2 Biological Consequences of the 1982–83 El Niño in the Eastern Pacific

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2.1 Introduction

The drastic changes in the abiotic environment caused by El Niño (EN) 1982–83 led to marked repercussions in the fauna and flora of the marine ecosystem, including pelagic and benthic marine subsystems and the seashore. Some of them were of a negative, others were of a positive nature. Mass mortalities of some species contrasted with enormous proliferations of others. Many species emigrated during EN from their traditional, cool upwelling areas, which had been converted to tropical or unusually warm conditions. Some moved towards deeper water, others poleward where conditions resembled those in their former habitat. Growth, body condition, reproduction and adult survival of some species were diminished. Also, changes in growth and survival of early life history stages affected recruitment of some species years later. At the same time dispersal stages of warm water species were transported south-/northward, and juveniles and adults actively invaded unusual areas. The biological effects of EN 1982–83 have been summarized in various conference volumes (Arntz et al. 1985b; CONCYTEC 1985; IFOP 1985; Robinson and del Pino 1985; Wooster and Fluharty 1985; IOC 1986; AGU 1987) and a number of reviews (Barber and Chávez 1983, 1986; Arntz 1984, 1986; McGowan 1984; Barber et al. 1985; Mysak 1986; Pearcy and Schoener 1987; Alvial 1988; Arntz and Fahrbach 1991).

Only part of the biological effects caused by EN are of major relevance to the Pacific pinniped populations, and we will concentrate on these changes and their underlying causes. Most effects were connected with changes in composition, distribution, abundance and thus availability of the prey of pinnipeds. We document these changes in order to understand the effects of the 1982/83 EN on pinniped populations along the eastern margin of the Pacific Ocean. We begin by describing the changes in the eastern tropical and subtropical Pacific where EN impacts were most severe and then document changes along the Pacific coast of North America. Documentation of EN effects along the coast of South America is less detailed and not as extensively published as for effects off North America. We therefore decided to give an overview of the effects off South America and treat the changes along the coast of North America in a species by species manner for the most important pinniped prey. In Section 2.4 we attempt to provide an overall view of the ways in which EN 1982–83 affected pinniped prey populations.

2.2 Biological Effects of EN 1982–83 off South America

2.2.1 *The Planktonic Community*

The Humboldt Current upwelling ecosystem, with a primary production of over 1000 g C m^{-2} yr^{-1} (Walsh 1981), is considered to be the most productive current system in the world. Within a narrow band covering only a tiny fraction of the world's ocean surface it was able to supply up to 22% of all the fish caught in the world in the 1970s (Idyll 1973). Under normal, non-EN conditions, effective year-round upwelling recycles remineralized nutrients from shallow depths (40–80 m) to the euphotic layer. There, immense populations of small diatoms make use of the nutrients and the sunlight, and provide a food base for small herbivorous zooplankton. Both phyto- and zooplankton are effectively grazed upon by small shoaling fish, mainly anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*), which are the staple food for most of the higher links in the different food chains which include predatory fish, guano birds and pinnipeds. Usually anchovy and sardine are easily accessible to predators; both species are normally found nearshore, close to the sea surface and in large shoals. Furthermore, they are small, relatively slow swimming species without dangerous defenses, like spines, and can easily be swallowed whole. Up to 1973, anchovy comprised 95% of the total pelagic fish biomass off Peru (Idyll 1973). Since then, the anchovy population has declined substantially, fluctuated markedly and temporarily been replaced by the sardine (Pauly and Tsukayama 1987).

The exceptionally strong 1982–83 EN severely disrupted this ecological system. During the peak of this EN upwelling in most areas became biologically ineffective, especially along the central and northern coast of Peru. Upwelling areas were compressed to narrow strips of 2–5 km width at sites where the cold water system normally extends several hundred kilometers offshore. Coastal winds were favorable for upwelling through March 1983 (Barber and Chávez 1986), but even though upwelling continued, the thermocline was depressed below the depth where water is entrained into the upwelling circulation. This meant that nutrients were concentrated below the depth of entrainment and were no longer transported into the euphotic layer.

EN thus enormously reduced the surface nutrient concentrations. Nitrate, phosphate and silicate values became extremely low for over 6 months (December 1982 to July 1983), and primary production was considerably diminished (Fig. 1). There was a clear N-S gradient in the intensity of the changes brought about by EN, but severe changes in the pelagic environment were registered as far south as 33°S (Muñoz 1985). In Peru, EN 1982–83 continued beyond March 1983 N of Pisco (14°S), whereas conditions returned to normal south of the Paracas peninsula in that month. However, some parts of northern Chile seem to have been affected as late as June 1983 (Avaria 1985b) and Alvial (1985) even suggested that it ended there between August and October 1983. In the Galápagos Islands, nutrient concentrations at the surface were extremely low from December 1982 to July 1983 (Kogelschatz et al. 1985). During March to May 1983, phytoplankton biomass near the center of the island group was reduced to 30% of the mean quantity present in September to

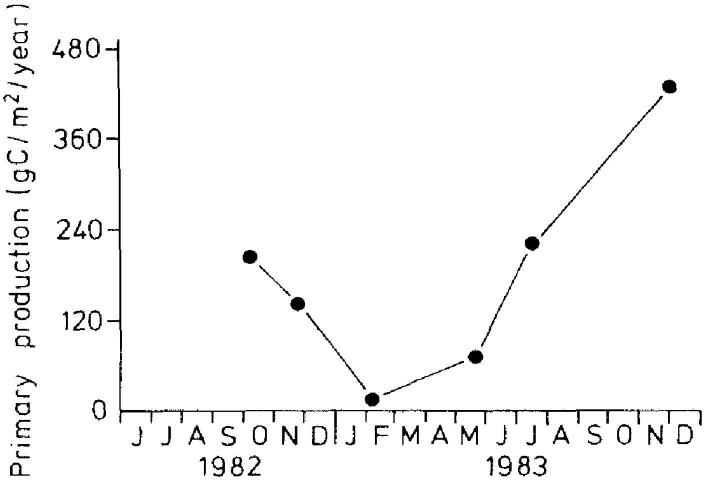

Fig. 1. Changes in primary productivity in the Peruvian upwelling system (redrawn after Chávez and Barber, unpubl.). Area weighed mean primary productivity along 85°W between the equator and 10.5°S

November 1983 (Kogelschatz et al. 1985); the reduction in the western area of the archipelago may have been even greater (Feldman 1984).

The reduction of nutrients by "nutricline depression" (Barber and Chávez 1986) and thus inefficient upwelling, or by temporary cessation of upwelling led to changes in the composition, biomass and production of phytoplankton. Small cold-water diatoms were reduced, (sub-)tropical dinoflagellates, including "red tide" species and large warm-water diatoms were transported into the area, and numerous indicators of oceanic or coastal equatorial waters appeared off Peru and Chile. At the peak of the event primary production in coastal waters off Paita was reduced by a factor of 20 (Barber and Chávez 1986), and biomass off central Peru may have been reduced even more (Rojas de Mendiola et al. 1985).

