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Seasonal variation in the diet of blue penguins (*Eudyptula minor*) at Oamaru, New Zealand

MAREE M. FRASER
Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand

CHRIS LALAS
P.O. Box 31, Portobello, Dunedin, New Zealand. *ithaki@xtra.co.nz*

Abstract The diet of blue penguins (*Eudyptula minor*) at Oamaru, New Zealand was examined by stomach flushing. The 22 species identified comprised 14 fishes, 1 cephalopod and 7 crustaceans. Slender sprat (*Sprattus antipodum*) accounted for more than half of the diet throughout most of the year while Graham's gudgeon (*Grahamichthys radiata*) and arrow squid (*Nototodarus sloanii*) were also important seasonally. Prey were either small, schooling, nearshore species or pelagic juveniles of larger species.

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INTRODUCTION

Blue penguins (*Eudyptula minor*) breed extensively around New Zealand and southern Australia (Marchant & Higgins 1990). Comprehensive studies of their diet in Australia (Klomp & Wooller 1988; Montague & Cullen 1988; Gales & Pemberton 1990; Cullen *et al*. 1992) have indicated consistent patterns; small, nearshore, pelagic and schooling species of fish predominate, especially sardines and anchovies (Clupeiformes). Size limits prey and many species are taken only as juveniles. The dominant prey species can differ not only geographically, but also seasonally and inter-annually, differences in diet that reflect differences in the abundance of prey species.

The only previous study of blue penguin diet in New Zealand was restricted to a one-week period at Codfish Island (46º 45′ S, 167º 40′ E), off Stewart Island (van Heezik 1990a). We sampled the diet of blue penguins monthly for one year, May 1994 to April 1995, at Oamaru (45º 06′ S, 170º 58′ E), South Island, New Zealand. In a 1992 census, Oamaru with 218 breeding pairs held the largest mainland aggregation of blue penguins along the south-eastern coast of South Island (Dann 1994). The penguins here nest along the foreshore abutting residential and commercial areas in two main concentrations <1 km apart (Dann 1994, map in Fraser 1999). One concentration is within Oamaru Harbour at the site of "Oamaru Blue Penguin Colony", a commercial tourist operation for penguin viewing that began in 1993. The other concentration borders the foreshore north of Oamaru Harbour and is a Wildlife Refuge closed to the public. During the 1994/95 breeding season encompassed within our diet study, there were 43 breeding pairs at "Oamaru Blue Penguin Colony" and 53 breeding pairs at the Wildlife Refuge (Perriman *et al.* 2000). In retrospect, our study coincided with a period of high reproductive success (Perriman *et al.* 2000). The annual cycle of blue penguins at Oamaru, as elsewhere comprised a breeding season in August - February and an annual moult in January - March (Marchant & Higgins 1990; Perriman *et al.* 2000).

Blue penguins forage at sea within 20 km of land (Collins *et al.* 1999). Adults are sedentary and colonial burrow-nesters, and come ashore at nightfall frequently throughout the year (Marchant & Higgins 1990). Foraging trips typically last 1 - 2 days during the breeding season, but are longer at other times of year (Weavers 1992; Collins *et al.* 1999). Consequently, the numbers of penguins coming ashore are lowest between completion of moult in April and the start of breeding in August (Marchant & Higgins 1990).

Periodic crashes in blue penguin populations attributed to food shortages have been recorded in Australian (Dann *et al.* 1992; Mickelson *et al.* 1992; Norman *et al.* 1992; Dann *et al.* 2000) and New

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Zealand (Powlesland 1984).. Since little is known of the diet of blue penguins in New Zealand, our study addresses this shortfall.

METHODS

Sampling regime

We followed the sampling procedure of Gales (1987) for retrieving stomach contents from live blue penguins by stomach flushing. Sampling was conducted under permits from Department of Conservation Otago Conservancy and the Committee on ethics in the care & use of laboratory animals, University of Otago. A limit of 10 birds per sampling night was set under these permits in order to minimise disturbance to the colony.

