

DIURNAL VERTICAL MIGRATIONS OF DEEP-WATER PLANKTON

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INTRODUCTION

Diurnal vertical migrations have long been known to play an important part in the lives of pelagic organisms. The numerous previous studies on these migrations in oceanic animals have been limited almost entirely to plankton living relatively near the surface. It was the purpose of the present investigation to continue and extend the observations made by Welsh, Chace, and Nunnemacher (1937) on the diurnal vertical migrations of deep-water animals. More specifically, our objectives were (1) to ascertain the vertical extent of these migrations for the bathyplankton,² (2) to determine the greatest depth in the sea at which these migrations still occur, and (3) to discover the relations of these phenomena to the changes in submarine illumination with time and depth.

HISTORICAL CONSIDERATIONS

The earliest knowledge of diurnal vertical migrations of marine organisms arose from the practical observations of fishermen. Thus man has known from time immemorial that under certain conditions if he wishes to obtain a good catch of herring, his nets should be set deep in the water during the daytime and shallower at night. Such observations were abundantly confirmed and extended for shallow-water animals by the work of a great many marine biologists (an extensive literature is cited by Rose, 1925; Russell, 1927; and Clarke, 1933*b*).

As far as the plankton of deeper water was concerned, a small amount of information was also already at hand by quite an early date. For example Rang (1828) observed that the pteropod, *Hyalocylis striata*, among others, could be taken at the surface of the sea only after sunset and before sunrise and sank into deeper water during the day. Recently Stubbings (1938) has found that this species descends during

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² See Ekman ('35, pp. 451-77) for a comprehensive general discussion of the bathypelagic fauna.

the day to 200–250 m. so that for at least part of the day it is a bathypelagic organism, i.e., one which lives in the intermediate depths rather than near the surface or the bottom of the sea. But the significance of this and other similar early observations was not appreciated until long afterwards since the existence of a bathyplankton had not been realized until the latter part of the nineteenth century when the data of the various great oceanographic expeditions were analyzed.

Murray (1885, p. 218) concluded from his experiences on the "Challenger" that, "the great majority of plankton organisms live at various depths down to and even deeper than 100 fathoms during the day . . . and only come to the surface at night. . . ." Other investigators came to similar general conclusions (e.g., Chun, 1890, pp. 82–4; Brauer, 1906, p. 337; 1908, p. 232). Brauer was among the first to point out the possible relation of these migrations to such interesting biological problems as bioluminescence, type and size of eye, and pigmentation in the bathyplankton.³ However, it remained for Fowler (1905, 1909) first to demonstrate by means of numerical data for schizopod and ostracod crustaceans the diurnal vertical migrations of moderately deep-living species. Soon afterwards Murray and Hjort (1912) showed clearly that such migrations were undertaken by organisms which were definitely "deep-sea" animals during the daytime; these investigators also emphasized the correlation of these phenomena with the general biology of the sea, sustaining and extending some of Brauer's suggestions by means of their more complete data.

The further inquiry into the exact and quantitative aspects of the subject presented considerable technical difficulties since for this purpose it is necessary to know accurately where the plankton has been caught, which is impossible when working with open nets. Hence the precise determination of the vertical extent of diurnal migrations and of the various depths at which they occur had to await the development of efficient deep-sea equipment for sampling populations at known depths without contamination from other strata.

Since the invention of the Sigsbee gravitating deep-sea trap (1880) and Palumbo's closing net (Chierchia, 1885, p. 81), many oceanographers have devised such apparatus; yet it was only very recently that reliable equipment has been available for these purposes.

METHODS

The observations were carried out in July, 1937, at "Atlantis" Station 2894 (39° 06' N., 70° 16' W.) which is in continental slope

³ For recent investigations of these problems see Welsh and Chace, 1937, 1938.

water about 300 miles east of Cape May, N. J. This position was chosen for several reasons: (1) The slope water, except for the superficial layers, is relatively free from currents (see Iselin, 1936, p. 11). (2) The station was far enough from both the Gulf Stream and coastal waters to be free of their influence. (3) The water was sufficiently deep to prevent benthonic organisms from confusing the results. (4) Data from the continental side of the Gulf Stream might offer some interesting points for comparison with results previously obtained (Welsh, Chace, and Nunnemacher, 1937) in the far more transparent waters of the Sargasso Sea.

In order to keep the ship in about the same geographic position the hauls were made in various directions while the work was being done. The maximum deviation from the original station was about 14 miles (see Table I).

TABLE I

Position of the ship at various times while the work was being carried out. The first position in the table is that designated as Station 2894.

Date	Time	Latitude	Longitude
July 18th.....	10 P.M.	39°06' N.	70°16' W.
19th.....	5 A.M.	38°57'	70°30'
19th.....	Noon	39°01'	70°30'
20th.....	Noon	39°06'	70°33'
21st.....	Noon	39°00'	70°30'
22nd.....	Noon	38°59'	70°30'

Horizontally hauled closing nets were used, modified from those employed by Leavitt (1935, 1938) as described by Welsh, Chace, and Nunnemacher (1937). These were 2 m. in diameter at the mouth and 9 m. long; the sides were of stramin, 6 threads to the centimeter, with a silk inset, about 20 threads to the centimeter (54 to the inch), in the tail. While the nets were open, the speed of the ship relative to the surface water was kept close to 2 knots. However, the actual speed of each net in relation to the water layer through which it was moving was not known. Since the water at various depths was probably moving at different velocities and possibly even in different directions, the results in such a situation might be very misleading as to the actual population distributions. But in the present case the fact that the hauls were made in various directions precludes the origin of systematic errors from this source. Furthermore, the evidence from the catches for a regular diurnal migration in the various organisms indicates that the relative

movements of the water were not of sufficient magnitude to confuse the results.

The depth at which a net was fishing was estimated by means of the trigonometric relation between wire angle and the amount of cable out. At 1,000 m. this estimate was probably accurate within about 10 per cent, being more accurate in shallower and less so in deeper tows.

Thirty-nine catches in a series of 16 hauls were made with the nets fishing for 2 hours at various depths and times throughout more than 2 diurnal cycles. Each entire haul took 4 hours so that 6 were made in a 24-hour period. Tows were made at 100, 200, 400, 600, 800, 1,000 and 1,200 meters, calculated depth, and since the bottom was at 2,860 m., the population thus sampled was purely pelagic. Although the closing nets worked very well in general, 4 of the 39 hauls failed; these are marked in Fig. 1 by asterisks.

Figure 1 represents graphically the times and depths of all the closing net hauls made at this station and shows that various depths were sampled on succeeding days. During the morning of the third day on station a series of tows at 100 and 1,200 m. was begun, but the sea became too rough to continue towing (force 5 on the Beaufort scale) so only one haul was made before work was stopped. In an attempt to fill in the gaps in our series we made tows at appropriate depths at noon and midnight on July 22, i.e., about 36 and 48 hours after the continuous series of hauls had been abandoned.

Throughout the periods when the plankton hauls were being made, a record was kept of the light intensity on deck; furthermore, two series of measurements of submarine illumination were carried out. The same submarine and deck photometer cases were employed and the same procedure followed as previously described by Clarke (1933a, 1938a).⁴ However, the Westinghouse "photox" cells in his apparatus were replaced by emission photoelectric cells of the "photronic" type (manufactured by the Weston Electrical Instrument Corp.) since the former had been found to be somewhat variable. To measure temperature changes, a small thermometer was installed inside the case of the deck photometer, beside the cell, where it could be read through the photometer window by raising the opal glass momentarily. The temperature inside the photometer case during the day was found to vary between a minimum of 19° C. and a maximum of 35° C. Correction factors throughout this temperature range were determined from tests carried out in the laboratory at the end of the cruise, in collaboration with

⁴ In making these measurements the shadow of the hull is avoided by heaving the ship to with her stern toward the sun and suspending the sea photometer from the end of the mizzen boom (compare criticism by Poole, 1938).

