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PROPAGULE PRODUCTION AND COMPETITION
IN SPECIES OF FUCUS

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A thesis submitted for the Degree of
Master of Science
in the Faculty of Science

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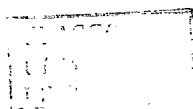
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SUMMARY

Several aspects of the ecology of Fucus propagules were studied.

To establish the order of magnitude of propagule production in Fucus, the rate of egg release for F. serratus was estimated in the laboratory, where it was found that the rate of release varied considerably between receptacles, but that there was a general trend to increased release during the second twenty-four hours in culture. This appeared to be associated with the trauma of introducing the plants to laboratory conditions. The rate of release appeared to be unaffected by different periods of exposure to air. It was estimated from the data that a fertile F. serratus plant may release fifty million eggs during a reproductive season and it was suggested that the eggs were released in a steady flow.

Little information was collected on the dispersal pattern of Fucus propagules once released. This was investigated on the shore for F. spiralis but was relatively unsuccessful, however, it was found that propagules preferentially settled in the minute depressions on the test substrata. This may be significant in providing the developing germling with protection from desiccation and grazers.

The density of propagule settlement was found to significantly affect the length, mean dry weight per plant and mean volume per plant of F. serratus, F. vesiculosus and F. spiralis germlings. The effect of density on the yield of a germling lawn was also recorded. These results appear to conform to the competition-density theory of higher plant studies.

A crowded stand of Fucus germlings was able to survive longer periods of aerial exposure in a tide-simulating apparatus than a sparse stand could. Crowding also appeared to have a very small protection effect against the grazer Littorina littorea, although crowding generally produced smaller individuals.

It is concluded that it would be beneficial for an upper shore species to recruit in dense lawns so that the germlings are better protected from desiccation and for mid to lower shore species to recruit in sparse lawns where rapid growth is required to escape the size class vulnerable to grazers. However, there is little evidence to suggest that they actually do so.

INTRODUCTION

INTRODUCTION

Most seaweeds release small, usually microscopic bodies as a means of reproduction, dispersal and colonisation. Such bodies may be termed 'disseminules' or 'propagules'. Propagules vary considerably in size and form between species and between stages in the life cycle of a species, some are motile, for example the zoospores produced by laminarian algae, whereas others are non-motile such as the carpospores and tetraspores of red algae. Sexually reproducing seaweeds generally produce non-motile oogonia and motile antherozoids although in many species of green algae both gametes are motile. Where there is an alternation of generations more than one type of propagule may be present but confined to different stages of the life cycle. The laminarian sporophyte, for example, produces zoospores and the microscopic gametophyte, oospheres and antherozoids.

Propagules vary considerably in size, in the brown algae they range from the minute laminarian zoospore 8-9 μm long (Kain 1979) to the large oogonia of Himanthalia elongata 250-300 μm in diameter (Gibb 1939); in the red algae they range from 34.3 μm in diameter for Chondrococcus carpospores (including their mucilage sheath) to 219.8 μm for the carpospores of Laurencia papillosa (Ngan and Price 1979); in the green algae the propagules are mostly small and vary little in size between species. Zoospores are generally larger than the oospores but still rarely exceed a size of 6 x 12 μm (Bliding 1963, 1968).

Propagules were described by Deysher and Norton (1982) as one of the most precarious stages in the life of any benthic organism.

Yet for most seaweeds they also represent the most important and indeed, often, the only dispersal mechanism. Despite their importance, propagules have been largely ignored by marine ecologists, in the past, attention has focused mainly on the adult plant. This is probably because on the whole, mature plants being macroscopic in size are easily recognisable on the shore. They also exhibit obvious changes in morphology and distribution with changing physical environments and are therefore attractive to study.

Propagules however present many problems to the investigator largely as a result of their microscopic size. It is very difficult to appreciate which factors are important in the environment of something only micrometres in dimensions and it is only recently that workers have tried to assess the environment on a scale appropriate to the size of propagules (Charters et al. 1973; Hruby and Norton 1979; Norton and Fetter 1981; Norton 1983). It is also very difficult to distinguish species at the propagule stage unless the parent plant is known.

However, a knowledge of propagule ecology is vital to an understanding of the ecology of the mature plant, for the distribution and abundance of benthic algae must initially depend on the production, dispersal, successful settlement and development of their propagules. In the past, particularly in colonisation studies, algal distribution patterns have been interpreted in terms of the seasonal availability of propagules (Rees 1940; Northcraft 1948; Harlin and Lindbergh 1977), the level on the shore and the type of substratum (Foster 1975; Harlin and Lindbergh 1977), but rarely has colonisation been considered in

relation to the size of the propagule inoculum and distance from the parent plant.

