

Abstract.—Food habits of the South American sea lion (*Otaria flavescens*) off Patagonia were studied by means of stomach content analysis. The samples were collected during 1982–1987 and 1990–1998 in northern and central Patagonia. The samples ($n=59$) came from individuals found dead on beaches and from animals recovered in incidental catches of the fishery. Forty-one prey species (including fishes, cephalopods, crustaceans, gastropods, polychetes, sponges, and tunicates) were identified; most important were Argentine hake (*Merluccius hubbsi*), red octopus (*Enteroctopus megalocyathus*), Argentine shortfin squid (*Illex argentinus*), “raneya” (*Raneya brasiliensis*), Patagonian squid (*Loligo gahi*), and Argentine anchovy (*Engraulis anchoita*). Differences in diet were found between sexes but not between geographical area of sampling, period of sampling, or source of samples. Females fed mostly on benthic species, whereas males fed mostly on demersal-pelagic species. The difference in diet between sexes was associated with different feeding grounds or different home ranges and could be produced by different constraints in the feeding behavior of each sex. These different constraints and restrictions could lead females to feed in more coastal and shallower waters than those waters where males feed. Some of the important prey were commercial species (Argentine hake, Argentine shortfin squid, Patagonian squid) consumed at both commercial and noncommercial sizes by sea lions. The presence of gastroliths was independent of the presence of stomach parasites; however, gastrolith weight was positively correlated with individual sea lion’s length, indicating that gastroliths could be involved in buoyancy control. In summary, these stomach content analyses indicate that South American sea lions feed primarily on demersal and benthic species and, in general terms, use resources according to their environmental availability.

Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina

Mariano Koen Alonso

Enrique A. Crespo

Susana N. Pedraza

Centro Nacional Patagónico (CONICET)
and Universidad Nacional de la Patagonia
Boulevard Brown 3600
(9120) Puerto Madryn, Chubut, Argentina
E-mail address: koen@cenpat.edu.ar

Néstor A. García

Centro Nacional Patagónico (CONICET)
Boulevard Brown 3600
(9120) Puerto Madryn, Chubut, Argentina

Mariano A. Coscarella

Centro Nacional Patagónico (CONICET)
and Universidad Nacional de la Patagonia
Boulevard Brown 3600
(9120) Puerto Madryn, Chubut, Argentina

The South American sea lion (*Otaria flavescens*) is one of the most common and abundant marine mammal species in the southwestern Atlantic and is distributed along the coasts of South America from Peru to southern Brazil in both the Pacific and Atlantic Oceans (Vaz Ferreira, 1982; Crespo¹). Most investigations on South American sea lions have been focused on social behavior, breeding biology, and population dynamics (Vaz Ferreira, 1982; Campagna and Le Boeuf, 1988; Cappozzo et al., 1991; Crespo and Pedraza, 1991; Crespo¹). Recent research has provided new data on the interactions between South American sea lions and fisheries (Crespo et al., 1994, 1997), on population size and trends (Reyes et al., 1999; Dans et al.²), and on diving behavior of lactating females (Werner and Campagna, 1995).

South American sea lions are considered opportunistic and broad-spectrum feeders, feeding on fish, squid, crustaceans, and occasionally

on sea birds (Vaz Ferreira, 1982; George-Nascimento et al., 1985; Crespo et al., 1997). In Chilean waters, their most important prey are the Patagonian grenadier (*Macruronus magellanicus*) and the kingclip (*Genypterus* spp.); no relationship has been found between predator and prey sizes (George-Nascimento et al., 1985). For Patagonian waters, only preliminary information has been published about feeding (Crespo et al., 1997). Several studies (Hamilton, 1934; Vaz Fer-

¹ Crespo, E. A. 1988. Dinámica poblacional del lobo marino del sur *Otaria flavescens* (Shaw, 1800) en el norte del litoral patagónico. Doctoral thesis, Facultad de Cs. Exáctas y Naturales, Universidad Nacional de Buenos Aires, Buenos Aires, Argentina, 298 p.

² Dans, S., E. A. Crespo, S. Pedraza, R. González, and N. García. 1996. Estructura y tendencia de los apostaderos de lobos marinos de un pelo (*Otaria flavescens*) en el norte de Patagonia. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica. Fundación Patagonia Natural (Puerto Madryn, Argentina) 13:1–21.

Table 1

Number of South American sea lion stomachs analyzed in our study by period of time, geographical area, sex, and source of sampling. The number of empty stomachs is given in parentheses.

Period	Area	Males		Females	
		Dead on shore	Caught incidentally	Dead on shore	Caught incidentally
1982–87	Northern Patagonia	6 (1)		3 (1)	
	Central Patagonia			1 (0)	
1990–98	Northern Patagonia	13 (4)		20 (4)	
	Central Patagonia	1 (1)	8 (0)	4(0)	3(0)

reira, 1982; George-Nascimento et al., 1985) have reported the presence of gastroliths in this species, and others (Taylor, 1993) have suggested functions for them (food processing, buoyancy control, elimination of internal parasites, and alleviation of hunger).

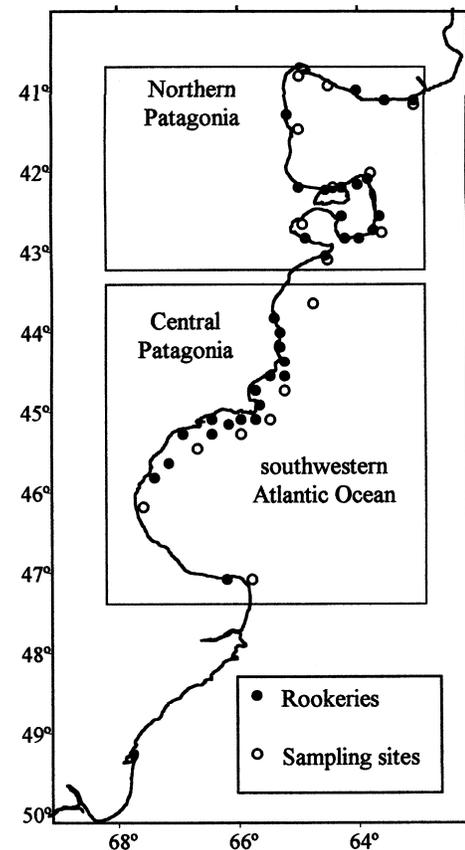
The marine ecosystem in Patagonia supports one of the most intense fisheries in the world, with approximately one million tons of catch per year during the 1990s (Anonymous, 1996). South American sea lions are reported to be caught incidentally in the trawl fisheries for Argentine hake (*Merluccius hubbsi*) and Argentine red shrimp (*Pleoticus muelleri*) (Crespo et al., 1994, 1997). Some of the target and bycatch species of these and other fisheries, such as the Argentine shortfin squid (*Illex argentinus*) fishery, are consumed by South American sea lions (Crespo et al., 1997). The development of the fisheries may have been one factor that slowed the recovery of the South American sea lion population after harvesting of this marine mammal species ended in the mid 1960s (Crespo and Pedraza, 1991).

The objectives of this research were to describe the diet of South American sea lions off Patagonia, to evaluate some hypotheses on the function of gastroliths, and to explore the possibility of trophic competition with commercial fisheries.

Materials and methods

Sample studied

The total sample was composed of 59 stomachs from 28 males and 31 females, obtained in the periods 1982–1987 and 1990–1998 (Table 1). Most of the 1982–1987 sample ($n=10$) was collected in the northern area of Patagonia (Fig. 1). These animals were found dead on shore. The 1990–1998 sample ($n=49$) was collected in the northern and central Patagonian areas (Fig. 1). During this period, the animals were

**Figure 1**

Study area, showing the two geographical areas considered in this work: northern and central Patagonia. The filled circles indicate the location of rookeries of South American sea lion and the empty circles indicate sampling sites.

