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Diet and Feeding Overlap of Two Otariids, *Zalophus californianus* and *Arctocephalus townsendi*: Implications to Survive Environmental Uncertainty

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Abstract

The San Benito Islands in Mexico host a population of about 7,000 California sea lions (*Zalophus californianus*) and have been recolonized by Guadalupe fur seals (*Arctocephalus townsendi*) since 1997. Due to similarities in natural history between the two species, we undertook a study to determine their feeding habits, measure diversity of their diets, examine trophic feeding level and overlap as indicators of competition, and estimate ability to adjust to changes in prey availability. During winter and summer 2001 and 2002, 289 sea lion scats and 218 fur seal scats were collected. To identify prey species, samples were sieved to recover otoliths and cephalopod beaks. A total of 1,495 structures were recovered from the sea lion scats: 83.8% otoliths and 16.2% cephalopod beaks. The most prevalent prey was in fish species (*Argentina sialis*, *Merluccius angustimanus*, and *Sebastes* spp.) and the squid (*Loligo opalescens*). Of the 1,866 structures recovered from the Guadalupe fur seal scats, 95.6% were cephalopod beaks and 4.4% were otoliths, with *L. opalescens* as the most prevalent prey. The diversity of the trophic spectrum (H') of the sea lion was greater than the fur seal in every one of the samples, placing it as a "generalist predator" (Levins Index B = 4.65) in comparison to the fur seal (B = 1.53). The only significant trophic overlap (Morisita-Horn Index) occurred during the summer of 2001 (CH = 0.73). Both species consumed prey at similar trophic levels (sea lion = 4.42; fur seal = 4.22), which placed them as secondary-tertiary carnivores. The evidence suggests that the California sea lion forages in both benthic and pelagic habitats, resulting in a broader feeding spectrum and better adaptations to cope with changes in prey availability than the Guadalupe fur seal.

Key Words: Diet, feeding overlap, feeding plasticity, California sea lion, Guadalupe fur seal

Introduction

The pinniped populations of the North Pacific were exploited at the end of the 19th and the beginning of the 20th centuries for their meat, oil, and skins (Lluch, 1969; Seagars, 1984). The California sea lion (*Zalophus californianus*) was the least exploited and recovered rapidly, becoming the most abundant pinniped of Mexico, with a population of about 90,000 individuals (Le Boeuf et al., 1983; Aurioles-Gamboa, 1993). The northern elephant seal (*Mirounga angustirostris*) was reduced to several dozen animals, which found refuge on Guadalupe Island. This population has also recovered to reach a population of about 160,000 animals (Le Boeuf & Bonnell, 1980). The Guadalupe fur seal (*Arctocephalus townsendi*) was reduced to a small group also on Guadalupe Island (Hamilton, 1951); its recovery, however, was less dramatic. The present population is about 12,000 individuals (Gallo, 1994).

In the 1980s, Guadalupe fur seals started to regularly visit the Channel Islands of California (Stewart et al., 1987), but a permanent colony has not yet been established on these islands. In 1997, 300 individuals were encountered on the island of San Benito del Este (Maravilla & Lowry, 1999), and by 2000 there were approximately 500 individuals (Aurioles-Gamboa & Hernández, 2001).

Guadalupe fur seals and California sea lions (adult females mainly) remain around their breeding sites for longer than 8 mo due to their lengthy lactation periods (Peterson & Bartholomew, 1967; Newsome et al., 2006), which forces them to maintain their feeding areas close to the area of reproduction (Costa, 1993; Gallo, 1994; Kuhn et al., 2006).

The Guadalupe fur seal feeds on average at depths of 30 m (Gallo, 1994), while females of the California sea lion dive as deep as 274 m off California and 345 m deep in the Gulf of California (Costa et al., 2001; Kuhn et al., 2003).

The diving capacity of marine mammals in general is determined by their oxygen and fuel stores and the rate of consumption due to their metabolism and can be aerobic or anaerobic (Kooyman, 1989). There is evidence indicating that the diving capacity of fur seals measured in their aerobic dive limit (ADL) is relatively smaller (1.6 to 1.7 min) compared to sea lions (2.3 to 3.8 min) (Costa et al., 2004), which imposes a constraint for the depth these pinnipeds are capable of reaching during foraging dives. There is no ADL available for the Guadalupe fur seal, but considering that other fur seal species of similar size have values around 1.7 min, whereas California sea lions vary their ADL from 2.7 to 3.8 min, it is reasonable to assume that the California sea lion is better suited to perform deeper dives than the Guadalupe fur seal. Considering this diving capacity difference among these two species, it is likely to suppose a higher susceptibility of the Guadalupe fur seal to variations in prey abundance than the California sea lion. If prey move to deeper waters, out of their physiological ability to hunt, the population will suffer.