The fecundity of the parent plant is important in determining the number of propagules available to colonise at a given moment, so too is the duration of their release, whether they are liberated all at once or over a long period of time. The dispersal pattern of the propagules once released is also significant, if many propagules settle close to the parent they may experience severe intraspecific competition. However, if they are dispersed far and wide then intraspecific competition may be reduced, but at the risk of many propagules possibly colonising unsuitable habitats.

There are many areas of propagule ecology where the knowledge is less than rudimentary. Little is known about what happens to propagules, how many are released, where they settle and whether they influence each others development if they settle in close proximity. In an attempt to increase our understanding of the subject, the ecology of Fucus propagules was investigated. Fucus seemed an ideal species as the ecology of the mature plant is well-studied (Knight and Parke 1950; Burrows and Lodge 1951; Schonbeck and Norton 1978; 1979a; 1979b; 1979c; 1980a; 1980b), and the propagules are quite large, having a diameter of between 60 and 100 μm (Evans 1962). It also is one of the most common of the British intertidal algae and therefore readily available. There are also several species available for study each with a different reproductive season, so that propagules of at least one species would be available throughout the year.

These species commonly exhibit a vertical zonation on the shore,

the upper limit of their distributions being controlled largely by tolerance of prolonged desiccation during tidal exposure (Schonbeck and Norton 1978) and their lower limit by biotic factors, mostly competition with other fucoids (Schonbeck and Norton 1980a). Three species of Fucus were chosen so that certain aspects of their propagule ecology could be studied in relation to the vertical zonation of the mature plants. The three species were F. spiralis L. from the upper shore, F. vesiculosus L. from the mid-intertidal and F. serratus L. from the lower shore. Details of the ecology and morphology of the three species are given in Table 1.

For the purpose of this study the subject of propagule ecology was subdivided into three main areas of research,

- i) Fecundity of the parent plant
- ii) Dispersal and settlement of the propagules
- iii) Intraspecific competition between newly settled germlings.

<u>Character</u>	<u>Fucus serratus</u>	<u>Fucus vesiculosus</u>	<u>Fucus spiralis</u>
<u>Shape of frond</u>	Flat	Flat	Spirally twisted
<u>Usual length at maturity</u>	400-1000 mm	400-1000 mm	150-350 mm
<u>Vesicles</u>	Absent	Present	Absent
<u>Margin of frond</u>	Serrated	Entire	Entire
<u>Midrib and wings</u>	Both prominent	Both prominent	Both prominent
<u>Receptacles</u>	Flat and forked, with serrated margin	Swollen, pointed and sometimes forked	Swollen, rounded with distinct flattened sterile margin
<u>Reproduction</u>	Dioecious	Dioecious	Monoecious
<u>Fertile period (Firth of Clyde)</u>	September - May	April - August	May - September
<u>Habitat and distribution in the British Isles</u>	Lower part of rocky shores	Middle and Upper part of rocky shores	Upper part of rocky shores
<u>Local distribution (Isle of Great Cumbrae, Schonbeck and Norton 1978)</u>	Centred at Mean Low Water Neap	Centred at Mean tide Level	Centred at Mean High Water Neap

TABLE 1: Features of the reproduction, morphology and ecology of
F. serratus, F. vesiculosus and F. spiralis

CHAPTER I

RATE OF EGG RELEASE IN FUCUS SERRATUS

A. INTRODUCTION

The fecundity of algae has generated relatively little research interest, mainly because of the difficulties involved in capturing and counting the propagules released by a plant over its entire reproductive season. Several methods have been employed in estimating propagule production. Bags have been attached to sporophylls or receptacles in the field to catch released spores, propagule output has been monitored in the laboratory, and potential release has been calculated from counts of the number of propagules forming within a plant.

