

Estimated food consumption by penguins at the Prince Edward Islands

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Abstract: The consumption of food by the four species of breeding penguins at the Prince Edward Islands is assessed on an annual and seasonal basis. Total annual food consumption was estimated at 880 000 t, of which king penguins accounted for 74%, macaroni penguins 21%, rockhopper penguins 5% and gentoo penguins <1%. Pelagic fish, almost entirely myctophids, were the most important prey (70% of total prey biomass), followed by pelagic crustaceans (18%) and cephalopods (11%). Demersal fish and benthic crustaceans accounted for <1% of total consumption, being consumed only by gentoo penguins. Peak demands of between 2 and 3.3 x 10⁶ kg d⁻¹ occurred from October–December when three of the four species were breeding, including the two demi-populations of king penguins. Food demand decreased to 1.2 x 10⁶ kg d⁻¹ during winter when only king and gentoo penguins were present. Much of the prey are presumably captured within 300 km of the islands. Assuming an even distribution of foraging effort within their respective foraging ranges, rates of food transferred to penguins in November ranged from 4.1 x 10⁻³ g m⁻² d⁻¹ for macaroni penguins to 1.24 x 10⁻² g m⁻² d⁻¹ for king penguins. In mid-July, transfer rates to king and gentoo penguins were 3.9 x 10⁻³ g m⁻² d⁻¹ and 6.7 x 10⁻³ g m⁻² d⁻¹, respectively. The importance of pelagic myctophid fish to penguin populations at the Prince Edward Islands is clear.

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Introduction

Concentrations of breeding seabirds, constrained by the need to return regularly to attend eggs and chicks, may consume substantial quantities of marine prey close to nesting areas. Six million seabirds of 27 breeding species reside at the Prince Edward Islands (Cooper & Berruti 1989). The four species of penguins, king (*Aptenodytes patagonicus*), gentoo (*Pygoscelis papua*), macaroni (*Eudyptes chrysolophus*) and rockhopper (*E. chrysocome*) account for 98% of the biomass of surface-nesting birds. Brown (1989) noted that although total food consumption of macaroni and rockhopper penguins amounted to 165 000 t during the seven-month breeding and moulting seasons, king penguins were probably the single most important avian consumer of food in the seas surrounding the Prince Edward Islands. Studies of food consumption by marine vertebrate predators in the Southern Ocean have generally underlined the importance of Antarctic krill in these high latitude marine food webs (Croxall & Prince 1982, Croxall *et al.* 1984, Croxall *et al.* 1985, Abrams 1985, Hunt 1985). However, away from breeding areas on the Antarctic continent and at lower latitudes, including the Prince Edward Islands, diet studies indicate fish may be as important a prey

of avian predators as pelagic crustaceans (Ainley *et al.* 1984, 1991, Adams & Klages 1987, Adams & Brown 1989, Brown & Klages 1987, Hindell 1988).

Based on a review of diets, energy expenditure and annual activity budgets, we present here estimates of the daily food consumption of the penguin populations at the Prince Edward Islands, including seasonal variation in consumption of different prey types. We have restricted estimates of food consumption to penguins because insufficient data exist to undertake similar analyses for other groups of seabirds at the islands.

Methods

The model used here is that of Croxall *et al.* (1984) modified to account for a) seasonal changes in diet, b) linear mortality in eggs and chicks over the incubation and chick rearing periods and c) foraging effort by each penguin species is assumed to be spread evenly over their estimated foraging ranges. Information on the sizes and activities of the non-breeding populations is sparse (see also Croxall *et al.* 1984 and Brown 1989) and the model computes food consumption by breeding populations only.

Breeding cycle and population sizes

King penguins at South Georgia may breed successfully twice in three years (Stonehouse 1960), but only once every two years at Isles Crozet (Barrat 1976). Recent data collected at Marion Island suggest a similar cycle to that reported at Crozet (FitzPatrick Institute unpublished data). The total moult and breeding cycle of king penguins at Marion Island extends over 14 months. Most birds commence their prenuptial moult in October with chicks eventually attaining independence by December the following year. In winter, the number of adults attending rookeries decreases dramatically and chicks are fed infrequently (Cherel *et al.* 1987). We assumed there were two demi-populations of king penguins present September to February, but at different stages of breeding.

