THE REPRODUCTIVE POTENTIAL OF A SINGLE CLONE OF PELMATOHYDRA OLIGACTIS

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Introduction

Very few metazoan animals reproduce asexually with sufficient rapidity and sustained repetition to render feasible a study of the theoretical asexual reproductive potential. After a culture of male *Pelmatohydra oligactis* had been maintained in a large aquarium for several years, during which it was observed that enormous increases in numbers by the process of budding occurred repeatedly, it appeared to the writer that it might be possible to determine the reproductive potential for males. The results are described in this paper.

Alternating periods of reproductive acceleration and depression were observed in the colony, the periods of acceleration coinciding roughly with abundance of food and the periods of depression to some extent with smaller quantities of food, but it was observed also that temporary declines in reproduction occurred even when food was abundant. Such a decline might have represented a general depression in the culture equivalent to senescence or a temporary resting stage. The only method of study which would yield results concerning a reproductive potential and the nature of the rhythms in reproduction appeared to be the method of isolating single specimens and following the reproductive history of the individuals and of their progeny. This method was pursued first by observing the increase in numbers in the progeny of a single specimen maintained in a mass and second, by separating the offspring from the parental animals as soon as they were detached and maintaining each in a separate culture.

Methods

Methods of culturing. A substitute for pond water was obtained by running tap water into a 50 gallon aquarium in which a quantity of the Bushy Pond Weed was maintained, and drawing off and filtering the water from time to time as needed for cultures. The water varied in pH but was always slightly alkaline. Temperatures varied from 22° to 28° C. No attempt was made to measure or to control light but the rather dim light in a corner of the laboratory was accepted as suitable since the large culture had flourished under these conditions.

The food supply was maintained at a high level. Hundreds of Entomostraca were placed daily in each culture jar. The hydra fed to capacity within a few hours and killed large numbers of animals which they did not consume. All dead food animals were removed at the end of six hours. The water in the culture jars was discarded and was replaced with fresh filtered water until the next feeding period. The high level of food supply would occur occasionally in nature but the sustained daily supply would not. Since hydra reproduced very slowly, if at all, when poorly fed, the sustained and abundant supply was considered necessary to secure maximal reproduction.

The observations on preliminary mass cultures from single individuals were made on specimens maintained in half liter jars. Culture jars of 125 cc. capacity were used for single isolated specimens.

Methods of Recording. In a preliminary mass culture which was carried on for only 17 days all specimens were removed from the jar every 24 hours, counted and then replaced. All hydranths, including buds in all stages of development, were counted.

Isolation cultures were examined every 24 hours and separate records were kept for each specimen. Samples of a 36 day record of specimen 5.1.1 and a 33 day record

TABLE I

Reproductive record of specimen 5.1.1

Day	Serial numbers of buds detached	Number of buds attached	Serial numbers of attached buds	Number of new buds produced daily
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	2	1, 2	2
5	1	3	2, 3, 4	2
6	2	3	3, 4, 5	1
7	3, 4	2	5, 6	1
8	5	1	6	0
9	0	1	6	0
10	6	2	7, 8	2
11	7, 8	2	9, 10	2
12	9	1	10	0
13	0	1	10	0
14	10	0	0	0
15	0	1	11	1
16	11	3	12, 13, 14	3
17	12, 13, 14	3	15, 16, 17	3
18	15	3	16, 17, 18	1
19	0	3	16, 17, 18	0
20	16, 17, 18	1	19	1
21	0	1	19	0
22	19	0	0	0
23	0	1	20	1
24	0	4	20, 21, 22, 23	3
25	20, 21	4	22, 23, 24, 25	2
26	22, 23, 24	3	25, 26, 27	2
27	25, 26	1	27	0
28	0	2	27, 28	1
29	27	3	28, 29, 30	2
30	28, 29	3	30, 31, 32	2
31	30, 31	5	32, 33, 34, 35, 36	4
32	32, 33	3	34, 35, 36	0
33	34	3	35, 36, 37	1
34	35, 36	3	37, 38, 39	1
35	37, 38, 39	1	40	1
36	40	1	41	1

