Spawning pattern and larval recruitment in Gulf of Nicoya anchovies (Pisces: Engraulidae)*

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Abstract: Monthly plankton collections (February to September, 1985) were made at three stations in and adjacent to the Punta Morales estuary, Gulf of Nicoya, to ascertain the importance of this mangrove system as a spawning and larval nursery ground for anchovies. Eggs were found to be abundant only at the estuary mouth and offshore, suggesting that most spawning occurred in nearshore waters, but not within the mangrove system itself. Densities of small larvae (< 5 mm TL) were also lower in the mangroves, but medium-sized individuals (5-12 mm TL) were common at all three sampling stations. Large larvae (12-20 mm TL) were nearly restricted to the inner estuary, suggesting that by this size fishes had moved into mangrove nursery grounds. Red tides in July and August apparently reduced the densities of eggs and larvae. Analysis of egg developmental stages indicated that spawning occurred around sunset, and that eggs developed in approximately 20-24 hours. Predation may be an important factor influencing the reproductive strategies of Gulf of Nicoya anchovies.

Mangrove estuaries are believed to be important fish nursery grounds and areas of reproduction, particularly for species of commercial value (Araya 1984, Krishnamurthy & Jeyaseelan 1981). Although numerous studies have documented the use of mangrove systems by the juvenile stages of fishes (Robertson & Duke 1987, Thayer, Colby & Hettler 1987, Bell *et al.* 1984, D'Croz & Kwiecinski 1980, Odum & Heald 1972, Austin 1971), very little is known about their role as nurseries for larvae or as spawning sites.

The Gulf of Nicoya is a large estuarine embayment that supports valuable commercial fisheries in Costa Rica (Kolberg *et al.* 1981). Its inner shoreline is lined with mangroves that frequently penetrate the coast in the form of inlets, or *esteros.* Previous studies(Araya 1984, Phillips 1983) and ongoing work (W.A. Szelistowski, unpubl. data) suggest that these *esteros* are utilized by the juveniles of a variety of fishes. Whether the young fishes migrate into these areas as juveniles or as larvae, or if they are spawned and remain there, is unknown.

This study examines the utilization of a mangrove *estero* by eggs and larvae of anchovies (Pisces: Engraulidae). Anchovies were selected because they are the most abundant group of fishes in the area, both as juveniles (W.A. Szelistowski, unpubl. data) and as larvae (Ramírez 1986), and because they play an important role in the Gulf of Nicoya food web (Peterson

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1956). Anchovies are treated at the family level because of taxonomic difficulties with their early life history stages. However, the common use of mangroves as a juvenile nursery ground by several species led us to hypothesize that general patterns in spawning and larval ecology may exist as well.

MATERIAL AND METHODS

Monthly plankton collections (February through September, 1985) were made in the vicinity of the Estero Punta Morales, a small (327 ha), secondary estuary of the Gulf of Nicoya (Fig. 1). Three sites were sampled, in the main channel approximately 1 km inside the estuary, at the estuary's mouth, and approximately 500 m offshore of the Punta Morales peninsula about 2 km from the mouth (Fig. 1). Mean depths at the sites were 4.1, 4.7, and 15.4 m, respectively. Four replicate tows were made at each site during incoming tides between 2030 and 0500 hours. Collections were made from a dinghy powered by a small outboard motor, using a 0.5 m diameter plankton net of 333 μm mesh fitted with a General Oceanics model 2030 flowmeter (calibrated monthly). The net was buoyed by a plastic gallon bottle attached by a cord and was towed behind the boat so that the upper rim of the net was maintained approximately 10 cm below the water surface, at 1.0-1.5 m/sec, for two minutes per tow. Samples were preserved in 10% formalin and transported to the laboratory.

Twenty-five per cent aliquots of all samples were sorted visually and engraulid eggs and larvae were separated from other ichthyoplankton. The remaining 75% unexamined portions were subsequently sorted at 100% for large larvae (defined below) to increase sample size for that group.

