

BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

VOLUME 6

1956

NUMBER 4

THE EFFECTS OF TEMPERATURE, ILLUMINATION AND PRESSURE ON THE VERTICAL DISTRIBUTION OF ZOOPLANKTON^{1, 2}

H. B. MOORE AND E. G. CORWIN

The Marine Laboratory, University of Miami

ABSTRACT

Thirteen 24-hour plankton stations were worked in the Florida Current and counts made for four species of siphonophores. Depth, temperature and illumination data accompanied all net hauls. An equation is developed relating the depth of each species at any given time to external conditions of temperature, illumination and pressure. This involves null value of each at which there is no stimulus to vertical movement, and factors giving relative response to each of the three environmental influences. The nulls are not solved here; the factors show a diurnal rhythm and also a progressive change from predominance of light control in the upper part of the population to predominance of temperature control in the lower part.

INTRODUCTION

In earlier studies (Moore, 1953, 1955; Moore, et al, 1953) it was shown that changes in the temperature and illumination are reflected in corresponding changes in the noon vertical distribution of various kinds of oceanic zooplankton. A balance appears to be attained, such that the stimulus to move upwards into warmer water just counteracts the stimulus to move downwards to a lower level of illumination. Furthermore, the deeper-living individuals in a population are more influenced by a given temperature change than the shallower ones while the latter are more influenced by a given change of illumination. That there is such a gradation of reaction through a population is to be expected since all individuals are not concentrated at a single depth but rather are spread over a wide range of external conditions.

In an attempt to relate, mathematically, the depth occupied and the external conditions, the general conditions of temperature and

¹Contribution No. 161 from The Marine Laboratory, University of Miami.

²Contribution No. 864 from the Woods Hole Oceanographic Institution.

illumination were expressed as the depths of a selected isotherm and isolume, and all data were translated into deviations from annual mean values of these depths at noon. Similarly the depth of the organism in question at noon was expressed as deviation from its annual mean noon depth. This had the advantage of allowing results for a number of different species to be grouped together and thus increasing the significance of results based on somewhat inadequate data. When the depths, temperatures and illuminations had been converted to deviations, partial regressions were calculated, and it was in this form that the plankton behavior was expressed. The population was separately analyzed at nine levels from 10% to 90%, the percentage representing the proportion of the population above that level. For each such level we solved the equation

$$d = T \text{ fac. } t + I \text{ fac. } i \quad (1)$$

where the factors are obtained as partial regressions and t , i , and d are the deviations from the mean of isotherm, isolume and plankton depth respectively.

This equation, in effect, related vertical movement of the animals to vertical movements of a given temperature and illumination level, and as such gave a close prediction of where the plankton would be found under widely varying conditions. At a test of its applicability, the equation predicted that the plankton at a station 40 miles east of Miami should be at least twice as deep as at a ten mile station. Roane (1954) verified this for the siphonophores, the mean day level, averaged for eight species, being 79 meters at the 10 mile station and 253 meters at the 40 mile station.

The type of equation given above yielded good values for the depth of the organism in terms of the displacement of isolines but proved useless in trying to relate depths with actual temperatures and illuminations *in situ*. Furthermore, some of the partial regressions obtained were greater than 1.0, suggesting an over-compensation by the animals. The present paper presents a modified equation which allows the actual values to be used rather than the deviations and appears to come closer to representing the actual mechanism involved.

Since we commence with counts of organisms in net hauls whose sampling variation is unknown, it seems valueless to attempt to determine the significance of the final figures arrived at. It must therefore be strongly emphasized that these figures should be considered as establishing certain general trends but not as being accurate