TABLE II

Reproductive record of specimen 5.1.40

Day	Serial numbers of buds detached	Number of buds attached	Serial numbers of attached buds	Number of new buds produced daily
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0
6	0	2	1, 2	2
7	0	3	1, 2, 3	1
8	1	3	2, 3, 4	1
9	2, 3	3	4, 5, 6	2
10	4, 5	1	6	0
11	0	1	6	0
12	0	1	6	0
13	0	1	6	0
14	0	1	6	0
15	0	1	6	0
16	0	1	6	0
17	0	2	6, 7	1
18	0	3	6, 7, 8	1
19	6, 7, 8	3	9, 10, 11	3
20	9, 10, 11	2	12, 13	2
21	12, 13	4	14, 15, 16, 17	4
22	14, 15	4	16, 17, 18, 19	2
23	16, 17	4	18, 19, 20, 21	2
24	18, 19, 20	3	21, 22, 23	2
25	21, 22	2	23, 24	1
26	0	2	23, 24	0
27	23	2	24, 25	1
28	24, 25	3	26, 27, 28	3
29	26, 27	4	28, 29, 30, 31	3
30	28, 29, 30, 31	3	32, 33, 34	3
31	32, 33	2	34, 35	1
32	34, 35	1	36	1
33	0	1	36	0

of specimen 5.1.40 are shown in Tables I and II. A record was begun when a bud was detached. Thereafter the daily record for this detached bud included the appearance of new buds, the number of attached buds and serial numbers of attached buds at the time of their first appearance, and the serial numbers of these same new buds at the time of their detachment. Such a method of recording has numerous advantages. It is possible to determine by simple inspection, (1) the extent and duration of pulses of reproduction, (2) the duration of reproductive depressions, (3) the duration of the attachment periods of buds and (4) the actual rate of reproduction expressed in the production of new buds as compared to the apparent rate of reproduction which would be indicated in the numbers of attached buds. Average daily rates of reproduction were secured by considering the total number of new buds in relation to the total number of days in the period of observation. A total of 184 cultures were followed for periods ranging from 7 to 75 days and the daily average rates of reproduction were recorded.

A second and supplementary method of recording the progress of reproduction in a single clone and of numbering the individuals is shown in Figure 2. As the buds of the parent animal (5) were detached they were numbered consecutively nos. 5.1, 5.2 etc., and the numbers were placed in a clockwise series upon a surrounding circle (Gen. 1). The records of the reproduction of the detached individuals of the first generation were placed in the second circle (Gen. 2), etc. The system has the advantages of visualizing the entire output of a single animal in a single scheme, of permitting continuous expansion of the records of earlier as well as later generations and of facilitating comparisons of the outputs of members of the same generation although they are separated in time. The scheme is not intended to indicate rates of reproduction but rather extent of reproduction which may be compared in the different lines of the strain. A terminal decline in any line would be clearly indicated if it should occur. It is obvious that a high rate of reproduction

