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The Biology of Colonial Hydroids. III. Influence of Temperature and Nutrition on Growth of *Eirene viridula* (Thecata-Leptomedusa: Capanulinidae)

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ABSTRACT: The temperature tolerance of the hydroid *Eirene viridula* Peron and Lesueur lies within the range 11°–31 °C. Colonies grow well between 19° and 27 °C, and optimally at 23 °C, provided that they receive sufficient food (*Artemia salina* larvae) every second day. If fed less often, growth slows down. When fed at 16-d intervals, phases of growth and regression alternate. After 29 days of starvation the colonies die.

INTRODUCTION

Due to the difficulties involved in studying the influence of external conditions on marine hydrozoans in the field, such effects are often examined by means of monofactorial analysis under laboratory conditions. The number of effective factors – which usually are interdependent and act jointly on the test organism – is relatively large. It is not surprising, then, that publications dealing with the responses of hydrozoans to temperature, food supply, light, salinity, pressure and dissolved gases are numerous (for reviews consult 'Marine Ecology', Volume I: Kinne, 1970, and Volume III: Kinne, 1977).

Eirene viridula can easily be cultivated in the laboratory (Hündgen, 1978), where it reproduces both sexually and asexually (Günzl, 1964; Bierbach and Hofmann, 1973; Germer and Hündgen, 1978); it has been employed as a sensitive indicator organism in tests of pollutant effects (Karbe, 1972). The present study on *E. viridula* is concerned with nutrition and temperature dependence of growth in secondary colonies which assume the form of a stolonial mat (Kinne, 1956) under laboratory conditions.

MATERIALS AND METHODS

Colonies of *Eirene viridula* were established on glass microscope slides standing vertically in 10-l aquaria. The culture medium used was filtered artificial sea water with a salinity of 35 ‰ S. The water was sufficiently well aerated so that it was not necessary to change it.

The experimental aquaria were kept in large tanks containing water maintained at 23 °C. Normally, the colonies were fed every 2 d by transferring the slides for 30 min to Petri dishes containing 3-d-old larvae of *Artemia salina*. The experiments were continued for 70 d. Exceptions to these standard conditions are noted in the text.

RESULTS

Eirene viridula colonies increase by branching stolonial growth (Fig. 1). When tips touch other stolons, fusion may occur at points of contact. In this way a

Fig. 1. *Eirene viridula*. Photograph of part of a living colony (4.5 X)

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stolonial network is formed, coarse-meshed at first, and rapidly covering a large area. If the area of the substrate is limited, the continued formation of new branches reduces the mesh size of the hydrorhiza; reduction below a certain mesh size is followed by growth cessation.

The criterion for colony growth was the number of polyps (buds) per colony (Paffenhöfer, 1968). These were counted during feeding. At the beginning of each series of experiments, several-week-old colonies were reduced to 10 hydranths each. The hydrorhiza of all these colonies were selected so as to have principally the same pattern of branching at this stage, because one factor determining the growth rate of small colonies is the number of stolon branches present.

Influence of Temperature

To assess the effect of temperature on colony growth we transferred 4 colonies to aquaria in which the water temperature was gradually changed over a period of 24 h from 23 °C to 4°, 7°, 11°, 15°, 19°, 23°, 27°, 31° or 39 °C. In water as cold as 4 °C or as warm as 39 °C all hydranths died within the two following days; during this time most of the coenenchyma of the stolons had been broken down. Figure 2 summarizes the growth curves (obtained at 7°–35 °C; each curve represents measurements conducted on four colonies).

