Mechanisms of Low Frequency Fluctuations in Sardine and Anchovy Populations

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1 Introduction

This review focuses on possible mechanisms associated with sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) “regimes” -- the very large, low frequency fluctuations and alternations exhibited by these small coastal pelagic species around the world. A wide variety of mechanisms has been proposed, but these mechanisms tend not to be exclusive of each other. Thus, both mechanism “A” and mechanism “B” may be acting simultaneously, and we can easily be misled by the results of conventional hypothesis tests of $H_A$ vs. $H_B$. The difficulties of studying these mechanisms is further compounded by differences among stocks in different geographic regions: mechanism “A” may predominate in one region, and mechanism “B” may predominate in another region. Even within a single region, mechanism “A” may predominate for several decades, and then the system may suddenly change behavior to favor mechanism “B”. Thus, during periods of low sardine productivity, it simply may not be possible to observe or study mechanisms associated with regimes of high sardine productivity: The mechanisms associated with high productivity may not be operating during a 20 to 30-year regime of low sardine productivity. This helps to explain why it has been so difficult to make progress toward a general understanding of productivity in sardine-anchovy systems (see Chapters 2 and 5, this vol.). Most of the associated coastal ecosystems have been monitored for little more than a single cycle of sardine or anchovy abundance, and the high serial correlation of physical and biological characteristics within a regime further reduces effective sample sizes. Strong co-variability of those characteristics can make it difficult to isolate causal factors from non-causal co-varying factors. The result is that existing historical data provide low statistical power to distinguish among competing hypotheses.
A long list of mechanisms can be compiled with regard to explaining annual fluctuations in recruitment (e.g., Bakun 1996), but the mechanisms listed here are selected as having potential for generating high contrast at interdecadal time scales. The evidence for these mechanisms is drawn mostly from four oceanic sardine-anchovy regions: The California Current (but excluding the Gulf of California in this discussion), the Humboldt Current, the Benguela Current and the Kuroshio Current (excluding the waters west of Japan). The Canary Current (where the resident sardine is of the genus Sardina rather than Sardinops) could have been included, but that region is poorly documented and would contribute little to this review. These four regions share many oceanographic features, and share remarkably similar guilds of pelagic fishes (Parrish et al., 1983). However, each region also has unique physical and biological properties. Thus, some of the proposed mechanisms may apply to several systems, while other mechanisms may be unique to one region. It is the presence of similar mechanisms operating in multiple regions that provides the best opportunity for achieving a general understanding of sardine-anchovy regimes.

2 An Initial Framework

Shifts in average sea surface temperature may be one of the most prominent features associated with sardine-anchovy regimes, but the preoccupation with temperature also may have been misleading: As Chavez et al. (2003) observed ‘It remains unclear why sardines increase off Japan when local waters cool and become more productive, whereas they increase off California and Peru when those regions warm and become less productive.’ MacCall (2002) identified flow, rather than temperature, as the likely unifying feature associated with worldwide regime shifts of small pelagic fish production. Warm temperatures in coastal currents off California,
Peru-Chile, and South Africa (where the source water is cold), and cold temperatures off Japan (where the source water is warm) all occur when the flow weakens. Patterns of flow have long been associated with sardine productivity in the Kuroshio Current System (Kondo, 1980). However, researchers outside Japan seem to have regarded flow patterns as an issue uniquely important to the highly energetic Kuroshio system, which is the only western boundary current exhibiting a major sardine-anchovy system. MacCall’s flow hypothesis extended some aspects of the Japanese view to the contrasting eastern boundary current sardine-anchovy systems. In all cases, patterns of flow are strongly associated not only with characteristic shifts in ocean temperature, but with shifts in the physical and biological structure of entire ecosystems. As will be show below, the flow hypothesis also provides an explanation for the mysterious near-synchrony of sardine-anchovy regime shifts on a worldwide scale (Kawasaki, 1983).

Before listing individual mechanisms, I propose the following hypothesized general physical and biological framework of sardine-anchovy regimes (the “Initial Framework”), reflecting three elements that seem to apply to most of the systems. These elements are:

1) Interdecadal alternation of strong and weak flow of the primary boundary current,
   1a) which in eastern boundary currents are associated with fluctuations in nutrient enrichment by both advective transport and by fluctuations in upwelling,
   1b) and which in the non-upwelling western boundary current system off Japan, involves correlated patterns of Kuroshio Current meandering and admixture of nutrient-rich Oyashio Current water.

2) Sardines move upstream and/or offshore to occupy spawning habitats that are favorable only during periods of weak current flow; sardine productivity is primarily associated with
flow conditions in the major currents.

3) Anchovies are restricted the nearshore region, and anchovy productivity is primarily subject to coastal nutrient fluctuations, especially by coastal upwelling.

