

# INTERANNUAL VARIATION OF ICHTHYOPLANKTON COMPOSITION AND ABUNDANCE RELATIONS OFF NORTHERN CHILE, 1964-83

VALERIE J. LOEB<sup>1</sup> AND OMAR ROJAS<sup>2</sup>

## ABSTRACT

Larval fishes were collected off of northern Chile during winter (July-September) ichthyoplankton surveys undertaken in 1964-70, 1972-73, and 1983. The 19-year timespan included a wide variety of hydrographic conditions in the Humboldt Current area (cold years, El Niño events, and intervening transition years); it also included the decline and collapse of the anchoveta fisheries and increases of sardine, mackerel, and jack mackerel stocks off northern Chile and Peru. The ichthyoplankton data are examined in relation to ambient hydrographic conditions as well as to possible chronological changes in environmental conditions which led to the increased Chilean sardine stocks and anchoveta fishery collapse.

More coherent patterns come from considerations of larval fish species composition in 1964-69 and 1970-73 data sets than from years of "similar" hydrographic conditions. A marked shift in relative abundances of nonfished mesopelagic species in 1969-70 is associated with changes within long-term physical data bases from Chile and Peru suggesting a large-scale environmental change. Sardine stock growth began with successful larval survival of 1968-69 and later year classes. Anchoveta stock decline began in 1972 probably due to poor larval survival. Affiliation of anchoveta and coastal species larval abundance implies that they are similarly influenced by coastal processes. An atmospherically driven oceanic circulation change beginning in the late 1960's and possibly involving onshore presence of subtropical and/or oceanic waters and altered coastal processes may have been responsible for the changes in the northern Chilean fish assemblages.

The Humboldt Current region, like the other major eastern boundary current systems (California, Benguela, and Canary Currents) is dominated by pelagic schooling fish stocks including anchoveta (*Engraulis*), sardine (*Sardinops*), hake (*Merluccius*), mackerel (*Scomber*), jack mackerel (*Trachurus*), and bonita (*Sarda*) (Parrish et al. 1983). These fish stocks, like those in the other eastern boundary current areas, exhibit extreme population fluctuations. Most notable in the past 30 years are the collapses of Peruvian and Chilean anchoveta stocks in the mid-1970's and their succession by sardine and, to a lesser extent, mackerel and jack mackerel stocks (Santander and Flores 1983; Serra 1983).

Hydrographic complexity and variability are characteristic of eastern boundary current systems. Included in the Humboldt Current region are equatorial, subequatorial, subantarctic, and antarctic oceanic water masses; northward flowing currents and opposing countercurrents; and wind driven, seasonally variable coastal upwelling (Wyrtki 1967). Additionally, the region is

subject to 1) large seasonal and longer period fluctuations in advection of water masses of markedly different properties and 2) large interannual differences in the timing and intensity of seasonal upwelling processes (Bakun 1987; Bernal et al. 1983; Parrish et al. 1983; Robles et al. 1976). The clearest and generally considered most important of the nonseasonal processes influencing the biology of the current system is the El Niño phenomenon (Bernal et al. 1983; Guillén 1983). El Niño events off Peru and Chile are marked by large-scale atmospherically driven southward and coastward advection of warm, high-salinity equatorial and subequatorial surface waters, weakening of coastal upwelling (or upwelling of warm nutrient-poor waters), and weakening of subsequent phytoplankton blooms. These El Niño or warm-water periods are variable in their intensity and duration (Guillén 1983; Santander and Flores 1983). In contrast to these periods are more "normal" cold-water events resulting from atmospherically driven intensification of northward flowing cold, low-salinity subantarctic waters and seasonal upwelling of cold, nutrient-rich water. Major El Niño events occurred in 1891, 1925-26, 1940-41, 1957-58, 1965, 1972-73, 1976, and 1982-83;

<sup>1</sup>Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, CA 95039.

<sup>2</sup>Instituto de Fomento Pesquero, Avenida Pedro de Valdivia 2633, Casilla 1287, Santiago, Chile.

major cold events over the past 20 years occurred in 1964, 1967–68, 1970–71, and 1974–75 (Guillen 1983).

The decline and ultimate collapse of the anchoveta fisheries of Peru began in 1970 and was finalized by the intense 1972–73 El Niño; the northern Chilean stock decline started in 1972 and was finalized by 1977. Factors facilitating these declines are generally believed to include overfishing and the devastating effects of the El Niño on anchoveta spawning behavior and intensity as well as on subsequent recruitment. Competition and/or predation pressure resulting from increasing abundances and distributions of sardine and mackerel have also been hypothesized (Santander and Flores 1983; Serra 1983).

Because of the great socioeconomic value of the dominant pelagic fish species of the Peru-Chile ecosystem, their population fluctuations have received a great deal of attention over the past 20 years. However, coincidental changes in the composition, abundance, or spawning intensities of other commercially less important and non-harvested species have not been examined. Information on the changes of these unfished species in relation to hydrographic conditions and fluctuations of the dominant pelagic fish stocks provide additional insight into the ecology of the Humboldt Current and may elucidate possible causes for the dramatic changes which occurred during the 1970's.

In the present work we examine the abundance and composition of total ichthyoplankton assemblages collected off of northern Chile (lat. 18°–24°S) during 1964–73 and 1983 in relation to ambient hydrographic conditions. "Normal" cold water as well as warm-water and El Niño events occurred during the 19-yr sampling span. We also examine our results with respect to possible chronological change in environmental conditions which led to the 1977 anchoveta fishery collapse off northern Chile. Our results may be applicable for interpreting coincidental changes in the Peruvian ecosystem and may also be broadly applicable for studies of similar changes in the other eastern boundary current ecosystems.

## METHODS

Samples were collected during 1964–73 and 1983 ichthyoplankton surveys conducted by the Instituto de Fomento Pesquero. The area most

intensively surveyed was a narrow coastal strip extending between Arica and Antofagasta (lat. 18°–24°S, long. 70°–72°W; Fig. 1). This area includes one of two major anchoveta (*Engraulis ringens*) spawning grounds off Chile and the primary sardine (*Sardinops sagax*) spawning area off Chile prior to 1973 (Fig. 2A, B). All samples used for interannual comparisons were collected during late July–September following peak winter anchoveta and sardine spawning periods. Between 21 and 87 samples from the 18°–24°S area were analyzed for each of 11 cruises (Table 1). In one case data from two cruises (August and September 1968) were pooled to provide adequate coverage. Sampling was done annually from 1964 to 1970 and in 1972 and 1973. There was a 10-yr hiatus before regular sampling was resumed in 1983.

The 1964–73 samples were collected with Hensen nets (0.28 m<sup>2</sup> mouth opening; 300 μm mesh). Prior to 1973 the vertical net hauls were 50–0 m; in 1973 haul depth was increased to 100 m. The 1983 100–0 m vertical hauls were made with WP2 nets (0.25 m<sup>2</sup> mouth opening; UNESCO 1968) of 300 μm mesh. Samples were preserved using buffered 5% formalin solution. Sea surface temperature and salinity data were collected at most sampling stations for all but two winter cruises; these data are lacking for 1970 and salinity data are minimal for 1967.

All fish eggs and larvae were removed from samples, and invertebrate zooplankton biomass was measured. Wet weight displacement volume was measured for 1964–73 samples; in 1983 the Yashnov (1959) technique modified by Robertson (1970) was used. A calculated correction factor of 1.44 (±3.34) was applied to the 1983 biomass values to permit comparison with the earlier data.

All fish larvae were identified to lowest taxon possible and counted. We herein treat the larvae of six commercially important species (anchoveta [*Engraulis ringens*], Pacific sardine [*Sardinops sagax*], jack mackerel [*Trachurus murphyi*; also known as *T. symmetricus* in U.S.A.], chub mackerel [*Scomber japonicus*], South Pacific menhaden [*Ethmidium maculatum*], and hake [*Merluccius gayi*]) separately from the other 35 identified taxa. These six species are referred to as the "PL" (larvae of pelagic schooling species). The other larval taxa considered together are the "OL". The PL and OL categories are treated separately because abundances of the PL (especially of anchoveta and sardine) mask abundance rela-



FIGURE 1.—Ichthyoplankton study area between Arica and Antofagasta, Chile (18°–24°S), 1964–83.

tions of the OL. The OL are further separated into myctophid, "other mesopelagic" and "coastal" fractions.

Ichthyoplankton abundances are expressed as numbers per 10 m<sup>2</sup> sea surface. Flow meters were not used with the vertical Hensen net hauls; numbers of larvae caught in each tow are multi-

plied by 30 to provide numbers per 10 m<sup>2</sup> estimates. A flow meter used with WP2 nets provided water volume measurements and more accurate abundance estimates. Based on these measurements the conversion factor applied to Hensen net catches appears to be reasonable: water volumes filtered by 100–0 m vertical WP2 net hauls aver-

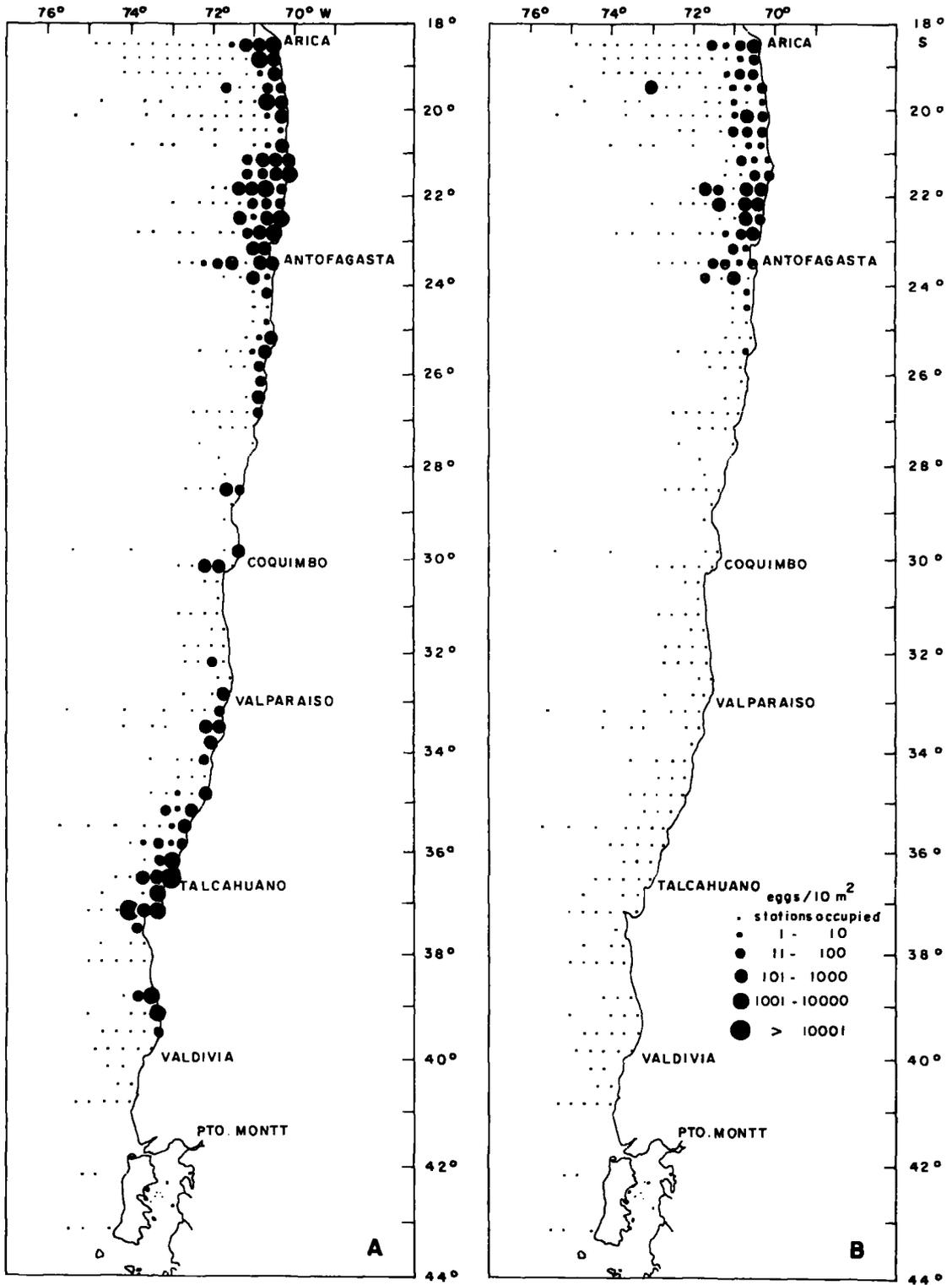


FIGURE 2.—Spawning areas of (A) anchoveta (*Engraulis ringens*) and (B) sardine (*Sardinops sagax*) off Chile based on egg abundances during July–September ichthyoplankton surveys, 1964–73.

TABLE 1.—Cruises yielding samples used for examination of ichthyoplankton abundance and composition variations off northern Chile. Only samples from 18°–24°S are used for interannual comparisons. Data from two 1968 cruises are combined; data from cruise 71(4)69CD are used for analysis of sampling depth-related catch differences. *N* = number of samples used in ichthyoplankton analyses. Tow types: H = Hensen net; WP2 = WP2 net; V = vertical.

| Year | Cruise     | Dates       | Location        |                 | <i>N</i> | Tow | Type | Depth (m) |
|------|------------|-------------|-----------------|-----------------|----------|-----|------|-----------|
| 1964 | 06(3)64GE  | 16/08-23/09 | 18°20', 23°38'S | 70°11', 71°50'W | 68       | H   | V    | 0–50      |
| 1965 | 13(3)65CD  | 15/08-09/09 | 18°20', 23°50'S | 70°00', 72°08'W | 76       | H   | V    | 0–50      |
| 1966 | 25(3)66CD  | 21/08-31/09 | 18°28', 23°52'S | 70°16', 72°16'W | 72       | H   | V    | 0–50      |
| 1967 | 37(3)67CD  | 17/08-10/09 | 18°25', 23°45'S | 70°05', 71°38'W | 59       | H   | V    | 0–50      |
| 1968 | 47(3)68NO  | 25/08       | 18°28', 23°00'S | 70°05', 70°58'W | 37       | H   | V    | 0–50      |
|      | 49(3)68NO  | 29/09       | 18°26', 23°01'S | 70°11', 70°59'W | 41       | H   | V    | 0–50      |
| 1969 | 70(3)69NO  | 23/08-25/08 | 18°29', 23°01'S | 70°09', 71°10'W | 35       | H   | V    | 0–50      |
|      | 71(4)69CD  | 03/12-17/12 | 28°29', 38°00'S | 71°22', 73°55'W | 43       | H   | V    | 0–100     |
|      | 71(4)69CD  | 03/12-17/12 | 28°29', 38°00'S | 71°22', 73°55'W | 39       | H   | V    | 0–50      |
| 1970 | 86(3)70NO  | 25/09-26/09 | 19°27', 21°58'S | 70°14', 71°03'W | 21       | H   | V    | 0–50      |
| 1972 | 109(3)72NO | 04/09-15/09 | 18°29', 22°58'S | 70°10', 71°25'W | 87       | H   | V    | 0–50      |
| 1973 | 130(3)73CP | 28/07-08/08 | 18°17', 23°08'S | 70°05', 72°20'W | 42       | H   | V    | 0–100     |
| 1983 | 277(3)83CP | 07/08-15/09 | 18°33', 23°48'S | 70°09', 71°38'W | 38       | WP2 | V    | 0–100     |

aged 28.3 m<sup>3</sup> yielding a raw count to numbers per 10 m<sup>2</sup> conversion factor of 35; this 17% increase in conversion factor is associated with a 12% decrease in mouth opening of WP2 vs. Hensen nets. Larval fish diversity is expressed as total numbers of taxa per sampling period and mean numbers of taxa per tow.

