Contributions from the Biological Laboratory of the U. S. Fish Commission,
Woods Hole, Massachusetts.

THE REPRODUCTIVE PERIOD IN THE LOBSTER.

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Whenever it is impracticable to determine the reproductive periods in an animal by watching its behavior, the structure of the ovary will usually furnish a clew. This is true of the crustacea, and probably of all other animals. My present aim is not only to illustrate this fact, but to settle certain questions concerning the breeding habits of the American lobster about which doubt is still expressed. To state the question briefly: How often does the adult animal lay eggs?—Every year, once in two years, or at longer intervals, for these diverse answers have been given by various writers.

Over ten years ago I found that a study of the comparative anatomy of the ovaries taken at different seasons seemed to prove the impossibility of annual spawning,* and to demonstrate that eggs were not laid oftener, as a rule, than every other year. This was further illustrated in a fuller work published in 1895.† While confident that these conclusions were reliable, the main evidence in their support was indirect, as I took pains to state at that time. It is now possible to supplement these earlier observations by direct experiments upon living animals, and the theory of biennial spawning is supported by a variety of testimony. The true answer to the question, How often does the mature lobster lay her eggs? is, therefore, Once in two years, as a rule.

We will now consider the evidence upon which this conclusion is based. Apart from the question of the frequency of spawning, the following facts are known: (1) The majority of the egg-producers for any given year lay at a definite season—namely, in summer. The breeding or egg-laying season at Woods Hole, Massachusetts, reaches its height during the latter part of July. (2) Following ovulation comes a long period of fosterage, inaccurately called incubation, which lasts from ten to eleven months, during which the eggs are carried under the "tail" or abdomen. (3) The hatching of this generation of external eggs follows in May or June.

To revert now to the question of the frequency of spawning. Do the berried females whose young hatch in May, 1902, lay again in July of that year, or not until July, 1903, or in some subsequent year?

In 1895 I recommended that the direct experiment should be tried of keeping female lobsters alive from the period of the hatching of their last broods until the

* Notes on the Habits and Larval Stages of the American Lobster, Johns Hopkins University Bulletin, No. 88, May 1891.
† The American Lobster; A Study of its Habits and Development. U. S. Fish Commission, Washington, 1895.

laying of the next generation of eggs, which upon the theory of biennial spawning would be due in one year.* Through the courtesy of the United States Fish Commission this experiment was made in 1900–1901. On June 19, 1900, Mr. Vinal Edwards placed in a floating car thirty-six lobsters from which the old external eggs had been removed, fed them regularly, and on the first of each month following caught one of the animals and preserved its ovaries. When the last survivor was taken, May 1, 1901, just ten months and twelve days from the beginning of the experiment, not one of the animals had laid eggs. Further, an examination of the ovaries disclosed no evidence of absorption of the ova or abnormal retardation of their growth, such as we might look for upon the theory of annual spawning—nothing in fact but a slow, regular growth of the organs.

