THE CALCOFI ICHTHYOPLANKTON TIME SERIES: POTENTIAL CONTRIBUTIONS TO THE MANAGEMENT OF ROCKY-SHORE FISHES

H. GEOFFREY MOSER, RICHARD L. CHARTER,

WILLIAM WATSON, DAVID A. AMBROSE Southwest Fisheries Science Center National Marine Fisheries Service P.O. Box 271 La Jolla, California 92038 Geoff.Moser@noaa.gov KEVIN T. HILL California Department of Fish and Game Southwest Fisheries Science Center 8604 La Jolla Shores Drive La Jolla, California 92037 PAUL E. SMITH, JOHN L. BUTLER, ELAINE M. SANDKNOP, SHARON R. CHARTER

Southwest Fisheries Science Center National Marine Fisheries Service P.O. Box 271 La Jolla, California 92038

ABSTRACT

Harvest of nearshore fishes off California, particularly species in the recently expanded live-fish fishery, has impacted many of these stocks. Important taxa are cabezon, sheephead, lingcod, greenlings, and the rockfishes included in the subgenus Pteropodus. Life-history information and fishery-independent abundance indices are badly needed for the development of management strategies for these stocks. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys can provide indices of abundance for larval stages of many species, including cabezon, sheephead, kelp and sand basses, lingcod, and several species of rockfishes. This paper presents, as examples, data on the distribution and abundance of cabezon, sheephead, and Paralabrax (kelp and sand bass) larvae in the Southern California Bight region and compares these with data from other nearshore ichthyoplankton surveys conducted in the region. Trends in landings for cabezon generally match trends in CalCOFI larval indices, supporting use of the larval catch data as fishery-independent abundance indices. The principal recommendation for improving nearshore larval time series is to reestablish plankton tow stations on CalCOFI survey cruises off central California, where standard plankton tows have not been taken since the survey area was reduced in 1985.

INTRODUCTION

The decline of West Coast rockfish (*Sebastes*) populations over the past several decades has left many stocks at dangerously low levels (Ralston 1998). Nowhere is this more evident than in the California trawl fishery, once dominated by bocaccio (*S. paucispinis*), a species that now is in rebuilding status (Ralston et al. 1996; MacCall et al. 1999). The contribution of recreational fisheries to the present condition of rockfish stocks is demonstrated by the severely depleted cowcod (*S. levis*), a species highly prized by both commercial and recreational fisheries. It, too, is in rebuilding status and has become a foundation species for new protective regulations in rockfish management (Butler et al. 1999). During the past decade, the growing popularity of the live-fish restaurant trade has produced a highly focused nearshore fishery that targets rockfishes of the subgenus *Pteropodus* (e.g., copper, grass, gopher, brown, and kelp rockfishes) and other associated shallow-water reef fishes (e.g., cabezon, greenlings, lingcod, sheephead). The impact of this fishery is superimposed on long-standing commercial and recreational fisheries for these species. Harvest of these nearshore stocks has progressed at a rate that may place them in the same status as those in deeperwater habitats (Pattison and Vejar 2000). Other key species in the nearshore environment are kelp and barred sand bass (*Paralabrax clathratus* and *P. nebulifer*), nonmarket species that have been mainstays of private and commercial sport fisheries in southern California.

The state of California has new responsibilities to manage and conserve nearshore fish species and their habitats. Among the most valuable assets for such stock assessments are long-term fishery-independent indices that originate well before the expansion of the fisheries and encompass the major shifts in ocean climate associated with the history of the fishery. The 51-year-long ichthyoplankton time series from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys provides such indices of abundance for larval stages of many species.

Although a primary objective of CalCOFI was to determine the cause for the decline of the Pacific sardine (Sardinops sagax) in the middle of the last century, CalCOFI data have been central to our understanding of population processes of a large array of marine organisms, from phytoplankton to mammals. CalCOFI has played an important role in the successful management of northern anchovy (Smith 1972; Lasker 1985) and Pacific sardine, which has rebounded dramatically during the past 20 years (Wolf 1992; Hill et al. 1999). Although CalCOFI surveys were designed to encompass the widespread open-ocean spawning of Pacific sardine, it is a surprising fact that trends in larval abundance of nearshore species in CalCOFI collections usually track changes in abundance of adults quite well, even when a species is greatly undersampled due to the offshore emphasis of the CalCOFI sampling pattern (Ralston et al. 1996;

[[]Manuscript received 15 February 2001.]

Butler et al. 1999). In addition to indices of larval abundance, the CalCOFI ichthyoplankton time series can provide valuable information on spawning seasons and temperatures as well as larval dispersion and mortality.

The objectives of this paper are to present current and potential contributions of the CalCOFI ichthyoplankton time series to nearshore fish management and ecology, and to compare CalCOFI larval indices with other available larval fish time series for this region. We examine trends in larval abundance of cabezon and sheephead, two important species currently under exploitation by the live-fish fishery, and kelp and barred sand bass, important nonmarket sport fishes, and then compare these with trends in the Southern California Bight (SCB) time series of the Natural History Museum of Los Angeles County (LACM) and MEC Analytical Systems (MEC), and with trends at Diablo Canyon off central California, monitored by Tenera Environmental Services (Tenera). Lastly, we consider how nearshore surveys could be augmented to produce more useful indices, and we discuss more costly methodologies, such as larval and egg production estimation techniques, that could provide direct measures of absolute fish abundance.

METHODS

Initially, CalCOFI conducted monthly surveys over a large portion of the California Current region from northern California to the tip of Baja California, Mexico—the spawning range of the Pacific sardine during the first decade of the CalCOFI program (see survey map on the inside back cover of this volume). Areal and temporal coverage contracted over subsequent decades; since 1985, the surveys have been limited to a pattern of 66 stations in the SCB region (Hewitt 1988; Moser et al. 1993, 1994). The Southern California Bight has been the most frequently occupied region of the overall CalCOFI survey pattern.

The oblique net tow time series for the species treated in this paper comprises 11,924 tows taken on 243 cruises during 1951–2000 within the boundaries of the present CalCOFI survey. These include all standard oblique CalCOFI survey tows taken since 1985, when occupancy of the present pattern was initiated. Oblique tows used prior to 1985 are a subset from the wider-ranging CalCOFI surveys (Hewitt 1988; Moser et al. 1993, 1994). On surveys prior to 1985 in the Southern California Bight, nearshore stations did not always correspond to the exact positions of the 66 nominal stations used on surveys since 1985. In order to expedite the construction of distribution maps, we assigned data for stations other than the nominal stations of the present pattern to the closest of the 66 nominal stations. Calculations for occurrence (proportion of positive tows) and abundance (larvae per 10 m² surface area) were consistent with procedures used in Moser et al. 2001. For these calculations, station 60 on each of the current CalCOFI lines defines the outer margin of the continental borderland and the Southern California Bight region; the SCB region includes line 77 (fig. 1), even though that line is north of Point Conception. Station 70 was used as the outer boundary for calculating occurrence of cabezon larvae because they were distributed farther off-shore than sheephead and *Paralabrax* spp. larvae (Moser et al. 2001).

