

Interannual variability of the diversity and structure of ichthyoplankton assemblages in the central Mexican Pacific

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ABSTRACT

We examined larval fish diversity and assemblage structure on the central Mexican Pacific (coast of Jalisco and Colima) using data from samplings carried out with a Bongo net at 12 stations during 27 months, from December 1995 through December 1998. A total of 132 taxa were recorded, and the dominant species were *Bregmaceros bathymaster* (90% of the total abundance), *Dormitator latifrons* (1.9%) and *Harengula thrissina* (0.8%). Only *B. bathymaster*, *D. latifrons* and *Gobionellus* sp. attained the 100 % of occurrence. The effects of the 1997-98 El Niño event in ichthyoplankton diversity were significant, however the prevalence of the normal seasonality could be observed. Diversity null models were used to determine structural changes in the assemblage due to El Niño effects; both species richness and evenness were highest during El Niño. The most parsimonious models of assemblage organization include the El Niño and seasonality as most significant environmental variability sources. The small-scale spatial variability expressed as the cross-shore gradient was not relevant. The dominant species group formed by *B. bathymaster*, *D. latifrons*, and *Vinciguerria lucetia* typify for similarity both the previous and El Niño period and the only change was the abundance difference among periods. The El Niño period was typified by the dominant species *Bentosema panamense* and *H. thrissina*, and by the rare species *Euthynus lineatus*, and species of the genus *Lujtanus*. The assemblage

shows a similar organization in the different seasons, sharing the same dominant species group. Seasonality produces only changes in the abundances and relative frequencies of dominant species and different rare species are characteristic of the different seasons. The average taxonomical distinctness, that could be considered as a measure of functional diversity, was highly sensitive to the seasonal change of the assemblages independently of the El Niño; this index showed lowest values during tropical and transition periods characterized by warm and oligotrophic waters.

Key words: El Niño Southern Oscillation, fish larvae, diversity null models, taxonomical distinctness, species richness, evenness, assemblages, tropical Pacific

INTRODUCTION

The El Niño events are the most important interannual source of environmental variability in the Pacific Ocean and their impacts and consequences on marine ecosystems and ecological processes are still being surveyed. A large knowledge base has been cumulated about the pelagic habitat and the primary and secondary production in equatorial, subtropical and temperate areas of the north Pacific (Bograd and Lynn, 2001; Chavez et al., 1999; 2002; Fiedler, 2002), which has allowed characterising the main direct effects of El Niño events. However, many gaps remain about the knowledge of the middle- and long-term effects on larval and postlarval fish populations and communities in coastal tropical waters.

During ENSO events four main responses could be observed in the pelagic habitats: 1) a physical-biological coupling; the decrease in the availability of nutrients produce an immediate response of phytoplankton and zooplanktic biomass (Bograd and Lynn 2001; Chavez et al. 1999; 2002); 2) evidence of the prevalence of an attenuated seasonal signal in the environment and the planktic communities (Chavez et al. 2002; Franco-Gordo et al. in review); 3) a differential response along the cross-shore gradient, the nearshore zone shows higher productivity levels than deep zones and support the highest plankton densities (Chavez et al. 2002; Franco-Gordo et al., in review); and 4) changes in the species composition that could be found in practically all plankton groups. A tropicalization of the plankton has been reported in subtropical and temperate areas of the Pacific Northwest (Gómez-Gutierrez et al., 1995, Funes-Rodríguez et al., 1998; Lavaniegos et al., 2002; Mackas and Galbraith, 2002; Marinovich et al., 2002; Avalos-Garcia et al., 2003; Brinton and Townsend, 2003; Lavaniegos et al., 2003; Lavaniegos and Ohman, 2003; Smith and Moser et al., 2003).

The relationships between larval fish assemblages in the Pacific Ocean and hydrographic features have been documented in a wide range of systems (e. g. Avalos-Garcia et al., 2003; Doyle, et al. 1993; Franco-Gordo et al. 2002;

2003; Funes-Rodriguez et al., 1998; Miller et al., 1985; Moser and Smith, 1993; Sanchez-Velasco et al., 2000; Smith and Moser, 2003). Larval assemblages have been further explained as the result of convergent spawning strategies among members of a given postlarval assemblage (e. g. Sherman et al., 1984; Doyle et al, 1993). However few studies have reported analytical procedures to weight the importance of the environmental factors, and the potential hierarchies among the several sources of variability have not been formally approached.

Diversity estimation and ordination of assemblages are the methods most frequently used in community analysis to identify conspicuous features of the ecosystems and the underlying ecological processes. In the marine environment, there exists little empirical information on the relationship between marine diversity, stability and resilience (Allison et al., 1996). In ichthyoplankton communities, diversity is a valuable index that has been used to evaluate temporal or spatial variations in the species composition and to infer environmental changes. This is particularly relevant in a zone, as the central Mexican Pacific, with a high variability at several temporal scales that affect coastal processes and, as a consequence, the spatial patterns of larval fish (Franco-Gordo et al. in review).

In the central Mexican Pacific, the plankton community shows a markedly seasonal response in the spatial distribution of the primary production, zooplanktic biomass and larval fish abundance (Franco-Gordo et al 2001a; b), and larval fish assemblages (Franco-Gordo et al., 2002). During the 1997-98 El Niño event the normal patterns of zooplanktic biomass and larval fish abundance cited above were decoupled (Franco-Gordo et al., in review). An attenuated seasonal signal was recorded while the spatial distribution pattern disappeared. Here we analyse the interannual variability of the most conspicuous structural features of the larval fish communities. Diversity and assemblage structure are scale-dependent processes, and for this reason we analyse the longest available series of larval fish abundances in the central Mexican Pacific to test a set of hypotheses about the temporal and spatial organization of the larval fish communities. In this work we hypothesize that

temporal oceanographic and climatic processes, as normal seasonality and the ENSO event (1997-1998), are reflected in the ichthyoplankton community structure and spatial distribution.

STUDY AREA

The surveyed area comprises a fringe along the continental shelf off the coasts of Jalisco and Colima, central portion of the Mexican Pacific located between Punta Farallón, in Jalisco (19°19'77"N, 105°00'28"W), and Cuyutlán, Colima (18°58'24"N, 104°13'51"W) (Fig. 1). The continental shelf is narrow, comprising, up to the 200 m isobaths, only 7-10 km (Filonov et al., 2000).

