

VARIATIONS IN TEMPERATURE AND LIGHT RESPONSE WITHIN A PLANKTON POPULATION

HILARY B. MOORE

The Marine Laboratory, University of Miami,¹ Coral Gables 34, Florida

Zooplankton tends to concentrate about a particular depth, this depth being characteristic of certain external conditions, of the species concerned, and frequently also of the stage of maturity and brood of the organism. Diurnal and seasonal rhythms in external conditions are frequently reflected in vertical migrations of the animals, and geographical gradients in such factors as light and temperature have been shown to be associated with correlated changes in the vertical distribution of the species concerned. There is an extensive literature on the subject, that part pertaining to the Crustacea having been well reviewed by Cushing (1951). He describes also the experiments on tropisms, taxes, etc., which have been made in an attempt to understand the behavior observed in the field. Although widely differing and sometimes contradictory results have been obtained by different workers, it appears that such differences are characters of particular species rather than of whole groups. So far as it is possible to visualize a typical copepod, etc., it appears that the general pattern of behavior is much the same at least in copepods, chaetognaths, siphonophores and pteropods (Moore *et al.*, 1953). With the exception of larval fishes, which rarely exhibit diurnal migration, it is probable that the principles are generally applicable to such zooplankton as are capable of vertical movements.

Cushing shows how light and temperature are generally accepted as the major environmental factors controlling vertical distribution, with only a minor part played by salinity, CO₂ and other factors. There are many instances where, during most of the 24 hours, the plankton migrates vertically as if it were following a level of optimal illumination. On the other hand, there are instances of a thermocline proving a barrier to the vertical movement of a species, and the upper or lower limits of some species have been shown to follow closely the seasonal movements of particular isotherms (Nikitine, 1929). Vertical movements in response to light and temperature stimuli have been demonstrated experimentally, although the results sometimes appear to conflict with observations of natural behavior. It has also been shown that the nature of the response to light may be modified by the temperature.

Laboratory experiments, at least with marine zooplankton, suffer from the difficulty of reproducing natural conditions. Comparatively few marine zooplankton have been successfully kept for any long period in the laboratory. The ecologist has the uncomfortable feeling that the more successful laboratory species are the least typical, and can be reared only because of this. There are factors such

¹ Contribution No. 756 from Woods Hole Oceanographic Institution; Contribution No. 137 from the Marine Laboratory, University of Miami.

as food, previous treatment, internal rhythms and others which may well modify behavior. On the other hand, any attempt to analyze behavior under natural conditions suffers from the large number of simultaneously varying factors, none of which can be controlled. It has the advantage, though, that the animals may be assumed to be behaving typically, and that, particularly in the tropics, a large number of species may be studied, so that the peculiarities of atypical species will not seriously affect the observations. The present paper is a study of the relative responses to temperature and light of some zooplankton in the Florida Current, and how these vary in a vertical section through the plankton population.

MATERIAL AND METHODS

The material was collected in a region of the Florida Current lying from ten to forty miles east of Miami, Florida. This is ocean water with isotherms sloping very steeply across the current so that a wide range of temperatures is available at any depth. Seasonal variations in the current pattern and velocity result in a wide range in conditions at any one station throughout the year. An account of the hydrographic conditions at the ten mile station has already been published by Miller *et al.* (1953) and the methods used in collecting plankton were described in the same paper. The material was drawn from samples, collected for other purposes, in part under a joint program of the Marine Laboratory of the University of Miami and the National Geographic Society, and in part by the Marine Laboratory under contract number NObsr-57146 for the Office of Naval Research. The analyses were carried out under the latter contract and under Bureau of Ships contract number NObsr-43270 at Woods Hole Oceanographic Institution. The siphonophore examination was carried out in part by the author and in part by D. C. Roane (1954). The chaetognaths were examined by H. Owre and her results will be included in a doctorate thesis at the University of Michigan. To all of these the author wishes to express his indebtedness.

The present work is restricted to the period within about two hours either side of noon, when the illumination is not changing rapidly, and it is assumed that the plankton has had time to stabilize at the depth at which it is found. Vertical temperature sections were available for each station. The vertical distribution of illumination was calculated by methods previously used (Moore, 1950) and from these the depths of selected isotherms and isolumes were obtained. For each station, the percentage vertical distribution of each species was calculated as follows. First, the count from each of the oblique net hauls was scaled to the equivalent of a tow of one mile, the factor being obtained from the trace on the depth-distance recorder towed along with the nets. Each count was assumed to be applicable to a column of water reaching from half way between the mid-depth of that tow and the mid-depth of the tow above it to half way to mid-depth of the tow below it. The top tow was assumed to terminate at the surface, and the lowest at the deepest point shown on its trace. Integration of the whole column was performed by multiplying each count by the length of water column to which it applied, and adding the products. By the use of a calculating machine, the levels were found corresponding to 10%, 20%, etc., of this total. These, referred to as the 10% level, etc., are the depths above which this percentage of the species occurred on the particular occasion. Values from 10% to 90% were

calculated, but the 0% and 100% levels were not sufficiently clearly defined to be usable.

