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PLANKTON OF THE FLORIDA CURRENT. III. THE CONTROL OF THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE DAYTIME BY LIGHT AND TEMPERATURE

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ABSTRACT

The four groups, pteropods, siphonophores, chaetognaths and copepods, have been studied separately and together in the plankton of the Florida Current. Vertical diffuseness of plankton was found to be under the control mainly of light at its upper levels and of temperatures at lower levels. This is true both within a population of a single species and, to some extent, between species living at different depths. Finally, in the copepods only, changes in level in response to temperature and light changes are superimposed on a seasonal change in level of the population which may be correlated with the presence of successive broods.

INTRODUCTION

In a study of the zooplankton of the Bermuda area (Moore, 1949), certain generalizations were made with regard to the behaviour and distribution of the organisms. The one to which the present work relates was the fact that the spread, or degree of vertical diffuseness, was slight in shallow-living species, but became progressively greater in deeper-living ones. In studies of the deep scattering layer and euphausids (Moore, 1950, 1952) it was shown that a workable explanation of the day-time vertical distribution could be obtained if it was assumed that two opposing factors were operative, temperature and illumination. During the descent and ascent periods of diurnal migration, illumination appeared to be the predominant control ex-

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cept at the greatest depths reached. During the latter, that is to say around noon, temperature usually superceded illumination as the controlling factor.

Finally, in a study of the siphonophores of the Florida current (Moore, 1953), it was found that the mid-day level occupied by the various species varied in close correlation with the changes in level of the isotherms. In fact the regression of change in level of the species on change in level of the 15°C. isotherm was 95%.

The behaviour of very few marine plankton species has been studied, either experimentally or by deduction from field observations. Experiments have suffered from the great difficulties of reproducing natural conditions and obtaining consistent results. For this reason, or because of wide differences in specific behavior patterns, little generalization has been possible with regard to the characteristics of plankton as a whole. In the Bermuda studies, the characteristics of each species were determined, and the resulting data treated as a whole for correlation studies. It was felt that the generalized view so obtained clarified points not readily seen in studies of single species. In addition, of course, it greatly increased the amount of material available for statistical analysis. The same method has been followed in the present work.

Material and Methods

The field work, and part of the study of the material was carried out as a joint program of the Marine Laboratory of the University of Miami and the National Geographic Society. An account of methods used as well as of the hydrographic conditions observed, has been published by Miller *et al.* (1953). An account of the siphonophores has also been published (Moore, 1953). The study on chaetognaths is part of a doctorate thesis to be submitted by H. Owre at the University of Michigan. That on copepods, by E. C. Jones, was incorporated in part in a masterate thesis at the University of Miami, and that on pteropods, by T. Dow, is part of a masterate thesis to be submitted at the same university. The work on the individual groups is that of the authors indicated, while the coordination is that of the senior author. This coordinated study is part of an investigation of the scattering layer carried out by the Marine Laboratory for the Office of Naval Research under contract number NObsr-57146. It was also carried out in part at Woods Hole Oceanographic Institution under Bureau of Ships contract number NObsr-43270. The authors wish to express their gratitude to all those members of both laboratories who have assisted in the work, and also to Mr. W. Shoemaker of Rochester Institute of Technology who helped greatly in obtaining the information on illumination.

A depth-distance recorder (Miller *et al.*, 1953) was used with all plankton hauls, and the counts of all species were corrected to a standard of one mile of towing. Generally, six or seven depths were sampled on each occasion. Owing to the strong currents in the area, it was not possible to hold the nets very close to a desired depth, but in general the water column was well sampled by a series of oblique hauls. The mid-depth of each haul was calculated, and from these, the depths half-way between each pair of hauls. It was assumed that each count was representative of the water column between two such half-way depths. The uppermost haul was assumed to extend to the surface, and the lowest, to the deepest recorded depth reached. For each species, and on each day, the total content of the water column was then integrated by cumulative multiplication of the counts and the lengths of the sections of water column to which they applied. A second integration was then performed from the top down, using the same figures, and the depths were noted at which 25, 50 and 75 percent of the above total were reached. In earlier work (Moore, 1949, 1953), the 50 percent depth so obtained was defined as the mean day level of the species, and the distance between the 25 and 75 percent levels as the spread. The mean day level, of course, varies widely in different species. In much of the present work it was convenient to eliminate the effects of such variation by expressing the values for each day as deviations from the annual mean for the species, the latter being the mean of all days for which data were available. In such cases, a positive value implies a depth greater than the mean, and a negative value, less than the mean. All depths are given in metres.

