

Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*

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ABSTRACT: Three fundamental foraging patterns in air-breathing marine vertebrates have been described: epipelagic, mesopelagic and benthic. Many sea lion species with access to extensive continental shelves have been described as benthic foragers. Coincidentally these species are considered threatened. The Galapagos sea lion *Zalophus wollebaeki*, a top predator in the Galapagos Islands, is also considered threatened in this ecosystem. Sea lions at the central part of the archipelago have access to a vast continental shelf. For this reason we hypothesized that sea lions within this region would dive benthically. In addition, effective protection and conservation of this species requires knowledge of their foraging patterns and habitat utilization. We investigated the diving behaviour and habitat utilization of female *Z. wollebaeki* of a centrally located colony situated inside the highest density area of the population using time-depth recorders and satellite telemetry. Three distinct foraging patterns were found and described (shallow, deep and bottom divers), and individuals utilizing each pattern foraged in different locations. Epipelagic, mesopelagic and benthic dives were exhibited in the sea lions' diving behaviour, but these dive types were not exclusively associated with a foraging pattern. Between foraging trips females hauled out more frequently on other islands than they did on their breeding colony. The finding of 3 distinct foraging patterns that differ spatially has direct implications for management, particularly with regard to fisheries interactions. Marine protected areas can be implemented in the regions described as *Z. wollebaeki* foraging areas. *Z. wollebaeki*'s wide foraging range coupled with their use of multiple haul-out sites should be considered in future studies when determining foraging trip lengths and habitat utilization since presence/absence from the colony does not reflect foraging trip length.

KEY WORDS: Diving behaviour · Foraging behaviour · Galapagos Islands · Habitat utilization · Individual specialization · Galapagos sea lion · *Zalophus wollebaeki*

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INTRODUCTION

Foraging patterns of air-breathing marine vertebrates may be classified by the habitats in which individual species forage. Epipelagic and mesopelagic foragers utilize the water column between 0–200 and 200–1000 m respectively; benthic foragers use the sea floor (Tremblay & Cherel 2000, Costa & Gales 2003). Epipelagic foragers include Antarctic fur seals *Arcto-*

cephallus gazella (Boyd & Croxall 1992), California sea lions *Zalophus californianus* (Feldkamp et al. 1989) and leatherback turtles *Dermochelys coriacea* (Eckert 2006). Among mesopelagic foragers are king penguins *Aptenodytes patagonicus* and northern elephant seals *Mirounga angustirostris* (LeBoeuf et al. 1986, Kooyman et al. 1992). Benthic foragers include pinnipeds such as Australian (*Neophoca cinerea*), New Zealand (*Phocarctos hookeri*) and Southern (*Otaria flavescens*) sea

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lions, sea turtles like loggerhead *Caretta caretta* and olive ridley *Lepidochelys olivacea* and seabirds such as cormorants (Phalacrocoracidae) (Cooper 1986, Thompson et al. 1998, Costa & Gales 2000, 2003, Hopkins-Murphy et al. 2003, McMahon et al. 2007). Diving patterns have been described for all extant sea lion species (Kooyman & Trillmich 1986, Feldkamp et al. 1989, Merrick & Loughlin 1997, Thompson et al. 1998, Costa & Gales 2000, 2003). However, diving behaviour of the Galapagos sea lion *Zalophus wollebaeki* has been investigated in only 4 individuals (Kooyman & Trillmich 1986).

Zalophus wollebaeki is endemic to the Galapagos Islands. The population is widely distributed among this archipelago, with the highest density of individuals at the central and southern islands (Salazar 2005). Current population estimates lie between 16 000 and 18 000 individuals (Salazar 2005) although an estimate of 20 000 to 50 000 individuals in 1963 suggests a dramatic decline in the population over the last 20 yr. (Heath 2002). The population fluctuates in size and is negatively affected by El Niño events (Trillmich & Limberger 1985).

The breeding season is protracted in *Zalophus wollebaeki* compared to other sea lion species. Births occur from June to March, but the peak pupping period varies among rookeries and years. Pups are weaned at a time when they are independently foraging—usually around 2 to 3 yr old (Trillmich 1986, Heath 2002).

Prey species found in the diet of *Zalophus wollebaeki* from multiple colonies include epipelagic fish (Clupeidae) of surface and coastal upwelling waters, mesopelagic fish (Myctophidae) found in deep waters of the open ocean, and demersal, benthopelagic or pelagic fish (Chlorophthalmidae, Serranidae and Mugilidae) found over muddy and sandy bottoms of the continental shelf or in shallow and deep waters between rocks (Salazar 2005, Froese & Pauly 2006).

Further, *Zalophus wollebaeki* provide an important ecosystem function as transporters of marine nutrients to terrestrial habitats of the Galapagos Islands (Fariña et al. 2003). Despite their vulnerability (Seal Specialist Group 1996) and importance, very little is known about the marine habitat utilization of these sea lions. The diving behaviour of this species was studied only once previously (Kooyman & Trillmich 1986) and at a different site, during a different time and with about half the number of individuals as the present study.

We investigated the diving behaviour and spatial habitat utilization of lactating female *Zalophus wollebaeki* at Caamaño Islet, south of Santa Cruz Island in the Galapagos Islands. The islet is characterized by an extensive continental shelf and access to a broad central underwater plateau. Pinniped species inhabiting

similar bathymetric conditions (e.g. Australian, New Zealand and Southern sea lions) are described as benthic foragers (Thompson et al. 1998, Costa & Gales 2000, 2003). Although some epipelagic and mesopelagic fish have been found in the *Z. wollebaeki* diet, we hypothesized that sea lions in this colony would dive predominantly benthically based on Caamaño Islet bathymetric conditions. Our objectives were to detail the at-sea habitat utilization and foraging behaviour of *Z. wollebaeki* centrally located within their range and to provide valuable data for conservation and protection measures.

