

**Abstract**—The Abrolhos Bank region off the eastern coast of Brazil, under the influence of the Brazil Current, constitutes a typical tropical coral reef ecosystem that is characterized by a high diversity of tropical fish. Results of three ichthyoplankton surveys conducted in this region during summer, autumn, and winter revealed that there were two dominant fish groups: mesopelagic fish and coral-reef-associated fish. From the 45,614 larvae collected, 83 taxa (77 families and 6 orders) were identified, in which the family Myctophidae was the most abundant accounting for more than 25% of the total catch in the three cruises. Among the Myctophidae, seasonal variation in abundance of *Myctophum affine* was significant; there was an outstanding peak in abundance of this species during the summer surveys. The summer peak in abundance of five other species (*Diaphus* spp., *Lepidophanes guentheri*, *M. nitidulum*, *M. obtusirostre*, and *Hygophum reinhardtii*) was not as pronounced. Larval distribution patterns of these six species showed no remarkable seasonal change, being evenly distributed over the oceanic area. The coral-reef-associated fish larvae were confined to the bank and adjacent waters. The spatiotemporal distribution patterns of these larvae was strongly influenced by hydrographic features and some seasonal variation was observed. Four larval fish assemblages were identified: Abrolhos Bank, neritic, transitional, and oceanic assemblages. The Abrolhos Bank assemblage was characterized by coral-reef-associated fish, mainly Gobiidae, occupying most areas of the bank on the three cruises. The oceanic assemblage was dominated by mesopelagic fish, especially Myctophidae in all seasons and their occurrence was limited to the open ocean. The transitional assemblage was characterized by a mixture of coral-reef-associated fish and mesopelagic fish, with a seasonal change of dominant groups. It occupied mainly the shelf break area. The small pelagic fish (sardine and anchovy) were the dominant group of the neritic assemblage and occupied the coastal region south of the Abrolhos Bank, where the influence of the South Atlantic Central Water was evident.

## Seasonal variation in larval fish assemblages in relation to oceanographic conditions in the Abrolhos Bank region off eastern Brazil

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The tropical marine ecosystem is characterized by 1) the presence of coral reefs, which support a large variety of fish communities and benthic fauna that are point sources of eggs and larvae and by 2) the open ocean, where mesopelagic fish dominate the fish community. Thus, the larval fish assemblages in tropical marine ecosystems are a result of the spawning activities of these two communities (Ahlstrom, 1971; 1972; Leis and Goldman, 1987; Flores-Coto and Ordonez-Lopez, 1991; Leis, 1993). The formation of larval fish assemblages is mainly influenced by the reproductive cycles of the adult fish populations. The seasonal cycle of fish spawning activities in the tropics is not pronounced because of a low level of variation in environmental conditions (Lowe-McConnell, 1987).

Distribution patterns of fish larvae in any region of the ocean are related to the reproductive activity of the adult population and to topographic and hydrographic features that affect the dispersal of the larvae. A study of the distribution patterns of fish larvae contributes to an understanding of the interrelationships among fish species during their early life stages, as well as an understanding of adult spawning patterns. In addition, information can be obtained on the reproductive strategies adopted by these fish in response to the physical and biological processes of the region. Distribution patterns among ichthyoplankton species arise from the synchronous reproductive activities of different species that are developed during evolutionary adaptation to geo-

graphic and oceanographic conditions. This information is important for a rational use of fishery resources and also for an understanding of the ecological status of the component species in a marine ecosystem.

Ichthyoplankton surveys in Brazilian waters are concentrated off southern Brazil (Matsuura and Olivar, 1999); only a small number of sampling cruises have been conducted off the eastern coast (Aboussousan, 1969; Matsuura, 1985).

In our study, temporal and spatial changes in larval fish assemblages in relation to physical processes of the Abrolhos Bank region were examined. Particular emphasis was placed on the seasonal variation of larval fish assemblages of abundant fish taxa. The objective of the present study is to understand the origin and maintenance of these larval fish assemblages and their relation to oceanographic conditions.

### Materials and methods

Three survey cruises were conducted along the eastern coast of Brazil. Two cruises of the FINEP Project (FINanciadora de Estudos e Projetos) were made with the RV *Prof. W. Besnard* in June and November–December of 1978. Sixty-four stations between latitudes 17°S and 23°S were sampled with a Nansen bottle containing a reversing thermometer for hydrographic data and with Bongo nets for collecting zooplankton. The third cruise, that of the JOPS II-9 (Joint Oceanographic ProjectS-II,

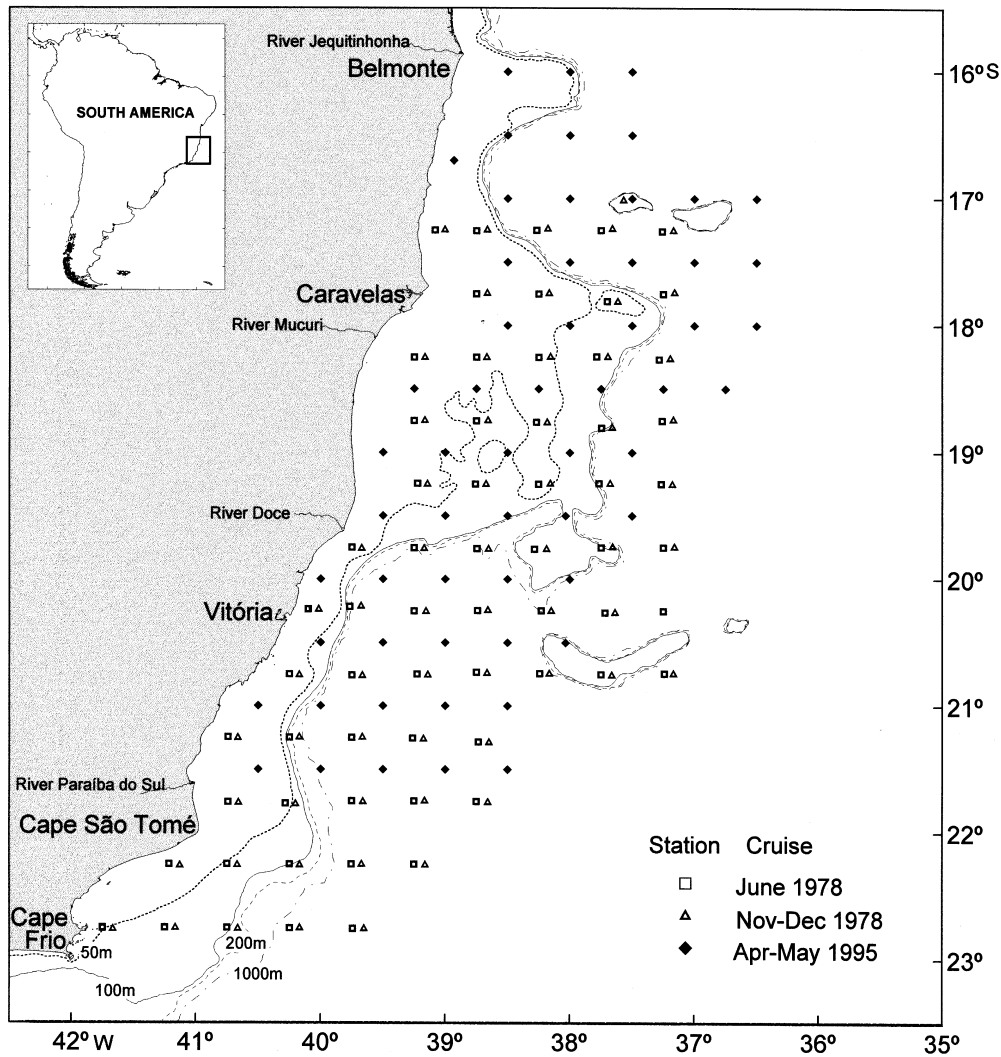


Figure 1

Survey area, sampling stations, and bathymetry off the eastern coast of Brazil.

leg 9), was conducted with the RV *Victor Hensen* in April–May 1995. Fifty-eight stations were sampled between latitudes 16°S and 22°S with a CTD cast for hydrographic data and with Bongo nets for zooplankton (Fig. 1). The interval between stations was 30 nautical miles.

