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POPULATION STRUCTURE OF *LITHOPHYLLUM INCRUSTANS* (PHILIPPI). (CORALLINALES RHODOPHYTA.) from south-west Wales

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ABSTRACT

The population structure and density of *Lithophyllum incrustans* (Philippi) at two sites in south-west Dyfed are described. Populations showed an age structure in which the greatest mortality occurs in the youngest age classes. Using size and population density data, the production and survival of spores was calculated for this alga and related to the survival of settled plants. The results are discussed in the light of using *L. incrustans* in the teaching of population dynamics.

INTRODUCTION

Lithophyllum incrustans (Philippi) is a rock-encrusting calcified red alga, common in intertidal pools and the shallow subtidal zone of Atlantic shores of the British Isles (Adey and Adey, 1973; Ford *et al.*, 1983). It is most abundant on exposed rocky shores where it grows in shallow rock pools which, due to grazing pressure, wave action and scouring, have little other algal growth.

Lithophyllum incrustans is the type species of its genus (subfamily Lithophylloideae, family Corallinaceae, class Rhodophyta). Like all encrusting forms in the Corallinaceae, it is difficult to identify and some of the taxonomy is undergoing reassessment (Woelkerling, 1983). The morphology of *L. incrustans* is variable, ranging from smooth, tightly adherent crusts to convoluted, loosely attached, forms. However the thallus is more bulky than most British Corallines and the colour, while dependent on the light intensity, is often more pink-orange to purple than other genera (Plate 1). The crusts have a central fertile area, containing the reproductive structures, known as conceptacles, surrounded by a sterile growing margin (Fig. 1a). Conceptacles are well-defined chambers, buried in the calcified thallus, and connect to the exterior by canals ending in pores on the thallus surface (Fig. 1b, c). Two types of thalli can be found, sexual and asexual (Edyvean and Moss, 1984). These have similar external morphologies but can be distinguished by the size and density of conceptacles when viewed in cross section, sexual conceptacles being smaller and more densely distributed than asexual conceptacles. While, with experience, *L. incrustans* can be recognised by external morphology, this species is particularly recognisable by the characteristic size and shape of asexual conceptacles in cross section (Edyvean and Moss, 1984) (Fig. 2). Asexual plants are dominant in littoral populations of *L. incrustans* around Britain (Ford *et al.*, 1983), though the proportion of sexual plants shows a clinal increase from north to south reaching 35% of populations in the far south-west of England (Edyvean and Ford, 1986). *L. incrustans* increases in size both peripherally and in thickness. The plants are fertile throughout the winter months (Edyvean and Ford, 1986) and asexual conceptacles are formed in seasonal layers in the thallus (Fig. 1c). This

