BIOLOGICAL BOARD OF CANADA

MANUSCRIPT REPORTS OF THE BIOLOGICAL STATIONS

No. 89

Title

The correlation between light intensity and the bathymetric distribution of marine copepods.

Author

Emma C. Odell

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Introduction

For some time the movements of pelagic organisms has been a subject for much discussion and it has been realized that these migrations are not merely a matter of chance but are controlled by definite factors of the environment. Much interest has been shown of late years in the movements of the planktonic forms, not only from an experimental standpoint but with a view to an economic application as well, since plankton constitutes the bulk of the material upon which most fish feed. Plankton is found at different depths of the sea at different times of the day. What is the cause of this phenomenon? Is it due to temperature change? Is it mechanical stimulus? Is it a reaction to light or is it a seeking after food that causes these organisms to migrate vertically in the sea?

For a number of years it has been understood that light plays an important part in the movements of pelagic organisms. Weismann (1877) believed "that light determined the upward and downward migration of pelagic animals and that most animals, being adapted to light of medium intensity retreated from the surface when the light increased and moved upward when it diminished." Chun (1877) maintained that temperature changes were responsible for daily migrations.

Groom and Loeb (1890), although they did "not deny the influence of temperature, concluded that light, not heat, was the chief factor in controlling migrations."

Loeb (1893) declares that many organisms "migrate periodically in a vertical direction, coming up to the surface during the night and going downwards during the day, but not deeper than 400 meters." Below this depth the intensity of the light is so small as to be negligible. The question then arises: what determines this periodic vertical migration? Loeb says that it is determined, to a certain extent at least, by the light. Animals negative to lights of high intensities descend until they reach a depth where the light is of a proper intensity; as the light conditions change (i. e. the intensity becomes less) they change their reaction (become positive) and migrate again towards the surface and the light. Hence there is a continual migration corresponding to the changes of light intensity. He also shows that temperature change has an influence on depth migrations and that animals which in winter are at the surface at night, in summer always remain at a certain depth below the surface.

G. H. Parker (1902) experimented at Woods Hole with Labidocera aestiva, one of the commonest summer copepods of that region. He says "that daily migrations of pelagic animals is not the result of as simple a combination of circumstances as was supposed, and further, what may be effective in bringing about migrations in one species may not in another. So far as the few copepods that have been studied are concerned, the chief factor seems to be light, although reaction to gravity has not been shown to be without influence, and heat and density of the sea water may play subordinate parts." Parker found that when Labidocera were put into an aquarium of sea water and placed near a window the animals separated into two distinct groups; the females frequented the top of the water at the light side of the jar and the males were distributed more or less uniformly throughout the aquarium. The question then arose as to whether the females were positively phototropic or negatively geotropic. He found that they remained at the surface in total darkness; he also proved that it was not oxygen that they were seeking, so he concluded that they were negatively geotropic. He found that they collected at the light side of the jar-hence were positively phototropic as well. He believes that the males are slightly negatively geotropic.

Parker found that although male Labidocera distributed themselves fairly evenly in the light the majority of them were found at the side of the jar away from the light, i.e. were slightly negatively phototropic. He also discovered that it was quite easy to drive male Labidocera horizontally across the jar by means of changing the position of the light, but it was impossible to drive them up and down through the water. Hence slight as the nagative geotropism of the male is, it is more effective than its phototropism. This might give the impression that the female Labidocera is found always at the surface of the sea instead of down in the daytime and up at night as is the case with copepods. The explanation is that there is a difference in their phototropisms when lights of different intensities are used. Parker found that the females are positive to lights of low intensities and negative to lights of high intensities; while the males are slightly negative to all intensities.

Parker uses artificial illumination (electric bulbs) and gives the measurement in candle power.

This paper is a discussion of copepods and light intensities: the relationship between them with respect to distribution. This problem was suggested by Dr. Huntsman who became interested in this particular phase of it during a visit to Bermuda where he had the opportunity of observing the influence of light (particularly moonlight) on the so-called "fire-worms" of the locality. These organisms are phosphorescent and are evidently very sensitive to light since they appeared and glowed at the surface of the water in the evening when the sun was down and the moon was not yet above the horizon at the exact moment when Dr. Huntsman could not read his watch. This is the only indication of the light value that Dr. Huntsman has. Evidently these "fire-worms" are strongly negatively phototropic since even moonlight drives them away from the surface. It was considered advisable to endeavor to find out in what way the reactions of the more northern planktonic forms were related to this. Copepods were selected as the subject for experimentation.

The copepods used were from a horizontal tow at a depth of from 18 to 20 meters taken at Prince Stations 5 and 6, Atlantic Biological Station, St. Andrews, New Brunswick. A surface tow was also taken at the same time and served as an indication of the difference in numbers. Tows were taken on dark nights and tows taken on moonlight nights were observed, the greater number of animals being found in the dark night tows.

The tows were brought to the laboratory in large glass containers; the copepods were immediately isolated as to genera and species and transferred in groups of ten to smaller glass jars containing sea water at sea temperature. These jars were kept cool by storing in a 0° chamber. Care was taken to use fresh normal specimens as much as possible.

