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Variability in the diet of New Zealand sea lion (*Phocarctos hookeri*) at the Auckland Islands, New Zealand

LAURELINE MEYNIER

New Zealand Wildlife Health Centre,
Institute of Veterinary, Animal and Biomedical Sciences,
Massey University,
Private Bag 11-222,
Palmerston North 4442, New Zealand
and

Institute of Food,
Nutrition and Human Health,
Massey University,
Private Bag 11-222,
Palmerston North 4442, New Zealand
E-mail: l.meynier@massey.ac.nz

DUNCAN D. S. MACKENZIE

Institute of Food, Nutrition and Human Health,
Massey University,
Private Bag 11-222,
Palmerston North 4442, New Zealand

PÁDRAIG J. DUIGNAN¹

New Zealand Wildlife Health Centre,
Institute of Veterinary, Animal and Biomedical Sciences,
Massey University,
Private Bag 11-222,
Palmerston North 4442, New Zealand

B. LOUISE CHILVERS

Marine Conservation Unit,
Department of Conservation,
P. O. Box 10-420,
Wellington 6011, New Zealand

PATRICK C. H. MOREL

Institute of Food, Nutrition and Human Health,
Massey University,
Private Bag 11-222,
Palmerston North 4442, New Zealand

¹Current address: Department of Agriculture and Food, Agriculture House, Kildare Street, Dublin, Ireland.

ABSTRACT

We examined the stomach contents of 121 New Zealand (NZ) sea lions (*Phocarcos bookeri*) caught by the squid fishery during the summer/autumn 1997–2006 around the Auckland Islands (51°S, 166°E). Dietary variation was assessed among juveniles, lactating females, nonlactating females and males, and between areas on the Auckland Islands shelf. The digested fraction of the contents consisted mostly of opalfish (*Hemerocoetes* spp.) (50.1% by number [N], 4.7% by mass [M]), rattail (*Coelorinchus* spp.) (12.0% N, 2.4% M), arrow squid (*Nototodarus sloani*) (14.1% N, 17.9% M), octopus (*Enteroctopus zealandicus*) (2.1% N, 27.8% M), and red cod (*Pseudophycis bachus*) (3.8% N, 4.3% M). Opalfish was found in greater proportions in the stomachs of females (lactating: 58.1% N, nonlactating: 62.4% N) and juveniles (56.9% N) than males (14.5% N). Juveniles caught smaller opalfish and rattail than adults did. Over all classes, sea lions ate larger prey in the east than in the north of the Auckland Islands shelf. The common prey—arrow squid and rattail—constitute an abundant resource at the edges of the Auckland Islands shelf, where lactating NZ sea lions forage. Although these key areas are far from the rookeries and impacted by the squid fishery, they may provide the only reliable resource able to support the cost of benthic foraging behavior in the deepest diver of all otariids.

Key words: diet, New Zealand sea lion, *Phocarcos bookeri*, feeding ecology, dietary variation, digested fraction.

The New Zealand (NZ) sea lion (*Phocarcos bookeri*) is one of the world's rarest and most highly localized pinnipeds, classified as "Threatened" under the NZ threatened classification system, and the NZ Marine Mammals Protection Act 1978 (Hitchmough 2002). The population size is estimated to be between 10,000 and 13,000 animals (Campbell *et al.* 2006) and has undergone a decline in pup production in the recent years (Chilvers *et al.* 2007). In addition to its low abundance, NZ sea lions have a restricted breeding range with 86% of the pup production at the Auckland Islands (51°S, 166°E; Campbell *et al.* 2006, Chilvers *et al.* 2007). In the past 8 yr, this species has been affected by three disease epidemics, which resulted in the mortality of half the pups born in 1998, and about a third of the pups in both 2002 and 2003 (Wilkinson *et al.* 2006). These events highlight the vulnerability of this restricted population, and they are still impacting on the recruitment of mature females (Chilvers *et al.* 2007).

Concern arose during the past decade over the interactions between NZ sea lions and the arrow squid (*Nototodarus sloani*) trawl fishery. This fishery operates on the Auckland Islands shelf between February and May each year (Gales 1995), which corresponds to the first months of the sea lion lactation period. Early observations of the NZ sea lion's feeding habits suggested that squid comprised a significant part of its diet (Cawthorn *et al.* 1985), leading to potential captures (bycatch) of sea lions in squid trawl nets. Since 1988, government observers have been placed on approximately 20% of the squid fleet every year (Wilkinson *et al.* 2003). The total number of bycaught sea lions is estimated by extrapolation of the number reported by the observers up to the entire fleet. It was calculated that up to 140 NZ sea lions were caught each year in fishing nets (Wilkinson *et al.* 2003; Baird 2005a, b).

Management efforts to date have focused on direct interactions, *i.e.*, bycatch, but not on the possible resource competition between the fishery and NZ sea lions. Knowledge of feeding habits of the NZ sea lion is essential to determine its trophic

interaction with fisheries, and its role in the Auckland Islands ecosystem. To date, only Childerhouse *et al.* (2001) have investigated the diet of sea lions at the Auckland Islands from the analyses of feces and regurgitates between 1994 and 1997. Two other diet studies from scat samples were carried out at sites visited by male NZ sea lions, Macquarie Island (54.5°S, 159°E, McMahon *et al.* 1999) and Otago Peninsula (South Island NZ, Lalas 1997). In these three locations, sea lions fed on a wide variety of prey, mainly fish species. However, scat analyses are known to be subject to biases such as differential retention/erosion rates of hard remains (Jobling and Breiby 1986; Jobling 1987; Harvey 1989; Tollit *et al.* 1997; Bowen 2000; Staniland 2002). Stomach analyses are hampered by biases similar to scat analyses, but to a lesser extent, as hard remains do not pass through the whole intestine. Moreover, the contents of each stomach can be directly related to the sex, age, and reproductive status of the animal.

In this study, the diet of the NZ sea lion was assessed by analyzing the stomach contents of animals bycaught between 1997 and 2006 by the squid trawl fishery. The data collected provided the first quantification by percentage mass of the diet of NZ sea lions. We also provide information on variation among age and sex classes, and between different locations on the Auckland Islands shelf.

MATERIAL AND METHODS

Sample Collection

Since 1997, NZ sea lions caught by the squid fishery operating off the Auckland Islands (Fig. 1) have been frozen and sent to Massey University for necropsy. The whole stomach was removed, and stored in a freezer at -20°C until further analysis. The sex/maturity status (immature [Im], lactating female [LF], nonlactating female [NLF] and male [Ma]) was recorded for each individual. Females without development of the mammary gland, and in the absence of *corpus luteum* or *corpus albicans* in the ovaries, were categorized as immature (Duignan *et al.* 2003). The maturity of the males was determined by histological examination of the testes: immature males had a lack of lumen in their seminiferous tubules, a high proportion of interstitial cells, and no spermatids or spermatozoa (Duignan *et al.* 2003). Immature females and males were pooled. Age of the animals was estimated using incremental growth layers in the dentine of canine teeth (Duignan *et al.* 2003). The average body mass of Im, LF, NLF, and Ma was calculated as it influences dive duration (Costa 1993), and thus may help understanding feeding behavior.

