MARINE MAMMAL SCIENCE, 14(3):552–574 (July 1998)

A PROTRACTED FORAGING AND ATTENDANCE CYCLE IN FEMALE JUAN FERNÁNDEZ FUR SEALS

JOHN FRANCIS[1]
DARYL BONESS
Department of Zoological Research,
National Zoological Park,
Smithsonian Institution,
Washington, DC 20008, U.S.A.
E-mail: jfrancis@ngs.org

HUGO OCHOA-ACUÑA
Department of Zoology,
University of Florida,
Gainesville, Florida 32611, U.S.A.

ABSTRACT

Previous studies of fur seals suggest that the attendance patterns and consequent temporal patterning of energy transfer from mother to pup follows a latitudinal cline. While data from subpolar, tropical, and some temperate latitude species support the postulated cline, data for the temperate latitude Juan Fernández fur seal do not. Maternal foraging trips and associated visits ashore were the longest of all otariids studied to date. The first foraging trip postpartum averaged 10.2 d (*n* = 51 females, range 1–22.5), foraging trips combined averaged 12.3 d (*n* = 100, range 1.0–25.0), and visits ashore averaged 5.3 d (*n* = 91, range 0.3–15.8) over the three seasons of study. Only duration of lactation was intermediate between subpolar and tropical strategies as predicted. Dive records suggest that these females feed almost exclusively at night at depths of less than 10 m and at distances of more than 500 km offshore. The prey species of this fur seal, primarily myctophids and squid, migrate to the surface at night and are patchily distributed. Foraging trip length varied between years in conjunction with shifts in sea-surface temperature and type of prey consumed. We suggest that distribution of prey, irrespective of latitude, dictates foraging patterns of fur seals and leads to the exceptionally long foraging trips and visits ashore observed in this species.

Key words: foraging, diving, otariid, fur seal, *Arctocephalus philippii*, maternal.

---

[1] Present address: National Geographic Television, 1145 17th St. N.W., Washington, D.C. 20036.

The maternal care of pinnipeds is unusual among mammals because females give birth on land or ice but feed entirely at sea. While all pinnipeds share this constraint, how females balance the requirements of aquatic foraging against those of terrestrial parturition and lactation varies considerably among species. Phocids, for the most part, do not forage during lactation and wean their pups within 4–50 d, whereas otariids conduct foraging trips throughout the course of lactation, weaning their pups in 4–36 mo (Oftedal *et al.* 1987*a*, Bonner 1984). In the only extant odobenid, the walrus, *Odobenus rosmarus*, females forage throughout lactation, suckle both on land and at sea, and wean their pups at 24 mo (Fay 1982, Miller and Boness 1983).

A previous synthesis of fur seal maternal strategies, which included data on the diving behavior of five fur seal and one sea lion species, suggests that the temporal patterning of energy transfer from mother to pup follows a latitudinal cline (Gentry *et al.* 1986). In subpolar species, females make long trips to sea followed by infrequent long periods on land, during which pups receive large amounts of high-fat milk and are weaned in approximately four months. In the tropical species, females make frequent short trips and spend short periods on land to feed their pups relatively low-fat milk, eventually weaning them in one to three years. Gentry *et al.* (1986) emphasized the need for additional data on temperate latitude species and suggested the additional influences of local effects such as temporal and spatial distribution of prey on maternal attendance patterns.

We present data on the attendance and foraging behavior of the previously unstudied, temperate latitude Juan Fernández fur seal, *Arctocephalus philippii*, and test whether latitude predicts the pattern of maternal care observed in this species. We examine the determinants of foraging trip duration and interannual variation in duration, using measures of diving behavior and location to clarify the relationship between foraging behavior and prey exploited. Finally, we discuss the available data on prey distribution and abundance and their relationship to the attendance patterns observed.

MATERIALS AND METHODS

Study Site and Animals

Forty lactating females were captured during their perinatal period at Los Harenes, Alejandro Selkirk Island, Chile (33°46′S, 80°47′W) in late November and early December of the 1988, 1990, and 1991 breeding seasons. For those females from which telemetry instruments were retrieved, a second capture was made approximately one month later. Twenty of these females were fitted with a MKIII+ Time Depth Recorder (TDR, 100 g, 2.5 cm diameter × 15.2 cm length—Wildlife Computers, Woodinville, WA) and a VHF radiotransmitter (81 g, 1.9 cm diameter × 10.2 cm length—Advanced Telemetry Systems, Isanti, MI) glued with Devcon 5-min epoxy to the fur on their backs. Females were marked on the head and flanks with orange fluorescent paint (Lenmar Paint, Baltimore, MD) for identification. Twenty females received radio-transmitters alone. Fifteen of the TDRs (those deployed in 1990 and 1991) were Geographic Location TDRs (GLTDRs) and measured light level and temperature to provide daily estimates of location at sea (DeLong *et al.* 1992). Data on diving behavior were collected from 9 of the 20 TDRs deployed. Of the 11 remaining, 2 were recovered but failed mechanically, 4 became detached from the females during a foraging trip, and 5 of the females were not seen after their departure to sea. To obtain more accurate and frequent measures of location at sea, in 1992 an additional three females were captured as above and outfitted with a 0.5-watt satellite-linked TDR (SLTDR, 450 g, 10.5 × 14.5 × 3.5 cm—Wildlife Computers). The SLTDR transmits dive records to satellites from which locations of better than 1 km accuracy can be calculated. Two of the three SLTDRs deployed provided records.

Fifty-one lactating females, marked remotely with paint pellets (Nelson Paint Co., Iron Mt., MI) at El Tongo rookery during 1988, 1990, and 1991, served as a control for the effect of instruments on attendance.

All females recaptured were stomach-lavaged with approximately two liters of fresh water and given an enema. The samples retrieved were washed through nested sieves to recover cephalopod beaks, fish otoliths, and tissue for identification of prey species consumed (Lowry 1986). Otoliths were identified to the level of genus or species through comparison to published material (Fitch and Brownell 1968, Fitch 1969, Hetch and Hetch 1981, Harkönen 1986) and to reference collections from locally caught fish and museum specimens. Squid beaks were identified using drawings and stereoscopic photos (Clarke 1962, 1986; Garcia-Tello 1965; Wolff 1982) in addition to reference beaks from museum specimens.

Data Collection and Analysis

The presence of each VHF-instrumented female was monitored automatically using a data logger and radio receiver (Advanced Telemetry Systems, Models 5040 and R2000) programmed by a laptop computer. The radio receiver and antenna were positioned approximately 200 m inland and at an altitude of 30 m, giving a range of at least 1 km with a line of sight to all resting locations regularly used by the study females at Los Harenes. To assure that females were not ashore at other sites, we surveyed adjacent beaches at 3–7 d intervals. The receiver and data logger were set to scan all transmitter frequencies once every 15 min, counting the number of pulses received for each in a 5-sec interval. An instrumented female was considered on land if the maximum five pulses was received during a scan. Records of less than five pulses usually indicated that females were rafting offshore as verified by TDR records and direct observation.

The presence of paint-marked females was monitored visually at El Tongo from 0900 through 2100 daily throughout the study period: in 1988 from 29 November to 23 December, in 1990 from 15 November through 28 February, and in 1991 from 19 October through 28 January. Departure and arrival dates for foraging trips were calculated to the nearest quarter hour for females with instruments and to the nearest hour for those observed visually, and these values were used for all calculations of trip and visit lengths presented. In cases where the paint-marked "control" females departed or arrived between observation periods, such as overnight, time was assigned as the midpoint between observations, usually 0300. A foraging trip was defined as any period encompassing 24 h or more during which a female was not recorded on land. This criterion has been employed in the majority of studies to which we compare. In this application it excludes trips to sea of several hours' duration occurring most often during the heat of the day (Francis and Boness 1991) but occasionally at night.