Anchovy eggs were identified on the basis of their oval shape, lack of filaments, oil globules and chorionic ornamentation, and the presence of segmentation in the yolk. Some engraulid species from the Gulf of Nicoya possess roughly spherical eggs (*Anchoa naso, Lycengraulis poeyi*; Peterson 1956). Due to the difficulties of separating these from those of other species with spherical eggs, this study was based entirely on oval eggs (*Anchoa argentivittata, A. curta, A. exigua, A. ischana, A. lucida, A. panamensis, A. walkeri, Anchovia macrolepidota,* and *Cetengraulis mysticetus;* Peterson 1956, Simpson 1959; shape unknown for 3 other species). Measurements of length (0.83 to 1.66 mm) and width (0.43 to 0.76 mm) of eggs selected randomly from each month suggested that several species were taken in the collections, although size overlap prevented the definition of distinct types. Therefore, this study treats all oval engraulid eggs together.

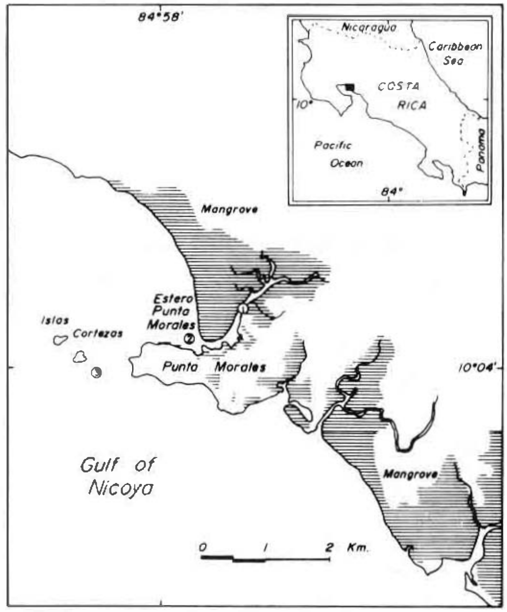

Fig. 1. Sampling stations at Punta Morales were located within the mangrove estuary (1), at the estuary mouth (2), and offshore (3).

Larvae were divided into three arbitrary classes: small (<5 mm TL), medium (5-12 mm TL), and large (12-20 mm TL), each analyzed separately. Large larvae were distinguished from clupeids based on the relative positions of the dorsal and anal fins, and small and medium-sized larvae based on the length of the gut (McGowan & Berry 1984). Fin-ray counts indicated a mixed assemblage of species among the large larvae.

A maximum of 600 eggs per sample were classified into the eleven developmental stages defined by Moser & Ahlstrom (1985).

Supplementary samples of eggs were collected from various times of the day and night over two days in October, 1986, in the same manner as the monthly samples. All eggs were staged as above.

Statistics followed Sokal & Rohlf (1981).