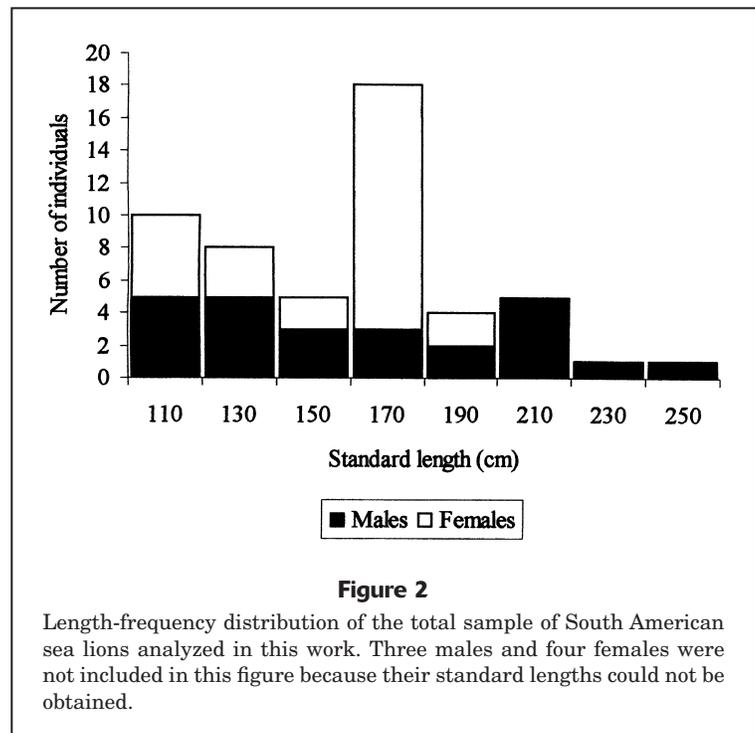
obtained from two sources: shores where animals were found dead (14 males and 24 females) and fisheries where animals were caught incidentally (8 males and 3 females) (Table 1). Samples were clumped

into geographical areas based on the spatial distribution of rookeries (Fig.1) and the reported animal movements between rookeries in northern Patagonia (Crespo and Pedraza, 1991; Crespo¹; Dans et al.²). Sex and standard length (SL, cm) were recorded when possible. Males ranged from 114 to 243 cm SL, whereas females ranged between 102 to 196 cm SL (Fig. 2).

Stomach content analysis

Stomach contents were preserved in 70% alcohol or frozen at -20°C . Hard pieces were recovered by using sieves of different mesh sizes (from 0.5 to 10 mm) flushed with water and by using decantation trays. Fish otoliths and bones, cephalopod beaks, crustacean exoskeletons and other hard remains were used to quantify and identify the prey species. Identification was made by using local species reference collections at the Marine Mammal Laboratory, Centro Nacional Patagónico, CONICET, and available catalogues (Clarke, 1986; Menni et al., 1984; Roper et al., 1984; Boschi et al., 1992; Gosztonyi and Kuba³). Complete and undigested elements (complete prey, otoliths and beaks) were measured with digital calipers. When digested and broken hard pieces were found in a stomach, the measurements for these elements were assigned from a random sample of undigested and whole parts of the same species obtained within the same stomach (Koen Alonso et al., 1998).

Size (total length ([TL]) of fish and dorsal mantle length ([DML]) of squid, cm) and wet weight (W, g) of prey were estimated from hard pieces by using allometric regressions (Clarke, 1986; George-Nascimento et al., 1985; Koen Alonso et al., 1998) (Table 2). In those cases where regressions were not available, regressions of related species were employed (Table 2). When related species regressions did not exist, weight was assigned by direct comparison with measured and weighed individuals of similar size for the same species or by weighing the fragments found in the stomach. The presence of stomach stones and parasites was recorded and all the gastroliths were weighed in each stomach.



Data analysis

The relative importance of prey species was evaluated by means of the index of relative importance (IRI) (Pinkas et al., 1971). The IRI was calculated for each prey species as

$$IRI = (\%N + \%W)\%FO,$$

Where $\%FO$ = the percent frequency of occurrence;
 $\%N$ = the percentage by number; and
 $\%W$ = the percentage by regression-estimated wet weight.

This IRI is a modified version of the index where the original term of percentage by volume was replaced by the $\%W$ term (Koen Alonso et al., 1998). In order to make easier the interpretation of the IRI, this index was expressed on a percent basis ($\%IRI$) (Cortés, 1997). Graphical representation of the diet was also employed to present some results (Cortés, 1997).

Two overlap indices, the general overlap index (GO) and the specific overlap index (SO) (Petraitis, 1979; Ludwig and Reynolds, 1988), were used to examine dietary differences. These indices were selected because they are based on the same theoretical framework, have associated statistical tests (Petraitis, 1979), and the GO presents a small bias even when the sample size is small (Smith and Zaret, 1982).

³ Gosztonyi, A., and L. Kuba. 1996. Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Informes Técnicos del Plan de Manejo Integrado de la Zona Costera Patagónica. Fundación Patagonia Natural (Puerto Madryn, Argentina) 4:1-29.

Table 2

Regressions used to estimate size and wet weight of prey of the South American sea lion off Patagonia, with their sample size (n), coefficient of determination (r^2), and source. Total length (TL) and dorsal mantle length (DML) are given in centimeters, otolith length (OL), lower rostral length (LRL), and lower hood length (LHL) are given in millimeters, and wet weight (W) is in grams.

Prey species	Regressions	n	r^2	Source
Teleosts				
<i>Engraulis anchoita</i>	$TL=2.36817+3.56OL$	79	0.70	Koen Alonso et al., 1998
	$W=0.0025TL^{3.353}$	81	0.93	Koen Alonso et al., 1998
<i>Seriolella punctata</i>	$TL=-0.1533+4.1987OL$	45	0.8956	present study
	$W=0.0182TL^{2.8635}$	22	0.8782	present study
<i>Stromateus brasiliensis</i>	$TL=3.042OL^{1.159}$	51	0.98	Koen Alonso et al., 1998
	$W=0.0006418TL^{3.917}$	63	0.98	Koen Alonso et al., 1998
<i>Nemadactylus bergi</i>	$TL=-3.8317+5.6735OL$	56	0.9079	present study
	$W=0.0144TL^{2.9301}$	23	0.9824	present study
<i>Merluccius hubbsi</i>	$TL=1.823OL^{1.072}$ if $OL<15$	447	0.93	Koen Alonso et al., 1998
	$TL=1.984OL^{1.05}$ if $OL\geq 15$	693	0.91	Koen Alonso et al., 1998
	$W=0.00476TL^{3.061}$ if $OL<15$	469	0.92	Koen Alonso et al., 1998
	$W=0.00972TL^{2.886}$ if $OL\geq 15$	742	0.96	Koen Alonso et al., 1998
<i>Acanthistius brasilianus</i>	$TL=10.4444+1.8673OL$	23	0.7816	present study
	$W=0.0082TL^{3.1713}$	11	0.9654	present study
<i>Pseudoperca semifasciata</i> ¹	$TL=-12.9242+4.6425OL$	27	0.9789	present study
	$W=0.005TL^{3.2066}$	13	0.9807	present study
<i>Gnyptherus blacodes</i>	$TL=-18.3696+5.6394OL$	45	0.7890	present study
	$W=0.0016TL^{3.2251}$	24	0.9783	present study
<i>Raneya brasiliensis</i>	$TL=-0.7671+3.1968OL$	52	0.6819	present study
	$W=0.0022TL^{3.2685}$	26	0.9349	present study
<i>Patagonotothen</i> spp. ²	$TL=-3.33204+4.21936OL$	121	0.7175	present study
	$W=0.0013TL^{3.668}$	75	0.9729	present study
<i>Triathalassothia argentina</i>	$TL=0.8116+2.775OL$	4	0.4278	present study
	$W=0.1987TL^{2.1123}$	4	0.6161	present study
<i>Paralichthys isosceles</i>	$TL=-0.9035+4.6962OL$	17	0.9436	present study
	$W=0.0013TL^{3.6036}$	8	0.9975	present study
Agnathans				
<i>Mixine</i> sp.	$W=0.003TL^{2.81089}$	7	0.9314	present study
Cephalopods				
<i>Illex argentinus</i>	$DML=-3.178+5.617LHL$	27	0.93	Koen Alonso et al., 1998
	$DML=0.08257+6.009LRL$	63	0.87	Koen Alonso et al., 1998
	$W=0.00982DML^{3.238}$	66	0.98	Koen Alonso et al., 1998
<i>Loligo gahi</i> ³	$DML=-0.712+4.622LHL$	98	0.76	Koen Alonso et al., 1998
	$W=0.026DML^{2.753}$	102	0.93	Koen Alonso et al., 1998
<i>Octopus vulgaris</i> ⁴	$W=e^{1.82+3.03Ln(LHL)}$	108	—	Clarke, 1986
<i>Eledone</i> sp.	$W=e^{1.68+2.85Ln(LHL)}$	214	—	Clarke, 1986

¹ These regressions were also used for *Pinguipes brasilianus*.