Various parametric and nonparametric tests were used for statistical analyses. Differences in mean abundances are tested with 2-tailed *Z* tests and Mann Whitney *U* tests (Dixon and Massey 1969; Conover 1971). Similarity of abundance ranks within data sets are tested with Kendall's concordance (*W*) test (Tate and Clelland 1969) and Spearman's rho ( $\rho$ ) correlation test (Conover 1971). Significant values resulting from these tests are indicated, but due to multiple testing these values should be used only as indicators of the relative strengths of relationships. Percent similarity indices (PSI; Whittaker 1975) are used for comparisons of species percentage composition. Because PSIs are strongly influenced by abundant species, we apply these tests to the OL fraction as well as to total larvae. We define as "high" all PSI values  $\geq 80$ , as "moderate" PSI's  $\geq 65$  and  $< 80$ , and as "low" values  $< 65$ .

## SAMPLING CONSIDERATIONS

### Sampling Depth Differences

The 100 m sampling depths in 1973 and 1983 potentially effect direct comparisons of abundance estimates and species composition in these vs. earlier data sets owing to individual species' depth distributions. Evaluation of depth-related sampling differences is possible through a comparison of data obtained from coincidental 50–0 m and 100–0 m Hensen net samples taken during December 1969 at 28°–38°S (Table 1). These data indicate that abundance estimates and percentage contribution of the PL to total larvae were higher in 50 m tows while those of the OL were higher in 100 m tows (Table 2). Four of five PL species caught were more abundant and frequent in the 50 m samples. The greatest differences were for *Trachurus murphyi*, which was 5 $\times$  more abundant and 3.6 $\times$  more frequent, and *Merluccius gayi*, which was present only in 50 m samples. Abundance estimates were higher for 11 of 16 OL taxa in 100 m tows although, with a few exceptions, catch frequencies were similar. The greatest difference was for *Triphoturus mexi-*

TABLE 2.—Catch comparisons of 50–0 m and 100–0 m Hensen net tows taken at lat. 28°–38°S, long. 71°–74°W during 3–17 December 1969. Abundances expressed as mean and standard deviations of numbers per 10 m<sup>2</sup>. F = percent frequency of occurrence in samples. Depth-related catch differences are shown as ratios of 50:100 m abundance estimates, species percentage contribution to total identified larvae, PL and OL percentage contribution to total larvae, and taxonomic diversity (mean numbers per tow and total numbers of taxa). N = number of samples. PL = larvae of pelagic species; OL = other larval taxa.

| Taxon                         | 50–0 m<br>(N = 43) |         |      |       | 100–0 m<br>(N = 39) |         |      |       | Ratio |
|-------------------------------|--------------------|---------|------|-------|---------------------|---------|------|-------|-------|
|                               | $\bar{X}$          | (S)     | F    | %     | $\bar{X}$           | (S)     | F    | %     |       |
| <i>Engraulis ringens</i>      | 34.2               | (122.8) | 23.2 | 13.42 | 22.3                | ( 69.4) | 15.4 | 7.23  | 1.53  |
| <i>Clupea bentincki</i>       | 6.3                | ( 28.2) | 9.3  | 2.47  | 1.5                 | ( 6.7)  | 5.1  | 0.49  | 4.20  |
| <i>Ethmidium maculatum</i>    | 0.7                | ( 4.6)  | 2.3  | 0.27  | 0.8                 | ( 4.8)  | 2.6  | 0.26  | 0.88  |
| <i>Merluccius gayi</i>        | 1.4                | ( 6.4)  | 4.6  | 0.55  |                     |         |      |       |       |
| <i>Trachurus murphyi</i>      | 4.2                | ( 14.0) | 9.3  | 1.65  | 0.8                 | ( 4.8)  | 2.6  | 0.26  | 5.25  |
| Total PL                      | 46.8               | (131.1) | 34.9 | 18.36 | 25.4                | ( 71.0) | 23.1 | 8.24  | 1.84  |
| <i>Bathylagus nigrigenys</i>  | 0.7                | ( 4.6)  | 2.3  | 0.27  | 0.8                 | ( 4.8)  | 2.6  | 0.26  | 0.88  |
| <i>Vinciguerria lucetia</i>   | 10.5               | ( 33.9) | 14.0 | 4.12  | 16.9                | ( 75.6) | 7.7  | 5.48  | 0.62  |
| <i>Diogenichthys</i> spp.     | 31.4               | (107.0) | 20.9 | 12.32 | 37.7                | ( 79.9) | 28.2 | 12.22 | 0.83  |
| <i>Hygophum bruuni</i>        | 121.4              | (238.2) | 56.1 | 47.64 | 166.2               | (291.0) | 53.8 | 53.86 | 0.73  |
| <i>Protomyctophum</i> sp.     |                    |         |      |       | 3.1                 | ( 9.2)  | 10.3 | 1.00  |       |
| <i>Diaphus</i> sp.            | 7.7                | ( 18.6) | 18.6 | 3.02  | 9.2                 | ( 24.0) | 17.9 | 2.98  | 0.84  |
| <i>Lampanyctus parvicauda</i> | 7.7                | ( 18.6) | 16.3 | 3.02  | 6.9                 | ( 21.2) | 15.4 | 2.24  | 1.12  |
| <i>Lampanyctus</i> sp.        | 1.4                | ( 6.4)  | 4.6  | 0.55  | 1.5                 | ( 6.7)  | 5.1  | 0.49  | 0.93  |
| <i>Triphoturus mexicanus</i>  | 7.7                | ( 21.8) | 14.0 | 3.02  | 18.5                | ( 57.4) | 20.5 | 5.99  | 0.42  |
| <i>Scopelosaurus</i> sp.      |                    |         |      |       | 0.8                 | ( 4.8)  | 2.6  | 0.26  |       |
| <i>Normanichthys crockeri</i> | 15.3               | ( 38.9) | 18.6 | 6.00  | 20.0                | ( 66.5) | 10.3 | 6.48  | 0.76  |
| <i>Sebastes</i> sp.           | 1.4                | ( 9.1)  | 2.3  | 0.55  | 0.8                 | ( 4.8)  | 2.6  | 0.26  | 1.75  |
| Blenniid A                    | 0.7                | ( 4.6)  | 2.3  | 0.27  |                     |         |      |       |       |
| Blenniid D                    | 0.7                | ( 4.6)  | 2.3  | 0.27  | 0.8                 | ( 4.8)  | 2.6  | 0.26  | 0.88  |
| Bothid                        | 0.7                | ( 4.6)  | 2.3  | 0.27  |                     |         |      |       |       |
| Unid. 2                       | 0.7                | ( 4.6)  | 2.3  | 0.27  |                     |         |      |       |       |
| Small damaged myctophids      | 4.8                |         |      |       | 9.2                 |         |      |       |       |
| Other unidentified            | 13.2               |         |      |       | 7.0                 |         |      |       |       |
| Total OL                      | 226.0              | (316.0) | 86.0 | 81.59 | 299.4               | (405.9) | 82.0 | 91.78 | 0.84  |
| Total larvae                  | 272.8              | (340.7) |      |       | 324.8               | (400.0) |      |       | 0.84  |
| No. taxa/tow                  | 2.5                | ( 2.0)  |      |       | 2.2                 | ( 2.0)  |      |       | 1.13  |
| Total no. taxa                | 18                 |         |      |       | 17                  |         |      |       | 0.94  |

*canus* which was 2.4× more abundant and 1.5× more frequent in 100 m tows. Because of the large catch variability, none of the species abundance differences nor the abundance differences of the PL, OL, and total larvae are significant (*Z* tests, *P*'s all >0.10). Additionally, species abundances within all positive tows from the two sampling depths are not significantly different (Mann Whitney U tests, *P* > 0.10 in all cases).

The overall species composition of 50 and 100 m tows was similar. Despite greater proportions of PL in 50 m tows, the PSI value from comparisons of total species lists was high (87.7). Species percentage contribution within the OL fraction of the two tow types was also quite similar (94.5). Species abundance rankings within the two total larval data sets are significantly correlated ( $\rho = +0.80$ ; *P* < 0.01). Species diversity estimates (total numbers of taxa and mean numbers of taxa per tow) are also similar.

From these comparisons it is apparent that the

PL predominantly occur within the upper 50 m. Similar shallow (e.g., ≤50 m) distributions have been described for dominant PL species off of Peru (anchoveta, sardine, and hake; Sameoto 1982). The generally lower 100 m abundance estimates of these species is puzzling, but suggests possibly shorter sampling time and/or less efficient sampling within the upper 50 m of these tows. Higher catch frequency and abundance of *T. mexicanus* in 100 m tows suggest that large proportions (e.g., 30–60%) of these larvae are at 50–100 m.

As a result of these catch differences we suggest caution in making direct numerical comparisons between the 1973 and 1983 vs. earlier data sets. Although the overall compositions and abundance relations should not be markedly altered, some accommodation should be allowed for the percentage contributions and across-year abundance ranks of PL species (especially *Trachurus*) and *Triphoturus mexicanus*.

**Net Type Differences**

There are no data available for a direct evaluation of catch differences between the vertical Hensen and WP2 net tows. However, comparisons of data from the 1983 WP2 net hauls (Table 3) do not indicate that this net is more or less efficient than the Hensen net. Mean abundances and species diversity (total numbers of taxa and mean numbers of taxa per tow) are within the ranges of values from Hensen net tows.

**Day-Night Catch Considerations**

Day and night sample data have been combined for each cruise. Day samples (0600–1800 hours) outnumbered (generally 55–64%) night samples during all cruises. In nine cases there were non-significant day-night larval catch differences (*Z* tests, *P* > 0.05) and overall similarity in night: day catch ratios (0.74–1.8:1; mode = 1.2:1). One cruise had a significantly higher night vs. day catch (2.5×; *P* < 0.01); this cruise and one with

TABLE 3.—Abundance estimates and diversity of larval fishes and abundance estimates of zooplankton collected in July-September samples off northern Chile (18°–24°S), 1964–83. Larval fish abundances as mean numbers per 10 m<sup>2</sup>. PL = larvae of commercially important pelagic species; OL = other larval taxa (myctophid, other mesopelagic, and other categories). Number of larvae is total raw count of identified larvae for each sampling period. Larval fish diversity expressed as total number of identified taxa and mean number of taxa per tow. Zooplankton abundance is mean displacement volume (cc/10 m<sup>2</sup>). N.A. = data not available.