Stomach Analysis

Following storage, stomach contents were thawed and washed through a 0.25-mm mesh sieve. Prey remains consisted mainly of whole or partially digested fish and squid, fish otoliths and bones, cephalopod beaks and eye lenses. Whole prey were identified by their morphologic traits using published guides (Paulin *et al.* 1989 for fish, Nesis 1987 for cephalopods) by technicians of the National Institute of Water and Atmospheric research (NIWA), Wellington, NZ. Fish otoliths, diagnostic bones (dentaries, premaxillaries, maxillaries, posttemporals, and hyomandibulars) and cephalopod beaks were identified using a reference collection held at Massey University and published guides (Clarke 1986; Smale *et al.* 1995). Within the same genus, some otoliths and beaks show no or little specific difference. In such cases, the

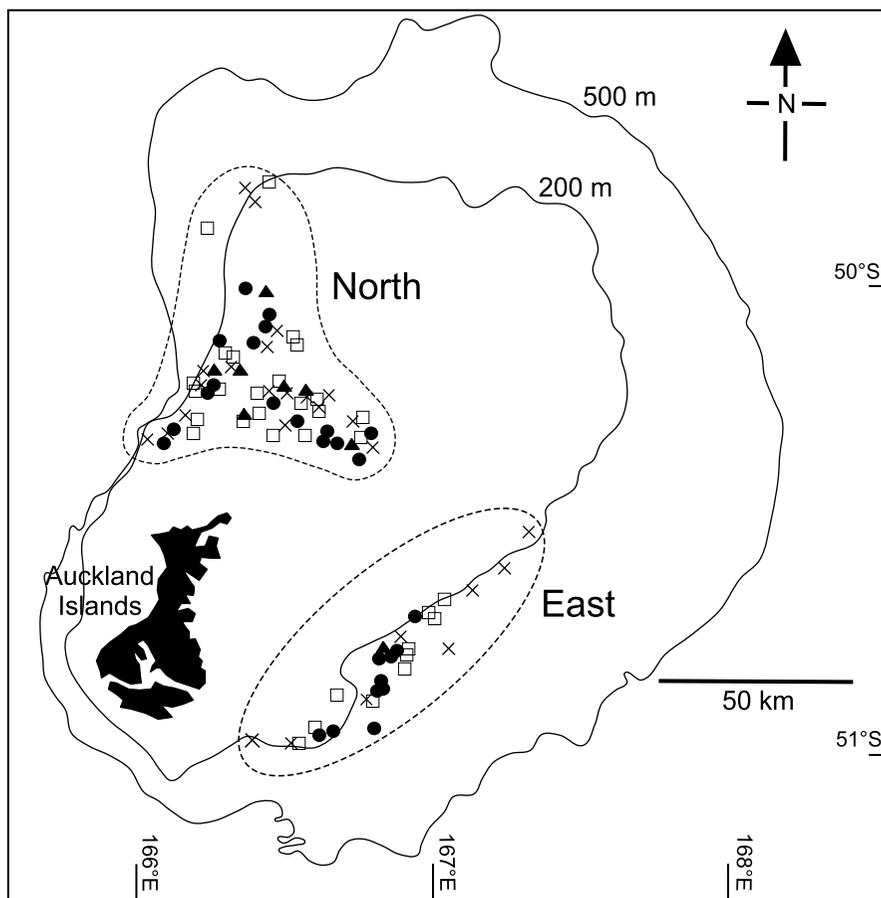


Figure 1. Location of the captures of New Zealand sea lions by the squid fishery between 1997 and 2006. Triangles are immature sea lions, solid circles are lactating females, crosses are nonlactating females, and empty squares are males. Bathymetric contours are shown in black lines. The Auckland Islands shelf is delimited by the 200-m boundary. The two studied areas "North" and "East" are represented by dotted lines. Map generated from NABIS, Ministry of Fisheries, New Zealand.

hard parts were attributed to the most abundant species occurring in the area from which the animal was taken. If more than one species belonging to the same genus was present in the area, the genus was noted as "spp." This is the case for jack mackerels *Trachurus* spp. (*T. declivis* or *murphyi*), warehouse *Serirolella* spp. (*S. brama*, *caerulea*, or *punctata*), rattails *Coelorinchus* spp. (*C. aspercephalus*, *bollonsi*, or *fasciatus*), lanternfish *Diaphus* spp. (*danae*, *budsoni*, or *meadi*), and opalfish *Hemerocoetes* spp. (*monopterygius*, *artus*, or *morelandi*). The sieved remains were stored in 70% ethanol except for bones and otoliths, which were kept dry.

All the animals sampled were bycaught from the squid fishery and hence from a region characterized by abundant squid. This may lead to an overestimation of the squid contribution to the diet. Indeed, almost all stomachs contained fresh

squid, which were ingested just before death. To minimize the overestimation of the squid contribution in the content, we distinguished a fresh and a digested fraction (Pusineri *et al.* 2007). The fresh fraction included whole prey and hard remains with some flesh attached (*e.g.*, skulls and vertebral columns) that were ingested shortly before the death of the animal. The digested fraction consisted of remains without associated flesh (*e.g.*, free otoliths, bones, and beaks), which were probably part of meals ingested from one to several days before the death (Bigg and Fawcett 1985; Dellinger and Trillmich 1988; Staniland 2002; Tollit *et al.* 2003). The digested fraction was assumed to be a better representation of the background diet of sea lions before they fed on squids in or close to the nets. Only this fraction was taken into account in the statistical analyses.

All diagnostic hard parts (otoliths, some bones, and beaks) were counted for each content, and the number of a taxon was determined as follows: the number of fish was estimated by the number of otoliths. If less than 10 per taxon were present, left and right otoliths were sorted, and the highest number was taken. If more than 10, the total number was simply divided by 2. The number of cephalopods was estimated by the number of upper or lower beaks, whichever was higher (Pierce and Boyle 1991).

Prey sizes and masses were estimated by measuring otolith length, or otolith width when the tip was broken, lower beak rostral length (*LRL* for squid) or lower beak hood length (*LHL* for octopods and sepiolids), and by using regressions from the literature or our own reference collection (see the Appendix). When a species was represented by >30 otoliths or beaks in a stomach, 30–40 were picked randomly and measured. In this case, a weighting factor (the ratio of measured prey to the total of prey) was multiplied with each measure (Santos *et al.* 2004). Only otoliths with no sign of erosion were measured in order to minimize the underestimation of size and mass.

The relative importance of each prey was estimated as the percentage of occurrence (number of stomachs in which the taxon was observed), the proportion of the total prey number in the sample set, and the proportion of the total reconstructed mass (product of the number of prey and the average body mass).

Statistical Analysis

Variation among areas (North and East, Fig. 1), and sex classes (combined sex/maturity factor: LF, NLF, Im, and Ma) was investigated on the number and median length of the common prey from the digested fraction. Prey were considered common when the occurrence was >30%, and occasional when the occurrence was <10% in the sample set.

