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The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion

Kathryn A. Ono*, Daryl J. Boness, Olav T. Oftedal

Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008, USA

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Summary. Observed changes in maternal investment due to an environmentally induced decrease in food supply (the 1983 El Niño-Southern Oscillation) are compared with *a priori* predictions for the California sea lion (*Zalophus californianus*). Changes in behavior, growth and mortality of offspring were also examined. Data collected in the first two months postpartum for the years before (PRE), during (EN), and the two years after (POST1 and POST2) the 1983 El Niño indicate that females initiated postpartum feeding trips earlier during the food shortage, and spent more time away on individual feeding trips in both the El Niño year and the year after. Perinatal sex ratios (♀:♂) in the years PRE, EN, POST1 and POST2 were 1:1, 1.4:1, 1.1:1 and 1:1.4, respectively. Fewer copulations were observed during the El Niño year, but this difference was not statistically significant. Pups spent less time suckling in the food shortage year and the year following, but attempted to sneak suckle more. Pups were less active and played on land less in the El Niño and following year. Finally, maternal investment as measured by milk intake of offspring was decreased, pups grew more slowly, and suffered increased mortality during the food shortage year. Despite expected sex differences in maternal investment and pup behavior in response to food shortage, there were no sex-biased differences in response in either females or pups. As expected, the food shortage did not affect adult males since they migrate north during the non-breeding season where the environmental perturbation was less severe.

Introduction

A considerable amount of theory has been advanced to explain the allocation of resources between parent and offspring (Trivers 1972; Trivers and Willard 1973; Maynard Smith 1980). With the exception of Trivers and Willard (1973) this theory concerns the expected patterns under normal environmental conditions. Here we empirically address the question of how maternal investment and mother and young behavior in the California sea lion (*Zalophus californianus*) changes in the face of a naturally occurring environmental perturbation, the El Niño.

The El Niño-Southern Oscillation is an irregularly occurring interannual oceanographic event evidenced by rises in sea level and sea-surface temperature in the eastern Pacific Ocean (Cane 1983). These increased ocean temperatures are correlated with increased salinity, decreased zooplankton (McGowan 1984), and decreased fish abundance (Barber and Chavez 1983).

The 1982–83 El Niño-Southern Oscillation was exceptional in being the strongest in recorded history as well as being extremely well documented (Cane 1983; Fielder 1984; Barber and Chavez 1983). However, most reports on the biological consequences of El Niño were restricted to the devastating effects near the heart of the El Niño in the eastern central Pacific Ocean and off the coast of South America where high mortality and even total reproductive failure of marine birds and mammals were the norm (Trillmich and Limberger 1985; Limberger et al. 1983; Barber and Chavez 1983; Simon 1983). In more northern latitudes, many populations were also severely affected, but in different ways. For instance, storm damage dis-

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* *Present address:* Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

rupted kelp beds off southern California (Dayton and Tegner 1984), and caused high mortality among Elephant seal pups (*Mirounga angustirostris*) (Le Boeuf and Condit 1983). We demonstrate that California sea lions breeding off the Southern California coast also suffered increased mortality of pups. Mortality in this species, however, was due to disruption of their food base rather than from the direct action of the physical environment.

Our study encompassed the years prior to (1982 = PRE) during (1983 = EN) and after (1984 = POST1; 1985 = POST2) the 1982–83 El Niño event as it affected the southern coast of California. Oceanographers found evidence of the El Niño along the California coast as early as October, 1982, and effects were still present as late as March, 1984 (McGowan 1984).

Natural history of the California sea lion

In order to understand the significance of the effects of El Niño on behavior and biology of this species, as well as the justification of our *a priori* expectations, a brief overview of its natural history is required. The natural history of the California sea lion has been well studied (Peterson and Bartholomew 1967; Odell 1972; Bartholomew and Hubbs 1952; Mate 1973). Throughout its range, the species is highly polygynous and is gregarious on land. Adult females and males begin arriving on reproductive areas simultaneously in May of each year. Females rest on land for a few days before giving birth to a single precocial pup. Parturition and nursing occur exclusively on land. Females remain with their pups for approximately one week before going to sea to feed. These attendance or "feeding cycles" in which females alternately feed at sea and return to nurse their pups continue for the remainder of the pairs' stay on the reproductive area. Except in rare cases of adoption, females nurse only their own pups. Females copulate once approximately three weeks postpartum (Heath and Francis 1983).