Spore production was quantified in the field for Macrocystis by enclosing intact sporophylls in polythene tubes for 15-30 minutes. The sporophylls were then removed and the spores counted (Anderson and North 1966). It was found that one cm^2 of sporophyll could release up to 76,000 spores per minute. There was considerable variation in the rate of release between plants and for the same plant at different times of the day. However it was possible to conclude that the average annual rates of release for healthy beds of Macrocystis lie in the range of 1,000-3,500 spores $\text{min}^{-1} \text{cm}^{-2}$ of sporophyll, which amounts to one adult plant releasing 8.64×10^9 spores per day (Neushul 1980). Spore production was also investigated in the laboratory, but sporophylls released ten times more spores in the laboratory than in situ (Anderson 1965; 1966; Anderson and North 1966). Propagule output was recorded in the

laboratory for Gelidium robustum and it was found that between 34,000 and 300,000 carpospores were released per plant per month and between 10,000 and 20,000 tetraspores (Guzmán del Prío et al. 1972).

Potential propagule output has been calculated for several species of seaweed. A fertile Rhodymenia pertusa plant was discovered to be a source of 83 million spores (Boney 1978) and the reproductive potential of Botrycladia pseudodichotoma was found to be 3.88×10^{11} tetraspores per day per adult female (Neushul 1980). It has also been calculated for Sargassum muticum, that a plant during its first reproductive season should be capable of releasing between 360,000 and 600,000 eggs, or even as many as 756,000 eggs (Norton unpublished).

From the few species investigated it can be concluded that the seaweeds are very fecund and may release millions of propagules per fertile season. In fact Kain (1975) estimated that for a Laminaria hyperborea forest during the reproductive season the number of spores released could amount to 3.3 million zoospores mm^{-2} of rock surface.

For this investigation it was decided to monitor propagule release in the laboratory because of the difficulties involved in securely attaching 'receptacle bags' to plants on the shore, without altering conditions surrounding the receptacle or causing damage to the plants. F. serratus seemed the ideal species for investigation because fertile material was available over a long period of time.

Reproduction in Fucus shows a clear-cut seasonal rhythm.

The exact onset of reproduction varies with geographical distribution and from year to year, but the whole process from initiation of gamete formation to the decay and loss of the reproductive apices may take most of a year (Knight and Parke 1950).

Gametangia are borne on a part of the thallus termed the receptacle, in small, flask-like depressions called conceptacles. The gametes are released from the conceptacles through a small opening, the ostiole. Thus prior to release, the gametes are in surroundings which show little environmental fluctuation regardless of changes that occur outside of the plant. In F. spiralis, a monoecious species, the male and female gametangia are borne within the same conceptacles, but both F. serratus and F. vesiculosus are dioecious and have male and female gametangia on different plants.

The oogonia develop directly on the inner wall of the conceptacle and in Fucus each oogonium produces eight oospheres. When mature, the oogonia have three-layered walls consisting of an inner endochiton, a mesochiton and an outer exochiton. The exochiton ruptures before release of the oogonium which passes into the sea enclosed within a two-layered wall. In the sea the mesochiton ruptures, then the endochiton dissolves, and the oospheres are liberated.

The male gametes are found within a two-walled structure, the antheridium. The antherozoids are released by rupture of the inner antheridium wall which occurs on immersion. Each antheridium

contains 64 antherozoids, 6 μm long and 1.4 μm in diameter.

They are motile, possessing paired flagella of unequal length.

No attempt was made in the present study to quantify the rate of release of antherozoids, although Baker (1910) did investigate this in relation to increasing periods of exposure to air. Antherozoids are even more difficult to collect and count than oospheres and thus were not studied, especially as the rate of release of antherozoids was not strictly relevant to the investigation.

B. METHODS

Fertile plants of F. serratus were collected from the stretch of shore between Keppel Pier and Farland Point, Isle of Great Cumbrae, Firth of Clyde (Figure 1). It was possible to determine the sex of a plant on the shore by examining the colour of the receptacles. The receptacles of a male plant when held up to the light were orange-brown and those of a female plant were green-brown. The preliminary identification was confirmed in the laboratory by examination of sections of receptacle under a microscope when oogonia or antheridia were clearly visible. Plants were returned to the laboratory in polythene bags where receptacles with 2-3 cm of vegetative thallus attached were examined from female plants and rinsed in seawater.

