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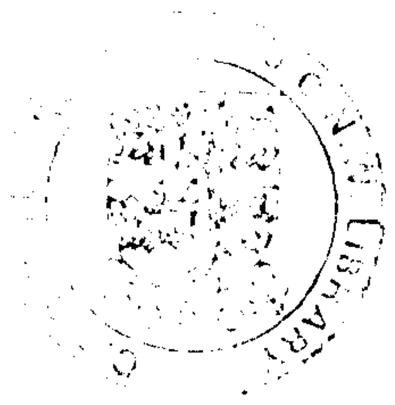

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Summary

Demographic aspects of the encrusting bryozoan Celleporella hyalina (L.) were investigated both at the colonial and the zooidal level. In the Menai Straits C. hyalina is the commonest epiphyte on the fronds of Laminaria saccharina (L.) Lamour. The life-span of C. hyalina on this substratum ranges from a few days to 5 - 6 months according to season and settlement location, substratum abrasion being the main mortality factor. Experimental rearing in the natural environment showed that on a permanent substratum C. hyalina survives more than 18 months. From April to September C. hyalina invests, at simultaneously high rates, in somatic growth and sexual reproduction, whilst during the rest of the year investment is mainly in growth, but at a low rate. In comparison with colonies experimentally grown in restricted water flow conditions, colonies of C. hyalina in higher water flow regimes achieved: (a) bigger colony size, (b) higher reproductive output (RO) (reproductive zooids/autozooids) and (c) higher investment in female functions. RO increases asymptotically as body size increases and can be experimentally depressed by reducing water flow, which presumably diminishes the supply of food to the colony. Colonies of C. hyalina start sexual reproduction at a small size and do not delay sex in favour of achieving a bigger size, probably because: (a) unpredictable life-expectancy in the natural environment favours an early reproduction, (b) viable larvae need brooding for 3 - 4 weeks and (c) the modular construction allows partitioning of functions among zooids in the colony, minimizing interference between sexual

activities and colonial growth. Resources are probably allocated to growth and reproduction in a similar way in other species of colonial organisms. Increasing the number of neighbouring colonies of C. hyalina reduces size and RO. Colonies isolated from foreign sperm produced larvae up to 40 days after isolation, suggesting that either self-fertilization or storage of foreign sperm takes place.

General Introduction

Organisms can be regarded as input-output systems that capture and transmit energy, information and material in such a way that the production of successful offspring throughout the organism's life-span is maximized (Pianka and Parker 1975, Pianka 1976, 1981, Calow 1977, 1979, 1981; Calow and Townsend 1981, Solbrig 1981). Although maximization of reproductive output can be assumed to apply to all organisms, the diversity of life histories and reproductive methods known, allows an extremely high number of successful ways of timing and allocating resources for reproduction. The demographic consequences of a particular reproductive method have been the subject of many notable papers (e.g. Cole 1954, Gadgil and Bossert 1970, Charnov and Schaffer 1973, Stearns 1976, 1977, 1980, May 1977, etc). In recent years numerous papers (especially those by Pianka 1976, 1981, Calow 1977, 1979, 1981), have stressed the physiological consequences of reproduction. This approach successfully deals with costs and benefits of a given reproductive method, taking into consideration the whole organism. Using energy as a common denominator, different activities of the organism can be directly compared, bringing together aspects of optimal foraging, behaviour, personal defense, reproduction, etc. (see Pianka 1976 and book edited by Townsend and Calow 1981). Similar approaches can be applied to populations and ecosystems (Slobodkin 1962).

Growth, reproduction and other activities of the organism, use the energy remaining after the metabolic "levy" has been taken

from the input to the organism (Calow 1981). Since energy used in reproduction is not available for other activities, present reproductive output is associated with costs that must be paid in terms of future growth and residual reproductive value (Wittenberger 1979, Calow 1979, 1981). In solitary animals it is well established that growth and reproduction are virtually mutually exclusive (Williams 1975, Pianka 1976, Muenchow 1978, Amir 1979, Calow 1981, Bell 1982). Similar principles seem to apply to plants (Harper 1977, Solbrig 1981, but see Cohen 1971, 1976, and Amir 1979) and to many clonal organisms with dissociated modules, (Williams 1975, Muenchow 1978, Hughes and Cancino, in press). Information regarding colonial organisms is, however, almost non-existent (Bell 1982, Hughes and Cancino, in press).

Throughout this thesis, a colony is regarded as a group of units or modules (synonymous with "ramet", Harper 1977) physically connected and sharing a common genotype. Production of new modules through budding, will be regarded as somatic growth (Hughes and Cancino, in press). Since every unit is an entity in itself, the proliferation of modules has been regarded by many authors as asexual reproduction (e.g.Sebens 1979, Bell 1982). From the demographic point of view, there are two levels of organization within clonal organisms: one is at the level of modules - n, the other at the level of genotypes - N, ("ramets" and "genets" of Harper 1977, 1980).

Colonial organisms are usually sedentary and because the modules in many species remain attached (e.g. Hydrozoa, Anthozoa, Bryozoa, Tunicata) they offer a unique material to test the applicability of life history theory to clonal organisms. All

living bryozoans are colonial (Ryland 1970, 1979b, Nicol 1978) and many species are polymorphic (Silen 1977). In some species with zooidal polymorphism the following types of zooids are recognized: autozooids that feed; androzooids that produce sperm; and gynozooids that produce eggs. Other special kinds of zooids, presumably for defense, are avicularia and vibracula (Silen 1977, Cook 1979, Ryland 1979b). Counting the number of zooids of different morphologies allows a rough estimate to be made of the relative investment per function. Such an approach, however, is not found in the literature.

Investigations of breeding seasons in Bryozoa are usually based on collections of colonies, of unknown age, at regular intervals; (e.g. Ryland 1963, Gordon 1970, Eggleston 1972, Hayward and Ryland 1975); or on observations of larval settlement on experimental substrata placed in the natural habitat (e.g. Ryland 1960, Withers and Thorp 1977, Vial and Wass 1981). Only Hayward and Ryland (1975) and recently Dyrynda (1981a, b), Dyrynda and King (1982) and Dyrynda and Ryland (1982) have simultaneously investigated growth and reproduction in species of Bryozoa. Growth and reproduction have, however, not been followed in individually identified colonies.

This thesis deals with demographic aspects of the encrusting bryozoan Celleporella hyalina (L.) both at the colonial level ("genets") and at the zooidal level ("modules"). Colonial growth and survival was followed on fronds of Laminaria saccharina L. (Lamour), the commonest habitat of C. hyalina in the Menai Straits. The dynamics of growth and production of sexual zooids

was investigated experimentally in colonies grown in the natural environment but under different conditions of water flow, the assumption being that water flow and food levels are correlated. If this assumption be true, we can learn about the way resources are allocated to somatic growth and reproductive output in C. hyalina. Male and female zooids in C. hyalina have different morphologies and do not eat, thus providing a suitable material for quantifying investment in gender, male vs female function, and in growth vs sexual reproduction. The possibility of inbreeding was also experimentally investigated.

Most of the observations on C. hyalina are probably relevant to other species of Bryozoa (i.e. Callopora lineata, Membranipora membranacea, Electra pilosa), that also use L. saccharina as a substratum. During the 3 years of the present study I gathered some information regarding growth of Electra pilosa, E. monostachys, Callopora dumerilli, C. lineata and Cryptosula pallasiana. Due to shortage of time those data are not presented as part of this thesis.

Errata:

Lünning, K. in Chapter 1 and in References should read Lüning, K.

Chapter 1

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Laminaria saccharina (L.) Lamour as a habitat for _Celleporella hyalina_(L.) and other encrusting bryozoans.

1.1. Introduction

Macroalgae provide marine invertebrates with a diversity of resources including: substratum for both sessile and non-sessile sedentary organisms, shelter and food (Hayward 1980, Seed and O'Connor 1982b). Different groups of algae offer these resources to different degrees; brown macroalgae, by virtue of their dominance on most temperate rocky coasts, their large size, broad fronds and usually massive holdfasts, are used as substrata and provide shelter to many marine invertebrates (Colman 1940, Ryland 1962, Jones 1971, 1972, 1973, Moore 1971, 1972, 1973c, 1978, Hayward 1980, Cancino and Santelices 1981, Seed and O'Connor 1981b). The sessile epifaunal communities occurring on fronds of macroalgae are subjected to very different constraints from those experienced by epifaunal communities on hard non-renewable marine substrata (Seed and O'Connor 1981b, Barnes and Hughes 1982). Predation and competition, two major organising forces in rocky shore communities (Connell 1961, Paine 1966, Dayton 1971, Menge and Sutherland 1976), seem to be relatively less important within macroalgal epifaunal communities (Stebbing 1973a, b, Hayward 1980, Seed and O'Connor 1981b). According to Seed and O'Connor (1981b) two major factors organising algal epifaunal communities are a) seasonal generation of new frond surface available for colonization (relieving inter- and intra-specific competition); and b) larval selection of habitats and position on the plant, resulting in partitioning of substratum. Another important factor is that most sessile epifaunal species are colonial and by virtue of their modular construction (Chapman and Stebbing 1980) they are able to re-direct growth towards the most favourable areas of

substratum (Gordon 1972, Ryland and Stebbing 1971, Stebbing 1973a, b, Buss 1979a, Jackson 1979). Most larvae of epifaunal species are highly selective with regard to both plant species used as substratum and position on the frond (Ryland 1959b, Ryland and Stebbing 1971, Stebbing 1972, Hayward and Harvey 1974a, Hayward 1980, Seed and O'Connor 1981b). These factors tend to create dense monospecific stands.

Intra-specific overgrowth within bryozoans has been reported to be uncommon (Stebbing 1973a, b, Seed and Boaden 1977, O'Connor et al. 1980, Wood and Seed 1980, Seed and O'Connor 1981b), it can be expected, therefore, that intra-specific overgrowth is not an important mortality factor within monospecific stands. Data on the survivorship of individually identified colonial epiphytes on macroalgae, necessary to confirm this prediction, are not available in the literature.

Most studies dealing with epifaunal communities on brown macroalgae have been carried out on Fucales and to a lesser extent on Laminariales. Many studies in Europe have dealt almost exclusively with the diverse epifauna on Fucus serratus (e.g. Hagerman 1966, Ryland and Stebbing 1971, Stebbing 1973a, b, Hayward and Harvey 1974a,b, Hayward and Ryland 1975, Boaden et al. 1975, 1976a,b, O'Connor et al. 1979, 1980, Seed and Boaden 1977, Seed et al.1981, Seed and O'Connor 1981a,b, Wood and Seed 1980, Wood 1983). Although several studies have been carried out on the holdfast communities of Laminariales (Scarrat 1961, Jones 1971, 1972, 1973, Moore 1971, 1972,1973a,b,c,d, McKenzie and Moore 1981), studies of epifauna occurring on the fronds of Laminariales

are few (Ebling et al. 1948, Sloane et al 1957, L'Hardy 1962, Kitching and Ebling 1967, Ryland and Stebbing 1971, Norton 1971, 1973, Stebbing 1972, Seed and Harris 1980). Studies on epifauna of Macrocystis pyrifera on the Pacific Coast of North America (Bernstein and Jung 1979, Dixon et al. 1981, Yoshioka 1982a,b) and that of Laminaria saccharina (Seed 1976) at Friday Harbour have also contributed to the knowledge of epifaunal community structure and dynamics on Laminariales.

Fronds of certain laminarians have been regarded as largely unacceptable to most species of sessile epiphytes (Seed and O'Connor 1981b), but this is certainly not the case of Laminaria saccharina, Sacchoriza polyschides, and Macrocystis pyrifera (L'Hardy 1962, Norton 1973, Bernstein and Jung 1979). Although the epifaunal communities on these macroalgae are less diverse than those on Fucus, these macroalgae act as substrata for several sessile species of Bryozoa, Hydrozoa, Polychaeta, Cirripedia and Urochordata (L'Hardy 1962, Norton 1971, Bernstein and Jung 1979, Seed and Harris 1980). The epifaunas of laminarian fronds are, moreover, fast-changing structures both in chemical composition (Black 1954, Kain 1979) and physical dimensions (Kain 1979 and below). Obviously such changes are of primary importance determining epifaunal life-span, colonization and probably degree of interaction amongst the members of these communities.

The fronds of Laminaria spp. behave like moving-belts of tissue (Mann 1972); frond tissue being generated at the base and abraded at the frond tip, (Parke 1948, Kain 1979). The growth of the fronds follows a seasonal pattern with maximum rates in late winter-spring and a minimum in summer-autumn (Parke 1948, Mann

1972, Kain 1979). Provided that light is not limiting, growth is in general controlled by the amount of nitrogen in the water (Chapman and Craigie 1977, Lünning 1979, Dieckman 1980, Anderson et al. 1981, Gagné et al. 1982). It has been shown experimentally (Chapman and Craigie 1977), that the reduction in growth rate during the summer is due to nitrogen depletion. Growth of Laminaria spp. occurring in areas with abundant supplies of nitrogen all year round follow the seasonal pattern of light (Dieckman 1980, Anderson et al. 1981, Gagné et al. 1982). Although nitrogen and light are the two main factors controlling the seasonal pattern of growth of Laminaria, many other factors have been reported to affect it. (For further details see Discussion).

The sporophytes (macroscopic plants) of Laminaria saccharina (L.) Lamour are found in Britain from the lower- midlittoral to about 25 m depth in the sublittoral zone (Burrows 1961, Norton and Milburn 1972). The species occurs on all types of substrata providing that they are sheltered from wave action (Burrows 1961, Kain 1962, Lewis 1962, Kain 1979; also see Druehl 1967 for distribution at Vancouver Island). The species occurs in the Atlantic from Portugal in the East to Massachussets in the West and it is also present in the Northern Pacific from California to inside the Polar Circle (Burrows 1961, Lünning et al. 1978, Hoek 1982). Many eco-physiological studies have shown that the species grows well under widely ranging conditions of temperature, salinity, irradiation, etc. (Burrows 1961, Druehl 1967, Kain 1969, Lünning et al. 1973, Johnston et al. 1977, Lünning 1979, Fortes

and Lünning 1980, Hoek 1982, further references and review in Kain 1979). The main work on the biology of L. saccharina is that of Parke (1948), who studied populations in Devon (South England) and Argyll (Scotland). Most of the recent works on this species come from Lünning and co-authors. References on L. longicruris are also relevant to L. saccharina since these two algae are probably con-specific (Chapman 1974, Lünning et al. 1978, Kain 1979).

A population of L. saccharina occurs in Anglesey, Wales towards the eastern mouth of the Menai Straits. The sea-water in this area of the Menai Straits, and as far westwards along the Straits as Brittania Bridge, is influenced by the oceanographic conditions in Liverpool Bay (Jones 1962). The cycle of nitrate-nitrogen follows the pattern typical for coastal waters, (Ewins and Spencer 1967, Lennox 1979); the cycles of active silicate and phosphorus are, however, slightly different from those of coastal waters (Jones 1962, Ewins and Spencer 1967). It had been reported (Ryland 1959a) that fronds of the local L. saccharina were inhabited mainly by the encrusting bryozoan Celleporella hyalina (L.), (=Hippothoa hyalina). C. hyalina also occurs as a major component on the epifauna of L. saccharina in France and the Isle of Man (L'Hardy 1962, Eggleston 1963, 1968, 1972), of Sacchoriza polyschides in Ireland and the Isle of Man (Ebling et al. 1948, Kitching and Ebling 1967, Norton 1971), of Macrocystis pyrifera in California (Bernstein and Jung 1979), and at a lesser extent of Fucus serratus (O'Connor et al. 1980) in Britain.

The present study was undertaken to gather information about both the biology of L. saccharina and that of the encrusting

epifauna. With regard to the plant, it will provide the first data of seasonal growth in this area of Britain, representing slightly different oceanographic conditions from previously published records. With regards to the epifauna, it will provide the first major study of the epifauna of L. saccharina in Britain. The general objective of the work was to understand the relationship between plant and epifauna. Justifications of this objective are: a) the few existing studies of epifaunal communities on fronds of Laminariales; b) the lack of a study integrating the biology of the plant and that of the epifauna; and c) lack of direct observations of survival times of individually identified sessile epihytes on this substratum. This last point is important in evaluating the role of competition on epiphyte mortality in this community.

1.2. Materials and Methods

Sixty one plants of L. saccharina were marked over a period of 602 days (Table 1.1), starting on 26 October 1980. The area studied was at Trwyn-y-Penrhyn, Menai Straits, Anglesey, Wales (SH 629 797). Five rocks, (A to E in Appendix 1), were selected in the sublittoral zone (sensu Lewis 1964), located between 60 and 80 cm above chart datum. On each rock, plants were individually marked with strings of different colours tied around the stipe (Plate 1.1). Frond growth was measured by following the displacement of a 4 mm diameter hole, (Plate 1.1), which was punched 10 cm from the base of the frond. Measured growth therefore, was the sum of both primary and secondary elongation (Parke 1948). A new hole was punched when the old one was about to reach the end of the frond. Plants were measured on 24 occasions (Table 1.1), at intervals of 15 to 31 days. On average 23 plants (SD 5.32, 15 minimum, 39 maximum) provided information about growth on 23 occasions (Table 1.1). Total length of the plant, length of the stipe and position of the hole were recorded on each occasion (all to the nearest 0.5 cm). From these data, the length of the frond, its growth rate and the rate of loss of tissue from its tip were calculated.

The present study was concerned with animals on the frond of L. saccharina and further analysis dealt only with the frond, but data on the stipe and total algal length are given in Appendix 1. Regression and correlation analyses were carried out between mean frond length, (mean value between two successive observations), and the growth rate per day observed during that interval. When a

statistically significant correlation was found, and observations existed for a similar period in another year (e.g. May 1981, May 1982), an analysis of covariance (Snedecor and Cochran 1967), was carried out. Data were pooled when the analysis of covariance showed no significant difference between years. In such cases only the pooled regression equation is given for that period (see Table 1.2). When differences between years were significant, separate regression equations are given. Rate of loss of tissue was treated in the same way as growth rate. Regression and correlation analyses were also carried out between growth rate and rate of loss of frondal tissue.

To determine if plants of different sizes were growing, or losing tissue at proportionally the same rate, data were standardized using an arbitrary frondal length of 100 cm. The standardized value of growth rate, or loss per day, was then plotted against mean frondal length. Since the scatter plots so obtained fitted curvilinear regressions, the values were transformed to natural logs. As before, data were pooled if a one-way analysis of variance (Kruskal-Wallis, Siegel 1956), carried out on the data before logarithmic transformation, showed no significant difference between years.

Survival time of the frond tissue was calculated throughout the year using a graphical method. Plant size was plotted against time and growth rate was integrated starting at each observation date. Survival time was estimated as the predicted time taken for newly formed tissue to reach the tip of the blade. Animal residence time was calculated in a similar way. (See Results for further details). Plant mortality was estimated from loss of

marked plants. The disappearance of a whole plant, or that of its frond, was regarded as death.

Surface water temperature was measured every 2 - 3 days at the Menai Bridge Pier (8 miles from the site studied). Information of the cycle of nutrients was obtained from Jones (1962), Ewins and Spencer (1967) and Lennox (1979).

The bryozoan populations on the fronds were studied by two methods. First, plants were randomly chosen and 3 transverse sections, Proximal, Central and Distal, cut in each frond. the Sections were 15 cm long and chosen so that the proximal one included the bryozoan ancestrulae settled nearest to the base of the frond. The distal section corresponded to 15 cm at the tip of the frond and the central one to the midpoint between the other two. Second, non-destructive repetitive samples were taken of areas 15 cm long on fronds of marked plants. Punched holes were used as reference points for these areas. All visible bryozoan colonies were mapped on acetate sheets. This technique was generally adequated to gather information about settlement, colony growth, survival and contact between individually identified colonies. Additional information on settlement of bryozoans and plant population structure was obtained on 9 occasions, over which a total of 967 plants were measured. A digitizer was used to measure areas of fronds and colonies on these plants.

1.3. Results

The results are presented in two sections, the first dealing with the plant and the second with the epifauna.

1.3.1. THE PLANT

1.3.1.1. Plant Population Structure.

The size of the fronds of the population studied varied during the year (Fig. 1.1). Most of the plants had fronds shorter than 100 cm from December to March, bigger plants being common from March to November. Fronds shorter than 20 cm were present in a variable percentage among all samples except in December 1981 (Fig. 1.1).

This fluctuation in size of the fronds was due to three factors: a) recruitment of new plants, b) mortality of whole sporophytes and c) balance between growth and loss of tissue on the fronds of older plants. Most of the plants with fronds shorter than 20 cm (Fig. 1.1) were newly recruited sporophytes. These were less frequent during the winter months (absent in December 1981) than during the rest of the year.

1.3.1.2. Survival and Growth of Marked Plants.

The mean mortality rate between successive observations of well grown marked sporophytes (fronds longer than 30 cm), was 9% (Fig. 1.2, see Table 1.1 for observations dates and number of plants observed). Mortality rates higher than 10% were recorded on 6 occasions (Fig. 1.2.b). High mortality rates, apparently, were not correlated with season. Fifty per cent of the marked plants died after 6 - 8 months (Fig. 1.2.a). The influence of age and plant size on the mortality rate were not investigated.

Fronds of marked plants were smaller during winter (December to February) than during the summer (June to September) (Fig. 1.3). This seasonal pattern was the result of the balance between growth rate (Fig. 1.4) and loss of tissue at the distal end of the frond (Fig. 1.5).

Frondal growth rate was at a maximum in April-May and at a minimum in November-December (Fig. 1.4). The rate of loss of tissue from the tip of the frond was lower from January to March 1981 (January to May in 1982) and higher from April to December 1981. The rates of loss of tissue were higher than the rates of growth from July 1981 to February 1982 (plants decreasing in size, Fig. 1.3) the reverse being the case between February and July 1981 and between March and June 1982 (plants increasing in size).

The growth rate of the fronds was not correlated with water temperature (Fig. 1.6). Plant growth rate decreased while the temperature was still rising and minimum growth rates were recorded 2 - 3 months earlier than the lowest temperatures (Fig. 1.4 and 1.6).

Frondal growth rate was positively correlated with plant size for most of the year (Fig. 1.7, Table 1.2). In November and December 1980 and 1981, however, all plants were growing at a very low rate and the correlation between growth rate and plant size was not significant.

All plants grew proportionally at the same rate from September to February (no significant correlation existed between frond size and growth rate per 100 cm of frond, Fig. 1.8.A). From February to June, however, smaller plants grew proportionally faster than bigger ones (Fig. 1.8.B). During July and August the

correlation changed sign, that is, bigger plants kept growing at proportionally higher rates than smaller plants. The rate of loss of tissue was correlated with mean frond size and with frondal growth rate on only a few occasions (Table 1.2). This was probably due to the loss of variable amounts of distal frond and to the fact that loss of tissue was not a continuous process.

1.3.1.3. Survival of Tissue on the Frond.

The mean survival time of frond tissue ranged from 2 to 9 months according to the time of the year at which it was generated (Fig. 1.9, 1.10). This seasonal pattern was the result of the interactions between growth rate, rate of loss of tissue and the total frondal length at different times of the year (Fig. 1.9). Due to differences in plant size and to mortality of whole plants, the individual estimates of survival time of frondal tissue (Fig. 1.10) were highly variable. Tissue generated in autumn survived about twice as long as tissue generated in spring.

1.3.2. THE EPIFAUNA

Fronds of L. saccharina provide a substratum for encrusting Bryozoa, Hydrozoa, Polychaeta, Cirripedia and Urochordata (see Introduction). The present study concerned only encrusting Bryozoa, particularly Celleporella hyalina, but other sedentary organisms will be subjected to similar constraints since they coexist on a common substratum.

Celleporella hyalina is the commonest encrusting bryozoan on fronds of L. saccharina (Table 1.3), representing about 99% of all colonies found on this substratum. All other species of

encrusting bryozoan found during this study (Electra pilosa, Callopora lineata and Membranipora membranacea) represented a very low percentage of colonies. Although colonies of E. pilosa and M. membranacea grew larger than those of C. hyalina, the latter was the most important species in terms of total area covered. The maximum colony size recorded for E. pilosa was 8 cm^2 and 150 cm^2 for M. membranacea. C. lineata was always smaller than C. hyalina (maximum recorded size 0.80 cm^2 and 2.50 cm^2 respectively).

1.3.2.1. Population Dynamics of C. hyalina on fronds of L. saccharina: A, a simple model.

According to evidence already presented (Fig. 1.10) it can be expected that colonies of C. hyalina will survive for different lengths of time depending on the time of the year at which they settle. The life expectancy of C. hyalina would be equal to that of the newly formed tissue of fronds of L. saccharina (Fig. 1.10) only if: a) settlement occurs at the zone of transition (between stipe and frond) and b) if post-settlement mortality, due to factors other than deterioration of the substratum, is equal to zero. However, neither (a) nor (b) seems to be true.

Larvae of C. hyalina do not settle on the youngest part of the fronds of L. saccharina. Settlement nearest to the transition zone occurred on average 12 cm from the base of the frond (Fig. 1.11). This distance varied throughout the year, being minimal from September to November and maximal in late April (Fig. 1.11). The proximal settlement-free zone was positively correlated with frond size (Table 1.4). At the time of the year when the distance of first settlement moved further from the transition zone, (January to April, Fig. 1.11), a percentage of fronds were found without C. hyalina (Table 1.4). Six per cent of fronds were also

found without C. hyalina on November 1981, but these were very small sporophytes.

Taking into account seasonal differences in the distance from the frondal base at which the most proximal settlement occurred (Fig. 1.11), a curve of life expectancy for C. hyalina was generated (Fig. 1.12, 1.13). On average, a maximum life-span of 7 months and a minimum of only 20 days is predicted if mortality of whole plants is taken into account (Fig. 1.13). These values would be reduced if the larvae settled further from the stipe than the mean distances given in Fig 1.11, or if factors other than substratum degradation affect colony survivorship.

Population Dynamics of C. hyalina on fronds of L. saccharina: B, some data on settlement and survivorship.

Repetitive sampling of areas on 12 marked plants (Fig. 1.14) showed that settlement occurred in 1981 from early June to November. The first settlement on area A, 10 cm from the transition zone on 5 May 1981, was detected on 3 June 1981, new colonies being continually recruited to this area until the substratum reached the end of the frond. Settlement on area B, 10 cm from the transition zone on 4 July 1981, was first detected on 1 August 1981. Subsequent settlement followed a temporal pattern similar to that in area A. In both areas the heaviest settlement took place during August.

The survivorship schedules of C. hyalina on fronds of L. saccharina are strongly affected by the continuous arrival of larvae. As a result of the dynamics of the generation and abrasion of frond tissue, the time of settlement on a given area

of the frond is an important factor affecting life expectancy. Colonies recruiting first at a given area should survive longer than later recruits. Fig. 1.15 clearly shows that this is so.

Survivorship of the whole population of recruits was near to 1 for 2-3 months in area B, whereas in area A there was increasing mortality rate with age (Table 1.5). Three factors: a) life expectancy of the substratum at settlement, b) number of larvae settling at a given time, and c) biological interactions, are likely to be responsible for the differences observed between the two survivorship schedules. Survivorship of colonies was very high until about 1 month before reaching the end of the frond (Fig. 1.16), life expectancy of the substratum being therefore quite important. Most colonies in area B recruited when this area had a life expectancy of 3 to 5 months whilst most colonies in A recruited when life expectancy was only between 2 and 4 months. An increasing number of later recruits (Fig. 1.17.A) produced the continuously decreasing survivorship curve in area A. The early colonization of area B (Fig. 1.17.B) resulted in a survivorship that approached closely that of the substratum.

Biological interactions seemed also to contribute to the differences observed between the survivorship schedules of the two areas. A close inspection of the curves in Fig. 1.16 reveals earlier mortality among later recruits than among slightly earlier recruits. Both the number of old colonies and the proportion of colonies touching neighbouring ones, increased with age of the frond (Fig. 1.17). A larva arriving when most of the area is covered by older colonies may be forced to settle in a less favourable place than those arriving first. Most earlier colonizers died later than colonies recruiting later, whence it

seems that older, bigger colonies are more resistant to abrasion or overgrowth.

The advantages of early recruitment to a given area and those of settling on low density areas are also revealed by following colony growth. Colonies that recruited earlier and at lower density reached a bigger size than colonies settling later at higher density (Fig. 1.19). The differences in growth rate between colonies recruited in June and those recruited on other months (Fig. 1.19.A) can be explained in terms of sea temperature (Fig. 1.16). In area B (Fig. 1.19.B), the colonies stopped growing 1.5 months after settlement, perhaps due to the combined effects of lower temperature (Fig. 1.16) and high density (Fig. 1.17.B).

1.3.2.2. Distribution Patterns of C. hyalina on fronds of L. saccharina.

According to evidence already presented, the heaviest settlement of C. hyalina on L. saccharina occurred in August. Seven plants were therefore sampled in September to estimate population structure and distribution along the fronds when occupation of the substratum is probably at its highest.

The distribution of the colonies of C. hyalina on the fronds of L. saccharina is not random, the larvae preferring to settle on concave surfaces (Ryland 1959b), with the result that a high concentration of colonies occurs along the two rows of depressions along the frond (Plate 1.1). On plants sampled in September, there was a more obvious bimodal pattern of colony distribution across the width of fronds in the proximal and central areas than

at the distal tip of the frond (Fig. 1.20). The difference between these patterns of distribution can probably be explained in terms of age of the frond and continuous recruitment of larvae to areas previously colonized.

There was a size gradient of C. hyalina colonies along the fronds of L. saccharina, the biggests colonies being found at the distal end of the frond and only small ones being present towards the proximal area (Fig. 1.21). This result was expected, since the tissue at the proximal end of fronds was too young for bigger colonies to be present. Although towards the distal end an increasing proportion of the frond was cover by older colonies, ancestrulae were the commonest size class in all 3 areas sampled (Fig. 1.21, 1.22, 1.23). The highest percentage cover by C. hyalina was recorded at the central area of one frond (31%, Fig. 1.22), the average percentage cover, however, was highest at the distal end (Fig. 1.22). When the area occupied by the colonies other than ancestrulae was subtracted from the total area of substratum sampled and the density of ancestrulae on this "colony-free" area was calculated, the densities of ancestrulae in the 3 areas of frond shown to be significatively different (Fig. 1.22, Kruskal-Wallis one way analysis of variance, $H = 14.32$, 2 d.f., $P < 0.001$), suggesting a preferential settlement towards the younger part of the frond.

In central and distal areas of the frond, between 50% and 100% of colonies touched neighbouring ones after they reached 2 mm in diameter (Fig. 1.23). The density of ancestrulae on the proximal area was higher than those previously observed (Fig. 1.17). Under such crowded conditions it would be expected to find

some early mortality due to biological interactions, after which the survivorship would follow that of the substratum.

1.4 Discussion

1.4.1. THE PLANT

The seasonal pattern of growth of Laminaria saccharina in the Menai Straits was similar to that previously reported for this and other species of the genus (Parke 1948, Mann 1972, Chapman and Craigie 1977, Lünning 1979, Kain 1979, Chapman and Lindley 1980, Gagné et al. 1982). In Nova Scotia, Chapman and Craigie (1977) and Gagné et al. (1982) found that growth of L. longicruris was controlled by the availability of nitrogen. In places where nitrogen was only abundant in winter, growth rate increased at this time and continued until late spring. However, where nitrogen was abundant in the water throughout the year, the growth followed the pattern of light (Gagné et. al 1982). This latter pattern has also been found for L. longicruris in Quebec, (Anderson et al. 1981), L. pallida in South Africa (Dieckman 1980), and L.digitata in Helgolander (Lünning 1979). Nitrogen and light are not the only factors regulating growth pattern, as shown by L. longicruris growing over summer in waters with low nitrogen content at Callahan Island, Nova Scotia, (Gerard and Mann 1979) and by L. saccharina and L. hyperborea which stopped growing at the beggining of the summer although nitrogen was still present in the water (Lünning 1979, Helgolander). Inhibition of growth in summer has also been thought to be due to high temperature (Gessner 1955, in Anderson et al. 1981), or to the combined

effects of irradiance and nutrient level (Chapman et al. 1978). Other factors that have been reported to affect growth pattern of Laminaria spp. are: low temperature (Anderson et al. 1981), plant morphology and water movement (Gerard and Mann 1979); reproductive cycle (spore formation) (Kain 1971, Lünning 1979, Dieckman 1980); plant reserves of organic and inorganic nutrients (Chapman and Craigie 1977, Anderson et al. 1981, Gagné et al. 1982); genetic differences and endogenous rhythms (Dieckmann 1980, Gagné et al. 1982), and interactions with epiphytes (Gerard and Mann 1979, Dieckman 1980). For effects of temperature, light intensity and day length on growth of L. saccharina see Fortes and Lünning (1980).

The cycle of nitrogen in the Menai Straits follows the typical pattern for temperate coastal waters, with a winter concentration of 15 g at $l^{-1}NO_3^-$ and a summer one between 0.5 and 3 g at $l^{-1}NO_3^-$ (Ewins and Spencer 1967, Lennox 1979). The NO_3^- saturation concentration for growth of L. saccharina is 10 g at l^{-1} (Chapman et al. 1978). Values higher than this are found in the Menai Straits from November-December until the onset of the spring phytoplankton bloom in April-May (Lennox 1979). Growth of L. saccharina started in January-February 1981 and in January 1982 (Fig. 1.4). If the cycle of nitrogen followed the pattern previously reported for the Menai Straits, factors other than nitrogen must have been controlling growth during these periods. Two such factors could have been low temperature and low irradiance. The latter is likely to have been the most important one as lowest temperature and lowest growth rate did not coincide. Furthermore, the amount of suspended matter in the Menai Straits

increases in winter (Buchan et al. 1967, 1973), reducing light penetration considerably. Field and laboratory studies on L. saccharina and related species have previously shown both the importance of irradiance and the ability of the species to grow at low temperatures (Mann 1972, Johnston et al 1977, Chapman and Lindley 1980, Anderson et al. 1981, Hoek 1982). In the Menai Straits growth of L. saccharina was faster in May 1981 and April 1982, the time of the year when the concentration of NO_3^- may be expected to drop below 10 g at l^{-1} (Ewins and Spencer 1967, Lennox 1979). This high growth rate in May-April and the growth later in the year is probably sustained, in part, by internal reserves of nitrogen (Chapman and Craigie 1977, Gagné et al. 1982).

The positive correlation between frond size and growth rate found in the present study had previously been reported for L. saccharina (Lünning et al 1973), and attributed to photosynthetic area and carbon requirements for growth. Most of the frond elongation in L. saccharina takes place in the proximal 10 cm (Parke 1948), but only 30% of the material needed for frond elongation is photosynthesised in this area, the extra 70% being translocated from older areas of the frond (Lünning et al. 1973). It is assumed that larger fronds, having bigger photosynthetic areas, are able to contribute more material for growth than shorter fronds. Experiments on L. longicruris have, however, supported these results only partially (Chapman and Craigie 1978).

Smaller plants have been found to have a higher turnover rate of tissue than larger ones (Mann 1972). In the present study

from February to June smaller plants produced frond tissue faster per unit length than larger plants (Fig. 1.8.B). During July and August the relation was reversed, larger plants being able to keep growing for a longer time, probably due to higher reserves of nitrogen. Parke (1948) and Lünning (1979) have stated that first year plants keep growing for a longer time in the slow-growing season than older ones, the differences being attributed (Lünning 1979) to higher amounts of energy spent on sporogeneous tissue by older plants. In the present study plant age was not determined, sorus formation however was observed sporadically and in very few plants, therefore nitrogen and energy reserves were most likely to have been committed mainly to growth.

The fluctuation in size of L. saccharina fronds throughout the year has been reported by several authors, (Spence 1918, Parke 1948, Lünning 1979, Kain 1979). The maximum size is reached in mid-summer and frond size increases as shelter and depth increases (Parke 1948, Lünning 1979). Due to mechanical reasons, a specific maximum plant size probably exists for a given place, depending on the degree of exposure to wave action and tidal level. This "optimum size" is likely to change throughout the year as a result of changes in both casting force (water movement) and frond strength, (frond thickness and width are correlated with growth rate and plant age, Parke 1948, Mann 1972, Gerard and Mann 1979). The rate of frond loss is, however, highly unpredictable. The only generalization possible to make is that some loss occurs all the year round. Loss-rates are variable between and within populations depending on exposure, tidal level, time of the year, plant age (Parke 1948, Johnston et al. 1977,

Lünning 1979) and, as found in the present study for a few months of the year, loss-rate was negatively correlated with plant size. All these factors contributed in making frond survival time highly variable.

Survival time of the frond tissue is variable between populations and throughout the year. The minimum and maximum values of frond survival found for L. saccharina in the Menai Straits were well within the limits reported for this species (Parke 1948, L'Hardy 1962, Lünning 1979). The seasonal pattern of frond survival time found in the present study agreed in general with that of L. saccharina in Devon, but it is different from the one reported for Argyll (data in Parke 1948, Plate IX - XI). The intertidal population in Devon showed lowest frond-tissue survival (2 - 3 months) in March-April and highest (6 - 8 months) from June to October. The subtidal population in Argyll showed less variable survival times throughout the year, (5 months between May and August and 6 - 7 months the rest of the year). These inter-population differences in frond-tissue survival time are probably due to different levels of exposure to wave action, plant age and tidal level also affect survival time (Parke 1948, Lüning 1979).

It can be concluded that sessile epifaunal species using fronds of L. saccharina as a substratum should necessarily be short-lived. Organisms with a life cycle longer than 6 - 7 months, (from settlement to larval production), would not be able to establish a breeding population. Because of the seasonal pattern of frond-tissue survival time, it can be expected that epiphyte recruitment will be maximal in the autumn. The following

section deals with the epifaunal community on this substratum.

1.4.2. The Epifauna.

1.4.2.1. The Epifauna on L. saccharina.

Epiphytes occuring on fronds of Laminaria spp., or on any other substratum with an age-dependent mortality, can be expected to achieve a maximum longevity by settling on the youngest area of the frond. Survival time could be prolonged further by directional growth towards the meristematic region of the alga. Both mechanisms have been reported for numerous epiphytes on seaweeds (Ryland 1959, Lutaud 1961, L'Hardy 1962, Ryland and Stebbing 1971. Reviews in Ryland 1976, 1977, Hayward 1980 and Seed and O'Connor 1981b).

Growth towards the meristematic region of the alga seems not to be a response to the age gradient of the frondal tissue but rather a consequence of responses of both the settling larva (taxes) and the growing colony (tropisms) to other factors such as light and water currents (Ryland 1977). The directional growth of Membranipora membranacea on fronds of Laminaria hyperbora, Fucus serratus and Sacchoriza polyschides (Ryland and Stebbing 1971, Norton 1973) is a positive rheotactic mediated response (Norton 1973, Ryland 1977). The orientated growth of Scrupocellaria reptans and Electra pilosa toward younger areas of the substratum (Ryland and Stebbing 1971, Stebbing 1971a) seems to result from the orientation of the larva at settlement, this determining the initial direction of growth. In these cases the responsible stimuli are light and water current respectively (Ryland 1974, 1977). Although directional growth towards the younger areas of the substratum can be achieved in response to different stimuli

according to the species of epiphyte, the ecological consequences of such behaviour are similar on all epiphytes. Orientated growth towards younger areas of the substratum might lead colonies toward areas free of competition thus increasing survivorship (Ryland and Stebbing 1971, Stebbing 1971a). Due to the short life-span of frond tissue of Laminariales, orientated growth of epiphytes may significantly increase residence time. This is likely to be more pronounced among fast growing epifaunal species (e.g. M. membranacea and E. pilosa; hydroids, etc., Menon 1972, Bernstein and Jung 1979, Yoshioka 1982b), and in summer and autumn when the plants are growing more slowly. Because of their small colony size, their concentric pattern of growth and their slow growth-rate (this is in comparison with M. membranacea and E. pilosa, personal observation), orientated growth does not significantly increase the life-span of species such as Callopora lineata and Celleporella hyalina.

Preferential settlement towards the younger areas of the substratum has been reported for bryozoans (Celleporella hyalina, Membranipora membranacea, Alcyonidium polyoum, Scrupocellaria reptans, Bugula flabellata and Crisia eburnea; Ryland 1959b, Ryland and Stebbing 1971, Stebbing 1971a, 1972, Elliot 1982), Serpulids (Spirorbis corallinae, Stebbing 1972) and hydroids (see review in Stebbing 1972). The mechanisms underlying selection of the younger areas remain unexplained, two ideas have however been put forward: a) older areas of fronds usually bear heavy encrustations, and are likely to die sooner, larvae may therefore avoid competition and increase prospects of survival by settling

on the younger areas (Ryland and Stebbing 1971, Stebbing 1971 a), and b) larvae may be responding to factors associated with the age gradient (e.g. microbial films, metabolic gradients, etc., Stebbing 1972; review in Seed and O'Connor 1981b). There is evidence (Grosberg 1981) that larvae of invertebrates are able to detect members of competitively dominant species and avoid settling near them. Absence of subordinated species from fronds of macroalgae on which competitively dominant species are present (Ebling et al. 1948, Kitching and Ebling 1967, Norton 1971, Bernstein and Jung 1979) can be the result of larval avoidance of other species at settlement. This could therefore be a mechanism explaining absence of newly settled colonies on old encrusted areas of frond, but does not explain how the old colonies came to be in that area.

Detection of age gradients on the plant could be achieved using clues such as microbial films and metabolic gradients. Many Bryozoa are known to require microbial films for a successful settlement (Ryland 1974, Scheltema 1976, Mihm et al. 1981, Brancato and Woollacott 1982), this could provide a factor associated with age of the substratum through which the larvae are able to differentiate between young and old tissue (Stebbing 1971a). Two results on the present study are relevant to this problem: Firstly: distance from the stipe of the first detected settlements of C. hyalina on fronds of L. saccharina (Fig. 1.11) varies throughout the year, following the pattern of plant growth. Secondly: this distance is positively correlated with plant size, slopes of linear regressions being higher from January to June than during the rest of the year (Table 1.4). Time for microbial

growth on the frond may be the main factor responsible for this pattern of settlement. Plants growing at higher rates have relatively younger tissue near to their stipes than plants growing slower. The same result regarding distance of first settlements could be expected if the colonies at the time of observation have already moved from their original position of settlement by virtue of plant growth. Furthermore, the similarity in the temporal pattern of settlement found on two areas of L. saccharina fronds (Fig. 1.14), despite the different position on the frond, suggests that the availability of larvae plays a major role in recruitment, age of the substratum probably being a subsidiary factor promoting settlement. Experiments, (such as those of Stebbing 1972), are needed to test larval preference for tissue of different ages.

It can also be argued that the larvae could be detecting factors other than microbial films. It is known that chemical gradients (concentration of mannitol, laminarian mineral reserves and antibiotic products) exist along the fronds of Laminaria spp. (Black 1954, Hornsey and Hide 1976b, Kain 1979). Mannitol is regarded as indicative of the amount of photosynthesis; it reaches the highest concentration one-third of the way up the frond, decreasing both towards the stipe and the tip (Black 1954). This gradient should be maintained by photosynthesis. The gradients of laminarian and minerals are present in the plant only during the low growing season and high mineral concentrations respectively (Black 1954, Haug and Jensen 1954, Hatcher et al. 1977, Kain 1979), therefore they cannot be used as age indicators at least during part of the year. Antibiotic production by the algae may

play a role in determining which part of the alga is colonized. L. saccharina and L. digitata produce antibacterial substances in higher concentrations in winter towards the frond tips (Hornsey and Hide 1974, 1976a,b). It is unknown if these substances are able to affect adult epiphytes in the same way that those produced by Sargassum (Sieburth and Conover 1965). These substances are however likely to interfere with larval settlement if the formation of a microbial film is inhibited. In L. saccharina antibiotic production is zero between May and October (Hornsey and Hide 1976a). This coincides with the higher observed percentage of encrusted fronds (Table 1.4) and with the higher settlements of C. hyalina on this alga (Fig. 1.14) in the Menai Straits. Epiphytes were also more common on L. saccharina in France between March and September (L'Hardy 1962), suggesting that this pattern may be of general occurrence. This could however be just a result of larval availability. This is also the time of the year at which life expectancy of the substratum is highest (Fig. 1.10) providing another selective force for heaviest settlement during this period.

The results presented in this study indicate that settlement of C. hyalina towards the younger areas of L. saccharina increases both the maximum survival time and the mean probability of survival until the substratum desintegrates. Longer living colonies will have more time to grow and to sexually reproduce, therefore they are likely to produce more larvae than colonies that live for a shorter time. Selective advantage is therefore confered to those individuals able to detect the younger parts of the frond. Colonization of the whole frond of L. saccharina,

however, seems to be only possible if frondal growth stops (personal observation), a situation also reported for S. polyschides (Norton 1971). Settlements of S. reptans were obtained on the younger areas of fronds of L. digitata collected in August-September, at which time growth of this alga is low (Kain 1979). Evidence therefore suggests that growth of the plant may be directly influencing selection of areas for settlement, very young or actively growing areas not being available for colonization. This may explain the puzzling results of Ryland (1959b) on settlement of C. hyalina. He found that L. saccharina was not preferentially selected by larvae of C. hyalina when a choice of different algae was given, the pieces of L. saccharina. offered, however came from the youngest part of the frond (Ryland 1959b, pp:629-630).

Selection of younger areas of fronds of different species of brown macroalgae (or other substratum with age gradient) by larvae of sessile epifauna is probably the result of different selective forces operating in each epiphyte community. Fast renewal of the frond of Laminaria spp. probably confers a selective advantage to epiphytes settling on the youngest areas. Settlement of epiphytes on younger areas of Fucus serratus does not necessarily guarantee a longer survival time since defoliation occurs due to plant reproduction (Knight and Parke 1950). In this case, and in that of epizoites on Flustra foliacea (a substratum lasting for up to 12 years, Stebbing 1971b), selection of younger parts of the fronds can be thought as a competition-avoidance mechanism (Stebbing 1971a, Ryland and Stebbing 1971, Seed and O'Connor

1981b), rather than selection of a persistant substratum. On L. saccharina, the correlation between the survival time of the sessile epifauna and that of the frond tissue is obvious. From studies of the survival time of frond tissue (Fig. 1.10) it is clear that a maximum life-span would be reached if the epiphyte were to settle in August-September. Earlier arrival on the frond, however, could be at premium since individuals of C. hyalina arriving earlier reached a bigger size than those arriving later. On the other hand, too early an arrival reduces life-span (Fig. 1.10). Size and number of sexual zooids in bryozoans are positively correlated (Hayward and Ryland 1975, Wood 1983, see Chapter 3 for C. hyalina). Early recruits, therefore, are likely to produce more larvae than individuals settling later on the season. Hayward and Harvey (1974) and Hayward and Ryland (1975) found that in Alcyonidium hirsutum, growth rate, final colony size and mortality were not affected by the density of colonies. However, a negative correlation between density and colony size has been found for A. hirsutum in the Menai Straits (Wood 1983).

A very high percentage of the larvae of C. hyalina settled on L. saccharina fronds formed colonies that survived until the substratum reached the frondal tip. The main cause of mortality was due to substratum abrasion. These results contrast with those obtained for A. hirsutum (Wood 1983), where only 17% of the total mortality was due to loss of the substratum. Seed and O'Connor (1981b) reported that the number of Spirorbis dying due to frond loss increased from the base to the tip of F. serratus, other factors (detachment or overgrowth) being more important as mortality factors toward the base of the plant. In the present

study it was found that inter- and intra-specific overgrowth was virtually absent from L. saccharina fronds.

Although C. hyalina is overgrown by M. membranacea (Bernstein and Jung 1979, personal observation), and in a few cases by E. pilosa (see Chapter 2), the density of the two latter species found in the present study was too low to account for a significant amount of the mortality of C. hyalina. Growth of C. hyalina usually stops when a conspecific colony is touched (see Chapter 2). This is the typical outcome of intra-specific contacts on bryozoans (Stebbing 1973a,b; Hayward and Harvey 1974b; Hayward and Ryland 1975, Seed and Boaden 1977, O'Connor et al. 1980, Wood and Seed 1980, Seed and O'Connor 1981b). The present findings confirm that intra-specific competition for substratum is not a major factor of mortality of colonial epifauna on algae.

Monospecific stands, as of Celleporella hyalina on fronds of L. saccharina, have been thought to be effective mechanisms preventing inter-specific competition (Crisp 1979, Schmidt 1982) and a meansof increasing the probability of cross-fertilization in hermaphrodite sessile animals such as tunicates, barnacles and bryozoans (Ryland 1973, Crisp 1979, Schmidt 1982). It is known that self-fertilization is possible in barnacles and tunicates, but survival of the progeny is low (Barnes and Crisp 1956, Sabbadin 1971). Currently it is generally accepted that most species of bryozoans cross-fertilize (see Chapter 4). C. hyalina, like most bryozoans, is a simultaneous hermaphrodite. In the present study, males and females were observed in small colonies of C. hyalina (4 mm diameter, March 1981), and since most colonies

were touching neighbouring ones, cross-fertilization was probably taking place in this population. The possibility of larval production by isolated colonies of C. hyalina will be discussed in Chapter 4.

Intra-specific competition within monospecific stands has been reported for barnacles (Crisp 1964) and Spirorbis (O'Connor and Lamont 1978). It is also likely to occur in bryozoans since denser settlements produce smaller colony sizes than more sparse settlements. This is likely to affect reproductive output. This will be the subject of further investigation (see Chapter 3).

1.4.2.2. The Epifauna on Other Susbtrata.

The 4 species of encrusting bryozoa (Celleporella hyalina, Electra pilosa, Callopora lineata and Membranipora membranacea), found on Laminaria saccharina fronds in the Menai Straits have been reported for a wide diversity of substrata along with their distributional ranges (Tables 1.6). In a particular place, however, these bryozoans occur in abundance in only a few substrata, usually brown macroalgae. M. membranacea is restricted to Phaeophyta, the other 3 species of bryozoans occur in a wider range of substrata (Table 1.6).

The algae providing substratum for C. hyalina, E. pilosa, C. lineata and M. membranacea can be classified as : a) those with short-lived frondal tissue (e.g. Laminaria spp, S. polyschides, and M. pyrifera; see North 1961, Norton and Burrow 1969, Kain 1979), and b) those with longer-lived frondal tissue (e.g. F. serratus, F. vesiculosus, R. californica; see Knight and Parke 1950, Bernstein and Jung 1979). Epiphytic communities on the

former group of algae (Ebling et al. 1948, Sloane et al. 1957, L'Hardy 1962, Norton 1971, Seed 1976, Bernstein and Jung 1979, Seed and Harris 1980, Dixon et al. 1981, and the present study) are less complex than those occurring on the latter group of algae (Hagerman 1966, Stebbing 1973a, Boaden et al. 1975,1976, Seed and Boaden 1977, Bernstein and Jung 1979, O'Connor et al. 1979, 1980; Seed and O'Connor 1980, 1981, Wood and Seed 1980). Although competitive abilities could be occasionally important for epiphytes living on algae of group (a) (e.g. on M. pyrifera, Bernstein and Jung 1979), the species on this substratum depend mostly on their colonizing abilities. Fast growth, early and continuous sexual reproduction being the key factors. The synchrony between growth and reproduction of M. membranacea and that of Laminaria spp. in the Isle of Man has been discussed by Eggleston (1972), for M. membranacea in California see Bernstein and Jung (1979) and Yoshioka (1982b). Epiphytes occurring on algae of group (b), (e.g. on F. serratus and R. californica) depend to a greater degree on competitive ability to maintain their position on the plant (Stebbing 1973a, b, Seed and Boaden 1977, Bernstein and Jung 1979, O'Connor et al. 1980, Wood and Seed 1980, Seed and O'Connor 1981b).

The competitively dominant species occurring on F. serratus (i.e. Frustrellidra hispida, Alcyonidiun hirsutum and A. polyoum) do not settle in high numbers on Laminaria spp. (Ryland 1959b), being probably excluded from this substratum by virtue of their long pre-reproductive life-span (Seed and O'Connor 1981b, Elliot 1982, Wood 1983). Species of Bryozoa normally occurring in high

densities on Laminaria spp., however, also settle on F, serratus (Table 1.6). On this substratum, overgrowth by F. hispida or Alcyonidium spp. can be avoided through partitioning of the substratum and habitat selection. E. pilosa and M. membranacea, species commonly overgrown on F. serratus in Strangford Lough, Northern Ireland (O'Connor et al. 1980), are more abundant on different levels of the plants or in different habitats than A. hirsutum and F. hispida. M. membranacea is especially abundant in quiet silt-free waters (Sloane et al. 1957, Kitching and Ebling 1967, O'Connor et al. 1979). C. hyalina is more tolerant of low water movement and high sediment concentration than most bryozoans (Sloane et al. 1957, Kitching and Ebling 1967, but see Moore 1973d), and is therefore able to use plants in habitats relatively free of competitive dominant species (e.g. on L. saccharina in the Menai Straits). Partitioning of S. polyschides among M. membranacea, C. hyalina, E. pilosa and C. lineata has been described by Ebling et al. (1948), Kitching and Ebling (1967) and Norton (1971). Partitioning of fronds of M. pyrifera among Spirorbis spirillum, C. hyalina, and Lichenopora buskiana have been discussed by Bernstein and Jung (1979). Continuous generation of substratum through plant growth and active larval choice are probably the major factors responsible for these patterns of distribution, and for the generally recognized low incidence of competitive interactions in organising epiphyte communities on seaweeds (Stebbing 1973, O'Connor et al. 1980, Seed and O'Connor 1981).

Finally, at Trwyn-y-Penrhyn, Menai Straits, there is an

extensive bed of L. saccharina long known to be used mainly by C. hyalina (Ryland 1959a). The colonizing abilities of the bryozoan, its early sexual maturity, its ability to produce larvae all year round (Eggleston 1963, 1968, Chapter 3), and the virtual absence of other encrusting bryozoans are likely to be some of the reasons for its success in this highly dynamic and ephemeral habitat. C. hyalina uses a great diversity of substrata (Table 1.6) within its geographical range. In Wales it uses concavities of L. saccharina, in California it has been reported on ridges of fronds of M. pyrifera (Bernstein and Jung 1979), and forming small erect reefs on rocks (Winston 1979); such versatility is probably one of the reasons for its wide distribution.

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Table 1.1. Numbers of plants of L. saccharina marked and measuredon successive dates.

Observation Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
DATE	26 Oct '80	22 Nov '80	21 Dec '80	20 Jan '81	20 Feb '81	20 Mar '81	9 Apr '81	5 May '81	3 Jun '81	4 Jul '81	1 Aug '81	31 Aug '81	16 Sep '81	14 Oct '81	13 Nov '81	12 Dec '81	10 Jan '82	9 Feb '82	10 Mar '82	26 Mar '82	8 Apr '82	24 Apr '82	23 May '82	25 Jun '82	TOTAL
Number of Plants marked on date:	21	--	12	--	--	--	--	19	--	--	1	--	2	--	--	--	6	--	--	--	--	--	--	--	61
recovered from previous date:	--	16	15	26	24	23	22	20	39	33	30	26	24	24	24	23	20	26	24	23	22	22	20	16	542

Table 1.2 Regression and correlations between different parameters measured on L. saccharina throughout the year. Observation dates are given in Table 1.1.

MF Mean Frond Size; GD Growth rate per day;

LD Frond Loss per day; LMF Natural log of MF;

LGD Natural Log of GD; N Number of plants;

r : correlation coefficient; b slope; a y intercept;

Levels of significance : N.S. non-significant.

* 0.05 > p>0.01
** 0.01 > p>0.001
** p < 0.001

For further information see text.

		MARCH (1982) EARLY		MARCH (1982) LATE		APRIL (1982) EARLY		APRIL (1982) LATE		MAY (1981/82)	
	N	23		22		21		21		39	
	r	0.7750		0.6999		0.7707		0.7895		0.8988	
MF/GD	b	0.59136E-02	***	0.55964E-02	***	0.6321E-02	***	0.81043E-02	***	0.93739E-02	***
	a	0.14603	*	0.32468	**	0.54528	***	0.70251	***	0.28970	***
	r	N.S.		0.6156		0.7706		0.7609		0.6707	
LMG/LGD	b			-0.40786	**	-0.51037	***	-0.45156	***	-0.26354	***
	a			1.7585	**	2.5174	***	2.5049	***	1.4238	***
	r	N.S.		N.S.		N.S.		0.5091		N.S.	
MF/LD	b							-0.38604E-02	*		
	a							0.13473	N.S.		
	r	N.S.		N.S.		N.S.		N.S.		N.S.	
GD/LD	b										
	a										

		JUNE (1981)		JULY (1981)		AUGUST (1981)	
	N	38		32		52	
MF/GD	r	0.7998		0.8626		0.7567	
	b	0.76016E-02	***	0.89544E-02	***	0.43226E-02	***
	a	0.44554	***	-0.21974	N.S.	-0.56555E-01	N.S.
	r	0.6296		0.4468		0.3398	
LMG/LGD	b	-0.41736	***	0.49100	*	0.40486	**
	a	2.1212	***	-2.7965	**	-3.0108	***
	r	N.S.		0.4370		0.4437	
MF/LD	b			-0.45517E-02	*	0.34442E-02	***
	a			-0.77826E-01	N.S.	-0.28720	N.S.
	r	N.S.		0.5766		0.4650	
GD/LD	b			0.53297	***	-0.63610	***
	a			0.17295	N.S.	-0.40671	***

		SEPTEMBER (1981)		OCTOBER (1981)		NOVEMBER (1980/1981)	
	N	23		23		39	
	r	0.5993		0.5804		N.S.	
MF/GD	b	0.14366E-02	**	0.99396E-03	***		
	a	0.13093E-01	N.S.	-0.54944E-02	N.S.		
	r	N.S.		N.S.		N.S.	
LMF/LGD	b						
	a						
	r	N.S.		0.5312		0.4289	
MF/LD	b			-0.31162E-02	***	-0.46805E-02	**
	a			-0.15460	N.S.	-0.11064	N.S.
	r	N.S.		N.S.		N.S.	
GD/LD	b						
	a						

		DECEMBER (1980/1981)	JANUARY (1981/1982)			FEBRUARY (1981/1982)			
	N	37	26		19	21		24	
	r	N.S.	0.5868		N.S.	0.6621		0.6211	
MF/GD	b		0.24517E-02	*		0.32369E-02	**	0.48297E-02	**
	a	N.S.	-0.62468E-01	N.S.		0.25795E-01	N.S.	0.22919E-01	N.S.
	r	N.S.	N.S.		N.S.	N.S.		N.S.	
LMF/LGD	b								
	a								
	r	N.S.	N.S.		N.S.	N.S.		0.4217	
MF/LD	b							-0.77961E-02	*
	a							0.11652	N.S.
	r	N.S.	0.4962		N.S.	N.S.		N.S.	
GD/LD	b		1.4768						
	a		-0.33698						

Table 1.3 Mean density of encrusting bryozoans on fronds of L. saccharina. Sampling units are cross-sections of fronds 15cm in length (see diagram of frond in Fig. 1.21).

DATE		May to Oct 1981	July to Dec 1981	18 Sept. 1982 POSITION ON FROND Proximal	Central	Distal	
No. sampling units		10	14	7	7	7	
$\bar{x}$ area (s) cm^2		181.776 (48.293)	204.863 (34.752)	143.320 (16.373)	173.790 (25.063)	156.162 (43.594)	%
C.hyalina	$\bar{x}$	63.800	92.786	267.000	214.430	149.000	99.24
	(s)	(55.501)	(65.377)	(191.786)	(80.247)	(77.071)	
E. pilosa	$\bar{x}$	0.600	0.417	0.143	0.143	1.714	0.38
	(s)	(0.843)	(0.669)	(0.378)	(0.378)	(1.38o)	
C.lineata	$\bar{x}$	0	1.615	0.143	0	0.143	0.24
	(s)		(3.841)	(0.378)	0	(0.378)	
M.membranacea	$\bar{x}$	0	0.286	0	0	0.857	0.14
	(s)		(0.611)			(1.464)	

Table 1.4 Seasonal occurrence of *C. hyalina* on fronds of *L. saccharina*.

r: regression coefficient; b: slope; a: y intercept; p probability; Only plants with *C. hyalina* were included in the regression analyses.

	DATE								
	15 Oct 1981	13 Nov	12 Dec	11 Jan 1982	9 Feb	9 March	24 Apr	25 June	18 Sept
No. of plants observed	112	122	62	82	89	66	98	154	76
% with *C. hyalina*	100	94.26	100	80.49	83.15	68.18	86.73	100	100

Regressions: Size of fronds/first settlements

r	0.4611	0.5090	0.5687	0.5817	0.7311	0.7470	0.8574	0.8887	0.8239
b	0.11081	0.10441	0.24565	0.33199	0.41014	0.47568	0.58856	0.36497	0.10689
a	8.8026	6.9172	-0.63698	7.3752	7.7307	0.89186	11.245	3.4087	2.4809
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 1.5. Survivorship of C. hyalina on L. saccharina fronds.

A: area with first settlement in May.

B: area with first setlement on 1st. August.

x	A (N = 371)	B (N= 544)
Age (months)	l (x)	l (x)
0	1.000	1.000
1	0.647	0.877
2	0.334	0.840
2.5	----	0.787
3.0	0.111	----
3.5	0.058	0.653
4.0	----	----
4.5	0.011	0.182
5.0	0.000	0.000

Table 1.6.

Substrata reported for the commonest species of encrustring bryozoans occurring on L. saccharina at Menai Straits. The records on this Table include information from the Pacific Coast of U.S.A. (Pinter 1961, Seed 1976, Bernstein and Jung 1979, Yoshioka 1982b); France (L'Hardy 1962) and Sweden (Hagerman 1966). All other references correspond to localities in Ireland, Isle of Man, Wales, and England.

(*) common to abundant, (1) holdfasts;

(2) see Yoshioka 1982a.

SUBSTRATA	*Celleporella hyalina*	*Electra pilosa*
PHAEOPHYCEAE		
Laminaria saccharina	Ryland 1959*, 1962; L'Hardy 1962.* Eggleston 1968*, 1972*; Ryland & Nelson-Smith 1975*.	Ryland 1962.
Laminaria digitata	Colman 1940 (1) Sloane *et al.* 1957; Ryland 1959, 1962 (1) Seed & Harris 1980	Ryland 1962 (1), Seed & Boaden 1977*,Seed & Harris 1980
Laminaria hyperbora	Sloane *et al.* 1957 Ryland 1962 (1), Moore 1973d (1)*	Ryland 1962 (1) Moore 1973d (1)*
Fucus serratus	Ryland 1959, 1962 O'Connor *et al.* 1980* Wood & Seed 1980, Seed & O'Connor 1981	Ryland 1962, Hagerman 1966* Ryland & Stebbing 1971, O'Connor *et al.* 1980*, Wood & Seed 1980, Seed & O'Connor 1981*
Saccorhiza polyschides	Ebling *et al.* 1948* Sloane *et al.* 1957* Ryland 1962, Norton 1971	Norton 1971
Macrocystes pyrifera	Pinter 1969 Bernstein & Jung 1979*	
Other Phaeoephyceae	Ryland 1959, 1962 Pinter 1969, Seed & Boaden 1977	Ryland 1962; Seed & Boaden 1977*
CHLOROPHYCEAE	Ryland 1959, 1962 Sloane *et al.* 1961 Pinter 1969	Sloane *et al.* 1961, Ryland 1962
RHODOPHYCEAE	Ryland 1959, 1962 Sloane *et al.* 1961 Pinter 1969 Bernstein & Jung 1979*	Sloane *et al.* 1961, Ryland Stebbing 1971
Erect HYDROIDS and BRYOZOANS	Ryland 1962 Eggleston 1963, 1968	Ryland 1962 Eggleston 1968
Shells	Ryland 1962	Ryland 1962
	Eggleston 1963, 1968	Eggleston 1968

Stones and Boulders	Lilly et al. 1953 Ryland 1962 Eggleston 1963, 1968 Winston 1979	Ryland 1962 Eggleston 1968
Artificial materials (panels,glass,etc)	Ryland 1960, Withers & Thorp 1977,	Ryland 1960 Withers & Thorp 1977

SUBSTRATA	Callopora lineata	Membranipora membranacea
PHAEOPHYCEAE		
Laminaria saccharina	L'Hardy 1962*, Eggleston 1968*, 1972*; Ryland & Nelson-Smith 1975*	L'Hardy 1962 Ryland 1962 Eggleston 1968 Seed 1976* (2)
Laminaria digitata	Colman 1940 (1), Ryland 1962 (1); Eggleston 1968 (1), Seed & Harris 1980	Sloane et al. 1957, Ryland 1962*, Eggleston 1968*, Ryland & Nelson-Smith 1975*, Seed & Boaden 1977* Seed & Harris 1980*
Laminaria hyperbora	Ryland 1962 (1) Eggleston 1968 (1) Moore 1973d (1)*	Sloane et al. 1957, Ryland 1962* Eggleston 1968* Ryland & Stebbing 1971
Fucus serratus		Ryland 1962 Ryland & Stebbing 1971* O'Connor et al. 1980
Saccorhiza polyschides	Ryland 1962 Norton 1971	Ebling et al. 1948*, Sloane et al. 1957* Norton 1971*, 1973*
Macrocystis pyrifera		Pinter 1969 Bernstein & Jung 1979*, Yoshioka 1982b*

Other Phaeophyceae	Ryland 1962 Pinter 1969 Seed & Boaden 1977, Bernstein & Jung 1979
CHLOROPHYCEAE	
RODOPHYCEAE	Ryland 1962
Erect HYDROIDS and BRYOZOANS	
Shells	Eggleston 1968
Stones and Boulders	Lilly et al. 1953 Ryland 1962 Eggleston 1968*
Artificial materials (panels,glass,etc)	

Plate 1.1.

