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The biological response to the 1977 regime shift in the California Current

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Abstract

Among the least understood interactions between physics and biology in the oceans are those that take place on the decadal scale. But this temporal scale is important because some of the greatest ecological events take place on this time scale. More than 50 years of measurement in the California Current System have revealed significant ecosystem changes, including a large, decadal decline in zooplankton biomass, along with a rise in upper-ocean temperature. The temperature change was a relatively abrupt shift around 1976–77, concurrent with other basin-wide changes associated with an intensification of the Aleutian Low-pressure system. This intensification generates temperature anomalies in the ocean by altering the patterns of net surface-heat fluxes, turbulent mixing, and horizontal transport. Changes in the mean abundance of zooplankton in the southern California Current have been attributed to variations in the strength of coastal upwelling, variations in the horizontal transport of nutrient-rich water from the north, or increased stratification due to warming, all of which could be affected by fluctuations in the Aleutian Low. Here we show that a deepening of the thermocline accompanied the warming and increased the stratification of the water column, leading to a decrease in the supply of plant nutrients to the upper layers. This is the most likely mechanism for the observed plankton decline, and subsequent ecosystem changes. A global change in upper-ocean heat content, accompanied by an increase in stratification and mixed-layer deepening relative to the critical depth for net production, could lead to a widespread decline in plankton abundance.

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1. Introduction

There is ample evidence of the ecological consequences of recent climate change (Gian-Reto et al., 2002; Walther et al., 2002). Much of this evidence comes from the terrestrial realm and lakes. Although the mechanisms linking terrestrial

populations and ecosystems with climate change are thought to be understood, the trajectories are not. The population changes are generally thought to be forced by climate warming. The rate of this warming, since 1977, has increased (Climate Change, 2001) and more such change is expected. Climate-related ecosystem changes also have been reported in the world's oceans, but, as opposed to the land, the intermediary mechanisms linking the two are, for the most part, speculative

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(Venrick et al., 1987; Aebischer et al., 1990; Ebbesmeyer et al., 1991; Francis and Hare, 1994; Polovina et al., 1995; Roemmich and McGowan, 1995; Brodeur et al., 1999; Hare and Mantua, 2000).

The California Current is a highly variable physical system and so are its populations and communities. But the 50-year time-series of physical and biological observations from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program have shown that the ecosystem does have some central tendency or pattern. There have been specific instances when climate-caused perturbations of the pattern have been documented: the 1957–59 El Niño and again in 1983–84 and 1997–98. These were of relatively short duration, and both the physical and biological systems “recovered” (Sette and Isaacs, 1960; Chelton et al., 1982; McGowan et al., 1996; Bograd and Lynn, 2001). But in the late 1970s a rapid shift to a persistent new state occurred in the North Pacific (Ebbesmeyer et al., 1991; Miller et al., 1994; Trenberth and Hurrell, 1994; Mantua et al., 1997; McGowan et al., 1998; Minobe, 1999; Hare and Mantua, 2000; Miller and Schneider, 2000; Parrish et al., 2000), and a similar rapid change of state has been reported in the terrestrial realm (Schaeffer et al., 2001). Most of the biological changes in the eastern North Pacific associated with this climate shift appear to be declines in populations and biomass and/or range shifts northward of some species. As with the terrestrial realm, we know little of the long-term consequences of such changes.

There have been three hypotheses for the mechanism(s) behind the decline of populations and biomass over time. All three could, in principle, be affected by the climate shift and might even act in concert. The most prominent of these hypotheses concerns coastal upwelling, a well-known process, and one frequently assumed to be the main reason for the biological richness of the California Current System (CCS). Variations in coastal upwelling intensity could change biological production by varying the input of deeper, nutrient-rich water to the lighted zone (Bakun, 1990). It also has been shown that interannual variations in horizontal input of cooler, fresher,

nutrient-rich water from the north are well correlated with interannual changes in zooplankton biomass in the southern CCS (Chelton et al., 1982). Finally, it has been suggested that the long-term warming and deepening of the mixed layer, post 1977, has led to an increase in stratification of the water column, resulting in a change in the source and therefore the nutrient content of the waters introduced into the euphotic zone from below (Roemmich and McGowan, 1995). Such a deepening of the mixed layer relative to the “critical depth” for net phytoplankton production also would lead to a decline in such production (Sverdrup, 1953). It is important to determine which of the hypotheses do not apply in order to enhance our understanding of the intermediary mechanisms by which climate variability, especially large-scale, low frequency, decadal variations, may be translated into ecosystem variability.

Here we present a brief overview of some of the known biological consequences in the CCS of the 1977 regime shift in North Pacific climate. Bograd and Lynn (2003) present a detailed account of the hydrographic and flow changes in the CalCOFI region associated with this shift. We test the three hypotheses for the intermediary mechanisms leading to the observed biological changes. But neither the atmospheric/oceanographic nor the biological phenomena are particularly well delineated and, in the case of biology, may have yet to play themselves out.

2. Biological response to the 1977 regime shift in the CCS

2.1. The North Pacific climate shift

There is great uncertainty about how variations in the atmosphere get translated into variations in the ocean and its populations. Among the least understood interactions are those between the ocean and atmosphere that take place on the decadal scale (Graham, 1994; Trenberth and Hurrell, 1994; Miller and Schneider, 2000), but this scale is important biologically because some of the greatest environmental events take place at this time scale. One such large shift in the climate–

ocean–biology system occurred in the Pacific during 1976–77 (Ebbesmeyer et al., 1991; Miller et al., 1994). The atmospheric changes were first noted as a deepening of the Aleutian Low-pressure system, a drop in sea-surface temperature (SST) in the central Pacific, and a rise of SST in the eastern Pacific including the California Current (Venrick et al., 1987; Cayan, 1992; Roemmich, 1992). The connection to oceanic ecology was evident when the step-like doubling of chlorophyll concentration in the deep chlorophyll maximum of the North Pacific Central Gyre coincided with an increase in winter winds and a decrease in SST (Venrick et al., 1987). Ebbesmeyer et al. (1991) showed that the changes of 40 different normalized environmental and biological variables formed a step-like shift during 1976–77. It appears that this 1976–77 shift in both the coastal and mid-Pacific regions was caused by a unique atmospheric state that persisted for many months before and during the 1976–77 winter.

