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Contrast in the importance of arrow squid as prey of male New Zealand sea lions and New Zealand fur seals at The Snares, subantarctic New Zealand

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Abstract New Zealand sea lions (*Phocarctos hookeri*) are threatened by incidental bycatch in the trawl fishery for southern arrow squid (*Nototodarus sloanii*). An overlap between the fishery and foraging sea lions has previously been interpreted as one piece of evidence supporting resource competition for squid. However, there is currently no consensus about the importance of squid in the diet of New Zealand sea lions. Therefore, we investigated this importance independently of spatial and temporal differences in squid availability through a simultaneous study with sympatric New Zealand fur seals (*Arctocephalus forsteri*), a species known to target arrow squid. Diet sampling at The Snares (48°01′S 166°32′E), subantarctic New Zealand, in February 2012 coincided with peak annual catch in the nearby squid fishery. Diets were deduced by analyses of diagnostic prey remains from scats (faeces) and casts (regurgitations). The contribution of each prey species to the diet was quantified using the per cent index of relative importance (% IRI) that combined frequency of occurrence, mass and number of prey items. Arrow squid was a minor component in sea lion scats (2 % IRI), and none was found in their casts. In contrast, arrow squid was the major component in fur seal scats and casts (93 and 99 % IRI, respectively). This study found that New Zealand sea lions ate minimal squid at a time when squid was clearly available as evidenced by the diet of New Zealand fur seals; hence, there was no indication of resource competition between sea lions and the squid fishery.

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Introduction

New Zealand sea lions (*Phocarctos hookeri*), hereafter referred to as NZ sea lions, have a breeding distribution extending from Otago Peninsula (South Island, New Zealand) south to subantarctic Campbell Island (Fig. 1). The species is classified as 'Vulnerable' by the International Union for the Conservation of Nature (IUCN) due to its small population and restricted distribution (IUCN 2012). New Zealand sea lions are the only endemic pinniped species in New Zealand and 86 % of the entire population breed at the subantarctic Auckland Islands (Chilvers et al. 2007; Chilvers 2008; Fig. 1). New Zealand fur seals (*Arctocephalus forsteri*), hereafter referred to as NZ fur seals, are more widespread, with a distribution encompassing Southern Australia, New Zealand and the Australasian subantarctic islands, and are classified as of 'Least Concern' (IUCN 2012). The distribution of NZ fur seals is expanding, and their population is increasing, following the cessation of human exploitation in New Zealand (Lalas and Bradshaw 2001; Harcourt 2005; Boren et al. 2006) and Australia (Goldsworthy et al. 2003). In contrast, the distribution of NZ sea lions is also expanding (Childerhouse and Gales 1998; McConkey et al. 2002a, b), but their total population size has decreased over recent years (Robertson and Chilvers 2011).

Mortalities through incidental catches in the squid trawl fishery around the Auckland Islands currently pose a major threat to NZ sea lions (Gales 1995; Wilkinson et al. 2003; Chilvers 2008, 2012a, b; Robertson and Chilvers 2011). This fishery typically operates from February to May each year (Ministry for Primary Industries 2012). Southern arrow squid (*Nototodarus sloanii*) is the most important commercial species of squid in New Zealand waters and is the only species fished in subantarctic waters (Ministry

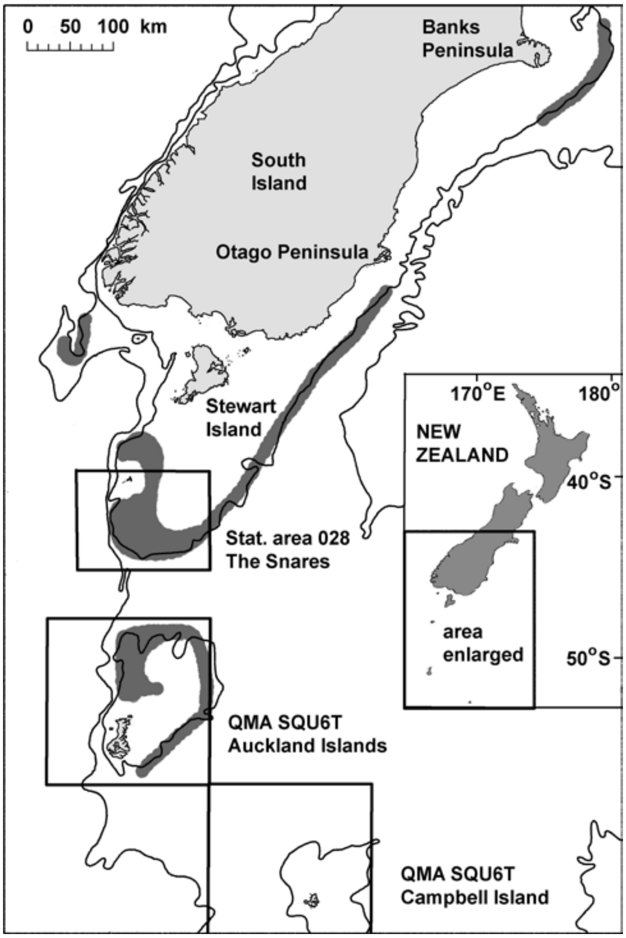

Fig. 1 Southern New Zealand region showing 200- and 1,000-m isobaths; main locations of trawl operations that target southern arrow squid (*grey*; from Gibson 1995; Jackson et al. 2000); The Snares, near the northern edge of statistical area 028; and Auckland Islands and Campbell Island within Quota Management Area (QMA) SQU6T

for Primary Industries 2012). Southern arrow squid have a distribution restricted to New Zealand waters from the south-east of the South Island to the Auckland Islands (Smith et al. 1987; Gibson 1995; Jackson et al. 2000). Fisheries catches closely correspond with the species' distribution and are typically concentrated along the continental shelf edge in water of 150–250 m depth, but with fishing largely restricted to beyond the 12-nm zone of territorial waters (Gibson 1995; Jackson et al. 2000; Fig. 1). Southern arrow squid are short lived, about 1 year (Uozumi and Ohara 1993; Gibson 1995), with large annual fluctuations in abundance that have been correlated with the Southern Oscillation Index (Waluda et al. 2004). For fisheries management purposes, southern arrow squid is split into two Quota Management Areas (QMA) considered to represent two different populations: the southern islands trawl fishery for southern arrow squid (QMA SQU6T; Fig. 1) is separated from the more northern fishery (QMA SQU1T) that also includes the congeneric *N. gouldi* (Gibson 1995; Langley 2001; Ministry for Primary Industries 2012). Trawlers operating in statistical area 028 (a rectangle with an area of 16,147 km^2 within QMA SQU1; Fig. 1), the fisheries management area encompassing The Snares, have accounted for about three-quarters of the annual estimated squid catch in QMA SQU1T through recent years (Ministry for Primary Industries 2012).