Gentoo penguins at Prince Edward Islands have a five-month breeding cycle with egg laying commencing in the austral winter. Failed breeders will relay, but breeding success is low (Williams 1980). The whole population is assumed to be resident at the islands throughout the year. The breeding and moult cycle of macaroni and rockhopper penguins covers six to seven months. The cycles are similar although macaroni penguins commence breeding three to four weeks earlier than do rockhopper penguins (Brown 1989).

Energy costs (see below) were allocated to eight defined activities: pre-laying attendance at the nest, laying fast, incubating, brooding and guarding chicks, at-sea foraging for chicks, chick growth, at-sea foraging for self, and moulting. During winter (June–August), when king penguin chicks ceased growth (Stonehouse 1960), we assumed breeding adults were only foraging for themselves, but remained within 300 km of the islands (Adams 1987). Although egg laying by king penguins at Marion Island was spread over four months and gentoo penguins will relay (Williams 1980), the model assumed the activities of breeding birds were synchronized and that eggs were not replaced (see Croxall *et al.* 1984). Recently fledged chicks and adults were assumed to feed in the vicinity of the islands for a week before and after the breeding and moulting season. Failed breeders were assumed to remain at sea in the vicinity of the islands, only departing at the end of the breeding and moulting cycle. Observations of Adélie penguins in the Ross Sea lends some support to such an assumption (Ainley *et al.* 1984).

Population sizes of all four penguin species breeding at Prince Edward Islands were from Watkins (1987), Cooper & Berruti (1989) and unpublished records of the FitzPatrick Institute. Figures for king and gentoo penguins were based on earlier counts presented in Siegfried *et al.* (1978) and Adams & Wilson (1987), respectively. Estimates of population size of king penguins are well over a decade old and may now be in error. Recorded increases in the numbers of adults breeding at small colonies, (FitzPatrick Institute unpublished data) suggest that the breeding population of king penguins at Marion Island may have increased over the past decade.

Egg loss and chick mortality from laying to independence were obtained from Williams (1980) and from unpublished data (FitzPatrick Institute). Breeding success of macaroni and rockhopper penguins at Marion Island has been recorded annually beginning in 1981/82 and 1983/84, respectively (FitzPatrick Institute unpublished data). Data for king and gentoo penguins were considerably more fragmentary. In the absence of data, the model assumed egg loss and chick loss decay linearly from laying to hatching and hatching to independence.

Diet

The diets of all four species of penguin breeding at Marion Island have been described quantitatively (Adams & Klages 1987, 1989, Brown & Klages 1987). In contrast to the situation at some high latitude sites (Croxall & Lishman 1987), there were considerable seasonal and annual changes in the diets of penguins at Marion Island. Dietary data were considered for 1984/85 only, but monthly changes in diet were incorporated into the model (Adams & Brown 1989). The presence of king and gentoo penguins throughout the year allowed sampling for 12 months. Samples from king penguins were obtained from adults returning to feed chicks or from large chicks immediately after feeding. Gentoo penguins attend chicks from July–December. During the remainder of the year non-breeding adults were sampled. Diet sampling of macaroni and rockhopper penguins was restricted to the chick-rearing period only. We assumed the proportion of different prey prior to chick rearing was similar to that in the diet of the first month sampled. Similarly, diet subsequent to chick rearing was assumed to be the same as the last month sampled. Diet composition was specified as

- 1) pelagic fish,
- 2) demersal fish,
- 3) pelagic crustaceans,
- 4) benthic crustaceans, and
- 5) cephalopods (from Adams & Brown 1989). Prey types comprising <1% of the diet by mass were ignored.