The zooplankton samples were collected by using 60-cm Bongo nets with mesh apertures of 300  $\mu\text{m}$  and 500  $\mu\text{m}$ . The nets were towed obliquely from the surface to a depth of 200 m or down to 5 m above the bottom at shallow stations as the vessel held a 45° wire angle (usually 1.5 knots vessel speed). Winch retrieval rate was 20 m per minute to the surface. In order to increase the water volume filtered, the nets were towed twice down near to the bottom at shallow water (<60 m) stations. The digital flowmeter attached at the center of the net was used to estimate the water volume that was filtered. The plankton samples collected with a 300- $\mu\text{m}$  mesh net were used for both the zooplankton and ichthyoplankton study. Zooplankton volume at each station was measured by using the replacement

method (Kramer et al., 1972) and expressed as  $\text{mL}/\text{m}^3$ . The number of fish larvae collected at each station was converted into the number under unit surface area (10  $\text{m}^2$ ) by using the following equation:

$$Y_i = (10 d_i x_i) / v_i,$$

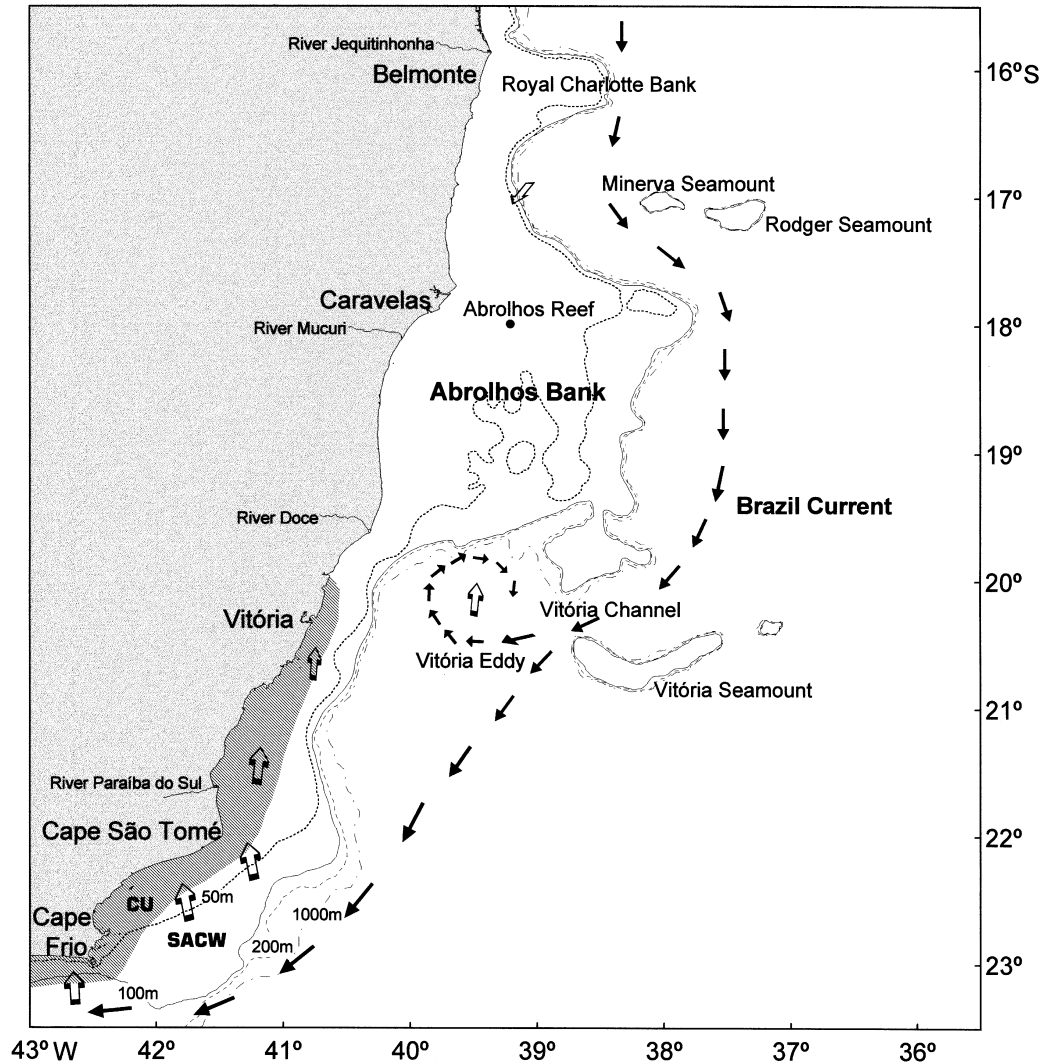
where  $Y_i$  = number of standardized larvae under 10  $\text{m}^2$  of sea surface at station  $i$ ;

$x_i$  = number of larvae taken at station  $i$ ;

$v_i$  = volume of water filtered ( $\text{m}^3$ ); and

$d_i$  = maximum depth of haul (m).

The total abundance of the larvae of each family was the sum of a standardized number of larvae from all the positive stations. The plankton samples were preserved in a solution of 4% buffered formalin, and the fish eggs and larvae were sorted by using a stereoscopic microscope in the laboratory. Identifications of fish larvae were



**Figure 2**

Hydrographic features of the Abrolhos Bank region. The dark arrow shows the main axis of the Brazil Current (BC); the blank arrow the upward movement of the South Atlantic Central Water (SACW), and the shadowed area the coastal upwelling (CU).

based on descriptions in the literature (Fahay, 1983; Leis and Rennis, 1983; Leis and Trnski, 1989; Moser et al., 1984; Moser, 1996; Nafpaktitis et al., 1977; Okiyama, 1988; Olivar, 1988; Olivar and Fortuño, 1991). Larval identification of coral-reef-associated fish is difficult; therefore identification was made only to the family level. The most abundant Myctophidae larvae were identified to species level.

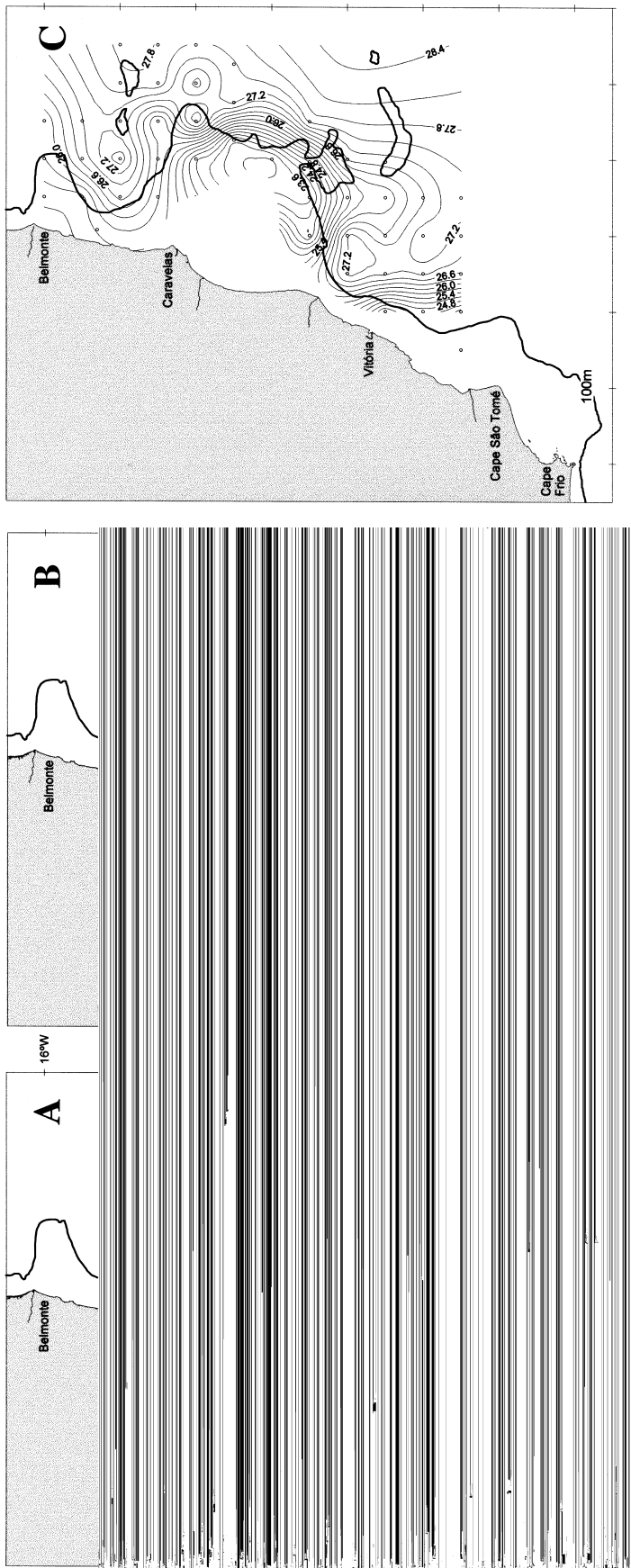
To determine the possible associations among stations, the distribution pattern, and larval abundance, a multivariate analysis of numerical classification was applied by using the two-way indicator species analysis (Hill et al., 1975; Hill, 1979), implemented by the program TWINSPAN. This is a divisive method that classifies stations and families and produces a sorted family by station table, showing the hierarchical classification in binary notation (see "Appendix"). The results of this analysis show the

clear ecological preferences of the family groups and are used to identify particular environmental conditions. Only the family groups with an occurrence of more than 10% in each cruise were used in this analysis.

