26 The Effects of El Niño on Pinniped Populations in the Eastern Pacific

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26.1 Introduction

Most hypotheses on adaptation stem from comparisons among species. The comparative method offers a way to study questions of ecological mechanisms and evolutionary adaptations, particularly in situations where experimentation is near impossible. Comparisons among species and areas in itself can advance the perspective greatly, but this approach suffers from unknown and uncontrollable variation among species and regions. Adding another dimension of comparison, a large ecological disturbance, to the system is extremely illuminating because it acts independently of preexisting species level and spatial variation and, therefore, simplifies comparisons by eliminating confounding variables. Thus, the chapters in this book are of interest because they not only chronicle the impact of El Niño (EN) on eastern Pacific pinnipeds, but they also provide new perspectives on the ecology, life history, and evolution of these species which could not otherwise have been obtained.

In the preceding chapters we described and analyzed the effects of EN on pinniped populations distributed over the Pacific east coast of the Americas from the Bering Sea (ca. 57°N) through California, Mexico, Ecuador (Galapagos), and Peru to northern Chile (ca. 23°S). We presented data on six species of pinnipeds, the northern fur seal (*Callorhinus ursinus*), the Galapagos fur seal (*Arctocephalus galapagoensis*), the South American fur seal (*Arctocephalus australis*), the South American sea lion (*Otaria byronia*), the California sea lion (*Zalophus californianus*), and the northern elephant seal (*Mirounga angustirostris*). Not only can we compare the effects of EN between two families of pinnipeds, the otariids and phocids, and between species of otariid seals, but we are also fortunate to have studies on different populations of the same species.

1. In the northern fur seal we can compare the colonies on the Pribilofs (at 57°N) and on San Miguel Island (34°N).
2. The South American fur seal was studied in Peru (15°S) and Chile (20–23°S), and the very similar Galapagos fur seal on the Galapagos (0°S).
3. For the California sea lion, data were obtained on the most varied aspects of behavior, physiology, and life history of any species in the book. These data originated from work on the California Islands, at the northernmost edge of the breeding range (33–34°N), and can be compared to information on the populations from Baja California (23°–28°N; the southernmost breeding range of *Z. c.*

californianus) and from the Galapagos Islands (at 0°N/S). The latter population is accorded subspecific status (*Z. c. wollebaeki*).

4. Lastly, we have detailed data on northern elephant seals from the center of their distribution on the California Channel Islands (33°–34°N) to the northern edge of their range at Año Nuevo Island (37°N) and on the Farallon Islands (38°N).

   Unfortunately, we have been unable to obtain substantial information on EN effects on the population of Steller sea lions (*Eumetopias jubatus*) in the north and obtained only limited information on the South American sea lion (*Otaria byronia*) in Chile and Peru (Guerra and Portflitt, Chap. 4; Majluf, Chap. 5). Data on the Harbor seal (*Phoca vitulina*) are also unavailable at present.

To structure this material for the following discussion (Sect. 26.2), we will first summarize our results (see Tables 1–3) with several general questions in mind:

1. How did effects on population parameters change with latitude?
2. What were the time courses of the various effects?
3. Were age groups and sexes differentially affected, and if so, how?
4. How did foraging behavior change during EN?

In Section 26.3 we then use this information on similarities and differences between species, and between sites within a species, to examine the stages in pinniped like cycles which suffer most from environmental disturbances. We then attempt to draw conclusions on the importance that environmental variance may have for the evolution of life history traits of phocids and otariids exposed to latitudinally different environmental regimes.

26.2 Summary

It is generally difficult to prove that changes in population parameters are directly caused by unusual environmental circumstances (Arntz et al., Chap. 2). This problem was demonstrated by Hatch (1987) in his report on seabirds in the Bering Sea: he observed substantial breeding failures during EN which were difficult to interpret since similar failures had been previously observed in non-EN years. Differential effects of EN among seabird species were weakly related to their foraging tactics, but showed marked geographical variation for a given species even within the area of the Bering and Chukchi Sea and the Gulf of Alaska. The variation in the response of these populations emphasizes how risky it is to ascribe changes in population parameters directly to EN. We are confronted with the same problem in the interpretation of our pinniped data.

Our data base, although in most cases encompassing several years, is not comprehensive enough to address all short- and long-term effects of this EN. Furthermore, most of our observations were made at the breeding sites and do not provide information on the nonbreeding season, during which extensive feeding occurs over wide areas (but see York, Chap. 9; Huber, Chap. 13). Since the migration period figures importantly in the life cycle of most pinniped species we are likely to underrate the importance of EN effects in our conclusions.

Table 1. Summary of the information on fur seals[a]

	C. ursinus Pribilof Islands	*C. ursinus* San Miguel Island	*A. galapagoensis* Galapagos	*A. australis* Peru
Latitude	57°N	34°N	0°	15°S
Pupping season	June-July	June-July	Sept.-Oct.	Oct.-Dec.
Pup mortality	No change	Increase	1982 100% Loss 1983 Normal	At least 41% increase
Juvenile mortality	Decreased by 15%	Presumably more than doubled in 1982 and 1983	100% Loss of 1980 and 1981 cohorts; partial loss of 1979 cohort	Increase
Adult female mortality	No change	50% Population decline mortality or decreased immigration? Increased emigration?	At least 30% lost in 1982–83	No exact data; most likely increase
Adult male mortality	No change	20% Less males; cause unclear	1982 100% Loss 1983 Back to normal	No quantitative data presumably increased
Number of pups born	No change	60% Decrease 1983 50% Decrease 1984	Normal 1982 89% Decrease 1983	No data
Pup growth rate	No data	1983 ca. 40% Decreased 1984 ca. 25% Decreased	1982 No growth 1983 Normal	1983 Decreased by 50%
Time to weaning	No data	No data	1982 All dead 1983 Normal	No data
Foraging trip duration	No change	Increased in 1983 Slight increase in 1984	About 3 times longer with larger variance	Increased
Prey composition	No change	Changed in 1983	Changed in 1983/84	Changed in 1983/84
Migration/ movement	No change on land	Local redistribution; more northward migration of juveniles	Local redistribution perhaps immigration into best habitats	Some movement into and establishment in northern Chile
Population recovery	No change	Still incomplete in 1987	Very slow	Established in Chile No date for Peru

Before we summarize our results, we need to define two terms for this summary. *Pups* are young animals which depend *entirely* on maternal milk for their energy input; juveniles are either recently weaned or living on a mixed diet of maternal milk and solid food for which they forage independently. Depending on the species, juveniles may be 4 weeks (*M. angustirostris*) to 3 years (*A. galapagoensis*) old. This definition stresses the change from total dependence on maternal care to partial or complete nutritional independence rather than absolute age (which is also used elsewhere in this book).

26.2.1 The Relationship Between the Impact of the EN Event on Population Parameters and Latitude

Because EN originates near the equator and is propagated poleward, the severity of EN-related impacts on pinniped populations declines from low to high latitudes

Table 2. The influence of El Niño on sea lions at various study sites (listed from N to S)[a]

	Channel Islands	Mexican Pacific	Sea of Cortez	Galapagos
Latitude	33–34°N	24°N	24–26°N	0°
Pupping season	June/July	June/July	June/July	Mostly Sept./Oct.
Adult female mortality	Slight?	No data	No data	Some?
Adult male mortality	No indication	No data	No data	Increased from 1982–83
Juvenile mortality	Increased on SC in 1984; no trend on SM	No data	No data	Strongly increased certainly >50%
Pup mortality	1982: 10% 1983 and 1984: 17% many abortions	No data	No change	ca. 100% in 1982 Normal (<10%) in 1983
Foraging trip duration	Increased in 1983 Almost normal in 1984	No data	No data	No data
Pup growth rate	Reduced in 1983 and 1984	No data	No data	No data
Number of pups born	30–70% Reduced in 1983	45% Reduced in 1983	No change	Reduced in 1983
Time to weaning	1984 More yearlings suckling	No data	No data	1982 Cohort lost
Migration/ movement	More animals migrate north	Less males on coast in 1982/83	No change	Unusual sightings on mainland Ecuador
Population recovery	Pup numbers in 1986 still < 1982	No data	No change	slow

[a]SC, San Clemente Island; SM, San Miguel Island, SN, San Nicholas Island.