2.1. Evidence for synchronous interdecadal fluctuations in ocean circulation

Coastal sea level is a well-established indicator of integrated boundary current flow (Chelton et al. 1982). I obtained long-term records of sea level from six coastal locations on the Pacific Rim and four coastal locations on the Atlantic Ocean (University of Hawaii Sea Level Center, http://uhslc.soest.hawaii.edu). The data were converted to a seven-year moving average to filter out El Niño influences. The dominant pattern of covariability given by the first empirical orthogonal function (a.k.a. principal component), accounted for 52 percent of the total variance (Figure 1). The loadings for all six locations from the Pacific (two each from California, Peru-Chile and Japan) were similar, suggesting a Pacific-wide tendency toward synchrony of fluctuations in sea levels and associated boundary current strengths. In the eastern Atlantic Ocean, fluctuations in sea level at Vigo, Spain (at the northern end of the fishery for *Sardina pilchardus*), also tended to be synchronous with those in the Pacific. Sea levels and current strengths off Namibia appear to vary inversely with those in the Pacific Ocean, and indeed, the South African sardine fishery has tended to fluctuate inversely to the Pacific *Sardinops* fisheries (Lluch-Belda et al., 1989, Schwartzlose et al. 1999). Sea levels on the Northwestern Atlantic coast also appear to vary inversely with those in the Pacific, but the Gulf Stream does not have a comparable resident sardine species.
2.2 Sardine movement upstream and utilization of offshore habitat

Kobayashi and Kuroda (1991) provide a clear illustration of the progressive offshore and upstream shift of Japanese sardine spawning between pre-regime conditions in the mid-1960s and the abundance peak in the late 1980s. There was also a large post-spawning downstream expansion of the Japanese sardine feeding migration: By the mid-1980s, the sardine range had expanded over 4000 kilometers eastward into the Kuroshio Extension (Wada and Kashiwai, 1991). The favorable period ended abruptly in 1988, and due to heavy exploitation, VPA estimates of parental spawning biomass dropped by 98% from 1988 to 1994 (Wada and Jacobson, 1998).

A similar offshore and upstream expansion of the California Current sardine occurred during the 1980s and 1990s. The California offshore population was not suspected until it was discovered in 1991. While conducting exploratory trawling for jack mackerel (Trachurus symmetricus) in international waters, the Russian survey vessel Novodrutsk encountered surprising abundances of sardines (Figure 2) as well as mackerel (Scomber japonicus)--at the farthest edge of the range previously covered by standard CalCOFI ichthyoplankton surveys, and outside the U. S. 200-mile Exclusive Economic Zone (Macewicz and Abramenkoff, 1993). Discovery of this offshore segment of the California sardine population helped explain the remarkably northern and offshore historical distributions of sardines seen in much earlier ichthyoplankton surveys of the California Current (surveys of 1929-1932, and 1939, reported by Scofield, 1934, and summarized by Smith, 1990).

Pacific sardines reappeared in British Columbia, Canada in 1992 after a nearly 40-year absence (Hargreaves et al. 1994). This was attributed to the increasing abundance of sardines off
California, and a northward shift in distribution due to the strong 1991-92 El Niño. The path taken by the northward-moving sardines is not clear, and on the basis of minimal sightings of coastal sardine schools between northern California and Washington, it is plausible that the migrating fish used the hypothesized corridor of offshore habitat to reach British Columbia. Tagging conducted during 1935-1942 indicated a low rate of movement from Central California to British Columbia, and consistent differences in length at age suggested lack of active mixing (Clark and Marr 1955).

An analogous situation appears to have occurred when in 1973 *Sardinops sagax* suddenly appeared in Talcahuano, Chile (37° S. Lat.), more than 1000 km. south (upstream) of traditional sardine fishing grounds near Iquique, Chile (Serra, 1983). The new spawning area in Talcahuano was thought to be a “colonization” event as described by Sharp (1980). The author proposes a modified hypothesis, based on the Initial Framework, that the Talcahuano colonization was made possible by an offshore corridor (similar to that hypothesized for North America) that connected the Iquique habitat to the newly favorable upstream habitat at Talcahuano, and that use of this hypothesized offshore corridor was not observed by surveys due to lack of sampling in sufficiently offshore areas: all of the existing samples were taken within ca. 100 nmi of the coast. However, there is supporting evidence in anecdotal reports that sardines were taken by the offshore Russian fishery for jack mackerel (M. Niquen, Pers. comm).

Historical evidence for an offshore segment of sardines is circumstantial off the Western Cape, South Africa. Crawford et al. (1983) observed that older fish formerly spawned off St. Helena Bay “in warm water outside the oceanic front” but that few fish later attained these ages due to heavy exploitation. In the recent productive period off South Africa, sardine spawning
initially overlapped with anchovy spawning in the Agulhas Bank area east of Cape Point, but in the 1990s shifted to a non-overlapping area west of Cape Point (van der Lingen et al. 2001). However, at the end of the 1990s, the South African sardines inexplicably shifted their spawning distribution over 500km eastward to the vicinity of Port Elizabeth in the Eastern Cape, completely abandoning the western spawning area (van der Lingen et al. 2005). Perhaps surprisingly, this shift is easily reconciled with the Initial Framework: the South African system is unique is that it has two alternative “upstream” regions, one extending off the Western Cape into the source of the Benguela Current in the open South Atlantic, and the other extending toward the Indian Ocean, up the Agulhas Current and the Eastern Cape. It appears that the South African sardines may be exploring both “upstream” possibilities. As van der Lingen et al. (2005) note, this eastward shift may have been favored by the intense exploitation of sardines in the Western Cape. In the author’s opinion, the shift was too sudden to have a genetic basis, but alternative mechanisms such as the “entrainment hypothesis” (see below) could be considered.