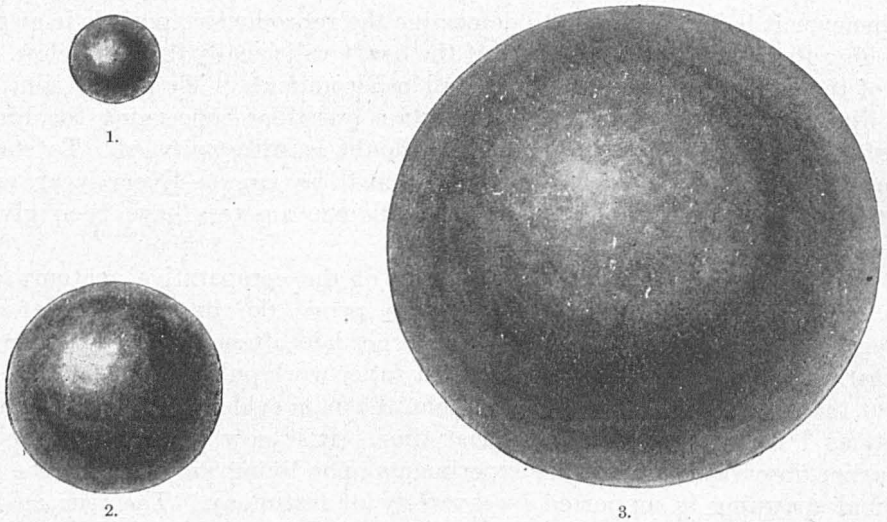

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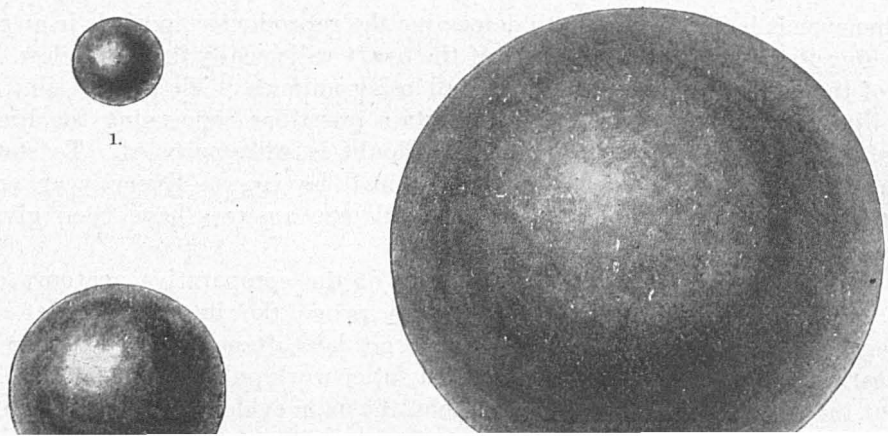
FIG. 1.—Initial stage of ovarian egg shortly after egg-laying in the lobster. Radius, 5.7 mm.; contents, 0.77 c. c. Animal taken 36 to 48 hours after egg-laying, July 29.

FIG. 2.—Ovarian egg in intermediate stage, one year after egg-laying. Radius, 14.1 mm.; contents, 11.71 c. c.; average of ten ova from animal taken June 19, and ten ova taken June 28.

FIG. 3.—Ovarian egg in final stage, when ready to be laid. Radius, 32 mm.; contents, 136.97 c. c.; average of five unextruded ova from the oviduct of a lobster which had recently laid eggs, August 17.

The testimony which is plainly borne by the structure of the ovaries of these animals is of much importance, and will be briefly analyzed.

In a single generation of ovarian eggs three stages are outlined as regards their growth, such as we might look for upon the theory of annual spawning—nothing in fact but a slow, regular growth of the organs.



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which serve as a handy and convenient chronometer. The ratio of growth in stages 1 and 2 can also be determined. The volume of the laid egg in the final stage is also known, so that it only remains to ascertain the time interval between stages 2 and 3.

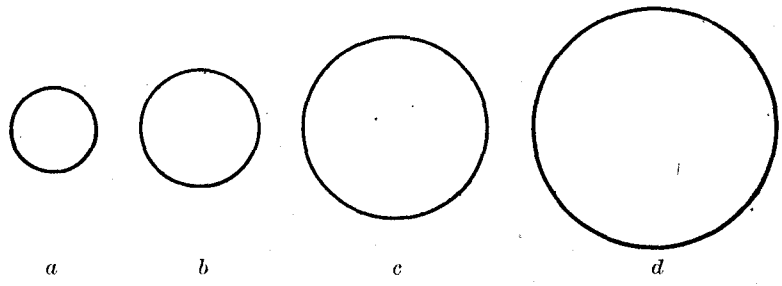

FIG. 4.—Series to illustrate the growth of the ovarian eggs during first year after spawning. (*a*) Ovarian egg in initial stage as shown in Fig. 1. (*b*) Ovarian egg fifteen days after egg-laying. External eggs borne on the swimmerets, in "nauplius" stage. Radius, 8.6 mm.; contents, 2.67 c. c., August 6. (*c*) Ovarian egg forty-two days after egg extrusion, the age being determined by state of development of attached ova. R. 12; contents, 7.22 c. c., August 21. (*d*) Ovarian egg, after approximately one year from egg-laying, average of ten ova from lobster taken June 19, 1900, with external egg ready to hatch. R. 16.2; contents, 17.77 c. c.

The relative volumes of the ovarian eggs at these successive periods are as follows: 0.77 c. c., 11.71 c. c., 136.97 c. c. Accordingly, during the first period of growth the ova increase in volume fifteen times, or the ratio of growth may be expressed by 1 : 15. Upon the theory of biennial spawning we should expect the ratio of growth for the second period to be approximately the same. The values

