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Original Research Article

Large-scale population assessment informs conservation management for seabirds in Antarctica and the Southern Ocean: A case study of Adélie penguins

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HIGHLIGHTS

- Adélie penguins and humans occupy similar terrestrial habitat in East Antarctica.
- One million Adélies, or one third of the mature population, breed close to stations.
- Limiting disturbance to breeding by protecting terrestrial areas varies regionally.
- Ecosystem-based fisheries need to protect food for dependent predators.
- Adélies consume 212 000 tonnes of krill and fish off East Antarctica while breeding.

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ABSTRACT

Antarctica and the Southern Ocean are increasingly affected by fisheries, climate change and human presence. Antarctic seabirds are vulnerable to all these threats because they depend on terrestrial and marine environments to breed and forage. We assess the current distribution and total abundance of Adélie penguins in East Antarctica and find there are 3.5 (95% CI 2.9–4.2) million individuals of breeding age along the East Antarctic coastline and 5.9 (4.2–7.7) million individuals foraging in the adjacent ocean after the breeding season. One third of the breeding population numbering over 1 million individuals breed within 10 km of research stations, highlighting the potential for human activities to impact Adélie penguin populations despite their current high abundance. The 16 Antarctic Specially Protected Areas currently designated in East Antarctica offer protection to breeding populations close to stations in four of six regional populations. The East Antarctic breeding population consumes an average of 193 500 tonnes of krill and 18 800 tonnes of fish during a breeding season, with consumption peaking at the end of the breeding season. These findings can inform future conservation management decisions in the terrestrial environment under the Protocol on Environmental Protection to develop a systematic network of protected areas, and in the marine environment under the Convention for the Conservation of Antarctic Marine Living Resources to allow the consumption needs of Adélie penguins to be taken into account when setting fishery catch limits. Extending this work to other penguin, flying seabird, seal and whale species is a priority for conservation management in Antarctica and the Southern Ocean.

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1. Introduction

Although Antarctica and the Southern Ocean are among the most remote regions on earth, the biota and ecosystems in these regions are being increasingly affected by fisheries, climate change, and other human disturbance over varying spatial scales. Antarctic land-breeding marine predators such as seabirds are vulnerable to a wide range of threats because they depend on terrestrial and marine environments to breed and forage (Croxall et al., 2012). Human activity in Antarctica such as tourism, scientific research, and the cumulative effects of close human presence may affect seabirds where humans spend time close to breeding colonies through disturbance, pollution, disease and the introduction of alien species (Micol and Jouventin, 2001; Trathan et al., 2008, 2015). Fishing in the Southern Ocean can directly affect Antarctic seabirds at regional scales through by-catch (Croxall and Nicol, 2004; Tuck et al., 2003) or indirectly by altering the food web and reducing prey (Cury et al., 2011; Trathan et al., 2015). Climate change may impact seabirds over large scales through effects on physical features of the breeding habitat (e.g. increased snowfall, Forcada and Trathan, 2009), foraging habitat (e.g. ice cover, Croxall et al., 2002) and food webs (Constable et al., 2014).

While the threats from climate change in Antarctica and the Southern Ocean are difficult to ameliorate directly (Trathan and Agnew, 2010), threats related to human impacts and fishing may be directly addressed through conservation management measures under the Antarctic Treaty System (ATS). Under the ATS, the Protocol on Environmental Protection (the Protocol) provides mechanisms for conservation in terrestrial and near-shore marine environments, and the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) provides mechanisms for conservation in marine environments. Although the area of application of the Protocol and CCAMLR overlap in near-shore marine environments, in many instances the mechanisms available under CCAMLR are most relevant to addressing the conservation challenges of the off-shore marine environment such as fishing.

Conservation measures under the Protocol include the designation of Antarctic Specially Protected Areas (ASPAs) and Specially Protected Species, the need for an environmental impact assessment prior to any activity, and protocols for minimizing harmful interference to wildlife, introduction of non-native species, and deleterious effects of waste and pollution. Of these measures, site protection is one of the most important conservation tools for managing threats to seabirds at their breeding sites (Croxall et al., 2012). ASPAs aim to protect, among other values, important or unusual assemblages of species including major colonies of land-breeding seabirds and marine mammals, and to keep areas free from human interference by limiting the number and frequency of visits so that future comparisons may be possible with localities that have been affected by human activities.

Conservation measures under CCAMLR include the ability to manage the catch within spatial management units to prevent local depletion of prey and protect marine areas by opening and closing areas to fishing. An important aspect of CCAMLR's conservation management for species that depend on harvested prey, which is embodied in Article II of the Convention, is the application of an ecosystem approach to managing fisheries (Constable et al., 2000). This requires that consumption or foraging needs of predators such as seabirds are taken into account when setting and managing catch limits. A second important aspect of CCAMLR's approach is the application of an Ecosystem Monitoring Program (CEMP) to detect the response of key ecosystem components to fluctuations in prey abundance and environmental conditions (Agnew, 1997). CEMP acknowledges the role of seabirds as potential indicators of marine conditions because they rely on marine prey and are relatively easy to monitor during the breeding season while at their land-breeding sites compared with solely marine species (Piatt et al., 2007).