This study was carried out in the Wildlife Refuge at Oamaru. Penguins were captured on the beach as they came ashore after dark. In most months, 10 penguins could be captured within two hours, but on nights when the target number was not reached, efforts were extended to three hours. A second sampling night was undertaken, if feasible, in months when the target was not reached. After capture, each penguin was held for 15 mins in a lidded 20 litre bucket to allow it to calm down. A plastic catheter, attached to the nozzle of a 5 litre garden pressure sprayer, was inserted into the mouth of the penguin and gently pushed down to the base of the stomach. Sea water (at ambient sea temperature) was then pumped into the penguin's stomach until it started flowing out of the corner of the mouth. The catheter was then quickly removed, the bird inverted over a bucket and pressure applied to the base of the stomach with the heel of the operator's hand. Each penguin was flushed three times then returned to its bucket and kept there for about 30 minutes before release. This was to ensure that the stomach flushing had not caused any immediate deleterious effects. After sampling during the breeding season, the penguins were force-fed slivers of filleted fish in order to avoid depriving chicks of food.

In a validation trial, Gales (1987) found that in some cases up to ten flushes were required to empty the stomach of a blue penguin completely. To minimise stress we decided on a maximum of three flushes for each penguin. This procedure was not always successful in retrieving the full stomach contents and some birds vomited after they had been returned to their bucket. These regurgitants were collected, but stored separately from the flushed portion of the sample.

Sorting of samples

The samples were frozen within three hours of collection for later analysis. After thawing, any articulated items were extracted. Other diagnostic remains were retrieved after the sample was washed through a 0.2 mm sieve. Intact fish were measured for standard length (mm SL). Otoliths were removed from crania of these fish and from any intact crania found in samples. Loose otoliths were sorted into left or right if possible. Otoliths too eroded to be separated into left or right were counted and the number divided by two to estimate the number of fish they represented. Otoliths too eroded to identify were termed "unidentifiable". All otoliths were air dried and then stored in sealed plastic bags. Each pair of otoliths removed from crania were stored in separate bags, and loose otoliths were stored by species. Squid beaks were identified as upper or lower beaks following Clarke (1986). All identifications of otoliths and squid beaks were confirmed by comparison with a reference collection held by CL and depicted in Lalas (1983). Crustaceans were identified by Dr Keith Probert, Department of Marine Science, University of Otago. Names and systematic listing of fishes follow Paulin *et al.* (1989).

Gales (1987) found that, except in very large meals, otoliths in blue penguin stomachs dissolved completely after 16 hours. Consequently, we assumed that otoliths retrieved from stomach contents represented foraging from that day only. However, we excluded squid beaks that were either broken or yellowed because they were likely to have originated from previous days.

Analysis of diagnostic remains

Original sizes of prey items were calculated from otolith size (fish), beak size (squid), and from extrapolations from individuals recovered intact and undigested (crustaceans). We inspected loose fish otoliths under a microscope and measured only those that appeared pristine, to avoid an underestimate of fish size. Slender sprat (*Sprattus antipodum*) and Graham's gudgeon (*Grahamichthys radiata*) typically had otoliths <1 mm long. To ensure that we measured only pristine otoliths from these species, only those extracted from crania were used. Total lengths of otoliths and rostral lengths of beaks were measured to 0.01 mm using a microscope. Fresh, but loose, beaks were included for measurement because, unlike loose fish otoliths, they do not erode in stomachs (Furness *et al.* 1984).

The two local species of sprat, slender sprat and stout sprat (*S. muelleri*), have visually indistinguishable otoliths but differ markedly in regression equations relating otolith size to fish size (CL pers. obs.). They differ in the shapes of their tongue and scales (Whitehead *et al.* 1985, Paulin *et al.* 1989). We verified only the presence of *S. antipodum* in blue penguin stomachs, and therefore assumed that all sprat found belonged to this species.

Pipefish (Syngnathidae) had otoliths that were too small (maximum 0.5 mm) to be extracted reliably from stomach contents (Lalas 1983). Of seven pipefish identified from body parts in samples, only one was sufficiently intact for species identification or measurement; a thread-like juvenile of longsnout pipefish (*Leptonotus norae*), ~210 mm TL, with estimated original mass 2 g (Lalas 1983). Therefore, we adopted a nominal mass of 2 g for pipefish.