Plants of Laminaria saccharina showing marking method. ph: punched hole, cs: coloured string. The scale is in cm.

Plate 1.1

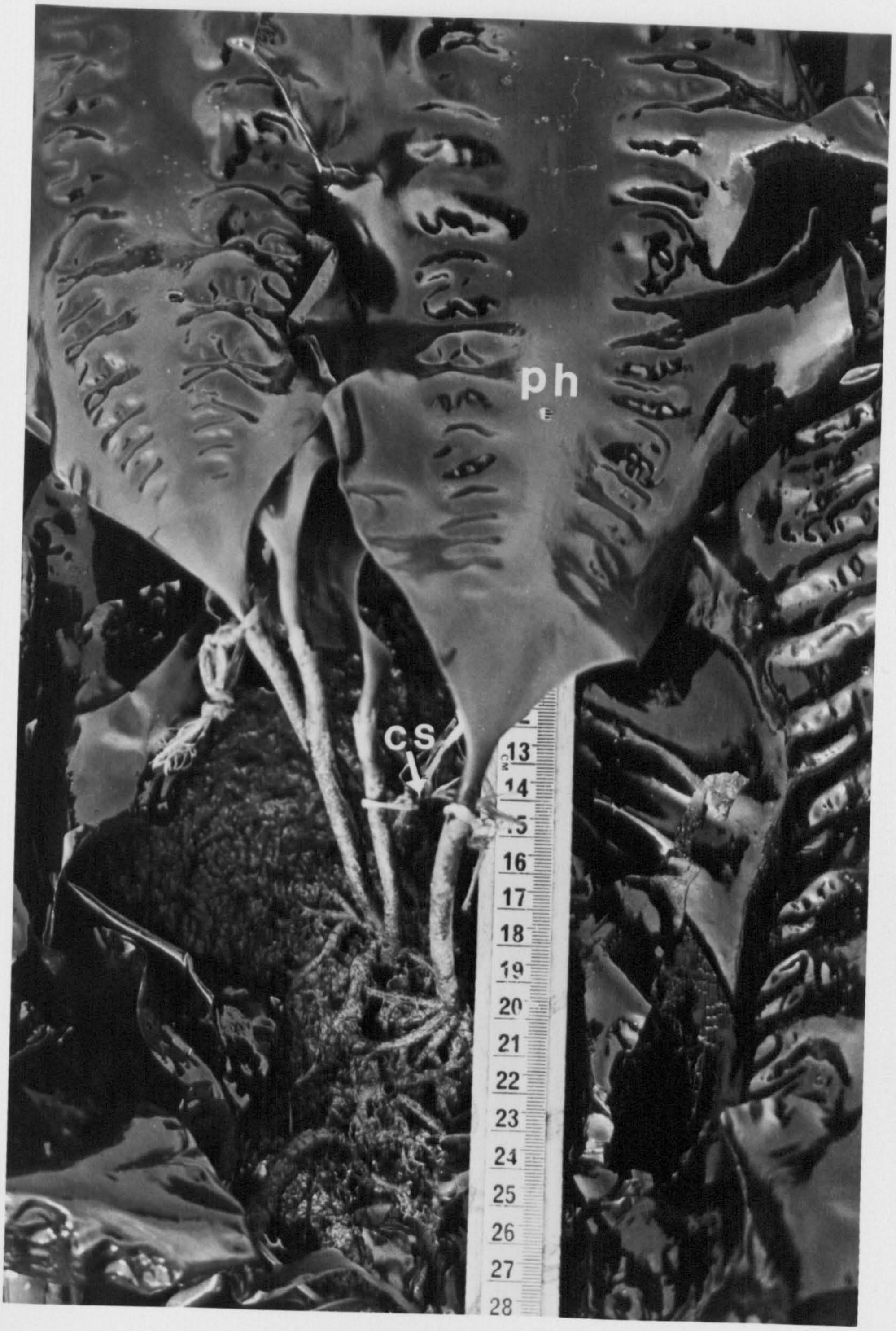


Figure 1.1.

Population structure (frond length) of L. saccharina at different months in 1981 and 1982.

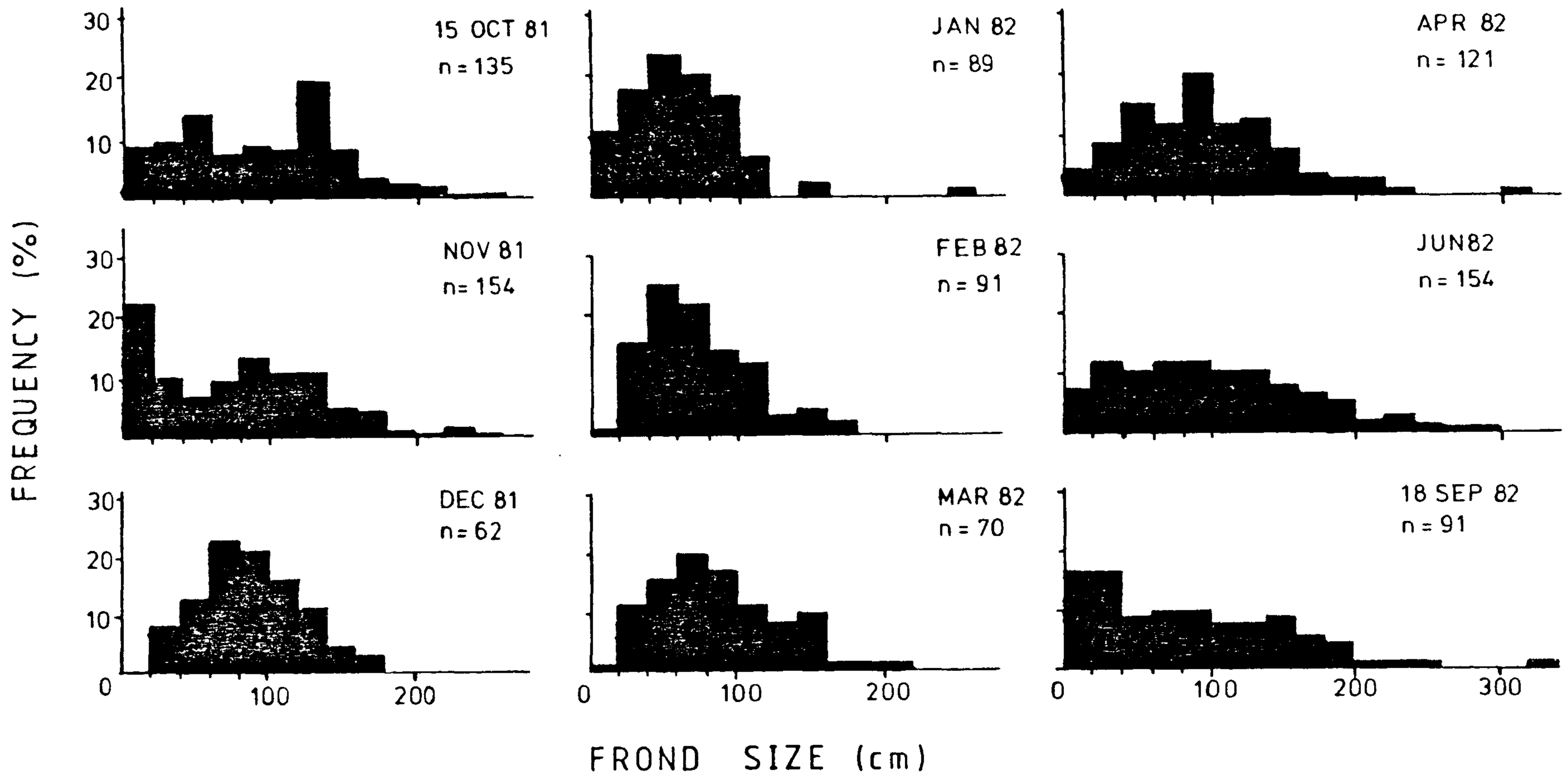
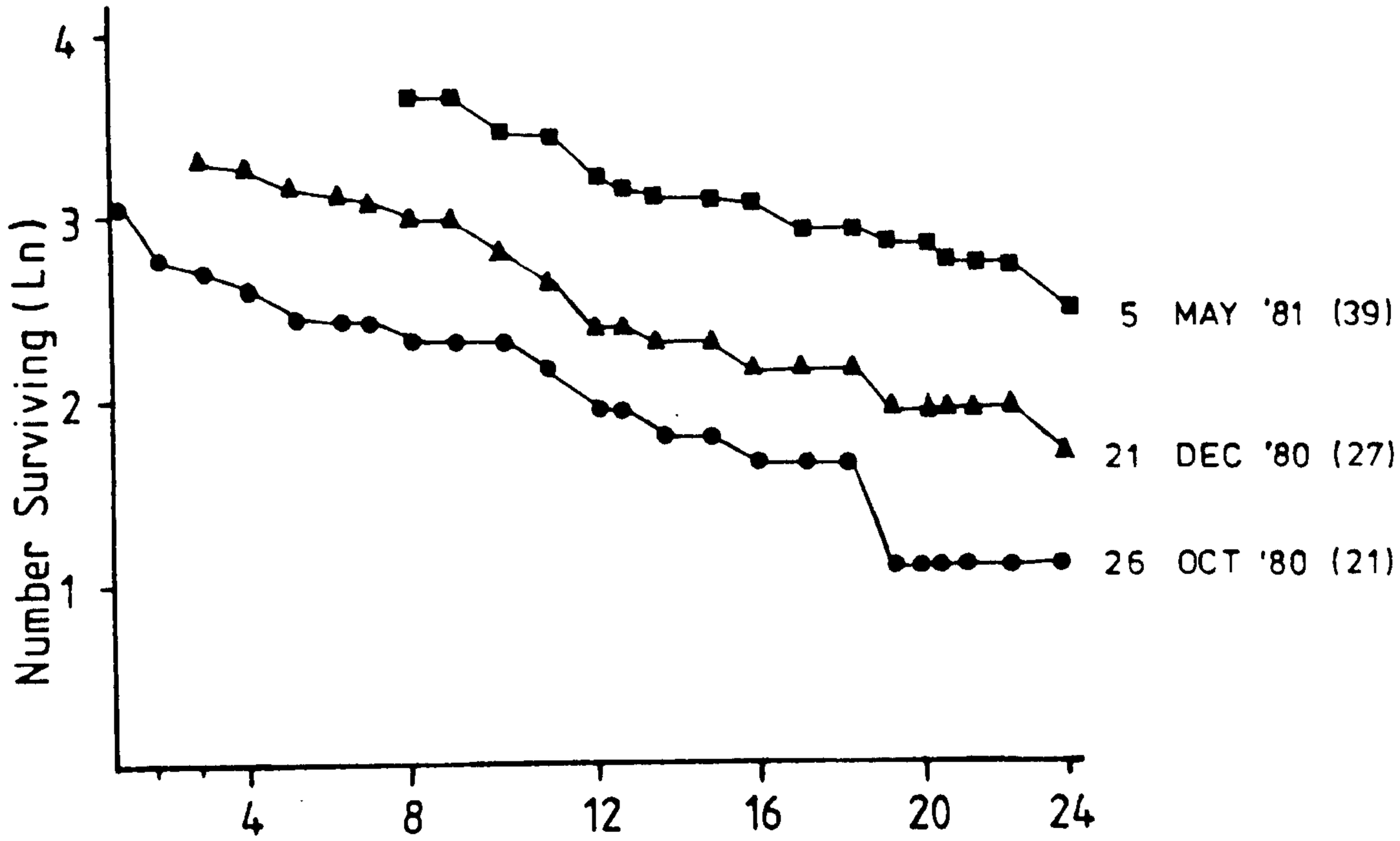

15 OCT 81
n = 135
JAN 82
n= 89
APR 82
n = 121
NOV 81
n= 154
FEB 82
n = 91
JUN82
n = 154
DEC 81
n= 62
MAR 82
n = 70
18 SEP 82
n = 91
FREQUENCY (%)
30
20
10
0
100
200
300
FROND SIZE (cm)

Figure 1.2.

Survival of marked plants of L. saccharina. A, gives number surviving after the 3 dates on the right. Values in brackets are initial numbers of plants. B, gives the proportion dying from one observation to the next.

Observation dates are given in Table 1.1.

A


Number Surviving (Ln)
4
3
2
1
4
8
12
16
20
24
5 MAY '81 (39)
21 DEC '80 (27)
26 OCT '80 (21)

B

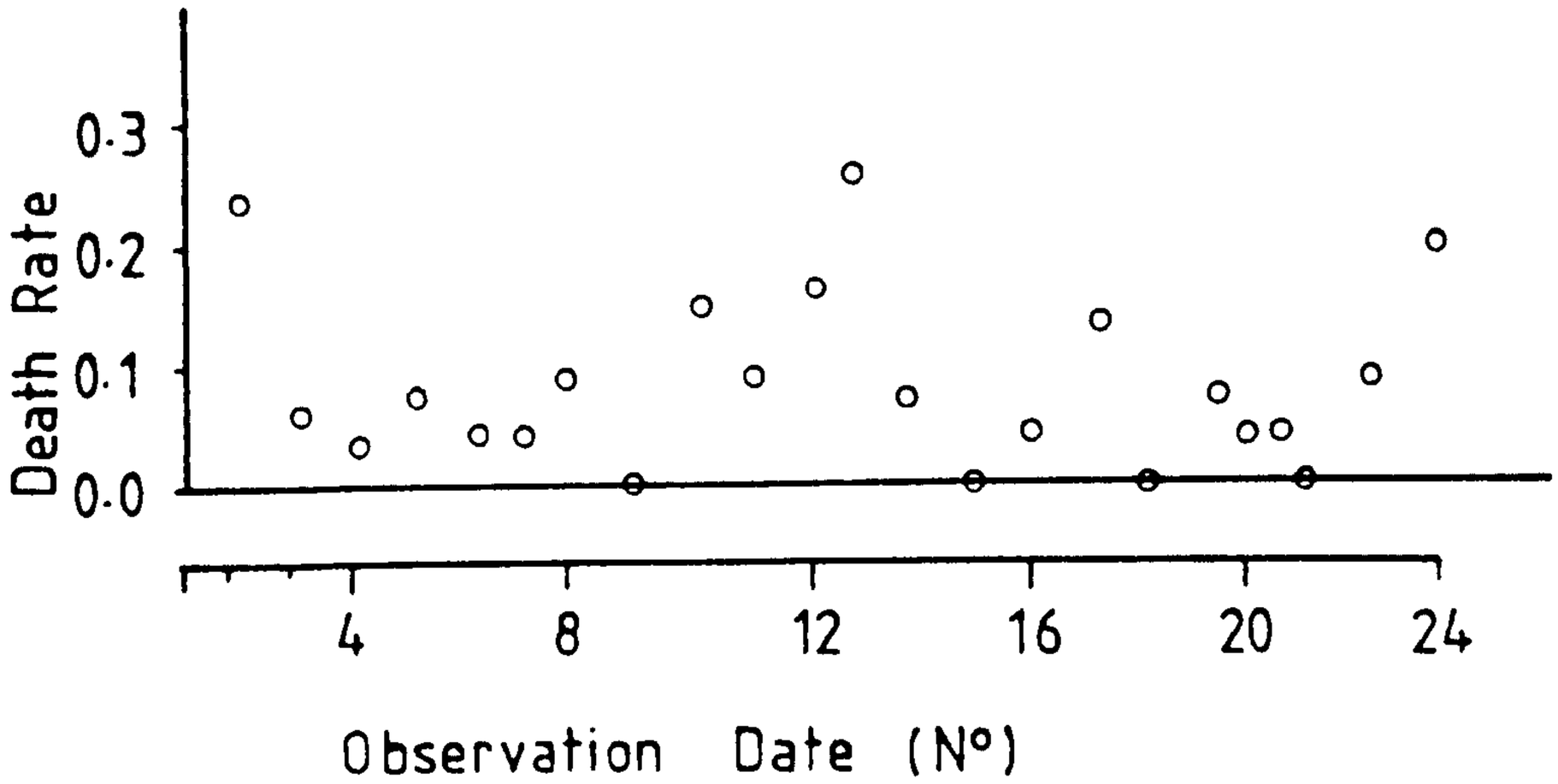

Death Rate
0·3
0·2
0·1
0·0
4
8
12
16
20
24
Observation Date (N°)

Figure 1.3.

Mean frond size of marked plants of L. saccharina

Vertical bars correspond to confidence intervals for the mean (α 0.05). Number of plants measured are given in Table 1.1. as "number recovered from previous date".

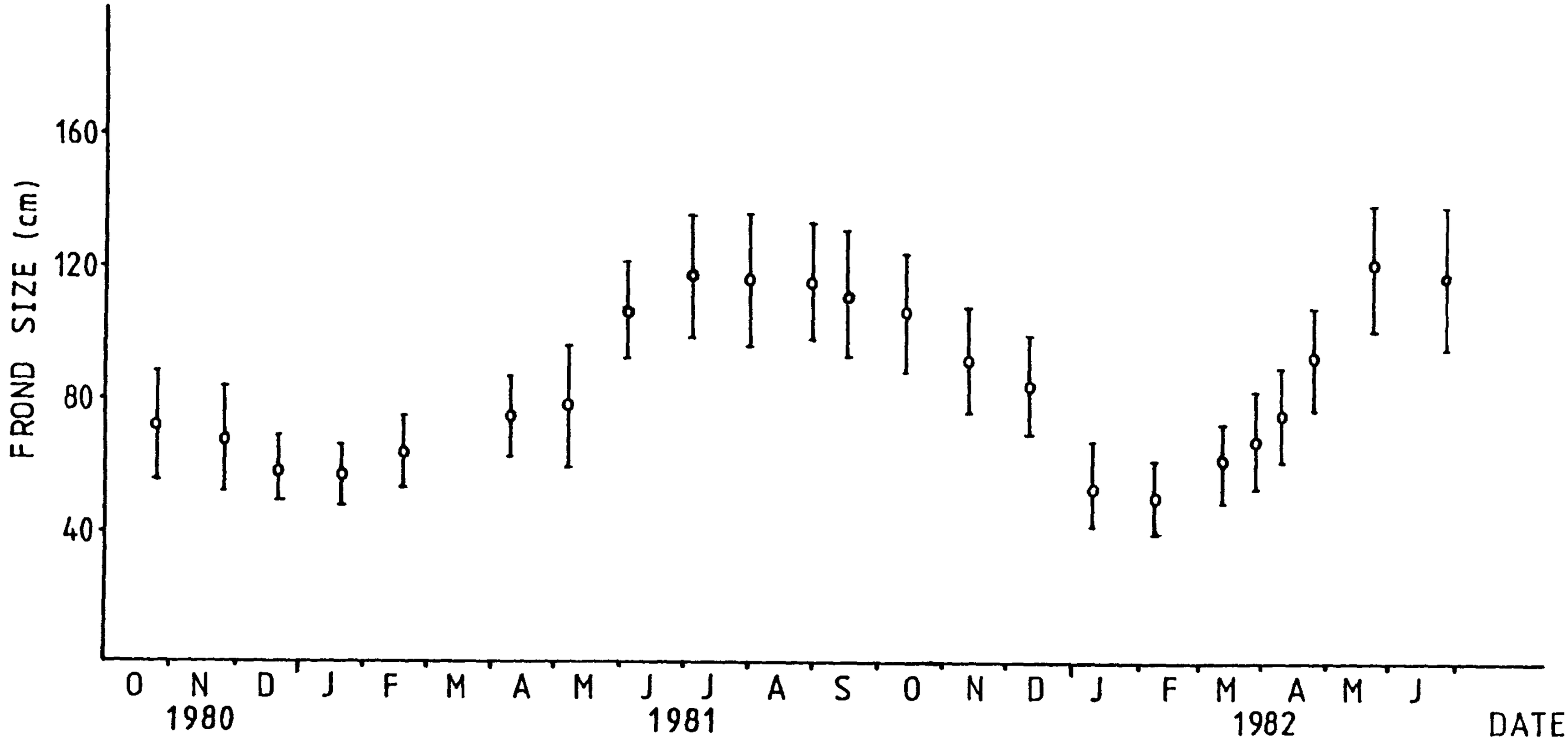

FROND SIZE (cm)
160
120
80
40
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1980
1981
1982
DATE

Figure 1.4.

Mean daily growth rate of L. saccharina fronds.

Vertical bars and number of plants as Figure 1.3.

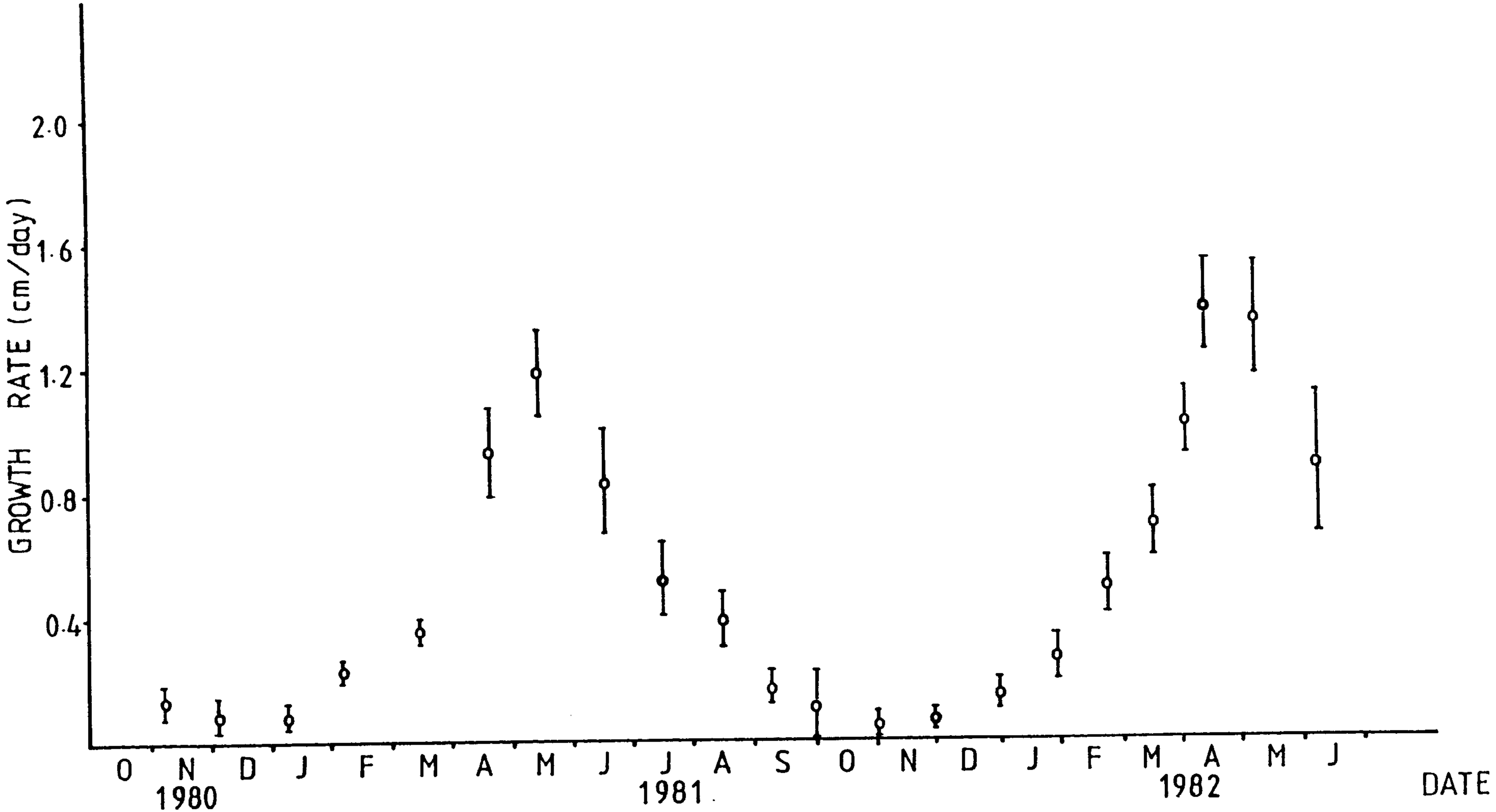

GROWTH RATE (cm/day)
2·0
1·6
1·2
0·8
0·4
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1980
1981
1982
DATE

Figure 1.5.

Mean frondal loss rate of L. saccharina. Symbols and number of plants as Figure 1.3.

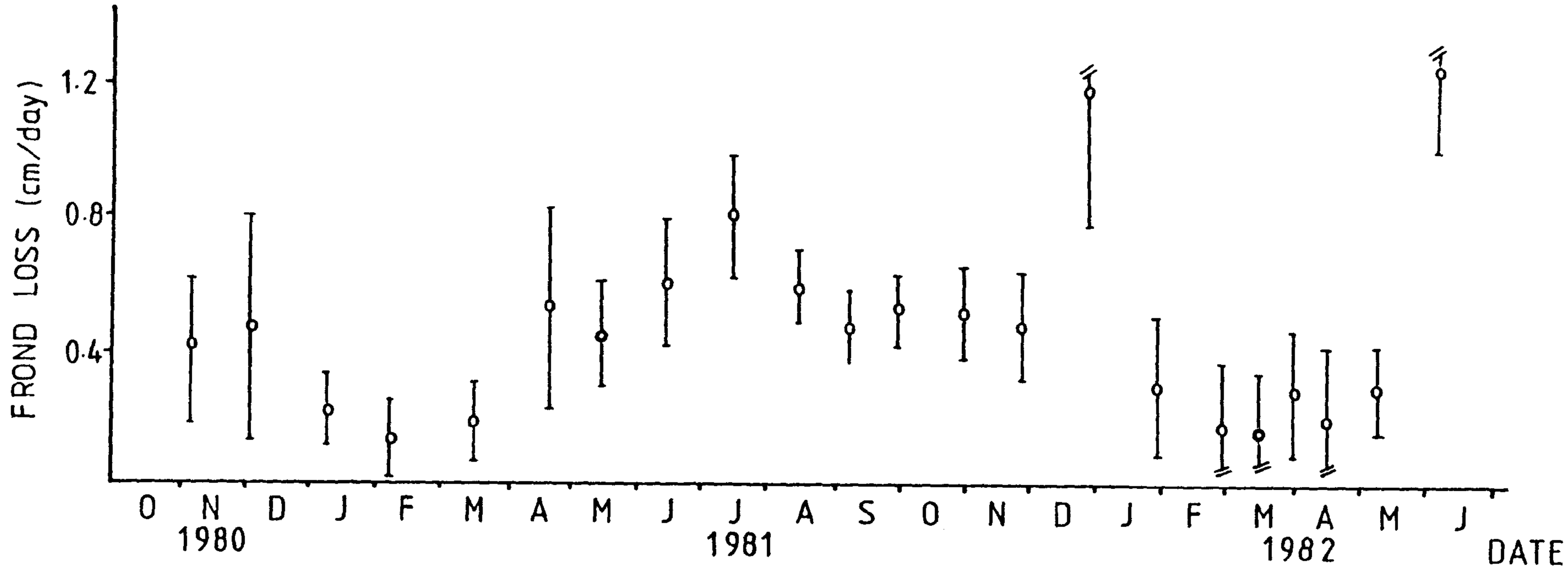

FRONT LOSS (cm/day)
1·2
0·8
0·4
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1980
1981
1982
DATE

Figure 1.6

Water temperature at Menai Bridge Pier.

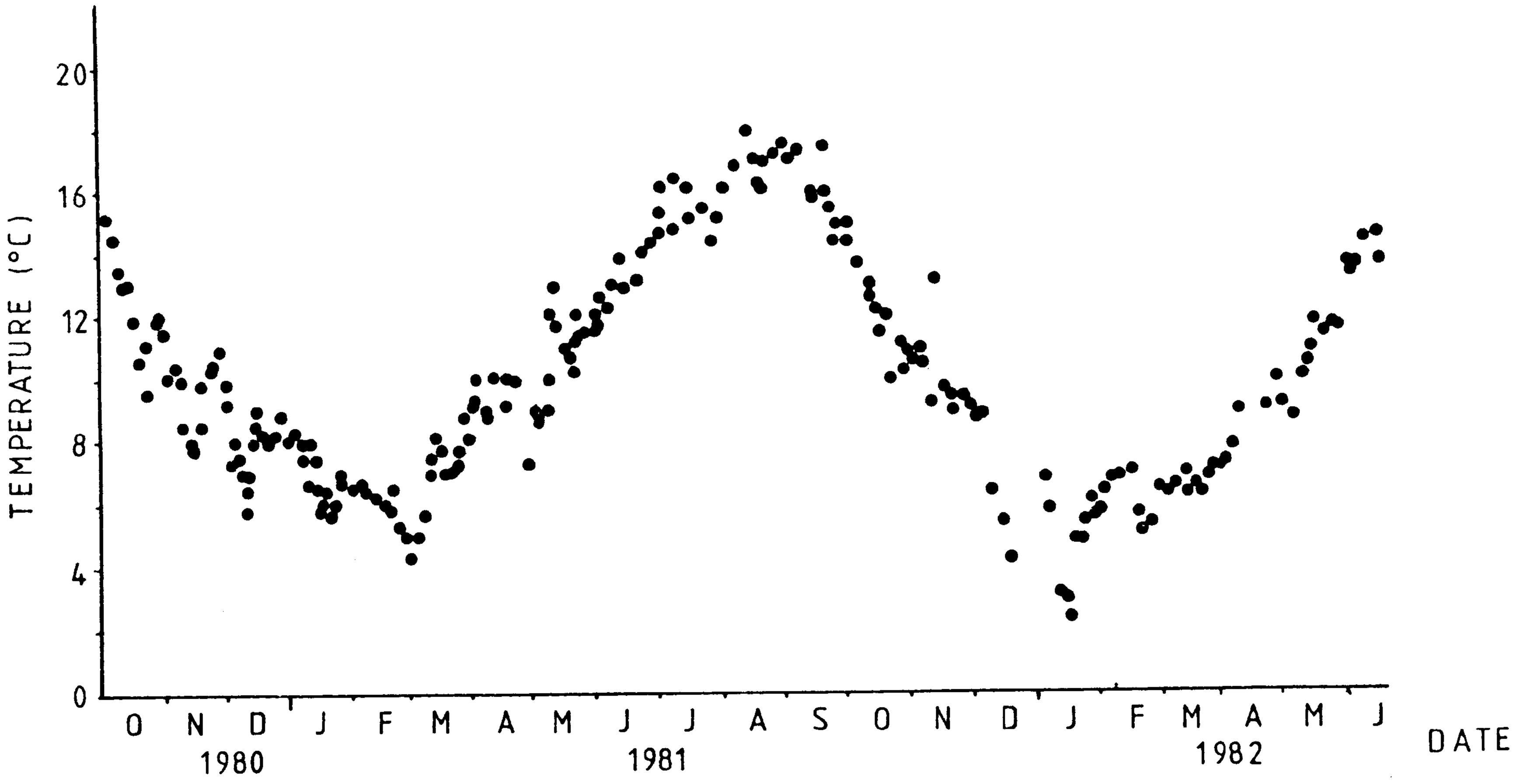

TEMPERATURE (°C)
20
16
12
8
4
0
O N D J F M A M J J A S O N D J F M A M J
1980
1981
1982
DATE

Figure 1.7

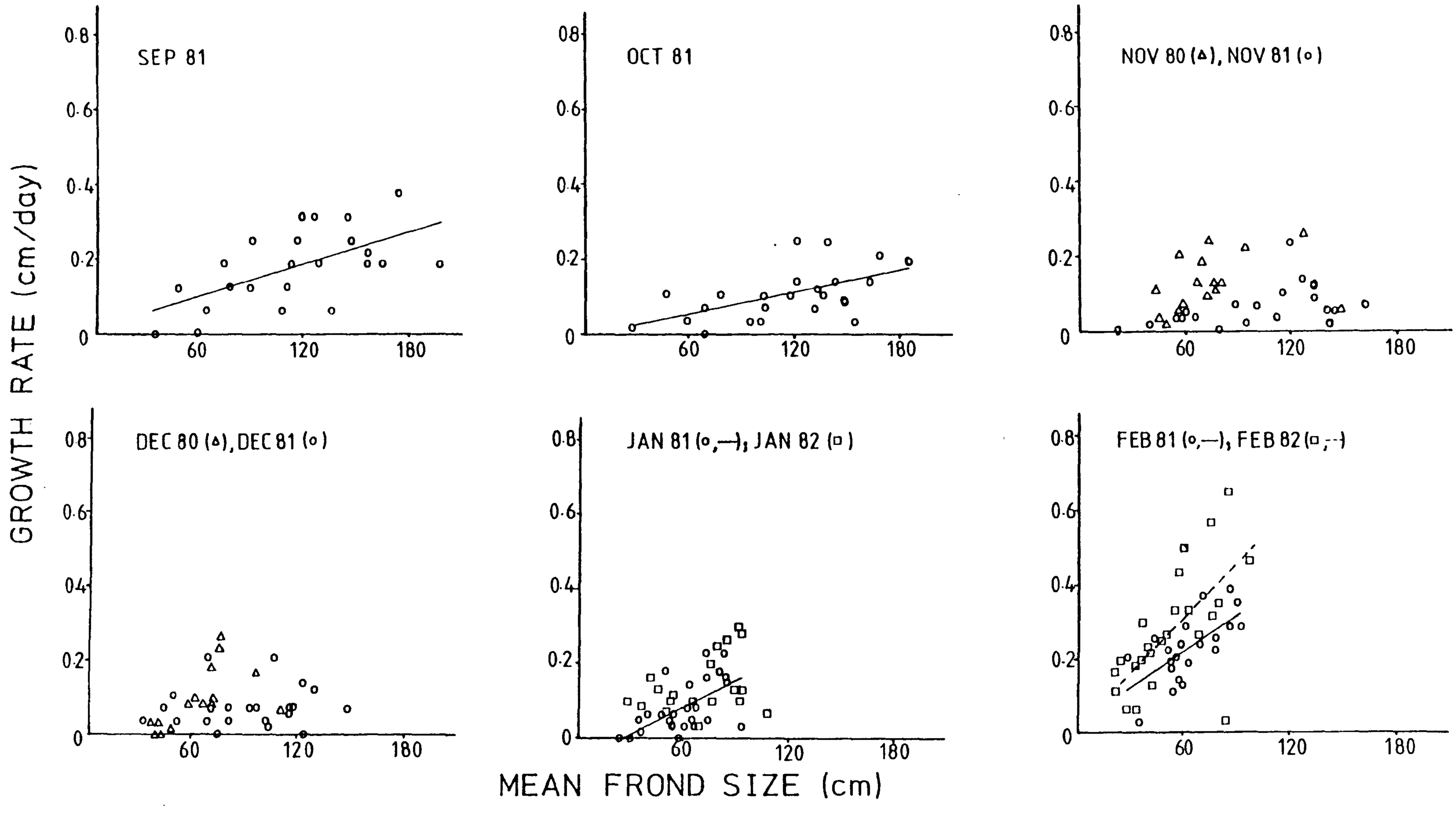
Scatter plots and Regression Lines of Growth rate as a function of mean frond size in L. saccharina.

A, September to February

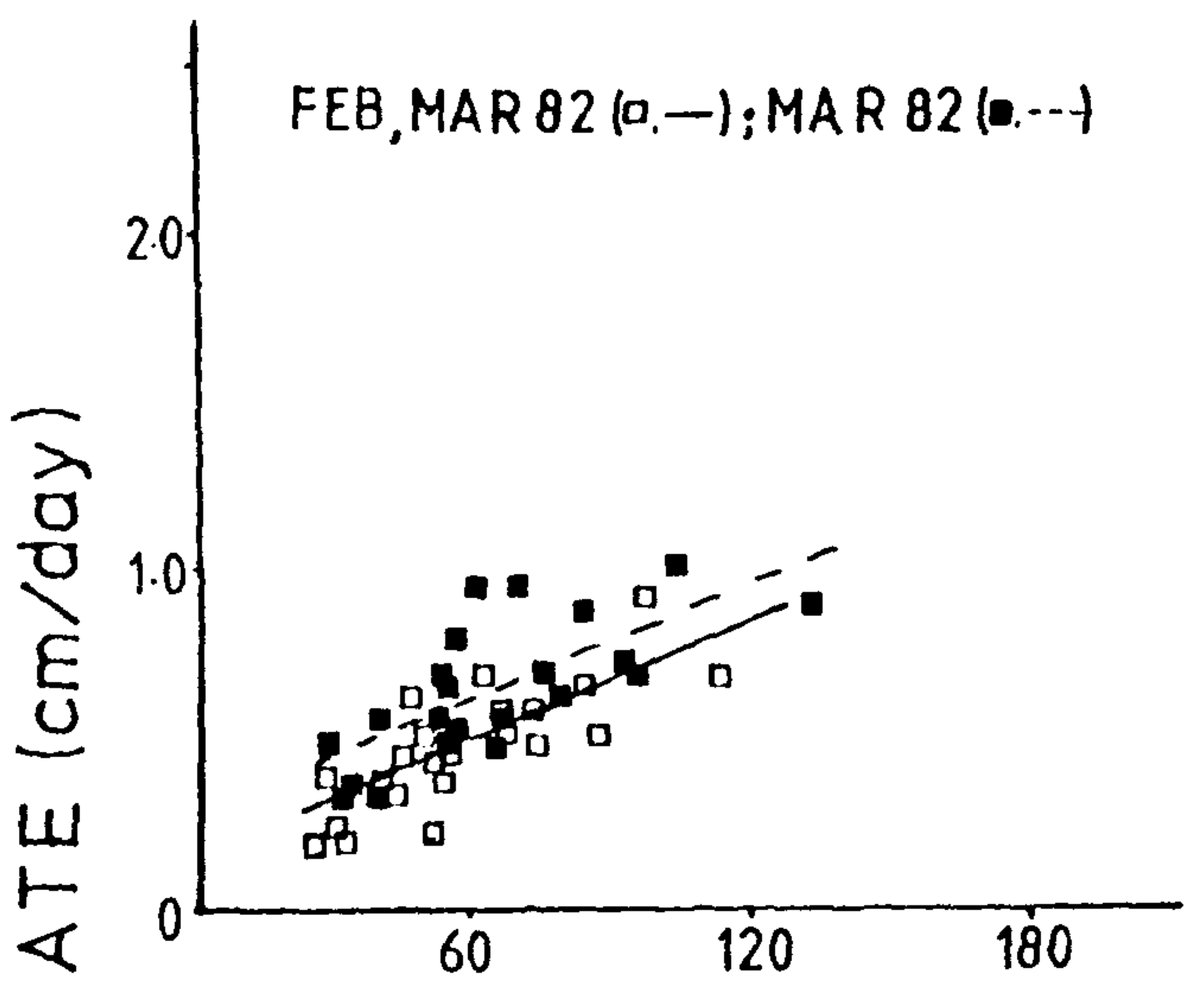
B, March to August

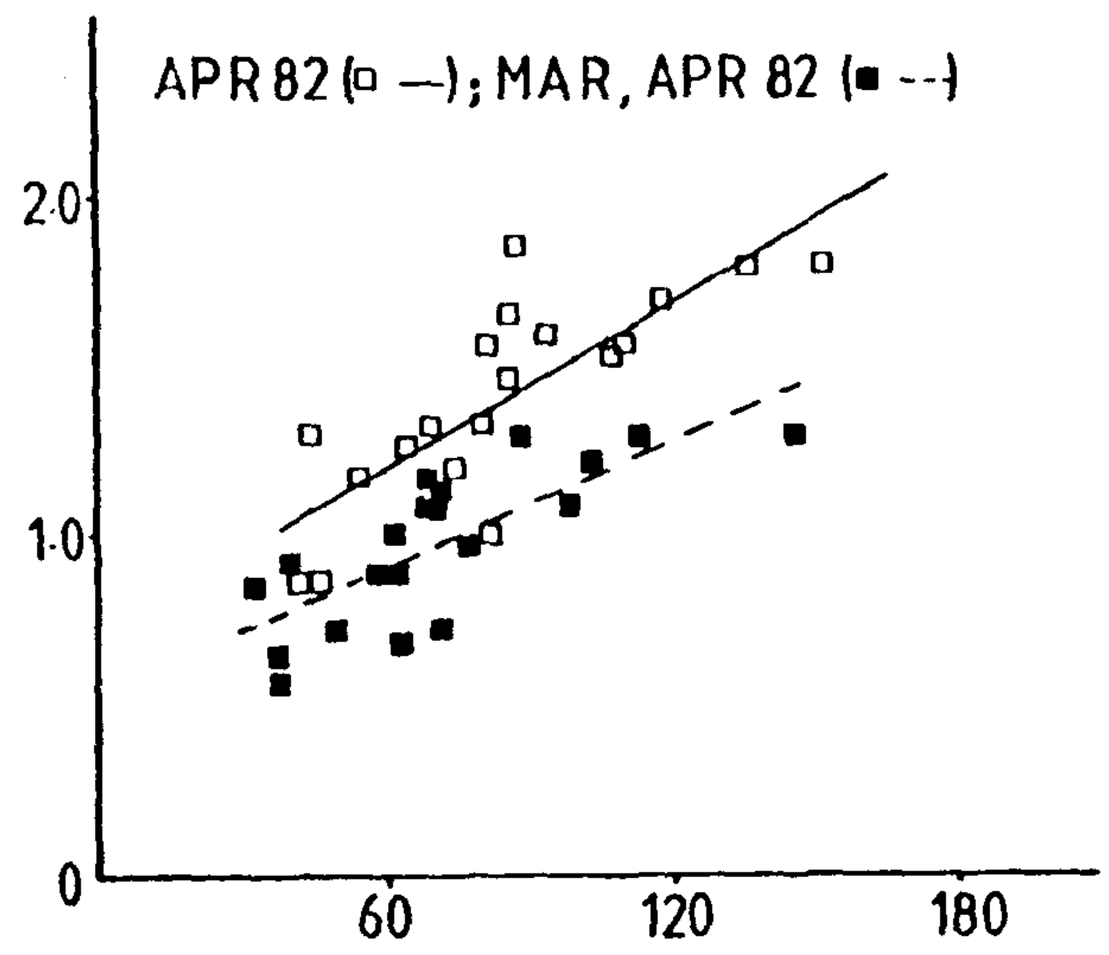
For further information see Table 1.2 and text.

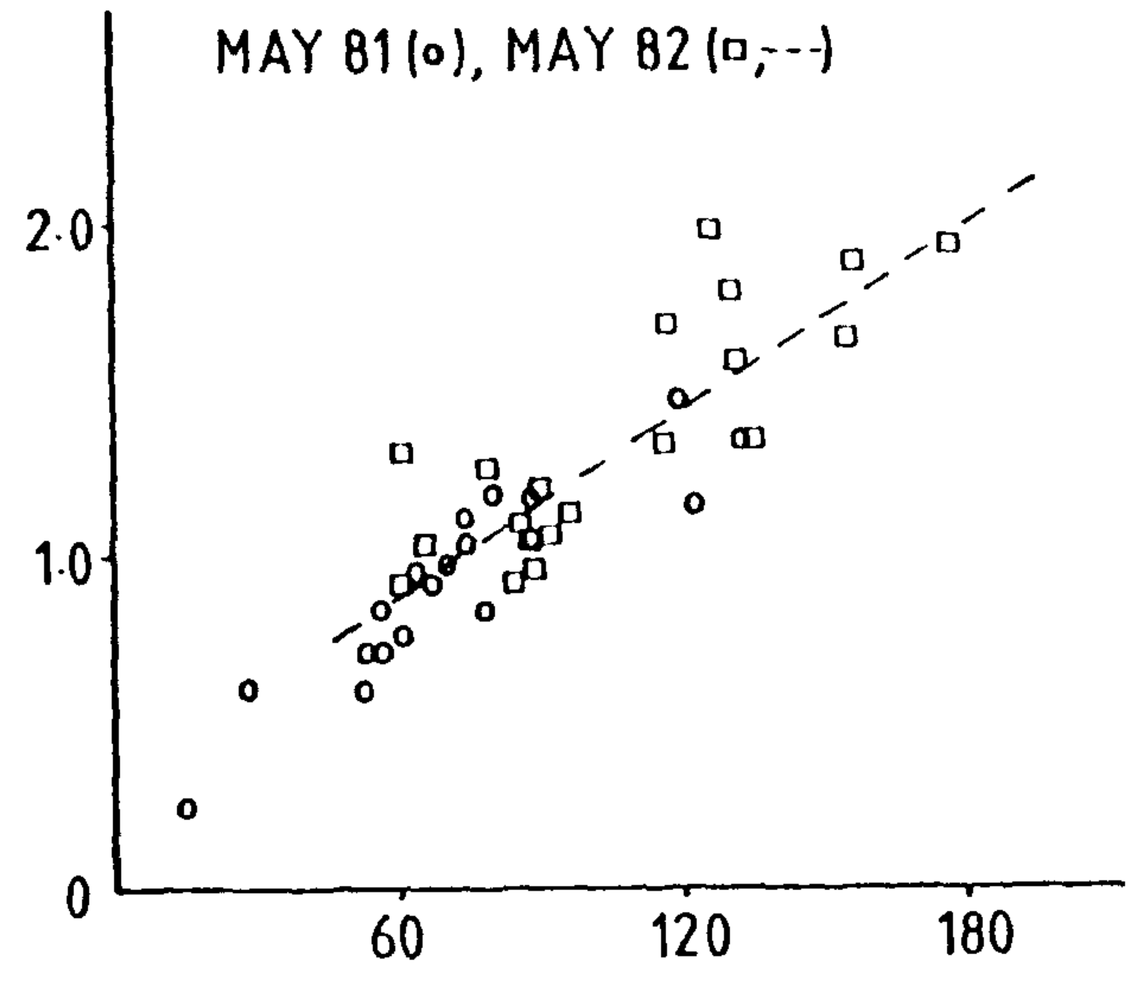
A


SEP 81
OCT 81
NOV 80 (△), NOV 81 (○)
DEC 80 (△), DEC 81 (○)
JAN 81 (○,—), JAN 82 (□)
FEB 81 (○,—), FEB 82 (□,--)
0·8
0·6
0·4
0·2
0
60
120
180
GROWTH RATE (cm/day)
MEAN FROND SIZE (cm)

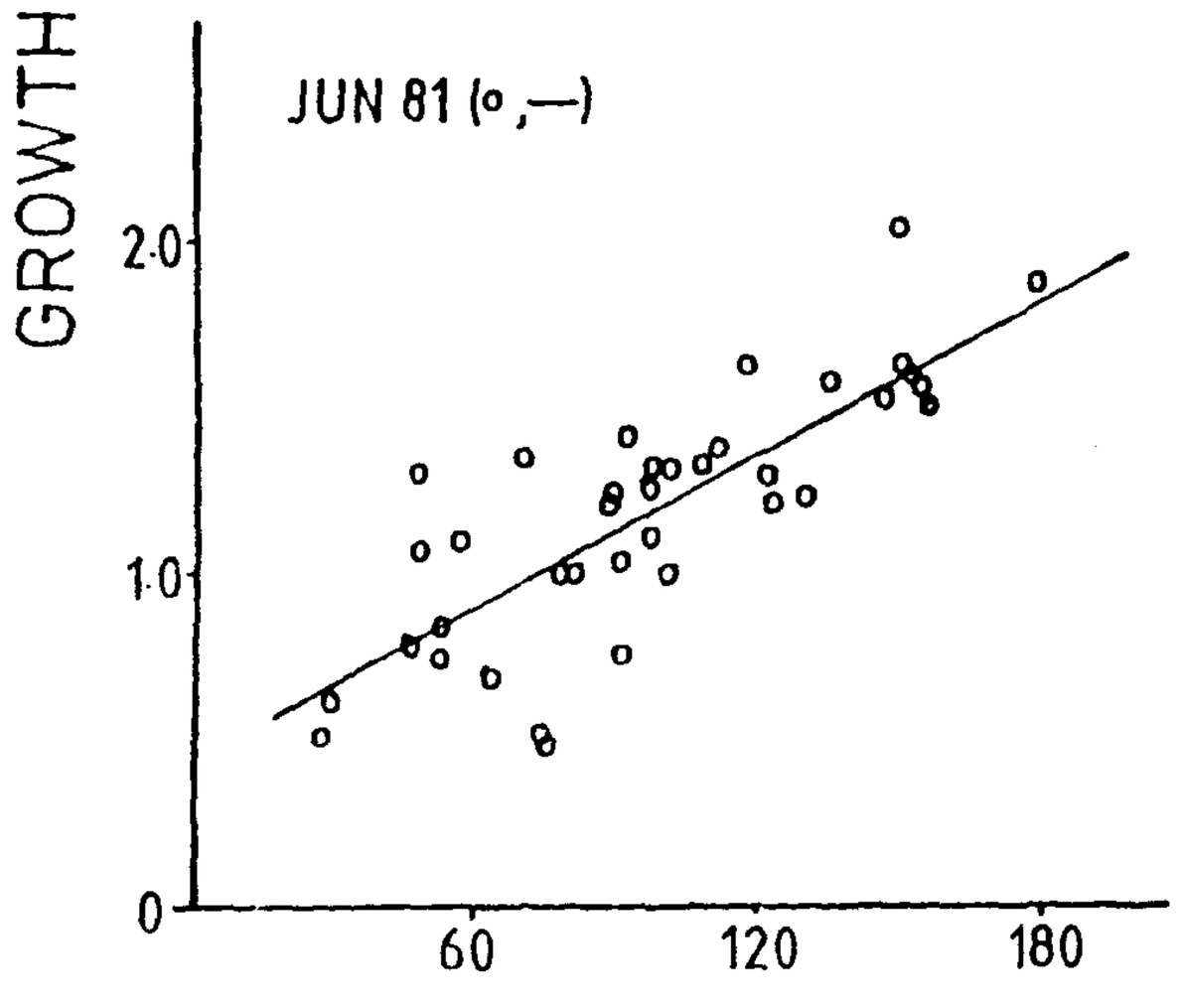
B

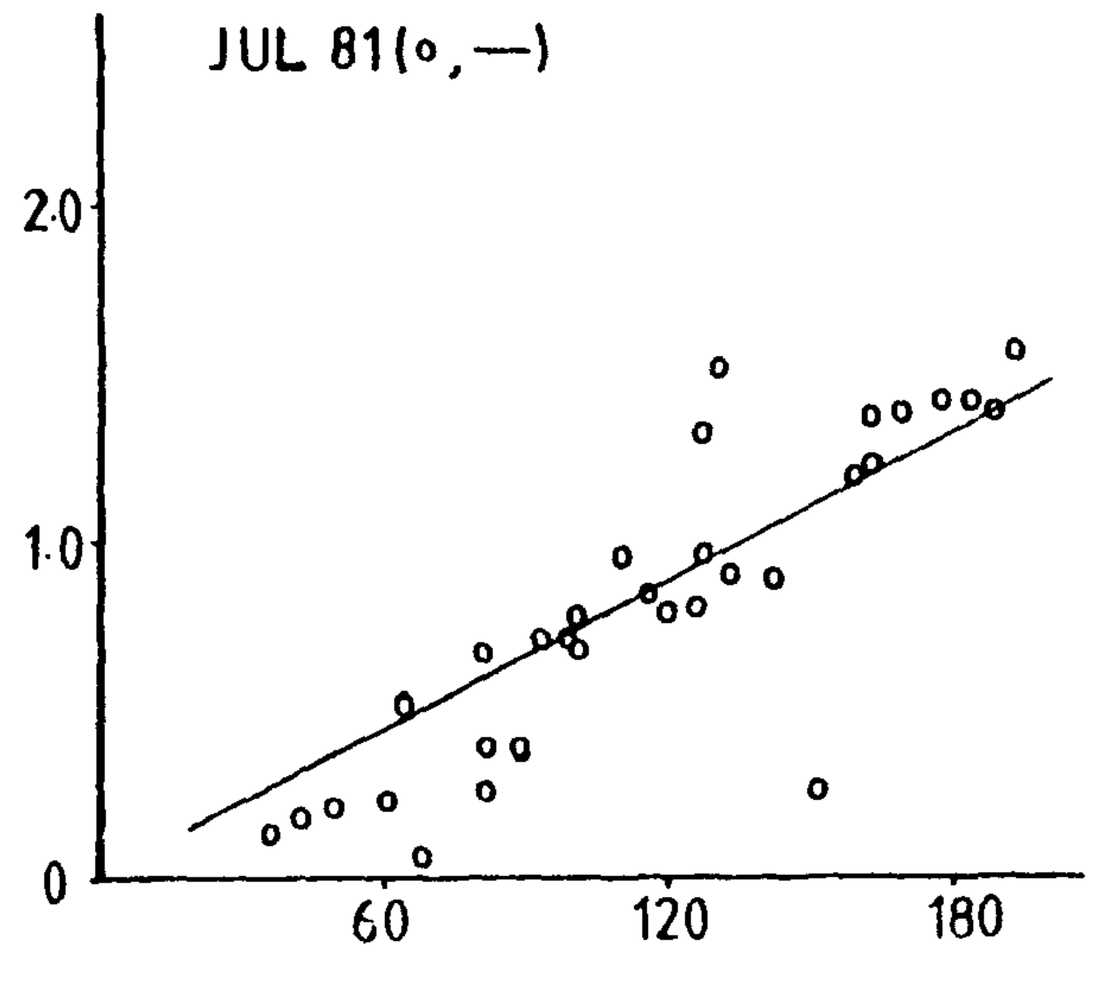


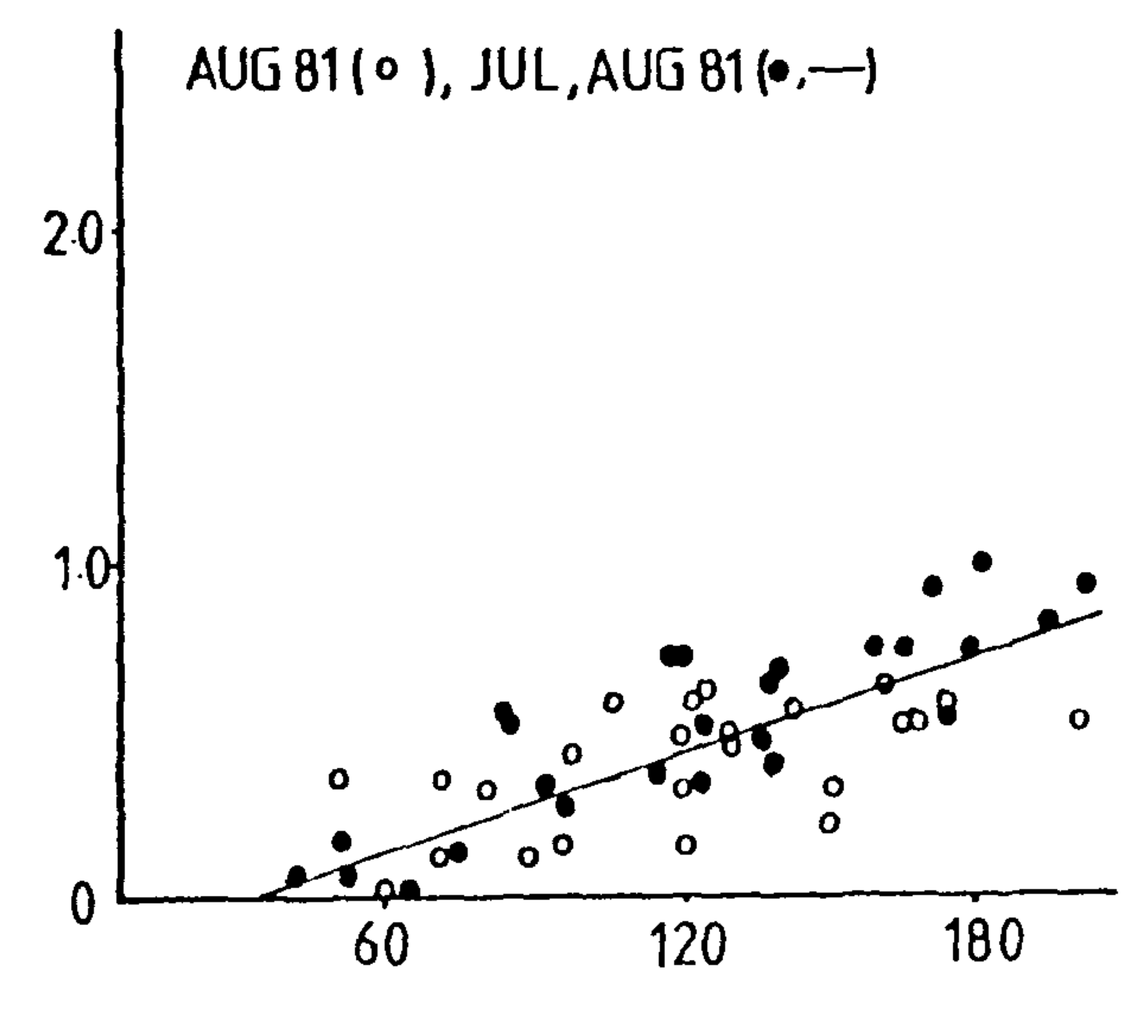




GROWTH RATE (cm/day)







MEAN FROND SIZE (cm)

Figure 1.8

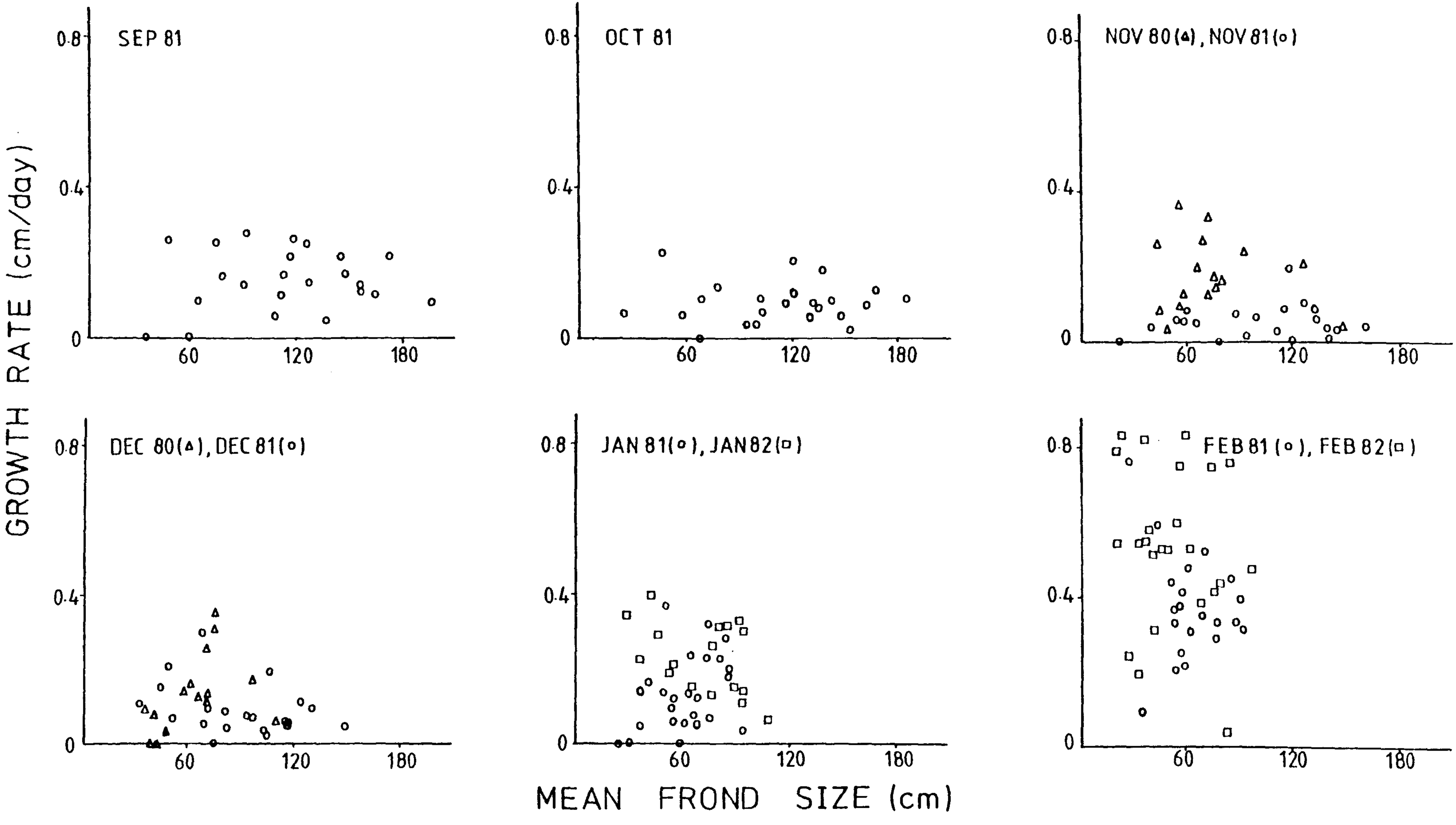
Scatter plots and Regression lines of Growth rate per 100 cm of frond as a function of mean frond size in L. saccharina.

