COUPLING OF THE PACIFIC SARDINE (*SARDINOPS SAGAX CAERULEUS*) LIFE CYCLE WITH THE GULF OF CALIFORNIA PELAGIC ENVIRONMENT

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ABSTRACT

The distribution of the Pacific sardine (*Sardinops sagax caeruleus*) in the Gulf of California led others to a conceptual model of the migration patterns over its life cycle. We examine the model in light of our recent understanding of the physical processes in this marginal sea. There appears to be a remarkable coupling between the two. The adult spawning migration from the northern feeding grounds and the subsequent spawning in the Guaymas Basin occurs in winter and early spring, at which time strong northwesterly winds predominate, and strong coastal upwelling is observed along the eastern margin of the gulf. The well-defined squirts and jets that result off the main capes appear to transport eggs and larvae across the gulf towards the Baja California coast, where juveniles concentrate. The summer conditions of southeasterly winds coincide with the migration of juveniles to the adult feeding grounds, thus closing the migratory life cycle. There are indications that the availability of adult Pacific sardines to the fishery depends on the intensity of the upwelling-favorable northwesterly winds and on interannual changes of thermal conditions occurring in the central gulf associated with the El Niño/Southern Oscillation (ENSO) phenomena. Density-dependent food competition among juveniles, and cannibalism on eggs and larvae are proposed as two possible mechanisms affecting recruitment during ENSO events, when the habitat of the Pacific sardine is compressed to the north.

RESUMEN

Un modelo conceptual del ciclo migratorio de la sardina (*Sardinops sagax caeruleus*) en el Golfo de California ha sido formulado por Sokolov y Wong basado en la distribución de los estadios juveniles y adultos. Este modelo es examinado incorporando el entendimiento reciente acerca de algunos procesos físicos que predominan en esta región. Notamos una correspondencia considerable entre ambos. La sardina adulta emigra del alto golfo hacia la cuenca de Guaymas para desovar en invierno y principios de primavera, cuando predominan los vientos del noroeste y se registran surgencias pronunciadas a lo largo del margen oriental del golfo. Los penachos de agua fría que se forman en extensión de los cabos y promontorios principales proporcionaría el mecanismo para transportar huevos y larvas hacia la costa de Baja California, donde se concentran los juveniles. Las condiciones de verano, con vientos del sureste, coinciden con la migración de los juveniles hacia las regiones donde se alimentan en su etapa adulta, cerrando así el ciclo migratorio. Existen indicaciones que la disponiblidad de sardina Monterrey a la pesquería depende de la intensidad de los vientos del noroeste, favorables a los procesos de surgencia, y de los cambios interanuales observados en la configuración térmica de las capas superficiales del golfo central como occurre, por ejemplo, durante un evento de El Niño. La competencia entre trófica juveniles, que depende de la densidad de la población, y el canibalismo de huevos y larvas por juveniles y adultos son propuestos como posibles mecanismos que afectan el reclutamiento durante eventos de El Niño, cuando el hábitat de la sardina Monterrey se encuentra reducido al norte.

INTRODUCTION

The Gulf of California is a semienclosed sea about 1000 km long and 100 to 200 km wide, bounded by the Baja California Peninsula on the west and by the states of Sonora and Sinaloa on the Mexican mainland to the east. The upper gulf, roughly one-third of its total length, is separated from the lower gulf by two large midriff islands and an irregular sill. The lower gulf comprises a series of basins, which deepen from approximately 2000 m off Guaymas to over 3000 m at the mouth. Most of the upper gulf is shallower than 200 m, except for the basins surrounding the pedestal of Ángel de la Guarda Island. Surface waters at the sill are typically cooler year-round than those of the lower gulf because of strong tidal mixing (Roden 1964; Badan-Dangon et al. 1985). The principal difference between the waters inside the Gulf of California and those of the adjacent open Pacific is the additional presence of a high-salinity water mass at or near the surface in the gulf. This water

is formed by evaporation in the upper gulf and appears to be modified by mixing with subsurface water from the eastern tropical Pacific (Roden and Groves 1959; Alvarez-Borrego and Schwartzlose 1979).

