

THE DAY AND NIGHT VERTICAL DISTRIBUTIONS OF CALANOID
COPEPODS IN THE WESTERN GULF OF MEXICO, WITH
REFERENCE TO FEEDING RELATIONSHIPS

A Thesis

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ABSTRACT

The Day and Night Vertical Distributions of Calanoid Copepods
in the Western Gulf of Mexico, with Reference to
Feeding Relationships. (August 1974)

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The day and night vertical distributions of total zooplankton and calanoid copepods were examined to a depth of 1000 m at a station in the western Gulf of Mexico. Interrelationships between abundant species with similar and varying feeding habits were analyzed as possible factors contributing to vertical distribution and migration.

The vertical distribution of the zooplankton at this station in the western Gulf was generally comparable with published results on vertical distribution in tropical oceanic regions. The greatest volumes of zooplankton and copepods in this study were found in the upper 50 m and they decreased rapidly with depth.

Zooplankton populations in the water column appear to co-exist through a complex assortment of interactions. Interspecific relationships may be important in determining vertical distributions and migrations. The most abundant particle grazing calanoid species were concentrated at 50 m at night and were generally distributed in deeper layers during the day. The common carnivores were most abundant in the upper 200 m of the water column during the day and at night. These

distributions suggest that partial escape from predation, through periodic movements into the deeper layers where carnivore densities are relatively low, may be an important advantage of vertical migrations.

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INTRODUCTION

The distribution of oceanic zooplankton varies in both the vertical and horizontal direction and the habitat of a zooplankter is therefore three dimensional. Zooplanktic organisms have been found distributed into the vast depths of every ocean. Most of them migrate towards the surface at night and away from it during the day. The most important specific triggering factor for these migrations is generally believed to be light intensity (Russell, 1927; Cushing, 1951). Considerable speculation still exists however, as to the advantage to the organism that compensates for the amount of energy expended in these migrations. Many theories, including protection from visual predators, the horizontal dispersion of organisms, and the exchange of genetic materials have been postulated but at best each seems to only partially answer the question (Vinogradov, 1968).

Diurnal migrations play an important role in the vertical distribution of zooplankton. Organisms have developed distributions into the deeper layers to escape excessive predation, competition, crowding, or other consequences resulting from high density populations at the surface. This provides additional ecological habitats and niches in the oceanic community. The photic zone in the open ocean, however, only extends several hundred meters down from the

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surface and phytoplankton, the primary source of energy for zooplankton, is therefore restricted to these upper layers. Vertical migrations allow the structuring of a complex energy flow web from phytoplankton to zooplankton. A working knowledge of vertical distribution and diurnal migration is therefore essential in understanding the structure of oceanic zooplankton communities.

One of the first oceanographic expeditions to establish the existence of zooplankton in the depths of the ocean was that of the "Challenger" (1872-1876). Most early investigations employed simple bridled plankton nets and made vertical tows. The advent of the closing net allowed the sampling of narrower vertical bands without excessive contamination. This method however still has several disadvantages. Vertical tows provide integrated samples over a range of depths and sample sizes are generally small. For these reasons, many studies have substituted the use of closely spaced horizontal tows for sampling vertical communities. Horizontal tows have the advantage of larger sample sizes and narrower depth horizons. Vinogradov (1968), discussing the advantages of vertical tows over horizontal tows, stated that the vertical distribution of zooplankton is not gradual and faunistic changes occur rapidly over short distances. This obstacle however, can be overcome by taking horizontal tows at short depth intervals. In this way, problems with the horizontal patchiness of zooplankton that arise with vertical tows can be avoided.

Work on the vertical distribution and diurnal migration of zooplankton in the open ocean has been extensive. References in this paper are mostly limited to major studies on total zooplankton and calanoid copepods using closing or opening-closing nets in the Atlantic Ocean.

In one of the first major studies on zooplankton vertical distribution, Fowler (1904) (cited in Vinogradov, 1968) examined horizontal and vertical tows to depths of 3660 m in the Bay of Biscay. Farran (1926) analyzed the copepods and compared some day and night samples. Wolfenden (1902, 1904) reported on copepods from various types of hauls to 2200 m in the Farøe Channel and the N.E. Atlantic. From cruises of the "Discovery I" and the R.R.S. "William Scoresby" in the S. Atlantic, Hardy & Gunther (1935) reported on zooplankton including copepods from both horizontal and vertical tows, mostly to 1000 m.

In the western N. Atlantic, Leavitt (1935, 1938) worked extensively on zooplankton and copepod volumes from horizontal hauls. Welsh, Chase & Nunnemacher (1937) towed horizontally at 400 and 800 m in the Sargasso Sea and examined the day and night distribution of copepods and other zooplankton. Lysholm & Nordgaard (1945) described the distribution of copepods to 1920 m in the N. Atlantic. Using oblique tows, Moore (1949) analyzed the vertical distribution of zooplankton including copepods mainly to 300 m by day and night and seasonally in the Bermuda area of the N. Atlantic.

From samples taken on the "Discovery II" cruises in the S. Atlantic, Foxton (1956) reported extensively on zooplankton volumes and their seasonal variations from vertical hauls to 1000 m. Menzel & Ryther (1961) reported seasonal changes of total zooplankton in the upper 2000 m using horizontal tows in the Bermuda area. Colman (1962) using vertically towed nets to depths of 1200 m in the day and 4000 m at night, studied the zooplankton and copepods in the Bay of Biscay. Using vertical tows to depths of 5000 m, Grice & Hulsemann (1965) reported on zooplankton volumes and the abundance and vertical distribution of copepods in the N.E. Atlantic. Wheeler (1970) studied copepods from depths between 2005 and 4100 m in the North and South Atlantic. In a very extensive study on calanoid copepods in the Canary Island area of the N. Atlantic, Roe (1972) analyzed day and night horizontal hauls to 960 m.

In the general area of the Gulf of Mexico, a large amount of work has been done in the Florida Current east of Miami. Miller, Moore & Kvammen (1953) briefly reported on the quantitative vertical distribution of zooplankton. In studying a limited number of species in the area, Moore & O'Berry (1957), Moore & Bauer (1960), Moore & Foyo (1963), and Roehr & Moore (1965) used samples from horizontal tows and attempted to relate day and night vertical distributions to various physical factors. Bsharah (1957) also used horizontal tows in the Florida Current and seasonally recorded day and

night dry weights for zooplankton including copepods to depths of 700 m.

Owre & Foyo (1964) reported on numerous species from horizontal tows to 1750 m in the Caribbean Sea and in 1967 they summarized data on the copepods of the Caribbean Sea and the Florida Current including data on vertical distribution and diurnal migration to depths around 300 m. Park (1970), using vertical tows, described numerous species and their vertical distributions to depths of 2800 m in the Gulf of Mexico and the Caribbean Sea.

Aside from Park (1970) little work has been done on the zooplankton in the open ocean waters of the Gulf of Mexico. In this paper I have attempted to examine some aspects of the zooplankton populations in the relatively stable water of the western Gulf. Samples were taken using opening-closing, paired, bridleless Bongo nets which were towed horizontally. The day and night vertical distribution of total zooplankton and calanoid copepods is reported to a depth of 1000 m and the interrelationships between abundant species with similar and varying feeding habits are examined as possible factors determining vertical distributions and migrations.

METHODS AND MATERIALS

Day and night horizontal tows were taken from the R/V *Alaminos* in an area with a radius of 20 nautical miles from a point, 25°13'N and 91°12'W, in the western Gulf of Mexico. This general area was chosen because of the minimal seasonal variations reported in subtropical oceanic regions (Bsharah, 1957; Heinrich, 1962; Vinogradov, 1968), and this specific station in the western Gulf of Mexico was chosen because of the general stability and relatively long residence time of the water in this area (Nowlin, 1970). According to Nowlin & Hubertz (1970), gyres or rings of water, which have detached from the loop current in the eastern Gulf, are not uncommonly found in the western Gulf region. In order to be certain that samples were taken in typical western Gulf water, the depth of the 22°C isotherm was monitored by using expendable bathythermographs. The depth of this isotherm will indicate whether a gyre has moved into the sampling area (Leipper, 1970; Nowlin & Hubertz, 1970).

The sampling gear consisted of opening-closing Bongo nets (McGowan & Brown, 1966) with 70 cm mouth openings. The net was made of Nitex (Tobler, Ernst & Traber, Inc., New York, N.Y.) with a 363µ mesh size (#2) and a non-filtering collar. A modified double messenger triggering mechanism was used for reliably opening and closing the nets at the desired depths.

Horizontal tows at varying intervals from the surface to 1000 m were taken day and night over a four-day period in May of 1973 (Table 1). The nets were open for one hour in all of the day tows and in the night tows above 500 m. Night hauls at 500 m and below were of longer duration, two hours, because of the low density of organisms present. Tows were not taken during hours nearing sunrise or sunset. The intervals were increased with depth because the structural changes in vertical communities occur more rapidly in the upper layers of the water column (Vinogradov, 1968). Although flow meters were not used, the wire angle and ship speed were kept relatively constant in order to allow the assumption of equal volumes of water being filtered for each one hour tow. A wire angle of 60° was generally maintained and the sampling depth for each tow was determined from the trigonometric relationship between the wire angle and the amount of wire out. Although this is not a precise method of determining sampling depth, large errors due to catenary should only be possible in the deep tows. The ship's speed remained roughly around three knots. The samples were preserved on the ship in 10% formalin.

In the laboratory, fish and organisms over 15 mm in length were removed from the samples before aliquotting in a Folsom Plankton Splitter. In this manner, nekton and the large rarely captured zooplankters such as salps and cnidarians were excluded from any further

TABLE 1. COLLECTION DATA

The sampling area was within a 20 nautical mile radius
from a point, 25°13'N and 91°12'W, in the
western Gulf of Mexico

Depth (m)	Date (1973)	Time
0	4-28	0829-0929
50	4-28	0945-1045
100	4-28	1104-1204
200	4-28	1231-1331
300	4-28	1409-1508
400	4-28	1545-1645
500	4-29	0844-0944
600	4-29	1035-1135
800	4-29	1251-1351
1000	4-29	1526-1626
0	4-26	1903-2005
50	4-26	2029-2129
100	4-26	2153-2253
200	4-26,27	2328-0027
300	4-27	0108-0208
400	4-27	0255-0355
500	4-27,28	2318-0118
600	4-28	0240-0440
800	4-28	1917-2117
1000	4-28,29	2227-0027

consideration. The removal of these large organisms also facilitated the splitting of the samples.

One-half aliquot was used from each sample to determine the displacement volume of total zooplankton. Mature and immature calanoid copepods were removed separately from smaller sub-samples and their displacement volumes were measured. One-eighth of the sample was sorted except in the 50 m day, 50 m night, and 100 m night samples where only 1/16 of the sample was sorted because of the large number of organisms present. The measured volumes from each side of the Bongo's were combined and all volumes were corrected to 1/2 aliquot of the total catch from both nets for a one-hour tow.

Displacement volumes were measured using the mercury immersion method of Yentsch & Hebard (1957). Vacuum filtration was substituted for blowing the water through the filter. In measuring total zooplankton volumes which were relatively large, filtration with 20" Hg of vacuum pressure was continued until water droplets ceased to form on the side of the filtration flask. Displacement volumes for adult and immature calanoids were relatively small and the filtration procedure was changed in an attempt to remove the same percentage of interstitial water in each sample. The vacuum pressure and time of filtration were standardized at 15" Hg and two minutes, respectively.

In sorting calanoid copepods, only those organisms that appeared to be living at the time of capture were removed (Wheeler, 1967). After laying their eggs, many calanoids of the families Calanidae and

Eucalanidae have little body tissue remaining and according to Vinogradov (1968), in the northwest Pacific *Calanus cristatus* is reduced to an "empty shell" after oviposition. Organisms from these families were defined as dead upon capture when the digestive tract and dorsal musculature were missing. Harding (1973) found that bacterial infection in dead *Calanus finmarchicus* spreads from the surface of the exoskeleton into the foregut and the intestinal tract is one of the first internal structures to decompose.

The adult calanoids from the sorted samples were identified and counted. In order to minimize the multiplication of observed numbers to correct for different size aliquots and towing durations, numbers were corrected to 1/4 aliquot of the total catch from both nets for a one-hour tow. The day and night vertical distributions of individual species are listed in Appendix Table 1. When possible, the total length of at least ten specimens of each species was measured. The mean length, range, and the number of specimens measured for each species are recorded in Table 2. Using the mean length of each species and the number of that species found at each sampling level, the mean length of the adult calanoids was calculated for each depth in the day and night.

In describing the day and night vertical distribution of the major families and their most abundant species, additional corrections had to be made to determine their percentages in the water column sampled. As previously explained, tows were not taken at

TABLE 2. SPECIES LIST

The mean size, range (in parentheses), and number of specimens measured are listed in that order for the females and males of each species.

All measurements are in millimeters.

