Journal of Fish Biology (2009) **75**, 630–646
doi:10.1111/j.1095-8649.2009.02327.x, available online at www.interscience.wiley.com

Interannual distribution of Pacific hake *Merluccius productus* larvae in the southern part of the California Current

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(Received 26 March 2008, Accepted 23 April 2009)

The interannual distribution of early life stages of Pacific hake *Merluccius productus*, within the southern part of the California Current (32–23° N) from 1951 to 2001, was examined to describe the relationship between spawning habitat and environmental conditions. Mean annual abundance was affected by different factors along the west coast of the Baja California Peninsula. In the northern areas (Ensenada and Punta Baja), reduced abundance of larvae coincided with the El Niño and a North Pacific Ocean climatic regime shift, but in the southern areas (San Ignacio to Bahía Magdalena), the drastic reductions suggested a fishery effect for large adults of the coastal migratory population, starting in 1966. Two spawning stocks, coastal and dwarf, were evident in comparisons of latitudinal differences in occurrence of early stages and differences in temperature preferences that seemed to break at Punta Eugenia.

Key words: Baja California Peninsula; California Current; larval distribution; *Merluccius productus*; Pacific hake.

INTRODUCTION

The life history of Pacific hake *Merluccius productus* (Ayres) was described by Alverson & Larkins (1969), who reported that the fish migrate annually between spawning grounds from central California to the Baja California Peninsula in winter to feeding grounds from central Oregon to northern Vancouver Island in summer. The spawning season of *M. productus* occurs from about October to May or June. Generally, it is strongly centred on January–March around the California Bight (Moser *et al.*, 1993; Smith & Moser, 2003).

Merluccius productus larvae were second in abundance and seventh in frequency of occurrence of fish larvae identified in the California Current from 1951 to 1984, with the highest mean values occurring off central California and the northern Baja California Peninsula and diminishing in the central part of the Baja California

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(Moser *et al*., 1993). In the southern part of the Baja California Peninsula, the highest mean abundance occurred within nearshore waters. The largest concentrations of larvae occurred at a depth of 50 m in the water column (Cass-Calay, 1997), with most larvae found near or within the thermocline at temperatures between 11·5 and 14·3° C (Ahlstrom & Counts, 1955).

Several environmental factors during the planktonic stages have important consequences for stock recruitment. One of the factors is advection of eggs and larvae away from favourable nursery areas (Bailey, 1981; Sakuma & Ralston, 1997). Others involve anomalous meteorological and oceanographic conditions, including high temperatures, reduced southerly flow of the California Current, weak upwellings and poleward currents (Mendelson & Schwing, 2002; Schwing *et al*., 2002; Bograd & Lynn, 2003; McGowan *et al*., 2003). Potential effects during cold or warm years for *M. productus* and other highly migratory fishes could also be related to changes in geographical distribution of eggs and larvae resulting from displacing spawning adults out of the normal spawning region (Hollowed, 1992; Phillips *et al*., 2007). Annual variation in the quantity of *M. productus* larvae in the Southern California Bight is large, declining after the North Pacific Ocean climatic regime shift (regime shift) of 1976–1977. Typically, a shift in abundance alternates triennially, closely tied to the strength of the California Current and its latitude-specific temperatures (Smith & Moser, 2003).

Two *Merluccius* species are found off the west coast of North America (*M. productus* and Panamanian hake *Merluccius angustimanus* Garman) and they mix off the northern part of Mexico (Grinols & Tillman, 1970). *Merluccius productus* has been exploited since 1966 along the west coast of the U.S. and Canada, and is documented in an extensive literature on its biology and ecology (Elorduy-Garay, 1986). *Merluccius angustimanus* is distributed from California southward to Colombia (Inada, 1981; Lloris *et al*., 2003), does not have a fishery at present and studies of their biology and ecology are rare (Lloris *et al*., 2003; Balart-Páez, 2005).

Merluccius productus occurs from the Gulf of Alaska to the Gulf of California (Eschmeyer *et al*., 1983), with two possible subpopulations (coastal migratory and dwarf) along the coast of the Baja California Peninsula (Bailey *et al*., 1982). The differentiation of the dwarf *M. productus* subpopulation from the migratory subpopulation may reflect local environmental effects rather than a genetic difference (Bailey *et al*., 1982). In this regard, several coastal pelagic fish species have population discontinuities in morphometric measurements, meristic counts and proportion of selected proteins polymorphs, suggesting restricted gene flow in the vicinity of Punta Eugenia, described as a provincial boundary caused by semi-permanent cyclonic eddies (Hewitt, 1981).

The identities of the dwarf and coastal stocks are controversial. Vrooman & Paloma (1977) believed the dwarf stock is limited to the west coast of the Baja California Peninsula and is morphologically and genetically distinct from *M. productus*. Only larvae attributable to the coastal migratory populations of *M. productus* have been identified in California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples (Ambrose, 1996), supporting the possibility that there is only one spawning stock. According to Iwamoto *et al*. (2004), levels of genetic differentiation between coastal migratory and inshore stocks (Strait of Georgia and Puget Sound) suggest that migratory and inshore populations are reproductively isolated. No genetic studies, however, have recently addressed the relationship between coastal migratory and dwarf populations.

The primary objective of the present study was to examine the interannual distribution of the early life stages of *M. productus* to identify preferences in spawning habitats related to environmental conditions in Mexican waters from Ensenada to the tip of the Baja California Peninsula between 1951 and 2001. Unique and long time-series data (50 years) were analysed to determine whether El Niño, regime shift and intensive fishing pressure affect the distribution of *M. productus* larvae in Mexican waters. The study also analysed whether latitudinal differences in abundance of larvae were related to two reproductive stocks of *M. productus*.

MATERIALS AND METHODS

The surveyed area extended from 32° N (near Ensenada, Baja California, Mexico) to 23° N (near the tip of the Baja California Peninsula) and extended from 9 to 185 km offshore (Fig. 1). In this area, the continental shelf is narrow, usually <37 km wide with a maximum of *c*. 65 km off Sebastián Vizcaíno and between San Ignacio and just north of Bahía Magdalena.