## Results

### Oceanographic conditions

The continental shelf of the eastern coast of Brazil is generally narrow (ca. 25 km) and is composed of calcareous sediments on the bottom; however, it widens to 230 km offshore at Caravelas (Lat. 18°S), forming the large Abrolhos Bank (AB) to the south (Fig. 2). The depth of shelf break in this region is 100 m with isobathic lines 200 m and 1000 m very close to it. Therefore, we have shown the margin of



**Figure 3** Horizontal distribution of water temperature at 50 m depth for three cruises: winter (A), summer (B), autumn (C) off the eastern coast of Brazil.

continental shelf with the 100-m isobath. This region is characterized by the southward flowing Brazil Current (BC), a typical western boundary current regime (Castro and Miranda, 1998). Because of the topographic impediment of the Abrolhos Bank, the main axis of the Brazil Current flows along the outer edge of the continental slope of the bank and passes through the Vitória Channel formed between the southeastern edge and the Vitória seamount at lat.  $20^{\circ}15'S$ . It flows southwestward from this point, approaching the coast near Cape São Tomé (Signorini et al., 1989). Schmid et al. (1995) detected a permanent cyclonic eddy which was formed south of the Abrolhos Bank from the meandering movement of the Brazil Current after passing through the Vitória Channel. Beneath the Brazil Current the South Atlantic Central Water (SACW) occupies the subsurface layer at 120–350 m depth. Prevailing northeast winds induce a coastal upwelling in the region from Cape Frio to Cape São Tomé which is more intense during the austral spring and summer, uplifting the SACW to the surface (Mascarenhas et al., 1971; Silva, 1973; Ikeda et al., 1974).

The horizontal distribution of the water temperature at a depth of 50 m showed a flow pattern similar to that of the Brazil Current on the three cruises, and the thermal front of the SACW of the Cape São Tomé reached the southern rim of the Abrolhos Bank (Fig. 3). The boundary between the Brazil Current and the coastal water was demarcated with a  $24.8^{\circ}C$ -isotherm line on the three cruises. The temperature gradient between two water masses on the autumn cruise was more pronounced (Fig. 3C). The sea surface temperature at 10 m depth over the Abrolhos Bank ranged from  $24.0$ – $25.6^{\circ}C$  in winter, and  $26.0$ – $26.4^{\circ}C$  in summer, to  $26.0$ – $28.3^{\circ}C$  in autumn. The salinity at 10 m depth ranged from 36.0 to 37.5 psu and showed no seasonal variation.

### Zooplankton

The displacement volume of macrozooplankton was low, ranging from  $0.07$  to  $1.54$   $mL/m^3$  over the bank and from  $0.01$  to  $0.41$   $mL/m^3$  in the open ocean (Table 1). However, when compared with the displacement volume of macrozooplankton in the north Pacific central gyre, which ranged from  $0.05$  to  $0.10$   $mL/m^3$  (Loeb, 1980), our values in the open ocean were slightly higher.

**Table 1**  
Displacement volume of macrozooplankton (mL/m<sup>3</sup>) from three survey cruises in the Abrolhos Bank region.

	Winter		Summer		Autumn	
	Shelf	Open Sea	Shelf	Open Sea	Shelf	Open Sea
No. of stations	26	35	30	34	23	35
Mean volume	0.32	0.09	0.28	0.12	0.26	0.07
Standard deviation	0.219	0.079	0.272	0.047	0.141	0.031
Minimum volume	0.10	0.03	0.07	0.04	0.07	0.01
Maximum volume	1.12	0.41	1.54	0.27	0.69	0.15

### Larval fish composition and abundance

A list of the family groups of fish larvae and their abundance is given in Table 2. From the 45,614 larvae collected, 83 taxa (77 families and 6 orders) were identified. The family Myctophidae was the most abundant, accounting for more than 25% of the total catch on the three cruises.

During the winter cruise, 58% of the total larvae taken represented five families in decreasing order of abundance: Myctophidae, Phosichthyidae, Sternoptychidae, Bregmacerotidae, and Serranidae, of which the first four belonged to the mesopelagic fish group.

The total number of larvae collected during the summer cruise was twice as high as that of the other two cruises. Myctophidae represented 27.6% of the total larvae, followed by Scaridae (11.6%), Sternoptychidae (8.2%), Carangidae (4.5%), and Phosichthyidae (4.2%). The following nine families were collected only on the summer cruise: Argentinidae, Clinnidae, Dactyloscopidae, Istiophoridae, Caproidae, Macrorhamphosidae, Malacanthidae, Percophidae and Symphysanodontidae, indicating that these groups spawned only in summer.

During the autumn cruise, the five most abundant families (Myctophidae, Scaridae, Gobiidae, Serranidae, and Phosichthyidae) represented 58.7% of the total larvae taken. Four families (Elopidae, Notosudidae, Scombro-labracidae, and Tripyterigiidae) were collected only in this season, indicating that for these families spawning peaked in autumn.

### Seasonal variation in abundance of fish groups

In relation to habitat of adult fish groups, two dominant fish groups were recognized in the survey area: mesopelagic fish and coral-reef-associated fish. Levels of abundance of three families of mesopelagic fish larvae (Myctophidae, Sternoptychidae, and Gonostomatidae) were highest during the summer cruise (Fig. 4). For three other families (Phosichthyidae, Bregmacerotidae, and Paralepididae) levels of abundance were highest for the winter cruise, decreased in summer, and were at a minimum during the autumn cruise. The summer peak in abundance for the myctophid *Myctophum affine* was outstandingly high (Fig. 5). Five other species (*Diaphus* spp., *Lepido-*

*phanes guentheri*, *M. nitidulum*, *M. obtusirostre*, and *Hygophum reinhardtii*) were most abundant in summer, but the seasonal differences were not pronounced.

Figure 6 shows a seasonal variation in abundance of the coral-reef-associated fish. Abundance of larval parrotfish (Scaridae) was at a peak in summer, followed by autumn and winter. The same trend was observed in six other families (Labridae, Holocentridae, Balistidae, Pomacanthidae, Acanthuridae, and Pomacentridae). Levels of abundance of larval grouper (Serranidae) were almost the same for three seasons. For the family Gobiidae, a peak in larval abundance was observed during the autumn cruise.

### Distribution patterns of fish larvae

Distribution patterns of six species of Myctophidae among each of the cruises are shown in Figure 7. Most of the *Diaphus* spp. larvae were collected at open ocean stations, but also at some coastal stations between Vitória and Cape Frio on the winter and summer cruises. Larvae of *Myctophum affine*, *M. obtusirostre*, *M. nitidulum*, *L. guentheri*, and *H. reinhardtii* were found predominantly at open ocean stations and some at the continental margin, but a considerable number of *Myctophum affine* larvae were also found at coastal stations between Vitória and Cape Frio on the summer cruise (Fig. 7E). The presence of these species along the coast coincided with the presence of the coastal upwelling observed in this area (Fig. 3).

Distribution patterns of the Gobiidae during the summer and autumn cruises were similar, with higher density over the Abrolhos Bank and seamount. Gobiid larvae during the winter cruise were concentrated over the Abrolhos Bank and only a small number of them were collected at open ocean stations south of the bank (Fig. 8). The distribution patterns of the parrotfish larvae (Scaridae) were similar during all three cruises, with higher density at open ocean stations. During the winter cruise the highest densities of grouper larvae (Serranidae) were found around the Vitória Channel, but the Abrolhos Bank stations also showed relatively high density. The stations with the highest densities of grouper larvae during the summer cruise were found along the shelf break and over the seamount. The distribution pattern of grouper larvae during the autumn cruise was different from the former

**Table 2**

Family groups represented in ichthyoplankton samples collected on the Arolhos Bank and in adjacent waters off eastern Brazil. Abundance is a sum of a standardized number of larvae from all positive stations and % is a percentage of total abundance.

