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PINNIPED POPULATION DYNAMICS IN CENTRAL CALIFORNIA: CORRELATIONS WITH SEA SURFACE TEMPERATURE AND UPWELLING INDICES

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ABSTRACT

We investigated effects of marine climate variability on pinniped populations and assessed the initial stages of recovery following implementation of the U.S. Marine Mammal Protection Act (MMPA) based on long-term (1973–1997) population surveys at the South Farallon Islands and Point Reyes Peninsula, central California. California sea lions increased over the study period, with peak numbers observed during and after major El Niño events. The rate of increase for California sea lions appears to have decreased in recent years. Steller sea lions decreased at the South Farallon Islands and remain depleted at Point Reyes Peninsula. Harbor seal populations increased in a logistic and non-linear fashion at Point Reyes Peninsula and the South Farallon Islands, respectively. Harbor seals were more abundant at the South Farallon Islands during years of relatively high sea-surface temperature, which may be related to their inability to find sufficient prey in coastal waters under these conditions. Northern elephant seal abundance increased in a logistic fashion over the study period at both the South Farallon Islands and Point Reyes Peninsula; however, productivity at the South Farallon Islands decreased in recent years. Maximum haul-out numbers for elephant seals at the South Farallon Islands increased in the 1970s, maintained an asymptote throughout the 1980s and early 1990s, but recently declined; additional studies are needed to investigate which age classes are associated with this decline. Protection afforded by the MMPA has facilitated partial to full recovery of all populations except for Steller sea lion. Oceanographic relationships do not appear to confound interpretations of population recovery and may help to explain changes in the Steller sea lion population.

Key words: California current marine ecosystem, climate variability, logistic growth, oceanographic conditions, pinniped population dynamics, population recovery.

The distribution and abundance of species varies with both intrinsic population processes and extrinsic forces, such as changes in environmental conditions. In the coastal marine ecosystem of California, both basin-wide (*e.g.*, El Niño) and local (*e.g.*, upwelling) physical oceanographic processes may influence the abundance of pinnipeds. Long-term trends in environmental conditions also have been identified (Roemmich and McGowan 1995). As an index to marine climate, sea-surface temperature (SST), measured at a series of sampling stations throughout the California current ecosystem, has increased considerably during the past decades. Changes in the abundance of both lower (zooplankton: Roemmich and McGowan 1995) and upper (fish: Francis and Hare 1994; birds: Veit *et al.* 1996) trophic-level organisms have been associated with the observed changes in SST (reviewed by Hayward 1997). Prey availability is the likely proximate mechanism influencing pinniped distribution and abundance during broad-scale or local, short- or long-term oceanographic change (Barber and Chavez 1983, Trillmich and Ono 1991). Marine climate change also may complicate interpretations concerning management or other protective measures.

Six pinnipeds occur in the Gulf of the Farallones, central California (Bonnell *et al.* 1983, Allen 1994): California sea lion (*Zalophus californianus*), Steller sea lion (*Eumetopias jubatus*), northern fur seal (*Callorhinus ursinus*), Guadalupe fur seal (*Artocephalus townsendi*), northern elephant seal (*Mirounga angustirostris*), and Pacific harbor seal (*Phoca vitulina richardsi*). Each requires terrestrial habitat for hauling out (*i.e.*, resting) and reproduction. From various shore-based sites it is possible to obtain an annual index of population size and investigate factors influencing the populations. Our specific objectives herein are to: (1) describe qualitatively and quantitatively changes in the breeding and haul-out populations of four pinnipeds in the Gulf of the Farallones from 1973 through 1997, (2) investigate whether annual variability in population size is associated with variability in certain oceanographic conditions, and (3) provide insight into the recovery, or lack thereof, of these species' populations following implementation of the U.S. Marine Mammal Protection Act and other protective measures.

Study Area and Methods

The Gulf of the Farallones is part of the California Current System, widely regarded as one of the most productive marine ecosystems in the world (Glantz and Thompson 1981). Hydrographic processes vary seasonally, including a period of intense coastal upwelling from March through May/June each year. Upwelling and ocean mixing during winter months may be especially important to the development of a robust marine food web in the region (Ainley *et al.* 1993). In particular, the combination of phasing and intensity of coastal upwelling may be crucial to food web development. Upwelling in the Gulf of the Farallones also varies annually, due in part to the influence of El Niño and other atmospheric relationships and teleconnections in the North Pacific Ocean (Emery and Hamilton 1985). These broad-scale oceanographic events

