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Studies on the Biology of Planktonic Coelenterates

by
Mary Needler Arai

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INTRODUCTION

In many fiords, such as the Alberni Canal, a sharp discontinuity is present between the upper water of low salinity and the lower water of a salinity closer to sea water. Where large amounts of pulpmill effluent are added, oxygen production even in the surface water is very low due to lack of light penetration. It is therefore important to determine what organisms brought into the inlet with the more saline water are using oxygen and in what amounts. It is also necessary to determine the distribution of these animals with reference to the water layers and any behaviour patterns tending to cause their aggregation.

The 1970 survey of plankton in the Alberni Canal indicated the presence of various hydromedusae and ctenophores including Aequorea, Sarsia, Phialidium, Aglantha, Rathkea, Eutonina and Pleurobrachia. Sarsia, Phialidium and Pleurobrachia were particularly abundant and have therefore been most extensively investigated in the present series of studies.

The research in the summer of 1972 has taken two main directions which will be included in this report. 1. Observations on the behaviour of coelenterates with reference to discontinuity layers. 2. Measurements of oxygen consumption of hydromedusae. Preliminary exploration was also made of the kinds of biological information on coelenterates which can be derived from plankton hauls carried out by other members of the Environmental Research Group in connection with productivity studies. A note on the biology of Aglantha digitale (O.F. Müller) coauthored with Mr. John Fulton will be published separately.

BEHAVIOUR OF COELENTERATES IN SALINITY DISCONTINUITY LAYERS

Introduction

Hansen (1951) showed by June hauls in Oslo fiord that Aglantha digitale occurred below the discontinuity layer with the layer as the upper boundary but that Sarsia tubulosa occurred only in or near the discontinuity layer. Harder (1952, 1954, 1957, 1968), Lance (1962) and Regan (1968) investigated the reaction of a variety of planktonic animals to discontinuity layers in experimental chambers. The only information on coelenterates included is a single experiment on Pleurobrachia pileus in which it was found to aggregate at an interface between 29.5‰ and 33.6‰ salinity water. The behaviour of Sarsia tubulosa, Phialidium gregarium, Pleurobrachia pileus and Aurelia aurita was therefore investigated in a chamber similar to Harder's in which the salinity was varied.

MATERIALS AND METHODS

Animals

Sarsia tubulosa (M. Sars, 1835), Phialidium gregarium (L. Agassiz, 1862), Aurelia aurita (Linnaeus, 1758) and Pleurobrachia pileus (O.F. Muller, 1776) were collected from Departure Bay, Vancouver Island.

The taxonomy of Pleurobrachia in western North American waters is controversial. Pleurobrachia bachei Agassiz was described by Agassiz (1860) from specimens obtained from the Gulf of Georgia. It was described from California by Torrey (1904). It has been considered by some authors to be a variety of the well known Pleurobrachia pileus (O.F. Muller) (Moser, 1909; Bigelow, 1912; Mayer, 1912) although this is disputed by Mortensen (1912). In the present paper Bigelow (1912) will be followed in considering the form as a variety of Pleurobrachia pileus. Since Bigelow eroneously ascribed the original description of P. pileus to Fabricius, his designation should be modified to Pleurobrachia pileus (O.F. Muller) var. bachei Agassiz.

All animals were dipped from the surface layers of water using small beakers or glass jars. They were immediately transferred to jars or cylinders containing sea water of the desired salinity and placed in a laboratory cooler. Sarsia tubulosa was fed frozen euphausids broken into small pieces. Aurelia aurita, Pleurobrachia pileus and Phialidium gregarium were fed young stages of Artemia salina.

In order to standardize, in as much as possible, the previous history of the animals, they were held for at least 3 days in a standard salinity and temperature. Surface salinities in which animals were caught varied from 23.0‰ to 25.8‰ for Sarsia tubulosa, 14.4‰ to 23.6‰ for Pleurobrachia pileus, 19.2‰ to 24.8‰ for Phialidium gregarium and 22.5‰ for Aurelia aurita. However, the sea water supply of the station with an intake approximately 60' below the surface varied from 26.5‰ to 28.5‰ during the same period. Similarly surface temperatures (all daytime) varied from 12.0°C to 15.0°C for Sarsia tubulosa, 14.5°C to 20.5°C for Pleurobrachia pileus, 12.2°C to 17.5°C for Phialidium gregarium and 14.0°C to 14.5°C for Aurelia aurita. As it was not known what portion of the water column the animals caught at the surface might have previously occupied an arbitrary temperature and salinity was chosen for holding. S. tubulosa was held and tested at 10°C, the other three species were held and tested at 13°C. All animals were held in 25.0‰ salinity except a series of P. pileus held at 20.0‰ for comparison of the effect of this salinity.

Sea water

Filtered sea water was obtained from the sea water system of the Pacific Biological Station, Nanaimo, the inflow of which is approximately 60' below the surface. As noted above, this supply varied from 26.5‰ - 28.5‰ salinity during the summer. It was diluted as required by distilled water with a specific resistance of less than 0.5 megohms. For routine mixing, salinity measurements were made with hydrometers. These hydrometers had been

calibrated in a series of sea water dilutions which had themselves been calibrated against standard sea water chlorinity 19.3755‰ using the lower precision titration method of Strickland and Parsons (1968). The salinity determinations of sea water dilutions used in the experiments were found to be accurate to better than 0.1‰ of salinity. Due to variation in the sea water supply as above and other technical difficulties, it was however sometimes necessary to use a wider range of salinities in what should ideally have been duplicate experiments. Where such variation occurs it is clearly stated on the graphs--note for example that the lowest layer used in the two experiments on Pleurobrachia pileus in the Regan chamber was 27.2‰ in one experiment and 27.4‰ in the other (Fig. 7).

Experimental chambers

The chamber used for most experiments was similar to that described by Harder (1952a, 1968) Fig. 1. Two 2-litre cylinders were used to contain the animals, one containing the experimental salinity (usually a discontinuity layer) and one acting as a control (usually with a homogeneous solution). These were separately enclosed in two chambers of a black painted wooden box through which water could be run from an attached Forma Scientific Model 70 cooler. Each chamber had a glass front through which the cylinders could be observed. The box had a hinged lid including a fluorescent light above frosted glass.

In establishing a discontinuity layer in one of the cylinders, the higher salinity water was first poured into the cylinder to 1000 ml. A disc was then floated on the surface of the water which supported the end of some flexible plastic tubing attached to a separatory funnel (Fig. 2). The tubing passed down through the outer edge of the disc and then curved upwards to an outflow in the center of the upper side of the disc. Water could thus be delivered at a rate controlled by the separatory funnel and was spread out by the disc to add to the water column with a minimum amount of turbulence. As shown by experiments using methylene blue dye, a very sharp interface could be so formed and was found to be stable for periods of several hours. If animals were introduced passage of these animals through the interface occasionally produced some mixing. The maximum such mixing seen was approximately 40 cc, i.e. a vertical distance of approximately 18 mm.

