

Ichthyoplankton assemblages in the Gulf of Nicoya and Golfo Dulce embayments, Pacific coast of Costa Rica

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Abstract: Ichthyoplankton surveys were conducted in December (rainy season), 1993 and February (dry season), 1994, during the RV Victor Hensen German - Costa Rican Expedition to the Gulf of Nicoya and Golfo Dulce, Costa Rica. Samples from the inner, central, and outer areas of each gulf were collected in oblique tows with a bongo net of 0.6 m mouth diameter, 2.5 m long and 1000- μ m mesh. A total of 416 fish larvae of 22 families were sorted out of 14 samples. Stations of both the maximum (11) and the minimum (1) family richness were located in Golfo Dulce. Mean total larval abundances were 124.9 and 197.2 individuals 10 m^2 for the Gulf of Nicoya and Golfo Dulce, respectively, while mean larval densities ranged from 95.3 larvae 10 m^2 in December to 236.7 larvae 10 m^2 in February. However, no statistical differences between gulfs or seasons were detected, due to the high within-group variability. Cluster Analysis, Multi-Dimensional Scaling (MDS), and non-parametric tests showed two well-defined major groups: (1) the Gulf of Nicoya neritic assemblage, represented by Engraulids, Sciaenids, and Gobiids (inner and central stations), and (2) the oceanic assemblage, dominated by Myctophids, Bregmacerotids, Ophiidids, and Trichiurids (outer stations off the Gulf of Nicoya and Golfo Dulce). A third, although less defined group, was an Ophichthid-dominated assemblage (typical in areas nearby coral or rocky reefs). These assemblages closely resemble the clusters based upon adult fish data of the beamtrawl catches of the same cruise. This publication is the first to report on the ichthyoplankton community of Golfo Dulce.

Key words: Ichthyoplankton, Eastern Tropical Pacific, fish larvae distribution, zooplankton, Golfo de Nicoya, Golfo Dulce.

The Gulf of Nicoya (GN) and Golfo Dulce (GD) are the major embayments of the Pacific coast of Costa Rica (Figs. 1 y 2). These systems are quite different in size, topography, hydrography, chemical oceanography, surrounding vegetation, and resource exploitation, among other features (Chaves *et al.* 1994, Wolff 1994, von Wangelin and Wolff, 1996).

The Gulf of Nicoya harbors the most important fishery grounds in the country, supporting a multi-species fishery of shrimp, finfish (drums and others), and sardines (Campos 1986). Zooplankton surveys in the gulf have emphasized the importance of the following groups: stomatopods (Dittel 1991), larval crabs (e.g., Dittel and Epifanio 1990, Dittel *et al.*

1991) as well as early developmental stages of fish (López 1983, López and Arias 1987, Ramírez *et al.* 1989, 1990). Ichthyoplankton assemblages offshore the Nicoya Peninsula and the Costa Rica Thermal Dome have been described by Rojas *et al.* (1991) and Aguilar-Ibarra (1993).

In Golfo Dulce, on the contrary, little is known about its planktonic communities. Its particular features as a 'tropical fjord' (von Wangelin and Wolff, 1996), its chemical oceanography (Chaves *et al.* 1994, Wolff 1994) and the presence of coral reefs (Cortés 1990), suggested plankton assemblages uncommon for tropical inshore waters. The plankton surveys of the recently conducted RV Victor Hensen expedition to the Golfo Dulce area yielded the