The reduced primary production also affected the herbivorous grazers in the upwelling system. Drastic changes were registered in species composition, density (reduced) and diversity (increased) of zooplankton. Oceanic copepods were found close to the shore, and large siphonophores, salps, jellyfish, euphausiids, appendicularians, pteropods and chaetognaths replaced the small copepods characteristic of the area during normal times. Biomass of small zooplankton became insignificant whereas that of the larger forms increased due to the much higher individual weight of the tropical species (Santander and Zuzunaga 1984; Carrasco and Santander 1987; Dessier and Donguy 1987).

2.2.2 Nektonic Animals – Pinniped Prey

Decisive changes at the lower levels of the food web, as referred to above, seem to have been the main reason for the alterations in the pelagic fish populations, which in turn influenced the food resources of their warm-blooded predators. In addition, the strong and abrupt increase in temperature and the increased oxygen concentrations near the seafloor may have been of major importance to forage fish.

Under normal conditions anchovy prefer cold water which keeps them in areas where plankton is most abundant (Barber and Chávez 1986). During the summer (January-March), when the coastal current is narrowest, they are densely concentrated in shallow waters and close to shore. At this time of the year they are readily available to fisheries, seabirds and pinnipeds (Idyll 1973; Arntz 1986). During the winter, when warm oceanic waters come closer to the shore, they disperse and remain at greater depths, below the deeper thermocline (Jordán and Chirinos de Vildoso 1965; Saetersdal et al. 1965). Spawning occurs in August and September during the winter and again on a smaller scale in January and February (Jordán and Chirinos de Vildoso 1965; Idyll 1973).

Anchovy carry out diel vertical migrations. During the day they remain in deeper waters, usually not below 50 m water depth, where they form dense shoals. Around dusk, they start dispersing and migrating upwards, until they reach the surface layers. They remain dispersed until dawn, when the whole process is reversed (IMARPE 1969). During spawning these migrations do not always occur (Jordán 1971).

Increased temperature and deteriorated feeding conditions during the 1982–83 EN affected anchovy (Fig. 2), sardine (Fig. 3), and the silverside (*Odontesthes regia*), an important item of the – nearshore – artisanal fishery. There were both behavioral and physiological responses, and both may have been of great importance for the pinnipeds feeding on pelagic fish. Silverside disappeared from shallow waters off Peru in February 1982 and returned only 2 years after EN; in the meantime no specimens were caught at all. Anchovy, sardine and silverside, while disappearing from near-surface waters, undertook active migrations to avoid high temperatures and barren food conditions in their traditional environment. These migrations seem to have been of three different kinds (cf. Valdivia 1978):

1. Some of the fish in Peru concentrated in the remnants of upwelling close to shore. Most of them were trapped there and apparently died, as indicated by occasional reports of dead fish in shallow water and the fact that seabirds or seals

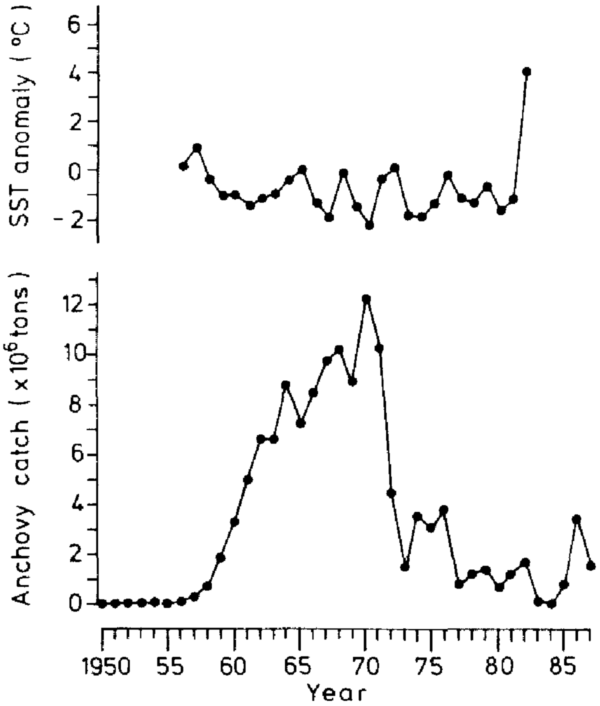

Fig. 2. 1982–1984 Temperature anomaly at Chicama (*above*) and anchovy catch off Peru (redrawn and slightly modified after Barber and Chávez 1986)

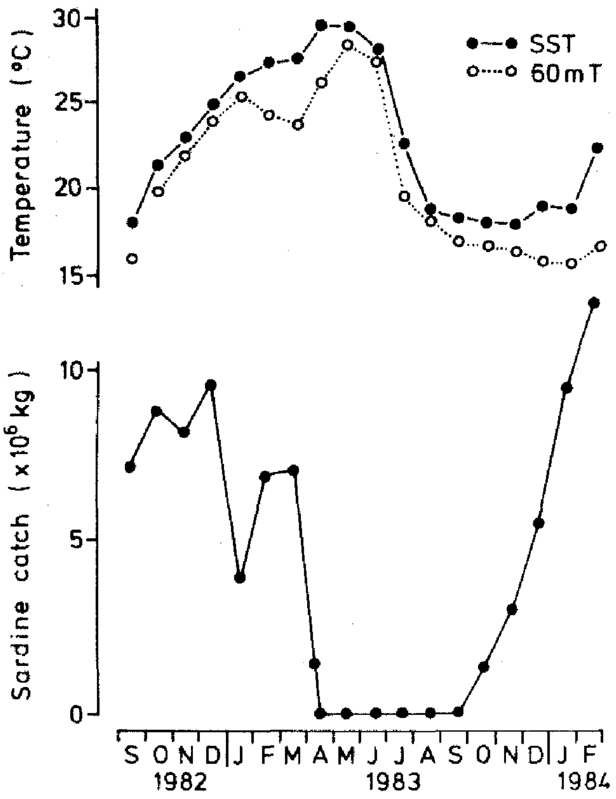

Fig. 3. 1982–1984 Temperature anomaly at Paita (*above*) and the sardine catch off Peru (redrawn after Barber and Chávez 1986)

never found any substantial fish concentrations nearshore in the later phase of EN.

2. Many fish – especially sardine – migrated south into Chilean waters where environmental changes were less drastic. A large proportion of them was caught by the Chilean purse seine fishery which landed nearly 3 Mt of sardine in 1983; few anchovy were caught, however, which means that either anchovy did not join the sardine in their southward migration, or that they were not available to the Chilean purse seines.
3. A third group of fish withdrew to deep water where temperatures were lower than near the surface, but where food conditions must have been miserable. Despite this fact, most of the fish, especially anchovy, that survived may have been those that migrated to deeper areas of the continental shelf, or even down part of the continental slope.