Table 3. The influence of El Niño on elephant seals at three study sites (years refer to the time when young weaned)

	Farallons	Año Nuevo	San Nicolas Island
Latitude	38°N	37°N	33°N
Pupping season	Dec./Jan.	Dec./Jan.	Dec./Jan.
Adult female mortality	No change	No change	No data
Adult male mortality	No change for dominant males; increase for subadults	Slight increase	No data
Juvenile mortality	Increase for 1982, 1983 and 1984 cohorts	Increased for 1982, 1983 and 1984 cohorts	No data
Pup mortality	No change; more stillbirths 1984 and 1985	Increase to 70% by storms in 1983	Increase from 4 to 20% in 1982/83
Time at sea between lactation and molt	No data	Increase in 1983 and 1984	Increase in 1983
Pup mass	No data	No change 1982 and 1984 No data 1983	No data
Number of pups born	Decrease in 1984 and 1985	No change	No data
Lactation duration	No change	No change	Shorter in 1983 and 1984
Skipped breeding season	More males and females skipped the 1984/85 breeding season	No data	No data
Age at primiparity	No data	Increase in 1983	No data

(Fahrbach et al., Chap. 1; Arntz et al., Chap. 2). At low latitudes EN effects were strongest during late 1982 until June 1983, whereas at temperate latitudes effects were strongest during the winter of 1982–83, lasted through 1983, and lingered on with strong aftereffects in 1984. It is instructive to examine how population parameters varied with latitude because this instantaneous picture of all populations is analogous to the responses that a population at one location may show to environmental perturbations of various magnitudes over time. This is suggested by the study of the South American fur seal in Peru where the strong EN of 1982–83 almost exterminated the 1982 cohort, whereas the weak EN of 1986–87 caused lower pup body mass at 1 month of age than in previous years, but apparently had no major effect on pup survival to 1 year of age (Majluf, Chap. 5).

We first summarize the effects on otariids and then on the elephant seal, the only phocid species for which we have detailed information.

Otariids

The effects of EN on otariid pup survival followed a latitudinal gradient. Pups experienced reduced milk intake during the years of EN effects, which led to reduced growth rate and associated reduced body mass for a given age. Consequently, survival of pups during their first 3 months of life decreased (Tables 1 and 2). The most severe negative effect was observed in the Galapagos Islands, where 100% mortality of fur seal pups in 1982 and nearly 100% mortality in the sea lions occurred (Table 1; Trillmich and Dellinger, Chap. 6). In the near-tropical population of the South American fur seal in Peru, 42% of pups died within a 22-day observation period in February 1983 (Trillmich et al. 1986; Majluf, Chap. 5). However, survival of pups in the insulated population of California sea lions in the Sea of Cortez did not appear to be affected (Aurioles and Le Boeuf, Chap. 11). Further north in more temperate latitudes on the California Channel Islands (about 33°–35°N) the 1982–83 EN had a less drastic effect on pup survival. In 1983 and 1984, it approximately doubled normal early postpartum pup mortality among California sea lions (Francis and Heath, Chap. 12; DeLong et al., Chap. 17) and northern fur seals on San Miguel Island (DeLong and Antonelis, Chap. 7). The very high latitude Pribilof population of northern fur seals was also unaffected (Gentry, Chap. 8).

The loss of juveniles from these populations varied with latitude in the same way as pup mortality. The most equatorial species, the Galapagos fur seal, lost the 1980 and 1981 cohorts completely and part of the 1979 cohort. In the area of the California Channel Islands, high mortality of underweight weanlings during their first year at sea was documented in juvenile California sea lions and northern fur seals (Tables 1, 2). Although exact mortality estimates are missing, an increase in the number of beached yearling sea lions and fur seals was noted (J. Antrim, Sea World, San Diego, pers. comm.; DeLong and Antonelis, Chap. 7). At 52°N, the 1983 year class of northern fur seals was of normal size initially, but its subsequent survival to 2 years of age may have been greater than normal, because of enhanced food supplies available to juveniles after weaning as shown by York (Chap. 9) for previous EN events. This may have occurred despite the fact that the 1982–83 EN had a less beneficial effect on fish stocks in the north than previous EN events even though they were not as strong in the tropics (Niebauer 1988; Fahrbach et al., Chap. 1; Arntz et al., Chap. 2).

During most EN events, the mortality effects on pups and juveniles may not show such an extreme equatorial-temperate trend as in the 1982–83 event. Weaker events appear to affect near-equatorial populations much less severely than the exceptional 1982–83 EN (Majluf, Chap. 5). In fact, moderate and weak ENs may only cause reduction in growth rates of pups in tropical areas and may have no effects on temperate populations.

Mortality of adult females was also increased during EN and varied with lati-tude. The effect was largest in the tropics, where an estimated 30–50% of the female fur seals on Galapagos died (Table 1). The larger Galapagos sea lion females had a lower mortality rate than the fur seals (Trillmich and Dellinger, Chap. 6). We have no estimates of fur seal mortality in Peru, but it is clear that female mortality there was high in 1983. Some animals may have escaped starvation by migrating south into Chile (Guerra and Portflitt, Chap. 4). Movement to more productive areas was not an option for the Galapagos species.

The data for the Channel Island populations of otariid pinnipeds showed no increase of female mortality among sea lions (Table 2), but marked shifts in distribution (Francis and Heath, Chap. 12; DeLong and Antonelis, Chap 7; DeLong et al., Chap. 17). A dramatic decline in the number of northern fur seal females on San Miguel was noted (Table 1). Whether this decline was due to migration from San Miguel or mortality is unknown (DeLong and Antonelis, Chap. 7). Female survival of northern fur seals in the Bering Sea was unaffected by the EN (Gentry, Chap. 8).

Adult males of otariid species, which fast during territory tenure, went to sea with their fat stores seriously depleted. Again, the effect of this depletion differed by latitude. The virtually complete loss of reproductive male Galapagos fur seals indicates how risky the reproductive fast is for males of polygynous pinnipeds (Table 1; Trillmich and Dellinger, Chap. 6). There was less mortality among Galapagos sea lion males than among the fur seals, but the extent of the mortality was not quantified (Trillmich and Dellinger, Chap. 6). In contrast, censuses for the California sea lion on the Channel Islands indicated no measurable change in adult male mortality (Table 2; Ono et al. 1987; Francis and Heath, Chap. 12). Since these males migrate north after the breeding season they may have been able to avoid the worst EN effects.

Female fertility decreased in almost all otariid species during EN (Tables 1, 2). Reproductive rates of adult females decreased most for the Galapagos fur seal (70–90%). Pup production of California sea lions on the outer coast of Baja California and on the Channel islands was reduced by about 50% in the first breeding season following the onset of EN (Table 2). These lower natalities were probably a result of undernutrition of females (Francis and Heath, Chap. 12). Female condition was not directly measured but appeared to be poor in 1983 as reflected by decreased copulation rates and increased abortion, resulting in decreased female fertility in 1983 and 1984 (Francis and Heath, Chap. 12). Pup births in the northern fur seal in California fell by about 60%, but in this case we cannot discriminate between reduced female fertility, and massive emigration combined with some mortality of reproductive females (DeLong and Antonelis, Chap. 7).

Another possible factor leading to decreased numbers of pups late in or immediately after the EN year 1983 may have been an increase in the age at first reproduction in tropical and temperate species. When marine productivity is high, food for recently weaned juveniles is abundant and causes fast growth which leads to early maturation as seen in northern fur seals (York 1983). Conversely, reduced growth early in life may lead to a later onset of reproduction. Juvenile females of the cohorts, which were born, maturing, or reproducing for the first time during EN, may have delayed their first pupping due to reduced food availability. Evidence for this effect was observed in northern elephant seals (see below).

