Energy requirements and food consumption of *Eudyptes* penguins at the Prince Edward Islands

CHRISTOPHER R. BROWN[1]

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa
[1] Present address: Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa

Abstract: Macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*) account for a substantial proportion of the avian biomass at the subantarctic Prince Edward Islands (47°S, 38°E) in summer, when both species are breeding at the islands. Information on breeding population sizes, breeding and moulting activities, and diets were combined with measurements of the penguins' energy expenditures to construct a bioenergetic model of their energy requirements and food consumption at the islands. Total energy requirements of adults and chicks amounted to 460×10^9 kJ and 162×10^9 kJ for macaroni and rockhopper penguins, respectively. Food consumption was estimated to amount to a total of 166 000 tonnes during the seven-month breeding and moulting cycle, of which macaroni penguins consumed 75%. Most, if not all, of this food is taken within a 200-km radius of the islands. Available information suggests that potential primary production in the immediate vicinity of the islands is sufficient to support the macaroni and rockhopper penguin populations. However, the importance in the diets of the penguins of several prey species more typical of Antarctic and subtropical regions suggests that the penguins rely to a large extent on the importation of prey populations from other areas.

Introduction

Seabirds frequently constitute a major class of predator in marine ecosystems (Croxall 1987). Quantitative assessments of their energy and food requirements provide information on energy flow through marine ecosystems (e.g. Wiens & Scott 1975), and allow assessment of the impact of seabirds on marine resources, of particular interest where these may conflict with commercially exploitable, or potentially exploitable, prey stocks (e.g. Furness 1978, 1981, Furness & Cooper 1982).

Bioenergetic models usually integrate counts, or estimates, of population sizes with estimates of individual metabolism. Basic information required includes population sizes, diet, activity budgets and energy requirements of the species concerned (Wiens 1984). A fundamental problem associated with modelling seabird energy requirements is that of estimating energetic costs associated with various activities. To date, most models have assessed existence metabolism (EM) from allometric equations and have subsequently assigned multiples of EM to other activities. However, estimates of population energy requirements are especially sensitive to the use of these equations and generate results with 95% confidence intervals of between 30% and 50% of the mean, depending on the equations used (Furness 1978, 1981). Despite evidence that the use of allometric equations result in large imprecisions in estimates of population energy requirements, they continue to be used in modelling seabird energetics, usually because of the lack of empirical data on individual energy expenditures of seabirds.

In addition to the above limitations, for reasons discussed by Croxall *et al.* (1984), most estimates of seabird energy and food requirements to date have focused on Northern Hemisphere, or low-latitude Southern Hemisphere, seabirds and few assessments have been made for Antarctic and subantarctic seabird communities. Mougin & Prevost (1980) made crude estimates of seabird consumption for the whole Antarctic and subantarctic region. Although based on early allometric equations and, in some instances, inappropriate methods, their results nevertheless emphasize the pre-eminent role of penguins in the region. Indeed, Croxall (1984) suggests that, in terms of biomass, 80% of the birds in the Subantarctic can be considered to be penguins and of these 50% are macaroni penguins (*Eudyptes chrysolophus* Brandt). More recently, Croxall & Prince (1982) and Croxall *et al.* (1984) assessed the impact of seabirds on marine resources in the vicinity of South Georgia (54°S, 37°W) and later extended this to include the Scotia Sea (Croxall *et al.* 1985). Although these studies also based existence metabolism of the birds on allometric equations, a significant departure from most models of seabird energetics was the use of empirical data for energetic requirements of the birds during incubation and moult (based on mass loss data during the fasts), for penguins swimming at sea (based on isotope dilution rates), and for chick-rearing (from meal sizes and

feeding frequency).

The Prince Edward Island group (47°S, 38°E), comprising Marion Island and the smaller Prince Edward Island, lies about 250 km north of the Antarctic Polar Front (Lutjeharms & Valentine 1984). Four species of penguins breed at the islands of which macaroni and rockhopper *(Eudyptes chrysocome* Forster) penguins are the most numerous, and comprise about 40% of the biomass of surface nesting species and an estimated 20% of the total avian biomass. In this paper, I combine measurements of the energy expenditures of macaroni and rockhopper penguins during their breeding activities at the Prince Edward Islands with information on their population sizes, activity patterns and diets to construct a bioenergetic model of the timing and magnitude of their food requirements. Total energy and food requirements of the two species during their 6- to 7-month breeding cycle at the Prince Edward Islands are estimated from the model.