By the end of 1982, the anchovy had suspended vertical migrations altogether and no longer formed large shoals. They always remained below 40–50 m, sometimes close to the seafloor, and between November 1982 and January 1983 were caught at depths between 70 and 130 m by R.V. “Humboldt’s” ground trawl. At the same time, the pelagic trawl caught none. During this same period, sardine disappeared altogether from coastal Ecuadoran waters (Arntz 1986; Maridueña 1986).

Anchovy caught at the beginning of summer 1983 had lost 30% of their body weight and sardines 15% of their normal weight (Dioses 1985), and their lipid content was reduced by about 56% (Romo 1985). Alamo and Bouchon (1987) registered weight losses of 10–20%, but up to 31% for Peruvian sardine in 1982–83. Sardine stomachs contained less and unusual food items compared to normal years, especially off southern Peru. As a consequence of the poor condition of the two species, anchovy spawning failed almost completely in 1982, 1983 and 1984, and sardine spawning was very weak off Peru and Chile in 1982 and 1983 (Santander and Zuzunaga 1984; Retamales and Gonzales 1985). In 1984 and 1985, sardine spawning was about normal, and in 1985 anchovy spawned in an expanded area up to 120 km offshore (Muck et al. 1987; Santander 1987).

Surprisingly, the stock of anchovy which before EN 1982–83 had declined to a very low level (Santander and Zuzunaga 1984) and showed serious depletion during the event, recovered from EN much better than the sardine. In 1985 relatively large concentrations were seen off central Peru, and in 1986, when purse seining for anchovy was opened again, considerable biomass of this species was located off Peru, Ecuador and northern Chile. A substantial proportion of 3–4-year-old anchovy were found among these fish which must have survived the 1982–83 EN, apparently at great depth.

Hake (*Merluccius gayi peruanus*), under non-EN conditions a semipelagic species restricted to the area N of Chimbote (9°S), and some other autochthonous demersal fish of the Peruvian upwelling areas responded to the 1982–83 EN by migrating to deeper waters, often onto the continental slope where they dispersed (Samamé et al 1985). At the same time they started a southward migration and disappeared from Ecuadoran waters (Herdson 1984), taking advantage of the improved O_2 and food conditions at the seafloor. If these fish were prey for sea lions and fur seals before EN, they clearly disappeared from the range of these species under EN conditions.

(Sub-)tropical and oceanic fish species that invaded the area during EN include two mackerel species (*Trachurus murphyi* and *Scomber japonicus*) which normally live further offshore and migrate towards the shore when waters become warmer, bonito (*Sarda chilensis*), dorado (*Coryphaena hippurus*), skipjack (*Katsuwonus pelamis*) and other tunas, and several sharks and rays. None of these species replaced the traditional dominants of the upwelling system as pinniped prey; their size is mostly unsuitable for smaller pinnipeds, some have spines, they never form dense shoals like anchovy and sardine, and are faster swimmers. In addition, the jack mackerel avoided the surface waters during EN, just as the anchovy did, as evidenced by acoustic surveys which showed it to be distributed mainly between 40 and 300 m (Santander and Zuzunaga 1984; Icochea 1989). The only fish species which increased during EN and might have provided suitable food for guano birds and pinnipeds were mullet species (*Lisa* sp.), but they never appeared in quantities comparable to the normal densities of anchovy and sardine.

Along the coast of Ecuador the incidental catches of small squids in the demersal fishery declined about tenfold during 1983. Limited observations in the Galápagos indicated that shallow-water fish did not spawn between October 1982 and April 1983, while in normal years January to April is the peak spawning season for most fish (Herdson 1984). No data are available for the pelagic fish around the Galápagos.

2.3 Biological Effects of EN Off North America

The influence of the 1982–83 EN along the west coast of North America was in many respects the mirror image of that found off South America. However, the biological changes that were coincident with this strong EN were most pronounced during 1983 and 1984, rather than 1982–83 as in the South Pacific. The effects of the EN lingered even though sea temperatures and sea level seemed normal in coastal waters during 1984 (Huyer and Smith 1985; McLain et al. 1985; Cole and McLain 1989).

The biological changes in phyto-zooplankton and nekton that were related to the 1982–83 EN in the Gulf of California, the California Current, the Alaska Current, the Gulf of Alaska, and in the Bering Sea are reviewed in the following.

2.3.1 *Gulf of California*

Changes in plankton and fish that occurred in the Gulf of California (or Sea of Cortez) during EN were markedly different from the rest of the west coast of North America and are therefore summarized separately. Primary production in the central gulf was very high in March 1983 before declining to pre-EN levels in November of 1984 (Baumgartner et al. 1987). This increased primary productivity was coincident with a 52% increase in the catch of sardine (*Sardinops sagax*) and a 49% increase in that of thread herring (*Opisthonema* spp.) for the 1982–83 fishing season (December-May) in comparison to 1981–82 (Mee et al. 1985). In contrast, the total fish catch in 1983–84 declined by 44%, with only 34% of the 1981–82 catch of thread herring. The high sardine catch in 1982–83 may reflect successful recruitment of sardine, whereas the 1983–84 decline in landings was presumably caused by a recruitment failure during EN (Mee et al. 1985). The thread herring migrated further north than normal into the gulf in 1982–83 due to the unusually warm waters. Under more normal thermal conditions during 1984, it penetrated much less deeply into the gulf. Thus, 1983 most likely was a year of unusually rich food resources for pinnipeds inside the Gulf of Cortez.

2.3.2 *The Planktonic Community*

Satellite imagery revealed warm sea surface temperatures (SSTs), with the greatest anomalies along the coast, weakened upwelling, changes in surface circulation, and reduced primary productivity from outer Baja California to British Columbia related to the EN event (Fiedler 1984a). In the California Current off San Diego, elevated SST and a depressed thermocline were detected in March 1983. By August 1983 the nutricline was deep, surface values of chlorophyll were very low and the subsurface chlorophyll maximum was deeper than normal (McGowan 1985). The same patterns were apparent off the west coast of Baja California (Torres-Moye and Alvarez-Borrego 1987).

Off Oregon, SSTs were also abnormally high and the deep thermocline reduced entrainment of cool, nutrient-rich water into the euphotic zone during the spring and summer of 1983. Chlorophyll concentrations were low and the non-upwelling pattern of chlorophyll distribution persisted through most of the summer of 1983, the time of the year that upwelling is usually well developed (Brodeur et al. 1985; Miller et al. 1985; Pearcy et al. 1985; Brodeur and Pearcy 1986).

