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A REVIEW OF THE DIET AND AT-SEA DISTRIBUTION OF PENGUINS BREEDING WITHIN THE CAMLR CONVENTION AREA

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Abstract

Managing fisheries in an ecologically sensitive manner demands that catches do not depress stocks within the foraging areas used by predators to levels that reduce their reproductive success or survival. Spatially–explicit bioenergetics models that estimate the amount of prey consumed by predators are required to inform such policy. These models require information on the number of predators in a population, their nutritional demands, their diet composition and their seasonal distribution in the marine environment. This paper reviews all published information on the diet and at-sea distribution of the six penguin species that breed in the CAMLR Convention Area, the methods used to collect these data and the uncertainties inherent in them. The review will be of utility to modellers as a source of parameters, and to penguin biologists by providing comparative information for their own findings and by highlighting significant gaps in existing knowledge and methods that could be used to fill these.

Introduction

A key objective for CCAMLR is to estimate the biomass of different prey species consumed by predators, especially harvested species such as Antarctic krill (*Euphausia superba*) within each of the management subareas of the Southern Ocean. Quotas can then be set at levels that ensure that stocks are not reduced to levels that will impact adversely on predator reproduction or survival. Moreover, research interest is increasingly focusing on fine-scale spatial distribution of food consumption by predators in the marine environment. This facilitates spatially explicit fisheries management that minimises the spatial overlap between predator food consumption and fishery catches. The bioenergetics models that produce estimates of total prey consumption require data on the number of individuals in a population, the energetic demands of each individual, and their diet composition (Boyd, 2002; Hill et al., 2007), while spatially explicit models require additional data describing the at-sea distribution of the population.

Aims and scope

The aim of this review is to summarise published data on penguins concerning the components of the models that relate to foraging ecology; namely their diet and at-sea distribution. Information of the distribution and size of penguin colonies and the energetic demands of penguins form the foci of other strands of Subgroup on Status and Trend Assessment of Predator Populations (WG-EMM-STAPP) work and will be presented elsewhere.

The review begins by giving an overview of methods for studying the diet and at-sea distribution of penguins and a commentary on the uncertainties associated with each approach. It then proceeds to review all published information on the diet and at-sea distribution of the six penguin species that regularly breed within the CAMLR Convention Area, broken down by division and subareas (for a map of these see www.ccamlr.org/en/organisation/convention-area). Information from divisions outside the CCAMLR region (namely the Falkland Islands and Macquarie Island) where three of the focal penguin species breed, is included in order to ensure that the review is comprehensive. The review only includes published literature to allow the reader to check the information at source. In the case of the review of diet, studies that only present data on composition within a specific taxonomic group (e.g. squid alone) are excluded.

The target audience of the review are penguin biologists and ecological modellers. Penguin biologists will find the information in the review useful for comparison with the findings of their own studies, to identify important gaps in current knowledge and to determine the most suitable methods that could be used to fill such gaps. Ecological modellers will be able to extract values of interest from the review and gain an improved understanding of the uncertainties that may be associated with these. Those readers wishing to extract large numbers of diet values may find it easier to do so from the online spreadsheet compiled by Raymond et al. (2011).

Estimating diet composition

Quantification of prey remains in stomach contents

Most diet studies of penguins are based on examination of the contents of the oesophagus, proventriculus and gizzard, typically referred to collectively (though anatomically inaccurately) as stomach sampling. The contents can be accessed by dissection, administration of emetics or by stomach flushing (also termed as water offloading, stomach pumping or gastric lavage). Dissection involves killing birds and cutting open the stomach to extract its contents; this is the most thorough method as all contents can be extracted (Croxall and Furse, 1980; Croxall and Prince, 1980; Volkman et al., 1980). This was only used in early studies of diet during the 1970s, and most researchers have subsequently considered it unjustifiable on ethical grounds. Emetics were also used in early studies (Jablonski, 1985; Volkman et al., 1980) but were ineffective and their use has been discontinued. Almost all studies since the mid-1980s have used stomach flushing, in which a tube is inserted down the oesophagus, down which warm water is poured until the stomach is full. The bird is then inverted over a bucket in which the regurgitated stomach contents are collected (Gales, 1987; Wilson, 1984). This procedure is often repeated for a fixed number of times or until only clear water is returned, depending on the study. The method does cause birds distress, and in exceptional cases results in death of a study animal, but it is less intrusive than killing birds for dissection.

Food recovered from stomachs is typically filtered through sieves with increasingly fine meshes to recover solid constituents, and prey remains are identified, counted and weighed. The main source of uncertainty is that prey are often heavily digested when recovered, which may cause problems with identification and estimation of their original mass upon ingestion (Gales, 1987). However, some parts of prey types resist digestion better than others and have sufficiently unique characters to allow identification to the level of genus or species. The beaks of squid, eye-capsules of crustaceans and sagittal otoliths of fish are particularly widely used in this respect. Counting these allows numbers consumed to be estimated, and original size of prey at digestion can be estimated from equations describing relationships between the size of the body parts and the whole body size, obtained from measurements of whole specimens captured in trawls (Hill et al., 1996). The resulting corrections from such analyses are usually referred to as reconstituted mass, as opposed to wet mass measured from raw stomach contents. Problems with this approach still remain, since erosion of these parts may result in underestimates of their numbers and size, and because these parts are digested at differing rates. For example, fish components are digested particularly rapidly, while squid beaks are extremely resistant to digestion and can accumulate in stomachs for several days or even weeks, resulting in overestimates of the squid component (Pütz, 1995; van Heezik and Seddon, 1989; Wilson et al., 1985). Most of the recent studies overcome the latter problem by only counting those squid beaks still attached to the buccal mass.

Data derived from stomach content studies can be presented in three ways. The simplest method is percentage occurrence, which is the percentage of stomachs in which at least one prey item of a given type is present. This tends to exaggerate the importance of small food items that tend to occur in most stomachs but are never significant in terms of numbers or mass. Percentage by number is the percentage of food items of a given type in a stomach, and is usually averaged across stomach samples. This tends to exaggerate the importance of numerous but small items and underestimates the importance of large items, which are inevitably less frequent owing to limitations of stomach volume. Percentage by wet mass or reconstituted mass are the percentage of the total mass of stomach contents comprised by a given prey type, and is the only measure that is of use in prey consumption models. The estimates authors choose to present often vary among studies, making direct comparison of values problematic.

Quantification of prey remains in faeces

Faeces can be collected either ashore or on sea-ice or icebergs. Prey remains, such as squid beaks, otoliths and crustacean eye-capsules can be identified and counted to quantify diet composition (Green, 1986; Green et al., 1998). This method has the advantage that faeces can be collected relatively easily and non-intrusively. However, the problems with digestion of prey and erosion of identifiable parts described for stomach sampling are magnified further owing to the prey being passed through the entire alimentary tract. Estimates are therefore even more biased in favour of prey types that have hard parts that are resistant to digestion.

An alternative approach that eliminates these biases is to identify prey in faeces from unique DNA markers present in different prey types (Deagle et al., 2007; Jarman et al., 2002). This involves collecting freshly deposited faeces and storing them in 70% ethanol at 4°C. DNA primers are extracted from faeces, amplified by PCR assay and separated on electrophoresis on gels before being revealed by staining with ethidium bromide. The resulting bands are compared with those obtained from DNA primers extracted from known prey types collected from stomach samples or trawls. Correspondence of these bands results in the prey type being classed as present in the sample. This is a powerful method for identification of prey types, but can only provide information on percentage occurrence in each faecal sample, not on percentage by number or mass.

Quantification of diet from analysis of tissues or feathers

The molecular components of all prey ingested by penguins are digested, absorbed and anabolised into their own tissues. These components often have molecular or sub-atomic signatures that provide information on the prey consumed, to varying levels of taxonomic resolution. There are two main approaches to inferring diets from tissues: fatty acid analysis and stable isotope analysis.

Fatty acid analysis

Different prey types often have unique types of fatty acids, and predators consuming them will incorporate these into their own blood and ultimately their adipose tissue or the yolk of their eggs (Raclot et al., 1998; Tierney et al., 2008a). Sampling blood provides an assessment of prey consumed in the previous couple of days and that in adipose tissue over the previous month, offering varying temporal coverage and resolution. Blood samples can be taken from a vein using a hypodermic syringe, and adipose samples by fat biopsies or by dissection of fresh cadavers. Samples need to be stored in chloroform and methanol (in a 2:1 ratio) or frozen in a deep freezer or using liquid nitrogen (Tierney et al., 2008a). Fatty acids are extracted from the samples using a solution of water, chloroform and methanol, and are separated using gas chromatography. The prey ingested can then be identified by comparing the fatty acid signatures from the sample with those of known prey types collected from stomach or trawls, or comparison with published fatty acid libraries (Tierney et al., 2008a). The approach only yields information on percentage occurrence of prey types in samples. A problem with this method is that fatty acids can be metabolised at different rates depending on energetic and physiological states of birds (e.g. chicks vs. adults), which results in biased estimation of diet composition (Tierney et al., 2008a). Nevertheless, it may represent a useful means of monitoring annual variation in diet composition within adult and chick age groups.

Stable isotope analysis

Some elements occur in two stable isotopic forms, and these exhibit different distributions relative to habitat types, geography or trophic level. The ratios of these isotopic forms in predator tissues can therefore provide insights into diet composition (Bearhop et al., 2006; Cherel, 2008; Cherel et al., 2007) and broad-scale distribution (Cherel and Hobson, 2007). The most commonly used stable isotope ratios used in diet studies are those of nitrogen (N^{15}/N^{14}; δN^{15}) and carbon (C^{13}/C^{12}; δC^{13}). δN^{15} gives an indication of the trophic level at which an animal feeds, while δC^{13} indicates primary sources of the trophic network, and can be used to infer the latitude and habitats (e.g. offshore vs. inshore or pelagic vs. benthic) where foraging occurs (Bearhop et al., 2006; Cherel et al., 2007). Isotope ratios are fixed following tissue formation, and varying turnover rates and timing of tissue formation can allow nutritional information to be averaged over differing time periods, or to be obtained from periods previous to the time of collection. For example, blood plasma infers diet over a matter of days, whole blood over several weeks, toenails or bone over several months or years and feathers the period prior to moult. Biodegradable samples (blood or flesh) need to be stored in 70% alcohol or frozen at –20°C, but feathers, toenails, eggshell and bone require no preservation and so historical dietary information can be obtained from museum specimens or sub-fossil remains (Emslie and Patterson, 2007; Hilton et al., 2006). Samples must be dried, powdered and washed in chloroform and methanol to remove lipids and contaminants, and acid to remove carbonates. The samples are homogenised and combusted and the relative abundance of δN^{15} and δC^{13} are then determined by continuous flow mass spectrometry of N_2 and CO_2 gasses. The drawback of the approach is that the taxonomic resolution is generally poor, offering information on only the broad habitat distribution and trophic levels that prey occupied. However, in cases where there are few types of prey with very different isotope signatures, it is possible to estimate the percentage diet composition by mass using isotope mixing models (Tierney et al., 2008b). The development of Bayesian isotope mixing models and a software package in which to fit these allows estimation of varied diet composition with measures of uncertainty (Parnell et al., 2010). Nevertheless, if prey types have strongly overlapping isotopic niches this method will be unable to discriminate reliably between them.

Sampling biases

Seasonal biases

Stomach sampling is typically conducted at the breeding colonies during chick rearing when adults return with crops full of food to deliver to their chicks. At other times of the year this approach is difficult to implement: during the arrival, incubation and pre-moulting periods adults often have little or nothing in their stomachs when they are ashore (Emison, 1968), while during winter most species are at-sea and unavailable to sample. Diets of penguins often vary through the year due to seasonal cycles in prey availability or shifts in foraging locations, and so samples in the chick-rearing period might not be representative of diets through the remainder of the year (Cherel et al., 2007; Tierney et al., 2008b). Moreover, in species with prolonged foraging trips, food returned to chicks may differ from that ingested by adults: prey adults bring back will have been caught during the latter part of the trip, since that captured earlier will already have been digested by the time they return (Cherel, 2008). Diet could vary through the trip owing to areas with different prey availabilities being exploited, or due to adults deliberately selecting different prey types for themselves and their chicks. Alternative methods can help to redress these biases. Faeces can be collected throughout the breeding season, or during winter on ice, and provide information on adult diet (Deagle et al., 2007; Green, 1986; Green et al., 1998). Stable isotope analysis of feathers allows inference of pre-moult diet, while analysis of tissues by this method or fatty acid analysis allows inferences of diet during the latter part of winter (Cherel et al., 2007; Tierney et al., 2008a, 2008b). The various methods of diet assessment are therefore complementary rather than competing paradigms (Tierney et al., 2008a).

Interannual biases

A small number of long-term studies of penguin diet reveal that composition can vary markedly from year-to-year (e.g. Barlow and Croxall, 2002; Crawford et al., 2003), often in response to environmentally driven changes in food availability within their foraging range. However, most studies of penguin diet only last one or two years, which will fail to fully capture annual variability in diet and risks sampling during a period when diet is atypical. Sites participating in the CCAMLR Ecosystem Monitoring Program (CEMP) often have complete time series of diet data, but there are often gaps or lags in the availability of these data in the published literature.

Geographic biases

Antarctic penguin species tend to have broad geographical ranges over which the available prey, and hence the diet of penguins, vary profoundly at the regional scale (see ‘Species accounts’). Reassuringly, at the scale of CCAMLR subareas, sampling coverage across each species’ biogeographic range is reasonably good, although a few notable species–region gaps do occur that need to be filled by empirical studies (see species accounts). However, notable variations in diet can occur at relatively fine spatial scales within regions owing to the effects of local marine habitat characteristics on prey availability within the foraging range of a colony (Bost et al., 1994; Clausen et al., 2005; Lescroel et al., 2004). Diet studies tend to be carried out at a limited number of colonies within a region, which could lead to spatial biases in estimates of diet composition across the region. Quantifying diet composition at each site is logistically impossible, but modelling diet as a function of habitat variables within the foraging range of each colony (derived from bathymetry maps and satellite remote sensing) may allow inference of spatial variation in diet composition.

Foraging range and habitat use

Transect surveys from ships

Penguin distribution at sea can be estimated by counting numbers of birds in transects at sea from ships (Ainley et al., 1984; Trathan et al., 1998; Zamon et al., 1996). Maps of bird density can then be constructed from the counts and the length, width and location of transect segments. Cruises can be designed specifically to map penguins, and can either follow a radial pattern from the colony to examine distances birds travel to feed (Trathan et al., 1998), or in successive parallel track lines to examine patterns of distribution within a study area (Zamon et al., 1996; Waluda et al., 2009). In many cases, however, counts of penguins are made opportunistically from vessels engaged in other operations, which may lead to spatial sampling biases. The advantage of transect surveys are that data can be obtained on a large proportion of the total population, and behavioural observations, associations with marine features, ice and other biota can be made concurrently with the counts. The drawback is that the breeding status and provenance of birds is often unknown, making inferences about distances travelled by breeders from a given colony difficult in most circumstances. The other problem is that the detection of penguins at sea is incomplete as they have dark upperparts, float low in the water when resting and are completely invisible when diving. These problems are likely to result in underestimates of density, although these issues can be overcome to some extent using distance sampling to account for decreasing likelihood of detecting birds with distance from the observer (Thomas et al., 2010). Birds that are underwater can be accounted for by combining distance sampling with mark-recapture methods (where data are available from a platform with two independent observers) or by incorporating independent data on surfacing rates and durations from depth recorders (Okamura, 2003; Okamura et al., 2003). Even then there are complications owing to variations in detectability at different stages of a foraging trip: commuting penguins porpoise and so are more visible than foraging ones that make frequent long dives and rest low in the water during dive intervals (Trivelpiece et al., 1986). Underestimates of foraging ranges and distribution may also occur if significant numbers of birds range beyond the outermost limits of the survey area (Zamon et al., 1996; Waluda et al., 2009).