The Pacific sardine, *Sardinops sagax caeruleus*, is distributed from the Gulf of California to Kamchatka, Alaska (Miller and Lea 1972). In the Gulf of California, it is found principally in the central region, where it supports, in terms of biomass, the most important pelagic fishery in the gulf. A hypothesis for the migration patterns of this species over its life cycle in the Gulf of California has been proposed by Sokolov and Wong-Rios (1973) and by Sokolov (1974). The purpose of this paper is to examine this migration hypothesis in light of recent observations augmenting our current knowledge of the physical variability in the pelagic ecosystem of the Gulf of California. We suggest that the general migration pattern of the Pacific sardine in the gulf can be explained by the seasonality of near-surface temperature and circulation patterns. We hypothesize that similar mechanisms will also vary the pattern of migration on an interannual scale and may thus affect adult availability to the fishery (as suggested by Lluch-Belda et al. 1986) as well as juvenile recruitment to the adult stock.

SATELLITE IMAGERY

Satellite data were received, archived, and processed at the Scripps Satellite Oceanography Facility. Infrared radiation propagating spaceward from the Gulf of California was measured with the Advanced Very High Resolution Radiometer (AVHRR) on the polar-orbiting NOAA-6 satellite. The spatial resolution of the AVHRR is 1.1 km at nadir. Visible radiance data from the Coastal Zone Color Scanner (CZCS, Nimbus-7 satellite) was used to calculate average chlorophyll *a* and phaeopigment concentration (one attenuation depth) using an algorithm based on Gordon et al. (1983). Without simultaneous shipboard measurements it is difficult to estimate the accuracy of pigment concentration calculated from satellite-measured sea-surface color; estimates should be taken as approximate. Relative spatial accuracy, however, is very good. The spatial resolution of the CZCS is about 0.8 km at nadir.

We chose to study April 7, 1980, because Badan-Dangon et al. (1985) showed this to be a day when the central gulf's frontal systems were very well developed and because both clear infrared irradiance and ocean color data were available. Although there is a time lag between surface

temperature and the biological response (for example, between initial upwelling and increased primary production), we used both infrared and CZCS images from the same day because no other CZCS data were available until April 23. All images were contrast-enhanced to improve pattern recognition, and were mapped so that warmer temperatures and lower pigment concentrations are associated with darker grey shades. The positional accuracy of the processed images is approximately ± 2.2 km.

VARIABILITY IN PHYSICAL ENVIRONMENT AND MIGRATION PATTERNS

The general circulation of the Gulf of California appears to be dominated by the regional wind field. During winter months, northwesterly winds predominate (Roden 1964; Candela et al. 1984, 1985); they are favorable for coastal upwelling along the eastern coast. During spring, the winds and resulting upwelling intensify, producing well-developed plumes of upwelled water across the gulf from off the capes near Guaymas and Yavaros (Badan-Dangon et al. 1985). During late spring, the wind changes to a southeasterly regime, which dominates throughout the summer months; summer upwelling occurs off the western Baja California coast, but is less intense than spring upwelling. Geostrophic calculations by Rosas-Cota (1977) indicate that the net flow at the surface is to the south during winter and spring, and to the north during summer and fall.

Figure 1 presents Sokolov and Wong-Rios's (1973) hypothesis in the line drawing beside an infrared satellite image indicating the surface thermal patterns of April 7, 1980. The remarkable similarity between the proposed larval transport pattern and the observed surface temperature pattern suggests a strong coupling of the two. Sokolov and Wong-Rios (1973) gathered information showing both adult and juvenile migration patterns. Because spawning was thought to be mostly on the east coast of the gulf, and juveniles were found concentrated on the west coast, they postulated that eggs and larvae are transported by the dominating surface circulation from the east to the western nursery grounds, but no mechanism was suggested. The satellite image presented in Figure 1 shows the formation of surface jets of cool water extending from the Guaymas and Yavaros spawning areas to the west coast of the gulf, thus providing a specific mechanism for such east-west egg and larval transport.

