

## Heat tolerance, growth and regeneration in three North Sea bryozoans exposed to different constant temperatures

N. R. MENON

Biologische Anstalt Helgoland (Meeresstation); Helgoland, Germany (FRG)

### Abstract

Three species of bryozoans — *Membranipora membranacea* (L.), *Electra pilosa* (L.) and *Conopeum reticulum* (L.) — are capable of acclimating to elevated temperatures, above the normal range experienced in nature, when exposed to a gradual increase in ambient temperature. Conspicuous differences in LD 50 values, as a consequence of acclimation, occur between representatives of the same species acclimated and grown at constant temperatures in the laboratory. The tolerance range of these species is influenced by their thermal history in the laboratory. While increased ambient temperatures accelerate growth rate, final colony size attained after prolonged exposure declines at higher temperatures. The size of zooecia attained is inversely proportional to the test temperature. Colonies of *E. pilosa* maintained at 22°C develop erect branches. Hence, it is probable that *E. pilosa* forma *erecta* is only a growth form of normally encrusting colonies of *E. pilosa*. Temperature affects rate of regeneration.

### Introduction

Considerable attention has been paid by marine biologists to the study of temperature effects on functions and structures of marine organisms (KINNE, 1970a). Temperature is one of the most important environmental factors in the life of marine animals (BRETT, 1970; GABSIDE, 1970; KINNE, 1970b). Hardly any study devoted to experimental ecology of marine animals can be conducted without paying proper attention to temperature effects.

In contrast to the above statements, there is a deplorable paucity of literature on the effects of various environmental factors — especially temperature, salinity and nutrition — on functions and structures of marine bryozoans. Important works which have dealt, in part, with such aspects are those by MARCUS (1926), GRAVE (1930), MAWATARI (1951), and BULLIVANT (1968).

Bryozoans are sessile colonial animals commonly encountered in sub-tidal regions. They constitute important and interesting test material for the study of organismic responses to environmental conditions for the following reasons:

(1) A colony contains numerous individuals; by cutting it into parts, genetically identical material can easily be obtained.

(2) Growth by asexual reproduction yields individuals developed under known environmental conditions within a short period of time.

(3) Each colony comprises a centripetal physiological gradient (age, reproductive condition) of zooids. The gradient begins with the oldest individuals in the centre and ends with the younger ones at the periphery.

(4) The translucent nature of the zooids in many ctenostomes and a few anascans facilitate easy observation.

The degree of temperature tolerance of a given species may change during its ontogeny (KINNE, 1970b). This seems to be especially true for species with long generation times. Possibly, such potential differences are less pronounced in bryozoans which reproduce largely asexually and undergo less marked structural changes throughout their life cycle. Of the 4000 known species of recent bryozoans (RYLAND, 1970), 8 are potentially capable of producing cyphonautes larvae which lead a planktonic life for 1 to 2 months. The majority of species produce lecithotrophic larvae of ephemeral existence. Since small adjustments in temperature tolerance are possible during early ontogeny, responses to different temperatures exhibited by a growing colony are likely to express the total thermal tolerance limit of the species concerned.

In regard to temperature effects on growth, bryozoans may exhibit considerable intraspecific differences. In temperate species, for example, growth is mainly restricted to periods of rising sea-water temperatures (RYLAND, 1970). In Japanese waters, *Bugula neritina* survives the winter in the form of small colonies (MAWATARI, 1951); but in the tropics, two species of the genus *Electra* grow continuously throughout the year (MENON and NAIR, in press).

A remarkable feature of bryozoans is their ability to degenerate and regenerate. Degeneration usually takes place under unfavourable environmental conditions, at the onset of the reproductive phase, or upon natural death of the polypide.

In the present study, attempts were made to assess heat tolerance, growth, and regeneration of 3

species, viz. *Membranipora membranacea*, *Electra pilosa* and *Conopeum reticulum*, commonly encountered in typical marine habitats. In the case of *E. pilosa*, representatives of both late-autumn and summer populations were tested, whereas only late-autumn specimens of *M. membranacea* and a summer population of *C. reticulum* were used. The work represented here comprises observations made over a period of 12 months.

### Material and methods

Experiments on tolerance were conducted on material collected during October and November, 1970, and June, 1971. Growth studies were made on specimens attached on *Laminaria hyperborea* collected during October/November, 1970, and on specimens settled on plexiglass slides exposed during April/May, 1971. All species were collected from the N/C Tonne near Helgoland (Southern North Sea). Tolerance tests were performed on two types of material: (1) colonies brought in from the sea and acclimated in the laboratory; (2) colonies grown in the laboratory at different constant temperatures and under uniform nutritional conditions. 500 to 700 zooids of each of the 3 species were used per test. After bringing the zooids from 8°C (*in situ* temperature) to 17°C in successive 3°C steps, further increases in temperature were affected in 1°C steps of 24 h duration each. Colonies, acclimated and grown at 22°C, were tested when the step-wise increased test temperature reached 22°C. No further temperature increase was made when 100% mortality occurred.

Growth rates under laboratory conditions were assessed by employing two criteria. In *Membranipora membranacea*, after acclimation in the laboratory (which usually took 10 to 14 days), parts of the same colonies were transferred to different temperature levels (ladder fashion). Each step of the ladder was 1°C, with a duration per step of 24 h. The steps were chosen so as to avoid shock reactions. Another set of specimens, collected during spring and used for growth studies, came from colonies which settled on plexiglass slides positioned at 8 m water depth at N/C Tonne in April, 1971. The species studied were *Electra pilosa* and *Conopeum reticulum*. *M. membranacea* did not settle on the plexiglass slides exposed during this period.

The procedure of taking the specimens to different temperatures was similar to that followed for the earlier experiments conducted in winter. Growth rate of colonies was assessed in *Membranipora membranacea* by counting the number of individuals which had been added to 5 initial rows of zooids. *M. membranacea* was transplanted from laminarian fronds to glass slides in the laboratory. Although the zooids continued to grow in the laboratory, all died after 20 days. It seems possible that the colony parts were damaged

due to transplantation (with a razor blade), or that the interrelationship between the laminarian fronds and *M. membranacea* had been disturbed.

