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Hector's dolphin diet: The species, sizes and relative importance of prey eaten by *Cephalorhynchus hectori*, investigated using stomach content analysis

ELANOR MILLER,[1] Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand; CHRIS LALAS, PO Box 31, Portobello, Dunedin, 9048, New Zealand; STEVE DAWSON, Department of Marine Science, University of Otago, PO Box 56, Dunedin, New Zealand; HILTRUN RATZ, PO Box 31, Portobello, Dunedin, 9048, New Zealand; ELISABETH SLOOTEN, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand.

Abstract

Stomach contents of 63 Hector's dolphins (*Cephalorhynchus hectori*) were collected between 1984 and 2006 from throughout New Zealand to provide the first quantitative assessment of prey composition. Twenty-nine taxa were identified. Those most commonly consumed were red cod (*Pseudophycis bachus*), ahuru (*Auchenoceros punctatus*), arrow squid (*Nototodarus* sp.), sprat (*Sprattus* sp.), sole (*Peltorhamphus* sp.), and stargazer (*Crapatalus* sp.). By mass, these six species contributed 77% of total diet. Red cod contributed the most in terms of mass (37%), while ahuru and Hector's lanternfish (*Lampanyctodes hectoris*) were consumed in large numbers. Prey ranged from <1 cm to >60 cm in total length, but the majority of prey items were <10 cm long, indicating that for some species, juveniles were targeted. Diets of dolphins from South Island east and west coasts were significantly different, due largely to javelinfish (*Lepidorhynchus denticulatus*) being of greater importance in west coast stomachs, and a greater consumption of demersal prey species in the east. The feeding ecology of Hector's dolphin is broadly similar to that of other *Cephalorhynchus* species. Hector's dolphin is shown to feed on species from throughout the water column, and differences in diet between populations are thought to reflect prey availability.

Key words: Hector's dolphin, Maui's dolphin, *Cephalorhynchus hectori*, stomach content analysis, diet, prey size, feeding ecology, habitat selection.

Dietary studies provide important insight into interactions among species and help to define a species' ecological role. Such studies not only increase ecological understanding, but can prove valuable to conservation efforts by aiding predictions of how a species will respond to anthropogenic disturbance and climate change (Heithaus and Dill 2002, Grémillet and Boulinier 2009).

Hector's dolphin (*Cephalorhynchus hectori*) is endemic to New Zealand, and is currently divided into two genetically distinct subspecies (Baker *et al.* 2002).

[1]Corresponding author (e-mail: elanorjh@gmail.com).

Hector's dolphin (*C. hectori hectori*) is distributed in three distinct regional populations throughout the South Island, and Maui's dolphin (*C. hectori maui*) is found along the North Island west coast (Pichler *et al.* 1998, Pichler 2002). Total abundance is estimated at 7,270 individuals (CV = 16.2%; Slooten *et al.* 2004) for the South Island population, which is classified as Endangered (IUCN 2012), and 111 individuals (CV = 44%; Slooten *et al.* 2006) for the Critically Endangered (IUCN 2012) Maui's dolphin.

For both subspecies, substantial population decline due to bycatch in gill and trawl nets (Dawson 1991, Dawson and Slooten 2005) has been indicated by stochastic population viability analyses (*e.g.*, Slooten *et al.* 2000, Slooten and Dawson 2010) and loss of genetic variation (Pichler and Baker 2000). Other potential threats include indirect fisheries interactions, habitat degradation associated with aquaculture and dredging, and impacts of tourism. Knowledge of the prey eaten by the dolphins and their relative dietary importance may help to predict where and when there is potential for such interaction, and help in understanding population recovery.

Hector's dolphins have a very patchy distribution both between and within populations (Dawson and Slooten 1988, Dawson *et al.* 2004, Rayment *et al.* 2011). Seasonal distributional patterns have been well documented, with the dolphins clustered inshore in summer and more evenly distributed in winter (Rayment *et al.* 2010). Being small cetaceans living in a cold water environment, Hector's dolphins have high energy requirements, so it is reasonable to hypothesize that their distribution will in part be driven by that of their prey. Dietary studies are the first step in investigating this link.

Hector's dolphin is one of four species in the genus *Cephalorhynchus*. All are small dolphins, endemic to coastal waters in the temperate Southern Hemisphere. They occur primarily in waters less than 150 m deep and are all susceptible to entanglement in net fisheries (Dawson 2009). The diet of the other *Cephalorhynchus* species has been described from a small number of bycaught individuals. Chilean dolphins (*C. eutropia*) have been found to eat primarily small schooling fish and squid (Torres *et al.* 1992). The main species found in stomach contents of Heaviside's dolphin (*C. heavisidii*) were demersal species, particularly juvenile hake (*Merluccius* spp.), as well as small pelagic fish (Sekiguchi *et al.* 1992). Hake was also found to be frequently consumed by Commerson's dolphin (*C. commersonii*), along with squid (Bastida *et al.* 1988, Crespo *et al.* 1997).

This study quantifies Hector's dolphin diet by analyzing diagnostic prey remains from the stomach contents of bycaught and beachcast individuals. We describe the prey species taken, quantify relative importance *via* estimation of prey size from fish otoliths and squid beaks, and investigate dietary differences between the two main Hector's dolphin populations on the South Island east and west coasts. Our results are discussed in the context of prey availability, based upon current knowledge of prey assemblages available to Hector's dolphin. Hector's dolphin diet is then compared to the feeding ecology of the other *Cephalorhynchus* species.

Methods

Sample Collection

We analyzed stomach contents from a total of 71 dolphins that had been bycaught and beachcast throughout New Zealand between 1984 and 2006.

Location and date of the incident were recorded, along with body measurements, sex (when possible), and the extent of decomposition. Of the 71 stomachs and esophagi examined for prey remains, four dolphins contained only eroded remains that could not provide accurate measurements. For another four, prey remains had degraded beyond use for species identification or measurement due to long-term storage in formalin or ethanol. Omission of these eight samples reduced the sample size suitable for quantitative analysis to 63 dolphins from the North Island west coast (n = 2), and the South Island east (n = 36), west (n = 23), and south (n = 2) coasts. Of these 63 dolphins, 79% were known to have been bycaught, and were found either entangled in nets or with significant net marks indicating entanglement as the cause of death. Markings on the remaining carcasses suggest the dolphins were bycaught and none are known to have stranded alive, which is a very rare occurrence for this species.