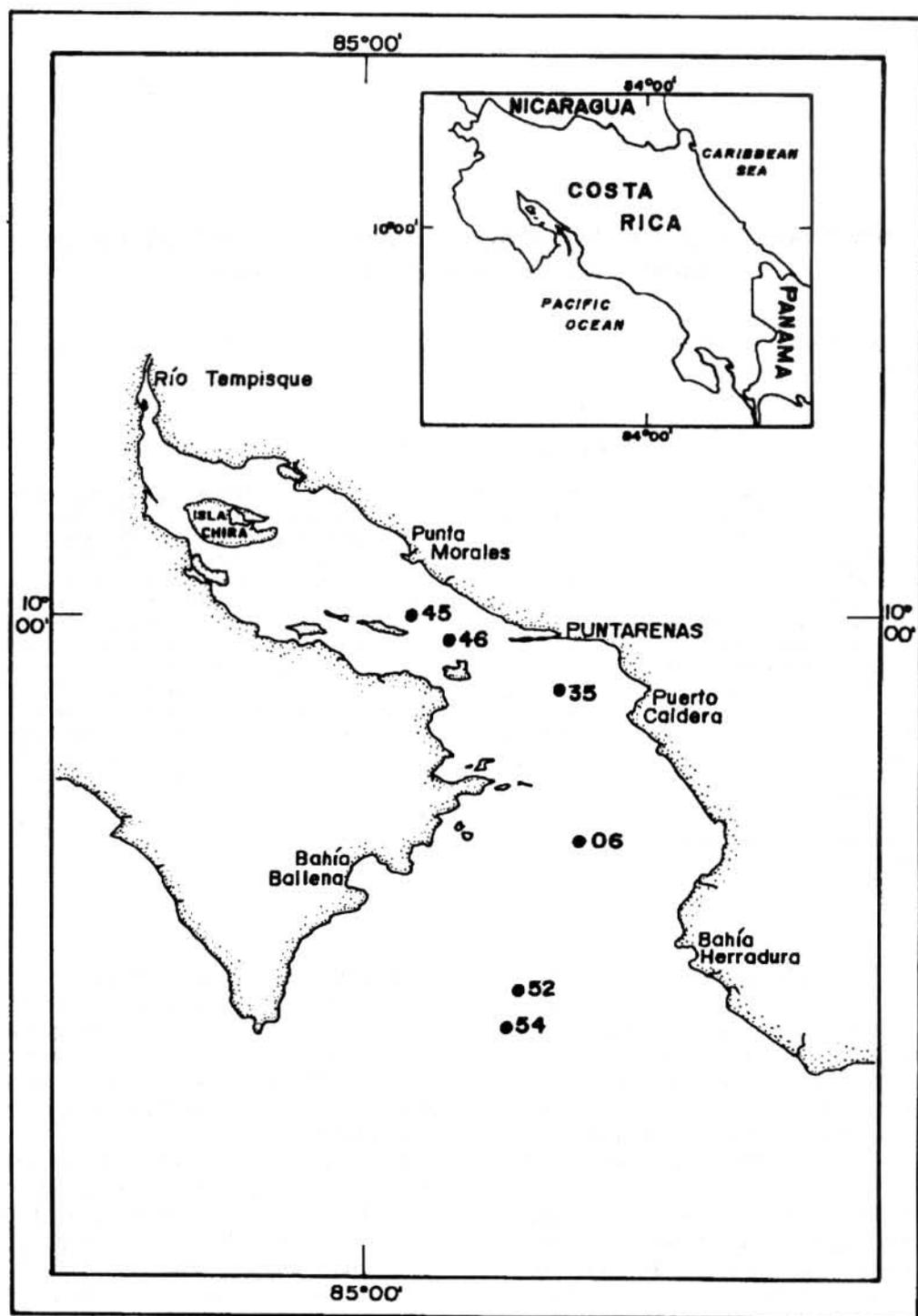


Fig. 1. Study area and sampling locations of the ichthyoplankton (1000- μ m fraction) component in Gulf of Nicoya. RV Victor Hensen Costa Rica Expedition, December 3-5, 1993 - February 3-5, 1994.