In *Electra pilosa* and *Conopeum reticulum*, an increase in the zooid number of whole colonies was recorded. This was possible as very young colonies with 10 to 20 zooids, attached to slides, could be sorted out. Hence, the data presented on growth rate consist of two categories: (1) number of new individuals added to 5 initial zooid rows (*Membranipora membranacea*), (2) increase in zooid number of the whole colony (*E. pilosa* and *C. reticulum*). For 60 days, zooid numbers were counted every 3 days; after this period, colonies were traced onto transparent paper at 30 day intervals and the area occupied computed with a planimeter. The number of zooids was then calculated from this area.

Many colonies of *Membranipora membranacea* and *Electra pilosa* collected during winter contained brown bodies and zooids at various stages of regeneration. In order to assess the influence of different temperature levels on the rate of regeneration, parts of some colonies with zoecia containing brown bodies were transferred directly to 8°, 12° and 18°C, and rate of regeneration observed.

The representatives of all species were fed with *Cryptomonas* sp. Each culture consisted of glass troughs containing 4 to 5 l aerated millipore (0.22 µ) filtered sea water of  $32.0 \pm 1.0\%$  S. Culture media were changed every week. 250 cm<sup>3</sup> of *Cryptomonas* culture (15000 cells/ml) was given as food once every 7 days. The cultures with specimens of *Membranipora membranacea* were kept in dim light, the others in total darkness.

## Results

### Tolerance

Temperature tolerance of *Membranipora membranacea*, *Electra pilosa* and *Conopeum reticulum* as a function of acclimation temperature is presented in Figs. 1 to 6, respectively. *M. membranacea* zooids acclimated to temperature in the field (Fig. 1) and in the laboratory (Fig. 2) show no significant differences in ultimate lethal temperature (ULT). On the other hand, LD 50-24 h occur at lower temperatures in laboratory-grown individuals. Although the temperature differences are slight (0.5° to 1.0°C), the results are statistically significant. Acclimation to high-temperature levels does not lead to a shift of LD 50 beyond the value obtained under field conditions. Even in 18°C-grown individuals, 25.3°C remains the lethal dose (LD 50-24 h).

*Electra pilosa*, acclimated and grown under defined acclimation temperatures in the laboratory, exhibit marked differences in tolerance. In 5°C-acclimated zooids, LD 50-24 h is 22.8°C; in 8°- and 12°C-acclimated zooids, it is around 25.7°C; in 18°C-acclimated

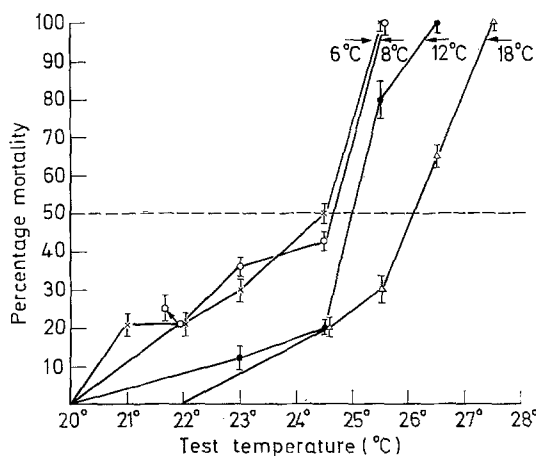


Fig. 1. *Membranipora membranacea*. Heat-death curves of zooids acclimated for 15 days to 4 different temperatures prior to tests. LD 50-24 h is indicated by horizontal broken lines. Each value represents average of 4 to 6 readings. Vertical lines: standard deviations

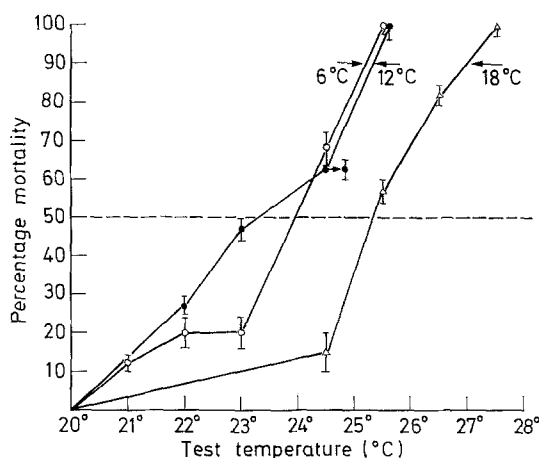


Fig. 2. *Membranipora membranacea*. Heat-death curves of zooids grown in the laboratory at 3 constant temperatures prior to tests. Each value represents average of 3 readings. Vertical lines: standard deviations

individuals 26.9 °C; and in 22 °C acclimated zooids 28.6 °C (Fig. 3). The grown representatives of the same species (Fig. 4) also showed an upward shift in the ULT. LD 50 occurred more or less at the same temperatures as in their acclimated counterparts from nature.

A comparison of the degree of tolerance in representatives of late-autumn and early-spring populations revealed (neither upon abrupt temperature increase nor after laboratory acclimation) no noticeable shifts which could be interpreted as seasonal effects.

*Conopeum reticulum* tolerated the highest temperature level (Figs. 5 and 6). The acclimation temperatures experienced in the laboratory affect both ULT and LD 50. The total resulting difference in LD 50 between 6°- and 22 °C-exposed individuals was 5.0 °C. A noticeable shift was evident in ULT, which was 30 °C for 22 °C-acclimated bryozoans and 32 °C for those grown under constant temperature conditions.

The lower lethal temperature (LLT) of zooids of the 3 species acclimated at 6° and 12 °C, was always below 0 °C. Death of polypides occurred only when they were taken to a temperature at which ice crystals appeared in the sea water (ca. -1.8 °C), whereas LLT was 1.5 °C for 18 °C- and 2.5 °C for 22 °C-acclimated specimens.

In *Electra pilosa*, kept at -4 °C for 14 days, the inner zooids died; however, rim individuals continued to regenerate. The animals which were maintained in 6 °C for 6 months were transferred to -4 °C over a period of 3 days. They were then kept in ice at -4 °C for 14 days. All the animals had been killed, but when brought to 6 °C by dissolving the ice, and kept in culture with food for 14 days, all the zooids at the rim of the colonies regenerated and functioned normally. This result shows that individual zooids of one colony may reveal different degrees of thermal resistance. Cold-tolerance decreases with age.

