Long-term change and stability in the California Current System: lessons from CalCOFI and other long-term data sets

Ginger A. Rebstock*

Department of Biology, University of Washington, Box 351800, Seattle, WA 98195-1800, USA

Received 8 March 2002; received in revised form 15 August 2002; accepted 1 November 2002

Abstract

The California Current System (CCS) is a highly variable system, both spatially and temporally, that is strongly affected by low-frequency climatic fluctuations. This paper reviews evidence for long-term (decadal-scale) change in the physics and biology of the CCS over the last 50–100 years, as well as evidence for stability in planktonic community structure and long-term persistence of populations. Increases in water temperature, thermocline depth and stratification in the CCS have been accompanied by changes in populations of kelp, diatoms, foraminifera, radiolarians, intertidal invertebrates, zooplankton, fish and seabirds. However, there is also evidence for stability in assemblages of larval fish, calanoid copepods and radiolarians. Statistical averaging (the portfolio effect) may explain some aspects of stability in assemblages. Advection of planktonic populations may account for rapid recovery of biomass and dominance structure following perturbations such as strong El Ni˜ no events. Planktonic populations in the CCS may be adapted to large-scale biotic and abiotic variability, through a combination of advection of populations and life history traits.

Several lessons may be learned from the California Cooperative Oceanic Fisheries Investigations and other long-term data sets: (1) long time series are needed to understand the dynamics of the ecosystem; (2) life histories are important determinants of species responses to environmental forcing, even in the plankton; and (3) the CCS is simultaneously variable and stable, and these properties are not necessarily in conflict.

© 2003 Elsevier Ltd. All rights reserved.

1. Introduction

The California Current System (CCS) forms the eastern boundary of the North Pacific subtropical gyre. As in other eastern boundary current systems, the euphotic zone is enriched by wind-driven upwelling as well as isopycnal shoaling due to geostrophic adjustment (Chelton et al., 1982). This enrichment of surface waters makes the CCS a highly productive system, supporting diverse marine life and major fisheries.

The CCS is highly variable both spatial and temporally. Mesoscale features such as fronts, eddies and jets produce steep gradients in physical and biological properties. Time scales of variability include events lasting days to weeks, such as passage of storms or wind-driven upwelling, as well as seasonal, interannual, interdecadal and longer periods.

The CCS is one of the best-studied oceanic areas in the world. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program...
began monitoring physical and biological properties of the CCS in 1949, in response to the collapse of the sardine fishery in California (Hewitt, 1988). The program continues and has expanded the number of properties measured over the years. Marine research institutions along the west coast of North America have also advanced our knowledge of the CCS.

Several climatic phenomena influence the CCS on interannual scales. The El Niño–Southern Oscillation (ENSO) has profound, if generally short-lived effects on the CCS (McGowan and Walker, 1993; but see Rebstock, 2002). During the El Niño or warm phase of the ENSO, equatorward transport is diminished, poleward transport in the counter-current increases, the thermocline deepens, primary production is reduced, the timing of the spring bloom may be altered, zooplankton biomass declines, and range boundaries of both planktonic and nektonic species shift (Lenarz et al., 1995; Mullin, 1998; Murphree and Reynolds, 1995; Roesler and Chelton, 1987; Smith, 1985). The La Niña or cold phase of the ENSO generally has opposite effects on the CCS, although La Niña has not been as well studied as El Niño (Murphree and Reynolds, 1995).

The ENSO is primarily a tropical phenomenon, and not all tropical El Niño events affect the CCS. Conversely, not all warm or cold events in the CCS are associated with a tropical ENSO event (Simpson, 1984). The strength and position of the Aleutian Low atmospheric pressure system also affects the CCS by altering the frequency, intensity and tracks of cyclonic storms in the North Pacific. Effects of a strong Aleutian Low are similar to those of a tropical El Niño (Norton and McLain, 1994).

In addition, local heating can affect water temperature and thermocline depth (McLain et al., 1985). Climatic phenomena that influence the CCS, including ENSO, the Aleutian Low and local heating, are not independent of each other, and their effects can be difficult to differentiate.