Stomach Analysis

Stomach contents were washed through a 0.5 mm sieve and examined for diagnostic prey remains, including fish otoliths, cephalopod beaks, crustacean exoskeletons, and remains of cartilaginous fish (*e.g.*, teeth, spines). These were removed, air dried, and sorted by taxon. Otoliths and exoskeleton parts were stored in airtight plastic bags and beaks in 5% isopropyl alcohol solution. Prey remains were identified to genus or species if possible, by comparison with diagnostic remains for invertebrates and fish from the South Island continental shelf (Lalas reference collection), and using the reference texts of Smale *et al.* (1995) and Furlani *et al.* (2007).

Remains were separated into left and right otoliths, upper and lower beaks, and those too eroded or broken to identify or measure. For fish, the minimum number of each species ingested was calculated as the total number of left or right otoliths (whichever was the greater) plus half the number of eroded otoliths. For cephalopods, the minimum number ingested was calculated as the total number of upper or lower beaks (whichever was the greater) plus half the number of broken beaks.

Data Analysis

To estimate the original length and mass of prey items from their diagnostic remains we calculated power equations (Appendix 1A, B), following Smale *et al.* (1995). Whole fish, cephalopods, and crustaceans in Lalas' reference collection were measured and weighed when freshly caught (to a precision of 1 mm and 1 g).

Prey remains from stomachs collected prior to 2002 were measured using digital calipers to the nearest 0.01 mm. Otolith length and width, and beak rostral length were recorded. Due to the small size and large quantity of otoliths in some samples, otolith remains gathered post 2002 were digitally photographed and measured using ImageJ software (Abramoff *et al.* 2004). To test the difference between the two measurement methods, a subsample of post 2002 otoliths from three species: ahuru (*Auchenoceros punctatus*), red cod (*Pseudophycis bachus*), and hoki (*Macruronus novaezelandiae*), were measured using both calipers and ImageJ software. These species were chosen as they provide a good representation of the range in size and shape of all otoliths examined. Otolith size results did not significantly differ between the two methods (paired t-test, $t_{72} = 1.355$, $P = 0.180$) and no measurement bias was found ($r^2 = 0.98$, $P < 0.001$).

For each species in each sample, the left or right otolith measurements (whichever were the more numerous) were used as input in the equations to estimate the size of the prey. Similarly, squid size was estimated from the size of upper or lower squid beaks. In the case where both categories contained the same number of measured samples, the measurements for left otoliths and lower beaks were used in the power equations.

In order to mitigate biases associated with the analysis of digested prey remains, and avoid underestimating prey size (Jobling and Breiby 1986, Pierce and Boyle 1991), eroded otoliths were not measured. Eroded otoliths were allocated either the average size of conspecifics in the same stomach, or if no others were present, conspecifics across all stomach samples (*e.g.,* Gannon and Waples 2004).

The relative importance of each species was estimated as %O (the percentage of stomachs examined containing that species), %N (the percentage of the total number of prey in all stomachs), and %M (the percentage of the total mass of prey in all stomachs). The total reconstructed mass of a prey species was calculated as the product of the number of prey items eaten and the average mass of that species. Each of these measures provides different information on the dolphins' feeding habits and the relative importance of prey species in their diet.

To assess sample size sufficiency in describing Hector's dolphin diet, the order of stomachs sampled was randomized 10,000 times, and the cumulative number of species discovered plotted as a function of stomach number (Ferry and Cailliet 1996, Cortés 1997).

Diet Variability

The size of our sample allows comparison of diet between males ($n = 30$) and females ($n = 27$) from the two main populations; the South Island east coast (SIEC; $n = 35$) and west coast (SIWC; $n = 22$). Both factors were analyzed in $R_{2.11.1}$ using the Scheirer-Ray-Hare (SRH) test, an extension of the Kruskal-Wallis test (Dytham 2011), with a sequential Bonferroni adjustment of α to minimize Type 1 errors (Rice 1989). Sample size was insufficient to compare diet across years, seasons or dolphin ages. The majority of samples (84%) were collected during spring and summer months.

Due to the large number of zeros typical of stomach content data, parametric testing using two-way ANOVA was not valid. The SRH test was used to compare both the number and mass of common prey consumed, as well as overall prey diversity, calculated using the Shannon-Weiner Diversity Index (H′) (Krebs 1989). Prey were considered common when their occurrence was >25% for any group of the sample set.

Categorization of prey species by habitat (Paulin *et al.* 2001) provides insight into where in the water column Hector's dolphins forage. Three habitat categories were defined as follows: Demersal: live and feed on or near the seafloor; Benthopelagic: live and feed at the seafloor and throughout the water column; Epipelagic: live and feed in surface waters. Occurrence of each prey type was examined for all stomachs collected, and compared between populations and sexes using the SRH test.

Results

Overall Diet Composition

In total, 22 fish, two cephalopod, and five crustacean species were identified from the diagnostic remains of all 63 stomachs examined (Table 1). This equated to a minimum number of 4,460 prey items with a total reconstructed mass of 55,104 g. In terms of number and mass eaten, fish contributed most to the dolphins' diet (95% and 87% respectively), followed by cephalopods (3% and 13%) and crustaceans (1% and <1%).

Thirteen of the 22 prey species occurred in >10% of all the stomachs examined (Table 2), while only four; red cod, ahuru, arrow squid (*Nototodarus* sp.) and sprat (*Sprattus* sp.); were commonly eaten (>25% O). Red cod and ahuru were the most frequently eaten prey, found in 59% and 49% of all stomachs respectively. Red cod, being a relatively large fish compared to ahuru, contributed little in terms of the number of fish eaten over all stomachs examined (4%, compared to 22% for ahuru), but made a high contribution in terms of mass (37% compared to 7% for ahuru). Arrow squid was the only other species contributing >10% in terms of mass, while Hector's lanternfish (*Lampanyctodes hectoris,* 21% N) and sole (*Peltorhamphus* sp., 17% N) were also eaten in relatively large numbers.

Stomachs of the six smallest Hector's dolphins analyzed in this study contained milk but no prey remains. These dolphins (six females, one male) were 77–90 cm standard length (SL: snout tip to tail notch). The next largest dolphin, measuring 99 cm SL (female), contained milk and arrow squid prey remains. Milk was not found in stomachs of any dolphins larger than 107 cm.

Only three items, two crab naupilii (length *ca.* 0.5 cm), and one parasitic isopod (length *ca.* 1 cm), were inconsistent with direct capture by dolphins and these were not included in analyses. One stomach contained only fresh and intact Graham's gudgeon (*Grahamichthys radiata*) measuring 3.0–5.6 cm. This verified that very small fish are taken directly by Hector's dolphins. None of the species and size mixtures in any stomachs were compatible with smaller items being derived from the stomach contents of larger prey.