Taxon	Winter Cruise		Summer Cruise		Autumn Cruise	
	Abundance	%	Abundance	%	Abundance	%
Myctophidae	17911	27.49	31165	27.58	14152	25.44
Scaridae	1224	1.88	13140	11.63	6341	11.40
Sternoptychidae	6042	9.27	9215	8.15	949	1.71
Carangidae	2049	3.14	5103	4.52	544	0.98
Phosichthyidae	6957	10.68	4723	4.18	2380	4.28
Gonostomatidae	414	0.64	4049	3.58	167	0.30
Scombridae	218	0.33	3254	2.88	152	0.27
Engraulidae	1148	1.73	3063	2.71	1075	1.93
Serranidae	3015	4.63	2860	2.53	3704	6.66
Paralepididae	2674	4.10	2527	2.24	672	1.21
Gobiidae	2245	3.45	2280	2.02	6088	10.94
Holocentridae	21	0.03	1976	1.75	54	0.10
Bregmacerotidae	3845	5.90	1657	1.47	1016	1.83
Labridae	114	0.17	1555	1.38	624	1.12
Balistidae	6	0.01	1335	1.18	21	0.04
Pleuronectiformes	625	0.96	1016	0.90	628	1.13
Scorpaenidae	332	0.51	919	0.81	397	0.71
Monacanthidae	94	0.14	857	0.76	353	0.63
Apogonidae	550	0.84	671	0.59	722	1.30
Clupeidae	1248	1.92	660	0.58	483	0.87
Mullidae	1236	1.90	591	0.52	57	0.10
Ophidiiformes	229	0.35	576	0.51	229	0.41
Tetraodontiformes	172	0.26	520	0.46	68	0.12
Pomacentridae	35	0.05	488	0.43	305	0.55
Priacanthidae	0	0	482	0.43	10	0.02
Pomacanthidae	334	0.51	454	0.40	229	0.41
Acanthuridae	44	0.07	424	0.38	127	0.23
Synodontidae	343	0.53	419	0.37	557	1.00
Callionymidae	275	0.42	327	0.29	1872	3.36
Anguilliformes	248	0.38	315	0.28	0	0
Stomiiformes	23	0.03	312	0.28	87	0.16
Triglidae	26	0.04	233	0.21	16	0.03
Gempylidae	110	0.17	210	0.19	84	0.15
Nomeidae	56	0.09	186	0.16	0	0
Lutjanidae	38	0.06	174	0.15	304	0.55
Chaetodontidae	60	0.09	164	0.15	0	0
Cirrhitidae	130	0.20	130	0.12	110	0.20
Exocoetidae	54	0.08	127	0.11	0	0
Syngnathidae	73	0.11	113	0.10	41	0.07
Coryphaenidae	6	0.01	102	0.09	49	0.09
Scopelarchidae	7	0.01	72	0.06	4	0.01
Blenniidae	124	0.19	53	0.05	60	0.11
Chiasmodontidae	42	0.06	50	0.04	75	0.13
Gerreidae	25	0.04	49	0.04	9	0.02
Sphyrnaeidae	11	0.02	46	0.04	48	0.09

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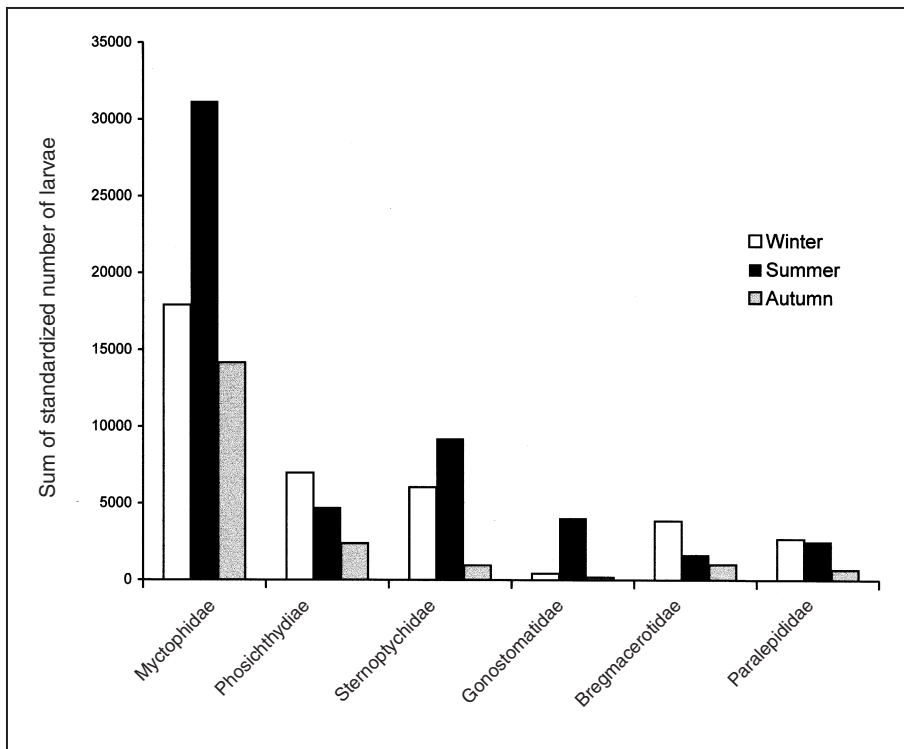
two and showed an even distribution pattern over the bank and along the shelf break.

The distribution patterns of Clupeidae and Engraulidae were similar; larvae were limited to coastal stations

(Fig. 8). The clupeid larvae collected in the coastal region between Vitória and Cape Frio belonged to *Sardinella brasiliensis* and *Harengula jaguana*, and those from the Abrolhos Bank were *Jenkinsia* sp., *Opisthonema* sp., and

