DIET OF THE YELLOW-EYED PENGUIN *MEGADYPTES ANTIPODES*, SOUTH ISLAND, NEW ZEALAND, 1991–1993

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SUMMARY

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Stomach samples were collected by using the water-flushing technique from Yellow-eyed Penguins *Megadyptes antipodes* from the south-east coast of the South Island, New Zealand. One hundred and ninety-eight samples were collected from 86 individuals during four breeding seasons from February 1991 to December 1993. Unworn otoliths were used to reduce bias in prey biomass calculations. Forty-three types of prey were identified, including 37 fish species, four cephalopod species and several crustacean species. Seven species (six fish and one squid) constituted 90% of the estimated biomass and 60% of the total prey number, and all fish comprised 90% of diet biomass and 80% of prey number. Opalfish *Hemerocoetes monopterygius*, a demersal (bottom-dwelling) species, was the most important component of the diet in terms of the total biomass, numbers and frequency at which it was eaten. Other important biomass components included demersal species and species often found near the bottom, such as Blue Cod *Parapercis colias*, Arrow Squid *Nototodarus sloani,* Silverside *Argentina elongata* and Red Cod *Pseudophycis bachus*, although pelagic prey such as Sprat *Sprattus antipodum* and krill *Nyctiphanes australis* were also eaten. Mean lengths of the main prey species were 5–17 cm and most prey items were < 25 cm long. There was significant temporal variation in diet composition for several prey species, such as increased proportions of Red Cod and Opalfish, and decreased Blue Cod and Arrow Squid in 1992/93. This coincided with a year of improved breeding success. Individual variation in diet may reflect differing foraging ranges. Nests with adults that were sampled for diet had lower breeding success than other nests.

INTRODUCTION

The Yellow-eyed Penguin *Megadyptes antipodes* is one of the world's rarest penguin species, and is found only in the New Zealand region (Marchant & Higgins 1990). The population on the South Island of New Zealand has undergone several declines, and at least partial recoveries, in recent years. The most dramatic population decrease occurred in early 1990, when about 150 adults died around the Otago Peninsula (Gill & Darby 1993). At the time there were estimated to be only 320 breeding pairs on the South Island from a total population of < 2100 pairs (Darby, in Marchant & Higgins 1990, Moore 1992). Although an unidentified toxin was suggested as a possible cause of the die-off in 1990 (Gill & Darby 1993), changes or shortages of food have usually been implicated in other years (Richdale 1957, van Heezik & Davis 1990, van Heezik 1990). There was some concern that the frequency of these poor seasons was increasing during the 1980s (van Heezik 1990) and that the species had become endangered on the South Island (Marchant & Higgins 1990).

In response to the 1990 event, we began a study involving diet, radio-telemetry and dive recording (Moore *et al.* 1995) which aimed to investigate how Yellow-eyed Penguins utilize the marine environment. By studying diet in consecutive breeding seasons at two areas of the South Island, New Zealand, we hoped to illustrate any geographic and temporal differences in the diet, whether it had changed since the previous study in the mid-1980s (van Heezik 1990), and how it might change during a season of food shortage.

METHODS

Study areas were the A1-Highcliff area of Boulder Beach (Otago Peninsula), and Long Point (Catlins), 110 km apart on the south-east coast of New Zealand's South Island (Fig. 1). The sampling regime (Table 1) encompassed two full breeding seasons (1991/92, 1992/93) at both localities and part of two more (1990/91, 1993/94) at Boulder Beach. At Boulder Beach, the same set of 14 birds was radio-tracked in October, December and January 1991/92 and 1992/93. Over three or four nights, these birds were caught preferentially, and extra birds completed a sample size of about 10 birds. At Long Point (and in July–August at Boulder Beach), birds were taken opportunistically on one or two evenings per sampling period, except in February, when radio-tracked birds were targeted. During the pre-breeding stage, birds were considered as breeders if they nested in later months. At Boulder Beach 77% of samples were from birds which were breeding at the time and at Long Point 51% of birds were known to be breeding. Breeding success was monitored at the main study areas and other areas for comparison: Sandfly Bay (Otago Peninsula); Nugget and Hayward Points (Catlins).

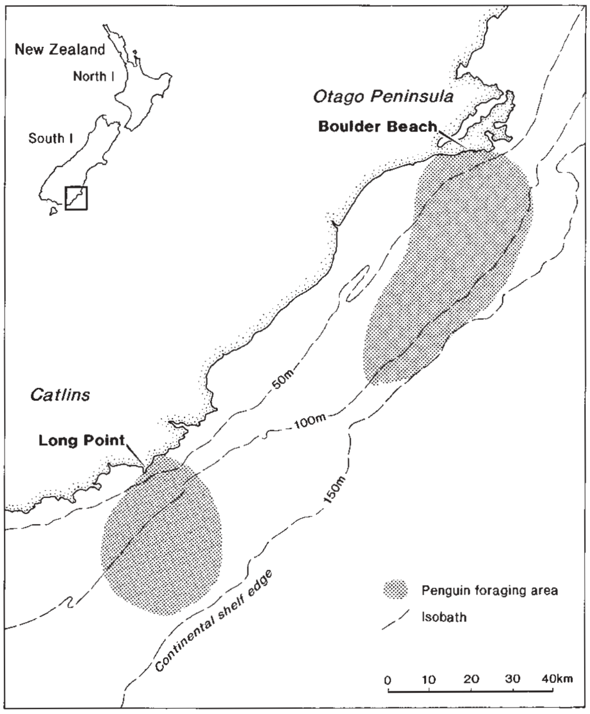

Fig. 1. *Location of study areas for Yellow-eyed Penguin diet, their approximate foraging range (Moore* et al. *1995) and offshore bathymetry, south-east coast of the South Island, New Zealand.*

The standard water-flushing technique for collecting diet samples from penguins was used (Wilson 1984, Duffy & Jackson 1986, van Heezik 1990) and afterwards they were fed Black Oreo *Allocyttus niger* fillets as a replacement meal.

Otoliths were identified using a reference collection from van Heezik (1990), photographs from Lalas (1983), and verification by C. Lalas (pers. comm.). Otoliths from skulls were weighed as pairs. Single otoliths were sorted into left and right for each species, and those from the most abundant side were weighed and the figures doubled to estimate pair mass. Cephalopod identifications were from Dell (1952), Clarke (1986) and M.J. Imber (pers. comm.). Some items were excluded from analysis because it was assumed that they were secondary prey (polychaetes, salps, pteropods, copepods) or taken up with stones (several types of shell), fell into the sample during the sieving process (terrestrial arthropods) or were parasites of the birds (nematodes).

It was assumed that most of the otoliths in the stomachs represented the remains of fish eaten during the day preceding capture, however there is likely to be a bias towards species with large otoliths; e.g. small otoliths such as Sprat *Sprattus antipodum* can be digested in eight hours (van Heezik & Seddon 1989). This could not be corrected for. Cephalopod beaks are much less digestible than fish parts, and therefore over-represented in stomachs (Wilson *et al.* 1985), but as they show signs of wear after 16 hours (van Heezik & Seddon 1989), we used only intact beaks of cephalopods for our diet analysis.

Calculation of fish size (total length or fork length, depending on the tail structure of the species) and biomass from otolith paired masses followed equations by Lalas (1983). An exception was the equation for Silverside *Argentina elongata:* $FL = 44.2 \times OW^{0.4}$, $FW = 3.1 \times 10^{-6} FL^{3.15}$, where FL = fork length (mm), OW = paired otolith mass (mg), FW = fish mass (g), which was calculated from raw data used by van Heezik (1990). Opalfish *Hemerocoetes monopterygius*: $FL = 52.8 \times OW^{0.5}$, $FW = 1 \times 10^{-5} FL^{2.82}$; *H. artus*: $FL = 49.7 \times OW^{0.4}$, $FW = 4 \times 10^{-6} FL^{3.01}$ had power curves fitted from data supplied by C. Lalas (unpubl. data). This differs from the single equation for Opalfish used by van Heezik (1990) which tended to overestimate maximum known sizes (Nelson 1979). The above equations could give a maximum error of 20–30% in estimation of prey biomass (Lalas 1983). Cephalopod lower beak rostral length was used to calculate biomass (Clarke 1986).

