EXPLORATIONS OF EL NIÑO EVENTS AND ASSOCIATED BIOLOGICAL POPULATION DYNAMICS OFF CENTRAL CALIFORNIA

WILLIAM H. LENARZ
National Marine Fisheries Service
Southwest Fisheries Science Center
3150 Paradise Drive
Tiburon, California 94920

DAVID A. VENTRESCA
California Department of Fish and Game
20 Lower Ragsdale Drive, Suite 100
Monterey, California 93940

WILLIAM MONTROSE GRAHAM
Marine Sciences Institute
UC Santa Barbara
Santa Barbara, California 95106

FRANKLIN B. SCHWING
National Marine Fisheries Service
Pacific Fisheries Environmental Group
1352 Lighthouse Avenue
Pacific Grove, California 93950

FRANCISCO CHAVEZ
Monterey Bay Aquarium Research Institute
160 Central Avenue
Pacific Grove, California 93950

ABSTRACT

During El Niño events off central California, temperatures were elevated, salinities were depressed, and there was evidence of poleward and onshore advection. El Niño conditions seemed to delay the annual phytoplankton bloom, affect the distribution and abundance of invertebrates, improve recruitment of southern fish species, cause recruitment failures of rockfish (*Sebastes* spp.), and cause poor growth and condition of adult rockfish. The 1992–93 El Niño off central California was less extreme than the 1982–83 event, but much stronger than the 1986–87 event. Water temperatures in 1992–93 were similar to the 1982–83 event, but poleward advection appeared to be weaker. Recruitment of southern species was higher in 1983 than in 1992; the condition of rockfish was better in the more recent event. Computer simulation indicated that fishery management practices can influence the intensity of El Niño effects on a fishery for rockfish. Possible causes of rockfish recruitment failures during El Niño events are discussed.

INTRODUCTION

Scientists familiar with waters off central California (figure 1) are aware that significant physical and biological changes are associated with El Niño events. However, little of the extensive scientific literature on El Niño events emphasizes central California. In this paper, we review some of the important papers dealing with El Niño characteristics in the northeastern Pacific Ocean, and then explore El Niño-related phenomena off central California, emphasizing the 1992–93 event, but also including the 1957–59, 1982–83, and 1986–87 events. We first examine physical oceanographic data, from shore stations and from oceanic surveys. We next present biological information for trophic levels ranging from primary production to planktivores. Finally, we show results of a computer simulation of El Niño effects on an exploited population of rockfish.

Most of the biological data come from research by the authors or close associates and have not been previously published in the peer-reviewed literature. Because of the review nature of this paper and the wide scope of the data, sources and descriptions of the data are provided in figure captions and the acknowledgments section rather than in a lengthy methods section.

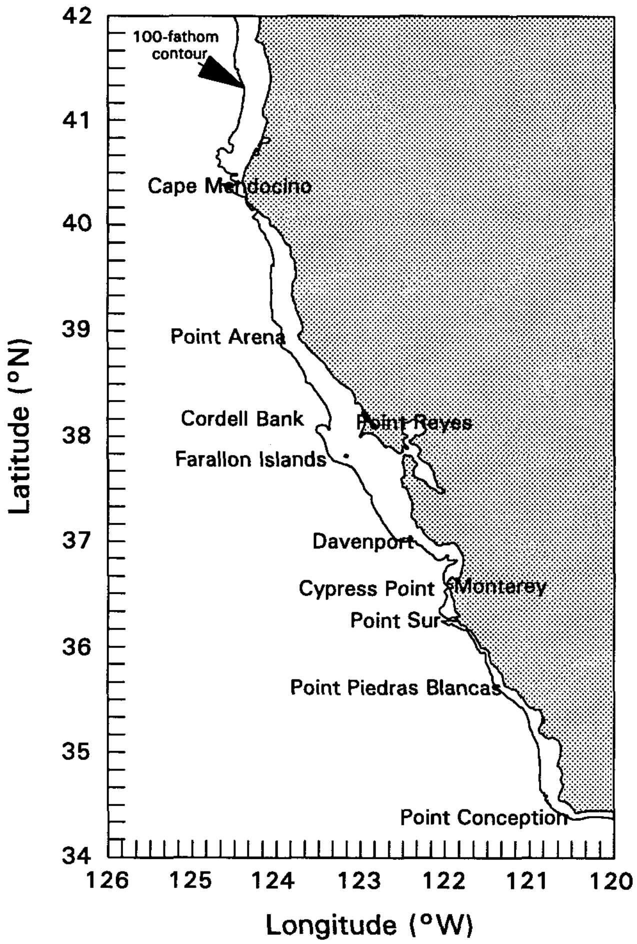

Figure 1. Map of central and northern California showing locations mentioned in text.

LITERATURE REVIEW

Researchers have documented numerous examples of physical and biological phenomena associated with El Niño events in the northeastern Pacific Ocean, including the very strong 1957–59 (*CalCOFI Reports*, vol. 7) and 1982–83 events (Wooster and Fluharty 1985). Mysak (1986) and Simpson (1992) presented extensive reviews of the physical dynamics of El Niño events, including proposed mechanisms that link events off the west coast of North America to events in the tropics. Although both of those papers addressed phenomena over much of the eastern Pacific Ocean, Mysak (1986) focused on British Columbia and Simpson (1992) on southern California. These authors concluded that El Niño events involve both onshore and poleward advection. They presented results indicating that onshore advection was forced by north Pacific atmospheric anomalies that appeared to be coupled with events at the equator. Poleward advection appeared to be caused by a combination of atmospheric anomalies and hydrodynamics related to the onshore movements. Both Mysak and Simpson expressed doubts about the importance of poleward advection being the result of forcing from tropical waters. Onshore advection appeared to cause nearshore salinities to be lower than normal. Both onshore and poleward advection could have caused elevated temperatures associated with El Niño events.

Both onshore and poleward advection during the 1982–83 El Niño were evident in the 1981–83 trajectory of a buoy drogued at 30 m, as reported by Emery et al. (1985). The buoy moved several hundred miles shoreward between December 1982 and late January 1983, approaching the coast at Point Arena. It then drifted rapidly northward, reaching Vancouver Island in late February 1983. Emery et al. (1985) presented evidence that North Pacific atmospheric anomalies caused the advection of surface waters and consequent movement of the drogue.

Although Mysak (1986) and Simpson (1992) question the importance of direct oceanic linkages of poleward advection with events at the equator, there is both theoretical and empirical work to indicate that direct oceanic linkages are plausible (e.g., Clarke and Van Gorder 1994). In addition, Norton and McLain (1994) correlated temperature data from the northeastern Pacific Ocean with atmospheric data from the tropics and the North Pacific. Although concluding that El Niño–related warming at depths below 100 m related to remote forcing through the ocean, they agreed with Mysak (1986) and Simpson (1992) that warming of surface waters involved North Pacific atmospheric anomalies.

Physical factors other than elevated temperatures, depressed salinities, and abnormal advection are associated with El Niño events off the West Coast. Hayward et al. (1994) associated reduced upwelling or increased downwelling, high sea level, thickened surface mixed layer, and depressed nutricline with the 1992–93 event.

Biological information related to El Niño events was reviewed by Radovich (1961). He noted many range extensions for fish along the West Coast associated with events of 1957–59 and earlier. Catch rates of some southern gamefish improved off southern California, and other species returned to areas of previous abundance. Although active swimming could explain most of the fish movements, Radovich hypothesized that several planktonic invertebrates had been advected northward. Several fish species appeared to reproduce successfully off southern California in areas north of their normal spawning region. Smith (1985) compared CalCOFI zooplankton catches off southern California during the 1957–59 event with adjacent years and found that effects varied among species, but overall zooplankton catch rates decreased dramatically during El Niño. Zooplankton volumes and chlorophyll concentrations were depressed off southern California during the 1982–83 (McGowan 1985) and 1992–93 El Niño events (Hayward et al. 1994). Pearcy et al. (1985) studied biological phenomena during the 1982–83 El Niño off Oregon and Washington. Surface chlorophyll levels were low during 1983 compared to 1982. Survival of salmon appeared to be poor, and their weights were low. Pearcy et al. also reported range extensions of several fish species, changes in the species composition of Oregon commercial landings, and shifts in species composition of fish and gelatinous zooplankton captured during a purse seine survey. Some of these biological effects of El Niño continued into the next year.

