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Research Article

Distribution and abundance of the ichthyoplankton assemblages and its relationships with the geostrophic flow along the southern region of the California Current

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ABSTRACT. The distribution of ichthyoplankton assemblages (summer 1999 and winter 2000) from the southern region of the California Current (CC) off the Baja California Peninsula were analyzed. Latitudinal and ocean-coast distribution limits of the assemblages were associated with the geostrophic flow, which showed the presence of cyclonic and anticyclonic eddies in the northern and central region of the Baja California Peninsula. The comparative analysis of distribution and abundance of the developmental stages (egg to preflexion, flexion, and postflexion larval stages), showed that each mesoscale eddy had a specific ichthyoplankton assemblage, and the ichthyogeographic regionalization of the study area was determined by the presence of eddies and fronts. Retention processes were observed on epipelagic and demersal species where the fish larvae were maintained near the coastal region.

Keywords: fish larvae, geostrophic flow, eddies, larval drift, Baja California Península.

INTRODUCTION

The main task on ichthyology has been to determine which are the most important factors driving the distribution and abundance of fish species. The establishment of Hjört´s hypothesis that recruitment success of fish populations depends on their egg and larval survival (Hjört, 1914), leads us to expect that factors driving the ichthyoplankton distribution could explain the general distribution patterns observed in the adults.

Environmental variables such as temperature, salinity, and oxygen concentration among others, stimulate spawning as well as egg and larval development (Boehlert & Mundy, 1988). It is also accepted that physical processes such as ocean currents, eddies, and upwellings can affect larval dispersion (Parrish *et al*., 1981; Haury *et al*., 1993; Moser & Smith, 1993; Inda-Díaz *et al*., 2010) as well as food and predator concentration, which in turn determines larval survival (Muhling & Beckley, 2007; Aceves-Medina *et al*., 2009). Hence, changes in regional oceanographic characteristics influence the larval fish distribution as well as recruitment success (Doyle *et al*., 1993).

The seasonal changes in larval fish composition and abundance in the area influenced by the California Current (CC) are determined mainly by the reproductive strategies of the different species in terms of spawning areas and seasons, as well as the hydrodynamic conditions (Loeb *et al*., 1983a, 1983b; Moser *et al*., 1987). Two main fish larvae species assemblages have been found in the CC area: a northern species group (mainly winter-spring spawners) with temperate-subarctic affinity and a southern group

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(mainly summer-fall spawners) with warm water affinity. The transitional area between both northern and southern ichthyoplanktonic groups seems to be located off Punta Eugenia (Moser & Smith, 1993), coinciding with the boundary between the Californian and Panamic biogeographic provinces (Briggs & Bowen, 2012).

Latitudinal changes in the environmental conditions, which affect the fish spawning areas and periods, are related to the southward flow intensity of the CC, the poleward flow of the California Undercurrent, as well as the intermittent seasonal coastal flow of the poleward superficial California Countercurrent (Durazo *et al.*, 2005). Changes in the transitional area between northern and southern ichthyoplankton faunas have been observed seasonally depending on the intensity of these currents (Moser & Smith, 1993). During winter, spring, and part of the summer, subarctic water is predominant in the area, while the influence of tropical and subtropical water is observed from the end of summer until fall (Durazo, 2009).

There is evidence from several areas of the ocean that mesoscale structures determine the distribution gradients of fish larvae and other plankton groups (Moser & Smith, 1993; Muhling *et al*., 2007; Okazaki & Nakata, 2007; Espinoza-Carreón *et al*., 2012). Mesoscale eddies, as well as oceanic upwellings and fronts, are common in the CC (Loeb *et al.*, 1983a, 1983b; Espinosa-Carreón *et al.,* 2012). Punta Eugenia's region (Fig. 1a) has the highest eddy production in the tropical-subtropical transition zone of the northeastern Pacific. The maximum generation of anticyclonic eddies happens during April, as for the cyclonic eddies, it occurs during June (Kurczyn *et al*., 2012). However, Durazo (2009) demonstrated that the all-time mean of dynamic heights at a 200 m depth from the CalCOFI (1950-1978) and IMECOCAL (1997-2008) time series showed two distinctive dynamic regimes, delineated by two large-scale subsurface cyclonic eddies off Baja California that detached near the vicinity of Punta Eugenia (28ºN), and are the most prominent along the Pacific coast. In this work, we try to prove that these hydrodynamic conditions explain the distribution of the fish larvae off Baja California.

For the study period of this work, Durazo *et al*. (2001) and Durazo & Baumgartner (2002) have already established that the geostrophic flow showed at least two contiguous eddies in summer 1999 and three during winter 2000 in the area between Ensenada and Punta Eugenia (Figs. 1b, 2a). For both seasons, the northernmost was the cyclonic Southern California Eddy (Bograd *et al*., 2000); it has been reported that the southern limit of this eddy at 30°N (Ensenada Front) drives strong changes in several variables in the pelagic ecosystem such as density, nutrients, productivity and fish larvae distribution (Moser & Smith, 1993). The anticyclonic eddy south of the Ensenada Front was characterized by oceanic waters (Durazo *et al*., 2001; Durazo & Baumgartner, 2002), and the area has been described as oligotrophic (Parrish *et al*., 1981; Baumgartner *et al*., 2008). The third eddy (cyclonic) was located off Punta Eugenia and was found only in winter.

Little is known about the effect of these contiguous eddies on the distribution and abundance of fish larvae assemblages from this and other regions of the world. In areas like the southern region of the CC, it has been suggested that the presence of fronts and eddies determines the location of the transition zone between the northern and southern faunas (Moser & Smith, 1993), but this has not been proved yet. This work analyzes the distribution of ichthyoplankton assemblages in the oceanic area of the southern region of the CC, off Baja California, and its relation with the geostrophic flow and the main environmental variables, based on the spatial comparative analysis of eggs, preflexion, flexion and postflexion larvae from two oceanographic surveys made during August 1999 and January 2000. We want to prove that the mesoscale structures evidenced by the geostrophic flow show different environmental characteristics that can determine the distribution and abundance of the ichthyoplankton assemblages.

MATERIALS AND METHODS

Data used in this work comes from two surveys from the Mexican monitoring program of the California Current, IMECOCAL (Investigaciones Mexicanas de la Corriente de California), which includes both neritic and oceanic stations off the Baja California Peninsula. Surveys took place during summer (August 8-22, 1999) with 79 zooplankton samples, and winter (January 14-31, 2000) with 89 samples. Zooplankton samples were taken along a sampling grid organized in 12 transects perpendicular to the coast, with a distance of 40 nm (~70 km) between them (lines 100 to 137) and 12 parallel transects with a distance of 20 nm (~35 km) between each one (Fig. 1a).

At each sampling station, measurements of conductivity, temperature, and pressure were taken with a Seabird CTD to 1000 m depth (when the depth allowed it); these measurements were used to calculate the Mixed Layer Depth (MLD) as well as dynamic heights. Surface geostrophic flows were estimated on the basis of the dynamic heights using reference levels of 0/500 db. The MLD and geostrophic flow used here were taken from Durazo *et al*. (2001) and Durazo &