Decadal-scale climatic variability also strongly influences the CCS. Periods of a decade or longer during which climatic and oceanographic variables fluctuate around some mean value have been termed climatic regimes, while more or less abrupt changes from one mean value to another are known as regime shifts (Isaacs, 1976; MacCall, 1996). A well-documented regime shift occurred in the North Pacific in the winter of 1976–77 (Ebbesmeyer et al., 1991; Graham, 1994). Other North Pacific regime shifts have been hypothesized around 1910 (Lluch-Belda et al., 2001), 1925, 1947 and 1989 (Beamish et al., 1999; Overland et al., 1999). Lluch-Belda et al. (2001) suggested that climatic regimes are not as prevalent or important to the ecosystem as warming or cooling periods, which may last decades.

Coherent, decadal-scale fluctuations have been identified in the dominant patterns (leading principal components) of winter (November—March) North Pacific sea-surface temperature and sea-level pressure. The variations in SST are known as the Pacific Decadal Oscillation or PDO (Mantua et al., 1997). Since the 1920s, the state of the PDO has reversed every two to three decades. A positive PDO is associated with an intense Aleutian Low, cool waters in the central North Pacific and warm waters in the CCS.

Interannual and decadal-scale variability are illustrated in Fig. 1, a time series of water temperature measured at the Scripps pier in La Jolla, California, USA. Interannual variations are obvious, including strong El Niño signals in the

![Fig. 1. Surface temperature at Scripps Institution of Oceanography pier, La Jolla, California, USA, 1916–96. Anomalies (°C) from the long-term mean for each month. Data provided by the Shore Station Program, Marine Life Research Group, SIO.](image-url)
late 1950s and the early 1980s. However, the later El Niño events do not stand out as clearly as the 1958–59 event, because they occurred during a warm-water regime (positive PDO), while the 1958–59 event occurred during a period of relatively cold water (negative PDO). Three decadal-scale regimes are apparent in the time series (see MacCall, 1996). Prior to the mid-1940s, the temperature was highly variable, but centered near the long-term mean. The period from the late 1940s through the early 1970s was characterized by cool water, interrupted by the 1958–59 El Niño. The 1976–77 regime shift is evidenced by a sudden increase in water temperature, beginning a warm regime.

In spite of physical and biological variability on many time scales, populations and some assemblages persist in the CCS for long periods, suggesting some kind of continuity or stability. A stable population, assemblage or system is one that remains at or returns to equilibrium when a disturbing force is applied. This equilibrium does not necessarily imply a constant value, but often involves fluctuations within limits. A persistent population is one that does not go extinct during some period (Connell and Sousa, 1983). Disturbance is often equated with aperiodic or episodic environmental variability (Floder and Sommer, 1999; McGowan, 1990). A perturbation is defined as a response of a population or community to a disturbance (Connell and Sousa, 1983). As seen in Fig. 1, large potential disturbances are frequent in the CCS and sometimes last for several years. Stability can be achieved either by resistance to potentially disturbing forces or by recovery following responses to disturbances (adjustment stability). Stochastic boundedness is another concept that may be applicable to the CCS. Population levels fluctuate within bounds; they neither go extinct nor return to the same values (Connell and Sousa, 1983).

In this paper, I review evidence for long-term change in the CCS, in both physical properties and biological populations, over the last 50–100 years. These changes may be manifestations of decadal or longer-scale fluctuations or of anthropogenic global change. Some population fluctuations caused by direct human persecution of species, such as pinnipeds and sea otters (MacCall, 1986), are not discussed. In spite of large fluctuations in the environment and in many populations, there is evidence for stability at the community or assemblage level in some cases. I also discuss this evidence and attempt to reconcile this observed stability and variability.

2. Long-term change in the California Current System

Decadal-scale oscillations or trends in climate are well known in the North Pacific (Latif and Barnett, 1994; Mantua et al., 1997; McGowan et al., 1998; Ware and Thomson, 2000). Climatic regime shifts occurred in the winter of 1976–77 (Ebbesmeyer et al., 1991), 1989 (Hare and Mantua, 2000) and around 1925 and 1947 (Beamish et al., 1999; Overland et al., 1999). ENSO events, which strongly influence the CCS (McGowan, 1985; Murphree and Reynolds, 1995) have increased in frequency since the mid-1970s (Trenberth and Hoar, 1997). Seasonal upwelling-favorable winds along the California coast have intensified (Bakun, 1990; Schwing and Mendelssohn, 1997). The frequency and intensity of winter cyclones, as well as extreme surface winds and wave heights have increased in the North Pacific over the last 50 years (Graham and Diaz, 2001).