PHYSICAL CHARACTERISTICS ASSOCIATED WITH EL NIÑO

Surface Temperature

The first evidence of the 1992–93 event came from positive surface temperature anomalies at the Farallon Islands shore station early in 1992 after several years of generally cool conditions (figure 2). Temperatures declined during summer and early fall of that year and

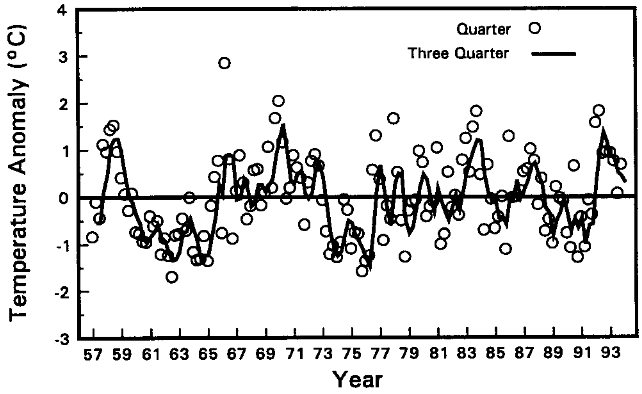

Figure 2. Quarter and three-quarter average temperature anomalies at the Farallon Islands shore station, 1957–93. Anomalies are deviations from monthly averages of 1957–93 data (Walker et al. 1992).

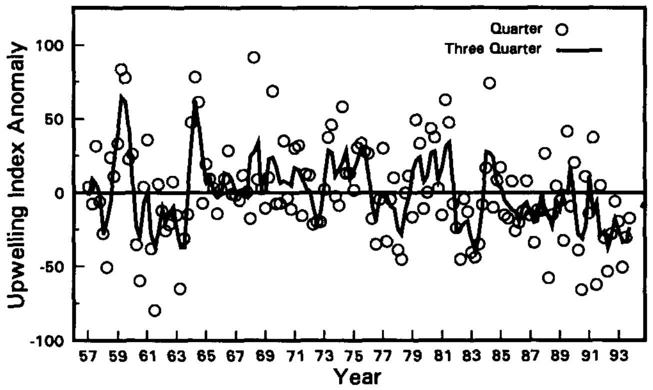

Figure 3. Quarter and three-quarter averages of the Bakun upwelling index anomalies [m^3s^{-1}/(100 m of coastline)] at 36°N, 1957–93. Anomalies are deviations from monthly averages of 1957–93 data (Bakun 1973).

then increased again, a pattern also noted for southern California (Hayward 1993; Lynn et al. 1995). The 1992–93 temperature pattern essentially mirrored that of the 1982–83 event. Temperature anomalies during the 1992–93 event were similar to those of the 1957–59, 1969–70, and 1982–83 El Niño events (figure 2). Temperature anomalies were lower during the 1986–87 event, but still positive. The cool period that preceded the 1992–93 event was the coolest since 1973–76. There was also an extensive period of below-normal temperatures between 1960 and 1965.

Upwelling Indices and Sea Level

Anomalies in the upwelling index at 36°N (Bakun 1973) were negative during 1992–93 (figure 3), indicating weaker-than-normal upwelling or downwelling. The values were similar to those of the strong 1982–83 and 1957–59 El Niño events. The low values of 1992–93 continued a trend that started in 1975, as observed by Bakun (1990), and anomalies tended to be negative even during the cool period that preceded 1992.

Monthly sea-level anomalies at San Francisco were generally positive during 1992–93 (figure 4). The highest values were observed during early 1992 and were similar to the maximum values measured during the 1986–87 El Niño. Values in 1982–83 were considerably higher than those of 1992–93. High sea levels are associated with northward flow (Chelton et al. 1982) and also are consistent with downwelling or reduced upwelling.

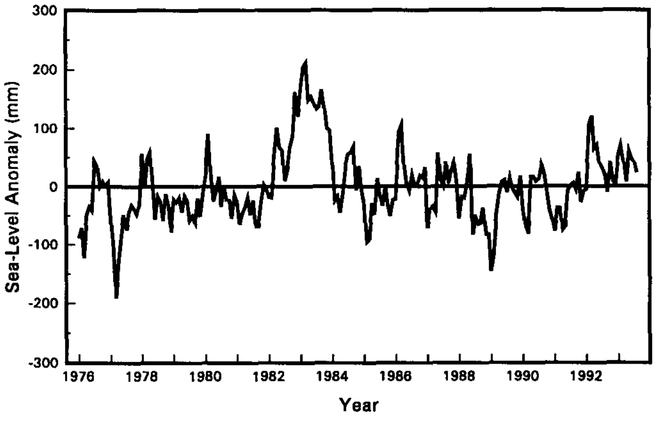

Figure 4. Monthly sea-level anomalies at San Francisco, 1976–93.

Vertical Temperature and Salinity Sections

Vertical temperature and salinity sections along a cross-shelf transect off Davenport in March and June during the 1992–93 event (figures 5–8) agree with the results of Simpson (1992) off southern California for the 1982–83 event. When compared to 1950–78 average conditions compiled by Lynn et al. (1982), temperatures were high and salinities low. The relatively high

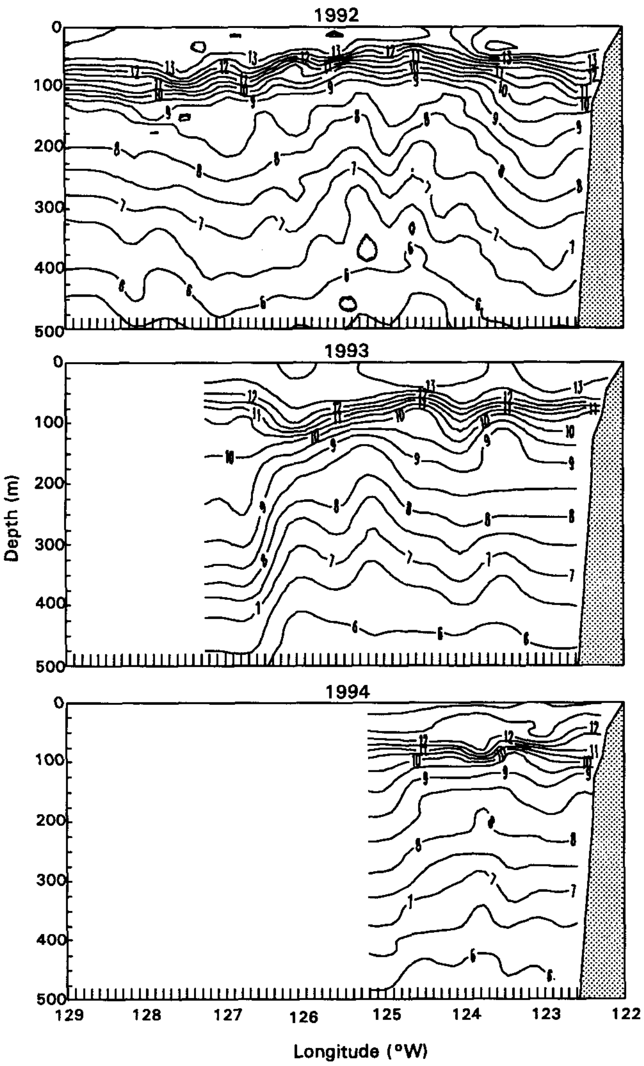

Figure 5. Vertical sections of temperature along a cross-shelf transect off Davenport (37°N), March 1992, 1993, and 1994. *Shaded areas* indicate the bottom. 1992 data were collected by a pre-FORAGE cruise. The 1993 and 1994 data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

