6 The Effects of El Niño on Galapagos Pinnipeds

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6.1 Introduction

The effects of the 1982–83 El Niño (EN) were most severe in the eastern tropical Pacific (see Fahrbach et al. and Arntz et al., this Vol.) and the seal populations in the area of Galapagos and Peru suffered most from the impact of this event. The ocean around the Galapagos warmed rapidly in September 1982 and remained warm until July 1983 with a short, somewhat cooler period in February/March 1983.

The climate of the Galapagos islands is seasonal despite the islands' position at the equator. During the cold season, from about May to December, waters around the archipelago are cool and upwelling along the western islands is strong, whilst during the warm season, from about January to April, water temperature increases and upwelling is diminished. This seasonal cycle comes about by the movement of the intertropical convergence zone which lies N of the islands in the cool season, but moves S during the warm season bringing the northeasternmost islands under the influence of warmer waters. A coincident drop in the strength of the southeastern trade winds weakens the Humboldt current which leads to reduced influx of cold water and this in turn slows the flow of the Cromwell countercurrent which upwells on the coasts of the western islands (Fahrbach et al., this Vol.).

Here, we describe the influence of EN on the Galapagos populations of fur seals (*Arctocephalus galapagoensis*) and sea lions (Zalophus californianus wollebaeki). Fur seals and sea lions reproduce predominantly during the cold season. The 1982–83 EN most severely affected these species during the 1982 breeding season. We summarize previously published material (Limberger et al. 1983; Limberger 1985; Trillmich 1985; Trillmich and Limberger 1985) and then address the long-term effects of EN on the two populations. Place names are shown in Fig. 1.

6.1.1 Background Information on the Natural History of the Galapagos Species

The Galapagos fur seal is nonmigratory and stays close to its breeding colonies year-round. Adult females of this species weigh about 30 kg and adult, territorial males between 60 and 70 kg (Trillmich 1987). This species thus shows the least sexual size dimorphism of any fur seal. Reproduction takes place between August and November, the local cold season. Females alternate between 1–2 day periods

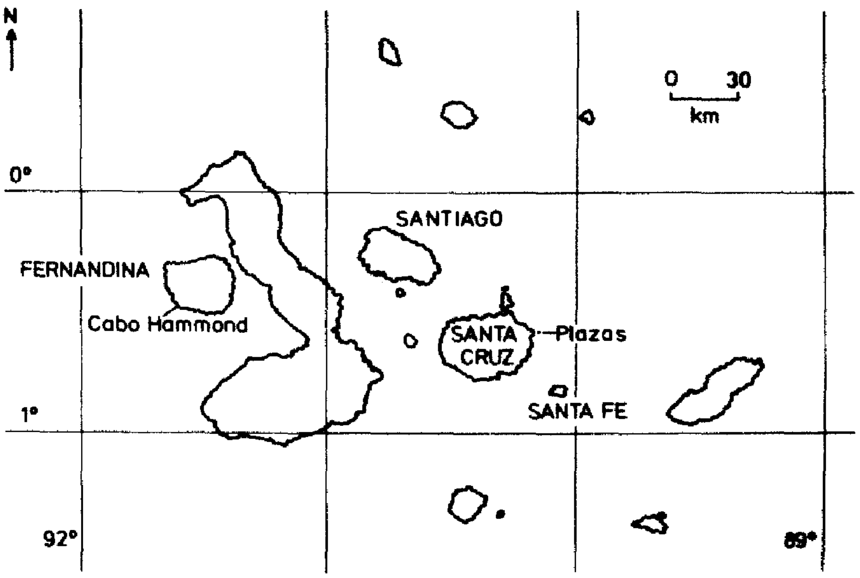

Fig. 1. Map of the Galapagos sites mentioned in the text

ashore, nursing the pup, and 1–4 day periods away, foraging at sea and resting elsewhere. Galapagos fur seals feed during the night on organisms which ascend to the ocean's surface during the dark hours from the deep scattering layer (Dellinger 1987). In most years young are weaned when about 2 years old (Trillmich 1986a).