Achieving effective conservation outcomes through these ATS mechanisms is reliant on sound scientific information. One of the fundamental needs for both the Protocol and CCAMLR is an accurate assessment of the population distribution and status of higher-order predators over spatial scales relevant to management in terrestrial and marine environments. For the Protocol, estimates of the distribution and abundance of predators breeding on ice-free land allow the level and location of potential disturbance from human presence to be assessed, and provide guidance on the representativeness of current site protection for seabird populations and on the future selection of sites to protect. For CCAMLR, estimates of the abundance of predators dependent on harvested prey, in combination with knowledge of bio-energetics, allow calculation of the amount of prey these species require. Discounting this consumption requirement of predators from spatial catch limits would enable the ecosystem approach in Article II of the Convention.

In response to these priority needs, we present an assessment of the current distribution and abundance of Adélie penguin (*Pygoscelis adeliae*) populations in East Antarctica and demonstrate how this information can be used to inform conservation management decisions in the terrestrial and marine environments. Notably, our work differs from most seabird population assessments by estimating both the breeding and non-breeding populations rather than just breeding populations. In relation to terrestrial conservation, we assess the current distribution of breeding populations in relation to permanently occupied research stations and ASPAs and determine the extent to which breeding populations close to human populations are afforded additional protection through ASPA management arrangements. For marine conservation, we apply a recently developed bio-energetics model for breeding Adélie penguins (Southwell et al., 2015c) to estimate the consumption needs of Adélie penguins breeding in CCAMLR management units across East Antarctica. Our results can inform conservation management decisions under the ATS and address both the terrestrial and marine needs of this species.

We focus on the Adélie penguin as an initial priority species because: (1) as an abundant predator it is an important consumer of marine prey and is therefore important for CCAMLR's ecosystem-based management approach, (2) it is the only predator species currently being used for CEMP monitoring in East Antarctica where this study is focused, (3) though

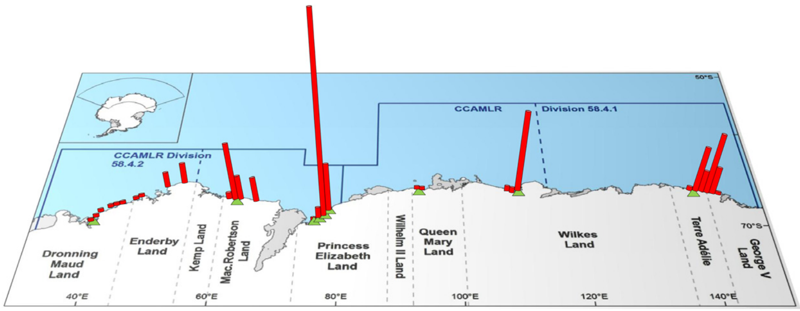

Fig. 1. Distribution of Adélie penguin breeding-age populations across East Antarctica. Vertical red bars aligned on the coastline indicate estimated abundance of breeding-age Adélie penguins at one-degree longitude resolution. For scale, the largest bar at 78°E represents approximately one million breeding-age individuals. Dark blue solid and dashed boundaries indicate CCAMLR Divisions and sub-divisions used for marine conservation management. Green triangles indicate locations of permanently occupied stations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

challenging, it is a relatively tractable Antarctic seabird species for large-scale population assessment, and (4) many breeding populations occur close to stations where impacts from human presence are likely to be greatest. We discuss the findings from our study in relation to other seabird species and stress that similar assessments of other seabird species' populations are critically important for improved conservation of seabirds in Antarctica and the Southern Ocean.

2. Materials and methods

2.1. Study region

The spatial extent of our study encompasses the terrestrial and marine environments along 5000 km of the Antarctic coastline from 30°E to 150°E (hereafter referred to as either the 'study region' or 'East Antarctica').

Terrestrial conservation in the region has to date been largely focused on areas of ice-free land close to the coastline where most terrestrial biodiversity, including seabird breeding populations, and human activity occurs. The area of ice-free land within 1 km from the ocean, which constitutes potential Adélie penguin breeding habitat (Southwell et al., 2016), totals approximately 900 km^2 in the study region. There are currently nine stations permanently occupied by humans in these ice-free areas (Fig. 1, Table A.1). Several of these were established in the 1950s. Since then the number of stations has increased steadily with the most recent established in 2012 (Table A.1). There are currently 16 ASPAs in the study region, 13 of which encompass seabird breeding sites and 8 of these have breeding Adélie penguins (Table A.2).

With regard to marine conservation, the study region spans the entire breadth of CCAMLR Statistical Area 58, which includes each of CCAMLR Divisions 58.4.1 and 58.4.2 and their eastern and western sub-Divisions (Fig. 1). A fishery for Antarctic krill (*Euphausia superba*), an important prey item for the Adélie penguin and several other Antarctic seabirds, operated off this coastline during the austral summers over three decades in the 1970s–1990s with the annual catch in Area 58 peaking at around 160 000 tonnes in 1981. Most of the catch occurred in Divisions 58.4.1 and 58.4.2 which are adjacent to the Antarctic coastline. Tracking studies of Adélie penguins breeding along this coastline indicate that foraging during the breeding season is within Divisions 58.4.1 and 58.4.2 and overlaps with the historical krill catch in space and time of year (Kerry et al., 1997). An exploratory fishery for Antarctic toothfish (*Dissostichus mawsoni*) has operated off the continental slope of East Antarctica since 2003 with an annual take of 100–500 tonnes.

2.2. Estimating Adélie penguin distribution and abundance in the study region

2.2.1. Population components

It is well known that seabird populations, including the Adélie penguin, comprise different life history stages including juveniles, pre-breeders, breeders and intermittent-breeders, and that most seabirds breed on land in dense breeding colonies. Compared with non-breeding birds, breeding seabirds and their chicks are readily observable at relatively accessible breeding sites and can be censused using standard count methods. The non-breeding population components, which include pre-breeders and intermittent-breeders, may not visit a breeding site in any given year and are hence largely or completely unavailable for standard population counts. Therefore, the breeding and non-breeding components of the population require different estimation procedures as outlined below.