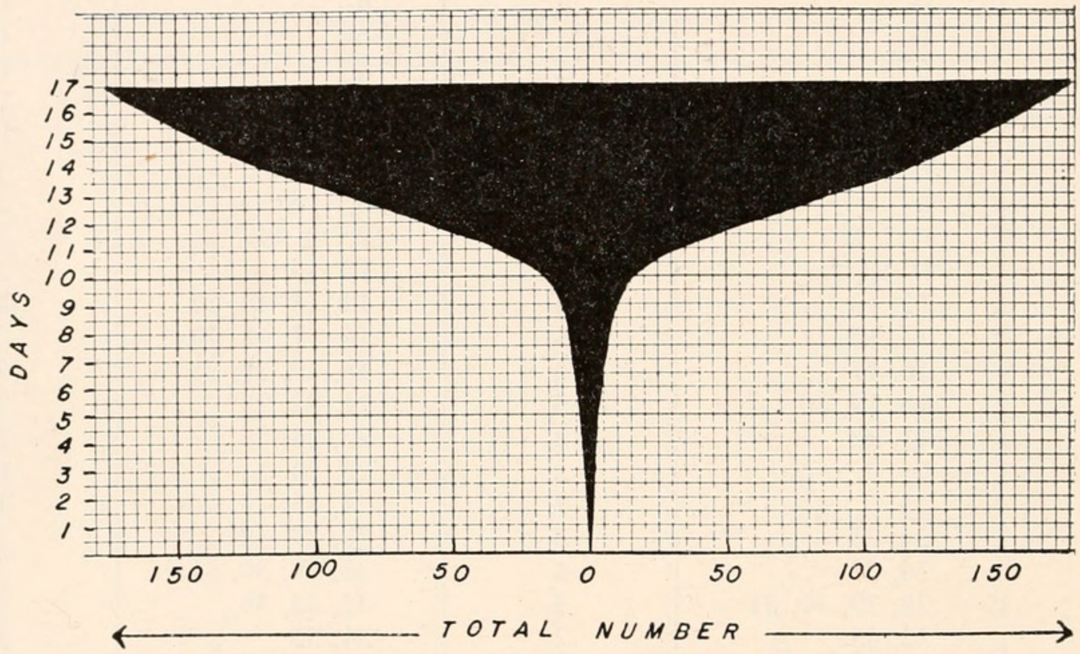

FIGURE 1. Bilateral graph showing the total number of individuals which are produced by budding by a single male specimen of *Pelmatohydra oligactis* in 17 days.

would result in such large numbers as to prohibit the culturing of all specimens and the keeping of a complete record. A complete record was kept of the first two generations but selected samples were run for the later generations. Approximately 3500 specimens from 184 cultures were recorded upon the scheme shown in Figure 2. Included in the 184 cultures were 15 cultures in which the reproducing individuals died during physiological depression.

Observations

Single clone mass culture. The specimen which produced the mass culture shown in Figure 1 was selected from a large tank in which hydra had been maintained for several years. The specimen was large, free from gonads and buds and was in a healthy condition. The results of culturing this individual along with its progeny with an optimal food supply are shown graphically in Figure 1. Single budding occurred within 2 days and by the end of the eighth day some of the specimens in the culture were bearing one bud, some were single and a few were bearing 2 buds. Specimens bearing 4, 5 and 6 buds appeared rapidly during the next 2 days but on the last day of the 17 day period there was an increase in the number of single specimens which were not budding. Increase in numbers was very high from the tenth to the fourteenth day but the rate of increase declined slightly from the fourteenth to the seventeenth day when the culture was discontinued. The production of