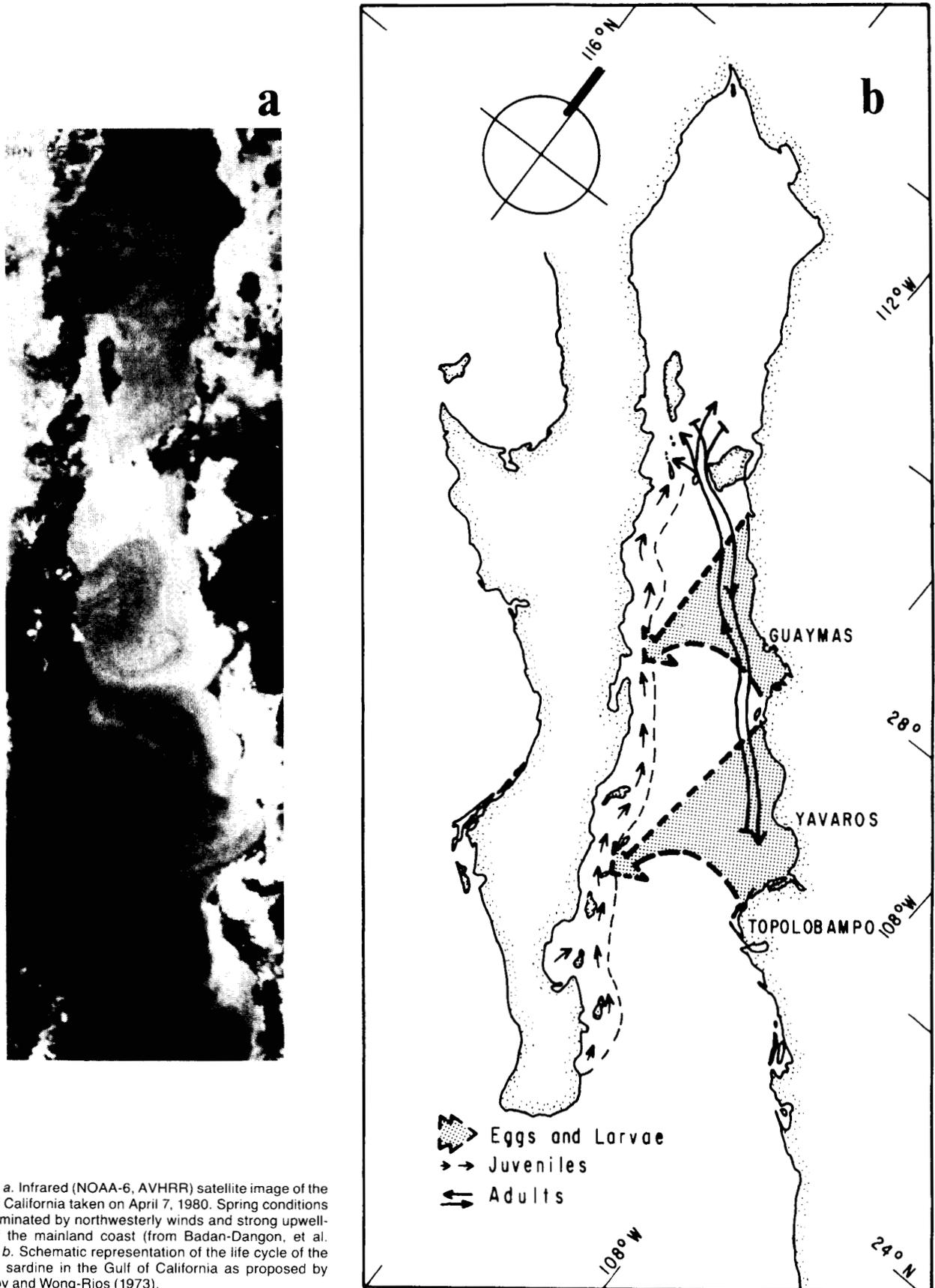Adults migrate along the east coast of the gulf