Only those species which occurred fairly consistently in adequate numbers, have been included. Not all these species were adequately represented on every day, so the numbers of pairs of figures available for comparison varies slightly throughout. The following species were included:

PTEROPODA

Limacina trochiformis (D'Orb.)
L. inflata (D'Orb.)
Creseis virgula Rang
C. acicula Rang
Diacria quadridentata (Lesueur)
Cavolinia longirostris (Lesueur)

SIPHONOPHORA

Chelophyes appendiculata (Esch.)
Diphyes bojani (Esch.)
D. dispar Chamisso & Eysenhardt
Eudoxoides mitra (Huxley)
E. spiralis (Bigelow)
Abylopsis eschscholtzii Huxley
A. tetragona Otto
Bassia bassensis (Quoy & Gaimard)

CHAETOGNATHA

Sagitta enflata Grassi
S. hexaptera D'Orb.
S. lyra Krohn
S. bipunctata Quoy & Gaimard
S. serratodentata Krohn
S. minima Grassi
S. decipiens Fowler
Pterosagitta draco (Krohn)
Krohnitta subtilis (Grassi)

COPEPODA

Neocalanus gracilis (Dana)
Undinula vulgaris (Dana)
Eucalanus attenuatus (Dana)
E. monachus Giesbr.
Rhincalanus cornutus (Dana)
Calocalanus pavo (Dana)
Euaetidius giesbrechti Cleve
Euchaeta marina (Prestand)
Scolethrix danae (Lubbock)
Temora stylifera (Dana)
T. turbinata (Dana)
Lucicutia flavicornis (Claus)
Haloptilus longicornis (Claus)
Candacia pachydactyla (Dana)
C. bispinosa (Claus)
Lubbockia squillimana (Claus)
Copilia mirabilis (Dana)
Acartia negligens (Dana)

At the station, approximately ten miles east of Miami, where this material was collected, the surface waters vary in origin. Water which has come through the Yucatan Channel is about 5°C. warmer than that from the Gulf of Mexico. None of the zooplankton species are restricted to one water mass only, although most show some relative variation in abundance in the two. The depth of the 15°C. isotherm was taken as a temperature standard. Its mean depth for the period was 151 meters, and its range, from 87 to 184 meters. The mean depth of the 50 percent level of the plankton, combining all species, was 93 meters. The selected isotherm is, therefore, deeper. However, the mean depth-temperature curve for the whole period was almost linear over the range of depths covered here, so the value of the standard temperature selected does not seriously affect the discussion.

Illumination was calculated by the method used in previous work (Moore, 1950), but making a small allowance for the effect of cloud.

The isolume selected was that with a value of 10^{-2}, which is approximately equivalent to one foot-candle. The mean depth of this for the period was 143 meters, and the range from 124 to 157 meters, which is considerably less than the temperature range. As with the 25, 50 and 75 percent levels of the plankton, the daily values for isotherm and isolume have, in most cases, been used as deviations from the mean for the period. Depths greater than the mean have a positive value, and lesser ones a negative value.

The Relation of Mean Day Level to Temperature and Illumination

Study of scattering layer records had indicated that, except in regions of slight temperature stratification, the mid-day level of the organisms concerned was likely to be under the almost complete control of temperature, with illumination exerting but little influence. An initial study of the Florida Current siphonophores showed a significant correlation between mean day level and the depth of the 15°C. isotherm. The regression of organism depth on isotherm depth was 95%. It should be noted that the latter figure differs from ones given later in the present paper since additional data have been incorporated in the present analysis. The coefficients of correlation between deviations from annual mean day levels and deviations of the depth of the 15°C. isotherm from its annual mean were worked out with the results shown in Table 1. The values are given for the four groups separately and for all species combined.

