

PATTERNS OF LOW-FREQUENCY VARIABILITY IN FISH POPULATIONS OF THE CALIFORNIA CURRENT

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ABSTRACT

Long-term data sets include sedimentary fish-scale paleochronologies, faunal surveys from the 1800s, and the records of game fish catches maintained by the Tuna Club at Avalon since 1898. These data suggest a mode of low-frequency biological variability over a cycle of 50 to 70 years that is associated with alternation of warm and cold physical regimes. The very warm conditions in the northeastern Pacific Ocean since 1976 seem similar to conditions experienced from about 1850 to 1870. Coastal pelagic fish abundances since 1930 indicate an orderly sequence of four or five dominant species through these cycles that is very similar to the order and timing of fluctuations in catches of similar pelagic fishes in Japanese waters. The consistency and predictability of this rotation and the biological relationship to low-frequency fluctuations in physical conditions are important areas for further research. These patterns of low-frequency variability result in boom-and-bust fisheries, and pose serious problems for "sustainable development."

INTRODUCTION

With recognition of the worldwide decline in fish stocks, the guideline of "sustainable development" is receiving international support as an explicit goal of fishery and ecosystem management. Ironically, this comes at a time when the biological basis of sustainability in some of the world's major fisheries is itself being questioned because of natural patterns of variability (e.g., Lluch-Belda et al. 1989; Beamish 1995). In a broader context, the science of ecology is moving away from static and equilibrium views of ecosystems. Rather, scientists are coming to perceive ecosystems as pulsing and fluctuating entities, driven by external sources of variability and by internal nonlinear dynamics. Odum et al. (1995) state the possibility that "what is sustainable in ecosystems, is a repeating oscillation that is often poised on the edge of chaos."

At the 1973 CalCOFI Symposium, John Isaacs (1976) took issue with the common implicit assumption in fisheries science that there is "some steady state . . . around which there is a normal distribution of perturbations." He continued,

This certainly does not seem to be the case. The assumption is that there are some normal statistics to all

kinds of conditions. Rather, there are probably a great number of possible regimes and abrupt discontinuities connecting them, flip-flops from one regime to another; multifarious regimes involving biology or climate, or oceanography, or migrations, temperature, or weather, or combinations of these . . . My main point is that there are no simple statistics in the ordinary sense. There are internal, interactive episodes locked into persistence, and one is entirely fooled if one takes one of these short intervals of a decade or so and decides there is some sort of simple probability associated with it . . . organisms must respond to more than just fluctuations around some optimum condition. Actually, many of their characteristics and fluctuations of populations must be related to these very large alternations of conditions.

Isaacs coined the term *regime* to describe distinct environmental or climatic states, and *regime shift* has recently gained acceptance as a term for the abrupt transitions between regimes. It is notable that publication of Isaacs' regime concept in 1976 itself coincided with a profound regime shift in the northeastern Pacific. That shift was not apparent at the time, and it required another decade for the oceanic warming (figure 1) to be recognized as a new and persistent condition (MacCall and Prager 1988; Trenberth 1990).

In this paper I examine variability in southern California

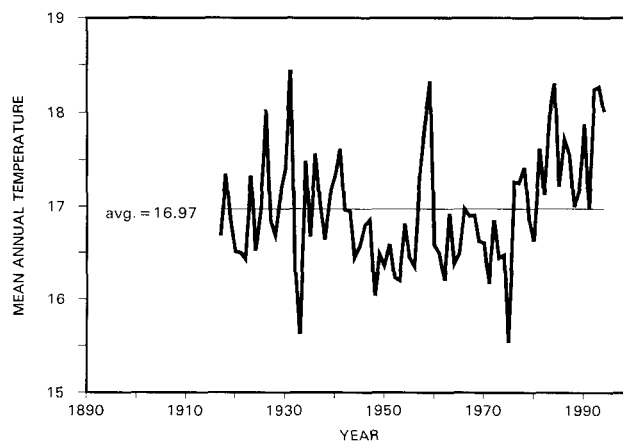


Figure 1. Mean annual temperatures (°C) at the Scripps Institution of Oceanography Pier, La Jolla, California.

fish populations over the longest time scales supported by the qualitative and quantitative information available. Even the quantitative time series are much too short for rigorous statistical analysis. My approach to these data is that of "historical science" (Gould 1989; Francis and Hare 1994); consequently, some of my interpretations are speculative.

Perhaps because fish are an important commodity, better long-term records exist for fishes than for any other biological component of the California Current System. Paleochronologies of fish debris preserved in anaerobic sediments provide invaluable information on prehistoric fluctuations and very-low-frequency variability. The earliest historical records indicative of fish abundance in the California Current are relatively qualitative and begin with the Pacific Railroad Survey of 1856. Quantitative big game fishing records have been maintained since the turn of the century by the Tuna Club at Avalon, on Santa Catalina Island. Although Tuna Club data have seen little use in scientific contexts, these records constitute the longest quantitative and unbroken series of biological observations in this region. The State of California began keeping systematic records of fish landings in 1916, and began comprehensive biological sampling of coastal pelagic fish landings in the 1930s. Good information on ichthyoplankton exists for much of the last 50 years due to the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and other fishery and oceanographic programs that were initiated following World War II.

For the purpose of this paper, I use ocean temperature as a simple proxy for the more complicated and poorly understood suite of oceanographic variables that influences biological populations. Sea-surface temperatures have been monitored continuously at the Scripps Institution of Oceanography Pier (Scripps Pier) in La Jolla, beginning in 1916 (figure 1), forming one of the longest time series of sea-surface temperatures on the Pacific coast. Earlier observations of sea-surface temperature from ships-of-opportunity are provided by the COADS data set (Mendelsohn and Roy 1996), but there are insufficient observations from southern California waters before 1920 to provide annual resolution of temperature fluctuations (R. Parrish, PFEG, NMFS, Pacific Grove, CA, pers. comm. 9/13/95). However, Parrish's examination of the post-1920 COADS data did demonstrate that low-frequency temperature fluctuations in southern California do not necessarily parallel temperature fluctuations off central or northern California. Thus, annual average Scripps Pier temperatures may provide a simplified representation of southern California ocean conditions but may not always be a reliable indicator of conditions in adjacent Pacific coastal regions such as central California.