Otoliths of three species of fish were unverifiable to family or genus because they were simply too small (≤0.5 mm) for irrefutable identification. These otoliths were all from small fish, almost certainly juveniles, up to a few cm long. The most numerous of these was from one of three families: Congiopodidae, Bovichthyidae or Nototheniidae (all three families have pelagic larvae and juveniles with indistinguishable otoliths) and most likely southern pigfish (Congiopodidae: *Congiopodus leucopaecilus*). Therefore, regression equations for southern pigfish (Lalas 1983) were used to calculate fish size from otolith size.

Calculations for prey size from otoliths and beaks

Lengths and masses of fish were calculated from size of otoliths from species-specific regression equations.

Equations for slender sprat (fish mass W (g) = 1.46 x $OL^{2.89}$, fish standard length SL (mm) = 54.15 x $OL^{0.87}$ where OL = otolith length (mm)) and Graham's gudgeon (W (g) = 0.67 x $OW^{0.94}$, SL (mm) = 39.24 x $OW^{0.24}$ where OW = mass of pair of otoliths (mg)) were provided by R.Arden (pers.comm.). Equations for hoki (*Macruronus novaezelandiae*) were from Gales & Pemberton (1990), and for all other fishes from Lalas (1983).

Because Jackson & McKinnon's (1996) relationship between beak size and squid size for arrow squid (*Nototodarus sloanii*) was established from data that included only one squid less than 15 cm dorsal mantle length (DML), we generated new regression equations from stored reference beaks of 45 *N. sloanii* with DML <15 cm (range 6 - 14 cm DML). Sizes of squid derived from articulated beaks in penguin stomach contents were calculated as the averages from the upper and the lower beak equations. Only one set of equations was used to derive size from loose beaks, either the upper beaks or the lower beaks, depending on which were the most numerous in each sample.

RESULTS

Calculations for squid size from beaks

We generated the following equations for the size of arrow squid from beak size:

$W = 0.13 \times DML^{2.28}$ ($n = 45$, $r^2 = 0.92$)
$DML = 7.27 \times LRL^{0.79}$ ($n = 44$, $r^2 = 0.58$)
$DML = 7.01 \times URL^{0.83}$ ($n = 41$, $r^2 = 0.60$)
$TL = 12.08 \times LRL^{0.77}$ ($n = 41$, $r^2 = 0.57$)
$TL = 11.39 \times URL^{0.84}$ ($n = 39$, $r^2 = 0.61$)

where W = squid mass (g), LRL = lower beak rostral length (mm), URL = upper beak rostral length (mm), DML = squid dorsal mantle length (cm), TL = squid total length (cm) = mantle plus arms (but excluding the pair of tentacles).

Number and size of samples

The target number of 10 penguins per month was reached in eight of the 12 months of sampling. Fewer than 10 were captured in April or May and none was encountered during a total of three nights' attempted sampling in June and July (Table 1). Twenty-six of the 99 penguins vomited while retained in the bucket for 30 min after being flushed. The mean number of items per stomach was considerably higher from the 26 penguins that vomited than from those that did not vomit (means of 184 items and 57 items, respectively). For the 26 penguins that vomited, inclusion of the vomited portion significantly increased the mean number of items per stomach from 70 (se 14.7) to 184 (*se* 26.0) (paired $t_{25} = 7.601$, $P < 0.001$). The vomited portion usually contained most of the loose otoliths of the sample and sometimes accounted for more than 100 fish. Vomit samples had a similar prey composition to that of flushed samples (Fraser 1999) and so they were included in all analyses of stomach contents.

Of the 99 stomach samples collected, 90 contained diagnostic prey remains (Table 1). Of the other nine, five contained no remains at all and were tinted green from bile, one contained no remains or bile, and three contained a slurry of unidentifiable digested tissue. The number of prey items per penguin varied both within and between months (Table 1). The mean number of prey items per penguin was higher from October to February than from March to September (Table 1).