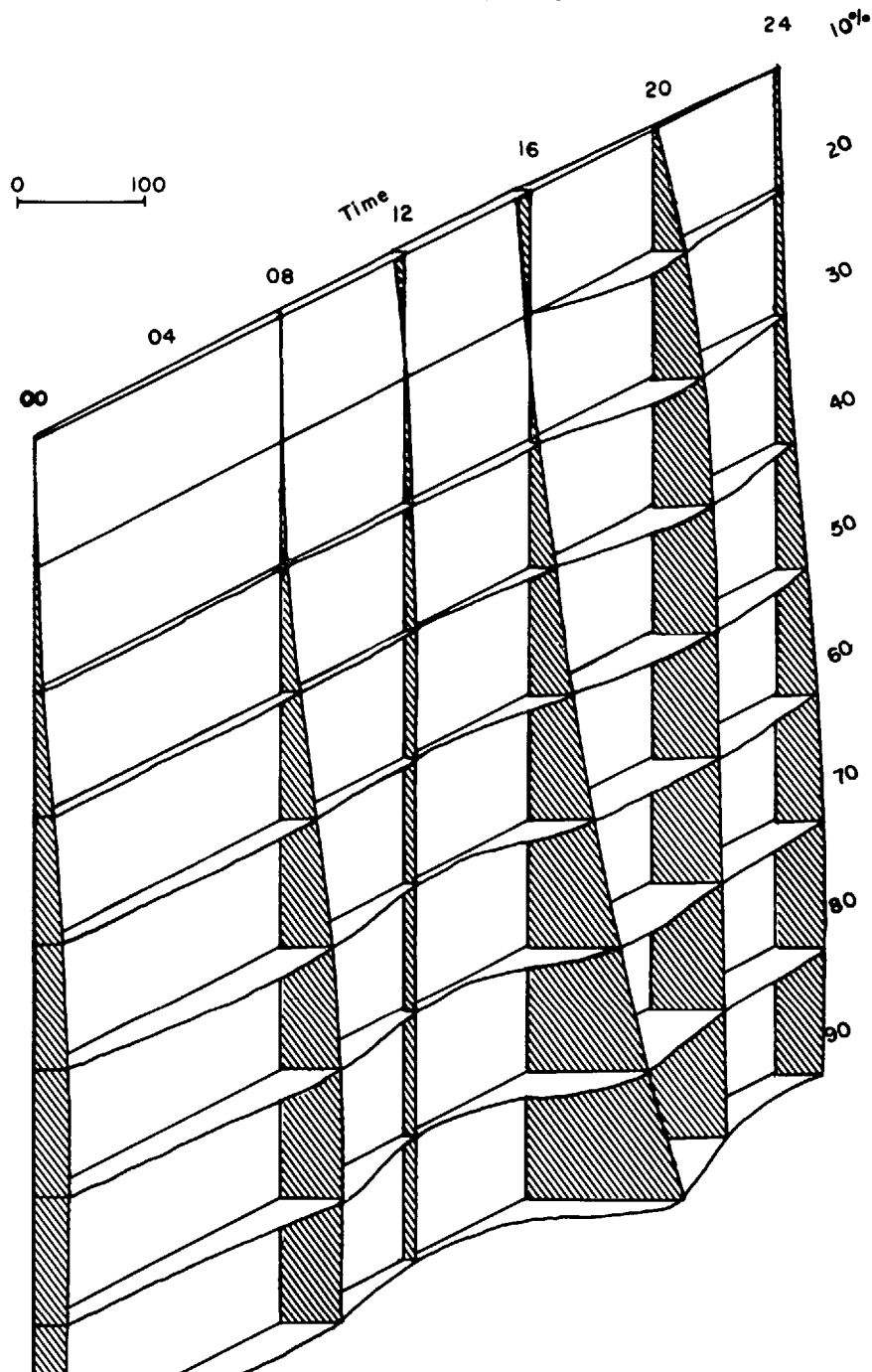


FIGURE 1. Mean values of T. factors for four Siphonophore species. The vertical coordinates represent percentage levels in the population. The horizontal coordinates are time and strength of factor. A vertical section (hatched) shows, for a given time, the variation in factor strength through the population. A horizontal section shows the diurnal change in the factor at a given percentage level.

in detail. It should be stated that the data used have served mainly for the development of methods. The diurnal rhythms found were considered questionable until more material had been collected and analyzed. Analysis of copepod behavior, based on a new and larger series of hauls, has confirmed the general pattern of these rhythms and has justified the presentation of the present series.

MATERIAL AND METHODS

Net hauls were available from thirteen stations at different locations in the Florida Current off Miami. At each, from six to nine hauls were made at different depths, and this series was repeated through a 24 hour period. However, weather and other conditions sometimes curtailed operation so that the number of stations usable varies with time of day. The collecting methods were those previously described. All counts were reduced to the equivalent of a one-mile tow and are accompanied by depth, temperature and illumination data. The full series of nets could not be towed simultaneously, so values have been interpolated at standard times at four hour intervals through the 24 hours.

The present treatment does not apply to conditions of complete darkness. We have therefore omitted those night hours when there was no moonlight. Unfortunately, these were mostly at 0400 hours so that the remaining data for this hour is insufficient for analysis.