Cayan (1992) has shown that monthly mean heat flux anomalies are organized in large-scale patterns that have strong influence on the ocean thermal structure. Although it is not yet clear how this affects atmospheric circulation, the patterns could be related to persistent regimes of mid-latitude ocean–atmosphere interaction, whereby feedback effects of heat transfer maintain the atmospheric thermal fields and wind stress maintains the oceanic SST field (Miller and Schneider, 2000).

Comparisons of models with observations indicate that large-scale deepening of the Aleutian Low can generate upper-layer temperature anomalies in the ocean by altering the spatial pattern of surface heat flux, by intensifying horizontal advection, and by increasing turbulent vertical mixing. One such model–observation comparison showed that the thermocline deepened from the 1970s to the early 1980s in the eastern Pacific at the same time it was raised in the northwestern Pacific due to changes in Ekman pumping (Miller, 1996; Miller et al., 1998). Both data and model agreed, but they revealed that a more gradual change in temperature occurs at depth than at the surface. More details on the physics of North Pacific regime shifts can be found in a number of recent

studies (Miller et al., 1994; Trenberth and Hurrell, 1994; Minobe, 1999; Miller and Schneider, 2000). Below we will show such thermocline changes in the CCS and the associated biological changes in plankton abundance.

2.2. *Biological changes in the CCS following 1977*

Our longest time series consists of a 50-year accumulation of zooplankton samples and hydrographic profiles from a fixed grid of stations in the main body of the CCS, collected under the auspices of CalCOFI (Fig. 1). The methods and locales have been described many times (Isaacs et al., 1971; Kramer et al., 1972; Ohman and Smith, 1995; SIO, 1999; Moser et al., 2001; Rebstock, 2001; Bograd and Lynn, 2003). There have been a few changes in both apparatus and sampling protocol over the years, but these have not biased our estimates of changes in plankton abundance or descriptions of hydrography.

These samples have been studied in many ways in the past for interannual and higher frequencies of temporal and spatial abundance changes (Brinton, 1981; Chelton et al., 1982; McGowan et al., 1996) and variations in relative abundance of major taxa (Fleminger et al., 1974; McGowan et al., 1998). Species biogeography and the associated habitat variables have been determined for species of copepods, euphausiids, chaetognaths, salps, doliolids, pteropods, heteropods, and squid and fish larvae from the first two decades of measurement (CalCOFI atlases 1–34). Species dominance structure also has been examined from samples close together in time and space (McGowan and Miller, 1980). These and other studies have provided us with a substantial understanding of the hydrography and quantitative biogeography of zooplankton during the first 20 years or so of this program, that is, the period prior to the late 1970s when the regime shift occurred.

There are three long-term studies of plankton species variability over the entire 50-year series: euphausiids (Brinton and Townsend, 2003), copepods (Rebstock, 2001) and larval fish (Moser et al., 2001). All of these cover the pre- and post-regime shift periods. Rebstock (2001) has examined the rank order of abundance (dominance structure) of

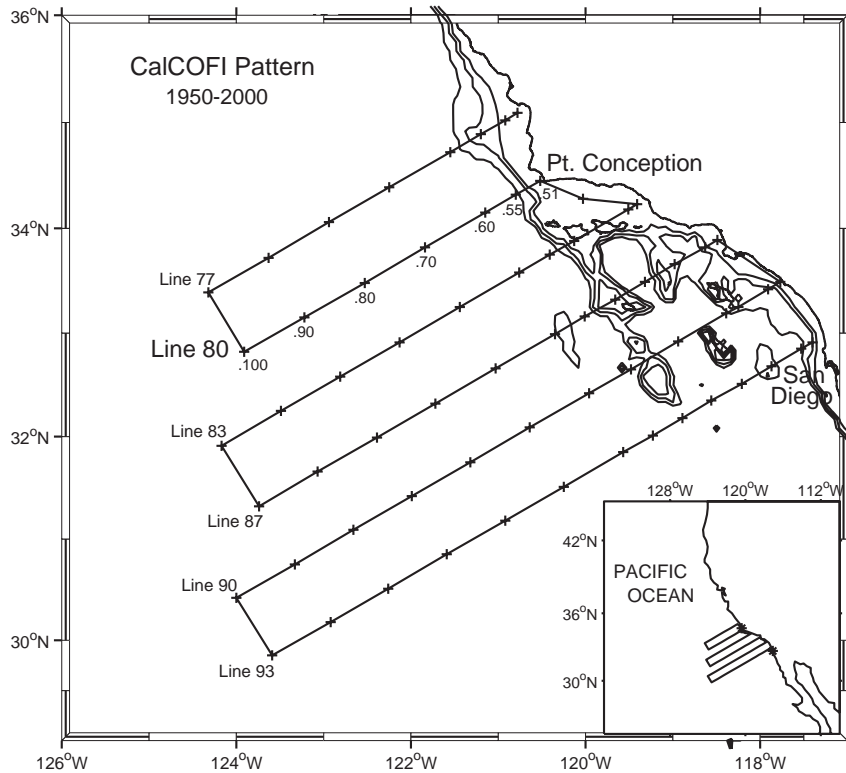


Fig. 1. The CalCOFI nominal sampling grid off southern California. Stations are marked by a +, and are labeled for line 80. Bathymetry contours at 300, 500, and 700 m are drawn. The Southern California Bight (SCB) is the region inshore of the submerged ridge extending southeast from Point Conception.

33 species of calanoid copepods from over 50 years of CalCOFI sampling in the CCS. She found the assemblage to be consistently and strongly dominated by only a few species. The two top dominants were *Calanus pacificus* and *Metridia pacifica*, both of which varied greatly in abundance during the five decades. Their interannual variability seems strongly tied to indices of climate driven variables, positively with the Southern Oscillation Index in the case of *Metridia pacifica* and negatively with deeper temperature anomalies in the case of *Calanus pacificus*. But *C. pacificus* also showed a great increase in the frequency of abundance anomalies from long-term means during the 1970s and 1980s, as did many other species of copepods. However, around 1990 the *C. pacifica* population fell to well below the long-term mean and stayed that way for a decade. The degree to which copepod species rank order of abundance

varied over time has changed greatly after the regime shift years of 1976–77. The rank order of abundance became much more variable during the following decades. Brinton and Townsend (2003) show that the populations of *Euphausia pacifica* and *Thysanoessa spinifera* were often below their long-term (1951–2000) mean after the late 1970s while those of *Nyctaphanes simplex* were anomalously high. That is, there was a change in species proportions and order of dominance. Variations such as these revealed by long-term studies are clear evidence of species population level responses to climatic variations such as El Niños and regime shifts.