2.2.2. Estimating the breeding population

We applied a staged approach to estimating the breeding population by: (1) locating all sites of potential Adélie penguin breeding habitat in the study region, (2) conducting occupancy surveys at these sites to identify which were currently occupied by breeding populations, (3) conducting counts of the population at each breeding site, (4) adjusting counts to a standardized population metric, and (5) aggregating standardized population estimates across sites for spatial regions relevant to important conservation management issues. To provide an accurate snapshot of the breeding population, we aimed to complete these steps from direct observations across the entire study region in a small number of consecutive breeding seasons using existing logistic capabilities of the Australian, Japanese and French Antarctic national Antarctic research programs. Details of these steps are provided below.

2.2.2.1. Locating potential breeding sites. We used the database and geographic information system (GIS) of potential Adélie penguin breeding sites in the study region developed by Southwell et al. (2016). Potential habitat is defined as ice-free land greater than 4000 m^2 in area and <1 km from the ocean. We refer to a discrete unit of potential breeding habitat (i.e. either an island or outcrop of continental rock) as a 'potential breeding habitat site' or 'site'. To facilitate the search effort in occupancy surveys, and if necessary clarify the location of historical count data, a unique label was allocated to each potential habitat site in the database and small-scale maps were produced from the GIS that together included all labelled sites in the survey region. The maps are available online (see Southwell et al., 2016).

2.2.2.2. Occupancy surveys. Potential habitat sites were searched for signs of breeding penguins (either penguins or guano) by observers in fixed-wing aircraft, helicopters, and from the ground. Observations were made by eye during surveys, or *post-survey* from visual inspection of photographs taken during surveys.

2.2.2.3. Population counts. For sites confirmed to have breeding Adélie penguins present, we conducted direct counts of the number of adults, occupied nests or chicks present. Counts were made from the ground or from aerial photographs. Small populations were counted entirely (i.e. census counts). Large populations were estimated from sample counts. The dates of counts varied from early-November to late-January. Details of population count methods are given in references listed in Appendix A.1.

2.2.2.4. Standardizing counts to a common population metric. It was important to standardize counts to a common breeding population metric because the dates of counts and population components counted varied across sites. We standardized raw counts to estimate the maximum number of breeding birds attending nests early in the incubation period before nests have failed (late-November to early-December). The population metric used was breeding birds, where breeding birds $= 2\times$ occupied nests or breeding pairs, instead of the commonly used breeding nests or pairs because it is a metric that is also appropriate to non-breeding birds, which would be counted or estimated individually. The standardization process applied the non-parametric bootstrap methods in Southwell et al. (2010) and McKinlay et al. (2010) to raw count data and adjustment data. Adjustment data were obtained from a network of 21 remotely-operating time-lapse cameras across East Antarctica (Southwell and Emmerson, 2015). The standardized population estimate for each breeding site that resulted from this bootstrapping process comprised a distribution of 1000 estimates which was summarized by the median and 95 percentiles.

2.2.2.5. Estimating current breeding abundance at sites where recent counts were not obtained. We constructed a recent population estimate from available historical count data for sites where recent counts were unavailable. Because many published Adélie penguin population estimates derived from historical counts in East Antarctica are subject to detection bias, we first re-constructed an unbiased population estimate and its uncertainty for the season of the count using the method in Southwell et al. (2015b), and then projected this estimate forward in time to the modal season of this study's survey period (2009/10) using estimates of regional population change from Southwell et al. (2015a) over the relevant time period of the most recent count at the site. The forward-projection incorporated uncertainty in the estimates of regional rates of change.

2.2.2.6. Estimating current breeding abundance at sites where Adélie penguins are known to breed but no direct counts have been made. If no recent or historical counts had been made at a site where Adélie penguins have been directly observed breeding, we used satellite-based estimates from (Lynch and LaRue, 2014) in lieu of direct counts. We did not use satellite estimates for any sites where Adélie breeding occupancy had been inferred from satellite observation only because of possible false positive detection of other species' guano, moulting sites, or physical features (Southwell et al., 2017).

2.2.3. Estimating the non-breeding population

We estimated abundance for two categories of non-breeders: (1) post-fledglings that had not reached breeding age (pre-breeders), and (2) breeding-age birds that skipped breeding in any particular breeding season (intermittent breeders). To estimate the size of these non-breeding population classes, we applied mark-recapture analysis methods and simple population modelling to a long-term Adélie penguin mark-resight dataset from Béchervaise Island (67.59°S, 62.81°E) in East Antarctica as outlined below.

2.2.3.1. Tagging and resighting. Up to 300 Adélie penguin chicks were tagged with subcutaneously implanted electronic identification devices at Béchervaise Island during each of 15 breeding seasons from 1991/92 to 2005/06. Tagged birds were resighted in later years by one of three methods: an automated penguin detection gateway, a manual island-wide detection survey of nesting birds, and nest censuses at several sub-colonies. In the first method, fences around several sub-colonies directed birds through two gateways as the birds moved between sub-colonies. A tag-reader on each gateway detected the presence and identity of implanted tags as birds passed through (Kerry et al., 1993a). In the second method, tagged birds were manually detected on nests on two occasions during the incubation period (23–29 November when mainly breeding males are present on the nest, and 11–18 December when mainly breeding females are present, (Kerry et al., 1993b)). This method detects ≥98% of birds sitting on nests (Emmerson and Southwell, unpub. data). All birds detected on nests during these periods were considered to be breeders and would have been included in population counts of breeding birds. In the third method, nests at several sub-colonies were monitored each day for the presence and identity of each breeding pair until chicks crèched. Any known deaths of individuals between the time of tagging and the time of departure at the end of the season were removed from the analysis.