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, in part under the contract number NObsr-57146 for the Office of Naval Research and in part under a grant from the Rockefeller Foundation. The analyses were carried out under contracts listed above and also under a National Science Foundation grant and under contract number NObsr-43270 at Woods Hole Oceanographic Institution.

EQUILIBRIUM EQUATION

The only formulation which would account for the observed facts required the inclusion of a third factor which was correlated linearly with depth. This is assumed to be pressure, and there is some evidence that pressure may control vertical movement of plankton (Hardy and Bainbridge, 1951; Knight-Jones and Quasim, 1955). Since our assumed pressure factor is derived from depths, the unit used is meters

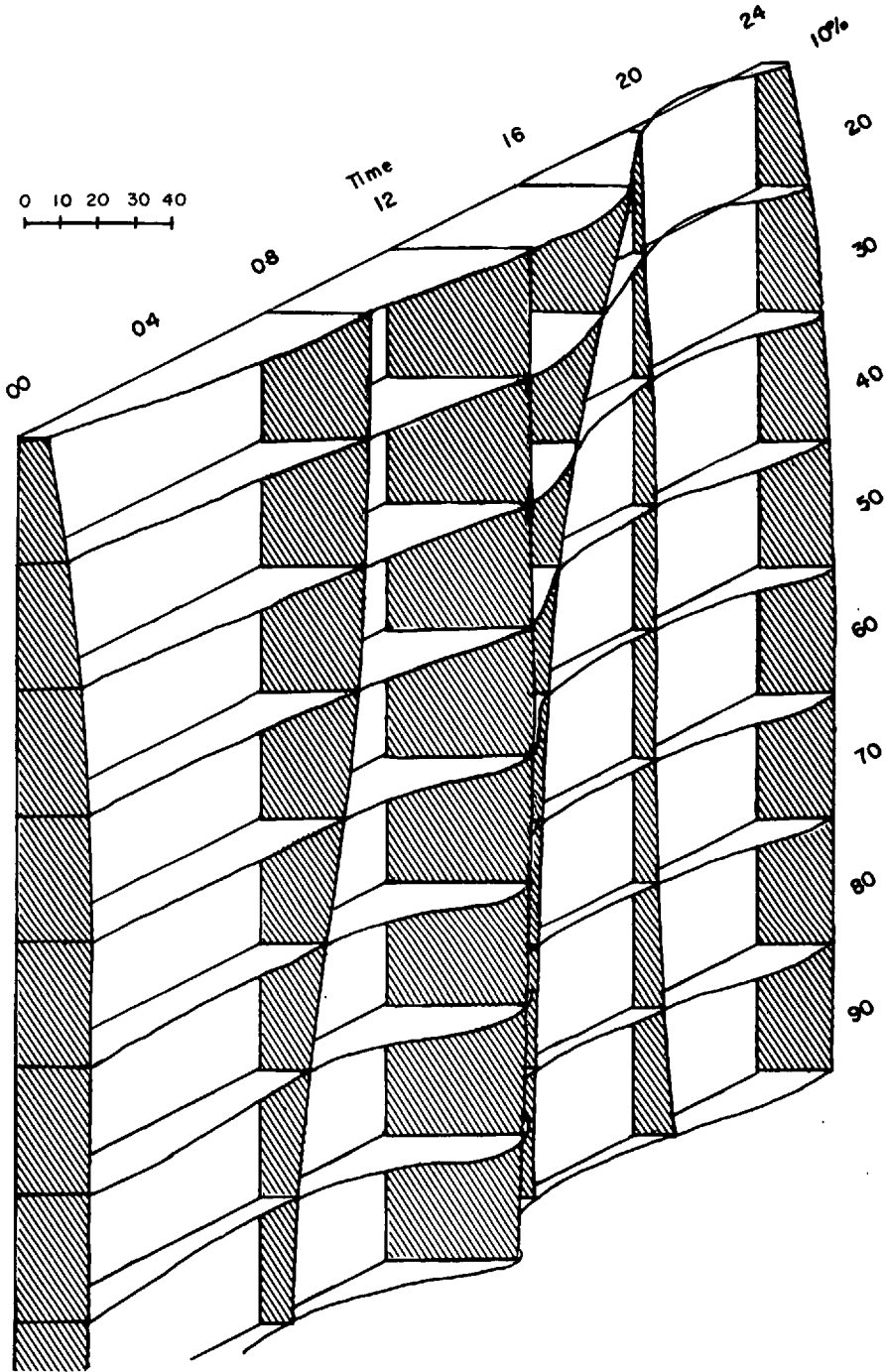


FIGURE 2. Mean values of I. factors for four Siphonophore species, represented as in Fig. 1.

of water. The light unit is the exponent to the base ten with full sunlight rated at 10^3 . Temperatures are in degrees centigrade.

