

DISTRIBUCION VERTICAL Y COMPOSICION DE LAS AGRUPACIONES DE ICTIOPLANCTON Y ZOOPLANCTON DE INVERTEBRADOS EN EL PACIFICO TROPICAL ORIENTAL

VERTICAL DISTRIBUTION AND COMPOSITION OF ICHTHYOPLANKTON AND INVERTEBRATE ZOOPLANKTON ASSEMBLAGES IN THE EASTERN TROPICAL PACIFIC

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RESUMEN

Se describe la composición y distribución vertical del ictioplancton y zooplancton de invertebrados del estrato 0-100 m. en la región NW del Pacífico Tropical Oriental, usando datos de 23 muestras de neuston y 166 muestras estratificadas de redes tipo "bongo". La máxima abundancia del zooplancton de invertebrados (número x 10 m^{-2}) se presenta durante el día en la zona inferior del estrato de mezcla (~ 40 m; definido por XBT) y en la zona superior del estrato de mezcla durante la noche; se presentan también altas concentraciones (número x 1000 m^{-3}) en el neuston tanto en el día como en la noche. La máxima abundancia y diversidad de ictioplancton (número de taxa) se presenta en la parte superior de la termoclina, encontrándose la mayoría de los individuos y especies por debajo de la profundidad de máxima abundancia de los taxa principales de zooplancton de invertebrados. La distribución del ictioplancton de profundidad y la dominancia numérica de las especies que son "habitantes de profundidad" en su fase larval y migradores activos para alimentarse en la superficie en su fase adulta, son únicas y características de esta región y distinguen la fauna de peces del Pacífico Tropical Oriental de aquella del giro central del Pacífico Norte. La estructura del conjunto de peces del Pacífico Tropical Oriental puede ser el resultado en parte de las altas concentraciones de zooplancton observadas en el estrato superficial, el cual provee: (a) de alimento abundante para los adultos migradores activos; y (b) intensa competencia trófica con, y/o predación sobre las larvas del hábitat somero. Las distribuciones de las larvas de peces de hábitat profundo puede también ser resultado en parte de la extrema heterogeneidad en la estructura térmica del estrato de mezcla a través de la región del Pacífico Tropical Oriental.

ABSTRACT

The composition and vertical distribution of ichthyoplankton and invertebrate zooplankton of the upper 100 m of the northwest eastern tropical Pacific have been described using data from 23 neuston and 166 stratified bongo samples. Maximum invertebrate zooplankton abundance (numbers 10 m^{-2}) occurs at the bottom of the mixed layer (~ 40 m; defined by XBT casts) by day, and in the upper mixed layer at night; high concentrations (numbers x 1000 m^{-3}) also occur in the neuston layer both day and night. Maximum ichthyoplankton abundance and diversity (numbers of taxa) occur in the upper thermocline, and most individuals and species occur below the depths of maximum abundance of major invertebrate zooplankton taxa. The deep ichthyoplankton distribution and numerical dominance by species which are "deep living" as larvae and actively migrating "surface" feeders as adults are unique, and distinguish the eastern tropical Pacific fish fauna from that of the North Pacific central gyre. Structure of the eastern tropical Pacific fish assemblage may result in part from high surface layer zooplankton concentrations which provide (a) abundant food for actively migrating adults; and (b) intense food competition with and/or predation upon shallow-living larvae. The deep larval fish distributions may also result in part from extreme heterogeneity in mixed layer thermal structure across the eastern tropical Pacific area.

INTRODUCTION

The eastern tropical Pacific ("ETP") is one of eight major Pacific Ocean ecosystems (McGowan, 1974, 1977). It differs from the

others in its hydrographic complexity. Circulation is zonal rather than gyral, and horizontal and vertical mixing are regionally and seasonally variable. Other unique features of

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the area include a permanent shallow thermocline, widespread regional upwelling, divergence-convergence ridge systems, and a thick, extensive and regionally shallow oxygen minimum zone (Brandhorst, 1958; Wooster and Cromwell, 1958; Wyrki, 1965, 1966, 1967; Tsuchiya, 1968, 1974). Because of the circulation system and extensive upwelling, near-surface nutrient concentrations are high, and support high levels of primary productivity and zooplankton standing stocks throughout the year (Holmes *et al.*, 1957; Reid, 1962; Blackburn *et al.*, 1970; Koblentz-Mishke *et al.*, 1970; Reid *et al.*, 1978).

Despite the hydrographic complexity, the ETP supports distinctive recurring assemblages of zooplankton and fish species, many of which are endemic (Bieri, 1959; Brinton, 1962; Ebeling, 1962, 1967; McGowan, 1974; Barnett, 1975). The distinctive nature of these assemblages is believed to be maintained by high productivity levels, predictability of physical properties, and recirculation of water due to counter current and eddy systems (Ebeling, 1967; McGowan, 1974). Additionally, the oxygen minimum zone may restrict some species horizontal distributions within the area (Ebeling, 1962, 1967; Johnson, 1974; Johnson and Glodek, 1975).

There is much information concerning the biology of the ETP (e.g., primary productivity [Owen and Zeitzschel, 1970]; phytoplankton and zooplankton [Blackburn *et al.*, 1970; Longhurst, 1976]; microzooplankton [Beers and Stewart, 1971]; ichthyoplankton [Ahlstrom, 1971, 1972]; mesopelagic fishes [Robinson, 1973]). Much of this information resulted from the 1967-68 EASTROPAC cruises which are based (as are prior works) on broad-scale sampling surveys, or are restricted to inshore areas. No previous work represents replicated sampling within any one locale.

The present study presents a detailed analysis of zooplankton and ichthyoplankton composition and vertical distribution based on 23 neuston samples and 166 stratified bongo samples collected in one area centered around 13°N, 130°W in the offshore northern portion of the ETP (Figure 1). Here we present vertical distribution information on 17 invertebrate zooplankton categories and 60 larval fish taxa, and compare our results with other work on ETP plankton and fish

assemblages. We also compare the distributions and compositions of these assemblages with those in the North Pacific central gyre ecosystem. We then consider factors possibly influencing overall structure of the ETP pelagic community.

METHODS

Zooplankton samples were collected near 13°N, 130°W (Figure 1) during two cruises conducted by Ocean Minerals Company of Mountain View, California. Forty-three of the 46 sampling sites were within 75 km of this coordinate; the other three were ~ 200 km to the southwest. Twenty-three surface layer (neuston) samples were collected from 7-27 March 1981 using a neuston sampler (mouth area 0.30 m²); fitted with 333 µm mesh net and a General Oceanics flowmeter. Tows lasted 15 min. at ~ 1 kt., and filtered the upper ~ 0.25 m of water; mean volume filtered was ~ 115 m³ per tow. Depth-stratified samples were collected at 23 stations from August 27-September 14, 1980 using open 505 µm mesh bongo nets (0.396 m² mouth area for each net; Scripps Institution of Oceanography, 1966). Volume filtered by each net was estimated using a calibrated flowmeter attached to the frame, and averaged ~ 450 m³. Target sample depth intervals were 0-25 m, 25-50 m, 50-75 m and 75-100 m. Nets were quickly lowered to the desired depth interval (as judged by wire angle and length of wire out), fished horizontally for 15 min. at ~ 2-3 kt., and then retrieved as quickly as possible to minimize in-transit filtration. The actual depths sampled (Figure 2) were monitored by a Marinc time/depth recorder fixed to the frame. These tows provided fairly good coverage of all depths except the upper 10 m of the 0-25 m stratum. Mixed-layer depth (~ 40 m) was determined from XBTs dropped at each bongo-net tow station. Samples were preserved with buffered 10% formalin in sea water.

Sample processing was done by Marine Environmental Consultants (MEC), Solana Beach, California. All fishes and fish eggs were sorted from 23 neuston samples and from 166 bongo samples (one sample = catch of one net on a bongo frame). Larval fishes were identified to the lowest taxon possible and enumerated by P. Jahn (MEC)

and V.J. Loeb. Invertebrate zooplankton samples were diluted to standard 100, 250 or 500 ml volumes, stirred and 5, 10 or 20 ml aliquots (depending on zooplankton concentrations), were pipetted out to provide subsamples for analysis. The major zooplankton components in these subsamples were identified and enumerated; the numbers were multiplied by appropriate factors to provide sample abundance estimates. A total of 23 invertebrate zooplankton taxa were identified. Data from all neuston samples, and 162 of the bongo samples were used for analyses.

The zooplankton and ichthyoplankton data are handled in two ways. (1) Abun-

dances of invertebrate zooplankton taxa and the larval fish category (pooled species) are based on values from individual neuston samples, and on averaged values from paired bongo samples at each station. In six cases, data from only one bongo net were utilized. This approach is used to reduce possible errors resulting from non-replicated subsamples. These abundances are expressed as mean numbers under 10 m² sea surface area (Smith and Richardson, 1979) to permit comparisons between concentrations in shallow (i.e., 25 cm deep) neuston and more vertically extensive (i.e., 25 m) bongo tows, and to provide estimates

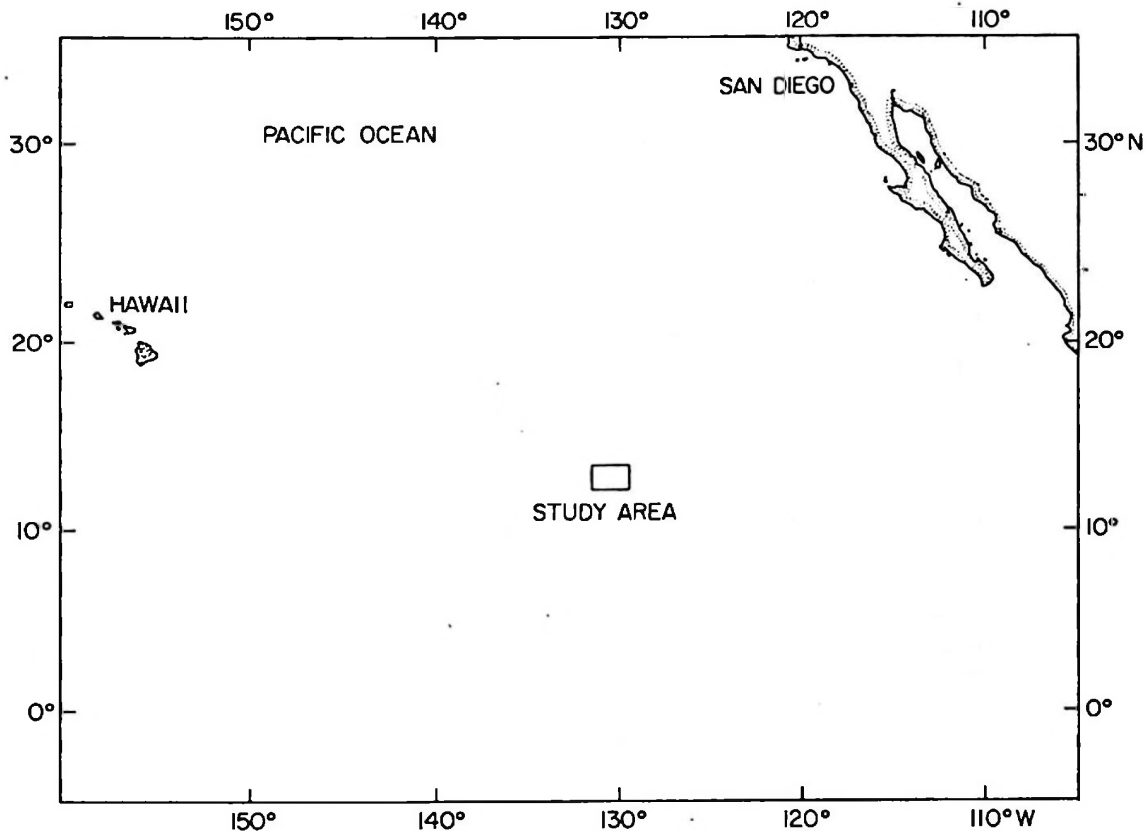


Figure 1. Eastern tropical Pacific sampling area.

of total 0-100 m abundances. The conversion is (numbers per 1000 m³) x (0.0025) for neuston samples, and x (0.25) for bongo samples. (2) Larval fish species abundances are based on values from individual neuston and bongo samples, because the larvae were not subsampled. Species abundances are expressed as mean numbers per 1000 m³ water filtered to provide a format comparable to that used in previous ichthyoplankton as-

semblage analyses (Loeb, 1979-1980a, b). Larval fish diversity is expressed as mean numbers of fish taxa per tow, and as total numbers of fish taxa taken by day and by night within each depth interval.

