THE VERTICAL DISTRIBUTION OF SOME PELAGIC COPEPODS IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

This study was based on zooplankton samples collected with standard, opening-closing bongo nets through eight depth intervals to 600 m or 800 m at 10 stations along a transect from 23°N to 3°S in the eastern tropical Pacific during May-June 1974. The investigation covered four environments: (1) the mouth of the Gulf of California, where some California Current species occurred at their southern limits: (2) the oxygen-deficient region ($0_2 < 0.1$ ml/l^{-1}); (3) the North Equatorial Countercurrent; and (4) the Equatorial Undercurrent. More than 60 species of calanoid copepods were identified and counted. The numerically dominant species—*Eucalanus subtenuis, Eucalanus subcrassus*, and *Rhincalanus nasutus*—constituted respectively 33.5%, 12.8%, and 9.5% of the total numbers. The quantitative, geographical, and vertical distributions of the most common and abundant species are described. Most of the species are subtropical or tropical, and oceanic in habitat. The ranges of vertical distribution of the abundant copepods are divided into several patterns: 0 to 200 m, 0 or 50 to 300 m, 200 or 300 to 400 m, and 400 to 800 m. The relationship between the distributions of copepods and current regimes is discussed.

RESUMEN

Este estudio está basado en las muestras de zooplancton colectadas con redes bongo estándares, a ocho profundidades, entre la superficie y 600 u 800 m de profundidad, en 10 estaciones ubicadas a lo largo de un corte entre 23°N y 3°S en el Pacífico Este tropical, en mayo-junio de 1974. Se cubrieron cuatro ambientes: (1) la boca del Golfo de California, la cual corresponde al límite Sur de distribución para algunas especies típicas de la corriente de California; (2) la región con bajas concentraciones de oxígeno (0_2<0.1 ml/l); (3) la Contracorriente Norecuatorial; y (4) la Corriente Ecuatorial Subsperficial. Más de 60 especies de copépodos calanoídeos fueron identificadas y contadas. Las especies numéricamente dominantes—*Eucalanus subtenuis, E. subcrassus*, y *Rhincalanus nasutus*—constituyeron 33.5%, 12.8%, y 9.5% respecitivamente del total. Se describen las distribuciones cuantitativas, geográficas, y verticales de las especies más abundantes y comunes. La mayoría de las especies es subtropical o tropical y de habitat oceánico. Los rangos de distribución vertical de aquellos copépodos abundantes muestran ciertos patrones; 0 a 200 m, 0 ó 50 a 300 m, 200 ó 300 a 400 m, y 400 a 800 m. Se discute la relación entre las distribuciones de copépodos y los regímenes de corrientes.

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INTRODUCTION

Copepods are an important component of the zooplankton in the tropical Pacific (Vinogradov and Voronina 1964). The general character of the tropical plankton's vertical distribution, and the peculiarities of distribution and migration of individual species have been studied by several authors (e.g., Vinogradov and Voronina 1962, 1963). The vertical distribution of some species of copepods in some areas of the tropical Pacific Ocean was also studied by King and Hida (1954, 1957), Motoda and Anraku (1955a, b), and Heinrich (1960, 1961). The data for individual species, however, were procured mainly from east and southeast of Japan (Motoda and Anraku 1955a, b; Heinrich 1961). This study uses zooplankton samples collected on the Krill Expedition (May-June 1974) to describe the composition and vertical distribution of copepods in the eastern tropical Pacific (ETP) and their relationship to its currents.

Past studies of the ETP's copepods are sporadic and incomplete. Giesbrecht (1895) presented a taxonomic report dealing with a few species found between the Galápagos Islands and the west coast of Mexico. Additional lists and descriptions of ETP copepods may be found in Wilson (1942), Grice (1961), Lang (1964), Heinrich (1960, 1973), Fleminger (1964a, 1964b, 1967a, 1967b, 1973), Fleminger and Hulsemann (1973, 1974), and Manrique (1977), but all deal with a few select species or represent limited localities within the region. There are no general references on the relation of copepod species and their horizontal and vertical distribution to ETP currents and water masses.

Tsuchiya (1974) detailed the currents and water masses of the ETP, each with unique physical and chemical features: (1) the California Current, (2) the North Equatorial Countercurrent, and (3) the Equatorial Undercurrent. Brinton (1979) presented an extensive review of the physical, chemical, and biological environments of the ETP. The California Current off central and southern California, 38°N to 33°N, supports zooplankton species with temperate affinities, notably *Euphausia pacifica* and the copepod *Calanus pacificus californicus* Brodskii. Their dominance diminishes southward, where their distributions are compressed shoreward along Baja California. At the western edge of the current, the temperate fauna is replaced by species of the subtropical Central Pacific Gyre. The central water species range eastward at 30°–33°N toward southern California and northern Baja California in a large meander and then drift westward off the Punta Eugenia upwelling center (e.g., Brinton 1962, Figure 118). Immediately to the north of the ETP, off Baja California, production is largely a consequence of coastal upwelling (Blackburn 1969). Within the ETP, high concentration of nutrients in the euphotic zone is associated with the shallow thermocline (Blackburn et al. 1970).

During late May-June west of the tip of Baja California near 23°30′N, part of the California Current turns westward in a series of temporally and spatially irregular anticyclonic eddies, and eventually joins the North Equatorial Current. Another part continues southward, though it is inconsistent in direction and speed while exchanging water with the Gulf of California (Roden 1958; Wyllie 1966). In the vicinity of the gulf, the California Current loses its faunistic and hydrographic identity. It is replaced by water containing the ETP assemblage of species. Sverdrup et al. (1942) designated this water "equatorial" because of its low oxygen content and its distinctive oceanic water mass indicative of local formation. The data presented here suggest that this boundary is less abrupt than that described by Brinton (1979). Brandhorst (1958), Wooster and Cromwell (1958), Cromwell and Bennett (1959), Austin (1960), Wyrtki (1965, 1966, 1967), Tsuchiya (1968, 1970, 1974), and Love (1971, 1972, 1973) also presented physical, chemical, and meteorological characteristics of the ETP.

The objective of this study is to investigate interrelationships between the distribution of calanoid species, the equatorial currents, and the steep hydrographic gradients of oxygen and temperature characterizing the ETP. The study covers a transect of 16 stations from 23°N to 3°S (northern Mexico to the coast of Equador; Figure 1).

MATERIALS AND METHODS

Zooplankton and hydrographic data were collected in May and June 1974 during the Krill Expedition on RV *Alexander Agassiz* of Scripps Institution of Oceanography. All but one of the samples reported on here (ten stations) were collected with 0.7-m-diameter, opening-closing bongo nets (Brown and McGowan 1966); at one station an open, 1-m-diameter net was used. Mesh size of both nets was 0.33 mm, and of the cod ends 0.22 mm. The volume of water strained, measured by flow meters, varied from 500 to 1000 m^3; estimates of plankton abundance were standardized to 1000 m^3 of water strained. Bongo net tows were made with four net pairs in series, which sampled depth increments of about 40 m in the 0-160-m layer, about 80 m in the 160-500-to-600-m layer, and about 80 m in the 600-800-m layer. The separation of about 10 m between the shallow and deep series minimized the possibility of overlap. Open-water net tows were oblique hauls to about 200-m depth. Separate day and night series were made at each station; the time of day of sampling was not consistent among stations. The deep, night series failed at station 12. Actual depths of the nets were estimated from a Benthos time-depth recorder attached to the bottom net. When the recorder failed, depths were calculated from meters of wire out and the mean wire angle. The bongo nets were opened by messenger at maximum depth, towed obliquely upward while the ship steamed at 1 to 15 m/sec, and closed by messenger at minimum depth. Temperature, salinity, oxygen, phosphate, nitrate, and nitrite were measured to 1000-m depth at all stations.

In the laboratory, one of the paired samples collected by the bongo nets from each depth interval was randomly selected for analysis. Aliquots of one percent by volume were removed with a 10-cc piston pipette and counted. Males, females, and late juveniles were tallied individually for numerically dominant species. Sufficient aliquots were counted to reach at least 100 individuals for commoner species. For rarer species, 10 aliquots were counted.

Brinton et al. (1986) reviewed the species of copepods reported from the Gulf of California and considered their biogeographical affinities and distributional characteristics. Brinton et al. recognized three categories: (1) temperate, (2) broadly tropical or tropical to subtropical, Indo-Pacific or cosmopolitan, and (3) narrowly tropical and endemic. They also assigned the species to habitat categories—estuarine waters, coastal waters, neritic waters, and oceanic waters. The biogeographical and habitat assignments have been used in the notes on individual species that follow.

RESULTS

Species Composition of Copepods

About 140 species of calanoid copepods have been reported for the ETP area. In this investigation 63 species of copepods were identified and counted (Table 1). The average abundance of all individuals of the ten numerically dominant species varied from 1.5% to 33.5% of copepods in the sample. Two species, *Eucal-*

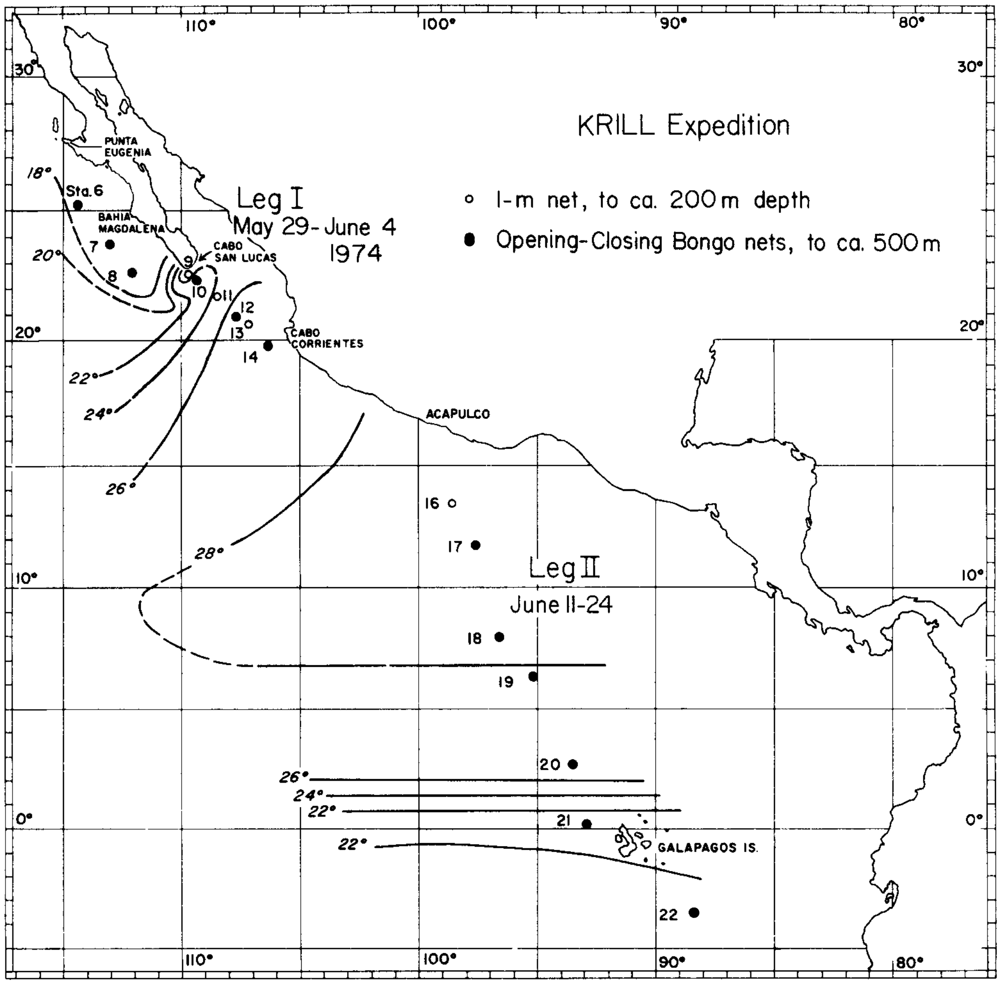

Figure 1. Localities occupied for plankton and hydrographic observations. Positions of surface isotherms beyond transect are generalized from published reports. From Brinton (1979).

anus subtenuis and *Eucalanus subcrassus*, produced the highest percentage (33.5% and 12.8%). Another 11 species were common, averaging 1.6% to 0.625% of all copepods, and 42 species were rare (< 0.5%). Two species averaged greater than 10%; 2 species from 5% to 10%; 11 species from 1% to 5%; and 6 species from 0.5% to 1% (Table 1). In general, frequencies were higher in night samples than in day samples.

