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Drastic effects of El Niño on Galapagos pinnipeds

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Summary. Population dynamics of pinnipeds living in the tropical upwelling ecosystem of the Galapagos were strongly influenced by the 1982–83 Southern Oscillation-El Niño (EN) event which was the strongest recorded in this century. The Galapagos fur seal (*Arctocephalus galapagoensis*) population lost the four youngest year classes (1980–1983) almost entirely and approximately 30% of the adult females and non-territorial males. Mortality of large territorial males was almost 100%. Most of the 1982 year class of Galapagos sea lions (*Zalophus californianus wollebaeki*) died and there was a much lower pup production in the breeding season following EN. Recurrent EN events must strongly influence age structure and average population size of these and other otariid species depending on tropical upwelling ecosystems.

El Niño (EN) events occur in the eastern tropical Pacific at irregular intervals, on average about once every 4 years. The strongest EN in this century was recorded between August 1982 and July 1983 (Arkin et al. 1983, Cane 1983, Rasmusson and Wallace 1983). During EN the southeast trade winds decrease or disappear, the flows of the Peru, South Equatorial and Cromwell counter-current diminish and warm waters accumulate in the eastern tropical Pacific (Wyrtki 1982). In Galapagos the arrival of EN was signalled by high sea surface temperatures due to reduced upwelling, heavy rainfall and a 30 cm increase in sea level. The causal chain of events leading from oceanographic changes to reduced primary and secondary productivity and the effect of reduced food abundance on sea bird populations are well documented (Idyll 1973, Barber and Chavez 1983, Schreiber and Schreiber 1984). The consequences of EN for marine mammals, however, are largely unknown (Limberger et al. 1983). We give the first detailed report of the effect of EN on the population of a marine mammal, based on our long term study of Galapagos fur seals at Cabo Hammond, Fernandina and some additional observations on Galapagos sea lions.

Material and methods

Galapagos fur seals were studied during their reproductive season (Aug–Nov) at Cabo Hammond, Fernandina; observations were made annually between 1976 and 1984, with the exception of 1978. Beginning in 1979 yearlings and older fur seals were permanently marked with Allflex tags applied to the trailing edge of the foreflipper. During the field seasons much less systematic observations on Galapagos sea lions were also gathered.

We interpret the disappearance of large numbers of fur seals from Fernandina as mortality because (1) the seals are not known to migrate away from the Galapagos, (2) within the Galapagos islands Fernandina is one of the coldest and therefore most suitable areas, making it unlikely that dispersal away from this area was greater than immigration into it, and (3) no tagged animals that disappeared during EN reappeared later.

Results

1. The Galapagos fur seal

Galapagos fur seals reproduce between Aug. and Nov. Females give birth to a single young. Mothers alternate bouts of suckling on shore (about 1 day) with foraging trips of 1 to 4 days. Females forage close to shore, presumably within the area of intense upwelling. They dive only at night, usually to depths of less than 30 m. Young are weaned when about 2 years old (Kooyman and Trillmich 1985a, Trillmich 1981, 1984, 1985a).

In 1979–81 about 80% of marked non-nursing females gave birth ($n=12$). During the early period of EN, in 1982, pup production appeared normal, but in Sep./Oct. 1983, shortly after the EN had ceased, pup production was only 11% of average (Table 1). In 1982 six pups, a few days old, were 9% lighter than predicted by the regression of pup growth on age derived from the 1979–1981 data (weight (g) versus age over the first 60 days of life is (i) for males: $w=57.9\,x+3879$ ($n=214$), (ii) for females: $w=42.7\,x+3661$ ($n=134$). Similarly, newborn pups in 1983 were about 10% lighter than those of 1981. Male pups weighed 3.3 ± 0.2 kg 1983 ($n=4$) versus 3.85 ± 0.4 kg in 1981 ($n=12$) ($p<0.02$) and female pups 3.06 ± 0.34 kg in 1983 ($n=10$) versus 3.35 ± 0.2 kg in 1981 ($n=11$) ($p=0.05$, both Mann Whitney U test). During EN females remained at sea for longer periods (Fig. 1) than had ever been measured, and pups were soon undernourished. After EN female absences were shorter again (Fig. 1). In 1979–81 about 95% of the pups survived the first month of life, and about 80% survived the first year (Trillmich 1985b). In contrast, during

