COMMUNITY ECOLOGY OF CALIFORNIA CHANNEL ISLANDS PINNIPEDS

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ABSTRACT

Six species of pinnipeds reside in or seasonally transit waters off the California coast. Four of those (California sea lion, northern elephant seal, Pacific harbor seal, and northern fur seal) breed in substantial numbers and share beach space at many sites on the southern California Channel Islands. But there appears to be little inter-specific competition for food among this guild of sympatrically breeding apex marine predators, evidently owing to seasonal, geographic, and vertical differences in foraging habitats. Northern elephant seals forage at great depths (350 to 1,600 m) mostly at great distances from the islands, harbor seals forage close to the islands on benthic and epibenthic fish and cephalopods at depths of 50 to 450 m, whereas California sea lions and northern fur seals forage principally in upwelling systems throughout the Southern California Bight, and well beyond in some seasons, at depths of 25 to 200 m. These differences in foraging niches may be adaptive responses to interspecific interactions and historic competition for prey resources (i.e., "the ghosts of competition past") or perhaps merely consequences of different phylogeny and adaptions to other selective pressures (i.e., "spandrels"). Regardless, these gross interspecific differences in foraging ecology have promoted long-term growth and maintenance of robust populations while permitting common use of the limited and unique terrestrial habitats of the Channel Islands by this diverse pinniped assemblage. Moreover, the population responses to and recoveries from periodic perturbations to ocean structure and prey communities, associated with El Niño-Southern Oscillation events, have evidently been tempered by these ecological differences. As yet, there is little unequivocal evidence of density-dependent influences on the population trajectories of any pinniped species except, perhaps, harbor seals.

Keywords: California Channel Islands, pinnipeds, harbor seal, northern elephant seal, California sea lion, northern fur seal, Steller sea lion, Guadalupe fur seal, community ecology, demography, foraging ecology.

INTRODUCTION AND METHODS

The southern California Channel Islands support the most concentrated taxonomic diversity of seals and sea lions (pinnipeds) in the world (cf. Reeves et al. 1992; Stewart et al. 1993). These populations have been hunted for subsistence, commercial use and profit, and as perceived competitive predators for centuries (Stewart et al. 1993). As a consequence, northern elephant seals (*Mirounga angustirostris*) and Guadalupe fur seals (*Arctocephalus townsendi*) were extinguished from the Channel Islands, perhaps prehistorically but certainly by the early in the nineteenth century, and indeed believed extinct by the late nineteenth century (Hubbs 1956; Cooper and Stewart 1983). Northern fur seals (*Callorhinus ursinus*) were also evidently extinguished from the Channel Islands prior to the twentieth century, though substantial numbers remained at the species primary rookeries in the Bering Sea despite long-term commercial harvesting (Trites and Larkin 1989; Reeves et al. 1992; Stewart et al. 1993). Similarly, California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina richardsi*) were relatively uncommon on the Channel Islands by the mid-twentieth century (Stewart et al. 1988; Stewart et al. 1993). In 1972, all direct and incidental killing of pinnipeds within U.S. jurisdiction was prohibited, with a few exceptions, with the enactment of the Marine Mammal Protection Act (16 U.S.C. §1361 et seq.). Since then, populations of all species but Steller sea lions (*Eumetopias jubatus*) have steadily increased with only minor interruptions (Stewart et al. 1993; Figure 1; and below).

A number of scientists have conducted various studies of demography, ecology, reproductive behavior, foraging patterns, diet, and physiology during this period of population growth. Here we provide a brief synthesis of some of the studies conducted and published by us and colleagues at the National Marine Mammal Laboratory (NMFS, NOAA, Seattle, WA; e.g., see DeLong and Melin 1999, this volume), the Southwest Fisheries Science Center (NMFS, NOAA, La Jolla, CA), and the California Department of Fish and Game in collaboration or independently. Our goal here is to provide a basic framework for understanding how these species live and coexist while interacting directly and indirectly in common terrestrial and marine habitats at and near the southern California Channel Islands and, more generally, in the northeast Pacific Ocean. Our specific objectives in this review are to highlight the resources that these pinnipeds use and the similarities and differences, on temporal and spatial scales (geographic and vertical), in their use of those resources.