Species	Females	Males	Percent of males ¹
Calanidae			
1. <i>Calanus tenuicornis</i> Dana, 1849	1.82(1.66-1.88), 11	1.77(1.52-1.88), 10	37.7
2. <i>Nannocalanus minor</i> (Claus, 1863)	1.92(1.76-2.04), 15	1.67(1.56-1.76), 15	53.4
3. <i>Neocalanus gracilis</i> (Dana, 1849)	3.40(3.12-3.76), 10	2.73(2.68-2.80), 4	55.4
4. <i>N. robustier</i> (Giesbrecht, 1888)	3.92(3.80-4.04), 2	-	0.0
5. <i>Undinula vulgaris</i> (Dana, 1849)	2.74(2.70-2.80), 3	2.50(2.40-2.60), 2	51.1
Megacalanidae			
6. <i>Bathycalanus richardi</i> Sars, 1905	8.92(8.92), 1	-	0.0
7. <i>Megacalanus princeps</i> Wolfenden, 1904	9.08(9.08), 1	9.16(9.16), 1	50.0
Eucalanidae			
8. <i>Eucalanus attenuatus</i> ² (Dana, 1849)	5.05(4.42-6.00), 13	3.13(2.96-3.24), 12	27.4
9. <i>E. crassus</i> Giesbrecht, 1888	3.20(3.20), 1	-	0.0
10. <i>E. hyalinus</i> (Claus, 1866)	5.80(5.58-6.17), 11	4.04(3.84-4.20), 10	15.5
11. <i>E. monachus</i> Giesbrecht, 1888	2.45(2.28-2.60), 11	-	0.0
12. <i>E. pileatus</i> Giesbrecht, 1888	2.21(2.08-2.38), 11	-	0.0
13. <i>E. subtenuis</i> Giesbrecht, 1888	3.32(3.32), 2	-	0.0
14. <i>Rhincalanus cornutus atlanticus</i> Schmaus, 1916	3.29(3.12-3.48), 13	2.73(2.48-2.88), 7	12.7

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
Paracalanidae			
15. <i>Acrocalanus andersoni</i> Bowman, 1958	1.23(1.18-1.26), 9	-	0.0
16. <i>A. longicornis</i> Giesbrecht, 1888	1.20(1.20), 3	-	0.0
17. <i>Paracalanus aculeatus</i> Giesbrecht, 1888	1.09(1.04-1.18), 9	-	0.0
18. <i>P. indicus</i> Wolfenden, 1905	0.73(0.73), 1	-	0.0
Calocalanidae			
19. <i>Calocalanus contractus</i> Farran, 1926	0.82(0.74-0.90), 2	-	0.0
20. <i>C. pavo</i> (Dana, 1849)	1.17(0.98-1.30), 13	-	0.0
21. <i>C. pavoninus</i> Farran, 1936	0.67(0.66-0.68), 3	-	0.0
22. <i>C. styliremis</i> Giesbrecht, 1888	0.72(0.70-0.74), 2	-	0.0
23. <i>Ischnocalanus plumulosus</i> (Claus, 1863)	1.20(1.20), 1	-	0.0
24. <i>Meyncocera clausii</i> Thompson, 1888	1.02(1.00-1.08), 1	-	0.0
Pseudocalanidae			
25. <i>Clausocalanus arcuicornis</i> (Dana, 1849)	1.37(1.26-1.44), 12	-	0.0
26. <i>C. furcatus</i> (Brady, 1883)	1.03(1.00-1.06), 10	0.90(0.90), 1	0.3
27. <i>C. jobei</i> Frost & Fleminger, 1968	1.30(1.24-1.36), 10	-	0.0
28. <i>C. mastigophorus</i> (Claus, 1863)	1.72(1.64-1.78), 10	1.31(1.20-1.38), 9	16.4
29. <i>C. parapergens</i> Frost & Fleminger, 1968	1.08(1.00-1.16), 5	-	0.0
30. <i>C. paululus</i> Farran, 1926	0.77(0.77), 1	-	0.0

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
31. <i>Ctenocalanus vanus</i> Giesbrecht, 1888	1.10(1.04-1.12), 6	-	0.0
32. <i>Farrania frigidus</i> (Wolfenden, 1911)	2.36(2.28-2.44), 4	-	0.0
Spinocalanidae			
33. <i>Mimocalanus cultrifer</i> Farran, 1908	1.30(1.24-1.36), 13	-	0.0
34. <i>M. nudus</i> Farran, 1908	2.36(2.36), 1	-	0.0
35. <i>Monacilla typica</i> Sars, 1905	2.22(2.14-2.32), 9	-	0.0
36. <i>Spinocalanus abyssalis</i> Giesbrecht, 1888	1.14(1.14), 1	-	0.0
37. <i>S. brevicaudatus</i> Brodsky, 1950	1.44(1.36-1.52), 3	-	0.0
38. <i>S. magnus</i> Wolfenden, 1904	2.10(2.08-2.12), 2	-	0.0
39. <i>S. oligospinosus</i> Park, 1970	1.40(1.38-1.42), 5	-	0.0
40. <i>S. parabyssalis</i> Park, 1970	0.86(0.86), 1	-	0.0
41. <i>S. spinosus</i> Farran, 1908	1.82(1.76-1.88), 11	-	0.0
Aetideidae			
42. <i>Aetideopsis multiserrata</i> (Wolfenden, 1904)	2.56(2.56), 1	-	0.0
43. <i>Aetideus acutus</i> (Farran, 1929)	1.63(1.50-1.70), 14	1.31(1.22-1.40), 17	37.0
44. <i>A. giesbrechti</i> (Cleve, 1904)	1.94(1.90-2.00), 8	1.60(1.56-1.62), 4	22.0
45. <i>A. mexicanus</i> Park, 1970	1.74(1.68-1.80), 4	1.66(1.60-1.72), 3	17.4
46. <i>Chirundina streetsii</i> Giesbrecht, 1895	4.92(4.75-5.08), 9	-	0.0
47. <i>Euchirella amoena</i> Giesbrecht, 1888	-	3.32(3.32), 1	100.0
48. <i>E. bitumida</i> With, 1915	5.67(5.50-6.00), 5	4.62(4.44-4.75), 3	42.9

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
49. <i>E. curticauda</i> Giesbrecht, 1888	3.74(3.68-3.80), 2	-	0.0
50. <i>E. maxima</i> Wolfenden, 1905	-	6.08(6.08), 1	100.0
51. <i>E. messinensis</i> (Claus, 1863)	4.86(4.72-5.08), 6	4.31(4.20-4.44), 6	46.2
52. <i>E. pseudotruncata</i> Park ³	4.38(4.16-4.56), 6	3.74(3.68-3.80), 4	40.0
53. <i>E. pulchra</i> (Lubbock, 1856)	3.38(3.16-3.72), 18	3.20(3.16-3.24), 2	10.6
54. <i>E. splendens</i> Vervoort, 1963	4.47(3.96-4.72), 4	3.96(3.96), 1	20.0
55. <i>Gaetanus armiger</i> Giesbrecht, 1888	2.90(2.80-2.96), 6	-	0.0
56. <i>G. kruppii</i> Giesbrecht, 1903	4.83(4.75-4.92), 3	-	0.0
57. <i>G. miles</i> Giesbrecht, 1888	4.14(4.04-4.24), 5	-	0.0
58. <i>G. minor</i> Farran, 1905	2.67(2.18-2.38), 10	1.97(1.94-2.00), 4	10.8
59. <i>G. minutus</i> (Sars, 1907)	2.63(2.48-2.80), 4	-	0.0
60. <i>G. pileatus</i> Farran, 1903	5.53(5.16-5.83), 15	4.75(4.67-4.83), 2	8.7
61. <i>Paivella inaciae</i> Vervoort, 1965	1.37(1.34-1.40), 10	-	0.0
62. <i>Pseudaetideus armatus</i> (Boeck, 1872)	3.04(3.04), 1	-	0.0
63. <i>Pseudeuchaeta brevicauda</i> Sars, 1905	5.25(5.25), 1	-	0.0
64. <i>Pseudochirella tuberculata</i> Tanaka, 1957	5.50(5.50), 1	-	0.0
65. <i>Undeuchaeta major</i> Giesbrecht, 1888	4.61(4.58-4.64), 2	4.20(4.20), 1	33.3
66. <i>U. plumosa</i> (Lubbock, 1856)	3.76(3.40-3.92), 10	3.32(3.12-3.48), 11	16.5
67. <i>Valdiviella insignis</i> Farran, 1908	10.67(10.67), 1	-	0.0
68. <i>V. oligartha</i> Steuer, 1904	9.00(9.00), 1	7.83(7.83), 1	33.3
Euchaetidae			
69. <i>Euchaeta aequatorialis</i> (Tanaka, 1958)	4.24(4.24), 1	-	0.0
70. <i>E. bisinuata</i> Sars, 1907	5.25(5.25), 1	-	0.0

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
71. <i>E. gracilis</i> Sars, 1905	6.67(6.67), 1	-	0.0
72. <i>E. marina</i> (Prestandrea, 1833)	3.17(2.96-3.48), 12	2.14(2.88-3.28), 11	25.2
73. <i>E. media</i> Giesbrecht, 188-	3.92(3.60-4.12), 10	3.55(3.44-3.76), 10	19.6
74. <i>E. paraconcinna</i> Fleminger, 1957	2.57(2.48-2.64), 4	2.50(2.48-2.56), 7	52.0
75. <i>E. pseudotonsa</i> Fontaine, 1967	6.15(6.04-6.25), 2	-	0.0
76. <i>E. pubera</i> Sars, 1907	4.08(4.08), 1	3.45(3.32-3.52), 5	83.3
77. <i>E. spinosa</i> Giesbrecht, 1892	6.58(6.35-6.91), 8	6.30(6.17-6.42), 2	21.4
Phaennidae			
78. <i>Phaenna spinifera</i> Claus, 1863	2.09(1.88-2.36), 10	1.90(1.90), 1	13.3
Scolecithricidae			
79. <i>Lophothrix frontalis</i> Giesbrecht, 1895	6.75(6.75), 1	-	0.0
80. <i>L. latipes</i> (T. Scott, 1894)	3.05(2.92-3.20), 13	-	0.0
81. <i>Racovitzanus levis</i> Tanaka, 1961	1.96(1.92-2.02), 7	-	0.0
82. <i>Scaphocalanus amplius</i> Park, 1970	1.66(1.54-1.74), 23	-	0.0
83. <i>S. brevirostris</i> Park, 1970	1.89(1.80-1.96), 38	1.94(1.80-2.02), 6	16.6
84. <i>S. curtus</i> (Farran, 1926)	1.28(1.28), 1	1.39(1.20-1.54), 8	98.2
85. <i>S. echinatus</i> (Farran, 1905)	2.25(2.20-2.36), 10	-	0.0
86. <i>S. longifurca</i> (Giesbrecht, 1888)	1.61(1.42-1.80), 2	-	0.0
87. <i>S. magnus</i> (T. Scott, 1894)	4.23(4.04-4.36), 5	-	0.0
88. <i>S. major</i> (T. Scott, 1894)	2.12(2.12), 1	2.27(2.26-2.28), 2	80.0
89. <i>S. subcurtus</i> Park, 1970	1.06(1.00-1.10), 8	-	0.0
90. <i>Scolecithricella abyssalis</i> (Giesbrecht, 1888)	1.99(1.94-2.04), 12	-	0.0
91. <i>S. ctenopus</i> (Giesbrecht, 1888)	1.54(1.48-1.60), 10	1.46(1.46), 1	3.6

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
92. <i>S. dentata</i> (Giesbrecht, 1892)	1.50(1.32-1.76), 23	1.47(1.34-1.64), 7	20.3
93. <i>S. ovata</i> (Farran, 1905)	1.98(1.88-2.08), 8	-	0.0
94. <i>S. pseudoarcurata</i> Park, 1970	2.37(2.34-2.40), 2	-	0.0
95. <i>S. tenuiserrata</i> (Giesbrecht, 1892)	1.15(1.06-1.24), 21	1.38(1.34-1.42), 9	3.3
96. <i>S. vittata</i> (Giesbrecht, 1892)	1.65(1.62-1.66), 11	1.62(1.56-1.66), 4	6.9
97. <i>Scolecithrix bradyi</i> Giesbrecht, 1888	1.22(1.14-1.34), 10	1.36(1.26-1.42), 10	33.0
98. <i>S. danae</i> (Lubbock, 1856)	2.07(2.00-2.20), 13	2.13(2.04-2.24), 10	24.6
99. <i>Scottocalanus backusi</i> Grice, 1969	5.34(5.00-5.67), 2	5.33(5.33), 1	50.0
100. <i>S. helenae</i> (Lubbock, 1856)	3.79(3.52-3.92), 9	3.95(3.74-4.04), 9	50.0
101. <i>S. securifrons</i> (T. Scott, 1894)	4.14(3.92-4.52), 8	4.68(4.64-4.72), 2	34.8
Tharybidae			
102. <i>Undinella brevipes</i> Farran, 1908	1.92(1.92), 1	-	0.0
103. <i>U. simplex</i> (Wolfenden, 1906)	1.42(1.42), 1	-	0.0
Temoridae			
104. <i>Temora stylifera</i> (Dana, 1849)	1.76(1.68-1.84), 11	1.74(1.58-1.84), 11	42.6
Metridiidae			
105. <i>Metridia brevicauda</i> Giesbrecht, 1889	1.77(1.70-1.80), 7	1.59(1.48-1.68), 11	15.2
106. <i>M. curticauda</i> Giesbrecht, 1889	2.31(2.24-2.36), 7	1.96(1.90-2.04), 6	14.6
107. <i>M. princeps</i> Giesbrecht, 1889	6.83(6.50-7.17), 3	6.58(6.58), 1	20.0
108. <i>M. venusta</i> Giesbrecht, 1889	2.80(2.68-2.92), 13	2.62(2.56-2.72), 8	52.5