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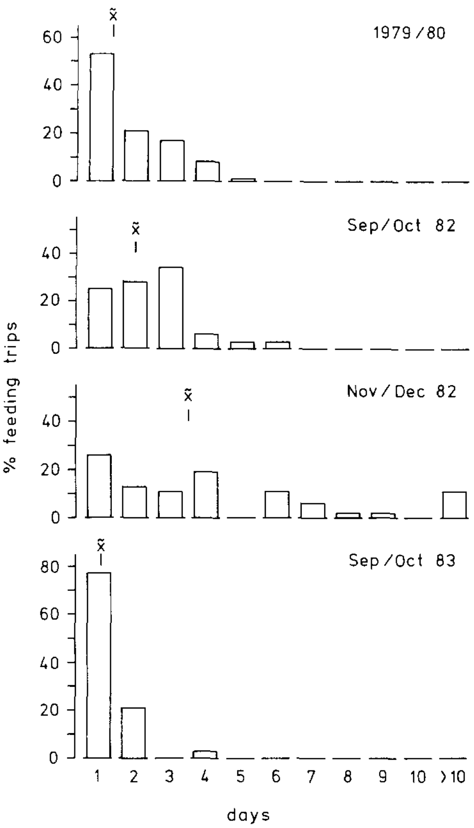

Fig. 1. Distribution of female feeding trip durations measured to the nearest day. Oct. to Nov. 1979/80 median is 1.3 days (*n* = 131), Sep/Oct 1982 median 2 days (*n* = 32), Nov/Dec 1982 median 3.5 days (*n* = 54), and Sep/Oct 1983 median 0.6 days (*n* = 39). Pre- and post-EN distributions are significantly different from distributions during EN

Table 1. Maximal number of fur seals of each age/sex class counted in the study area (180 m coastline) during the peak of the reproductive seasons in Sep/Oct 1979–81 and 1983. — : no data

Year	Territorial males	Other males	Adult females	1–3 year olds	Pups[a]
1979	15	25	132	164	162
1980	14	18	118	112	228
1981	15	32	146	120	—[b]
1983	3	17	96	1	21
1983 as percent of average 1979–81	21	68	73	0.8	11

[a] total pup production over 530 m coastline
[b] pups present in large numbers, but no count made

Table 2. Number of sea lion pups and yearlings in study areas on several islands in 1983 compared to earlier years. — : no data

Island	Date	No. of pups	No. of yearlings
Caamano	Oct. 21, 1976	53	34
(Santa	Nov. 5, 1977	45	42
Cruz)	Oct. 31, 1983	14 (29%)[a]	7 (18%)[a]
Fernandina	Nov. 7, 1977	93	42
	Oct. 2, 1983	6 (6%)	3 (4%)
Santa Fe[b]	Dec. 25, 1981	149	—
	Dec. 26, 1982	140	—
	Dec. 29, 1983	94 (65%)	—
Santiago	Sep. 11, 1976	94	—
	Nov. 16, 1977	54	—
	Oct. 26, 1983	2 (3%)	—
South Plaza	Nov. 17, 1976[c]	202	—
	Oct. 29, 1983	60 (30%)	—

[a] 1983 census as percent of average number in earlier counts
[b] Andrew Laurie pers. comm.
[c] Birgit Voigt pers. comm.

EN, in late 1982, only 67% survived the first month of life and 100% had died within five months after birth (*n* = 18). Only 2 yearlings were found in the entire colony of about 200 females after EN in Sep/Oct 1983 indicating that almost all pups born in 1982 had died. First-month survival of 21 pups born in 1983 was 90% again.

The effects of EN were also apparent on the yearlings, which were still largely dependent on their mothers in 1982. According to daily observations, 7 of the 9 regularly observed yearlings disappeared between Jan. and March, 1983. The previous emaciated appearance of these animals suggests that they had died from starvation. After EN had subsided in late 1983, we searched the same area and found no survivors of this age class. Animals born in 1980, about 2 years old at the onset of EN, initially seemed to have survived better than the yearlings: of the 13 regularly observed individuals only 3 had disappeared by March 1983. However, at the end of EN in Sep/Oct 1983 this year class, of which 143 had been tagged, was also entirely missing. Pups born in 1979 and about 3 years old at the onset of EN were also affected, although they had been weaned before it began. Of the 18 tagged individuals resighted in late 1982 only 6 (33%) were seen again in late 1983.

Animals larger than 3-year olds were classified as adults. The maximal number of adult females in late 1983 amounted to 73% of the maxima of previous years (Table 1). The number of Galapagos fur seals ashore varies with the lunar cycle (Trillmich and Mohren 1981). Comparable data, covering the complete lunar cycle exist for 1979 and 1983. A Fourier analysis of number of females ashore versus lunar phase was made and the maxima of the resulting Fourier syntheses for 1979 and 1983 were then compared. From this comparison the numbers of females in 1983 were estimated to be only 66% of the 1979 value.