The general hydrography of the study area is described by Wyrtky (1965) for the eastern Pacific Ocean and is characterized by a northeastward flow during summertime and southwestward in winter. The surface layer is formed by a seasonal, variable mixture of tropical surface water, and water from the California Current (CC). In winter and spring the area is influenced mainly by CC that is mixed with the Equatorial Countercurrent and the North Equatorial Current between 15°N and 20°N. In summer and autumn, the CC is weakened and the area is affected mainly by the northward flow of the tropical waters transported by the Equatorial Countercurrent through the North Equatorial Current and the Costa Rica Coastal Current (Pacheco-Sandoval, 1991; Wyrtky, 1965). In Jalisco and Colima coast the current patterns are defined by two main phases: The first one is influenced by the CC, the cool waters affect the area from January to May; the second phase characterized by a tropical water mass from the North Equatorial Countercurrent is present for the period July to November, a third phase is determined by the transition between both previous phases, characterized by a non-defined conditions in June and December. These environmental patterns determine the seasonal variability in the coastal ecosystem in the study area and affect the primary production (Franco-Gordo et al., in review) zooplanktic biomass and larval fish abundance (Franco-Gordo et al 2001), and larval fish assemblages and diversity (Franco-Gordo et al., 2002; 2003).

METHODS AND DATA

Samplings

The area was surveyed using a 12-station plan on board the BIP-V oceanographic vessel (Fig. 1) exclusively over the continental shelf. Zooplankton samplings were carried out monthly at night (20:00 to 07:00 h) from December 1995 through December 1998. No samplings were made in some months due to adverse climatic conditions or problems with the vessel. Zooplankton tows were performed following Smith and Richardson (1977). Samples were collected by means of a Bongo net with a 0.505 mm mesh size. This gear was hauled obliquely and the net was sent down tried to cover the most water column. A digital flowmeter was adapted to the net mouth in order to estimate the amount of water filtered. Previously to each tow, a profile of temperature and salinity was recorded using a CTD profiler SBE-19. Abundance data were standardized into number of larvae per 10 m² (Smith & Richardson, 1977).

Diversity

Diversity was analytically decomposed in its components using estimates of richness, evenness, and taxonomical distinctness. Species richness and evenness were estimated using two null models (Gotelli and Graves 1996, Gotelli and Entsminger 2001): rarefaction curves and the probability of an interspecific encounter (PIE). Data were pooled by cruise and depth strata and monthly estimates of diversity were obtained. In both rarefaction and PIE the calculus procedure employed the Monte Carlo method to generate mean and a confidence interval (95%) of diversity estimates. Several zooplankton studies have reported that the species assemblages during El Niño events are strongly recomposed and other species with different biogeographical affinities replace to the local communities. These make that a simple diversity index could be unable to detect the community changes, being necessary other diversity indexes such as those based on taxonomical relations. The taxonomical

distinctness has been proposed as a biodiversity index based on taxonomic (or phylogenetic) relatedness patterns within an assemblage (Clarke and Warwick 2001a), and is estimated by the average taxonomic distinctness and the variation in taxonomic distinctness. The average taxonomic distinctness (AvTD) is the average path length between every pair of species traced through a taxonomic tree:

$$\Delta^+ = \left[\sum \sum_{i < j} \omega_{ij} \right] / [s(s-1)/2]$$

where s is the number of species present, the double summation is over the set ($i = 1, \dots, s; j = 1, \dots, s$, such that $i < j$), and w_{ij} is the distinctness weight between species i and j . The taxonomic levels considered for us were from species to order. The variation in taxonomic distinctness (VarTD) is defined as:

$$\Lambda^+ = \left[\sum \sum_{i \neq j} (\omega_{ij} - \bar{\omega})^2 \right] / [s(s-1)]$$

Monthly estimates of both taxonomic distinctness indices by depth strata were obtained using pooled abundance-species data and the software Primer v5 (Clarke and Warwick, 2001b). To determine the influence of both seasonal and interannual source of variability in taxonomical distinctness measures (AvTD and VarTD) a two-way ANOVA was carried out.

The diversity estimates employed here are considered robust to abundance and effort biases (see Gotelli and Graves 1996; Clarke and Warwick 2001a). However, the Lambda index is not exactly unbiased as sample size changes Clarke and Warwick (2001a) but the bias is very small and could be not relevant.

Generalized linear models (GLM) were used to analyse the spatial and temporal patterns of the diversity components and their relationships with the environmental variables. The following environmental variables were used:

- Inshore and offshore sea surface temperature (SST) and salinity.

- The Multivariate ENSO Index MEI (Wolter & Timlin, 1993; 1998) as an indicator of El Niño/La Niña conditions in the tropical Pacific. The MEI is based on six highly correlated observed variables in the tropical Pacific: SST, atmospheric sea level, pressure (SLP), surface winds, zonal and meridional surface air temperature and total cloudiness. (Details on the computation of the MEI are available at: <http://www.cdc.noaa.gov/~kew/MEI/mei.html>).

- The upwelling index (UI) at 21° N (available at <http://www.pfeg.noaa.gov>).

Assemblage structure

We assume that the seasonality and interannual events as El Niño are the most influent temporal sources of variability in the pelagic habitat in the study area, whereas cross-shelf variability defines the main spatial gradient. A set of *a priori* hypotheses were designed to test a wide range of multivariate models of increasing complexity to explain assemblage structure variability in relation with environmental variables (seasonality, El Niño event and cross-shore distance). Three groups of models are considered: the first group include the full model (all the single variables and interactions) and models constructed removing one interaction in each step (the order was based in the factor weight). The second group (basic models) include only one single variable by model, and the third (other model) are constructed following the single factor weight including the highest factors.