Larvae of *M. productus* collected during three data series were examined for patterns of distribution in Mexican waters from 1951 to 2001. Data bases from CalCOFI (1951–1981) were originally published in CalCOFI atlases (Moser *et al*., 2001). The first decade of monthly CalCOFI cruises (1951–1960) was changed to quarterly cruises (1961–1968); cruises were monthly in 1969, but with considerable variation in geographic coverage. The grid was

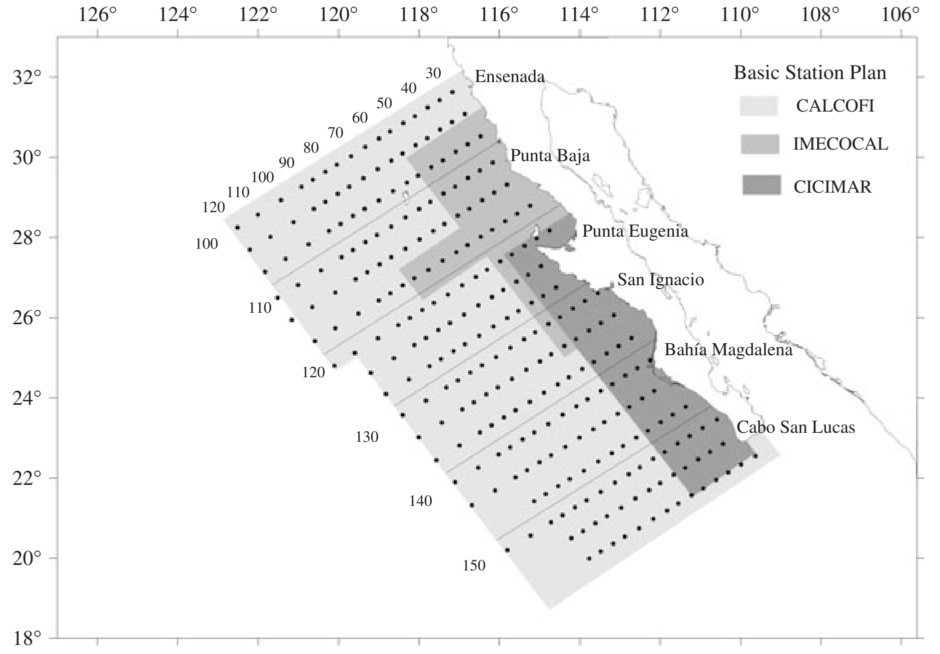

FIG. 1. Study area and sampling grid of the California Cooperative Oceanic Fisheries Investigations (CalCOFI 1951–1985), Centro Interdisciplinario de Ciencias Marinas (CICIMAR 1982–1994) and Investigaciones Mexicanas de la Corriente de California (IMECOCAL 1987–2001) along the west coast of the Baja California Peninsula.

completely sampled, but changed to triennial surveys from 1970 to 1984; from 1972 to 1984, there were six or seven monthly cruises per year. Beginning in 1985, quarterly sampling resumed but the CalCOFI grid was reduced to include only station lines 77–110 (Avila Beach, California to Punta Baja, Baja California). The other two data series were based on quarterly surveys conducted by Centro Interdisciplinario de Ciencias Marinas (CICIMAR) from 1982 to 1994 and Investigaciones Mexicanas de la Corriente de California (IMECOCAL) from 1997 to 2001 (Fig. 1).

The region was divided into six study areas following the nomenclature of the CalCOFI basic station plan in Mexican waters (Fig. 1 and Table I): Ensenada lines (97–107), Punta Baja (110–117), Punta Eugenia (120–127), San Ignacio (130–137), Bahía Magdalena (140–147) and Cabo San Lucas (150–157). Areas between Ensenada and San Ignacio were sampled most frequently by the CalCOFI (1951–1985) and IMECOCAL (1997–2001) surveys. The San Ignacio and Bahía Magdalena areas were principally sampled by CalCOFI (1951–1960) and

TABLE I. Summary of sampling effort (*n* samples per transect; see Fig. 1) for surveys conducted during the first half of the year (January to June) and number of samples containing *Merluccius productus* larvae (parenthesis) along the Pacific coast of the Baja California Peninsula from 1951 to 2001

Year	Ensenada	Punta Baja	Punta Eugenia	San Ignacio	Bahía Magdalena	Cabo San Lucas
1951	150 (85)	107 (48)	56 (32)	66 (37)	21 (12)	8 (4)
1952	122 (72)	109 (47)	111 (43)	102 (57)	5 (5)	1 (1)
1953	152 (84)	110 (64)	97 (48)	106 (48)	8 (8)	
1954	194 (119)	173 (126)	160 (93)	97 (50)	10 (10)	2 (2)
1955	144 (99)	140 (103)	140 (65)	73 (42)	29 (27)	10 (9)
1956	172 (99)	143 (68)	105 (38)	67 (38)	31 (23)	11 (4)
1957	149 (75)	109 (59)	73 (30)	86 (36)	39 (21)	5 (2)
1958	192 (104)	138 (67)	110 (54)	89 (37)	33 (23)	
1959	105 (29)	88 (29)	61 (16)	100 (34)	10 (6)	
1960	163 (75)	161 (72)	99 (39)	106 (56)	18 (11)	1 (1)
1961	45 (32)	25 (18)	30 (18)	20 (11)		
1962	78 (57)	36 (27)	32 (24)	26 (18)	6 (5)	
1963	63 (51)	46 (29)	32 (17)	24 (12)	2 (2)	
1964	62 (50)	26 (17)	20 (11)	34 (19)	3 (3)	
1965	103 (68)	41 (21)	37 (25)	44 (33)	7 (7)	
1966	63 (51)	46 (29)	32 (17)	24 (12)	2 (2)	
1968	32 (17)	6 (6)	6 (3)	10 (10)	1 (1)	
1972	114 (68)	45 (19)	17 (4)	44 (25)	7 (4)	
1975	133 (51)	63 (22)	13 (7)	24 (13)		
1978	48 (21)	15 (5)	1 (1)	24 (16)		
1981	52 (18)	14 (7)	5 (4)	4 (4)		
1982				5 (5)	24 (14)	
1983			9 (0)	33 (1)	29 (5)	1 (0)
1984	16 (6)	1 (0)	15 (1)	16 (2)	20 (7)	
1985	8 (0)	2 (0)	12 (0)	16 (0)	15 (0)	
1986		9 (0)	17 (0)	13 (0)	17 (0)	3 (1)
1989			6 (0)		15 (1)	17 (0)
1991				4 (1)	28 (8)	37 (6)
1994	7 (0)	9 (0)	34 (1)	22 (6)	33 (7)	
1998	21 (0)	23 (0)	19 (0)	6 (1)		
1999	38 (11)	43 (7)	19 (5)			
2000	21 (6)	25 (0)	20 (2)	22 (4)		
2001	21 (1)	16 (0)	21 (0)	14 (3)		

CICIMAR (1982–1994). The Cabo San Lucas area was less frequently sampled (CalCOFI 1951–1958; CICIMAR 1986–1994) (Table I).

