DEVELOPMENTAL RATES AT VARIOUS TEMPERATURES OF EMBRYOS OF THE NORTHERN LOBSTER (*Homarus americanus* MILNE-EDWARDS)

HERBERT C. PERKINS[1]

ABSTRACT

The rates of development, time from extrusion to hatching at various temperatures, and differential developmental rates at the same temperature of lobster embryos are presented. The eyes of the embryos were measured to monitor the rates and degree of embryo development.

Herrick (1890, 1896) discussed developmental rates for lobster embryos in the early stages at 20° to 22° C. Templeman (1940) determined the times required at various temperatures for lobster eggs to reach the 16-cell stage, and up to the formation of eye pigment. The information from these studies is valuable for determining the rates of early development in lobster egg-embryos but is not adequate for the accurate assessment of developing embryos once eye pigment has been formed. By monitoring the rate of development of lobster embryos throughout the embryonic period at various temperatures one can predict hatching times of larvae and control hatching times by manipulating the water temperature in tanks holding egg-bearing females, so that larvae can be available over a wide period of time for use in experiments. This paper presents the rates of development and time required to complete the embryonic period by lobster embryos at various temperatures and a method of continually monitoring that development. The work was conducted at the National Marine Fisheries Service, Biological Laboratory, Boothbay Harbor, Maine, as part of the Laboratory's investigation of the early life history of the lobster.

METHODS AND MATERIALS

Most of the egg-bearing lobsters used in this study came from the offshore canyons of the continental shelf, south and east of New England. A few came from the Boothbay Harbor area and are so noted. All egg-bearing females were kept in tanks at seasonal water temperatures or in water warmed to various constant temperatures. Water from the laboratory's seawater system was piped to the heated tanks at rates consistent with the capacity of the heaters. Salinity averaged 31‰ and ranged from 29 to 32‰ throughout the study period.

Five egg-bearing females were kept in a tank through which natural seawater at seasonal temperature was circulated during the developmental period of their eggs. The purpose of holding these females at seasonal temperatures was to determine the rates of development of their embryos in a natural temperature regime. Fourteen female lobsters from the offshore canyons, with recently extruded eggs (eggs in prenaupliar condition), were kept at constant temperatures from 6.9° to 24.6° C. The primary objective at the higher temperatures (20°-24.6° C) was to force the eggs to hatch before the time they would do so at seasonal temperatures. Of further interest was the rate of development of the embryos at constant, rather than fluctuating, temperatures, and the time required for the eggs to hatch at these temperatures from a given point in their development.

The rates and extent of development of the embryos were determined by measuring the size of their eyes. Measurements were made to the nearest micron with an ocular micrometer in a dissecting microscope at a magnification of 50×. When measuring an eye, I took its greatest width and greatest length, combined these figures and

[1] National Marine Fisheries Service, Northeast Fisheries Center, Boothbay Harbor Laboratory, W. Boothbay Harbor, ME 04575.

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divided by two. The resulting figure was used as an index of development only and was not meant to represent the actual increase or growth of the eye. Samples of 15 to 20 eggs were removed from the periphery of an egg mass whenever a measurement was desired (usually once a week). From these samples five eggs were selected randomly, and one eye of each embryo measured. A mean of these five measurements was used as a working figure or index. Eggs were taken from the peripheral layer of the mass as these are the furthest advanced in development and are the first to hatch. Variation in the eye measurements of eggs from this layer ranges from zero to 5%. When the eyes first appear and are large enough to measure, they are but thin crescents, darkly pigmented and surrounded by a halo of lighter material. The dark crescents only were measured. The eyes are very distinct for most of the developmental period and are easily measured, the crescents gradually becoming tear-drop in shape. The index of the eye is about 70μ when it is first measurable; the index is about 560μ at hatching. All eyes were measured after the eggs had been preserved in a 5% solution of Formalin in seawater. Preservation in Formalin caused significant swelling in the eggs themselves but had no determinable effect on the size of the eyes.