There have been two sharp drops in zooplankton biomass associated with Californian El Niños, which were well correlated, at a lag, with tropical ENSO conditions. These occurred during the 1957–59, 1983–84, and 1997–98 episodes. There

was a clear recovery to former levels after 1960, but the 1983–84 and later the 1997 decline were superimposed on a much larger and more persistent shift to less biomass and elevated SST, i.e. the regime shift of 1977. At this writing there is no clear evidence for a widespread and persistent recovery of zooplankton biomass to the pre-regime shift condition, especially offshore. The systematic decline of plankton was clearly associated with the surface mixed-layer warming and lower salinities (Roemmich, 1992; Roemmich and McGowan, 1995; McGowan et al., 1996). The 1977 shift also led to a significant change in zooplankton phenology. The seasonal mean peak in biomass was July during the cold regime 1951–76, but this peak shifted about two months earlier during the 1977–98 warm regime (Fig. 2a).

There also have been pronounced shifts in the abundance and proportions of larval fish. Over 8 million eggs of all species were collected between 1951 and 1976. From 1977 to 1998 only 3.4 million were found. Prior to 1975 the abundance of fish eggs (from over 300 species) fluctuated during the decades with a sharp, brief decline following the 1959–60 El Niño and then a spectacular recovery and increase until 1976, when the population essentially crashed (Fig. 2b). As of 1999 there is no convincing evidence of a recovery. The abundance of fish eggs is generally thought to be an index of the size and/or condition of the adult population that gave rise to them. The annual variations in larval fish abundance followed a similar pattern to that of the fish eggs but at a several-year lag (Moser et al., 2001).

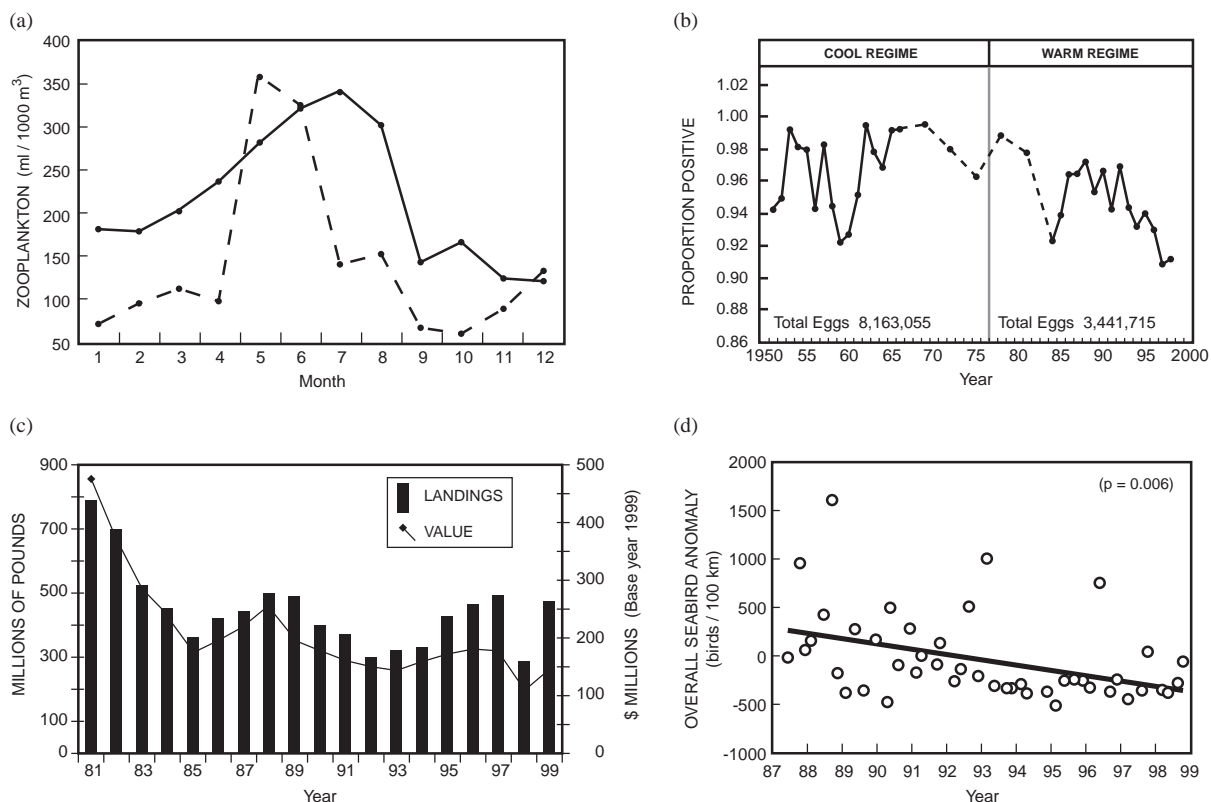


Fig. 2. (a) The shift in the seasonal peak of zooplankton biomass abundances. Solid line is the pre-1977 cool period, dashed line is the post-1977 warm period (after Moser et al., 2001). (b) Change in frequency (proportion of samples with eggs) and abundance of fish eggs in the water column of the CalCOFI area. Over 300 species are represented (after Moser et al., 2001). (c) Volume and ex-vessel value of all commercial fish landings in California (after Thomson, 2001). (d) Number of seabirds per 100 km averaged over CalCOFI cruise lines (see Fig. 1; after Hyrenbach and Veit, 2003).