MATERIALS AND METHODS

Field site and general procedures. During March 2005 we captured 9 lactating female Galapagos sea lions *Zalophus wollebaeki*, which were suckling small pups 4 to 5 mo after peak pupping season at Caamaño Islet (0.759°S, 90.278°W) in the Galapagos Islands. Caamaño Islet holds a population of approximately 970 individuals, and, together with Santa Cruz Island, represents the second largest colony: 14% of the total population (Salazar 2005, Wolf & Trillmich 2007). Sea lions were captured with hoop nets and anesthetized with isoflurane gas (0.5 to 2.5%) with oxygen via a portable field vaporizer, administered through a cone shaped mask and then with an endotracheal tube (Gales & Matlin 1997). Individuals were instrumented with SPOT4 satellite platform terminal transmitters (PTT) (Wildlife Computers) for large-scale tracking, time-depth recorders (TDR) (2 Mk6, 2 Mk8 and 5 Mk9 models, Wildlife Computers) to obtain diving behaviour data, and radio transmitters (VHF, Sirtrack) to locate the sea lions for instrument recovery when on land. We mounted instruments on mesh netting and glued them to the dorsal pelage of the lower back and between the shoulders of the sea lions using 5 min quick set Loctite epoxy. The total weight of the attached instruments was 230 g (approximately 0.23% of the sea lions' mass). We weighed sea lions in a sling using a tripod and a 250 kg (± 0.1 kg precision) capacity digital scale. We recaptured all the sea lions after 7 to 11 d. The equipment was removed by physically restraining individuals without anesthesia. Epoxy mounts fall off within a few months during the sea lions' annual moult.

Tracking data analysis. To determine the sea lions' habitat utilization and foraging range we used a program from the IKNOS toolbox (custom software developed by Y. Tremblay) to filter satellite location data obtained through ARGOS. The algorithm uses several criteria to remove unlikely locations: (1) realistic travel speeds of a subject between 2 fixes (≥ 10 km h⁻¹),

(2) change in azimuth between successive fixes, (3) Argos location class and (4) time lapse between 2 consecutive fixes. We plotted filtered locations on a map in Matlab (The MathWorks).

Diving behaviour data analyses. We analysed dive data in Matlab using a custom-written dive analysis program (Y. Tremblay unpubl. data) which allows for a zero offset correction at the surface and the identification of dives based on a minimum depth and duration. All Mk9 and Mk8 recorders had a 0.5 m depth resolution and sampled every 2 s. One Mk6 had a 2 m resolution and the other a 4 m resolution; both sampled every 4 s. The minimum depth for a dive was set at 5, 6 or 8 m, depending on the sampling depth resolution of the TDR used (0.5, 2 or 4 m respectively). These depths accounted for instrument error while detecting the minimum depths possible by the dive analysis program. The minimum duration for a dive was set at 12 s to standardize the different sampling intervals of the tags (2 and 4 s) and by setting a minimum of 3 sampling points for dive identification by the dive analysis program.

Sea lions exhibit characteristic sequences of shallow dives when travelling to different locations; this behaviour has been described as 'porpoising' (Blake 1983, Williams 2001). The depth of these shallow dives peaks on a frequency distribution diagram of maximum dive depths (Tremblay & Cherel 2003), making porpoising depth evident. Following similar procedures as in Tremblay & Cherel (2003), porpoising dives in our data were restricted to the upper 10 to 12 m and were discarded from the analysis because their recognition was dependent on the type of recorder used. By eliminating these porpoising dives we also limited the effects of the dissimilarity in sampling resolution between the different recorders used. This was consistent with our goal of analysing potential foraging dives (i.e. feeding or search dives).

We conducted multivariate analyses in SYSTAT 10.2 to classify diving behaviour. Data were tested for normality by visual examination of probability plots and no transformations were needed. Results presented are means \pm 1 SD. Variables used are averages of the following for each dive: maximum depth (m), dive duration (s), bottom time (s), number of 'wiggles' at the bottom of a dive (number of ascent and descent movements at the bottom of the dive, which can imply foraging behaviour; Kuhn 2006), descent and ascent rate (m s^{-1}), dive rate (dives h^{-1}) and mass (kg).

Principal component analysis (PCA) was used to reduce the number of variables, followed by a hierarchical cluster analysis (HCA) to classify diving behaviour. We used Latent root criterion, a minimum Eigen value of 1.0 and a varimax rotation for the PCA. This analysis is suitable for this type of data because

the diving variables are strongly correlated (McGarigal et al. 2000). Standardized PCA factor scores were input as variables in the HCA, which we conducted using Euclidean distance and average linking method. Hierarchical clustering is ideal for small data sets as in this study (McGarigal et al. 2000).

To further characterize diving behaviour, we used the intra-depth zone (IDZ) (Tremblay & Cherel 2003). IDZ provides an index of the tendency to repeatedly dive to a given depth. An IDZ of 1 indicates a maximum dive depth is within a user-defined zone of the maximum depth of the previous dive. An IDZ of 0 means a dive does not fall within the maximum depth of the previous dive. Considering that 4 m was the lowest depth resolution of the instruments, we applied a user-defined zone of ± 10 m of the maximum depth of the previous dive (i.e. 5 m above or below the previous depth).

RESULTS

Habitat utilization and foraging trips

Satellite tracking duration varied from 8 to 11 d (mean = 8.55 ± 1.13 d), generating 28.8 ± 4.2 (range = 24–36) filtered satellite locations for each female, $71.5 \pm 17.9\%$ of which were at sea. TDR deployment duration also varied from 8 to 11 d, with data collected over a mean of 9.29 ± 0.89 d. Females performed 6.22 ± 2.16 unique trips to sea (4 to 10 trips, $N = 9$ females), spending $59 \pm 11\%$ of their time at sea. Average maximum distance recorded from the rookery per female was 41.76 ± 20.27 km (range: 14.3 to 76 km) (Table 1). Females hauled out at islands other than their breeding colony 79% of the time (3 to 9 haul-out periods recorded per sea lion, $N = 48$). They used 9 haul-out areas in addition to the Caamaño Islet rookery, which was used only 21% of the total haul-out time (Fig. 1). Foraging trips (time at sea between haul-out periods) lasted 23.87 ± 11.03 h on average ($N = 9$ females) (range = 7.5 h to 4.9 d, $N = 56$ trips). Haul-out times between foraging trips ranged between 1.12 and 35.5 h ($N = 47$ haul-out periods) with a mean of 11.9 ± 2.9 h ($N = 9$ females). Trip durations from the rookery, or the time away from their pups, ranged between 9.1 h and 9.13 d ($N = 19$ trips from rookery), with a mean duration of 4.18 ± 2.06 d (mean range = 1.3 to 8 d, $N = 9$ females). Although females tended to repeatedly haul out at the same sites (other than their breeding rookery), they also visited different haul-out sites during different foraging trips. Females showed preferences in their haul-out behaviour: some individuals hauled out at night, some during the day, and others during the day and at night.