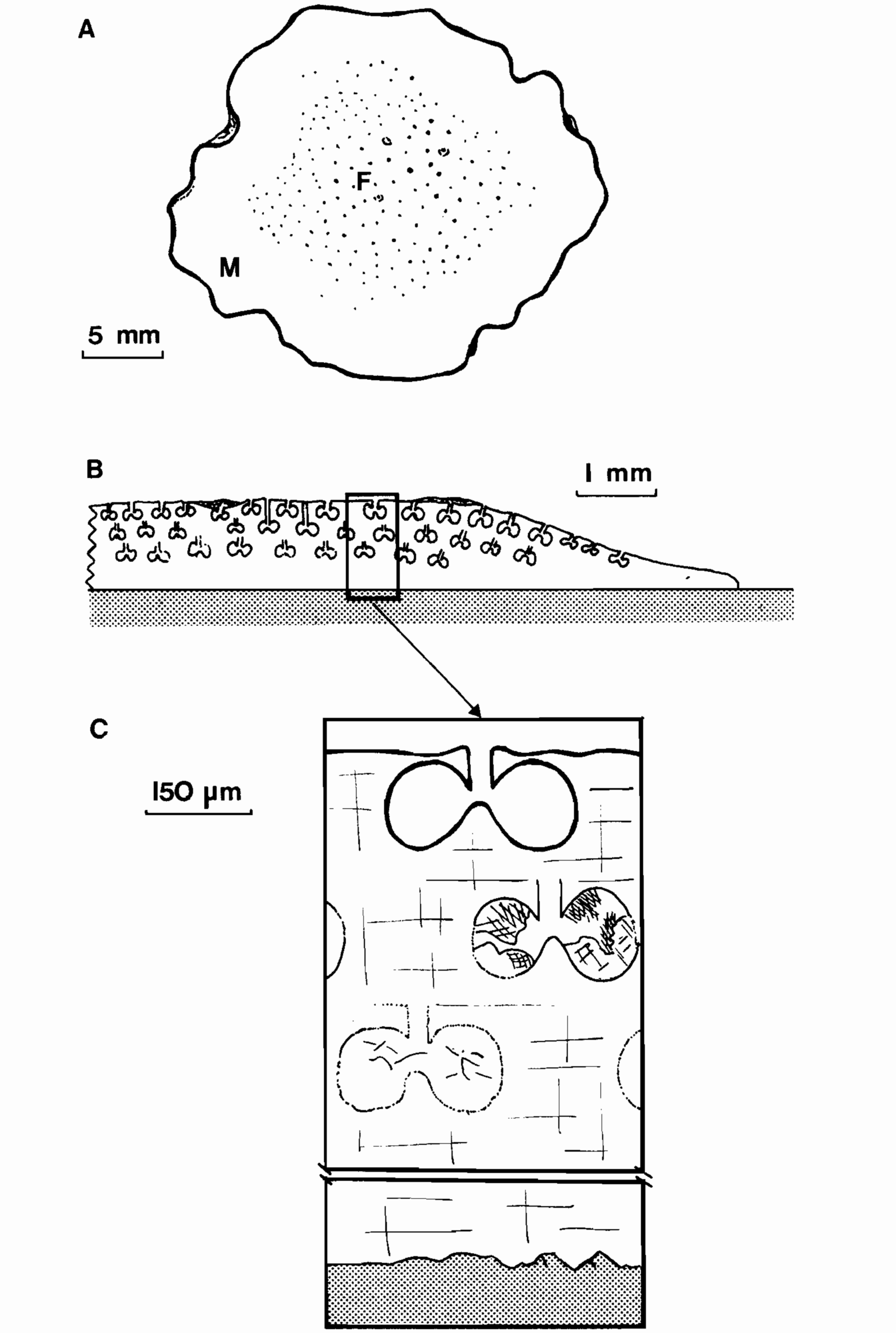

FIG. 1.

Morphology of *Lithophyllum incrustans*. (A) Surface of thallus showing the central fertile area, F, with the surface pores of conceptacles, and the sterile margin, M. (B) Cross section through an age class 3 plant showing the layered nature of conceptacles. (C) Close up of part of the cross section from (B) showing an active conceptacle at the surface and old conceptacles lower in the thallus becoming filled with calcium carbonate deposits.