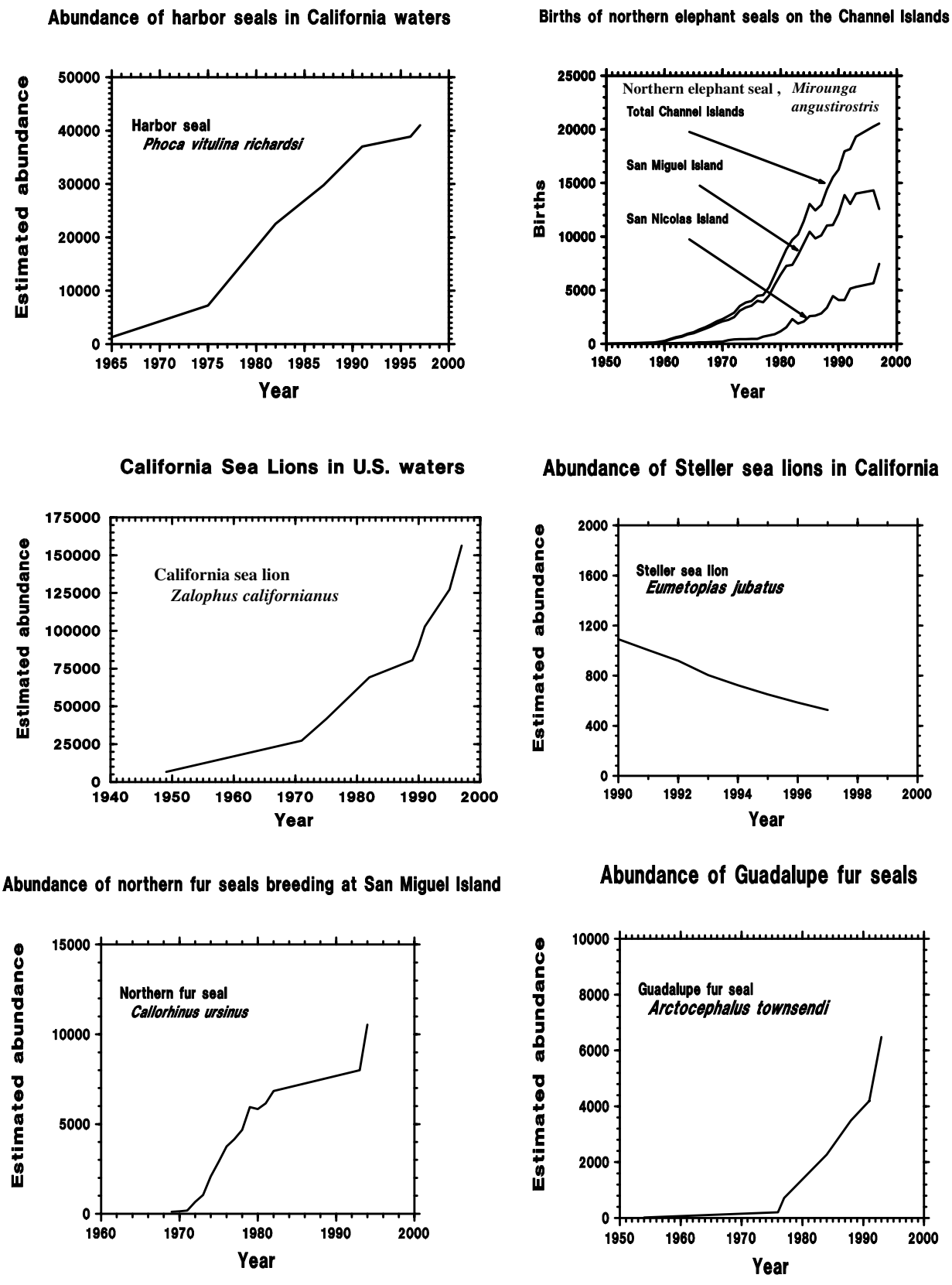

Figure 1. Population trends of California pinnipeds.

RESULTS

Distribution and Seasonal Abundance on the California Channel Islands

Harbor seals haul out and breed on all of the southern California Channel Islands (although numbers are relatively small at San Clemente and Santa Barbara islands) using sheltered coves, intertidal ledges and offshore reefs at fairly consistent locations (e.g., Stewart 1981a; Stewart and Yochem 1984, 1994; Yochem 1987; Yochem et al. 1987). Numbers ashore are greatest in late spring and early summer, when seals are molting, and least in winter (Stewart and Yochem 1994). Harbor seals give birth beginning in late February (although in some years viable pups appear as early as late January); births generally peak in late March and most pups are weaned by late April. Mating occurs in April, May, and early June (Stewart 1981a; Yochem 1987).