The original prey mass represented in the 90 stomach contents that contained diagnostic prey remains ranged from 0.1-350 g (mean 56 g, *se* 8.5). There were significant seasonal differences in prey mass (Fig. 1). Prey mass in summer was significantly greater than in autumn, winter and spring, but there were no significant differences in prey mass between autumn, winter or spring (ANOVA, $F = 10.050$, $df = 97$, $P < 0.001$, Fisher's least significant difference test).

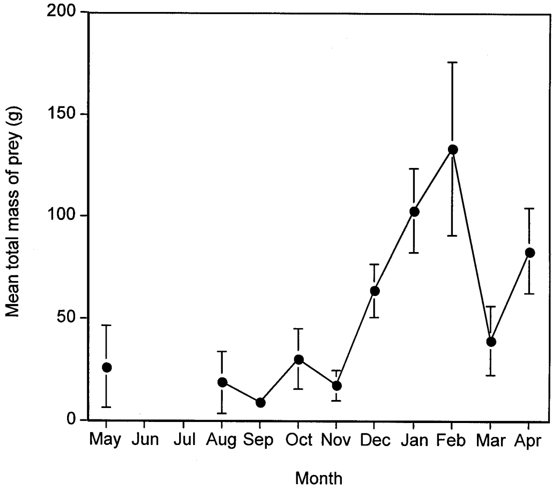

Figure 1 Monthly mean masses (± *se*) of prey from stomachs of blue penguins at Oamaru, May 1994 - April 1995. Sample sizes as in Table 1.

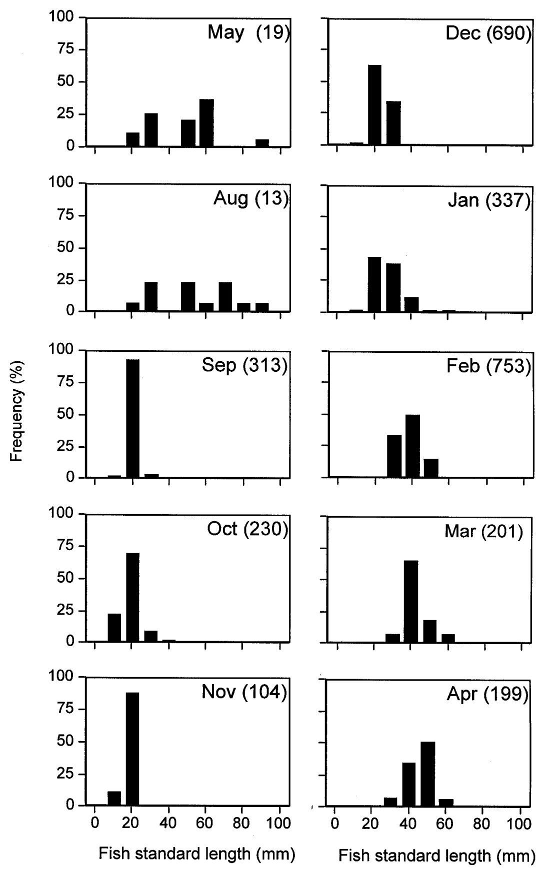

Figure 2 Monthly length frequency distributions of slender sprat eaten by blue penguins at Oamaru, May 1994 - April 1995, calculated from pairs of uneroded otoliths (sample sizes in brackets).

Diversity and relative importance of prey taxa

Twenty-two species were represented in blue penguin stomach contents: one cephalopod, seven crustaceans and 14 fishes (Table 2). Fish dominated the diet throughout the 12 month study. They occurred in 89 (99%) of the 90 stomach samples that contained diagnostic remains and accounted for about 97% of the 8561 total items by number and 90% of the summed original prey mass of about 5150 g. Cephalopods occurred in 21 (23%) of the 90 samples and accounted for about 0.5% by number, but about 10% by mass in the diet. Crustaceans occurred in 14 (16%) of the samples and accounted for about 2.5% by number, but only 0.1% by mass in the diet. The largest crustaceans recorded were ectoparasitic isopods with a mass up to 0.2 g. These were probably injested with fish prey. The other crustaceans recorded were each no more than 0.05 g, average about 0.03 g.