The method consists in the use of canonical correspondence analysis (CCA) to measure the fit of model to data, and the use of a selection model procedure to determine the best model. Multivariate model selection, using the principle of parsimony and the hierarchical relation among the environmental factors explaining spatial and temporal variability of the ichthyoplankton

community, were carried out following the procedure proposed by Godínez-Domínguez and Freire (2003). The method use the Akaike information criterion (AIC):

$$AIC = -2\log[\ell(\hat{\theta})] + 2K$$

where k = the number of parameters. Simple transformations of the estimated residual sum of squares (RSS) allow obtaining the value of $\log [\sigma^2(\theta)]$ using least-squares estimation with normally distributed errors rather than the likelihood method. For all standard linear models, we can take

$$\log_{(\sigma^2)} [\sigma^2(\hat{\theta})] = -\frac{1}{n} \log \hat{\sigma}^2$$

where $\log = \log_e$, n is sample size and $\sigma^2 = \text{RSS}/n$. The trace obtained by each model using the canonical correspondence analysis (CCA) (ter Braak and Smilauer 2002) was employed to estimate the residual sum of squares (RSS):

$$\text{RSS} = (\text{sum of all eigenvalues}) - \sum_{i=1}^h \text{trace}_i$$

Partial canonical correspondence analysis (Borcard et al. 1992) was carried out to determine the individual weight of the spatial and temporal factors and their interactions. The procedure described above allows to determine the most parsimonious model however the variance decomposition allow us to quantify the weight of the variables (single variables and interactions of them) employed in the fitted models.

Non-metric multidimensional scaling (MDS) (Clarke and Warwick 2001b) was used to explore visually the ordination patterns of the most parsimonious models. The species assemblages that typify to the most parsimonious spatial-temporal models were determined by similarity-dissimilarity rank using the

SIMPER procedure (Clarke and Warwick 2001b). Bray-Curtis index and four-root transformation were used for both MDS and similarity-dissimilarity analyses.

RESULTS

The relative abundance of the 132 taxa sampled off Jalisco and Colima during 1995-1998 is shown in Table 1. *Bregmaceros bathymaster* was the dominant species in the assemblage representing 90.4% of the total number of larvae, whereas the following taxa showed low relative abundances, as *Dormitator latifrons* (1.9%), *Harengula thrissina* (0.9%), and Engraulidae (0.85%). This pattern of relative abundance shows clearly an uneven structure of the assemblage. *B. bathymaster*, *D. latifrons* and *Gobionellus* sp. were the only taxa that appeared in all the samples.

Diversity

During El Niño period the species richness was slightly higher than during the previous normal period in both offshore and inshore zones. The evenness index (PIE) showed an important increase during El Niño period and its variance decreased (Fig. 2). The seasonal pattern of diversity was prevalent both during El Niño and non-El Niño, but the main scale of temporal variability was interannual related to the ENSO events. The lowest diversity values were obtained during the period when the colder, more productive California Current flows along this coast southward from higher latitudes. These conditions produce decreases in diversity and allow the dominance of one or a few species.

The average taxonomic distinctness index (AvTD) did not show interannual patterns (ENSO effect) neither inshore nor offshore (Fig. 3). However lowest values of months corresponding to tropical period (July to November) and transition (December and June), and the anova results corroborate this statement (Table 2). The variation of taxonomical distinctness (VarTD) was in general larger than expected and this result could represent a

widespread of higher taxa or taxonomic richness during the normal periods and during El Niño (Fig. 3).

The generalized linear models GLMs (Table 3) confirm that the El Niño event was the most important source of temporal variability of the diversity. The multivariate ENSO index (MEI) and sea surface temperature (SST) were the main factors included in the models fitted for richness and evenness.

Assemblages

The most parsimonious model explaining the assemblage organization includes the ENSO event and seasonality, the second best model only include the ENSO event and the third best model include ENSO, seasonality and the interaction among them (Table 4). The parsimony is rooted in the concept of simplicity and considers only the minimum number of parameters or variables to explain a phenomenon. In this case, the best model only included seasonality and ENSO events to explain the variability of the larval fish assemblages, and posterior increases in the number of parameters in the model could add more complexity than information. The rank of models obtained by the procedure employed can be understood as a hierarchy of the models and implicitly as a hierarchy of environmental factors. The variance decomposition shows the single weight of the variables considered as the environmental variability. Season is the variable that more variance explains followed by ENSO, however season has three possible states (CC, tropical and transition) while ENSO only two (normal and ENSO period) and these is taken in account by the Akaike procedure. The spatial variability, expressed as inshore-offshore gradient is not considered as an important factor in the assemblage organization, and factors as interactions between ENSO and season, showed highest values of explained variance (see table 4).

Seasonal assemblage organization

The highest similarity of the species that typify the seasons of the period previous to the El Niño event reflect a high dominance of *B. bathymaster*. CC

period of 1996, tropical 1996 and CC in 1997, with values of similarity of 98, 87 and 96% respectively (Table 5);. The tropical seasons during El Niño period (Jul-Nov 1997 and 1998) showed more even similarity values. *B. bathymaster* was also during El Niño the dominant species, and only during the tropical period of 1997 *Harengula thrissina* recorded a highest similarity value.

Interannual assemblage organization

Similar species typified for similarity the assemblages for the normal and El Niño periods (*B. bathymaster*, *D. latifrons*, *Gobionellus* sp. Gobidae and *Vinciguerria lucetia*) (Table 6). The species that typify to dissimilarity are *B. bathymaster* Sciaenidae, *H. thrissina*, Engraulidae *Euthynus lineatus* and *Bentosema panamense*. *B. bathymaster* typifies for both similarity and dissimilarity of the community and this feature is due to the abundance differences between periods. Sciaenidae taxa and *Symphurus elongatus* and *Symphurus atramentatus* showed affinity for the normal period while *H. thrissina*, *E. lineatus*, *B. panamense*, and species of *Lutjanus* genus showed affinity for El Niño period.

DISCUSSION

Different processes related to spawning, oceanography and larval life histories affect the composition and distribution of the larval fish communities (Mullin, 1993), and during the El Niño these three aspects could be altered. The convergence of spawning strategies observed in fish communities (Dayle et al., 1993) could be due to the common goal of increasing the survival by coupling spawning with production processes and circulation-retention patterns (Parrish et al., 1981; Iles and Sinclair, 1982; Frank and Leggett, 1983; Werner et al., 1999; Winemiller and Rose 1992). In the central Mexican Pacific the peaks in the larval fish abundance coincide with primary and secondary production patterns and reproductive seasonality of the fish community (Franco-Gordo et al., 2001a; b; in review), corroborating that the spawning strategies in fish populations have evolved in synchrony with prevailing oceanographic

processes. However during El Niño event, spawning patterns, food availability and transport mechanisms could be modified and decoupled, and as a consequence the larval fish survival could decrease.