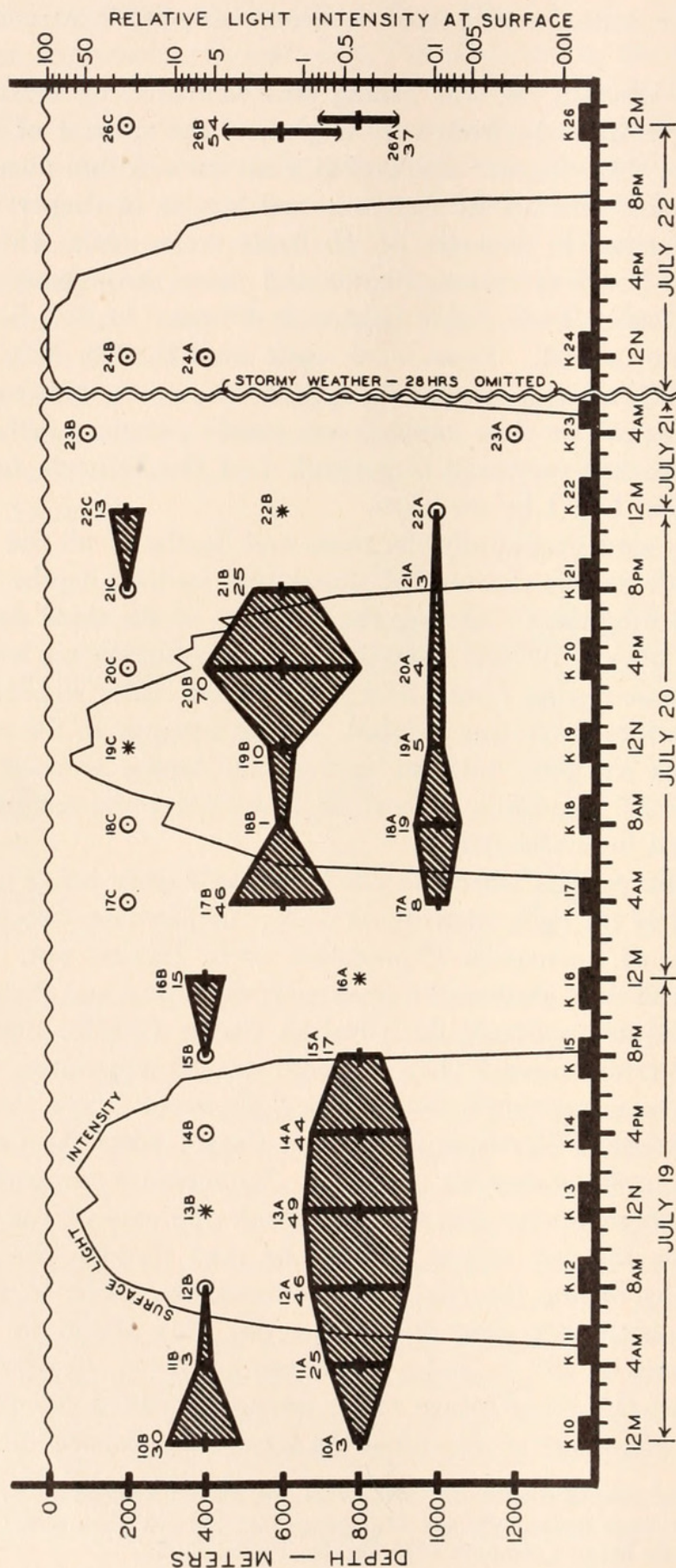


FIG. 1. Distribution in depth and time of the closing net hauls at Station 2894. The numbers of the hauls and their duration are shown by the heavy bars along the time axis. The numbers of the individual nets and their depth are indicated by the small numerals (10A, 10B, etc.) above the histograms. Those catches which failed are denoted by asterisks. The larger numerals and the vertical bars of the histograms represent the number of adult *Gemadys elegans* taken in each net. Hauls which contained none are designated by an open circle. The changes in the relative surface light intensity are also shown.

Dr. W. R. Sawyer. The proper correction, varying up to a maximum of $12\frac{1}{2}$ per cent, has been applied to each of the photometer readings.

In the first series of measurements of the penetration of light into the water (Series 450) the photronic cell was used with opal diffusing disc, but no filter. Thus the spectral sensitivity of the photometer was that of the photronic cell itself (See Weston Electrical Instrument Corp. Circ. TD-10), the sensitivity of which reached a maximum at 5800 Å. and dropped off to 10 per cent of this value at 7080 Å. and 3420 Å. In the second series (Series 451) the "green" filter combination (Schott-Jena BG-18 and GG-11) used previously and the opal disc were employed. The transmission of this green filter combination exhibited a maximum at about 5100 Å. and fell to 10 per cent of this value at about 6460 Å. and 4640 Å. When these filters were used their selective action was superimposed upon that of the photronic cell with the result that the point of maximum sensitivity of the whole instrument fell between 5800 Å. and 5100 Å.

RESULTS

This paper presents the results on the occurrence and diurnal vertical migrations of the eleven most numerous malacostracan crustaceans. The decapod, *Gennadas elegans* (Smith), has been chosen for detailed analysis of the data since its presence in significant numbers (526 specimens), its apparent freedom from marked swarming, and its definite diurnal migrations make it a favorable form for our purpose. This prawn was taken at all depths except 100 and 1,200 m. although 83 per cent of the adults captured occurred at 600 and 800 m.

Figure 1 shows that during the first day the number of *Gennadas* present at 800 m. showed a 15-fold increase between midnight and 8 A.M., followed by a further small increase by noon. By 4 P.M. the population present at this depth had decreased to 35 per cent of the number there at noon. Since *Gennadas* disappeared entirely from 400 m. or shallower after 4 A.M. and was not found at this depth again until midnight, the catches strongly suggest that individuals appearing at 800 m. between 4 A.M. and noon had migrated down from lesser depths. The series of hauls at 200, 600, and 1,000 m. on the second day confirmed this indication by showing that the *Gennadas* stock which was present at 200 m. at midnight moved downward a considerable distance during the morning and returned again to shallow water during the afternoon and evening. The numbers taken at 600 m. at various hours of the day suggest further that the bulk of the *Gennadas* stock has gone below 600 m. at the deepest extent of this vertical migration. It is noteworthy that the only hour at which these crus-

taceans were taken at 200 m. was midnight when a significant number of them were taken at that depth. Clearly a shifting of the population of this species by nearly 400 m. took place on both days when hauls were made.

The conclusions drawn from the above horizontal histograms (Fig. 1) appear even more clearly when the results of the different days are combined and regraphed in the conventional vertical histograms (Fig. 2). It is furthermore apparent from this graph that the vertical spread of the population remained about the same throughout the 24 hours in spite of its bodily translation up and down. Hence these migrations involved a concerted vertical movement of the population as a whole rather than massing and scattering effects due to relative movements between various parts of it.