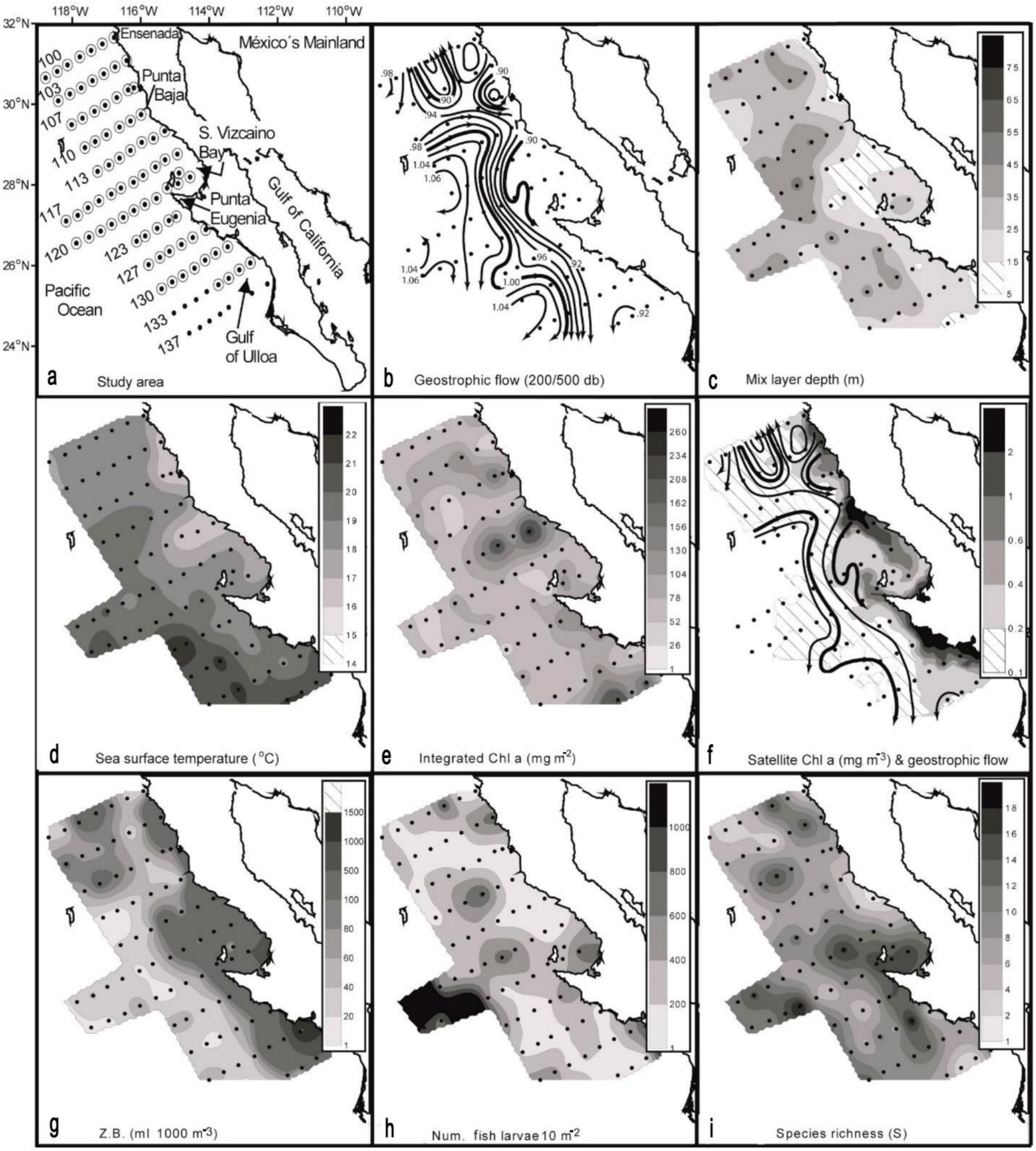

Figure 1. a) Study area with sampling stations during summer 1999 (O) and winter 2000 (●), b-i) physical and biological variables distribution during summer 1999. Arrows in Figure f represent the main geostrophic flow (between 0.9 and 1.2 db), overlapped with satellite Chl-*a* imagery.

Baumgartner (2002). The geostrophic flow was related to the distribution and abundance of ichthyoplankton.

Water samples were obtained at each sampling station with 5 L Niskin bottles at depths of 0, 10, 20, 50, 100, 150 and 200 m, and used to obtain chlorophyll-*a* (Chl-*a*) concentrations using a Turner fluorometer, following Hansen *et al*. (1965) and Venrick & Hayward (1984) methods. Discrete Chl-*a* data were used to calculate the water column integrated Chl-*a* concentration. In addition, representative composite Chl-*a* images for each survey (summer 1999 and winter 2000) were obtained from the SeaWiFS satellite (http://oceancolor.gsfc.nasa.gov). Both images were composed values of surface Chl-*a* values or 8 days (August 13-20, 1999 and January 17-24, 2000) with a resolution of 9×9 km.

Zooplankton samples were obtained using cylindrical-conical Bongo nets (3 m in length, 0.6 m in diameter and 505-µm net mesh) equipped with a flowmeter at the mouth, to estimate the filtered water volume (Smith & Richardson, 1977). Oblique Bongo tows were made from a maximum depth of 210 m up to the surface or 15 m above the bottom when depth was less than 210 m. Small zooplankton biovolume (ZB) of each sample was obtained measuring the displaced biomass (Beers, 1976) and standardized to mL 1000 m^{-3} of filtered water as in Smith & Richardson (1977) and Kramer *et al*. (1972).

Samples were fixed in 10% formalin buffered with a borax saturated solution. Only the ichthyoplankton material from one of the nets was used. Ichthyoplankton was sorted from each zooplankton sample and identified with a stereoscope using the identification guides of Moser (1996). Organisms were counted by species and by developmental stage (egg, preflexion, flexion and postflexion larvae) as in Ahlstrom *et al*. (1976) and Kendall *et al*. (1984). Ichthyoplankton abundance was standardized to the number of organisms under 10 m^2 of sea surface as in Smith & Richardson (1977).

Most of the fish larvae were identified to species level (91%). In the cases when larvae were identified to genus (8.5%) or family (0.5%), organisms were named as different morphological entities (*e.g.*, *Sebastes* sp. 1, *Sebastes* sp. 2, *Labridae* sp. 1) according to their meristic characteristics and their pigmentation patterns. A detailed description of the species composition and abundance of fish larvae for each survey is found in Jiménez-Rosenberg *et al*. (2007, 2010). In this work, the database used corresponds to the most abundant species (85% of the total larvae collected), as well as those species that although not abundant, were present in at least 15% of the sampled stations in each survey. Since there are no descriptions for most eggs of fish species in the surveyed region, only some of them were identified to species level. For this reason, eggs were not taken into account in the statistical analyses for species assemblages.

In order to determine if there was an ontogenetic spatial segregation related to the geostrophic flow and the environmental gradients observed, distribution maps of the assemblage's abundance by developmental stage (egg, preflexion, and postflexion) were made. When the eggs of species contained in an assemblage could not be identified, the distribution of preflexion larvae was compared with those of the flexion and postflexion stages.

To observe the relation between larval abundance and environmental variables, a canonical correspondence analysis was performed (CCA), with larval abundance as the main matrix; the secondary matrix was formed using MLD, sea surface temperature (SST), Chl-*a* and ZB. Species assemblages were obtained through a cluster analysis (CA) using the same larval abundance matrix. Species dendrograms were performed based on Bray-Curtis similarity index. Prior to CCA and CA analyses, larval abundance was transformed using the formula Log ($1+ x_{i,n}$), where "x" is the abundance of the *i-eth* species at the *n-th* sampling station.

RESULTS

During summer, the dynamic heights at 30ºN (Fig. 1b) indicated two flows with a different direction, one towards the north and other flowing from the oceanic region toward the coast that later turn southward (Fig. 1b). This pattern changed during winter (Fig. 2a) when the flow was from the northwest of the study area and later bifurcated with a branch flowing coastward and turning northward off Punta Baja (~29ºN), and a second branch that formed an anticyclonic eddy between 29 and 27ºN. South of this eddy, a meander that flowed southward and formed a cyclonic eddy was observed near to the Punta Eugenia region (Durazo, 2009; Espinoza-Carreón *et al*., 2012).

The patterns of the geostrophic flow observed for each season showed a strong relationship with the environmental conditions that are characteristic of the pelagic ecosystem off the Baja California Peninsula.

