Marine Biology 9, 267—273 (1971)

Growth of *Flustra foliacea* (Bryozoa)

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Abstract

The perennial bryozoan *Flustra foliacea* L. has annual growth-checks which leave lines across the fronds. These growth-checks have been used to determine the age and the pattern of growth of the colonies in terms of height and numbers of zooids. Monthly samples have been used to find the annual growth cycle. Heavy encrustations of epizoites on the *F. foliacea* colonies reduce growth rate. As the fronds increase in height, frontal budding of zooids thickens, and thereby strengthens, the holdfast.

Introduction

EGGLESTON (1963), in an unpublished thesis, noted that the lines which cross the fronds of the perennial bryozoan *Flustra foliacea* at intervals are the result of an annual cessation of growth from October to February; and that these lines could probably be used to determine the age of the colonies. However, he gave no empirical evidence to substantiate this interesting observation. The objects of the present study were first, to verify EGGLESTON's observations and second, to use this method of age determination to study the growth of *F. foliacea* colonies.

Examination of *Flustra foliacea* fronds from Oxwich Point, South Wales, has shown that these growth-check lines are more pronounced on the older parts of the frond. When looked at under a low power stereomicroscope, many of the zooids along these lines can be seen to lack spines and often have distorted lateral walls. When recently formed, soon after growth restarts in spring, the lines are difficult to see. However, with age they become more conspicuous; it appears that the force of water movement on the younger parts causes the frond to bend along what are evidently lines of weakness. This constant flexing presumably results in the loss of spines and distortion of the lateral walls of the zooids along these lines. *Membranipora membranacea*, which is typically found on the fronds of laminarians, has gaps in the calcification of the zooidal lateral walls which allow the bryozoan colony to bend with the laminarian (RYLAND, 1970, p. 76). There appears to be no such adaptation in *F. foliacea*, so the annual growth-check lines may give the colonies flexibility.

Initially, growth of *Flustra foliacea* colonies is unilamellar and adherent to the substratum (Fig. 1). How long the colonies grow in this way before becoming erect and bilamellar is not clear. For the purposes of this paper, the first winter of the colony is considered to be represented by the first growth-check on the erect frond near the holdfast. Therefore, a colony during its fourth summer (Fig. 1) would have 3 lines, representing growth-checks, across the frond. The fourth line would be formed along the distal edge during the following winter.

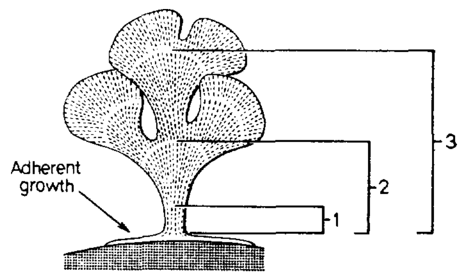

Fig. 1. *Flustra foliacea.* Diagram of frond showing growth-check lines, and height and age of frond in years with respect to these lines

The growth history of *Flustra foliacea* colonies over the observable part of the life span was determined (in terms of height of the fronds and numbers of zooids) by back measurement. The annual pattern of growth in height was worked out from monthly samples over a complete year. At the same time, observations were made on the effects of encrustations of epizoites on growth rates, and the part played by frontal budding in strengthening the holdfast.

Habitat

Samples of *Flustra foliacea* were dredged by R V "Ocean Crest" at approximately monthly intervals from a depth of 15 to 20 m in an area about 0.5 nautical mile south of Oxwich Point, on the Gower Peninsula, South Wales. Here, ridges and hummocks of carboniferous limestone project through the gently undulating, coarse sandy bottom. To these are attached numerous clumps of *F. foliacea* colonies, interspersed with colonies of *Nemertesia antennina* and *Chartella papyracea*.