One of the more striking features of the behavior of the *Gennadas* population shown in Fig. 2 is that the animals were apparently not at the same depths at each midnight. Examination of Fig. 2 shows that the *Gennadas* as a whole are considerably deeper in the water in the second midnight histogram than they are in that for the first midnight. Reference to Fig. 1 demonstrates that the difference between these two histograms depends on the deeper distribution of this prawn on the midnight following the storm of the twenty-first than at the same hour on the preceding days. Specifically, on the midnight of the fourth day none were taken at 200 m. in contrast to the 13 taken there two days before, whereas twelve times as many were taken on this occasion at 800 m. as were taken at the same time and depth four days before.

Our data yield some further details concerning the behavior of *Gennadas elegans*. There were no significant differences in vertical distribution and migration between the males and females (adult). On the other hand, there were notable differences appearing between the behavior of the adult and the post-larval specimens. All of the 67 post-larvae of *Gennadas* taken in our hauls were caught at 600 m.; none appeared at any other depths. Thus, if the post-larvae underwent diurnal migrations, the vertical extent of these was not great enough to bring the animals at any time, in sufficient quantities to be caught, within strata sampled by the other nets.

The evidence at hand for *Hymenodora glacialis* (Buchholz) is unfortunately more circumstantial than conclusive (Fig. 3A). Adults were taken only at 1,000 m. and in small numbers; from these facts and from the results of previous work (see Welsh and Chace, 1937, p. 63) it is clear that the adults of *Hymenodora* live generally deeper in the water than our nets fished. The post-larval and immature specimens of this crustacean were living shallower so that a considerable

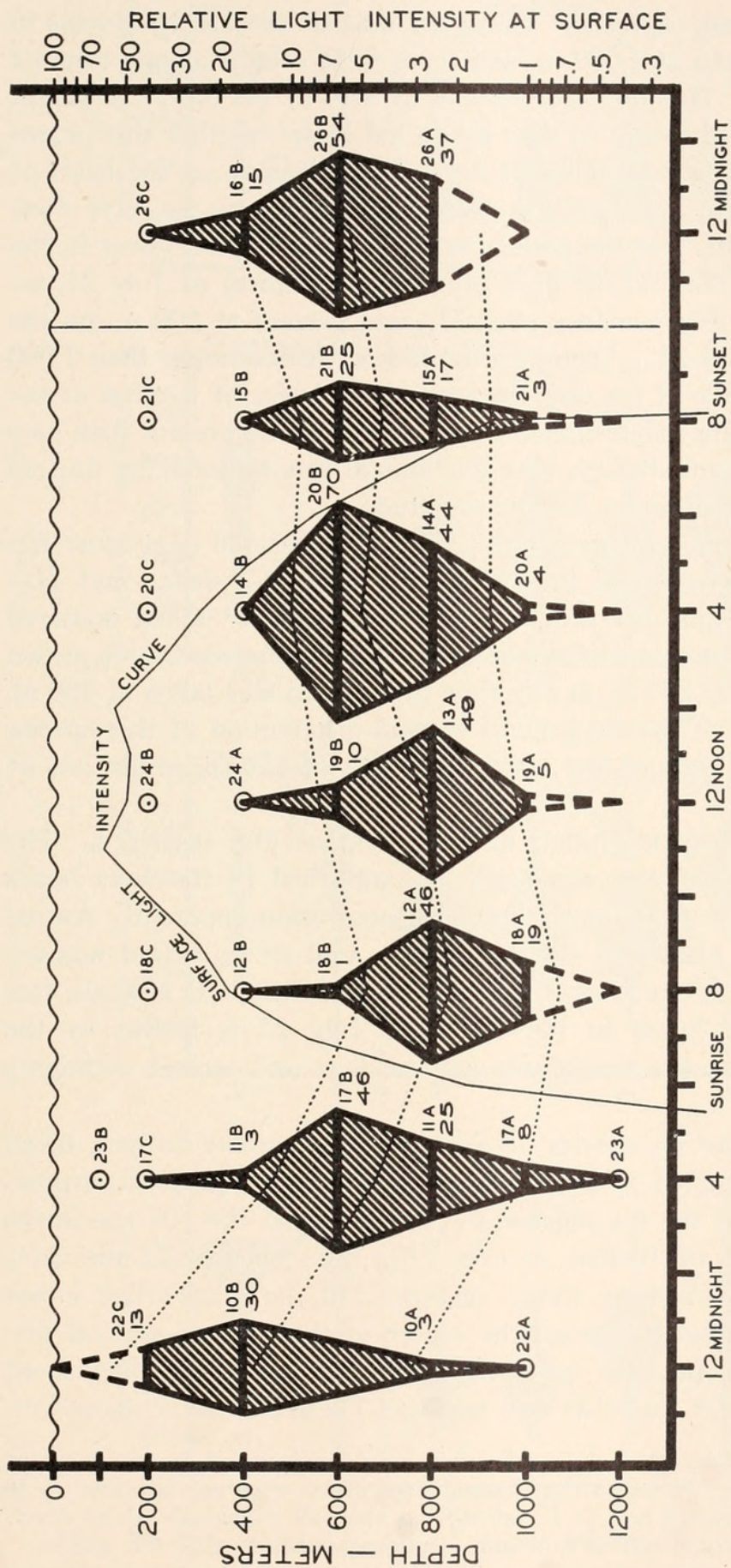


FIG. 2. *Gennadas elegans*: distribution of the adults in the various catches so arranged as to represent the position of the population at the different hours of the day. The small numerals (22C, 10B, etc.) to the right of the histograms are the numbers of the nets, which are given so that the method of combining the data of the different days will be clear from a comparison with Fig. 1. The vertical dashed line separating the second midnight histogram from the rest emphasizes the fact that 3 of the 4 nets in the group were hauled after the storm of July 21. The horizontal bars of the histograms and the larger numerals represent the numbers of animals. The upper and lower dotted lines delimit boundaries of 80 per cent of the population and the middle dotted line represents its center. The light intensity curve is an average for the 4 days measured.

number of them was captured. Sixty per cent of the 153 specimens in the hauls were taken at 1,000 m. and none were caught at any time of day above 800 m. It is unfortunate that the 600 m. net on the midnight of July 20–21 failed to fish so that we do not know whether this prawn was present at this crucial point or not. If we assume on the basis of evidence afforded by some of the other crustaceans, as we have done above for *Gennadas*, that the population was about 200 m. lower in the water on July 22 than on the days preceding the storm of July 21, we can conclude that *Hymenodora* probably was present at 600 m. on the midnight of July 20–21. Owing to the lack of hauls deeper than 1,000 m. during the middle of the day, the lower boundaries of five out of the seven histograms are indeterminate. Indecisive as the present data may be, it is probable, nevertheless, that this animal was undertaking diurnal vertical migrations of about 200 m. amplitude.

Parapasiphaë sulcatifrons Smith (Fig. 3B) was the next most numerous decapod crustacean in our catches after *Gennadas* and *Hymenodora*. Fifty-nine per cent of the 123 specimens⁵ taken occurred at 800 m. and 10 per cent of them at 1,000 m. Furthermore, this prawn was never caught at 200 m. at any time of day and was taken at 400 m. only at midnight. Thus the general vertical distribution of this species was appreciably deeper in the water than that of *Gennadas* but not of *Hymenodora*.

A diurnal vertical migration of *Parapasiphaë* also occurred. The downward movement was essentially accomplished in the four hours from midnight to 4 A.M. and the upward migration apparently started slowly in the late afternoon although 75 per cent of its extent was accomplished more rapidly after 8 P.M. The fact that these animals, too, were considerably lower in the water on July 22 is shown by the differences between the histograms for the first and second midnights in Fig. 3B.