Table 1. *Zalophus wollebaeki*. Female trip durations from time-depth recorder (TDR) records (mean \pm SD) between haul-out periods (mean trip duration) and between haul-outs at the rookery (mean trip duration from rookery). Caamaño Islet, March 2005

Female ID	# Foraging trips recorded	Mean trip duration (h)	# Foraging trips from rookery	Mean trip duration from rookery (h)	Mean haul-out duration (h)	# Haul-out periods recorded	Total # days recorded	Max. dist. traveled from rookery (km)	# Haul-out sites used (including rookery)
CAAF01	8	15.1 \pm 3.6	2	84.6 \pm 7.4	11.6 \pm 9.7	7	9.5	35.5	3
CAAF02	5	40.2 \pm 45.5	3	81.3 \pm 119.4	17.4 \pm 15.7	4	11.3	54.2	3
CAAF03	6	24.4 \pm 13.4	2	89.2 \pm 39.4	13.4 \pm 12.4	5	9.4	54.2	3
CAAF05	10	12 \pm 1.9	3	62.3 \pm 58.7	9.9 \pm 3.8	9	9.5	43	2
CAAF06	8	10.9 \pm 1.8	1	154.7	9.6 \pm 5.3	7	9.3	19.7	2
CAAF08	4	25.3 \pm 15.2	1	131.1	10 \pm 8.1	3	8.1	14.3	2
CAAF09	4	32.1 \pm 25.9	4	32.1 \pm 25.9	10.6 \pm 0.2	3	9.2	23.5	1
CAAF10	4	35.4 \pm 26.6	2	77.5 \pm 7.4	16 \pm 16.5	3	8.7	55.2	2
CAAF11	7	19.3 \pm 11.4	1	191.5	9.3 \pm 1.5	6	8.6	76.2	2

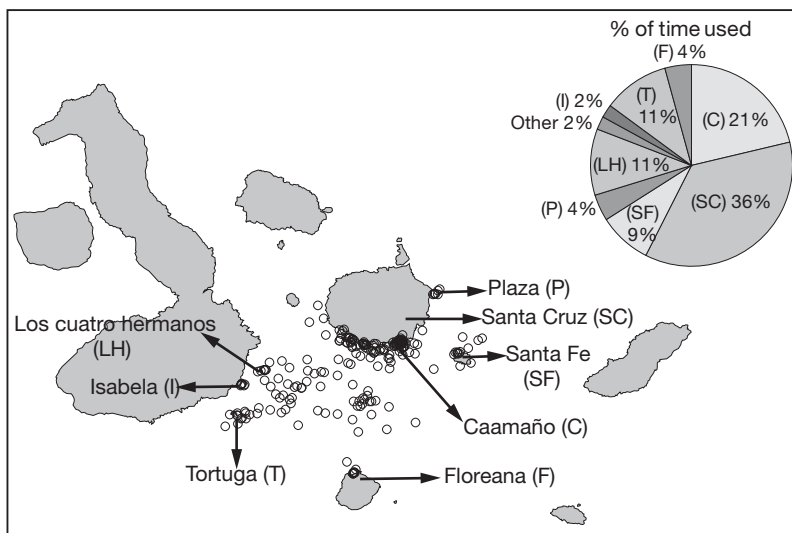


Fig. 1. *Zalophus wollebaeki*. Locations of alternate haul-out sites used by 9 females from Caamaño Islet, March 2005. Pie chart indicates percentage of the total number of haul-outs at these alternate sites

Diving behaviour and foraging strategies

Elimination of travelling dives resulted in the analysis of 997 ± 293 (range = 595 to 1636) dives per female, accounting for 62.46 to 100% of the total number of dives. One female (CAAF08) showed no travel dives and foraged coastally around the rookery.

At sea, females spent $53 \pm 14\%$ of their time diving. Mean individual dive depth ranged from 45 to 149 m and averaged 91.8 ± 35.2 m ($N = 9$). Mean individual dive durations ranged from 2.9 to 5.8 min, with an average of 4.0 ± 0.9 min ($N = 9$) (Table 2). Sea lions also varied in the time of day they dived. Four females dived exclusively during the day, 2 individuals dived exclusively during the night and the remaining 3 individuals exhibited no diel pattern (Fig. 2).

The multivariate analysis revealed 2 factors from the PCA that explained 82.16% of the variance and therefore were used for the subsequent HCA. Dive depth, dive rate, and mass explained most of the variance in factor 1. Factor 2 was driven by bottom time, descent and ascent rate (Table 3). The HCA identified 3 distinct groups of sea lions; the maximum Euclidean distance for a group to be considered was 1.07 based on the cluster tree produced by the HCA. Taking into account diving behaviour characteristics, groups were classified as (1) shallow divers, (2) deep divers and (3) bottom divers (Fig. 3).

Females in Group 1 (shallow divers: CAAF05, CAAF06) had the shallowest mean dive depths (44.8 ± 21.6 and 46.3 ± 18.6 m respectively), shortest mean dive duration (2.94 ± 1.17 and 2.94 ± 1.16 min respectively) and highest mean dive rate (13.5 ± 6.1 and 11.4 ± 4.51 dives h^{-1} respectively) of all females. They were also the smallest (55 and 62 kg respectively), primarily dove at night and spent on average 60.9% of their time at sea diving.