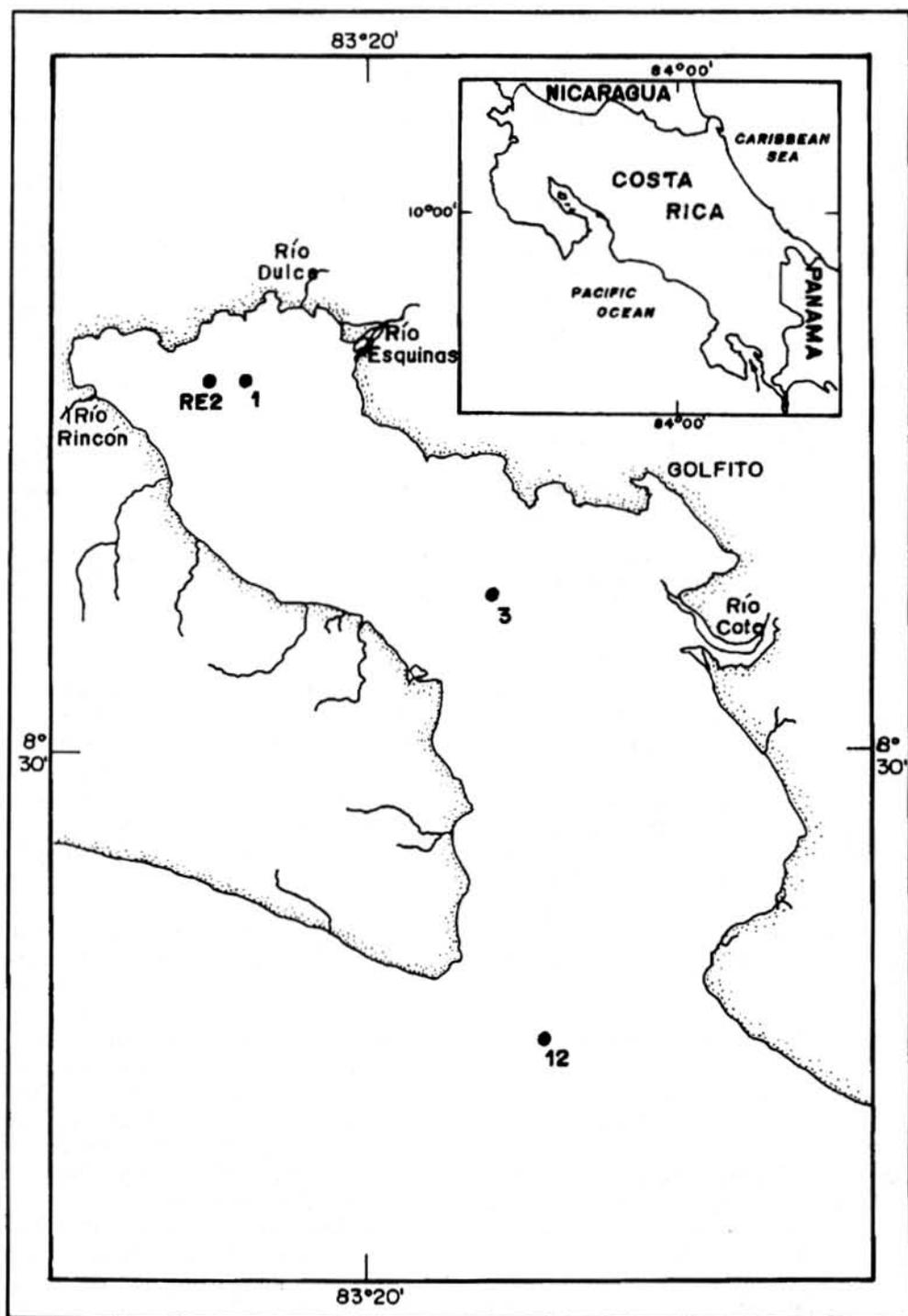


Fig. 2. Study area and sampling locations of the ichthyoplankton (1000- μ m fraction) component in Golfo Dulce. RV Victor Hensen Costa Rica Expedition, December 7-9, 1993 - February 7-9, 1994.

TABLE 1

*Ichthyoplankton stations of the RV Victor Hensen Costa Rica Expedition,
Gulf of Nicoya and Golfo Dulce (December 1993-February 1994)*

Station	Date (d/m/y)	Time (GMT)	Latitude	Longitude	Bottom DEPTH (m)	Tow DEPTH (m)	Vol. FILTERED (m ³)
N06-D	4/12/93		09°N 45.25'	084°W 45.87'	45	30	135.12
N35-D	5/12/93	14:57	09°N 55.08'	084°W 47.51'	17	10	98.23
N45-D	5/12/93	20:10	10°N 02.99'	085°W 00.51'	60	40	36.64
N52-D	3/12/93	19:20	09°N 36.05'	084°W 50.04'	100	85	92.80
N54-D	3/12/93	21:17	09°N 33.82'	084°W 50.16'	220	100	123.08
N46-F	3/2/94	17:11	10°N 02.10'	084°W 57.00'	16	10	97.72
N52-F	5/2/94	14:56	09°N 35.88'	084°W 50.06'	110	90	69.72
N54-F	5/2/94	16:59	09°N 33.43'	084°W 50.11'	300	180	214.43
Golfo Dulce							
D01-D	8/12/93	14:24	08°N 41.39'	083°W 23.18'	204	180	293.57
D03-D	7/12/93	23:04	08°N 34.68'	083°W 15.57'	190	140	165.66
D12-D	7/12/93	13:24	08°N 20.51'	083°W 13.29'	200	90	130.03
D01-F	8/2/94	16:25	08°N 34.70'	083°W 15.83'	190	160	144.45
D02-F	9/2/94	22:30	08°N 42.16'	083°W 25.15'	196	118	168.63
D12-F	8/2/94	12:07	08°N 20.50'	083°W 13.98'	215	180	175.41

* Station nomenclature: first letter indicates the gulf (N= Nicoya, D=Dulce); the two digits indicate station number (following previous works) and the last letter belongs to the month of collection (D=December 1993, F=February 1994). E.g., N45-D is station 45 of Gulf of Nicoya sampled in December, while D12-F is station 12 in Golfo Dulce collected in February.

first reports on meso- and macrozooplankton (von Wangelin and Wolff 1996), and the Chaetognath and Copepod components (Höbfeld 1996, Morales, 1996). Presently, Copepod (Morales and Cubero in prep.) and Ostracod studies (Jakob in prep.) are being conducted. The present paper represents the first report on the ichthyoplankton community of Golfo Dulce. Its objective was to compare the taxonomic composition and relative abundance of the ichthyoplankton of the Gulf of Nicoya (GN) and Golfo Dulce (GD) embayments.