Main prey species

Slender sprat accounted for over 50% of the diet by mass in nine of the 10 months, and >90% of the diet in four months (Table 4). The balance of the diet was contributed mostly by four species: Graham's gudgeon, arrow squid, pigfish and common smelt (*Retropinna retropinna*).

Blue penguins consumed a broad size range of slender sprat (Table 3), more so in May and August than in other months (Fig. 2). Monthly length frequency distributions of sprat from blue penguin stomachs showed a distinct modal progression from September to April (Fig. 2) and the length of sprat increased significantly through this period (Fig. 3: $n = 2827$, $r^2 = 0.88$, $P < 0.001$).

DISCUSSION

Fish prey of blue penguins have small otoliths that are quickly digested and so an unquantifiable amount of food is completely digested before penguins return to land (Gales & Pemberton 1990). Gales & Green (1990) estimated that a non-breeding blue penguin required an average of 315 g of food per day. In common with all previous studies that have quantified original masses of stomach contents of blue penguins (Klomp & Wooller 1988; Montague & Cullen 1988; Gales & Pemberton 1990), we found that mean masses were lower than that required for self maintenance. Stomach content samples are only representative of true diet if the birds forage consistently throughout the day. If the pattern changes diurnally, then the contents retrieved from the stomachs will only be representative of foraging in the latter part of the day.

The dominant prey

Slender sprat contributed more than half of the mass of prey in nine out of the 10 months for which

Table 1 Number of little blue penguins whose stomachs were flushed at Oamaru, May 1994 – April 1995, and the number of identifiable items per stomach.

	Number of stomach contents		Number of items per stomach (for stomachs with diagnostic remains)		
Month	total number of penguins flushed	number without diagnostic remains	mean	se	range
May	7	2	60	35.3	1 - 183
Jun	0	-	-	-	-
Jul	0	-	-	-	-
Aug	14	3	17	5.2	1 - 51
Sep	10	2	57	10.4	7 - 107
Oct	10	0	138	35.7	5 - 396
Nov	10	0	56	22.1	6 - 212
Dec	10	0	178	36.8	43 - 370
Jan	10	0	123	26.1	5 - 220
Feb	10	0	167	56.9	17 - 583
Mar	10	1	43	15.5	3 - 114
Apr	8	1	65	12.9	25 - 120
Total	99	9	93	11.0	1 - 583

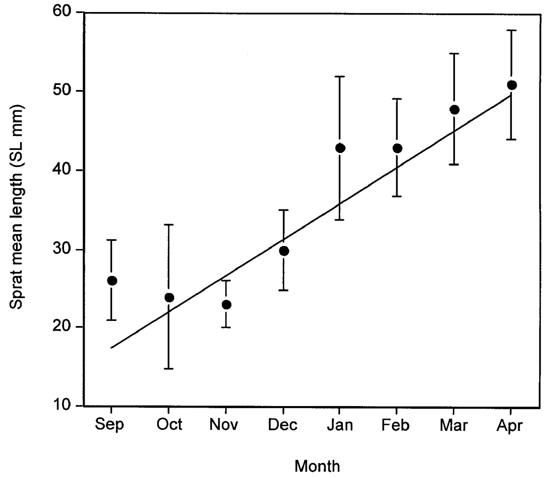

Figure 3 Monthly mean lengths (± *sd*) of slender sprat eaten by blue penguins at Oamaru, for eight consecutive months, September 1994 ($x = 1$) to April ($x = 8$) 1995. See Figure 2 for monthly sample sizes. The plotted straight line of best fit is $y = 12.9 + 4.6x$ ($n = 2827$, $r^2 = 0.88$, $P < 0.001$).

Table 2 Prey species identified in 90 blue penguin stomachs at Oamaru, May 1994-April 1995, the number of each retrieved, and their mass.