Females in Group 2 (deep divers: CAAF01, CAAF02, CAAF03, CAAF09) had the deepest mean dive depths (range = 101.8 to 114.6 m), shortest mean bottom time (range = 1.1 to 1.5 min), lowest mean dive rate (range = 6.3 to 8.4 dives h^{-1}) and lowest proportion of IDZ dives (similar depths on consecutive dives) (31.3 to 65.6%) of all females in the study, except 1 female in Group 3 (CAAF11, deepest mean depth = 149 m and shortest mean dive rate = 5.2 dives h^{-1}). These sea lions dived predominantly during the day and spent an average of 44.1% of their time at sea diving.

Lastly, females in Group 3 (bottom divers: CAAF08, CAAF10, CAAF11) had the longest mean bottom time

Table 2. *Zalophus wollebaeki*. Mean (\pm SD) and max. dive parameters. Caamaño Islet, March 2005. IDZ (intra-depth zone): similar max. dive depth on consecutive dives

Dive strategy	Female ID	Mass (kg)	Dive depth (m)	Dive duration (min)	Bottom time (min)	Mean # bottom wiggles	Mean descent rate (m s ⁻¹)	Mean ascent rate (m s ⁻¹)	Mean dive rate (dives h ⁻¹)	% IDZ	% Time diving at sea
Shallow	CAAF05	55	44.8 \pm 21.6	2.9 \pm 1.2	1.6 \pm 1.0	8.1 \pm 5.1	1.1 \pm 0.3	1.2 \pm 0.4	13.5 \pm 6.1	63	68
Shallow	CAAF06	61.8	46.3 \pm 18.6	2.9 \pm 1.2	1.7 \pm 1.0	2.1 \pm 1.6	1.1 \pm 0.3	1.4 \pm 0.2	11.4 \pm 4.5	61.4	54
Deep	CAAF01	78	114.6 \pm 112.4	4.1 \pm 2.4	1.5 \pm 1.0	8 \pm 6.9	1.1 \pm 0.7	1.0 \pm 0.5	6.8 \pm 4.2	39.5	48
Deep	CAAF02	78	104.1 \pm 95.5	3.5 \pm 2.0	1.1 \pm 0.8	5.8 \pm 5.5	1.2 \pm 0.7	1.1 \pm 0.6	6.4 \pm 4.3	31.3	28
Deep	CAAF03	95.6	112.2 \pm 91.0	3.9 \pm 2.2	1.3 \pm 1.0	7.2 \pm 6.2	1.2 \pm 0.6	1.1 \pm 0.5	6.3 \pm 3.7	43.6	40
Bottom	CAAF09	71.6	101.8 \pm 58.6	3.9 \pm 1.7	1.5 \pm 1.0	8.2 \pm 6.8	1.2 \pm 0.5	1.3 \pm 0.5	8.4 \pm 4.3	65.6	59
Bottom	CAAF08	72.6	57.8 \pm 11.0	3.9 \pm 1.1	2.6 \pm 1.0	14.5 \pm 7.0	1.5 \pm 0.3	1.4 \pm 0.3	10.2 \pm 3.4	88.9	70
Bottom	CAAF10	78.2	96.0 \pm 41.6	5.1 \pm 1.7	2.9 \pm 1.3	17.5 \pm 9.9	1.4 \pm 0.4	1.4 \pm 0.4	7.7 \pm 3.2	75.8	64
Bottom	CAAF11	75.4	149.0 \pm 65.3	5.8 \pm 1.6	2.5 \pm 1.1	4.5 \pm 2.4	1.4 \pm 0.3	1.4 \pm 0.3	5.2 \pm 2.2	73.8	43