MATERIAL AND METHODS

Ichthyoplankton surveys were conducted during Leg 1 (December 2-9, 1993) and Leg 4 (February 2-9, 1994) on board the German research vessel Victor Hensen. The stations were selected based on studies by Voorhis *et al.* (1983) for the Gulf of Nicoya (Fig. 1) and Richards *et al.* (1971) for Golfo Dulce (Fig. 2). The sampling strategy was designed such that the inner, central, and outer parts of both gulfs were surveyed. December collections represented the end of the rainy season, while the February sampling took place in the middle of the dry season for both ecosystems.

Standard MARMAP procedures (Smith and Richardson 1977) were followed, using a Bongo-net sampler frame with paired bongo nets. The nets (0.6 m mouth diameter and 2.5 m length each) had a 500- μ m and a 1000- μ m mesh size, respectively. Hydrobios flowmeters, attached at the mouth of each net, were used to determine the volume of water filtered.

The nets were towed obliquely with a wire angle of approximately 45-50°, at an average speed of 1.5 to 2.0 knots (0.76 - 1.03 ms⁻¹), to and from a maximum depth of 193 m or a minimum of 5 m above the sea floor. Towing time varied between 8 and 15 minutes, depending on water depth and the Secchi reading. Both the wire angle and the required length of wire to reach the chosen tow depths, were determined by a clinometer. Table 1 summarizes the main descriptors of each station.

Samples were immediately fixed with 4% buffered formaline solution. Within six months after each collection, formalin was replaced by 70% ethanol for long term preservation. The 1000- μ m samples were processed at the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) of the Universidad de Costa Rica (UCR), sorted

and identified to the lowest taxon possible, enumerated and measured to the nearest 0.1 mm. Most identifications were checked by the Ichthyoplankton Laboratory personnel, UCR.

Because ichthyoplankton surveys usually take oblique tows, which integrate all larvae between the deepest point reached by the net and the surface, larval densities must be expressed in terms of amount of individuals under a given unit of surface area, with a formula given by Smith and Richardson (1977). In this study, this formula was adapted for a unit of surface area of 10 m^{-2} due to the low abundances of certain taxa:

$C = 10 (a b c^{-1})$, where

C=number of fish eggs or larvae beneath a unit sea surface area (10 m^{-2})

a=number of fish eggs or larvae in the sample

b=maximum depth of tow (in meters)

c=volume filtered=area of the mouth of the bongo net*# revs in flowmeter * 0.3

Differences in total abundances between gulfs and between seasons, as well as the gulf-season interaction effect, were tested by Two-way Analysis of Variance (ANOVA). Stations were compared to each other in terms of species composition with the non-parametric statistical Kendall's Coefficient of Concordance Test, by calculating Kendall's Concordance Coefficient W of the species ranks. (Tate and Clelland 1959, Zar 1984). Also, multivariate hierarchical agglomerative Cluster Analysis (based upon Bray-Curtis Similarity matrix with square root transformation) and the non-parametric Multi-Dimensional Scaling (MDS) were conducted in order to display any possible seasonal or geographical patterns of distributions that may arise (Clarke 1993, Clarke and Warwick 1994).

RESULTS AND DISCUSSION

A total of 416 fish larvae were sorted out of 14 samples of the 1000- μm fraction during both legs of the expedition. Larval stages of 22 families were identified to the lowest taxonomic level possible; the dry-season outer GD sample had the greatest family richness (11

families), while the minimum richness occurred during the rainy season at the inner GD station (Table 2).

When comparing between gulfs and between seasons, no gulf-season interaction effects were significant (Two-way ANOVA $F=0.702$, $P=0.4304$), which allowed to compare abundances between gulfs and between seasons independently. The mean total larval abundance for the 14 samples was 155.9 per 10 m^2 ; in the Gulf of Nicoya there were 124.9 larvae per 10 m^2 , while Golfo Dulce had 197.2 larvae per 10 m^2 . Comparisons of larval abundances between gulfs resulted in non-significant differences (Two-way ANOVA $F=0.251$, $P=0.6328$), likely due to the high variability of larval abundances within each gulf (Table 2). However, rankings of total ichthyoplankton abundances by family showed highly significant differences among all stations ($W=42.76$, $0.01 < P < 0.001$), which indicated different types of assemblages.

The higher mean abundance value for Golfo Dulce apparently contradicts the observation that the Gulf of Nicoya was far more productive in terms of adult ichthyofauna than Golfo Dulce during the same cruise (Bussing and López 1994). The high larval densities collected at station 12 during February (Table 2) account for such high global values. Thus, considering only the inner and central stations of each gulf, GN showed similar values (72.8 larvae 10 m^{-2}) as GD (72.0 larvae 10 m^{-2}) with no statistical differences (Two-way ANOVA $F=0.000$, $P=0.9998$).

Concerning seasonal variations, no particular patterns were observed. Although December showed lower global densities (95.3 larvae 10 m^{-2}) than February (236.7 larvae 10 m^{-2}), the high within-group variation brought about a non-significant difference between rainy and dry seasons (Two-way ANOVA $F=1.472$, $P=0.2529$).