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
109. <i>Pleuromamma abdominalis abdominalis</i> (Lubbock, 1856)	3.11(2.76-3.60), 10	3.10(2.80-3.36), 10	26.9
110. <i>P. abdominalis edentata</i> Steuer, 1932	2.98(2.84-3.12), 2	-	0.0
111. <i>P. gracilis gracilis</i> (Claus, 1863)	1.85(1.72-2.00), 11	1.75(1.68-1.80), 10	53.9
112. <i>P. piseki</i> Farran, 1929	1.92(1.84-2.04), 10	1.76(1.68-1.88), 10	72.8
113. <i>P. xiphias</i> (Giesbrecht, 1889)	4.84(4.58-5.08), 10	4.66(4.48-5.25), 10	42.7
Centropagidae			
114. <i>Centropages caribbeanensis</i> Park, 1970	2.03(1.96-2.12), 15	1.91(1.84-2.00), 4	29.6
115. <i>C. velificatus</i> (de Oliveira, 1947)	1.80(1.80), 1	-	0.0
Lucicutiidae			
116. <i>Lucicutia clausi</i> (Giesbrecht, 1889)	1.75(1.68-1.80), 10	1.80(1.72-1.96), 17	49.3
117. <i>L. curta</i> Farran, 1905	2.11(1.92-2.22), 7	-	0.0
118. <i>L. flavicornis</i> (Claus, 1863)	1.50(1.38-1.96), 41	1.50(1.38-1.70), 12	21.7
119. <i>L. gaussae</i> Grice, 1963	1.39(1.30-1.48), 7	1.33(1.28-1.40), 7	17.5
120. <i>L. gemina</i> Farran, 1926	1.64(1.56-1.72), 9	1.51(1.34-1.70), 29	67.2
121. <i>L. longiserrata</i> (Giesbrecht, 1889)	2.35(1.98-2.84), 29	1.96(1.82-2.32), 7	28.4
122. <i>L. lucida</i> Farran, 1908	-	3.24(3.24), 1	100.0
123. <i>L. magna</i> Wolfenden, 1903	3.16(2.88-3.40), 23	3.16(2.96-3.42), 7	34.0
124. <i>L. oblonga</i> Brodsky, 1950	-	2.90(2.68-3.12), 20	100.0
125. <i>L. ovalis</i> (Giesbrecht, 1889)	1.47(1.40-1.54), 14	1.33(1.26-1.42), 9	38.3
126. <i>L. paraclausi</i> Park, 1970	1.61(1.48-1.82), 17	1.58(1.42-1.82), 25	40.4

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
Heterorhabdidae			
127. <i>Disseta palumboi</i> Giesbrecht, 1889	7.00(6.75-7.25), 6	6.63(6.17-6.92), 4	47.4
128. <i>Heterorhabdus abyssalis</i> (Giesbrecht, 1889)	2.41(2.02-3.24), 51	2.31(2.08-2.76), 41	55.2
129. <i>H. medianus</i> Park, 1970	2.55(2.40-2.72), 6	-	0.0
130. <i>H. papilliger</i> (Claus, 1863)	1.88(1.80-1.96), 10	1.83(1.76-1.88), 10	34.7
131. <i>H. spinifer</i> Park, 1970	1.80(1.68-1.82), 11	1.79(1.72-1.86), 10	43.6
132. <i>H. spinifrons</i> (Claus, 1863)	3.22(3.04-3.48), 15	3.01(2.82-3.20), 7	36.7
133. <i>H. tenuis</i> Tanaka, 1964	-	2.36(2.20-2.52), 3	100.0
134. <i>H. vipera</i> (Giesbrecht, 1889)	2.38(2.30-2.52), 6	2.60(2.52-2.72), 8	65.0
135. <i>Heterostylites longicornis</i> (Giesbrecht, 1889)	2.76(2.64-2.88), 9	2.76(2.68-2.96), 7	23.8
136. <i>H. major</i> (Dahl, 1894)	3.96(3.88-4.00), 3	3.91(3.56-4.12), 5	50.0
137. <i>Mesorhabdus brevicaudatus</i> (Wolfenden, 1905)	-	3.58(3.56-3.60), 2	100.0
Augaptilidae			
138. <i>Augaptilus longicaudatus</i> (Claus, 1863)	3.82(3.60-4.20), 12	3.09(2.84-3.24), 6	25.0
139. <i>A. megalurus</i> Giesbrecht, 1889	4.60(4.40-4.80), 4	4.00(4.00), 1	16.7
140. <i>Centraugaptilus ratrayi</i> (T. Scott, 1894)	5.00(5.00), 1	-	0.0
141. <i>Euaugaptilus hecticus</i> (Giesbrecht, 1889)	2.66(2.40-2.88), 22	2.43(2.36-2.52), 12	16.9
142. <i>E. palumboi</i> (Giesbrecht, 1889)	2.15(2.04-2.22), 13	1.89(1.88-1.90), 2	13.2

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
143. <i>Haloptilus acutifrons</i> (Giesbrecht,	3.38(3.20-3.62), 13	-	0.0
144. <i>H. austini</i> Grice, 1959	3.08(3.04-3.12), 2	-	0.0
145. <i>H. fertilis</i> (Giesbrecht, 1892)	-	2.96(2.84-3.08), 2	100.0
146. <i>H. longicirrus</i> Brodsky, 1950	2.96(2.96), 1	-	0.0
147. <i>H. longicornis</i> (Claus, 1863)	2.21(2.08-2.32), 11	-	0.0
148. <i>H. ornatus</i> (Giesbrecht, 1892)	4.39(4.28-4.76), 13	-	0.0
149. <i>H. paralongicirrus</i> Park, 1970	2.58(2.48-2.68), 10	-	0.0
150. <i>H. spiniceps</i> (Giesbrecht, 1892)	4.63(4.32-4.90), 8	-	0.0
151. <i>Pachyptilus eurygnathus</i> Sars, 1920	5.25(5.25), 1	-	0.0
Arietellidae			
152. <i>Paraugaptilus buchani</i> Wolfenden, 1904	3.19(3.18-3.20), 2	-	0.0
153. <i>Phyllopus bidentatus</i> Brady, 1883	2.72(2.72), 2	2.80(2.80), 3	60.0
154. <i>P. helgae</i> Farran, 1908	2.23(2.14-2.28), 5	2.29(2.20-2.40), 4	44.4
155. <i>P. impar</i> Farran, 1908	2.74(2.68-2.80), 4	2.75(2.72-2.76), 3	40.0
Candaciidae			
156. <i>Candacia bipinnata</i> (Giesbrecht, 1889)	2.72(2.72), 1	2.40(2.40), 1	50.0
157. <i>C. curta</i> (Dana, 1849)	2.40(2.24-2.48), 11	2.17(2.08-2.22), 3	14.8
158. <i>C. ketchumi</i> Grice, 1961	2.02(1.96-2.08), 4	1.95(1.92-1.98), 3	27.3
159. <i>C. longimana</i> (Claus, 1863)	3.16(2.88-3.32), 11	3.01(2.88-3.16), 9	38.4
160. <i>C. pachydactyla</i> (Dana, 1849)	2.90(2.80-3.00), 6	2.83(2.72-2.96), 7	41.2
161. <i>C. tenuimana</i> (Giesbrecht, 1889)	2.22(2.18-2.26), 2	2.03(2.00-2.06), 2	50.0
162. <i>C. varicans</i> (Giesbrecht, 1892)	2.43(2.32-2.56), 8	2.34(2.24-2.52), 9	61.9

TABLE 2. (continued)

Species	Females	Males	Percent of males ¹
163. <i>Paracandacia bispinosa</i> (Claus, 1863)	1.87(1.80-1.96), 11	1.93(1.84-2.00), 7	66.7
164. <i>P. simplex</i> (Giesbrecht, 1889)	2.01(1.90-2.12), 16	2.04(1.92-2.16), 17	42.4
Pontellidae			
165. <i>Pontellina plumata</i> (Dana, 1849)	1.86(1.86), 1	-	0.0
Bathypontiidae			
166. <i>Bathypontia minor</i> (Wolfenden, 1906)	2.80(2.80), 1	-	0.0
167. <i>B. similis</i> Tanaka, 1965	2.75(2.72-2.78), 2	2.76(2.76), 1	50.0
168. <i>Temorites brevis</i> Sars, 1900	-	1.82(1.82), 1	100.0
Acartiidae			
169. <i>Acartia danae</i> Giesbrecht, 1889	1.23(1.06-1.30), 12	-	0.0

¹These numbers represent the percentage of males among the total examined individuals of each species

²In a recent paper, Fleminger (1973) has separated this group into several species. *Eucalanus sewelli* Fleminger, 1973 is represented here, but larger forms that have not been critically examined are also present.

³In press.

consistent depth intervals. Each sampling depth was given a correction factor to compensate for the average depth range covered by that sample. These numbers increased with depth and distance between sampling layers. For example, the 0 m tow represented the 25-0 m interval and was given a correction factor of 1. The 50 m tow represented the 75-25 m interval and was given a correction factor of 2. These corrected values were only used in determining percentages in the water column.

In order to examine the feeding relationships of copepods, each major family was categorized as to its predominant feeding habits. The percentages of each feeding type at specific depths were also calculated.

RESULTS AND DISCUSSION

General

From 29,136 specimens of adult calanoid copepods examined, 169 species were identified (Table 2). The following 161 specimens were not identified to species:

<i>Spinocalanus sp.</i>	1 ♀
<i>Chiridiella spp.</i>	4 ♀
<i>Chiridius spp.</i>	28 ♀
<i>Aetideidae</i>	1 ♀
<i>Phaenidae</i>	1 ♂
<i>Xanthocalanus sp.</i>	1 ♀
<i>Scaphocalanus spp.</i>	1 ♀
	10 ♂
<i>Scolecithricella spp.</i>	4 ♀
	7 ♂
<i>Scottocalanus spp.</i>	2 ♀
	1 ♂
<i>Scolecithricidae</i>	7 ♀
	1 ♂
<i>Heterorhabdus sp.</i>	1 ♂
<i>Euaugaptilus spp.</i>	52 ♀
	27 ♂
<i>Haloptilus spp.</i>	10 ♂
<i>Phyllopus sp.</i>	1 ♂
<i>Bathypontia sp.</i>	<u>1</u> ♂

161

All adult calanoids were included in the calculations of the number and mean length of specimens at each depth. From the above list of unidentified specimens, only the individuals that were identified to genus and that I was certain were single species were included in counts of species at each depth. These included *Spinocalanus sp.*,

Xanthocalanus sp., *Heterorhabdus* sp., *Phyllopus* sp., and *Bathypontia* sp.

Contamination in the samples collected in this study appeared to be insignificant. Possible contaminants were determined from reports by Grice & Hulsemann (1965) and Roe (1972). Only 28 specimens from the entire collection could be considered contaminants and 25 of these were *Clausocalanus furcatus* found below 100 m. These "contaminant" species are noted in Appendix Table 1, but none of the specimens were excluded from the calculations for some species may have distribution peaks at specific depths and also be distributed in smaller numbers throughout other parts of the water column.

Zooplankton and Copepod Abundance

Displacement Volumes

During the day, the greatest volume of zooplankton was at 50 m with the values dropping rapidly in both the upward and downward direction (Fig. 1). There was a small increase in volume at 600 m. At night, the greatest volume was at the surface. This bulk consisted mainly of small euphausiids which did not appear to be concentrated to the same extent at any other depth in the day or night samples.

The distributions of total calanoid (Fig. 2) and adult calanoid (Fig. 3) displacement volumes were similar with the major biomass peaks, both day and night, at 50 m. Volumes below 100 m decreased at

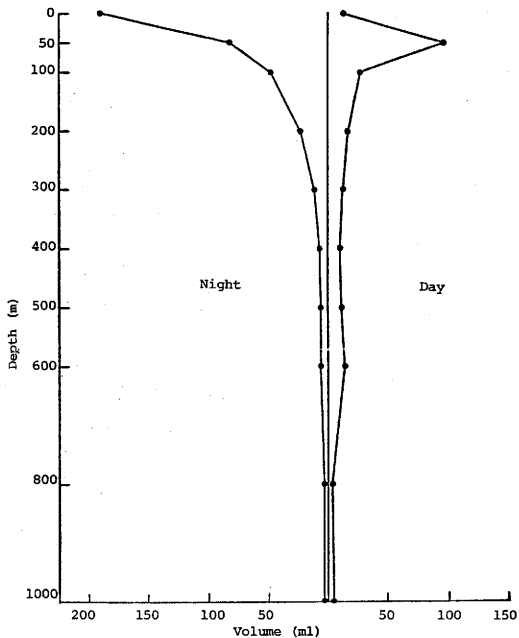


Fig. 1. Day and night total zooplankton displacement volumes at each sampling depth. These are estimated volumes for 1/2 aliquot of the total catch from both nets for a one-hour tow.

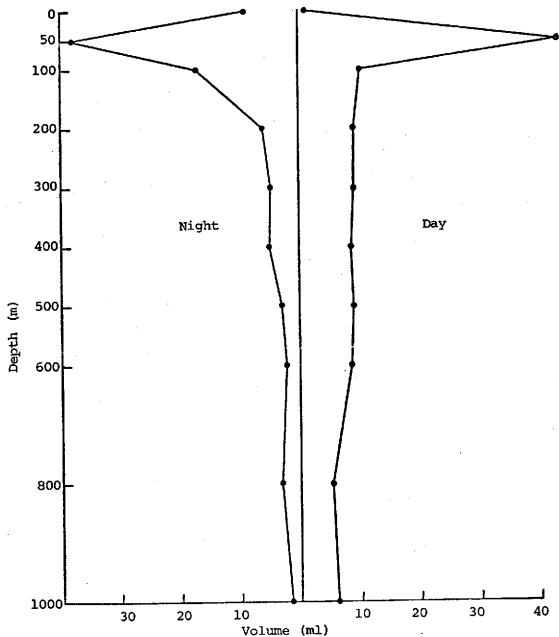


Fig. 2. Day and night total calanoid copepod displacement volumes at each sampling depth. These are estimated volumes for 1/2 aliquot of the total catch from both nets for a one-hour tow.