It is assumed that there are null values of temperature, illumination and pressure (T_n , I_n and P_n) at which an animal has no tendency to move upwards or downwards. This does not exclude the possibility of their oscillating between two limiting values since the null would represent the mean of these. It is further assumed that the strength of the animal's response is linearly proportional to the difference between the null values and the *in situ* values of the condition to which the animal is exposed. While this is improbable, it is necessary as an approximation if the solution is not to become impossibly complex at the present stage.

We may therefore represent the strengths of the stimuli to vertical movement as $T - T_n$, $I - I_n$ and $P - P_n$ where T , I , and P are the temperature, illumination and pressure *in situ*, and T_n , I_n and P_n , the null values of each. To equate relative responses to the three stimuli, it is necessary to designate three factors, T fac., I fac., and P fac. Since these are determined relatively and not absolutely, one of them, P fac., is assumed to be always equal to one. If it varies, certain changes are implied, which will be discussed later.

If the animals of a given part of the population, and at a given time, have achieved an equilibrium between their responses to the three stimuli, then

$$T \text{ fac. } (T - T_n) + I \text{ fac. } (I - I_n) + P \text{ fac. } (P - P_n) = 0 \quad (2)$$

It is initially assumed that the organisms at different percentage levels of the population may differ in their responses and in their nulls. There may also be differences in diurnal rhythm. There may be some delay in response to changing conditions but both net hauls and scattering layer records have frequently demonstrated the ability of plankton to keep pace in its vertical movements with the rapidly changing illumination at sunrise and sunset. Thus, for each time and percentage level we have an array of occasions with different, known values of T , I and P . With these it is possible to obtain a solution to part of the equation, namely the three factors. Equation 2 may be rewritten:

$$T \text{ fac. } T + I \text{ fac. } I + P \text{ fac. } P = T \text{ fac. } T_n + I \text{ fac. } I_n + P \text{ fac. } P_n \quad (3)$$

and the sum of the right hand part may be temporarily designated Tot. fac.

Solution by partial regressions gives us the best fitting values of T fac., I fac. and Tot. fac.; P fac. is assumed to equal one. The

values for T and I factors are given in Tables 5-8, while Figures 1 and 2 are smoothed curves drawn from the mean value for the four. The 0400 hour series, as stated above, is missing, and the 2000 hour means are based on two species only. The other two being inadequately represented.