While their mothers are present on the breeding area, pups spend most of their time in close proximity to their mothers, generally resting or suckling. In their first 2–3 weeks of life pups tend to rest alone while their mothers are away. As they grow older, pups gather in groups or "pods" and play and explore small pools of water. Later, pups spend much of their time swimming and playing in larger tidepools and protected coves.

Adult males compete for the opportunity to remain on reproductive areas through fighting and ritualized displays. Established males do not feed during their entire tenure on the breeding areas which may last up to 55 days (unpubl. data). Males migrate northward post-season as far as British Columbia (Bigg 1973; Mate 1973; Hancock 1970; Bartholomew 1967).

Methods

The study was conducted on San Nicolas Island, Channel Islands, California (33° N, 119° W), which lies approximately 96 km off the Southern California coast. Our behavior study area (Trailer Cove) was located on the northwest tip of the island (area 1A in Peterson and Bartholomew 1967). The area consists of a rocky flat shale shelf measuring 120 × 85 m. It is bounded to the north by a small cove, to the south by an area of large boulders and cobble, to the west by open ocean and to the east by a restricted access dirt road over a stabilized dune.

Shortly after the peak of births on the study area (late June), pups were weighed, measured and individually marked with hair bleach. Pups were again weighed, measured and tagged (red Reise tags, Dalton Supplies Ltd., England) in early August in order to obtain individual growth rates. Growth rates used in this paper were calculated for individual marked pups by subtracting June weight from the August weight and dividing by the number of days between weighings. Sexual differences in pup size existed for all weighings (Boness, Oftedahl, and Ono, in preparation).

Adult females were marked remotely with a combination of hair dye (Nyanzol) that was injected into blown eggs and thrown, and paint pellets propelled from a wrist rocket. Adult males were sufficiently scarred to permit identification without further marking.

Data on female and pup activity patterns were collected daily from 0600–1800 h from a blind approximately 30 m from the animals from mid-May through July during the years 1982–84. Instantaneous scan samples of mother and pup behavior were taken hourly throughout the season. Since all pups were not observed the same number of times, pup behavior was analyzed for each pup as the proportion of total observed time spent on each activity. Since these proportions showed no sexual differences, yearly means for combined sexes were calculated. Sample sizes for each year indicate the number of pups used for the analyses. Data from pups that died during the season were not used in the analyses, except for mortality calculations. Categories of pup behavior analyzed here are defined as follows:

Rest: Lying in a prone position, motionless.
Suckle: Suckling or searching for nipple.
Sneak suckle: Suckling from any female other than the mother.
Active: Behaviors which presumably require moderate to large expenditures of energy. Includes all play, interactive (other than suckle) and locomotory components. Play, swim and aggression defined below are subcategories of Active.
Play: On land non-social exploration and manipulation of objects as well as non-aggressive social interactions.
Swim: In water activities including non-social and social play, diving, moving in water from place to place.
Aggression: Social interactions which include components biting at, threatening, and barking.

Data were collected on female attendance (feeding cycles) for the years 1982–85. Analyses of female feeding cycles were confined to weeks 2 through 11 postpartum since the period of time between parturition and the initial departure varied between years from about 5 to 8 days. Females were scored by the half day as being present, absent, or uncertain. Uncertainties were recorded when the female was not seen and her pup was not observed for at least 3 h.

Studies of milk intake were performed on pups residing on reproductive areas located 0.3–8.8 km from the behavior study area. A deuterium oxide (D_2O) dilution technique was used to approximate the amount of milk consumed by pups (Oftedal et al. 1987). As our initial intent was simply to monitor milk intake in *Zalophus* pups at different ages, pups were not studied in the same months each year. Some pups were excluded from the analysis presented here because their growth was abnormal (below the 1st percentile of normal growth), and we were unable to determine if environmental or human disturbance factors were the cause. Intake measurements used in this analysis were taken on 14 pups in June of PRE, on 9 pups in July of EN, and for 8 pups in June and 8 pups in July of POST1.

Minimum mortality was calculated as the proportion of marked pups actually observed dead. Most of these pups were in an emaciated condition up to several weeks before death and were, therefore, watched closely. Healthy pups which disappeared suddenly from the study area were generally resighted on another reproductive area.