Only one of the six species of *Sergestes*, *S. arcticus* Kröyer, taken at this station occurred in sufficient numbers for our present purpose. An examination of the distribution in the catches of the 104 specimens of carapace length of 10 mm. or over (Fig. 3C) shows that the older stages of this prawn were living shallower in the water than either *Parapasiphaë* or *Gennadas* since the center of the average vertical distribution of the population was just above 600 m. rather than about 800 m. as it was for the other two forms. These *Sergestes*, moreover,

⁵ Immature, post-larval, and larval specimens were included in this count as well as in the figure. Although the immature specimens were not identified as to species, they were included here as *P. sulcatifrons* since all individuals whose development was sufficiently advanced to permit identification belonged to this species.

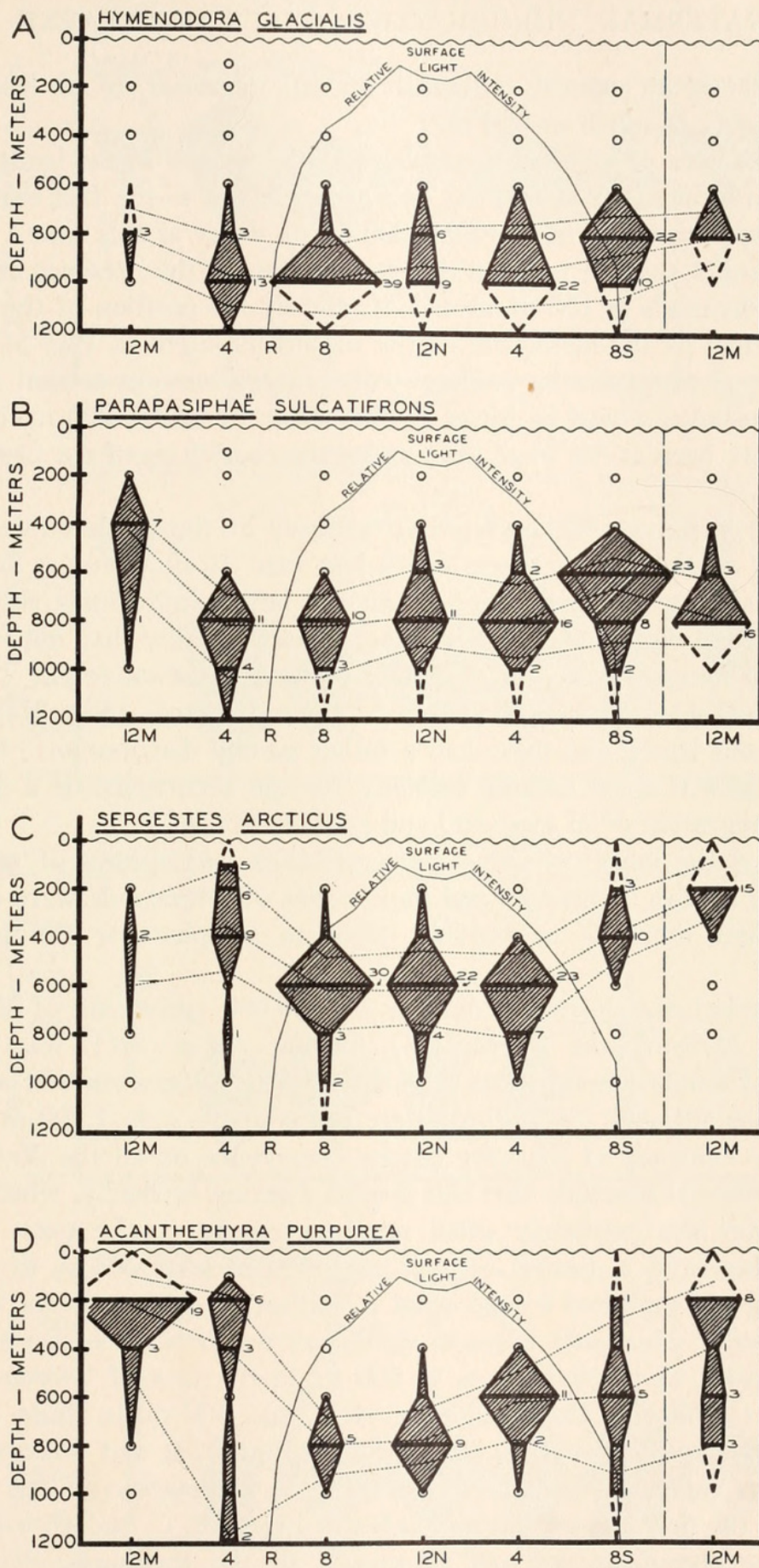


FIG. 3. Decapods: data condensed as in Fig. 2. The numerals to the right of the histograms represent the numbers of specimens taken. These figures include: *A*, larval, post-larval, and immature stages; *B*, all stages; *C* and *D*, adults.

also exhibited an extensive diurnal vertical migration of at least 200 and probably as much as 400 m.

The absence of significant numbers of the species in the hauls made for the first midnight of Fig. 3C was probably due to the fact that most of the population was in less than 200 m. of water at this time. Some circumstantial support is given this explanation by the presence of some of these decapods at 100 m. at 4 A.M. and by the position of the population shown by the histogram of the second midnight in Fig. 3C since the stock of *Sergestes* by analogy with observations on several of the other Crustacea would be lower in the water by about 200 m. than it would have been at the same time under the conditions of the preceding days.

There is some evidence from an analysis of the catches that those *Sergestes arcticus* of carapace length less than 10 mm. live at and migrate to slightly shallower levels than the larger individuals shown in the figure and discussed above, but hauls closer together than ours would have been necessary to determine this relation quantitatively.

Only 68 *AcanthePHYRA purpurea* A. Milne-Edwards (Fig. 3D) were taken in our hauls, and these had a rather patchy distribution. Nevertheless, there is some definite evidence for the occurrence of a diurnal vertical migration of at least 400 and possibly 600 m.

Among the more primitive malacostracans two species of euphausiids, two species of mysids, and two species of amphipods were caught in sufficient numbers to provide adequate samples for the present analysis.

The relatively enormous number of 180,000 specimens of the euphausiid, *Nematoscelis megalops* G. O. Sars (Fig. 4A), was taken. The 1,543 adults among these were living mainly between 400 m. and the surface although 12 of them were taken in the only 1,200 m. haul. From the evidence of the very patchy occurrence of all the *Nematoscelis*, one would conclude that this species swarms markedly, which may account for the extremely small numbers caught in the noon hauls. Clearly, however, a diurnal vertical migration at least 200 m. in extent was being accomplished by the adult *Nematoscelis*, shown in the figure.