Most of the copepods were tropical, oceanic species occurring throughout most of the tropical Pacific. Some species are endemic to the ETP; others are widespread in tropical latitudes.

Distribution of the Numerically Dominant Species

Eucalanus subtenuis. This species was the most abundant copepod sampled, constituting 33.5% of the total catch in combined day and night samples. It was more numerous in day samples—56.5% of the total daytime catch—and, in agreement with Timonin and Voronina's (1977) results, maximum numbers by day exceeded those of night samples. The distribution of this species was marked by large concentrations. Greatest numbers extended from 25 to 175 m, and adults were concentrated at 50-100 m at stations 17 and 19. In the daytime the maximum densities of females were 175,000 per 1000 m^3 (station 17, 0-150 m) and 11,700 per 1000 m^3 (station 19, 50 m). The maximum number of females between 0 and 100 m at station 17 was 183,000 individuals per 1000 m^3. Adults and juveniles together ranged from 25 to 50 m at stations 10 and 19. Their maximum densities in night samples, 44,400 and 483,000 individuals per 1000 m^3, were similar to those of day sampling. Maximum numbers of females, concentrated at stations 18 and 12, were 21,600 and 5,460 individuals per 1000 m^3, respectively. The number of males and of juveniles was less than that of females. Diel vertical migration was not apparent. The overall range of vertical distribution extended from the surface to 630 m (Figure 2).

Eucalanus subcrassus. This was the second most abundant species in the Krill Expedition's zooplankton samples. Its horizontal distribution was irregular; the species appeared at stations 10-14 (20°-23°N) and stations 18-22 (8°N-4°S) (Figure 3). The trend of vertical distribution was similar to that of *E. subtenuis*, occurring mainly above 200 m, but the overall vertical range

TABLE 1
Abundance of Copepod Species Observed in Bongo Net Samples from Krill Expedition

Species	Mean Percentage Day	Night	Combined	Species	Mean Percentage Day	Night	Combined
1. *Eucalanus subtenuis*	56.5	10.5	33.5	12. *Pleuromamma abdominalis*	0.8	1.3	1.1
2. *Rhincalanus nasutus*	5.9	13.2	9.6	13. *Temora discaudata*	0.7	1.0	0.9
3. *Eucalanus inermis*	5.9	7.2	6.6	14. *Haloptilus longicornis*	0.7	1.1	0.9
4. *Eucalanus subcrassus*	5.4	20.1	12.8	15. *Pleuromamma indica*	0.6	3.0	1.8
5. *Nannocalanus minor*	4.7	1.3	3.0	16. *Aetideus pacifica*	0.5	1.4	0.9
6. *Eucalanus attenuatus* s.l.	2.9	2.2	2.6	17. *Centropages furcatus*	0.2	2.2	1.1
7. *Cosmocalanus darwini* s.l.	2.8	4.5	3.7	18. *Haloptilus orientalis*	0.2	1.1	0.6
8. *Rhincalanus rostrifrons*	1.6	1.6	1.6	19. *Scolecithrix danae*	0.1	1.3	0.7
9. *Pleuromamma gracilis*	1.4	2.1	1.5	20. *Euchaeta rimana*	0.1	4.9	2.4
10. *Euchaeta media* and *acuta*	0.8	5.0	2.9	21. *Canthocalanus pauper*	0.1	1.0	0.6
11. *Lucicutia flavicornis*	0.8	1.5	1.2				

The following species all occurred at abundances less than 0.5%.

Calanus chilensis
Calanus pacificus californicus
Candacia bipinnata
Candacia curta
Candacia pachydactyla
Candacia truncata
Clausocalanus spp.
Clytemnestra rostrata (Harpacticoid)
Euaetideus acutus and *giesbrechti*
Eucalanus hyalinus
Euchaeta longicornis
Euchaeta spinosa
Euchirella maxima
Euchirella sp.
Gaetanus minor
Haloptilus bradyi
Haloptilus ornatus
Haloptilus oxycephalus
Heterorhabdus papilliger
Heterostylites major
Labidocera acuta
Labidocera sp.
Lophothrix sp.
Lucicutia clausi
Lucicutia ovalis
Metridia sp.
Neocalanus gracilis
Neocalanus robustior
Pachyptilus sp.
Parauchaeta sp.
Phaenna spinifera
Phyllopus integer
Pleuromamma xiphias
Pontellina plumata
Pontellina sobrina and *morii*
Scaphocalanus minuta
Scaphocalanus sp.
Scolecithricella abyssalis
Scolecithricella ctenopus
Scolecithricella nicobarica
Scolecithrix bradyi
Undinula vulgaris

was deeper. Diel vertical migration was not indicated in a comparison of day and night samples (Figure 3). The vertical range of males was shallower than that of females and extended to 250 m in day samples and 150 m in night samples.

Eucalanus attenuatus s.l. This category includes *E. attenuatus* s.s. and *E. sewelli* s.s., which were not counted separately. They were distributed mainly between 25 and 100 m (Figure 4). Their vertical distribution was mainly confined to depths above 100 m at stations 14-16. They appeared only in the surface between 18°N and 20°N. The distribution of males and females was similar, but the females were more numerous, and the number of juveniles was less than that of males. At the mouth of the Gulf of California they were found only between 25 and 75 m at station 10. The maximum concentration was 30,700 individuals/1000 m^3. Numbers were higher in night samples. Diel vertical migration was not obvious. Generally, the species were distributed above 100 m. At stations 10 and 12 abundance was highest above 50 m, and the maximum number was 26,500 individuals/1000 m^3. Female numbers were higher in night samples. The species were not observed in samples from the oxygen-deficient layer or from stations near Mexico.

Eucalanus inermis. This was one of the most numerically important species in the ETP. Its vertical distribution ranged from the surface to the deepest layer sampled. Adults occurred mainly at three stations: 17, 18, and 19; thus its principal horizontal distribution extended from 6°N to 11°N with greatest abundances from 300 to 600 m. Females were more abundant than males, being concentrated mainly from 500 to 800 m in the day samples. The trend of vertical distribution of juveniles was similar to that of the females, whereas males occurred at shallower depths. Adults were less frequent at the surface (Figure 5), especially at stations 12, 14, 16, 17, and 20-22. At stations influenced by the California Current, *E. inermis* was found at the surface. The distribution of juveniles differed from that of the adults: juveniles occurred mainly near the surface at stations 14 and 16 and at mid- and deep depths at stations 17 and 18. Juveniles appeared below 500 m at stations 19-21. At station 22, which was located south of the equator, adults and juveniles were found in large numbers.

Rhincalanus nasutus. Although *R. nasutus* is distributed widely in tropical latitudes, its distribution in the ETP is restricted to the middle and maximum depths sampled. South of 8°N its distribution appears to have been influenced by the Equatorial Countercurrent (Figure 6). The maximum concentration occurred between 500 and 600 m. At station 21, the maximum number of females was 11,100 individuals/1000 m^3 at about 500 m. From 20°N to near the equator, *R. nasutus* was not present from middle depths to the surface. Numbers of females were higher than those of the male, and diel vertical migration was not apparent.

Rhincalanus rostrifrons. This species was less abundant than *R. nasutus*, but its distribution was more extensive. In day samples, *R. rostrifrons* occurred mainly beneath 50 m south of 11°N. In general, both females and males were concentrated above 400 m. The highest densities reached 5000 individuals/1000 m^3 (Figure 7). The species occurred in lower numbers and at fewer depths at stations 12 and 14. Diel vertical migration was not apparent. *R. rostrifrons* appears to be better adapted to the ETP than *R. nasutus*.

Cosmocalanus darwini s.1. This category includes *C. darwini* s.s. and *C. caroli* s.s., which were not counted separately. They constituted about 3.65% of the total number of copepods and occurred mainly from 3°N to 4°S above 200 m at stations 20-22. The maximum number of females (17,900 individuals/1000 m^3) was concentrated between 100 and 150 m (Figure 8). Apart from this, there were other high concentrations above 120 m at stations 14, 12, and 10 between 23° and 20°N. Although diel vertical migration was not apparent, the numbers at night were much higher than the numbers in day samples. The species were concentrated between 50 m and the surface. Female numbers were higher than those of males.

Pleuromamma indica. The numbers of this species were the highest for the genus *Pleuromamma* in the ETP. The species was found at most of the stations occupied (Figure 9). Females occurred primarily between 250 m and 600 m during the day. The depths of maximum concentrations were from 350 to 400 m between 6°N and 8°N. Maximum numbers were 2800 individuals/1000 m^3. Female vertical distribution at night was from 150 to 300 m between 20°N and 3°N. It appears that vertical distribution was shallower north of 12°N than south of this latitude. The data suggest that the species undergoes diel vertical migration.

Pleuromamma gracilis. The numbers of this species were less than that of *Pleuromamma indica*. *P. gracilis* was distributed at most of the stations occupied except stations 16 and 17. Females occurred mainly from 200 to 600 m between 5°S and 8°N in day samples. The depths of maximum concentrations were from 300 to 450 m. Females occurred only above 200 m between 20°N and 22°N. Maximum numbers were 11,600 individuals/1000 m^3. Most males occurred mostly above 200 m in night samples (Figure 10).

Pleuromamma abdominalis. The numbers of this species were the lowest for the genus in the ETP. Females were distributed at most of the stations except stations 16 and 17. Females usually occurred between 200 and 600 m, but at stations 18-20 they occurred at depths below 400 m in day samples. The ranges of vertical distribution of females and males were similar. The maximum concentration was 1000 individuals/1000 m^3 and was found between 300 and 450 m. The shallow depths of females and males in night samples suggest pronounced diel vertical migrations over an extensive vertical range (Figure 11).

Euchaeta rimana. *E. rimana* was confused with *E. marina* until it was separated by Bradford (1974). Its number (2.42%) occupied ninth position among copepods of the ETP area. It was found in lower numbers in day samples than in night samples. Its vertical distribution extended from the surface to 600 m, but in general it was concentrated above 100 m. The maximum number was 35,600 males, 13,800 females, and 62,400 juveniles per 1000 m^3. The species occurred in low numbers (130-800 individuals/1000 m^3) below 200 m.

Euchaeta acuta and *media*. *E. acuta* and *E. media* were not distinguished from one another in the present study. Together they constituted the most abundant category of *Euchaeta* in the ETP. They were less frequent in day samples than in night samples. Their horizontal distribution was vast, extending from the California coast to the southernmost stations. Their vertical distribution was from the surface to the deepest depths. They were not found at the surface or subsurface in the oxygen-deficient area north of 6°N.

Nannocalanus minor. Although this is a tropical to subtropical, oceanic species, *N. minor* was found mainly at station 10, which was dominated by hydrographic conditions indicative of the California Current. The maximum number of females reached 11,900 individuals/1000 m^3 in day samples and 119,000 individuals/1000 m^3 in night samples. It also was found at station 22 (about 4°S), where it was concentrated mainly above 200 m in day samples. Elsewhere *N. minor* occurred mainly above 100 m. Its overall depth distribution tended to coincide with the depth of the thermocline.