| Taxon                         | Mean abundance for |      |         |       |      |       |       |         |         |       |  |
|-------------------------------|--------------------|------|---------|-------|------|-------|-------|---------|---------|-------|--|
|                               | 1964               | 1965 | 1966    | 1967  | 1968 | 1969  | 1970  | 1972    | 1973    | 1983  |  |
| <i>Engraulis ringens</i>      | 302.0              | 36.7 | 3,478.3 | 224.7 | 72.3 | 181.7 | 620.0 | 1,634.1 | 1,816.4 | —     |  |
| <i>Sardinops sagax</i>        | 5.3                | 5.1  | 12.5    | 4.6   | 21.1 | 24.9  | 1.4   | 327.2   | 52.1    | 594.9 |  |
| <i>Ethmidium maculatum</i>    | —                  | —    | —       | —     | —    | 2.6   | —     | 0.7     | —       | —     |  |
| <i>Trachurus murphyi</i>      | 2.6                | 7.1  | 10.8    | 3.1   | 0.4  | 6.8   | 5.7   | 100.3   | 2.1     | —     |  |
| <i>Scomber japonicus</i>      | —                  | 0.4  | —       | —     | —    | —     | —     | 25.9    | —       | —     |  |
| <i>Merluccius gayi</i>        | —                  | —    | —       | —     | —    | —     | —     | —       | 0.7     | 2.6   |  |
| Total PL                      | 309.9              | 49.3 | 3,501.6 | 232.4 | 93.8 | 216.0 | 627.1 | 2,086.2 | 1,871.3 | 597.5 |  |
| <i>Bathylagus nigrigenys</i>  | 4.0                | 5.1  | 6.7     | 9.7   | 6.2  | 0.9   | 7.2   | 56.6    | 35.0    | 31.5  |  |
| <i>Vinciguerria lucetia</i>   | 3.1                | 0.4  | 2.9     | 6.1   | 3.1  | 2.6   | 21.4  | 54.8    | 18.6    | 3.7   |  |
| <i>Sternoptyx diaphana</i>    | —                  | —    | —       | —     | —    | —     | —     | 0.7     | 0.7     | 1.0   |  |
| <i>Chauliodus</i> sp.         | —                  | —    | —       | —     | —    | —     | —     | 0.3     | —       | —     |  |
| <i>Stomias</i> spp.           | —                  | —    | —       | —     | —    | —     | —     | —       | —       | 1.9   |  |
| <i>Lestidiops pacificum</i>   | —                  | —    | —       | —     | —    | —     | —     | 0.3     | 0.7     | —     |  |
| <i>Melamphaes</i> sp.         | —                  | —    | —       | 0.5   | 0.4  | —     | —     | 0.3     | 2.1     | —     |  |
| Beryciform                    | —                  | —    | —       | —     | —    | —     | 1.4   | —       | —       | —     |  |
| Other mesopelagics            | 7.1                | 5.5  | 9.6     | 16.3  | 9.7  | 3.5   | 30.0  | 113.0   | 57.1    | 38.1  |  |
| <i>Diogenichthys</i> spp.     | 6.2                | 18.9 | 14.6    | 30.5  | 7.3  | 14.6  | 21.4  | 59.3    | 39.3    | 114.2 |  |
| <i>Hygophum bruuni</i>        | —                  | 2.8  | 1.2     | 3.6   | —    | —     | —     | —       | —       | 0.9   |  |
| <i>Hygophum atratum</i>       | —                  | —    | —       | —     | —    | —     | —     | —       | —       | 6.7   |  |
| <i>Metelectrona ventralis</i> | —                  | —    | —       | —     | —    | —     | —     | —       | —       | 0.9   |  |
| <i>Myctophum nitidulum</i>    | 0.4                | —    | 0.4     | —     | 0.4  | 0.9   | —     | 4.8     | 4.3     | 4.6   |  |
| <i>Diaphus</i> sp.            | —                  | 0.4  | 0.4     | —     | —    | —     | 1.4   | 0.3     | —       | 4.5   |  |
| <i>Lampanyctus parvicauda</i> | 41.0               | 32.0 | 65.8    | 63.0  | 10.8 | 38.6  | 5.7   | 29.7    | 12.1    | 15.5  |  |
| <i>Lampanyctus</i> spp.       | —                  | —    | 0.8     | —     | 1.1  | —     | —     | —       | 0.7     | —     |  |
| <i>Triphoturus mexicanus</i>  | 31.8               | 15.8 | 20.8    | 29.0  | 4.6  | 31.7  | 11.4  | 19.7    | 23.6    | 33.6  |  |
| Myctophids                    | 79.4               | 69.9 | 104.0   | 126.1 | 24.2 | 85.8  | 39.9  | 113.8   | 80.0    | 180.9 |  |
| <i>Normanichthys crockeri</i> | 17.2               | 1.5  | 281.2   | 5.6   | 2.3  | 26.6  | 10.0  | 2.4     | 31.4    | —     |  |
| <i>Sebastes</i> sp.           | 0.4                | —    | 2.5     | 1.0   | 0.8  | —     | —     | —       | 0.7     | —     |  |
| Gadiform D                    | —                  | —    | 0.8     | —     | —    | —     | —     | —       | —       | —     |  |
| Macrourid A                   | —                  | —    | —       | 0.5   | —    | —     | —     | —       | 0.7     | —     |  |
| Macrourid C                   | —                  | —    | —       | 0.5   | —    | —     | —     | —       | —       | —     |  |
| Blenniid A                    | 0.4                | —    | 0.8     | —     | 1.2  | —     | —     | —       | 1.4     | —     |  |
| Blenniid B                    | —                  | —    | 0.4     | —     | —    | —     | —     | —       | —       | —     |  |
| Blenniid C                    | —                  | —    | —       | 1.5   | —    | —     | —     | 0.3     | —       | —     |  |
| Blenniid D                    | 5.3                | 0.4  | 16.7    | 7.1   | 4.2  | 2.6   | —     | 2.8     | 8.6     | 1.0   |  |
| Gobiesocid A                  | 0.4                | —    | 0.8     | —     | —    | —     | —     | 1.0     | 0.7     | —     |  |
| Gobiesocid B                  | —                  | —    | —       | —     | 0.4  | —     | —     | —       | —       | —     |  |
| Unid. 1                       | —                  | —    | —       | —     | 0.8  | —     | —     | —       | 5.7     | 8.6   |  |
| Unid. 2                       | —                  | —    | 0.4     | —     | —    | —     | —     | 0.3     | 12.1    | —     |  |
| Unid. 3                       | —                  | —    | —       | —     | 0.4  | 1.7   | —     | 0.3     | 0.7     | —     |  |
| Unid. 4                       | —                  | —    | —       | —     | —    | —     | —     | 0.3     | 0.7     | —     |  |
| Ophiid                        | —                  | —    | —       | 1.0   | 0.8  | —     | —     | —       | —       | —     |  |
| <i>Hippoglossina</i> sp.      | —                  | —    | —       | —     | —    | —     | —     | 0.3     | —       | —     |  |
| Other larvae                  | 23.7               | 1.9  | 303.6   | 17.2  | 10.9 | 30.9  | 10.0  | 7.7     | 62.7    | 9.6   |  |
| Total OL                      | 110.2              | 77.3 | 417.2   | 159.6 | 44.8 | 120.2 | 79.9  | 234.5   | 199.8   | 228.4 |  |

TABLE 3.—Continued.

| Taxon                               | 1964  | 1965  | 1966    | 1967  | Mean abundance for |       |       |         |         |       |
|-------------------------------------|-------|-------|---------|-------|--------------------|-------|-------|---------|---------|-------|
|                                     |       |       |         |       | 1968               | 1969  | 1970  | 1972    | 1973    | 1983  |
| Larval fish abundance and diversity |       |       |         |       |                    |       |       |         |         |       |
| Total ID PL                         | 309.9 | 49.3  | 3,501.6 | 232.4 | 93.8               | 216.0 | 627.1 | 2,088.2 | 1,871.3 | 597.5 |
| Total ID OL                         | 110.2 | 77.3  | 417.2   | 159.6 | 44.8               | 120.2 | 79.9  | 234.5   | 199.8   | 228.6 |
| Total ID larvae                     | 420.1 | 126.6 | 3,918.8 | 392.0 | 138.6              | 336.2 | 707.0 | 2,322.7 | 2,071.1 | 826.1 |
| Unid/missing OL                     | 10.2  | 4.4   | 17.0    | 22.0  | 3.4                | 11.9  | 7.2   | 104.5   | 57.2    | 76.6  |
| Total larvae                        | 430.3 | 131.0 | 3,935.8 | 414.0 | 142.0              | 348.1 | 714.2 | 2,427.2 | 2,128.3 | 902.7 |
| Number of larvae                    | 953   | 321   | 9,406   | 771   | 360                | 650   | 495   | 6,738   | 2,900   | 893   |
| Number of taxa                      | 15    | 14    | 20      | 19    | 20                 | 13    | 12    | 26      | 25      | 19    |
| Number of taxa/tow                  | 2.2   | 1.6   | 3.2     | 2.5   | 1.4                | 1.9   | 2.3   | 5.3     | 4.1     | 3.7   |
| Number of samples                   | 68    | 76    | 72      | 59    | 78                 | 35    | 21    | 87      | 42      | 38    |
| Zooplankton abundance               |       |       |         |       |                    |       |       |         |         |       |
| Number of samples                   | 333.9 | 242.2 | 406.5   | 370.8 | 279.2              | 141.0 | N.A.  | 301.7   | 100.6   | 168.7 |
|                                     | 85    | 124   | 72      | 59    | 78                 | 35    |       | 110     | 42      | 30    |

a 1.8:1 night:day catch ratio were represented by fairly equal day (55–57%) and night samples.

## TAXONOMIC PROBLEMS

The 576 samples used for interannual comparisons yielded a total of 41 taxa including 19 species, 7 genera, and 11 higher taxa (Table 4). The PL and most mesopelagic forms were identified to species. During several cruises there were large proportions of small *Diogenichthys* spp. (Mycetophidae) larvae which could not be identified to species. As a consequence, data on the two species, *D. atlanticus* and *D. laternatus*, were lumped to permit reasonable between-year taxonomic composition comparisons. In all but one cruise, *D. laternatus* dominated (77–100%) the identifiable *Diogenichthys* larvae. Total within-year *Diogenichthys* spp. abundances were multiplied by proportions of identified *D. laternatus* and *D. atlanticus* larvae to provide between-year abundance rankings for each species.

Species identifications of coastal forms are limited by inadequate taxonomic information and by the presence of generally early larval developmental stages in samples. These larvae are primarily classified at familial and ordinal levels. Because the classifications include few multispecies groupings and those were numerically rare the taxonomic limitations offer no severe analytical problems.

Largest taxonomic problems occurred in cruises when large numbers of small unidentifiable larvae were caught (e.g., 1972 and 1983; Table 3). Additionally, most cruises had "missing" larvae (e.g., "other larvae" enumerated when the samples were first processed but not accounted for during later species identification

work). With the exception of 1983 the unidentified and missing larvae made up  $\leq 5\%$  of the total larval abundance for each sampling period.

## RESULTS

### Overall Ichthyoplankton Composition

The 576 July–September samples used for interannual comparisons yielded a total of 23,487 identified larvae. These larvae were dominated (85.1%) by PL species (Table 4). Overall dominants were anchoveta (*Engraulis ringens*; 74.3%) and sardine (*Sardinops sagax*; 9.3%). The other PL species were relatively rare: *Trachurus murphyi* contributed 1.2% and *Scomber japonicus*, *Merluccius gayi*, and *Ethmidium maculatum* together formed 0.3% of the total. The larval abundances of these species off of Chile are strongly influenced by sampling time and location. *Merluccius gayi* occurs primarily to the south of the study area (24°–43°S) and *Scomber japonicus* and *Trachurus murphyi* have later summer (November–February) spawning peaks.

The OL were dominated by mesopelagic fishes (18 taxa, 10.6% of total larvae). Mycetophids were most abundant (8.0%) primarily because of the large numbers of *Diogenichthys* spp., *Lampanyctus parvicauda*, and *Triphoturus mexicanus*, which together made up 7.7% of the total. One bathylagid (*Bathylagus nigrigenys*) and one gonostomatid (*Vinciguerria lucetia*) were also relatively abundant (together 2.5%). Coastal fish larvae (14 taxa) made up 4.2% of the total; a scorpaeniform (*Normanichthys crockeri*; 3.4%) and blenniid (Blenniid D; 0.4%) dominated this group.

Eighteen taxa were relatively frequent (e.g., in

≥50% of cruises) and/or abundant across the 10 sampling periods (Table 4). These taxa (four PL species, seven myctophid taxa, two other mesopelagic species, and five coastal forms) made up 99.6% of the identified larvae; they also contributed 97–100% of the identified larvae (91.2–99.6% of total larvae) and included the top 9–12 ranked taxa within each sampling period (Table 5).

TABLE 4.—Ichthyoplankton species collected in July–September samples off northern Chile (18°–24°S, 70°–72°W), 1964–83. Relative abundance (ROA) and percentage composition based on summed cruise mean abundances (no./10 m<sup>2</sup>) of all identified forms. Frequency is number of total 10 sampling periods when taxon was caught. Categories are PL (commercially important pelagic species) and other taxonomic components (M = myctophids; OM = other mesopelagic taxa; C = coastal forms).

| Taxon  | ROA    | %      | Frequency | Category |
|--|--------|--------|-----------|----------|
| <i>Engraulis ringens</i>                               | 1      | 74.29  | 9         | PL       |
| <i>Sardinops sagax</i>                                 | 2      | 9.33   | 10        | PL       |
| <i>Normanichthys crockeri</i>                          | 3      | 3.36   | 9         | C        |
| <i>Diogenichthys laternatus</i> + <i>D. atlanticus</i> | 4      | 2.90   | 10        | M        |
| <i>Lampanyctus parvicauda</i>                          | 5      | 2.79   | 10        | M        |
| <i>Triphoturus mexicanus</i>                           | 6      | 1.97   | 10        | M        |
| <i>Bathylagus nigrigenys</i>                           | 7      | 1.44   | 10        | OM       |
| <i>Trachurus murphyi</i>                               | 8      | 1.23   | 9         | PL       |
| <i>Vinciguerria lucetia</i>                            | 9      | 1.04   | 10        | OM       |
| Blenniid D   | 10     | 0.43   | 9         | C        |
| <i>Scomber japonicus</i>                               | 11     | 0.23   | 2         | PL       |
| <i>Myctophum nitidulum</i>                             | 12     | 0.14   | 7         | M        |
| Unid. 1  | 13     | 0.13   | 3         | C        |
| Unid. 2  | 14     | 0.11   | 3         | C        |
| <i>Hygophum bruuni</i>                                 | 15     | 0.075  | 4         | M        |
| <i>Diaphus</i> sp.                                     | 16     | 0.062  | 5         | M        |
| <i>Hygophum atratum</i>                                | 17     | 0.060  | 1         | M        |
| <i>Sebastes</i> sp.                                    | 18     | 0.050  | 5         | C        |
| Blenniid A   | 19     | 0.034  | 4         | C        |
| <i>Ethmidium maculatum</i>                             | 20.5   | 0.030  | 1         | PL       |
| <i>Merluccius gayi</i>                                 | 20.5   | 0.030  | 2         | PL       |
| Unid. 3  | 22     | 0.028  | 4         | C        |
| <i>Melamphaes</i> sp.                                  | 23.5   | 0.026  | 3         | OM       |
| Gobiesocid A   | 23.5   | 0.026  | 4         | C        |
| <i>Lampanyctus</i> spp.                                | 25     | 0.024  | 3         | M        |
| <i>Sternoptyx diaphana</i>                             | 26     | 0.020  | 3         | OM       |
| <i>Stomias</i> spp.                                    | 27     | 0.017  | 1         | OM       |
| Blenniid C   | 28.5   | 0.016  | 2         | C        |
| Ophidiid   | 28.5   | 0.016  | 2         | C        |
| Beryciform   | 30     | 0.012  | 1         | OM       |
| Macrourid A  | 31     | 0.011  | 2         |          |
| <i>Lestidiops pacificum</i>                            | 32.5   | 0.009  | 2         | OM       |
| Unid. 4  | 32.5   | 0.009  | 2         | C        |
| <i>Metelectrona ventralis</i>                          | 34     | 0.008  | 1         | M        |
| Gadiform D   | 35     | 0.007  | 1         |          |
| Macrourid C  | 36     | 0.004  | 1         |          |
| Blenniid B   | 37.5   | 0.0036 | 1         | C        |
| Gobiesocid B   | 37.5   | 0.0036 | 1         | C        |
| <i>Chauliodus</i> sp.                                  | 39.5   | 0.0030 | 1         | OM       |
| <i>Hippoglossina</i> sp.                               | 39.5   | 0.0030 | 1         | C        |
| Total number of identified larvae:                     | 23,487 |        |           |          |
| Total number of samples:                               | 576    |        |           |          |
| Total number of taxa:                                  | 41     |        |           |          |

## INTERANNUAL VARIATIONS IN ABUNDANCE AND COMPOSITION

The ichthyoplankton demonstrated extreme interannual variations in abundance and composition (Tables 3, 5; Fig. 3A, B). Most obvious are the 1) total larval and PL abundance peaks of 1966, 1972, and 1973 and 2) shift from anchoveta to sardine dominance between 1973 and 1983. The maximum total larval abundance values in 1966, 1972, and 1973 were 2.4–30 × higher than those of other years; the PL had 3–71 × higher abundances during these vs. other years. Interannual abundance variations during the seven years of lower abundance were also large for total larvae (to 6.9 ×) and the PL (to 12.7 ×). Anchoveta dominated the ichthyoplankton through 1973 (29.0–88.8%) and was directly responsible for the extreme abundance variations; anchoveta were absent from the 1983 samples, and sardine larvae (72.0%) contributed to the moderately high total larval and PL abundances (Table 5).

The OL fraction had less extreme abundance variations than the PL: maximum 1966, 1972, 1973, and 1983 mean abundance values ranged from 1.4 to 9 × those of the other years; mean values within the six years of lower abundance varied to 3.8 ×. Unlike the PL, OL abundance fluctuations were not attributed to any one taxonomic component (Fig. 3B): the 1966 peak was largely due to coastal taxa (73% of OL); myctophids and other mesopelagic taxa equally dominated the 1972 peak (48%); myctophids dominated (79%) in 1983; and all three components were relatively abundant (29–40%) in 1973. Myctophids were generally the dominant component (50–90%) during the six years of lower OL abundance. Abundance fluctuations (as range of mean abundance values) across the 10 years were less extreme for myctophids (8.1 ×) than for the other mesopelagic taxa (32.3 ×) and coastal forms (160 ×).