The following species, used in previous work, were present in sufficient numbers to be significant. It should be noted that, with the inclusion of more stations, some of the regressions obtained differ from ones previously quoted.

SIPHONOPHORA

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

CHAETOGNATHA

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

The various species characteristically occupy different levels. In order that the data for the various species could be combined, the mean 10%, 20%, etc., levels were calculated for each species, these being the means of all stations. For each station, the results were then expressed as deviations from the mean on that occasion, a positive value being deeper, and a negative shallower. The deviation of a typical siphonophore on that occasion was the mean deviation for the eight species available, and that of a typical chaetognath was the mean for nine species. For comparison, the levels of the 15° C. isotherm and of the 10⁻² isolume were similarly expressed as deviation from their respective means.

After testing for correlations between the deviations of the plankton and the isolume and isotherm, and finding that these were significant, partial regressions were calculated with the results shown in Figures 1 and 2. The regression coefficients show the extent of vertical movement of the plankton in relation to a one-meter shift in the 15° C. isotherm or 10⁻² isolume. In all cases the coefficients are positive, that is to say, the plankton movement is in the same direction as the movements of the isotherm and isolume.

For simplicity it may be assumed that the temperature and light graphs in the above figures are straight lines. If the regressions of plankton movements on isotherm and isolume movements are referred to as temperature and light responses, then the regressions of the responses on percentage level can be calculated. From these, the levels occupied by the typical siphonophore or chaetognath may be predicted for any given hydrographic conditions for this region. As a verification of the goodness of fit between such predicted levels and those actually observed, six stations were selected which offered a particularly wide range of hydrographic conditions. Figures 3 and 4 show the comparison of the values from the 10, 50 and 90% levels as predicted and as observed. These cover a more than five-fold range of depth under different conditions, and the agreement appears to be good.

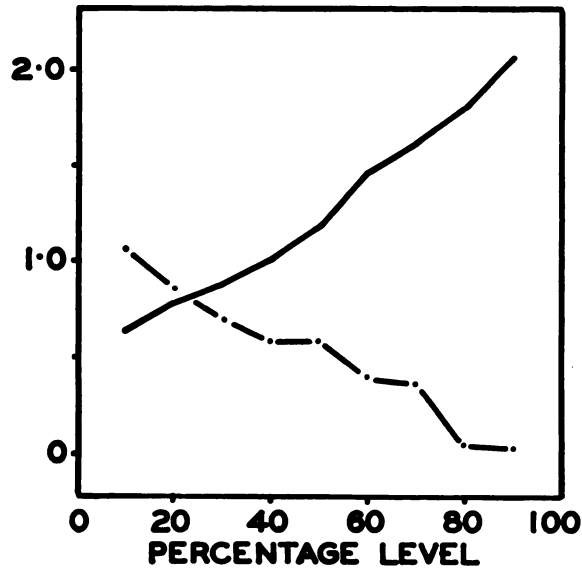


FIGURE 1. Typical siphonophores. Partial regression of plankton movement on movement of the 15° C. isotherm (whole line) and of the 10³ isolume (broken line), and the variation of these regressions with percentage level; 0% represents the top, and 100% the bottom of the plankton column.

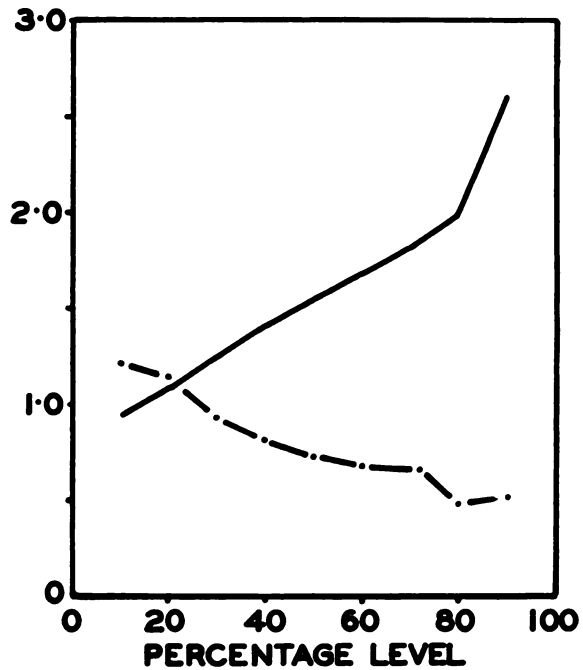


FIGURE 2. Typical chaetognath regressions indicated as in Figure 1.