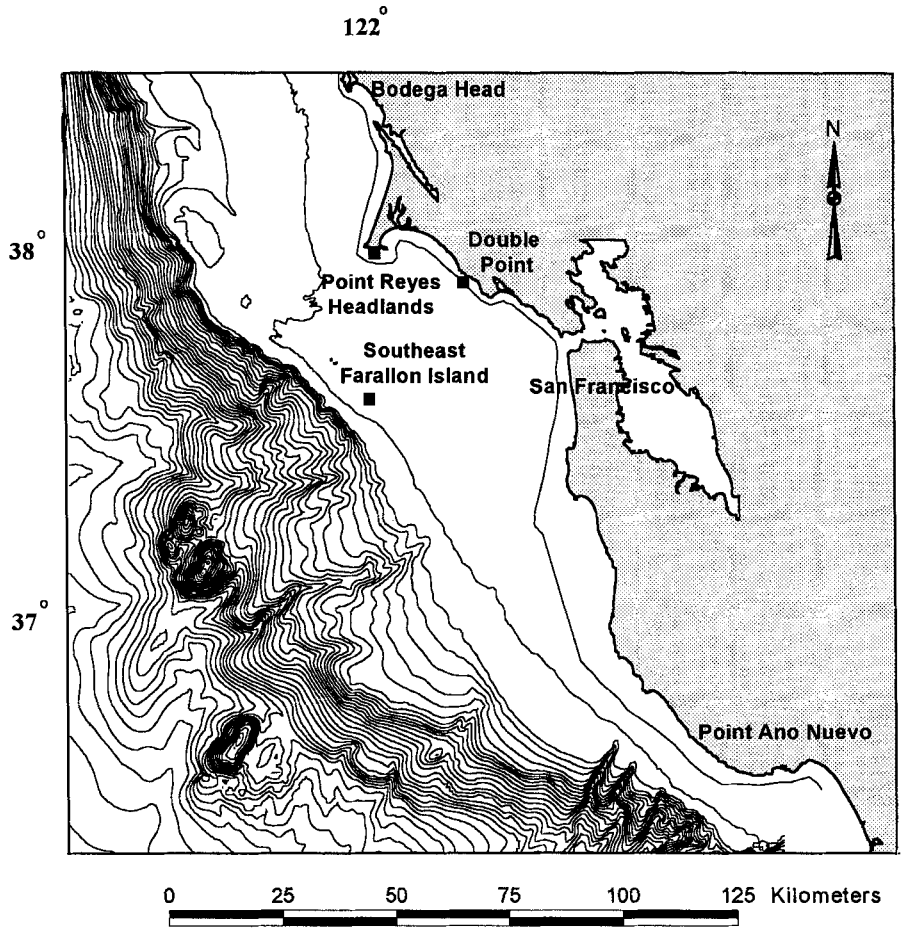

Figure 1. Map of Gulf of the Farallones, central California, showing locations of Point Reyes, Double Point, and South Farallon Islands. Studies of California and Steller sea lions and harbor and elephant seals conducted at South Farallon Islands. Studies of northern elephant seals conducted at Point Reyes and of harbor seals at Double Point.

may disrupt or prevent effectual upwelling, thereby affecting food web development. In turn, marine mammals and other upper trophic level marine predators generally demonstrate reductions in population size, productivity, and/or survival during years of poor oceanic productivity (Trillmich and Ono 1991, Ainley *et al.* 1995).

We studied pinniped populations at the offshore South Farallon Islands and the mainland sites of Point Reyes headlands (Point Reyes Peninsula) and Double Point (Fig. 1). South Farallon Islands and Point Reyes Peninsula are separated by approximately 30 km of ocean habitat. The South Farallon Islands are situated on the edge of the continental shelf, thereby affording pinnipeds relatively quick access to deep ocean waters. Point Reyes Peninsula juts out

from the mainland into the ocean and is indirectly responsible for a persistent plume of upwelled water which develops off this section of coastline; this plume often encircles the South Farallon Islands. Double Point, located ~10 km south of the Point Reyes Peninsula headlands, is a large pocket beach isolated by two small coastal promontories. All of these locations are under protection: the South Farallon Islands are protected as the Farallon Islands National Wildlife Refuge under the jurisdiction of the U.S. Fish and Wildlife Service; Point Reyes Peninsula headlands and Double Point are part of the Point Reyes National Seashore, under the U.S. National Park Service.

Breeding Populations

During winter, northern elephant seal rookeries are found on both South Farallon Islands and Point Reyes Peninsula (Stewart *et al.* 1994). By observing tagged and/or individually marked females and regularly censusing both rookeries, we estimated the number of pups born each year at each site (for additional details see Huber *et al.* 1991, Sydeman *et al.* 1991). During spring, we estimated the number of harbor seal pups born at Double Point by counting adults and pups a minimum of four times during the peak of the breeding season (mid April–mid May). The Double Point harbor seal breeding population estimates are conservative, based on direct counts of live and dead pups. We assessed the breeding population size of Steller sea lions on the South Farallon Islands based on numbers of pups born by conducting a minimum of eight surveys during the peak of the breeding season (May–July). Because few pups are produced on the South Farallon Islands, we estimated changes in population size based upon numbers of females. Production of California sea lions at South Farallon Islands has been limited to few pups over the past two decades (Point Reyes Peninsula Bird Observatory, unpublished data). Due to the infrequent nature of reproduction of California sea lions in central California, we omitted these data from further consideration.

Haul-Out Populations

At South Farallon Islands, we surveyed haul-out populations weekly between 1000 and 1600 throughout the year. We conducted between 40 and 53 censuses annually (Point Reyes Peninsula Bird Observatory, unpublished data). We counted pinnipeds hauled out on the island from vantage points located atop Lighthouse Hill (110 m) and atop Corm Blind Hill (35 m) or by counting from the edges of surge channels. Animals were tallied with respect to various age classes, but only a limited portion of these data are presented herein (see Hastings and Sydeman 1998 for details). At Point Reyes Peninsula and Double Point, we were unable to conduct haul-out population surveys because of disturbance to other wildlife and logistical difficulties. Although fur seals (both northern and Guadalupe) were recorded on the South Farallon Islands and Point Reyes Peninsula during the study period, these species were omitted from analyses due to infrequent observation.

Table 1. Oceanographic correlates of pinniped populations (annual maxima at South Farallon Islands, except where noted) in central California, 1973–1997. Pearson correlation coefficients presented (* = $P < 0.05$). Species abbreviations: NES (northern elephant seal); HS (harbor seal); CSL (California sea lion); SSL (Steller sea lion); FEM (female Steller sea lion). SST refers to sea-surface temperature collected at SFI. UI refers to NOAA/PFEG upwelling indices derived at 36°N. Season abbreviations: FALL (fall); WIN (winter); SPR (spring). See text for details.

Species Seasons	NES (n = 25)	HS (n = 25)	HS[a] (n = 22)	CSL (n = 25)	SSL (n = 24)	FEM (n = 24)
SST–FALL	0.053	0.060	0.212	0.105	−0.075	0.033
SST–WIN	0.371	0.454*	0.321	0.384	−0.162	−0.086
SST–SPR	0.417*	0.592*	0.407*	0.456*	−0.477*	−0.402*
UI–FALL	0.026	0.069	−0.302	0.162	0.041	−0.189
UI–WIN	−0.139	−0.185	−0.010	−0.066	0.162	−0.086
UI–SPR	−0.372	−0.458*	−0.400*	−0.325	0.456*	−0.345

[a] Refers to annual maxima at Double Point, central California. See Figure 1.