The basic plankton tow methodology for oblique tows and sample handling were consistent throughout the time series (Kramer et al. 1972; Smith and Richardson 1977; Moser et al. 1993, 1994). Neuston tows have been taken at each station on all CalCOFI survey cruises since 1978 with a manta net (Brown and Cheng 1981; Moser, Charter, Reilly et al. 2000). Hauls were made at a ship speed of 1.0–2.0 knots for 15 minutes, except in 1978 when tow duration was 3 minutes. The manta net time series for the species in this paper includes 4,733 tows taken on 88 cruises.

Data were available from LACM and MEC surveys, conducted over shelf areas of the SCB in the years between 1978 and 1986, and from Tenera surveys conducted at the Diablo Canyon power plant in central California from 1990 to the present. With minor exceptions, gear and tow methodology used by LACM, MEC, and Tenera were similar to those of CalCOFI. The MEC oblique tows were taken in 30-second steps, but equivalent volumes of water were filtered for all portions of the water column. Surface tows taken by Tenera within the intake bay at Diablo Canyon employed a 0.5 m ring net towed just below the surface on the same transect on a weekly basis.¹

RESULTS

Demersal Habitats in the SCB

The inner third of the present CalCOFI survey pattern overlies the continental borderland of southern California, a region of complex topography that includes the mainland continental shelf and slope, deep-water basins, and numerous islands and banks and their shelves and slopes (fig. 1). The islands and banks extend coastal habitats >100 nmi offshore, and the basins provide deepwater habitats and zoogeographic refugia for many midwater species. Point Conception forms the zoogeographic boundary between the Oregonian shore fauna to the north and the San Diegan fauna, which extends southward to about Magdalena Bay, Baja California Sur,

¹Tenera Environmental Services. 2000. Diablo Canyon Power Plant, 316(b) demonstration report. Prepared for Pacific Gas and Electric Company. San Francisco, Calif.



Figure 1. Bathymetry of the nearshore part of the current CalCOFI survey pattern, showing total bottom areas of shelf and upper slope for the region within the Southern California Bight. Shelf (0–200 m), medium shading; upper slope (200–500 m), dark shading; deeper isobaths, 1,000 m and 2,000 m. Station locations are shown as circles; on each survey line station 60 is denoted by a filled circle.

Mexico. The offshore region of the continental borderland has 40% more shelf habitat and more than twice as much upper slope habitat than the mainland coast (fig. 1). The Santa Rosa–Cortez Ridge represents essentially a second coastline equivalent in shelf and slope area to the mainland coast. Because of this, most CalCOFI stations in the SCB, out to station 60, are near sources of rocky-shore fish larvae (fig. 1). Although only ~30% of the stations in the present survey pattern are over or adjacent to the continental shelf or upper slope, the circulation pattern over the SCB (see below) favors the dispersal of larvae from nearshore habitats to regions well seaward of their origins.

The topographic complexity of the continental borderland is matched by its complex hydrography. The coastal jet of the California Current courses equatorward along the central California coast, sweeps around Point Conception, and continues along the outer margin of the continental borderland; a coastward branch of the current turns poleward to form the Southern California Eddy, centered on the outer Channel Islands (Lynn and Simpson 1987). The inshore poleward component of the eddy circulation is augmented seasonally

and episodically by the Inshore Countercurrent flowing from Baja California. Another major feature is the extensive undercurrent that flows poleward at slope depths over the borderland (Lynn and Simpson 1990). Surface waters overlying the continental borderland are richer than the relatively more oligotrophic offshore waters as a result of seasonal coastal upwelling and the complex pattern of mesoscale circulation (Hayward and Venrick 1998). Three oceanic water masses (Subarctic, Pacific Central, and equatorial water of the eastern tropical Pacific) converge in the SCB region, where complexity is heightened by a field of mesoscale eddies that extends from the inner margin of the California Current into the SCB, and by a persistent frontal zone (Ensenada Front) at the southwest corner of the bight (Lynn and Simpson 1987; Haury et al. 1993).

Rocky-Shore Species in the CalCOFI Time Series

The larvae of rocky-shore fishes are an important, although not numerically dominant, part of the ichthyoplankton in CalCOFI samples. In oblique plankton tows, coastal pelagic fish larvae are the dominant cate-

TABLE 1
Taxonomic Composition and Relative Abundance (Percentage of Total Abundance) of Larval Fish Categories
in CalCOFI and LACM Time Series in the Southern California Bight Region

Habitat	CalCOFI		LACM	
	Taxonomic composition (%)	Relative abundance (%)	Taxonomic composition (%)	Relative abundance (%)
Coastal pelagic	4.4	69.7	8.5	72.4
Other pelagic	6.7	0.2	0	0
Midwater	37.7	20.5	10.6	1.4
Rocky substrate	26.3	7.4	45.1	3.5
Soft substrate	24.9	2.2	35.9	22.7

TABLE 2 Larvae of Rocky-Shore Fish Taxa* Identified in CalCOFI Oblique Tow Samples in the Southern California Bight Region, by Overall Abundance

Common name	Scientific name	Rank	Time series
Fisheries species			
Bocaccio	Sebastes paucispinis	22	1951-2000
Cowcod	Sebastes levis	97	1951-2000
Aurora rockfish	Sebastes aurora	47	1951-2000
Kelp and sand bass	Paralabrax spp.	49	1951-2000
Pacific barracuda	Sphyraena argentea	55	1951-2000
Chilipepper	Sebastes goodei	66	1951-1969
Cabezon	Scorpaenichthys marmoratus	86	1951-2000
Sheephead	Semicossyphus pulcher	112	1961-2000
Lingcod	Ophiodon elongatus	184	1951-2000
Other species			
Shortbelly rockfish	Sebastes jordani	9	1951-2000
Señorita	Oxyjulis californica	38	1961-2000
Blacksmith	Chromis punctipinnis	48	1951-2000
Blackeye goby	Coryphopterus nicholsii	68	1985-2000
Mussel blenny	Hypsoblennius jenkinsi	84	1985-2000
Garibaldi	Hypsypops rubicundus	90	1957-2000
Red brotula	Brosmophycis marginata	95	1951-2000
Roughcheek sculpin	Ruscarius creaseri	105	1985-2000
Painted greenling	Oxylebius píctus	107	1951-2000
Rubynose brotula	Cataetyx rubrirostris	129	1985-2000
Bluebanded goby	Lythrypnus dalli	136	1985-2000
Halfmoon	Medialuna californiensis	142	1951-2000
Opaleye	Girella nígricans	146	1951-2000
Deepwater kelpfish	Cryptotrema corallinum	151	1985-2000
Zebra goby	Lythrypnus zebra	158	1985-2000
Blind goby	Typhlogobius californiensis	159	1985-2000
Smoothhead sculpin	Artedius lateralis	160	1985-2000
Rock wrasse	Halichoeres semicinctus	168	1961–2000
Bay blenny	Hypsoblennius gentilis	173	1985-2000
Yellowfin fringehead	Neoclinus stephensae	175	1985-2000
Rough ronquil	Rathbunella alleni	177	1985-2000
Salema	Xenistius californiensis	181	1985-2000
Scalyhead sculpin	Artedius harringtoni	189	1985-2000
Slimy snailfish	Liparis mucosus	190	1985-2000
Padded sculpin	Artedius fenestralis	192	1985-2000