To assess the accuracy of methodology previously employed in the study of female attendance patterns in otariids, we also calculated time at sea and time ashore to the nearest day. As with previous investigators (*e.g.*, Gentry and Holt 1986, Heath *et al.* 1991), we assumed that if a female was sighted on land during the daily observation period, she was present the entire day. These values were then compared to the primary data analyzed at an accuracy of a quarter hour or hour for the instrumented and control females, respectively.

TDRs were programmed to record depth every 10 sec when the instrument was wet and to record only time when dry. Depth was measured to an accuracy of 2 m in 1988 and 1 m in 1990 and 1991; however, because of some drift in the measurement of zero depth inherent in the TDR design, only dives greater than 2 m were considered for 1990 and 1991 records. For 1988 records, due to more extreme drift in zero depth measures and a lower precision of the instrument, only depth measurements greater than 10 m were considered. For comparison to the 1988 data and also to previous studies, records from 1990 and 1991 were analyzed also at a 10-m minimum depth.

Dive frequency was calculated over the total time at sea. This contrasts with other studies where dive frequency was calculated within dive bouts (Gentry and Kooyman 1986, Feldkamp *et al.* 1989). Dives were not distributed over time in this study such that dive bouts could be identified from log-survivorship plots of durations at the surface, for either 3-m or 10-m minimum records.

Daily locations at sea were calculated for five females using GLTDRs which measured light levels at each surfacing. The light levels were converted to dawn and dusk times which were used to obtain latitude and longitude values from standard navigational algorithms within the GEOLOCATION program (Wildlife Computers) (DeLong *et al.* 1992). Predicted locations and empirical tests (DeLong *et al.* 1992) suggest that a conservative interpretation of our data would place the actual location of the animals in this study within a 250 km × 250 km zone. Data plotted are the central points of each predicted location zone.

SLTDRs have been used in a number of marine mammal studies (Stewart *et al.* 1989, McConnell *et al.* 1992, Merrick *et al.* 1994). Accuracy of the locations depends on the number of signals received during a satellite pass. In our study 10% of the signals were of Class 2 accuracy (±350 m each in latitude and longitude), 27% were Class 1 (±1 km), and 63% were Class 0

Table 1. Duration (days) of visits ashore and trips to sea during foraging cycles of uninstrumented female Juan Fernández fur seals from El Tongo Rookery, Alejandro Selkirk Island. Values presented are mean, ± SD, (*n*), and range.

	1988	1990	1991	*F*	*P*	$\bar{x}$ (88–91)
Perinatal period	11.3 ± 4.26 (16)	12.1 ± 2.62 (12)	10.7 ± 2.97 (21)	0.63	n.s.	11.3 ± 3.35 (49) 6.6–20.6
1st trip	9.5 ± 4.48 (14)	14.3 ± 5.64 (12)	8.4 ± 5.36 (21)	5.12	<.01	10.2 ± 5.64 (47) 1.0–22.5
1st visit	5.2 ± 1.89 (11)	5.9 ± 2.99 (12)	4.1 ± 2.01 (21)	2.32	n.s.	4.9 ± 2.36 (44) 0.8–12.0
		1990	1991	*F*	*P*	$\bar{x}$ (90–91)
2nd trip		16.0 ± 5.75 (11)	13.1 ± 6.69 (19)	1.21	n.s.	14.2 ± 6.42 (30) 2.5–25.0
2nd visit		6.6 ± 2.69 (10)	5.7 ± 2.02 (18)	0.97	n.s.	6.0 ± 2.27 (28) 1.7–10.5
3rd trip		16.4 ± 4.16 (10)	12.6 ± 6.52 (13)	1.58	n.s.	14.2 ± 5.82 (23) 1.7–23.0
3rd visit		4.7 ± 2.83 (9)	5.4 ± 4.35 (10)	0.41	n.s.	5.0 ± 3.63 (19) 0.3–15.8
Trips 1–3						12.3 ± 6.19 (100) 1.0–25.0
Visits 1–3						5.3 ± 2.67 (91) 0.3–15.8

(unknown accuracy). Locations plotted are averages of 1–9 sightings for each day an animal was located.

RESULTS

Attendance Pattern

Juan Fernández fur seal females in this study that were not carrying instruments spent an average 11.3 d on land with their newborn pups prior to departing on their first foraging trip (Table 1). The mean duration of foraging trips was 12.3 d and visits ashore averaged 5.3 d. Attendance patterns varied considerably within and between females (Fig. 1). Female attendance periods ranged from 0.3 to 15.8 d and trips to sea from 1.0 to 25.0 d.

Females frequently made trips to sea for less than one day, and these trips were considered separately from the above analyses. TDR records from six females in 1990 and 1991 show that females went on 1.36 (SD = 0.74, n = 6) short trips per day. The majority (82%) of these trips occurred during the middle of the day and were associated with increases in solar radiation (see Francis and Boness 1991). Daytime trips for the TDR females averaged 2.2 h in length (SD = 1.46, n = 64). Nighttime short trips recorded with the TDRs were longer (mean = 9.3 h, SD = 5.10, n = 14, Student's t-test, t =

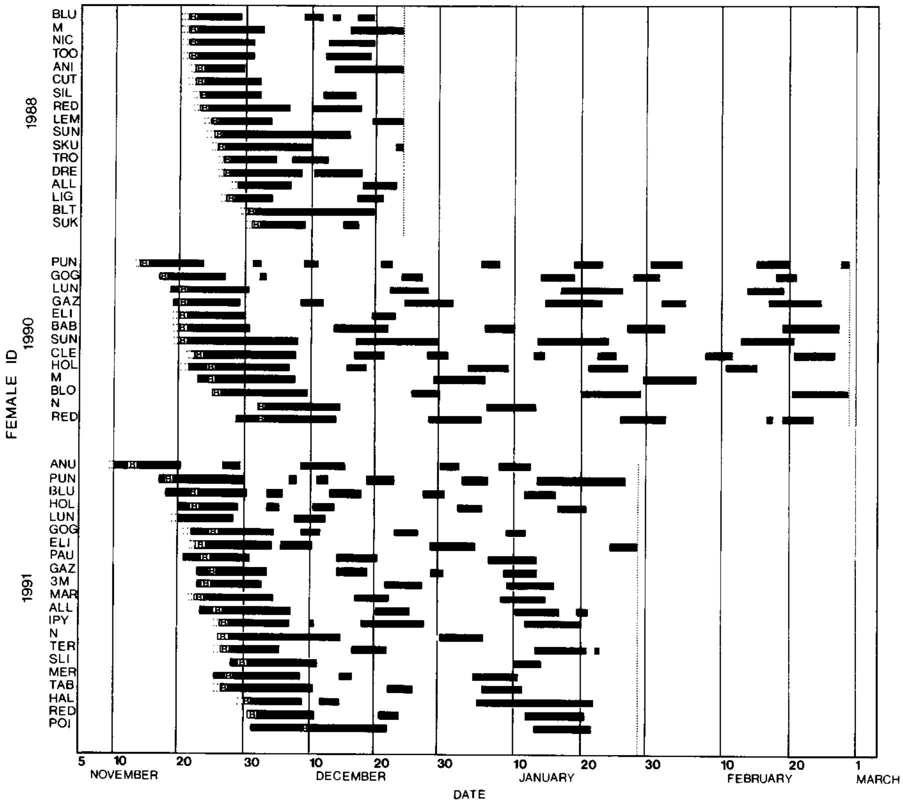

Figure 1. Attendance patterns of individual, non-instrumented females, Alejandro Selkirk Island, 1988–1991. Birth date of pup represented as "B." Solid bars indicate days female was present on land. Dotted vertical lines indicate end of observation period.