In both approaches, day and night data are treated separately; tows taken between 1 h before sunrise and 1 h after sunset are considered "day" samples.

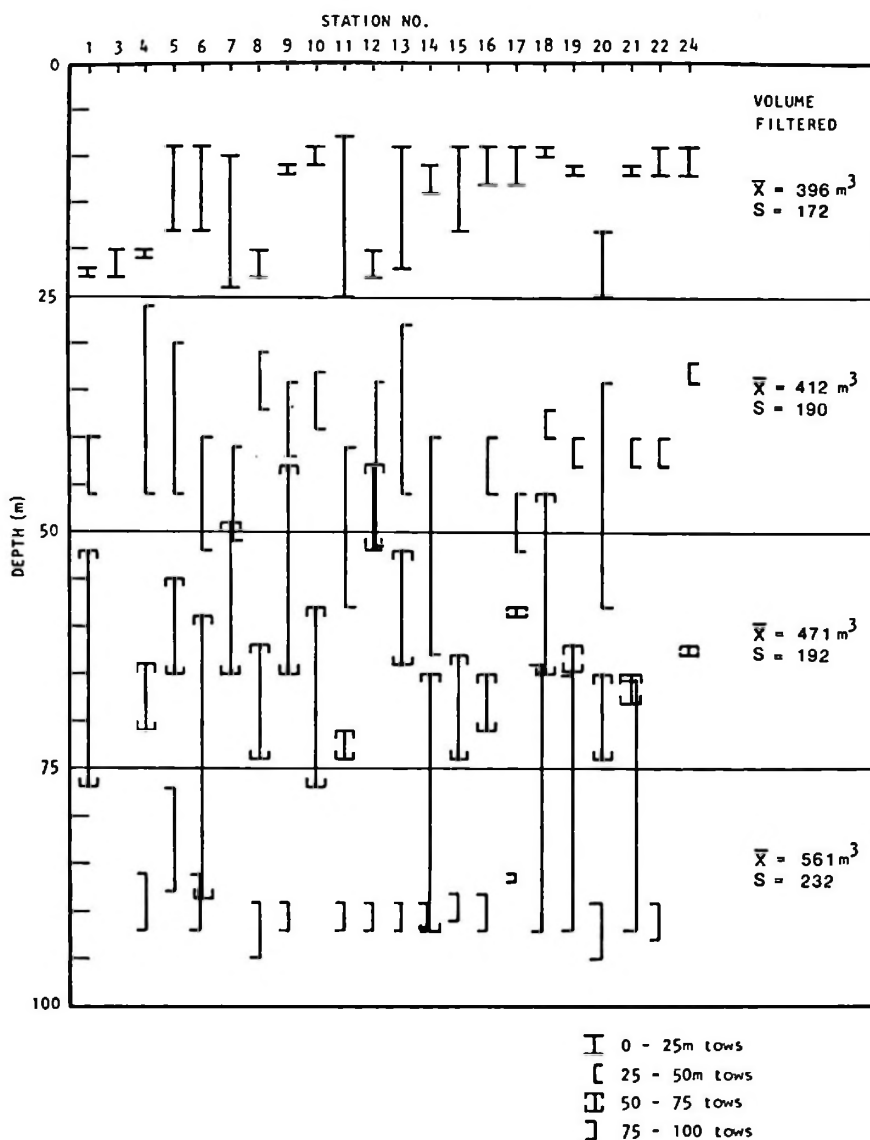


Figure 2. Depth intervals sampled and mean water volume filtered by bongo net tows within four 25 m strata in the eastern tropical Pacific. Actual sample depths monitored by a time-depth recorder fixed to the net frame.

Statistical Analyses

Sample variability due to patchiness within each depth interval is described by an index of dispersion (S^2/\bar{x}) tested against an expected Chi-Square distribution (Pielou, 1977); we consider that $P \leq 0.05$ indicates "significant" aggregation, and $P > 0.05$ implies "randomness". Significance of day-night and between-interval differences in abundance and diversity are determined with Z tests (two-tailed) on sample means and standard deviations (Dixon and Massey, 1969).

Within and between-interval comparisons of ichthyoplankton and zooplankton taxonomic composition are made using Percent Similarity Indices (PSIs; Whittaker, 1975). PSI values compare two taxonomic lists based on relative proportions of individual taxa within each list, and may range from 0 (no taxa in common) to 100 (all taxa and their proportions are identical). PSIs are strongly influenced by abundant taxa. We define as "high" all $PSI > 80$, as "moderate" $60-80$, and as "low" $PSI < 60$. Simpson's diversity index, calculated from individual taxon proportions ($\lambda = \sum Pi^2$) is used here in conjunction with PSI values to show day-night and between-interval differences in larval fish species dominance (Whittaker, 1975). High diversity values indicate dominance by one or a few species; low values indicate more equitable species abundances.

Kolmogorov-Smirnov (K-S) tests (Conover, 1971) are based on the maximum differences between cumulative percent curves for two sets of data. They are used here to identify significant day-night and between-taxon differences in depth distributions based on taxon proportions within each depth interval.

Comparisons of rank order of abundance of taxa between sets of data are made using Kendall's tau and rank difference correlation tests (Tate and Clelland, 1957); both provide correlation coefficients which are measures of similarity between orders of rankings within two data sets.

Data and Sampling Considerations

Although collected during different seasons and with different mesh sizes, neuston and bongo tow data are treated together here to provide generalized abundance and composition information of the surface layer

relative to the rest of the upper 100 m. Seasonal changes in zooplankton and ichthyoplankton abundances in the eastern tropical Pacific are minor; winter abundances of both are 2X the summer value (Blackburn *et al.*, 1970; Ahlstrom, 1972). The smaller neuston net mesh size could increase surface abundance estimates by a factor of ~ 1.6 (see Lenarz, 1972). However, increased avoidance by larger or more agile forms, and erratic depth sampling associated with neuston nets, may cause decreased surface abundance values relative to the bongo samples. Consequently, direct comparisons between the neuston and bongo data sets must be interpreted with caution.

There were varying degrees of overlap in depths sampled by some of the 25-50 m, 50-75 m, and 75-100 m tows (Figure 2); this probably will reduce the significance of differences between abundances and compositions of plankton assemblages within these depth intervals.

Use of open nets in stratified depth sampling may allow significant contamination of deep samples by shallow-living organisms. Although nets were lowered and retrieved quickly to minimize contamination, mean flow volumes (Figure 2) at 50-75 m and 75-100 m were 19% and 42% larger, respectively, than at 0-25 m. These larger volumes may have resulted from depth-related differences in currents or sampling gear characteristics, and/or in-transit filtration. The occasional presence of surface-dwelling larval fish species (i.e., exocoetids and no-meids), and shallow-living species (i.e., *Cyclothone* spp. and *Diplophos taenia*) in deeper samples probably indicates contamination. However, such individuals contributed $< 0.4\%$ of total 50-75 m and 75-100 m larvae, suggesting that such contamination is not a major problem. In-transit filtration will most strongly affect ichthyoplankton abundance and diversity estimates of 75-100 m samples, but is probably less important than the sampling overlap in deep intervals. Zooplankton abundance estimates for both 50-75 m and 75-100 m intervals may be more affected by in-transit filtration than those of ichthyoplankton due to surface layer zooplankton abundance peaks.

Despite these sampling problems, significant between-interval and day-night within-interval differences occur in abundance and composition of both ichthyoplankton and in-

vertebrate zooplankton assemblages. This indicates that patterns of vertical structure within these assemblages are quite pronounced.

RESULTS

Overall Composition of the Zooplankton

Zooplankton of the upper 100 m were numerically dominated by six invertebrate categories: copepods, chaetognaths, euphausiids, siphonophores, larvaceans and amphipods (Table 1). Together, these taxa include 88% of captured individuals. They generally dominated zooplankton assem-

blages within each 25 m depth interval, and included 84-92% of individual zooplankters in each interval, both day and night samples. Larval fishes ranked seventh in overall abundance (2% of total individuals). Pteropods, ostracods, thaliaceans, and decapods (ranks 8-11) were also common zooplankters in each depth interval, both day and night. At night, mysids were the second most abundant taxon in the neuston layer (15% of individuals); they were rare or absent at all other depths. Copepods were consistently the most abundant category both day and night, and contributed 40-71% of total individuals within all five depth intervals. Ranks and percentages of other taxa varied with depth and time of day (Figure 3).

TABLE 1

Plankton categories collected in the upper 100 m of the eastern tropical Pacific. Total day and night abundances are mean numbers of individuals per 10 m² sea surface from pooled bongo and neuston tow data.

Overall Rank	Taxon	Total Abundance		Abundance				Night:
		N ^o 10 m ⁻²	%	Day N ^o 10 m ⁻²	%	Night N ^o 10 m ⁻²	%	Day Ratio
1	Copepod	14,233	51.45	16,021	54.94	12,445	47.57	0.78
2	Chaetognath	4,400	15.91	5,129	17.59	3,671	14.03	0.72
3	Euphausiid	2,196	7.94	775	2.66	3,617	13.82	4.67
4	Siphonophore	1,549	5.60	1,582	5.43	1,515	5.79	0.96
5	Larvacean	1,226	4.43	1,377	4.72	1,075	4.11	0.78
6	Amphipod	923	3.34	1,327	4.55	519	1.98	0.39
7	Larval fish	608	2.20	529	1.81	687	2.62	1.30
8	Pteropod	522	1.89	511	1.75	533	2.04	1.04
9	Ostracod	492	1.77	427	1.46	556	2.12	1.30
10	Thaliacean	485	1.75	597	2.05	373	1.42	0.62
11	Decapod	350	1.27	266	0.91	434	1.66	1.63
12	Crustacean larva	206	0.74	192	0.66	220	0.84	1.15
13	Cephalopod	140	0.51	84	0.29	197	0.75	2.35
14	Heteropod	132	0.48	139	0.48	126	0.48	0.91
15	Medusa	76	0.27	91	0.31	60	0.23	0.66
16	Polychaete	64	0.23	81	0.28	47	0.18	0.58
17	Mysid	40	0.14	1.1		79	0.30	71.82
18	Echinoderm	16	0.06	22	0.08	11	0.04	0.50
19	Gastropod	2		4	0.01			
20	Cladocera	1.8		1.5		2.2		1.47
21	Turbellaria	0.2		0.1		0.4		4.0
22	Nudibranch	0.14		0.06		0.22		3.67
23	Ctenophore	0.03		0.06				
24	Salp	0.02		0.05				
Total zooplankton:				29,156		26,168		0.90