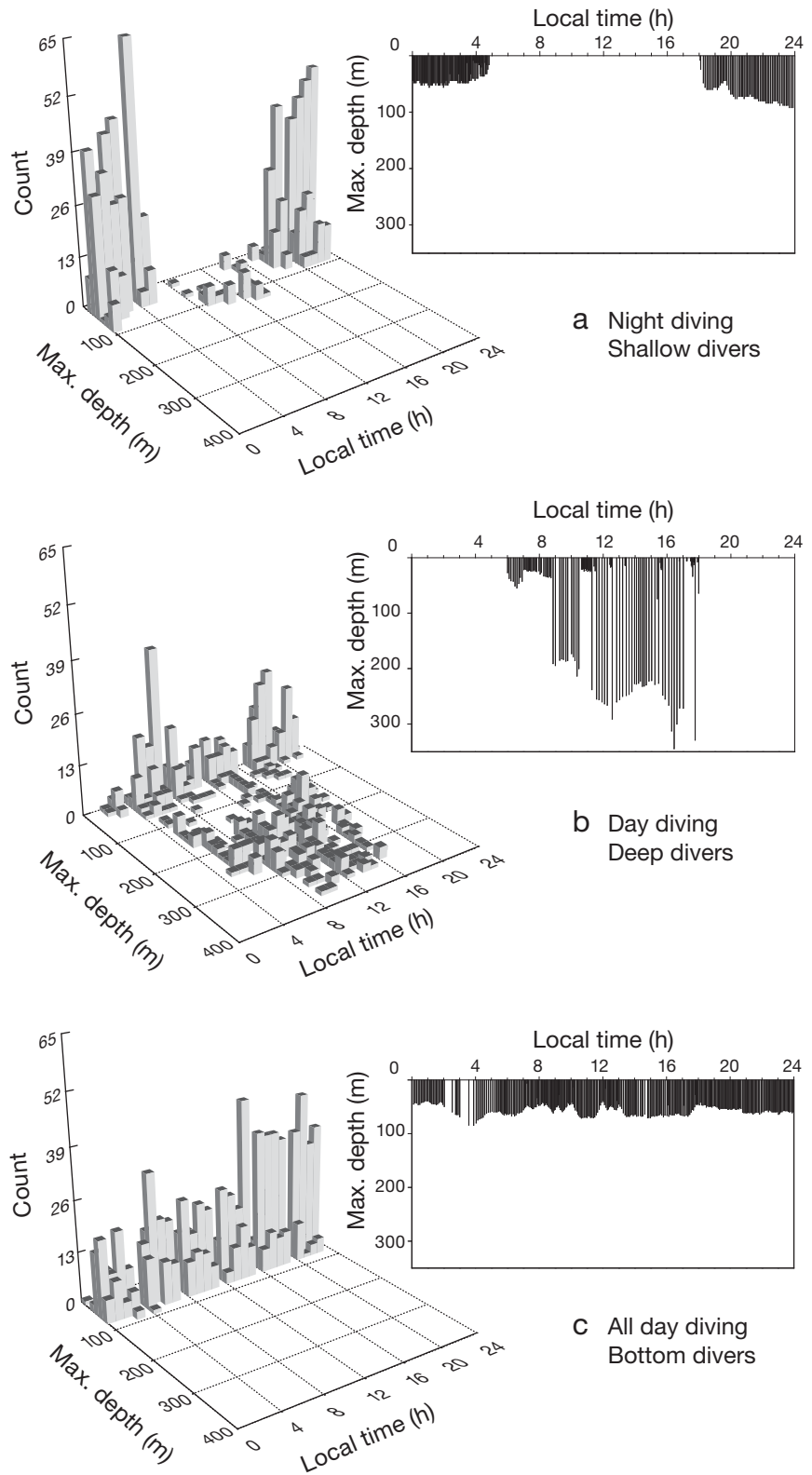


Fig. 2. *Zalophus wollebaeki*. Left: number of dives by depth and time of day; right: dive profiles of females from Caamaño Islet, March 2005. (a) Night diving, shallow divers group (CAAF06); (b) day diving, deep divers group (CAAF01); and (c) all day diving, bottom divers group (CAAF08)

Table 3. *Zalophus wollebaeki*. PCA rotated loading matrix (SYSTAT 10.2) for dive parameters used in the diving behaviour analysis of 9 females from Caamaño Islet during March 2005. In bold are loadings for the diving variables that contributed the most for Factors 1 and 2

Dive parameter	Factor 1 (41.78%)	Factor 2 (40.38%)
Mean dive depth	0.957	-0.018
Mean dive duration	0.720	0.611
Mean bottom time	0.000	0.981
Mean # bottom wiggles	0.007	0.654
Mass	0.847	-0.044
Mean descent rate	0.363	0.871
Mean ascent rate	-0.296	0.840
Mean dive rate	-0.985	0.011

(2.5 to 2.9 min), longest mean dive duration (3.9 to 5.8 min), highest mean ascent and descent rates (1.4 and 1.4 to 1.5 m s⁻¹ respectively) and highest proportion of IDZ dives (73.8 to 88.9%) of all females. These sea lions dived at all times of day and spent an average of 59.2% of their time at sea diving (Table 2, Fig. 2).

Consistent with the different diving depths, the 3 diving groups showed spatial segregation in their foraging locations as observed from their ARGOS positions (Fig. 4). Shallow divers foraged coastally south of Santa Cruz Island, staying within the 100 m isobath. The foraging range of deep divers was broader and the most widespread, comprising deeper waters over the 200 and 500 m isobaths between Santa Cruz, Isabela, Floreana and Santa Fe Islands. Bottom divers utilized

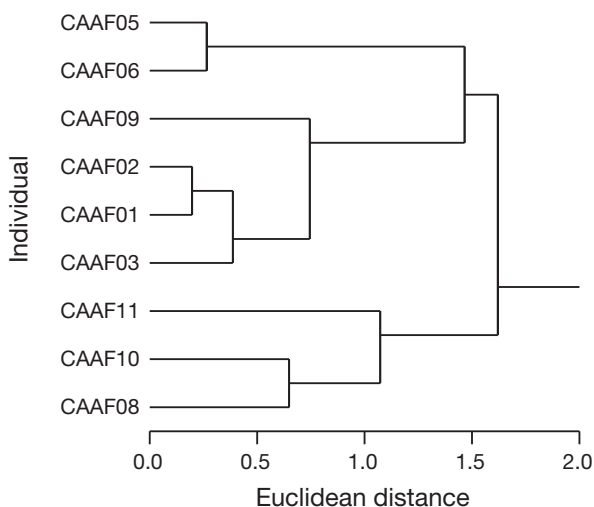


Fig. 3. *Zalophus wollebaeki*. Cluster tree (SYSTAT 10.2) of dive parameters from 9 females, Caamaño Islet, March 2005, showing 3 distinct groups. Euclidean distance considered for clustering was 1.07, based on the unique shared characteristics of each group

the southwest waters between Santa Cruz and Isabela Islands, staying within the 200 m isobath. Dive depth, dive duration and trip duration from the rookery were all greater in Caamaño Islet (this study) vs. Fernandina Island (Kooyman & Trillmich 1986) sea lions. Additionally, sea lions from Fernandina exhibited similar diving behaviour between them (Kooyman & Trillmich 1986), possibly exhibiting one diving strategy compared to the 3 strategies found in this study (Table 4).

DISCUSSION

Diving behaviour and foraging strategies

Different modes of marine predator foraging patterns or strategies (epipelagic, mesopelagic and benthic) (Costa et al. 2004) are typically associated with different geographic regions or habitats. Rarely are all 3 foraging patterns observed in one population, one location, or one sex and age group. Most species tend to exhibit one foraging pattern exclusively. For example, king penguins from Crozet Island feed mesopelagically (Bost et al. 1997). Blue-eyed shags *Phalacrocorax atriceps*, Australian, New Zealand and Southern sea lions forage almost exclusively on the benthos (Croxall et al. 1991, Thompson et al. 1998, Costa & Gales 2000, 2003). California sea lions in California and Antarctic fur seals at South Georgia Island forage epipelagically (Feldkamp et al. 1989, Boyd & Croxall 1992). Some species like female northern fur seals *Callorhinus ursinus* (Goebel et al. 1991), rockhopper penguins *Eudyptes chrysocome* (Tremblay & Chérel 2000) and Gentoo penguins *Pygoscelis papua* (Williams et al. 1992) employ 2 foraging patterns at the same location, diving either epipelagically or benthically.