Energy content of prey

We used values for energy content of prey (wet mass) given by Brown (1987a) for crustaceans (4.68 kJ g⁻¹) and cephalopods (3.25 kJ g⁻¹). These values are close to the 4.35 and 3.57 kJ g⁻¹ given by Croxall *et al.* (1984). Energy content of fish was taken as 3.97 kJ g⁻¹ wet mass (Clarke & Prince 1980). We did not account for any seasonal changes in energy content, although such changes have been demonstrated for Antarctic krill (Clarke 1984). Measured assimilation efficiencies of king and gentoo penguins fed on fish averaged 75.5%. King penguins assimilated squid with a mean efficiency of 73%

(Adams 1984, N.J. Adams unpublished data). Assimilation efficiency of gentoo penguins fed Antarctic krill was 71.7% (N.J. Adams unpublished data). We assumed macaroni and rockhopper penguins assimilated the various prey types at similar efficiencies.

Energy costs

Energy requirements of male adult king, macaroni and rockhopper penguins merely attending breeding sites (pre-laying attendance) were assumed to be equivalent to Average Daily Metabolic Rates (ADMR) of resting penguins (Adams 1990, Brown 1984). Average energy cost of egg formation was estimated to be 7.2% of Basal Metabolic Rate BMR (Adams 1992) and was added to ADMR to determine energy cost of pre-laying attendance of female penguins. During this period male and female gentoo penguins continued to go to sea regularly and these energy costs were taken from Davis *et al.* (1989). Similarly, during incubation, both gentoo and king penguin partners alternate shifts and regularly go to sea (Adams 1990, Williams 1980). Integrated energy costs over the incubation period of king penguins were determined from measurements of oxygen consumption of birds incubating in the colony (Adams 1990) and at-sea costs (see below). Corrections were made for differences in activity budgets between male and female penguins. Energy costs of gentoo penguins during incubation were taken from Davis *et al.* (1989). Macaroni and rockhopper penguins divide incubation duties into two shifts only (Brown 1989). Energy expenditure at the nest was taken from rates of oxygen consumption measured over 24 h (Brown 1984). King and gentoo penguins alternate brood and guard shifts in a similar way to their incubation duties (Stonehouse 1960, Williams 1980). Energy costs to king penguins were determined by combining measurements of ADMR and at-sea costs. Energy costs to gentoo penguins were again taken from Davis *et al.* (1989). Brooding and guarding duties of *Eudyptes* penguins were undertaken exclusively by males. Energy costs to macaroni penguins were from Davis *et al.* (1989). Costs to rockhopper penguins were calculated from this on a mass-specific basis. At-sea energy costs have been measured for king penguins (Kooyman *et al.* 1982), macaroni and gentoo penguins (Davis *et al.* 1989). Costs to rockhopper penguins were calculated from mass-specific equivalents measured for macaroni penguins. Measurements of the energy cost of feeding chicks of gentoo and macaroni penguins account for species-specific activity budgets during chick rearing. King penguins are assumed to spend negligible time ashore while feeding large chicks and costs are taken directly from Kooyman *et al.* (1982). Male and female penguins are assumed to divide foraging effort equally once they begin feeding large chicks. At-sea costs of king penguins were measured using tritiated water whereas those of gentoo and macaroni penguins were based on dilution rates of doubly labelled water. Energy costs of failed breeders were assumed

to be equivalent to at-sea energy expenditure of penguins foraging for themselves. Total food requirements during chick rearing were calculated from the addition of food required to meet at-sea energy costs and that required to meet the cost of growth and maintenance of surviving chicks (Adams 1990, Brown 1987a) corrected for assimilation efficiency. Moulting costs were determined as average daily energy expenditure during moult measured from rates of oxygen consumption (Brown 1985, Adams & Brown 1990). To account partly for accumulation of fat reserves prior to moult, we assumed a feeding rate during moult commensurate with these energy costs. Normally during moult, penguins are restricted to land and no feeding takes place. Masses of male and female penguins vary through the breeding season as a consequence of fast and periods of food accumulation. Energy expenditures during different breeding activities take into account these changes in body mass.