TABLE I

Coefficients of Correlation between Deviations of Mean Day Levels of the Species from their Annual Means and Deviations of the Depth of the 15°C. Isotherm from its Mean. Values with a Significance of P=>5% Are in Parentheses. P Is the Frequency with which the Observed Results Might Be Expected To Occur by Chance.

Pteropods	+.26
Siphonophores	+.33
Chaetognaths	+.24
Copepods	(+.04)
All species	+.18

Similar correlations between mean day level deviations and deviations in the depth of the 10^{-2} isolume showed no significant values, although the coefficient for the chaetognaths was sufficiently large to suggest the possibility of a relationship there. No significant change was observed when the relationships to temperature and illumination were treated as partial correlations.

In the Bermuda work, no relationships were found between behaviour and temperature since there was so little day-to-day variation in the vertical temperature distribution. Night reaction to moonlight was rather closely correlated with the day level occupied by the species, but daytime reaction to cloudiness appeared to be a specific characteristic, not correlated with the depth of the species. It showed some correlation, however, with the extent of diurnal migration of the species, and the latter, in turn, was correlated with the depth of the day level of the species. In the Florida Current material, the closeness of correlation between day level deviations and isotherm deviations showed no relation to depth. On the other hand, it did appear to be a group characteristic. The pteropods did not give a significant value, probably because too few species were available for study. The coefficients were about the same, though, for pteropods, siphonophores, and chaetognaths. On the other hand, the copepods, with more data available than any other group, showed no correlation at all.

It is known that, in temperate waters, some chaetognaths and copepods change level seasonally (Russell, 1936). These level changes do not correspond with seasonal movements of either isotherms or isolumes, and appear to be specific characteristics of the successive broods, on which the adjustments of diurnal migration, and day-to-day level changes, are superimposed. It seemed possible that a correlation between day level and isotherm level might be masked in the Florida copepods by a similar seasonal rhythm. To test this possibility, partial correlations were calculated between deviations of day level and isotherm deviations, as well as between day level deviations and isolume deviations, but including a third variable, deviation from a given date. A series of six alternative dates was tested, namely the first of October, November, December, January, February and March. Of these, October 1 gave the highest partial correlation with change in day level, and was therefore used to recalculate the partial correlations of day level deviations with isotherm and isolume deviations. Allowing for the seasonal level change, these now became +.57 and +.40 respectively, both significant with a value of $P = < 1$ percent. To demonstrate the nature of the seasonal vertical rhythm of the copepods, the partial regression coefficients of level deviation on isotherm and isolume deviations were calculated. These were +105 percent and +81 percent respectively. Using these factors, the effects of the daily differences in isotherm and isolume depths were allowed for, and Figure 1 shows what the seasonal changes in day level of an average copepod would have been had there been no changes in temperature or light. The pteropod data were inadequate for such treatment, but