All studies of the diet of NZ fur seals within the distribution of southern arrow squid found these squid to be an important prey species that typically accounted for >50 % of estimated total mass of prey. These studies extended from Banks Peninsula (South Island) south to The Snares (Fig. 1), with diet deduced from undigested flesh in stomach contents (Street 1964; Rapson 1969) or from regurgitated or defecated remains (Tate 1981; Fea et al. 1999; Holborow 1999; Harcourt et al. 2002; Allum and Maddigan 2012). Arrow squid was found to be unimportant in studies of the diet of NZ sea lions assessed from regurgitated or defecated remains when compared with similar studies for NZ fur seals. For Otago Peninsula (the northern limit of breeding for NZ sea lions), squid constituted about 2 % of prey mass from males sampled throughout 1 year (Lalas 1997) and about 15 and 4 % of mass from females sampled in two consecutive autumns (Augé et al. 2012); and for the Auckland Islands about, 1 % of prey items from samples collected December–February in three consecutive years for both sexes combined (Childerhouse et al. 2001). In contrast, the contribution of arrow squid was higher from NZ sea lions killed in the Auckland Islands squid trawl fishery: 18 % of estimated mass of prey from the digested fraction in stomach contents (Meynier et al. 2009) and 18–28 % mass from quantitative fatty acid signature analysis (Meynier et al. 2010). However, the diet of sea lions killed in the fishery could be expected to be biased towards squid as they were caught by trawlers targeting squid (Chilvers 2008). The idea that arrow squid is an important prey of NZ sea lions (Wilkinson et al. 2003; Robertson and Chilvers 2011) has not been substantiated. Instead, the overlap between the fishery and foraging sea lions has been interpreted to imply that arrow squid is targeted by sea lions.

Robertson and Chilvers (2011) concluded that the two most parsimonious hypotheses for the population decline of NZ sea lions at the Auckland Islands were attributable to fisheries through resource competition (an indirect effect) and bycatch mortalities (a direct effect). The likely causes of a population decline have been well studied for Steller sea lions (*Eumetopias jubatus*) in the Bering Sea. Here, population size was found to be most affected by changes in prey species composition, availability and abundance likely caused by oceanographic factors; rather than the effects of fisheries (e.g. Wolf and Mangel 2008; Mangel 2010). Robertson and Chilvers (2011), however, state that the indirect effects of fishing on NZ sea lions remain unclear and should therefore be a priority for future work. Here, we aim to examine the contribution of arrow squid to the diet of NZ sea lion in order to investigate the question of resource competition.

Beaks of ingested cephalopods resist digestion and accumulate in the stomach until regurgitated or defecated (e.g. Klages 1996). Their resilience contrasts with that of sagittal otoliths, the key diagnostic remains of teleost fishes, that are subject to digestive erosion (e.g. Smale et al. 1995; Tollit et al. 1997, 2006). Quantification of cephalopods in the diet of pinnipeds is confounded further, because beaks are typically over-represented in regurgitated prey remains and under-represented in defecated prey remains (e.g. Gales and Cheal 1992; Lalas 1997). Although theses biases confound accurate quantification of pinniped diets from the analyses of prey remains in scats and casts, they do not preclude spatial or temporal comparisons (Tollit et al. 2006). By simultaneously sampling two sympatric species of pinniped, we were able to conduct a diet study that was independent of locational, seasonal and annual differences in the availability and abundance of southern arrow squid.

The Snares are a small subantarctic island group (48°01′S 166°32′E) situated about 100 km south-west of Stewart Island, New Zealand (Fig. 1). Few NZ sea lions breed at The Snares and males predominate (Crawley and Cameron 1972; McNally 2001), with the population in 1998 estimated at 252 (95 % CI 187–348) males and seven females (McNally 2001). New Zealand fur seals breed at The Snares, and the population is considered stable, with counts in 1997 of 1,142 adults and 155 pups ashore on North East Island, the largest island in The Snares group (Carey 1998). The Snares are a fortuitous location to compare the diets of NZ sea lions and NZ fur seals, because they are situated about 20 km east of the continental shelf edge, and so a variety of foraging habitats are readily accessible: coastal, and continental shelf, slope and rise. Knowledge of the diets of these two pinniped species, particularly with regard to arrow squid, is essential for determining the potential for competition with fisheries.

Materials and methods

Diet sampling regime

Prey remains analysed in this study were derived from two sources: scats and casts. Faecal material of the same colour and texture and within close proximity (<50 cm) was judged to be produced in one sitting by the same animal and assigned as one scat sample. This procedure minimised the likelihood of duplication of prey remains among different pieces of the same scat sample. Regurgitations of indigestible prey remains were designated as ‘casts’, replacing the terms ‘regurgitates’, ‘regurgitations’, ‘vomits’ or ‘spews’ used in previous accounts of pinniped diets. This term was adopted from Green et al. (1998), who differentiated material regurgitated by albatrosses into two categories: ‘casts’ contain only indigestible remains, whereas ‘regurgitations’ also contain flesh. Note was made if a cast and nearby scat sample were considered to have been produced by the same animal, but were analysed separately.

All scats and casts were collected on North East Island, from 3 to 6 February 2012. Samples from NZ sea lions and NZ fur seals were easily differentiated by both species segregation on land and differences in size, shape, consistency and colour. All fresh scats and casts were collected as they were encountered. Although samples could not be assigned to individuals, samples could be confidently assigned to males, as females were absent from the areas sampled. Fresh samples from NZ sea lions and NZ fur seals were collected within 100 m of the shoreline from Seal Point to Ho Ho Bay (48°01.0′S 166°36.7′E) on the east side of North East Island. This was the main region frequented by NZ sea lions at The Snares (Crawley and Cameron 1972; McNally 2001) and an area where male NZ fur seals were abundant, but females were absent (Carey 1998).

Samples were sieved (mesh size 0.5-mm) in water either on-site or aboard RV *Polaris II*. Prey remains were then collected and soaked in labelled sample pots containing water and laundry detergent. Diagnostic prey remains were cleaned, sorted, washed in 50 % ethanol and, after measurement and analysis, stored dry in labelled plastic bags. The diagnostic remains were then identified to genus or species level by comparison with specimens in a comprehensive reference collection held by CL and reference texts of teleost otoliths (Schwarzhans 1984; Williams and McEldowney 1990; Smale et al. 1995; Furlani et al. 2007), teleost bones (Cannon 1987; Leach 1997), elasmobranch teeth (Last and Stevens 2009), chimaerid tooth plates (Leach 1997; Last and Stevens 2009) and cephalopod beaks (Clarke 1986; O’Shea 1999; Xavier and Cherel 2009). Parasitic crustaceans (copepods and isopods) ingested with host fish were excluded from this study. Otoliths and other paired bones of teleost fish were sorted into left and right, and cephalopod beaks were sorted into upper and lower. Uneroded diagnostic measures of prey remains were measured to the nearest 0.01 mm. Photographs of bones and otoliths and associated measurements were taken with a Dino-Lite digital microscope using software DinoCapture 2.0 (version 1.0.2). Measuring cephalopod beaks from photographs can cause parallax error; to avoid this, beaks were measured with electronic callipers in the correct orientation (from the rostral tip to the jaw angle parallel to the jaw edge; Clarke 1986).