The major warming that began about 1976 is clearly visible in the Scripps Pier temperature record. This event was widespread and occurred over the entire northeastern Pacific Ocean, from Mexico to Alaska (Cole and McLain 1989). However, the geographic extent of earlier temperature regimes and regime shifts is less clear. An earlier regime shift occurred about 1940, beginning a long period of cold temperatures. Consequently the Scripps Pier record consists of three conspicuous temperature regimes: a moderate and highly variable period from the beginning of the time series to about 1940, a cold period from 1940 to 1976, and a warm period since 1976. Ware (1995) describes similar alternations of temperature regimes off British Columbia.

It is not clear how these low-frequency temperature regimes are related to the El Niño/Southern Oscillation. However, brief warm events related to both El Niño and variability in the Aleutian Low (Wooster and Hollowed 1995) are superimposed on these underlying temperature regimes. Major warm events have occurred at a transition (1940), in the midst of a cool period (1958–59), and in the midst of a warm period (1982–83 and 1992–93).

FISH ABUNDANCES

The anaerobic sediments of the Santa Barbara Basin provide a remarkable paleochronology of fish scale-deposition rates (Soutar 1967). Soutar and Isaacs (1974) developed a 160-year time series of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) scale-deposition rates that indicated large natural long-term fluctuations in both of those species. Baumgartner et al. (1992) extended and refined these studies, and developed a paleochronology spanning the last 1,700 years at a temporal resolution of 10 years (figure 2). Power spectra of these long time series show high variability in both sardine and anchovy scale-deposition rates at a period of approximately 60 years, and at longer periods that differ for the two species. Ware's (1995) analysis of a much shorter physical and biological data set also indicated a spectral peak in the range of 50 to 75 years. Neither Baumgartner et al. (1992) nor Ware (1995) was able to identify a physical mechanism associated with this low-frequency variability.

Anecdotal Information

Biological surveys of the Pacific coast began in the mid-1800s, and provide useful indications of presence or absence of species but have poor resolution for the purpose of estimating the timing and duration of environmental regimes. However, in comparison with conditions during most of the twentieth century, some of the early survey information is so peculiar that Hubbs

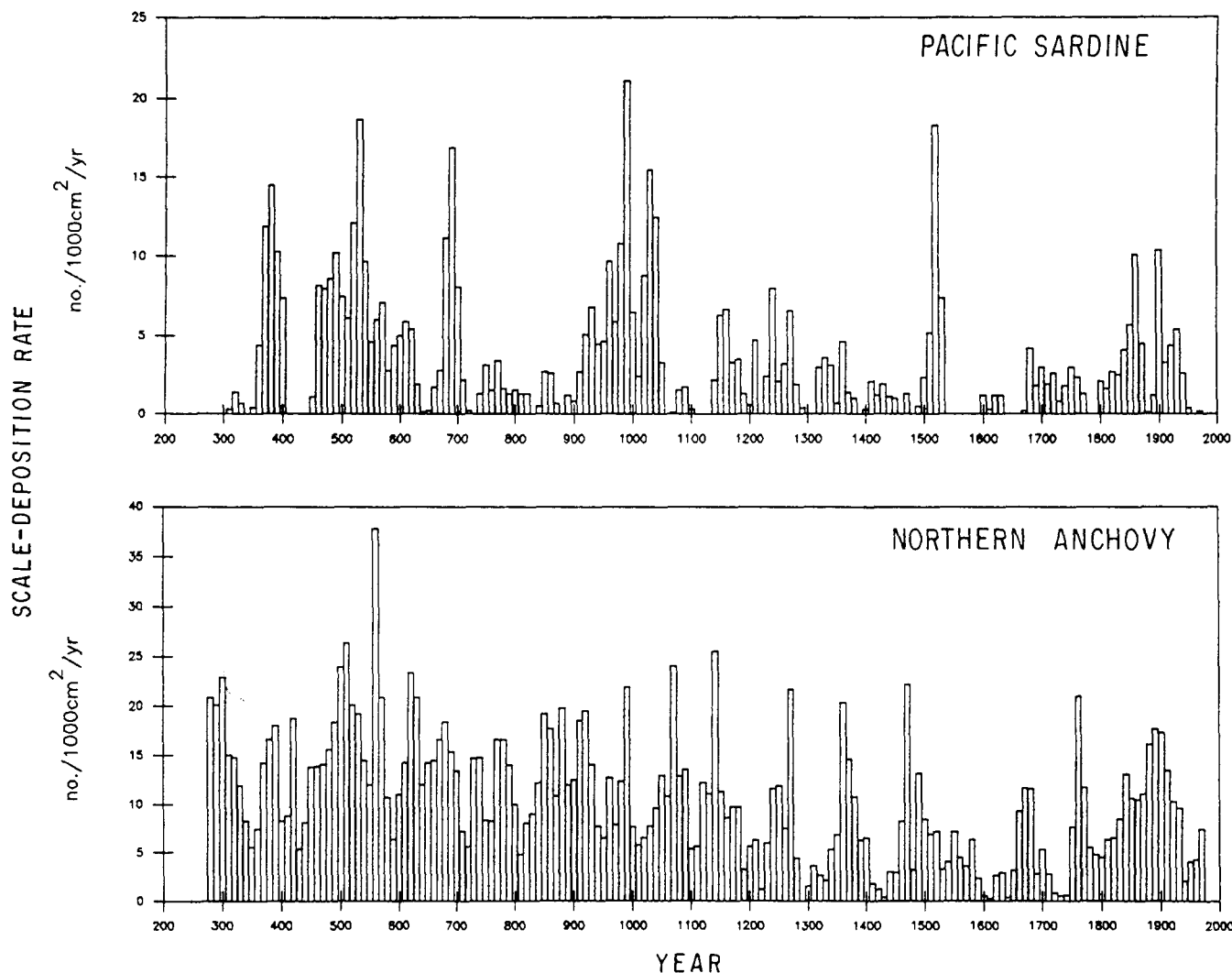


Figure 2. Sardine and anchovy scale-deposition rates in the Santa Barbara Basin (reproduced from Baumgartner et al. 1992).