There are about 20 species that make up the bulk of the larval fish population from the CalCOFI record, which consists of nearly 300 species identified over the period 1951–98. But the adults of only six of the dominant 20 are harvested commercially. This suggests that the massive decline in eggs and larvae, post 1976, may not be due entirely to fishing pressure on the adults, but rather to some additional factor, perhaps habitat change. For example, *Leuroglossus stilbius*, which ranked third in larval numerical abundance and is a non-commercial species, fell from 243,017 larvae collected between 1951 and 1976 to 121,321 between 1977 and 1998. *Stenobranhus leucop-sarus*, which ranked sixth and is also non-commercial, fell from 141,434 to 82,409 during the same period.

Commercial fish landings also provide evidence for a biotic response to an abrupt environmental change in the late 1970s. Total commercial fish landings have dropped precipitously since about 1981 (Fig. 2c). During this time the number of fishing vessels also declined, so an increase in fishing pressure does not seem to be the cause of this decline of landings (Thomson, 2001). The declines have been across trophic levels and habitats. Coastal pelagic fishes such as anchovy, sardines, mackerel and others were once the most important commercial fish in the California Current and important zooplankton predators as well. But the combined landings of these fish have dropped about 30% post-1977 in spite of the limited recovery of the California sardine (Chavez et al., 2003). Groundfish, another commercially important group that includes about 80 bottom dwelling species, are almost all at or below 25% of their pre-1977 abundance.

Seabirds in the CCS also have responded to climate events, both at El Niño and lower frequencies. They are apex predators and, because they are unharvested, variations in their population sizes should reflect changing availability of their prey. Systematic surveys of seabird abundance did not begin until 1987 but have continued on all CalCOFI cruises since then (Veit et al., 1996, 1997; Hyrenbach and Veit, 2003). Fortunately, there are earlier observations and estimates of abundance at several different locales within the

CCS so temporal comparisons may be made (Ainley et al., 1995). The CalCOFI seabird survey consisted of 159,000 sightings on 45 cruises over a distance of 70,000 km. A total of 68 species were counted. Hyrenbach et al. (2003) have confirmed and extended the Veit et al. (1997) report that there has been a large and significant decrease in seabird abundance during this period, particularly in the nearshore region, where five of the six dominant species declined (Fig. 2d). Hyrenbach et al. (2003) also have demonstrated that, along with the drop in zooplankton biomass, there has been a drop in the intensity of plankton patchiness nearshore, where foraging seabirds depend on such patches. Ainley et al. (1994, 1995) and Sydeman et al. (1997) showed that the size, diet, and reproductive success of locally breeding seabirds have changed in response to warming of the CCS.

2.3. The nearshore changes

Holbrook et al. (1997) studied Southern California nearshore reef fishes for over 20 years at two sites and found significant shifts in species richness and dominance, with southern species becoming dominant over time and an overall decrease of fish abundance by an average of 69%. These changes followed the abrupt shift to warmer nearshore temperatures over the entire coast of California in the late 1970s. Other nearshore changes also have occurred. Barry et al. (1995) compared the species counts of invertebrates at a site surveyed twice, 60 years apart (1931–33 and 1993–94). There was a clear change in species structure, with a general increase in “southern” species and decrease in “northern” species. Sagarin et al. (1999), in a study of an expanded data set of 62 species from the same locale in central California, supported the earlier Barry et al. (1995) conclusions about the relationships between changes in invertebrate abundance and the increase in nearshore temperature. They also evaluated several alternative hypotheses to explain such changes. These included habitat changes, anthropogenic effects (pollution), indirect biological interactions, El Niño events, and upwelling, all

of which were considered to be “less important than climate change” (Sagarin et al., 1999).

An aerial survey in 1967 showed a total of 180 km² of kelp canopy along the entire California coast. A similar survey conducted in 1989 reported 104 km². During the most recent statewide kelp forest survey in 1999 a total of 45 km² was charted along the coast (Bedford, 2001). These kelp forests are of commercial importance and are special habitat and nursery areas for almost 800 species. Bull kelp forests (*Macrocystis*) have always varied in density seasonally and interannually, being especially sensitive to episodic warm water events such as Californian El Niños. Storm disturbances and perhaps pollution also play a role. But Parrish and Tegner (2001) found that SST is the best predictor of Bull kelp harvest and aerial extent, and that the nearshore ocean warming following the 1977 regime shift has been associated with large decreases in the size of kelp plants. A depressed thermocline also limits intrusions of deep, cooler, nutrient-rich waters from offshore, yielding kelp mortality (Parrish and Tegner, 2001).

2.4. The state change

Taken together, the evidence strongly points to a major change of state of the California Current ecosystem extending from the open ocean pelagic zone to the nearshore. The shift involved many populations from at least four trophic levels. The shift was relatively rapid for the lower level, short-lived organisms, but there appeared to be a lag at the predator level of large fish and seabirds. We are hampered here in pinpointing the timing of the change across trophic levels, because of differences in the frequency of measurements. But there is substantial concordance among all of the biotic groups studied and in all of the habitats that a very substantial change has taken place since 1977, and that this change was associated with a relatively abrupt ocean warming. The warming event may be distinguished from the interannual, El Niño-driven, warming episodes in the California Current both by its decadal persistence and its appearance in concert with an interdecadal shift in the large-scale atmospheric dynamics of the North Pacific.

The almost universal observation is that many populations declined in abundance, although there is ample evidence that there were also range shifts to the north of both pelagic and nearshore species (Lluch-Belda et al., 1989; Karpov et al., 1995; Sagarin et al., 1999). These extensive ecosystem changes have persisted for at least 20 years. Although there is some evidence for a recent cooling of the California Current and some populations may be “recovering”, nothing resembling a major system-wide shift back to pre-1977 conditions has thus far been documented.

To what may we attribute this spectacular response of the biota to such a climate event? Clearly warming has something to do with it, but the persistent large-scale warming of the California Current amounted to less than 1°C when averaged over the upper mixed layer where the greatest changes took place. Physiological effects sufficient to affect population dynamics of entire trophic levels seem unlikely from this small a temperature increment. It has been suggested in several places that the mechanism for input of the basic inorganic nutrients required for primary production has changed due to the climate shift. Below we examine the three hypothesized mechanisms whereby this could occur.