Statistical Analyses

We used the maximum count of each species each year and the total number of annual births for northern elephant and harbor seals to assess population trends. To investigate changes in pinniped abundance through time, we fit logistic functions to breeding population estimates. We also fit exponential models to haul-out and breeding population estimates to evaluate rates of population change during different time periods. Assuming exponential population growth, we regressed log-transformed ($\log_e$) abundance estimates against year and then converted exponential rates to finite (*i.e.*, annual) rates of increase using the formulae $\lambda = e^r$ (Caughley 1977; also see Stewart 1992), where $r = \beta_{1,2,\ldots k}$, and β_k refers to each regression coefficient in multiple regression analyses. We report the coefficient of determination (R^2) to assess whether logistic functions or other models fit the data for each species at each location well and to compare competing models. Models with insignificant terms are not reported.

To investigate oceanographic correlates of pinniped abundance and population trends, we correlated log-transformed ($\log e$) annual maxima with sea-surface temperature (SST) and the Upwelling Index (UI; Table 1); we do not report oceanographic correlates of northern elephant seal and harbor seal pup counts because none were statistically significant. We measured SST daily at South Farallon Islands and obtained UI data from National Oceanic and Atmospheric Administration/Pacific Fisheries Environmental Group. We pooled oceanographic measurements into three seasons: fall (October–November), winter (December–February) and spring (March–May) and correlated these values with estimates of pinniped abundance (Table 1). Due to multiple testing, P-values for these correlations should be interpreted with caution. We followed correlation analysis by developing a multiple regression model for each species. We selected the season with the highest correlation coefficient

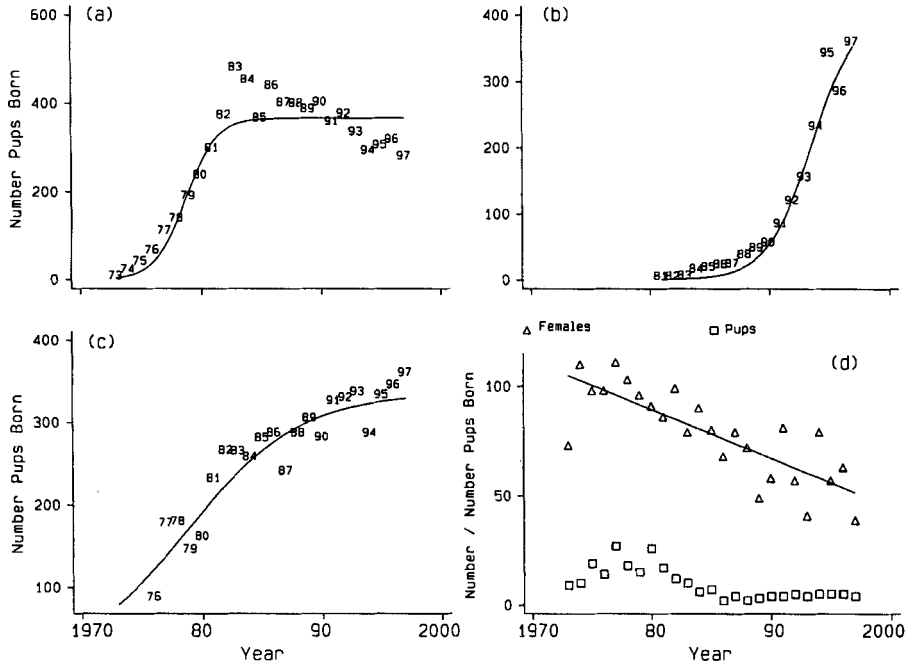

Figure 2. Changes in breeding populations of pinnipeds in central California: (a) northern elephant seals on South Farallon Islands; (b) northern elephant seals at Point Reyes headlands; (c) harbor seals at Double Point, Point Reyes Peninsula; (d) Steller sea lions on South Farallon Islands.

for each oceanographic variable and entered these simultaneously with year (and higher-order time terms [year^2, *etc.*], when necessary) in multiple linear regression models. In this manner we investigated whether oceanographic changes were associated with trends in populations and whether there were significant relationships between pinniped abundance and oceanographic parameters after accounting for population trends.

Results

Breeding Populations

Northern elephant seals recolonized the South Farallon Islands as a rookery in 1972 (Le Boeuf *et al.* 1974, Stewart *et al.* 1994). Numbers of northern elephant seal births followed a pattern of logistic growth (Fig. 2a; β_1 = 366.58, t = 26.79, $P < 0.001$; β_2 = 0.775, t = 3.57, P = 0.002; β_3 = 78.71, t = 189.49, $P < 0.001$, R^2 = 0.976). From 1973 through 1983, the numbers of pups born increased at an average rate of 56.5% *per annum,* whereas from 1983 through 1997 the number of births declined by 3.4% per year. In 1983 a peak of 475 pups was born, while in more recent years number of pups has fluctuated between 200 and 300.

Northern elephant seals recolonized Point Reyes Peninsula in 1981 (Allen *et al.* 1989*b*). The rookery at Point Reyes Peninsula also has grown in a logistic fashion (Fig. 2b; $\beta_1 = 409.85$, $t = 8.50$, $P < 0.001$; $\beta_2 = 0.528$, $t = 5.75$, $P < 0.001$; $\beta_3 = 93.56$, $t = 147.82$, $P < 0.001$, $R^2 = 0.985$). From 1981 to 1988, this population increased by 74.2% per year, whereas from 1988 to 1997 growth was reduced to a rate of 32.8% per year.

Few (<10) harbor seal pups have been born on South Farallon Islands during the past 25 yr (Point Reyes Peninsula Bird Observatory, unpublished data). At Double Point, the number of harbor seal births followed a pattern of logistic growth (Fig. 2c; $\beta_1 = 336.27$, $t = 19.35$, $P < 0.001$; $\beta_2 = 0.210$, $t = 4.48$, $P < 0.001$; $\beta_3 = 78.61$, $t = 107.32$, $P < 0.001$, $R^2 = 0.991$). The population grew at 13.7% per year from 1976 to 1983 and 2.2% per year from 1983 to 1997. The overall rate of population growth was 4.6% per annum ($\beta_1 = 0.045$, $t = 6.98$, $P < 0.001$, $R^2 = 0.71$).