Data in a stomach analysis consist of many zero values for each prey distribution, which makes the application of parametric tests such as ANOVA difficult. The Scheirer-Ray-Hare (SHR) test is a nonparametric equivalent of a two-way ANOVA (Dytham 1999), and was used to reveal significant differences in the number of common prey within areas and sex classes. *Post hoc* comparisons were performed using Tukey tests. The median lengths of common prey were tested using a Kruskal–Wallis test and *post hoc* Mann–Whitney tests for sex classes, and using a Mann–Whitney test for areas. We set the statistical significance α at 0.10 to take into account the low statistical power of our analyses (low sample size). Tests were performed with the MINITAB package (MINITAB Release 14.1, MINITAB Inc. 2003), and all arithmetic means are followed by the standard deviation (SD).

RESULTS

Overall Diet

A total of 121 stomach contents of NZ sea lions incidentally caught between February and May from 1997 to 2006 were examined. Mature sea lions of both sexes were well represented in each area (Table 1). In total, mature males represented a third of the sample set, and mature females were more numerous with half of them lactating.

Overall, 35 different prey taxa were found with fish comprising the bulk of the diet (Table 2). Cephalopods ranked second and crustaceans occurred only sporadically. In total, 6,004 diagnostic hard remains were recovered from the stomachs, which corresponded to an estimated 3,627 individual prey of which 2,309 were fish, 1,311 squid, six crustaceans, and one bird. Only nine out of 35 taxa had a frequency of occurrence >10%. The common prey species were arrow squid *Nototodarus sloani* (86.9% by occurrence [O], 33.4% by number [N], 43.0% by mass [M]), rattail *Coelorrinchus* spp. (55.7% O, 10.0% N, 1.8% M), opalfish *Hemerocoetes* spp. (48.4% O, 35.5% N, 2.4% M), octopus *Enteroctopus zealandicus* (38.5% O, 3.1% N, 14.4% M), and red cod *Pseudophycis bachus* (32.0% O, 3.1% N, 3.2% M). Hoki, *Macruronus novaezealandiae*, and hake, *Merluccius australis*, contributed significantly to the total mass (17.8% M), but they were present in only 16% of the stomachs.

The same prey species were common in both the total content and the digested fraction; however, they were not in the same order of importance (Table 2). In the analysis of the digested fraction, opalfish was the most commonly eaten (50.4% O), followed by rattails (54.0% O) and arrow squid (33.6% O). Opalfish represented half of the diet by number but was still low by mass (4.7% M) due to a small individual mass (Table 3, 20 ± 13 g). In contrast, octopus was the first prey by mass (27.8% M) due to a high individual mass ($1,788 \pm 2,322$ g). Red cod, hoki, and hake occurred in the same proportions in the digested fraction as in the total content (Table 2). The majority of the fresh fraction was composed of arrow squid (82.2% O, 78.1% N, 78.5% M).

The estimated prey lengths from hard remains found in the stomach contents ranged from 1.6 cm (sepiolids) to 119.5 cm (hake), but common prey were less than 30 cm long (Table 3). The intraspecific length variation was also important with coefficients of variation higher than 20% for all common prey but opalfish. The largest prey were fish that made a minor contribution to the diet such as hake, hoki, barracouta, and ling.

Table 1. Distribution of the number of stomachs of New Zealand sea lions analyzed according to the bycatch location and whether they were immature (Im), lactating females (LF), nonlactating females (NLF), or males (Ma) together with their average body mass (BM \pm SD). The first number in each category is the total number of stomachs analyzed. The second number in parenthesis is the number of stomachs containing some digested material (digested fraction). The difference between the two numbers is the number of stomachs containing fresh prey only.

Category	North	East	Unknown location	Total	BM (kg)
Im	8 (7)	3 (1)	1 (1)	12 (9)	91 \pm 13
LF	21 (20)	12 (12)	1 (1)	34 (33)	108 \pm 14
NLF	23 (23)	8 (8)	4 (3)	35 (34)	104 \pm 16
Ma	22 (20)	11 (9)	7 (7)	40 (36)	167 \pm 60
Total	74 (70)	34 (30)	13 (12)	121 (112)	

Table 2. Composition of the New Zealand sea lion's diet expressed as % occurrence (% O; percentage of stomachs in which the taxon was observed), % number (% N; percentage of the total prey number across all samples), and % reconstructed mass (% M; percentage of the number of prey times the average body mass) of the total content, the digested fraction only and the fresh fraction only. Bold numbers represent the principal contributions. Common and occasional prey have an occurrence > 30% and < 10%, respectively.

Fraction (no. of stomachs) Diet picture	Total (121)			Digested (112) 1-2 d before death			Fresh (101) Just before death		
	%O	%N	%M	%O	%N	%M	%O	%N	%M
FISH									
Argentinidae <i>Argentina elongata</i> (silverside)	3.3	0.3	0.1	2.7	0.3	0.2	1.0	0.3	0.1
Bramidae <i>Brama brama</i> (sea bream)	0.8	< 0.05	0.2	0.9	< 0.05	0.4			
Carangidae <i>Trachurus</i> spp. (jack mackerels)	8.2	0.7	3.0	7.1	0.7	2.6	5.9	0.6	1.6
Centrolophidae <i>Seriotelella</i> spp. (warehou)	4.1	0.2	1.0	2.7	0.1	1.2	2.0	0.3	1.1
Congiopodidae <i>Congiopodus coriaceous</i> (pigfish)	11.5	0.7	0.1	9.7	0.6	0.1	4.0	0.8	0.1
Congridae <i>Gnatophis habenatus</i> (silver conger)	1.6	0.1	0.1	1.8	0.1	< 0.05			
Emmelichthyidae <i>Emmelichthys nitidas</i> (redbait)	0.8	< 0.05	< 0.05	0.9	< 0.05	< 0.05			
Gadidae <i>Micromesistius australis</i> (southern blue whiting)	2.5	0.1	< 0.05	1.8	0.1	< 0.05	1.0	0.1	< 0.05
Gempilidae <i>Thysites atun</i> (barracouta)	7.4	0.5	4.6	5.3	0.5	5.8	5.0	0.4	3.0