Tracking devices

Tracking devices can be fitted to penguins to collect data on their foraging movements and environments. Generally, the advantage of telemetry is that it allows characteristics of foraging trips by individuals of known status and provenance to be acquired. Devices can also collect data on external variables (e.g. water temperature) that allow marine habitat use to be inferred, and even allow penguins to be used as oceanographic platforms (Charrassin et al., 2002; Sokolov et al., 2006). The drawbacks of this approach are that the fitting of the devices may alter the animals' behaviours, producing biased results, and the weight of a device and the drag (influenced by dimensions, shape and presence of external aerials and where on the bird it is fitted) can increase the costs of locomotion (Bannasch et al., 1994; Bost et al., 2008; Ropert-Coudert et al., 2007a, 2007b; Wilson et al., 2004). Several studies have found adverse effects of devices on penguin foraging trip parameters and breeding success when compared to unencumbered control birds (Ballard et al., 2001; Hull, 1997; Ropert-Coudert et al., 2000b, 2007a, 2007b; Taylor et al., 2001). A number of technologies to study penguin foraging movements are available, each with strengths and weaknesses.

Radio tracking involves equipping penguins with radio transmitters, which broadcast a radio signal on a frequency unique to each transmitter. This signal is detected by two radio receiving stations, which are generally situated at elevated positions at least several hundred metres apart (Ainley et al., 2004; Kato et al., 2003; Trivelpiece et al., 1986). Observers at the stations rotate the antennae of the receivers until the signal strength is at its greatest, and record the bearing from a compass rose. The position of the penguin can then be determined by triangulation, and a foraging track can be constructed by repeating this process at regular intervals. Signals cannot be received if the transmitter is underwater, and so diving or swimming activity can be determined from the pattern of intermittent signals (Trivelpiece et al., 1986). The main problem with this approach is that the range over which the transmitter can be detected (known as the radio horizon) is limited (Davis et al., 1988). The distance depends on the strength of the radio transmitter and the altitude of the receiving station, but is generally less than 100 km which is insufficient to describe foraging range for many species, at least at certain stages of the breeding cycle. Signals are also lost if the bird moves behind land or icebergs. The radio horizon can be extended using light aircraft equipped with receivers, though it is expensive and potentially hazardous (Davis et al., 1988). Radio tracking is also labour-intensive as it requires at least two people to operate antennae at frequent intervals to obtain fixes.

Satellite tracking involves fitting birds with platform transmitter terminals (PTTs), also known as satellite tags, that transmit a unique radio signal that is received by orbiting Argos satellites (Clarke and Kerry, 1992; Davis and Miller, 1992; Jouventin et al., 1994; Pütz et al., 2003). The Doppler shift in signal strength as two or more satellites pass over the transmitter is used to triangulate position of the tag on the earth's surface (Argos, 2008). This position is relayed to a ground station and then sent by email to the researcher, offering near real-time recording of the study animal's movements. The benefits of PTTs are that they allow an animal's location to be determined anywhere in the world, and that there is no need to recover the tag in order to obtain the data. This makes PTTs particularly useful for studying long-range winter movements of penguins up to the point of battery expiry (Bost et al., 2004; Pütz et al., 2000; Stokes and Boersma, 1998; Trivelpiece et al., 2007). The disadvantages are that the number of fixes is determined by the number of times two or more satellites are in view overhead simultaneously (Argos, 2008). Transmissions cannot be detected underwater, and so no fixes are obtained when penguins dive even if two or more satellites are overhead. This results in the rate of fix acquisition being c. 20 per day, which does not provide sufficient resolution to describe fine-scale movements. The accuracy of fixes depends on a number of factors such as how many satellites receive the signal at the same time, their geometry and electromagnetic interference. Accuracy can range from within 150 to over 1 500 m, and Argos assigns each fix to a location quality class to assist with post-processing. Inaccurate positions need to be filtered, which leads to further loss of fixes or the errors modelled to reposition erroneous fixes (Austin et al., 2003; Jonsen et al., 2005; Sumner et al., 2009; Tremblay et al., 2009). Notwithstanding these problems, PTT-based studies have produced the overwhelming majority of information about penguin movements to date.

Global positioning system (GPS) tracking involves equipping birds with GPS tags that calculate position from the phase shift in a pseudo-random code transmitted by 24 orbiting satellites. The advantage of this system is that the accuracy of the signals is greater and less variable than those from PTTs (accurate to within 50 m), and fixes can be recorded almost continuously. GPS tags require 15 to 120 seconds of uninterrupted exposure to the satellite constellation to acquire a fix (known as time to first fix – TTFF). GPS signals are not received while the tag is submerged, and so when these devices are deployed on penguins, acquisition of positions is frequently interrupted by immersion in water (Ryan et al., 2004). This results in a reduced number of fixes and prolonged TTFF, which results in high power drain on the tag battery and an associated reduction in the duration of operation (Ryan et al., 2004). This problem has recently been overcome using rapid acquisition GPS loggers: these simply record the raw GPS signal for processing after the device is recovered, at which time advanced algorithms are used to recreate the satellite constellation and calculate the position (Trathan et al., 2008). This reduces TTFF to 60 ms, providing tracks of unrivalled precision and resolution and extended battery life (Bishop et al., 2007; Trathan et al., 2008). This technology is relatively new and has been little used on penguins to date, though it is likely to be used more widely in the future. The drawbacks of GPS loggers are that devices need to be recovered in order to retrieve the data and they have a relatively short battery life. However, the latest generation of GPS tags overcomes these problems by including options for solar-charging, ultra-low battery drain and the wireless download of data to a base station positioned by the colony. Devices that transmit GPS readings to the Argos or Iridium satellite systems have also been developed for marine mammals but these are presently too large to be deployed on penguins.

Geolocation involves fitting birds with geolocator tags that record time and ambient light levels at one minute intervals (Moore et al., 1999; Pütz, 2002; Wilson et al., 1998a). These are archival tags that need to be recovered in order to download the data. Algorithms estimate the time of sunrise and sunset from thresholds in light curves, from which latitude can be estimated from day length and longitude from the coordinated universal time (UTC) of midday. The approach yields two fixes per 24-hour period, with an accuracy of 190 km for flying birds (Phillips et al., 2004). Latitude cannot be estimated during the equinoxes owing to day length being the same globally. Accuracy can be improved, particularly at the equinoxes, by including data on sea-surface temperature (Schaffer et al., 2005; Sumner et al., 2009; Thiebot and Pinaud, 2010) but fix accuracy never rivals those of PTT or GPS tags. Geolocation is therefore only suitable for tracking long-distance foraging movements, since local movements cannot be discriminated from fix inaccuracy. The tags have a long lifespan and can record data for up to three years, while their small size (the smallest suitable for penguins are a mere 3 g) means that they can be attached to padded leg rings so that they remain attached for such long deployments. They are inexpensive compared to other devices, which allows larger sample sizes to be tracked for a given budget. The use of geolocation to track the overwinter movements of penguins has increased markedly in the past five years (Ballard et al., 2010; Bost et al., 2009; Dunn et al., 2011; Thiebot et al., 2011a). Time-depth recorders (TDRs) can also provide geolocation data owing to strong and consistent relationships between penguin relative dive depths and light levels (Wilson et al., 1993): a process known as behavioural geolocation (Green et al., 2009).

Reconstructing tracks by dead reckoning involves equipping penguins with activity recorders that log heading, swimming speed and depth at frequent intervals. These tags need to be recovered in order to obtain data. The track followed from the colony and back can be reconstructed from the time and speed (giving distance) travelled along each bearing while allowing for vertical movements during dives, a process known as dead reckoning (Wilson and Peters, 1999; Wilson et al., 1991). The speed recorded is the speed of the penguin relative to the water around it, and the heading is the direction of the bird's long axis relative to magnetic north. This approach can produce accurate and high-resolution tracks in situations where the water that penguins travel through is relatively still. However, where penguins encounter currents on their foraging trips, the resulting drift will bias the heading and speed estimates (Shiomi et al., 2008; Wilson and Wilson, 1988). Any inaccuracies can, however, be identified by closing errors (i.e. the distance between the estimated end point of the foraging trip and the colony location), and corrections for displacements can be made using information on current direction and strength and by coercing the trip's end point to the known colony location (Wilson et al., 2007; Wilson and Wilson, 1988).

The tracking devices described above collect data on horizontal movements of birds, but deploying them in tandem with other devices has potential to allow identification of areas where foraging occurs. Prey capture and ingestion can be inferred from sensors that detect movements of the bird's beak, or temperature sensors in the stomach or oesophagus that detect drops in temperature when cold prey items are ingested (Charrassin et al., 2001; Pütz et al., 1998; Ropert-Coudert et al., 2000a; Wilson et al., 2002). TDRs and accelerometers can be used to reconstruct dive profiles and speed, and foraging activity can be inferred from the depth of dives and the number of 'wiggles' (sudden changes of depth associated with prey pursuit) or rushes (sudden increases in speed) at the bottom of dives (Bost et al., 2007, 2008). When combined with horizontal tracking, these data allow commuting corridors and foraging zones to be discriminated, which is clearly valuable in the context of spatially explicit consumption models.

Sampling biases

Both ship-time and electronic devices are expensive, and so the number of studies and their spatial and temporal coverage are relatively limited. Telemetry studies have generally been conducted at colonies near research stations owing to logistic considerations and the ease with which birds can be captured and recaptured. The locations for which distribution data are available are therefore a small, and potentially biased, sample of the wider population. The results of these studies can be generalised to the wider population in two distinct ways. The most simple is to estimate the radius within which predators spend a given proportion of time within a given season and apply this to all breeding colonies within the area of interest. This has the advantage of simplicity but it lacks parsimony as predators often focus foraging effort on certain habitats within the area available to them, such that much of the radius that contains unsuitable habitat is never used. Modelling approaches that predict distribution of birds based on habitat variables and intrinsic constraints (such as distance from colony, size of colony, size and distances of adjacent colonies) provide a more parsimonious and mechanistic method of predicting at-sea distribution of penguins around unsampled colonies (Wakefield et al., 2009, 2011).

Emperor penguin (*Aptenodytes forsteri*)

Diet

Diet comprises fish (mostly nototheniids, particularly Antarctic silverfish (*Pleuragramma antarcticum*)), crustaceans (mostly *E. superba*) and squid (most commonly *Psychroteuthis glacialis*). Proportions vary enormously among studies due to season and location: crustaceans tend to dominate in winter at colony sites close to shelf edge, whereas fish and squid dominate in summer in colonies adjacent to more extensive shelf areas.

Studies have been conducted largely by stomach flushing of birds returning to feed chicks. This has potential to cause biases owing to adults feeding chicks on different prey to themselves, although a stable isotope study showed no difference in signatures among these age classes (Cherel, 2008). Accumulation of cephalopod beaks could cause overestimation of the squid component (Pütz, 1995): treatment of these varies among studies, although most exclude beaks free of flesh from analysis. Two studies focused on prey remains in faeces. Seasonal sampling is better than for most penguin species, since breeding cycle results in birds being available to sample during the winter months. Presentation of results differs among papers (percentages of occurrence, numbers and mass) making comparisons across sites problematic. Samples have been taken within most of the CCAMLR management units, though at a limited number of sites within each and often in a limited number of years and seasons. Sampling is particularly sparse in Subarea 48.5 given the number and size of colonies there (Fretwell and Trathan, 2009). The marked spatio–temporal variability in diet evident from these studies indicates that more frequent sampling at more sites is needed, though the remote and inhospitable locations in which colonies occur make this impractical. Inferences of diet composition at colonies for which no data exist may be possible by modelling diet as a function of bathymetry around each colony (see below).

In Subarea 48.5, Piatkowski and Pütz (1994) conducted stomach flushing of 58 adult birds during January and February of both 1990 and 1992 at the Drescher Inlet. Analysis was of percentage of stomachs (squid 93%, fish 74%, krill 67%, amphipods 55% and isopods 22%) in which prey occurred, with more detailed analysis of the squid component. Of the squid component alone, by mass, *Kondakovia longimana* comprised 48–50%, *Alluroteuthis antarcticus* 29–37% and *P. glacialis* 13–23%. Pütz (1995) conducted stomach flushing of 29 adults at the Dresher Inlet in January and February of both 1990 and 1992 (Fish composition by mass was 75% (mostly *P. antarcticum* and *Pagothenia borchgrevinki*) and crustaceans composition by mass was 25% (almost entirely *E. superba*)). Squid beaks were excluded from analysis, as a feeding experiment showed they could accumulate for several weeks without signs of erosion. Ainley et al. (1992a) undertook stomach flushing of 18 birds captured on sea-ice in the Weddell Sea in March 1986, and eight at the Weddell–Scotia Sea confluence in July–August 1988. Of diet by mass, 99% comprised squid: 48% *P. glacialis*, 32% *K. longimana*, 14% *Gailteuthis glacialis* and 5% *Gonatus antarcticus*. Klages (1989) undertook stomach flushing of 34 adults in October–November 1986 at Dresher Inlet. Fish comprised 38.1% by mass, squid 9.8% and crustaceans 52.1%. Of the fish component alone by number, 66.3% were *P. antarcticum* and 30.5% *Notolepsis coatsi*. Of the squid component alone by number, 90.8% were *P. glacialis* and the crustacean component was almost entirely *E. superba*.

In Division 58.4.1, Offredo and Ridoux (1986) conducted stomach flushing of 29 birds in November 1984 at Pointe Géologie. Fish comprised 95%, cephalopods 3% and crustaceans 2%; almost all fish were nototheniids. Cherel (2008) took blood samples from 11 adults and eight chicks in the austral spring of 2002 at Pointe Géologie. Whole blood was subjected to carbon and nitrogen stable isotope analysis in order to infer trophic niches in the months prior to sample collection. The isotope signatures of penguins closely matched that of *P. antarcticum*, and no differences were evident between adults and chicks. Opportunistic, qualitative inspection of spontaneous regurgitates confirmed birds were eating *P. antarcticum*, and also some *P. glacialis* and *E. superba*.

