RESEARCH ARTICLE

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Larval fish assemblages in Independencia Bay, Pisco, Peru: temporal and spatial relationships

Abstract The structure of the larval fish assemblages in Independencia Bay on the coast of Peru was examined using a combination of univariate and multivariate techniques. The plankton of Independencia Bay was sampled during 2000, to ascertain ichthyoplankton composition, abundance, and seasonality. These data were used to assess the function of the bay as spawning and nursery grounds and were related to the regional oceanography. In total, 16,156 fish larvae, representing 34 families, 48 genera, and 48 species were collected. Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae, and Atherinidae comprised 96.8% of the larvae captured; the remaining 3.2% included 26 families. Greatest mean larval fish densities, 319–1,381 per 100 m^3, were recorded between September and November, suggesting a major spring spawning period. The most abundant fish larvae during this period were preflexion stage mote sculpins (Normanichthyidae) and newly hatched and preflexion stage anchovies (Engraulidae). A second, smaller summer peak was dominated by preflexion stage anchovies, followed by preflexion stage mote sculpins. The occurrence of high larval fish densities and the wide range of larval stages suggest that Independencia Bay is a regionally important spawning and nursery ground for marine fish. The principal component analysis showed that temperature and salinity were the dominant variables within the first two principal components, which accounted for 74.4% of the variation in environmental conditions. These conditions varied over time, station, and depth; however, interaction terms could not clearly be identified. Fitting a multinomial logistic model showed that larval fish assemblages and environmental conditions were associated in a complex way. The spring and summer ichthyoplankton abundance peaks in Independencia Bay coincided with high zooplankton standing stock and also coincided approximately with the periods of increased upwelling in the area.

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Introduction

One of the most productive fishing areas in existence lies off the coast of Peru (Fahrbach et al. 1980). Strong coastal upwelling in this region results from moderately deep (50–100 m) water forced to the surface as compensation for surface water driven offshore by a combined effect of trade winds, Coriolis force and Ekman transport, bringing nutrient-rich, cool water to the surface (Arntz and Fahrbach 1991). The phytoplankton, which thrives within this upwelling zone, is fed upon by a variety of creatures including fish larvae. The biomass feeds an important food web, culminating in predatory fish, guano birds, and mammals (Mendo 1997). Coastal regions are important nursery grounds for littoral and shelf fish populations, with shallow areas offering suitable food supply, shelter, and ecophysiological conditions for development of all stages from eggs to juveniles (Blaber and Blaber 1980). It is well documented that many populations of coastal fish depend on such critical areas, at least during part of their life cycle (Weinstein 1979; McHugh 1985).

The knowledge of ichthyoplankton and its ecology is still limited (e.g. Richards 1985); this is especially true for the Pacific coast of South America. Marine fish

diversity is high in Peruvian waters, but little is known about larval stages (e.g. Vélez et al. 2003). Despite the importance of knowing the processes affecting the dynamics of the coastal ichthyoplankton, most of the ichthyoplankton studies carried out in Peru have focused on mesoscale surveys over the continental shelf and are concentrated on fish with commercial value (Guzmán and Ayón1995; Guzmán and Carrasco1996). To date, no scientific information is available on the ecology of ichthyoplankton in Independencia Bay, although it is an area of upwelling and possibly an important spawning and nursery area. It is important to increase our ecological knowledge of Independencia Bay, because, as with the entire Pacific basin, it is affected by developments that are tied to the major economic activities of fisheries. A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fishes during their early life stages, as well as to an understanding of adult spawning patterns. This paper describes the seasonal abundance of ichthyoplankton in Independencia Bay. The objectives were to: (1) determine the taxonomic composition of fish larvae and (2) assess the seasonal variations of the dominant families. These data are used to assess the inferred function of the bay as a spawning and nursery ground for marine fish in the region.

Materials and methods

Study area

The study was done in Independencia Bay (14°06–14°20′S; 76°00′–76°18′W), a large, shallow bay situated within the Paracas National Park, Pisco, Peru (Fig. 1). Independencia Bay is ca. 21 km long and 6.5 km wide, much of the bay is 22–25 m deep. There are two islands, La Vieja and Santa Rosa. The larger, La Vieja Island, is 5.6 km long and 2.4 km wide, and occupies much of the southern half of the mouth of Independencia Bay. It is located in the Humboldt Current marine ecoregion and is a marine upwelling site with elevated levels of primary production all year long, with a higher peak during winter and spring seasons.

Sample collection

Larvae were collected monthly during January–May and August–November in 2000. March–April was combined as one sampling period. Plankton was collected with two net types. A 60-cm Bongo (with a 0.505-mm mesh net and cod end on one side and a 0.333-mm Nitex net and cod end on the other) was towed at a depth of 10 m. A 0.5-m ring net (0.333-mm Nitex mesh) was towed at the surface. Both samplers were equipped with calibrated flowmeters. All tows were taken at a speed of about 1.5 m s^{-1} for 10 min, and samples were preserved in 4%

formalin solution immediately after collection. A total of 64 horizontal tows was made during daytime (between 0830 and 1400 hours) at four stations (Santa Rosa, Panteón, Tunga, Pampa) (Fig. 1). An additional 37 daytime tows were made in September. At three stations (MorroQuemado, Pan deAzúcar, Laguna Grande), one sample was taken. At Panteón, two additional samples were taken. At Panteón and Tunga, 32 samples were taken, one every 3 h, during a 24-h period. This 24-h sampling is the subject of a separate paper, and it is not included here except for use in compiling the most complete ichthyoplankton species list possible for the bay. The 37 additional samples (Table 1) were included in the composition analysis of the ichthyoplankton, but were not used for distributional analyses.

Using a Nisken bottle, temperature, salinity, pH, and dissolved oxygen were measured at four depths (0, 5, 10, and 20 m) during each collection at the four standard stations (Santa Rosa, Panteón, Tunga, Pampa). The physical data for June, July, and December were kindly provided by Dr. J. Tarazona (unpublished data, UniversidadNacional Mayor de San Marcos, Lima, Peru). In the laboratory, zooplankton biomass was measured from each sample using the displacement volume method (Beers 1976), and all fish larvae were sorted from the samples and identified to the lowest taxon possible. Larvae were identified by the series method (Moser1996; Leis and Carson-Ewart2000), using a combination of meristic and developmental characters that permitted definitive identification.

Fig. 1 Study area, Independencia Bay, Pisco, Peru. Sampling locations indicated [*closed circles* main stations (standard sampling); *open circles* extra stations (additional sampling)]

Table 1 Number of tows (*tows*), total number of individuals (*N*), total number of taxa (*taxa*), and densities (*D* , *N* per 100 m³) at the surface and mid-water across the sampling period. Data of the additional sampling during September are listed below the standard sampling data

	Surface				Mid-water				Total		
	Tows	N	Taxa	D	Tows	N	Taxa	D	Tows	N	D
Standard sampling											
Jan	4	11	6	6	4	214	21	97	8	225	103
Feb	4	1	1	1	4	1,200	16	2,491	8	1,201	2,492
Mar–Apr	4	29	3	16	4	881	12	484	8	910	500
May	4	26	1	14	4	30	6	14.8	8	56	29
Jun	–	–	–	–	–	–	–	–	–	–	–
Jul	–	–	–	–	–	–	–	–	–	–	–
Aug	4	6	3	3	4	145	14	128.5	8	151	132
Sep	4	20	1	17	4	557	18	302.1	8	577	319
Oct	4	104	7	207	4	5,935	13	7,286.1	8	6,039	7,493
Nov	4	13	5	29	4	1764	12	1351.2	8	1777	1,380
Total	32	210	–	–	32	10726	–	–	64	10936	
Additional sampling											
Panteón 24 h	8	201	5	230	8	3,754	21	1710	16	3955	1,940
Tunga 24 h	8	52	5	80	8	497	26	310	16	549	390
Laguna Grande	–	–	–	–	1	3	1	3	1	3	3
Pan de Azúcar	–	–	–	–	1	8	2	6	1	8	6
Morro Quemado	–	–	–	–	1	48	4	61	1	48	61
Panteón	–	–	–	–	2	657	9	294	2	657	294
Total	16	253	–	–	21	4,967	–	–	37	5,220	–

Treatment and data analysis

Because some specimens could not be identified to genus or species level, abundance data were summed at the family level in the quantitative analyses. The most abundant families in this study were identifiable to species. In each tow, numbers of fish larvae and zooplankton biomass were standardized to the number per 100 m³ of water filtered. A multivariate ANOVA was used to test for differences in the vector of environmental variables over time, station, and depth. Three test statistics were considered for this purpose (Wilk's lambda, Pillai's trace, and the Hotelling–Lawley trace), each of which measures specific aspects of the multivariate distances. In order to avoid conclusions on the basis of ambiguous decisions, an effect was considered to be present only if all three test statistics produced a significant result. Pairwise comparisons between months, stations, and depths were performed by multivariate contrasts with Bonferroni correction. Here, all three previously mentioned statistics coincide, because only two groups are compared. If not stated otherwise, an α error of 0.05 was used in statistical tests.