TABLE 1

Number of diet samples and date of collection from Yellow-eyed Penguins at Boulder Beach and Long Point, 1991–1993

Stage of breeding cycle	Boulder Beach date	No.	Long Point date	No.
Pre-breeding	23–24 Jul 1991	7		
	8 Aug 1991	6	5 Aug 1991	15
	14–15 Jul 1992	11	19, 23 Jul 1992	6
	20–21 Jul 1993	10		
Incubation	27–31 Oct 1991	11	24–26 Oct 1991	5
	28–30 Oct 1992	11	6 Nov 1992	1
	25–28 Oct 1993	10		
Early chick-rearing	12–15 Dec 1991	12	18–19 Dec 1991	11
	8–10 Dec 1992	12	11,17 Dec 1992	8
	9–11 Dec 1993	10		
Late chick-rearing	11–12 Feb 1991	9		
	28–31 Jan 1992	12	13 Feb 1992	9
	18 Feb 1992	1	11–12 Feb 1993	10
	26–27 Jan 1993	11		
Total samples		133		65
Total individuals		43		43

Erosion of otoliths leads to the underestimation of the original prey size (Gales 1988, Robertson *et al.* 1994). Previous workers (e.g. van Heezik 1990) used all otoliths in a stomach, regardless of the degree of wear, to calculate fish size. To reduce the bias this creates (Gales 1988) we used an "unworn otolith" method, whereby the average mass of unworn otoliths in a stomach was used to estimate prey size and masses for the other items which had worn otoliths. Where there were no unworn otoliths for a prey type in a sample, the average for the same locality and sampling period was used.

As in previous studies, the calculated prey biomass was analysed in terms of overall percent mass, based on the combined mass of prey from all samples. The statistic used in most of our analyses though was mean percent mass per sample, to limit the effect of very large samples and allow the use of analysis of variance testing.

An analysis of variance model was formulated (*Datadesk 4.1*, Data Decription Inc. PO Box 4555, Ithaca NY 14852-4555, U.S.A.) for the mean percent mass data which allowed for uneven sample sizes and predicted the results expected from a more even sample design. Although the percent compositional data did not satisfy normality assumptions of analysis of variance, the standard arc-sine transformation did not either, because of the multitude of zeros. Consequently, percent figures were used and the most significant effects were looked for. The initial model used six factors: site (n = 2), year (n = 4), month (n = 4 stages of the annual cycle), breeding status (whether breeding or not at time of sampling), sex (n = 2) and individual (n = 73); and two factor interactions of all factors except individual, which was nested within both sex and site. Birds of unknown sex were removed from analysis, leaving an overall sample size of 184 stomachs of the original 198. The multivariate analysis of variance allowed us to assess the evidence for significant effects, and allowed for correlations between different prey.

RESULTS

Between February 1991 and July 1993, 198 stomach contents from 86 individual penguins were collected from Boulder Beach and Long Point. There were 24 410 prey items from 43 species or prey categories (Table 2). Most categories of fish represented different species, on the basis of recognisable differences in otoliths, although some, such as Triplefins Tripterygiidae, may have represented more than one species. Most Opalfish otoliths appeared to be of *H. monopterygius*, and some of the larger ones were *H. artus* but because differences are minor, some small *H. artus*, and species such as *H. pauciradiatus*, may have been incorrectly identified as *H. monopterygius*. Krill were mainly *Nyctiphanes australis*, but at least two other unidentified species were eaten. Crustacea were an assemblage, including Lobster Krill *Munida gregaria* (19% by number), crabs (22%), amphipods (27%), isopods (9%), shrimps and mantis shrimps. Stones were found in 86% of samples (mean mass per sample 16.1 g, s.d. = 15.7).

Of 19 961 fish prey, 24% were identified from otoliths dissected from skulls, a further 39% had otoliths that were considered relatively unworn, and the remaining 37% showed varying degrees of wear. Prey with small otoliths (e.g. Sprat, Graham's Gudgeon *Grahamichthys radiata*) generally had unworn otoliths.

Seven species (six fish and one squid) constituted 90% of the estimated biomass ("unworn otolith method") and 60% of the total prey number (Tables 2,3). All fish combined comprised 90% of diet biomass and 80% of prey number.

Frequency of occurrence of prey in the diet

Crustacea, Opalfish, Arrow Squid *Nototodarus sloani* and Blue Cod *Parapercis colias* occurred in the greatest number of stomachs (>50%). Six other prey occurred in 30–50% of samples, six in 10–30%, and the remainder were in less than 10% of samples (Table 2).

Prey number

The median number of prey items per stomach was 66 (lower to upper hinge 34–123, range 3–1575, n = 198). Only 7.6% of samples had >250 prey items. Two samples had 1200–1400 krill, one sample had 1498 Graham's Gudgeon and four samples had 600–1100 Red Cod *Pseudophycis bachus*. Small prey, such as Red Cod, have low medians, but the occasional high numbers skew the frequency distribution and give high means (Table 3). Large prey, such as Blue Cod and Arrow Squid, were eaten in low numbers (max. = 21 and 22, respectively). Ahuru *Auchenoceros punctatus* were eaten infrequently but usually in moderate numbers, resulting in the highest median (Table 3). Opalfish were also eaten in moderate numbers (max. = 200).

Opalfish, Red Cod and krill each constituted >10% of the total number of prey items eaten in all 198 stomachs combined (Tables 2, 3). Mean percent number of prey per sample (Table 3) was less affected by individual samples with numerous items; e.g., Opalfish had the highest mean, because of its high frequency of occurrence and the high proportion of samples where it reached >75% of prey number, whereas Red Cod and Krill/Crustacea had lower means because there were fewer samples in which the species predominated (Table 3).

Mean prey diversity was 6.3 taxa per stomach (s.d. = 2.4, range 1–14). This was positively correlated with calculated meal mass ($R = 0.399$, $P < 0.001$).

Prey size

Mean prey sizes, as calculated from unworn otoliths, were between 49–173 mm for the main prey types (Table 2). All common prey were < 300 mm long, and the majority were < 250 mm. The longest intact prey item was a Lamprey *Geotria australis* (500 mm, 101 g). Seasonal patterns of prey size are shown in Fig. 2. Different size classes eaten at different times of the year are clearly shown for Red Cod, Silverside, Ahuru, Tarakihi *Nemadactylus macropterus* and Sprat. Of the main prey, only Blue Cod shows little seasonal pattern in size, apart from a mode of 170–190 mm in October and December. Although the range in sizes of Opalfish were similar at each time of the year, size frequency distributions showed a modal peak around 90–140 mm in December–February and 140–180 mm in later months. Small Arrow Squid of < 20 g were eaten at all times, but larger squid (20–240 g) were more often taken in January–February.

Prey mass

The mean masses per prey item, as calculated from unworn otoliths, cephalopod beaks or intact specimens, are shown in Table 2. The average Opalfish was equivalent in mass to 618 krill, and the average Blue Cod was equivalent to 35 Red Cod.