Larvae were sampled by oblique tows with a 1 m ring net from 1951 to 1976 and with bongo nets after 1976. The depth of the tows was 140 m from 1951 to 1968 and 210 m thereafter. Counts of fish larvae were converted to number under 10 m^2 sea surface (Smith & Richardson, 1977). Mean annual abundances of larvae were calculated for each of the six areas to analyse interannual trends, based on positive stations where larvae occurred in surveys conducted during the first half of each year (January to June). This represents the period when this species consistently occurred at locations over the continental shelf or in oceanic waters near the continental slope in the southern part of the Baja California Peninsula (Moser *et al*., 1993). Years with only one cruise (January to June) were removed (Table I). In addition, monthly anomalies (between January and December) were calculated by areas using the whole data series (1951–2001) to compare differences when surveys were monthly *v*. years when they were quarterly.

Time series of environmental conditions along the coast of the peninsula were obtained from different sources. The NOAA Climate Diagnostic Center provided the Multivariate El Niño Indices (www.cdc.noaa.gov) and the NOAA Pacific Fisheries Environmental Laboratory provided the average monthly values of the upwelling index in m^3 s^{-1} 100 m^{-1} coast line (www.pfeg.noaa.gov) at three locations (30° N, 119° W; 27° N, 116° W; and 24° N, 113° W). Spearman rank order correlations(r_s; $P < 0{\cdot}05$) were used to examine the relationships between abundance of larvae and environmental data in each of the six areas. Temperature at each station (depth 50 m) was extracted from the CalCOFI hydrographic database (1951–1985) and the CICIMAR and IMECOCAL cruises (1982–2001). These temperature data were used as an environmental indicator, varying with latitude, with relatively cold water to the north and warm water to the south. Larval occurrence (number of positive stations) was grouped by temperature intervals at a depth of 50 m. Standard lengths (L_S) of fish larvae were grouped and graphed to detect regional differences during 1982–2001.

RESULTS

Mean annual abundance of larvae in the Ensenada area was variable, with relatively high values of >100 larvae 10 m^{-2} from 1951 to 1957 and extraordinarily high values of >300 larvae 10 m^{-2} during the La Niña events of 1956 and 1975. A rapid decline in abundance began during El Niño 1957–1958 and relatively low abundances of 50–100 larvae lasted until 1972, but with increases in 1963 and 1966 to 200 larvae. A major decline to <50 larvae occurred from 1978 to 2001 (Fig. 2), following the 1976–1977 shift to a warm regime; since there was no sampling during the regime shift, it would be difficult to say whether variability was lower or not during the shift.

The Punta Baja area followed the same trend described for Ensenada, with increases during the 1955–1957 and 1975 La Niña events. After El Niño 1957–1958, densities remained low until a peak in 1975, followed by a second decline after the regime shift (Fig. 2). Similarly, monthly anomalies showed the same trends in the northern areas (Ensenada and Punta Baja), except that increases in density were not always detected as positive anomalies, which suggested that calculations of anomalies were influenced by the period of high larval abundance from 1951 to 1957 (Fig. 3).

Distinct trends in abundance were observed in the southern areas, specifically between Punta Eugenia to Bahía Magdalena areas. Punta Eugenia had low values of <50 larvae, with a moderate increase to 100 larvae 10 m^{-2} during La Niña events in 1956 and 1999, but no evidence of responses to El Niño or the regime shift (Fig. 2). Monthly anomalies showed the same pattern, except for increases in 1956 and 1961

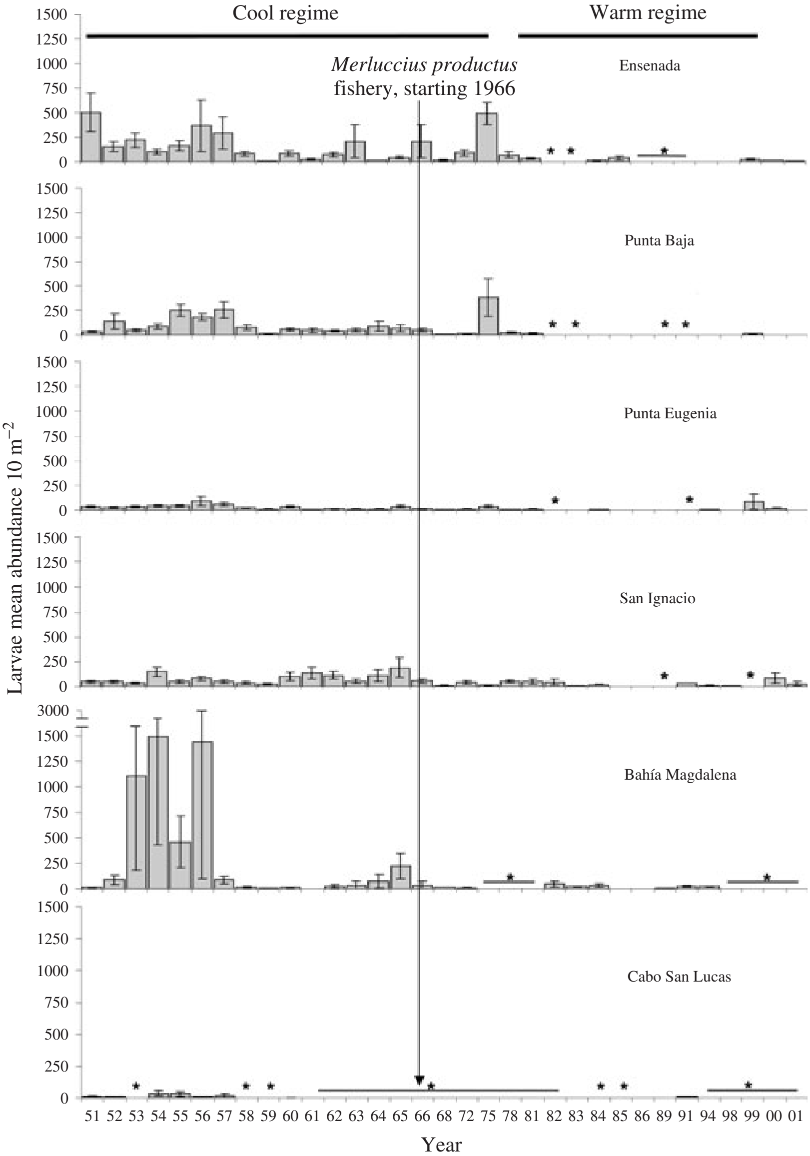

FIG. 2. Mean ± S.E. abundance of *Merluccius productus* larvae by area, determined from surveys from January to June from 1951 to 2001 along the west coast of the Baja California Peninsula. Years when surveys were not conducted are marked (⋆).