### Growth

The rates of growth of the 3 species are presented in Figs. 7 to 11.

In *Membranipora membranacea*, growth at 6 °C was very slow. It accelerated considerably at 12° and 18 °C. After 32 days, growth rate at 18 °C were higher than at 12 °C.

The colonies of *Membranipora membranacea* brought in from the field initially contained 15 to 20 rows of zooids at various stages of development. Before adding new zooids at the rim, these zooids completed their growth and started feeding, before budding additional zooids. This was true in the case of all colonial parts exposed to different temperatures. However, the time taken for this process was 29 days at 6 °C, 10 days at 12 °C and 6 days at 18 °C.

The rate of growth of *Electra pilosa* is given in Figs. 8 and 9. Growth rate was very slow at 6 °C. Growing at an equal pace to the 12 °C-exposed colonies to begin with, those individuals at 18 °C eventually outpaced the former. In 22 °C, the growth distinctly increased. However, after an initial accelerated growth for 4 months, a retardation occurred and, after 6 months, the final growth was more or less similar to that of individuals exposed to 18 °C.

Figs. 10 and 11 give the rate of growth of *Conopeum reticulum*. Growth at 12 °C was distinctly less than that of colonies exposed to 18 °C. Another dif-

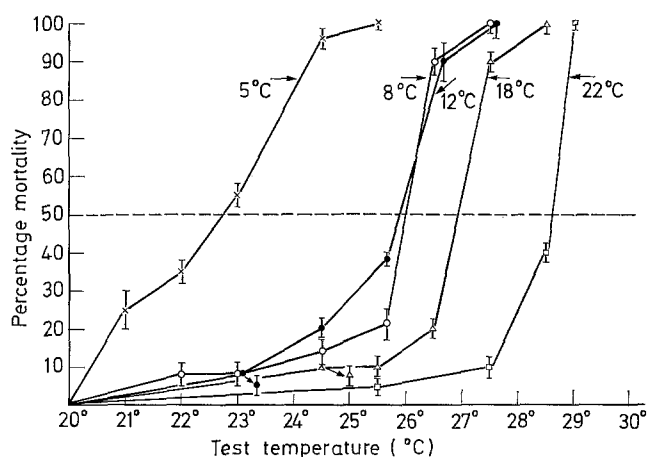


Fig. 3. *Electra pilosa*. Heat-death curves of zooids acclimated for 15 days to 5 different temperatures prior to tests. LD 50-24h is indicated by horizontal broken line. Each value represents average of 4 to 6 readings. Vertical lines: standard deviations

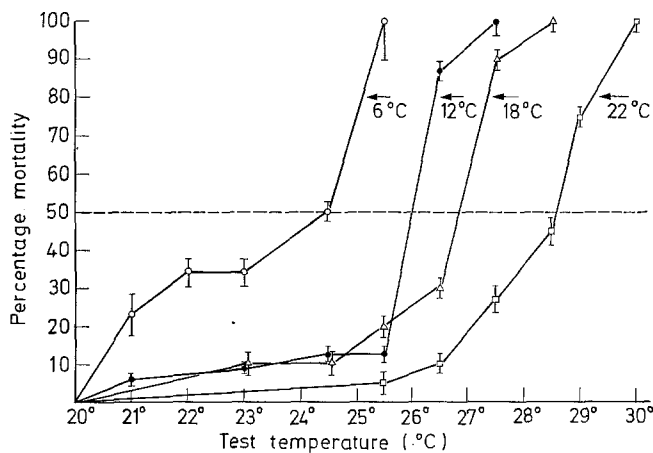


Fig. 4. *Electra pilosa*. Heat-death curves of zooids grown in the laboratory at 4 constant temperatures prior to tests. LD 50-24h is indicated by horizontal broken line. Each value represents average of 4 readings. Vertical lines: standard deviations

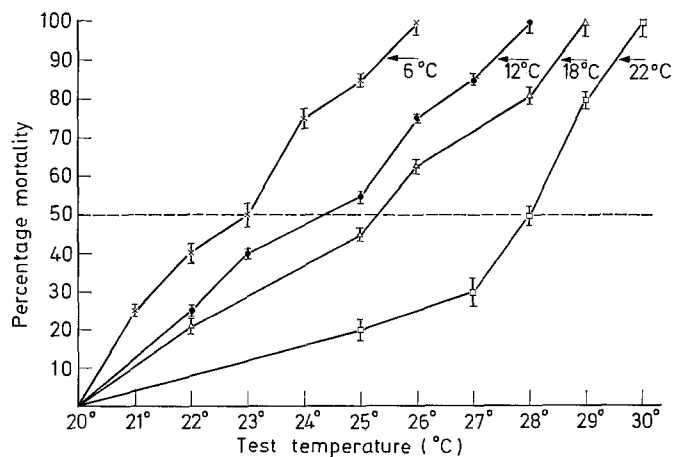


Fig. 5. *Conopeum reticulatum*. Heat-death curves of zooids acclimated for 15 days to 4 different temperatures prior to tests. LD 50-24h is indicated by horizontal broken line. Each value represents average of 4 readings. Vertical lines: standard deviations

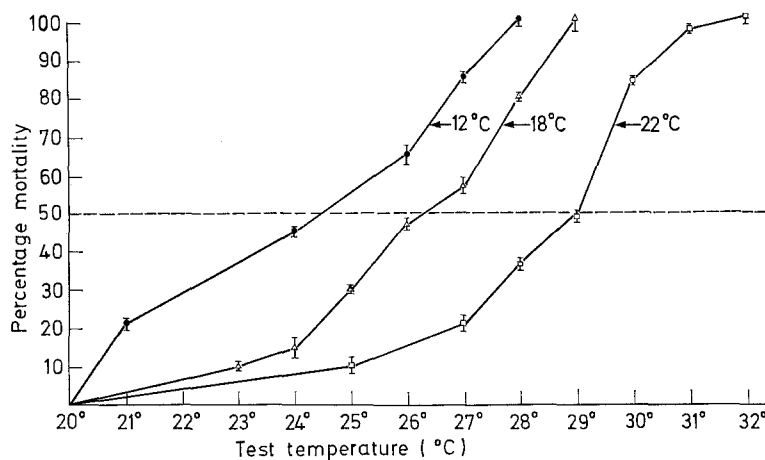


Fig. 6. *Conopeum reticulatum*. Heat-death curves of zooids grown in the laboratory at 3 constant temperatures prior to tests. LD 50-24 h is indicated by horizontal broken line. Each value represents average of 3 readings. Vertical lines: standard deviations