Foraging range

Total distance travelled during foraging excursions of all four species of penguins during chick rearing at Marion Island have been estimated using time-speed meters (Adams 1987, Adams & Wilson 1987, Brown 1987b). Foraging ranges were calculated as half the total distance travelled. Foraging ranges of macaroni and rockhopper penguins were for adults feeding large and small chicks, respectively.

To calculate prey transfer rates, we assumed the foraging effort of penguins was distributed uniformly within their exclusive foraging zones (gentoo inshore, rockhopper intermediate, king and macaroni offshore). We have some circumstantial evidence which suggested foraging zones may be mutually exclusive (Adams & Brown 1989).

Total food requirements of the penguin community at the Prince Edward Islands were estimated by summing food requirements for all four species. We may have overestimated the energy consumption of the breeding populations in the area. At-sea energy requirements of failed breeders are likely to be less than those of birds attending chicks. In addition, we have assumed failed breeders remain feeding in the vicinity of the island. This may not be true, particularly for king penguins, since during winter, reduced chick feeding rates suggest limited availability of prey in waters surrounding the islands. However, we have not considered the impact that the pre-breeding population has on marine resources. Subantarctic penguins begin breeding at between two and five years of age, depending on the species (Croxall 1984). Immature penguins return to breeding sites to moult and are presumably in the surrounding waters feeding for some time before and after moult. Pre-breeders of some penguin species may comprise up to 40% of the breeding penguin population (Croxall & Prince 1982) and, therefore, will consume substantial quantities of marine prey. Other errors are likely to arise because foraging ranges, calculated as half total distance travelled during a foraging excursion, probably

overestimate actual ranges. In addition, it is unlikely that penguins distribute their foraging effort uniformly around the islands. For instance, gentoo penguins may feed largely in shallow shelf waters that lie between Marion and Prince Edward islands (Adams & Wilson 1987).

Results and discussion

We did not conduct any formal sensitivity tests to determine confidence limits around food consumption estimates. On the basis of Monte Carlo simulations on a model developed to determine the food consumption of the seabird community at Foula, Shetland Islands, Furness (1978) indicated that changes in input values of existence metabolism equations, population size, flight or swimming activity levels and their energy costs had a large effect on output values. Because actual measurements of the energy costs of many activities are now available, greatest errors are likely to arise from use of varying population size inputs. The importance of obtaining better estimates of breeding and especially non-breeding populations has been stressed repeatedly (Croxall *et al.* 1984, Brown 1989).

Total food consumption

Total annual food consumption of the breeding penguin community at the Prince Edward Islands was close to 900 000 t. Pelagic fish (mainly Myctophidae) account for 70% of the total consumption, pelagic crustaceans 18% and cephalopods 11%. Benthic crustaceans and demersal fish were consumed almost exclusively by the small gentoo penguin population and accounted for <1% of total consumption (Table I). Much of the pelagic fish was consumed by king penguins which took 74% of total consumption. Macaroni penguins accounted for 21% of consumption and rockhopper penguins 5%.

The importance of pelagic fish as prey for penguins at the Prince Edward Islands was in marked contrast to the situation at many sites south of the Antarctic Polar Front where energy flux to top predators is primarily through pelagic crustaceans (Croxall *et al.* 1984, 1985). Subantarctic seabird assemblages breeding at localities north of the Antarctic Polar Front may

be operating generally as higher order predators than is the case for many crustacean-dominated food webs farther south.

Seasonal food consumption: predators

During October–April, when three of the four penguin species breed or moult, peak food demand occurred (Fig. 1). Food consumption rates over this period ranged from $1.9\text{--}3.3 \times 10^6 \text{ kg d}^{-1}$ and decreasing to $1.1 \times 10^6 \text{ kg d}^{-1}$ during winter. Daily consumption rates compared here are considerably higher than those presented by Adams & Brown (1989), which were calculated from predictive equations relating body mass to feeding rate (Nagy 1987). However, the pattern of penguin population consumption rates decreasing with decreasing average foraging range of the respective species, was consistent (see Adams & Brown 1989).