Although it is not apparent that during the 1990s sardine spawning moved offshore to the extent described by Crawford et al. (1983), the recent sampling pattern did not extend sufficiently offshore to provide a clear answer; sardine eggs were found at the most offshore stations sampled, ca. 60 nmi offshore, leaving the offshore extent undetermined. Davies (1956) similarly found evidence of sardine spawning at about the same distance off St. Helena Bay, without determining the offshore limit of the spawning area.

The relationship between the South African and Namibian (Walvis Bay) sardine stocks is problematic. These two stocks are now generally considered to be independent, though the potential analogy to the California-British Columbia and Iquique-Talcahuano cases may be
worth consideration. The nearshore region north of St. Helena Bay is too cold for sardine reproduction, and is considered to be a barrier to migration between the Western Cape and Walvis Bay. An extensive tagging study conducted from 1957 to 1966 (Newman, 1970a, 1970b) showed a very low amount of movement from Walvis Bay to the Western Cape (and no movement in the opposite direction), which appeared to be evidence that the two stocks were independent. However, much of the tagging study was conducted during the historical collapse of Western Cape sardines; estimated migration rates were based on results for years 1963 to 1966 (Newman 1970b). A sequence of recruitment failures began in the early 1960s, and spawning biomass estimated by VPA declined by 95% from 1961 to 1967 (Butterworth, 1983), suggesting that the favorable regime had already ended by 1963, and if so, the hypothesized offshore habitat corridor required for potential migration past the cold nearshore region may no longer have existed by the time the tagging program was conducted, which would be consistent with the results. This is potentially an example of the regime-related problem described in the Introduction, where mechanisms associated with a productive regime cannot be studied during an unproductive regime. In the author’s opinion, existing information is insufficient to support or to disprove the hypothesized possibility of an offshore corridor between the Western Cape and Walvis Bay during regimes of high sardine productivity and abundant older fish.

2.3 Anchovy restriction to nearshore habitat

Sardines and anchovies are both capable of feeding on small plankton, by both filtering and biting, depending on prey size and concentration, and show a strong overlap in food habits (Blaxter and Hunter, 1982, also see van der Lingen et al., Chapter 8, this vol.). However,
anchovies are generally not found far offshore in any system. MacCall (2002) speculated that their smaller body size and associated limitation in swimming capacity may restrict anchovies may to nearshore areas. Presumably their small size renders them more susceptible to predation and less able to maintain their position in a persistent current, and they are therefore unable to utilize the offshore habitat that episodically becomes available to sardines.

The ecological importance of anchovies in the four systems ranges from relatively low significance in Japan (which is not an upwelling-driven system) to ecological dominance in the Humboldt Current, which is the strongest upwelling system. Anchovies in eastern boundary currents are highly dependent on nearshore plankton production associated with upwelling (Parrish et al. 1983), and their relative abundance in the various systems is correlated with the corresponding intensity of upwelling-driven productivity. Periods of weakened boundary current flow are associated with reduced upwelling productivity and reduced plankton abundance in the three eastern boundary currents (e.g., Muck (1989) for the Humboldt Current, and Roemmich and McGowan (1995) for the California Current) and abundance of anchovy stocks also tend to decline. Conversely, upwelling productivity increases during periods of stronger eastern boundary current flow, and anchovy stocks tend to increase in abundance. Most importantly, this Initial Framework contains little direct linkage of mechanisms favoring or disfavoring sardines and anchovies respectively. The impression of sardine-anchovy alternation is circumstantial, and should not necessarily be expected to be a consistent feature of these systems. It is easy to envision oceanic conditions under which both species may be abundant or scarce simultaneously. Thus, the lack of correlation or even positive correlation (as opposed to the conventionally expected negative correlation) between California’s anchovy and sardine
paleosedimentary scale deposition rates initially observed by Soutar and Isaacs (1974) and confirmed by Baumgartner et al. (1992) is entirely consistent with this Initial Framework. However, Baumgartner et al. do observe that most of the positive correlation arises from intercentennial patterns in the paleosedimentary record. At higher frequencies, fluctuations in the scale deposition rates of the two species are uncorrelated.

3 Physical Processes

3.1 Retention

The characteristic temperature patterns would be seen if a parcel of water takes a shorter or longer time to move through the system. If the length of time is sufficiently long for offspring to develop from eggs to fully mobile juveniles, weak flow (or equivalent conditions discussed below) is tantamount to improved retention, one of Bakun’s (1996) fundamental processes needed for recruitment. One of the simplest mechanisms is that the same volume of water can be transported at reduced velocity if the current becomes wider, or deeper. For example, the mixed layer depth increased in both Japan and Peru ca. 1969 (J. Alheit, Pers. comm.), at the beginning of productive regimes for sardines and the characteristic temperature shifts in both areas.