Macrozooplankton standing stocks were reduced to about 50% of average values in March-May 1983 and about 10% of average in July-September 1983 off southern California (McGowan 1985), to about 30% of non-EN years off Oregon (Miller et al. 1985) and to about 50% off Vancouver Island, British Columbia (Seften et al. 1984). The species composition of zooplankton was altered during the 1983 summer off Oregon, with a persistence of southern species, which typically disappear in the summer (Miller et al. 1985).

The abundance of larval fish was several times lower off Oregon during the summer of 1983 and the species composition was unusual. Species of larvae normally found offshore were found inshore, and the inshore species were reduced in abundance. Northern anchovy larvae (*Engraulis mordax*) were abundant in April 1983, months earlier than in previous years. They were also found closer to shore, indicative of inshore spawning, or onshore advection of eggs and larvae. Osmerid larvae, usually the most common inshore larval fish, were virtually absent in 1983 (Brodeur et al. 1985).

Changes in ocean circulation and productivity and the northward shift of the Subarctic Boundary during 1983 presumably resulted in a lower biomass and smaller individual size of zooplankton in the northern portion of the California Current than found in normal years. These changes may affect the feeding effectiveness and growth rates, and possibly survival, of juvenile salmonids (Fulton and LeBrasseur 1985) and other planktivorous fish. If zooplankton standing stocks decrease in the California Current during strong ENs, they may increase in the Gulf of Alaska. Frost (1983) observed that year to year variations in the zooplankton biomass at Station "P" (50°N, 145°W) were opposite to those in the California Current system.

2.3.3 Nektonic Animals – Pinniped Prey

The following sections are devoted to fish and squids that are known to be important prey for seals, sea lions and fur seals in the California Current, Alaska Current, the Gulf of Alaska, and in the Bering Sea (Table 1). Some species were not considered that are sometimes important prey (such as capelin, sand lance, Pacific saury, gonatid and onychoteuthid squids) because little or no quantitative data are available to assess their abundances. We use a species by species approach, proceeding poleward from species that occupy the southern part of the California Current to those in the Alaska Current, Gulf of Alaska, and then the Bering Sea.

Table 1. Important prey species for pinnipeds in the North Pacific Ocean[a]

	Southern California Current	Northern California Current	Alaska Current Gulf of Alaska	Bering Sea
Northern anchovy	X	X		
Pacific sardine	?			
Pacific mackerel	X			
Jack mackerel	X			
Market squid	X	X		
Pacific whiting	X	X		
Pacific herring		X	X	X
Pacific salmon		X	X	X
Walleye pollock			X	X
Pacific cod			X	X
Atka mackerel			X	X

[a] From Antonelis and Fiscus (1980); Bigg (1985); Perez and Bigg (1986); York (1987); Kajimura and Loughlin (1987).

Northern Anchovy – *Engraulis mordax*

The northern anchovy is an important prey for pinnipeds in the California Current off California (DeLong et al., DeLong and Antonelis, this Vol.; Antonelis and Perez 1984; Perez and Bigg 1986; York 1987). During 1983 and 1984 spawning of the central stock of the northern anchovy expanded farther offshore and to the north than during previous years due to the shift in sea temperature boundaries (Fiedler 1984a; Hewitt 1985; Fiedler et al. 1986). This northward movement of anchovy probably explains the dramatic increase of this species in the diet of California sea lions and northern fur seals on the Channel Islands from 1982 to 1983 (DeLong et al., DeLong and Antonelis, this Vol.).

The total spawning biomass of the stock, which experienced a long-term decline between 1975 and 1983, was not severely affected in 1983, but it reached its lowest level in 20 years in 1984 (Methot and Lo 1987; see Table 2). Anchovy were less available in surface waters to fishermen, and perhaps to pinnipeds, as a result of the deep thermocline during 1983. Aerial spotters detected few schools (CalCoFi 1984; R. Methot pers. comm.). This northward shift in the distribution also occurred for the southern stock which apparently moved into the Southern California Bight from Baja California (R. Methot pers. comm.).

Mortality of yolk-sac larvae was high in 1983 (Fiedler et al. 1986), and the 1983 year class was weak (Methot and Lo 1987). Although the growth of larval anchovy was not affected by low availability of food during the 1982–83 EN, the growth of juvenile anchovy was retarded. Lengths of 1-, 2-, and 3-year-old anchovy were shorter than expected beginning in early 1983, and year classes experienced abrupt increases in length during the fall of 1984 (Fiedler et al. 1986; Butler 1987). Survival of the 1984 and 1985 year classes was higher than that for the 1983 year class (Methot and Lo 1987).

The reduced growth and survival of northern anchovy during EN were most likely caused by the reduced availability of zooplankton which was significantly lower in

Table 2. Summary of abundances, availability and year class success of some important species during 1983 and 1984 along the west coast of North America

Species/stocks	Availability abundance		Year-class strength	
Northern anchovy	1983 – Northward movement	Hewitt (1985) Fiedler et al. (1986)	1983 – Weak	Methot and Lo 1987)
(Central pop.)	1983 – Spawning biomass average 1984 – Spawning biomass low	Methot and Lo (1987) CalCoFi (1984), R. Methot (pers. comm.)	1984 – Average	Methot and Lo (1987)
Pacific sardine	1984 – Large schools in Monterey Bay 1983 – Catches largest in 20 years	CalCoFi (1985)	1983 – Strong	CalCoFi (1985, 1986, 1987)
Pacific mackerel	1983/84 – Northward movement 1983 – Poor catches California	MacCall et al. (1985) Pearcy et al. (1985) R. Klingbeil (pers. comm.)	1983 – Weak 1984 – Weak	MacCall et al. (1985) CalCoFi (1988)
Jack mackerel	1983/84 – Reduced availability California	CalCoFi (1984, 1985)	1983 – Weak 1984 – Strong	
Market squid	1983/84 – Both California fisheries failed	CalCoFi (1984, 1985, 1988) T. Dickerson (pers. comm.)	1983 – Weak?	
	1983/84 – Decreased catches Oregon/Washington 1983 – Increased catches in Puget Sound	Pearcy et al. (1985) Schoener and Fluharty (1985)		
Pacific whiting	1983 – Migrated farther north	R. Methot (pers. comm.) D. Ware (pers. comm.)	1983 – Average 1984 – Strong	Shaw et al. (1988) Hollowed et al. (1988)
Pacific herring	*Spawning biomass*			
N Calif. (S.F. Bay)	1983–84 Season – low	Spratt (1987a)	1983 – Strong 1984 – Strong	CalCoFi (1988), Sprat (1987b)
Oregon	1983/84 Seasons – average	J. Butler (pers. comm.)	1983 – Strong 1984 – Average	J. Butler (pers. comm.)
Washington (Puget Sound)	1983/84 Seasons – average	D. Day (pers. comm.)	1983 – Average 1984 – Average	D. Day (pers. comm.)
British Columbia				
Southern Georgia Strait	1983/84 – Average	Haist et al. (1988)	1983 – Strong 1984 – Average+	Haist et al. (1988) Haist et al. (1988)
Northern Georgia Strait	1983/84 – Low	Haist et al. (1988)	1983 – Strong 1984 – Average	Haist et al. (1988) Haist et al. (1988)

