

The Reproduction of the Lobster.

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The Habits and Development of the Lobster, and their bearing upon its Artificial Propagation. By Francis H. Herrick, Professor of Biology in Adelbert College. *Bulletin of the United States Fish Commission*, vol. xiii. 1893.

The Reproduction of the Lobster. By Francis H. Herrick. *Zoologischer Anzeiger*, xvii. August, 1894, and xviii. June, 1895.

Lobster Reproduction. By S. Garman, Mus. Comp. Zool. Cambridge, Mass. U.S.A. *Zoologischer Anzeiger*, xviii. Feb. 1895.

Der Helgolander Hummer ein Gegenstand deutscher Fischerei, von Dr. Ernst Ehrenbaum. *Wissenschaftliche Meeresuntersuchungen herausgegeben von der Komm. z. wiss. Untersuch. d. deutschen Meere in Kiel u. d. Biol. Aust. auf Helgoland*, Neue Folge, heft i. 1894.

Amongst the numerous subjects which have occupied the attention of the fishery authorities of the United States, that of the great decline in the productiveness of the lobster fishing industry has received much consideration, and several competent naturalists have, in consequence, devoted themselves to a scientific study of the habits and life-history of the American species. This species (*Homarus Americanus*) is so nearly allied to the European lobster (*Homarus vulgaris*), that the results arrived at for it, with regard to such questions as the time of year at which spawning takes place, the length of time during which the eggs are carried by the female attached to the under side of the abdomen, and the time of year at which the eggs are hatched, might be expected to apply, to some extent at least, to the latter. That this is so, appears to be abundantly proved by Dr. Ehrenbaum's study of the lobsters which frequent the shores of Heligoland, and certain observations which I have been able to make on lobsters taken in the neighbourhood of Plymouth during the last two years, in the course of my work on the nervous system of the embryo, also tend to confirm this view.

In America, the investigation of the subject seems to have been carried on independently, at about the same time, by Herrick and

Bumpus, working at the U.S. Fish Commission Station, at Woods Holl, Mass., and by Garman, in connection with the State Fish Commission, of Massachusetts. It would appear that Herrick's work was commenced during the season of 1889, his most important results being published in May, 1891,* whilst Garman turned his attention to the subject in 1890, and reported his conclusions to the Massachusetts State Fish Commission, in December, 1891. On most points of importance, the independent researches of these different investigators are so much in accord, that there can be little doubt as to their correctness.

The time of year during which eggs are laid by the American lobster appears, from Herrick's recent papers † to be less restricted than had previously been supposed. As the result of his earlier work, he was of opinion that the period of egg-laying was confined to the summer months, and that the eggs were carried by the female until the summer following, when they were hatched. A similar view is also taken by Garman. This statement of the facts, however, Herrick now regards as only partially true, for, whilst the greater number of females deposit their eggs during the months of June, July, and August, a considerable number—probably, at least, ten per cent.—lay eggs during the autumn, winter, and spring months.‡

For eggs laid during the summer, Herrick, Bumpus, and Garman agree as to the time occupied in development. They are carried by the female from ten to eleven months before being hatched, this event taking place, in the majority of cases, during June and July of the year following that in which they are laid. During the first few weeks development proceeds rapidly, the eyes being already visible after a month from the time of laying. As the colder weather comes on the process is much retarded, and advance is slow during the winter. According to Herrick, however, the period of fosterage varies considerably in eggs not produced in the summer, some of which may hatch in the fall, and possibly in the winter months.

On these points Ehrenbaum is able to give valuable information concerning the Heligoland lobsters. Special opportunities for the study of the subject are afforded at this place, as the fishermen and dealers keep great numbers of lobsters in large, floating cages for considerable periods, especially in summer. In these cages, however, the females do not, in the majority of cases, deposit their spawn, probably on account of their being shut up in a confined space with a number of their

* *Johns Hopkins Univ. Circulars*, vol. x. no. 87, and *Zool. Anzeiger*, nos. 361 and 362.

† *Zool. Anzeiger*, August, 1894, and June, 1895.