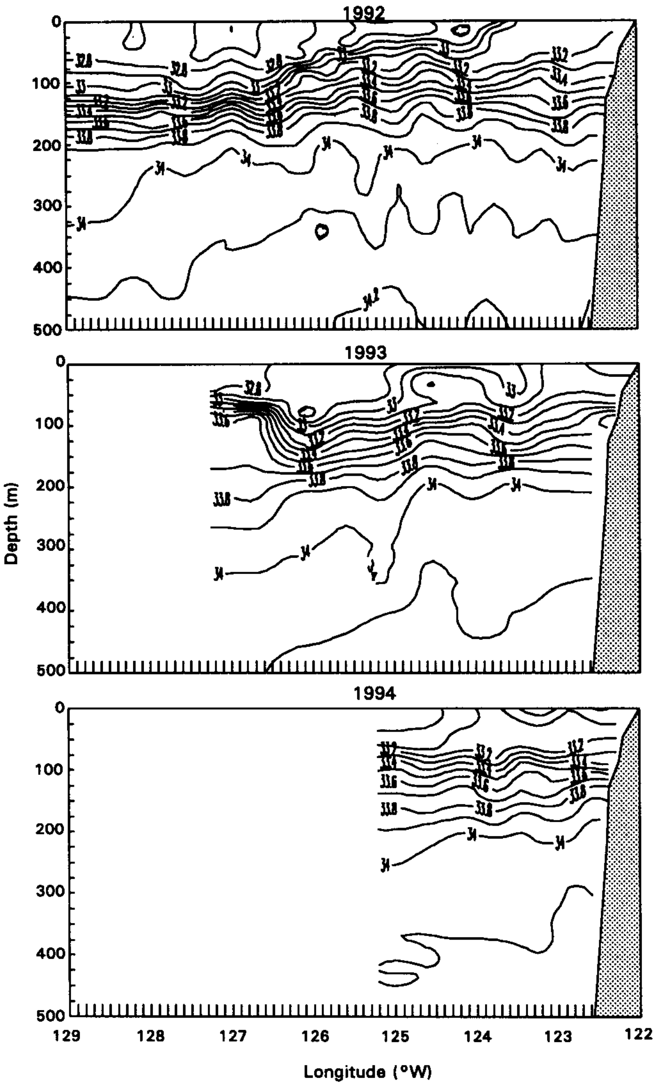

Figure 6. Vertical sections of salinity along a cross-shelf transect off Davenport (37°N), March 1992, 1993, and 1994. *Shaded areas* indicate the bottom. 1992 data were collected by a pre-FORAGE cruise. The 1993 and 1994 data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

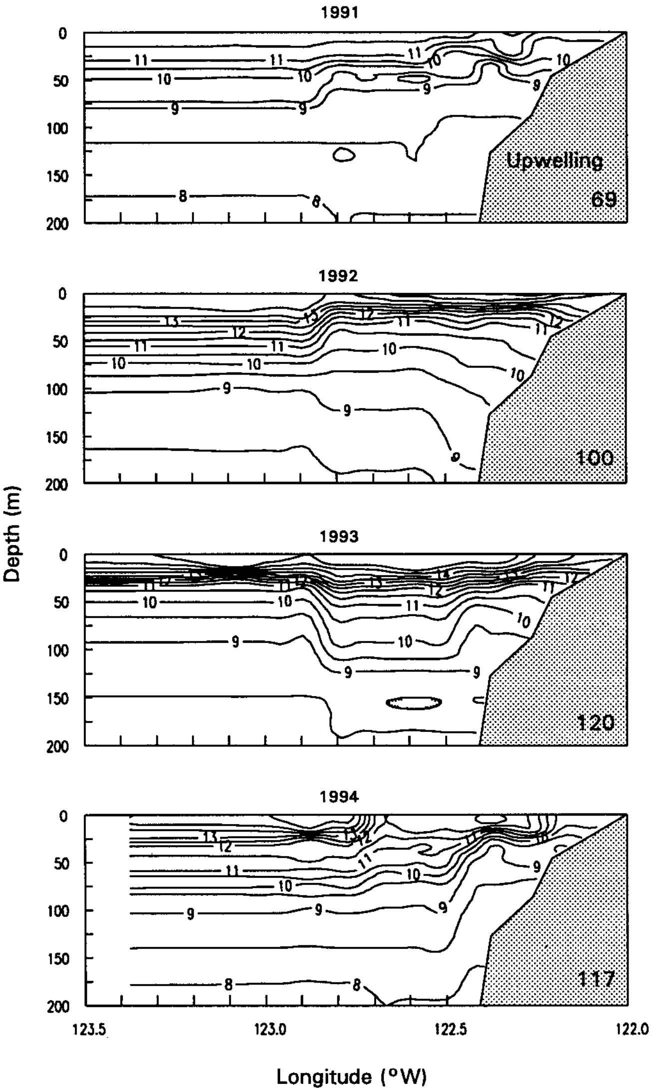

Figure 7. Vertical sections of temperature along a cross-shelf transect off Davenport (37°N), early June 1991–94. *Shaded areas* indicate the bottom. Five-day averages of the Bakun upwelling index [m^3s^{-1}/(100 m of coastline)] are shown in the *shaded areas*. Temperature data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

temperatures combined with relatively low salinities suggest onshore advection, because climatological salinities decrease to the west and north and temperatures increase to the west and south (Lynn 1967; Lynn et al. 1982). Temperature and salinity fronts defining the eastern boundary of the California Current in June appear to be closer to shore than in March, and closer to shore relative to the climatology (Lynn 1967; Lynn et al. 1982), implying an onshore component of advection. In March 1992, temperatures on level surfaces down to 500 m tended to tilt down toward the coast inshore of 124°W (figure 5), which is contrary to typical conditions at that time of year. However, salinities tended to tilt up in an easterly direction, as is normal (figure 6).

Sakuma and Ralston (1995) calculated northward geostrophic flow to about 100 km off central California during March 1992. Direct shipboard acoustic Doppler current profiler measurements in late February support this (P. M. Kosro and R. J. Lynn, pers. comm.). By June 1992, the geostrophic flow was southward, except for a region of extremely strong subsurface poleward current over the continental slope (Lynn et al. 1995). The surface geostrophic circulation was southward during March 1993 as well (Sakuma and Ralston 1995). These observations indicate that both onshore and poleward advection occurred off central California during at least part of the 1992–93 period. The complete time history of these periods of anomalous advection is not known.

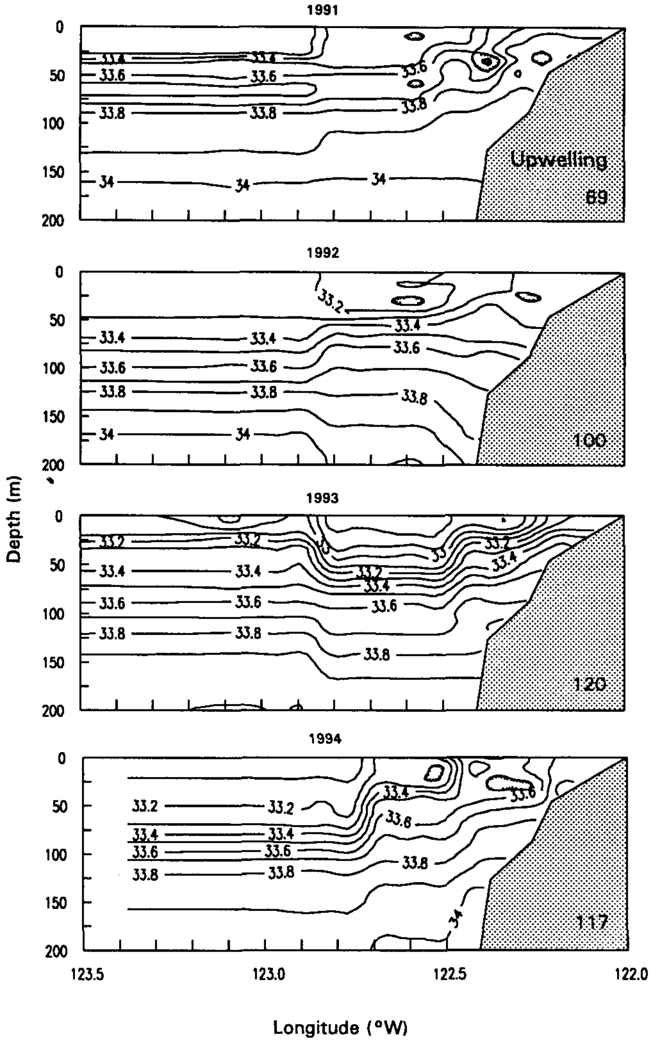

Figure 8. Vertical sections of salinity along a cross-shelf transect off Davenport (37°N), early June 1991–94. *Shaded areas* indicate the bottom. Five-day averages of the Bakun upwelling index [m^3s^{-1}/(100 m of coastline)] are shown in the *shaded areas*. Data were collected by the Tiburon Laboratory (Sakuma et al. 1994).

An upwelling center appears off Davenport in June during normal years and was evident in the temperature and salinity data during 1991, 1993, and 1994 (figures 7 and 8). There was little evidence of upwelling in the hydrographic data during 1992, even though the upwelling index for the five-day period immediately preceding the survey was similar to that of the other years. Large-scale poleward advection, possibly caused by remote forcing (Norton and McLain 1994), may have been strong enough to overwhelm evidence of local wind-induced upwelling during this time. In addition, short-term upwelling-favorable wind events, as defined by the upwelling index and direct wind measurements off central California, may not be sufficient to counter the seasonal effects of the anomalously weak equatorward stress observed throughout 1992.