*Limited to taxa with 100 or more total larvae (larvae per 10 m², summed over the time series).

gory, with about 70% of total larvae contributed by only 4% of the total taxa (table 1). Midwater fish larvae have the most taxa (38%) and are second in abundance, with 20% of the total larvae. Rocky-shore fishes contribute about 1/4 of the taxa but represent only 7% of the total larval abundance. In the LACM nearshore larval surveys, bottom fish taxa constitute ~80% of the total taxa (nearly

half the total are rocky-substrate taxa) and, as expected, the larvae of midwater species represent only 11% of the total taxa and ~1% of the total larval abundance. As in the CalCOFI surveys, larvae of coastal pelagic fishes dominate the LACM surveys with >70% of the total abundance contributed by 8.5% of the taxa (table 1). In the LACM surveys, larvae of soft-substrate fishes are ten times more abundant than in CalCOFI surveys.

Although few of the Sebastes larvae taken in CalCOFI samples are identifiable to species, some important species can be identified (table 2). Four of these (bocaccio, cowcod, aurora rockfish, and chilipepper) are heavily exploited. Shortbelly rockfish has the potential to be an important fishery because of a large biomass that may approach a half-million tons (Pearson et al. 1991). Larvae of lingcod, a heavily impacted species, are neustonic and thus not abundant in CalCOFI oblique tows; however, they are a prominent species in CalCOFI manta tows. Pacific barracuda is an important species in recreational fisheries and, as a voracious fish predator, plays an important ecological role in the nearshore habitat. Its larvae are moderately abundant in CalCOFI oblique tows. Although larvae of kelp bass (Paralabrax clathratus) and barred sand bass (P. nebulifer) are not identifiable to species, the time series representing them in aggregate (Paralabrax spp.) may prove to be a useful index. Larvae of spotted sand bass (P. maculatofasciatus) are not differentiable from the other two *Paralabrax* species, but it is unlikely that they are present in CalCOFI samples because they are primarily bay inhabitants. Cabezon and sheephead are important species in nearshore fisheries and are well represented in the CalCOFI time series as well as in the nearshore time series. Abundance trends for larvae of cabezon, sheephead, and *Paralabrax* spp. are described below.

Cabezon. Cabezon are exploited in all nearshore fisheries. The most consistent record is from the commercial passenger fishing vessel (CPFV) catch, beginning in 1936 (fig. 2). Cabezon catch rose rapidly after WWII to a peak in 1956 and then showed a trend of irregular decline. Catch was distinctly seasonal, with a minimum during winter months and then a steady increase to a summer peak.



Figure 2. Total catch (numbers of fish) of cabezon from commercial passenger fishing vessels off California by year (*above*) and month (*below*); from database described in Hill and Schneider 1999.

Highest average abundance of cabezon larvae in oblique tows is at CalCOFI survey stations north of Point Conception and in the northern sector of the SCB (fig. 3). This reflects the more northerly distribution of this wide-ranging (central Baja California to southeast Alaska) species, whose population center appears to be off northern California (O'Connell 1953; Doyle 1992a, b; Moser et al. 1993). Although highest average abundances were at stations over the shelf or upper slope, about half of the positive stations were over deep water (fig. 3). Abundance was relatively high at stations well offshore of Point Conception, and transport of cabezon larvae into the SCB from the north probably is affected by variation in the speed and degree of offshore divergence of the California Current in the Point Conception region. The pattern of distribution and abundance of cabezon larvae in manta tows in the SCB was similar to the pattern for oblique tows, except that average abundance was approximately five times higher in manta samples (fig. 4). In contrast to oblique tows, average abundance in manta tows was consistently as high at stations in the northern sector of the SCB as at stations north of Point Conception.

Time series of occurrence of cabezon larvae in oblique tows show a generally decreasing trend since the 1950s,



Figure 3. Average abundance of cabezon larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region, 1951–2000.



Figure 4. Average abundance of cabezon larvae in manta tows at CalCOFI survey stations in the Southern California Bight region, 1978–2000.



Figure 5. Occurrence (proportion of positive tows) of cabezon larvae in CalCOFI oblique tows in the Southern California Bight region, 1951–2000. Dashed line indicates the period of triennial surveys.

with an approximately decadal cycle of high and low occurrence (fig. 5). Generally, occurrence peaked during cold episodes (1954–56, 1963–65, 1972–75, 1988–89, 1999), with the peaks tending to be progressively lower through the time series. Low occurrence was generally associated with years within warm episodes (e.g., 1957–59, 1978–81, 1997). The trends in larval occurrence match the trends in CPFV landings fairly closely. Average oc-



Figure 6. Occurrence (proportion of positive tows) of cabezon larvae in CalCOFI manta tows in the Southern California Bight region, 1978–2000. Dashed line indicates the period of triennial surveys.

currences of cabezon larvae in manta tows for the years 1978–2000 are in general agreement with occurrences in oblique tows for that segment of the time series (fig. 6). Cabezon larvae are well represented in surface samples taken by Tenera at the intake bay for the power generating plant at Diablo Canyon (fig. 7). Occurrence declined during the years 1990–98 and is in general agreement with CalCOFI oblique and manta tow time



Figure 7. Occurrence (proportion of positive tows) of cabezon larvae in CalCOFI manta and oblique tows in the Southern California Bight region, 1990–2000, compared with occurrence of cabezon larvae in surface tows taken by Tenera Environmental Services at the intake bay of the Diablo Canyon power station, 1990–1998.