The statistical packages SPSS (Statistical Package for the Social Sciences) and SPSSPC were used to analyze aspects of the data. Analysis of feeding cycle data was performed using ANOVA with the Bonferroni technique for comparisons between years (Neter et al. 1985). Since there was no difference between data from mothers of male and female pups, data for both sexes were combined. Analysis of pup weight and growth data was done by analysis of covariance. The effect of sex was partialled out in the comparison of weights at 2 months of age, and both sex and initial weight were removed in the comparison of growth rates to adjust for size dependent differences in growth. Pup behavior was analyzed using Mann-Whitney *U* tests to compare between years and the Bonferroni adjustment for multiple comparisons. Milk intakes were compared using analysis of covariance with pup weight and sex controlled.

A priori expectations of the El Niño effect

Most of the hypotheses tested in this paper were based on *a priori* expectations. The rationale for these expectations are explained here. The major direct effect of the El Niño on the California sea lion in the Channel Islands appeared to be a reduction in the normal food supply for lactating females. Evidence for this food supply depression can be obtained from several sources. Costa et al. (1985) administrated doubly labeled water to lactating females leaving on feeding trips. They found that females increased their metabolism at sea during the El Niño year, indicating an increase in foraging effort. They also found an increase in time spent foraging while at sea.

Studies of *Zalophus* stomach contents and scat samples indicate that anchovies, squid, hake, rockfishes, jack mackerel, and herring are common prey species (Scheffer and Neff 1948; Fiscus and Baines 1966; Heath and Francis 1984; Antonelis et al. 1984). Fisheries statistics indicate that four of these species declined in commercial catches between PRE and EN, and the other two remained essentially the same (U.S. Department of Commerce 1982, 1984; McGowan 1984). A further decline occurred in all six prey species in POST1 (U.S. Department of Commerce 1985). Plankton samples also revealed a dramatic drop in EN off southern California (Fielder 1984; McGowan 1984). This decrease in the lower food chain may have yielded both immediate and longer term drops in available prey for sea lions.

Terrestrial behavior may also have been influenced by the unusually warm weather experienced during the breeding season. Maximum daily air temperature during June and July in EN was higher than in PRE (PRE: $\bar{x}=18.9°$ C, $sd=4.1$; EN: $\bar{x}=20.4$, $sd=4.0$, $P<0.02$, unpubl. data).

The effect of an El Niño may be manifest in many different aspects of biology and behavior in these animals. In the case of a depression in food supply females must balance the growth and survival of their single pup of the year against their own survival and future reproduction, while pups must trade off energy allocated to growth (and fat deposition) with energy needed for socialization, muscle strengthening, and the acquisition of swimming skills. The El Niño provided us with an opportunity to test our understanding of the biology of this species by first making hypotheses regarding the way we throught components should change given the relevant theoretical and experimental evidence, then by comparing our hypotheses with the observed results. We expected that females would need to spend more time foraging, and less time with their pups during EN. For a highly polygynous species such as *Zalophus*, sex ratio theory (Trivers and Willard 1973; Maynard Smith 1978) leads us to expect a greater proportion of female pups born during the lean year. Nutritional stress has been shown to decrease or suppress the frequency of estrus as well as cause decreases in the frequency of sexual behavior and copulations in other species (Loy 1970; Guilbert and Goss 1932; Lochmiller et al. 1986; Southwick 1967). We might, therefore, expect a decrease in copulations during the El Niño year, and a decrease in pup production in subsequent years.

We expected that pups would attempt to maximize energy intake by spending a larger proportion of time suckling during EN, and also by attempting to sneak suckle more often. Pups should conserve their energy by by participating less in high energy utilizing behaviors and Resting more. Behaviors such as Active, Play on land and Swim require large amounts of energy and, therefore, should be curtailed under nutritional shortage. Nutritional stress has been shown to cause an increase in aggression in other species (Zimmerman et al. 1974, 1975; Dasmann and Taber 1956). We would, therefore, expect pups to be more aggressive during EN. If females were undergoing a food shortage, then pups should also receive a smaller quantity of milk from their mothers during EN. Pups should be smaller, grow slower, and suffer an increase in mortality during EN. Since large body size is critical to males, we expected that male pups and mothers of male pups would attempt to compensate more for the decrease in food supply. Lastly, we expected the El Niño to have negligible effect on adult males, since they do not feed during their tenure on land, do not have the added energy drain of lactation, and migrate north during the nonbreeding season where the effects of EN were less severe (Gentry and Kooyman 1986).