The effect of EN on the population of males of maximal size was even more dramatic. In 1980 and 1981 we recorded 31 and 32 large males holding territory during at least part of the reproductive period. In 1982 no count of males was made, but approximately the same number was present; but in the 1983 reproductive season, after EN, there were no maximally-sized males in our study area. Only 1 or 2 were seen in the entire population, although it appears that all females were reproductively active. The disappearance of maximally-sized males that were territorial in 1982, implies a close to 100% mortality. In 1983 only 5 males, clearly smaller than average territorial males, established dominance status at some time during the reproductive season over about 800 m^2, whereas average territory size is 200 m^2

(Trillmich 1984). This made it impossible for them to exclude other males. Consequently many small males copulated with females. These small males apparently suffered no more mortality during EN than the adult females (Table 1).

2. The Galapagos sea lion

Our information about EN effects on the Galapagos sea lion is based on less systematic observations. Sea lion females weigh about 80 kg (nearly three times as much as Galapagos fur seal females), stay away from their pups for about 1 day and forage during the day, mainly at depths between 20 and 60 m (Kooyman and Trillmich 1985b, Trillmich 1985c).

In 1977 Galapagos sea lion pup mortality before 7 months of age was 5% in a study colony on Santiago ($n=20$), and the same during the first 2 months of life on Fernandina ($n=19$). During EN in Feb. 1983 pups began to show signs of starvation (Limberger et al. 1983), and between Feb. and April 1983 sea lion pup mortality increased rapidly on Santa Fe island where only 19 of 140 pups survived the first 5 months (A. Laurie pers comm). During March and April 1983 most pups on Santa Fe were abandoned by their mothers and starved to death. After EN yearling sea lions were extremely scarce on all islands which we visited, and the two quantitative comparisons possible (Table 2) showed that the yearling age class was reduced to between 5 and 20% of its normal size. Pup production in 1983 was less than 30% of normal on most of the islands censused, but varied widely from colony to colony (Table 2). The effect of EN on adult numbers was not determined.

Discussion

Most of the surviving females could not accrue enough resources to sustain the added energetic cost of pregnancy under EN conditions. This is shown by reduced pup production in both species and reduced birth weights of the few pups born in the Galapagos fur seal colony. The unusually long nursing period of about 2 years (Trillmich 1981) may buffer young fur seals against minor EN-events which occur frequently enough (Cane 1983, Quinn and Zopf 1984) to make extended lactation a useful maternal adaptation against environmental uncertainty. Galapagos sea lion females also nurse for about 1 year, longer than mothers in the Californian population (about 9 months). However, during the recent EN food resources deteriorated to such an extent (Feldman et al. 1984) that even this strategy could not save dependent young from starvation. As young, small seals are presumably less efficient divers than adults (Kooyman et al. 1983, Gentry et al. 1985) they were also unable to sustain themselves by independent foraging. Under EN conditions, in late 1982-early 1983, territorial fur seal males apparently could not recover from their weight loss during territory tenure and suffered almost 100% mortality. This indicates that even under less severe conditions there may be a significant cost to fasting during the reproductive season.

Yearling sea lions weigh almost as much as adult female fur seals (ca. 25 versus 27 kg) and adult fur seal males as much as small adult sea lion females (ca. 60 versus 50–100 kg). Nevertheless neither yearling sea lions nor adult male for seals survived EN, indicating their inability to switch to the other species' feeding technique. This suggests either a phenotypic or genetic (physiological, morphological or behavioral) constraint allowing sea lions to hunt more effectively during the day and fur seals during the night.

Strong EN events create dramatic discontinuities in the age structure of these long-lived mammals and must have large effects on the future reproductive output of populations. However, not every EN has such profound effects on Galapagos pinnipeds. During the weak 1976 EN no exceptional starvation mortality was noticed in pups of either species. There were no deaths amongst 12 Galapagos fur seal pups observed during Dec 1976 and only 17% of the 30 Galapagos sea lion pups observed during Oct 1976 died. Thus only strong EN events may lead to increased mortality in populations of tropical marine mammal populations which depend on upwelling ecosystems. Nevertheless, besides imposing density-independent mortality, by reducing resource levels EN events also decrease the average carrying capacity of the environment. They may thus contribute to keeping tropical otariid populations much smaller than those of similar temperate or sub-polar species.

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