Phocids

The range of our study sites of northern elephant seals was about 400 km, too limited to reveal a latitudinal trend in pup mortality (Table 3), but site effects were important. Pups of this species were well buffered against EN effects while they were still suckling. Only direct storm effects increased the mortality rate of pups during early 1983 and the effect was site-specific. At the Farallon Islands (38°N) pup mortality rates were normal (Huber et al., Chap. 24). At Año Nuevo Island (37.5°N), pup mortality roughly doubled (Le Boeuf and Reiter, Chap. 23). At San Nicolas Island (33°N), the pup mortality rate was five times above normal (Stewart and Yochem, Chap. 25). At both of the latter locations mortality increased due to a coincidence of unusually strong winter storms and high sea levels which accompanied EN at temperate latitudes (Fahrbach et al., Chap. 1). The same storms struck the Farallon islands, but mortality did not differ from non-EN years because the animals there were on high ground, away from the sea.

The difference in storm effects among these islands was a function of population density and beach topography rather than of latitude. Population density was highest at Año Nuevo (cf. Table 1 in Le Boeuf and Reiter, Chap. 23). When the animals had to move during storms, high population density led to more trampling of pups and a greater probability of mother-pup separation. If, in addition, the animals were unable to reach higher ground because of cliffs at the back of the beach, pups drowned. Therefore, increased mortality of northern elephant seal pups occurred where high population density, limited beach space, and cliffs behind the beach exacerbated the storm effects (Le Boeuf and Reiter, Chap. 23; Stewart and Yochem, Chap. 25).

In conclusion, EN 1982–83 had a highly negative influence on several pinniped species at or near the equator, and a moderately negative influence in the temperate zone. The effect was negligible for the variables monitored in the subpolar northern fur seal.

26.2.2 Differential Effects of EN on Age Classes and Sex

The impact of EN on pinnipeds was strongly influenced by the age and sex of individuals. Age is a good measure of physical maturation and behavioral experience, and is therefore expected to influence the resistance of an individual to environmental perturbations. All the species studied show strong sexual dimorphism in size, and size influences the diving abilities of pinnipeds (Kooyman 1989). Furthermore, the reproductive strategies of males and females of these species differ widely and exert different constraints on the patterning of foraging time and the migratory behavior of the sexes. The way in which EN affects a pinniped individual is therefore also expected to be influenced by its sex.

Otariids

During the lactation period, otariid pups rely on the foraging success of their mothers. Pup growth rate will depend on foraging conditions, if, at lower food availabilities, females do not allocate increasing amounts of their resources to pups. During acute food shortages these pups may be more susceptible to EN impacts than are juveniles and adults since pups cannot contribute independently to their energy intake. Consequently, pups suffer more than any other age class wherever EN-related changes in the marine environment have negative effects on maternal foraging efficiency (Tables 1, 2).

Male otariid pups demand more milk from their mothers than female offspring, mainly because male pups are bigger and grow faster than female pups (Kerley 1985; Costa and Gentry 1986; Trillmich 1986b: Oftedal et al. 1987b). This suggests another way in which females may cope with reduced food resources. According to the Trivers and Willard (1973) hypothesis, mothers may produce more female offspring during times of food scarcity. Previously reported data for the Galapagos fur seal (Trillmich and Limberger 1985; Trillmich 1986b) and the California sea lion (Ono et al. 1987) showed no significant relationship between environmental quality and secondary sex ratio measured during the following EN. However, two studies in this volume have indicated instances of sex bias in California sea lion pups in relation to EN. When all 4 years of study on California sea lions (1982–1985) were considered simultaneously, the secondary sex ratio was shown to be female-biased during EN on San Nicolas Island (Ono and Boness, Chap. 20). Also, the sex ratio among pups 2 months of age on San Nicolas and Santa Barbara Islands was weakly female-biased during EN compared to the 2 years prior to EN (Francis and Heath, Chap. 21). Sex ratio changes in the predicted direction were mentioned for northern elephant seals on San Miguel Island (Stewart and Yochem, Chap. 25), but were not corroborated by more extensive observation on the same species on Año Nuevo and the Farallon Islands. The problem of adaptive sex ratio shifts clearly needs more investigation since it is hard to imagine how pinniped females could predict foraging conditions 1 year ahead of time in order to shift sex ratio in an adaptive way at the time of conception. They would have to make such a prediction because there is a 1-year delay between fertilization of the egg and birth of the pup. Alternatively, females may resorb embryos of the wrong sex previous to parturition, and thereby lose a major part of their lifetime reproductive effort. Such a mechanism has not been documented in pinnipeds and would a priori seem to be of questionable adaptive value.

Temperate and tropical otariid species are flexible in the timing of weaning (Gentry et al. 1986a; Trillmich 1986b; Francis and Heath, Chap. 21). Under poor conditions these species delay weaning and can thus reduce, or at least delay, mortality of juveniles during periods of low food availability. In fact, more California sea lion yearlings were suckling following the EN than in other years (Francis and Heath, Chap. 21). While the proportion of suckling male yearlings increased in

1984, there was no significant change across years in the proportion of juvenile females suckling. Differences between years in migratory behavior of yearling males may account for this finding: males in 1984 were more likely to stay on their island of birth and therefore remain in contact with their mothers. In addition, their mothers were less likely to have new pups to compete for milk than in years before EN. This difference in migratory behavior of male yearlings may have accounted for the lack of sex difference in juvenile mortality. Older sea lion juveniles migrated in greater than usual numbers from southern to central California during 1983 and 1984 and may thus have avoided the worst impact of EN (Huber, Chap. 13). Data from the South American fur seal in Peru also indicate that under EN conditions weaning is delayed (Majluf 1987).

Adults were most resistant to EN-related changes since they were the most efficient foragers (see Sect. 26.2.3). Moreover, they sometimes reacted to changes in the marine habitat by emigrating (Tables 1, 2).

In otariids, the extent of the increase in adult mortality during EN was related to sex-specific differences in foraging and migration. After the reproductive season, males have to recover from the territorial fast. Similarly, females must restore their body reserves after the initial 7-day fast following parturition. Recovery from poor body condition depends not only on food resources after this stressful period, but also relates to a sex difference in foraging options. California sea lion males migrate north, into areas less affected by EN, immediately after the end of the breeding season. Consequently, if they have enough reserves to get away from the breeding grounds after the fast, they are free to forage wherever they find food most plentiful. In contrast, female sea lions continue to forage near the breeding colonies and do so under the additional stress of lactation. They would therefore seem to be in greater danger than males when feeding conditions deteriorate since they cannot escape by migrating away without potentially losing the young of the year. In Galapagos fur seals and sea lions, on the other hand, both sexes appear to be resident and forage in the same upwelling areas near the islands. Under these conditions reproductive males clearly suffered higher mortality than females (Tables 1, 2). The combination of a more marked EN effect together with a more restricted foraging environment in the tropics may explain why sea lion males on Galapagos were more likely to die during EN than their conspecifics in California.

Females showed a marked reduction in fertility after the EN, whereas no such effect was noted for males. If males survived the stressful reproductive period they were able to forage continually during the nonbreeding season. This apparently provided them enough opportunities to recover and store reserves for the next breeding attempt. In contrast, females must spend a large percentage of their time ashore to suckle their pup during which they obviously cannot feed and must also incur the cost of lactation (Ono et al. 1987; Heath et al., Chap. 14; Costa et al., Chap. 16; Boness et al., Chap. 18). As a consequence, they were often unable to produce the extra energy necessary for a simultaneous pregnancy.

Phocids

Data on northern elephant seals do not suggest major differential sex effects of EN. Mortality of pups and juveniles appeared to be indiscriminate with respect to sex.

The studies showed no negative effect of EN on lactation in elephant seals, and presumably pup growth during nursing was also normal. No data on pup mass are available for pups born in December 1982 to January 1983. Mean weaning mass in 1982 and 1984 was no different from preceding and succeeding years.