‡ Nielsen states that, in Newfoundland, the larger lobsters spawn from the middle of June till the middle of August, whilst the smaller do not lay until the latter part of October and November. (*Annual Report, Newfoundland Fisheries Commission*, 1889, p. 12.)

fellows. In cases where the ova are mature, but are not shed, a curious physiological process is set up, the yolk of the unlaidd eggs being re-absorbed, and passing into the blood. The blood, in this way, becomes dark green, or almost black, and the dark colour is visible through the thin membranes, especially on the under side of the abdomen. Such animals are known as "black" lobsters, and, if the process has been allowed to proceed far, they are unsaleable. The first appearances of this blackening are, therefore, carefully watched for by the owners of the cages, in order that the animals may be sold before they become valueless. "Black" lobsters begin to appear about the end of July. Ehrenbaum states also, that, in individual cases, lobsters in the cages have spawned, the dates given being 20th, 23rd, and 26th July, the first days of August, and the 28th August. He is also able in two cases to give direct information as to the time the female lobsters carry their eggs. In the first case, eggs spawned during the early days of August, 1892, commenced to hatch on the 20th July, 1893. In the second case, the eggs were laid on the 28th August, 1893, and the majority of the larvæ hatched on the 21st July, 1894. This would give about eleven months as the period of incubation. It should be noted, however, that the lobsters must have been kept in a state of confinement during the time that the eggs were developing.*

My own observations on our English lobster (*Homarus vulgaris*), although not made systematically for the purpose of determining these points, but, rather, from the necessity of examining numerous egg-bearing females at different times of the year, in connection with other investigations, agree with those of Ehrenbaum in pointing to the conclusion that, on the whole, the history of the reproduction of this species is similar to that of the American representative of the genus.

Females with newly-laid eggs were first obtained during the latter half of July, but out of a large number of lobsters examined, only two specimens in this condition were found. During August and September my work on the subject was interrupted, but on taking it up again in October (1893), females carrying eggs were plentiful, but all the eggs were either in the nauplius stage, with no eye-pigment yet deposited, or in stages in which eye-pigment was just commencing to be seen. These facts, namely, that newly-laid eggs were scarce during the

* In the sixth *Annual Report of the Fishery Board for Scotland*, p. 196, Prof. Ewart and Dr. Fulton state that in Rothesay Aquarium, a female, with ova, being placed in the tanks in August, 1886, hatching was only completed in August, 1887, some of the young lobsters being hatched as early as April. It seems fairly certain from this result, that confinement tends to produce an abnormal rate of development, as, in the case of lobsters captured when the eggs are nearly ready to hatch and placed in the tanks of the Plymouth Laboratory, hatching is usually completed within a week, at most, from the time it commences.

latter half of July, whilst they were numerous, but all were at least in the nauplius stage, in October, would seem to show that August is the month during which most of the females spawn. Development during the winter months took place very slowly.

The first lobster which I was able to obtain during the following year with eggs on the point of hatching, was brought to the Laboratory on the 20th of March, and larvæ were set free on the 29th of the same month. This lobster, which was stated to have been taken in deep water off the Eddystone, appears, however, to have been quite exceptional, for, in spite of repeated endeavours, no specimen could be again procured with ripe eggs until the middle of May. From this time they became more frequent, the largest number being obtained in June. By the middle of July only occasional specimens were seen, whilst after the end of that month no more could be obtained. During the last fortnight of July the two seasons appeared to overlap, very few lobsters being in berry at all; whilst of those which were, the number having ripe eggs appeared to be about equal to that of those whose eggs were newly spawned.

On the whole, therefore, it is probable that, in this district, the majority of lobsters lay their eggs during August, and the majority of eggs are hatched during June, the period of fosterage being at least ten months.

Coming to the question of the interval which elapses between the hatching of one brood of eggs and the laying of the next, the authors are agreed that this must be at least a year, whilst Ehrenbaum would make it considerably longer. The reasons brought forward by the American naturalists in support of their conclusions on this head are, in the first place, the immature condition of the ovaries of females which have recently hatched their eggs, and the slow rate of maturation of the eggs in the ovary, which render it impossible that the eggs should be ready for laying during the summer in which a brood has hatched; and, secondly, the fact that during the winter months a large proportion of the females captured do not carry eggs.

As already stated, Ehrenbaum makes the interval much longer, and considers that, on the average, a female lobster produces eggs only once in four years. This result is so extraordinary, and if the conclusion can be maintained, is so important, that it is worth while stating in full the evidence on which it is based, and I give, therefore, the following translation of Ehrenbaum's remarks on the subject:

"If eggs were laid every year, then, in consequence of the long duration of the hatching period, females bearing no eggs on the abdomen would seldom occur, which is by no means the case. It can rather be proved with tolerable certainty that the intervals between two

consecutive spawnings extend over two, three—or, indeed, more—generally over four years. . . .