Northern elephant seals breed in large numbers at San Miguel and San Nicolas islands, in increasing numbers at Santa Rosa Island, and in relatively small numbers at Santa Barbara and San Clemente islands (Stewart and Yochem 1986; Stewart 1989; Stewart et al. 1993; Stewart et al. 1994). Elephant seals breed at San Miguel and San Nicolas islands from late December through mid-February and then occur again in relatively large numbers from April through July when they are molting (Stewart and Yochem 1984; Stewart 1989). During the breeding season they use virtually all beaches along the southern coastline of San Miguel and San Nicolas islands and only a few locations on the islands' northern shorelines (Stewart 1989, 1992). Numbers ashore are lowest from late summer through early December, when most adults and juveniles are foraging at great distances north from the Southern California Bight (cf. Stewart and DeLong 1995; Stewart 1997a).

California sea lions occur principally at San Miguel and San Nicolas islands, with substantially smaller numbers occurring at Santa Barbara, San Clemente, and Anacapa islands and even fewer at Santa Cruz and Santa Catalina islands (Stewart et al. 1993). At San Miguel Island, most sea lions haul out and breed at the island's western tip, Point Bennett (Stewart et al. 1993), though the numbers of sea lions hauling out seasonally at beaches along the south side of the island, including Crook Point and Cardwell Point, have increased in recent years. At San Nicolas Island, California sea lions now haul out and breed along virtually the entire south coastline (Stewart and Yochem 1984; B. Stewart and P. Yochem, unpubl. data), a substantial expansion of range since the early 1970s (cf. Peterson and Bartholomew 1967; Odell 1975). They are most numerous ashore during the breeding season from late May through early August, and least abundant in autumn and winter when adult and subabdult males, many juveniles, and some adult females are foraging in areas off northern and central California, Oregon, Washington, and British Columbia (Stewart and Yochem 1984; Stewart et al. 1993; Melin 1995).

Historically, Steller sea lions occurred at Point Bennett and Castle Rock at and off the western end of San Miguel Island, respectively, and at a few isolated locations on Santa Rosa Island, Santa Cruz Island and, perhaps, San Nicolas Island (e.g., Bartholomew 1967; Stewart et al. 1993). Steller sea lions breed from late May through early August, when they occur in greatest seasonal abundance at central California rookeries (e.g., Orr and Poulter 1965). Historically, they occurred at the northern Channel Islands during that season at least, though little is known about their former occurrence in other seasons (Stewart et al. 1993). None have bred on the Channel Islands since 1982, and only a couple of individuals have been seen occasionally about San Miguel Island since then (Stewart et al. 1993; B. Stewart, unpubl. data.; DeLong and Melin 1999, this volume).

In southern California, northern fur seals haul out and breed seasonally at San Miguel Island (Adams Cove, Point Bennett) and nearby Castle Rock (DeLong 1982; Stewart et al. 1993; DeLong and Melin 1999, this volume), and a few northern fur seals have hauled out in summer at San Nicolas Island during the past decade (B. Stewart, unpubl. data). They are most abundant ashore during the breeding season at San Miguel Island (Point Bennett and Castle Rock) from late May through July, and most animals leave rookeries and haulouts by early autumn (DeLong 1982; Stewart et al. 1993). Nonetheless, a small number of northern fur seals, mostly juveniles and subadult males, do haul out at Point Bennett throughout winter and spring.

Guadalupe fur seals occasionally appear at isolated spots along the southern coastlines of San Clemente Island (B. Stewart, unpubl. data), San Nicolas Island (Stewart 1981b; Stewart et al. 1987; B. Stewart, unpubl. data) and San Miguel Island (Stewart et al. 1987; B. Stewart, unpubl. data; DeLong and Melin 1999, this volume). Adult males and juveniles have been seen ashore almost exclusively during the summer breeding season, from late May through July, although a female was observed ashore at San Miguel Island in January 1991 (B. Stewart, unpubl. data) and another gave birth at San Miguel Island in 1997 (DeLong and Melin, this volume). In Baja California waters, few seals are ashore in winter (Fleischer 1987; Gallo-Reynoso 1994), although their whereabouts at sea are unknown.