Results

Effects on females

Attendance behavior. As expected, many aspects of female feeding cycles were affected by the El Niño. The duration of time between parturition and the first departure on a feeding cycle was significantly shorter for females in EN than for PRE, POST1 and POST2 (Table 1). Females left about 2 days earlier during EN than any of the other three years.

Table 1. Feeding cycle parameters of female *Zalophus californianus* for the years 1982–1985. Comparisons between years were made with a one-way ANOVA and a priori family wide significance was determined by the Bonferroni technique. Means, standard deviations, sample sizes and significant comparisons are given

Activity	PRE (1982)			EN (1983)			POST1 (1984)			POST2 (1985)			Comparisons	
	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	Years	$P<$
Parturition to first departure (days)	7.90	1.66	10	6.09	0.97	11	7.96	1.05	13	7.69	1.33	32	$83<82,84,85$	0.01
Proportion of time spent on land	0.59	0.11	16	0.42	0.14	14	0.42	0.14	25	0.52	0.09	21	$82>83$ $82>84$	0.001 0.0001
Duration of feeding trips (days)	1.39	0.32	14	2.05	0.78	14	2.47	0.72	22	1.63	0.55	21	$83>82$ $84>82, 85$	0.05 0.0001
Duration of periods present (days)	1.48	0.43	13	1.58	0.69	14	1.40	0.34	22	1.70	0.35	21	$84<85$	0.05
Number of feeding trips per week	1.45	0.33	12	1.88	0.73	13	1.81	0.53	21	2.01	0.38	18	$82<85$	0.05

Females also spent a smaller porportion of their time on land during EN and POST1 than in PRE (Table 1). Computed per week postpartum, females spent 59% of their time at the study area in PRE and 42% during EN and POST1. POST2 was intermediate and not singificantly different than any other year. The duration of individual feeding trips was shorter in PRE than EN, increased in POST1 and was larger than for PRE and POST2 (Table 1). Females spent 1.39 days on feeding trips in PRE, but increased their foraging effort to 2.05–2.47 days per trip in the following years. The only difference in duration of periods females were present on the reproductive area occurred between POST1 and POST2 (Table 1). Finally, females made a greater number of feeding trips in POST2 than PRE, with no differences between any other years (Table 1). Thus, females did not leave more often on feeding trips during EN and POST1, but took longer trips, and departed earlier postpartum in the EN season.

Sex ratios, pup production, and copulations. Sex ratios were calculated from Trailer Cove study area pups that were caught at the first weighing session, when they were less than 14 days old. As there were very few still births on the study area in any year (≤ 2) these were not included in the sex ratios given here. No pups died before these data were collected so that it is close to the secondary sex ratio. In PRE we found 31 female and 31 male pups in our marked sample. There were 27 female and 19 male pups in EN (1.4:1), and 24 female and 21 male pups in POST1. Our data, then, parallel theoretical predictions but deviations from a 50:50 sex ratio are non-significant (PRE vs. EN, $Z=0.90$, $P<0.18$). The 1985 season was considered a fully recovered year by other measures such as pup weights and growth rates (Boness, Oftedahl, and Ono, in preparation). Sex ratios for 1985 were 22 female and 31 male pups (1:1.4). There was a significant differences between EN and POST2 ($Z=1.70$, $P<0.04$).

Pup production was also low during the EN and POST1 years. Since we collected all pups in our study area at the same time each year and the mean birth date for pups did not differ between years, our marked sample should be a reasonable indication of pup production. We found 62 pups in PRE, 46 pups in EN, and 45 pups in POST1. Pup production on the study area increased to 54 pups in POST2.

Although we observed few copulations each year, the number decreased, though not significantly, during EN. Since the number of copulations observed is a function of the number of females present (given that male ability to copulate successively is not limiting and a fixed proportion of the females present will come into estrus) we define the copulation rate as the number of copulations observed divided by the mean number of females present per day during the period of time (days) in which copulations took place. This rate was 0.14 for both PRE and POST1, and 0.08 for EN. The 43% reduction in copulations observed in EN is not significantly different from the surrounding years ($X^2=1.11$, $P=0.29$).