“The report by J. C. Ewart, on the Scotch lobster fishery, already referred to (6th Annual Report of the Fishery Board for Scotland, 1888, p. 196), contains the statement that, according to the testimony of the lobster fishermen, about 30 per cent. of all the lobsters caught are females bearing spawn. But as males and females are represented in about equal numbers in the catches—I have found 2,200 males to 2,030 females,* in an enumeration extending over the whole year—according to the statement made above, about 60 per cent. of all the females carry eggs, which would indicate an interval of scarcely two years between two consecutive spawnings.

“The matter was of sufficient interest and importance to justify closer investigation, and I have therefore made statistical observations extending over the whole year, whenever suitable opportunity offered, on the number and percentage of egg-bearing females in the catches. In doing this I have not counted the individual catches, but those collected by the dealers in the lobster cages, and have obtained the following results:—†

Date.	Total Number.		Females with Eggs.		Eggs newly laid.	“Black” Females.	Eggs far developed.	Remarks.				
	Males.	Females.	Number.	Percent.								
1892. July 25th .	38	21	...	—	...	—	...	All just before or just after moulting.				
	15	61	...	29	...	—	...					
Aug. 13th .	86	75	...	35	46.6	...	4	...	7	...	—	
Sept. 14th .	97	91	...	40	44.0	...	—	...	7	...	—	
Nov. 8th .	123	78	...	23	29.5	...	—	...	—	...	—	Unsorted catches.
Dec. 7th .	207	162	...	31	19.1	...	—	...	—	...	—	“ ”
„ 10th .	94	67	...	9	13.5	...	—	...	—	...	—	“ ”
„ 14th .	61	102	...	25	24.7	...	—	...	—	...	—	“ ”
„ 20th .	276	160	...	27	16.9	...	—	...	—	...	—	“ ”
1893. Feb. 20th .	310	212	...	49	23.1	...	—	...	4	...	—	“ ”
May 17th .	277	270	...	46	17.0	...	—	...	—	...	5	“ ”
June 13th .	246	309	...	64	20.7	...	—	...	—	...	—	Caught since May 17th.
July 13th .	111	138	...	64	46.4	...	—	...	—	...	21	Caught since June 13th.
„ 25th .	106	171	...	45	26.3	...	2	...	—	...	3	Unsorted catches.

“For the better understanding of these figures, the following must be mentioned:—

“The “black” females are reckoned as egg-bearing, since, under natural conditions, *i.e.*, if they had not been confined in the cages, they would have spawned.

* Herrick found, however, among about 3,000 animals, a slight excess of females.

† Herrick (*Zool. Anz.* 1891, p. 134) has given a similar table, which, however, does not give the same result.

"As regards the first three entries, which relate to July 25th, August 13th, and September 14th, 1892, it cannot be maintained that the catches still retained sufficiently closely the natural composition which they possessed when first taken. In the summer the dealer sorts his wares, in order to render selection for sale more easy. He divides the small from the large, puts such lobsters as are about to moult in a special part of the cage (it is in this way that the animals enumerated on the 25th July, 1892, are divided), and prefers to sell the females without eggs on the abdomen first, in order to guard against their becoming "black." The latter circumstance is the cause of the percentage of egg-bearing females, in the first three entries on the list, being somewhat higher than in the following. In calculating the mean, however, this is hardly noticeable. The last ten enumerations are all made, on the other hand, on material which had not yet been sorted, and which therefore possessed the original constitution of the catch. Care was also taken that nothing should be counted twice, for each time new cages which had not previously been looked through were examined.

"Reckoning the whole thirteen entries, the mean percentage of egg-bearing females is 25.4 per cent.; the last ten, it is only 23 per cent.