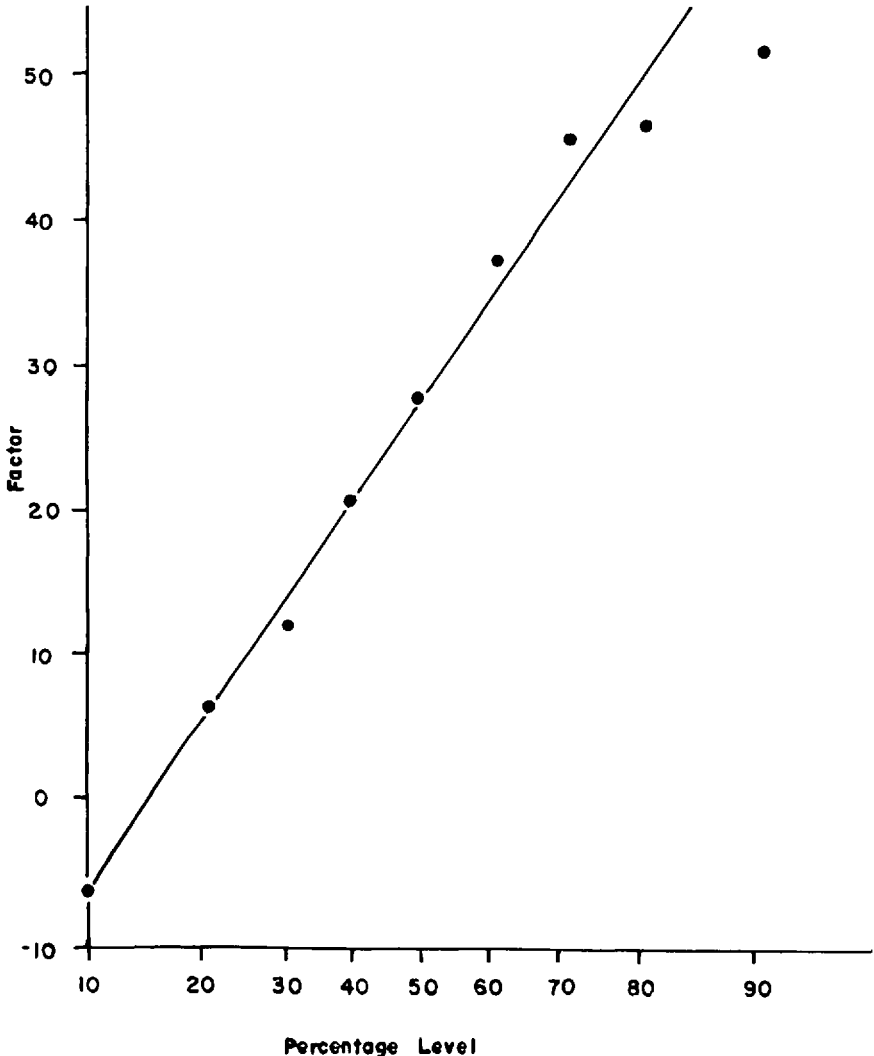


FIGURE 3. Mean of T. factors for four Siphonophore species, taking all times, in relation to percentage level. These are plotted on linear probability paper.

Bearing in mind that only generalizations, and not details, should be taken from these results, one or two particular aspects may be considered. In the first place, earlier work indicated a change from dominant illumination sensitivity in the upper part of the population to dominant temperature sensitivity in the lower part. If we take the means for all hours for the present data we find this to be true here also. In the earlier work it was stated that the partial regressions, which were not strictly equivalent to the present ones, seemed to vary linearly with percentage level. The present values approach a straight line on linear probability paper (Figs. 3, 4) which suggest that they represent a more or less normal distribution of the two factors through the population. Again we must not draw too detailed inferences from the data. The misfit of the 90% values, particularly for the I factor, may well be due to the inadequacy of the original sampling since this is the sparsest part of the population.

We originally assumed that the pressure factor was constant with a value of one. In view of the variation in the other two factors it seems probable that the pressure factor also varies. Since they are measured in units relative to the pressure factor at any given time and percentage level, the values shown in Figures 1 and 2 would have to be correspondingly modified. This might result in a change in the gradient of a factor through the population or in its diurnal rhythm in itself or one of the other two factors. Changes in the pressure factor could, however, in no way modify the diurnal and percentage level changes in the relative strengths of the temperature and illumination factors. In other words the change from shallow illumination sensitivity to deep temperature sensitivity is real, as is the diurnal change in their relations.

The second generalization which may be made from the data is that there is a marked diurnal rhythm in the factors. In general there is a marked noon drop in the temperature factor with a corresponding increase in the illumination factor. The 1600 hours series appears to indicate an over-compensation following the noon condition. The 2000 hours and 0800 hours conditions are so similar that it seems unlikely that the missing 0400 hours series would be much different.

It can be shown that, even if the pressure factor varies, there will still be a diurnal rhythm in the relative strengths of the temperature and illumination factors. The ratio $\frac{T \text{ fac}}{I \text{ fac}}$ can be calculated, and

expressed as the mean for all percentage levels. To eliminate the effects of the few negative values for the factors, a constant can be added throughout which makes all values positive. This does not affect the general trend of the means. Table 1 shows the mean values

of $\frac{T \text{ fac.} + 14}{I \text{ fac.} + 3}$

TABLE 1

Time	00	04	08	12	16	20
Ratio	17.73	—	3.06	0.45	4.66	10.22

DISCUSSION

At an earlier stage in these studies it was shown that there was a very similar pattern of response to temperature and illumination in widely different groups of plankton animals (Moore, et al, 1953). An average siphonophore (mean of 8 species) was very similar to an average chaetognath (9 species), pteropod (6 species) or copepod (18 species). The depth at which they were found most closely reflected isolume movements in the upper part of the population and isotherm movement in the lower part. This was later confirmed in more detail for siphonophores and chaetognaths (Moore 1955). Coming to individual species, the pattern is the same, although here we are relating depth to actual temperature and illumination, and not to movements of isotherms and isolumes. If we take, for each species, the mean value of temperature and illumination factor for all percentage levels, and exclude 2000 hours, for which only two of the species were analyzed, we obtained the following values:

TABLE 2
MEAN VALUES OF FACTORS

	T fac.	I fac.
<i>Abylopsis eschscholtzii</i>	20.7	21.1
<i>A. tetragona</i>	17.3	19.9
<i>Eudoxoides mitra</i>	23.6	20.0
<i>Chelophyes appendiculata</i>	24.9	20.1

The differences are very small and perhaps not even significant. Yet these species characteristically live at very different levels. The following mean day levels are given by Roane (loc. cit.). In the Florida Current the cold water comes closer to the surface at the 10 mile than at the 40 mile station. Depths at the 40 mile station are the means of Roane's values for the two generations.