A type of oyster dredge was used which was developed locally for use on the rough bottom (KING and OSBORN, 1969). The dredge bag was lined with hessian and/or shrimp netting to prevent the loss of small fronds and motile epifauna through the coarse meshes. Occasionally, collections and observations were also made by diving. After sorting to remove all free-living organisms, which form the subject of separate studies, the *F. foliacea* samples were preserved in 70% alcohol. The sessile fauna of the *F. foliacea* fronds is dealt with in another paper (STEBBING, in press).

Off Oxwich Point, the habitat of *Flustra foliacea* is subject to strong tidal flow. This agrees with the conclusions of Mr. E. I. S. REES (personal communication), who found that, around Anglesey, *F. foliacea* is most abundant in areas where the mean surface current speed at spring tides is 2.0 to 3.5 knots (1.0 to 1.8 m/sec).

Methods

Measurements were made with a transparent ruler from the holdfast to the peripheral growing edge of the longest branch of the frond. Measurements of the height of the colonies at different ages were made in a similar fashion, but to the most distal part of each growth-check line. The increase in numbers of zooids was determined by weighing. As the zooids of *Flustra foliacea* are of approximately equal size both on different parts of one frond and on different fronds, they are assumed to be of approximately uniform weight when damp. The number of zooids should, therefore, be directly proportional to the weight of a frond. To find the relationship between frond area, weight and numbers of zooids, ten 1 cm^2 pieces of frond were cut out and weighed. Their mean damp weight was 0.07009 g/cm^2 (SD $\pm$ 0.007902). The zooids on one side of each square were counted and the figures doubled to allow for the zooids on the other side of the bilamellar squares of frond. The mean number of zooids was 1788/cm^2 (SD = $\pm$ 136) The relationship between zooids and weight is, therefore, 25510 zooids/g.

Only LOPPENS (1905) seems to have related the weight of a *Flustra foliacea* colony to the number of zooids that constitute it. He found a colony weighing 13 g and estimated that it consisted of 1,333,000 zooids. His figures suggest that he weighed the frond dry, or nearly so. In order to examine this further, the 10 squares which had been used to calculate the relationship between damp weight, area and numbers of zooids were weighed again after drying in air. The mean weight of the 10 squares was then 0.01128 g. In this state, a 13 g dry colony would consist of 2,060,643 zooids, compared with only 331,630 zooids/13 g damp colony.

The number of zooids in a colony at each age was calculated by first weighing the entire colony. The most recent annual increment, adjacent to the growing edge, was then removed from the colony by cutting along the previous winter's growth-check line, and the colony was then reweighed. The next annual increment was removed in the same way and the colony reweighed and so on. Where possible, colonies free from epizoites were used but, in order to obtain data from as large a number of colonies as possible, it was sometimes necessary to include lightly encrusted fronds from which the epizoites had been removed.

Results

Annual pattern and season of growth

The annual cycle of growth of *Flustra foliacea* was found by taking measurements of 40 fronds at random from each of the monthly samples. It will be shown that growth rate in height does not vary significantly with age (Fig. 3). In studying the annual pattern of growth in height, it was, therefore, considered unnecessary to deal with the year classes separately. Measurements were made from the peripheral growing edge to the previous winter's growth-check along the longitudinal rows of zooids. The data are plotted graphically in Fig. 2, in which the date order of samples has been arranged so that the pattern of growth for one complete growing season can be seen most clearly.

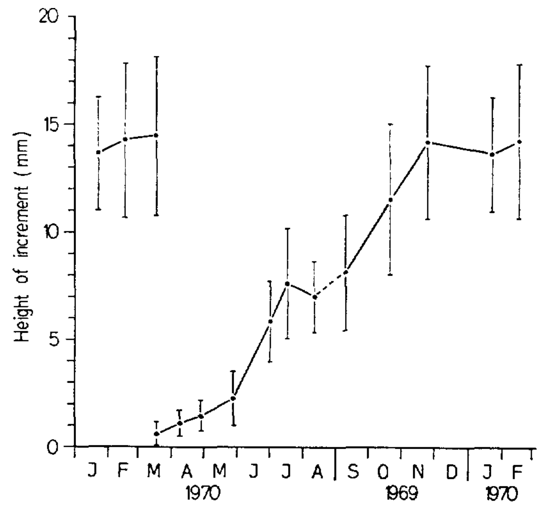

Fig. 2. *Flustra foliacea*. Annual pattern of growth in height. Measurements represent mean distance between growing edge and previous winter's growth check-line, from samples dredged at approximately monthly intervals