(Fig. 3). Larvae reached maximum abundance of >1000 larvae 10 m^{-2} from 1953 to 1956 in the Bahía Magdalena area, which was not observed in the San Ignacio area in the same period. In the San Ignacio area, mean annual abundances of *c*. 50 larvae were relatively similar from 1951 to 1982, with a moderate increase of 100 larvae 10 m^{-2} during 1960–1965, except in 1963 (50 larvae) and 1965 (192 larvae). El Niño 1957–1958 was not strong in the San Ignacio area, but a drastic decline

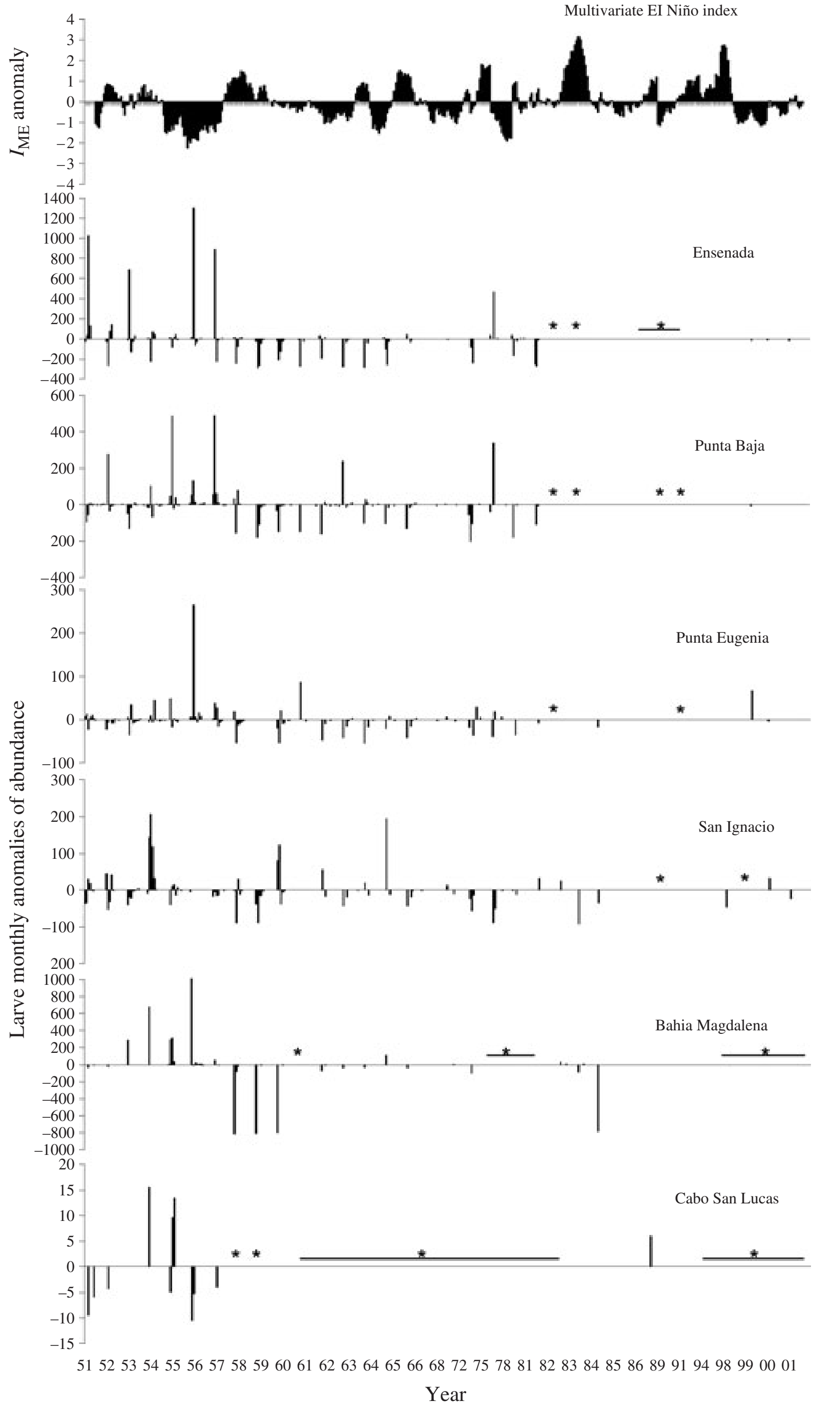

FIG. 3. Monthly anomalies of abundance of *Merluccius productus* larvae by area from 1951 to 2001 along the west coast of the Baja California Peninsula. The multivariate El Niño index (I_{ME}) is shown. Years when surveys were not conducted are marked (*).