Galapagos sea lion females weigh about 80 kg. No adult male weights are available. Mothers usually forage during the daytime (Trillmich 1986c) and are absent on foraging trips for about 1 day. Sardines are their staple food (Dellinger 1987). Galapagos sea lions, just like the fur seals, reproduce mainly during the cold season with the peak of births occurring between October and November. However, the pupping season of the sea lion lasts much longer, in the extreme case of the Plaza Islands (in the center of the archipelago, Fig. 1) from about June of one year to March of the next. On Santiago, in 1977, pups were born from June to September; on Santa Fé and Fernandina sea lions pup from about October to January. Young are suckled for about 1 year, but if a mother does not pup after 1 year, suckling may be continued for up to 3 years.

6.2 Methods

Galapagos fur seals were studied from 1976 to 1985, and in March/April 1986 at Cabo Hammond (0°28'S, 91°37'W) on Fernandina Island, the westernmost island of the Galapagos. Observations were made every year, except for 1978, during the reproductive season from approximately September-November and during the warm seasons of 1978 (February) and 1986 (March and April). The fur seal study site extended over a section of coastline of about 800 m of which 180 m were censused regularly (for further methodological details, see Trillmich and Limberger 1985).

During these field seasons much less systematic observations were gathered on a nearby sea lion colony which comprised about 150 animals living on a flat rocky shelf with a number of tide pools.

The diet of these species was determined from scats collected during the 1983–85 cold seasons (Dellinger 1987).

6.3 Results

6.3.1 The Galapagos Fur Seal

Pup production in the study area at Cabo Hammond fluctuated at around 200 pups per year from 1979–1982 (Fig. 2). For the years 1981 and 1982 no exact pup counts are available, but the observers' impression was that these were years of normal pup production. In contrast, pup production in September-October 1983, right after the end of EN, was only 11% of normal (Fig. 2). In 1984 a large number of pups were born, but in 1985 pup production was about half of the pre-EN level (Fig. 2). This effect was caused by the synchronizing effect of EN on the reproductive status of fur seal females: in normal years about half of all females suckle yearlings or 2-year-olds and, as a consequence of the energetic stress of lactation, the majority of them do not produce a pup (Trillmich 1986b). Thus, before EN, only about half of the reproductive females produced a pup in any given year. During EN, in 1982, all females lost their pups, due to starvation, and very few produced one in 1983 so that nearly all of them lived without the energetic drain of lactation for all of 1983 and most of 1984, up to the reproductive season in September-October. Nearly 100% of the adult females pupped in 1984, but then many of them did not pup again in 1985 due to the lactation effort. Therefore, 1985 pup production is more comparable to production before EN than production in 1984. Thus, the 1985 pup number can be

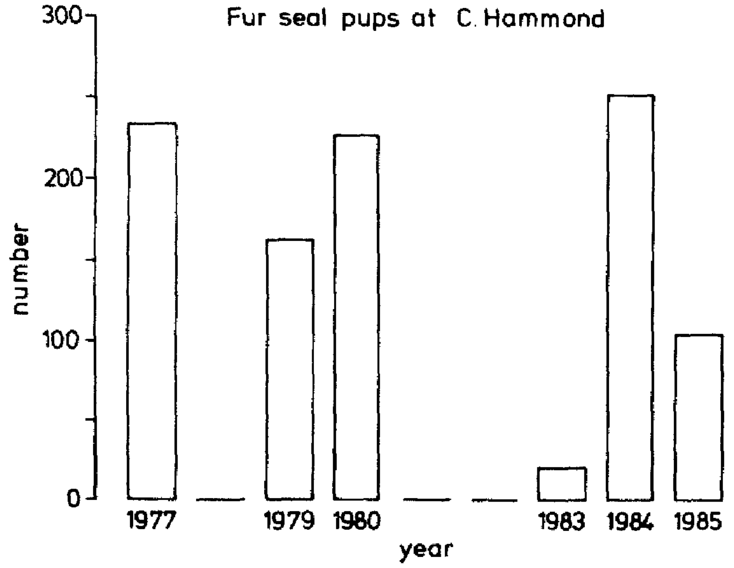

Fig. 2. Pup numbers of the Galapagos fur seal at the Cabo Hammond study site on Fernandina. No data available for the years 1978, 1981, and 1982

used as another index of the decrease in the number of reproductive females due to EN. This would indicate a ca. 50% decrease of adult females (Fig. 2).