Hydrographic conditions in the CCS have changed, apparently in response to climatic regime shifts. Upper ocean temperature increased off southern California between the 1950s and the 1990s (Roemmich, 1992; Roemmich and McGowan, 1995a). This surface-intensified warming has been accompanied by an increase in thermocline depth and water-column stratification (McGowan et al., 2003; Miller, 1996). Weinheimer et al. (1999) presented evidence from microfossils of increasing thermocline depth and stratification in the 1940s and in 1960. Increased stratification and thermocline depth tend to counteract the enriching effect of the increase in upwelling that might be expected due to changes in wind intensity. Pennington and Chavez (2000) also found higher temperatures and stronger stratification in the upper 100 m in fall
and winter in Monterey Bay, in addition to a delay in the onset of upwelling in spring.

Biological populations spanning several trophic levels and representing many different taxa have also undergone long-term change in the CCS. Evidence exists for change in populations of kelp, diatoms, foraminifera, radiolarians, intertidal invertebrates, zooplankton, fish and seabirds.

Much has been published on the Pacific sardine (*Sardinops sagax*) since the catastrophic fishery collapse of the 1940s that spawned the CalCOFI program. Sediment cores from an anoxic basin off southern California contain evidence that the Pacific sardine as well as the northern anchovy (*Engraulis mordax*) has undergone interdecadal fluctuations in abundance for at least the last 1700 years (Baumgartner et al., 1992; Soutar and Isaacs, 1969). Sardine and anchovy stocks in the CCS and other parts of the world have undergone similar fluctuations in historical times (e.g., Lluch-Belda et al., 1992).

In addition to sardine and anchovy, many other fish stocks show decadal-scale population fluctuations in the CCS. Other pelagic fishes such as hake (*Merluccius productus*), mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*) as well as large predatory fishes such as tuna (*Thunnus* spp.) and marlin (*Tetrapturus audax*) have undergone long-term change in abundance or seasonal timing of migration (MacCall, 1996). Salmon (*Onchorhynchus* spp.) catches in the northeastern Pacific appear to fluctuate with the PDO. Positive states of the PDO are associated with low catches of salmon in the CCS, but high catches in Alaska (Mantua et al., 1997). Declines in abundance of nearshore reef fishes in the Southern California Bight have been accompanied by shifts in dominance from northern to southern species (Holbrook et al., 1997). Off southern California, the distribution of larvae of a number of species shifted between 1951–76 and 1977–98. In particular, several species of myctophids, midwater fish that are not commercially exploited, expanded their larval distributions to the north and/or inshore after the mid-1970s (Moser et al., 2001).

The fluxes of planktonic diatoms (Lange et al., 1990), foraminifera (Lange et al., 1990; Weinheimer et al., 1999), and radiolarians (Weinheimer and Cayan, 1997) to the sediments of the Santa Barbara Basin, off southern California, have varied over the last 50–100 years. The diatom flux declined sharply in the early 1970s, while the foraminiferan flux has declined more gradually since the 1950s, accompanied by a shift in species composition around 1970 (Lange et al., 1990). The percentage of deep-dwelling radiolarians decreased over the last century, with a sharp decline in the early 1940s (Weinheimer et al., 1999). Total radiolarian flux was high in the late 1800s, low in the early 1900s and high since the 1950s. Fluctuations were coherent among several biogeographic groups, suggesting changes in the carrying capacity of the system. Although radiolarian assemblages appear to be generally stable, decreases in rank correlation among years and increases in diversity occurred around 1955 and 1976–77 (Weinheimer and Cayan, 1997).