TABLE 2

Prey types identified in the diet of Yellow-eyed Penguins 1991–1993, and diet composition in terms of % mass of the total calculated diet biomass, % prey number and % occurrence, mean mass and length of prey (* calculated from unworn otoliths except: [a] from intact prey , [b] from worn otolith or [c] estimated where no formulae available)

Prey type	**% Calculated mass**		**% No.**	**% Occ.**	**Mass (g)***			**Length (mm)***		
	All otoliths	**Unworn**			**Mean**	**s.d.**	**N**	**Mean**	**s.d.**	**N**
Crustacea										
Krill *Nyctiphanes australis*	0.1	<0.1	15.2	37.4	0.02[a]	0	100			
Other Crustacea	0.1	0.1	3.1	80.3	0.28[a]	0.1	26			
Cephalopods										
Arrow squid *Nototodarus sloani*	14.4	10.3	1.7	59.6	55.0	72.7	418			
Moroteuthis ingens	<0.1	<0.1	<0.1	1.5	6.8	3.4	3			
Octopus *Octopus ?maorium*	0.1	0.1	0.4	26.8	1.1	0.9	103			
Sepioloidea pacifica	<0.1	<0.1	<0.1	1.0	1.8	2.9	5			
Fish										
Lamprey *Geotria australis*	5.9	4.2	0.4	14.6	101.3[a]	15.8	3			
Sprat *Sprattus antipodum*	2.2	1.8	6.8	34.8	2.2	2.4	1436	63.2	22.8	1436
Sandfish *Gonorynchus gonorynchus*	<0.1	<0.1	<0.1	1.0	3.0[a]		1			
Silverside *Argentina elongata*	10.0	8.7	5.4	40.9	16.2	6.7	768	133.1	18.0	768
Smelt *Retropinna retropinna*	<0.1	<0.1	<0.1	2.5	2.0	1.0	5	66.6	10.9	5
Lanternfish *Lampanyctodes hectoris*	<0.1	<0.1	<0.1	1.5	0.5[b]		1			
Ahuru *Auchenoceros punctatus*	4.8	4.9	5.8	13.6	7.7	2.3	710	114.0	13.9	710
Rock Cod *Lotella* sp.	<0.1	<0.1	<0.1	1.0	0.6	0.1	4	21.2	1.8	4
Red Cod *Pseudophycis bachus*	7.4	8.3	22.3	45.5	2.7	10.3	3834	48.9	28.3	3834
Hoki *Macruronus novaezelandiae*	0.2	0.2	1.0	11.6	1.6	1.1	219	75.7	14.8	219
Rattail *Coelorinchus* sp.	0.3	0.2	0.1	1.5	14.8	4.7	34	159.9	15.5	34
Ling *Genypterus blacodes*	0.2	0.2	<0.1	3.5	41.0	44.3	4	198.2	71.5	4
Sea Horse *Hippocampus abdominalis*	<0.1	<0.1	<0.1	1.0	0.01[a]		1			
Pipefish *Lissocampus filum*	<0.1	<0.1	<0.1	0.5	2.3[a]		1			
Sea Perch *Helicolenus percoides*	<0.1	<0.1	<0.1	0.5	58.5		1	154.5		
Tarakihi *Nemadactylus macropterus*	2.3	2.3	0.9	39.4	22.2	20.6	131	99.6	30.8	131
Stargazer *Kathetostoma giganteum*	<0.1	<0.1	<0.1	2.0	10.1	2.5	7	73.2	6.4	7
Sanddiver *Tewara cranwellae*	<0.1	<0.1	<0.1	0.5	2.1[a]		1	81.9[a]		1
Opalfish *Hemerocoetes ?artus*	1.0	0.7	0.2	12.6	26.6	5.8	57	184.0	11.9	57
Opalfish *Hemerocoetes monopterygius*	27.6	35.2	22.7	78.3	14.2	11.4	2060	142.3	39.3	2060
Blue Cod *Parapercis colias*	18.3	18.4	1.8	54.5	94.3	74.4	247	172.8	48.1	247
Triplefin Tripterygiidae	1.3	1.1	1.5	36.9	7.1	3.9	251	80.1	12.4	251
Gudgeon *Grahamichthys radiata*	0.2	0.1	8.2	4.5	0.2	0.1	2008	33.0	1.8	2008
Barracouta *Thyrsites atun*	0.1	<0.1	<0.1	1.0	43.0	10.2	2	205.3	15.1	2
Blue Warehou *Seriolella brama*	1.2	1.1	2.0	13.6	5.5	5.5	304	62.5	19.9	304
Silver Warehou *Seriolella punctata*	2.8	1.7	0.1	5.0	186.3	51.5	17	218.9	19.6	17
Lemon Sole *Pelotretis flavilatus*	<0.1	<0.1	<0.1	0.5	2.5[b]		1			
Sole *Peltorhamphus novaezeelandiae*	0.2	0.2	0.1	0.5	21.9	8.4	9	140.3	16.0	9
Leatherjacket *Parika scaber*	<0.1	<0.1	<0.1	0.5	2.2		1	51.3		1
?Gadiformes	<0.1	<0.1	0.1	3.5	3.0[c]					
?Ling	<0.1	<0.1	<0.1	1.0	4.2[a]		1			
?hake/Eel	0.1	0.1	<0.1	1.0	116.4	90.4	2	291.1	77.9	2
?Sea Perch	<0.1	<0.1	<0.1	1.0	4.7	2.3	2	71.0	10.7	2
?Scorpionfish	<0.1	<0.1	<0.1	1.0	2.0[c]		1			
?Opalfish	<0.1	<0.1	<0.1	0.5	20.9[c]		1			
Unknown L	<0.1	<0.1	<0.1	0.5	2.0[c]		1			
Unknown O	<0.1	<0.1	<0.1	0.5	0.5		1	24.5		1

The mean sample wet mass was 430 g (s.d. = 278, range 0.6–1410 g, n = 198). This overestimated stomach content mass because of extra water retained in the slurry during the seiving process; e.g., birds weighed before and after stomach flushing had a mean mass difference of 332 g (s.d. 137, range 100–600 g, n = 14) compared with the mean wet mass of 434 g for the same samples. A few individuals were almost empty of stomach contents, either because of advanced digestion or lack of prey eaten. The mean meal mass, calculated from unworn otoliths, was 1131 g (s.d. = 708, median = 1003, range 37–4754 g, n = 198), compared with a mean of 812 g if all otoliths were used, regardless of wear.

Analysis of variance for log meal size using factors of site, year, month, sex, breeding status, individual and several interactions, found that only month was significant ($F_{3,184} = 4.2$, $P<0.01$). This was because October meals (mean = 1635 g) were significantly larger than in other months. Foraging trips tend to be longer at that time and for birds with known foraging times (<1 day at sea, 2, 3, 4 and 6 days), there was a positive correlation between number of foraging days and meal mass ($R = 0.229$, $P<0.05$, n = 73). However, the relationship was not significant when one sample larger than 2000 g was removed from the sample. Also, for day-trips when the exact time at sea was known (mean = 13.1 h, range 8.7–16.3 h, n = 29) there was a poor correlation between meal size and time at sea ($R = –0.183$, $P = 0.3$).

Opalfish had the highest percent mass (>30%) of the total calculated prey biomass and the mean percent mass per sample (Tables 2,3). Blue Cod and Arrow Squid were the only other species which made up >10% of biomass, followed closely by Silverside and Red Cod (Table 2). In the Other Fish category, Lamprey (5.6% mean mass) was a major component, followed by Tarakihi, Sprat and Silver Warehou *Seriolella punctata* (Table 2).

When the main species are ranked for percent mass, number and occurrence and these ranks are added together (Duffy & Jackson 1986), Opalfish, Red Cod, Blue Cod, Arrow Squid, Silverside, Sprat and Ahuru were the seven most important species. Because prey mass should have a more direct relationship to nutrition than prey number or frequency of occurrence, further more detailed analyses will deal with mean percent mass only.

Diet variation

Fig. 3 illustrates the mean percent mass of the main prey types at the two sampling localities. The diet composition was similar at both sites for most prey except Ahuru, which was eaten mainly at Long Point in July 1991, and Blue Cod, which was eaten more at Boulder Beach.