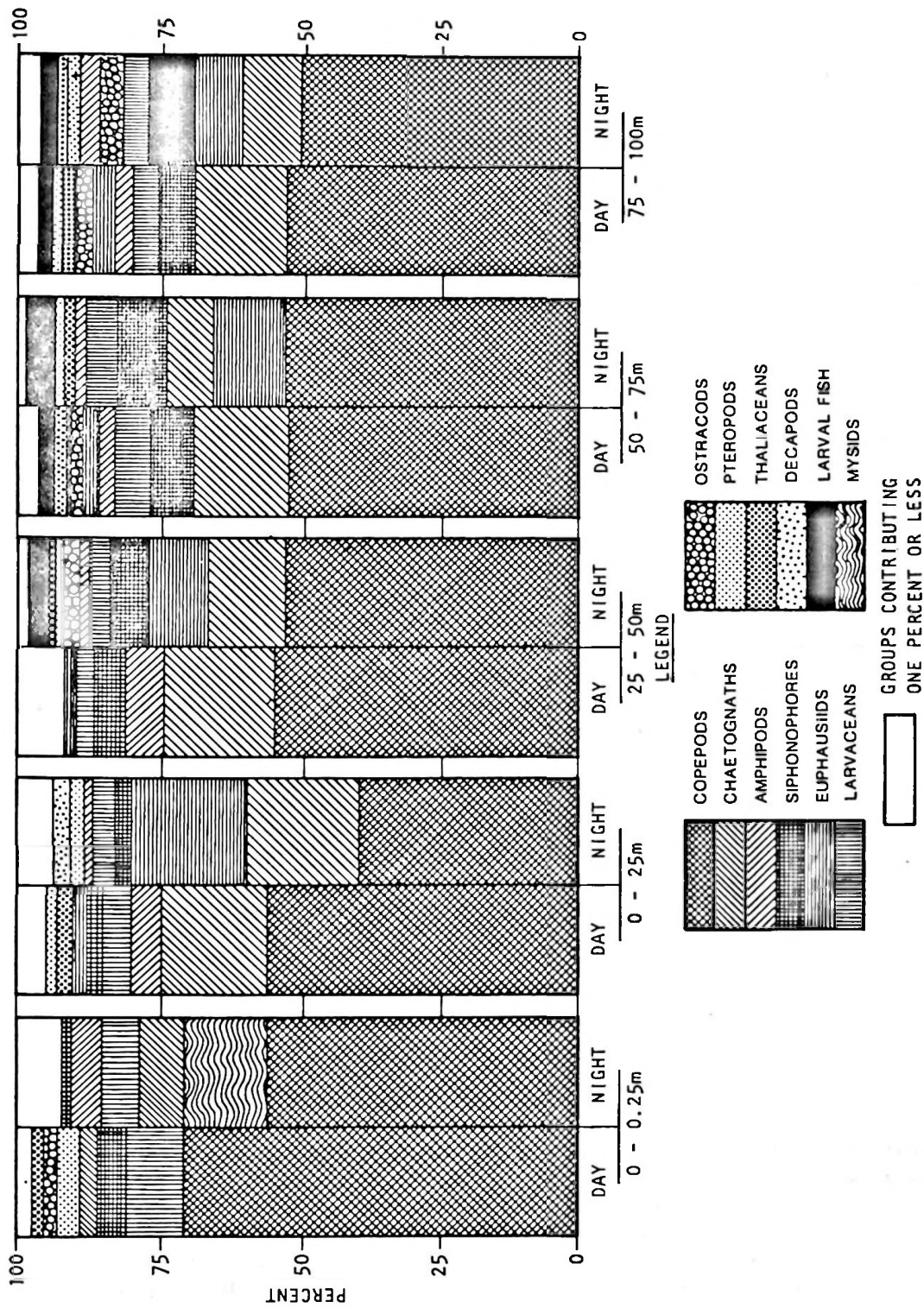


Figure 3. Relative proportions of major zooplankton taxonomic categories collected in day and night samples of the neuston layer, and four 25 m depth intervals in the eastern tropical Pacific.

Vertical Distribution and Abundance of the Invertebrate Zooplankton

Day and night vertical distributions of invertebrate zooplankton are presented in Figure 4. Tow-to-tow abundances varied widely within each depth interval, and standard deviations are large (Table 2). Index of dispersion values (S^2/\bar{x}) based on concentrations are also large, and indicate a high degree of aggregation or patchiness within each depth interval. The most extreme patchiness occurred at night within the neuston layer and 0-25 m interval. The most even distributions occurred at 75-100 m during day, and 25-50 m at night.

Despite sample variability, statistically significant ($P < 0.001$) increases in abundance occurred within the neuston layer at night, and at 25-50 m during the day. Moderate

night vs day abundance increases occurred at 0-25 m, and minimal decreases occurred at 50-75 m and 75-100 m (Table 2).

Mean zooplankton concentrations (numbers 1000 m^{-3}) in the neuston layer were 1.8-2.7 times larger by day, and 5.7-10.8 times larger by night than those in deeper intervals. However, zooplankton numbers per 10 m^2 sea surface area represented in this 0.25 m layer were minimal compared to those in the 25 m intervals (Table 2). At most, 2% of total invertebrate individuals were present in the neuston layer at night. Maximum day zooplankton abundance ($> 32\%$) occurred at 25-50 m in association with the bottom of the mixed layer ($\sim 40 \text{ m}$), and maximum night abundance ($> 36\%$) was at 0-25 m. Total 0-100 m day abundance was 10% higher than night abundance, but the difference was not significant.

TABLE 2

Day and night abundance estimates for invertebrate zooplankton collected in five depth intervals in the eastern tropical Pacific. Abundances expressed as means and standard deviations of numbers of zooplankton (23 categories combined) per 10 m^2 sea surface area, and percent of total 0-100 m zooplankton represented in each depth interval. N = numbers of single neuston samples and paired bongo net tows used for abundance estimates. Significance of day-night abundance differences based on Z tests (two-tailed).

Depth Interval (m)	Day				Night				Night: Day Ratio	Significance Level
	N	\bar{X}	S	%	N	\bar{X}	S	%		
0-0.25	14	164	120	0.6	9	540	228	2.1	3.3	$P < 0.001$
0-25	15	5960	4111	20.8	8	9368	7020	36.8	1.6	N.S.
25-50	14	9253	3218	32.3	7	5117	1568	20.1	0.6	$P < 0.001$
50-75	12	7250	3131	25.3	8	5437	2450	21.3	0.7	N.S.
75-100	11	6000	2284	21.0	6	5019	3204	19.7	0.8	N.S.
Total		28,627				25,481			0.9	

Vertical Distribution and Abundance of Invertebrate Zooplankton Categories

Marked differences in day-night and between-interval abundances occur among various zooplankton taxa (Table 3). Copepods, chaetognaths, larvaceans, amphipods, decapods, medusae, and mysids had significantly higher ($P < 0.01$) night than day abundances in the neuston layer. Night abundances were significantly lower ($P < 0.05$) than day abundances at 25-50 m for

copepods, chaetognaths and amphipods, at 50-75 m for chaetognaths, and at 75-100 m for chaetognaths and decapods. Euphausiids had higher night vs. day abundances in all 25-m intervals ($P < 0.05$). Additionally, marked day-night differences occurred in total 0-100 m abundances of several taxa (Table 1): night $>$ day for euphausiids (4.7 X), mysids (7.2 X), cephalopods (2.4 X), and decapods (1.6 X); day $>$ night (2.6 X) for amphipods.

TABLE 3.

Day and night distributions of 17 zooplankton taxa in five depth intervals in the eastern tropical Pacific. Abundances expressed as percent of total day and of total night abundance within each depth interval. Asterisks indicate significantly larger day or night values based on Z test comparisons of abundance within each depth interval: *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001.

Taxon	Day/ Night	Percent of Total				
		0-0.25 m	0-25 m	25-50 m	50-75 m	75-100 m
Copepod	D	0.7	21.0	33.5***	24.7	20.1
	N	2.4***	30.6	22.5	23.3	21.2
Chaetognath	D	0.1	21.4	34.9***	24.6**	19.0*
	N	1.1***	51.1	19.5	13.3	15.0
Euphausiid	D	—	21.2	28.5	27.2	23.1
	N	0.1***	52.3**	14.4*	20.4***	12.9*
Siphonophore	D	0.5	12.1	28.6	33.7	25.1
	N	0.8	20.7	25.0	29.2	24.3
Larvacean	D	1.2	22.6	21.7*	36.0	18.5
	N	3.1**	36.3	15.1	25.0	20.6
Amphipod	D	0.02	25.3	36.3**	14.8	23.6
	N	5.7**	24.8	13.6	20.6	35.3
Larval Fish	D	0.04**	3.5	24.4	43.6	28.4
	N	0.01	8.8***	25.2	39.1	26.9
Pteropod	D	1.4	22.6	27.5	25.7	22.9
	N	1.0	48.6	15.1	15.6	19.6
Thaliacean	D	0.5	29.7	22.2	21.7	25.8
	N	1.1	23.3	22.6	28.0	24.9
Ostracod	D	0.9	0.6	22.5	26.6	49.4
	N	0.02	4.0	41.7	14.6	39.6
Decapod	D	0.2	28.8	22.9*	22.7	25.5**
	N	1.2***	83.1	4.9	6.6	4.2
Medusa	D	1.0	15.6	32.2	24.1	27.1
	N	15.0***	32.2	18.1	13.8	21.0
Crustacean Larva	D	0.2	15.9	42.1	30.3	11.4
	N	0.3	44.6	12.7	17.9	24.4
Cephalopod	D	—	22.0	33.9	22.8	21.3
	N	0.2	15.7	7.4	47.1	29.7
Heteropod	D	0.01	21.6	31.4	26.6	20.4
	N	—	54.1	0.8	29.7	15.4
Polychaete	D	0.02	26.4	22.4	24.7	26.5
	N	4.9	41.9	—	36.6	16.6
Mysid	D	3.7	—	96.3	—	—
	N	100**	—	—	—	—

In several cases, marked day-night abundance differences were associated with changes in vertical distributions. Maximum daytime copepod and chaetognath abundances were at 25-50 m; at night, maximum abundances of copepods, chaetognaths, and euphausiids occurred at 0-25 m. The abun-

dance shifts of these three dominant taxa are responsible to a great extent for the substantial day-night differences in total zooplankton distribution (Figure 4). Vertical distribution changes of chaetognaths and euphausiids are reflected in significant day-night differences in their proportions

within depth intervals (Table 3; K-S test, $P < 0.05$ in both cases). Decapods, medusae, heteropods, crustacean larvae, cephalopods, and mysids also had significantly different day and night vertical profiles (K-S tests, $P < 0.05$ in all cases). These differences were (except for cephalopods) due to larger proportions within the upper 25 m at night than during the day. Such distribution shifts suggest diel vertical migrations.

Vertical Distribution and Abundance of the Ichthyoplankton

Unlike many zooplankton taxa, larval fishes were relatively rare in the shallower depths: abundances were insignificant in the neuston (0.02% of total larvae), and only

6.5% of total larvae occurred at 0-25 m. Most larvae ($> 66\%$) were caught below the mixed layer with maximum abundance ($> 39\%$) at 50-75 m within the upper thermocline (Figure 5).

Ichthyoplankton abundances estimates varied widely (4-21 fold) among day and night tows within each interval (Figure 5). Resulting large indices of dispersion indicate significant ($P < 0.01$) horizontal and vertical patchiness throughout the upper 100 m.