Temperatures of the upper water column were slightly lower in March 1994 than during the preceding two years, but remained higher than normal (figure 5). Salinities remained low during March 1994 (figure 6). June 1994 nearshore temperatures dropped to 1991 levels, but temperatures remained warm offshore (figure 7). June 1994 nearshore salinities approached 1991 levels, but offshore salinities were similar to 1992 and 1993 levels (figure 8). This suggests that normal upwelling had recommenced in 1994, but a large anomalous water mass remained in the seaward portion of the survey region.

El Niño events are often associated with deeper-than-normal thermoclines (e.g., Norton and McLain 1994). It is difficult to characterize thermocline depth in our area because of the complex dynamics of upwelling and the California Current. The vertical sections off Davenport (figures 5 and 7) illustrate the difficulty in concluding that thermocline depth increases in our study area during El Niño events. However, the data indicate considerably more vertical thermal stratification during El Niño events than during other years (figures 5 and 7).

BIOLOGICAL CHARACTERISTICS ASSOCIATED WITH EL NIÑO

Primary Productivity

Primary productivity has been measured in Monterey Bay since 1989. Climatological primary production for the cool years of 1989–91 shows a peak in May–June at around 2.3 $gC/m^2/d$ (figure 9). In 1992 productivity was bimodal, with peaks in May and July–August of around 1.7 $gC/m^2/d$, about 25% lower than the 1989–91 average. However, and perhaps more important, the start of the productive season was delayed about two months compared to the 1989–91 climatology (figure 9). During the cool years, productivity began to increase from the winter low in late January. In 1992, productivity did not begin to increase until late March. The early months of the year are particularly important for members of the upper trophic level, as will be discussed below. When analyzing productivity effects during El Niño, it is obviously necessary to consider the change in the pattern as well as in the amplitude. The productive season was delayed only slightly in 1993; in contrast, the latter half of the year was substantially less productive than the 1989–91 climatology (figure 9). During 1993, the average productivity peaked in April at around 1.8 $gC/m^2/d$. Averaged over the year, primary production during 1992 was 28% lower than the 1989–91 climatology, and 1993 was 21% lower. Primary production did not return to pre-1992 levels in 1994.

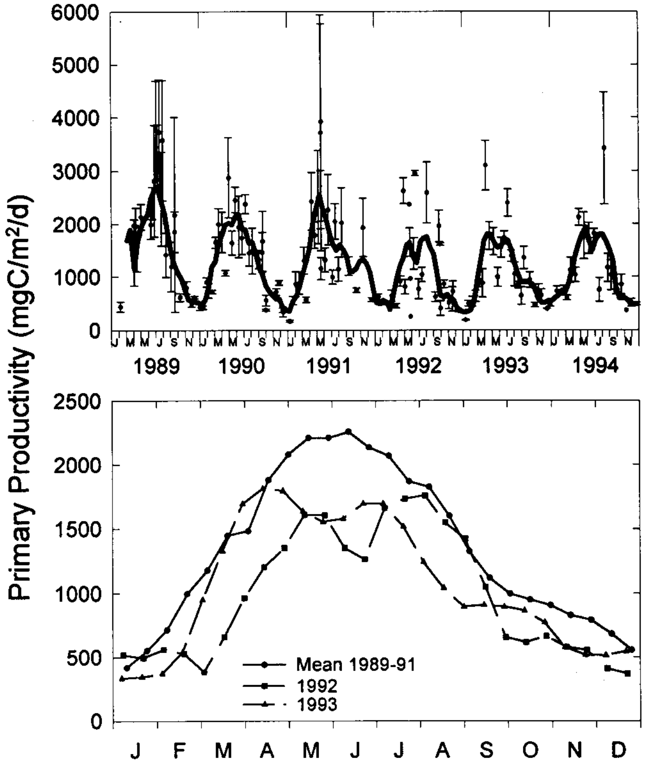

Figure 9. Time series of primary productivity for Monterey Bay for 1989–94 (*upper panel*). Primary productivity was measured by Francisco Chavez using incorporation of ^{14}C over 24 hr in simulated in situ incubations. Sampling was done at 2–5 stations and on intervals ranging from daily to monthly. Shown in the *upper panel* are the means and standard errors for stations occupied each day. The *solid line* represents a 4-point smooth of data that had been interpolated to biweekly intervals. The smoothed data were averaged for the period 1989 to 1991 and compared to the smoothed data from 1992 and 1993 (*lower panel*).

Invertebrates

Graham (1994) analyzed annual May–June midwater trawl survey (MWTS) catches of the scyphomedusa *Chrysaora fuscescens* between Cypress Point and Point Reyes since 1985. For the MWTS, the NMFS Tiburon Laboratory uses a square-mouthed trawl with 26.5 m sides and a 1 cm mesh cod end. The survey is conducted during the night at stations shown in figure 10. The MWTS is further described by Wyllie Echeverria et al. (1990). Three main localities (northern Monterey Bay, Gulf of the Farallons, and Point Reyes) usually accounted for most of the medusa biomass within the survey region.

There were two major low-abundance periods of *C. fuscescens* between 1985 and 1993 (figure 11). Except for the 1985–86 period, Point Reyes tended to have lesser year-to-year variation than the southern coastal sites. The 1986 and 1992 low abundances are consistent with the decline off Oregon in 1983 (Pearcy et al. 1985). Although the 1986 reduction in abundance off central California was evident over the breadth of the entire trawling region, Graham (1994) explained the 1992 reduction as a distributional shift of *C. fuscescens* towards the north. The distribution of the medusae towards the north is consistent with northward advection, but it should be noted that concentrations did not increase off Point Reyes during El Niño years. Lower concentrations in the southern regions may also be explained by weaker cross-shelf density gradients as a result of both weakened upwelling intensity and a warmer mixed layer. As previously mentioned, there was little evidence of upwelling off Davenport during 1992 (figure 7). However, there was some upwelling off Point Reyes during May–June 1992 (Sakuma et al. 1994).

Graham (1994) also documented changes in benthic juvenile crab distributions as a consequence of the 1992

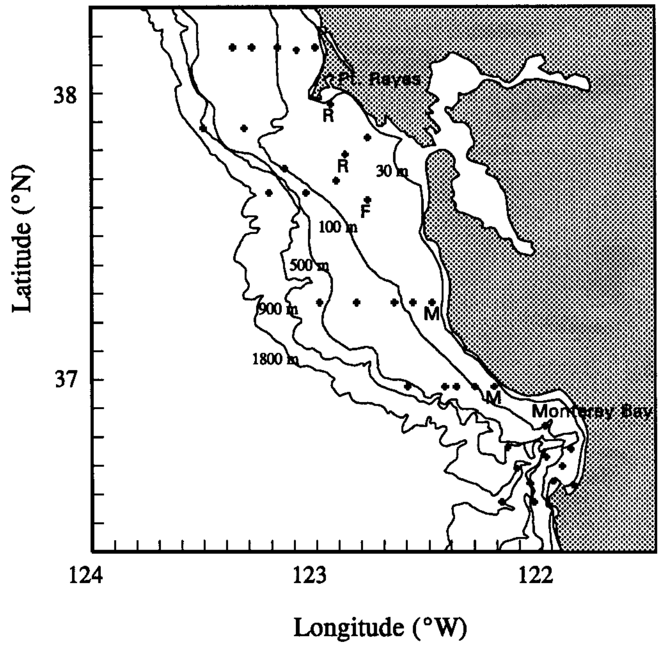

Figure 10. Locations of midwater trawl stations sampled annually during May–June since 1983 by the Tiburon Laboratory (Wyllie Echeverria et al. 1990). The Point Reyes area comprises the stations labeled *R*; the Gulf of the Farallons area contains the station labeled *F*; and the northern Monterey Bay area comprises stations labeled *M*.

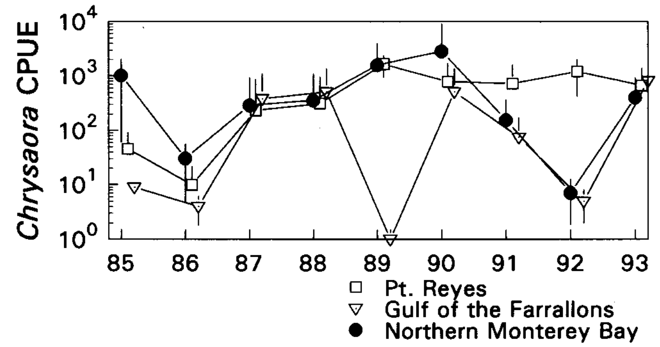

Figure 11. Average catch of *Chrysaora fuscescens* per trawl by the Tiburon midwater trawl survey at the nearshore areas shown in figure 10, 1985–93 (Graham 1994).

event. Megalopae of the crab *Cancer gracilis* cling to the tentacles of *C. fuscescens*, where they molt to a juvenile stage and eventually fall to the seafloor. During normal upwelling years, when medusae are concentrated in convergences south of upwelling centers, these juveniles are concentrated at the front away from shore. But during 1992, when medusae were generally absent from Monterey Bay, these crabs were concentrated on the seafloor significantly closer to the coast. Graham (1994) attributes this shift to the distribution shift of the *C. fuscescens*.