A, September to February

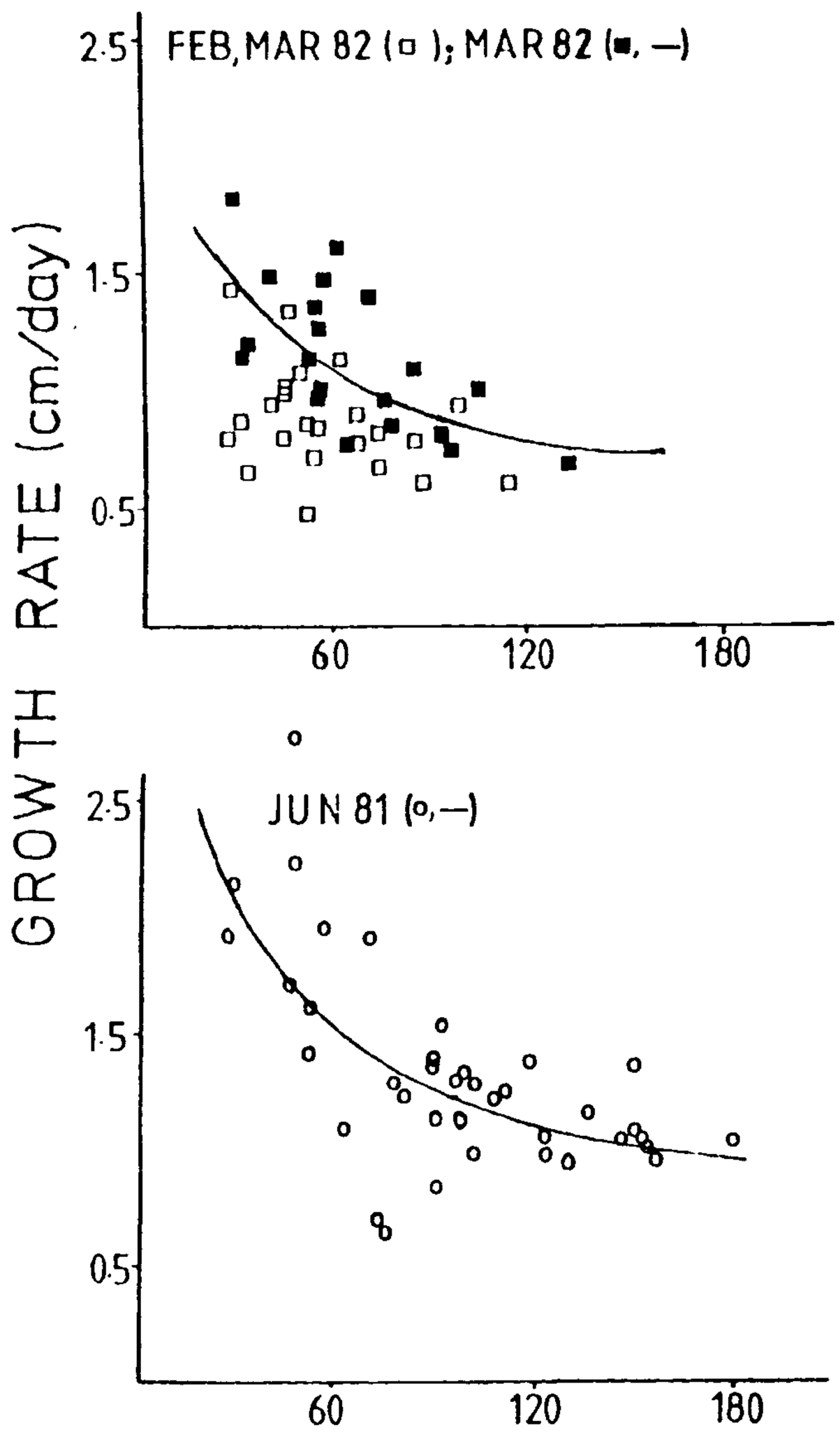
B, March to August.

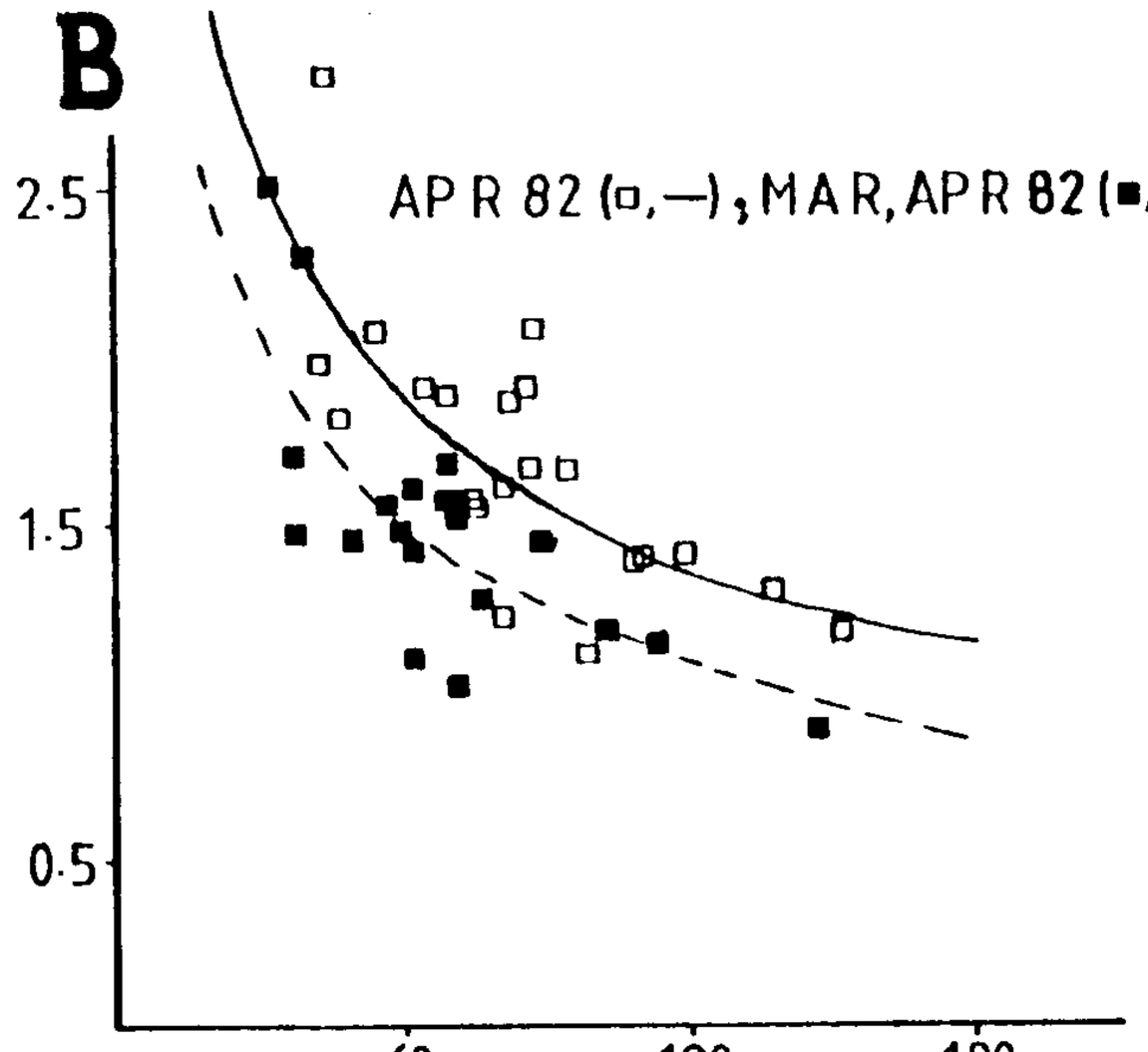
Further details on Table 1.2 and text.

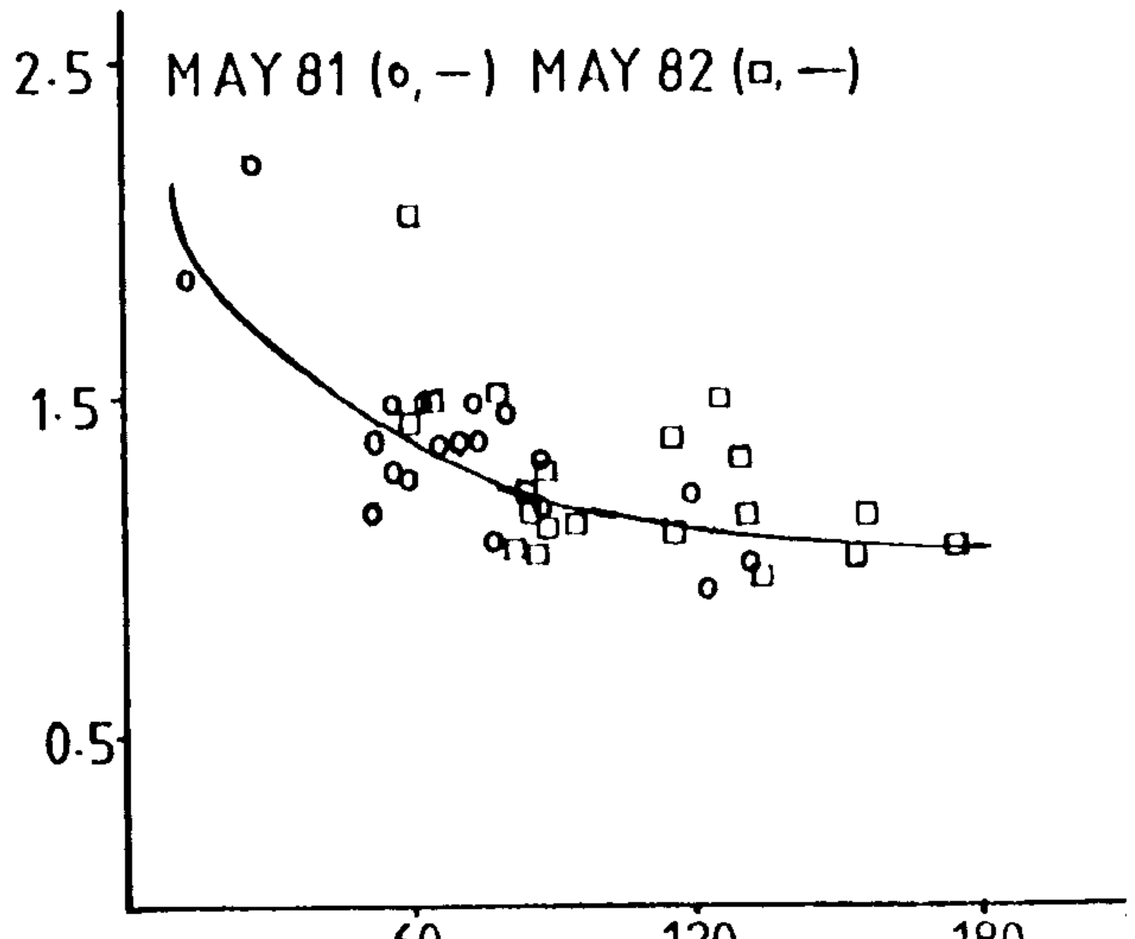
A

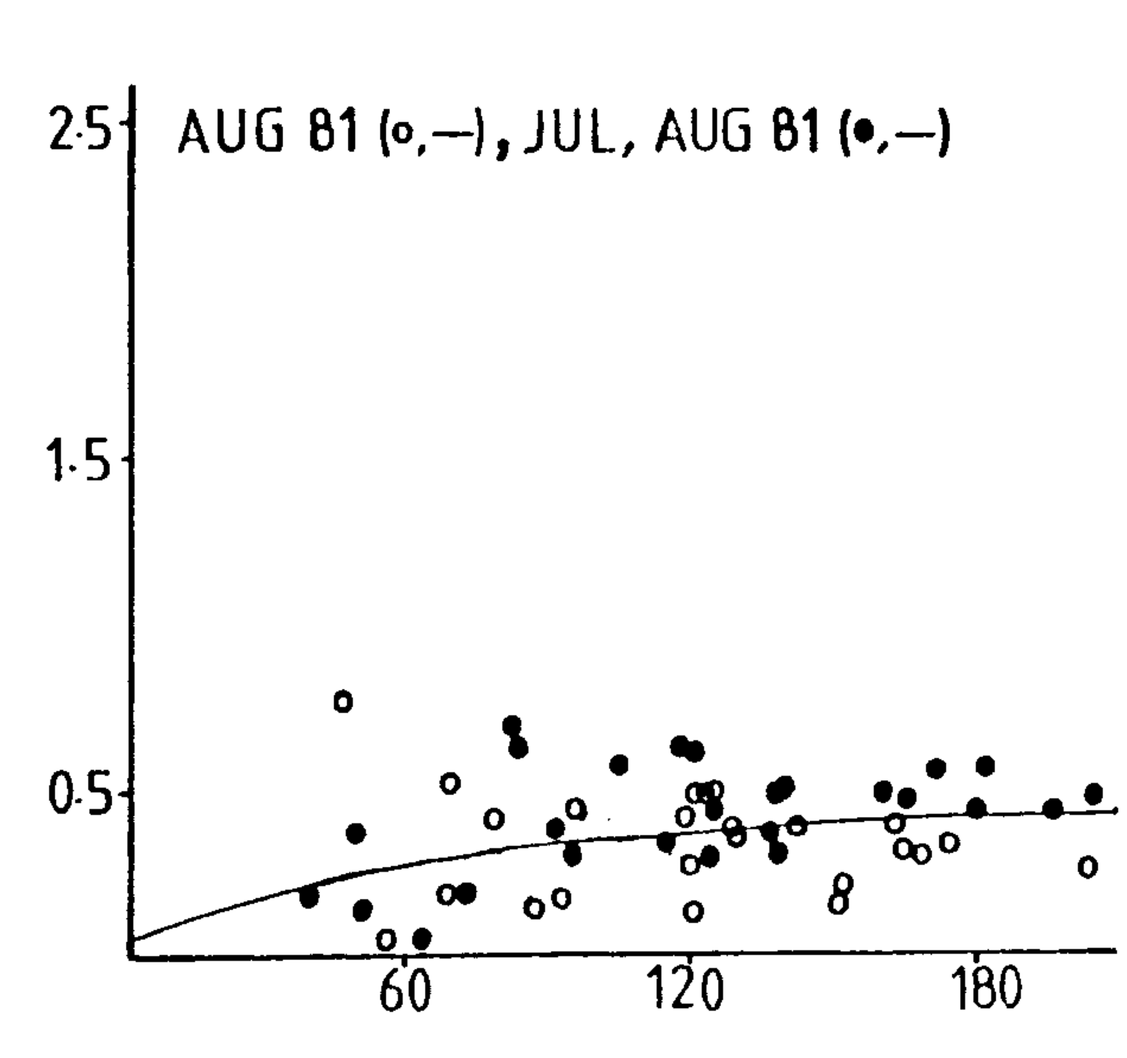

SEP 81
OCT 81
NOV 80(Δ), NOV 81(o)
DEC 80(Δ), DEC 81(o)
JAN 81(o), JAN 82(□)
FEB 81(o), FEB 82(□)
0·8
0·4
0
60
120
180
GROWTH (cm/day)
MEAN FROND SIZE (cm)

B









MEAN FROND SIZE (cm)

Figure 1.9

Frond size and cumulative growth (ignoring loss from frondal tip) of L. saccharina. Based on mean values of frond length and growth rates (Fig. 1.3 and 1.4 respectively). The sigmoidal curves correspond to cumulative growth starting at different dates (numbers refer to observation dates on Table 1.1.).

□ Total length

△ Stipe length

S.T. Survival Time

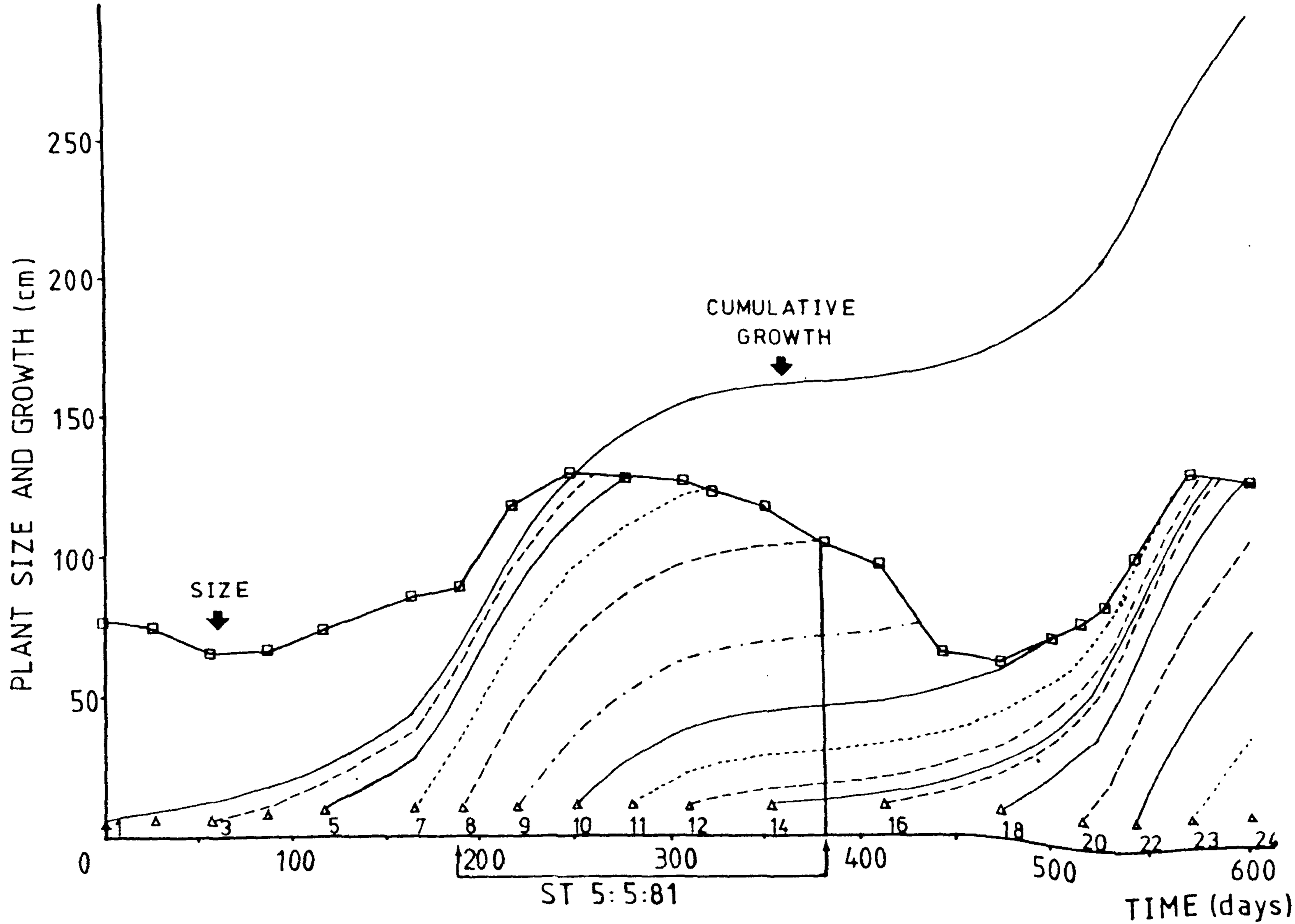

PLANT SIZE AND GROWTH (cm)
250
200
150
100
50
0
CUMULATIVE
GROWTH
SIZE
1
3
5
7
8
9
10
11
12
14
16
18
20
22
23
24
100
200
300
400
500
600
ST 5:5:81
TIME (days)

Figure 1.10

Survival time of frond tissue of L. saccharina throughout the year. Date refers to time at which the tissue was generated.

Obtained : (O) using mean plant size and mean growth rate (Fig. 1.9) and with (●)mean value (± CI) of 57 plants (worked in same way as Fig. 1.9).

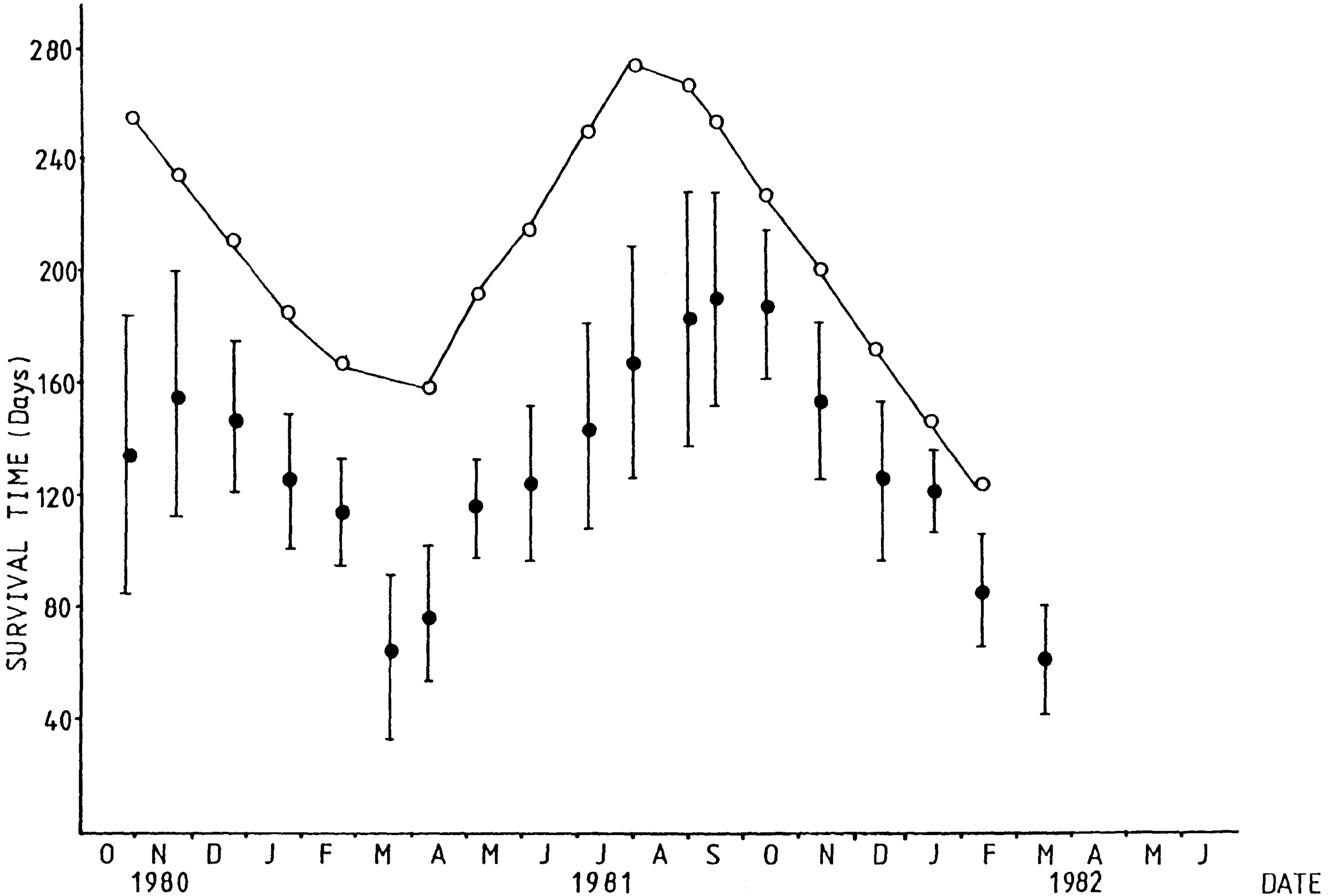

280
240
200
160
120
80
40
SURVIVAL TIME (Days)
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1980
1981
1982
DATE

Figure 1.11

Laminaria saccharina. Frond length and settlement of *Celleporella hyalina*.

○ mean size of fronds with settlement of *C. hyalina*.

● distance from the base of frond to the first settlement.

Vertical bars are confidence intervals for the mean (α 0.05).

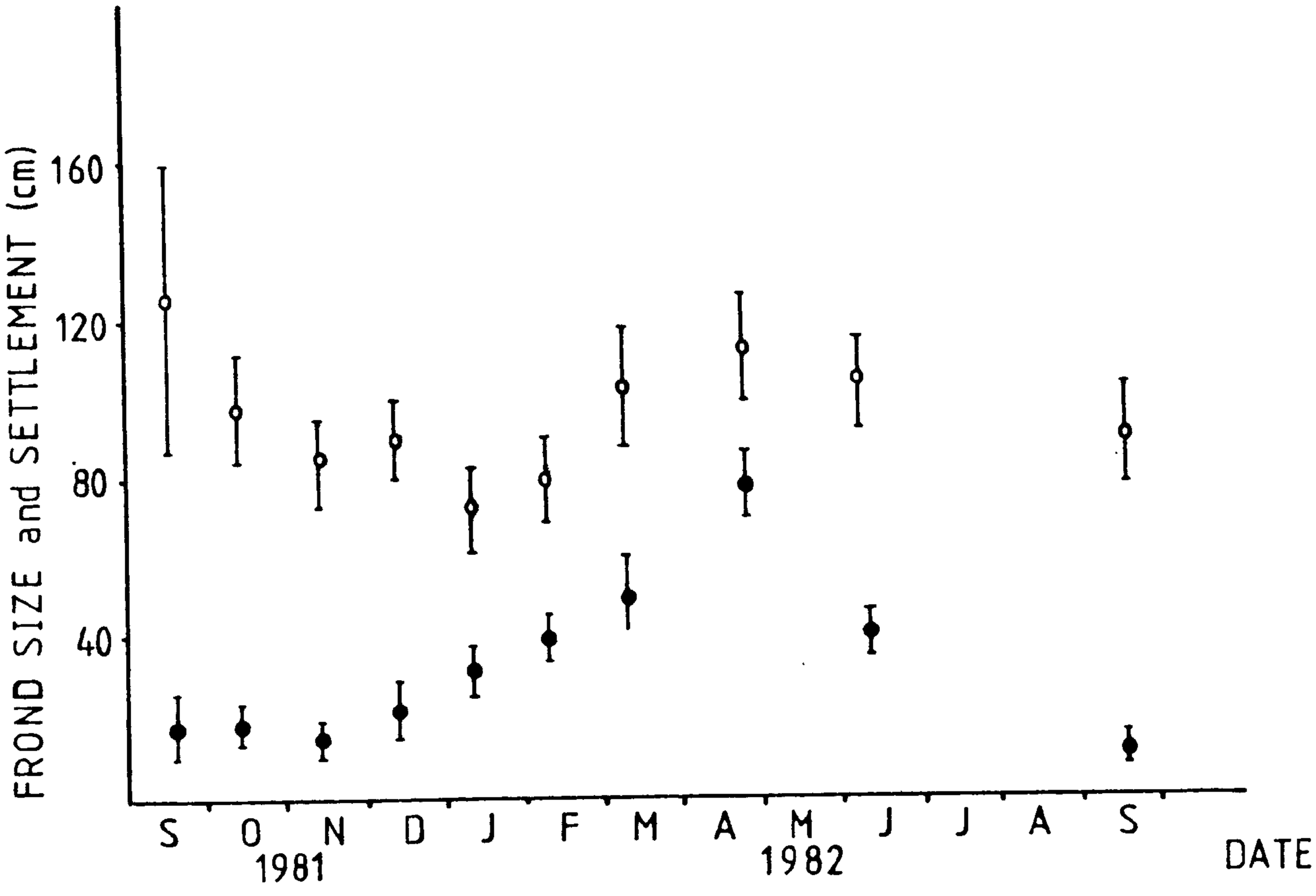

FROND SIZE and SETTLEMENT (cm)
160
120
80
40
S
O
N
D
J
F
M
A
M
J
J
A
S
1981
1982
DATE

Figure 1.12

Average frond size and growth of L. saccharina from 26 October 1980.

Cumulative growth curves start at the place on the frond where first settlement was observed at each observation date (numbers 1 to 23, see Table 1.1.)

□ Total length

Δ Stipe length

S.T. Survival Time

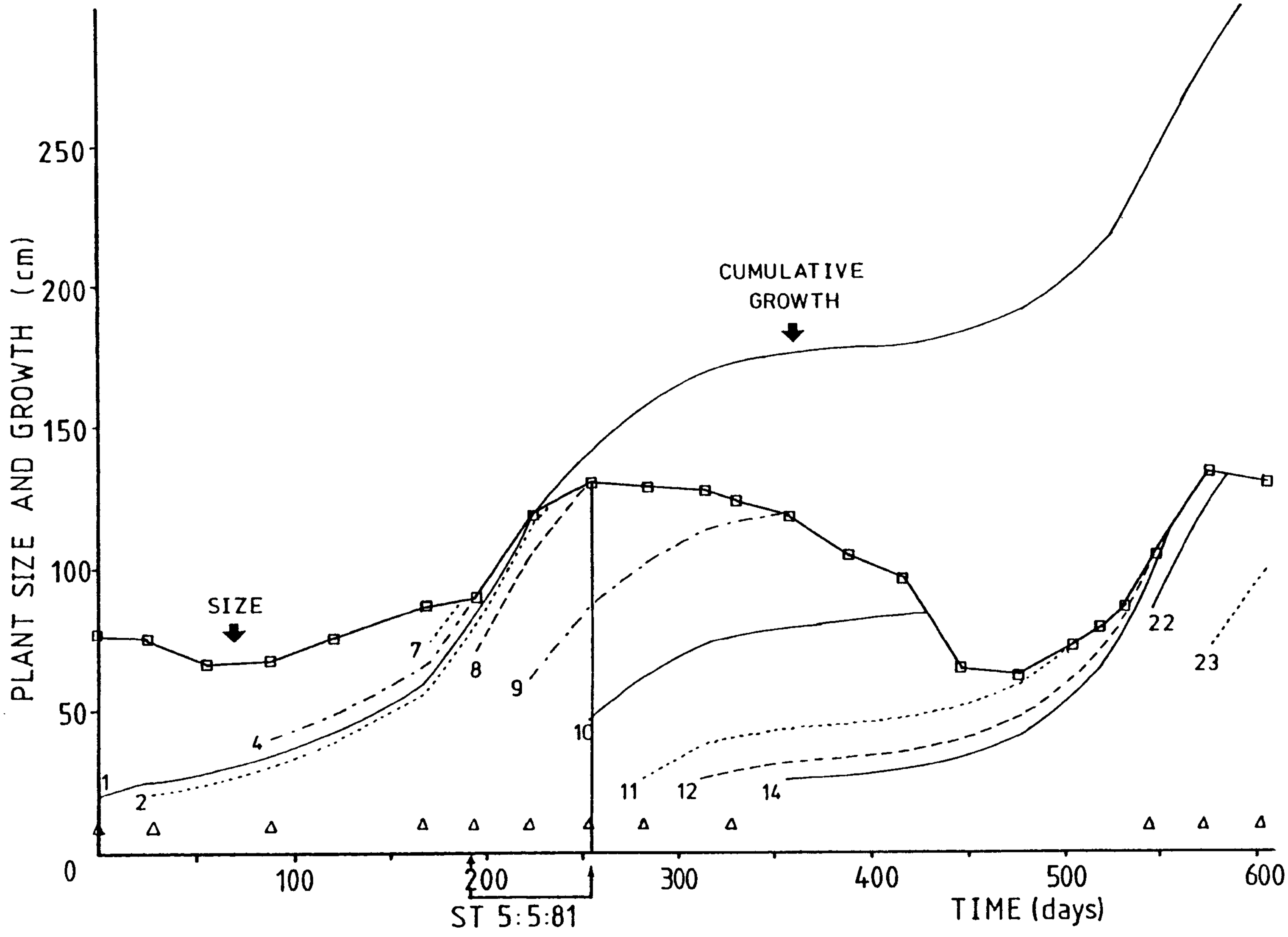

PLANT SIZE AND GROWTH (cm)
250
200
150
100
50
0
SIZE
CUMULATIVE
GROWTH
1
2
4
7
8
9
10
11
12
14
22
23
100
200
300
400
500
600
ST 5:5:81
TIME (days)

Figure 1.13

Survival time of C. hyalina obtained from Fig. 1.16 (O) and mean values (●) (± CI) obtained with a similar method on 57 plants of L. saccharina.

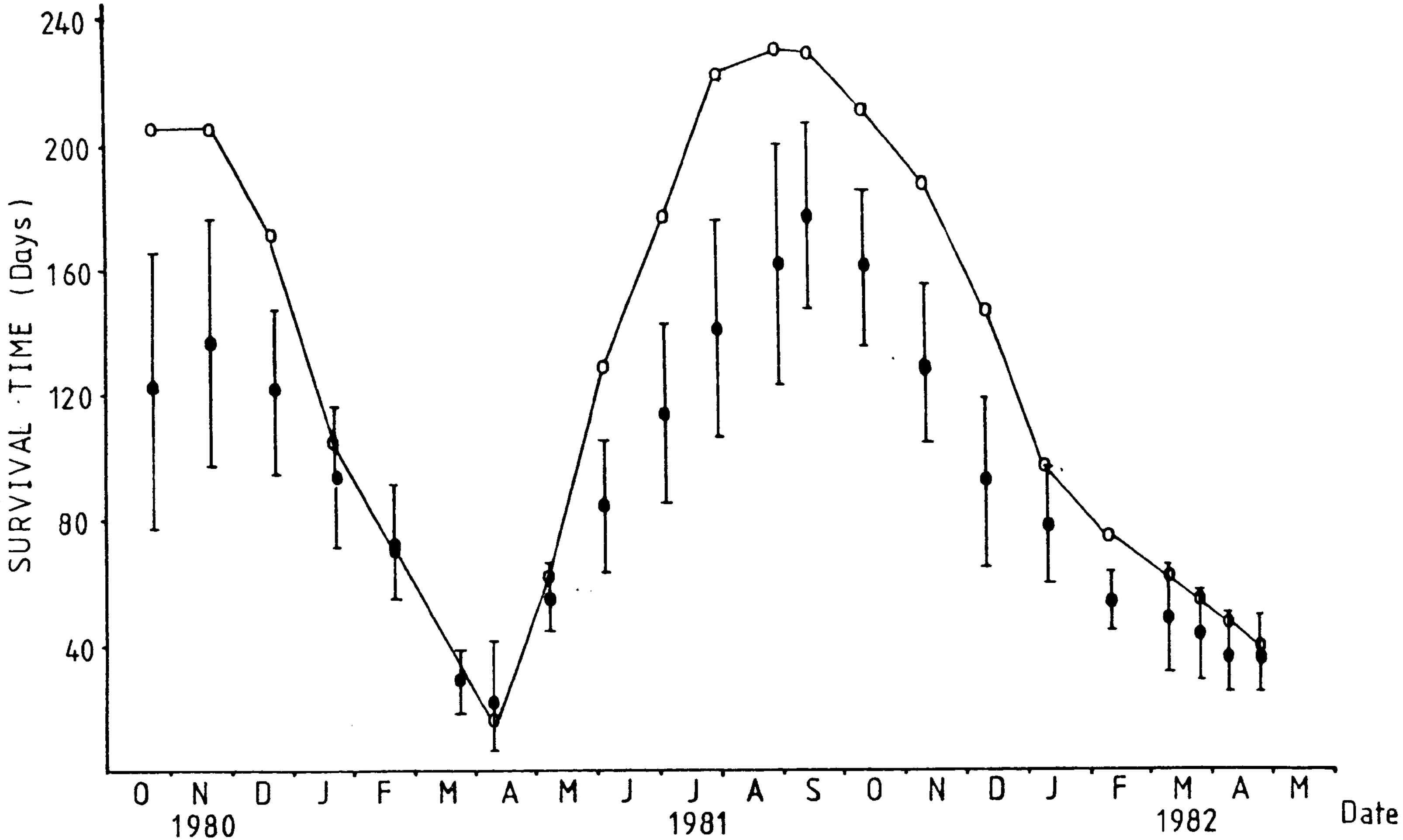

240
200
160
120
80
40
SURVIVAL TIME (Days)
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1980
1981
1982
Date

Figure 1.14

Mean number of C hyalina settled since previous observation in two areas of L. saccharina fronds. Position of the areas on the frond and time of the year are indicated. Number refer to number of fronds sampled. Horizontal bars are S.E. for position on the frond, vertical bars are S.E. for the number of new colonies.

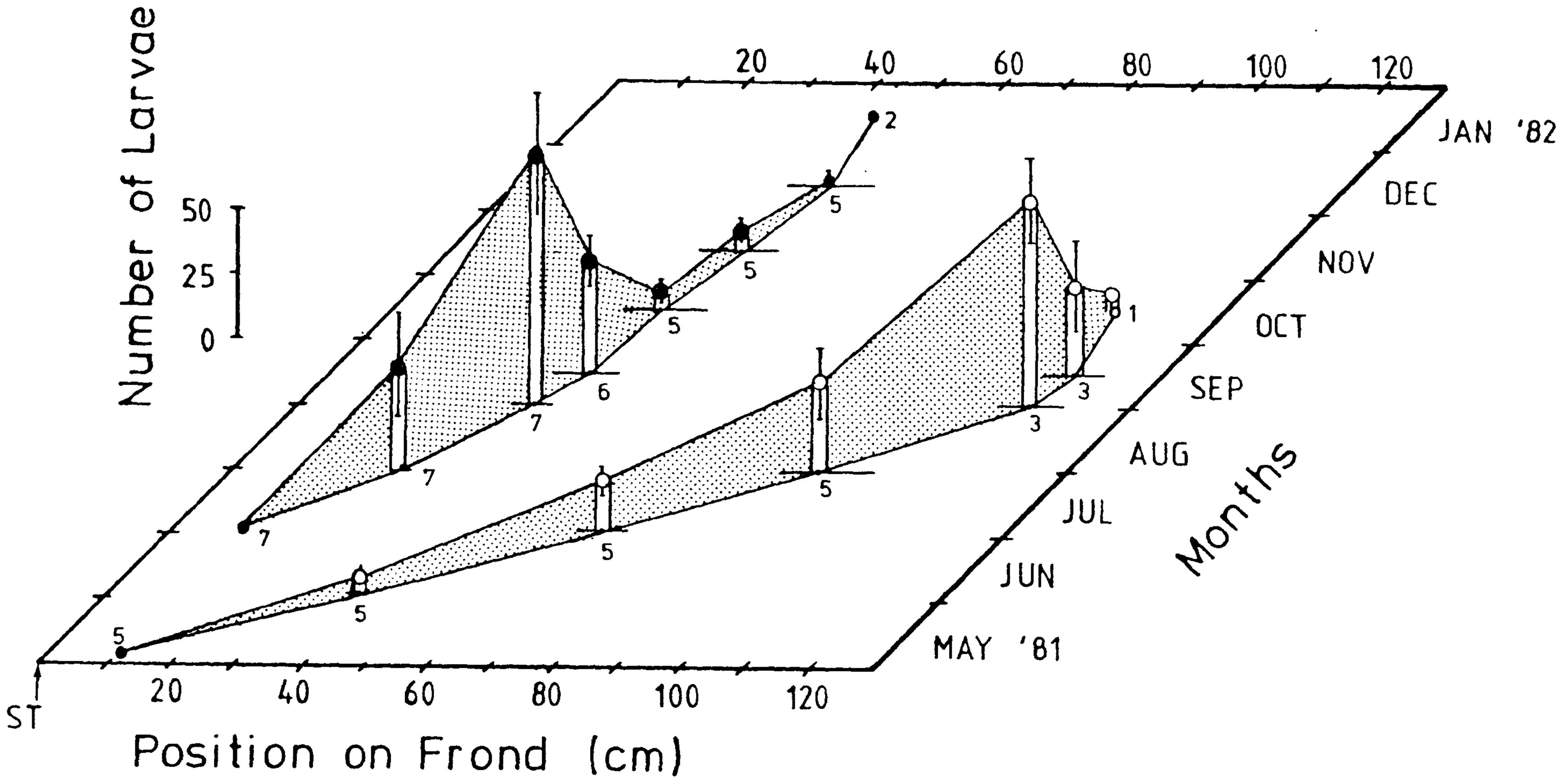

Number of Larvae
50
25
0
20
40
60
80
100
120
JAN '82
DEC
NOV
OCT
SEP
AUG
JUL
JUN
MAY '81
Months
ST
Position on Frond (cm)
2
5
5
6
7
7
7
5
5
5
3
3
1

Figure 1.15

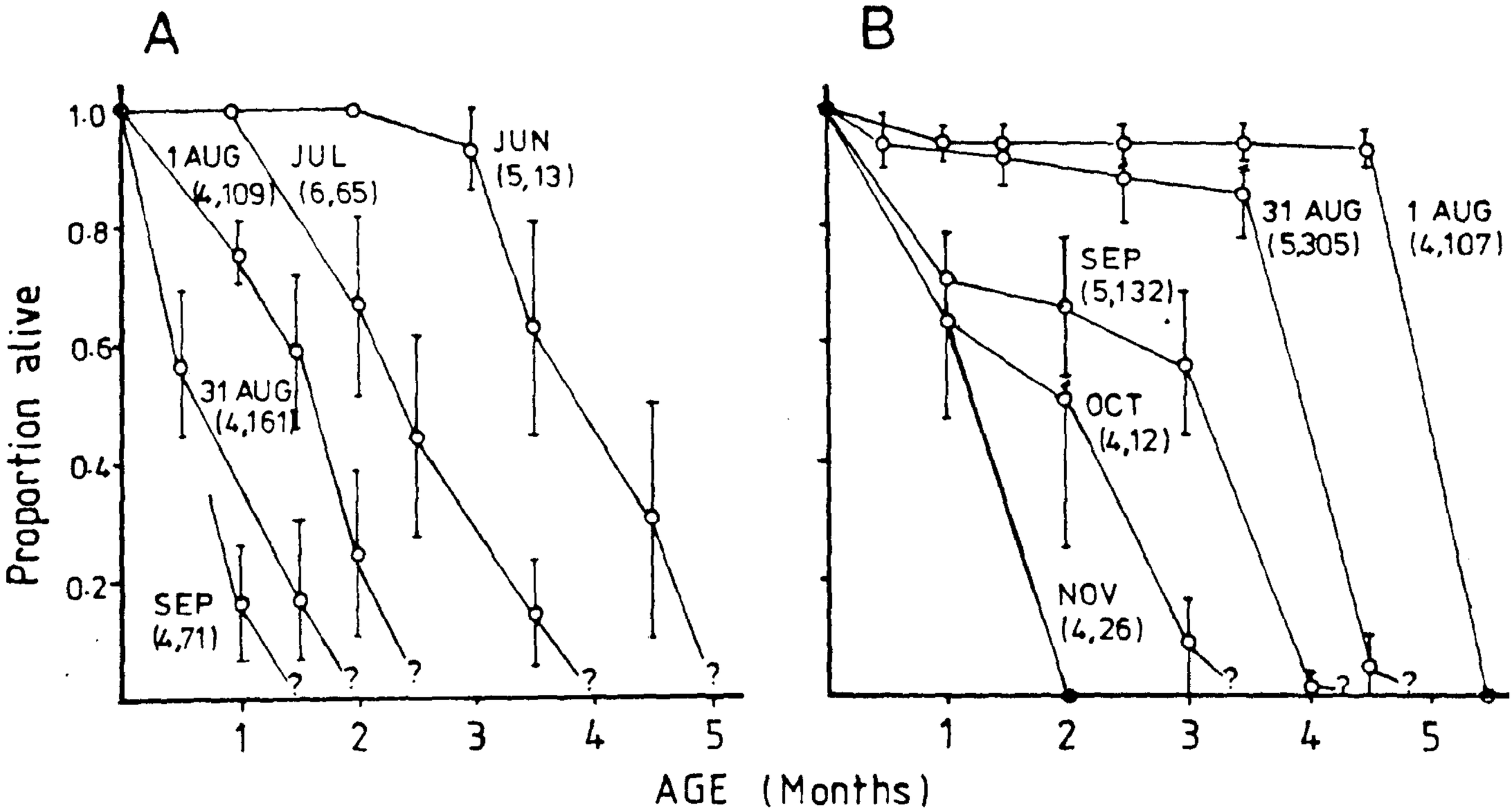
Survival of C. hyalina settled at different dates on 2 areas of L. saccharina fronds.

A area sampled from 5 of May, B from 4 July 1981. Values in brackets are number of areas sampled and initial number of colonies observed. Vertical bars are S.E. around the mean.

Figure 1.16

Survival curves of C. hyalina settled on L. saccharina at different times of the year.

(A and B as Figure 1.14).


A
B
1·0
0·8
0·6
0·4
0·2
Proportion alive
1 AUG (4,109)
JUL (6,65)
JUN (5,13)
31 AUG (4,161)
SEP (4,71)
SEP (5,132)
31 AUG (5,305)
1 AUG (4,107)
OCT (4,12)
NOV (4,26)
1
2
3
4
5
AGE (Months)

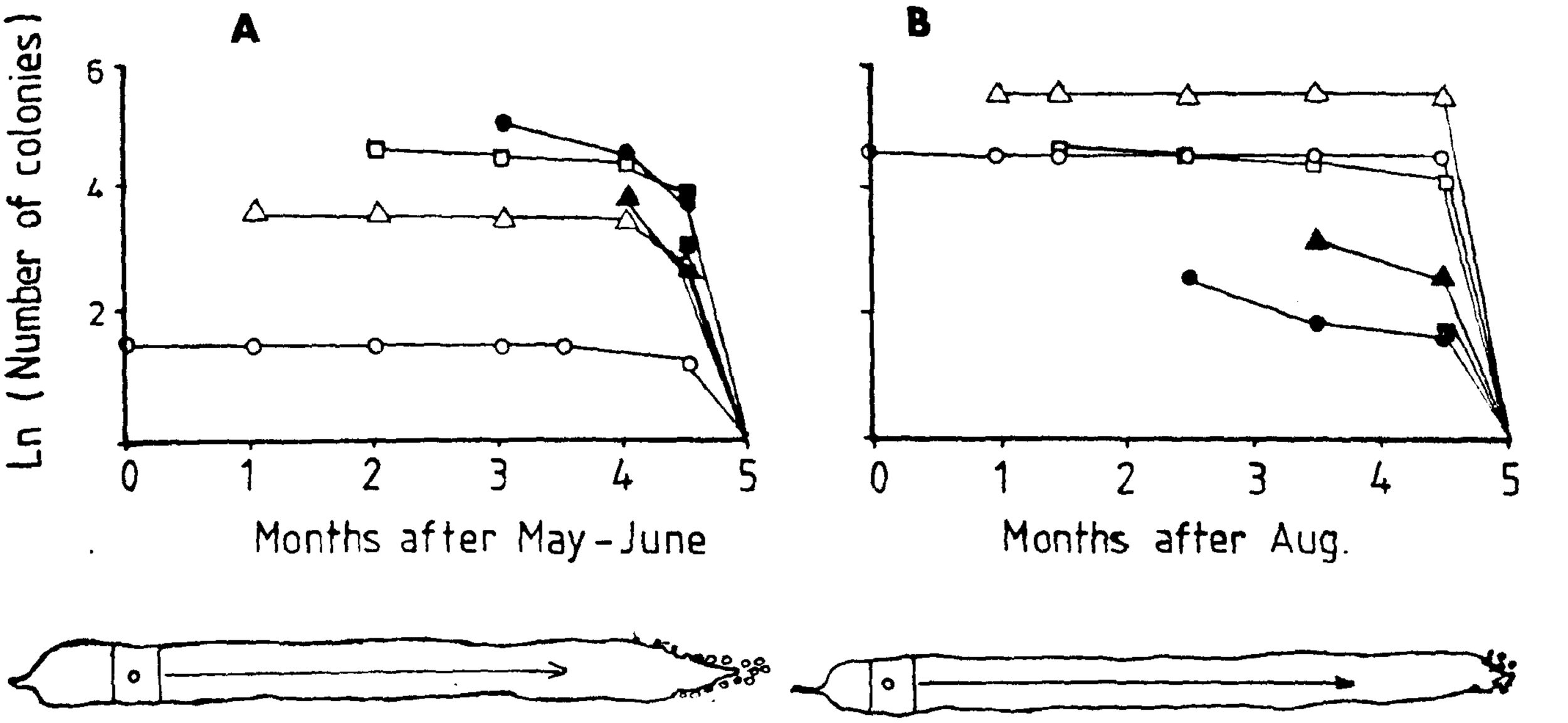

A
B
Ln (Number of colonies)
6
4
2
0
1
2
3
4
5
Months after May-June
Months after Aug.

Figure 1.17

Mean number of colonies older than 1 month (●), total number of alive colonies (○) and proportion of colonies touching neighbouring ones (△), on 2 areas of L. saccharina fronds.

(A and B as Figure 1.14). Vertical bars are S.E.

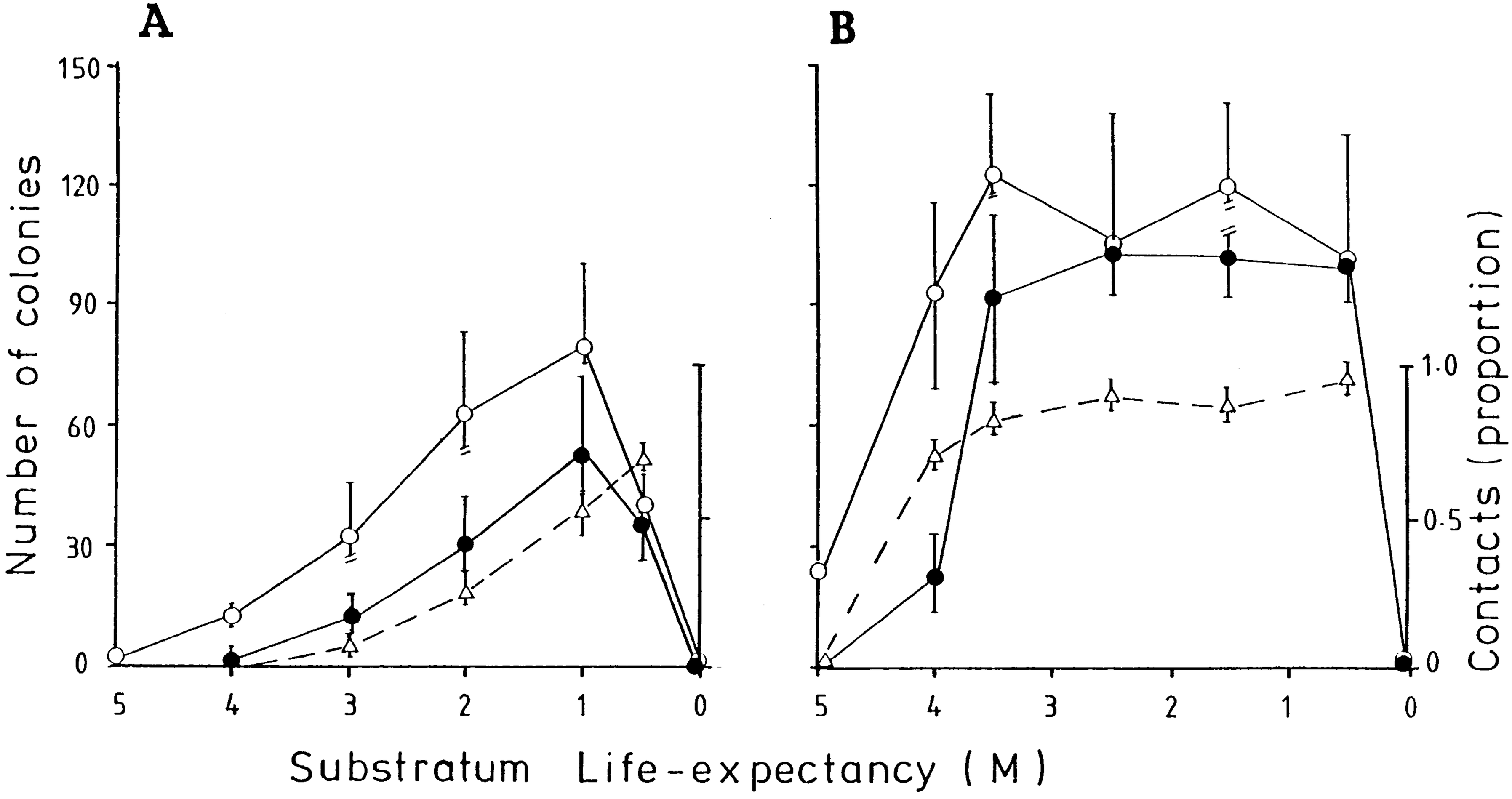

A
B
150
120
90
60
30
0
Number of colonies
1·0
0·5
0
Contacts (proportion)
5
4
3
2
1
0
Substratum Life-expectancy (M)

Figure 1.18

Timing of mortality of C. hyalina according to life-expectancy of L. saccharina fronds and date of settlement. Values given are proportions (mean ± S.E.) of colonies dying between observations in two areas of the frond (A and B, as Fig. 1.14). The arrows indicate settlement date.

(A and B as Figure 1.14).

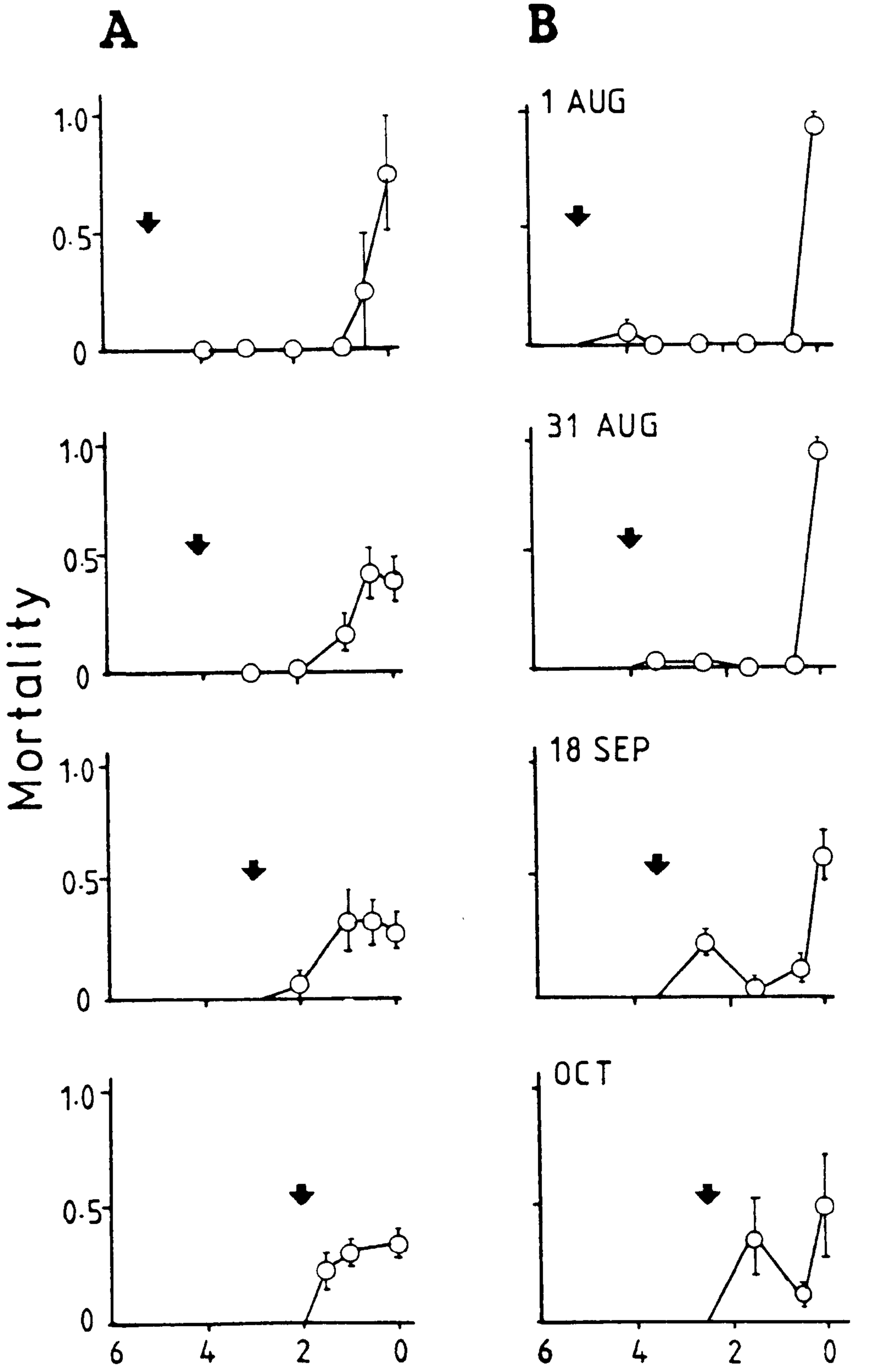

A
B
1 AUG
31 AUG
18 SEP
OCT
1·0
0·5
0
Mortality
Substratum Life-expectancy (M)
6
4
2
0

Figure 1.19

Growth of C. hyalina settled at different dates on fronds of L. saccharina.

A, area sampled from 5 of May, B from 4 July 1981.

Numbers in brackets represent number of colonies followed, dates indicate time at which the colonies were observed first. Values given are mean colony area ± S.E.

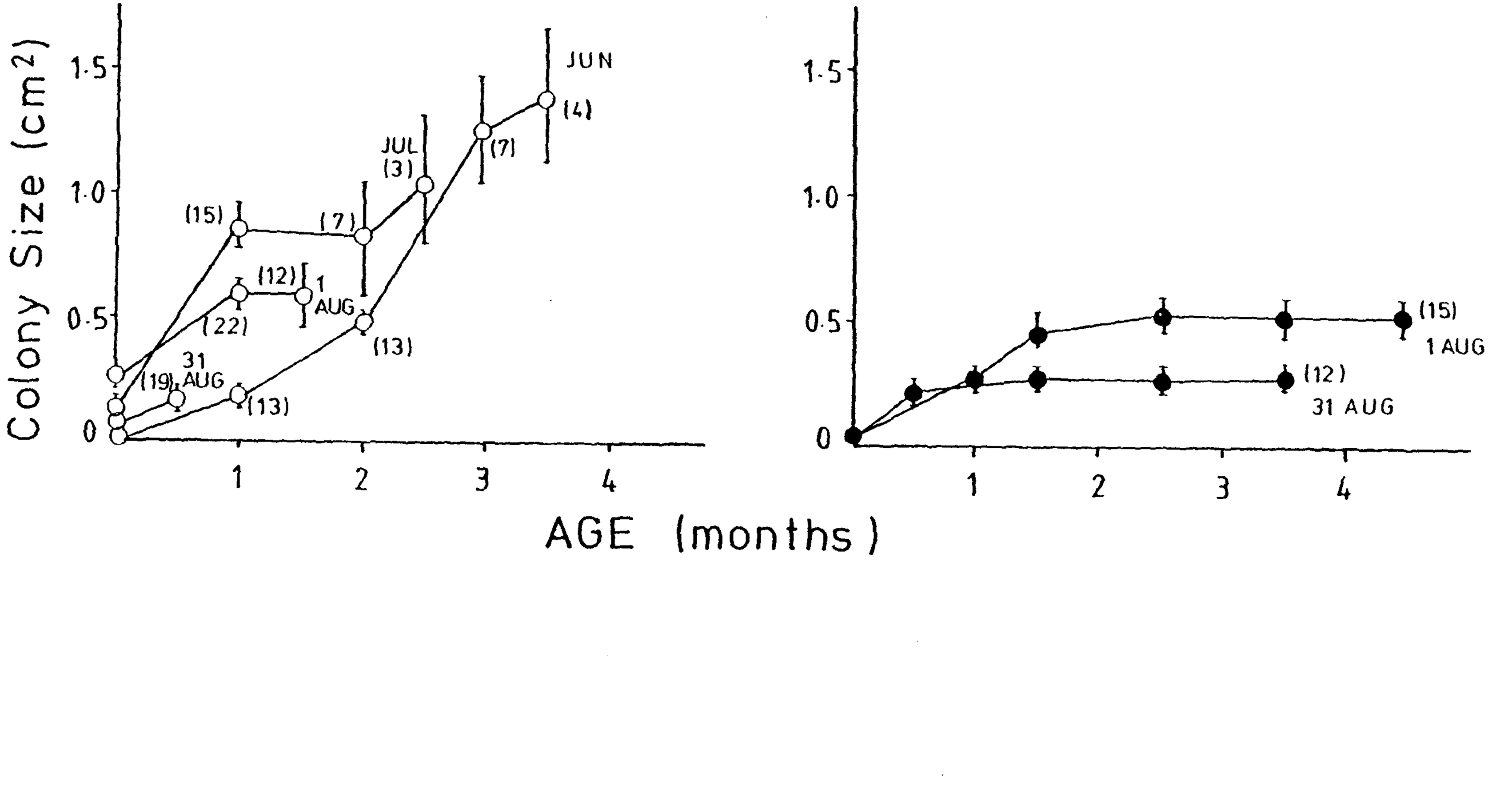
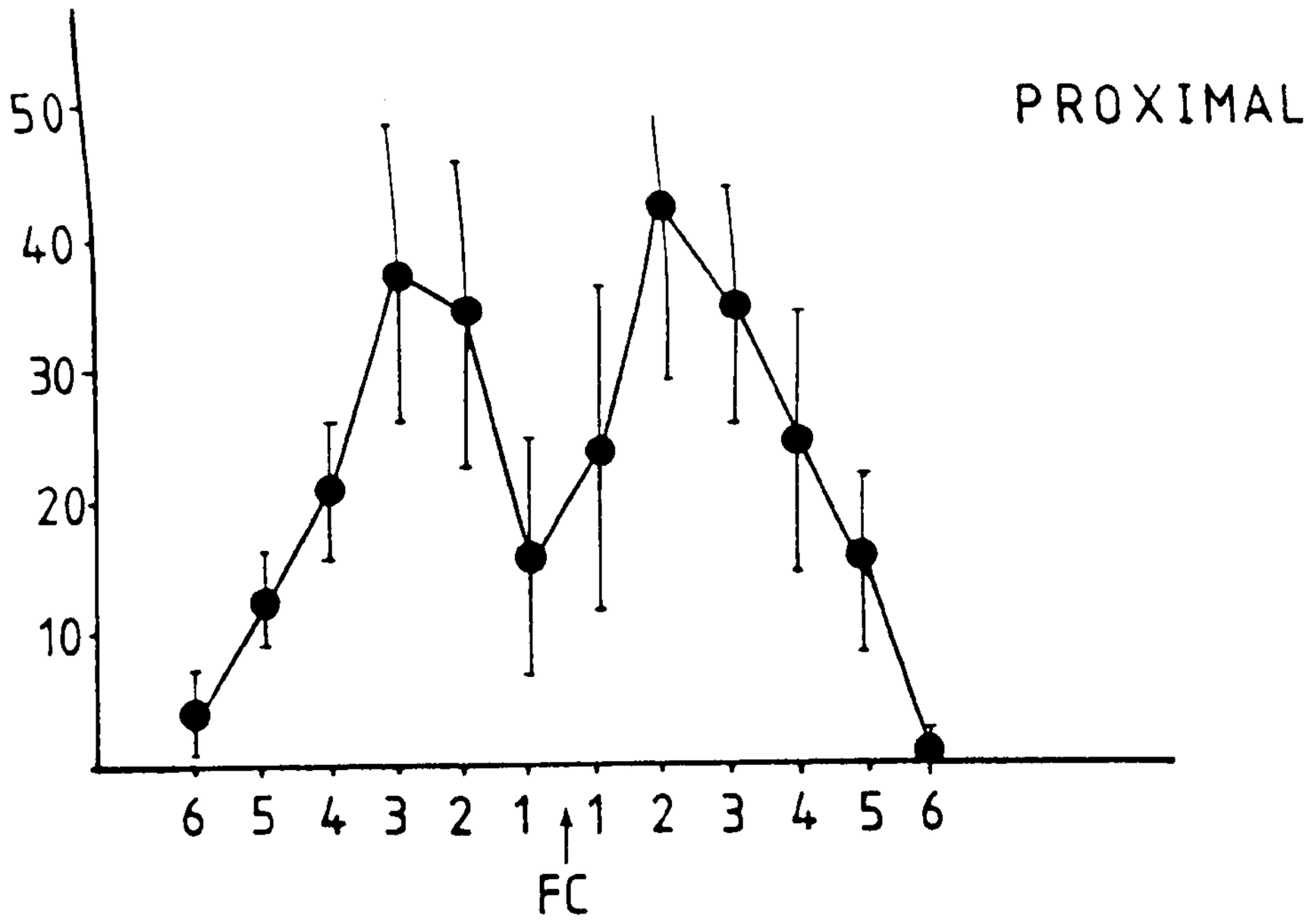
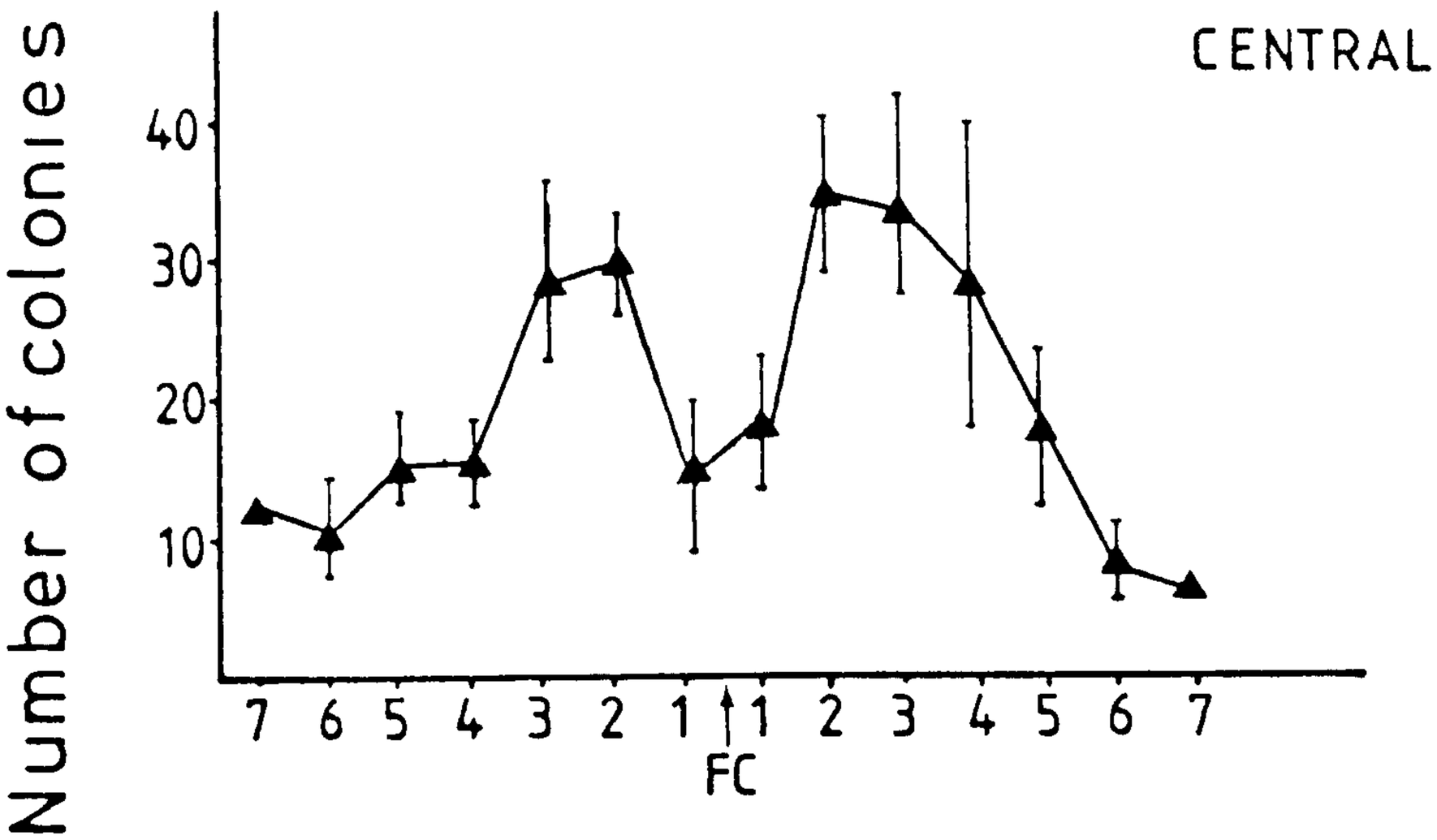
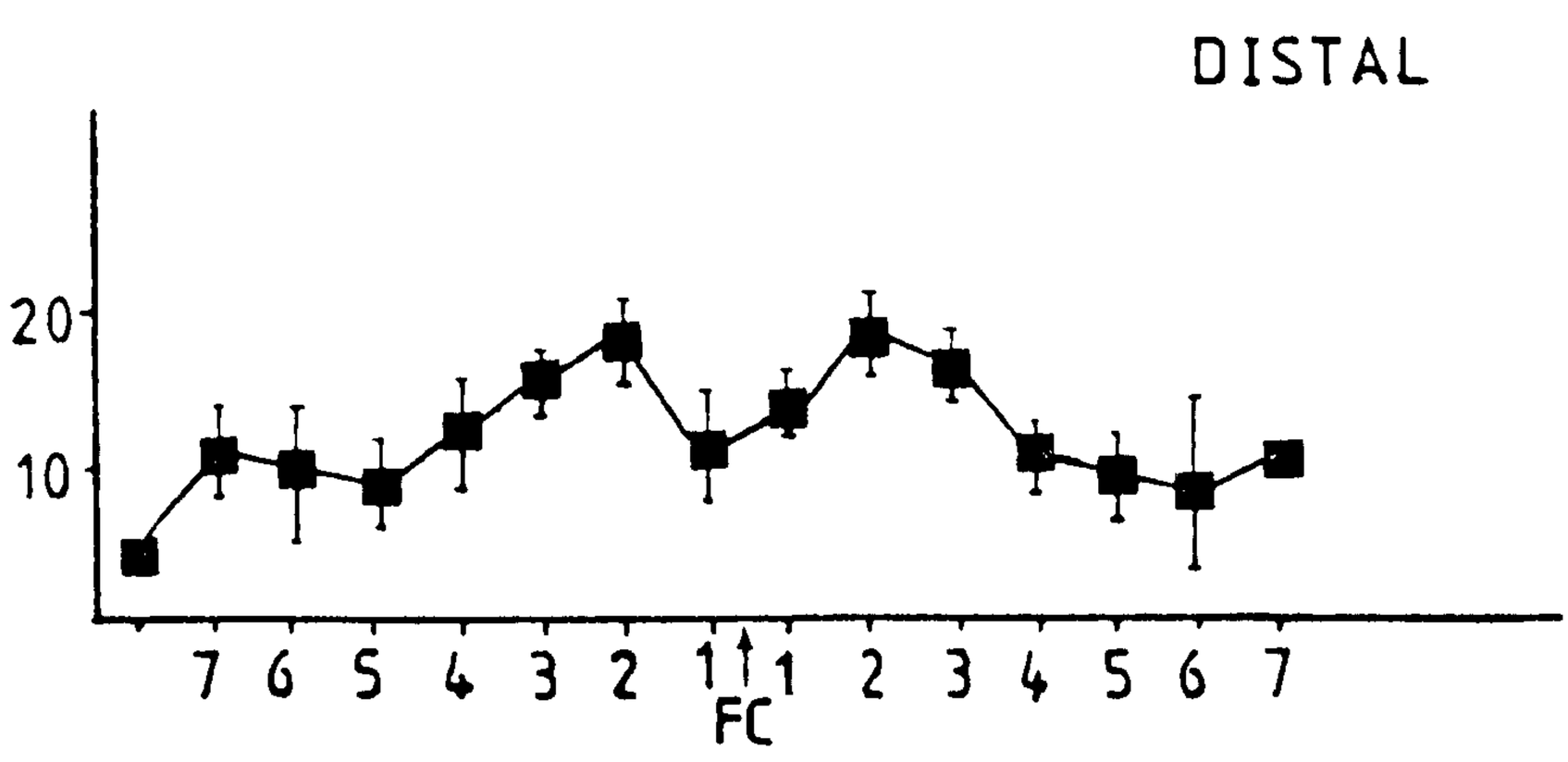

A
B
Colony Size (cm²)
1·5
1·0
0·5
0
(15)
(7)
JUL
(3)
(7)
JUN
(4)
(12)
1
AUG
(22)
31
(19) AUG
(13)
(13)
1
2
3
4
(15)
1 AUG
(12)
31 AUG
AGE (months)

Figure 1.20

Mean number of colonies of C. hyalina (± S.E.) on longitudinal sections (15 cm long, 1 cm width) of L. saccharina fronds. FC refers to Frond Center, the number on the abscissa being position on the section (highest number nearest to the edge).