Growth probably starts in late February or early March; by mid-March the new growth is clearly visible. Growth continues until November, except for what appears to be a brief check during August. From November until the following late February or early March there is no growth. This is very similar to the season of growth which EGGLESTON (1963) observed for *Flustra foliacea* off the Isle of Man, except that there, growth continued only until October.

It is difficult to be sure whether the apparent growth-check in July and August is typical, peculiar to 1970, or merely the result of sampling error. Certainly, it is sometimes possible to discern a faint line across the fronds, midway between the winter growth-checks, which may represent a cessation of growth. Bryozoans are phytoplankton feeders (RYLAND, 1970, p. 44), so that a brief check in growth might be expected, because phytoplankton is not nearly as plentiful in the summer as during the spring and autumn (HARVEY et al., 1935).

After the recommencement of growth in March, the buds which constitute the growing edge are fresh and white in appearance. The occurrence of a new line across the fronds, very close to the growing edge, is evidence that the lines represent the position of the growing edge during the winter cessation of growth, as EGGLESTON (1963) first noted.

Growth in height by back measurement

To determine the pattern of growth in height, 20 colonies of year classes 1 to 6 and fewer of the older year classes were taken from one sample dredged on 9 September, 1969. Although this was a large sample of fronds, there were less than 20 colonies in each of year classes 7 to 9. The height of each frond at each age was measured. From these data the mean height and standard deviation of each year class at each age were calculated. The data are plotted graphically in Fig. 3.

It can be seen that the rate of growth in height was remarkably constant for all year classes at all ages, and that the rates of growth of different year classes were very similar. Furthermore, there is little deviation of measurements from their means.

Growth in zooids by back measurement

More significant than growth in height is the growth rate of the colony in terms of numbers of zooids. As before, 20 colonies of year classes 1 to 5 and fewer of year classes 6 and 7 were taken from the sample dredged on 9 September, 1969. As described, the colonies were weighed and re-weighed after the removal of each annual increment. The mean weights of the colonies at each age and their standard deviations were calculated; the data are plotted graphically in Fig. 4. Ordinates show both weights and numbers

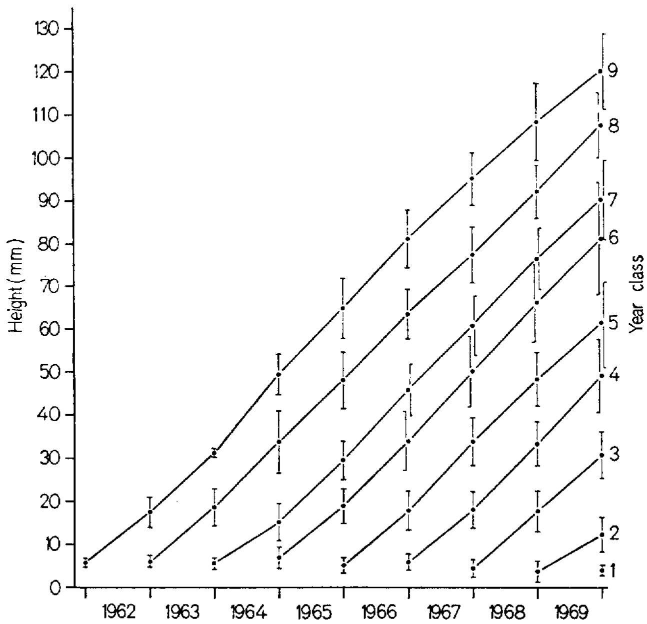

Fig. 3. *Flustra foliacea*. Growth in height of colonies as shown by back measurements