However, the impact of EN varied strongly with the age of elephant seals. Mortality of juvenile elephant seals was elevated for the 1982 (i.e., born Dec. 81-Feb. 82), 1983 and 1984 cohorts compared to previous and later years (Table 3; Le Boeuf and Reiter, Chap. 23; Huber et al., Chap. 24), an effect that was most marked for the 1983 cohort. Juveniles, who enter the sea after a 2.5-month postweaning fast, appeared to suffer from reduced food availability during their first year(s) at sea. Compared to previous cohorts, less than half the normal number of females from the 1983 cohort appeared to reach sexual maturity.

Mortality among adult female elephant seals did not change on Año Nuevo or at the Farallon Islands, but mortality of adult males increased on Año Nuevo and, at the Farallons, subadult males seemed to suffer even more than adults (Huber et al., Chap. 24; Table 3). This finding is unexpected since the fully adult, dominant males presumably spend more energy during the reproductive season fighting and guarding females than subadults and hence have more to recover.

EN reduced the probability of breeding, and thus reduced lifetime fertility, of both sexes (Table 3; Huber et al., Chap. 24). More females than usual skipped 1 or 2 years of pupping and a few males also skipped a breeding season on the Farallons (Huber et al., Chap. 24). The data do not reveal whether males or females were more likely to skip a breeding season. In addition, age at first reproduction also increased significantly for the 1983 female cohort at Año Nuevo Island, an effect that may have been caused by reduced growth rates of that cohort during the first years at sea.

26.2.3 Effects of EN on Foraging and Energetics of Mothers and Pups

Otariids

EN was obviously a time of food shortage for temperate and tropical pinnipeds. In otariids, lactating females were ideal subjects for studying the effects of food shortage on foraging behavior because they forage between periods of pup nursing. This restricts them to a foraging site relatively close to the rookery. A pup's physical condition is a sensitive indicator of its mother's foraging success.

During EN, female otariids stayed away from their pups increasingly longer between nursing visits on land (Tables 1, 2; Trillmich and Limberger 1985; Ono et al. 1987; Majluf, Chap. 5; Trillmich and Dellinger, Chap. 6; Heath et al., Chap. 14; Feldkamp et al., Chap. 15). The effects were most marked in the tropics where females more than doubled the time away from their pups. It is important to note the distinction between *time away* from the pup and *time at sea*. This is best demonstrated by the data for the California sea lion (Feldkamp et al., Chap. 15). Here, and in Galapagos fur seals (Trillmich and Kooyman unpubl.), females sometimes rested elsewhere on land before returning to the pup. This observation supports the hypothesis by Costa and Gentry (1986) and Costa et al. (Chap. 16) that females attempt to restore their physical condition to an upper threshold of body mass before returning to their pups to lactate.

During EN, the time mothers spent away from their pups lengthened to the extent that the energy budget of many pups became negative; they lost mass and finally died. Reduced milk transfer (Oftedal et al. 1987b; Iverson et al., Chap. 19) was the main reason for mass loss and this reduction was reflected in decreased suckling times (Ono and Boness, Chap. 20). In the Galapagos, the mean absence duration of mothers was no longer than under normal warm season conditions. Nevertheless, pups starved to death because the variance associated with the mean was very high (Trillmich and Dellinger, Chap. 6). In California sea lions, pups with mothers gone for more than 9 days died (Heath et al., Chap. 14). Although pups decreased their activities, these compensatory mechanisms were insufficient to balance the reduced energy intake during the peak of EN effects (Ono et al. 1987; Boness et al., Chap. 18; Iverson et al., Chap. 19; Ono and Boness, Chap. 20).

As a consequence of EN, foraging females were also faced with changes in prey composition and abundance while at sea (Arntz et al., Chap. 2). Changes in prey availability were reflected to a certain degree in changes in the diet of several species (Majluf, Chap. 5; Trillmich and Dellinger, Chap. 6; DeLong and Antonelis, Chap. 7; DeLong et al., Chap. 17). The most obvious example is the increase of northern anchovy in the diet of northern fur seals and California sea lions in 1983. This was apparently caused by a northward shift in the distribution of this species (Arntz et al., Chap. 2). On the other hand, the proportion of scats with market squid changed little from 1982 to 1983 (DeLong and Antonelis, Chap. 7; DeLong et al., Chap. 17) despite the crash of the fishery for market squid in central California (Arntz et al., Chap. 2). Northern fur seals and California sea lions were apparently flexible enough in their diet choice to change to other food items where and when it was profitable, but also kept hunting for organisms that were decreasing in abundance.

The data on foraging behavior and energetics of female California sea lions (Feldkamp et al., Chap. 15; Costa et al., Chap. 16) suggest the mechanism by which foraging females attempted to compensate for reduced prey abundance. They appeared to reduce the time spent swimming and resting, and to increase the percentage of time spent diving (as in Antarctic fur seals, Costa et al. 1989). Dive bouts, which may reflect active foraging on individual prey patches (Gentry et al. 1986a; Feldkamp et al., Chap. 15), increased in length during 1983 when compared with the previous year.

The apparent decline in percent time swimming, while diving effort increased (Feldkamp et al., Chap. 15), suggests that sea lions do not initially travel further away to search for prey. Transit times to the first dive bout were not different between pre-EN and EN years. Prey were apparently found at similar distances from the islands in 1983 as in 1982, but occurred at lower density in 1983. Sea lions increased their search effort by spending a greater percentage of their time diving instead of swimming long distances in search for prey. Diving depths and durations showed a tendency to increase, perhaps reflecting an increased search effort for less available prey. Sea lions examined during the EN years appeared to make a greater percentage of their dives to greater depths or for longer durations (Feldkamp et al., Chap. 15). The South American fur seal (Majluf, Chap. 5) and the Antarctic fur seal (Costa unpubl. data) appear to compensate in a similar fashion for lowered prey availability.

All the above compensatory mechanisms were obviously not sufficient to balance reduced prey availability. The animals found it increasingly difficult to find and capture enough prey to satisfy their energy demands. While the rate of food intake (in biomass) appeared to be constant between years in California sea lions, more energy was expended to obtain this intake, compared with pre-EN years (Costa et al., Chap. 16). Furthermore, the energy content of prey may have been lower, resulting in a reduced energy intake per unit of biomass eaten. The decline in foraging efficiency manifested itself through increased time spent feeding at sea, and through a decline in the amount of milk provided to the offspring (Heath et al., Chap. 14; Boness et al., Chap. 18; Iverson et al., Chap. 19). It may be significant that under non-EN conditions, in 1982, all California sea lion females with time-depth recorders returned to their pups, while in 1983 three of five did not return. The animals that did not return may have been unable to make up for the additional energy demand required by carrying the instrument. They gave up their pups and did not return to the site of capture. The animals from which we obtained dive data are therefore perhaps exceptionally efficient foragers.

Phocids

Similar effects must have influenced the elephant seals. Females spent more time at sea in 1983 between the end of lactation and molt than in any other year (Table 3; Le Boeuf and Reiter, Chap. 23; Stewart and Yochem, Chap. 25). It is not clear how EN affected their food resources since elephant seals forage off the continental shelf at great depth, 98.5% of their dives are deeper than 200 m (Le Boeuf et al. 1988). Perhaps, EN reduced prey abundance off the shelf. This is likely since we know that Pacific hake is prey of elephant seals and these fish seemed to be distributed more to the north and offshore during 1983 than in normal years (Arntz et al., Chap. 2). If the distribution of other prey species also changed, this would explain the reduced survival of elephant seal juveniles of the 1982 and 1983 cohorts (Le Boeuf and Reiter, Chap. 23; Huber et al., Chap. 24) which – as smaller and less experienced animals – are presumably less able divers than adult females.