Position on Frond

Figure 1.21

Colony size of C. hyalina in 3 areas of L. saccharina fronds. Vertical bars on the histrograms are standard errors (S.E.). Shaded areas represent number of colonies touching neighbouring ones. The diagram on the left hand side shows the position of the area sampled.

(○) mean stipe lenght, (●) first settlements of C. hyalina, (▲) position of central area, (■) mean total lenght. Vertical boxes around the symbols are S.E. All values given are means of 7 plants collected on 18 September 1982.

A: ancestrulae.

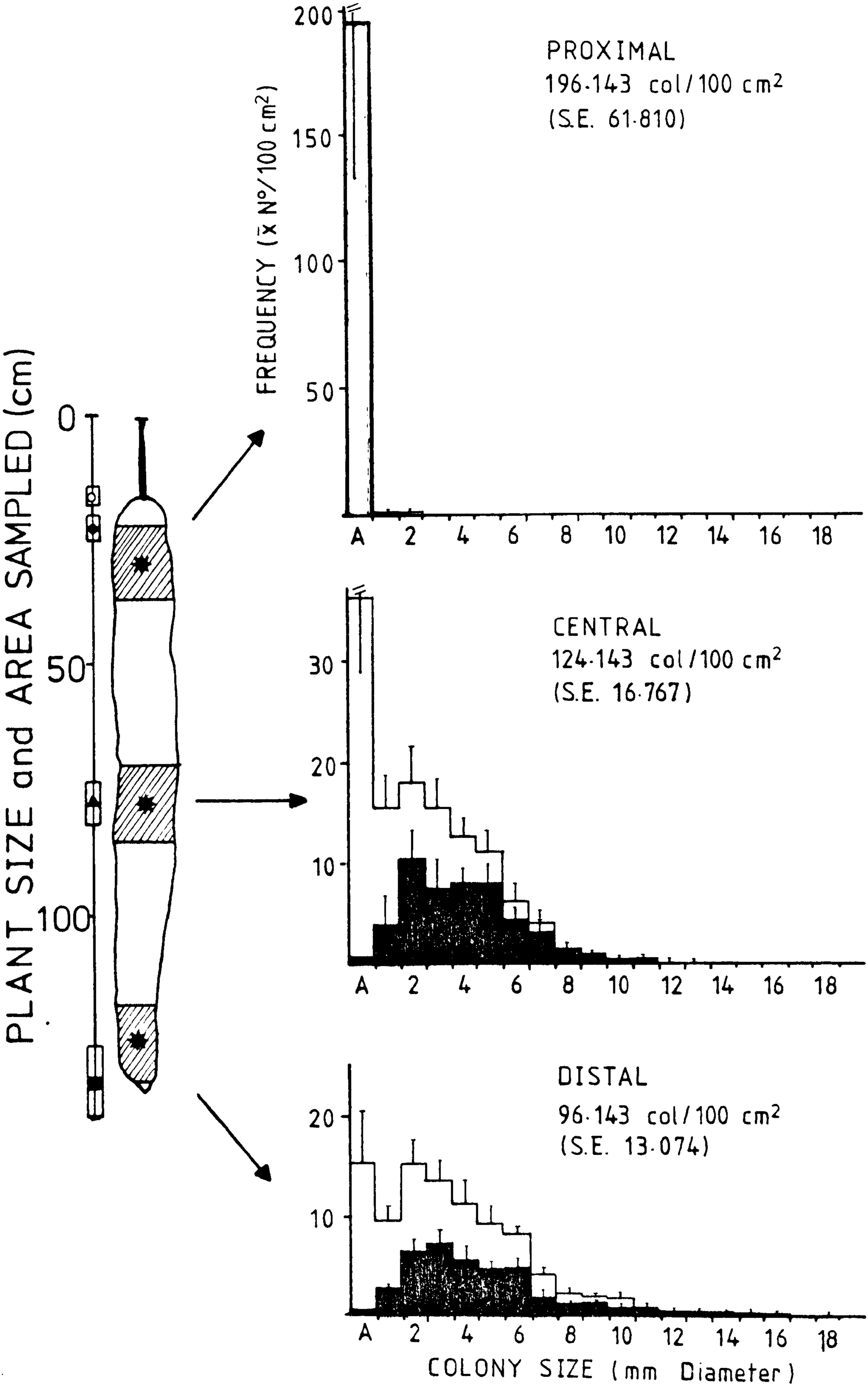
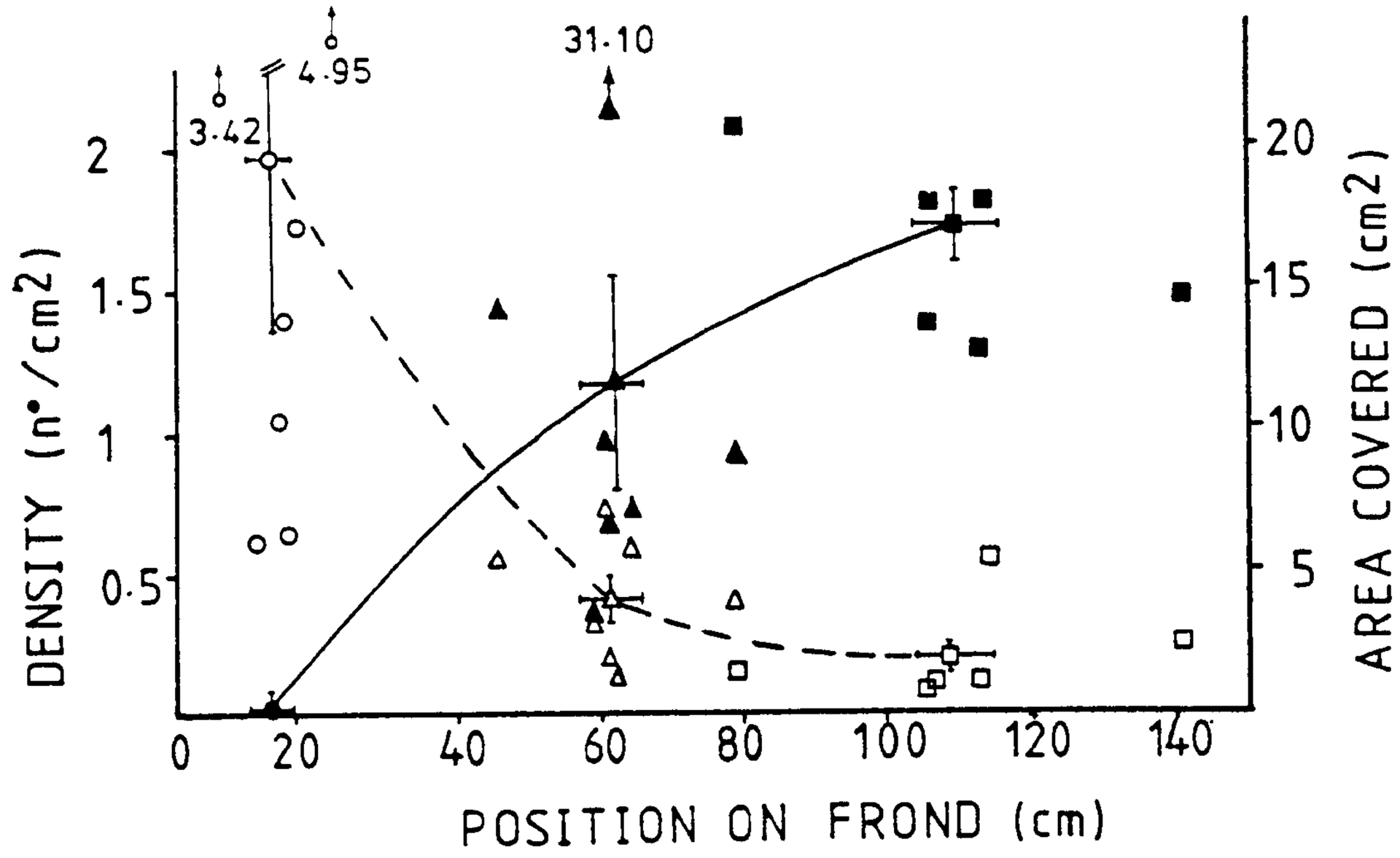

PLANT SIZE and AREA SAMPLED (cm)
0
50
100
FREQUENCY (x̄ N°/100 cm²)
200
150
100
50
PROXIMAL
196·143 col/100 cm²
(S.E. 61·810)
A 2 4 6 8 10 12 14 16 18
30
20
10
CENTRAL
124·143 col/100 cm²
(S.E. 16·767)
DISTAL
96·143 col/100 cm²
(S.E. 13·074)
COLONY SIZE (mm Diameter)

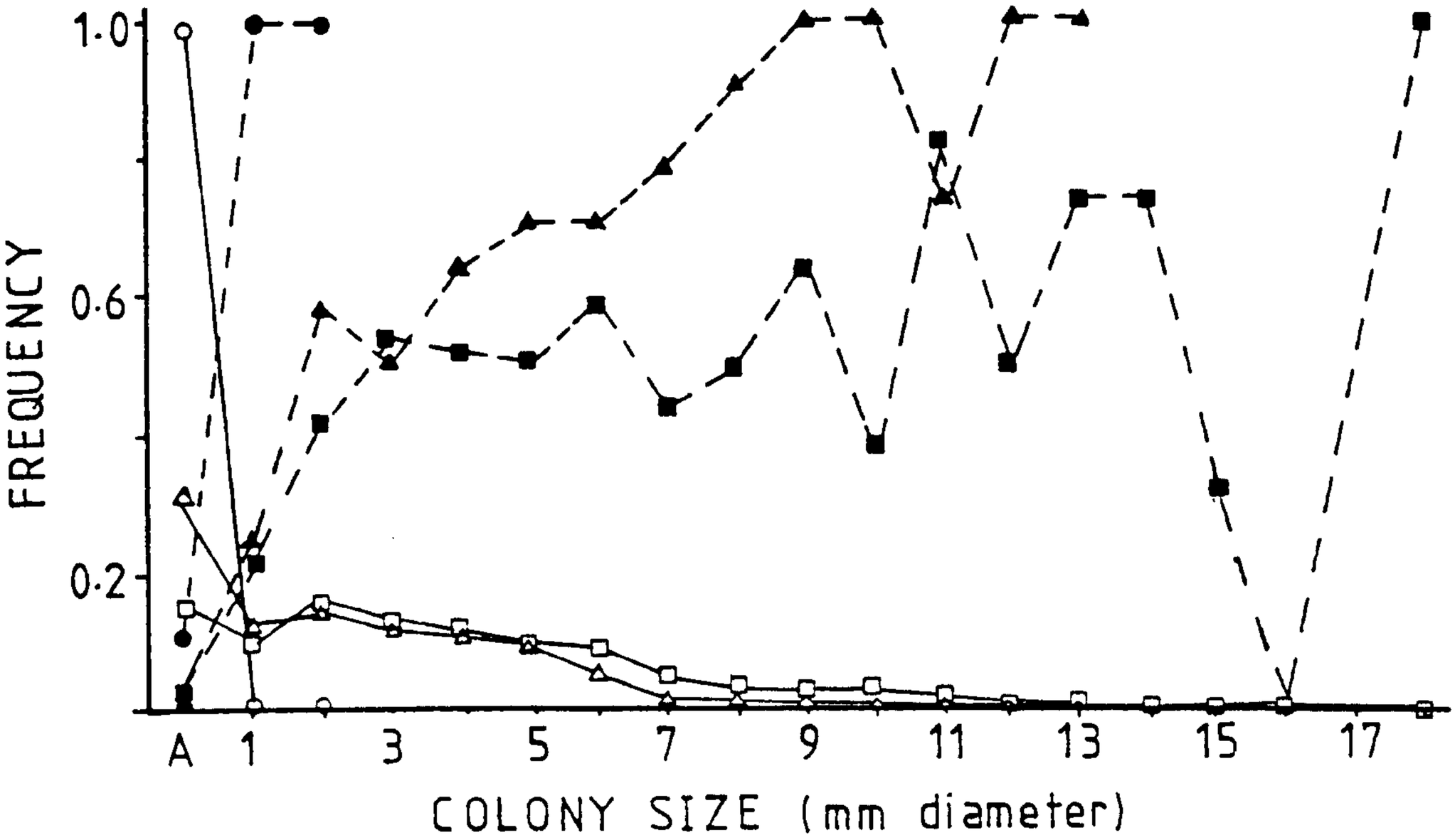
Figure 1.22

Density of C. hyalina (open symbols) and area covered by colonies other than ancestrula (filled symbols) on 100 cm^2 of L.saccharina fronds. Curves drawn by eye through the mean values at: Proximal (○), Central (△) and Distal (□) areas. Vertical and horizontal bars : S.E. for the mean.

Figure 1.23

Size distribution of C. hyalina on 3 areas of L. saccharina frond (open symbols) and proportion of colonies touching neighbouring ones (filled symbols). Circles. triangles and squares as in Fig. 1.22.


31·10
4·95
3·42
2
1·5
1
0·5
DENSITY (n°/cm2)
20
15
10
5
AREA COVERED (cm2)
0
20
40
60
80
100
120
140
POSITION ON FROND (cm)


1·0
0·6
0·2
FREQUENCY
A
1
3
5
7
9
11
13
15
17
COLONY SIZE (mm diameter)

Chapter 2

The Life History of *Celleporella hyalina* (L.)

I. Zooidal polymorphism and astogeny.

2.1 INTRODUCTION

2.2. MATERIALS AND METHODS

2.3 RESULTS

2.3.1 Early astogeny and zooidal polymorphism.

2.3.2. Interactions between colonies.

2.3.3. Effects of season and water flow on colony shape and growth rate.

2.3.4. Other patterns of early astogeny and premature metamorphosis.

2.4 DISCUSSION.

2.1. Introduction

The encrusting bryozoan Celleporella hyalina (L.) is commonly found in the Menai Straits on fronds of Laminaria saccharina. In this habitat in summer, the colonies reach up to 25 mm in diameter and have a maximum life-span of about 4 months (Chapter 1). The species has also been reported from a wide diversity of substrata along with its distributional range. Some of these substrata are even more ephemeral than L. saccharina fronds, (e.g. fronds of Macrocystis pyrifera North 1961, Bernstein and Jung 1979). Preliminary observations (Bernstein and Jung 1979, Chapter 1) indicate that C. hyalina starts sexual reproduction at a small colony size (4 mm in diameter, Chapter 1). This is in agreement with what is expected from an opportunistic species living in ephemeral habitats.

The terminology used below to describe topographical position within colonies of C. hyalina is that of Hayward and Ryland (1979). The surface in contact with the substratum is referred to as basal, the opposing surface as frontal. The end bearing the orifice is distal, the opposite end proximal.

Early studies on the polymorphism of C. hyalina (Marcus 1937, 1938) showed that the colonies are formed by 3 types of zooids: autozooids that feed, and non-feeding male and female zooids (androzooids and gynozooids respectively, Silen 1977). Sexually mature colonies have 2 or more layers of zooids (multilaminar, Pinter 1973), with autozooids forming the basal layer, whilst sexual zooids are the commonest in the frontal layer (Ryland and Gordon 1977, Hayward and Ryland 1979).

Sexually mature colonies of C. hyalina in Brazil have been

found to be unilaminar or multilaminar (Marcus 1937, 1938). Ryland and Gordon (1977) and Ryland (1979), however, have argued that Marcus' description was based in two species, namely C. hyalina and C. carolinensis. These two species have been described as having a different astogeny, only the latter one being unilaminar when sexually mature (Ryland 1979b). The present study describes the different patterns of astogeny and the spatial distribution of auto- male and female zooids within colonies of C. hyalina experimentally reared in the Menai Straits. The aim of the work has been to characterize the species in this locality, providing a base-line for possible comparison with this and closely related species in other localities. Furthermore, a comprehensive study of growth and sexual reproduction of C. hyalina is not found on the literature, but for reasons discussed above, and in the General Introduction and in Chapter 3, such a study is urgently needed. The present chapter will also deal with the feasibility of experimentally manipulating the species.

Rearing of bryozoans under laboratory conditions has been attempted by numerous authors with different degrees of success (review in Jebram 1977). Although growth of colonies has been reported in many cases (e.g. Wood 1971, Menon 1972, Jebram 1973, 1977, 1980a,b; Winston 1976, 1977), sexual reproduction has not occurred (Winston 1976) or has not so far been reported in colonies kept a long time in laboratory conditions. Some authors (e.g. Ström 1969, Silen 1945, 1966, Cook 1962, Nielsen 1981, Dyrynda 1981a) have, however, kept freshly collected bryozoans alive in the laboratory for a few weeks and studied different

aspects of sexual reproduction such as sperm release, ovogenesis, egg transfer, larval development, brooding-time, etc. Both the difficulty in providing a diet able to sustain good growth in laboratory conditions (see for example Jebram 1980b) and the failure of laboratory-reared colonies to sexually reproduce (Winston 1976, Thorpe 1977) suggest that studies of the relationship between growth and reproduction in bryozoans must be carried out in the field. Furthermore, C. hyalina has been reported (Jebram 1977) to survive in the laboratory for only a short time. Successful settlement, growth, and sexual reproduction of marine bryozoans in the field have been observed on many man-made materials (e.g. glass: Dudley 1973; perspex: Ryland 1960, Wass and Vail 1978, Vial and Wass 1981; ceramic tiles: Sutherland and Karlson 1977; tufnol: Ryland 1960, 1974; for a review see Soule and Soule 1977). It was decided, therefore, to attempt rearing C. hyalina on glass petri dishes and slides under field conditions. The methods used are modified from Dudley (1973) and Wood (1971, 1973).

2.2. Materials and Methods

All observations were carried out on colonies established by settlement of larvae released in the Laboratory. The procedure for obtaining larvae was similar to that previously reported by Ryland (1959a,b; 1960). Fronds of Laminaria saccharina bearing colonies of Celleporella hyalina were collected at different dates between January 1980 and September 1982 at two localities; Twyn-y-Penrhyn SH 629797 and Menai Bridge Pier SH 559720 in the Menai Straits, Anglesey, Wales. In the laboratory at Bangor, the fronds were kept in the darkness in running sea-water for 24 to 36 hrs. To release larvae, the fronds were illuminated after being placed in a transparent plastic tank filled with freshly collected sea-water from the Menai Straits. The released larvae, being initially positively phototactic, swam to the surface (Ryland 1960), where they were carefully collected with a plastic pipette and placed in small dishes containing the substrata for settlement. Larvae were settled on glass petri dishes 10 cm in diameter and on glass slides measuring 3.8 x 7.7 cm. Settlement was successful only when the surface of the glass had previously been conditioned for 6 to 14 days in the Menai Straits.

Two to three days after settlement, the animals were taken to the field. One slide-holder (Fig. 2.1.) and several boards to hold petri dishes were used to suspend the colonies beneath Menai Bridge Pier, (Plate 2.1 C, Fig 2.2). The boards and slide-holder were tied to the Pier through chains and ropes (Fig. 2.2.C), whilst weights were used to keep the boards horizontal and continuously submerged at about 80 cm below the surface. The

distance between the boards and the sea-bed varied from about 30 cm and 6 m according to the state of the tide (Plate 2.1). To prevent silting of the colonies, the surfaces with C. hyalina were kept facing downwards. Overgrowth by algae was prevented in two ways: a) the slide-holder was located in a dark place between the pontoons of the Pier and b) covers made of linoleum (synthetic floor cover) were placed on the upper surface of each petri dish, preventing light penetration. This was a modification of the technique used by Wood (1973) for rearing fresh-water bryozoans. Water temperatures were measured at the surface at the Menai Bridge Pier throughout the period of study (Fig. 2.3).

Water flow around the colonies was controlled using linoleum conical baffles (Fig. 2.2 A) of two different sizes. The procedure for making the baffles is given in Appendix 2.1. Details about the boards are found in Appendix 2.2. The amount of water circulating over the petri dishes was assumed to be directly proportional to the amount of weight-loss by gypsum hemispheres (Muss 1968, Doty 1971) placed in the center of each petri dish (Appendix 2.3).

The colonies were taken to the Laboratory at regular intervals and observed under the binocular microscope. Growth and sexual reproduction was followed for individually identified colonies. To do this, a camera lucida was used to draw all zooids in small colonies and all zooids within sample-areas of larger colonies. The colonies were usually kept in the laboratory for less than 24 hrs, but large colonies were kept occasionally for up to 72 hrs. While in the cold room, the colonies were kept in a 60

l tank with recirculating unfiltered sea-water. The sea-water came from the Menai Straits and was usually replaced every two days. A chamber with recirculating sea-water, driven by a TEP pump (Fig. 2.3), was used to maintain the colonies at the correct temperature while observations under the binocular microscope were being made.

Areas of the colonies were measured from the camera lucida drawings using a digitizer, which is a device able to take coordinates as a tracer is moved round the periphery of the area to be measured. Coordinates were stored on disk (PDP-11 micro computer) and the information used to calculate the area inside the perimeter. In a few cases the information was transferred to a Dec-10 computer and the shape of the colony and position of the opening of autozooids plotted (e.g. Plate 2.5 C).

For scanning electron microscopy, larvae and colonies of different ages, grown on glass slides, were fixed in glutaraldehyde, dehydrated through ethanol and acetone and transferred to liquid CO_2 for critical-point-drying. Gold coating was carried out using a Polaron SEM Coating Unit E 5000. The micrographs were taken using an M-7 SEM, International Scientific Instruments. Some colonies were sonicated for 5 minutes while in acetone. Details of timing are given in Appendix 2.4.

2.3. Results

2.3.1. Early astogeny and zooidal polymorphism.

The lecithotrophic larvae of Celleporella hyalina (Plate 2.2 a) become photonegative and settle within 1.5 to 4 hrs after release. At 15° C metamorphosis takes two days, the recently settled larva becomes dome-shaped (Plate 2.2 b,c) giving rise to a schizoporelloid (Gordon and Hasting 1979) ancestrula. Calcification starts basally, progressing towards the frontal area, and the area around the orifice of the ancestrula is calcified last (Plate 2.2 C).

Normally, the ancestrula produces a single disto-lateral bud, either at the left or right hand side, and a second zooid is produced between the ancestrula and the first zooid (Plate 2.2 d to h). The first zooid arises on either side of the ancestrula with equal frequency (Table 2.1, total X^2 3.683, 1 d.f., $P > 0.005$). Other infrequent budding patterns found in C. hyalina will be presented on section 2.3.4.

The basal layer of the C. hyalina colony is formed by autozooids (Plate 2.2, f,g,h; Plate 2.3 a to d). The autozooids produced in the vicinity of the ancestrula are smaller than those produced later. Eventually however, the size of the autozooid stops increasing, further produced autozooids being of about the same size (Plate 2.2; Plate 2.5). New autozooids are formed distally, (i.e. at the edge of the colony), by fusion of pore-chambers budded from the proximal autozooids (Plate 2.3 d). Frontal budding gives rise to males, females and autozooids (Plate 2.3 e, f, Fig. 2.4 A, D; Fig. 2.5 A). Male zooids have a

relatively smaller orifice and are smaller in overall size than basal autozooids, but are not necessarily smaller than frontal budded autozooids (Plate 2.3 e). The females are provided with a globular ovicell that is usually completed within a week of the production of the female's body (Plate 2.3 e to g).

Frontal budding starts in the older areas of the colony and progresses towards the edges as the colony increases in size (Fig. 2.4 B, E; Fig. 2.5 B). Frontally budded autozooids are commoner in areas around the ancestrula than in other areas of the colony (Fig. 2.4.A, D; Fig. 2.5.A). Male and female production starts near the ancestrula and progresses towards the edge of the colony (Fig. 2.5.C, F; Fig. 2.6.C). Towards the edge of the colony the abundance of sexual zooids normally decreases, but males and females are produced near the edge of colonies that have stopped growing due, for example, to contacts with neighbouring colonies (Fig. 2.5.G).

Male zooids are easily identified under the binocular microscope by their small size, by their milky-white colour when producing sperm and by their lack of a digestive tract. Although males have a lophophore, this is not normally visible. In three years of study the protruded male lophophore was observed only 3 times. Male zooids were observed in the basal layer of some colonies, especially over winter, but not a single case of female production in the basal layer was observed. Nine to twelve frontal pores on the ovicells of C. hyalina are visible under the binocular microscope (see Hincks 1880, Marcus 1938, Ryland and Gordon 1977, Hayward and Ryland 1979). However, only small depressions on the ovicells were seen with the scanning microscope

(Plate 2.3, f, g,), indicating that the cuticle, or periostracum (sensu Tavern-Smith and Williams 1972) covers non-calcified areas of the ovicell.

Eggs are produced in the body of the female, they are visible 2 to 3 days before being transferred to the ovicell. Eggs and early larval stages are bright yellow (Eggleston 1963, 1970; Ryland and Gordon 1977), the later larval stages are whitish. The embryo increases in size while in the ovicell from about 90 μ m to 185 - 200 μm in diameter (fig. 2.7 and Ryland 1959b, for larval size). Ciliary movement was observed in all embryos bigger than 140 μm (Fig. 2.7).

2.3.2. Interactions between colonies.

The highly organized, even distribution of zooids in colonies of C. hyalina is altered when growing edges of the same or other colonies are juxtaposed (Plate 2.4 a to d). Actively growing colonies procede to form autozooids distally, the tubular connections produced by the autozooids of neighbouring colonies intermingle and fail to form zooids or form deformed ones. In some cases contacting colonies form a ridge.

Intra-specific contacts between colonies of C. hyalina very occasionally result in ovegrowth that contrasts with the outcome of inter-specific contacts as seen from Table 2.2.

2.3.3. Effects of season and water flow on colony shape and growth rate.

Colonies of C. hyalina recruited in spring and summer become circular in shape and start growing concentrically 4 - 5 weeks after larval settlement (Plate 2.5, a,b; Table 2.3 A). During

winter however, the colonies remain elongated or fan-shaped (Plate 2.5 c to e) for a longer time, becoming circular only after 5 - 6 months (Table 2.3 B). With the onset of winter (Plate 2.5 B), well grown colonies start to produce finger-like projections and lobules at the edges, the circular shape being reformed during the next spring.

Water flow in the 3 treatments, unrestricted (no baffle), semi-restricted (short-baffle), and restricted (long baffle) was in the ratio of 3.0:1.8:1.0 (Appendix 2.3). Colonies on petri dishes with unrestricted water flow were subjected to relatively lower water flow than colonies on Laminaria saccharina (Appendix 2.3). Water flow did not have any effect on colony shape during spring (Table 2.3. A). During winter, however, colonies grown on petri dishes with restricted and semi-restricted water flow became circular earlier than colonies grown in unrestricted water flow (Table 2.3 B)

Colonies under different water flow regimes showed initially a similar growth rate, but eventually a different size was achieved in each treatment (Fig. 2.8, also compare length of X axe in Fig. 2.5, Fig. 2.6).

2.3.4. Other patterns of early astogeny and premature metamorphosis.

Eight ancestrulae in a thousand were found to produce the first zooid disto-medially (Plate 2.5 g) and 3 in a thousand produced two zooids simultaneously (Plate 2.5 f, Table 2.1). These colonies produced males and females similar in morphology to those produced by colonies in which the first zooid had been produced unilaterally.

Three colonies with a similar budding pattern to that of C. hyalina, but with zooids of smaller size, were found during this study (Plate 2.5 h), but unfortunately breeding was not observed.

Larvae of C. hyalina undergo metamorphosis prematurely if mishandled when transferred with a pipette. If a substratum is not offerred for settlement the ancestrulae become avoid and lack a sinus at the orifice (Plate 2.4 e,f). Metamorphosis is completed in about 5 hrs at 15°C.

2.4. Discussion

The rearing technique used in the present study, which combined larval settlement and observations in the laboratory with cultivation in the field, has proven adequated to gather information of the life history of Celleporella hyalina. This technique could be applied to other bryozoans, overcoming the difficulties in rearing Bryozoa under laboratory conditions and providing useful information regarding growth and sexual reproduction under natural conditions.

The following 5 features have been emphasized by Ryland and Gordon (1977) as distinctive of C. hyalina: 1) the schizoporelloid ancestrula; 2) the unilateral initial budding pattern; 3) sexual zooids usually frontally budded and smaller than the autozooids; 4) almost orbicular orifice of auto- and male zooids with a broad shallow sinus, and 5) ovicells provided with numerous frontal pores. The present study has shown that there are some variations regarding features 2 and 3. In relation to 5, the pores, as seen under the light microscope, do not open to the surface, being therefore "windows" (Banta 1973).

The patterns of early astogeny are generally regarded as distinctive of species and considered to be fairly constant within species (Ryland and Gordon 1977, Hasting 1979, Gordon and Hasting 1979, Ryland 1979b). Most of the population of C. hyalina in the Menai Straits showed unilateral initial budding pattern. A few ancestrulae, however, produced simultaneously 2 disto-lateral zooids while others produced a single disto-medial zooid. These two types of initial budding have been described as characteristic

of species of Celleporella, Hippothoa and Plesiothoa not found in British waters. Ancestrulae of C. bathamae, C. delta, C. tongima from New Zealand (Ryland and Gordon 1977) and C. carolinensis from North Carolina (Ryland 1979), produce two disto lateral zooids. All these species, however, differ from C. hyalina in being unilaminar, with male and female zooids produced by lateral budding (see Ryland and Gordon 1977 for other differences between these species). The initial production of a single disto-medial zooid by the ancestrula has apparently not been previously described for any species of Celleporella, but is found in some species of Hippothoa and Plesiothoa (Ryland and Gordon 1977, Gordon and Hasting 1979). Marcus (1938) illustrated a unilaminar, sexually mature, colony of C. hyalina from Brazil with 2 disto lateral zooids budded from the ancestrula. Ryland and Gordon (1977) and Ryland (1979) have argued that Marcus (1937, 1938) based his description of C. hyalina on two species, namely C. hyalina and C. carolinensis. Since ancestrulae of C. hyalina in the Menai Straits were able to produce simultaneously two disto-lateral buds in the way described for C. carolinensis (Ryland 1979b), this may not be a good character for distinguishing between these two species. The results of the present study, however, agree with Ryland and Gordon (1977), and Ryland (1979b) in that colonies of C. hyalina always produce females by frontal budding and that the female zooids are always about half the size of autozooids. Marcus (1937, 1938) believed that, depending on the season, C. hyalina produced sexual zooids by lateral or frontal budding and that the females can be as big as the autozooids; this latter feature is certainly one of C.

carolinensis (Ryland 1979b).

In the Menai Straits, numerous colonies of C. hyalina produced males in the basal layer. This had been previously reported for C. hyalina (Ryland and Gordon 1977). Males in the basal layer were commoner in winter and in areas of contiguous growing edges. Some of these zooids were smaller than autozooids and never fed. Others, however, functioned as autozooids for one or two months, becoming males after degeneration. Similar changes from autozooiods to males were also observed in frontal budded zooids.

Colonies of C. hyalina did not always follow the spiral pattern of astogenesis, reported as typical for the species in Europe and California (Hayward and Ryland 1979, Pinter 1973). Larvae recruited in late autumn - early winter gave rise to elongated and fan-shaped colonies; these colonies eventually adopted a circular shape but at a size 3 - 4 times bigger than that of colonies recruited during spring - summer. Temperature is probably the main factor influencing the budding pattern, but food and water movement cannot be ruled out. In winter, colonies grown on petri dishes with short and long baffles (restricted water flow) started to adopt a circular shape earlier than colonies with unrestricted water flow, indicating that this can be a factor influencing colony shape. Spratt (1980) has shown that the number of extended lophophores of Membranipora membranacea and Frustrellidra hispida reaches a maximum in intermediate water velocities, extension of the lophophore being inhibited at velocities higher than 0.3 $m.s^{-1}$. I used a jet of water to

inhibit extension of lophophores of C. hyalina while drawing colonies in the laboratory, and this suggests therefore that C. hyalina may respond to water velocity in a similar way to F. hispida. If feeding is prevented during winter, due to rough seas, this is more likely to affect colonies subjected to unrestricted water flow than those growing in restricted water flow. This supposition agrees with the observed higher growth rate in petri dishes with long baffles and with the earlier adoption of a circular colony shape in a few colonies under restricted water flow (Table 2.3). More than 50% of colonies grown on petri dishes with long baffle, however, remained fan-shaped for a month longer than colonies on other treatments, suggesting that other factors became important towards early spring.

Food has been found to influence colony shape and colony size of the bryozoans Conopeum tenuissimum (Winston 1976, 1977), Bowerbankia gracilis (Jebram 1973) and Electra pilosa (Jebram 1980b). Bryozoans cultured in a medium of poor nutritional quality grew slowly and resulted in elongated colonies, while colonies cultured in a medium of better nutritional quality grew faster and produced dense mats of zooids (B. gracilis) or colonies with zooids arranged in a continuous sheet (C. tenuissimum). A high number of zooids per unit area has been interpreted as a feature that allows the use of resources at a favourable site, while an elongated colony, with less zooids per unit area, would facilitate location of more favourable sites, maximizing substrate covered (Winston 1976, Buss 1979a). This would not be the case if a poor ration prevented the colony from reaching further stages in

the astogeny. Colonies of Electra monostachys that settled in October in the Menai Straits initially produced 3 radiating arms (personal observation). The arms grew by distal budding, whilst zooids were also produced laterally and eventually the zooids of neighbouring arms met, producing a circular colony. This event occurred by the time the branches were about 20 zooids long, the whole colony having 400 - 500 zooids and being about 5 months old. Experiments lasting for a short time, and those reducing growth rate due to malnutrition, may prevent colonies with similar patterns of astogeny from reaching the later astogenic stages, the results being therefore misleading. In Celleporella hyalina, however, it is clear that the pattern of early astogeny differs from early spring - summer to winter, being spiral during the former and tending to linear during the latter. Initially, colonies grew at similar rates in all three water flow conditions, but as the colonies increased in size, growth rates began to differ. Similar results have been reported for C. tenuissimum (Winston 1976) grown with diets of different quality.

Scanning micrographs of the areas of contact between neighbouring colonies of C. hyalina have revealed the mechanism by which growth of colonies stops at the area of contact. The process seems more complicated in C. hyalina, and probably more energy consuming, than in species such as Alcyonidium polyoum, A. hirsutum, E. pilosa and Frustellidra hispida (Stebbing 1973a, b), in which marginal budding does not involve the production of tubular connections. As in other species of Bryozoa (Jackson 1979), the outcome of overgrowth between colonies of C. hyalina

depends on the angle of encounter between the colonies. Fan-shaped colonies could easily be overgrown if the ancestrula is contacted first. Incidences of intra-specific overgrowth were observed rarely and this never resulted in the death of the overgrown colony, corroborating field data obtained on fronds of Laminaria saccharina (Chapter 1).

Ryland (1960) has referred to the pipetting effect, encountered while working with bryozoan larvae. He observed inmediate metamorphosis of some larvae of Bugula neritica and Escharoides coccineus on the surface film of the water and observed premature photonegative responses in other species including C. hyalina. Larvae of C. hyalina metamorphosing in this way differ in morphology from ancestrulae generated through settlement. The whole process takes only a few hours; a more detailed study of this is certainly warranted.

Acknowledgments

I thank the following people for help received. R.G. Hickson, G. Lightfoot and T.B. Tilley for providing me with the materials and making the rearing apparatus. Dr. N.W. Runham, D.A. Davies and A.V. Buckland for help with scanning electron microscopy. E.W. Pritchard for photographs, D.A. Davies for use of the digitizer. A. Newton for translating some papers from the Portuguese. Mr D. Roberts for computing programmes, A. Rossitter and P. Beverley for occasional help with handling of heavy rearing boards. And very specially, my supervisor Dr. R.N. Hughes for constant discussion of ideas and encouragement.

Table 2.1. Side of Production of First Autozooid by Ancestrulae of Celleporella hyalina.

DATE	Uni-Lateral Right	Uni-Lateral Left	Bi-Lateral	Disto-Medial	Total
16 April 1980	122	118	1	9	250
19 Sep. 1981	484	423	3	1	911
TOTAL	606	541	4	10	1161

Table 2.2 Outcome of inter- and intra-specific contacts between colonies growing on glass slides and petri dishes, June 1981.

Species A	B	Total no. of interactions	% A overgrowing B	% B overgrowing A	% neutral or mutual
C. hyalina v/s	*C. hyalina*	208	5.77	5.77	94.23
	E. pilosa	124	68.55	13.71	17.74
	C dumerilli	12	0	58.33	41.67
E.pilosa v/s	*E. pilosa*	27	11.11	11.11	88.89
	C. dumerilli	3	0	100	0

Table 2.3. Percentage of C. hyalina colonies with circular shape (autozooids have been produced proximally to the ancestrula as in Plate 2.5 a).

A. Settled 19 April 1980.

	Number of colonies	Weeks after Settlement 2	3	4	5
Unrestricted	15	0	40.0	93.3	100
Short-baffle	19	0	31.57	84.21	100
Long-baffle	60	0	46.67	86.67	100

B. Settled 20 October 1980

	Number of colonies	Months after Settlement 1	5	5.5	6	7
Unrestricted	14	0	0	28.57	100	100
Short-baffle	16	0	12.5	43.75	100	100
Long-baffle	14	21.43	21.43	28.57	42.86	100

Plate 2.1.

Field experimental site. (a), (b) Menai Bridge Pier at low and high tide respectively. The arrows indicate the wooden platform under which rearing boards were located, the white bar is 2 m long. (c) rearing boards (bo), for holding petri dishes (pe), weight (w), buffer (bu).

Plate 2.1

a

b

c

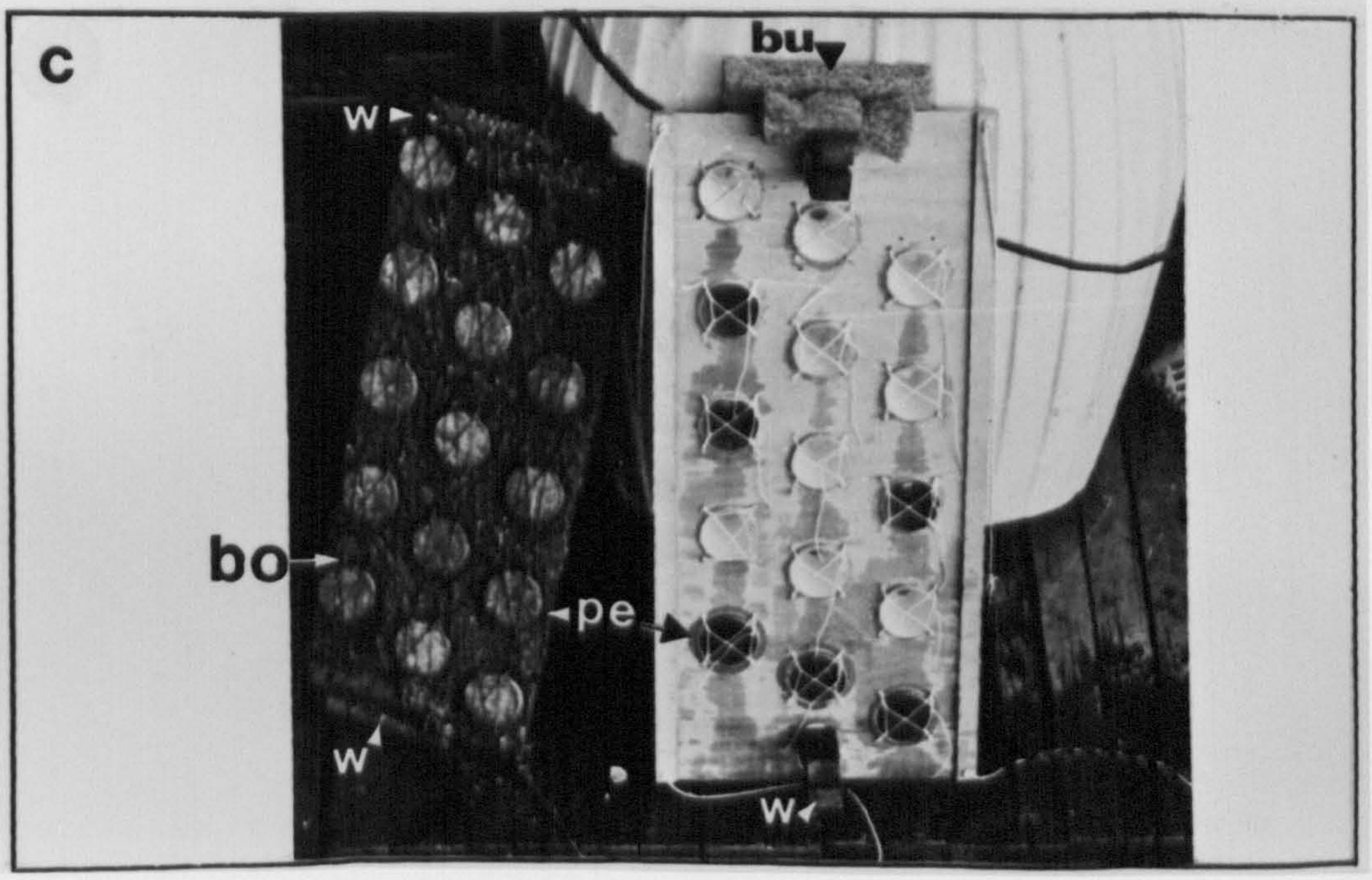
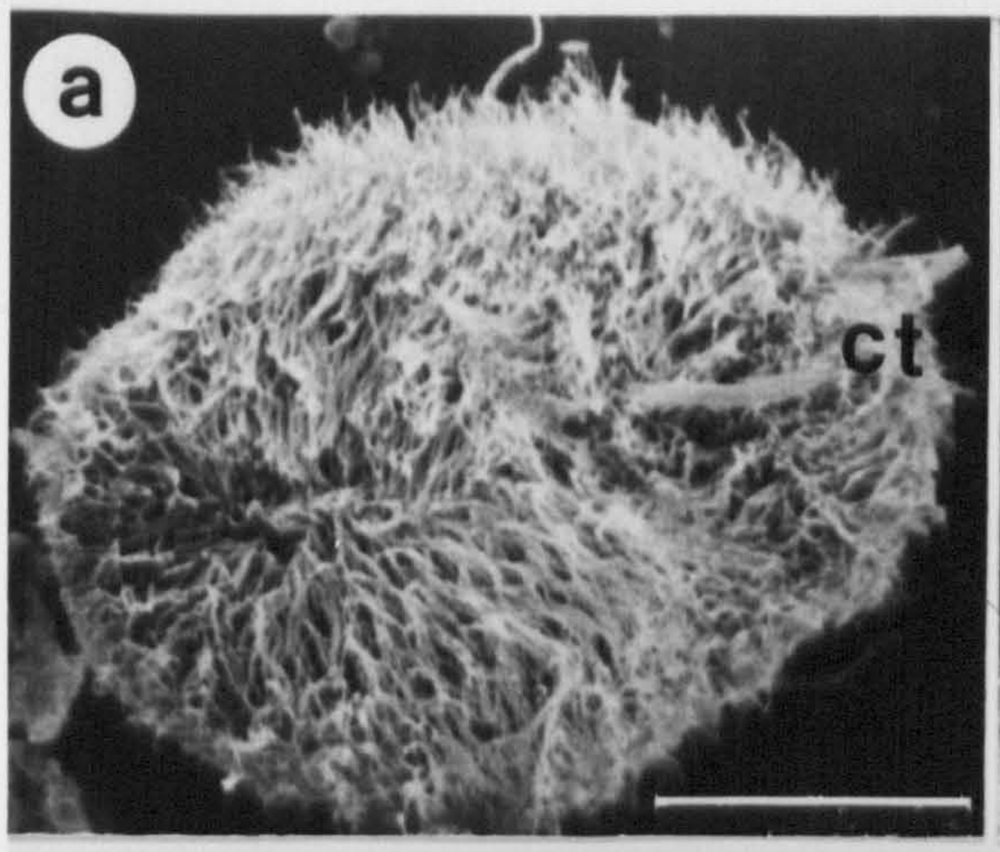


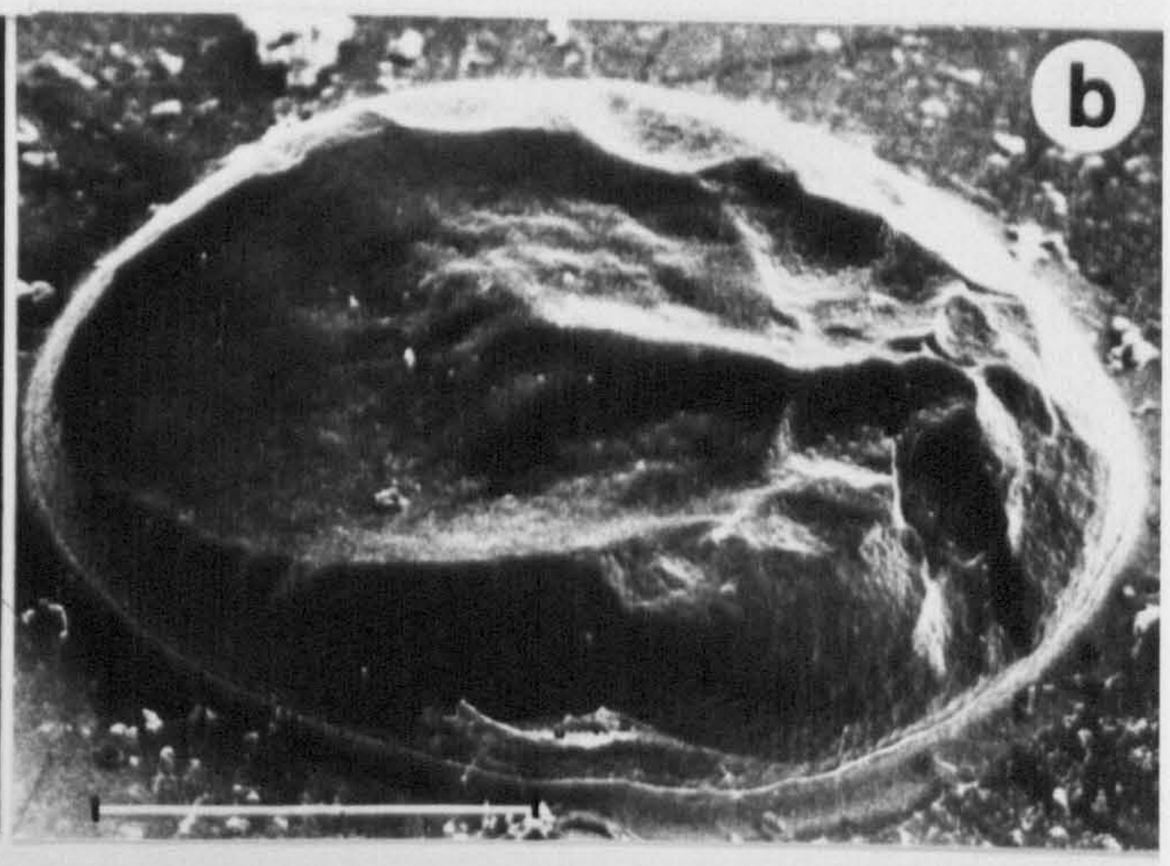
Plate 2.2.

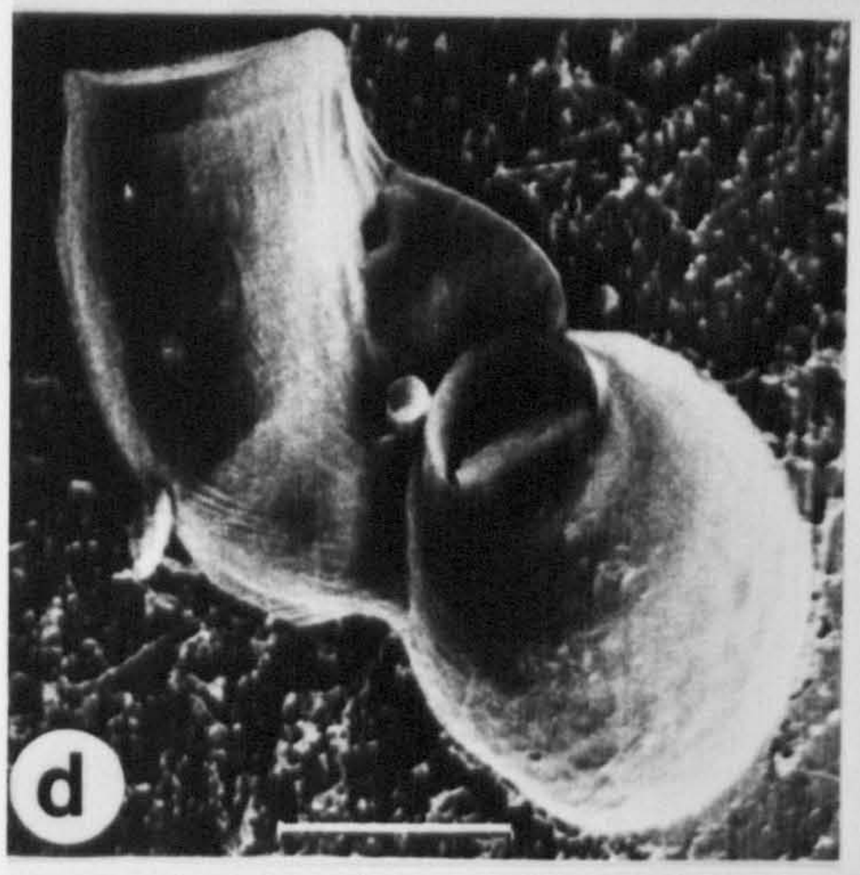
Larva, metamorphosis and early astogeny of Celleporella hyalina. (a) larva 15 minutes after release, (ct) ciliated tuft; (b) and (c) recently settled larvae showing two successive stages of metamorphosis; (d) and (e) ancestrula and early stages of unilateral budding. Both photographs show the initial stages of the first two zooids in the colony being produced at the left and right hand side of the ancestrula. (f) and (g) more advanced stages in the astogeny of the colony; (h) autozooids of a colony settled on a glass slide, as seen through the binocular microscope. The stomach is hardly visible at the moment the autozooid first begin to feed (ff), but becomes very obvious with increasing age of the zooid. During degeneration (deg) the stomach enlarges, other organs of the zooid being lost, and subsequently shrinks, producing the brown body (bb). The ancestrula (an) in this colony has recently regenerated, the brown body has been excreted.

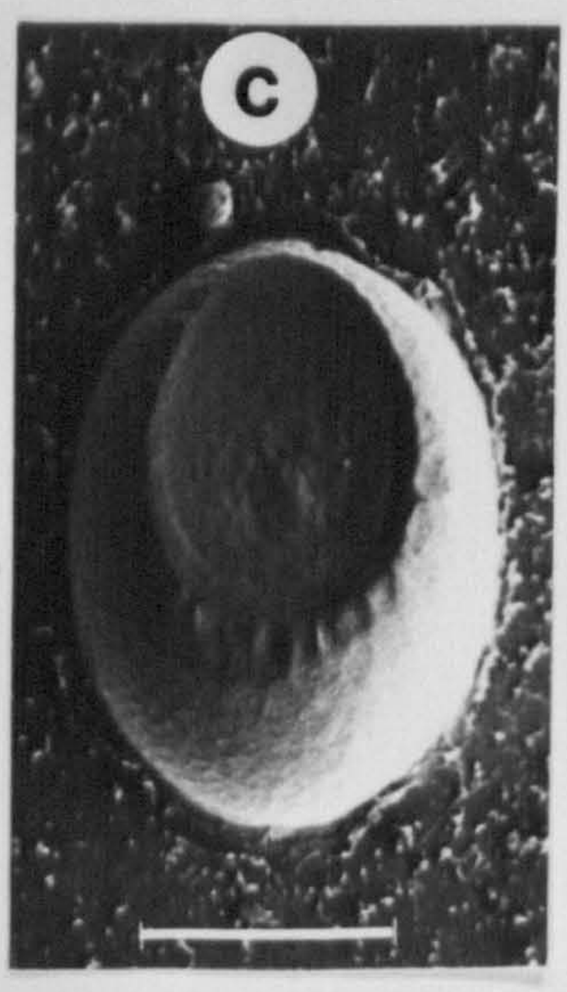
Scale bars: (a) 50μm, (g) 500μm, all others 100μm.

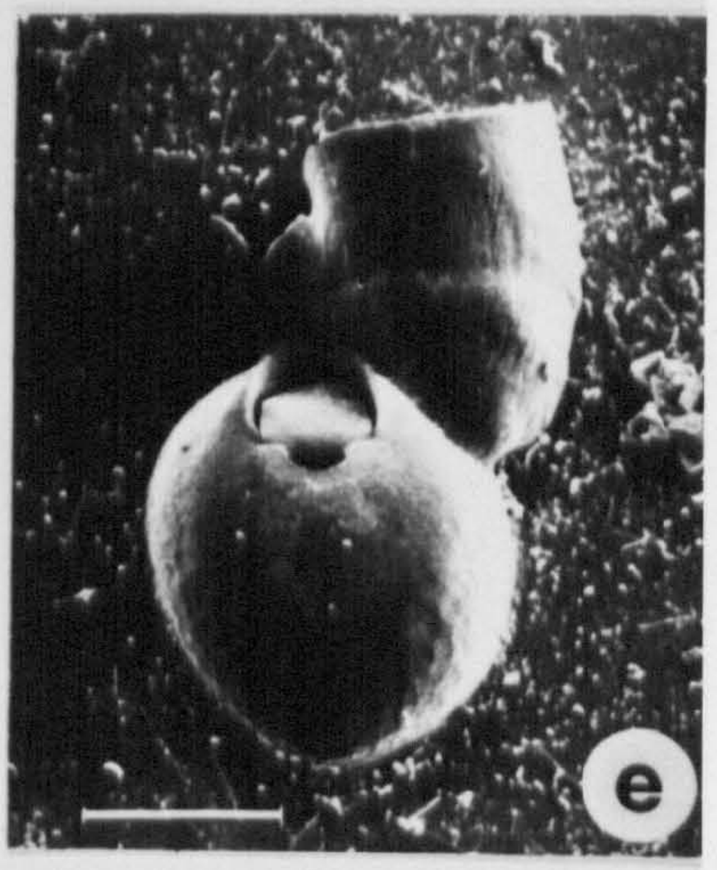
Plate 2.2











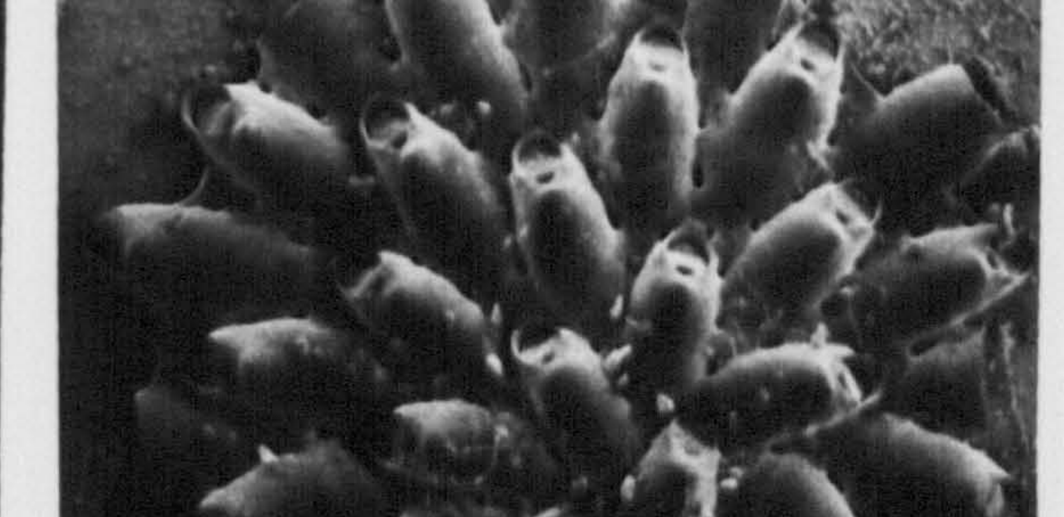
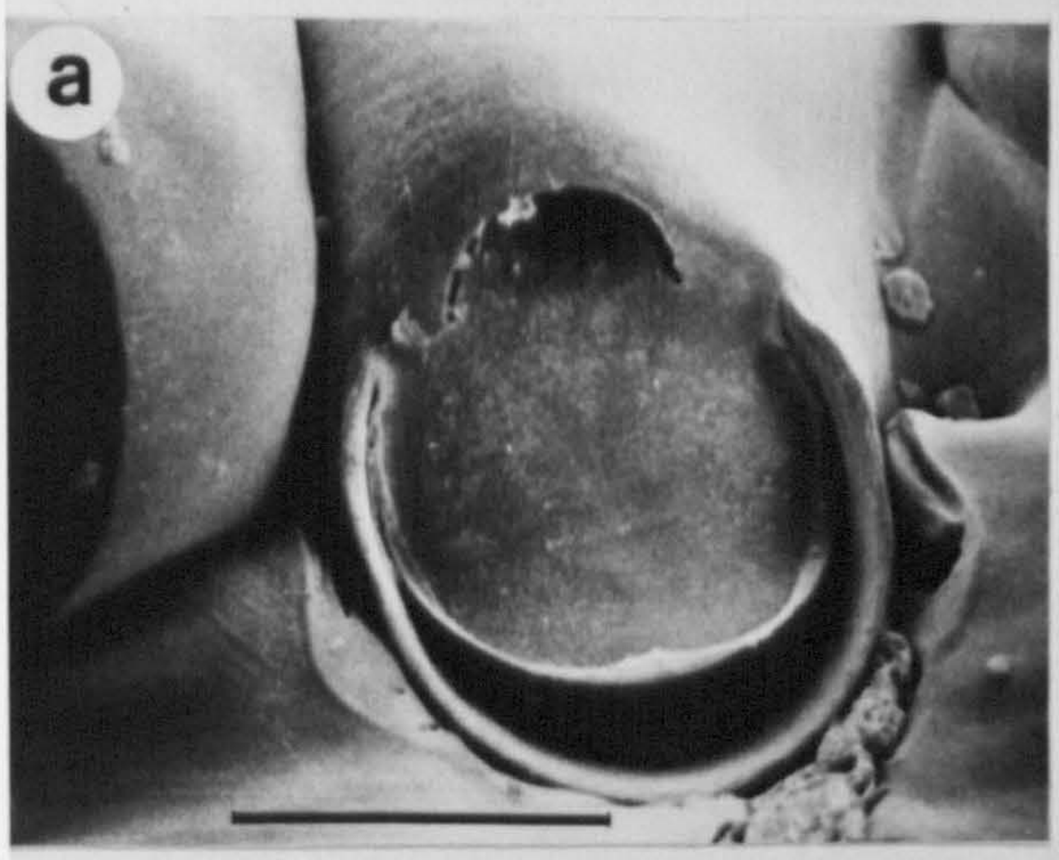


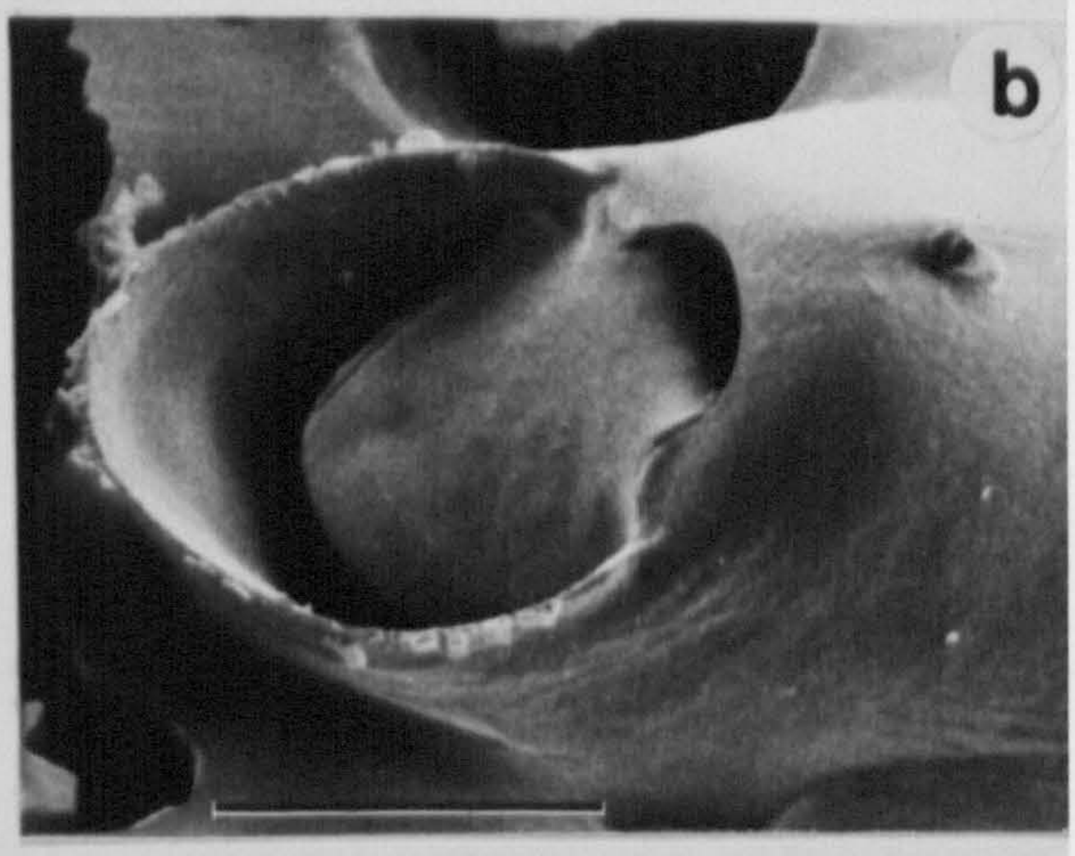
Plate 2.3.