Figure 1. a. Infrared (NOAA-6, AVHRR) satellite image of the Gulf of California taken on April 7, 1980. Spring conditions are dominated by northwesterly winds and strong upwelling off the mainland coast (from Badan-Dangon, et al. 1985). b. Schematic representation of the life cycle of the Pacific sardine in the Gulf of California as proposed by Sokolov and Wong-Rios (1973).

from their summer feeding grounds in the northern gulf toward their spawning grounds, principally in the region of Guaymas and Yavaros, from January to April. Spawning generally occurs during this period (Wong-Rios 1974), although recent work has found spawning as early as November (Cisneros-Mata et al. 1987); after spawning, the adults return north. This adult southern migration occurs during the period of cool southerly flow and intense coastal upwelling along the eastern coast; the return north coincides with summer warming and the decreased upwelling off the eastern coast associated with the general flow to the north shown by Rosas-Cota (1977). Juveniles are found on the west coast during the period of western upwelling; they migrate north to join the adults in the northern gulf with the late-summer northern flow.

Although the similarity between the larval transport pattern proposed by Sokolov and Wong-Rios (1973) and the thermal patterns on Figure 1 are quite striking, it is important to recognize that sea-surface temperature derived from infrared satellite imagery originates only from a thin surface film (approximately 0.02 mm), and may not represent the temperature and thus the flow at greater depths (Stewart 1985). Therefore it is important to examine more closely whether the circulation patterns reported by Badan-Dangon et al. (1985) could represent a net transport of the eggs and larvae throughout a significant depth in the near-surface layers of the gulf. Because sea-surface color results from processes integrated approximately over the euphotic zone (Morel and Gordon 1980), color is helpful for gauging a minimum depth of these circulation patterns. The concentration of chlorophyll-like pigments in the surface layer (one attenuation depth) greatly contributes to the observed color (Stewart 1985). Sea-surface color, therefore, should better represent net transport of water in the surface layer and may therefore be a better indicator of egg and larval transport. Clearly, pigment concentrations also indicate the relative food availability for first-feeding larvae.

A pattern in the satellite image of sea-surface color is quite similar to that observed in surface temperature (Figure 2), suggesting that the circulation pattern extends down through at least the surface layers. Figueroa and Robles (1987) have shown evidence that the surface patterns are part of a deep baroclinic circulation that may extend to the bottom of the gulf. That the coolest water shows the highest pigment concentration indicates that upwelled, nutrient-rich water from the eastern coast of the gulf is carried by the jets, resulting in

higher productivity within the filaments and lower productivity in the surrounding waters.

Temperature and phytoplankton pigment concentration are important measurements to represent the general surface environment. Mean surface temperatures at Guaymas range from about 17.5°C in January to roughly 32°C in August (Cisneros-Mata et al. 1987). Tibby (1937) found the optimum temperature range for Pacific sardine spawning to be between 15° and 18°C for the Pacific coast population. Satellite imagery shows that the surface temperatures on April 7, 1980, ranged from approximately 16° to 19°C (Figure 2). Although typical chlorophyll a concentrations have not been reported for the Gulf of California, an average concentration of approximately 5.6 mg chlorophyll a m^{-3} was found near Guaymas in March 1983 during the 1983–84 El Niño event (estimated from vertical profiles in Valdez–Holguin 1986); the depth of maximum chlorophyll a concentration at this station was about 17 m. A year later, during March 1984, the average concentration was approximately 1.8 mg chlorophyll a m^{-3}, and the depth of maximum chlorophyll concentration was about 60 m, below the depth of 1% surface irradiance. Average surface-layer chlorophyll-like pigment concentrations as determined by satellite imagery ranged from approximately 0.5 to 3.0 mg chlorophyll a + phaeopigments m^{-3}; very near the coast, over 6.0 mg chlorophyll a + phaeopigments m^{-3} were found (Figure 2).