Foraging patterns of species also vary geographically. Antarctic fur seals from South Georgia Island feed epipelagically on krill (Boyd & Croxall 1992), whereas near Kerguelen Island they feed on mesopelagic myctophid fish (Chérel et al. 1996). Staniland et al. (2004) identified 4 categories of trip durations in female Antarctic fur seals *Arctocephalus gazella* depending on the location of foraging. To our knowledge this is the first time any sea lion species of the same sex and age class has been reported to exhibit 3 foraging patterns or strategies in one geographic area, classified as shallow, deep and bottom divers.

Shallow divers most likely dive on the shallow benthos, but they also presented some epipelagic dives during the study period. A bimodal distribution of bottom time frequencies with peaks at a short and longer bottom time reflects 2 dive types in this group. Dives with short bottom time and shallow depth reflect epipelagic dives and dives with longer bottom times

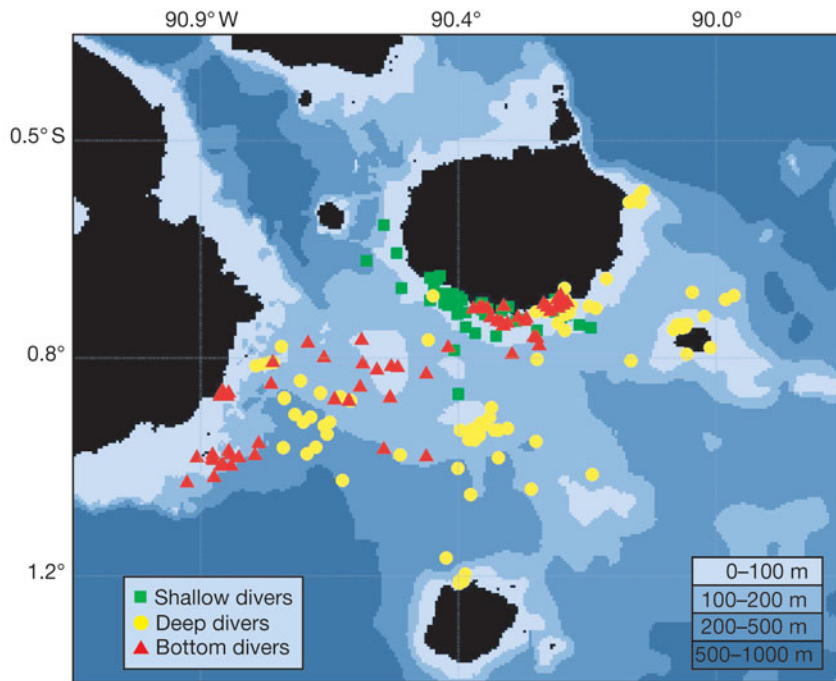


Fig. 4. *Zalophus wollebaeki*. Satellite locations from 9 females instrumented at Caamaño Islet, March 2005. Different colors/shapes show spatial segregation of 3 diver type groups

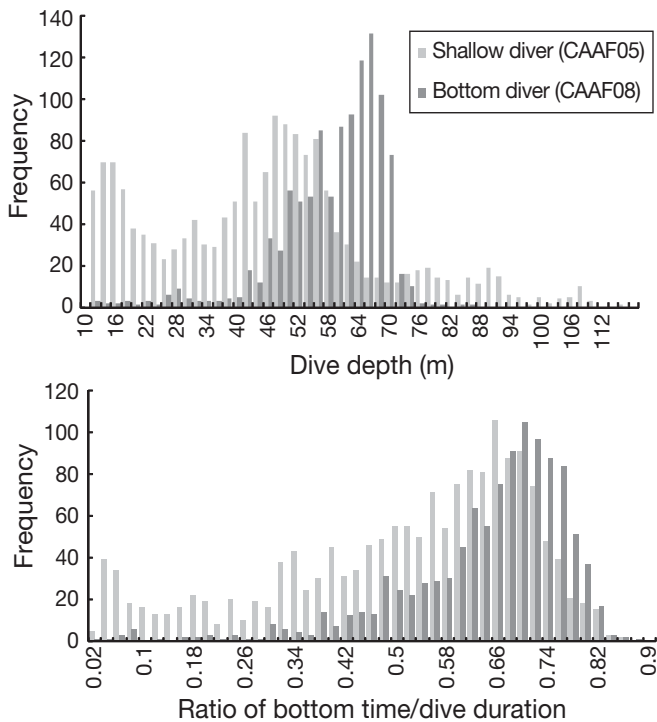


Fig. 5. *Zalophus wollebaeki*. Frequency distribution of dive depth (m) and ratio of bottom time/dive duration for 2 females, a shallow diver (CAAF05) and a benthic diver (CAAF08), showing shallow epipelagic dives (low bottom time/dive duration) in the shallow diver and deeper benthic dives (higher bottom time/dive duration) in the bottom diver

and deeper depths could indicate benthic dives. When compared to sea lions from the bottom divers group, the presence of 2 dive types is more evident (Fig. 5). Because shallow divers dived mostly at night and in characteristically shallow areas close to the shoreline, they likely fed on vertically migrating prey. Dolphins of New Zealand foraging at night were found to feed on the deep scattering layer as it came up along the shore (Benoit-Bird et al. 2004).

The deep divers presented characteristically deep dives, and had the lowest percentage of consecutive dives to the same IDZ, indicating that they were not likely feeding on the benthos. Some dives were most likely mesopelagic—this group exhibited the highest percentage of dives deeper than 200 m (15%), over water of 500 m depth compared to the other groups. Although the absolute depth and durations differed, general diving patterns are similar to those of other mesopelagic predators

such as king penguins and northern elephant seals (LeBoeuf et al. 1986, Kooyman et al. 1992).