In Division 58.4.2, Green (1986) collected 151 droppings at the ice edge 100 km from the Amanda Bay colony from August to October 1984. They were analysed in terms of frequency of occurrence of prey items by month. Fish occurred in 88% of droppings in August and 100% in other months, cephalopods in only 1.6–5.1%; the main species identified from otoliths was *P. antarcticum*. Crustaceans increased throughout the study: amphipods from 13.7% in August to 51.3% in October, isopods from 7.8% to 33.3% respectively. Euphausiids and mysids were rare (<4%). Gales et al. (1990) conducted stomach flushing of 35 birds in autumn 1986 at Amanda Bay. Fish comprised 98.6% of diet by mass, cephalopods 2.7% and crustaceans < 1%. Of the total sample, the fish *P. antarcticum* comprised 78.1%, *Trematomus/Pagothenia* spp. 9.5% and Channichthyid species 7.9%. Robertson et al. (1994) conducted stomach flushing of 153 adults returning to feed chicks at Auster and Taylor Glaciers in 1988. Fish comprised 55% by mass at Auster and 30.7% at Taylor; cephalopods 44.7% and 69.3% respectively. Crustaceans occurred in over 80% of samples but were so heavily digested that numbers and mass could not be determined. Nototheniidae (notably *T. eulepidotus* and *P. antarcticum*) were the dominant fish component, with various species of the families Bathydraconidae and Channichthyidae each totalling less than 10% by mass. The squid component was dominated by *P. glacialis* and *A. antarcticus*. Kirkwood and Robertson (1997a) undertook stomach flushing of 17 females returning to feed chicks at Auster Glacier from July to early August 1993. Fish comprised 27% (*P. antarcticum* 13%), squid 3% (all *P. glacialis*) and crustaceans (all *E. superba*) 70% by mass. Kirkwood and Robertson (1997b) also undertook stomach flushing of 94 adult penguins returning to feed chicks at Auster Glacier and 27 at Taylor Glacier from late August to early December 1993. Percentage composition by prey groupings varied considerably among sampling days; fish 10.9–74.8%, squid 5.2–64.2% and *E. superba* 0.7–67.5%. The *E. superba* component declined with a seasonal trend, from 68% in August to < 1% in December, while the squid component increased markedly throughout the season but decreased abruptly in December. The fish component was dominated by nototheniids (22% by mass of all prey types), with *Trematomus* sp. (27% by number), *P. borchgrevinki* (25%) and *P. antarcticum* (8%) being the most important. The myctophid *Electrona antarcticum* comprised 1.9%, and was found mostly in October–early November, and the paralepid *N. coatsi* comprised 1.7%. The cephalopod component was dominated by *P. glacialis* (25.6% of mass of all prey types); the next most common squid (*A. antarcticus*) comprised only 3.4%. Wienecke and Robertson (1997) flushed the stomachs of 20 females and 20 males on their first return trip to feed their chicks in mid-July and late August 1994. Female diet comprised 72% fish by mass (34.5% *Trematomus* sp., 19.3% *P. antarcticum*), 16% squid (*P. glacialis*) and 12% crustaceans (*E. superba*). For males these values were 55.1, 18.1, 28.9, 1.9 and 43.0% respectively.

In Subarea 88.1, Cherel and Kooyman (1998) stomach-flushed a total of 40 birds at Cape Washington in November and December of 1986, 1989, 1990 and 1992. Fish comprised 88.6–94.9% by mass, crustaceans 5.1–11.4% and squid were absent. *Pleuragramma antarcticum* comprised 89% of fish component by number and an unidentified channichthyiid 11%. Of the crustacean component by number, 30.3% were *Abyssorchomene rossi/plebs*, 23.7% *E. crystallorophias*, 22.3% *Eusirus microps* and 11.4% *Epimeriella macronyx*. The same study also collected seven frozen natural regurgitates at Coulman Island, and four at Cape Roget in 1993. Diet comprised 88.0% and 93.3% fish, 11.6% and 6.6% squid and 0.4% and 0.1% crustaceans at Coulman Island and Cape Roget respectively. Of the fish component by number, 97% were *P. antarcticum* and squid were almost entirely *P. glacialis*.

In Subarea 88.2, Kooyman et al. (2004) collected 54 scats along pelagic transects in the eastern Ross Sea from December 1999 to February 2000 during pre- and post-moult periods. Sixteen were red and contained euphausiids and 16 were black and contained either fish or squid. These colour classes were used to identify broad prey categories from deck-based observations throughout the entire cruise. Fish and squid type scats were mostly over shelf waters and krill predominated in deeper, offshore waters.

Movements and habitat

Foraging movements and habitat vary according to season. After laying in the early austral winter, females walk tens of kilometres across fast-ice to forage in pack-ice or polynyas over shelf areas, usually within 150 km of the colony, in trips lasting c. 76 days. Meanwhile males remain on fast-ice to incubate their eggs. Upon hatching in the austral spring, males and females both forage for the chick in trips of shorter duration (2–25 days) in similar areas and habitats. After completion of breeding, adults undertake long pre-moult foraging movements, often into deep water north of the ice edge, to gain mass before the moult. Moulting occurs in sea areas that support stable areas of fast-ice throughout the summer, often far from the colony. Juveniles travel further north still to the Antarctic Polar Front (APF) for the remainder of the austral summer. With the onset of the austral winter, adults return to the breeding colonies, while juveniles return to the marginal-ice and pack-ice zones.

Tracking studies have mostly used PTTs, and have only been carried out at a relatively small proportion of the total number of known colonies (Fretwell and Trathan, 2009). The lack of studies in Subarea 48.5, despite the large number of colonies there, represents a major knowledge gap. Tracking was conducted using PTTs in all studies, mostly of females during the incubation period and of both sexes during chick rearing. Sample sizes at each site when summed across studies are adequate to describe foraging ranges and habitat use in most cases. Two studies of pre-moult movements and of moulting distribution exist, and one of juvenile dispersal. Data from other sites is desirable.

In Division 58.4.1, Ancel et al. (1992) fitted four males with PTTs in August 1990 at Pointe Géologie. Birds walked over fast sea-ice to reach polynyas, and the two birds that reached a polynya with the PTTs still transmitting travelled for 156 and 269 km. Rodary et al. (2000) equipped four males departing for sea after completion of incubation in August 1996 and six in August 1997 with PTTs. Average maximum distances from colony were 90 km in 1996 and 60 km in 1997. Foraging occurred in pack-ice areas near the fast-ice edge in waters 200–300 m deep, with most dives being benthic. Zimmer et al. (2008) equipped birds with PTTs throughout the 2005 breeding period: three females post-laying (four trips), two males (two trips) post-hatching, 10 adults (21 trips) during chick rearing and five successful or failed breeders during their pre-moult period. After laying, females departed the colony following laying in a north-easterly direction, with an average maximum range from the colony of 94 km. Trips lasted 72 days, 5–11 days of which was spent walking over fast-ice. Males after incubation also headed northeast, with a mean maximum distance from the colony of 106 km. Trips lasted 24 days, with two days walking over fast-ice. During chick rearing, foraging was over the shelf areas to the northeast of the colony with an average maximum distance from the colony of 85 km and duration of 2–19 days. Once their breeding cycle ended, adults moved into deep water up to 660 km off the Adélie land coast before returning to sea-ice areas to moult during trips lasting 42 days. Four non-breeding or failed breeders showed similar long-distance movements.

In Subarea 48.5, Kooyman et al. (2000) conducted transect counts of moulting penguins in the Weddell Sea. Large numbers observed centred on 72°S 50°W, on ridged ice floes that are durable and provide protection from wind. This is believed to represent the main moulting areas for all colonies in the Weddell Sea, between 550 and 1 400 km away.

In Division 58.4.2, Kirkwood and Robertson (1997a) equipped three female birds with PTTs in May 1993 at Auster Glacier. All walked to reach the fast-ice edge (one PTT failed here), and then swam a further 40 km through the pack-ice to reach a polynya where they remained until mid-July when the remaining two PTTs failed. Expansion of fast-ice subsequently would have forced birds further offshore. Kirkwood and Robertson (1997b) equipped three male birds departing the Auster colony to forage for their chicks with PTTs from late July to August 1993. Only one operated long enough to provide a foraging track. It walked northeast across 60 km of fast-ice to reach a polynya where it foraged for 25 days, after which the PTT failed. It returned to the colony 13 days after this. Wienecke and Robertson (1997) fitted 12 females departing for sea after laying with PTTs and TDRs in late May 1994 and three males departing after hatching in August–September. Birds had to walk

50–70 km to reach the edge of the fast-ice. Foraging of both sexes mostly occurred in pack-ice along a narrow band of the shelf slope within 120 km of the colony. 50% of foraging occurred within two areas occupying 15% of this total area, one being adjacent to a polynya and the other over a canyon, which may have enhanced marine productivity. Two females exhibited far greater foraging ranges, moving east to maximum distances from the colony of around 500 km. Wienecke et al. (2004) tracked movements of nine adults from Auster and Taylor Glacier colonies equipped with PTTs during the pre-moult period from December 2000 to February 2001. All Auster birds and two of the Taylor birds moved an average of 478 km north of the colony to latitudes less than 64°S, where water was deep (>3 000 m) and ice-free. Two Taylor birds remained close to the edge of the fast-ice and moved west to distances of 300–600 km from the colony. Three moult locations were identified for six birds: these were all well to the west of the breeding colony at Cape Boothby, Steffanson Bay and Casey Bay, where small but stable areas of fast-ice persisted through the moult period.

In Subarea 88.1, Ancel et al. (1992) fitted six birds (three female, one male, two unknown gender) with PTTs in October–December during chick rearing at Cape Washington, eastern Ross Sea. The lengths of track-lines were 164–1 454 km along looping courses. Kooyman et al. (2000) fitted a total of 12 PTTs to adults departing four western Ross Sea colonies (Capes Washington, Crozier and Roget and Coulman Island) to moult in November and December of 1992 to 1994. Birds travelled for c. 30 days to areas of perennially consistent pack-ice in the eastern Ross Sea and western Amundsen Sea over 1 000 km from their colonies, where they proceeded to moult. Observations in the Weddell Sea showed birds moulted in areas where sea-ice was ridged, providing shelter from wind. Kooyman and Ponganis (2007) fitted 10 juveniles with PTTs on their first trip from the Cape Washington colony in December of 1994 to 1996. Six hand-reared chicks were also grown to fledging weights greater than those in the wild so that they could be fitted with larger PTTs with longer operational life: these were released at the ice edge off McMurdo Sound in January 2001. Wild birds all swam northeast to open water at latitudes between 64°S and 57°S. Released birds swam north also, though only reached latitudes of 63°S, where they either remained or turned back south. The conclusion was that after fledging birds migrate to the APF until March, after which they spend the winter in the marginal ice zone or within the pack-ice.

King penguin (*Aptenodytes patagonicus*)

Diet

Generally, summer diet comprises fish of the family Myctophidae, particularly *Krefftichthys anderssoni* and *E. carlsbergi* in varying proportions according to geography, season and year. During winter, chicks are fed infrequently on smaller meals, with other fish taxa and squid becoming more important. Adults are likely to continue to self-feed on myctophids based on stable isotope study at a single site (Cherel et al., 2007). Crustaceans comprise a trivial component of diet in all studies.

Quantitative studies of diet have been conducted at most colonies worldwide so there is little uncertainty due to spatial bias in sampling. Most studies sampled diet by stomach flushing at breeding colonies, which will be biased by variable digestion rates of different prey types. The method is only representative of what adults bring back to their chicks rather than for self-maintenance. In view of the long foraging trips this species undertakes, and the rapid rate of fish digestion, prey ingested early in the trip may differ from that captured during the latter part of the trip that is fed to chicks. This bias is particularly acute during winter, when adults are absent for a month or more and return to feed chicks on prey captured locally. A small number of studies based on fatty acid and stable isotope analysis give information on adult diet but lack taxonomic resolution. Diet composition varied at sites annually and seasonally, creating uncertainty in the representativeness of studies from a small number of years or only from certain parts of the season.

In the Falkland Islands, Cherel et al. (2002) flushed the stomachs of 10 birds at Volunteer Point in February 2001. Diet by mass was 88.1% *Protomyctophum choriodon* and 4.7% *E. carlsbergi*. Piatkowski et al. (2001) conducted stomach flushing of 23 adults of various stages at Volunteer Point from September to October 1996. Diet by mass was mostly myctophid fish but this component of samples was not quantified; the squid component comprised 60.4% *Martialia hyadesi* and 23.3% *Moroteuthis ingens*.

At South Georgia in Subarea 48.3, Olsson and North (1997) stomach-flushed 115 breeding adults at St Andrew's Bay during November 1991 and March 1994. *Krefftichthys anderssoni* was most important by mass, followed by *N. coatsi*, *E. carlsbergi* and *P. choriodon*. The *K. anderssoni* component declined with season and was lower in 1993/94, which was associated with low breeding success.

At the Kerguelen Islands in Division 58.5.1, Bost et al. (2002) stomach-flushed 22 breeding adults in March 1995. Diet by mass was 31.6% *K. anderssoni*, 30.1% *Mureanolepis marmoratus* and 13.7% *P. bolini*. Diet differed significantly from trawl samples within foraging areas, but the closest match found during the day was from depths at which king penguins foraged.

At Heard Island in Division 58.5.2, Klages et al. (1990) conducted stomach flushing of 24 birds of unknown status from November 1986 to January 1987. Fish comprised 99.4% by mass, mostly *K. anderssoni*, *E. carlsbergi* and *Champsocephalus gunnari*. Moore et al. (1998) conducted stomach flushing of 98 adults from February to November 1992. Diet by mass comprised 71% fish, mostly *K. anderssoni* (48.0%) and the paralepidedid *Magnisudis prionosa* (16.7%) and squid 28.5%, mostly *M. hyadesi*, taken only in winter. Wienecke and Robertson (2006) undertook stomach flushing of eight breeding birds from 20 December 2003 to 27 February 2004. Diet by percentage number comprised fish 28.4%, mostly *K. anderssoni* (25.4%); squid 71.6%, mostly *M. ingens* (33.6%) and *Kondakovia longimana* (22.8%).

In Subarea 58.6 at the Crozet Islands, Ridoux (1994) had 23 adults stomach-flushed from November 1980 to February 1981. Diet by percentage mass comprised 35.6% *E. carlsbergi*, 28.6% *K. anderssoni*, 24.4% *P. tenisoni*. Squid comprised 7.6%; mostly *M. knipovitchi* and *K. longimana*. Raclot et al. (1998) had eight chicks and eight adults killed for fatty acid analysis during spring and autumn 1987. Diet of both chicks and adults comprised mostly myctophids, which agreed with dissected stomach samples that comprised *E. carlsbergi*, *P. tenisoni* and *K. anderssoni*. Cherel and Ridoux (1992) undertook stomach flushing of 20 breeding adults with chicks during February 1989. Diet by mass was 73.7% *E. carlsbergi* and 13.4% *K. anderssoni*. Cherel et al. (1993) conducted stomach flushing of 45 breeding adults from February to October 1990. *Krefftichthys anderssoni*, *E. carlsbergi* and *P. tenisoni* accounted for > 98% of diet by number in summer and spring, but only for 67% in winter, with other fish and squid becoming more frequent. Cherel et al. (1996) conducted stomach flushing of 47 adults in June and July of 1990 to 1992. Diet by mass was 56% squid *M. ingens*, 13% the myctophid fish *Gymnoscopelus piabilis*, and a wide range of other taxa, each < 5%. Bost et al. (1997) undertook stomach flushing of 10 adult birds in both February 1993 and 1994. In 1993, samples contained *K. anderssoni* 15%, *Protomyctophum* sp. 14.3% and *E. carlsbergi* 70.1% and in 1994 36.6%, 48.1% and 15.3% respectively. Cherel and Hobson (2007) and Cherel et al. (2007) stomach-flushed 10 adults tending chicks at Possession Island in 2002. Diet by percentage number comprised 97.6% fish; 68.2% *K. anderssoni*, 19.1% *E. carlsbergi* and 6.9% *P. tenisoni*; the remainder comprised various species of squid. Studies of stable isotope ratios in adult king penguin tissues and feathers showed diets broadly similar seasonally, although the niche widened during winter.