Table 2. (*continued*)

Species/stocks	Availability abundance		Year-class strength	
Southwest Vancouver Is.	1983/84 – Average	Haist et al. (1988)	1983 – Average 1984 – Weak	Haist et al. (1988), D. Ware (pers. comm.) Haist et al. (1988)
Northwest Vancouver Is.	1983/84 – Low	Haist et al. (1988)	1983 – Average? 1984 – Average	Haist et al. (1988) Haist et al. (1988)
Central B.C. Coast	1983/84 – Average	Haist et al. (1988)	1983 – Weak 1984 – Weak?	Haist et al. (1988) Haist et al. (1988)
Prince Rupert District	1983/84 – Average	Haist et al. (1988)	1983 – Average? 1984 – Strong	Haist et al. (1988) Haist et al. (1988)
Queen Charlotte Islands	1983/84 – Average	Haist et al. (1988)	1983 – Weak 1984 – Weak	Haist et al. (1988) Haist et al. (1988)
Alaska				
Sitka Sound	1983 – Average	Funk and Savikko (1989)	1983 – Average 1984 – Strong	Funk and Savikko (1989) Funk and Savikko (1989)
Prince William Sound	1983 – Average 1984 – Average	Funk and Savikko (1989)	1983 – Weak 1984 – Strong	Funk and Savikko (1989) Funk and Savikko (1989)
Kamishak	1983 – Low 1984 – Low	Funk and Savikko (1989)	1983 – Strong 1984 – Strong	Funk and Savikko (1989) Funk and Savikko (1989)
Togiak District	1983 – Average 1984 – Average	Funk and Savikko (1989)	1983 – Average	Funk and Savikko (1989)
Security Cove	1983 – Average 1984 – Average	Funk and Savikko (1989)	1983 – Average	Funk and Savikko (1989)
Goodnews Bay	1983 – Average 1984 – Average	Funk and Savikko (1989)	1983 – Average	Funk and Savikko (1989)
Nelson Island	—		1983 – Average	Funk and Savikko (1989)
Nunivak Island	—		1983 – Average	Funk and Savikko (1989)
Cape Romanzof	1983 – Average 1984 – Average	Funk and Savikko (1989)	1983 – Average	Funk and Savikko (1989)
Norton Sound	1983 – High 1984 – Average	Funk and Savikko (1989)	1983 – Weak	Funk and Savikko (1989)

Table 2. *(continued)*

Species/stocks	Availability abundance		Year-class strength	
Salmon	*Catch and escapement*		*Year of ocean entry*	
Chinook				
California	1983 – Low	PFMC (1984, 1985)	1983 – Average	Pearcy and Fisher (unpubl.), Pacific salmon comm. (unpubl.)
	1984 – Low		1984 – Strong	Pearcy and Fisher (unpubl.), Pacific salmon comm. (unpubl.)
Southern Oregon	1983 – Low	Nicholas and Hankin (1988)	1983 – Average	Pearcy and Fisher (unpubl.)
		Johnson (1988), PFMC (1984)	1984 – Strong	Pacific salmon comm. (unpubl.)
Northern Oregon	1983 – Average+	Johnson (1988)	1984 – Average	Pearcy and Fisher (unpubl.), Pacific salmon comm. (unpubl.)
			1984 – Average	Pearcy and Fisher (unpubl.), Pacific salmon comm. (unpubl.)
Columbia River Tule	1983 – Low	Johnson (1988)		
Coho				
Oregon prod. area	1983 – Low	PFMC (1989)	1983 – Weak	Johnson (1988)
	1984 – Low	PFMC(1989)	1984 – Weak	Fisher and Pearcy (1988)
Washington	1984 – Low	PFMC (1985)		
Carnation Creek, B.C.			1983 – Weak	B. Holtby (pers. comm.)
			1984 – Weak	B. Holtby (pers. comm.)
			1983 – Average	B. Holtby (pers. comm.)
Central British Columbia			1984 – Average	B. Holtby (pers. comm.)
Sockeye				
Barkley Sound, B.C.			1983 – Weak	K. Hyatt (pers. comm.)
			1984 – Weak	K. Hyatt (pers. comm.)

Table 2. (*continued*)

Species/stocks	Availability abundance		Year-class strength	
Central British Columbia			1983 – Average	K. Hyatt (pers. comm.)
			1984 – Average	K. Hyatt (pers. comm.)
Bristol Bay	1983 – High	Eggers and Dean (1987)	1983	D. Eggers (pers. comm.)
	1984 – Average	Eggers and Dean (1987)	1984	D. Eggers (pers. comm.)
Pink Salmon				
Southeast Alaska	1983 – High	Eggers and Dean (1987)	1983 – Strong	D. Eggers (pers. comm.)
	1984 – Average+	Eggers and Dean (1987)	1984 – Strong	D. Eggers (pers. comm.)
Walleye Pollack	*Stock biomass*			
Gulf of Alaska	1983 – Average	Megrey (1989)	1983 – Weak	Megrey (1989)
	1984 – Average	Megrey (1989)	1984 – Weak?	Megrey (1989)
Shelikof Strait	1983 – High	Megrey (1988)	1983 – Weak	Nunallee and Williamson (1988)
	1984 – Average	Nunallee and Williamson (1988)	1984 – Strong?	Nunallee and Williamson (1988)
Eastern Bering Sea	1983 – Average	Wespestad and Traynor (1990)	1983 – Weak	Bakkala et al. (1987)
	1984 – Average	Wespestad and Traynor (1990)	1984 – Average	Wespestad and Traynor (1990)
Pacific cod				
Hecate Strait, B.C.	1983 – Low	Foucher and Tyler (1988)	1983 – Weak	Foucher and Tyler (1988)
	1984 – Low	Foucher and Tyler (1988)		
Gulf of Alaska	1983 – Average	Zenger (1989)	1983 – Average?	Zenger (1989)
	1984 – Average	Zenger (1989)	1984 – Average+	Zenger (1989)
Eastern Bering Sea	1983 – Average	Thompson and Shimada (1990)	1983 – Average	Thompson and Shimada (1990)
	1984 – Average		1984 – Average	
Atka mackerel				
Aleutian Islands	1983 – Low	Kimura and Ronholt (1990)	1993 – Average	Kimura and Ronholt (1990)
	1984 – High	Kimura and Ronholt (1990)	1984 – Average	Kimura and Ronholt (1990)

1983 (McGowan 1985). The influx of zooplankton predators from the south may have affected survival and availability of prey for anchovy. The pelagic red crab (*Pleuroncodes planipes*), a voracious planktonic predator, increased in occurrence in net catches and strandings in 1983 and 1984 (P.E. Smith 1985) and in the diet of California sea lions, northern fur seals and northern elephant seals (Hacker 1986; Antonelis et al. 1987; DeLong et al., DeLong and Antonelis, this Vol.). Pelagic red crabs, which are normally found off the southern tip of Baja California, first appeared in California in October 1982; they reached the waters of the Channel Islands by December 1982, remained in California waters through 1983 (Stewart et al. 1984), and sometimes were caught in huge numbers in bottom trawls (CalCoFi 1984). Predation on anchovy by scombrid predators migrating into California waters from the south may also have increased during 1983 (Bernard et al. 1985).