The other schizopods taken in significant numbers were also migrating vertically, as much perhaps as 600 m. in the case of *Thysanopoda acutifrons* Holt and Tattersall (Fig. 4B), and 400 m. in those of the mysids, *Boreomysis microps* G. O. Sars (Fig. 4C), and *Eucopeia unguiculata* (Willemoes-Suhm) (Fig. 4D). A comparison of the histograms of the first and second midnights in Figs. 4B, C, and D, indicates that these organisms, as well as several of the previously discussed Crustacea, were 200 m. deeper in the water after the storm of July 21

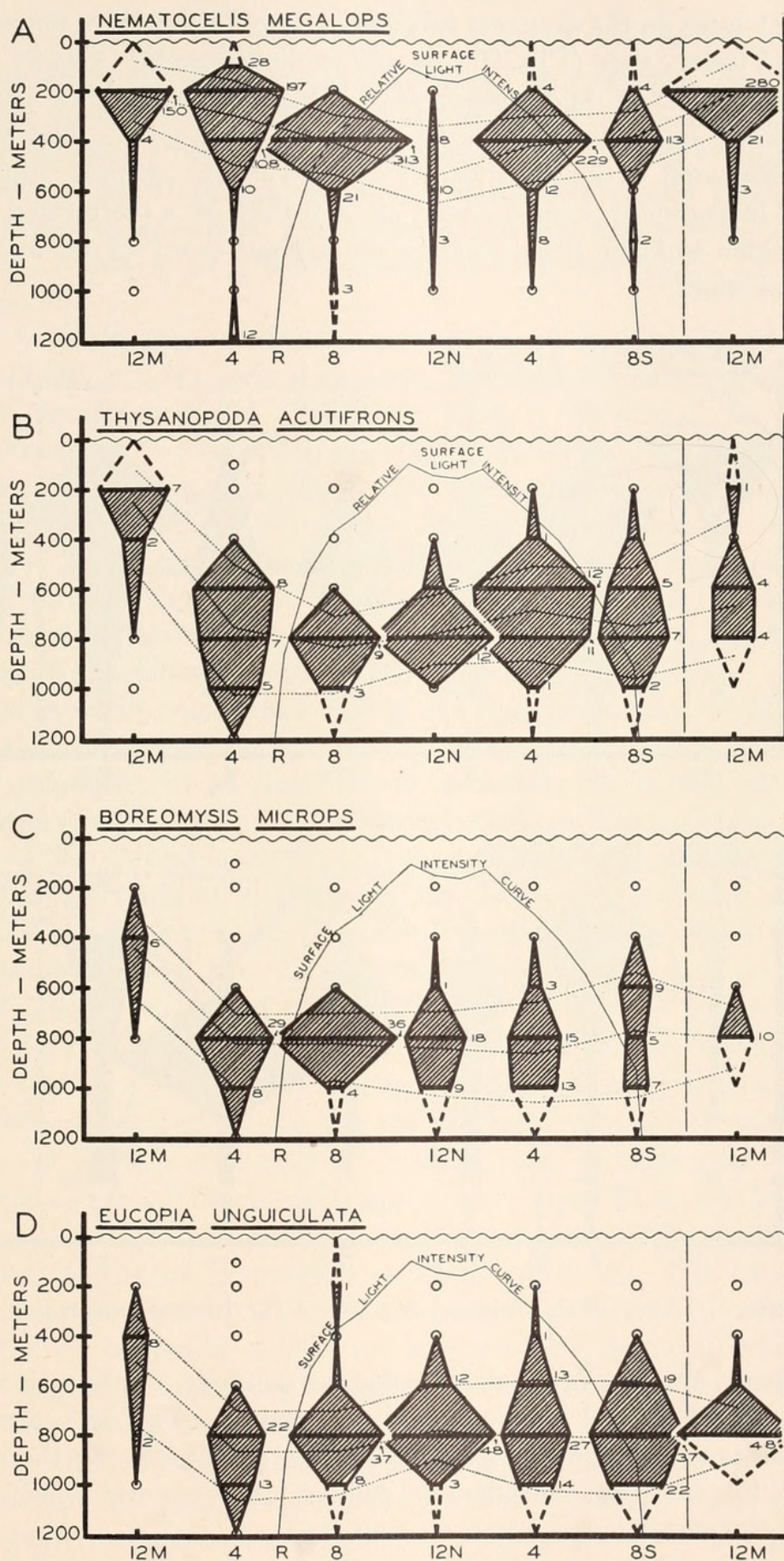


FIG. 4. Euphausiids and mysids. *A*, large adults; *B* and *C*, adults; *D*, all stages. See Fig. 2 for further explanation.

than they were on the previous two days. It is furthermore noteworthy that the *Thysanopoda* (Fig. 4B), as well as the *Gennadas* (Fig. 2), *Parapasiphaë* (Fig. 3A), and *Acantheephyra* (Fig. 3D) apparently began to move slowly upwards in the water almost as soon as they had reached the lowest point of its downward excursion in the morning; this slow upward migration was succeeded at about 8 P.M. by a more rapid movement which brought the animal to the highest point of its migration about midnight.

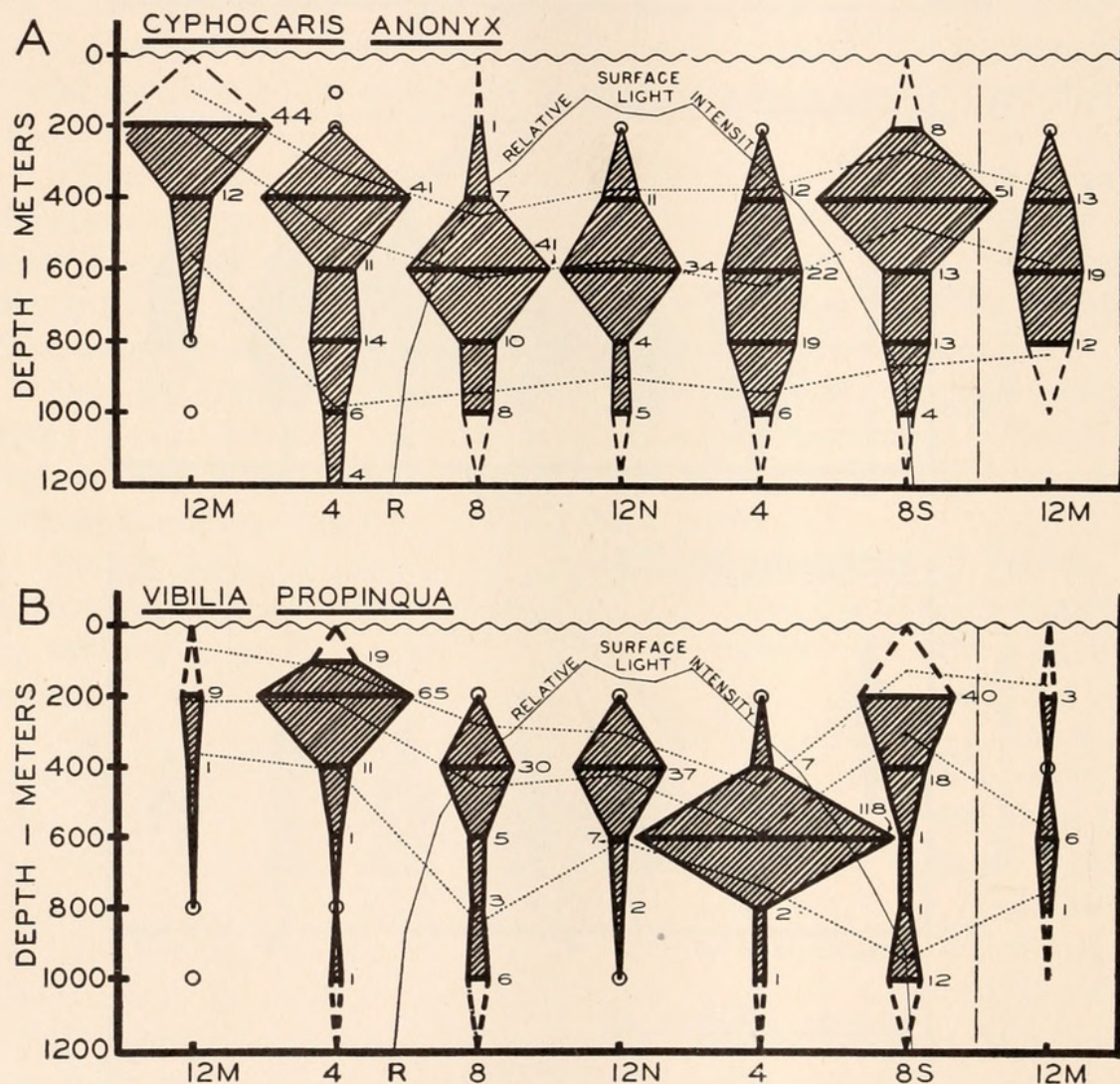


FIG. 5. Amphipods. Adults. See Fig. 2 for further explanation.