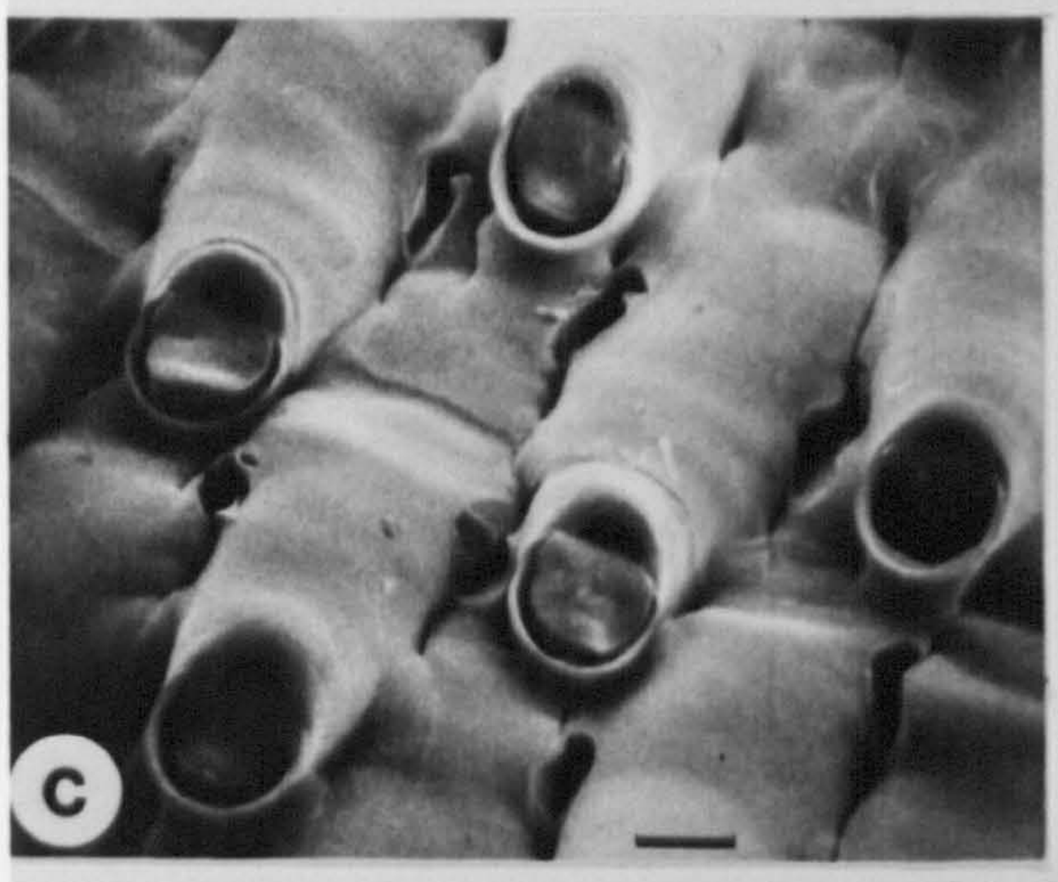
Interzooidal connections and zooidal polymorphism in Celleporella hyalina.

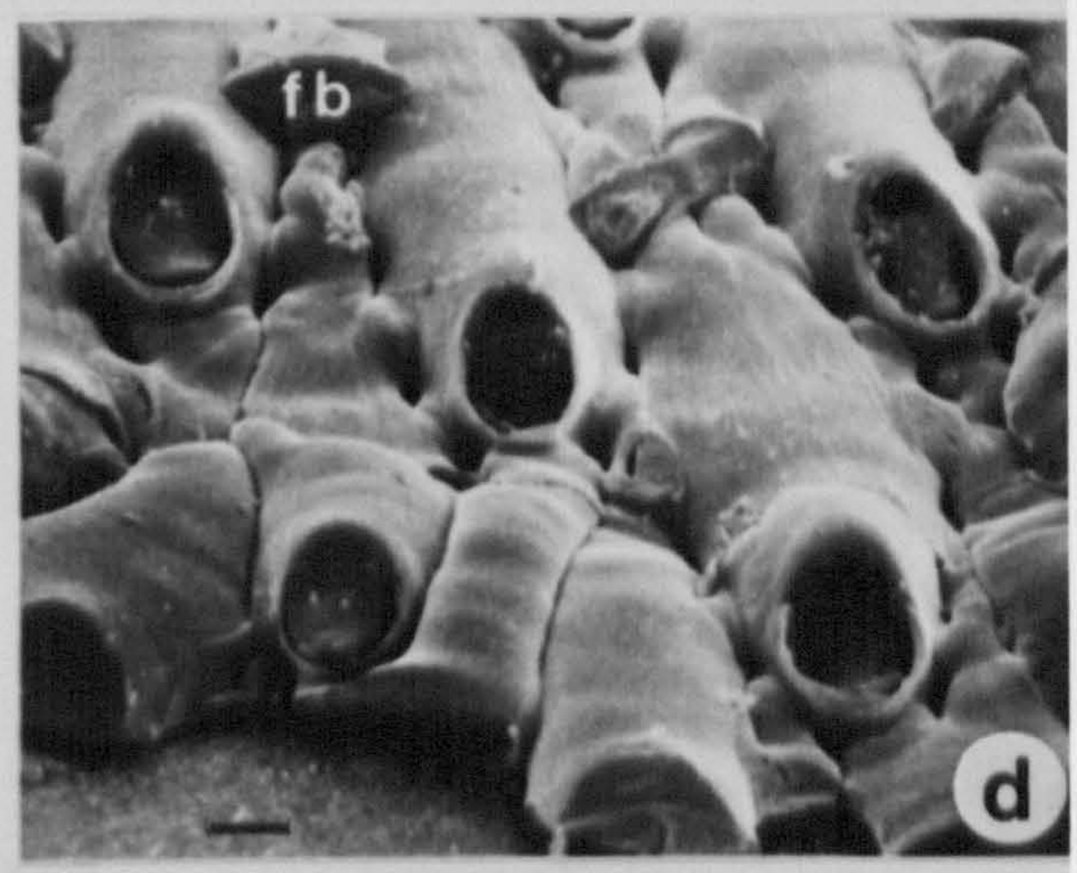
(a) and (b), frontal and lateral view of the opening and opercular plate of an autozooid; (c) and (d), arrengement of autozooids on the base of the colony. Frontal buds (fb) originate on the roof of the tubular connections (pore-chambers) between autozooids. In (c) the areas where frontal buds would originate have been destroyed by sonication; (d), growing edge of the colony; (e) and (f), morphology of the 3 types of zooids in the colony; (au) basal autozooids, ♀ , female and ♂, male. Females, males and occasionally autozooids (af) originate by frontal budding (fb). The body of the female (bo in photograph f) is formed first; the ovicell (ov) is formed as a double walled structure growing from the base towards the frontal area (iov= incomplete ovicell); (g), an ovicell about to be completed. All scale bars 100 μ m.

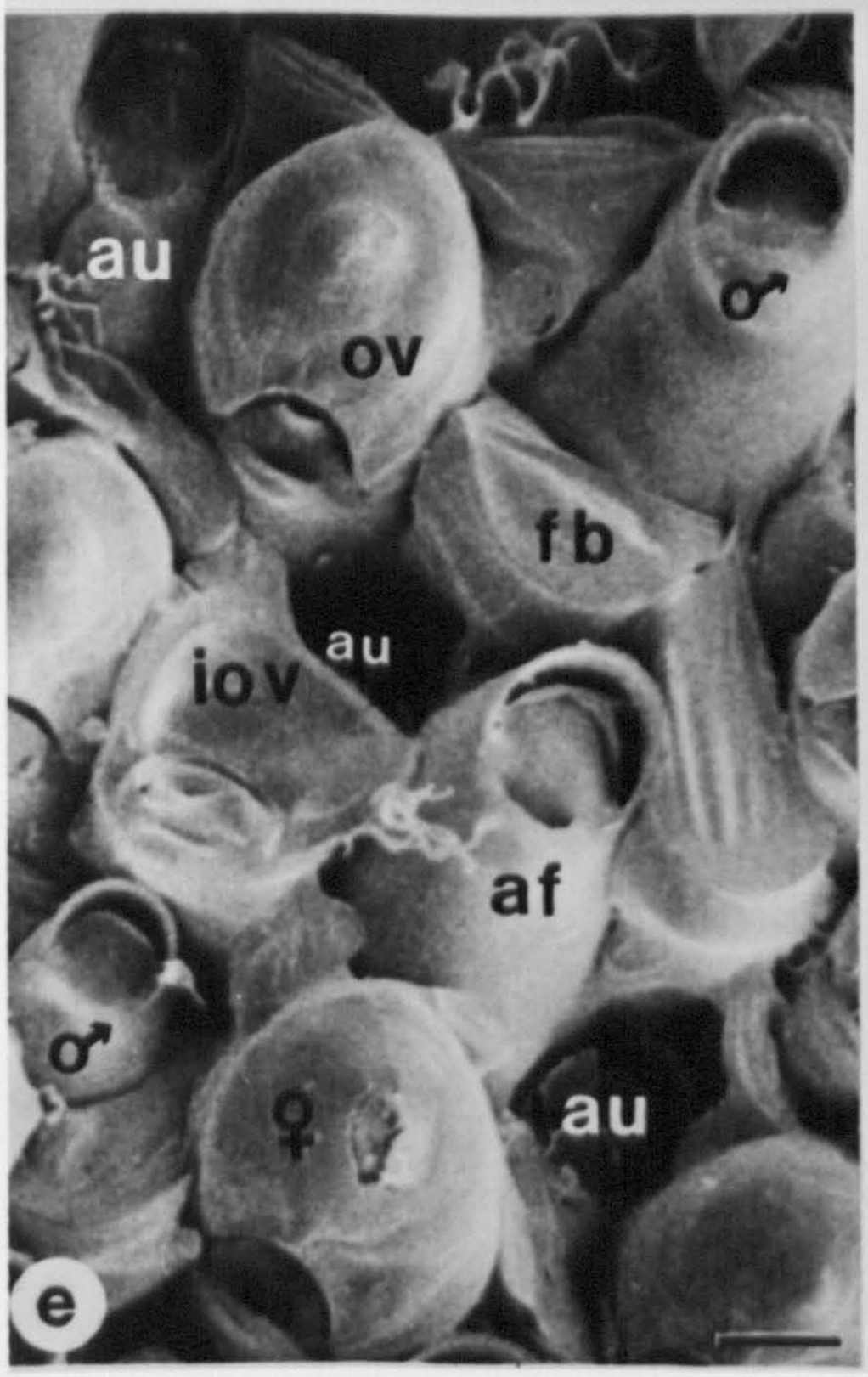
Plate 2.3

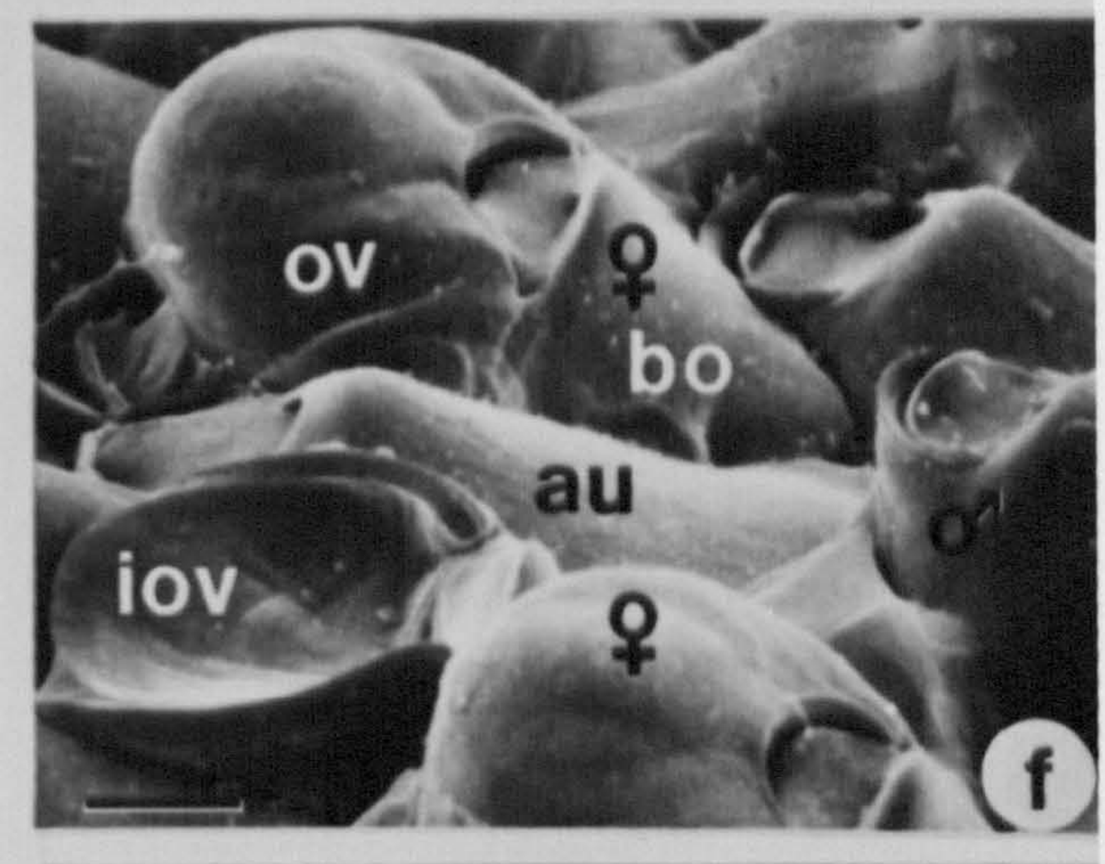












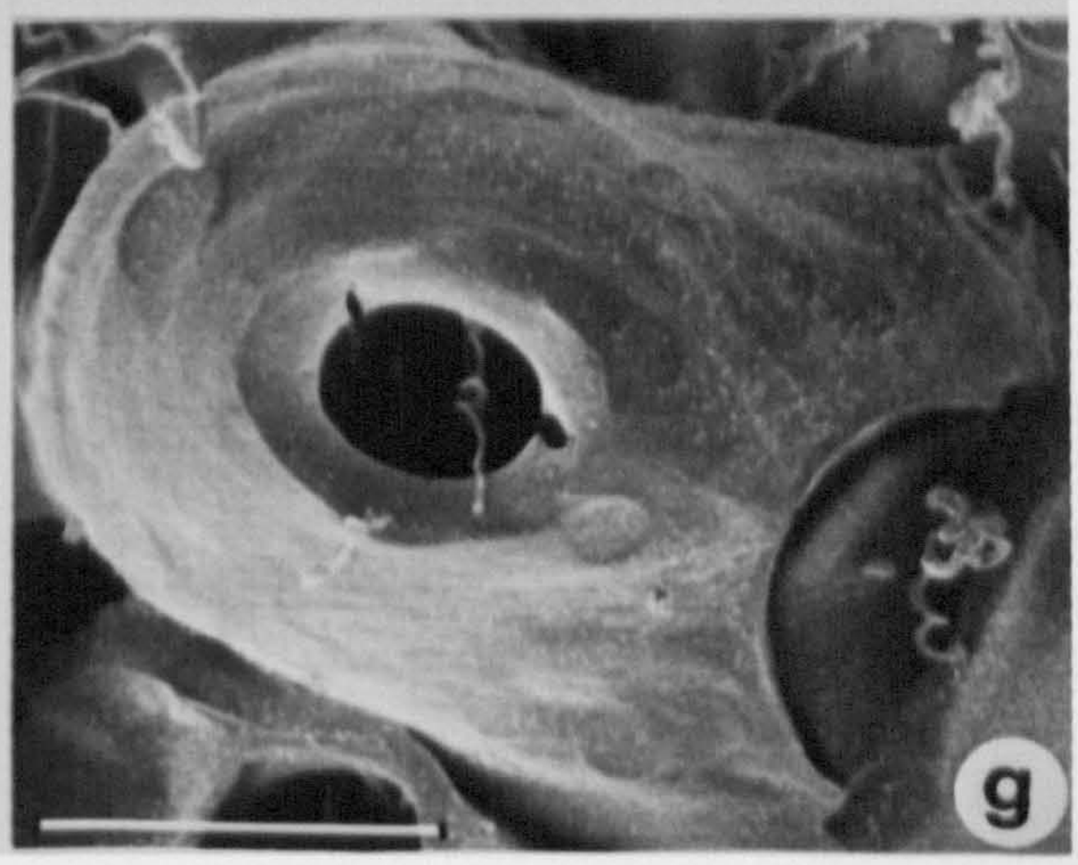


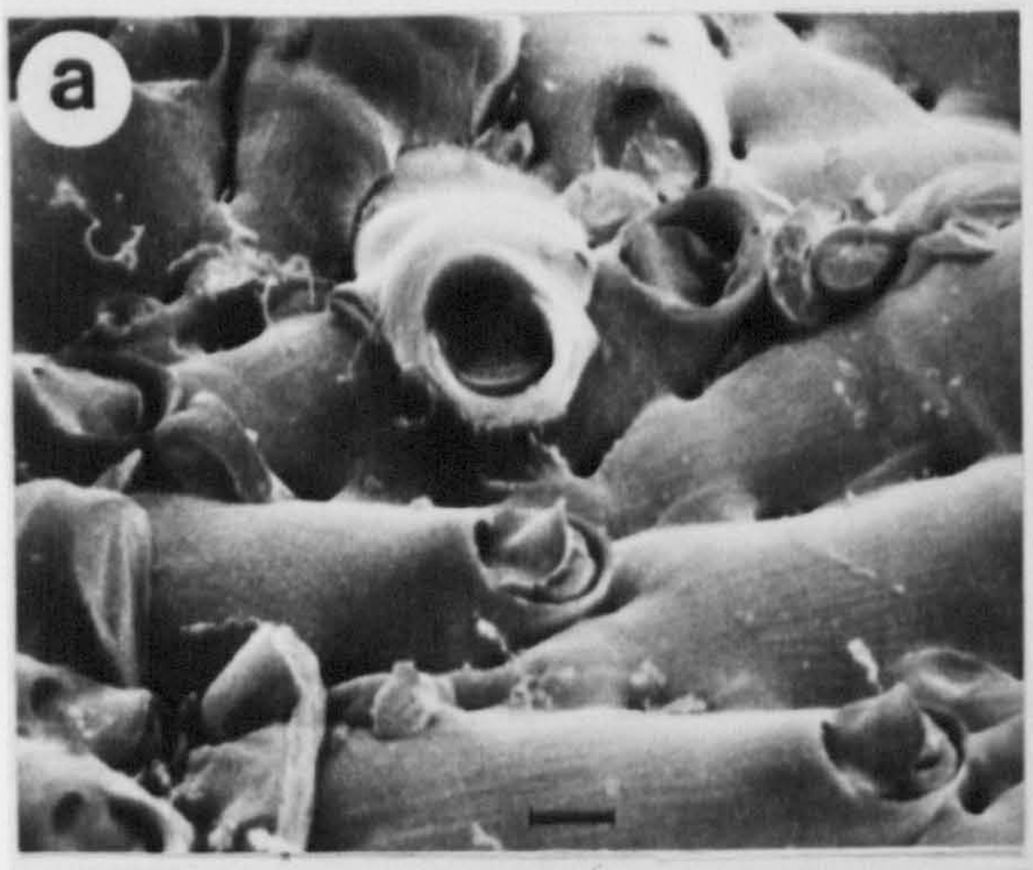
Plate 2.4

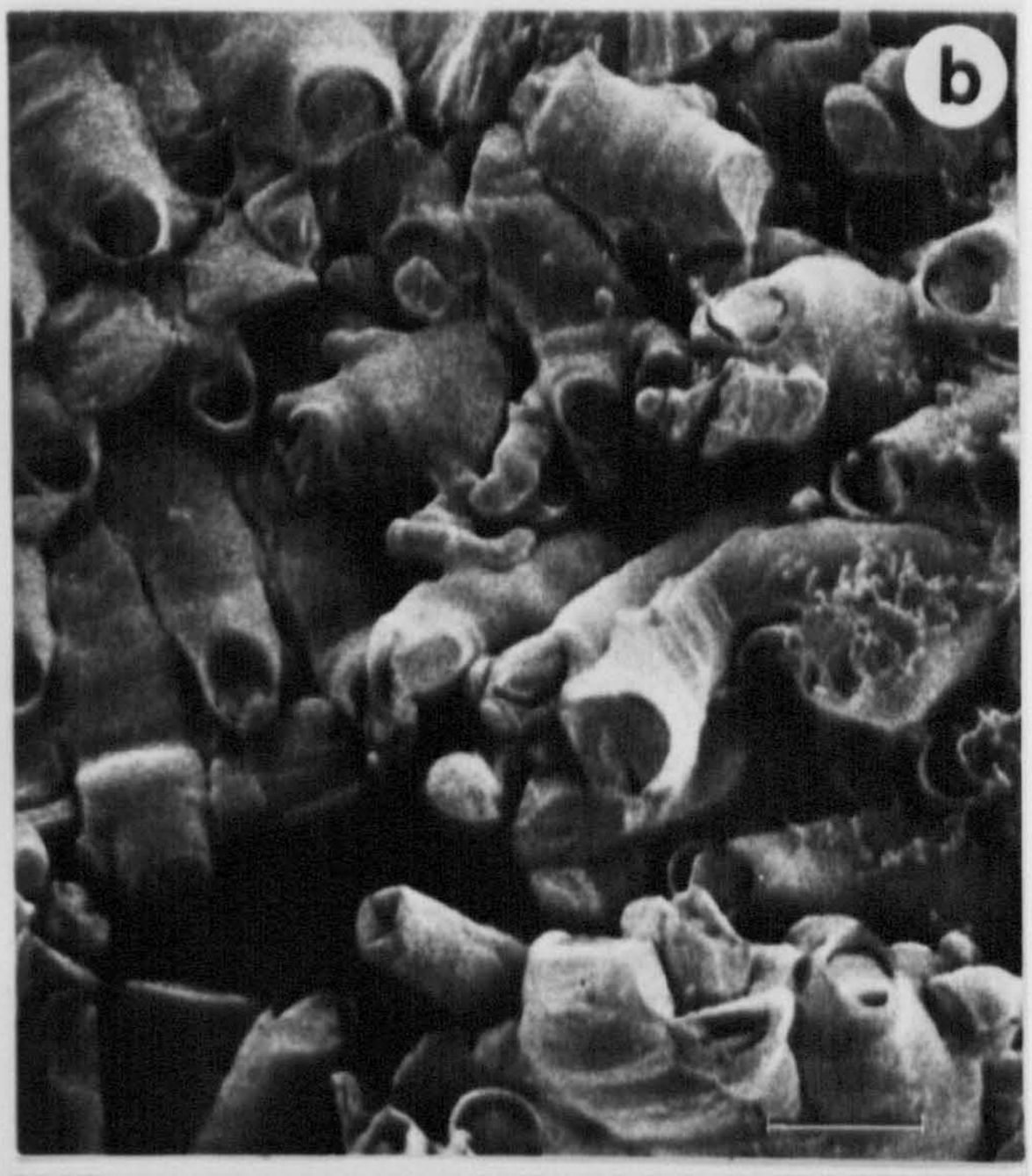
(a) to (d) intra- and inter- colonial contacts between growing edges of Celleporella hyalina.

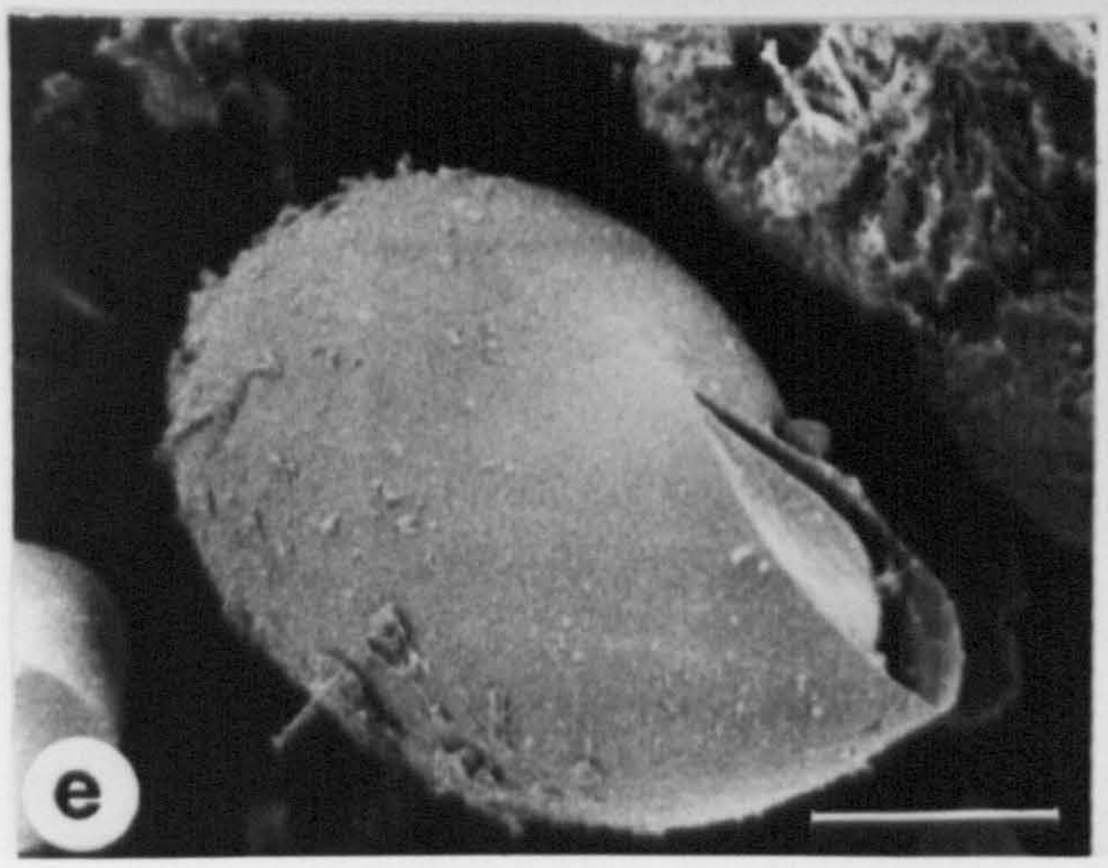
(a) encounter between growing edges of same colony; (b) contacts among 3 colonies showing deformed zooids and long tubular connections; (c) and (d) contacts between two colonies, males and females are seen near to the area of contact, which is indicated by arrows and broken white line; (e) and (f) ancestrula resulting from premature metamorphosis.

Scale bars: (a) 100 μm, (b) to (d) 250 μm, (c) and (f) 50μm.

Plate 2.4







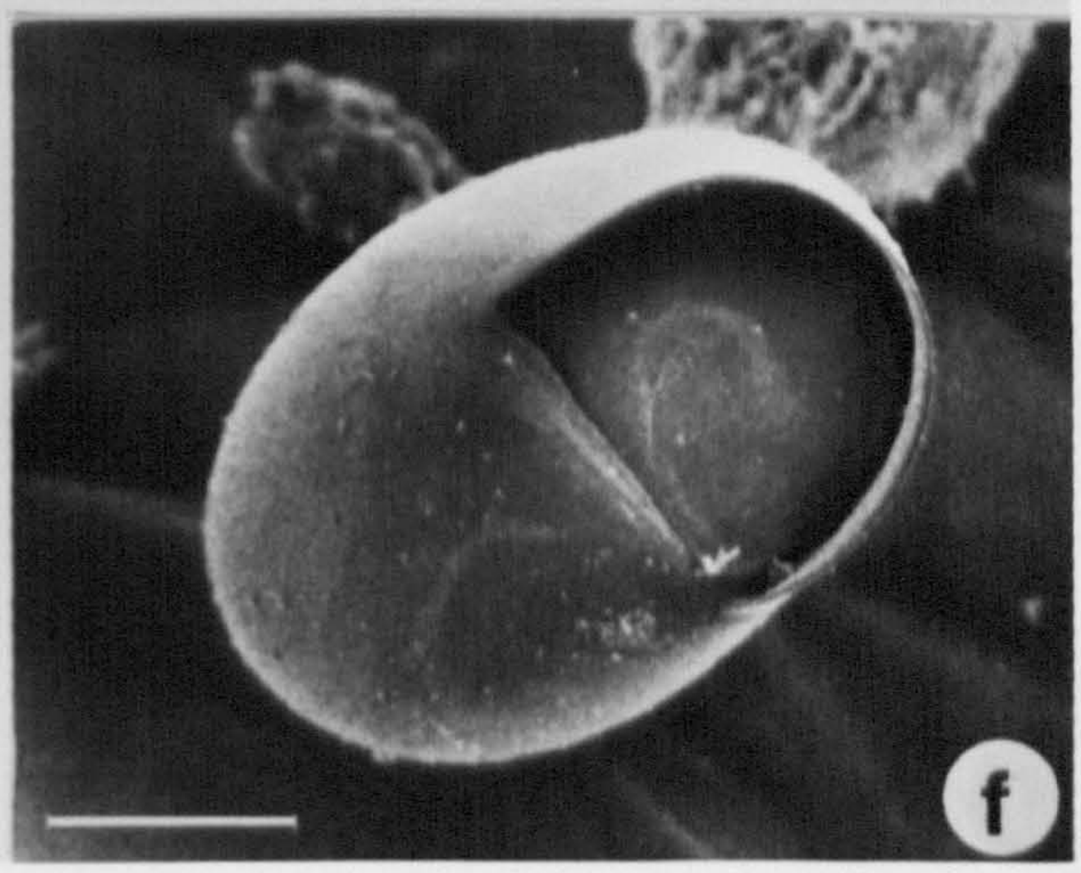
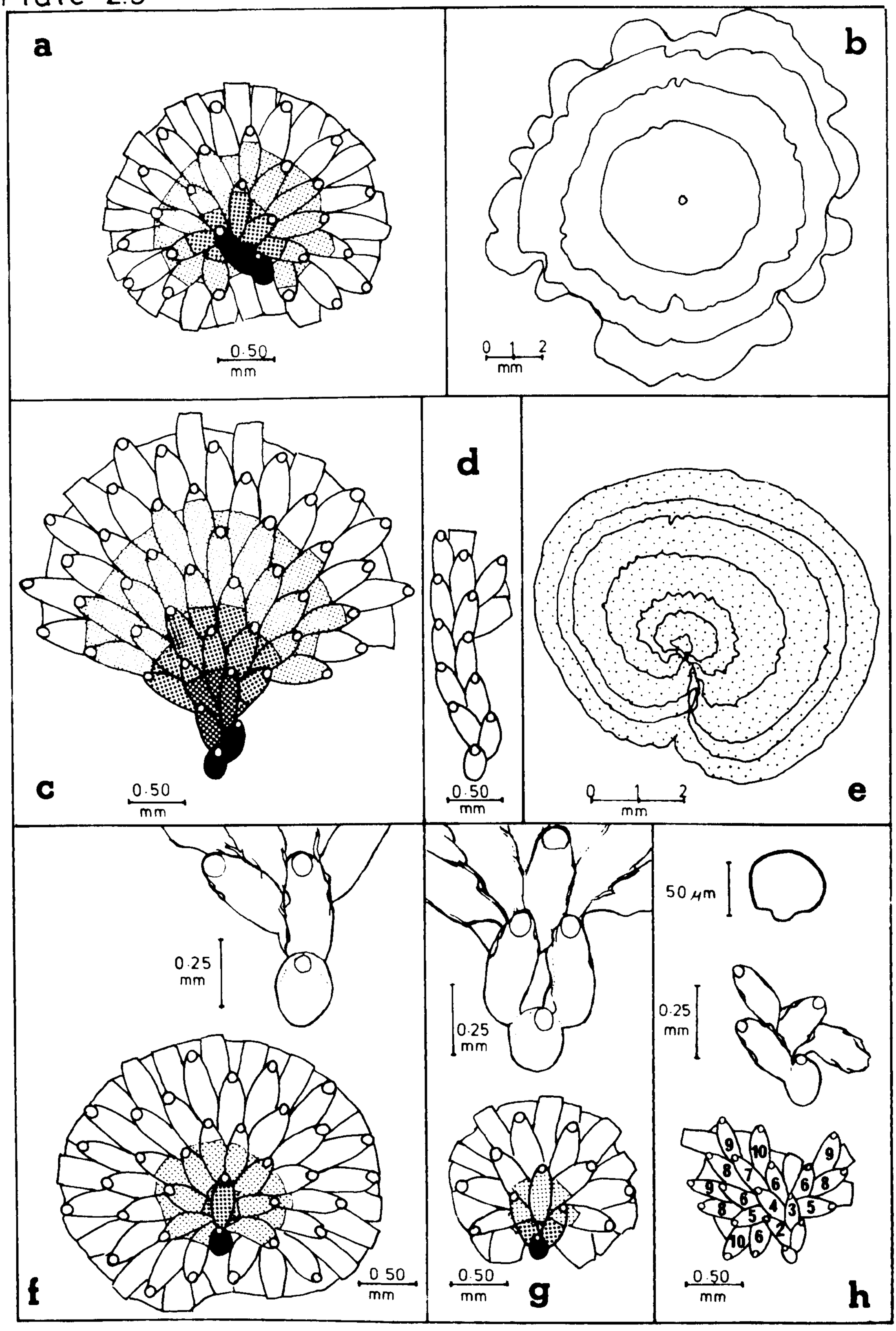


Plate 2.5

Colonial astogeny in Celleporella hyalina.

(a) and (b) pattern found in colonies settled at the end of May 1981; (a) colony size and shape at weekly intervals; (b) the concentric growth pattern, the lines correspond to the perimeter of the colony at 4, 8, 12, 18, and 27 weeks after settlement; (c), (d) and (e) pattern found in colonies settled in autumn; (c) colony shape at intervals of 2 weeks, settlement occurred on 7 October 1980; (d) a colony of unknown age found on 9 August 1980; (e) shape of a colony at 1, 4, 10, 17, 22, 23 and 25 weeks after settlement on 20 October 1980, dots in this figure are orifices of autozooids; (f), (g) and (h) atypical patterns of early astogeny in C. hyalina; (f) the first zooid was produced disto-medially; (g) two disto-lateral zooids produced by the ancestrula. The bottom figures on (f) and (g) show colony shape at weekly intervals starting on 14 of May 1980; (h) a form with the typical uni-lateral budding pattern of C. hyalina but with smaller size. The bottom figure represents a colony found on 6 November 1980 at which time the ancestrula and the first autozooid were already present, the numbers superimposed on autozooids represent weeks after the above date at which the zooids were generated. The middle figure was drawn from a photograph of another colony taken on 14 October 1981. The top figure represents the orifice of an autozooid, drawn from a scanning electron micrograph, of a colony collected on 20 July 1982. The zooid was located 3 autozooids away from the ancestrula, in relatively the same position as autozooid 7 of the bottom figure.

Plate 2.5


a
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c
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e
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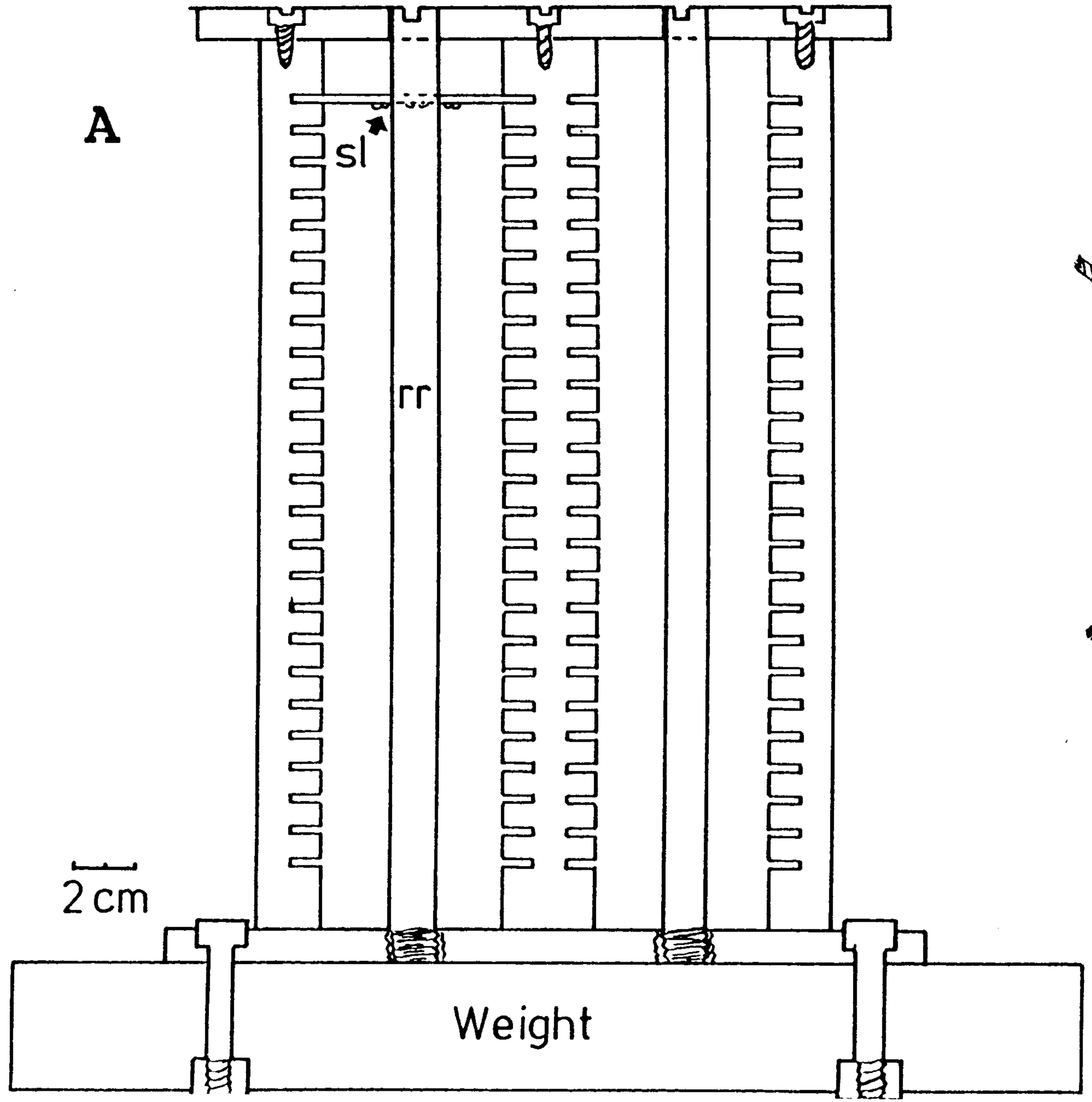
6
9
6
6
8
4
3
5
2
f
0 50
mm
0·50
mm
g
0·50
mm
h

Figure 2.1.

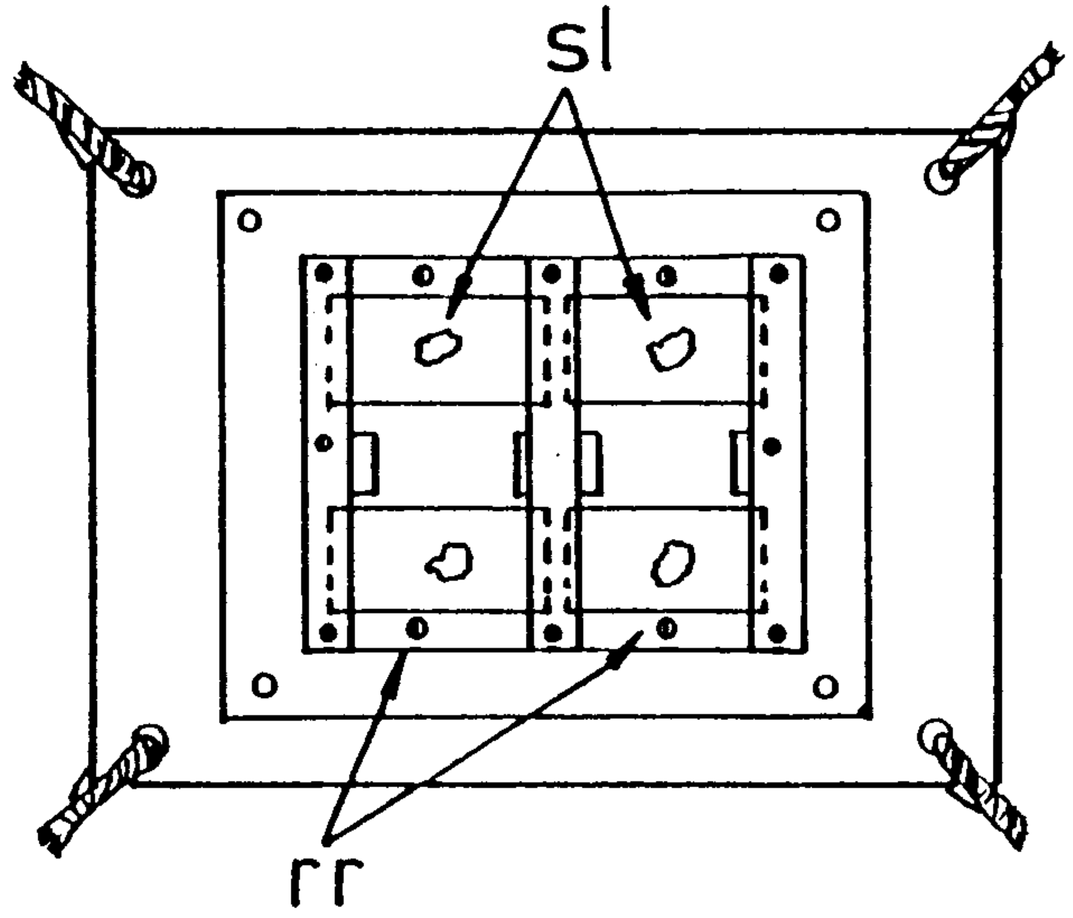
Housing for rearing Celleporella hyalina on glass slides in the field. The housing was made out of perspex and it was attached to a thick piece of slate which acted as a weight and provided 4 points by which the housing was tied to the Pier. The housing holds 100 glass slides (sl) which are kept in position by the retaining rods (rr).

A, side view; B, upper view.

A



B

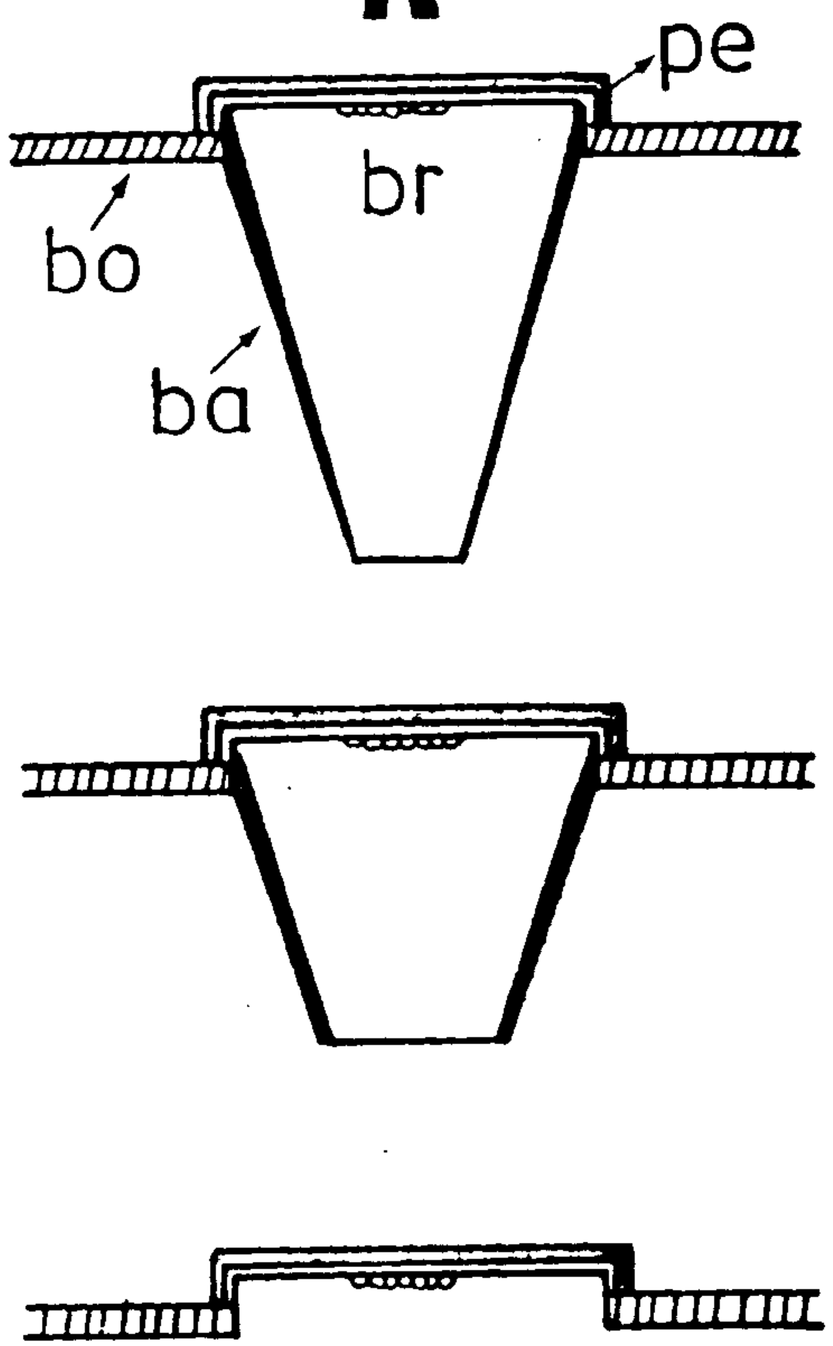


5 cm

Figure 2.2.

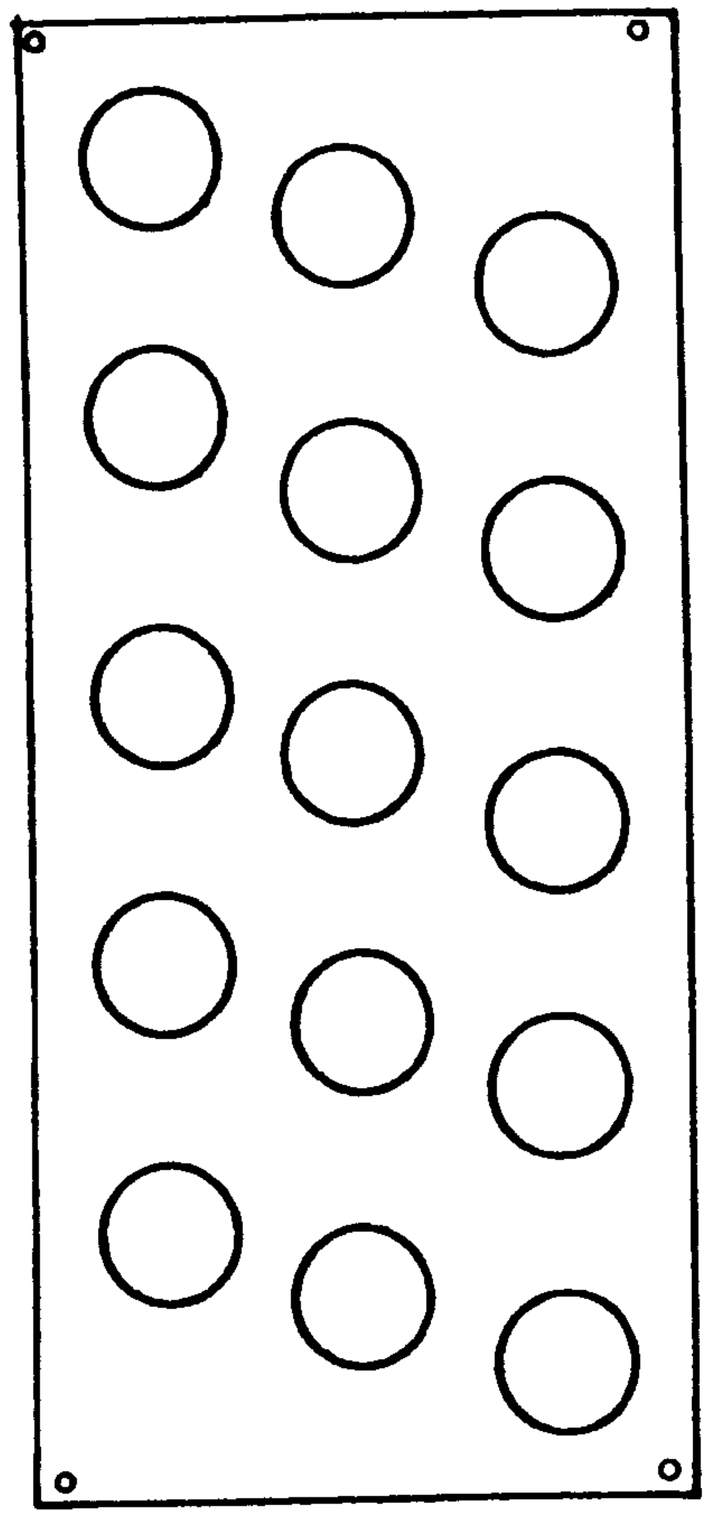
Apparatus for rearing bryozoans on petri dishes in the field. A, side view of petri dishes (pe), with baffles (ba); B, rearing board (bo); C, orientation of the rearing boards when suspended beneath Menai Bridge Pier. br bryozoan colony; ch chain; dwf direction of water flow; po pontoon; wl water level; wp wooden platform.

A



5 cm

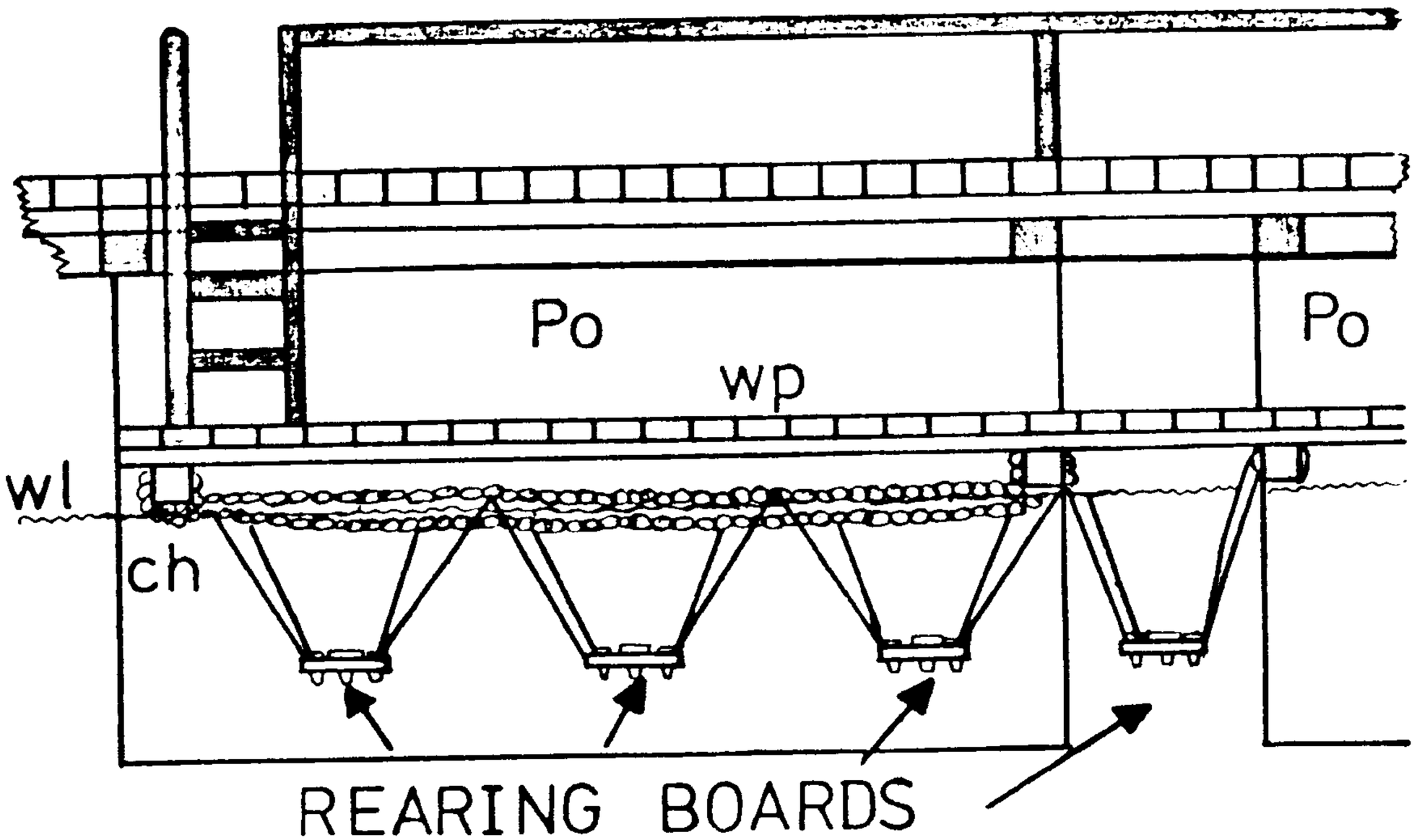
B



10 cm

dwf

C

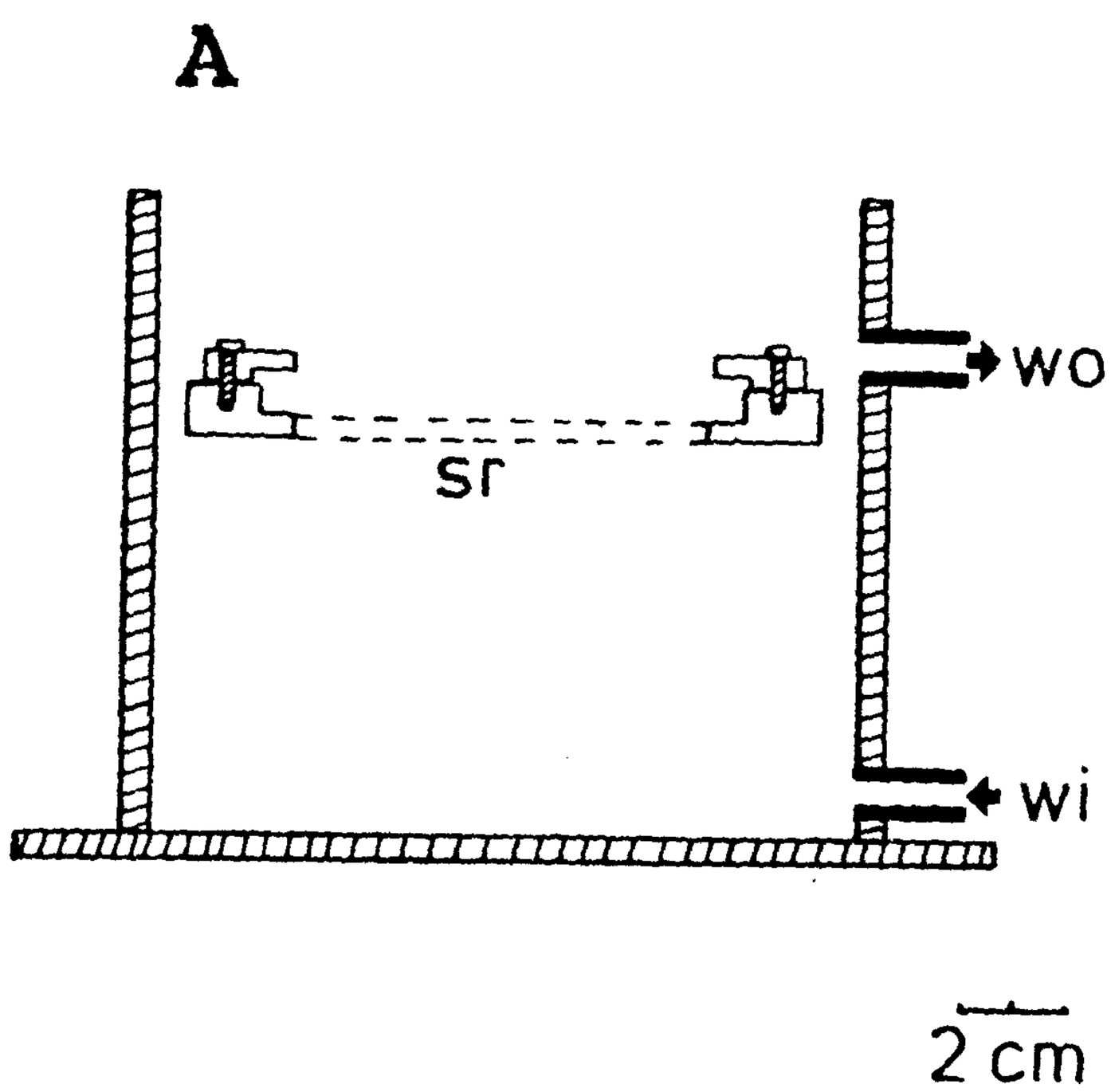


1 m

Figure 2.3

Chamber for observation of bryozoans under the binocular microscope. Colonies grown on petri dishes can be observed from above and from underneath by rotating the supporting ring (sr) which hold the petri dish.

A, side view; B, cross section at the level of the water outlet. Ca, catch; wi water inlet; wo water oulet.


A
wo
sr
wi
2 cm

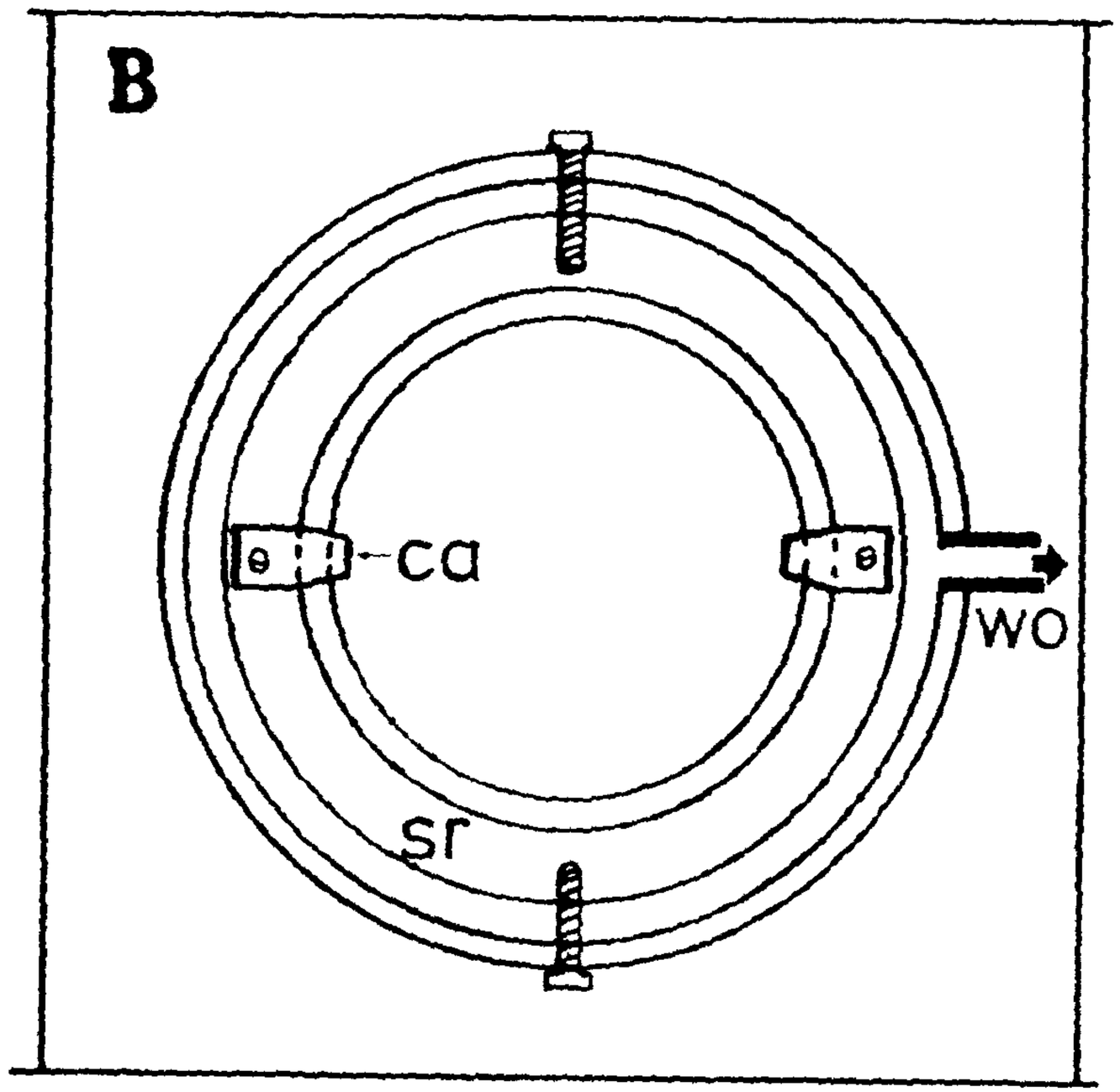

B
ca
wo
sr

Figure 2.4

Temperature of the water measured at the surface at the Menai Bridge Pier.