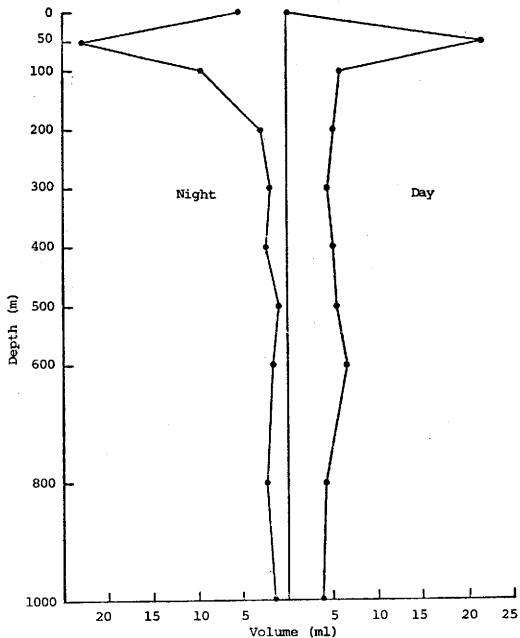


Fig. 3. Day and night adult calanoid displacement volumes at each sampling depth. These are estimated volumes for 1/2 aliquot of the total catch from both nets for a one-hour tow.

night and the surface volume increased at night indicating a slight overall upward migration. A small secondary peak in the day at 600 m in the distribution of adults that does not appear in the distribution of total calanoids is due to the high percentage (77%) of adults in this sample (Fig. 4B).

The percentage of zooplankton formed by calanoid copepods increased erratically with depth both during the day and at night (Fig. 4A). Below 100 m, this percentage was generally greater in the day series of samples than the night series. This could be the result of a migration of euphausiids from a widely distributed group during the day to the highly concentrated mass that was found in the surface layers at night. The percentage of copepods that were adults increased slightly with depth but generally did not vary excessively throughout the sampling range (Fig. 4B). The 0 m day percentage may not be accurate due to the small number of specimens present.

Numbers of Copepods

The numbers of adult calanoids (Fig. 5) agree well with the volumes in Figure 3. The abundance peaks were at 50 m in the day and at night. The differences between the surface layers and the deeper layers are more pronounced in the numerical representation due to the increase in mean size with depth (Fig. 6A). The small biomass peak at 600 m in the day does not appear in the numerical representation due to the large mean length (3.59) of the calanoids in this sample.

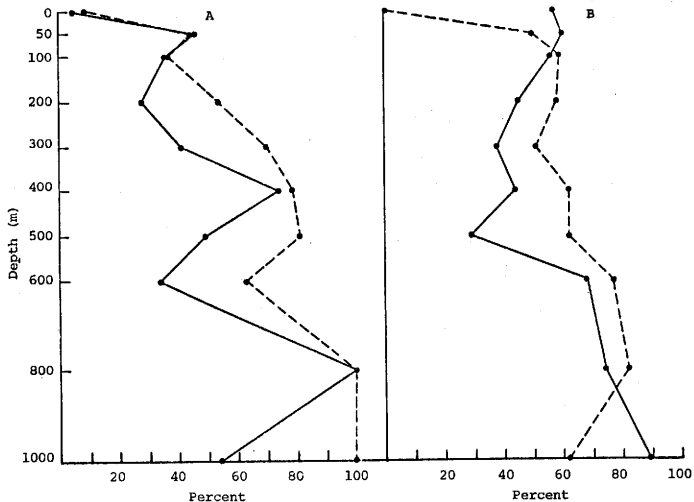


Fig. 4. A. Percentage of zooplankton due to calanoid copepods at each sampling depth. B. Percentage of calanoids that are adults at each sampling depth. In both cases the percentage is by volume and / = night, / = day.

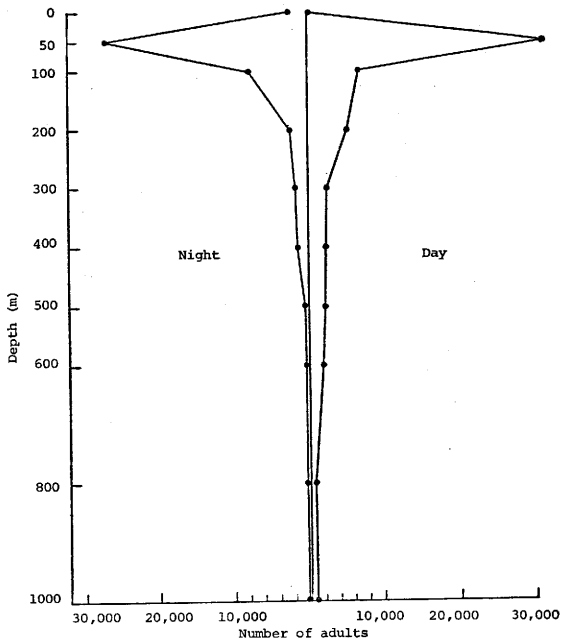


Fig. 5. Day and night numbers of adult calanoids at each sampling depth. These numbers are estimated for 1/4 aliquot of the total catch from both nets for a one-hour tow.

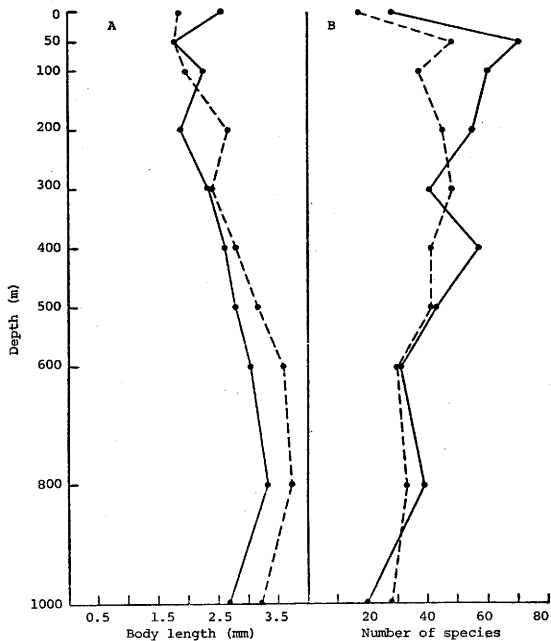


Fig. 6. A. Mean body length of adult calanoids at each sampling depth. B. Number of calanoid species at each sampling depth. In both cases / = night, / = day.

The abundance peaks at 50 m were relatively large in relation to the numbers found in deeper layers. During the day, adult calanoids were 38 times more abundant at 50 m than at 1000 m. At night, the number found at 50 m was 137 times greater than the number at 1000 m.

Previous Investigations

The vertical distributions of zooplankton and copepods as groups have been extensively studied in the Atlantic Ocean, but the results are quite variable. Comparing specific results on displacement volumes and abundances is difficult due to the varying mesh sizes, types of collecting gear, and methods of towing used in previous studies (Fleminger & Clutter, 1965; Clutter & Anraku, 1968). Water mass movements and, in the cold and temperate areas, seasonal migrations also affect the vertical distribution of zooplankton in the upper layers (Vinogradov, 1968). For these reasons, results are compared generally here as to the trends found in different areas.

In the relatively high latitudes of the North Atlantic, subsurface abundance peaks are frequently evident due to water mass differences or the presence of seasonal migrants. Farran (1926) found the greatest number of copepods between 458 and 275 m in day samples. Leavitt (1935) reported the largest volumes of zooplankton in the upper 300 m and in 1938 he found a large variation in the level with the greatest volume, but always found the largest biomass above 1000 m. For copepods, the greatest volume was at 800 m with a secondary peak

at 1600 m. Moore (1949) generally found the greatest volumes of total zooplankton in the upper 100 m in the day and in the night. He also reported slight seasonal changes in the vertical distribution. Colman (1962) reported the greatest number of copepods in the 100-45 m layer in the day and the 50-0 m layer at night. At their two relatively low latitude stations (ca. 30°N and 40°N), Grice & Hulsemann (1965) found the greatest volume of zooplankton in the upper 100 m. At their northern station, northwest of the Shetland Islands, the greatest amount of zooplankton was in the 500-200 m layer with a secondary peak at 50-0 m. At all stations the maximum number of copepods was found in the 50-0 m interval and at the Shetland Island station there was a secondary peak in the 500-200 m interval. Most of the samples were taken in the day. Roe (1972) did not sample above 40 m, but found the greatest day and night volumes of calanoids at 500 m. The majority (91%) of this volume was made up of copepodites. He found the greatest number of adult calanoids at 40 m in the day and 50 m at night.

In the South Atlantic, Foxton (1956) found that zooplankton volumes in the Antarctic and sub-Antarctic zones were concentrated in the surface layers, day and night, during the summer months. In the winter, zooplankton volumes were greatest in the deeper layers.

In the tropical latitudes, where seasonal migrations are minimal, the largest biomass of zooplankton is generally found in the upper 50 m and decreases steadily with depth (Vinogradov, 1968). The

sub-tropical and tropical regions of the Atlantic have not been studied as extensively as the temperate and polar regions. In the Caribbean Sea, Jespersen (1935) found the greatest zooplankton volumes near the surface and reported, "a very poor plankton fauna in the deeper layers." Owre & Poyo (1964) also worked in the Caribbean Sea and reported that copepods were least diverse and most abundant in the upper 100 m. In the Florida Current, Bsharah (1957) found seasonal changes in the zooplankton and copepod populations in the upper 600 m to be minimal. He reported the greatest zooplankton volume at 650 m in the day, and at night the maximum was at the surface with a secondary peak at 700 m. Recording dry weights for copepods, the greatest biomass during the day was at 150 m with another peak at 450 m. At night, the greatest biomass was at the surface with a secondary peak again at 450 m. Copepod numbers were shown to peak at approximately 75 m in the day and at the surface at night.

There have been a number of studies done in the tropical areas of other oceans. In the central equatorial Pacific, King & Hida (1957), using open horizontal nets to 240 m, found the largest zooplankton volume at the surface. Also in the tropical Pacific, Vinogradov (1962) used vertical nets to 8000 m and found a steady decrease with depth in zooplankton volume from a peak at the surface. In the Indian Ocean, Sewell (1948) used open horizontal nets and found two distinct maxima in copepod abundance, the greatest one near the surface and another maximum at about 600 m.

The results of this study, indicating no distinct maxima below 50 m for displacement volumes or numbers, generally agree with published results for sub-tropical and tropical oceanic zooplankton populations. According to Vinogradov (1968), the daytime maximum biomass is almost always found in the 50-25 m or 100-50 m layers in tropical regions. The rapid decrease in plankton density with depth is also typical of tropical areas.

Copepod Mean Lengths and Species Diversity

Both day and night curves show a general increase in the mean length of calanoid copepods with depth (Fig. 6, p. 30). Copepods of maximum size were found at 800 m in the day and night. Mean day lengths were consistently larger than night lengths below 100 m, and from 100 m to the surface the night lengths were larger than the day lengths. This indicates an upward migration of the larger forms at night.

Grice & Hulsemann (1965) found that in the upper 1000 m, the greatest mean size was in the 1000-500 m layer. Roe (1972) generally found an increase in mean size with depth to a maximum at the deepest layer sampled of approximately 900 m.

The number of species generally decreased with depth below 50 m (Fig. 6B, p. 30). During the day, the greatest number was at 50 and 200 m, both with 48 species. At night, the number of species was greatest at 50 m (70 species) with a secondary peak at 400 m (57

species). In the upper 200 m the number of species found at night was considerably larger than the number found during the day. This increase in the surface waters indicates an upwards migration at night.

Previous investigations generally report the greatest number of species at deeper levels than those reported here. Farran (1926) found the greatest number of species below 732 m. Hardy & Gunther (1935) reported the peak number of species at about 600 to 700 m. Using samples to 4000 m, Grice & Hulsemann (1965) found that most species inhabited the upper 1000 m. Roe (1972) reported the greatest number of species below 500 m in the day and at night. In the Caribbean Sea, Owre & Foyo (1964) also reported the greatest number of species below 500 m, but in the Indian Ocean, Sewell (1948) reported the maximum number of species at the surface.

The general disagreement of the results of this study with other published results can best be explained by sample sizes. The plankton at this station was found to be sparse in the deeper layers. Comparing the 50 and 1000 m layers, it can be seen that the number of adult calanoids found at 50 m was 38 times greater than the number at 1000 m in the day, and 137 times greater at night. These large differences will undoubtedly affect the number of species found in the deeper layers. These variations in sample sizes were less intense in the studies listed above, and the greatest number of specimens was frequently found in the deeper layers.