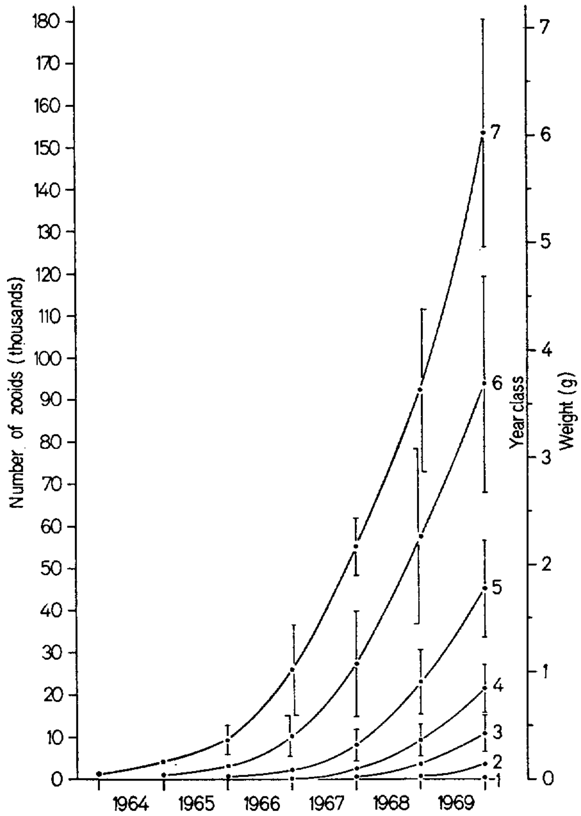

Fig. 4. *Flustra foliacea*. Growth of colonies in numbers of zooids as shown by back measurements

of zooids according to the relationship given under "Methods" p. 268. The pattern of increase in numbers of zooids is exponential. In none of the older year classes does there appear to be any decline in the rate at which zooids are added to the colonies. The standard deviations of the numbers of zooids in the colonies at each age are quite considerable (Fig. 4), when compared with those of the height of the colonies at each age (Fig. 3). A more realistic comparison can be made by calculating the coefficients of variation of each set of data. From these figures it appears that the rate of increase in width of the fronds, or the frequency with which the longitudinal row of zooids bifurcate, is a more variable factor than the rate at

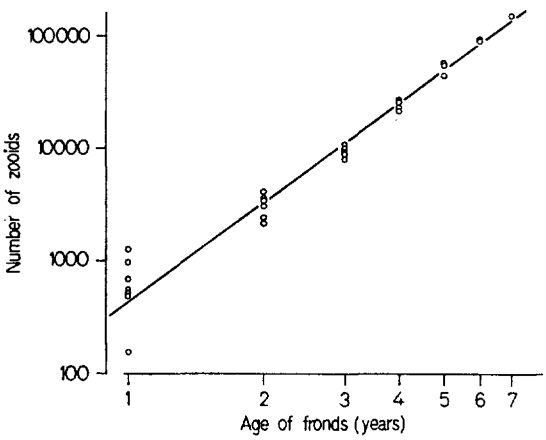

Fig. 5. *Flustra foliacea.* Growth in estimated numbers of zooids, by back measurements. Numbers of zooids (derived from data used in Fig. 4) and age of fronds in years are plotted on logarithmic scales. A regression line is fitted

which the fronds increase in height. Thus, one might expect fast growing colonies to be fan-shaped, while slow growing colonies would tend to have more parallel-sided fronds.

When the growth data are plotted on logarithmic scales, the relationship between time and numbers of zooids is linear. The data shown in Fig. 4 were replotted so that the abscissa represents the age of the frond (Fig. 5), rather than specific years (as in Figs. 3 and 4). All the colonies of all year classes are considered as if they began life simultaneously. Their growth curves are thus superimposed upon one another. The relationship appears to be linear for most of the life span of the colonies.