RESULTS AND DISCUSSION

TRENDS OF EMBRYONIC DEVELOPMENT IN WATER OF SEASONAL TEMPERATURES

The developmental patterns, from onset of eye pigment to hatching, of the embryos of the five females held at seasonal temperatures are shown in Figure 1, as is the cycle of water temperature for the same period. The trends of embryonic development were plotted by using periodic (usually weekly) measurements of the eye index of each egg mass. These five lobsters had extruded their eggs in the laboratory tanks so the age of each egg mass was known. From the latter part of November to the first of May of the following year, water temperatures were no higher than 6° C. Embryonic development during this period ceased in some of the egg masses and was barely discernible in others, at least by the method of eye index measurement. Squires (1970), using the amount of yolk material in the eggs as a criterion, reported a standstill in development during the winter in embryos of Newfoundland lobsters.

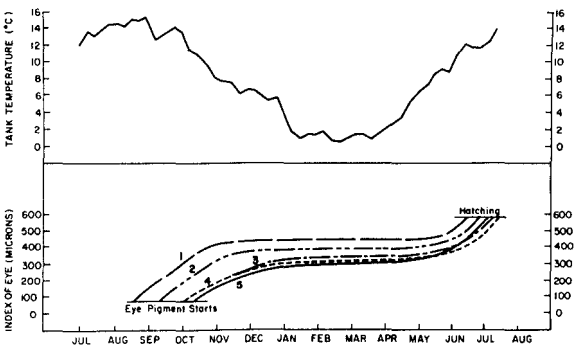

FIGURE 1.—Trends of development of the embryos of five female lobsters held in water of seasonal temperature at the Boothbay Harbor Laboratory and the temperature cycle during the period. The lines showing developmental trends are derived from plots of periodic measurements of the embryos' eye indices. The lines are numbered in accordance with the age of the egg mass; the lower the number, the older the egg mass.

DIFFERENTIAL RATES OF DEVELOPMENT

The developmental rates of lobster embryos appear to be governed not only by their thermal environment, but by the age or extent of development at which they are subjected to that environment. During the experiments I conducted the older or more advanced embryos developed at slower rates than those less advanced, though all were maintained in the same tank. The oldest egg mass of the five females held under seasonal conditions was extruded 7 weeks before the youngest, but the total time for development of the younger egg mass was 4½ weeks less than the older; the younger embryos had developed considerably faster. Measurements of the eye index of embryos in all five egg masses were made for the first time on November 7. In Fig-

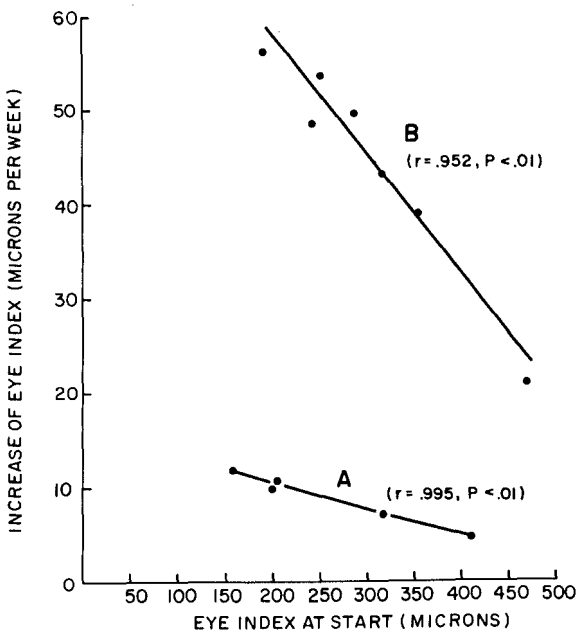

FIGURE 2.—Line A represents the different rates of increase of the eye index, in microns per week, of the embryos of the five lobsters held in the same tank, under seasonal conditions, from November 7, until hatching. Line B represents the different rates of eye increase of the embryos of seven females held at a constant temperature of 22.6° C. Size of eye index at the starting time is plotted against the corresponding rate of increase of the eye index up to the time of hatching.