TABLE 3
MEAN DAY LEVELS. DEPTHS IN METERS

	Bermuda	Florida Current	
		10 Mile	40 Mile
<i>Abylopsis eschscholtzii</i>	40	58	171
<i>A. tetragona</i>	55	104	188
<i>Eudoxoides mitra</i>	125	134	270
<i>Chelophyes appendiculata</i>	75	74	221

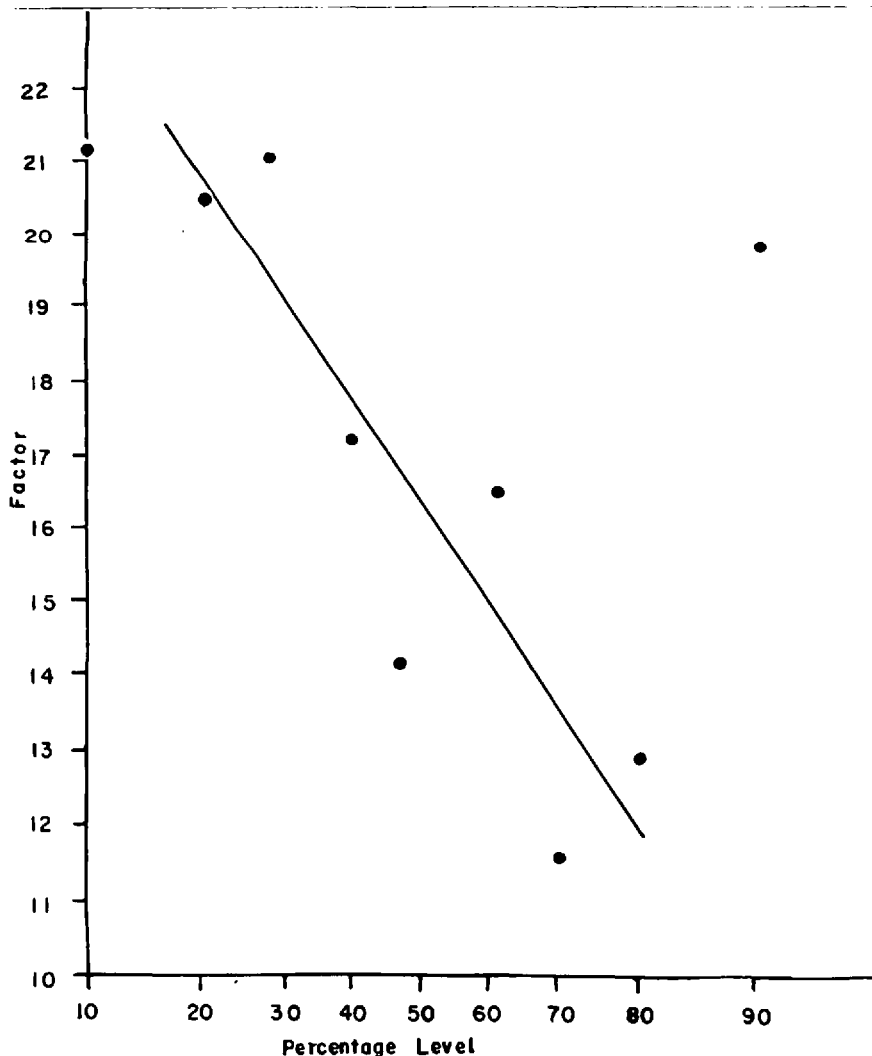


FIGURE 4. Mean of I. factors for four Siphonophore species, taking all times, in relation to percentage level. These are plotted on linear probability paper.

The present paper does not present the analysis of the second part of the equation, which yields the null values of temperature, etc., at which the animals are not stimulated to vertical movement. The similarity of their responses to unit change of temperature, etc., suggests that the difference in the levels characteristically occupied is more likely to reflect specific differences in their null values.