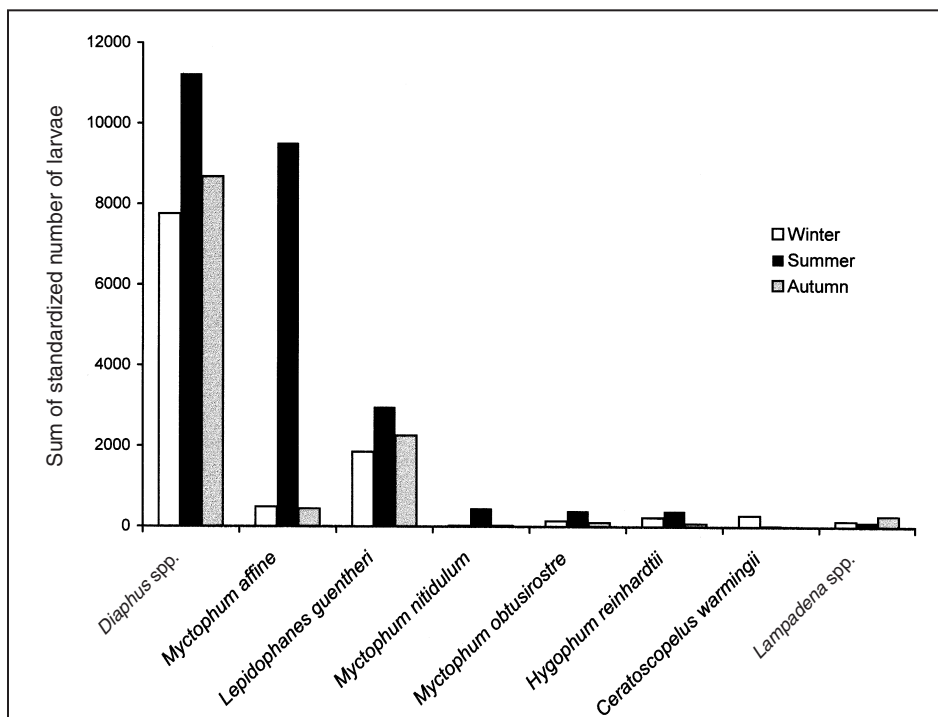
**Table 2 (continued)**

Taxon	Winter Cruise		Summer Cruise		Autumn Cruise	
	Abundance	%	Abundance	%	Abundance	%
Sciaenidae	136	0.21	46	0.04	49	0.09
Fistulariidae	17	0.03	39	0.03	29	0.05
Istiophoridae	0	0	31	0.03	0	0
Lophiiformes	22	0.03	25	0.02	0	0
Percophidae	0	0	22	0.02	0	0
Ostraciidae	0	0	21	0.02	22	0.04
Ogcocephalidae	0	0	20	0.02	6	0.01
Symphysanodontidae	0	0	19	0.02	0	0
Malacanthidae	0	0	18	0.02	0	0
Pomatomidae	11	0.02	18	0.02	2	0
Caproidae	0	0	17	0.02	0	0
Antennariidae	0	0	15	0.01	37	0.07
Carapidae	15	0.02	15	0.01	56	0.10
Echeneidae	0	0	14	0.01	10	0.02
Argentinidae	0	0	13	0.01	0	0
Sparidae	10	0.02	12	0.01	0	0
Trichiuridae	273	0.42	8	0.01	57	0.10
Acropomatidae	153	0.23	6	0.01	400	0.72
Labrisomidae	8	0.01	6	0.01	0	0
Clinidae	0	0	6	0.005	0	0
Macrorhamphosidae	0	0	4	0.004	0	0
Dactyloscopidae	0	0	4	0.003	0	0
Aulostomidae	9	0.01	3	0.003	99	0.18
Mugilidae	11	0.02	2	0.002	0	0
Opistognathidae	15	0.02	2	0.002	4	0.01
Astronesthidae	7	0.01	0	0	5	0.01
Chlorophthalmidae	33	0.05	0	0	0	0
Elopidae	0	0	0	0	8	0.02
Gadidae	24	0.04	0	0	0	0
Hemiramphidae	12	0.02	0	0	7	0.01
Kyphosidae	6	0.01	0	0	0	0
Melanostomiidae	68	0.10	0	0	15	0.03
Microdesmidae	15	0.02	0	0	10	0.02
Notosudidae	0	0	0	0	31	0.06
Scombrobracidae	0	0	0	0	4	0.01
Stromateidae	5	0.01	0	0	0	0
Tripyteriidae	0	0	0	0	4	0.01
Xiphiidae	14	0.02	0	0	6	0.01
Not identified	9856	15.13	13970	12.36	9909	17.81
Total	65154	100.00	112998	100.00	55634	100.00
No. of taxa	65		70		62	



**Figure 4**

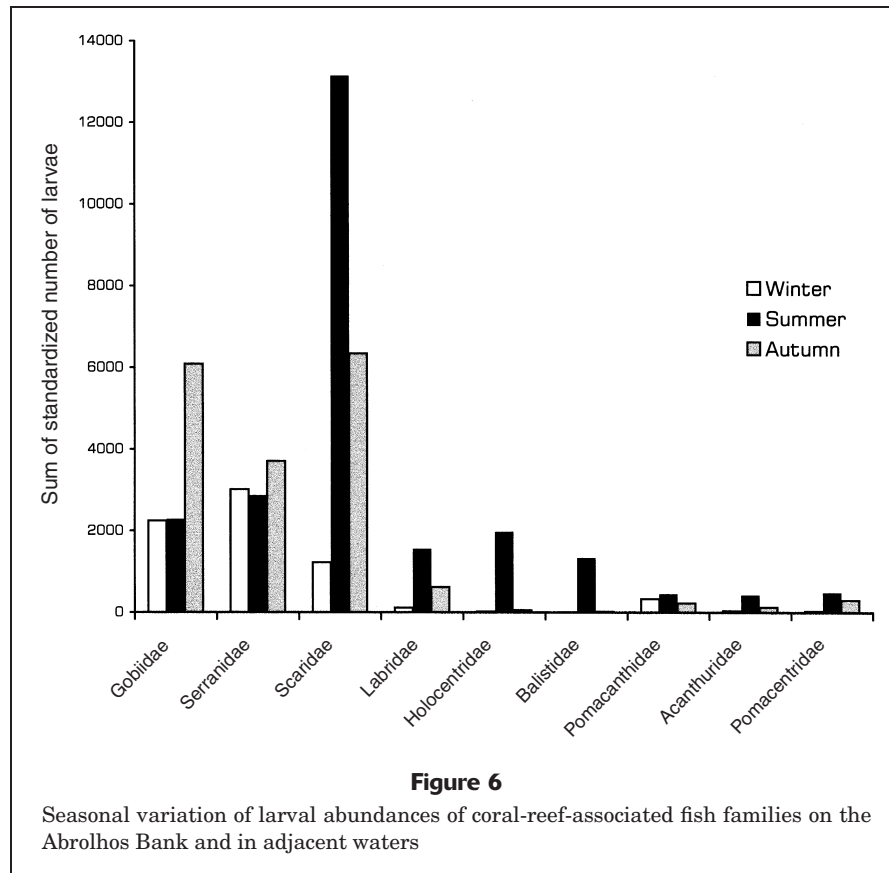
Seasonal variation of larval abundances of mesopelagic fish families in the Arolhos Bank and adjacent waters.



**Figure 5**

Seasonal variation of larval abundances of lanternfish (Myctophidae) on the Arolhos Bank and in adjacent waters.





un-identified clupeid larvae. Most of the engraulid larvae collected at coastal stations between Vitória and Cape Frio in winter and autumn were *Engraulis anchoita*, but some larvae found over the AB belonged to *Anchoa* and *Anchovia* that were not identified to species.

### Larval fish assemblages

A figure of fish families by station created with the TWINSPAN program is shown in Appendix 1. Clustering the families based on their occurrence and abundance at each station resulted in four major oceanographic groupings: 1) Abrolhos Bank, 2) neritic, 3) transitional, and 4) oceanic.

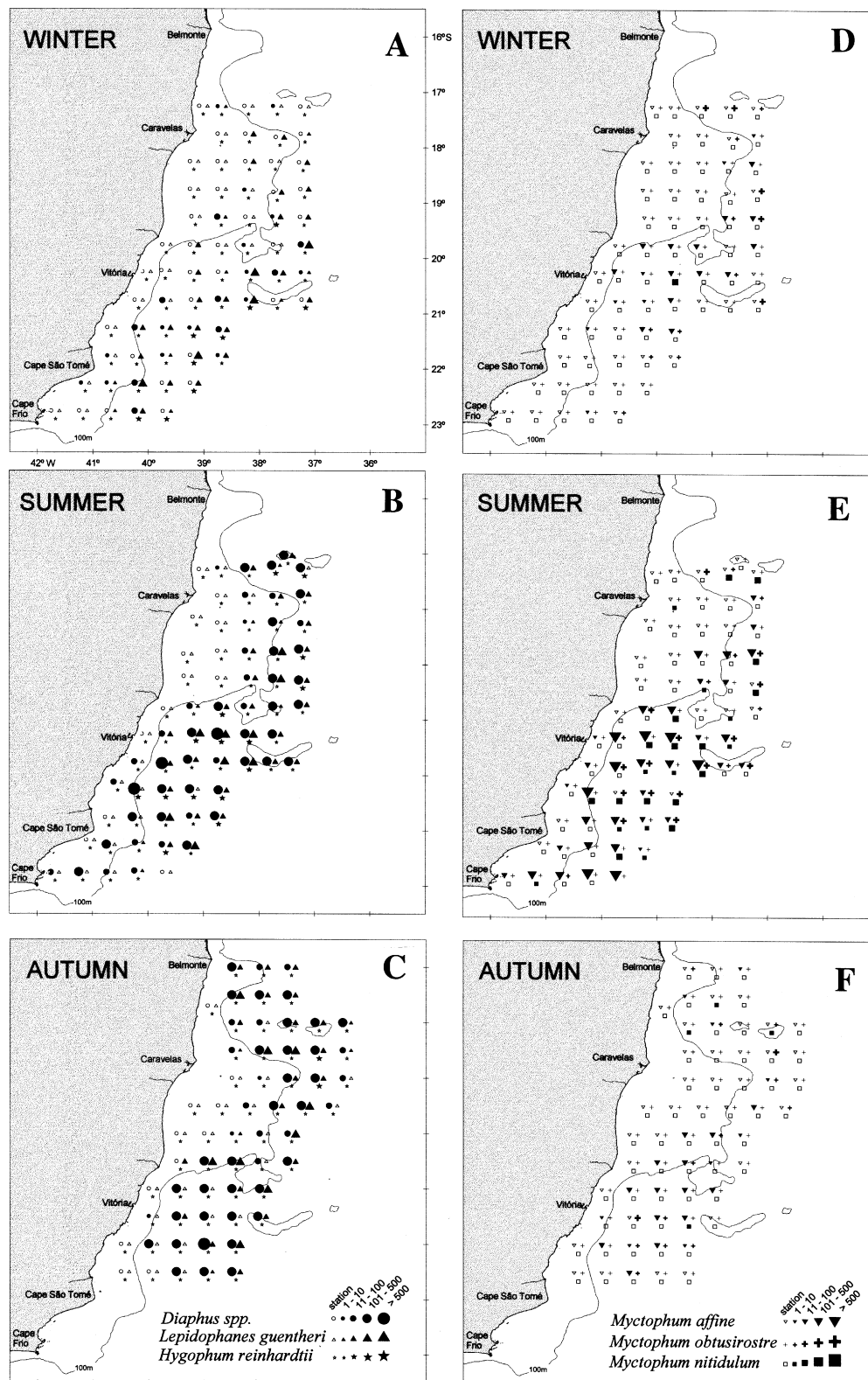
**Abrolhos Bank assemblage** The Abrolhos Bank assemblage was situated over the Abrolhos Bank (Fig. 9). During the autumn cruise another subgroup was identified in the coastal region and named “the Abrolhos Bank-coastal assemblage.” Taxonomic composition of this assemblage was characterized by the presence of coral-reef-associated fish. The composition was influenced by the seasonal variation of taxa, with the exception of Gobiidae which was the dominant family on all the cruises. The dominant groups of this assemblage were Serranidae, Scaridae, Carangidae, Clupeidae, Apogonidae, Blenniidae, and Labridae.