Day-night ichthyoplankton catch differences were minor. Overall 0-100 m night: day abundance ratio was 1.3:1 (Table 4). Within the neuston, mean abundances were significantly larger ($P < 0.05$) during day than night. Night abundance estimates exceeded day values for all four deeper inter-

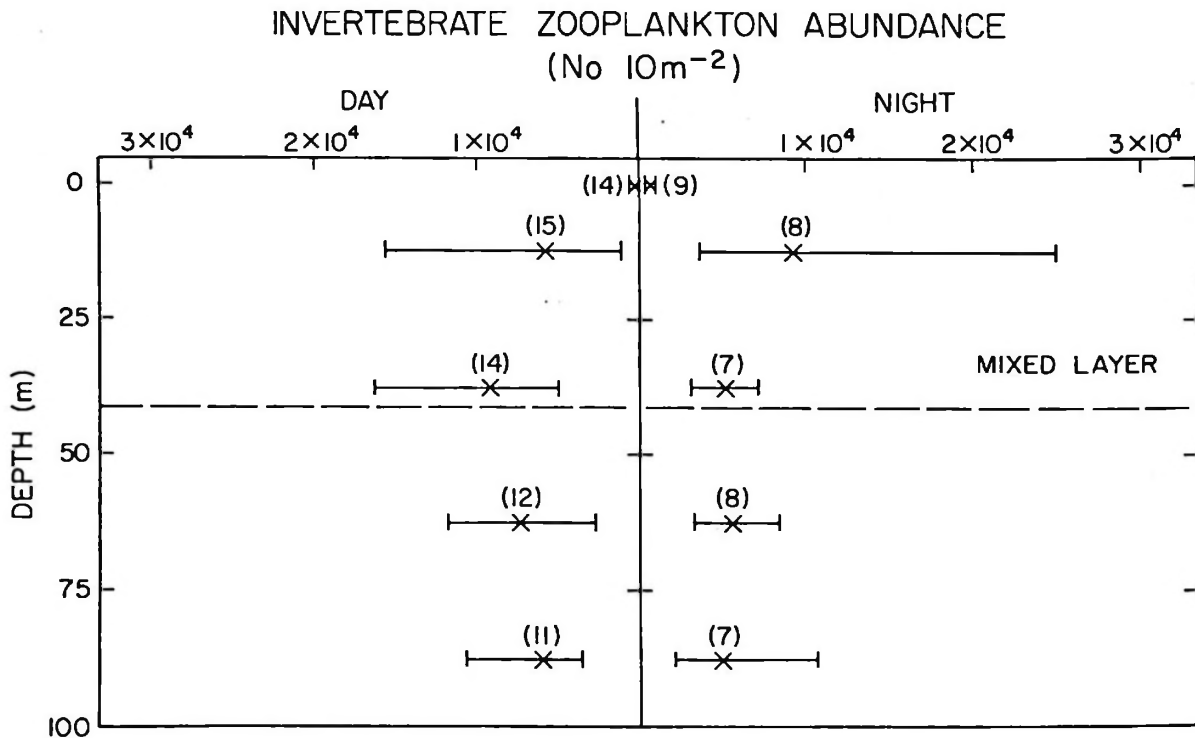


Figure 4. Day and night vertical distribution of invertebrate zooplankton as mean (\bar{x}) and range (horizontal line) of numbers per $10 m^2$ sea surface area. (N) is number of tows represented.

vals, but the difference was significant ($P < 0.05$) only at 0-25 m. Unlike many of the other zooplankton categories (Table 3), there were no marked day-night differences in proportions of the total ichthyoplankton between depth intervals (i.e., no obvious

overall diel migration). However, individual species did show significant diel changes in abundance and proportions within each depth interval, possibly resulting from diel changes in net avoidance and/or vertical migration.

TABLE 4.

Day and night abundance estimates for larval fishes collected in five depth intervals in the eastern tropical Pacific. Abundances expressed as means and standard deviations of numbers per 10 m^2 sea surface area, and percent of total 0-100 m larval fishes represented in each depth interval. N = numbers of single neuston samples, and paired bongo net tows used for abundance estimates. Significance of day-night abundance differences based on Z test (two-tailed).

Depth Interval (m)	Day				Night				Night: Day Ratio	Significance Level
	N	\bar{X}	S	%	N	\bar{X}	S	%		
0- 0.25	14	0.20	0.12	0.04	9	0.08	0.10	0.01	0.4	$P < 0.05$
0- 25	15	18.6	14.6	3.5	8	60.4	46.2	8.8	3.2	$P < 0.05$
25- 50	14	129.2	98.0	24.4	7	173.0	142.6	25.2	1.3	N.S.
50- 75	12	230.2	180.7	43.5	8	269.0	128.6	39.1	1.2	N.S.
75-100	11	150.4	63.0	28.5	7	184.8	114.4	26.9	1.2	N.S.
Total Larvae		528.6				687.3			1.3	

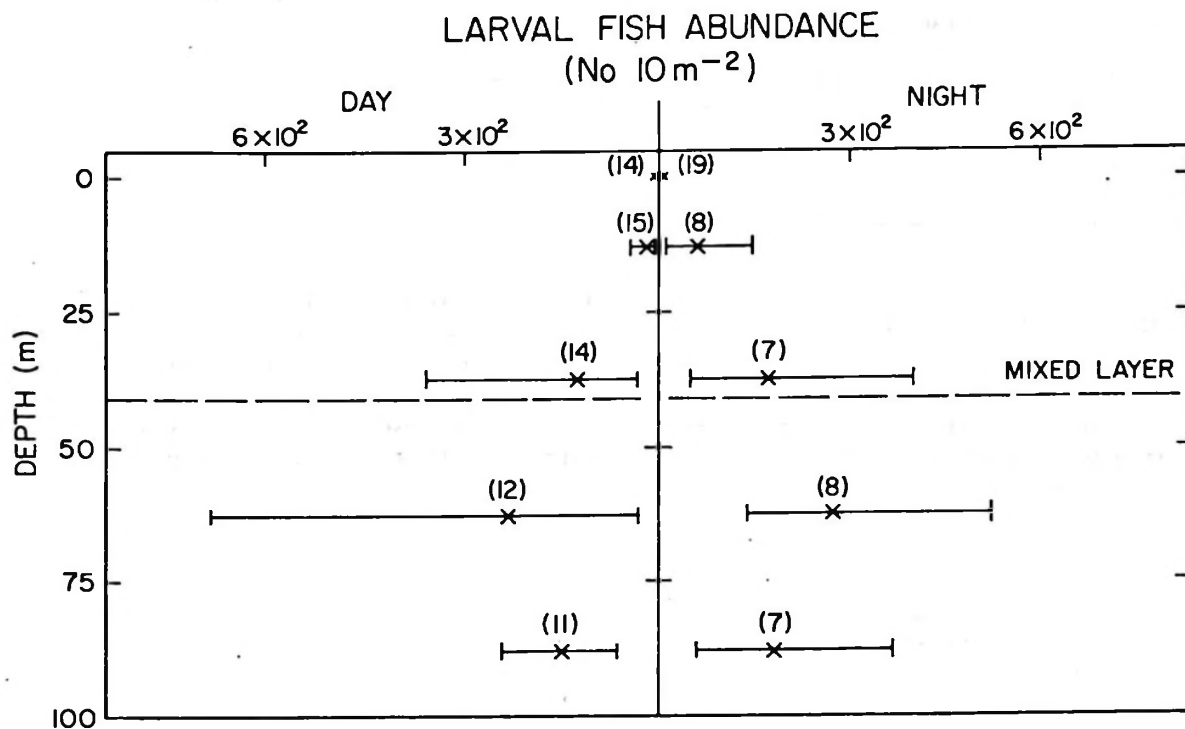


Figure 5. Vertical distribution of ichthyoplankton as mean (x) and range (horizontal line) of numbers per 10 m^2 sea surface area. (N) is number of tows represented.

Larval fishes comprised only 2% of the total 0-100 m zooplankton assemblage (Table 1). However, due to differences between ichthyoplankton and invertebrate zooplankton vertical distributions, the relative importance of ichthyoplankton varied with depth (Table 5). Larval fishes contributed 0-0.5% of the zooplankton in neuston samples, and 0.07 to 2.8% in 0-25 m tows.

The relative abundance of larval fishes at the three deeper intervals was greater; proportions ranged from 0.20 to 6.5% (day), and from 0.53 to 13.7% (night) of total zooplankton per tow. Highest mean percentages (3.1 and 4.7%) occurred at the 50-75 m depth of maximum ichthyoplankton abundance. Here, larval fishes were the fifth most abundant taxon.

TABLE 5.

Relative abundance of ichthyoplankton within total zooplankton (23 taxa combined) in upper 100 m of the eastern tropical Pacific. Abundance relations are as ranges and means of ichthyoplankton percentage contribution to zooplankton caught in day and night tows within five depth intervals, and as overall relative rank of mean ichthyoplankton abundance. Rank difference correlation coefficients (R.D. Corr.) for each depth interval (calculated from individual neuston sample and mean bongo tow rankings of total invertebrate zooplankton and ichthyoplankton abundances) indicate spatial and temporal relationships between these two plankton categories.

Depth Interval (m)	Day Percent of Total			R.D. Corr.	Night Percent of Total			R.D. Corr.
	Range	Mean	Rank		Range	Mean	Rank	
0- 0.25	0.00-0.46%	0.15%	12	+0.09	0.00- 0.04%	0.01%	17	+0.15
0- 25	0.12-1.0	0.31	12	+0.51	0.07- 2.8	0.6	9	-0.69
25- 50	0.20-4.7	1.4	9	+0.02	0.78- 9.5	3.3	6	+0.25
50- 75	0.42-6.5	3.1	5	+0.57	1.6 -13.7	4.7	5	-0.60
75-100	1.2 -5.0	2.5	9	+0.44	0.53- 7.1	3.4	8	-0.09
Overall 0-100		1.8%	8			2.6%	6	

Ichthyoplankton Composition

Neuston ichthyoplankton (232 larvae, 23 samples) included 12 taxa (Table 6), all but one of which (*Oxyphorhamphus micropterus*) were also represented in bongo samples.

Epipelagic forms dominated: flying fishes (Exocoetidae) were the most abundant (76.8%); two epipelagic stromatioid families (Nomeidae; Coryphaenidae) contributed 13.2%. Five mesopelagic families contributed only 10% of total neuston larvae.

TABLE 6.

Composition and abundance of ichthyoplankton collected in 23 neuston tows in the eastern tropical Pacific. Abundances of each taxon expressed as means and standard deviations of numbers per 1000 m³ by day and night, and as total numbers per 1000³ based on mean of day and night values. The percent contribution by each taxon to the total ichthyoplankton is also provided.

