23 Biological Effects Associated with El Niño Southern Oscillation, 1982–83, on Northern Elephant Seals Breeding at Año Nuevo, California

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23.1 Introduction

This chapter presents vital statistics on northern elephant seals, *Mirounga angustirostris*, inhabiting the rookery at Año Nuevo, California over a period that included EN 1982–83. Our approach involves comparisons of baseline data collected routinely in the years before, during, and after EN 1982–83. Specifically, we examine:

1. Direct effects on mortality and distribution of adults caused by a rise in sea surface level, high coastal winds, high surf, and winter storms associated with El Niño (Fahrbach et al., this Vol.), and
2. Indirect or long-term effects on mortality, reproduction, and foraging effort associated with fluctuations in water currents, upwelling, and water temperature—perturbations that might have caused changes in the composition, distribution, abundance, and availability of the food base of these phocids (Arntz et al., this Vol.).

Northern elephant seals are deep-diving pelagic seals that forage along the continental slope from mid-Baja California, Mexico to southern Alaskan waters. Depending on sex and age, individuals remain at sea for 2.5 to 8 months at a time. During the 2.5-month period at sea following lactation, adult females dive virtually continuously to mean depths in the range, 400 to 700 m (Le Boeuf et al. 1986, 1988, 1989b; Naito et al. 1989). Females average 2.5 to 3 dives per hour around the clock; 99% of these dives are to depths greater than 200 m. It is clear that much of the time spent diving is spent feeding because all females studied increased their mass over the period at sea. Seven females monitored in 1985 and 1986 gained a mean of 76.5 ± 13.9 kg during a mean of 72.5 ± 5.0 days at sea (Le Boeuf et al. 1988).

Given their deep-diving habits, one might expect elephant seals to be less affected by fluctuations in sea temperature, sea level, and currents than shallow water feeding sea lions. EN 1982–83 seemed to have less of an effect on deep-water organisms, which comprises most elephant seal prey, than on organisms living close to the surface that sea lions exploit. Thus, one might predict that the weather and sea perturbations that influenced the distribution of marine life during EN 1982–83 had a less deleterious effect on elephant seals than on Pacific coast sea lions and fur seals. We test this prediction.
23.2 Methods and Background Information

We were in a good position to assess the effects of EN 1982–83 on the elephant seals at Año Nuevo because the colony has been under close observation every breeding season since 1968. In 1975, when elephant seals began breeding on the mainland, the study was enlarged to cover both the mainland and the island. The long-term study involves routine monitoring of data such as the following: number of pups born, weaned and pup mortality rate; number and distribution of adults and juveniles; fecundity and reproductive success of marked known-age females and the sex ratio of pups produced; and the length of the foraging trip to sea by marked females following breeding.

In general, observations were continuous throughout daylight hours on both the island and the mainland during the entire breeding season from mid-December to mid-March, and observations were conducted approximately once a week during the rest of the year. Censuses and monitoring of pup deaths were conducted daily during each breeding season.

For most analyses, we attempt to compare the data from El Niño years to those of preceding and succeeding years.

23.3 Direct Immediate Effects

Mortality Due to Storms. On three consecutive days, from 27 to 29 January 1983, giant storm-driven waves cresting above the year’s highest tides smashed the coast of California. The surf pounded Año Nuevo island and the mainland at the peak of the breeding season, a time when the maximum number of females were giving birth and nursing their pups. The scene on Año Nuevo Island (Fig. 1) was described as follows (Le Boeuf and Condit 1983, p. 14):

“The Año Nuevo Island rookery was packed with animals when giant waves curling over a 6.6-foot tide inundated the harems on the morning of 27 January. Wedged together on the large sandy Point Beach on the lee side of the island were 95 males, 936 nursing or pregnant females, and at least 510 pups. There were also 20 females, 20 suckling pups, and a few males in a small cove on the island’s weather side. For three hours the unusually high surf pounded the island. Waves flooded the beaches and sent logs, boulders, and flotsam careening against animals, over cliffs, and onto the highest reaches of the island. Piers, catwalks, and retaining walls erected by the U.S. Coast Guard in the 1930s were demolished and washed away. The tight group of over a thousand seals was wrenched apart and dispersed. With each incoming surge bodies were hurled pell mell over others and against cliffs and were then swept back to sea in the strong aftertow. As hundreds of pups were swept away hundreds of mother seals bobbed about in the white foam, calling to their helpless offspring. About two hundred females with pups managed to cling to higher ground at the base of the cliffs in about a foot of water.”