Off Oregon, the northern stock of northern anchovy spawned earlier in 1983 than in other non-EN years and larvae were unusually abundant in the warm waters close to the coast (Brodeur et al. 1985). Large schools of anchovy that usually occur in the Columbia River plume and estuary were not observed (R. Emmett, pers. comm.).

Pacific Sardine – *Sardinops sagax caeruleus*

Trends in the abundance of the Pacific sardine were opposite those of the northern anchovy (Table 2). Catches, and presumably abundance, have increased from 1974 to 1987. The 1983 year class was strong, dominating the catches in 1984, the year in which the largest catch in 20 years occurred. Sardine, like anchovy, were more available in waters to the north in 1984 than in previous years. Schools were seen in Monterey Bay, California and a substantial portion of the total catch during that year was landed in Monterey (CalCoFi 1985, 1986, 1987).

Pacific Mackerel – *Scomber japonicus*

The total biomass of Pacific mackerel (age 1+) increased sharply in 1977, attained a peak in 1982, and then decreased substantially in 1983 and 1984 because of poor recruitment (MacCall et al. 1985). The 1983 year class was very weak and the 1984 year class was weak in subsequent landings (CalCoFi 1988; R. Klingbeil pers. comm.). This was unexpected since Sinclair et al. (1985) found that EN events and associated high sea levels favored survival of the early life history stages of this species in the California Current.

During 1983–84, this species migrated to the north in large numbers. Schools of Pacific mackerel were abundant in Monterey Bay, the Gulf of Farallon off San Francisco and off Oregon and Washington, and were reported in Puget Sound, along the west coast of Vancouver Island and around the Queen Charlotte Islands (Ashton et al. 1985; MacCall et al. 1985; Pearcy et al. 1985). Off Oregon and Washington, Pacific mackerel was the most abundant nektonic animal in purse seine catches during 1983 and 1984, although it did not even rank among the top ten species during 1979–1982 or 1985 (Brodeur and Pearcy 1986; Pearcy and Schoener 1987). Because of the impressive northward movement of Pacific mackerel, the fishery essentially collapsed in southern California during 1983 (Klingbeil, pers. comm.). This probably explains why this species decreased in importance in the diet of California sea lions on San Miguel and San Clemente Islands between 1982 and 1983 (DeLong et al., this Vol.).

Jack Mackerel – *Trachurus symmetricus*

Landings of jack mackerel declined dramatically during 1983 and 1984 because of their reduced availability in surface waters to purse seines. They were largely unavailable off southern California, but moderate landings were made off central California. Catches continued to be low between 1985 and 1987 (CalCoFi 1984, 1985, 1988). The 1983 year class of jack mackerel was weak (J. Mason, pers. comm.), the 1984 year class strong (T. Dickerson, pers. comm.).

This fish also expanded its range to the north, probably as a response to ocean warming during EN, and was abundant in purse seine catches off Oregon and Washington in 1983 and 1984 compared to other years (Pearcy et al. 1985; Brodeur and Pearcy 1986). The decrease in occurrence of jack mackerel in the diet of California sea lions of the Channel Islands off southern California (DeLong et al., this Vol.) was again likely caused by northward migration out of this area.

Market squid – *Loligo opalescens*

Two fisheries exist for market squid in California: one off southern California, the other off Monterey. Both of these fisheries failed in 1983 (Table 2). The southern fishery had its worst year since the 1960s. Catches in both fisheries were even lower in 1984, either because of reduced abundance or availability on the spawning grounds. Both fisheries rebounded in 1985 and catches have continued to increase since then in southern California with the highest catches on record reported in 1988 (CalCoFi 1984, 1985, 1986; T. Dickerson, pers. comm.). Poor catches of market squid are correlated with their decreased occurrence in the stomachs of California sea lions between 1982 and 1983 (DeLong et al., this Vol.).

Off Oregon and Washington, market squid was usually the most abundant nektonic animal in purse seine catches during the non-EN years of 1979–1982 and in 1985. However, it decreased in rank to sixth in 1983 and to fifth in 1984 (Pearcy and Schoener 1987). Landings of market squid in Puget Sound, Washington, increased substantially in 1983 and 1984 compared with other years (Schoener and Fluharty 1985). This increase was partially due to the use of purse seines and lampara nets only during these years (L. Palensky, pers. comm.).

Pacific Whiting or Hake – *Merluccius productus*

This species, one of the most abundant marine fish in the California Current System, and an important prey for sea lions and fur seals, spawns during the winter off Baja California and juveniles and adults migrate northward during the spring as far north as British Columbia before returning to their winter spawning grounds (Bailey et al. 1982). Neither catches nor spawner biomass of this relatively long-lived fish was depressed during 1983–84. The 1983 year class was weak, but the 1984 year class was strong (Hollowed et al. 1988; Shaw et al. 1988).

Obvious changes in the depth distribution of whiting were not noted during 1983 or 1984. All age groups of Pacific whiting migrated farther to the north in

1983 than in other years (Table 2). Ware (pers. comm.) found that Pacific whiting were farther northward and seaward in 1983 than in the 4 years after 1983. This northward, farther offshore distribution may explain the decreased occurrence of this species in the diet of California sea lions in the Channel Islands off southern California (DeLong et al., this Vol.).

Pacific Herring – *Clupea harengus pallasi*

Because of the many separate spawning stocks of Pacific herring from central California to the Bering Sea, this species, like species of Pacific salmon, can provide unique information on the latitudinal effects of major EN events. The Pacific herring is also an important prey for pinnipeds throughout its range (e.g. Bigg 1985; Perez and Bigg 1986; York, this Vol.). Catches of the herring fishery in San Francisco Bay declined by 40% between 1982 and 1983, and the following winter season of 1983–84 was the poorest since the fishery began in 1973 (CalCoFi 1984, 1985). Spratt (1987a,b) believed that the EN caused unusually high natural mortality of 2–5-year-old San Francisco Bay herring and decreased the abundance of Tomales Bay herring because of altered migration patterns during EN. Growth of herring was also poor during the 1983 EN year. In 1983 there was no weight gain by San Francisco Bay herring (Spratt 1987c). Growth was good during 1984 and the San Francisco fishery recovered from the transitory effects of the EN during the 1984–85 season (CalCoFi 1986; Spratt 1987c).