-5.20, $P < 0.0001$) than daytime trips. As a rule, diving was infrequent during these short trips (see section on diving behavior, below).

The data on nighttime short trips recorded with TDRs can be applied to data from non-instrumented females to calculate the effect of their inclusion on the average foraging trip length. TDR females averaged 0.22 nighttime short trips per day ashore (SD = 0.205, $n = 6$). Non-instrumented females averaged 5.3 d ashore per foraging trip to sea. Assuming the TDR data apply to these females, we can calculate that the average female takes 1.17 short trips for every foraging trip recorded. Using the sample of foraging trips for this study (mean 12.3 d, $n = 100$) and adding 117 short trips of 9.3 h gives an average of 5.83 d per trip.

Average weight and length of instrumented females at first capture were 48.1 kg (SD = 9.92) and 142.1 cm (SD = 6.97), respectively, and did not differ significantly between years (ANOVA df = 37, 2; $F = 1.71$ and 0.68, respectively, $P = 0.19$).

Intra-annual and interannual variation—The first foraging trip was shorter than the second and third foraging trips (Table 1 for both 1990 and 1991 (paired t-tests, $P < 0.05$), with the exception of the second foraging trip in 1990 ($P = 0.08$). The first visit was shorter than the second in 1991 but not in 1990 ($P = 0.45$). Second and third foraging trips and visits were not significantly different from each other. A regression of trip length on days postpartum was not significant ($F = 1.552$, df = 110, 1), despite the shorter trips immediately postpartum.

Foraging trip length varied significantly between years. The first foraging trip of females with and without instruments was 60% longer in 1990 than 1991 and 1988 (Tables 1 and 2). Subsequent foraging trips also tended to be longer in 1990 than 1991 (the only years for which data were available) but pooled data within year was not significant (paired t-test, $P = 0.055$, Table 1). In contrast, duration of visits ashore did not vary significantly between years.

Instrument effect—In all three years VHF transmitters and TDRs attached to females had a significant effect on foraging trip length (Table 2). Though the tendency was for females with TDRs to be at sea longer than females with radio-transmitters and shortest with females carrying no instruments, not all years showed significant differences (SNK multiple comparisons test between means). In 1990 the effect was most pronounced: the first foraging trip of TDR females was four times longer than females without instruments and half again longer than for females carrying radio transmitters. In 1988 TDR females were at sea twice as long as for females without instruments, and in 1991 none of the means were significantly different.

Effect of precision in measuring attendance patterns—In many previous studies duration of feeding cycles has been measured to the nearest day assuming the female is ashore all day if seen at least once. In this study we analyzed trip and visit durations both to the nearest hour and to the nearest day to measure the effect of this assumption. As before, absences of less than 24 h were not defined as trips and thus were excluded from this analysis.

Analysis to the nearest day resulted in significantly longer visits ashore and shorter trips to sea than measurements to the nearest hour. Visits of instrumented and non-instrumented females combined were 0.64 d longer on average (paired t-test, $t = -16.78$, $n = 106$, $P < 0.0001$) and trips were 0.71 d shorter ($t = 26.06$, $n = 158$ visits, $P < 0.0001$) than comparable data analyzed to the nearest hour.

Diving Behavior

The TDR records cover the first month of foraging after birth and show the pattern of relatively shallow, nighttime diving found in other arctocephalines (see fig. 15.5 in Gentry *et al.* 1986). Dives reached maximum depths of 50–90 m, with the majority to less than 10 m (Fig. 2, Table 3). Frequency of diving, however, was low for an arctocephaline: only 0.6 dives/h to a depth of 10 m or greater. Minimum depth used in the analysis strongly affected

Table 2. Duration (days) of first trip to sea of female Juan Fernández fur seals with and without instruments. Values presented are mean, ± SD, (*n*), and range (t = TDR, r = radio-transmitter, n = no instrument).

	1988	1990	1991	*F*	*P*	SNK
No instrument	9.5 ± 4.48 (14) 1.9–15.8	14.3 ± 5.64 (12) 7.7–22.5	8.4 ± 5.36 (21) 1.0–21.7	5.12	<.01	90 > 91 = 88
Radio-transmitter	13.2 ± 3.48 (9) 9.1–18.5	36.2 ± 5.25 (3) 30.5–40.8	17.7 ± 9.29 (7) 7.8–31.6	14.22	<.01	90 > 91 = 88
TDR	17.5 ± 3.37 (5) 11.2–20.5	55.1 ± 20.40 (7) 20.9–75.3	17.5 ± 18.60 (3) 5.7–39.0	9.73	<.01	90 > 91 = 88
F	7.54	24.50	4.58			
P	<.01	<.01	<.05			
SNK	t > n t = r r = n	t > r > n	t = r = n			

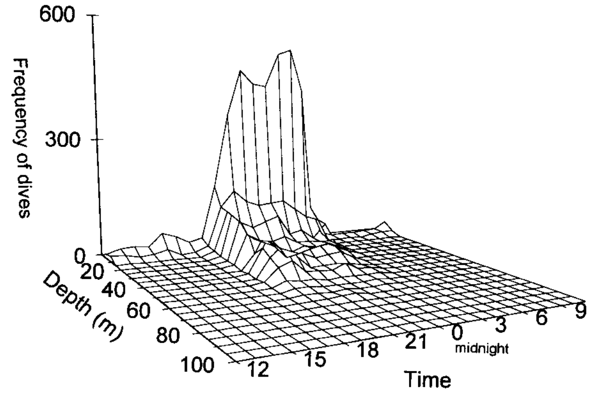

Figure 2. Three-dimensional plot of frequency of dives by depth and time of day. Composite for nine females and 7,557 dives. Measurements for three females from 1988 (n = 342 dives) are included for which dives <10 m were not recorded.

mean dive depth. Using a 10-m minimum depth, the mean was double that calculated for a 3-m minimum depth.

Diving occurred almost exclusively at night: 99.5% of all dives occurred between 2000 and 0700. Females usually began frequent diving around 2200 on the evening following their departure from land, although shallow dives typically began within minutes of entering the water. The first dive to 10 m or deeper occurred without exception in the nighttime, in 7 of 12 cases between 2100 and 2400. Transit time, defined as the time between departure and first dive to 10 m or more (see Gentry and Kooyman 1986) averaged 11.2 h (SD = 11.09, n = 12; 3.8% of average total time at sea). Transit time was positively correlated with the latency between departure and dusk (r = 0.84, $P < 0.05$) for the eight daytime departures recorded. Time between last dive (to 10 m or more) and arrival ashore was 6.1 h (SD = 9.07, n = 5).