Methods and data base

Breeding cycle

The breeding cycles (here taken to include the post-breeding moult) of the two species are similar, although macaroni penguins begin breeding earlier than do rockhopper penguins (Warham 1963, 1971). However, the activity patterns of the sexes differ during at least a part of the breeding cycle. Both species are absent from their breeding sites at the Prince Edward Islands for about five months of the year. Although their whereabouts during the winter months are unknown, a number of records of moulting individuals of both species on the southern African coast indicates that they are capable of long-distance dispersal (see Cooper 1987 and references therein). Consequently, the birds are assumed to be dispersed away from the islands when not breeding.

Population sizes

Population numbers (breeding pairs) of macaroni penguins at Marion Island were based on a census conducted in 1983 (Watkins 1987) and those of breeding rockhopper penguins on a census conducted in 1987 (FitzPatrick Institute, unpublished data). Numbers of breeding macaroni and rockhopper penguins at Prince Edward Island were based on earlier estimates (Siegfried et al. 1978); the only figures currently available.

The number of pairs actively breeding from incubation until chicks fledged was estimated on a weekly basis from mortality data of eggs during incubation and of chicks during brooding and guarding and subsequently until fledging (Williams 1980). Rates of mortality from week to week during each stage were assumed to be linear and failed

breeders were assumed to remain at sea feeding in the vicinity of the islands and to return ashore to moult with successful breeders. For simplicity, it was assumed that all activities of breeding birds were synchronous (i.e. all birds of each sex were involved in the same activity at the same time).

Energetic costs of breeding activities

Daily energetic costs of breeding activities were based on measured values. In most cases, where testable, metabolic rates of the two sexes were not significantly different so slight weight differences between the sexes were ignored.

Pre-laying activities

Energy expenditures of adults during pre-laying activities at the nest were considered to be equivalent to average daily metabolic rates, about 15% higher than measured resting levels and 25% higher than predicted basal metabolic rate (Brown 1984).

Egg formation

The energetic cost of forming the clutch of two eggs was not measured. However, based on an estimate of Grau (1982) for Fjordland-crested penguins *(Eudyptes pachyrhynchus* Gray), maximum energy costs of egg formation in macaroni and rockhopper penguins were estimated to amount to less than 10% of their daily energy expenditures during pre-laying activities and were consequently not taken into account when calculating energy requirements.

Incubation

Energy expenditure during incubation was taken from rates of oxygen consumption measured over 24 h during incubation (Brown 1984).

At sea

Energy expenditures of five species of penguins, while feeding at sea, have been measured using dilution rates of either tritium (Kooyman et al. 1982, Davis et al. 1983) or doubly-labelled water (Nagy et al. 1984, Costa et al. 1986). Energy expenditure of macaroni and rockhopper penguins at sea were estimated from the relationship relating energy expenditures at sea to body mass from the above studies using a lean body mass of 4800 g for macaroni penguins and

2500 g for rockhopper penguins. Estimated energy expenditures were 3456 and 2493 kJ d⁻¹ for macaroni and rockhopper penguins, respectively. These values integrate time spent swimming (between 30 and 40% of their time at sea in macaroni and rockhopper penguins; Brown 1987a), time spent resting on the water and, in some instances, time spent ashore feeding chicks.

Brooding and guarding

During the first three weeks of chick-rearing, males remain at the nest brooding and guarding the chicks. Energy expenditure during this period has been measured for macaroni penguins by Davis et al. (1983) using dilution rates of tritiated water. Energy expenditure of rockhopper penguins was estimated from this on a mass-specific basis. During the guard period, chicks of macaroni and rockhopper penguins are fed by the females who spend about two-thirds of their time at sea foraging and one-third (usually at night) at the nest (Brown 1987a). Daily energy requirements of females during this period were calculated from their at-sea and at-nest energy expenditures using the above proportions.

Chick-rearing

The energetic cost of chick-rearing comprises the cost of the adults at sea (assuming that time spent ashore feeding chicks after initial brooding is negligible) plus the cost of growth and maintenance of surviving chicks. The energetic cost of the latter was calculated from energy budgets for chicks of the two species (Brown 1987b).