Egg release was monitored over 7 and 9 day periods by culturing the excised receptacles in a spore accumulator. This is a vertical perspex pipe 34 cm long by 12 cm in diameter and sealed at

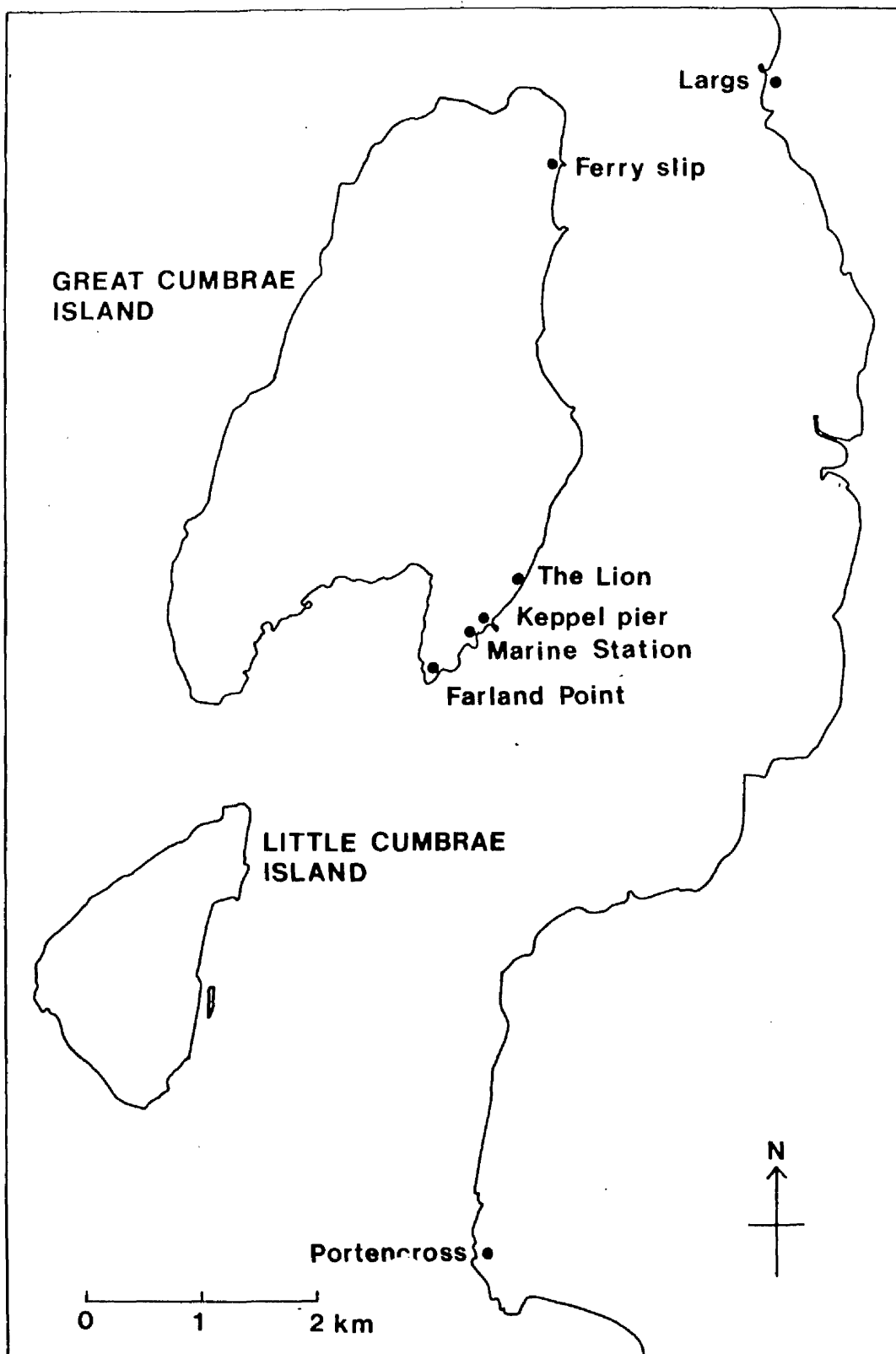


FIGURE 1: Part of the Firth of Clyde showing the location of the experimental sites.

(O.S. Map Sheet 63, 1: 50000 First Series)

the base. Air under pressure fed into the bottom of the pipe is broken into bubbles by a fine plastic mesh traversing the interior, 5 cm above the base. The bubbles surge to the surface of the culture medium filling the pipe, and the resulting turbulence prevents any oospheres in the medium from settling (Deysher and Norton 1982). Details of culture conditions are given in Appendix A, and the composition of the culture medium in Appendix B.

Several medium-sized receptacles were selected for each spore accumulator so that approximately the same surface area of receptacle was in each. As the receptacle in F. serratus is flat the surface area of each receptacle could be measured in cm^2 using a surface area meter (Lambda Instrument Corporation: Model LI-3000). The mean of ten readings for each receptacle was used and this value was doubled to account for both sides of the receptacle.