This has been confirmed during El Niño events for the Galapagos fur seals, when the thermocline and the vertical distribution of potential prey are found deeper, and it has had a greater impact on the fur seals than on Galapagos sea lions (Trillmich & Ono, 1991).

Since the California sea lion and the Guadalupe fur seal maintain populations on the same islands throughout the year, one might expect a higher degree of competition for food between these two species. In this study, we examined similarity and flexibility of the diets for both otariids, with the aim of estimating the degree of feeding overlap and prey diversity during four seasonal samplings. By analyzing the diet of the two species, we attempt to explore their feeding plasticity to cope with changes in prey availability caused by environmental disturbances and to provide information to help to understand the differences in their recent historic population fates (Gerber & Hillborn, 2001; Costa et al., 2004).

Materials and Methods

The study was carried out on San Benito Islands (28° 18' N, 115° 32' W), Mexico, where four periods of sampling the feces for both species were undertaken during the winter and spring of 2001 and 2002 (Table 1). Collections were made in areas where the terrain was occupied almost exclusively by one or the other species. It was possible to clearly distinguish the scat of each species based on evident differences in size, color, and consistency. Sea lion scats were larger and soft with a light brown color, while fur seal scats were dark colored, fibrous, and very dry. Only fresh feces were collected during the initial visit, and all of the uncollected scats in the sampling area were destroyed. During subsequent visits, both fresh and partially dried scats were collected.

Table 1. Total number of scats collected during each sampling season

		Number of scats	
Sampling season	Date	California sea lion	Guadalupe fur seal
Winter 2001	7-21 February	80	51
Summer 2001	20-24 July	71	57
Winter 2002	19-26 January	69	54
Summer 2002	14-22 September	69	56

The scats were placed in water with detergent for 12 to 36 h and then passed through a set of 2.0, 1.19, and 0.71 mm^2 mesh-size sieves to separate the otoliths and cephalopod beaks. The otoliths were preserved dry, and the cephalopod beaks were preserved in ethyl alcohol. The prey was identified based on the otoliths collection at the Pinniped Ecology Laboratory of the Centro Interdisciplinario de Ciencias Marinas (CICIMAR) and by photographs and figures obtained from literature (Fitch, 1966, 1967, 1968, 1970; Iverson & Pinkas, 1971; Wolff, 1984).

Due to the total or partial digestion of the prey remains (Lance et al., 2001), the presence of certain prey might have been underestimated, although a study of the digestion of the California sea lion (*Z. californianus*) and the South American fur seal (*A. australis*) by Dellinger & Trillmich (1988) found that such bias decreased with large sample sizes. In order to evaluate the degree of representation the sample size needed to achieve stability in prey diversity, diversity curves (Colwell, 1997) were constructed for each sampling season. The diversity curves and the diversity of the feeding spectrum of both species were determined using the Shannon Index, with the following formula:

$$H' = -\sum_{i=1}^{S} pi \, ln \, pi$$

where pi is the proportion of prey i in the grouped excreta and s is the number of species.

The importance of the prey within the trophic spectrum of each species was determined using the Importance Index (IIMPi) modified by García-Rodriguez & Aurioles-Gamboa (2004):

$$IIMPi = \frac{1}{U}\sum_{j=1}^{u}\frac{xij}{Xj}$$

where xij is the number of observations of species i in scat j, Xj is the total number of identifiable structures in scat j, u is the number of scats in which the taxon i was found, and U is the number of scats for which the appearances were counted.

In this study, we considered the principal prey those that follow the criterion of representing 10% or more of IIMPi (Lowry et al., 1991; García-Rodríguez, 1995; García-Rodriguez & Aurioles-Gamboa, 2004).

The values of the IIMPi were used to classify the different samples based on the agglomerative method and their information content using the *ANACOM 3.0* program (De la Cruz, 1994).

As a measurement of the diet plasticity, we estimated the breadth of the diet of each predator using Levins Index (Krebs, 1999),

$$B = \frac{1}{\sum p_j^2}$$

where pj is the proportion of resource j in the diet of the predator. Values lower than this index (B < 3) are considered to reflect a specialized diet while high values (B > 3) indicate a generalist diet (Gibson & Ezzi, 1987).

To answer the question of the degree of overlap between the trophic spectrum of both otariid species, we used the simplified Morisita-Horn Index (Krebs, 1999),

$$C_H = \frac{2\sum_i^n p_{ij}p_{ik}}{\sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2}$$

where pij is the proportion of resource i utilized by species j, pik is the proportion of resource i utilized by species k, and n is the total number of resources. The value of the index varies between 0 and 1; values less than 0.29 indicate a low degree of superposition, 0.30 to 0.65 a moderate superposition, and high superposition is associated with index values greater than 0.65 (Langton, 1982).