Effects on pups

Suckling behavior. Pups spent a larger proportion of their time suckling in PRE than in either EN

Table 2. Between year comparison for selected behaviors of *Zalophus californianus* pups on San Nicolas Island for the years 1982–1984. Data presented are mean percent of observations per pup, standard deviation and number of pups. PLAY, SWIM and AGGRESSION are subcatagories of the ACTIVE classification. Comparisons between years were made with the Mann-Whitney *U* Test, and the Bonferroni method was used to adjust for multiple comparisons

Behavior	PRE (1982)			EN (1983)			POST1 (1984)			Comparisons	
	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	Years	$P<$
SUCKLE	19.24	4.84	15	13.51	4.82	17	12.42	3.94	23	82>83 82>84	0.01 0.0005
REST	38.80	6.81	15	41.13	7.63	17	36.83	4.26	23	NS	
ACTIVE	32.02	4.46	15	25.41	6.53	17	21.87	5.68	23	82>83 82>84	0.005 0.0001
PLAY	9.09	3.57	14	5.22	2.54	17	2.99	1.60	23	82>83 83>84 82>84	0.02 0.02 0.005
SWIM	5.97	3.34	14	5.60	2.80	17	5.92	2.94	23	NS	
AGGRESSION	0.17	0.48	14	0.38	0.47	17	0.32	0.54	23	NS	

or POST1 (Table 2). Pups spent 19.2% of their time suckling in PRE, 13.5% in EN and 12.4% in POST1 when including those observations taken both when the mother was present and when she was absent. However, females spent a larger proportion of their time at sea during EN and POST1 (the complement of "proportion of time spent on land" in Table 1). Pups then, would have to spend a greater proportion of the time that their mothers were available to them suckling, in order to compensate for the longer absence of their mothers. This proportion, however, was not greater for EN or POST1, and pups suckled for less than a third of a time that their mothers' were present in any year (average time spent suckling while mother present = 27.2% ± 9.3, no differences between years with Mann-Whitney *U* Test), so that the amount of time spent suckling was not constrained by the availability of their mother. Also, the duration of periods that females were present on the study area did not differ among the three years, though females were away at sea for a longer period of time during each feeding cycle (Table 1). Lastly, females did not appear to restrict suckling behaviorally, since pups initiated and terminated most suckling bouts in all years (unpubl. data). Thus, our evidence does not indicate that pups suckled longer to compensate for the reduced availability of their mother, or that mothers restricted suckling during EN or POST1.

Pups attempted to sneak suckle significantly more in EN and POST1 than in PRE (χ^2:$P<0.0005$ for PRE vs. EN and PRE vs. POST1). Of the marked pups, 6.4% attempted to sneak suckle at least once in PRE, 54.4% in EN, and 42.2% in POST1. Although pups attempted to sneak suckle more in EN and POST1, sneak suckling did not appear to contribute substantially to increased intake in any year, since 93% and 88% of the attempts by pups were totally unsuccessful in EN and POST1, respectively. The mean duration of successful attempts was less than one minute in either year ($\bar{x} = 52 \pm 86$ s in EN, and $\bar{x} = 39 \pm 31$ s in POST1).

Other behavior. Other aspects of pup behavior varied between years. The behavioral category "Active" includes relatively high energy utilizing behaviors such as walking, playing and swimming. Pups spent 32% of their time in Active behaviors in PRE compared with 25% to 22% in the following years (Table 2). On the other hand, pups did not appear to Rest more in EN and POST1 when compared with PRE. There were no significant differences in the amount of time pups spent Resting in any of the three years (Table 2). In general, pups spent abot 40% of their time resting.

The percent of total time spent in Play on land varied significantly between all three years. Pups spent the greatest amount of time Playing in PRE (9.1%), and the least in POST1 (3.0%) (Table 2). The percent of time pups spent Swimming and playing in the water was not significantly different between years (~6%, Table 2). Pups were not involved in significantly more Aggressive interactions in EN than in either PRE or POST1 (Table 2).