Diving during short trips to sea—Diving occurred infrequently during short trips to sea. Females dove to 3 m or more on only 42% of all short trips and on average dove only 1.4 times per trip. Dive frequency on short trips averaged 0.49 dives per hour (SD = 0.44, n = 6 females), one fourth that of the 1.94 dives per hour recorded during foraging trips (trips greater than one day long). Most of the dives during short trips were shallow, 3 and 4 m deep. Dives 10 m deep or deeper occurred on only five trips, four of which had only one dive exceeding 10 m. The fifth trip was exceptional and had numerous dives both deep and shallow, which occurred predominantly from 2040 to 2340. Of the total 78 short trips recorded, only this trip and one other occurring in the daytime showed repeated diving.

Locations at Sea

Locations at sea for five females carrying GLTDRs (Fig. 3) show that they traveled primarily south and west of Alejandro Selkirk Island to locations up

Table 3. Characteristics of diving behavior for nine Juan Fernández fur seal females. Values presented are means and (SD).

Year	*N* females	Total dives	Record length (h)	Mean depth (m)	Maximum depth (m)	Mean duration (min)	Maximum duration (min)	Dives/ hour at sea	Time to first dive (h)
Analysis with 10-m minimum depth									
1988	3	114.0	333.3	31.6	74.7	2.02	3.46	0.44	11.4
		(119.2)	(172.7)	(2.1)	(18.2)	(0.18)	(1.24)	(0.17)	(7.4)
1990, 1991	6	474.2	625.1	23.8	61.8	1.71	3.41	0.74	10.5
		(390.4)	(64.8)	(7.1)	(14.7)	(0.54)	(0.74)	(0.57)	(11.6)
Total	9	354.1	525.4	26.4	66.1	1.81	3.43	0.64	10.8
		(362.3)	(175.6)	(6.9)	(16.1)	(0.46)	(0.85)	(0.48)	(10.0)
Analysis with 3-m minimum depth									
1990, 1991	6	201.7	621.5	12.3	61.8	0.81	3.71	1.94	
		(564.0)	(64.8)	(7.6)	(14.7)	(0.35)	(0.80)	(0.86)	

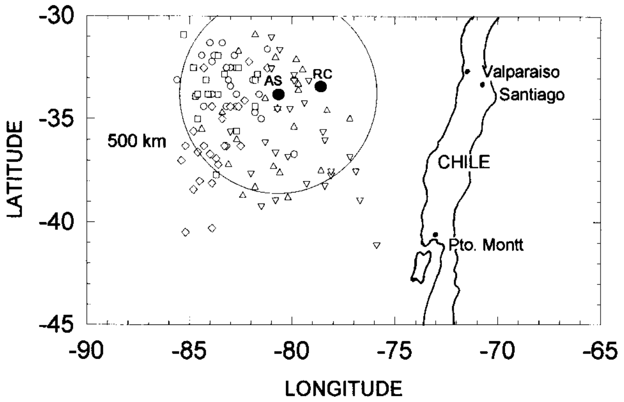

Figure 3. Distribution of locations at sea for five females outfitted with Geographic Location Time Depth Recorders. AS = Alejandro Selkirk Island and RC = Robinson Crusoe Island. Circle = 500 km radius around AS.

to 889 km distant. All females were located more than 550 km from the island (mean = 653 km, SD = 139.3). Distribution of locations varied among females: females 1-90 and 6-90 traveled to the west and southwest to a maximum 594 and 556 km, respectively; females 7-90 and 6-91 to the southwest 667 and 559 km, respectively; and female 10-91 to the southeast 889 km. Actual progression of daily movements could not be calculated given the imprecision of the measurements. However, sea-surface temperatures recorded with the TDRs showed that females 7-90, 6-91, and 10-91 foraged in water as cold as 14.7°C for two to three days each. At the time of deployment the 14°–15° thermocline was located south of 37°S latitude (Oceanographic Monthly Summary–NOAA), confirming a southerly movement on the order of 400 km for these females. Data on successive foraging trips, available for the two females in 1991, showed a similar distribution of locations at sea during each trip.

Data from SLTDRs also showed that females traveled far offshore while foraging. Female 6-92 went 377 km south southeast of the Alejandro Selkirk Island and returned to within 75 km of it by its 24th day when the SLTDR stopped producing signals. The SLTDR carried by female 8-92 recorded a complete 25-d foraging trip 462 km southwest of the island (Fig. 4). Average maximum distance moved for all SLTDR and GLTDR females combined was 586 km (SD = 162.8, n = 7).

Food Habits

Fish remains were obtained from enemas of 10 of 12 females recaptured. Lavage was less successful, leading to recovered hard parts in only 3 of 12 females. Myctophids and cephalopods predominated among prey remains identified through enema, occurring in 48.2% and 37.9%, respectively, of the samples which contained otoliths or beaks. The myctophids identified were

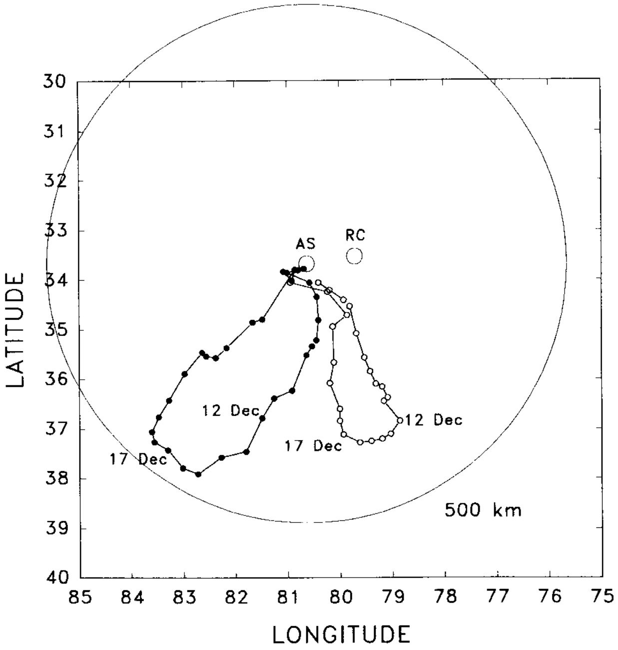

Figure 4. Daily average locations and path of travel for two females outfitted with Satellite-Linked Time Depth Recorders.

Symbolophorus species D, 50% prey occurrence, and *Symbolophorus* species B, 29% (see McGinnis 1982 for treatment of *Symbolophorus* species complex); *Myctophum phengodes,* 7%; and *Lampanychtus* sp., 7%. Cephalopod remains included *Onychoteuthis banksii,* 43%; *Todarodes filippovae,* 28%; and *Tremoctopus violaceus,* 7%. The remaining prey species identified in the enema samples were *Scomberesox saurus scromboides,* 7% and *Decapterus pinnulatus,* 7%.

Duration of Lactation

During all years of observation, females were observed suckling only pups of the year. Lactation lasts for at least 7 mo, since many pups at Los Harenes in June 1991 were observed suckling (M. Ricci, personal communication). In mid-October of the same year the island was barren of females and pups, indicating a maximum weaning date of 11 mo for this species. This is probably an overestimate since sealers during the late 18th century reported that seals traditionally vacated the island by early September (Magee 1795, Delano 1817, Appleton 1947).