It can be noted from the data expressed graphically in Figs. 4 and 5, that the weight of colonies at the end of the first year of erect growth tends to be greater in the older year classes. These data do not represent the true growth in the first year, because this part of the frond becomes secondarily thickened with age by frontal budding and, therefore, increases in weight. Accurate measurements of the weight of colonies during their first year can only be derived from colonies 1 or 2 years old. This phenomenon, described more fully in the section on frontal budding (below), probably accounts for the wide scatter of points representing colonies of 1 year old in Fig. 5.

The effect of epizoites on growth rates

The fronds of *Flustra foliacea* are typically encrusted by large numbers of epizoites. The most frequent are the bryozoans *Scrupocellaria reptans* and *Crisia eburnea*. These and other epizoic bryozoans and hydroids encrust the fronds at a density of about 1 colony/cm^2 of frond (STEBBING, in press). Their presence in such large numbers poses the question of their possible effect on the growth rate of the fronds.

Table 1. *Flustra foliacea. Mean values of the increment in height of encrusted and non-encrusted fronds following the previous winter's growth check. The probability that the two mean values could be due to chance is $P < 0.001$*

Fronds	Mean height of increment	Standard deviation
Encrusted	8.625	± 2.959
Non-encrusted	16.875	± 3.560

Fronds which were either well encrusted by epizoites, or not encrusted at all, were sorted from a sample dredged on 11 August, 1970, so that a comparison of their growth rates could be made. The distance between the previous winter's growth-check and the growing edge was measured on 40 encrusted fronds and 40 fronds free from epizoites. The mean height and standard deviation of the increments for each group are given in Table 1. It can be seen that the mean size of the increment of well encrusted fronds is significantly less than those not encrusted. This indicates that epizoites cause a reduction in the growth rate of *Flustra foliacea* fronds.

Frontal buds

Zooids of *Flustra foliacea* are capable of giving rise to frontal buds. They originate from the distal wall, which seems to become elevated above the level of the neighbouring zooids. A membranous primary bud arises first, distal to the parent zooid. Two secondary buds then arise distally (but each slightly to one side) from the primary bud (Fig. 6). The buds are separated from each other by thin calcareous walls. Such buds are found scattered over all but the

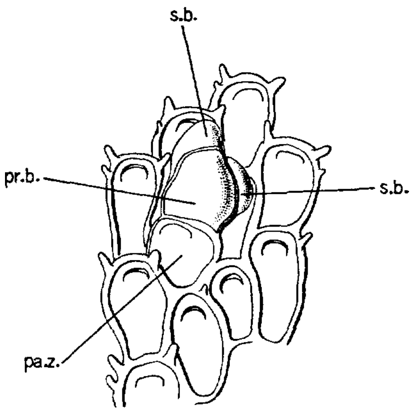

Fig. 6. *Flustra foliacea.* Frontal bud and its initial development. *pa. z.*: parent zooid; *pr. b.*: primary bud; *s. b.*: secondary buds

most recently added parts of the fronds; they increase in density towards the holdfast. On the younger parts of the frond, where the growth of these buds is not restricted by similar buds produced by neighbouring zooids, a small, ovoid, unilamellar layer of zooids may grow outward from the parent zooid. These small "colonies" are close to the surface of the frond and cause the degeneration of underlying zooids. They may sometimes give rise to erect bilamellar branches. Their development, therefore, seems similar to that of colonies which originate from larvae in the normal way.

On the holdfast region, frontal buds are very numerous. On colonies more than 3 years old, almost all the zooids of the holdfast region have produced frontal buds. However, their density seems to prevent the development of unilamellar "colonies" in the manner described above. These membranous buds coalesce to form a haphazardly arranged layer, overlying and obscuring the regular pattern of their parent zooids. As the colony becomes older, the first layer of frontal buds gives rise to, and is overlaid by, further irregular layers of buds. With increasing age and size of the frond, the holdfast is in this way thickened and, therefore, strengthened. In Fig. 7 the relationship between the height of the frond and the largest numbers of layers counted across each transverse section of 92 holdfasts is plotted graphically. It is clear that there is a linear relationship, and that additional layers are added at a constant rate as the fronds increase in height.