*Vertical Distribution of Families and
Their Abundant Species*

The day and night vertical distributions of the 13 most abundant families of calanoid copepods were examined in detail. Reference should be made to Appendix Table 1 throughout this section. The percentage of each family at specific depths is listed in Table 3. These 13 families represented 98.5% of the calanoids in the water column sampled. Small numbers of the following 10 families were also recorded from the samples:

Megacalanidae
Paracalanidae
Spinocalanidae
Phaennidae
Tharybidae
Temoridae
Centropagidae
Arietellidae
Pontellidae
Bathypontiidae

Calanidae

This family was abundant in the surface layers (Fig. 7) and was represented by five species which together formed 15.9% of the estimated total number of calanoids in the water column. The two predominant species, *Nannocalanus minor* (73.8%) and *Calanus tenuicornis* (20.5%) made up 94.4% of the family in the water column. All of the species found except *Neocalanus gracilis* were mainly limited to the upper 100 m.

TABLE 3. THE DAY AND NIGHT PERCENTAGE OF CALANOIDS FORMED BY

COMMON FAMILIES AT SPECIFIC DEPTHS

FAMILY		Depth (m)									
		0	50	100	200	300	400	500	600	800	1000
Calanidae (Herbivores)	D	41.8	45.1	21.0	0.5	3.3	5.2	5.7	0.4	-	-
	N	2.8	11.1	6.5	0.8	3.8	0.9	3.8	3.1	0.7	-
Eucalanidae (Herbivores)	D	7.1	2.1	10.5	58.1	10.8	4.6	11.3	46.3	57.2	65.1
	N	9.7	5.3	1.1	25.4	23.6	31.4	36.7	49.5	37.6	41.4
Calocalanidae (Herbivores)	D	6.1	4.3	0.0	-	-	-	-	-	-	-
	N	1.2	8.4	4.2	0.1	-	-	-	-	-	-
Pseudocalanidae (Herbivores)	D	11.2	11.8	0.2	2.0	0.7	0.6	0.5	0.6	0.8	1.2
	N	0.4	9.2	2.1	0.5	-	0.6	0.5	0.3	0.2	2.0
Aetideidae (Omnivores)	D	-	0.6	4.2	7.8	2.1	3.9	3.5	3.9	2.8	4.1
	N	0.2	2.3	14.2	2.8	4.3	4.0	9.0	3.4	4.4	5.6
Scolecithricidae (Omnivores)	D	1.0	11.1	8.2	5.7	21.6	9.2	9.8	1.5	0.5	0.5
	N	11.3	11.9	9.3	15.4	7.8	14.3	5.7	1.0	1.5	-
Metridiidae (Omnivores)	D	1.0	-	-	1.5	46.0	57.7	37.8	38.4	14.1	13.0
	N	2.2	22.8	8.5	0.7	6.9	12.3	17.4	26.1	17.5	16.7
Lucicutiidae (Omnivores)	D	1.0	3.9	31.3	12.9	4.0	1.9	2.6	6.1	14.9	9.9
	N	2.0	10.2	11.9	7.4	27.3	9.9	10.3	9.5	26.7	25.3

TABLE 3. (continued)

		Depth (m)									
		0	50	100	200	300	400	500	600	800	1000
Acartiidae (Omnivores)	D	-	4.1	-	-	-	-	-	-	-	-
	N	0.5	6.3	0.2	-	-	-	0.3	-	0.2	-
Total particle grazers	D	69.2	83.0	76.3	88.5	88.5	83.1	71.2	97.2	80.3	93.8
	N	30.3	87.5	58.0	53.1	73.7	73.4	83.7	92.9	88.8	91.0
Euchaetiidae (Carnivores)	D	-	2.4	-	0.4	2.0	10.1	23.3	1.6	-	0.2
	N	40.5	0.7	2.9	0.5	1.5	0.8	2.2	3.4	0.5	0.5
Heterorhabdiidae (Carnivores)	D	-	3.1	0.1	3.4	5.8	2.9	1.0	0.3	4.9	2.7
	N	1.7	0.4	3.1	6.8	12.4	4.2	9.2	2.4	4.1	3.5
Augaptilidae (Carnivores)	D	-	8.4	19.8	6.7	1.4	0.2	0.1	0.2	0.5	0.2
	N	-	9.7	34.9	35.2	9.8	11.8	1.1	0.3	0.7	-
Candaciidae (Carnivores)	D	0.5	2.4	2.3	0.1	0.2	3.0	2.9	-	-	-
	N	3.2	1.5	0.6	0.1	-	-	-	-	-	-
Total carnivores	D	0.5	16.3	22.2	10.6	9.4	16.2	27.3	2.1	5.4	3.1
	N	45.4	12.3	41.5	42.6	23.7	16.8	12.5	6.1	5.3	4.0
TOTAL	D	69.7	99.3	98.5	99.1	97.9	99.3	98.5	99.3	95.7	96.9
	N	75.7	99.8	99.5	95.7	97.4	90.2	96.2	99.0	94.1	95.0

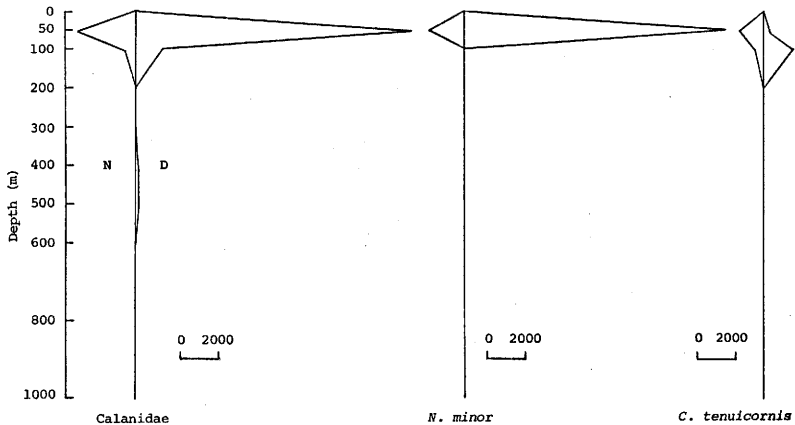


Fig. 7. The vertical distribution of the family Calanidae, *Nannocalanus minor*, and *Calanus tenuicornis*. The day distribution is shown to the right of the axis and the night distribution to the left. The values plotted are estimated numbers for 1/4 aliquot of the total catch of each group from both nets for a one-hour tow. Note that the data cannot show distributions below 1000 m.

Nannocalanus minor.--The greatest concentration of this species appeared to be at 50 m both during the day and at night. There was a large decrease in the number caught at this depth, however, from 13,824 in the day to 1716 at night, suggesting a nocturnal migration away from 50 m.

Calanus tenuicornis.--The day and night distribution of this species indicates a slight vertical migration. The greatest concentration of the population moved from 100 m in the day to 50 m at night.

This family is generally considered herbivorous (Conover, 1960; Anraku & Omori, 1963; Itoh, 1970; Timonin, 1971). The relatively large number of individuals present and the intermediate size of its members probably makes this group one of the most important food sources for predatory zooplankton. Members of this family generally remain in the upper layers in the day and night, while many other forms migrate away from the surface during the day. This is also suggested by the increased percentage of this group in relation to other calanoids in the surface layers during the day (Table 3). This family probably serves as a major source of food for surface-living carnivores and migratory predators invading the upper layers at night.

Eucalanidae

Members of this family were found at every depth sampled (Fig. 8). It formed 16.2% of the estimated total number of calanoids in the water column and was represented by seven species. *Rhincalanus*

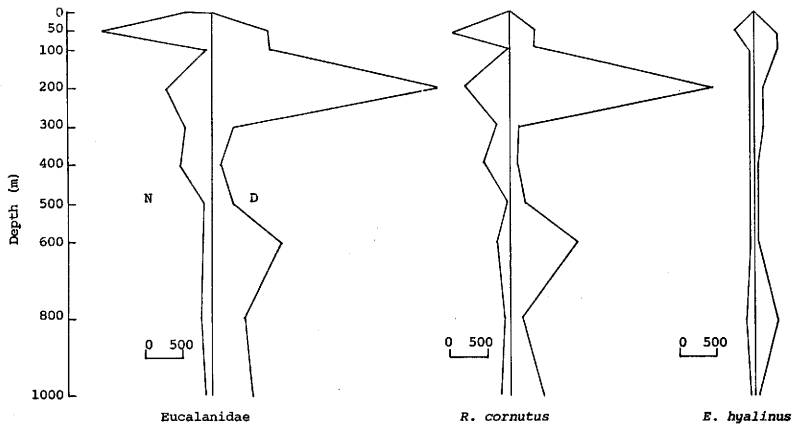


Fig. 8. The vertical distribution of the family Eucalanidae, *Rhincalanus cornutus*, and *Eucalanus hyalinus*. Plotted as in Fig. 7 (page 39).

cornutus (72.6%), *Eucalanus hyalinus* (16.3%) and *E. monachus* (6.7%) made up 95.6% of the family in the water column. These three species were distributed over a wide depth range and exhibited varying degrees of migration.

Rhincalanus cornutus.--This species ranged from 0 to 1000 m both during the day and at night. Its vertical distribution appeared to have two centers of abundance. Part of the shallow maximum at 200 m in the day evidently migrated to 50 m at night and a deeper maximum at 600 m in the day apparently moved into the upper 500 m at night.

Eucalanus hyalinus.--The range of this species extended from 50 to 1000 m in the day and at night. The evidence for vertical migration was conflicting. Relatively large numbers of the day population were found at 50, 100, and 800 m. At night, these numerical peaks were only at 50 and 800 m. This indicates that part of the population moved from 100 m in the day to 50 m at night. The number caught at 50 m however, decreased from 256 in the day to 212 at night. The day and night abundance peaks at 800 m suggest that part of the population remained at this depth. The decrease in the total number caught from 1160 in the day to 452 at night may partially explain these puzzling distributions. The population may not have been sampled adequately at night.

Eucalanus monachus and *E. pileatus*.--These less abundant species in the family were distributed over narrower depth ranges. *E. monachus* was found in mid-water and appeared to have a reverse migration with the center of abundance of the population moving from 200 m in

the day to 300 m at night. *E. pileatus* was found only in the upper 100 m.

This family is considered herbivorous (Wickstead, 1962; Mullin, 1966; Itoh, 1970; Timonin, 1971). Its numerical importance in the water column and the relatively large mean size of its most abundant members, *R. cornutus* (3.29 mm) and *E. hyalinus* (5.80 mm), make this one of the largest herbivorous groups, in terms of biomass, present in this area at the time of sampling.

The day and night distribution of this family, which generally reflects the distribution of *R. cornutus*, showed large numbers distributed from 500 to 1000 m in the day which were not present at night. This suggests that this group may be an important link in the food chain between the primary producers in the surface layers and the carnivores in the deeper layers. Vinogradov (1972) referred to organisms that functioned in this manner as interzonal filter-feeders. These organisms inhabit the "dynamic photic zone", feeding near the surface and constituting a food source for predators in the deeper levels.

The percentage of calanoids formed by this family at the various sampling depths indicated that this group made up a large number of the calanoid copepods between 600 and 1000 m (Table 3). At 800 and 1000 m these percentages decreased at night but still remained relatively high. These high percentages in the deeper layers may be partially due to the fact that in this family in particular, the condition of the specimens decreased steadily with depth. In the

deep layers, deciding whether the organisms were dead or alive at the time of capture proved difficult. Some of the specimens counted in these samples may have actually been carcasses. This could also explain the lack of migration of *E. hyalinus* at 800 m.

Calocalanidae and Pseudocalanidae

Members of these two families were abundant in the surface layers (Fig. 9). They exhibited little or no vertical migration.

The family Calocalanidae was represented by six species which formed 3.2% of the estimated total number of calanoids in the water column. The greatest numbers were found at 50 m both during the day and at night. *Calocalanus pavo* formed 95.5% of the family in the water column.

Calocalanus pavo.--The evidence for vertical migration in this species was inconclusive. Although the bulk of the population was at 50 m in the day and night, there was a large increase in the number caught at this depth from 1232 in the day to 2208 at night. This indicates a migration from some other level to 50 m at night.

The family Pseudocalanidae was represented by eight species which formed 5.2% of the estimated total number of calanoids in the water column. The greatest abundance was at 50 m, but smaller numbers of various species were distributed throughout the water column. *Clausocalanus arcuicornis* (45.9%) and *C. furcatus* (34.6%) made up 80.5% of the family.

Clausocalanus arcuicornis and *C. furcatus*.--The evidence for

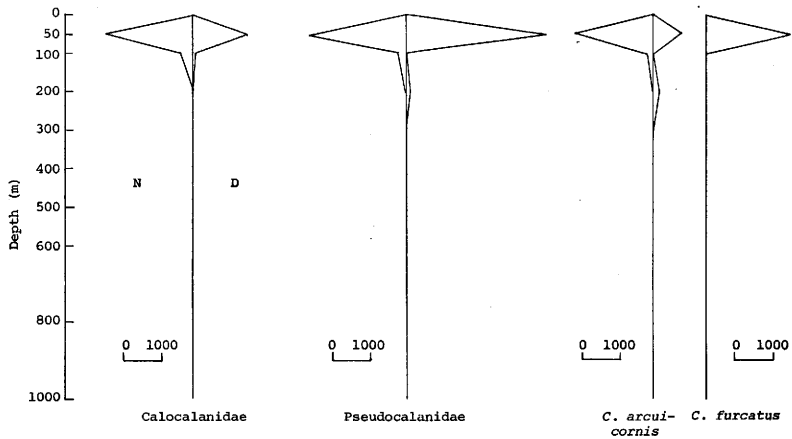


Fig. 9. The vertical distribution of the two families Calocalanidae and Pseudocalanidae and *Clausocalanus arcuicornis* and *C. furcatus*. Plotted as in Fig. 7 (page 39).

vertical migration in these species was inconclusive. Their greatest numbers were at 50 m both during the day and the night, but apparently they were distributed over a narrow depth range and the populations were not sampled adequately.

