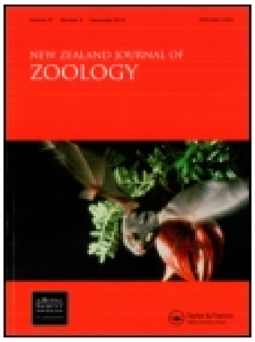

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Seasonal, geographical, and age-related variations in the diet of the yellow-eyed penguin (*Megadyptes antipodes*)

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Abstract A quantitative study of yellow-eyed penguin diet was carried out at two mainland breeding areas over a 2-year period, and at five other breeding areas over shorter time periods. Yellow-eyed penguins (*Megadyptes antipodes*) ate 26 prey species, with fish comprising 87% of the weight and 91% of the total number of prey items. Sprat occurred in the largest number of stomachs (70%) with red cod, opalfish, and squid in 49%, 42%, and 46%, respectively. Most prey items were <200 mm long. Prey were mainly pelagic species but also demersal species. The absence of inshore species in the diet and the distributions of prey species indicated that penguins travel away from the coast before beginning to feed, but remain over the continental shelf. Juvenile penguins ate more squid and less fish than adults, and weighed less. Differences in diet composition, body weights, and meal sizes were found between birds from different breeding areas, and between breeding seasons of contrasting reproductive success. Evidence from preferred prey and daily foraging patterns suggested that yellow-eyed penguins are selective feeders, and as such, are vulnerable to fluctuations in populations of their preferred prey.

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Keywords diet; prey; penguin; yellow-eyed penguin; *Megadyptes antipodes*

INTRODUCTION

Yellow-eyed penguins (*Megadyptes antipodes*) are present throughout the year at their breeding areas which are scattered along the south-east coast of New Zealand's South Island, Stewart Island, the Auckland Islands, and Campbell Island. During most of the year penguins leave the breeding area at dawn to feed and return at dusk, although this pattern may become less regular when feeding chicks (Richdale 1957). The total population is estimated at 7000 individuals, with only 600–700 pairs breeding on mainland New Zealand (J. T. Darby pers. comm.).

Recent censuses indicate that numbers have decreased since counts were last made (1936–1954) (L. E. Richdale 1942, unpublished manuscript, Hocken Library, Dunedin, New Zealand; 1957; J. T. Darby pers.comm.). Poor reproductive success seems to be because of destruction of nesting habitat and increasing predation (Darby 1985). In some seasons, starvation of chicks and adults, and low fledging weights result in mortality, and hence poor recruitment into the breeding population (van Heezik & Davis 1990). The frequency of such poor seasons may be increasing; Richdale (1957) recorded only one season with mortality resulting from starvation in 18 years, whereas starvation occurred in three years between 1983 and 1988 (van Heezik 1988).

Knowledge of diet is necessary to determine the extent to which yellow-eyed penguins depend on particular prey. The aims of this study were to outline diet composition, to describe diet in terms of prey size and variety of prey items, and to compare the diets of adults and juveniles. As variations in reproductive success were found between breeding areas (van Heezik 1988), diet was studied at several breeding areas to determine whether its composition was the same, and if not, whether differences in composition might explain variations in reproductive success. Diet was also compared between two seasons to help determine whether diet composition was related to reproductive success.

METHODS

The study animal. The yellow-eyed penguin breeds on the south-eastern coast of the South Island, New Zealand, and on Stewart, Auckland, and Campbell Islands (Falla et al. 1981). Usually two eggs are laid between late September and early October, followed by an incubation period of about 43 days (Richdale 1957). Eggs hatch in the first 3 weeks of November. During the first 6 weeks chicks are guarded by one or other of the parents, after which both parents forage each day and return to feed chicks in the afternoon or evening. Total fledging period is about 105 days, and chicks are fed right up until their departure, although frequency of feeding may taper off (Richdale 1957).

Sampling regime. The main study was carried out at two breeding areas: Nugget Point (46°20′S, 169°40′E), from March 1984 to June 1986, and Boulder Beach (45°50′S, 170°30′E), from July 1984 to August 1986. Stomach sampling was undertaken at these and six other breeding areas along the east coast of the South Island, New Zealand: Moeraki (45°20′S, 170°40′E), April –August 1984; Shag Point (45°20′S, 170°40′E), May – August 1984 and December 1984–July 1985; Bobbys Head (45°30′S, 170°35′E), March–August 1984; Penguin Bay & Hina Hina Cove (= Catlins) (46°30′S, 169°34′E), May & August 1984 and March 1985; and Falls Creek (46°30′S, 169°18′E), May 1984 and March 1985.

Breeding groups of this species are small, (5–7 breeding pairs at Shag Point, 9–17 pairs at Boulder Beach), so to minimise disturbance I visited breeding areas once monthly, except for Nugget Point (35–50 pairs) which was visited twice monthly. Penguins were caught as they came ashore at dusk.

Stomach contents were obtained using the water-flushing method (Wilson 1984). Two flushes were usually adequate to clear the stomach of its contents. The presence of small stones in the vomit confirmed that the entire contents had been flushed, as stones rest on the bottom of the stomach. Two to seven birds were sampled per evening. All penguins caught were weighed and banded. During breeding, adults were fed with blue cod (*Parapercis colias*) or yellow-eyed mullet (*Aldrichetta forsteri*) after flushing to ensure that offspring did not miss a meal. Samples were stored fresh and sorted the following day, or frozen until sorted.