In Subarea 58.7 at Marion Island, Adams and Brown (1989) and Adams and Klages (1987) conducted stomach flushing of 115 breeding adults from March 1984 to March 1985. Diet by mass was dominated by myctophids: 27% *K. anderssoni* and *P. tenisoni* combined, and 51% *E. carlsbergi*. Squid made up 13% overall (mostly *K. longimana*), with importance greater during winter.

At Macquarie Island, Hindell (1988a) stomach-flushed 118 breeding adults from November 1984 to November 1985. Diet by mass comprised 37.7% *K. anderssoni*, 53.2% *E. carlsbergi*; the former dominated summer diet, and the latter in winter. Wienecke and Robertson (2006) conducted stomach flushing of 10 breeding birds from 15 December 1998 to 28 January 1999. Fish made up 52.4% by number, mostly *K. anderssoni* 28.3% and *E. carlsbergi* 12.5%; squid was 46%, mostly *M. ingens* 15.2%, *Mastigoteuthis* sp. 11.7%, *P. glacialis* 7.6% and *K. longimana* 6.0%.

Movements and habitat

During summer, birds at most colonies commute to the APF, or mesoscale eddies associated with it, such that foraging ranges and direction are dictated by the position of the colony relative to these features. Consequently, foraging trips can span long distances and may cross boundaries of CCAMLR management units. King penguins forage mostly by day, with dive depths being shallower in morning and evening than in the day, associated with diel vertical movements of myctophid prey. Maximum dive depths of 343 m have been recorded (Pütz and Cherel, 2005). Myctophid densities are elevated and more predictable at the APF and below the thermocline which explains horizontal and vertical distribution of foraging by king penguins (Charrassin and Bost, 2001). During winter, thickening of the surface mixed layer (SML) results in myctophids descending to depths inaccessible to king penguins: birds then move into Antarctic waters, especially the marginal ice zone, where the SML is thinner and potential prey are concentrated.

Studies of horizontal foraging distribution using PTTs, GPS or GLS loggers have been conducted at all major colonies, often over multiple years with adequate sample sizes. These have mostly been conducted on breeding birds during summer. Studies of birds rearing chicks in the winter and non-breeding birds exist for a limited number of sites, and all are based on small sample sizes.

In the Falkland Islands, Pütz (2002) tracked five adult birds, some for multiple trips, using GLS from Volunteer Beach on the west coast of the island in each season (early winter, late winter and early summer 1996). In early winter, birds foraged over 1 000 km south of the Falkland Islands around the South Shetland Islands, with one moving into the Weddell Sea. Those in late winter foraged to the north along the Patagonian shelf break up to 45°S, with only a single short trip to the south of the Falkland Islands. In summer, foraging was to the east and northeast of the colony with highest densities around 49–51°S 55°W. Pütz and Cherel (2005) recorded 15 tracks for 12 birds fitted with GLS and TDR tags during brooding in February 2001 at Volunteer Point. Foraging locations were similar to a previous study: 500 km to the northwest of the island associated with the sub-Antarctic Front and Patagonian shelf break.

At South Georgia in Subarea 48.3, Pütz (2002) recorded three foraging trips of one bird during the chick-rearing season at Husvik Bay using a GLS tag. Foraging trips increased in length as season progressed; two were to the north-northeast and one to the west, with two reaching the APF. Scheffer et al. (2010) and Trathan et al. (2008) fitted six birds with rapid-acquisition GPS tags and 14 with PTTs during the incubation stage from December 2005 to January 2006 at Hound Bay. Average trip duration was 18.6 days (SD 1.8). Birds commuted northwards along narrow corridors to forage in waters at the APF ranging from 5.0 to 5.5°C and lying between 49–50°S and 40–30°W. King penguins appeared to target predictable mesoscale features in the Polar Frontal Zone (PFZ), either a warm-core eddy in the PFZ or regions of strong temperature gradients at oceanic fronts. Foraging therefore occurs mostly within Subarea 48.3 with birds merely commuting through the small-scale management units around South Georgia.

In Division 58.5.1 at the Kerguelen Islands, Bost et al. (2002) and Koudil et al. (2000) tracked nine birds with chicks at crèche stage during March 1995, fitted with PTTs at Ratmanoff colony in the east of the island. Maximum distance of foraging trips from the colony was c. 300 km, all falling within a narrow sector between east-northeast and east-southeast. Trips were all within Division 58.5.1. Pütz (2002) fitted four birds with GLS tags in March 1995 at Ratmanoff colony on the east coast of the island. Foraging distributions were similar to those described by Bost et al. (2002) at the same colony and time. Charrassin et al. (2002, 2004) fitted 18 breeding adults at brood-guard stage from Ratmanoff colony with PTTs in February–March 1998–2001. Most birds foraged over the Kerguelen shelf near the shelf break to the southeast of the colony, on average 304 km from the colony (max. 603 km). Three tracks went to the south of Kerguelen to the western shelf break and one to the northeast. All fell within Division 58.5.1. Foraging birds targeted a sub-surface tongue of cold water flowing along the shelf break or Polar Front. Foraging areas of colonies elsewhere on this large island were not documented, but were probably within Division 58.5.1. The foraging distributions of winter breeders and non-breeders are unknown.

At Heard Island in Division 58.5.2, Moore et al. (1999) fitted 55 breeding birds with GLS tags during chick rearing in autumn, winter and spring

1992/93. During autumn, birds foraged almost entirely east of Heard Island from 71° to 79°E and over a wide longitudinal range from 46° to 58°S, taking them north to the APF and to the south end of the Kerguelen Plateau. Some of the samples coincided with the equinox, which may have contributed to this wide range. Positions in spring were almost all to the north-northeast of Heard Island, to and beyond the APF. Foraging ranges during spring, autumn and likely summer therefore fell within Divisions 58.5.1, 58.5.2 and 58.4.3. During winter, one bird travelled south and east to 49–54°S and 78–95°E which corresponded to the ice-edge and another to 65°S which was deep in the pack-ice, but small sample size makes representativeness of tracks uncertain. Wienecke and Robertson (2006) fitted 21 incubating birds with PTTs during 2003/04. Foraging concentrated in an area to the east of the colony occupying 7 400 km^2 between 75 and 300 km from the colony, with none travelling beyond 80°E, or 55°S. Two birds foraged to the north and west of the island. Hence, most foraging during summer occurred within Division 58.5.2, with minor activity in Division 58.5.1.

Many published studies exist for Possession Island at the Crozet Islands in Subarea 58.6. Many overlap with respect to the data presented. In combination, these suggest most of the foraging in spring, summer and early autumn are within Subarea 58.6 and Division 58.4.4b, while in late autumn and winter birds spend most of their time in Divisions 58.4.2, 58.4.4a and 58.4.4b. Jouventin et al. (1994) fitted 18 birds with PTTs, covering all stages of breeding from January 1992 to August 1993. Average foraging trip duration was 16.8 days (SD 7.8) and foraging range was 471 km (SD 299). Trip durations and foraging ranges were shortest during brooding, intermediate during incubation and longest during guard stage. Little foraging activity occurred to the west of the island; most trips were long and linear to the south; with a smaller number of shorter circular trips to the northeast. In winter, the single bird tracked travelled south to the ice edge. Guinet et al. (1997) tracked 20 birds fitted with PTTs in the 1992–1994 summers (including four summer 1992 tracks described above). Most birds foraged to the south in waters of 4–5°C associated with the APF; those foraging to the east in waters of 8–10°C were associated with the southern limit of the sub-Antarctic Front. Bost et al. (1997) used stomach temperature loggers on a sub-sample of these birds to show that highest rates of prey capture occurred on the outbound trip and at fronts; little was ingested on the return journey. Pütz et al. (1998) equipped seven birds with GLS tags during chick rearing from January to March 1993. Most positions were 250 km south of the island 48–49°S, though some as far south as 51°S. Pütz et al. (1999) had breeding birds fitted with GLS tags during January–March 1994 and January–June 1995. In summer, birds went to the APF 300 km south of the colony; those in 1995 travelled farther south than in 1994. Two birds tracked in winter travelled to the ice edge at 60°S at distances 16 000–18 000 km from the colony. Charrassin and Bost (2001) tracked 44 birds using PTTs during the entire annual cycle in 1994 and 1997. During summer, 14 satellite-tracked birds foraged at the APF 340–450 km south of the colony, and temperature profiles from 12 birds carrying TDRs only indicated they also foraged there. In autumn and winter, eight PTT-tracked birds and temperature readings from eight TDR-equipped birds, showed that these foraged in Antarctic waters. 70% of PTT-tracked birds reached the pack-ice limit. In spring during post-moult, four PTT-tracked birds resumed feeding at the APF. Birds generally dived through the SML to forage below the level of the thermocline: the depth of the SML increases in winter at the APF which likely explains the move of birds to Antarctic waters where the SML is thinner. The exception is in spring when foraging resumes at the APF despite the SML being deeper than maximum dive range. Bost et al. (2004) fitted 10 breeders during crèche stage at Possession Island with PTTs in winter from 5 June to October in 1996 and 1997. All birds moved south to the marginal ice zone between 55.8° and 57°S and from 40° and 70°E. Pack-ice, floes and open water were used less than marginal ice zone. Trips were longer compared to untagged birds and six of 10 birds abandoned chicks, indicating that adverse effects of tags is greater in winter. Cotte et al. (2007) tracked 43 birds with PTTs during summer 2002–2005. Penguins travelled to foraging zones rapidly using ocean currents, slowing down to forage in regions of high thermal gradients, such as fronts and mesoscale eddies, and ignored currents on return journeys.

At Macquarie Island, Sokolov et al. (2006) and Wienecke and Robertson (2002, 2006) fitted 24 incubating birds with PTTs between 1998 and 1999. Tracks ran clockwise and were teardrop-shaped; outbound trips took a southeast heading to 58–59°S before returning north and then east to return to the colony. Foraging concentrated between the northern and southern branches of the APF, between 250 and 600 km from the colony. There is reasonable certainty that foraging by breeding birds in summer occurs outside the CAMLR Convention Area, but no information on winter breeders and non-breeding birds that could plausibly feed in Subareas 88.1, 88.2 or Division 58.4.1, based on winter movements from other colonies, is available.

Adélie penguin (*Pygoscelis adeliae*)

Diet

Diet is dominated by euphausiid crustaceans and fish in all studies, with squid and amphipods making relatively small contributions. Diet varies according to habitat around the colony: birds foraging over the shelf feed mostly on *E. crystallorophias* and fish (especially *P. antarcticum*), while those feeding over the shelf slope or in oceanic waters feed on *E. superba*. Relative contribution of fish to the diet varies among years and seasonally in several studies, and generally becomes more common during chick rearing. A single study of winter diet suggests squid may become more important then, although sample sizes are small.

Studies are mostly based on stomach flushing of adults returning to feed chicks; these are likely to be unrepresentative of diet composition at other times of the year, or that of adult birds during chick rearing. Three studies of diet using stable isotopes, one using fatty acid analysis and one using genetic signatures in faeces confirm these biases. Studies have been carried out at colonies throughout the species range, though only a small proportion of the colonies in each subarea have been sampled, and the variation in diet among sites is large. Estimating diet composition at unsampled sites may be possible by modelling it as a function of the percentage of the foraging range that is on the continental shelf, since this explains much of the spatial variation in diet.

In Subarea 48.1, Volkman et al. (1980) dissected the stomachs of 48 birds throughout the breeding period at Point Thomas, King George Island, from November 1977 to February 1978. Percentage composition by mass was 99.6% euphausiids; of these 98.4% were *E. superba* and 1.6% *E. crystallorophias*. Jablonski (1985) sampled the stomachs of 600 birds using stomach flushing, emetics or dissection. Diet composition by percentage mass was 72.7% euphausiids, 3.9% amphipods and 11% an indeterminate mixture of the two; fish comprised 7%. Euphausiids were mostly *E. superba* with small numbers of *E. crystallorophias*. Amphipods were mostly *Themisto gaudichaudii* and fish were *P. antarcticum*. Fish were taken only during chick rearing and prior to moult, with proportion by mass varying among years (1.9–24%). Nagy and Obst (1992) stomach-flushed five birds near Palmer Station, Anvers Island, during January 1984. Diet by percentage mass was 100% *E. superba*. Coria et al. (1995) stomach-flushed 41 birds during chick rearing at Esperanza Bay from 13 December 1987 to 28 January 1988. Diet composition by mass was 93.6% *E. superba* during guard stage and 99.7% during crèche. The remainder comprised fish that included three nototheniids, six *P. antarcticum* and one *E. antarctica*. A small quantity of hyperiid amphipods were also recorded. Polito et al. (2011) took 14–15 eggshell samples from 11 sites around the South Shetland Islands and Antarctic Peninsula to infer female winter diet using stable isotope analysis. A stable isotope mixing model predicted that the percentage of the diet comprising euphausiids was 37–53% depending on region, with the remainder being fish.

In Subarea 48.2, White and Conroy (1975) conducted stomach flushing of 10 birds at Signy Island, South Orkney Islands, during 1972 and 1973. Samples comprised almost entirely *E. superba* with small numbers of amphipods. Lishman (1985) dissected the stomachs of birds during the breeding season at Signy Island (15 in 1980/81 and 13 in 1981/82). Percentage composition by mass was 98.3% euphausiids in the first year and 99.1% in the second. Fish comprised most of the remainder, along with traces of amphipods. Lynnes et al. (2004) undertook stomach flushing of 30–50 birds during chick rearing at Gourlay Peninsula, Signy Island, from 1997 to 2001. *Euphausia superba* comprised 99.5% by mass across all years, with little annual variation. Libertelli et al. (2003) conducted stomach-flushing of 35–47 birds from December to January in 1997/98 and 1998/99 at Laurie Island, South Orkney Islands. Diet by percentage mass exceeded 99% *E. superba* in all three years, with the amphipods *T. gaudichaudii* and the fish *E. antarctica*, *T. newnesi* and larval nototheniids comprising the remainder. Polito et al. (2011) took 15 eggshell samples from both Signy and Coronation Islands to infer female winter diet using stable isotope analysis. A stable isotope mixing model predicted that the percentage of the diet comprising euphausiids was 47%, with the remainder being fish.

In Subarea 48.5, Ainley et al. (1992a) conducted stomach flushing of birds captured on sea-ice in the Weddell and Scotia Seas: 11 in autumn 1986 and 29 in winter 1988. Composition by mass was 30% crustaceans (28% *E. superba*, 2% *Thysanoessa macrura*), 14% fish (all *E. antarctica*) and 54% squid (44% *K. longimana*, 10% *P. glacialis*).