26.2.4 Time Lags of Effects on Pinnipeds Relative to the Onset of EN

The time scale of EN effects on pinnipeds ranged from the immediate to those with a lag of several years. "Immediate" effects were caused mainly by physical, oceanographic disturbances such as storms, shifts of the thermocline, and the accompanying changes in the distribution of prey species (Fahrbach et al., Chap. 1; Arntz et al., Chap. 2). In contrast, effects which showed up one to several years after the phenomenon and were potentially long-lasting were primarily caused by slower biological processes affecting mortality and fertility schedules of prey (Arntz et al., Chap. 2) and predator. Following the time course of effects provides clues to the causal chain through which EN influenced pinniped populations.

The most immediate effects of EN were created by the increase in sea level combined with heightened storm activity in the eastern Pacific. The best example of this was the large storm-related mortality of elephant seal pups described in Section 26.2.1.

The rapid change in SST accompanied by the drop in thermocline to greater depth during EN also had an immediate effect on pinnipeds by causing changes in the local distribution of prey. Deepening of the thermocline together with reduced upwelling in the shelf ecosystem, the otariids' foraging habitat, caused a decline in phyto- and zooplankton density near the surface. This in turn diminished the near-surface food resources of fish and cephalopod prey species of pinnipeds. This led to a decrease in body condition of fish, best documented for the Humboldt current system off Chile and Peru (Arntz et al., Chap. 2). It seems likely that changed vertical migration (i.e., fish stayed deeper) and increased dispersal of fish shoals made foraging increasingly difficult for pinnipeds (sea Sect. 26.2.3).

A second effect of EN was large-scale movement of prey organisms. This came about simultaneously with local redistribution and produced longer-lasting effects. Off Peru, benthic fish migrated to greater depths after the onset of EN, while fish with a strong cold preference initially gathered in remaining coastal pockets of cold water upwelling. The South American fur seal in Peru may have experienced this change as an initial increase in prey availability with a subsequent decline as local resource depletion and migration of fish to depth or south to cooler waters occurred. Similar migrations influenced the food resources of pinniped species in temperate zones (Arntz et al., Chap. 2; see Sect. 26.2.3). Redistribution and decrease in energy content of prey species thus had strong and almost immediate effects on pinnipeds.

The decline in prey availability associated with EN 1982–83 led to an observable reduction in body condition of adult animals of some species. Decreased physical condition of adult females then caused reduced milk production (Iverson et al., Chap. 19), decreases in the number of estrus females, or reduced pregnancy rates as indicated by the reduced number of copulations (Francis and Heath, Chap. 12). In gray seals (*Halichoerus grypus*), implantation is closely linked to an increase in food availability resulting in fast deposition of blubber (Boyd 1984). The reduction in pregnancy rates during EN may indicate that pinniped females have to increase fat reserves before reproduction (for similar effects in humans, see Frisch 1985, 1988).

The lowered growth rates of pups of many species led to poor condition of surviving young and to long-term reduced survival of cohorts born during the peak of EN (Tables 1, 2). For elephant seals, reduced juvenile survival occurred as a consequence of lower prey availability (see Sect. 26.2.3), even though initial growth of pups appeared normal during EN (Le Boeuf and Reiter, Chap. 23; Huber et al., Chap. 24; Stewart and Yochem, Chap. 25).

Most of these effects became evident while the meteorological and oceanographic signals of EN were still recognizable; but other effects of EN on pinniped food resources became obvious only when these signals had largely disappeared. The delay was apparently caused through loss (by mortality or migration) and reduced fertility of adult fish. Smaller fish stocks, with individuals of low body condition, reproduced little or not at all in the EN year or the year following it (Arntz et al., Chap. 2). Thus, whole cohorts of prey species were lost with the corollary that fish standing stocks were decreased for one to several years after EN. These effects on prey stocks may explain the lasting influence of EN on pinnipeds after the oceanographic signals had subsided. York (Chap. 9) discusses the ways in which a

4-year delay between an EN event and its positive effect on cohort survival can come about in subpolar areas. For northern fur seals, this is probably related to better juvenile survival of some fish like herring which in turn then provide more food to juvenile fur seals when they begin independent foraging.

Interestingly, the rebound of the marine ecosystem appeared to be more rapid in the tropical Pacific where initial effects were more extreme (Arntz et al., Chap. 2). At temperate latitudes, full EN effects took longer to develop and lasted longer than in the tropics. For example, in the Peruvian system the food chain is especially short and usually ends with a single species, the anchovy. Anchovy consume most of the primary production and produce most of the biomass that is harvested by top predators (Pauly and Tsukayama 1987). Fast recovery of this species can therefore mean a quick return of the ecosystem to an apparently normal state. Perhaps the less complex food web of tropical upwelling systems recovers faster from population crashes or the component species of tropical ecosystems are better adapted to swings from boom to bust conditions than those of temperate systems.

The longest lags in EN effects on pinnipeds are caused by changes in population structure due changes in mortality and fertility. Adult mortality coupled with the loss of several cohorts (Majluf, Chap. 5; Trillmich and Dellinger, Chap. 6) and partial loss of one or two cohorts as observed in temperate zone pinnipeds (DeLong and Antonelis, Chap. 7; Francis and Heath, Chap. 12; Le Boeuf and Reiter, Chap. 23; Huber et al., Chap. 24; Stewart and Yochem, Chap. 25) will change the population composition and its reproductive output for a long time. Full recovery to pre-EN population sizes will vary with latitude and with the number of year classes affected. Twenty years after an intentional kill of females, the Pribilof Island population of northern fur seals was still not fully recovered due to the loss of potential female recruits (York and Hartley 1981). The Galapagos fur seal population, which lost a large proportion of adult females and three full cohorts during EN 1982–83, will similarly show the effects for many years to come. More temperate populations can be expected to experience less dramatic, but nevertheless significant, long-term reductions in numbers due to a decrease in the number of female recruits. EN aftereffects will show up as a decline in the number of pups born when females of the reduced cohorts are entering reproductive age.

In summary, the most important long-term population effect of EN, with delays on the order of one to several generation times, is increased adult female mortality. Next in importance (and for elephant seals perhaps the most important EN effect) is the loss or partial loss of cohorts of juveniles and pups. Another major long-term population change was brought about by large-scale emigration. In California sea lions on the Channel Islands, this may have led to a major population redistribution (DeLong et al., Chap. 17), and in northern fur seals on San Miguel Island, it temporarily reversed the long-term trend of a population increase (DeLong and Antonelis, Chap. 7). Emigration may also have caused a major loss to the Peruvian population of the South American fur seal (Guerra and Portflitt, Chap. 4; Majluf, Chap. 5).

26.3 Conclusions

26.3.1 Comparison of Pinnipeds and Seabirds

During the 1982–83 EN, ornithologists gathered extensive data on seabirds in the same area of the eastern Pacific as the pinniped studies reported in this book. A comparison between these two widely differing groups is of interest because pinnipeds and seabirds have to deal with similar ecological problems. Similarities and differences in the effects of EN on the two groups can therefore be used to expose, and increase understanding of, specific adaptations and constraints in the way in which species deal with environmental disturbances.

During the migration period, phocids and otariids behave like open ocean foraging birds, which are free to follow food-rich currents or stay in patches of high food abundance (Hunt and Schneider 1987). Nonmigratory and lactating otariids resemble inshore feeding seabirds during the breeding season when they are tied to the local food resources in their sometimes large "patch" of nearshore habitat. Although the monogamous mating system permits seabirds to share the burden of chick rearing, seabirds as well as otariid pinnipeds have to leave their young while hunting at sea and to return to them at intervals. The length of the feeding cycle partially depends on the distance to the foraging areas. Thus seabirds, like otariids, follow a central-place rearing strategy.

There are, of course, pronounced differences in the physiology and ecology of pinnipeds and seabirds. For allometric reasons (Lindstedt and Boyce 1985), as well as to maintain flying ability, even a maximally fat seabird will store less fat relative to metabolic demand than a much larger pinniped. Only the penguins, because of their size and flightlessness, can build up substantial nutrient deposits to cover their own metabolic needs while fasting for prolonged periods during chick rearing.