(1948) was able to infer the existence of an unusually warm ocean climate during the mid 1800s.

According to Hubbs, the Pacific Railroad Survey sampled fish fauna in the San Diego area during the period 1853–57. This superficial survey encountered many “southerly” fish species that no longer occur in southern California. Hubbs reported that when Jordan and Gilbert conducted a thorough sampling of the California coast in about 1880, the fish fauna from Monterey Bay and southern California still had an unusually strong representation of subtropical species. These anomalies led Hubbs to infer that southern California experienced exceptionally warm oceanic conditions from about 1850 to 1870; the beginning and ending dates are imprecise.

In 1857, the Pacific Railroad Survey encountered five specimens of Pacific seahorse (*Hippocampus ingens*) in San Diego Bay (figure 3). This species is normally found much farther to the south and was exceedingly rare in

California until a small population reappeared in San Diego Bay about 1984 (Jones et al. 1988). The San Diego Bay population has remained viable over the past decade (R. Burhans, SIO, UCSD, La Jolla, CA, pers. comm. 2/15/96). Hubbs’ inference of warm oceanic conditions in the mid-nineteenth century is consistent with reappearance of the Pacific seahorse at San Diego during the warming since 1976.

Tuna Club Records

The Tuna Club was formed at Avalon, Catalina Island, in the summer of 1898, shortly following the discovery of the sport of angling for large ocean game fishes by its founder, Dr. C. F. Holder (Macrate 1948). The club’s records, which now span nearly 100 years, document sizes and numbers of several fish species taken in annual tournaments. From 1909 to 1919, a summer tournament was held from May 1 to September 30, and a

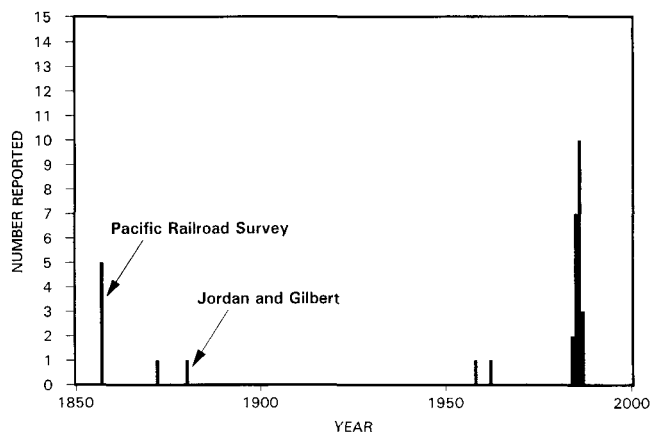


Figure 3. Number of Pacific seahorses reported by various sources (data from Jones et al. 1988).

separate winter tournament was held from October 1 to April 30. From 1920 on, annual tournaments corresponded to calendar years.

The nature of the Tuna Club data differs among groups of fish. Naturally, tunas were of greatest interest, and the club yearbooks provide information on the largest fish caught each year, catch by month, average weight of all fish reported, and date of first catch. Unfortunately the club did not distinguish among several species of large tunas, which include northern bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*). The Tuna Club considered striped marlin (*Tetrapturus audax*) and swordfish (*Xiphias gladius*) to be worthy alternatives to large tuna and kept separate records for those species. Club yearbooks also provide data on the largest fish caught in each annual tournament for a number of "lesser" species, including albacore (*Thunnus alalunga*), white seabass (*Atractoscion nobilis*), yellowtail (*Seriola lalandi*), and giant sea bass (*Stereolepis gigas*).

Tunas were landed in large numbers in many tournaments through the 1920s (figure 4), but were very rare

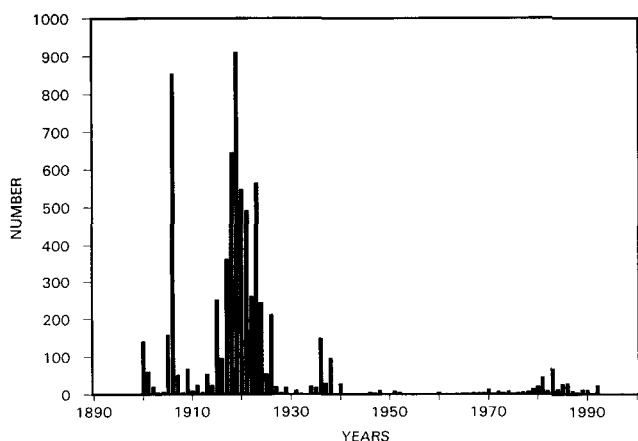


Figure 4. Number of tuna reported in Tuna Club annual tournaments.

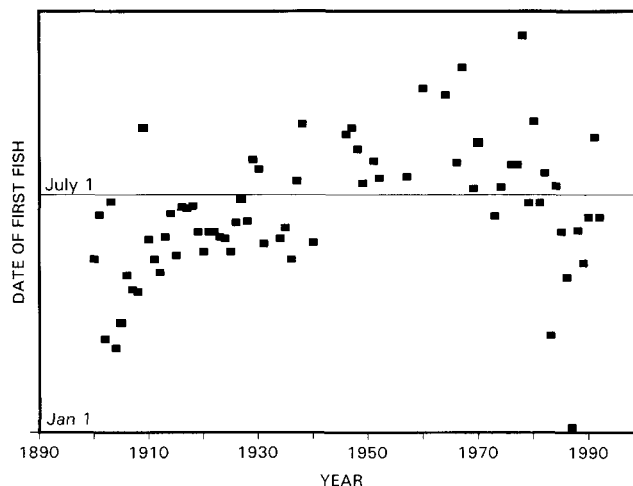


Figure 5. Dates at which first tuna were caught in Tuna Club annual tournaments.

during the extended cold regime from 1940 to 1976. Moderate numbers of tuna reappeared in the annual tournaments following the 1976 warming. The two periods of abundance reflect different species of tuna: pre-1940 catches consisted mainly of northern bluefin tuna, while post-1976 catches have been mostly yellowfin and bigeye tunas. Interpretation is also complicated by the growth of commercial fishing for tunas in southern California during the 1920s (Bayliff 1992; Wild 1992), with consequent declines in abundance and size.