A larger cylinder was borrowed from Dr. L. Regan in which multiple salinity layers could be established (see Regan 1968). This chamber did not incorporate a control cylinder.

Experimental procedure

Usually each cylinder was filled to close to the 1900 cc line as described above, the discontinuity, if present, being at the 1000 cc line. Five animals were then placed in each cylinder, being transferred with as little accompanying water as possible in a 5 cc beaker attached to a glass rod (Fig. 2B) and the water level was adjusted precisely. In cases where the lower portion of the column was filled with a salinity higher than that in which the animals had been held, the animals were added to this water before

the 1000 cc line was reached and then the column filled. Unless otherwise stated the room was darkened with black curtains, and the overhead light of the chamber turned on.

The position of the animals (top of the bell in the medusae, top of the body in Pleurobrachia) was recorded at five minute intervals for one hour. In order to allow the animals to recover from the transfer, the data presented is that collected in the second half hour of recording. Unless otherwise stated each experiment was run twice. The animals used in each experiment were fixed in 10% formalin neutralized with an excess of magnesium carbonate.

RESULTS

Sarsia tubulosa

The first animal examined was Sarsia tubulosa. It was found that this animal is strongly attracted to light as noted by Romanes (1885). When animals were placed in a cylinder of 24.4‰ salinity water as a control they were found to aggregate at the top of the column (Fig. 3), i.e. toward the overhead light.

The animals were then placed in cylinders with three types of discontinuity layers (Fig. 3). When 19.9-20.4‰ water was placed over 24.4‰ the animals aggregated at the discontinuity layer and did not penetrate into the upper less saline portions of the column (Fig. 3A). When the upper layer is made slightly more saline (i.e. the ΔS is reduced to $1.7 \pm .1$‰) the animals became distributed between the discontinuity layer and the top of the column (Fig. 3B). When 24.4‰ water is placed over more saline water (28.3-28.6‰) the animals again aggregate at the discontinuity layer and the top of the column (Fig. 3C).

It is obvious in the case shown in Fig. 3C that the aggregation of the interface represents a preference for the interface since there is no possible density barrier between the interface and the top of the column where it aggregates in a homogeneous column of the same water. However when the upper portion of the column is less saline as in Fig. 3A, it seemed possible that the less saline water was acting as a barrier above which the animal was physically unable to rise. This impression was strengthened when the animals were found to go to the bottom of a homogeneous 19.9‰ column and to the top in a homogeneous 28.0‰ column (Fig. 4). However, when sucrose was added to 15‰ to give a density equal to that of 19.9‰ the animals were now able to aggregate at the top of the column, i.e. the aggregation at the interface rather than the surface is not due to an inability to reach the surface.

Harder (1968) had attempted to distinguish between salinity gradients per se and density gradients by adding sucrose to various sea water dilutions to adjust density. In the present experiments however sucrose caused changes in behaviour of S. tubulosa in homogeneous control columns as noted above so this approach was dropped.

During the experiments on Sarsia, records were kept not only of the position of each animal but also of its behaviour. Each animal was rated as swimming (involving pulsation of the bell, usually associated with movement of the manubrium and somewhat shortened tentacles), fishing (with tentacles directed to the side and then bending vertically downward and extended), floating (mid-water, neither swimming or fishing), or sitting on the bottom. Animals when first placed in the columns occasionally exhibited the "crumple" reaction described by Hyman (1940) and Mackie and Passano (1968), but this never occurred in the second half hour of the experiments. The results of this analysis are shown in Table I. It may be noted that in homogeneous columns the amount of swimming increased with increased salinity. Also the amount of fishing activity was markedly increased in any column including a discontinuity layer compared with any of the homogeneous columns.

Table I. Percentage Sarsia tubulosa involved in various activities (second half hour each experiment.

Salinity	Swimming	Fishing	Floating	Sitting on Bottom	No. Expts.
19.9‰	3.3	.8	7.5	88.3	4
24.4-24.7‰	29.7	56.1	14.2	0	8
28.0‰	61.6	25	13.3	0	2
19.9-20.4/24.4‰	8.3	91.7	0	0	2
22.9-23.1/24.7‰	5	78.3	16.7	0	2
24.4/28.3-28.6‰	3.3	90	6.7	0	2
15.0‰ + Sucrose to Density = 19.9‰	0	1.7	98.3	0	2

It should be noted that the above behavioural categories differ somewhat from the behaviour described by Agassiz (1849). The criteria for fishing were based on the description by Henschel (1935) of tentacle extension in response to "muscle juice." In the chambers, tentacle extension only occurred with the tentacles directed outwards and then bent down. Agassiz (1849) however describes the stretching of the tentacles sideways as a resting position involving a maximum tentacle extension of three times the diameter of the bell. He then describes a further state of relaxation in which the tentacles hang vertically and extend up to five times the diameter of the bell. In the present experiments, data on degree of tentacle extension was not kept but preliminary photographs were obtained of animals with tentacles extended up to 12 times the diameter of the bell and these still showed the tentacles extending sideways from the margin and then downward. The only occasions on which animals were seen with extended tentacles in a vertical position to the margin were when they began to swim from a fishing position.

Pleurobrachia pileus

In preliminary tests, when P. pileus, which had been held in 25‰, were placed in a control column of 25‰ they showed a tendency to aggregate at the top and bottom of the column whether the overhead light was turned on or not. In all definitive experiments, the overhead light was kept on to facilitate observation.

Three sets of experiments were then run in which the reactions of these animals to three types of discontinuity layers were tested (Fig. 5). In each case a column of 25.0‰ was used as a control. As noted above, the control columns showed aggregation at the top and bottom of the cylinder. When a layer of 20.0‰ was placed over 25.0‰, it was found that animals aggregated at the interface with little penetration into the upper portion of the column. This result corresponds with Harder's (1968) single observation on Pleurobrachia pileus. He used 29.5‰ over 33.1‰, i.e. ΔS of 3.6‰. That these show a true preference rather than a barrier is demonstrated by the lack of animals on the bottom of the cylinder in each case. When the salinity gradient was reduced to 23.0‰ over 25.0‰ there was still some tendency to remain at the interface; however, animals again showed a tendency to remain at the top or bottom of the column. Experiments were also run in which 25.0‰ water was placed over 27.8‰ (Fig. 5) and in homogeneous cylinders of 27.8‰ and 20.0‰ water (Fig. 6). In the former, animals aggregated in the upper half of the cylinder, above the 27.8‰ water, even when placed in the 27.8‰ water prior to addition of the 25.0‰. Surprisingly, the animals showed the same distribution in a homogeneous 27.8‰ column as in 25.0‰. In 20.0‰ they tended to sink to the bottom.

Animals were held in 20.0‰ water for 7-8 days and tested as above to see if the behaviour could be modified by prior history. As shown in Fig. 6, they still showed a tendency to sink to the bottom in 20.0‰. However, in 25.0‰ they tended to aggregate at the top of the column, and when 19.9‰ water was placed over 25.0‰, they largely aggregated in the upper half of the cylinder even though animals were added to the 25.0‰ water prior to addition of the 19.9‰. By comparison with the previous experiments with 25.0‰ held animals tested at these salinities, it can be seen that the 20.0‰ held animals have indeed changed in behaviour.