An analysis of variance model was formulated for the mean percent mass data (see methods) of 10 species groupings: Arrow Squid, Ahuru, Opalfish (two spp.), Silverside, Blue Cod, Red Cod, Sprat, Krill/Crustacea, Other Cephalopods and Other Fish. An overall Wilks test suggested there were significant effects ($P < 0.05$) of individuals, site*year, site*month, site*breeding, year*month. In further modelling Ahuru was removed from the dataset because it had the strongest significant effects over several factors and interactions. This was because almost all penguins in July 1991 (one evening of sampling) at Long Point had eaten Ahuru, accounting for 97% of the total mass of this species. Other Cephalopods and Krill/Crustacea were also deleted because they were minor mass components. Individual models were then produced for the other seven prey types, using the six standard factors and any interaction terms which produced significant effects. This allowed us to look more closely at the effects for each prey type, while ignoring the correlations inherent in the earlier model. The significant factors and interactions are summarised in Table 4. The table compares the observed and “predicted” mean percent masses. Not shown in Table 4 are the significant effects of individuals which occurred for Arrow Squid ($P < 0.05$), Opalfish ($P < 0.01$), Silverside ($P < 0.001$), Blue Cod ($P < 0.001$), Sprat ($P < 0.05$) and Other Fish ($P = 0.06$), i.e. some individuals ate more of these prey types than did others.

The significant effects of year and month*breeding for Arrow Squid were caused by less being eaten in 1992/93 than in other years, and much more being eaten in January–February, particularly by the non-breeder/failed breeder group (Table 4). Significant factors for Opalfish were year*month (Table 3) because of high proportions in October 1992 and 1993 and low in July 1993. Silverside was significant for month, year*site and site*sex (Table 4), mainly because little was eaten at Boulder Beach in the first and last years or during January–February. Blue Cod had significant effects of site and

TABLE 3

Yellow-eyed Penguin diet composition in terms of mean and median number (non-zero) of prey eaten per sample, percent number of total prey items (N = 24 410 items), mean percent number of prey items per sample (N = 198 samples), percent of total calculated biomass eaten (224 kg) and mean percent per sample

	Mean no.	Median no.	No. samples occurs	% No.	Mean % no.	s.d.	% mass	Mean % mass	s.d.
Krill/Crustacea	26.1	4	171	18.3	1.1	19.0	0.1	0.2	0.7
Arrow Squid	3.5	2	118	1.7	5.1	12.2	10.3	10.8	20.8
Ahuru	52.8	45	27	5.8	6.0	20.6	4.9	4.7	17.8
Opalfish (2spp.)	36.3	19	154	22.9	33.1	31.3	35.9	31.3	31.7
Silverside	16.1	5	81	5.4	11.0	24.1	8.7	9.3	22.7
Blue Cod	4.1	3	108	1.8	5.8	11.7	18.4	18.0	25.2
Red Cod	60.5	5	90	22.3	10.6	21.9	8.3	8.4	18.3
Sprat	26.0	4	64	6.8	2.5	10.4	1.8	3.5	13.1
Other Ceph.	2.1	1	54	0.5	0.6	2.0	0.1	0.2	1.0
Other Fish	23.3	4	152	14.5	12.2	18.5	11.6	13.6	21.3

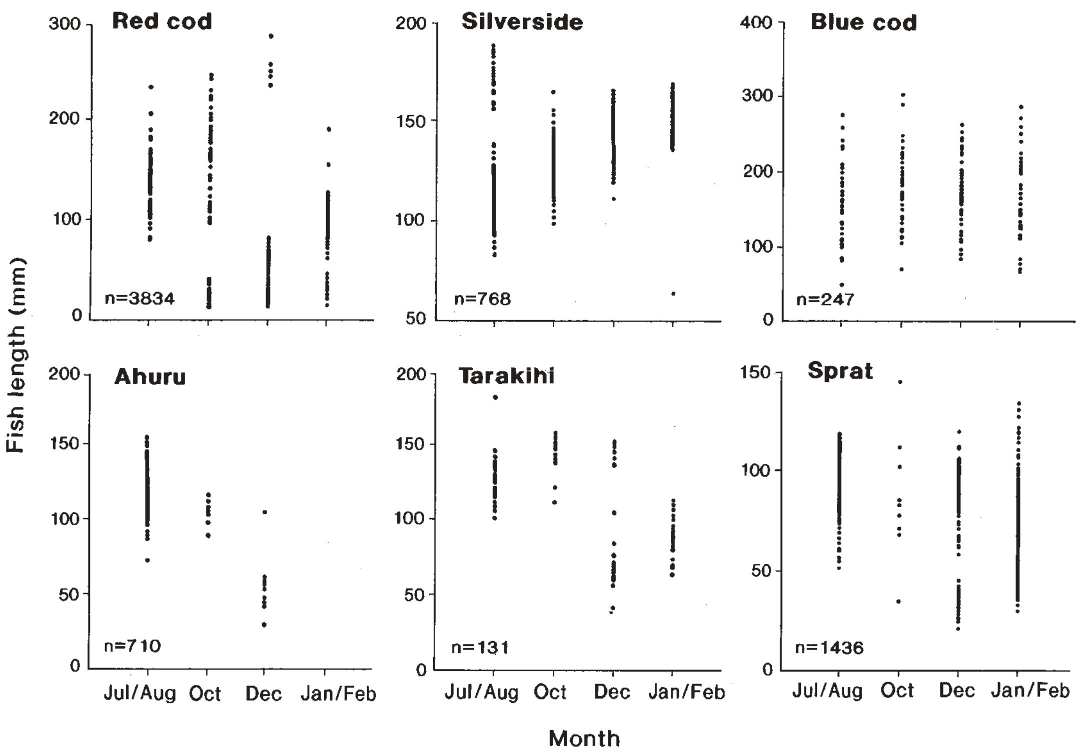

Fig. 2. Lengths of Yellow-eyed Penguin prey at different times of the year (July–August, October, December, January–February), calculated from sizes of unworn otoliths in penguin stomachs. Data are pooled for different years (1991–1993) and sites.

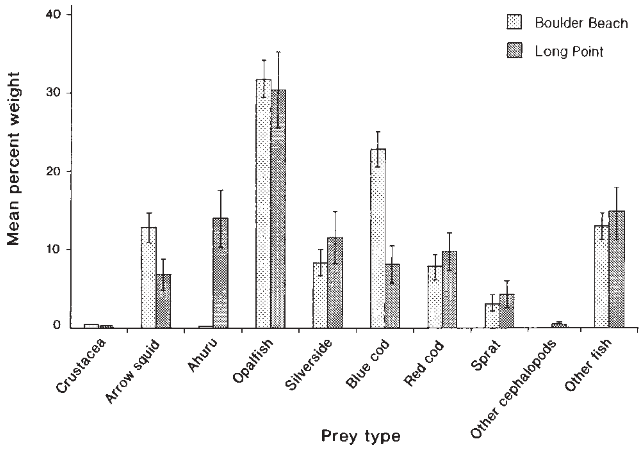

Fig. 3. Mean percent calculated mass of main prey groupings per Yellow-eyed Penguin stomach sample at Boulder Beach and Long Point. Data are pooled for different years (1991–1993) and standard errors shown (n = 198 samples).