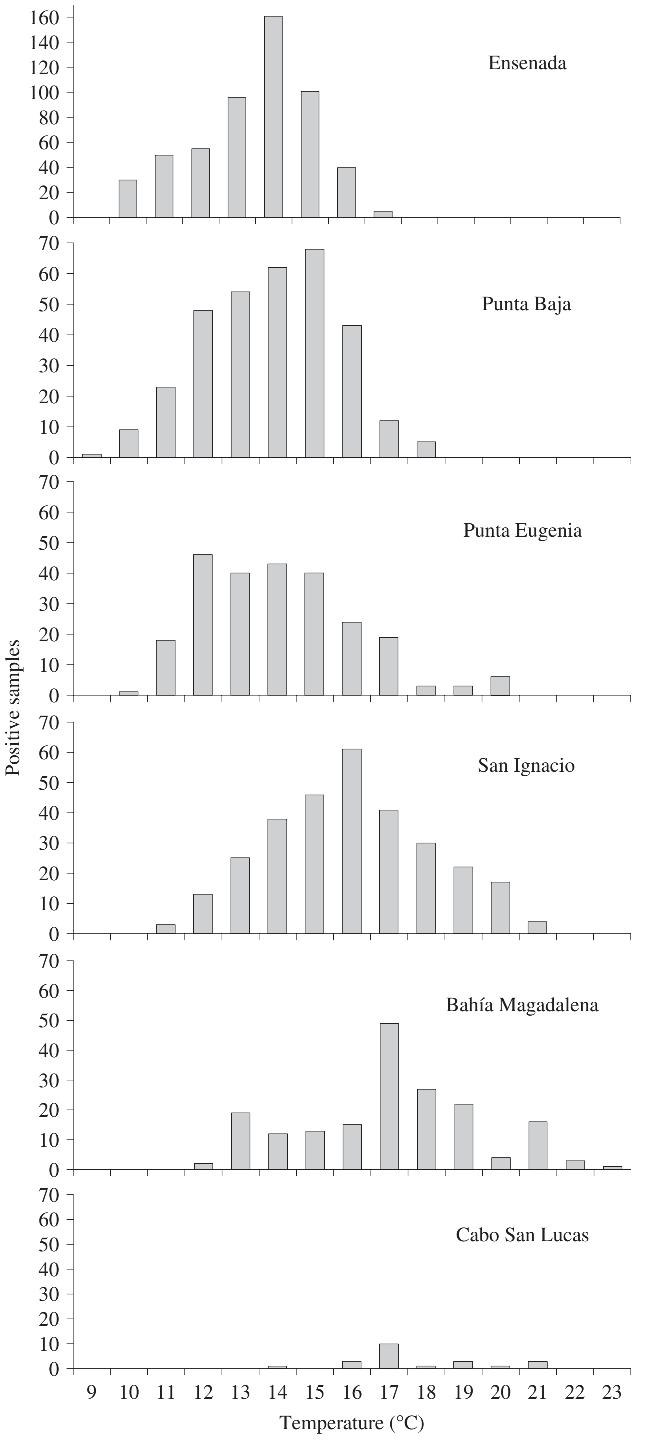

FIG. 4. Occurrence of *Merluccius productus* larvae (number of positive samples) in relation to temperature at 50 m depth in each area from 1951 to 2001 along the west coast of the Baja California Peninsula.

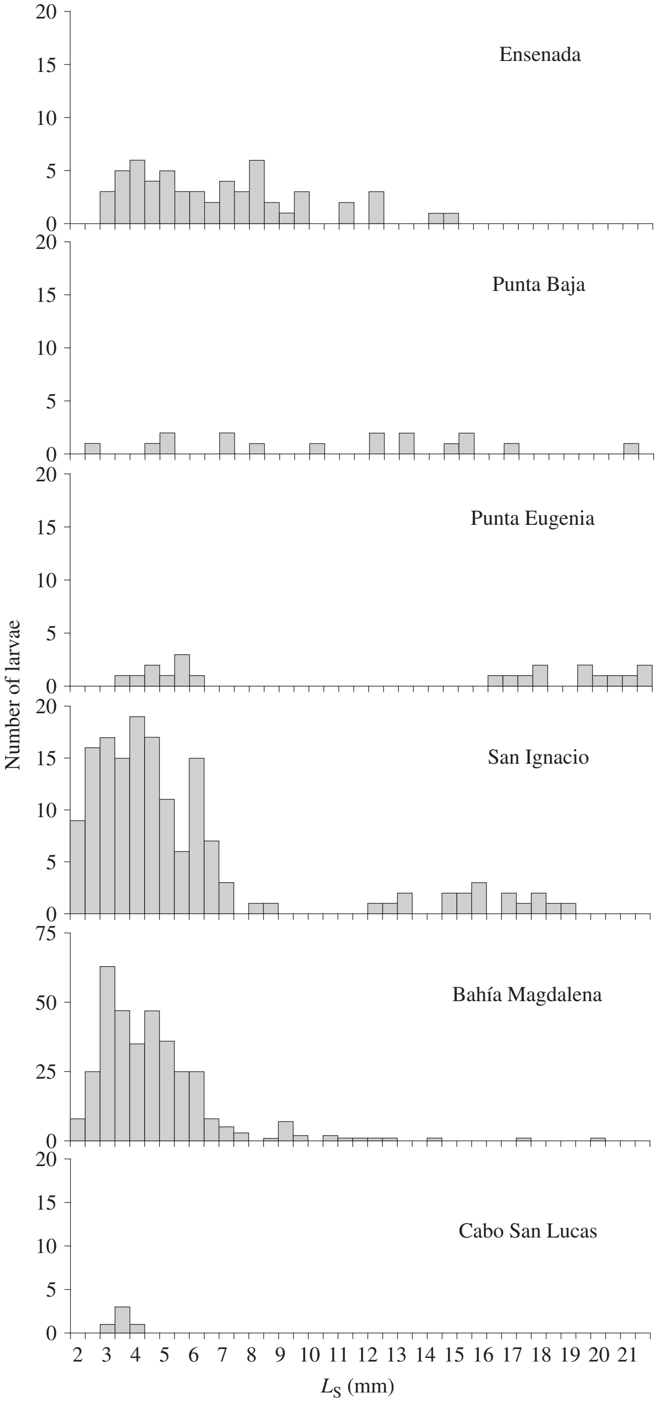

FIG. 5. Standard-length (L_S) frequency of *Merluccius productus* larvae by area from 1982 to 2001 along the west coast of the Baja California Peninsula.

occurred in the Bahía Magdalena area. Although evidence of the regime shift was absent in the southernmost areas, a drastic decline in the San Ignacio area coincided with an intensive commercial fishery for large adults off the Oregon-Washington coast, starting in 1966 (Figs 2 and 3). No evidence in environmental conditions related to the regime shift or fishery effects were found in the Bahía Magdalena or Cabo San Lucas areas (Fig. 3).

El Niño or La Niña events appeared to decrease or increase larvae in some areas; however, abundance was not significantly correlated to the multivariate El Niño