² These regressions were used for *Patagonotothen cornucola*.

³ These regressions were also used for *Loligo sanpaulensis*.

⁴ This regression was used for *Enteroctopus megalocyathus* and *Octopus tehuelchus*.

The GO evaluates the probability of obtaining the utilization curve of each group from the common utilization curve of all groups (Petraitis, 1979). This index has a minimum value which depends on the

sample size and the number of prey species considered. To compare the index obtained from different samples, it was adjusted to vary between 0 and 1 (GO_a) (Ludwig and Reynolds, 1988). The null

hypothesis of a complete overlap ($GO=1$) can be statistically tested by using the V -statistic (Ludwig and Reynolds, 1988).

The SO is a pairwise nonsymmetric index which evaluates the probability of obtaining the utilization curve of one group from the utilization curve of the other (Petraitis, 1979; Ludwig and Reynolds, 1988). The probability of obtaining the utilization curve of the group i from the utilization curve of group k is denoted by SO_{ik} . The null hypothesis of a complete overlap ($SO_{ik}=1$) can be tested with the U -statistic (Ludwig and Reynolds, 1988).

The comparisons made were 1) geographical area of sampling (between northern Patagonia and central Patagonia), 2) period of sampling (between 1982–1987 and 1990–1998), 3) source of sampling (between dead animals on shore and entangled animals in the fishery), and 4) sex (between males and females). Because entangled individuals were mostly males and were obtained only during the 1990–1998 period (Table 1), comparisons were made between entangled and nonentangled males in the period 1990–1998.

The data employed for this analysis were those data on the occurrences of prey species that presented an %IRI greater than 2% in the pooled sample. Inherent in the use of occurrences of prey species is the assumption that each prey species in a stomach was consumed independently. For this reason, the correlations between the prey species used in our analyses were evaluated with the Spearman rank correlation coefficient (r_s) (Siegel and Castellan, 1995). The use of occurrences of prey species as data also increases the sample size for these comparisons because the stomach of one sea lion usually contained more than one prey species.

Differences in prey sizes consumed were tested by using the nonparametric two-sample Mann-Whitney U test in those cases where differences were detected (Siegel and Castellan, 1995).

The relationship between mean length of prey in each stomach and predator SL was evaluated using the r_s (Siegel and Castellan, 1995). This analysis was performed by using the pooled sample and analyzed by sex of predator.

The function of gastroliths

The role of gastroliths in eliminating stomach parasites and the potential function of gastroliths in buoyancy control were investigated. The independence between the presence of gastroliths and the presence of parasites in the stomachs was tested with Fisher's exact test. The relationship between SL and total weight of gastroliths found in the stomach

(GW) was evaluated with the Spearman rank correlation coefficient (r_s) (Siegel and Castellan, 1995). This relationship was analyzed by considering each sex and the pooled sample.

Results

Prey species

Forty-eight of 59 stomachs analyzed contained food remains (Table 1). Approximately 37 prey species were identified, mostly fishes and cephalopods (Table 3). Additionally, the stomach of one female found dead on the beach contained two sponge species, tube polychetes, nudibranchs and hagfish (*Mixine* sp.). Because this specimen was considered sick and anomalous, it was excluded from the analysis.

The collection analyzed was composed of 1449 individual prey, and the total estimated weight was 209.9 kg.

Males consumed a broader trophic spectrum of 32 prey species (Table 3), dominated by Argentine hake, followed by Patagonian squid, *Loligo gahi*, Argentine shortfin squid, "raneya," *Raneya brasiliensis*, and red octopus, *Enteroctopus megalocyathus*. Only the Argentine hake had a %IRI greater than 10%. The total number of prey found in male sea lions stomachs was 738 and the total estimated biomass was 91.4 kg. The five most important prey represented 74.0% by number and 74.6% by weight.

Twenty-nine species were found in female sea lion stomachs. The important prey were red octopus, Argentine shortfin squid, Argentine hake, "raneya," and Argentine anchovy (*Engraulis anchoita*) (Table 3). Only the first three species had %IRIs greater than 10%. The total number of prey found in the female stomachs was 711 and the estimated weight of this collection was 118.5 kg. The five most important prey represented 75.5% by number and 91.3% by weight.

Homogeneity of the sample

Six species (Argentine hake, red octopus, Argentine shortfin squid, Patagonian squid, "raneya," and Argentine anchovy) had an %IRI greater than 2% in the pooled sample (Fig. 3). All pairwise correlations for these prey species were nonsignificant ($P>0.05$). Data on the occurrences of these species were used in the overlap analysis.

Considering the GO , no differences in diet were found between geographical areas and between periods of sampling (Table 4). However, the SO indicates differences in diet between the periods 1990–1998 and

Table 3

Number (*n*), percent frequency of occurrence (%*FO*), percent number (%*N*), percent estimated wet weight (%*W*), and percent index of relative importance (%*IRI*) of prey of the South American sea lion off Patagonia. The ecological group for each species is shown in parentheses (P=pelagic, B=benthic, DP=demersal pelagic, DB=demersal benthic, NA=not assigned). Ecological groups were assigned following Angelescu (1982), Menni (1983), Menni et al. (1984), Angelescu and Prenske (1987), and Boschi et al. (1992).

Prey	Females					Males				
	<i>n</i>	% <i>N</i>	% <i>W</i>	% <i>FO</i>	% <i>IRI</i>	<i>n</i>	% <i>N</i>	% <i>W</i>	% <i>FO</i>	% <i>IRI</i>
Teleosts										
<i>Merluccius hubbsi</i> (DP)	101	14.2	9.0	34.6	11.9	286	38.8	52.4	72.7	68.6
<i>Raneya brasiliensis</i> (DB)	151	21.2	3.0	19.2	6.9	67	9.1	2.8	40.9	5.0
<i>Engraulis anchoita</i> (P)	123	17.3	2.0	15.4	4.4	33	4.5	0.8	27.3	1.5
<i>Patagonotothen cornucola</i> (DB)	34	4.8	0.3	7.7	0.6	40	5.4	0.4	22.7	1.4
<i>Paralichthys isosceles</i> (B)	18	2.5	0.7	7.7	0.4	8	1.1	2.6	18.2	0.7
<i>Triathalassothia argentina</i> (B)	13	1.8	0.4	15.4	0.5	5	0.7	0.2	9.1	0.1
<i>Genypterus blacodes</i> (DB)	12	1.7	0.7	3.8	0.1	3	0.4	3.4	9.1	0.4
<i>Pseudoperca semifasciata</i> (DB)	3	0.4	0.9	3.8	0.1	3	0.4	11.4	9.1	1.1
<i>Stromateus brasiliensis</i> (DP)	5	0.7	0.7	3.8	0.1	5	0.7	1.4	9.1	0.2
<i>Acanthistius brasiliensis</i> (DB)	1	0.1	0.4	3.8	<0.1	2	0.3	1.4	9.1	0.2
<i>Seriola punctata</i> (DP)	—	—	—	—	—	9	1.2	0.5	4.5	0.1
<i>Ilucoetes fimbriatus</i> (DB)	—	—	—	—	—	7	0.9	0.2	4.5	0.1
<i>Percophis brasiliensis</i> (DB)	1	0.1	0.8	3.8	0.1	1	0.1	0.6	4.5	<0.1
<i>Pinguipes brasiliensis</i> (DB)	2	0.3	<0.1	3.8	<0.1	1	0.1	0.1	4.5	<0.1
Unidentified fish (NA)	1	0.1	<0.1	3.8	<0.1	1	0.1	0.1	4.5	<0.1
<i>Nemadactylus bergi</i> (DB)	—	—	—	—	—	3	0.4	0.2	4.5	<0.1
<i>Prionotus punctatus</i> (B)	—	—	—	—	—	1	0.1	0.1	4.5	<0.1
<i>Trachurus picturatus</i> (P)	1	0.1	0.1	3.8	<0.1	—	—	—	—	—
Elasmobranchs (DB)	6	0.8	3.0	7.7	0.4	1	0.1	0.5	4.5	<0.1
Agnathans										
<i>Mixine</i> sp. (B)	—	—	—	—	—	18	2.4	0.7	13.6	0.4
Cephalopods										
<i>Enteroctopus megalocyathus</i> (B)	54	7.6	61.7	53.8	55.0	21	2.8	9.3	27.3	3.4
<i>Illex argentinus</i> (DP)	108	15.2	15.7	38.5	17.5	27	3.7	8.2	54.5	6.7
<i>Loligo gahi</i> (DP)	18	2.5	0.2	26.9	1.1	145	19.6	1.9	40.9	9.1
<i>Octopus tehuelchus</i> (B)	6	0.8	0.1	11.5	0.2	9	1.2	0.4	22.7	0.4
<i>Eledone</i> sp. (B)	6	0.8	0.1	7.7	0.1	18	2.4	0.3	13.6	0.4
<i>Loligo sanpaulensis</i> (DP)	3	0.4	<0.1	7.7	0.1	1	0.1	<0.1	4.5	<0.1
<i>Semirossia tenera</i> (DB)	2	0.3	<0.1	3.8	<0.1	3	0.4	<0.1	4.5	<0.1
Crustaceans										
Crabs (B)	9	1.3	<0.1	15.4	0.3	4	0.5	<0.1	13.6	0.1
<i>Pleoticus muelleri</i> (DB)	3	0.4	<0.1	3.8	<0.1	6	0.8	0.1	9.1	0.1
Amphipods (P)	12	1.7	<0.1	3.8	0.1	—	—	—	—	—
<i>Munida subrugosa</i> (B)	2	0.3	<0.1	3.8	<0.1	1	0.1	<0.1	4.5	<0.1
<i>Munida gregaria</i> (B)	—	—	—	—	—	2	0.3	<0.1	9.1	<0.1
<i>Serolis</i> sp. (B)	—	—	—	—	—	2	0.3	<0.1	9.1	<0.1
<i>Peisos petrunkevitchi</i> (DB)	—	—	—	—	—	5	0.7	<0.1	4.5	<0.1
<i>Heterosquilla platensis</i> (B)	1	0.1	<0.1	3.8	<0.1	—	—	—	—	—
Polychetes										
<i>Eunice argentinensis</i> (B)	8	1.1	<0.1	3.8	0.1	—	—	—	—	—
Tunicates										
<i>Pedicle tunicate</i> (B)	7	1.0	<0.1	7.7	0.1	—	—	—	—	—