Gonorynchidae	0.8	< 0.05	< 0.05	1.0	0.1	0.1
<i>Gonorynchus gonorynchus</i> (sand fish)						
Macrouridae <i>Coelorinchus</i> spp. (rat tails)	55.7	10.0	1.8	54.0	12.0	2.4
<i>Lepidorhynchus</i> <i>deniculatus</i> (javelin fish)	9.0	3.3	0.4	7.1	4.3	0.7
Unidentified Macrouridae	1.6	0.3	0.6	1.8	0.1	0.9
Total Macrouridae	59.0	13.6	2.8	57.5	16.4	4.0
Merlucciidae <i>Macrurus</i> <i>novaezelandiae</i> (hoki)	11.5	2.2	9.6	12.4	3.1	15.5
<i>Merluccius australis</i> (hake)	4.1	0.3	7.4	3.5	0.3	3.7
Unidentified Merlucciidae	1.6	< 0.05	0.8	1.8	0.1	2.6
Total Merlucciidae	16.4	2.5	17.8	15.9	3.5	21.8
Moridae <i>Austrophycis</i> <i>marginata</i> (dwarf cod)	6.6	0.9	< 0.05	7.1	1.1	0.1
<i>Pseudophycis bachus</i> (red cod)	32.0	3.1	3.2	30.1	3.8	4.3
Total Moridae	36.1	4.0	3.2	36.3	4.9	4.4
Mugiloididae <i>Parapercis</i> <i>colias</i> (blue cod)	0.8	< 0.05	< 0.05	0.9	< 0.05	< 0.05
Myctophidae <i>Diaphus</i> spp.	0.8	< 0.05	< 0.05		1.0	0.1

(Continued)

Table 2. (Continued)

Fraction (no. of stomachs) Diet picture	Total(121)			1-2 d before death			Fresh (101) Just before death		
	%O	%N	%M	%O	%N	%M	%O	%N	%M
<i>Lampanyctodes bectori</i>	4.1	0.7	< 0.05	4.4	0.9	< 0.05			
<i>Myctophum</i> sp	0.8	0.1	< 0.05	0.9	0.1	< 0.05			
Total Myctophidae (lanternfish)	5.7	0.8	< 0.05	5.3	1.0	< 0.05	1.0	0.1	< 0.05
Norosudidae <i>Scopelasmaurus</i> sp	0.8	< 0.05	< 0.05	0.9	< 0.05	< 0.05			
Ophidiidae <i>Gemmyterus</i> <i>blacodes</i> (ling)	13.1	0.9	4.4	14.2	1.5	8.8			
Percophidae <i>Hemerocoetes</i> spp. (opalfish)	48.4	35.5	2.4	50.4	50.1	4.7	5.0	5.2	0.3
Psychrolutidae <i>Neophrymichthys latius</i> (dark toadfish)	10.7	1.0	< 0.05	9.7	1.2	< 0.05	3.0	0.4	< 0.05
Scorpaenidae <i>Helicolenus</i> <i>peroides</i> (scarpee)	0.8	< 0.05	0.1				1.0	0.1	0.2
Unknown species A	7.4	0.7	< 0.05	8.0	1.0	< 0.05			
Total Scorpaenidae	8.2	0.7	0.1	8.0	1.0	< 0.05	1.0	0.1	0.2
Rajidae <i>Raja nasutta</i>	3.3	0.3	0.2				2.0	0.2	0.3
Unidentified fish	10.7	0.5	0.2	6.2	0.4	—	5.0	0.5	—
CEPHALOPODS									
octopodidae <i>Enteroctopus</i> <i>zealandicus</i> (octopus)	38.5	3.1	14.4	28.3	2.1	27.8	15.8	4.5	6.0
Octopoteuthidae?	0.8	< 0.05	< 0.05	0.9	< 0.05	< 0.05			
Unknown species									
Ommastrephidae <i>Nototodarus sloani</i> (arrow squid)	86.9	33.4	43.0	33.6	14.1	17.9	82.2	78.1	78.5
Onychoteuthidae <i>Moroteuthis ingens</i> (wary squid)	3.3	0.9	1.9	3.5	1.1	2.9			

Sepioidae Unknown species	2.5	0.1	<0.05		1.0	0.1	<0.05
Unidentified squid	0.8	< 0.05	—	0.9	<0.05	—	
CRUSTACEANS (swimming crabs)	4.9	0.2	—	0.9	<0.05	0.5	—
unknown genus	2.5	0.1	—	0.9	<0.05	0.2	—
Palinuridae <i>Jasus</i> sp (crayfish)							
BIRDS							
Procellariidae <i>Pachyptila</i> sp (prion)	0.8	< 0.05	<0.05		1.0	0.1	0.1
Total number of taxa/species		35		29		23	
Total of prey		3627		2732		895	

Table 3. Length and mass ($\bar{x} \pm SD$) of New Zealand sea lion's common prey (in bold) and minor prey species with a commercial value. CV is the coefficient of variation. Length is the total length for fish and dorsal mantle length for cephalopods, except for barracouta and opalfish for which standard length was calculated. Lengths and masses were back-calculated from measurements of specific hard parts using regressions in Appendix.

Prey species	N	Length (cm)		Range	Mass (g)
		$\bar{x} \pm SD$	CV (%)		
FISH					
<i>Trachurus</i> spp. (jack mackerels)	27	40.9 \pm 3.9	10	31.9–50.8	991 \pm 307
<i>Micromesistius australis</i> (southern blue whiting)	40	30.7 \pm 5.9	19	17.0–41.2	116 \pm 98
<i>Thyriscus atun</i> (barracouta)	22	75.1 \pm 10.4	14	41.2–84.8	2,070 \pm 1,005
<i>Coelorhynchus</i> spp. (rattails)	520	19.4 \pm 6.2	32	5.1–43.8	48 \pm 52
<i>Macrurus novaezelandiae</i> (hoki)	97	71.9 \pm 11.2	16	50.2–97.4	1,034 \pm 460
<i>Merluccius australis</i> (hake)	17	92.3 \pm 11.2	12	77.7–119.5	6,117 \pm 1,275
<i>Pseudophycis bachus</i> (red cod)	195	25.0 \pm 10.4	42	4.9–54.7	263 \pm 306
<i>Genypterus blacodes</i> (ling)	57	61.2 \pm 19.3	32	23.0–95.2	1,193 \pm 1,040
<i>Hemirocoetes</i> spp. (opalfish)	1,027	12.4 \pm 1.6	13	9.3–25.0	20 \pm 13
CEPHALOPODS					
<i>Enterocoptus zealandicus</i> (octopus)	110	13.5 \pm 9.0	67	2.5–37.1	1,788 \pm 2,322
<i>Nototodarus sloani</i> (arrow squid)	963	23.0 \pm 5.4	24	6.6–36.5	347 \pm 189
Smallest prey = sepiolids	3	1.7 \pm 0.1	1	1.6–1.7	2
Largest prey = hake	17	92.3 \pm 11.2	12	77.7–119.5	6,117 \pm 1,275

Dietary Variation (Digested Fraction)

SHR tests on the numbers of common prey did not reveal any significant interactions between the factors sex/maturity and area; thus, these factors can be treated independently. No significant difference existed between the North and the East of the shelf (SHR test, $P > 0.10$). Opalfish was the only common prey showing a significant difference between sex classes (SHR test, $F_{3,99} = 2.33$, $P = 0.10$), though this was at the limit of the statistical significance. Tukey tests revealed that fewer opalfish were retrieved from the stomachs of males (14.5% *N*) than those of lactating (58.1% *N*) and nonlactating females (62.4% *N*) and immatures (56.9% *N*). The number of different taxa eaten by an individual sea lion was similar among sex classes and averaged 3 ± 2 .