During summer (Fig. 1), the pelagic ecosystem depicted three main regions: 1) a coastal region that was characterized by a shallow MLD (5-25 m), low SST values (16.5-20.5ºC), high Chl-*a* (29-257 mg m^{-2}) and high ZB (70-1579 mL 1000 m^{-3}) (Figs. 1c, 1g); 2) an oceanic region north of 30ºN, the southernmost extension of the southern California eddy (Bograd *et al*., 2000), in which the MLD was deeper (15-35 m), higher SST (16-17ºC) relative to the SST near the coast at the same latitude, and lower values of Chl-*a* (28-100 mg m^{-2}) and ZB (20-500 mL 1000 m^{-3}); and 3) an oceanic region south of 30ºN characterized by the deepest values of MLD (25-45 m), highest SST (18-23ºC), the lowest Chl-*a* (20-80 mg m^{-2}) and minimum ZB values (1-60 mL 1000 m^{-3}) (Figs. 1c-1g).

Despite the fact that during winter an onshore-offshore gradient was observed (mainly north of Punta Eugenia), the main gradient was latitudinal (Fig. 2).

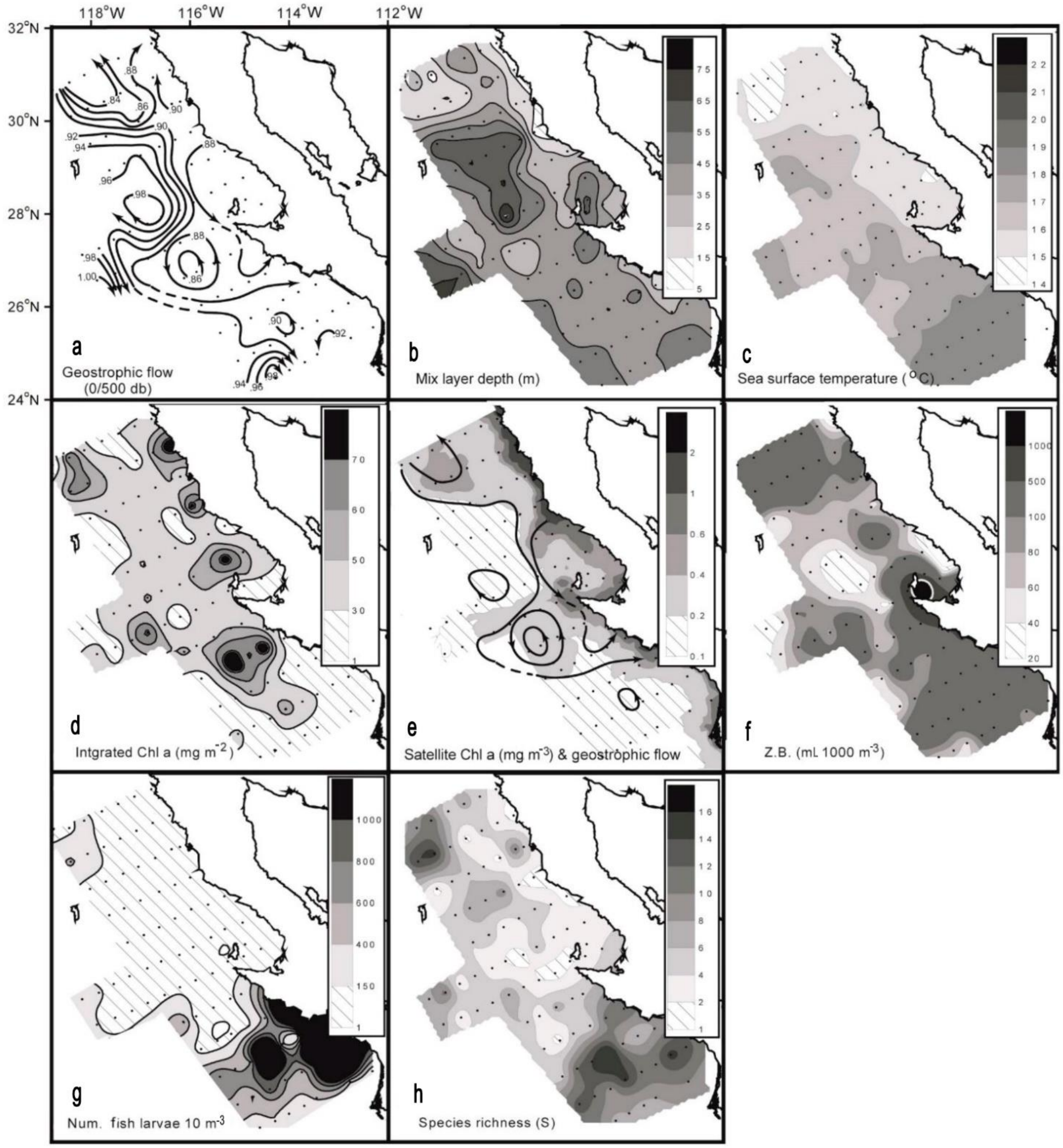

Figure 2. Physical and biological variables distribution during winter 2000. Arrows in figure e represent the main geostrophic flow (between 0.9 and 1.2 db), overlapped with satellite Chl-*a* imagery.

The presence of northern, central**,** and southern eddies during winter established three main regions on the pelagic ecosystem: 1) a region north of 30ºN, characterized by a shallow MLD (5-45 m), low SST (15-17ºC), intermediate Chl-*a* values (6-80 mg m^{-2}). and low values of ZB (20-334 mL 1000 m^{-3}); 2) a central region between 30º and 27.5ºN that had the deepest MLD (25-79 m), a small increment in SST (15-18ºC), intermediate values of Chl-*a* (1-70 mg m^{-3}) and low ZB values (30-395 mL 1000 m^{-3}) and; 3) a region south of Punta Eugenia, where MLD had intermediate values (21-52 m), the highest SST (18-19ºC), intermediate Chl-*a* values (17-95 mg m^{-2}), and the highest ZB values (49-465 mL 1000 m^{-3}) (Fig. 2).

In both summer and winter seasons, the overlapping of the geostrophic flow on the satellite Chl-*a* images and the ZB distribution maps showed a remarkable agreement with the dynamic height isolines (Figs. 1f, 1g, 2e-2f).

In summer, a total of 27,189 larvae were collected, with a mean abundance of 274 organisms per sample, while during winter the total number of larvae increased to 29,549 organisms with a mean abundance of 399 organisms per sample (Table 1). The total number of taxa identified to species level was 99 for summer and 74 for winter (Jiménez-Rosenberg *et al*., 2007, 2010). However, the most abundant and frequent species were 21 for summer and 23 for winter which together represented more than 90% of the total abundance for each season (Table 1).

The most abundant species during summer were *Vinciguerria lucetia*, *Triphoturus mexicanus*, and *Engraulis mordax*, which together represented 67% of the total abundance. During winter, the most abundant species were *E. mordax*, *Diogenichthys laternatus*, *V. lucetia*, *Sardinops sagax* and *Scorpaena* sp. 1 which represented 75% of the total larvae collected (Table 1). The remaining species (18 in both surveys) had abundances lower than 3% each (Table 1).

Environmental gradients associated with the geostrophic flow had a spatial match with the general ichthyoplankton distribution for both seasons. During summer, fish larvae distribution and species richness showed a latitudinal division at 30ºN where a gap area of low abundance and diversity of fish larvae were found, in coincidence with the limits of the northern eddy. South of 30ºN, a higher larval abundance was found in the oceanic area while a higher diversity was found in the coastal area (Figs. 1h, 1i). The larval fish distribution and diversity patterns coincide with the station clusters observed in the Q mode CA (Fig. 3a).

During winter, there was a notable latitudinal difference in the fish larvae abundance north and south of Punta Eugenia. To the south, the highest abundance and diversity of larvae was observed (Fig. 2g). Low species diversity was associated with the anticyclonic eddy in the central region (Fig. 2h). The CA in Q mode for winter showed two different groupings north and south of Punta Eugenia. The limits of those associations were defined by the limits of the cyclonic and anticyclonic eddies observed in the area. Also, associations corresponding to each mesoscale structure were observed (Fig. 3b).

In both periods the CCA showed that fish larvae abundance gradients were mainly influenced by the physical variables since the highest correlation values with statistical significance on Axis 1 were with the SST and the MLD. Axis 1 explained 13.1% of the total variance for summer and 11.4% for winter (Table 2). ZB had a significant correlation on Axis 2 (12.5% of the total variance explained in summer and 10.5% winter), and Chl-*a* only during summer on Axis 3 (1.6% of the total variance explained; Table 2).