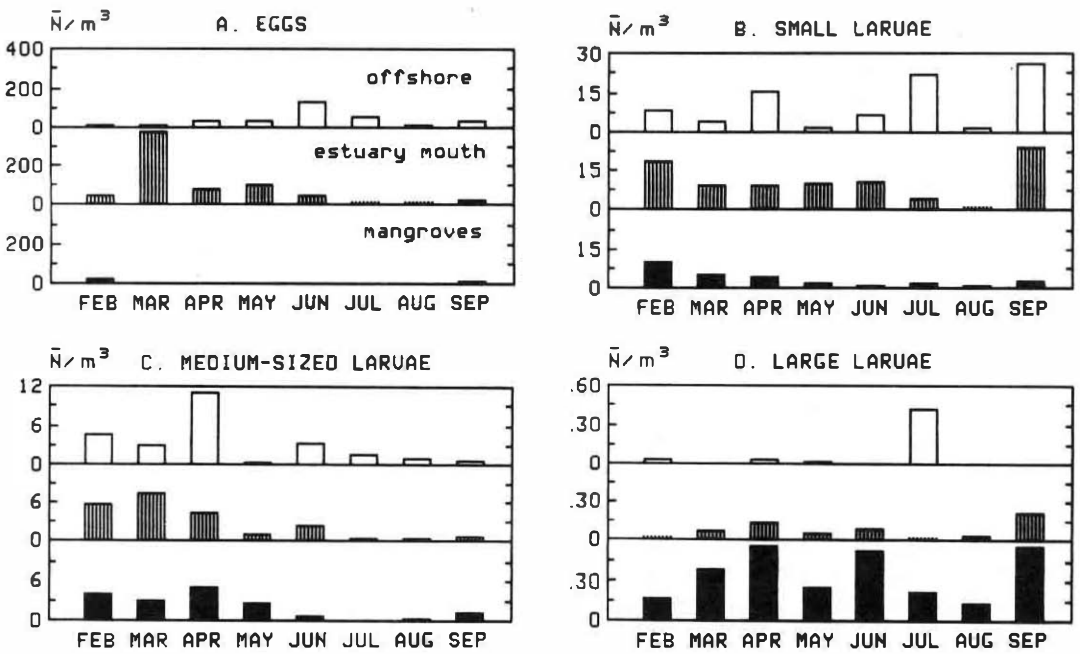

Fig. 2. Densities of anchovy eggs and larvae. Solid bars represent the estuary interior, lined bars the estuary mouth, and open bars the offshore site.

RESULTS

Egg densities differed significantly between stations ($p < .01$, Friedman's method for randomized blocks, subsequently referred to as FMRB), and were found to be lower in the mangroves than at and the estuary mouth offshore ($p < .01$ and .05, respectively, Wilcoxon's signed-ranks test, subsequently refferred to as WSR). No difference in egg abundance was observed between the latter two locations ($p > .05$, WSR, Fig. 2a).

Egg densities in July were low both within the estuary and at its mouth ($X = 0$ and 3.12 eggs/m^3, respectively), whereas moderate egg densities ($X = 54.03/m^3$) were found offshore. This pattern paralleled the distribution of red tides (Víquez 1985) that in July extended from within the mangroves to beyond the estuary's mouth, but not to the offshore site. During the August collections, red tides affected the entire area and egg densities were correspondingly low at all sities (maximum 2.36 eggs/m^3). By September the red tides had dissipated and egg densities had returned to higher levels.

No significant differences in abundance were detected between stations for small and medium -sized larvae in *a priori* comparisons (FMRB, $p > .05$, Fig. 2 b,c), and larvae of up to 10 mm TL were common at all three sites. However, application of *a posteriori* tests (WSR) showed a lower concentration of small larvae inside the estuary relative to its mouth ($p < .05$). Distributions of small and medium-sized larvae paralleled that of eggs during the time of the red tides in July and August, with relatively high densities present only in the unaffected, offshore station during July, and densities uniformly low in August when the red tide affected all stations (Fig. 2 b,c).

Densities of large larvae (12-20 mm) differed significantly between stations (FMRB, $p < .01$), and were found to be greater in the estuary than at its mouth ($p < .01$, WSR) and offshore ($p < .05$, WSR, Fig. 2d). Large larvae were virtually absent offshore in all months except July, when red tides affected the other two sites.

Mean egg developmental stages are presented in Table 1. Eggs from all monthly samples were in relatively early stages of development. Of nearly 12,000 eggs examined (72 collections),

TABLE I

Mean egg developmental stages for Gulf of Nicoya anchovy eggs, 1985. Stage values range from 1 (freshly spawned) to 11 (hatching imminent). Standard deviations and sample sizes (SD, N) are in parentheses. Dashes indicate no eggs in collections.

Date	Inner Estero	Estero Mouth	Offshore
February 15-16	3.14 (0.44, 814)	3.12 (0.42, 1309)	4.48 (0.68, 231)
March 15-16	---	2.62 (0.49, 1960)	3.08 (0.46, 122)
April 16-19	4.00 (0.00, 2)	3.00 (0.21, 1638)	3.15 (0.44, 387)
May 17-19	---	3.34 (0.77, 170)	3.03 (0.60, 498)
June 15-18	---	2.99 (0.18, 1009)	2.88 (0.61, 1728)
July 14-16	---	3.13 (0.45, 48)	2.98 (0.22, 1086)
August 17-18	---	2.63 (0.93, 11)	3.63 (1.19, 45)
September 18-19	3.12 (0.46, 140)	4.09 (0.41, 149)	3.88 (0.50, 308)

none was more advanced than the sixth of the eleven possible stages. No difference in development was found between eggs from the estuary mouth and the offshore station ($p > .05$, WSR). The presence of recently-spawned eggs in the 2040 h supplementary collection and nearly linear progression of development (Fig. 3) indicate late afternoon or early evening spawning. The lack of late stage eggs in the early evening (Fig. 3) suggests an egg development period of around 20-24 h. The fact that some anchovy eggs tend to sink just before hatching (Simpson 1959) could make this estimate somewhat low.