Taxon	Total Abundance N° 1000 m ⁻³	Percent of Total	Day		Night	
			x	(S)	x	(S)
Gonostomatidae						
<i>Cyclothone</i> spp.	0.4	0.7			0.8	(2.3)
<i>Diplophos</i> spp.	0.4	4.4			4.8	(11.9)
<i>Vinciguerria lucetia</i>	0.4	0.7			0.8	(2.3)
Astronesthidae						
Unid. Astronesthid	0.4	0.7			0.8	(2.3)
Ceratioid fishes						
Unid. Ceratioid	0.5	0.9	1.0	(2.6)		
Exocoetidae						
<i>Cypselurus</i> sp.	24.6	45.0	46.4	(33.9)	2.7	(5.7)
<i>Oxyphorhamphus micropterus</i>	16.4	30.0	29.1	(22.3)	3.6	(7.1)
Unid. Exocoetids	1.0	1.8				
Coryphaenidae						
<i>Coryphaena</i> sp.	0.8	1.5	0.7	(2.7)	1.0	(2.7)
Chiasmodontidae						
Unid. Chiasmodontid	0.9	1.6			1.8	(3.6)
Gempylidae						
<i>Gempylus serpens</i>	0.5	0.9			1.0	(3.0)
Nomeidae						
<i>Cubiceps paucerradiatus</i>	6.4	11.7			12.8	(35.8)
Unidentified Larvae			4.4		1.8	
Total Larvae			77.7		33.6	
Number of Samples			14		9	

Ichthyoplankton collected in bongo samples (45,221 larvae, 166 samples) included 59 taxa (26 families and three higher categories; Table 7). In contrast to the neuston, mesopelagic fishes dominated, with over 95% of the larvae coming from the mesopelagic families Gonostomatidae (78.3%) and Myctophidae (16.6%). The eight next most abundant families were the mesopelagic Scopelarchidae (1.2%), Paralepididae (1.0%), Bathylagidae (0.9%), Idiacanthidae (0.7%), Bregmacerotidae

(0.3%), Melamphaeidae (0.2%), Gempylidae (0.1%), plus the epipelagic Scombridae (tunas; 0.1%). Larvae of the remaining 16 families and three higher taxa contributed only 0.7% of the total.

Overall species diversity (total numbers of species) was low and numerical dominance by a few species was high. Four species contributed 91% of all larvae (*Vinciguerria lucetia*, *Diogenichthys laternatus*, *Symbolophorus evermanni* and *Diaphus pacificus* [?]). *Vinciguerria lucetia* dominated (77% of total) and

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	Range	Mean	Rank		Range	Mean	Rank	
0- 0.25	0.00-0.46%	0.15%	12	+0.09	0.00- 0.04%	0.01%	17	+0.15
0- 25	0.12-1.0	0.31	12	+0.51	0.07- 2.8	0.6	9	-0.69
25- 50	0.20-4.7	1.4	9	+0.02	0.78- 9.5	3.3	6	+0.25
50- 75	0.42-6.5	3.1	5	+0.57	1.6 -13.7	4.7	5	-0.60
75-100	1.2 -5.0	2.5	9	+0.44	0.53- 7.1	3.4	8	-0.09
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			\bar{x}	(S)	\bar{x}	(S)
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Chiasmodontidae						
Unid. Chiasmodontid	0.9	1.6			1.8	(3.6)
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Total Larvae			77.7		33.6	
Number of Samples			14		9	

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TABLE 7

Taxon	Total Abundance N° 1000 m ⁻³	Percent of Total	0-25 m				25-50 m				50-75 m				75-100 m				
			Day		Night		Day		Night		Day		Night		Day		Night		
			\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	\bar{x}	(S)	
BATHYLAGIDAE																			
<i>Bathylagus virgatus</i>	30.8	0.90			0.4	1.7			2.0	6.6			22.9	(42.5)	16.4	(30.8)			
GONOSTOMATIDAE																			
<i>Gonostoma</i> spp.	19.7	0.85	10.5	(12.6)	12.4	(15.6)	2.8	(3.4)	1.9	(3.2)	2.7	(3.4)	1.7	(2.4)	2.1	(3.0)			
<i>Diplophus tenuis</i>	8.5	0.37	4.6	(4.7)	6.5	(8.0)	1.6	(2.5)	0.8	(1.3)	1.1	(1.2)	1.2	(2.8)	0.1	(0.5)			
<i>Vinciguerra</i> sp.	1780.8	77.10	40.8	(54.5)	199.9	(188.5)	467.2	(394.9)	574.1	(515.2)	614.9	(643.3)	850.2	(556.8)	522.2	(395.0)			
STERNOPTYCHIDAE																			
<i>Argyrops</i> sp.	0.2														0.4	(1.6)			
STOMATOID FISHES																			
Unid. Stomatoids	1.5	0.06			0.2	(0.7)	0.4	(0.9)	1.0	(2.0)	0.4	(1.1)	0.2	(0.8)	0.1	0.5	0.7	1.9	
ASTRONESTHIDAE																			
Unid. Astronesthid	0.2													0.1	(0.7)	0.2	0.7		
IDIACANTHIDAE																			
<i>Idiacanthus</i> sp.	16.0	0.69			0.7	(2.8)			3.0	(9.0)	0.4	(1.0)	14.4	20.8	15.5	26.4			
MELANOSTOMIATIDAE																			
<i>Balophthalmus filifer</i>	4.0	0.17			2.6	(4.9)	2.6	(4.9)	2.6	(5.5)	1.5	(2.6)	0.7	(1.0)	0.6	1.1	0.1	0.3	
<i>Eutoniscus</i> sp.	0.05				0.1	(0.7)													
Unid. melanostomiatid	0.2																		
CHLOROPHTHALMIDAE																			
Unid. Chlorophthalmid	0.06																	0.1	(0.5)
PARALEPIDIDAE																			
Type A	2.8	0.12			1.4	(4.8)	1.4	(4.8)	1.5	(2.3)	0.7	(2.4)	0.6	(1.1)	0.6	(2.8)	1.0	(2.5)	
Type B	5.6	0.24	0.3	(1.6)	0.3	(0.7)	0.3	(1.1)	1.6	(3.1)	2.2	(4.0)	4.1	(4.7)	1.3	(2.6)	1.2	(1.8)	
<i>Stenomacrus macrura</i>	12.5	0.54			1.7	(3.4)	1.7	(3.4)	7.5	(5.9)	4.8	(5.4)	6.6	(7.2)	1.8	(2.5)	2.1	(1.9)	
Unid. Paralepidids	1.9	0.08			0.6	(1.6)			0.7	(1.3)	0.3	(1.0)	1.5	(1.8)	0.2	(0.7)	0.3	(0.8)	
EVERMANNELLIDAE																			
Unid. Evermannellid	0.05				0.1	(0.5)													
SCOPELARCHIDAE																			
<i>Scopelarchoides nicholsi</i>	27.5	1.18			0.3	(0.8)	0.4	(1.3)	8.8	(21.3)	7.6	(11.4)	25.4	(22.5)	12.1	(11.7)			
NOTOSUDIDAE																			
Unid. Notosudid	0.1				0.2	(0.6)													
MYCTOPHIDAE																			
S.F. LAMPANCTINE-																			
<i>Bolimichthys</i> sp.	3.1	0.13	2.1	(4.5)	1.7	(3.2)	1.6	(5.1)	0.4	(1.0)	0.4	(0.9)	0.1	(0.3)			1.6	(4.6)	
<i>Geraiscopus</i> sp.	1.9	0.08	0.1	(0.4)	0.3	(0.9)			1.8	(6.5)							14.2	(17.0)	
<i>Diaphus</i> (prob. <i>parvicus</i>)	58.4	2.53	0.4	(1.0)	1.1	(1.8)	22.2	(29.1)	19.5	(19.4)	26.7	(48.0)	27.7	(19.0)	5.0	(6.0)	1.9	(3.4)	
<i>Lampargyreus idonigra</i>	3.7	0.16			0.2	(0.6)			0.2	(0.6)	1.8	(4.2)	1.5	(4.2)	2.2	(2.4)	0.3	(0.8)	
<i>L. ornata</i>	2.4	0.10			2.3	(6.9)	2.3	(6.9)	0.6	(0.8)	1.0	(2.6)	0.2	(0.7)	0.3	(0.8)	0.6	(2.4)	
<i>L. parvicus</i>	7.2	0.31	1.2	(3.0)	0.8	(1.9)	2.8	(3.7)	2.9	(3.2)	2.6	(4.0)	1.7	(1.9)	1.2	(3.0)	1.2	(1.5)	
<i>Lampargyreus</i> spp.	2.4	0.16			0.1	(0.4)	0.3	(1.1)					1.2	(1.8)			3.3	(8.9)	
S.F. MYCTOPHINAE																			
<i>Bruchoeris</i> sp.	0.2																		
<i>Diogenichthys laermatus</i>	184.3	7.98	1.2	(2.6)	0.9	(2.8)	0.4	(1.2)	1.0	(2.3)	56.3	(164.8)	45.6	(93.1)	177.7	(125.0)	86.7	(66.6)	
<i>Goniichthys lunisculus</i>	3.8	0.16			0.1	(0.5)	0.1	(0.3)	1.7	(4.2)	1.8	(3.7)	2.2	(4.0)	1.9	(2.7)	7.8	(6.4)	
<i>Hypophthalmus atretum</i>	6.5	0.28			0.1	(0.3)	4.3	(6.6)	1.9	(3.6)	12.0	(13.8)	13.7	(12.5)	9.2	(10.5)	5.0	(6.9)	
<i>H. prasinum</i>	23.0	1.00			0.7	(1.4)	2.2	(4.1)	1.5	(5.0)	0.1	(0.6)					1.7	(2.6)	
<i>Myciophthalmus auroblattarum</i>	7.2	0.31															0.2	(0.7)	
<i>M. nidulium</i>	0.2																0.1	(0.5)	
<i>Myciophthalmus</i> spp.	0.3	0.01			0.2	(0.9)	1.1	(2.9)	3.0	(7.5)	34.1	(41.2)	26.8	(30.0)	53.5	(51.1)	0.3	(0.9)	
<i>Synalphegurus covvmani</i>	78.8	3.41	0.3	(1.0)	0.2	(0.9)	0.1	(0.3)	0.2	(0.6)							39.0	(52.6)	

was also the most abundant species both day and night within all 25 m intervals (Table 8). *Diogenichthys laternatus* was second in overall abundance (8%); *S. evermanni* and *D. pacificus* (?) were third (3.4%) and fourth (2.5%), respectively. *Scopelarchoides nicholsi* and *Hygophum proximum* (ranks 5 and 6) each constituted 1% of total larvae. A number of other species, although rare relative to total ichthyoplankton, were abundant within one or more depth intervals (Table 8).

Diversity increased with depth, with

greatest numbers of taxa represented at 75-100 m at night (Table 9). These diversity increases are associated with increased volume filtered with depth (Figure 2), and could result from in-transit contamination. However, neither day nor night samples within each interval yielded significant correlations between volume filtered and larval diversity (rank difference correlation coefficients [-0.19 — + 0.37]; $P > 0.05$ in all cases), suggesting that these diversity patterns are real. Species dominance relations

TABLE 8

Day-night abundance differences of the most abundant larval fish taxa in five depth intervals in the eastern tropical Pacific. Abundances expressed as relative rank of numbers per 1000 m³, and percentage of the total ichthyoplankton at each depth by day and by night for the six most abundant taxa in neuston samples, and the ten most abundant species in bongo samples. Significant day-night catch differences based on data provided in Tables 6 and 7 (Z test, two-tailed; only significant Z-values are indicated).