1982–1987 (Table 4). The Argentine anchovy was not found in the small sample for the period 1982–1987, and was the least important of the six prey species

selected for the overlap analysis. When the analysis was performed excluding this prey species, no differences were found between periods in either of the

two overlap indices (Table 4). No differences were also found between entangled and nonentangled males in the period 1990–1998 (Table 4).

When the difference in feeding between sexes was analyzed, no differences were found with the GO, but the SO indicated significant differences in diet (Table 4). Taking into account that the GO analyzes the differences between the utilization curves of the groups with reference to a common utilization curve, whereas the SO analyzes one utilization curve with respect to the other one, our data suggest that there are some differences in the diet between sexes.

Prey size

No differences were found in the sizes of Argentine hake ($U=13,785.5$; $n_{\text{males}}=286$; $n_{\text{females}}=101$; $P=0.496$), Argentine shortfin squid ($U=1,331.5$; $n_{\text{males}}=27$; $n_{\text{females}}=108$; $P=0.486$), and Argentine anchovy ($U=1,627$; $n_{\text{males}}=33$; $n_{\text{females}}=123$; $P=0.080$) consumed by the two sexes. Seventy-four percent of the Argentine hake eaten by sea lions were less than 30 cm TL. Argentine shortfin squid consumed by sea lions had a DML greater than 15 cm, whereas Argentine anchovy consumed by sea lions were mostly between 12 and 17 cm of TL (Fig. 4). Red octopus consumed by males weighed significantly less than those consumed by females ($U=194.5$; $n_{\text{males}}=21$; $n_{\text{females}}=54$; $P<0.0001$). Patagonian squids consumed by males were larger than those consumed by females ($U=880$; $n_{\text{males}}=145$; $n_{\text{females}}=18$; $P=0.024$), but the range of DMLs of squid consumed by females was greater than that of squid eaten by males. Larger "raneya" was consumed by male sea lions than "raneya" eaten by female sea lions ($U=2,681$; $n_{\text{males}}=67$; $n_{\text{females}}=151$; $P<0.0001$) (Fig. 5).

No relationships were found between mean length of prey and predator SL with the pooled sample ($r_s=0.007$; $n=37$; $P=0.964$), with males only ($r_s=0.004$; $n=19$; $P=0.985$) or with females only ($r_s=0.118$; $n=18$; $P=0.641$).

Gastroliths

Of the stomachs analyzed, 60.4% had gastroliths and 87.9% had parasites. The parasites found in the stomachs were mostly nematodes. The presence of parasites and gastroliths was independent (Fisher exact test; $P=0.999$). A positive correlation was found between the SL of South American sea lions and GW ($r_s=0.572$; $n=45$; $P<0.0001$) (Fig. 6).

Gastroliths were found in 56.7% of females sea lions and 90.0% of females had parasites. The pres-

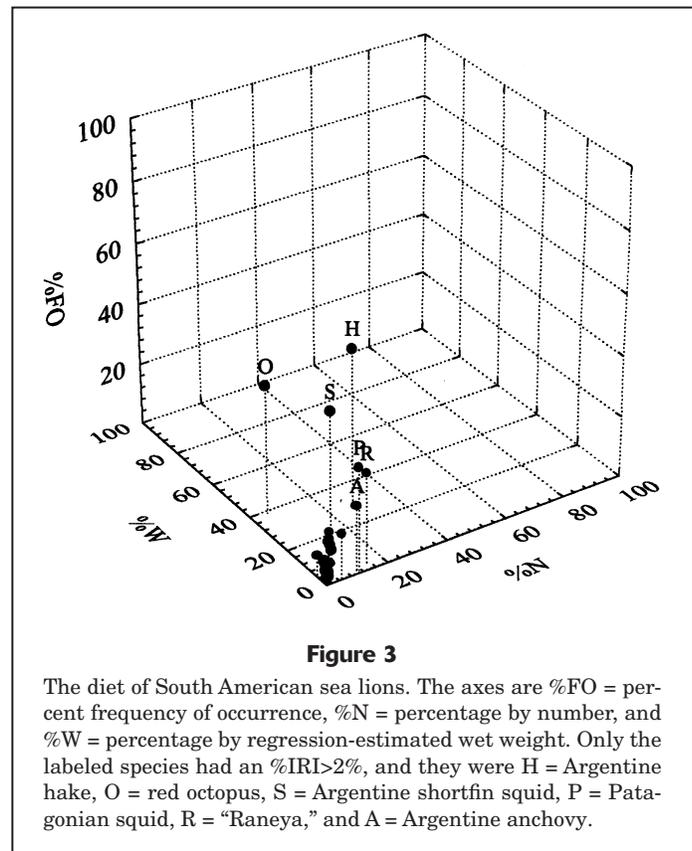


Figure 3

The diet of South American sea lions. The axes are %FO = percent frequency of occurrence, %N = percentage by number, and %W = percentage by regression-estimated wet weight. Only the labeled species had an %IRI>2%, and they were H = Argentine hake, O = red octopus, S = Argentine shortfin squid, P = Patagonian squid, R = "Raneya," and A = Argentine anchovy.

ence of gastroliths and parasites was independent (Fisher exact test; $P=0.5645$). A positive correlation was found between SL and GW ($r_s=0.66$; $n=23$; $P=0.0006$).

Gastroliths were found in 85.7% of the male sea lion stomachs, and 64.3% of males had parasites. The independence between the presence of gastroliths and parasites could not be rejected (Fisher exact test; $P=1$), and a positive correlation was found between SL and GW ($r_s=0.599$; $n=22$; $P=0.0032$).