To determine whether the seasonal abundance changes of larvae of the most common families were statistically significant, Poisson regressions (McCullagh and Nelder 1989) using the number of fish larvae and volume of water filtered per tow were performed on untransformed count data, with months and stations as classification factors. These procedures were run in the GLM (general linear model) module of SAS (SAS 2001). The relations between species assemblage and environmental variables were analyzed by a multinomial logistic model (McCullagh and Nelder 1989), using the LOGIS-TIC module of SAS (2001). Multivariate analyses, based on the dominant species collected with the bongo (0.333-mm mesh) and surface nets, were used to examine temporal (seasonal) and spatial (vertical dimension) patterns of the larval fish assemblages. To further examine temporal patterns, and to calculate the similarities between stations and taxa, the Bray–Curtis dissimilarity coefficient was calculated using $\log(x +1)$-transformed standardized abundances for each month, station, season, and depth (0 and 10 m) where the samples were taken. The $\log(x +1)$ transformation was used to reduce the contribution from numerically dominant species and to reveal changes among less dominant species (Field et al. 1982). Abundances of taxa were summarized in separate matrices for each factor analyzed; only the eight most abundant taxa were included. A classification (cluster analysis, complete linkage) of the similarity matrices was made for all stations and taxa. Non-metric multidimensional scaling (MDS) was used to graphically display two-dimensional ordination plots of the inter-relationships among samples, based on the relative abundance of each taxon. A low (< 0.2) MDS stress coefficient indicates that the multivariate similarity pattern is represented by the plot without much distortion. The PRIMER program was used for these analyses (Clarke and Warwick 1994).

Results

Taxonomic composition of the ichthyoplankton

A total of 16,156 fish larvae (Table 1)—representing 34 families, 48 genera, and 48 species—was collected;

29 families, 35 genera, and 36 species were identified (Table 2), and 99% of the total larvae were identifiable to at least the level of family. Eight families accounted for 96.8% of total larval abundance: Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae, and Atherinidae (Table 2). The remaining 26 families and unidentified taxa contributed 3.2% to the total larvae. Most larvae not identified to the family level (0.9%) were yolk-sac stage, or damaged larvae. None of the rare taxa contributed >0.6% to the total larvae. The three most abundant taxa, the anchovy *Engraulis ringens*, the mote sculpin *Normanichthys crockeri* and the blenny *Scartichthys* sp., together contributed 82.2% to the larvae. These three taxa were found during all months. The next five most abundant families were found during 7 months (Gobiesocidae, Labrisomidae, and Pinguipedidae), 6 months (Haemulidae), or 5 months (Atherinidae); 28 taxa appeared only in a single month.

Spatial and temporal distribution

Total larval abundance was significantly higher at Santa Rosa than at the other stations; however, there were no statistically significant differences between stations in the total values for any of the dominant families. For surface samples, larval abundance was also highest at Santa Rosa, followed by Panteón, Pampa, and Tunga, and the number of taxa was highest at Santa Rosa and Panteón (9), followed by Tunga and Pampa (4) (Table 3). More total individuals, higher standardized total abundance, and more taxa were encountered in the mid-water samples than in the surface samples at all stations, and the highest values at both depths were at Santa Rosa (Table 3). There was a distinct temporal pattern in occurrence in surface and mid-water layers (Table 1), and the highest value in total larval abundance at both depths occurred in October. A pronounced seasonal variability was observed (Fig. 2), with two peaks in the

Table 2 Total number (*N*), percent contribution to all fish larvae caught (*D* dominance), and percent frequency (*F*) of capture of the ichthyoplankton taxa collected in Independencia Bay during 2000 (additional sampling is included)

Family	Genus/Species	N	D	F	Family	Genus/Species	N	D	F
Atherinidae	*Odontesthes regiaregia*	218	1.3	53.3	Labrisomidae	*Labrisomus* (*philippii*?)	263	1.6	73.3
Blenniidae	*Scartichthys* sp.	2,898	18.0	86.7	Nomeidae	*Nomeus gronovii*	2	<0.1	13.3
	Hypsoblennius sp.	90	0.6	60.0	Normanichthyidae	*Normanichthys crockeri*	5,155	31.9	80
Carangidae		3	<0.1	6.7	Ophidiidae		5	<0.1	13.3
Centropomidae		1	<0.1	6.7	Paralichthyidae	*Paralichthys adspersus*	77	0.5	46.7
Chaenopsidae	*Emblemaria* sp.	2	<0.1	6.7		*P. microps*	12	<0.1	13.3
Cheilodactylidae	*Cheilodactylus variegates*	1	<0.1	6.7		*Etropus ectenes*?	6	<0.1	6.7
Coryphaenidae	*Coryphaena hippurus*	2	<0.1	6.7		*Hippoglossina* sp.	3	<0.1	13.3
Clupeidae	*Sardinops sagaxsagax*	7	<0.1	13.3	Pinguipedidae	*Prolatilus jugularis*	232	1.4	53.3
Engraulidae	*Engraulis ringens*	5,225	32.3	93.3	Pomacentridae	*Chromis* sp.	9	<0.1	26.7
Ephippidae	*Parapsettus* (*panamensis*?)	1	<0.1	6.7		*Abudefduf* (?) sp.	1	<0.1	6.7
Gerreidae	*Eugerres periche*	12	<0.1	13.3	Sciaenidae	*Sciaena* sp.	4	<0.1	13.3
Gobiesocidae	*Gobiesox marmoratus*	1346	8.3	73.3	Scombridae	*Auxis* sp.	3	<0.1	13.3
	Sicyases sanguineus	22	0.13	6.7	Scorpaenidae	*Sebastes capensis*	12	<0.1	13.3
	Tomicodon petersi	2	<0.1	6.7	Serranidae		1	<0.1	26.7
Gobiidae	*Evermannia zostetura*	50	0.31	40.0	Sphyraenidae	*Sphyraena idiastes*	1	<0.1	6.7
Haemulidae	*Anisotremus* sp.	329	2.0	53.3	Syngnathidae	*Leptonotus blainvillianus*	12	<0.1	6.7
Kyphosidae	*Doydixodon* sp.	1	<0.1	6.7	Unidentified		146	0.94	26.7
Labridae		2	<0.1	13.3					

Table 3 Total number of fish larvae (*N*), total density (*D*, *N* per 100 m³), total number of taxa (*taxa*), number of tows (*tows*), and temperature ranges (temp., in °C) at the surface and at mid-water level pooled across the four stations during the study period (standard sampling only)

Station	Surface					Mid-water level					Total D
	N	D	Taxa	Tows	Temp.	N	D	Taxa	Tows	Temp.	
Pampa	25	73	4	8	14.4–20.3	1,718	1,815	20	8	13.9–15.7	1,888
Tunga	33	55	4	8	14.4–19.1	736	1,099	19	8	13.5–17.0	1,154
Panteón	37	95	9	8	14.0–17.1	1,285	1,514	20	8	13.7–16.9	1,609
Santa Rosa	115	509	9	8	13.7–16.9	6,987	7,685	23	8	13.4–15.8	8,194