Sorting techniques. Intact prey items were rarely encountered. These were measured and weighed. Loose otoliths (sagittal) were separated into left- and right-hand side, and dried at room temperature. Otolith pairs recovered from skulls were dried separately as a pair. When numbers of left- and right-hand otoliths of any one species in a single stomach differed, the number of prey in the stomach was taken as the larger number of the two. Otoliths were identified using the reference collection of Lalas (1983) and weighed. When large numbers of otoliths were present in one stomach (i.e., >50), otoliths were clumped into groups of not more than 20 similarly-sized individuals, weighed, and a mean value calculated for each size group.

Estimation of stomach contents. Fish lengths (total) and weights were estimated using the allometric equations of Lalas (1983), which relate otolith-pair weight to fish length, and fish length to fish weight. Cephalopod beaks were identified, measured (upper rostral length), and the allometric equations of Lalas (1983) applied to determine squid weights. All beaks showing excessive breakage or erosion were treated as being not from that day's foraging (van Heezik & Seddon 1990), and were excluded from the estimated stomach composition. A study of beak digestion in yellow-eyed penguins showed that all beaks had broken and abraded wings after 24 h, and after 36 h all surfaces were smooth and rounded (van Heezik & Seddon 1990). Relative to fish, the amount of squid in the diet is likely to be slightly overestimated; however, yellow-eyed penguin stomachs did not contain large numbers of beaks, and so a correction factor was not ascribed. Meal weights were estimated from the combined calculated weights of all prey species.

Contribution of each species to the diet was expressed as a mean percentage of the total calculated meal weight ingested of all stomachs sampled, mean percentage of the total number of prey items identified, and mean percentage frequency of occurrence (number of stomachs containing the species as a percentage of the total number of stomachs sampled).

Measurements of the horizontal relaxed gape of the penguins were made using Vernier calipers (accurate to ± 1mm), in order to relate gape width to sizes of prey items consumed.

Seasons are defined as follows; autumn (March–May), winter (June–August), spring

(September–November) and summer (December–February).

RESULTS

Prey species. The mean contributions of prey species in the diet of the yellow-eyed penguin from all seven breeding areas are shown in Table 1. Six fish and one squid species made up 94% of the weight and 97% of the number of prey items. None of the remaining 20 taxa made up more than 1% of the diet by weight. The diet of juveniles differed from that of adults in that it contained less fish and more squid by weight (χ^2=36.0, d.f.=1, P<0.001), (Table 2).

The percentage frequency of each length class for each season are plotted for red cod (*Pseudophycis bachus*), opalfish (*Hemerocoetes monopterygius*), sprat (*Sprattus antipodum*), silversides (*Argentina elongata*), and ahuru (*Auchenoceros punctatus*); and each weight class for arrow squid (*Nototodarus sloanii*) (Fig.1). Most prey were less than 200 mm long, although opalfish consumed were up to 350 mm long. Most squid eaten weighed less than 100 g. The mean relaxed horizontal-gape of yellow-eyed penguins was 34 mm (SD=2.2, n=187). Regression equations relating total fish length (x) to maximum body depth (y) are: red cod, y=0.191x −1.0114, (n=11, r=0.985); opalfish, y= 1.104 + 0.095x, (n=13, r=0.991). The figure for the mean relaxed horizontal-gape of yellow-eyed penguins is about the same as the maximum body depth of an opalfish of 360 mm, and a red cod of 180 mm total length.

Inter-locality variation in diet composition. Percentage contributions in terms of weight and percentage occurrences of the seven principal diet species were calculated for each of the seven breeding areas (Fig. 2). This combination of seven prey species comprised at least 87% and as much as 95% of the total calculated weight at all breeding areas. Sprat occurred in 61–84% of all stomachs from everywhere except Boulder Beach, where it was found in 49% of the total. Opalfish, red cod, and squid were found at all breeding areas in at least 23%, and as many as 65%, of the samples.

Variation in diet between the 1984/85 and 1985/86 seasons. The 1985/86 season was identified as being one of poor reproductive success (van Heezik & Davis 1990). Fledging weights were significantly lower at Nugget Point in the 1985/86 season (1984/85; $\bar{x}$=5.62 kg, SD=0.59, n=24, range, 4.3–7.1 kg, 1985/86; $\bar{x}$=4.12 kg, SD=0.96, n=15, range, 2.25–5.55 kg, t=6.1, P<0.001), but were not