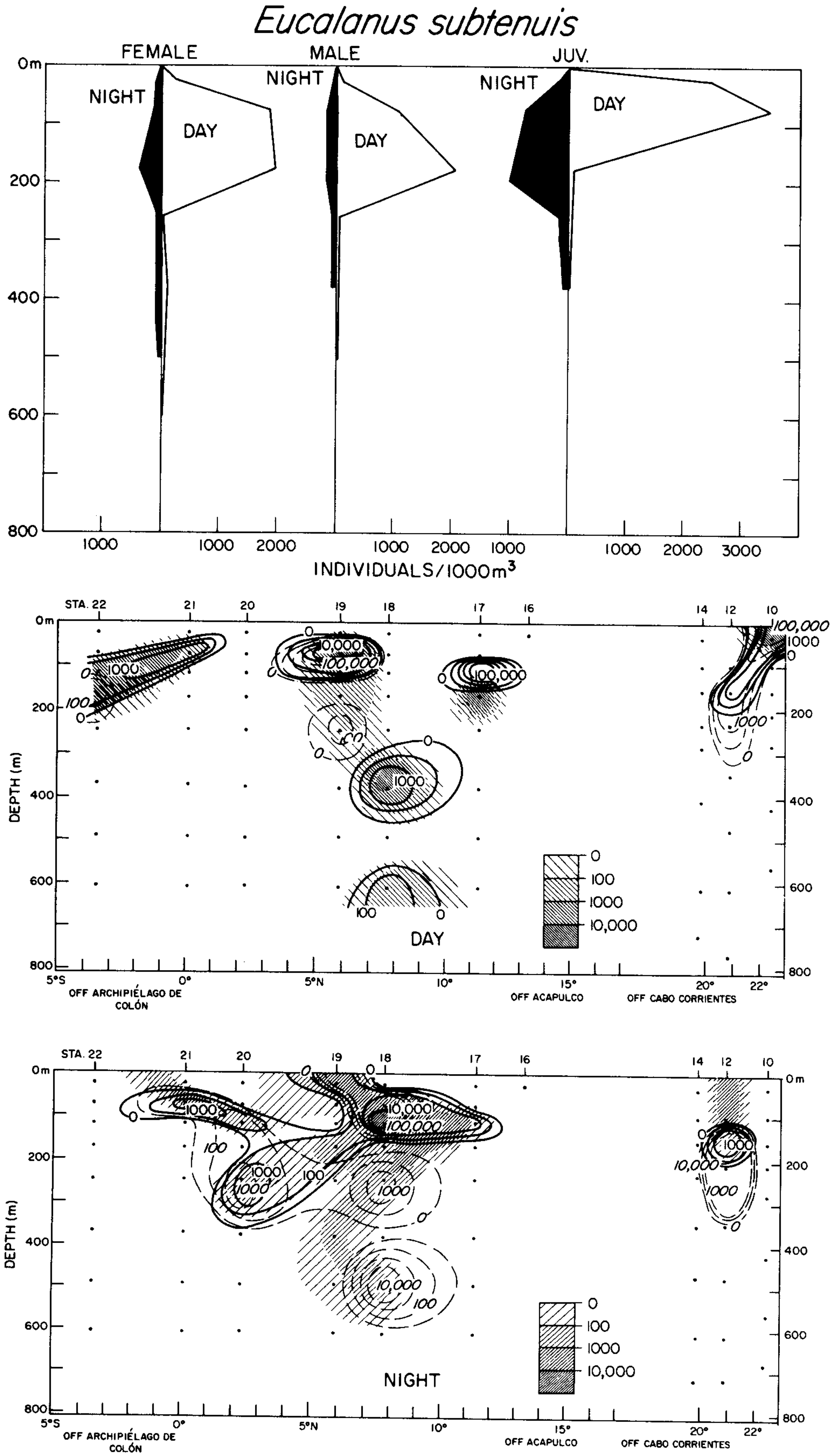

Figure 2. *Eucalanus subtenuis*. *Top panel:* Vertical profile of mean abundance (no./1000 m^3) of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. Night values to left, day values to right. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Sampling stations are shown across top, latitudes across bottom, and vertical depth scale along sides of middle and bottom panels. Dots represent midpoints of oblique tows.

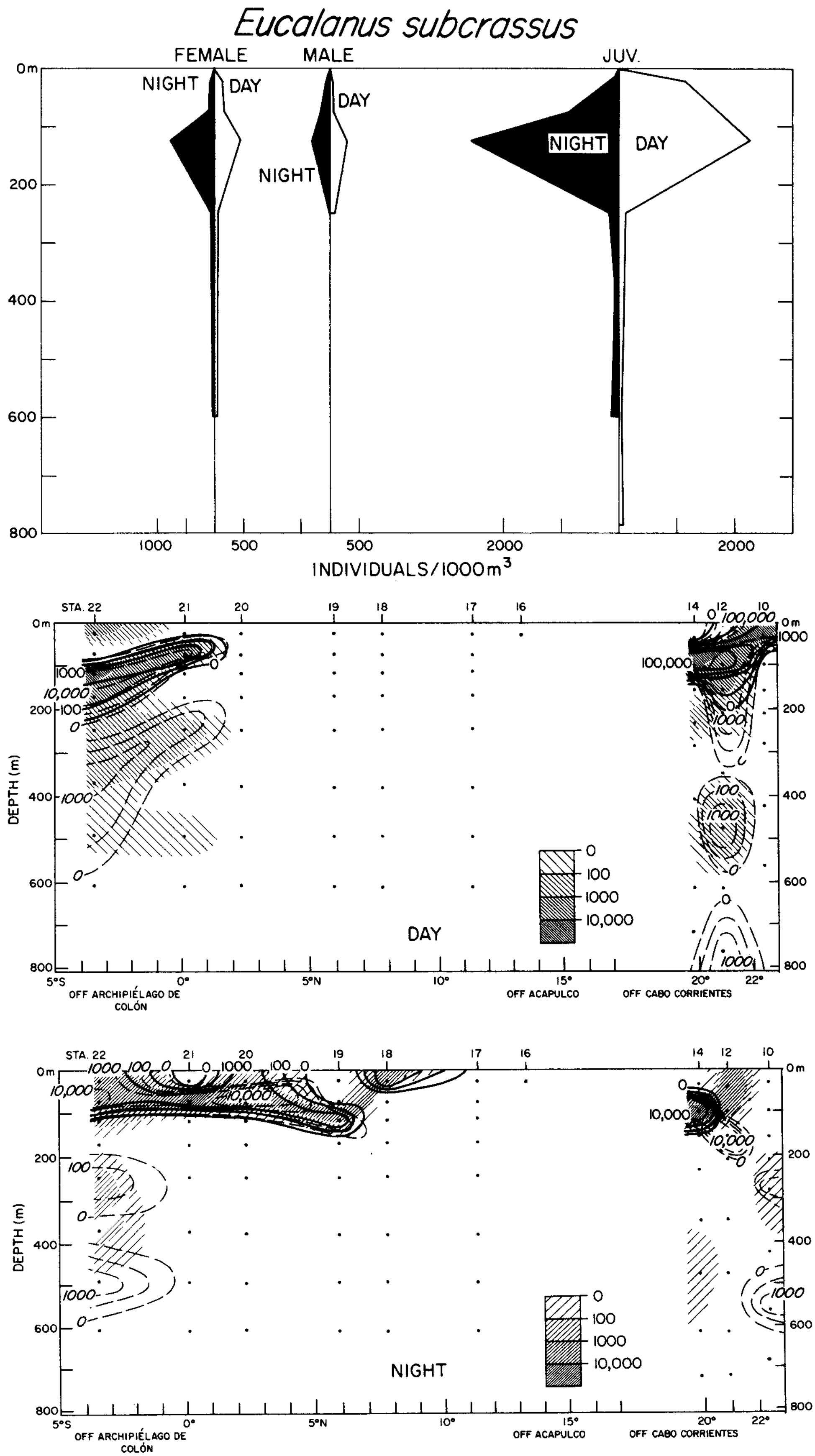

Figure 3. *Eucalanus subcrassus. Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

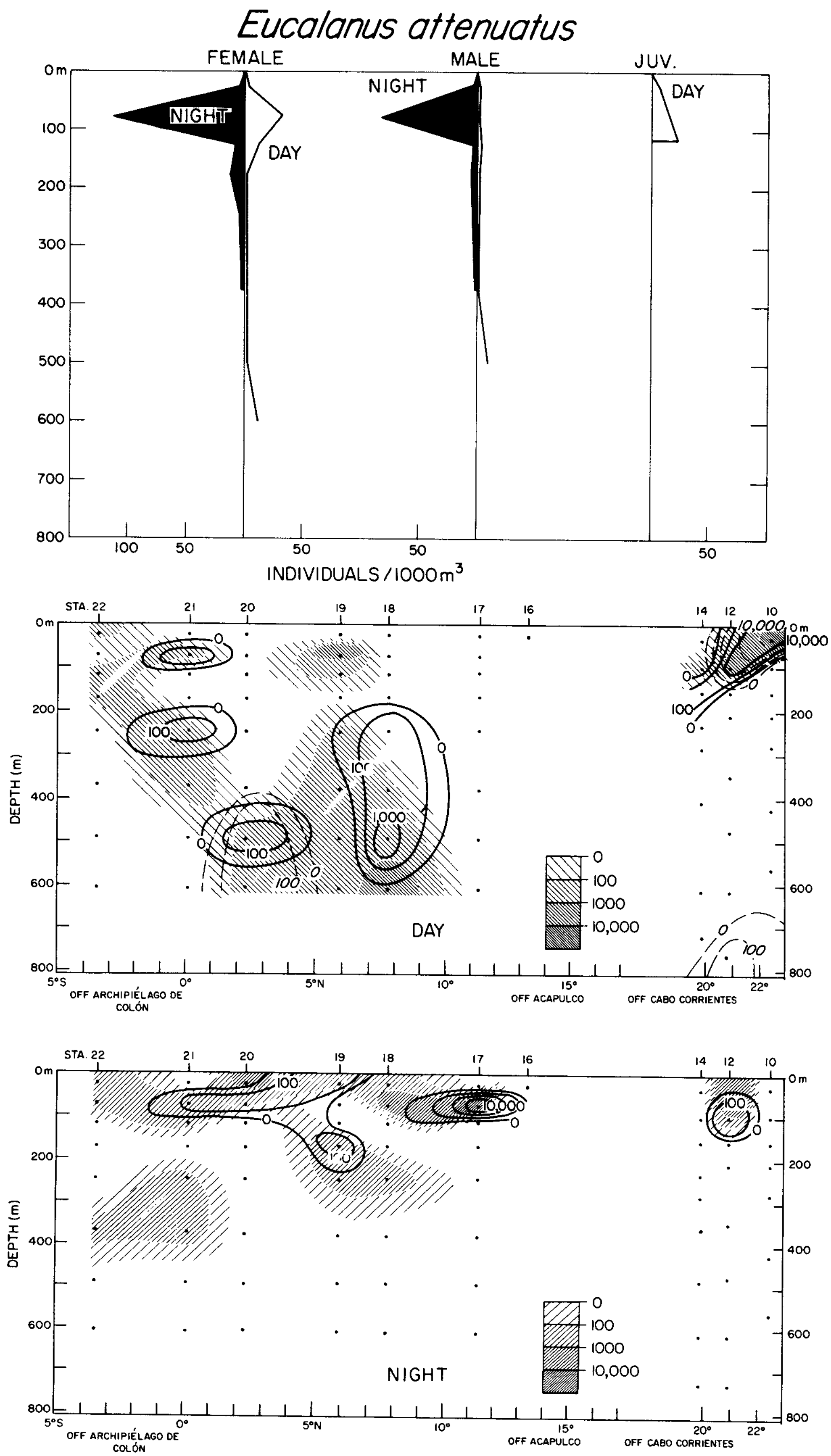

Figure 4. *Eucalanus attenuatus* s.l. *Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