The mean mass of newborn pups produced in 1982 and 1983 was about 10% lower than in normal years (Trillmich and Limberger 1985). Most of the pups born in 1982 lost weight rapidly before starving to death. The pups of the 1983 cohort, born about 2 months after the end of EN, grew normally.

Thirty-three percent of the pups born in 1982 died during their first month of life and 100% were dead after 5 months. In contrast, 90% of the pups born shortly after the end of EN in 1983 survived the first month as observed in other "normal" years. During the period of September 1982 to March 1983, both 1- and 2-year-olds, from the 1980 and 1981 year classes, of which many were tagged, suffered 100% mortality and about 70% of the 1979 year class (3-year-olds) also perished (Trillmich and Limberger 1985). Figure 3 (upper panel) roughly illustrates the fate of the 1979–1982 cohorts.

The reason for starvation of pups and dependent juveniles during EN in 1982–83 lies in the unusually long (foraging) absences of mothers. Absence duration of females during the cold (breeding) season from August-November varied little between years; females rarely stayed away for more than 4 days (Fig. 4a,b). During EN 1982, at a time of year which is normally the Galapagos cold season, mean absence duration lengthened significantly (Mann-Whitney U-test; $p < 0.01$) and variance in absence duration increased drastically (Fig. 4c). Interestingly, mean absence duration during the 1986 warm (nonbreeding) season was even slightly longer than during EN, but the variance of the warm season data was much smaller (Fig. 4d; F-test; $F_{54,27} = 8.3$, $p < 0.001$).

Between 1979 and 1981 the maximal number of adult females censused ashore in the study site averaged 132. In 1983 this number declined to about 70% of its former value (Trillmich and Limberger 1985). By 1984 numbers returned to pre-EN

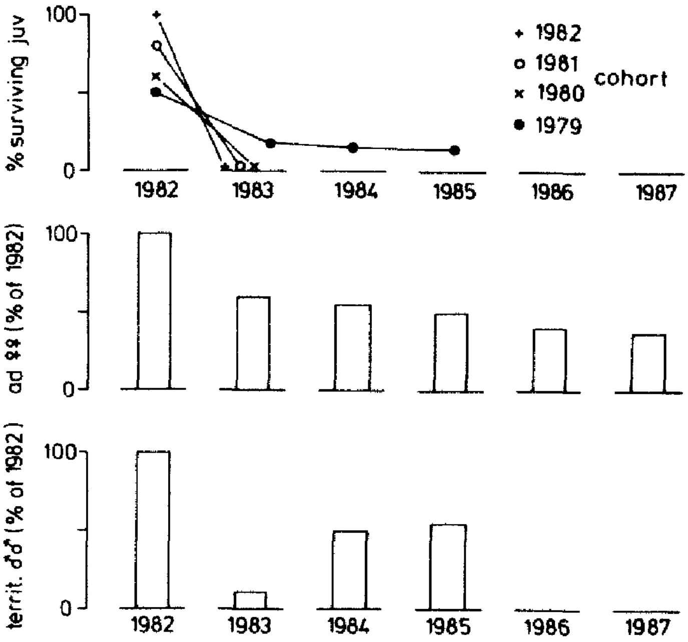

Fig. 3. A graphic summary of EN effects. *Upper panel*: the percentage of juveniles surviving from the cohorts 1979–1982. No data for 1986 and 1987. Estimated survival of a given cohort to 1982 is taken into account; therefore, the various cohorts begin at different percentages of juveniles surviving at the beginning of EN. *Middle panel*: effects on the number of mature females relative to the numbers in 1982. *Lower panel*: effects on the number of territorial males in the study area relative to those in 1982. No data for 1986 and 1987