Consumption remained high for individual species during chick rearing when adults were collecting food for their chicks and failed breeders were assumed to be in the vicinity of the islands (Figs 2a–d). This assumption is supported by observations of Adélie penguins in the Ross Sea (Ainley *et al.* 1984). Peak demands coincided with premoult foraging excursions (Adams & Brown 1990) and the presence of recently fledged chicks feeding in the vicinity of the islands, and were a consequence of the model assuming synchrony of activity. Such peaks in food consumption are unlikely to be as high in the natural situation. Periods of reduced consumption occurred when the population or a proportion of the population was confined to land, for example, during incubation or moult.

Patterns of food consumption of the two congeneric species, the macaroni and rockhopper penguins, were similar, reflecting their matched activity patterns (Fig. 2). Consumption rates were highest during February and March immediately after chicks attained independence (Fig. 2a & b). Values for food consumption of macaroni and rockhopper penguins from this study were 49% and 11% higher, respectively, than those presented by Brown (1989) for the same site. The differences were partly accounted for by the higher at-sea costs used here. Previous estimates based on dilution of tritiated water (Davis *et al.* 1983) and used by

Table I. Estimated number of breeding pairs and annual food requirements of the penguin community at the Prince Edward Islands

| Penguin species | Population size | Food consumption (tonnes per annum) | | | | | Total |
|-----------------|-----------------|-------------------------------------|---------------|---------------------|---------------------|-------------|---------|
| | | Pelagic fish | Demersal fish | Benthic crustaceans | Pelagic crustaceans | Cephalopods | |
| Macaroni | 422 084 | 30 176 | 0 | 0 | 120 833 | 34 769 | 185 778 |
| Rockhopper | 172 652 | 3 111 | 0 | 0 | 41 368 | 933 | 45 412 |
| Gentoo | 1 543 | 96 | 674 | 397 | 310 | 28 | 1 505 |
| King | 220 230 | 583 630 | 0 | 0 | 0 | 64 523 | 648 153 |
| Total | 615 509 | 617 013 | 674 | 397 | 162 511 | 100 253 | 880 847 |

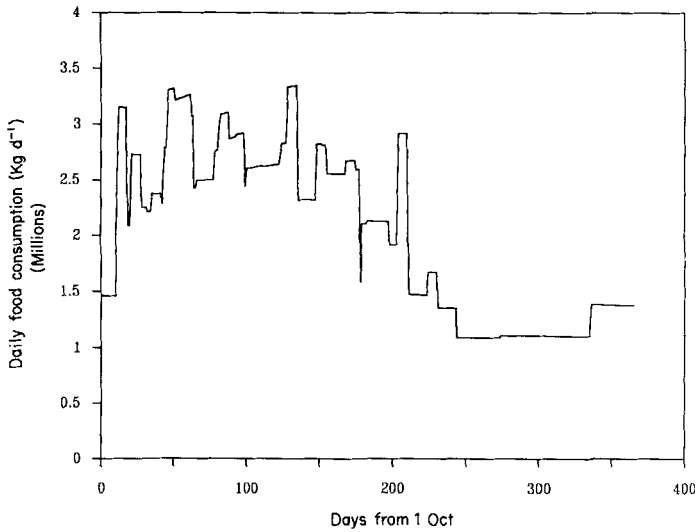


Fig. 1. Seasonal variation in the daily food consumption of penguins at the Prince Edward Islands.

Brown (1989) may have underestimated actual costs (Davis *et al.* 1989). The closer coincidence of consumption figures for rockhopper penguin in the two studies were due to the use of revised population estimates. While recognizing other differences in the biology of sympatric congeneric penguin species that result in ecological separation, Croxall & Lishman (1987) and Trivelpiece *et al.* (1987) have stressed the importance of differences in timing of breeding as a mechanism to ensure staggering of food demands by chicks. However, the relatively long chick-rearing period is nearly three times the length of the differences in the timing of breeding. This coupled with the observation that energy requirements of chicks accounted for only 4–9% of the total energy budget of *Eudyptes* penguins (Brown 1989), such an argument is not entirely convincing. Energy constraints on individual breeding penguins may be most severe during brooding and guarding when chicks require frequent feeds, but potential foraging time is halved by the necessity of one adult having to remain at the nest site. It may be that the interspecific staggering of brooding is the more important factor in trophic segregation.