Since seabird parents cannot store nutrients in their own body tissues for later transfer to young, they must transport food to their chicks in their stomachs (Costa 1990). This method of provisioning young contrasts strongly with the ability to digest food and convert it into blubber and milk, which are easier to store and higher in energy content. Lactation thus allows pinnipeds to store large amounts of energy and nutrients over a relatively long period for later feeding of young. As a consequence of their lack of storage ability, adult seabirds and their chicks are less capable than pinnipeds of bridging long intervals of food shortage.

Differences in the foraging ecology of the two groups are also marked: most seabirds gather their food from the surface or from a thin upper layer of the ocean. Only penguins, alcids, and perhaps cormorants appear able to dive consistently to depths greater than 20 m (Kooyman and Davis 1987; Kooyman 1989). During warm water conditions, only these species may thus be expected to follow prey species to depths as pinnipeds seem able to do, whereas all other surface-feeding seabird species would be cut off from their food supply.

26.3.1.1 Effects on Mortality and Breeding Success

From these differences in size, provisioning strategy and foraging ecology between seabirds and pinnipeds one would expect stronger EN effects on seabirds than on pinnipeds. This is indeed the general pattern. In the tropical Pacific (Galapagos and Peru) boobies, cormorants, pelicans, and penguins abandoned their nests, eggs, and chicks leading to almost total breeding failure (Arntz 1986; Valle et al. 1987; Duffy et al. 1988; Schreiber and Schreiber 1989). In addition, adult mortality in seabirds was far more massive than in pinnipeds. Duffy et al. (1988) estimated adult mortality of Peruvian boobies (*Sula variegata*), Guanay cormorants (*Phalacrocorax bougainvillii*), and Peruvian pelicans (*Pelecanus occidentalis*) as near 85% (cf. our pinniped data in Tables 1, 2).

Data for the northern hemisphere show the same trends, but the responses of seabirds in this area were more varied (Ainley et al. 1988; Schreiber and Schreiber 1989). Along the coast of North America, EN effects on seabirds were delayed by 1 year, i.e., most pronounced in 1983 and 1984 as we noted for pinnipeds. All seabird species on the especially well-studied Farallon Islands were strongly affected during 1983. Adult mortality of cormorants and alcids was higher than normal, breeding success was reduced, and chick growth was slowed, leading to longer times to fledging and lower fledging weights (Ainley et al. 1988). Species feeding locally on benthic organisms (pigeon guillemots, *Cepphus columba*, and pelagic cormorants, *Phalacrocorax pelagicus*) were most strongly affected. Even further north, along the Oregon coast, researchers noted deleterious effects of EN on seabirds in 1983 (Hodder and Graybill 1985). Finally, in Alaskan waters, effects were noted in 1983 but were hard to interpret, as mentioned earlier (Hatch 1987).

In general, latitudinal trends in seabird mortality and the reduction in breeding success parallel effects found in pinnipeds, but EN effects and after effects seem to have caused stronger negative effects on chick growth and survival and perhaps adult mortality among seabirds than among pinnipeds. This may be related to the lower fasting tolerance of seabirds.

26.3.1.2 The Role of Emigration

The majority of seabirds can emigrate from areas of poor food conditions much faster than pinnipeds (or penguins). The ability to emigrate large distances from the core of the EN event may have saved many adult seabirds. In Peru, boobies, cormorants, and pelicans were observed to emigrate southward, and Galapagos blue-footed boobies (*Sula nebouxii*) apparently moved toward mainland South America. The return of thousands of adults of these species shortly after the end of EN in 1983 indicated that emigration had been successful for many. Similarly, the Humboldt penguin (*Spheniscus humboldti*) colony in Punta San Juan, Peru, was reduced to only 1% of the birds during EN (Duffy et al. 1988). Later on, many returned and by 1985 colony size was back to normal (Hays 1986).

In Galapagos, nearshore feeders (the Galapagos penguin, *Spheniscus mendiculus*, and the flightless cormorant, *Nannopterum harrisi*) showed the strongest adult mortality (77% and 49%, respectively; Valle et al. 1987). Given these species' limited traveling speeds and body reserves, they may have been unable to emigrate successfully to more suitable habitat, a problem which they apparently shared with the Galapagos pinnipeds.

Along the coast of North America major movements of seabirds were also noted. Cool water species migrated further offshore and many subtropical species followed warm water further north than their usual northern limit (Ainley et al. 1988). Increased northward migration of pinnipeds was also noted by Huber (Chap. 13), particularly for immature California sea lions. In summary, dispersal appears to have been a successful strategy to avoid the worst impact of EN-related changes in food resources for both seabirds and pinnipeds. But this strategy was not open to species feeding locally on benthic organisms, like many of the seabirds mentioned above, or to species which were stuck in the isolated food patches of near-coastal habitat.

Monitoring seabirds would therefore appear to provide a faster indication of changes in marine conditions than similar monitoring of pinnipeds. On the other hand, most seabirds more easily abandon breeding attempts and emigrate from disturbed oceanic areas than pinnipeds and therefore pinnipeds, and especially lactating females, may provide better indicators of local long-term effects.

26.3.1.3 Other Effects on Population Dynamics

An interesting phenomenon that deserves further attention in studies of pinniped populations was noted by ornithologists on the Farallon Islands during EN. The assumption of stability of some seabird populations over the period of EN proved to be erroneous since different individuals were breeding before and after EN (Ainley et al. 1988). Previously nonbreeding birds moved in to fill vacancies left by the mortality of breeding birds. This was demonstrated for populations of banded western gulls (*Larus occidentalis*) and Cassin's auklets (*Ptychoramphus aleuticus*) on the Farallons.

In some species of seabirds the breeding failure during EN was followed by an apparent population increase after the event ended. This was most likely caused by more synchronous breeding of the remaining birds, the majority of which responded with a breeding attempt when food resources returned to a more favorable state (Ainley et al. 1986, 1988). We have noted the same phenomenon in the Galapagos fur seal (Trillmich and Limberger 1985; Trillmich and Dellinger, Chap. 6). This effect will, in both groups, speed up recovery from environmentally caused population crashes.

Seabird observations also suggest another interpretation of the delayed onset of breeding seasons during and after EN, which was observed in two pinniped species (DeLong and Antonelis, Chap. 7; Stewart and Yochem, Chap. 25). Later onset of seabird breeding seasons on the Farallons could have been a secondary consequence of the changed age structure of the populations (Ainley et al. 1988). If floaters entered the population of breeders after EN, their lower efficiency may have caused later onset of breeding and reduced mean fertility in 1984 (Ainley et al. 1988). We cannot presently decide whether this effect might also have contributed to the later arrival of breeding female pinnipeds ashore.

26.3.2 Phocid-Otariid Differences in Reproductive Strategy

Pinnipeds face a foraging versus reproduction dilemma. They forage at sea and breed on land because their young are initially bound to land. Females of the two families of pinnipeds, the phocids and otariids, use two entirely different strategies in dealing with this dilemma. In most phocids, reproductive events are isolated from foraging in space and time while in otariids the two activities are intertwined.

Elephant seals forage most of the year without returning to the breeding grounds except to molt. Females travel as far as necessary and stay in good food patches as long as profitable while storing large amounts of nutrients. Costa et al. (1986) calculated that a female elephant seal need only increase her food intake by about 10% per day above her own needs to gather all the nutrient reserves needed for the 28-day period of lactation ashore. As in most phocids, lactation is then fueled entirely from body reserves. Therefore, the location of breeding areas is largely independent of the location of concentrated food resources. Fasting proves to be the key strategy phocids use for solving the food versus reproduction dilemma.

In phocids, large amounts of high energy milk are transferred to the young in a very short time, 4 days to about 6 weeks depending on the species. At the end of this period young are abruptly weaned and are left to their own devices. At this stage they have about 25% of the mother's body mass (Costa 1990). Much of the mass of recently weaned young is a large energy deposit stored as subcutaneous fat which enables them to live up to several months without feeding until they begin to feed on their own.