DISCUSSION

The observation of Pacific sardine spawning in the Gulf of California in areas of intense upwelling is quite different from the spawning of pelagic fishes in the California Current. Parrish et al. (1981) suggested that northern anchovy avoid spawning in strong upwelling areas to prevent their eggs and larvae from being transported offshore. Smith and Lasker (1978) wrote that the effect of upwelling should favor northern anchovy adults but would be detrimental to their embryos and larvae. In the gulf, the Pacific sardine seem to spawn preferentially in these areas to enhance the cross-gulf transport of their eggs and larvae. Of course, this does not simply move them offshore, as would be the case in the California Current, but takes them to the western shore. Satellite imagery suggests that eggs and larvae are entrained in cross-gulf squirts and are transported to the west along with high-productivity water. Similar offshore entrainment for eggs and larvae has been described by Fiedler (1986) for the northern anchovy in the
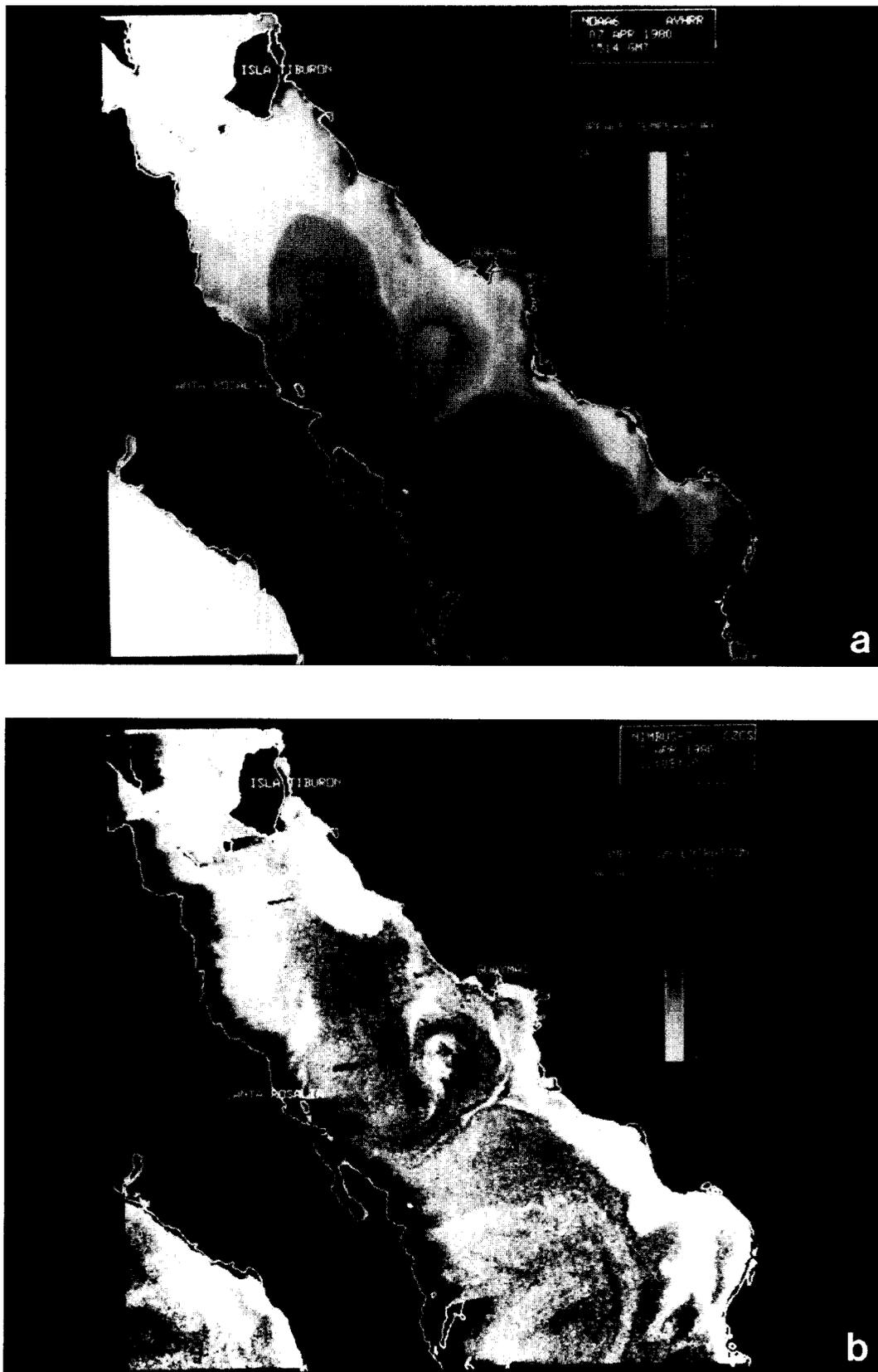
Figure 2. Satellite images of the central Gulf of California on April 7, 1980. *a*. A portion of Figure 1*a* calibrated to derive surface temperature. *b*. The corresponding NIMBUS-7 Coastal Zone Color Scanner image showing the distribution of chlorophyll-like pigments, corresponding markedly to the pattern of surface temperature shown in *a*.