Another feature of the feeding habits of interest was the trophic position, determined with the algorithm proposed by Christensen & Pauly (1992),

$$TL = 1 + \sum_{j=1}^{n} D_{cij} * TL_j$$

where D_{cij} is the proportion of prey j in the diet of species i, TL_j is the trophic level of prey j, and n is the number of groups in the system. The trophic level of the prey was obtained from the Internet database FISHBASE (www.fishbase.org) and the literature (Mearns et al., 1981; Rau et al., 1983). When a trophic level for a particular prey could not be found, a trophic level corresponding to another species having similar feeding habits and from the same area was assigned. This procedure was applied in only 8% of the cases, however. In order to define the type of feeding strategy for sea lions and fur seals, all the prey species were characterized to be in one of the following habitats: pelagic (epipelagic and mesopelagic) for those prey living in the water column from surface to 1,000 m, and demersal and benthic for prey dwelling at or near the bottom.

Results

A total of 507 scat samples were collected at San Benito Islands based on two winters and two summers (Table 1). Scat sample sizes were slightly larger for California sea lions (Figure 1), but the diversity prey curves related to sample size reached the asymptote at around 10 samples in the case of the Guadalupe fur seal (except for the summer 2002) and around 30 for the California sea lion (except for summer 2001).

Feeding Habits of the California Sea Lion

Of the total of 289 scats collected, 71% contained remains of prey. Of these remains, 65% of occurrences were of fish, 25% of cephalopods, and 7% of crustacean remains. A total of 1,253 otoliths and 242 cephalopod beaks were recovered.

In 2001, the diet of the sea lions consisted mainly of fish, and the most consumed prey were *Merluccius angustimanus* during winter and *Loligo opalescens* during summer. In 2002, the fish *Argentina sialis* was the most hunted prey and, although it did not occur in all of the samples, its presence was common over the entire length of the study (Table 2).

The sea lion showed a trophic spectrum of great diversity, which places the species as a generalist with Levins Index levels close to or greater than 3 (Table 3). This feature was also reflected in the diversity curves for each seasonal sampling (Figure 1).