3.2 Meandering

The pattern of Kuroshio Current meandering has long been associated with fluctuations in pelagic fish productivity off Japan (Nakai, 1949, 1962). Notably, it is the most extreme or “A-type” meandering that is thought to be associated with sardine productivity and the associated
cold temperatures (Hayasi, 1983). A meandering path increases the length of time needed to transport a water parcel from one end of the system to the other, so in terms of larval retention, increased meandering can be considered roughly equivalent to a slowing down of the current system. However, meandering may have additional effects such as extending the length of frontal regions that may be important feeding areas for both adults and offspring. Increased admixing of cold, nutrient-rich Oyashio Current water is beneficial to sardine production, and seems to be enhanced by some patterns of Kuroshio meandering (Kondo, 1980).

3.3 Cyclonic eddies

Logerwell and Smith (2001) have shown that offshore mesoscale cyclonic eddies in the California Current are associated with elevated densities of sardine larvae. Logerwell et al. (2001) modeled the spatial bio-energetics of such an offshore eddy, and concluded that they are likely to be a significant source of sardine recruitment. This mechanism has not yet been confirmed by direct quantitative comparison of eddy activity and resulting recruitment strengths estimated by stock assessments. With respect to mechanisms associated with productivity regimes, an important oceanographic question is whether eddy formation is enhanced during periods of weak boundary current flow, as was postulated by MacCall (2002).

3.4 Latitudinal shifts in source water

Parrish et al. (2000) analyzed North Pacific atmospheric observations and concluded that the North Pacific regime shift in 1976 was associated with distinct changes in wind patterns influencing the North Pacific Current. They found that the total eastward transport actually
increased, but that the portion of the water entering the California Current had a more equatorward source than before 1976. This not only accounts for the post-1976 warming of the California Current, but also accounts for the decrease in nutrients and plankton production observed by Roemmich and McGowan (1995). This post-1976 North Pacific wind pattern also was associated with an extreme cooling in the Kuroshio-Oyashio mixing area that Japanese sardines used as nursery habitat, and may have contributed to nutrient enrichment. A comparable analysis of South Pacific atmospheric observations (if sufficient data exist) would be worthwhile, given the very similar post-1972 Peruvian pattern of declining zooplankton and increased offshore temperatures (Muck, 1989).

4 Biological Mechanisms

4.1 Life history and reproduction

4.1.1 Indeterminate fecundity and access to forage

Unlike herring, anchovies and sardines are indeterminate spawners: their seasonal fecundity is not fixed at the beginning of a spawning season, and they have the capacity to generate and unlimited supply of new oocytes and convert current food intake into successive batches of gametes as long as abundant forage is available (Blaxter and Hunter, 1982). This is an important aspect of their life history, and is undoubtedly a key to their productivity. Hunter and Goldberg (1980) used incidence of postovulatory follicles to infer that anchovies spawn at intervals of 6-8 days during a protracted period of active spawning. Hunter and Leong (1981) calculated that a typical female anchovy in southern California may produce 20 batches of eggs in a year, only about two-thirds of which could be attributed to fat stored during the pre-
spawning period. Similarly, Le Clus (1989) estimated that large sardines off Namibia may produce 80 batches of eggs in a year.

This direct linkage of plankton production to net fecundity is especially important for sardines. Richard Parrish (Pers. comm.) has hypothesized that regime conditions favorable to sardines in the California Current provide the spawning population access to the high production of plankton at the upstream end of the system at a time when the California Current otherwise exhibits a substantial decline in primary and secondary production (Roemmich and McGowan 1995). Abundant food for sardines is nearly always present at the upstream end of the California Current, but during periods of strong flow the upstream temperature is too cold for sardine larvae to develop, and sardines abandon the northern area. However during periods of weaker flow, upstream temperatures are warm enough to allow larval development and successful reproduction. Sardines extend their feeding range northward where they can convert the abundant forage supply into a substantial increase in fecundity. This provides the enrichment and concentration aspects of Bakun’s (1996) “fundamental triad.” The third component of the triad, which is retention, is provided by the combination of upstream spawning and slower transport of eggs and larvae through the system (MacCall, 2002).

4.1.2 Age-dependent fecundity and reproductive age structure

Although spawning biomass has long been used as a measure of stock reproductive potential, it is an inappropriate measure of reproductive potential for indeterminate spawners such as anchovies and sardines which increase their fecundity with age. Parrish et al. (1986) estimated that a 4-year-old female anchovy produces about 50 times the egg output of a 1 year
old (Table 1). Le Clus (1989) estimated that Namibian sardines increased their annual number of spawning batches by 50 to 70 percent for each 1-cm. increase in length. Murphy (1967) warned that risk of stock collapse is greatly increased by the tendency of fisheries to reduce the number of reproductive cohorts in a population. The pattern of increasing fecundity reported by Parrish et al. (1986) and Le Clus (1989) suggest that for anchovies and sardines, the risk is greater than was envisioned by Murphy.

### 4.1.3 Life history plasticity

A remarkable regime-related alternation in growth, maturation and natural mortality rates of anchovies and sardines has been documented in the California Current system. It is unknown whether, or to what extent these patterns are seen in other systems.