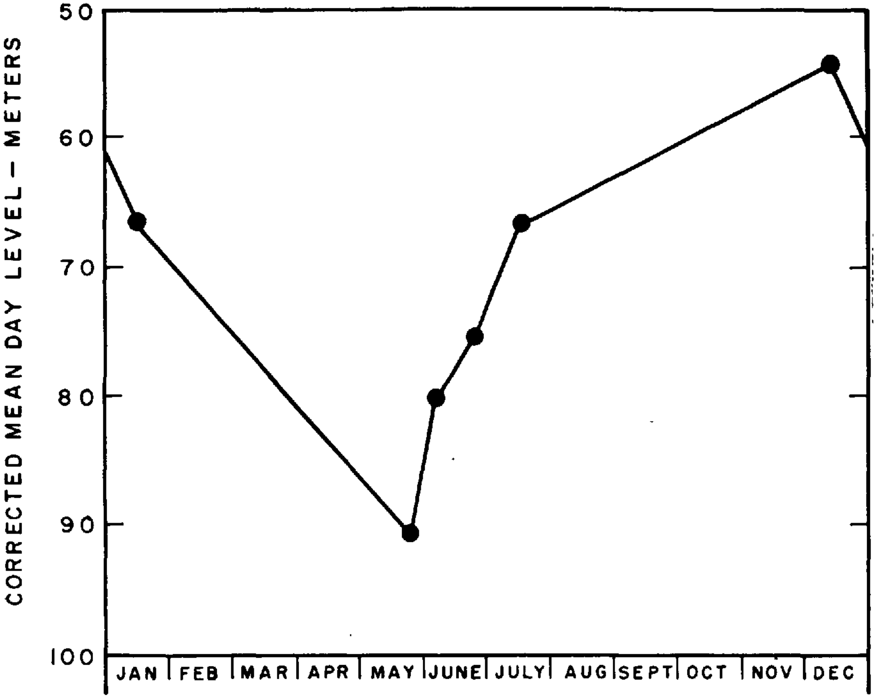

FIGURE 1. Seasonal variation in mean day level of copepods after correction for effects of variations in temperature and illumination.

neither siphonophores nor chaetognaths showed any significant seasonal level shift of this type. It remains possible, of course, that within these groups, individual species do show such a seasonal rhythm, but that these rhythms are not sufficiently similar in phase to appear as a group characteristic.

THE RELATION OF SPREAD TO TEMPERATURE AND ILLUMINATION

The vertical distribution pattern of a typical plankton species may be roughly represented by a kite, where the diameter of the figure at any depth corresponds to the concentration of the organisms there. In such a kite, the lower tail is characteristically longer than the upper part. A more accurate picture would probably be given if the sides of the kite were skewed normal distribution curves. However, lacking adequate information as to the form of the curve, we have chosen the 25 and 75 percent levels as useful parameters for considering the outlying parts of the population. The distance between the two, or spread, has been used as an index of the diffuseness of the population.

The Bermuda data showed that, for all species combined, there was a significant increase in spread in the deeper-living species. This held true in the Florida material also, the correlation coefficient between spread and mean day level being +.44 ($P = < 1\%$). The separate groups all showed positive correlations, but only that for the copepods was significant ($r = +.55$; $P = < 1\%$).

In one group or another it has been shown that the degree to which the mean day level is correlated with temperature and illumination is itself dependent on the depth characteristically occupied by the species in question. It is probable, then, that a similar difference in reaction to these two factors exists at different levels in a population of a given species. Reactions at the 25 percent level may differ from those at the 75 percent level. If this is so, then variations in spread may be more simply explained in terms of reactions at the two limits which define it. Partial correlation coefficients were therefore calculated for each level with isotherm and isolume deviations. Significant values were obtained in most groups at one level or the other. Since we are concerned with the reaction of the plankton to movements of the isotherms and isolumes, it is clearer if the results are shown as regression coefficients. This is done in Table II, where the figures indicate the percentage response of the plankton to a given shift of an isotherm or isolume. For completeness, the responses of the 50 percent level also have been included. Since responses of the 50 percent level of copepods had been

TABLE II

Coefficients of Regression of the Deviations of the 25, 50 and 75% Levels on Deviations of the 15°C. Isotherm (above) and of the 10^{-2} Isolume (below). Values in Parentheses Are Significant with a Value of $P > 5\%$.

	Pteropods	Siphonophores	Chaetognaths	Copepods	All Species
25%	(+20%)	+32%	+ 36%	+ 62%	+ 22%
50%	+66%	+61%	+ 39%	+105%	+ 31%
75%	+71%	+76%	+ 41%	+151%	+ 42%
25%	— 7%	(+67%)	+116%	+ 75%	+137%
50%	(+10%)	(+21%)	(+ 84%)	+ 81%	+ 31%
75%	(+29%)	(+26%)	(— 52%)	(+ 22%)	+ 43%

found to be largely masked by the seasonal rhythm present, allowance has been made for this in calculating the partial regression coefficients in that group. Since, however, this seasonal effect has not been found in the other groups, the seasonal effect on copepods has not been allowed for in calculating the values for all species combined, and the values in this column are, therefore, probably somewhat lower than they should be. If the regression coefficients are considered as an index of the response of the plankton to changes in level of isotherms and isolumes, it is clear that there is a general tendency for the upper levels of the plankton to be more under the control of light and the the lower levels more under the control of temperature. This is not to be interpreted as a difference in response between shallow and deep species, since the effects of the differing characteristic levels occupied by the various species have been eliminated. The response differences exist between the upper and lower parts of the populations of a single species.