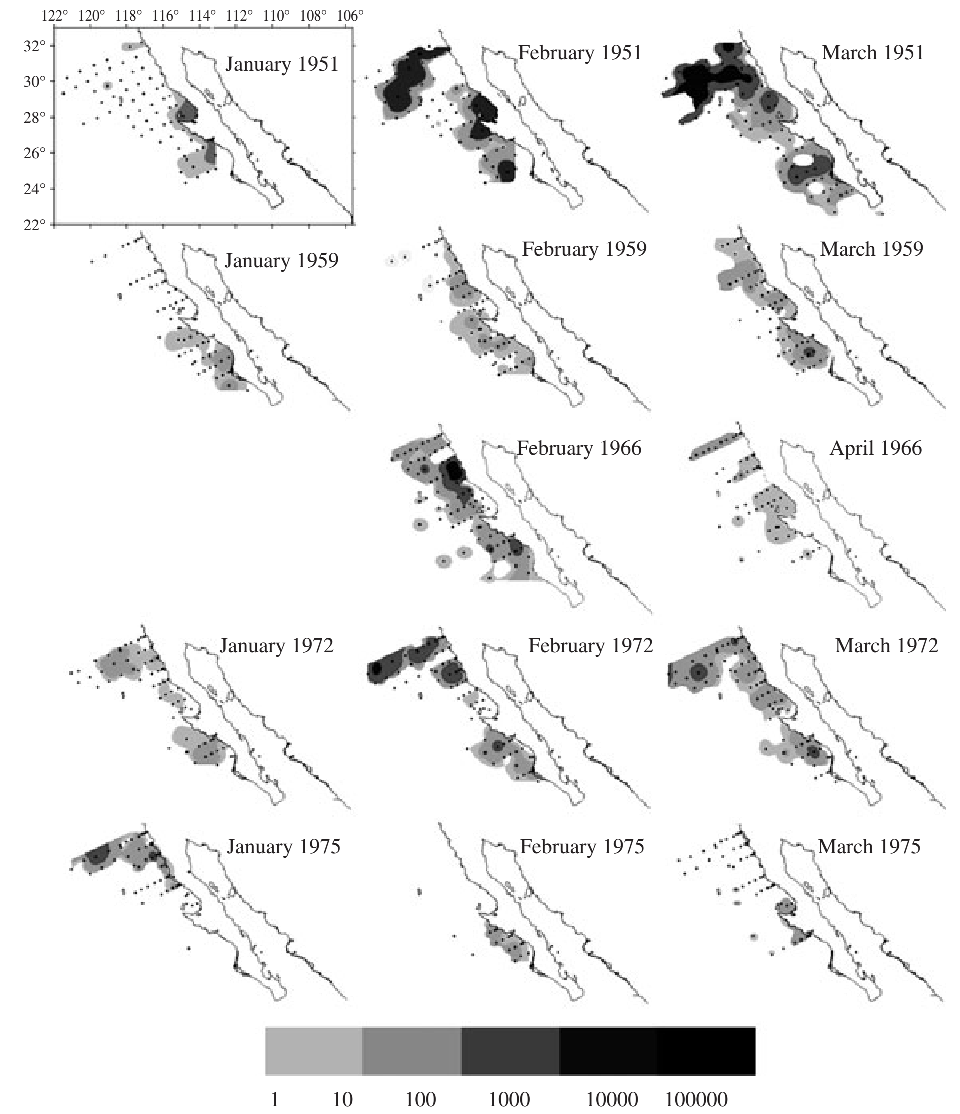

FIG. 6. Abundance distribution of *Merluccius productus* larvae during cruises in 1951, 1959, 1966, 1972 and 1975 along the west coast of the Baja California Peninsula.

index I_{ME} ($P < 0{\cdot}005$). This probably was a reflection of spawning seasons being principally modified for 3–4 years during and after the strongest events. Upwelling indices and abundance were negatively correlated ($P < 0{\cdot}01$) for all areas, except Cabo San Lucas.

The temperature range at 50 m depth at stations where larvae were collected in Ensenada and Punta Baja areas (northern Baja California), was relatively cold (9–18·0° C) with peak concentrations of larvae in Ensenada waters at 14° C. In the areas of San Ignacio, Bahía Magdalena and Cabo San Lucas (south central and southern Baja California) water at 50 m depth was warmer (11–23° C); peak concentrations of larvae occurred at 16° C in the San Ignacio area and 17° C in the Bahía Magdalena area (Fig. 4).

Early stages of *M. productus* larvae (2·0–4·0 mm L_S) were found in all six regions, with greater occurrences from the Bahía Magdalena to the San Ignacio areas. This suggests its importance as a spawning area. Large larvae (>12·0 mm)

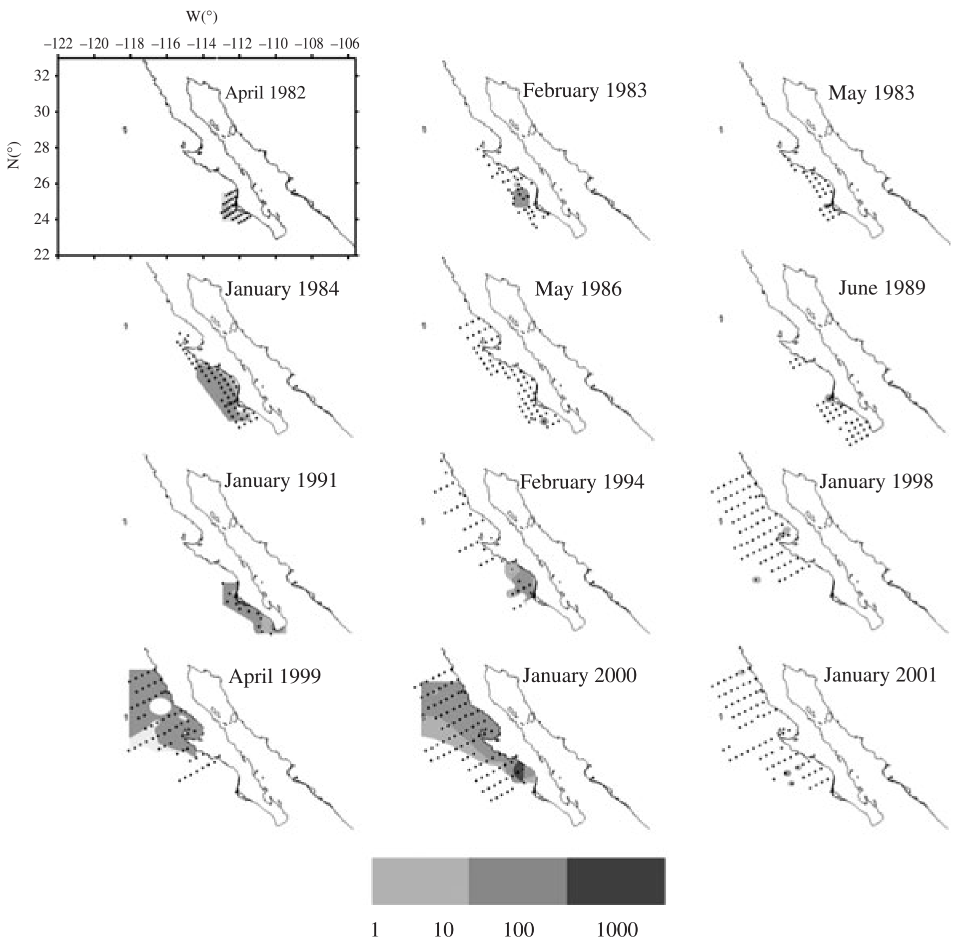

FIG. 7. Abundance distribution of *Merluccius productus* larvae during cruises from 1982 to 2001 along the west coast of the Baja California Peninsula.

were more concentrated off Punta Eugenia in 1999 and San Ignacio in 2000 (Fig. 5), during a La Niña period. Areas with more extensive continental shelf are probably important for recruitment of large larvae and juveniles.