**Neritic assemblage** The neritic assemblage was found over the continental shelf between Vitória and Cape Frio.

The neritic assemblage was composed of pelagic fish, such as the Clupeidae, Engraulidae, Carangidae, and Bregmacerotidae, as well as the demersal fish Gobiidae and Pleuronectiformes. During the summer cruise the neritic assemblage was limited to the area between Cape São Tomé and Cape Frio, and another subgroup was identified in the northern part between Vitória and Cape São Tomé, named the neritic-north assemblage. This assemblage was characterized by Gobiidae, Engraulidae, and Clupeidae, which accounted for 60% of the total larvae.

**Transitional assemblage** The transitional assemblage was found mainly along the shelf break area. During the winter cruise the transitional assemblage occurred in two shelf break areas: between Caravelas and Vitória and between Vitória and Cape São Tomé (Fig. 9A). This assemblage was dominated by mesopelagic fish belonging to Myctophidae, Sternoptychidae, Bregmacerotidae, Phosichthyidae, and Paralepididae, but also by the coral-reef-associated fish, such as Serranidae, Carangidae, Mullidae, Pomacanthidae, Apogonidae, and Callionymidae.

The transitional assemblage found during the summer cruise was situated along the outer edge of the Abrolhos Bank, including the oceanic area of the Minerva and Vitória Seamounts (Fig. 9B). Its taxonomic composition was characterized by the great diversity of coral-reef-associated and mesopelagic fish. A transitional-Vitória subassemblage was identified to the south of the Abrol-



**Figure 7**

Distribution patterns of lanternfish (Myctophidae) larvae in the Abrolhos Bank region during winter, summer and autumn cruises. (A-C): *Lepidophanes guentheri*, *Hygophum reinhardtii*, *Diaphus* spp. (D-F): *Myctophum affine*, *M. obtusirostre*, *M. nitidulum*.

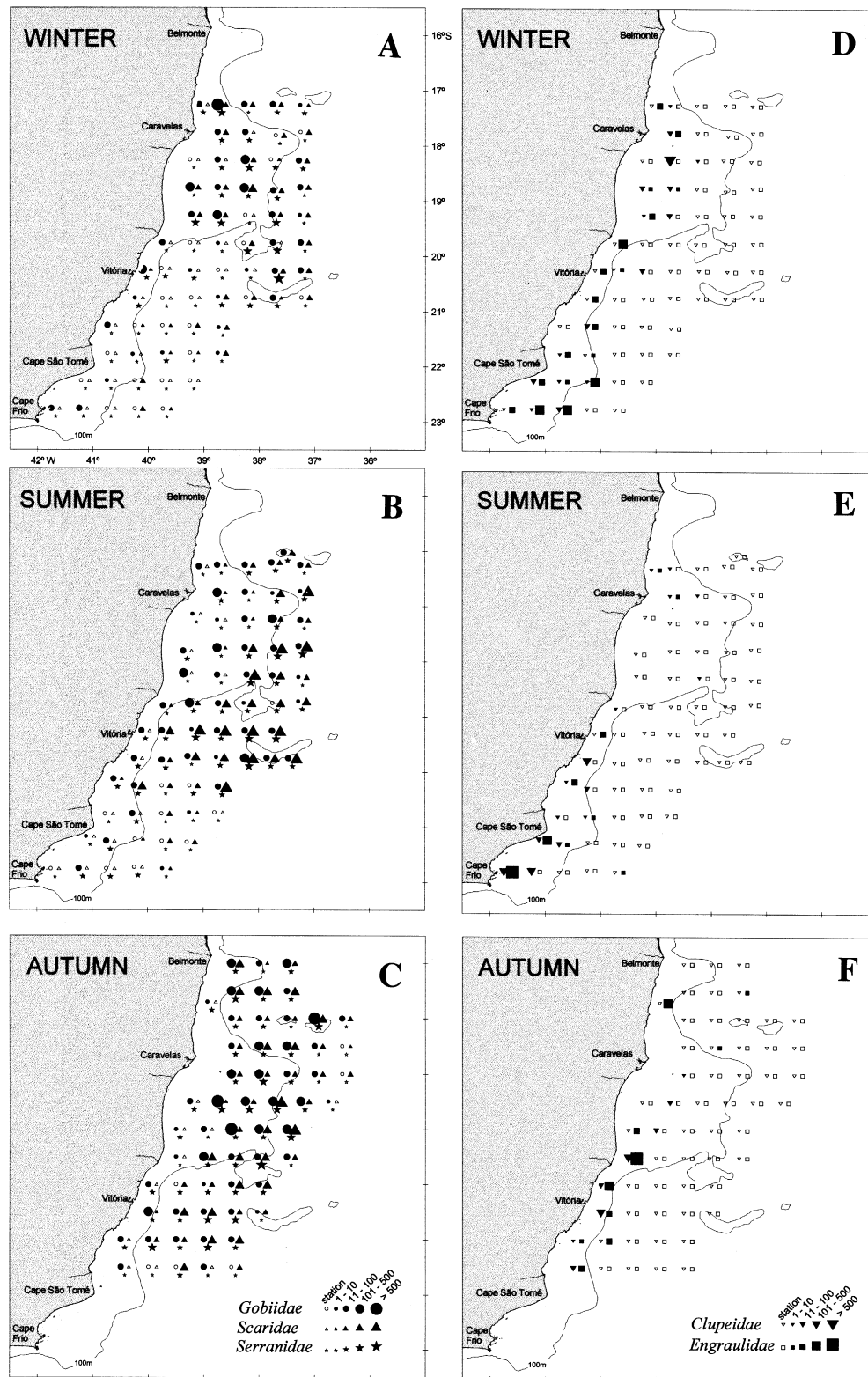
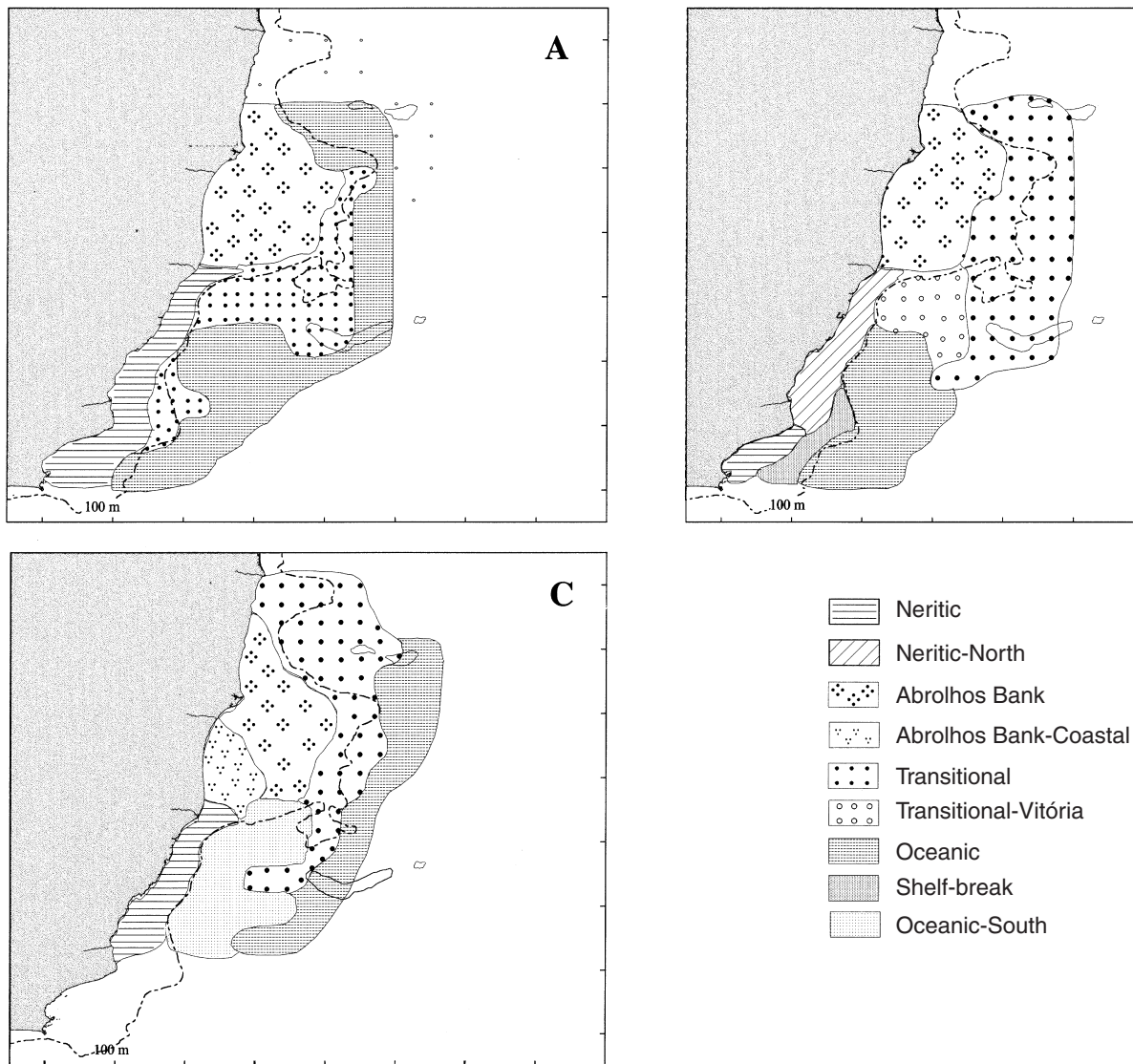