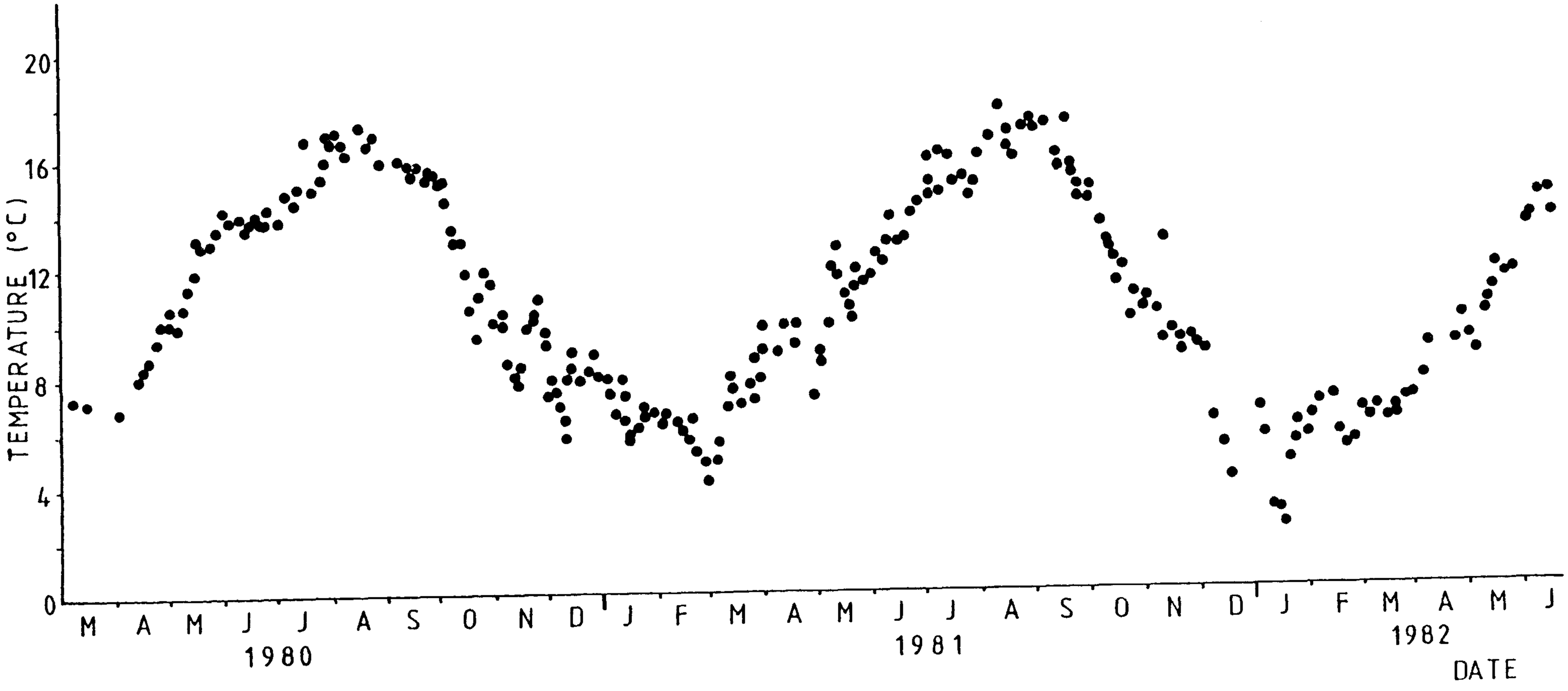

TEMPERATURE (°C)
0
4
8
12
16
20
M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1980
1981
1982
DATE

Figure 2.5.

Distribution of basal (●) and frontally budded (○) autozooids (A, D); incomplete frontal zooids and undifferentiated frontal buds (B, E); females (○) and males (△) (C, F, G), in colonies of different size. All colonies were grown on petri dishes from 15 April to 21 July 1980. A, B and C, mean ±S.E. of 4 colonies grown with long baffles; D, E, F, mean ± S.E. of 2 colonies grown with short baffles; G mean ±S.E. of two transects on a colony grown under unrestricted water flow and touching a neighbouring colony at its edge E_2. Letters on the abscissa are: A ancestrula, E_1 edge of the colony in the direction of production of first zooid, E_2 edge of the colony at 180° to E_1.

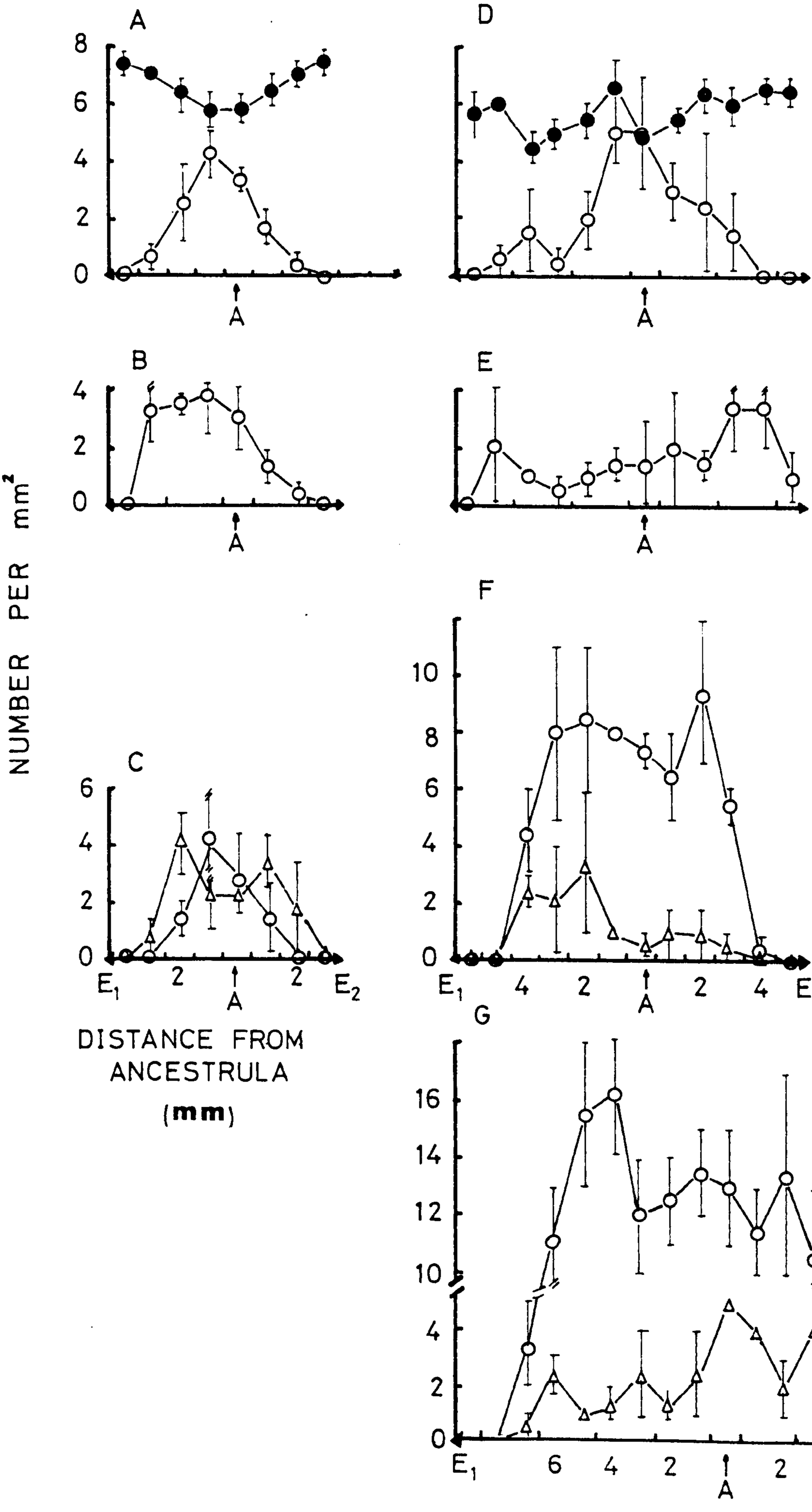

A
B
C
D
E
F
G
NUMBER PER mm²
DISTANCE FROM ANCESTRULA (mm)
A
E1
E2

Figure 2.6

Distribution of basal (●) and frontally budded (○) autozooids (A); incomplete frontal zooids and undifferentiated frontal buds (B); females (○) and males (△) (C); on colonies grown on petri dishes from 15 April to 21 July 1980, under unrestricted water flow conditions. Values given are mean ± S.E. of 5 colonies. Letters on abscissa represent: A ancestrula; E_1 edge of the colony in the direction of the production of the first zooid; E_2 edge of the colony at 180° to E_1.

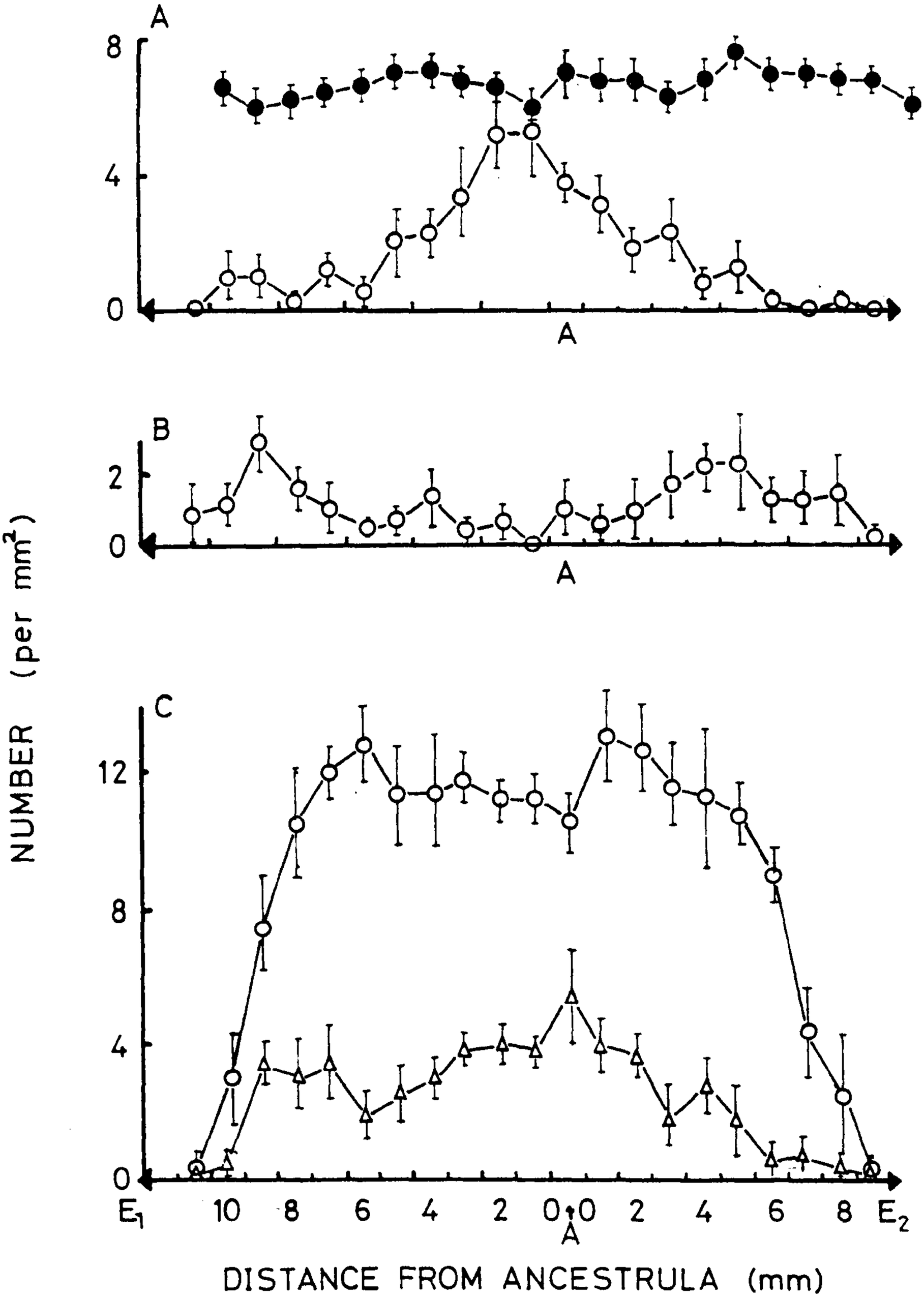

A
8
4
0
A
B
2
0
A
C
12
8
4
0
E1
10
8
6
4
2
0
0
2
4
6
8
E2
A
NUMBER (per mm²)
DISTANCE FROM ANCESTRULA (mm)

Figure 2.7

Size (maximum diameter) of embryos dissected from ovicells of C. hyalina on 4 July 1980. The parental colony had been grown on a petri dish with short baffle from April 1980. N= 37.

Dark area represents embryos in which ciliary movement was observed.

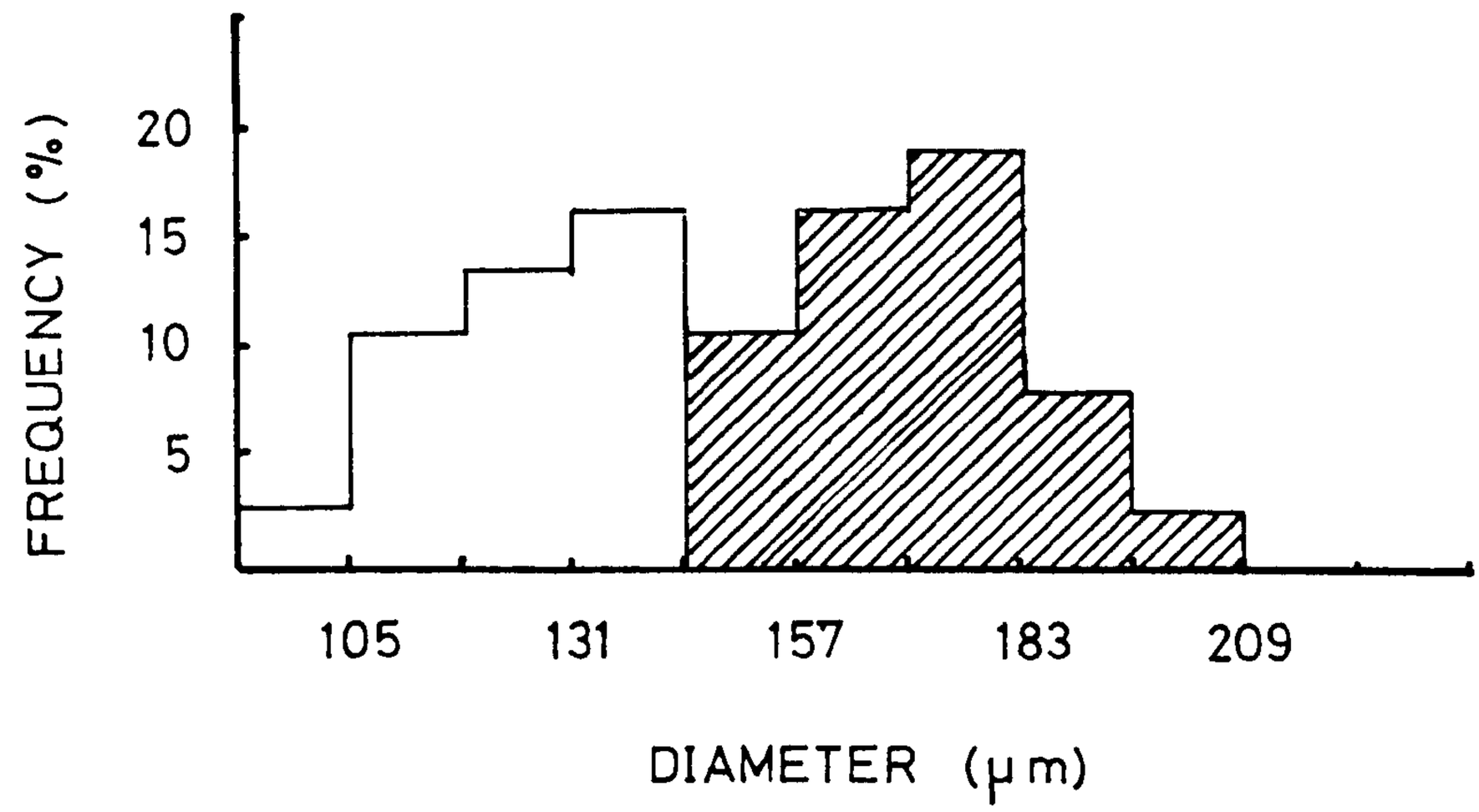
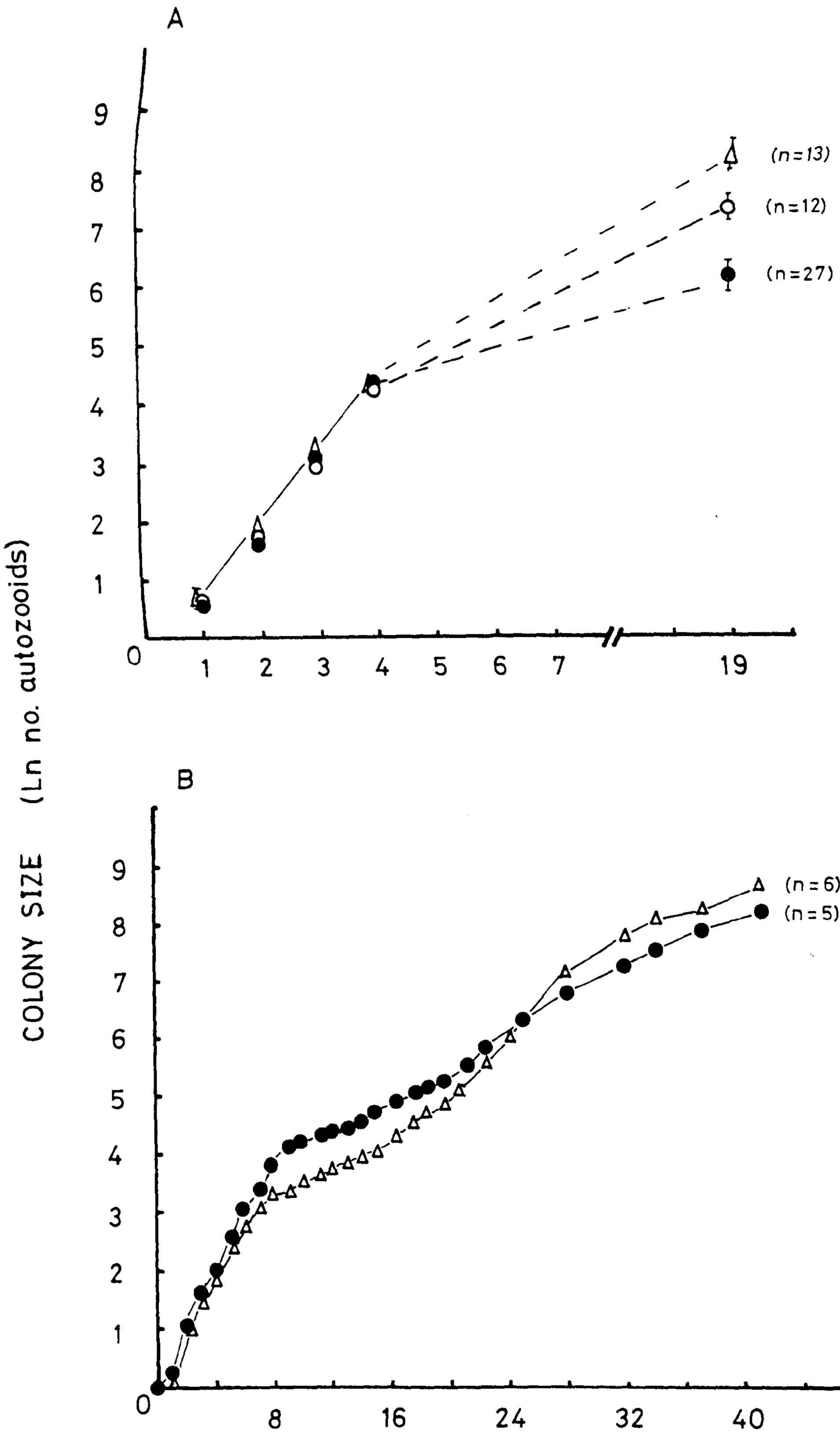

FREQUENCY (%)
20
15
10
5
105
131
157
183
209
DIAMETER (μm)

Figure 2.8

Growth of C. hyalina colonies on petri dishes under unrestricted (Δ), semi-restricted (short baffle, ○) and restricted (long baffle, ●) water flow conditions. A, colonies settled in April; B, colonies settled in October. Only two treatments are shown in B, the other treatment showed intermedium values. Vertical bars are S.E., ommitted in B for clarity.


A
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
19
(n=13)
(n=12)
(n=27)
B
9
8
7
6
5
4
3
2
1
0
8
16
24
32
40
(n = 6)
(n = 5)
COLONY SIZE (Ln no. autozooids)
AGE (weeks)

Chapter 3

The Life History of *Celleporella hyalina* (L.).

II. Experiments on the effect of water flow and neighbouring colonies on growth and sexual reproductive output.

3.1. Introduction

Within Bryozoa there is a great diversity of sexual reproductive patterns (Hyman 1959, Brien 1960, Ryland 1967, 1970, 1974, 1976, Ström 1977), ranging from species that release eggs and spermatozoa into the water to non-placental and placental brooders (Dyrynda and Ryland 1982). In terms of life-span there is a progression from short-lived species which reproduce all year round, to annual and perennial species with well-defined seasons of growth and reproduction (Ryland 1970, Eggleston 1972, Dyrynda and Ryland 1982). In a review of the data then available Ryland (1970) concluded that the commonest annual cycle found in bryozoans in temperate waters was characterized by rapid somatic growth in the early part of the year and a peak of sexual reproduction in late summer. Sexual reproduction at the end of the growing season, however, has only been described for Flustra foliacea (Eggleston 1972). In other species it is not clear whether colonial growth and reproduction occur simultaneously, but the evidence available suggests that this may be so (see below).

Sebens (1979) pointed out that the energy assimilated by the modules must be available at the growing points of the colony if it is to contribute to colonial growth. If the translocation of materials within the colony is limited, growth could be sustained by modules at the perimeter of the colony, while units in the center could put surplus energy into sexual reproduction (Sebens 1979). Bands, or zones, with zooids at different ontogenic stages have been described for colonies of several species of Bryozoa (Starch 1938, Correa 1948, Silen 1966,

Eggleston 1972, Ryland 1979, Ryland and Dyrynda 1982). In all cases there is a band of zooids at the periphery involved in budding, while older areas of the colonies are involved in sexual reproduction. This indicates simultaneous growth and reproduction, but sequential observations on individual colonies, needed to fully understand the process, are largely missing. The present study was undertaken to investigate different aspects of growth and reproduction in Celleporella hyalina (L.).

Colonies of C. hyalina are often found on ephemeral habitats, thus sexual reproduction starts at a small colony size (Chapter 1, Bernstein and Jung 1979), but on fronds of Laminaria saccharina, the colonies reach up to 25 mm diameter (Chapter 1). In the context of the theoretical trade-off between growth and reproduction (General Introduction, Pianka 1976, Calow 1981), it is of interest to know whether these two functions are mutually exlusive or occur simultaneously.

As with all marine bryozoans, C. hyalina is a sedentary species that captures particulate food using water currents created by the ciliated crown of tentacles (Ryland 1970, Winston 1977). If water flow is experimetally altered around the colony, it can be assumed that food supply is also altered. Organisms grown under a shortage of food, or with food of poor quality, may never reach sexual maturity (Giese 1959), or may grow at a low rate and take a long time to reach sexual maturity (Sebens 1979). In situations where food supply is sufficient to sustain growth and sexual reproduction, different response to food levels can be expected, depending on whether the species is able, or unable, to delay sex until fecundity is maximized. (See Discussion).

Experimental manipulation of water flow, presumably correlated with food supply, also allows current ideas (Ghiselin 1969, Clark 1978, Heath 1979, Charnov 1979, 1982) regarding investment in gender (male vs female functions) to be investigated.

3.2 Materials and Methods

The methodology used to obtain larvae for settlement and for rearing in the field has been presented on Section 2.2. The present Section will deal only with the methods used to sample the three types of modules: auto- male and female zooids in colonies of C. hyalina. From settlement until a colony-size of about 100 zooids was reached, a weekly record of total number of zooids was kept. All zooids were drawn under the binocular microscope using a camera lucida and 32 X magnification. Each week, newly formed zooids were added to the drawing with a different colour code. By the time the colonies reached about 50 mm^2, this method was very time consuming. For bigger colonies, the procedure used to calculate the total number of zooids on the colony was as follows: number of basal autozooids was calculated from linear regressions of zooid number on colony area. Number of frontal auto- male and female zooids were estimated by counting all zooids in a drawing of a small area of the colony. Size of this subsample varied from 10% to 50% of the total area with sexual zooids. The area sampled was a triangular sector of the colony, converging from circumference to center. In each colony, the same area was sampled at regular intervals, newly formed zooids being added to the drawing with a different colour code. Ovicells stained with alsian blue were used as reference points. The stain was injected through the opening of the ovicell using a glass micro-pipette mounted on a micro-manipulator. The stain remained visible on the ovicell for 2 to 4 months.

Destructive sampling was used in a few instances. For this,

a very fine needle was used to destroy zooids one by one under the binocular microscope. This procedure was used in 1980 to calibrate the linear regression of area on basal autozooids and in 1982 for the experiments on effect of neighbouring colonies on growth and reproduction. For the latter experiment, only 25% of the area of each colony was sampled. When subsampling was used, the total number of zooids (Nz) of a given type in the colony was calculated as :

$$Nz = \frac{No}{Ao} \times TA$$

where No = number of zooids observed (counted) on Area (Ao), and TA is total area on the colony with that type of zooid.

Numbers of frontal zooids predicted by non-destructive sampling (drawings) were compared in 1980 with those obtained by destructive sampling. Estimates from these two methods did not differ by more than 16%. Areas were estimated from drawings both gravimetrically (1980) and by using a digitizer (1981 - 1982). Reproductive output (RO), was calculated as:

$$RO = \frac{\text{Number of reproductive zooids}}{\text{Number of autozooids}}$$

Colonies were grown under 3 water flow conditions: a) restricted (long baffle), b) semi-restricted (short baffle), and c) unrestricted (without baffle). (See Section 2.2).

3.3. Results

3.3.1. Water flow regime and its effect on colony growth, size at first sexual reproduction and on reproductive output.

3.3.1.1. Preliminary results: spring - summer 1980.

Sixty-seven colonies of Celleporella hyalina were grown under 3 water flow conditions between March and August 1980 (Table 3.1). Although colonies in all treatments initially grew at an equal rate, (instantaneous rate of increase per zooid per day observed for 7 weeks from 26 of March was 0.125), colonies under conditions of higher water flow reached a bigger size, and produced more sexual zooids than colonies under conditions of lower water flow (Table 3.1, Fig 3.1.A). Furthermore, reproductive output (RO) was higher in higher water flow than in lower water flow (Fig. 3.1.B). In all 3 treatments, RO reached a plateau after the colonies attained a certain size (Fig. 3.1.B). The mean values of RO for colonies of asymptotic size were in the ratio of 1.0: 2.0: 3.6 (Table 3.1 last column) when grown in restricted to unrestricted water flow respectively. For use in future experiments, the feasibility of estimating total number of autozooids, females and males through non-destructive subsampling was investigated. Linear regression analyses provided a good estimate of the number of basal autozooids as a function of the area of the colony (Fig. 3.2). Subsamples of areas of the colony gave a good estimate of number of reproductive zooids (Table 3.2).

3.3.1.2. The dynamics of growth and sexual reproduction of individually identified colonies.

Colonies recruited in October 1980 grew exponentially for

the first 50 days (Fig. 3.3., 3.4). The growth rate declined for the next 2 months (mid December to mid February) but then regained a higher level (Fig. 3.3, 3.4).

Two colonies grown under restricted water flow conditions (Fig. 3.3) were damaged when small and thereafter remained smaller than the undamaged colonies. The initial growth rate of undamaged colonies in restricted water flow conditions was higher than that of colonies grown in unrestricted water flow conditions, the instantaneous rate of growth per zooid per day being 0.0693 and 0.0529 respectively (Fig. 3.4 and 3.4).

In the period of faster growth in the following spring (March to May 1981), colonies in unrestricted water flow grew at a lower rate than colonies in unrestricted water flow conditions. This was so for autozooids as well as for the total number of zooids (Fig. 3.3.A, B and 3.4.A, B). The instantaneous rate of growth per zooid per day observed during the spring of 1981 was lower than the values observed for the same colonies when they were smaller (autumn 1980) (Fig. 3.3 and 3.4).

Sexual reproduction, in colonies settled on 20 October 1980, started at different ages in different water flow conditions but approximate at the same colony size (Table 3.3). Colonies settled on glass slides on 20 September 1981 started sexual reproduction (male production) on 20 October 1981 at a mean colony size of 57 autozooids (SD 14.175, N= 28). The smallest colony of C. hyalina observed bearing male zooids had only 21 feeding zooids (summer 1981).

The total number of reproductive zooids was positively correlated with the number of autozooids in the colony (Fig. 3.5),

the relationship being linear beyond a colony size of 500 - 700 autozooids. The slope of the regression for colonies grown in restricted water flow conditions was significantly lower than that of colonies grown in unrestricted water flow conditions (Fig. 3.5).

Reproductive output (RO) increased until the colony reached a size of 1000 to 2000 autozooids (Fig. 3.6). Thereafter the values of RO tended to remain constant (Fig. 3.6 shows an exception). Colonies grown under restricted water conditions achieved a lower asymptotic RO than those grown under unrestricted water flow conditions (Fig. 3.6).

The total number of active reproductive zooids (male with sperm + female with eggs and/or larva) was also higher in colonies grown under unrestricted than under restricted water flow conditions (Fig. 3.7.A, B). Colonies in both treatments showed a peak of sexual activity during June 1981, the number of active sexual zooids decreasing thereafter (Fig. 3.7.B).

3.3.1.3. Effect of translocation between treatments.

Thirty-seven colonies were grown from May to September 1981 under two water flow regimes (Table 3.4). At this later date, colony size, number of reproductive zooids and reproductive output were significantly different between treatments (Table 3.4). On 25th September 1981 the colonies in each treatment were divided into two groups. One of these groups, control, was kept under the same water flow conditions as before 25th of September. The second group, experimental, was transferred to the other water flow regime. Growth of the colonies and production of sexual

zooids were followed after translocation for 240 and 100 days respectively (Fig. 3.8, 3.9, Table 3.5). Colonies translocated to, or kept under, unrestricted water flow conditions grew considerably faster than colonies translocated to or kept under, restricted water flow conditions (Fig. 3.8, Table 3.5). After 100 days the increments in area, in number of autozooids and in number of reproductive zooids, were significantly different between translocated colonies and those kept with the same treatment (Table 3.5). Reproductive output was also different between experimental and control colonies previously grown in restricted water flow, but was not different in colonies previously grown in the unrestricted water flow regime (Table 3.5).

The number of active sexual zooids, compared to the value at translocation, was higher in colonies kept in, or translocated to, unrestricted water flow conditions, (Fig. 3.9), than in colonies kept in, or translocated to, restricted water flow conditions. The number of active sexual zooids increased above the initial value only in colonies translocated from restricted to unrestricted water flow conditions (Fig. 3.9).

3.3.1.4. A summary of the effect of water flow conditions.

The 3 sets of experiments already presented in section 3.3.3.1. can be summarized as follows: a) Given time, colonies grown under higher water flow conditions reach bigger sizes than colonies grown under lower water flow conditions. b) As colony size increases, the number of reproductive zooids increases. c) Reproductive output increases asymptotically with colony size.

Reproductive output, calculated on the last observation in each of the 3 sets of experiments, was always lower in colonies

grown in lower water flow than in higher water flow conditions (Fig. 3.10). Both treatment and size had a significant effect on reproductive output (Table 3.6).

3.3.2. Effect of number of neighbouring colonies on size and reproductive output.

The effect of neighbouring colonies on growth and sexual reproduction was investigated during spring-summer 1982 on 43 colonies of C. hyalina (Table 3.7). The colony size achieved after 4 months, the number of basal autozooids and the number of sexual zooids were significantly lower in colonies grown at higher than at lower densities (Table 3.7). Care was taken to stop the experiment before neighbouring colonies came into contact.

Reproductive output (RO) was found not to differ within treatments (P= 0.097). However, if increasing the number of neighbours has a similar effect on food supply to reducing the water flow, it can be assumed that RO would be lower at higher than at lower densities, in which case a one-tail t test would be appropiate. Such a test showed significant differences in reproductive output between treatments at the 5% level (Table 3.7). There was no significant difference, however, in sex ratio and in number of frontally budded autozooids between treatments.

3.3.3. Investment in autozooids vs investment in sexual zooids.

Colonies of C. hyalina from April to September grew and reproduced sexually at a higher rate than during the rest of the year (Fig. 3.11). During the former period, production of autozooids and sexual zooids occurred simultaneously, both functions being positively correlated (Fig. 3.11.A). If

production of autozooids is regarded as growth. growth and sexual reproduction occurred simultaneously.

3.3.4. Sex Ratio.

Sex ratios, calculated as females/males, were very variable (Fig. 3.12, 3.13). Male zooids were produced first in all colonies of C. hyalina observed, female zooids being produced as colony size increased. The sex ratio therefore increased as a function of colony size (Fig. 3.12, 3.13.A). Some colonies, however, produced about 16 males per females during the entire period observed (Fig. 3.13). Mean sex ratio increased as a function of colony size until the colonies reached a size of about 1000 autozooids and varied between 2 and 4 thereafter (Fig. 3.12). A wider range of sex ratios, however, were recorded among individually identified colonies (Fig. 3.13).

An analysis of variance carried out on colonies bigger than 900 autozooids showed that water flow significantly affected the sex ratio. There was also a significant interaction between colony size and water flow, but size on its own did not have a significant influence (Table 3.8).

3.3.5. Zooidal longevity.

Reproductive output (RO), as measured in the previous sections, does not take into account zooidal life-span. But an accurate estimate of number of active zooids in the colony is difficult to achieve. This is particularly true regarding autozooids that undergo cycles of degeneration and regeneration.

Observations carried out on the first zooids of colonies recruited on October 1980 showed that autozooids feed for 3 to 4 weeks, degeneration and regeneration taking place within 1 to 2 weeks.

During the 3 months of observations, zooids were observed to undergo 3 cycles of degeneration and regeneration. The maximum number of cycles of degeneration-regeneration that an autozooid is able to survive is unknown. The centres of the colonies, however, were observed to be inactive after 3 - 4 months. This is in agreement with the observed longevity of reproductive zooids (Fig. 3.14, 3.15).

In a colony observed for 180 days after 1 October 1980, male zooids had a life-span of 2 to 3 months (Fig. 3.14). Female zooids were active for 3 to 4 months, 2 to 3 larvae being produced for each female during this period (Fig. 3.15). Eggs were observed in the body of females at the moment the ovicells were empty or an old larva was about to leave the ovicell (Fig. 3.15). Sexual reproduction was at minimum over winter, but new male and female zooids were formed from March onwards (Fig. 3.14, 3.15). Reproductive zooids formed in the previous reproductive season were, in general, not used in the second reproductive season. Active autozooids were always observed near to active sexual zooids.

3.4 Discussion

Experimental manipulations of water flow around colonies of Celleporella hyalina affected growth rate, reproductive output, and sex ratio. A similar response to that of restricting water flow was induced by increasing the number of neighbouring colonies, suggesting that food may have been the main causal factor. In all conditions of water flow presented, colonies of C. hyalina had enough food for growth and sexual reproduction.

When sexual reproduction has a negative effect on somatic growth (see Calow 1981, and General Introduction), sexual maturity should be delayed until the size that maximizes fecundity is reached. This principle can be expected to apply to the following types of organisms: (1) those living in relatively stable environments and with low mortality rates so that the probability of reaching the optimum size for reproduction is high; (2) those living in temporary but predictable environments, and which are able to transform energy reserves into gametes in a short time if adult mortality is imminent. Delayed maturity is not expected if early reproduction is at a premium, as in expanding populations, or in situations where later recruitment is negatively correlated with survival of the juveniles.

Celleporella hyalina started sexual reproduction at a small colony size, 21 - 113 autozooids. There was no difference in the size at first reproduction in different water flow regimes, suggesting that reproduction was not delayed in favour of achieving a bigger colony size.

Celleporella hyalina cannot be expected to delay sex for the following reasons: (1) the commonest substratum used by C. hyalina

is ephemeral, lasting for only a few months (Chapter 1); (2) although longevity of the substratum varied seasonally in a predictable way (Chapter 1), it is very likely that C. hyalina is unable to detect such a cycle, therefore mortality is unpredictable; (3) larvae of C. hyalina need a period of 3 to 4 weeks in the ovicells to be viable; (4) number of sexual zooids increases linearly with colony size, therefore there is not a significant advantage in delaying sex (there would be an advantage if fecundity were an exponential function of body size, see Calow (1981) for this argument); (5) sexual reproduction seems not to supress growth to any significant extent (but see below).

From April to September autozooids and sexual zooids were produced simultaneously at a maximum rate, suggesting that current sexual reproduction is not negatively affecting current growth. This is probably achieved through partitioning of functions, as suggested by Sebens (1979). Zooids at the perimeter of the colony could be putting energy into budding while zooids at the center of the colony put energy into sexual reproduction. If in encrusting colonies growth is sustained mainly by the zooids at the perimeter of the colony, it can be expected that the growth rate decreases as colony size increases. Colonies of C. hyalina grew at a higher rate when smaller. Bigger colonies, however, were also putting energy into sexual reproduction and the decreased growth rate, therefore, could be attributable to diversion of energy from growth to reproduction. Temperature was also important as shown by the decrease in growth rate during thecolder months of the year. The observed differences in growth rate between small and large colonies of C. hyalina cannot be attributed to temperature,

however, since during March-April small colonies grew twice as fast as bigger colonies, (instantaneous rate of growth per zooid per day 0.125 and 0.0506 respectively, Sections 3.3.1.1. and 3.3.1.2.).

Evidence in the literature suggests that growth and reproduction occur simultaneously also in other species of Bryozoa (see references in the Introduction and review in Ryland 1979 under the title of Age-correlated zones). Information on another 3 species has been published recently: zooids of Epistomia bursaria do not regenerate after degeneration, therefore the zooids must provide energy for budding and sexual reproduction before death. Zooidal life-span is not known, but is shorter than that of the colony (Dyrynda 1981b, Dyrynda and King 1982). Zooids of Bugula flabellata and of Chartella papyracea are recycled. In B. flabellata, zooids in the first generation, (after first degeneration and near to the growing tips), provide energy for colonial growth, spermatogenesis, ovogenesis and for early embryogenesis (Dyrynda and Ryland 1982). In C. papyracea, first-generation zooids provide energy for budding, while after regeneration zooids put energy into reproduction. During the growing season, however, mainly androzooids are formed (Dyrynda and Ryland 1982). Simultaneous growth and reproduction can also be expected in bryozoans that are usually associated with ephemeral habitats. Such bryozoans are known to start sexual reproduction at a small colony size (e.g. Conopeum tenuissimum, Dudley 1973). Information also exists on simultaneous growth and reproduction in Entoprocta (Mukai and Makioka 1980).

It has been assumed often in the literature that unconstrained bryozoan colonies grow exponentially (e.g. Bushnell 1966, Menon 1972, Dudley 1973. Thorpe 1979, review in Ryland 1976). The only data that support the idea of exponential growth throughout the life of the colony are those of Stebbing (1971b) for Flustra foliacea. Other published data (e.g. Hayward and Ryland 1975, Winston 1977) show that growth is exponential, (linear relationship between log of colony area and time), for only short periods of time. Taking into consideration the geometry of the colonies, Kaufman (1973) argued that encrusting bryozoans show Gompertzian growth (growth becomes asymptotic after a phase of exponential growth). Wass and Vial (1978) have published data supporting the idea that the growth of encrusting bryozoans is a linear function of the square root of colonial area. The area of a circular colony is equal to the perimeter times a factor of 0.5 r, consistent with the idea of growth as a linear function of colony perimeter. Whether this is the result of energy being put into growth only by the zooids near the periphery, or just a consequence of colonial geometry, remains to be determined.

Reproductive output, as measured in the present study, is likely to be an adequate index of reproductive effort (Pianka 1976), since each autozooid can be regarded as a unit providing a certain amount of energy to the colony. Each reproductive zooid on the other hand can be regarded as costing a fixed amount of energy to the colony. Certainly a more accurate index of reproductive effort would be one that takes into account number of active zooids of each type at a given time. But this would be

very difficult to assess, especially after the colony has reached a large size. The fact that active autozooids were always observed close to active reproductive zooids suggests that the index of reproductive effort used in the present study is a good estimate of allocation of resources to sexual vs somatic tissues.

Translocation experiments showed that C. hyalina could be induced to increase reproductive output only when transferred from restricted to unrestricted water flow conditions. Such translocation is equivalent to increasing the energy input to the colony. Stebbing (1980) experimentally induced an increase in reproductive effort in Campanularia flexuosa. Several other examples of a similar response have been reviewed in Hughes and Cancino (in press). It has been suggested (op. cit.) that colonial organisms may respond differently to constraints, depending on whether the organism is likely to survive the deletereous consequences, diverting all available energy to reproduction if death is imminent, or stopping reproduction if conditions are likely to improve (reduced food supply fits into this last category). Diversion of energy is possible only if reserves are available. If the organism is using all available energy in growth and reproduction, as C. hyalina probably does, an increased reproductive effort could be achieved reducing growth rate in favour of sexual reproduction. Colonies of C. hyalina transferred from unrestricted to restricted water flow conditions grew slower than control colonies, but showed no significant differences in reproductive output. If restricted water flow reduces food supply, however, colonies in this treatment must have

increased their relative investment in reproduction for their reproductive output to equal that of the controls. More experimental work is needed to confirm this suggestion.

The lower reproductive output observed in colonies grown under restricted water flow conditions can be explained in terms of energy requirements for the production and maintenance of reproductive zooids. In theory, if sexual zooids cost a fixed amount of energy, fewer of these units can be supported by an autozooid in situations of limited food supply (restricted water flow). On only one occasion during this study (spring-summer 1980) was it found that the reproductive output of colonies grown under 3 water flow regimes were in the proportion of 1.0:2.0:3.6, values that agree almost exactly with the relative amounts of water flow in the experimental treatments, as measured by the loss in weight of gypsum hemispheres (Appendix 2.3).

In the present study the effect of neighbouring colonies was similar to that of decreasing water flow, and this result more generally may be applicable to fauna underneath boulders or in crevices. Buss (1979b) showed that there can be interference between feeding currents of adjacent colonies of Bryozoa. The results of the present study showed that interference is present even when colonies are not in direct contact. Indeed, any organism reducing water flow in the neighbourhood of a filter feeder may reduce the fitness of the latter.

Simultaneous hermaphroditism, both in animals and plants, is assumed to confer the possibility of altering allocation of resources to male and female functions according to environmental and metabolic factors (Ghiselin 1969, Heath 1977,1979, Maynard

Smith 1978, Charnov 1979, 1980, 1982, Primack and Lloyd 1980, Lovett and Cavers 1982). It is frequently assumed that female functions are limited by the availability of resources (Charnov 1979, 1982) or of space to accommodate eggs or larvae, (Heath 1977, 1979, Clark 1978), proportional development of the female function usually increases with increasing body size, (see Lovett and Cavers 1982 for plants), which is attributable to an increase in the ability to gather resources, (but see Maynard Smith (1978) for an argument that male and female function are equally expensive). C. hyalina always produces males first and females later. Similarly Chartella papyracea produces mainly androzooids at the beginning of the growing season, diverting energy to production of gynozooids later (Dyrynda and Ryland 1982). In the entoproct, Barentsia discreta, male zooids outnumbered female zooids in the early part of the breeding season and along the actively growing stolons later in the season (Mukai and Makioka 1980).

The experimental manipulations carried out during the present study showed that: (1) Most colonies of C. hyalina produce more female than male zooids as colony size increased; (2) In most individual colonies the sex ratio varied throughout the period studied. Wider oscillations in sex ratio were observed in newly formed sexual zooids, indicating a constant adjustment of investment into gender. (3) Sex ratio was significantly affected by water flow conditions, more females being produced in unrestricted than in restricted water flow conditions. This gave support to the idea of higher investment into femaleness as more resources become available for reproduction. (4) There was no

significant difference in sex ratio between colonies grown in different densities. Colonies in high density, however, produced slightly more females per male than colonies in low density, suggesting that presence of neighbours could have a different effect on sex ratio than that of water flow. More investigation is needed regarding this point. (5) Some colonies put most energy into males even though they reached sizes as big as colonies producing mainly females. Colonies of this type were found in all water flow conditions, suggesting that some colonies do not alter their gender. More investigation is needed to elucidate the mechanism controlling such behaviour.

Table 3.1 Area and number of zooids in colonies of C. hyalina grown under 3 water flow regimes from March to August 1980. Results were obtained with destructive sampling of colonies 3 to 5 months old. The last column shows the mean reproductive output (Reproductive zooids/autozooids of the bigger colonies in each treatment).

		Area (mm^2)	No. Autozooids Basal	No. Autozooids Frontal	No. Males	No. Females	Reproductive/Autozooids All	Reproductive/Autozooids Bigger
TREATMENT UNRESTRICTED:								n=12
n = 15	$\bar{x}$	190.346	1120.467	99.600	390.667	1504.00	1.4164	1.628
	s	88.403	529.484	59.568	258.429	917.988	0.5100	0.2645
SEMI-RESTRICTED								n=12
n = 24	$\bar{x}$	71.858	424.917	56.458	274.625	125.417	0.470	0.897
	s	78.194	393.318	108.954	404.300	168.566	0.465	0.233
RESTRICTED								n=19
n = 28	$\bar{x}$	49.593	302.259	44.185	67.333	84.667	0.368	0.447
	s	36.781	202.786	62.299	78.802	76.459	0.236	0.214

Table 3.2. Number of reproductive zooids in 3 colonies of C. hyalina; determined by (A) direct counting (destructive sampling), and (B) from drawings of sections of the colonies.

	A No. counted	B No. predicted	% error
Female zooids		2336	+ 8.18
	2145	2321	+ 8.22
		3445	+ 5.72
	3248	3346	+ 3.08
		2632	+ 16.32
	2262	2597	+ 14.81
		876	- 1.46
	889	922	+ 3.71
Male zooids		656	+ 5.81
	620	651	+ 5.00
		537	- 4.62
	563	645	+ 14.56

Table 3.3 Age and size at first reproduction of colonies of C. hyalina grown under 3 conditions of water flow starting the 20th October 1980. Values given are means ± confidence intervals, α = 0.005.

		WATER FLOW		
		Restricted	Semi-restricted	Unrestricted
		n= 5	n= 4	n= 6
Appearance of first males	Age (days)	91.0 ± 31.094	139.5 ± 65.200	125.667 ± 16.110
	Number of autozooids	99.2 ± 71.085	84.0 ± 59.020	113.330 ± 18.01
Appearance of first females	Age (days)	138.6 ± 71.085	153.25 ± 4.50	157.75 ± 15.87
	Number of autozooids	246.4 ± 341.49	251.75 ± 119.44	422.00 ± 391.85

Table 3.4 Size and reproductive activities of colonies grown within conical funnels restricting water-flow, compared with colonies grown under conditions of unrestricted water-flow. Colonies settled 27th May 1981, grown until 25th Sept. 1981.

		Area (mm^2)	No. Autozooids	No. Reproductive zooids	Proportion of active ♂+♀	Reprod. / Autozooids	No. colonies observed
Restricted	$\bar{x}$	148.15	868.76	707.28	0.284	0.807	25
water flow	s	58.03	353.28	338.32	0.206	0.250	
Unrestricted	$\bar{x}$	699.03	3912.667	5053.33	0.227	1.223	12
water flow	s	187.81	1180.87	1766.01	0.127	0.235	
p (t-test)		<0.001	<0.001	<0.001	N.S.	<0.001	

Table 3.5 Growth and reproductive activities of colonies (specified in Table 3.4), observed for 100 days from 25 September 1981. Some were translocated to or from funnels, others left in or out of funnels as controls.

Treatment	% Increase in Area	% Increase in No. Autozooids	% Increase in No. Reprod. zooids	% Reproductive zooids / % Auto zooids	No. colonies observed
1. From restricted to unrestricted water-flow	133.830	131.384	15.989	0.150	9
2. Control (restricted water-flow)	33.198	31.805	2.531	0.104	8
p(Mann-Whitney test	<0.01	<0.01	<0.01	<0.05	
3. From unrestricted to restricted water-flow	13.760	13.304	2.524	0.31	5
4. Control (unrestricted water-flow)	60,786	58,280	19,608	0,320	5
p(Mann-Whitney test)	<0,01	<0,01	=0,05	N,S	

Table 3.6 Two-way analysis of variance on reproductive output partitioned according to treatment and colony size.

A. REPRODUCTIVE OUTPUT: mean and (standard deviation).

	Colony Size (number of autozooids)		
	900 to 1600	1601 to 3290	3291 to 5700
Restricted Waterflow	n= 17 0.90 (0.24)	n= 10 1.29 (0.16)	n= 4 1.48 (0.14)
Unrestricted Waterflow	n= 4 1.24 (0.17)	n= 11 1.73 (0.43)	n= 11 1.93 (0.36)

B. FINAL ANOVA

SOURCE	DF	SS	MS	F	Prob.
Cells	5	8.81			
Treatment Eliminating Size	1	1.94	1.94	22.51	<0.0001
Size Eliminating Treatment	2	3.03	1.52	17.61	<0.0001
Treatment by Size	2	0.02	0.01	0.14	0.8714
Within	51	4.39	0.09		
TOTAL	56				

Table 3.7 Effect of number of neighbouring colonies on size and number of auto- and reproductive zooids in C. hyalina. Colonies were grown for 4 months, (settlement on 29 May 1982), on petri-dishes under restricted water flow conditions and at two densities: High = 7 - 8 colonies per petri., Low = 2 colonies per petri. Values given are Means (SD) as observed on 29 September 1982.

		Number of Autozooids				Reproductive	Sexual Ratio
	Area (mm^2)	Basal	Frontal	Males	Females	Autozooids	(♂♂ / ♀♀)
High density	228.549	1512.478	83.565	525.435	1073.739	1.006	0.530
N = 23	(66.604)	(387.193)	(83.228)	(286.969)	(440.765)	(0.293)	(0.263)
Low density	367.469	2283.70	89.850	962.600	1707.650	1.162	0.696
N = 20	(75.585)	(478.609)	(54.269)	(456.7131)	(482.134)	(0.304)	(0.664)
"t-test"							
t	6.408	5.839	0.288	3.810	4.503	1.700	1.108
p 2-tail	<0.0001	<0.0001	0.7748	0.0002	0.0001	0.0967	0.1372
p 1-tail	<0.0001	<0.0001	0.3874	0.0002	0.0001	0.0484	0.0686

Table 3.8 Two-way analysis of variance on sex ratio partitioned according to treatment and colony size.

A. SEX RATIO: mean and (standard deviation).

	Colony size (number of autozooids)		
	900 to 1600	1601 to 3000	3001 to 7000
Restricted	n= 19	n= 31	n= 7
Waterflow	1.68 (1.50)	2.54 (1.60)	2.44 (1.82)
Unrestricted	n= 7	n= 7	n= 12
Waterflow	4.48 (1.69)	3.29 (1.73)	2.18 (1.35)

B. FINAL ANOVA

SOURCE	DF	SS	MS	F	Prob
Cells	5	46.01			
Treatment Eliminating Size	1	20.02	20.02	8.03	0.0059
Size Eliminating Treatment	2	9.19	4.59	1.84	0.1654
Treatment by Size	2	23.70	11.85	4.75	0.0113
Within	77	192.00	2.49		
TOTAL	82				

Figure 3.1

Total number of reproductive zooids (A) and reproductive output (B) of colonies of C. hyalina grown under 3 water flow conditions from March to August 1980. The symbols represent: ○ unrestricted, x semi-restricted and ● restricted water flow.

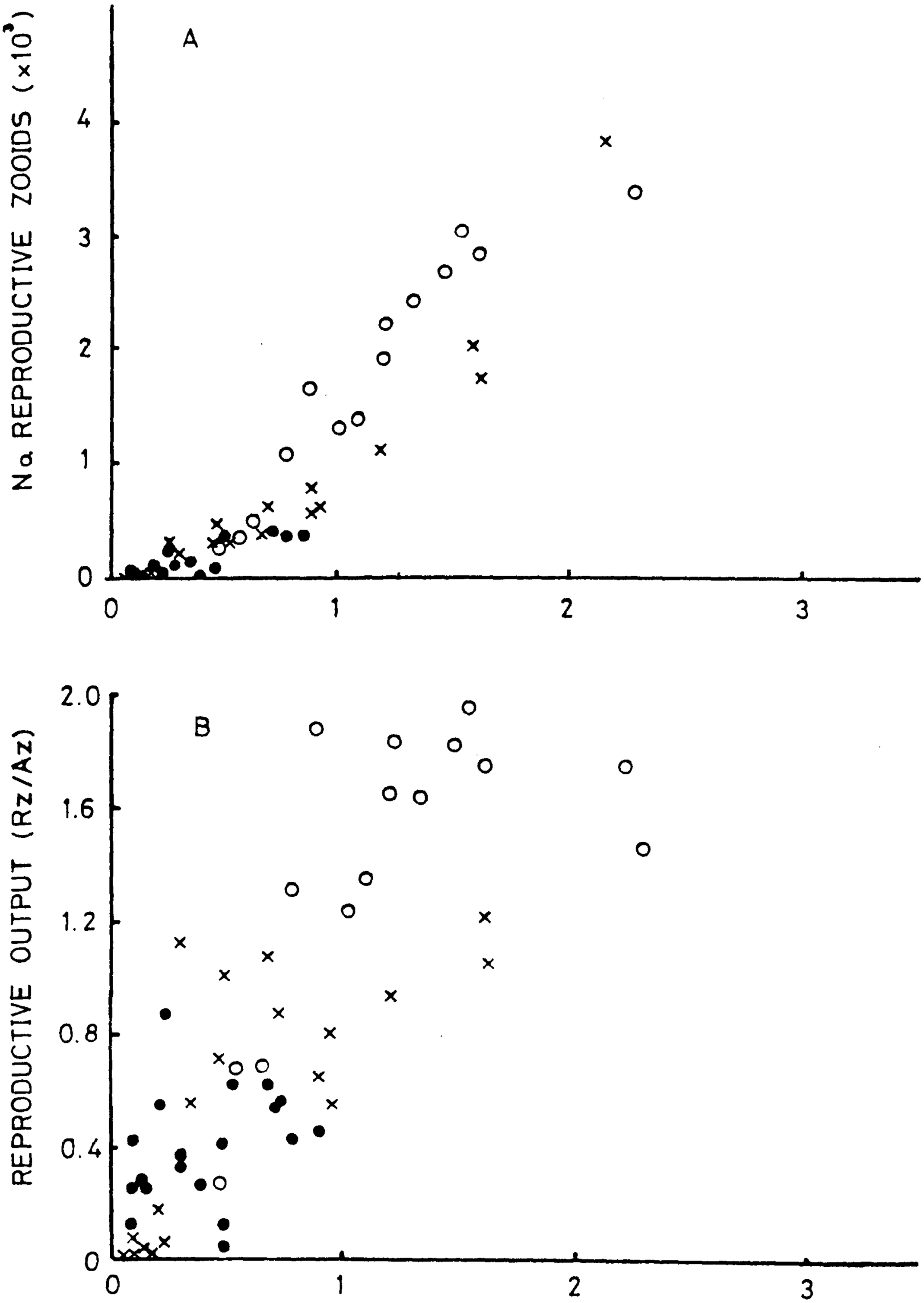

A
No. REPRODUCTIVE ZOOIDS (×10³)
0
1
2
3
4
0
1
2
3
B
REPRODUCTIVE OUTPUT (Rz/Az)
0
0.4
0.8
1.2
1.6
2.0
0
1
2
3
No. AUTOZOOIDS (×10³)

Figure 3.2

Relationship between area of colonies of C. hyalina and number of basal autozooids in a population grown on petri dishes under 3 water flow conditions (O unrestricted, x semi-restricted, and ● restricted water flow). Colonies only a few days old and up to an age of 5 month are included. The linear regression fitted is given by equation y= 27.412 + 5.726 X; r= 0.967, N= 65, with x in mm^2.

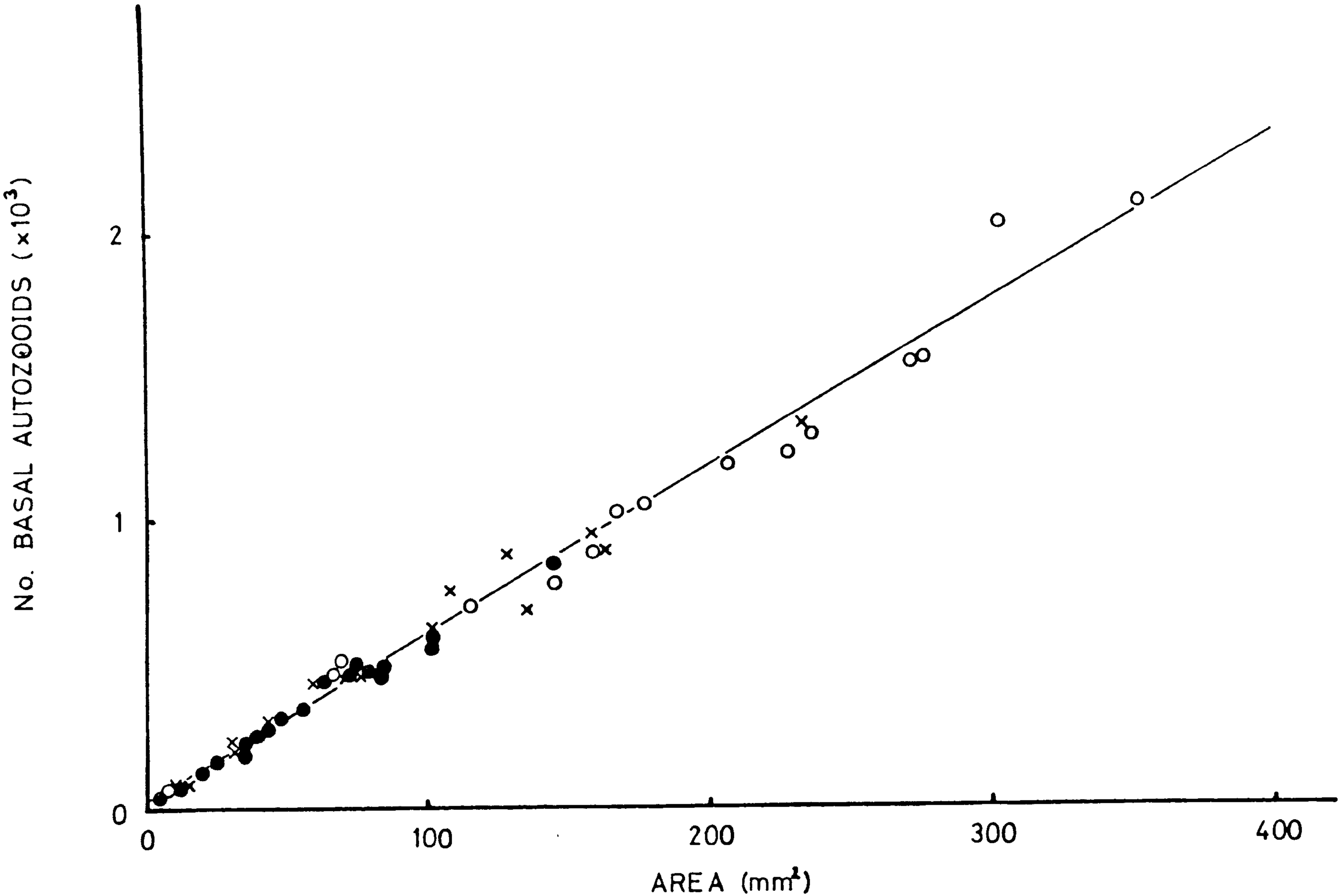

No. BASAL AUTOZOOIDS (×10³)
2
1
0
0
100
200
300
400
AREA (mm²)

Figure 3.3

Growth curves of C. hyalina grown under restricted water flow regime from 20th October 1980. The growth curve for number of autozooids (A) and for total number of zooids (B) are shown. The slopes of the straight lines represent the instantaneous rate of growth per zooid in periods of fast exponential growth. During this period the number of zooids at time (t) can be estimated from the formula $N_t = N_o^{ert}$, where N_o = number of zooids at the beginning of the period, r = a constant equal to the slope of the straight line and t = time in days. The estimated values of r are : (a) 0.0693; (b) 0.0233 and (c) 0.0321.