Discussion

The samples analyzed was collected over a broad range of time and space and were derived from two sampling sources. For that reason several subsamples were tested for homogeneity before a sample could be considered to be representative of the diet of South American sea lions. Those subsamples were tested by means of the GO and SO indices because they have associated statistical tests. The GO has only a small bias related to the difference in sample sizes even when the total sample size is relatively small (Smith and Zaret, 1982), and both overlap measures do not change if the resources are divided

Table 4

Diet overlap analyses between the major sources of variation in the sample studied. GO = general overlap index; GO_a = adjusted general overlap index; V = the statistic to test the null hypothesis that $GO = 1$; df = degrees of freedom; P = probability of the statistic; SO_{ik} = specific overlap of group i onto group k ; U = statistic to test the null hypothesis that $SO_{ik} = 1$. The number of prey occurrences in each category are indicated in parentheses.

Source of variation	General overlap index					
	GO	GO_a	V	df	P	
Period of time	0.987	0.953	2.870	5	0.720	
Period of time ¹	0.997	0.990	0.585	4	0.965	
Geographic area	0.986	0.971	2.989	5	0.702	
Source of sampling	0.983	0.966	1.715	5	0.887	
Sex	0.970	0.940	6.514	5	0.259	
Source of variation	Specific overlap index					
	i	k	SO_{ik}	U	df	P
Period of time	1982–1987 (11)	1990–1998 (96)	0.869	3.078	5	0.688
	1990–1998 (96)	1982–1987 (11)	0.197	311.532	5	<0.001
	1982–1987 ¹ (11)	1990–1998 ¹ (86)	0.971	0.658	4	0.956
	1990–1998 ¹ (86)	1982–1987 ¹ (11)	0.969	5.367	4	0.252
Geographic area	central Patagonia (38)	northern Patagonia (69)	0.942	4.545	5	0.474
	northern Patagonia (69)	central Patagonia (38)	0.937	8.951	5	0.111
Source of sampling	nonentangled males (29)	entangled males (22)	0.932	4.066	5	0.540
	entangled males (22)	nonentangled males (29)	0.933	3.037	5	0.694
Sex	females (49)	males (58)	0.870	13.606	5	0.018
	males (58)	females (49)	0.894	13.029	5	0.023

¹ Analysis performed excluding the Argentine anchovy.

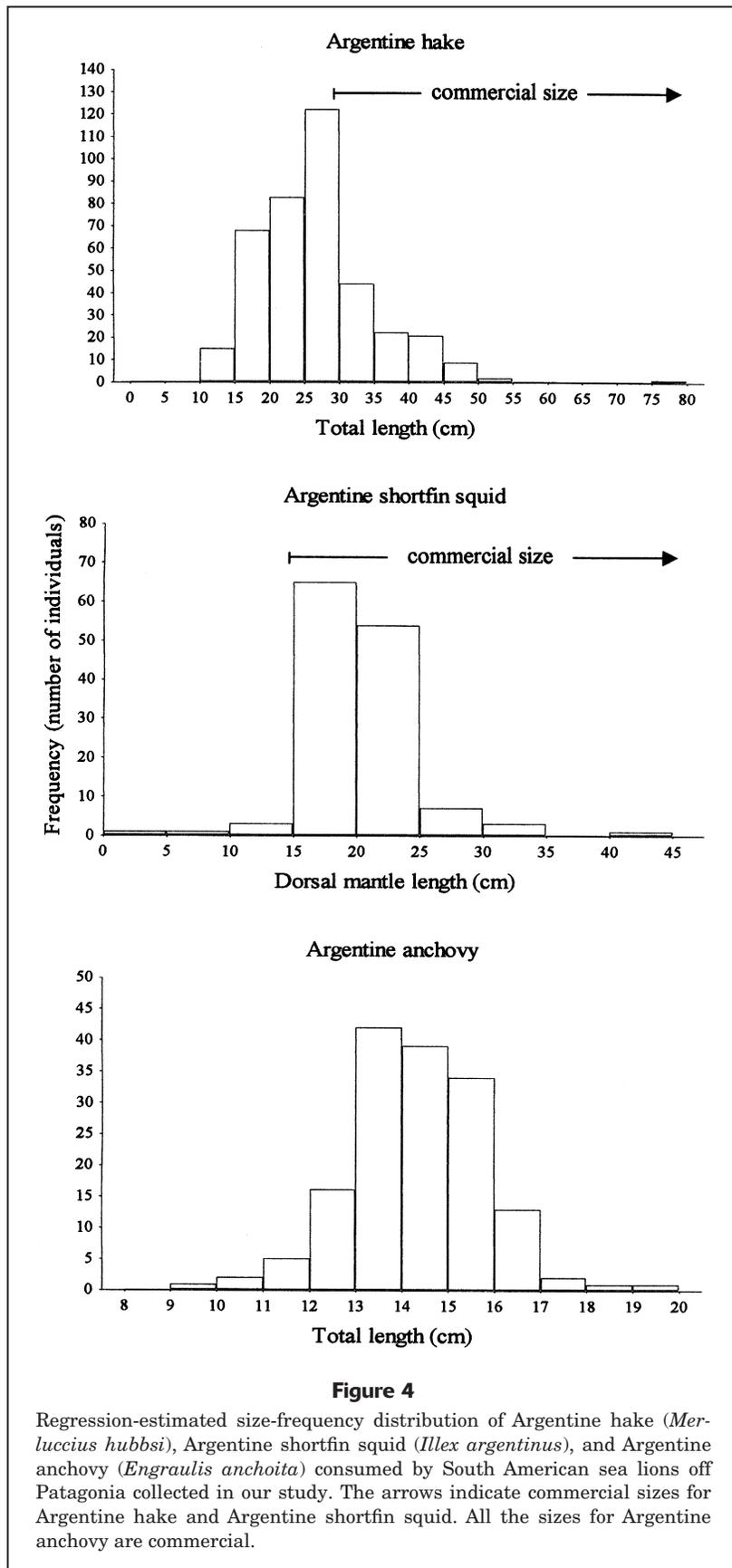
into classes below the organism's level of discrimination (Petraitis, 1979). However, one cannot evaluate the interaction between sources of variation with these analyses. For this reason, as in any statistical test, the lack of a difference for a particular source of variation does not indicate the absence of a difference, it means only that there is not enough information to affirm that this source of variation is significant.

The marine communities for both areas in this study comprise the same species and are considered to be relatively homogeneous along the entire geographical areas range covered by the study area (Fig. 1) (Menni, 1983; Menni and López, 1984; Angelescu and Prenski, 1987). In addition, the trend of sea lion stocks in northern and central Patagonia has followed a pattern of decline and recovery during recent decades. The northern Patagonia stock declined to one fifth of its original population size between 1930 and the mid-1960s as a consequence of intense harvesting. Then it remained stable between 1972 and 1990, when it began to recover (Crespo and Pedraza, 1991). The central Patagonia stock had not been har-

vested but declined in a similar proportion during the mid-century and has shown evidence of population increase in recent years—a fact that suggests a strong connection and interchange of individuals between these regions (Reyes et al., 1999). In addition, preliminary results based on electrophoresis analysis of blood enzymes and proteins codified by 10 loci have indicated that nine of these loci are monomorphic, suggesting that South American sea lions from both areas have had a strong gene flux between them and possibly constitute an unique biological population (Crespo⁴).

Regarding the two sampling periods, the differences in the diet detected with the SO are surely associated with the absence of Argentine anchovy in the 1982–1987 samples. The SO indicated that the utilization curve of food resources of the period 1990–1998 could not be drawn from the utilization

⁴ Crespo, E. A. 1998. Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico (CONICET). Boulevard Brown 3600, (9120) Puerto Madryn, Chubut, Argentina. Personal commun.



curve in the period 1982–1987. Nevertheless, when the Argentine anchovy is excluded from the analysis, no differences were found between the two periods in either at the two overlap indices. Probably, the absence of Argentine anchovy in the period 1982–1987 is related to the small size of the sample collected and to the fact that Argentine anchovy was the least important prey species among the six prey species selected for the overlap analysis (Fig. 3) because the available information indicates that the abundance of Argentine anchovy was high and roughly constant during the entire study period (Ciechomski and Sánchez, 1988; Pájaro et al.⁵).