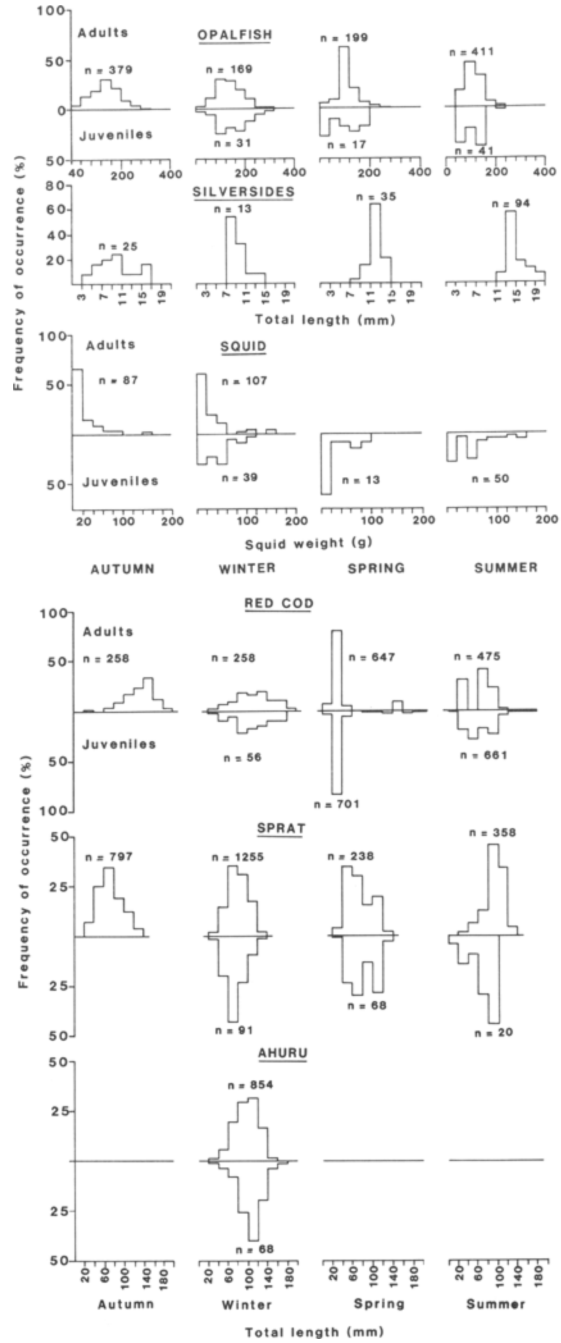

Fig. 1 Size-frequency distributions (percentage of total) of six prey species of the yellow-eyed penguin. Adult yellow-eyed penguin intake is shown above the x axis and juvenile yellow-eyed penguin below.

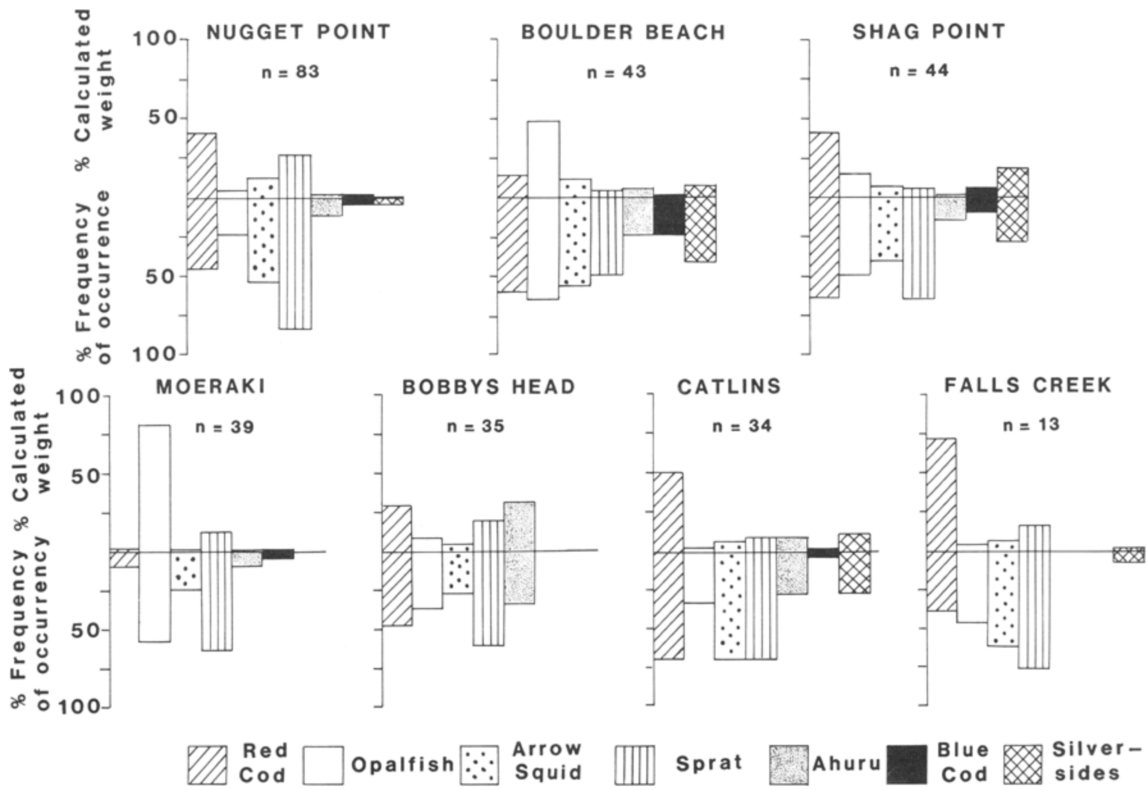

Fig. 2 Diet composition of adult yellow-eyed penguins at seven breeding areas, over one year of sampling. Numbers of penguins sampled are given as *n* values. Number of sampling dates are as follows: Nugget Point (21) Boulder Beach (9) Shag Point (11) Moeraki (7) Bobbys Head (7) Catlins (3) Falls Creek (2).

Table 1 The food of 512 adult yellow-eyed penguins from seven breeding areas on the Otago coast.