Even though the MWTS was designed to sample pelagic young-of-the-year (YOY) rockfish, the (1.27 cm mesh cod end) trawl retains considerable quantities of euphausiids (mostly *Euphausia pacifica* and *Thysanoessa spinifera*). Catches of euphausiids were not quantified until 1990. Euphausiid abundance was considerably lower in 1992 than in 1991 or 1993, but catch rates were also low during the non-El Niño year of 1990.

Southern Fishes

Scuba divers have estimated the abundance of YOY blacksmith (*Chromis punctipinnis*), bluebanded goby (*Lythrypnus dalli*), and California sheephead (*Pimelometopon pulchrum*) near Monterey since 1981 (figure 12). These southern species were absent as YOY in most years, but were abundant in 1983, and some were common in 1992. Some also occurred in low numbers in 1993 and 1987. Adult bluebanded gobies are usually absent from the area. We believe that YOY bluebanded gobies were present in 1983 because of poleward advection. Adult blacksmith and California sheephead have occurred in the area and may have successfully reproduced only during the El Niño years.

Other evidence suggests that recruitment of California sheephead during El Niño years was the result of poleward advection. California sheephead were taken by recreational divers in spearfish meets along central California when they were available. Fish smaller than 356 mm (14 in.) did not qualify for competition but were occasionally speared. One large sheephead was landed in 1980; subsequently, none were landed until 1987, when two small fish were taken (figure 13). More than 60 fish were landed in 1988, followed by a declining catch through 1993. Average size slowly increased each year between 1987 and 1993, but did not reach the size of the one fish landed in 1980. The data suggest that sheephead were scarce or absent from the area between 1980 and 1983. As previously noted, YOY recruited to the area during the 1983 El Niño. The 1983 year class apparently had grown to sizes attractive to divers by 1987. The absence of catches in 1982 and 1983 suggests that large sheephead were not in the area and that recruitment in 1983 was the result of advection. If YOY that recruited to the area in 1992 survive and if their growth is similar to the 1983 year class, they should begin to recruit to the sport fishery in 1996. YOY sheephead abundance was not as high in 1992 in comparison with 1983.

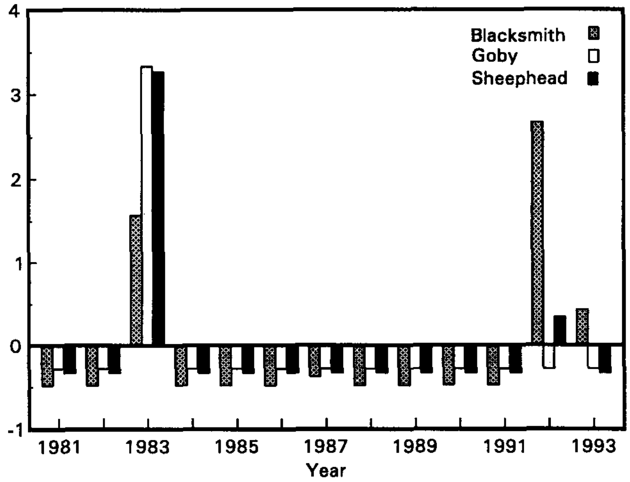

Figure 12. Standard deviates of diver counts of YOY blacksmith, bluebanded gobies, and California sheephead at the Monterey Jetty, 1981–93. Survey was made along standardized tracks (D. VenTresca, unpublished data).

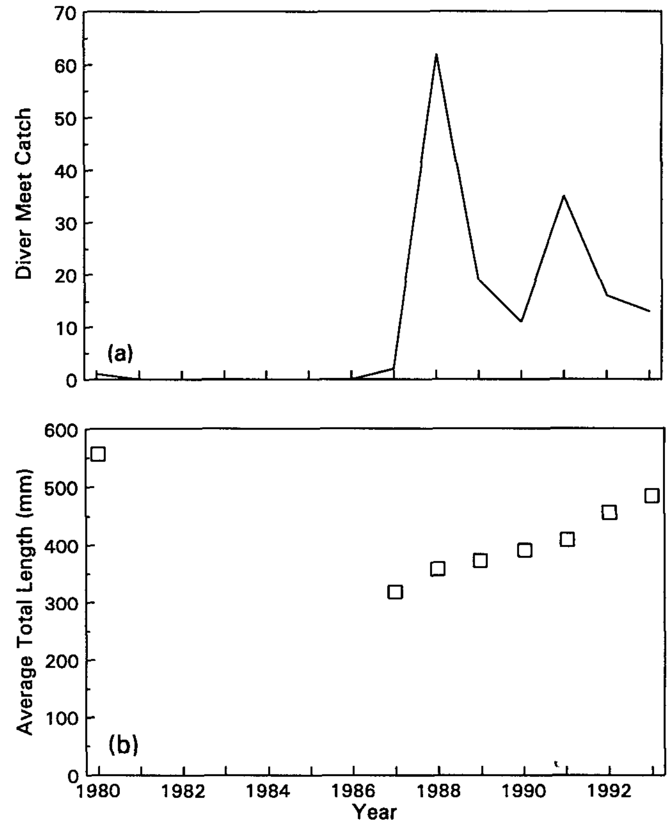

Figure 13. Catches (*a*) and average sizes (*b*) of California sheephead in recreational spearfish meets along the central California coast between Monterey and Piedras Blancas, 1980–93. Minimum size to qualify for the meets was 356 mm (14 in.), but smaller fish were occasionally taken. Data were collected by D. VenTresca.

Thus the 1992 year class is unlikely to affect the fishery as much as the 1983 year class.

Cowen (1985) presented evidence to support the argument that prevailing currents make Point Conception the northern boundary of the normal range of southern fish such as California sheephead. He proposed that recruitment does not occur in normal years because currents are southward and there are no sources of eggs and larvae to the north. He concluded that temperature is not the main factor because populations of these species are successful in cold-water upwelling areas off north-central Baja California.

Rockfish

The MWTS has followed a consistent sampling plan since 1986 (figure 10). Annual indices of abundance of YOY rockfish are estimated from the survey catches. The surveys are conducted at the end of the pelagic stage of juvenile rockfish, by which time we believe that year-class strength has been established. Ralston and Howard (in press) found that abundance indices calculated from MWTS results correlated well with diver estimates of settled YOY rockfish abundance between Cape Mendocino and thirty miles south of Point Arena. Thus the MWTS results appear to be representative of much of central California. The YOY rockfish abundance index was very low in 1986 and in 1992, as well as in 1990 (figure 14). A limited MWTS and diver counts indicate that it was also very low during 1983 (pers. comm., E. Hobson, NMFS, 3150 Paradise Dr., Tiburon, CA 94920).

Shortbelly rockfish (*Sebastes jordani*) usually constitute 70% or more of MWTS YOY rockfish catches, but the catches of two years differ markedly. The first half of 1991 was cold compared to other years since the survey began (figure 2), and shortbelly rockfish made up less than 50% of the catch in that year. Northern species of rockfish constituted a larger portion of the catch in 1991 than in other years, and for the first time, Puget Sound rockfish (*S. emphaeus*) were recorded south of Cape Mendocino. The other unusual catch composition occurred during the 1992–93 El Niño. The 1993 index of abundance was the fourth highest of the series (figure 14). However, shortbelly rockfish constituted less than 50% of the catch, and catches of brown rockfish (*S. auriculatus*) were much higher than in any previous year.