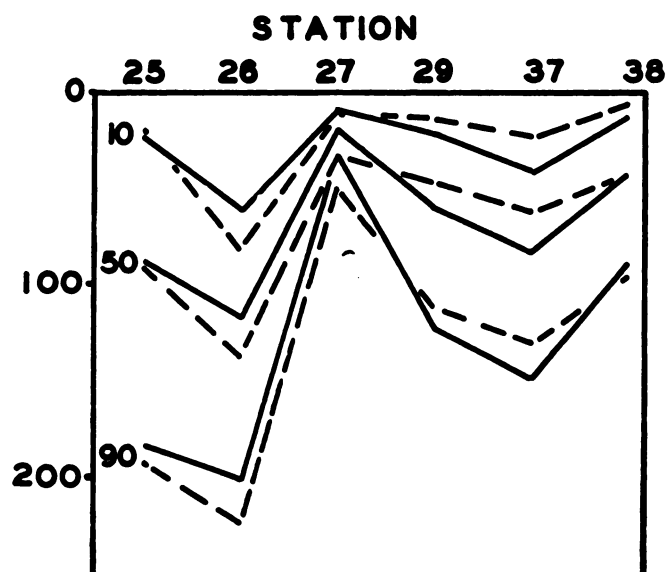


FIGURE 3. Typical siphonophore. Comparison of the observed depths, in meters, of the 10%, 50% and 90% levels at six stations (whole lines) with the depths predicted by the regressions referred to in the text (broken lines).

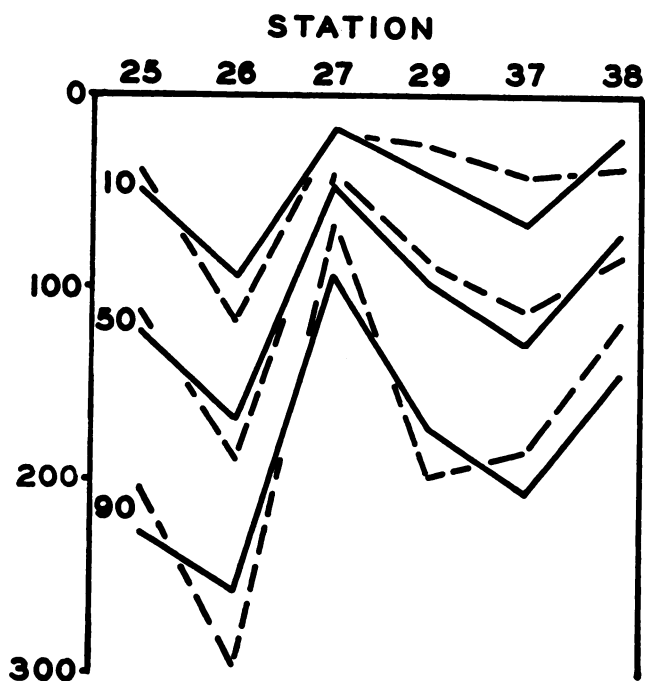


FIGURE 4. Typical chaetognath comparisons indicated as in Figure 3.

DISCUSSION

Cushing (1951) summarizes many examples of plankton whose day level varies on different occasions. Where these variations have been correlated with changes in an environmental factor, this has usually been illumination. The Florida Current provides an unusually wide range of temperature variation at depth, and so may be particularly advantageous for demonstrating the role of temperature. Further, most previous workers have been concerned with the level of maximum concentration of the plankton and have not differentiated between the behaviors of the shallower and deeper members of the population of a given species. In an earlier study (Moore, 1953; Moore *et al.*, 1953) in which considerably fewer data were available than in the present work it was shown that there was an increase in temperature response and a decrease in light response in the lower levels of the plankton as a whole. The same trend was indicated in the four separate groups studied, but many of the values could not be considered statistically significant. J. B. Lewis (in press) has studied the euphausiids of this area, and shown that illumination plays the major part in controlling both day level and vertical diffuseness, with little or no demonstrable effect of temperature. Roane (1954) compared the average day level of a group of siphonophores at two stations in the Florida Current and found these to be 79 and 253 meters. The corresponding extinction coefficients were 0.062 and 0.051 while the depths of the 15° C. isotherms were 151 and 619 meters, respectively. It seemed probable that the great range in depth of the animals was associated with both illumination and temperature differences. The present work shows that the observed vertical distributions can be accounted for if both temperature and light play a part in regulation of level, and if it is assumed that their effects are additive.