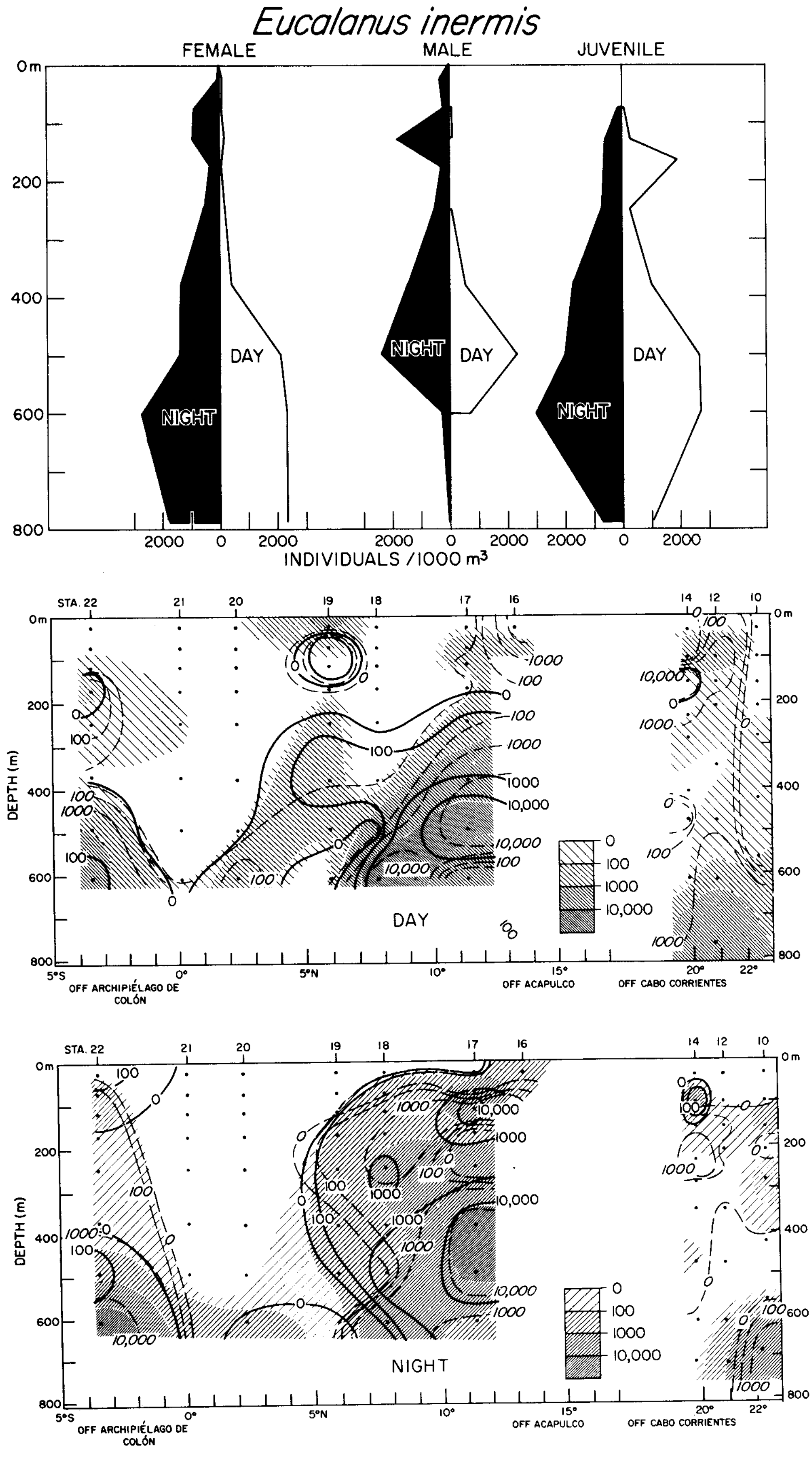

Figure 5. *Eucalanus inermis*. *Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

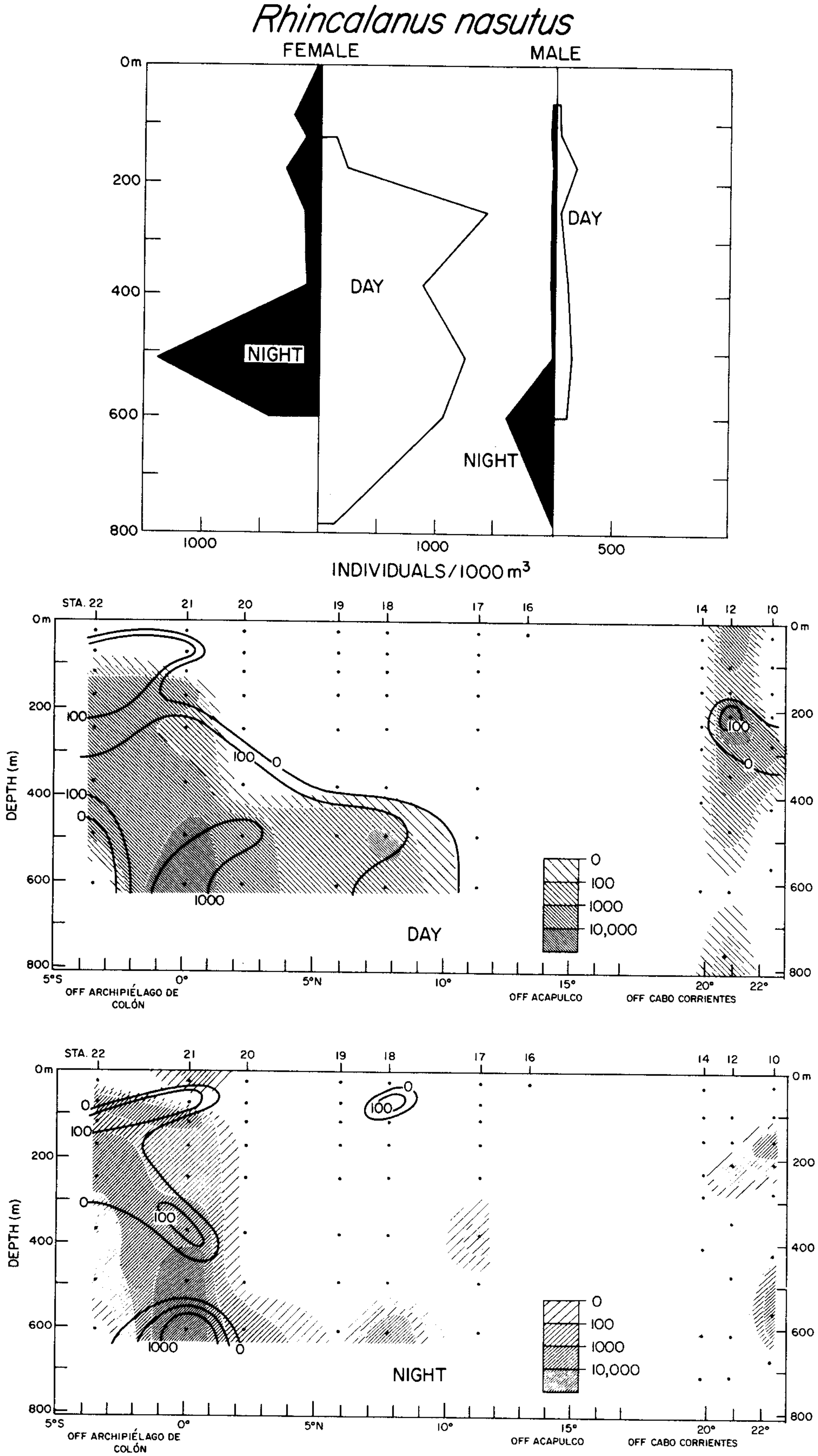

Figure 6. *Rhincalanus nasutus. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

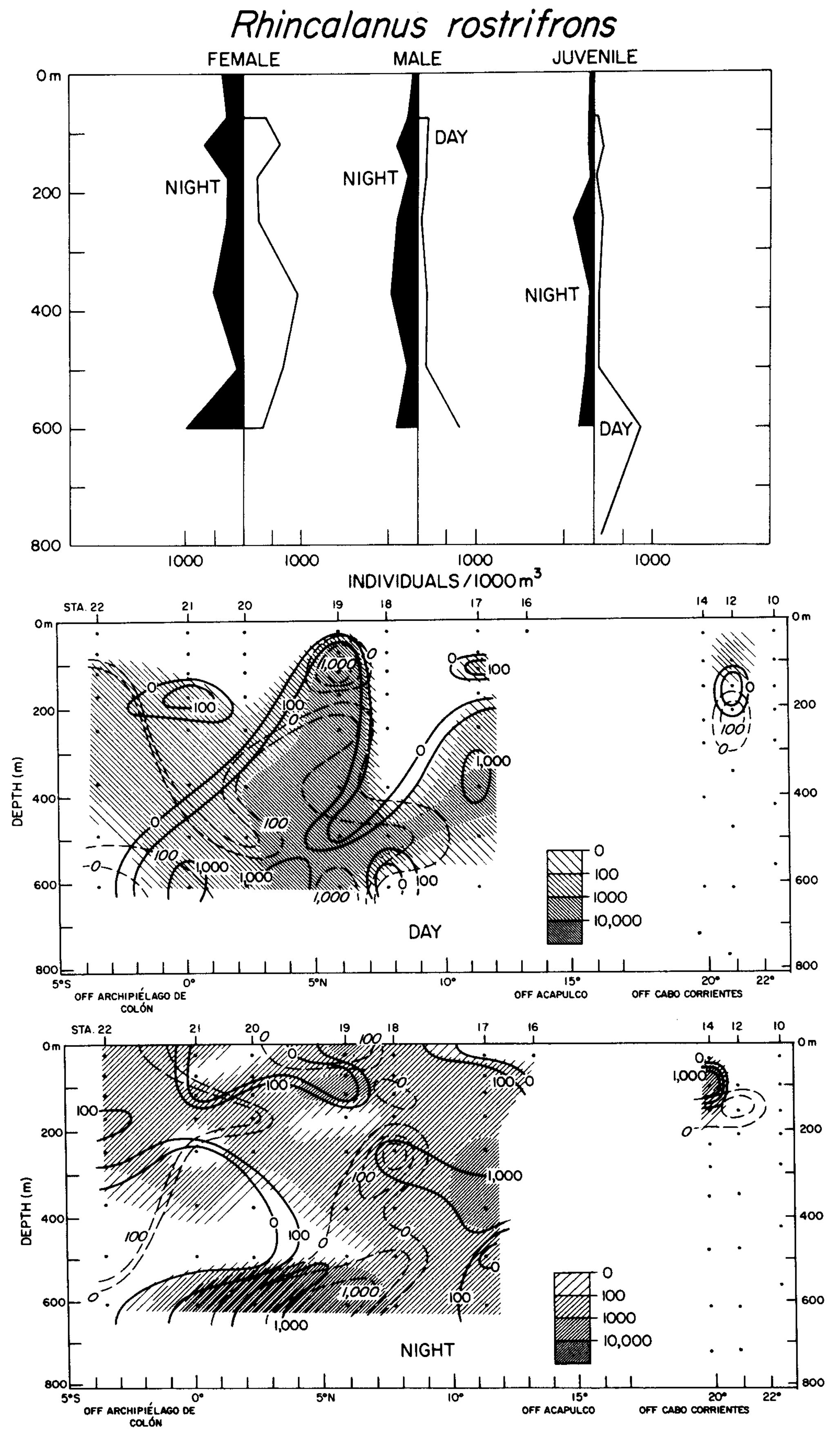

Figure 7. *Rhincalanus rostrifrons. Top panel:* Vertical profile of mean abundance of females, males, and late copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of copepodites (broken line), males (continuous line), and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of copepodites (broken line), males (continuous line), and females (crosshatching). Dots represent midpoints of oblique tows.