The dates on which the first tuna was taken in the annual tournaments also coincide with the large shifts in Scripps Pier temperatures (figure 5). The post-1976 pattern is similar to that prior to 1940, when the earliest catches were often made in April or May. During the long cold regime, the few tuna that were caught first appeared in July or August. Remarkably, the earliest annual appearance of tuna in club records is March 4, and first appearances were in March of three of the four years 1902–5. Sea-surface temperatures are normally quite cold in March, and immigration of bluefin tuna to southern California would be unlikely at that time of year, suggesting that there may originally have been a small resident population of tuna in southern California. A recent anomaly in figure 5 is a tuna that was caught on January 3, 1987, in waters far to the south of the usual fishing grounds near Catalina Island.

Catches of striped marlin increased sharply in the 1930s, providing an alternative to tuna, which were becoming scarce. Although there is little long-term pattern to annual marlin catches (figure 6), the size of the largest fish dropped conspicuously about 1940. In contrast to many changes associated with the 1940 regime shift, large marlin did not reappear after 1976 (figure 7). And unlike the dates for tuna, the dates of the first marlin caught each year have been virtually constant,

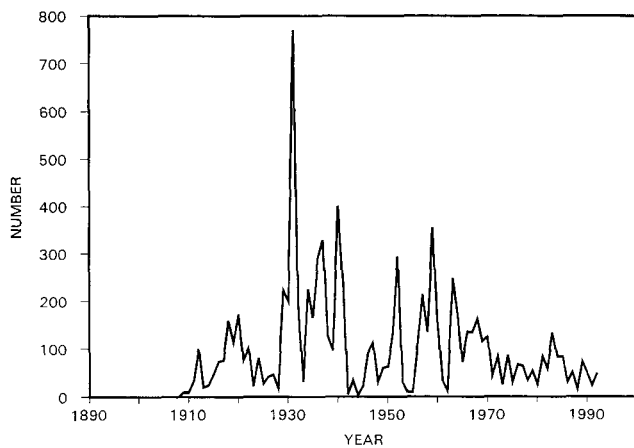


Figure 6. Number of marlin reported in Tuna Club annual tournaments.

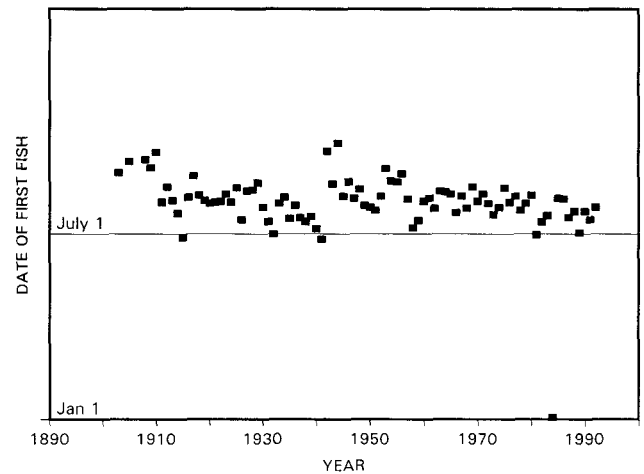


Figure 8. Dates at which first marlin were caught in Tuna Club annual tournaments.

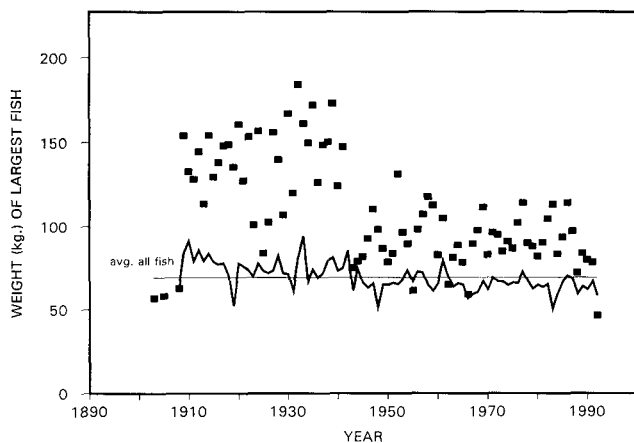


Figure 7. Largest (points) and annual average (solid line) weight of marlin taken in Tuna Club annual tournaments.

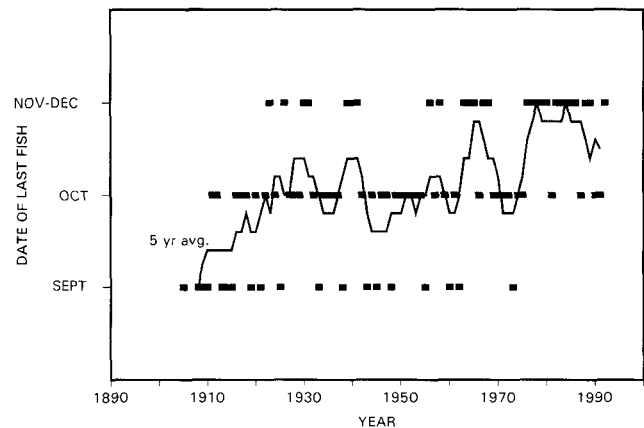


Figure 9. Month in which the last marlin was caught in Tuna Club annual tournaments.

except for one fish caught in southern waters on January 1, 1984 (figure 8). However, marlin appear to be departing southern California waters later in the warm period since the mid-1970s (figure 9).