DISCUSSION

The foraging cycle of the Juan Fernández fur seal is the longest reported for any otariid. The 11.3 d spent on land with their newborn pups prior to

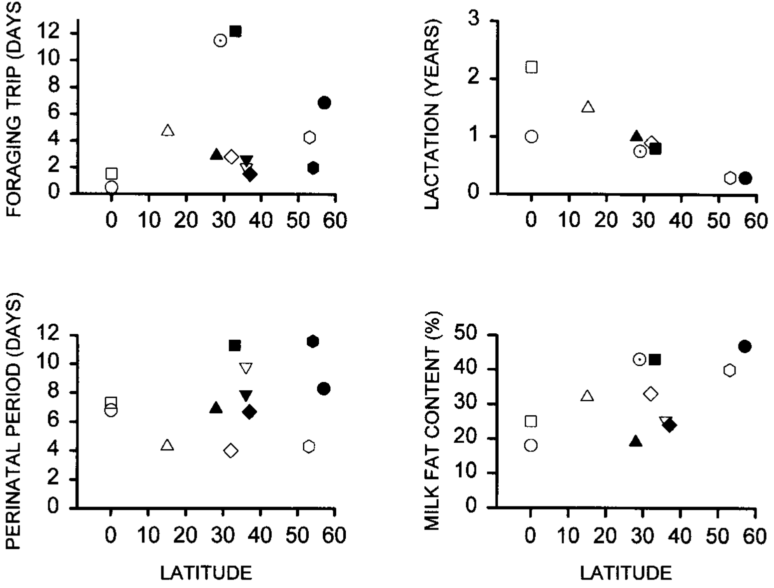

Figure 5. Relationship between latitude and parameters of maternal care (perinatal period, first foraging trip, milk fat content, and duration of maternal care) for thirteen species of otariids. Data are from Gentry *et al.* (1986) pp. 222, 224 or as follows: ○—Galapagos sea lion (Trillmich and Lechner 1986); □–Galapagos fur seal (Trillmich and Lechner 1986); △—South American fur seal (Ponce de Leon 1984) (Majluf 1987); ▲—South African fur seal (Rand 1956); ⊙—Guadalupe fur seal (Figueroa 1994); ◇—California sea lion (Oftedal *et al.* 1987*b*), (Heath *et al.* 1991); ■—Juan Fernández fur seal: this study; ▽—Australian sea lion (Higgins and Gass 1993); ▼—New Zealand fur seal (Goldsworthy 1992); ◆—Steller sea lion (Higgins *et al.* 1988); ⬡—Antarctic fur seal; ⬢—subantarctic fur seal (Goldsworthy 1992); ●—northern fur seal.

departing on their first foraging trip is half again as long as that found in most otariids (Fig. 5). Further, the average 10.2 d on the first trip at sea foraging, 12.2 d at sea for all trips combined, and the 5.3-d visits ashore are two to four times longer than those found in most fur seals and sea lions. Only the closely related Guadalupe fur seal (Repenning *et al.* 1971) approaches the Juan Fernández fur seal in foraging cycle duration (11.5 d at sea, 5.0 d on land, Figueroa 1994).

The exceptionally long foraging cycles of the Juan Fernández fur seal do not fit the predictions of the latitudinal cline hypothesis proposed by Gentry *et al.* (1986). Also contrary to the predicted cline, Juan Fernández fur seal milk is among the richest (about 41% fat) found in eared seals (Francis *et al.* 1989; Ochoa-Acuña 1989; H. Ochoa-Acuña, J. M. Francis, O. Oftedal, unpublished data). Only the length of lactation in this species is intermediate between tropical and subpolar otariid species as predicted by their temperate latitude habitat. These findings suggest that while lactation length may be linked to the differences in seasonality and predictability of food associated with latitude (Gentry *et al.* 1986), parameters of foraging cycles and milk composition are more likely related to local ecological conditions, irrespective of latitude.

Visit Duration

The extremely long visits ashore in the Juan Fernández fur seals are likely a product of the long foraging trips discussed in detail below. Interspecific comparison (Fig. 6) and an intraspecific study of the Antarctic fur seal (Boyd *et al.* 1991) show a positive correlation between visit and trip length.

Visit duration may be determined by amount of energy available for transfer to the pup combined with the capacity of the pup to receive the nutrients. Experiments on mother-pup pairs in the northern fur seal suggest that the duration of a shore visit by a female to nurse her pup depends on the amount of contact with her pup (Gentry and Holt 1986). Pup demand can be expected to increase with increased fasting associated with long foraging trip duration. Thus, maximal demand in conjunction with limits in digestive capacity, as suggested by temporal partitioning of suckling in otariids (Bowen 1991), could result in extended visits ashore in the Juan Fernández fur seal. Further, longer periods at sea as observed in the Juan Fernández fur seal might result in greater amounts of energy stored, which require greater transfer time for the mother and her pup. These conjectures are substantiated by a comparison of five otariid species showing that mass-specific energy delivered to a pup during a visit correlates positively with foraging trip length (Costa 1991).

In the case of the Juan Fernández fur seal, higher fat content of milk in addition to longer visits ashore may provide the increased energy necessary to help sustain pups over the long fasts imposed by long foraging trips. Fat content of milk has been positively correlated with foraging trip length across a number of otariids (Trillmich and Lechner 1986), and the data for the Juan Fernández fur seal corroborates this finding.

Foraging Trip Duration

Applying the chief prediction of central place foraging theory (Orians and Pearson 1979, Stephens and Krebs 1986), as suggested by Gentry *et al.* (1986), we would expect foraging trip duration (specifically time spent foraging) to increase as distance to foraging patch increases. Testing this hypothesis requires data on distance to foraging patches and data that distinguish time spent traveling from time spent foraging.

Our data, when compared with other otariids, are consistent with this hypothesis. Lactating Juan Fernández fur seal females, in addition to having the longest-duration foraging trips, traveled on average 586 km offshore, the farthest for any otariid measured to date. Similar findings for Guadalupe fur seal females (mean = 444 km) in association with their unusually long foraging trips (Gallo 1994) further substantiates this relationship. The northern fur seal, the only other species for which direct measures are available, travels a maximum 137–406 km offshore during a foraging trip (Loughlin *et al.* 1987,

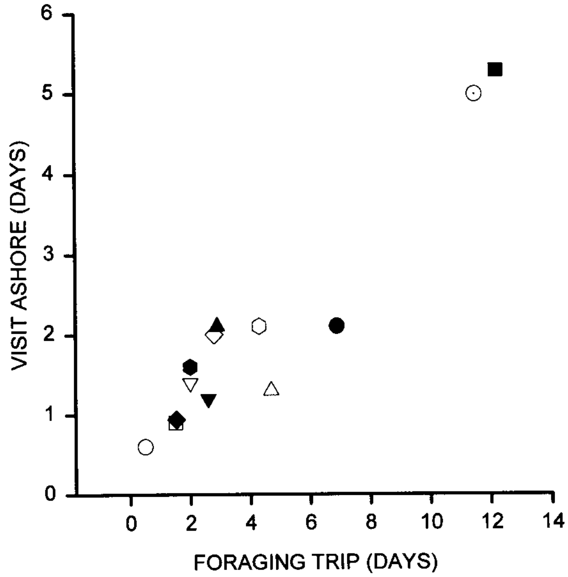

Figure 6. Relationship between first foraging trip and visit length in thirteen species of otariids. Symbols and references as in Figure 5.

Antonelis *et al.* 1990, Baba *et al.* 1991, Goebel *et al.* 1991). Other otariids are estimated to travel a maximum 44–220 km based on foraging trip duration (Gentry *et al.* 1986, Kooyman *et al.* 1986, Antonelis *et al.* 1990).