Analysis of diets

Prey size was estimated from species-specific power equations applied to key measures on diagnostic remains. These included previously unpublished equations for one species of crab calculated from claws, two species of cephalopod calculated from beaks and 11 species of teleost fish calculated from otoliths (Table 1). For southern arrow squid, two size-specific equations were applied to estimate dorsal mantle length (DML cm) from upper rostral length (URL mm) and lower rostral length (LRL mm). Separate equations were used for squid with rostral lengths <4.0 and ≥ 4.0 mm to avoid either underestimating or overestimating DML. Size-specific equations for this species were used in preference to the published single equations by Jackson and McKinnon (1996). Equations for six of the ten teleost species applied the normal measure of total length of the otolith. The equations for the other four species applied unconventional, but robust measures that facilitated measures of some broken or partially eroded otoliths that had unmeasurable total lengths (Table 1).

Published equations to estimate prey size from diagnostic remains were used for the octopus *Macroctopus maorum* (Lalas 2009) and the lanternfish *Diaphus hudsoni* (Smale et al. 1995). Estimates for sizes of deepsea smelt (*Bathylagus* sp. and *Nansenia* sp.) were inaccurate, with each derived from only three fish in the CL reference collection, with depictions of otoliths for *Bathylagus* spp. in Williams and McEldowney (1990) and Smale et al. (1995), and for *Nansenia* spp. in Hecht (1987) and Smale et al. (1995). Identifiable fish bones were used to increase the likelihood of detecting prey species [following Browne et al. (2002), Tollit et al. (2006), Waite et al. (2012a)]. Published equations were used for estimating fish size from jaws of blue cod (*Parapercis colias*; Leach et al. 1997a) and red cod (*Pseudophycis bachus*; Leach et al. 1997b). Lengths of some fish were estimated by interpolation from specimens in the CL reference collection: pharyngeal dentition of wrasse (*Notolabrus* 2 spp.), following Leach et al. (2001); caudal bones of slender mackerel (*Trachurus murphyi*) and barracouta (*Thyrsites atun*); hyoid and pectoral bones of blue cod; orbital, tail and alar thorns of rough skate (*Raja*

Table 1 Previously unpublished equations to calculate size of prey at The Snares from diagnostic remains

Species	Diagnostic item (mm)		Prey length equation (cm)						Prey mass equation (g)			
	Measure	Depiction	Length	Range	*n*	*A*	*b*	r^2	*n*	*A*	*b*	r^2
Swimming crab *Nectocarcinus bennetti*	PTL	1 S	CW	1.8–8.5	8	0.29	0.82	1.00	31	0.44	2.77	0.99
Southern arrow squid *Nototodarus sloanii*	URL <4.0	–	DML	3.0–23	168	7.09	0.84	0.87	313	0.016	3.08	0.99
	URL ≥ 4.0	–	DML	23–43.5	116	11.2	0.52	0.79				
	LRL <4.0	3S	DML	3.0–23	177	6.94	0.84	0.90				
	LRL ≥ 4.0	3S	DML	23–43.5	136	10.3	0.57	0.78				
Octopus *Octopus huttoni*	UHL	7 S	VML	1.5–4.8	8	1.83	0.93	0.90	8	1.15	2.39	0.96
	LHL	7S	VML	1.5–4.8	8	2.42	0.93	0.94				
Waryfish *Scopelosaurus* sp.	OAL	6 G	FL	5.2–26.5	15	1.53	1.74	0.97	12	0.0010	3.46	1.00
Barracudina *Macroparalepis* sp.	OTL	4, 6 G	FL	7.5–30.3	19	7.02	1.21	0.97	18	0.0036	2.62	0.99
Red cod *Pseudophycis bachus*	ONL	8 S	TL	3.2–73.5	267	0.81	1.62	0.98	252	0.0074	3.07	1.00
Javelinfish *Lepidorhynchus denticulatus*	OTL	8 S	TL	7.1–69.5	33	2.09	1.23	0.98	21	0.00081	3.29	0.99
Jock stewart *Helicolenus percoides*	OAL	8 S	TL	5.7–44.5	118	2.35	1.14	0.97	99	0.0099	3.20	1.00
Redbait *Emmelichthys nitidus*	OSL	6, 8 S	FL	10.0–42.5	47	3.44	1.26	0.96	42	0.0053	3.25	1.00
Scarlet wrasse *Pseudolabrus miles*	OTL	8 G	FL	18.8–31.2	8	2.33	1.43	0.88	7	0.017	3.04	0.81
Giant stargazer *Kathetostoma giganteum*	OTL	8 G	TL	6.7–64.5	65	4.16	1.07	0.97	59	0.022	2.92	1.00
Opalfish *Hemerocoetes artus*	OTL	2 G	FL	4.2–22.6	51	2.43	1.53	0.94	46	0.0080	2.77	0.99
Blue warehou *Seriolella brama*	OTL	8 S	FL	2.6–66.5	82	2.30	1.19	0.99	85	0.014	3.09	0.99

Equations are in the form $y = Ax^b$, where for length equation x = measure of diagnostic item and for mass equation x = prey length; *A* entered to two decimal places or two significant figures

Measures for diagnostic item: PTL maximum length of claw (cheliped) between proximal and distal tips of the propodite; URL upper rostral length; LRL lower rostral length; UHL upper hood length; LHL lower hood length; otolith measures parallel to the sulcus—OAL antirostrum to posterior tip; OTL anterior to posterior tips; ONL anterior tip to posterior dorsal notch of sulcus opening; otolith measure diagonal to the sulcus—OSL from antirostrum to posterior end of sulcus

Depiction of item: (1) Main (1974), (2) Schwarzhans (1984), (3) Clarke (1986), (4) Hecht (1987), (5) Williams and McEldowney (1990), (6) Smale et al. (1995), (7) O'Shea (1999), (8) Furlani et al. (2007), where S = same species and G = congeneric species

Prey length: *CW* carapace width, *DML* dorsal mantle length, *VML* ventral mantle length, *FL* fork length, *TL* total length *nasuta*); and tooth plates of dark ghost shark (*Hydrolagus novaezelandiae*).