Total food consumption of the gentoo penguin population was small compared to the other three penguin species. Consumption rates of gentoo penguins were highest at the beginning of January when adults were at sea immediately prior to moult (Fig. 2c). In contrast to their activities during the remainder of the year, gentoo penguins spend this period at sea continuously and may feed away from the immediate vicinity of the islands. For the remainder of the year, there was little variation in food consumption rates of 3000–5000 kg d⁻¹.

The high food demands of king penguins can be ascribed to their large population size and long breeding season. King penguins had their greatest impact on marine resources during the first part of summer when the breeding activities

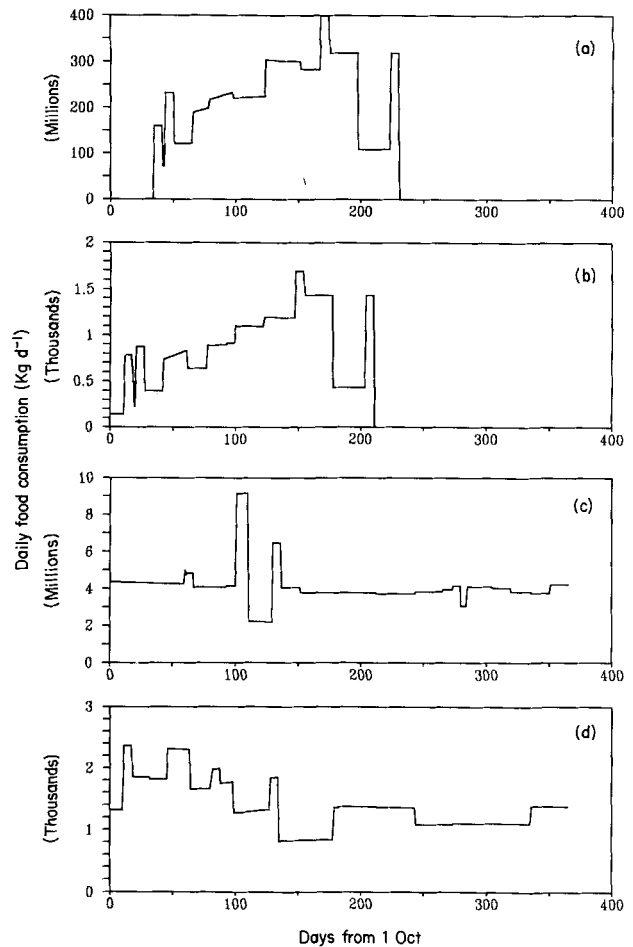


Fig. 2. Seasonal variation in the daily food consumption of penguins at the Prince Edward Islands a. rockhopper, b. macaroni, c. gentoo and d. king.

of the two demi-populations overlapped (Fig. 2). Consumption was lowest during January and February when adults were incubating, and during July and August when it was assumed that adults remain in the vicinity of the islands, but do not attempt to feed chicks.

Seasonal food consumption: prey

Daily consumption rates of benthic crustaceans, mainly the shrimp *Nauticaris marionis*, ranged from zero to 2 600 kg d⁻¹ during March when it accounted for over 70% of the diet of gentoo penguins (Fig. 3a). Consumption rates of the other dietary components restricted to gentoo penguins, demersal fish and mainly juvenile Antarctic cod (Nototheniidae), peaked at 8 000 kg d⁻¹ for 10 days coinciding with the end of the premoult foraging excursion when we assumed gentoo penguins were at sea continuously (Fig. 3b). From March–May consumption fell to zero. Consumption rates during the remainder of the year were close to 2 000 kg d⁻¹.