As a final experiment in this species, 20 animals at a time were placed in the Regan chamber which had been filled with layers of water of six salinities from 15.0‰ to 27.2-27.4‰. It can be seen (Fig. 7) that although animals previously held at 25.0‰ become distributed from 20.0‰ to 27.2‰, they show a strong tendency to aggregate at the interfaces.

Phialidium gregarium

A series of experiments similar to those carried out above were begun placing P. gregarium, previously held in 25.0‰, into cylinders with discontinuity layers, and in control cylinders of 25‰ (chamber light on). It soon became apparent that a great deal of variability was present in the control cylinders. It did not prove possible to remove this variation by

control of length of acclimation or of salinity of water from which the animals had been collected. In four experiments in which the animals had been collected from surface water salinity 24.5-24.8‰, acclimated for 4 days to 25.0‰, and tested in 25.0‰, one experiment resulted in approximately half the animals each at top and bottom of the cylinder, one experiment resulted in aggregation at the bottom of the cylinder, and two resulted in intermediate states. Similarly in three experiments in which the animals had been collected from surface water of 19.2‰, acclimated for 6-7 days to 25.0‰, and tested in 25.0‰, one experiment resulted in aggregation at the top of the cylinder, one experiment resulted in aggregation at the bottom of the cylinder and one showed approximately one half each at top and bottom of the cylinder. The experimental series was therefore terminated.

The few experiments on discontinuity layers run before the series was terminated indicate that the reaction of P. gregarium to discontinuity layers is also variable. Of 4 experiments in which 20.0‰ water was placed over 25.0 aggregation was seen in one case. Of 2 experiments in which 25.0‰ was placed over 28.0‰ aggregation also occurred in one case.

Aurelia aurita

One experiment (duplicated) was run on ephyrae of Aurelia aurita with a discontinuity layer of 20.0‰ over 25.0‰ and a control of 25.0‰. As shown in Figures 8 and 9, there was some aggregation at the discontinuity layer as well as the top and bottom of this column and the control column.

DISCUSSION

In the experiments described above, it was demonstrated that Sarsia tubulosa and Pleurobrachia pileus show preferences for salinity discontinuities of as little as 2‰. Phialidium gregarium is probably relatively unresponsive. It is less clear how such aggregation is accomplished. No distinction can yet be made between the effects of salinity per se and the effects of density.

A number of experiments have been carried out by other authors in which animals have been enclosed in chambers, the pressure varied and the reactions noted. Sarsia tubulosa has been shown to move toward a light source as pressure increases, and to decrease activity and sink as pressure decreases (Rice, 1964). Pleurobrachia pileus has been shown to move upward with pressure increase and actively downward with a pressure decrease as small as 50 millibars irrespective of light direction or absence (Knight-Jones and Quasim, 1955; Rice, 1964; Knight-Jones and Morgan, 1966; Digby, 1967). Phialidium hemisphaericum also moves upward with increased pressure and downward with decreased pressure (Knight-Jones and Quasim, 1955; Knight-Jones and Morgan, 1966; Digby, 1967). Such results may be correlated with (for example) the greater amount of swimming of S. tubulosa in more saline water.

However, it is very difficult to relate experiments on pressure per se to density discontinuities which represent changes in the gradient of pressure increase with depth.

Each of the species investigated is euryhaline and likely to encounter salinity discontinuity layers. Lindquist (1958) summarizes previous data indicating that Pleurobrachia pileus can survive in salinities as low as 6.5‰. It has been shown to penetrate into the mesohaline zones of the Weser estuary (Kuhl and Mann, 1969) and the Eider estuary (Kuhl and Mann, 1971) as did Sarsia tubulosa in the latter case. McCormick (1969a) found Phialidium gregarium in salinities of less than 9.9‰ in Yaquina Bay, Oregon.

The ecological advantage of aggregation in around a discontinuity layer may be the concentration of food organisms in the layer. Fraser (1970) summarizes his own and previous work indicating that Pleurobrachia are miscellaneous feeders but that crustacea, particularly copepods, are the dominant food. Lebour (1922) found that Sarsia tubulosa ate only copepods. McCormick (1969b) found the main constituent of the diet of Phialidium gregarium to also be copepods. Although not all copepods become concentrated in or near the discontinuity layers, a number of species do so (Hansen, 1951; Lance, 1962; Harder, 1952b, 1954, 1968).

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FIGURES

In each of the experiments using the Harder chamber the experiments run as controls are paired with the results from the experimental cylinder run simultaneously. The observations from two experiments are lumped, or if three experiments were run, these three are lumped and prorated. Observations of the position of 5 animals per cylinder were made every 5 minutes for an hour in each experiment. In the graphs the results for the last 30 minutes are recorded, i.e. each graph represents 2 experiments $\times$ 5 animals $\times$ 6 times of observation = 60 observations.