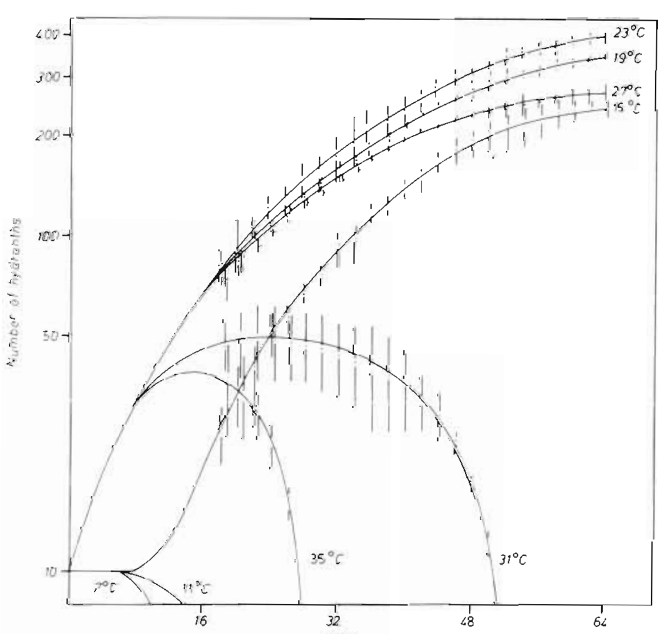

Fig. 2. *Eirene viridula.* Relation between number of hydranths and time of exposure (days) to the different temperatures indicated. Results of four experiments are combined in each curve. Points represent average measurements; vertical bars indicate ranges

In control experiments without temperature change (23 °C in Fig. 2) colonies grew exponentially for 15 d, then more slowly. Toward the end of the 70-d experiment these colonies attained their final size with ca 400 polyps. At this time, the slide serving as a substrate was completely covered by the colony. Colonies at 19° and 27 °C responded similarly, although the final polyp count was less: 350 and 270 polyps, respectively.

Even at high temperatures (31° and 35 °C in Fig. 2) initial growth was exponential, but then growth rates began to decrease drastically. At 31 °C the number of individuals began to decrease from the 25th day on. All hydranths were resorbed after 55 d. The coenosarc remained visible for a few more days, but in this condition could not be initated to form new hydranths by lowering the temperature to 23 °C. The situation was similar at 35 °C; however, decrease in growth began as early as the 15th day, with resorption of all polyps after 30 d.

When the optimal environmental temperature (23 °C) was lowered by more than 5 C°, growth stagnated. At 15 °C, growth stagnation turned, after about one week into a period of exponential growth (15 °C in Fig. 2). Final colony size, with ca 240 polyps, was not appreciably smaller than at 27 °C. Reduction of the temperature to 11° or 7 °C caused immediate growth cessation followed after one week by colony regression. All hydranths were resorbed after 40 d at 11 °C, after only 15 d at 7 °C. The temperature range tolerated by *Eirene viridula*, then, lies above 11 °C and below 31 °C. Growth is optimal at 23 °C (Fig. 3).

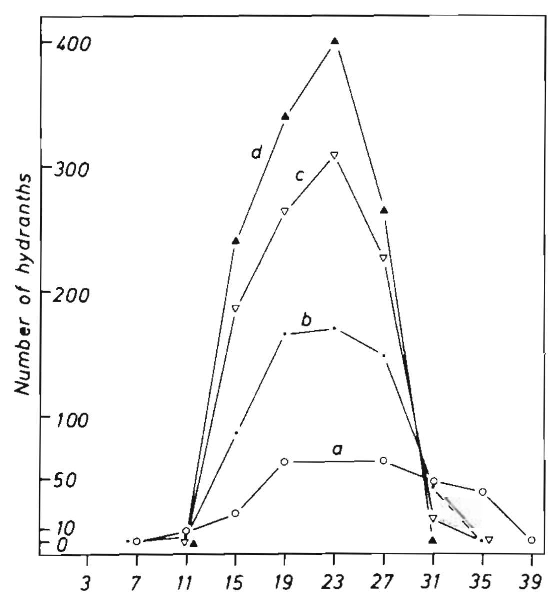

Fig. 3. *Eirene viridula.* Influence of temperature on growth (number of hydranths). Time of exposure to test temperatures: (a) 16 d; (b) 32 d; (c) 48 d; (d) 64 d. Results of four experiments are combined in each curve

Influence of Food

The effect of food supply on growth was measured by feeding *Eirene viridula* colonies at various intervals, namely 2, 4, 8, 16 or 32 d. Four colonies were studied under each condition. Daily feeding was not included in this programm, because pilot observations showed that growth rate did not differ from colonies fed at 2-d intervals. Figure 4 summarizes the results obtained. Colonies fed at short intervals (Fig. 4a), grew most rapidly. For these colonies average growth corresponds to the control curve obtained at 23 °C (Fig. 2). Increase of the intervals between feedings to 4 and 8 d causes the growth curves to flatten (Fig. 4b and c). With feeding at 16-d intervals (Fig. 4d) the curves undulate: each feeding is followed by growth which continues for about one week and then gives way to regression. At the next feeding, regression is interrupted by a new growth phase. Because the increase in number of polyps during the growth phases is greater than the decrease during the phases of regression, there is a slight overall rise in the growth curve. The colonies do not survive a longer period (28 d) of food deprivation.