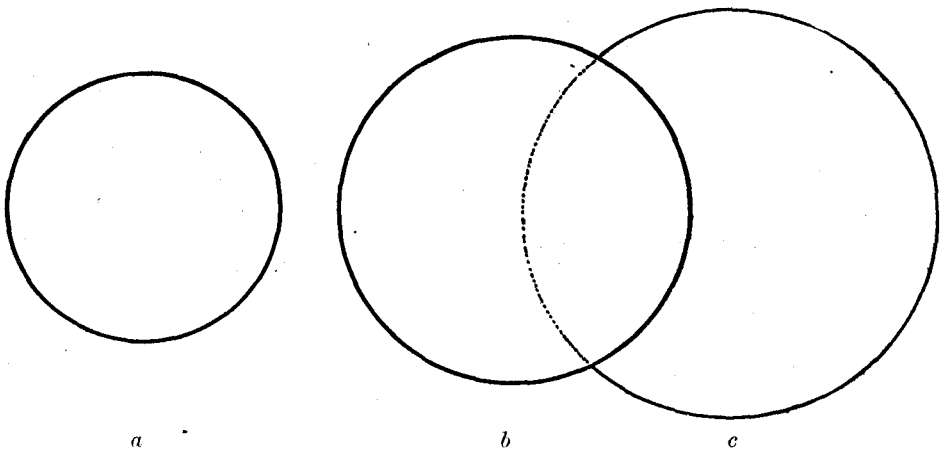

FIG. 5.—Series illustrating the growth of the ovarian eggs during the second year after spawning. (*a*) Ovarian egg one year ten months after egg-laying. The female from which this ovary was taken was kept in a floating car from June 19, 1900 (period of hatching), until May 1, 1901. Radius 17.9; contents, 23.97. (*b*) Average size of two fresh ova, taken August 19. These eggs were soon to be laid as shown by their size, color, and general appearance of ovary. (*c*) Unextruded ovarian eggs, taken about three days after egg-laying. The external eggs were in segmentation. Radius, 27.1; contents, 83.19 c. c.

given above, for which only a relative degree of accuracy can be maintained, give this ratio as 1 : 12. This result supports the conclusion that the ovarian ova which in spring following the last ovulation attain the size shown in fig. 2, experience a second period of rapid growth and are laid during the following summer. This is rendered

all the more certain from the characteristic appearance of the ovaries of certain lobsters taken in summer in the very midst of the spawning season. There are certain infallible signs which prove that the ovarian eggs are due in the current season, the most conspicuous of which is the color change. From a light pea-green the ovary becomes a dark olive or rather a greenish-black color, which is often noticeable at the very beginning of the period of rapid growth, or at least when many of the ova are scarcely more than ½ mm. in diameter (see fig. 5, *a*), and not due for some weeks. Then with the further growth of the ova the transparent elastic wall of the ovary becomes distended and assumes a beaded appearance. As the period of ovulation approaches, the ovarian eggs become free, and, if the wall is cut, flow out in a stream. It is thus evident that during the second year the ovary undergoes little change with respect to the size of the ova up to the beginning of summer or of the second period of rapid growth. Further direct observations upon lobsters kept alive for upwards of ten months after the hatching of a brood demonstrate that their ovarian eggs attain that size which the theory of biennial spawning demands.

Accordingly, a very slight change from the condition shown in stage 2 ushers in a second period of rapid growth, and this period, beginning usually sometime in June or early July, is brought to a close in the course of a few weeks, when the new generation of eggs is extruded.

The rapidity of growth of the ovarian eggs for a period of six weeks, as measured from the initial stage by means of the chronometer provided by the eggs attached to the swimmerets, is illustrated by figures 4 and 5. The egg more than doubles in volume during the first fortnight, while in seven weeks the initial volume has been increased 9.3 times.

While we speak of "stages" and "periods of growth" as a matter of convenience, it is hardly necessary to be reminded that every change is gradual, and that no abrupt transitions are known.

The theory of biennial spawning is supported: (1) By the statistics of the fishery; (2) by the anatomy of the ovary of the adult female taken at different seasons; (3) by the ratio of growth of a given generation of ovarian ova for stated periods; (4) by observation on animals kept alive for long periods; (5) by the evidence of the rapid growth of ovarian eggs of spawners for any given year during the height of the breeding season.

It is to be expected that the rule to which the majority conforms has many exceptions in individual cases, for variation is the rule of life. It seems quite probable that occasionally a lobster may lay eggs in two consecutive seasons, and that in other cases the normal biennial period may be even prolonged, but I have nothing to offer under this head.

I have shown in an earlier work* that a considerable number of spawners laid their eggs out of season, as in the fall and winter months. How can we account for these fall and winter eggs? An experiment tried by Mr. Cunningham,† in the summer of 1897, on the European lobster, suggests an answer to the question. At Falmouth, England, five female lobsters bearing external eggs about ready to hatch

* Ibid, p. 44.

† Contributions to the knowledge of the national history of the lobster and crab. Journ. Royal Inst. Cornwall, No. XLIV, 1897.

were placed in a floating box in summer time. When their ova had all hatched out these females were kept confined with two males until after October 14, when one was found to have newly spawned. This proves that it is possible for the European lobster to spawn in two successive years, but it does not prove that this is the common habit of the species. It also strongly suggests that these October eggs correspond to the "fall" and "winter" eggs occasionally produced in the American form. By accelerated growth of the ovary, eggs might be laid in fall or winter when not normally due until the summer following. Under such circumstances the ovarian eggs would come to maturity in fifteen instead of twenty-three months. It would be interesting to know when these fall eggs hatch. As already suggested, it is possible that they do not give rise to the regular summer broods. In the American species hatching of larvæ has been casually detected in November and January.