In Division 58.4.1, Ridoux and Offredo (1989) flushed the stomachs of 105 birds during chick rearing at colonies in Terre Adélie in January and February 1982. Diet by mass comprised 79% euphausiids (41% *E. superba*, 38% *E. crystallorophias*), 18% fish (*T. newnesi* were the only identifiable fish remains) and 3% squid (*P. glacialis*). Percentage mass of *E. crystallorophias* increased in February to over 75% in 28 of 33 samples. Kent et al. (1998) undertook stomach flushing of 41 birds rearing chicks at Shirley Island, near the Casey Station in January 1992. Diet by percentage mass comprised 48.7% fish (41.9% *P. antarcticum*), 48.3% euphausiids (39.7% *E. superba* and 8.5% *E. crystallorophias*), and 3% amphipods and squid combined. Watanuki et al. (1997) stomach-flushed 28 birds in 1996/97 at a colony by Dumont d'Urville station. Diet composition by percentage mass was 75% *E. superba*, 4% *E. crystallorophias*, 17% nototheniid fish and 1% amphipod. Wienecke et al. (2000) conducted stomach flushing of 30 birds at Petrel Island, Dumont d'Urville station, and 26 birds at Shirley Island through the 1995/1996 chick-rearing period. Diet by percentage mass comprised approximately 75%–80% euphausiids during the guard phase and 55–60% during crèche at Petrel Island and Shirley Island respectively. Fish comprised the remainder, apart from small proportions of amphipods at Petrel Island. Composition of euphausiid component varied by stage and site: at Petrel Island *E. superba* comprised 27% at guard stage and 38% at crèche, *E. crystallorophias* 39% and 22% respectively. At Shirley Island these values were 22%, 0.3%, 53% and 51% respectively. These differences among colonies were reflected by relative abundance of the two euphausiids in offshore trawls. The fish that could be identified included *P. antarcticum*, *E. antarctica* and channichthyiids. Ropert-Coudert et al. (2002) conducted stomach flushing of 13 birds from Petrel Island during January 1997. Diet by mass comprised 68% euphausiids, with *E. superba* and *E. crystallorophias* in equal proportions, and the remainder fish in the form of *P. antarcticum*. Cherel (2008) undertook stomach flushing of 10 adults during chick rearing, and sampling of whole blood from 10 adults during the arrival period in spring, 10 during breeding and eight chicks at Pointe Géologie in 2002. Crustaceans comprised 93.6% by mass, and fish 6.2%. The main prey species by number was *E. crystallorophias* (93.9%) with only 4.4% of *E. superba*. Fish were *P. antarcticum* and unidentified channichthyiids. δN^{15} isotope values were similar to those of euphausiids during arrival, intermediate for adults during chick rearing and highest for chicks, the latter being more similar to values for fish. This indicates adults self-fed increasingly on fish through the season, but moreover provisioned chicks with a diet more rich in fish than their own.

In Division 58.4.2, Puddicome and Johnstone (1988) conducted stomach flushing of 574 birds at Magnetic Island from December 1982 to February 1983 and from October 1983 to December 1984. Diet by percentage mass was 42% *E. crystallorophias*, 31.8% fish (mostly *P. antarcticum*, *Trematomus* sp. and *P. borchgrevinki*) and 24% *E. superba*. The fish component was most important during crèche and fledging periods. Green and Johnstone (1988) conducted stomach flushing of 132 birds at Magnetic Island from January to February 1984 and October 1984 to January 1985. Diet by percentage mass during the pre-hatching period was 58% amphipods, 15.8% euphausiids (with *E. superba* and *E. crystallorophias* in equal proportions), 13.1% unidentified crustaceans and 3.6% fish, with the remainder of mass unidentified. After hatching in 1984, euphausiids comprised 95.2% (*E. superba* 76.9%) and fish 4.7%, while in 1985 these values were 79.6%, 66.3% and 20%. Fish were *P. antarcticum*, *Pagothenia* sp. and nototheniids. Thomas and Green (1988) undertook stomach flushing of 10–50 birds per week during chick rearing in 1983/84, and throughout the breeding period in 1984/85, at two colonies on Magnetic Island, Prydz Bay. Euphausiids consistently contributed over 80% by percentage mass in 1983/84, fluctuated between 30 and 85% in October–December 1983 and increased to > 85% in January–February 1984, but were low at 0–45% in October–December 1984 before increasing to 60–80% in January–February 1985. *Euphausia crystallorophias* dominated during October–December (generally > 90% of euphausiid component) and *E. superba* increased during January–February (20–90%). Watanuki et al. (1994) conducted stomach flushing of 142 birds during chick rearing (January–February) 1989–1991 at Hukuro Cove and 16 in 1991 at Cape Hindoe, both on the Prince Olav Coast, Enderby Land. Diet composition by mass: 67.9% *E. superba*, 1.4% *E. crystallorophias* and 2.4% the amphipod *Paramoera walkeri*. Fish comprised 27.9%, *P. antarcticum* 10.4% and *P. borchgrevinki* 17.5%. Watanuki et al. (1997) presented a subsample of the previous study, plus stomach flushing of 52 birds returning to feed chicks at Magnetic Island in Prydz Bay during December 1992 to February 1993 (only latter reviewed here). Diet by percentage was 58% *E. superba*, 2% *E. crystallorophias*, 8% *P. antarcticum* and 26% other fish of undisclosed identity. Clarke et al. (1998) flushed the stomachs of five birds every five days through chick rearing at Béchervaise Island, Mawson Coast (1991/92–1994/95). Diet comprised mostly *E. superba* and fish (*P. antarcticum* and *T. newnesi*) in varying proportions according to stage of season and year. Krill content was particularly high in 1993/94 and 1994/95 during guard stage. Kato et al. (2003) and Watanuki et al. (2002) conducted stomach flushing of 55 birds at Hukuro Cove during December–January in 1995/96 and 1996/97 and 27 at Magnetic Island in 1992/93. Diet composition by percentage mass at Hukuro Cove was 35% *E. superba* in 1995/96 and 41% in 1996/97, but much higher at 69% at Magnetic Island. *E. crystallorophias* comprised 11%, 6% and 22% respectively, and nototheniid fish (mostly young *P. borchgrevinki*) comprised 54%, 47% and 0% respectively. Amphipods comprised 7% of diet in 1996/97 at Hukuro Cove, and *P. antarcticum* 8% at Magnetic Island, but were absent from samples in other site-years. Jarman et al. (2002) undertook stomach flushing of three birds at Béchervaise Island during January–February 1997, and collection of faecal samples from October 2001 to February 2002 for DNA-based prey identification. Conventional stomach samples comprised 30% *E. superba*, 40% *E. crystallorophias* and 30% fish. DNA analysis of faeces identified *T. macrura* and *E. superba* among the euphausiids consumed. Nicol et al. (2008) conducted stomach flushing of 40 birds during chick rearing in each year 2001 and 2003 at Béchervaise Island. *Euphausia superba* abundance was three times higher in 2001 than in 2003 due to late melting of sea-ice in the latter year. Diet by percentage mass was 82% *E. superba* in 2001 but only 34% in 2003. Most of the remainder in both years comprised fish (mostly *P. antarcticum*). Tierney et al. (2008a, 2008b) conducted stomach flushing of 83 birds near Mawson Station during chick rearing in 2001 and 2002. Diet by percentage mass in 2001: 66.7% *E. superba*, 2.5% *E. crystallorophias*, 4.5% unidentified krill, 23.9% fish and 1% amphipods. In 2002, values were 25.5%, 1.5%, 3.4%, 66.7% and 1.8% respectively; a substantial increase in fish content. Tierney et al. (2008b) also collected 92 feathers during moult from 2000 to 2002, and blood samples from 87 adults throughout the breeding period and from 28 chicks during the crèche stage in 2001 and 2002 for stable isotope analysis. Percentage of chick diet comprising krill based on isotope mixing model was 58.5% in 2001 and 16.1% in 2002, and did not differ significantly from stomach content analysis. Krill composition of adult diets was 64.2% in adults during the 2000 moult. During 2001 krill composition was 45.7% during arrival and increased throughout the season to 90.5% by moult. In 2002, the percentage of krill in adult diet was over 70% during arrival and incubation, dropped to 27.8% in the guard stage, 2.7% at crèche stage and then increased to 67.4% during moult. Tierney et al. (2008a) analysed fatty acid signatures of 77 adult and 88 chick blood samples collected during 2001 and 2002. Differences in fatty acid signatures broadly corresponded to results of stable isotope and stomach content analysis: a mix of krill and fish consumed in the early part of the breeding season in both years, krill dominating the diet during the chick-rearing periods in 2001, and fish in 2002. Different metabolic and physiological demands between stages may also have influenced signatures.

In Subarea 88.1, Emison (1968) undertook stomach flushing or dissection of 201 birds at Cape Crozier and six at Beaufort Island and Franklin Island during the 1964/65 and 1965/66 breeding seasons. Percentage composition by number at Cape Crozier was 91.5% euphausiids (99.2% of which were *E. crystallorophias*), 7.8% fish (mostly *P. antarcticum* and Chaenichthyidae spp.) and 1.2% amphipods. A small sample at Beaufort Island contained more fish (31.5%) and amphipods (4.8%). Paulin (1975) dissected eight stomachs and flushed a further seven at Cape Bird during the 1973/74 breeding season. Composition by percentage volume was 46% *E. crystallorophias*, 44% fish (of which only *P. antarcticum* were identifiable) and 10% amphipods. Ainley et al. (1984) dissected the stomachs of five birds collected on ice: two over the continental shelf at 71°32'S 171°19'E in December 1977 and two at the shelf slope at 76°02'S 166°20'E in January 1980. Composition by percentage mass was 97.7% crustacean and 2.3% fish over shelf, and 99.9% and 0.1% respectively at the shelf slope. Crustaceans comprised 99.0% *E. superba* at the shelf slope and 99.6% *E. crystallorophias* over the shelf. van Heezik (1988) undertook stomach flushing of 16 birds during incubation at Cape Bird, Ross Island, in November and December 1985. Percentage by number was > 94% *E. crystallorophias* in 13 samples, 77.8% in one and absent in the others. Other prey included small numbers of amphipods, *E. superba* and fish. Clarke et al. (1998) undertook stomach flushing of five birds every five days throughout chick rearing at Edmonson Point, Ross Sea (1994/95 and 1995/96). Diet by mass comprised > 90% fish (*P. antarcticum* and *T. newnesi*) and *E. crystallorophias* in varying proportions according to stage of season and year. Ainley et al. (2003, 1998) conducted stomach flushing of 4–7 chicks weekly for 1–7 weeks during chick rearing at three colonies (Capes Bird, Crozier and Royds) from 1994 to 2000. Chick toenails at these colonies plus a fourth (Beaufort Island) were collected for stable isotope analysis. Conventional samples revealed diet by mass comprised > 95% *P. antarcticum* or *E. crystallorophias*, although the proportions of these varied markedly. The prevalence of *P. antarcticum* was negatively related to the amount of ice cover around the colony, and also increased throughout the season, and was especially high in 1996 and low in 2000. δN^{15} values of chick toenails correlated with percentage of fish in conventional diets in each colony-year. Diet at the Beaufort Island colony could therefore be inferred from isotope signatures, and did not differ significantly from that at other sites studied.

Movements and habitat

Foraging is mainly confined to pack ice, and seasonal variations in the distribution of this cause marked seasonal and spatial variations in foraging ranges, migration routes and wintering areas. Foraging ranges during incubation are generally large (often > 100 km), with birds commuting to pack-ice by walking over fast-ice and swimming through polynyas. Breaking out of fast-ice in summer often results in birds foraging in pack-ice or open water nearer to the colony (often < 100 km), although at some colonies this persists throughout the breeding season forcing birds to forage in tide-cracks very close to the colony (< 20 km). Migrations tend to follow the coastline during autumn where pack-ice occurs, moving north ahead of the advancing fast-ice to remain in the pack-ice over oceanic waters.

Studies of foraging range and habitat use have been conducted using PTTs and radio tags. Radio tag studies generally underestimate range owing to birds travelling beyond the radio horizon. Studies were conducted at many colonies throughout the species range, and throughout the annual cycle. Only a small proportion of the colonies within each subarea have been studied, but generalisations to the remainder should be possible based on available data. Coverage in Subarea 48.5 is lacking however, and further studies are desirable considering the number and size of colonies occurring here.

In Subarea 48.1, Wilson (2010) fitted compass-speed loggers to 18 birds rearing chicks at Ardley Island, King George Island, from December 1991 to January 1992, with positions calculated using dead-reckoning. Birds spent most time in an area 5 km to the southeast of the colony, with only one trip to a distance of 35 km from the colony.

In Subarea 48.2, Lynnes et al. (2002) fitted PTTs to birds rearing chicks at Signy Island, South Orkney Islands: nine in 2000 and 10 in 2001. Birds foraged on the continental shelf to the south and southwest of Signy Island out as far as the shelf break in both years, although in 2000 the area used was more extensive. Average maximal distances from the colony were 99 km in 2000 and 58 km in 2001, and the greatest distances from the colony were 177 and 163 km respectively. Dunn et al. (2011) equipped five birds with PTTs and 54 with GLS tags (20 recovered with data) at Signy Island, South Orkney Islands, during the end of chick rearing from December 2004 to January 2005, to track overwinter movements. After leaving the colony in late January, birds moved rapidly south to an area of dense pack-ice between 65°S and 71°S, 41°W and 50°W where they moulted, covering the 888 km average distance in four weeks. After moult in April, birds moved north within the expanding pack-ice, spreading west to 6°W before beginning their return migration to the colony in September and arriving in October.

In Division 58.4.1, Kerry et al. (1997) and Wienecke et al. (2000) fitted PTTs to 28 birds rearing chicks at Petrel Island, Dumont d'Urville, and 13 at Shirley Island from December 1995 to January 1996. Mean maximal distances from the colony were 36–37 km at Petrel Island throughout chick rearing, but at Shirley Island were 68 km during guard and 113 km during crèche. Foraging was over the continental shelf at both sites, and at Shirley Island birds also foraged at the shelf break, although avoided the oceanic waters beyond. Angelier et al. (2008) fitted PTTs to nine birds rearing chicks at Pointe Géologie, Terre Adélie. Maximal foraging ranges were 64 km for males and 94.7 km for females (differences not significant).