Estimates of maximum foraging distance vary in quality depending on type. Transit times and distance to deep water, while perhaps useful as indicators of minimum distance to foraging grounds, are misleading indicators of foraging range for at least two species. In the northern fur seal (Loughlin *et al.* 1987, Baba *et al.* 1991, Goebel *et al.* 1991) and the Juan Fernández fur seal (this study), transit times of about 12 h, multiplied by an average swimming speed of 7 km/h (Loughlin *et al.* 1987, Ponganis *et al.* 1990) give gross underestimates of maximum distance traveled. Likewise, distance to continental shelf margins, while roughly agreeing with distances calculated from transit times in the northern fur seals at the Pribilof Islands (Gentry *et al.* 1986), do not agree with empirical locations of foraging, which are beyond the shelf (see Loughlin *et al.* 1987, Goebel *et al.* 1991, and Baba *et al.* 1991). For the Juan Fernández fur seal, water more than 1,000 m deep is within 10 km of shore, yet females travel hundreds of kilometers offshore while foraging.

One can estimate maximum foraging range based on swimming speed and time spent traveling, as for the Galapagos fur seal and sea lion, the California sea lion, and Antarctic fur seal (Gentry *et al.* 1986, Kooyman *et al.* 1986, Antonelis *et al.* 1990). However, correlations cannot be drawn between these variables because foraging range is calculated from duration. Ideally, to test hypotheses relating foraging trip duration to distance traveled, more direct data on foraging location must be obtained from a number of species.

We must also be cautious in drawing conclusions on foraging range when instruments can be shown to affect trip duration. In this study, for example, instrumented females stayed at sea two and three times longer than control females. If trip duration is related to distance traveled, then non-instrumented females should have smaller foraging ranges than those measured carrying instruments.

Is Diving Equivalent To Foraging?

Several lines of evidence suggest that Juan Fernández fur seals feed at the surface, shallower than the 3-m limit used to define a dive in this study. First, the rate of diving to depths >10 m in this species is ten times lower than other otariids (Table 4). Since Juan Fernández fur seal pups grow at a rate similar to that of other otariids (H. Ochoa-Acuña *et al.*, in press) females must catch more fish per dive, or feed at the surface, in order to provide equivalent energy to pups, assuming prey quality and other factors are comparable. Second, dive frequency increases with shallower depths up to the 3-m minimum, and 2-m readings not considered as dives in this study are at the highest frequency of all. Third, prey species consumed by this fur seal, predominantly squid and myctophids (Ochoa-Acuña and Francis 1995; this study) migrate to the surface at night (Roper and Young 1975, Pearcy *et al.* 1977, Gjosaeter and Kawaguchi 1980). Fourth, Antarctic fur seals have been observed feeding with high intensity on surface-swarming krill (Fraser *et al.* 1989), diving to shallow depths not detectable by TDRs.

These findings emphasize the need for measurements of prey capture to broaden our understanding of the relationship between foraging and diving. Such information, especially for surface feeding species, would improve our assessment of effort during foraging trips and help identify whether shallow dives are associated with foraging or other behaviors such as traveling.

Further, for the Juan Fernández fur seal, prey capture data would clarify whether foraging occurs during short daytime trips, which at present appear to be thermoregulatory in function. Short trips at night, of duration similar to those found in this study, have also been observed in the subantarctic and Antarctic fur seals (Goldsworthy 1992). Though records for the Juan Fernández fur seal show little diving, it is still quite possible that females feed at or near the surface on these short trips. However, until we can document feeding activity during these short trips of variable function, we recommend using a >24-h criterion in defining foraging trips to be conservative and consistent with the majority of previous studies.

Prey Distribution and Foraging Strategy

Foraging trip duration and visit duration varies inversely with primary productivity across otariid species (Figueroa 1994), a correlation further strengthened by our data on the Juan Fernández fur seal. The exact relationship between low primary productivity and the availability of prey for the Juan Fer-

Table 4. Characteristics of diving behavior for eight otariid species.

Species	Mean depth (m)	Maximum depth (m)	Mean duration (min)	Maximum duration (min)	Dives/ hour	Source
Analysis at 10-m minimum depth						
Arctocephalus philippii	26	94	1.8	3.7	0.6	this report
A. gazella	30	101	<2.0	4.9	3.4	Kooyman *et al.* 1986
A. galapagoensis	26	115	<2.0	4.2	5.6	Kooyman and Trillmich 1986
A. australis	43	170	2.5	5.3	4.5	Trillmich *et al.* 1986
A. pusillus	45	204	2.1	7.5	2.7	Kooyman and Gentry 1986
Callorhinus ursinus	68	207	2.2	7.6	1.5	Gentry *et al.* 1986
Zalophus californianus californianus	62	241	2.1	9.9	8.4	Feldkamp *et al.* 1989
Z. c. wollebaeki	37	186	<2.0	6.0	8.0	Kooyman and Trillmich 1986
Analysis at 3-m minimum depth						
Arctocephalus philippii	12		0.85	1.9		this report
A. gazella	30		0.93	8.7		Boyd *et al.* 1991

nández fur seals is unknown. There is little information on the distribution of myctophids (Gjosaeter and Kawaguchi 1980) or cephalopods in southeastern Pacific waters, but what is available suggests that the prey species of the Juan Fernández fur seal are abundant though patchily distributed. Craddock and Mead (1970) provide data on the abundance of midwater fishes in a transect extending 2,000 km from the Chilean coast westward across the Juan Fernández Islands. They found the most abundant species in all samples to be myctophids, representing 88.3% of all fish encountered above 500 m. In all, 22 species of lanternfishes were encountered, of which the most frequently captured in surface tows were the principal prey species of the Juan Fernández fur seal, *Symbolophorus boops* and *Myctophum phengodes.* Lanternfish of these two genera are known to concentrate in the uppermost 10 m or less of the ocean at sunset and return to the upper mesopelagic zone below 200 m at dawn (Gjosaeter and Kawaguchi 1980).

Horizontal distributions of *Myctophum* and *Symbolophorus* were patchy, like many of the lanternfish sampled around the Juan Fernández Islands. Surface tows captured from 0 to 100 individuals of these two species depending on the sample longitude.

We are unable to locate similar data for squid distribution around the Juan Fernández Islands. The distribution of squid in this region may, to some extent, follow that of myctophids, since squid feed on mesopelagic fish (Okiyama 1965, Zuev and Nesis 1974). Squid are found with mesopelagic fish in mixed species aggregations at the surface, and some squid have been caught containing as many as 60 lanternfish otoliths (R. McGinnis, personal communication).

The myctophid otoliths collected in our study were too large relative to the beaks collected to have been acquired secondarily through predation on squid (H. Ochoa-Acuña and J. Francis, unpublished data). Juan Fernández fur seals may be exploiting large myctophids and small squid brought together in these interspecific aggregations, the distribution and abundance of which may dictate foraging patterns observed.

Interannual Variability

The Juan Fernández fur seals had significantly longer trips to sea in 1990 than in 1988 or 1991. It is also noteworthy that the lengthening of foraging trips associated with instrument deployment was greatest in 1990 as compared to the other two years. The more pronounced instrument effect, as well as longer foraging trips for control females, may have resulted from reduced food availability as has been shown to occur in a number of seal species (Trillmich and Ono 1991). Though we have no direct measurements of prey availability around Alejandro Selkirk Island during our study, we did observe a significant shift in the diet toward squid in 1990, as compared to the other years between 1987 and 1991 (Ochoa-Acuña and Francis 1995). In conjunction, late summer (January, February) average sea surface temperatures at Alejandro Selkirk Island were 1.0°–1.5° higher than usual in 1988 and 1989 (Anonymous 1989, 1990).