Despite the impact of EN on the availability and survival of spawners, the San Francisco population of herring produced a series of four consecutive relatively strong year classes (1982, 1983, 1984, 1985) (Spratt 1987b; CalCoFi 1988). Considering that California is the southern limit of major herring spawning concentrations along the west coast of North America, it is surprising that stocks were not affected more by the strong 1982–83 EN (Spratt 1985).

The spawner biomass of herring in Yaquina Bay, Oregon, was about average during the 1983 and 1984 seasons. A strong year class was produced in 1983 which has contributed substantially to the 1986–1988 catches. The 1984 year class was not exceptional (J. Butler, pers. comm.).

The stock size and catch of herring in the Strait of Georgia (Washington) has experienced long-term decline since the early 1970s, and no unusual trends are apparent in either the spawner biomass or year class strength for 1983 and 1984 (D. Day 1987, pers. comm.).

In British Columbia, the estimated spawning stock biomass of herring was about average during 1983 and 1984 for most of the seven districts, but was low during the 1983–84 season in the northern Georgia Strait and northwest Vancouver Island. Year-class strength did not vary consistently among the regions. D. Ware (pers. comm.) concluded that 1983 year-class strength was average and that no striking decrease in size-at-age occurred in 1983 for herring off the west coast of Vancouver Island. Ware and McFarlane (1986) and D. Ware (pers. comm.) reported a strong negative correlation between year-class strength of herring along the west coast of Vancouver Island and SST, which they suspected resulted from the extended northward movement of piscivorous Pacific whiting during warm years. The average year class of herring produced during the warm year of 1983 is an exception to this trend that may be explained by the unusual offshore distribution of whiting during 1983 (D. Ware, pers. comm.; see above).

In Alaskan waters, the stock biomass of herring from Sitka Sound and Prince William Sound was about average during 1983 and 1984 compared to other years. Data are available which compare the spawner biomass in 1983 and 1984 with other years for five of the seven herring fishing areas in the Bering Sea. All stock biomasses were about average during 1983 and 1984 except for higher than average biomass in Norton Sound (Funk and Savikko 1989).

Over the west coast range of herring, these results suggest that the 1982–83 EN only had drastic effects on the availability and survival of adult herring in the southern part of its range in 1983 and 1984. However, these years were correlated with good survival of the larvae that hatched early in 1983 for stocks of herring from San Francisco, Oregon and Georgia Strait. The 1984 year class of several stocks along the Gulf of Alaska also enjoyed good survival.

Strong year classes of herring were correlated with previous ENs and warm-water conditions in the northern part of their range (Pearcy 1983; Bailey and Incze 1985; Mysak 1986; York, this Vol.), perhaps because high sea levels and onshore convergence during EN reduce offshore transport of larvae (Taylor and Wickett 1967; Pearcy 1983). The strong 1958–59 EN was associated with unusually strong year classes in the northern part of the range and poor year classes in central California (Bailey and Incze 1985). This appears to be the opposite of the 1982–83 EN where strong year classes were most pronounced in southern British Columbia and southward.

Pacific Salmon – *Oncorhynchus* spp.

Both otariids and phocids are known to feed on salmon in the California Current, Gulf of Alaska and the Bering Sea (Antonelis and Fiscus 1980; Perez and Bigg 1986; York 1987; Kajimura and Loughlin 1988). Pacific salmon, like Pacific herring, have many discrete stocks ranging from central California to the Arctic Ocean. Stocks in the southern part of the range were severely impacted by the 1982–83 EN. Runs farther to the north were not unusually depressed, and in Alaska good production was recorded during these years.

The 1982–83 EN may have altered migration patterns of salmonids in the ocean. The migration of Fraser River sockeye around Vancouver Island is the classic example of migratory pathways that are related to ocean temperatures. During the recent years of high sea level and warm sea temperatures, a high percentage of the run has returned through the northern passage on the east side rather than along the west side of Vancouver Island (Groot and Quinn 1987). The highest diversion rate was recorded in 1983, when the effects of the EN were most pronounced.

Walleye Pollock – *Theragra chalcogramma*

The pollock fishery currently ranks as one of the most productive fisheries in the world. Walleye pollock are especially abundant in the Gulf of Alaska and the Bering Sea. Pollock is an important prey for Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*) and harbor seals (*Phoca vitulina*) and other phocids in the Gulf of Alaska and the Bering Sea (Kajimura and Fowler 1984; Hacker and Antonelis 1986; Perez and Bigg 1986; Lowry et al. in press). Based on trawl surveys, the stock biomass of walleye pollock in the Gulf of Alaska and the eastern Bering Sea was about average during 1983 and 1984, except that high biomass was reported in Shelikof Strait in 1983. The strength of the 1983 and 1984 year classes was below average in the western Gulf of Alaska based on Fishery data (Megrey 1988), but the 1984 year-class strength was thought to be strong in Shelikof Strait based on acoustic surveys (Nunallee and Williamson 1988). The 1983 year class was weak and the 1984 year class was above the 1980–1987 average in the eastern Bering Sea (Bakkala et al. 1987; Wespestad and Traynor 1988).

Pacific Cod – *Gadus macrocephalus*

Pacific cod is listed as a preferred prey of harbor seals, Steller sea lions and northern fur seals in the Gulf of Alaska (Kajimura and Loughlin 1988). Landings and catch per effort of Pacific cod in Hecate Strait, British Columbia, decreased since 1979 and this trend continued into the years 1983–84 when catches were also low. Based on the numbers of age-3 cod, the 1983 year class in British Columbia was the lowest since 1961 (Foucher and Tyler 1988). Farther north in the Gulf of Alaska and in the Bering Sea (Thompson 1988), both the abundance and the year classes of 1983 and 1984 were about average.

Atka Mackerel – *Pleurogrammus monopterygius*

This species, which is sometimes important prey for northern fur seals in western Alaska and the Bering sea (York 1987), produced low catches in 1983 and high catches in 1984 around the Aleutian Islands. Numbers of age-3 fish indicated that the 1983–84 year classes were not exceptional, stronger than the 1978–1981 year classes, but weaker than the strong 1975 and 1977 year classes (Kimura and Ronholt 1988).

2.3.4 Discussion of Effects on EN Along the Coast of North America

Obvious effects of this EN seemed to be confined to the California Current System from Vancouver Island to the south as evidenced by catches, spawner biomass and survival of Pacific herring and Pacific salmon, two groups of fish that spawn in both the California Current and farther north in the Gulf of Alaska and the Bering Sea. The availability of market squid and herring were severely affected on their traditional spawning grounds in California. However, the EN years produced surprisingly strong year classes of San Francisco Bay herring. Farther to the north unprecedented mortality of coho salmon (*Oncorhynchus Kisutch*) occurred during 1983 off Oregon and California. Returning adult coho and chinook (*O. tshawytscha*) salmon were extremely small, and coho smolts migrating to sea during both 1983 and 1984 survived poorly.