Figure 8. Occurrence (proportion of positive tows) of cabezon larvae in CalCOFI manta tows in the Southern California Bight region compared with occurrence of cabezon larvae in manta tows taken by MEC Analytical Systems off San Onofre, 1978–1986. Dashed line indicates the period of triennial surveys.

series during those years, although the minimum occurrence (~0.2 in 1993) was only slightly less than the proportion of positive tows in the year of highest average annual occurrence (1999) in CalCOFI manta tows. The trend for occurrence in CalCOFI oblique tows from the entire continental borderland closely matched the trend for surface tows at Diablo Canyon but was approximately tenfold lower (fig. 7). Within the SCB, occurrence of cabezon larvae in manta tows taken by MEC over the shelf at San Onofre shows an irregularly decreasing trend from 1978 to 1986 (fig. 8). Occurrence of cabezon larvae in CalCOFI manta tows over the entire continental borderland during that period was on the same scale; however, a year-to-year comparison of the two time series is precluded because of the missing years between CalCOFI triennial surveys. Cabezon larvae were too rare in LACM manta tows over the shelf in the central SCB to permit comparison with MEC and CalCOFI tows.



Figure 9. Total catch (numbers of fish) of sheephead from commercial passenger fishing vessels off California by year (*above*) and month (*below*); from database described in Hill and Schneider 1999.



Figure 10. Occurrence (proportion of positive tows) of sheephead larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region, 1961–2000. Dashed line indicates the period of triennial surveys.

Sheephead. Sheephead, like cabezon, are exploited by all nearshore fisheries. Commercial party vessel catch was stable from 1945 to the early 1960s, when it doubled (fig. 9). After 1966 it declined irregularly and more



Figure 11. Average abundance of sheephead larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region, 1977–2000 (1998 excluded).



Figure 12. Average abundance of sheephead larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region in 1998.

gradually than the cabezon CPFV catch. Like cabezon, the sheephead catch peaked during summer and early fall (fig. 9).

Identification of sheephead larvae in CalCOFI ichthyoplankton time series began in 1961. Peak occurrence of sheephead larvae in oblique tows in 1965 was followed by an abrupt decline in 1966 and 1969, and larvae were absent from the SCB during the prolonged cold episode of the early 1970s (fig. 10). The increase in 1981 corresponds to generally warm ocean conditions in the early to mid 1980s. The abrupt increase in larval occurrence in 1998 may represent an increase in transport of larvae northward from Baja California by the unusually strong Inshore Countercurrent generated during the 1997–98 El Niño. This is demonstrated by the distribution of sheephead larvae in the SCB during 1977-2000 (except 1998; fig. 11) compared to the distribution during 1998 (fig. 12). The general pattern is similar in both maps, with positive stations close to the mainland shore in the southern and northern sectors of the SCB and some positive stations offshore in the southern region of the SCB. Average abundance, however, was three times higher during the 1997-98 El Niño, and occurrence was consistently higher in the southern sector of the SCB compared with the 1977-2000 period. If we look at occurrence of sheephead larvae on individual CalCOFI cruises in the SCB during El Niño we see that larvae were absent until the summer cruise of 1998 and then peaked at >20% positive tows in the fall cruise of 1998 (fig. 13). Lynn and Bograd (in press) show that poleward transport measured on CalCOFI cruise 9711 was the largest ever documented in the entire CalCOFI time series (fig. 13). This and the much smaller transport event of summer 1998 may have contributed to the relatively high occurrence in the fall of 1998 (figs. 12 and 13).

A more direct response to the anomalously strong Inshore Countercurrent of 1997–98 was shown by the larvae of Diogenes lanternfish (Diogenichthys laternatus), an eastern tropical Pacific species, whose average occurrence in the SCB was six times higher in 1998 than in the highest previous year in the time series (fig. 14). The proportion of positive tows began to increase in the summer of 1997, reaching a peak of >30% positive tows in February 1998 (fig. 13). Approximately 23% of the total occurrences and 40% of the total larvae of this species in the entire CalCOFI time series from the present survey pattern were taken on this cruise. The sudden decrease in April was followed by another less spectacular increase in the fall cruise of 1998 and then a return to no occurrences in subsequent cruises. These transport events brought D. laternatus larvae to the SCB from waters off Baja California. The tropical affinity of D. laternatus is clearly shown in a map of larval abundance in the SCB (1998 excluded), where there are no



Figure 13. Occurrence (proportion of positive tows) of larvae of sheephead and Diogenes lanternfish (*Diogenichthys laternatus*) on CalCOFI cruises 9702 through 9904. Values for *D. laternatus* were calculated from all stations within the current CalCOFI survey. Shaded area indicates total transport (million m³/sec) of water by the Inshore Countercurrent from cruise 9702 to 9809 (data provided by Ronald Lynn, SWFSC, from Lynn and Bograd, in press).



Figure 14. Occurrence (proportion of positive tows) of *Diogenichthys laternatus* larvae in oblique tows in CalCOFI surveys, 1951–2000. Dashed line indicates the period of triennial surveys.

occurrences north of CalCOFI line 87 (fig. 15) and average abundance is comparatively low over the continental borderland. In 1998 abundances were extremely high in coastal stations, where the Inshore Countercurrent was strongest and larvae were advected as far north as line 77, north of Point Conception (fig. 16).

Occurrence of sheephead larvae in oblique tows taken over the continental shelf in the SCB by LACM and MEC during 1978–86 follow similar trends, with the highest proportion of positive tows in 1979 and 1982 (fig. 17). Occurrence of sheephead larvae in CalCOFI oblique tows over the entire continental borderland during that period was on the same scale; however, years of



Figure 15. Average abundance of *Diogenichthys laternatus* larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region, 1951–2000 (1998 excluded).



Figure 16. Average abundance of *Diogenichthys laternatus* larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region in 1998.



Figure 17. Occurrence (proportion of positive tows) of sheephead larvae in CalCOFI oblique tows in the Southern California Bight region compared with occurrence of sheephead larvae in oblique tows taken over the shelf by MEC Analytical Systems off San Onofre, 1978–1986, and by the Natural History Museum of Los Angeles County (LACM) in the central region of the Southern California Bight. Dashed segment of CalCOFI line indicates the period of triennial surveys



Figure 18. Total catch (numbers of fish) of kelp bass from commercial passenger fishing vessels off California by year (*above*) and month (*below*); from database described in Hill and Schneider 1999.

relatively high occurrence of sheephead larvae in the LACM and MEC time series (1979 and 1982) were not sampled by the triennial CalCOFI surveys.

Paralabrax spp. Kelp and barred sand bass are exploited primarily by private and commercial recreational fish-



Figure 19. Total catch (numbers of fish) of barred sand bass from commercial passenger fishing vessels off California by year (*above*) and month (*below*); from database described in Hill and Schneider 1999.

eries. Trends for CPFV catches are strikingly different for these two species in the SCB (figs. 18 and 19). In the decade following WWII kelp bass catch was approximately three times greater than during the prewar period, and then doubled in the early 1960s, peaking at >1.2 million fish in 1966. Catch declined abruptly in the early 1970s to between 200,000 and 400,000 fish, with a trend of gradual decline to the present (fig. 18). Barred sand bass showed low catches until 1970, when the catch increased to a peak of >700,000 fish in 2000 (fig. 19). It appears that the two species have a compensatory catch history, with barred sand bass becoming targeted after the decline of kelp bass. Catch for both species peaks in July, but high catches of sand bass are restricted to summer months, whereas catches of kelp bass are relatively high from May to September (figs. 18 and 19).