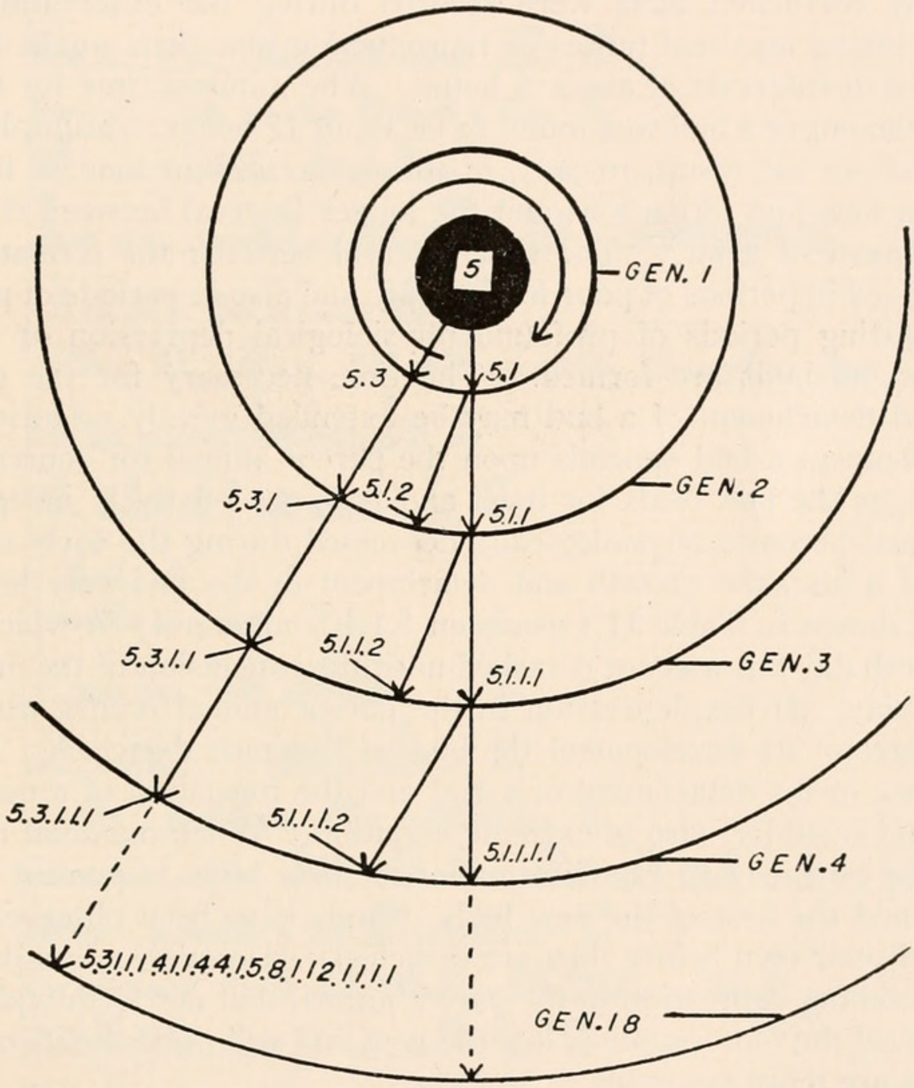

FIGURE 2. Scheme for recording the population produced by a single hydra. The scheme is capable of recording a continually expanding population and of indicating the relations of specimens by generations. The scheme does not express relations in time.

350 specimens in a period of 17 days from a single specimen was a remarkable performance which was repeated by other specimens cultured under the same conditions. One of the cultures maintained for 22 days was marked by a steady decrease from the maximal rate of reproduction after the thirteenth day. The beginning of a decline in reproductive rate was not a result of an accumulation of decomposition products in the culture water since the water was changed daily. Neither was it due to crowding or a lack of food or oxygen. It was concluded from this preliminary set of observations that some internal physiological state in the strain was responsible for

the reduction in reproductive rate but that the situation could be studied better in pedigreed individuals rather than in masses, and consequently the method of isolating single specimens as soon as they were detached was substituted for mass culturing.

Reproduction in isolated cultures. Prolonged observations upon isolated cultures were made with the primary objectives of determining the pattern in reproductive rate and of discovering whether a clone maintained under the conditions described would continue to reproduce indefinitely or would become senescent and die out. Many correlated facts were secured during the observations. It was observed that during maximal pulses of reproduction new buds might be produced by an individual at intervals of about 5 hours. The minimal time for the development and detachment of a bud was found to be about 17 hours. Multiple buds upon a parent animal are the result, in part, of the differences in time of the short intervals between new bud formations and the longer interval between the formation and the detachment of a bud. The time interval between the formation of buds is greatly extended in periods of poor food supply and also in periods of physiological depression. During periods of profound physiological depression or in complete absence of food no buds are formed. The time necessary for the growth, differentiation and detachment of a bud may be extended greatly. During the early stages of development a bud depends upon the parent animal for sources of energy but in later stages the bud feeds for itself and becomes relatively independent. If the parent animal becomes physiologically depressed during the early stages of the development of a bud, the growth and detachment of the bud may be postponed. An instance is shown in Table II (specimen 5.1.40, column 4) in which bud no. 6 arose on the tenth day but was not detached until the conclusion of the depression on the eighteenth day. If the depression in the parent animal occurs when a bud is in the later stages of its development the bud will become detached. The interval between the time of the detachment of a bud and the formation of a new bud upon the detached bud is subject also to extreme variation. When maximal reproduction is occurring the tendency to rapid formation of new buds is present in both the parent animal and the first of the new buds. Buds have been observed frequently to form buds of their own before they are detached. However, a bud detached in a period of approaching depression in the parent animal will not form buds of its own immediately and if the food supply is low the new bud will postpone its own budding until conditions are more favorable.

An examination of Tables I and II brings out the fact that there is a general correlation between the number of buds detached per day and the number of buds attached to the parent at about the same time. There is also a general correlation between the number of buds attached to the parent animal at one time and the production of new buds at the same time. The occurrence of several buds upon a parent animal is an indication of a period of rapid reproduction but it cannot be taken as an exact index of reproductive rate. For example, in Table I it is indicated that on the thirty-first day 5 attached buds were present on specimen 5.1.1 and the number of new buds formed on that day was 4. On the thirty-second day 3 attached buds were present but no new buds were formed on that day. In Table II it is shown that a bud (no. 6) was present upon the parent animal from the ninth to the eighteenth day. A casual observation of the fact would indicate that the parent animal was reproducing at a low rate when, in fact the parent animal was in a state of depression and did not form a new bud for seven days. Because of these apparent discrepancies between the number of buds attached or detached on any one day and the number of new buds formed on the same day, the rate of new bud formation was selected as the best criterion of an index for reproduction rate.