"It will not, therefore, be an error to maintain that never more than the fourth part of the female lobsters capable of reproduction actually carry eggs; or, in other words, that a female lobster, as a rule, actually produces eggs only once in every four years."*

Few will be inclined to object to the author's exclamation, "Das ist eine Thatsache, die allerdings zu denken giebt!" but whether, as a result of the thinking, all will be ready to accept the conclusion arrived at, is another question. At first sight, the argument presented appears to be conclusive, but a little consideration will, I think, lead to the conclusion that at least one other explanation of the facts is possible, for it must be borne in mind that Ehrenbaum was not dealing with the number of lobsters living in the sea, but with the number caught in the traps. It is, to say the least, not improbable that a female bearing eggs would be much more wary of entering a trap than one not so encumbered, especially if the trap already contained other lobsters, including females without eggs. The pugnacious habits of these animals are matters of common experience, and I have, on several occasions, known two of them, confined in one tank, continue their

* "A false interpretation of the facts can only be possible in so far that perhaps, sometimes, females may have been counted as 'not egg-bearing,' although they were slightly under 24 c.m. (9½ inches) long, and therefore not yet capable of reproduction. So far as could be judged by the eye, however, the young animals not yet capable of reproduction during the enumeration, were always left on one side."

warfare until one or the other has been killed. The loss of claws and legs is of quite frequent occurrence; and the fisherman, before confining lobsters in a store-pot, invariably cuts the pincer muscles of the big claws, in order to prevent them injuring each other. Even if no instinct corresponding to maternal jealousy exists amongst these animals, a female bearing eggs is placed at such a physical disadvantage, that it is not unlikely that she would be more cautious of entering a confined space with other lobsters. At any rate, this consideration should be borne in mind when drawing conclusions from the results arrived at by Ehrenbaum.

An examination, made at the end of July, of the ovary of a female whose brood had just been hatched, did not appear to me, in itself, to offer evidence for or against the view that eggs would not be laid even during the same summer. The ovaries were found to extend from the anterior end of the œsophagus to the middle of the third segment of the abdomen. The eggs were of a dark green colour, and in a lobster 30.5 cm. long, many of them had a diameter of as much as 1.2 mm. If no further evidence of a different kind were forthcoming, one would, I think, have been inclined to expect that these eggs would be laid during the same summer. It seems to be very important for the settlement of these questions that the rate of development of the eggs in the ovaries of lobsters kept under conditions as normal as possible should be determined, but this, of course, involves many difficulties. It could, probably, only be satisfactorily undertaken where the lobsters could be confined in a large tidal pond from which they were unable to escape but from which the water could at intervals be drawn off completely.

The number of eggs laid by a lobster becomes very much greater as the age of the animal advances. This appears to be true, both of the American and European species. A female 8 inches long, according to Herrick, carries from 3,000 to 9,000 eggs, whilst in one measuring 16½ inches, the number was 85,000. As the result of an examination of nearly a thousand individuals, this author finds that "the numbers of eggs produced by a female lobster at each reproductive period vary in geometrical series, while the lengths of the lobsters producing these eggs vary in arithmetical series."

Thus an American lobster

8	inches	long	produces	5,000	eggs.
10	"	"	"	10,000	"
12	"	"	"	20,000	"
14	"	"	"	40,000	"
16	"	"	"	80,000	"

Ehrenbaum finds a similar state of things in the Heligoland lobster, although the actual number of eggs on individuals of the same length appears to be less in the European than in the American species. The following table gives the German naturalist's chief results on this head* :

Total length of Lobster.	Number of eggs counted.	Estimated number of eggs, including those lost after animal is caught.
25.4 cm. (10 inches)	7,026	8,000
28.1 cm. ($11\frac{1}{8}$,,)	7,376	8,000—8,500
29.1 cm. ($11\frac{1}{2}$,,)	8,420	9,009—9,500
29.5 cm. ($11\frac{3}{8}$,,)	13,532	14,000
29.2 cm. ($11\frac{1}{2}$,,)	10,330	11,000
31.0 cm. ($12\frac{3}{8}$,,)	16,800	17,500
31.1 cm. ($12\frac{1}{2}$,,)	10,307	11,000
35.5 cm. (14 ,,)	20,016	22,000
37.3 cm. (15 ,,)	29,000	32,000

An account of the number of eggs produced by the individual leads to the consideration of what Herrick calls the "law of survival of the larvæ." From the figures given for the American species, it is evident that the total number of eggs produced during the entire life of a female which reaches the length of 16 inches, must be very large, even should Ehrenbaum's conjecture that spawning takes place only once in four years prove to be correct. The question which presents itself is, what proportion of this large number of eggs must develop into sexually mature lobsters, in order to maintain the species in its existing numbers; and the answer to this question would be completely given if we knew (1) the relation of the total number of females existing to the total number of males, and (2) the number of eggs produced on the average by a sexually mature female during the whole of her life; for it is only necessary that each female should give rise to two sexually mature individuals in order to accomplish the result, if the number of males is not greatly in excess of the number of females.