Figure 1 indicates that when sampled in random order, the first 30 stomachs examined accumulate on average 24 of the 29 prey species. Overall, our samples appear to be approaching an asymptote.

Length Distribution

Reconstructed prey lengths show that Hector's dolphins consume prey ranging from less than 1 cm to greater than 60 cm in total length (Fig. 2). The distribution of prey size is highly skewed, with over 75% of the prey items measuring less than 10 cm (Fig. 2). Prey consistently larger than 10 cm were pilchard (*Sardinops neopilchardus*), yelloweyed mullet (*Aldrichetta forsteri*) and rattail (*Coelorinchus aspercephalus*), from which only a small number of otoliths were available for measurement (n = 9, 10, 7, respectively). The largest prey item found was a 60.8 cm long arrow squid, far above the mean length for this species in this study (17.1 cm total length; Table 1).

Table 1. A list of all prey identified and their reconstructed mass and length. Data were collected from diagnostic remains from 63 stomach contents of Hector's dolphins bycaught and beachcast throughout New Zealand between 1985 and 2006.

Prey			Mass (g)			Length (cm)		
		n	Mean ± SD	Minimum	Maximum	Mean ± SD	Minimum	Maximum
Fish								
Sardinops neopilchardus	Pilchard	9	24.6 ± 9.4	11	41	13.3 ± 1.7	11	16
Sprattus sp.	Sprat	86	12.1 ± 13.0	2	91	10.4 ± 2.1	7	19
Engraulis australis	Anchovy	29	4.0 ± 1.9	2	8	7.8 ± 1.2	6	10
Lampanyctodes hectoris	Hector's lanternfish	365	2.1 ± 0.9	0.7	7	5.9 ± 0.7	4	9
Auchenoceros punctatus	Ahuru	520	4.0 ± 3.8	0.1	20	8.3 ± 3.3	2	16
Pseudophycis bachus	Red cod	170	107.6 ± 135.6	0.1	830	17.9 ± 10.1	2	44
Macruronus novaezelandiae	Hoki	15	93.3 ± 63.8	2	266	28.9 ± 8.9	8	45
Merluccius australis	Hake	32	65.0 ± 64.6	4	313	20.0 ± 6.6	9	37
Coelorinchus aspercephalus	Oblique banded rattail	7	60.9 ± 33.3	16	104	23.1 ± 4.7	16	28
Lepidorhynchus denticulatus	Javelinfish	106	21.9 ± 28.1	0.1	162	18.6 ± 5.7	3	28
Paratrachichthys trailli	Common roughy	1	92.6	-	-	9.5	-	-
Nemadactylus macropterus	Tarakihi	15	12.4 ± 4.5	7	25	9.2 ± 1.0	8	12
Aldrichetta forsteri	Yelloweyed mullet	10	158.3 ± 107.3	20	302	21.0 ± 6.6	12	28

(Continued)

Table 1. *(Continued)*

Prey		*n*	Mass (g)			Length (cm)		
			Mean ± SD	Minimum	Maximum	Mean ± SD	Minimum	Maximum
Notolabrus sp.	Wrasse	1	215.8	-	-	22.3	-	-
Crapatalus sp.	Stargazer	128	14.7 ± 25.1	0.8	128	10.2 ± 4.1	5	24
Forsterygion sp.	Triplefin	1	2.0	-	-	6.0	-	-
Grahamichthys radiata	Graham's gudgeon	160	0.5 ± 0.4	0.1	2	4.1 ± 0.6	3	6
Thyrsites atun	Barracouta	6	27.6 ± 14.9	3	44	18.2 ± 4.8	9	22
Seriolella brama	Blue warehou	4	28.2 ± 32.4	3	73	10.2 ± 4.5	6	16
Pelotretis flavilatus	Lemon sole	1	195.8	-	-	27.8	-	-
Peltorhamphus sp.	Sole	1,258	5.4 ± 48.0	0.1	1282	4.4 ± 4.0	0.5	50
Rhombosolea sp.	Flounder	1	37.0	-	-	18.6	-	-
Cephalopod								
Nototodarus sp.	Arrow squid	75	48.3 ± 118.9	0.1	960	17.1 ± 9.4	3	61
Sepioloidea pacifica	Pacific bobtail squid	4	4.3 ± 1.8	2	6	1.8 ± 0.2	2	2
Crustacean								
Pontophilus australis	Sand shrimp	1	0.4	-	-	3.6	-	-
Halicarcinus sp.	Pillbox crab	46	0.1 ± 0.1	0.1	0.7	0.6 ± 0.2	0.3	1
Macrophthalmus hirtipes	Mud crab	3	2.5 ± 0.6	2	3	1.9 ± 0.2	2	2
Nectocarcinus antarcticus	Red swimming crab	1	0.2	-	-	0.9	-	-
Ovalipes catharus	Paddle crab	4	3.6 ± 5.7	0.2	12	2.1 ± 1.3	1	4

Table 2. Composition of stomach contents from Hector's dolphins from the South Island east coast (SIEC), west coast (SIWC), south coast (SISC), and North Island west coast (NIWC). Diet composition is presented for male and female dolphins, and those of unknown sex, and is defined by three measures (%O/%N/%M): percentage by occurrence, number, and mass. The symbol "+" is used to indicate <0.5%.

	All samples	SIEC			SIWC			SISC	NIWC	
		Male	Female	Unknown	Male	Female	Unknown	Female	Male	Female
Prey	n = 63	n = 19	n = 16	n = 1	n = 11	n = 11	n = 1	n = 2	n = 1	n = 1
Fish										
Pilchard	3/+/1				18/1/5					
Sprat	25/8/7	26/20/16	19/4/2		45/5/7	18/+/+	100/56/63			
Anchovy	11/2/1		6/+/+		27/5/3	27/2/1				
Hector's lanternfish	14/21/3	11/8/1	6/3/+	100/96/73	27/24/9	18/31/5				
Ahuru	49/22/7	37/17/3	56/19/6		64/16/15	45/45/9	100/17/1		100/100/100	100/43/6
Red cod	59/4/37	79/4/39	63/8/60	100/3/21	27/+/1	36/6/42	100/7/17	100/17/27		100/40/7
Hoki	10/+/3	5/+/3			18/+/8	27/+/6				
Hake	13/1/4	16/1/1	6/1/3		27/1/19	9/+/3				
Oblique banded rattail	5/+/1	5/+/1	6/+/2			9/+/1				
Javelinfish	8/3/5				27/4/12	18/6/13				
Common roughy	2/+/+					9/+/1				
Tarakihi	3/1/1	5/2/2			9/1/1					
Yelloweyed mullet	14/+/3	26/+/9	13/+/2			9/+/+	100/7/5			