Historically, Steller sea lions pupped at Point Reyes Peninsula, but they have not done so since the mid 1970s (Chan 1979; S. Allen, personal observation). At South Farallon Islands, few Steller sea lion pups were born each year, making it difficult to assess trends in the breeding population based on this index. Nonetheless, there appears to have been a decline in the number of pups born at the South Farallon Islands since the early 1980s (Fig. 2d). The abundance of females (annual maxima) declined at an average rate of 3.6% per year (Fig.2d; from 1974 to 1997; $\beta_1 = -0.035$, $t = -7.14$, $P < 0.001$, $R^2 = 0.70$). The female population was largest in 1977. Notably, during the last six years the abundance of females has fluctuated greatly. The abundance of females was negatively correlated with spring SST (Table 1). However, this relationship was not significant when time trends were accounted for in a multiple linear regression model.

Haul-out Populations

Northern elephant seals are present year-round in central California but are most abundant during the spring molt or the fall juvenile haul-out period (Le Boeuf and Laws 1994; Point Reyes Bird Observatory, unpublished data). We did not have a sufficient continuous-year sample of maximum elephant seal numbers during the spring molt or fall haul-out period for Point Reyes Peninsula to permit statistical analyses for this site. Maximum annual counts of northern elephant seals at the South Farallon Islands increased at 29.1% per year between 1973 and 1978 (Fig. 3a; $\beta_1 = 0.255$, $t = 11.99$, $P < 0.001$, $R^2 = 0.97$), leveled off from 1978 to 1994, and declined in 1995–1997; a significant parabolic pattern of population growth and decline was determined ($\beta_1 = 1.17$, $t = 9.99$, $P < 0.001$; $\beta_2 = -0.007$, $t = -9.77$, $P < 0.001$, $R^2 = 0.86$). Peak numbers fluctuated between 800 and 1,000 animals each year until 1995, when numbers decreased by about 25%. We found a correlation between maximum elephant seal abundance at South Farallon Islands and spring SST (Table 1), but this variable was not statistically significant in a multiple regression analysis including year and its square. The apparent recent

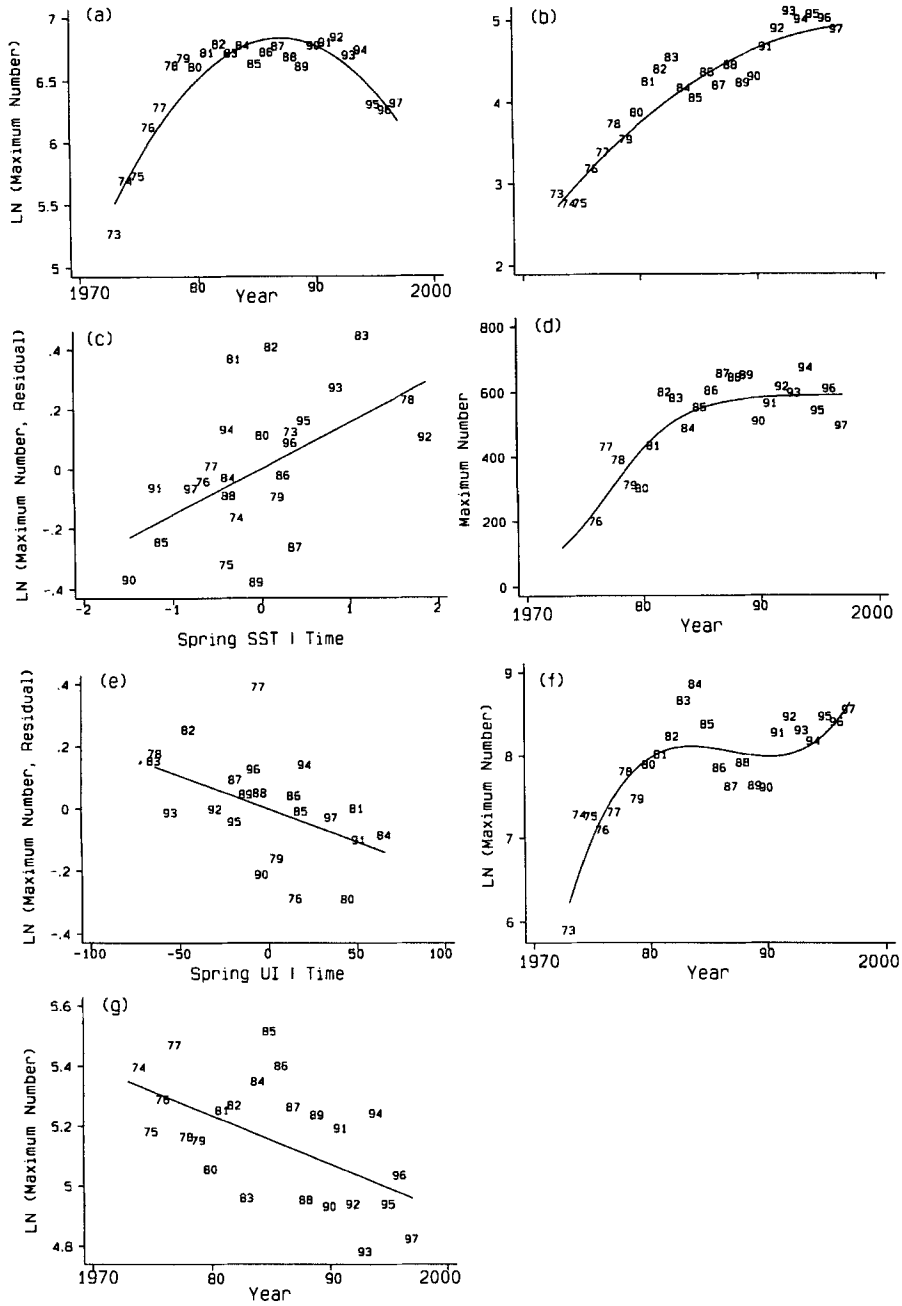

Figure 3. Changes in and oceanographic correlates of haul-out populations of pinnipeds in central California: (a) northern elephant seals on South Farallon Islands; (b) harbor seals on South Farallon Islands; (c) relationship between spring sea-surface temperature (SST) and harbor seal abundance on South Farallon Islands; (d) harbor seals at Double Point, Point Reyes Peninsula; (e) relationship between spring Upwelling Index (UI) and harbor seal abundance at Double Point; (f) California sea lions on South Farallon Islands; (g) Steller sea lions on South Farallon Islands. LN = natural log.