Many fish species exhibit latitudinal trends in life histories: individuals in the more poleward segments of fish populations tend to grow larger, live longer, and mature at a larger size and/or older age. In the California Current, the northern anchovy (*E. mordax*) strongly exhibits this latitudinal structure (Mais, 1974, Parrish, et al. 1985). Mais (1981) reported a very sudden change in southern California anchovy age and size composition, beginning in 1977, where fishery catches had previously been mostly 2 and 3-year-old fish, and suddenly catches were mostly 0- and 1-year-old fish. In hindsight, this demographic change coincided with what has since become a well-known regime shift in 1976, at which time ocean temperatures increased markedly. After 1976, southern California anchovies experienced warmer conditions similar to those previously characteristic of Baja California waters, and the fish now exhibited slower growth, earlier maturity and shorter life spans previously typical of Baja California fish.
Lasker and MacCall (1983) found paleosedimentary evidence for the same demographic shift in the mean sizes of anchovy scales taken from the Santa Barbara Basin, and concluded that anchovies had about half the average body weight during periods of sardine abundance as compared with periods of sardine scarcity (Figure 3). Because of the age-dependent fecundity pattern described above, changes in lifespan may strongly influence population productivity. The environmental trigger for these changes in the anchovy life table is presumably water temperature experienced during early life stages, perhaps coincident with mortality rates associated with environmentally-driven changes in the predator field.

The California Current’s sardines also show a regime-dependent change in the life table. Murphy (1966) reports that in the early years of the historical fishery, about half of the 2-year-olds spawned, but that in the late 1950's, all of the 2-year-olds spawned. Anecdotal accounts suggest that one-year-old sardines were actively spawning in the 1960's and early 1970's. In the early 1930s, at the beginning of the historical fishery, sardines achieved maximum ages of at least 13 years (the plus group reported by Mosher and Eckles, 1954), seen both in Central California and in British Columbia. In the early 1970's, 4-year-olds were rare, despite a harvest moratorium. Murphy (1966) concluded that the natural mortality rate of sardines approximately doubled in the 1950s, when sardine abundance was declining to low levels.

Thus during California Current regimes with cold water temperatures, and during which anchovies and sardines occupy the same coastal habitats, the two species have very similar life tables. However, during regimes favorable to sardines, with typically warmer water temperatures and a more offshore distribution of sardines, the two species occupy different habitats and the life tables of the two species diverge sharply. Anchovies become short-lived,
while sardines become relatively long-lived. It can be rationalized that in an oceanic habitat, sardines benefit from a larger body size and corresponding swimming ability. However the mechanism of the change in sardine life history is unknown.

It is possible that a similar shift in sardine age at maturity occurred in South Africa. Fairweather et al. (2006) document a 53-year history of sardine lengths at 50% maturity covering two separate regimes favorable to sardines. There is a strong correlation between length at maturity and spawning abundance. However, the lengths at maturity increased in the mid to late 1980s in advance of the population growth. This phase relationship allows the possibility that the change in length at maturity was not simply abundance-dependent, but rather was a more direct response to the new environmental conditions that allowed subsequent population growth.

4.1.4 Temperature optima

Sardine and anchovy fluctuations are strongly correlated with temperature fluctuations (e.g., Chavez et al., 2003), but it is difficult to distinguish direct influences of temperature from effects of correlated variables. Nonetheless, Butler et al. (1993) analyzed stage-based sardine and anchovy life tables, and concluded that temperature-related changes in the duration of egg and early larval stages could have a strong influence on population productivity. Associations of spawning activity and temperature have been described by for sardines and anchovies in the California Current system (Lluch-Belda et al., 1991), and in the Japanese system (Takasuka and Aoki, 2006, A. Takasuka, Pers. comm.), and are summarized in Table 3. Eggs and larvae in the California Current system have a bimodal temperature distribution, corresponding to separate spawning populations off California and off Southern Baja California. Temperature associations
in Japanese waters show a separation between spawning habitats of sardines and anchovies, and Takasuka and Aoki (2006) have demonstrated that growth rate of anchovy larvae has a peak value at about 22 °C independently of the availability of food. In contrast to Japan, California Current sardines and anchovies tend to spawn at similar temperatures, but show a difference among stocks. The temperature associations of sardine spawning in the far northern California Current was not covered by the data available to Lluch-Belda et al., and that cold region is not represented in Table 3.

4.2 Behavioral mechanisms

4.2.1 Behavioral imprinting

Cury (1994) hypothesized that small pelagic species may exhibit a form of behavioral imprinting—a “natal homing” tendency for an individual spawning fish to return to habitats or environmental conditions similar to those experienced in its own early life history. This behavioral tendency would amplify species productivity, and also is consistent with the geographic shift of sardine spawning during favorable regimes.

4.2.2 The entrainment hypothesis

An International Council for Exploration of the Sea Working Group (Petitgas et al. 2006) has explored a hypothesis that the navigational path of spawning migrations may be learned from experienced older fish by recruits to the migrating fish schools. The importance of learning migratory paths from older experienced individuals is well established in bird migration (Able and Able 1998) and strengthens the plausibility of this hypothesis for fish migration. In the case
of the tendency for sardines to occupy offshore/upstream habitats during favorable regimes, this hypothesis helps account for the delay between the shift to a physically favorable ocean condition and utilization of the newly available habitat by the fish stocks. Important considerations include the contrast between optimal habitat locations in unfavorable and favorable regimes, and the extent to which older “knowledgeable” fish remain in the population at the time the shift occurs.