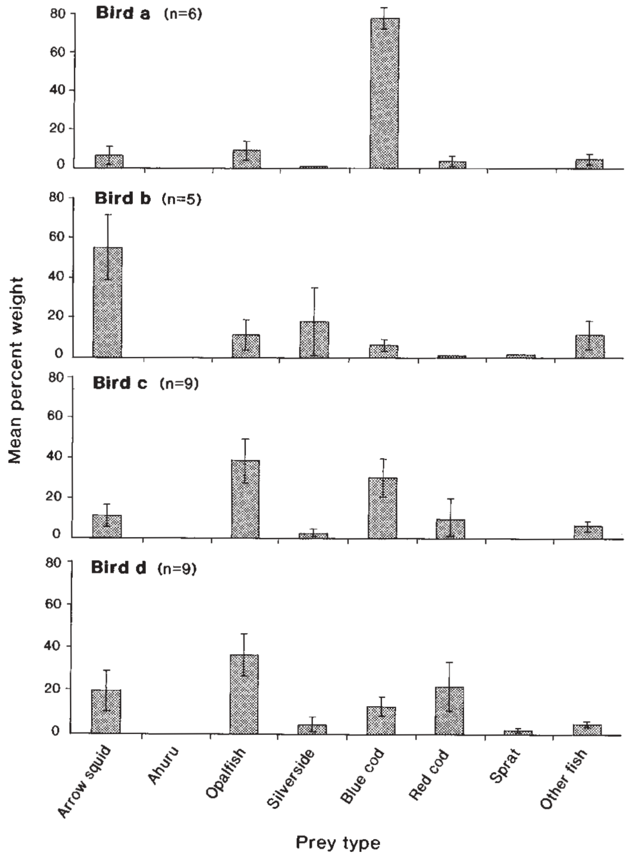

Fig. 4. Individual variation in mean percent calculated mass of main prey groupings per Yellow-eyed Penguin stomach sample, four examples (a–d) of birds with multiple samples. Data are pooled for different years (1991–1993) and standard errors shown.

year*month (Table 4), since more was eaten at Boulder Beach, particularly in October–December 1991, whereas little was eaten in October 1992 or July 1993. Red Cod had a significant interaction of year*month, caused by higher percent mass figures in December 1992 to July 1993 than previously. The Sprat model produced significant effects of year*month, with higher proportions eaten in July 1992, January–February 1993 and December 1993 than at other times, and females ate more of this species than did males. The final category, Other Fish, had interactions of year*month (Table 4). One of the causes of this was Lamprey, which was eaten in July–August every year at both sites.

Individual variation in diet

During the study, 40 individuals were sampled for diet once, 23 twice and the remaining 23 were sampled 3–9 times (but usually only once per sampling period). Some of the penguins with multiple samples were shown to have consistent patterns of dietary intake, and were different from the average pattern, examples of which are shown in Fig. 4. The first example (Fig. 4a) consistently ate more Blue Cod, and the second (Fig. 4b), although showing variation, ate more Arrow Squid. The other two birds illustrated had an average type of dietary intake. Another example of individuality was shown by one bird, which was sampled five times, and was responsible for 79% of the total number of krill eaten by all birds. The two specimens of Sea Horse *Hippocampus abdominalis* found during the study came from another individual which ate higher than average levels of Silverside (70–72% prey number, 49–68% prey mass, n = 3). We have little measure of daily variation in diet, apart from two birds that were sampled twice within two to three days. One showed consistently high levels of Opalfish,

TABLE 4

Comparison between observed (Obs.) mean % mass and that predicted (Pred.) from an ANOVA model. Prey types and interaction terms are those that have significant ($P < 0.05$) differences between predicted means (ahuru, krill-crustacea and other cephalopods are not shown)
BB = Boulder Beach, LP = Long Point. 1990 = 1990/91 annual cycle

		Mean % mass of prey									
Interaction		**Opalfish**		**Blue Cod**		**Red Cod**		**Sprat**		**Other fish**	
Year*month		**Obs.**	**Pred.**	**Obs.**	**Pred.**	**Obs.**	**Pred.**	**Obs.**	**Pred.**	**Obs.**	**Pred.**
1990	February	29.2	26.8	21.8	7.8	0.3	3.0	0	3.3	6.1	25.7
1991	Jul–Aug	16.2	17.1	7.0	15.1	9.0	1.7	1.7	4.2	18.0	16.8
	October	40.9	15.4	36.2	36.5	3.9	1.4	0.1	0.6	7.4	4.5
	December	45.6	44.5	24.2	25.5	0.01	0	0	0.8	9.4	5.6
	Jan–Feb	33.7	26.8	15.5	8.2	0.3	5.4	0.02	1.9	3.6	5.7
1992	Jul–Aug	42.8	42.8	17.1	14.0	0	0	7.7	11.4	14.5	17.5
	October	33.9	62.6	17.2	1.0	7.1	0	0	2.8	22.2	34.9
	December	23.8	34.2	16.9	11.6	20.9	21.4	0.8	0	21.7	11.4
	Jan–Feb	27.9	17.0	15.0	7.4	16.4	22.6	16.9	15.2	8.0	13.5
1993	Jul–Aug	15.2	7.5	1.4	0	20.2	22.0	1.7	2.1	48.4	57.0
	October	33.3	61.9	37.2	23.4	1.4	9.5	0.2	0	4.1	8.0
	December	36.1	33.0	15.0	10.7	16.1	16.4	13.2	8.5	9.0	19.0
P-value			*0.003*		*0.02*		*0.005*		*0.04*		*0.001*

Arrow Squid		
Year	**Obs.**	**Pred.**
1990	41.7	15.0
1991	10.7	17.1
1992	7.0	8.6
1993	10.8	15.5
P-value		*0.002*

Silverside			
Year*site		**Obs.**	**Pred.**
1990	BB	0.04	12.8
1991	BB	12.2	9.9
	LP	14.1	18.7
1992	BB	10.3	12.2
	LP	7.0	2.5
1993	BB	1.3	3.3
			0.002

Silverside		
Month	**Obs.**	**Pred.**
Jul–Aug	10.7	5.5
Oct	7.9	7.4
Dec	13.0	10.9
Jan–Feb	5.1	0
		0.006

Arrow Squid			
Breed*month		**Obs.**	**Pred.**
Bred	Jul–Aug	5.4	5.0
	Oct	5.6	4.9
	Dec	4.2	7.6
	Jan–Feb	20.1	23.7
Nonbr.	Jul–Aug	3.5	9.6
	Oct	9.5	11.2
	Dec	2.8	0.8
	Jan–Feb	53.0	49.5
			0.002

Blue Cod		
Site	**Obs.**	**Pred.**
BB	22.8	15.9
LP	8.1	1.6
P-value		*0.03*

Silverside			
Site*sex		**Obs.**	**Pred.**
BB	male	4.4	4.4
	female	11.3	14.7
LP	male	12.8	7.2
	female	3.6	0
			0.01

Sprat		
Sex	**Obs.**	**Pred.**
male	1.3	0
female	6.4	3.6
		0.02

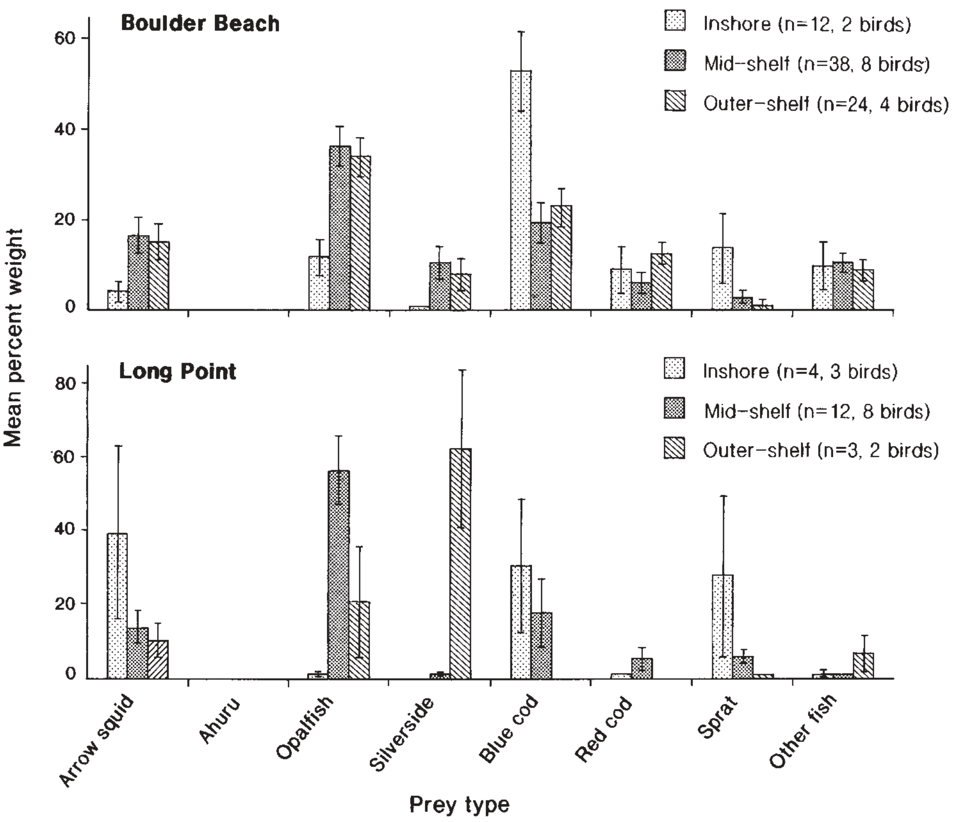

Fig. 5. *Comparison of mean percent calculated mass of main prey groupings per stomach sample of radio-tracked Yellow-eyed Penguins at two sites. The birds were categorised as predominantly inshore, mid-shelf or outer-shelf feeders on the basis of their centre of activity of foraging range. Data are pooled for different years (1991–1993) and standard errors shown.*