Teleost fish and cephalopods were enumerated after accounting either for paired left and right otoliths and other diagnostic bones or for paired upper and lower beaks, respectively (Lalas 2009). Cephalopods and teleost fishes represented only by unmeasurable diagnostic remains were excluded from estimates of prey size. However, they were included in counts of prey, and each was assigned a nominal mass estimated either from a qualitative assessment of size of the prey remains or as the average mass of other conspecifics represented in the same sample. Species of cartilaginous fish identified only from teeth, thorns or vertebrae were considered to represent a single individual per sample. Here, sharks were assigned nominal masses: 1 kg for spiny dogfish (*Squalus acanthias*), the average deduced from jaws and dorsal spines from diet studies of NZ sea lions at Otago Peninsula (CL unpublished data), and 5 kg for school shark (*Galeorhinus galeus*), the nominal mass assigned by Holborow (1999) from teeth during previous diet studies of NZ fur seals at The Snares. The occurrence of seabirds was indicated by the presence of bones and/or feathers, and their presence in a sample was considered to represent a single individual. New Zealand fur seals in scats or casts from NZ sea lions were indicated by the presence of their fur (pelage), teeth, flippers, claws and/or bones. Guard hairs in the pelage of young NZ fur seal pups are black or dark brown and distinctly darker than the usual grey-brown of older animals (Harcourt 2005). This difference was a key indicator for size of fur seals. In addition, sizes of teeth, toenails and bones were compared against a reference collection held by CL. Remains of NZ fur seal pups were assigned a nominal mass of 7 kg, their average mass at the start of February at Otago Peninsula, South Island (Bradshaw et al. 2003). The size of NZ fur seals older than pups could not be determined from the colour of guard hairs. Any estimate for mass of these fur seals is speculative in the absence of measureable bones. The largest NZ fur seal recorded as prey of NZ sea lions was a subadult male at Otago Peninsula, length 152 cm (Lalas et al. 2007) with a mass estimated as 59 kg from an equation in McKenzie et al. (2007). Other than pups, the main class of NZ fur seals eaten by NZ sea lions at Otago Peninsula are adult females (CL unpublished data) that have an average mass of 39 kg (Harcourt 2005). Consequently, 40 kg was assigned as the nominal mass for NZ fur seals older than pups.

Indices for diet composition were calculated separately for scats and for casts, and then for the combination of scats and casts for comparison with other diet studies using this method. In each case, four indices were calculated: frequency of occurrence (% O), the proportion of samples containing each prey species; numerical frequency (% N), the number for each prey species as a proportion of the total number of prey items; mass frequency (% M), the estimated original mass contributed by each prey species as a proportion of the estimated total mass of prey items; and index of relative importance (% IRI). The IRI was created by Pinkas et al. (1971) to incorporate occurrence, total number and total mass for each prey species into a single measure, where IRI = % O(% N + % M), in order to rank species. Cortés (1997) transformed IRI into a proportion, where % IRI represented the IRI for each prey species as a proportion of the sum of IRIs from all prey species. Fish names and taxonomic listing followed Paulin et al. (2001). Names, taxonomic listing and body masses of seabirds followed Marchant and Higgins (1990). A Bray–Curtis similarity analysis (Bray and Curtis 1957) was used to assess the compositional differences in diet between NZ sea lions and NZ fur seals and to assess the overlap between the two. Based on the prevalence of each prey species, a similarity index (between 0 and 1) was calculated for % O, % N, % M and % IRI, where a value of 0 indicated that the diets have the same species composition and 1 indicated that the diets did not share any of the same species.

Southern arrow squid and fisheries

Spawning by southern arrow squid has been recorded through most of the year throughout their distribution, but egg hatching peaks in July and August (Uozumi and Ohara 1993). Length frequency distributions may be bimodal, indicating two cohorts, and contemporary squid generally are larger around the Auckland Islands than around The Snares (Gibson 1995). Length frequencies for random samples of arrow squid recorded by government observers aboard trawlers targeting squid in statistical area 028 were supplied by the New Zealand Ministry for Primary Industries. The sample of squid caught from 27 January to 5 February 2012 were considered contemporary with prey remains collected 3–6 February at The Snares during this study. Length frequency distributions of DML from squid caught in the fisheries and from squid represented by beaks in prey remains were assigned to 5-cm length classes. The likelihood of differences in length frequencies among arrow squid from scats and casts of NZ sea lions and NZ fur seals and fisheries was investigated using *G* tests with William's correction, following Sokal and Rohlf (1995), specifically to assess any overlap or competition with the squid fishery. *G* tests were used in preference to comparisons of means for two reasons: first, sizes of squid from prey remains were derived from beak size, rather than direct measure of DML, and second, large sample sizes can produce statistically significant results for small differences that are not biologically meaningful.

The Ministry for Primary Industries supplied data for monthly estimated catch of arrow squid and total fishing hours by trawlers that targeted squid in statistical area 028, for the 2011–12 fishing year, the duration that encompassed this study. Corresponding monthly catch data were also supplied for QMA SQU1T and in QMA SQU6T. The New Zealand fishing year begins 1 October and ends 30 September in the following year. Analyses of fisheries data were restricted to comparisons of monthly estimated catch, because changes in fishing effort reflected regulatory protocols rather than squid availability and precluded further analyses of catch data.

Results

Twenty-two species totalling c. 150 kg of prey were represented in 44 NZ sea lion scat samples (Table 2), and 16 species totalling c. 30 kg of prey in 42 NZ fur seal scat samples (Table 3). Two species totalling c. 141 kg of prey were represented in NZ sea lion casts, and three species totalling c. 22 kg of prey in NZ fur seal casts. No regurgitations containing undigested flesh were found. All diet samples from NZ sea lions were from subadult or adult males. The youngest NZ sea lion encountered was a tagged subadult male (tag number 6906) aged 5 years. Only two female sea lions were encountered; both were adult and one had a pup. It is unlikely that either of these females was sampled, as no scats or casts were found in their vicinity. All diet samples for NZ fur seal were from males.