2.2.3.2. Mark-resight data analysis. To estimate the pre-breeder and intermittent-breeder population components, we used models from the mark-recapture software MARK incorporated with simple population modelling techniques. To estimate the size of the pre-breeder population, we used estimates of annual survival probability from 1991 to 2005 (Emmerson and Southwell, 2011), the proportion of each tagged cohort attempting to breed for the first time each year, and the number of fledglings produced in each year. Our survival estimates were based on a fully time-dependent Cormack–Jolly–Seber model with age structure in the recapture and survival sub-models. The transition rates between the pre-breeder and breeder states were based on the detection of birds tagged as chicks in subsequent years on nests. The transition between breeder and intermittent-breeder states for birds that had previously bred at least once was estimated with a robust design model in MARK which allows the estimation of transition rates between observable and unobservable states. Transition rates were estimated between each of the 15 breeding seasons from 1991/92 to 2005/06. The transition and survival rates were then applied to a count of breeding birds at Béchervaise Island in the same years to estimate the number of intermittent-breeders in each year. Further details of the estimation procedures are in Appendix A.2.

2.2.4. Combining breeding and non-breeding population estimates

We used the ratios of intermittent-breeders and pre-breeders to breeders at Béchervaise Island over 11 breeding seasons to develop adjustment factors for converting breeding bird estimates to breeding-age (breeding + intermittent-breeding) and total (pre-breeding + breeding + intermittent-breeding) population estimates. We then applied these ratios to breeding population estimates at breeding sites across East Antarctica to develop estimates of the non-breeding population over large spatial scales. The estimates of pre-breeders and intermittent-breeders in the 11 breeding seasons at Béchervaise Island were first standardized to the number of breeders counted in the same season. The mean and standard deviation of the adjustment factors across the 11 breeding seasons were then calculated and these summary statistics were used to generate normal distributions of 1000 adjustment factors for breeding-age and total populations. In the final step, the 1000 bootstrap replicates from breeding abundance distributions were multiplied by replicates from the adjustment distributions to generate bootstrap distributions of breeding-age and total population estimates, and these distributions were summarized with the median and 95 percentile values.

2.3. Assessing potential disturbance and site protection for breeding populations

One of the potential direct threats for Adélie penguin populations breeding on land is disturbance by humans living and working at stations. This is particularly true in East Antarctica where several permanently occupied stations exist but relatively little tourism occurs. Assuming that the potential for disturbance is related to the distance between a breeding site and the nearest station, we calculated these distances for the centroid of each breeding site and summed population estimates across sites within 10 km distance increments to assess the size of breeding-age populations in relation to a gradient of potential disturbance. To assess the level of protection from potential disturbance, we further summed population data within and outside ASPAs across breeding sites close to (<20 km) a station. This analysis was applied to estimates of breeding-age populations for the six regional populations where stations occur (Fig. 1).

2.4. Estimating prey consumption

We used the population data and a bio-energetics model for breeding Adélie penguins (Southwell et al., 2015c) to estimate the amount of prey (krill and fish) consumed in CCAMLR management units. The bio-energetics model predicts the amount of prey consumed by a breeding Adélie penguin to provision itself and its chicks throughout the breeding season from the time it arrives at its colony until after it moults. It incorporates uncertainty in model parameters using Monte Carlo simulation with foraging success estimated through the calibration procedure outlined in Green et al. (2007) based on observations of body mass and reproductive success. We used the same individual input values for the model as in Southwell et al. (2015c) which were derived from birds at Béchervaise Island and from the literature, and scaled-up individual consumption estimates to consumption estimates for each of four CCAMLR management units (58.4.1 east and west, 58.4.2 east and west) using breeding population estimates for each unit. This analysis rests on the expectation that breeding birds forage in the same CCAMLR management unit that their breeding sites are located in, which has been confirmed by several tracking studies in the study region (Clarke et al., 2006; Cottin et al., 2012; Kerry et al., 1997; Kato et al., 2009; Wienecke et al., 2000).

Table 1
Estimated abundance of Adélie penguin breeding individuals and their consumption of krill and fish during the breeding season in CCAMLR Divisions 58.4.1 and 58.4.2 and their sub-divisions. Values are medians and 95 percentile ranges for 1000 bootstrap estimates and Monte Carlo simulations.

CCAMLR management unit	Abundance (number of breeding individuals)		Krill consumption (tonnes during the breeding season)		Fish consumption (tonnes during the breeding season)	
58.4.1 East (115°E–150°E)	696 500	(552 600–1 153 900)	49 300	(15 400–88 100)	4750	(800–9760)
58.4.1 West (80°E–115°E)	392 300	(371 400–412 800)	26 800	(10 100–42 800)	2480	(450–4760)
All of 58.4.1	**1 090 200**	**(938 000–1 547 600)**	**75 000**	**(21 200–128 100)**	**7370**	**(1280 –14 560)**
58.4.2 East (55°E–80°E)	1 592 400	(1 525 800–1 657 800)	106 900	(36 200–172 200)	10 160	(1850–19 790)
58.4.2 West (30°E–55°E)	178 500	(175 000–229 100)	12 500	(4700–20 600)	1160	(180–2260)
All of 58.4.2	**1 773 000**	**(1 707 200–1 867 200)**	**118 500**	**(40 700–193 900)**	**11 470**	**(2120 –22 050)**

Table 2
Abundance estimates for components of the Adélie penguin population in East Antarctica. Values are medians and 95 percentile ranges for 1000 bootstrap estimates.