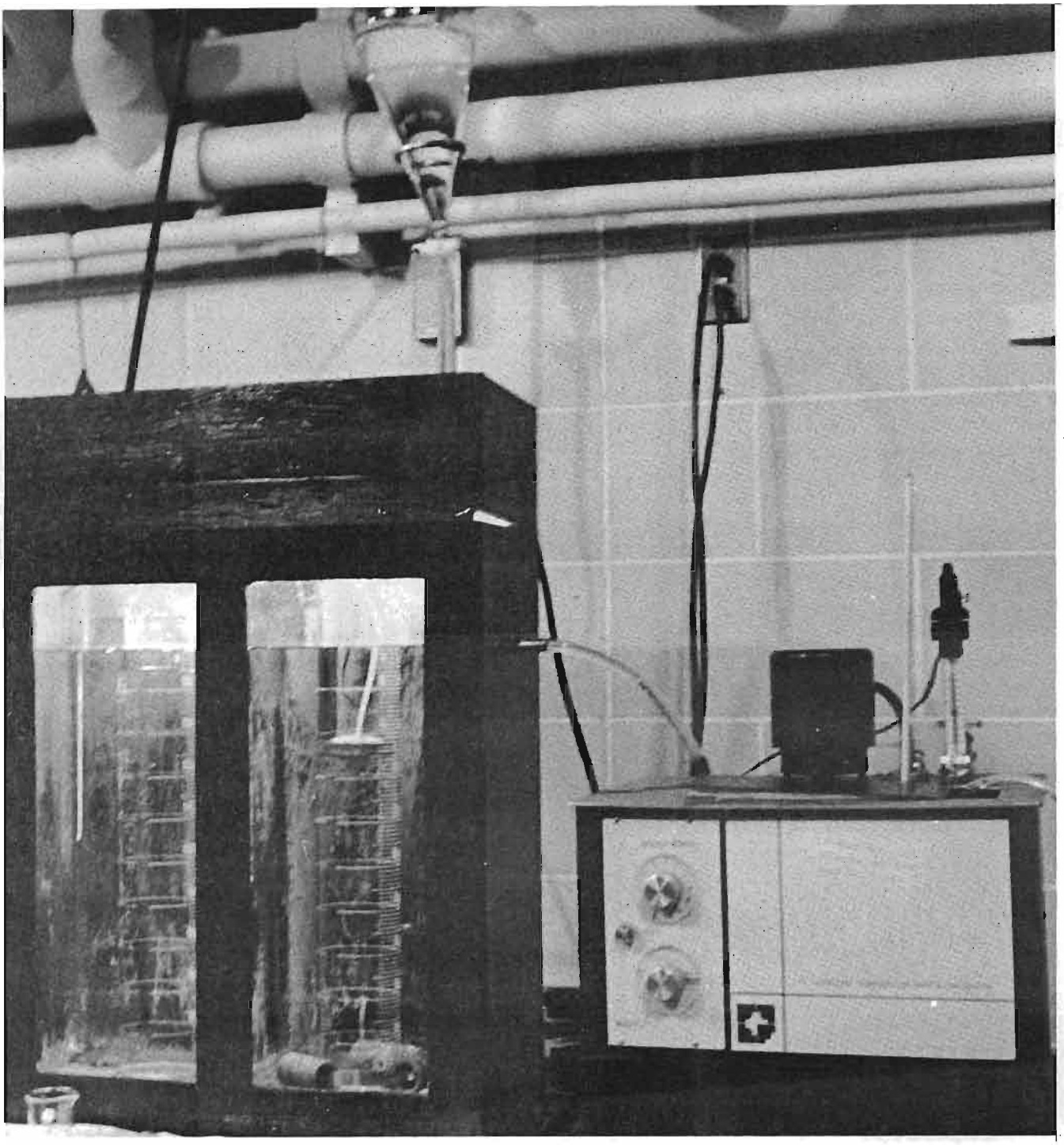

Fig. 1. General view of the Harder chamber and cooler. The right cylinder is being filled from the separatory funnel above but the top of the chamber is in its normal experimental position in order to illuminate the cylinders.

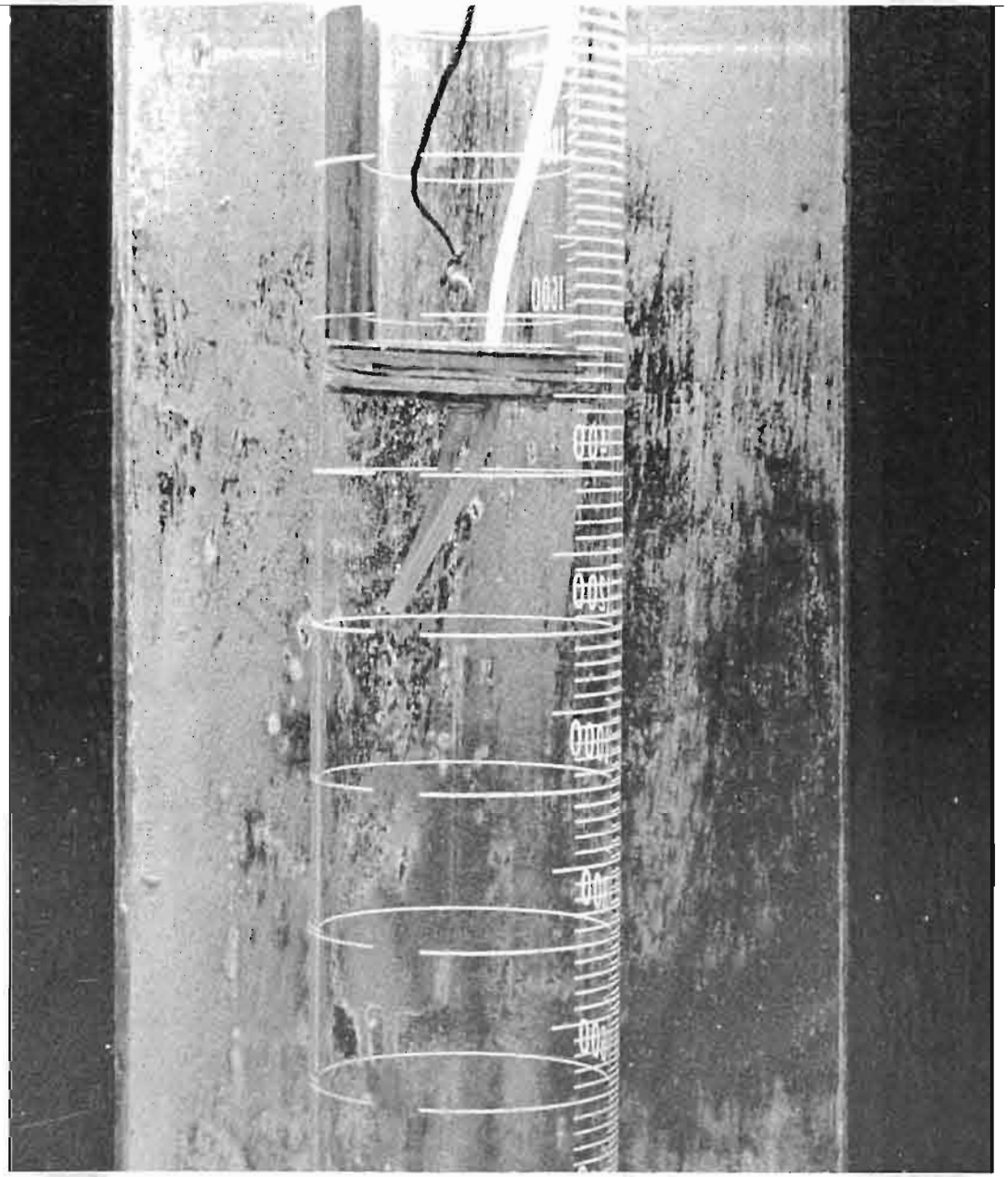

Fig. 2A. The top of a cylinder being filled to show the floating disc and attached tubing.