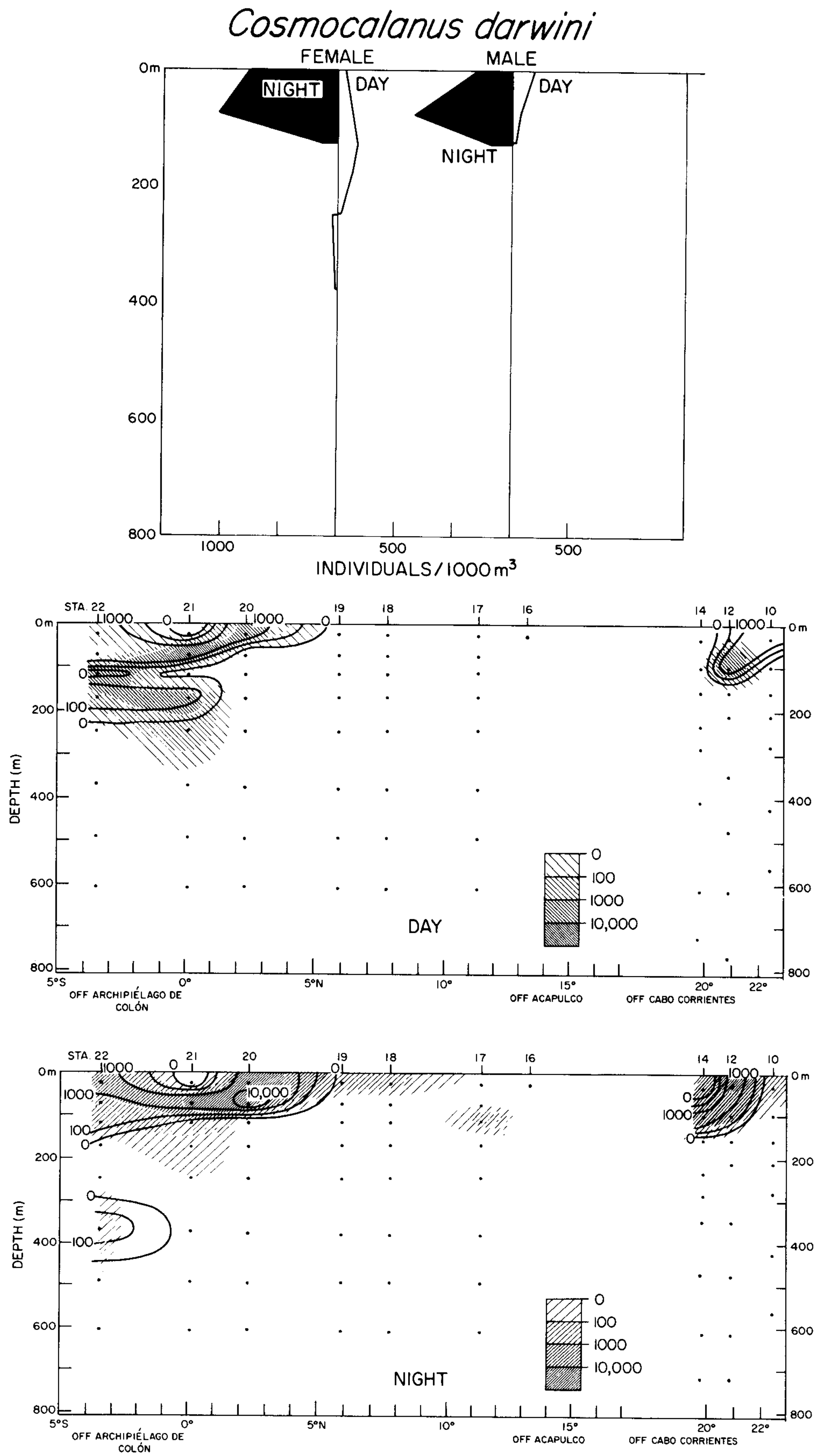

Figure 8. *Cosmocalanus darwini* s.l. *Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

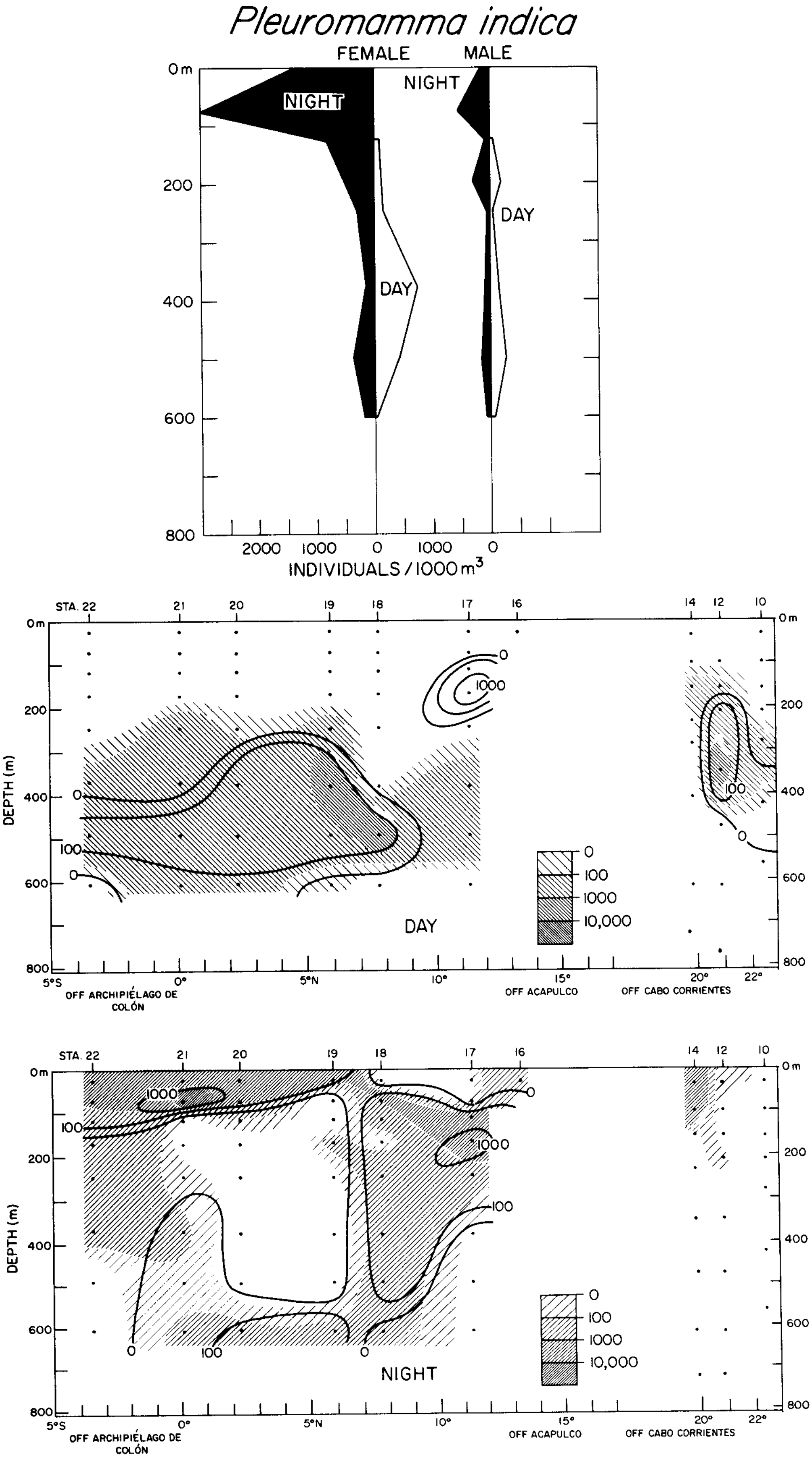

Figure 9. *Pleuromamma indica. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

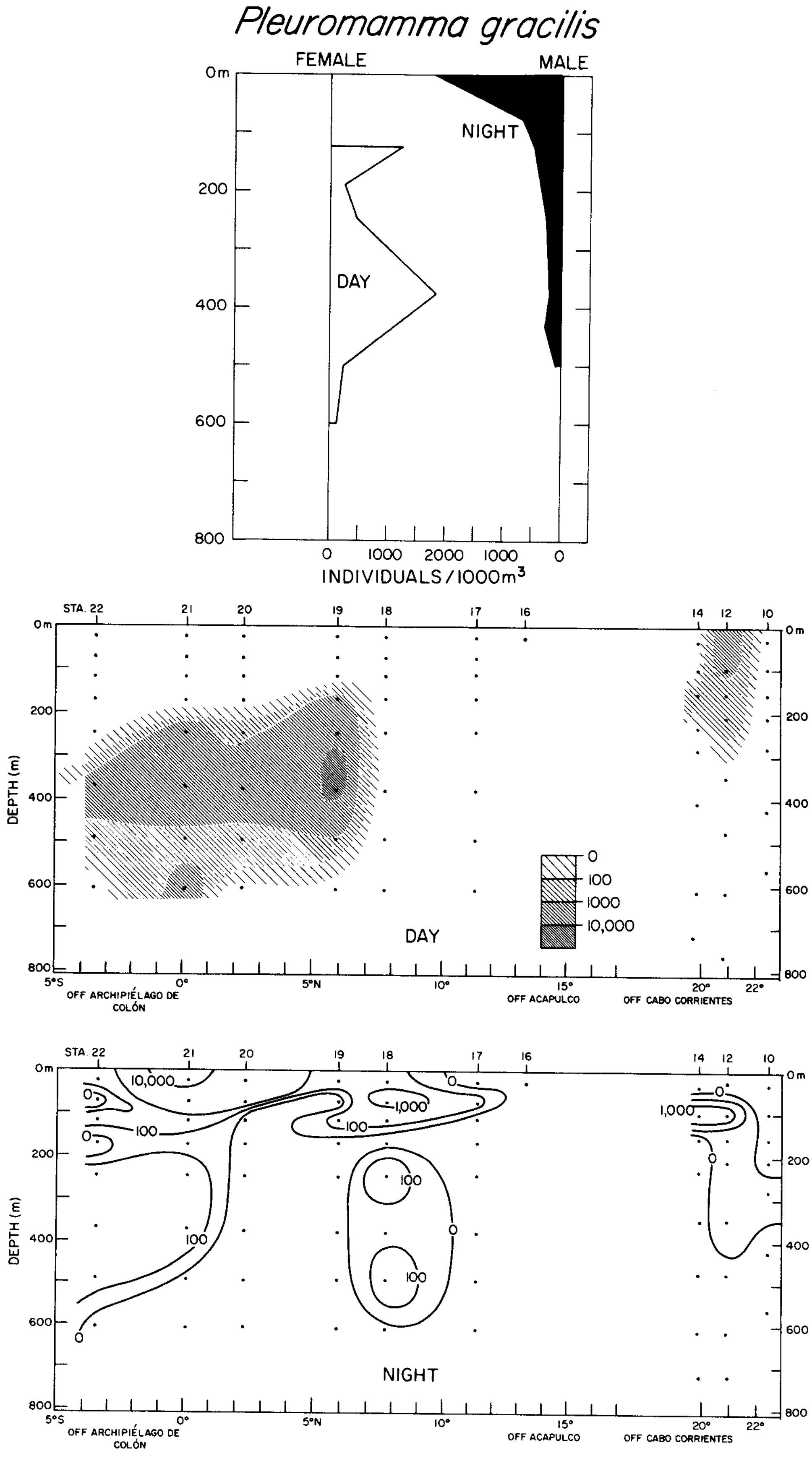

Figure 10. *Pleuromamma gracilis. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m^3) in day samples of females. *Bottom panel:* Vertical profile of contoured abundance in night samples of males. Dots represent midpoints of oblique tows.