Population component	Number of individuals (Median, 95% percentile range)	
Breeding population	2 868 800	(2 690 700–3 321 900)
Breeding-age population	3 490 300	(2 923 600–4 206 400)
Total population (prior to breeding season)	5 073 000	(3 950 100–6 520 700)
Total population (after breeding season)	5 800 200	(4 205 600–7 646 600)

2.5. Ethics

All counting, tagging and re-sighting activities were conducted in accord with permits issued by the Australian Antarctic Ethics Committee, the Committee on Bioscience Program at the National Institute of Polar Research for Japanese Antarctic Research Expeditions, and Terres Australes et Antarctiques Françaises authorities under the Institut Paul Emile Victor, Zone Atelier de Recherches sur l'Environnement Antarctique et Subantarctique (CNRS-INEE), and Terres Australes et Antarctiques Françaises.

3. Results

3.1. Estimates of breeder, intermittent-breeder, pre-breeder and total populations

The Adélie penguin breeding population in East Antarctica at the time of surveys was estimated to be 2.87 (2.69–3.32) million individuals (=1.43 million breeding pairs, Tables 1 and 2) at 247 known breeding sites. This population estimate is based on direct counts over seven breeding seasons (2006/07–2012/13, modal year 2009/10) at 183 breeding sites, forward-projected estimates from earlier direct counts at 56 sites, and indirect estimates from satellite-detected guano at 8 sites (Lynch and LaRue, 2014) where Adélie penguins have been directly observed breeding but have never been directly counted. Our estimate may be an under-estimate because the initial occupancy survey, while very extensive, was incomplete. The main gaps in direct search effort are along the coastlines of Enderby Land between 47°E and 50°E, Kemp Land between 56°E and 59°E, and George V Land between 145°E and 150°E (Table A.3). However, satellite observations have not detected any guano in those areas (Lynch and LaRue, 2014; Schwaller et al., 2013) so it is unlikely that there are any large Adélie populations breeding in these unsearched areas. The distribution of Adélie breeding populations along the East Antarctic coastline is clustered into several regional populations and is numerically dominated by the large population along the Princess Elizabeth Land coast (Fig. 1, Table A.3). Breeding populations in the four CCAMLR management areas varied by an order of magnitude (range 178 500–1 592 400, Table 1).

The mark-recapture analysis estimated that on average 14% (SD = 8.3%) of breeding-age penguins at Béchervaise Island skipped breeding in any given year and hence would not have been included in counts of breeding penguins at breeding sites. Most of the birds that skipped breeding in any given year bred in the following year (mean = 85%, SD = 7.9%). Survival estimates and population modelling estimated that the pre-breeding population was on average 0.58 (SD = 0.12) times the breeding population just before a breeding season commenced and 0.85 (SD = 0.19) times the breeding population just after a breeding season ceased. This difference is due to a pulse of pre-breeders produced during the breeding season and high mortality of first-year pre-breeders through the winter between successive breeding seasons (Emmerson and Southwell, 2011).

Combining population components, we estimate that over the 11 breeding seasons (1995/96–2005/06) where population estimates sufficiently incorporated the complex age structure of the population, the breeding-age population at Béchervaise Island was on average 1.21 times the number of breeding individuals. By applying this factor to breeding population estimates across all breeding sites in the study region, we estimate the total breeding-age population (breeder + intermittent-breeder) in the region was 3.49 (2.92–4.21) million individuals (Table 2). Further, the total population (pre-breeder + breeder + intermittent-breeder) was estimated on average to be 2.01 times higher than the breeding population at the end of a

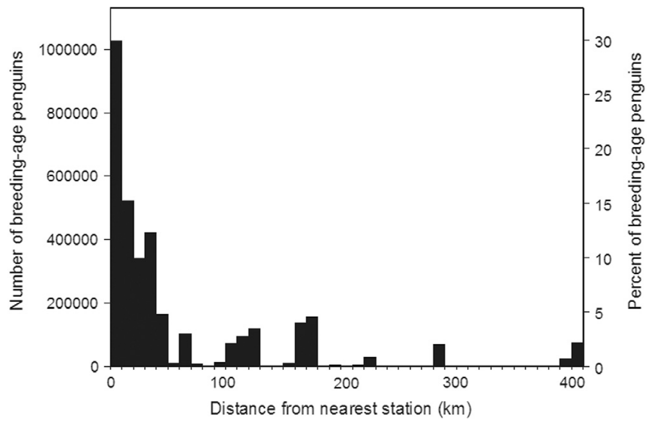

Fig. 2. Adélie penguin breeding-age abundance in relation to distance from the nearest permanently occupied station.