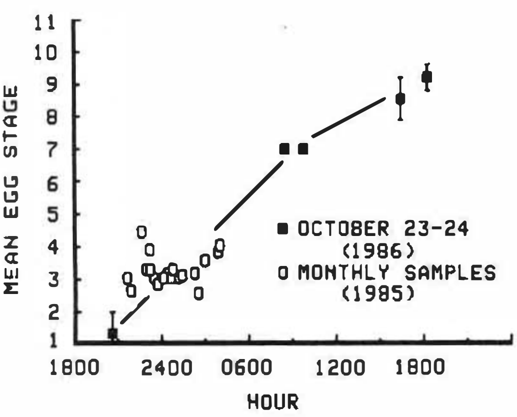

Fig. 3. Mean egg developmental stages for monthly, 1985, samples and a series of supplementary collections made in 1986. The 0824h and 0950h, 1986, samples are each composed of three combined tows made within 50 minutes of each other. Bars (± 1 SD) bracket mean values for the supplementary samples only. Supplementary samples without SD bars contained eggs of only one stage.

DISCUSSION

The value of mangroves as nursery grounds for juvenile fishes has been established in tropical and subtropical systems world-wide (Bell *et al.* 1984, Krishnamurthy & Jeyaseelan 1981, D'Croz & Kwiecinski 1980, Odum & Heald 1972, Austin 1971); however, almost no data are available to evaluate their importance to earlier life history stages. In one of the few studies considering mangrove ichthyoplankton, Krishnamurthy & Jeyaseelan (1981) found the Pichavaram system in India to harbor rich populations of juveniles, but eggs and planktonic larvae were uncommon. A similar phenomenon was seen in this study, as the mangroves were nearly devoid of oval engraulid eggs. This pattern probably applied to engraulids with spherical eggs also, since densities of total spherical eggs were also low in the mangroves (MS is preparation). Spawning apparently took place in adjacent areas with tidal mixing probably accounting for the occurrence of smaller larvae in the estuary. Since all collections in this study were made during incoming tides, we can't eliminate the possibility that spawning occurs within the mangroves during high or outgoing tides. However, we have occasionally sampled the area during outgoing tides, and have found minimal numbers of eggs in the estero, and in waters that have left it. Offshore collections at these times contained moderate densities of early-stage eggs (authors' pers. obs.).

Krishnamurty & Jeyaseelan (1981) discussed the hazards that planktonic fish eggs may face in Pichavaram mangroves, including high turbidity, elevated bacterial densities associated with organic-rich sediments, and loss of buoyancy induced by brackish waters. Although the authors were impressed by the large numbers of juvenile fishes present, many of which were carnivorous, they failed to consider the possible effect that predation may have on egg survival. At Punta Morales, young planktivorous fishes make up a major portion of the fish community, and at least one common species (*Oligoplites altus*) consumes anchovy eggs (W. A Szelistowski, unpubl. data). Although spawning in mangrove areas might maximize the chance that larvae are in a favorable location from which to recruit, a disadvantage may lie in their vulnerability to zooplanktivores. An optimal strategy might be to spawn in nearby, presumably more predation-free areas.

Similarly, predation pressure might also explain the timing of spawning in Gulf of Nicoya anchovies. Holt, Holt & Arnold (1985) found evening spawning to be a general phenomenon among sciaenid (croaker) species, and suggested that this behavior functions to minimize egg predation by ensuring that planktonic eggs have dissipated to low densities by daytime when predation levels are highest. Anchovies also commonly spawn at night (Blaxter & Hunter 1982, Breder & Rosen 1966), and Simpson (1959) found that ten species studied in the Bay of Panama all spawned very late in the afternoon or in the evening. Evening spawning may thus be a general behavior in anchovies as well, functioning to reduce predation on the egg stage.