Dispersion diagrams obtained with the CCA (Fig. 4), as well as dendrograms in R mode from the CA (Fig. 5), showed that in both seasons there was a spatial segregation of the abundance, which indicated that larval fish assemblages were determined by the adults' habitat. This resulted in two main species groups: an oceanic group constituted by mesopelagic species assemblages, and a coastal group constituted by larval fish assemblages associated with demersal and coastal-epipelagic environments.

Inside the main species clusters obtained from the CA in R mode (mesopelagic and coastal assemblages), there were also latitudinal distribution differences associated with the geostrophic flow. During summer (Fig. 5), a mesopelagic cluster was constituted by an assemblage composed of the subtropical-subarctic species *Lestidiops ringens* and *Lampadena urophaus* (SMG1), which were distributed mainly south of 30ºN (Fig. 6a) associated with the flow from the central Pacific. A second assemblage (SMG2) composed of one subarctic-temperate species (*Nannobrachium ritteri*), a central water mass species (*Diogenichthys atlanticus*) and a transitional species (*Symbolophorus californiensis*), that was distributed north of Punta Eugenia, with higher abundance and frequency north of 30ºN and offshore of the southward flow (Fig. 6b). A third assemblage (SMG3) composed of species with tropical-subtropical affinity was distributed throughout the study area (Fig. 6c).

For the mesopelagic cluster, only eggs of *V. lucetia* from SMG3 could be identified. Even though, fish larvae of the six species forming SMG3 had a wide distribution in the study area (Fig. 6c), the spatial distribution of the different developmental stages (egg to postflexion) of *V. lucetia* was practically the same, suggesting a very low dispersion of eggs and larvae coastward (Figs. 6d-6e).

The coastal-pelagic and demersal species cluster had an assemblage named SCG1 composed by *E. mordax* and *Chromis punctipinnis* distributed through the entire coastal region (Fig. 6g). A second coastal assemblage (SCG2) composed by *Etrumeus teres*, *S. sagax*, and *Prionotus ruscarius* had the same distribution except in the area north of 30ºN (Fig. 6h). Eggs of *E. teres* and *S. sagax* having the same spatial distribution as the larvae suggest a strong retention of the early life stages of this species in the coastal waters, which seems to be related with the main geostrophic flow (Fig. 6i).

Table 1. Most abundant fish larvae species during summer 1999 and winter 2000. AB: total standardized abundance and %: relative abundance.

Summer 1999	AB	%	Winter 2000	AB	%
Vinciguerria lucetia	12,382	45.5	*Engraulis mordax*	10,730	36.3
Triphoturus mexicanus	5,195	19.1	*Diogenichthys laternatus*	3,337	11.3
Engraulis mordax	831	3.1	*Vinciguerria lucetia*	2,930	9.9
Prionotus ruscarius	719	2.6	*Sardinops sagax*	2,744	9.3
Sardinops sagax	662	2.4	*Scorpaena* sp. 1	2,526	8.5
Bathylagoides wesethi	578	2.1	*Macroramphosus gracilis*	813	2.8
Etrumeus teres	569	2.1	*Synodus lucioceps*	569	1.9
Ceratoscopelus townsendi	546	2.0	*Triphoturus mexicanus*	488	1.7
Diogenichthys laternatus	519	1.9	*Merluccius productos*	479	1.6
Chromis punctipinnis	423	1.6	*Protomyctophum crockeri*	391	1.3
Cyclothone acclinidens	381	1.4	*Sebastes* sp. 1	342	1.2
Cyclothone signata	290	1.1	*Nannobrachium idostigma*	279	0.9
Symbolophorus californiensis	245	0.9	*Citharichthys stigmaeus*	258	0.9
Protomyctophum crockeri	237	0.9	*Citharichthys fragilis*	206	0.7
Diogenichthys atlanticus	218	0.8	*Nannobrachium ritteri*	202	0.7
Melamphaes lugubris	179	0.7	*Symbolophorus californiensis*	188	0.6
Notoscopelus resplendens	148	0.5	*Hygophum atratum*	177	0.6
Scorpaena guttata	140	0.5	*Cyclothine signata*	152	0.4
Lampadena urophaos	131	0.5	*Chiasmodon niger*	142	0.4
Nannobrachium ritteri	129	0.5	*Diogenichthys atlanticus*	133	0.4
Lestidiops ringens	117	0.4	*Leuroglossus stilbius*	128	0.4
			Cyclothone acclinidens	127	0.4
			Stomias atriventer	105	0.4
Totals of main species	24,640	90.6	Totals of main species	27,447	92.6
Remaining 78 species	2,549	9.4	Remaining 51 species	2,102	7.4
Total abundance (summer)	27,189		Total abundance (winter)	29,549	

During winter, the CA showed again a cluster composed only of mesopelagic species and the second one of coastal-pelagic and demersal species, except for *Leuroglossus stilbius* which is a mesopelagic species (Fig. 5b). Three main mesopelagic species assemblages were found. One was the group WMG1 with three species of warm affinity including the Eastern Tropical Pacific, *V. lucetia*, *D. laternatus* and *T. mexicanus* together with *Protomyctophum crockeri* of transitional affinity. This group was distributed in the entire study area (Fig. 7a). However, spawns of *V. lucetia* were exclusively oceanic south of Punta Eugenia; *V. lucetia* preflexion larvae had a distribution similar to the eggs, while flexion and postflexion larvae reached the central and northern region of the study area within the anticyclonic eddy (Figs. 7d-7f).

A second mesopelagic assemblage (WMG2) was composed by *Nannobrachium idostigma*, *Hygophum atratum*, *Cyclothone acclinidens* and *Stomias atriventer*. The general distribution of this group was mainly southern-oceanic off the Gulf of Ulloa and in some sampling stations over the outside northern limits of the anticyclonic eddy (Fig. 7b). Spatial location of eggs, preflexion and postflexioned larvae of *S. atriventer* suggest that its northern distribution was defined by the southern limits of the anticyclonic eddy off Punta Eugenia (Figs. 7g-7h).

The third mesopelagic assemblage (WMG3) was composed by species from the Central Water mass such as *N. ritteri*, *Cyclothone signata*, *D. atlanticus* and *S. californiensis*, which were distributed mainly between the oceanic area south of 30°N and Punta Eugenia (Fig. 7c). No eggs of these species were identified, but the distribution of preflexion larvae of the most abundant species of this group (*N. ritteri*) was practically restricted to the anticyclonic eddy between Punta Baja and Punta Eugenia, suggesting southward advection of the fish larvae with the geostrophic flow (Fig. 7i).

In the case of the coastal winter species cluster, the first assemblage (WCG1) was composed by demersal species such as *Sebastes* sp. 1, *Citharichthys stigmaeus* and *C. sordidus* (Fig. 5b). No eggs of these species were identified as well, but preflexion, flexion and postflexion larvae were exclusive to the cyclonic eddy and the