The highest average abundance of *Paralabrax* spp. larvae in oblique tows typically was at the most nearshore station of survey lines within the SCB (fig. 20). On the three southernmost lines (87, 90, 93) abundance on the most nearshore station was 3–5 times greater than on the adjacent seaward station; however, abundance at the most nearshore station of line 83 was slightly lower than on the adjacent station. Except for stations associated



Figure 20. Average abundance of *Paralabrax* spp. larvae in oblique tows at CalCOFI survey stations in the Southern California Bight region, 1963–2000.

with offshore islands, abundance declined sharply seaward of the two most nearshore stations on each line. Average abundance was comparatively low at nearshore stations on the northernmost survey lines (77 and 80), reflecting the warm-water affinity of the genus (fig. 20).

Time series of occurrence of *Paralabrax* spp. larvae in oblique tows showed a series of decadal oscillations since 1963, with a pronounced decline from 1989 to 1995 and a generally decreasing trend for the available time series (fig. 21). The trend for incidence of Paralabrax spp. larvae is not directly comparable to the CPFV time series of the separate species since catches of kelp and sand bass follow opposite courses and appear to be compensatory; however, it is probable that the sand bass catch, like the kelp bass catch, will eventually decline with continued fishing pressure. Moreover, the trend for Paralabrax spp. larvae is similar to the CPFV trend for the numerically dominant kelp bass and may be a useful index of general population health for the genus. Occurrence of Paralabrax spp. larvae in CalCOFI oblique tows taken over the borderland and in MEC oblique tows taken over the continental shelf during 1978-86 followed similar trends (fig. 22). Occurrences in MEC tows showed



Figure 21. Occurrence (proportion of positive tows) of *Paralabrax* spp. larvae in CalCOFI oblique tows in the Southern California Bight region, 1963–2000. Dashed line indicates the period of triennial surveys.

a dome-shaped curve with highest values during 1982 and 1983. These years were not sampled by the triennial CalCOFI surveys, but the general agreement of values for years sampled by both surveys suggests that the MEC data could be used to estimate missing data in CalCOFI time series of *Paralabrax* larvae.



Figure 22. Occurrence (proportion of positive tows) of *Paralabrax* spp. larvae in CalCOFI oblique tows in the Southern California Bight region compared with their occurrence in oblique tows taken by MEC Analytical Systems off San Onofre, 1978–1986. Dashed segment of CalCOFI line indicates the period of triennial surveys.

DISCUSSION

Estimation of the size of marine fish populations by quantitative sampling of their larvae has become a useful tool in fishery management (Hunter and Lo 1993) despite the sources of potential imprecision inherent in this approach (Hauser and Sissenwine 1991). The daily egg production method provides a more direct means of estimating biomass and reduces the number of assumptions required in larval techniques (Lasker 1985; Hunter and Lo 1993); however, the method is relatively costly and is most useful for pelagic spawners. A modification of the technique, the daily fecundity reduction method, has proven useful for demersal spawners (Lo et al. 1992, 1993).

The value of indices of larval abundance or occurrence is dependent on the duration and sampling intensity of the time series from which they are derived. The CalCOFI surveys, designed for prolific, wide-ranging, pelagic spawners with dynamic life-history characteristics, have comparatively low sampling intensity in coastal regions. Nonetheless, larval indices of commonly occurring demersal species, derived from CalCOFI surveys, have proven to be effective means of tuning biomass models based on age-structured fisheries catch data. Formal population assessments of bocaccio and cowcod, incorporating CalCOFI larval abundance indices, have resulted in new harvest regulations by the Pacific Fisheries Management Council (PFMC) and the California Department of Fish and Game (CDFG) that are designed to conserve and rebuild these stocks (Ralston et al. 1996; Butler et al. 1999). Larval indices of rocky-shore species with less commonly occurring larvae may prove equally useful in developing management strategies. A formal population assessment of cabezon, planned for 2001, will rely on larval indices from CalCOFI time series for fishery-independent population trends, and a future assessment of sheephead is equally feasible. Catch curves for cabezon generally match trends in CalCOFI larval indices, supporting use of the larval catch data as fisheryindependent abundance indices.

How could CalCOFI larval indices be improved? Enhancing our ability to identify the larvae of nearshore rockfish species would be an important advance, particularly for species in the subgenus *Pteropodus*. This has proven difficult in the past because of the similarity of larval morphology and pigment patterns. The pigment pattern of Pteropodus larvae off central and southern California may be sufficiently distinct from patterns in larvae of co-occurring Sebastes species to permit identification to subgenus (Watson and Robertson, manuscript in prep.). Development of a time series of larval abundance of Pteropodus from reexamination of specimens in the archived CalCOFI ichthyoplankton collection would be useful but would require a large investment of effort and time. Direct identification of individual Pteropodus larvae by genetic markers is equally labor-intensive (Cynthia Taylor, pers. comm.). Ethanolpreserved samples from oblique tows taken on CalCOFI survey cruises over the past several years provide a means to genetically determine the extent that Pteropodus larvae occur in CalCOFI samples and the proportion of various species of the subgenus that may occur from year to year. This information could be used in combination with aggregate indices of Pteropodus larvae from CalCOFI archives to estimate historical changes in the abundances of individual Pteropodus species. Similarly, genetic identification of larvae of Paralabrax species from recent cruises could improve the CalCOFI time series of kelp and sand bass larvae.

An immediate improvement of the nearshore CalCOFI ichthyoplankton time series would be to reestablish plankton tows on CalCOFI survey cruises off central California north of line 77, the only line north of Point Conception on which standard plankton tows have been taken since the survey area was reduced in 1985 (see map of overall CalCOFI survey pattern on inside back cover of this volume). Prior to 1985, central California was surveyed, usually north to Point Arena (line 60), on approximately 60% of the CalCOFI cruises from 1951 to 1984. Since 1997, winter and spring CalCOFI surveys have occupied lines 60, 63, 67, and 70 off central California, taking continuous underway pump samples to measure sardine egg abundance. With one to two extra days of ship time, bongo and manta samples could be taken at the 18 historical stations on these lines out to, and including, station 60. Reestablishment of these net tow stations would permit comparison of current larval indices of rocky shore species with historical CalCOFI indices prior to 1985 and would provide information critical to the management of nearshore fishes. Ideally, net tow stations could be added

seaward of station 60 off central California if resources and research vessel time were to become available.