Merluccius productus larvae were widespread along the Peninsula from 1951 to 1966, the beginning of the *M. productus* fishery (1966) and were before the regime shift (Fig. 6). A period of drastic decline occurred from 1975 to 1998 followed by a slight increase during La Niña 1999–2000 (Fig. 7). Differences in abundance of larvae were clearly separated at Punta Eugenia, suggesting different reproductive stocks between the northern and southern Baja California Peninsula (Figs 6 and 7; January 1951, 1959, 1984 and 2001, February 1983 and 1994, and March 1975).

Larvae collected from California and the southern Baja California Peninsula during different seasons showed no differences in general morphology and pattern of pigmentation; however, ray counts in anal fins and second dorsal fins (36 or 37) in large larvae (17–18 mm L_S) captured in southern Baja California were clearly different from ray counts with a mode of 40 rays for both fins in larvae captured off the California coast.

DISCUSSION

Sampling efforts in Mexican waters varied in coverage and intensity during the study period. To compensate, several procedures described in the methods section were taken to minimize these differences, since the monthly (1951–1960) and quarterly surveys (1961–2001) cannot be considered equivalent surveys. Although the CalCOFI portion of the data has been intensively analysed, the data compiled from Mexican investigations is mostly unpublished and is of considerable value for evaluating causes for changes in distribution and abundance surrounding El Niño, La Niña and regime shifts.

Mean annual abundance of *M. productus* larvae was affected by different environmental conditions within each defined area of the west coast of the Baja California Peninsula. Southerly flow of the California Current, upwelling intensity and anomalous poleward currents (Mendelson & Schwing, 2002; Schwing *et al.*, 2002; McGowan *et al.*, 2003), as well as warming related to the 1976–1977 regime shift (Mendelson & Schwing, 2002; Bograd & Lynn, 2003), probably coincided with abrupt latitudinal changes in populations of larvae along the peninsula.

The northern areas (Ensenada and Punta Baja) had high larval abundance from 1951 to 1957, which changed to relatively low abundance starting with El Niño 1957–1958 and lasting until 1972, with the exception of extraordinarily high values during the La Niña events of 1956 and 1975. A major decline through 2001 followed the 1976–1977 regime shift, probably related to the stronger nearshore poleward flow during the warm regime (Bograd & Lynn, 2003). In contrast, annual variations were low in the Southern California Bight (SCB) from 1951 to 1985. Abundances and variations in the SCB were on about the same scale as those in the Punta Baja area until the regime shift, followed by high variability with strong spawning events in 1986 and 1988, and low concentrations from 1993 to 2000 (Moser *et al.*, 2001; Smith & Moser, 2003).

Ratios of triennial averages of abundance of larval *M. productus* and differences of triennially averaged water temperatures, typically shifted above and below a 1:1 ratio about every 3 years, although not always in phase with *M. productus*, as Smith & Moser (2003) indicated. This suggests a relationship with temperature, but probably not a direct linear one and temperature is related, at least in part, to the strength of the California Current. Increasing or decreasing abundance of larvae in the SCB appears to reflect El Niño events and regime shifts, but a consistent La Niña effect is not so clear (Moser *et al*., 2001). Fluctuations related to El Niño and La Niña, however, were more evident in Ensenada and Punta Baja. Most likely, variations in latitudinal distribution of spawning associated with temperature is indicated because, in warm years, when subtropical water expanded northward, spawning occurred at higher latitudes (Bailey *et al*, 1982; Saunders & McFarland, 1997), and in cool years *M. productus* spawned further south (Hollowed, 1992).

Spawning in the southern areas (Punta Eugenia to Bahía Magdalena) probably is not completely related with El Niño and regime shift. The change in larval abundance during El Niño 1957–1958 was not strong in the Punta Eugenia and San Ignacio areas, but a drastic decline occurred in the Bahía Magdalena area. Although no evidence of a response in larval abundance to the regime shift was detected in the southern areas, a drastic decline of larvae in the southernmost regions occurred earlier. The *M. productus* fishery, starting in 1966 off the Oregon-Washington coast (Smith, 1975), probably affected the area of spawning by removing the large spawners, which migrate farther north in the feeding season and probably farther south in the spawning season. As a consequence, larvae contributed by the migratory stock were considerably reduced from 1966 until the late 1990s. It also is possible that the southern spawning area was already decimated before inception of the fishery. No evidence currently exists to indicate that changes in the ocean environment are connected to the redistribution during this period (Bailey, 1980).

Merluccius productus larvae have been collected principally at stations over the continental shelf or in oceanic waters over the continental slope in the southern part of the Baja California Peninsula (Moser *et al*., 1993), closely related to the habitats used by the adults. Smaller larvae were more common between the Bahía Magdalena and San Ignacio areas, while larger larvae were more abundant in the Punta Eugenia and San Ignacio areas. This pattern suggests that these areas are important for spawning or recruitment for larger larvae. Funes-Rodríguez *et al*. (2002) proposed that the distribution of fish larvae assemblages reflected the location of the preferred habitats and spawning grounds of mature adults; however, assemblage differences are also influenced by oceanic dynamics, including El Niño events.

Merluccius productus larvae occur from about October to June; the peak of abundance typically is January to March within the California Current, with the highest densities in two regions: along the coast from San Francisco southward to northern Baja California and in the southern part of the Baja California Peninsula (Moser *et al.,* 1993). This bimodal gradient, with higher abundances in the north and south, and intervening lower abundance in the middle off the central Baja California Peninsula, appears to be related to environmental conditions. For example, higher abundance in northern Baja California from 1951 to 1957 was opposite to what prevailed in the SCB (Smith & Moser, 2003) and off central California where annual means were very low (Bailey, 1980). Larvae along the central California coast are more affected by wind stress transport than are larvae off the coast of the Baja California Peninsula and the low numbers off central California during 1951–1957 may reflect transport offshore, away from suitable nursery areas, as a result of strong upwelling in some of those years (Bailey, 1980). The opposite occurred from the mid-1960s to 1979, when larvae were much less common off the northern Baja California coast and more common off the central California coast (Bailey, 1980). This implies that upwelling was reduced along the central California coast during the mid-1960s to 1979. Alternatively, Bailey (1980) hypothesized that the *M. productus* fishery removed the fish that would have spawned in the south, and that accounted for the change in relative larval abundances between central California and Baja California.