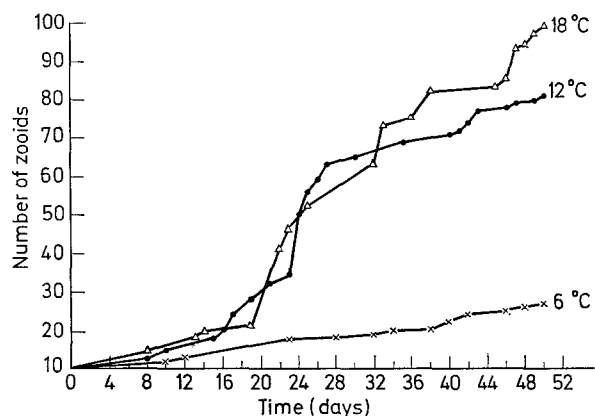


Fig. 7. *Membranipora membranacea*. Growth rate based on increase in zooid number of 5 initial rows of zooids exposed at 3 constant temperatures

ference which could be noticed in the growth of this species was the uniform trend in growth maintained by colonies exposed at 18° and 22 °C. The data gathered at the end of 6 months shows that the colonies at 22 °C have considerably reduced their pace of growth.

In the laboratory, the colonies of *Electra pilosa* and *Conopeum reticulatum* kept at 6° and 22 °C never attained sexual maturity, as evidenced by the absence of ova and sperms. Those at 12° and 18 °C became sexually mature within 48 and 31 days, respectively. However, none of the colonies bred in the laboratory.

#### Structural responses

##### Size

The dimensions of zooecia developed under different constant temperatures in the laboratory are given in Table 1.

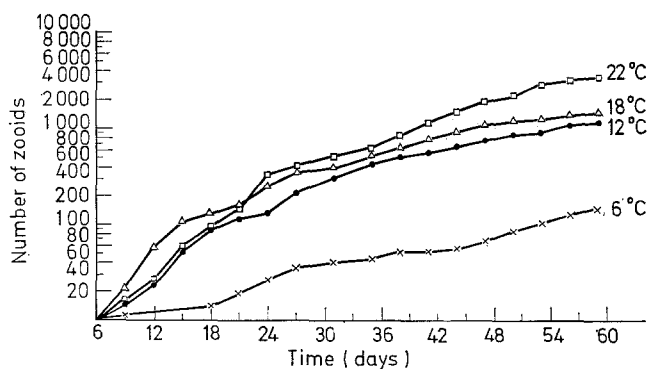


Fig. 8. *Electra pilosa*. Growth rate of colonies exposed to 4 constant temperatures

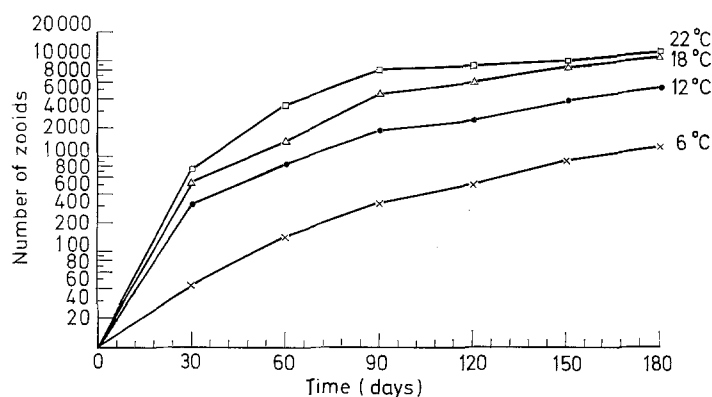


Fig. 9. *Electra pilosa*. Growth rate of colonies at 30 day intervals for 180 days at 4 constant temperatures

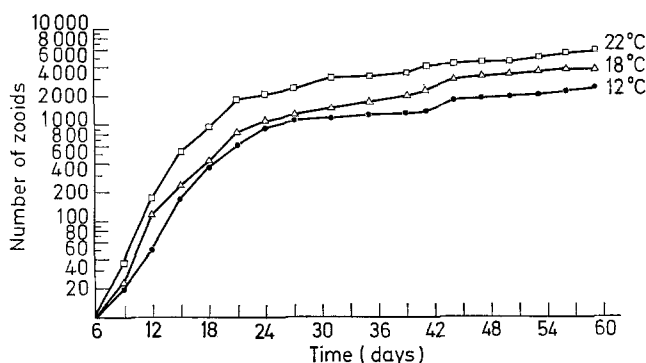


Fig. 10. *Conopeum reticulum*. Growth rate of colonies exposed to 3 constant temperatures

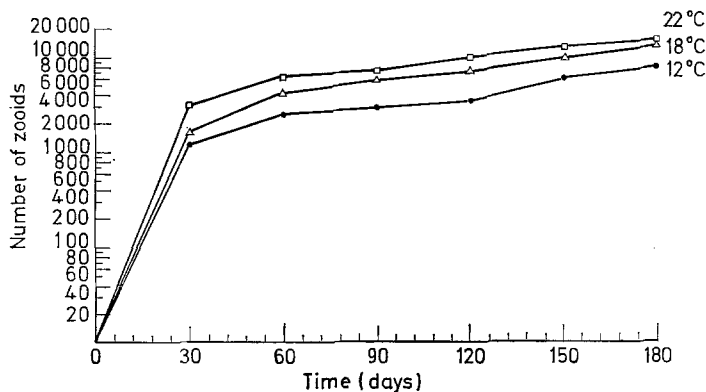


Fig. 11. *Conopeum reticulum*. Growth rate of colonies at 30 day intervals for 180 days at 3 constant temperatures

It is evident from Table 1 that, in both *Electra pilosa* and *Conopeum reticulum*, increased temperature has resulted in a reduction of the final zoecial size.