Taxon	DAY		NIGHT		Night: Day Ratio	Probability Level
	Rank	% of Total	Rank	% of Total		
0-0.25 m						
<i>Cypselurus</i> sp.	1	60.1	4	8.4	0.06	P<0.01
<i>Oxyphorhamphus micropterus</i>	2	37.4	3	11.2	0.12	P<0.01
Ceratioid fish	3	1.3				
<i>Coryphaena</i> sp.	4	0.9	7.5	3.1	2.7	
<i>Cubiceps pauciradiatus</i>			1	39.9		
<i>Diplophos taenia</i>			2	15.0		
0-25 m						
<i>Vinciguerria lucetia</i>	1	62.4	1	85.6	4.9	P<0.01
<i>Cyclothone</i> spp.	2	16.2	2	5.3	1.2	
<i>Diplophos taenia</i>	3	7.0	3	2.8	1.4	
<i>Bolinichthys</i> sp.	4	3.2	5	0.7	0.8	
<i>Gempylus serpens</i>	5	2.8	4	1.5	1.9	
<i>Lampanyctus parvicauda</i>	6.5	1.8	9	0.2	0.7	
<i>Diogenichthys laternatus</i>	6.5	1.8	8	0.4	0.8	
<i>Diaphus</i> sp. (prob. <i>pacificus</i>)	9	0.6	6.5	0.5	2.8	
<i>Thunnus</i> sp.	10	0.1	6.5	0.5	12.2	
<i>Coryphaena</i> sp.	8	0.8	27	0.1	0.3	
25-50 m						
<i>Vinciguerria lucetia</i>	1	90.0	1	90.8	1.2	
<i>Diaphus</i> sp. (prob. <i>pacificus</i>)	2	4.3	2	3.1	0.9	
<i>Stemonosudis macrura</i>	9.5	0.3	3	1.2	4.4	P<0.01
<i>Cyclothone</i> spp.	4.5	0.5	4	0.8	1.8	P<0.05
<i>Hygophum proximum</i>	3	0.8	8	0.3	0.4	
<i>Lampanyctus parvicauda</i>	4.5	0.5	6	0.5	1.0	

Tabla 8 (continuación)

<i>Bathophilus filifer</i>	6	0.5	7	0.4	1.0	
<i>Symbolophorus evermanni</i>	14	0.2	5	0.5	2.7	
<i>Myctophum aurolaternatum</i>	8	0.4	11	0.2	0.7	
<i>Diplophos taenia</i>	11.5	0.3	12.5	0.2	0.8	
50-75 m						
<i>Vinciguerria lucetia</i>	1	78.1	1	84.2	1.2	
<i>Diogenichthys laternatus</i>	2	7.0	2	4.5	0.8	
<i>Symbolophorus evermanni</i>	3	4.3	4	2.7	0.8	
<i>Diaphus</i> sp. (prob. <i>pacificus</i>)	4	3.4	3	2.7	1.0	
<i>Hygophum proximum</i>	5	1.5	5	1.4	1.1	
<i>Scopelarchoides nicholsi</i>	6	1.1	6	0.8	0.9	
<i>Stemonosudis macrura</i>	7	0.6	7	0.6	1.4	
<i>Myctophum aurolaternatum</i>	10.5	0.4	9	0.4	1.3	
Paralepidid type B	12	0.3	8	0.4	1.9	
<i>Bregmaceros</i> spp.	10.5	0.4	10	0.3	0.9	
75-100 m						
<i>Vinciguerria lucetia</i>	1	46.9	1	69.5	1.8	P<0.05
<i>Diogenichthys laternatus</i>	2	28.6	2	11.5	0.5	P<0.01
<i>Symbolophorus evermanni</i>	3	8.6	3	5.2	0.7	
<i>Bathylagus nigrigenys</i>	4	3.7	4	2.2	0.7	
<i>Scopelarchoides nicholsi</i>	5	4.1	7	1.6	0.5	P<0.05
<i>Idiacanthus</i> sp.	6	2.3	6	1.8	0.9	
<i>Diaphus</i> sp. (prob. <i>pacificus</i>)	8	0.8	5	1.9	2.8	P=0.05
<i>Hygophum proximum</i>	7	1.5	10	0.7	0.5	
<i>Bregmaceros</i> spp.	13	0.3	9	0.9	3.4	P<0.05
<i>Lampanyctus idostigma</i>	9	0.4	16	0.2	0.9	

(Simpson's index; Table 9) reflect the relative abundance of *Vinciguerria lucetia* within each depth interval; maximum dominance occurred at 25-50 m, where this species constituted 90% of total larvae. The most equitable species abundance relations were in the neuston, and at 0-25 m and 75-100 m during the day, where *V. lucetia* was relatively less abundant (< 63% of total).

Ichthyoplankton composition and abundance relations varied with depth and time of day (Table 9). Within each depth interval, night tows generally caught more kinds of larvae than did day tows, but the difference was significant only at 0-25 m and 25-50 m (Table 9). Greatest day-night differences in composition and abundance relations occurred in the neuston. Nine neuston night tows caught 3 times as many taxa as did 14 day tows, and taxon proportions and ranked abundances changed radically from day to night (PSI = 20.5; Kendall's tau = 0.10, $P > 0.20$, indicating no agreement of taxon

ranks). These changes were associated with shifts from day dominance by exocoetid larvae (97.5%) to less pronounced night dominance by the nomeid *Cubiceps paucerradius* (39.9%), and mesopelagic fish larvae (28.1%); exocoetid larvae were relatively rare at night (25.8%) (Table 6). Moderate day-night changes in species proportions occurred at 0-25 m (PSI = 74.8), and at 75-100 m (PSI = 73.2). In both cases, there was a night increase in dominance (per Simpson's index), but no marked change in species ranked abundance (Kendall's tau, $P < 0.05$, indicating significant agreement of species ranks). At both depths, day-night changes in species proportions were due to significantly larger night catches of *Vinciguerria lucetia* (Table 8). Exclusion of *V. lucetia* from PSI calculations ("other" PSIs) for the 0-25 m and 75-100 m intervals result in increased values (79.3 and 80.0; Table 9), showing day-night similarity of proportions of other species. Species proportions and do-

minance relations were stable at 25-50 m and 50-75 m (both PSIs > 93), primarily due to relatively constant high abundances of *V. lucetia* (Table 8). Day and night species abundances, and ranks of abundance, were similar at 50-75 m, and the "other" PSI value was high (87.9; Table 9). However, at 25-50 species ranked abundance shifted markedly (Kendall's tau = 0.38, $P > 0.05$) due to a significant ($P < 0.01$) night abundance increase of the paralepidid *Stemonosudis macrura* and marked decrease of *Hygophum proximum* (Table 8), and the "other" PSI value was relatively low (72.4; Table 9).

The uniqueness of the neuston ichthyoplankton assemblage and dominance by *Vinciguerria lucetia* at greater depths are reflected in PSI values from between-depth interval comparisons of species proportions (Table 10A). The neuston assemblage bore little resemblance to that of any deeper interval; PSI comparisons between the neuston and 25 m intervals ranged from 0 to 1.1 (day), and 2.6 to 9.1 (night). PSI values for comparisons between 25 m intervals were much higher (i.e., 50.4 to 84.8 day; 72.0 to 96.3 night), and reflected similarity in the relative proportions of *V. lucetia*. Highest

TABLE 9

Comparison of diversity and composition of ichthyoplankton caught by day and night within five depth intervals in the eastern tropical Pacific. Diversity expressed as mean and standard deviation of numbers of taxa caught per tow, and as total numbers of taxa caught. Significance of day-night differences in mean numbers of taxa caught based on Z tests; species dominance expressed as Simpson's Index (λ). Day-night differences of species proportions expressed as percent similarity index (PSI) values for total species and for species other than *Vinciguerria lucetia*. Day-night differences of species rank order of abundance (10 most abundant species in bongo tows, all species in neuston tows) expressed as Kendall's Tau. Asterisks denote significant day-night differences in diversity and significant agreement of species rank order of abundance at probability levels $P < 0.05$ (*), and $P < 0.01$ (**).

Depth Interval (m)	Day				Night				Composition		
	N ^o Taxa/Tow		Total		N ^o Taxa/Tow		Total		PSI Total	PSI Other	Kendall's Tau
	\bar{X}	(S)	N ^o taxa	λ	\bar{X}	(S)	Taxa	λ			
0-0.25	2.0	(0.8)	4	0.504	1.8	(1.9)	11	0.212	20.5	20.5	0.10
0-25	4.6	(1.9)**	19	0.423	6.0	(1.5)**	27	0.737	74.8	79.3	0.60*
25-50	6.7	(3.0)**	29	0.812	9.3	(3.4)**	32	0.826	96.6	72.4	0.38
50-75	11.5	(2.7)	35	0.618	13.0	(3.3)	35	0.713	93.1	87.9	0.69**
75-100	12.9	(2.2)	33	0.313	14.2	(2.9)	39	0.500	73.2	80.0	0.69**

similarity occurred between the 25-50 m and 50-75 m intervals. Exclusion of *V. lucetia* from PSI comparisons between the 25 m intervals results in lowered values (11.6 - 66.8 day, 14.5 - 69.9 night; Table 10B) with greatest similarity of proportions of other taxa occurring between the 50-75 m and 75-100 m intervals. As suggested by these lowered PSI values, species composition and abundance relations within each interval

were unique (Table 8); ranked abundances of the ten most abundant species within each interval by day and by night were (with one exception) different from those in all other intervals (Kendall's tau test, $P > 0.05$, indicating no significant agreement of species ranked abundances). The exception was similarity of daytime species ranks at 50-75 m and 75-100 m (Kendall's tau = 0.47; $P < 0.05$).

TABLE 10

Between-depth percent similarity index (PSI) values of ichthyoplankton composition by day and night with (A), and without (B) *Vinciguerria lucetia* included in calculations.

A. Total Larvae

Depth (m)	Day				
	0-0.25	0-25	25-50	50-75	75-100
Night:					
0-0.25	X	1.1	0	0	0
0-25	9.1	X	66.2	66.4	50.8
25-50	3.5	89.0	X	84.8	50.4
50-75	2.8	86.7	96.3	X	65.0
75-100	2.6	72.0	74.2	82.4	X

B. Other Larvae (*V. lucetia* excluded)

Depth (m)	Day			
	0-25	25-50	50-75	75-100
Night:				
0-25	X	22.9	14.3	1.6
25-50	28.7	X	38.0	12.0
50-75	16.9	44.0	X	66.8
75-100	14.5	23.0	69.9	X

Day-night differences in total abundance, within-interval abundance, and vertical distributions of some of the more abundant species (Table 8) suggest significant day-night changes in net avoidance and/or vertical migration. Increased night over day abundances throughout the depth ranges of predominantly shallow-living *Vinciguerria lucetia*, *Cyclothone* spp., *Gempylus serpens*, *Thunnus* sp. and Paralepidid B probably resulted primarily from visually aided net avoidance. Significantly lower night abundance at 0-25 m ($P < 0.05$) in conjunction with a significantly shallower night distribution (K-S test, $P < 0.05$) of *Bolinichthys* sp. strongly suggests vertical migration into the undersampled 0-10 m range at night. The day increased 0-100 m abundances, and marked 75-100 m abundance peaks of deep-living *Diogenichthys laternatus*, *Symbolophorus evermanni*, *Scopelarchoides nicholsi*, and *Bathylagus nigrigenys* indicate that indivi-

duals may migrate into the upper 100 m from greater nighttime depths. Both *Stemonosudis macrura* and *Bregmaceros* spp. had substantial overall night abundance increases with concurrent changes in vertical distribution (K-S tests, $P \leq 0.01$ in both cases), possibly resulting from nocturnal upward migration and (for *S. macrura*) decreased net avoidance.

DISCUSSION

Invertebrate Zooplankton

Day-night zooplankton distribution changes appear to be primarily due to upward nocturnal migrations to 0-25 m and/or the neuston by forms which have maximum daytime abundances near the bottom of the mixed layer (~ 40 m), and by forms which undertake extensive migrations from depths > 100 m (i.e., euphausiids, decapods, and mysids). Relatively small day-night changes

occur in abundances, compositions, and proportions of zooplankton taxa at 50-75 m and 75-100 m relative to changes within the three shallower intervals (Table 2; Figure 3).