Bailey and Incze (1985) concluded that the strong 1958–59 EN appeared to be beneficial for some fish that spawned at the northern end of their ranges, including subtropical stocks of Pacific sardine, northern anchovy and jack mackerel, which had strong 1958 and/or 1959 year classes off California. This also applied to some temperate stocks at the northern end of their ranges, such as the Pacific herring stocks off Canada, in the Gulf of Alaska and in the Bering Sea, which had unusually strong year classes in 1958 or 1959. They noted that strong ENs may have disastrous effects on recruitment of stocks that inhabit the southern end of their ranges, e.g., Pacific cod off British Columbia and Pacific herring off California, both of which produced weak year classes in 1958.

Bailey and Incze's predictions that strong ENs and abnormally warm years will have severe impacts on temperate stocks living at the equatorial ends of their geographic ranges and more favorable effects on subtropical stocks spawning towards the poleward end of their ranges were not always substantiated during 1983–84 off North America. Herring stocks in the southern part of their range often realized better than average year classes in 1983, and particularly strong year classes of herring were not common in 1983–84 north of Vancouver Island. Among the more subtropical species at the northern end of their ranges, only the Pacific sardine had a strong year class in 1983. Jack mackerel, Pacific mackerel and northern anchovy produced weak 1983 year classes. Since we have included only several of the 58 stocks that Bailey and Incze (1985) listed, for which recruitment data will eventually become available for the 1983–84 year classes, our conclusions are preliminary. Nevertheless, it is obvious that the 1982–83 EN had effects on pelagic species of the northeastern Pacific that were different from the 1958–1959 EN, the only other big northern EN for which considerable data are available. On the other hand, as Sharp (1980) and Bailey and Incze (1985) predict, those species in the California Current that experienced the most significant effects during 1983 and 1984 were species that home to specific localized spawning sites, such as herring, salmon and squid. Nomadic or migratory species were apparently able to find suitable conditions for spawning outside their normal ranges.

Ocean climate may be one of the reasons why ENs of similar magnitude have different impacts. The 1982–83 EN was unusual in timing and hydrographic changes (McGowan 1985; Fahrbach et al., this Vol.). It is also well documented that EN in 1982–83 influenced the Bering Sea much less than previous EN events since the position of the Aleutian low moved unusually far eastward (Niebauer 1988; Fahrbach et al., this Vol.).

Furthermore, the strong 1982–83 EN produced a signal that was embedded in longer-term, climatic events in the Pacific ocean. Along the west coast of North America, for example, a warming trend commenced years before the 1982–83 EN. Elevated sea levels and high SSTs occurred along the coast after 1976 (Norton et al. 1985; Cole and McLain 1989). This climatic change in 1976 is correlated with low survival of coho salmon off Oregon (Pearcy 1988), increased availability and northward expansion of Pacific mackerel, increased catches of Pacific sardine, and decreased catches of northern anchovy in California (CalCoFi 1984, 1985, 1986, 1987, 1988), and decreased catch per effort of Pacific cod in Canada (Foucher and Tyler 1988). These long-term changes in the pelagic ecosystems, which are independent of EN events, may have effects on the population biology of pinnipeds as important as isolated EN events. The long-term decline in the population of the Steller sea lion on the extreme southern end of its breeding range on the Channel Islands off California (Bartholomew 1967) may be the result of such a change in ocean climate.

A final caveat: it must be emphasized that Eastern Boundary Current Systems are inherently variable, and that it is difficult to ascribe changes observed during an EN event unequivocally to that event. We have correlations and can only try to interpret which is cause and which effect (Paine 1986; Pearcy and Schoener 1987).

2.4 Conclusions

Major similarities in the response of pelagic fish to the EN in both the southern and the northern hemisphere were the strong poleward migrations, the intrusion of oceanic and subtropical species toward the coasts, and the poor conditions for feeding, growth and survival of some species. Differences included the earlier impacts off South America than off North America and the return to normal conditions earlier in the South Pacific. Effects on fish populations were obvious farther from the equator in the North Pacific (50°N) than in the South Pacific (33°S), but this may be partly a consequence of missing observations in the far south. Those species in the California Current that experienced the most significant effects during 1983 and 1984 were species that home to specific localized spawning sites, such as herring, salmon and squid. Nomadic or migratory species were apparently able to find suitable conditions for spawning outside their normal ranges.

The EN had both short- and long-term effects on the prey populations of pinnipeds. The most obvious short-term responses were changes in the availability of prey caused by poleward, inshore-offshore, or bathymetric movements observed for anchovy, sardine, mackerel and hake in both hemispheres. Actual changes in the abundance and age structure of populations were related to higher mortality rates of adult, juvenile or larval stages. Body condition, growth rates and reproductive capacities were also reduced. The influx of new predators, such as subtropical scombrids, into an area modified the abundance and availability of the usual prey populations. All of these changes could affect the availability, vulnerability and nutritive value of prey populations to marine mammals and therefore the quantity, quality and the ease of capture of prey.

Delayed responses to a major EN perturbation are less obvious than immediate effects because they may affect recruitment years after the event. Elevated temperatures can alter the time of spawning, fecundity and viability of eggs, rates of development and metabolism, as well as the species composition and seasonal timing of prey and predator populations; changes in the circulation of water can affect the dispersal or retention of eggs and larvae (Bailey and Incze 1985). All of these factors can influence the survival of early life history stages and the strength of year classes. Hence, weak year classes resulting from EN could alter the availability of pinniped prey years after the EN event.

Pinnipeds (and seabirds) find themselves confronted with a number of difficulties during and shortly after major EN events which seriously interfere with normal feeding:

1. Their food is not where it used to be; fish emigrate to cooler (deeper, more poleward, or remaining upwelling) areas;
2. Food can no longer be found near the surface where it is easily accessible at low energetic cost;
3. Even if food can be reached (e.g., by deep-diving pinnipeds), it is of poor quality and occurs at lower density; e.g., Peruvian anchovy had decreased fat content;
4. Invading species such as mackerel or tropical immigrants are unsuitable as pinniped food due to their size, strong defenses, and high swimming speeds; some of them also live in deeper water and do not form dense shoals like anchovy and sardine;
5. In addition, these invading species are often predators of early life history stages of the normal pinniped prey;
6. There may be major time lags in the recruitment of anchovy, sardine, pollock, capelin and other species caused by EN which render the feeding situation insecure in the years following the event;
7. Physical manifestations of EN are strongest near the equator and become attenuated towards higher latitude; biological effects are pronounced near the equator and on species that are near the equatorial ends of their ranges and have localized spawning grounds. At high latitudes (e.g., Chile or Alaska) the resulting warming may even have been beneficial.

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