In Division 58.4.2, Clarke et al. (2006) summarised and updated a series of preceding papers (Clarke et al., 1998; Clarke and Kerry, 1992; Kerry et al., 1997, 1995) including PTT tracking of a total of 359 birds during incubation, chick rearing and pre-moult at Béchervaise Island, Mawson Coast, from 1991/92 to 2002/03. Median maximal distances from the colony reached by foraging birds were 272, 60, 125 and 380 km in the incubation, guard, crèche and pre-moult stages of breeding respectively for all years pooled. Birds foraged over the continental shelf and beyond during incubation, walking over the fast-ice to a polynya and swam rapidly through it to reach the extensive pack-ice beyond. During the guard stage, foraging was over the shelf area close to the colony and over a submarine canyon to the north. During the crèche stage, foraging over the shelf and break was more extensive, and extended beyond into deeper water (although less so than during incubation). Prior to moult, birds were mostly confined to shelf waters, but travelled extensively along the coastline far from the colony. These variations are explained by variations in ice extent, demands for time and energy by offspring and adult body condition. Clarke et al. (2003) fitted PTTs to seven fledglings and four post-moult adults during the winters of 1995/97 and 1998 respectively, all from Béchervaise Island, except one of the fledglings which was at Magnetic Island. All fledglings travelled northward initially, then westward along the edge of the fast-ice or in the pack-ice, reaching distances of between 536 and 1 931 km west of their colonies before transmissions ceased. Adult birds travelled west until July, then moved north within the expanding pack-ice to areas of high euphausiid concentration before returning east toward their colonies. Kerry et al. (1997) fitted PTTs to birds rearing chicks: three at Magnetic Island in 1994, five at Scullin Monolith in 1996 and six at Ufs Island in 1996. All birds foraged over the continental shelf out as far as the shelf break, with maximum distances of 200 km for the former site and 100–120 km for the remainder. Kato et al. (2003), Watanuki et al. (1999, 2003) conducted radio tracking of 22 birds from December 1995 to January 1996, 8 December 1996 to January 1997 and 40 in 1999/2000 at Hukuro Cove. The sea around the colony was covered in fast-ice in all years for most of the breeding period. Birds walked to forage in tide cracks along the shore (within 3 km of the colony), or those further away around islands and grounded icebergs (up to 6 km away). However, in 1996/97, open water became increasingly available throughout the season, with an associated increase in penguin foraging range out to 7 km, where they crossed the radio horizon.

In Subarea 88.1, Davis et al. (1988) tracked nine birds from Cape Bird, Ross Island, fitted with radio tags prior to the first foraging trip of the incubation period, from November to December 1985. Positions were determined by triangulation from two hilltops on the island and by searches for tagged birds from a helicopter, enabling a 100 km radio horizon from the colony. All birds crossed this horizon within two to 12 days: four did so to the west of the colony which took them to the edge of the pack-ice, and five to the east or northeast. Sadleir and Lay (1990) fitted radio tags to 17 birds during the guard stage in December 1986, and 20 during incubation in November 1987, at Cape Bird, Ross Island. Positions were determined by triangulation from hilltops: both on the island in 1986 and on the mainland shore 78 km to the west in 1987. During guard stage, most fixes occurred in the sector between north and west, and within 20 km of the colony. During incubation, the highest density of fixes was along a corridor northwest of the island out to 150 km, after which they passed the radio horizon. Davis and Miller (1992) fitted four females with PTTs at Cape Bird, Ross Island, prior to their first foraging trip after laying in November 1988. Average maximal radial distance travelled from colony was 112 km, range was 46–260 km. Direction travelled varied: one to the southwest, two to the north and one to the northeast. All birds remained over the continental shelf, and one foraged in association with the ice edge. Davis et al. (1996, 2001) fitted two post-moulting birds with PTTs at Cape Bird in February 1991 and one at Cape Hallett in February 1998, to track winter migration. All birds followed the coast north to Cape Adare and then northeast along the coast to 155°E, upon which they travelled north to an area of sea to the northeast of the Balleny Islands. Migration routes and wintering areas occur mainly within areas where dense pack-ice occurs. Kerry et al. (1997) fitted 25 birds with PTTs at Edmonson Point during incubation and chick rearing in 1995 and 1996. During incubation, birds foraged to the east and southeast, the latter in association with a polynya, while during chick rearing they foraged to the east, generally within 120 km of the colony. Ainley et al. (2004) fitted radio tags to a total of 15–19 birds at each of four colonies (Beaufort Island and Capes Crozier, Bird and Royds) during each of four seasons (December–January 1997/98–2000/01). Positions were determined by triangulation from a number of elevated points around the study area. Average foraging distances across all colony-years was 17 km, ranging between seven and 37 km. PTT tracking showed that upper limits were probably underestimated owing to birds travelling beyond the radio horizon. Range increased with size of the colony and varied among years in different patterns among sites. Areas used grew throughout the season, especially for that of the largest colony. Foraging areas around small colonies overlapped, but that of the largest colony was exclusive. Huge icebergs limited foraging area of the largest colony in latter years. Ballard et al. (2010) equipped a total of 98 birds with GLS tags (41 recovered with data) at Cape Crozier and Cape Royds during late chick rearing in January 2004, 2005 and 2006 to track winter migration. These data were augmented with tracks from 10 PTTs in order to examine movements during post-breeding when day length was 24 hours and geolocation was not possible. After leaving the colony in February, birds migrated north-northeast to the Eastern Ross Sea to moult on the nearest residual pack-ice. During moult they drifted northwards on ice floes to the vicinity of the continental shelf break. Subsequently, they moved farther north occasionally visiting the Balleny Islands polynya but mostly remaining relatively near the ice edge. By late winter they moved eastward along the ice edge before moving south and west to their breeding colonies during late September and October.

Chinstrap penguin (*Pygoscelis antarctica*)

Diet

Diet in all studies comprised almost entirely *E. superba*, except for one study in the South Shetland Islands where fish were also an important component, this varying according to year and stage of season.

Studies were all based on stomach flushing of adults during chick rearing, which may be unrepresentative of diet at other times of year. Studies have been conducted at colonies in most of the archipelagos in which the species breeds abundantly, except for the South Sandwich Islands where many large colonies occur. It is likely that a reliance on *E. superba* is typical for chinstrap penguins, at least during the breeding season, because most of the world population resides in the Scotia Sea where krill is by far the most abundant pelagic crustacean.

At the South Shetland Islands in Subarea 48.1, Croxall and Furse (1980) dissected 46 stomachs sampled from five sites in the Elephant Island Group from 20 December 1976 to 2 February 1977. Diet by mass averaged 95.4% *E. superba*, 1.0% *Thysanoessa* sp. and 3.6% fish. Volkman et al. (1980) flushed the stomachs of 29 birds at Point Thomas, King George Island, from November 1977 to 21 February 1978. Diet comprised 99.6% *E. superba*, 0.3% fish and 0.1% amphipods. Jablonski (1985) analysed the contents of 159 bird stomachs sampled by dissection, stomach flushing or emetics from several colonies at King George Island from 5 December 1978 to 16 February 1979 and from 10 December 1979 to 14 March 1981. Diet by percentage mass during incubation averaged 69.9% crustaceans (mostly *E. superba*), 14.2% fish and 16.2% other. During chick rearing, these values were 55.1%, 38.8% and 6.1% and during the period between completion of breeding and moult 47.5%, 44.7% and 7.8% respectively. Crustacean component was markedly lower and fish higher in 1980/81 compared to other years. Jansen et al. (1998) undertook stomach flushing of a total of 75 chick-rearing birds in January–February 1993 and 1994 at Seal Island. In 1993 *E. superba* comprised 100% by mass on diurnal foraging trips, 96% on overnight trips, with the remainder fish. In 1994, diet was split between intact and digested components and proportions in these categories were not given, such that overall diet composition was indeterminable. Of the intact portion, krill comprised 100% of the diet following diurnal trips and 96% following overnight trips, with the remainder comprising fish. Of the digested portion, krill comprised 98% of the diet following diurnal trips and 42%

following overnight ones. The remainder were fish, of which 95% were myctophids and 5% *N. coatsi*.

At the South Orkney Islands in Subarea 48.2, Lishman (1985) dissected the guts of 21 birds during the 1981/82 breeding season and 17 during 1982/83 at Signy Island. Composition by weight in 1981/82 was 97.0% *E. superba*, 2.9% fish and 0.1% amphipods; in 1982/83 it was 99.8%, 0.1% and 0.1% respectively. Fish were the nototheniids *T. eulepidotus* and *T. hansoni*. Rombola et al. (2003, 2006) conducted stomach flushing of a total of 173 penguins during chick rearing from 1998 to 2002 at Point Martin, Laurie Island. Diet comprised over 99.4% *E. superba* by mass in all years. Lynnes et al. (2004) undertook stomach flushing of 43–55 birds per annum during chick rearing from 1997 to 2001 (237 in total) at Signy Island. Diet was comprised entirely of krill (>99.0%) in all years except 1997, when it was 95.1% and the remainder *T. gaudichaudii*. Takahashi et al. (2003) conducted stomach flushing of 16 birds during chick rearing at Signy Island in January 2002. Diet was comprised entirely of *E. superba* except for one small amphipod.

In Subarea 48.6, Cooper et al. (1984) dissected the stomachs of three birds at Nyrøysa, Bouvet Island, in December 1982; two stomach contents were comprised entirely of *E. superba*, the third additionally included 80 *E. carlsbergi* otoliths and an unidentified squid beak. Isaksen et al. (1997) undertook stomach flushing of 20 adult birds returning to feed chicks at Nyrøysa from December 1996 to February 1997. Diet by percentage mass comprised 99.6% *E. superba*, with the remainder being nototheniid fish.

Movements and habitat

Foraging ranges during the chick rearing stage were relatively short (<60 km from the colony). After moult, most birds appear to stay in the vicinity of the archipelago on which their colonies are situated, but some undertake long migrations across oceanic waters to visit other archipelagos within the species' wider breeding range. Chinstrap penguins tend to forage in open water and avoid areas of pack-ice (Ainley et al., 1992b).

Studies have been based on PTTs, GLS and dead-reckoning loggers. The number of sites and years studied, and number of individuals tracked during each, is relatively small, and no information is available from the South Sandwich Islands where several large colonies occur. Studies include chick rearing, pre-moult and post-moult periods, but never for the same site and published information on incubation stage and winter movements are lacking.

In Subarea 48.1, Wilson et al. (1998b) fitted GLS tags to five birds after their moult at Admiralty Bay, King George Island, in April 1995, of which one was recovered. This bird travelled 200 km south to the eastern tip of the Antarctic Peninsula for 20 days, before moving east-northeast along the Scotia Ridge past the South Orkney Islands. It then spent July and the first half of August to the southeast of the South Sandwich Islands 1 500 km away. Wilson and Peters (1999) and Wilson (2010) equipped 17 birds with dead-reckoning loggers at Ardley Island, off King George Island, during December and January of 1991/92 and 1995/96. Birds followed looping courses to the southeast of the colony, mostly within 20 km of the colony, and the maximum being 33.5 km. Trivelpiece et al. (2007) fitted two post-moult birds with PTTs in late February–early March of 2000 at Cape Sheriff, Livingston Island, and three in both 2000 and 2004 at Admiralty Bay, King George Island. Most birds foraged between the South Shetland Islands and the shelf break during the winter of 2000, typically 40–70 km from their colonies, but in 2004 they foraged further offshore in pelagic waters of the Drake Passage up to 300 km from the colony. This difference was likely due to prey distribution being affected by a strong shelf-slope front in 2000 that was absent in 2004. Two birds from Admiralty Bay undertook long easterly migrations away from the South Shetland Islands before their tags failed, one reaching the South Orkney Islands and the other waters to the southeast of the South Sandwich Islands; 800 and 1 336 km away from the colony respectively.

In Subarea 48.2, Lynnes et al. (2002) fitted 24 birds with PTTs in January–February 2000 and 2001 at Gourlay Point, Signy Island, South Orkney Islands, providing fixes during 102 foraging trips. In 2000, foraging trips were further from the colony than in 2001 (57.8 vs. 35.1 km), probably due to krill availability being lower in 2000 compared to 2001. The area used for foraging in 2000 was more extensive and contained two discrete hotspots of activity, whereas that in 2001 was smaller and contained a single hotspot immediately to the south of the colony.

In Subarea 48.6, Biuw et al. (2010) fitted one bird with a satellite tag at Nyrøysa, Bouvet Island, during late chick rearing in January 2008. Maximum ranges of 12 foraging trips during chick rearing were within 10 km of the colony, one extended to 32km southwest and one 48 km to the northwest. After completion of breeding, the bird migrated to Montagu Island in the South Sandwich Islands (1 863 km to the west), where it presumably moulted. Six other birds fitted with PTTs during the pre-moult period remained within 300 km of their breeding colony and returned there to moult.

Gentoo penguin (*Pygoscelis papua*)

Diet

Diet composition generally comprises a wide range of crustacean fish taxa, with crustaceans typically being less important than for other *Pygoscelis* or *Eudyptes* spp. breeding at the same site. Relative importance of the main prey types often varies among years, throughout the season and among individuals. Spatial variation in diets is profound, both regionally in response to geographic prey distribution, and locally according to the marine habitats around the colony and specificity of prey types to these. The short foraging ranges of gentoo penguins result in the spatial variation in diet composition being marked even at fine spatial scales.

Studies of diet composition have been carried out almost entirely by stomach flushing, mostly during chick rearing. However, several studies of diets in all other seasons, these being facilitated by the fact that gentoo penguins return to the shore to roost at night throughout the year. Biases due to digestion are reduced in this species compared to other penguins owing to foraging trips typically lasting only one or two days. Studies have been carried out at a large number of colonies throughout the species' range, although at a relatively small proportion of the colonies within each CCAMLR subarea. The high variation in diet composition at small spatial scales makes diets at unsampled colonies difficult to infer, though this could be estimated by modelling diet as a function of region and the marine habitat characteristics within foraging range from the colony.

In the Falkland Islands, Clausen and Pütz (2002) and Pütz et al. (2001) conducted stomach flushing of 252 birds from six sites during various stages of the breeding season from 1986/87 to 1999/2000. Overall composition by percentage mass was 53% fish, 36% crustaceans and 11% squid. Relative importance of prey types varied considerably among years. Fish dominated in northern colonies, fish and crustaceans in the south and squid/crustaceans in the west. Crustaceans were mostly *Mundia gregaria*. Squid species identified included *Loligo gahi*, *Illex argentinus*, *G. antarcticus* and *M. ingens*. Fish species taken included several nototheniid species, gadoids (predominantly *Merluccius* spp. and *Micromesistius australis*), *Agonopsis chiloensis* and *Sprattus fuegensis*. Clausen and Pütz (2003) conducted stomach flushing of 56 birds throughout the winter from May to October 2000 at Kidney Cove. Diet by percentage mass comprised 34% fish, 47% squid, 18% crustaceans. Of the items identified to species, the most important by percentage mass were the squid *L. gahi* (53%), the fish *Patagonotothen ramsayi* and the crustacean *M. gregaria*. Clausen et al. (2005) conducted stomach flushing of 4–11 breeding birds at each of five colonies along the western coast and Beauchêne Island in the south from 10 to 20 October 2000. Overall, diet by percentage mass comprised crustaceans 46% (mostly *Mundia* sp.), fish 33% (mostly *S. fuegensis* and *Patagonotothen* sp.) and squid 20.8% (*M. ingens* and *L. gahi*). Diet varied according to marine habitat: *Mundia* sp. in sheltered shallow waters, *S. fuegensis* and squid in exposed, deeper waters. Masello et al. (2010) conducted stable isotope analysis of 13 blood samples from birds breeding on New Island, with proportions of prey types estimated using a stable isotope mixing model. Diet comprised c. 45% fish, 25% *M. gregaria*, 20% squid and 10% other krill species.