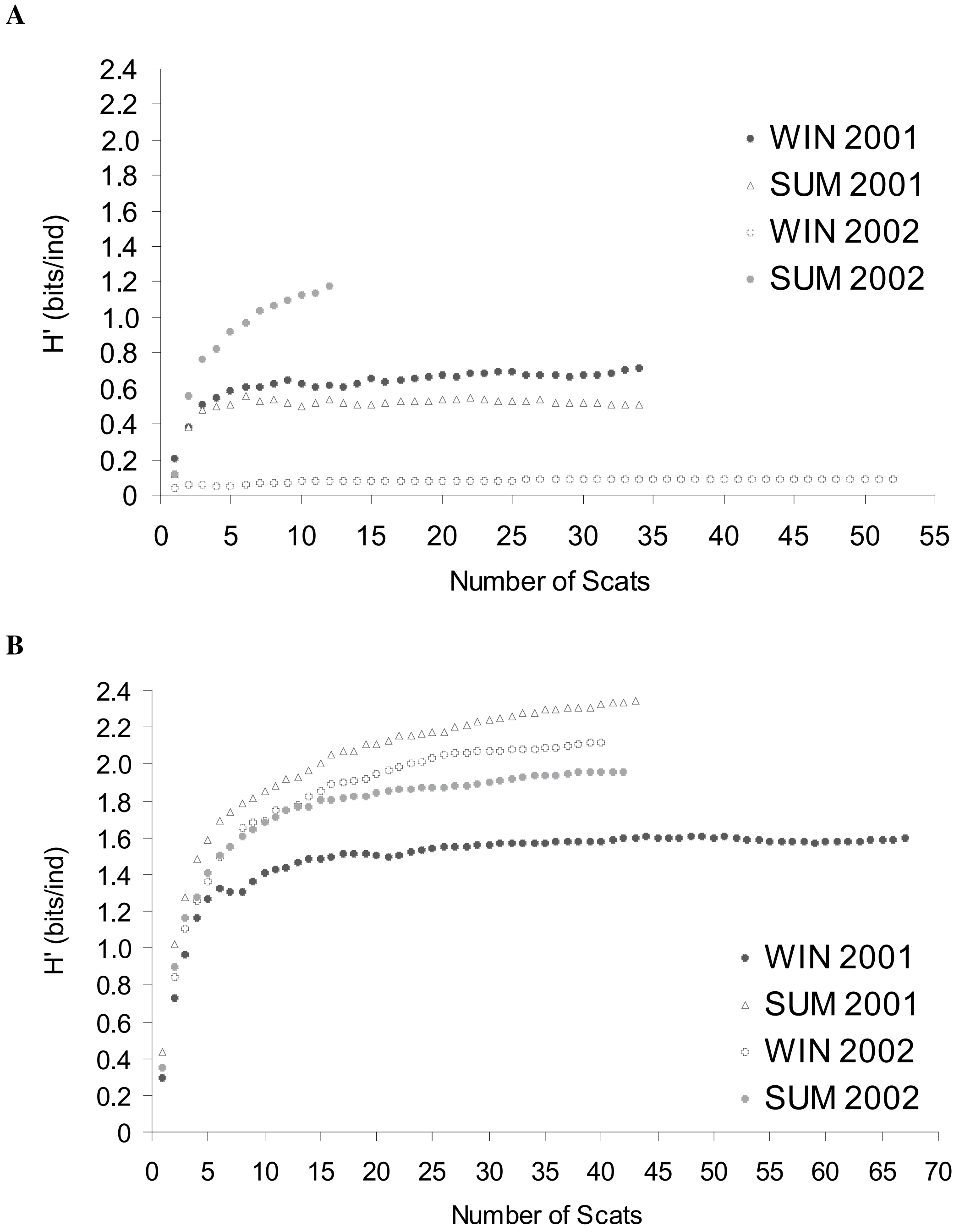

Figure 1. Diversity curves for scat of the California sea lion (A) and the Guadalupe fur seal (B) in each sampling season; WIN 2001, winter 2001; SUM 2001, summer 2001; WIN 2002, winter 2002; and SUM 2002, summer 2002.

Feeding Habits of the Guadalupe Fur Seal

Only 66% of the 218 scats collected had remains of prey, of which cephalopods appeared in 62%, followed by fish with 12% and crustaceans (likely *Pleuroncodes planipes*) with 2%. Overall, 1,803 cephalopod beaks and 83 otoliths were recovered. As opposed to the sea lion samples where sea grass was not found, fragments of sea grass

Table 2. Temporal variation of the importance of prey in California sea lions and Guadalupe fur seals at San Benito Islands, Mexico, 2001-2002

Prey species	Prey habitat	California sea lion					Guadalupe fur seal				
		Winter 2001	Summer 2001	Winter 2002	Summer 2002	Average	Winter 2001	Summer 2001	Winter 2002	Summer 2002	Average
Cephalopods											
Loligo opalescens	Pelagic	7.47	24.04	21.20	5.70	14.60	66.58	65.52	95.89	33.33	65.33
Gonatus sp.	Pelagic	--	2.38	2.29	2.38	1.76	7.18	12.79	--	8.33	7.08
Dosidicus gigas	Pelagic	--	3.88	--	3.17	1.76	0.98	--	0.55	32.87	8.60
Stenoteuthis oualaniensis	Pelagic	1.49	--	--	--	0.37	--	--	0.15	4.17	1.08
Ommastrephidae	Pelagic	--	3.10	--	2.38	1.37	--	--	0.21	16.67	4.22
Onychoteuthis banksii	Pelagic	--	--	1.25	--	0.31	0.20	--	0.26	--	0.12
Octopus sp1	Benthic	3.73	4.03	3.76	3.59	3.78	1.11	6.37	--	--	1.87
Octopus sp2	Benthic	--	--	--	0.30	0.07	--	--	1.92	--	0.48
Fishes											
Opisthonema sp.	Pelagic	0.17	0.78	--	--	0.24	--	--	--	--	--
Sardinops caeruleus	Pelagic	6.06	3.88	4.25	--	3.55	2.94	--	--	--	0.74
Engraulis mordax	Pelagic	3.00	--	--	--	0.75	7.11	--	--	--	1.78
Argentina sialis	Demersal	13.45	16.01	28.26	26.42	21.04	2.94	--	--	--	0.74
Synodus sp.	Demersal	0.25	4.19	2.82	2.38	2.41	4.22	1.18	--	--	1.35
Physiculus nematopus	Demersal	0.75	2.96	--	1.19	1.22	--	--	--	--	--
Merluccius angustimanus	Demersal	33.28	4.00	4.58	6.14	12.00	3.43	11.19	--	4.63	4.81
Lepophidium sp.	Benthic	0.25	2.99	0.14	--	0.85	0.26	1.47	--	--	0.43
Ophidion scrippsae	Benthic	--	1.09	--	--	0.27	--	--	--	--	--
Porichthys notatus	Benthic	0.37	0.78	0.07	2.38	0.90	0.13	--	--	--	0.03
Leuresthes tenuis	Demersal	--	2.30	--	0.22	0.63	--	--	--	--	--
Sebastes sp1	Demersal	13.79	5.51	12.34	17.86	12.38	--	--	--	--	--
Sebastes sp2	Demersal	6.67	3.10	0.50	11.29	5.39	--	--	--	--	--
SCORP2	Demersal	--	0.16	--	--	0.04	0.13	--	--	--	0.03
Icelinus sp.	Demersal	--	0.78	--	--	0.19	0.98	--	--	--	0.25
Paralabrax clathratus	Demersal	--	4.65	--	--	1.16	--	--	--	--	--
Pronotogrammus multifasciatus	Demersal	3.81	--	--	5.17	2.25	--	--	--	--	--
Trachurus symmetricus	Pelagic	2.65	3.96	14.69	--	5.32	1.23	--	0.05	--	0.32
Lycodes pacificus	Demersal	2.13	--	1.25	2.08	1.37	--	--	--	--	--
Scomber japonicus	Pelagic	--	1.16	0.73	4.76	1.66	--	--	--	--	--
Citharichthys stigmaeus	Benthic	--	3.16	1.74	0.30	1.30	0.59	1.47	0.96	--	0.76
Lyopsetta exilis	Benthic	0.12	0.42	--	0.22	0.19	--	--	--	--	--
Microstomus pacificus	Benthic	0.55	0.72	0.14	0.28	0.42	--	--	--	--	--
sp32		--	--	--	1.79	0.45	--	--	--	--	--