(Continued)

Table 2. (*Continued*)

Prey	All samples	SIEC			SIWC			SISC	NIWC	
		Male	Female	Unknown	Male	Female	Unknown	Female	Male	Female
	n = 63	n = 19	n = 16	n = 1	n = 11	n = 11	n = 1	n = 2	n = 1	n = 1
Wrasse	2/+/+	5/+/1								
Stargazer	21/5/6	21/6/9	38/21/11		9/+/1	18/1/1				
Triplefin	2/+/+	5/+/+								
Graham's gudgeon	13/11/+	21/33/1	19/12/+		9/1/+					
Barracouta	3/+/+		6/1/1			9/+/+				
Blue warehou	6/+/+	5/+/1			9/+/+	18/1/+				
Lemon sole	2/+/+		6/+/1							
Sole	21/17/7		38/21/10		18/40/11	18/3/5	100/3/1	50/8/40		100/15/86
Flounder	2/+/+									100/2/1
Cephalopod										
Arrow squid	37/3/13	26/4/12	26/6/1	100/1/6	36/1/7	55/3/12	100/10/13	100/75/33		
Pacific bobtail squid	6/+/+	5/+/+	19/1/+							
Crustacean										
Sand shrimp	2/+/+		6/+/+							
Pillbox crab	11/1/+	24/4/+	13/1/+		9/+/+					
Mud crab	3/+/+		13/+/+							
Red swimming crab	2/+/+	5/+/+								
Paddle crab	5/+/+	5/+/+	13/+/+							

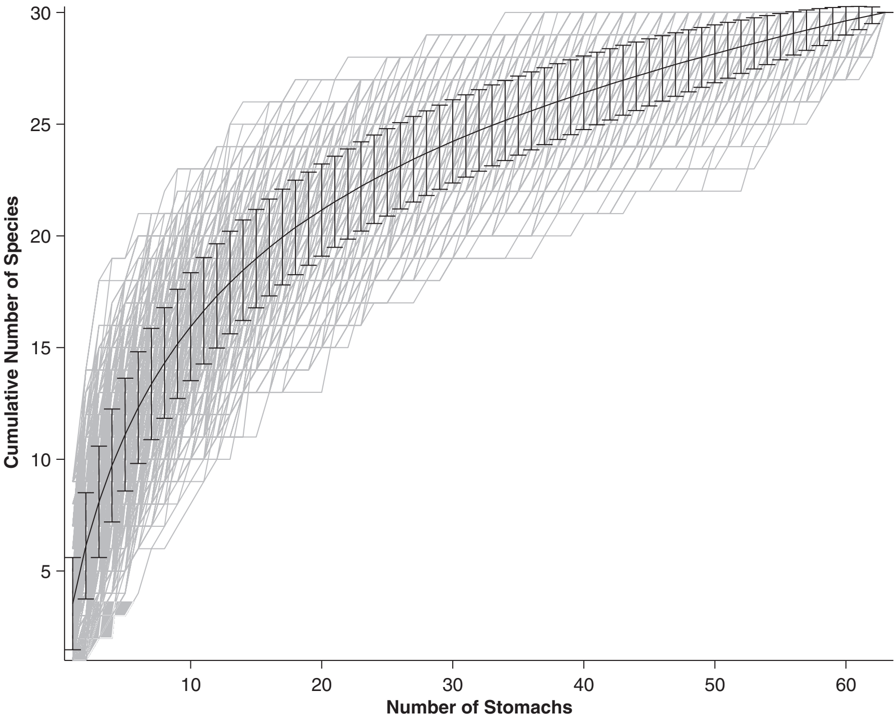

Figure 1. The cumulative number of species discovered as a function of stomach number for 10,000 randomized selections of the stomachs examined (shown in gray). The black line indicates the mean cumulative number of species ± standard deviation.

Diet Variability

SIEC samples contained a total of 25 prey species (18 fish, two cephalopod, and five crustacean) from 36 stomach samples (Table 2). A minimum number of 2,024 prey items were eaten, with a total reconstructed mass of 29,491 g. Overall, commonly consumed prey (>25% O) were ahuru, red cod, and arrow squid. Sprat and yelloweyed mullet were found in 26% of male stomachs while 38% of females had consumed stargazer (*Crapatalus* sp.) and sole. Red cod contributed most to prey mass, particularly for females, while Graham's gudgeon, sprat, stargazer, sole, and ahuru were eaten in large numbers.

SIWC samples contained a total of 20 prey species (18 fish, one cephalopod, and one crustacean) from 23 stomach samples (Table 2). This equated to a minimum number of 2,363 prey items, with a total reconstructed mass of 20,513 g. On the west coast, other species commonly consumed were anchovy (*Engraulis australis*), Hector's lanternfish, hake (*Merluccius australis*), hoki, and javelinfish (*Lepidorhynchus denticulatus*). Only red cod contributed substantially to the mass of prey, while large numbers of ahuru, sole, and Hector's lanternfish were eaten.

All comparisons revealed no significant interaction between population and sex (SRH test, $P > 0.05$) so these factors can be examined independently. A significantly greater number and mass of javelinfish were eaten on the SIWC than the

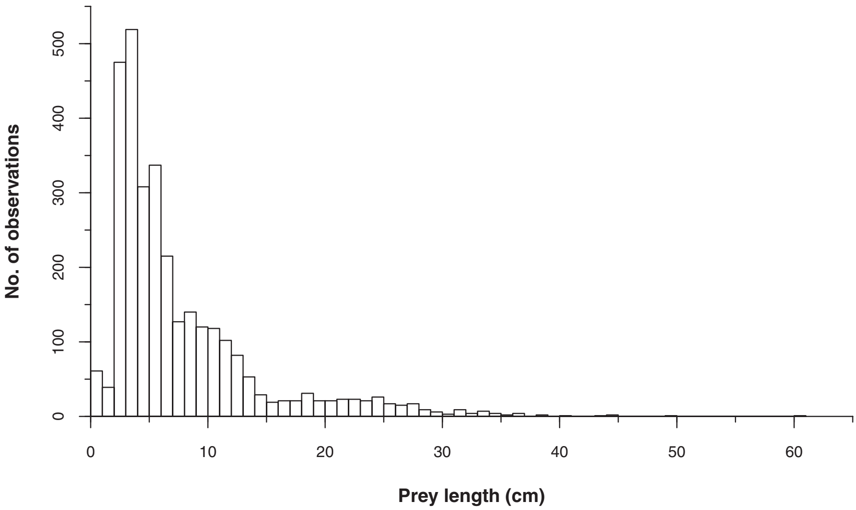

Figure 2. Length distribution of prey consumed by Hector's dolphins throughout New Zealand, combined across all stomachs examined ($n = 63$).