In contrast, otariids reproduce in a way that we described above as central-place rearing. They give birth to their young in places where high food-abundance ecosystems are nearby and permit fast gathering of food during short foraging trips. Mothers alternate between short 1–3 day long stays ashore and hunting sojourns at sea which may last from 1 to 8 days depending on the species. Trip length is constrained by the pups' ability to fast and to maintain a net mass gain over time. Given that otariid milk never contains much more than 50% fat, and that there is a limit to the quantity of milk a female can produce, otariid foraging trips appear limited to about 7 days. This constraint makes the location of otariid breeding grounds dependent on a combination of distance to and food density in foraging areas: they can afford to travel farther if resources are richer. Mothers must not only replenish their own body stores during the time at sea, they must also pay for the cost of travel between breeding and foraging site and store enough nutrients for lactation during the next stay ashore with the pup. The metabolic overhead of this strategy is much larger than of the phocid rearing strategy, since considerable energy is expended for shuttling between the breeding colony and the foraging grounds. In addition, otariids take more time before weaning their pups, usually between 4 and 12 months, but in exceptional cases up to 36 months. Pups also begin feeding on their own before weaning. They are weaned when they have attained between 40 and 55% of maternal body mass.

As expected from the differences in the lactation strategies of otariids and phocids, starvation of pups due to insufficient milk transfer did not play a role in elephant seal pup mortality. Even if our studies spanned a wider range of latitudes and species we would not expect phocids to show the same tropical-temperate gradient of EN effects on pup mortality as otariids.

Another difference between phocids and otariids that follows from the differences in rearing strategy is that phocids, and to some extent subpolar otariids, provide their young with fat stores and wean them when they are still naive about foraging. This results largely from the short time they spend at maternal care. This strategy can only be successful if food is relatively easy for an unexperienced animal to catch. Temperate and tropical otariids, on the other hand, wean young that are not very fat, but that have some foraging experience. If food is less abundant or difficult to catch, gaining more foraging experience while still supported by maternal milk may be critical for juvenile survival and the otariid strategy allows for this.

Both phocid and otariid males fast during the reproductive season because intrasexual competition does not permit them to forage intermittently at sea. If they did, they would lose opportunities for reproduction and may risk losing their territories or dominance positions to other males. The obvious solution to this problem is to forage more or less independently of a land base during most of the year gathering body stores. These reserves are then used for maintenance during the breeding season on shore. Males are thus shielded from fluctuations in prey abundance during the breeding season, but are fully impacted by whatever conditions they meet upon returning to the sea.

Knowing about the differences in the life history of female otariids and phocids and male vs female pinnipeds, we are now in a position to evaluate the differences found in the effects of EN on otariids and phocids. This can tell us which stages in their life cycles are most susceptible to environmental fluctuations.

26.3.3 The Influence of the Timing of EN Effects

Otariids

The onset of EN will have different effects depending upon which stage of the life cycle is affected. We observed EN effects at various stages of the otariid reproductive cycle, although our data set is confounded by the change in latitude and the corresponding change in the strength of the effects. We can adjust for some of these confounding variables by also observing the effects of weaker ENs on the same population as e.g. in Peru (Majluf, Chap. 5).

In Galapagos, EN began during the peak of the birth season of fur seals and sea lions. In both species growth rates of pups decreased immediately as mothers' time at sea increased (Trillmich and Dellinger, Chap. 6). Decreased provisioning rates led to almost complete pup mortality within a few months of the onset of the event. However, where EN is not as strong, flexibility in the duration of maternal care buffers the impact. Buffering is best demonstrated by Majluf's data for the South American fur seal in Peru. During the 1987 EN, growth rates of pups decreased but mortality rates did not increase. Even though pups were small at 4 months of age, they nevertheless survived as well as other cohorts which grew much faster (Majluf, Chap. 5).

Otariid mothers are continuously exposed to and informed about foraging conditions during lactation, and therefore, are immediately affected by deterioration of the food supply. This may actually work to their advantage. If pup survival becomes unlikely, the earliest possible cessation of investment will allow a female to attend to her own survival as well as garner energy for subsequent offspring. The mechanism by which maternal effort is ended may lie in maternal physiology. Since lactating females forage longer during poor food conditions (see Sect. 26.2.3) in order to obtain enough resources for lactation as well as their own metabolic demands, pups may starve to death during very protracted feeding trips, especially if such trips are consecutive. This effectively constitutes pup "abandonment".

Otariids in the California system were not affected by EN in 1982 before their young were 3–4 months old. The only clear change here was an increase in the period of maternal care (Francis and Heath, Chap. 21) thus reducing the impact of EN. However, increased maternal care entailed a great cost to mothers through reduced fertility. This effect was more pronounced in otariids than in phocids (Tables 1–3; cf. DeLong et al., Chap. 17, on sea lions; DeLong and Antonelis, Chap. 7, on fur seals; Aurioles and Le Boeuf, Chap. 11, on sea lions; Le Boeuf and Reiter, Chap. 23, and Huber et al., Chap. 24, on elephant seals). While phocid mothers showed only slight decreases in pup production, sea lions produced only half as many pups in 1983 as in 1982.

Reproductive output of otariid mothers was reduced even when lactation was not extended: in 1983, northern fur seals at San Miguel weaned their young as usual after about 4 months. Nevertheless, they produced fewer young in 1984. The mortality of recently independent northern fur seal young also appeared to increase during the subsequent months (DeLong and Antonelis, Chap. 7 see also Sect. 26.3.4). Even in the tropics, otariid populations began to recover immediately after the end of EN as soon as feeding conditions returned to normal. This is possible because mothers do not depend on body reserves for pup rearing but on food available at the time of rearing. In California, recovery in the otariid populations did not occur until 1985 since the long-term effects of the EN carried over into 1984 (see above).

Phocids

EN in 1982 first influenced temperate waters in Sept./Oct. when elephant seal mothers had already gathered the majority of the nutrient reserves needed for successful pup rearing. Consequently, the period of pup rearing showed few effects of EN (aside from the direct physical storm effects). However, the subsequent stages in the cycle, foraging to recover some of the resources lost in lactation prior to molting, and foraging until the next pupping season, were affected as shown by the longer foraging of females before returning to molt (Le Boeuf and Reiter, Chap. 23) and by reduced natality in the next season (Huber et al., Chap. 24).

Phocid pups are shielded from the effects of environmental fluctuations while still dependent on their mothers, but juveniles are adversely affected when they begin foraging at times of low food abundance. This was most noticeable in the reduced long-term survival of the 1983 cohort. Juveniles are expected to be less capable of sustained deep diving than their mothers because of lower body size. This has been shown for the Weddell seal, *Leptonychotes weddelli* (Kooyman et al. 1983), where the 13-min aerobic dive limit (i.e., the time they can spend under water without incurring an oxygen debt) of juveniles was about half the 20–25-min aerobic dive limit of adult animals (see also Gentry et al. 1986a). However, this explanation may not apply to elephant seals. By 14 months, juvenile elephant seals showed the same dive depth/duration pattern as adult females (Le Boeuf unpubl. data). Alternatively, less hunting experience of juveniles as compared to adults may cause the decreased survival of juvenile elephant seals when food is scarce.

The unusually long duration of the 1982–83 EN provided the opportunity to record the effects of long-term reductions in food supply on a phocid. The 1984 elephant seal reproductive season was preceded by a year of EN influence. This had no effect on adult female mortality or on the number of pups born on Año Nuevo island (Le Boeuf and Reiter, Chap. 23), but it increased the females' tendency to skip one reproductive season, and decreased the number of pups born on the Farallon Islands (Huber et al., Chap. 24). Apparently, the animals at the species' northern distribution limit were affected more by the changes than were Año Nuevo animals. The reasons for this difference are not known, but clearly food shortages can influence a female's ability to implant the fertilized egg or to pay the metabolic cost of gestation. Thus, the phocids are most sensitive to food shortages during the long foraging period at sea, the nonreproductive season. As a corollary of reduced food intake during their first year at sea, growth of juveniles is presumably retarded, and age at primiparity is delayed.