There are few studies available about the effect of the El Niño event on the spawning activity in fish communities of the tropical zones, or the differential responses of some fish populations. It is possible to assume that the environmental stress reduces in a different way the reproductive activity of different species, and by the other hand it is possible to assume variations in the ability of larval fish species in responding to the effects of impoverished environments, and these factors should be part of the mechanisms of resilience of the community in the Pacific region. Some species in subtropical areas as the sardine in the Gulf of California modify their spawning activity and distributional range as a consequence of ENSO events (Nevárez-Martínez et al., 2001, Sánchez-Velasco et al., 2002), which can diminish the larval abundance and shift their spatial distribution. The consequences of poor spawning during the El Niño alter the recruitment to adult populations in the following years (Sánchez-Velasco et al., 2002).

The changes of the abundance of coastal fishes in the central Mexican Pacific during El Niño event (Godínez-Domínguez et al., 2000; Madrid and Sánchez, 1997) could be produced by changes in their catchability, because extreme environmental changes could modify the spatial distribution of fish populations. Apparently, pelagic species as *Katsuwonus pelamis* and the sardine *Opisthonema libertate* move towards inshore waters during warm periods searching for food (Godínez-Domínguez et al 2000). The main environmental changes in the study area during El Niño event are positive temperature anomalies and the impoverishment of primary and secondary production (Franco-Gordo et al., in review). The shortage of food could produce the displacement of fish populations and reductions in the spawning activity, and these factors could be the reason because the larval fish assemblage shows higher values of species richness, evenness and lower abundances.

One of the most cited effects of the El Niño events in zooplankton studies in the subtropical, temperate and subarctic waters of the Pacific has been the tropicalization of the communities. These effects have been reported for most of the zooplanktonic groups (see Franco-Gordo et al., in review), including the ichthyoplankton communities. The irruption of a warmer water mass from the south modifies the oceanographic conditions and produces a displacement of the local communities by others with more tropical affinities. So, what could we expect in tropical areas about the assemblage composition and structure?

In our case, both components of diversity, species richness and evenness, show a slight increase during El Niño event due mainly to the abundance decrease and the shift toward inshore waters of the fish community. Unfortunately there are not studies focused in the determination of changes of the larval fish diversity under El Niño events. The main effects reported in larval fish communities during warm periods are the abundance decrease and assemblage recomposition (Avalos-García et al., 2003; Smith and Moser, 2001; Funes-Rodríguez et al., 1995), but assemblage structure has not been analyzed.

The average taxonomical distinctness (AvTD) of the assemblages showed significant seasonal differences but not interannual changes. The values of the AvTD were similar in both pre- and ENSO periods, however the lowest values were observed during the tropical and transition seasons. According to Clarke and Warwick (2001a) low values of this statistic denote environmental stress or disturbance; the first species disappearing are predominantly representative of higher taxa that are relatively species-poor, the remaining species pertain to taxonomic groups relatively more species-rich. AvTD, together with species richness and evenness, showed the existence of a low diversity assemblage during the tropical season, which is formed by a small group of species closely related phylogenetically. Taxonomical diversity could be related with functional diversity, and in this sense AvTD index could be interpreted in this case as a functional diversity measure indicating a decrease in functional diversity of the larval assemblage during a season defined by warm and oligotrophic waters inclusive of the El Niño event.

B. bathymaster was the most important species and typify for both similarity and dissimilarity in the previous and El Niño period. Other dominant species in both periods were *D. latifrons*, *Gobionellus* sp., Gobidae and *V. lucetia*. The species that discriminate the El Niño period are: *H. thrissina*, *E. lineatus*, *B. panamense* and larvae of the genus *Lutjanus*. The interannual variability due to El Niño event does not implies a drastic change in the species composition of the tropical larval assemblages, and, specially, the dominant species group remains constant. The main effects are defined by a decrease of abundance and changes in the dominance patterns due to an increase in evenness. The seasonal variability of the assemblages was similar to the interannual variability, because no changes in the dominant species group were observed, however during the tropical period (mainly during El Niño event) the similarity was most even and other species as *E. lineatus*, *V. lucetia*, *D. latifrons* and *Lutjanus* typified this assemblage.

During El Niño 1997-98, a drastic seasonal recomposition of the larval fish assemblages was observed in the Gulf of California (an area close to the present study area): the southern assemblage (central Gulf) was dominated by mesopelagic species as *B. panamense*, *V. lucetia* and showed a lower change than the northern assemblages which showed a more drastic seasonal recomposition of species with tropical and temperate-subarctic affinity (Avalos-García et al., 2003). Typical species of the tropical Pacific as *B. panamense* and *V. lucetia* have been reported as the most frequent and dominant in the Gulf of California (Aceves-Medina et al 2002; Moser et al., 1974), however the abundance recorded during El Niño 1997-98 for *B. panamense* reached 44 to 65% of the relative abundance per cruise (Avalos-García 2003). The tropicalization of the assemblages could be determined by the ocean warming generated by El Niño, but also by the seasonal irruption of the tropical water mass in the Gulf of California.

Interannual changes could be masked by long-term shifts of some larval species. *V. lucetia* has showed a sustained increase in abundance of nearly 200-fold from the 1976-77 regime shift in the Southern California Bight region

(Smith and Moser, 2003). The seasonal and interannual expansion of the tropical community towards the north together with other decadal scale variability in the Pacific, are the main forces that determine the large-scale distributional changes of ichthyoplankton. According to Smith and Moser (2003), the effect in the middle-term of environmental variability in temperate waters could be different for demersal and pelagic fish species and they suggest that other factors outweigh the shift described above, as fishing and other environmental variability sources, making difficult to find conclusive patterns.