By 30 January, no pups remained on the exposed Cove Beach. The sandy Point Beach, the prime breeding area for the seals, was reduced to 10% of its normal size and only 290 pups remained in the harem. Scores of pregnant females and at least
Fig. 1. Photograph of the Point Harem on Año Nuevo Island at peak season on a calm day at high tide (top). The same harem is shown during a storm with attendant high surf at the peak of the breeding season in 1983 (bottom).
Table 1. Number of pups born and pup mortality rate at Año Nuevo Island and mainland from 1977 to 1987

<table>
<thead>
<tr>
<th>Year</th>
<th>Island No. Pups born</th>
<th>Percent died</th>
<th>Mainland No. Pups born</th>
<th>Percent died</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>798</td>
<td>20.0</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>1978</td>
<td>908</td>
<td>44.0</td>
<td>86</td>
<td>9.3</td>
</tr>
<tr>
<td>1979</td>
<td>1072</td>
<td>36.4</td>
<td>101</td>
<td>20.8</td>
</tr>
<tr>
<td>1980</td>
<td>1194</td>
<td>36.0</td>
<td>159</td>
<td>3.1</td>
</tr>
<tr>
<td>1981</td>
<td>900</td>
<td>40.0</td>
<td>325</td>
<td>11.1</td>
</tr>
<tr>
<td>1982</td>
<td>1100</td>
<td>25.0</td>
<td>369</td>
<td>7.6</td>
</tr>
<tr>
<td>1983</td>
<td>975</td>
<td>70.0</td>
<td>591</td>
<td>11.3</td>
</tr>
<tr>
<td>1984</td>
<td>956</td>
<td>48.5</td>
<td>729</td>
<td>7.8</td>
</tr>
<tr>
<td>1985</td>
<td>1016</td>
<td>37.8</td>
<td>685</td>
<td>8.3</td>
</tr>
<tr>
<td>1986</td>
<td>889</td>
<td>40.2</td>
<td>853</td>
<td>6.2</td>
</tr>
<tr>
<td>1987</td>
<td>716</td>
<td>22.6</td>
<td>808</td>
<td>8.9</td>
</tr>
</tbody>
</table>

125 mothers that lost their pups abandoned the ravaged island for the relative safety of adjacent mainland beaches.

Pup mortality on the island, from December 1982 to March 1983, was estimated as 70% of pups born; 683 pups died out of 975 pups produced. The mortality rate in 1983 far exceeded that observed in preceding and succeeding years (Table 1). Since the island colony reached carrying capacity in 1977, variation in the pup mortality rate has been highly correlated with storms at peak season. Before 1977, when colony number was increasing, the entire breeding beaches were not fully occupied and storms had a less deleterious effect. During the years, 1968 to 1976, the pup mortality rate ranged from 13 to 26% of pups born (Le Boeuf and Briggs 1977).

Many pups died as a result of being washed out to sea. Many evidently drowned but some may have been eaten by white sharks, *Carcharodon carcharias*. Over 250 dead pups washed ashore during the few days following the storms. However, the majority of pups died a weak or two later because of separation from their mothers caused by the physical disruption of the harems (Le Boeuf and Briggs 1977). Storms and high surf increase crowding in harems, heighten aggression between females, and make mother-pup separation more likely. Orphans not reunited with their mothers within 2 days must attempt to steal milk from other nursing females or they die of starvation. Most females nursing their own pups bite milk thieves. Starvation and trauma caused by female bites is the major cause of pup death in most years (Le Boeuf and Briggs 1977).