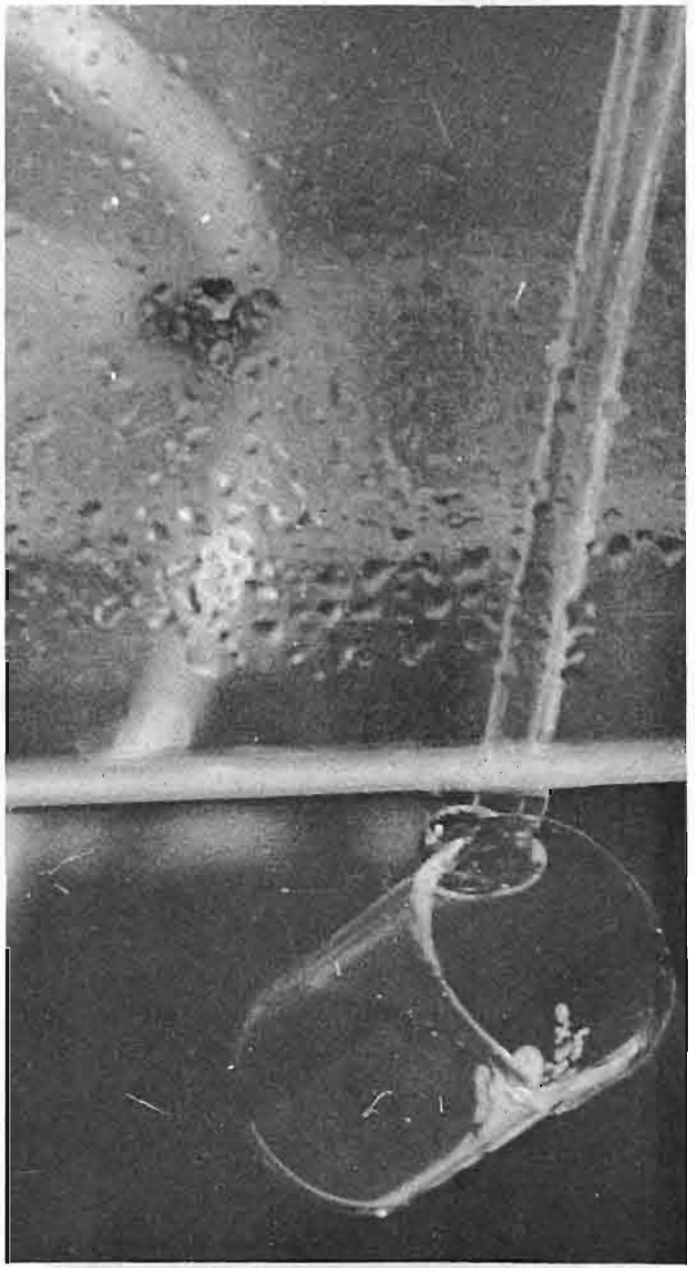

Fig. 2B. A Pleurobrachia being transferred to the experimental cylinder in a 5-cc beaker attached to a glass rod.

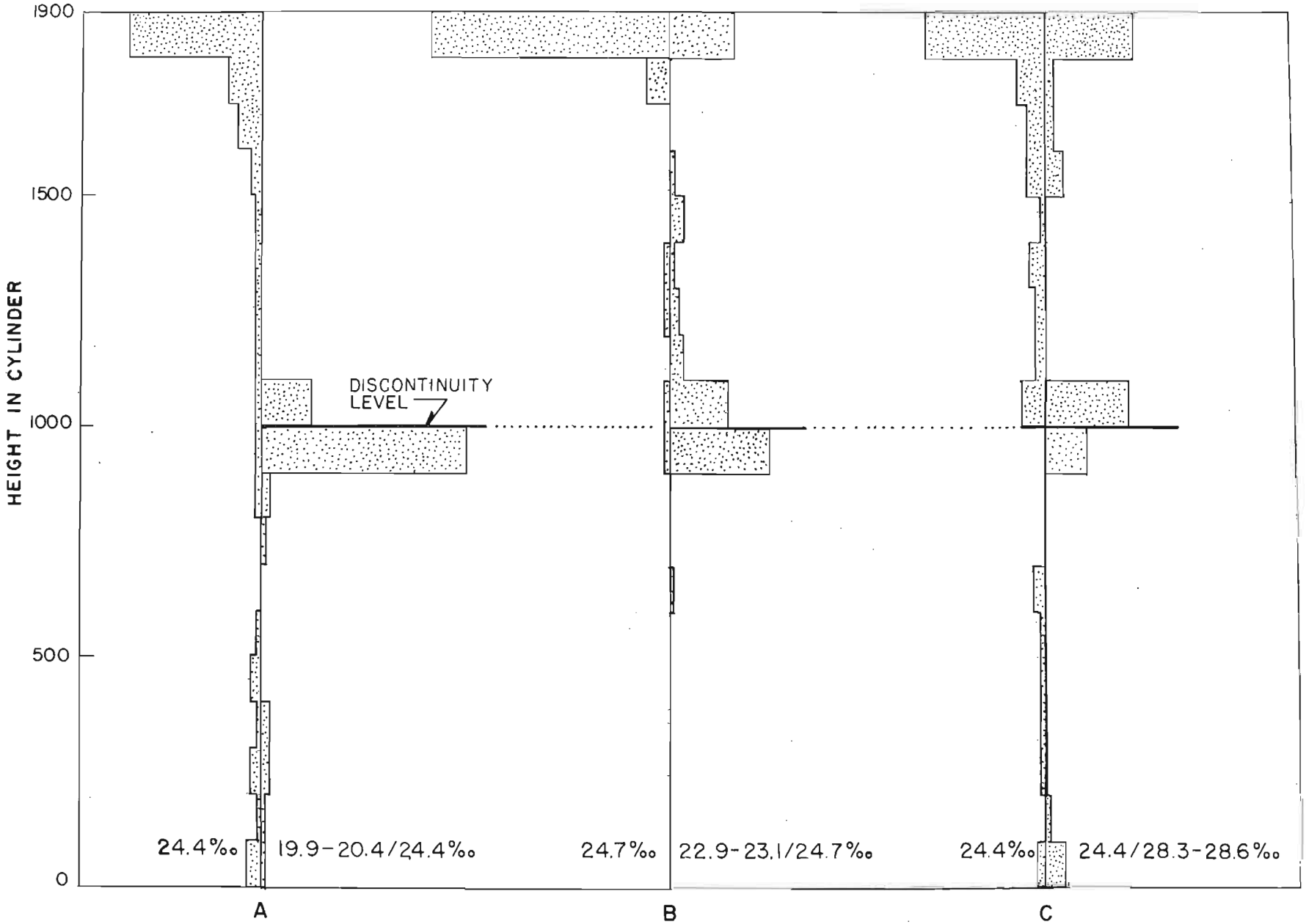

Fig. 3. Position in Harder chamber of Sarsia tubulosa, previously held in 25.0‰ water, tested with 24.4-24.7‰ as control and with discontinuity layers present (A. 19.9-20.4/24.4‰; B. 22.9-23.1/24.7‰; C. 24.4/28.3-28.6‰).