#### External characters

One colony of *Electra pilosa* kept at 22 °C produced erect branches. Usually this occurred at places in the

colony where two growing tips met. The daughter zooids produced at such meeting-points maintained a slanting position and, by the addition of new zooids, an erect branch was formed. A tendency to grow erect was also noticed when a growing tip collided with an encrusted portion of the same colony (Fig. 12). The spinous adornment, characteristic of zoecia of erect portions of colonies collected from nature, was totally

Table 1. Means ( $\bar{x}$ ) and standard deviations ( $s$ ) of length and breadth of 50 zoecia of bryozoan colonies maintained at different constant temperatures

*Electra pilosa*

Temperature (°C)	6°	12°	18°	22°
Length	$\bar{x}$ 686.34 $\mu$ $s$ 175.23 $\mu$	$\bar{x}$ 596.37 $\mu$ $s$ 41.60 $\mu$	$\bar{x}$ 586.35 $\mu$ $s$ 29.57 $\mu$	$\bar{x}$ 577.00 $\mu$ $s$ 36.70 $\mu$
Breadth	$\bar{x}$ 303.61 $\mu$ $s$ 36.35 $\mu$	$\bar{x}$ 311.81 $\mu$ $s$ 25.09 $\mu$	$\bar{x}$ 314.37 $\mu$ $s$ 32.64 $\mu$	$\bar{x}$ 314.30 $\mu$ $s$ 51.20 $\mu$

*Conopeum reticulum*

Temperature (°C)	12°	18°	22°
Length	$\bar{x}$ 558.31 $\mu$ $s$ 51.34 $\mu$	$\bar{x}$ 518.65 $\mu$ $s$ 43.64 $\mu$	$\bar{x}$ 500.00 $\mu$ $s$ 49.02 $\mu$
Breadth	$\bar{x}$ 315.27 $\mu$ $s$ 26.57 $\mu$	$\bar{x}$ 285.18 $\mu$ $s$ 46.72 $\mu$	$\bar{x}$ 314.24 $\mu$ $s$ 34.70 $\mu$

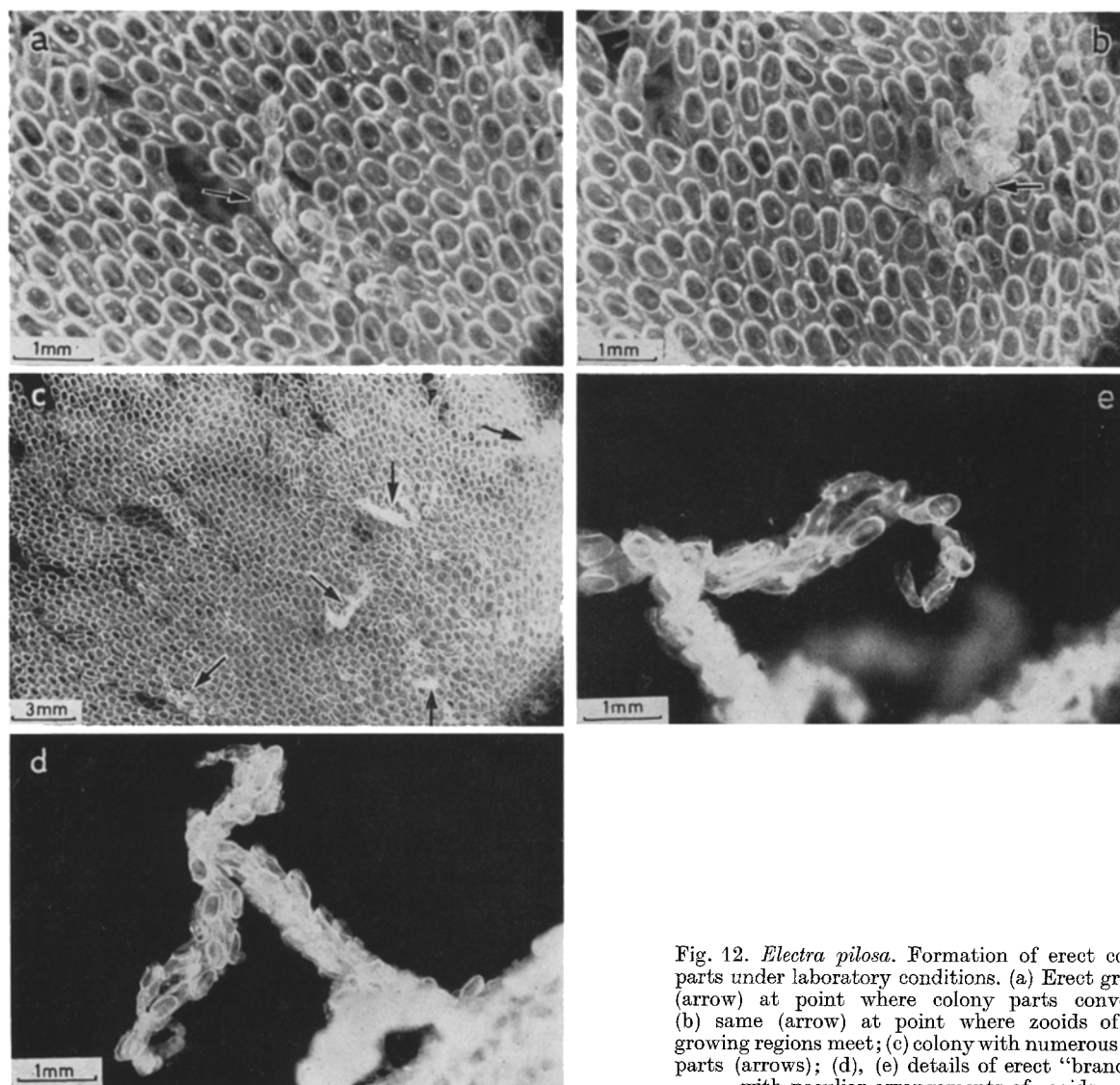


Fig. 12. *Electra pilosa*. Formation of erect colony parts under laboratory conditions. (a) Erect growth (arrow) at point where colony parts converge; (b) same (arrow) at point where zooids of two growing regions meet; (c) colony with numerous erect parts (arrows); (d), (e) details of erect "branches" with peculiar arrangements of zooids