Despite evidence for upward nocturnal migration, night zooplankton abundance was 10% less than the day value. This is caused primarily by night decreases in total numbers of copepods, chaetognaths and amphipods (Table 1). Decreased night abundances of copepods, and chaetognaths occurred at 25-50 m, 50-75 m, and 75-100 m; amphipod abundances decreased at all depths except the neuston. These decreases suggest nocturnal downward migration out of the upper 100 m and/or upward migration into the undersampled 0-10 m layer by some members of these taxa.

Overall composition, vertical abundance profiles, and diel abundance variations of invertebrate zooplankton described here are apparently characteristic of much of the ETP. Longhurst (1976) described general patterns of ETP zooplankton distribution relative to physical and biological parameters, and found that various features persisted despite regional and seasonal hydrographic variations: (a) The zooplankton were abundant and diverse (predominantly copepods, chaetognaths and euphausiids) within the mixed layer and upper

thermocline (the "epiplankton"). This epiplankton was distinct from the sparser plankton below, and from a vertically migrating fraction ("interzonal species"; predominantly euphausiids and adult mesopelagic fishes) which entered the epiplankton from greater depths (i.e., 250-300 m) at night, primarily increasing its biomass (not numbers). (b) Maximum zooplankton abundance occurred within the epiplankton, and was closely associated with the bottom of the mixed layer (and with the depth of maximum primary productivity). (c) There was generally a secondary near-surface zooplankton maximum, distinct from the rest of the epiplankton. (d) Generally, nocturnal shoaling of the epiplankton was evident, but some taxa exhibited nocturnal "sinking". Because of the similarities between our observations and Longhurst's general patterns, we feel that the following description of zooplankton and ichthyoplankton assemblages at our study site may be broadly applicable to the offshore ETP.

Ichthyoplankton Distribution and Abundance Relative to Invertebrate Zooplankton

The overall vertical distributions of ichthyoplankton and invertebrate zooplankton were significantly different (Figure 6;

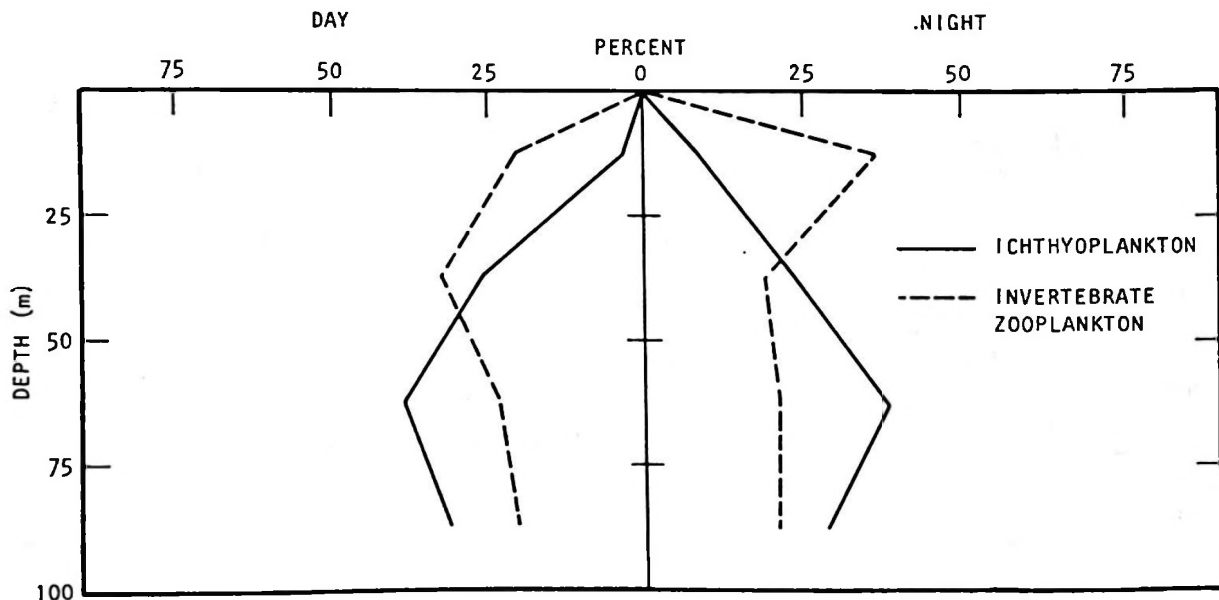


Figure 6. Vertical distribution of ichthyoplankton in relation to invertebrate zooplankton in the upper 100 m of the eastern tropical Pacific. Vertical profiles based on the proportion of total 0-100 m abundance (numbers per 10 m² sea surface area) present by day and night within each of five depth intervals.

K-S test, $P < 0.01$) both day and night. By day and night, most larval fishes were distributed below the depths of maximum zooplankton abundance. Despite these overall distributional differences, strong positive correlations (rank difference correlations $> +0.40$) occurred between zooplankton and ichthyoplankton abundance in individual day tows at 0-25 m, 50-75 m, and 75-100 m, and strong negative correlations (≤ -0.60) occurred in night tows at 0-25 m and 50-75 m (Table 5). While not significant, these correlations show trends of within-depth larval fish and zooplankton abundance relations similar to those reported from the North Pacific central gyre (Loeb, 1979). The strong positive correlations may indicate local aggregation of visually-feeding larvae and zooplankton taxa in response to increased food availability. It is possible that zooplankton concentrations and/or composition at the 25-50 m depth of maximum day abundance are not conducive to such aggregations. At night, relatively large negative correlations could result from predation on larval fish by concentrations of interzonal vertical migrators (e.g., euphausiids).

Ichthyoplankton Composition and Vertical Distribution

Our ichthyoplankton species list resembles that of EASTROPAC ichthyoplankton (Ahlstrom, 1971, 1972); however, relative abundances of dominant families differ markedly between the data sets (Table 11). These differences are in part due to differences between sampling depths of the two surveys. EASTROPAC tows were to ~ 220 m, over twice the depth range of our samples, and so yielded more deeper-living larvae (e.g., sternoptychids [Badcock and Merrett, 1976; Loeb, 1980a]).

The marked difference between ranks and proportions of gonostomatids and myctophids in the two surveys is partly due to extreme dominance by *Vinciguerria lucetia* (77.1%), and low relative abundance of *Diogenichthys laternatus* (8.0%) in our samples, vs. large numbers of *D. laternatus* (38.1% of total larvae), and relatively low abundance of *V. lucetia* (18.0%) in EASTROPAC tows. This suggests that most *D. laternatus* larvae in our area occurred below 100 m. Certainly, *D. laternatus* larvae were most abundant at 75-100 m (Table 8), and appeared to undergo

TABLE 11

The ten most abundant families of fishes and their percentage contribution to the total ichthyoplankton collected during August-September in 0-220 m tows taken on EASTROPAC II cruise (1967), and in tows within upper 100 m taken near 13°N, 130°W during August-September 1980. EASTROPAC II data from Ahlstrom (1972).

	EASTROPAC II		August-September 1980	
	Rank	%	Rank	%
Myctophidae	1	52.0	2	16.6
Gonostomatidae	2	19.7	1	78.3
Sternoptychidae	3	6.0	45.5	0.0008
Bathylagidae	4	4.8	5	0.9
Bregmacerotidae	5	2.5	7	0.3
Paralepididae	6	2.0	4	1.0
Nomeidae	7	1.2	36	0.02
Melamphaeidae	8	1.1	8	0.2
Engraulidae	9	1.1		
Idiacanthidae	10	0.6	6	0.7
Scombridae	20	0.2	10	0.09
Scopelarchidae	15	0.2	3	1.2
Gempylidae	14	0.3	9	0.1
Others		8.3		1.9

substantial upward nocturnal migration into this interval. Relative abundances of these two species may be more alike in our area than in the extensive EASTROPAC II area. Samples collected at nine EASTROPAC II stations closest to our study area (11-14°N, 119°W; Ahlstrom, 1972) contained almost equal numbers of *V. lucetia* and *D. laternatus* larvae. However, this still implies that most *D. laternatus* larvae occurred below 100 m in our area. Other myctophids which had maximum abundances at 75-100 m (*Gonichthys tenuiculus*, *Hygophum atratum*, *Myctophum nitidulum*, *Symbolophorus evermanni*) may also be more abundant at depths > 100 m, and so be under-represented in our samples. Other families which were relatively more abundant in the EASTROPAC II survey than in ours (Table 11) may also occur mostly at 100-220 m: Bathylagidae, Bregmacerotidae, Melamphaeidae and Idiacanthidae larvae all had maxima at 75-100 m in our samples.

ETP vs. North Pacific Central Gyre Fish Assemblages

Loeb (1979; 1980a, b) presented data on larval fishes collected in stratified bongo net samples taken at 28°N, 155°W within the North Pacific central gyre. Because our ETP samples are roughly analogous to those collected in the central gyre (i.e., night samples collected during August-September with bongo nets fitted with 505 µm mesh, fished at four 25 m intervals between 0-100 m, with flow volumes ~ 300 m³; mixed layer depth ~ 40 m; SIO, 1974; Loeb, 1980 a, b), direct comparisons may be made of abundances, diversities, distributions and compositions of night-caught ichthyoplankton of these two oceanic ecosystems.

Estimated total 0-100 m nighttime ETP ichthyoplankton abundance was ~ 2 X that of the central gyre. Mean concentrations at 0-25 m and 25-50 m (mixed layer) were similar (ETP values 0.78 X and 0.95 X, respectively, those in the central gyre). However, abundances at 50-75 m and 75-100 (upper thermocline) were significantly larger (4.1 X and 4.7 X; $P < < 0.001$ in both cases) than in the central gyre. Abundance profiles differ significantly (Figure 7-A; K-S test, $P < 0.01$): 70.2% of 0-100 m central gyre larvae occur-

red within the mixed layer, while 66.0% of ETP larvae were below the mixed layer. In the central gyre, 97% of the estimated 0-600 m larval fish abundance was between 0-100 m; indications are that a substantial proportion of the ETP ichthyoplankton occurs at depths > 100 m.

ETP ichthyoplankton was much less diverse than that of the central gyre: 40 central gyre bongo samples caught 83 taxa vs. 59 taxa in 166 ETP tows. In the central gyre, from 1.3-1.9X more taxa were collected within each depth interval (10 tows/interval), and in all cases, significantly more ($P < 0.05$) taxa were caught per tow than in the ETP.

Both ETP and central gyre ichthyoplankton assemblages were dominated (> 91%) by gonostomatids and myctophids, but the vertical distributions and species compositions of these families differed greatly. Both families had significantly deeper distributions in the ETP than in the central gyre (Figures 7A-B; $P < 0.01$ in both cases). The dominant central gyre gonostomatids *Cyclothone* spp. (27%), and *Vinciguerria nimbaria* (9%) had maximum abundances at 25-50 m (Loeb 1980a, b). In the ETP, shallow-living *Cyclothone* spp. larvae were rare (< 1.0% of total), and dominant *Vinciguerria lucetia* (maximum abundance at 50-75 m) occurred significantly deeper ($P < 0.01$) than its central gyre congener. In both areas, larvae of the myctophid subfamily Lampanyctinae occurred significantly shallower ($P < 0.01$) than larvae of subfamily Myctophinae. In the central gyre, larval lampanyctines outnumbered myctophines by 4:1; in the ETP, larval myctophines outnumbered lampanyctines by 4:1. Additionally, both subfamilies occurred significantly deeper in the ETP than in the central gyre (Figure 7-B; $P < 0.05$ in both cases).