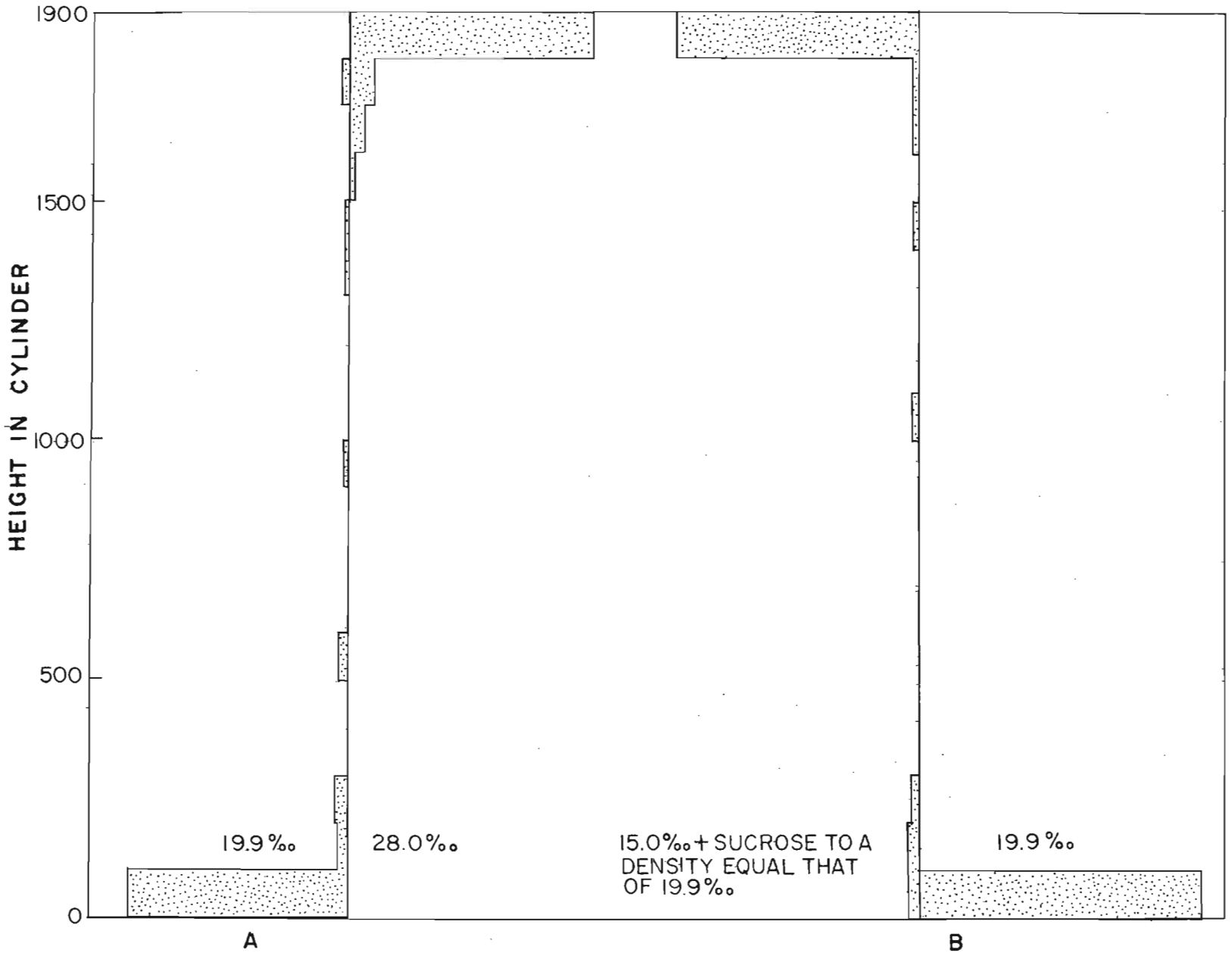

Fig. 4. Position in Harder chamber of Sarsia tubulosa previously held in 25.0‰ water, tested in homogeneous columns of 19.9‰, 28.0‰ or 15.0‰ adjusted with sucrose to a density equal to 19.9‰.

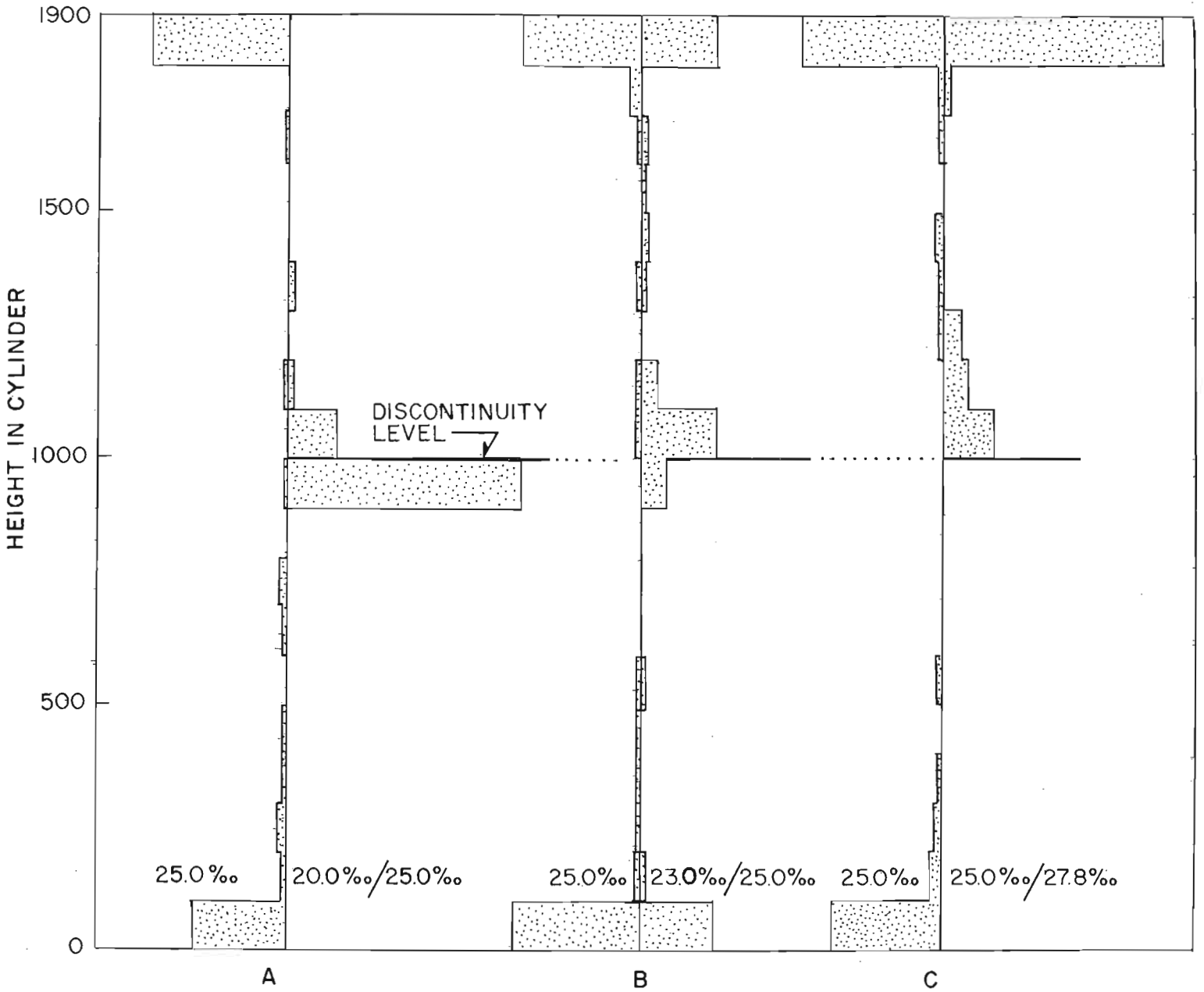

Fig. 5. Position of Pleurobrachia pileus in Harder chamber. Animals previously held at 25.0‰, tested in 25.0‰ as control and with discontinuity layer present (A. 20.0/25.0‰; B. 23.0/25.0‰; C. 25.0/27.8‰). B and C are each based on three experiments.