All scat samples collected from NZ sea lions contained quantifiable prey remains (Table 2). Fifteen (34 %) of the scat samples contained only one species, including 10 (23 %) that contained only redbait (*Emmelichthys nitidus*), two samples that contained only NZ fur seal and one sample each containing only rough skate, blue cod and barracouta. Redbait was the major prey species represented in NZ sea lion scat samples comprising 50 % IRI (15 % M). Rough skate was the second major prey species represented in NZ sea lion scats (23 % IRI, 29 % M). Red cod was the

Table 2 Composition of the diet represented in scats of male New Zealand sea lions at The Snares in February 2012

Prey species	Occurrence		Number		Mass		Importance		Length of prey (cm)				
	n	%O	*n*	%N	kg	%M	IRI	%IRI	*n*	Measure	Mean	SD	Range
Lobster krill *Munida gregaria*	1	2	1	<1	0.0	0	1	<1	1	CL	1.0		
Swimming crab *Nectocarcinus bennetti*	10	23	15	8	0.1	<1	172	3	14	CW	2.7	0.7	1–3
Salp *Iasis zonaria*	1	2	1	<1	0.0	0	1	<1	1	TL	2.3		
Southern arrow squid *Nototodarus sloanii*	7	16	10	5	1.6	1	96	2	10	DML	18.3	5.3	13–31
Octopus *Octopus* sp. (probably *O. huttoni*)	3	7	10	5	0.3	<1	35	<1	10	VML	3.9	0.5	3–4
Octopus *Macroctopus maorum*	4	9	4	2	10.7	7	83	2	4	VML	18.0	1.2	16–18
Spiny dogfish *Squalus acanthias*	4	9	4	2	4.0	3	42	<1	0				
School shark *Galeorhinus galeus*	1	2	1	<1	5.0	3	9	<1	0				
Rough skate *Raja nasuta*	15	34	15	8	43.2	29	1,235	23	6	TL	73.9	7.3	65–85
Red cod *Pseudophycis bachus*	10	23	29	14	13.0	9	525	10	24	TL	32.4	13.6	8–54
Javelinfish *Lepidorhynchus denticulatus*	1	2	6	3	0.9	<1	8	<1	2	TL	39.4		38–40
Jock Stewart *Helicolenus percoides*	3	7	6	3	2.2	1	30	<1	5	TL	26.4	2.7	22–29
Slender mackerel *Trachurus murphyi*	3	7	3	2	3.7	3	27	<1	2	FL	49.7		48–50
Redbait *Emmelichthys nitidus*	24	55	68	34	22.4	15	2,660	50	30	FL	29.6	5.0	20–39
Wrasse *Notolabrus cinctus* or *N. fucicola*	2	5	2	1	0.3	<1	6	<1	2	TL	21.9		20–23
Scarlet wrasse *Pseudolabrus miles*	1	2	1	<1	0.2	<1	1	<1	1	FL	22.3		
Giant stargazer *Kathetostoma giganteum*	2	5	3	2	3.3	2	17	<1	3	TL	40.2	7.2	34–48
Opalfish *Hemerocoetes* sp. (probably *H. artus*)	2	5	3	2	0.0	0	7	<1	3	FL	12.2	1.0	11–13
Blue cod *Parapercis colias*	6	14	12	6	7.2	5	146	3	6	TL	32.8	8.2	22–43
Barracouta *Thyrsites atun*	1	2	1	<1	3.8	3	7	<1	1	FL	92.5		
Common storm-petrel *Pelecanoides urinatrix*	2	5	2	1	0.3	<1	5	<1					
New Zealand fur seal *Arctocephalus forsteri*	4	9	4	2	28.0	19	187	4					

Percentages: frequency of occurrence (%O) from 44 scat samples containing prey remains; numerical frequency (%N) from a minimum total of 201 prey items; mass frequency (%M) from a total estimated mass of prey of 150.4 kg; and proportion of the sum of index of relative importance (%IRI)

Prey length measure: *CL* carapace length, *CW* carapace width, *TL* total length, *DML* dorsal mantle length, *VML* ventral mantle length, *FL* fork length only other prey species with ≥10 % IRI from NZ sea lion scat samples (9 % M). Numerical frequency of NZ fur seal was low, but mass frequency was high (19 % M). Arrow squid was not important in the diet of NZ sea lion as it comprised only 2 % IRI.

Thirty-five (83 %) of the scat samples collected from male NZ fur seals contained identifiable prey remains (Table 3). Twenty-five (71 %) scat samples contained only one species; including 21 (60 %) that comprised only arrow squid, two samples contained only redbait, one only deep-sea smelt (*Nansenia* sp.) and one sample only the lanternfish *Lampanyctodes hectoris*. Arrow squid was by far the most important prey species in NZ fur seal scat samples as it comprised 93 % IRI. No other species accounted for more than 10 % of total mass or IRI. The only other species that was considered of any consequence was *L. hectoris*, an oceanic mesopelagic fish. Mesopelagic fish were represented in NZ fur seal scat samples by six genera from four families: deepsea smelt (Bathylagidae 2 genera), waryfish (Notosudidae 1 genus), barracudina (Paralepididae 1 genus) and lanternfish (Myctophidae 2 genera). Together, they represented high numbers of prey in scat samples but only a small proportion of total mass.

Six casts were collected from NZ sea lions and each contained quantifiable prey remains. All of the cast samples contained diagnostic remains of NZ fur seal (including fur, teeth, bones, toenails and part of a fore flipper). Three of these casts contained remains of pups (nominal mass 7 kg) and the other three contained remains of individuals older than pups (nominal mass 40 kg) to produce a total estimated mass of c. 141 kg. Two of the casts were associated with scat samples as they were likely to be from the same animal. Both of these casts contained NZ fur seal pup remains, and both of the scat samples contained pup fur. The only other prey remains found among the six NZ sea lion casts represented one swimming crab (*Nectocarcinus bennetii*) with an estimated mass of 33 g.

Eight casts were collected from NZ fur seals and each contained quantifiable prey remains. All of the cast samples included arrow squid as prey (100 % O). Six (75 %) of these casts only contained arrow squid, and the other two casts contained one fish each, slender mackerel in one and barracouta in the other. Arrow squid accounted for 105 (98 % N) of items found in casts and a total mass of 17.9 kg (86 % M, 98 % IRI). Estimates for size of the two fish found in NZ fur seal casts were quantified from caudal bones: FL 52.8 cm, mass 1.5 kg for the slender mackerel, and FL 65.5 cm, mass 1.3 kg for the barracouta.