No differences in diet were detected when shore and entangled individuals were analyzed, even though several sources of bias could be operating at the same time. The diet information obtained from individuals found dead onshore could be biased, depending on the degree of digestion of the stomach contents. In our study, the use of several (and complementary) hard remains, such as otoliths and bones, allowed us to reduce this source of bias. Even when a small otolith was totally digested, the fish bones (mostly skull bones) permitted us to identify and quantify these prey. Thus, estimating prey size by regressions avoided underestimating the importance of small or highly digested prey. In some cases, when we used the regression of a related species, the results were likely partially biased. Samples from entangled sea lions probably did not hold any of these biases because all the stomach contents were presumably composed of fresh materials. The source of bias in this case would have been due to individuals that fed inside the net. Nevertheless, a comparison

⁵ Pájaro, M., R. Sánchez and G. Macchi. 1997. Evaluación de la biomasa de adultos desovantes de la población norteña de anchoíta (*Engraulis anchoita*) en el período 1993–1996. Abstracts of the XII Simposio Científico-Tecnológico de la Comisión Técnica Mixta del Frente Marítimo, Montevideo, Uruguay, November 12–14, 1997, 4 p.

of dead, beached males with entangled males did not show any significant difference.

The only difference in diet found between subsamples was that shown by sexes. In this case differences in behavior and feeding habits could reflect differences in diet. Even if each sample source may have had different potential biases and the overlap analysis between them did not detect differences, we consider our sample to be, even with its limitations, a reasonable approximation of the diet of South American sea lions in Patagonia.

The diversity of prey species (Table 3) found in the diet of the South American sea lion indicates that it is a broad-spectrum predator. Some of these prey species (Argentine hake, Argentine shortfin squid, and Argentine anchovy) are abundant key species in the Patagonian continental shelf ecosystem and have commercial value (Angelescu, 1982; Angelescu and Prenski, 1987; Brunetti, 1990; Bezzi et al., 1994).

Argentine hake and Argentine shortfin squid are the two major target species of the Argentine fleet (Anonymous, 1996), and Patagonian squid is also exploited in the Falkland (Malvinas) Islands (Hatfield, 1996). Sea lions ate these prey species at both commercial and noncommercial sizes (Fig. 4).

The fishery catches Argentine hake with length modes between 35 and 40 cm TL (Cañete et al., 1986), and the minimum commercial size of this species is 30 cm TL. Mostly noncommercial sizes of Argentine hake (less than 30 cm TL) were consumed by South American sea lions (Fig. 4). Estimates of stock number by age by using virtual population analysis indicated that the most abundant Argentine hakes are those of age-1 and age-2 year classes (approximately 30 cm or less in TL), which represent around 56% in number of the estimated hake stock (Bezzi et al., 1994). These data indicate that sea lions are feeding on this species according to prey-size distribution and availability in the environment. Hakes smaller than 10 cm

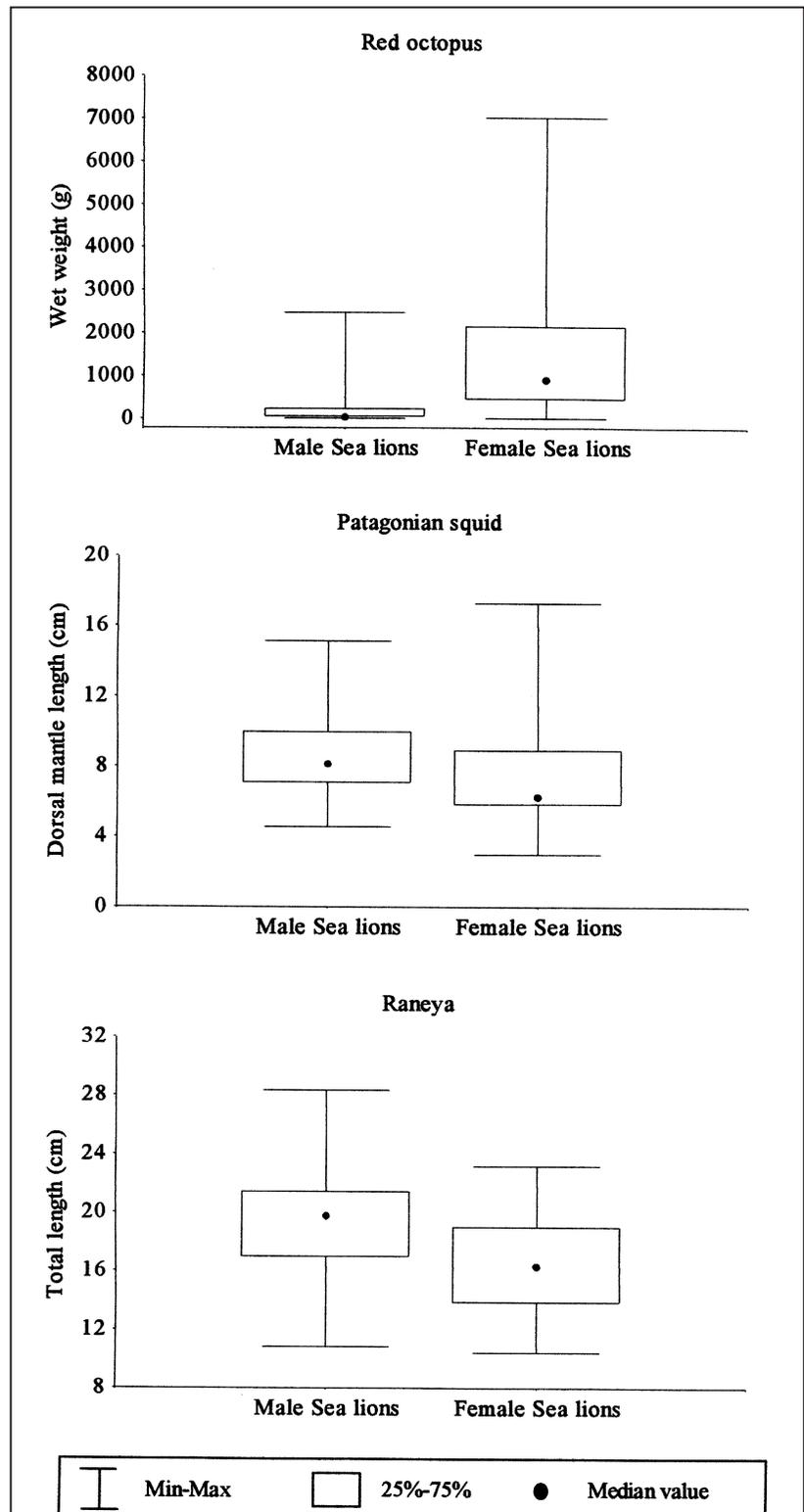


Figure 5

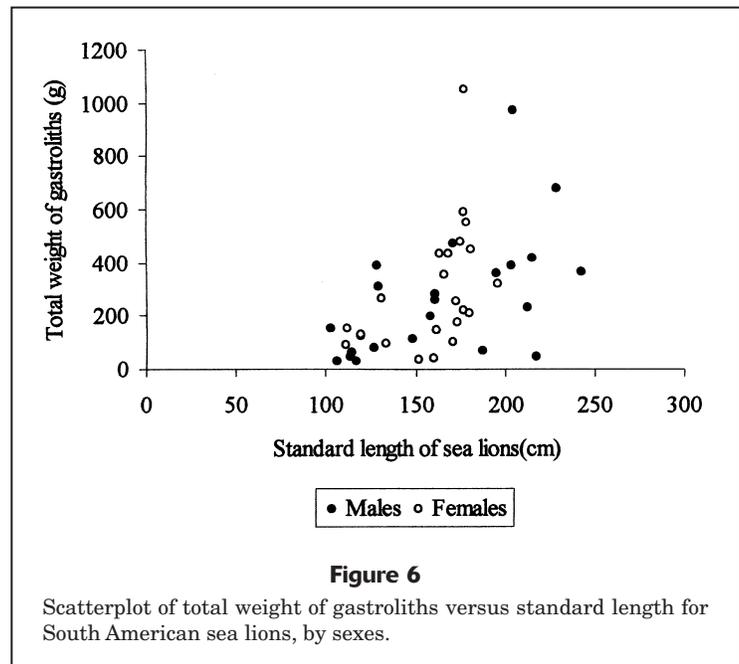
Box plots of regression-estimated size of red octopus (*Enteroctopus megalocyathus*), Patagonian squid (*Loligo gahi*), and "raneya" (*Raneya brasiliensis*) consumed by male and female South American sea lions collected in our study.

TL are not caught by either sea lions or the fishery because of the pelagic behavior of fish in this size range (Angelescu and Prenschi, 1987).