Milk intake. Since changes in intake with the stage of lactation may confound the comparison be-

Table 3. Milk intake (ml/day) as a percent of body weight for California sea lion pups during the first two months of life. Milk intake was estimated using a deuterium oxide dilution technique. An analysis of covariance with sex and weight controlled revealed that the June PRE (1982) and POST1 (1984) samples are significantly different ($P < 0.026$). The July samples for EN (1983) and POST1 are not significantly different ($P > 0.05$). Data presented here are derived from Oftedal et al. (1987)

		PRE (1982)			EN (1983)			POST1 (1984)		
		$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*
June	Male	8.01	0.69	7				7.06	0.89	4
	Female	7.37	0.64	7				6.82	0.42	4
July	Male				5.96	0.91	5	6.11	0.49	5
	Female				5.93	0.93	4	6.00	0.93	3

Table 4. Between year comparison of *Zalophus californianus* pup early postnatal weight and growth parameters. Due to significant differences between sexes the means, standard deviations, and sample sizes for male and female pups are presented separately. Early postnatal weight (<7 days of age) was obtained from the entire San Nicolas Island population; weight at <14 days, 2 months and growth rate were calculated from the same individuals residing on Trailer Cove. Sex was an independent factor in all analyses. A covariance analysis tested for differences between years in growth rate with the initial (<14 days of age) pup weight used as a covariate. Adjustments for multiple comparisons were made using the Bonferroni method

Parameter	PRE (1982)			EN (1983)			POST1 (1984)			POST2 (1985)			Comparisons	
	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	$\bar{x}$	*sd*	*n*	Years	$P<$
$\bar{x}$ weight (kg) <7 days of age:														
Males	9.0	0.9	21	9.0	1.1	15	9.0	1.0	14	9.6	0.7	9	NS	
Females	7.8	0.8	32	7.3	0.8	20	7.8	0.7	10	8.1	1.1	16		
$\bar{x}$ weight (kg) <14 days of age:														
Males	10.3	1.0	16	9.6	1.5	14	9.9	0.8	14	10.2	1.7	25	NS	
Females	8.5	0.9	10	8.3	1.2	13	8.6	1.2	18	8.8	1.2	14		
$\bar{x}$ weight (kg) approx. 2 mos.:														
													83<84	0.05
Males	17.2	2.0	16	14.8	2.8	14	15.7	2.9	14	16.5	2.4	25	83<85	0.005
Females	14.1	2.0	10	11.8	2.5	13	13.3	2.4	18	13.4	1.8	14	83<82	0.005
$\bar{x}$ growth rate (kg/day):														
													83<84	0.05
Males	0.15	0.04	16	0.12	0.04	14	0.14	0.04	14	0.15	0.03	25	83<85	0.005
Females	0.12	0.04	10	0.08	0.05	13	0.11	0.03	18	0.11	0.03	14	83<82	0.005

tween pups differing in age, we can only compare the PRE June data with the POST1 June data, and the EN July data with the POST1 July data (Table 3). Also, since weight and sex of pups affect milk intake, these concomitant variables were statistically standardized using an analysis of covariance. A singificant decrease in milk intake was found from PRE to POST1, but there was no difference between samples for EN and POST1 (Table 3). From this we infer that PRE intakes were greater than those during the same month of EN. A strong correlation between growth rate and intake ($r = 0.72$, $P < 0.01$), supports this conclusion; the growth rate of pups was significantly lower during EN when compared with PRE, POST1, and POST2 (see next section).

Growth and mortality. Although there were no differences in mean birth measurements between years (<7 days of age), by the age of approximately two months (August) pups were larger in all other years compared to EN (Table 4). An ANOVA revealed significant differences with or without the effect of sex removed.

The weight gain of pups measured at both June and August weighings was significantly less in EN compared to all other years (PRE, POST1, POST2), when the effects of sex and initial weight were removed via ANCOVA (Table 4). Pup growth rate did not differ significantly between any other years.

Pup mortality increased during the El Niño year. Mortality of marked pups between late May and early August was 0% in PRE, 10.9% in EN, 2.2% in POST1, and 2.0% in POST2. These differences were significant for the PRE versus EN comparison ($P<0.01$, Fisher's Exact Test). For all pups observed, the apparent cause of death was starvation even though some pups were nursed by their mothers regularly.