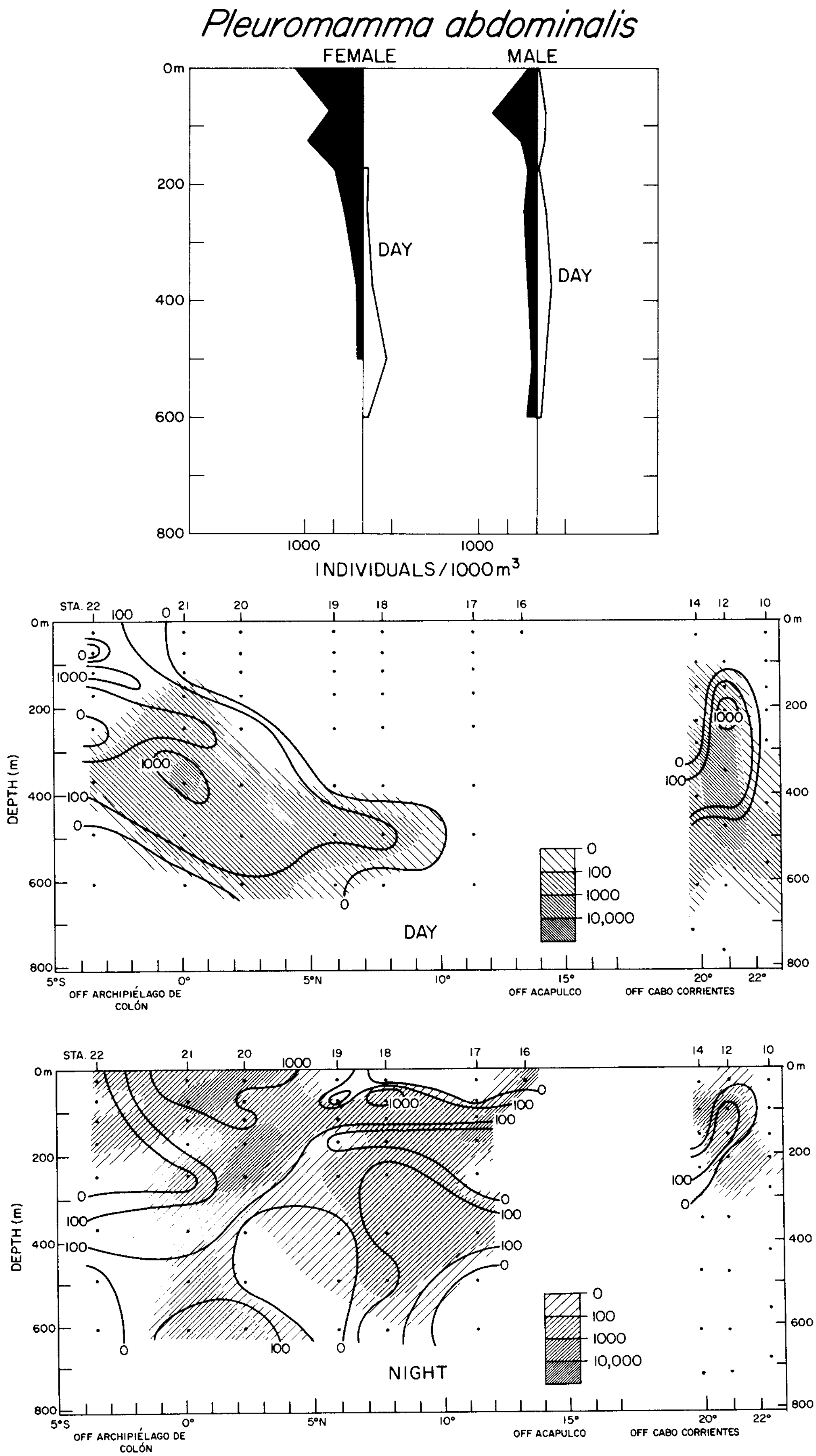

Figure 11. *Pleuromamma abdominalis. Top panel:* Vertical profile of mean abundance of female and male copepodites at mean sampling depth intervals, data from all stations pooled. Night values to left, day values to right. *Middle panel:* Vertical profile of contoured abundance (values of intervals in no./1000 m³) in day samples of males (continuous line) and females (crosshatching). *Bottom panel:* Vertical profile of contoured abundance in night samples of males (continuous line) and females (crosshatching). Dots represent midpoints of oblique tows.

Scolecithrix danae. This broadly tropical oceanic species was found everywhere except in the oxygen-deficient area of the ETP. The main concentrations occurred above 150 m, especially in night samples. The maximum numbers were 300-1500 individuals/1000 m^3 at station 14 from 0 to 100 m. In day samples the total numbers were lower, but female numbers were higher. Vertical distribution tended to coincide with the thermocline. Abundance declined from north to south.

Aetideus pacifica. This species occurred mainly below 100 m. In general, it ranged from 100 to 350 m at abundances varying from 200 to 500 individuals/1000 m^3. The maximum female concentration was 8160 individuals/1000 m^3. Female numbers were higher than those of males and juveniles. In night samples *A. pacifica* was found in the uppermost 100 m. A maximum of 13,600 individuals/1000 m^3 was observed between 0 and 100 m at station 14; the species also occurred at 600 m. It was not found in the oxygen-deficient area.

Temora discaudata. This species is found commonly in coastal waters of tropical to warm-temperate areas. It occurred mainly above 400 m over the entire area of investigation, except for the oxygen-deficient region. Its main concentrations were found between 50 to 100 m. Its maximum concentration (11,000 individuals/1000 m^3) was in a day sample from 0 to 50 m at station 10, although numbers were usually higher in night samples than in day samples.

Neocalanus gracilis. This species was found mainly in mid-depth to surface samples taken south of 10°N (stations 18-22). The greatest depth of occurrence was 500 m, where the number (142 individuals/1000 m^3) was less than that at 50 m. In night samples the species was found, in greater numbers than in day samples, between 0 and 350 m. The maximum number was 1020 individuals/1000 m^3 in 0-50 m at station 21. *N. gracilis* was not present in the oxygen-deficient area.

DISCUSSION

Hydrographic Conditions

To understand the distributions indicated above, it is necessary to review oceanographic environmental conditions along the Krill Expedition's cruise track. These conditions were originally described by Brinton (1979).

Between stations 10 and 11, flow appeared easterly, as indicated by the slope of the σ_t surface and the surface temperatures of 23.8° and 24.9°C (Figures 12 and 13). At station 12, near 21°N off the middle of the mouth of the gulf, subsurface influence of the California Current was evident from the higher oxygen content (Figure 13b) and from the presence of northern euphausiid species, although surface temperatures were > 24°C (Figure 13a). Stations 13 and 14 were south of 21°N, lying in waters considerably warmer at all depths than those to the north, and showed fully developed characteristics of the ETP, evidently associated with northerly or easterly flow toward the gulf.

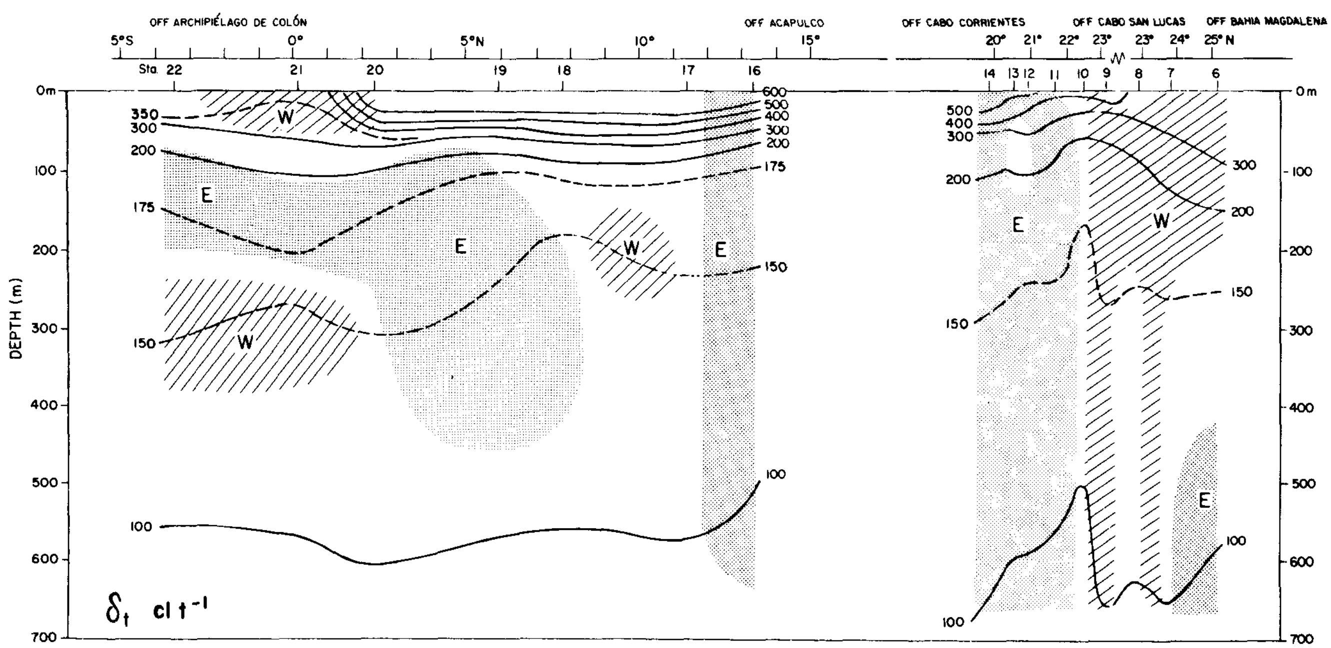

Figure 12. Vertical distribution of thermosteric anomaly σ_t (cl_t^{-1}). Direction of zonal components of flow is inferred from slopes of isopleths; inferences within about 2° of the equator are least reliable. From Brinton (1979).