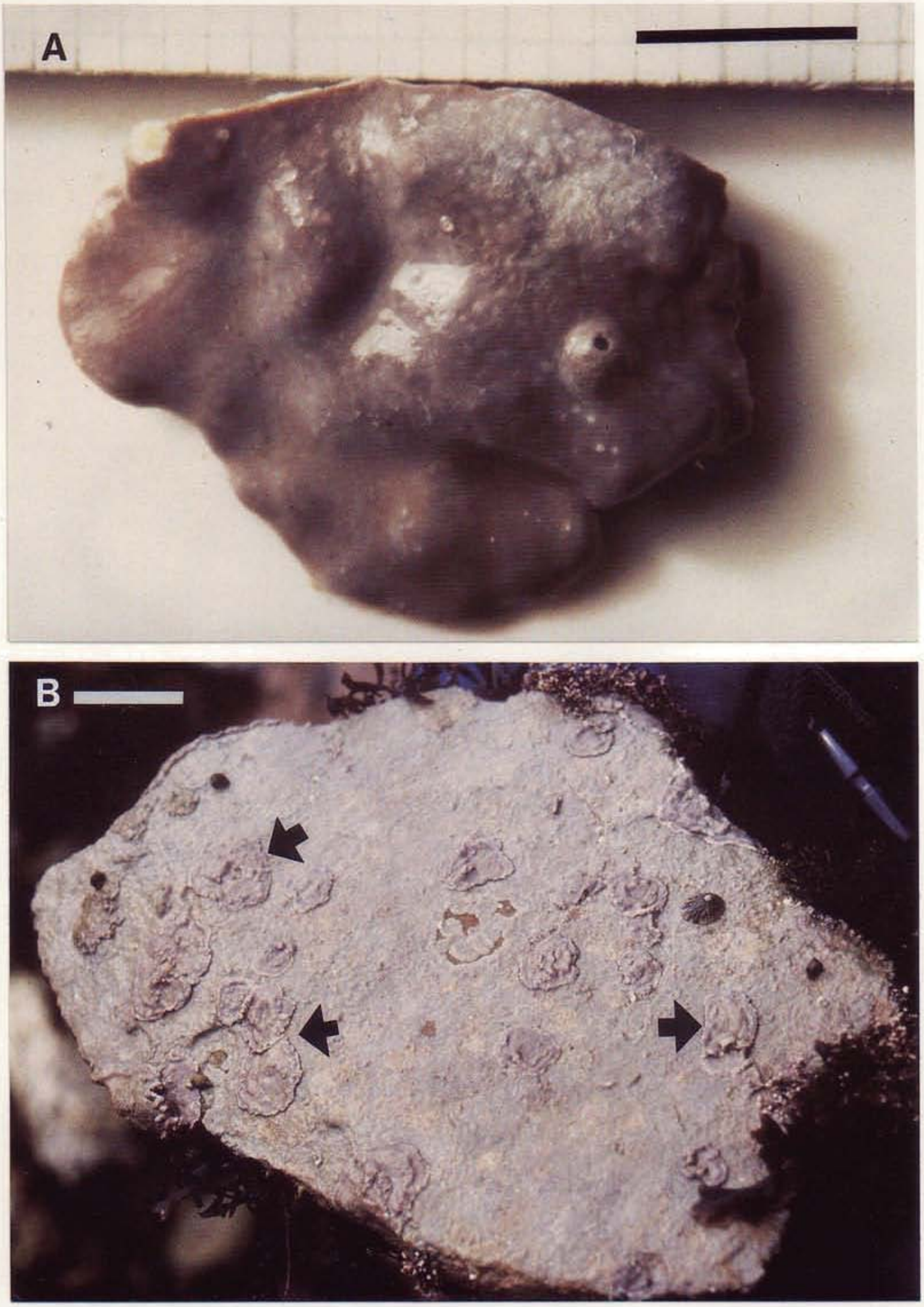

PLATE 1.

Lithophyllum incrustans. (A) Part of a thallus removed from the substratum. Note its bulky nature. Bar = 5 mm. (B) *Lithophyllum incrustans* growing on top of other coralline algae (examples arrowed). Note how the bulky morphology distinguishes this species from others. Bar = 5 cm. (Photograph courtesy of Dr L. A. Terry.)