Principal species		% Caculated Weight X	SD	% Numbers X	SD	% Occurrence X	SD
red cod	*Pseudophycis bachus*	36	22	34	21	47	20
opalfish	*Hemerocoetes* spp.	22	30	15	16	44	15
arrow squid	*Nototodarus* sp.	9	7	3	2	47	18
sprat	*Sprattus antipodum*	12	6	28	15	67	11
ahuru	*Auchenoceros punctatus*	7	11	11	14	17	11
blue cod	*Parapercis colias*	2	3	1	1	6	8
silversides	*Argentina elongata*	6	7	5	6	15	16

Occurring occasionally—barracouta *Thyrsites atun*, cockabully *Trypterygion* spp., warehou, *Seriolella brama*, ling *Genypterus blacodes*, tarakihi *Nemadactylus macropterus*, hoki *Macruronus novaezelandiae*, rattails Macrouridae, hake *Merluccius australis*, giant stargazer *Kathetostoma giganteum*, N.Z. sole *Peltorhamphus novaezeelandiae*, long-snouted pipefish *Stigmatophora macropterygia*, seahorse *Hippocampus abdominalis*, silver conger eel *Gnathophis habenatus*, short-finned eel *Anguilla australis*, lamprey *Geotria australis*, warty squid *Moroteuthopsis ingens*, octopus *Octopodidae*, cuttlefish *Cephalopoda*, squillid shrimp *Heterosquilla* spp., salps Thaliacea.

significantly different at Boulder Beach (1984/85; $\bar{x}$=4.94 kg, SD=0.45, n=11, range, 4.25–6.20 kg, 1985/86; $\bar{x}$=4.83 kg, SD=0.67, n=18, range, 3.6–6.1 kg, t=0.5, P>0.05). At both breeding areas the range of weights included very light birds (<4.0 kg), and this was reflected in lower recovery rates of these fledglings as juveniles; <1% from 1985/86 compared to 26% from 1984/85 at Nugget Point, and <1% from 1985/86 compared to 18% from 1984/85 at Boulder Beach. At Nugget Point 18% of chicks starved to death.

Table 2 Composition of juvenile (82 stomachs sampled) compared with adult (512 stomachs sampled) yellow-eyed penguin diet.

	% Caculated weight		% Occurrence	
	Juvenine	Adult	Juvenile	Adult
arrow squid	49	9	44	47
red cod	29	36	58	47
blue cod	7	2	5	6
sprat	3	12	59	67
ahuru	3	7	27	17
silversides	3	6	7	15
opalfish	2	22	39	44
miscellaneous	4	6	32	39

Three kinds of fish and arrow squid made up most of yellow-eyed penguin diet between March 1984 to July 1985 at Nugget Point, and August 1984 to July 1985 at Boulder Beach, whereas in the following year (August 1985 – August 1986 at both breeding areas) the proportion of the three fish species decreased, whereas squid, blue cod and miscellaneous groups increased (Table 3).

A comparison of the two breeding seasons showed a trend of decreasing principal fish species and increasing proportions of other prey, in particular, arrow squid (Table 4, Fig. 3). Significant differences were found between the absolute quantities of most of the principal prey species or prey groups consumed in each breeding season. During a particular year there were also significant seasonal fluctuations in relative intake of various species (Fig. 3). Between early 1984 to mid-1985 sprat, opalfish, and miscellaneous species intake varied significantly at Nugget Point (Kruskal-Wallis, d.f.=12, H=23.3, H=34.5, H=44.1, P<0.05, respectively) and red cod, sprat, and opalfish varied significantly at Boulder Beach (d.f.= 7, H=19.2, H=27.1, H= 25.6, P<0.05, respectively). There was no significant difference in the relative intake of squid throughout the year at either breeding area.

Table 3 The percentage contribution of each prey species to the intake (biomass) of the yellow-eyed penguin over two years, and over two seasons (Dec–April).

% Calculated weight	year 1		year 2		P	breeding season 1		breeding season 2		P
Nugget Point										
red cod	45		41			52		13		
sprat	18	66	4	46	*	30	88	2	16	**
opalfish	3		1		Z=72	6		1		Z=146
ahuru	17		2			<1		<1		
blue cod	1		8			0		10		
squid	10		34			12		63		
miscellaneous	6		11			<1		12		
Boulder Beach										
red cod	15		3			17		3		
opalfish	53	77	32	49	*	65	93	23	29	**
silversides	9		14		Z=70	11		3	Z=100	
blue cod	2		9			3		6		
squid	15		30			4		56		
miscellaneous	5		12			1		7		

Year 1 (Nugget Point) = March 1984–July 1985, (Boulder Beach) = August 1984–July 1985
Year 2 (both breeding areas) = August 1985–August 1986.
breeding season 1 = Dec–April 1984/85, 2 = Dec–April 1985/866.
*differences between proportions tested following Zar (1984); * = P<0.05, ** = P<0.01.