In contrast to the ichthyoplankton, July–September zooplankton biomass values were relatively constant between years and exhibited only a 4 × range in values (Table 3).

Despite large between-year variability in relative proportions of the PL and OL, there is a significant agreement of their ranked mean abundances across the 10 years ( $\rho = +0.81$ ,  $P < 0.01$ ). There is also a general agreement of the ranked mean abundances of PL and the three OL components across the 10 years ( $W = 0.44$ ;  $P = 0.05$ ). These categories were generally more abundant

TABLE 5.—Comparisons of relative abundances of dominant larval fish taxa collected off of northern Chile (18°–24°S, 70°–72°W) during July–September sampling periods, 1964–83. Relative abundances within each year are presented as (A) percentage contribution to total identified larvae and (B) ranked abundance. Taxa are listed in order of total summed 10-yr mean abundances.

| Taxon   | 1964  | 1965  | 1966  | 1967  | 1968  | 1969  | 1970  | 1972  | 1973  | 1983  |
|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| A. Percentage contribution to total identified larvae |       |       |       |       |       |       |       |       |       |       |
| <i>Engraulis ringens</i>                              | 71.89 | 28.99 | 88.76 | 57.32 | 52.20 | 54.05 | 87.69 | 70.35 | 87.70 | —     |
| <i>Sardinops sagax</i>                                | 1.26  | 4.03  | 0.32  | 1.17  | 15.23 | 7.41  | 0.20  | 14.09 | 2.52  | 72.01 |
| <i>Normanichthys crockeri</i>                         | 4.09  | 1.18  | 7.18  | 1.43  | 1.66  | 7.91  | 1.41  | 0.10  | 1.52  | —     |
| <i>Diogenichthys</i> spp.                             | 1.48  | 14.93 | 0.37  | 7.78  | 5.27  | 4.34  | 3.03  | 2.55  | 1.90  | 13.82 |
| <i>Lampanyctus parvicauda</i>                         | 9.76  | 25.28 | 1.68  | 16.07 | 7.80  | 11.48 | 0.81  | 1.28  | 0.58  | 1.88  |
| <i>Triphoturus mexicanus</i>                          | 7.57  | 12.48 | 0.53  | 7.40  | 3.32  | 9.43  | 1.61  | 0.85  | 1.14  | 4.07  |
| <i>Bathylagus nigrigenys</i>                          | 0.95  | 4.03  | 0.17  | 2.47  | 4.48  | 0.27  | 1.02  | 2.44  | 1.69  | 3.81  |
| <i>Trachurus murphyi</i>                              | 0.62  | 5.61  | 0.28  | 0.79  | 0.29  | 2.02  | 0.81  | 4.32  | 0.10  | —     |
| <i>Vinciguerria lucetia</i>                           | 0.74  | 0.32  | 0.07  | 1.56  | 2.24  | 0.77  | 3.03  | 2.36  | 0.90  | 0.45  |
| Blenniid D  | 1.26  | 0.32  | 0.43  | 1.81  | 3.03  | 0.77  | —     | 0.12  | 0.42  | 0.12  |
| <i>Scomber japonicus</i>                              | —     | 0.32  | —     | —     | —     | —     | —     | 1.12  | —     | —     |
| <i>Myctophum nitidulum</i>                            | 0.10  | —     | 0.01  | —     | 0.29  | 0.27  | —     | 0.21  | 0.21  | 0.56  |
| Unid. 1   | —     | —     | —     | —     | 0.56  | —     | —     | —     | 0.27  | 0.96  |
| Unid. 2   | —     | —     | 0.01  | —     | —     | —     | —     | 0.01  | 0.57  | —     |
| <i>Hygophum bruuni</i>                                | —     | 2.21  | 0.03  | 0.92  | —     | —     | —     | —     | —     | 0.11  |
| <i>Diaphus</i> sp.                                    | —     | 0.32  | 0.01  | —     | —     | —     | 0.20  | 0.01  | —     | 0.54  |
| <i>Hygophum atratum</i>                               | —     | —     | —     | —     | —     | —     | —     | —     | —     | 0.81  |
| <i>Sebastes</i> sp.                                   | 0.10  | —     | 0.06  | 0.26  | 0.58  | —     | —     | —     | 0.03  | —     |
| Other taxa  | 0.19  | —     | 0.09  | 1.02  | 3.03  | 1.28  | 0.20  | 0.19  | 0.43  | 0.78  |
| B. Ranked within-year abundance                       |       |       |       |       |       |       |       |       |       |       |
| <i>Engraulis ringens</i>                              | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | —     |
| <i>Sardinops sagax</i>                                | 6.5   | 6.5   | 7     | 9     | 2     | 5     | 10    | 2     | 2     | 1     |
| <i>Normanichthys crockeri</i>                         | 4     | 9     | 2     | 8     | 9     | 4     | 5     | 12    | 5     | —     |
| <i>Diogenichthys</i> spp.                             | 5     | 3     | 6     | 3     | 4     | 6     | 2.5   | 4     | 3     | 2     |
| <i>Lampanyctus parvicauda</i>                         | 2     | 2     | 3     | 2     | 3     | 2     | 7.5   | 7     | 8.5   | 5     |
| <i>Triphoturus mexicanus</i>                          | 3     | 4     | 4     | 4     | 6     | 3     | 4     | 9     | 6     | 3     |
| <i>Bathylagus nigrigenys</i>                          | 8     | 6.5   | 9     | 5     | 5     | 12.5  | 6     | 5     | 4     | 4     |
| <i>Trachurus murphyi</i>                              | 10    | 5     | 8     | 11    | 17    | 7     | 7.5   | 3     | 13.5  | —     |
| <i>Vinciguerria lucetia</i>                           | 9     | 11.5  | 10    | 7     | 8     | 9     | 2.5   | 6     | 7     | 10    |
| Blenniid D  | 6.5   | 11.5  | 5     | 6     | 7     | 9     | —     | 11    | 10    | 13.5  |
| <i>Scomber japonicus</i>                              | —     | 11.5  | —     | —     | —     | —     | —     | 8     | —     | —     |
| <i>Myctophum nitidulum</i>                            | 12.5  | —     | 18.5  | —     | 17    | 12.5  | —     | 10    | 12    | 8     |
| Unid. 1   | —     | —     | —     | —     | 12.5  | —     | —     | —     | 11    | 6     |
| Unid. 2   | —     | —     | 18.5  | —     | —     | —     | —     | 20.5  | 8.5   | —     |
| <i>Hygophum bruuni</i>                                | —     | 8     | 12    | 10    | —     | —     | —     | —     | —     | 15.5  |
| <i>Diaphus</i> sp.                                    | —     | 11.5  | 18.5  | —     | —     | —     | 10    | 20.5  | —     | 9     |
| <i>Hygophum atratum</i>                               | —     | —     | —     | —     | —     | —     | —     | —     | —     | 7     |
| <i>Sebastes</i> sp.                                   | 12.5  | —     | 11    | 13.5  | 14    | —     | —     | —     | 21    | —     |

in 1966, 1972, and 1973 and relatively rare in 1965 and 1968. The ranked abundance patterns of each of the components differ from one another (e.g., all pairwise correlation coefficients [ $\rho = -0.21$  to  $+0.61$ ] are nonsignificant). Larval diversity is strongly correlated with total larval abundance ( $\rho = +0.88$ ,  $P < 0.01$ ).

There are no significant correlations between abundance ranks of invertebrate zooplankton biomass and total larvae ( $\rho = +0.27$ ) or any of the larval categories ( $\rho = -0.03$  to  $+0.22$ ;  $P > 0.05$  in all cases).

### Species Abundance Variations and Relations

The top 10 ranking larval fish taxa were caught

during at least 9 of the 10 sampling periods (Table 4). All of these taxa exhibited large interannual abundance fluctuations (Table 3). Most marked were the abundance changes of anchoveta, sardine, and coastal species *Normanichthys crockeri*. This latter species (rank 3 in overall abundance) was frequently abundant prior to 1983; like anchoveta it was absent from 1983 samples. Among the 10 taxa only *Triphoturus mexicanus* had  $<10\times$  changes in mean abundance values;  $<20\times$  changes occurred for *Lampanyctus parvicauda* ( $11.5\times$ ) and *Diogenichthys* spp. ( $18.4\times$ ); all other taxa had  $>20\times$  mean abundance changes over the 10 years. The abundance fluctuations of these 10 taxa are primarily responsible for the interannual abundance and composition variations (Table 5; Fig. 3A, B).

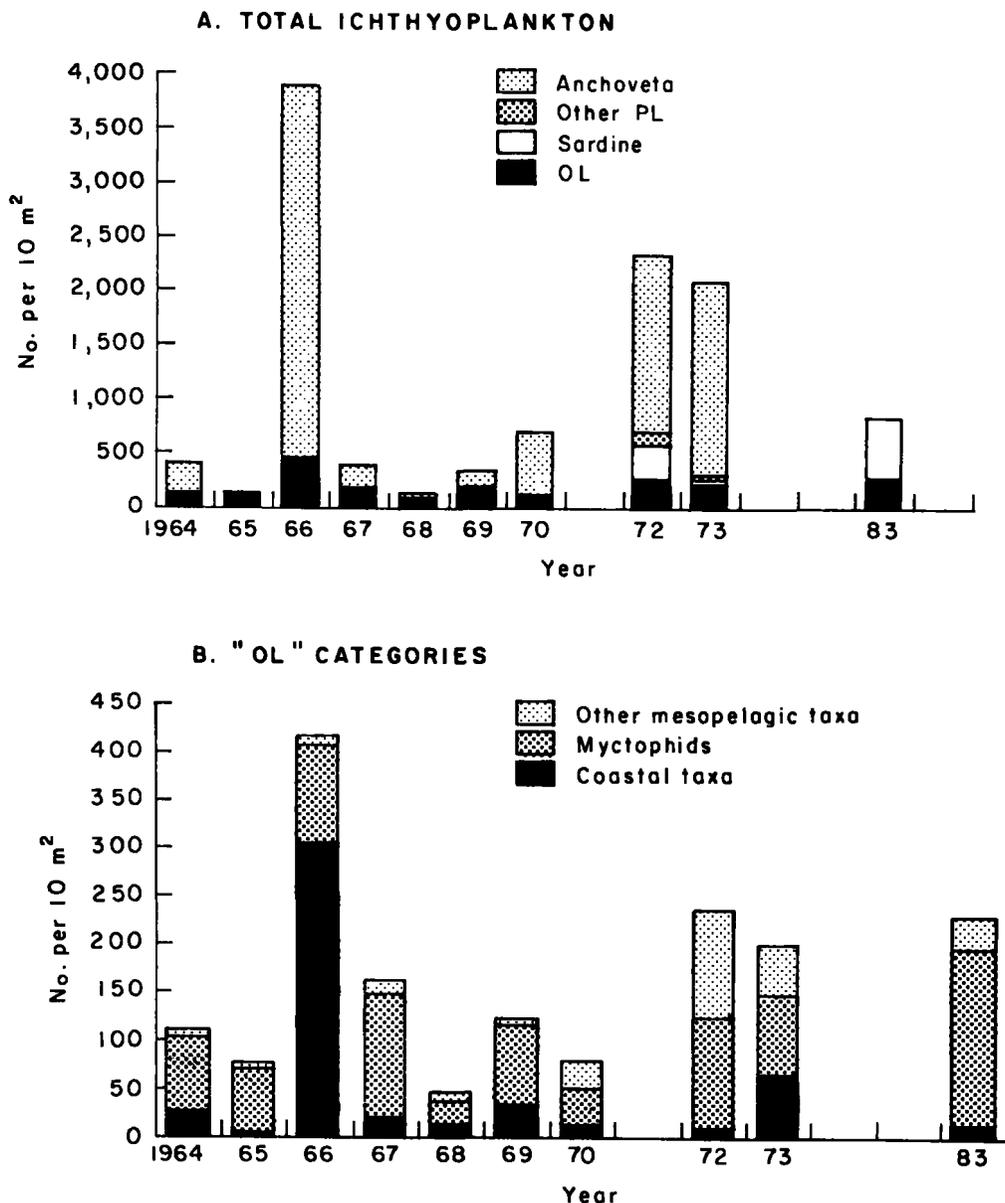


FIGURE 3.—Mean abundance (numbers per 10 m<sup>2</sup>) of (A) total ichthyoplankton and major PL components and (B) total OL and major OL components collected off northern Chile (18°–24°S) during July–September sampling periods, 1964–83.

Between-year comparisons of the species percentage compositions of total larvae give a wide range of PSI values (3.3–95.0; Table 6A) which primarily reflect similarity in percentages of anchoveta; 51% of these values are moderate to high (e.g.,  $\geq 65$ ). Highest values (91.5–95.0) come from comparisons between 1966, 1970, and 1973 when anchoveta contributed  $>87\%$  of the larvae. High

values (80.7–82.5) also result from comparisons between 1964, 1967, and 1969 and result from moderate anchoveta abundance (54.0–71.9%) and relatively similar proportions of other taxa. Lowest values (3.3–31.0) result from comparisons of 1983 vs. all other years and reflect the absence of anchoveta larvae in 1983 samples. The 1973 and 1983 PSI values are little affected (e.g.,  $\leq 2.3$ ) by

TABLE 6.—Between-year percent similarity index (PSI) values from comparisons of (A) total larvae and (B) the OL (other larval taxa) fraction collected during July–September sampling periods off northern Chile (18°–24°S), 1964–83.

|                 | PSI values for |       |       |       |       |       |       |       |       |
|-----------------|----------------|-------|-------|-------|-------|-------|-------|-------|-------|
|                 | 1965           | 1966  | 1967  | 1968  | 1969  | 1970  | 1972  | 1973  | 1983  |
| A. Total larvae |                |       |       |       |       |       |       |       |       |
| 1964            | 52.44          | 79.94 | 82.22 | 71.25 | 80.70 | 79.70 | 77.89 | 80.30 | 10.30 |
| 1965            | X              | 33.95 | 67.41 | 55.54 | 62.38 | 38.16 | 45.32 | 38.74 | 28.47 |
| 1966            |                | X     | 62.69 | 57.83 | 65.08 | 91.55 | 73.65 | 91.88 | 3.32  |
| 1967            |                |       | X     | 77.96 | 82.47 | 67.75 | 68.21 | 66.82 | 18.05 |
| 1968            |                |       |       | X     | 79.39 | 62.81 | 76.39 | 63.68 | 30.95 |
| 1969            |                |       |       |       | X     | 62.95 | 69.67 | 63.50 | 18.80 |
| 1970            |                |       |       |       |       | X     | 79.06 | 94.95 | 7.31  |
| 1972            |                |       |       |       |       |       | X     | 79.42 | 22.02 |
| 1973            |                |       |       |       |       |       |       | X     | 8.95  |
| B. OL fraction  |                |       |       |       |       |       |       |       |       |
| 1964            | 69.88          | 47.01 | 75.76 | 57.56 | 85.16 | 45.99 | 36.08 | 51.29 | 33.15 |
| 1965            | X              | 29.22 | 88.07 | 60.36 | 68.42 | 55.43 | 54.30 | 47.13 | 54.39 |
| 1966            |                | X     | 34.96 | 36.78 | 50.09 | 30.53 | 26.15 | 37.50 | 18.48 |
| 1967            |                |       | X     | 70.21 | 71.01 | 53.92 | 52.55 | 55.68 | 49.12 |
| 1968            |                |       |       | X     | 58.46 | 54.85 | 61.57 | 67.92 | 51.92 |
| 1969            |                |       |       |       | X     | 48.98 | 39.22 | 51.92 | 37.18 |
| 1970            |                |       |       |       |       | X     | 74.35 | 68.40 | 60.21 |
| 1972            |                |       |       |       |       |       | X     | 66.23 | 58.74 |
| 1973            |                |       |       |       |       |       |       | X     | 58.61 |

accommodations for possible sampling depth-catch differences of *Trachurus gayi* and *Triphoturus mexicanus*.