3. Potential mechanisms for the biological regime shift in the CCS

Availability of inorganic nutrients in the euphotic zone, the portion of the water column receiving sufficient light energy for primary production, acts as a control on biological production in the CCS. Although CalCOFI did not begin systematic nutrient measurements until 1984, a close relationship has been found between temperature and nitrate in the CCS (Kamykowski and Zentara, 1986; Hayward and Venrick, 1998; Bograd and Lynn, 2001), allowing use of the 50-year temperature series as a proxy for nutrient concentrations. Profiles of mean temperature and nitrate concentration reveal a substantially shallower thermocline and nutricline at the nearshore end of line 80, although constant values of 12°C and 10 µmol/l appear to be representative of

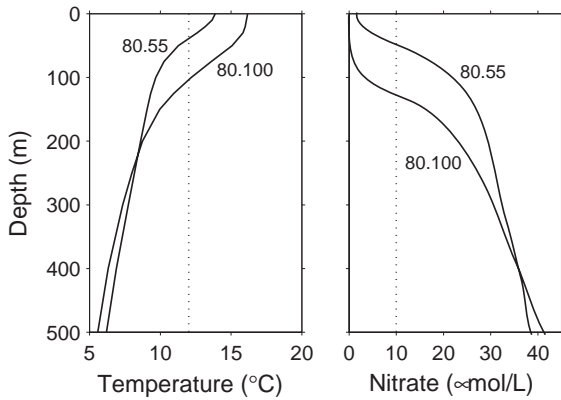


Fig. 3. Mean profiles of (a) temperature (1950–2000 base period) and (b) nitrate (1984–2000 base period) for stations 80.55 and 80.100 (see Fig. 1). The 12°C and 10 μmol/l values, marked by dashed lines, are representative of thermocline and nutricline depth, respectively. We confine the present analysis to line 80, which has a well-defined, seasonally varying productive zone off Point Conception driven, in part, by coastal upwelling, and is unencumbered by topographic steering of the near-surface flow, as within the SCB.

thermocline and nutricline depth, respectively, along the extent of the line (Fig. 3). Thermocline depth and nutricline depth, thus defined, are well correlated ($r \approx 0.9$) at all stations on line 80 for the 17-year period in which nutrient data exist, confirming our use of the temperature proxy.

There is an unambiguous visual and statistical correlation between thermocline depth and zooplankton biomass along line 80 over the period 1950–2000 (Figs. 4a–d and Table 1). The time series have been separated into two 25-year periods, with the dividing year (1976) being the approximate time of the well documented regime shift in North Pacific climate (Ebbesmeyer et al., 1991; Miller et al., 1994; Trenberth and Hurrell, 1994; Mantua et al., 1997; Hare and Mantua, 2000). Year-to-year variability is prevalent in both fields, with particularly energetic El Niño events in 1957–58, 1982–83 and 1997–98 forcing a deepening of the thermocline nearshore and presumably leading to significant reductions in the input of nutrients, a depressed primary production, and a reduced secondary production of zooplankton biomass (Bograd and Lynn, 2001). Variability at the offshore end of line 80 is of lower frequency.

Even with high-amplitude interannual variability throughout the record, both fields appeared to shift to different mean states following the 1976–77 climate event, rather than follow a continuing trend of upper-ocean warming and zooplankton decline (Roemmich and McGowan, 1995; McGowan et al., 1998). The section-mean 74% decline in zooplankton biomass between 1950–75 and 1976–2000 (before and after the regime shift) was coincident with a 17% deepening of the thermocline (nutricline).

If a significant portion of the zooplankton decline can be attributed to suppression of nutrient input into the upper water column, one question is whether a change in horizontal advection or vertical transport played a larger role. We investigate this issue by looking at two factors which have been implicated in forcing zooplankton variability in the CCS: (a) alongshore volume transport (Wickett, 1967; Chelton et al., 1982), which can advect nutrients and zooplankton into the region from the north as well as deflect isopycnals upward via geostrophic adjustment, and (b) upwelling index (Bakun, 1990), which is a measure of wind-driven coastal upwelling (Figs. 4e and f). Net transport is almost always equatorward, reflecting the dominant California Current (Lynn and Simpson, 1987), but fluctuates greatly on seasonal and interannual time scales. The upwelling index is dominated by interannual variability in seasonal wind forcing. Neither series, however, has a strong long-term trend, nor is either series significantly correlated with variations in thermocline depth or zooplankton biomass ($r = 0.09$ for line-mean zooplankton anomalies vs. volume transport anomalies, $r = 0.04$ for line-mean zooplankton anomalies vs. upwelling index anomalies). Indeed, alongshore winds increased after the 1977 regime shift, which by itself should lead to cooler temperatures and higher salinities in the CCS (Fig. 5). While the offshore CalCOFI region had a decrease in wind stress curl (i.e., more downwelling) following 1977, the nearshore region had a year-round increase in curl, again implying increased upwelling. However, we may conclude that although equatorward transport and coastal upwelling can greatly impact water properties, vertical structure, and biological production across