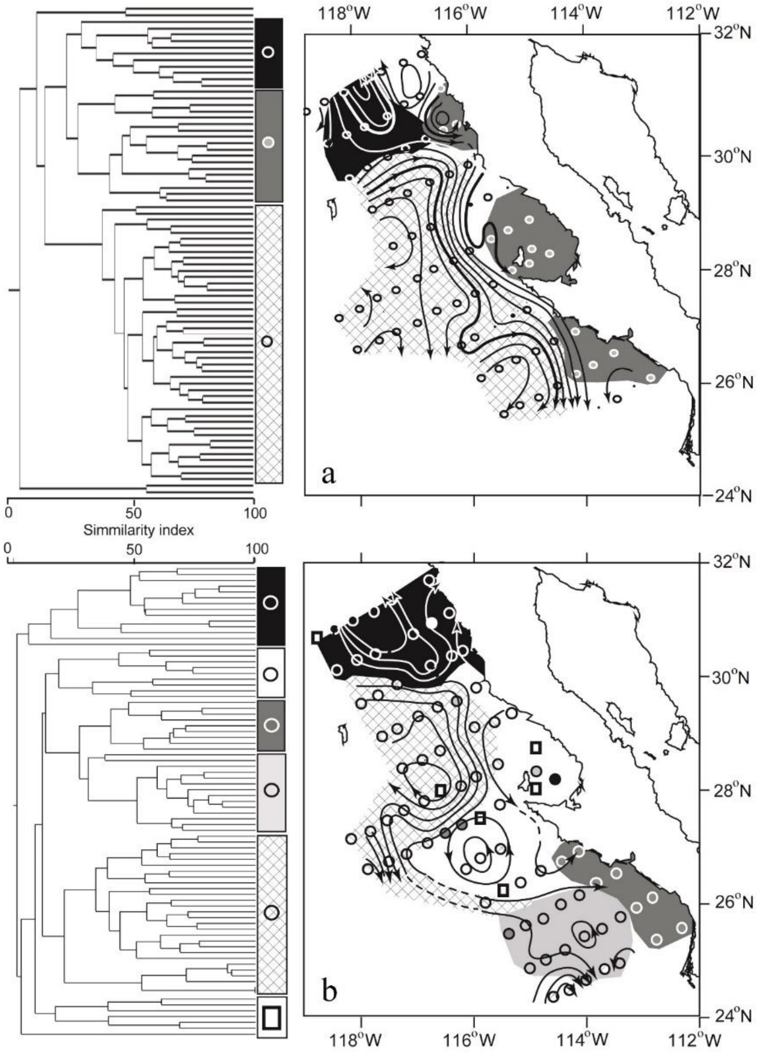

Figure 3. Cluster analyses in Q mode during a) summer 1999 and b) winter 2000. Arrows represent the geostrophic flow for each sampling period.

Table 2. Explained variance (EV) and correlation values of the environmental variables for each of first three axes from the CCA (summer 1999 and winter 2000).

	Summer 1999			Winter 2000		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
EV (%)	13.1	12.5	1.6	11.4	10.5	1.00
1 SST	0.68	0.64	-0.18	-0.92	0.09	-0.08
2 MLD	0.72	-0.46	-0.25	-0.24	0.72	0.29
3 Chl-*a*	0.19	-0.07	0.94	0.46	0.41	-0.30
4 ZB	-0.25	0.92	-0.16	-0.18	-0.63	-0.09

coastal area north of Punta Baja with few larvae off Punta Eugenia (Fig. 8a).

The second group (WCG2) was formed by one mesopelagic (*L. stilbius*) and one deep demersal (*Merluccius productus*) species. Eggs of both species were observed throughout the study area (even in the central region), but larvae were only found at the edges of the area forming both northern and southern subgroups (Figs. 5b, 8b, 8c). The third assemblage was constituted by coastal pelagic and demersal species (WCG3) such as *E. mordax*, *S. sagax*, *Synodus lucioceps*, *Scorpaena* sp. 1, and *Citharichthys xanthos-*

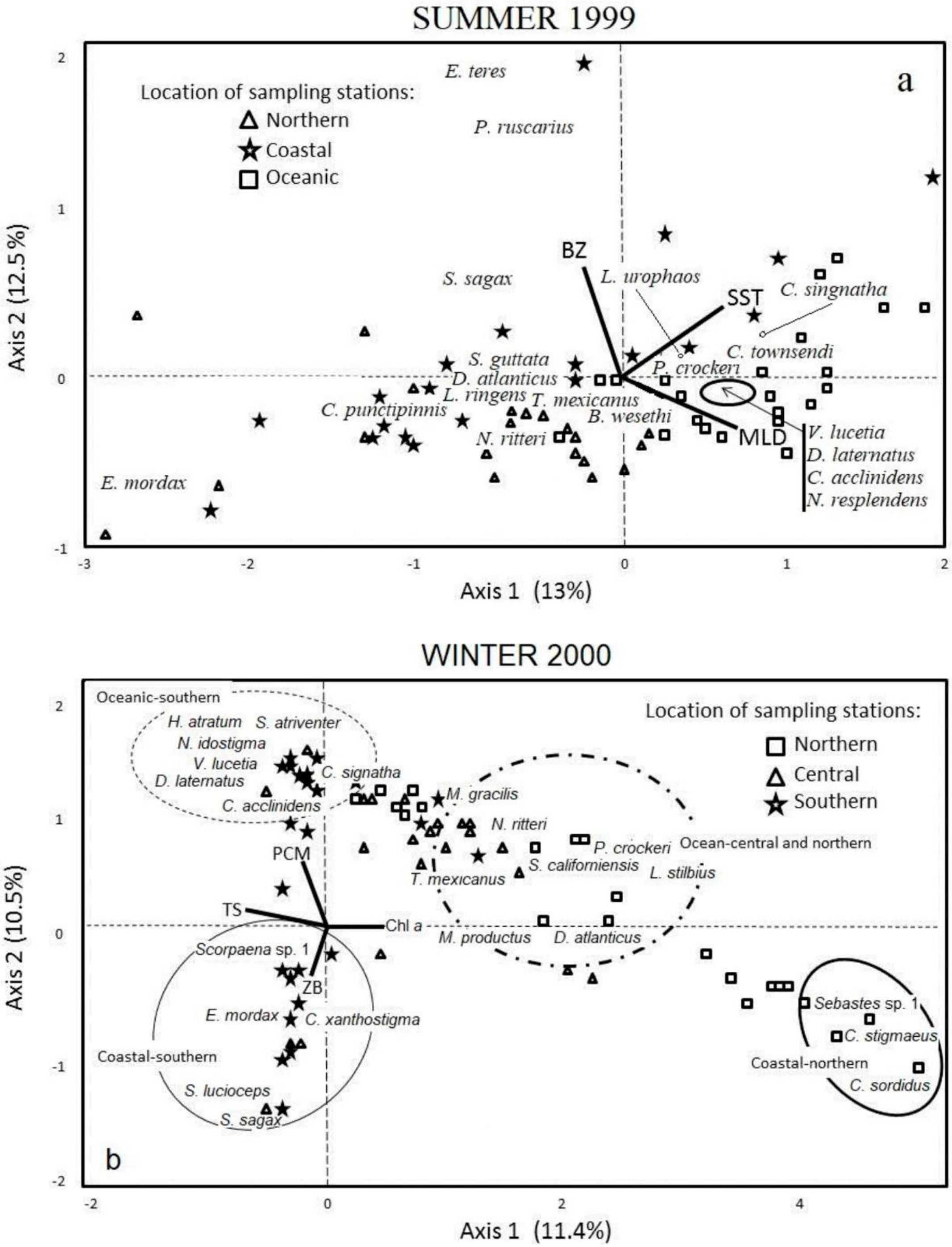

Figure 4. Dispersion diagram from the Canonical Corresponding Analyses. a) summer 1999 (northern stations Δ, coastal stations ★, oceanic stations □), b) winter 2000 (northern stations Δ, central stations ★, southern stations □).

tigma (Fig. 5b) distributed south of Punta Eugenia, mainly in the Gulf of Ulloa (Fig. 8c). Egg distribution of the first three species showed three main spawning areas: Sebastian Vizcaino Bay, the coast of the Gulf of Ulloa and a small region in the oceanic edge of this gulf. Distribution of eggs (Fig. 8e) and larval stages (Fig. 8c) suggest larval retention in the coastal region of the Gulf of Ulloa and Sebastian Vizcaino Bay, which was associated to the main flow of the current toward the coast south of Punta Eugenia. However, some larvae drifted to the oceanic region between the anticyclonic and cyclonic eddies off Punta Eugenia (Fig. 8c).