Tuna Club catches suggest that albacore were abundant in southern California during the first two decades of this century, but catches declined severely in the late 1920s and again declined in the late 1980s, paralleling difficult periods for California's commercial albacore fishery (Lauri and Dotson 1992). From 1910 to 1919, when winter tournament records were kept separately, albacore continued to be caught after October 1, and the largest "winter" fish was consistently larger than the largest "summer" fish (figure 10). This phenomenon cannot have lasted long after the winter tournaments were discontinued, because large albacore disappeared altogether from the annual tournaments shortly after 1920. Large late-season albacore reappeared in southern California waters about 70 years later, and in the mid-

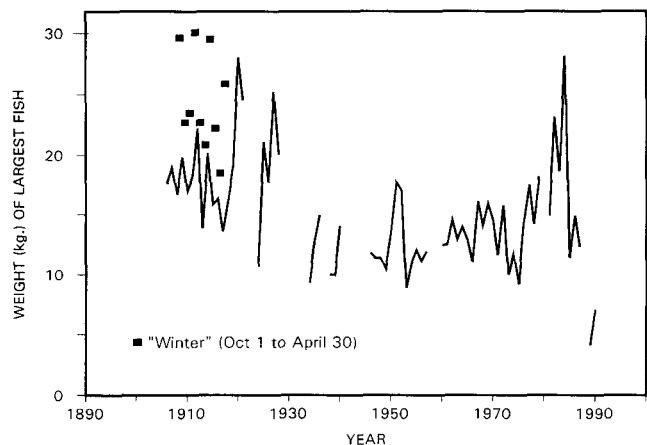


Figure 10. Largest albacore taken in Tuna Club annual tournaments. Winter records were not maintained after 1920.

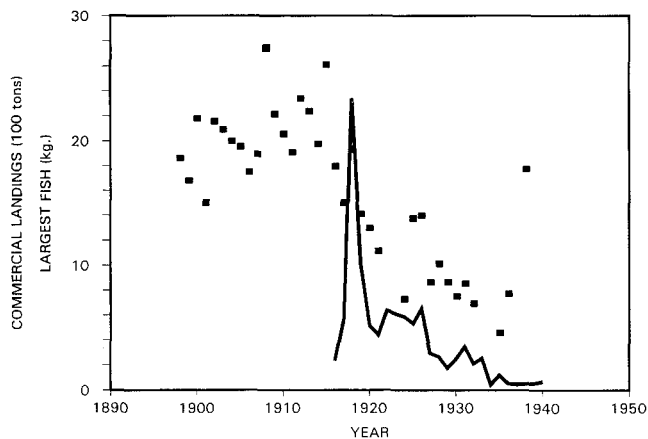


Figure 11. Association of commercial harvesting (solid line) with decrease in size of largest yellowtail (points) taken annually by Tuna Club members.

1980s once again were encountered very late in the year (T. Foreman, IATTC, La Jolla, pers. comm., 1987). In both the 1920s and 1980s, the appearance of large late-season albacore was followed by a severe decline in southern California catches. The links to climate variability are unclear, and may be related to environmental conditions in distant waters. These albacore fluctuations show a 60-year pattern that seems out of phase with the temperature regimes. An intriguing possibility is that the albacore patterns seen in the 1920s and 1980s consistently lead a regime shift to colder conditions by ten to fifteen years.

Tuna Club records of yellowtail, white seabass, and giant sea bass caught in the annual tournaments do not show clear long-term patterns other than a severe impact from commercial fishing during the period 1916 to 1930. Southern California's giant sea bass were commercially depleted by 1930, after which catches by members of the Tuna Club were rare. For yellowtail, the coincidence of intense commercial harvesting and a decline in size is striking (figure 11). After the 1920s, southern California's catches of these species were maintained by seasonal migration of younger fish from distant waters.

There may have been resident California populations of several species of fish, including bluefin tuna, yellowtail, and giant sea bass. The strongest evidence for a resident population exists for white seabass, which supported continuous harvests in the San Francisco area between 1880 and 1916 (Skogsberg 1939). Ragen (1990)—summarized by Dayton and MacCall (1992)—developed a population model that relates maximum size of fish caught each year to the rate of exploitation, and used the Tuna Club and California commercial catch data to estimate preexploitation abundances of three species. Ragen concluded that initial biomasses of white seabass and yellowtail would have been each about 20,000 tons,

and that the initial biomass of giant sea bass was at least 1,300 tons in southern California waters.

Like the Pacific seahorse described earlier, the northern populations of these species are probably established or strengthened during prolonged warm periods, such as occurred during the mid to late 1800s. During cooler regimes, these populations would no longer be self-sustaining, and would slowly decline due to lack of recruitment (cf. Jacobson and MacCall 1995). In the absence of fishing, adults of these species have low mortality rates, and a substantial population could remain resident for decades. However, during cold regimes even a moderate fishery would deplete the population very rapidly.

Small Pelagic Fishes

Patterns and causes of fluctuations in pelagic fish populations of the California Current have long been fundamental issues of study by CalCOFI. Reviews include MacCall (1986) and the Pacific Fishery Management Council (1996). Historical fluctuations in several species of small pelagic fishes are summarized very briefly here.

Scientific monitoring of California's pelagic fish resources began in the 1920s, and useful estimates of sardine landings by age group were provided by the California Division of Fish and Game's Bureau of Commercial Fisheries beginning in 1932. But it wasn't until Murphy (1966) developed a formal technique now known as virtual population analysis (VPA) that consensus could be reached on the detailed historical pattern of sardine population abundance. The Pacific sardine reached a peak abundance in 1934, declined sharply, and recovered to a secondary peak in 1941 before declining to unmeasurably low levels over the following 30 years. The recent sardine recovery was first detected in the early 1980s (Watson 1992; Wolf 1992), and the population has grown steadily since then (Barnes et al. 1992), not yet having shown evidence of a peak in abundance. Jacobson and MacCall (1995) have described a temperature-dependent relationship between recruitment and parental stock for sardines that links the long-term cycle of sardine abundance to the low-frequency variability of sea-surface temperatures.