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Table 1. Summary of the abundance and occurrence of the larval fish taxa found in the central Mexican Pacific during the 1995-1998 period. Taxa are sorted by mean abundance (organisms / 10 m²).

	Mean abundance	% of the total count	Cumulative percentage	Monthly abundance range		Frequency of occurrence
				% minimum	% maximum	
1 <i>Bregmaceros bathymaster</i>	15948.1	90.43	90.43	1.984	98.42	100.00
2 <i>Dormitator latifrons</i>	332.9	1.89	92.32	0.229	11.31	100.00
3 <i>Harengula thrissina</i>	150.3	0.85	93.17	0.040	42.06	59.26
4 Engraulidae	149.1	0.85	94.01	0.017	38.72	62.96
5 <i>Vinciguerria lucetia</i>	120.4	0.68	94.70	0.015	25.74	85.19
6 <i>Euthynus lineatus</i>	110.5	0.63	95.32	0.006	22.63	66.67
7 <i>Benthoosema panamense</i>	96.8	0.55	95.87	0.007	7.67	74.07
8 Sciaenidae	84.7	0.48	96.35	0.030	3.42	62.96
9 <i>Gobionellus</i> sp.	78.4	0.44	96.80	0.039	3.53	100.00
10 Gobiidae	66.5	0.38	97.17	0.012	6.85	96.30
11 <i>Syacium ovale</i>	33.2	0.19	97.36	0.008	2.49	88.89
12 Pomacentridae	32.7	0.19	97.55	0.030	5.34	51.85
13 <i>Lutjanus</i> spp.	26.8	0.15	97.70	0.024	18.67	25.93
14 <i>Lutjanus argentiventris</i>	25.7	0.15	97.85	0.024	18.40	29.63
15 <i>Auxis</i> sp.	25.0	0.14	97.99	0.016	4.66	74.07
16 <i>Lutjanus novemfaciatus</i>	23.6	0.13	98.12	0.025	9.47	29.63
17 <i>Symphurus elongatus</i>	20.3	0.12	98.24	0.004	0.76	48.15
18 <i>Caranx caballus</i>	19.4	0.11	98.35	0.004	5.17	51.85
19 <i>Cetengraulis mysticetus</i>	16.6	0.09	98.44	0.016	0.73	18.52
20 <i>Xyrichtys</i> sp.	15.9	0.09	98.53	0.009	0.85	85.19
21 <i>Sphoeroides annulatus</i>	15.5	0.09	98.62	0.017	1.01	51.85
22 Eleotridae	14.9	0.08	98.70	0.015	2.71	29.63
23 <i>Opistonema</i> sp.	11.3	0.06	98.77	0.016	0.17	22.22
24 <i>Synodus sechurae</i>	10.8	0.06	98.83	0.005	2.81	51.85
25 <i>Engraulis</i> sp.	9.5	0.05	98.88	0.850	17.50	7.41
26 <i>Cubiceps pauciradiatus</i>	9.1	0.05	98.93	0.025	1.64	48.15
27 <i>Lutjanus guttatus</i>	9.0	0.05	98.98	0.035	3.82	29.63

Table 2. Results of two-way ANOVAs to test the effects of seasonality and El Niño in the the average taxonomic distinctness (AvTD) and the variation of taxonomic distinctness (VarTD).

Average taxonomic distinctness

Effect	d.f.	F-value	<i>p</i>
Season	2	6.29	0.003
El Niño	1	2.05	0.158
season*El Niño	2	0.87	0.427
error	47		

Variation of taxonomic distinctness

Effect	d.f.	F-value	<i>p</i>
Season	2	1.35	0.268
El Niño	1	0.46	0.502
season*El Niño	2	0.24	0.790
error	47		

Table 3. Generalized linear models (GLM) fitted to diversity components following the AIC to select the most parsimonious model. MEI (Multivariate ENSO index), SST (sea surface temperature), UI (upwelling index). The value of the parameters included in the most parsimonious models are showed.

	MEI	SST	UI	Season	d.f.	AIC	<i>p</i>
Richness inshore	0.959				1	149.77	0.314
Richness offshore		1.750			1	134.07	0.001
PIE inshore	0.107				1	13.81	0.047
PIE offshore	0.084	0.087			2	11.01	0.007

Table 4. Results of the procedure for selection of the most parsimonious model of assemblage structure using the Akaike information criterion. (a) The models are detailed (X indicate the variable or parameter include in the model). (b) Results of CCA and the permutation test of the fitted models, and the ranking of the models estimated using AIC.

		Full model	Basic models plus interactions					Basic models				Other models			Factor weight	
a	Distance	Inshore	x	x	x	x	x	x			x					0.015
	ENSO	El Niño	x	x	x	x	x	x			x	x	x			0.148
	Season	California Current	x	x	x	x	x	x	x							0.154
		Tropical	x	x	x	x	x	x	x							
	Interactions	ENSO*Calif. Current	x	x	x	x	x									0.026
		ENSO*Tropical	x	x	x	x										0.057
		ENSO*Inshore	x	x	x											0.016
		Inshore*Calif. Current	x	x												0.017
		Inshore*Tropical	x													0.017
	b	Sum of all canonical eigenvalues	0.441	0.433	0.416	0.4	0.343	0.317	0.153	0.147	0.015	0.435	0.385	0.302		
K (parameters number)		9	8	7	6	5	4	2	1	1	8	5	3			
P-value 1st canonical Axis		0.008	0.002	0.002	0.002	0.002	0.002	0.02	0.02		0.002	0.002	0.002			
P-value all canonical Axis		0.16	0.09	0.05	0.02	0.01	0.012	0.05	0.004	0.9	0.09	0.006	0.006			
AICc		-161.684	-164.696	-166.837	-170.115	-169.352	-171.389	-170.829	-172.786	-168.703	-165.987	-171.651	-173.155			
w _i		0.001	0.004	0.012	0.061	0.042	0.115	0.087	0.231	0.030	0.008	0.131	0.278			
model ranking		12	11	9	6	7	4	5	2	8	10	3	1			

* the factor weight include the explained variance of both seasons: CC period and tropical period

Table 5. Percentage contribution of typifying species similarity within seasonal groups of the larval fish assemblages of the central Mexican Pacific. Only species up to 90% of the cumulative similarity are showed.