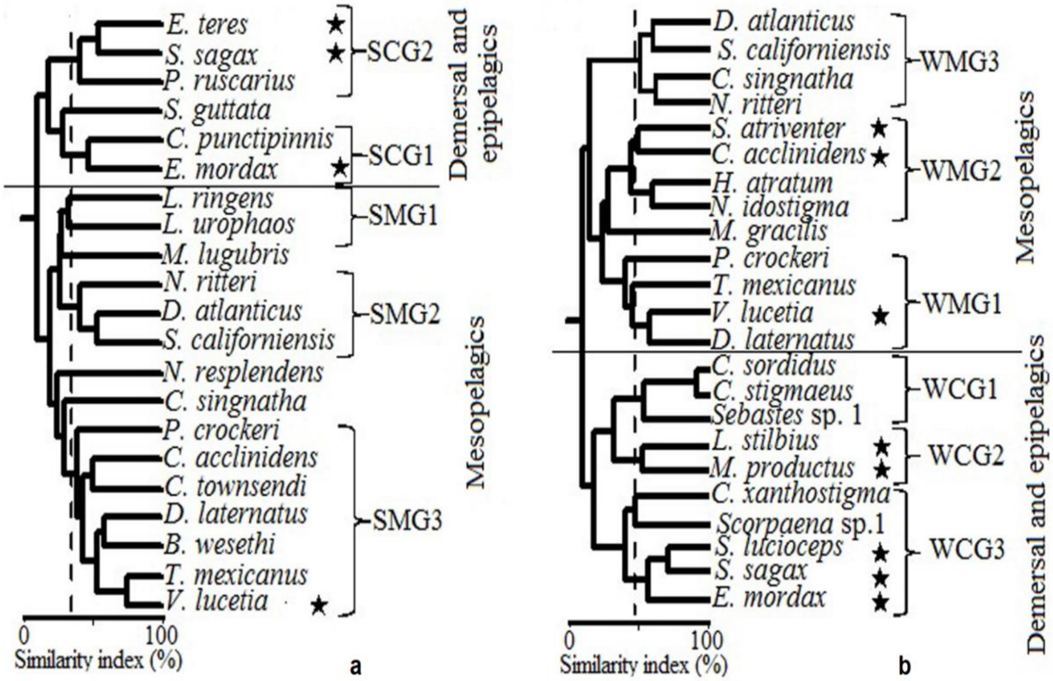

Figure 5. Dendrogram from the Cluster Analyses in R mode during: a) summer 1999 and b) winter 2000. S: summer, W: winter, C: coastal, M: mesopelagic, G: group. Stars indicate those species whose eggs could be identified.

DISCUSSION

This study examined the relationship between the geostrophic flow and the ichthyoplankton composition and abundance in the southern region of the CC during summer 1999 and winter 2000. This region includes an area north of Punta Eugenia (28°N), where subarctic waters dominate the upper ocean layer (0-100 m) all year long, and another to the south, where there is influence of tropical and subtropical water during summer and autumn, as well as waters of subarctic origin in winter (Durazo *et al*., 2001; Durazo, 2009).

These latitudinal differences in the distribution of water masses between summer and winter establishes the greatest environmental contrast in the area throughout the year and determine the two main faunistic complexes found here and in previous works (Loeb *et al*., 1983a, 1983b; Moser *et al*., 1987; Moser & Smith, 1993). Taking this into consideration, the assemblages' regionalization, as well as their relationship with the environmental conditions observed in this study, can be considered as representatives for each region and seasonal period.

As has been observed in similar areas (Olivar *et al*., 2016) data obtained in this work showed that during both analyzed periods, surface circulation explained the temperature distributions as well as MLD. The dispersive property of cyclonic eddies (Condie & Condie, 2016) explained the lowest SST, the shallowest MLD as well as the high density of photosynthetic pigments and ZB compared with the surrounding areas of each eddy. In contrast, warm core anticyclonic eddies were associated with the deepest MLD and lowest density of Chl-*a* and ZB.

It is noted that although distribution patterns of the physical and biological variables used here established environmental gradients in the marine pelagic ecosystem off the Baja California Peninsula, which determined the fish spawning sites, the relationship observed with the CCA (Fig. 4) between species abundance and environmental gradients (SST, MLD, Chl-*a* and ZB) is also a co-variation of these parameters driven by the geostrophic flow. Due to this, although the comparison between the distribution of the different development stages suggests in some cases dispersal processes of eggs and larvae, this dispersion seems to happen in the limits of the structures marked by the geostrophic flow, since each one of them has a different fish larvae association.

For example, the geostrophic flow and the physical characteristics of the water column observed in this study at 30°N (Durazo *et al*., 2001; Durazo & Baumgartner, 2002) demonstrate the presence of the southern boundary of Southern California Eddy (Bograd *et al*., 2000), known as the Ensenada Front (Haury *et al*., 1993). For both summer and winter, the

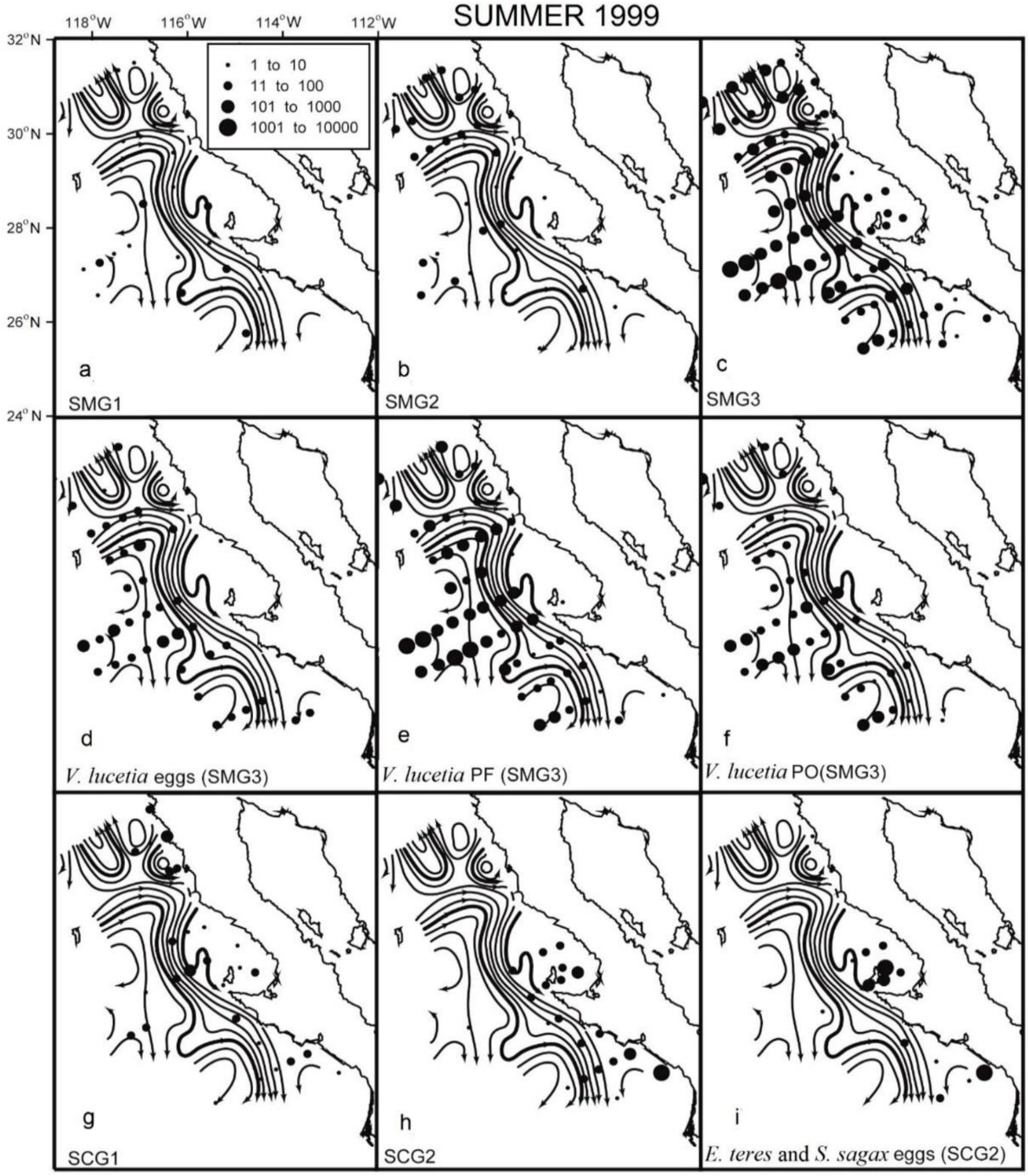

Figure 6. Distribution and abundance of a) SMG1, b) SMG2, c) SMG3, d) *V. lucetia* eggs, e) *V. lucetia* preflexion larvae, f) *V. lucetia* postflexion larvae, g) SCG1, h) SCG2, i) *E. teres* and *S. sagax* eggs. S: summer, M: mesopelagic, C: coastal, G: group, PF: preflexion, PO: postflexion. Abundance scale is given in individuals per 10 m^2 of the sea surface. Arrows represent the geostrophic flow.