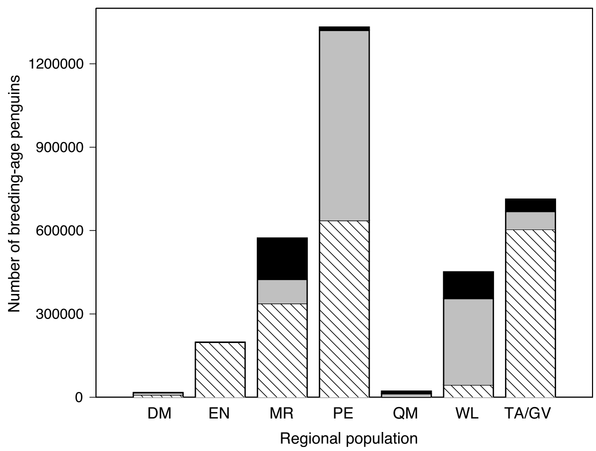

Fig. 3. Number of breeding-age Adélie penguins breeding >20 km from a permanently occupied station (cross-hatched) and <20 km from a station (black + grey) in seven regional populations across East Antarctica. Penguins breeding <20 km from a station are further partitioned according to whether they are located outside (grey) or inside (black) an Antarctic Specially Protected Area. The regional populations are named according to the adjacent sectors of 'land' shown in Fig. 1 (DM: Dronning Maud, 39°E–47°E; EN: Enderby, 50°E–54°E; MR: Mac. Robertson, 59°E–67°E; PE: Princess Elizabeth, 75°E–79°E; QM: Queen Mary, 92ºE–94ºE; WL: Wilkes, 107°E–112°E; TA/GV: Terre Adélie/George V, 139°E–145°E).

breeding season and 1.76 times higher at the beginning of a breeding season, leading to estimates of the total number of Adélie penguins foraging in the ocean off East Antarctica being highest at 5.80 (4.21–7.65) million individuals just after the breeding season when chicks had fledged and pre-breeders were most abundant, and lowest at 5.07 (3.95–6.52) million individuals prior to the next breeding season after early mortality of pre-breeders (Table 2).

3.2. Potential disturbance and site protection for breeding populations

Analysis of the distribution of breeding-age populations in relation to distance from stations revealed that overall around one million individuals, or 29% of the East Antarctic breeding-age population, breed within 10 km of a station, and 44% within 20 km of a station (Fig. 2). However, the proportion of populations close to stations varies regionally (e.g. there are no stations along the Enderby Land coast where Adélie penguins breed, but almost all the populations along the Wilkes Land coast are within 20 km of Casey station, Fig. 3). The 16 ASPAs along the East Antarctic coastline encompass 10% of the total East Antarctic breeding-age population. Again, this varies regionally, with larger proportions of populations occurring within ASPAs in the Mac. Robertson, Queen Mary and Wilkes regions than in other regions (Fig. 3). ASPAs offer protection from potential human disturbance to substantial proportions of Adélie populations close to stations in four of six regional breeding populations where stations exist (Fig. 3). The two regions lacking substantial protection are Dronning Maud Land and Princess Elizabeth Land. The Dronning Maud region has several small breeding Adélie populations but no ASPAs within 20 km of Syowa station. The Princess Elizabeth Land region has around 1.35 million breeding-age birds (Table A.3), of which 700 000 breed within 20 km of four stations (Davis, Progress, Zhong Shan and Bharati, Table A.1). There are two ASPAs (Hawker Island and Stornes, Table A.2) within 20 km these stations, but they contain <2% of the breeding-age population.

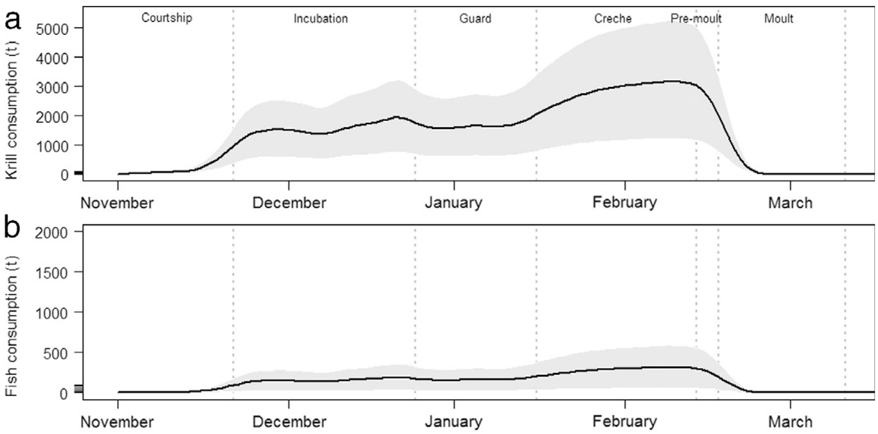

Fig. 4. Model predictions for daily consumption of (a) krill and (b) fish by the breeding Adélie penguin population in East Antarctica during the breeding season. The solid black line indicates total daily ingested krill or fish consumed by breeding Adélie penguin males and females combined and averaged across years, and grey shading indicates 95% confidence intervals for inter-annual variation. Dotted grey vertical lines indicate major phases of the breeding cycle.

3.3. Prey consumption

We estimate that the breeding Adélie penguin population of 2.87 million individuals consumes a total of 193 500 (57 700–313 700) tonnes of krill and 18 840 (2900–37 300) tonnes of fish in a breeding season in CCAMLR Divisions 58.4.1 and 58.4.2 (Table 1). The wide confidence interval primarily reflects variation in diet and breeding success from year to year and uncertainty in our population estimates. Over half (55%) of the krill consumed were taken in the eastern sector of Division 58.4.2 (Table 1) associated with the large penguin population in the Princess Elizabeth Land region. The model predicts a gradual increase in consumption across the breeding season with a peak towards the end of the season as chicks grow and adults forage prior to their moult (Fig. 4).