At the South Shetland Islands in Subarea 48.1, Volkman et al. (1980) dissected the alimentary tracts of 46 penguins at Point Thomas, King George Island, between 1 November 1977 and 21 February 1978. Composition by percentage wet weight was 84.5% crustaceans (all *E. superba*), 15.4% fish (all *P. antarcticum*) and 0.1% amphipods. Males consumed more fish (22.8%) than females (7.3%). Jablonski (1985) analysed contents of 244 bird alimentary tract sampled by dissection, stomach flushing or emetics from several colonies at King George Island from 5 December 1978 to 16 February 1979 and from 10 December 1979 to 14 March

1981. Diet by percentage mass was 55.8% crustaceans (*E. superba* and amphipods), 34.9% fish (small *Notothenia rossii* and *P. antarcticum*) and 9.1% other (mostly squid). Repeated sampling of 46 individuals throughout the season showed 24 specialised in krill, seven in fish and 15 took a mixture of both. The fish component increased and crustaceans decreased during the chick rearing and winter periods. Polito et al. (2011) took 88 eggshell samples from 13 sites throughout the South Shetland Islands and Antarctic Peninsula to infer female winter diet using stable isotope analysis. A stable isotope mixing model predicted that the percentage of the diet comprising krill was 39–44% depending on region, with the remainder being fish.

At the South Orkney Islands in Subarea 48.2, Coria et al. (2000) conducted stomach flushing of 37 birds sampled in 1993, 46 in 1995 and 42 in 1996, between March and June at the east coast of the Mossman Peninsula, Laurie Island, South Orkney Islands. Fish by percentage mass comprised 25% in 1993, 81% in 1995 and 60% in 1996. Fish were almost all nototheniids of five species. Crustaceans by percentage mass represented 70%, 18% and 38% respectively, mostly *E. superba*. Squid comprised the remainder and were almost entirely *P. glacialis*.

At South Georgia in Subarea 48.3, Croxall and Prince (1980) dissected 43 stomachs at Bird Island from 28 December 1976 to 11 February 1977. Diet composition by percentage mass was 68.9% *E. superba*, 1.2% *E. frigida*, 32.6% fish and 0.3% squid. The few fish identified to species were *N. rossii*, *Lepidonotothen larseni* and *C. gunnari*. Croxall et al. (1988, 1997) conducted stomach flushing of 40 birds throughout the chick-rearing period at Bird Island in 1986. Overall diet was 51.4% *E. superba* and 48.5% fish (mostly nototheniids and *C. gunnari* in equal proportions). Williams (1991) undertook stomach flushing of birds from two colonies on Bird Island in winter (May, July and September): 25 in 1987 and 69 in 1988. *Euphausia superba* comprised 87% or more by weight in September 1987 and May–September 1988. In July–August 1987 crustaceans formed 87% of the diet of females but fish formed 83% of the diet of males. The main fish species taken were *L. larseni* and *C. gunnari*. Kato et al. (1991) flushed the stomachs 18 birds at Bird Island in July 1989. A marked dietary shift was observed during the month: crustaceans (mostly *E. superba*) rose from 25% by mass in the first half to 95% in the second half, with the remainder comprising unidentified fish. Croxall et al. (1999) undertook stomach flushing of 25 adults during chick rearing at Bird Island in 1994, a year of low krill availability. Diet by percentage weight was 12.9% crustaceans, 85.9% fish and 1.2% cephalopods. Crustaceans comprised mostly *E. superba* (9.0% of total) and *T. gaudichaudii* (3.6%), fish *C. gunnari* (80.5%) and *Parachaenichthys georgianus* (4.4%). Berrow et al. (1999) conducted stomach flushing of birds from May 1996 to January 1997 throughout the season at Bird Island, comparing sampling in one day with sampling of the same number of birds spread over two weeks. Months, sample sizes and percentage of *E. superba* by mass were: May, 22 birds, 89.3–95.2%; June–July, 24 birds, 73.3–80.8%; August–September, 24 birds, 36.3–45.3% and January, 24 birds, 42.6–61.3%. The remainder of samples were fish, *C. gunnari* and *L. larseni* (66% and 29% by number of otoliths recovered respectively). Hill et al. (2005) undertook stomach flushing of 40 birds during the crèche period in each year from 1991 to 2002 (except for 1998). Diet composition by mass averaged 56% fish, with half of this component comprising *C. gunnari*. Other fish species taken included *L. larseni*, *Pseudochaenichthys georgianus*, *M. microps*, *E. carlsbergi*, *P. choriodon* and *E. antarctica*. Forty-two percent of the average diet was *E. superba*, and small amounts of other species, mainly *T. gaudichaudii*, were also eaten. The relative importance of prey types varied between years: *C. gunnari* dominated in 1999 and *E. superba* dominated in 1992, 1993 and 2002, while *L. larseni* made up an average of 41% of the fish component in 1996.

At the Kerguelen Islands in Division 58.5.1, Bost et al. (1994) undertook stomach flushing of birds from three colonies at different stages throughout the breeding cycle: 56 in 1987 and 30 in 1989. Diet by mass was 84–86% crustaceans (mostly *E. vallentini* and lower numbers of *T. gaudichaudii*) and fish the remainder (mostly the nototheniids, *Harpagifer kerguelensis* and *C. gunnari*). Lescroel et al. (2004) undertook stomach sampling of birds from four colonies: Cape Ratmanoff and Ronarch and Jeanne d'Arc Peninsula which were adjacent to open sea, Nuageuses Islands which was by open sea near the APF and Morbihan Gulf within a shallow inlet. A total of 159 samples were collected in 1987 and 53 in 1989. There was little yearly variation but striking differences among colonies according to adjacent marine habitat.

Site and percentage composition of crustaceans, fish, cephalopods and annelids respectively: Cape Ratmanoff: 13.1%, 71.2%, 9.7%, 6.0%; Ronarch and Jeanne d'Arc: 28.3%, 38.0%, 13.4%, 20.3%; Nuageuses: 1.3%, 94.6%, 4.1%, 0.0%; Morbihan: 84.3%, 13.0%, 0.1%, 2.7%. *Euphausia vallentini* and *P. gaudichaudii* were the dominant crustaceans, nototheniids, *C. gunnari*, *Zanclorhynchus spinifer* and *H. kerguelensis* were most common among the fish. Cephalopods included *G. antarcticus*, *K. longimana* and octopods, while all identified annelids were *Platynereis magellanica*.

At Heard Island in Division 58.5.2, Klages et al. (1990) undertook stomach flushing of 64 birds at the Spit Bay colony between December 1986 and January 1987. Diet by percentage mass comprised 90.5% fish, 7.8% crustacean and 1.7% squid. Myctophids comprised most of the fish (57% by number, of which *K. anderssoni* was the most common), with small nototheniids comprising 24%. Crustaceans were almost all *E. vallentini*. Green and Wong (1992) sampled 30 faeces from the north of Heard Island spit and 29 from the south. Data are presented as frequency of occurrence north then south. *Themisto gaudichaudii* occurred on 87% and 97% of faeces, *E. vallentini* in 47% and 0%, fish in 57% and 48% and squid in 47% and 31%. Myctophids, particularly *K. anderssoni*, dominated the fish component.

At the Crozet Islands in Subarea 58.6, Ridoux (1994) conducted stomach flushing of 23 adults of unknown breeding status from 7 November 1980 to 5 January 1981 and 94 from 29 May to 12 December 1982. Diet by percentage mass comprised 54.2% crustaceans, 43.9% fish and 1.8% squid. Crustaceans were mostly *E. vallentini*, with the benthic, hyppolytid shrimp *Nauticaris marionis* occurring at significant levels in some samples. Fish composition increased in spring and summer, and species taken varied seasonally: myctophids were taken mostly in spring and summer and comprised *G. nicholsi*, *K. anderssoni* and *P. tenisoni*, these being augmented by *Paradiplospinus gracilis* for a short period in summer. Nototheniids were consumed all year round, although more consistently in winter. Squid comprised *K. longimana* and onchyteuthiids.

At Marion Island in Subarea 58.7, La Cock et al. (1984) conducted stomach flushing of 64 birds during September 1982. Fish comprised 70% by mass, with 92.7% of fish otoliths being *H. georgianus* and the remainder nototheniids. Crustaceans made up 30% by mass, all *N. marionis*. Adams and Wilson (1987) conducted stomach flushing of 27 birds from four colonies during September and October 1984. Percentage composition by mass was 46.2% crustacean, 53.2% fish and 0.6% cephalopod. Eleven samples contained only *N. marionis*, 11 only *N. squamifrons*, and two only *E. vallentini* and the remainder were mixed. Adams and Brown (1989) and Adams and Klages (1989) undertook stomach flushing of 144 birds of unknown status from three colonies from March 1984 to March 1985. Diet by percentage mass comprised 44.4% crustacean, 53.5% fish and 9.8% cephalopods. Crustaceans dominated in March–June 1984, after which fish were most common; cephalopods only exceeded 10% in February and March 1985. Crustaceans were predominantly *N. marionis* from March to September 1985, after which E. *vallentini* became dominant. Fish mostly nototheniids and myctophids, with *Channichthys rhinoceratus* comprising 6–24% in the last three months of the study. Cephalopods were mostly small octopods.

At Macquarie Island, Hindell (1989) conducted stomach flushing of 33 birds at Bauer Bay from June to November 1985. Diet composition by percentage mass was dominated by fish (81.3%), mostly comprising myctophids (59%), *E. carlsbergi* 27.5%, *Gymnoscopelus* spp. 15.7%, *K. anderssoni* 15.1% and also nototheniids (20%), particularly *Paranotothenia magellanica*. Cephalopods comprised 18.6%, mostly *Moroteuthis* spp. and *M. hyadesi*. Crustaceans comprised a trivial amount of the diet. Robinson and Hindell (1996) undertook stomach flushing of 82 birds from 30 October 1993 to 15 January 1994 (chick rearing) at the Hasselborough Bay colony. Fish comprised 91.6% by mass, cephalopods 8.3% and crustaceans a trivial amount. The most important fish species by mass were *P. magellanica* (28.0%), *L. squamifrons* (22.7%), *Z. spinifer* and *Gymnoscopelus* spp. (13.7%). Cephalopods were *M. knipovitchi* and *M. hyadesi*.

Movements and habitat

Foraging ranges during the breeding season are relatively short (<50 km, and often much less) owing to multi-day foraging trips being relatively rare. During winter the requirement to return to land to roost means birds seldom travel over

50 km from the coast, but they may range considerable distances from their breeding colonies, while remaining within the same archipelago.

Studies of movements have been conducted using PTTs, radio tags and dead-reckoning loggers. Few studies exist relative to other penguin species, perhaps because PTT fixes lack the spatial and temporal resolution to describe their short foraging trips during the breeding season adequately. Further studies using rapid-acquisition GPS loggers at a number of sites throughout the species range would be desirable, since these provide the frequency and accuracy of fixes required to study gentoo penguin foraging tracks (Ratcliffe, unpublished data).

At the Falkland Islands, Clausen and Pütz (2003) equipped two birds with PTTs during winter at two sites in the East Falklands. One bird generally remained in shallow water close to coast and returned to land most evenings, often to different colony sites. The other made journeys to sea of several days' duration, and afterwards would remain ashore for one or more days. Both birds made extended trips to the north coast of the West Falklands. Masello et al. (2010) tracked 13 bird from two colonies for 46 foraging trips from New Island during the 2008/09 breeding season using GPS loggers. Foraging trips concentrated within 20 km of the colonies, although one bird ranged c. 60 km from the colony. Areas used by the two colonies at the north and south ends of New Island showed little overlap, suggesting segregation of foraging areas.

At the South Shetland Islands in Subarea 48.1, Trivelpiece et al. (1986) fitted radio tags to seven birds at Point Thomas, King George Island, between 26 January and 12 February 1984. Positions triangulated from two points 200 m high and 3 km apart, and a third receiver recorded signals continuously on a strip chart, providing data on surface and submersion times. The track of one gentoo penguin trip followed an elliptical course within Admiralty Bay, with the furthest distance c. 3 km from the colony. Wilson (2010) and Wilson et al. (1998a) conducted tracking of 37 birds (10 incubation, 14 brood guard and 13 overwinter (only three recovered with data)) from Ardley Island using GLS and dead-reckoning loggers during December 1991 to November 1996. During incubation, 80% of time was spent within 50 km of the colony, most trips were to the north or south of King George Island into Bransfield Strait and Drake Passage. During brood guard almost all time was spent within 5 km of the colony, within Maxwell Bay. During winter, average distance from colony was 80 km, and the maximum was 268 km, mostly to the west of King George Island.

At South Georgia in Subarea 48.3, Tanton et al. (2004) fitted five birds with PTTs over winter at Bird Island in 2001. 95% of fixes were within 30 km of Bird Island and 96% within 17 km of land; birds returned to land to roost each night, although not always to the release site. One bird travelled to the south end of South Georgia, 180 km away from the release site, and stayed there for 21 days.

At the Kerguelen Islands in Division 58.5.1, Lescroel and Bost (2005) tracked seven birds from three colonies on the east coast of Kerguelen, two birds at each of two colonies facing the open sea and three birds at one colony within the Morbihan Gulf during incubation and chick rearing, from 2002 to 04. Birds at open-sea colonies travelled east up to 46 km to feed on demersal fish at the shelf edge, while birds from the closed-sea colony foraged within 11 km and fed on pelagic crustaceans. Thiebot et al. (2011b) attached PTTs to six juveniles from two colonies on the east coast of the Kerguelen mainland. Birds mostly remained along the eastern and northern coastline with forays into open water over the shelf and to the shelf break, with one bird moving south to shelf waters off Heard Island.

Macaroni (*Eudyptes chrysolophus*) and royal (*Eudyptes schlegeli*) penguins

Diet

Royal penguins are found only on Macquarie Island and macaroni penguins at all other localities described in this section. Diet comprises mostly euphausiid crustaceans and myctophid fish throughout their biogeographic range, with small contributions by amphipods and squid. Relative importance and species composition of euphausiid and fish components vary geographically. *Euphausia superba* dominate diet at South Georgia in most seasons, but this is largely absent from more northern and eastern sites. There, *E. vallentini* and *T. gregaria* tend to be the dominant crustaceans, and myctophid fish generally comprise a significant proportion of the diet.

Most studies are based on stomach flushing of adults throughout the breeding season, with one also using genetic identification of prey in faeces. Three studies of diet during winter utilise stable isotopes, but taxonomic resolution during this period is lacking. Studies have been carried out at all of the major breeding localities for each species, although information from Kerguelen is sparse and studies are based on a small number of years at all sites other than Marion and South Georgia.

At the South Shetland Islands in Subarea 48.1, Jablonski (1985) dissected the alimentary tracts of five birds killed on King George Island from 1978/79 to 1980/81. Diet by mass comprised 96% crustaceans, 4% fish and < 1% cephalopods. Croxall and Furse (1980) dissected the alimentary tracts of nine birds killed on Clarence Island, and four on Gibb's Island in January 1977. Diet by percentage mass comprised *E. superba* 37%, *Thysanoessa* sp. 38% and fish 25%.