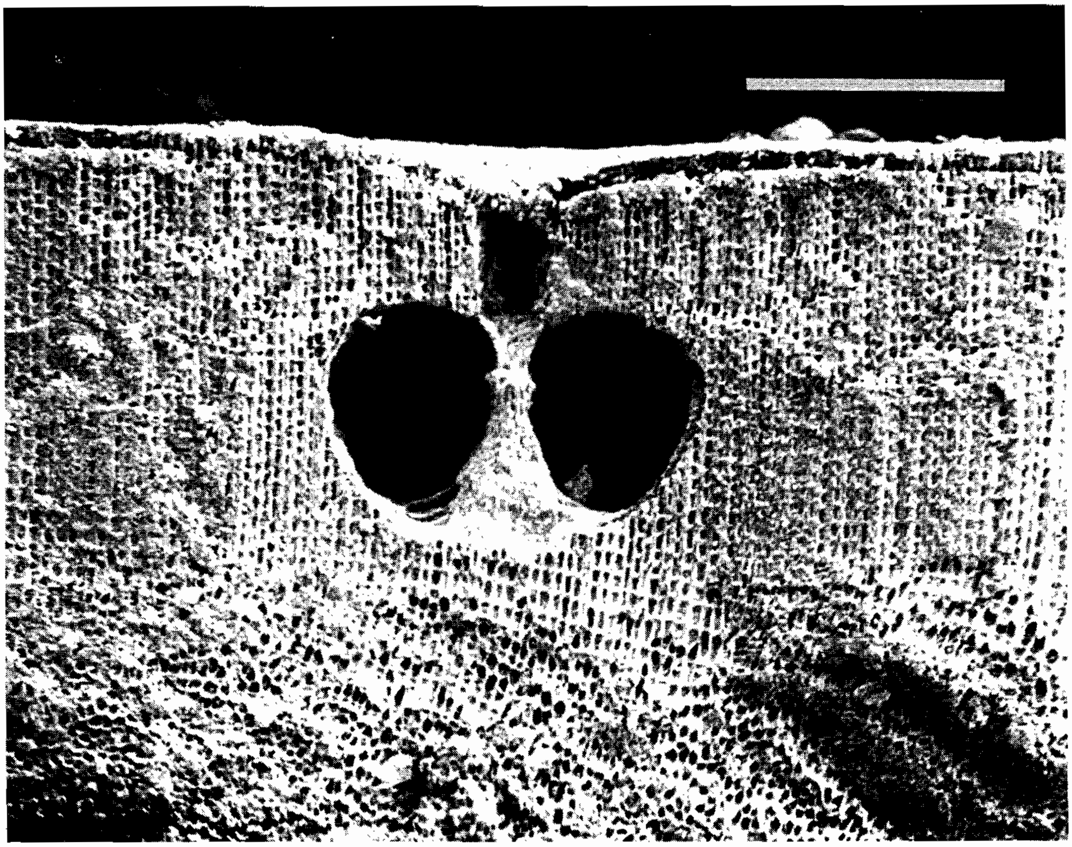

Fig. 2.
Scanning electron micrograph of a cross section through a thallus of *Lithophyllum incrustans* showing the characteristic shape of an asexual conceptacle. Bar = 200 µm.

makes *Lithophyllum incrustans* unique amongst the British corallines as it allows the age of plants to be readily estimated according to the number of conceptacle layers, age class 0 being plants up to 1 year old having no sign of conceptacles, age class 1 being in the second year of growth having 1 layer of conceptacles and so on.

Two types of reproductive spores, bispores and tetraspores, are produced by asexual plants, the production of tetraspores being correlated to the percentage of sexual plants (Edyvean and Ford, 1986). Both types of spore undergo a similar developmental sequence. The spores develop in sporangia from spore mother cells and they remain attached to the base of the conceptacle by a stalk cell until just before release. The developmental sequence of bispores in the conceptacle is shown in Fig. 3a–c. Once the spores are released they swell slightly, round off and separate into individual spores (Fig. 3d, e). A similar developmental sequence is shown by tetraspores, both within the conceptacle (Fig. 3f–h) and after release (Fig. 3i, j). Bispores are thought to form by mitotic divisions and to develop into asexual thalli. Tetraspores are thought to form by meiotic division and to develop into sexual thalli (Edyvean and Ford, 1986).

While the population biology of this species has been studied at various sites around Britain (Ford *et al.*, 1983; Edyvean and Ford, 1984*a, b*), no studies have, until now, been made of populations from Dyfed. This work was undertaken to determine the age structure, density and reproductive strategies of populations of *L. incrustans* in the vicinity of Orielton Field Centre for comparison with sites studied in other parts of the British Isles.

MATERIALS AND METHODS

Populations of *Lithophyllum incrustans* from a series of small intertidal rockpools were sampled at Manorbier (SS 056976), and at two sites in West Angle Bay (SM 851035). One of these was natural and the other an artificial pool created by staff from Orielton Field Centre in 1975. Collections were made between May 3–6 1985.