California Current, but this is not a normal occurrence.

Although the estimated distribution and abundance of Pacific sardine eggs and larvae in the Gulf of California during 1956–57 (Moser et al. 1974) did not reflect the surface patterns in temperature and chlorophyll *a* content shown by satellite imagery, or the pattern of transport proposed by Sokolov (1974), the spatial scale of the stations was too coarse to detect such directed transport. The surface jets seen in the satellite images were also not observed in the surface geostrophic flows (Rosas-Cota 1977) calculated from data collected from the same cruises in which Moser et al. (1974) sampled the ichthyoplankton. This emphasizes that satellite imagery is very important to adequately define the surface structure of the ecosystem over the temporal and spatial scales that are meaningful to the Pacific sardine. Additional habitat and ichthyoplankton survey data would also greatly help in this regard.

Larval mortality may also be affected by variability in surface conditions. Increased pigment concentrations in the jets suggest an increased food supply. Nevertheless, food may not be limiting outside the jets. Butler (1987) has shown that for larval northern anchovy, the growth rate was not affected by the low food availability that occurred with the 1983 El Niño event. For the northern anchovy population on the Pacific coast, the 1982–83 El Niño did, however, greatly affect the growth rate of juveniles (Fiedler et al. 1986; Butler 1987).

Most fishing effort for the Pacific sardine in the Gulf of California occurs near the eastern coast, principally offshore of the port of Guaymas. Data for the period 1969–80 show that interannual variation in the landings and catch-per-unit-effort (CPUE) of Pacific sardine are correlated with the El Niño/Southern Oscillation (ENSO) phenomena; during El Niño events, the landings and CPUE decreased. The reverse was found to be the case for the more tropical *Opisthonema* spp. (Huato-Soberanis and Lluch-Belda 1987). Lluch-Belda et al. (1986) proposed that fluctuations in Pacific sardine catches can be explained almost entirely by temperature-induced fluctuations in their availability. Under cooler, more temperate conditions during anti-El Niño years, the Pacific sardine can move farther south for a longer period and thus be available to the fishery for more time over a larger area, resulting in increased landings. If this is true, variation in current fishery landings for Pacific sardine in the Gulf of California may not reflect recruitment variation.

Since 1977, larger boats with greater range have been added to the sardine fleet in the Gulf of California; these vessels have the capability to fish where Pacific sardine are available. This has tended to reduce the correlation between the ENSO anomalies and Pacific sardine catch and CPUE; the catch of the smaller, limited-range vessels may still reflect this relation, however. This relation may also be due to changes in recruitment to the stock or to changes in the stock's availability to the fleet. Cisneros-Mata et al. (1987) have reported that the Pacific sardine population in the gulf is beginning to show signs of overexploitation (e.g., reduction in average age and length in the fishery). Huato-Soberanis and Lluch-Belda (1987) suggested that 5+ year cycles in mean sea level and mean surface temperature associated with the El Niño-Southern Oscillation are reflected in stock recruitment, as suggested by a similar cycle in the average length of commercially landed sardines. Nevertheless, one cannot escape the disadvantage of working with spatiotemporally selective commercial landings.