Farrania frigidus.--This species is mentioned here because its vertical distribution was not typical for a member of this family. A small number of specimens were found exclusively at 1000 m.

The numerical importance of these two families may have been incorrectly estimated. The large differences in the day and night catch of several of the species indicates that they are distributed over a narrow depth range. Although samples were taken at short depth intervals near the surface to alleviate this problem, the sampling procedures apparently still did not sample all of the populations adequately.

These two families are considered herbivorous (Itoh, 1970; Minoda, 1971; Timonin, 1971). The relatively small size of these organisms suggest that they make up a lesser percentage of the herbivorous biomass in the water column than the larger families (Calanidae, Eucalanidae). There is generally an inverse relationship however, between body size and respiration per standard weight in copepods (Raymont, 1963). Consequently, the secondary production derived from these species and their effect on the energy flow in the water column may be larger than their relative biomass would indicate.

Aetideidae

This family formed 3.9% of the estimated total number of calanoids in the water column and was represented by 27 species. There was no numerically predominant species with *Aetideus acutus* (29.8%), *Gaetanus minor* (21.6%), *Paivella inaciae* (15.7%), *Undeuchaeta plumosa* (9.3%), and *Euchirella pulchra* (6.4%) together making up 82.8% of the family in the water column. Most of the abundant species exhibited vertical migrations and this is reflected in the day and night distribution of the family (Fig. 10).

Aetideus acutus.--The distribution of the male and female of this species were different. Although the greatest number of females were found at 50 m during the day and night, the distributions and the increase in the number caught at 50 m from 176 in the day to 416 at night indicate a possible migration to this depth at night. Males were found almost exclusively at 100m both during the day and at night.

The vertical distributions of the three species found in the genus *Aetideus* appeared to be related. *A. acutus* was found in the shallow depths, *A. giesbrechti* was found in the intermediate layers and *A. mexicanus* occurred in the deeper samples.

Gaetanus minor.--The evidence for vertical migration in this species is strong. The center of the population moved from 400 m in the day to 100 m at night.

Paivella inaciae.--A short vertical migration was strongly

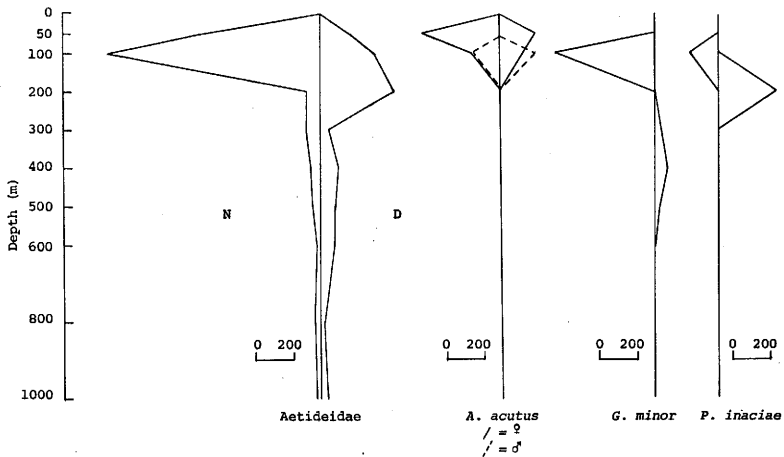


Fig. 10. The vertical distribution of the family Aetideidae, *Aetideus acutus*, *Gaetanus minor*, and *Paivella inaciae*. Plotted as in Fig. 7 (page 39).

indicated in this species. Almost the entire population moved from 200 m in the day to 100 m at night.

The members of this family are generally considered to be omnivorous (Wickstead, 1962; Mullin, 1966; Timonin, 1971). Although numerically it is not as important as many other families in the water column, some of the less common species are relatively large and may account for considerable biomass. The percentage of calanoids formed by this family at the sampled depths (Table 3) remained relatively constant with the slightly elevated values at 200 m in the day and 100 m at night corresponding to the abundance peaks in the distribution.

Euchaetidae

This family was represented by nine species which together formed 2.8% of the estimated total number of calanoids in the water column. The two predominant species, *Euchaeta media* (62.2%) and *E. marina* (29.7%), made up 91.9% of the family. Both species exhibited definite vertical migrations and the distribution of the family as a whole is much deeper in the day than at night (Fig. 11).

Euchaeta media.--Vertical migration was strongly indicated in this species. The bulk of the population moved from 500 m in the day to the 50 and 100 m levels at night.

Euchaeta marina.--Although this species was found only in the upper 50 m, the evidence strongly indicates a vertical migration from 50 m in the day to the surface at night.

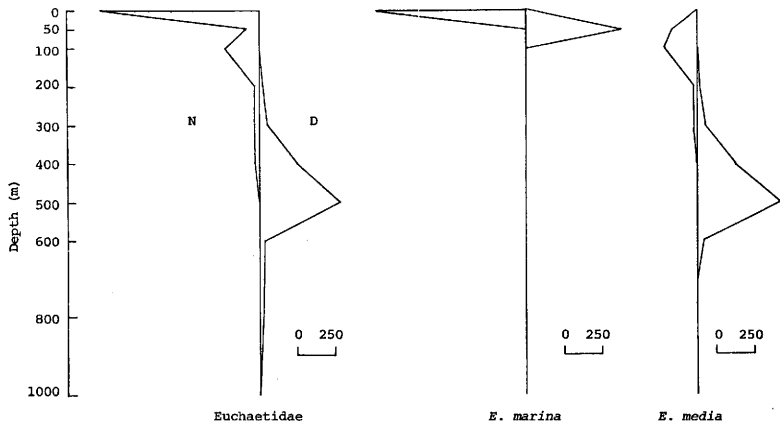


Fig. 11. The vertical distribution of the family Euchaetidae, *Euchaeta marina*, and *E. media*. Plotted as in Fig. 7 (page 39).

The members of this family are generally considered carnivorous (Wickstead, 1962; Mullin, 1966; Timonin, 1971). The only depths where this family was well represented in relation to the other calanoids present were at 500 m in the day and 0 m at night. These depths coincide with major abundance peaks of the family. This group evidently feeds on the smaller forms present in the surface levels at night.

Scolecithricidae

This family was represented by 23 species which together formed 9.7% of the estimated total number of calanoids in the water column. No single species predominated. *Scolecithrix danae* (26.6%), *Scolecithricella dentata* (19.5%), *Scolecithrix bradyi* (17.7%), and *Scolecithricella tenuiserrata* (11.7%) made up 75.5% of the family in the water column. The three most abundant species displayed some evidence for vertical migration, and the family as a whole increased slightly in numbers in the surface layers at night (Fig. 12).

Scolecithrix danae.--A part of the population moved from 50 m in the day to the surface at night. There was also a large decrease in the number of specimens found at 50 m from 2768 in the day to 472 at night which indicates a nocturnal migration away from this depth.

Scolecithricella dentata.--An extensive vertical migration was indicated in this species. The bulk of the population moved from 300 m in the day to the 50 and 100 m levels at night.

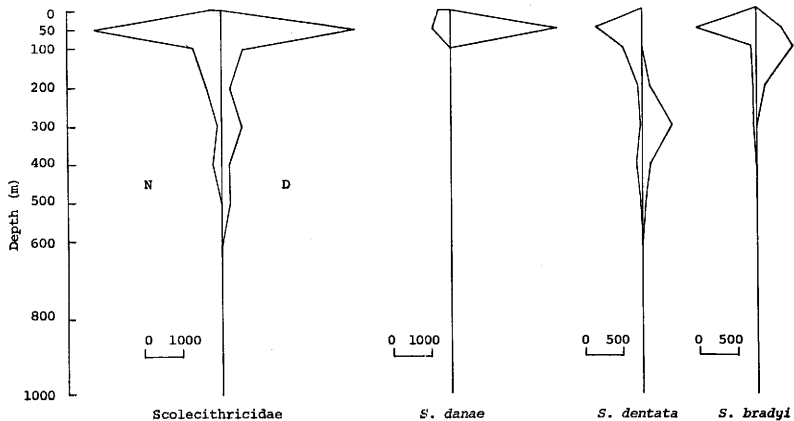


Fig. 12. The vertical distribution of the family Scolecithricidae, *Scolecithrix danae*, *Scolecithricella dentata*, and *Scolecithrix bradyi*. Plotted as in Fig. 7 (page 39).

Scolecithrix bradyi.--The evidence for migration in this species was convincing. In the day the species was widely distributed with its center of abundance at 100 m and at night it was concentrated at 50 m.

This family is generally considered omnivorous (Esterly, 1916; Mullin, 1966; Minoda, 1971; Timonin, 1971). Mullin (1966) stated that the gut contents of *Scolecithrix* suggested predominantly carnivorous feeding, but Wickstead (1962) examined gut contents and found both phytoplankton and crustacea remains. The percentage of calanoids formed by this species was relatively stable with depth (Table 3). The only high percentage (21.6%) was found at 300 m in the day which corresponds to the relatively deep water abundance peak in the day distribution.

Metridiidae

This family was represented by 9 species which together formed 14.0% of the estimated total number of calanoids in the water column. The species *Pleuromamma gracilis* (39.4%), *P. abdominalis abdominalis* (22.6%), *P. xiphias* (14.0%), and *P. piseki* (13.9%) made up 89.9% of the family. The vertical distribution of the group as a whole (Fig. 13) reflects the distribution of *Pleuromamma*, which migrated extensively. *Metridia* was found in smaller numbers and in the deeper layers.

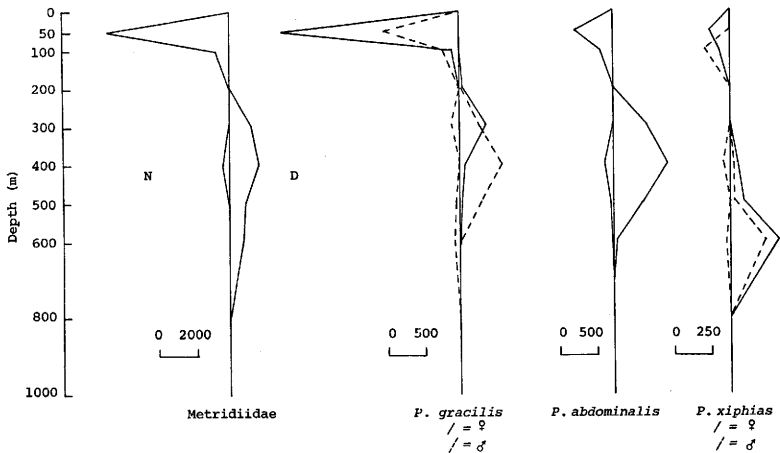


Fig. 13. The vertical distribution of the family Metridiidae, *Pleuromamma gracilis*, *P. abdominalis abdominalis*, and *P. xiphias*. Plotted as in Fig. 7 (page 39).

Pleuromamma gracilis.--The distributions of the males and females of this species were slightly different. Both sexes showed evidence of extensive vertical migration. In the day, the center of the female population was at 300 m and the male population at 400 m. At night, the bulk of both populations was at 50 m.

Pleuromamma abdominalis abdominalis.--The evidence indicates a strong vertical migration in this species. The population was centered at the 300 to 500 m levels in the day and moved to 50 m at night.

Pleuromamma xiphias.--The females of *P. xiphias* migrated farther than the males. During the day, both populations were centered at 600 m. At night, the bulk of the male and female populations moved to 100 and 50 m, respectively. Apparently the female population migrated in its entirety. Not a single specimen was found at night in the range of depths inhabited by the species in the day.

This family is generally considered omnivorous (Esterly, 1916; Wickstead, 1962; Mullin, 1966; Timonin, 1971). Conover (1960) and Minoda (1971) however, considered its members herbivorous. The extensive migrations, large numbers found, and the relatively large mean size of the abundant species in this family, make this group important in the transfer of energy from the surface to the deeper layers. The percentage of calanoids formed by this family (Table 3) in the upper 600 m reflects the abundance of *Pleuromamma* in the day and night. The relatively high percentages below 600 m reflect the

presence of *Metridia*.

Lucicutiidae

This family was represented by 11 species which together formed 10.3% of the estimated total number of calanoids in the water column. *Lucicutia flavicornis* was predominant, forming 57.1% of the family. *L. paraclausi* (13.3%), *L. ovalis* (9.8%), and *L. clausi* (8.7%) were also abundant. Together these four species made up 88.9% of the family in the water column. The members of this family appeared to be distributed in two groups (Fig. 14). Group I, *L. clausi*, *L. flavicornis*, *L. gaussae*, *L. gemina*, and *L. paraclausi* was found mainly in the upper 400 m. Group II, *L. curta*, *L. longiserrata*, *L. lucida*, *L. magna*, *L. oblonga*, and *L. ovalis* was found exclusively at the 400 m level or below.

Lucicutia flavicornis.--There were two forms of females of this species present in the samples. Form I and the males found were synonymous with *Lucicutia flavicornis* (Claus, 1863). The mean size of the form I female was 1.52 mm and the size range was from 1.40 to 1.96 mm. The mean size of the male was 1.50 mm with a range from 1.38 to 1.70 mm. A vertical migration was evident, with the bulk of the population moving from 100 m in the day to 50 m at night.