This may have reduced recruitment of myctophids in the following year, as apparently occurred in the Galapagos Islands in 1984 following the strongest El Niño in recorded history (Trillmich and Dellinger 1991).

Conclusion

This study of the Juan Fernández fur seal reveals the ability for females to acquire resources over long trips to sea while their pups fast, remarkably, for up to three weeks. Future studies of the Juan Fernández fur seal should address, in addition to the previously discussed questions about prey distribution and foraging effort, the ability of the female to store energy resources and at the same time to retain the capacity to lactate over long periods without suckling. Prey capture measurements should be used to determine the relationship of foraging to diving behavior. Finally, studies of milk intake (H. Ochoa-Acuña, J. Francis, and O. Oftedal, in preparation) and growth in pups (H. Ochoa-Acuña *et al.*, in press) should address how they respond to the record-length fasts presented by their mothers' protracted foraging cycles.

Acknowledgments

We would especially like to thank Roger Gentry for frequent discussions and guidance throughout this project and for the stimulating research he and his collaborators have offered this field. Daniel Torres and the World Wildlife Fund provided support through the initial phases of this study. Juan Carlos Cárdenas, Hernán Diaz, and Marisol Sepulveda assisted in many aspects of the field research. John Bengtson, Don Croll, Roger Hill, Richard Merrick, Brent Stewart, and Mike Goebel provided advice on time depth recorders and radiotelemetry systems. Thanks to Markus Horning, Roger Gentry, Dan Costa, Burney Le Boeuf, and two anonymous reviewers for helpful comments on this manuscript. Corporación Nacional Forestal (CONAF) of Chile, Cascadia Research Collective, and Museo Nacional de Historia Natural, Santiago, provided institutional support, and the Zenith Corporation, Achilles, USA, and Wildlife Computers, Inc., provided material support. Financial support was provided by the Friends of the National Zoo, several Smithsonian Institution grants (Scholarly Studies Fund, Research Opportunities Fund, and International Exchange Program) and by the National Geographic Society, grants 3707-87 and 3979-88.

Literature Cited

Anonymous. 1989, 1990. NOAA Oceanographic Monthly. Department of Commerce, National Weather Service, Washington, DC 20233.

Antonelis, G. A., B. S. Stewart and W. F. Perryman. 1990. Foraging characteristics of female northern fur seals *(Callorhinus ursinus)* and California sea lions *(Zalophus californianus)*. Canadian Journal of Zoology 68:150–158.

Appleton, N. 1947. Nathaniel Appleton's journal of the voyage of the ship Concord around the world October 1799 to July 1802. Essex Institute Historical Collections, Vol. 83:146–161, 220–246. Essex Institute, Salem.

Baba, N., M. Kiyota, Y. Kazumoto, T. R. Loughlin and G. A. Antonelis. 1991. Satellite tracking of northern fur seal. Pages 104–107 *in* Biotelemetry XI. Proceedings of the Eleventh International Symposium on Biotelemetry. Yokohama, Japan. 29 August–4 September 1990. Waseda University Press, Tokyo.

Bonner, W. N. 1984. Lactation strategies in pinnipeds: Problems for a marine mammalian group. Symposium of the Zoological Society of London 51:253–272.

Bowen, W. D. 1991. Behavioural ecology of pinniped neonates. Pages 66–127 *in* D. Renouf, ed. The behaviour of pinnipeds. Chapman and Hall, London.

Boyd, I. L., N. J. Lunn and T. Barton. 1991. Time budgets and foraging characteristics of lactating Antarctic fur seals. Journal of Animal Ecology 60:577–592.

Clarke, M. R. 1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. Bulletin of the British Museum (Natural History). Zoology 8:422–482.

Clarke, M. R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford.

Costa, D. P. 1991. Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. Pages 300–344 *in* D. Renouf, ed. The behaviour of pinnipeds. Chapman and Hall, London.

Craddock, J. E., and G. W. Mead. 1970. Midwater fishes from the eastern South Pacific Ocean. Scientific Results of the Southeastern Pacific Expedition, Anton Bruun Report 3:3–46.

Delano, A. 1817. A narrative of voyages. E. G. House, Boston, MA.

DeLong, R. L., B. S. Stewart and R. Hill. 1992. Documenting migrations of northern elephant seals using day length. Marine Mammal Science 8:155–159.

Fay, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Fish and Wildlife Service, North American Fauna, No. 74, pp. 1–279.

Feldkamp, S. D., R. L. DeLong and G. A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus.* Canadian Journal of Zoology 67:872–883.

Figueroa, A. L. 1994. Early lactation and attendance behavior of the Guadalupe fur seal females *(Arctocephalus townsendi).* M.Sc. thesis. University of California, Santa Cruz, CA. 63 pp.

Fitch, J. E. 1969. Fossil lanternfish otoliths of California, with notes on fossil Myctophidae of North America. Contributions in Science, Los Angeles County Museum, No. 173.

Fitch, J. E., and R. L. Brownell. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. Fisheries Research Board of Canada 25: 2561–2574.

Francis, J. M., and D. J. Boness. 1991. The effect of thermoregulatory behavior on the mating system of the Juan Fernández fur seal, *Arctocephalus philippii.* Behaviour 119:104–126.

Francis, J., D. Boness and O. Oftedal. 1989. Foraging behavior and lactation strategy of the Juan Fernández fur seal. Abstract. Eighth Biennial Conference on the Biology of Marine Mammals. Pacific Grove, CA. 7–11 December 1989.

Fraser, W. R., R. L. Pitman and D. G. Ainley. 1989. Seabird and fur seal responses to vertically migrating winter krill swarms in Antarctica. Polar Biology 10: 37–41.

Gallo, J. P. 1994. Factors affecting the population status of Guadalupe fur seal, *Arctocephalus townsendi* (Merriam, 1897) at Isla de Guadalupe, Baja California, Mexico. Ph.D. thesis. University of California, Santa Cruz, CA. 187 pp.

Garcia-Tello, O. P. 1965. Utilización de la mandíbula inferior de la jibia *Dosidicus gigas* (D'Orbigni) en el cálculo de su peso total (Mollusca, Cephalopoda, Ommastrephidae). Revista de Biología Marina 12:185–197.

Gentry, R. L., and J. R. Holt. 1986. Attendance behavior of northern fur seals. Pages 41–60 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

Gentry, R. L., and G. L. Kooyman. 1986. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

GENTRY, R. L., D. P. COSTA, J. P. CROXALL, J. H. M. DAVID, R. W. DAVIS, G. L. KOOYMAN, P. MAJLUF, T. S. MCCANN AND F. TRILLMICH. 1986. Synthesis and conclusions. Pages 220–264 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

GJOSAETER, J., AND K. KAWAGUCHI. 1980. A review of the world resources of mesopelagic fish. FAO Fisheries Technical Paper No. 193. FAO, Rome. 151 pp.

GOEBEL, M. E., J. L. BENGSTON, R. L. DELONG, R. L. GENTRY AND T. R. LOUGHLIN. 1991. Diving patterns and foraging locations of female northern fur seals. Fishery Bulletin, U.S. 89:171–179.

GOLDSWORTHY, S. D. 1992. Maternal care in three species of southern fur seal (*Arctocephalus* spp.). Ph.D. thesis, Monash University. 182 pp.