Apparatus

Three different copepods were used: Calanus finmarchicus, Tortanus discaudatus, and Eurytemora herdmani. The apparatus concerned consisted of a glass cylinder approximately 40 cm. in length and open at one end. This was blackened (leaving a strip along the side through which to observe the copepods) and was marked off in centimeters. This cylindrical jar was filled with sea water and slipped through an opening in the top of a light-proof box so that the jar stood up-right. This box had one side open and covered with a black curtain made of several thicknesses of black sateen, which could be wound around the observer's head and shoulders and quite successfully excluded the light while the readings were being taken.

The idea was to observe the copepods under as normal conditions as possible in this miniature ocean. The first thing necessary to do was to devise some means of keeping the temperature of the sea water constant. This was accomplished by means of a galvanized and copper ice-container which fitted around the cylindrical jar. The light-proof box rested on a frame of convenient height. The top of the jar was covered with a piece of glass of the same thickness as the bottom. It was found necessary to do this because the source of light had to be changed from the top to the bottom and since it had to pass through the glass bottom of the cylinder, glass was added to the top also, in order to make the lights comparable.

Procedure

Ten copepods were used in each experiment and they were subjected to three different conditions of illumination: that of sunlight, skylight and moonlight. In the cases of sunlight and skylight natural light was used; for moonlight, an artificial moon was made from an electric light bulb.

The apparatus was first set up under skylight conditions, the jar was filled with sea water and the copepods introduced at the top; i.e. zero centimeters. The apparatus was tilted toward the light in each case so that the light passed straight down the cylinder. The angle of inclination was ascertained by means of a goniometer measurement of the sun's rays as shown by the diaphragm system of the pyrheliometer. The readings were taken at 5 minute intervals and the distribution of the copepods recorded. The intensity of the light was measured in each case with a Drem Photometer which was calibrated against the pyrheliometer, the Neutral Wedge, and the Ecological Photometer. After the experiment was completed in the skylight the apparatus was moved to the sunlight and thence to moonlight. The gradient curves for the sunlight and skylight conditions were obtained by readings made with the Spectrophotometer and under as nearly the same light conditions as possible.

The accompanying sets of curves- two for each of the three species of copepods- show in graphic form the distribution of the animals with relation to light intensities. Let the abscissa represent the depth of the cylindrical jar. It is marked off in centimeters, 0- 42, the top and bottom of the jar, respectively. The left hand ordinate represents percentage light values and the right hand ordinate, percentage distribution of copepods. The unbroken line is the curve of the gradient of light under sunlight conditions. This was obtained by averaging the Drem Photometer readings for the ten experiments, then taking the

Spectrophotometer readings in terms of this Drem reading and reducing them to a percentage basis. The broken line (thus,-..-..-) is the sky curve and was obtained in the same way. The distribution of animals for these two light conditions is shown (on separate graphs) by the dotted line (thus. . . . .) The animal curve was obtained by dividing the jar into five sections, counting the number of copepods in each section, adding together the results for the ten experiments and reducing to a percentage basis.

Taking these sets of curves in groups of two- one species under the two light conditions- the graphs show quite clearly that the relationship between light intensity and the distribution of copepods is one of reciprocals; the greater the light intensity, as represented by the greater area bounded by the sun curve, the smaller the area of the jar occupied by the copepods. The lower the light intensity, as represented by the area bounded by the sky curve, the greater the area of the jar occupied by the copepods. i.e. the lower the light intensity the less negatively phototropic are the copepods. The same relationship obtains in the sets of curves for Tortanus and Eurytemora.

The accompanying tables- two for each of the three species of copepods show numerically the distribution of the copepods in the ten experiments. A, B, C, D, and E represent the divisions of the jar. The light value for the experiments are given in Drem Photometer readings in terms of A (the darkest screen).

These results indicate that all three copepods are negatively phototropic to the intensities of light used. Calanus gives the most definite reaction and is easily the most readily affected by light. When it was noticed that the copepods distributed themselves so persistently toward the bottom of the jar the question arose: is it because they retreat from the light or is it some other factor (e.g. gravity) that is keeping them down? The apparatus was then rearranged so that the jar rested on the bottom of the light-proof box and a hole the size of the bottom of the cylinder was cut in it. A false bottom was arranged which could be slipped in and out at will. A light-proof cover was placed over the top of the cylinder, the false bottom was then removed and the light focused by means of mirrors on the bottom of the cylinder. It was found that both Calanus and Eurytemora could be driven away from the light- Calanus again giving the most definite reaction; they moved immediately to the dark end of the jar and were found at the surface of the water. Eurytemora retreated from the source of light but did not go to the surface of the water. They would move upwards until they reached a point where the light was of a sufficiently low intensity to be comfortable, so to speak, or approximately half way up the jar (20 cm.) and would then distribute themselves fairly evenly over the dark half. Thus we can quite safely conclude that neither Calanus nor Eurytemora are geotropic.