Fig. 2 Mean monthly density (ind. per 100 m³) of total larvae at the four stations (**A–D**) sampled during 2000. Note the different abundance scales for the different stations
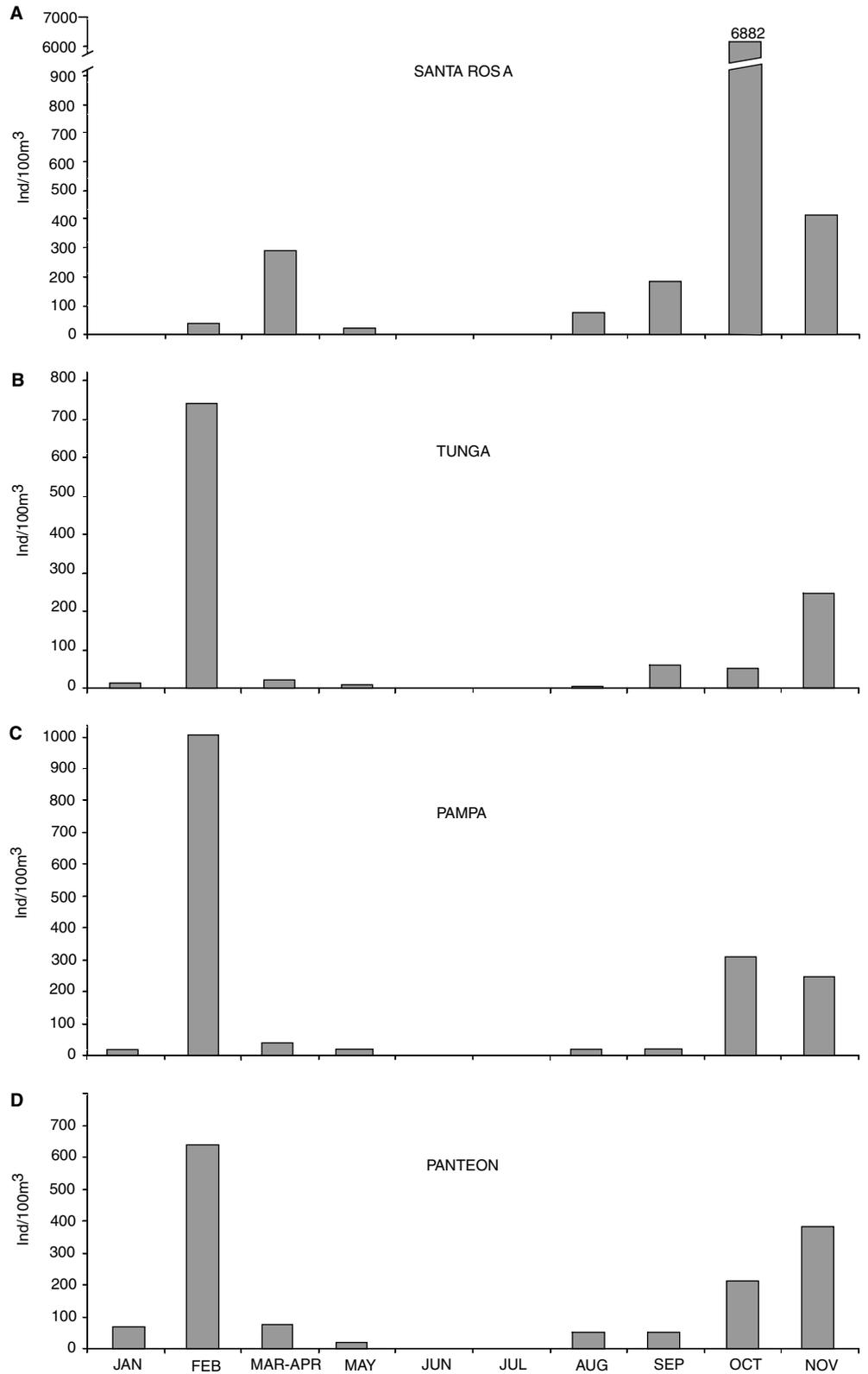
monthly mean abundance of total fish larvae: one in spring (September–November), dominated by newly hatched mote sculpins and anchovies, both pelagic shelf species, and a second in summer (January–March), dominated by preflexion stage anchovies, followed by newly hatched mote sculpin. Greatest mean total abundance during the spring peak was in October (7,493 larvae per 100 m³), suggesting a major

spawning period, whereby Santa Rosa presented the highest abundance. At the summer peak, the greatest mean total abundance was in February (2,492 larvae per 100 m^3), with highest values at Pampa, Tunga, and Panteón. At the summer peak, we found 33.3% of the total taxa, and at the spring peak, 29.2%. Figure 3 gives some insight into seasonal variation in abundance of the dominant ichthyoplankton taxa in Independencia Bay. Both abundance peaks are clearly distinguishable.

Most individuals of all the most abundant families except Atherinidae were captured in the 10-m (midwater) stratum (Table 4). The abundances of Engraulidae, Gobiesocidae, Labrisomidae, Normanichthyidae, and Pinguipedidae were higher at Santa Rosa than at the other stations, while Atherinidae and Haemulidae were more abundant at Tunga, and the Blenniidae were most abundant at Panteón.

Seasonal spawning, inferred from larval abundances, could be classified into four general patterns (Fig. 3). These were: winter–spring spawning, as exemplified by *Odontesthes regiaregia* (Fig. 3H); and spawning throughout much or all of the year, but with a distinct spring maximum, exemplified by *Gobiesox marmoratus* (Fig. 3D) and *Normanichthys crockeri* (Fig. 3B), with a principal spawning peak in spring and a smaller peak in summer, exemplified by *Engraulisringens* (Fig. 3A), *Prolatilus jugularis* (Fig. 3G), *Labrisomus* sp. (Fig. 3F), and *Scartichthys* sp. (Fig. 3C), and with a principal peak in summer and a smaller peak in spring, exemplified by *Anisotremus* sp. (Fig. 3E).

O. regiaregia was present in 5 months (Fig. 3H) at all four stations, with peak abundance in September (24 larvae per 100 m^3); the high September and November abundances were at Tunga, and the high values during the other months were at the other stations. Larvae appeared only at the surface, except in May and August, when a few were also captured at 10 m depth at Santa Rosa.

G. marmoratus was present most of the year (Fig. 3D) at all four stations, with peak abundance in October (307 larvae per 100 m^3); the peak was apparent at all four stations. Larval abundance at Pampa was slightly higher in summer than during October. *G. marmoratus* was found only at 10 m depth, except in August when some larvae were captured at the surface at Panteón. *N. crockeri* was found throughout the year (Fig. 3B) at all four stations, with peak larval abundance in October