The two amphipods caught in sufficient numbers, *Cyphocaris anonyx* Boeck (Fig. 5A) and *Vibia propinqua* Stebbing (Fig. 5B), also show a diurnal vertical migration of about 400 m. amplitude. In the case of *Vibia*, however, the considerable amount of swarming which is apparent obscures this migration somewhat.

DISCUSSION

Since the hauls were made in such a way that our data give us information about points separated in effect by 200 m. and 4 hours, a detailed analysis of the diurnal vertical migrations is clearly impossible. Nevertheless, our results show that all of the crustaceans investigated were accomplishing vertical migrations 200 to 400, and possibly 600 m. in extent, which is in general agreement with the results of recent investigators.

For instance, certain of the larval stages of euphausiids taken by Fraser (1936, p. 154) were apparently moving upward 200–250 m. to reach the surface at night. Stubbings (1938, p. 27) found that species of the pteropods, *Creseis* and *Hyalocylis*, underwent a diurnal migration of 200 m. vertical extent and that some of the other pteropods may have been migrating even further. The copepod, *Pleuromamma robusta*, was shown by Mackintosh (1934, p. 92) to exhibit the most pronounced vertical migration of all the plankton animals of the antarctic surface waters; this crustacean rose into the upper 100 m. around midnight and descended apparently below 600 m. during the day. Among the malacostracan crustaceans Hardy and Gunther (1935, p. 240) observed that *Euphausia frigida* and *E. triacantha* underwent a diurnal vertical migration of at least 200 m. and that the amphipod, *Parathemisto gaudichaudi*, migrated a vertical distance of about 60 m. in the course of its diurnal movement. Since the latter animal was taken within the upper 100 m. at all hours, this observation is similar to those made on other shallow water plankton. Clarke (1934a, Figs. 2 and 3), for example, showed that *Calanus finmarchicus* adults and copepodid stages IV and V exhibited a diurnal migration of about 100 m.

The rate of the diurnal vertical migrations may be roughly calculated from our results. If the speeds of downward movement of the centers of the populations for the various species, as shown in the figures, are taken to represent the average rates of movement for the organisms concerned, these are found to vary from 29 m. per hour for *Nematoscelis* to 125 m. per hour for *Thysanopoda*. The average for the eleven species of crustaceans is 67 m. per hour. The only comparable data are those of Hardy and Gunther (1935, p. 240) mentioned above for the migration of the two species of *Euphausia* in which the upward migration apparently occurred at a rate of 100–200 m. per hour.

In some of these organisms a slower upward movement during the day preceded the more rapid upward migration shortly before midnight. This phenomenon has been observed in shallow-water zoöplankton by a number of workers and has been explained on the basis of a gradual

light adaptation of the animals (see Russell, 1931, p. 402; Kikuchi, 1938, p. 37). In spite of this slow upward trend, however, our observations suggest that the upward migration in the early evening hours was as rapid as the downward movement in the early morning.

A comparison of the swimming speeds of the animals in the plankton with the rates of these diurnal vertical migrations would be of great interest. Unfortunately, there are no data available for these or comparable plankton organisms. Measurements have been made, however, of the rates of locomotion of several copepods and crustacean larvae (Russell, 1927, p. 221; Welsh, 1933). The latter found that *Centropages* would swim towards a light of an intensity that might be found 20–30 m. below the surface on a clear day at a rate of 82 m. per hour (actually measured over a path only 10 cm. long). As Parker (1902), Gardiner (1933), and Seiwel and Seiwel (1938) have shown, gravity alone causes copepods to sink at a rate of about 24 m. per hour.

Thus, if any organism to which the above quoted rate of sinking is applicable were migrating downward 400 m. in 8 hours, it would sink 192 m. merely through the effect of gravity and would have to swim downward through the remaining 208 m. at an average rate of 26 m. per hour. For the upward trip the gravitational effect would add the 192 m. to the distance to be swum (see Clarke, 1934*b*) so that the animal would have, in effect, to swim upward at a rate of 592 m. in 8 hours or 74 m. per hour. To consider it in another way, the organism in order to accomplish the downward migration would have to be actively swimming towards the bottom at the experimentally determined rate of 82 m. per hour for only about one-third of the 8-hour period, whereas in order to move upward to the original level in the same length of time it would have to be swimming towards the surface at this rate during 7 of the 8 hours.

As the pelagic malacostracans such as those discussed in this paper are known to be very active swimmers, they could presumably accomplish such vertical migrations with greater ease than the animal postulated above on the basis of data obtained from copepods. The Crustacea in our analysis are larger, moreover, and, other things being equal, would sink more rapidly through the water than the copepods so that an even greater proportion of their downward movement may be effected by the mere absence of any persistently oriented swimming activity. Many experiments have shown that several environmental variables, such as light and temperature, will affect the locomotor activity of zoöplankton, but, as Clarke (1934*b*) pointed out, these factors under natural conditions would seem to work in the wrong direction to explain distribution as it is found.

Since the great majority of previous workers have recognized that light is the most significant single environmental factor in diurnal vertical migrations, it is interesting to correlate these phenomena with the changes in the intensity of illumination at various hours of the day (Fig. 1). During the first hour after daylight became measurable, its intensity increased at an exceedingly rapid rate. Similarly, the illumination diminished at an equally rapid rate during the hour preceding the last measurement of the day. During the four hours in the middle of the day the illumination remained relatively constant and such changes in intensity as resulted from different degrees of cloudiness were of a much lower magnitude than those of early morning and late afternoon.

The most striking point which appears in a comparison of the biological and the light intensity data is that much of the migration apparently occurred when there was no light more intense than starlight even at the surface. Before sunrise most of the animals had already descended about half of their total downward distance, and several, such as *Boreomysis*, *Eucopia*, and *Parapasiphaë*, had reached the deepest point in their migration by sunrise. In most cases, furthermore, the greater part of the upward migration must have been accomplished between the time of sunset and midnight.

It is clear from these facts that the vertical migrations of these organisms cannot be explained simply on the basis of a negative phototropism which overshadowed a negative geotropism in the daytime and left it with a free hand at night.

Similarly the hypothesis that the animals aggregate by means of a tropistic mechanism (Michael, 1911; Russell, 1934) in a region of optimum light intensity and follow the latter as it moves vertically at various hours of the day apparently will not explain the situation here. Such an hypothesis is further weakened by the lack of evidence in the present case for a general vertical scattering of the population throughout the water column at night when it would be free of the concentrating effect of light.