Figure 8

Distribution patterns of coral-reef-associated fish and clupeoid larvae in the Abrolhos Bank region for three cruises: winter (A, D), summer (B, E) and autumn (C, F).



**Figure 9**

Temporal and spatial distributions of four groups of larval fish assemblages based on the two-way indicator species analysis (TWINSPAN program). (A) winter, (B) summer and (C) autumn.

hos Bank in the oceanic area. The taxonomic composition of this subgroup was similar to that of the transitional assemblage, but mesopelagic fish, such as Myctophidae, Sternoptychidae, and Phosichthyidae dominated.

The transitional assemblage found during the autumn cruise extended along the shelf break area from Royal Charlotte Bank to the Vitória Seamount (Fig. 9C). Its taxonomic composition was predominantly Myctophidae, Scaridae, Gobiidae, Serranidae, Callionymidae, and Apogonidae.

**Oceanic assemblage** The oceanic assemblage consisted principally of mesopelagic fish (Myctophidae, Phosichthyidae, Sternoptychidae, Paralepididae, and Gonostomidae). The oceanic assemblage was found in the entire

oceanic area from the Minerva Seamount to Cape Frio during the winter cruise. During the summer cruise the same assemblage was limited to the oceanic area between Vitória and Cape Frio. The oceanic subassemblage was detected over the outer continental shelf between River Paraiba do Sul and Cape Frio, named the shelf-break subassemblage. This group was represented by a small number of taxa, predominantly Sternoptychidae. During the autumn cruise the oceanic assemblage was located in the oceanic area from the Roger Seamount to Cape São Tomé and consisted of Myctophidae. The oceanic subassemblage was identified to the south of the Abrolhos Bank, and consisted predominantly of Myctophidae, Phosichthyidae, Scaridae, and Serranidae.

## Discussion

The warm and salty tropical water which covers the entire survey area, is transported southward by the Brazil Current. The cold South Atlantic Central Water occupies the subsurface layer beneath the Brazil Current but owing to the deep thermocline (80–120 m), the nutrient rich SACW does not come up to the euphotic zone in the survey area, with exception of the coastal region of Cape Frio-Cape São Tomé. Consequently this area is known to be oligotrophic with a low concentration of nitrates, chlorophyll-*a* biomass, and primary production (Gaeta et al., 1999). The primary production of the nutrient-depleted surface layer is supported principally by autotrophic and heterotrophic picoplankton which use the recycled nutrients in the water. The heterotrophic dinoflagellates and ciliates are responsible for the transfer of energy produced by picoplankton to the upper trophic levels (Susini-Ribeiro, 1999).

There was a time gap between the first two cruises (June and November–December in 1978) and the last one (April–May in 1995); therefore the seasonal variations of hydrographic conditions and larval distribution in this region could have been the result of interannual variation. The El Niño year in the tropical Pacific normally causes a drought in the northeastern Brazil and a flood in the south. Bearing in mind that 1978 and 1995 were not atypical El Niño years, we assumed that the interannual variation in hydrographic conditions between these two periods could be ignored. We had no any other information on the interannual variation in oceanographic conditions in this region.

The fish larvae in the Abrolhos Bank region off the eastern coast of Brazil were produced by a diverse collection of fish species that can be divided into two dominant groups: mesopelagic fish and tropical reef fish. The high diversity of taxa (77 families and 6 orders) is characteristic of the tropical marine ecosystem and similar taxonomic diversity of larval fish is known from the eastern tropical Pacific (Ahlstrom, 1971; 1972) and the Gulf of Mexico (Richards et al., 1993).

The most surprising results were the occurrence of many reef-fish larvae along the shelf break areas. Assuming that the reef fish larvae found along the shelf break area off the Abrolhos Bank are transported southward by the main axis of the Brazil Current, most of them should be trapped in the Vitória eddy after passage through the Vitória Channel. Consequently they can be recruited at the southern margin of the bank. In order to prove this hypothesis, an intensive sampling program, coupled with an application of aging technique for postsettlement juveniles, is necessary in this region.

The dominant taxonomic groups (family) from the three cruises showed a distinct seasonal pattern in abundance. The overall larval abundance of the summer cruise was the highest. Among the Myctophidae, the larval abundance of *Myctophum affine* was highest in summer and insignificant in other seasons. Other species (*Diaphus* spp., *Lepidophanes guentheri*, *Myctophum nitidulum*, *M. obtusirostre*, *Hygophum reinhardtii*) also showed relatively

high values in summer. Many dominant species concentrate their spawning activities during the austral summer. Myctophid fish in the temperate and subtropical seas are known to spawn mainly from late winter to summer, coinciding with the seasonal peak of zooplankton production in the area (Clarke, 1973; Doyle et al., 1993). The mean displacement volume of macrozooplankton in the open ocean was 33–50% higher in summer than during winter and autumn, suggesting that many fish species have evolved spawning patterns that are synchronized with zooplankton production in this region.

The composition of dominant myctophid larvae in this region is different from that observed on the other side of the South Atlantic, i.e. the *Lampanyctodes hectoris*, a commercially exploited lanternfish, is the most abundant in the Benguela Current, followed by *Symbolophorus* and *Diaphus* (Ahlstrom et al., 1976; Olivar and Shelton, 1993). Meanwhile, the four abundant genera (*Diaphus*, *Myctophum*, *Lepidophanes*, and *Hygophum*) in the eastern tropical Pacific (Ahlstrom, 1971; 1972) were also found in the survey area. Most of the *Maurolicus muelleri* larvae were collected from south of Abrolhos Bank in winter and summer, but their occurrence during the autumn cruise was at a minimum. Because the highest densities of *M. muelleri* larvae were recorded in oceanic waters from south Brazil Bight (23–29°S) (Ribeiro, 1996), those found in the survey area may represent only a northern extension of the southern population.