TABLE 5

Yellow-eyed Penguin breeding success, fledging age, fledging mass and adult body mass during separate breeding seasons

	1990/91[a]		1991/92		1992/93		1993/94	
Breeding success	**No. chicks/nest**	**No. nests**	**No. chicks/nest**	**No. nests**	**No. chicks/nest**	**No. nests**	**No. chicks/nest**	**No. nests**
Boulder Beach								
Diet nests[b]	1.0	4	0.73	11	0.79	14	0.73	15
Other nests	0.64	11	1.4	15	1.54	13	1.38	16
Sandfly Bay	0.57	7	1.27	15	1.67	15	0.85	13
Long Point								
Diet nests[b]			1.0	10	1.64	14		
Other nests	0.36	11	0.92	12	1.29	17	1.34	35
Nugget/Hayward Point	0.27	11	0.75	16	1.4	15	1.58	12
Chick age and mass	**Mean**	**s.d., N**	**Mean**	**s.d., N**	**Mean**	**s.d., N**	**Mean**	**s.d., N**
Chick fledging age (days)[c]	104	3.7,15	111	8.4,44	103	6.8,56	104	6.1,42
Chick fledging mass (kg)[c]	5.6	0.6,15	5.2	0.7,43	5.8	0.6,56	5.8	0.5,29
Adult mass (kg)[d]	5.8	0.5,14	5.6	0.5,83	5.8	0.4,54	5.6	0.5,33

[a] Most nests were reduced to single egg nests by Department of Conservation staff to safeguard adults from a predicted food shortage (Darby & Paterson 1991), therefore chick production is not comparable with other years.

[b] Nests where one or both adults had diet sample(s) taken during the year.

[c] Mean for Boulder Beach / Sandfly Bay. Fledging age is the difference between estimated hatching date (error usually 0–2 days) and fledging date (error usually ±4.5 days). Fledging masses are the last mass taken before the chick leaves for sea.

[d] Masses of birds (males and females combined) caught coming ashore after feeding at sea.

but the other changed from Blue Cod to Opalfish as the dominant mass component.

Individual differences in diet may relate to foraging location. Radio-tracking of penguin foraging ranges was conducted during February 1990/91, October, December and January 1991/92 and 1992/93 at Boulder Beach and February 1991/92 and 1992/93 at Long Point (Moore *et al.* 1995). Although foraging ranges overlapped, they were categorized as inshore, mid-shelf and outer-shelf feeders, based on the centres of activity of their radio fixes (approximately <5, 5–16, >16 km from the nearest shoreline). Note that Figure 4a was an inshore feeder, Figure 4b was on average a mid-shelf feeder (although at times travelled farther than the others) and Figures 4c, d were outer-shelf feeders. Figure 5 illustrates the mean % mass data for radio-tracked birds that had diet samples taken. The main differences shown at Boulder Beach were that inshore feeders ate less Opalfish and more Blue Cod than their mid-shelf and outer-shelf counterparts. They also ate less Arrow Squid and Silverside, but more Sprat. At Long Point, inshore feeders also ate less Opalfish and outer-shelf feeders ate the most Silverside, on average.

Breeding success

Breeding success is summarized in Table 5. Deaths were attributed to starvation (from prior mass loss), injury or trampling in the nest, or predation (wounds or confirmed losses at neighbouring nests), but often the cause of death or disappearance was uncertain. Despite control of predators (Stoats *Mustela erminea*, Ferrets *M. putorius* and feral Domestic Cats *Felis catus*), there were occasional outbreaks of predation (e.g. Sandfly Bay in 1993/94), resulting in lower breeding success (Table 5). Apart from 1992/93, when no chick deaths were positively attributed to starvation, at least 5–13% of chicks died from this cause each year. These were a result of food shortage, poor parenting or loss of a parent. In the first two years, a few chicks starved to death late in the rearing period.

At Boulder Beach, nests with adults that had diet samples taken produced fewer chicks than other nests (Table 4; Pearson Chi-Square = 16.8, d.f. 2, $P < 0.001$ for comparison of number of nests with 0,1 or 2 chicks for the last three years combined). At Boulder Beach in 1990/91 and at Long Point, diet-sample nests had similar or higher success than other nests (Table 5). This was partly biased by successful breeders in February being selected to have transmitters and subsequently being sampled for diet, but the nests that were sampled earlier had similar success to other nests (1.2 and 1.26 chicks/nest, respectively; data too sparse for Chi-Square test). Nests at Boulder Beach may have been more susceptible to disturbance because it was more likely for diet samples to have been taken from both partners, more than once a year, and in consecutive years. However, there was a non-significant trend to higher success (0.95 chicks per nest; n = 21) for highly disturbed nests (multiple applications of transmitters and one to four diet samples for one or both adults) than nests with adults that were only sampled once or twice a year (0.57 chicks per nest; n = 21).

Disregarding the first year of study (because eggs were removed), 1991/92 had significantly lower success (Pearson Chi-Square = 10.1, d.f. 4., $P < 0.05$ for comparison of 0,1 and 2 chick nests) because of a high proportion of failures at Catlins breeding areas (Long, Nugget and Hayward Points). In 1991/92, chicks were lighter at Otago Peninsula sites (Table 5; ANOVA: $F_{3,139} = 9.0$, $P < 0.001$) and older ($F_{3,153} = 12.4$, $P < 0.0001$) at fledging time than in other years, but adult masses did not vary significantly.

DISCUSSION

Prey ecology

Yellow-eyed Penguins at Boulder Beach (Otago Peninsula) and Long Point (the Catlins) ate a wide range of species, although only a few were eaten in sufficient numbers and mass to be considered important. Opalfish, a widespread demersal (bottom-dwelling) New Zealand genus (Ayling & Cox 1982), was the mainstay of the diet, comprising the greatest calculated mass eaten, the highest total number of prey items, and occurring in the second highest number of stomachs. Most were *Hemerocoetes monopterygius*, which is abundant within the northern range of Yellow-eyed Penguins (South Island, Stewart Island), and is found in 4–178-m deep water (Nelson 1979). Because Opalfish seldom exceed 25 cm (Nelson 1979, Ayling & Cox 1982), all size classes are available to penguins.