Whether we assume that external environmental or internal physiological factors are controlling the diurnal migrations, the intensity of illumination penetrating from the surface must play an important rôle in these phenomena since it is the only daily environmental variable in deep water. It may act in combination with other external factors, such as temperature and gravity, since many investigators have shown experimentally that interactions of such factors may cause a tropistic reversal (Kikuchi, 1938, pp. 35-6). Or it may merely keep in phase cyclic internal physiological conditions of the organisms which themselves regulate these migrations (see Russell, 1927, p. 225; Welsh,

Chace, and Nunnemacher, 1937, p. 195). Many cases are known (Welsh, 1938, p. 136) of the persistence of internal diurnal rhythms under constant external conditions, but one would expect that in nature at least an occasional action of the external factor to which it owes its origin, in this case light, would be necessary to maintain the synchrony indefinitely.

A second problem is posed by the fact that most of the Crustacea here considered were about 200 m. lower in the water on the midnight of July 22 than they were at the same hour two or three days before. Furthermore, the maximum illumination at the surface on July 22 was 66 per cent greater than the maximum on July 19. Previous studies have shown that certain organisms appear to live at depths where the light intensity is of a particular magnitude, i.e., an optimum intensity for the organism in question; these organisms may, as a consequence, appear in shallower waters on dull days or in high latitudes (Russell, 1933, p. 569; Murray and Hjort, 1912, p. 664-6); thus the light intensity itself may have been responsible for the observed difference in distribution.

It is clear, however, that the amount of illumination could not explain so great a change in distribution. Since actual measurements down to 84 m. (Fig. 6) showed that the light is reduced by a factor of 10, for every 25 m. of water, the observed change in light intensity at the surface would result in a difference of only about 5.5 m. in the depth at which any given intensity of light would be found. Even in the clearest sea water yet measured (see below) this change in light intensity at the surface would result in a maximum change of only 50 m. in the depth to which any particular intensity of light would penetrate.

An alternative causal or contributory factor to the observed lower position of the plankton on July 22 may have been the storm of the previous day, but it is not likely that a relatively mild disturbance of this sort at the surface would be appreciable at a depth of over 200 m. Furthermore, Hardy and Gunther (1935, p. 268) conclude from their observations that, "... the state of the sea has little or no bearing on the number of organisms in the surface layers. . . ."

A more important point is the fact that simultaneous measurements on the horizontal patchiness of the plankton were not made. Consequently we cannot tell whether or not the observed difference might rather be due to the fact that on the later day we were sampling a different population with a different vertical distribution pattern from that of the previous days (Russell, 1933, p. 569; Hardy, 1936).

One of the most important questions raised by previous work on the diurnal vertical migrations of bathypelagic organisms is how deep

down in the water do such migrations occur. Most of the crustaceans showing diurnal vertical migrations discussed in this paper were living at depths of 600–800 m. during the four hours during the middle of the day. If, as pointed out above, we recognize the necessity of light in one way or another for the vertical migrations of these animals, we must assume that at some time during the day the organism is affected

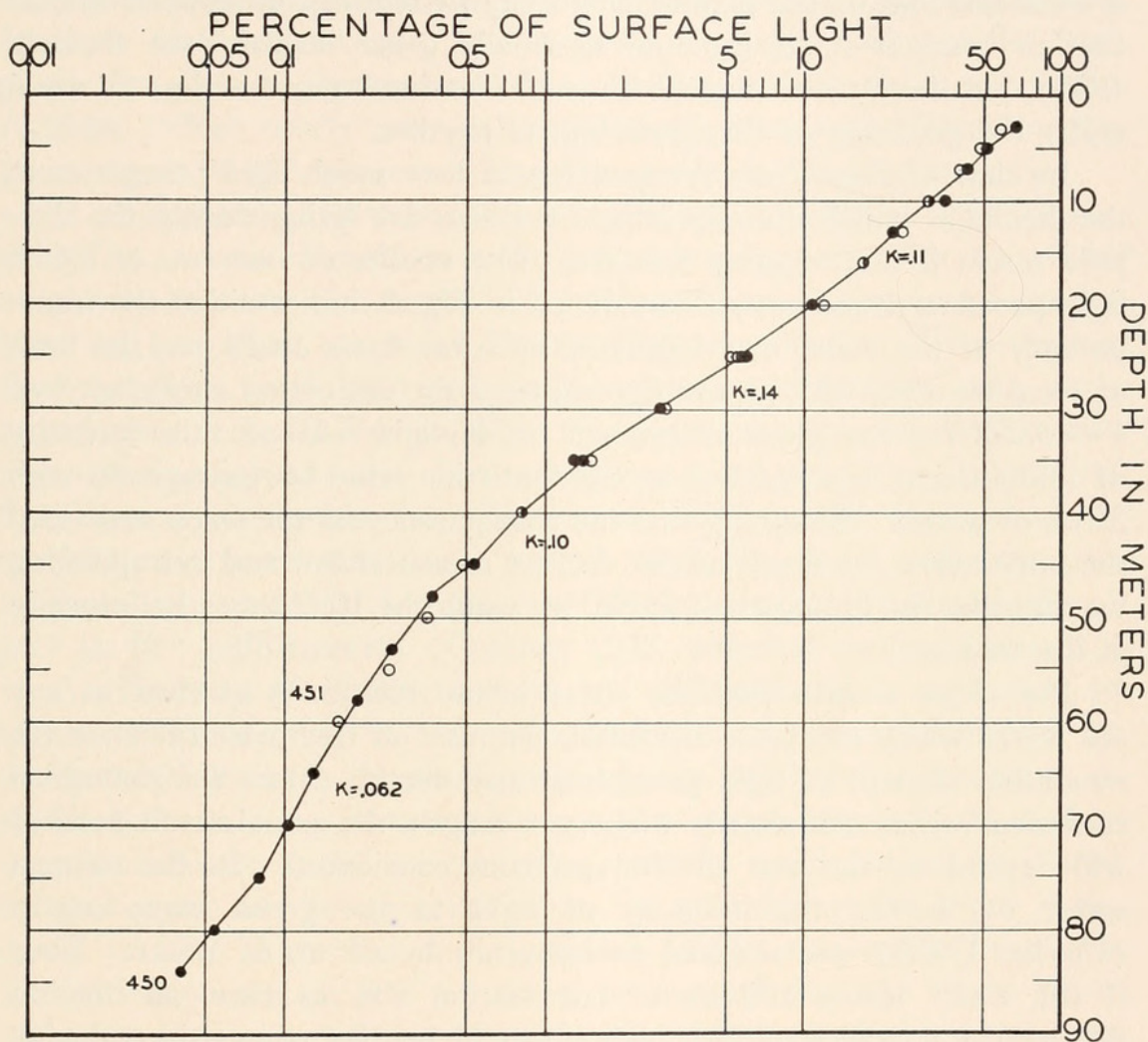


FIG. 6. Relation between depth and irradiation expressed as a percentage of the light just over the surface (logarithmic scale). Station 2894. Lat., $39^{\circ} 06' N.$; Long., $70^{\circ} 16' W.$ July 22, 1937. Sky: clear. Sea: moderate, white caps. Series 450 measured by photronic cell with opal disc. Series 451 measured by photronic cell with "green" filter combination (Schott-Jena BG-18 and GG-11) and opal disc.

by light. Clearly, under any given physiological conditions, there is a minimum intensity of illumination which would be just sufficient to affect any particular animal; in the open sea there would be a definite maximum depth beyond which this minimum light intensity would never penetrate even at noon on the brightest days. A diurnal vertical migration in which illumination from the surface was supposed to have any

controlling effect would thus be impossible below this depth. As pointed out above, however, vertical migrations could be temporarily maintained under constant conditions by a diurnal physiological rhythm within the organism. Thus, if unusual conditions such as a storm should cut down the incident light so that deep-living animals did not come under the influence of light for several days, there would not be a wholesale loss of the population through continued downward migration or random scattering into unusually great depths (see Russell, 1930), but the diurnal migrations would continue more or less as usual under the guidance of the physiological rhythm.