FIGURE 3. Block graph showing the daily production of buds by the single parent hydra and 18 specimens of the second and third generation. The symbol ⊏ indicates that the strain was terminated intentionally or was lost accidentally. The symbol □ indicates that the specimen died during a depression.

The rate of new buds produced per day by the original member of clone 5 and of 183 bud descendants representing samples from 18 generations has been plotted and 52 typical samples are shown in Figures 3, 4 and 5. Records followed by the symbol ⊏ are those which were intentionally terminated or were lost by accident. The 5 records followed by hollow rectangles indicate lines which died during physiological depression. The average rate of reproduction for each generation and for all individuals cultured is shown in Table III. The average daily production of new buds per day for all individuals cultured was 1.14 (Table III). The inclusion in the fifth and sixth generations of several cultures which died during depressions is responsible for the low rates per day shown in the Table. The reproductive rates of specimens which eventually do not survive a depression is considerably lower than the average rate for all specimens.

FIGURE 4. Block graph of 17 specimens from the third and fourth generations.

An analysis of reproduction and reproductive rates as illustrated in the graphs and Tables I and II reveals the following facts: (1) Reproduction occurs in rhythms characterized by periods of acceleration and shorter periods of rest or lowered rates per day, (2) There is no sustained reproduction at the highest level. The highest rate of reproduction for any one day is 5 and this rate is attained only twice. The longest period of sustained production of 4 or more buds per day is 2 days and 22 such periods are shown on the graphs. The longest period during which, on consecutive days, 3 or more buds are produced per day is 3 days. Eleven days marks the longest continuous period for the production of 2 or more buds per day and in no instance is there a period of more than 24 consecutive days in which one or more buds are produced. (3) In addition to the one or two day interruptions which oc-