Form II females differed from form I in the structure of the third exopod of P5, the length and position of the caudal rami, and the shape of the genital segment. The mean size was 1.46 mm and the

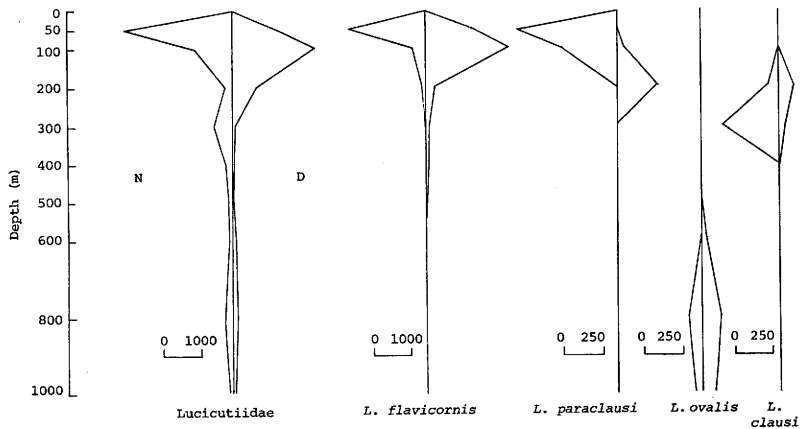


Fig. 14. The vertical distribution of the family Lucicutiidae, *Lucicutia flavicornis*, *L. paraclausi*, *L. ovalis*, and *L. clausi*. Plotted as in Fig. 7 (page 39).

range was from 1.38 to 1.56 mm. There was little evidence for vertical migration in this form. There was a large increase in the estimated total number caught from 36 in the day to 380 at night, but the greatest number of specimens was found at 100 m both during the day and at night.

Both forms will be described in detail at a later date, but the form I and the form II specimens have been combined in all of the tables and figures in this paper. The number of form II specimens was relatively small and the vertical distribution was generally similar to that of form I. Form II specimens made up 8.0% of the *L. flavicornis* population in the water column.

Lucicutia paraclausi.--This species exhibited a short vertical migration. The bulk of the population moved from 200 m in the day to the 50 and 100 m levels at night.

Lucicutia ovalis.--The evidence indicated little or no vertical migration for this species. Its depth range extended from 400 to 1000 m and the greatest numbers were at 800 m during the day and at night.

Lucicutia clausi.--The evidence for vertical migration is inconclusive for this species. The bulk of the population appeared to move down from 200 m in the day to 300 m at night, but there was a large increase in the total number of specimens caught from 142 in the day to 454 at night which may indicate that the day population was not sampled adequately.

There has been little agreement as to the feeding habits of this family. Itoh (1970) considered its members omnivorous. Minoda (1971) and Timonin (1971) listed them as herbivores. A herbivorous mode of feeding seems especially unlikely for the members of group II of this family. The percentage of calanoids formed by this family at the various depths generally reflects the abundance peaks of its distribution (Table 3). The relatively high percentages at the 800 and 1000 m levels reflect the presence of the group II species.

Heterorhabdidae

This family was represented by 11 species which together formed 2.7% of the estimated total number of calanoids in the water column. There was no single predominant species. *Heterorhabdus papilliger* (32.0%), *H. spinifer* (27.4%), and *H. abyssalis* (19.7%) made up 79.1% of the family. The two most abundant species exhibited a slight reverse migration and *H. abyssalis* did not migrate appreciably. The distribution of the family as a whole reflects this with the number found in the surface layers decreasing at night (Fig. 15).

Heterorhabdus papilliger.--The distributions of the male and female of this species were different. Both were mainly found in the upper 400 m. In the day, the male and female populations were centered at 50 m. At night, part of the female population apparently moved to the surface and part moved into the deeper layers. The males did not move into the surface layers but exhibited a reverse

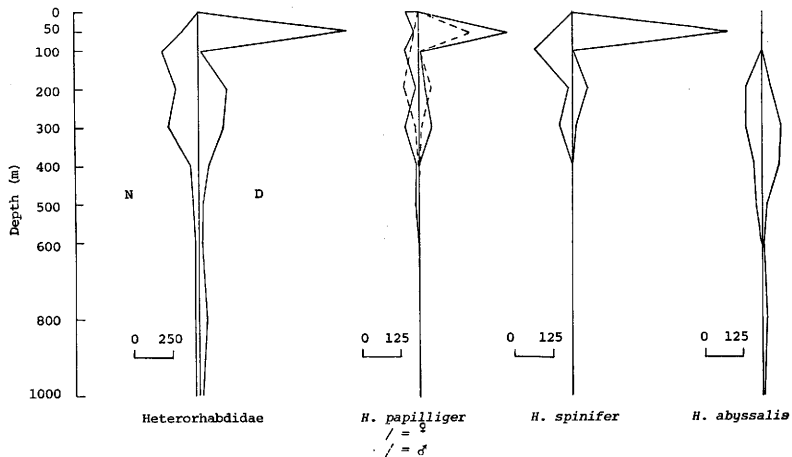


Fig. 15. The vertical distribution of the family Heterorhabdidae, *Heterorhabdus papilliger*, *H. spinifer*, and *H. abyssalis*. Plotted as in Fig. 7 (page 39).

migration, moving into the 100 and 200 m levels.

Heterorhabdus spinifer.--The evidence for a reverse migration in this species was substantial. The center of the population moved from 50 m in the day to 100 m at night.

Heterorhabdus abyssalis.--This species was distributed in slightly deeper water and most of the population was found between 200 and 500 m. Little evidence for migration was found.

This family is considered carnivorous (Itoh, 1970; Minoda, 1971; Timonin, 1971). The percentage of calanoids formed by this group at the various depths was generally stable (Table 3). The elevated value of 12.4% at 300 m in the night was the result of the downward movement of *H. papilliger* and *H. spinifer* and the presence of *H. abyssalis*.

Augaptilidae

This family was represented by 14 species which together formed 10.9% of the estimated total number of calanoids in the water column. The number of species in the family was undoubtedly larger due to the specimens of *Euaugaptilus* which were not identified. Numerically however, these specimens represented only a small percentage of the family. *Haloptilus longicornis* (56.2%) and *H. paralongicirrus* (36.5%) formed 92.7% of the family in the water column. The day and night distribution of the family was concentrated in the upper layers (Fig. 16).

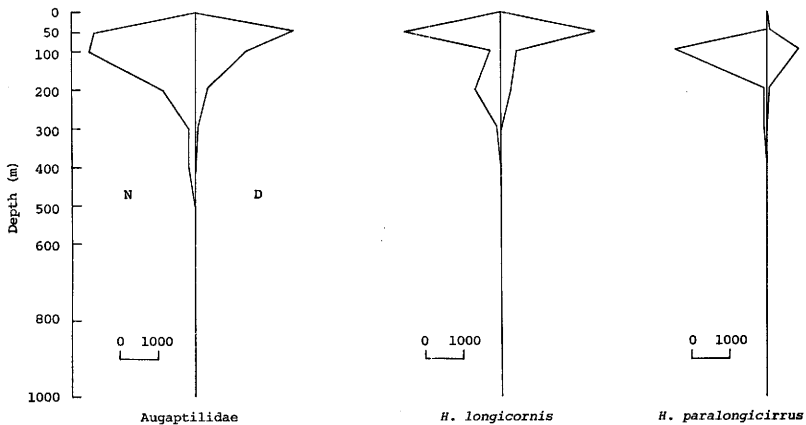


Fig. 16. The vertical distribution of the family Augaptilidae, *Haloptilus longicornis*, and *H. paralongicirrus*. Plotted as in Fig. 7 (page 39).

Haloptilus longicornis.--The greatest concentrations of this species were found at 50 m both during the day and at night. There was some evidence for a reverse migration with part of the population moving to 200 m at night.

Haloptilus paralongicirrus.--This species exhibited no vertical migration and was distributed slightly deeper than *H. longicornis*. The greatest concentrations were found at 100 m in the day and night.

This family is generally considered carnivorous (Mullin, 1966; Itoh, 1970; Minoda, 1971; Timonin, 1971) and as such it represents the most abundant carnivorous group found in the water column. It was most abundant in the sub-surface layers which is reflected in the percentage of calanoids formed by this family at these levels (Table 3).

Candaciidae

This family was mainly distributed in the upper 200 m (Fig. 17) and was represented by nine species which together formed 1.4% of the estimated total number of calanoids in the water column. *Paracandacia simplex* (46.6%), *Candacia longimana* (18.5%), and *Paracandacia bispinosa* (13.3%) made up 78.4% of the family.

Paracandacia bispinosa and *P. simplex*.--Both of these species were found in the surface layers. *P. bispinosa* was found only at 50 m in the day. The night hauls entirely missed the population. Apparently, this species inhabits a very narrow depth range. *P. simplex*

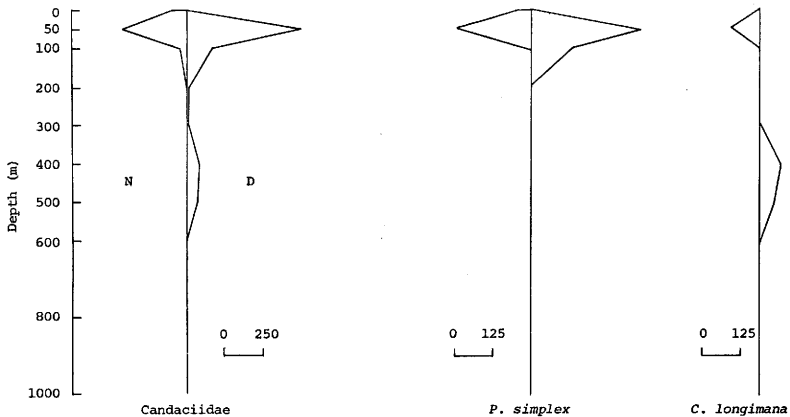


Fig. 17. The vertical distribution of the family Candaciidae, *Paracandacia simplex*, and *Candacia longimana*. Plotted as in Fig. 7 (page 39).

exhibited a slight vertical migration. Although the bulk of the population remained at 50 m, the range moved upwards at night.

Candacia longimana.--During the day, this species was found in mid-water. An extensive vertical migration was indicated with the bulk of the population moving from the 400 and 500 m levels in the day to 50 m at night.

This family is considered carnivorous (Wickstead, 1959, 1962; Mullin, 1966; Itoh, 1970; Timonin, 1971). It was the least abundant carnivorous group examined and was found mainly in the surface layers.

Acartiidae

This family was represented by one species, *Acartia danae*, which formed 2.7% of the estimated total number of calanoids in the water column. Almost the entire population was found at 50 m both during the day and the night. *Acartia* is considered omnivorous (Itoh, 1970; Timonin, 1971).

Distribution of Dominant Particle Grazers and Carnivores; the Adaptive Value of Vertical Migrations

In many instances there have been disagreements by various investigators as to the feeding habits of calanoid copepods. The families Euchaetidae, Heterorhabdidae, Augaptilidae, and Candaciidae are usually considered carnivorous but the feeding habits of the

other families investigated here, Calanidae, Eucalanidae, Calocalanidae, Pseudocalanidae, Aetideidae, Scolecithricidae, Metridiidae, Lucicutiidae, and Acartiidae have not always been agreed upon. In examining the selective feeding in the laboratory of a number of species from many of these families, Mullin (1966) found no obligate herbivores and concluded that the term particle grazers would more aptly fit their mode of feeding. Until more work has been done on natural feeding preferences, this appears to be a reasonable approach and these families will be considered as particle grazers in any further discussion.

Dominant species of particle grazers and carnivores were determined on the basis of their percentage in the water column. In many instances, the effect of a species on its environment may be more closely related to its relative abundance at individual depths. The following method of analysis therefore, should be interpreted as a general examination of the relationships present.

The vertical distributions of the abundant particle grazing species are quite varied. The dominant forms have been listed in Table 4 according to their relative abundance in the water column, and the 11 species represented 67.4% of the nine particle grazing families considered. Specific details on the day and night vertical distribution of these species are given elsewhere in this paper, but the distributions of the four most abundant species and also *Eucalanus hyalinus* and *Pleuromamma abdominalis abdominalis* are shown again

TABLE 4. DOMINANT CALANOID PARTICLE GRAZERS IN
THE WATER COLUMN SAMPLED

Rank	Species	Percent of calanoids in water column
1.	<i>Rhincalanus cornutus</i>	11.8
2.	<i>Nannocalanus minor</i>	11.7
3.	<i>Lucicutia flavicornis</i>	5.9
4.	<i>Pleuromamma gracilis</i>	5.5
5.	<i>Calanus tenuicornis</i>	3.3
6.	<i>Pleuromamma abdominalis</i>	3.2
7.	<i>Calocalanus pavo</i>	3.1
8.	<i>Eucalanus hyalinus</i>	2.6
9.	<i>Scolecithrix danae</i>	2.6
10.	<i>Clausocalanus arcuicornis</i>	2.4
11.	<i>Acartia danae</i>	<u>2.3</u>
		54.4

in Figure 18. Through consideration of size and numerical abundance, these six species appear to represent the greatest particle grazing biomass in the water column. All of the species have night abundance peaks at 50 m, but during the day, significantly different vertical distributions are evident. *Rhincalanus cornutus*, *Pleuromamma gracilis*, and *P. abdominalis* migrate extensively to the 400 to 600 m depths and these species undoubtedly play an important role in the transfer of energy from the surface layers to these depths. *Eucalanus hyalinus* also has an abundance peak in deep water but this may have been due to the counting of specimens that were actually dead at the time of capture as has been previously explained.