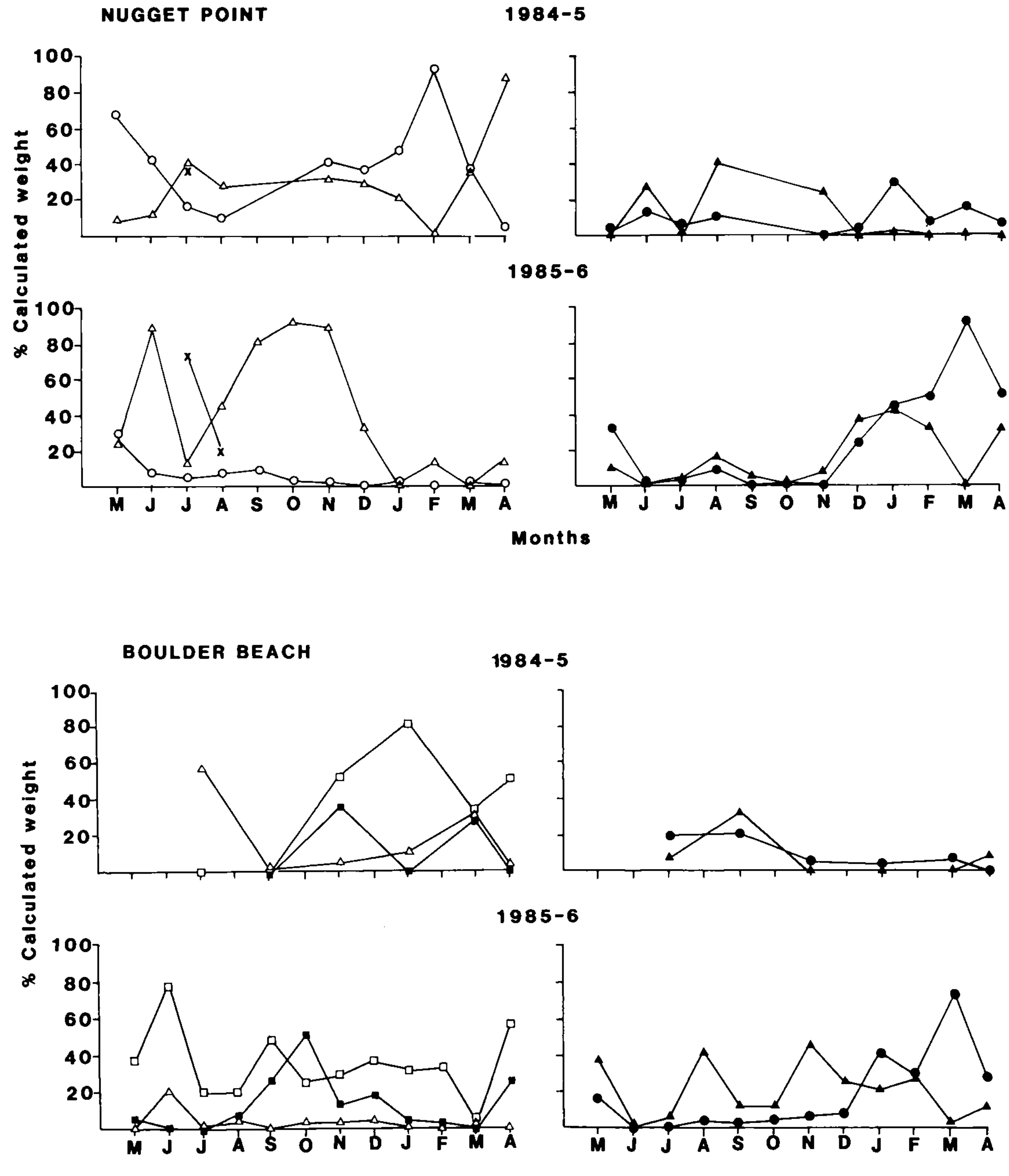

Fig. 3 Percentage contribution to the total calculated intake (weight) of yellow-eyed penguins over two seasons: (1) 1984/85: (2) 1985/86 at two breeding areas: (a) Nugget Point; (b) Boulder Beach, of six prey items: (open circle) sprat; (open triangle) red cod; (closed circle) arrow squid; (closed triangle) miscellaneous group; (open square) opalfish; (closed square) silversides; (cross) ahuru.