In the case of Tortanus, however, the copepods persisted in staying in the lower part of the jar whether the light was admitted from the top or from the bottom. In a horizontal box which allowed the light to enter at one end and where the geotropic force was practically nil, Tortanus sought the light end. Thus it would seem that Tortanus are both positively geotropic and positively phototropic. Their distribution in the sea is probably a balance between the two.

Low Intensity Experiments.

In the experiments carried on with lights of low intensities, of which moonlight was taken as an example, the apparatus was set up in a dark room in the basement of the laboratory. The jar was filled with sea water and the copepods introduced at the top, as before. First, the distribution in total darkness was determined. Observations made by flashing an electric light on the cylinder showed the distribution to be thus:

Calanus- evenly distributed throughout cylinder.

Tortanus- all at the bottom.

Eurytemora- evenly distributed throughout cylinder.

An artificial moon was constructed by cutting down the light from a 25 watt bulb with parchment paper and a green gelatin filter until it approached moonlight. The light from this moon was measured at a height of one foot above the top of the jar with the Ecological Photometer and was found to be .00011% full noon June sunlight. A Photometer measurement of actual moonlight showed it to be .00018% full noon June sunlight.

The spectral quality of actual moonlight is mostly green, with blue, orange and a bit of red. The spectral quality of the artificial moon showed more green than real moonlight, along with blue, orange, and a bit of red. That is, the green quality of real moonlight was emphasized in the artificial moon.

This moon was arranged so that it could be shifted to different heights above the cylinder and thus different light intensities could be obtained. Heights of ½ foot, 1 foot, 2 feet, and 4 feet were used so that the Inverse Square Law would apply. The idea was to get the lowest intensity of light that would drive the copepods definitely down in the jar. Under the influence of light of lower intensities than this, the animals were found to become evenly distributed. Hence we can assume that this fact accounts for their coming up nearer the surface at night. It is more of a case of free will to go where they please rather than a rise toward the light.

The following tables show the results with low intensities.

CALANUS.

Ht. of moon	Light Value (F.N.J.S)	Effect
4 ft.	.0000068%	none- even distribution
3 ft.	.000012%	none- even distribution
2 ft.	.000027%	animals definitely down.

That is, the lowest light intensity that drives Calanus definitely down is .000027% full noon June sunlight , or very near this value.

Tortanus.

Ht. of Moon	Light Value (F.N.J.S)	Effect
4 ft.	.0000068%	none- even distribution
2 ft.	.000027%	animals near surface
1 ft.	.00011%	animals lower in cylinder
½ ft.	.00044%	animals at bottom

Thus for Tortanus the lowest light intensity that drives them definitely down is between .00011% and .00044% full noon June sunlight.

The artificial moon had no effect on Eurytemora- it was of too low an intensity. It was found necessary to use a 100 watt Tungsten bulb (light value .3% full noon June sunlight).

Eurytemora.

Ht. of lamp	Light Value (F.N.J.S.)	Effect
2 ft.	.075%	none- even distribution
1 ft.	.3%	animals lower in jar
$\frac{1}{2}$ ft.	1.2%	animals definitely down

With low intensities as with sunlight and skylight, Calanus gave the most definite reaction. They, as compared with the other species, were responsive to the lowest intensity of light. Of the three species, Eurytemora required the greatest intensity of light to bring about a reaction. The above results also show that Tortanus, which is both positively phototropic and positively geotropic, rise to the surface in lights of low intensities; i.e. with low intensities, their phototropism is stronger than their geotropism.

We have-

Calanus driven definitely down by light of .000027% F.N.J.S.

Tortanus driven definitely down by light of .00044% F.N.J.S.

Eurytemora driven definitely down by light of 1.2% F.N.J.S.

Actual moonlight is .00018% F.N.J.S. Hence from the above results we would expect to find both Tortanus and Eurytemora quite near the surface of the water under moonlight conditions, and very few, if any, Calanus.

Summary

1. In the three species under experimentation, the relationship between light intensity and the distribution of the copepods is one of reciprocals: the greater the light intensity the more negatively phototropic are the copepods; and conversely, the lower the light intensity the less negatively phototropic are the copepods.

2. Of the three species Calanus gives the most definite reaction and is easily the most readily affected by all intensities of light. It is strongly negatively phototropic.

3. Eurytemora is also negatively phototropic but not to the same degree as Calanus.

4. Tortanus is both positively phototropic and positively geotropic. Under the influence of light of high intensities it acts as though it were negatively phototropic. This is due to the geotropic force exerting its influence. Under lights of low intensities the phototropism of Tortanus is the stronger of the two forces, since Tortanus rises to the surface under weak lights.