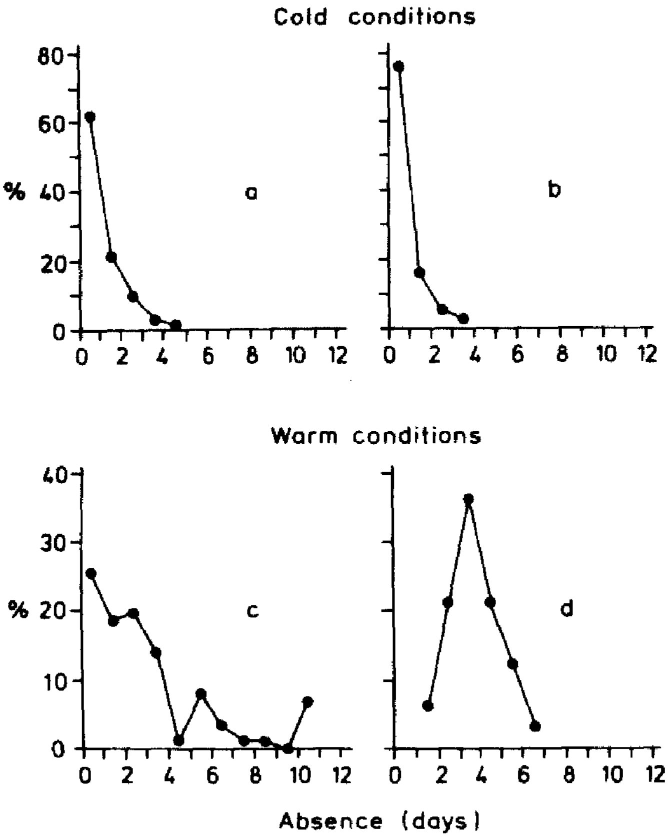

Fig. 4a-d. Comparison of the distributions of the duration of maternal absence under cold and warm conditions. **a** (*Upper left*) values from the months Sept.-Nov. 1979, 1980, 1981, 1984, 1985 (n = 345 trips). **b** (*Upper right*) values from Sept.-Nov. 1983, immediately after the end of EN effects (n = 38). **c** (*Lower left*) values during EN-related warm conditions in Sept.-Dec. 1982 (n = 86). **d** (*Lower right*) values from February 1978 and March-April 1986 (n = 33), normal warm seasons

levels in the study area: the maximal number counted was 155 females; but large surrounding areas of fur seal habitat, which had been used by fur seals in former years, remained empty. Apparently, the reduced population had concentrated into the most suitable habitat. If we estimate the reduction in female numbers from the 1985 pup production (see above), 50% of the adult female population may have been lost during EN. Figure 3 (middle panel) shows these estimates and indicates that due to the loss of the 1980–1983 cohorts, the number of adult females must have kept declining at least until 1987 when the first females of the 1984 cohort may have matured.

In contrast to adult females, territorial males suffered close to 100% mortality during EN. In 1980 and 1981 we recorded 31 to 32 males, respectively, holding territories of about 200 m^2 each in our study area (Trillmich 1984). Males fast for up to 6 weeks while holding territories during the reproductive season between August and November. In 1982 about the same number of territorial males appeared to be present. At the end of their fast these males returned to a warm ocean which was apparently providing very sparse food supplies, as also evidenced by the unusually long foraging absences of mothers with pups (see above; Fig. 4). None of these males were observed again in the 1983 breeding season, immediately after the end of EN; they all must have starved to death. Instead, only five smaller males, of about 80% of normal breeding-male size (which in other years would have been categorized as subadult males) established dominance status over huge areas of about 800 m^2, and males of female size, i.e., less than half the mass of normal breeding males, were able to sneak many copulations during this season (Trillmich and Limberger 1985). By 1984, 15 bigger males were in the study area and the territorial system, except for unusually large territory sizes, was established again. This trend continued into 1984 (see Fig. 3, lowest panel). Two of the males observed in 1984 had been tagged as subadults before EN and had obviously grown at an increased rate between the 1983 and the 1984 reproductive season.

6.3.2 The Galapagos Sea Lion

The most complete data set on pup production and mortality during EN stems from Santa Fé (A. Laurie, pers. comm.). About 145 pups were born there in 1981 and 1982 (Table 1). Although the sea surface temperature began rising in September 1982, this had no noticeable impact on pup production in 1982. However, pup production in 1983 was about 30% lower than in previous years (Table 1). The breeding season also began later, as we only counted 26 pups on November 2, 1983 (Trillmich and Limberger 1985), whereas in previous years about 50% of the pups were already born by that date. The number of pups born in 1984 was the same as before EN, but in 1985 it declined to roughly 74% of the pre-EN value (Table 1). Presumably, a synchronization effect, as described above for the fur seals, influenced sea lion pupping on Santa Fé as well.