The median length of rattail was significantly smaller in the stomachs of immature sea lions (14.2 ± 3.1 cm) than in the stomachs of lactating females (18.8 ± 5.3 cm) and adult males (21.0 ± 6.1 cm) (Kruskal–Wallis test; $H_{3,55} = 9.54$, $P = 0.023$; Mann–Whitney tests, $P < 0.10$). Similarly, immature sea lions fed on opalfish of smaller size (11.7 ± 0.6 cm) than did lactating females (13.0 ± 1.3 cm) and males (13.4 ± 1.6 cm) (Kruskal–Wallis test; $H_{3,54} = 8.49$, $P = 0.041$; Mann–Whitney tests, $P < 0.10$). The median lengths of rattail, red cod and arrow squid were significantly larger in the eastern area than in the northern area (Mann–Whitney tests; $P = 0.001$ for rattail; $P = 0.032$ for red cod; $P = 0.009$ for arrow squid). Indeed, the length distributions of rattail and red cod (Fig. 2a, b) showed that most of the largest fish eaten were from the East. This difference in size distribution between the two areas was well marked for the arrow squid (Fig. 2c) with a peak at 29–30 cm in the East and a peak at 20–21 cm in the North.

DISCUSSION

Common prey of sea lions incidentally caught as bycatch during the early lactation period were opalfish, rattail, arrow squid, octopus and red cod, which are bottom living species, or living at depth >200 m. Diet variation between males and females concerned only opalfish, whereas lactating and nonlactating females showed no difference in their diet. Immatures that were 3–4 yr old fed on the same diet as adults, but targeted smaller opalfish and rattail. These results are consistent with the benthic foraging behavior described previously in diving studies (Gales and Mattlin 1997; Chilvers *et al.* 2006). Nonetheless, ontogenic variation in our study may have been underestimated due to the nature of the sample set (bycatch) and the small number of individuals analyzed in each sex class.

Limitations of the Study

Total stomach contents were divided into fresh and digested fractions. The fresh fraction includes all items ingested over a similar period, and probably during the same “meal.” It provides an unbiased estimate of actual intake although over a restricted period (Pierce *et al.* 2004; Pusineri *et al.* 2007). However, in our study, the composition of the fresh fraction is obviously biased in that the individuals sampled were caught in fishing nets targeting squid. The comparison between the fresh (78.1% *N*, 78.5% *M*) and the digested fraction (14.1% *N*, 17.9% *M*) confirmed

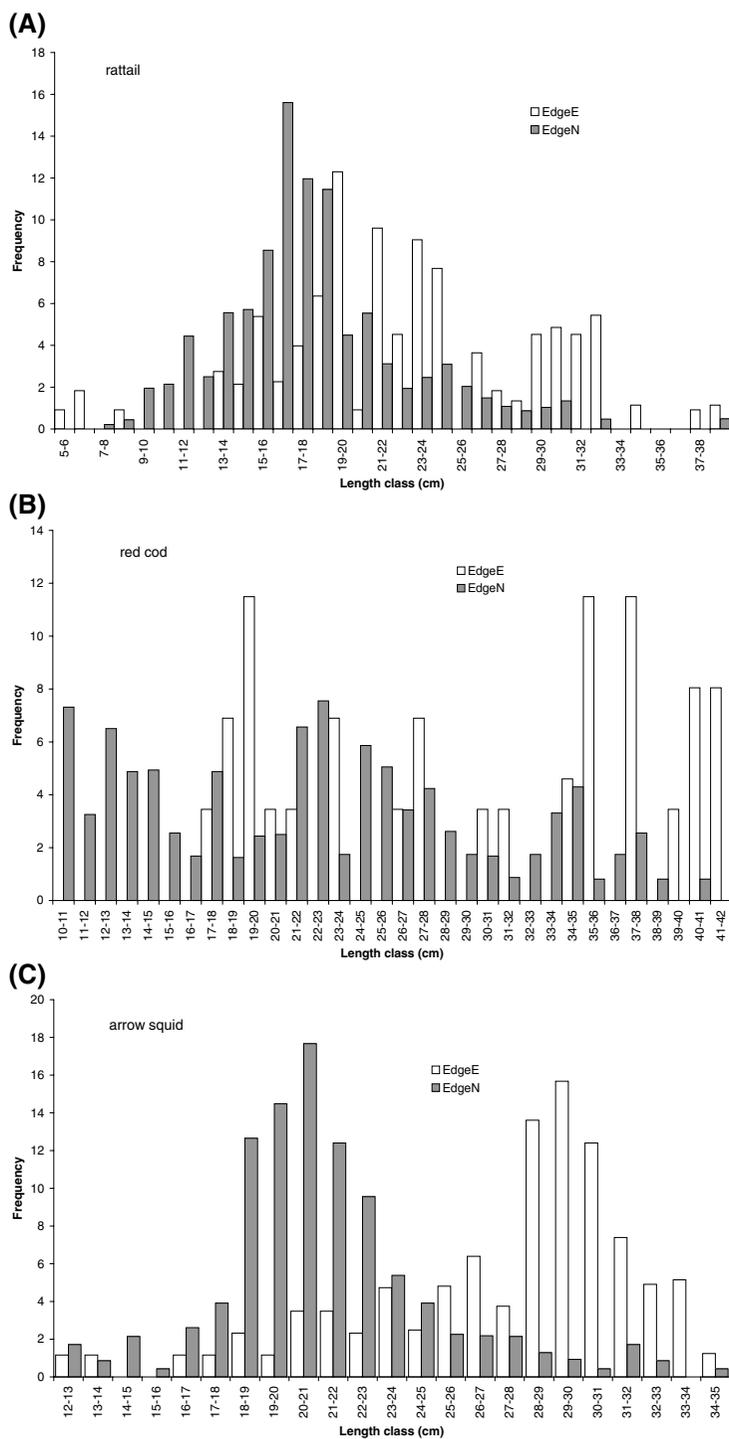


Figure 2. Length distribution of (A) rattail, (B) red cod, and (C) arrow squid retrieved from stomachs of New Zealand sea lions according to the area of capture.

that total stomach contents overestimated the percentage of arrow squid in the diet (Table 2). The digested fraction is also subject to biases, related to differential digestion rates and hard part accumulation. Firstly, fish otoliths may be partially or completely digested in stomachs of pinnipeds (Murie and Lavigne 1985; Dellinger and Trillmich 1988) and fish with small otoliths tend to be underestimated. To reduce this bias, an "all-structure" approach was used (Tollit *et al.* 2003), in which both otoliths and diagnostic bones were identified. Secondly, cephalopod beaks are not affected by digestion and tend to accumulate in the stomach (Bigg and Fawcett 1985). Individuals of all classes have been seen regurgitating beaks on rookeries (B. L. Chilvers, unpublished data), which may reduce the accumulation of cephalopod beaks. Consequently, we believe that the biases encountered in the digested fraction were minimized in this study, and that this fraction better represented the diet of NZ sea lions than the whole stomach content or the fresh fraction.