The high mortality rate on Año Nuevo Island in 1983 was due to the coincidence of several events:

1. Higher than normal sea level and the highest tides of the year coupled with high coastal winds and storms created unusually high surf that inundated traditional breeding areas.
The storms struck when the number of females and suckling pups were at their highest peak.

The island colony was at carrying capacity.

All space on the large breeding area on the Island, the Point Beach, was taken up by the animals, and high cliffs prevented the animals from retreating to higher ground. Flooding of the breeding beaches on the island was the worst that we have ever observed.

In contrast to the island, the pup mortality rate on the adjacent mainland, separated from the island by a 200-m channel, was 11% of pups born, only slightly higher than in previous years (Table 1). Although mainland beaches also took a physical pounding that eroded cliffs and caused large areas of dunes to be washed away, females and pups on the mainland had one advantage. They were widely dispersed along the shore, breeding in 10 small harems containing 10 to 150 females, and most importantly, most females and pups could move inland to high and dry areas away from the dangerous surf. However, where high cliffs inhibited retreat, pup mortality was high. For example, one mainland beach being used for the first time, housed 12 suckling pups before the storm. All of them were swept away when the first high seas washed over the beach. Even when females moved inland, beaches behind them were often cut away, leaving meter-high vertical banks that prevented lagging pups from following their mothers inland to safety.

Other exposed elephant seal rookeries in California also incurred high pup mortality rates. All 20 pups born in the newly established breeding colony at Cape San Martin in Big Sur were killed. Numerous starving or dead pups washed ashore in southern California, evidently from the offshore rookeries on San Miguel or San Nicolas islands, where 2000 pups were estimated to have died (Le Boeuf and Condit 1983).

Indirect Effects

If foraging was more difficult for pregnant females during the El Niño years, they did not respond by remaining at sea longer and delaying parturition. The normally distributed curve of females present on the rookery during the breeding season (Fig. 3 in Le Boeuf and Briggs 1977), which also shows the onset and rate of female arrivals and the rate at which females return to sea, did not change significantly from 1968 to 1988 despite a sevenfold increase
in the population of females (from 247 giving birth in 1968 to 1742 giving birth in 1986) and despite storms and bad weather at peak season in the years, 1973, 1978, 1981 and 1983. The time and slope of female arrivals and departures varied little over the years; females began arriving in early December and the last breeding female departed on about 10 March. In all years, female numbers peaked between 26 January and 2 February. The timing of parturition, nursing, and mating is evidently deeply fixed and unresponsive to environmental fluctuations.

**Postlactation Foraging Duration.** At the end of lactation, adult females go to sea to feed for about 70 days. This post-reproductive foraging period would appear to be a critical time for females. They have just lost approximately 42% of their mass during a 4-week nursing period during which they do not feed or drink (Costa et al. 1986) and, being fertilized, they are beginning another pregnancy. It is likely that they go directly to food. Much of their time at sea appears to be spent feeding since females increase their mass, on average, by 1 kg/day, which would require that they consume about 20 kg of prey per day (Le Boeuf et al. 1988). Upon their return from a period at sea lasting approximately 70 days, they are 25% heavier than at the end of lactation during initial water entry. If foraging was difficult during the El Niño years, one might expect that the females would have stayed at sea longer.

We determined the duration of the period at sea between the end of lactation and the beginning of the molt for females that weaned their pups successfully during the years 1976 to 1987. We simply noted the departure and return dates of marked, tagged females. The sample sizes for these years were 31, 18, 17, 12, 4, 38, 21, 23, 16, 20, 55, and 33, respectively. Figure 2 shows that the mean duration at sea was significantly higher by 5–15% in the years 1982 to 1985 than in preceding or

![Fig. 2. Mean duration at sea during the period between lactation and molting as a function of breeding year among female elephant seals that weaned pups successfully](image)
succeeding years ($F = 5.32, df = 11, 275, P < 0.05$). The highest mean duration at sea was in 1984 but the longest periods at sea immediately following lactation were recorded in 1983. One female bearing a diving instrument (not included in the sample) was at sea for 127 days (Le Boeuf et al. 1986); one female, unencumbered by an instrument, was at sea 104 days.