Prey common name	Prey scientific name	Number of months recorded	Total number of individuals	Total reconstituted mass (g)	Mean mass per item (g)
Cephalopods					
Arrow squid	*Nototodarus sloanii*	7	52	492	9.5
	All cephalopods	7	52	492	9.5
Crustaceans					
Planktonic copepod	*Neocalanus tonsus*	1	1	<1	<1
Mantis shrimp	*Heterosquilla tricarinata*	1	3	<1	<1
Mysid krill	Unidentified sp.	1	1	<1	<1
Ectoparastic isopod	Unidentified sp. or spp.	4	5	1	<1
Planktonic amphipod	Unidentified 2 spp.	2	151	3	<1
Euphausid krill	*Nyctiphanes australis*	2	46	2	<1
	All crustaceans	8	207	7	0.03
	Crustaceans excluding parastic isopods	6	202	6	0.03
Fishes					
Slender sprat	*Sprattus antipodum*	10	6958	4305	0.60
Common smelt	*Retropinna retropinna*	4	50	51	1.0
Whitebait	*Galaxias* sp.	3	9	2	<1
Pearlside	*Maurolicus muelleri*	1	1	est. 1	est. 1
Lanternfish	*Electrona* sp.	1	1	est. 1	est. 1
Red cod	*Pseudophycis bachus*	1	2	<1	<1
Hoki	*Macruronus novaezelandiae*	2	12	2	<1
Pipefish	*Leptonotus* sp.	4	7	est. 14	est. 2
Seaperch	*Helicolenus* sp.	1	2	<1	<1
Pigfish	*Congiopodus* sp.	4	854	177	0.21
Opalfish	*Hemerocoetes* sp.	1	1	<1	<1
Graham's gudgeon	*Grahamichthys radiata*	8	403	99	0.25
Unidentified (2 spp.)	(otoliths not recognised)	3	5	est. ±1	<1
Unidentifiable	(otoliths too eroded)	1	2	est. <1	<1
	All fish	10	8307	4652	0.56
	Total items		8561	5150	

Table 3 Numbers and size ranges of the five most numerous species of fishes and cephalopods recorded from blue penguin stomachs at Oamaru, May 1994 – April 1995.

Species	Total number in stomach samples	Number quantified for length & mass	Proportion quantified	Length Measure	Length range (mm)	Mass range (g)
Slender sprat	6958	2859	41%	SL	20 - 100	0.03 - 9
Pigfish	854	385	45%	FL	15 - 45	0.02 - 1
Graham's gudgeon	403	253	63%	SL	20 - 40	0.1 - 1
Arrow squid	52	47	90%	TL	80 - 150	5 - 20
Smelt	50	42	84%	FL	40 - 65	0.3 - 2

Table 4 Monthly contributions to the diet of blue penguins at Oamaru, May 1994-April 1995, of the five most commonly identified species.

	May	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Frequency of occurrence										
Number of stomachs	5	11	8	10	10	10	10	10	9	7
Slender sprat	60%	82%	100%	100%	70%	100%	100%	100%	100%	100%
Graham's gudgeon	80%	9%	88%	40%	80%	20%	-	20%	11%	-
Arrow squid	-	-	-	20%	20%	80%	50%	20%	11%	14%
Pigfish	-	-	63%	90%	30%	10%	-	-	-	-
Smelt	-	27%	88%	-	10%	-	30%	-	-	-
Total number of species identified	5	7	4	5	8	9	4	4	4	2
Proportion by number										
Total number of fish and squid	294	138	458	1385	557	1782	1233	1672	388	453
Slender sprat	21%	91%	76%	53%	45%	98%	97%	99%	99%	100%
Graham's gudgeon	78%	<1%	17%	2%	11%	<1%	-	<1%	<1%	-
Arrow squid	-		-	-	<1%	<1%	2%	<1%	<1%	<1%
<1%										
Pigfish	-	-	3%	44%	41%	<1%	-	-	-	-
Smelt	-	4%	4%	-	<1%	-	2%	-	-	-
Total for these 5 species	99%	96%	100%	100%	98%	100%	100%	100%	100%	100%
Proportion by mass										
Total mass of fish and squid (g)	167	360	101	306	127	680	1093	1306	416	585
Slender sprat	72%	99%	55%	51%	17%	59%	86%	97%	98%	98%
Graham's gudgeon	26%	<1%	23%	2%	17%	<1%	-	<1%	<1%	-
Arrow squid	-	-	-	7%	20%	40%	11%	3%	2%	2%
Pigfish	-	-	3%	40%	41%	<1%	-	-	-	-
Smelt	-	<1%	19%	-	<1%	-	3%	-	-	-
Total for these 5 species	99%	100%	100%	100%	97%	100%	100%	100%	100%	100%

samples were collected. When the 10 monthly proportions were averaged, slender sprat accounted for 75% of the penguin's diet by mass.