The accumulation of large (>12 mm) larvae within the mangroves combined with their disappearance from offshore collections suggests the death of offshore individuals, a deeper vertical distribution offshore, or a shoreward migration. Death of nearly all large larvae offshore, by starvation or other causes, seems unlikely. No data are available on the vertical distributions of any tropical eastern Pacific anchovies, and we were unable to address it in this study. Studies in shallow, temperate waters have shown that large anchovy larvae are commonly concentrated in bottom strata (Brewer & Kleppel 1986, Schlotterbeck & Connally 1982), though at night some individuals may make surface migrations and become more dispersed relative to day-time distributions (Brewer & Kleppel 1986). Blaxter and Hunter (1982) concluded that in general, clupeoid larvae tend to move up and become more spread out in the water column at night. Spreading out could result in a "diluting effect" of larvae in a deep water column, and could potentially account for the low densities of large larvae found offshore in this study. It cannot explain, however, the significantly higher densities of large larvae in the mangroves than at the estuary mouth, where depths were approximately equal. Onshore migration may thus be the most plausible explanation for the accumulation of large larvae in the mangroves. Onshore migration could occur by relatively passive behavioral mechanisms as has been proposed for some other estuarine fishes (Pollock, Weng & Morton 1983, Weinstein *et al.* 1980, Grahn 1972), or by actively swimming inshore. Movement onshore might be related to the development of schooling behavior, and schooling anchovies as small as 14 mm have been observed at Punta Morales (pers. obs.). This is consistent with other studies reporting the onset of schooling in anchovies at about 10-15 mm in length (Blaxter & Hunter 1982, Hunter 1981).

The possible effects of red tides on temperate zone ichthyoplankton were discussed by White (1982), who stressed the potential impact on recruitment and subsequent year-class strength. Data demonstrating the effects of red tides on ichthyoplankton are sparse, however, and this study may present some of the first field evidence for such an effect. It is unknown if the low concentrations of ichthyoplankton during red tides resulted from reduced spawning activity, mortality, or migration. The high density of large larvae offshore in July may indicate a migration away from the red tide, as has been suggested for mobile, adult fishes (Wardle, Ray & Aldrich 1975). However, other possibilities could also account for an abundance of large larvae in offshore surface waters at this time, including an upward vertical migration, or normal patchiness in distribution. Although it is difficult to assess the impact of red tides on the population dynamics of Gulf of Nicoya anchovies, the effect on stocks would be expected to be least severe in tropical areas like the Gulf where breeding seasons are generally protracted.

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RESUMEN

Se realizaron muestreos mensuales de ictioplanction (de febrero a setiembre de 1985) dentro, en la boca y afuera del estero de Punta Morales, Golfo de Nicoya con el propósito de determinar la importancia de este manglar como sitio de desove y crianza de larvas de anchoas. La abundancia de huevos fue baja en la región interna del estero, mientras que fue alta en la boca del mismo y cerca de la costa, lo que sugiere que la mayor parte del desove ocurre en aguas abiertas cerca de la orilla. Densidades de las larvas pequeñas (LT $<$5 mm) también fueron menores en la región interna del estero, sin embargo las de tamaño mediano (LT 5-12 mm) fueron semejantes en las tres estaciones de muestreo. Las larvas grandes (12-20 mm) se encontraron casi exclusivamente en el interior del estero, lo que sugiere que a esta talla los peces se han movilizado dentro de estas zonas de crianza. Las densidades de huevos y larvas obtenidos mostraron una diminución en los meses de julio y agosto, coincidiendo con un período de marea roja. El análisis sobre el estado de desarrollo de los huevos indicó que el desove se realiza al atardecer y que el desarrollo se completa en aproximadamente 20-24 horas. Se sugiere que la depredación es un factor importante que influye en las estrategias reproductivas de las anchoas en el Golfo de Nicoya.

LITERATURE CITED

Araya, H.A. 1984. Los sciaénidos (corvinas) del Golfo de Nicoya, Costa Rica. Rev. Biol. Trop. 32(2):179-196.

Austin, H.M. 1971. A survey of the ichthyofauna of the mangroves of western Puerto Rico during December, 1967-August, 1968. Carib. J. Sci. 11(1-2):27-39.

Bell, J.D., D.A. Pollard, J.J. Burchmore, B.C. Pease & M. J. Middleton. 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. Aust. J. Mar Freshw. Res. 35:33-46.

Blaxter, J.H.S. & J.R. Hunter. 1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20:3-223.

Breder, C.M. Jr. & D.E. Rosen. 1966. Modes of reproduction in fishes. T.F.H. Publi., Inc., Neptune City, N.J.

Brewer, G.D. & G.S. Kleppel. 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217-226.

D'Croz, L. & B. Kwiecinski. 1980. Contribución de los manglares a las pesquerías de la Bahía de Panamá. Rev. Biol. Trop. 28(1): 13-29.