4. Discussion

The large-scale population data from this study substantially improves knowledge of Adélie penguin status in East Antarctica by providing a comprehensive estimate of the breeding population derived almost entirely from direct counts and for the first time estimating the size of the non-breeding population. These new population data revise recent estimates derived from indirect methods and indicate the population is substantially larger than previously thought. The findings provide insights into management where penguins could come into contact with humans in the terrestrial environment and have direct relevance to the management of fisheries in the ocean off East Antarctica.

4.1. Distribution and abundance

Most estimates of seabird abundance understandably focus on the readily observable breeding populations (Griffiths et al., 1982; Harris and Wanless, 1991) and do not include the significant numbers of non-breeders. As this study shows for Adélie penguins, non-breeders may be as or more abundant than the breeders. Non-breeding birds are crucial for species conservation because they are a 'reservoir' of future breeders (Clobert and Lebreton, 1991). Estimating the entire population is important for terrestrial conservation management because a variable and substantial proportion of breeding-age seabirds may skip breeding and hence the total population potentially exposed to human impacts when breeding on land over multiple years will be larger than the number present in any given year. Similarly, estimating the size of the total population is critical for marine conservation to ensure that the consumption needs of the total population are taken into account when managing fisheries. Our results also highlight the magnitude of temporal variation in the number of birds foraging in the ocean, and hence in their consumption of prey and the level of potential competition with fisheries, due to fluctuations in the number of intermittent-breeders and pre-breeders between and within years.

Our estimate of 2.87 million breeding individuals in the survey region, which is based on direct counts over six breeding seasons (2006/07–2012/13, modal season 2009/10), is substantially higher than a largely satellite-based estimate of 2.28 million individuals obtained over a similar period (Lynch and LaRue, 2014, modal year 2010/11). Some of this difference may be due to the unavailability of satellite imagery and lack of recent direct counts for a number of East Antarctic breeding sites in Lynch and LaRue's global assessment. For the purpose of estimating prey consumption, we recommend using our higher, more complete population estimate in accord with CCAMLR's precautionary approach. The direct population data from this study will be valuable for assessing satellite population estimation in East Antarctica in the future.

Our results have broad implications for assessing the global population status of Adélie penguins and for conservation management in other CCAMLR management areas. Although seabird researchers commonly use breeding pairs as a metric for population status, the IUCN uses the metric of 'mature individuals' to assess species conservation status (IUCN, 2012). For seabirds, including Adélie penguins, this metric is most appropriately represented by breeding-age birds rather than just breeding birds. The most recent global estimate of Adélie populations (3.79 million pairs or 7.58 million birds, Lynch and LaRue 2014) is for breeding birds and does not include breeding-age birds that skip breeding in a given year. Extrapolating our results from East Antarctic, where approximately one third of the global population breeds, to the global population suggests that the breeding-age or mature population around Antarctica would be considerably higher than the 7.58 million breeding birds estimated in (Lynch and LaRue, 2014). Assuming the non-breeding population component around Antarctica is similar to that estimated at Béchervaise Island in East Antarctica, and taking the breeding bird estimates for East Antarctica from this study, for the western Ross Sea from Lyver (2016) for the season closest to the modal year of our study, and for the remainder of Antarctica from (Lynch and LaRue, 2014), we suggest a more likely estimate of the global population using the IUCN metric would be around 9.55 million breeding-age or mature individuals (3.49 million in East Antarctica; 2.96 million in the western Ross Sea; 0.55 million in the Amundsen/Bellingshausen Sea; 1.95 million in the Antarctic Peninsula; 0.60 million in the Scotia Sea). Furthermore, we suggest that the global total population foraging in the Southern Ocean could be around 14–16 million individuals. It would be useful to confirm these estimates with additional analyses of mark-resight data from populations in other regions around Antarctica.

4.2. Terrestrial conservation

In demonstrating that nearly one third of the East Antarctic breeding-age population numbering over a million individuals breeds within 10 km of permanently occupied stations, this study highlights the potential for human activities to impact Adélie penguin populations in the future despite the species' large population size. This potential for impact arises because the preferred habitat of breeding Adélie penguins has features similar to areas preferred for station locations (ice-free, relatively flat land with easy access to open ocean for 're-supply') and the small, finite area of this habitat in East Antarctica. For seabirds, detrimental impacts could take a number of forms including direct interference or disturbance of breeding activities by humans visiting breeding sites (Giese, 1996), disturbance from close approach of aircraft or all-terrain vehicles (Giese and Riddle, 1999), pollution of waters around breeding sites, and introduction or spread of disease (Kerry and Riddle, 2009; Leotta et al., 2006). Our analysis shows that the current ASPAs do not protect all regional Adélie populations that are close to stations. By identifying significant penguin breeding populations located in close proximity to stations that are not within the current suite of ASPAs, our results can inform priorities for designation of new ASPAs and the application of other management measures.

The use of distance from station as a proxy for potential disturbance and site protection as an amelioration measure is a simplification of a complex suite of potential terrestrial impacts or responses and management measures that may play out in the future if human presence and activities increase. It is possible, for example, that potential detrimental effects of interference or disturbance could be ameliorated if penguins become habituated to frequent contact with humans. Also, site protection through the designation of ASPAs under Annex V of the Protocol is just one management tool that can be used to minimize disturbance from human visitation. Our demonstration of the strong overlap between breeding Adélie penguins and human occupation in East Antarctica emphasizes the importance of maintaining vigilance against disturbance or interference of seabirds and other wildlife outside of ASPAs, and against other impacts such as disease, pollution and the introduction of alien species which can have long-lasting effects on wildlife and their environments, through the implementation of other protocols developed in accord with Annexes I–IV of the Protocol.