The commercial squid species found in the diet of sea lions (Argentine shortfin and Patagonian squid) form schools of restricted size range (Brunetti and Ivanovic, 1992; Hatfield, 1996). Therefore, it is difficult to determine if the consumed sizes represent the environmental availability of these prey species. The commercial size of shortfin squid is approximately 15 cm DML, and this species was consumed by sea lions at commercial sizes (Fig. 4). Patagonian squid was consumed mostly at noncommercial sizes (less than 10 cm DML) because that most of the squid catches in the Falkland fishery were between 10 and 15 cm DML (Hatfield, 1996).

These results indicate some overlap between the South American sea lion diet and fishery catches but not enough to conclude that competition exists with the fishery. The population of South American sea lions in northern Patagonia has been increasing during recent years at a rate of increase greater than 3% (Crespo and Pedraza, 1991; Dans et al.²). There is no indication that fishery catches affect the availability of food for sea lions at the present time. More detailed estimates of food consumption by South American sea lions are needed. Also, estimates of the catch and bycatch of the fishery are needed to evaluate conclusively the existence of ecological competition.

Differences in the diet between sexes are probably associated with different utilization of common and frequent food resources, suggesting some kind of differential feeding behavior between the sexes. The South American sea lion is a dimorphic and polygamous species. Therefore each sex must have different ecological constraints. Adult female feeding trips last for about three days during reproductive (Cappozzo et al., 1991) and nonreproductive (Reyes and Crespo⁶) seasons. Nursing pups may limit the distance that females can travel to feeding ground. Males are not restricted by nursing pups and their feeding trips seem to be less constant (Reyes and Crespo⁶). There is also some evidence obtained from sightings from fishing vessels that males move farther offshore than do females which remain closer



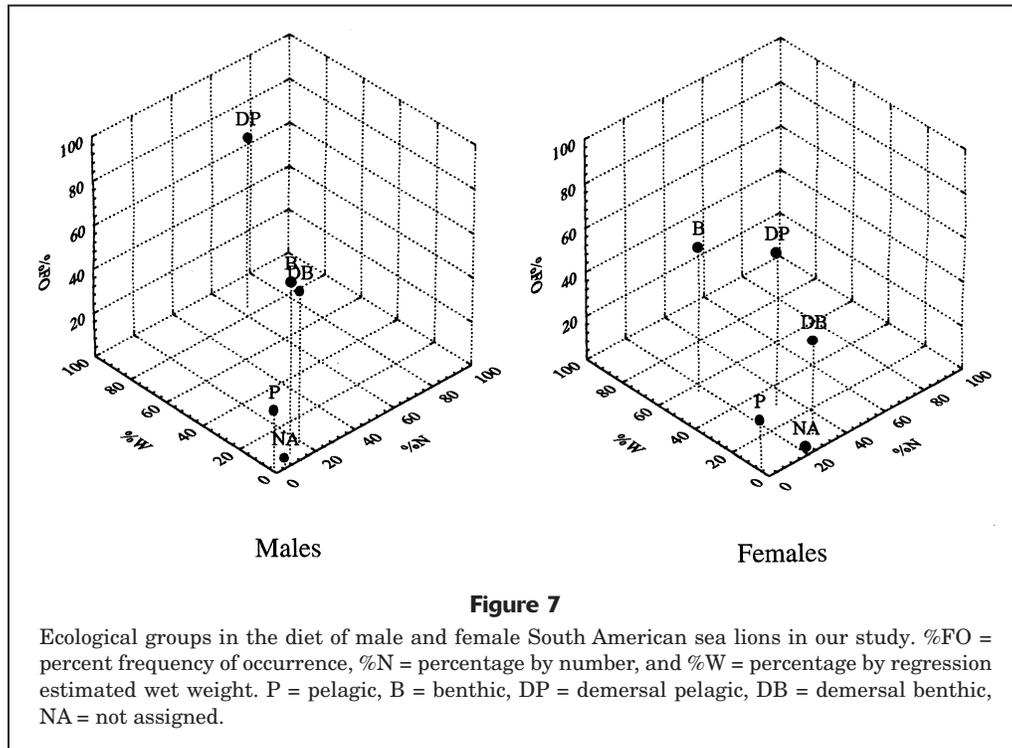
to the coast (Crespo et al., 1997). Thus, differences in the diet could be associated with different feeding grounds or different home ranges between the sexes.

The prey of female South American sea lions were more evenly distributed within ecological groups than the prey of males (Fig. 7). The prey of females were mostly benthic and demersal-pelagic species. The mean dive depth recorded by lactating females in Patagonia was 60.9 m, and 69% of the dives were flat-bottomed and U-shaped (Werner and Campagna, 1995)—data that agree with the bottom and coastal feeding behavior suggested by the stomach contents. On the other hand, the most important prey of males were demersal-pelagic species (Fig. 7).

The Patagonian squid spawns in shallow waters, and the new generation migrates offshore to feed, grow, and mature (Hatfield, 1996). This migration pattern implies that small Patagonian squid must be more abundant in shallow, coastal waters than in deeper, offshore areas, but their size range in the coastal area must be broader than that in offshore areas because mature (and large) squids return to shallow waters to spawn. The consumption of larger Patagonian squid by male sea lions and the broader range size of Patagonian squid eaten by female sea lions agree with the hypothesis that females feed in more coastal and shallower waters than do males.

The red octopus lives mostly in caves on rocky bottoms (Ré, 1998) and is the most important prey species of female South American sea lions. Red octopus reach maturity around 120 mm DML and 850 g of total weight (Ré, 1998); male sea lions consumed

⁶ Reyes, L. M., and E. A. Crespo. 1993. Variaciones diarias y lunares y viajes de alimentación en el lobo marino del sur *Otaria flavescens* en el norte de Patagonia. Abstracts of the Jornadas Nacionales de Ciencias del Mar "93," 19–25 September 1993, Puerto Madryn, Argentina, 156 p.



mostly immature individuals whereas female sea lions consumed mature ones. If females search for prey on rocky bottoms, they will catch the mature and larger red octopus. Instead, if male South American sea lions feed mostly in the water column near the bottom, they could catch the younger red octopus when they are actively moving on the bottom. Younger octopus could be more vagrant than adults, and in some species, posthatching octopuses do exhibit pelagic behavior (Boletzky, 1977). The difference in the size of red octopus that South American sea lion consumed could be associated with this characteristic in prey biology, thus supporting the hypothesis of different feeding behavior between the sexes.

In regard to gastrolith function, the hypothesis of buoyancy control has been postulated with the evidence of the presence of gastroliths in several living and extinct tetrapods that swim using their limbs in the form of an underwater fly (Taylor, 1993). Taylor (1993), in an extensive comparative study, demonstrated that there is no correlation between the presence of gastroliths and diet, but he found a correlation between gastroliths and underwater flying. Another explanation for the ingestion of stones is that gastroliths “grind up” parasitic worms that usually infest seals (Riedman, 1990). The role of stomach stones seems to be better explained as “buoyancy control” than as “elimination of stomach parasites” because of the independence between the presence of para-

sites and gastroliths, and the significant correlations between predator size and gastrolith weight. Gastroliths found in the South American sea lions could be considered “ballasts” that allow the sea lions to regulate their buoyancy. Moreover, the gastroliths can also be quickly swallowed and vomited, allowing sea lions to change buoyancy according to their needs (Harrison and Kooyman, 1968).

In summary, these stomach content analyses indicate that South American sea lions feed primarily on demersal and benthic species and, in general terms, use resources according to their environmental availability. Males and females appear to have different constraints in their feeding behavior and these restrictions could lead females to feed in more coastal and shallower waters than those where males feed. These potential differences in feeding grounds or home ranges, or both, could explain the observed differences in diet between the sexes.

Acknowledgments

The authors wish to thank Pablo Mariotti, Bárbara Berón Vera, Nancy Mora, Pablo Nepomnaschy and Laura Reyes for their help with the stomach contents analysis; Silvana L. Dans, Pablo Yorio and Guillermo Harris for their critical reading and useful comments on earlier versions of the manuscript; and all of the

fishermen and wildlife wardens for their help aboard ship and in the field. Three anonymous reviewers (especially no. 817) and Sarah Shoffler made important and useful comments that enhanced the analysis of results and the expression of the ideas. As always, Sharyn Matriotti gave us important help with this article. Institutional support was provided by Centro Nacional Patagónico (CONICET), Universidad Nacional de la Patagonia, Fundación Patagonia Natural, Prefectura Naval Argentina, and the government of Chubut Province. The fishing companies Harengus S.A. and Alpesca S.A. collaborated with the authors in the retrieval of entangled sea lions and gave their permission for work onboard their fishing vessels. This work was carried out with the financial support of the National Geographic Society (Grant 5548/95 to E.A. Crespo and A.C.M. Schiavini), the Whale and Dolphin Conservation Society, the Patagonian Coastal Zone Management Plan (GEF/UNEP FPN/WCS) and the Programa de Cooperación Científica con Iberoamérica (1996–1998).