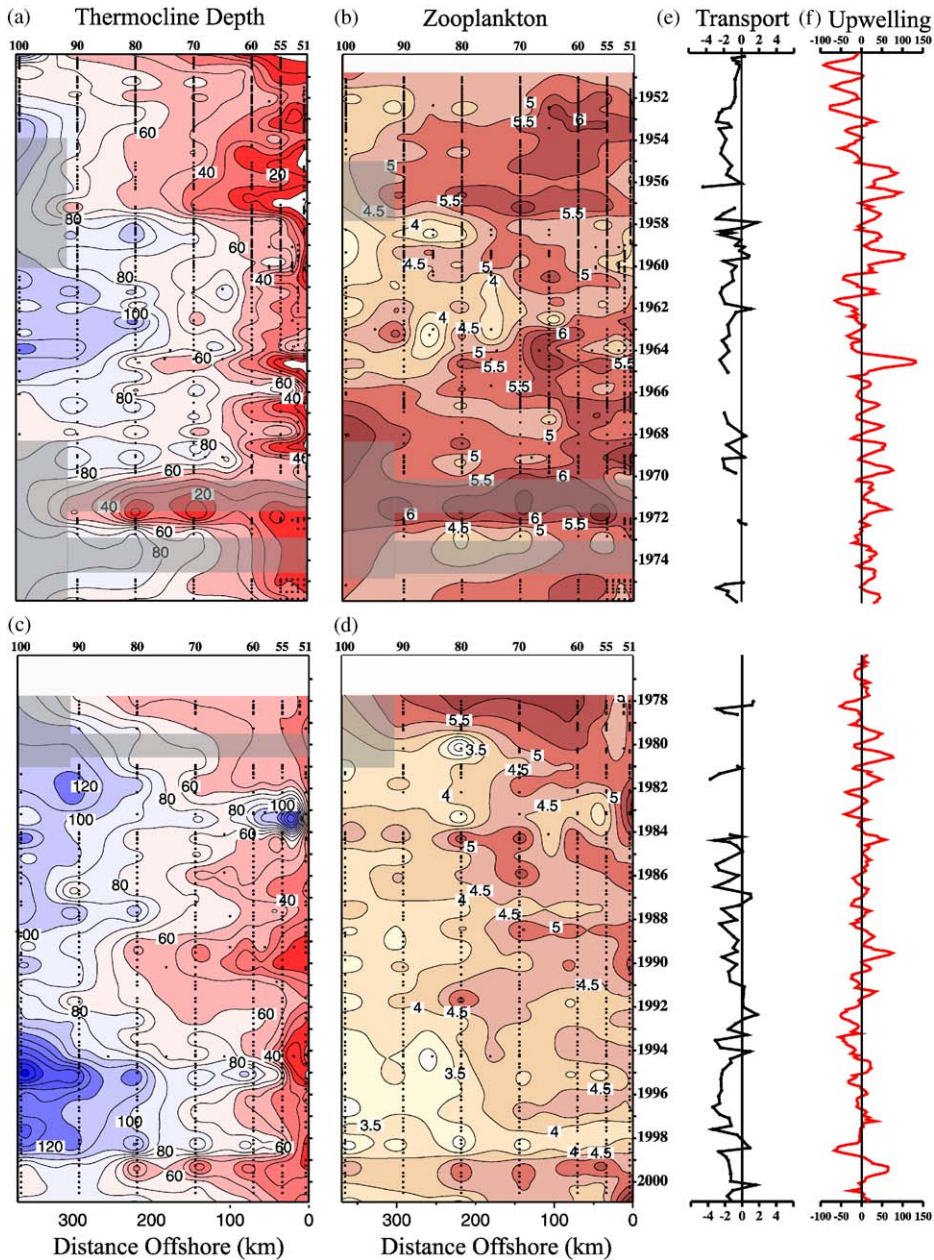


Fig. 4. Line 80 time-distance plots of depth of the 12°C isotherm (m; a proxy for thermocline depth and nutricline depth) for (a) 1950–75 and (c) 1976–2000, and log_e of macrozooplankton displacement volume (cm³ 1000 m⁻³) for (b) 1950–75 and (d) 1976–2000. Regions requiring significant interpolation or extrapolation are shaded gray, and nearshore areas in white are where the 12°C isotherm outcrops. Stations are marked by a dot and their labels are given on the top axis of each plot. A total of 1391 (1750) station occupations comprise the 50-year hydrographic (zooplankton) time series on line 80. Time series of (e) alongshore volume transport (10⁶ m³ s⁻¹), calculated between stations 80.55 and 80.90 for each cruise, and (f) monthly upwelling index anomalies (m³ s⁻¹ 1000 m⁻¹; base period 1946–1997), which are estimates of offshore Ekman transport driven by the alongshore geostrophic wind stress at 34°N, 120°W, are shown to the right of the time-distance plots.

Table 1

Correlations between the CalCOFI line 80 thermocline depth and macrozooplankton displacement volume time series for periods 1 (1950–75) and 2 (1976–2000)

	80.100	80.90	80.80	80.70	80.60	80.55
n_1, r_1	41, -0.45	103, -0.38	100, -0.47	112, -0.16	113, -0.13	107, -0.25
n_2, r_2	58, -0.49	78, -0.31	80, -0.47	80, -0.14	83, -0.27	83, -0.36
T_1/T_2	95/115	84/102	75/81	57/65	42/55	32/46
Z_1/Z_2	116/63	211/86	197/150	277/169	333/217	325/152
ΔTherm (%)	+17	+18	+7	+12	+24	+30
$\Delta Z_{\text{oo}_{\text{sm}}}$ (%)	-84	-145	-31	-64	-53	-114
$\Delta Z_{\text{oo}_{\text{tot}}}$ (%)	+61	-13	+4	-59	-63	-61

These are unlagged correlations based on same-month observations between the series. The number of common estimates (n) and the correlation coefficients (r) are given for each station (top row) and each of the two time periods (1, 2). Correlations that are significant at the 99% confidence level are bold. Mean values of thermocline depth (T ; m) and zooplankton displacement volume (Z ; $\text{cm}^3 1000 \text{m}^{-3}$) for both periods are given for each station, as are the percentage changes in thermocline depth (ΔTherm) and zooplankton displacement volume ($\Delta Z_{\text{oo}_{\text{sm}}}$) between periods 2 and 1. The last row gives the percentage changes in *total* zooplankton displacement volume ($\Delta Z_{\text{oo}_{\text{tot}}}$; megalozooplankton) between periods 2 and 1. Net decline in macrozooplankton biomass along line 80 is -74%, -17% for megalozooplankton.

many time scales, neither process can be invoked to fully explain the dramatic long-term changes observed in upper ocean heat content and zooplankton biomass on line 80.

Earlier studies (Roemmich and McGowan, 1995; McGowan et al., 1998) have speculated that upper-ocean warming could result in increased stratification, less lifting of the thermocline by vertical mixing and upwelling (coastal and offshore), and hence a shallower, nutrient-poor source of upwelled waters. We have documented a section-mean 17% increase in thermocline depth in the CCS, in agreement with modeling results (Miller and Schneider, 2000). We further explore this mechanism by looking at the vertical structure of water property changes on line 80 between the two 25-year periods (Fig. 6). Warming has occurred at all depths down to at least 200 m, although the warming is surface-intensified across most of the line (Fig. 6a). The largest change ($>1.2^\circ\text{C}$) occurred at 50–100 m depth at station 80.100, and may be a result of more frequent incursions of water from the Subtropical Gyre and/or a different make-up of the source waters of the California Current (Bograd and Lynn, 2003). Strong warming is also evident in the upper 40 m at the nearshore end of the line (stations 80.51–80.60), while the center of the line has had the weakest change. The largest change in salinity, a freshening of more than 0.07 psu, also occurred in

the upper 40 m at the nearshore end of the line (Fig. 6b).