It is known, from observation, that the males are not greatly in excess, but the average number of eggs produced by females during the course of their lives is more difficult to ascertain, as we have no knowledge of the number of individuals destroyed at different ages. Many, no doubt, of those which lay their first brood are destroyed before the eggs are hatched, whilst of those which survive, a constantly diminishing number produce a second, third, or fourth lot of young. This, however,

* In comparing Ehrenbaum's figures with those of Herrick, it must not be forgotten that those of the latter author are based on an examination of nearly a thousand individuals, whilst those of the former are in each case the result of counting the eggs of a single female.

is in part compensated by the fact that the number of eggs produced increases so rapidly with the increase in size of the lobster.

Herrick makes the exceedingly moderate statement that, taking into account "the fact that the species, as a whole, does not appear to be maintained at present at an equilibrium, but rather to be actually on the decline, a little reflection will convince anyone that the destruction of the young of this species in nature, must be much greater than that entailed by the survival of 2 in 10,000."

But this estimate appears, from a consideration of all the facts, to be considerably too low, and we should, I believe, be well within the mark in placing the figures at 2 in 30,000. It must not be lost sight of that the number of eggs that it is necessary for a female to produce to maintain the species at an equilibrium, in other words, the number of eggs actually produced by each female, had become a fixed quantity before there was any interference on the part of man in the way of lobster fishery, as we must suppose that the species was then adapted to its conditions. But, since the introduction of lobster-fishing has done nothing to increase or diminish the dangers to which the larva is exposed after it has become free,* the number of eggs now produced, on an average, by a female lobster during her lifetime, will give us an indication of the minimum number of eggs necessary, in order to ensure the survival to sexual maturity of two individuals.

From the *Report of the Newfoundland Department of Fisheries* for 1893, p. 39, it appears that from a total of 96,098 female lobsters taken from 1890 to 1893, the number of eggs collected was 2,247,908,000, which would give an average of 23,000 eggs for each female. This is the average number of eggs actually carried. But a female with 23,000 eggs would, according to Herrick's results, have a length of more than 12 inches, and would, therefore, from the known average age at which spawning commences, be carrying, at least, her second brood. Under these circumstances 30,000 eggs, on the average, to each female during her lifetime, must be well within the mark and the number of survivors necessary, therefore, to maintain the species cannot be more than 2 to every 30,000 eggs.

As Herrick points out, attempted remedial measures, which are confined to the mere hatching of lobster eggs, and turning the larvæ immediately into the sea, can have but little practical effect. The rate of destruction will be at least as great as in the case of larvæ hatched by the parent, and, on the estimate given above, two, at most, will survive out of every 30,000. This method of attempting to benefit the lobster industry has been extensively used in Newfoundland, and it is

* It may, of course, be maintained that the capture of other fish has tended to reduce the number of enemies of the larvæ.

interesting to calculate what the probable effect of the operations there being carried on is likely to be.

From the *Report of the Newfoundland Department of Fisheries* for 1893, it appears that the largest number of ova dealt with in any one year was 696,517,690, in 1891. Calculating the number of survivors at 2 in 30,000 (as a matter of fact, 20 per cent. were lost before hatching, a much greater number than would be lost under natural conditions), this would give 46,434 adult lobsters added to the neighbourhood. Even if all these 46,434 were caught, the percentage of increase on the whole fishery (a little over 5,000,000 in 1893) would be 0.9 per cent.

A consideration of the steps by which this conclusion has been reached will, I think, leave the impression that it is still far too high, and that a very much smaller percentage would much more nearly represent the truth. As to whether the result is sufficient to justify the trouble and expense involved in bringing it about, I will not venture to express an opinion.

If the larvæ could be reared through their early pelagic stage and not liberated until their natural instincts lead them to seek the bottom and hide themselves, the result would, as Herrick maintains, be probably very different; but if this could be successfully done on a large scale, as no doubt it might be if sufficient capital were put into the undertaking, there seems no reason why the young lobsters should not be reared to the adult stage, and to marketable size, and not turned into the sea at all. An undertaking of this kind, carried out on a scale similar to that upon which oyster-farming is conducted on the Continent, might very probably be made a success.