Literature cited

- Angelescu, V.**
1982. Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*). Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero), Contribution 409, 83 p.
- Angelescu, V., and L. B. Prenski.**
1987. Ecología trófica de la merluza común del Mar Argentino (Merlucciidae, *Merluccius hubbsi*). Parte 2. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y las evaluaciones de los efectivos en su área de distribución. INIDEP, Contribution 561, 205 p.
- Anonymous.**
1996. Captura 95. *Redes* 88:24–40.
- Bezzi, S., G. Cañete, M. Pérez, M. Renzi, and H. Lassen.**
1994. Report of the INIDEP working group on assessment of hake (*Merluccius hubbsi*) north of 48°S (Southwest Atlantic Ocean). INIDEP Doc. Cient. 3:5–28.
- Boletzky, S. V.**
1977. Post-hatching behavior and mode of life in cephalopods. *Symp. Zool. Soc. Lond.* 38:557–567.
- Boschi, E. E., C. E. Fischbach, and M. I. Iorio.**
1992. Catálogo ilustrado de los crustáceos estomatópodos y decápodos marinos de Argentina. *Frente Marítimo* 10 (sec. A):7–94.
- Brunetti, N. E.**
1990. Evolución de la pesquería de *Illex argentinus* (Castellanos, 1960). *Inf. Técn. Inv. Pesq.* 155, 19 p.
- Brunetti, N. E., and M. L. Ivanovic.**
1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. *ICES J. Mar. Sci.* 49:175–183.
- Campagna, C., and B. J. Le Boeuf.**
1988. Reproductive behavior of Southern sea lions. *Behaviour* 104:233–261.
- Cañete, G. R., R. G. Perrotta, and J. A. Pérez Comas.**
1986. Aspectos comparativos entre muestreos de desembarque y muestreos en alta mar de la especie merluza (*Merluccius hubbsi*), considerando el descarte efectuado por la flota marplatense en el período julio 1979–Setiembre 1980. *Publ. Com. Téc. Mix. Fr. Mar.* 1:447–453.
- Cappozzo, H. L., C. Campagna, and J. Monserrat.**
1991. Sexual dimorphism in newborn Southern sea lions. *Mar. Mamm. Sci.* 7(4):385–394.
- Clarke, M. R.**
1986. A handbook for the identification of cephalopods beaks. Clarendon Press, Oxford, 273 p.
- Cortés, E.**
1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 54:726–738.
- Crespo, E. A., J. F. Corcuera, and A. López Cazorla.**
1994. Interactions between marine mammals and fisheries in some coastal fishing areas of Argentina. In *Gillnets and cetaceans* (W. F. Perrin, G. P. Donovan, and J. Barlow, eds.), p. 269–281. *Rep. Int. Whal. Comm.* (special issue 15).
- Crespo, E. A., and S. N. Pedraza.**
1991. Estado actual y tendencia de la población de lobos marinos de un pelo (*Otaria flavescens*) en el litoral norpatagónico. *Ecología Austral* 1:87–95.
- Crespo, E. A., S. N. Pedraza, S. L. Dans, M. Koen Alonso, L. M. Reyes, N. A. García, M. Coscarella, and A. C. M. Schiavini.**
1997. Direct and indirect effects on the high seas fisheries on the marine mammal populations in the northern and central patagonian coast. *J. Northwest Atl. Fish. Sci.* 22:189–207.
- de Ciechowski, J. D., and R. P. Sanchez.**
1988. Análisis comparativo de las estimaciones de biomasa de la anchoíta (*Engraulis anchoita*) en el Atlántico Sudoccidental en diferentes años y con distintas metodologías. *Publ. Com. Téc. Mix. Fr. Mar.* 4:117–132.
- George-Nascimento, M. F., R. A. Bustamante, and R. C. Oyarzun.**
1985. Feeding ecology of the Southern sea lion *Otaria flavescens* Shaw, 1800: food contents and food electivity. *Mar. Biol. Prog. Ser.* 21:135–143.
- Hamilton, J. E.**
1934. The Southern sea lion *Otaria byronia* (de Blainville). *Discovery Rep.* 8:269–318.
- Harrison, R. J., and G. L. Kooyman.**
1968. General physiology of the Pinnipedia. In *The behavior and physiology of pinnipeds* (R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman, eds.), p. 221–296. Appleton-Century-Crofts, New York, NY.
- Hatfield, E. M. C.**
1996. Towards resolving multiple recruitment into loliginid fisheries: *Loligo gahi* in the Falkland Islands fishery. *ICES J. Mar. Sci.* 53:565–575.
- Koen Alonso, M., E. A. Crespo, N. A. García, S. N. Pedraza, and M. Coscarella.**
1998. Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina. *Fish. Bull.* 96:366–374.
- Ludwig, J. A., and J. F. Reynolds.**
1988. Statistical ecology. John Wiley and Sons, New York, NY, 337 p.
- Menni, R. C.**
1983. Los peces en el medio marino. Estudio Sigma S.R.L., Buenos Aires, Argentina, 169 p.

- Menni, R., and H. L. López.**
1984. Distributional patterns of Argentine marine fishes. *Physis* 42 (issue 103, sec. A):71–85.
- Menni, R. C., R. A. Ringuelet, and R. A. Aramburu.**
1984. Peces marinos de la Argentina y Uruguay. Editorial Hemisferio Sur S.A., Buenos Aires, Argentina, 359 p.
- Petraitis, P. S.**
1979. Likelihood measures of niche breadth and overlap. *Ecology* 60(4):703–710.
- Pinkas, L., M. S. Oliphant, and I. L. K. Iverson.**
1971. Food habits of albacore, bluefin tuna and bonito in California waters. U.S. Dep. Fish. Game, Fish Bull. 152:1–105.
- Ré, M. E.**
1998. Pulpos octopódidos (Cephalopoda, Octopodidae). In *El mar argentino y sus recursos pesqueros* (E. Boschi, ed.), tomo 2: Los moluscos de interés pesquero. Cultivos y estrategias reproductivas de bivalvos y equinoideos, p 99–114. Instituto Nacional de Investigación y Desarrollo Pesquero, Secretaría de Agricultura, Ganadería, Pesca y Alimentación, Mar del Plata, 231 p.
- Reyes, L. M., E. A. Crespo, and V. Szapkievich.**
1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Patagonia, Argentina. *Mar. Mamm. Sci.* 15(2):478–493.
- Riedman, M.**
1990. The pinnipeds: seals, sea lions and walruses. Univ. California Press, Berkeley, CA, 439 p.
- Roper, C. F. E., M. J. Sweeney, and C. E. Nauen.**
1984. FAO species catalogue: an annotated and illustrated catalogue of species of interest to fisheries, vol. 3: Cephalopods of the world. FAO Fish. Synop. 125, 277 p.
- Siegel, S., and N. J. Castellan.**
1995. Estadística no paramétrica aplicada a las ciencias de la conducta, 4th Spanish edition. Editorial Trillas S.A., Mexico D.F., Mexico, 437 p.
- Smith, E. P., and T. M. Zaret.**
1982. Bias in estimating niche overlap. *Ecology* 63(5): 1248–1253.
- Taylor, M. A.**
1993. Stomachs stones for feeding or buoyancy? The occurrence and function of gastroliths in marine tetrapods. *Philos. Trans. R. Soc. Lond. (B Biol. Sci.)* 341:163–175.
- Vaz Ferreira, R.**
1982. *Otaria flavescens* (Shaw), South American sea lion. In *Mammals of the world*, FAO Fish. Series 5(IV), p 447–495. FAO, Rome.
- Werner, R. and C. Campagna.**
1995. Diving behavior of lactating southern sea lions (*Otaria flavescens*) in Patagonia. *Can. J. Zool.* 73:1975–1982.