FORAGING HABITATS

Vertical Habitat Use

In southern California waters, harbor seals forage at depths of 10 to 446 m (Figure 2). Most dives, however, are to modal depths of 10, 70, or 100 m, although a deeper mode (280 m) is occasionally apparent in their diving patterns (Stewart and Yochem 1994).

Northern elephant seals forage principally at depths between 250 to 550 m although occasionally they dive to nearly 1,600 m (DeLong and Stewart 1991; Stewart and DeLong 1993, 1994, 1995; Figure 2).

While in southern California waters, California sea lions forage mostly at depths averaging 50 to 100 m although in some warm water years they may forage as deep as 400 to

500 m (Feldkamp et al. 1989, 1991; Melin et al. 1993; B. Stewart and P. Yochem, unpubl. data).

There are no data on dive patterns for Steller sea lions that may forage in southern California waters. In the Gulf of Alaska and off the Aleutian Islands, however, Steller sea lions forage at depths of 10 to 50 m and, on rare occasion, deeper than 250 m (Merrick and Loughlin 1997).

Foraging dives of lactating northern fur seal females breeding at San Miguel Island are relatively shallow, averaging around 25 to 50 m (Figure 2; Stewart and DeLong 1999).

There are no data on dive patterns of Guadalupe fur seals that may forage in U.S. waters, although a record for one female foraging near Isla de Guadalupe in Mexican waters indicated that most dives were shallow, between 10 and 25 m, with a maximum of 82 m (Gallo-Reynoso 1994).

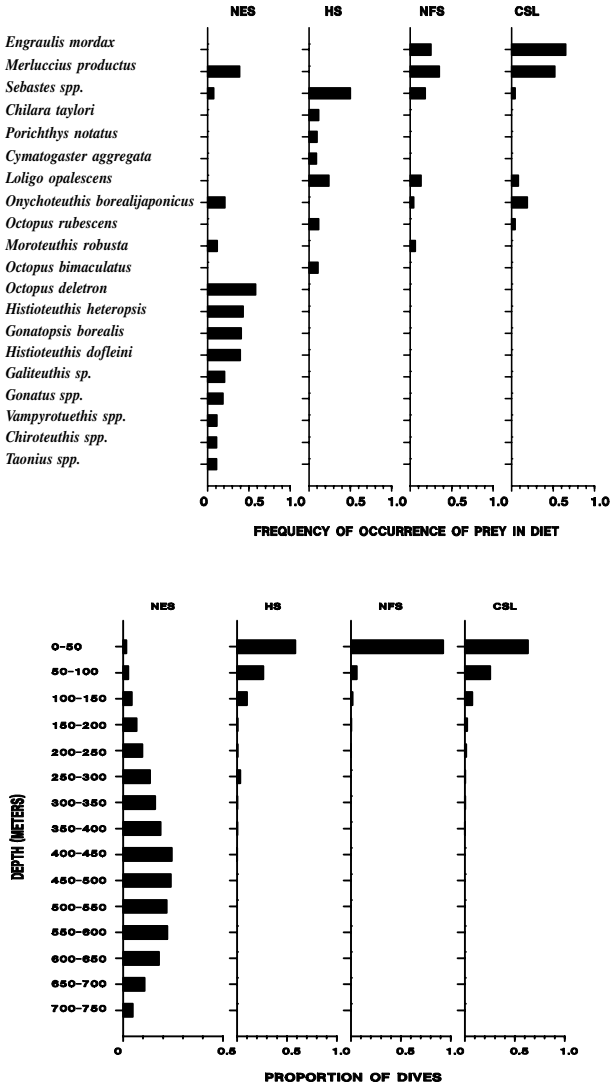

Figure 2. Predominant prey (top) and foraging depths (bottom) of Channel Islands pinnipeds (NES = Northern elephant seal; HS = Harbor seal; NFS = Northern fur seal; CSL = California sea lion).

Geographic Habitat Use

Most harbor seals appear to remain near the Channel Islands year round and forage relatively near island coastlines, although some seals may occasionally move beyond the Southern California Bight seasonally (Stewart and Yochem 1994). Data are not yet sufficient to determine whether harbor seals make intra- or inter-annual migrations or simply disperse to some extent at certain ages.