Multivariate community analyses based on family level suggested some trends. A Cluster Analysis showed two well-defined major groups and a third more loose category (Fig. 3): I- Inner and central stations from the Gulf of Nicoya; II- Outer stations from both GN and GD; III- Inner and central GD with outer GN. A Multi-Dimensional Scaling Analysis (MDS) confirmed these three clusters on a two-dimensional plot (Fig. 4); the low stress value, i.e.,

TABLE 2

Families of fish on the RV Victor Hensen Costa Rica Expedition, Gulf of Nicoya and Golfo Dulce (December 1993 - February 1994). Abundances are standardized to # 10 m³

Family	N45-D	N35-D	N06-D	N52-D	N54-D	N46-F	N52-F	N54-F	D01-D	D03-D	D12-D	D02-F	D03-F	D12-F	Total/ Family
Ophichthidae	0	0	0	18	0	0	0	0	67	0	0	0	66	10	162
Engraulidae	98	3	11	0	0	36	13	0	0	0	0	0	0	31	192
Myctophidae	0	0	0	0	16	0	13	201	0	8	28	0	0	41	308
Bregmacerotidae	0	0	0	0	146	0	77	25	0	25	21	0	0	585	880
Ophidiidae	0	0	0	0	16	0	0	8	0	0	7	0	11	0	43
Gobiesocidae	0	0	0	27	0	0	0	0	0	0	0	0	0	0	27
Exocoetidae	0	0	0	0	0	0	0	8	0	0	0	0	0	0	8
Serranidae	0	0	0	0	0	0	0	0	0	17	0	0	0	0	17
Carangidae	0	0	0	0	8	0	13	8	0	0	0	0	0	10	40
Lutjanidae	0	0	0	27	8	0	0	0	0	0	0	0	0	0	36
Gerreidae	0	4	7	0	0	0	0	0	0	0	0	0	0	0	11
Haemulidae	11	3	0	0	0	2	0	0	0	0	0	0	0	0	16
Sciaenidae	33	2	16	0	0	3	0	0	0	25	0	21	0	0	100
Ephippidae	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Gobiidae	11	0	11	0	16	38	13	0	0	8	0	0	0	21	118
Trichiuridae	0	0	0	0	0	0	0	0	0	0	14	0	0	10	24
Scombroidae	0	0	0	0	8	0	13	0	0	0	0	0	0	0	21
Stromateidae	0	0	0	0	0	0	0	0	0	0	0	0	0	21	21
Bothidae	0	0	0	0	0	0	0	0	0	0	7	0	11	0	18
Paralichthyidae	0	0	0	0	0	0	0	0	0	0	7	0	0	21	27
Cynoglossidae	0	0	0	18	8	0	0	0	0	0	0	0	22	51	100
Balistidae	0	0	0	0	0	0	0	0	0	0	0	7	0	0	7
Total/station	153	12	47	92	228	79	142	252	67	85	83	28	111	800	

measure of goodness-of-fit, of 0.025 for the MDS plot, indicates that it gives an excellent representation of the sample relationships (Clarke and Warwick 1994).

Both the Cluster dendrogram and the MDS plot (Figs. 3 and 4) suggest that geographic differences account for more variation than the seasonal differences did. Thus, the Inner-Central GN Group (N45-D, N06-D, N35-D, N46-F), with a similarity of about 58%, is characterized by a neritic assemblage of Engraulids, Sciaenids and Gobiids, with Gerreids and Haemulids in smaller numbers (Table 2). This type of assemblage closely resembles the ones described by Ramírez *et al.* (1990) in the Punta Morales estuary, located on the East shore of central Gulf of Nicoya (Fig. 1).

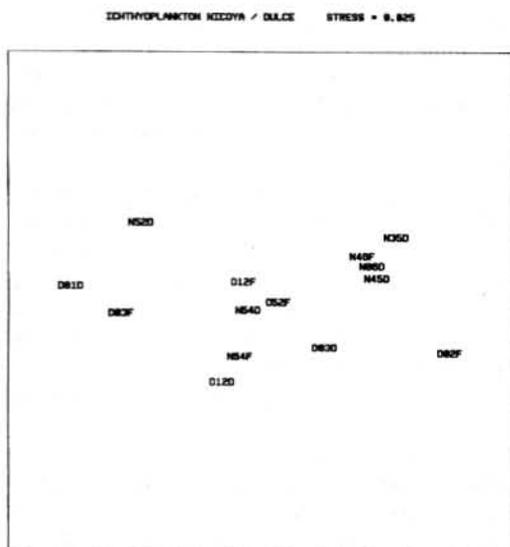


Fig. 3. Multi-dimensional Scaling (MDS) ordination of Gulf of Nicoya (GN) and Golfo Dulce (GD) ichthyoplankton samples, December 1993-February 1994.