To simulate natural conditions on the shore at the lower end of the F. serratus zone, receptacles were removed from the spore accumulators and exposed to air for one hour, some received this treatment daily, some every third, fifth or seventh day and others received continuous submergence. However, this procedure was simplified to some receiving one hour of exposure daily and others continuous submergence. The experiments were terminated as soon as the receptacles started to decay. The culture medium was changed daily and to collect the released oospheres, it was poured into a beaker and the oospheres allowed to sediment out. Some of the supernatant was then carefully poured off and the remainder

removed by pipette until the oosphere suspension was just sufficient to fill a 3.5 cm diameter petri-dish. The petri-dish was placed on graph paper and the number of oospheres in each of 15 regularly spaced mm squares was counted, using a binocular microscope. Care was taken not to move the oospheres when moving the petri-dish across the field of view. It was thus possible to estimate the total number of oospheres in the dish. When only a few oospheres were present, for example less than one hundred, all the oospheres in the whole dish were counted. Oospheres were counted and not oogonia because over the collection period the majority of the oogonia had ruptured and released their oospheres. Each oogonium contained eight oospheres so when an intact oogonium was found it was counted as eight oospheres. No test was made of the viability of the eggs.

The effect of exposure to air on the number of eggs released was investigated by laying excised receptacles for varying lengths of time on absorbant paper in a constant temperature room. The periods of exposure used were 1, 2, 3, 4, 5, 7 and 9 hours. Each receptacle after a period of exposure was placed in a 150 ml flask of culture medium, sealed with aluminium foil and left for 24 hours in the constant temperature room. Three replicates were used for each exposure and the whole experiment was immediately repeated with the same material. The eggs were collected using the method described above.

It was observed that receptacles released a moderate number of eggs during the first 24 hours in culture but that there was a

substantial increase in propagule output during the second 24 hours of culture. It was decided to investigate this further.

Plants were collected and divided into two groups. Plants in group one had their receptacles excised immediately after they were introduced into the laboratory. These receptacles received different periods of exposure to air before being allowed to release for 24 hours whilst submerged. The numbers of oospheres released were recorded and the experiment repeated. Group two plants were left intact for 24 hours, immersed in tanks of seawater. Their receptacles were then excised, exposed to air for different lengths of time and left to release for 24 hours whilst submerged. The numbers of oospheres released were then counted.

C. RESULTS

C.1 Egg release over time

The numbers of oospheres released by receptacles during the seven and nine day investigation periods are presented in Tables 2 and 3. The data from the two different treatments of daily one hour exposure to air and continuous submergence were amalgamated as they appeared to have had no effect on the overall trend in egg release. The number of oospheres collected varied considerably from day-to-day and between spore accumulators. The greatest number collected over 24 hours from seven receptacles was more than 200,000 and the least was eight.

Days from start of experiment	Number of Oospheres	
	Mean	Range
1	14,939	100 - 36,786
2	76,672	4,294 - 211,143
3	3,081	73 - 10,200
4	11,135	1,633 - 44,100
5	1,649	146 - 6,100
6	159	48 - 315
7	35	8 - 56
8	22	8 - 48
9	28	8 - 56

TABLE 2: The mean number of oospheres (and range) collected from seven spore accumulators each containing seven F. serratus receptacles. The mean number of oospheres released per receptacle on day one was 2,134.

Days from start of experiment	Number of Oospheres	
	Mean	Range
1	3,462	1,338 - 6,344
2	18,250	10,800 - 28,967
3	2,170	681 - 4,033
4	1,180	440 - 2,830
5	1,527	808 - 2,533
6	6,550	833 - 12,833
7	24,028	244 - 55,125

TABLE 3: The mean number of oospheres (and range) collected from four spore accumulators each containing seven F. serratus receptacles. The mean number of oospheres released per receptacle on day one was 495

The number of oospheres released declined with time in experiment one but not in experiment two, where the most oospheres were collected on the last day observations were made. One trend which features in both tables is a peak in the number of oospheres released on the second day that the receptacles were in culture.

C.2 The effects of exposure to air

Results from the investigation into the effect of exposure to air on oosphere release are shown in Table 4. It is impossible to detect any significant trends in the data associated with an increase in the period of exposure to air because the variation in oosphere release between receptacles is very large. The greatest number of oospheres collected per receptacle on day one was over 15,000 and the least was zero, with a mean of 1,287 oospheres receptacle⁻¹. On day two the greatest number collected was 173,800 and the least was over 5,000, with a mean of 78,059 oospheres receptacle⁻¹. This indicates a 10-100 fold increase in the number of oospheres released by receptacles from day one to day two.