Lastly, the behaviour of bottom divers was consistent with benthic foraging. These sea lions had the highest ascent and descent rates, longest bottom times, and greatest percentage of consecutive dives to the same IDZ (Tremblay & Cherel 2000). Dives were similar to the benthic dives observed in Australian, New Zealand and Southern sea lions (Thompson et al. 1998, Costa & Gales 2000, 2003). Even though benthic dives were found in other groups as well, the 'bottom divers' classification relies on the fact that these sea lions spent most of their dive time at the bottom, as observed in their bottom time duration and descent and ascent rates.

It is important to indicate that each of the 3 groups of diving patterns was described with only a very small number of individuals. While this only allows general conclusions to be drawn, it is interesting to note that dive types found in these groups are consistent with prey species found in the diet of the Galapagos sea lion. These include epipelagic Clupeids, mesopelagic Myctophids found in deep waters (200 to 1000 m), shallow and deep benthic Serranids, and shallow benthic Mugilids (0 to 120 m) among others (Salazar 2005). This also suggests that frequency of each diving pattern may be high in the population since rare events are very unlikely discovered with small samples.

Individualized foraging specializations might be expected to occur more frequently in apex predators (Estes

et al. 2003) such as the Galapagos sea lion. Individual specialization observed in this study could result from intraspecific competition due to seasonal changes in prey resources. Intraspecific competition resulting in the exploitation of different prey types and niche separation was found in the sea otter *Enhydra lutris* (Estes et al. 2003, Tinker et al. 2007). Ecological prerequisites of foraging specializations stated by Estes et al. (2003) include weak interspecific competition coupled with strong intraspecific competition for limited resources. Prey resources were likely to be limited during our study as it was conducted during the warm season characterized by reduced upwelling and lower productivity. Although we lack information about other species like sharks and dolphins that may target similar prey, sea lions in Caamaño Islet are the only pinniped present and no other pinnipeds are found around their foraging areas, suggesting weak interspecific competition.

Variability in the sea lions' diving behaviour can also be explained by the mass range of individuals used in this study (55 to 95.6 kg). Sea lions in the shallow divers group were the smallest and exhibited the shallowest dives, foraging coastally. The size of an individual influences its physiological capabilities, which in turn limits its diving behaviour. A smaller individual has proportionally lower oxygen storage capacity for a dive, causing shorter duration aerobic dives (Costa et al. 2004, Weise & Costa 2007). The diving behaviour of the shallow divers group appears to have an ontogenetic component given that their diving capacity could be constrained by body size. The other 2 groups do not seem to be influenced by body size; their mass varied with no particular pattern across both groups (Fig. 6).

Variability in diving behaviour could have also been influenced by pup age, which influences the mother's trip duration, affecting, in turn, her dive behaviour. Although all instrumented females were observed with small (by mass) pups, the pups could have differed in age. Growth of young in this species varies widely,

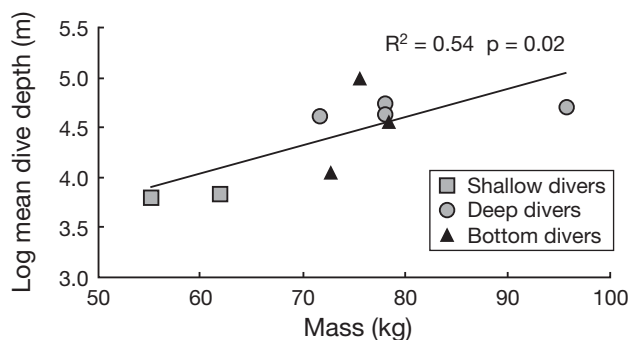


Fig. 6. *Zalophus wollebaeki*. Linear regression of mass (kg) vs. log-transformed mean dive depth (m) of 9 females instrumented at Caamaño Islet, March 2005, showing a significant relationship ($R^2 = 0.54$, $p = 0.02$)

making age classification very difficult (F. Trillmich pers. comm.). Unfortunately, we did not capture pups and thus lack information regarding their sex and/or age.

Foraging trips

Female Galapagos sea lions spend more time away from their pups (2.5 h to 8 d) than the 21 h to 5 d reported for other sea lions species (Feldkamp et al. 1989, Merrikk & Loughlin 1997, Thompson et al. 1998, Costa & Gales 2000, 2003, Kuhn 2006). As these females were lactating, their pups fasted longer than those of other species, indicating that these pups may face higher nutritional stress. Longer trips are in part caused by the propensity of Galapagos sea lion females to haul out at locations other than their rookery, which to our knowledge has only been reported for one other sea lion species, the South American sea lion (Thompson et al. 1998). The necessity to haul out at other areas could be caused by shark predation risk and thermoregulatory energetic costs. It is energetically expensive to swim to shore but these factors might make it more expensive to remain at sea, as hypothesized by Thompson et al. (1998). Longer trip durations from the rookery indicate that females have to spend longer times at sea to locate food and meet energy requirements, causing them to haul out at areas away from their pups. This creates a conflict between continuing to forage and returning to the rookery to suckle their pup (Costa 2008). Longer fasting durations for pups influence their growth, survival rates, maternal dependence and, ultimately, population trends. Galapagos sea lion populations from the southern central archipelago may increase slowly or decrease quickly, as seen during El Niño events (Trillmich & Limberger 1985), as a result of pups having to sustain long fasting periods.

Boyd et al. (1997) showed that fur seals with attached devices increased the duration of their foraging trips by 33.8% compared to those without them. The mass of these devices represented 0.62% of the total mass of the individual. In our study the total mass of the attached devices represented only one-third of the percentage of total body mass they represented in Boyd et al.'s study, that is, 0.23% of the sea lion's mass in this study. Devices used in this study also had a lower profile than the ones used in Boyd et al.'s study. Given that the 2 main components (mass and profile) potentially affecting the sea lions' behaviour were smaller than in Boyd et al.'s study, we believe the effect of attached devices on our sea lions' behaviour was small and that our results are representative of the natural behaviour of these individuals.