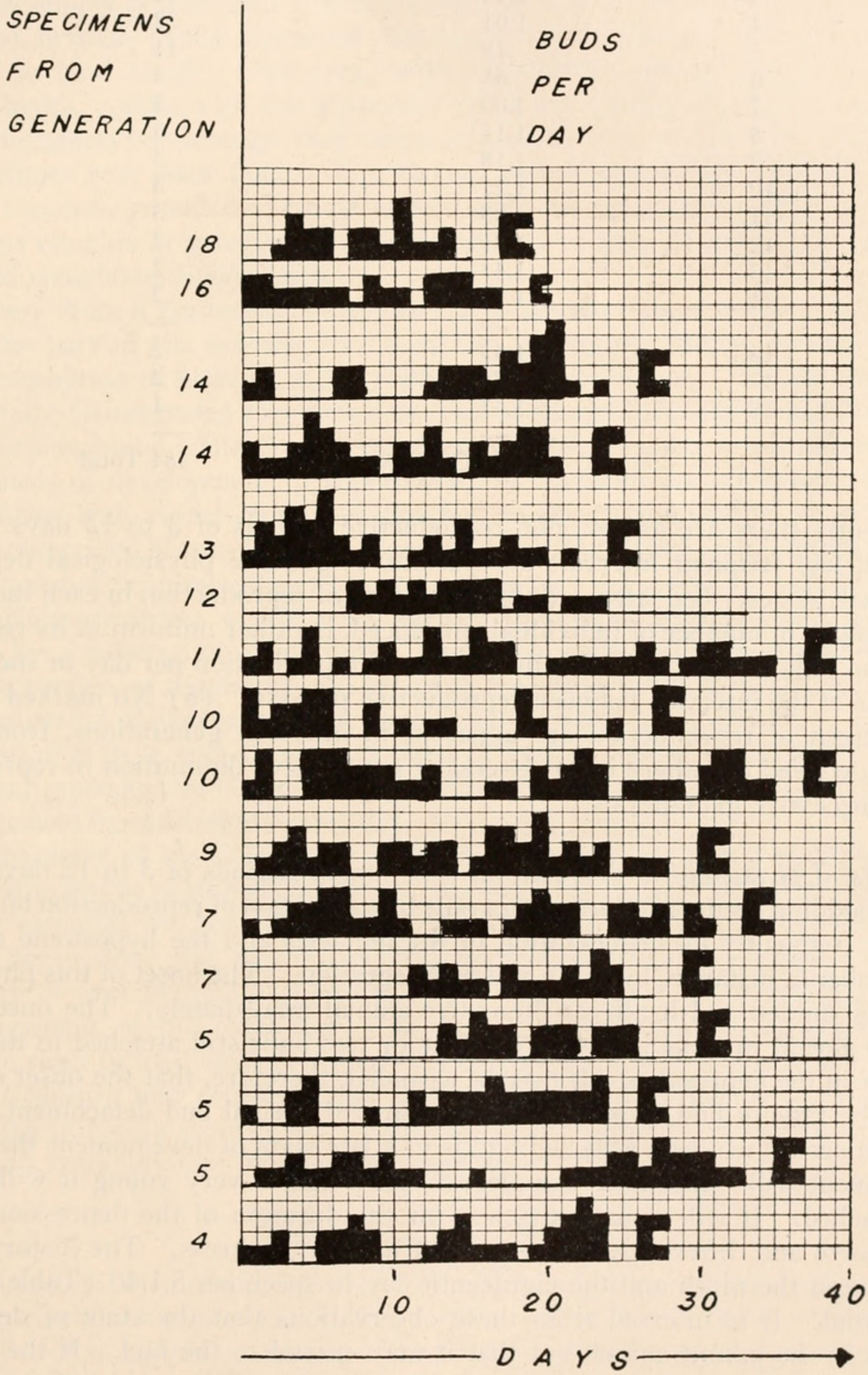

FIGURE 5. Block graph of 16 specimens from the fourth to the eighteen generations.

TABLE III

Rate of reproduction as indicated by production of new buds per day in all cultures

Generation	Average of new buds per day	Number of cultures
1	.96	22
2	1.05	50
3	1.10	42
4	1.04	22
5	.78	14
6	.65	8
7	1.00	3
8	1.15	3
9	1.18	3
10	1.27	3
11	1.05	3
12	1.31	2
13	1.43	2
14	1.24	2
15	—	—
16	1.43	2
17	1.75	2
18	1.67	1
	1.14 Gen. Av.	184 Total

cur frequently there are longer, non-reproductive periods of 3 to 12 days. These longer and less frequent intervals are periods of genuine physiological depression and they will be described later. (4) The pattern of reproduction in each individual, while irregular in number of individuals produced, is rather uniform in its repetition. There is no indication of a decline in the rate of reproduction per day or increase in the lengths of the intervals between reproductive periods. (5) No marked changes in the pattern of reproduction are apparent in different generations, from which it may be deduced that there is no general or progressive diminution in reproductive vigor in successive generations.

Periods of physiological depression. The longer periods of 3 to 12 days during which no budding occurs are marked not only by a cessation of reproduction but also by inactivity, frequently by degeneration of the tentacles and the hypostome and in a lesser number of instances by death and disintegration. The onset of this physiological state is sudden and it affects the entire animal immediately. The onset of the state is so abrupt in some instances that one or two buds still attached to the parent are caught in the depression. It may be assumed, therefore, that the onset occurred between the time of bud formation and the time of normal bud detachment. If the depression occurs while an attached bud is in a late state of development the process of detachment will continue to completion. If a bud is very young it will not become detached. It will remain attached for the duration of the depression during which growth and differentiation in the bud will not progress. The history of bud no. 6 between the ninth and the eighteenth day in specimen 5.1.40 (Table II) is a case in point. It is inferred from these observations that the state of depression originates in the parent animal but that it may extend to the bud. If the bud has established a sufficient degree of independence it will not be much affected by the depression in the parent animal. The fact that young buds do not grow and develop during depressions indicates that the state of depression extends to the processes of growth and differentiation as well as activity and reproduction.

The state of depression is set off sharply from the state which exists in partial starvation. If food is provided for a partially starved hydra the hydra reacts immediately and vigorously. If the food supply is meager the animal will produce buds slowly. If the food supply is abundant it will produce buds at an accelerated rate. On the other hand, animals in the depressed state react slowly to tactile stimulation and do not react to food at all. Cladocera, which would be captured immediately by a vigorous hydra, collide with the depressed hydra and evoke no reaction in the tentacles or nematocysts although they frequently come into contact with the tentacles and sometimes rest upon them. The starved animal possesses a full capacity for vigorous reaction, growth and reproduction while the depressed animal is incapable of vigorous reaction or growth or reproduction and in deep depression the most differentiated structures disintegrate.