When the PL are excluded, comparisons between the OL taxa yield generally lower PSI values than those of the total larvae: only 24% of the 18.5–88.1 values are moderate to high (Table 6B). Moderate to high values (69.9–88.1) come from comparisons between 1964, 1965, 1967, and 1969, and in part result from similar proportions of *Lampanyctus parvicauda* (32.1–41.4%) and *Triphoturus mexicanus* (18.2–28.9%) during those years. Moderate values (66.2–74.4) also come from comparisons of 1967 vs. 1968 and 1969 (similar proportions of *L. parvicauda*, *T. mexicanus*, and *Diogenichthys* [12.2–39.5%]); 1970 vs. 1972 (similar proportions of *Vinciguerria lucetia* and *Diogenichthys* [23.4–26.8%]); and 1972 vs. 1973 (similar proportions of *Bathylagus nigrigenys*, *V. lucetia*, and *Diogenichthys* [9.3–25.3%]). Lowest PSI values (<30) result from comparisons of 1966 vs. 1965, 1970, 1972, and 1983, and are due largely to extreme dominance by *Normanichthys crockeri* (67.4% of OL) in 1966. Recalculations to accommodate for possible depth-related increased catches of *T. mexicanus* in most cases decrease 1973 and 1983 PSI values (e.g., by 2.6–7.2) and in two cases (1968 and 1970 vs. 1973) change the value characterization from moderate (67.9 and 68.4) to low (63.8 and 64.5). With one exception

(1972 vs. 1973, PSI = 67.0) all of the other adjusted values are low.

### Species Across-Year Ranked Abundance Patterns

Individual species across-year abundance rankings demonstrate a variety of patterns. Three patterns are shared by nine of the more frequently occurring taxa (Table 7). These involve 1) a group formed by anchoveta and three coastal forms; 2) a group formed by one myctophid and two other mesopelagic species; and 3) a species pair consisting of sardine and a myctophid. Another species pair (two myctophids) can be formed if the 1973 and 1983 abundances of *T. mexicanus* are adjusted.

Group I includes anchoveta, *Normanichthys crockeri*, Blenniid D, and *Sebastes* sp. (Table 7). There is a significant concordance among these species as to years of highest (1966 and 1973) and lowest (1965 and 1983) abundance ( $W = 0.69$ ,  $P < 0.01$ ). The abundance rankings of anchoveta and *N. crockeri* ( $\rho = +0.79$ ) and of Blenniid D and *Sebastes* ( $\rho = +0.88$ ) are significantly correlated ( $P \leq 0.01$ ). None of the correlations between species of the two pairs are significant due to differences in 1967–68 vs. 1970–72 relative abundances.

The three Group II species, *Diogenichthys later-*

natus, *Bathylagus nigrigenys*, and *Vinciguerria lucetia*, have a concordance of higher abundances in 1972, 1973, and 1983 vs. other years ( $W = 0.81$ ,  $P < 0.01$ ). The abundance rankings of *B. nigrigenys* are strongly correlated with those of *D. laternatus* and *V. lucetia* ( $\rho = +0.82$ ,  $P < 0.01$  in both cases); the correlation between *D. laternatus* and *V. lucetia* is not significant.

The abundance rankings of sardine and *Myctophum nitidulum* (Pair I species) are significantly correlated ( $\rho = +0.96$ ,  $P < 0.01$ ); both species were rare or absent in 1970 and most abundant in 1972, 1973, and 1983.

With adjustment to 1973 and 1983 abundances of *T. mexicanus*, its abundance rankings are strongly correlated with those of *Lampanyctus parvicauda* (Pair II species;  $\rho = +0.84$ ,  $P < 0.01$ ). Highest relative abundances of both species were in 1964, 1966, 1967, and 1969.

Three relatively frequent species (*Trachurus murphyi*, *Diogenichthys atlanticus*, and *Diaphus*

sp.) do not conform to any of the above patterns. If the 1973 *Trachurus* abundance is adjusted to accommodate for possible undersampling, its abundance pattern is similar to that of anchoveta ( $\rho = +0.68$ ,  $P = 0.05$ ) but not to any of the other Group I species ( $\rho = +0.03$  to  $+0.46$ ).

## VARIATIONS IN ABUNDANCE AND COMPOSITION RELATIVE TO HYDROGRAPHIC CONDITIONS

Ichthyoplankton abundances in the 10 years sampled show no consistent patterns relative to warm water-cold water events (Table 8). High PL and OL abundances occurred during strong El Niño events (1972 and 1983) and during cold or transition years immediately following El Niños (1966 and 1973). Lowest abundances of both fractions were associated with the 1965 El Niño and warm 1968. Neither the PL nor OL have significant correlations with ranked (high to low) July-

TABLE 7.—Larval fish taxa grouped according to similar across-year (1964–83) ranked abundance patterns. Significant agreement of group rankings indicated by Kendall's concordance ( $W$ ) values. Correlations between species pair rankings indicated by Spearman's rho ( $\rho$ ) values. Significant values at  $P \leq 0.05$  are indicated, but note use of multiple testing. \*\* = abundance ranks adjusted to accommodate for possible sampling depth related catch differences (Table 2).

| Species                                       | Abundance rank for            |      |      |      |      |      |      |      |      |      |
|---|-------------------------------|------|------|------|------|------|------|------|------|------|
|   | 1964                          | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | 1972 | 1973 | 1983 |
| Group I                                       |                               |      |      |      |      |      |      |      |      |      |
| <i>Engraulis ringens</i>                      | 5                             | 9    | 1    | 6    | 8    | 7    | 4    | 3    | 2    | 10   |
| <i>Normanichthys crockeri</i>                 | 4                             | 9    | 1    | 6    | 8    | 3    | 5    | 7    | 2    | 10   |
| Blenniid D                                    | 4                             | 9    | 1    | 3    | 5    | 7    | 10   | 6    | 2    | 8    |
| <i>Sebastes</i> sp.                           | 5                             | 8    | 1    | 2    | 3    | 8    | 8    | 8    | 4    | 8    |
|   | $W = 0.69$ ( $P < 0.01$ )     |      |      |      |      |      |      |      |      |      |
| <i>E. ringens</i> - <i>N. crockeri</i>        | $\rho = +0.79$ ( $P = 0.01$ ) |      |      |      |      |      |      |      |      |      |
| Blenniid D- <i>Sebastes</i> sp.               | $\rho = +0.88$ ( $P < 0.01$ ) |      |      |      |      |      |      |      |      |      |
| <i>E. ringens</i> -Blenniid D                 | $\rho = +0.59$                |      |      |      |      |      |      |      |      |      |
| <i>E. ringens</i> - <i>Sebastes</i> sp.       | $\rho = +0.44$                |      |      |      |      |      |      |      |      |      |
| <i>N. crockeri</i> -Blenniid D                | $\rho = +0.61$                |      |      |      |      |      |      |      |      |      |
| <i>N. crockeri</i> - <i>Sebastes</i> sp.      | $\rho = +0.48$                |      |      |      |      |      |      |      |      |      |
| Group II                                      |                               |      |      |      |      |      |      |      |      |      |
| <i>Diogenichthys laternatus</i>               | 10                            | 5    | 7.5  | 4    | 9    | 7.5  | 6    | 2    | 3    | 1    |
| <i>Bathylagus nigrigenys</i>                  | 9                             | 8    | 6    | 4    | 7    | 10   | 5    | 1    | 2    | 3    |
| <i>Vinciguerria lucetia</i>                   | 6.5                           | 10   | 8    | 4    | 6.5  | 9    | 2    | 1    | 3    | 5    |
|   | $W = 0.81$ ( $P < 0.01$ )     |      |      |      |      |      |      |      |      |      |
| <i>B. nigrigenys</i> - <i>D. laternatus</i>   | $\rho = +0.82$ ( $P < 0.01$ ) |      |      |      |      |      |      |      |      |      |
| <i>B. nigrigenys</i> - <i>V. lucetia</i>      | $\rho = +0.82$ ( $P < 0.01$ ) |      |      |      |      |      |      |      |      |      |
| <i>D. laternatus</i> - <i>V. lucetia</i>      | $\rho = +0.52$                |      |      |      |      |      |      |      |      |      |
| Pair I  |                               |      |      |      |      |      |      |      |      |      |
| <i>Sardinops sagax</i>                        | 7                             | 8    | 6    | 9    | 5    | 4    | 10   | 2    | 3    | 1    |
| <i>Myctophum nitidulum</i>                    | 6                             | 9    | 6    | 9    | 6    | 4    | 9    | 1    | 3    | 2    |
| <i>S. sagax</i> - <i>M. nitidulum</i>         | $\rho = +0.96$ ( $P < 0.01$ ) |      |      |      |      |      |      |      |      |      |
| Pair II                                       |                               |      |      |      |      |      |      |      |      |      |
| <i>Lampanyctus parvicauda</i>                 | 3                             | 5    | 1    | 2    | 9    | 4    | 10   | 6    | 8    | 7    |
| <i>Triphoturus mexicanus</i> **               | 1                             | 6    | 4    | 3    | 10   | 2    | 8    | 5    | 9    | 7    |
| <i>L. parvicauda</i> - <i>T. mexicanus</i> ** | $\rho = +0.84$ ( $P < 0.01$ ) |      |      |      |      |      |      |      |      |      |

TABLE 8.—Range, mean, standard deviation and ranked (high to low) values of sea ichthyoplankton sampling periods, 1964–83. *N* = number of observations. N.A. = data not (1976), Bernal et al. (1982), and Kelly and Blanco (1983).

|                         | 1964        | 1965        | 1966        | 1967        | 1968        |
|-------------------------|-------------|-------------|-------------|-------------|-------------|
| Temperature (°C)        |             |             |             |             |             |
| <i>N</i>                | 85          | 128         | 72          | 55          | 81          |
| Range                   | 13.5–17.9   | 13.6–18.1   | 13.7–17.1   | 13.3–16.0   | 14.3–18.6   |
| $\bar{X}$               | 15.7        | 16.5        | 15.3        | 14.8        | 16.5        |
| (S)                     | (1.0)       | (1.0)       | (0.8)       | (0.8)       | (0.9)       |
| Rank                    | 7           | 3.5         | 8           | 9           | 3.5         |
| Salinity (‰)            |             |             |             |             |             |
| <i>N</i>                | 84          | 124         | 72          | 4           | 81          |
| Range                   | 34.51–34.99 | 34.80–35.40 | 34.53–35.03 | 34.74–34.82 | 34.69–35.23 |
| $\bar{X}$               | 34.74       | 35.06       | 34.83       | 34.78       | 34.92       |
| (S)                     | (0.12)      | (0.12)      | (0.11)      | (0.04)      | (0.12)      |
| Rank                    | 9           | 2           | 6           | 8           | 4           |
| Hydrographic condition: |             |             |             |             |             |
|                         | Cold        | El Niño     | Transition  | Cold        | Warm        |

September mean temperature and salinity values; larval diversity (mean number of taxa/tow) also shows no correlation with these values (Table 9). Within the PL, anchoveta were most abundant during years immediately following El Niños (cold 1966, transition 1973), the 1972 El Niño, and cold 1970; lowest abundances were during the 1965 and 1983 El Niños (Table 8). There are no significant correlations between ranked anchoveta abundances and ranked values of temperature or salinity (Table 10). Sardine larvae were most abundant during and after the 1972 El Niño; prior to this moderate abundances and relatively large percentage contributions to the ichthyoplankton occurred only during the warm 1968–69 period (Tables 5, 7). Lowest sardine abundances were during cold years 1964, 1967, and 1970 and the 1965 El Niño. Despite low abundances during the 1965 El Niño, there is a significant positive correlation between ranked sardine abundance and temperature ( $\rho = +0.69$ ,  $P < 0.05$ ). Ranked larval anchoveta and sardine abundances are not correlated ( $\rho = -0.07$ ).

The only apparent warm-cold year abundance pattern among the OL categories is that of the coastal taxa; this group had lowest abundances during the 1965, 1972, and 1983 El Niños and highest abundances in subsequent 1966 and 1973 transition years. The ranked abundance pattern of this category has negative correlations ( $P \leq 0.05$ ) with ranked temperature ( $\rho = -0.69$ ) and salinity ( $\rho = -0.68$ ) values (Table 9). Both the myctophid and other mesopelagic categories appear to have abundance patterns unrelated to warm-cold hydrographic conditions (Table 9).

TABLE 9.—Correlations of across-year abundance ranks of zooplankton and ichthyoplankton categories with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods off northern Chile, 1964–83. Correlations based on Spearman's rho tests. Significant values at  $P \leq 0.05$  are indicated, but note use of multiple testing. PL = larvae of pelagic species; OL = other larval taxa.

|  | Temperature (°C) | Salinity (‰)     |
|--|------------------|------------------|
| Zooplankton                              | -0.48            | -0.37            |
| PL                                       | -0.10            | -0.17            |
| OL                                       | -0.02            | +0.05            |
| Larval diversity:<br>(mean no. taxa/tow) | +0.12            | 0.00             |
| Myctophids                               | +0.02            | +0.12            |
| Other mesopelagic<br>taxa                | +0.28            | +0.12            |
| Coastal taxa                             | -0.69 $P < 0.05$ | -0.68 $P = 0.05$ |

Zooplankton biomass values show negative but nonsignificant correlations with temperature and salinity (Table 9). This is in agreement with the time-series analysis results of Bernal et al. (1983) which demonstrated no consistent relations of zooplankton biomass with cold- or warm-water events.