Consumption of pelagic crustaceans was confined mainly

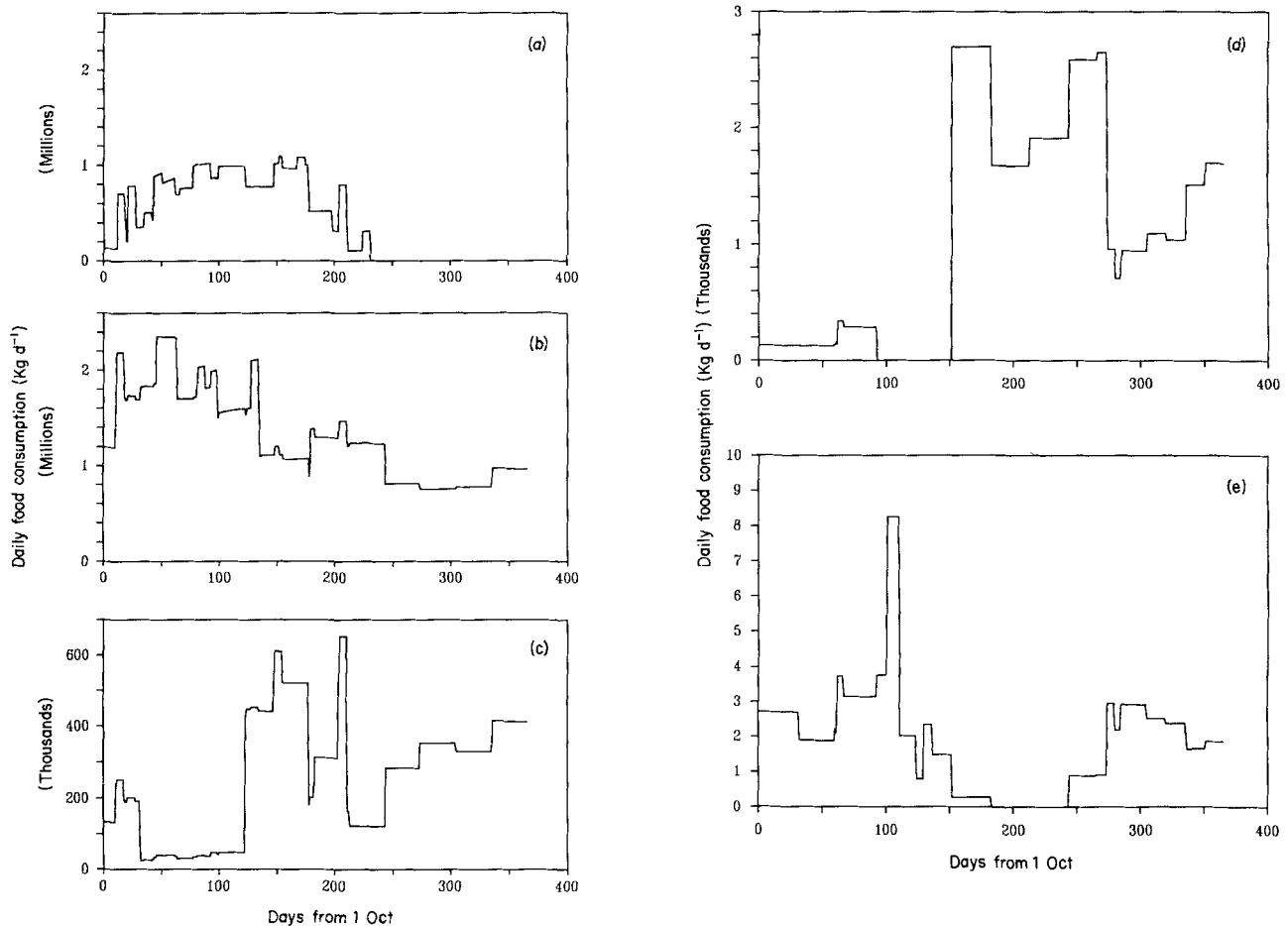


Fig. 3. Seasonal variation in daily food consumption rates of **a.** pelagic crustaceans **b.** pelagic fish **c.** cephalopods **d.** benthic crustaceans and **e.** demersal fish by penguins at the Prince Edward Island.