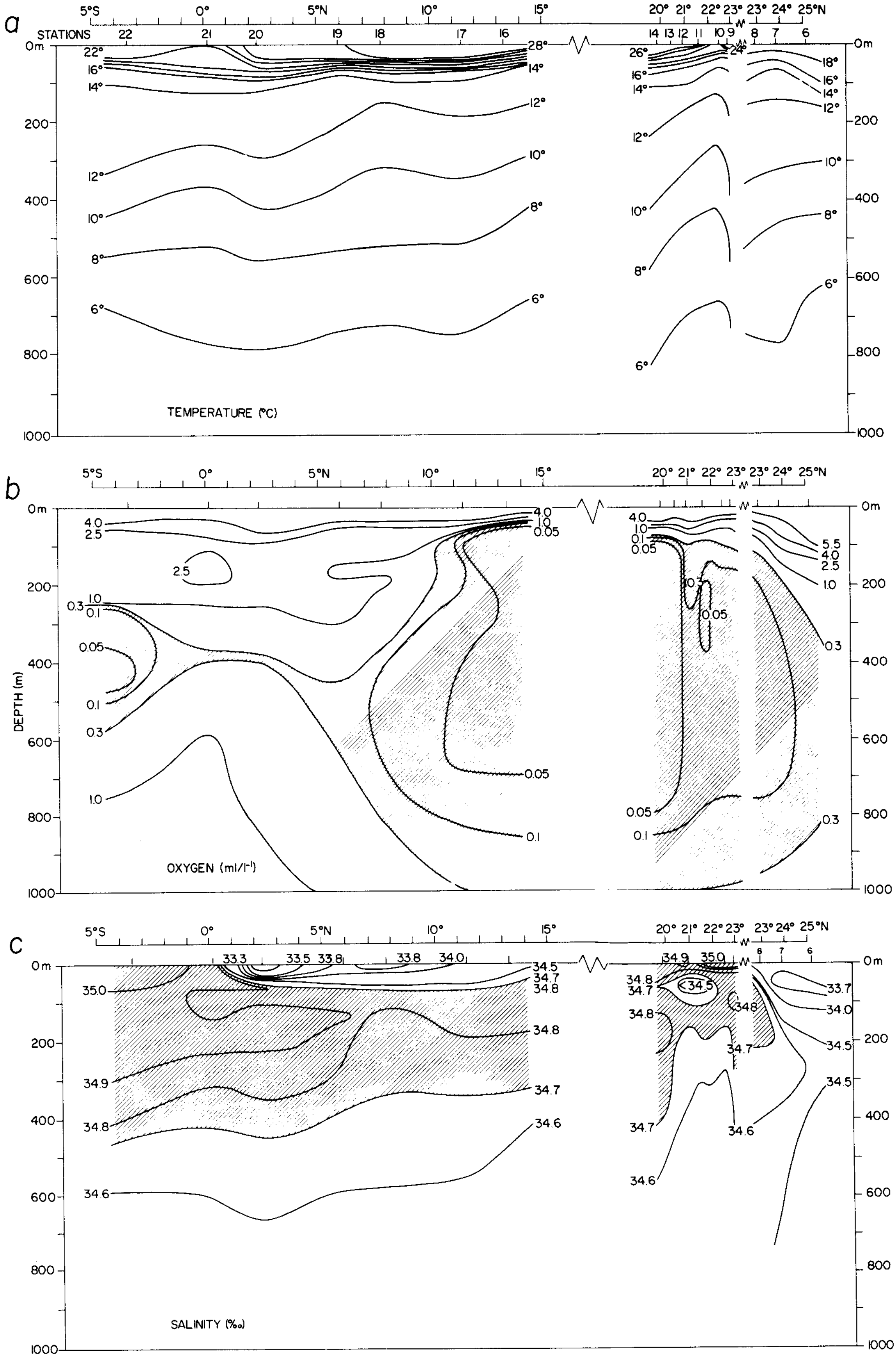

Figure 13. Profiles of *(a)* temperature, *(b)* dissolved oxygen, with depths having < 0.3 ml/l^{-1} crosshatched, and *(c)* salinity, with depths having >34.7‰ crosshatched. From Brinton (1979).

Along the Krill Expedition's cruise track, the weak thermocline at 50-100 m off Baja California gave way to the strong ETP thermocline between 25 and 60 m off the gulf (Figures 12 and 13a).

The distribution of oxygen (Figure 13b) also showed strengthening of ETP characteristics along the southerly track, as oxygen values in the minimum layer progressively decreased south of 25°N, where the lowest measurable value (< 0.05 ml/l^{-1}) was first encountered. This low value was uniformly distributed in a thick, oxygen-deficient layer between 11°N and 21°N (Figure 13b). Extremely low oxygen concentrations (< 0.05 ml/l^{-1}) were also present at some depths at stations 11 and 22.

Salinity (Figure 13c) was < 34‰ above 100-m depth off Baja California, indicating water of northern origin. The core of the flow appeared in the 33.7‰ southerly tongue at 50-100 m. The axis of the deep countercurrent of the California Current (Reid et al. 1958) was evident at 200-400 m, where water having salinity in excess of 34.5‰ extended northward. To the south, ETP salinities were high (34.6-35.0‰), except for a localized subsurface patch off the mid-gulf (station 12), where salinity was lower (34.5‰) and associated with an increase in oxygen above 300 m and with plankton species indicative of California Current influence.

The Krill Expedition's transect (stations 16-22) across the ETP was between the 88°W and 98°W meridians. Tsuchiya's (1974) April-May 1967 chart of flow above 500-m depth showed flow varying between easterly and westerly in the area where stations 16 and 17 were situated (ca. 13°N and 11°N off southern Mexico). On the Krill Expedition's transect, the slope of σ_t surface (Figure 12) indicated an easterly component of flow at all observed depths between stations 16 and 17; however, south of station 17 there was a westerly component centered near 200-m depth. In these latitudes the characteristic ETP oxygen minimum was highly developed beneath 70 m, indicating little dilution by other water masses (Figure 13b). High temperature (> 28°C) and low salinity (< 34‰) were found in the 50-m-thick mixed layer (Figure 13a,c). Stations 18 and 19 were occupied between 6°N and 8°N, typically the zone of the North Equatorial Countercurrent. Tsuchiya (1974) showed easterly flow across 97°E between 4°N and 6°N during April and May 1967, and Love (1971) reported easterly flow between 4°N and 8°N during July 1967. Wyrtki and Kendall (1967) provided evidence that eastward geographic flow in the countercurrent is maximal from March through June, overlapping the time of the present observations. Brinton (1979) reported finding considerable faunistic evidence of the countercurrent's influence in this zone.

At station 20 (2°41′N), extremely low surface salinity (< 33.3‰) indicated westerly flow in the mixed layer. However, the presence here of 13°C water (Jones 1973) and a secondary oxygen maximum at 100-200 m indicated a contribution from the easterly Equatorial Undercurrent, which mixed with ETP water beneath and lateral to the undercurrent's core. At equatorial station 21, 0°19′N, stronger evidence of the undercurrent's activity was seen between 100- and 225-m depth in the 13°C water, the secondary oxygen maximum in excess of 2.5 ml/l^{-1}, and the secondary salinity maximum. Station 22, south of the Galápagos Islands, was also in water of high surface salinity, again indicating little or no contribution of westerly water by the South Equatorial Current. Salinity was homogeneous between 60 and 275 m, but an oxygen maximum near 150 m intercepting the generally oxygen-deficient water beneath the mixed layer indicated penetration by water from a direction other than the east. Faunistically, this locality was mixed, but without the easterly intrusions found at the equator (Brinton 1979).

Patterns of Vertical Distribution of Copepods in the ETP

Vertical distribution of copepods in the Krill Expeditions transect varied, probably because of the different environmental conditions encountered along the cruise track. It is necessary to consider the variations in vertical distribution among the species in order to understand relationships within the ETP.

Table 2 shows that patterns of vertical distribution of ETP copepods can be divided as follows:

From the surface to 200 m. Sixteen species occurred between the surface and 200 m. They constituted about 28% of the total calanoid numbers identified and were mainly tropical and oceanic. Environmental conditions were rather different above than below 200 m. The thermocline layer extended from 50 to 80 m, and the temperature gradient tended to be very steep. The range of temperature differed in different areas; thus it was 14°-28°C south of 15°N, while north of 20°N it was 12°-26°C. Salinity ranged from 33.3 to 34.9‰ above 200 m. The low salinity suggests the possible influence of neritic waters, and the zooplankton included some broadly neritic species such as *Centropages furcatus* and *Temora discaudata*.

From the surface or 50 m to 320 m. The range of vertical distribution of five ETP copepods was from the surface to 300 m. *Phaenna spinifera* was distributed between 200 m and 320 m in day samples and between the surface and 200 m in night samples. *Lophothrix* sp. was rare and occurred only from 200 to 320 m where hydrographic conditions are relatively stable (12°-14°C, 34.0-34.8‰).

TABLE 2
Maximum Depth Range of More Abundant Copepod Species in Day (▭) and Night (▬) Samples