ure 2(A) the rate of eye increase (microns per week) of the embryos in each egg mass for the remainder of the developmental period is plotted against the corresponding eye index taken on November 7. The same result is obtained if the age of an egg mass is substituted for its eye index on the abscissa. Rates of increase were calculated by dividing the total increase of the eye index by the total number of weeks the embryos took to complete development after November 7. The increase in eye index (microns per week) of embryos in each egg mass, for the period January 10 to March 26, is presented in Table 1. During this time the water temperature ranged between 0.1° and 1.5° C; the mean was 1.0°. This was the coldest 10-week interval of the developmental period. The embryos in the oldest egg mass exhibited no noticeable or measurable increase in development during this time, whereas some development was noted in the embryos of the other egg masses. In fact, the embryos in the oldest egg mass showed no measurable increase from the second week of December to the middle of the following April. The number of weeks during the winter in which no development could be measured, for each egg mass, was as follows (as in Table 1, lobsters are numbered according to the age of their egg mass):

TABLE 1.—Lobster number, carapace length of female, age of eggs 10 January, increase of eye index of embryos from 10 January to 26 March, and the total developmental time for the embryos of the five female lobsters held under seasonal water conditions at the Boothbay Harbor Laboratory.

Lobster number	Carapace length (mm)	Area of capture	Age of eggs 10 January (weeks)	Increase of eye index (microns/week) 10 Jan.-26 Mar.	Total weeks to hatching
1	97	Boothbay Harbor	29	0.00	51.4
2	94	Boothbay Harbor	26	0.46	50.6
3	147	Veatch Canyon	24	0.65	50.0
4	124	Hudson Canyon	23	1.49	49.4
5	94	Boothbay Harbor	22	2.52	47.0

Lobster number	*Number of "dormant" weeks during winter*
1	18
2	14
3	8
4	6
5	0

The rates of increase (microns per week) in eye index for the embryos of seven lobsters held at a constant temperature of 22.6° C are indicated in Figure 2(B). These females came from offshore canyons of the continental shelf, off New England. The ages of these egg masses were not known, but the eye index of the embryos in each was measured before the females were placed in the warm water. The increase in eye index of the embryos in each egg mass was monitored weekly until hatching. Times and rates pertain only to the time spent at 22.6° C. Although one might expect that in a given time interval, at the same temperatures, younger embryos would develop faster than older ones, it might also be expected that the younger embryos would assume the slower growth rate of the older when they eventually reached the same age. Of

the five females held in water of seasonal temperature, the youngest eggs were at lower temperatures than the older at the same age, making assessment of differential developmental rate difficult. However, of the seven egg masses held at 22.6° C the embryos of least development at the start developed faster at comparable levels of development than the more advanced embryos. The differential rate of development of lobster embryos, at the same temperature, seems to imply that in a given population where extrusion of eggs may be somewhat staggered in time among the females, hatching of the eggs would occur during a more limited period, providing the egg-bearing females occupied the same thermal environment.