**Survival to the Next Year Following Reproduction.** If the increased time at sea reflects a more difficult time obtaining food or more energy spent securing it, we might expect this to be reflected in a lower rate of survival to the next year or decreased probability of producing or weaning a pup in the next year, possibly because of a reduced amount of energy transferred to the pup.

We calculated the percentage of tagged females that were resighted 1 year after producing a pup by conducting a search in each of the 3 years following the breeding episode. Searches were made daily during the breeding season and once a week during the rest of the year. Virtually all females resighted were observed during the breeding season at Año Nuevo or the rookery at southeast Farallon Island.

Table 2 shows the minimum number of females that survived from one breeding season to the next from 1981 to 1986. It is clear that the minimum survival rates did not vary substantially over the sample period whether one makes the comparison 1, 2, or 3 years after breeding (Chi-square = 1.34, df = 4, $P > 0.05$). The minimum survival rate was as high in El Niño years as in non-El Niño years. Moreover, adjusting for an estimated 6% tag loss per year (Le Boeuf and Reiter 1988), the best estimate of annual survival during this period is in the range, 60 to 69%.

**Reproductive Success: Pup Production Following Reproduction.** Because 97% or more of the females observed on a rookery give birth to a pup, observation of a female on a rookery can be virtually equated with giving birth. Thus, it follows that reproductive success, as measured by pups produced, also did not vary significantly across the sample years indicated in Table 2. In any case, we did not observe a decrease in natality during the EN years.

**Table 2.** Percent annual survivorship of female northern elephant seals from one breeding season to the next during the years 1981 to 1985. The percentage of females surviving to the year after breeding was calculated by searching for tagged females during 1, 2, and 3 years after breeding.

<table>
<thead>
<tr>
<th>Breeding season</th>
<th>n</th>
<th>Percent females surviving to next year based on observation in year:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>1981</td>
<td>151</td>
<td>47.1</td>
</tr>
<tr>
<td>1982</td>
<td>204</td>
<td>53.9</td>
</tr>
<tr>
<td>1983</td>
<td>183</td>
<td>53.0</td>
</tr>
<tr>
<td>1984</td>
<td>193</td>
<td>44.6</td>
</tr>
<tr>
<td>1985</td>
<td>162</td>
<td>47.5</td>
</tr>
</tbody>
</table>
23.4.2 Pups

Mass. If foraging conditions were poorer in El Niño years, females might have transferred less energy to their pups and weaned them at reduced weights compared to other years. This was clearly not the case in 1982 and 1984. In a study by Le Boeuf (1989a), using annual sample sizes in the range 28 to 98, mean mass of pups at weaning (both sexes combined) was 127 ± 36 in the years 1978, 1982, 1986, and 1987. Mean weaning mass was higher in 1980 (146 ± 31), 1984 (134 ± 19), and 1985 (137 ± 23). Pups were not weighed in 1983.

Survivorship. Although pups appear to have started life in as good condition in 1982 and 1984 as in other years (as reflected by mass), was pup survival over the first period at sea as high as in other years? This is a vulnerable time for pups for they must avoid predators and feed on their own after a 2.5-month fast. On average, only 45% survive the first period at sea to 1 year of age (Le Boeuf and Reiter 1988). Preliminary data indicate that they are shallower divers than adult females (P. Thorson and B. Le Boeuf, unpubl. data) and hence, may exploit different prey. Their prey distribution may have been changed during the El Niño years making it more difficult for them to feed. If so, one would predict low mass and poor condition when the animals return from sea, or in the extreme, a lower survivorship rate during the El Niño years than in other years.

From annual tagging studies and tag recovery observations, we calculated the survivorship curves shown in Fig. 3 for the years 1981 to 1984. The survivorship curve is lowest for the peak El Niño year, 1983, with the adjacent years, 1982 and 1984, being intermediate to the non-El Niño year, 1981. The survivorship curve in 1981 is similar to the survivorship curves of 1976 to 1980 (B. Le Boeuf, unpubl. data).