The relative importance of arrow squid was not altered, when diets were assessed from the combination of scats and casts rather than separately for each of these two sources; 96 % IRI from NZ fur seals and 2 % IRI from NZ sea lions (Table 4). Among the other prey species, the only dramatic changes in diet indices generated from the

Table 3 Composition of the diet represented in scats of male New Zealand fur seals at The Snares in February 2012

Prey species	Occurrence		Number		Mass		Importance		Length of prey (cm)				
	n	%O	*n*	%N	kg	%M	IRI	%IRI	*n*	Measure	Mean	SD	Range
Southern arrow squid *Nototodarus sloanii*	30	86	174	50	18.5	61	9,528	93	145	DML	17.0	2.8	8–26
Dark ghost shark *Hydrolagus novaezelandiae*	1	3	1	<1	1.6	5	16	<1	1	SL	64.6		
Deepsea smelt *Bathylagus* sp.	1	3	4	1	0.1	<1	5	<1	3	FL	18.0	1.7	16–19
Deepsea smelt *Nansenia* sp.	3	9	6	2	0.1	<1	17	<1	3	FL	12.7	2.7	9–14
Waryfish *Scopelosaurus* sp.	1	3	7	2	0.2	<1	8	<1	7	FL	17.6	5.6	10–25
Barracudina *Macroparalepis* sp.	1	3	4	1	0.1	<1	5	<1	4	FL	32.1	4.3	27–37
Lanternfish *Diaphus* sp. (probably *D. hudsoni*)	1	3	7	2	0.1	<1	6	<1	5	FL	8.6	1.0	7–9
Lanternfish *Lampanyctodes hectoris*	4	11	108	31	0.3	<1	366	4	67	FL	5.6	1.6	3–8
Red cod *Pseudophycis bachus*	4	11	12	3	2.5	8	134	1	10	TL	19.0	18.0	3–45
Jock Stewart *Helicolenus percoides*	1	3	1	<1	0.6	2	7	<1	1	TL	31.7		
Redbait *Emmelichthys nitidus*	4	11	14	4	3.0	10	161	2	11	FL	24.5	3.7	16–30
Greenbone *Odax pullus*	1	3	1	<1	0.2	<1	3	<1	1	FL	26.1		
Opalfish *Hemerocoetes* sp. (probably *H. artus*)	1	3	1	<1	0.0	<1	1	<1	1	FL	14.6		
Blue warehou *Seriolella brama*	3	9	3	1	0.0	<1	8	<1	2	FL	8.2		8–8
Unidentified teleost fish (unidentifiable remains)	2	6	2	<1	0.1	<1	4	<1					
Snares penguin *Eudyptes robustus*	1	3	1	<1	3.0	10	29	<1					

Percentages: frequency of occurrence (%O) from 35 scat samples containing prey remains; numerical frequency (%N) from a minimum total of 346 prey items; mass frequency (%M) from a total estimated mass of prey of 30.4 kg; and proportion of the sum of index of relative importance (%IRI)

Prey length measure: *DML* dorsal mantle length, *SL* length excluding caudal filament, *FL* fork length, *TL* total length combination of scats and casts were for NZ fur seals as prey of NZ sea lions: 58 % M and 26 % IRI from scats and casts combined, in contrast to the respective two extremes of 19 % M and 4 % IRI from scats and 100 % M and 100 % IRI from casts. The Bray–Curtis similarity analysis confirmed that there were large differences in diet composition between NZ sea lions and NZ fur seals. Only scats were used for this analysis, because there was no overlap at all in prey composition of casts. Bray–Curtis indices (%O = 0.784, %M = 0.792, %N = 0.868, %IRI = 0.953) were much closer to 1 than 0 and indicated that there was little overlap in diet.

The DML of arrow squid was calculated from beak measurements for all ten squid recorded from NZ sea lion scat samples (mean = 18.3 cm, SD = 5.3, range = 13–31 cm) (Table 2; Fig. 2). No squid were recorded in cast samples from NZ sea lions. The estimated DML of arrow squid was calculated for 145 (83 %) squid recorded from NZ fur seal scat samples (mean = 17.0 cm, SD = 2.8, range = 8–26 cm; Table 3; Fig. 2), and for 99

Table 4 Composition of the diets of male New Zealand sea lions and New Zealand fur seals at The Snares in February 2012 deduced from the combination scats and casts

Prey species	Occurrence (%O)		Number (%N)		Mass (%M)		Importance (%IRI)	
	Sea lion	Fur seal	Sea lion	Fur seal	Sea lion	Fur seal	Sea lion	Fur seal
Lobster krill *Munida gregaria*	2	–	<1	–	<1	–	<1	–
Swimming crab *Nectocarcinus bennetti*	22	–	8	–	<1	–	4	–
Salp *Iasis zonaria*	2	–	<1	–	<1	–	<1	–
Southern arrow squid *Nototodarus sloanii*	14	88	5	62	<1	72	2	96
Octopus *Octopus* sp.	6	–	5	–	<1	–	<1	–
Octopus *Macroctopus maorum*	8	–	2	–	4	–	<1	–
Spiny dogfish *Squalus acanthias*	8	–	2	–	1	–	<1	–
School shark *Galeorhinus galeus*	2	–	<1	–	2	–	<1	–
Rough skate *Raja nasuta*	30	–	7	–	15	–	14	–
Dark ghost shark *Hydrolagus novaezelandiae*	–	2	–	<1	–	3	–	<1
Deepsea smelt *Bathylagus* sp.	–	2	–	1	–	<1	–	<1
Deepsea smelt *Nansenia* sp.	–	7	–	1	–	<1	–	<1
Waryfish *Scopelosaurus* sp.	–	2	–	2	–	<1	–	<1
Barracudina *Macroparalepis* sp.	–	2	–	<1	–	<1	–	<1
Lanternfish *Diaphus* sp.	–	2	–	2	–	<1	–	<1
Lanternfish *Lampanyctodes hectoris*	–	9	–	24	–	<1	–	2
Javelinfish *Lepidorhynchus denticulatus*	2	–	3	–	<1	–	<1	–
Red cod *Pseudophycis bachus*	20	9	14	3	4	5	8	<1
Jock Stewart *Helicolenus percoides*	6	2	3	<1	<1	1	<1	<1
Slender mackerel *Trachurus murphyi*	6	2	1	<1	1	3	<1	<1
Redbait *Emmelichthys nitidus*	48	9	33	3	8	6	41	<1
Wrasse *Notolabrus* sp.	4	–	1	–	<1	–	<1	–
Scarlet wrasse *Pseudolabrus miles*	2	–	<1	–	<1	–	<1	–
Greenbone *Odax pullus*	–	2	–	<1	–	<1	–	<1
Giant stargazer *Kathetostoma giganteum*	4	–	1	–	1	–	<1	–
Opalfish *Hemerocoetes* sp.	4	2	1	<1	4	<1	4	<1
Blue cod *Parapercis colias*	12	–	6	–	2	–	2	–
Barracouta *Thyrsites atun*	2	2	<1	<1	1	2	<1	<1
Blue warehou *Seriolella brama*	–	7	–	<1	–	<1	–	<1
Unidentified teleost (unidentifiable remains)	–	5	–	<1	–	<1	–	<1
Snares penguin *Eudyptes robustus*	–	2	–	<1	–	6	–	<1
Common storm-petrel *Pelecanoides urinatrix*	4	–	1	–	<1	–	<1	–
New Zealand fur seal *Arctocephalus forsteri*	20	–	5	–	58	–	26	–

Percentages for sea lions and fur seals, respectively: frequency of occurrence (%O) from 50 to 43 combined scat and cast samples containing prey remains; numerical frequency (%N) from a minimum total of 208 and 453 prey items; mass frequency (%M) from a total estimated mass of prey of 291 and 52.2 kg