Feeding Ecology of the NZ Sea Lion

Although the diet of caught NZ sea lions during the early lactation period of 1997–2006 was diverse, only five prey—opalfish, rattail, arrow squid, octopus, and red cod—were considered common (Table 2). These prey also comprised a significant part of the diet estimated from scats and regurgitates between 1994 and 1997 (Childerhouse *et al.* 2001). Both opalfish and octopus are benthic species occurring on the shelf, living in sandy beds and in rock holes, respectively (Paul 2000). Arrow squid occurs not only in the water column over the shelf but also at the edge of the plateau and offshore, where they form large aggregations down to 300 m (Jackson *et al.* 2000). The edge is also the habitat of rattails which live near the bottom at depths >200 m (Paul 2000). Benthic foraging is consistent with previous studies on the diving behavior of female NZ sea lions (Gales and Mattlin 1997, Chilvers *et al.* 2006), where most of the dives were in waters >150 m, consecutively at similar depths, and with a U-shaped dive, which is typical of diving to the sea bottom. Most of the uncommon prey are demersal or benthic living species, but few species are from the pelagic region such as barracouta and jack mackerel. NZ sea lions may opportunistically catch these prey at the beginning or the end of a dive. This is consistent with the conclusions of a study conducted at Otago (South Island, NZ) on male NZ sea lions (Lalas 1997), where the diet consisted of a wide range of benthic species with several pelagic species. The examination of prey sizes (Table 3) emphasizes this opportunistic behavior: all but one of the common prey displayed a coefficient of variation higher than 20%, showing that NZ sea lions do not target a particular length of prey, but instead are likely to eat what is available.

During summer, lactating female NZ sea lions forage over and at the edge of the shelf (Chilvers *et al.* 2005), where they dive continuously to depths >150 m (Chilvers *et al.* 2006). The energy cost of deep diving is greater than transiting between locations (Costa and Gales 2000). Consequently, these benthic divers need a sufficient energetic income at each dive to balance their energetic budget, and are likely to forage on areas with predictable and concentrated resources. The edges of the Auckland Islands shelf appear to be a preferred foraging region for lactating females where they concentrate most of their time during a foraging trip (Chilvers *et al.* 2005). Although it is far from the rookeries (>50 km), it may represent an energetic risk worth taking based on foraging returns from greater density of prey than would be available on the shelf. Indeed, arrow squid and rattails, two of the

common prey, are schooling species forming large aggregations at depths >200 m (Jackson *et al.* 2000; Paul 2000). In contrast, opalfish and octopus live at the bottom of the shelf (Paul 2000) and are not in schools. Therefore, it appears that by foraging at the edge of the Auckland Islands shelf in depths >200 m, NZ sea lions have access to concentrated food resources where great quantities can be consumed in a short time period, increasing their energetic investment per dive.

Ontogenic Variation in Diet

Dietary differences between adult females and males are most likely to be driven by different physiological constraints, metabolic requirements and reproductive strategies (Costa 1993). In this study, though body mass variation of males was important (Table 1), the average mass was a third heavier than that of females. Body mass influences dive capability in such a way that heavier animals are able to dive longer than lighter ones (Costa 1993). Furthermore, foraging trips of males are not constrained in duration by pup nursing; thus, they may undertake trips of longer duration than females and access different resources. The only difference found in our study between the diet of males and females was the amount of opalfish (demersal species occurring on the shelf, Paul 2000), which was significantly greater in the diet of females (approximately 60% *N* vs. 14.5% *N* for males). Males are able to dive deeper because of their greater body size, and may focus their food search at depths >200 m, where opalfish are less abundant. This hypothesis could only be validated by the comparison of satellite-TDR data on males and females, but to date foraging studies have focused on lactating individuals only (Gales and Mattlin 1997; Chilvers *et al.* 2005, 2006). The lack of strong difference between the diet of female and male sea lions in our study may originate from the method used and the sample set: first, stomach contents give a diet picture over a foraging trip only, and may not be representative of the "routine" diet of females and males during the early lactation period. Second, most of the males in our sample set were nonterritorial animals during the breeding season. Territorial bulls are likely to show more dietary differences with females than the nonterritorial animals, because they tend to disperse further from the study area after the breeding season (Robertson *et al.* 2006).

Incidentally caught lactating and nonlactating females did not show any difference in their diet. Nonlactating females are not constrained to return to the breeding site to nurse when foraging; thus, they can increase their time at sea and forage on a different resource. However, lactating females are seen to have high site fidelity to certain foraging zones, which is thought to represent long-term learnt foraging behavior (Chilvers 2008). Therefore, it is expected that these foraging habits would be similar whether they were rearing a pup or not.

The bycatch location and our dietary results indicated that bycaught immature NZ sea lions are able to feed on the same prey and at the same locations as mature animals. Their diet consists of bottom-dwelling (octopus, opalfish) and deepwater species (arrow squid, rattail), implying that they are able to forage on the bottom of the shelf and at depths >200 m. Similarly to females, immature sea lions fed on a greater percentage of opalfish than did adult males. Moreover, the length of opalfish and rattail were significantly smaller than that of adults. The predation of smaller prey by juvenile otariids compared to adults has been reported before (*e.g.*, Page *et al.* 2005), and is an expected result given their lower mass (Table 1). Nevertheless, it must be stressed that the class "immatures" in our study comprises animals from 3 to

4 yr old, which have a mass close to that of females (Table 1), being able to forage on deep prey at depths >200 m. This may explain their capacity of capturing red cod, arrow squid and octopus of the same size as adults. Yearlings or 2-yr-old juveniles, not represented here, are likely to forage in shallower areas closer to the rookeries. This hypothesis is consistent with studies on the diving patterns of young, 1–2 yr of age, of other otariid species (e.g., Fowler *et al.* 2007, *Neophoca cinerea*; Spence-Bailey *et al.* 2007, *Arctocephalus pusillus doriferus*; Baylis *et al.* 2005, *A. forsteri*).

Geographical Variation in Diet

Individuals were grouped according to their bycatch location, either north or east of the Auckland Islands (Fig. 1). The diet from stomach analyses showed no difference between the two locations, suggesting no difference in prey distribution between the north and east of the Auckland Islands shelf. However, sea lions caught in the east ate larger rattails, red cod and arrow squid than those caught in the north (Fig. 2). It is difficult to verify if these prey stocks in the Auckland Islands show size differences between areas as their biology is poorly known. The only length distribution available in the region is from the arrow squid fishery, which catches bigger squid in the southern than in the northern part of the Auckland Islands shelf (Gibson 1995). This is consistent with our results showing that squid eaten by sea lions in the eastern zone, which is also south of the shelf (Fig. 1), were 10 cm larger than those from the north (Fig. 2). The areas east of and north of the shelf are exploited by sea lions from different breeding colonies of the Auckland Islands (B. L. Chilvers, unpublished data), and a stock of larger prey may be energetically advantageous for animals foraging in the eastern area.