Comparison of diving behaviour studies

Two studies have been conducted on *Zalophus wollebaeki* diving behaviour, one by Kooyman & Trillmich (1986) and the present research. They differ in geographic location, surrounding bathymetry and season. Kooyman & Trillmich's (1986) study was conducted on the northwestern region of the Galapagos archipelago at Fernandina Island, the youngest and westernmost island of the Galapagos. The continental shelf is almost non-existent on its western side. In contrast, we performed our research in the central region, at Caamaño Islet, surrounded by an extensive shelf and broad central underwater plateau accessible to sea lions breeding at this colony. The former study took place during the dry season (October to November 1980), while our study was carried out during the wet season (March 2005). The wet season is characterized by lower upwelling, warmer water temperatures, reduced productivity and consequently prey abundance (Pak & Zanveld 1973, Feldman 1986). Furthermore, *Z. wollebaeki* at Fernandina Island coexist with Galapagos fur seals *Arctocephalus galapagoensis*, whereas sea lions at Caamaño Islet are the only pinniped present.

Although the Kooyman & Trillmich (1986) study had a smaller sample size ($n = 4$), was carried out over 20 yr ago (different devices used) and during a different season, the contrasting results suggest that sea lions may forage differently at different areas of the Galapagos Archipelago. Diet results from Dellinger & Trillmich (1999) support this suggestion, showing that sea lions at the west part of the archipelago fed almost exclusively on sardines, compared to Salazar's (2005) results which showed that clupeids, myctophids, serranids and mugilids, among others, are present in the diet of sea lions from the central part of the archipelago. Differing oceanographic and bathymetric features among sites influence the presence of distinct prey. Furthermore, possible competition with sympatric Galapagos fur seals *Arctocephalus galapagoensis* at Fernandina

Island could also be driving the specialized diet found in *Zalophus wollebaeki* at this site.

Implications of individual specialization and management

Individual specialization has implications for demographic, ecological and evolutionary dynamics. Specialization is expected to be higher in environments with fewer competing species (Bolnick et al. 2003) and intraspecific competition is diversifying (Roughgarden 1972). Our results support these statements, showing individual specialization as 3 distinct diving behaviours at Caamaño Islet, an area where sea lions are the only pinniped present. Further, populations with individual specialists may be open to future evolutionary diversification (Rosenzweig 1978, Lomnicki & Ombach 1984, Doebeli 1996). Individual specialization can also produce a delayed response to fluctuations in prey availability (Werner et al. 1981). This might explain why the Galapagos sea lion population, particularly in the central area of the archipelago (which includes this study location), appears to be so sensitive to El Niño events, when prey availability is significantly diminished (Trillmich & Limberger 1985).

Furthermore, because individual specialization is diversifying, if the high degree of individual specialization shown in these Galapagos sea lions persists through time, this population would be of great importance as it holds vast evolutionary potential, which could, in the future, increase the great diversity that already characterizes this archipelago. Galapagos sea lions are a vulnerable species (Seal Specialist Group 1996) with a fluctuating population (Trillmich & Limberger 1985). Not only breeding but also foraging and other terrestrial habitats require protection for the species to survive.

In this study we determined for the first time the marine and terrestrial habitat utilization of Galapagos sea lions inhabiting the densest area of its population, using satellite telemetry. The foraging range of these individuals is wide and is situated within a commercially exploited area. Terrestrial habitat use is broad as well. Female sea lions used several haul-out areas other than their breeding rookery. These areas included Islas Plazas and Las Palmas in Santa Cruz Island, Los Cuatro Hermanos Islets, Tortuga Island, Santa Fe Island, Floreana Island and Punta Veintimilla at Isabela Island (Fig. 1). Taking into consideration the sea lions' wide foraging range, management plans should

Table 4. Comparison of Galapagos sea lion dive behaviour in this study with Kooyman & Trillmich (1986). Mean dive duration (\pm SD) for this study is presented

	Kooyman & Trillmich (1986)	This study
Date/season	Oct–Nov 1980, dry season	Mar 2005, wet season
Location	Fernandina Island	Caamaño Islet
Sample size	4 females	9 females
Mean dive depth (m)	Similar, 37 or 38	Variable, 45–149
Max. dive depth (m)	115–186	84.5–371
Max. dive duration (min)	5 or 6	6.4–9.8
Mean dive duration (min)	<2	4 \pm 0.9
Dive rate (dives h ⁻¹)	5–13	5–13.5
Time of day diving	Daylight	Daylight, night & all day

also consider protecting a wider marine area in contrast to only the immediate area around the breeding rookery.

The fact that individuals adopt a range of strategies, hunting prey in epipelagic, mesopelagic and benthic environments, suggests that they do not have a strong, reliable prey resource. Interactions with fisheries represent a great threat to the species, particularly because the number of registered fishers in Galapagos has shown a consistent increase over time (Baine et al. 2007) and some of the sea lion prey species are targeted by fisheries. The identification of distinct foraging strategies with distinct geographic and depth zones found among this population can be incorporated into new regulations to manage spatial and temporal aspects of the local fishing effort. That is, knowing the most frequented depths and areas in which sea lions dive, a regulation can be implemented to avoid fishing at those particular depths around these areas. Of particular interest are the areas around Santa Cruz Island from Isla Sin Nombre to Islas Plazas, around Santa Fe Island within the 100 m isobaths and waters between Santa Cruz, Floreana and Isabela Islands below 0° 40' S and within the 500 m isobath.

Lastly, to better understand the Galapagos sea lions' habitat utilization and diving behaviour, further studies should be performed in different seasons and with larger sample sizes to determine if the distinct foraging strategies and habitat utilization found in this study continue throughout the year, or if seasonal and resource changes generate a behavioural and/or habitat utilization change in the population. If the latter is the case, management strategies and regulations to alleviate negative effects on both sea lions and fishermen can be imposed seasonally. Similar studies on different demographic groups such as males and juveniles will contribute greatly to understanding the behaviour of the population as a whole. Further studies at different sites (e.g. San Cristobal and Floreana Islands) will allow for better determination of sea lion habitat utilization and foraging range within the population's densest area. Demography and diet studies should be continued to monitor population status and fisheries interactions, particularly during El Niño and La Niña years.

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