Would we improve our ability to assess nearshore fish populations by increasing the number of nearshore plankton tows on CalCOFI surveys within the SCB? Larval trends based on the present survey pattern have been adequate for formal PFMC biomass assessments of deepwater rockfish species (Ralston et al. 1996; Butler et al. 1999); however, species whose larvae remain close to shore may not be adequately sampled by the present CalCOFI survey pattern.

Average larval abundance of *Paralabrax* spp. was consistently low from the beginning of the time series until 1963, when nearshore net tow stations were added to the survey pattern, about a dozen on survey lines within the SCB. *Paralabrax* spp. larvae occur primarily in nearshore waters (fig. 20), and their low abundance prior to 1963, as well as the comparison with the MEC collections over the shelf, reflects inadequate sampling of this habitat. The larger CalCOFI catches since 1963 indicate that these larvae are dispersed seaward to some extent from the nearshore spawning sites, so that the seaward end of the larval distribution now falls within the CalCOFI sampling area.

Larval distributions of other important species may be even closer to shore than *Paralabrax* spp., and additional nearshore stations would improve larval indices for these species. Also, additional nearshore stations would improve indices for nearshore species whose larvae are relatively rare on CalCOFI surveys, and would reduce the chances of having zero occurrences for any given year.

Certainly we would need a higher station density to accomplish a biomass assessment of nearshore species based on egg or larval production. For example, during 1990-97, 88 to 124 (average of 112) samples per year were taken in the area of the CalCOFI survey pattern where cabezon larvae occur, during the months when they are present. Incidence of cabezon larvae was low, with the proportion of positive tows typically 0.01 to 0.02 for these years (fig. 5). The number of tows per year would have to be increased to 325-750 (average of 519) to obtain an acceptable coefficient of variation (e.g., CV of proportion positive = 0.4). Thus, a biomass estimate of cabezon based on larval production would require approximately five times as many samples as are presently taken on CalCOFI surveys (Nancy Lo, pers. comm.). Obtaining required age data of the larvae and data on fecundity and age structure of adults would add substantially to the cost of this method of assessment.

The shorter-term nearshore ichthyoplankton time series of LACM, MEC Analytical Systems, and Tenera Environmental Services provide data from shelf waters and are valuable adjuncts to CalCOFI time series. The most recent of these surveys, the sampling program conducted by Tenera at Diablo Canyon, is just north of CalCOFI survey line 77 and proximate to CalCOFI station 77.49. Overall, Tenera took 8,657 tows (898 surface, 4,693 vertical, 3,066 oblique) in the vicinity of the Diablo Canyon power plant. The longest-running and most continuous part of Tenera's sampling program is the series of surface tows taken at weekly intervals at the intake cove at Diablo Canyon.² Fish larvae from these samples have been identified for the years 1990–98, but unsorted samples for 1999 and 2000 could be processed if funding were available. Retrieval of these data from existing samples would be highly cost-effective, as would support to continue this sampling program in the future.

The intensive sampling programs conducted over the SCB shelf by MEC and LACM are valuable complements to CalCOFI survey data. MEC took 3,023 tows (985 surface, 1,044 oblique, 994 epibenthic) at quarterly to weekly intervals on two transects in the San Onofre area from 1978 to 1986. LACM took a total of 2,518 tows (485 surface, 1,648 oblique, 385 epibenthic) between 1978 and 1985, but not all sites were sampled in all years. During 1978–79, the first year of the program, 10 shelf transects encompassing the entire SCB were sampled with a full array of samplers. In the following year, 1979-80, 20 shelf transects spanning the SCB were sampled with oblique tows. These were augmented by surface and epibenthic samples on three transects in the central SCB. During 1982-85 sampling was restricted to oblique tows at 4 shelf transects in the central SCB (off Ormond Beach, Playa Del Rey, Seal Beach, and San Onofre). Thus, the LACM series provides data on a wider selection of sites in the SCB than the MEC time series but is less site-consistent. LACM's synoptic bightwide surveys of 1978-80 are the only such surveys ever taken over the SCB shelf.

Data from these nearshore surveys can be used to fill in missing data from years when CalCOFI surveys were run on a triennial basis. Another important feature of these additional surveys was their comprehensive sampling of the entire water column with surface, oblique, and epibenthic nets. Information on vertical distribution of larval stages resulting from this approach is important in interpreting life-history strategies and in quantitative evaluation of each type of tow. For example, some nearshore species-e.g., white croaker (Genyonemus lineatus), queenfish (Seriphus politus), and other croakersproduce planktonic eggs, but a large fraction of the larvae settles to the epibenthos early in the larval period (Schlotterbeck and Connally 1982; Barnett et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). Undersampling the larvae of these species with oblique tows is further complicated by diel behavior that results

²See footnote 1 on page 113.

in higher concentrations of larvae in the epibenthos during the day than at night (Jahn and Lavenberg 1986). Larvae of another croaker species, white seabass (Atractoscion nobilis), settle to the epibenthos soon after hatching and recruit to submerged drift algae in the subtidal zone (Allen and Franklin 1992). Many nearshore species (e.g., some gobies, cottids) that brood eggs in nests produce larvae that settle to the epibenthos soon after hatching (Barnett et al. 1984; Jahn and Lavenberg 1986) and would be poorly sampled by oblique tows even if the tows reached the epibenthic layer. Marliave (1986) showed that larvae of some cottid, stichaeid, pholid, and gobiesocid species remain within several meters of the rocky shoreline, even at newly hatched stages. They appear to school early in the preflexion stage and have the capacity to maintain their position near rocky substrate features. Other species, including nearshore rockfish species, may be able to maintain proximity to shore, but this has not been demonstrated. Species whose larvae are primarily neustonic (e.g., cabezon, lingcod, greenlings) are undersampled by oblique net tows because the surface layer is filtered only briefly at the beginning and end of each tow. The manta net time series, begun on CalCOFI survey cruises in 1978, permits better sampling of these species.

An important facet of CalCOFI survey data is the information that they can provide on the relation between larval production and ocean climate. The potential for advection of larvae northward into the SCB from Baja California by the Inshore Countercurrent during El Niño episodes has been discussed in this paper. Such transport events could be important sources of larvae and pelagic juveniles of species such as sheephead, with large populations off Baja California. Cowen (1985) found anomalously large numbers of newly settled sheephead in 1983 at the northern Channel Islands within the SCB and noted similar settlement success at other localities as far north as Monterey Bay, California. He suggested that this could have resulted from advection of sheephead larvae into the SCB from population centers off Baja California by the strong Inshore Countercurrent that developed during the 1982-83 El Niño. Information presented in this paper on the distribution and abundance of larval sheephead and Diogenes lanternfish during the 1998 El Niño supports Cowen's (1985) hypothesis and suggests that a strong 1998 year-class could have resulted from these events.