4.2.3 Mixed-species schooling and the “school trap”

Bakun and Cury (1999) cited widespread observations that during unproductive periods, species experiencing low abundance often join schools of other more abundant fish species of similar size or swimming speed. Unlike Radovich (1979), who hypothesized that the scarce species benefits from the protection offered by the schools of the abundant species, Bakun and Cury (1999) hypothesized that the scarce species could suffer disadvantages from mixed schooling, and this mechanism could provide the kind of dynamic instability that allows prolonged dominance of one species or the other.

4.2.4 “School-mix feedback” and behavioral imprinting

Bakun’s (2001) “school-mix feedback” hypothesis is an extension of Bakun and Cury’s “school trap” hypothesis that adds elements of behavioral imprinting (see preceding) and predator-prey dynamics. The result is a hypothesized tendency for multispecies cycling. This behavioral tendency presumably would contribute to regime-like population behavior, but it is difficult to quantify the periodicity or amplitude or explain the worldwide synchronization of the
resulting population cycles.

4.2.5 “Basin model” of habitat selection

MacCall (1990) proposed a “basin model” of habitat selection mechanism to account for the tendency of fish populations to expand and contract with changes in abundance (a related hypothesis, also based on the “ideal free distribution” was proposed by Wada and Kashiwai, 1991). Because relative density near the center of the distribution tends to vary less than population abundance as a whole, this population behavior renders fish stocks more vulnerable to centrally-foraging predators and fishermen during stock declines, and less vulnerable during stock increases, potentially increasing contrast between favorable and unfavorable periods.

The basin model originally described the population size-dependent distribution of anchovies off California, but is occasionally applied to sardines by analogy. The basin model predicts that spawning area should vary approximately as the square or cube root of abundance. In the case of the Japanese sardine, Zenitani and Yamada (2000) found that a power function was indeed the best mathematical model, and that the exponent of abundance was in the range of 0.32 to 0.46, in accordance with a basin model. However, Barange et al. (1999) concluded that unlike anchovies, the distribution of South African sardines did not conform to the basin model, and that sardines and anchovies “may have different strategies of occupying space.” Smith (1990) showed that the California Current sardine spawning area has been approximately proportional to spawning biomass (i.e., a power function exponent of 1.0) over the full range of historically observed sardine abundance, which again does not agree with behavior predicted by a basin model. Whereas MacCall’s basin model would suggested that Smith’s (1990) offshore
expansion of the sardine spawning grounds (considered as “effect”) was in response to the increase in abundance (considered as “cause”), the Initial Framework proposed here reverses the interpretation of cause and effect, so that the improvement of offshore spawning habitat (now the “cause”) is itself the source of the increased reproductive rate and consequently increased abundance (now the “effect”). Thus the Initial Framework freely allows Smith’s proportional relationship, and does not assume that a basin model necessarily applies to the productive phase of sardine populations. It is possible that a basin model fits sardine populations, as in Japan, but it may be best suited to describing coastally-constrained populations such as anchovies, and perhaps sardines during their unfavorable periods (MacCall 1990, Barange et al. 1999).

4.3 Multispecies mechanisms

4.3.1 Trophic dynamics

Biological oceanography has a long history of research on trophic control of marine ecosystems, specifically whether productivity is controlled by the primary production rate or by predation from higher trophic levels. Abundant small pelagic fishes may even exert controlling influences on both higher and lower trophic levels (“wasp-waist” control, Rice, 1995). This is a large area of research, and is reviewed in Chapters 8 and 9 of this volume.

With the possible exception of Japanese waters, bottom-up control of sardines is unlikely: In eastern boundary currents, primary and secondary production tends to be lower during productive sardine regimes than during regimes of low sardine productivity (e.g., Muck, 1989, Roemmich and McGowan 1995). Unlike the eastern boundary currents, the source of
Japan’s Kuroshio Current is tropical nutrient-poor water. Sardines live in the mixing area between the warm, nutrient-poor Kuroshio Current and the cold and nutrient-rich Oyashio Current, and benefit from conditions of increased mixing (Kondo, 1980), suggesting a possible bottom-up trophic influence on Japanese sardines. Eastern boundary current production of anchovies is dependent on nutrient enrichment by coastal upwelling, and may also experience a bottom-up trophic influence. Importantly, the trophic dynamics may be substantially different in regimes favoring sardines or anchovies, respectively.

4.3.2 Species competition

Classic competition was the first multispecies mechanism proposed to explain the shift from sardines to anchovies. Murphy (1966) reviewed specific mechanisms for sardine-anchovy competition in the California Current, which included direct competition among larvae for food, and adult feeding on the competitor’s eggs and larvae, but neither was supported by evidence. Stander and Le Roux (1968) similarly suggested that competition from anchovies was a factor in the decline of South African sardines. In both cases, the main evidence was circumstantial: anchovy abundance increased after sardines declined, and sardines showed little ability to recover from their low abundance. In California, Murphy and others strongly advocated an “experimental fishery” on anchovies that was designed to reverse the apparent equilibrium and bring back the sardines (McEvoy, 1986). The experiment was not conducted. However, it is interesting to imagine the result of such an experiment: Because we now know that California’s sardines began increasing after 1976, the experiment would have appeared successful whether or not it had any influence on actual events.
4.3.3 Predator-prey dynamics

On a predator-prey basis similar to the earlier competition hypothesis, Muck (1989) similarly argued for increasing the Peruvian fishery for mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus murphyi*), on the premise that these predators were preventing the anchoveta from recovering. This “ecosystem-oriented” policy was not implemented, but it too would have appeared to be successful: The anchoveta increased rapidly in abundance after 1988.