At present, the rate of Pacific sardine recruitment in the Gulf of California is not known. If decreased landings and CPUE during El Niño events, for example, are in part due to a decrease in recruitment, one could suggest the following: with the northern penetration of tropical, warm surface waters during an ENSO event (Baumgartner and Christensen 1985; Robles and Marinone 1987), the spawning area of the Pacific sardine in the gulf will be confined to the cool waters in the north, and thus be compressed. Furthermore, the nursery areas of the larvae and juveniles will be compressed northward. Santander and Flores (1983) also described similar adjustments in the distribution of spawning of both anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) with El Niño conditions off Peru.

Although food concentrations in the gulf are very high, an increased population density in a decreased habitat area may cause food to limit growth or fecundity. Butler (1987) showed that limiting food resources for juvenile northern anchovy greatly affects their growth rate and may increase their mortality. Also, when juveniles and adults coexist with eggs and larvae, cannibalism and predation of eggs and larvae by other species may increase in importance. The potential of egg and larval cannibalism as a density-dependent mechanism to control the populations of northern anchovy (Hunter and Kimbrell 1980) and Peruvian anchovy (Santander et al. 1983; Alheit 1987) has

been clearly demonstrated. Typically, the adult migration of the Pacific sardine separates them from their eggs and larvae. Under compressed habitat conditions, as may occur with an El Niño event, they may continue to coexist.

Although cannibalism has not been reported for the Pacific sardine, it is unlikely that they would be capable of selecting against their eggs and larvae in the particulate food field. For Pacific sardine in the Gulf of California, Wong-Rios (1974) reported the occurrence of unidentified fish eggs in the stomach contents of over 25% of those analyzed. Off Peru, individual sardines were reported to consume three times the number of anchovy eggs compared to individual adult anchovies, and the degree of consumption was related to the abundance of eggs in the water (Santander et al. 1983). On a per-weight basis, Alheit (1987) found that sardines were more efficient at consuming eggs than anchovy. Therefore, the potential for cannibalism in Pacific sardine in the Gulf of California under compressed habitat conditions is very high. Mechanisms like those described here may partly explain the relation between ENSO conditions and Pacific sardine landings as recruitment becomes more important than adult availability to the fleet in the future.

CONCLUSIONS

We have shown that the general pattern of migration for the Pacific sardine in the Gulf of California proposed by Sokolov and Wong-Rios (1973) and Sokolov (1974) is consistent with the seasonal changes in near-surface temperature and circulation. We have also suggested a mechanism by which interannual variations in recruitment may be related to the occurrence and strength of El Niño/Southern Oscillation events. Nevertheless, these hypotheses imply various assumptions that must be tested.

First, because most information on the adult spawning area is derived from gonad analysis of fishery-caught animals, it is not known if adults spawn where the fleet does not fish; when sardines are available near the port of Guaymas, the vessels do not search farther. Second, the relation between mesoscale oceanographic structures like the cross-gulf jets and eddies shown here, and egg and larval transport has not been verified by ichthyoplankton collections; samples taken on more meaningful time-and-space scales are necessary. Third, it is not known how often the cross-gulf jets that coincide with the spawning season of the Pacific sardine occur in the Gulf of California. Serial

analysis of satellite images will allow us to better describe the temporal as well as the spatial spawning habitat. Finally, our discussion here has ignored the importance of competition with or predation by other pelagic species in the environment. Butler (1987) described important interactions between the Pacific sardine and the northern anchovy in the California Current; northern anchovy has been recently reported in the Gulf of California (Hammann and Cisneros-Mata, in press), but its ecological role in the gulf is still not clear.

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