### Species Groups and Hydrographic Conditions

The species groups formed by similarity of between-year abundance ranks demonstrate both positive and negative correlations with cold- and warm-year conditions (Table 10). Group I and Pair II and their member species have negative correlations with ranked temperature and salinity values indicating a tendency for higher

surface temperature (°C) and salinity (‰) values during July–September available. Hydrographic “condition” descriptions for these periods are from Robles et al.

|                         | 1969        | 1970 | 1972        | 1973        | 1983        |
|-------------------------|-------------|------|-------------|-------------|-------------|
| Temperature (°C)        |             |      |             |             |             |
| <i>N</i>                | 35          | N.A. | 110         | 43          | 24          |
| Range                   | 14.6–17.5   |      | 15.5–18.5   | 14.3–17.4   | 15.1–19.0   |
| $\bar{X}$               | 16.0        |      | 17.2        | 15.8        | 17.2        |
| (S)                     | (1.0)       |      | (0.7)       | (0.9)       | (0.9)       |
| Rank                    | 5           |      | 1.5         | 6           | 1.5         |
| Salinity (‰)            |             |      |             |             |             |
| <i>N</i>                | 35          | N.A. | 108         | 43          | 20          |
| Range                   | 34.60–35.19 |      | 34.75–35.96 | 34.60–35.13 | 34.81–35.39 |
| $\bar{X}$               | 34.87       |      | 35.05       | 34.82       | 35.09       |
| (S)                     | (0.16)      |      | (0.18)      | (0.13)      | (0.19)      |
| Rank                    | 5           |      | 3           | 7           | 1           |
| Hydrographic condition: |             |      |             |             |             |
|                         | Warm        | Cold | El Niño     | Transition  | El Niño     |

TABLE 10.—Correlations of across-year abundance ranks of larval fish species groups and member species with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods, 1964–83. Correlations based on Spearman's rho tests. Group correlations based on ranks of summed within-year ranks of member species. Significant values at  $P \leq 0.05$  are indicated but note use of multiple testing. \*\* = abundance ranks adjusted to accommodate for apparent large sampling depth-related catch differences.

| Species                         | Temperature (°C) | Salinity (‰)     |
|---------------------------------|------------------|------------------|
| Group I                         | -0.78 $P < 0.05$ | -0.78 $P < 0.05$ |
| <i>Engraulis ringens</i>        | -0.52            | -0.62            |
| <i>Normanichthys crockeri</i>   | -0.69 $P < 0.05$ | -0.72 $P < 0.05$ |
| Blenniid D                      | -0.74 $P < 0.05$ | -0.77 $P < 0.05$ |
| <i>Sebastes</i> sp.             | -0.67            | -0.55            |
| Group II                        | +0.27            | +0.20            |
| <i>Diogenichthys laternatus</i> | +0.45            | +0.50            |
| <i>Bathylagus nigrigenys</i>    | +0.27            | +0.20            |
| <i>Vinciguerria lucetia</i>     | +0.12            | -0.14            |
| Pair I                          | +0.70 $P < 0.05$ | +0.49            |
| <i>Sardinops sagax</i>          | +0.69 $P < 0.05$ | +0.50            |
| <i>Myctophum nitidulum</i>      | +0.61            | +0.35            |
| Pair II                         | -0.62            | -0.57            |
| <i>Lampanyctus parvicauda</i>   | -0.68 $P = 0.05$ | -0.48            |
| <i>Triphoturus mexicanus</i> ** | -0.50            | -0.53            |

abundances during colder, lower salinity periods. The rankings of Group I (based on ranks of summed within-year member species ranks) are significantly correlated ( $P < 0.05$ ) with both temperature and salinity ( $\rho = -0.78$  in both cases). Within this group the rankings of *Normanichthys crockeri* and Blenniid D are correlated ( $P < 0.05$ ) with temperature and salinity ( $\rho = -0.69$  to  $-0.77$ ); the correlation of *Sebastes* with temperature is also relatively strong ( $\rho = -0.67$ ). Within Species Pair II, *Lampanyctus parvicauda* abundance has a relatively strong

negative correlation with temperature ( $\rho = -0.68$ ).

Group II and Pair I and their member species have positive correlations of ranked abundance with temperature and (with one exception) salinity values (Table 10) suggesting a tendency for higher abundances during warmer, higher salinity conditions. These correlations are all non-significant and generally weak for Group II and its member species (*Bathylagus nigrigenys*, *Vinciguerria lucetia*, and *Diogenichthys laternatus*). Pair I has a positive correlation ( $P < 0.05$ ) with temperature ( $\rho = +0.70$ ) primarily due to sardine abundance ranks.

### Species Percentage Composition Relative to Hydrographic Conditions

Ichthyoplankton percentage composition shows no striking warm year vs. cold year related patterns. Total ichthyoplankton composition comparisons between years of “similar” hydrographic conditions do not give overall higher PSI values than do comparisons between years of different conditions (Table 11A). PSI values (ranges, means, and proportions of high and moderate values) from comparisons of cold, transition, and warm years are similar. However, highest values (91.6–94.9) come from cold vs. transition year (1970 vs. 1966 and 1973) and between-transition year (1966 vs. 1973) comparisons. Additionally, intercomparisons of the transition, warm, and El Niño years give relatively lower values than do cold-year comparisons. Comparisons between El Niño years give generally PSI low values.

TABLE 11.—Within- and between-hydrographic period ichthyoplankton composition comparisons presented as range, mean, and standard errors of percent similarity index (PSI) values and numbers (N) out of total comparisons having moderate to high (e.g.,  $\geq 65$ ) values. A. Total larvae. B. OL (other larval taxa) fraction.

|                                     |       | PSI values for |            |           |           |
|-------------------------------------|-------|----------------|------------|-----------|-----------|
|                                     |       | Cold           | Transition | Warm      | El Niño   |
| <b>A. Total larvae</b>              |       |                |            |           |           |
| Cold years<br>(1964, 1967, 1970)    | Range | 67.8–82.2      | 62.7–94.9  | 62.8–82.5 | 7.3–79.1  |
|                                     | X     | 76.6           | 79.4       | 73.0      | 46.5      |
|                                     | (SE)  | ( 4.5)         | ( 5.2)     | ( 3.6)    | ( 9.6)    |
|                                     | N     | 3/3            | 5/6        | 4/6       | 4/9       |
| Transition years<br>(1966, 1973)    | Range |                |            | 57.8–65.1 | 3.3–79.4  |
|                                     | X     |                | 91.9       | 62.5      | 39.7      |
|                                     | (SE)  |                |            | ( 1.6)    | (12.9)    |
|                                     | N     |                | 1/1        | 1/4       | 2/6       |
| Warm years<br>(1968, 1969)          | Range |                |            |           | 18.8–76.4 |
|                                     | X     |                |            | 79.4      | 52.3      |
|                                     | (SE)  |                |            |           | ( 9.2)    |
|                                     | N     |                |            | 1/1       | 2/6       |
| El Niño years<br>(1965, 1972, 1983) | Range |                |            |           | 22.0–45.3 |
|                                     | X     |                |            |           | 31.9      |
|                                     | (SE)  |                |            |           | ( 7.0)    |
|                                     | N     |                |            |           | 0/3       |
| <b>B. OL</b>                        |       |                |            |           |           |
| Cold years<br>(1964, 1967, 1970)    | Range | 46.0–75.8      | 30.5–68.3  | 47.0–85.2 | 33.2–88.1 |
|                                     | X     | 58.6           | 48.0       | 64.6      | 57.6      |
|                                     | (SE)  | ( 8.9)         | ( 5.7)     | ( 5.4)    | ( 5.9)    |
|                                     | N     | 1/3            | 1/6        | 3/6       | 3/9       |
| Transition years<br>(1966, 1973)    | Range |                |            | 36.8–67.9 | 18.5–66.2 |
|                                     | X     |                | 37.5       | 51.7      | 41.0      |
|                                     | (SE)  |                |            | ( 6.4)    | ( 7.8)    |
|                                     | N     |                | 0/1        | 1/4       | 1/6       |
| Warm years<br>(1968, 1969)          | Range |                |            |           | 37.2–68.4 |
|                                     | X     |                |            | 58.5      | 53.1      |
|                                     | (SE)  |                |            |           | ( 5.2)    |
|                                     | N     |                |            | 0/1       | 1/6       |
| El Niño years<br>(1965, 1972, 1983) | Range |                |            |           | 54.3–58.7 |
|                                     | X     |                |            |           | 55.8      |
|                                     | (SE)  |                |            |           | ( 1.5)    |
|                                     | N     |                |            |           | 0/3       |

The OL percentage composition similarly does not demonstrate clear hydrographically related patterns (Table 11B). As with the total larvae, comparisons of cold vs. other years yield most of the moderate to high PSI values. Highest values (88.1 and 85.2) come from comparisons of cold vs. El Niño (1965 vs. 1967) and cold vs. warm (1964 vs. 1969) years. Comparisons within and between transition, warm and El Niño years give primarily low values. Recalculation of PSIs to accommodate for *Triphoturus mexicanus* lowers mean values for comparisons with 1973 and 1983 by only 0.4–2.3 and does not affect the overall results.

### Chronological Considerations of Species Composition

When the total larval and OL PSI data are considered in terms of chronological rather than hy-

drographic periods, various patterns become apparent (Table 12). For the total ichthyoplankton, comparisons within the 1964–69 data set and between this and the 1970–73 data set give similar means, ranges, and proportions of moderate to high values. In contrast, comparisons within the 1970–73 data set provide more similar values and a significantly higher mean value than results from comparisons within the 1964–69 set ( $Z$  test,  $P < 0.01$ ). This suggests that, despite the varied hydrographic conditions represented during the 1970–73 period, conditions were favorable for a repeated fairly similar anchoveta-dominated ichthyoplankton assemblage during July–September months.

Chronologically grouped comparisons of the OL fraction provide somewhat different patterns from those of the total ichthyoplankton (Table 12B) and indicate a marked change in species

proportions between 1964–69 and later years. Comparisons within the 1964–69 OL data set yield all of the high and most of the moderate PSI values. The mean PSI value from these comparisons is significantly higher ( $P < 0.05$ ) than that from 1964–69 vs. 1970–73 comparisons. As with the total larvae, the 1970–73 PSI values are similar and moderately high and the 1983 comparison values are relatively low compared with other

years. Accommodation for *T. mexicanus* abundance reduces slightly (1.1–3.1) the mean values from comparisons with 1970–73 and 1983 data sets and strengthens the significance of difference ( $P < 0.01$ ) between 1964–69 and 1964–69 vs. 1970–73 mean values.

The difference in OL PSI values between 1964–69 and 1970–83 is, to a great extent, due to abundance shifts of Group II and Pair II species. The abundance ranks of all three Group II species (Table 7) indicate significantly higher abundances during 1970–83 than in earlier years (Man Whitney U tests, all  $P$ 's  $\leq 0.05$ ). Additionally, the averaged abundance estimates from these four years are significantly higher than from earlier years ( $Z$  tests;  $P < 0.01$  for *Bathylagus nigrigenys* and *Vinciguerria lucetia*,  $P < 0.05$  for *Diogenichthys* spp.). Together *B. nigrigenys*, *V. lucetia*, and *Diogenichthys* spp. (primarily *D. laternatus*) contributed 46.5–72.8% of the OL collected during 1970–83 compared with 5.8–37.1% during 1964–69 (Table 13).

In contrast, Pair II species *Lampanyctus parvicauda* and *Triphoturus mexicanus* were relatively less abundant during 1970–83 than in previous years. These two species contributed 21–66% of the OL during 1964–69 compared with <22% during 1970–83 (Table 13). With adjustments to *T. mexicanus* abundance these species proportions in 1973 and 1983 decrease to 11.8% and 13.2%, and those of the Group II species increase to 49.9% and 71.4%, respectively. The relative abundance decrease of Pair II was primarily

TABLE 12.—Within- and between-time period ichthyoplankton composition comparisons presented as ranges, means, and standard errors of percent similarity index (PSI) values and numbers ( $N$ ) out of total comparisons having moderate to high (e.g.,  $\geq 65$ ) values. A. Total larvae. B. OL (other larval taxa) fraction.

|                        |       | PSI values for |           |           |
|------------------------|-------|----------------|-----------|-----------|
|                        |       | 1964–69        | 1970–73   | 1983      |
| <b>A. Total larvae</b> |       |                |           |           |
| 1964–69                | Range | 33.9–82.5      | 38.2–91.9 | 3.3–31.0  |
|                        | X     | 67.4           | 67.7      | 18.2      |
|                        | (SE)  | ( 3.6)         | ( 3.6)    | ( 4.3)    |
|                        | N     | 9/15           | 11/18     | 0/6       |
| 1970–73                | Range |                | 79.1–95.0 | 7.3–22.0  |
|                        | X     |                | 84.4      | 12.8      |
|                        | (SE)  |                | ( 5.2)    | ( 4.7)    |
|                        | N     |                | 3/3       | 0/3       |
| <b>B. OL</b>           |       |                |           |           |
| 1964–69                | Range | 29.2–88.1      | 26.2–67.9 | 18.5–54.4 |
|                        | X     | 60.2           | 48.4      | 40.7      |
|                        | (SE)  | ( 4.6)         | ( 2.5)    | ( 5.6)    |
|                        | N     | 7/15           | 1/18      | 0/6       |
| 1970–73                | Range |                | 66.2–74.4 | 58.6–60.2 |
|                        | X     |                | 69.7      | 59.2      |
|                        | (SE)  |                | ( 2.4)    | ( 0.5)    |
|                        | N     |                | 3/3       | 0/3       |

TABLE 13.—Percentage contribution by dominant OL (other larval taxa) species collected during July–September sampling periods, 1964–83. Species arranged according to group affiliations based on across-year ranked abundance patterns.

|                               | Percentage contribution for |       |       |       |       |       |       |       |       |       |
|-------------------------------|-----------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|                               | 1964                        | 1965  | 1966  | 1967  | 1968  | 1969  | 1970  | 1972  | 1973  | 1983  |
| <b>Group I</b>                |                             |       |       |       |       |       |       |       |       |       |
| <i>Normanichthys crockeri</i> | 15.61                       | 1.94  | 67.40 | 3.51  | 5.15  | 22.13 | 12.52 | 1.02  | 15.72 | —     |
| <i>Sebastes</i> sp.           | 0.36                        | —     | 0.60  | 0.63  | 1.79  | —     | —     | —     | 0.35  | —     |
| Blenniid D                    | 4.81                        | 0.52  | 4.00  | 4.45  | 9.40  | 2.16  | —     | 1.19  | 4.31  | 0.44  |
| Group total                   | 20.78                       | 2.46  | 72.00 | 8.59  | 16.34 | 24.29 | 12.52 | 2.21  | 20.38 | 0.44  |
| <b>Group II</b>               |                             |       |       |       |       |       |       |       |       |       |
| <i>Bathylagus nigrigenys</i>  | 3.63                        | 6.60  | 1.61  | 6.08  | 13.87 | 0.75  | 9.01  | 24.14 | 17.53 | 13.78 |
| <i>Vinciguerria lucetia</i>   | 2.81                        | 0.52  | 0.70  | 3.82  | 6.94  | 2.16  | 26.78 | 23.37 | 9.31  | 1.62  |
| <i>Diogenichthys</i> spp.     | 5.63                        | 24.45 | 3.50  | 19.11 | 16.33 | 12.15 | 26.78 | 25.29 | 19.68 | 49.96 |
| Group total                   | 12.07                       | 31.57 | 5.81  | 29.01 | 37.14 | 15.06 | 62.57 | 72.80 | 46.52 | 65.36 |
| <b>Pair I</b>                 |                             |       |       |       |       |       |       |       |       |       |
| <i>Myctophum nitidulum</i>    | 0.36                        | —     | 0.10  | —     | 0.89  | 0.75  | —     | 2.05  | 2.15  | 2.01  |
| <b>Pair II</b>                |                             |       |       |       |       |       |       |       |       |       |
| <i>Lampanyctus parvicauda</i> | 37.21                       | 41.40 | 15.77 | 39.47 | 24.16 | 32.11 | 7.13  | 12.67 | 6.06  | 6.78  |
| <i>Triphoturus mexicanus</i>  | 28.86                       | 20.44 | 4.99  | 18.17 | 10.29 | 26.37 | 14.27 | 8.40  | 11.82 | 14.70 |
| Pair total                    | 66.07                       | 61.84 | 20.76 | 57.64 | 34.45 | 58.48 | 21.40 | 21.07 | 17.88 | 21.48 |

due to the increased numbers of Group II species and decreased numbers of *L. parvicauda*. The 1970–83 averaged abundance of *L. parvicauda* is significantly lower ( $Z$  test;  $P < 0.01$ ) than that of 1964–69. *Triphoturus mexicanus* averaged abundance (both adjusted and unadjusted values) is similar ( $P > 0.05$ ) between the two time periods.