It is not surprising that there should be a regular change through the population in the relative strength of temperature and illumination response. It is true that random movement about an optimal depth would result in vertical spread but it is hard to believe that animals with identical behavior characteristics would tolerate the wide range of external conditions which they would encounter. Roane (loc. cit.) gives the following vertical spreads between the 25% and 75% levels. For the entire population, 0% - 100%, these would be still greater.

TABLE 4
VERTICAL SPREAD IN METERS

	Bermuda	Florida Current	
		10 Mile	40 Mile
<i>Abylopsis eschscholtzii</i>	80	51	219
<i>A. tetragona</i>	25	63	234
<i>Fudoxoides mitra</i>	105	65	209
<i>Chelophyes appendiculata</i>	130	81	134

If such spreads are not due to random movement they must represent a sorting of the population resulting from individually different behavior characteristics.

The existence of a diurnal rhythm in degree of response to the same stimulus is also in accord with the numerous examples of rhythms known in other animals. While some of these are timed by varying external conditions, many others are known to be timed by an internal "clock." It has been suggested that the observed rhythm reflects a conditioning to the much more intense light in the middle of the day or is even an effect of the response scale not being linearly related to the illumination scale. This at first sounds reasonable, since the light changes many million-fold diurnally, whereas the temperatures and pressures encountered have a far smaller range. However, the animals to a great extent regulate their level so as to follow a constant illumination and the actual light

changes they encounter during their diurnal movement are of comparable magnitude with the temperature and pressure changes.

It is interesting to make a tentative comparison of the relative effects of the three environmental conditions considered. A change of one light unit represents a ten-fold change in light. Temperature is in degrees centigrade and one pressure unit is equivalent to one meter of water or about a tenth of an atmosphere. Both temperature and illumination factors have mean values of about twenty, so a ten-fold light change, or a 1°C temperature change is equivalent to about two atmosphere. Dr. P. F. Scholander suggested that it would be more logical to consider volume changes rather than pressure changes and that the reciprocal of the pressure might yield better correlation than the pressure itself. This was tested, but found not to be true.

We wish to express our indebtedness to many people for assistance. The Captain, crew and various scientists on board made possible the extensive collecting at sea. This work was done from The Marine Laboratory R/V *PHYSALIA*. Illumination and temperature data were worked up by various members of the Laboratory staff. The counting was done partly by the senior author and partly by D. C. Roane (1954). Thanks are due to various members of Woods Hole Oceanographic Institution for helpful criticism and suggestions. Finally invaluable assistance in statistics was received from Dr. F. Smith of the University of Michigan, Dr. C. C. Taylor of the U. S. Fish and Wildlife Service in Woods Hole, Mrs. Helen Roberts of Woods Hole Oceanographic Institution, and Miss A. Feinstein, of The Marine Laboratory, University of Miami.

TABLE 5
Abylopsis eschscholtzii

TEMPERATURE FACTORS				
%	00.00	08.00	12.00	16.00
10	+3.8	-5.1	-3.3	-17.0
20	+8.0	-11.9	-15.1	-18.7
30	+9.4	-11.8	-1.2	+0.6
40	+13.6	+1.9	+16.3	+20.5
50	+12.1	+6.7	+37.7	+38.2
60	+47.8	+36.0	-4.6	+57.4
70	+178.4	+25.6	-3.3	+52.5
80	+12.3	+42.4	+22.5	+63.6
90	+15.3	+41.8	+3.3	+69.8

TABLE 5 (Cont.)
ILLUMINATION FACTORS

%	00.00	08.00	12.00	16.00
10	+2.0	+21.0	+38.2	+37.9
20	+6.7	+37.9	+47.3	+23.9
30	+21.3	+43.5	+40.8	+12.8
40	+16.0	+33.7	+26.6	+5.4
50	—0.6	+33.6	+3.4	+13.9
60	+2.2	+36.2	+65.3	+11.2
70	—58.1	+15.1	+53.6	+20.7
80	+32.2	+4.8	+11.9	+12.7
90	+30.7	+7.9	+44.6	+4.6

TABLE 6
Abylopsis tetragona

TEMPERATURE FACTORS				
%	00.00	08.00	12.00	16.00
10	—5.3	+11.7	+8.8	—9.8
20	—1.4	+16.2	—0.9	+0.9
30	+6.9	+2.8	—0.5	+4.6
40	+26.9	+15.3	+5.8	+11.4
50	+12.4	+30.3	—3.8	+31.0
60	+24.6	+46.1	—4.1	+37.3
70	+22.7	+46.2	—2.6	+43.8
80	+25.1	+52.0	—1.7	+40.7
90	+33.1	+33.9	—2.8	+62.7