Another potential use of the CalCOFI ichthyoplankton time series is to separate the effects of fishery removals from those of ocean climate by comparing larval production of species that share similar habitats and life-history characteristics but differ in degree of exploitation. One such pair is the heavily exploited bocaccio and the relatively unexploited shortbelly rockfish

(Moser, Charter, Watson et al. 2000). Time series of these two species show that both had a general trend of decreasing abundance, with sharp declines in both species during the 1957-59 El Niño and a sharp decline during the transition from the cool to the warm ocean regime in 1976–77. The fact that both species declined during the transition from cool to warm regime even though one was exploited and one was not suggests an environmental effect on larval production. The contrasting trends in larval abundance for these species during the warm regime suggest that other factors are affecting larval production as well. The larval trend for bocaccio followed the steadily declining trend for adult biomass (MacCall et al. 1999) and suggests that fishery removals were the principal cause. In contrast, the recovery of shortbelly larval production during the warm regime suggests that some other factor, possibly one or more good year-classes, resulted in a sustained increase in larval abundance that peaked in 1991 (Moser, Charter, Watson et al. 2000).

The CalCOFI ichthyoplankton time series has proven to be an important resource in the monitoring and management of coastal pelagic fish stocks and promises to be equally useful for nearshore species that have experienced increasing pressure from fisheries and environmental perturbation. In addition to providing indices for individual species, the CalCOFI time series could be used to construct long-term indices of community structure in the nearshore environment. For example, one could calculate the ratio of abundances of the larvae of fished rocky-shore species to the larvae of unfished, or lightly fished, species (e.g., those listed under "other species" in table 2). Essentially this would be a dimensionless index of ecosystem "health," with the standard for the ratio being data collected 50 years ago. One could then monitor trends in the community (i.e., the ratio over time) to track the extent to which the fished species become a smaller fraction of the community. This index could include nearshore soft-substrate species (table 3), or a separate index could be constructed for them. The CPFV data are beginning to indicate increasing fishing effort on shallow-water soft-substrate species because of fishing restrictions on rocky-substrate fauna. Pre-crisis assessment and monitoring of these stocks by means of fishery-independent abundance indices would be prudent.

ACKNOWLEDGMENTS

This study was made possible by the many people who contributed to CalCOFI over the past half-century. We are indebted to those who served on the survey cruises, particularly David Griffith, Ronald Dotson, and Amy Hays, who conducted the plankton collections during CalCOFI survey cruises for the past decade or more and who are responsible for the high quality of

TABLE 3
Larvae of Soft-Substrate Fish Taxa* in CalCOFI
Samples in the Southern California Bight Region,
by Overall Abundance

Common name	Scientific name	Rank	Time series
Fisheries species			
White croaker	Genvonemus lineatus	26	1981-2000
Pacific sanddab	Citharichthys sordidus	28	1954-1960;
	1		1984-2000
English sole	Parophrys vetulus	44	1952-2000
California halibut	Paralichthys californicus	50	1951-2000
Dover sole	Microstomus pacificus	71	1951-2000
Rex sole	Glyptocephalus zachirus	104	1951-2000
Longspine thornyhead	Sebastolobus altivelis	155	1985-2000
Shortspine thornyhead	Sebastolobus alascanus	194	1985-2000
Other species			
Speckled sanddab	Citharichthys stigmaeus	16	1954-2000
Pacific argentine	Argentina sialis	37	1951-2000
Slender sole	Lyopsetta exilis	45	1951-2000
Hornyhead turbot	Pleuronichthys verticalis	56	1951-2000
Pacific butterfish	Peprilus simillimus	59	1951-2000
Queenfish	Seriphus politus	67	1981-2000
California tonguefish	Symphurus atricaudus	76	1951-2000
Basketweave cusk-eel	Ophidion scrippsae	88	1951-2000
Bigmouth sole	Hippoglossina stomata	93	1951-2000
Bay goby	Lepidogobius lepidus	100	1985-2000
Yellowchin sculpin	Icelinus quadriseriatus	101	1985-2000
Spotted cusk-eel	Chilara taylori	106	1951-2000
C-O turbot	Pleuronichthys coenosus	108	1951-2000
Spotted turbot	Pleuronichthys ritteri	122	1951-2000
California lizardfish	Synodus lucioceps	124	1951-2000
Longspine combfish	Źaniolepis latipinnis	125	1985-2000
Curlfin turbot	Pleuronichthys decurrens	132	1951-2000
Longfin sanddab	Citharichthys xanthostigma	134	1954-1960;
0			1985-2000
Fantail sole	Xystreurys liolepis	137	1951-2000
Sand sole	Psettichthys melanostictus	153	1951-2000
Diamond turbot	Hypsopsetta guttulata	157	1951-2000
Shortspine combfish	Zaniolepis frenata	163	1985-2000
Roughback sculpin	Chitonotus pugetensis	176	1985-2000
Rock sole	Lepidopsetta bilineata	179	1951-2000
Blacktip poacher	Xeneretinus latifrons	183	1985-2000
Pygmy poacher	Odontopyxis trispinosus	188	1985-2000
Bluebarred prickleback	Plectobranchus evides	191	1985-2000

*Limited to taxa with 100 or more total larvae (larvae per 10 m^2 , summed over the time series).

the net tows and associated data, as well as for the excellent condition of the fish eggs and larvae captured in the nets. Lucy Dunn has been the mainstay of our group of plankton sorters over the past three decades. Susan Manion was responsible for data entry during this project. We are especially indebted to Susan Jacobson for her contributions in data management and programming. We thank Henry Orr for his work on the graphics and Richard Cosgrove for his help with bathymetric data. We thank Nancy Lo for helpful discussions on sampling and for her estimates of sampling requirements. We are indebted to John Hunter, Chief of the Fisheries Resources Division, for his support, encouragement, and helpful suggestions. Karen Green, MEC Analytical Systems, provided advice on the MEC ichthyoplankton database, and Steven Schroeter, Marine Science Institute,

Univ. Calif. Santa Barbara, made the MEC database available to us and provided advice on its use. Richard Feeney, Natural History Museum of Los Angeles County, provided data from the LACM ichthyoplankton program and offered helpful information and advice. Chris Ehrler, Tenera Environmental Services, provided data from the Diablo Canyon ichthyoplankton database and many helpful discussions. We are grateful to Ron Lynn for advice on oceanography, always graciously given, and for his generosity in providing data on the strong Inshore Countercurrent generated by the 1998 El Niño.