CA shows two distinct associations on both sides of the front.

During summer, the distribution limits of the northern species such as those forming the SMG2 (Fig. 6b) were closely related to the Ensenada Front. This was also observed during winter, where the Ensenada front represented the distribution limit for the WCG1group (Fig. 8a). Strong changes in phytoplankton and zooplankton abundance between the Southern California Bight and northern Baja California have been explained as a result of the restriction of the southward transport of coastal water from central and southern California, plus the reduction of productive coastal habitat to the south by the constriction of the oceanic habitat into the coast (Parrish *et al*., 1981; Baumgartner *et al*., 2008). These constraints favor environmental gradients across the Ensenada front in several variables such as density, dissolved oxygen, nutrients, productivity, etc., which also affect fish larvae distribution (Moser & Smith, 1993). Although

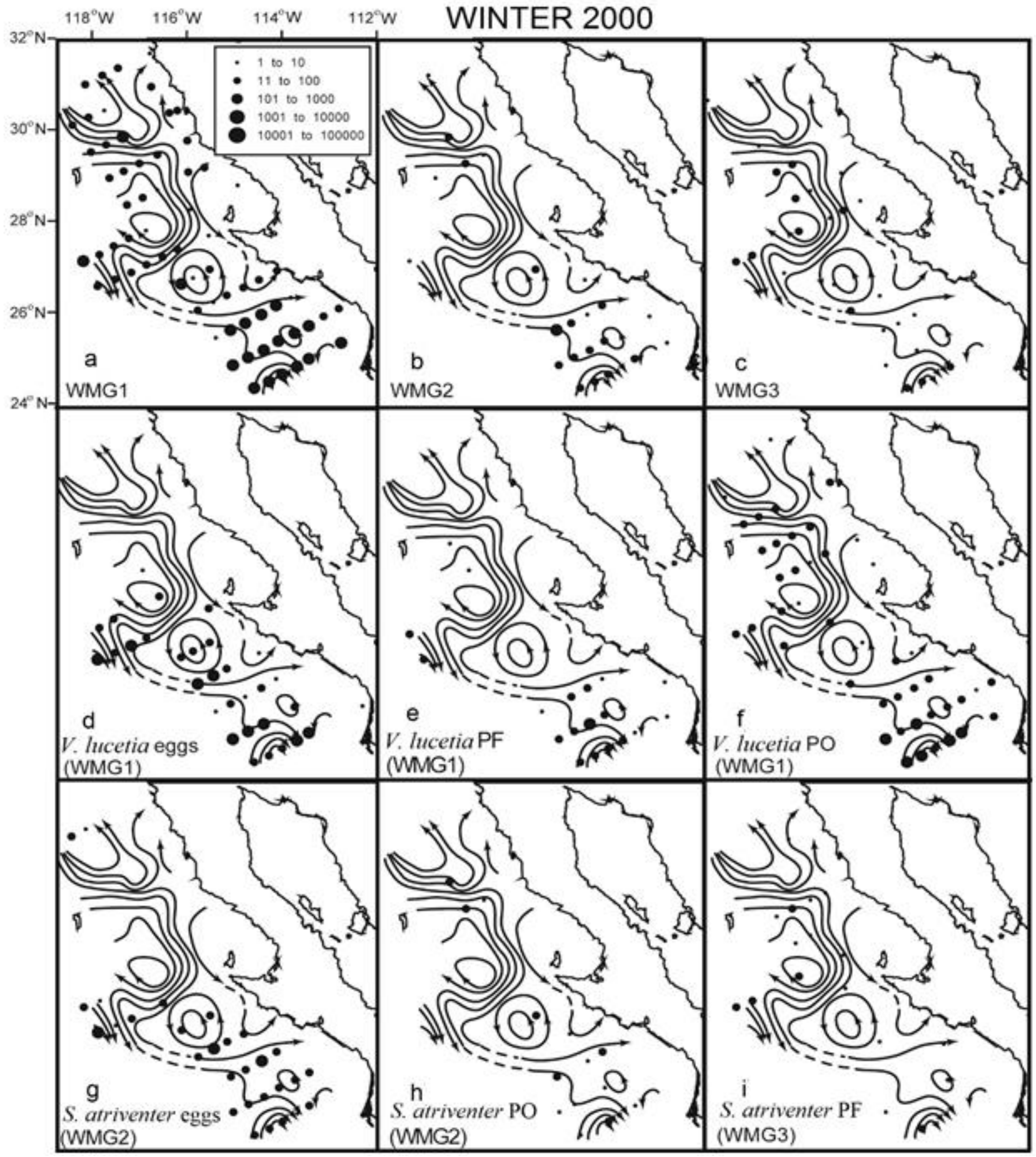

Figure 7. Distribution and abundance of a) WMG1, b) WMG2, c) WMG3, d) *V. lucetia* egg, e) *V. lucetia* preflexion larvae, f) *V. lucetia* postflexion larvae, g) *S. atriventer* egg, h) *S. atriventer* postflexion larvae, i) *N. ritteri* preflexion larvae. W: winter, M: mesopelagic, C: coastal, G: group.

the effect of the Ensenada Front on the distribution of fish larvae has already been described by Moser & Smith (1993), they only observed a marked effect on the summer mesopelagic species, whereas in this study we verify an effect in winter on coastal species like *C. sordidus*, *C. stigmaeus*, and *Sebastes* sp. 1, of temperate affinity and whose distribution limits were observed north of the Ensenada Front.

During summer, south of the Ensenada Front, the neritic species maintained an onshore distribution, while oceanic species are clearly situated away from the coast (Fig. 6) as a consequence of the offshore advection produced by the upwelling processes typical of spring-summer months (Loeb *et al*., 1983a, 1983b) and the limits established by eddies. Spatial segregation between coastal and oceanic species can be seen in both