Moult

Penguins undergo a rapid moult lasting, in the case of macaroni and rockhopper penguins, about four weeks, of which about 25 days are spent ashore fasting (Brown 1986). Energy expenditure during this period comprises maintenance energy expenditure, cost of new feather synthesis and cost of thermoregulation during a period of reduced feather insulation. Average energy expenditure during moult has been measured from rates of oxygen consumption (Brown 1985).

Food requirements

Mean energy content of the diets of macaroni and rockhopper penguins was calculated from the energy content of each prey type and its proportional representation in the diets. Diets comprised 62% crustaceans, 25% fish and 13%

cephalopods for macaroni penguins and 81% crustaceans, 14% fish and 5% cephalopods for rockhopper penguins (Brown & Klages 1987). Energy content of crustaceans and cephalopods in the diet, measured by bomb calorimetry, averaged 4.68 and 3.25 kJ g⁻¹ wet mass, respectively (C.R. Brown, unpublished data). Energy content of fish in the diet was not measured and a value of 3.97 kJ g⁻¹ wet mass (Clarke & Prince 1980) was used.

Measured assimilation efficiencies of penguins range from 74% for jackass penguins (Spheniscus demersus Linnaeus) fed on fish (Cooper 1977) to 81% for king penguins (Aptenodytes patagonicus Miller) fed on squid (Adams 1984). White-chinned petrels (Procellaria aequinoctialis Linnaeus) fed on a mixture of crustaceans, fish and squid had assimilation efficiencies averaging 76% (Jackson 1986) and this figure was assumed for macaroni and rockhopper penguins.

Additional energy and food requirements

Macaroni and rockhopper penguins undergo fasts during the breeding season, notably during incubation, brooding and moulting. Energy reserves (lipid and protein) to sustain them through the fast must be accumulated in the period at sea prior to the fast and are in addition to normal at-sea maintenance and activity energy requirements. Synthesis of energy reserves may require an energy intake equivalent to 1.2–2.1 times that available to the birds through oxidation of the reserves (Kendeigh et al. 1977). For present purposes, production efficiency of energy storage was assumed to be 75% (Ricklefs 1974). Consequently, daily energy requirements prior to fasts, plus the cost of synthesis of energy reserves and food requirements prior to fasts were calculated as normal maintenance and activity requirements while at sea, plus total food requirements for the fasting activity, multiplied by the reciprocal of production efficiency (1.33) and divided by the number of days spent at sea before the fast. This correction was not applied to food requirements prior to the pre-laying fast because it was assumed that energy reserves for this period were accumulated before the birds' arrival in the immediate vicinity of the islands.

Results and discussion

Energy requirements and food consumption was highest during the pre-moult foraging trip when the entire breeding population and their surviving, newly fledged chicks were assumed to be at sea in the vicinity of the islands (Figs 1, 2). In addition to normal at-sea energy and food requirements, breeding adults were also laying down energy reserves to sustain them for their four-week moult fast ashore.