One hundred plants were sampled at each site along transects across the pools. Two diameters were measured on the nearest identifiable plant to every station, at 25 cm intervals, along the transect. These plants were collected, by chipping them from the base rock with a hammer and chisel, and taken to the laboratory for determination of age, sex, and the type of spores being produced by asexual plants. The plants were broken across the centre of the crust and the annual layers of conceptacles counted, using a low power binocular microscope (×15) to give an estimation of the age of the plant (Fig. 1b). Temperature and salinity shocks cause the conceptacles to release their contents and this was utilised to distinguish between bisporic and tetrasporic asexual plants. The thallus surface was scrubbed under fresh running water and the plant examined under the low power microscope (×25) with overhead illumination. Spores could be observed emerging from the conceptacle pores and differentiated into bispores or tetraspores. The density of plants in the natural pool at West Angle Bay was calculated by determining the surface area of the pool, to give an estimation of pool bottom area (the pool is shallow and flat), and then counting the total number of *L. incrustans* in the pool. Plants can be recognised from a diameter of about 5 mm upwards and while several individuals may be growing together the margins of each individual can usually be easily recognised. Density, in number of individuals per square metre, was determined from these data.

RESULTS AND DISCUSSION

The population parameters of *Lithophyllum incrustans* are given in Table 1. All three populations sampled show low percentages (3% or less) of sexual plants. All the sexual plants (a total of four) were male. Nearly all asexual plants were producing bispores. One plant was found to be producing tetraspores (at Manorbier) and one was found to be producing both bispores and tetraspores (also at Manorbier). The low level of sexual plants was surprising in view of the geographical cline in the occurrence of sexual plants from 0% in the north of Scotland to 35% or more on the south coast of Cornwall (Edyvean and Ford, 1984*a*). The low level in Dyfed indicates that the percentage of sexual plants in a population is not just correlated with latitude but is affected by other, perhaps more local, influences.

The age distributions of the populations are given in Figs 4, 5 and 6. All the populations show a stable age distribution with many young plants and rapidly diminishing numbers of older plants. If constant recruitment is assumed, the age structures correspond to Deevy Type II–III curves, in which the greatest risk of death occurs in the youngest age classes (Edyvean and Ford, 1984*a*). The age distribution of plants from the artificial pool constructed at West Angle Bay in 1975 shows no plants above age class 7 (Fig. 6). This reaffirms the assumption that conceptacles are formed in annual layers and implies that the