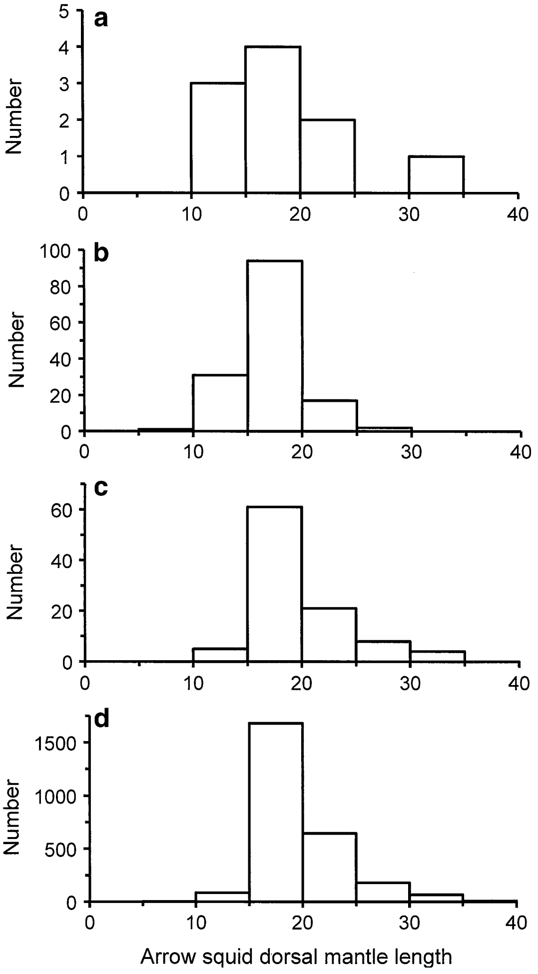

Fig. 2 Length frequency distribution of southern *arrow* squid for **a** 10 squid in scats from NZ sea lions; **b** 145 squid in scats from NZ fur seals; **c** 99 squid in casts from NZ fur seals; and **d** contemporary sample of 2,665 squid from catches in the nearby trawl fishery from data supplied by Ministry for Primary Industries

Table 5 Monthly estimated catch (t) of arrow squid by trawlers that targeted squid in the 2011–2012 fishing year (October 2011–September 2012) for statistical area 028, the part of Quota Management Area (QMA) SQU1T encompassing The Snares, and for QMA SQU1T (New Zealand waters north of the Auckland Islands) and QMA SQU6T (encompassing the Auckland Islands)

Month	Area 028	SQU1T	SQU6T
October	2	3	0
November	0	0	0
December	9	10	0
January	4,521	4,583	0
February	650	2,833	3,147
March	2,438	4,963	3,062
April	1,867	2,809	4,149
May	928	1,728	2,051
June	8	175	1,117
July	30	82	0
August	0	1	0
September	27	48	0
Annual total	10,480	17,234	13,526

From data supplied by Ministry for Primary Industries

(94 %) of arrow squid recorded from NZ fur seal casts (mean = 19.9 cm, SD = 4.2, range = 11–34 cm; Fig. 2). Length frequency distributions were placed in four length classes (<15, 15–20, 20–25, >25 cm) in order to avoid small sample sizes (<5). Contemporary samples of arrow squid caught locally in the squid trawl fishery had a mean DML of 19.2 cm ($n = 2{,}665$, SD = 3.8, range 7–37 cm) (Fig. 2). Comparisons using 2 × 4 G tests ($df = 3$) indicated that the length frequency distribution of squid represented in NZ fur seal casts was not significantly different from squid caught in the fishery ($G = 1.77$, $P = 0.62$). However, the casts ($G = 28.1$, $P = <0.001$) and the fishery ($G = 84.9$, $P = <0.001$) both contained squid on average larger than those represented in NZ fur seal scats. The sample size of 10 arrow squid from NZ sea lion scats was too small to generate meaningful statistical comparisons, but a qualitative comparison indicated a length frequency distribution similar to those from fur seals (Fig. 2).

The annual estimated catch of arrow squid by the squid trawl fishery from around The Snares (statistical area 028) through the 2011–12 fishing year totalled 10,480 t, accounted for 61 % of the annual total from QMA SQU1T, and was equivalent to 77 % of the annual estimated catch from around the Auckland Islands (QMA SQU6T; Table 5). The monthly maximum estimated catch of arrow squid in statistical area 028 was in January. Both the monthly catch of 4,521 t and the average catch rate of 3.6 t/h of arrow squid in January were about double the respective values from other months with relatively high catches in statistical area 028: 2,438 t at 1.3 t/h in March and 1,867 t at 1.5 t/h in April. This January catch coincided with our diet study at The Snares and exceeded the maximum monthly estimated catch of arrow squid from the Auckland Islands, 4,149 t in April 2012 (Table 5).

Discussion

Southern arrow squid was unimportant as a prey species for NZ sea lions, but it was the most important prey species for NZ fur seals based on the analyses of prey remains collected at The Snares at the start of February 2012. Squid occurred in 16 % of NZ sea lion scat samples, where it accounted for only 1 % of estimated total prey mass and 2 % IRI, and in none of six casts. In contrast, arrow squid occurred in 81 % of NZ fur seal scat samples, where it accounted for 61 % of estimated total prey mass and 91 % IRI, and in all eight casts, where it accounted for 86 % of estimated total prey mass and 98 % IRI.

The contrast in importance of squid as prey between NZ sea lions and NZ fur seals could be attributable to interspecific differences in foraging zones and behaviour. For NZ sea lions, studies of females off Otago Peninsula (Augé et al. 2011) and all sex and age classes off Auckland Islands indicate that they typically forage throughout the day and night across the continental shelf and shelf edge, usually with demersal dives (e.g. Crocker et al. 2001; Chilvers et al. 2011; Chilvers 2009; Leung et al. 2012). Studies of foraging by NZ fur seals within the distribution of NZ sea lions have been restricted to adult females off Otago Peninsula where they typically only forage offshore at night over the continental shelf edge and slope, usually with pelagic dives (Harcourt et al. 2001, 2002). Southern arrow squid are concentrated along the edge of the continental shelf where they undergo diel migrations and are demersal by day and pelagic by night (Gibson 1995), features that coincide with foraging by NZ fur seals. These differences in foraging patterns reflect those from other comparisons of foraging and diet between sympatric fur seals and sea lions (e.g. Dellinger and Trillmich 1999; Waite et al. 2012a, b). Galápagos fur seals (*A. galapagoensis*) forage further offshore than Galápagos sea lions (*Zalophus wollebaeki*), with squid only being important in the diet of the fur seals (Dellinger and Trillmich 1999). In the Russian Far East, northern fur seals (*Callorhinus ursinus*) forage further offshore than Steller sea lions (*Eumetopias jubatus*), with squid important only in the diet of the fur seals (Waite et al. 2012a, b).