Two characteristics of the graphs in Figures 1 and 2 call for explanation. The temperature and light responses change more or less linearly with percentage level, and the regressions of plankton movement on isotherm and isolume movement may have values well in excess of unity. The author has, so far, been able to find little information on how the nature or strength of a reaction varies among the individuals in an invertebrate population. The frequency distribution may perhaps be expected to follow either a symmetrical or a skewed normal curve. The latter is true in what is perhaps a parallel case, the variations in rate of hemolysis of red cells in a sample (Ponder, 1930, 1932). Too much reliance cannot be placed on the exact form of the present curves, and unfortunately the ends of the curves are lacking, even the 10% and 90% values probably being based on too small counts to have much significance. It seems clear, though, that they cannot represent a frequency distribution rising to a marked peak at any particular value. Subsequent work on single species suggests that they may, with more data available, prove to be flat-peaked curves. Another explanation of their shape lies in the probability that, as shown below, temperature and light are not sufficient alone to account for the observed behaviors, and a further environmental factor will have to be considered.

The extent to which the regression coefficients may exceed unity can hardly be attributed to error due to inadequate data. They indicate that the animals may respond to a change in depth of an isotherm or isolume by moving considerably further. In other words, although the movements of the animal are in such direc-

tion as could maintain them at a constant temperature or illumination, they do not, in fact congregate at the depth corresponding to such a constant value. Finally, very much poorer correlations are obtained if an attempt is made to relate the depth at which the animals are found to *in situ* temperatures and illuminations, than if the correlations are made between the depth changes of the animals, the isotherms and the isolumes. All this suggests that a third factor, related to depth, and which we tentatively suggest may be pressure, must be included in the complex. Although pressure has received much less consideration in this connection than the other two factors, there is some evidence that it may affect vertical movement of zooplankton (Hardy and Bainbridge, 1951).

The similarity of Figures 1 and 2 gives support to the statement already made that there may be a pattern of depth control mechanism typical of widely different animals. Within the species which we have grouped together, specific differences may be expected both in the strengths of the responses and in the relative response to light and temperature. Such would be in agreement with the very different behavior patterns observed in the many forms which have been worked with. We have found a marked difference in response in different parts of a population. There is no evidence as to whether this represents permanent differences among the individuals or whether it represents a sorting, resulting from varying responses, of individuals whose responses fluctuate continually. Differences between individuals may be expected, but so may changes in the reactions of a single individual. The latter might be more or less random, they might vary in relation to previous condition or to some control such as a feeding cycle, or they might vary with an inherent diurnal or other rhythm. Whatever may prove to be the case, a significant point seems to emerge in connection with the interpretation of experiments with plankton. Firstly, if the experimental animals are not always collected from the same part of the plankton column then differences may be expected in the nature of the experimental behavior. Secondly, experiments made with animals taken from the top or bottom of the population may yield results which are not applicable to the main concentration of the population.

LITERATURE CITED

- CUSHING, D. H., 1951. The vertical migration of planktonic crustacea. *Biol. Rev.*, **26**: 158-192.
- HARDY, A. C., AND R. BAINBRIDGE, 1951. Effect of pressure on the behaviour of decapod larvae (Crustacea). *Nature*, **167**: 4244, 354-355.
- 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**: 465-485.
- MOORE, H. B., 1950. The relation between the scattering layer and the Euphausiacea. *Biol. Bull.*, **99**: 181-212.
- MOORE, H. B., 1953. Plankton of the Florida Current II. Siphonophora. *Bull. Mar. Sci. Gulf and Caribbean*, **2**: 559-573.
- MOORE, H. B., H. OWRE, E. C. JONES AND T. DOW, 1953. Plankton of the Florida Current. III. The control of the vertical distribution of zooplankton in the daytime by light and temperature. *Bull. Mar. Sci. Gulf and Caribbean*, **3**: 83-95.
- NIKITINE, B., 1929. Les migrations verticales saisonnières des organismes planktoniques dans la Mer Noire. *Bull. Inst. Océanogr. Monaco*, **540**: 1-24.
- PONDER, E., 1930. The form of frequency distribution of red cell resistances to saponin. *Proc. Roy. Soc. London, Ser. B*, **106**: 543-559.
- PONDER, E., 1932. On certain correction terms required in the equations for the kinetics of simple haemolysis. *Proc. Roy. Soc. London, Ser. B*, **110**: 1-17.
- ROANE, D. C., 1954. A study of some siphonophores of the Florida Current. Thesis for Masterate at the University of Miami, 1-77.