4.3. Marine conservation

A fundamental tenet of CCAMLR's management of fisheries in the Southern Ocean is the application of an ecosystem approach to management to ensure that ecological relationships between harvested and dependent populations are maintained, and irreversible changes in the marine ecosystem are avoided. Rigorous estimates of the amount of prey consumed by dependent species such as the Adélie penguin are central to this management goal. The prey consumption estimates presented here are an important first step in accounting for the consumption needs of Adélie penguins when setting fishery catch limits. Estimating prey consumption is currently limited by the scope of the bio-energetics model to just breeding Adélie penguins during the breeding season, and by parameterization of the model with data from only one site (Béchervaise Island). Now that estimates of the size of non-breeding Adélie population in East Antarctica are available, extending the model to estimate prey consumption by non-breeders, to cover the period between breeding seasons, and using data from additional populations is high priority future work for CCAMLR.

The approach taken in this study is a model that could be extended to other penguin and seabird species and other CCAMLR regions such as Area 48 (the Antarctic Peninsula) where the krill fishery is currently focused (Nicol et al., 2012). While substantial progress in estimating prey consumption by penguins around Antarctica is now possible, progress in estimating consumption by flying seabirds is limited by the current scant knowledge of their large-scale distribution and abundance. Flying seabird populations are difficult to estimate over large spatial scales because they are cryptic and patchily distributed when breeding on land, and wide-ranging and largely inaccessible when foraging at sea. New approaches, or intense and concerted efforts using existing methods, will be required to improve this significant knowledge gap.

Pack-ice seals are another group of dependent predators that are important to consider in CCAMLR's ecosystem approach to fisheries management. The Antarctic Pack Ice Seal program (Anonymous, 1995) undertaken under the auspices of the Scientific Committee on Antarctic Research in the late 1990s and endorsed by CCAMLR, similarly aimed to estimate the abundance of pack-ice seal populations, in particular the abundant crabeater seal, and their consumption of prey around Antarctica. Although estimates of pack-ice seal abundance are now available for the Ross/Bellingshausen Sea, Antarctic Peninsula, Queen Maud Land/eastern Weddell Sea and East Antarctic regions (Bengtson et al., 2011; Forcada et al., 2012; Gurarie et al., 2016; Southwell et al., 2008), presently prey consumption has only been estimated for the Antarctic Peninsula population. Extending estimates of prey consumption to these other regions would also be a major contribution to CCAMLR's ecosystem approach to fishery management.

The distribution and abundance data from this study can contribute to CCAMLR's spatial management in a number of other ways. CCAMLR has placed a high priority on designating a representative system of marine protected areas (MPAs) in the Southern Ocean in recent years (Brooks, 2013), and CCAMLR member nations have agreed on a conservation measure outlining a general framework for establishing MPAs (CCAMLR, 2011). The breeding distribution data from this study, in conjunction with foraging distribution from tracking studies, were ecological inputs to help define boundaries and locations in a recent proposal to CCAMLR for a representative system of MPAs in East Antarctica (CCAMLR, 2013). A second potential application of the breeding distribution and abundance data is the delineation of smaller scale management units than presently exist in East Antarctica. Shortly after the adoption of CCAMLR, the Convention area was divided into three broad management Areas corresponding to the Atlantic, Indian and Pacific Oceans (Areas 48, 58 and 88, respectively). These were further divided into management Subareas and Divisions on the basis of ocean characteristics, fish stock distributions and the location of fishing activities for catch reporting and management purposes (Everson, 1977). More recently CCAMLR has recognized these units are too large for management to prevent local depletion of krill and their dependent predators, and consequently established small-scale management units in Subareas 48.1, 48.2 and 48.3 by integrating fine-scale information on the distribution of the harvested species, the krill fishing effort, and the breeding and foraging distributions of dependent predators (Constable and Nicol, 2002). The extensive Indian Ocean sector immediately north of East Antarctica is currently divided into two Divisions (58.4.1 and 58.4.2), each with eastern and western sub-divisions (Fig. 1), on the basis of oceanographic features and krill distribution. The fine-scale distribution and abundance data from this study provide a basis for incorporating predator requirements into spatial management if the delineation of small scale management units is extended to East Antarctica for management of a future krill fishery in this region.

Smaller management units also provide a spatial framework for extending monitoring for the CEMP, which is currently undertaken at just a few predator breeding sites in Divisions 58.4.1 and 58.4.2. When CEMP was established in the 1980s the methods for ecosystem monitoring that existed at the time proved difficult to apply over large areas or numerous locations because they were labour-intensive. CCAMLR has subsequently acknowledged that CEMP needs to be more spatially extensive to effectively monitor impacts from fishing. Smaller scale management units, in combination with new methods and technologies for population monitoring over large scales, will be important components of improved ecosystem management and monitoring in the future.

4.4. Conclusions

Although the Adélie penguin is currently widespread and highly abundant in Antarctica and the Southern Ocean, this study highlights potential threats from human disturbance and fisheries and provides critical scientific data that contribute to effective conservation management in the future. This work provides a model for addressing conservation-related data gaps for other Antarctic seabird species, species groups, and regions. Priorities for future work include improving the currently scant knowledge of flying seabird distribution and abundance, extending estimates of prey consumption to non-breeding seabirds, the non-breeding season, and to other penguin, flying seabird, seal and whale species, and undertaking tracking studies to understand the level of functional overlap of predator foraging with fisheries. These data can most effectively contribute to conservation management by informing the decision-making processes under the Protocol and CCAMLR.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2016.12.004.

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