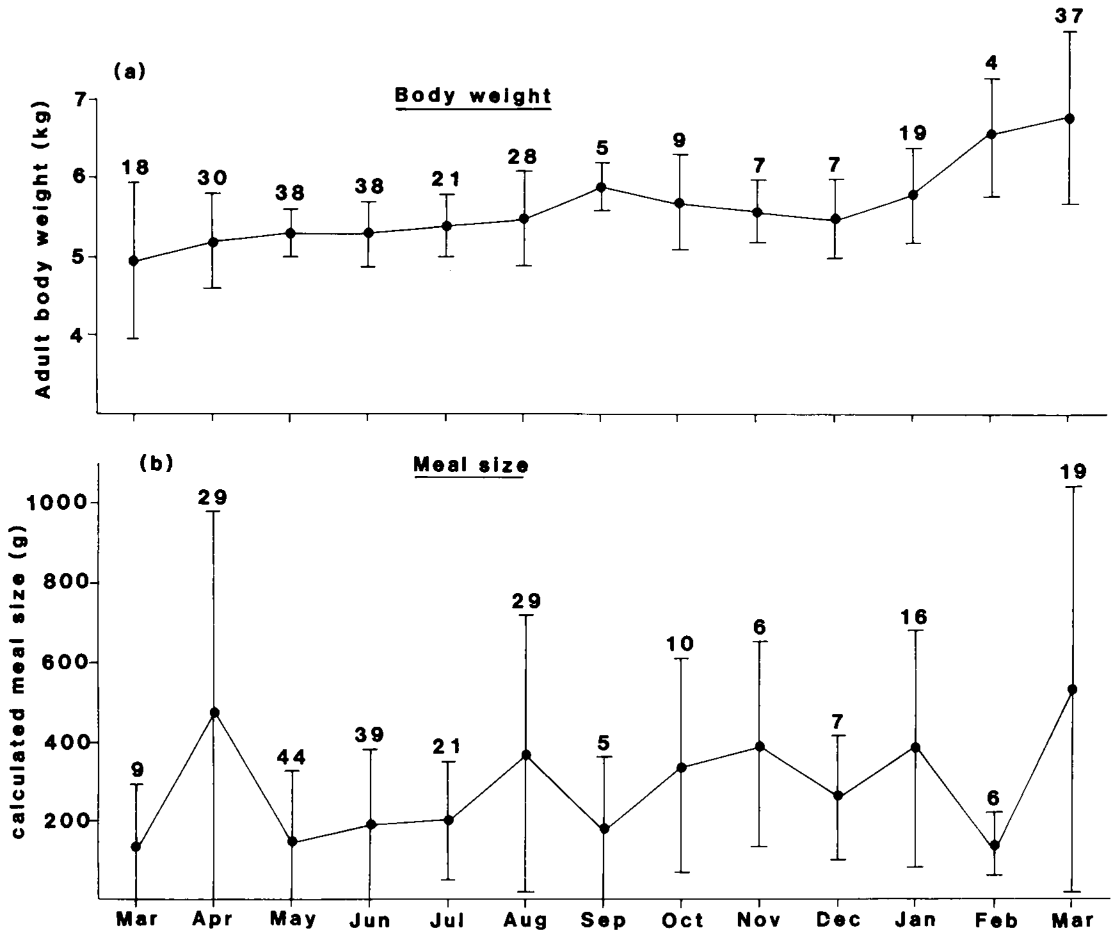

Fig. 4 Monthly means, from all study areas combined, of (a) body weight and (b) meal size of yellow-eyed penguins, ± one standard deviation. Sample sizes are given.

Table 4 Mean weights (calculated) of prey species from yellow-eyed penguin stomachs sampled at two localities during two breeding seasons (December–April). Quantities tested for significance using the Mann–Whitney μ test

	Nugget Point			Boulder Beach		
	Mean stomach weight(g)			Mean stomach weight(g)		
	1984/85	1985/86		1984/85	1985/86	
Species	n=31	n=66	P	n=14	n=24	P
red cod	137	85	ns	102	33	*
sprat	62	11	***	–	–	–
opalfish	–	–	–	402	228	*
silversides	–	–	–	67	34	ns
blue cod	0	68	–	–	–	–
squid	42	421	***	163	424	*
miscell.	6	128	***	18	117	*

*=P<0.05; ***=P<0.001.

Body weights and daily adult intake. Mean adult body weight was 5.5 kg (n=256, SD=0.70) and was heavier than the mean juvenile (first year birds) body weight of 5.1kg (n=96, SD=0.70), (t=4.2, d.f.=352, P<0.05). Mean adult body weights fluctuated significantly throughout the year (Fig. 4),(Kruskal-Wallis, H=53.3, d.f.=12, P<0.05). Variation in adult body weights between localities was also significant (Fig. 5), (Kruskal-Wallis, H=14.7, d.f.=4, P<0.05).

The mean calculated adult meal size was 340 g (n=281, SD= 390), 6% of the mean adult body weight. No significant variation was found in meal size throughout the year (Fig. 4), (Kruskal-Wallis,

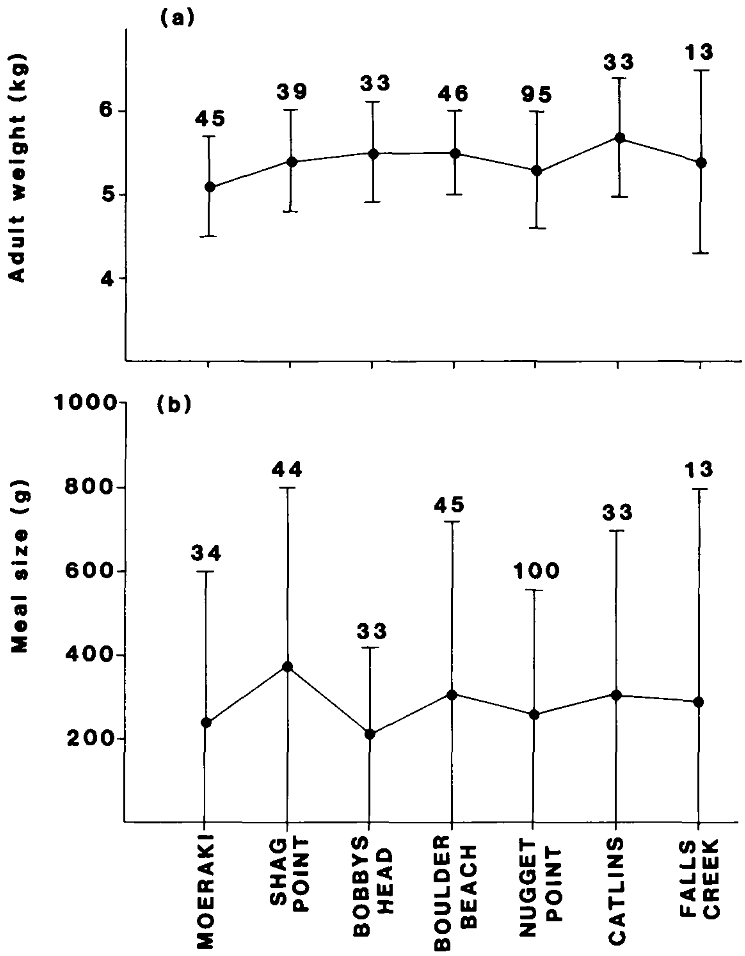

Fig. 5 Yellow-eyed penguin mean adult body weights (a), and mean meal weights (b) ± one standard deviation, at seven breeding areas: MO – Moeraki; SP – Shag Point; BH – Bobbys Head; BB – Boulder Beach; NP – Nugget Point; CA – Catlins; FC – Falls Creek. Sample sizes are given.