Interactions with Fisheries

Of the common prey species found in the stomachs of NZ sea lions taken as bycatch, only arrow squid and red cod have commercial value. Some of the minor prey are also harvested by fisheries, such as hoki, hake, barracouta, ling, southern blue whiting, and jack mackerel (Table 2; Ministry of Fisheries 2007). These fish along with red cod and arrow squid accounted for 24.1% *N* and 58.6% *M* of the total prey in the digested fraction of the stomach contents (Table 2). The Auckland Islands are the southern limit of the NZ sea lion's historical breeding range (Childerhouse and Gales 1998), but host 86% of the current pup production (Chilvers *et al.* 2007). This environment has been considered a marginal habitat for NZ sea lion females, which dive deeper than any other otariid, and operate at their physiological limits when foraging (Gales and Mattlin 1997; Costa and Gales 2000; Chilvers *et al.* 2005, 2006). Therefore, the recovery of this species depends on the development of new colonies around NZ main islands. A fragile recolonization is visible in the South Island of NZ (Childerhouse and Gales 1998; Wilkinson *et al.* 2003), but this region is also an important ground for deepwater fisheries (hoki, hake, barracouta; Ministry of Fisheries 2007). The hoki fishery, which is the most important fishery in NZ, targets fish of a size >60 cm (Ministry of Fisheries 2007), similar to the size range exploited by NZ sea lions (Table 3). Also, the NZ sea lion seems to eat what is the most available in the benthos or deep waters, and is capable of eating a wide size range (Table 3). This opportunistic behavior, also reported in animals not caught as bycatch

(Lalas 1997; McMahon *et al.* 1999), may lead to direct and indirect interactions with fisheries occurring around the developing colonies in the future.

Conclusion

We investigated the diet of NZ sea lions and its variation from stomach contents of bycaught animals. The main prey species are benthic dwelling or deepwater fish and squid, which is consistent with the results of diving studies showing benthic foraging. Lactating, nonlactating females, males, and juveniles of 2–3 yr old commonly forage on the same prey, but the lack of differences on prey numbers in the diet between the different categories may be an effect of the small sample set. Future studies using techniques relying on biopsies and not on dead animals, such as fatty acid analysis, are needed to further investigate the dietary differences between classes of the population. However, the present study highlights the importance of the edges of the Auckland Islands shelf, where common prey of NZ sea lions such as schooling fish and squid aggregate. Though these key areas are far from the rookeries and impacted by the squid fishery, they may provide the only predictable and abundant resource needed to cover the cost of benthic foraging in the deepest diver of all otariids.

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APPENDIX

Regression equations used to estimate the length and mass of prey from otolith/beak measurements. HL is the hood length in mm, LRL is the lower rostral length in millimeters, DML is the dorsal mantle length in millimeters, M is the reconstructed biomass in grams, OL is the otolith length in millimeters, OD is the longest otolith diameter in millimeters, SL is the standard length and TL is the total length. For these last two measurements, the unit is specified in the equations. N is the number of measurements used to construct the equations, r is the correlation coefficient. *No regression was available within the same family thus a regression of a species from a related family has been used.

Prey species	Species used for length estimate	Estimated length	N	r	Source	Species used for mass estimate	Estimated mass	N	r	Source
FISH										
<i>Argentina elongata</i>	<i>A. silus</i>	$TL_{cm} = 3.87 OL$	15	0.95	Leopold <i>et al.</i> 2002	<i>A. silus</i>	$M = (0.16TL_{cm})^{3.46}$	7	0.99	Leopold <i>et al.</i> 2002
<i>Brama brama</i>	Same	$\ln TL_{mm} = 5.2987 + 0.5586 \ln OD$	43	0.787	Smale <i>et al.</i> 1995	Same	$\ln M = 3.5947 + 2.1934 \ln OD$	43	0.772	Smale <i>et al.</i> 1995
<i>Trachurus</i> spp.	Same	$TL_{mm} = 17.82 OL^{1.325}$	65		Fea <i>et al.</i> 1999	Same	$M = 0.034OL^{4.285}$	44		Fea <i>et al.</i> 1999
<i>Seriolella brama</i>	<i>Seriolella</i> spp.	$TL_{mm} = 40.475 OL^{1.043}$	10	0.79	L. Meynier, unpublished data	<i>Seriolella punctata</i>	$M = 0.0193TL_{cm}^3$			Froese and Pauly 2007
<i>Seriolella caerulea</i>	<i>Seriolella</i> spp.	$TL_{mm} = 40.475 OL^{1.043}$	10	0.79	L. Meynier, unpublished data	<i>Seriolella punctata</i>	$M = 0.0193TL_{cm}^3$			Froese and Pauly 2007

<i>Seriolella punctata</i>	<i>Seriolella</i> spp.	$TL_{mm} = 40.475 OL^{1.043}$	10	0.79	L. Meynier, unpublished data	Same	$M = 0.0193TL_{cm}^3$	Froese and Pauly 2007
<i>Seriolella</i> spp.	Same	$TL_{mm} = 40.475 OL^{1.043}$	10	0.79	L. Meynier, unpublished data	<i>Seriolella punctata</i>	$M = 0.0193TL_{cm}^3$	Froese and Pauly 2007
<i>Congiopodus coriaceus</i>	<i>C. spinifer</i>	$\ln TL_{mm} = 3.799 + 1.1698 \ln OD$	46	0.923	Smale et al. 1995	<i>C. spinifer</i>	$\ln M = -0.0974 + 3.5938 \ln OD$	45 0.919 Smale et al. 1995
<i>Gnathobobis habenatus</i>	<i>Bassanago albescens</i>	$\ln TL_{mm} = 4.1576 + 1.0912 \ln OD$	43	0.919	Smale et al. 1995	<i>Bassanago albescens</i>	$\ln M = -2.1867 + 3.9603 \ln OD$	43 0.916 Smale et al. 1995
<i>Enmelichthys nitida</i>	Same	$\ln TL_{mm} = 3.2242 + 1.2005 \ln OD$	40	0.983	Smale et al. 1995	Same	$\ln M = -2.4456 + 3.8311 \ln OD$	42 0.983 Smale et al. 1995
<i>Micromesistius australis</i>	<i>M. pontassou</i>	$TL_{cm} = 5.65 + 2.660L$	101	0.99	Leopold et al. 2002	Same	$M = 0.004688TL_{cm}^{3.0931}$	441 0.98 O'Driscoll and Bagley 2001
<i>Thysites atun</i>	Same	$\ln SL_{mm} = 3.9602 + 1.1198 \ln OD$	53	0.98	Smale et al. 1995	Same	$\ln M = -1.7389 + 3.9189 \ln OD$	61 0.994 Smale et al. 1995

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APPENDIX (Continued)