decline may be attributed to population changes in a variety of age classes, because maximum numbers were obtained during the spring molt, when both adult females and subadults of both sexes were counted.

The abundance of harbor seals at the South Farallon Islands (Fig. 3b) increased significantly, although differently than the pattern shown at Double Point (Fig. 3d). At the South Farallon Islands, numbers of harbor seals peaked in 1983, levelled off, and then began to increase again, displaying an overall increase of 9.5% per annum ($\beta_1 = 0.091$, $t = 11.81$, $P < 0.001$, $R^2 = 0.86$). Growth of the South Farallon Islands harbor seal population, however, has slowed in recent years ($\beta_1 = 0.616$, $t = 3.49$, $P = 0.002$; $\beta_2 = -0.003$, $t = 2.97$, $P = 0.007$, $R^2 = 0.90$). From 1973 to 1985, this population grew at an average rate of 15.9% per year, whereas from 1985 to 1997, the rate was 9.0% per year. Abundance of harbor seals at the South Farallon Islands was positively correlated with winter and spring SST and negatively correlated with spring UI (Table 1). A multiple regression including the variables spring SST, UI, and year and its square, revealed a significant positive relationship with spring SST (Fig. 3c) but no influence of spring UI. Together, year and spring SST explained 93% of the variation in harbor seal numbers at South Farallon Islands.

At Double Point, maximum annual harbor seal numbers increased and leveled off during the study period, following a pattern of logistic growth (Fig. 3d; $\beta_1 = 590.74$, $t = 21.85$, $P < 0.001$; $\beta_2 = 0.330$, $t = 2.97$, $P = 0.008$; $\beta_3 = 77.18$, $t = 95.54$, $P < 0.001$, $R^2 = 0.982$). The population grew at 7.6% per year from 1976 to 1989. There were statistically significant correlations between spring SST and spring UI and annual maximum numbers at Double Point (Table 1). A multiple regression including the variables year and its square, spring SST, and spring UI indicated a significant negative relationship between abundance and the spring UI (Fig. 3e) but no influence of spring SST.

California sea lions at South Farallon Islands increased during the study period, following a pattern of reverse sigmoidal population growth (Fig. 3f; $\beta_1 = 18.77$, $t = 3.56$, $P = 0.002$; $\beta_2 = -0.216$, $t = -3.49$, $P = 0.002$; $\beta_3 = 0.001$, $t = 3.41$, $P = 0.003$, $R^2 = 0.73$). Over the entire period the average rate of population growth was 6.0% per year ($\beta_1 = 0.058$, $t = 4.42$, $P < 0.001$, $R^2 = 0.46$). Growth between 1973 and 1979 was 23.1% per year, whereas growth declined to 3.6% per year from 1979 through 1997 (1983–1984 excluded). Peak abundance (~7,000 individuals) was observed in 1983–1984 (and again in winter 1998; Point Reyes Peninsula Bird Observatory, unpublished data), in association with severe El Niño conditions. Omitting data from 1983 and 1984 did not significantly alter estimates of population growth ($\beta_1 = 0.061$, $t = 5.55$, $P < 0.001$, $R^2 = 0.59$). The effect of El Niño on California sea lion abundance at the South Farallon Islands was reflected in a correlation between annual maxima and spring SST (Table 1). A multiple regression investigating this variable, year, and its square and cube, however, revealed no significant relationship with spring SST.

At South Farallon Islands, Steller sea lion haul-out populations were present

year-round, but numbers were often greatest during the breeding season. Steller sea lion haul-out populations varied considerably and declined at an overall rate of 1.6% per annum at the South Farallon Islands (1974–1997; $\beta_1 = -0.016$, $t = -3.20$, $P = 0.004$, $R^2 = 0.32$; Fig. 3g). The abundance of Steller sea lions was correlated with spring SST and the spring UI (Table 1). A multiple regression, however, revealed no significant relationships between Steller sea lion annual maxima and these oceanographic variables.

Discussion

Historically, pinniped populations in central California were exploited for fur, oil, and meat, and many animals were killed due to their interactions with commercial fisheries (Scammon 1874, Ainley and Lewis 1974, Bonnell *et al.* 1983, Lowry *et al.* 1992, Barlow *et al.* 1997). With implementation of protective measures including the U.S. Marine Mammal Protection Act of 1972, the Endangered Species Act of 1973 (U.S. Public Law 93–205), and protected status for terrestrial habitats (*i.e.*, Farallon National Wildlife Refuge and Point Reyes National Seashore), populations have, in general, recovered significantly. While the degree of recovery is difficult to interpret because preexploitation numbers are generally unknown, northern elephant seals on the South Farallon Islands and harbor seals at Double Point appear to have reached current terrestrial carrying capacity. In contrast, while growth of northern elephant seals at Point Reyes Peninsula and harbor seals at the South Farallon Islands appears to be slowing, we suspect that these populations will continue to increase.