Total energy requirements of the macaroni and rockhopper penguin populations over a single breeding season, including
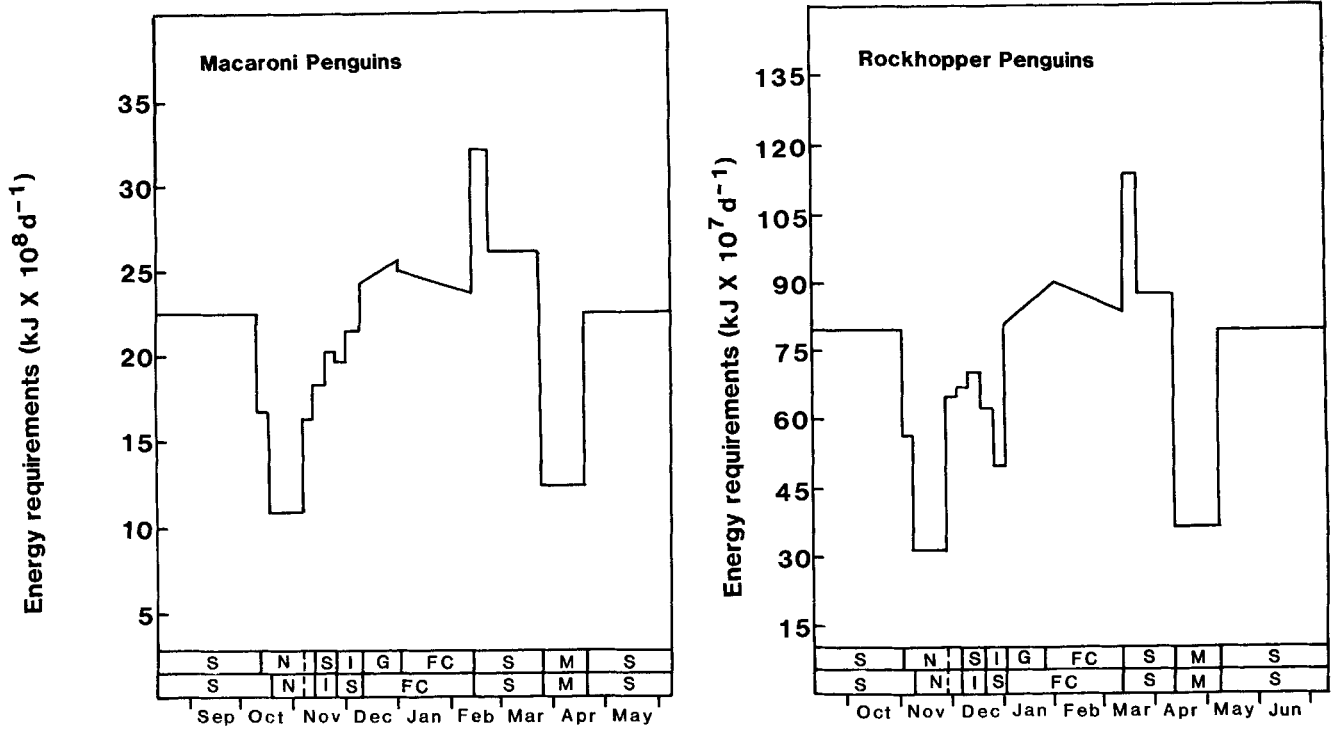
Fig. 1. Seasonal changes in energy requirements of macaroni and rockhopper penguins at the Prince Edward Islands. Approximate breeding and moulting schedules of macaroni and rockhopper penguins at the islands, based on data from Warham (1963, 1971), FitzPatrick Institute (unpublished data) and personal observation, are included below. N = nest and courtship activities, S = at sea, I = incubation, G = brooding and guarding chicks, FC = feeding chicks, and M = moulting. Dashed lines indicate the beginning of egg laying.
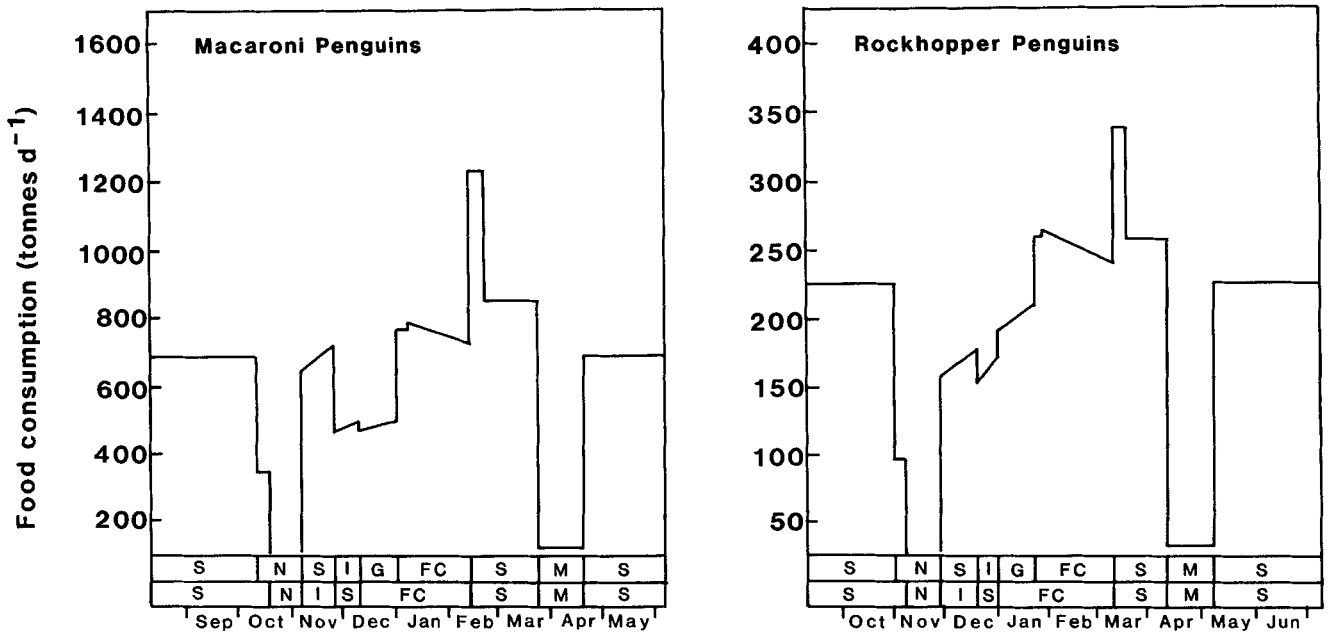