Prey species	Species used for length estimate	Estimated length	N	r	Source	Species used for mass estimate	Estimated mass	N	r	Source
<i>Gonorynchus gonorynchus</i>	Same	$\ln TL_{mm} = 4.4773 + 1.0094 \ln OD$	25	0.988	Smale <i>et al.</i> 1995	Same	$\ln M = 0.7456 + 3.3375 \ln OD$	25	0.988	Smale <i>et al.</i> 1995
<i>Coelorinchus</i> spp.	<i>C. aspercephalus</i>	$TL_{cm} = 1.488 OL^{1.271}$			Holborow 1999	<i>C. aspercephalus</i>	$M = 0.0110L^{3.946}$			Holborow 1999
<i>Lepidorhynchus denticulatus</i>	Same	$TL_{cm} = 2.216 OL^{1.153}$			Holborow 1999	Same	$M = 0.010L^{3.697}$			Holborow 1999
<i>Macraronus novaezelandiae</i>	Same	$TL_{mm} = 16.31 OL^{1.238}$			Fea <i>et al.</i> 1999	Same	$M = 0.004771TL_{cm}^{2.8796}$			O'Driscoll and Bagley 2001
<i>Merluccius australis</i>	<i>Macraronus novaezelandiae</i>	$TL_{mm} = 16.310L^{1.238}$			Fea <i>et al.</i> 1999	Same	$M = 0.004771TL_{cm}^{2.8796}$			O'Driscoll and Bagley 2001
<i>Anstrophyxis marginata</i>	<i>Pseudophycis bachus</i>	$TL_{mm} = 7.2670L^{1.625}$			Fea <i>et al.</i> 1999	<i>Pseudophycis bachus</i>	$M = 0.0030L^{4.979}$			Fea <i>et al.</i> 1999
<i>Pseudophycis bachus</i>	Same	$TL_{mm} = 7.2670L^{1.625}$			Fea <i>et al.</i> 1999	Same	$M = 0.0030L^{4.979}$			Fea <i>et al.</i> 1999
<i>Paraperchis colias</i>	<i>Haliidesmus scapularis</i> *	$\ln TL_{mm} = 4.2174 + 1.3009 \ln OD$	93	0.883	Smale <i>et al.</i> 1995	Same	$M = 0.01TL_{cm}^{3.1}$	93	0.875	Froese and Pauly 2007
<i>Diaphus danae/budonil meadi</i>	<i>D. budoni</i>	$\ln SL_{mm} = 2.7179 + 1.0077 \ln OD$	24	0.959	Smale <i>et al.</i> 1995	<i>D. budoni</i>	$\ln M = -2.1402 + 2.487 \ln OD$	23	0.937	Smale <i>et al.</i> 1995
<i>Lampanyctodes bectori</i>	Same	$SL_{mm} = 21.880L^{1.239}$			Fea <i>et al.</i> 1999	Same	$M = 0.1230L^{3.838}$			Fea <i>et al.</i> 1999

<i>Myctophum bigyphum</i>	<i>Lampanyctodes bectori</i>	$SL_{mm} =$ 21.880L ^{1.239}	Fea et al. 1999	<i>Lampanyctodes bectori</i>	$M = 0.1230L^{3.838}$	Fea et al. 1999
<i>Scopelosaurus</i> spp.	<i>Saurida in-</i> <i>disquani</i> *	$\ln TL_{mm} =$ 3.0124 + 1.1711 $\ln OD$	0.969	<i>S. adleri</i>	$M = 0.00097L_{cm}^{3.4867}$	0.964 Froese and Pauly 2007
<i>Genypterus blacodes</i>	<i>G. capensis</i>	$\ln TL_{mm} =$ 2.393 + 1.563 $\ln OD$	0.984	<i>G. capensis</i>	$\ln M = -6.4094 +$ 5.2076 $\ln OD$	0.984 Smale et al. 1995
<i>Hemerochetes artus</i>	<i>Hemerochetes</i> spp.	$SL_{mm} = 34.297$ + 32.553 OL	0.46	L. Meynier, unpublished data	$M = 3 \cdot 10^{-8} SL_{mm}$ ^{3.9565}	0.9 L. Meynier, unpublished data
<i>Hemerochetes monopterygius</i>	<i>Hemerochetes</i> spp.	$SL_{mm} = 34.297$ + 32.553 OL	0.46	L. Meynier, unpublished data	$M = 3 \cdot 10^{-8} SL_{mm}$ ^{3.9565}	0.9 L. Meynier, unpublished data
<i>Hemerochetes</i> spp.	Same	$SL_{mm} = 34.297$ + 32.553 OL	0.46	L. Meynier, unpublished data	$M = 3 \cdot 10^{-8} SL_{mm}$ ^{3.9565}	0.9 L. Meynier, unpublished data
<i>Neophrystichthys latus</i>	Same	$TL_{mm} =$ -73.201 + 81.024 OL	S. Childerhouse, unpublished data	<i>Helicolenus dacty-</i> <i>lopterus</i> *	$\ln M = -3.2748 +$ 3.8463 $\ln OD$	0.982 Smale et al. 1995

(Continued)

APPENDIX (Continued)

Prey species	Species used for length estimate	Estimated length	N	r	Source	Species used for mass estimate	Estimated mass	N	r	Source
<i>Halicolinus peronii</i>	<i>H. dactylopterus</i>	$\ln SL_{mm} = 2.6947 + 1.2357 \ln OD$	195	0.977	Smale <i>et al.</i> 1995	<i>H. dactylopterus</i>	$\ln M = -3.2748 + 3.8463 \ln OD$	171	0.982	Smale <i>et al.</i> 1995
SpA Scorpaenidae	<i>H. dactylopterus</i>	$\ln SL_{mm} = 2.6947 + 1.2357 \ln OD$	195	0.977	Smale <i>et al.</i> 1995	<i>H. dactylopterus</i>	$\ln M = -3.2748 + 3.8463 \ln OD$	171	0.982	Smale <i>et al.</i> 1995
CEPHALOPODS										
<i>Enteroteuthis zealandicus</i>	<i>Octopus vulgaris</i>	$DML = 5.39 + 24.9HL$			Clarke 1986	<i>Octopus vulgaris</i>	$\ln M = 1.82 + 3.03 \ln HL$			Clarke 1986
Octopoteuthidae	<i>Octopoteuthis</i> sp.	$DML = -0.4 + 17.3LRL$			Clarke 1986	<i>Octopoteuthis</i> sp.	$\ln M = 0.166 + 2.31 \ln LRL$			Clarke 1986
<i>Nototodarus sloani</i>	<i>Nototodarus</i> spp. (east coast)	$\ln DML = 4.18 + 0.788 \ln LRL$			Clarke 1986	<i>Nototodarus</i> spp. (east coast)	$\ln M = 1.79 + 2.41 \ln LRL$			Clarke 1986
<i>Moroteuthis ingens</i>	Same	$DML = 39.61LRL - 13.58$	137	0.92	Jackson 1995	Same	$\ln M = -0.068 + 3.5 \ln LRL$			Clarke 1986
Sepiolidae	<i>Sepiolla</i> spp.	$DML = 5.39 + 24.9HL$			Clarke 1986	<i>Sepiolla</i> spp.	$\ln M = 0.4 + 0.35 \ln HL$			Clarke 1986