In view of these facts the question of how much light penetrates to the depths at which the migrating Crustacea are living during the daylight hours is one of great interest. The results of our two series of light penetration measurements, shown in Fig. 6, indicate that the transparency of the water was relatively uniform down to 84 m., the limit of measurement, with an average value of the extinction coefficient⁶ of $k = 0.092$ for the green component of daylight. Hence, the intensity of illumination was reduced to one-tenth its value by passage through 25 m. of water. Assuming that the transparency of the water remained the same below the depth of our deepest measurement and extrapolating we find that the illumination at 800 m. would be 10^{-32} times its intensity at the surface.

But if we assume that the water below 100 m. is as clear as any sea water which has been measured, we may on this basis calculate the maximum amount of light possible at any depth. Since the extinction coefficient varies enormously with wave-length, the actual result reached will depend on the part of the spectrum considered. In the clearest water yet known the intensity of light in the green wave-lengths (Clarke, 1938*b*) was reduced to one-tenth by 61 m. of water. Thus if the water below 100 m. at our station was as clear as this, at 800 m. the intensity of illumination would be 10^{-15} times the value at the surface. In the clearest water yet known the blue wave-lengths were reduced to one-tenth their intensity in 230 m. (Clarke, 1933*a*).⁷ If water of like transparency existed below 100 m. at our station, the illumination of 800 m. would be a little less than 10^{-7} times the surface intensity;⁸ this value is between 100 and 1,000 times higher than the threshold intensity for human vision.

⁶ In the equation $I/I_0 = e^{-kL}$, where L is the thickness of the water layer in meters through which the intensity is reduced from I_0 to I .

⁷ Basing our calculations on the most transparent strata only.

⁸ Assuming the same reductions in the upper 100 m. for the blue component as for the green, which is known (Oster and Clarke, 1935) to be approximately true in this region of the Atlantic.

We have some evidence, however, that conditions as favorable for penetration as this latter case for blue light did not exist at our slope water station since on a bright, calm day Beebe (1934, p. 276) observed through the window of the bathysphere that at a depth of 610 m., the water appeared absolutely dark to the human eye. But Beebe was not able to look upward in the water so that he could not tell at what depth the downward component of the light had become indistinguishable from the blackness below.⁹ On the other hand, the water of the Sargasso Sea, where Beebe made his observations, is characteristically (Clarke, 1936*a*) nearly twice as transparent in the upper 100 m. for the green region of the spectrum as was the water at our present station.

It would be of great interest to compare the amounts of light present at 800 m., where migrations were definitely going on, with the visual sensitivity of these Crustacea. Unfortunately, no experimental studies have yet been made on vision in any deep-sea animals. Nevertheless, from previous work on crustaceans and other arthropods with compound eyes, it is possible to draw two extremely general conclusions: first, that arthropods are more sensitive to the blue wave-lengths of light than to the green (see Waterman, 1937, p. 464 for table summarizing pertinent data) and second, that for these organisms the minimal light intensity for response is of the order of magnitude of 10^{-6} to 10^{-7} millilamberts (Crozier, 1938, personal communication).¹⁰

An intensity of illumination of 10^{-6} millilamberts is equivalent to about 10^{-10} times that of full noon sunlight and is the value used by Clarke (1936*b*) as a threshold intensity for determining the depth at which fish can see. A crustacean with a visual threshold of such a magnitude in the green wave-lengths certainly could not be stimulated by this region of the spectrum when the intensity of the latter is reduced to 10^{-15} times that at the surface. Since this would be the illumination present at 800 m., when we assume that the water below 100 m. was as clear as any sea water that has been observed, we may conclude that under these conditions the crustaceans could not be re-

⁹ Presumably this directional effect would still be appreciable at great depths since directional differences in intensity were recorded photographically by Helland-Hansen (Murray and Hjort, 1912, p. 252) at 500 m. and since more recent work of Whitney (1938, p. 211) has demonstrated that in optically homogeneous waters the ratio of the intensities of light passing downward to those of the light scattered upward is a constant (see also Pettersson, 1938). Of interest in this connection is the occurrence of upwardly (dorsally) directed "telescopic" and stalked eyes in a number of different families of deep-sea fishes of the "twilight zone" of the seas (Brauer, 1908, p. 233) which would suggest that this directional difference in the light intensities is of biological significance even at considerable depths.

¹⁰ Any value obtained for a sensory threshold will, of course, depend largely on the exact experimental conditions under which it was determined.

sponding to light from the surface. But if the crustacean had an equally low visual threshold for blue light, our calculations have shown that in the clearest water observed there would be almost 1,000 times as much light present at 800 m. as would be necessary for the threshold of vision. Under such maximum conditions even at 1,000 m., where the immature *Hymenodora* in our catches possibly gave some indications of a diurnal vertical migration, more than 100 times the necessary amount of light would be present. The threshold intensity for vision, 10^{-10} of full sunlight intensity, would occur at a depth of nearly 1,500 m. under such conditions.

Thus, the water below the surface layers could be, as it probably was, considerably less transparent than the clearest sea water ever observed and still permit sufficient visible light for affecting the reactions of bathypelagic organisms to penetrate to depths of about 800 m.

The preceding discussion makes it clear that several important aspects of this problem must be investigated more thoroughly before a satisfactory solution will be possible. These are in brief: (1) actual measurements of the transparency of the water at greater depths and of the relative intensities of the light in various directions; (2) more detailed work on the maximum depth at which diurnal vertical migrations occur; (3) measurements of the photosensitivity of deep-sea animals and correlations of the maximum wave-length sensitivity to the wave-length of the most penetrating part of the spectrum; (4) experimental studies on deep-sea animals designed to elucidate the nature of any diurnal physiological rhythms and their relation to the organisms' behavior in the sea.

SUMMARY

1. A study was made with the aid of closing nets of the diurnal vertical migrations of bathypelagic organisms at a station in continental slope water of the western North Atlantic.

2. While the hauls were being made a continuous record of the light intensity at the surface was kept.

3. The penetration of light into the upper 84 m. of water was directly measured photometrically; the average extinction coefficient for green light was $k = 0.092$.

4. All of the malacostracan Crustacea (to which the detailed results presented in this paper are limited) which occurred in sufficient numbers for analysis exhibited diurnal migrations 200 to possibly 600 m. in vertical extent.

5. The speed of vertical movement in these migrations varied from 24 to 125 m. per hour among the various crustaceans.

6. A considerable part of the migrations took place while the light intensity even at the surface was no greater than starlight.

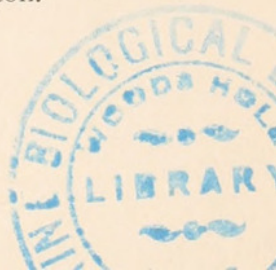
7. Several Crustacea living at 800 m. during the day showed extensive diurnal vertical migrations.

8. It is concluded, however, that whether the migrations are regulated by external environmental or by internal physiological factors, at some time of day the organisms concerned are affected by light penetrating from the surface.

9. Calculations made from the light penetration data indicate that the amount of light probably present during the middle of the day at the depths where the animals were migrating was adequate to support this conclusion (8).

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