![Survivorship curve](image)}

Fig. 3. Log survivorship of elephant seals of both sexes from the 1981 to 1984 cohorts.
Moreover, the discrepancy in survivorship between the years 1982–1984 and 1981 increases with advancing age. This effect is shown more clearly in Fig. 4. First, it is clear that survivorship to 1 year of age varied significantly across cohorts (Chi-square = 112, df = 13, P < 0.05). The 1983 cohort has low survivorship to age 1 but no more so than the years 1973 and 1979. However, survivorship during the intervals, age 1 to 2, 2 to 3, and 3 to 4, reveals that the 1983 cohort is always significantly lower than other cohorts (Chi-square goodness of fit = 41, df = 1, P < 0.05). Other significant differences include adjacent years: 1984 to years 1, 3, and 4, and 1982 to years 2 and 4. By the time pups reached 4 years of age, only 7.5% of the 1983 cohort was still living. Next in line were the cohorts of 1982 (12.5%), 1975 (13.0%), 1973, and 1976 (about 17%). Survivorship to age 4 was highest in 1971, 1979, 1980, being slightly over 20%.

Age at Primiparity. The last point we address is cohort variation in age at primiparity. If body condition is positively correlated with onset of reproductive age (see Boyd 1984), and the female cohort from 1983 had a more difficult time finding food, the onset of reproduction might be later relative to other cohorts.

Table 3 shows that 1982, 1983, and 1984 were poor cohorts in terms of the low percentage of females that were primiparous at age 3, 4, or 5. The 1983 cohort had the poorest record. The 1982 and 1984 cohorts were somewhat more successful but less so than in other years. It is not clear whether this effect is due to reduced survival or deferrment of reproduction or a combination of both variables. The aberrant
### Table 3. Percentage of females from various cohorts that were primiparous at age 3, 4, or 5 and older

<table>
<thead>
<tr>
<th>Cohort year</th>
<th>N</th>
<th>3</th>
<th>4</th>
<th>5+</th>
<th>3, 4 or 5+</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>293</td>
<td>3.8</td>
<td>9.9</td>
<td>5.5</td>
<td>19.1</td>
</tr>
<tr>
<td>1978</td>
<td>476</td>
<td>5.5</td>
<td>9.0</td>
<td>4.8</td>
<td>19.3</td>
</tr>
<tr>
<td>1979</td>
<td>97</td>
<td>5.2</td>
<td>8.2</td>
<td>11.3</td>
<td>24.7</td>
</tr>
<tr>
<td>1980</td>
<td>113</td>
<td>8.8</td>
<td>10.6</td>
<td>6.2</td>
<td>25.7</td>
</tr>
<tr>
<td>1981</td>
<td>227</td>
<td>4.8</td>
<td>15.9</td>
<td>5.3</td>
<td>26.0</td>
</tr>
<tr>
<td>1982</td>
<td>332</td>
<td>1.8</td>
<td>8.4</td>
<td>4.2</td>
<td>14.5</td>
</tr>
<tr>
<td>1983</td>
<td>277</td>
<td>1.1</td>
<td>5.4</td>
<td>2.9</td>
<td>9.4</td>
</tr>
<tr>
<td>1984</td>
<td>471</td>
<td>1.5</td>
<td>11.7</td>
<td>2.3</td>
<td>15.5</td>
</tr>
<tr>
<td>1985</td>
<td>221</td>
<td>3.6</td>
<td>8.6</td>
<td>n.a.*</td>
<td>n.n.</td>
</tr>
<tr>
<td>1986</td>
<td>231</td>
<td>3.5</td>
<td>n.a.</td>
<td>n.a.</td>
<td>n.a.</td>
</tr>
</tbody>
</table>

*Not available.

distribution for the 1979 cohort, with a higher percentage of females being primiparous at age 5 than age 4, may reflect difficult foraging for 4-year-olds in 1983 that resulted in the postponement of reproduction.