Logistic population growth, that is a sigmoidal curve approaching a stable carrying capacity, for pinniped populations has been demonstrated rarely. Our ability to demonstrate logistic population growth is facilitated by the use of extensive time-series of data and the fact that our studies were initiated early in the growth phase of these species' populations. Factors generally thought to limit population growth include prey and habitat availability, acting through density-dependent intraspecific competition. The leveling-off of northern elephant seal abundance at the South Farallon Islands came at the end of an era of relatively rapid expansion of ~8%–14% per year from the early to late 1900s (Cooper and Stewart 1983, Stewart 1992, Stewart *et al.* 1994). Associated with this increase has been range expansion and colonization of mainland beaches in central (Le Boeuf and Panken 1977, Allen *et al.* 1989*b*) and northern California (Jacques and Strong 1995) and Oregon (Hodder *et al.*, in press). Availability of, and access to, high quality breeding habitat may now be limiting the South Farallon Islands northern elephant seal breeding population. Up until 1983, the principle breeding area on the South Farallon Islands was a beach known as Sand Flat. During the El Niño of 1983, large swells associated with storms washed the majority of sand off Sand Flat and out of access routes. Ingress to Sand Flat is now severely limited. Coincident with these habitat changes, there was a substantial decline of breeding females on Sand Flat, from a peak of ~180 in 1983 to about 75 in 1997 (Point Reyes

Peninsula Bird Observatory, unpublished data). Many permanently marked (*i.e.*, tagged) animals moved from Sand Flat to another subrookery, known as Shell Beach, and others have been recorded at Point Reyes Peninsula (Point Reyes Bird Observatory and Point Reyes National Seashore, unpublished data). Consequently, habitat limitations, some associated with deterioration of access routes and others related to quality breeding space, appear primarily responsible for leveling-off and possible decline of the South Farallon Islands northern elephant seal population.

Other factors, such as predation by white sharks (*Carcharodon carcharias*) may also be playing a role in limiting the size of the South Farallon Islands northern elephant seal population. Predation on juvenile and subadult elephant seals hauled out on the South Farallon Islands during fall each year has increased with time (Pyle *et al.* 1996). It is possible that current levels of shark predation are limiting recruitment. Incidental take (*i.e.*, by-catch) in commercial fisheries is not thought to play a major role in elephant seal population dynamics (Barlow *et al.* 1997), although it may affect certain age classes and populations more than others.

Whereas the South Farallon Islands northern elephant seal population appears to have reached carrying capacity, populations at newer locations continue to grow. The Point Reyes Peninsula colony has been growing exponentially, but appears to be beginning to level-off. Coincidentally, there have been recent distributional shifts in the locations of animals on the Point Reyes Peninsula (Allen 1995). While the rookery was limited to a single headlands pocket, animals began breeding in Drakes Bay and at Point Reyes Beach in 1995 (Point Reyes National Seashore, unpublished data). Overall, there appears to be ample habitat (~32 km of sandy beach; Allen 1995) to support a considerably larger breeding population on the Point Reyes Peninsula, but other factors, such as human disturbance, may preclude the establishment of additional rookeries.

The central California harbor seal population has grown considerably over the past two decades, as it has throughout much of the eastern North Pacific Ocean (Allen *et al.* 1989*a*, Huber *et al.* 1994, Barlow *et al.* 1997), but the rate of increase has declined in recent years. Habitat saturation and/or prey limitation may be influencing the population dynamics of harbor seals. The fact that changes in annual oceanographic conditions had demonstrable effects on both the South Farallon Islands and Double Point harbor seal populations suggests that food availability may be involved. Also, a marked peak in harbor seal abundance at the South Farallon Islands occurred in 1983 during an exceptionally strong El Niño event. This observation may be explained by poor food availability during El Niño, which may force seals to leave traditional neritic foraging grounds in search of food in more pelagic waters. Similarly, Brown and Mate (1983) hypothesized that under poor foraging conditions harbor seals in Oregon moved from coastal to estuarine habitats in search of food. The overall increase in abundance at South Farallon Islands must be the result of immigration rather than internal recruitment because of the small number of offspring produced at the South Farallon Islands over the preceding

years. We are unclear as to the limiting factors now affecting harbor seals in central California, but we suspect undisturbed habitat may be limiting breeding populations on the mainland. Incidental mortality in drift and set nets (Barlow *et al.* 1997) and predation by sharks (Ainley *et al.* 1985) also may be limiting population growth.

California sea lion abundance at the South Farallon Islands has fluctuated but appears to be increasing overall. Notably, there was little population growth in the late 1980s, but that pattern changed in the early 1990s (Fig. 3f). Production of California sea lions dropped appreciably during the 1983 El Niño and did not recover to pre-1983 levels until 1987 (Lowry *et al.* 1992, Barlow *et al.* 1997). It is likely that poor production during the mid 1980s explains the relative lack of population growth at the South Farallon Islands during the mid-to-late 1980s. Nonetheless, the overall South Farallon Islands population increase, roughly 6% *per annum* from 1973 to 1997, is comparable to estimated rates of increase based upon studies of pup production at southern California rookeries during roughly the same period (DeMaster *et al.* 1982, Lowry *et al.* 1992). Despite the fact that the California sea lion population is growing, incidental take in commercial fisheries may be limiting the rate of population increase. Barlow *et al.* (1997) reported that entanglement in set and drift nets was responsible for mortality of thousands of animals each year in the early 1990s. California sea lions at the South Farallon Islands increased during the 1983 and 1992 (and 1997–1998) El Niños due, in part, to a general migration northward from southern California breeding grounds. These movements were associated with poor food availability in the Southern California Bight (Trillmich and Ono 1991).