	Califor. Current Jan-May 1996	Tropical Jul-Nov 1996	Califor. Current Jan-May 1997	Tropical Jul-Nov 1997	Califor. Current Jan-May 1998	Tropical Jul-Nov 1998
<i>Bregmaceros bathymaster</i>	97.8	86.9	96.4	16.3	84.5	19.0
<i>Dormitator latifrons</i>		3.3		16.1	6.5	2.3
<i>Harengula thrissina</i>				24.2		
<i>Euthynus lineatus</i>				10.8		10.2
<i>Vinciguerria lucetia</i>				5.5		4.1
<i>Benthoosema panamense</i>				3.2		
<i>Lutjanus novemfaciatus</i>				10.6		
<i>Gobionellus</i> sp.				3.1		2.0
Gobiidae				1.7		9.7
<i>Lutjanus</i> spp						15.4
<i>Lutjanus argentiventris</i>						15.1
Engraulidae						11.8
Pomacentridae						2.3

Table 6. Percentage contribution of typifying species similarity within the discriminated species groups and dissimilarity within interannual periods

	Similarity			Dissimilarity between groups
	Previous El Niño	El Niño		
<i>Bregmaceros bathymaster</i>	25.79	13.75	<i>Bregmaceros bathymaster</i>	7.78
<i>Dormitator latifrons</i>	10.18	10.77	Sciaenidae	2.88
<i>Gobionellus</i> sp.	6.29	6.85	<i>Harengula thrissina</i>	2.65
Sciaenidae	5.15		Engraulidae	2.64
Gobiidae	4.67	7.88	<i>Euthynus lineatus</i>	2.56
<i>Xyrichtys</i> sp.	4.43	2.58	<i>Benthoosema panamense</i>	2.44
<i>Vinciguerria lucetia</i>	3.64	5.91	<i>Vinciguerria lucetia</i>	1.93
<i>Syacium ovale</i>	3.19	5.81	<i>Lutjanus</i> spp	1.9
<i>Symphurus atramentatus</i>	2.16		Pomacentridae	1.82
Engraulidae	2.07	3.32	<i>Lutjanus argentiventris</i>	1.73
<i>Auxis</i> sp.	2.02		<i>Symphurus elongatus</i>	1.71
<i>Symphurus chabanaudi</i>	1.83		<i>Caranx caballus</i>	1.69
<i>Benthoosema panamense</i>	1.65	5.77	<i>Symphurus atramentatus</i>	1.64
<i>Symphurus elongatus</i>	1.61		<i>Lutjanus novemfaciatus</i>	1.58
Pomacentridae	1.52		<i>Gobiesox</i> sp.	1.54
<i>Chloroscombrus orqueta</i>	1.49		<i>Symphurus chabanaudi</i>	1.49
<i>Euthynus lineatus</i>	1.48	4.88	<i>Sphoeroides annulatus</i>	1.47
<i>Etropus crossotus</i>	1.44		<i>Cubiceps pauciradiatus</i>	1.45
<i>Halichoeres dispilus</i>	1.34		<i>Synodus sechurae</i>	1.42
Moringuidae	1.22		<i>Auxis</i> sp.	1.41
<i>Synodus sechurae</i>	1.17		<i>Chloroscombrus orqueta</i>	1.37
<i>Harengula thrissina</i>	1.14	3.5	<i>Halichoeres dispilus</i>	1.31
<i>Caranx sexfasciatus</i>	0.88		Eleotridae	1.31
<i>Abudefduf troschelli</i>	0.86		<i>Syacium ovale</i>	1.29
<i>Labrisomus multiporosus</i>	0.86		<i>Mugil cephalus</i>	1.22
<i>Ophidion</i> sp.	0.86		<i>Etropus crossotus</i>	1.21
<i>Mugil cephalus</i>	0.76	1.35	Moringuidae	1.2
Eleotridae	0.67		<i>Abudefduf troschelli</i>	1.19
<i>Auxis</i> sp.		3.2	<i>Labrisomus multiporosus</i>	1.19
<i>Gobiesox</i> sp.		2.58	<i>Lutjanus guttatus</i>	1.19
<i>Cubiceps pauciradiatus</i>		2.24	<i>Xyrichtys</i> sp.	1.16
<i>Caranx caballus</i>		2.17	<i>Dormitator latifrons</i>	1.15
<i>Lutjanus</i> spp		1.99	<i>Caranx sexfasciatus</i>	1.15
<i>Sphoeroides annulatus</i>		1.9	<i>Cetengraulis mysticetus</i>	1.13
<i>Lutjanus argentiventris</i>		1.54		
Pomacentridae		1.28		
<i>Lutjanus novemfaciatus</i>		1.06		