Pacific mackerel (elsewhere known as chub mackerel, *Scomber japonicus*) experienced two major peaks in abundance, in 1932 and again in 1982 (Parrish and MacCall 1978; MacCall et al. 1985; Pacific Fishery Management Council 1996). The northern anchovy (*Engraulis mordax*) appears to have been at a very low abundance when the CalCOFI ichthyoplankton surveys began in the early 1950s, but increased in the mid-1960s and experienced a brief period of high abundance in the mid-1970s (Methot 1989; Pacific Fishery Management Council 1996). The abundance of northern anchovy is unclear before 1954, but MacCall (1986) interpreted ichthy-

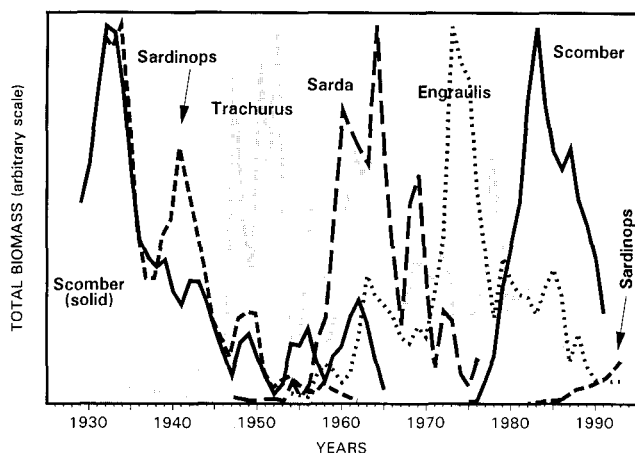


Figure 12. Abundances of major pelagic fishes in southern California, with each species scaled to unit maximum.

oplankton information from 1939–40 as indicating a moderate level of abundance, somewhat higher than was seen during the early 1950s. Pacific bonito (*Sarda chilensis*) has long been harvested commercially in southern California waters, but recruitment of young-of-the-year was rare before a major increase in southern California abundance that began in the mid-1950s (Collins et al. 1980; MacCall 1986).

Jack mackerel (*Trachurus symmetricus*) abundance has not been monitored, and the history of fishery landings has been strongly influenced by the availability of alternative fishing targets such as sardine, anchovy, and Pacific mackerel. But length distributions reported by MacCall and Stauffer (1983) suggest that there may have been a recruitment pulse in the mid to late 1940s, at about the same time the southern California fishery suddenly increased. The evidence for a large jack mackerel population around 1950 is much weaker than the evidence for other species.

Pelagic fish fluctuations appear to be unpredictable when they are considered individually, but a pattern emerges when the time series of historical abundances of these fishes are viewed simultaneously (figure 12). In order to emphasize the temporal pattern, I have scaled abundances to a unit maximum for each species peak (i.e., where two widely separated peaks occur, each is rescaled separately). Sardine and Pacific mackerel were simultaneously abundant in the early 1930s; unfortunately, pre-1950 information on other species is weak or lacking. In the late 1940s and early 1950s no species appears to have been abundant, with the possible exception of jack mackerel.

Since the 1950s, peak abundances have occurred sequentially at regular intervals of about a decade. Currently, Pacific mackerel is declining in southern California, and Pacific sardine continues to increase. Peak abundances

of these pelagic fishes are strongly separated, so that in recent years no two of these species have simultaneously been highly abundant. The sequence of the four well-documented species alternates between piscivores (bonito and Pacific mackerel) and planktivores (anchovy and sardine). An implication of this pattern is that biological interactions may play a substantial role in determining the patterns of peak abundances. Yet the timing of these peaks also appears to be strongly conditional on regime-scale physical fluctuations such as the 1976 transition from cold to warm conditions.

Fishing pressure undoubtedly influences these fluctuations, but its effect is difficult to isolate. In the absence of intense sardine fishing, it is likely that the partial sardine recovery, reaching 2.5 million tons (age 2 and older; Murphy 1966) in 1941, would have produced a much higher abundance, probably exceeding that of 1934 (3.6 million tons). The potential magnitude of the 1941 peak has been estimated quantitatively by MacCall (1979), who simulated historical sardine abundances under alternative fishing pressures. MacCall's simulated 1941 peak was higher than the 1934 peak in scenarios where the simulated fishing intensity was less than about half the actual historical rate. Thus it is reasonable to speculate that a valid sardine peak occurred in 1941, nine years after the Pacific mackerel peak in 1932. Thus the early mackerel-sardine sequence is not necessarily inconsistent with the sequence seen in the 1980s and 1990s, and the coincidence of historical peaks in the early 1930s may have been an artifact of fishery development.

Relationship to the Northeastern Pacific

The southerly portion of the California Current treated in this paper bears a special relationship to the contiguous ecosystems to the north, extending from central California to southwestern Alaska. A large symposium (Beamish 1995) recently addressed climatic effects on fishes in this northern area. Many pelagic fishes (e.g., sardines, Pacific mackerel, jack mackerel, and Pacific whiting, *Merluccius productus*) seem to move to the southern portion of the California Current for reproduction in late winter through early summer. As older adults, these fishes migrate in the summer and fall to northerly waters, especially under conditions of high abundance and warm ocean temperatures. Low-frequency fluctuations in these species are more apparent at the northern and southern ends of the range.

Sardines were abundant off British Columbia in the 1930s, when they supported a substantial fishery (Murphy 1966). Under intense harvesting and a regime shift to colder conditions, they subsequently disappeared from that area for over 40 years. In the 1990s sardines are once again becoming abundant from the Columbia River to British Columbia (Hargreaves et al. 1994).

It is unclear whether *Scomber* was abundant in British Columbia in the 1930s, but in the El Niño events of 1982–83 and 1992–93 it was common enough in the Pacific Northwest to be considered a potentially important predator of young salmon (D. Ware, Pacific Biological Station, DFO, Nanaimo, pers. comm., 1996).

Brodeur and Ware (1995) showed that jack mackerel were abundant in the southern Gulf of Alaska during 1955–58, but were almost entirely absent when the area was resampled in 1980–89.

Salmon (*Oncorhynchus* spp.) in the northeastern Pacific have shown a strong response to regime shifts. Francis and Hare (1994) show that Alaskan salmon catches dropped abruptly with the shift to a cold regime, which they identify as having occurred in 1946, and rose abruptly with the 1976 shift to a warmer regime. Beamish and Bouillon (1995) also examined long-term fluctuations in fish catches from the northeastern Pacific, and found major shifts around 1940 and 1976 for both salmon and nonsalmon species. They conclude that these fluctuations in aggregate catch are closely related to low-frequency fluctuations in the Aleutian Low.