In spite of protection, the South Farallon Islands Steller sea lion population is declining, and the northern fur seal population, which may have numbered upwards of 50,000 on the South Farallon Islands in the late 1700s (Ainley and Lewis 1974), has only recently recolonized the island (Point Reyes Bird Observatory, unpublished data). Furthermore, Steller sea lions have not reestablished a rookery on Point Reyes Peninsula. In 1990, the Steller sea lion was listed as a threatened species under the Endangered Species Act of 1973, mainly because of substantial declines in southwestern Alaska (Merrick *et al.* 1987, Loughlin *et al.* 1992, National Marine Mammal Laboratory 1995). In California, the decline of Steller sea lions on the South Farallon Islands (−3% p.a.) and at Año Nuevo Island (Le Boeuf *et al.* 1991, Ono 1993) is comparable, though less in absolute terms, than the decline (−8% *p.a.*) in southwestern Alaska (National Marine Mammal Laboratory 1995). There may be several factors affecting population parameters of Steller sea lions in California. First, a general warming trend of the ocean may have affected characteristics of the California Current food web, thereby reducing prey availability (Roemmich and McGowan 1995). Second, the expanded California sea lion population may be competing with Steller sea lions for prey. Third, there is evidence that contaminants, disease, and possible synergistic interactions between these factors may be influencing this population. At the South Farallon Islands premature births (some stillborn) accounted for 20%–65% of pup mortality be-

tween 1973 and 1983 (Huber 1984, Hastings and Sydeman 1998). Organochlorine and trace metal contaminants in central California Steller sea lion pups have decreased during the last decade, but levels are still elevated (Jarman *et al.* 1996). Viral and bacterial diseases, such as San Miguel Sea Lion virus and *Leptospira interrrogans serovar pomona,* also have been found in debilitated animals. Finally, small populations may demonstrate unpredictable variability in demographic characterisics (Burgman *et al.* 1993). Irregularities in reproduction (*e.g.*, low birth rates) support the idea that demographic stochasticity is influencing the South Farallon Islands population.

The short-term prognosis for pinniped populations in central California, with the exception of the Steller sea lion, is excellent. Protective measures have facilitated population recovery, some to a level where relative stability may be demonstrated. Moreover, effects of long-term change in the coastal marine food web on pinniped populations have yet to be examined. Although interannual variability in marine conditions did not appear to have long-term detrimental effects on populations, there were clear short-term effects on Gulf of the Farallones pinniped productivity and dispersal characteristics (see also Trillmich and Ono 1991). As the frequency of El Niño and other warm-water oceanographic events has increased in recent times (Quinn *et al.* 1987, Hayward 1997), population-level effects may be more pronounced in the future. Anthropogenic mortality and other demographic effects, most related to incidental take in fisheries, pollutants, and disturbance, also may have slowed population growth. Given changes in environmental conditions and relatively constant, albeit low-level anthropogenic mortality factors, the future of pinniped populations in central California cannot be accurately predicted.

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Literature Cited

Ainley, D. G., and T. J. Lewis. 1974. History of Farallon Island marine bird populations, 1854–1972. Condor 76:432–446.

Ainley, D. G., R. P. Henderson, H. R. Huber, R. J. Boekelheide, S. G. Allen and T. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. Memoirs of the Southern California Academy of Sciences 9:109–122.

Ainley, D. G., W. J. Sydeman, R. H. Parrish and W. H. Lenarz. 1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California: A predator's perspective. California Cooperative Oceanic Fisheries Investigations Report 34:133–139.

Ainley, D. G., W. J. Sydeman and J. Norton. 1995. Upper trophic level predators indicate interannual positive and negative anomalies in the California Current food web. Marine Ecology Progress Series 118:69–79.

Allen, S. G. 1994. The distribution and abundance of marine birds and mammals in the Gulf of the Farallones and adjacent waters, 1985–1992. Ph.D. dissertation, University of California, Berkeley, CA. 379 pp.

Allen, S. G. 1995. Northern elephant seal management plan for Point Reyes National Seashore. Final Report to the Point Reyes National Seashore, Point Reyes National Seashore, Point Reyes, CA. 36 pp.

Allen, S. G., H. R. Huber, C. A. Ribic and D. G. Ainley. 1989*a*. Population dynamics of harbor seals in the Gulf of the Farallones, California. California Fish and Game 75:224–232.

Allen, S.G., S. C. Peaslee and H. R. Huber. 1989*b*. Colonization by northern elephant seals of the Point Reyes peninsula, California. Marine Mammal Science 5:298–302.

Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. Science 222:1203–1210.

Barlow, J., K. A. Forney, P. S. Hill, R. L. Brownell Jr., J. A. Caretta, D. P. Demaster, F. Julian, M. S. Lwory, T. Ragen and R. R. Reeves. 1997. U.S. Pacific marine mammal stock assessments: 1996. NOAA Technical Memorandum NMFS-SWFSC-248. 223 pp.

Bonnell, M. L., M. O. Pierson and G. D. Farrens. 1983. Pinnipeds and sea otters of central and northern California, 1980–1983: Status, abundance and distribution. Final Report to Minerals Management Service, Center for Marine Studies, University of California, Santa Cruz, CA. 220 pp. Available from Minerals Management Service, 770 Paseo Camarillo, Camarillo, CA.

Brown, R. F., and B. R. Mate. 1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. Fishery Bulletin, U.S. 81:291–301.

Burgman, M. A., S. Ferson and H. R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London.

Chan, G. L. 1979. Reconnaissance survey of Double Point, Point Reyes headland, and Bird Rock. Report to California Department of Fish and Game and the State Water Resources Control Board No. 79–15, 80–01, and 80–02. 51 pp. Available from point Reyes Bird observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

Cooper, C. F., and B. S. Stewart. 1983. Demography of northern elephant seals, 1911–1982. Science 219:969–971.

Demaster, D. P., D. J. Miller, D. Goodman, R. L. DeLong and B. S. Stewart. 1982. Assessment of California sea lion fishery interactions. Transactions of the 47th North American Wildlife and Natural Resources Conference, 1982. Wildlife Management Institute, Washington, DC. Pp. 253–263

EMERY, W. J., AND K. HAMILTON. 1985. Atmospheric forcing of interannual variability in the northeast Pacific Ocean: Connections with El Niño. Journal of Geophysical Research 90:857–868.

FRANSCIS, R. C., AND S. R. HARE. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: A case for historical science. Fisheries Oceanography 3:279–291.

GLANTZ, M. H., AND J. D. THOMPSON, EDS. 1981. Resource management and environmental uncertainty. Wiley, New York, NY.