The vertical distributions of the common carnivorous species were generally limited to the upper layers (Fig. 19). The predominant copepod carnivores are shown in Table 5 and the eight species listed represent 85.9% of the organisms in the four carnivorous families considered. *Haloptilus longicornis* and *H. paralongicirrus* were by far the most abundant predatory calanoids in the water column and were found almost exclusively in the upper 200 m. *Euchaeta media* was the major deep living form, migrating from the upper 100 m at night to 500 m in the day.

The distributions of common carnivores indicate that predatory pressure by calanoids is greatest in the surface layers. Other zooplankton forms, including many carnivores such as chaetognaths and some euphausiids (Timonin, 1971), were also relatively abundant in

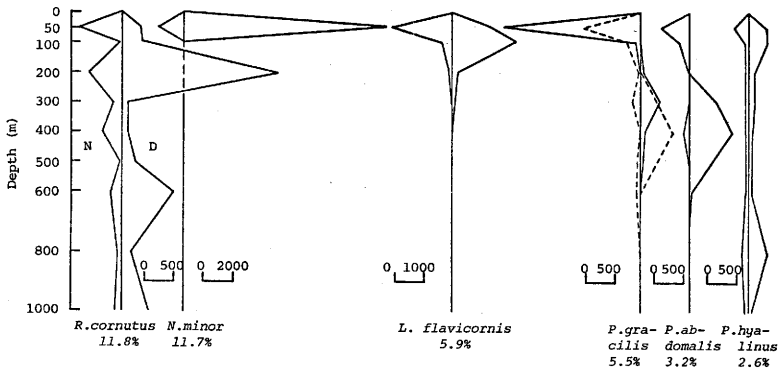


Fig. 18. The day and night vertical distributions of the dominant calanoid particle grazers *Rhincalanus cornutus*, *Nannocalanus minor*, *Lucicutia flavicornis*, *Pleuromamma gracilis*, *P. abdominalis abdominalis*, and *E. hyalinus*. Plotted as in Fig. 7 (page 39). The percentage of calanoids in the sampled water column formed by each species is shown beneath each diagram.

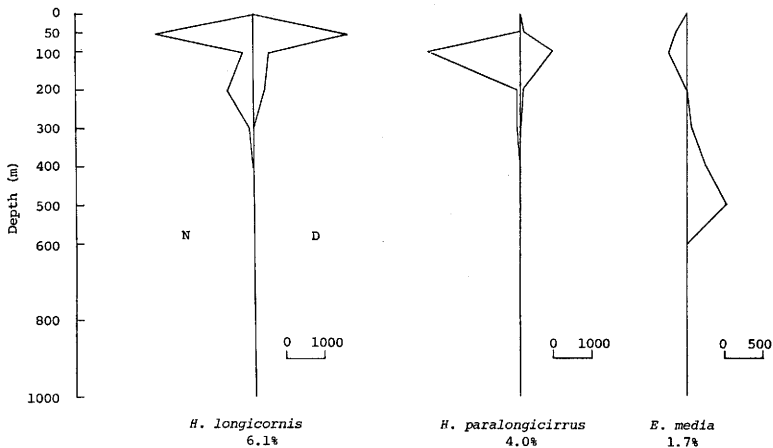


Fig. 19. The day and night vertical distributions of the dominant calanoid carnivores *Haloptilus longicornis*, *H. paralongicirrus*, and *Euchaeta media*. Plotted as in Fig. 7 (page 39). The percentage of calanoids in the sampled water column formed by each species is shown beneath each diagram.

TABLE 5. DOMINANT CALANOID CARNIVORES
IN THE WATER COLUMN SAMPLED

Rank	Species	Percent of calanoids in water column
1.	<i>Haloptilus longicornis</i>	6.1
2.	<i>Haloptilus paralongicirrus</i>	4.0
3.	<i>Euchaeta media</i>	1.7
4.	<i>Heterorhabdus papilliger</i>	0.9
5.	<i>Euchaeta marina</i>	0.8
6.	<i>Heterorhabdus spinifer</i>	0.7
7.	<i>Paracandacia simplex</i>	0.6
8.	<i>Heterorhabdus abyssalis</i>	<u>0.5</u>
		15.3

abundant in the upper layers of the water column (Fig. 4A, p. 28). It would therefore seem to be advantageous for prey species to move periodically out of the surface zone and this may be the reason for many vertical migrations, especially by particle grazing species. In recognizing the advantage of migrations in escaping from predation, it has generally been emphasized that the plankters are attempting to escape from visual planktophages by feeding under the cover of darkness at night and migrating into the deeper darker layers during the day. This has led to numerous attacks on the hypothesis by citing examples that apparently negate this advantage (e.g. Vinogradov, 1968). One of the major objections to this idea has been centered around the fact that during the day, light intensities do not change enough over many migratory ranges to make a significant difference in the visual capabilities of predators. Despite these objections, at least in reference to the zooplankton in this region, migrating out of the surface layers moves the organisms out of the distribution ranges of many abundant carnivores. Migrations to the deeper layers where carnivore densities are lower should decrease the probability of predator contact. Light, the triggering factor, may be incidental. If periodic migrations to deeper levels are advantageous, rhythmical changes in light intensity might be expected to act as a triggering mechanism. Selective pressure would therefore work towards perpetuating a response to light intensities. Why this is a negative response in the vast majority of zooplanktic

organisms is still unknown. In concordance with this theory however, migrations of extremely small magnitude and even reverse migrations could be advantageous by moving an organism away from optimum densities of specific predators. This paper has already shown that in many instances, calanoid copepods inhabit narrow depth ranges. Species that apparently do not migrate extensively away from the surface are generally smaller in size and may also combat predatory pressure with greater reproductive capabilities.

Carnivores may migrate away from the surface to escape from predation by other carnivores or they may be following their prey. With the exception of *Euchaeta media* however, vertical migrations were not very extensive among the common carnivorous calanoids. Some vertical distributions of carnivorous species could be explained through competitive exclusion. As an example, the distributions of the two most abundant calanoid carnivores can be examined.

Haloptilus longicornis and *H. paralongicirrus* are similar in size and morphology (Park, 1970) and may be expected to feed on similar organisms. Their distributions in the water column appear to be distinctly separated. *H. longicornis*, the most abundant form, was found to be concentrated at 50 m in the day and night, where the highest concentration of total copepods also occurred. *H. paralongicirrus* was found just below this level with its greatest numbers at 100 m in the day and night. This apparent spatial separation suggests that *H. longicornis* may be more competitive in utilizing the

food source at 50 m thus displacing *H. paralongicirrus* into the deeper layers.

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APPENDIX

TABLE 1. DAY AND NIGHT VERTICAL DISTRIBUTION OF INDIVIDUAL SPECIES

The numbers are estimated numbers, the sexes are combined,
and the numbers marked * could be considered contaminants

CALANIDAE

Depth (m)	<i>Calanus tenuicornis</i>		<i>Nannocalanus minor</i>		<i>Neocalanus gracilis</i>		<i>N. robustier</i>	
	D	N	D	N	D	N	D	N
0	.	.	24	28	.	8	.	6
50	240	1200	13824	1716	24	94	.	12
100	1428	464	.	.	.	44	.	.
200	24	.	2	.	.	16	.	.
300	4	.	.	2	76	60	.	.
400	128	12	.	.
500	.	.	4	.	124	14	.	.
600	8	9	.	.
800	3	.	.
1000
Estimated total	1696	1664	13854	1746	360	250	.	18

TABLE 1. (continued)

Depth (m)	<i>E. crassus</i>		<i>E. hyalinus</i>		<i>E. monachus</i>		<i>E. pileatus</i>	
	N	D	N	D	N	D	N	D
0	144	12	.
50	76	4	212	256	32	56	56	4
100	.	.	44	278	120	.	.	.
200	.	.	8	90	202	12	.	.
300	.	.	14	110	106	198	.	.
400	.	.	56	54	26	42	.	.
500	.	.	8	2	66	60	.	.
600	.	.	5	36	2	.	.	.
800	.	.	99	268
1000	.	.	6	66
Estimated total	220	4		1160	312	554	72	

TABLE 1. (continued)

<i>Paracalanus aculeatus</i>	D	6	136	26	16	2*	42	144
	N							
<i>P. indicus</i>	D	8					8	
	N							
CALOCALANIDAE								
<i>Calocalanus contractus</i>	D	8					4	8
	N							
<i>C. pavo</i>	D	10	60				1302	
	N	32	332	2			2574	
Depth (m)	0							
	50	2208	1232					
	100	332	60					
	200							
	300							
	400							
	500							
	800							
1000								
Estimated total							2574	1302

TABLE 1. (continued)

PSEUDOCALANIDAE

Depth (m)	<i>Clausocalanus arcuicornis</i>		<i>C. furcatus</i>		<i>C. jobei</i>		<i>C. mastigophorus</i>		Estimated total
	N	D	N	D	N	D	N	D	
0	.	4	
50	100	696	8	18	2	232	472		
100	32	8	20	2332	204	.	6		
200	2	124	8	2*	4	.	4		
300	.	2	4*	.	.	.	4		
400	.	10	.	6*	.	.	4		
500	.	.	2*	8*	.	.	4		
600	.	.	1*	.	.	.	12		
800	.	.	1*	4*	.	.	.		
1000	.	.	4*	6*	.	.	.		
Estimated total	134	814	52	2276	210	232	506		2182

TABLE 1. (continued)

Depth (m)	<i>A. mexicanus</i>		<i>Chirundina streetsii</i>		<i>Euchirella amoena</i>		<i>E. bitumida</i>	
	N	D	N	D	N	D	N	D
0
50	4	.	.	.
100
200
300
400	.	4
500	.	16
600	.	12
800	.	2
1000	.	8
Estimated total	.	22	.	.	4	.	.	14
		56						

TABLE 1. (continued)

<i>E. curticauda</i>	D	2	2
	N	.	.	4	4
<i>E. maxima</i>	D	2	2
	N
<i>E. messinensis</i>	D	2	.	2	.	16	.	.	20
	N	.	8	1	.	.	9
<i>E. pseudotruncata</i>	D	.	.	.	20	20
	N
Depth (m)		0	50	100	200	300	400	500	600	800	1000	Estimated total	

TABLE 1. (continued)

Depth (m)	<i>E. pulchra</i>		<i>E. splendens</i>		<i>Gaetanus armiger</i>		<i>G. kruppi</i>	
	N	D	N	D	N	D	N	D
0	40	•	•	•	•	•	•	•
50	•	•	8	•	•	•	•	•
100	•	•	•	•	•	•	•	•
200	•	2	•	4	•	•	•	•
300	•	•	•	•	•	•	•	•
400	•	•	•	•	•	•	•	•
500	1	•	•	•	•	•	•	•
600	2	•	•	•	•	•	•	•
800	•	18	1	•	•	•	•	•
1000	5	10	•	•	5	2	•	•
	7	16	•	•	1	•	•	•
Estimated total	55	82	9	4	6	2	2	4

TABLE 1. (continued)

METRIDIIDAE

Depth (m)	<i>Metridia brevicauda</i>		<i>M. curticauda</i>		<i>M. princeps</i>		<i>M. venusta</i>	
	N	D	N	D	N	D	N	D
0
50
100
200
300
400	32	.	24
500	7	.	1	.	4	.	7	116
600	6	6	16
800	9	.	40	16	.	2	6	6
1000	.	.	18	20
Estimated total	54	174	83	36	4	2	54	122

TABLE 1. (continued)

Depth (m)	<i>L. curta</i>		<i>L. flavicornis</i>		<i>L. gaussae</i>		<i>L. gemina</i>	
	N	D	N	D	N	D	N	D
0	.	.	.	3
50	.	.	52	1160	.	56	.	.
100	68	.	1996	2072	128	.	.	.
200	80	.	432	211	68	.	80	.
300	16	.	14	50	.	.	6	.
400	8	.	36	26	2	.	6	.
500	3	.	62	22	.	.	6	.
600	1	.	10	2	.	.	1	.
800	.	.	3	2
1000	.	.	.	4
Estimated total	176	98	2605	3549	198	56	98	7

TABLE 1. (continued)

Depth (m)	<i>H. medianus</i>		<i>H. papilliger</i>		<i>H. spinifer</i>		<i>H. spinifrons</i>		Estimated total
	N	D	N	D	N	D	N	D	
0	
50	.	.	40	.	4	.	.	.	
100	.	.	48	448	56	512	.	.	
200	8	.	72	4	120	2	.	.	
300	.	4	56	52	10	44	10	.	
400	8	.	46	44	40	12	18	.	
500	.	.	12	10	.	.	2	.	
600	.	.	11	.	.	2	.	.	
800	.	.	1	.	.	.	6	.	
1000	.	.	2	
	.	.	1	6	
Estimated total	16	4	289	564	230	572	79	38	

TABLE 1. (continued)

Depth (m)	<i>C. curta</i>		<i>C. ketchumi</i>		<i>C. longimana</i>		<i>C. pachydactyla</i>	
	N	D	N	D	N	D	N	D
0	34	•	•	•	•	•	6	1
50	64	32	•	•	88	•	•	104
100	•	•	•	•	4	2	•	•
200	•	•	•	•	•	•	•	•
300	•	•	•	•	•	2	•	•
400	•	•	•	4	•	70	•	•
500	•	•	•	18	•	46	•	•
600	•	•	•	•	•	•	•	•
800	•	•	•	•	•	•	•	•
1000	•	•	•	•	•	•	•	•
Estimated total	98	32	•	22	92	120	6	105

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