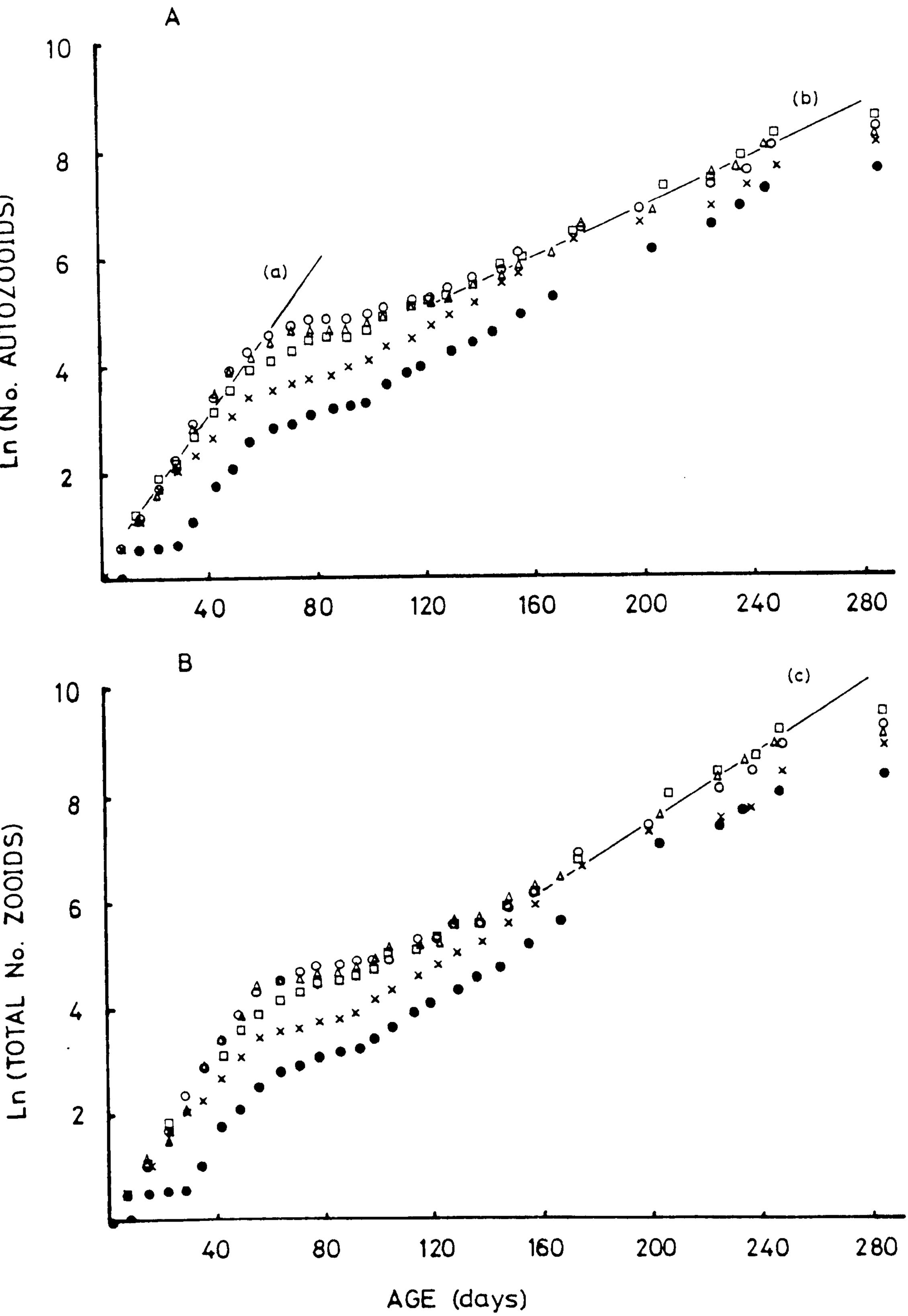
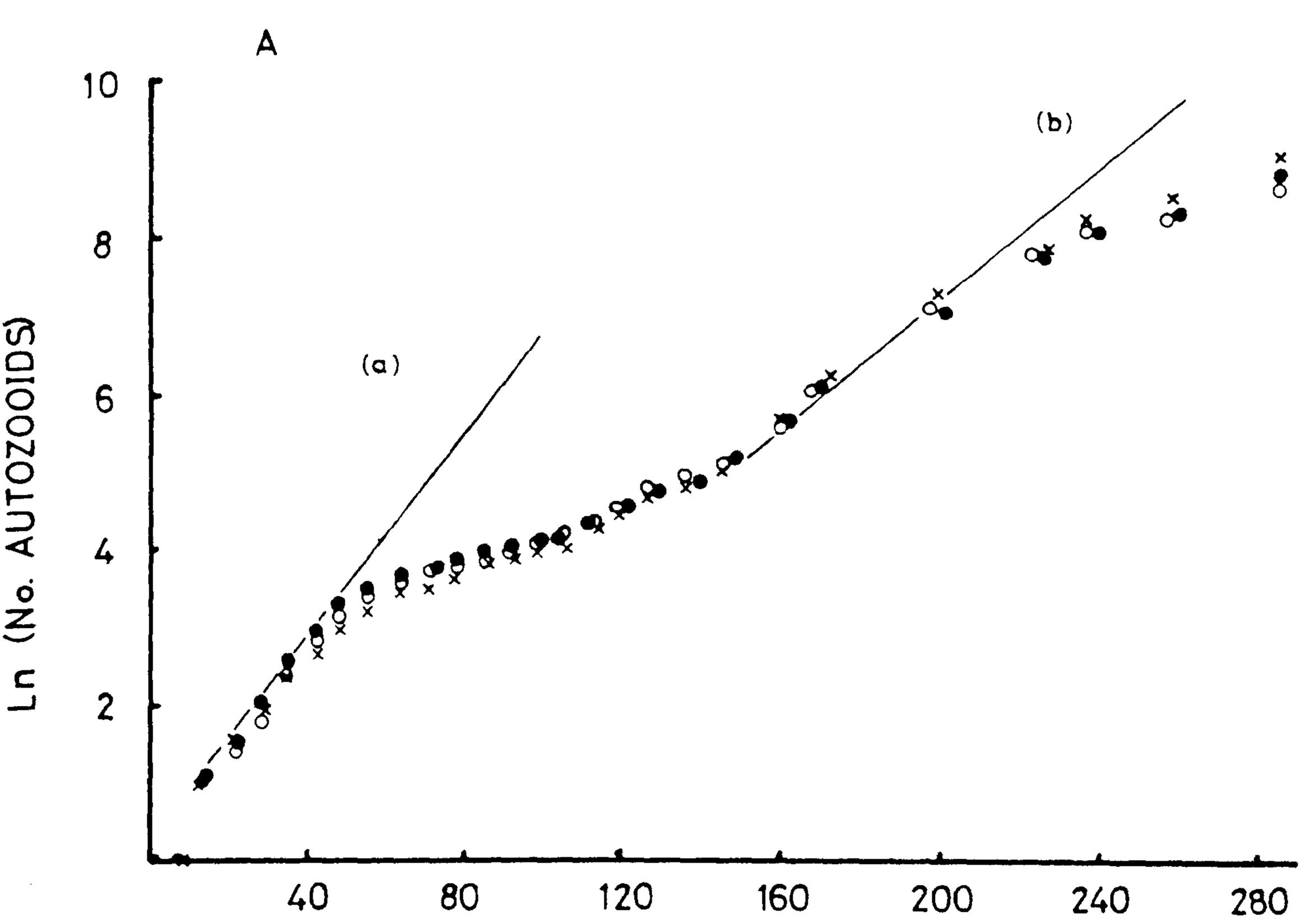

A
B
(a)
(b)
(c)
Ln (No. AUTOZOOIDS)
Ln (TOTAL No. ZOOIDS)
10
8
6
4
2
40
80
120
160
200
240
280
AGE (days)

Figure 3.4

Growth curves of C. hyalina grown under unrestricted water flow regime from 20th October 1980. Only 3 colonies have been included, information is available for 3 other colonies which follow exactly the same curves as the ones plotted. A and B as in Fig. 3.3. Values of r are as follows: (a) 0.0529; (b) 0.0478 and (c) 0.0506.


A
10
8
6
4
2
Ln (No. AUTOZOOIDS)
(a)
(b)
40
80
120
160
200
240
280

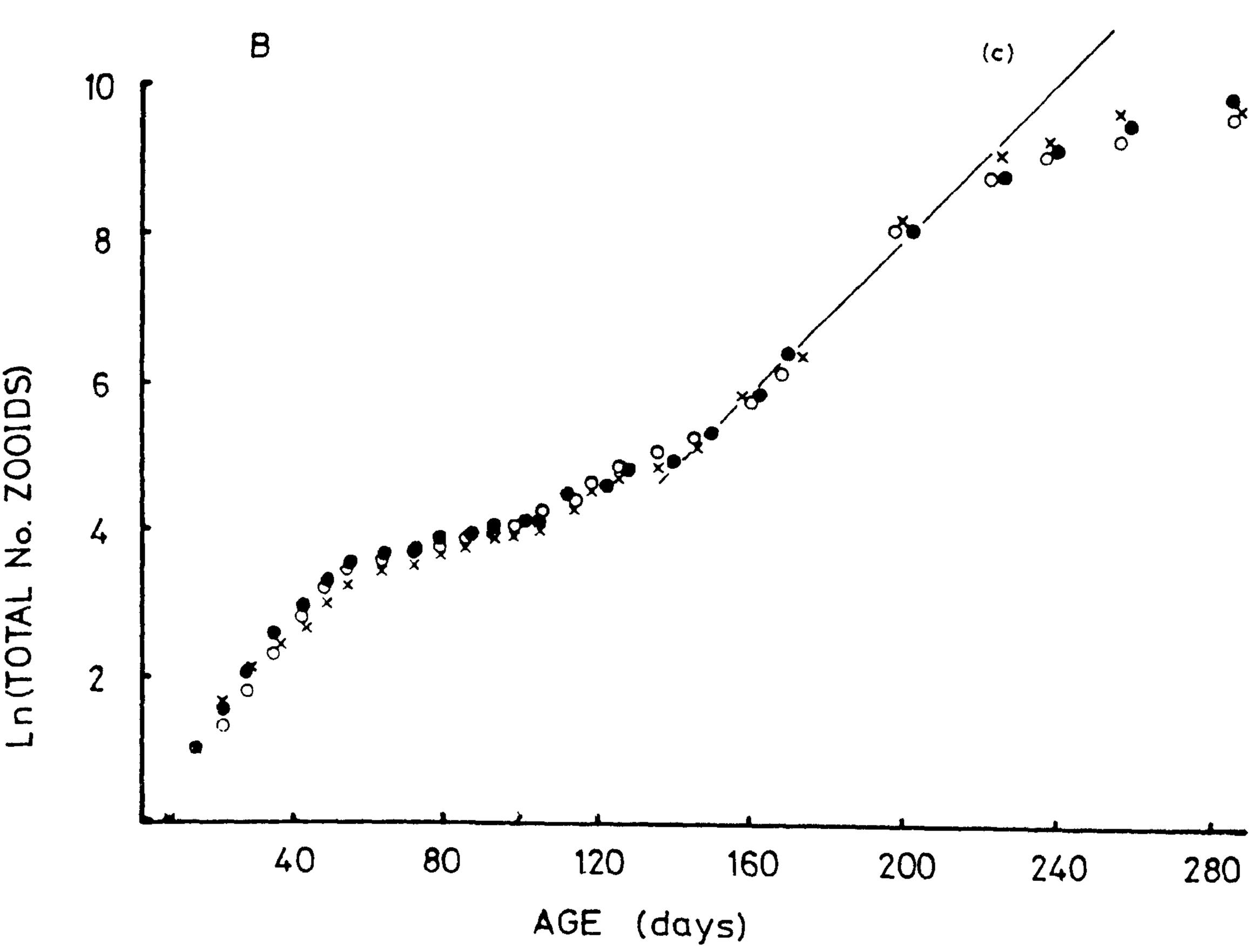

B
10
8
6
4
2
Ln (TOTAL No. ZOOIDS)
(c)
40
80
120
160
200
240
280
AGE (days)

Figure 3.5

Relationship between colony size, expressed as number of autozooids, and total number of reproductive zooids in colonies of C. hyalina grown under 2 water flow regimes (o unrestricted and ● restricted flow). The linear regression fitted to data for colonies with more than 700 autozooids are:

Unrestricted: y= 2.0439X - 806.93; r= 0.967, N= 34

Restricted: y= 1.5776X - 633.66; r= 0.988, N= 33

Analysis of covariance gave a value of F= 14.4 (P < 0.001) between treatments.

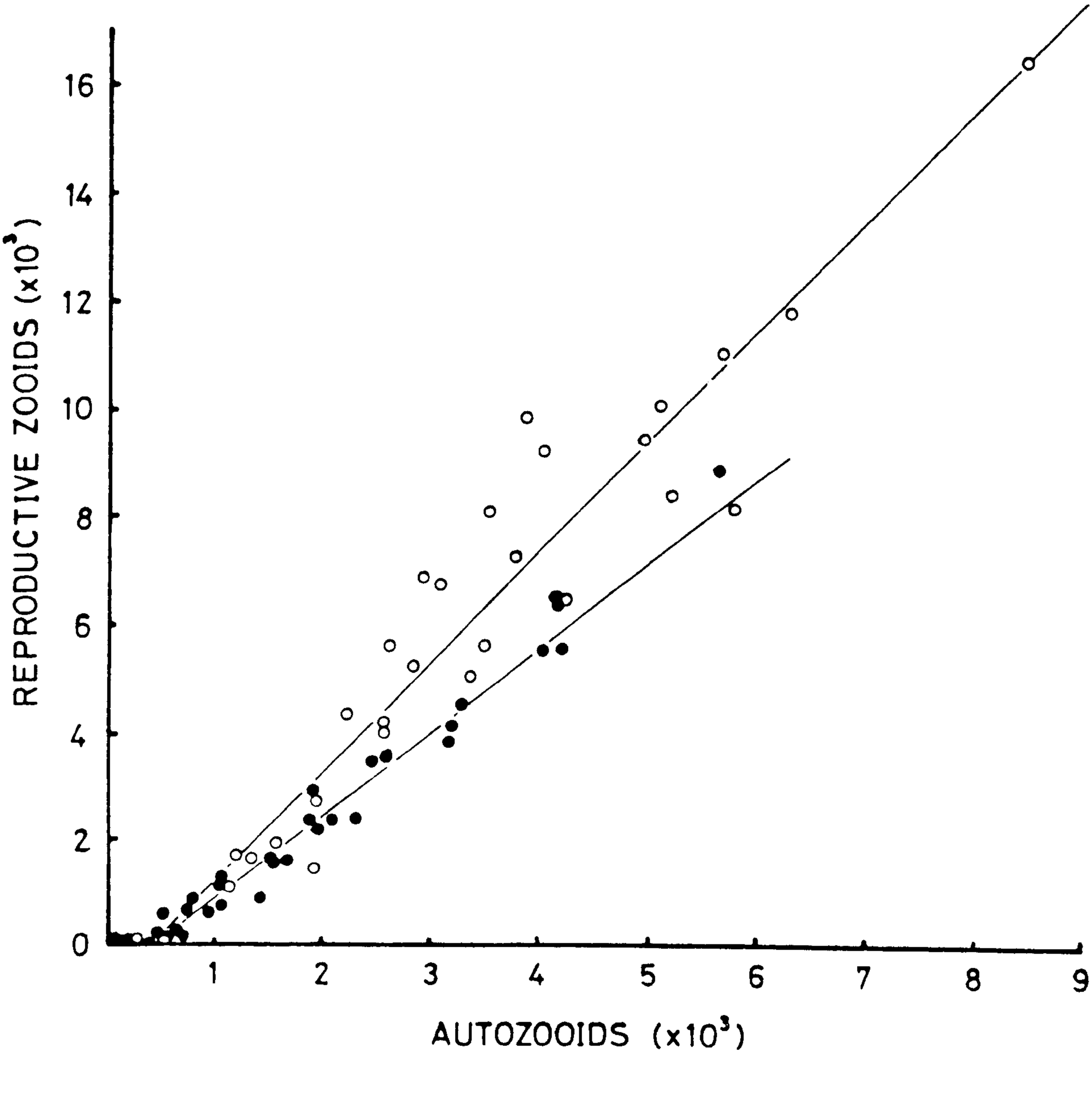

REPRODUCTIVE ZOOIDS (x10³)
0
2
4
6
8
10
12
14
16
1
2
3
4
5
6
7
8
9
AUTOZOOIDS (x10³)

Figure 3.6

Reproductive output as a function of colony size in individually identified colonies grown under two water flow conditions; (O) unrestricted and (●) restricted; after settlement on 20 October 1980.

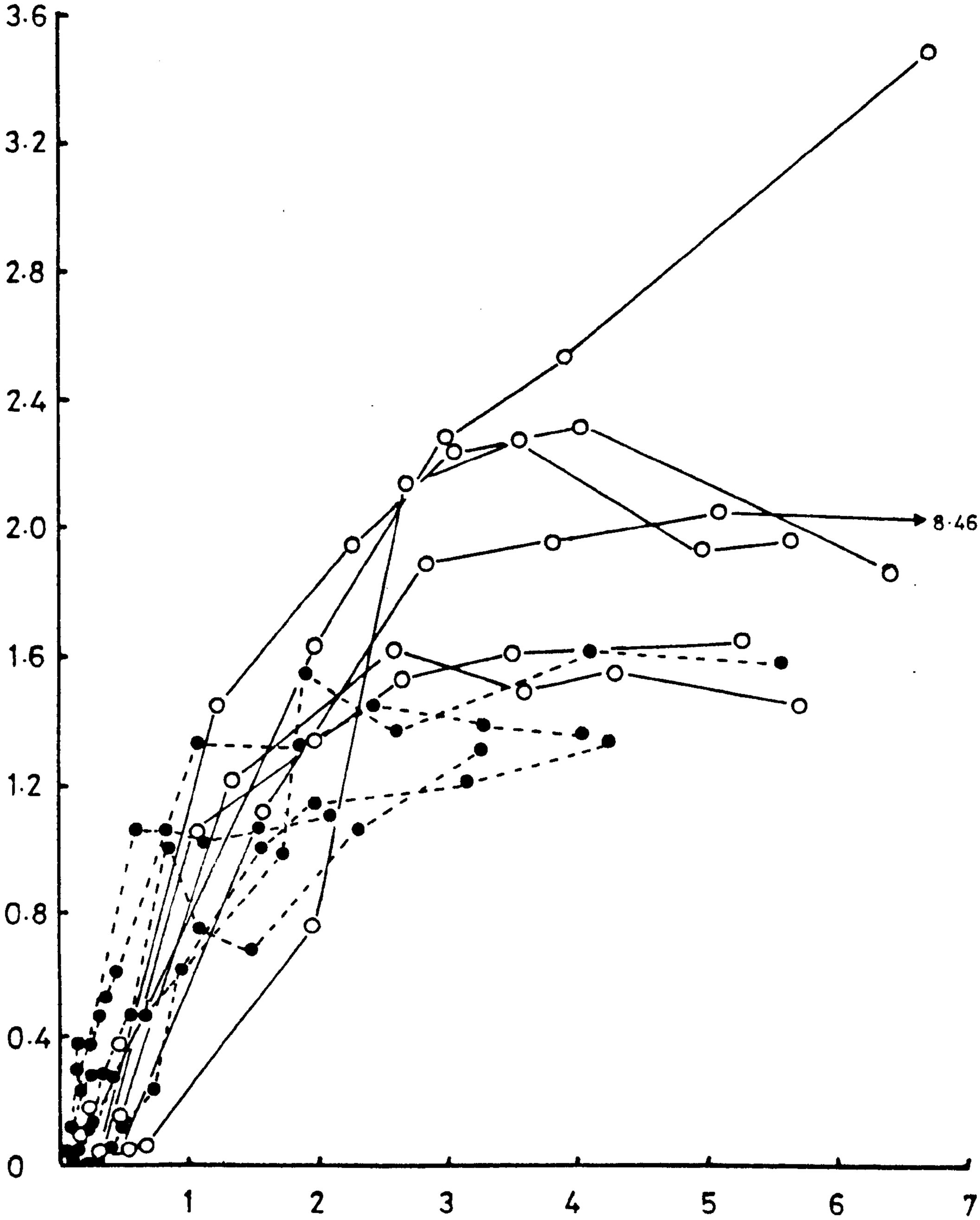

3·6
3·2
2·8
2·4
2·0
1·6
1·2
0·8
0·4
0
REPRODUCTIVE OUTPUT (rep. zooids/autozooids)
8·46
1
2
3
4
5
6
7
COLONY SIZE (no. autozooids x10³)

Figure 3.7

Number of active reproductive zooids (male with sperm + female with egg or/and larva) as a function of colony size (A) and time of the year (B). Colonies were grown under 2 water flow conditions; ○ unrestricted and ● restricted; after settlement on 20 October 1980.

A

B

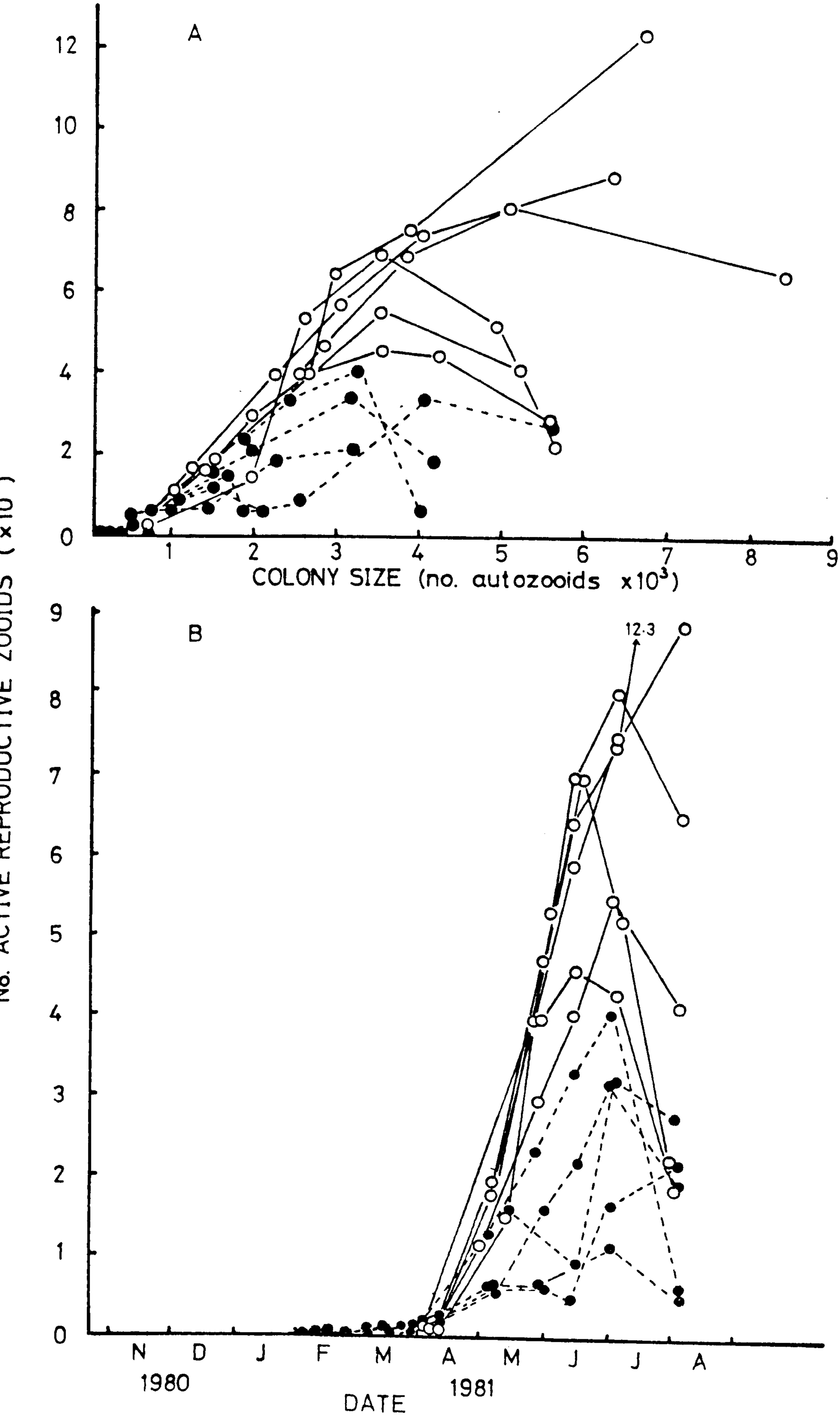

12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
COLONY SIZE (no. autozooids x10³)
No. ACTIVE REPRODUCTIVE ZOOIDS (x10³)
12·3
N
D
J
F
M
A
M
J
J
A
1980
1981
DATE

Figure 3.8

Size of colonies of C. hyalina grown until 25 September 1981 under restricted (A) and unrestricted (B) water flow conditions. On 25 September colonies in each treatment were divided into two groups. One group (●) was placed under restricted water flow, the other group (O) was left under unrestricted water flow regime. Arrows indicate translocation date. Values given are means (± S.E.).

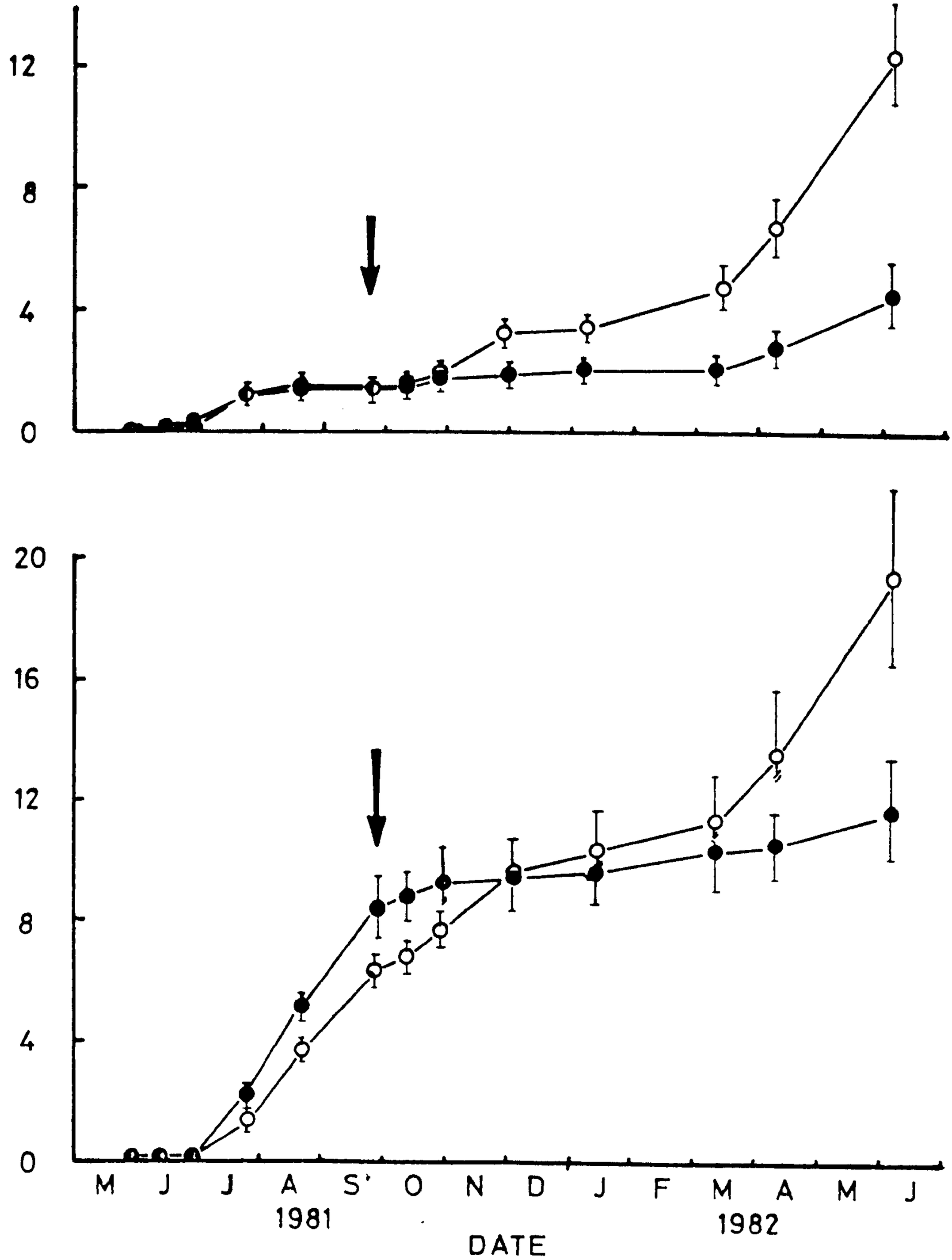

MEAN COLONY SIZE (cm²)
0
4
8
12
16
20
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1981
1982
DATE

Figure 3.9

Changes in the frequency of active reproductive zooids in colonies of C. hyalina translocated on 25 September 1981 from:

○ : restricted to unrestricted water flow

● : restricted to restricted water flow (control)

▲ : unrestricted to restricted water flow

△ : unrestricted to unrestricted water flow (control)

Values given are means (± S.E.) referred to the moment of translocation.

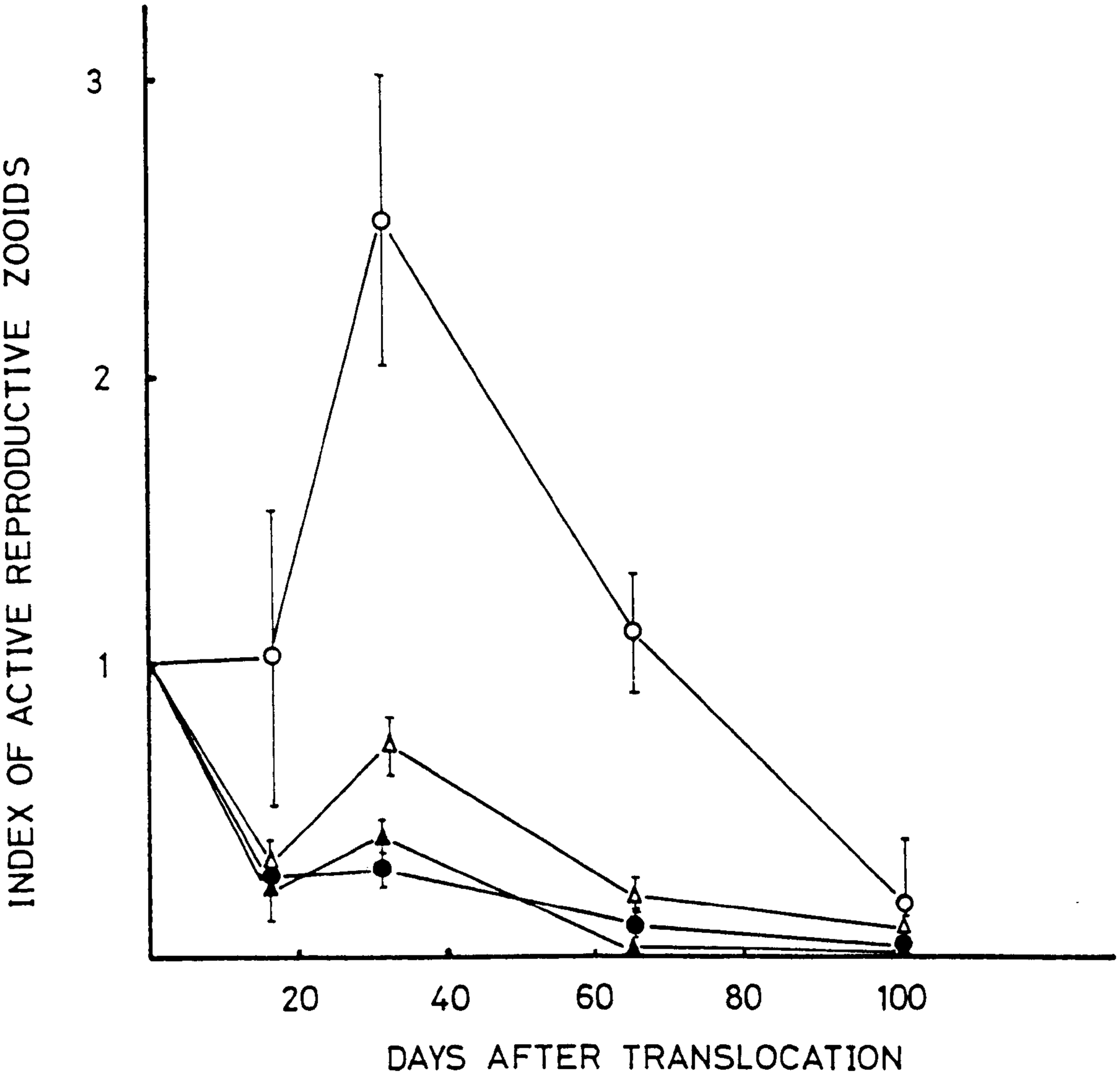

INDEX OF ACTIVE REPRODUCTIVE ZOOIDS
3
2
1
20
40
60
80
100
DAYS AFTER TRANSLOCATION

Figure 3.10

Reproductive output (Reproductive zooids/ Autozooids), as a function of water flow. Values given are means (± confidence intervals, α 0.05) as observed on the following sets of experiments: (O) colonies grown from March to August 1980; (Δ) colonies grown from October 1980 to August 1981; and (□) colonies grown from May to September 1981.

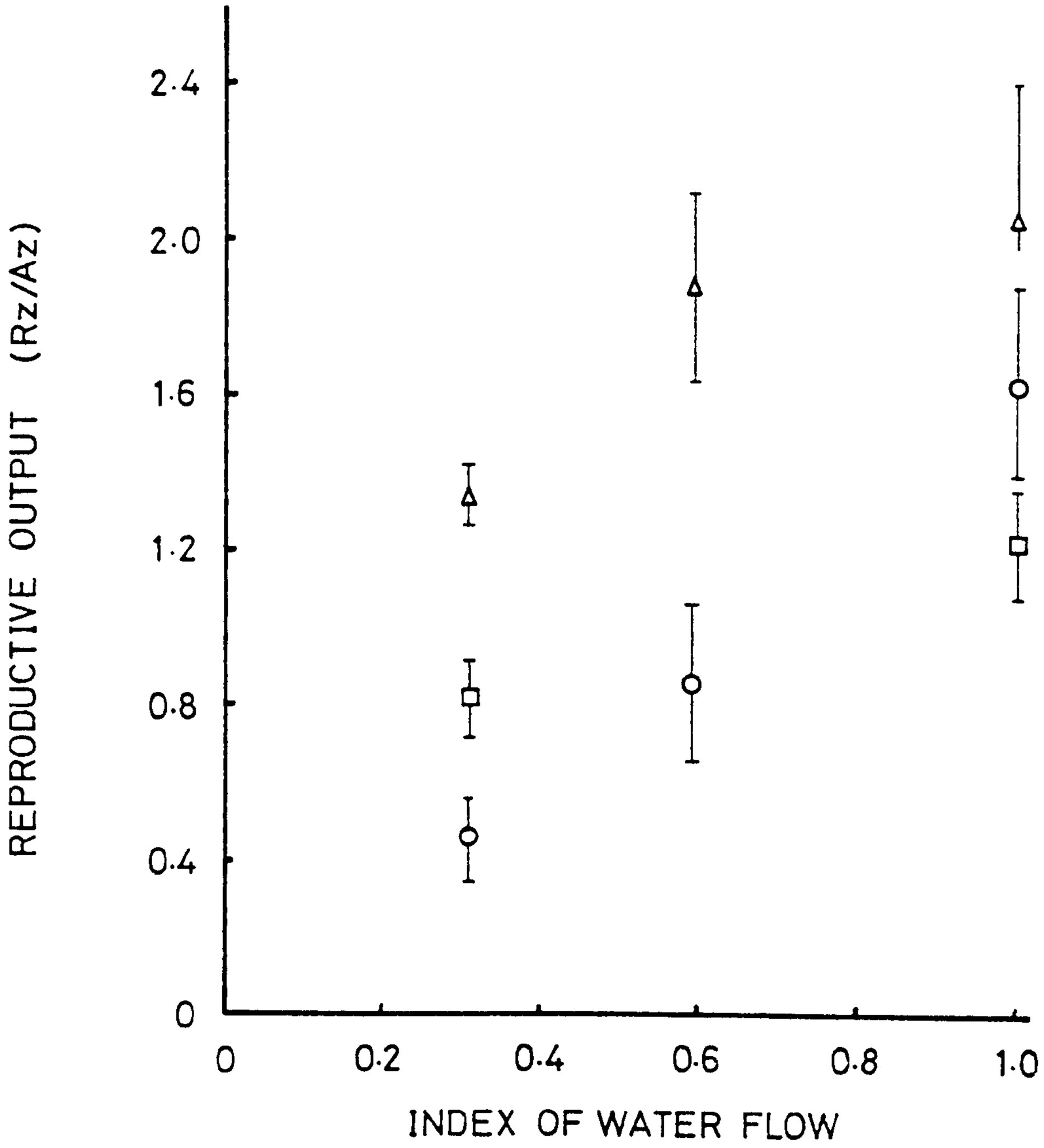
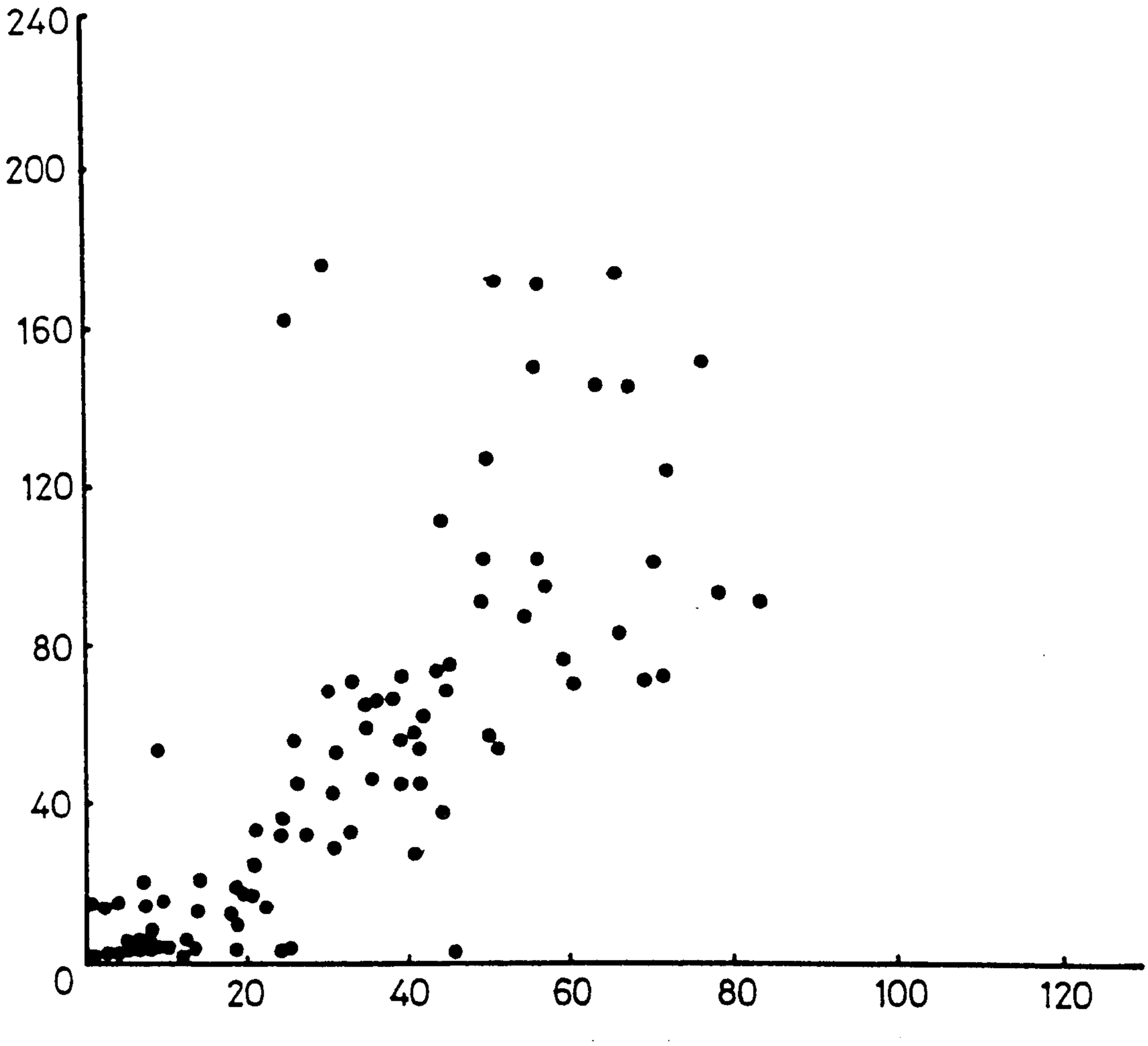

REPRODUCTIVE OUTPUT (Rz/Az)
2.4
2.0
1.6
1.2
0.8
0.4
0
0
0.2
0.4
0.6
0.8
1.0
INDEX OF WATER FLOW

Figure 3.11

Seasonal investment in production of autozooids and sexual zooids. Based on 23 colonies observed, on average, every 16 days for a minimum period of 9 months.

A APRIL TO SEPTEMBER



B OCTOBER TO MARCH

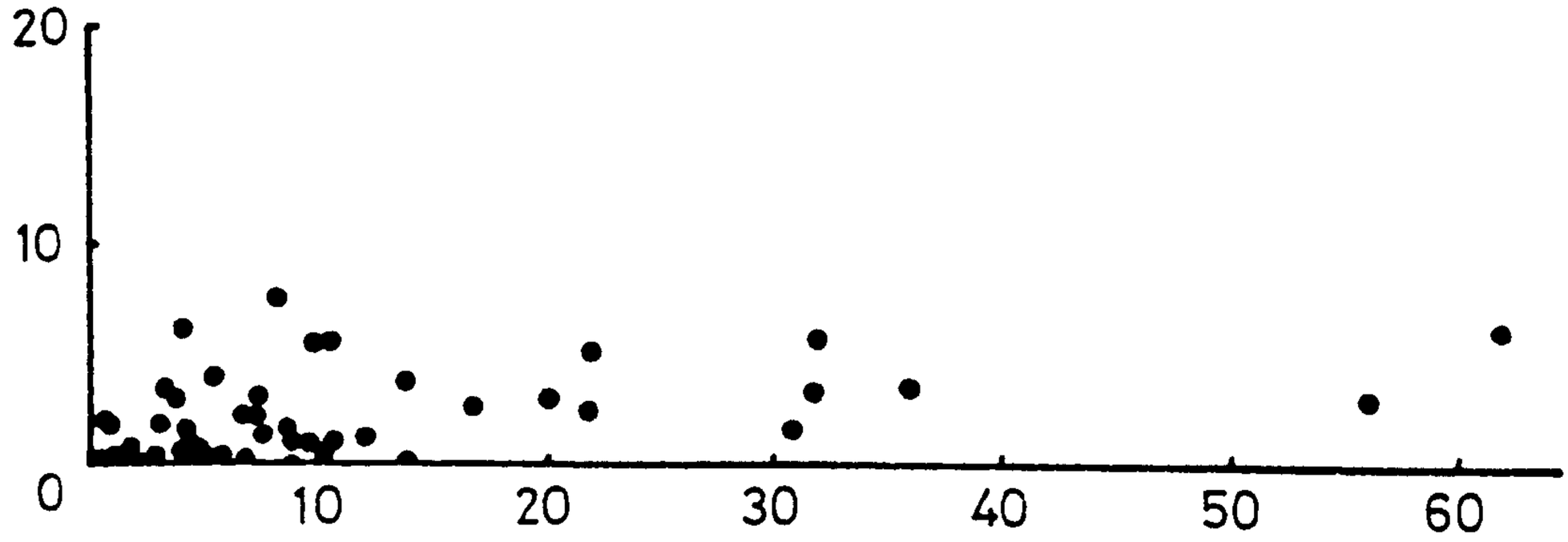


Figure 3.12

Sex ratio as a function of colony size and water flow (open symbols = unrestricted; closed symbols = restricted , and symbols with an x = semi-restricted). Values given are means (± confidence intervals, α 0.05) as observed in the following sets of experiments: (○) colonies grown from March to August 1980; (△) colonies grown from October 1980 to August 1981; (□) colonies grown from May to September 1981 and (◇) from May to September 1982. In this last set of experiments, all colonies were grown under restricted water flow but at two densities; (◆) 7 - 8 colonies per petri dish and (◇) 2 colonies per petri dish.

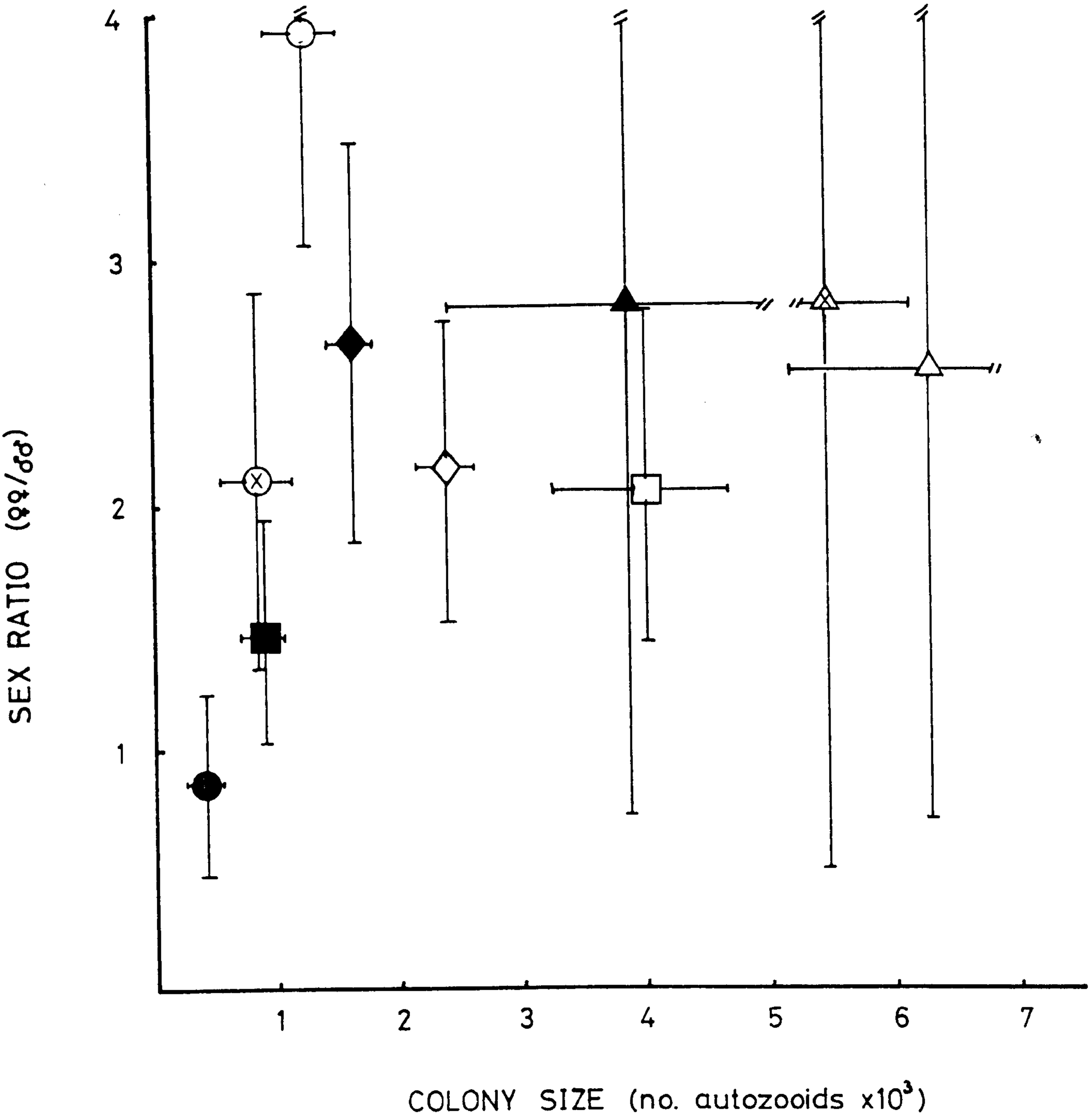
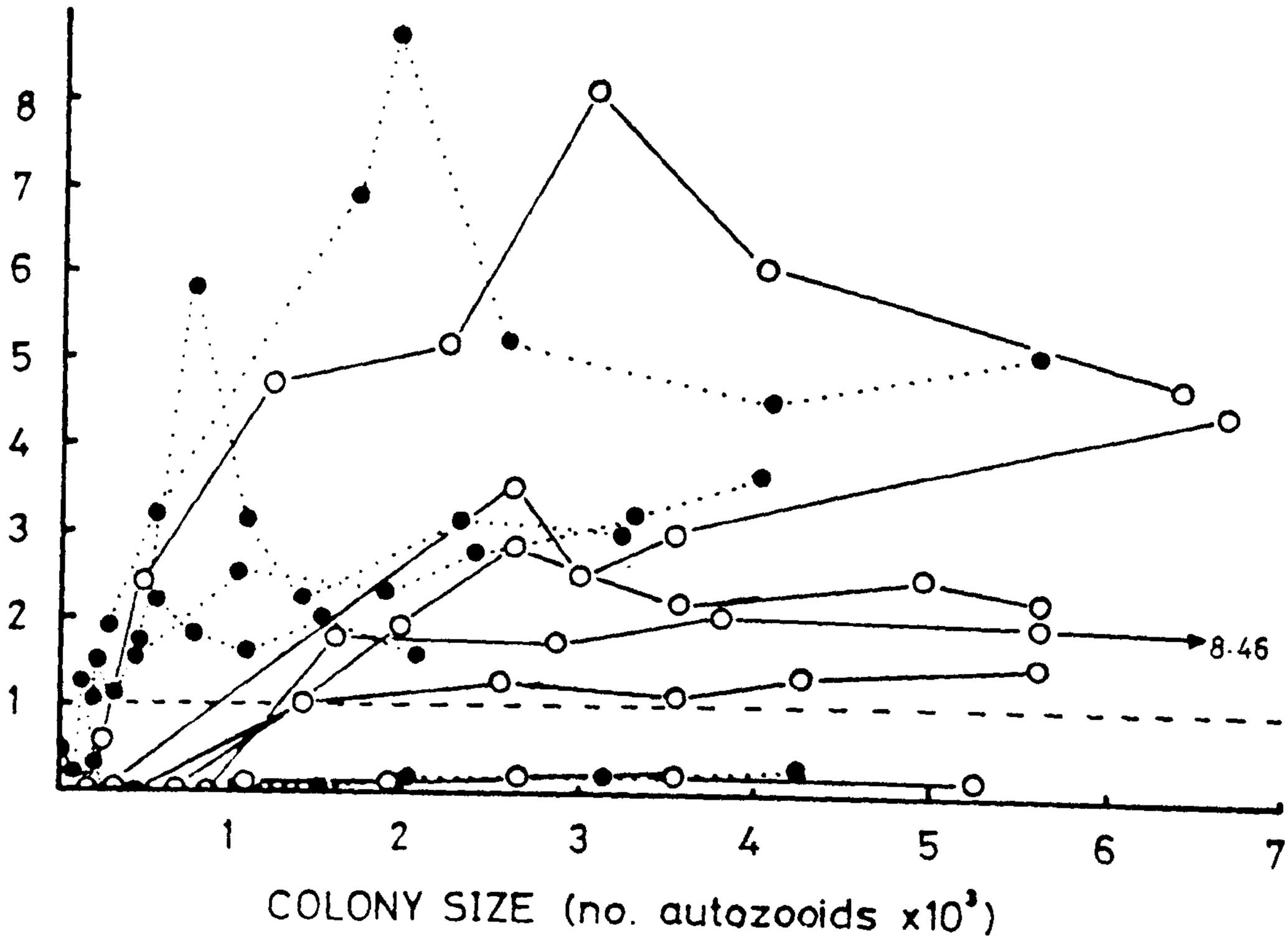

SEX RATIO (♀♀/♂♂)
4
3
2
1
1
2
3
4
5
6
7
COLONY SIZE (no. autozooids x10³)

Figure 3.13

Sex ratio as a function of colony size in individually identified colonies of C. hyalina grown under two water flow regimes, (○ unrestricted, ● restricted). The values given in B are sex ratios of the newly formed sexual zooids plotted against the mean size of colony between observations.

A


8
7
6
5
4
3
2
1
8·46
1
2
3
4
5
6
7
COLONY SIZE (no. autozooids x10³)

SEX RATIO (♀♀/♂♂)

B

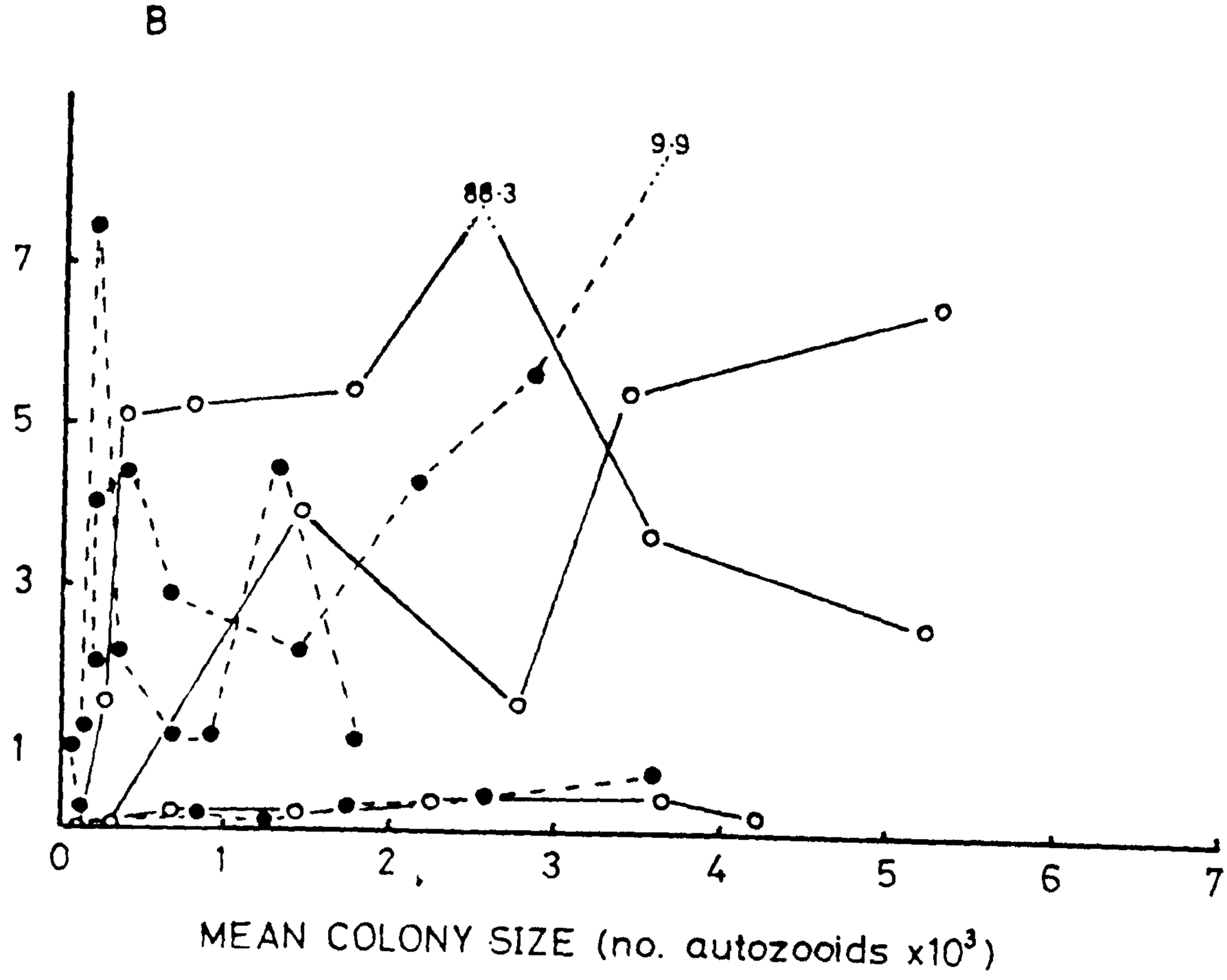

9·9
8·3
7
5
3
1
0
1
2
3
4
5
6
7
MEAN COLONY SIZE (no. autozooids x10³)

Figure 3.14

Production of male zooids (□) by a colony of C. hyalina after 1 October 1980. Capitals letters (A to C) represent cohorts of males formed: A, before 1 Oct 1980; B, between 1 October and 25 October and C, between 25 October and 18 November. The open circles represent number of males containing sperm within each cohort.

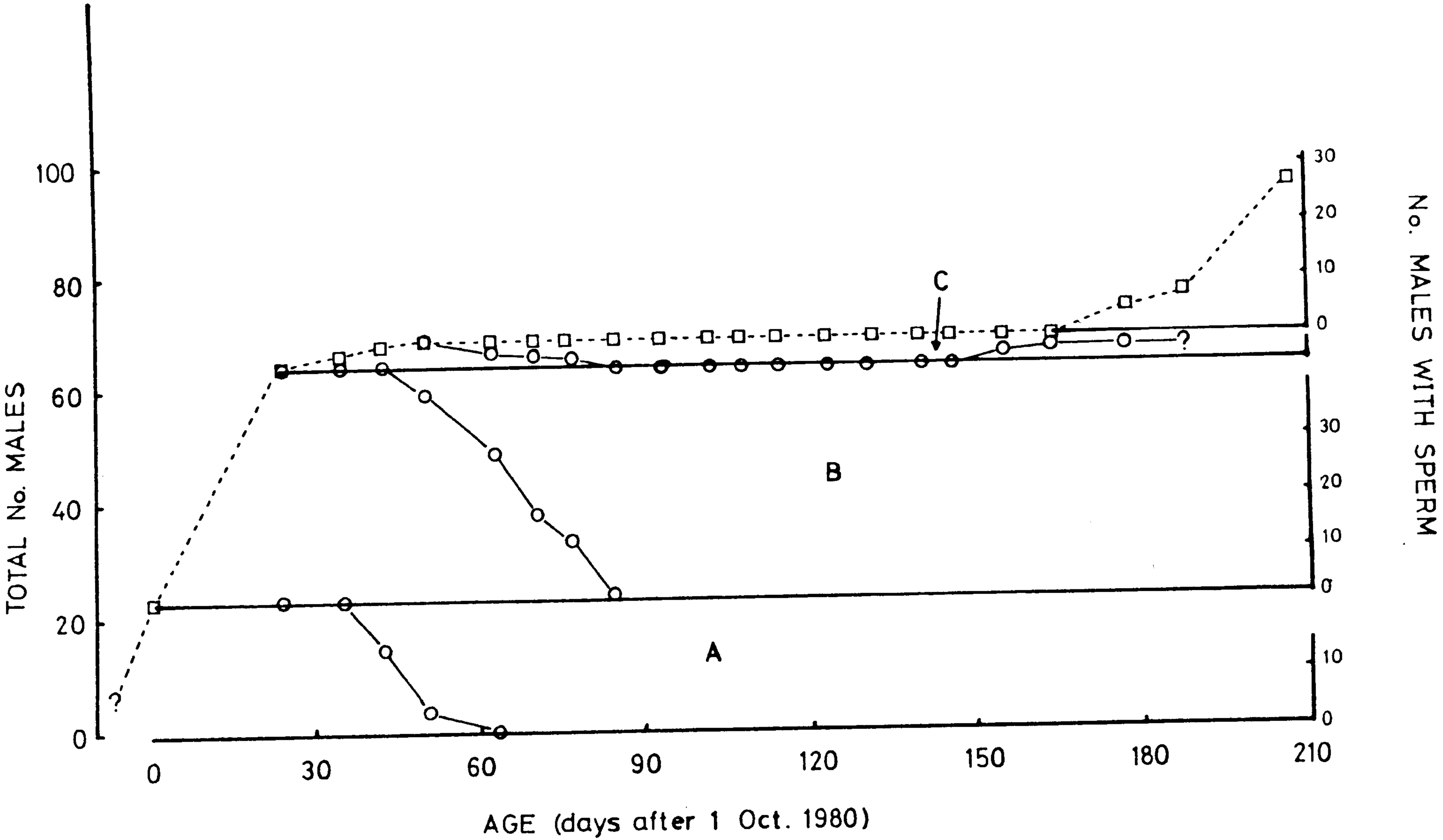
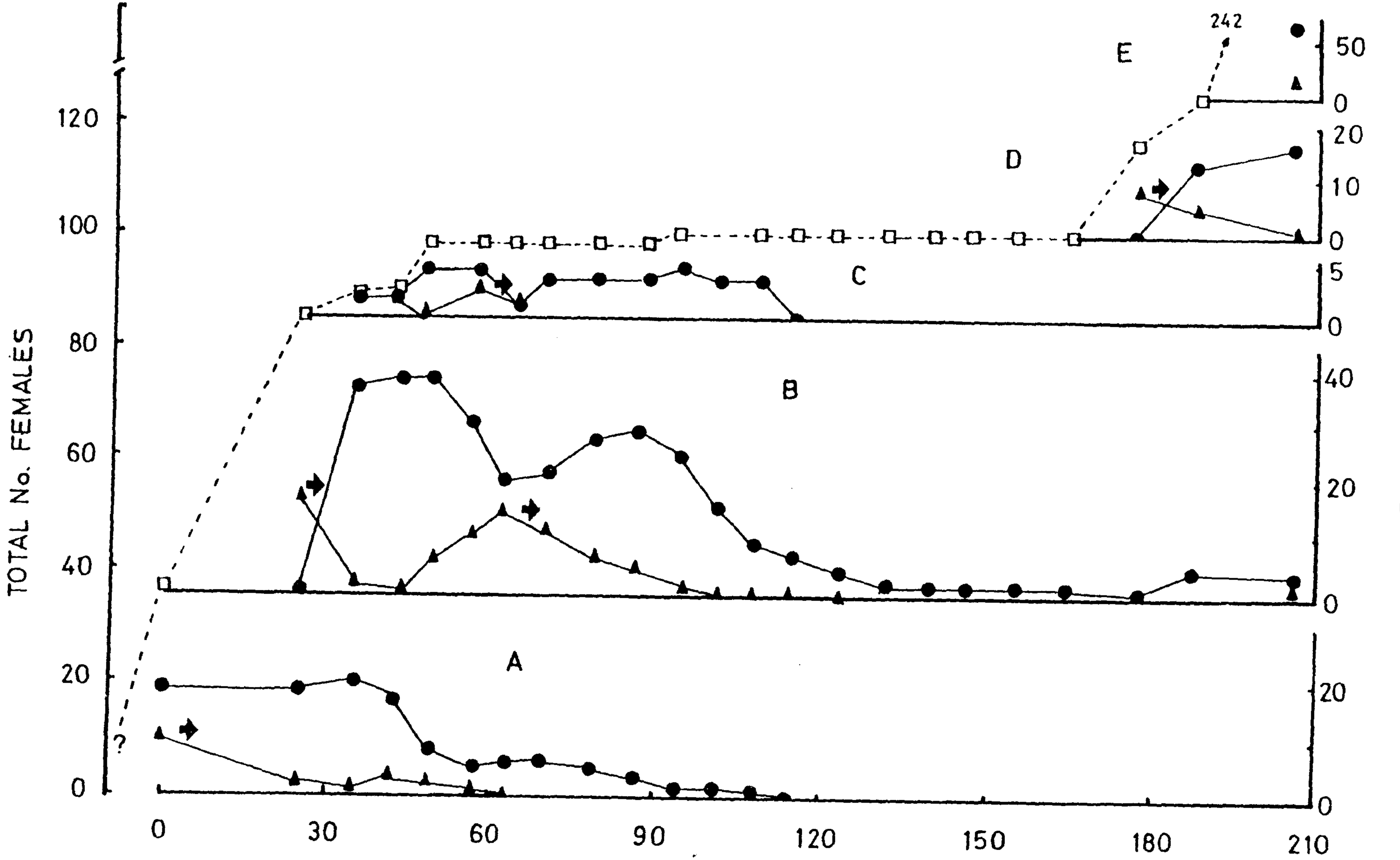

TOTAL No. MALES
100
80
60
40
20
0
No. MALES WITH SPERM
30
20
10
0
30
20
10
0
10
0
C
?
B
A
?
0
30
60
90
120
150
180
210
AGE (days after 1 Oct. 1980)

Figure 3.15

Production of female zooids (□), eggs (●), and larvae (▲) by one colony of C. hyalina. after 1 October 1980. Capital letters (A to E) represent cohorts of females formed: A, before 1 October 1980; B, between 1 October and 25 October; C, between 25 October and 18 November; D, between 9 March and 1 April 1981; and E between 1 April and 18 April. Arrows indicate transference of eggs to ovicells.


TOTAL No. FEMALES
No. EGGS & LARVAE
AGE (days after 1 Oct. 1980)
A
B
C
D
E
242
0
30
60
90
120
150
180
210
20
40
60
80
100
120
5
10
50

Chapter 4

Investigation of the possibility of self-fertilization in *Celleporella hyalina*.