SIEC ($H_1 = 8.566$, $P = 0.003$; $H_1 = 8.543$, $P = 0.003$, respectively). SIWC dolphins also consumed a significantly greater number of anchovy ($H_1 = 9.658$, $P = 0.002$). No significant differences were found between sexes with sequential Bonferroni correction.

Prey diversity (H′) varied from 0, for stomachs containing only one prey species, to 1.66. On average, SIEC dolphins had higher prey diversity (H′ = 0.60) than those from the SIWC (H′ = 0.55). Female prey diversity (H′ = 0.60) was slightly higher than the average for males (H′ = 0.57). None of these comparisons was statistically significant (SRH test, $P > 0.05$).

Both demersal and benthopelagic prey species were found in a high percentage of all stomachs examined (Fig. 3). Comparisons of the number of prey species consumed from each habitat indicated no significant interaction between population and sex, and no significant effect of sex (SRH test, $P > 0.05$). SIEC and SIWC dolphins were found to forage to a different extent in each habitat, however. As indicated by Figure 3, significantly more benthopelagic and epipelagic species were eaten on the west coast ($H_1 = 5.708$, $P = 0.017$; $H_1 = 8.487$, $P = 0.004$, respectively), while SIEC dolphins consumed a greater number of demersal species ($H_1 = 11.332$, $P = 0.001$).

Discussion

Dietary Composition and Prey Distribution

Hector's dolphins eat a wide variety of prey species, with a total of 29 identified from the 63 stomachs examined. The rate of species discovery suggests that while the analysis of additional stomachs may reveal new prey species, the current sample represents the diet of Hector's dolphins fairly well. While a broad range of species were eaten, only a few were common and contributed

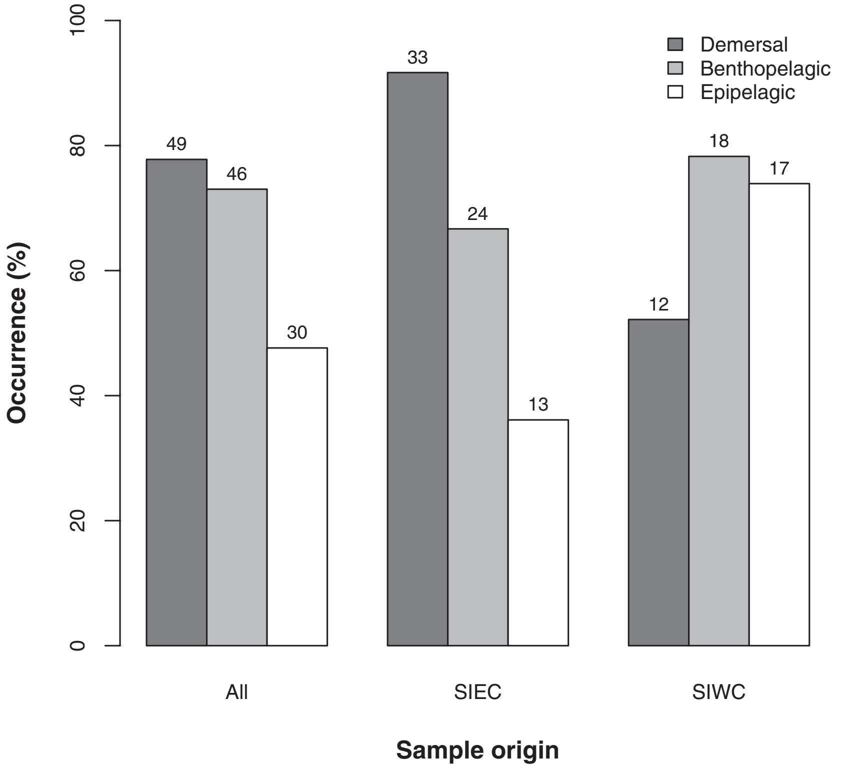

Figure 3. Occurrence (%) of prey types in all stomachs examined (n = 63), and those collected from the South Island east coast (SIEC; n = 36) and west coast (SIWC; n = 23). Numbers above each bar indicate absolute occurrence (the number of stomachs containing each prey type).

substantially to the dolphins' diet. Overall, the two prey species with the greatest contribution were red cod and ahuru. These prey were the most commonly consumed and contributed most in terms of mass and number respectively.

Hector's dolphins evidently forage throughout the water column. The prey species identified in this study come from a wide range of habitats. Both epipelagic prey and those living near the seafloor frequently occurred in the stomachs examined, but overall, demersal and benthopelagic prey were most prevalent. This is consistent with incidental observations of foraging behavior made during long-term photo-identification studies of Hector's dolphins at Banks Peninsula. Surface feeding is not common, but has been observed throughout the year, in a range of water depths from 2 to 25 m, on small fish including sprat, pilchard, and yelloweyed mullet. White-fronted terns (*Sterna striata*) are often seen diving in an apparent commensal association with surface-feeding dolphins, likely due to increased accessibility of prey (Bräger 1998). Feeding at depth is not directly observable, but is assumed to be the main activity during "long-diving" in which dolphins dive for up to *ca*. 90 s (Slooten and Dawson 1994). Hector's dolphins have been observed following inshore trawlers in large groups in water 9–32 m deep (Rayment and Webster 2009), and are likely to be taking fish stirred up, but not caught by the trawl net. The trawl net and steeply descending traces consistent with dolphins diving to the seafloor around the net are regularly observed on the echosounder during these occasions.

Significant differences were found between the diets of dolphins from the South Island east and west coasts. One contributing factor to these differences was the presence of javelinfish in several west coast individuals. This species did not occur in samples from other regions. All five stomachs containing this species were collected near Haast in southern Westland, where deep water can be found close to shore. In this region, the 100 m and 500 m depth contours lie only approximately 9 and 17 km from shore, respectively. This contrasts with the wide continental shelf around Banks Peninsula on the east coast, where water is less than 100 m deep out to 37 km. from shore. Adult javelinfish have been found most commonly in water 80–450 m deep (*e.g.,* Last *et al.* 1983), but have also been recorded from as shallow as 60 m depth in Australian waters (Gomon *et al.* 1994).