Slender sprat grow to 120 mm SL (Whitehead *et al.* 1985), are sexually mature at about 100 mm SL (Coleman 1979), and are winter spawners (Robertson 1980). Most sprat prey of blue penguins at Oamaru were less than 1-year old. In May and August the size range of slender sprat recorded was 20-100 mm SL and included adult (1-year old) fish. We speculate that 1-year-old sprat probably formed the bulk of the diet through June and July, though no samples were collected. Only juvenile sprat were recorded from the other eight months, September to April. Lengths of slender sprat taken showed a distinct modal progression from 20 - 30 mm in September to 50 - 60 mm in April. This increase in size probably represents growth in the cohort of slender sprat spawned in winter 1994. The absence of adult sprat in the diet in most months indicated that they were unavailable during most of the year.

Van Heezik & Davis (1990) found that high fledgling masses and growth rates coincided with a prevalence of slender sprat in the diet of Yellow-eyed Penguins (*Megadyptes antipodes*) at Otago and van Heezik (1990b) suggested that sprat were targeted because they were oil-rich. However, oil content in sprat is age-related and high only in adults (Harris & Hislop 1978). During the chick-rearing period (September to March), blue penguins at Oamaru were taking only juvenile sprat, not adults, and so they were apparently not targeting sprat for their high oil content.

Graham's gudgeon grow to only 55 mm SL, live for up to one year and are continuous spawners (Davison 1981). They were recorded in the diet in eight months but exceeded 2% of mass in only three months with their peak contribution being in May and September. Prevalence of arrow squid and pigfish through the four months September to December coincided with the period when the modal length of slender sprat as prey was less than 30 mm SL. Our interpretation is that penguins switched to alternative prey because these small sprat yielded too little energy for the effort expended.

Foraging area

Practically all blue penguin prey species at Oamaru are found over the continental shelf. Slender sprat and smelt are nearshore, pelagic, schooling fish which occur in surface waters (Ayling & Cox 1987). Juvenile stages of red cod (*Pseudophycis bachus*), hoki (*Macruronus novaezelandiae*), longsnout pipefish (Ayling & Cox 1987), southern pigfish (Robertson 1980) and arrow squid (Mattlin *et al.* 1985; Uozumi & Forch 1995) are also pelagic although adults of these species are demersal. Graham's gudgeon have been defined as a nearshore "bentho-pelagic" species (Davison 1981). Our anecdotal records indicate that Graham's gudgeon up to ~45 mm SL are pelagic juveniles and larger fish are benthic adults (CL unpubl. data). Hence, only the pelagic juveniles were taken as prey even though the adults were well within the size range normally taken.

We recorded two oceanic fish species amongst the prey, each represented by one individual: pearlside (*Maurolicus muelleri*) and lanternfish, *Electrona* sp.. Both species are abundant and widespread surface and mid-water dwellers over southern hemisphere continental slopes (Smith & Heemstra 1991). Finding only two individual oceanic fish strongly indicated that foraging by Oamaru blue penguins was restricted to coastal waters. Because lanternfish (Myctophidae) have very large otoliths relative to fish size (Smale *et al.* 1995) their otoliths would have persisted in stomach contents if the penguins were feeding beyond the continental shelf.

Other diet studies

The only previous study of diet of blue penguins in New Zealand was restricted to one week in October 1984 at Codfish Island where the main prey was ahuru (*Auchenoceros punctatus*) (van Heezik 1990a). Although sprat was the main prey at Oamaru in October 1994, none was recorded at Codfish Island, and no ahuru was recorded as prey at Oamaru. In common with sprat, ahuru is a short-lived schooling near-shore fish that is common off Otago, including Oamaru (Lalas 1983; Ayling & Cox 1987). At Otago, ahuru is the main prey species of spotted shags (*Stictocarbo punctatus*) throughout the year (Lalas 1983) and so its absence from the blue penguin diet at Oamaru is a puzzle.