## DISCUSSION

The northern Chilean ichthyoplankton data set is obviously weakened by lack of information from the 1974–82 period; this missing information is critical for an appreciation of the temporal extent and relative constancy of the apparent ichthyoplankton composition change in 1970–73 vs. earlier years. This data set also suffers from limited seasonal coverage which prohibits examination of between-year variations in spawning time and intensity as a cause of interannual abundance fluctuations and apparent composition change. However, the existing data set does provide coherent coverage over varied hydrographic conditions between 1964 and 1973 and is sufficient to test for correlations with short-term (e.g., year to year) fluctuations in hydrographic conditions.

The large interannual changes in abundance and composition of the northern Chilean ichthyoplankton can to a certain extent be related to interannual changes of hydrographic conditions in the Humboldt Current. This has been demonstrated through correlations of ranked temperature and salinity values and abundances of coastal species, sardine, and *Lampanyctus parvicauda* (Tables 9, 10). The temperature and salinity values used in these correlation tests represent ambient conditions during the July–September spawning period and therefore possibly reflect only conditions affecting egg and early larval (e.g., to stages capable of substantial net avoidance) survival. These values do not necessarily reflect longer term conditions affecting abundance, distributions, and fecundities of adult populations or later larval survival and recruitment. However, there is a generally good correspondence between these values and reported longer term hydrographic conditions in the Humboldt Current over the 19-yr timespan (e.g., Table 8; Robles et al. 1976; Bernal et al. 1983; Guillén 1983; Bakun 1987).

Despite significant correlations between abundances of some ichthyoplankton components and

temperature and salinity values, there is no apparent consistency of total larval or OL species percentage compositions during years of "similar" hydrographic conditions (Table 11). More coherent patterns emerge from considerations of the 1964–69 and 1970–73 data sets (Table 12). This chronological separation is also supported by the ranked abundance patterns of the various species groups and pairs (Table 7).

Among the least confusing across-year abundance patterns demonstrated by the ichthyoplankton are 1) generally greater abundance of Group II species after 1969, 2) greatest abundance of Pair I species after 1970, and 3) predominantly higher abundances of one of the Pair II species prior to 1970 (Table 7). Associated with the Group II and Pair II abundance patterns are large shifts in their relative proportions (Table 13).

The shift from relatively large percentage contributions by *Lampanyctus parvicauda* and *Triphoturus mexicanus* to larger proportions of *Diogenichthys* spp., *Bathylagus nigrigenys*, and *Vinciguerria lucetia* after 1969 is notable. The abundances of these mesopelagic species, unlike those of anchoveta and sardine, are not directly influenced by man's fishing activities and so may be interpreted as indicators of environmental change. Furthermore, the timing of these species absolute and relative abundance changes preceded by several years the dramatic changes in anchoveta and sardine stocks off of northern Chile (Fig. 4) and so cannot be directly related to biological consequences of change in the dominant pelagic schooling fish stocks.

Although fragmentary, there is evidence for a change in zooplankton biomass values off northern Chile ( $18^{\circ}$ – $24^{\circ}$ S) occurring in 1969 (Fig. 5) which, like OL percentage composition, suggests a possible environmental change. Time series analysis of quarterly zooplankton biomass values during 1964–73 indicate generally lower biomass during 1969–73 relative to the 1964–68 period. As with total larval abundance (Table 9), these zooplankton biomass variations do not appear to be related to warm year-cold year events (Bernal et al. 1983).

The changes in OL composition and zooplankton biomass suggest that there was subtle but large-scale (low-frequency) environmental transition occurring in the 1969–70 period. Various indications of environmental change occurring about this time are present in long-term physical data bases from Chile and Peru. Predominantly

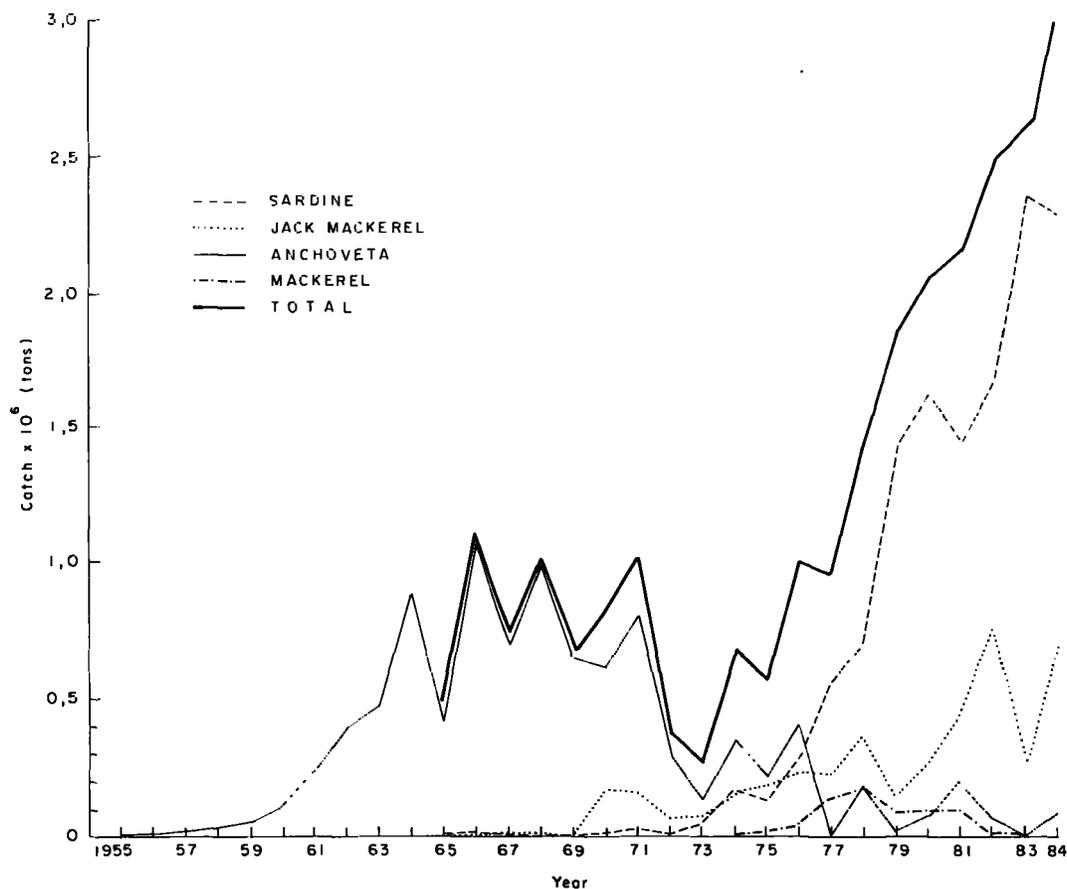


FIGURE 4.—Total catch and catch of dominant species taken in the northern Chilean pelagic fishery, 1955–84.

negative sea surface atmospheric pressure anomalies occurred off of Arica from 1960 to 1972 with a strong negative anomaly occurring in 1969; predominantly positive anomalies occurred there after 1972 (Fig. 6A). A similar but less extreme change from negative or neutral anomalies to predominantly positive anomalies occurred off Iquique ( $20^{\circ}\text{S}$ ) in 1970 (Fig. 6B; Kelly and Blanco 1983).

Off Peru ( $5^{\circ}$ – $15^{\circ}\text{S}$ ) the wind driven turbulent mixing index of surface waters shows a general increase during and after the 1972 El Niño event (Fig. 7A; Bakun 1987). A probable result of this increased turbulence is an increase in standard deviations associated with monthly temperature values; standard deviations above the 30-yr mean generally persisted throughout the year from 1972 to 1984 (Fig. 7B) and suggest increased physical variability and heterogeneity in this later period. Comparable data sets from northern Chile are not available to determine if these lat-

ter two features were also characteristic of the Chilean area.

How these observed atmospherically related changes could be related to changes in the marine environment off northern Chile is uncertain. It is possible that the observed changes in atmospheric pressure off Arica and Iquique have associated changes in advection of water mass and faunal sources. Bernal et al. (1983) discussed El Niño related changes in water mass distribution off Chile in 1972 and 1973 relative to cold-year 1967. These changes involved southerly extensions of oceanic subtropical and equatorial subsurface waters, strengthening of the spring-summer thermocline, and cessation of coastal upwelling. These authors did not examine water mass distributions in the 1968–70 period. However, lowered zooplankton biomass starting in 1969 and the OL composition change starting around 1970 suggest that the hydrographic conditions attributed to the 1972 El Niño may have been an intensification of

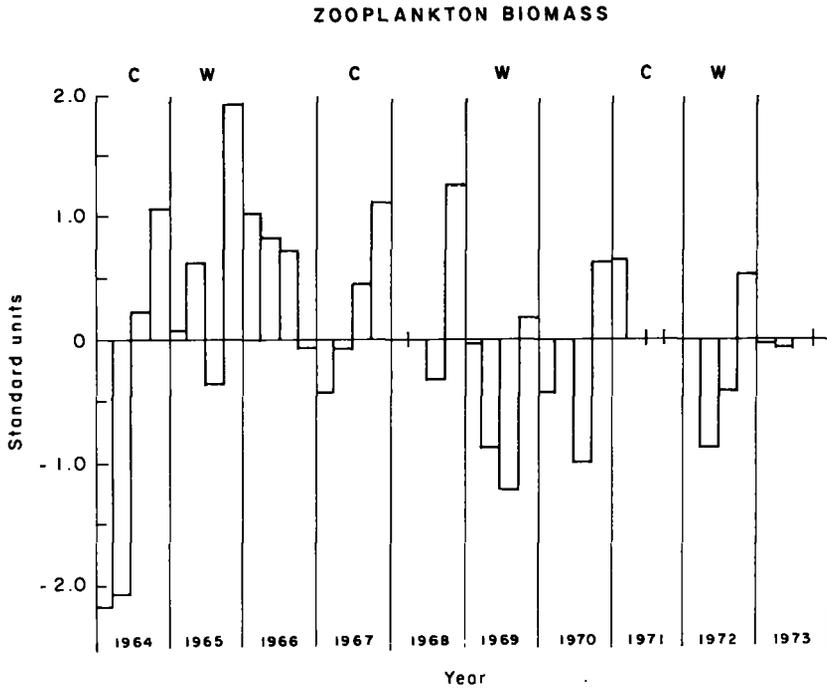


FIGURE 5.—Time series estimates of quarterly zooplankton biomass values from northern Chile (18°–24°S), 1964–73, standardized according to the long term standard deviation. W = warm years; C = cold years. From Bernal et al. 1983.

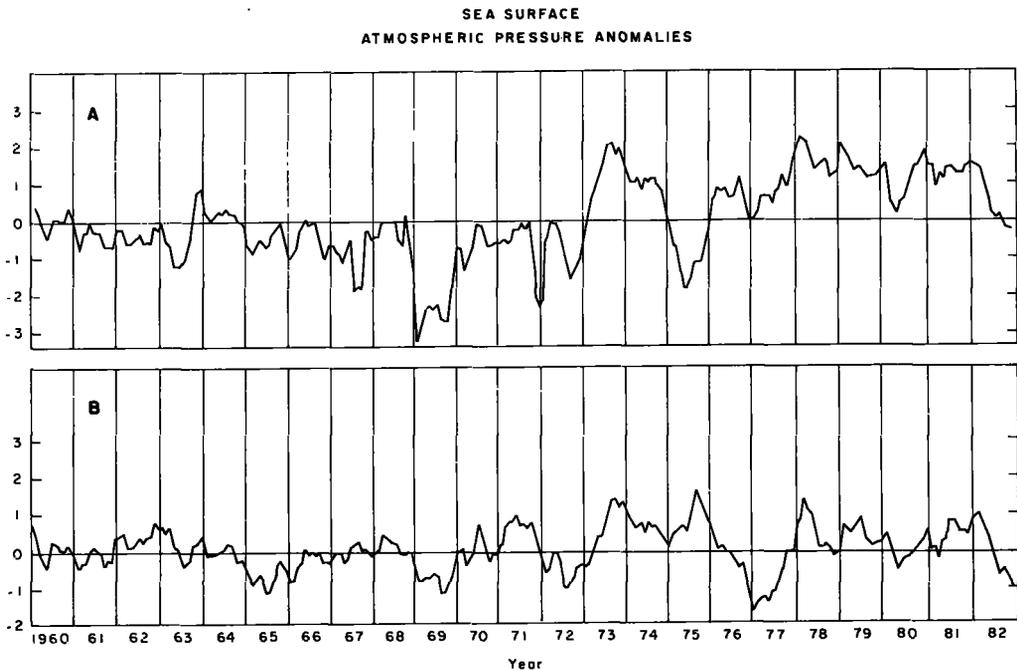


FIGURE 6.—Sea surface atmospheric pressure anomalies off of (A) Arica (18°S) and (B) Iquique (20°S), 1960–82. From Kelly and Blanco 1983.