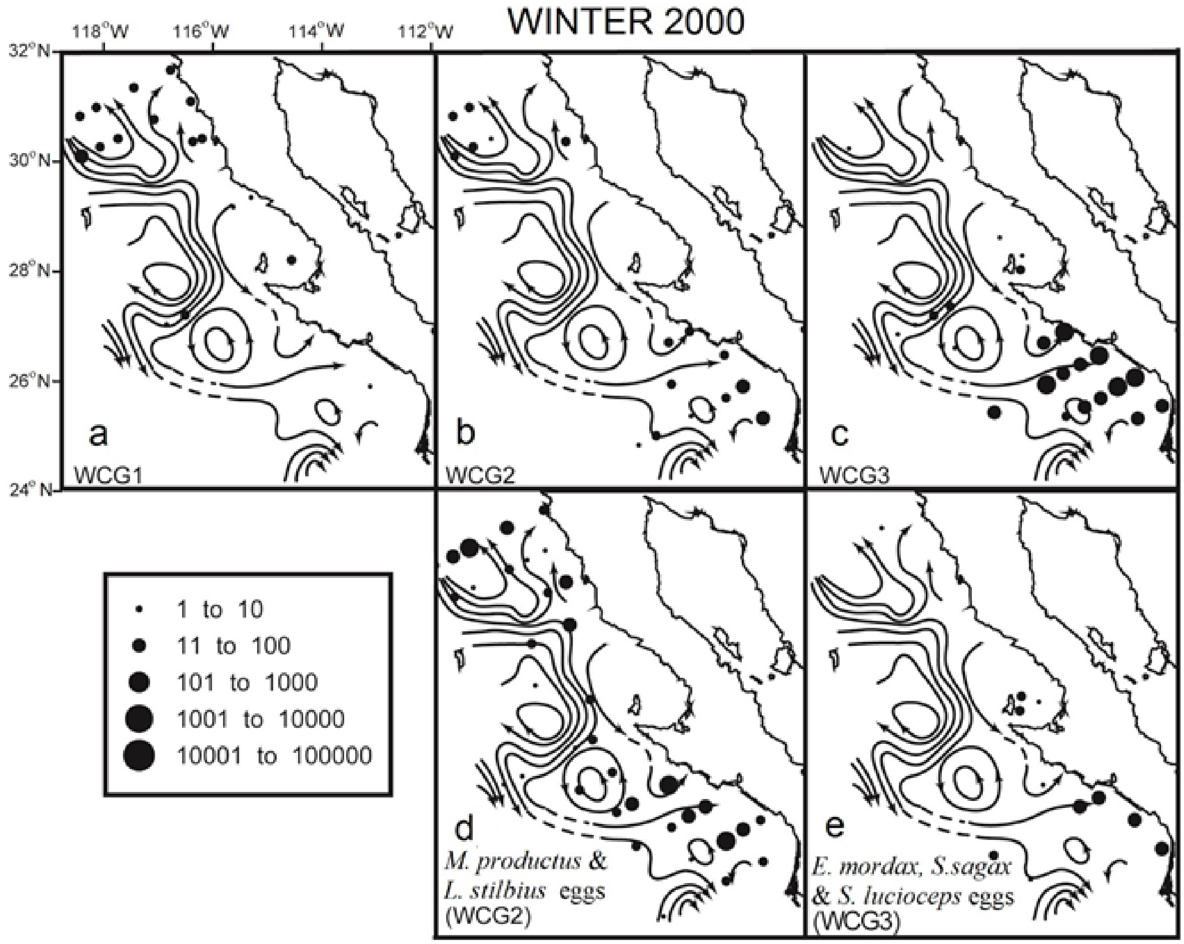

Figure 8. Distribution and abundance of a) WCG1, b) WCG2, c) WCG3, d) *M. productus* and *L. stilbius* egg, e) *E. mordax*, *S. sagax*, and *S. lucioceps* eggs. W: winter, M: mesopelagic, C: coastal, G: group, PF: preflexion, PO: postflexion. Abundance scale is given in individuals per 10 m^{-2} of the sea surface. Arrows represent the geostrophic flow.

egg and larvae distributions south of 30ºN (Fig. 6), which in all cases had the same distribution, and was defined by each of the mesoscale structures observed. Spawning areas of the coastal epipelagic species in SCG2 (*E. teres* and *S. sagax*) and the corresponding distribution of its larvae (Figs. 6h-6i), suggest retention of coastal-pelagic and demersal larvae along the entire coastal region of the peninsula. However, the spawning areas of some mesopelagic species such as *V. lucetia* compared with its larvae distribution, suggest that coastward dispersion of these larvae was limited by the mesoscale structures (Figs. 6e-6f) such as has been observed in the Kuroshio Branch Current (Hsieh *et al*., 2017). Studies in the Canary Current system showed that combined effect of the upwelling front and a cyclonic-anticyclonic eddy dipole is likely to be a successful retention mechanism for coastal species and support the current belief that retention may be higher than previously thought in an upwelling area (Moyano *et al*., 2014).

During winter, when cyclonic and anticyclonic eddies were more evident off the peninsula (Bograd *et al*., 2000; Durazo *et al*., 2001; Durazo & Baumgartner, 2002; Espinosa-Carreón *et al*., 2012) and upwelling processes decreased (Bograd *et al*., 2000), the major gradients observed in the ichthyoplankton distribution and abundance were in the latitudinal direction. The region between the Southern California Eddy (30°N) and Punta Eugenia was a zone with few primary producers and zooplankton organisms. South of the Southern California Eddy (30°N), the water flows eastward and is characterized by oligotrophic waters (Baumgartner *et al*., 2008) where a predominance of mesopelagic species such as *V. lucetia*, *T. mexicanus* and *D. laternatus* (WMG1), whose distribution was driven by the anticyclonic eddy north of Punta Eugenia, was found (Fig. 7a). In this case, developmental stages distribution south of Punta Eugenia showed that while the main spawning areas of the WMG1 and WMG2 were found in the oceanic region, late larval stages were transported from the spawning site throughout the anticyclonic eddy off Sebastian Vizcaino Bay, reaching the coastal area (Fig. 7). Thus, although the ontogenetic spatial segregation suggests larval dispersion processes, data shown here indicates this segregation occurs inside an area with similar characteristics (physical and biological) defined by the mesoscale eddies and the main direction of the geostrophic flow.

Although the anticyclonic eddiy facilitates the transport of oceanic larval species toward the coast during winter, it also favored a partition of the nursery habitat for other species, as in the case of the WCG2 species (*M. productus* and *L. stilbius*) (Fig. 8), which spawned along the entire study area, but the eddy apparently promoted disjunctive larval distribution in both north and south of its edges (Fig. 8b). It is important to note that at approximately 28°N, discontinuities in morphometric measurements, meristic counts, and proportion of selected protein polymorphs were observed in pioneering works between north and south fish populations of *E. mordax*, *S. sagax* and *M. productus* (Hubbs, 1925; Clark, 1947; Vrooman & Paloma, 1976; Owen, 1980; Parrish *et al*., 1981). Spatial coincidence between these biological discontinuities and strong semi-permanent eddies suggest that these mesoscale structures also act as mechanisms that promote the presence of geminate species north and south of Punta Eugenia, especially on populations that time their spawning with these eddies (Hewitt, 1981; Parrish *et al*., 1981). This work supports the previous hypothesis which is based on the effect of eddies on the planktonic stages, as we were able to see that eddies affect the distribution of the eggs and fish larvae.

It is important to note that during the summer, the distribution of neritic species of subtropical affinity and the mesopelagic species of warm waters of the central Pacific reached 30ºN. However, during winter there were no coastal associations in Vizcaíno Bay, and the distribution limits of tropical and subtropical neritic species only reached Punta Eugenia. Nevertheless, the mesopelagic species of warm water affinity maintained their distribution limit to the north in the Ensenada Front. This difference in the distribution of fish larvae associations is related to the presence of the system of both cyclonic and anticyclonic eddies off Punta Eugenia in winter, which showed a low diversity and abundance (Fig. 2), and represent the transition zone between the northern and southern fauna obtained in the CA (Fig. 3b). According to this, we suggest that both eddies located off Punta Eugenia determined the transition zone between the northern and southern neritic fauna of the CC.

According to the findings, distribution of the fish larvae assemblages off the west coast of the Baja California Peninsula are determined seasonal and locally by environmental variables such as the SST and food availability, among others, which are stimuli for spawning (Lynn, 2003) and precursors of the larval fish assemblages (Jiménez-Rosenberg & Aceves-Medina, 2009). However, as has been noted in other regions (Moyano *et al*., 2014; Olivar *et al*., 2016; Hsieh *et al*., 2017) it is the ocean currents and determining the distribution of ichthyoplankton assemblages. their inherent mesoscale structures (eddies, meanders, etc) that seem to be the local factors

Specifically for the western coast of the Baja California peninsula, the Ensenada front acts as a border for northern and southern communities of mesopelagic species, whereas in winter, the establishment of a system of eddies (cyclonic and anticyclonic) off Punta Eugenia determines the limits of distribution to the north of tropical and subtropical coastal fauna.

Even though ontogenetic segregation of some species showed evidence for dispersion inside mesoscale structures, physical barriers established during early summer (coastal upwellings) and winter (mesoscale eddies) determine larval dispersion processes to the north and south of the study area, particularly for those coastal epipelagic and demersal species.

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