Since temperature has the largest influence on the equation of state in subtropical waters, the density difference section (Fig. 6c) has a pattern much like that of temperature. The critical parameter for vertical nutrient transport, however, is water column stability, defined here simply as the vertical gradient of density (Fig. 6d). As described in Bograd and Lynn (2003), stability has increased from the coast to 300 km offshore on line 80, with the maximum increase occurring at 30–50 m depth. Mean profiles of Brunt-Väisälä frequency at station 80.55 also indicate a substantial increase in water column stability following the regime shift (not shown). This pattern would act to limit the lifting of nutrient-rich waters, rendering upwelling less biologically effective and reducing productivity at these stations. The strongest warming and freshening has occurred in the near-surface waters of stations 80.55 and 80.60, just above the peak stability changes. This supports the idea that there was a shallower source of upwelled waters following the regime shift (Bograd and Lynn, 2003), even though the amplitude of coastal upwelling may have increased (Fig. 5). These patterns are consistent with a long-term trend with a positive feedback: as near-surface warming has occurred stratification has increased, resulting in reduced vertical trans-

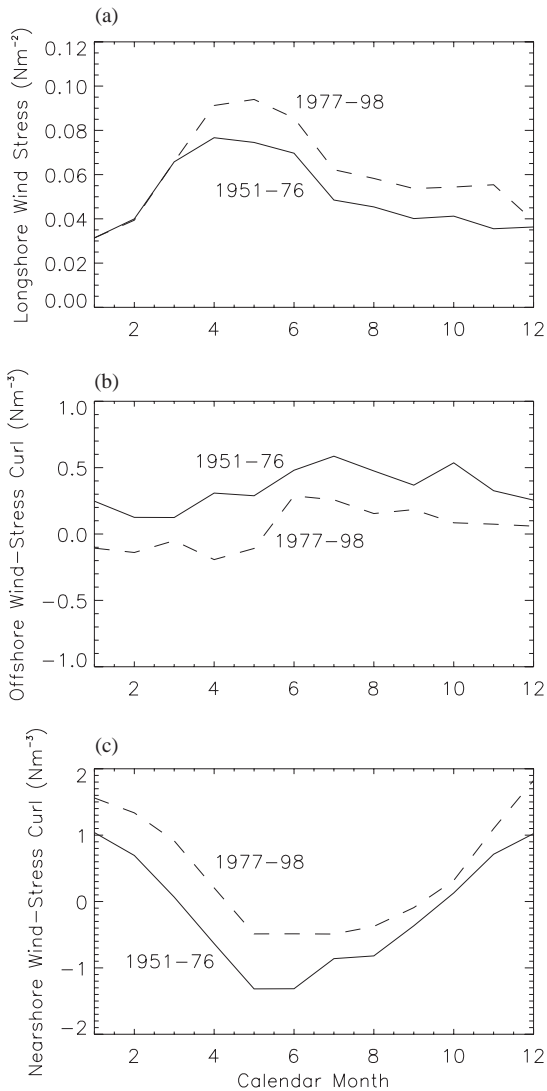


Fig. 5. The climatological annual cycle of (a) alongshore wind stress, (b) wind-stress curl in the offshore CalCOFI region (average over 7 atmospheric grid points from the outer half of the nominal CalCOFI grid), and (c) wind-stress curl in the nearshore CalCOFI region (average over 4 atmospheric grid points from the inner half of the nominal CalCOFI grid) for the periods 1951–76 (solid lines) and 1977–98 (dashed lines). Wind data are from the National Centers for Environmental Prediction.

port by upwelling or mixing of cooler, more saline (and more nutrient-rich) waters, a process which would then work to increase stratification further. This is an important point to consider, for if the

observed warming is less transient than regime-scale dynamics, for example a signature of a global warming trend (Barnett et al., 2001; Levitus et al., 2001), the impact on biological production could be profound and widespread. The details of how altered upper-ocean temperature can change the source waters of the coastal upwelling field need to be examined further through combined observational and modeling studies.

Our results are consistent with the hypothesis that the recent warming in the CCS, which we have associated with the 1976–77 regime shift, led to an increase in water column stability. The mechanism for the surface-intensified warming, which can act to deepen the thermocline, is not clear. Modeling studies have shown that altered air–sea heat fluxes acted to warm the surface mixed layer after the shift (Miller et al., 1994) and that changes in wind stress curl have forced the thermocline downward (Miller et al., 1998) in the offshore California Current region. Remote forcing by oceanic signals propagating along the eastern Pacific boundary from the tropics (Meyers et al., 1996; Clarke and Lebedev, 1999), due to a preponderance of tropical warm (El Niño) events following the regime shift, also may have contributed to the thermocline depression and near-surface warming in the eastern North Pacific. Each mechanism is plausible and may be acting concurrently, although the present data are not sufficient to distinguish their relative importance. Our observations are also consistent with the “optimal stability window” hypothesis (Gargett, 1997), which argues that increased water column stability along the eastern boundary of the North Pacific would reduce (enhance) biological production at southern (northern) latitudes, where productivity is nutrient (light) limited. Variability in thermal structure of the upper water column appears to have been the dominant mechanism responsible for the stability increase in the CCS, while salinity changes were more important at northern latitudes (Freeland et al., 1997; Overland et al., 1999; Whitney and Freeland, 1999).