LITERATURE CITED

- Allen, L. G., and M. P. Franklin. 1992. Abundance, distribution, and settlement of young-of-the-year white seabass *Atractosion nobilis* in the Southern California Bight, 1988-89. Fish. Bull. 90:633–641.
- Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. Fish. Bull., U.S. 82:97–111.
- Brewer, G. D., and G. S. Kleppel. 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.
- Brown, D. M., and L. Cheng. 1981. New net for sampling the ocean surface. Mar. Ecol. Prog. Ser. 5:224–227.
- Butler, J. L., L. D. Jacobson, J. T. Barnes, and H. G. Moser. 1999. Stock assessment of cowcod. *In* Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, Ore. 97201.
- Cowen, R. K. 1985. Large scale pattern of recruitment by the labrid, Semicossyphus pulcher: causes and implications. J. Mar. Res. 43:719–742.
- Doyle, M. J. 1992a. Patterns in distribution and abundance of ichthyoplankton off Washington, Oregon, and northern California (1980–87). U.S. Dep. Commer., NMFS, Alaska Fish. Sci. Ctr. Proc. Rep. 92–14. 344 pp.
- Doyle, M. J. 1992b. Neustonic ichthyoplankton in the northern region of the California Current ecosystem. Calif. Coop. Oceanic Fish. Invest. Rep. 33:141–161.
- Haury, L. R., E. L. Venrick, C. L. Fey, J. A. MacGowan, and P. P. Niiler. 1993. The Ensenada Front: July 1985. Calif. Coop. Oceanic Fish. Invest. Rep. 34:69–88.
- Hauser, J. W., and M. P. Sissenwine. 1991. The uncertainty in estimates of the production of larval fish derived from samples of larval abundance. ICES J. Mar. Sci. 48:23–32.
- Hayward, T. L., and E. L. Venrick. 1998. Near surface pattern in the California Current: coupling between physical and biological structure. Deep-Sea Res. II 45:1617–1638.
- Hewitt, R. P. 1988. Historical review of the oceanographic approach to fishery research. Calif. Coop. Oceanic Fish. Invest. Rep. 29:27–41.
- Hill, K. T., and N. Schneider. 1999. Historical logbook databases from California's commercial passenger fishing vessel (partyboat) fishery, 1936–1997. SIO Ref. Ser. 99-19. 13 pp.
- Hill, K. T., L. D. Jacobson, N. C. H. Lo, M. Yaremko, and M. Dege. 1999. Stock assessment of Pacific sardine (*Sardinops sagax*) for 1998 with management recommendations for 1999. Calif. Dep. Fish Game, Marine Region Admin. Rep. 99-4. 94 pp.
- Hunter, J. R., and N. C. H. Lo. 1993. Ichthyoplankton methods for estimating fish biomass. Introduction and terminology. Bull. Mar. Sci. 53(2): 723–727.
- Jahn, A. E., and R. J. Lavenberg. 1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. Mar. Ecol. Prog. Ser. 31:223–231.
- Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zwiefel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech. Rep. NMFS Circ-370, 38 pp.
- Lasker, R., ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36. 99 pp.

- Lo, N. C. H., J. R. Hunter, H. G. Moser, and P. E. Smith. 1992. The daily fecundity reduction method: a new procedure for estimating adult fish biomass. ICES J. Mar. Sci. 49:209–215.
- ——. 1993. A daily fecundity reduction method of biomass estimation with application to Dover sole *Microstomus pacificus*. Bull. Mar. Sci. 53(2): 842–863.
- Lynn, R. J., and S. J. Bograd. In press. Dynamic evolution of the 1997–99 El Niño–La Niña cycle in the southern California Current system. Prog. Oceanogr.
- Lynn, R. J., and J. J. Simpson. 1987. The California Current system; the seasonal variability of its physical characteristics. J. Geophys. Res. 92: 12,947–12,966.
- ------. 1990. The flow of the undercurrent over the continental borderland off southern California. J. Geophys. Res. 95:12,995–13,008.
- MacCall, A. D., S. Ralston, D. Pearson, and E. Williams. 1999. Status of the bocaccio off California in 1999 and outlook for the next millennium. *In* Appendix to the status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catches for 2000. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, Ore., 97201.
- Marliave, J. B. 1986. Lack of planktonic dispersal of rocky intertidal fish larvae. Trans. Am. Fish. Soc. 115:149–154.
- Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, S. R. Charter, C. A. Meyer, E. M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest. Atlas 31. 233 pp.
- ———. 1994. Distributional atlas of fish larvae in the California Current region: taxa with less than 1000 total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest. Atlas 32. 181 pp.
- Moser, H. G., R. L. Charter, S. B. Reilly, D. A. Ambrose, S. R. Charter, E. M. Sandknop, and W. Watson. 2000. Ichthyoplankton and station data for surface tows taken during the 1987 eastern tropical Pacific dolphin survey on the research vessels *David Starr Jordan* and *McArthur*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-287. 45 pp.
- Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, J. L. Butler, S. R. Charter, and E. M. Sandknop. 2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation. Calif. Coop. Oceanic Fish. Invest. Rep. 41:132–147.

- Moser, H. G., R. L. Charter, P. E. Smith, D. A. Ambrose, W. Watson, S. R. Charter, and E. M. Sandknop. 2001. Distributional atlas of fish larvae and eggs in the Southern California Bight region: 1951–1998. Calif. Coop. Oceanic Fish. Invest. Atlas 34. 166 pp.
- O'Connell, C. P. 1953. The life history of the cabezon Scorpaenichthys marmoratus (Ayres). Calif. Dep. Fish Game Fish Bull. 93. 76 pp.
- Pattison, C., and A. Vejar. 2000. Nearshore finfish. In Review of some California fisheries for 1999: market squid, Dungeness crab, sea urchin, prawn, abalone, groundfish, swordfish and shark, ocean salmon, nearshore finfish, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass, and recreational, L. Rogers-Bennett, ed. Calif. Coop. Oceanic Fish. Invest. Rep. 41:17–18.
- Pearson, D. E., J. E Hightower, and T. H. Chan. 1991. Age, growth, and potential yield for shortbelly rockfish Sebastes jordani. Fish. Bull. 89:403–409.
- Ralston, S. 1998. The status of federally managed rockfish on the U.S. west coast. In Marine harvest refugia for West Coast rockfish: a workshop, M. M. Yoklavich, ed. NOAA, NMFS, Tech. Memo. NOAA-TM-NMFS-SWFSC-255, pp. 6–16.
- Ralston, S., J. Ianelli, R. Miller, D. Pearson, D. Thomas, and M. Wilkens. 1996. Status of the bocaccio in the Conception/Monterey/Eureka INPFC areas in 1996 and recommendations for management in 1997. *In* Appendix (vol. 1) to the status of the Pacific Coast groundfish fishery through 1996 and recommended acceptable biological catches for 1997. Pacific Fishery Management Council, 2130 SW Fifth Avenue, Suite 224, Portland, Ore. 97201.
- Schlotterbeck, R. E., and D. W. Connally. 1982. Vertical distribution of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*). Fish. Bull., U.S. 80:895–902.
- Smith, P. E. 1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull. 70:849–874.
- Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175. 100 pp.
- Wolf, P. 1992. Recovery of the Pacific sardine and the California sardine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 33:76–86.