Recovery from a depression is marked by a resumption of activity and feeding and, on the part of the animals that have not undergone partial disintegration, a prompt resumption of budding if the food supply is abundant. The animals which have partially disintegrated regenerate the lost parts and frequently exhibit a partial loss of morphogenetic control. The regenerated apical region is sometimes double and instances of development of supernumerary tentacles are common. In a few rare instances buds, which remained attached to the parent during the depression and were depressed themselves, on recovery from the depression remain attached to the parent but acquire sufficient independence to form a colony with the parent. Structural abnormalities which arise during depression and recovery are slowly corrected by a process of regulation. The remarkable adjustments which occur during the process of regulation will be made the subject of a separate paper. The length of a period of depression is not necessarily a mark of its severity. A depression period of 8 days may be characterized by nothing more severe than a loss of activity and reproductive output while a 3 day depression in another specimen may be accompanied by disintegration of tentacles and hypostome.

The character of the depression aside from the affects described above is not known. It might be postulated that there is a loss during rapid reproduction of some substance essential for normal metabolism, but the fact that the animals recover from the depressions and regenerate lost parts without feeding indicates rather a disturbance of arrangement of substances or processes prior to the depression and a rearrangement of the materials or processes during depression. Recovery of capacity to react to food and to metabolize the new intake would necessarily precede the actual capture and utilization of food. With the resumption of feeding and metabolizing of food a store of energy would be furnished, a part of which could be diverted to a resumption of the process of budding.

Reproductive Potential

A satisfactory formula for the theoretical reproductive potential of an animal should be capable of expressing a reproductive output for a stated period and be capable also of unlimited expansion if the factors which control reproduction are invariable. Such a formula is easy to construct in the case of a sexually reproducing animal which has a limited life span and undergoes senescence and death on the part of the parent animal. Only the progeny need be considered as the reproducers of the future. In the sexually reproducing animal the number of viable gametes, the numbers of new generations per year or season and the span of time during which the parent is able to reproduce are most important. The situation is different in an animal which reproduces asexually and in which both parent and offspring survive to reproduce on equal terms. The parent reproduces continually and long spans of time elapse between the production of the first bud and a much later one. All of the buds from a single individual belong to the same generation but the origin of the members of the single generation is spread through a long span of time. The continuity of reproduction in all generations at the same time makes it impossible to estimate the total output which constitutes one generation, or to separate the generations in time. A different method of approach must be employed if the total theoretical production is to be expressed in terms of time.

When hydra produces a mature individual by budding, and both the bud and the parent survive and continue to bud, a mathematical doubling occurs each time a bud is produced. With continual budding the doubling increases exponentially. If a rate of budding (doubling) can be established this rate can be used as the exponent of 2. If the rate is expressed in days and the daily average rate is known the following formula can be used for any stated length of time:

Reproductive output for n days = $2^n \times$ average daily rate.

The only factor which might vary would be the average daily rate of doubling. Reproduction in the original member of clone 5 and in the samples of its progeny has many minor fluctuations and long periods of depression, and some strains die out during depressions. However, an average daily rate of bud production has been obtained by including these depressed strains among the 184 samples. The records of the specimens which became depressed and eventually died have been included because each specimen was an actual or potential reproducer as long as it was alive. It has been shown also that, within the limit of 75 days at least, there is a general continuity of the daily rate in the over-all performances of individuals and of different generations. The daily average has been shown to be 1.14 under the favorable conditions described. Using 75 days as the period of time during which it is desired to express a total output, the total output under the conditions described can be expressed as follows:

$$\text{Reproductive output for 75 days} = 2^{75} \times 1.14.$$

The possibility that the potential indicated above for 75 days applies in longer periods was tested tentatively in the following procedure. Three of the oldest individuals reported for the 75 day period were observed for 48 days longer before they were accidentally lost. The average number of buds produced by these individuals for the total period of 123 days was 136. The average daily bud production was 1.10. Also two cultures of the most recently produced individuals from the 75 day period were maintained for an additional period to determine whether the production of succeeding generations would decline. The number of generations was raised to 28 in one culture and 26 in the other before they were lost accidentally. If these results are added to those described for the 75 day period it appears that there is no decline in the average daily rate of bud production or in the capacity of new buds to produce new generations, and that the formula for the total output can be used to cover a period of at least 123 days.