Our results also show a variable biological response on the inshore (80.55–80.70) and offshore (80.80–80.100) stations (Table 1), suggesting that different physical mechanisms may be dominant in

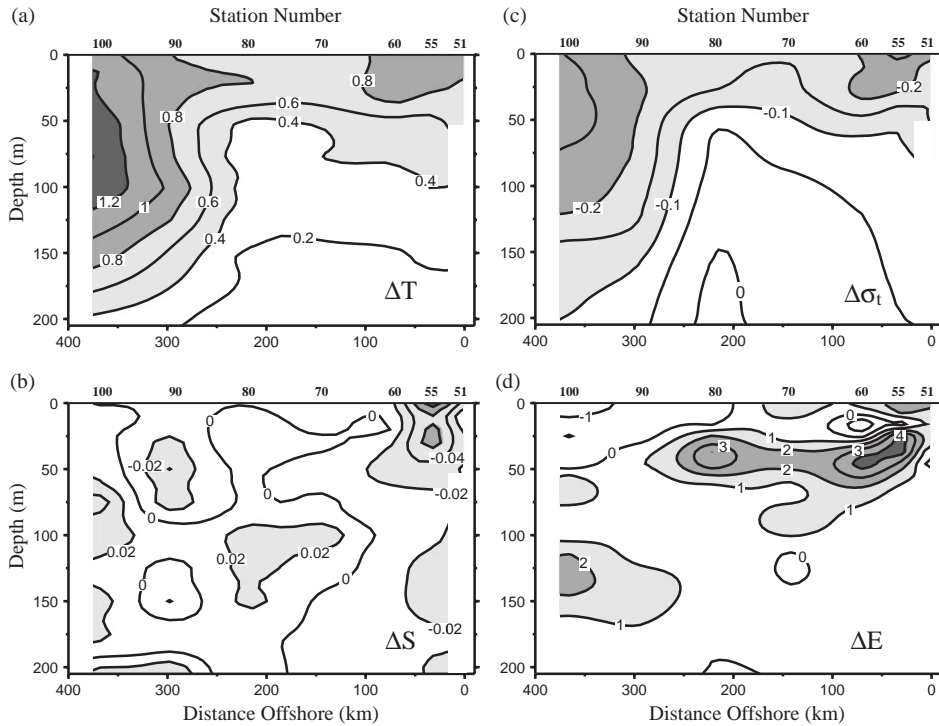


Fig. 6. Line 80 sections in the upper 200m showing the mean regime differences (1976–2000 mean minus 1950–75 mean) for (a) temperature (ΔT ; $^{\circ}\text{C}$), (b) salinity (ΔS ; psu), (c) density ($\Delta\sigma_t$; kg m^{-3}), and (d) stability (ΔE ; $10^{-3} \text{ kg m}^{-3} \text{ m}^{-1}$), which is defined here as the vertical gradient of density based on 10-m spline-interpolated density profiles.

these regions. This difference is consistent with the dynamics of the oceanic seasonal cycle in this region, in which a coastal upwelling jet dominates inshore flows while thermocline fluctuations forced by wind stress curl dominate deep-ocean flows (Di Lorenzo, 2003). The thermocline depression and stability increase inshore are coincident with decreases in all size classes of zooplankton sampled. The offshore end, which experienced a comparable deepening of the thermocline but a broader warming with a smaller impact on water column stability, has had either a smaller decline or an increase (station 80.100) in larger zooplankton (Table 1). The biological changes offshore may be a response to changing source waters of the California Current, or to a community reorganization following the warming and thermocline depression. It does appear, however, that the combined effects of a deeper thermocline (nutri-cline) and increased stability in the CCS have led to a reduced supply of nutrients to the euphotic

zone following the 1976–77 regime shift in both the nearshore and offshore environments.

Recent studies (Schwing and Moore, 2000) have suggested that the North Pacific may have entered into a new climate regime, during which cooler waters and heightened biological production might be expected along the West Coast. This was indeed the case in the CCS following the decay of the 1997–98 El Niño, when near-surface temperatures were anomalously cool, the nutricline shoaled, and in situ measurements of vertically integrated chlorophyll and zooplankton biomass were at their highest levels in more than 15 years during early 1999 (Bograd et al., 2000; Bograd and Lynn, 2001). Although much of that signal appeared to be associated with short-term anomalies in wind-driven coastal upwelling within the CCS (Schwing et al., 2000), Minobe (1999) has suggested that a new regime shift, triggered by resonance of North Pacific atmospheric variability at different time scales, is imminent, if it has not already occurred.

It is too early to tell whether the coupled physical-biological changes in the CCS represent transient signals associated with a North Pacific climate regime shift, an extratropical response to decadal variability in the tropics, or a continuing trend associated with global warming, or some combination of these and other effects.

4. Discussion

It has become quite clear from the results of both terrestrial and marine studies that low frequency interannual and interdecadal perturbations, such as we show here, are of greater amplitude and broader spatial scale than those of higher frequencies. These low-frequency disturbances are ecologically significant with long-term, widespread effects on ecosystem structure and function. Haury et al. (1978) proposed, in a time/space conceptual diagram, that lower-frequency variations of abundance of plankton tend to have greater amplitude departures from baseline than do higher frequencies. They also suggested that the biomass anomalies on different scales have different forcings. Thus extrapolating “cause” from one scale to another was not justified. The results presented here involve the interdecadal scale of temporal variability and 50–1000 km on the Haury diagram. Earlier time-series analysis of this system focused on the non-seasonal interannual scale of variability (Chelton et al., 1982). They found that a strong positive correlation between interannual variations in the transport of cool, high nutrient water from the north and variations in plankton abundance over most of the CCS. Cause and effect were clearly implied. But here we show that no such correlation exists at the interdecadal time scale. At this longer time scale it seems there is an in situ process dominating nutrient flux into the system, rather than a large-scale horizontal advective one. There is a diminution of the vertical flux of cool, high-nutrient, high-salinity water into the euphotic zone from below, due to very large spatial scale warming and enhanced stratification.

In spite of its inherent variability we can see that a large, persistent and pervasive change has taken place in the California Current ecosystem follow-

ing the 1977 regime shift. This change lasted for at least 20 years and involved all parts of the trophic levels we have measured regularly and well. The consequences of such a great perturbation may be felt far into the future. It may be possible, now that we have much more knowledge of our complex system in terms of climate–ocean–biology interactions, to begin the difficult task of distinguishing between human-caused (e.g., over-harvesting) and climate-caused variability or change in populations. This ability will be required if we are to model future marine population trends for the purpose of conservation or management.

Our results demonstrate, however, that significant changes in near-surface heat and freshwater balances can greatly alter marine community ecosystem structure and productivity, sounding the alarm to the potential impacts of a global warming trend. Continued monitoring is essential to distinguish the relevant mechanisms of climate change and marine ecosystem response.

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