SCORP2 refers to an unidentified scorpaenid fish, and sp32 refers to an unidentified species coded with number 32.

Table 3. Values of the Shannon, Levins, and the Morisita-Horn Indexes

Season	Shannon Index		Levins Index		Morisita-Horn Index
	California sea lion	Guadalupe fur seal	California sea lion	Guadalupe fur seal	
Winter 2001	1.60	0.72	2.75	1.39	0.06
Summer 2001	2.34	0.51	5.29	1.27	0.73
Winter 2002	2.12	0.09	5.99	1.02	0.27
Summer 2002	1.96	1.18	5.03	2.46	0.09

(*Phyllospadix* sp.) were found in 40% of the fur seal scats.

The diet of the fur seal was composed principally of cephalopods and was dominated by *L. opalescens*, except in summer, when other squid, such as *Gonatus* sp. in 2001 and *Dosidicus gigas* in 2002, appeared in some of the prey remains (Table 2). The fur seal diet showed low diversity and, by consequence, the Levins Index was always less than 3, indicating a specialized diet (Table 3).

Classification and Trophic Overlap

Cluster analysis of the diet by sample and by species revealed two groups separating the diets of the Guadalupe fur seal and the California sea lion (Figure 2). The difference in the diet of both species were defined by the squid *L. opalescens* and the fish *A. sialis* because when the same analysis is performed without these two prey, the cluster pattern vanishes and is replaced by another that is incoherent.

In the cluster formed by the sea lion samples, two subgroups were generated. The first was formed by samples from the winter 2001 and summer 2002 seasons when consumption of the fishes *Sebastes* sp. and *M. angustimanus* was greater. In the second subgroup, formed by samples from summer 2001 and winter 2002, the squid *L. opalescens* was also abundant in the diet (Table 2).

Within the fur seal grouping, both winter seasons (INV01, INV02) and the summer of 2001 formed a subgroup due to the dominance of the squid *L. opalescens.* The summer of 2002 remained separate because the prevalence of *L. opalescens* was shared with other squid (*D. gigas* and other omastrephidae).