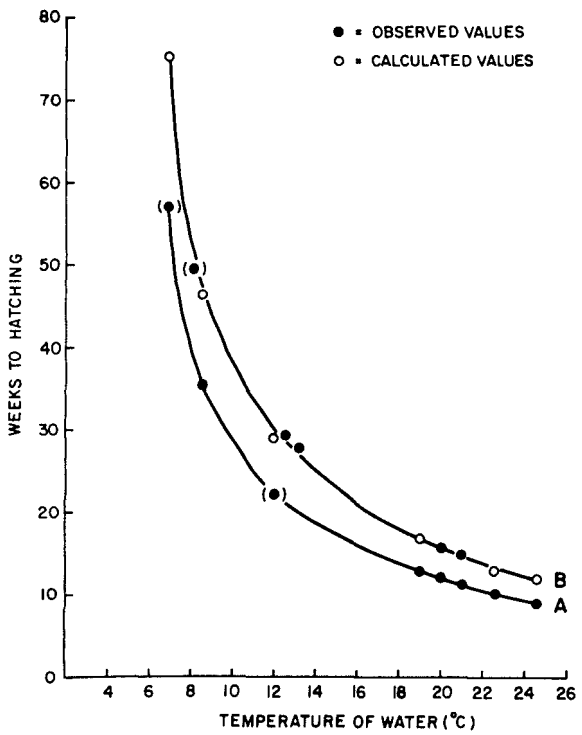

FIGURE 3.—The number of weeks for lobster eggs to complete the embryonic period at various temperatures. Line A represents the time required from onset of eye pigment in the embryos; line B represents the time required from extrusion to hatching. Points in parentheses indicate times required at the mean temperature of a fluctuating thermal environment.

RATES OF DEVELOPMENT AT VARIOUS TEMPERATURES

The times required for the embryos to hatch at various temperatures are shown in Figure 3. Line A represents the time required for the embryos to hatch after the formation of eye pigment; line B represents the time required from extrusion to hatching. Most of the points in each line indicate the time required to complete development at constant temperatures. A few (points in parentheses), representing the time required for total development at the mean temperature of a fluctuating thermal environment, have been included as well. For example, the average time required for total development of the eggs of the five females held under seasonal conditions was 49.7 weeks. The mean water temperature during the period was 8.1° C. These values are virtually the same as would be expected if the water was held constantly at 8° C.

All values showing time from onset of eye pigment to hatching were observed. The times required from extrusion to hatching at five temperatures were also observed. To find the unknown time required from extrusion to hatching, at other temperatures, I used the following equation:

$$\frac{A_1}{X_1} = \frac{A_2}{X_2}$$

where A_1 was the observed time from onset of eye pigment to hatching at 20° C; A_2 was the observed time from extrusion to hatching at 20° C; X_1 was the observed time required from

TABLE 2.—Number of weeks required from extrusion to onset of eye pigment, onset of eye pigment to hatching, and to hatching at certain temperatures, at salinities near 31‰.

Water temperature (° C)	Weeks required from		
	Extrusion to onset of eye pigment	Onset of eye pigment to hatching	Extrusion to hatching
5	40	120	160
10	9	30	39
15	5	18	23
20	4	12	16
25	3	9	12

onset of eye pigment to hatching at a given temperature; and X_2 is the unknown time required from extrusion to hatching at the same temperature as X_1. Templeman (1940, p. 74) used a similar method to find unknown developmental rates. The requisite times for development of lobster embryos at certain temperatures are summarized in Table 2. The relationship between water temperature and the average increase in eye index of lobster embryos, in microns per week, is linear at temperatures between 5° and 25° C. The index of the embryonic eye must increase to approximately 560μ at hatching. If eggs are encountered with eyed embryos, their eye index may be subtracted from 560 and the difference divided by the value calculated from the following equation:

$$\hat{Y} = -8.3151 + 2.6019(X)$$

where Y is the increase of the eye index in microns per week, and X is the developmental temperature. The resulting quotient is the average number of remaining weeks required for the embryos to hatch, depending on genetic variation and the differential rate of development noted earlier.

SUMMARY

1. Once eye pigment has been formed, the course and rate of development of lobster embryos may be monitored by the periodic measuring of the eye of the embryos.

2. Lobster embryos develop differentially, under the same thermal conditions, depending on their age or extent of development when they are subjected to a given thermal environment.

3. As water temperature has a direct effect on the developmental rate of lobster embryos, that rate may be manipulated by adjusting the water temperature of holding tanks to insure periodic hatches of larvae throughout the year.

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