ILLUMINATION FACTORS

%	00.00	08.00	12.00	16.00
10	+7.2	+16.6	+25.5	+36.4
20	+20.6	+21.4	+38.7	+26.1
30	+21.5	+28.3	+38.1	+22.8
40	+12.9	+16.9	+21.3	+18.1
50	+21.3	+10.1	+38.9	+10.4
60	+16.0	+4.0	+40.0	+7.5
70	+15.2	+5.4	+37.6	+4.7
80	+16.2	+1.1	+37.0	+11.9
90	+15.3	+13.7	+37.5	+2.1

TABLE 7
Eudoxoides mitra

TEMPERATURE FACTORS					
%	00.00	08.00	12.00	16.00	20.00
10	+4.8	—13.3	—2.8	—7.0	—0.1
20	+5.0	—6.7	—3.4	—6.0	+36.2
30	+6.8	+15.8	—9.7	+9.9	+39.7
40	+21.5	+29.6	—3.4	+19.5	+56.5
50	+31.3	+45.5	—4.2	+34.2	+55.1
60	+36.6	+58.6	—2.7	+56.7	+72.0
70	+42.7	+65.6	—7.2	+99.8	+73.2
80	+63.2	+71.6	—5.5	+105.2	+79.2
90	+34.7	+46.1	—2.0	+4.6	+67.7

ILLUMINATION FACTORS					
%	00.00	08.00	12.00	16.00	20.00
10	+25.5	+25.5	+37.9	+30.8	+1.6
20	+24.4	+26.0	+38.6	+29.1	+3.8
30	+24.6	+17.1	+45.4	+19.5	—3.3
40	+21.0	+11.6	+37.1	+15.5	+7.1
50	+19.5	+5.5	+38.0	+10.7	+7.8
60	+18.5	+0.8	+37.0	+4.7	+9.4
70	+16.7	+0.0	+37.0	—8.1	—2.7
80	+5.6	—1.5	+36.4	—17.4	+6.1
90	+15.3	+13.3	+38.5	+21.0	+7.3

TABLE 8
Chelophyes appendiculata

TEMPERATURE FACTORS					
%	00.00	08.00	12.00	16.00	20.00
10	+5.3	—	—	—	—
20	+8.3	+6.9	+31.2	+17.4	+12.5
30	+10.5	+3.8	+17.3	+25.6	+38.2
40	+18.7	+0.6	+13.4	+27.6	+30.0
50	+26.2	+34.1	+26.9	+40.1	+26.4
60	+36.5	+24.9	+9.7	+58.9	+42.0
70	+33.8	+33.0	+8.2	+68.9	+31.6
80	+30.9	+37.7	+19.2	+72.5	+64.7
90	+54.2	+35.3	+5.6	—	+34.9

TABLE 8 (Cont.)
ILLUMINATION FACTORS

%	00.00	08.00	12.00	16.00	20.00
10	—7.4	—	—	—	—
20	—6.7	+24.1	+22.8	+20.3	—1.8
30	+15.4	+25.9	+32.2	+14.4	—0.1
40	+14.5	+26.3	+33.1	+12.0	+4.7
50	+12.6	+9.5	+25.6	+6.4	+4.8
60	+11.6	+13.2	+35.4	+1.4	+3.3
70	+15.6	+10.2	+36.9	+6.3	+8.7
80	+21.2	+8.6	+31.1	+11.2	+11.6
90	+13.8	+12.8	+35.8	—	+17.6

REFERENCES

HARDY, A. C. AND R. BAINBRIDGE

1951. Effect of pressure on the behavior of decapod larvae (Crustacea).
Nature, 167 (4244): 354-355.

KNIGHT-JONES, E. W. AND S. Z. QUASIM

1955. Response of some marine plankton animals to change in hydrostatic pressure. Nature, 175: 941-942.

MOORE, H. B.

1953. Plankton of the Florida Current. II. Siphonophora. Bull. Mar. Sci. Gulf and Caribbean, 2 (4): 559-573.

1955. Variations in temperature and light response within a plankton population. Biol. Bull., 108 (2): 175-181.

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.

ROANE, D. C.

1954. A study of some siphonophores of the Florida Current. Thesis for Masterate of the University of Miami, 1-77.