Barry et al. (1995) presented evidence for a shift in community composition in a rocky intertidal area in Monterey Bay between the early 1930s and the early 1990s. Invertebrate species with a southern biogeographic affinity tended to increase, while northern species tended to decrease. Cosmopolitan species did not show a clear pattern, with some species increasing and others decreasing. Water temperature at the site, particularly the average summer maximum, increased over the same period.

Veit et al. (1996) reported a decline in overall seabird numbers over 8 years off southern California, although some species increased in abundance. The decline was led by a 90% decrease in numbers of sooty shearwaters (*Puffinus griseus*), the numerically dominant species in the CCS. Sydeman et al. (2001) reported species-specific changes in reproductive performance, a more sensitive indicator of environmental change than population size, of seabirds breeding on islands off California between 1969 and 1997. They also found changes in diet composition of several species, especial a decline of juvenile rockfish (*Sebastes* spp.) around 1989.

Kelp (*Macrocystis pyrifera*) forests off San Diego have undergone large interannual to interdecadal change in canopy extent and plant size, although it is more difficult to separate effects of
climate change from those of direct human disturbance such as pollution and dredging in this nearshore environment (Tegner et al., 1996). Median and maximum plant size, but not plant density declined between the 1950s and the 1990s. Macrozooplankton biomass undergoes large changes on interannual to interdecadal scales (e.g., Bernal, 1981; Chelton et al., 1982). These low frequencies (periods greater than 1 year) account for a large portion of the variability in zooplankton biomass in the CCS (Bernal, 1981). Off southern California, zooplankton displacement volume, an index of biomass, has declined by 70% since the 1950s (Roemmich and McGowan, 1995a, b).

Off Baja California, the zooplankton volume has also undergone large interannual and interdecadal fluctuations (Lavaniegos et al., 1998). Although the large, long-term decline seen off southern California was not obvious, perhaps because of the paucity of samples since about 1970, zooplankton volumes in the 1990s were the lowest on record. Upwelling-favorable winds increased in the region, but without an increase in zooplankton standing stocks.

Species-level analyses using CalCOFI samples have been completed for some groups of zooplankton and are underway for others. Hyperiid amphipods and presumably their gelatinous hosts have declined in abundance and species richness off southern California since the mid-1970s (Lavaniegos and Ohman, 1999).

I found evidence for species-specific responses to climatic conditions in calanoid copepods off southern California (Rebstock, 2002). Between 1951 and 1999, 19 out of 24 species analyzed showed abrupt step changes or more gradual monotonic trends in density. Most of the step changes occurred around 1977 and 1990, coincident with climatic regime shifts. Rare warm-water species as a group increased in frequency of occurrence in samples after 1977. Other step changes occurred in the late 1950s and the early 1980s, probably triggered by major El Niño events. The changes are not easily explained by simple advection of copepod assemblages. For example, the seven species that abruptly increased in density in the mid-1970s (no species declined at this time) include warm-water species as well as cool-water Transition Zone species (Rebstock, 2002). Differences in life history traits in the two dominant species of calanoid copepods off southern California may explain their different responses to climatic forcing.

Several perturbations occurred in the species composition of the calanoid copepods between 1951 and 1999, in which dominance structure was temporarily altered. Most of these perturbations were associated with warm-water events in the CCS. Five of the six perturbations have occurred since the mid-1970s (Rebstock, 2001), perhaps a response to an increased frequency in El Niño events.

3. Stability in the California Current System

Little has been published on biological stability in the CCS and other eastern boundary currents, either because few populations or communities appear stable, or because few researchers have looked for stability. Although individual species undergo large fluctuations in abundance in the CCS, there is evidence for stability at the assemblage or community level. Recurrent groups of larval fish were found to persist over decades (Moser and Smith, 1993). In spite of large fluctuations in abundance, patterns of association of species with environmental conditions have remained constant.

The dominance structure of calanoid copepods in spring off southern California has also remained stable over the last 50 years (Rebstock, 2001). The rare species have remained rare and the dominant species have remained dominant. Perturbations to this dominance structure occurred in 6 years between 1951 and 1999, but in each case, the usual structure recovered within 1 or 2 years.