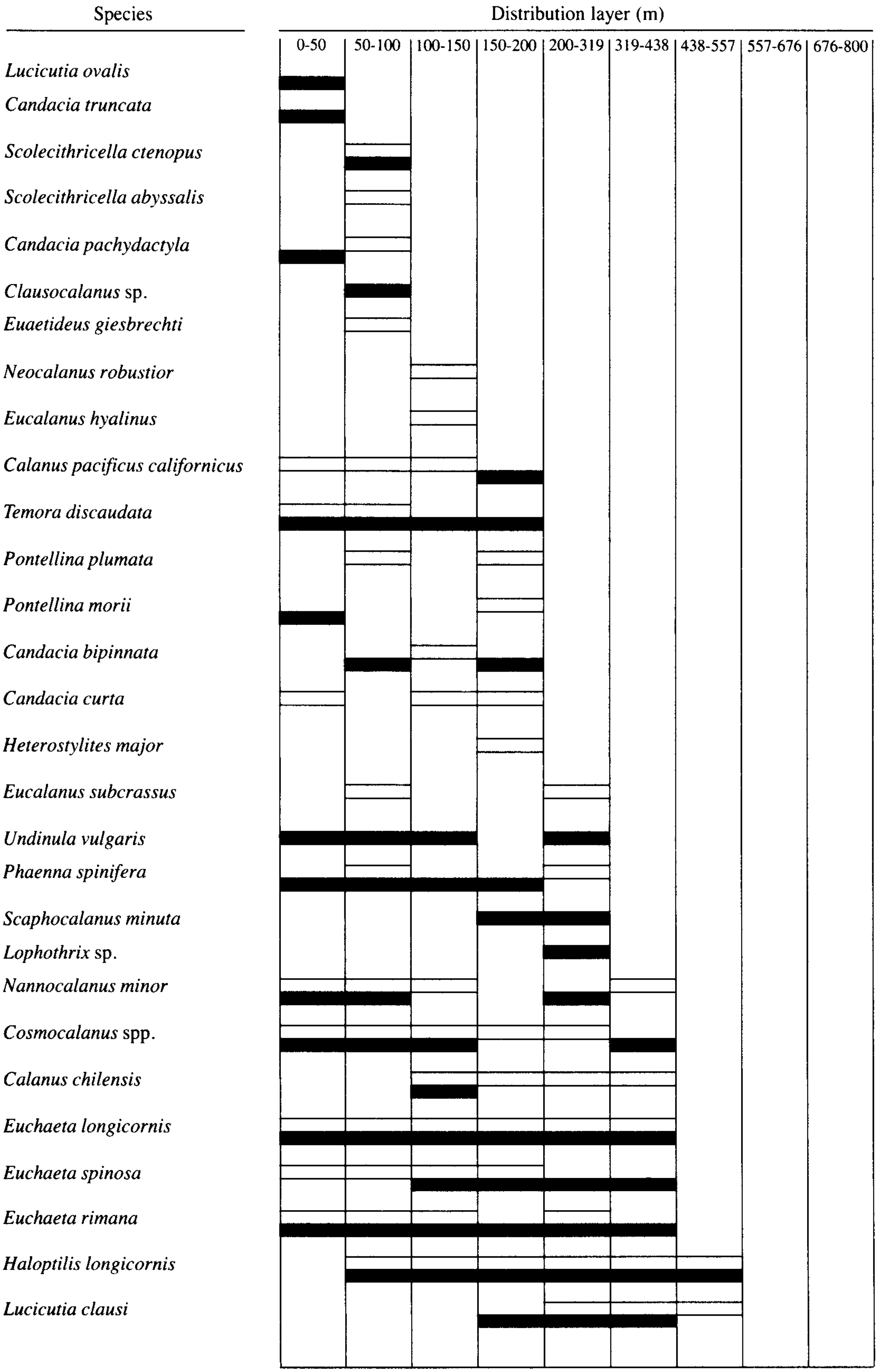

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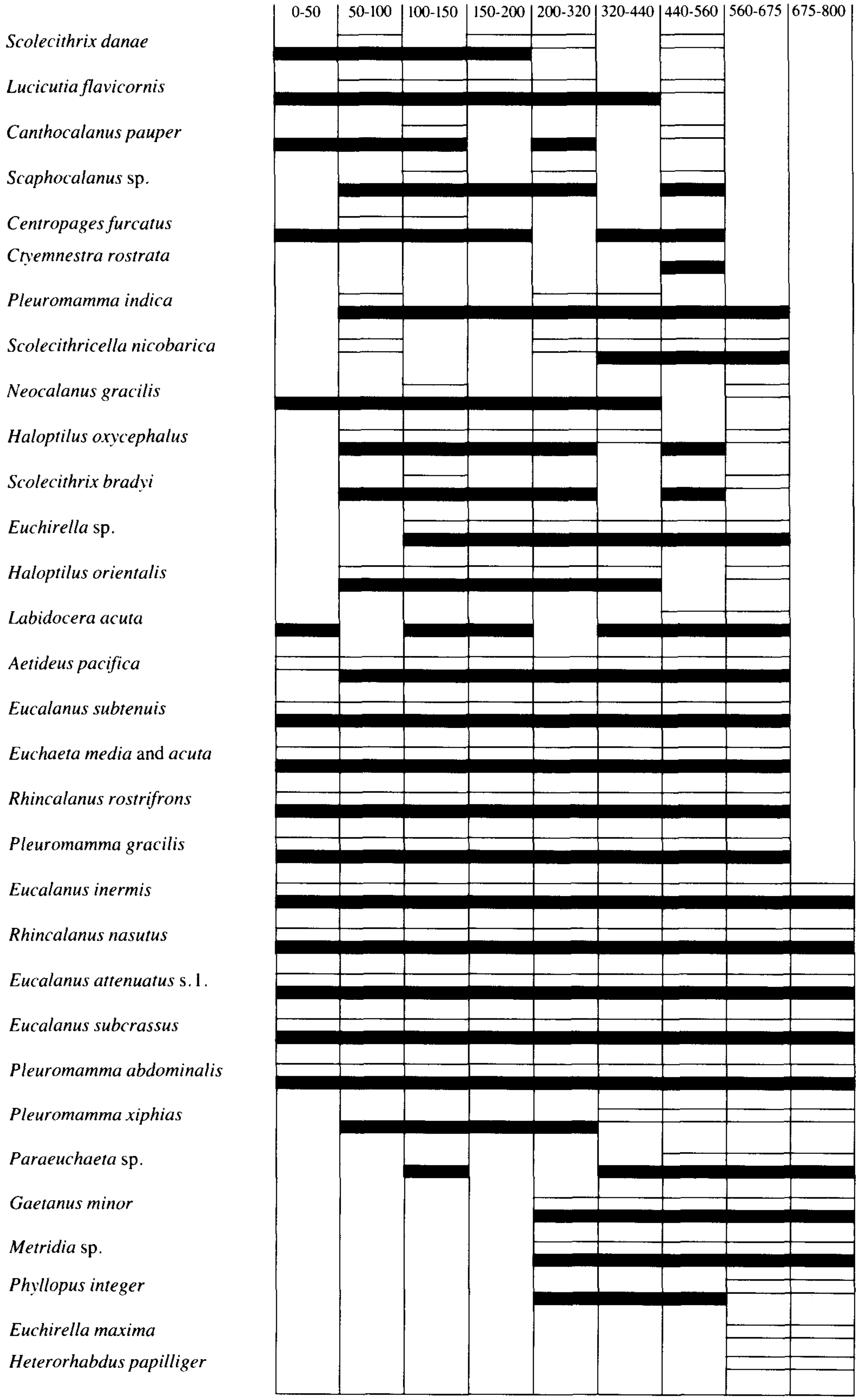
TABLE 2—*Continued*

Maximum Depth Range of More Abundant Copepod Species in Day (▭) and Night (▬) Samples



From the surface to 440 m. Six species were restricted to depths above 440 m in the ETP.

From 440 to 800 m. Thirty-two species, or about half of the total species list, were found in samples taken between 440 and 800 m. These species can be subdivided into several subgroups on the basis of vertical ranges as follows:

1. Distribution above 560 m. *Lucicutia clausi, Canthocalanus pauper, Scolecithrix danae,* and *Lucicutia flavicornis* reached this depth in day samples, but they occurred in shallow water (above 150 m) in night samples.
2. Distribution above 680 m. Thirteen species occurred above 676 m. Twelve species were found in day samples and nine species in night samples. The vertical range of five species (*Eucalanus subtenuis, Rhincalanus rostrifrons, Euchaeta media* and *acuta, Pleuromamma gracilis*) extended from the surface to 680 m in both day and night samples.
3. Distribution to 800 m. Twelve species occurred in the samples obtained from 800 m. Five of these species were distributed from the surface to 800 m in both day and night samples. They were numerically dominant species in the ETP. The range of vertical distribution of three species (*Gaetanus minor, Metridia* sp., and *Phyllopus integer*) was from 200 to 800 m. *Euchirella maxima* and *Heterorhabdus papilliger* were found only below 560 m.

Relationship between Currents and the Distribution of Copepods in the ETP

Brinton (1979) described four environments in the ETP that differ in physical and chemical conditions as well as in their euphausiid species. He reported that stations from 25°N to 21°N were located in a transition between the California Current and the ETP, merging a coastal upwelling regime with strongly stratified tropical water. The copepods in this sector were characterized by temperate species of the California Current region. In California Current water (23°N-25°N) above 200 m, the temperature was 12°-18°C. South of 23°N the temperature above 100 m increased, varying from 14° to 26°C, and the temperature gradient increased (Figure 13a).

Station 10 was located at a transition from California Current water to Gulf of California water. The zooplankton obtained at this station was a mixture of the two biogeographically different regions. Numerically dominant ETP species included *E. subtenuis, E. attenuatus* s.l., and *E. subcrassus*. The numerically dominant California Current species was *Calanus pacificus californicus*. All occurred in high concentrations in the mixed waters above 70 m, where the temperature ranged from 18° to 24°C.

The oxygen-deficient region of the ETP between 21°N and 10°N has tropical water forming a shallow surface layer (Brinton 1979). At the bottom of the shallow oxycline, oxygen was < 0.05 ml/l^{-1}, and temperatures were compressed in a steep gradient ranging from 28° to 14°C (Figure 13a). The vertical distribution of the oxygen-deficient layer extended from 25 m to as deep as 600 m. The changes in depth reflect the influence of the Equatorial Countercurrent.

According to Brinton (1979), euphausiids have adapted to the oxygen minimum in two ways. First, one group of species has a vertical distribution that is limited to all or part of the mixed layer, day and night. Second, a group of strongly migrating species tolerates oxygen-deficient waters in their daytime depths of 200-400 m and moves up into the oxygenated mixed layer at night. Comparing the distribution of ETP copepods with euphausiids (Brinton 1979) in the oxygen-minimum layer of the ETP, the patterns of vertical distribution of the former can be divided as follows:

First pattern. About 15 species (e.g., *Eucalanus subcrassus, E. attenuatus* s.l., *E. crassus, E. subtenuis,* and *Cosmocalanus darwini* s.l.) resided in the mixed layer above the oxygen-deficient layer at station 14 or 17.

Second pattern. Some dominant or common species are distributed in both shallow and deep layers, ranging from the surface to 630 m. *Eucalanus inermis* was a typical example of this pattern. Some species in this category also migrated into shallower depths at night. *Pleuromamma indica* and *Pleuromamma gracilis* were found deeper than 300 m in daytime samples but occurred between 100 and 150 m in night samples

Third pattern. Some species occurred in the deepest layers in both day and night samples. Representative species in this pattern were *Euchaeta acuta* and *media, Gaetanus minor, Heterorhabdus papilliger, Haloptilus orientalis,* and *Haloptilus oxycephalus.*

Copepods of the North Equatorial Countercurrent

The copepods residing within middle depths (100-400 m) north of the equator, a zone approximately from 0° to 10°N, were characterized by species considered tropical and oceanic. Stations 18 and 19 (ca. 6°N-8°N) were located in the North Equatorial Countercurrent. Tsuchiya (1974) showed easterly flow across 97°E between 4°N and 6°N during April and May 1967. Wyrtki and Kendall (1967) provided evidence that eastward geostrophic flow in the countercurrent is at a maximum during June. Evidence of the countercurrent's influence on the copepods of this zone was found at stations 18 and 19. Twenty-five species were found in the North Equatorial Countercurrent flow. The representative species were *Eucalanus at-*

tenuatus s.l., *Rhincalanus rostrifrons*, *Aetideus pacifica*, *Gaetanus minor*, *Heterorhabdus papilliger*, and *Euchaeta acuta* and *media*. Most of them are tropical oceanic species abounding in the central equatorial Pacific (Timonin and Voronina 1977) and living in or above the thermocline where oxygen values exceed 1 ml/l. Some of these species appeared to show diel vertical migration. A few neritic species, such as *Eucalanus subcrassus*, were also found in the North Equatorial Countercurrent. *Euchirella* sp., distributed in middle-layer waters at all stations but station 10, seemed endemic to the ETP.

The Equatorial Undercurrent Species

Station 21, located at the equator, lies within the Equatorial Undercurrent (Brinton 1979), and 13°C water at this station implies strong evidence of undercurrent activity (Figure 13a). The westerly South Equatorial Current occupies the surface layer at the equator and extends to greater depths on each side of it. The easterly Equatorial Undercurrent (Cromwell Current) is about 160 km wide in the eastern Pacific (Jones 1969), and the velocity core is consistently at 50-150 m (Taft and Jones 1973).

The range of vertical distribution and migration of copepods in equatorial waters can be divided into different categories as follows:

a. Three species (*Pleuromamma indica*, *P. abdomnalis*, *P. gracilis*) resided mainly below the 200-m layer in day samples and ascended to above 100 m at night. This vertical range could have allowed these species to maintain substantial east-west equilibrium. Easterly transport by the undercurrent during the day, balanced by usually westerly surface transport at night establishes the possibility of locally resident stocks' using opposite-flowing currents of the equatorial system to maintain a relatively fixed geographical position, if current speeds are similar. This vertical range of copepod migration was similar to that of some euphausiids such as *Euphausia eximia* and *Euphausia distinguenda* (Brinton1979).

b. *Scolecithrix danae*, *Euchaeta longicornis*, and *Eucalanus subtenuis*—like *Stylocheiron carinatum*, a euphausiid—had shorter spans of vertical range and nighttime levels even more surface-linked. This was also reported by Timonin and Voronina (1977) and Vinogradov (1970).

c. The vertical distribution exceeded 200 m during the day and 300-500 m or deeper at night. Species showing this distribution include *Metridia* sp., *Scaphocalanus minuta*, *Gaetanus minor*, and *Haloptilus longicornis*. They occurred beneath the thermocline and undercurrent, where horizontal flow is presumed much weaker.

d. *Eucalanus attenuatus* s.l. and *Cosmocalanus darwini* s.l. occurred at and beneath the thermocline at depths of the undercurrent. They appeared to be nonmigrating at the equator and seemed to be entrained within the undercurrent, which would ensure easterly drift toward unsuitable waters. In comparison with the data of Timonin and Voronina (1977), *Eucalanus attenuatus* s.l. was distributed deeper at the equator in this investigation.

It is necessary to note that the higher surface salinity at station 22, located near the Galápagos Islands, indicates that this locality was not strongly influenced by westward flow from the South Equatorial Current. The presence of *Calanus chilensis* at stations 21 and 22 indicated mixing of several different water currents, including an intrusion of the Peru Current, which may account for the oxygen-deficient water beneath the mixed surface waters.

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