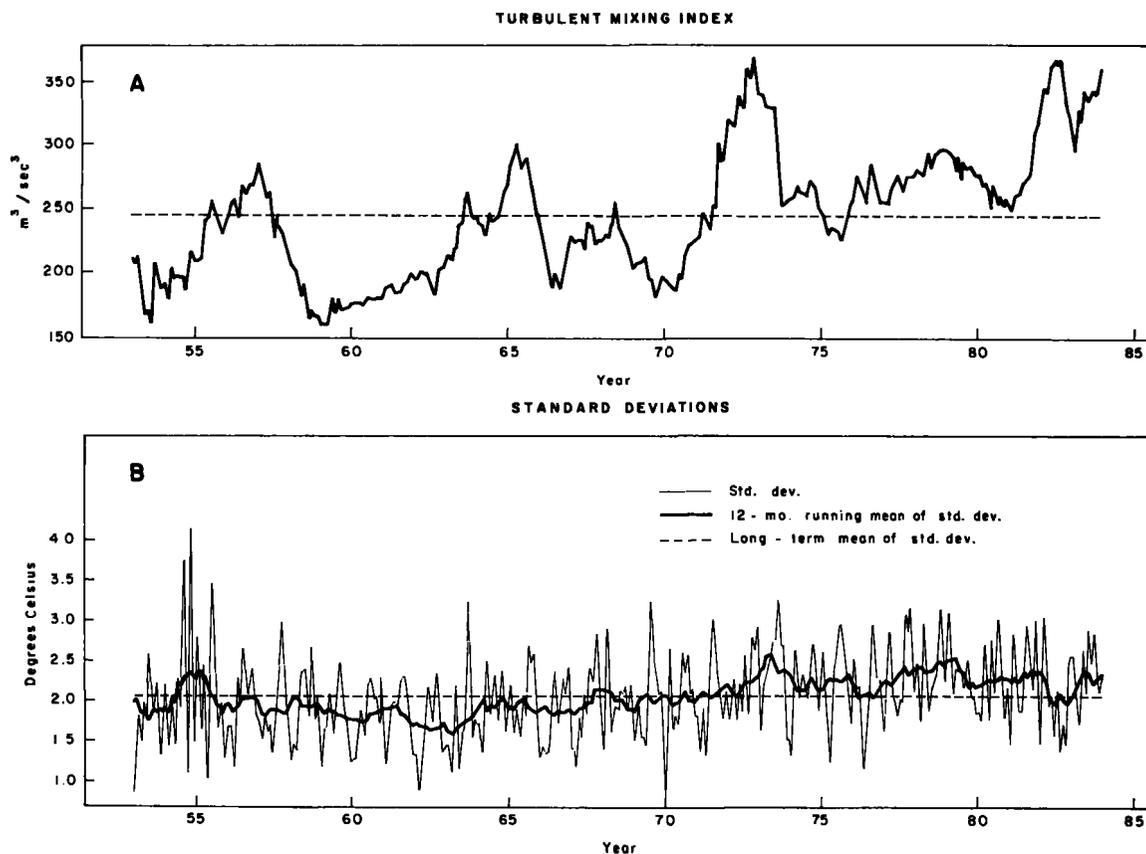


FIGURE 7.—(A) Surface layer turbulent mixing index values and (B) standard deviations and 12-mo running mean of standard deviations associated with mean monthly sea surface temperature values off of Peru ( $5^{\circ}$ – $15^{\circ}$ S), 1953–84. Dotted lines represent long-term mean values of each index. From Bakun 1987.

conditions initiated during the warm 1968–69 period; these could possibly have persisted and intensified again during the 1976 and 1983 El Niño events.

It is also likely that the 1970 change in OL composition is related to onshore advection of northern or oceanic water masses and associated faunal assemblages, but this cannot be confirmed. All involved species are relatively abundant in coastal Peruvian and south eastern tropical Pacific waters (Ahlstrom 1971, 1972; de Castillo 1979; Santander and de Castillo 1979) and in more southern coastal Chilean waters (Table 2), but their wintertime relative abundances in these areas have not been documented. It is also possible that the changes in species composition are related to locally lowered zooplankton abundance (e.g., that the Group II species are relatively more successful than *Lampanyctus parvicauda* and *Triphoturus mexicanus* during periods of lowered secondary productivity levels). Alternatively, the

observed change could be due to altered seasonal spawning activity which is not treated in the present study. However, whatever the cause, there is evidence for an environmental change in the study area, and this may be also implicated in changes occurring within the PL ichthyoplankton fraction.

Increased abundances of sardine and *Myctophum nitidulum* (Pair I species) during and after 1972 may be further evidence for a changed marine environment off of northern Chile. Additionally, the significant correlation between larval sardine abundance and temperature (Table 10) suggests that elevated temperatures may have been important for increased spawning activity and/or increased success of hatching and early larval survival. Given this observation one may speculate that the increased sardine catches after 1973 (Fig. 4) are related to increased frequency of warm-water events in the 1964–84 period relative to earlier years. Increased sardine

catches in 1973 resulted from apparently extremely good survival and recruitment of individuals spawned during the warm 1968–69 period (Serra<sup>3</sup>). Similarly, good survival of the large 1972 El Niño spawn could explain the huge catch increases in 1976 and later years (Fig. 4). However, mean biomass estimates of age groups contributing to the Chilean fisheries catch from 1974 to 1981 (Serra 1983) indicate increasing contributions after the 1967 year class with marked increases beginning with the 1970 year class; this suggests that factors other than temperature (e.g., environmental change starting in 1969–70) may also be responsible for increased larval survival and recruitment. A possible cause is increased nearshore influence of equatorial and subtropical waters (Santander and Flores 1983). Because the sardine abundance increase was initiated prior to the 1972 anchoveta decline off northern Chile (Fig. 4), it is difficult to implicate reduced anchoveta competition as the cause of the early sardine population growth in this area.

The grouping of anchoveta with three coastal species (Group I), and significant correlation of anchoveta and *Normanichthys crockeri* larval abundances are extremely interesting and imply that the spawning intensity and/or early stage survival of these four species are influenced in similar ways by interannual changes off northern Chile. Unfortunately, little is known about the natural histories or population abundances of the coastal species. Because of the group composition, it is logical to suspect that coastal processes are important factors influencing their larval abundance. The significant negative correlation of the group as a whole, and of two of the coastal species, with ranked temperature and salinity values (Table 10), suggests that coastal upwelling and/or increased coastal influence by subantarctic waters, and theoretically enhanced food supplies, are important factors.

Given the present data set and information from recent publications, a case can be made for a low-frequency environmental change influencing the abundances of anchoveta and sardine larvae as well as the larvae of coastal and mesopelagic species during the 1964–84 period. The Chilean OL composition suggests an environmental change (e.g., an atmospherically related oceanic circulation change) starting with the 1968–69 warm-water event. This coincided with apparent

successful survival of sardine larvae and markedly increased recruitment by 1968 and later year classes despite varied warm water-cold water events between 1968 and 1973. Physiological anomalies of Peruvian anchoveta stocks in 1971 suggest that these fishes may have experienced environmental change at that time. Unusually low proportions (e.g., 40% vs. typically 90%) of potential spawning-sized fish were sexually mature during the 1971 spawning season and fat content of the 1971–72 catch was anomalously high, indicating unusually low transfer of body fat to gonadal products (Sharp 1980). Starting with the 1972 El Niño was 1) an obvious increased incidence of penetration of subtropical surface waters toward the Peruvian coast, 2) coincidental onshore and southward expansion of sardine spawning activity off both Peru and Chile, 3) southward expansion of Peruvian anchoveta spawning activity into new spawning areas between 14°S and 18°S (e.g., to northern Chile), and 4) a succession of years of poor anchoveta larval survival off Peru and Chile (Santander and Flores 1983; Serra 1983). Environmental conditions favorable for growth of sardine populations, as well as of mackerel and jack mackerel populations, off both Chile and Peru have persisted since the early to mid-1970's (Santander and Flores 1983; Serra 1983).

The lack of Chilean ichthyoplankton data from the 1974–82 period precludes evaluation of the constancy of altered species composition during that time. However, there are indications that change is once more occurring off northern Chile. Preliminary analysis of ichthyoplankton samples collected between Arica and Antofagasta during 4–14 August 1985 indicates a clear dominance by anchoveta larvae at a markedly higher mean abundance level than encountered in the 1964–83 samples; sardine and *Trachurus* larval abundances are comparable to those in the 1973 samples (Table 14). The other species have not yet been analyzed, but *Normanichthys crockeri* is

TABLE 14.—Mean abundance estimates and standard errors (numbers per 10 m<sup>2</sup>) and percent frequency of occurrence (F) of PL taxa, OL and total larvae collected in 81 100–0 m WP<sub>2</sub> net samples off northern Chile (18°–24°S) during 4–24 August 1985.

| Species                  | $\bar{X}$ | (SE)      | (F)    |
|--------------------------|-----------|-----------|--------|
| <i>Engraulis ringens</i> | 5,535.3   | (1,844.1) | (90.4) |
| <i>Sardinops sagax</i>   | 63.8      | ( 24.9)   | (26.6) |
| <i>Trachurus murphyi</i> | 1.2       | ( 0.9)    | ( 2.1) |
| Other species            | 233.7     | ( 28.4)   | (92.5) |
| Total                    | 5,834.0   | (1,838.2) |        |

<sup>3</sup>Serra, R. Unpubl. manusc. Subsecretaria de Pesca, Teatinos 120, Piso 11, Of. 44, Santiago, Chile.

once again noted to be among the abundant OL taxa. It will be of great interest to see the recruitment resulting from this 1985 anchoveta spawn. If the 1985 anchoveta year class is relatively successful during this period of continued large sardine stocks, it will lend support to the idea that the anchoveta-sardine population fluctuations have been primarily regulated by low-frequency hydrographic events. In a long-term context such events may not be unusual to the Humboldt Current area. Fish scales present in sediment records from coastal Peruvian waters indicate that sardine replacements of typically dominant anchoveta stocks have occurred at infrequent intervals over the past 11,000 years (De Vries and Pearcy 1982). In light of this, the ecological events of the past 20 years may be naturally occurring, physically mediated, but probably fisheries enhanced, fluctuations in this hydrographically complex region. Because of our limited time reference, we have not previously acknowledged such fluctuations as being "normal".

### ACKNOWLEDGMENTS

We extend our appreciation to Dick Parrish and Andy Bakun, Pacific Fisheries Environmental Group (SWFC/NMFS/NOAA), whose interest in eastern boundary current comparison studies has made this work possible. We also thank Rodolfo Serra and Gary Sharp for their valuable comments and discussions of the manuscript. Appreciation is extended to numerous other people including ship captains and crew and laboratory assistants, especially Hernan Miles, who have helped in sample collection and processing over the 20-yr period.

This work was funded by NMFS/NOAA Solicitation WASC-84-00075.

### LITERATURE CITED

- AHLSTROM, E. H.  
1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. *Fish. Bull.*, U.S. 69:3-77.  
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.*, U.S. 70:1153-1242.
- BAKUN, A.  
1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations, 1953-84. In D. Pauly and I. Tsukayama (editors), the anchoveta and its ecosystem, p. 46-74. International Center for Living Aquatic Resources Management (ICLARM), Manila.
- BERNAL, P. A., F. L. ROBLES, AND O. ROJAS.  
1983. Variabilidad fisica y biologica en la region meridional del sistema de corrientes Chile-Peru. *FAO Fish. Rep.* 291:683-711.
- CONOVER, W. J.  
1971. *Practical nonparametric statistics*. John Wiley and Sons, N.Y., 462 p.
- DE CASTILLO, O. S.  
1979. Distribucion y variacion estacional de larvas de peces en la costa Peruana. *Inf. Inst. Mar Peru* 63:1-32.
- DE VRIES, T. J., AND W. G. PEARCY.  
1982. Fish debris in sediments of the upwelling zone off central Peru: a late quarterary record. *Deep-Sea Res.* 28(1A):87-109.
- DIXON, W. J., AND F. M. MASSEY, JR.  
1969. *Introduction to statistical analysis*. McGraw-Hill, N.Y., 638 p.
- GUILLÉN, O.  
1983. Condiciones oceanograficas y sus fluctuaciones el Pacifico sur oriental. *FAO Fish. Rep.* 291:607-658.
- KELLY, R., AND J. L. BLANCO.  
1983. Fluctuaciones ambientales y su relacion con la abundancia de recursos pelagicos en la zona norte-centro de Chile. *Inst. Fom. Pesq.* 830040, 22 p.
- PARRISH, R. H., A. BAKUN, D. M. HUSBY, AND C. S. NELSON.  
1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. *FAO Fish. Rep.* 291:731-777.
- ROBERTSON, A.  
1970. An improved apparatus for determining plankton volume. *Fish. Bull.*, S. Afr. 6:23-26.
- ROBLES, F. L., E. ALARCON, AND A. ULLOA.  
1980. Water masses in the northern Chilean zone and their variations in the cold period (1967) and warm periods (1969, 1971-73). *Proceedings of the workshop on the phenomenon known as "En Niño"*, p. 83-174. UNESCO.
- SAMEOTO, D.  
1980. Distribution and abundance of six species of fish larvae in Peruvian waters and their relationship with the physical and biological environment. *Bol. Inst. Mar Peru Callao* 5:164-170.
- SANTANDER, H., AND O. S. DE CASTILLO.  
1979. El ictioplancton de la costa Peruana. *Bol. Inst. Mar Peru Callao* 4:69-112.
- SANTANDER, H., AND R. FLORES.  
1983. Los desoves y distribucion larval de cuatro especies pelagicas y sus relaciones con las variaciones del ambiente marino frente al Peru. *FAO Fish. Rep.* 291:835-867.
- SERRA, J. R.  
1983. Changes in the abundance of pelagic resources along the Chilean coast. *FAO Fish. Rep.* 291:255-284.
- SHARP, G. D.  
1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. In G. D. Sharp (editor), *Workshop on the effects of environmental variation on the survival of larval pelagic fishes*, Lima, Peru, April-May 1980. Workshop Report No. 28, p. 15-59. Intergovernmental Oceanographic Commission, UNESCO, Paris.
- TATE, M. W., AND R. C. CLELLAND.  
1957. *Nonparametric and shortcut statistics in the social, biological and medical sciences*. Interstate Printers and Publishers, Danville, IL, 171 p.

UNESCO

1968. Zooplankton sampling. Monographs on oceanographic methodology 2. Imprimeries Populaires, Geneva, 174 p.

WHITTAKER, R. H.

1975. Communities and ecosystems. MacMillan Publishing Co., N.Y., 385 p.

WYRTKI, K.

1967. Circulation and water masses in the eastern equatorial Pacific Ocean. *Int. J. Oceanol. Limnol* 1:117-147.

YASHNOV, V. A.

1959. A new model of a volume meter for rapid and precise plankton evaluation under field conditions. *Zool. Zh. (Moscow)* 38:1741-1744.