The Outer GN - GD Group (N54-D, N52-F, D12-F, N54-F, D12-D), with ca. 44% similarity (Fig. 3) is represented by Myctophids, Bregmacerotids (*Bregmaceros bathymaster*), and Ophiids. Trichiurids (*Trichiurus nitens*) and Paralichthyids (flatfish) were collected only from the two GD outer stations (Table 2). These are typical oceanic assemblages, similar to those

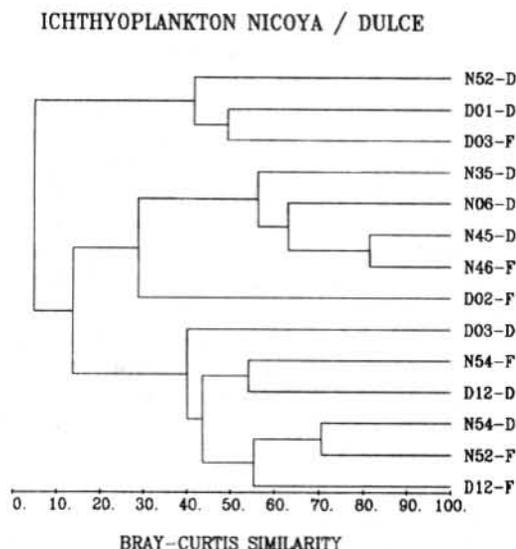


Fig. 4. Hierarchical agglomerative clustering of ichthyoplankton communities from Gulf of Nicoya and Golfo Dulce, December 1993 - February 1994. The Bray-Curtis Similarity is presented in terms of percentage.

found off the Sierpe-Térraba region nearby Caño Island (Molina 1994). The dominant families of the GN outer stations were the same that were most abundant offshore the Nicoya Peninsula (Rojas *et al.* 1991); Myctophids also showed the highest densities on ichthyoplankton assemblages from the Thermal Dome of Costa Rica, even though Bregmacerotids were not so abundant there (Aguilar 1993).

Larval fish of the families Carangidae, Gobiidae, and Cynoglossidae (*Symphurus* spp.) also occurred off GN in the December stations of this cluster, while flatfish larvae (Bothidae) were present off GD. The latter families have both neritic and oceanic species (Ramírez *et al.* 1990, Rojas *et al.* 1991, Aguilar-Ibarra 1993), so they would be expected to appear anywhere inside and outside the gulf. During February, other families such as Exocoetidae and Scombridae were also part of the GN offshore assemblages in this study, as well as off the Nicoya Peninsula (Rojas *et al.* 1991).

This Outer GN-GD group, however, could actually be divided into two subclusters: Assemblage A (N54-D, N52-F and D12-F), and Assemblage B (N54-F, D12-D), with a similarity of about 55% each (Fig. 3). The MDS plot (Fig. 4) confirmed this subdivision. These results support the lack of seasonal patterns as well.

The third group (N52-D, D01-D, D03-F) did not hold either a tight geographic or seasonal unity; the presence of high numbers of Ophichthid leptocephali is the only common feature among these samples. Snake eels are nocturnal fish distributed in coastal areas of tropical to warm temperate oceans (Nelson 1994), and the adults are usually found in areas of mixed sand, gravel, and coral/rocky rubble adjacent to shallow coral reefs, on sand flats or shallow grass beds (Humann 1994).

Because inner GN has a muddy bottom and it is mostly surrounded by mangrove with almost no rocky or coral areas (Voorhis *et al.* 1983), it would be unlikely to find snake eel leptocephali within this area. No larval Ophichthids have been reported in estuaries from the inner Gulf of Nicoya (Ramírez *et al.* 1990); their larval stages are rather more oceanic (Rojas *et al.* 1991, Aguilar-Ibarra 1993, López, Myrna 1995. Pers. Comm.). On the contrary, the outer GN is surrounded by rocky cliffs and sandy beaches (Voorhis *et al.* 1983), and the major coral reefs within GD, i.e., Punta Islotes, Punta El Bajo, and Sándalo reef areas (Cortés 1990), are close to the inner and central stations D01, D02 and D03 (Fig. 2).

The assemblages here described closely resemble the adult fish clusters of the beam-trawl catches, based on a biomass/abundance descriptor obtained by Wolff and Jesse (1994) during the same legs of the cruise. They found three major groups (inner-central GN, offshore stations, and GD stations), which showed well defined geographic ranges.

The present results, however, coincided only partially with their results of ottertrawl catches. The adult fish assemblages in GD were, in general, more similar to those of the outer part of GN, such as it is also seen in the ichthyoplankton component in this study. Nevertheless, the most important difference is that in GN, ottertrawl, central stations were clustered together with outer stations (Wolff and Jesse 1994), which suggests a more oceanic influence into GN for the larger nekton component.