The percentage index of relative importance was adopted in preference to proportion by mass as the main indicator of the importance of prey species. This index mitigated the likely underestimate of importance of small prey eaten frequently in large numbers and overestimate of importance of large prey eaten infrequently; these biases were highlighted by Joy et al. (2006) for the analyses of seal diets. Studies of seal diet deduced from defecated and regurgitated prey remains have presented results from these two sources either separately, because their contents are affected by different biases, or combined, because biases are considered to be compensated by random sampling (e.g. Fea et al. 1999; Harcourt et al. 2002). For diet studies within the distribution of southern arrow squid, results from defecated and regurgitated prey remains from NZ fur seals have been presented separately (Tate 1981; Allum and Maddigan 2012), combined (Holborow 1999), and both separately and combined (Fea et al. 1999; Harcourt et al. 2002); however, results were presented combined for all three studies of NZ sea lions (Lalas 1997; Childerhouse et al. 2001; Augé et al. 2012). The choice of indices for diet or for sources of prey remains did not affect the outcome of the assessment of the importance of squid in this study. The dominance of southern arrow squid in the diet of NZ fur seals and its insignificance in the diet of NZ sea lions at The Snares remained unchanged regardless of whether the index applied was mass or IRI, and similarly unchanged whether diet was assessed from only scats, only casts or the combination of scats and casts.

It is likely that some of the small prey species (mass <50 g) identified in the diet samples from NZ sea lions represented secondary occurrence (originating from larger prey items): lobster krill (*Munida gregaria*), swimming crab (*Nectocarcinus bennetti*), salp (*Iasis zonaria*), small octopus (*Octopus huttoni*) and opalfish (*Hemerocoetes artus*). Some of these species have been reported as among the most numerous prey of NZ sea lions at the Auckland Islands (Childerhouse et al. 2001) and Otago Peninsula (Lalas et al. 2007), but none were numerous in this study. Secondary occurrence may also have accounted for some of the small fish (mass <50 g) recorded from NZ fur seals at The Snares, where the lanternfish *L. hectoris* accounted for 31 % of the number of prey in scat samples, second only to arrow squid at 50 %, and small mesopelagic fish overall accounted for 40 %. This possibility is supported by a study of southern arrow squid that found mesopelagic fish, including *L. hectoris*, predominated in their diet on the Chatham Rise, east of Banks Peninsula, South Island (Dunn 2009).

The only previous investigation into pinniped prey at The Snares was restricted to NZ fur seals and deduced from 104 scats collected during five visits in 1996–1997 by Holborow (1999). Arrow squid accounted for only 6 % of the number of prey and 8 % of total prey mass from scats, and no casts were found (Holborow 1999). This was in marked contrast to the results from our study where arrow squid was the most important prey by number and mass in scats and casts. Other than the proportion of arrow squid, the composition of the diet of NZ fur seals at The Snares was similar for both studies. In particular, prey found by Holborow (1999) included the first record of redbait as prey of NZ fur seals in New Zealand waters. Redbait, a schooling midwater fish over the continental shelf, has been recorded as important prey of NZ fur seals in Australia (Goldsworthy et al. 2003; Furlani et al. 2007). Redbait was also the most important prey of NZ sea lions during this study and accounted for 50 % IRI from scats and 41 % IRI from the combination of scats and casts. The only previous record for redbait as prey of NZ sea lions was two fish among 3,627 prey items recovered from the stomach contents of NZ sea lions caught in fisheries around the Auckland Islands (Meynier et al. 2009). Three other species accounted for $\geq$5 % IRI from scats, casts or the combination of scats and casts from NZ sea lions at The Snares. For the combination of scats and casts, NZ fur seal accounted for 26 % IRI, rough skate for 14 % IRI and red cod for 8 % IRI. Five species were found in this study that have not been previously recorded in the diet of NZ fur seals: greenbone (*Odax pullax*), lanternfish (*Diaphus* sp.), dark ghost shark (*Hydrolagus novaezelandiae*), Snares crested penguin (*Eudyptes robustus*) and barracudina (*Macroparalepis* sp.). Common storm-petrel (*Pelecanoides urinatrix*) was the only species not recorded previously as prey of NZ sea lions.

An assessment of the potential impact of incidental catches in fisheries was beyond the scope of this study, but is addressed here briefly, because mortalities in the Auckland Islands squid trawl fishery are considered a major threat to the viability of NZ sea lions (e.g. Robertson and Chilvers 2011; Chilvers 2012a, b). Incidental catches of NZ sea lions and NZ fur seals occur in trawl fisheries in the vicinity of The Snares. Model-based analyses indicated an estimated total of 3–9 (mean 5.9) NZ sea lions caught annually over 14 fishing years from 1995/1996 to 2008/2009 (Thompson and Abraham 2010b). Similar analyses for NZ fur seals (Smith and Baird 2009; Thompson and Abraham 2010a) were not directly comparable to those for NZ sea lions, because the areas analysed were more extensive; the area encompassing The Snares extended further north and east to include southern South Island, although maps showed that most trawl tows and seal captures were in statistical area 028. An indication of incidental catches of NZ fur seals in the vicinity of The Snares was generated by applying estimated annual catch rate per tow through the six fishing years 2003/2004 to 2008/2009 from Thompson and Abraham (2010a) to respective annual number of tows in statistical area 028 from Thompson and Abraham (2010b). This produced an estimated total 18–112 (mean 55) NZ fur seals caught annually, about 10 times the estimate for NZ sea lions in statistical area 028. The effects of these on-going mortalities on the viability of NZ sea lions and NZ fur seals at The Snares remain unknown.

This study showed that southern arrow squid was unimportant in the diet of NZ sea lions at The Snares during a period that coincided with peak seasonal squid catches by the nearby squid trawl fishery. The sample population consisted only of subadult and adult males, and so this result cannot be extrapolated to encompass females and juvenile males. However, no sex- or age-related differences in the size and amount of arrow squid eaten were found in stomach contents of NZ sea lions killed in the squid trawl fishery around the Auckland Islands (Meynier et al. 2008, 2009, 2010). Consequently, our result could be applicable to all NZ sea lions. We found no indication of resource competition between NZ sea lions and the squid fishery; NZ sea lions ate few squid at a time when squid was clearly available as evidenced by its predominance in the diet of NZ fur seals. Rather than speculating, the simplest way to deduce the importance of squid in the diet of NZ sea lions at the Auckland Islands would be to repeat our study there during February–May to coincide with the seasonal peak in squid catches by the Auckland Islands squid trawl fishery.

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