5. Neither Calanus nor Eurytemora are geotropic.

6. Neither Tortanus nor Eurytemora are affected to any great extent by moonlight- Calanus is.

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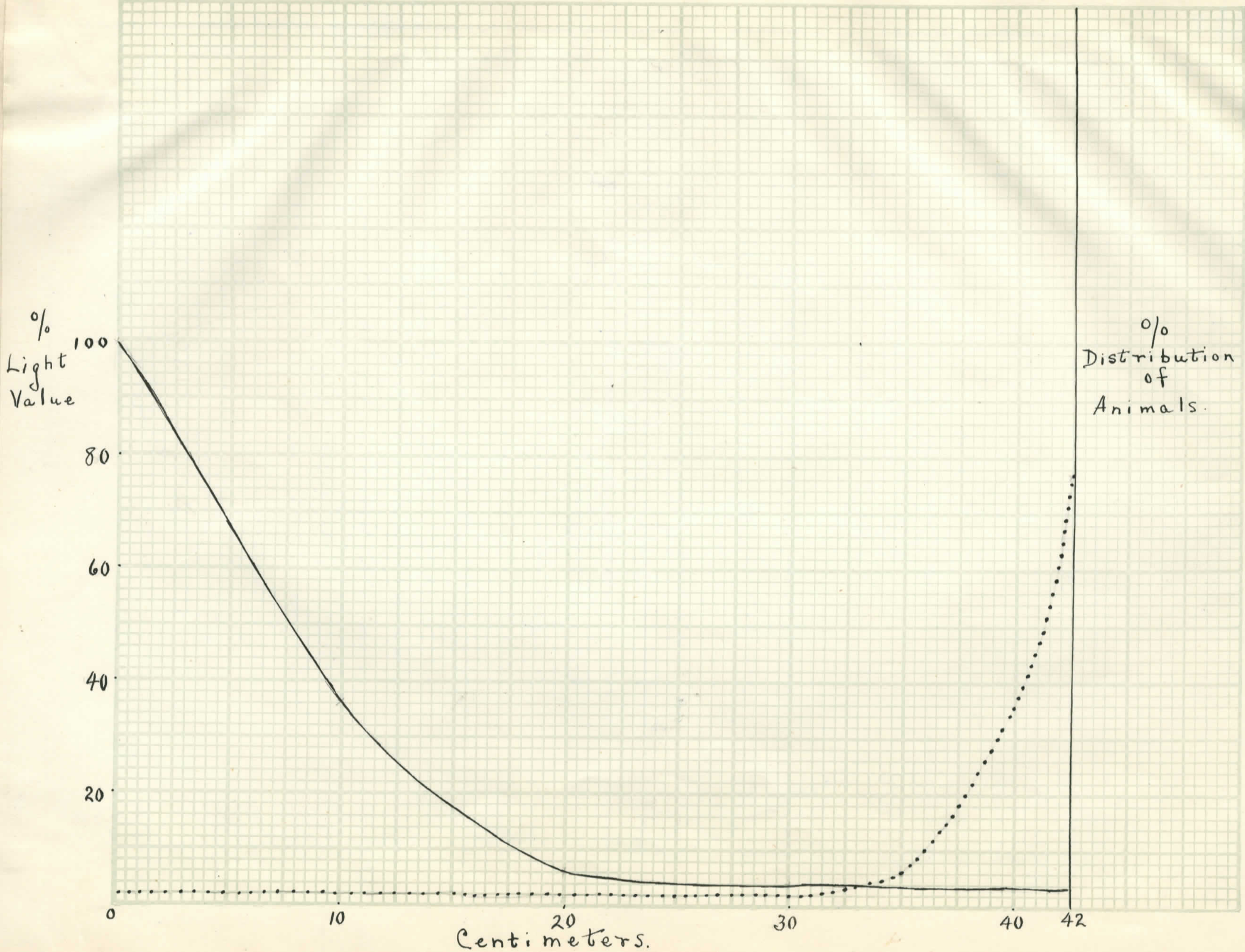
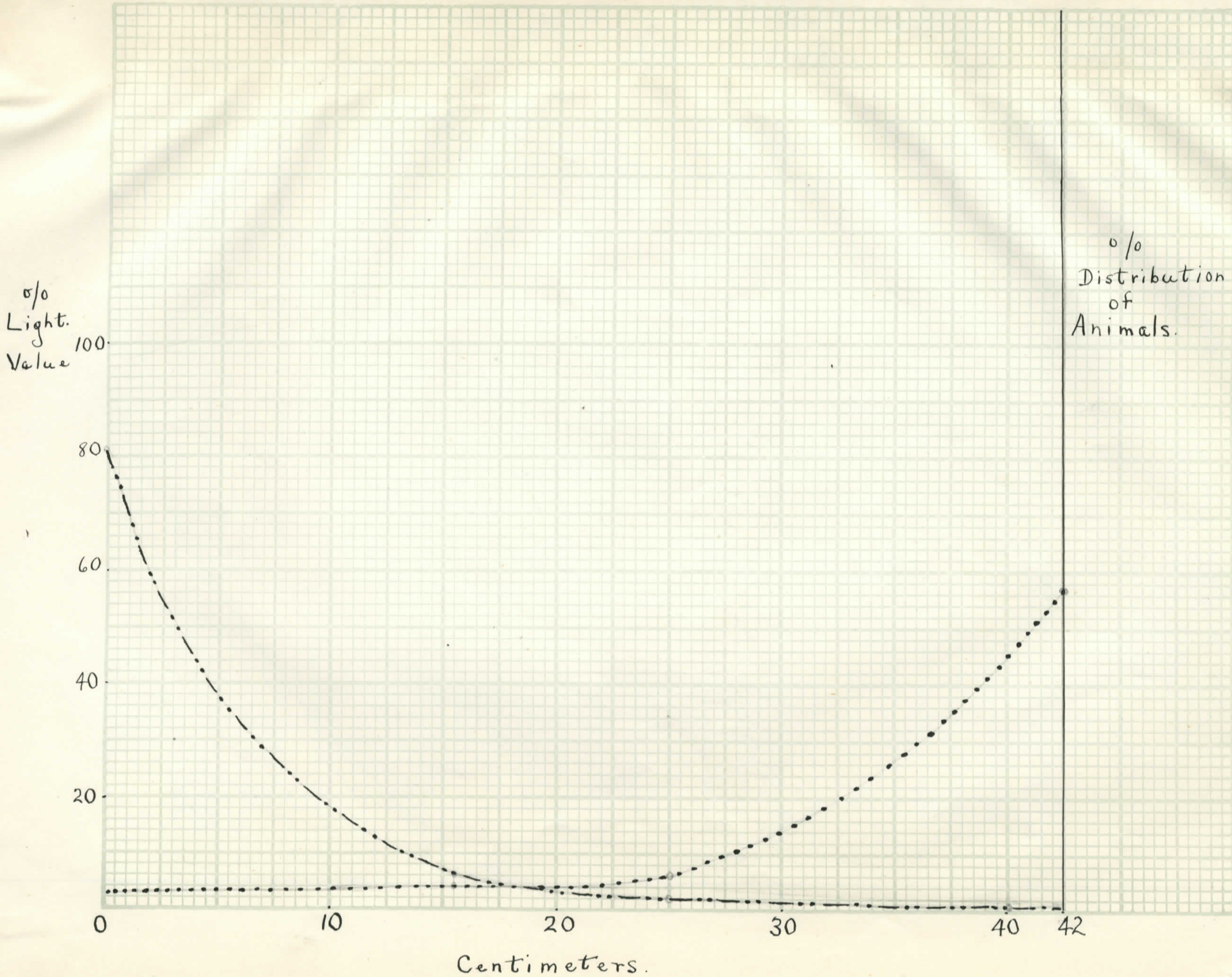
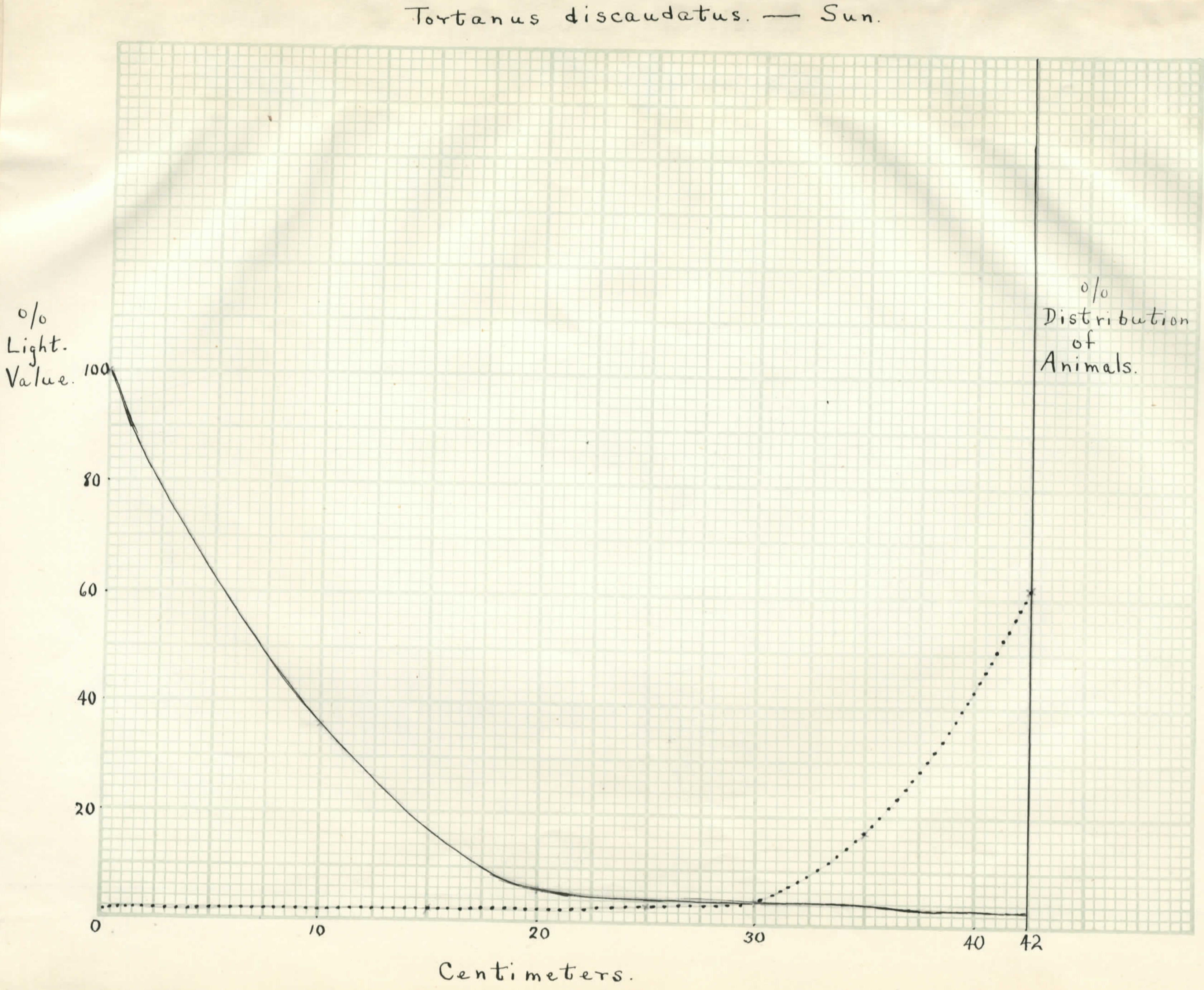
Calanus finmarchicus — Sun.