Fig. 2. Seasonal changes in food consumption of macaroni and rockhopper penguins at the Prince Edward Islands. Conventions for breeding schedule as in Fig. 1.

Table I. Energy requirements (kJ × 10⁹) of breeding macaroni and rockhopper penguins at the Prince Edward Islands during the breeding and moulting seasons.

| | Populations | Energy requirements | | | | |
		Males	Females	Failed breeders	Chicks	Total
Macaroni penguins						
Marion Island	405 100	138.1	141.4	125.2	29.0	433.7
Prince Edward Island	17 000	5.8	5.9	5.3	9.3	26.3
Rockhopper penguins						
Marion Island	157 600	48.9	49.4	28.9	5.0	132.2
Prince Edward Island	35 000	10.8	11.0	6.4	1.1	29.3
Grand total						621.5

Table II. Food requirements (tonnes) of breeding macaroni and rockhopper penguins at the Prince Edward Islands.

	Macaroni penguins	Rockhopper penguins	Total
Marion Island	120 000	33 400	153 400
Prince Edward Island	5 000	7 400	12 400
Total	125 000	40 800	165 800

a period of seven days prior to their arrival at the islands and after their departure, when the birds were assumed to be in the vicinity of the islands, were estimated to be 460.0×10^9 kJ for macaroni penguins and 161.5×10^9 kJ for rockhopper penguins (Table I). Energy requirements of males and females of both species were similar, despite differences in breeding activities. Energy requirements of chicks, the end product of a breeding attempt, comprised only 8.3% and 3.8%, respectively, of the total energy requirements of macaroni and rockhopper penguins during the breeding season.

Total estimated food consumption of macaroni and rockhopper penguins at both islands over a single breeding season (about 200 days) was 165 800 tonnes (Table II), of which macaroni penguins consumed 75%, consistent with their larger body size and higher population numbers. Of the total food consumption of both species, 110 600 tonnes comprised crustaceans, 36 590 tonnes fish and 18 620 tonnes cephalopods. Most, if not all, of this food is removed from within a 300 km, and probably closer to 200 km, radius of the islands (Brown 1987a).

Potential primary production in the immediate vicinity of the Prince Edward Islands ranges from about 140 mg C m⁻² d⁻¹ to as much as 4200 mg C m⁻² d⁻¹ (Mitchel-Innes 1967, El-Sayed et al. 1979, Parker 1984, Allanson et al. 1985, D.G.M. Miller, personal communication 1987). Assuming 0.4 g C g⁻¹ dry weight of prey (Curl 1962), macaroni and rockhopper penguins feeding within 200 km of the islands require an estimated 0.6 mg C m⁻² d⁻¹ (0.4 % of the primary production) during their seven-month breeding and moulting cycles.