The ecology of penguin prey, particularly of the juvenile and small size classes, is poorly understood. Because of this, van Heezik (1990) considered that penguins were likely to feed mainly from the upper portion of the water column. However, in addition to Opalfish, other important prey are predominantly demersal, or often found close to the bottom, e.g. Red Cod (including at least a proportion of juveniles; Beentjes 1992, 1995), Silverside, Ahuru, Tarakihi and Triplefin (Ayling & Cox 1982, Paulin *et al.* 1989). Even Arrow Squid, which are found at the surface at night, school near the bottom during the day (Gibson 1995), and juveniles (<19 cm) comprise 47% of bottom trawls (Mattlin *et al.* 1985). Furthermore, dive depth data has shown that penguins often forage at or near the bottom (Moore *et al.* 1995). Prey which are probably pelagic species include Sprat (Ayling & Cox 1982) and krill (Young *et al.* 1993), although the latter may migrate diurnally (Blackburn 1980). Lamprey are known as parasites of other fish, but judging by the quantities consumed by albatrosses at South Georgia, they may also be free-swimming in their marine phase (Potter *et al.* 1979). Most prey of Yellow-eyed Penguins are either juveniles (e.g. Arrow Squid), small size classes (e.g. Red Cod, Blue Cod) or adults of species that do not grow beyond 25–30 cm (e.g., Silverside, Ahuru and Sprat).

Comparison with a previous study

Despite a decrease in sample size from 1984–1986 (512 samples from seven areas; van Heezik 1990) to 1991–93 (198 from two areas) there was an increase in prey diversity (26 species, including four not found in our study; cf. 43 types). This is partly an artefact of prey categorisation, since prey identified as one species in 1984–1986 were split to two-three species in 1991–1993 (e.g. Opalfish, Warehou, Sole; Table 2). Most of the difference in diversity comes from 16 prey types that were only found once or twice in 24 410 items, and seven of these were of uncertain identification (Table 2). Of the remaining “new” species, three occurred in 2–4% of samples in low numbers, while Graham’s Gudgeon was a numerous but very small prey.

A notable difference between the two studies was the reported lack of krill and other crustacea in 1984–1986 (van Heezik 1990). Because they occurred only occasionally in stomach samples, it was considered likely to have been secondary prey released from fish or squid stomachs (Y.M. van Heezik pers. comm.). In contrast, we found one penguin which ate large numbers of *Nyctiphanes australis* and it occurred in 37% of all stomachs, although usually in low numbers (< 5). Other crustaceans, including *Munida gregaria*, occurred in 77% of samples, but to what extent they may have been secondary prey cannot be determined.

In 1984–1986, Red Cod, Opalfish, Sprat, Arrow Squid, Ahuru, Silverside and Blue Cod (in order of importance) comprised 94% of the total mass consumed at seven areas (Table 6; van Heezik 1990). In 1991–1993 these species were also important (86% total mass at two areas), but the top seven species were Opalfish, Blue Cod, Arrow Squid, Silverside, Red Cod, Lamprey and Ahuru. Because the seven areas varied in predominance of prey species, Boulder Beach data only are compared in Table 6. Whereas acknowledging that different sampling regimes will have contributed to variation in the figures, the main similarity between the two study periods is that Opalfish was the most important prey and Red Cod, Sprat and Ahuru were less important than at the collective seven study areas in 1984–1986. The most notable difference is the higher proportion of Blue Cod in 1991–1993 (Table 6).

The trend in meal size between the two Yellow-eyed Penguin studies was inconsistent. The average meal size for 1984/85 was only 340 g and increased to about 710–840 g in the following year, although the higher level occurred at Boulder Beach in both years (van Heezik 1990: Table 4). The increased consumption of poorer quality food such as squid and Blue Cod was thought to be the reason why meal sizes were larger in 1985/86 (van Heezik 1990). In contrast, the mean meal size for 1991–1993 of 812 g (or 1131 g if unworn otoliths were used to calculate biomass) did not vary significantly between years.

Food shortage and quality

One of the aims of our study was to investigate the effects of food shortage, however no major shortage was apparent subsequent to the population crash of 1989/90. Numbers of birds nesting in our five study areas have increased (49 nests in 1990/91, 83 in 1991/92 and 103 in 1994/95), although similar increases at other areas were caused by the proportion of adults breeding rather than recruitment (M. Efford & J.T. Darby pers. comm.). Also there has been moderate to high mean breeding success of 1.21 chicks produced per nest (s.d. = 0.18, range 1.03–1.39, n = 3 years 1991–1994; combined data from five breeding areas, Table 5), compared with 1.09 chicks per nest from four areas in 1936–1953 (calculated from Richdale 1957) or 1.13 chicks per nest at eight areas in 1981–1986 (calculated from Darby & Seddon 1990). Of our years of study, 1991/92 had the lowest overall level of breeding success in terms of chick production, fledging masses and development time (Table 5).

Some trends in our study, although less marked, were similar to van Heezik (1990). Years of high breeding success (1984/85, 1992/93, 1993/94) when compared with those of poorer breeding success (1985/86, 1991/92) showed higher incidence of Red Cod and Opalfish, and lower proportions of Squid and Blue Cod (Tables 4, 6). Sprat, although a minor component, also showed an increase in 1992–1994. Opposite trends between the two studies are shown for Silverside and miscellaneous prey. A dietary shift was implicated in causing high chick and juvenile mortality, slower chick growth, lower fledging masses and delayed moult, particularly at Nugget Point in 1985/86 (van Heezik & Davis 1990). Because of its importance at Nugget Point, Sprat was identified as a key species for Yellow-eyed Penguin nutrition (van Heezik 1990, van Heezik & Davis 1990). By implication, Red Cod and Opalfish may also be nutritious prey, and Squid and Blue Cod of poor quality.

The relationship between prey species and nutrition is likely to be complex, and our assumptions are hindered by the paucity of data on chemical composition of prey, and how this changes seasonally or with age. Van Heezik (1990) suggested that Sprat would provide a richer energy source than Opalfish or Red Cod, based on high energetic values and oil composition of large (>104 mm) Northern Hemisphere Sprat *Sprattus sprattus* (Harris & Hislop 1978). However, small *S. sprattus*, in the size range normally eaten by Yellow-eyed Penguins, had intermediate oil and energy levels (Harris & Hislop 1978). Other known oil and energy levels of prey do not match what we would expect from the above trends in consumption. Red Cod has low values (Vlieg 1984a, Pickston *et al.* 1982), Blue Cod has low oil content but higher energy levels (Johnson 1920, 1921, Vlieg & Body 1988) and Arrow Squid has an oil content and energy level in the range of most of the above fish prey (Vlieg 1984b). It may be that digestibility of protein is more important than the oil content or energy value (Harris & Hislop 1978, Heath & Randall 1985). For example, squid is considered a poor diet for penguins because of a poor ability to assimilate its protein, and creation of an ion imbalance and calcium deficiency (Heath & Randall 1985).

TABLE 6

Yellow-eyed Penguin diet composition at Boulder Beach during 1984–1986 (van Heezik 1990: Tables 1–2) and 1991–1993. Overall % mass was calculated using all otoliths (both worn and unworn)

	% Calculated mass					
	All sites	Boulder Beach		Boulder Beach		
	1984–1986	1984/85	1985/86	1991/92	1992/93	1993/94
Red Cod	36	15	3	1	11	12
Opalfish	22	53	32	25	29	31
Arrow Squid	9	15	30	21	10	9
Ahuru	7	0	0	0	1	0
Blue Cod	2	2	9	33	19	22
Silverside	6	9	14	12	12	2
Sprat	12	}	}	0.2	2	4
Miscellaneous	6	}5	}12	9	16	21

Prey selection

To what extent Yellow-eyed Penguins are generalists, eating the most abundant and easily captured prey, or specialists, selecting the most nutritious prey, cannot be determined without data on prey availability. Van Heezik (1990) suggested they were selective, based on the small number of main prey and low diversity per stomach, the lack of krill or inshore species, and the difference in diet between adults and juveniles, the latter eating proportionally more squid. Yellow-eyed Penguins might then be vulnerable to decreased availability of their principal prey species (van Heezik 1990). Randall & Randall (1986) suggested that the high incidence of a few fish species, especially anchovy *Engraulis capensis*, in the diet of African Penguins *Spheniscus demersus* indicated selectivity. However, they also pointed out that the favoured prey species were probably the most abundant or available prey. Some Yellow-eyed Penguin prey species have spatially and temporally patchy distributions (e.g. Red Cod, Beentjes 1995), so, the differences in penguin diet between sites and years could reflect these differences in prey availability. During our study it was noted at times that some radio-tracked birds confined their foraging close inshore for short periods, indicating that prey availability or location changed over short time-scales. Individual differences in diet could relate to the availability of prey in different foraging zones, rather than active selectivity. For example, the bird which ate proportionally high levels of Blue Cod foraged inshore, and was likely to have been in more rocky habitat favoured by Blue Cod. This diet preference may have developed with age, since the same bird had not eaten Blue Cod when it was sampled twice in 1984–1986 (van Heezik 1990, raw data), or abundance of this species may have changed. Six of the other nine birds that were sampled during both studies showed similarities in diet, although sample sizes for comparison were low.