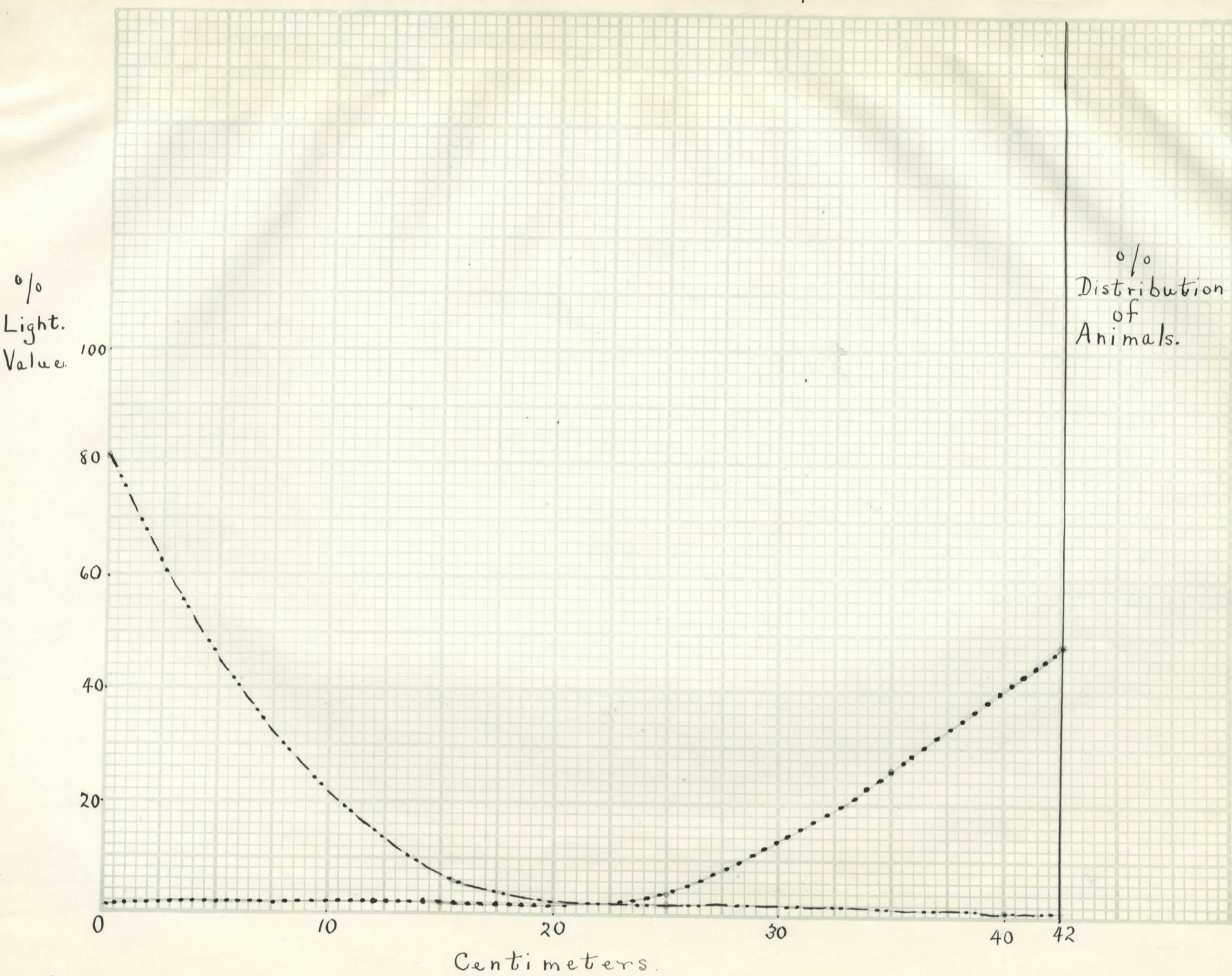


Calanus finmarchicus - Sky.