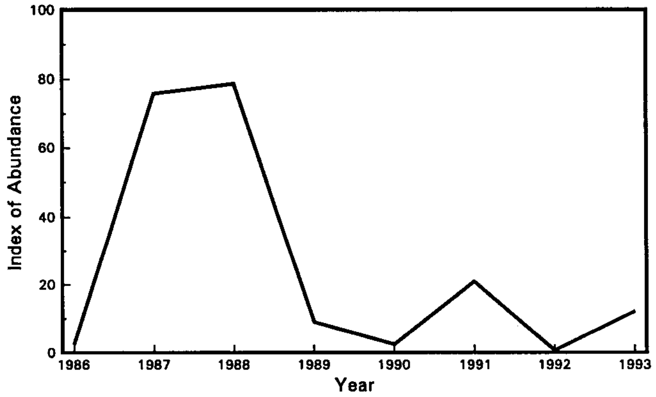

Figure 14. Index of abundance of pelagic YOY rockfish off central California, 1986–93. Index is calculated from catches by the Tiburon midwater trawl survey (Ralston 1994).

Brown rockfish belong to the nearshore demersal group. Adults of these species—kelp rockfish (*S. atrovirens*), brown rockfish, gopher rockfish (*S. carnatus*), copper rockfish (*S. caurinus*), black and yellow rockfish (*S. chrysomelas*), quillback rockfish (*S. maliger*), china rockfish (*S. nebulosus*), and grass rockfish (*S. rastrelliger*)—tend to be solitary individuals closely associated with the bottom in shallow water.

Another distinct group, structure schoolers, comprises widow rockfish (*S. entomelas*), yellowtail rockfish (*S. flavidus*), black rockfish (*S. melanops*), blue rockfish (*S. mystinus*), and olive rockfish (*S. serranoides*). Adults of these species often form midwater schools associated with structures such as pinnacles and kelp, and tend to occur in water deeper than the nearshore demersal group.

Pelagic YOY of the nearshore demersal group are relatively more abundant during El Niño years than during other years in comparison to structure schoolers (figure 15). In addition, fishes in the nearshore demersal group are captured higher in the water column than the structure schoolers (figure 16). The nearshore demersal group, therefore, may benefit from the onshore advection, or the reduced offshore advection, of surface

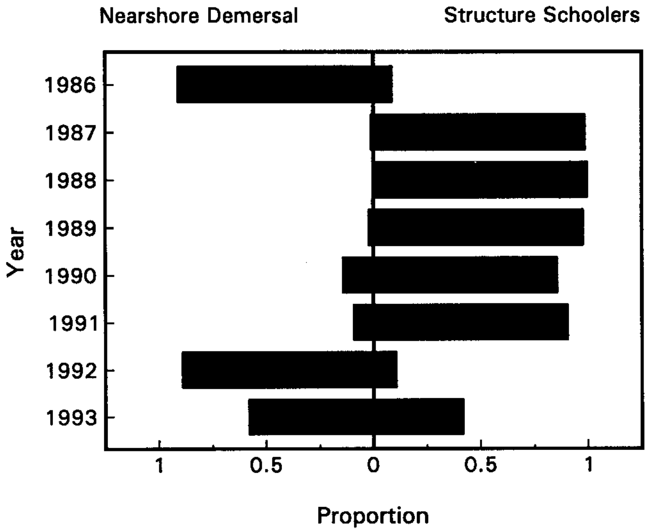

Figure 15. Relative proportions of nearshore demersal and structure schooler YOY rockfish captured by the Tiburon midwater trawl survey, 1986–93 (proportions calculated as fraction of combined catch of the two groups). See text for group definitions.

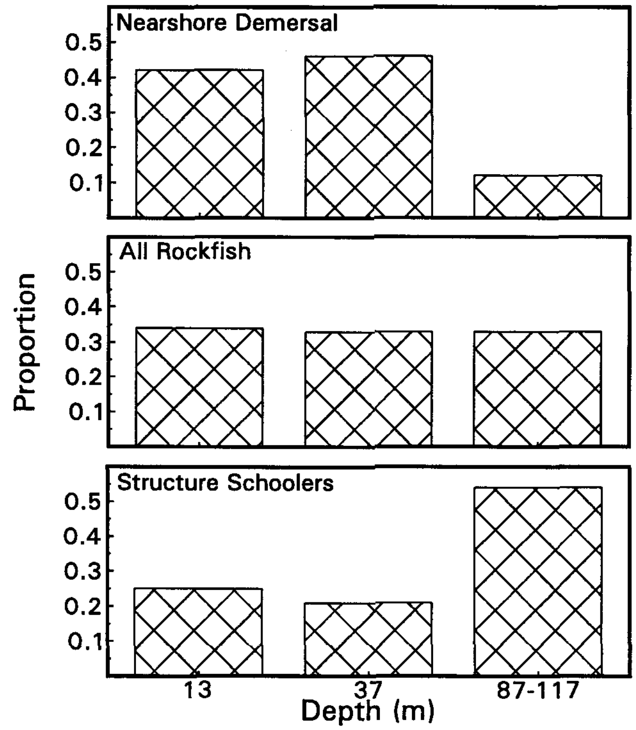

Figure 16. Unweighted average depth distributions of catches of YOY rockfish by the Tiburon midwater trawl survey, 1983–93. Depth-distribution estimation procedures were described by Lenarz et al. (1991).

waters that characterizes El Niño years. Conversely, the structure schoolers may benefit from onshore advection of deeper waters during non-El Niño years (Moser and Boehlert 1991).

The nearshore demersals and structure schoolers differ in another way that could affect their relative reproductive success during El Niño and non-El Niño years. Off central California, the peak parturition season for structure schoolers tends to be January and February, whereas that of the nearshore demersal group tends to be later. Peak parturition for blue rockfish occurs in January, and for black, widow, and yellowtail rockfish, in February (Wyllie Echeverria 1987). For the copper rockfish, parturition peaks in February (Wyllie Echeverria 1987), and for black and yellow rockfish, it peaks in March or possibly April (although little data are available for April; Zaitlin 1986). Parturition peaks in May for kelp rockfish (Romero 1988; figure 17), and June for brown rockfish (Wyllie Echeverria 1987).

Distributions of back-calculated birthdates of surviving YOY shortbelly rockfish and most other common species of rockfish captured by the MWTS varied considerably among years (figure 18 and Woodbury and Ralston 1991). However, adult samples and CalCOFI fish larvae surveys indicate that the parturition season varies much less than do back-calculated birthdate distributions of YOY that survive to the pelagic juvenile stage. MacGregor (1986) showed that there was little interannual variability in the seasonal distribution of shortbelly rockfish larvae caught by CalCOFI surveys. Wyllie Echeverria (1987) summarized data on gonad state of rockfish collected between 1981 and 1985 in routine samples of commercially landed rockfish. She found that peak months of parturition for widow rockfish ranged from January to February; peak months of chilipepper parturition varied from December to February; and peak months of bocaccio parturition varied from December to March. David Woodbury (pers. comm., NMFS, 3150 Paradise Dr., Tiburon, CA 94920) was concerned that

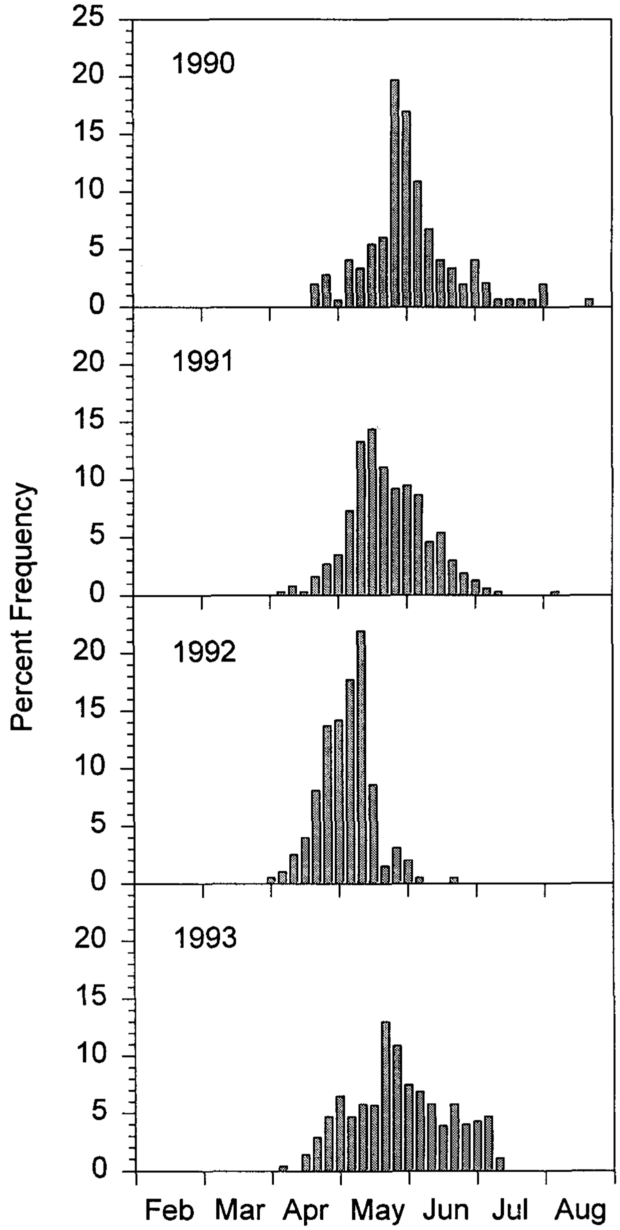

Figure 17. Back-calculated birthdate distribution of YOY kelp rockfish recruited to nearshore areas off central California, 1990–93. Fish were collected by D. VenTresca.