It appears that, if light penetrates deeper, the upper levels of the plankton move deeper also, but the lower levels show little response. On the other hand if the isotherms move upwards, the lower plankton levels move upwards, and there is little response in the upper plankton levels. The spread of the plankton is therefore related to the relative positions of isotherms and isolumes. To test this, the distance between the selected 15°C. isotherm and 10^{-2} isolume was calculated for each occasion. The deviations of this from its mean value for the period were then compared with the spread deviations with the results shown in Table III.

TABLE III

Coefficients of Correlation (above) and of Regression (below) between Deviations of the Distance between the 15°C. Isotherm and the 10^{-2} Isolume and Deviations of Spread. The Pteropod Data were Inadequate for Inclusion. All Figures Are Significant with a Value of $P = < 1\%$.

	Siphonophores	Chaetognaths	Copepods	All Species
r	+.66	+.63	+.40	+.48
b	+ 95%	+ 89%	+ 51%	+ 62%

As would be expected, the copepods agree well with the other groups in this case, since their seasonal rhythm affects all levels together and not spread. With more data available, some seasonal rhythm might well be looked for in spread in all groups, since, in most areas, there is some seasonal change in the depths of both isotherms and isolumes. The present locality is unusual in that such effects are likely to be masked by much greater changes due to water mass variation.

It was found, in Bermuda, that the spread of the plankton as a whole increased with depth. After elimination of the effects of isotherm and isolume movements, such relation was found also in the Florida material as shown in Table IV. Only the values for chaetognaths were not significant.

TABLE IV

PARTIAL CORRELATION COEFFICIENTS BETWEEN SPREAD AND THE 50% LEVEL OF THE SPECIES, OMITTING THE EFFECTS OF CHANGES IN ISOTHERM AND ISOLUME DEPTHS. THE VALUES FOR CHAETOGNATHS ARE NOT SIGNIFICANT, BUT THE REST ARE SIGNIFICANT WITH A VALUE OF $P=<1\%$. PTEROPOD DATA WERE INADEQUATE FOR INCLUSION.

	Siphonophores	Chaetognaths	Copepods	All Species
r	+.53	+.19	+.29	+.32

The regression coefficients were only small: —23 percent for all species combined.

A residual increase in spread with depth has been found. Spread is itself a resultant of differential movements of the upper and lower parts of the population. These upper and lower parts differ in the relative strength of their reactions to light and temperature. Some correlation may therefore be looked for between the strengths of these reactions of the upper and lower levels and the depths characteristically occupied by the species in question. For each species, the coefficient of regression of deviation of the 25 percent level on deviations of the 10^{-2} isolume were determined. The coefficient of correlation between these regression coefficients and the mean 25 percent level of the species was then calculated. It was significant only in the case of the siphonophores, with a value of —.72 ($P=<5\%$). Where the correlation was made with the 50 percent level of the species, the chaetognaths showed a significant value of —.73 ($P=2\%$). The direction of the correlation is as might be expected. The upper levels of a deep-living species tend to be less responsive to light changes than those of a shallow species.

A similar comparison was made between response to temperature at the 75 percent level and the 75 percent level of the species. Using regression coefficients, as above, no significant values were obtained. Using, instead, the coefficients of correlation between 75 percent level deviations and isotherm deviations, a value of +.74 ($P=2\%$) was obtained in the case of the chaetognaths. There is, therefore, some indication that the lower levels of the population are more closely controlled by temperature in deep-living species than in shallower ones.

Discussion

The present study has been limited to conditions in the middle of the day when it is assumed that an equilibrium has been established after the morning descent. Scattering layer records indicate that such an equilibrium is rapidly established, and that, in fact, the organisms responsible for the phenomenon can migrate vertically faster than is needed to keep pace with the changing illumination. This is probably true also of even such small organisms as copepods, for which very rapid ascents and descents have been recorded. The basic data used were the levels occupied on different occasions by selected fractions of the plankton and by a selected isotherm and isolume. The three values being compared are, therefore, all depths. Within the range of depths under consideration, the rate of change with depth of both illumination and temperature is approximately linear. Changes in depth of isotherms and isolumes may therefore be considered as indices of the strength of temperature and illumination stimuli, and as having an approximately linear relation to them. It seems reasonable, then, to consider movement of the plankton in relation to movement of an isotherm or isolume as equivalent to a measure of response to a given temperature or light stimulus. Then a value of +100 percent, obtained as the regression coefficient of plankton movement on isotherm movement, indicates a response of the plankton exactly sufficient to maintain it under conditions of constant temperature.