Fig. 3 Mean monthly densities (ind. per 100 m^3) of the most abundant ichthyoplankton taxa (**A–H**) collected in Independencia Bay during 2000. Note the differences in scale
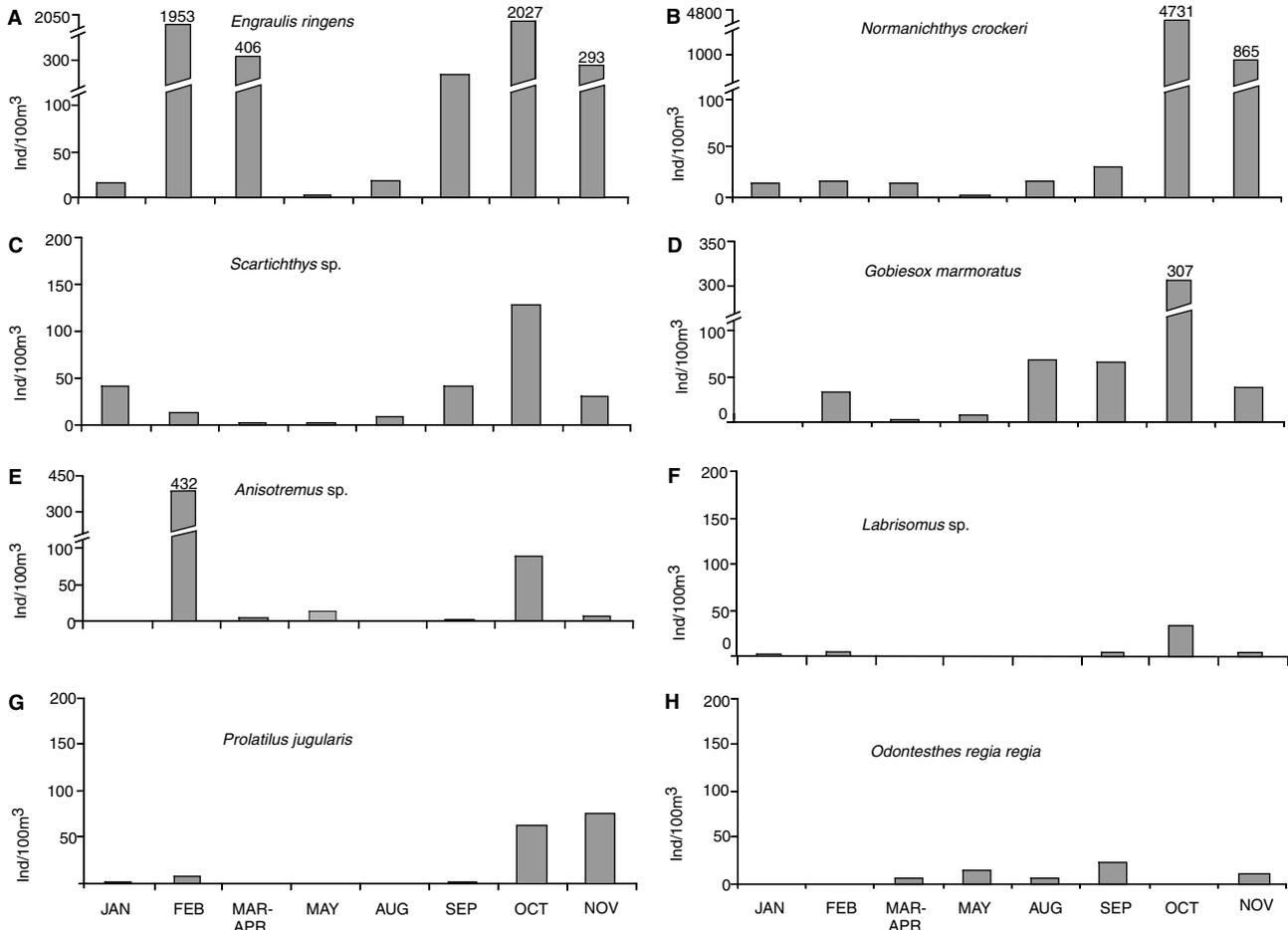
Table 4 Total density (larvae per 100 m^3), dominance (D, percent contribution to the summed abundance of the dominant taxa), percent in upper and lower regions of the water column, and adult habitats (N neritic; B benthic; CP coastal pelagic) of dominant taxa during 2000 in Independencia Bay (standard sampling only)

Taxa	Total density	D	Upper (%)	Bottom (%)	Adult habitat
Engraulisringens	48,462	40.0	2.8	97.2	CP
Normanichthyscrockeri	56,947	46.9	2.1	97.9	N
*Scartichthys*sp.	2,749	2.3	0.7	99.3	B
Gobiesoxmarmoratus	5,183	4.3	1.4	98.6	B
*Anisotremus*sp.	4,428	4.5	0.9	99.1	N
*Labrisomus*sp.	456	0.4	0	100	B
Prolatilusjugularis	1,452	1.2	1.0	99.0	B
Odontesthesregiaregia	643	0.5	90.6	9.4	N

(4,731 larvae per 100 m^3); this peak was primarily at Santa Rosa and Pampa. Abundances during November were highest at Panteón and Tunga. Larvae were present only at 10 m depth, except in October when some were captured at the surface at Santa Rosa, and in October and November at Pampa.

E. ringens was present throughout the year (Fig. 3A) at all four stations, with peaks of abundance in October (2,027 larvae per 100 m^3) and February (1,953 larvae per 100 m^3). The October peak was primarily at Santa Rosa, and the February peak was at the other stations. Larvae were collected primarily at 10 m depth; a few were collected at the surface at Santa Rosa and Panteón. *P. jugularis* occurred during most of the year (Fig. 3G) at all four stations, with peaks in October–November (59.9–72.7 larvae per 100 m^3) and February (8.3 larvae per 100 m^3). The spring peak was most apparent at Tunga, Panteón, and Santa Rosa, and the small summer peak occurred only at Pampa. *P. jugularis* was present mainly at 10 m depth; a few were collected at the surface at Panteón and Tunga. *Labrisomus* sp. occurred throughout most of the year (Fig. 3F) at all four stations, with peak larval abundance in October (32 larvae per 100 m^3) and February (3.3 larvae per 100 m^3). Only the spring peak was apparent at Panteón and Santa Rosa; the small summer peak occurred at Tunga and Pampa. In September there was another period of relatively high abundance (3.2 larvae per 100 m^3) at Tunga. Larvae were collected only at 10 m depth. *Scartichthys* sp. occurred throughout the year (Fig. 3C) at all four stations, with abundance peaks in October (130 larvae per 100 m^3) and summer (January, 43 larvae per 100 m^3; February, 14.5 larvae per 100 m^3). The October peak was primarily at Panteón, Pampa, and Santa Rosa, and the summer peak at Tunga. *Scartichthys* sp. was present only at the 10 m depth, except in October when some larvae were captured at the surface at Santa Rosa.

Anisotremus sp. was found most of the year (Fig. 3E). *Anisotremus* sp. was present at all four stations, with peak abundance in February (433 larvae per 100 m^3) and possibly in October (86.3 larvae per 100 m^3). The summer peak was at Tunga and Pampa, and the spring peak was at Santa Rosa and Panteón. Larvae were found only at 10 m depth.

Environmental variables

The oceanographic conditions of Independencia Bay are typical of cold coastal waters, due to coastal upwelling. In general, vertical similarities in temperature and salinity reflect the extent of vertical mixing in the bay (Fig. 4). Because each of the environmental parameters tended to follow a similar seasonal pattern at each of the four depths sampled, ee present here only the two depths (0 and 10 m) where the fish larvae were collected. Results of MANOVA, principal component (PCA), and multivariate multiple comparison analyses on the environmental data are summarized in Tables 5, 6, 7, and 8. The MANOVA results for the comparison of environmental variables showed significant main effects for month, station, and depth (Table 5). Only the 0 and 10 m levels where the fish larvae were collected were included in the analysis. Clear indications for significant interaction terms could not be found; instead, the three test statistics produced an indifferent picture, with at least one statistic always being non-significant. For this reason, interaction terms were not incorporated in the subsequent analysis. Pairwise comparisons (with Bonferroni correction) of the environmental data vector over stations and months were calculated as multivariate contrasts and are summarized in Tables 6 and 7. In the tables, months and stations with the same letter constitute groups of environmental variables that are not significantly different from one another. Table 8 summarizes the principal components of the environmental data. The structure of the principal components showed that temperature was the hydrographically dominant component (explaining 44.8% of the variation), followed by salinity (29.6%); together these two components explained 74.4% of the variability in the oceanographic data. The other two parameters (oxygen and pH) were relatively unimportant.