Archaeological evidence shows that giant bluefin tuna have been taken by artisanal fisheries off Vancouver Island and the Queen Charlotte Islands on many occasions during the last 5,000 years (Crockford 1994). Although bluefin tuna have been absent from that area during the twentieth century, Crockford reports an oral account of artisanal harpoon fishing that must have taken place during the decade of the 1880s. The tuna were said to have appeared during brief, exceptionally warm periods in August. Unfortunately, dating of archaeological remains is too imprecise to establish a statistically useful time series, but this pattern is consistent with other evidence of low-frequency variability.

Relationships to Other Ecosystems

Throughout the world, sardine and anchovy stocks exhibit low-frequency fluctuations (Lluch-Belda et al. 1989), many of which appear to be in phase. A remarkable hemispheric coincidence of *Sardinops* spp. fluctuations in Japanese waters and off the west coasts of both North and South America has been described by Kawasaki (1991). In the Peru–Chile system, a large sardine (*Sardinops sagax*) fishery developed following the collapse of the anchoveta (*Engraulis ringens*) fishery in the early 1970s. In the 1990s there is evidence that the sardine resource is declining off Peru and Chile, and that the anchoveta is achieving higher levels of abundance and productivity (R. Parrish, PFEG, Pacific Grove, pers. comm., 1996). Other pelagic fish species in the Peru–Chile system have not been monitored closely enough to discern their relationships to the fluctuations in sardine and anchoveta.

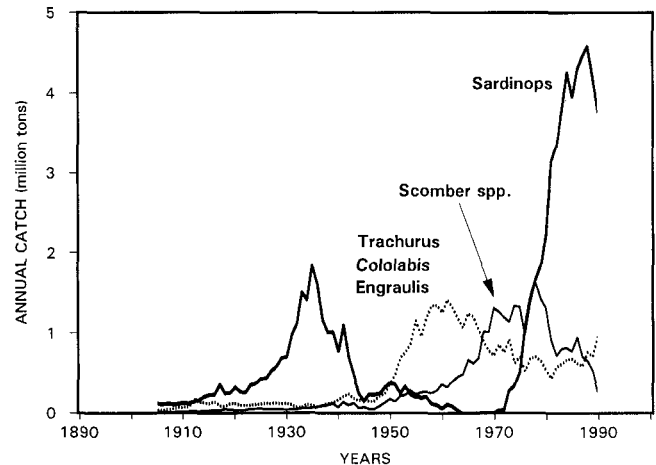


Figure 13. Annual catches of several groups of pelagic fishes in Japanese waters (redrawn from Matsuda et al. 1992).

The waters off Japan have supported harvests of several small pelagic fish species for centuries. Qualitative analysis of historical fish market records kept since 1550 indicates strong low-frequency fluctuations in catches of sardine (*Sardinops melanosticta*), with major peaks occurring every 100 to 120 years (Ito 1961). Reliable pelagic fish catch records exist for most of the twentieth century, but Japanese fishery statistics are maintained separately by many independent agencies, and it is difficult to obtain comprehensive summary statistics. In a study of alternations in pelagic fish abundances off Japan, Matsuda et al. (1991, 1992) proposed a cyclic dominance model (A defeats B, B defeats C, and C defeats A) to explain the temporal pattern of pelagic fish catches off Japan (figure 13). Matsuda et al. identified three pelagic fish groups, consisting of chub mackerels (mostly *Scomber japonicus*), Japanese sardine (*Sardinops melanostictus*), and a mixed-species group composed of anchovy (*Engraulis japonica*), horse mackerels (*Trachurus japonica* and *Decapterus muroadsi*), and Pacific saury (*Cololabis saira*).

There are remarkable similarities between the sequence of pelagic fish species groups in Japanese waters and the sequence of similar groups off California. In both cases, *Sardinops* is followed by *Engraulis*, then by *Scomber japonicus*, and then returns. Matsuda et al. combined *Engraulis* and *Trachurus* into a single group; these two genera may have formed separate peaks in California, but if they were combined, they would occupy the same sequential position as in Japan. The Japanese system does not appear to have an analog of California's Pacific bonito, which intervened between California's tentative *Trachurus* peak and the *Engraulis* peak. In California, sequential peaks in pelagic fish abundance have occurred at near-regular intervals of slightly over a decade (figure 12). In Japan, the peaks in catches of pelagic fish groups are less distinct, but appear to occur at intervals of about

TABLE 1
 Dates of Peak Abundance for Similar Pelagic Fishes in
 Japan and California

Species group	Japan	California
<i>Scomber</i>		1932
<i>Sardinops</i>	1936	1934 (1941?)
<i>Trachurus</i>	} combined, 1955-65	late 1940s?
<i>Engraulis</i>		<i>Sarda</i> * 1960-64 1973-75
<i>Scomber</i>	1971-78	1983
<i>Sardinops</i>	1988	after 1995

**Sarda* is not present in the Japanese system.

15 years (figure 13); the longer interval may also be related to the smaller number of identified fish groups.

In both systems many pelagic species were at low abundance in the 1940s, following the initial decline of sardine and, in California, immediately following the shift to a cold regime. In the Japanese system, low catches could have been caused by low fishing effort during the post-World War II economic depression. In California actual abundances appear to have been simultaneously low, with the possible exception of *Trachurus*. Future periods of generally low pelagic fish abundance (possibly following a sardine peak or a regime shift) could pose problems for the related industries in both California and Japan.

In California, the peaks in *Scomber* abundance are separated by 51 years (table 1). In Japan, the two peaks in annual harvest of sardines are separated by 52 years. The date of California's second sardine peak has yet to be determined, but the interval will be at least 62 years (i.e., 1934 to 1996 or later). Although the California and Japanese systems appear to have been in synchrony before 1950, a five- to ten-year time lag is now present. If this time lag continues, changes in Japan's pelagic fish populations may presage similar changes in California; if a general predictive relationship exists, the utility of such a predictor would be high, and the phenomenon merits long-term monitoring.