4.3.4 The “cyclic advantage” hypothesis, and cyclic dominance of pelagic species

Matsuda et al. (1991, 1992) observed a historical sequence of three dominant pelagic species groups off Japan, and proposed a cyclic dominance model (a.k.a. the “rock-paper-scissors” game, where A defeats B, B defeats C, and C defeats A) to explain the temporal pattern. Their species groups were sardines (*Sardinops melanosticta*), chub mackerels (mostly *Scomber japonicus*), and a combined group of anchovies (*Engraulis japonica*), horse mackerels (*Trachurus japonica* and *Decapturus muroadsi*) and saury (*Cololabis saira*). Matsuda et al. (1992) and Matsuda and Katsukawa (2002) developed a simple biologically-driven asymmetric competition model, and identified parameter values that could approximately reproduce the observed species replacement cycle. They acknowledged that environmental variability could influence some aspects of the pattern, but considered biological interactions to be the primary force in the system.

Documented cases of cyclic dominance exist for behavioral interactions among individuals, but to the author’s knowledge no cases have been documented for this pattern of
interactions at the population level. Evolutionary theory indicates that a single strategy should prevail unless each species of the trio has a fitness advantage when rare (Maynard-Smith 1982, Sinervo and Lively 1996). It is difficult to envision any of these species having a fitness advantage during their periods of low abundance, and, as reviewed above, Bakun and Cury’s (1999) “school trap” hypothesis argues that these pelagic species may suffer a disadvantage when scarce.

MacCall (1996) observed a similar sequence of dominant pelagic species off California, where at least four groups of species were present. As in Japan, the cycle follows a characteristic order: sardine (Sardinops spp.)-jack mackerel (Trachurus spp.)-anchovy (Engraulis spp.)-chub mackerel (Scomber japonicus)-sardine. Note that MacCall splits the multispecies anchovy-horse mackerel group of Matsuda et al., but that their combined position in the sequence remains the same. Thus the classically-accepted (though perhaps not as well established in fact) pattern of sardine-anchovy alternations may be a subset of a larger multispecies sequential pattern. The timing of species transitions is closely linked to physical regime shifts: Sardines and anchovies become abundant during respectively favorable environmental regimes, while jack mackerel and chub mackerel become abundant during the transitions between those environmental regimes. MacCall also noted that the two regime-transition fishes (Scomber and Trachurus) are piscivorous and are potential predators of the preceding planktivorous species (Engraulis and Sardinops) in the cycle, providing some circumstantial biological support for the cyclic dominance mechanism of Matsuda et al. However, MacCall favored the hypothesis that the cycle of sequential dominance is primarily a response to a consistent pattern of decadal shifts in the physical system.
MacCall (1996) also noted a loose synchrony in the timing of similar species transitions in Japan and California. The Initial Framework proposed here suggests that trans-Pacific synchrony may result mainly from the strong response of sardines to mutually experienced decadal fluctuations in current flow. The timing of transitions and peak abundances of the other pelagic species may result from a combination of biological interactions (competition and predation) and from other biological and physical properties of the environment that are associated with decadal-scale cycling of flow patterns.

4.3.5 Predator outbreaks

A speculative addition to this list of mechanisms is the possibility that predator outbreaks may hasten the end of sardine regimes in eastern boundary current systems where persistent warm water may allow an influx of sub-tropical predators. During the present decade, the jumbo squid, *Dosidicus gigas*, has become unusually abundant in the upstream portions of the California and Humboldt Currents, whereas it was formerly found mainly at the tropical ends of these systems (Field et al., In press 2007). There has been plausible speculation that this recent outbreak of piscivorous squid contributed to a massive decline in hake (*Merluccius gayi*) abundance off Chile (Contreras, 2005), and it is equally possible that the North American squid could contribute substantially to sardine mortality. *Dosidicus* was previous abundant off California in the 1930s, at a time when the sardine population was declining rapidly (Croker 1937).

In a review of early faunal surveys in California, Hubbs (1948) noted that in 1880, ichthyologists Jordan and Gilbert encountered substantial abundances of subtropical predators in
Monterey Bay, central California. The year 1880 was near the end of an extraordinarily warm period inferred by Hubbs from faunal range extensions, including several prominent predators. The paleosedimentary sardine record of Baumgartner et al. (1992) shows a very sharp decline in sardine scale deposition rate during from the 1870s to the 1880s (see Chapter 4, Figure x ??).

4.3.6 Environmental “loopholes”

Bakun and Broad (2003) proposed that transient conditions of poor ocean productivity, such as El Niño, can impact predator populations so that production of small pelagics is enhanced in subsequent years. This mechanism could account for interannual variability, but it is more difficult to accept Bakun and Broad’s argument that it can account for interdecadal variability.