Penguins feed at the third and fourth trophic levels. Assuming a 10 % efficiency of trophic transfer, a potential 1.5–46.0 mg C m⁻² d⁻¹ of primary and secondary consumers (crustaceans, fish and cephalopods) would be produced. However, primary production at the Prince Edward Islands

has only been measured during austral spring and autumn, when phytoplankton production levels are generally high. Furthermore, all measurements were made within about 50 km of the islands where primary production is enhanced by an island mass effect (Allanson et al. 1985), the influence of which is unlikely to extend to ranges at which the penguins forage when food requirements are highest. Nevertheless, even the lowest estimate of primary production suggests that there is potentially sufficient food in the vicinity of the islands to support the large breeding populations of macaroni and rockhopper penguins, although pre- and non-breeders have not been taken into account. However, net-hauls in the vicinity of the Prince Edward Islands frequently contain several species of crustaceans more typical of subtropical and Antarctic waters than of subantarctic waters, the presence of which are thought to occur through advection and eddying of foreign water masses past the islands (Boden & Parker 1986). Despite the apparent high productivity in the vicinity of the islands, the importance of subtropical and Antarctic prey species in the diets of macaroni and rockhopper penguins (Brown & Klages 1987) suggests that these birds rely, to a large extent, on importation of prey-stocks from other areas. Apart from qualitative data from net hauls, little information is available on the abundance, distribution and movements of these important prey species in the vicinity of the Prince Edward Islands and quantitative data should be considered a priority for future marine research in the area.

Despite refinements, the model still suffers several limitations. Population estimates for breeding macaroni and rockhopper penguins at Marion Island are good, but an up-to-date census of both species at Prince Edward Island is overdue.

Data on energetics of the species are considered good, although measurements of incubation costs in the field using doubly-labelled water are desirable to validate those made in metabolic chambers. However, substantial refinements of energy expenditures are probably not warranted until better information is available on individual activity budgets, and foraging distribution, especially outside the breeding season.

Dietary information for the two species is good during the chick-rearing period but, as at other localities, little is known of the diets outside this period. For this reason, seasonal and year to year changes in diets (Brown & Klages 1987), and consequently energy intake, have not been considered in the

model.

Probably the largest, single limitation of the present model, and also that of Croxall *et al.* (1984), is the lack of information on numbers of birds too young to breed (pre-breeders) and non-breeding penguins. As pointed out by Croxall *et al.* (1984), demographic data are, at present, inadequate to assess the size of these populations, although Croxall & Prince (1982) estimated the pre-breeding population of macaroni penguins to be 40% of the breeding population. Extrapolating this figure to the Prince Edward Islands, and assuming that pre-breeding birds spend half the breeding period ashore and half at sea, their food requirements could amount to an additional 49 200 tonnes and 15 700 tonnes for pre-breeding macaroni and rockhopper penguins, respectively.

In most respects, the pattern of daily food consumption of macaroni penguins corresponds very closely with that of the same species at South Georgia (Croxall *et al.* 1984), with the notable exception of food requirements of pre-moulting birds at sea. However, Croxall *et al.* (1984) point out that they did not include additional food required to establish energy reserves for moult and thus recognized that food consumption during this period was an underestimate. Overall, Croxall *et al.* (1984) estimated that 8×10^6 breeding pairs of macaroni penguins in the vicinity of South Georgia consumed 4 million tonnes of food, chiefly krill. This amounted to 51% of the total annual food consumption of all seabirds at South Georgia, although Croxall *et al.* (1984) assumed that the penguins were feeding in the vicinity of the island throughout the year. Nevertheless, macaroni penguins are an important consumer at South Georgia and seasonal patterns of food consumption largely reflect the consumption of this species. Although macaroni and rockhopper penguins account for a substantial proportion of the avian biomass at the Prince Edward Islands, their impact on marine resources is difficult to assess at present because of lack of information on consumption by other breeding species. Preliminary estimates (C.R. Brown, unpublished data) suggest that the estimated 50 000, 80 000 and 1.7 million breeding pairs, respectively, of white-chinned petrels, blue petrels (*Halobaena caerulea* Gmelin) and Salvin's prions (*Pachyptila vittata salvini* Mathews) at Marion Island take a total of 35 720 tonnes of food, comprising 15 250 tonnes of crustaceans, 13 700 tonnes of fish and 6770 tonnes of cephalopods. This is approximately 20% of the consumption of macaroni and rockhopper penguins, but does not include the populations at Prince Edward Island for which there are no reliable estimates of burrowing petrel numbers. Consumption of these may amount to three times that of the same species at Marion Island. However, only a few prey species of blue petrels and Salvin's prions are common also to macaroni and rockhopper penguins (Steele & Klages 1986, Gartshore *et al.* in press) and the extent to which their foraging ranges overlap with those of the penguins is unknown. The king penguin is probably the most important single consumer of marine resources in the area. A preliminary estimate suggests that the 220 000 breeding pairs of king penguins which are resident at the islands throughout the year, consume about 280 000 tonnes of food per year, most of which is removed from within a 300-km radius of the islands (Adams 1987, N.J. Adams, unpublished data).