to summer, largely reflecting the presence at the islands of their major consumers, macaroni and rockhopper penguins (Fig. 3c). Consumption rates averaged $7.0 \times 10^5 \text{ kg d}^{-1}$ and peaked at $1.1 \times 10^6 \text{ kg d}^{-1}$. In 1984/85, the most important crustaceans consumed were the euphausiids *Euphausia vallentini* and *Thysanoessa vicina* (Brown & Klages 1987). Preliminary estimates of the rate of advection of potential prey species on to the shelf region suggest this would supply sufficient pelagic crustaceans for all the terrestrial breeding marine predators (birds and seals) at the Prince Edward Islands (Perissinotto *et al.* 1990, Perissinotto & Mcquaid 1992). However, such a process is inadequate to support the estimated consumption rate of pelagic myctophid fish (see below) (Perissinotto & Mcquaid 1992).

Daily consumption of pelagic fish, largely myctophids, averaged $1.7 \times 10^6 \text{ kg d}^{-1}$. In late summer the consumption by macaroni penguins increased, but rates were still less than during early summer when the king penguins were present (Fig. 3d).

Highest consumption rates of cephalopods occurred during

February and March when the proportion of cephalopods in the diet of macaroni penguins increased sharply. Intake consisted almost entirely of small *Kondakovia longimana*. Consumption of this species was sustained through winter by king penguins at around $3.5 \times 10^6 \text{ kg d}^{-1}$ before falling to less than $1.0 \times 10^6 \text{ kg d}^{-1}$, from November–January.

Prey transfer rates to populations of the different penguin species in November ranged from $9.6 \times 10^{-3} \text{ g m}^{-2} \text{ d}^{-1}$ for king penguins feeding offshore to $5.69 \times 10^{-2} \text{ g m}^{-2} \text{ d}^{-1}$ for rockhopper penguins feeding closer to shore (Table II). By mid-July only king and gentoo penguins remain at the Prince Edward Islands and a far more even distribution of foraging effort is suggested with maximum transfer rates to king penguins of $3.9 \times 10^{-3} \text{ g m}^{-2} \text{ d}^{-1}$ and $6.6 \times 10^{-3} \text{ g m}^{-2} \text{ d}^{-1}$ to gentoo penguins.

While we have accounted for seasonal variations in diet in this model, we have not addressed the problem of year to year variation in diet composition (see Brown *et al.* 1990) and breeding populations and their effects on consumption rates. Large changes in the annual food consumption of seabirds have occurred in other marine systems (Briggs & Chu 1987,

Table II. Food transfer rates to penguins at the Prince Edward Islands assuming mutually exclusive foraging ranges

| Penguin species | Foraging range km | Daily consumption | | | |
|-----------------|-------------------|---|--|---|--|
| | | Nov (Day 36) g d ⁻¹ x 10 ⁶ | g m ⁻² d ⁻¹ x 10 ⁻³ | July (Day 288) g d ⁻¹ x 10 ⁶ | g m ⁻² d ⁻¹ x 10 ⁻³ |
| King | 300 | 1 755 | 9.5 | 1 104 | 3.9 |
| Macaroni | 178 | 397 | 4.1 | - | - |
| Rockhopper | 33 | 160 | 56.9 | - | - |
| Gentoo | 14 | 4 | 7 | 4 | 6.7 |

Duffy & Siegfried 1987). Considerable fluctuations in breeding success of particularly krill-eating seabirds at South Georgia (Croxall *et al.* 1988) and macaroni penguins at Marion Island (FitzPatrick Institute unpublished data) suggested similar year to year variability in breeding populations and food consumption in higher latitude waters. Similarly although the diets of penguins at some breeding sites south of the Antarctic Polar Front show little seasonal or interannual change (Croxall & Lishman 1987) there is considerable variation at Marion Island (Brown *et al.* 1990). Future modelling exercises should attempt to address these problems and evaluate the magnitude of such interannual variation in prey consumption.

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