Fig. 6A. Position in Harder chamber of Pleurobrachia pileus previously held in 25.0‰, tested in homogeneous columns of 20.0‰ or 27.8‰.

6B and C. Position in Harder chamber of Pleurobrachia pileus previously held in 20.0‰, tested in homogeneous columns of 19.9-20.0‰, or 25.0‰, or in a discontinuity layer of 19.9‰/25.0‰.

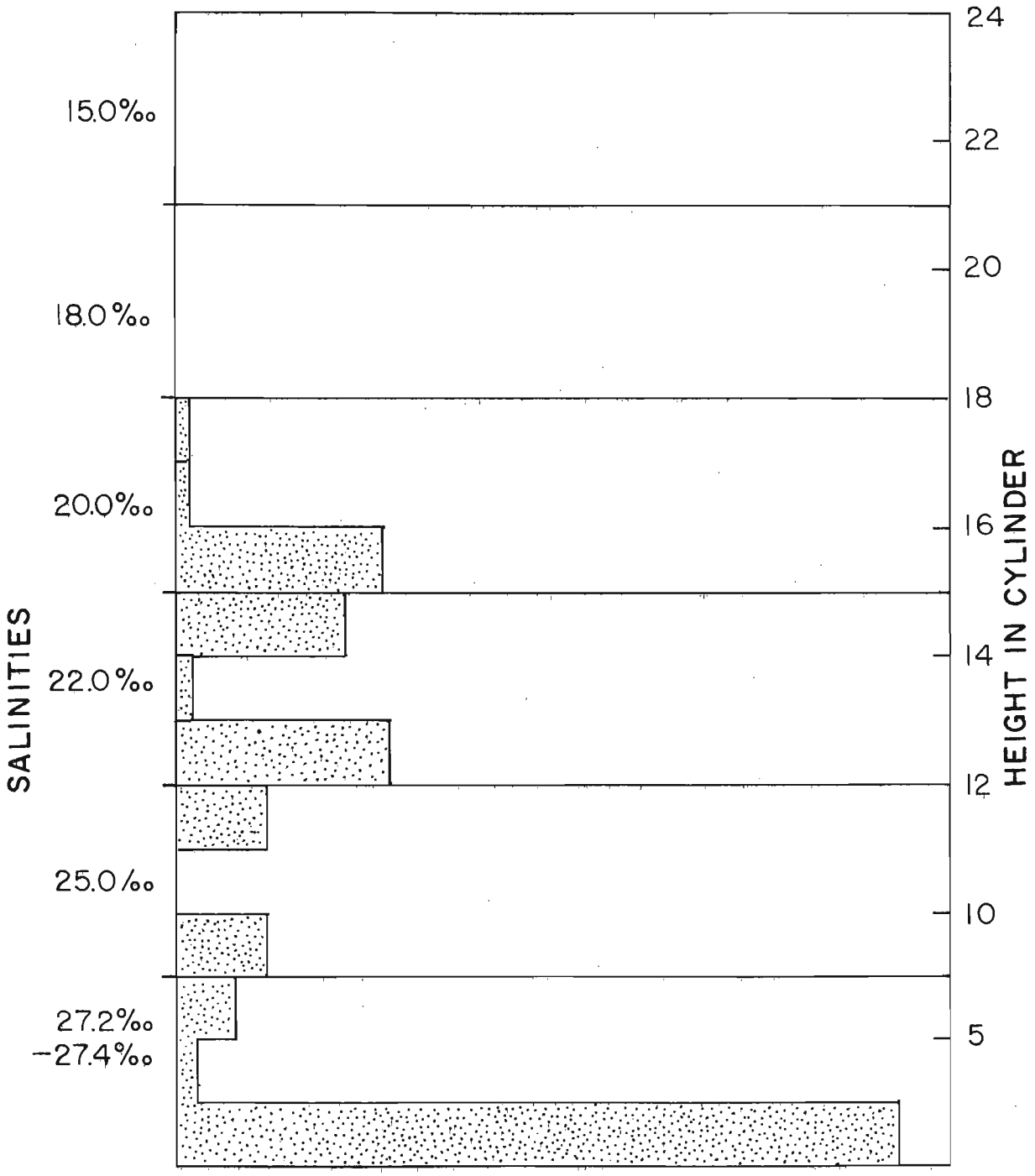

Fig. 7. Position in Regan chamber of Pleurobrachia pileus previously held in 25.0‰ showing reactions to multiple discontinuity layers. Twenty animals were used in each of 2 experiments and observations recorded at 5-minute intervals, the second half hour of each experiment being graphed.