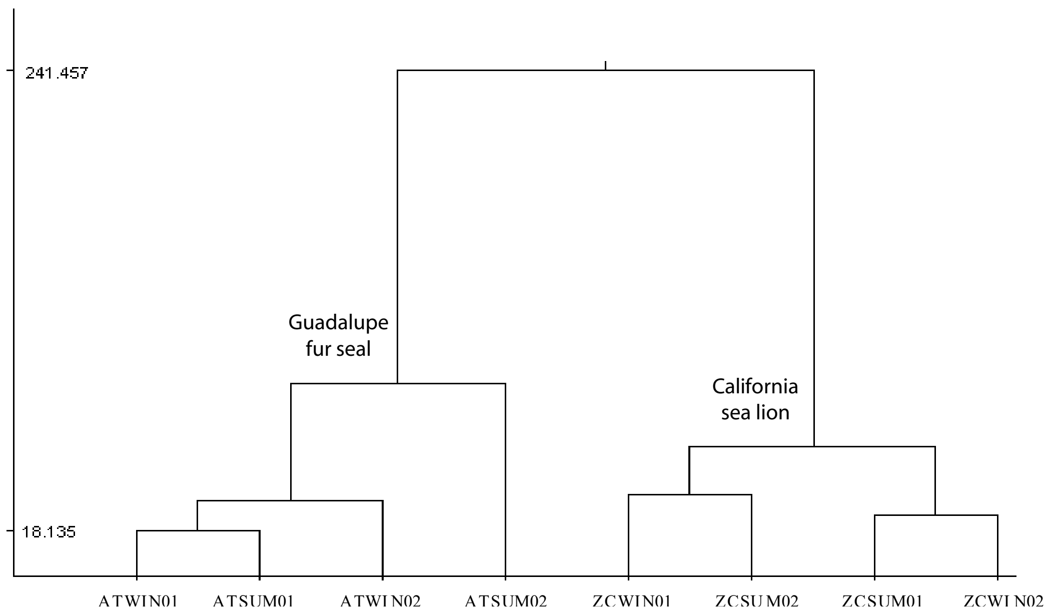

Figure 2. Cluster diagram of the trophic spectrum of the fur seal and the sea lion; ATINV01 fur seal – winter 2001; ATVER01 fur seal – summer 2001; ATINV02 fur seal – winter 2002; ATVER02 fur seal – summer 2002; ZCINV01 sea lion – winter 2001; ZCVER01 sea lion – summer 2001; ZCINV02 sea lion – winter 2002; ZCVER02 sea lion – summer 2002.

Trophic overlap was significantly higher during the summer of 2002 when the Morisita-Horn Index was greater than 0.66 (Table 3). This overlap was determined by a greater consumption of squid by the two species.

Both otariids presented trophic levels corresponding to secondary-tertiary carnivores (Mearns et al., 1981), although the fur seal had a slightly lower trophic level (4.22) compared to the California sea lion (4.42).

Prey Habitat and Feeding Strategy

By considering the type of habitat of the prey (e.g., pelagic, demersal-benthic), it was possible to define the general feeding strategy for sea lions and fur seals (Table 2). Because demersal and benthic prey force the predator to dive near the bottom, we combined the number of demersal and benthic fishes to define a broader category in which the animal separates clearly from a pelagic feeder that concentrates its foraging in the column of water. California sea lions and Guadalupe fur seals were compared on their general feeding strategy: the sea lion shows a tendency to feed mostly near the bottom (60%), whereas the fur seal shows a more biased pelagic feeding strategy (90%).

Discussion

In general, the otariid diet includes a large variety of species, which has led them to be considered opportunistic predators or plastic specialists (Antonelis & Fiscus, 1980; Lowry et al., 1991); however, only two to five prey species account for the greatest portion of energy in their diet in a given season or geographic area (Reynolds & Rommel, 1999). This characteristic was also observed in the San Benito Islands, where the California sea lions feed on a large variety of prey but particularly the Pacific argentine (*A. sialis*), the Baja California hake (*M. angustimanus*), the Pacific jack mackerel (*T. symmetricus*), and the rockfish (*Sebastes* spp.), as well as the market squid (*L. opalescens*) (Table 2). These prey have also been reported in the trophic spectrum of the sea lion in other parts of its geographic distribution, although with a different order of importance (Antonelis et al., 1984; De Anda, 1985; Salazar, 1989; Lowry et al., 1991; García-Rodríguez, 1995; García-Rodríguez & Aurioles-Gamboa, 2004).

In the case of the market squid, it is one of the most important prey of sea lions in southern California, occurring in 35 to 44% of the scat samples from San Nicolas Island, San Clemente Island, and Santa Barbara Island (Lowry & Carretta, 1999).

For its part, the Guadalupe fur seal on the San Benito Islands specializes on cephalopods and market squid in particular (Table 2). Squid prey was previously identified by Gallo (1994) at Guadalupe Island and by Hanni et al. (1997) on the coast of California, USA.

A high proportion of *Phyllospadix* spp. (40%) found in the scat of fur seals is more difficult to explain since they may be ingested incidentally as the food of the market squid, a demersal species living on the continental shelf (Jackson, 1998). Because it appears so frequently, it may be considered that its consumption is not casual but serves the function of purging the animal's digestive system or as an aid in the digestion of its prey as occurs in some terrestrial mammals.

In general, the most significant differences in the diet of the sea lion and the fur seal were (1) the presence of a large variety of fishes in the trophic spectrum of the former and of almost exclusively cephalopods in the diet of the latter and, as a consequence, (2) a more generalist regime with slightly higher trophic level for the sea lion and a specialized diet and lower trophic level for the Guadalupe fur seal, and (3) a clear trophic separation between the diets of both otariids.

California sea lions and Guadalupe fur seals only overlapped significantly in their diets during summer 2001 (Table 3), when sea lions had 24% consumption of *L. opalescens* and fur seals had 65.5% (Table 2). It is interesting to note that the importance of *Loligo* increased in the Guadalupe fur seal diet for the following season (winter 2002) to almost 96%, whereas for the sea lion, it remained in similar proportion (21%).