4.1.- Introduction

Fertilization in Bryozoa remains to be observed and has been a matter of controversy for more than a century (Silen 1966, Bell 1982). After the observation of simultaneous hermaphroditism in zooids of Bugula avicularis (Huxley 1856) and early reports of possible autogamy in other species of freshwater (Allman 1856, Braem 1897, Marcus 1934), and marine bryozoans, (for a review see Silen 1966), it was generally accepted that self-fertilization was the rule. Today, however, it is thought that most bryozoans are potential outbreeders. (Silen 1972, Ryland 1976).

The possibility of outbreeding in marine Bryozoans has been supported by direct observations of sperm released into water and by genetical studies. Although there were earlier reports of the release of sperm into water (Hincks 1800, Joliet 1877, Marcus 1938) the first clear account of this phenomenon was reported by Silen (1966). The same author has more recently (Silen 1972) reviewed all species in which the release of sperm has been observed. These included 11 Cheilostomata, 3 Ctenostomata, and 2 Stenolaemata. Aditional observations for 2 species of Cheilostomata have been reported by Chimonides and Cook 1981. In all these species the sperms are released through the tentacles. In non-brooding species, (Membranipora membranacea, Electra posidoninae, E. crustulenta and probably Farella repens and Triticella koreni), fertilization occurs either in the intertentacular organ while the ova are being discharged into water or in the sea, therefore being external. (Silen 1966, 1972, Ryland 1976). In brooding species, fertilization is thought to be

internal (Silen 1972, Ryland 1976, Chimonides and Cook 1981, Dyrynda and King 1982). The sperm probably locate the ova through chemotaxis (Clark 1981), similar to that described for hydroids (Miller 1966a, b, 1976, Miller and Brokaw 1970). Studies of gene frequency for isozyme loci have supported the idea of routine outbreeding in 2 species of Cheilostomata, (Bugula stolonifera and Schizoporella errata) (For a review see Schopf 1977). In these two species, gene frequencies have been found to conform to the Hardy-Weinberg equilibrium, thus suggesting random mating (Schopf 1977). The release of sperm provides the possibility of outbreeding, but is also possible that some sperm could be taken in again by the same colony (Ryland 1976, Bell 1982). Sterility mechanisms have not yet been described for Bryozoa, therefore it is possible that in natural populations some inbreeding takes place (Ryland 1976, Bell 1982).

Sexual reproduction in fresh-water bryozoans seems to be more common in tropical than temperate or arctic waters (Wesenberhund 1907, Bell 1982). In recent long lasting studies larvae have not been observed (Wood 1973) or have been observed only sporadically (Bushnell 1966). Apart from the earlier reports of possible autogamy, already mentioned, no direct observations on fertilization of fresh-water bryozoans exist. Two authors (Clark 1981, Bell 1982), have recently put forward ideas supporting the possibility of self-fertilization in Phylactolaemata. Cross-fertilization through sperm released into water seems to be restricted in fresh-water to animals with low osmolarity of their body fluids and therefore able to produce sperm that survive a long time in the water (eg. Hydra viridissima, Anodonta cygnea and

probably spongillids). Animals with high osmolarity of their body fluids (eg. Oligochaeta, Crustacea, Pisces, Gastropoda), either copulate or show a close pairing of partners before gamete release (Clark 1981). Unfortunately there is not information regarding osmolarity of body fluids of freshwater Bryozoa.

Self-fertilization has been reported in many simultaneous hermaphroditic animals under experimental conditions and in natural populations, (see Ghiselin 1969, Clark 1978 and Bell 1982 for reviews). Among colonial animals, autogamy is known to take place exceptionally in tunicates, (Sabbadin 1971, Berrill 1975), and has also been reported for a hermatypic coral (Kojis and Quinn 1981). Although simultaneous hermaphroditism is known for several species of sponges (Fell 1974), Entoprocta (Mariscal 1974, Mukai and Makioka 1980) and a few hydroids (Campbell 1974), autogamy has not yet been observed in any of these groups (Bell 1982).

Celleporella hyalina (L.) is a simultaneous hermaphrodite, with separate feeding, male and female zooids (Chapter 2). Sperm have, however been reported in all three types of zooids (Marcus 1938), and it has been suggested that sperm migrate within the colony (Marcus 1938, 1941). Although release of sperm into water has not yet been observed in C. hyalina, it is supposed that this process takes place through the male lophophore and that sperm subsequently enter females of neighbouring and probably also of the same colony (Ryland and Gordon 1977). Either of these mechanisms (intra-colonial migration of sperm or released sperm entering females of the same colony), could result in self-fertilization. In the Menai straits C. hyalina forms dense mono-

specific stands on fronds of L. saccharina (Chapter 1). Such aggregations in bryozoans have been postulated as a mechanism preventing self-fertilization (Ryland 1973). If such is the case, it can be expected that C. hyalina is normally outbreeding in natural populations. The present study was designed to investigate whether isolated colonies of C. hyalina would produce larvae. A positive answer to this query would unfortunately not prove that self-fertilization has taken place since the possibility of storage of foreign sperm acquired before isolation (Marcus 1941, Correa 1948, Dyrynda 1981a), and of parthenogenesis (Robertson 1903) must also be taken into account. On the other hand, a negative answer would show that C. hyalina is an obligate out-breeder that does not store sperm. Whatever the answer, it will be relevant to the problem of fertilization in bryozoans, a field so far experimentally neglected.

4.2.- Materials and Methods

Larvae of Celleporella hyalina were obtained from colonies on Laminaria saccharina collected at Menai Bridge Pier on 28 of May and 13 of July 1982. The larvae were released using the standard method (see section 2.2) and settled on conditioned 38x70 mm glass slides. The new colonies were grown beneath Menai Bridge Pier in a housing designed to hold glass slides (Fig. 2.1). When the first males and females started to appear, the colonies were moved to the Laboratory. Here they were kept in 1 litre tanks with aerated running sea water. (Fig. 4.1).

In order to kill any extraneous sperm, the sea water was passed through 7 mm diameter glass coils within which it was heated to 65°C and then cooled to 16°C, prior to flowing over the colonies. (Fig. 4.2.). A thermostat connected to the pump allowed water to circulate only after 65°C had been reached. The sea-water was subsequently cooled using 3 separated stages, the first 2 using fresh water and the final one using sea water (Fig. 4.3). Direct observations showed that the sperm stopped moving well below 65°C. The chemical quality of the water reaching the rearing tanks was essentially the same as before heating, (pH 8.13; salinity 33‰, and O_2 content near saturation). Temperature was recorded every 40 minutes throughout the experiments, values are given below.

To prevent possible interchange of sperm among colonies in different rearing tanks, the following precautions were taken: a) Inlet tubes did not touch the surface of the water of the rearing tank and they were provided with a non-return valve (Fig.

4.1 A). b) Each rearing tank was individually isolated within plastic walls, (this prevented splash created by air bubbles from reaching neighbouring tanks).

Two set of experiments were carried out. The first, commencing on 30th June 1982 and lasting for 30 days, involved 6 rearing tanks, 3 with solitary, experimental colonies, and 3 with neighbouring, control, colonies. Water flow was 73 ml min^{-1} per tank, and temperature was 16 - 20° C (S.E. ± 0.046, 397 observations). The second, commencing on 8th August 1982 and lasting for 60 days, involved 4 rearing tanks, 2 with solitary colonies and 2 with neighbouring, control, colonies. Water flow was 109 ml min^{-1} per tank, mean temperature was 15.9° C (S.E.± 0.048, 460 observations). (Fig. 4.3).

Both experiments were carried out with natural light in a space provided at the Menai Bridge Marine Station. During the last 4 weeks of the second set of experiments it was necessary to cover the tanks with black plastic sheets to stop algal growth on the colonies.

The colonies were observed under the binocular microscope every 6 - 7 days during the first set of experiments and the first 40 days of the second set, and every 2 - 3 days for the last 20 days of the second set of experiments. All males, females, eggs and larvae were mapped using a camera lucida. Colony areas were measured from drawings using a digitizer (see also section 2.2).

4.3 Results

Very few larvae were produced by the colonies in the first set of experiments (Table 4.1). After 3 weeks in the Laboratory, most of the feeding zooids had degenerated, growth in all colonies and sexual reproduction had stopped. It is worth noting, however, that solitary colony E produced 2 larvae after 14 days in isolation.

In the second set of experiments, all colonies showed a substantial growth and sexually reproduced whilst in the laboratory (Table 4.2, Fig. 4.4). Two colonies (A.3, D.1), produced only males, but all others produced both, males and females. Females generated whilst in the laboratory produced eggs and larvae only in control colonies (Table 4.2, last 2 columns).

Females that completed the ovicell produced in average 2 larvae; but up to 5 larvae were produced by individual females (Fig. 4.5). The larvae stayed in the ovicells for 13 to 18 days (Figs, 4.6, 4.7). An average of 14.62 days (S.E.± 0.417, n=13) was obtained with observations every 2 - 3 days (after 17 of September 1982), and assuming that the larvae were produced or released half a way between 2 observations. The eggs were visible in the female's body for 2 to 8 days. Frequent observations after 17 of September gave an average of 3.78 days (S.E.± 0.332, n=23). In most cases by the time a larva was ready to leave the ovicell a fully grown egg was seen in the female's body ready to enter the ovicell (Figs. 4.6, 4.7).

Solitary colony D (Table 4.2, Fig. 4.7) produced 9 larvae that completed development, one of them 40 days after isolation.

Two larvae stayed in the ovicells for about 8 days and so it was assumed that they were aborted. Two eggs produced by this colony never reached the ovicells. Abortions were also observed in colony C and in control colonies as evidenced by the difference between total egg production and the number of larvae completing development (Table 4.2). Settlement of larvae occurred only in rearing tanks A and B (3 and 4 larvae respectively; giving as probability of settlement of 0.056) If the same probability of settlement applied to larvae produced by colony D, then it is not surprising that settlement was not observed. Judging from the timing and changes in size and colour, all 9 larvae that completed development in colony D were normal ones.

4.4.- Discussion

Three explanations, namely sperm storage, parthenogenesis, and self-fertilization, could account for the production of larvae by colonies in isolation. Since the colonies used in the present study were initially grown with other colonies nearby, the first larva produced in isolation by each female may have been the product of outcrossing. The larvae produced subsequently by a female could be product of outcrossing only if storage of sperm exists. Many hermaphroditic invertebrates are able to store sperm (see Ghiselin 1969, Clark 1978, 1981), and utilize stored sperm with high efficiency (e.g. insects, Parker 1970; nematodes, Ward and Carrel 1979), such mechanisms, however, seem to be restricted to animals that transfer sperms through copulation.

Among Bryozoa, sperm have been observed associated with inmature ovocytes of several species of Gymnolaemata (Marcus 1938, 1941, Correa 1948, Dyrynda 1981a, Dyrynda and King 1982). Marcus (1938) found precocius insemination in ovocytes 200 - 300 times smaller than the fully mature ovocyte. Precocius insemination could provide a possible mechanisms of sperm storage; and if present in C. hyalina, it could account for the production of larvae by isolated colonies. The restriction of larval production by females generated in the laboratory to cases where other colonies were nearby, suggests that only cross-fertilization took place and that sperm storage mechanisms could have been involved in the production of larvae by isolated colonies. Unfortunately , too few solitary colonies were observed and they produced too few new females to be conclusive.

Although parthenogenesis is rather common among

invertebrates (eg. Gastrotricha, Rotifera, Nematoda, Oligochaeta, Gastropoda, some Arachnida, Crustacea,Insecta, Symphyla, Diplopoda, Tardigrada) (Bell 1982, Hughes and Cancino, in press), within the bryozoans it has been reported as likely to occur only in Crisia (Robertson 1903). The lack of conclusive evidence to support the occurence of parthenogenesis in bryozoans cannot be taken as proof of its absence. In extensively studied cases, (eg. slugs), what was thought to be selfing proved to be apomictic parthenogenesis (Nicklas and Hoffmann 1981).

Most hermaphroditic animals and plants seem to suppress autogamy if outcrossing is possible (Williams 1975, Heath 1977, Maynard-Smith 1978, Lewis 1979). Selfing, nevertheless, has been reported in many invertebrates, both in the laboratory and in natural populations. (see Ghiselin 1969, Clark 1978 and Bell 1982 for reviews; Colton and Pennypacker 1934 and Hyman 1967 (fresh-water snails); Barnes and Crisp 1956 (barnacles); Noble and Noble 1961 (flukes and tapeworms); Gee and Williams 1965 (polychaetes); Sabbadin 1971 (tunicates); Reeve and Walter 1972 (Chaetognatha); Cain 1974 (sea-anemones); Pianka 1974 (Ctenophora); Ward and Carrel 1979 (nematode); McCracker and Selander 1980 (terrestrial slugs); Kojis and Quinn 1981 (coral); and Mulvey and Vrijenhoek 1981 for a terrestrial snails). Within the Bryozoa, self-fertilization seems probable among Phylactolaemata, (Braem 1897, Marcus 1934, (both cited by Silen 1972), Clark 1981, Bell 1982) and has been suggested as probable in the cheilostome, Epistomia bursaria (Dyrynda and King 1982). The present study suggests that selfing may take place in C. hyalina if both sperm storage and

parthenogenesis are absent.

The question of self and cross-fertillization in marine bryozoans remains unanswered, mainly due to the difficulties of rearing colonies in laboratory conditions. Such difficulties have been pointed out by several authors (e.g. Winston 1977, Jebram 1977, Jebram 1980a). Breeding has been reported in colonies kept in the laboratory for only a relatively short time (eg. Silen 1945, Ström 1969, Nielsen 1981). In the present study, larval production was observed to increase when water flow was increased. This is in agreement with results obtained in experiments in the field (Chapter 3) and observations of Silen (1945) on Callopora dumerilli. Further work using a technique similar to that used in the present study, but with a higher water flow and supplementary diets, might provide the answer to the question of fertilization in Bryozoa.

The present study has shown that isolated colonies of C. hyalina are able to produce larvae, in laboratory conditions, up to 40 days after isolation. Further study is needed to determine the nature of the mechanism allowing breeding in isolated colonies (parthenogenesis, sperm storage or self-fertilization). In nature, C. hyalina should be able to establish populations even from very low initial densities.

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Table 4.1.- First experiment.

Larvae produced by colonies of C. hyalina reared in the laboratory for 31 days.

CONTROL			SOLITARY		
Colony	Larva produced Total	After 14 days	Colony	Larva produced Total	After 14 days
A.1	4	2	B	1	0
A.2	1	0	E	3	2
A.3	0	0	F	1	0
C.1	5	3			
C.2	8	3			
D.1	0	0			
D.2	0	0			
TOTAL	18	8		5	

Table 4.2 Size and production of males, females, eggs and larvae by colonies of Celleporella hyalina reared in the laboratory. (1) Females produced while in the lab, the figure in brackets indicates how many females developed an ovicell.

(2) Larva that completed the development.

a) Control. 2 rearing tanks with 4 colonies each.

		INITIAL (9 AUG)			FINAL (7 OCT)				PRODUCTION OF EGGS & LARVA TOTAL		IN NEW	
	Colony	Area mm²	No. ♂♂	No.♀♀ (ovicells)	Area (mm²)	No. ♂♂	Total no♀ (ovicells)	New♀♀ (1)	Eggs	LCD (2)	Eggs	LCD
COLONIES	A.1	103.74	14	6(2)	123.76	26	19(14)	13(9)	30	19	17	6
	A.2	114.65	22	9(1)	252.99	27	10(5)	1(0)	12	12	0	0
	A.3	75.83	18	0(0)	163.01	19	0(0)	0(0)	-	-	-	-
	A.4	126.80	35	2(0)	207.72	54	5(3)	3(2)	6	6	2	2
	B.1	180.83	60	0(0)	429.38	108	0(0)	0(0)	-	-	-	-
	B.2	78.89	14	2(0)	80.66	25	5(2)	3(2)	3	2	3	2
	B.3	103.33	23	1(0)	110.13	49	7(4)	6(3)	11	7	8	6
	B.4	150.82	20	10(3)	226.63	37	44(33)	34(24)	87	80	54	50
	b) Solitary colonies											
	C	119.57	20	6(0)	136.54	68	6(2)	4(0)	1	0	0	0
	D	100.73	10	17(1)	224.71	49	18(6)	1(1)	13	9	0	0

Figure 4.1

Tank for rearing C. hyalina in the Laboratory. A, side view; B, cross section; sl, slide with bryozoan; ss, supporting strap; wi, water inlet; wl, water level; wo, water oulet.

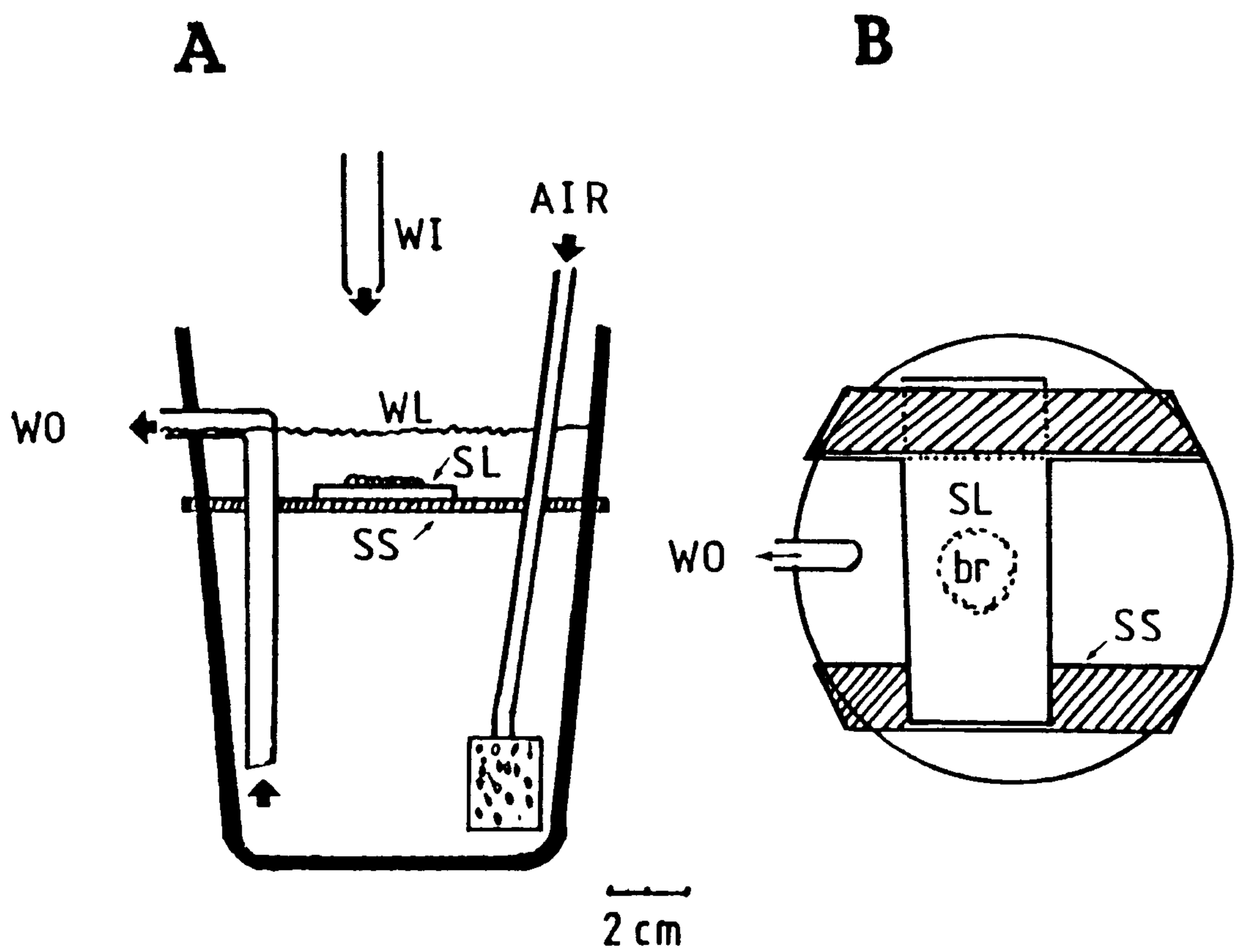

A
B
WI
AIR
WO
WL
SL
SS
SL
br
WO
SS
2 cm

Figure 4.2

Schematic representation of the apparatus used in the self-fertilization experiment with C. hyalina under laboratory conditions. Arrows indicate the direction of flow.

fsw, floating switch; fw, fresh water; ma, mains; nrv, non-return valve; pu, pump; sw, sea water; th, thermostat.

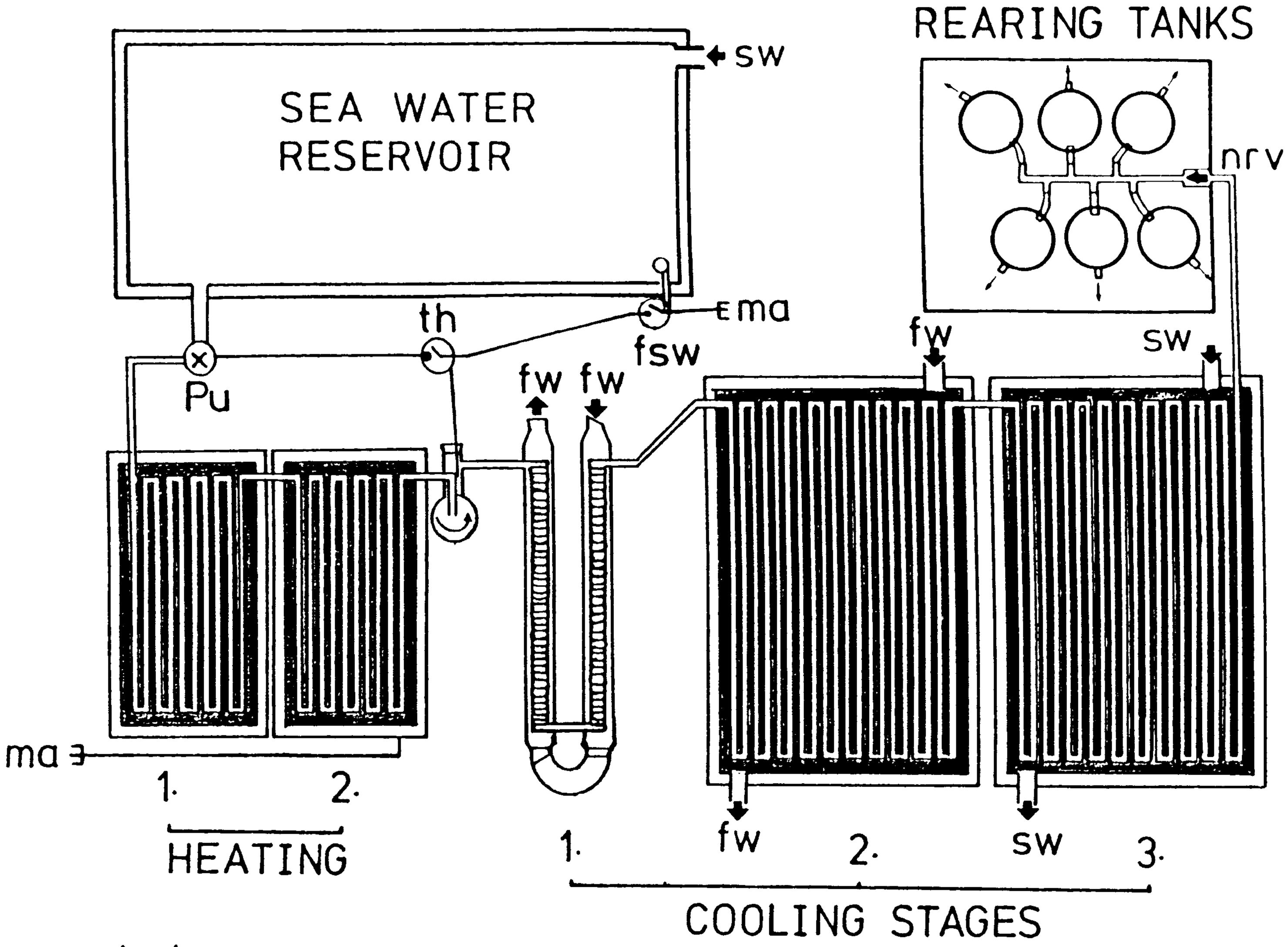

REARING TANKS
SEA WATER
RESERVOIR
sw
nrv
ema
th
fsw
Pu
fw
sw
fw fw
ma
1.
2.
HEATING
1.
fw
2.
sw
3.
COOLING STAGES
10 cm

Figure 4.3

Daily temperature (mean ± C.I., α = 0.05) in rearing tanks during the second set of experiments.

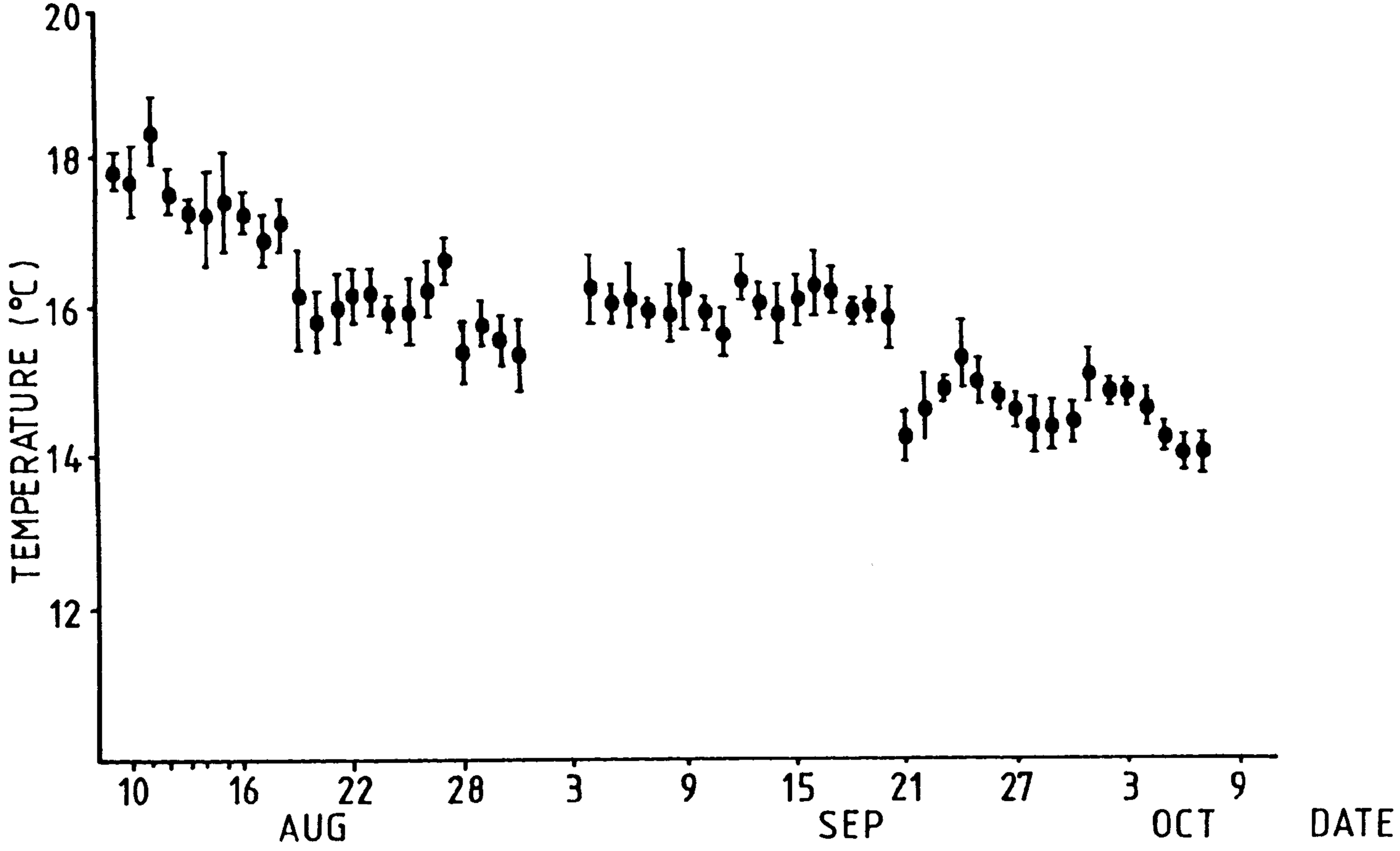

20
18
16
14
12
TEMPERATURE (°C)
10
16
22
28
3
9
15
21
27
3
9
AUG
SEP
OCT
DATE

Figure 4.4

Second experiment. Mean size (± SD) of colonies of C. hyalina. reared in the laboratory.

O--- Control, N=8

●— Experimental, N=2

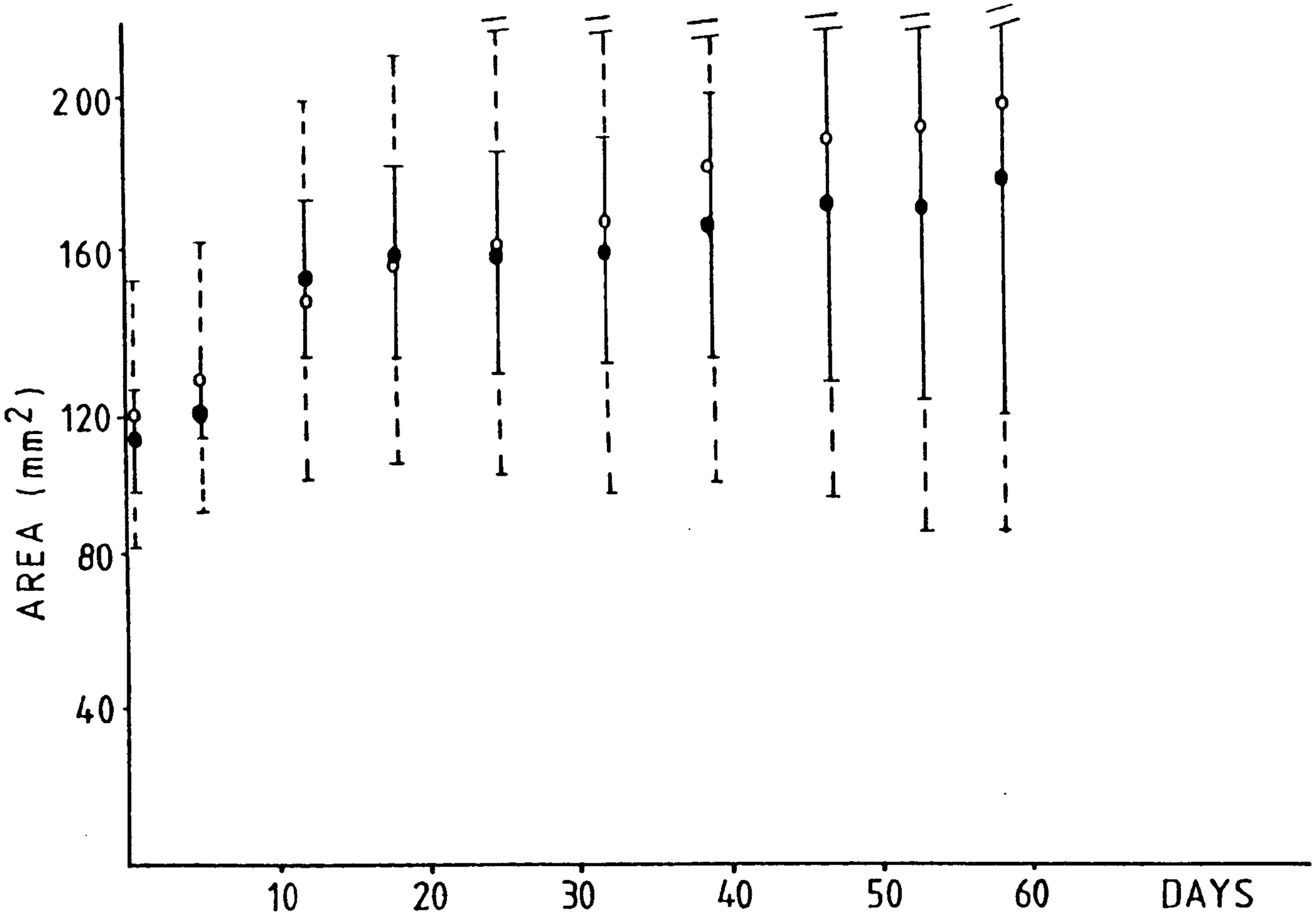

200
160
120
80
40
AREA (mm²)
10
20
30
40
50
60
DAYS

Figure 4.5

Second experiment. Number of larvae produced per female in colonies of C. hyalina reared in the laboratory for 60 days.

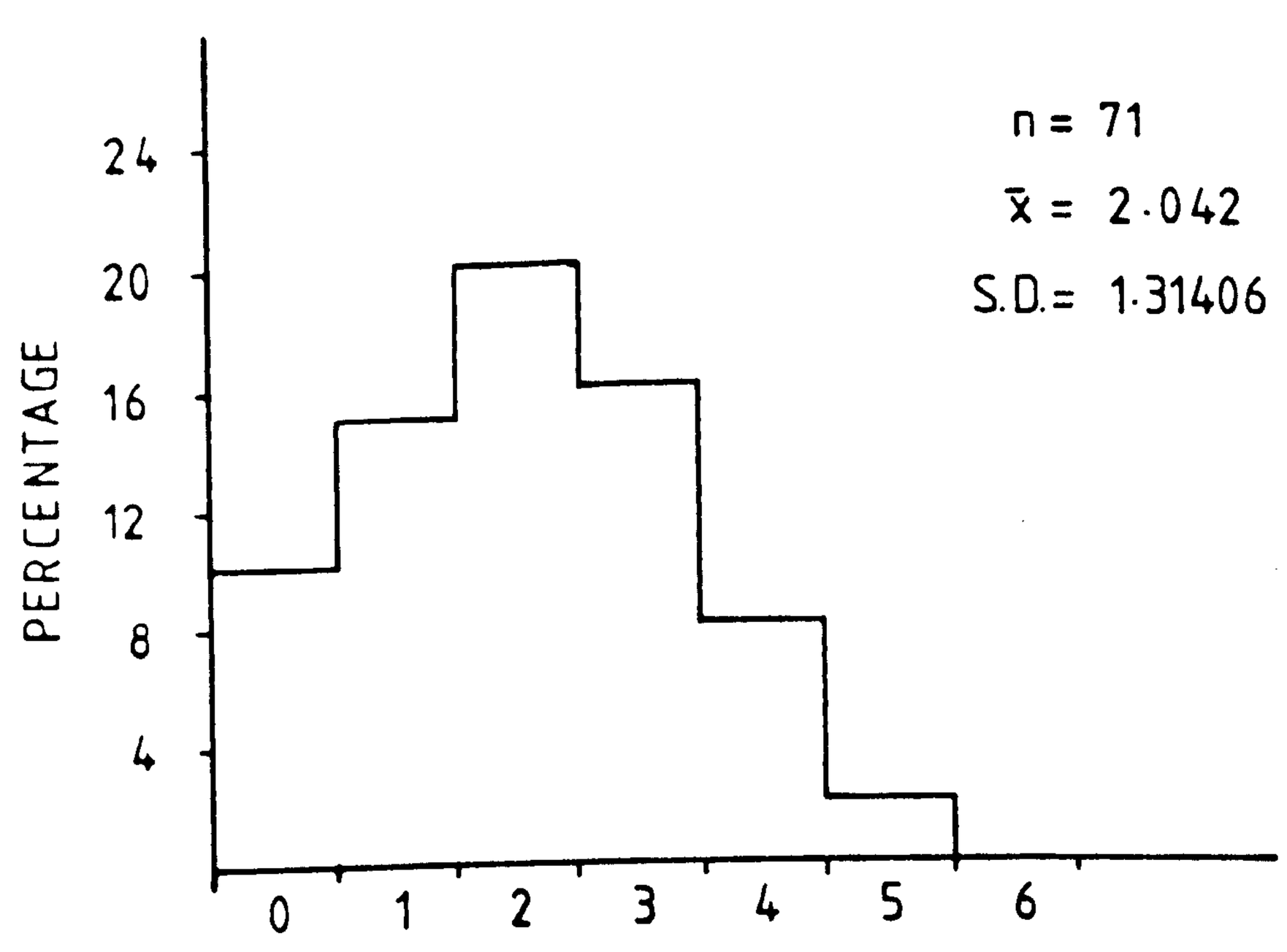

n = 71
x̄ = 2·042
S.D.= 1·31406
PERCENTAGE
24
20
16
12
8
4
0
1
2
3
4
5
6
NUMBER OF LARVAE

Figure 4.6

Timing of larval production by a few selected females in control colonies. Female number refers to individual females within the colony. (*) indicates that egg was seen in the body of the female before passing to the ovicell. Vertically pointing arrows indicate observation dates.

AUGUST SEPTEMBER OCTOBER

8 12 16 20 24 28 1 5 9 13 17 21 25 29 3 7

Colony A. 1 egg new larva old larva

♀#1 ♀#3 ♀#6

Colony A. 2

♀#1 ♀#3 ♀#6

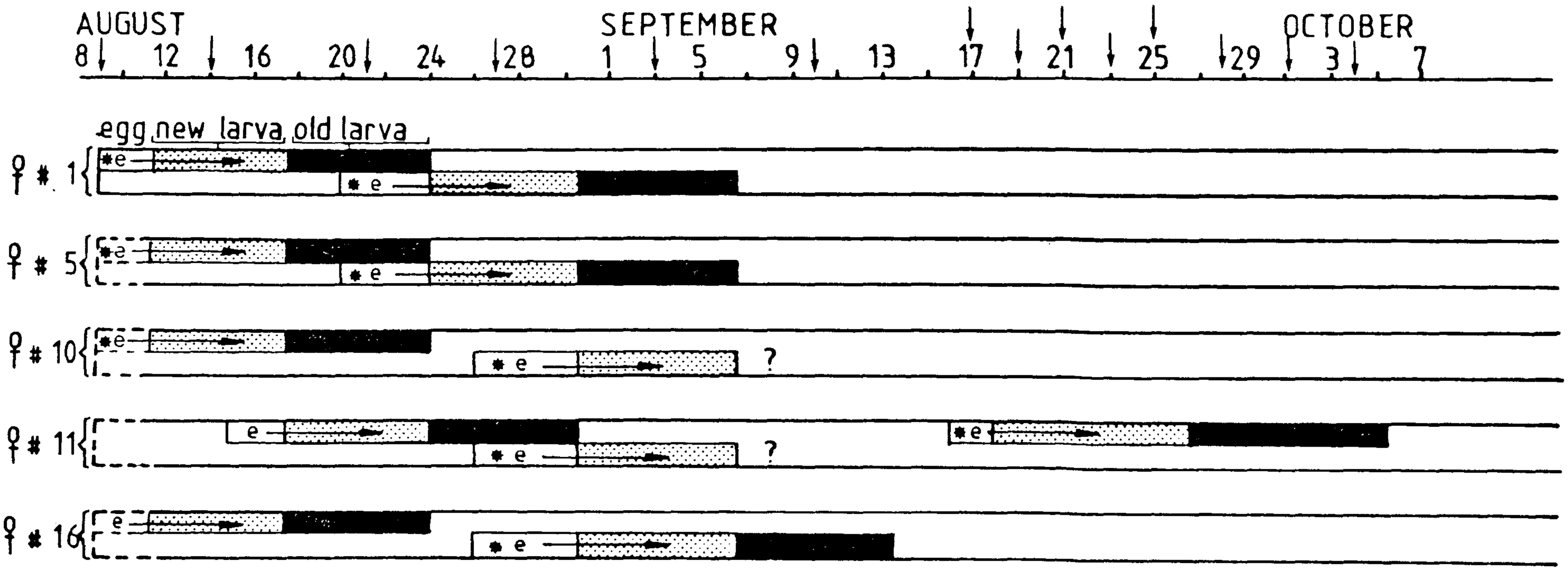
Colony B. 4

♀#1 ♀#9 ♀#15

Figure 4.7

Timing of larval production by colony D. Female number refers to individual females within the colony. Only female #1 had an ovicell on 9 August 1982. (*) indicates that the egg was seen in the body of the female before passing to the ovicell. Vertically pointing arrows indicates observation dates.

SOLITARY COLONY "D"



General Discussion

When given a permanent substratum Celleporella hyalina (L.) is able to survive for up to 18 months (observations of the colonies was stopped at this time). Although C. hyalina has been reported from a wide range of susbstrata, it is commonest on ephemeral substrata such as fronds of Laminariales (Chapter 1). The present study provided some evidence to explain why C. hyalina selects such ephemeral substrata in spite of limiting its life-span by doing so. During the plant growing season, substratum free of competitors is continuously produced, but long lived-species, usually of higher competitive ability, are excluded by the ephemerality of the frondal tissue. Overgrowth of C. hyalina is usually by other bryozoan species (Chapter 2), but on fronds of Laminaria saccharina (L.) Lamour inter-specific contacts are uncommon and intra-specific overgrowth rarely causes mortality (Chapters 1 and 2).

Species living in ephemeral habitats and those associated with substrata of unpredictable durability are usually fast growing and must start sexual reproduction at an early age (Cohen 1971, 1977, Harper 1977, Bernstein and Jung 1979). Because of the trade-off between growth and sexual reproduction (Cohen 1971, 1977, Pianka 1976, Smith 1976, Calow 1981, and General Introduction), it is optimal to delay sexual reproduction until the size that maximizes fecundity is reached. Many examples of solitary and clonal organisms that follow this pattern are known (Pianka 1976, 1981, Hughes and Cancino, in press). In temporary

habitats where the parent dies at the end of the growing season, sex can be delayed only if the timing of mortality is predictable and energy can be diverted to sex within a short time (Chapter 3). Many plants and freshwater clonal animals follow this pattern (Cohen 1971, 1977, Hughes and Cancino in press).

Plants living in habitats in which the timing of mortality is not predictable show a long period of simultaneous flowering and vegetative growth (Cohen 1971, 1977, Harper 1977). Similarly C. hyalina on fronds of L. saccharina has an unpredictable life-span that depends on where the larva settles on the frond and on the fate of the plant (Chapter 1). C. hyalina starts sexual reproduction at an early age, (3 to 4 weeks old in summer), simultaneous growth and sexual reproduction being maintained until death (Chapter 3). During winter, energy is allocated mainly to growth and survival, but some sexual reproduction also takes place (Eggleston 1972 and Chapter 3).

The modular construction of the colonies of C. hyalina allows partitioning of functions, probably minimizing interference between growth and sexual reproduction. It remains to be established if the depression on growth rate observed in sexually mature colonies (Chapter 3) is due to energy being preferentially allocated to sexual activities rather than to growth. For geometrical reasons, however, encrusting species with circular colonies are expected to have a quadratic growth curve (Kaufman 1973 and Chapter 3).

If modular construction allows partitioning of functions, hence minimizing interference between growth and reproduction, simultaneous growth and reproduction should be of common

occurrence among modular organisms. Long reproductive seasons are common among short-lived species of Bryozoa (Eggleston 1972) and among corals subjected to continuous disturbances (see review in Hughes and Cancino, in press). The effect of continuous and early sexual reproduction on future reproduction (residual reproductive value, Calow 1981, Hughes and Cancino, in press) is not relevant to species limited in longevity to a single reproductive season by ephemerality of the habitat.

Within Bryozoa, including species living on permanent substrata, some of the constraints favouring reproduction at an early age or reproduction concurrent with growth are: (a) that larval brooding is common (Dyrynda and Ryland 1982). (b) that autozooids have a limited life-span (Dyrynda 1982 and Chapter 3) and (c) that the season favourable for growth is also the one favourable for larvae (this is common to all invertebrates living in seasonal environments and with delicate larvae, see Hughes and Cancino, in press). Brooding usually takes place in ovicells which are limited in number, the commonest frequency being one ovicell per autozooid. Furthermore, ovicells hold only few larvae, usually one, at a time (Eggleston 1972, Dyrynda and Ryland 1982, and Chapter 3), therefore early production of ovicells maximizes the number of larvae produced in the reproductive season. Autozooids in many species of bryozoans have a short life-span (Chapter 3), thus the scope for sexual activity is limited if it depends on the energy surplus produced by all autozooids in the colony. If autozooids fail to regenerate, there will be a concomitant reduction in the number of functional

ovicells in the colony, hence if sexual reproduction is maintained at a constant rate, further growth to accomodate new ovicells must take place. Similarly, if all ovicells are being used to full capacity and surplus energy is available, further growth can provide space for accommodating new ovicells.

Finally, two advantages commonly attributed to simultaneous hermaphrodites are the ability to : (a) allocate energy to either male or female functions according to environmental conditions (Chapter 3) and, (b) to establish a population from low densities (from only one individual if self-fertilization takes place (Chapter 4). Colonies of C. hyalina showed widely ranging values of sex ratios both throughout the life of the colony and between colonies at a given time. This is probably a reflection of the ability of C. hyalina to regulate energy allocation to gender (Chapter 3). The production of larvae by colonies of C. hyalina isolated from foreign sperms suggests that the species should be able to establish a population even from very low densities of founder colonies.

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Appendix 1

Data on Laminaria saccharina (L.) Lamour at Trwyn-y-Penrhyn, Menai Strait, Anglesey (SH 629797). Plants were marked and followed individually on 5 rocks at different levels in the upper-sublittoral zone (named A to E from the highest to the lowest respectively). For each plant, st = stipe, lg = total length and gr = frond elongation since the previous observation, (all measured to the nearest 0.5 cm).

Question marks denote lack of information.

Location and Plant No.		DATE: 26 Oct 1980	22 Nov	21 Dec	20 Jan 1981	20 Feb	20 March	9 April	5 May	3 June	4 Jul	1 Aug	31 Aug	16 Sept	14 Oct	13 Nov	12 Dec	10 Jan 1982	9 Feb	10 Mar	26 Mar
1A	st	4																			
	lg	37																			
	gr	-																			
2A	st	4																			
	lg	31																			
	gr	-																			
3A	st	2																			
	lg	31																			
	gr	-																			
4B	st	4																			
	lg	73																			
	gr	-																			
5B	st	4																			
	lg	62																			
	gr	-																			
6A	st	7	7																		
	lg	62	50																		
	gr	-	0.5																		
7A	st	4	5	5																	
	lg	70	53	54																	
	gr	-	1.5	0.5																	
8A	st	3	5	5	4																
	lg	67	60	35	22																
	gr	-	2	0	0																
9D	st	6	6	5	6																
	lg	52	46	43	41.5																
	gr	-	3	0	1.5																
10B	st	4	4	4	4	4		4													
	lg	76	78	73	67	48		12													
	gr	-	6.5	5.5	1.5	5.5		?													
11B	st	4	4	4	4	4		4													
	lg	78	43	38	31	32		9													
	gr	-	5.5	1	0	6.5		?													
12A	st	6	8.5	8.5	8.5	10	10	10	10	10.5	10										
	lg	75	75	66.5	61	74	64	72	84	87	67										
	gr	-	3.5	3	2	4.5	7	8	24	14	2										
13A	st	8	10.5	9.5	10	11	11	11	12	12	12	10									
	lg	89	84	80.5	85	93	88	92	90	96	89	12									
	gr	-	3.5	3	5	7	7	11	22	29	8	?									
14A	st	9	12	11	12	13	14	13.5	15	15	15	16									
	lg	118	93	82	88	94	90	101	108	100	105	13									
	gr	-	6	8	7	8	7	12	27.5	35	12	?									
15B	st	9	7	6	6.5	7		6.5	7	7	8	8	7	7							
	lg	135	131	75	7.3	80		71	58	97	118	106	100	97							
	gr	-	7	5	2.5	7.5		15.5	19	39	24	17	13	4							

DATE

Location and Plant No.		26 Oct 1980	22 Nov	21 Dec	20 Jan 1981	20 Feb	20 March	9 April	5 May	3 June	4 Jul	1 Aug	31 Aug	16 Sept	14 Oct	13 Nov	12 Dec	10 Jan 1982	9 Feb	10 Mar	26 Mar	9 Apr	24 Apr	23 May	25 Jun
16D	st	3	2.5	2.5	3	?		2	2	3	2	2	?	2	1.5	2.5									
	lg	88	62	60	43	?		51	67	65	58	43	?	30	27	21.5									
	gr	-	2.5	2.5	2	?		?	22	20	7	2	?	0	0.5	0									
17B	st	5	4.5	5	4	4		4.5	5	5	5	6	5	5	5	5	5	6	6						
	lg	90	79	65	59	55		63	90	101	94	79	69	12	12.5	12.5	12	10.5	6						
	gr	-	3.5	2.5	0	6		13	25.5	30	22	16	4	?	?	?	?	?	-						
18D	st	7	7.5	7.5	7	7.5		10	8	9	9	9	9	9	9	9	8	9	9						
	lg	169	141	96	88	99		123	160	165	190	184	183	181	173	135	141	55	64						
	gr	-	1.5	2	4.5	12		26	35	45	43	22	18	6	6	1.5	3.5	4	8						
19D	st	3.5	3.5	3.5	3.5	3.5		4	4.5	5	5.5	6	6	6	6	6	6	6	6.5	6	6.5	6	6.5	7	7
	lg	52	4.5	45	43	51		59	79	110	119	125	126	119	100	88	87	84	100	110	113	131	158	214	201
	gr	-	1	1	2	8		17.5	25	36	29.5	21	15	4	2	2	2	7.5	19.5	26	16	16	27	54	43
20D	st	7	7	7	7	7		7	8	8	9	9	9.5	9	9.5	9	9	9	9	9	9	9	9.5	9.5	9
	lg	75	78	88	92	103		124	140	180	205	173	171	160	144	139	126	79	93	102	110	118	141	194	162
	gr	-	5	7	7	11		19	30	46	44	29	19.5	3.5	4	3.5	4	8.5	9.5	15	11	15	25.5	46	37
21D	st	6	6	6	6.5	6.5		6.0	7	7	9	9	9	9	9	10	9	9	10	9.5	10	10	10	10	11
	lg	87	79	76	72	67		81	83	128	140	105	100	99	75	76	80	30	32	44	56	67	85	119	103
	gr	-	3	2.5	1	6		19	29	38	25	11	5	2	3	1	6	4	5	11.5	9	9	19	33.5	20
22B	st			10.5	10.5	11																			
	lg			54	67	77																			
	gr			-	5.5	9																			
23D	st			9	9	9																			
	lg			89	98	95																			
	gr			-	5	9																			
24D	st			7	7	7.5		7.5	8	8															
	lg			70	71	86		27	45	67															
	gr			-	4.5	11.5		?	16	31															
25B	st			7.5	6.5	7		6.5	7	7.5															
	lg			75.5	63	68		77	43	65															
	gr			-	2.5	7.5		16	16	23															
26A	st			11	11.5	11	12	12	12	13															
	lg			91	80	61	70	82	93	80															
	gr			-	1.5	4	4	11	27	15															
27A	st			11	11.5	12	11	12	12	12.5															
	lg			49	47	47	50	58	64	66															
	gr			-	0.5	1	1.5	11	20	24.5															
28A	st			10	10	10	10	10	10	10	10														
	lg			71	58	65	68	70	30	44	47														
	gr			-	1	?	?	15	?	15	4														
29A	st			17	16	18	17	17	18	18.5	18	18													
	lg			78	76	70	66	75	68	74	60	51													
	gr			-	1	3.5	6.5	8	19	21.5	6.5	2													

DATE

Location and Plant No.		26 Oct 1980	22 Nov	21 Dec	20 Jan 1981	20 Feb	20 March	9 April	5 May	3 June	4 Jul	1 Aug	31 Aug	16 Sept	14 Oct	13 Nov	12 Dec	10 Jan 1982	9 Feb	10 Mar	26 Mar	9 Apr	24 Apr	23 May	25 June
30B	st			4.5	4.5	?		4	4	4	5	4	5	5	4	4.5	5	4	5	4	4.5	5	5	6.5	
	lg			43.5	27	?		15	22	44	50	52	52	54	48.5	40.5	35	31	34	40	47	42	55	83	
	gr			-	0	?		?	7	18	5.5	5	11	2	3	0.5	1	3	2	6	5.5	7	13	25.5	
31D	st			7.5	7.5	?		9	8.5	8.5	9	10	10	9	9	9.5	9	9	9	9	9.5	9	10	10.5	
	lg			87	90	?		82	114	147	154	139	140	134	126	118	105	99	58	70	78	88	96	95	
	gr			-	5.5	?		30.5	30.5	37.5	27.5	19	15	3	4	1	1	3	8	11	7.5	9	15	25.5	
32B	st			4.5	4.5	5		5	5	5	6	6	5	7	6	6	6	6	6	7	6.5	6	7	7.5	9
	lg			56.5	59	63		71	103	143	128	128	126	126	127	123	102	93	70	80	90	105	128	162	129
	gr			-	1.5	6.5		17	31	47	47	10	18	5	7	7	6	9	17	15	10	16	23	37.5	30
33D	st			8	10	8		9	9	?	?	9	9	9	10	10	10	11	11	10	10	10	10.5	11	11
	lg			110	96	105		115	145	?	?	149	155	153	143	129	122	31	34	40	46	57	76	109	103
	gr			-	1	9		20	38	———	———	89	17	5	7	4	2	3	3.5	6	6	11.5	17.5	35	27
34B	st								6	6															
	lg								101	115															
	gr								-	38															
35E	st								10	9															
	lg								128	137															
	gr								-	35															
36C	st								9	9.5	9.5														
	lg								123	157	165														
	gr								-	35.5	8														
37D	st								11	11	12	12													
	lg								134	188	212	201													
	gr								-	59	43	24													
38E	st								9	8	9	9													
	lg								102	96	84	77													
	gr								-	22	12	4													
39B	st								7	8	9	10	9												
	lg								44	67	78	66	65												
	gr								-	38	16	1	1												
40C	st								6	7	10	8	8												
	lg								116	120	153	140	136												
	gr								-	40	30	20	14												
41B	st								7	7	7	6	7	8	8	8.5	9								
	lg								79	119	146	140	125	114	106	100	58								
	gr								-	41	41	12	19	2	3	0.5	1								
42E	st								9	10	11.5	12	12	11.5	12	12	11								
	lg								178	200	208	220	211	206	188	159	160								
	gr								-	54	48.5	27	16	3	5.5	2	2								
43E	st								10	10	9	10	9	10	10	10	9								
	lg								110	113	100	100	93	83	74	64	58								
	gr								-	29	22	10	4	2	0	1	1								

DATE

Location and Plant No.		26 Oct 1980	22 Nov	21 Dec	20 Jan 1981	20 Feb	20 March	9 April	5 May	3 June	4 Jul	1 Aug	31 Aug	16 Sept	14 Oct	13 Nov	12 Dec	10 Jan 1982	9 Feb	10 Mar	26 Mar	9 April	24 April	23 May	25 June
44C	st								9	10	10	11	10	11	10.5	11	11	11	10	12	12				
	lg								152	168	170	180	170	164	153	135	122	70	70	90	104				
	gr								-	47	37	22	16	3	2.5	2.5	2	8	15	77	14				
45C	st								6	6.5	7	8	7	7	8	7	7	7	8	8	8	7.5	9	8	
	lg								88	119	133	129	125	115	101	90	75	40	43	56	65	67	92	102	
	gr								-	36.5	24.5	15	10	3	1	2	0	2	5.5	11	9	11	20	29.5	
46D	st								7	7	7	8	8	8	8	7.5	7	8	7	7.5	8	8	8	8	9
	lg								47	80	92	89	85	80	74	61	52	48	60	59	67	77	90	101	90
	gr								-	32	21	15	10	3	2	1.5	3	5	7.5	12.5	8	11	18	30.5	16
47D	st								8	8	8	8	9	8	8	8	8	8.5	8.5	8.5	9	8	9	9	10
	lg								71	100	116	88	67	68	66	59	47	43	41	38	44	50	63	89	81
	gr								-	29	21	8	4	0	1	1	2	2.5	2	7.5	5.5	8	13	28.5	16
48E	st								7.5	9	11	11	11	11	11	12	12	11	12.5	12	12	12	12.5	13	13
	lg								91	122	129	130	138	136	119	105	83	49	61	74	84	87	112	153	150
	gr								-	32	26	21	18	5	3	2	1	3.5	4	13	9	13.5	25	47	35
49E	st								11	12	13	13	14	14	14	14	14	13	14	14	14	14	14	14	15
	lg								147	189	193	178	152	150	139	112	103	75	68	85	85	90	113	152	132
	gr								-	43	44	16	7	1	2	1	2	6	13	20	15	14	22	37	14
50E	st								9	10	11	11	11	11	11	11	10	11	11	11	11	11	12	11	11
	lg								100	136	150	142	122	116	95	84	79	49	53	60	75	89	99	103	92
	gr								-	38	28	14	5	1	1	0	2	3	7	13	12.5	13.5	20	26.5	15
51C	st								6	5.5	6	6	6	5	6	5.5	6	5	6	6				6	7
	lg								120	162	173	178	172	167	153	137	123	103	79	38				78	50
	gr								-	45.5	42.5	27	16	3	1	1.5	0	2	1	7	→			23	7
52C	st								11.5	12	13	14	14	14	14	14	14	14	13	14	14.5	14	14	15	15
	lg								141	175	176	169	163	160	139	119	103	77	75	102	114	116	134	164	150
	gr								-	44	38	22	10	4	3	3	2	3	10	14	11.5	13.5	23.5	44	32
53B	st											9	8	8											
	lg											79	75	71											
	gr											-	11	1											
54C	st													9	9	9.5	9	9.5	10	10					
	lg													180	163	137.5	114	93	88	103					
	gr													-	4	0.5	1.5	4	10.5	19					
55E	st													10	9.5	9.5	9	10	10.5	10	9	10.5	10		
	lg													149	135	123	104	55	50	59	69	81	106		
	gr													-	3.5	0	0.5	1	6.5	10	10.5	12.5	23.5		
56E	st																	3.5	3	3	4	3.5	5	7.5	
	lg																	24	30	33	33	43	58	82	
	gr																	-	6	7	8	10.5	19.5	36.5	
57E	st																	8	8	8.5	8.5	8.5	9	10	
	lg																	42	47	60	69	77	94	111	
	gr																	-	6	12.5	8.5	8.5	18	29.5	

Location and Plant No.		DATE																							
		26 Oct 1980	22 Nov	21 Dec	20 Jan 1981	20 Feb	20 March	9 April	5 May	3 June	4 Jul	1 Aug	31 Aug	16 Sept	14 Oct	13 Nov	12 Dec	10 Jan 1982	9 Feb	10 Mar	26 Mar	9 April	24 April	23 May	23 June
58E	st																	9	9	9	9	9			
	lg																	72	57	61	64.5	77	9	9.5	10
	gr																	-	10	15	11	11	93	123	118
																							18	31.5	20
59E	st																	6	6	6.5	7	8			
	lg																	38	47	61	76	83	8	9	12
	gr																	-	9	18	15	14.5	111	165	184
																							28	55	48
60C	st																	8	9	8.5	8.5	8.5			
	lg																	100	114	133	150	164	9	9.5	9
	gr																	-	14	19.5	14	16	160	178	174
																							27	52.5	46
61C	st																	5	5	5	6	6			
	lg																	?	73	85	79	90	6	6.5	8
	gr																	-	7	17	11	12	113	165	150
																							24	50	63

Appendix 2:

Methods used for building rearing apparatus, measuring water circulation and for scanning electron microscopy.

2.1. CONSTRUCTING BAFFLES.

1) Cut a disk (D) of linoleum of 15 cm radius.

2) Mark areas (A) of 117° with vertice on the center of D.

3) For long baffles (Fig. 2.2 A, upper figure) cut in the center of D a small disk (d) 4.0 cm radius and cut out area A.

4) For short baffles (Fig. 2.2 A, middle) make d= 7.5 cm radius and cut as in 3.

5) Bend area A to form a cone (wider opening being perimeter of D and narrower opening being perimeter of d). Glue using silicon-rubber and strips of linoleum (= 1.5 cm width).

The baffles made following this procedure fit inside standard sized petri dishes (9.8 cm internal diameter) and sit inside holes 9.6 to 9.7 cm in diameter. I glued them to the boards using silicon-rubber.

2.2 BOARDS

The boards were made of marine-ply of 0.9 cm thickness. Three rows of holes 9.6 cm diameter were cut. To diminish the interference of baffles on water flow of neighbouring petri dishes, the rows of holes were orientated diagonally in relation to the direction of water flow (Fig. 2.2 B). The petri dishes were tied to the boards with strings (Plate 2.1 C). After the petri dishes were tied to the board and the board placed in the water, care was taken to remove air trapped inside the down-facing petri dishes; this was achieved by turning the board upside down and allowing it to re-adopt the normal position without touching the surface of the water.

2.3. MEASURING WATER CIRCULATION

Water flow inside petri dishes and on algae was measured as follows:

1) Ten hemisphers of 3 cm diameter were made from a mixture of 55 g of calcium sulphate ($CaSO_4 \cdot 5 H_2O$) and 40 cc tap water. Sections of ping-pong balls 1 cm height were used as moulds. A piece of string 10 cm long was put in each hemisphers

2) The hemispheres were dried in a stove (62° C) until constant weight was achieved, this normally took 36 - 48 h.

3) Disks were weighed and reduced to equal weight using sand-paper. The hemispheres used range between 3.3 and 5.0 g (Table 2.3.1).

4) Hemispheres were tied to algae or to the inner surface of petri dishes provided with a small piece of linoleum for such purpose.

5) Petri dishes bearing gypsum hemispheres were tied to boards and left in the water for 24 hours. Afterwards the hemispheres were carefully removed, washed in fresh-water, dried to constant weight and the amount of weight lost calculated.

6) Mean values of weight lost are given in Table 2.3.1. The values given are angular-tranformed percentages (Snedecor and Cockram 1967).

2.4. TIMING FOLLOWED TO FIX AND COAT MATERIAL FOR SCANNING ELECTRON MICROSCOPY.

1) Fix for 1 hr in 10% glutaraldehyde in 80% sea-water.

2) Rinse in filtered sea-water every 9 minutes for 45 minutes.

3) Dehydrate in 25%, 50%, 75% and 100% ethanol (5 - 10

minutes each).

4) Transfer to 100% acetone for 12 hrs, changing twice.

5) Transfer to liquid CO_2 at a temperature of approximately 20° C. Keep in this medium for at least 4 h, flushing every 0.5 h. Instrument used was a Polaron Critical Point Drying Apparatus E 3000.

6) Stop CO_2 circulation and increase temperature of the chamber to 32 - 36° C for critical point drying.

7) Coating with gold was carried out using a Polaron Equipment Limited SEM Coating Unit E 5000, using N_2. Coating lasted 5 minutes at 10 mA.

Sonication for 5 minutes before step 6 was found to give very clean colonies (see Plate 2.3 A, B, C) but destroyed all their membranes at the growing edges, for this reason it was used infrequently.

Table 2.3.1 Initial weight and weight lost in 24 hrs by gypsum hemispheres on algae (L. saccharina) and petri-dishes subjected to different water-flow regimes.

		12-13 March 1980	14-15 March 1980	28-29 April 1980	5-6 May 1980	12-13 May 1980	20-21 May 1980	25-26 Dec 1980	20-21 Jan 1981	General Proportion x and S.E.
Initial weight (gr)		3.683	4.493	4.507	3.364	4.494	4.782	4.918	4.667	
S.E.		0.0018	0.0015	0.0022	0.233	0.0048	0.0079	0.0811	0.0560	
n		16	17	12	11	12	17	9	12	
%	Algae:loss $\bar{x}$	65.033	61.366	-	-	-	55.615	-	-	4.332
	S.E.	11.102	8.995				2.950			0.556
	Petri: Unrestricted									
$\bar{x}$ %	loss	43.719	53.9506	48.929	49.542	50.921	47.301	42.470	38.464	3.081
	S.E.	2.778	1.149	1.491	3.579	1.406	1.995	1.088	0.607	0.230
	Petri: semi-restricted									
$\bar{x}$ %	loss	25.395	35.353	26.835	31.367	27.600	22.107	30.727	23.641	1.818
	S.E.	1.784	0.361	1.126	3.734	1.649	1.591	1.360	1.456	0.142
	Petri: Restricted									
$\bar{x}$ %	loss	12.340	14.008	15.293	15.9679	13.931	16.622	23.047	14.747	1.00
	S.E.	0.175	0.517	2.121	1.022	0.647	1.301	0.576	0.425	