Acknowledgements

References

ADAMS, N.J. 1984. Utilization efficiency of a squid diet by adult king penguins (*Aptenodytes patagonicus*). *Auk*, **101**, 884–886.

ADAMS, N.J. 1987. Foraging range of king penguins *(Aptenodytes patagonicus)* during summer at Marion Island. *Journal of Zoology, London*, **212**, 475–482.

ALLANSON, B.R., BODEN, B., PARKER, L. & DUNCOMBE-RAE, C. 1985. A contribution to the oceanology of the Prince Edward Islands. *In* SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., eds. *Antarctic nutrient cycles and food webs*. Berlin: Springer-Verlag, 38–45.

BODEN, B.P. & PARKER, L.D. 1986. The plankton of the Prince Edward Islands. *Polar Biology*, **5**, 81–93.

BROWN, C.R. 1984. Resting metabolic rate and energetic cost of incubation in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*). *Comparative Biochemistry & Physiology*, **77A**, 345–350.

BROWN, C.R. 1985. Energetic cost of moult in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*). *Journal of Comparative Physiology*, **155B**, 515–520.

BROWN, C.R. 1986. Feather growth, mass loss and duration of moult in macaroni and rockhopper penguins. *Ostrich*, **57**, 180–184.

BROWN, C.R. 1987a. Traveling speed and foraging range of macaroni and rockhopper penguins at Marion Island. *Journal of Field Ornithology*, **58**, 118–125.

BROWN, C.R. 1987b. Energy requirements for growth and maintenance in macaroni and rockhopper penguins. *Polar Biology*, **8**, 95–102.

BROWN, C.R. & KLAGES, N.T. 1987. Seasonal and annual variation in diets of macaroni (*Eudyptes chrysolophus*) and southern rockhopper (*E. chrysocome chrysocome*) penguins at sub-Antarctic Marion Island. *Journal of Zoology, London*, **212**, 7–28.

CLARKE, A. & PRINCE, P.A. 1980. Chemical composition and calorific value of food fed to mollymauk chicks at Bird Island, South Georgia. *Ibis*, **122**, 488–494.

COOPER, J. 1977. Energetic requirements for growth of the jackass penguin. *Zoologica Africana*, **12**, 201–213.

COOPER, J. 1987. New data on rarely recorded seabirds in southern Africa. *Cormorant*, **14**, 53.

COSTA, D.P., DANN, P. & DISHER, W. 1986. Energy requirements of free-ranging little penguins, *Eudyptula minor*. *Comparative Biochemistry and Physiology*, **85A**, 135–138.

CROXALL, J.P. 1984. Seabirds. *In* Laws, R.M., ed. *Antarctic ecology*.

London: Academic Press, 533–619.

CROXALL, J.P. 1987. Introduction. *In* CROXALL, J.P., *ed. Seabirds: feeding ecology and role in marine ecosystems.* Cambridge: Cambridge University Press, 1–5.

CROXALL, J.P. & PRINCE, P.A. 1982. A preliminary assessment of the impact of seabirds on the marine resources at South Georgia. *Comité National Français des Recherches Antarctiques*, 51, 501–509.

CROXALL, J.P., PRINCE, P.A. & RICKETTS, C. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. *In* SIEGFRIED, W.R., CONDY, P.R. & LAWS, R.M., *eds. Antarctic nutrient cycles and food webs.* Berlin: Springer-Verlag, 516–533.

CROXALL, J.P., RICKETTS, C. & PRINCE, P.A. 1984. Impact of seabirds on marine resources, chiefly krill, of South Georgian waters. *In* WHITTOW, G.C. & RAHN, H., *eds. Seabird energetics.* New York: Plenum Publishing Corp., 285–317.

CURL, H.S. 1962. Analyses of carbon in marine plankton organisms. *Journal of Marine Research*, 20, 181–188.

DAVIS, R.W., KOOYMAN, G.L. & CROXALL, J.P. 1983. Water flux and estimated metabolism of free-ranging gentoo and macaroni penguins at South Georgia. *Polar Biology*, 2, 41–46.