In California, *Z. californianus* ate market squid year-round but predominantly during autumn and winter, with consumption highly variable over seasonal periods, fluctuating from 0 to 90% of their diet (Lowry & Carretta, 1999). The differential consumption of market squid between both otariids from winter to summer suggests that this squid species is a preferential prey for *A. townsendi* and an opportunistic prey for the sea lion, which may take advantage of higher abundances of the cephalopod available in its foraging area.

There are no available data of squid abundance in the area of study, but in southern California (500 km north of the San Benito Islands), there is an important fishery of market squid that shows a regular increase of landings from October to January. A historical analysis of the fishery in southern California (1981 to 2003) revealed a marked increase from 1999 to 2001 (Zeidberg et al., 2006), a period that coincides with this study.

The differences in the composition of the diet between these otariids may indicate that each species hunts in areas having different types of food availability. Utilization of different food resources may occur when the distributions of two or more otariid species overlap (Dellinger & Trillmich, 1988; Page et al., 2005).

Fiscus (1982) mentioned that fish should constitute the greatest portion of the diet of marine mammals over the continental shelf, while squid would be the most important prey in oceanic waters. The Guadalupe fur seals do appear to feed more in oceanic waters as indicated by their feeding excursions. These may take them as far away from their areas of reproduction or hauling areas as 444 ± 151 km while spending an average time at sea of 14 ± 8.2 days (Gallo, 1994). The sea lion, in contrast, travels 10 to 100 km, with an average of 50 km (Kuhn et al., 2003). These differences in feeding areas may determine the low overlap in the diet of the two otariids, except maybe when a particular prey is very abundant in the region where the feeding areas of the two predators overlap (more likely the region around the islands). It is known that large aggregations of *L. opalescens* occur to lay eggs and mate on the bottom between 20 to 60 m of depth from April to November (Forsythe et al., 2004; Macewicz et al., 2004). These shallow breeding areas of the market squid places the squid in locations available for both species of otariids.

The reduced feeding spectrum of the fur seal is reflected in a lower diversity compared to the sea lion (Table 3) and may be due to a preference for squid over other pelagic prey. Sinclair et al. (1994) found that the northern fur seal (*Callorhinus ursinus*), despite a large variety of species available in dives, concentrated feeding on a small number of prey. A study in northern fur seals captured in the central Pacific indicated that 85 stomach contents were composed of only squid species and dominated by the mesopelagic firefly squid (*Watasenia scintillans*), which occurred 94% of the time (Mori et al., 2001).

The limited diving depth of the Guadalupe fur seal may influence the lower diversity of prey in its diet. For example, the average depth of the dives of a female Guadalupe fur seal is 16.9 ± 10.3 m, with a range of 3 to 82 m, but very few dives deeper than 30 m (Gallo, 1994). *L. opalescens*, its main prey off the San Benito Islands, makes circadian migrations to the surface only at night (Zeidberg, 2003), when most of the Guadalupe fur seal dives occur (Gallo, 1994).

California sea lion females, conversely, can dive as deep as 350 m in the Gulf of California (Kuhn et al., 2003). This is confirmed by the variety of prey in their scats: *A. sialis* lives between 11 to 274 m, *M. angustimanus* lives between 80 and 500 m, *T. symmetricus* lives down to 150 m, and the rockfishes can be found down to 425 m (Fischer et al., 1995).

No defined pattern was found with respect to the winter-summer variation of prey. The diet of many pinnipeds, especially otariids that live in temperate and tropical climates, does not vary markedly between seasons, although it does vary from year to year (Riedman, 1990).

The California sea lion and Guadalupe fur seal presented near trophic levels (4.42 and 4.22, respectively). The lower trophic position of the fur seal is probably due to a higher consumption of squid, particularly *L. opalescens*, which feeds primarily on euphausiids (Fischer et al., 1995), while the prey of the sea lion present a higher trophic level because they feed mostly on fish and in less proportion on cephalopods and crustaceans (Pauly et al., 1998).

The evidence at the time the Guadalupe fur seal began the recolonization of San Benito Islands demonstrates that the California sea lion is not a trophic competitor of the Guadalupe fur seal in the San Benito Islands; however, both otariids may take advantage of the temporary abundance of some prey, such as squid, causing a slight overlap in their diets. Similar results were obtained when comparing the diet of the sea lion (*Z. wollebaeki*) and the Galapagos fur seal (*A. galapagoensis*), where there was no significant degree of feeding overlap (Dellinger & Trillmich, 1999). In that study, myctophidae and bathylagidae fish were a regular prey of the fur seals, whereas for the sea lion it was the sardine (*Sardinops sagax*).