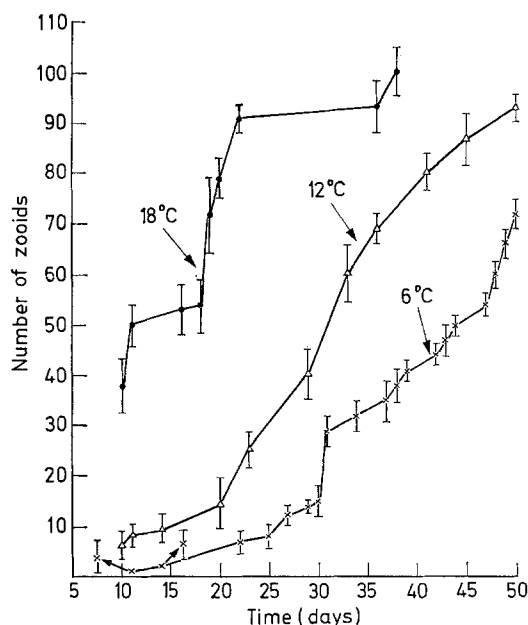


Fig. 13. *Membranipora membranacea*. Rate of regeneration of degenerated zooids, exposed to 3 constant temperatures. Each value is average of 4 to 5 readings. Vertical lines: standard deviations

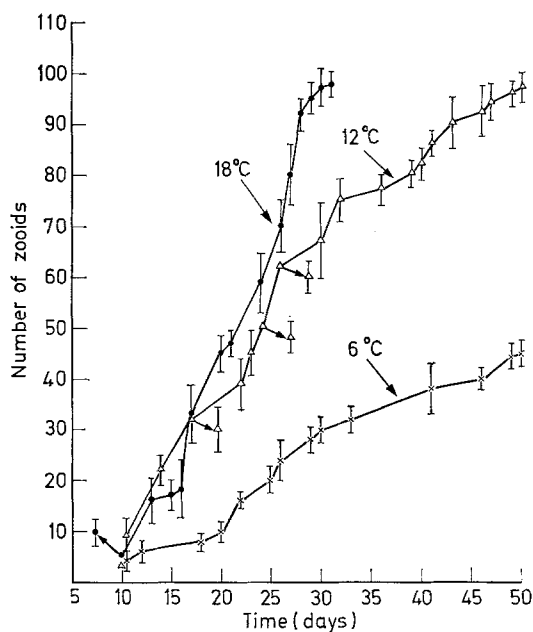


Fig. 14. *Electra pilosa*. Rate of regeneration of degenerated zooids, exposed to 3 constant temperatures. Each value is average of 3 to 4 readings. Vertical lines: standard deviations

absent in those grown in the laboratory. The development of spines, in general, showed retardation. This suppression of spine development in the laboratory cultures (observed in *Callapora lineata* also) is inter-

esting, and a correct interpretation of this phenomenon could be given only by a study of calcium deposition, which promises interesting results.

The enlargement of the triangular opesial spaces in *Conopeum reticulum* occurred conspicuously only in colonies maintained at 18 °C. The reticulum zooids, which are found in large numbers at the centre of the colonies exposed to 18 °C, assume larger dimensions in the course of time. The maximum size attained is 232.2  $\mu$  length, 129.0  $\mu$  breadth. Here, the development of operculum, and a feeding individual very comparable to an autozooid, occur. In the majority of cases, the reticulum zooids contain only granulated brown bodies and no opercula.

### Regeneration

Rate of regeneration in *Membranipora membranacea* and *Electra pilosa* is shown in Figs. 13 and 14. It is quite clear from the figures that temperature has a direct bearing on the rate of regeneration. Regeneration of the zooids took place from the periphery of the colony parts towards the centre. This indicates that the capacity to regenerate is greater in the young zooids than in the old ones. The life of a polypide under different temperature regimes was never uniform. The "age" of polypides varies from 10 to 32 days. The capacity to regenerate may be lost only at very extreme temperatures.

### Discussion and conclusions

KINNE has aptly stated that the determination of lethal temperatures is a useful tool for assessing (1) inter- and intraspecific differences in temperature tolerance, (2) the physiological condition, (3) the status of acclimation to a given temperature" (KINNE, 1963, p. 307). The present study helps to elucidate two points of the above statement, viz. the inter- and intraspecific differences in temperature tolerance and the status of acclimation to a given temperature.

Whether brought from the sea and acclimated in the laboratory or grown under constant temperatures, the tolerance rate increases as a function of increased acclimation temperature. The zooids of *Membranipora membranacea* tested are genetically identical, as they were obtained from the same colony. Nevertheless, the difference in tolerance (LD 50) between the 6 °C-acclimated and 18 °C-acclimated animals amounts to 1.6 °C. Comparison of the difference in tolerance between the zooids acclimated at different temperatures and those grown under constant temperatures in the laboratory shows that the degree of temperature tolerance was equal. The zooids which grew at a constant temperature and under uniform nutritional conditions did not experience the cyclic variations in temperature and nutrition of their counterparts which settled under field conditions in late summer. The



observed similarities in the total tolerance-range reveal that, although adjustments are possible, the ULT is species specific.

*Electra pilosa*, which enjoys a wider range of distribution than *Membranipora membranacea*, exhibits a high capacity for thermal acclimation. The ULT was 25.5 °C in 5 °C-acclimated animals, whereas it was 29 °C for 22 °C-acclimated animals. The total gain in resistance acquired was 3.5 °C.

*Conopeum reticulum*, a cosmopolitan, showed the highest tolerance. The difference between 6 °C-acclimated and 22 °C-acclimated forms as well as colonies grown under defined acclimation-temperatures of 12° and 22 °C in the laboratory was 4 °C.