HARKÖNEN, T. 1986. Guide to the otoliths of the bony fishes of northeast Atlantic. Danbiu ApS, Hellerup, Denmark.

HEATH, C. B., K. A. ONO., D. J. BONESS AND J. M. FRANCIS. 1991. The influence of El Niño on female attendance patterns in the California sea lion. Pages 138–145 *in* F. Trillmich and K. Ono, eds. Pinnipeds and El Niño: Responses to environmental stress. Ecological Studies. Vol. 88. Springer-Verlag, Berlin.

HETCH, T., AND A. HETCH. 1981. A descriptive systematic study of the otoliths of the neopterygean marine fishes of South Africa, Part IV. Transactions of the Royal Society of South Africa 44:401–440.

HIGGINS, L. V., AND L. GASS. 1993. Birth to weaning: Parturition, duration of lactation, and attendance cycles of Australian sea lions (*Neophoca cinerea*). Canadian Journal of Zoology 71:2047–2055.

HIGGINS, L. V., D. P. COSTA, A. C. HUNTLEY AND B. J. LE BOEUF. 1988. Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. Marine Mammal Science 4:44–58.

KOOYMAN, G. L., AND R. L. GENTRY. 1986. Diving behavior of South African fur seals. Pages 142–152 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

KOOYMAN, G. L., AND F. TRILLMICH. 1986. Diving behavior of Galapagos fur seals. Pages 186–195 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

KOOYMAN, G. L., R. W. DAVIS AND J. P. CROXALL. 1986. Diving behavior of Antarctic fur seals. Pages 115–125 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

LOUGHLIN, T. R., J. L. BENGTSON AND R. L. MERRICK. 1987. Characteristics of feeding trips of female northern fur seals. Canadian Journal of Zoology 65:2079–2083.

LOWRY, M. S. 1986. Documentation of procedures and computer programs used for food-habit analysis of California sea lion *(Zalophus californianus)* scats and spewings. Administrative Report LJ-86-04. National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA.

MAGEE, BERNARD. 1795. Observations of the islands of Juan Fernández . . . from the journal of Bernard Magee. Collections of the Massachusetts Historical Society for the year 1795. pp. 247–260.

MAJLUF, P. J. 1987. Reproductive ecology of female South American fur seals at Punta San Juan, Peru. Ph.D. thesis, University of Cambridge. 127 pp.

MCCONNELL, B. J., C. CHAMBERS, K. S. NICHOLAS AND M. A. FEDAK. 1992. Satellite tracking of grey seals (*Halichoerus grypus*). Journal of Zoology, London 226:271–282.

MCGINNIS, R. F. 1982. Biogeography of lanternfishes (Family Myctophidae) south of 30°S. Biology of the Antarctic Seas XII. Antarctic Research Series v. 35:1–110.

MERRICK, R. L., T. R. LOUGHLIN, G. A. ANTONELIS AND R. HILL. 1994. Use of satellite-linked telemetry to study Steller sea lion and northern fur seal foraging. Polar Research 13:105–114.

MILLER, E. H., AND D. J. BONESS. 1983. Summer behaviour of the Atlantic walrus

(*Odobenus rosmarus rosmarus*) on Coats Island, NWT. Zeitschrift für Säugetierkunde 48:298–313.

Ochoa-Acuña, H. 1989. Composición láctea en el lobo fino de Juan Fernández *Arctocephalus philippii* (Peters 1866), durante el primer mes de la lactancia. Veterinary Thesis, Universidad de Chile, Santiago. 55 pp.

Ochoa-Acuña, H., and J. Francis. 1995. Food habits of the Juan Fernández fur seal. Canadian Journal of Zoology 73:1444–1452.

Ochoa-Acuña, H., J. M. Francis and D. J. Boness. In press. Interannual variation in birth mass and postnatal growth of Juan Fernández fur seals. Canadian Journal of Zoology.

Oftedal, O., D. Boness and. R. Tedman. 1987*a*. The behavior, physiology, and anatomy of lactation in the pinnipedia. Current Mammalogy 1:175–245.

Oftedal, O., S. Iverson and D. Boness. 1987*b*. Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. Physiological Zoology 60:560–575.

Okiyama, M. 1965. On the feeding habit of the common squid, *Todarodes pacificus* Steenstrup, in the off-shore region of the Japan Sea. Bulletin of the Japanese Sea Regional Fisheries Research Laboratory 14:31–41.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 783–801 *in* D. J. Horn, R. D. Mitchell and T. F. Stairs, eds. Analysis of ecological systems. Ohio State University Press, Columbus, OH.

Pearcy, W. G., E. E. Krygier, R. Mesecar and F. Ramsey. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Research 24:223–345.

Ponce de Leon, A. 1984. Lactancia y composición cuantitativa de la leche del lobo fino sudamericano *Arctocephalus australis* (Zimmerman, 1783). Industria Lobera Pesquera Estado, Montevideo, Uruguay, Anales 1984:43–58.

Ponganis, P. J., E. P Ponganis, K. V. Ponganis, G. L. Kooyman, R. L. Gentry and F. Trillmich. 1990. Swimming velocities in otariids. Canadian Journal of Zoology 68:2105–2112.

Rand, R. W. 1956. The Cape fur seal, *Arctocephalus pusillus* (Schreber), its general characteristics and moult. Union of South Africa Department of Commerce and Industries. Division of Fisheries Investigative Report No. 21:1–52.

Repenning, C. A., R. S. Peterson and C. L. Hubbs. 1971. Contributions to the systematics of southern fur seals, with particular reference to the Juan Fernández and Guadalupe species. Pages 1–34 *in* W. H. Burt, ed. Antarctic Pinnipedia. Antarctic Research Series Vol. 18. American Geophysical Union.

Roper, C. F. E., and R. E Young. 1975. Vertical distribution of pelagic cephalopods. Smithsonian Contributions to Zoology, No. 209. 51 pp.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, NJ.

Stewart, B. S., S. Leatherwood, P. K. Yochem and M. P. Heide-Jorgensen. 1989. Harbor seal tracking and telemetry by satellite. Marine Mammal Science 5:361–376.

Trillmich, F., and E. Lechner. 1986. Milk of the Galapagos fur seal and sea lion, with a comparison of the milk of eared seals (Otariidae). Journal of Zoology, London 209:271–277.

Trillmich, F., and T. Dellinger. 1991. The effects of El Niño on Galapagos pinnipeds. Pages 66–74 *in* F. Trillmich and K. Ono, eds. Pinnipeds and El Niño: Responses to environmental stress. Ecological Studies. Vol. 88. Springer-Verlag, Berlin.

Trillmich, F., and K. A. Ono, eds. 1991. Pinnipeds and El Niño: Responses to environmental stress. Ecological Studies. Vol. 88. Springer-Verlag, Berlin.

Trillmich F., G. L. Kooyman, P. Majluf and M. Sanchez-Griñan. 1986. Attendance and diving behavior of South American fur seals during El Niño in 1983. Pages

153–167 *in* R. L. Gentry and G. L. Kooyman, eds. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, NJ.

WOLFF, G. A. 1982. A key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size. Fishery Bulletin, U.S. 80: 357–370.

ZUEV, G. V., AND K. N. NESIS. 1974. The role of squids in the food chains of the ocean. *In* Squids—biology and fisheries. Translation series (Canadian Fisheries and Marine Service) (3315):8 Translation of Rol'kal'marov v pishchevykh tsepyakh okeana, 1971.

Received: 5 December 1996
Accepted: 14 July 1997