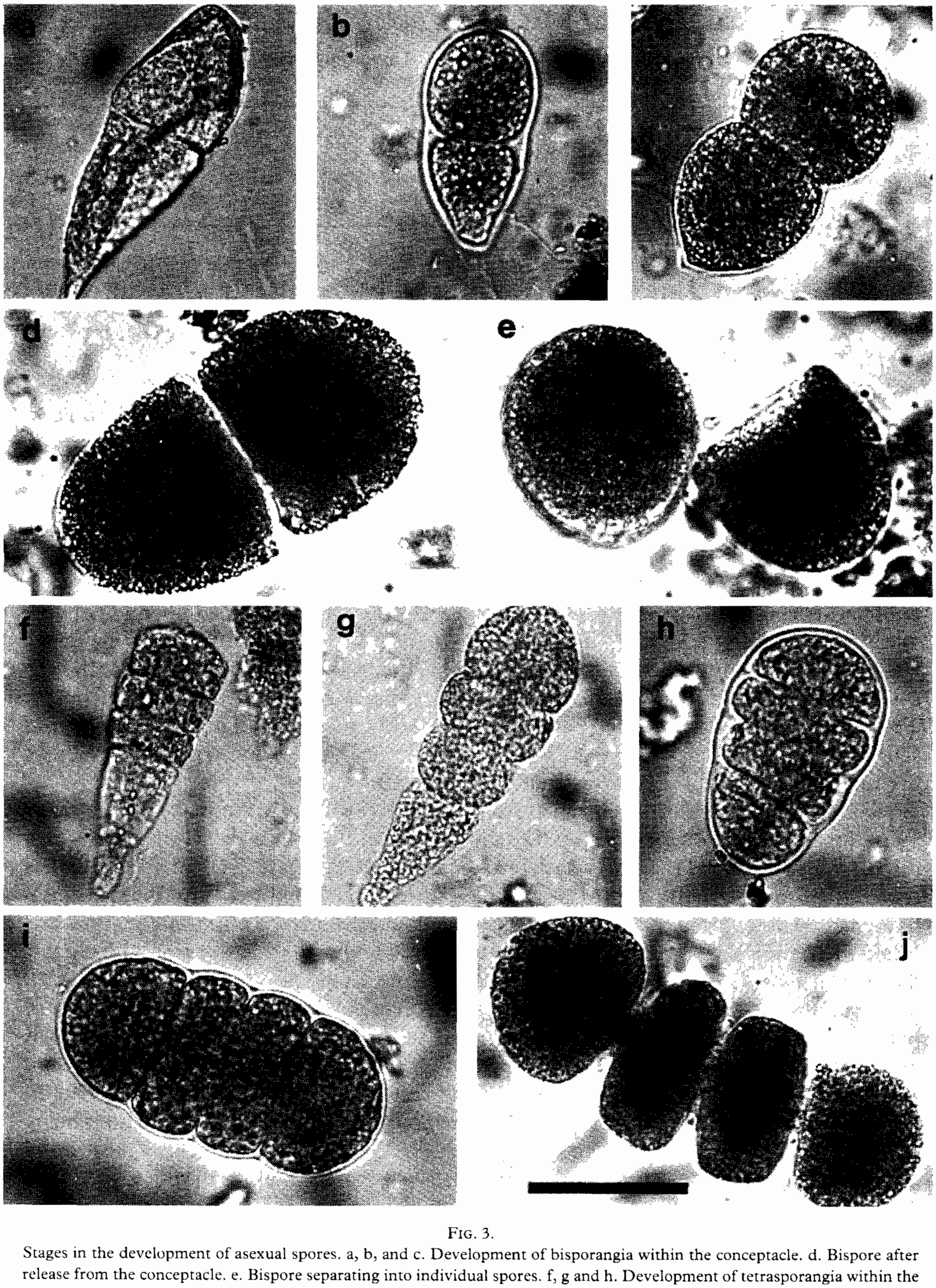

FIG. 3.

Stages in the development of asexual spores. a, b, and c. Development of bisporangia within the conceptacle. d. Bispore after release from the conceptacle. e. Bispore separating into individual spores. f, g and h. Development of tetrasporangia within the conceptacle. i. Tetraspore after release from the conceptacle. j. Tetraspore separating into individual spores. Bar = 50 μm.

Table 1. *Population parameters of* Lithophyllum incrustans *from south-west Dyfed*

Site	Percentage of mature plants		Percentage of mature asexual plants producing		
	Asexual	Sexual	Bispores	Tetraspores	Bi- and tetraspores
Manorbier	98.5	1.5 (♂)	96.8	1.6	1.6
West Angle Bay (natural pool)	97.0	3.0 (♂)	100.0	0	0
West Angle Bay	98.5	1.5 (♂)	100.0	0	0

oldest plant sampled settled in the pool in the winter of 1977–78. The lack of older plants, representing the 1975–76 and 1976–77 spore release periods may be due to two main factors. Firstly, there may be low numbers of older plants in the pool, which due to their scarcity did not occur in the sample, and secondly there may be a lag period before a new habitat becomes suitable for settlement. The pool was acid-cleaned when constructed and experienced initial blooms of ephemeral algae (diatoms, *Enteromorpha* spp., etc. (Dr R. G. Crump, *personal communication*). These adverse conditions, coupled with a low survival rate of spores being washed into the new pool on the rising tide (*L. incrustans* appears to release spores at low tide, which would facilitate settlement in the parental pool rather than other pools) could explain the lag period in colonisation. This situation was repeated in another artificial pool, constructed in 1980, which, by 1985, contained only a few, very small, individuals of *L. incrustans*.

The problem with determining population parameters from settled plants is that the early stages of reproduction, spore release, settlement and germination are ignored. The number of spores produced per plant is obviously very large, though the number of settled juveniles is relatively small. This indicates that the greatest mortality occurs between spore release and development to a viable size.