*Electra pilosa* and *Conopeum reticulum* have been reported from tropical (GAUTIER, 1962; MENON and NATR, 1967) as well as from boreal waters. It is, therefore, evident that populations of these species which can tolerate very wide ranges in temperature do exist. Of these two species, *E. pilosa* is more abundant in the temperate and boreal waters. Tolerance experiments show that, if slowly acclimated, this species grows very well and fast at 22 °C, which should, therefore, be a temperature range reasonably below the ULT of this species. The inability (no matter whether acclimated or grown under defined artificial conditions) to tolerate temperatures above 30 °C, suggests that 30 °C represents the ULT of the population occurring in this part of the North Sea.

Studies which deal with the growth of bryozoans under laboratory conditions are those of MARCUS (1926), GRAVE (1930), SCHNEIDER (1959), and JEBRAM (1968, 1970). In these papers, little or no attention has been paid to temperature influences on growth of representatives of the same population.

Information on the effects of temperature on the growth of other colonial invertebrates under laboratory conditions is mainly confined to the studies of KINNE (1956, 1958), FULTON (1962), KINNE and PAFFENHÖFER (1966) and PAFFENHÖFER (1968).

In general, rates of metabolism and activity increase with rising temperatures within the range tolerated and then decrease suddenly near the ULT. Our data on growth rates support this statement (also data on O<sub>2</sub> consumption and feeding rates substantiate this assumption; unpublished own results). There was a noticeable difference in growth between animals maintained at 6° and 12 °C and those kept at 22 °C in the initial stages of the experiments. However, long-term observation (24 weeks) show that there is a tendency to "level off" and the possibility that colonies growing at 12 °C finally "outgrow" those kept at 22 °C.

The bryozoans grew exponentially in the laboratory, similar to the mode of growth observed in nature. When the data on the increase in area of field colonies was fitted to the equation  $y = a X x^n$ , the equation, after taking logarithm to the base 10, reduces to a

straight line of the form  $y = a X n X x$  (MENON and NATR, in press).

Rate of growth of *Electra pilosa* and *Conopeum reticulum* in situ at N/C Tonne during the period June to September was faster than that in the laboratory. It is quite possible that the restricted food supply of uniform quality and quantity (*Cryptomonas* sp. 250 cm<sup>3</sup> per week) was not sufficient for these bryozoans. Because of practical difficulties, an increase in food ration was not possible.

An examination of the percentage growth of *Electra pilosa* and *Conopeum reticulum* at different levels of temperature shows that the period required to attain 50% of the total recorded growth for 6 months at 12°, 18° and 22 °C was 18, 16 and 12 weeks, respectively for both species. This clearly indicates that growth at the upper temperature is fast to start with, but that the same pace is not maintained throughout.

In the laboratory, KINNE and PAFFENHÖFER (1966) found that the doubling-time of polypide numbers for *Clava multicornis* is progressively reduced with increasing temperature. From the data now available, it is clear that this is also true during the initial phase of colonial growth in *Electra pilosa* and *Conopeum reticulum*.

The data on the size of zoecia achieved at different temperatures show that those individuals which developed at lower temperatures attained a larger size; although the difference is not outstanding, considering the fact that zoecial dimensions are important morphological characters, the observed variations are interesting. KINNE (1963) regarded that a larger final body-size may be related to reduced metabolic rate and growth, with a concomitant postponement of sexual maturity and prolongation of life.

JEBRAM found that the triangular or rounded inter-opesial spaces develop into reticulum zooids in *Conopeum reticulum*, and reported fully-functioning polypides: "some of the polypides in the reticulum zooids attain the size of the polypides in the auto-zooids" (JEBRAM, 1968, p. 126). In the present investigation, the size of the feeding individual never equalled that of the autozooid. Further, as the development of these structures occurred at the central region of the colonies (where usually more than one lamina of zooids is present) it is doubtful whether the larger reticulum zooids represent suppressed auto-zooids.

The development of erect branches in *Electra pilosa* reveals that *E. pilosa* forma *erecta* represents a temperature modification of the encrusting parent colony. JEBRAM (1970, p. 288) noticed rudimentary development of erect branches in his cultures, but could not gather conclusive evidence as his culture "died from a defect of food". During the present investigation, erect branches (as many as 23) developed in a colony kept in still water in the laboratory. The

beginnings of erect branches were observed 10 days after the colony was brought to 22 °C (15 days acclimation from 8° to 22 °C). JEBRAM (1970, p. 289) remarked "I have not observed the growth of such structures typical of *E. pilosa* forma *erecta* in still water in the laboratory". This observation, and the evidence that *E. pilosa* shows positive rheotropism, led him to the conclusion that negative geotropism can be due to the influence of slow water-current speed. These contrasting observations suggest that a factor apart from water movement could influence the formation of *E. pilosa* forma *erecta*. As erect branches occur only at 22 °C, accelerated growth and differentiation seem of primary importance. All the erect colonies collected around Helgoland during August and September, 1971 were found in association with *Phylloporhpora membranifolia* and *Chaetomorpha melagonium* (Dr. K. LÜNING, BAH, kindly identified the algae), which offer comparatively little space for encrustation. It is evident from the studies of FRIEDL (1925) that, in *Schizoporella sanguinea* of temperate waters, maximum growth occurs in August/September, both in the autumn generation which survived the winter, and in the freshly settled summer generation. This clearly indicates that temperature elevation triggers faster growth in this species. NAIR (1962) found maximum growth of bryozoans in the fjords of Norway during late spring and summer, when the temperature moved upward from 8 °C in May to 16.5 °C in July. STEBBING (1971) discerned accelerated growth from mid-March to November, and recorded practically no growth for November until late February.

Rate of regeneration depends on temperature in *Membranipora membranacea* and *Electra pilosa*. This indicates that, in the sea, increasing temperatures during spring and summer will initiate regeneration of zooecia which degenerated during the cold winter.

### Summary

1. The bryozoans *Membranipora membranacea* (L.), *Electra pilosa* (L.) and *Conopeum reticulum* (L.) were acclimated and grown under defined laboratory conditions for periods ranging from 50 to 180 days and thermal tolerances of acclimated colonies assessed in terms of ultimate lethal temperature (ULT) and lethal dose (LD 50).