#### 23.4.3 Males

We determined the percentage of identifiable males that returned to Año Nuevo from one breeding season to the next, i.e., the minimum annual survival rate (Fig. 5). The lowest minimum survival rate from 1 year to the next was from 1983 to 1984 (40.2%) followed by 1984 to 1985 (44.4%). However, differences across years are not statistically significant (Chi-square = 2.84, df = 6, P > 0.05). The sample size for a single year is also too small to determine what age class had the lowest survival rate. However, summing all years across age classes confirmed an effect reported earlier (Le Boeuf 1974). Annual survival rate decreased systematically with age, from 63 to 48% in 4-7-year-olds to 45% or below in adult males 8 years of age or older.

#### 23.5 Conclusions

The year, 1983, and to a lesser extent, 1982 and 1984, were poor years for elephant seals breeding at Año Nuevo, California. As a large-scale natural experiment that caused changes in weather, sea temperatures, and currents, EN 1982–83 exerted diverse, depressing effects on survival and reproduction.

The principal effects of EN 1982–83 on the Año Nuevo colony can be summarized as follows:

1. A 44% increase in pup mortality in 1983 relative to other years, due to inundation of breeding beaches at peak season.
Fig. 5. Percent annual survivorship of tagged male northern elephant seals on Año Nuevo from one breeding season to the next during the years 1980 to 1986. For example, only 40% of the males present in 1983 were observed in 1984. All males were known-age adults, 5 to 14 years of age, that were born on Año Nuevo. The sample sizes for the years 1980 to 1986 were 124, 86, 79, 87, 81, 124, and 129, respectively.

2. Reduced survivorship of pups born in 1983 to age 2, 3, and 4, relative to other cohorts.
3. Lower reproductive success of female pups born in 1983 relative to other cohorts, as measured by proportion of females primiparous at ages 3 and 4.
4. An increase in the length of the foraging period at sea of females following reproduction during the years, 1982-1985.
5. Reduced survival of breeding males from 1983 to 1984 relative to other years.

We found no evidence for predictions that during the El Niño years:
1. Females would be late arriving on the rookery to reproduce (arrival to give birth, nurse, and mate);
2. Breeding females would exhibit a lower survival rate to the next breeding season;
3. Breeding females would produce fewer pups the following breeding season;
4. The mean mass of weaned pups would decline (tested in 1984 but not in 1983); and that
5. Survivorship of pups to 1 year of age would be lower than usual.

Consideration of the causes of these effects, and the sex and age class affected, is illuminating, especially for comparisons with other species.

The devastating effect of the winter storms of 1983 on elephant seal colonies along the coast of California was only partly due to El Niño. The high pup mortality on Año Nuevo Island and on some other rookeries in central and southern California was due to the concomitance of several events - bad weather with high winds.
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and high surf, high tides, peak number of females and suckling pups present, crowded conditions allowing little room for escape to dry land, and higher than normal water level. Only the latter condition was unique to El Niño. The bad weather and storm conditions were associated with El Niño, but storms and high surf occur in any year. The timing of the storm, 19–21 January, was the key to the high mortality in 1983. Even a milder storm at the same time of year would have caused numerous pup deaths on Año Nuevo Island, given the number of pups present and the lack of access to safety. Equally bad storms in previous years (1969, 1978, and 1981) caused less pup mortality because the storm struck before peak season or because the storm struck at peak season before the colony was at carrying capacity. The effect of the 1983 storms on pup mortality was also a matter of location. Where females and their pups could retreat inland from the dangerous surf, such as on the Año Nuevo mainland, pup mortality was no higher than usual. Lastly, the storm effect on elephant seal pup mortality had no parallel among sea lions and fur seals that breed in the Pacific during the summer months.

Of equal importance is how possible changes in the distribution of prey or abundance and condition of prey, associated with perturbations in sea temperature and currents, affected foraging and subsequent survival and reproduction. This discussion is speculative because we do not know precisely what northern elephant seals from Año Nuevo were eating and where they were foraging. In general, we know that seals associated with central California rookeries are most often observed north of their rookeries off California, Oregon, Washington, and Vancouver Island, British Columbia; a few individuals have been sighted as far north as the southern Aleutian Islands in Alaska (Condit and Le Boeuf 1984).