In spite of step changes and monotonic trends in density of many species of calanoid copepods, the density of the total calanoid assemblage showed no long-term trends between 1951 and 1999 (Rebstock, 2002). For total calanoid copepods, interannual fluctuations seem to be more important than decadal-scale fluctuations.
Weinheimer and Cayan (1997) noted that the radiolarian community structure in the Southern California Bight has remained stable over the last 100 years. Although decreases in rank correlation between years were seen in two periods, most rank correlations were significant. Weinheimer and Cayan concluded that no changes in source water of the radiolarian assemblage had occurred during the period of record.

Many populations in the CCS, in spite of undergoing large fluctuations in abundance on interannual and interdecadal scales, show long-term persistence. These populations respond to changes in their physical and biotic environment with large departures from their mean abundances, but do not go extinct. Small pelagic fish generally show this persistence, in spite of the additional disturbance of overfishing (Beverton, 1990). Biomass of the Pacific sardine off California, for example, was reduced between 2 and 3 orders of magnitude and remained at virtually undetectable levels for over 20 years (Beverton, 1990), but the stock is now considered fully recovered (California Department of Fish and Game, 1999). These populations may best be described as stochastically bounded (Connell and Sousa, 1983).

Much of the discussion of any kind of stability in eastern boundary currents comes from the literature on small pelagic fishes. Walsh (1978) suggested that pelagic populations or communities shift location in response to climatic change and our perception of variability is at least partly due to our Eulerian rather than Lagrangian perspective. However, he noted that some populations, such as guano birds in Peru, suffer declines during El Niños because they are unable to migrate with their prey. Mathisen (1989) hypothesized that variations in timing of spawning of small pelagic fish help buffer the populations against environmental perturbations.

Bakun (2001) noted that physical variability in the oceans is red-shifted, that is, variability is higher at lower frequencies. Marine populations must be able to track these low-frequency variations or go extinct. He argued that serial spawning in different environments by small pelagic fish results in different generations being adapted to different conditions. Some of these generations are likely to be adapted to new conditions in the event of long-term environmental change. Populations need to track long-term changes but not interannual variability such as ENSO events. Adapting to short-term events would leave the population poorly adapted to more average conditions. This implies that interannual fluctuations in populations may be part of an evolutionary strategy to cope with large long-term environmental change. Bakun suggested that the presence of several reproductive age classes in a population and the greater fecundity of older classes act as a low-pass filter for environmental variability. Cury et al. (2000) also contended that multiple reproductive age classes buffer populations of higher trophic level predators from high-frequency variability. A weak cohort has little effect on the population if many other age classes are also breeding.

4. Reconciling stability and change

It has long been known that communities may be more stable than the individual species making up those communities. On theoretical grounds, May (1974) noted “These models illustrate very clearly how instability in the populations of individual species may be found alongside stability in the total population of the overall community”. Statistical averaging (the portfolio effect) may account for the higher stability of assemblages compared to individual species, if the species are not concordant in their fluctuations (Lehman and Tilman, 2000). This portfolio effect may explain the lack of a long-term trend in total calanoid copepods, but it cannot explain the stability of species composition seen in copepods and radiolarians. In addition, the macrozooplankton assemblage off southern California has undergone a long-term decrease in abundance, in spite of the lack of decline in the calanoid copepods, a major component of the zooplankton. MacCall (1986) suggested that the ecosystem of the CCS may be adapted to large fluctuations in abundance of component species such as the anchovy. These variations may have little effect on other components of the system. Anchovy and
sardine have undergone large population changes in the CCS for at least 1700 years (Baumgartner et al., 1992; Soutar and Isaacs, 1969). These fluctuations have continued in recent times, with only very weak correlations with calanoid copepod populations off southern California (Fig. 2). However, higher trophic level components of the system, such as fishes, marine mammals and seabirds, have been impacted by fisheries and direct persecution by humans in historical times. We lack the data on most component species or assemblages to determine if populations fluctuated coherently before large-scale human disturbances.