EN events of more "normal" duration, the composite ENs of Wyrtki (see Fahrbach et al., Chap. 1), may begin to affect the temperate areas off California in January. This would presumably lead to less pronounced changes in adult behavior and fertility, but may influence juvenile survival similarly as we found for the 1982–83 EN.

Unlike lactating otariids, breeding phocids of both sexes as well as breeding male otariids do not gather information on feeding conditions during the reproductive season. During very strong ENs they may not be able to replenish body reserves lost during the reproductive season quickly enough. Could such an effect be responsible for the absence of phocids in the eastern tropical Pacific?

26.3.4 Potential Selective Effects of Environmental Fluctuations Like EN on Pinnipeds

None of our results are sufficiently detailed to permit direct measurements of selection due to EN conditions. Nevertheless, on the basis of the documented effects, we consider it useful and of value for future studies to build hypotheses on the selective effects of environmental variance on pinniped life history.

26.3.4.1 Effects on Maternal Strategies

What effect could recurrent EN events have on the evolution of the patterning of maternal care in otariids? We noticed no effect of EN on the population of northern fur seals in the Bering Sea (Gentry, Chap. 8), but a severe one on the small population which recently colonized temperate San Miguel Island (DeLong and Antonelis, Chap. 7). This species invariably weans its young after about 4 months. It shares this characteristic with its southern counterpart, the Antarctic fur seal (*Arctocephalus gazella*) which also lives in a relatively predictable subpolar environment. Populations of both species suffered high pup mortality under adverse environmental conditions (Croxall et al. 1988; Costa et al. 1989; DeLong and Antonelis, Chap. 7). Apparently, the maternal strategy of these subpolar species is not flexible enough to compensate for periods of low food availability by increasing the lactation period, thus helping juveniles to ease into independent foraging and increasing their probability of survival.

These results are of great interest because they are our only example of the impact of EN on a population with a fixed time to weaning. Growth of the San Miguel colony presently still partially depends on continuing immigration. This apparently precludes genetic adaptation to local conditions in the California Current system. Northern fur seals on San Miguel followed a rigid, genetically programmed time course in their pup rearing. This strategy is probably adaptive in the subpolar areas where they normally breed, but has major disadvantages when animals live under temperate conditions. The same applies to Antarctic fur seals which breed on temperate Marion Island (Kerley 1985).

All other otariids, sea lions and fur seals alike, are much more flexible in the duration of lactation, which allows them to buffer their young against unpredictable reductions in food resources. It seems logical that a more flexible patterning of maternal effort will be selected for when environmental circumstances vary unpredictably, if the benefit of lengthening the lactation period (i.e., increased juvenile survival) outweighs any decrement in future offspring production (i.e., reduced female fertility).

At the same time, lengthening of the nursing period should allow juveniles to gather foraging experience before they become totally independent. In such a variable rearing system there needs to be communication between young and their mothers as to the degree of nutritional dependence or independence. While such a system is open to cheating from the side of the young (Trivers 1974), it allows females to adjust maternal effort in relation to environmental circumstances. EN could be one source of variation selecting for increased flexibility of the maternal strategy. This agrees with the degree to which this flexibility is observed at different latitudes: at high latitudes with highly predictable seasonality northern fur seals (and Antarctic fur seals) show no flexibility of weaning age, whereas at low latitudes Galapagos fur seal mothers wean their young at any time between 10–36 months. A similar though lower flexibility was also noted for the South American fur seal in Peru (Majluf, Chap. 5) and the California sea lion (Francis and Heath, Chap. 21).

Whereas very strong EN events like the one in 1982/83 destroy all offspring of a given cohort, as in the Galapagos fur seal, less violent fluctuations will lead to differential survival of young as observed in the California otariids and the fur seal in Peru. If such events recur frequently enough they could lead to selection on mothers for giving up the current reproductive effort in favor of a future one if the probability of less severe environmental conditions in the next reproductive cycle is sufficiently high. During EN in 1982/83 many female otariids were at sea for so long that their young starved to death. It has been postulated for the northern fur seal that mothers return to their pups when they have replenished their body stores up to a set threshold (Costa and Gentry 1986). They then transfer milk to the pup until their body stores reach a lower threshold whereupon they leave again to forage. Interindividual variation in the position of the upper and lower threshold could well become a target for selection. Mothers in a relatively predictable environment may face less of a survival cost if they allow body stores to fall to a lower setpoint than animals in a less predictable environment. This would apply if lowered fat stores imply more of a mortality risk to a mother in an unpredictable environment.

In phocid seals, it is more difficult to envisage how selection would act on maternal strategies since survival of both mother and pup depend on body stores during and at the end of lactation. Bigger females may have an advantage during periods of food shortage since they can carry and transfer more reserves to their young than smaller mothers (Lindstedt and Boyce 1985). To young, the advantage of being bigger (bigger in terms of more lean body mass) may consist of increased diving ability once they begin their independent foraging. In addition, pups with larger fat stores at weaning can spend more time gaining hunting experience once they enter the sea before their body stores fall to critically low levels (Reiter et al. 1978).

For mothers, being bigger could also be disadvantageous, since in absolute terms a bigger animal utilizes more food per unit time. This need for more food could become critical for a big female under conditions of food shortage, whereas at the same time the larger size of the young of a big mother (Costa et al. 1988) would confer an advantage to her due to a higher survival probability of her offspring. Without detailed modeling it is hard to guess where the optimum size of a female would fall under conditions of variable prey abundance, but it seems a worthwhile exercise to model this problem of a size-dependent shift in the trade-off between fertility and survival.

In the elephant seal, age at primiparity was delayed in cohorts grown up under EN conditions (Le Boeuf and Reiter, Chap. 23; Huber et al., Chap. 24). If large size of mother and pup alike confer a survival advantage, unpredictable variance in environmental conditions could select for delayed primiparity in both phocids and otariids. This would allow females to grow to a larger size before first reproduction. Costa et al. (1988) have shown that in the Antarctic fur seal female size is correlated positively with pup size. Thus, bigger mothers produce bigger pups and may increase the survival chances of their pup. If under fluctuating prey abundance, growth rates of subadults fluctuate strongly between cohorts, age at primiparity may come more under the control of body size rather than of age per se and this could result in greater variance in the age at primiparity in more tropical pinniped populations. We presently have no data to test this hypothesis.

26.3.4.2 Effects on Male Size and Sexual Selection

A decrease in male size reduces the absolute amount of food needed for maintenance metabolism. If food shortages occur frequently and cannot be evaded by migration to more productive areas, this could select for reduced male size. These arguments may explain why the Galapagos fur seal has the least pronounced sexual size dimorphism of all otariids. Similarly, fully adult male California sea lions on Galapagos (*Zalophus californianus wollebaeki*) appear smaller than males in California (*Z. c. californianus*), but exact morphometric data on California sea lion males from the Galapagos population are not available.

Environmental fluctuations, which decrease male adult or juvenile survival for certain cohorts, may decrease the average intensity of intrasexual selection. During EN, increased mortality or skipping of reproductive seasons among breeding males was observed in many species (Tables 1–3). Nearly 100% of the territorial male fur seals died in the Galapagos. If many breeding males die during EN, male-male competition among the survivors necessarily decreases. The extent of this decrease in male-male competition depends on the proportion of fully adult males that actually become territorial in a given season. Males, which are subadult at the time that breeding males experience increased mortality, also face less fierce competition by older males in the next breeding season. Similarly, males born in, just before, or just after the cohort(s) with reduced survival at the pup stage also face less competition when they become territorial.

The intensity of male-male competition is considered the selective process responsible for the major size difference between male and female polygynous pinnipeds (e.g. Bartholomew 1970). Environmental fluctuations, which cause increased male mortality, would therefore be expected to reduce intrasexual selection for large male size. This agrees with the latitudinal trend in size dimorphism found in otariids: at nearly equal female body mass, male northern fur seals have five to six times higher body mass than females, whereas male Galapagos fur seals weigh only about twice as much as females.