Many fish surveys are carried out well beyond the typical extent of Hector's dolphin distribution, but available inshore data does provide some information on the assemblages present in Hector's dolphin habitat. Research trawls on the SIEC continental shelf and upper slope (10–400 m depth) have found two of the identified prey species; red cod and barracouta (*Thyrsites atun*) to be among the three most abundantly caught demersal fish, along with spiny dogfish (*Squalus acanthias*) (Beentjes *et al.* 2002). The characteristic teeth and dorsal fin spines of spiny dogfish were not present in our samples, so there is no indication that this species is eaten. During these trawls, several other prey species were also found to be among the most abundant in water <100 m deep, including tarakihi (*Nemadactylus macropterus*), sole, lemon sole (*Pelotretis flavilatus*), arrow squid and rattails (Beentjes *et al.* 2002). In these fish surveys, cod-end mesh size varied from 7.4 cm in winter surveys to 2.8 cm in the summer. The majority of red cod measured around 35 cm length, though individuals <20 cm were also caught. Tarakihi size peaked at 13–18 cm and arrow squid matched the size distribution of those eaten by Hector's dolphins well, with peaks at 10, 21, and 30 cm mantle length (Beentjes and Stevenson 2000).

Research trawl surveys on the SIWC in water 20–400 m deep (Stevenson and Hanchet 2010) found spiny dogfish, red cod, barracouta, and silver dory (*Cyttus novaezealandiae)* to make up over 51% of the total catch by weight. Arrow squid (*N. sloanii*), barracouta, and spiny dogfish occurred in over 90% of the tows. Tows shallower than 200 m caught 95% of the red cod biomass, with the highest catches between 25 and 100 m. In these surveys, a 6 cm cod-end mesh size was used. Again, relatively few captured red cod were smaller than 20 cm in length. Tarakihi were mainly >25 cm long, with >62% biomass caught between 100–200 m deep. Captured hoki were mainly 17–26 cm long.

Despite extensive surveys, Hector's dolphins are very rarely seen in water deeper than 90 m on the SIEC (*e.g.,* Rayment *et al*. 2010) and 60 m on the SIWC (*e.g.,* Rayment *et al.* 2011). Trawl surveys often do not cover the close inshore habitat <20 m deep where Hector's dolphins are most often encountered, especially in summer (Rayment *et al.* 2010). It is likely that many of the very small prey eaten by the dolphins (both juveniles of larger prey species such as red cod, and adults of smaller species such as triplefins [*Forsterygion* sp.]) are captured in these areas, particularly in bays and harbors. For example, in a study of fish species within a tidal flat of the Manukau Harbour, Morrison *et al.* (2002)

observed several Hector's prey species, including yelloweyed mullet, sole, flounder (*Rhombosolea plebeia*), anchovy, and Pacific bobtail squid (*Sepioloidea pacifica*). Most individuals they caught measured <10 cm long.

Hector's dolphins consumed prey up to 60.8 cm in total length, but the majority of prey measured <10 cm. Some species found in the stomach contents, including javelinfish and hake, are generally thought of as mid- to deep-water species, but it appears that Hector's dolphins are preying upon juvenile individuals, which range into shallower water. Hake adults for example, commonly occur in areas deeper than 350 m (Hurst *et al.* 2000), but immature individuals 25–40 cm long are widespread in water shallower than 100 m around the South Island (Patchell 1981). Juvenile red cod have been caught around New Zealand, mostly in water shallower than 250 m (Hurst *et al.* 2000). Tarakihi juveniles have been caught in bottom trawls mainly off the SIEC in water depth <100 m (Hurst *et al.* 2000), and are thought to be abundant in many rocky inshore areas, not available to trawl sampling (Annala 1987). Juvenile *N. gouldi* squid have been found mainly between the North Taranaki Bight and Westland <200 m deep, while *N. sloani* are distributed inshore to the east and south of the South Island (Hurst *et al.* 2000). Adult sole and flounder have been caught in research trawls mainly in <100 m of water (Anderson *et al.* 1998) while juveniles occur close inshore and seasonally use estuaries and harbors as nurseries (*e.g.,* Roper and Jillet 1981). Young blue warehou (*Seriolella brama*) are often found in small schools in harbors and bays (Ayling and Cox 1982) while adults range deeper out to 400 m (Hurst *et al.* 2000).

Hector's lanternfish were eaten by the dolphins in relatively large numbers. This species is considered to be one of the shallowest living myctophids, and is common over shelf and slope waters (Robertson 1977). The occurrence of lanternfish in Hector's dolphin stomachs suggests that some individuals of this fish species occur in shallow water. Lanternfish adults are frequently associated with the deep scattering layer, rising from deeper water to the surface at night, but current knowledge of Hector's dolphin movements indicates no evidence of foraging in such areas. Extensive visual observations during daylight hours indicate that the dolphins inhabit inshore waters shallower than *ca.* 90 m deep (*e.g.,* Rayment *et al*. 2010). Day and night acoustic surveys of dolphin density at Banks Peninsula have found no evidence of diel variation in movements (Rayment *et al*. 2009) and so it is unlikely that the dolphins gain access to prey such as lanternfish by moving out over deeper offshore water at night.

Several fish species have been found to increase in density inshore, in areas 30–100 m deep during the summer, with lower densities recorded in winter. Trawl surveys on the SIEC have found this to be the case for several Hector's prey species including red cod, barracouta, rattails, and tarakihi (Beentjes *et al.* 2002). As well as using protected inshore areas as nurseries, these patterns are possibly linked to movements of food sources. Red cod, for example, are known to feed extensively on squat lobster (*Munida gregaria*) during summer and autumn, which occur in large shoals throughout inshore waters and harbors during that time (Carter and Malcolm 1926). The habitat preferences of marine mammals are similarly assumed linked to prey to some degree (*e.g.,* reviewed by Stevick *et al.* 2002).

Cooperative feeding such as herding or corralling of prey has only rarely been observed for Hector's dolphins, though it has been described for related species, including Commerson's (Goodall *et al.* 1988) and Chilean dolphins (Heinrich

2006). Such behavior is often linked to the abundance of schooling prey in the region. When prey is more patchily distributed or less abundant, dolphins are more likely to forage individually (Würsig 1986).

Overall, our knowledge of Hector's dolphin diet and distribution suggests that these predators primarily consume small and often juvenile prey, the distribution of which corresponds to the dolphins' close proximity to shore, particularly in the summer months. Prey consumption appears to reflect species availability, which differs between the South Island east and west coasts, likely due in part to the bathymetric differences between these two regions.