On the other hand, even though the innermost GN station from December (N45-D) appeared to be peculiar with respect to adult fish distributions (Wolff and Jesse 1994) and high nutrient concentrations (Chaves *et al.* 1994), the ichthyoplankton assemblage was

80% similar to N46-F and more than 60% to the central station N06-D (Fig. 3).

The two remaining stations that were not included within any cluster belonged to GD (inner and central). The GD central D03-D station showed a mixed assemblage dominated by Bregmacerotids and Sciaenids, while Serranids and Gobiids had lower numbers. This suggests that Golfo Dulce does not have a distinctive zonation as seen in the Gulf of Nicoya. The D02-F sample, in the innermost area of the gulf, was also very deep (Table 1); only Sciaenids and Balistids (*sensu* Nelson 1994) were collected. The presence of the latter family is related to the coral reef habitats nearby; no adult specimens were collected during the same cruise (Bussing and López 1994) due to the fact that no trawls were conducted close enough to the reefs, where the adults live. Thus, the inner waters of GD are also important for early developmental stages of coral reef fishes.

The results discussed above support the observation that the Golfo Dulce ichthyofauna is more uniformly distributed across the basin. On the contrary, the Gulf of Nicoya is represented by two distinctive assemblages: neritic and oceanic. In this particular set of data no seasonal patterns arose, but a follow-up study of given key species might reveal some trends. The elucidation of ichthyoplankton biosystematics must be pursued for more years, in order to identify the specimens to the species level. This is no easy task in a tropical environment where species richness is so high.

The MDS analysis gives a good background information that may become useful when comparing these present assemblages described herein with future works. MDS has proved to be very useful in showing spatial and temporal patterns, such as impacts of coral mining on reef-fish communities (Clarke 1993, Clarke and Warwick 1994). The present work gives a baseline for the Golfo Dulce ichthyoplankton community to be used as reference for future zooplankton studies.

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RESUMEN

Se recolectó ictioplancton en diciembre (época lluviosa) de 1993 y febrero (época seca) de 1994 durante la expedición del barco de investigación alemán Victor Hensen al Golfo de Nicoya y al Golfo Dulce, Costa Rica. Se realizaron arrastres oblicuos en estaciones en las zonas interna, central y externa de cada golfo, con una red de 0.6 m de diámetro de boca, 2.5 m de largo y 1000- μ m de poro. En 14 muestras se extrajo un total de 416 larvas de 22 familias de peces. Tanto la estación con máxima riqueza de familias (11) como la mínima (1) están localizadas en Golfo Dulce. En el Golfo de Nicoya la densidad promedio fue de 124.9 larvas 10 m², mientras que en Golfo Dulce fue de 197.2 larvas 10 m². En diciembre se encontró un promedio de 95.3 larvas 10 m² y en febrero fueron 236.7 larvas 10 m². Sin embargo, no se registraron diferencias estadísticamente significativas de las abundancias totales entre golfos o entre épocas, debido a la alta variabilidad dentro de los grupos. Mediante Análisis de Conglomerados y de Escala Multidimensional, se establecieron dos tipos de comunidades ictioplanctónicas definidas: (1) el Grupo Nerítico del Golfo de Nicoya, representado por las familias Engraulidae, Sciaenidae y Gobiidae (estaciones internas y centrales), y (2) el Grupo Oceánico, dominado por Myctophidae, Bregmacerotidae, Ophiididae y Trichiuridae (fuera de la boca de ambos golfos). Un tercer grupo, más disperso, estaba constituido por estaciones dominadas por larvas leptocéfalas de la familia Ophichthidae, y fue típico en zonas aledañas a los arrecifes coralinos o rocosos. Esta clasificación se asemeja a la descrita para las comunidades de peces adultos recolectados durante el mismo crucero con una red de arrastre. Esta publicación constituye la primera descripción de la comunidad ictioplanctónica del Golfo Dulce.