No specific oceanographic or biological mechanisms are known that account for these patterns and phase relationships within and among ecosystems. Caution should also be taken from Baumgartner et al. (1992), who found no consistent phase relationships between anchovy and sardine scale-deposition rates in the southern California paleosedimentary record. However, the timing and sequence of recent species peaks in Japan and California strongly suggest that the mechanisms determining sequences and relative abundance of these species are similar or interrelated.

It is plausible that sharp physical regime shifts, such as from the very cold pre-1976 period to the very warm post-1976 period, would favor distinct sequential changes

in dominant pelagic fish species. In contrast, an intermediate and prolonged physical regime (such as pre-1940) could result in less temporal separation of dominant populations, perhaps consistent with the coincidence of high sardine and mackerel biomasses around 1930.

DISCUSSION

Fortunately, the Santa Barbara Basin paleosedimentary record is sufficiently long to establish conclusively that there is low-frequency or interdecadal variability in anchovy and sardine scale-deposition rates (figure 2). Excluding the paleochronologies, even our longest data sets (e.g., Tuna Club records) are inadequate for analysis of very-low-frequency variability, and will remain so for at least another century. Even the 80-year time series of temperatures at Scripps Pier does not yet definitively encompass a complete regime cycle—one more regime shift is still needed.

The most promising approach to extending our time series is to reconstruct conditions between Hubbs' warm period of 1850-70 and the beginning of the Scripps Pier record in 1916. The southern California paleosedimentary record of sardine scales shows a brief but sharp decline in sardine scale-deposition rate around 1890, suggesting very cold temperatures according to the temperature-dependent reproductive model of Jacobson and MacCall (1995). However, Tuna Club records indicate an abundance of warm-water fishes at the turn of the century. If a post-1870 cold period existed, it must have been relatively short (less than 25 years). Alternatively, if there was no distinct cold period in the late 1800s, the pre-1940 moderate temperature regime may have been very long (nearly 70 years).

Although there appears to be a low-frequency warm-cold alternation of physical conditions, this does not necessarily result in only two simple alternative ecological states or regimes. Although the pre-1940 period was warm relative to the subsequent 1940-76 period, it was substantially cooler than the post-1976 warm period. The Pacific seahorse population, which presumably was abundant in San Diego Bay during the 1850s, was re-established there around 1984 (Jones et al. 1988), 127 years after it was first seen by the Pacific Railroad Survey. Notably, a seahorse population was not established in San Diego Bay during the pre-1940 moderate period. As another example, the large marlin recorded regularly by the Tuna Club before 1940 have not reappeared in the post-1976 warm period (figure 7).

Sequences and timing of peak abundances could be modified by interventions by opportunistic species that are not typical elements of the species rotation. The increase of Pacific bonito in southern California during the 1960s may have been such an intervention. Hubbs (1948) reports that surveys conducted at Monterey Bay

by Jordan and Gilbert and by others around 1880 encountered remarkable abundances of barracuda (*Sphyræna argentea*), Pacific bonito, and even Spanish mackerel (*Scomberomorus concolor*). In this century, barracuda and bonito have seldom reached Monterey Bay, and catches of *Scomberomorus* have been restricted to southern Baja California.

CONCLUSION

The low-frequency fluctuations of pelagic fish populations in the southern California region are somewhat cyclic, and are related to the alternation of warm and cold temperature regimes on periods of 50 to 70 years. The fluctuations in pelagic fishes are also correlated with fluctuations in other geographical areas such as Peru-Chile and Japan, a phenomenon climatologists call teleconnections. The remarkable similarity of temperate pelagic fish assemblages in these distant areas indicates a larger suite of physical and biological similarities that favor persistence of these particular species types (Bakun and Parrish 1980). Given general physical and biological similarities, we should also expect there to be similarities in the population dynamics of these species and in the interactions among them. From this viewpoint, it is reasonable to hypothesize that the worldwide similarity of fluctuations in sardine and anchovy stocks (Lluch-Belda et al. 1989; Kawasaki 1991) may extend to the full assemblage of major pelagic fishes in those systems. In the near future, the only hope of testing that hypothesis must come from paleochronologies or from long-term data that have already been collected from other comparable ecosystems; within any single system, we otherwise have little hope of gaining further insight during our lifetimes.

It is difficult to resist speculating on what the near future may hold. The present warm regime is now 20 years old, and it has been 56 years since the 1940 shift to a cold regime (figure 1). The appearance of large late-season albacore and the subsequent decline in southern California catches in the mid-1980s resembles events in the mid-1920s that preceded the regime shift by 10 to 15 years. Also, Japanese sardine catches peaked in 1988 and have since declined sharply. If the recent pattern of time lags remains consistent (table 1), we should expect California's peak sardine abundance about a decade later, around 1998. These biological indicators suggest that a transition to a cooler regime is likely in the next decade or so. On the basis of spectral patterns, Ware (1995) has boldly predicted that the transition could occur around the year 2001. Unfortunately, we do not know whether it will be intense or moderate.

Even with the limited understanding provided by historical science, it is clear that the ecosystems and pelagic fish resources of California, Peru-Chile, Japan, and many

other ecologically similar locations experience low-frequency variability that is incompatible with a simple interpretation of "sustainable development." However, an analogous principle is vitally needed to guide fishing industries and their management through inevitable boom-and-bust cycles. It is first necessary to recognize the importance of low-frequency variability or regime behavior of ecosystems in contrast to standard steady-state assumptions. This step has taken nearly 20 years (cf. Isaacs 1976), but perhaps some of the delay has been due to the need for a clear object lesson. That lesson was provided by the sharp regime shift in the northeastern Pacific Ocean about 1976.

We are now beginning to understand this low-frequency variability and the corresponding biological responses (e.g., Jacobson and MacCall 1995). Fortunately, there appears to be substantial pattern and statistical predictability in the long-term physical and biological variability of the California Current ecosystem. The scientific problems now faced by CalCOFI are perhaps more complicated than was originally envisioned, and are of fundamental importance to fields such as climatology, oceanography, and ecosystem management. It may be taken as a sign of institutional and intellectual health that as our view of the California Current ecosystem matures, the need for and value of CalCOFI monitoring and research continues to grow.

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