Upwelling indices and larval *M. productus* abundance are negatively correlated off the Baja California Peninsula, suggesting that the fish avoid spawning in areas where intense upwelling is present. Upwelling transports eggs and larvae farther offshore where postlarvae or juveniles probably have low survival (Bailey, 1981). Pelagic species spawn primarily in areas characterised by weak or intermediate coastal upwelling (Bailey, 1981; Parrish *et al.*, 1981; Lluch-Belda *et al.*, 1991). *Merluccius productus* minimizes offshore transport of larvae by spawning in early winter when offshore Ekman transport is at a seasonal low in the spawning region (27–36° N) (Bailey, 1981), and the vertical distribution of eggs and larvae at the base of the thermocline provides further protection from offshore transport (Bailey, 1980; Moser *et al.*, 1997). Favourable environmental conditions during spawning and especially inshore Ekman transport are associated with large populations of *M. productus* (Bailey *et al.*, 1982; Hollowed, 1992; Sakuma & Ralston, 1997). In the southern part of the peninsula, a deeper thermocline (50–70 m) could be a mechanism that prevents larvae from being transported offshore because eggs and larvae are below the Ekman layer and are protected from transport offshore (Bailey, 1980).

Controversies remain over whether *M. productus* occurs as a cline or separate stocks (Bailey *et al.,* 1982) and whether early stages of *M. angustimanus* occur in Mexican waters (Inada, 1981). Since adults of both species have been reported in these latitudes (Grinols & Tillman, 1970), there is the possibility that early stages of these species were mixed. A few female *M. angustimanus* with ripening eggs were collected in the Bahía Magdalena area and immediately to the north in the CalCOFI survey of January 1970, which suggests that spawning began in April and continued until June or later (Inada, 1981).

Larval *M. productus* from California and the southern part of the Baja California Peninsula showed no differences in general morphology and pigmentation patterns (Ahlstrom & Counts, 1955; Ambrose, 1996). Recently, fish larvae identified as *M. angustimanus* (5 mm L_S) were found in shallow water (1 m, 29·2° C, 18·8 salinity) in Ensenada de Utría, Colombia (6° 00′ *N*; 77° 18′ W) in July 1996 (Beltrán-León & Ríos-Herrera, 2000). The features (primarily pigmentation) of these larvae are quite different from *M. productus*. Consequently, the possibility of a mix of *M. angustimanus* with early stages of *M. productus* is rejected. Discontinuities in distribution and occurrence at various temperatures are probably related to clines or other types of ecological factors, most probably latitudinal differences in the seasonal properties of the California Current and the area. Dwarf *M. productus* have several different morphometric and meristic characteristics compared with coastal fish (Vrooman & Paloma, 1977; Bailey *et al.*, 1982) and Iwamoto *et al.* (2004), working with coastal migratory and inshore stocks in the north-west Pacific demonstrated that regional genetic differentiation can occur between reproductively isolated stocks. Nevertheless, separate dwarf and coastal *M. productus* stocks remain controversial (Bailey *et al*., 1982).

Punta Eugenia has been recognized as a province boundary for several fishes (Hubbs, 1960; Hewitt, 1981). This area is characterized by a negative wind stress curl associated with downwelling that affects the coast at Punta Baja and Eugenia (Parrish *et al*., 1981). This feature, associated with semi-permanent cyclonic eddies, is evident north and south of Punta Eugenia (Hewitt, 1981). Limited communication between eddies suggests a mechanism that could reduce connectivity around Punta Eugenia, for species that time their spawning to coincide with strong eddy formation (Hewitt, 1981). Local reductions in abundance in some years around Punta Eugenia presumably reflect interannual differences in the strength of the eddies that could favour development of more or less distinct subpopulations, or reproductive stocks of *M. productus*. Parrish *et al*. (1981) noted that gyral circulation patterns appear to create favourable spawning conditions that lead to distinct subpopulations of pelagic fishes off the coast of the Baja California Peninsula.

The largest concentrations of larvae occurred at 14° C in the Ensenada area, indicating a preference for low temperatures, as on the coast of central California (8·6–18·5° C), where large concentrations of larvae occurred at temperatures between 10·6 and 15·0° C and only *c*. 4% of the specimens came from waters at temperatures $>16°$ C (Ahlstrom & Counts, 1955). The range of water temperatures where larvae were collected off southern Baja California suggests adaptability to warmer conditions (11–23° C), where the temperature along the Mexican coast is mostly related to seasonal changes and latitudinal influence of the California Current. For example, larvae were abundant and widely distributed during winter from 1951 to 1972, except during El Niño years (Ahlstrom, 1969; Moser *et al*., 2001).

The distribution of *M. productus* larvae off the southern part of the Baja California Peninsula suggests the presence of a southern (dwarf) reproductive stock separate from the coastal migratory population extending from Canada to the southern tip of the Baja California Peninsula. This conclusion is supported by: (1) reproductive stocks that occupied different thermal regimes, with moderate spawning at the warm end of the temperature range in the southern areas of the Baja California Peninsula (11–23·0° C) and in cooler water north of Punta Eugenia (9·0–18·0° C), similar to central California, (2) abundances of larvae that are clearly higher north and south of Punta Eugenia in most years, suggesting different reproductive stocks between the northern and southern Baja California Peninsula during the spawning season and (3) differences in fin-ray counts in anal and second dorsal fins between larvae from the southern Peninsula and California. Together, these suggest the presence of two spawning stocks, coastal migratory and dwarf, adapted to different environmental conditions along the west coast of the Baja California Peninsula. Finally, there is insufficient evidence of common spawning grounds along the coast of the Baja California Peninsula of two species, the common *M. productus* and the very rare *M. angustimanus*.

We thank the staff at the Plancton y Ecología Marina Laboratory and Centro de Investigación Científica y Educación Superior de Ensenada for collecting and processing the samples. This project was funded by grants from SIP-IPN, FONSEC-CONACYT and IMECOCAL. We also thank the reviewers for their valuable comments.

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