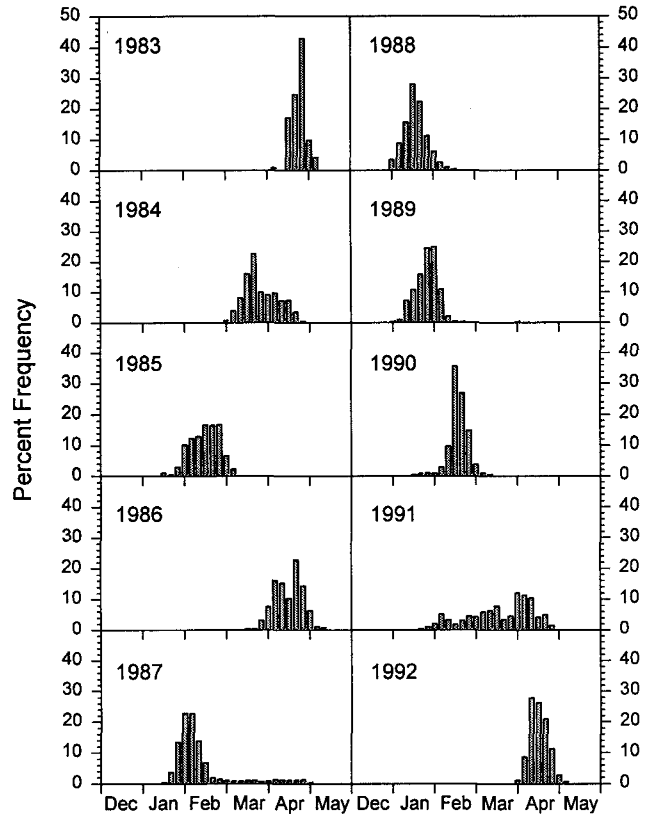

Figure 18. Back-calculated birthdate distribution of pelagic YOY shortbelly rockfish captured by the Tiburon midwater trawl survey.

sample size in the Wyllie Echeverria study was too small to adequately describe the parturition season and made a special effort to obtain chilipepper samples from commercial landings during 1990–92. He found that peak months of parturition were January and February in each of the three years. We believe that interannual variations in date-of-parturition-dependent survival rates are the primary cause of the variability in birthdate distributions shown in figure 18.

Back-calculated birthdate distributions of pelagic YOY of several important species of rockfish, including structure schoolers, covary with birthdate distributions of shortbelly rockfish (Woodbury and Ralston 1991); although these authors did not have data from the nearshore demersal group, the recent data for kelp rockfish (figure 17) indicate little interannual variability in back-calculated birthdate distributions, suggesting that the birthdate distributions of the nearshore demersal group do not covary with the structure schoolers. Survival of rockfish larvae released during January and February of 1983 and 1986 was poor (Woodbury and Ralston 1991). In those years and in 1992, most surviving shortbelly rockfish were larvae released during April (figure 18). In the other years, relatively few surviving shortbelly rockfish were released later than March.

Perhaps the seasonality of parturition is an important factor related to the interannual variation in relative reproductive success of the nearshore demersal and structure schooler groups. As previously shown, the annual primary productivity cycle started two months later than normal in Monterey Bay in 1992. Dominant prey of small larval rockfish are calanoid copepod nauplii (Sumida and Moser 1984) and calanoid copepod eggs (Bainbridge and McKay 1968). Mullin (1993) showed that food (phytoplankton) can limit egg production by calanoid copepods off California. Thus delayed phytoplankton blooms could indirectly cause failure of early-season rockfish parturition in El Niño years.

The low larval survival during the early season of El Niño years could also be related to onshore advection. There is some evidence that rockfish life-history stages are adapted to offshore waters. A summary of catches of rockfish larvae off central California by CalCOFI surveys taken during 1951–81 showed that the larvae were relatively abundant in offshore waters (Moser and Boehlert 1991). Pelagic juvenile YOY rockfish are often found off the continental shelf prior to settlement. Then they apparently undergo a behavioral change, sometimes supplemented by upwelling relaxations, that brings them onshore to settlement habitats (Larson et al. 1994). Ahlstrom (1959) found that rockfish larvae mainly occurred in the upper water column, which tends to be advected offshore in normal years.

The MWTS captured a gravid brown rockfish near the surface at a 55 m station during 1994 (pers. comm., David Woodbury). Until this capture, we had thought that adult brown rockfish were always associated with the bottom. The capture suggests that brown rockfish may swim into the upper water column to release reproductive products, as does another scorpaenid, the California scorpionfish (*Scorpaena guttata*). This species was thought to be closely associated with the bottom until Love et al. (1987) showed that it rose into the upper water column to spawn. While not conclusive, the evidence suggests that rockfish are adapted to an existence in offshore waters during their larval and pelagic juvenile phases.

Onshore advection and downwelling during El Niño events may bring young rockfish into nearshore waters that they are not adapted to, thus resulting in high mortality. Hobson and Howard (1989) found that a slightly more advanced life stage of shortbelly rockfish suffered high mortality in nearshore waters when southerly winds caused ocean currents that brought the fish inshore. The fish were apparently unable to avoid contact with the bottom. It is also possible that earlier life stages are not adapted to nearshore predators or prey.

Onshore advection is likely to be most severe during the early reproductive season, because average upwelling is weakest at that time (Bakun 1973). The high sea levels of early 1983, 1986, and 1992 (figure 4) are consistent with coastal downwelling and onshore advection.

El Niño events also appear to affect the growth and somatic condition of adult rockfish. The annual otolith growth increments in length (measured as the square root of surface area increments) of yellowtail and widow rockfish were 15%–20% lower in 1983 than in several adjacent years (pers. comm., Woodbury). Assuming that otolith growth increments are proportional to growth in body length, the decrease in annual otolith increment translates to about a 45% decrease in body-weight increment because of the cubic relationship between weight and length.

The condition of adult rockfish also deteriorated during El Niño events. We used length-specific weight as a condition measure for chilipepper, yellowtail, and blue rockfish, as did Winters and Wheeler (1994) for Atlantic herring. The specified lengths were common and sampled during each sampling period. We interpret condition as a measure of the well-being of a typical member of the species that is available to the sampling gear employed.

The condition of chilipepper was lowest during 1983 and early 1984 (about 5% below normal) and then recovered in late 1984 (figure 19). The other species were not measured for condition during 1983, although all three species had relatively low condition during 1992. Condition of yellowtail rockfish continued to be low in late 1993 through early 1994, but the condition of blue rockfish was high during the second half of 1993. Then the condition of blue rockfish deteriorated to about average levels during the first half of 1994. The condition of the three species was below average in late 1989 through early 1990, which was not during an El Niño. Condition was relatively high during 1988. Blue rockfish were not sampled until 1987. Condition for the other two species was about average during 1986, and tended to be above average for all three species during 1987. Thus the 1986–87 El Niño did not appear to adversely affect condition of the three species of rockfish. Lenarz and Wyllie Echeverria (1986) and VenTresca et al. (1995) also showed that condition of yellowtail and blue rockfish off central California deteriorated during El Niño events.

Simulated Effects of El Niño on Rockfish Population

We examined the combined effects of a severe El Niño and exploitation rates on a hypothetical population of chilipepper with a spreadsheet simulation model. We assumed that weight was reduced by 5% (as occurred in chilipepper during 1983) and that growth in weight was reduced by 45% (as occurred for widow and yellowtail rockfish in 1983). These factors were assumed to return to normal in the following year. Recruitment was assumed to be zero in the El Niño year and average in the other years. Growth, natural mortality, and the age-specific pattern of exploitation rates followed Rogers and Bence (1993). The simulation was run for three years because quotas are set at three-year intervals for some species of rockfish on the West Coast.