In contrast to MacCall’s (1986) hypothesis, Cury et al. (2000) presented evidence that small pelagic fish are capable of exerting both top-down control of their prey and bottom-up control of their predators. However, they did not find a significant relationship between pelagic fish catch and zooplankton biomass in the CCS, even with an overall decline in zooplankton biomass and a generally increasing trend in catches of pelagic fish. MacCall’s (1986) hypothesis of ecosystem adaptations to large fluctuations in biomass of component species implies some compensating mechanisms that he did not comment on. McGowan and Walker (1993) suggested one possible mechanism. They noted the recovery of zooplankton biomass in the CCS following perturbations such as strong El Niño events, and suggested that advection of populations into the CCS is more important than biological processes within it in maintaining zooplankton communities. Weinheimer and Cayan (1997) also noted the importance of source water in maintaining planktonic assemblages. They concluded that no major changes in source water for radiolarians have occurred off southern California during the last 100 years. The correlation between zooplankton biomass and volume transport in the CCS (Chelton et al., 1982) supports the idea that advection is an important process in structuring planktonic communities, although it is not clear how much direct advection of planktonic biomass occurs. The correlation also could be the result of increased local productivity associated with higher volume transport (e.g., Roesler and Chelton, 1987). The occurrence of subarctic and equatorial species of copepods off California (Fleminger, 1964, 1967; Rebstock, 2002) and the shifting of range boundaries north and south with changes in transport in the CCS (Brinton and Reid, 1986; Roesler and

![Fig. 2. Rank correlations (Spearman’s ρ) between copepod population densities in spring and anchovy larvae densities in spring, summer, autumn and winter. Time lags range from spring of the previous year (anchovy leads copepods) to spring of the following year (copepods lead anchovy). Densities are number per 10 m² for anchovy, and number per m² for copepods. All densities are averaged over CalCOFI lines 80–93.3, offshore to station 70 on each line. Winter is defined as December–February, spring as March–May, Summer as June–August, and Autumn as September–November. Only samples collected at night were used. Dashed lines indicate approximate critical values for ρ; based on the Fisher z transformation (Zar, 1984). The critical values are low, due to uncorrected autocorrelation in the time series. (a) Rank correlations between C. pacificus females and northern anchovy larvae. (b) Rank correlations between M. pacifica females and northern anchovy larvae. (c) Rank correlations between total female calanoid copepods and northern anchovy larvae.](image-url)
Chelton, 1987) provide some evidence that long-distance advection occurs.

In situ biological processes also may play a role in regulating planktonic populations in the CCS. *Calanus pacificus* and several other calanoid species may take a decade to recover high population levels following strong El Niño events, while species such as *Metridia pacifica* may recover within a year (Rebstock, 2002). *C. pacificus*, one of the dominant copepod species off southern California (Rebstock, 2001), overwinters in deep basins in the region (Alldredge et al., 1984), and the overwintering stock may reseed the regional population each spring (Osgood and Checkley, 1997). The overwintering strategy of some species, including *C. pacificus*, may buffer populations against moderate El Niño conditions, which generally affect the CCS most strongly in fall and winter (Lynn et al., 1995). Note that part of the *C. pacificus* population off southern California remains active during winter (Mullin and Brooks, 1967; Ohman et al., 1998), possibly poised to take advantage of a shift to more favorable winter conditions.

Several mechanisms for buffering populations of higher trophic level species against high-frequency variability in eastern boundary currents have been proposed. They include spawning at different times (Mathisen, 1989) and locations (Bakun, 2001), presence of more than one reproductive year class (Bakun, 2001; Cury et al., 2000), ability to migrate with prey populations or shifting hydrographic conditions (Cury et al., 2000; Walsh, 1978), prey switching (Cury et al., 2000), and genetic variation within species (Cury et al., 2000). Some of these mechanisms may be valid for zooplankton as well. Zooplankton biomass in the southern parts of the CCS does not have a strong seasonal cycle (Roesler and Chelton, 1987). The breeding season is extended or year-round in many calanoid copepods off southern California (e.g., Mullin and Brooks, 1967). As long as adverse conditions do not last more than 1 year, part of the population should be reproducing during more favorable conditions. Planktonic populations are advected with their water masses to some degree, thereby remaining with favorable hydrographic conditions. Many calanoid copepods are fairly generalist grazers, feeding on particles within a size range regardless of composition (Mullin, 1966). They presumably switch prey readily. Little is known about genetic diversity or life history traits of most planktonic species but differences in overwintering strategies among calanoid copepod species (Ohman et al., 1998) suggest that species-specific life history traits are varied and may represent different strategies for coping with environmental variability in the CCS.