Professor Prince, who rejects the idea of a biennial spawning period, expresses surprise that the notion first advanced by persons wholly untrained and unqualified to form a reliable judgment has received support recently from men of scientific standing. A statement of mine is given a construction which might seem to support the idea that eggs are laid in consecutive years. Thus he says that I found in paper-shell lobsters in July that just after the brood had hatched and the molting was over the eggs in the ovaries were no less than half the size of mature ova. I speak of the diameter of these ova which, if by size is implied their volume, is quite a different matter.*

Again, it is said that I do "not hesitate to affirm concerning this supposed biennial spawning that to prove it requires only the dissection of a female with eggs ready to hatch in June, July, or August, and it will be found that "the ovarian eggs have had, in all these cases, from ten months' to a year's growth"—the very point, in fact, being assumed which requires proof." It would be a work of supererogation to go over in detail this ground again, but I can reaffirm the statement with added emphasis. That the majority of female lobsters which spawn in summer carry their eggs attached to the swimmerets until these same eggs hatch ten or eleven months later is a proved and settled fact admitting of no doubt. It was proved at Woods Hole, and the same experiment was conducted on a large scale by Mr. R. P. Greenleaf, at Southport, Me.† In July and August, 1892, he placed 300 egg lobsters in a pound at that place. In April, 1893, he seined and found the females still carrying their eggs; again, he seined the pound in June, when most of the eggs were hatched. Moreover, I have determined the rate of growth of the external eggs from actual observation, from the time of extrusion to hatching. The external summer eggs are a perfect chronometer for measuring the rate of growth of the ovary during the first period—that is, during the fall, winter, and spring following any given ovulation.

"The fact," says Prince, "that the lobster spawns annually is evidenced by: (1) The fairly uniform proportion of 'berried' females taken season after season. (2) The occurrence of the berried conditions in all sizes of females from 7 inches to 18 inches. It might be expected that females of certain specified sizes would never or rarely be found with eggs were biennial spawning a fact. (3) Exact researches upon

*Ibid, p. 152. †Ibid, p. 58.

allied decapod crustaceans prove the greater frequency of spawning. (4) The rapid growth of ovarian eggs so familiar to embryologists is unfavorable to the biennial theory."

The last two clauses (3 and 4) may be ruled out because this is a matter of fact concerning a specific animal, not a question of analogy with what may or may not occur with other species.

The first clause (1) is somewhat obscure. So far as my observations at Woods Hole have gone, the proportion of berried to adult females without berries is fairly uniform—that is, about one-half the adult females captured in winter and spring are without eggs. Whether this is what Professor Prince means or not, the fact is fatal to the theory of annual spawning. For, upon this hypothesis, during late winter or spring every female of breeding age should carry eggs, excepting here and there a solitary individual which had postponed egg-laying to an extraordinarily late period, or which had met with an accident and lost her cargo. I have never found a single instance of egg-laying in spring. On the other hand, the records of the catches made under my directions by the United States Fish Commission at Woods Hole confirm the statement just made and support the biennial theory of spawning, the proof of which has been given. Thus, in the month of March, 1894, 71 female lobsters 10 inches or more in length were captured in Woods Hole Harbor. Of these, only 9 bore external eggs. How are facts of which this is a sample to be explained on the theory of annual spawning, according to which all such animals should have borne eggs, or, at least, all but a very few which may not have reached maturity? The second statement—"the occurrence of the berried conditions in all sizes of females, from 7 inches to 18 inches," has no bearing on the question of frequency of spawning, since there is no fixed limit at which lobsters mature.* Again, the remark "it might be expected that females of certain specified sizes would never or rarely be found with eggs were biennial spawning a fact," is open to the same objection. New female recruits, of all sizes from 8 inches up, come to their first spawning period every year, and would do so whatever the length of the reproductive cycle.

In conclusion I wish to quote the brief summary which was placed under the description of a drawing of the ovary, which I believe gives a true picture of the growth of the ovarian eggs: "We thus see that a generation of ovarian ova grow very rapidly during the first summer following the last ovulation. They then enter upon a period of quiescence, growing but slowly, like the external embryos during the succeeding winter. At the beginning of the third summer after ovulation this generation of eggs is ready for extrusion. That the spawning periods are thus two years apart is a valid inference drawn from the study of the anatomy of the reproductive organs." †

* Ibid, p. 68. † Ibid, p. 246.