As nearly all the frontal buds lack orifices and polypides, the question arises as to how the buds which occur on the holdfast are sustained, for there may be no zooids capable of feeding nearby. It may be that nutrients pass down to the holdfast from parts of the frond where there are feeding zooids.

Regeneration

Flustra foliacea fronds were often found from which areas of one layer of the bilamellar frond were missing. This may be the result of predation by nudibranchs or *Psammechinus miliaris*, which is known to graze on *F. foliacea* (MILLIGAN, 1916).

It appears that, when only one layer of zooids is missing from the frond, regeneration may occur, for the growth of zooids surrounding a grazed area becomes orientated towards its centre and the grazed area is replaced by new growth. However, where

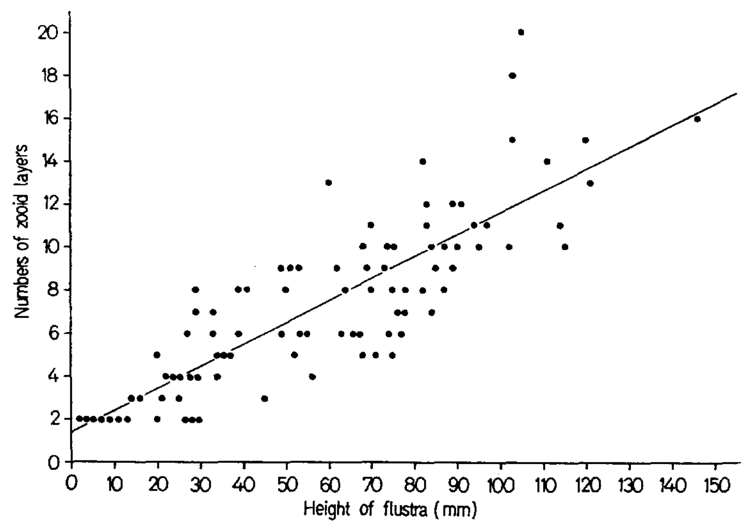

Fig. 7. Relationship between the number of layers of zooids and frontal buds seen in transverse sections of holdfasts and the height of *Flustra foliacea* fronds. A regression line is fitted

the regenerative growth meets, it does not stop growing. Growth then becomes erect, with the basal walls of the zooecia touching, and a new bilamellar branch to the colony is formed.

Discussion

It has been shown that the pattern of growth in height of *Flustra foliacea* is linear, and that growth rates for year classes of all ages are very similar (Fig. 3). Several other workers have given data which show that growth in height of *Bugula* species occurs at a constant rate (GRAVE, 1930; McDOUGALL, 1943; KAWAHARA, 1960). However, these studies have never followed the growth for more than a few months, and in some colonial animals growth rates in height appear to decline with age (GRAVE, 1933, a hydroid; SKERMAN, 1959, *Bugula* spp.). Interpretation of data may sometimes be difficult when derived from interval samples of a population of colonial animals, such as the data on the annual growth cycle of *F. foliacea* given in this paper. Back measurements (where possible) seem reliable, but the ideal method is to follow the growth of numerous individual colonies as BUSHNELL (1966) and GORDON (1968) have done.

The rate of increase in the number of zooids in *Flustra foliacea* colonies is shown by back plotting to be exponential (Fig. 4). It appears from the literature that this is generally true in colonial animals (GRAVE, 1930, a cheilostomatous bryozoan; GRAVE, 1933, a hydroid and a tunicate; BRAVERMAN, 1963, a hydroid; BUSHNELL, 1966, a phylactolaematous bryozoan). In one species of colonial protozoan a decrease in growth rate occurs after a long exponential phase (FAURE-FREMIET, 1930). However, all these observations were also made over relatively short periods of time. It is, therefore, interesting that, although the rate of growth of *F. foliacea* is not as spectacular as some species of colonial animals, the exponential pattern is maintained for at least 7 years (Fig. 4). In this way the growth resembles that of unlimited increase in a population of free living animals, as pointed out by BUSHNELL (1966). However, in colonial animals the rate of increase in the number of zooids is closely related to colonial morphology. Clearly, the potential rates of increase in zooids of adherent and branching erect forms differs, given a constant rate of linear growth. In *F. foliacea* the increase in frond width in relation to height sometimes becomes so great that any further increase in width is only possible if the frond bends or branches, allowing the two new branches to overlap as their width increases further.