The hypothesis that advection of populations maintains planktonic community composition and biomass in the CCS assumes some stability in the source region. The CCS is dominated by equatorward flow and, at least in terms of the calanoid copepods, by Transition Zone species (Fleminger, 1964). Although the CCS may be considered an ecotone rather than an ecosystem, it has a characteristic planktonic fauna (McGowan, 1974), which even large low-frequency environmental changes have not substantially altered over the last 100 years.

5. Summary and lessons

In summary, the CCS has undergone long-term change in hydrographic properties over the last century, apparently in response to low-frequency fluctuations in climate. There is also ample evidence for long-term change in populations in the CCS, including kelp, diatoms, foraminifera, radiolarians, intertidal invertebrates, zooplankton, fish and seabirds. At the same time, there is evidence for stability in assemblages of larval fish, calanoid copepods and radiolarians. Few attempts have been made to reconcile these apparently conflicting observations, but the answer probably lies in a combination of statistical, physical and biological factors. Finally, even populations that undergo large fluctuations in abundance persist over long periods in the CCS. Responses of populations to climatic change are interesting and informative, but stability of assemblages and persistence of populations can also inform us on the dynamics of the California Current ecosystem.

Several lessons may be learned from the long-term data sets discussed here. First, long time
series are necessary for a full understanding of the system dynamics, especially with respect to decadal-scale climate variability. Studies lasting only a few years could give very different pictures depending on timing in relation to ENSO events and climatic regime shifts. Only over longer periods, spanning several disturbances, recoveries and regime shifts, do we begin to sense the dynamic stability of the CCS.

Second, life histories and biological interactions are important, even in the plankton. In spite of the presumed importance of physical advection, fluctuations in density of calanoid copepods are not always concordant among species with similar biogeographic affinities (Rebstock, 2002). The two dominant species of calanoid copepods off southern California, C. pacificus and M. pacifica, are both Transition Zone species, yet their population fluctuations are apparently driven by different environmental stimuli. Differences in their life history traits may explain these different responses.

Finally, the CCS is simultaneously a highly variable and stable system. Populations in the CCS undergo large fluctuations in abundance, species composition, and range boundaries on interannual to interdecadal scales, in response to climatic variations. However, they are apparently adapted to low-frequency variability in both biotic and abiotic conditions. In addition to stability in total abundance of assemblages of some planktonic organisms resulting from statistical averaging, some compensating mechanisms, possibly including advection of populations and life history traits, provide stability in species composition. Even species that undergo large fluctuations in abundance persist in the CCS. Variability and stability are both properties of the CCS and are not necessarily in conflict.

Acknowledgements

First and foremost, I acknowledge the CalCOFI program. The program has been kept going by many dedicated people for over 50 years and their hard work has yielded much of our knowledge of the long-term dynamics of the CCS. I also thank the Pelagic Invertebrates Collection at Scripps Institution of Oceanography (SIO) for granting access to the plankton samples, and Annie Townsend for her cheerful assistance in obtaining the samples. Melissa Carter and Kirk Ireson provided invaluable assistance with sample preparation. The SIO pier temperature data were provided by the Shore Station Program at SIO. The anchovy data were provided by Paul Smith, National Marine Fisheries Service, La Jolla. Comments by two anonymous reviewers greatly improved the manuscript. My work on the CalCOFI samples was supported by graduate fellowships from the US Office of Naval Research and Environmental Protection Agency (STAR Graduate Fellowship), as well as a grant from the US GLOBEC program, jointly funded by the National Science Foundation and the National Oceanic and Atmospheric Administration. This is GLOBEC contribution #395. This research was supported in part under NSF grant OCE-9711369. This paper was also supported in part by the National Sea Grant College Program of the US Department of Commerce’s National Oceanic and Atmospheric Administration under NOAA Grant #NA06RG0142, project number R/F-72PD, through the California Sea Grant College Program. The views expressed herein do not necessarily reflect the views of any of those organizations.

References