Prey abundance and fisheries

Some temporal changes in prey abundance and penguin diet may also be shown by the annual catches of commercial fisheries. Reported annual catches of the Red Cod fishery peaked in 1984/85, decreased by 78% over the next two years and did not reach high levels again until 1992/93 (Annala 1994). There is some similarity in the Yellow-eyed Penguin diet composition trend, with the proportion of Red Cod being highest in 1984/85 and 1993/94 (Table 6), although a lag would be expected between a year of high penguin consumption (< 2 year-old fish) and one of high catch in the fishery (3–4 year old fish, Beentjes 1992). The jig fishery catch tonnage and fishing effort for Arrow Squid peaked in 1983/84 and decreased over the next two years, although catch per day increased in 1985/86 at a time when penguin consumption also increased (Table 6). Subsequent fishing effort and catch of squid varied from a peak in 1988/89 to very low (including low catch per day) in 1991/92 and increasing the following year (Gibson 1995). Conversely, consumption of Arrow Squid by penguins decreased (Table 6). Blue Cod catch increased after 1985 to the highest level in 1992/93, although this may relate to new methods being used (Annala 1994). Penguin consumption of Blue Cod was also higher in the latter time period (Table 6), suggesting a change in abundance.

Over-exploitation of fish stocks has been implicated in seabird population declines, e.g., guano birds of Peru (Duffy 1994) or the African Penguin in southern Africa (Randall & Randall 1986). Direct competition with fisheries by Yellow-eyed Penguins is probably limited because they eat juveniles and sub-adults (i.e. small size classes) of commercial species, they are not solely reliant on these prey, and generally they do not overlap with the main fishing zones; e.g., the main Red Cod fishery is north of Otago Peninsula (Annala 1994), and the Arrow Squid fishery is usually near the edge of the continental shelf (A. Shaw pers. comm.). Although the mean size of Red Cod has decreased considerably since earlier this century, there are natural fluctuations in abundance from high mortality, short lifespan, fast growth and recruitment variation (Beentjes 1992, Annala 1994). Similarly, squid, being an annual species, has a variable and unpredictable biomass between years, which is independent of fishing pressure (Annala 1994, Gibson 1995). There may be indirect effects of fisheries activities that are impossible to estimate, such as changes to the food chain, or problems of bycatch mortality of non-commercial species. There is also the concern that fisheries activities directly kill penguins, as more than 50 birds were reported drowned in set nets over a 10-year period (J.T. Darby pers. comm.).

Environmental change

Environmental changes and their effects on prey abundance, although poorly understood, are the most plausible explanations for variations in Yellow-eyed Penguin survival and breeding success. There has been a perception that years of poor foraging have increased (van Heezik 1990) but as early as the 1930s, Richdale (1957) suggested that poor breeding success or high mortality of juveniles and adults were caused by "some unusual event at sea affecting the food supply." The worst season of 18 years was 1938/39, but there were five other years of below average adult survival and/or breeding success (Richdale 1957).

Because penguins are adapted to cold or cool water Southern Hemisphere systems (Croxall & Lishman 1987), warm sea temperatures tend to be deleterious; e.g. causing breeding failures of Galapagos Penguins *Spheniscus mendiculus* (Boersma 1978) and a decrease in numbers of Rockhopper Penguin *Eudyptes chrysocome* (Cunningham & Moors 1994). ENSO (El Niño Southern Oscillation) events, or large-scale, irregular sea-saw variation (every two to seven years) in atmospheric pressure associated with anomalous warming of the tropical Pacific Ocean (Mysak 1986, Wilson 1991), cause dramatic short-term effects in sea surface temperature and salinity, weather patterns, winds, currents, turbulence and sea level (Mysak 1986). These in turn affect primary productivity and fish survival and migration, for example causing the crash in the anchovy fishery off the coast of Peru in the early 1970s (Barber & Chavez 1983).

In New Zealand, El Niño events (with a negative Southern Oscillation Index) result in lower sea surface temperatures in coastal waters, although turbulence, eddies, currents and upwelling create variation (Greig *et al.* 1988). High sea surface temperatures generally occur during La Niña (positive SOI). These changes influence the spawning success of fishes and their food chains (Paul 1990, Francis & Evans 1993). It appears that La Niña and/or warm water events coincided with years of poor penguin breeding success and adult survival in 1938/39 (Richdale 1957, Gordon 1985), 1984–1986 (Greig *et al.* 1988, van Heezik & Davis 1990) and 1988–1990 (Francis & Evans 1993, Gill & Darby 1993). Subsequent to 1990 there have been mild El Niños, associated cool sea temperatures (Francis & Evans 1993) and relatively productive years for the penguins.

Foraging zones

Prior to this study, it was considered that Yellow-eyed Penguins fed away from the coast (van Heezik 1990) between 7–13 km offshore (Seddon & van Heezik 1990). Smith (1987) related Yellow-eyed Penguin distributions to the wide areas of continental shelves (>14 km wide) and high levels of primary production. At Otago and the Catlins, the shelf is about 35 km wide. This may be a productive zone for penguin prey, as a wide area of medium-sized pebbles (Andrews 1973) has a distinctive and species-rich benthic fauna (Probert & Batham 1979, Probert & Wilson 1984) and the cool subtropical Southland Current promotes zooplankton and fish spawning (Jillett 1969, 1976, Robertson 1980). Foraging range estimation from radio-telemetry has confirmed the importance of the continental shelf (Fig. 1), with birds mostly foraging 5–25 km from the breeding area (mean 16 km, max. 57 km) (Moore *et al.* 1995). Dive depth data has also shown the importance of foraging near the bottom, generally in 40–80 m deep water at Otago Peninsula, and 80–120 m at the Catlins (Moore *et al.* 1995), and the diet composition gives further evidence for this strategy.

Disturbance

The finding that sampling of diet using the water-flushing technique may decrease breeding success differs from other studies (e.g. Robertson *et al.* 1995). This may reflect species differences or the higher frequency of disturbance in our study. There is no doubt that birds are stressed during diet sampling and there may be cumulative effects of further sampling in other months or years, and revisiting nests to weigh chicks. However, the most frequently disturbed birds were more successful than those that were rarely sampled for diet. Of the birds that were sampled for diet, 54% had two or more samples taken (max. nine), compared with 41% (max. six) at two main study areas in 1984–1986 (Y.M. van Heezik unpubl. data). In 1994/95, when no diet samples were taken, breeding success at Boulder Beach was 1.5 chicks per nest (n = 30), and twice as many chicks were produced from the nests that had been disturbed the previous year.

Conclusions

Bottom-dwelling prey, particularly Opalfish, were important components of Yellow-eyed Penguin diet during our study. Diet composition was similar in the early 1990s to that found in the mid-1980s (van Heezik 1990), although several new, but rarely eaten, prey types were identified. Although we did not witness a year of major food shortage, there was significant temporal variation in dietary composition. Years of higher proportions eaten of Red Cod, Opalfish and Sprat, and lower proportions of Arrow Squid and Blue Cod coincided with years of improved breeding success. Dietary variation between sites and between individual penguins may have reflected different prey abundances and foraging ranges. Changes in prey abundance are likely to be caused by environmental factors such as sea temperature, which are in turn influenced by the El Niño Southern Oscillation.

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