Sexual differences. There were no differences in female attendance behavior associated with pup sex in any year. As noted above, the pup sex ratio did not differ significantly from 1:1 in EN. With one expection, there were no differences in behavior between male and female pups. Males spent a larger proportion of their time suckling ($\bar{x}=14.6\%$, $sd=3.3\%$) when compared to female pups ($\bar{x}=10.7$, $sd=3.6\%$) in POST1 ($P<0.05$, Mann-Whitney U with Bonferroni adjustment). Male pups received more milk per day than females in all years (Oftedal et al. 1987), however, a contrast analysis showed no difference in the magnitude of this difference between years (PRE and EN, $t=0.19$, $P=0.85$). The magnitude of growth rate differences between males and females did not change between years. Mortality did not differ between sexes in any year or for all years combined.

Effects on adult males

Male tenure. Since breeding males do not feed during their tenure on the reproductive areas, and migrate north after the breeding season, we did not expect to find any major behavioral differences in males as a result of the El Niño. As expected, male tenure (the number of days between the arrival and departure of a male on the reproductive area) did not differ between years. Males spent about 45 days on the study area in all four years. In addition we did not observe a decline in male numbers as seen in the Galapagos fur seal (Trillmich and Limberger 1985). The number of adult males on the study area remained approximately the same in all four years (1982–1985), and many of the same individually identifiable males were present in all four years.

Discussion

Maternal behavior

Our results show an impact of El Niño encompassing many aspects of female and pup biology. The shorter initial postpartum period of attendance in EN may have reflected poor reserves in females. Prepartum conditions appeared to be improved by POST1 in that the initial period of attendance by females was virtually identical to that of PRE and POST2. However, in POST1 the proportion of time females spent on the study area was closer to EN; females apparently still had to forage longer. Indeed, the values for POST1 were closer to EN than PRE in half of the comparisons, and intermediate to PRE and EN in half of the yearly comparisons presented here. This indicates a longer-term effect of El Niño on the sea lion population. It is evident that the sea lions were still under its influence during the 1984 breeding season. The impact was lessened, however, as evidenced by the increased growth rate and decreased mortality. The system appears to have recovered by 1985; the POST2 data show a high similarity to PRE (1982).

An increase in the duration of female feeding trips has been observed in other otariids experiencing El Niño. Further south, where El Niño effects were more pronounced, the duration of periods of absence increased in the Galapagos fur seal (*Arctocephalus galapagoensis*) and Southern sea lion (*Otaria byronia*) on the South American coast (Limberger et al. 1983; Trillmich and Limberger 1985).

Pup behavior, growth and sexual differences

Increases in the amount of time spent foraging as a response to food shortage has been observed in other species (Loy 1970; Muller-Schwarze et al. 1982). We also expected that pups should suckle more during the El Niño year, reflecting an increased "effort" to obtain milk. Contrary to expectations, pups suckled more in PRE than EN or POST1. The amount of time pups spent suckling, then, may instead reflect a positive relationship with the amount of milk mothers were producing, rather than reflecting effort on the part of pups. Trillmich (1986) found that suckling bout length correlated significantly with the amount of milk transferred to young in Galapagos fur seals. If this is also true for *Zalophus*, pups would simply have wasted energy by continuing to suckle after the depletion of this limited resource.

Sneak suckling represents an opportunity for pups to obtain additional nutrients as in the increase in foraging observed in other species, however, at some risk. Pups risk physical harm from being bitten or tossed by unrelated females while sneak suckling (pers. obs.). Therefore, sneak suckling includes a possible large cost with only a small probability of benefit, since most sneak suckling attempts by pups are unsuccessful. The increases in sneak suckling observed in EN and POST1 demonstrate that under nutritional stress, any additional nutrient input may be worth the risk.

Although pups were more active in PRE as expected, they did not rest more in EN. Part of this difference may be due to thermoregulatory constraints, that is, pups may have needed to move back and forth from the water more often during EN since maximum air temperature was warmer than for PRE. Also, the search for sneak suckling opportunities may drive pups to greater activity during an El Niño year, yielding less time spent resting. There was no difference in the amount of time pups spent swimming and playing in water between years. Development of swimming skills may be too important to pups to be curtailed for energy conservation purposes.