EL-SAYED, S.Z., BENON, P., DAVID, P. & GRINDLEY, J.R. 1979. Some aspects of the biology of the water column studied during the 'Marion Dufresne' cruise 08. *Comité National Français des Recherches Antarctiques*, 44, 127–134.

FURNESS, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. *Journal of Animal Ecology*, 47, 39–53.

FURNESS, R.W. 1981. Estimating the food requirements of seabird and seal populations and their interactions with commercial fisheries and fish stocks. *In* COOPER, J., *ed. Proceedings of the symposium on birds of the sea and shore.* Cape Town: African Seabird Group, 1–13.

FURNESS, R.W. & COOPER, J. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. *Marine Ecology Progress Series*, 8, 243–250.

GARTSHORE, N.A., STEELE, W.K. & KLAGES, N.T. In press. Summer diet of the Salvin's prion at sub-Antarctic Marion Island. *South African Journal of Zoology.*

GRAU, C.R. 1982. Egg formation in the Fjordland crested penguin (*Eudyptes pachyrhynchus*). *Condor*, 84, 172–177.

JACKSON, S. 1986. Assimilation efficiencies of White-chinned Petrels (*Procellaria aequinoctialis*) fed different prey. *Comparative Biochemistry and Physiology*, 85A, 301–303.

KENDEIGH, S.C., DOLNIK, V.R. & GAVRILOV, V.M. 1977. Avian energetics. *In* PINOWSKI, J. & KENDEIGH, S.C., *eds. Granivorous birds in ecosystems.* New York: Cambridge University Press, 127–204.

KOOYMAN, G.L., DAVIS, R.W., CROXALL, J.P. & COSTA, D.P. 1982. Diving depths and energy requirements of King penguins. *Science*, 217, 726–727.

LUTJEHARMS, J.R.E. & VALENTINE, H.R. 1984. Southern Ocean thermal fronts south of Africa. *Deep-Sea Research*, 31, 1461–1475.

MITCHEL-INNES, B.A. 1967. Primary production studies in the southwest Indian Ocean, 1961–1963. *Investigation Report of the Oceanographic Research Institute (Durban)*, No. 14, 1–20.

MOUGIN, J.L. & PREVOST, J. 1980. Evolution annuelle des effectifs et des biomasses des oiseaux Antarctiques. *Terre et la Vie, Revue d'Ecologie*, 34, 101–133.

NAGY, K.A., SIEGFRIED, W.R. & WILSON R.P. 1984. Energy utilization by free-ranging jackass penguins (*Spheniscus demersus*). *Ecology*, 65, 1648–1655.

PARKER, L.D. 1984. A contribution to the oceanology of the Prince Edward Islands. M.Sc. Thesis, Rhodes University, South Africa. 97 pp. [Unpublished.]

RICKLEFS, R.E. 1974. Energetics of reproduction in birds. *In* PAYNTER, R.A., *ed. Avian energetics.* Cambridge, Massachusetts: Nutthall Ornithological Club, 152–292.

SIEGFRIED, W.R., WILLIAMS, A.J., BURGER, A.E. & BERRUTI, A. 1978. Mineral and energy contributions of the eggs of selected species of seabirds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research*, 8, 75–87.

STEELE, W.K. & KLAGES, N.T. 1986. Diet of the blue petrel at sub-Antarctic Marion Island. *South African Journal of Zoology*, 21, 253–256.

WARHAM, J. 1963. The rockhopper penguin (*Eudyptes chrysocome*) at Macquarie Island. *Auk*, 80, 229–256.

WARHAM, J. 1971. Aspects of breeding behaviour in the royal penguin (*Eudyptes chrysolophus schlegeli*). *Notornis*, 18, 91–115.

WATKINS, B.P. 1987. Population sizes of king, rockhopper and macaroni penguins and wandering albatrosses at the Prince Edward Islands and Gough Island, 1951–1984. *South African Journal of Antarctic Research*, 17, 150–157.

WIENS, J.A. 1984. Modelling the energy requirements of seabird populations. *In* WHITTOW, G.C. & RAHN, H., *eds. Seabird energetics.* New York: Plenum Publishing Corp., 255–284.

WIENS J.A. & SCOTT, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. *Condor*, 77, 439–452.

WILLIAMS A.J. 1980. Offspring reduction in macaroni and rockhopper penguins. *Auk*, 97, 754–759.