Comparison with Other Species

Seasonal changes in distribution, potentially related to prey movements have also been reported for other small cetaceans including Chilean dolphin (Heinrich 2006) and Commerson's dolphin (Goodall 1988). Like most aspects of their biology, the diets of the other *Cephalorhynchus* species are less well-known than that of Hector's dolphin. It appears the diets are broadly similar however, as all species are reported to feed throughout the water column on demersal and pelagic prey, with both fish and cephalopods making a large dietary contribution. There are also similarities in the size of prey eaten, as juveniles appear to be targeted. All members of the genus have a coastal distribution, occurring primarily in waters shallower than 150 m (Dawson 2009) and so their diets of juvenile coastal species reflect their habitat preferences.

Like Hector's dolphins, Chilean dolphins have been observed surface feeding in association with terns, as well as long-diving (Ribeiro *et al.* 2007). Dietary information for this species comes from a small sample of twenty individuals, and little quantitative information has been reported. Known prey include pelagic species: anchovetas (*Engraulis ringens*), Chilean jack mackerel, (*Trachurus murphyi*), and herring (*Clupea bentincki*); as well as species associated with the seafloor: drum (*Cilus gilberti*), Patagonian blenny (*Eleginops maclovinus*), and Patagonian squid (*Loligo gahi*) (Torres *et al.* 1992). Patagonian squid were found in 30% of stomach contents examined. Several of these prey species inhabit estuaries and sheltered bays, especially in spring and summer.

From the stomach analysis of nine Commerson's dolphins in the San Jorge Gulf (Crespo *et al.* 1997), the most important prey were found to be juvenile hake (*Merluccius hubbsi*) and shortfin squid (*Illex argentinus*). Other species include Patagonian squid, bobtail squid (*Semirossia tenera*), anchovy (*Engraulis anchoita*), butterfish (*Stromateus brasiliensis*), and southern cod (*Patagonotothen ramsayi*). Hake consumed were *ca*. 10 cm long; smaller than those caught in a nearby fishery. Off Tierra del Fuego, the main prey were sprat (*Sprattus fuegensis*), hoki (*Macruronus magellanicus*), Patagonian squid, southern cod, and silverside (*Austroatherina* sp.) (Bastida *et al.* 1988). Iñíguez and Tossenberger (2007) observed Commerson's dolphins surface feeding on silverside, often herding the fish against anchored ships and piers, and close to kelp forests.

Sekiguchi *et al.* (1992) examined 21 stomach contents of Heaviside's dolphin, collected from stranded and bycaught individuals between 1969 and 1990. Overall, five cephalopod and 12 fish species were identified. Demersal prey, particularly hake and *Octopus* sp. contributed the most, though pelagic prey including goby (*Sufflogobius bibarbatus*) were also present. The hake and goby consumed were mainly juveniles, averaging 19.5 cm and 5.3 cm in length, respectively.

Interactions with Fisheries

There is no indication that Hector's dolphins scavenge fish from gill nets. Hickford *et al*. (1997) examined the size selectivity of mesh sizes commonly used by some commercial gill net fishermen in New Zealand. They found that 3.5 in. mesh catch peaked at 25 and 40 cm fork length, while 4.5 and 5.5 in. mesh mostly caught fish of 35 and 50 cm fork length. These sizes are well above the typical length of Hector's dolphin prey. Hector's dolphins are most often caught in inshore gillnet fisheries targeting rig (*Mustelus lenticulatus*), elephant fish (*Callorhyncus milii*), and school shark (*Galeorhinus galeus*) (Dawson 1991). These nets typically have larger mesh sizes (6.5–7 in., up to 9 in. for school shark) than tested by Hickford *et al.* (1997), hence are even less likely to catch fish small enough for Hector's dolphins to eat.

It is more likely that Hector's dolphins are susceptible to gill net entanglement because they feed throughout the water column, not only in surface waters but on the seafloor, and because their diet is similar to that of the targeted catch species. School sharks, for example, are known to feed on barracouta, anchovy, cod, crustaceans, small cephalopods, and demersal reef fish (Olsen 1954). Similar overlap in food sources is indicated for target species in the Gulf of Maine gill net fishery and harbor porpoise (Gannon *et al.* 1998), a species also very susceptible to gill net entanglement (Read and Gaskin 1988). Spatial overlap between commercially targeted Chondrichtyhans and Hector's dolphins is greatest in summer, when rig, elephant fish, and school shark are all well known to aggregate in inshore coastal waters (Francis 1998).

Of the main prey species, red cod is also important to both commercial and recreational fishermen. Over the course of this study, this species has been a key target species in the Southern Inshore Trawl Finfish Fishery (Ministry of Fisheries 2007) and biomass trends have shown a substantial decline since the mid-1990s (Ministry of Fisheries 2011). Red cod recruitment varies considerably between years, however the length and magnitude of decline in commercial and recreational catch indicate that fishing pressure may also be responsible for the decreased abundance (Ministry of Fisheries 2007). This is particularly the case on the SIEC, including Banks Peninsula, a stronghold for Hector's dolphins. This region has been important for recreational fishing of red cod in the past, but recently, local fishermen have found that what used to be one of the most abundant species is now relatively uncommon catch (Ministry of Fisheries 2007). As this study has shown red cod to contribute most in terms of mass to Hector's dolphin diet, this raises concern. Dietary analyses should continue in the future to assess whether decreased red cod availability is reflected in the current diet.

Limitations of this Method

Stomach content analysis has inherent biases which have been discussed extensively in the literature (*e.g.,* reviewed by Pierce and Boyle 1991). In this study, one potential limitation comes from the fact that our samples were not randomly gathered, but came from individuals found beachcast or recovered dead from gill nets. Sampling is therefore somewhat opportunistic, and so sample size is limited. Small sample sizes can lead to single individuals having a high influence on overall results. In this study for example, four of the five dolphins containing javelinfish remains were found entangled in the same net and so are potentially not representative of the west coast population as a whole.

Stomach content analysis only provides information on what has been recently ingested; the method does not take into account the different digestibility of prey items. This could lead to some prey species being more easily detected than others. Some prey remains, for example cephalopod beaks, may be retained in stomachs for long periods (Pitcher 1980), and prey with no hard parts or with cartilaginous skeletons are likely to be underestimated (Pierce and Boyle 1991). Partially digested otoliths could lead to an underestimation of original prey size (Jobling and Breiby 1986), which is why we did not measure eroded otoliths. Some prey remains may also be lost due to regurgitation; a few individuals in this study had prey remains in the esophagus.