Depth-related composition differences also exist between other more abundant central gyre and ETP families. Shallow-living evermannellids, apogonids, stomiatoids and notosudids were among the ten most abundant taxa collected in 0-100 m central gyre tows; they were rare or absent in ETP samples. In contrast, deep-living bathylagids, idiacanthids and scopelarchids were relatively abundant in ETP samples, but rare in central gyre samples. An exception to this trend was increased relative abundance of deep-

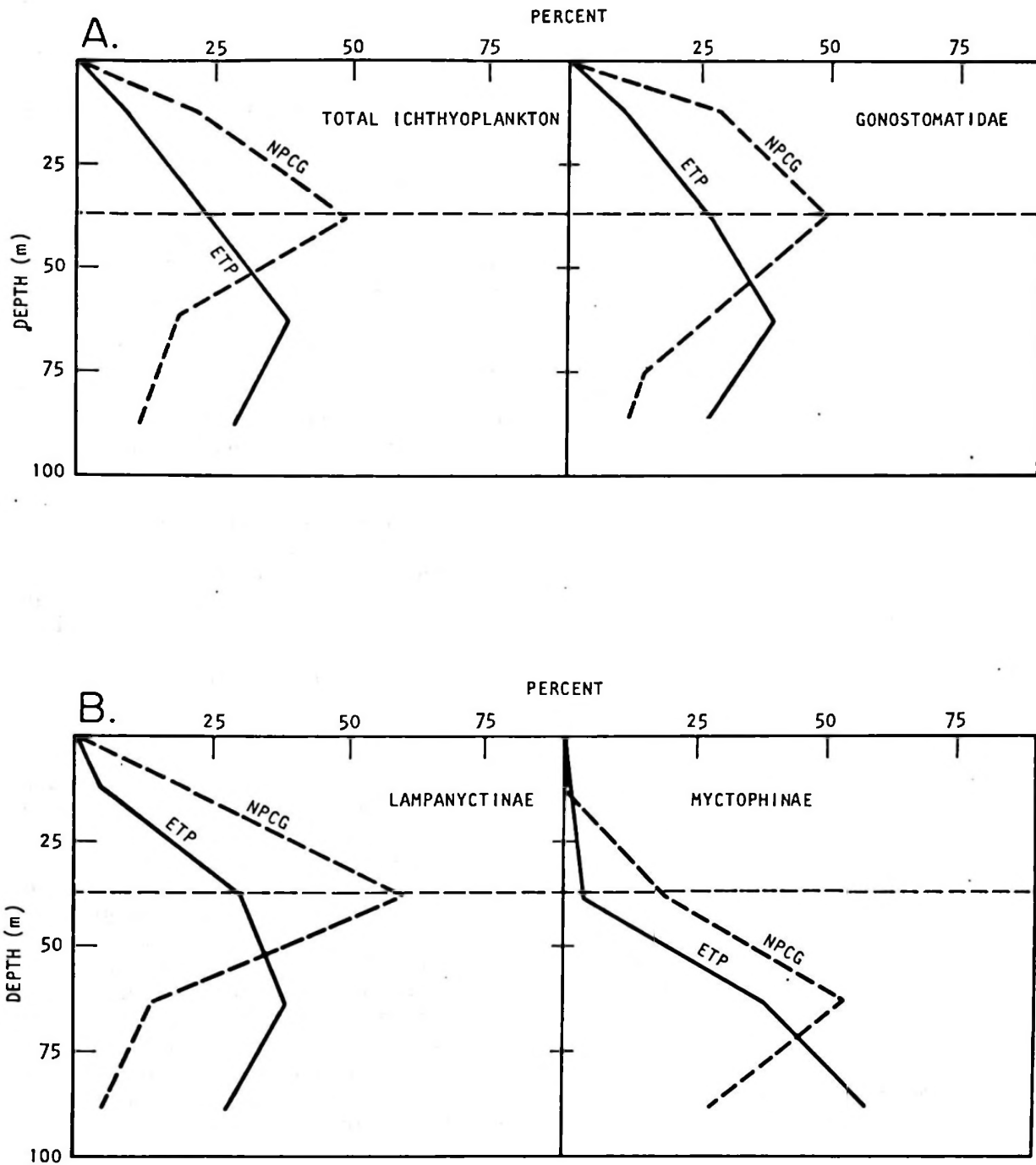


Figure 7. Nighttime vertical distribution of total ichthyoplankton and of major components of the ichthyoplankton of the eastern tropical Pacific (ETP) and North Pacific central gyre (NPCG) based on percentage of total 0-100 m nighttime abundance present within each of four 25 m depth intervals. (A) Total ichthyoplankton and Family Gonostomatidae. (B) Myctophid Sub-families Lampanyctinae and Myctophinae. Dashed line represents mixed layer depth.

living bregmacerotid larvae in the central gyre; however, as mentioned above these may have been greatly undersampled in our study (Table 11). Other exceptions were shallow-living gempylids, paralepidids, and deep-living melamphaeids, which had similar ranks and proportions in both areas.

The major differences between the ETP and central gyre ichthyoplankton composition and depth distribution imply different migratory habits of the dominant adult populations. *Cyclothone* spp., the central gyre dominants, are non-migrators; *Vinciguerria lucetia*, the ETP dominant, migrates to the upper 100 m at night (Robison, 1973). In the central gyre, myctophine myctophid adults generally migrate to the surface or mixed layer, while lampanyctine adults generally do not (Loeb 1980a). A similar situation exists in the ETP. According to Robison (1973) and Wisner (1976), adults of six of our seven myctophine species migrate to the surface at night; the exception (*Diogenichthys laternatus*) is most abundant at 50-100 m at night. In contrast to the central gyre, the adults of two of the four lampanyctine species we caught (*Lampanyctus parvicauda*, *L. omostigma*) migrate to the surface at night; the other two (*Diaphus pacificus*, *L. odostigma*) are caught at depths > 100 m. Additionally, the adult ETP mesopelagic fish assemblage described by Robison (1973; 25 families, 60 species) is mostly composed of vertical migrators. Thus, the ETP mesopelagic fish assemblage appears to be dominated by actively-migrating "near-surface" (Robison, 1973) adult forms that have deep-living larvae; the North Pacific central gyre assemblage is dominated by less actively migrating or non-migrating, deeper-living adult forms with shallow-living larvae.

Differences in ichthyoplankton abundance, diversity, composition and depth distribution, as well as differences in composition and migratory habits of dominant adult populations of the ETP and central gyre reflect fundamental differences between environmental conditions affecting both larval and adult stages in these two areas. Larger ETP ichthyoplankton abundance is associated with the high productivity of the ETP relative to the more oligotrophic central gyre (Holmes *et al.*, 1957; Reid, 1962; Blackburn *et al.*, 1970; Koblentz-Mishke, *et al.*, 1970). The 2 X higher summer (and possibly 4 X winter) ETP

abundances are in accordance with 2-8 X higher ETP zooplankton standing stock estimates (Brandhorst, 1958; Reid, 1962; McGowan and Williams, 1973). Relatively low ETP fish diversity may result from the hydrographic complexity and variability in the ETP as compared to the stability and predictability of the central gyre (Barnett, 1975; Haury, 1976; McGowan, 1977).

The differences in larval depth distributions and in migratory habits of dominant species of the ETP and central gyre fish assemblages may result from differences in (a) uniformity of surface layer parameters, and (b) zooplankton distribution and abundance between the two areas.

Surface layer conditions in the North Pacific central gyre are relatively stable and predictable. Physical, chemical and biological properties of the upper several hundred meters are laterally homogeneous across the water mass. Seasonal changes are moderate, and involve a 6-7 °C cooling and deepening of the mixed layer (40 m in summer, 110-140 m in winter; McGowan, 1977; McGowan and Hayward, 1978; McGowan and Walker, 1979).

In contrast, ETP surface layer conditions are complex and variable. Surface current direction and intensity vary regionally and seasonally. Seasonal changes in mixed layer temperatures and depths also vary considerably (Wooster and Cromwell, 1958; Wyrski, 1965, 1966, 1967; Tsuchiya, 1968, 1974). Across the ETP, the summer mixed layer ranges from 17 °C to > 29 °C, and < 10 m to > 70 m; the winter mixed layer ranges from 22 °C to > 28 °C, and from < 10 m to > 60 m (Love, 1971; 1972a, b; 1973). These within-season regional differences far exceed seasonal changes across the central gyre. In the central gyre, significant ichthyoplankton composition changes are associated with seasonal changes in mixed layer temperature and depth, and central gyre upper water column thermal structure appears to be a major factor regulating ichthyoplankton species and spatial structure (Loeb, 1980b). It is possible, therefore, that the extreme heterogeneity of mixed layer conditions across the ETP is not favorable for most larvae, and that more favorable conditions (i.e., laterally homogeneous) exist within the thermocline. Among potentially favorable physical conditions are continuous isothermal layers (i.e., 15-20 °C) and density

surfaces which could provide uniform physical environments in near-surface waters throughout most of the area to stenothermal larvae and/or early, less active (i.e., buoyancy dependent) larval stages. This may in part explain the widespread constancy of ETP ichthyoplankton species composition (Ahlstrom, 1971, 1972) despite heterogeneity of ETP surface-layer conditions.

While physical conditions in the mixed layer may affect overall ichthyoplankton depth distribution and species composition, the distribution and concentrations of invertebrate zooplankton are probably also important. Both our study and Longhurst's (1976) work indicate that an abundant invertebrate zooplankton assemblage is always present within the mixed layer, and often present within the near-surface/neuston layer of the ETP. Comparable depth stratified data do not exist which would allow direct comparisons of central gyre and ETP zooplankton vertical abundance profiles. However, 0-300 m ETP zooplankton standing stock estimates (~ 50 - 200 ml/1000 m³; Brandhorst, 1958; Reid, 1962) are about 2-8X those for the central gyre (~ 21 - 24 ml/1000 m³; McGowan and Williams, 1973). Most ETP zooplankton biomass (50-60%; Blackburn, 1966) is concentrated within the mixed layer, and zooplankton abundance decreases substantially at depths > 150 m (Longhurst, 1976). This very abundant, shallow zooplankton could directly affect the composition of the adult fish assemblage by providing a selective advantage to predatory fishes migrating into surface layers to feed; this would result in a fish assemblage dominated by actively migrating and surface-associated species. In the central gyre, the overall low water column productivity and only

moderately increased zooplankton biomass values in surface layers at night probably offer a selective advantage to moderate or low-energy vertical migrators and non-migrating species.

Vertical distributions of invertebrate zooplankton can also directly affect larval fish distributions through competition for food. This may favor the survival of larval forms in the upper thermocline, where food resources are relatively rich (i.e., abundances of copepod nauplii and post-nauplii, and other micrometazoans similar to those within the mixed layer; Beers and Stewart, 1971), but where potential competition for food is markedly reduced relative to the mixed layer. Additionally, nighttime predatory activities of vertical migrators concentrating within the neuston and mixed layers may also skew survival of larval fishes toward deeper waters. Mesopelagic fishes contribute much of this migratory fauna (Blackburn, *et al.*, 1970; Longhurst, 1976); the deep distribution of their larvae may generate additional selective advantage through reduced incidence of cannibalism.

Although the shallow oxygen minimum layer may restrict horizontal distributions of some fish species within the ETP (e.g., evermannellids and scopelarchids; Johnson, 1974; Johnson and Glodek, 1975), it probably does not directly affect the overall structure of the fish assemblage. We agree with Ebeling (1962, 1967) that the distinctive nature of the ETP fish assemblage is probably related to the ETP's high productivity and high hydrographic complexity, and suggest that the structure of this assemblage is in part related to the vertical distributions of productivity and hydrographic heterogeneity, and their influences on both larval and adult stages.

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