2. Both ULT and LD 50 levels vary significantly as a function of acclimation temperature.

3. Growth in all 3 bryozoans is exponential.

4. Increased temperatures accelerate growth rates.

5. Growth rates obtained in the laboratory are lower than those occurring under *in situ* conditions.

6. *E. pilosa* develop erect branches at 22 °C. Presumably, acceleration of growth and differentiation as well as insufficient space for encrustation, result in erect growth.

7. Reduction in average zooecia size is caused by increasing temperatures.

8. The majority of reticulum zooids in *C. reticulum* lack opercula. Feeding individuals formed in the remainder are much smaller than normal autozooids.

**Acknowledgements.** I am deeply indebted to Professor Dr. O. KINNE, Leading Director and Professor of the Biologische Anstalt Helgoland (FRG) for introducing me to experimental ecology. With a warm sense of gratitude I acknowledge his help and encouragement and his personal interest during my stay on Helgoland. I am thankful to Mr. K. KLÖCKNER for allowing me to use his underwater installation for the collection of bryozoans and record my gratitude to other members of staff of the Biologische Anstalt Helgoland who helped me during my work. Thanks are due to Mrs. I. MENON for her assistance in preparing the manuscript and to Mrs. R. FRIEDRICH for her help in editing the paper. I am grateful to DAAD, Bad Godesberg (FRG), for financial assistance, and to the authorities of the University of Agricultural Sciences, Bangalore (India), for granting study leave.

### Literature cited

- BRETT, J. R.: Temperature. Animals: fishes. (Functional responses). In: Marine ecology. Vol. I. Environmental factors, Part 1. pp 515—560. Ed. by O. KINNE. London: Wiley Interscience 1970.
- BULLIVANT, J. S.: The rate of feeding of the bryozoan *Zoobotryon verticillatum*. N. Z. J. Freshwat. Res. 2, 111—134 (1968).
- FRIEDL, H.: Koloniebildung, Besiedlung und Wachstum bei marinen Bryozoen. Arb. zool. Inst. Univ. Innsbruck 2, 139—168 (1925).
- FULTON, C.: Environmental factors influencing growth of *Cordylophora*. J. exp. Zool. 151, 61—78 (1962).
- GARSDALE, E. T.: Temperature. Animals: Fishes. (Structural responses). In: Marine ecology. Vol. I. Environmental factors, Part 1. pp 561—573. Ed. by O. KINNE. London: Wiley Interscience 1970.
- GAUTIER, Y. U.: Recherches écologiques sur les bryozoaires cheilostomes en Méditerranée occidentale. Recl Trav. Stn mar. Endoume 38, 1—434 (1962).
- GRAVE, B. H.: The natural history of *Bugula flabellata* at Woods Hole, Massachusetts, including the behaviour and attachment of the larva. J. Morph. 49, 355—383 (1930).
- JEBRAM, D.: A cultivation method for salt water Bryozoa and an example for experimental biology. 1st I.B.A. International Conference on Bryozoa. S. Donato Milanex. 1968. Atti Soc. ital. Sci. nat 108, 119—128 (1968).
- Preliminary experiments with Bryozoa in a simple apparatus for producing continuous water currents. Helgoländer wiss. Meeresunters. 20, 278—292 (1970).
- KINNE, O.: Über den Einfluß des Salzgehaltes und der Temperatur auf Wachstum, Form und Vermehrung bei dem Hydroidpolypen *Cordylophora caspia* (PALLAS), Athecata, Clavidae. Zool. Jb (Abt. allg. Zool. Physiol. Tiere) 66, 565—638 (1956).
- Über die Reaktion erbgleichen Coelenteratengewebes auf verschiedene Salzgehalts- und Temperaturbedingungen. Zool. Jb. (Abt. allg. Zool. Physiol. Tiere) 67, 407—486 (1958).
- The effects of temperature and salinity on marine and brackish water animals. I. Temperature. Oceanogr. mar. Biol. A. Rev. 1, 301—340 (1963).
- (Ed.) Marine ecology. Vol. I Environmental factors, Part 1. 681 pp. London: Wiley Interscience 1970a.
- Temperature. Animals: invertebrates. In: Marine ecology. Vol. I. Environmental factors, Part 1. pp 407—514. Ed. by O. KINNE. London: Wiley Interscience 1970b.

- and PAFFENHÖFER, G.-A.: Hydranth structure and digestion rate as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). Helgoländer wiss. Meeresunters. **12**, 329—341 (1965).
- — Growth and reproduction as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). Helgoländer wiss. Meeresunters. **13**, 62—72 (1966).
- MARCUS, E.: Beobachtungen und Versuche an lebenden Meeresbryozoen. Zool. Jb. (Abt. Syst. Ökol. Geogr. Tiere) **52**, 1—102 (1926).
- MAWATARI, S.: The natural history of a common fouling bryozoan *Bugula neritina* (LINNAEUS). Misc. Rep. Res. Inst. nat. Resour., Tokyo **19/21**, 47—54 (1951).
- MENON, N. R. and N. B. NAIR: The ectoproctous bryozoans of the Indian waters. J. mar. biol. Ass. India **9**, 430—433 (1967).
- The growth rates of four species of inter-tidal bryozoans in Cochin backwaters. Bull. natn. Inst. Sci. India. (In press).
- NAIR, N. B.: Ecology of marine fouling and wood boring organisms of western Norway. Sarsia **8**, 1—88 (1962).
- PAFFENHÖFER, G.-A.: Nahrungsaufnahme, Stoffumsatz und Energiehaushalt des marinen Hydroidpolypen *Clava multicornis*. Helgoländer wiss. Meeresunters. **18**, 1—44 (1968).
- RYLAND, J. S.: Bryozoans, 175 pp. London: Hutchinson 1970.
- SCHNEIDER, D.: Der Aufbau der *Bugula*-Tierstöcke und seine Beeinflussung durch Außenfaktoren. Biol. Zbl. **78** (2), 250—283 (1959).
- STEBBING, A. R. D.: Growth of *Flustra foliacea* (Bryozoa). Mar. Biol. **9**, 267—273 (1971).
- Author's address: Dr. N. R. MENON  
College of Fisheries  
University of Agricultural Sciences  
Mangalore-1  
India

Date of final manuscript acceptance: February 15, 1972. Communicated by N. K. PANIKKAR, Panaji