Northern elephant seals range widely in the North Pacific Ocean and spend relatively little time in the Southern California Bight other than when ashore to breed in winter (one to three months depending on age and sex) and to molt (one month in spring or summer; see Stewart and Huber 1993 for review). Indeed, adults are at sea for about eight to ten months each year and pass quickly through southern California waters once departing island haulouts and rookeries enroute to distant foraging areas in the North Pacific Ocean, Gulf of Alaska and along the eastern Aleutian Islands (Stewart and DeLong 1993, 1994, 1995). The patterns of juveniles and subadults are similar but more variable (Stewart 1997a).

During the breeding season, lactating California sea lions forage relatively near rookeries, primarily in productive upwelling areas around the islands or near Point Conception (Antonelis et al. 1990; Melin et al. 1993: Stewart and Yochem, unpubl. data). Non-lactating females, juveniles, and adult and subadult males are known to depart southern California waters in autumn, particularly the latter which migrate to foraging areas off central and northern California, Oregon, Washington, and British Columbia (e.g., Mate 1975; Huber 1991; Melin et al. 1993; Melin 1995; B. Stewart, unpubl. data.) and evidently forage little in southern California waters.

Nothing is known about the foraging areas or seasonal migrations of Steller sea lions in California waters, although lactating females in the Gulf of Alaska may forage relatively near rookeries year-round (Merrick et al. 1994; Merrick and Loughlin 1997).

The available data for lactating northern fur seal females indicate that they forage mostly in upwelling areas near and west of Point Conception in summer (Antonelis et al. 1990). Presumably they forage further offshore and perhaps further north from autumn through spring, as do most northern fur seals that breed at rookeries in the Bering Sea (cf. Bigg 1990).

Guadalupe fur seals that haul out on the Channel Islands in summer likely forage near the islands during that season, and some fur seals from rookeries in Baja California may migrate into waters of the Southern California Bight and even further north at other seasons (cf. Stewart 1981b; Stewart et al. 1987; Hanni et al. 1997). In Baja California waters, several lactating females that were monitored in summer foraged in deep offshore waters south of rookeries at Isla de Guadalupe (Gallo-Reynoso 1994). Nothing else is

known of the foraging areas nor, indeed, the whereabouts of most Guadalupe fur seals from autumn through spring, when they evidently remain at sea.

Diet

Although harbor seals consume a great variety of fish, cephalopods, and invertebrates, their diet around the Channel Islands is dominated by six prey (Figure 2; Stewart and Yochem 1994; Henry 1997; Henry et al. 1998): rosy rockfish (*Sebastes rosaceus*), chilipepper rockfish (*S. goodei*), spotted cusk-eel (*Chilara taylori*), plainfin midshipman (*Porichthys notatus*), market squid (*Loligo opalescens*), and red octopus *(Octopus rubescens*).

Northern elephant seals prey mostly on epi-, meso-, and bathy-pelagic squid *(Octopoteuthis deletron*, *Histioteuthis heteropsis*, *Gonatopsis borealis*, *H. dofleini*) though some fish (e.g., Pacific whiting, *Merluccius productus*), skates, and rays are also eaten on occasion (Figure 2; Antonelis et al. 1987; Antonelis et al. 1994; Stewart and DeLong 1993).

In southern California waters, prey of California sea lions is predominately market squid, Pacific whiting, jack mackerel (*Trachurus symmetricus*), rosy rockfish, shortbelly rockfish (*Sebastes jordani*), and shiner perch (*Cymatogaster aggregata*) (Figure 2; Antonelis et al. 1984; Antonelis et al. 1990; Lowry et al. 1991; Henry 1997; Henry et al. 1998).

Nothing is known of the diet of Steller sea lions in southern California waters. In northern and central California and in the Gulf of Alaska, they are known to prey on Pacific whiting, walleye pollock (*Theragra chalcogramma*), rockfish (*Sebastes* spp.), cod (*Gadus macrocephalus*), herring (*Clupea harengus*), and squid (Gonatidae) (e.g., Ainley et al. 1982; Reeves et al. 1992; Merrick and Calkins 1996).

Northern fur seals breeding at San Miguel Island eat mostly Pacific whiting, northern anchovy (*Engraulis mordax*), California lanternfish (*Symbolophorus californiensis*), rockfish (*Sebastes* spp.), nail squid (*Onychoteuthis borealijaponicus*), market squid, and north Pacific giant squid (*Moroteuthis robusta*) (Figure 2; Antonelis et al. 1990; DeLong and Antonelis 1991).