HASTINGS, K. K., AND W. J. SYDEMAN. 1998. History, status and seasonal variation in counts of Steller sea lions, *Eumetopias jubatus*, at the South Farallon Islands: 1927–1996. Final Report to NMFS, Southwest Fisheries Science Center, Point Reyes Bird Observatory, Stinson Beach, CA. Contract number 40JGNF00336. 28 pp. Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

HAYWARD, T. L. 1997. Pacific Ocean climate change: Atmospheric forcing, ocean circulation and ecosystem response. Trends in Ecology and Evolution 12:150–154.

HODDER, J. R., R. BROWN AND C. CZEISAL. In Press. Northern elephant seals in Oregon: A pattern of regular onshore occurrence and breeding range expansion. Marine Mammal Science.

HUBER, H. R. 1984. Premature pupping in northern sea lions on the Farallon Islands. Final Report to the Gulf of the Farallones National Marine Sanctuary, Point Reyes Bird Observatory, Stinson Beach, CA. 12 pp. Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.

HUBER, H. R., A. C. ROVETTA, L. A. FRY AND S. JOHNSTON. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. Journal of Mammalogy 72:535–534.

HUBER, H. R., S. JEFFRIES, R. BROWN AND R. DELONG. 1994. Harbor seal stock assessment in Washington and Oregon 1993. Annual Report to the MMPA Assessment Program, Office of Protected Resources, NMFS, NOAA.

JACQUES, D. L., AND C. S. STRONG. 1995. 1995 Survey of northern elephant seals and other pinnipeds at Castle Rock National Wildlife Refuge. Final Report to the U.S. Fish and Wildlife Service—San Francisco Bay National Wildlife Refuge and Oregon Department of Fish and Wildlife, Cresent Coastal Research, Cresent City, CA. 12 pp. Available from Cresent Coastal Research, 7700 Bailey Road, Cresent City, CA 95531.

JARMAN, W. M., K. A. HOBSON, W. J. SYDEMAN, C. E. BACON AND E. B. MCLAREN. 1996. Influence of trophic position and feeding location on contaminant levels in the Gulf of the Farallones food web as revealed by stable isotope analysis. Environmental Science and Technology 30:654–660.

LE BOEUF, B. J., AND R. L. LAWS. 1994. Elephant seals: An introduction to the genus. Pages 1–28 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

LE BOEUF, B. J., AND K. J. PANKEN. 1977. Elephant seals breeding on the mainland in California. Proceedings of the California Academy of Sciences 41:267–280.

LE BOEUF, B. J., D. G. AINLEY AND T. J. LEWIS. 1974. Elephant seals of the Farallones: population structure of an incipient breeding colony. Journal of Mammalogy 55: 370–385.

LE BOEUF, B. J., K. ONO AND J. REITER. 1991. History of the Steller sea lion population at Año Nuevo Island, 1961–1991. Administrative Report LJ-91–45C. National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla. 9 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038.

LOUGHLIN, T. R., A. S PERLOV AND V. VLADIMIROV. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Marine Mammal Science 8:220–239.

LOWRY, M. S., P. BOVENG, R. L. DELONG, C. W. OLIVER, B. S. STEWART, H. DEANDA

AND J. BARLOW. 1992. Status of the California Sea Lion (*Zalophus californianus californianus*) Population in 1992. Administrative Report LJ-92-32. National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla. 24 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92138.

MERRICK, R. L., T. R. LOUGHLIN AND D. G. CALKINS. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–1986. Fishery Bulletin, U.S. 85:351–365.

NATIONAL MARINE MAMMAL LABORATORY. 1995. Status review of the United States Steller sea lion (*Eumetopias jubatus*) population. National Marine Fisheries Service, Seattle, WA. 61 pp. Available from the National Marine Mammal Laboratory, 7600 Sand point Way N.E., Seattle, WA 98115.

ONO, K. A. 1993. Steller Sea Lion Research at Año Nuevo Island, California, during the 1992 Breeding Season. Administrative Report LJ-93–21C. National Marine Fisheries Service, Southwest Fisheries ScienceCenter, La Jolla. 7 pp. Available from Southwest Fisheries Science Center, P. O. Box 271, La Jolla, CA 92038.

PYLE, P., S. ANDERSON AND D. G. AINLEY. 1996. Trends in white shark predation at the South Farallon Islands, 1968–1993. Pages 375–379 *in* A. P. Klimley and D. G. Ainley, eds. Great white sharks: The biology of *Carcharodon carcharias*. Academic Press, San Diego, CA.

QUINN, W. H., V. T. NEAL AND S. E. ANTUNEZ DE MAYOLO. 1987. El Niño occurrences over the past four and a half centuries. Journal of Geophysical Research 92:14449–14461.

ROEMMICH, D., AND J. MCGOWAN. 1995. Climatic warming and the decline of zooplankton in the California Current. Science 267:1324–1326.

SCAMMON, C. M. 1874. The marine mammals of the north-western coast of north America. Dover Publications, New York, NY. (Reprint).

STEWART, B. S. 1992. Population recovery of northern elephant seals on the southern California Channel Islands. Pages 1075–1086 *in* D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Appied Science Press, New York, NY.

STEWART, B. S., B. J. LE BOEUF, P. YOCHEM, H. R. HUBER, R. DELONG, R. JAMESON, W. J. SYDEMAN AND S. G. ALLEN. 1994. History and present status of the northern elephant seal population. Pages 29–48 *in* B. J. Le Boeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

SYDEMAN, W. J., H. R. HUBER, S. D. EMSLIE, C. A. RIBIC AND N. NUR. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology 72:2204–2217.

TRILLMICH, F., AND K. A. ONO, EDS. 1991. Pinnipeds and El Niño: Responses to environmental stress. Springer-Verlag, Berlin.

VEIT, R. R., P. PYLE AND J. A. MCGOWAN. 1996. Ocean warming and long-term change in pelagic bird abundance in the California current system. Marine Ecology Progress Series 139:11–18.

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