At South Georgia in Subarea 48.3, Croxall and Furse (1980) conducted stomach flushing of 40 adults during January and February 1977 at Bird Island. *Euphausia superba* comprised 98% and fish 2%. Croxall et al. (1988) flushed the stomachs of 40 birds per week throughout chick rearing in 1986 at Bird Island. Diet was 93.5% by mass *E. superba*, 5% small *N. rossii* and 1.5% *T. gaudichaudii*. Croxall et al. (1997) undertook stomach flushing of 40 adult penguins returning to feed chicks at Bird Island in February 1986. Crustaceans comprised 97.7% by mass: *E. superba* 95.0% and *T. gaudichaudii* 2.7%. Fish comprised 2.3% and included assorted myctophid spp. and *C. gunnari*. Hill et al. (1996) compared krill samples in the previous study with those caught in nets, and found evidence of selection for larger female krill. Croxall et al. (1999) conducted stomach flushing of 40 adults returning to feed chicks on Bird Island during 1994: a year of low krill abundance. Diet by percentage mass was 84% crustaceans, 15% fish and 1% cephalopods. Crustaceans comprised mostly *T. gaudichaudii* (67.3%) with some *E. superba* (13.1%) and *Thysanoessa* sp. (3.6%). Fish comprised 9% myctophids (especially *K. anderssoni*) and 4.3% *P. georgianus*. Barlow et al. (2002) conducted stomach flushing of 80 birds throughout January and February from 1989 to 2000 at Bird Island. Percentage of *E. superba* by mass varied markedly among years: over 90% in 1989, 1990, 1992, 1996 and 1997, yet below 20% in 1994 and 2000. The composition of the remainder of the diet was not given. Bearhop et al. (2006) used stable isotope analysis to show females have wider niches than males, with evidence for a bimodal foraging strategy among individuals, with some targeting inshore waters and the remainder foraging offshore.

At Bouvet Island in Subarea 48.6, Isaksen et al. (1997) undertook stomach flushing of 45 adults returning to feed chicks at Nyrøysa from 10 January to 19 February 1997. Diet comprised fish (mostly myctophids) and euphausiid crustaceans (mostly *E. superba*) in varying proportions throughout the season. Fish comprised > 95% in early and late January, but was less than 50% in mid- to late February, with the difference being made up by euphausiids.

At the Kerguelen Islands in Division 58.5.1, Bost et al. (2009) conducted stable isotope analysis of blood samples collected from an unspecified number of birds returning to the colony in spring. Isotopic signatures suggested birds were feeding on crustaceans, although the latitude at which birds foraged precludes the species being *E. superba*.

At Heard Island in Division 58.5.2, Klages et al. (1989) conducted stomach flushing of a total of 66 adults from three colonies from 15 December 1986 to 7 January 1987. Percentage diet by mass was 76.7% crustaceans, 23.2% fish and 0.1% squid. Higher-level taxonomic information was only presented as percentage occurrence. *Krefftichthys anderssoni* occurred in 75% of samples, *C. gunnari* in 27%, *E. vallentini* in 65%, *T. macrura* in 87.5% and *T. gaudichaudii* in 27%. Green et al. (1998) undertook stomach flushing of eight birds from a colony to the northwest of the island in February 1992 and 50 at one to the southeast during January and February 1993. In February 1992, composition by mass was 37% *T. gaudichaudii*, 22% *E. vallentini* and 41.4% fish. In 1993 samples were heavily digested and estimation of percentage by mass was not possible. Number of *E. vallentini*, expressed as a percentage of *E. vallentini* and *K. anderssoni* combined, was high in early–mid January, intermediate in early February (35.6–28.5%) and low in late February (5.1%). Deagle et al. (2007) conducted stomach flushing of 69 adults (although only 53 contained sufficient content for analysis) through the chick-rearing period, mid-December 2003 to mid-January 2004. Euphausiids comprised 69% by mass, fish 22%, amphipods 8% and cephalopods

< 1%. Euphausiids were more important in the guard phase than during crèche. Most of the euphausiids were *E. vallentini* and *T. macrura*, almost all fish were myctophids (especially *K. anderssoni*) and all but one of the amphipods were *T. gaudichaudii*. Genetic analyses of frequency of occurrence of prey types in faeces found similar diet composition and seasonal patterns.

At the Crozet Islands in Subarea 58.6, Ridoux (1994) conducted stomach flushing of 10 adults during incubation, 10 during guard stage and 10 during crèche in 1980/81 at Possession Island. Diet comprised 59.4% by mass crustaceans, 28.0% fish and 12.1% squid. Crustaceans were mainly *E. vallentini* (38.1% of total mass) and *T. gaudichaudii*. Fish were mainly *K. anderssoni* (18.5%) and *E. carlsbergi* (8.2%) and squid *K. longimana* (7.1%). Cherel et al. (2007) undertook stomach flushing of 10 adults rearing chicks at Possession Island in 2002. Crustaceans made up 97.9% by number, comprising *T. gaudichaudii* (45.4%), *E. vallentini* (27.9%) and *Primno macropa* (16.1%). Fish comprised 1.9% by number, and were almost entirely *K. anderssoni*. Cephalopods comprised a trivial dietary component (0.2% by number). Stable isotope analyses showed diets were similar in summer and winter, but larger variance in δC^{13} during winter suggests the range of latitude occupied is greater than that in summer.

At Marion Island in Subarea 58.7, Williams and Laycock (1981) flushed stomachs of 20 adult birds from January to March in 1973 and 1974. All stomachs contained *T. macrura* and three contained *Euphausia* spp. (in one sample identified as *E. vallentini*). Brown and Klages (1987) undertook stomach flushing of 30 birds from December to February in 1983/84 and 45 from December to February in 1984/85. Crustaceans comprised 62.1% by mass in 1983/84, 80.8% in 1984/85, fish 24.7% and 14%, and cephalopods 13.2% and 5.2% respectively by year. *Nauticaris marionis* and *T. gaudichaudii* dominated the crustacean component by number in year one, and the euphausiids *E. vallentini* and *T. vicinia* in year two. Fish were myctophids, with *P. tenisoni* dominating in both years, *E. carlsbergi* being important in the first year and *P. normani* in the second. Almost all squid identified to species were *K. longimana*, and most unidentified ones were assigned to the family Onchoteuthidae, to which this species belongs. Adams and Brown (1989) undertook stomach flushing of an unspecified number of penguins from April 1984 to March 1985 along the east coast of Marion Island. Diet by mass was dominated by euphausiids *E. vallentini* (32.2%) and *T. vicinia* (21.9%). The amphipod *T. gaudichaudii* comprised 6.2%. Fish comprised 25% of diet, mostly *P. tenisoni* (12.7%), *P. normani* (6.7%) and *G. nicholsi* (9.5%). Squid comprised 13.1%, all of which were *K. longimana*. Crawford et al. (2003) undertook stomach flushing of 30–45 chick-rearing adults from December to February annually from 1994/95–2001/02 at Bullard Beach. Crustaceans comprised the greatest proportion by mass in all years but one (46–96%), fish component was variable (0–53%), and cephalopods consistently rare (1–9%). Components were not identified to higher taxonomic levels.

At Macquarie Island, Horne (1985) conducted stomach flushing of royal penguins during chick rearing in January 1982: 29 samples were taken from the colony on the west coast, 21 from one on the east. Euphausiids (mainly *T. gregaria* and *E. vallentini*) comprised 3% by mass on the west coast and 26% on the east. Amphipods (*P. macropa* and *T. gaudichaudii*) comprised 8% of mass on the east coast and 0.5% on the west. Fish comprised 54% of mass on the east coast and 62% on the west; high levels of digestion made identification to species level impossible in most cases, although *K. anderssoni* were present in two samples and *E. carlsbergi* and *H. bispinis* both occurred in one sample. Only three samples contained intact squid, although beaks were present in c. 30% of samples. Hindell (1988b) undertook stomach flushing of 182 adults from November 1984 to February 1985 and from September to November 1985 at a colony to the northeast of the island. Euphausiids comprised 51.3% by mass (*E. vallentini* 32.1%, *T. gregaria* 10.3%, unidentified 8.9%), fish 45.5% (*K. anderssoni* 23.7%, *E. carlsbergi* 9.7%, *Primno* spp. 3.84%, *Gymnoscopelus* spp. 4.03%), cephalopods 3% (mostly *Moroteuthis* spp.). Fish component was important only in late November and December, *T. gregaria* only occurred from December to early February. Samples collected at a colony on the west coast in December 1984, January 1985 and November 1985 showed that *E. vallentini* comprised a smaller proportion of the diet there. Hull (1999a) conducted stomach flushing of a total of 540 birds during 1993/94, 1994/95 and 1995/96, sampled from all stages of the breeding season at a colony on the east coast. Percentages by mass were: 26.7% euphausiids, mostly *E. vallentini* and 51.7%

fish (mostly *K. anderssoni*). Only a small proportion of the diet comprised cephalopods (3.4%; mostly *M. knipovitchi* and *M. hyadesi*) and other crustaceans (4.4%, mostly *T. gaudichaudii*). No substantial differences were found in diet among years or stages of the breeding season.

Movements and habitat

Macaroni penguins are known to forage 500–600 km from the colony during the pre-moult and incubation periods, but generally remain within 150 km during chick rearing. Birds select PFZ or shelf-edge foraging habitats, depending upon season. Birds travel to feeding sites along relatively narrow corridors at right angles to the coast, and are segregated among adjacent colonies. During winter, birds range far from the breeding colonies and forage in association with the APF.

Studies of foraging distribution and habitat use during the breeding season using PTTs, GLS and transect surveys have been carried out on royal penguins at Macquarie Island and macaroni penguins at Heard Island, Kerguelen Islands and South Georgia. Data is lacking from the other important breeding locality at Marion Island; studies there are desirable. Recent GLS studies of movements during the wintering period were conducted from colonies at Crozet and Kerguelen Islands; studies at other main breeding localities are required.

At South Georgia in Subarea 48.3, counts of birds (Trathan et al., 1998) along ship-based transects radiating from the major colonies at the northwest of South Georgia out to 130 km were used to infer foraging range during the crèche stage in 1986. Birds were mainly over the continental shelf, with over 70% within 40 km of the nearest breeding colony. There was no evidence of significant variation in density among radial sectors. A predictive model of foraging areas around each colony in South Georgia is presented. Barlow and Croxall (2002) used PTTs to track 13 birds from Bird Island during incubation (2000 and 2001), 29 females during brood-guard and 21 during the crèche stage (1999 and 2000). Foraging trips were longest during incubation: the average maximum range was 572 km for males and 367 km for females. Birds travelled in a northwest direction to Maurice Ewing Bank or the PFZ. During chick rearing both sexes foraged relatively close (average maximum range 62 km) over the continental shelf, but also to the northwest. Trathan et al. (2006) deployed PTTs on females during the brood-guard stage at multiple colonies in South Georgia (69 at Fairy Point, Bird Island, from 1999–2005; eight at Goldcrest Point, Bird Island, in 2003; eight at Macaroni Cwm, Bird Island, in 2003; nine from a colony on the south shore of Willis Main Island in 2004 and 10 from Rookery Bay on the north shore of the South Georgia mainland in 2004). Foraging was mostly over shelf areas and often in association with the Southern Antarctic Circumpolar Current Front. Foraging from Goldcrest and Fairy Points was similar to that described by Barlow and Croxall (2002), but that from Macaroni Cwm occurred to the east of this despite close proximity. Birds from Willis Island foraged to the south and those from the Rookery Bay to the north of their colonies. Thus, all birds seemed to head out to sea with a restricted set of orientations that were generally at right-angles to the coastline, and certainly not covering the wider area of sea and potential foraging habitat available to them. These results suggest segregation of foraging zones among adjacent colonies. Green et al. (2009) implanted TDRs into 15 birds during incubation in 2001/02, 17 during pre-moult in 2001/02, and 15 during pre-moult in 2002/03. These were used to estimate positions using known relationships between dive patterns and daylight to allow geolocation. The mean maximum distance from the colony during the pre-moult period was 634 km in 2001/02 and 697 km in 2002/03, and during incubation it was 570 km. With a few exceptions, tracks were in a northerly direction to the PFZ in all periods. Thus, birds may forage outside FAO Subarea 48.3 during some periods. Waluda et al. (2009) tracked 14 birds during crèche and four during pre-moult foraging trips with PTTs. Foraging concentrated to the northwest of the island to and beyond the shelf break, but well short of the PFZ, during crèche. During the pre-moult period, birds also travelled in a general northwest direction but trips were much longer, reaching the PFZ and Shag Rocks. A ship-based transect survey covering a narrow rectangle from the west tip of South Georgia out beyond Shag Rocks during the pre-moult period confirmed the highest densities of penguins occurred around Shag Rocks, though a high proportion of PTT fixes during this same period fell outside the surveyed area.

At the Kerguelen Islands in Division 58.5.1, Bost et al. (2009), Thiebot et al. (2011a, 2011b) fitted GLS tags to 21 birds in March–April 2006 and data were recovered from 12 of these the following spring. All birds departed east from Kerguelen, and dispersed widely along a narrow latitudinal band (47°–49°S) within the central Indian Ocean (70°–110°E), corresponding to the position of the PFZ.

At Heard Island in Division 58.5.2, Green et al. (1998) conducted GLS tagging of 10 birds during incubation and 19 during chick rearing. Most locations were in an arc from north-northwest to east-southeast of the island extending out as far as the shelf break nearly 300 km away; very few locations were to the south. Deagle et al. (2008) fitted PTTs to 43 chick-rearing birds in 2003/04. Tracks were generally east or southeast with an average maximum distance from the colony of 47 km during the guard stage and 115 km during the crèche stage. Foraging trips fell into two strategies: long offshore trips with deep dives to capture myctophids, and shorter inshore trips with shallow dives to capture euphausiids. Individuals switched between these strategies often. Inshore trips showed characteristics of benthic foraging.

At the Crozet Islands in Subarea 58.6, Thiebot et al. (2011b) equipped 18 birds with GLS tags (11 were recovered with data) from a colony on the north coast of Possession Island. Birds mostly moved westwards within the PFZ and showed no overlap with the distribution of conspecifics from the Kerguelen Islands.

At Macquarie Island, Hull et al. (1997) attached PTTs to five birds during incubation, four during guard and one during crèche stages during the 1994/95 and 1995/96 breeding seasons. Maximum average distance from colony was 544 km during incubation, 115 km during guard and 330 km during the crèche stages. Trips were in a southeast direction to the PFZ, in water greater than 2 000 m deep. Hull (1999b) fitted 37 birds with light and temperature sensors in 1994/95 and 1995/96. Geolocation lacked the accuracy required to describe foraging trips, but duration of foraging trips and temperature data suggested birds were ranging to the PFZ. Foraging was therefore entirely within Area 81 and outside the CAMLR Convention Area.

Conclusions

This review summarised the enormous body of literature describing the diet and at-sea distribution of penguins that breed in the CCAMLR region. Despite the large number of studies, significant gaps are evident in the data and there is considerable potential for bias according to spatial location, seasonality and annual variation. Modelling of diet and distribution in relation to habitat variables around the colony provides an avenue for reducing such bias and for extrapolation of available information across populations or regions. However, there is need for further data collection to fill key information gaps, particularly diet and distribution of penguins in winter. Modellers and penguin biologists need to work together closely to develop models and collect further data required by these in order to provide the information required to manage fisheries within the CAMLR Convention Area in an ecologically sensitive manner.

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