Pup production in 1983, after the end of EN, varied widely between colonies on different islands with a highest value of 65% of pre-EN values on Santa Fé, an island where sea lions produce their pups late in the year, and a low of only 3% of the pre-EN value of Santiago. Only six pups were born in the Fernandina colony where in former years more than 100 had been born. Similar to the fur seals, sea lions on Fernandina produced unusually many pups (166) in 1984, but only 97 were born in 1985.

The survival of pups born in 1982 was much lower than usual. Normal pup mortality during the first 6 months of life is about 5% (Trillmich and Limberger 1985). On Santa Fé, mothers abandoned their pups in March-May 1983, when oceanographic EN effects reached a second peak (Fahrbach et al., this Vol.). Only 19 (14%) of the 140 pups counted in December 1982 were still alive by April 1983. During the 1982–83 EN, pups on Fernandina began to show signs of starvation in February 1983, shortly after the first peak of EN and only about 4% of the pups born in 1982 survived to the age of 1 year.

Table 1. Sea lion pup counts on Santa Fé (data courtesy of A. Laurie)

Date	Pup number
Dec. 29, 1981	149
Dec. 26, 1982	140
Dec. 29, 1983	94
Dec. 29, 1984	140
Dec. 31, 1985	108

High yearling mortality apparently occurred throughout the Galapagos during EN, in late 1982 and early 1983. Counts in October 1983 on various islands showed that the 1982 yearling cohort was reduced to between 5 and 20% of the size of previous cohorts. The 20% value most likely is an overestimate of actual survival rate, since sea lions moved, just like fur seals, from less preferred into better habitats after EN.

Adult numbers clearly decreased during EN, but no censuses are available. Assuming that the number of pups born in 1985 of Santa Fé (Table 1) can serve as an index to the number of adult females left after EN, it seems likely that about 20% of the adult sea lion females died. Robinson (1985) had the impression that the so-called sea lion pox disease (the infectious agent responsible for the disease is unknown) became much more prevalent during 1982–83 and killed many animals. Inhabitants of the Galapagos also saw many dead adult animals, and their reports suggest that the mortality of territorial males was particularly severe.

6.4 Discussion

During EN decreased upwelling, increased sea surface temperatures and a depressed thermocline all contributed to a rapid depletion of nutrients for phytoplankton growth (Kogelschatz et al. 1985). This in turn led to reductions in zooplankton. Finally, fish starved, died, and emigrated or migrated to greater depths. There are no data on pelagic fish for the Galapagos area. However, Feldman et al. (1984) have shown that the phytoplankton concentration around the western islands was still high (>1 mg m^{-3}) in February 1983, but had decreased dramatically by March 1983. This is exactly the time when the first signs of starvation became noticeable in Galapagos sea lion pups on Fernandina (Limberger 1985), suggesting that sardine availability decreased around this time. Barber and Chávez (1986) reported a decrease of sardine catches to almost zero in mainland Ecuadoran waters. Local Galapagos fishermen claimed that benthic fish disappeared from their usual depth but returned immediately after EN, indicating that many fish indeed migrated to greater depths during the warm water phase.

Fish living in the deep scattering layer are the main food resource of the fur seals which hunt for this prey when vertical migration brings it near the surface at night. In normal cold seasons Galapagos fur seals feed mostly on myctophid and, to a lesser extent, on bathylagid fish (Table 2; Dellinger 1987). The starvation of pups and adults alike suggests that these fish either died or moved to a depth where they could not be reached easily or in sufficient quantity. After EN, in late 1983, fur seals fed on unusual prey such as sardine (*Sardinops sagax*; 6% of otoliths) and *Selene declivifrons* (5%), suggesting that myctophids – although representing the majority of the prey with 81% (Table 2) – were still not as abundant or energy-dense as in other years. Apparently, the recruitment of myctophids failed during 1983 leading to reduced availability of this prey type in 1984. Bathylagids then became a more dominant part of the fur seals' prey (Table 2). But, in both 1984 and 1985, fur seals were again feeding almost exclusively on organisms from the deep scattering layer.