5 Impacts of fisheries

Most small pelagic species are now subject to fisheries, and exploitation plays an influential role in their population dynamics. Intense exploitation following the end of favorable regimes has in several cases depleted the reproductive potential of the resource within a very few years; with compounded loss due to age-dependent fecundity (see above). Subsequent increases in abundance when conditions again become favorable are an exponential growth process, and potentially are limited by the initial “seed” abundance. In some systems, the exponential growth rate is sufficiently high that the initial abundance is unimportant, but in other systems a lower growth rate makes initial conditions much more important.

Inter-regime fluctuations in sardine productivity in Japan and California provide a useful
comparison. The recruitment per spawning biomass of Japanese sardines is twenty-fold higher during a favorable regime (Wada and Jacobson 1998). This allows an intense fishery to be sustained during productive periods, and perhaps decreases the importance of maintaining a seed stock during unfavorable periods. However, when the system suddenly becomes unfavorable for sardines, the remaining stock is depleted very rapidly. In contrast, the California sardine experiences only a doubling of recruitment per spawning biomass during favorable regimes (Jacobson and MacCall 1995). In the absence of fishing, the population growth rate during favorable conditions off California is about 40 percent per year. At this relatively low growth rate, even low fishing rates and the initial size of the California stock have strong influences on the growth trajectory—the stock required twenty years to approach its asymptotic abundance following the beginning of favorable conditions in 1976. Recent sardine fishery management in California has been conservative, which may have contributed to continuing abundance, in contrast to the rapid post-1988 depletion of the Japanese and South American sardine stocks.

In addition to their influence on exponential growth rates, fisheries also cause truncation of the age structure. Older, larger individuals play an important role in many of the hypothesized mechanisms presented in this review, both directly, through their high fecundity, and indirectly through their behavior, especially migratory behaviors in the case of sardines.

It is doubtful that sufficient understanding of pelagic fish demographics and dynamics will soon be gained to identify an optimal harvesting policy for these small pelagic fishes. The first anchoveta fishery off South America lasted perhaps 15 years, and the present anchoveta fishery is now about that old. Both recent sardine fisheries in Japan and South America lasted little more than 20 years under heavy exploitation. The present South African sardine population
appears viable, but is heavily exploited, has strangely abandoned its traditional spawning grounds, and is still less than 20 years old. The California Current’s intentionally small sardine fishery is exceptional, in that it is still viable after 30 years (assuming it began in 1976, though little fishing was allowed for much of the first two decades in order to allow maximal population growth). This raises the question of whether this 30-year record has been the lucky result of continuing favorable environment, or whether it has been the earned result of unusually conservative management that seeks to maintain older individuals in the population and to provide sufficient abundance to endure the inevitable shift to a prolonged unfavorable regime. As with most pelagic fish questions, we are unlikely to have an answer for a very long time.

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Table 1. Age specific per capita fecundity of northern anchovy (from Parrish et al. 1986).

<table>
<thead>
<tr>
<th>age</th>
<th>Number of spawnings</th>
<th>Eggs/g/yr</th>
<th>Avg wt. (g)</th>
<th>annual fecundity (10^6)</th>
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<tbody>
<tr>
<td>1</td>
<td>5.3</td>
<td>2803</td>
<td>11.6</td>
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<tr>
<td>2</td>
<td>11.9</td>
<td>6550</td>
<td>16.5</td>
<td>1.29</td>
</tr>
<tr>
<td>3</td>
<td>19.2</td>
<td>11434</td>
<td>20.7</td>
<td>4.54</td>
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<tr>
<td>4+</td>
<td>23.5</td>
<td>13861</td>
<td>26.6</td>
<td>8.66</td>
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Table 2. Comparison of California Current anchovy and sardine life histories during respective productive and unproductive ocean conditions.

<table>
<thead>
<tr>
<th>Regime</th>
<th>Productive</th>
<th>Unproductive</th>
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<tbody>
<tr>
<td>Sardine</td>
<td>warm</td>
<td>cool</td>
</tr>
<tr>
<td>Age of Maturity</td>
<td>2-3</td>
<td>1-2</td>
</tr>
<tr>
<td>Approx. Maximum Age</td>
<td>&gt;13</td>
<td>4</td>
</tr>
<tr>
<td>Anchovy</td>
<td>cool</td>
<td>warm</td>
</tr>
<tr>
<td>Age of Maturity</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Approx. Maximum Age</td>
<td>6</td>
<td>4</td>
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</table>

Table 3. Temperature (°C) associated with peak abundance of eggs and larvae

<table>
<thead>
<tr>
<th>Region</th>
<th>Sardines</th>
<th>Anchovies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Japan</td>
<td>16.5</td>
<td>22</td>
</tr>
<tr>
<td>California</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>So. Baja California</td>
<td>24</td>
<td>25</td>
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</table>
Figure 1. Empirical orthogonal function (principal component) loadings of 7-year averaged sea level associated with the largest eigenvalue.
Figure 2. Location of sardines encountered off California by the Russian survey vessel Novodrutsk in 1992 (circles), shown in comparison with standard CalCOFI sampling stations (squares). Filled symbols are positive for sardines. Figure taken from Macewicz and Abramennoff (1993).
Figure 3. Cumulative frequency distributions of anchovy scale widths from anaerobic sediments of the Santa Barbara Basin. A. Periods of high sardine scale deposition rate. B. Periods of low sardine scale deposition rate.