Relationships between environmental variables and larval fish assemblage

The relation between environmental variables and the larval fish assemblage, analyzed by a multivariate logistic model (backward selection), showed that all four
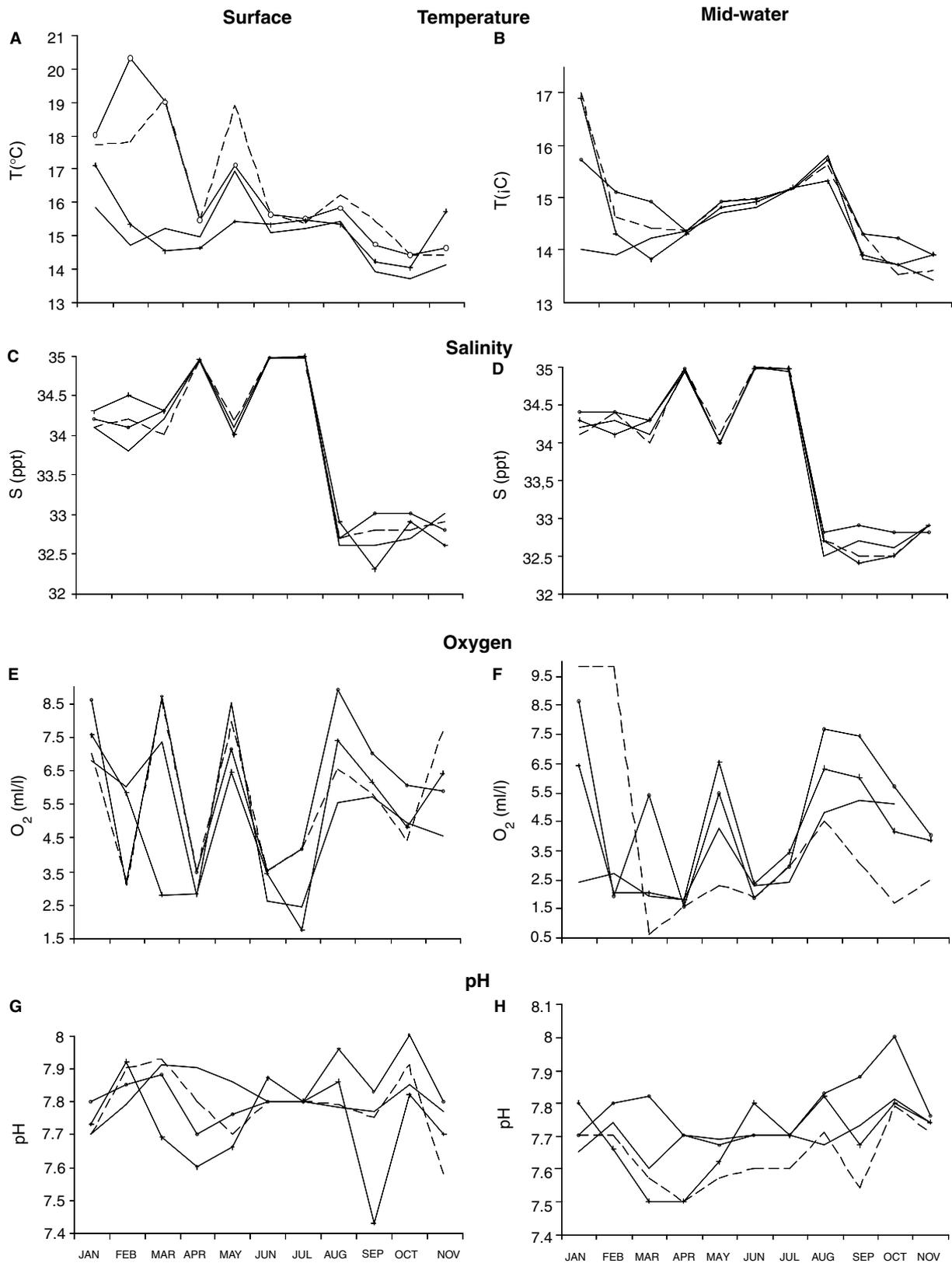
Fig. 4 Spatial and temporal variations in mean temperature (**A, B**), salinity (**C, D**), oxygen (**E, F**), and pH (**G, H**) at the surface (*left panels*) and 10 m depth (*right panels*) for each station in Independencia Bay during 2000 (*solid line* Santa Rosa; *dashed line* Tunga; *solid line with circles* Pampa; *solid line with cross* Panteón)

environmental parameters had significant effects on species assemblage and that all twofold interactions, with the exception of temperature×oxygen, were also significant (Table 9).

Table 5 Summary of the MANOVA results for the environmental data. Temperature, salinity, O₂, and pH jointly constituted the dependent vector (*df*, *num.* degrees of freedom for the numerator of the *F*-statistic; *df*, *den.* degrees of freedom for the denominator of the *F*-statistic)

Source of variation	Wilk's lambda				Pillai's trace				Hotelling–Lawley trace			
	P	*F*	*df*, num.	*df*, den.	*P*	*F*	*df*, num.	*df*, den.	*P*	*F*	*df*, num.	*df*, den.
Main effects												
Month	< 0.0001	15.48	28	66.32	< 0.0001	4.31	28	84	< 0.0001	112.83	28	36.16
Station	0.0004	3.8	12	47.91	0.0014	3.21	12	60	0.0008	4.27	12	27.46
Depth	< 0.0001	15.0	4	18	< 0.0001	15.0	4	18	< 0.0001	15.0	4	18
Interaction terms												
Month×Station	0.0494	1.46	84	73.55	0.0459	1.45	84	84	0.0841	1.46	84	44.77
Month×Depth	0.0502	1.65	28	66.32	0.0800	1.50	28	84	0.0438	1.83	28	36.16
Station×Depth	0.0481	1.98	12	47.91	0.0421	1.98	12	60	0.0711	1.96	12	27.46

Table 6 Mean values and pairwise multivariate comparisons with Bonferroni correction of the environmental data vector (temperature, salinity, oxygen, and pH) over months. Means with the same letter (in the grouping column) are not significantly different (*N* number of observations)

Month	N	Temp. (°C)	Salinity (ppt)	O₂ (ml l⁻¹)	pH	Grouping
300 net						
Jan	4	15.90	34.25	6.80	7.71	A
Feb	4	14.48	34.30	4.10	7.73	A
Mar–Apr	4	14.33	34.18	2.48	7.62	A
May	4	14.83	34.03	4.62	7.64	A
Aug	4	15.60	32.68	5.81	7.76	B
Sep	4	14.08	32.63	5.41	7.71	B, C, D
Oct	4	13.78	32.60	4.15	7.85	C
Nov	4	13.70	32.88	3.69	7.65	D
Standard net						
Jan	4	17.15	34.18	7.49	7.73	A
Feb	4	17.03	34.15	4.51	7.87	A
Mar–Apr	4	16.95	34.20	6.86	7.85	A
May	4	17.08	34.08	7.51	7.75	A
Aug	4	15.68	32.73	7.10	7.85	B
Sep	4	14.55	32.68	6.16	7.70	B
Oct	4	14.13	32.85	5.05	7.90	B
Nov	4	14.70	32.83	6.13	7.71	B

Table 7 Multiple comparison analyses (Scheffe's test) of the environmental data. Mean values for the stations are listed. Means with the same letter (in the grouping column) are not significantly different (*N* number of observations)

Station	N	Temp. (°C)	Salinity (ppt)	O₂ (ml l⁻¹)	pH	Grouping
300 net						
Pampa	8	14.84	33.55	5.76	7.81	A
Panteón	8	14.58	33.40	4.65	7.70	A
Santa Rosa	8	14.19	33.41	3.87	7.66	A
Tunga	8	14.74	33.40	4.24	7.66	A
Standard net						
Pampa	8	16.74	33.51	6.92	7.86	A
Panteón	8	15.19	33.48	5.92	7.73	A
Santa Rosa	8	14.96	33.39	6.18	7.80	A
Tunga	8	16.74	33.46	6.38	7.78	A

Table 9 shows that there clearly is a statistical relation between environmental parameters and the larval assemblage. The many significant interaction terms

Table 8 Principal components (*PC1–4*, loadings) of the environmental data

	PC1	PC2	PC3	PC4
Temp. (°C)	0.6376	0.2361	−0.0451	−0.7318
Salinity (ppt)	0.2821	0.7758	0.3006	0.4775
O₂ (ml l⁻¹)	0.5743	−0.2472	−0.6307	0.4595
pH	0.4288	−0.5302	0.7139	0.1585

show that this relation is of a complex nature. Further conclusions are hard to make, as the environmental quantities did not emerge from a designed laboratory experiment, but were measured in the field, leading to highly correlated values, as could already be seen from the PCA in Table 8. For this reason, no attempt was made to attribute changes in the larval assemblage to one or more particular environmental parameters.