Table 2. Numerical composition of Galapagos fur seal and Galapagos sea lion food during the cold seasons 1983–85. Data are given as percent of total numbers of otoliths found in scats (lowest line). Only the most frequent prey items are listed for a minimum of 90% (numerically) of the diet

	Fur seal			Sea lion		
	1983	1984	1985	1983	1984	1985
Myctophidae	81.0	41.7	77.4	0.2	1.0	0.6
Bathylagidae	4.7	56.8	21.6	–	0.6	–
Sardinops sagax	6.2	0.4	0.2	70.7	74.8	84.8
Chlorophthalmus sp.	–	–	0.1	23.1	21.1	5.0
No identified "type 34"	–		–	–	–	4.5
Total otoliths (n)	4545	3136	4766	416	659	1450

The diet of Galapagos sea lions is always dominated by sardines which contribute over 70% by number of otoliths to the diet (Dellinger 1987). However, *Chlorophthalmus* sp. (presumably *agassizii*; T. Hecht, pers. comm.) contributed 23% and 21% of the diet in 1983 and 1984, but only 5% in 1985 when the proportion of sardine otoliths reached 85% (Table 2). Apparently, as a consequence of EN, there was some shift in sea lion food resources as well. In October 1983, shortly after the end of EN, sea lions regurgitated more frequently than observed in previous or later years, actually vomiting whole stomach-fulls of partly digested sardines. Only at that time did we find about as many spewings as scats on land, an observation which may indicate illness or overeating of the previously starved sea lions.

In both species reduced food availability during EN made it far more difficult for mothers to gather sufficient food for their own and their pup's metabolic needs. Fur seals were probably affected more severely than sea lions since the former appear to forage farther away from the coast and can spend less time under water. Judging from the time they need from leaving the coast until foraging dive bouts begin, sea lions forage roughly 4–5 km from the colony (at least near Fernandina), while fur seal mothers travel about 16 km before they begin to forage (Kooyman and Trillmich 1986a,b). During EN, the cost of foraging became so high that fur seal mothers reduced the numbers of round trips and stayed at sea for very prolonged periods. The mothers' absence times exceeded their pups' fasting abilities. Females still returned and nursed their pups, but it seems like that milk transfer was minimal. In the otariid rearing strategy the effect of food shortage thus becomes immediately noticeable during pup rearing since mothers cannot rely on fat reserves gathered prior to the pup rearing period as phocids do (see Trillmich et al., this Vol.).

Larger pinnipeds can stay under water longer than small ones (Gentry et al. 1986a). If fur seal and sea lion prey stayed at greater depth and/or decreased in abundance during El Niño, then yearlings of both species would have had more difficulty catching prey than conspecific adults. This could explain the much higher mortality rates of juveniles, and perhaps, the more dramatic mortality observed in the smaller species, the fur seal.

Extrapolating from our study site, the 1982–83 EN has caused a loss of three cohorts in fur seals and a reduction in the size of two cohorts in sea lions. This extrapolation is probably an underestimate of the population reduction, as the ocean area around Fernandina is the most productive within the Galapagos archipelago. Loss of whole cohorts through exceptionally strong ENs is a rare and random event. If such an event does not reduce the pinniped populations to a very small size (on the order of 100 or less productive females), sampling drift is unlikely to significantly influence the evolution of the species. However, a reduction in the size of cohorts could po- tentially be a very strong selective agent. For example, slow growing young may survive better during food stress due to lower energy and material requirements.

The differential mortality of most large, territorial males in 1982, as observed for fur seals and suspected for sea lions, may influence selection for sexual size dimorphism. In otariid pinnipeds sexual selection through male-male conflict favors males large in size, because only large males can successfully fight for and maintain territories during the reproductive season. Repeated natural (survival) selection against exactly these largest males during periods of EN-induced food shortages will oppose sexual selection for ever-increasing male size. This could explain why the Galapagos fur seal, and most likely the Galapagos sea lion as well, have much less sexual dimorphism in body size than their close relatives in cooler environments.

Lastly, EN events occur unpredictably over the lifetime of a female. Aperiodic unpredictable reductions in food availability could select females to maintain larger body reserves at the cost of a reduction in pup growth and survival since the survival of the mother is far more important to her lifetime reproductive success than the survival and rapid growth of a given pup. This could explain the evolution of an extreme phenotypic flexibility of pup growth rate and time to weaning as found in the Galapagos fur seal.

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