It has been shown that the presence of epizoites on the fronds decreases rate of growth. The way in which this occurs is not clear. One might expect that only interference with the growing edge itself would reduce the rate at which zooids are added to it. However, the great majority of epizoites are not on the growing edge, although the larvae of some species of epizoites have been shown to settle preferentially on or near it (STEBBING, in press). The buds which constitute the growing edge must be provided with nutrients by the more proximal zooids until they acquire a gut and tentacular feeding apparatus. If growth is dependent on the passage of nutrients from zooids some distance back from the growing edge, the deleterious effect of epizoites can be easily understood. Zooids of *Flustra foliacea* often degenerate irreversibly as a result of stolons of hydroids growing over their orifices; the stolons of *Bugula flabellata* have a similar effect by growing through the zooids. Furthermore, sediment accumulates around the rhizoids of other epizoic bryozoa and their very presence attached to the fronds must hinder the feeding of the *F. foliacea* zooids. Less serious is the possibility of competition for food between the zooids of epizoites and *F. foliacea*.

Colonies of *Flustra foliacea* from Oxwich Point have been found which are 12 years old. This raises the question of what determines their life span, for colonial animals do not seem to become senescent. It seems possible that fronds become too large for the strength of the holdfast, and are eventually torn from the substratum by water movement. However, those colonies stranded on Oxwich beach, apparently from the population used in this study, did not appear significantly larger than those in dredged samples.

It seems likely that the high growth rates of colonial animals, which do not seem to decline with the age of the colony, must be of considerable advantage when in competition for space with non-colonial animals. This may explain why colonial animals of various phyla are often the dominant organisms in sessile marine communities.

Summary

1. *Flustra foliacea* L. is shown to have an annual growth season between March and November.

2. During the dormant winter period, when no growth occurs, a line is left across the fronds which allows their age to be determined in years.

3. By back measuring, growth of the fronds in height is shown to be linear for year classes 1 to 9 at all ages.

4. Growth by addition of zooids is similarly shown to be exponential for at least 7 years.

5. The presence of heavy encrustations of epizoites on the fronds reduces the growth rate of *F. foliacea*.

6. The frontal buds are capable of giving rise to new branches of the frond in a way similar to the development of new colonies from larvae.

7. Frontal buds thicken, and thereby strengthen the holdfast region of the fronds as they grow larger.

8. In two instances, the most feasible explanation of the observations would be the passage of nutrients from one part of the frond to another.

9. Colonies appear to be able to regenerate areas of the frond which have been removed by grazing. Regenerative growth can result in new branches.

10. The patterns of growth of *F. foliacea* found by back measuring are discussed in the light of other work on the growth of colonial animals.

Acknowledgements. I am most grateful to Dr. J. S. Ryland who supervised the work described in this paper, and to Professor E. W. Knight-Jones in whose Department the work was done. Both my supervisor and Dr. D. A. Hancock read and improved drafts of this paper by their valuable suggestions. I am pleased to thank the Captains and crew of R V "Ocean Crest", from which all the dredging and most of the diving was done. I am also very grateful to Mr. P. D. Stebbing who drew Figs. 1 and 6. Finally, I would like to thank the National Environment Research Council for a Research Studentship which made it possible for me to carry out this work.

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Date of final manuscript acceptance: January 20, 1971. Communicated by J. H. S. Blaxter, Oban