Nothing is known of the diet of Guadalupe fur seals in southern California waters. Analyses of five scats collected at Isla de Guadalupe in Mexican waters, however, identified remains of mesopelagic squid (Enoploteuthidae, Onychoteuthidae, Ommastrephidae), and scombrid (*Scomber japonicus*) and clupeid (*Sardinops sagax*) fish (Gallo-Reynoso 1994).

DISCUSSION

Populations of California sea lions, harbor seals, and northern elephant seals have increased steadily in California waters throughout the second half of the twentieth century and are now relatively robust (Figure 1; Stewart et al. 1993; Stewart and Yochem 1994; Stewart et al. 1994).

Northern fur seals and Guadalupe fur seals have also increased in number (Figure 1), although the latter still breed almost exclusively at Isla de Guadalupe in Mexican waters (Stewart et al. 1993; Gallo-Reynoso 1994; Maravilla-Chavez and Lowry 1999). All have demonstrated relatively remarkable resilience to periodic, natural oceanographic perturbations. Even substantial mortality of California sea lions from incidental entanglement in gill nets in the 1980s (cf. DeMaster et al. 1982) evidently had little impact on population vitality.

Populations of harbor seals appear to have stabilized, at the Channel Islands at least (Stewart and Yochem 1994), and their abundance appears to be limited by local benthic and epibenthic prey resources, as there is little evidence for seasonal migration.

Northern elephant seals capitalize on evidently rich, yet poorly known, distant deep-water biological communities to support their breeding and molting tenures on the Channel Islands, when they are completely independent of regional food resources.

During the summer breeding season, lactating California sea lions are limited in their foraging range in the Southern California Bight by the fasting abilities of dependent pups left on land. Dynamic upwelling systems in the Southern California Bight in spring and summer are key to the foraging success of lactating female California sea lions, and consequently to local patterns of sea lion demography. Similarly, such upwelling systems appear to be key to annual reproductive success of northern fur seals at San Miguel Island as substantial declines in natality and great increases in neonatal mortality of both California sea lions and northern fur seals occur during warm water, El Niño-Southern Oscillation events (e.g., DeLong et al. 1991; DeLong and Antonelis 1991; Stewart et al. 1993; B. Stewart and P. Yochem unpubl. data) when those upwelling systems fail.

The reasons for the long-term, substantial decline of Steller sea lions in the Gulf of Alaska and Aleutian Islands, the heart of their range, and the correlative retreat of the southern limits of their range in Southern California, continue to be debated (e.g., Alverson 1992; Pascual and Adkison 1994). However, it arguably appears to be due to substantive long-term shifts in the composition of oceanographic communities owing in part, perhaps, to human intrusion and exploitation of living marine resources.

The simultaneous, long-term, sustained increases of harbor seals, northern elephant seals, California sea lions, northern fur seals, and Guadalupe fur seals along the western coast of North America have evidently been facilitated by intra- and interspecific differences in their spatial (vertical and geographic) and temporal use of marine habitats.

There appears to be little inter-specific competition for food among this guild of sympatrically breeding apex marine predators, evidently owing to seasonal, geographic, and vertical differences in foraging habitats. Northern elephant seals forage at great depths (350 to 1,600 m), mostly at great distances from the islands; harbor seals forage close to the islands on benthic and epibenthic fish and cephalopods at depths of 50 to 450 m; and California sea lions and

northern fur seals forage principally in upwelling systems throughout the Southern California Bight, and well beyond in some seasons, at depths of 25 to 200 m. These differences in foraging niches may be adaptive responses to interspecific interactions and historic competition for prey resources (i.e., the "ghosts of competition past," cf. Connell 1980) or perhaps merely consequences of different phylogeny and adaptations to other selective pressures (i.e., "spandrels," cf. Gould and Lewontin 1979). In any event, these gross interspecific differences in foraging ecology have undoubtedly promoted long-term growth and maintenance of robust populations while permitting common use of the limited and unique terrestrial habitats of the Channel Islands by this diverse pinniped assemblage. Moreover, their population responses to and recoveries from periodic perturbations to ocean structure and prey communities, associated with El Niño-Southern Oscillation events, have evidently been tempered by these ecological differences. Continued study of this diverse pinniped community will offer unique opportunities for evaluating the roles of natural and human-related factors in the limitation and regulation of these important apex predators.

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