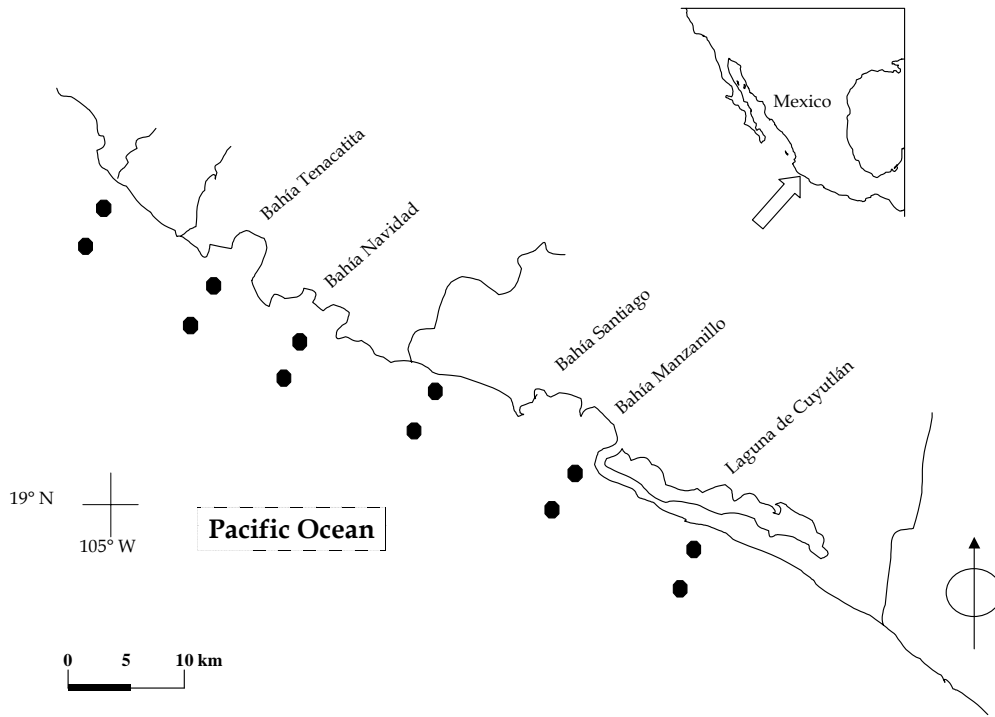


Figure 1. Study area, dots indicate the zooplankton sampling sites

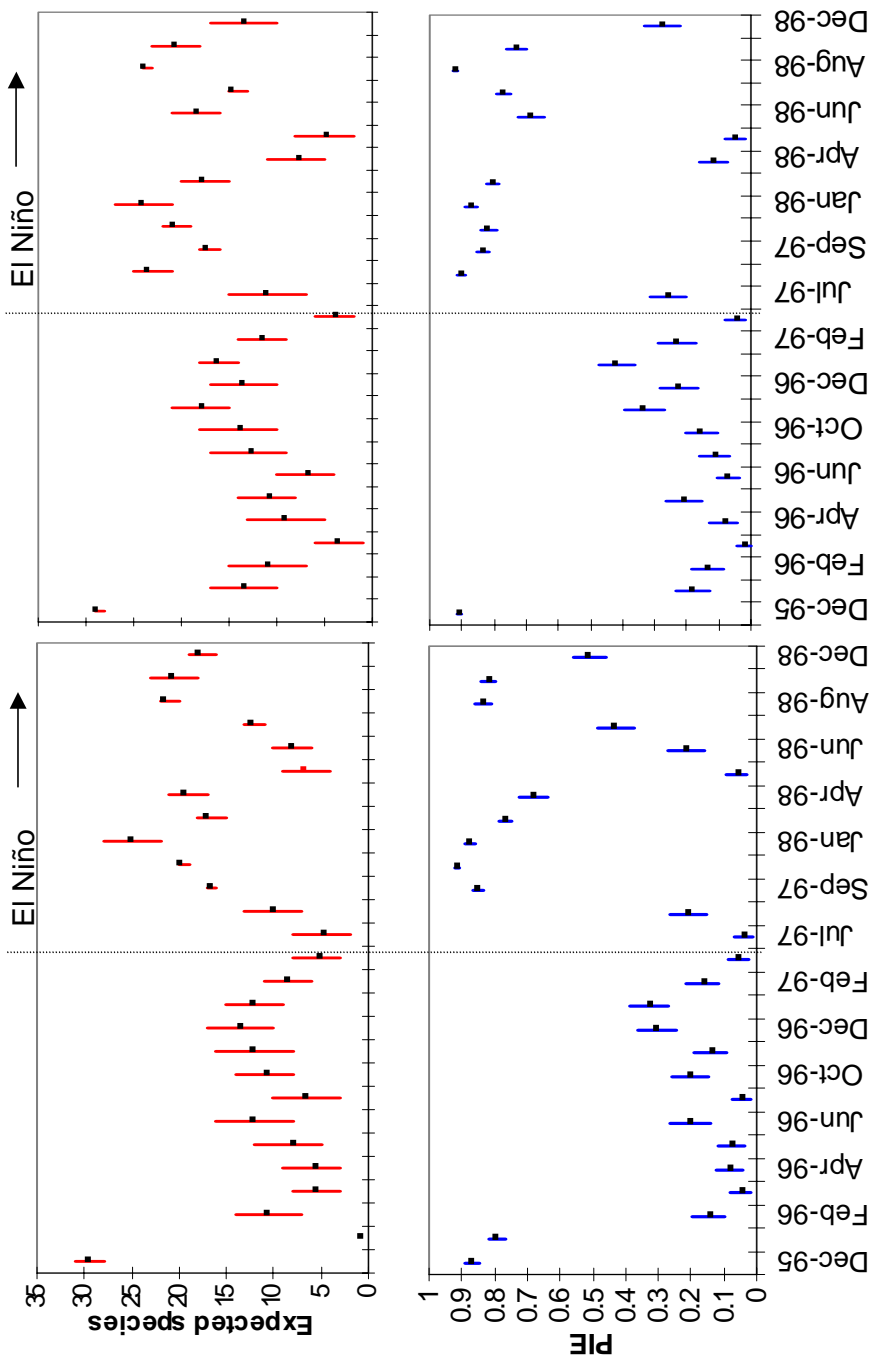


Figure 2. Temporal distribution of the species richness and evenness (PIE) of the larval fish assemblages of the central Mexican Pacific (mean and 95% confidence intervals are showed).