We recorded 22 species (14 fishes, 1 cephalopod, 7 crustaceans) from stomach contents of blue penguins at Oamaru, a broad diversity but similar to that recorded from seasonal Australian studies, e.g. Klomp & Wooller (1988) in Western Australia (18 species: 16 fishes, 1 cephalopod and 1 crustacean); Montague & Cullen (1988) in Victoria (28 species: 21, 5, 2, respectively); Gales & Pemberton (1990) in Tasmania (24 species: 19, 2, 3, respectively). We found that the contribution of crustaceans was negligible.

Clupeiform fish (sardines, anchovies, sprats) are also eaten by blue penguins in Australia. Anchovy (*Engraulis australis*) and pilchard (*Sardinops neopilchardus*) are important prey in Victoria and Tasmania seas (Montague & Cullen 1988, Gales & Pemberton 1990, Cullen *et al.* 1992). Both occur in New Zealand but neither range as far south as Oamaru (Ayling & Cox 1987). Consequently, we would expect that these two species would feature in the diet of blue penguins in New Zealand north of Oamaru.

Fish taken by blue penguins at Oamaru were 15 - 100 mm SL (except the thread-like juveniles of longsnout pipefish ~200 mm long), and weighed up to 10 g. The largest prey were juvenile arrow squid, range 80 -150 mm TL (50-90 mm DML), which weighed up to 20 g. This pattern of squid prey larger than fish was also seen in Australia (Montague & Cullen 1988; Gales & Pemberton 1990).

Oceanic and weather influences

Prey species of blue penguins, being short-lived, vary in abundance and availability both seasonally and inter-annually (Hobday 1992) and are impacted by hydrological perturbations (Gibbs 1992). Fluctuations in food availability can impact detrimentally on breeding success of seabirds (e.g. van Heezik 1990b, Cullen *et al.* 1992). However, blue penguins may deal with a variable food supply by breeding early when food is plentiful and delaying breeding when food is scarce (Cullen *et al.* 1992). Not only does their ability to lay replacement clutches allow them to compensate for an initial failure in the breeding season but also they can take advantage of extended availability of food by fledging two sets of chicks in one season (Gales 1985).

The effects of El Niño-Southern Oscillation (ENSO) have resulted in mass mortalities and reproductive failures of seabirds at South America (e.g., Hays 1986), across the Pacific (Schreiber & Schreiber 1984) and southern Africa (e.g., La Cock 1986). In contrast to increased sea surface temperatures in the eastern and central Pacific, El Niño events are accompanied by the reverse effect of lower sea surface temperatures around southern New Zealand (Greig *et al.* 1988). Slender sprat are winter spawners that exhibit increased breeding success in winters with cold sea surface temperatures (Robertson 1980). Therefore, we would expect that slender sprat would have particularly high breeding success and be most abundant in years of El Niño and, as a corollary, be least abundant and productive in La Niña years.

Our study coincided with a period of high reproductive success for the penguins and embraced part of a prolonged El Nino that extended from October 1992 to December 1994 (www.bom.gov.au). Perriman *et al*. (2000) concluded that blue penguins breed earlier and better in El Niño or normal years than in La Nina years. With the results presented in our paper, we can match seasonal changes in the penguin diet with the annual cycle of blue penguins at Oamaru and present two testable hypotheses:

1. The timing of initiation of egg-laying could be dependent on the availability of adult slender sprat in May to August. These 1-year old sprat would be most abundant, and the initiation of breeding earliest, in calendar years following a winter El Niño. In corollary, the initiation of breeding would be latest in calendar years following a winter La Niña.
2. Reproductive success through the second half of the breeding season (January-March), and adult survival rates through the annual moult following the breeding season, would be dependent on the abundance of juvenile slender sprat spawned through the previous winter. The abundance of these <1-year old sprat would vary with the winter ENSO regimes in the same calendar year as the initiation of the breeding season.

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