Vertical assemblages

Five major depth groups were determined by cluster analysis (Fig. 5A) at the 20% similarity level. Groups I and II consisted exclusively of surface samples, where *O .regiaregia* was most abundant and overwhelmingly dominant. Group III consisted only of one sample in summer at Santa Rosa. Group IV was composed predominantly (84.6%) of samples collected at 10 m depth, where *N .crockeri* , *E .ringens* and *Scartichthys* sp. were dominant. Group V consisted mainly of mid-water samples (78%). The MDS (Fig. 5B) plot also showed that the assemblage at the surface and 10 m differed. Depth stratification of assemblages was evident although the water column was well mixed in this shallow bay.

Seasonal assemblages

The cluster analysis distinguished four seasonal groups at a 20% similarity level, corresponding to larval fish assemblages (Fig. 6A). Group I is composed of summer samples, group II is composed of March–April samples,

Table 9 Results of fitting a multinomial logistic model to species assemblage. Only the main families were included (*df* degrees of freedom; *SE* standard error)

Parameter	df	Estimate	SE	Wald chi-squared	P
Intercept Atherinidae	1	−1,982.2	348.9	32.2743	< 0.0001
Intercept Blenniidae	1	−1,980.4	348.9	32.2164	< 0.0001
Intercept Engraulidae	1	−1,976.7	348.9	32.0982	< 0.0001
Intercept Gobiesocidae	1	−1,976.5	348.9	32.0900	< 0.0001
Intercept Haemulidae	1	−1,976.4	348.9	32.0888	< 0.0001
Intercept Labrisomidae	1	−1,976.4	348.9	32.0882	< 0.0001
Intercept Normanichthyidae	1	−1,972.1	348.9	31.9492	< 0.0001
Intercept Paralichthyidae	1	−1,971.6	348.9	31.9310	< 0.0001
Temperature	1	3.6487	6.4344	0.3216	0.5707
Salinity	1	50.2196	11.7772	18.1828	< 0.0001
Oxygen	1	26.2364	3.7506	48.9330	< 0.0001
pH	1	275.4	46.1096	35.6667	< 0.0001
Temperature×Salinity	1	0.4619	0.1025	20.3065	< 0.0001
Temperature×pH	1	−2.2206	0.8366	7.0454	0.0079
Salinity×Oxygen	1	−0.2252	0.0331	46.3835	< 0.0001
Salinity×pH	1	−7.1925	1.5428	21.7337	< 0.0001
Oxygen×pH	1	−2.4054	0.4621	27.0912	< 0.0001

group III is composed of surface samples collected predominantly (86%) in autumn and winter, with just over half the samples (57%) taken in autumn, and group IV contains predominantly spring through autumn samples (93%). The ordination plot (Fig. 6B) clearly shows the small summer and winter groups (I, II) and the mixture of seasons in the other groups.

Discussion and conclusions

Independencia Bay is a productive marine ecosystem that contains cold, low-salinity waters derived from the adjacent Humboldt Current. Independencia Bay is also subject to physical variability, influenced by strong currents. Perhaps owing to its variability, and probably owing also to the high production, the bay supports an abundant and varied ichthyoplankton. However, only a small proportion of the total taxa (16.7%: eight species) contributed most of the total abundance of fish larvae (96.8%). The numerically dominant taxa were Engraulidae, Normanichthyidae, Blenniidae, Gobiesocidae, Haemulidae, Labrisomidae, Pinguipedidae, and Atherinidae. All of these, except Engraulidae, are resident taxa that most likely complete their life cycles within the bay.

Composition of the larval fish assemblage

The composition of larval fish assemblages in coastal waters is generally related to the local current regimes, habitat types, and water masses occurring in the region. All of the families listed in Table 10 have species that are most abundant in bays, but also may occur to some extent near shore along the open coast, as well as species that are most abundant inshore along the open coast, but also occur in bays (Hildebrand 1946; Mongard1981; Leis 1994; Beltran-Leon and Rios2000). The dominant species in these families that we found during our study

are primarily those associated with bays, based on these earlier studies. Fish larvae from this study could be divided into four groups on the basis of their adult habitat (Table 10): (I) inshore, benthic species; (II) inshore, neritic species; (III) coastal pelagic species that do not complete their life cycle exclusively in the bay; and (IV) epi- and mesopelagic oceanic species. Most of the members of groups I and II are very common in Independencia Bay as adults (Reynaga and Mendo2002), and, as evidenced by collections of eggs, preflexion, and flexion stages, we suspect that they spawn and complete their life cycles within the bay. The larvae of these two groups constituted > 66.6% of all larvae collected at all stations. Group III constituted 32.5% of the total larvae collected, of which 99.4% was constituted by*Engraulisringens*. Group IV, the oceanic taxa, contributed < 1% of the total larvae in the bay. Apparently the bay is not an important nursery area for the oceanic species, but it supports a suite of inshore species and is likely to be a critical habitat for them.