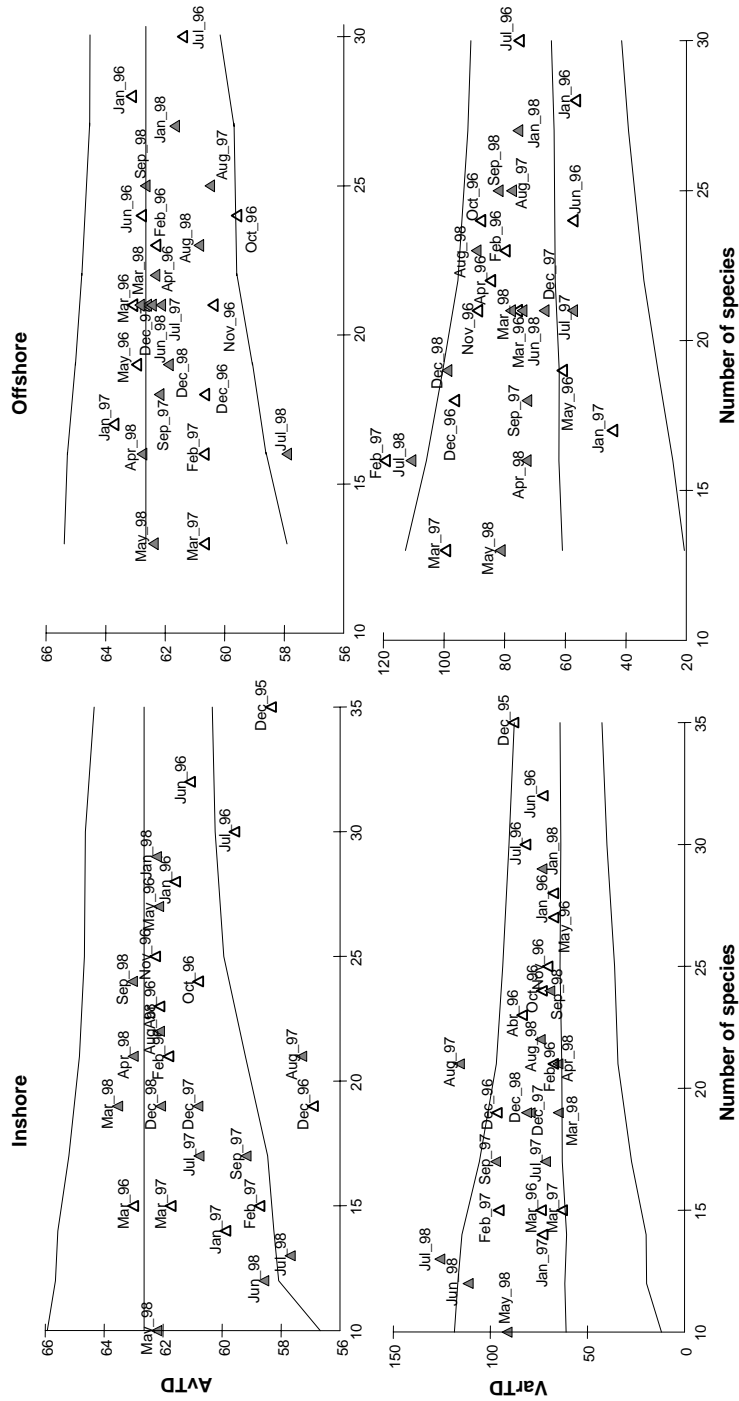
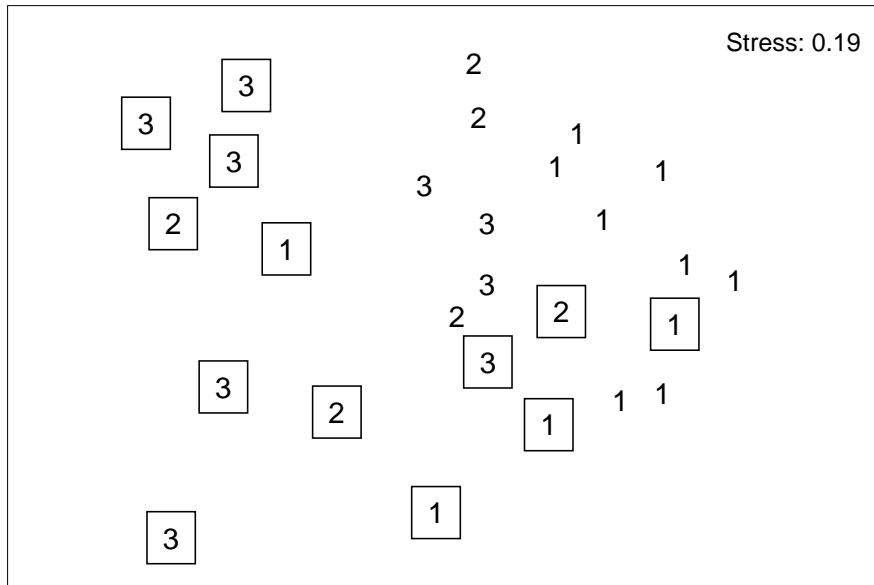


Figure 3. Average (AVTD) and variation of taxonomic distinctness (VarTD) of larval fish assemblage in the inshore and offshore zones. Filled triangles represent the monthly values of El Niño period. Lines represent the 95% probability funnels.

Inshore



Offshore

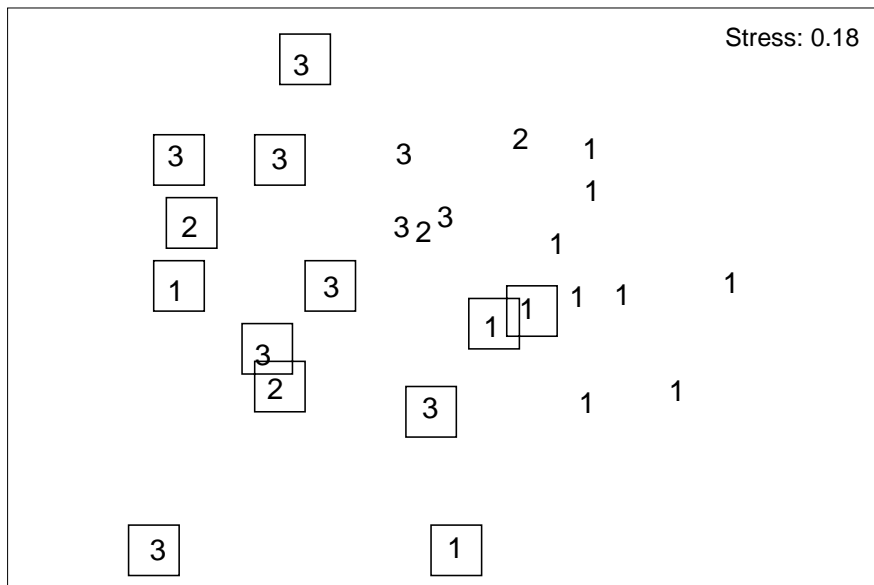


Figure 4. Ordination patterns using non-parametric multidimensional scaling (nMDS) of the larval fish assemblages of the Mexican central Pacific. 1 = CC period, 2 = transition, 3 = tropical period. Numbers with frames are the months of El Niño period.