The trophic flexibility of the sea lion might have been one of the reasons for its rapid recuperation compared to the Guadalupe fur seal. This same trophic flexibility may explain why during El Niño events, when the California sea lion is sympatric with the Galapagos fur seal, the sea lion suffers less drastic losses in population (30%) than does the fur seal (between one half to 70%) (Trillmich & Ono, 1991).

During El Niño, the trade winds weaken, and warm water in the Pacific Ocean moves east, producing a depression of the thermocline in the eastern Pacific. As a consequence, coastal upwelling along South and North America are unable to bring up to euphotic zone the cold, nutrient-rich water from beneath it, reducing the supply of chemical nutrients for the phytoplankton. The drastic decline in phytoplankton production, then, has adverse effects along the higher levels of the marine food chain (Arntz et al., 1991). Common preys of otariids, such as fish and squids, respond to warm conditions in three ways: (1) concentrating in the remnants of the upwelling where the deteriorating conditions eventually may produce mass mortalities of fish and otariids; (2) migration of the preys to areas far away from the sea lions' and fur seals' foraging distribution; and (3) sinking of fish or squid to depths where temperature is more suitable, although with poorer nutritional conditions, reducing its availability for otariid predation and affecting the body growth of the preys (Arntz et al., 1991; Jackson & Domeier, 2003).

Since longer dive capacity of marine mammals is mostly determined by their oxygen concentrations, which relates to body size (Costa et al., 2004), California sea lions are more suited than Guadalupe fur seals to reach deeper waters where food may be found during warming events. In Figure 3, a hypothetical model of the spatial differences of California sea lions and Guadalupe fur seals from San Benito Islands is presented. The Guadalupe fur seal has a wide horizontal and shallow foraging area around the islands, whereas the California sea lion shows a horizontally restricted but deeper foraging area.

Very specialized benthic feeding may also lead to limited habitat exploitation such as that of the Australian and New Zealand sea lions (Costa & Gales, 2003; Costa et al., 2004). In the case of the California sea lions at San Benito Islands, around 35% of their prey was pelagic and 65% benthic, suggesting a more balanced use of the pelagic and benthic habitats and resulting in a more diverse diet and foraging plasticity to better survive oceanographic perturbations such as El Niño.

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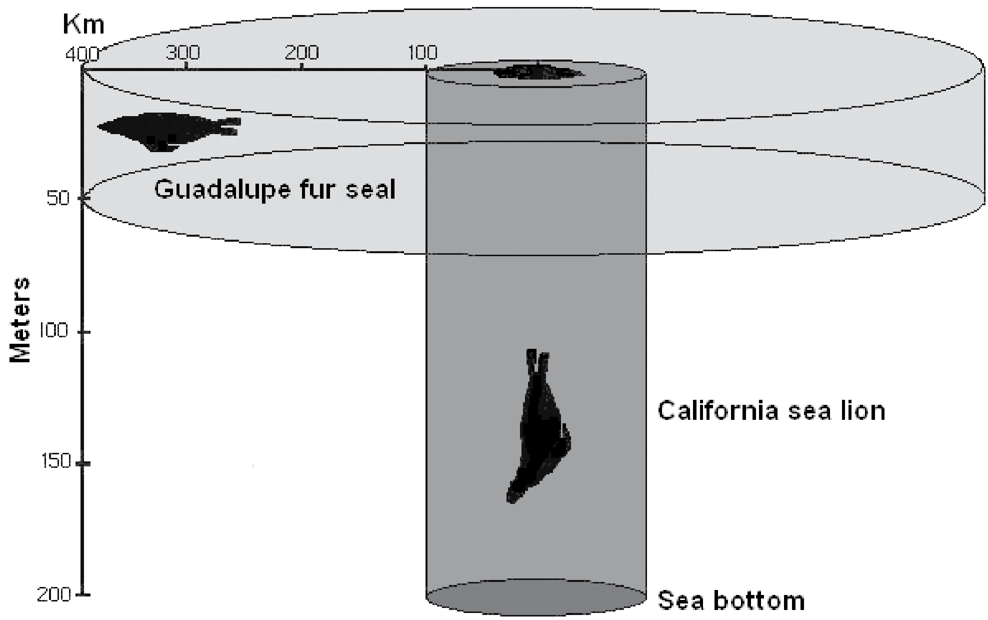

Figure 3. Spatial difference in foraging areas of Guadalupe fur seals and California sea lions from San Benito Islands based on feeding habits and information of diving behavior; California sea lions exploit deeper but narrower columns of water reaching the bottom over the continental shelf, whereas Guadalupe fur seals disperse over an extended horizontal layer, usually no deeper than 50 m.

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