H=20.9, d.f.=12, 0.10 >P>0.05), but meal size did vary between breeding areas (H=27.1, d.f.=5, P<0.05), (Fig. 5).

Of the 281 adult stomachs, 3% were empty and 5% contained more than 20% of mean adult body weight (=1100 g). Otoliths of the heavy samples showed minor signs of erosion only, indicating they had been in the stomach less than 1 day (van Heezik & Seddon 1990).

Mean juvenile meal size was 366 g (n=59, SD=648), 7% of the mean juvenile body weight, and was not significantly different from mean adult meal size (t=0.4, d.f.=338, P>0.05). The standard deviation of juvenile meal size was larger than that for adults, indicating a wider range of meal sizes were taken by juveniles. Of 66 juveniles 3% were empty and 7% contained meal sizes of a weight equal to more than 20% mean juvenile body weight.

DISCUSSION

Diet composition. Twenty-six prey species were found, with fish comprising about 85% of the calculated weight and 94% of the total number of prey items. Sprat occurred in the largest number of stomachs sampled (70%), with red cod, opalfish, and arrow squid occurring in just under half. Although squid were taken in small quantities throughout much of the first 18 months their contribution was possibly overestimated as beaks can be retained undamaged for periods longer than a day (van Heezik & Seddon 1990). The relatively higher quantities of squid eaten in the second season was not because of large numbers of small beaks; rather, a few large individuals were often regurgitated almost intact. Hence, the increase in squid consumption was not caused by increased retention of large numbers of beaks. Conversely, rapid digestion of small otoliths ingested early in the foraging trip may result in an underestimation of fish species with small otoliths, i.e., sprat and small opalfish. Planktonic krill were absent from the diet, even though *Munida gregaria* and *Nyctiphanes australis* are abundant in the area north of 46°30′S, although not in every year nor continuously throughout each year (Zeldis 1983; Murdoch 1985). The juvenile diet differed from that of adults in that squid comprised the largest portion of the biomass (47%), but meal size was similar. Very few adult and juvenile penguins had empty stomachs.

Prey size. Fish larger than 200 mm were seldom taken. Opalfish as long as 300 mm were captured, but this species is more slender than other prey, and longer individuals could be ingested whole. In many fish-eating birds that swallow their prey whole, it is the width of the gape rather than the length of the bill that restricts ingestion of large prey (Swennen & Duiven 1977; Hulsman 1981). Hence, it is the maximum depth of the fish's body rather than its length that determines whether it can be swallowed. Slightly larger individuals will be able to be swallowed when the beak opens wide and the width of the gape is stretched. In yellow-eyed penguins the mean relaxed gape size corresponded to opalfish of about 350 mm length and red cod about 180 mm long, values close to the maximum size of each of these prey species taken by yellow-eyed penguins.

Yellow-eyed penguins were feeding on adult opalfish, sprat, and ahuru, juvenile silversides and arrow squid, and 0+ year class red cod (Ayling & Cox 1984; Mattlin et al. 1985), (Fig. 1). Juvenile yellow-eyed penguins took relatively less fish than adult penguins, but the sizes of prey in diets of juveniles were similar to those in adult diet. In spring, most red cod found in stomachs were postlarval (20–60 mm length) individuals from the previous winter's spawning.

Prey distribution. All prey species eaten are found over the continental shelf: sprat, ahuru, silversides, juvenile arrow squid, and young red cod are all mid-water species, opalfish are distributed demersally, and blue cod are common over and near rock reefs (Ayling & Cox 1984; Mattlin et al. 1985). Juvenile arrow squid are most abundant towards the surface, i.e., at depths of 50–100 m, where they have been found to represent 47% of the total commercial squid catch (Mattlin et al. 1985). This suggests that yellow-eyed penguins forage over the continental shelf, mainly from the upper portion of the water column, but also demersally (see also Seddon & van Heezik 1990).

Feeding appears to occur away from the coast, as shallow coastal-fish species common in marine shags (Lalas 1983) are absent in the diet of yellow-eyed penguins, even though penguins and shags nest in the same areas. The brief appearance of ahuru in the diet in winter may reflect a short period of inshore feeding, although it may also because of a change in the distribution of ahuru, which may move further off the coast during spawning.

Variations in diet composition. Seasonal and inter-locality differences in body weight, meal size, and reproductive success may be caused by variations in diet composition. Adults in this study gained weight before egg-laying and then slowly lost weight during the incubation and guard phases of the breeding cycle (Fig. 4).

Changes in adult body weight were not paralleled by changes in meal sizes, indicating that other factors also play a role in determining body condition, such as frequency of feeding, the effort required to capture food, physiological demands associated with feeding offspring or moulting, and meal composition. When feeding frequencies of breeding adults were lower, (in October and November incubating birds undergo unrelieved spells at the nest ranging from 1–7 days; Seddon 1989), meal sizes tended to be relatively larger. In January some non-breeding adults begin to gain weight in preparation for moulting. High body weights in February and March are of pre-moult adults. The physiological demand of a 40% weight gain before moulting is accompanied by larger meal sizes than at any other time. Daily intake amounting to 45% body weight was observed in captive jackass penguins *Spheniscus demersus*, 1–2 weeks before visible signs of moulting, and after completion of the moult (Gailey-Phipps & Sladen 1982).