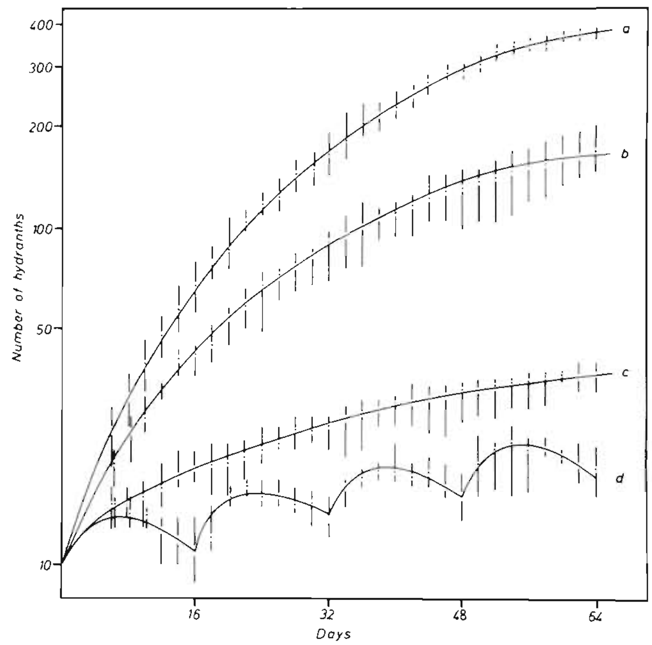

Fig. 4. *Eirene viridula*. Influence of feeding schedule (interval between feedings) on growth. Cultures were grown at 23 °C and fed to saturation for 30 min. The results of four experiments are combined in each curve. Points represent average measurements; vertical bars indicate ranges. Intervals between feedings: (a) 2 d; (b) 4 d; (c) 8 d; (d) 16 d; (e) 32 d

DISCUSSION

Coelenterates are widely used as test material for laboratory experiments and their cultivation has received considerable attention (Loomis, 1954; Kinne, 1956, 1977; Crowell, 1957; Fulton, 1960, 1962, 1963; Bick, 1966; Werner, 1968; Bierbach and Hofmann, 1973). In the experiments described here, we followed primarily recommendations by Fulton (1962).

Eirene viridula colonies grow less well after transfer to 27 °C than at 23 °C. Similar findings have been reported by Bierbach and Hofmann (1973) for *E. viridula*, by Kinne (1956) for *Cordylophora caspia* and by Crowell (1957) for *Campanularia flexuosa*. Physiological competition between polyp and medusa buds, postulated by Günzl (1964) to explain the lower rate of increase in Polyp number of *Dipurenia reesi* at increased temperatures, was not confirmed in our experiments; most of the medusae were formed in the first week of the experiment, during which growth at 19°, 23° and 27 °C was more or less the same (Fig. 2).

During the first days following a change in temperature, the colonies exhibit two types of response: initial growth stagnation (15°, 11° and 7 °C in Fig. 2) or exponential growth (19°, 27°, 31° and 35 °C in Fig. 2). However, the second type may also represent a 'successive response' (Kinne, 1956), in which adaptation lasts less than 2 d and thus was not detectable in our experiments.

Growth stagnation at the end of the experiment can be ascribed to the restricted size of the slide providing the substrate; after 70 d it was covered more or less completely by the stolon network of the *Eirene viridula* colony. When the experiments were continued beyond 70 d, the cultures sometimes departed from their two-dimensional form of growth building up in the third dimension.

Larvae of *Artemia salina* have proved a favorable food source for polyps (Loomis, 1954; Davis, 1971); the optimal amount to offer, however, can vary (Fulton, 1962). Whereas one feeding every second day produces optimal growth in *Eirene viridula*, *Campanularia flexuosa* grows best when fed twice a day (Crowell, 1957). With *Hydra littoralis* (Loomis, 1954) and *Chlorohydra viridissima* (Muscatine and Lenhoff, 1965), one feeding per day is sufficient for optimal growth. If feedings are more frequent than required for optimal growth, signs of regression eventually appear (Brinckmann, 1964; Davis, 1971). The duration of tolerable starvation periods also varies from species to species. As in the reef coral *Favia fragum* (Lewis, 1974), in *Eirene viridula* lack of food results in a reduction of hydranth size.

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