An idea of survivorship from spore release to the sessile growing plant can be made by performing some calculations on the combined data from all three sites. The average diameter (and thus surface area) was determined for each age class. Each mature plant has an actively growing sterile margin surrounding the central fertile area; thus the reproductively active area is somewhat less than the total surface area. This sterile margin was found to average 3.58 mm in width with little variation for age or size of plant. Using this figure, the average fertile area was also calculated for each age class of plant (Table 2). These data were then applied to the West Angle Bay natural pool where the density of plants was known (222.2 m^{-2}). The percentage of the population in each age class was determined for this pool from the results given in Fig. 5 and the total and fertile areas of *L. incrustans* in the pool were calculated. The results, given in Table 2, show that *L. incrustans* occupies a total of 15.77% of the pool floor with 10.18% of the pool floor being covered by reproductive tissue. This gives a figure of 101,837 mm^2 of fertile *L. incrustans* per square metre. Using this figure the reproductive output (numbers of spores produced m^{-2}) can be calculated. Previous work has shown that there are, on average, 5.4 conceptacles per square millimetre of fertile thallus surface (Edyvean and Ford, 1986) and each bisporic conceptacle produces an average of 32 individual spores (Edyvean and Ford, 1984*a*). This gives a figure of 549,920 conceptacles and 17,597,434 spores produced per square metre. In terms of survival the 17.6 million spores m^{-2} released each year result in

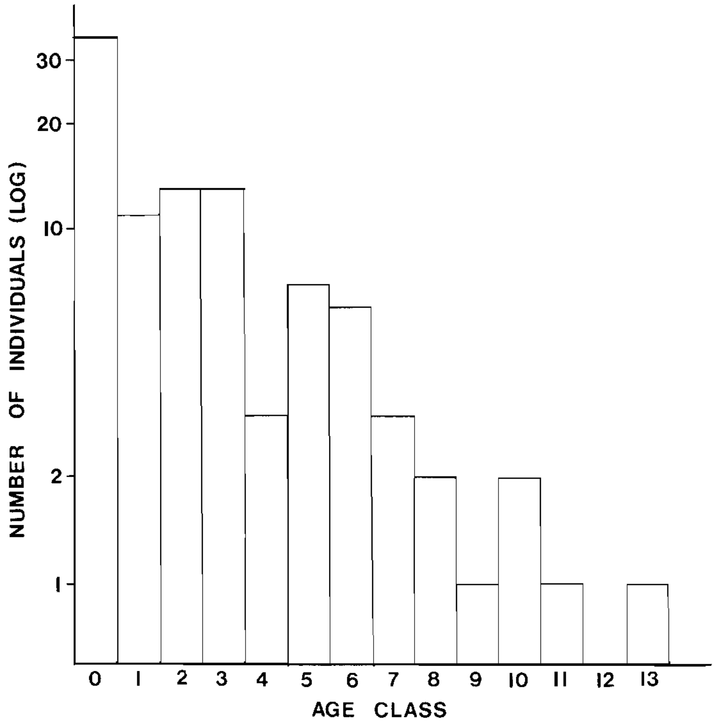

FIG. 4.
Age distribution of the *Lithophyllum incrustans* population from Manorbier.

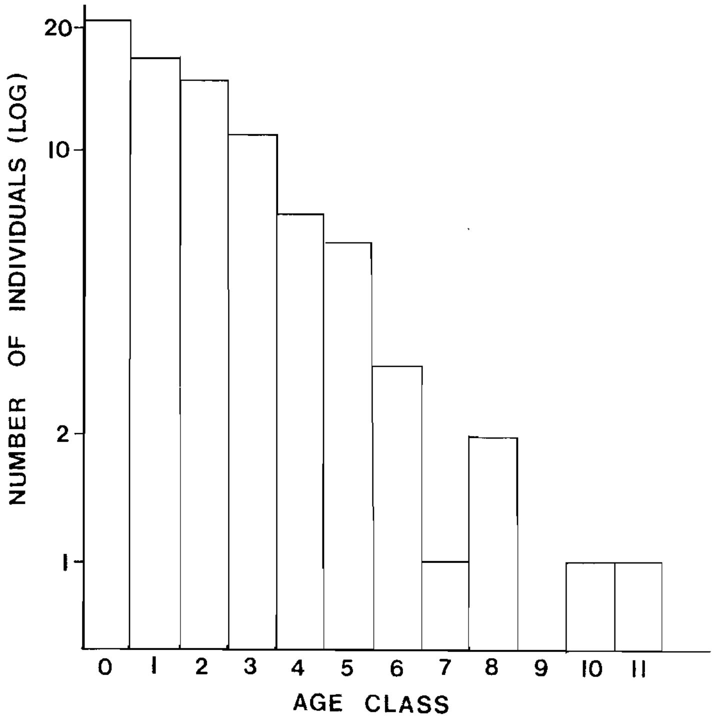

FIG. 5.
Age distribution of the *Lithophyllum incrustans* population from a natural rock pool at West Angle Bay.