In general, when some ecological condition of an organism is shown to be under the simultaneous control of two factors, and can be expressed as functions of each, then the condition resulting from the simultaneous variation of both factors is best expressed as the product of the two factors. In the present case it has been assumed that the deviation of the plankton level from its mean position may be considered as the sum of the movements which would have resulted had temperature or light operated alone. Whether or not this is strictly true is open to question, and will probably not be settled until more data are available. The assumption has, however, been made since it greatly simplifies the partial regression analysis. It can, however, be shown that the assumption that the reaction of the plankton is a function of the product of the temperature and illumination changes results in values, the sum of the squares of whose errors is about four times that obtained assuming that the effects of the two factors are additive.

It is found that the mean day level of the various species studied followed the isotherm changes, but was influenced little, if at all, by light changes. This is in agreement with what is most usually found in the scattering layer in the North Atlantic. In the Mediterranean, where there is only very slight temperature stratification, this does not hold for the scattering layer. In Bermuda, where the temperature at the level concerned varied very little throughout the year, a correlation was found between the mean day level of the zooplankton as a whole and the cloudiness of the sky, but no more exact information on the vertical distribution of illumination is available.

Comparison of the responses of the plankton at its 25, 50 and 75 percent levels showed a transition from dominant light control at the top to dominate temperature control below. Three possible conditions are suggested which might produce such results. The responses of all the individuals in the population might be similar, and the observed vertical distribution might reflect either random "diffusion" around a center of distribution, or random movement more or less modified by the light and temperature conditions encountered away from this center. This is inherently unlikely since individual variation in reactions would be expected to occur in a population. The second alternative is that the observed vertical variation in relative reaction to light and temperature directly reflects the distribution within the population of individual reactions to these two factors. The distribution curves tentatively arrived at so far cast doubt of the likelihood of this. The third alternative combines the second with a modification of individual reaction by some third factor such as pressure. Further discussion of these alternatives must await considerable further analysis and probably calls for the examination of night levels also, and of the levels occupied during the morning descent and evening ascent.

When allowance was made for the effects of temperature and illumination on the 25 and 75 percent levels of the plankton, and through them on the spread, there still remained some residual tendency for the spread to be greater in deep-living than in shallower-living species. This agreed with observations in Bermuda. Furthermore, there was some slight indication that the upper (25 percent) levels are more responsive to light in shallow-living than in deep-living species, and conversely that the deeper-living species are the more responsive to temperature at their lower levels. These two effects were, however, not universal.

Finally, in the case of the copepods, there was a residual seasonal change in level after variations due to temperature and illumination had been allowed for, and it was suggested that this resulted from different levels being characteristically occupied by successive broods, over and above any responses to temperature and light conditions. Such a seasonal vertical range has previously been demonstrated in a few plankton species.

REFERENCES

JONES, E. C.
1952. A preliminary survey of the copepods of the Florida Current. Master's Thesis, The Marine Laboratory, University of Miami.

MILLER, S. M., H. B. MOORE AND K. R. KVAMMEN
1953. Plankton of the Florida Current. I. General conditions. Bull. Mar. Sci. Gulf and Caribbean, *2*(3):465-485.

MOORE, H. B.
1949. The zooplankton of the upper waters of the Bermuda area of the North Atlantic. Bull. Bingham oceanogr. Coll., *12*(2):1-97.
1952. Physical factors affecting the distribution of euphausids in the North Atlantic. Bull. Mar. Sci. Gulf and Caribbean, *1*(4):278-305.
1953. Plankton of the Florida Current. II. Siphonophora. Bull. Mar. Sci. Gulf and Caribbean, *2*(4):559-573.

RUSSELL, F. S.
1936. A review of some aspects of zooplankton research. Rapp. Cons. Explor. Mer., *95*(1):3-30.