Other studies have shown that long-term food shortages and experimentally induced protein malnutrition have caused increases in aggressive encounters and decreases in play (Muller-Schwarze et al. 1982; Zimmerman et al. 1975; Dasmann and Taber 1956; Smart 1981). The decreases in play behavior from PRE to EN and POST1 found in our results are consistent with long-term food deprivation models. We found no differences in the proportion of time spent in aggressive encounters, but the nonsignificant trend was for an increase in EN and POST1.

Pup growth rate increased in POST1 when compared to EN, while food supply as measured by fisheries catches continued to decline. Many alternative hypotheses can be evoked to explain this result: perhaps other factors besides food supply are also responsible for the observed effects of El Niño, or fisheries statistics are not an accurate measurement of available sea lion prey. Fisheries statistics used for this comparison did not include catch as a function of effort. If fishing industry effort varied between years, the statistics may be misleading. Female sea lions may have become more adept at catching scarce prey, or may have shifted to other prey species by the second year. Females may also have had less competition for food in POST1 since fewer pups were born that year.

Since larger body size is more critical to adult males than to females in order for them to reproduce, we might expect male pups and mothers of male pups to put more effort into counterating the effects of EN. In other words, we might expect sexual differences in the extent of effect of EN. However, we found no systematic differences in the effect of EN on the sexes; EN appeared to affect male and female pups equally.

Population dynamics

Longer lasting effects on population parameters are indicated by these data. In concordance with our data, Heath and Francis (1984) found a 35% decrease in pup production in counts of all breeding beaches on San Nicolas Island in EN compared with PRE. The numbers of pups remained essentially the same in POST1 (1% decrease from EN) (J. Francis and C. Heath pers. comm.). In addition to this decrease in production, there was also an increase in pup mortality. Studies of other breeding areas on San Nicolas estimated pup mortality to be 11% in PRE and 17% in EN during the first few months of life (Heath and Francis 1983, 1984). High rates of mortality in the El Niño cohort continued throughout the year (unpubl. data), and were probably much higher than in other years due to the emaciated condition of pups observed as late as December. We also observed large numbers of emaciated *Zalophus* juveniles during the EN breeding season as well as later that year in December. Low production rates coupled with high mortality over the period of one or two years will have an impact on *Zalophus* given that this El Niño affected the entire breeding range of this species. Pinniped species residing farther south were even more severely impacted. Galapagos fur seals had an estimated 33% pup mortality during the El Niño season compared with 5% for "normal" years, and also suffered a dramatic decrease in pup production (11% of average) in the season immediately following El Niño (Trillmich and Limberger 1985). South American fur seals (*Arctocephalus australis*) were observed to have a pup mortality rate in excess of 40% (Limberger et al. 1983).

Future pup production may also be at risk. Heath and Francis (1984) found that the number of copulations on their study areas decreased 50% from PRE to EN and suggested that this might account for the low number of pups produced in subsequent years. This concurs with our observed decrease in copulation rate of 43%. Copulation rates have been observed to decrease in populations of other species undergoing food shortages (Loy 1970; Southwick 1967). This stands to reason in that nutritionally stressed females are known to defer estrus (Guilbert and Goss 1932; Lochmiller et al. 1986; Hafez 1974). If pregnancy and lactation during the El Niño year overtaxed females' resources, then we would expect a lower estrus rate.

The 1982–83 El Niño was an extremely strong event and the magnitude of effect observed was probably not typical. Weak El Niño events may have a negligible effect on *Zalophus* breeding on the Channel Islands, but El Niño events strong enough to adversely effect pinnipeds as far north as Año Nuevo Island, California (37° N, 122° W) may occur as often as every ten years (Ono unpubl. obs. on *Eumetopias jubatus*, 1972–73; McGowan 1984, Fig. 2; Gentry and Kooyman 1986, Fig. 1.1). Detrimental perturbations of this frequency may be quite important over evolutionary time. Gentry and Kooyman (1986) attribute many of the differences in life history patterns between temperate and tropical breeding otariids to the environmental uncertainty imposed by recurrent El Niño events.

In conclusion, there were consistent changes in many aspects of mother and pup behavior and biology in relation to the 1982–83 El Niño event, attributable to decreases in food availability for pregnant and lactating female sea lions. The short-term or individual parameters appear to have returned to "pre-El Niño" values in the 1985 season. Our data also demonstrate the long-lasting nature of these effects, however; for population parameters, the return of this and other affected pinniped populations to "pre-El Niño" values will probably take many years.

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