Spatial and temporal distribution

The young age of most larvae collected in this study (mostly preflexion stage) suggests that the temporal and spatial patterns mainly reflect spawning seasons and localities (i.e. inside or outside the bay) of adults. Most of the abundant taxa, except engraulids, probably spawn primarily or entirely inside the bay;*E .ringens* spawns mainly along the open coast (Ayón2001a, 2001b; Girón2001). In the Pisco area larval abundance of *E .ringens* is high in the coastal zone to 46.3 km from shore (Ayón2001b), but it clearly spawns in Independencia Bay, too. In the bay, where fish larvae are predominantly species that most likely complete their life cycles inside the bay (groups I and II, Table 10), the larvae probably are retained by the circulation pattern within the bay and possibly by larval behavior. Yamashiro et al. (1990), Moron and Campos (1998) and Moron
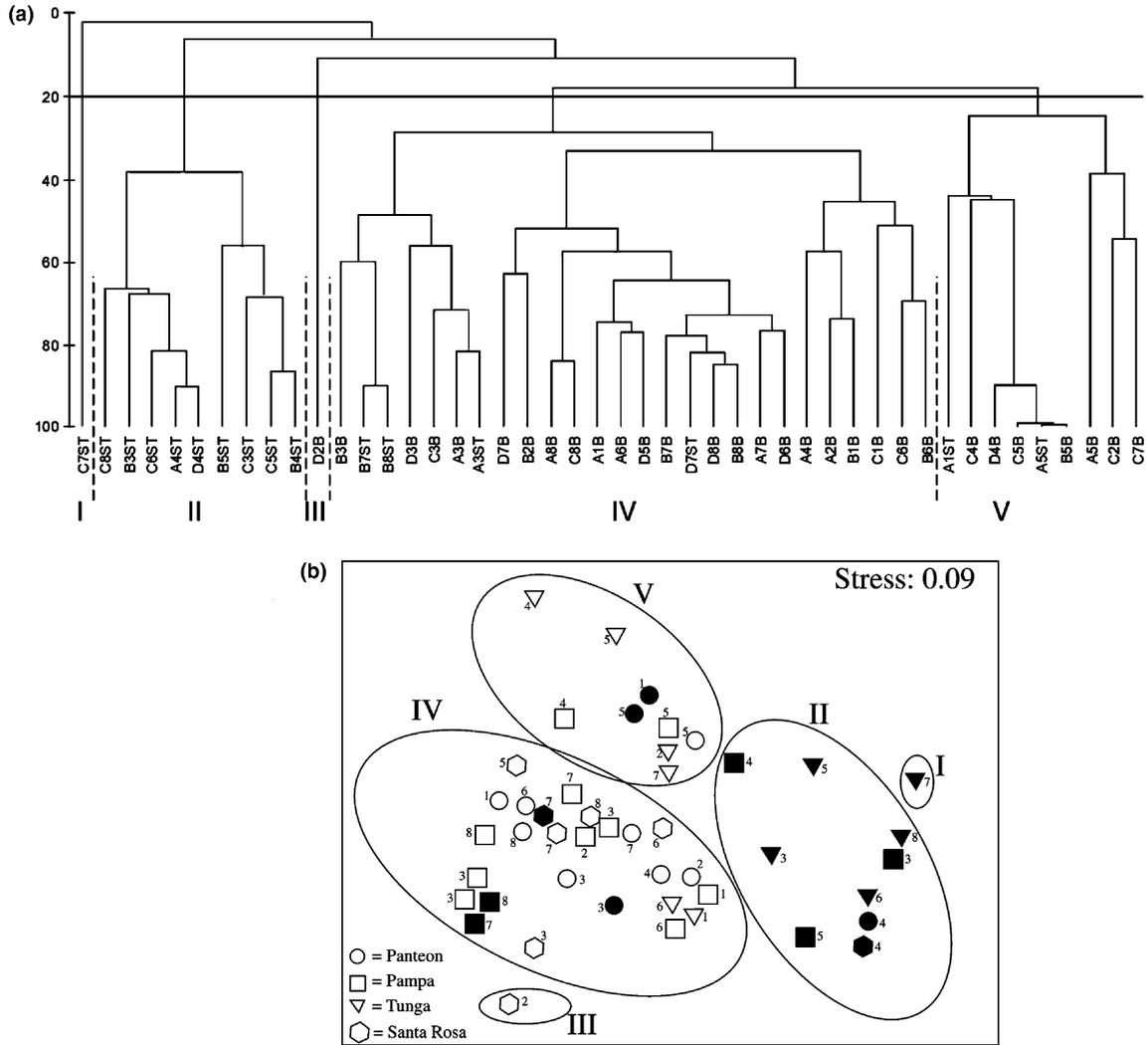
Fig. 5A, B Vertical classification of the ichthyoplankton sampled in Independencia Bay during 2000. Data are log($x+1$) transformed. Only the dominant taxa were included in this analysis. **A** Dendrogram of similarities (Bray–Curtis index) (*A* Panteón; *B* Pampa; *C* Tunga; *D* Santa Rosa; *ST* surface net; *B* bongo net). **B** MDS ordinations (*closed symbols* surface samples; *open symbols* 10 m samples). Numbers in both plots refer to the month of sampling (*1* January; *2* February; *3* March–April; *4* May; *5* August; *6* September; *7* October; *8* November)

(personal communication) demonstrated the presence of anticyclonic circulation in the central bay. The central bay (north of La Vieja Island) is relatively rich in plankton and consistently holds high abundances of fish eggs and larvae. Larvae of all sizes were retained in the anticyclonic eddy. Although no larval length or current measurements were made in this study, a qualitative examination of the samples suggested that larvae tended to be larger at Santa Rosa than at the other stations. The apparent larger larval sizes at Santa Rosa may reflect an inability of the smaller larvae to maintain position in the stronger currents at this station, which is closer to the open ocean. Alternatively, it might reflect preferential movement of the older larvae into the area, possibly

because of higher food availability (zooplankton volumes were always higher at Santa Rosa than at the other stations), or for settlement. Hydrographic conditions that retain planktonic eggs and larvae within bays (Doyle et al. 1993), together with enhanced densities of food, may allow developing larvae to grow rapidly, thus helping them to avoid predators and resist being dispersed by currents (Bourne and Govani 1988; Olney and Boehlert 1988). The species composition differed between summer and spring, but the dominant species were found in both seasons, except *Odontesthes regiaregia*, which was absent in both February and October, but present in November. The reason for this different seasonal spawning pattern is unclear, because we do not see any difference between the stations during the peak. Since *O .regiaregia* larvae are neustonic, wind-driven surface transport may be important, and the wind pattern would favor larval retention in the bay. Another possibility to consider is that there may be some adult spawning habitat requirement that is available only during part of the year and that drives the pattern. The spring and summer ichthyoplankton abundance peaks in Independencia Bay coincided with high zooplankton
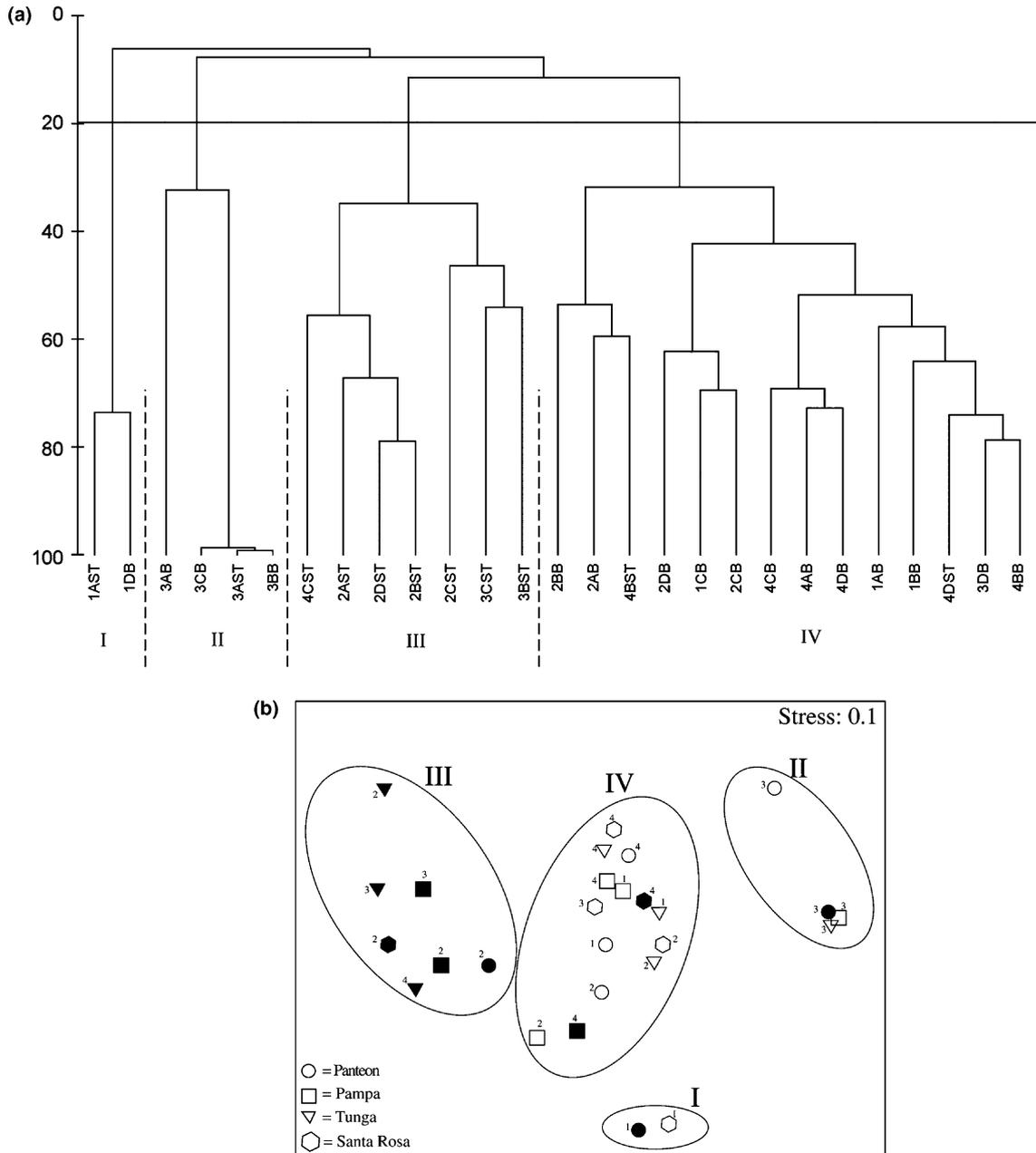
Fig. 6A, B Seasonal classification of the ichthyoplankton sampled in Indendencia Bay during 2000. Data are $\log(x+1)$ transformed. Only the dominant taxa were included in this analysis. **A** Dendrogram of similarities (Bray–Curtis index) (*A*Panteón; *B* Pampa; *C* Tunga; *D* Santa Rosa;*ST* surface net; *B* bongo net). **B**MDS ordinations (*closed symbols* surface samples; *open symbols* 10 m samples). Numbers in both plots refer to the season of sampling (*1*summer; *2* autumn;*3* winter; *4* spring)