REFERENCES

- Aguilar-Ibarra, A. 1993. Larvas y juveniles de peces del Domo Térmico de Costa Rica (Otoño 1981 y Verano 1982). Tesis de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F. 149 p.
- Bussing, W.A. & M.I. López. 1994. Demersal fish and macrofauna: report on the fish collections. In: Wolff, M. & J. Vargas (eds.). RV Victor Hensen Costa Rica Expedition 1993/1994. Zentrum für Marine Tropenökologie (ZMT) Contribution 2. p. 18.
- Campos, J.A. 1988. Fisheries development in Costa Rica. Conference on Artisanal Fisheries and Economic Development. University of Quebec, Remouski, Canada. April 1986.
- Chaves, J., M. Birkicht, S. León & A. Madrigal. 1994. Nutrient profiles. In: Wolff, M. & J. Vargas (eds.). RV Victor Hensen Costa Rica Expedition 1993/1994. Zentrum für Marine Tropenökologie (ZMT) Contribution 2. p. 10-17.
- Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18: 117-143.
- Clarke, K.R. & R.M. Warwick. 1994. Change in marine communities; an approach to statistical analysis and interpretation. Natural Environment Research Council and Plymouth Marine Laboratory, United Kingdom. 144 p.
- Cortés, J. 1990. The coral reefs of Golfo Dulce, Costa Rica: distribution and community structure. *Atoll Res. Bull.* 344: 1-37.
- Dittel, A.I. & C.E. Epifanio. 1990. Seasonal and tidal abundance of crab larvae in a tropical mangrove system, Gulf of Nicoya, Costa Rica. *Mar. Ecol. Prog. Ser.* 65: 25-34.
- Dittel, A.I., C.E. Epifanio & O. Lizano. 1991. Flux of crab larvae in a mangrove creek in the Gulf of Nicoya, Costa Rica. *Est. Coast. Shelf Sci.* 32: 129-140.
- Dittel, A.I. 1991. Distribution, abundance and sexual composition of stomatopod Crustacea in the Gulf of Nicoya, Costa Rica. *J. Crust. Biol.* 11: 269-276.
- Hossfeld, B. 1996. Distribution and biomass of species of Chaetognaths in Golfo de Nicoya and Golfo Dulce, Costa Rica. *Rev. Biol. Trop.* 44. Suppl 3: 157-172.
- Humann, P. 1994. Reef fish identification; Florida, Caribbean, Bahamas. New World, Florida. p. 362-375.
- López, M.I. 1983. *Lycodontis verrilli* (Pisces: Muraenidae), descripción de su larva leptocéfala del Golfo de Nicoya, Costa Rica. *Rev. Biol. Trop.* 31: 75-101.
- López, M.I. & C. Arias de la P. 1987. Distribución del ictioplancton en el Estuario de Pochote, Bahía Ballena, Pacífico de Costa Rica. *Rev. Biol. Trop.* 35: 121-126.

- Molina, H. 1994. Zooplankton: ichthyoplankton. In Wolff, M. & J. Vargas (eds.). RV Victor Hensen Costa Rica Expedition 1993/1994. Zentrum für Marine Tropenökologie (ZMT) Contribution 2. p. 47-50.
- Morales-Ramírez, A. 1996. Checklist of copepods from Gulf of Nicoya, Coronado Bay and Golfo Dulce, Pacific coast of Costa Rica, with comments on their distribution. *Rev. Biol. Trop.* 44. Suppl. 3: 103-113.
- Nelson, J.S. 1994. *Fishes of the world*. 3rd ed. John Wiley & Sons., New York. 600 p.
- Ramírez, A.R., W.A. Szelistowski & M.I. López. 1989. Spawning pattern and larval recruitment in Golfo de Nicoya anchovies (Pisces: Engraulidae). *Rev. Biol. Trop.* 37: 55-62
- Ramírez, A.R., M.I. López & W.A. Szelistowski. 1990. Composition and abundance of ichthyoplankton in a Gulf of Nicoya estuary. *Rev. Biol. Trop.* 38: 463-466.
- Richards, F.A., J.J. Anderson & J.D. Cline. 1971. Chemical and physical observations in Golfo Dulce, an anoxic basin on the Pacific coast of Costa Rica. *Limnol. Oceanogr.* 16: 43-50.
- Rojas, D.E., X. Lara & M.I. López. 1991. Taxonomía del ictioplancton costero del Pacífico Norte de Costa Rica. *Rev. Biol. Trop.* 39: 215-218.
- Smith, P.E. & S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larval surveys. *FAO Fish. Tech. Rep.* 175: 100 p.
- Tate, M.W. & R.C. Clelland. 1959. *Non-parametric and shortcut statistics*. Interstate, New Jersey. 171 p.
- Von Wangelin, M. & M. Wolff. 1996. Comparative biomass spectra and species composition of the zooplankton community of the Golfo Dulce and Golfo de Nicoya, Pacific coast of Costa Rica. *Rev. Biol. Trop.* 44 (Suppl 3): 135-155.
- Voorhis, A., C.E. Epifanio, D. Maurer, A. Dittel & J.A. Vargas. 1983. The estuarine character of the Gulf of Nicoya, an embayment on the Pacific coast of Central America. *Hydrobiologia* 99: 225-237.
- Wolff, M. 1994. Overview on oceanographical conditions in the study areas: CTD - Temperature, salinity and oxygen profiles. In Wolff, M. & J. Vargas (eds.). RV Victor Hensen Costa Rica Expedition 1993/1994. Zentrum für Marine Tropenökologie (ZMT) Contribution 2. p. 5-10.
- Wolff, M. & S. Jesse. 1994. Quantitative assessment of fish and crustaceans. In Wolff, M. & J. Vargas (eds.). RV Victor Hensen Costa Rica Expedition 1993/1994. Zentrum für Marine Tropenökologie (ZMT) Contribution 2. p. 25-37.
- Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, New Jersey. p. 352-358.