Graham J.J. 1972. Retention of larval herring within the Sheepscot Estuary of Maine. Fish. Bull. 70(2): 299-305.

Holt, G.J., S.A. Holt & C.R. Arnold. 1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27:1-7.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. *In*: R. Lasker (Ed.), Marine Fish Larvae, pp. 33-77, Washington Sea Grant, Univ. of Washington.

Kolberg, W., R. Pollnac, D. Stevenson & J. Sutinen. 1981. The setting: Costa Rica, El Salvador and Guatemala: *In*: J.G. Sutinen and R. B. Pollnac (Eds.), Small scale fisheries in Central America: Acquiring information for decision making, pp. 7-43, ICMRD, Univ. of Rhode Island.

Krishnamurthy, K. & M.J.P. Jeyaseelan. 1981. The early life history of fishes from Pichavaram mangrove ecosystem of India. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:416-423.

McGowan, M.F. & F.H. Berry. 1984. Clupeiformes: development and relationships. *In*: H.G. Moser and W.J. Richards (Eds.), Ontogeny and systematics of fishes, pp. 108-126, Am. Soc. Ich. Herp. Spec. Publ. 1.

Moser, H.G. & E.H. Ahlstrom. 1985. Staging anchovy eggs. *In*: R. Lasker (Ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, pp. 37-41, U.S. Dept. Commerce, NOAA Tech. rep. NMFS 36.

Odum, W.E. & E.J. Heald. 1972. Trophic analyses of an estuarine mangrove community. Bull. Mar. Sci. 22: 671-738.

Peterson, C.L. 1956. Observations on the taxonomy, biology, and ecology of the engraulid and clupeid fishes in the Gulf of Nicoya, Costa Rica. Bull. Inter-Amer. Trop. Tuna Comm. 1(5):139-279.

Phillips, P.C. 1983. Diel and monthly variation in abundance, diversity and composition of littoral fish populations in the Gulf of Nicoya, Costa Rica. Rev. Biol. Trop. 31(2):297-306.

Pollock, B.R., H. Weng, & R.M. Morton. 1983. The seasonal occurrence of postiaval stages of yellowfin bream, *Acanthopagrus australis* (Gunther), and some factors affecting their movement into an estuary. J. Fish. Biol. 22:409-415.

Ramírez C., A.R. 1986. Importancia de un estuario como habitaculo de ictioplancton. Punta Morales, Pacífico de Costa Rica. Tesis de Licenciatura, Universidad de Costa Rica. 112 pp.

Robertson, A.I. & N.C. Duke. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Mar. Biol. 96:193-205.

Schlotterbeck, R.E. & D.W. Connally. 1982. Vertical stratification of three nearshore southern California larval fishes (*Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*). Fish. Bull. 80(4): 895-902.

Simpson, J.G. 1959. Identification of the egg, early life history and spawning areas of the anchoveta, *Cetengraulis mysticetus* (Gunther), in the Gulf of Panama. Bull. Inter-Amer. Trop. Tuna Comm. 3(10):441-580.

Sokal, R. R. & F.J. Rohlf. 1981. Biometry. W.H. Freeman Co., San Francisco, 859 pp.

Thayer, G.W., D.R. Colby & W.F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in south Florida. Mar. Ecol. Prog. Ser. 35:25-38.

Víquez, R. 1985. Problemática de la marea roja en el Golfo de Nicoya. *In*: O Blanco (Ed.), Memorias del Primer Seminario sobre la Problemática Pesquera de Costa Rica, Puntarenas, Costa Rica, 14 pp.

Wardle, W.J., S.M. Ray & A.S. Aldrich. 1975. Mortality of marine organisms associated with offshore summer blooms of the toxic dinoflagellate *Gonyaulax monilata* Howell at Galveston. Texas. *In:* V.R. LoCicero (Ed.). Toxic Dinoflagellate Blooms, pp. 257-263, Proc. lst Int'l Conf.. Mass. Science & Technol. Found., Wakefield.

Weinstein, M.P., S.L. Weiss, R.G. Hodson, & L.R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull. 78(2):419-436.

White, A.W. 1982. The scope of impact of toxic dinoflagellate blooms on finfish in Canada. Can. Tech. Rep. Fish. Aqua. Sci. 1063, 5 pp.