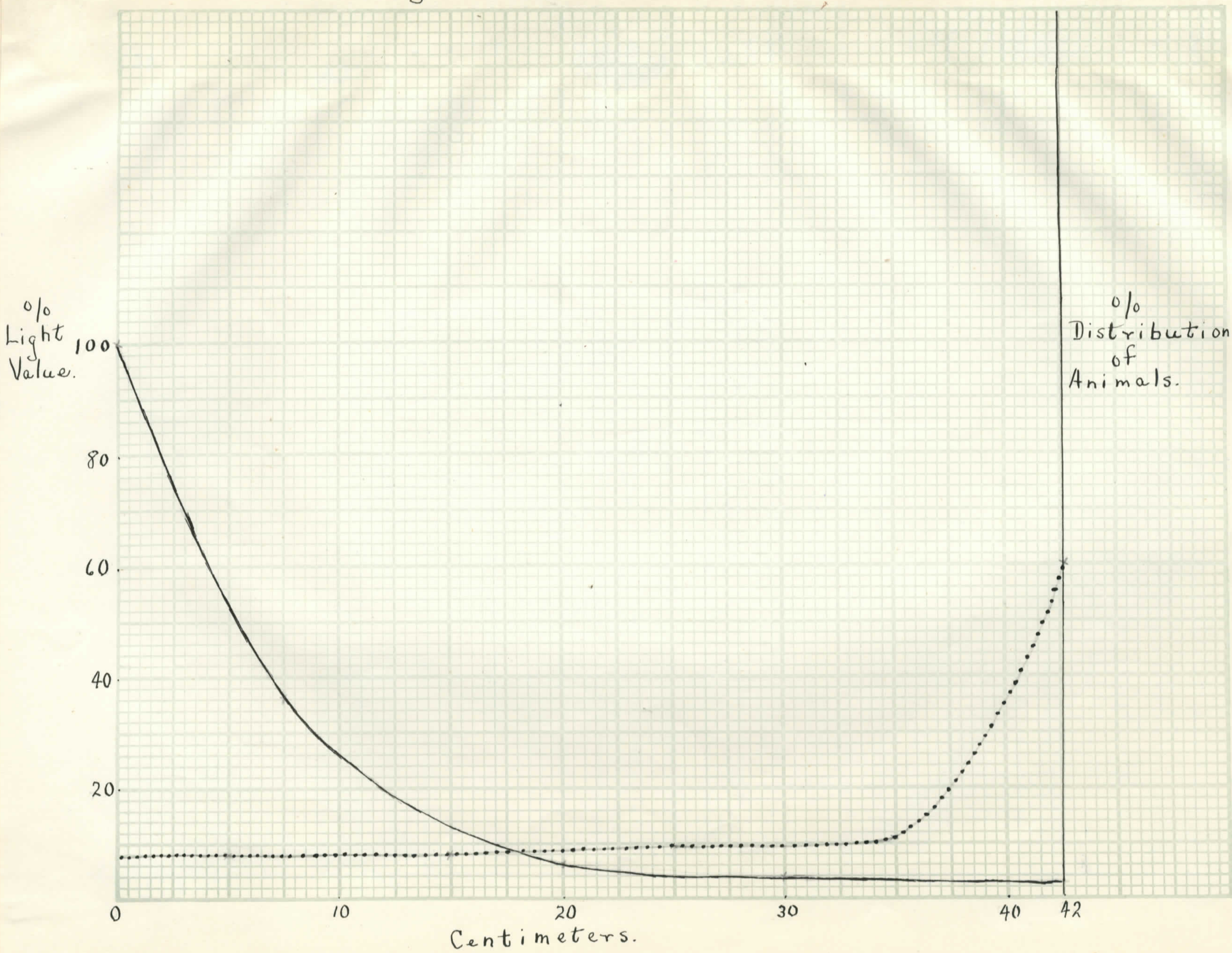


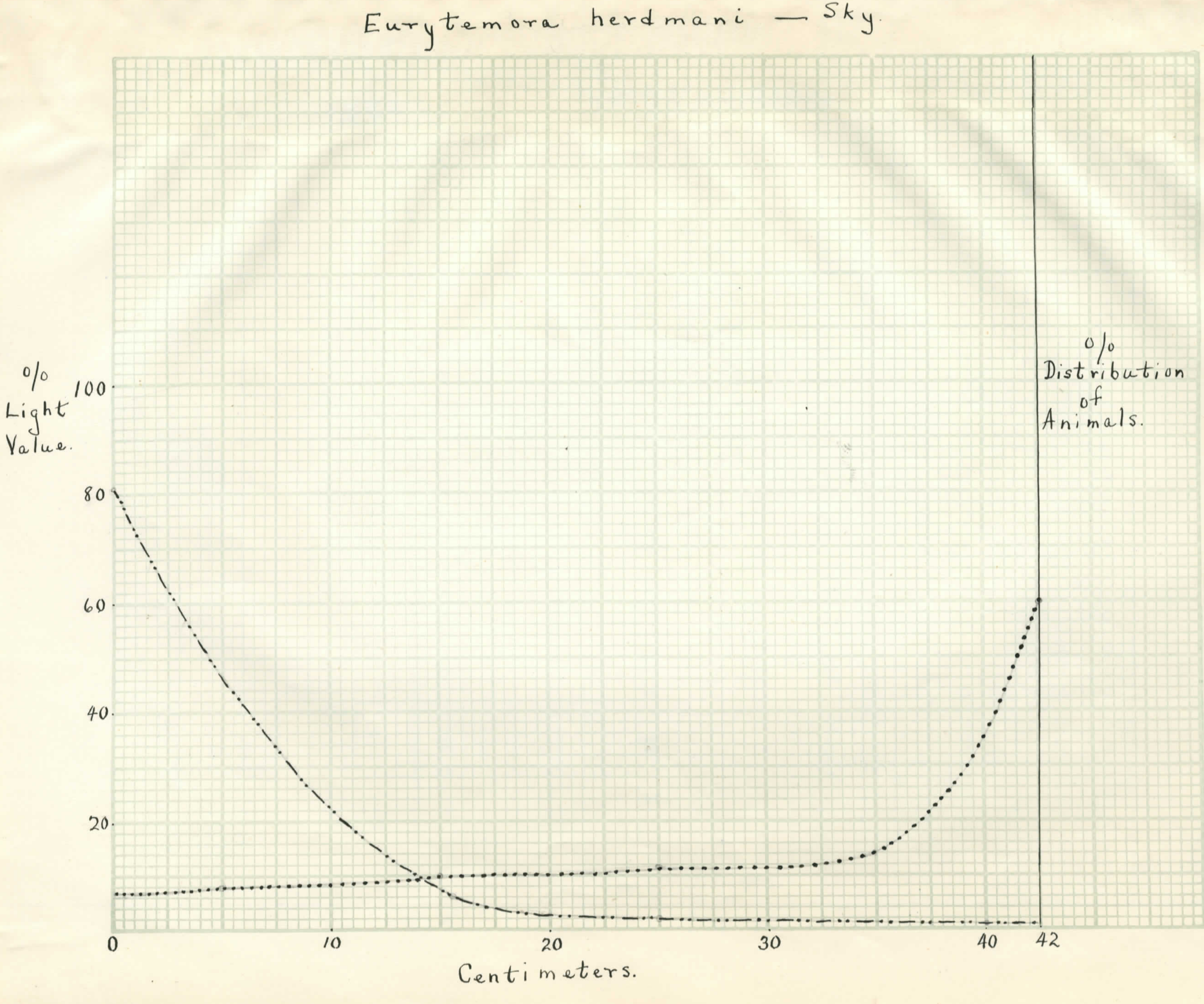

Tortanus discaudatus. — Sun.
③
%
Light.
Value.
100
80
60
40
20
0
10
20
30
40
42
Centimeters.
%
Distribution
of
Animals.

Tortanus discaudatus — Sky.



Eurytemora herdmani – Sun.




Eurytemora herdmani — Sky.
%
Light
Value.
100
80
60
40
20
%
Distribution
of
Animals.
0
10
20
30
40
42
Centimeters.

Calanus finmarchicus

Sky

cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A		1		3		2	2		1	1
10-20	B							1			
20-30	C		1				1	1		1	
30-38	D	2	2		1	4	1		1	1	1
38-42	E	8	6	10	6	6	6	6	9	7	8
Light Value Drem Reading		A=5	A=9	A7.5	A7	A7	A9	A9	A10	A7.5	A7

Calanus finmarchicus

Sun

cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A	2	1		1		2				
10-20	B		1		1						
20-30	C	1			1						
30-38	D	1	1	1		2		1			
38-42	E	6	7	9	7	8	8	9	10	10	10
Light Value Drem Reading		A7.5	A7.5	A17	A10	A11	A10	A11	A12	A12	A23

Tortanus discaudatus

Sky

cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A	6			2			1			
10-20	B	1			2						
20-30	C	1			2	2					
30-38	D	2	2	3		1				1	2
38-42	E		8	7	4	7	8	9	10	9	8
Light Value Drem Reading		A5	A4.8	A8	A7	A9	A7	A6.3	A9	A5	A10

Tortanus discaudatus

Sun

cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A	4			1						
10-20	B	1									
20 -30	C	2			1	1					
30-38	D	2				3		2			1
38-42	E	1	10	10	8	6	10	8	10	10	9
Light Value Drem Reading		A5	A7	A9	A7	A7	A16	A16	A13	A23	A12

Eurytemora herdmani

Sky

cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A		3			1	1	1		1	
10-20	B	1				2	2			2	1
20-30	C	1		1	1	1		1		1	2
30-38	D	4	1	3	1			1	3	1	
38-42	E	4	6	6	8	6	7	7	7	5	7
Light Value Drem Reading		A6.3	A5	A7	A9.5	A7.5	A7.5	A8	A7	A7	A7.5

Eurytemora herdmani

Sun

Cm.		I	II	III	IV	V	VI	VII	VIII	IX	X
0 -10	A					1		1	1	1	4
10-20	B					1	2	2	1	1	2
20-30	C	1	1	2	1		1	1	2	1	
30-38	D	2	1	1	1	2	1	1		1	1
38-42	E	7	8	7	8	6	6	5	6	6	3
Light Value Drem readings		A6.3	A7	A8	A9.5	A7.5	A9	A6.3	A8	A8	A8