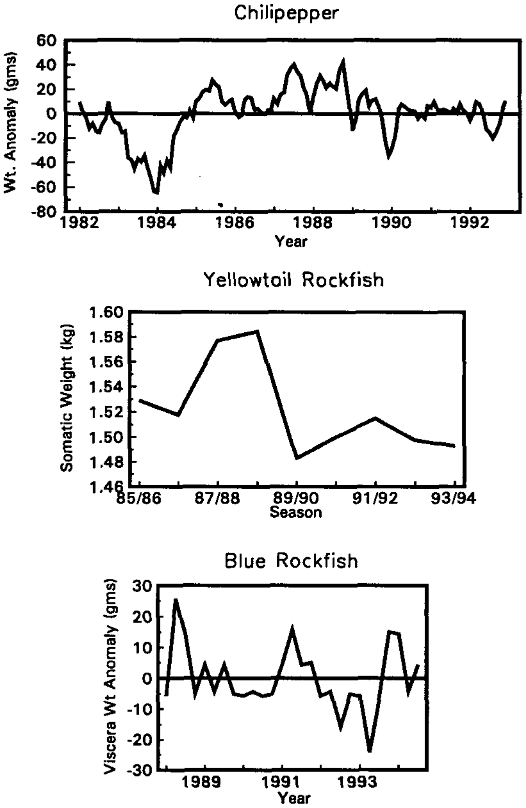

Figure 19. Weight at specified lengths for chilipepper, yellowtail rockfish, and blue rockfish. Chilipepper data are quarterly averages of monthly total weight anomalies of 400 mm fish sampled from commercial landings between San Francisco and Eureka, 1982–92. Expected weights were estimated using the methodology of Lenarz (1994). Yellowtail rockfish data are November–February averages of weight (with ovaries removed) of 400 mm female fish that were captured at Cordell Bank. Blue rockfish anomalies are deviations from quarterly averages of viscera weight without ovaries of 375 mm female fish captured in nearshore waters between Cape Mendocino and thirty miles south of Point Arena. Expected weights of blue and yellowtail rockfish were calculated by means of linear regression of log-transformed data. *Tic marks* on X-axes represent the beginning of the year.

The biomass of the stock dropped about 15% during the El Niño year (figure 20), recovered some in the next year, and then dropped as the failed year class did not replace losses due to natural and fishing mortality. Since the fishery still took the fixed quota from the reduced biomass, fishing mortality increased in the El Niño year and lowered the biomass more than would have occurred if the quota had been adjusted for El Niño conditions. Fishing mortality dropped in the following year and then increased slightly again because of the missing year class. The population was more strongly affected by

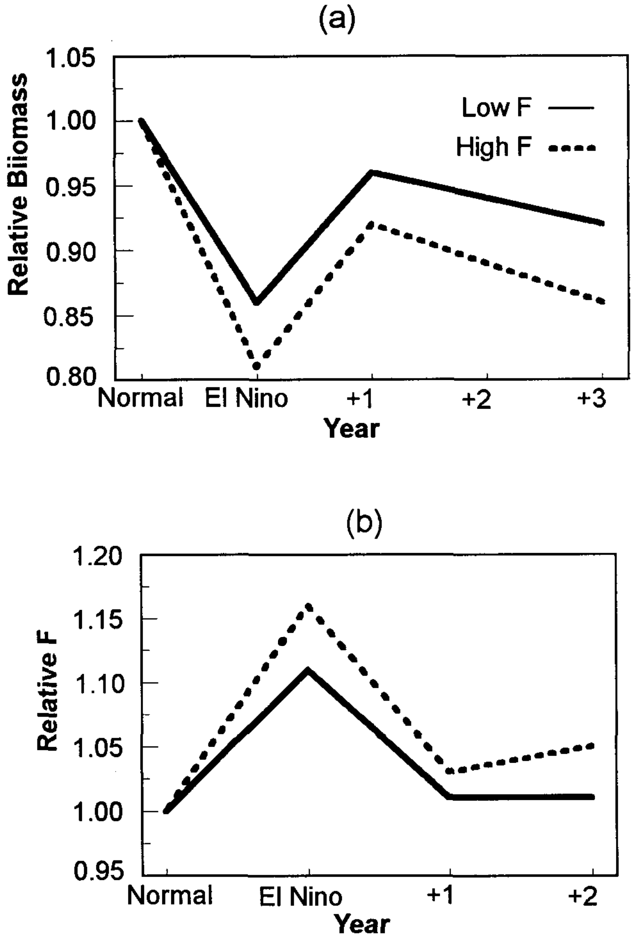

Figure 20. Results of computer simulation of how a severe El Niño would affect an exploited population of chilipepper rockfish: (*a*) relative biomass, and (*b*) relative fishing mortality (F).

El Niño when highly exploited than under low exploitation. The simulation demonstrated that fishery management practices can extend El Niño effects if harvest is not decreased in response to El Niño-related decrease in biomass.

GENERAL DISCUSSION

Physical phenomena associated with El Niño events were evident off central California during 1992–93. Temperatures were elevated, and salinities were depressed in 1992. The anomalies that appeared in 1992 remained to some degree in 1993 and 1994, with 1994 showing evidence of a return to more typical non-ENSO conditions. The observations also suggest that these anomalous conditions resulted from a combination of onshore and poleward advection, possibly combined with reduced upwelling. Although surface temperatures were equal to observations during the 1957–59 and 1982–83 events, coastal sea level was not as high during 1992–93 as during the 1982–83 event. Thus, poleward advection was probably not as strong off central California during the recent event as it was during the 1982–83 event. There was little physical evidence that the 1986–87 El Niño affected waters off central California. During this El Niño, temperature anomalies were less elevated than during the other El Niño events, and there was only a short period of high sea-level anomalies.

Physical aspects of El Niño events are better understood than biological repercussions off the West Coast; however, certain patterns are emerging. Primary productivity and zooplankton abundance appear to be reduced during El Niño events. There is considerable evidence of northward movement of southern species of fish, and some evidence of poleward advection of early life-history stages of some species. Reproductive success of most important species of rockfish tends to be poor off central California. The important early (January–February) parturition season seems to be particularly adversely affected. Condition of adult rockfish also appears to be poor off central California, similar to that of salmon off Oregon (Pearcy et al. 1985). Recruitment of southern fish was lower during the 1992–93 event than during 1982–83, and the condition of rockfish was higher during the more recent event. The 1986–87 event had little effect on either recruitment of southern fish or condition of rockfish.

Comparison of the three events indicates that the 1982–83 event was the strongest and the 1986–87 event was the weakest off central California. It appears that reproductive success of many species of rockfish off central California is very sensitive to El Niño conditions, because it was very poor during 1983, 1992, and 1986. Some El Niño physical attributes, such as elevated temperatures and depressed salinities, were still very evident off central California during the 1993 reproductive season, and rockfish reproduction was moderately successful (figure 14). Sea-level anomalies were considerably higher during the early parturition seasons of 1983, 1986, and 1992 than during 1993. Thus poleward advection or downwelling appear to be important factors in El Niño-associated rockfish reproductive failures off central California.

Just as some oceanic warm periods off the West Coast are not associated with tropical El Niño events, some of the biological characteristics observed during El Niño events off central California also occur during non-El Niño years. Rockfish condition was poor during late 1989 and early 1990. Rockfish reproduction was poor and euphausiid abundance was low during 1990. The 1989–90 event apparently also affected southern California waters. The condition of northern fur seals on San Miguel Island was relatively poor during 1990 (pers. comm., Robert DeLong, NMFS, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115).

Although oceanographers relate non-El Niño occurrences of El Niño-like physical phenomena to North Pacific atmospheric anomalies, we do not have a similar explanation for the biological events. Recognition of El Niño events and the wide geographical range of their effects has led to considerable progress toward understanding the dynamics of physical and biological ocean characteristics. The biological events of 1989–90 suggest that there may be another important oceanic regime awaiting discovery. Recognition of such a regime would give scientists another tool for understanding and perhaps predicting biological changes.

Longer time series are needed to ascertain that the El Niño–associated biological phenomena that we documented in this study are indeed common features of El Niño events off central California. The temporal sample size is small. Only a few events have been monitored. Considerably more work is required before we can do much more than speculate on the mechanisms that link the biological and physical phenomena. A better understanding of these mechanisms would reduce the variability that has hindered development of models relating fish reproduction success to adult population size and environmental factors. Much of the uncertainty in providing scientific advice on management of fisheries is due to a poor understanding of the recruitment process. Thus a better understanding of the mechanisms that link the biological and physical phenomena would have considerable pragmatic implications.

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