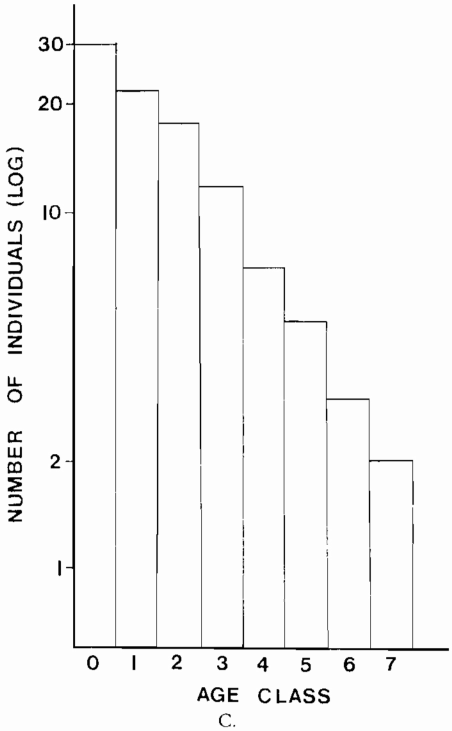

FIG. 6.
Age distribution of the *Lithophyllum incrustans* population from an artificial pool at West Angle Bay.

Table 2. *Age class, size and surface area parameters of* Lithophyllum incrustans *calculated for the West Angle Bay natural pool*

Age class	Percentage in age class	Average diameter, mm	Average fertile diameter, mm	Area occupied per sq m (sq mm)	Fertile area per sq m (sq mm)
0	24.70	7.99	0	2752	0
1	20.00	20.47	13.31	14626	6184
2	17.65	23.76	16.60	17390	8488
3	12.94	31.12	23.96	21857	12966
4	8.23	37.64	30.48	20350	13345
5	7.06	45.44	38.28	25443	18058
6	3.53	44.38	37.22	12132	8535
7	1.18	50.83	43.67	5321	3928
8	2.35	72.50	65.34	21550	17511
9	0	70.83	63.67	—	—
10	1.18	61.88	54.72	7885	6168
11	1.18	64.00	65.84	8436	6654
			Total	157742	101837

the recruitment of 54.89 age class 0 plants m^{-2}, a survival rate of 0.000003119% (3.1192×10^{-6}).

It could be argued that this figure is not a true representation of survival as, despite the spore release mechanism which favours spores remaining in the parental pool, there will be an unknown number of emigrant spores that survive and develop in other pools. However, it is equally likely that spores from other pools will develop in the pool under study and thus the calculation of survivorship is valid. The balance between emigration and immigration would only be upset if newly created pools were to be colonised. Such pools may be formed naturally, by the movement of rocks and erosion processes or, as in the case at West Angle Bay, artificially created by man. In such cases the pool may provide a suitable habitat without initially contributing spores for emigration, though even this would have only a very small effect on the survival rate.

The high spore mortality is typical of a species with a low cost/low survival reproductive strategy. Many spores will become food for planktonic organisms, or be grazed during the very early stages of settlement when they are still poorly calcified. Some sporelings will be outcompeted for space by their own or other species and others will settle in areas which are unsuitable for further development.

The data presented here can be used as the basis of a useful non-destructive student project. The field work (determining the density of plants in a pool) is straightforward once the species has been recognised and can be completed in one visit to the shore. A few plants can be collected for microscopical examination of thallus structure and spore release. The average data given in Table 2 are typical of most sites the authors have studied and, using them, students can perform the calculations shown above and determine the mortality of spores. Such a study provides a good practical example of a low-cost/low-survival reproductive strategy in an alga not normally studied on school/undergraduate field-trips.

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