standing stock and also coincided approximately with the periods of increased upwelling in the area (Fig. 7). Presumably, spawning in the bay during summer and early spring, in association with strong upwelling periods, permits larvae to take advantage of the increased planktonic production. The May sample had the lowest monthly mean larval density (29.2 larvae per 100 m^3). Cabello et al. (2002) detected in mid-May to mid-June 2000 high concentrations of oil and grease coming from fishery effluents and discussed the presence of a red tide associated with an increase in total suspended solids, pH, and dissolved oxygen at Paracas Bay (north of Independencia Bay). The red tide was also observed during the May ichthyoplankton sampling in Independencia Bay, and it is possible that the low larval abundance in that month could be related to these phenomena. Comparing the abundances of *E .ringens*, the most important Peruvian fisheries resource, with results from IMARPE studies during 2000 in other areas along the Peruvian coast shows that larval abundances generally were of the same order of magnitude both in the bay and off the open coast. Abundance was higher in the bay than along much of the coast and was comparable to that in localized high-abundance areas along the

Table 10 Families of fish larvae grouped on the basis of their adult habitats reported in the literature (Nelson 1994)

Group I (inshore, benthic species)		Group II (inshore, neritic species)	Group III (coastal pelagic fish, not bay dependent)	Group IV (epi- and mesopelagic species)
Blenniidae	Labrisomidae	Atherinidae	Engraulidae	Nomeidae
Chaenopsidae	Ophidiidae	Centropomidae	Clupeidae	Scombridae
Cheilodactylidae	Paralichthyidae	Haemulidae	Coryphaenidae	
Ephippidae	Pinguipedidae	Labridae	Kyphosidae	
Gerreidae	Scorpaenidae	Normanichthyidae	Sphyraenidae	
Gobiesocidae	Serranidae	Pomacentridae	Carangidae	
Gobiidae	Syngnathidae	Sciaenidae		
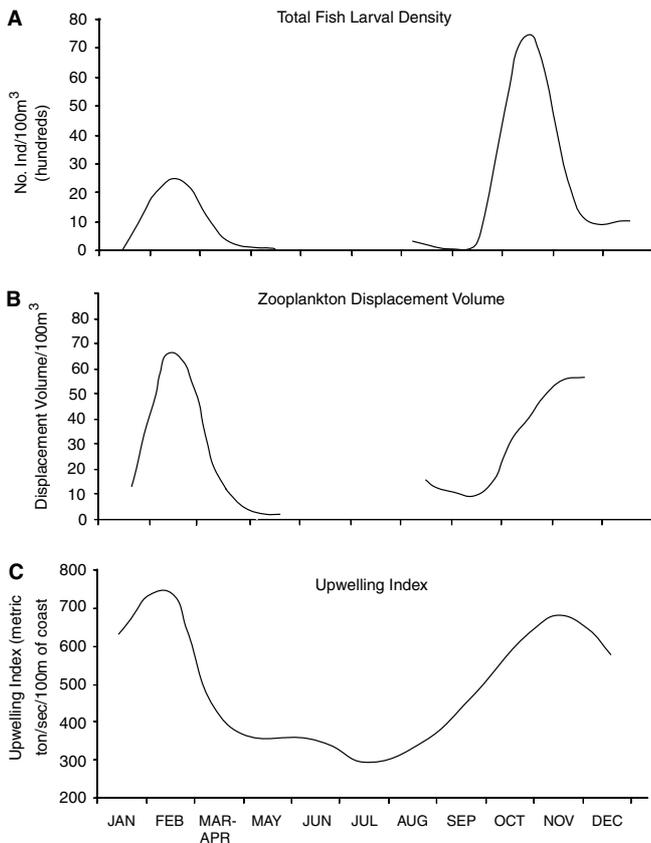
Fig. 7 A Total fish larval density (ind. per 100 m³), **B** zooplankton displacement volume (ml sample⁻¹), and **C** upwelling index (metric tons per second per 100 m of coast) during 2000. Upwelling index of waters adjacent to Pisco (15°S; 77°W), from Pacific Fisheries Environmental Laboratory, NOAA (http://www.pfeg.noaa.gov/products/pfel/modeled/indices/upwelling/sa/sp_upwell_data.html)

Peruvian coast (Ayón 2001a; Girón 2001). Higher abundance of larval *E. ringens* in Independencia Bay compared with waters along much of the open coast suggests that the bay may, to some extent, serve as a nursery area for this species. In addition, it is possible that the bay could serve as a refugium during El Niño events for species such as *E. ringens*. In the California Current region plankton production near shore remains relatively high during El Niño events compared with more seaward waters, thus providing food and increasing

larval survival of species such as *Sardinops sagax* in the near-shore zone compared with the oceanic regions.

Vertical distributions of larvae in Independencia Bay were well defined; thus, larvae apparently are able to maintain vertical position despite the strong vertical mixing suggested by the apparent lack of a thermocline at all four stations throughout the study. Because Hewitt (1980) found essentially no difference in catches of small larvae between a ring and a bongo net, and, because most of our larvae were small, we feel justified in making a comparison between the catches from the ring and bongo nets. Overall, more taxa were caught at the 10 m depth than at the surface, and the classification analyses revealed that depth was more important in distinguishing assemblages than horizontal location, which had little effect on structuring the assemblages. Only one of the nine most abundant taxa, the atherinid *O. regia regia*, was consistently most abundant at the surface at all locations; similar neustonic distributions have been reported for other atherinids as well (Leis 1991; Schmitt and Leis 2000). The distribution patterns in the bay coincide with those found elsewhere in other studies (Ahlstrom 1959; Boehlert et al 1985; Leis 1991). Larval Blenniidae (*Scartichthys* sp.), Engraulidae (*Engraulis ringens*), Gerreidae (*Eugerres periche*), Gobiesocidae (*Gobiesox marmoratus* and *Tomicodon petersi*), Normanichthyidae (*Normanichthys crockeri*), Paralichthydae (*Paralichthys microps*), Pinguipedidae (*Prolatilus jugularis*), Kyphosidae [*Doydixodon* sp. (*laevifrons*?)], Labrisomidae [*Labrisomus philippi* (?)], and Haemulidae (*Anisotremus* sp.) were found at least once at the surface in different months, usually at night during the additional sampling (Table 1), but they were never more numerous at the surface than at 10 m depth (Vélez et al., unpublished data). The results of this study are consistent with the hypothesis that fishes in Independencia Bay synchronize their reproductive seasons in response to local environmental factors to take advantage of currents and favorable larval feeding conditions in the bay. Larvae of most species in the bay apparently have a mechanism to stay in the bay (retention), and the coastal pelagic fish larvae (e.g. anchovies, sardines) temporarily use the bay as a nursery area. Those nearshore species that do not complete their life cycles exclusively in embayments (group III, Table 10) may time their spawning peaks to coincide with times of reduced currents, and bay species in groups I and II

spawn in a pattern that is less dependent upon seasonal current shifts. Because seasonal patterns in primary and secondary productivity in Independencia Bay are poorly documented and because this is the first ichthyoplankton study in the bay, inter-study comparisons are not possible. However, this study suggests that the seasonal assemblages of early larvae reflect the seasonal spawning patterns of adult fish. Future ichthyoplankton studies in the bay should focus on obtaining better resolution of small-scale larval patchiness and links to food and predators.

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