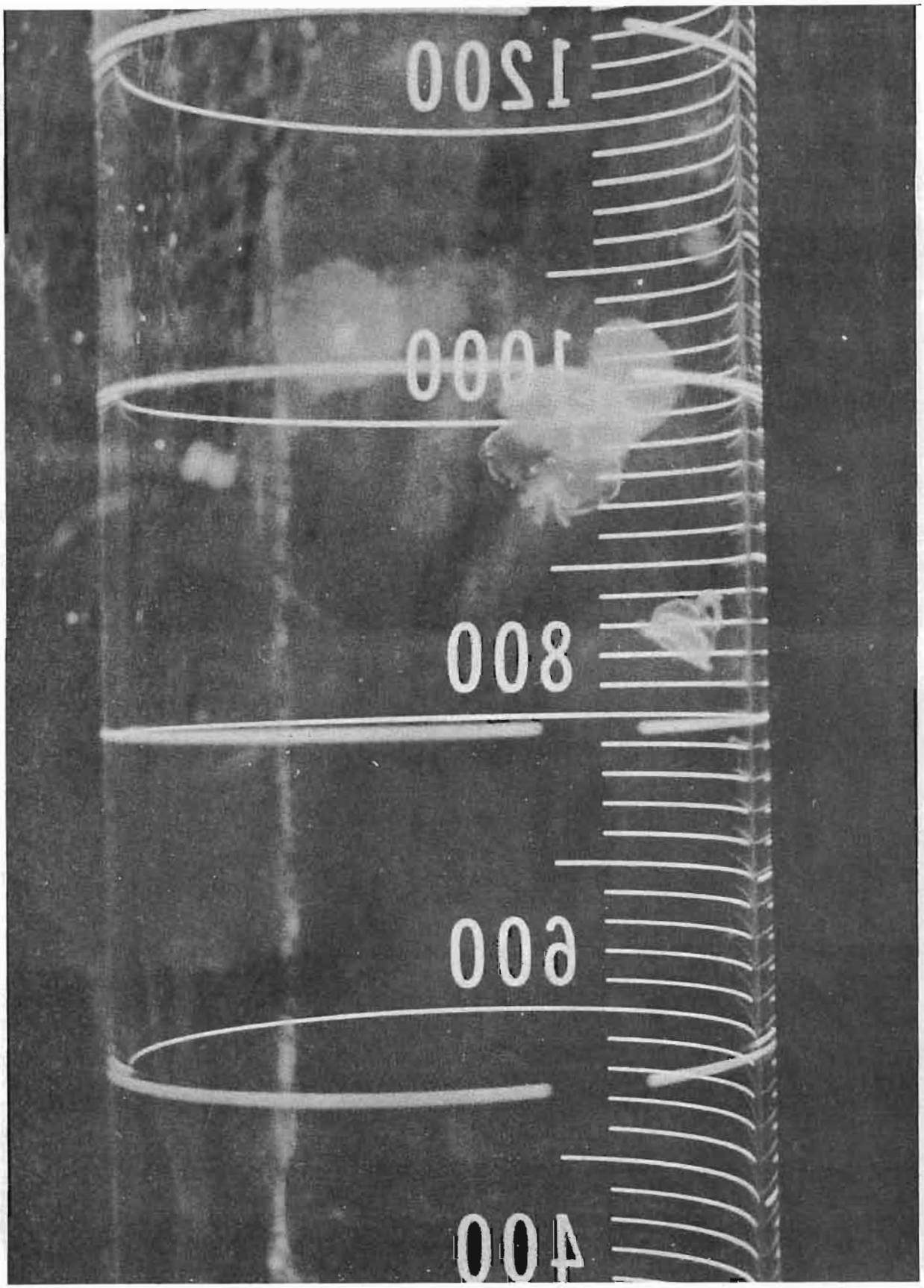

Fig. 8. Aurelia aurita in an experimental cylinder containing a discontinuity layer at the 1000 cc level. Note aggregation around this layer.

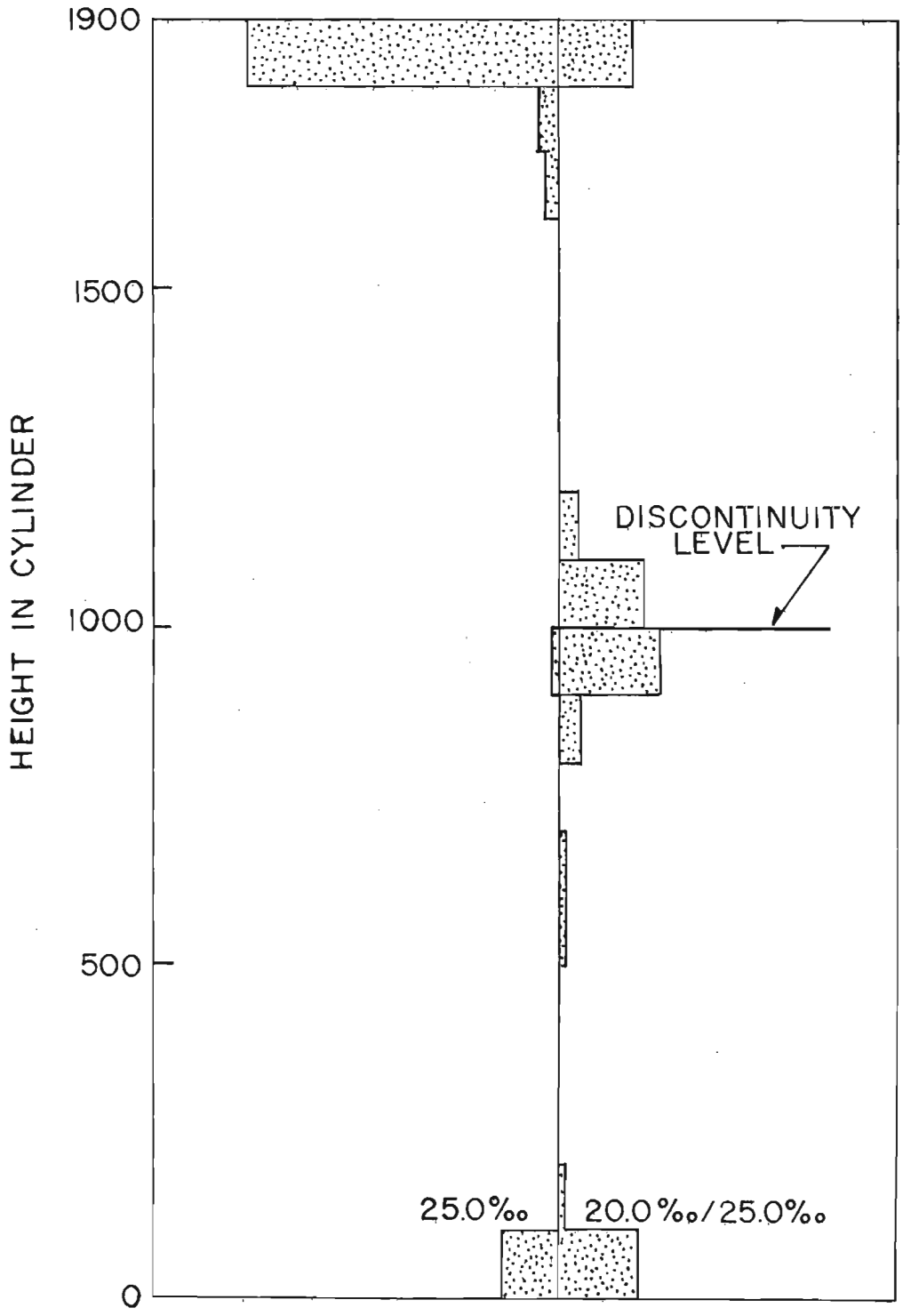

Fig. 9. Position in Harder chamber of Aurelia aurita, previously held in 25.0‰ water, tested with 25.0‰ as a control and with a discontinuity layer of 20.0‰ over 25.0‰.

OXYGEN CONSUMPTION OF HYDROMEDUSAE

Introduction

Virtually no work has been done on the oxygen consumption of hydromedusae. In a brief note Rajagopal (1962) states that Gonionemus sp. uptake is 1.5µl O_2/mg dry weight/hour at 29°C. Vernon (1895) investigated the oxygen consumption of Carmarina. The present study was therefore initiated to investigate oxygen consumption of one of the common hydromedusae of British Columbia waters, Phialidium gregarium.

METHODS AND RESULTS

Preliminary tests were run using the micro-winkler method of Fox and Wingfield (1938) to measure the oxygen consumption of Phialidium gregarium. The necessary micro-syringe pipette was built and calibrated, modifications being included to allow ease in cleaning.

Chambers were constructed utilizing 50 cc beakers. A glass tube was attached vertically to the inside by which samples could be obtained by pushing a hypodermic needle through a rubber cap. In the main portion of the chamber a frame was built of PVC to support a disc of nitex over a stirring magnet. A second removable disc was supported above the first to allow inserting of the medusae but prevent the medusae reaching the surface of the water with which the chamber was filled. The surface was then sealed with paraffin oil.

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