Studies of gut contents and observations of feeding indicate that elephant seals feed on a variety of prey that includes cephalopods, crustaceans, tunicates, and fish (Condit and Le Boeuf 1984; Antonelis et al. 1987). Several species of pelagic squid and octopus make up the largest number of prey species found in seal stomachs. Pacific hake, Merluccius productus, is the most frequently occurring teleost fish and several species of sharks, rays, and ratfish are common cartilaginous fish prey. The prey of elephant seals suggest that they are capable of foraging in a variety of marine environments from epipelagic to benthic. However, the diving pattern of adult females indicates that most foraging is in the mesopelagic zone between 400 to 700 m (Le Boeuf et al. 1988).

The effect of the aberrant sea temperature and currents on elephant seal foraging was not as visible and dramatic as it was on some otariids. The sea lion and fur seal pattern consists of females alternatingly foraging for 2–7 days and feeding their pups for about 2 days (Gentry et al. 1986a). Clearly, good foraging must be available close to the rookery. In contrast, female elephant seals wean their pups after 27 days of nursing during which they do not feed, drink, or enter the water (Le Boeuf et al. 1972; Reiter et al. 1981; Costa et al. 1986). Although the tax on the body is great, when females return to the water to feed, they are not constrained to remain near their pups as are otariid females. They have more freedom to move to where the prey are located. We do not know whether females traveled further afield in 1983, but they spent more days at sea than usual, a result also observed in California sea lions breeding at San Miguel and San Nicolas Islands in southern California.
(Boness et al. 1985; Costa et al., this Vol.; Heath et al., this Vol.). Indeed, the seals spent more days at sea in 1984 than in any other year. This may have been caused by the necessity of traveling further north to feed on known prey such as market squid, *Loligo opalescens*, which decreased in catches off California and Oregon but increased off the coast of Washington in 1983 and 1984 (CalCoFi Report 1985; Pearcy et al. 1985). We have no evidence that spending more days at sea than usual had a deleterious effect on female survival or reproduction the following year. Adult males breeding in 1983 showed a reduced survival rate to the next breeding season. This sex difference suggests that males may have had a more difficult time finding or catching prey than females. This could have arisen if males feed on different prey, consume more prey per unit time away, or forage in different locations than females.

At present, we have no information on the diving or foraging behavior of males that bears on this speculation.

Our most significant result is the poor survival and reproductive record of the 1983 cohort. This was due to the combined direct and indirect effects associated with El Niño. First, bad weather caused high pup mortality prior to weaning and, second, some unknown mechanism (possibly poor forage) caused reduced survivorship to reproductive age of females. The decreased survivorship of the 1983 cohort was not apparent at age 1 but became more and more pronounced with age. Decreased survival to reproductive age, a major component of reproductive success in female elephant seals (Le Boeuf and Reiter 1988), coupled with a reduced percentage of females giving birth for the first time at ages 3 and 4, indicates that the 1983 cohort will leave significantly fewer progeny than adjacent cohorts. Moreover, the 1983 cohort will not have the substantial advantages – the "compound genetic interest" effect – that females accrue from reproducing early (Lewontin 1965). Regardless of the underlying mechanisms, it is clear that significantly fewer progeny will be produced by the 1983 cohort than by others that immediately preceded or succeeded it. In the long run, the reproductive performance of the elephant seals born at Año Nuevo, California, in 1983 may be as low as some of the sea lions and fur seals whose first year class was decimated (Limberger et al. 1983). The underlying mechanisms might be different but the end results are similar.

Cohort variation in reproductive success is widespread in nature and the factors that cause this variation are significant forces in selection (Clutton-Brock 1988). Our data show that the 1982–83 El Niño Southern Oscillation produced a complex of physical perturbations that apparently caused extensive cohort variation in survival of elephant seals breeding in central California.

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