Meal composition varied seasonally and between breeding areas. Consumption of some species was not continuous throughout the year; e.g., ahuru only appeared in the diet in July and August. Between breeding areas principal species remained the same, but the percentage contribution of each of these species to the total biomass differed (Fig. 2). However, sprat was found consistently in the largest proportion of stomachs at all breeding areas except Boulder Beach; opalfish, red cod, and squid appeared consistently in samples from all breeding areas, and made up a larger part of the diet during the months of chick feeding and moult.

A comparison of two seasons of contrasting reproductive success (1984/85, 1985/86) showed that the combined proportion of the three principal fish species decreased from 88% to 16% at Nugget Point, and from 93% to 29% at Boulder Beach (Table 3). However, meal sizes were heavier in the second season (Table 4), with the difference being made up by a large increase in the amount of squid (from 12% to 63% at Nugget Point, and 4% to 56% at Boulder Beach), as well as increases in blue cod at Nugget Point and miscellaneous species at both localities. Quantities of sprat were smaller in 1985/86 at Nugget Point, and red cod and opalfish at Boulder Beach. Larger quantities of squid, blue cod, and miscellaneous species were eaten at Nugget Point and Boulder Beach. During the second season it was not so much an absolute food shortage as a shortage of certain prey items.

Prey species and diet quality. Sprat is an oily fish and provides a richer energy source than opalfish or red cod. The presence of fat increases the caloric value of fish considerably (Johnson 1920), and the northern sprat *Sprattus sprattus* has been shown (Harris & Hislop 1970) to have the highest caloric values of any of the species eaten by puffins (*Fratercula arctica*). Harris (1984) found puffins grew best on oil-rich fish, and Gailey-Phipps & Sladen (1982) suggest that the fat content of fish is important in diets of captive penguins, as health problems occur when penguins are kept on low-fat diets. Seasons of abundant sprat in yellow-eyed penguin diet may result in high fledging weights and optimal growth rates (e.g., Nugget Point 1983/84 and 1984/85 seasons, van Heezik & Davis 1990), whereas low quantities of sprat may result in depressed growth rates and starvation. The value of sprat is also indicated by its high frequency of occurrence in all stomachs sampled. Arrow squid and red cod are of low oil content (Vlieg 1984a, b). A diet of squid resulted in slow growth, low fledging weights, and poor plumage development when fed to jackass penguin chicks (Heath & Randall 1985).

High caloric values of sprat may also explain the larger inconsistencies between mean meal size and adult body weight at two of the breeding areas; at Bobbys Head meal sizes were low but body weights were high, possibly because 20% of the intake consisted of sprat. At Shag Point, meal size was highest but body weights less than average, and diet consisted of opalfish and juvenile red cod and silversides, which are likely to be of low caloric value since fat content of other species has been shown to be less in juvenile forms (Harris 1984). That squid has a lower nutritional value is also suggested by lower body weights of juvenile penguins, which eat proportionately more squid and less fish.

Selective or opportunistic feeding. Certain characteristics of foraging indicate that yellow-eyed penguins are more likely to be selective than opportunistic: (1) only seven species comprise between 87–98% of their total intake over all mainland breeding areas sampled; (2) krill was not eaten; (3) the absence of inshore species; (4) the low mean number of species recovered from any one meal; and (5) the difference in diet between adult and juvenile penguins. Juvenile pelicans *Pelecanus occidentalis* (Brandt 1984) and juvenile jackass penguins (Wilson 1985) have been identified as being less efficient foragers than adults. Juvenile jackass penguins are not able to swim as fast as adults, rendering certain species of prey unavailable to them. The time that juvenile yellow-eyed penguins spend at sea after leaving the natal breeding area is also the period of highest mortality (Richdale 1957), and even after returning to land their weight is lower than adult weight. Juveniles may be forced to spend as much time feeding as possible, and be less selective than adults in their choice of prey.

Penguin diet and fisheries. Seabirds and industrial fisheries may exist in direct competition for pelagic fish (Furness 1978; Furness & Cooper 1982; Duffy 1983). The overexploitation of pelagic fish stocks by the commercial purse-seine fishery has been suggested as being responsible for declining jackass penguin numbers, as jackass penguins are selective in their choice of prey (Crawford & Shelton 1978; Randall & Randall 1986). The selectivity of the yellow-eyed penguin also makes it vulnerable to decreased availability of its principal prey species. Red cod and arrow squid are fished commercially off the east coast of the South Island. However, interactions between penguins and fisheries are complex, and competition between seabirds and fisheries cannot be invoked to explain changes in seabird numbers until the competition mechanism has been examined (Duffy et al. 1987). The inference that penguins are competing with fisheries because they take large amounts of a commercially exploited species need not necessarily apply (Duffy et al. 1987). The reduction in sprat and opalfish consumption observed in this study was not directly attributable to fishing, as they are not commercially exploited species in this region. A reduction in consumption may not be caused by a decrease in prey population numbers, but may result from a natural change in the availability of these species. The increasing incidence of breeding seasons of poor reproductive success indicate feeding conditions may have changed since Richdale's study (1957) during the years 1936–1954. More information on prey populations and interrelationships between trophic levels within the marine system is required before any cause-effect conclusions can be made concerning the impact of commercial fisheries on reproductive success.

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