Discussion

Tremendous hydra populations have often been noted in natural uncontrolled situations. Some of these populations have been noted as to quantity and date with no observations as to duration. Fishing nets in Lake Erie, (Clemens, 1922) Lake Michigan (Welch and Loomis, 1924) and Lake Superior have been described as covered with hydra, in some cases for thousands of feet. Immense populations have been observed in the inland lakes of New York and Wisconsin. In some instances the inlets of water systems have been clogged with hydra. The duration of a large population in Lake Douglas, Michigan has been studied by Welch and Loomis. The large population existed during late spring and early summer but declined in late summer after the water temperature rose permanently to a point above 70° F. Large populations have been observed in other cases in late July, in November and in January, February and March in natural habitats with low temperatures at other seasons. It is indicated by these observations of hydra in natural habitats that accelerated reproduction is not seasonal except as seasonal conditions are responsible for low temperatures, food supply and dissolved oxygen in the water. In a large tank in which favorable conditions have been maintained throughout the year, the writer has observed reproductive pulses resulting in the production of thousands of specimens in each month of the year. It is clear that hydra may enter a period of reproductive acceleration at any time but, as indicated in the graphs, the periods of acceleration are sure to be followed by periods of depression. Under natural conditions a few hydra, which have survived unfavorable conditions and are in a semi-starved state, will form an enormous population within two or three weeks when favorable conditions exist. If favorable conditions prevail for several weeks the extent of the population will be limited, for the most part, by the death of specimens which become depressed. During the depression specimens do not move about and the ability to undertake vertical migrations into cooler water is lost. These specimens do not feed during the depressed period and if the food supply should decline in the immediate vicinity during the depression the animals would be in an unfavorable situation on their recovery. It seems, therefore, that great populations are reduced in part by extrinsic unfavorable factors in the environment but that an important contributing factor is the intrinsic depression which inevitably follows any initial burst of reproductive acceleration.

The phenomenon of depression was first noted by Trembley in 1744 and has been studied by numerous investigators (R. Hertwig, 1906; Frischholz, 1909; Rehm, 1925; Goetsch, 1922; Grosz, 1925). Hyman (1928) has made an extensive study of the metabolic rate during depression, recovery from depression and starvation. She agrees with earlier investigators that depression may be induced by long continued feeding, extremes of temperature, insufficient oxygen and changes from pond water to tap water, but she comes to the conclusion that the primary cause is the condition of senescence during which there is a general lowering of the rate of metabolism. It follows that recovery from the depression, marked by a regeneration of lost parts and a resumption of budding, indicates a process of rejuvenescence. In none of the studies mentioned above has accelerated reproduction been emphasized as a causative factor for the depression. In the observations described by the writer depression has occurred only at the end of a period of rapid budding. It would appear that some substance necessary for normal metabolism is exhausted by rapid budding or that some toxic substance is formed incident to the rapid budding and that the lowered rate of metabolism may be caused thereby.

Senescence in highly differentiated animals is terminal and results in death. If the process of depression is a process of senescence in hydra, it is terminal for a relatively small number of specimens. The others, after partial senescence, undergo rejuvenescence and the specimens survive and resume reproduction by budding. It appears that in hydra partial senescence has been substituted for terminal senescence for most specimens and that, given favorable conditions for recovery and reproduction after depression, reproduction by budding can go on indefinitely.

Summary

1. A single *Pelmatohydra oligactis*, when maintained under favorable conditions of temperature and water and given maximal amounts of food, reproduces rapidly and continually. New buds are formed every five hours when reproduction is at its height and buds may be detached in 17 hours after their first appearance.

2. Periods of maximal reproduction alternate with periods of depression during which specimens become inactive and in many instances degenerate at the apical ends. Some specimens die during the periods of depression but most of them regenerate the lost parts and resume reproduction by budding.

3. The average daily rate of bud production in 184 specimens, including those which eventually died during depressions, was 1.14.

4. There is no general decline, during a 75 day period, in reproductive vigor and rate in single specimens or in succeeding generations. During the 75 day period 18 generations were produced.

5. The total potential production by a single animal for a 75 day period can be obtained by using the average total number of doubling (budding) for the period, 75×1.14, as an exponent of 2.

6. Sudden reductions in population may be directly caused in natural habitats by unfavorable environmental factors, but the physiological depressions which follow rapid reproduction contribute to the decline by rendering the animals inactive and unable to accommodate themselves to changing conditions.

7. The depressions which follow rapid reproduction are basic intrinsic physiological states which may be genuine states of senescence. They may be caused by exhaustion of some substance essential to normal metabolism or to the accumulation of some substance which interferes with metabolism. Specimens appear capable of repeating the cycles of reproduction and depression indefinitely under favorable circumstances.

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