Multivariate analysis of the dominant taxa in the region suggests the existence of geographically distinct larval fish assemblages that show significant seasonal variation. Observed distribution patterns of dominant groups are the result of synchronous and geographically coherent spawning activities of different groups of adult fish. The Abrolhos Bank assemblage was characterized by coral-reef-associated fish, predominantly Gobiidae, on the three cruises. Small pelagic fish were the dominant group in the neritic assemblage. The transitional assemblage was characterized by a mixture of coral-reef-associated fish and mesopelagic fish and a seasonal change of dominant groups. The oceanic assemblage was dominated by the presence of mesopelagic fish, especially the Myctophidae in all seasons.

The general geographic positions of the four larval fish assemblages showed similar distribution patterns on winter and autumn cruises, but those of the summer cruise were slightly different. The oceanic assemblage, which extended in the offshore area from the Minerva Seamount to Cape São Tome in autumn and winter, was limited to the area between Vitória and Cape Frio during the summer cruise. The offshore area between the Minerva and Vitória Seamounts was occupied by the transitional assemblage in summer. The Abrolhos Bank and neritic assemblages consistently occupied most parts of the continental shelf during the three cruises, but different larval fish assemblages occupied the offshore area south of the Abrolhos Bank. This finding can be interpreted as a result of the seasonal variation of hydrographic conditions in this specific area, such as the formation of the Vitória eddy and the intensity of coastal upwelling.

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## Literature cited

- Abousoan, A.  
1969. Sur une petite collection de larves de Téléostéens récoltée au large du Brésil (Campagne <Calypso> 1962). *Vie et Milieu* 20(3A):595–610.
- Ahlstrom, E. H.  
1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. *Fish. Bull.* 69(1):3–77.  
1972. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. *Fish. Bull.* 70(4):1153–1242.
- Ahlstrom, E. H., H. G. Moser, and M. J. O'Toole.  
1976. Development and distribution of larvae and early juveniles of the commercial lanternfish, *Lampanyctodes hectoris* (Günther), off the west coast of southern Africa with a discussion of phylogenetic relationship of the genus. *Bull. South Calif. Acad. Sci.* 75:138–152.
- Castro, B. M. and L. B. Miranda.  
1998. Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S coastal segment (4, W). *The Sea* 11:209–251.
- Clarke, T. A.  
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull.* 71(2):401–434.
- Doyle, M. J., W. W. Morse, and A. W. Kendall Jr.  
1993. A comparison of larval fish assemblages in the temperate zone of the northeast Pacific and northwest Atlantic oceans. *Bull. Mar. Sci.* 53(2):588–644.
- Fahay, M. P.  
1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. *J. Northwest Atl. Fish. Sci.* 4:1–423.
- Flores-Coto, C., and U. Ordonez-Lopez.  
1991. Larval distribution and abundance of Myctophidae, Gonostomatidae, and Sternoptychidae from the southern Gulf of Mexico. U.S. Dep. Commer., NOAA Tech. Rep., NMFS 95:55–64.
- Gaeta, S. A., J. A. Lorenzetti, L. B. Miranda, S. M. M. Susini-Ribeiro, M. Pompeu, and C. E. S. Araujo.  
1999. The Vitória eddy and its relation to the phytoplankton biomass and primary productivity during the austral fall of 1995. *Arch. Fish. Mar. Res.*, 47(2/3):253–270.
- Hill, M. O.  
1979. TWINSPAN-A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, NY, 40 p.
- Hill, M. O., R. G. H. Bunce, and M. W. Shaw.  
1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *J. Ecol.* 63:597–613.
- Ikeda, Y., L. B. Miranda, and N. J. Rock.  
1974. Observations on stages of upwelling in the region of Cabo Frio (Brazil) as conducted by continuous surface temperature and salinity measurements. *Bolm Inst. oceanogr.*, S Paulo 23:33–46.
- Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel.  
1972. Collecting and processing data on fish eggs and larvae in the California Current region. U.S. Dep. Commer., NOAA Tech. Rep., NMFS Circ. (370):1–38.
- Leis, J. M.  
1993. Larval fish assemblages near Indo-Pacific coral reefs. *Bull. Mar. Sci.* 53(2):362–392.
- Leis, J. M., and B. Goldman.  
1987. Composition and distribution of larval fish assemblages in the Great Barrier Reef lagoon, near Lizard Island, Australia. *Aust. J. Mar. Freshwater Res.* 38:211–223.
- Leis, J. M., and D. S. Rennis.  
1983. The larvae of Indo-Pacific coral reef fishes. New South Wells Univ. Press, Sydney, 269 p.
- Leis, J. M., and T. Trnski.  
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, HI, 371 p.
- Loeb, V. J.  
1980. Patterns of spatial and species abundance within the larval fish assemblage of the North Pacific Central Gyre during later summer. *Mar. Biol.* 60:189–200.
- Lowe-McConnell, R. H.  
1987. Ecological studies in tropical fish communities. Cambridge Univ. Press, Cambridge, 382 p.
- Mascarenhas Jr., A. S., L. B. Miranda, and N. J. Rock.  
1971. A study of the oceanographic conditions in the region of Cabo Frio. *In* The fertility of the sea (J. D. Costlow, ed.), p. 285–308. Gordon & Breach, New York, NY.
- Matsuura, Y.  
1985. Distribution and abundance of skipjack larvae off the coasts of Brazil. *Proc. ICCAT Conf. Intern. Skipjack Year Prog.*, Madrid, p. 285–289.
- Matsuura, Y., and M. P. Olivar.  
1999. Fish larvae. *In* South Atlantic zooplankton (D. Boltovskoy, ed.), p. 1445–1496. *Buckhuys Publ.*, Leiden.
- Moser, H. G. (ed.).  
1996. The early stages of fishes in the California Current region. *Calif. Coop. Oceanic Fish. Invest.*, Atlas 33:1–1505.
- Moser, H. G., W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson, (eds.).  
1984. Ontogeny and systematics of fishes. *Am. Soc. Ichthyol. Herpetol. Spec. Publ.* 1, 760 p.
- Nafpaktitis, B. G., R. H. Backus, J. E. Craddock, R. L. Haedrich, B. H. Robison, and C. Karnella.  
1977. Fishes of the western North Atlantic. Part 7: Order Iniomi (Myctophiformes). *Memo. Sears Found. Mar. Res.*, New Haven, CT, 299 p.
- Okiyama, M. (ed.).  
1988. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo, 1154 p.
- Olivar, M. P.  
1988. Planktonic stages of lanternfishes (Osteichthyes, Myctophidae) in the Benguela upwelling region. *Invest. Pesq.* 52(3):387–420.

- Olivar, M. P., and J. M. Fortuño.  
1991. Guide to Ichthyoplankton of the southeast Atlantic (Benguela Current Region). *Scientia Marina* 55(1):1–383.
- Olivar, M. P., and P. A. Shelton.  
1993. Larval fish assemblages of the Benguela Current. *Bull. Mar. Sci.* 53(2):450–474.
- Ribeiro, M. R.  
1996. Estudos sobre o desenvolvimento larval, abundância e distribuição de ovos e larvas de *Maurolicus muelleri* (Gmelin, 1789) (Teleostei: Sternoptychidae), e possíveis potencialidades ao largo da costa sudeste brasileira, compreendida entre 23°S (Cabo Frio, RJ) e 29°S (Cabo de Santa Marta Grande, SC). Master thesis presented at the Instituto Oceanográfico da Universidade de São Paulo, 160 p.
- Richards, W. J., M. F. McGowan, T. Leming, J. T. Lamkin, and S. Kelley.  
1993. Larval fish assemblages at the loop current boundary in the Gulf of Mexico. *Bull. Mar. Sci.* 53(2):475–537.
- Schmid, C., H. Schäfer, G. Podestá, and W. Zenk.  
1995. The Vitória eddy and its relation to the Brazil Current. *J. Phys. Oceanogr.* 25:2532–2546.
- Signorini, S. R., L. B. Miranda, D. L. Evans, M. R. Stevenson, and H. M. Inostroza.  
1989. Corrente do Brasil: estrutura térmica entre 19° e 25° circulação geostrófica. *Bolm Inst. Oceanogr., S. Paulo* 37(1):33–49.
- Silva, P. C. M.  
1973. A ressurgência em Cabo Frio (I). *Publ. Inst. Pesquisa Marinha* 24:1–31.
- Susini-Ribeiro, S. M. M.  
1999. Biomass distribution of pico-, nano- and microplankton on the continental shelf of Abrolhos, East Brazil. *Arch. Fish. Mar. Res.* 47(2/3):271–284.