Conclusion

This study presents the first quantitative analysis of Hector's dolphin diet, based on detailed analysis of stomach contents from 63 dolphins. The results indicate that Hector's dolphins take a wide variety of prey throughout the water column, but that their diet is dominated by a few demersal and mid-water species. Small and juvenile prey are targeted, the movements of which appear to reflect Hector's dolphins' coastal distribution. Comparable diets have been reported for related species with similar habitat preferences. Knowledge of Hector's dolphin diet may assist in interpreting habitat preferences and behavioral patterns. Using this as a baseline, future research can aim to determine how prey availability influences Hector's dolphin movements, and could identify which habitats have the greatest potential for future population recovery of this endangered species.

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APPENDIX 1A

Family	Genus and species	Common name	*n*	Fish length (cm)	Length equation (cm)			Mass equation (g)		
					A	b	r^2	A	b	r^2
Clupeidae	*Sardinops neopilchardus*	Pilchard	Furlani *et al*. (2007)		3.25	1.37		0.322	4.243	
Clupeidae	*Sprattus antipodum*	Slender sprat	110	FL 3.6–13.4	5.62	0.916	0.97	1.079	3.322	0.97
Engraulidae	*Engraulis australis*	Anchovy	Furlani *et al*. (2007)		4.71	0.74		0.694	2.501	
Myctophidae	*Lampanyctodes hectoris*	Hector's lanternfish	Jackson *et al*. (1998)		1.94	1.49		0.064	4.628	
Moridae	*Auchenoceros punctatus*	Ahuru	134	TL 2.8–14.9	1.7	1.498	0.99	0.019	4.674	0.98
Moridae	*Pseudophycis bachus*	Red cod	171	TL 3.2–73.5	0.83	1.534	0.98	0.004	4.752	0.98
Merlucciidae	*Macruronus novaezelandiae*	Hoki	65	TL 14.5–58.5	1.92	1.178	0.98	0.032	3.384	0.98
Merlucciidae	*Merluccius australis*	Hake	46	TL 5.7–23.1	1.52	1.149	0.97	0.017	3.542	0.97
Macrouridae	*Coelorinchus aspercephalus*	Oblique banded rattail	125	TL 5.9–49.5	1.47	1.25	0.98	0.004	4.241	0.98
Macrouridae	*Lepidorhynchus denticulatus*	Javelinfish	67	TL 11.5–60.5	2.02	1.227	0.98	0.008	4.039	0.98
Trachichthyidae	*Paratrachichthys trailli*	Common roughy	22	FL 14.3–28.5	1.37	1.088	0.94	0.066	3.216	0.91
Cheilodactylidae	*Nemadactylus macropterus*	Tarakihi	59	FL 9.0–46.3	3.37	1.155	0.96	0.466	3.665	0.96
Mugilidae	*Aldrichetta forsteri*	Yelloweyed mullet	82	FL 4.4–37.5	2.91	1.031	0.99	0.163	3.407	0.99
Labridae	*Notolabrus* sp.	Wrasse	20	TL 6.5–38.5	3.16	1.38	0.94	0.125	5.258	0.96
Leptoscopidae	*Leptoscopus macropypus*	Estuary stargazer	19	TL 6.0–30.8	1.5	1.386	0.98	0.022	4.331	0.98
Tripterygiidae	*Forsterygion bathytaton*	Deepwater triplefin	28	TL 4.0–11.3	2.99	0.94	0.97	0.23	3.058	0.97
Eleotridae	*Grahamichthys radiata*	Graham's gudgeon	17	TL 3.7–5.7	5.05	0.6	0.83	0.938	3.196	0.9
Gempylidae	*Thyrsites atun*	Barracouta	90	FL 6.7–52.5	3.46	1.19	0.98	0.15	3.684	0.99
Centrolophidae	*Seriolella brama*	Blue warehou	41	FL 6.7–28.6	2.66	1.072	0.98	0.354	3.162	0.91
Pleuronectidae	*Pelotretis flavilatus*	Lemon sole	36	TL 9.0–38.5	2.83	1.423	0.9	0.588	3.799	0.79
Pleuronectidae	*Peltorhamphus* sp.	Sole	42	TL 5.4–29.8	2.48	1.711	0.93	0.077	5.557	0.95
Pleuronectidae	*Rhombosolea plebeia*	Sand flounder	29	TL 3.0–34.9	2.66	1.675	0.97	2.256	3.51	0.92

Note: Equations to estimate the length (FL: fork length; TL: total length) and mass of fish prey from length of saccular otoliths (mm). Equations are in the form $y = Ax^b$.

Appendix 1B

						Length equation (cm)			Mass equation (g)		
Family	Genus and species	Common name	*n*	Fish length (cm)		A	b	r^2	A	b	r^2
Ommastrephidae	*Nototodarus* sp.	Arrow squid	308	DML 3.0–43.5	URL	12.35	0.76	0.99	0.93	2.186	0.93
					LRL	11.89	0.79	0.99	0.79	2.315	0.95
Sepiadariidae	*Sepioloidea pacifica*	Pacific bobtail squid	14	DML 1.9–6.3	UHL	1.12	0.87	0.86	0.17	1.843	0.81
					LHL	1.56	1.02	0.93	0.42	1.97	0.88
Crangonidae	*Pontophilus australis*	Sand shrimp	18	TL 2.0–5.8					0.11	2.95	0.91
Hymenosomatidae	*Halicarcinus* sp.	Pill-box crab	13	CW 4.0–1.1					0.42	2.97	0.94
Macrophthalmidae	*Macrophthalmus hirtipes*	Mud crab	20	CW 1.6–3.2					0.6	2.84	0.98
Portunidae	*Nectocarcinus antarcticus*	Red swimming crab	31	CW 1.1–6.7					0.22	3.05	0.99
	Ovalipes catharus	Paddle crab	14	CW 7.4–12.4					0.18	3.02	0.98

Note: Equations to estimate the length and mass of invertebrate prey from measures of diagnostic remains (mm). Equations are in the form $y = Ax^b$. Body length of squid: DML = dorsal mantle length, TL = total length (for squid = mantle, head and tentacles but excluding pair of extendable arms). Measures of squid beaks: UHL = upper beak hood length; LHL = lower beak hood length; URL = upper beak rostral length; LHL = lower beak rostral length. Body length of crustaceans: TL = total length; CW = carapace width.

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