An increase in the number of oospheres released by receptacles during the second day of culture had been observed on other occasions, and therefore was considered to be worthy of further investigation.

Time in culture (hours) Period exposed to air (hours)	28		48	
	Mean	Range	Mean	Range
0	992	109 - 2,200	73,000	16,100 - 170,450
1	70	0 - 210	58,048	5,433 - 126,643
2	558	149 - 883	70,822	23,900 - 99,100
3	5,737	150 - 15,633	123,133	57,850 - 164,150
4	89	16 - 236	47,933	41,350 - 58,900
5	526	16 - 1,546	105,100	56,600 - 173,800
7	43	24 - 56	91,783	58,200 - 138,650
9	2,269	56 - 6,400	54,650	20,350 - 95,550

TABLE 4: The mean number of oospheres (and range) released by a F. serratus receptacle in 24 hours after different periods of exposure to air, for the first and second days in culture. The receptacles used had a mean surface area of $30.02 \text{ cm}^2 \pm 2.02 \text{ cm}^2$ (S.E.).

C.3 The effects of receptacle excision

The number of oospheres released may increase on day two in the laboratory in response to an environmental stimulus. It is unlikely that the large release of eggs is the norm because where the receptacles were cultured for several days a large release of eggs was not maintained. It was hypothesized that the 'second day peak' was a delayed response to the plants being removed from their natural habitat. It was impossible to isolate all of the changes that occurred when a plant was removed from the shore and introduced to the laboratory, but an obvious one to investigate was the excision of the receptacles. Plants introduced to culture at the same time were divided into two groups and by removing the receptacles from one group immediately, but not from the other until 24 hours later it was possible to differentiate between the effect of excision and any other effects. If the plants were responding to changes in the environment between the shore and the laboratory then an exaggerated rate of release would have been found in both groups. However if it was a specific response to the excision of receptacles then only those plants which had had their receptacles excised immediately would have shown an increased rate of egg release.

It was found that receptacles immediately excised released a mean of 276 (\pm S.E. of 83) oospheres per receptacle on day one (Table 5) and showed no obvious response to the different periods of exposure to air. On day two the mean number of oospheres released per receptacle was 17,386 (\pm S.E. of 5,756), an increase of 60-fold

Sample	A		B
Time in culture (h)	24	48	48
Time of excision of receptacles after introduction to culture (h)	0	0	24
Period of exposure to air (h)			
0	32 8 - 72	15,301 1,302 - 35,700	527 231 - 1,042
1	876 24 - 1,446	10,905 820 - 19,767	8,205 2,865 - 13,250
2	249 8 - 532	10,848 310 - 18,433	23,020 459 - 47,633
3	206 48 - 498	13,652 2,819 - 35,188	23,654 1,632 - 64,067
4	124 8 - 276	9,167 2,800 - 20,401	20,300 12,333 - 35,833
5	347 16 - 750	4,750 2,178 - 6,321	24,385 1,022 - 52,133
7	405 24 - 917	6,248 1,975 - 13,920	16,531 4,093 - 27,033
9	13 8 - 24	19,514 2,350 - 53,300	3,233 1,500 - 4,967

TABLE 5: The mean number of oospheres (and range) released by a F serratus receptacle in 24 hours after different periods of exposure to air, for immediately excised receptacle (A) and for receptacles left intact for 24 hours (B)

and day two. Receptacles left intact overnight released an average of 14,982 (\pm S.E. 3,700) oospheres per receptacle, and again showed no response in the number of oospheres released to the different periods of exposure to air.

The results were very similar for the receptacles left intact and for day two, of those immediately excised. This suggests that the 'second day peak' is not a response to the receptacles being excised but a response to some other change(s) in the environment.

D. DISCUSSION

The rate of egg release from receptacles during their first day in the laboratory suggests that a F. serratus receptacle may release up to fifteen thousand eggs in a single day. If this approximates to the magnitude of actual release in the field, then using Vernet's unpublished observation that an average plant bears 70 receptacles (although as many as 4,000 receptacles were recorded on one plant by Knight and Parke 1950) indicates that in the order of one million eggs per day would be released. Extending this rate of release over a fertile period of 1-2 months means a F. serratus plant represents a potential source of approximately 50 million eggs. Vernet (personal communication) calculated the potential egg production of F. serratus and other fucoids from the number of receptacles per plant, the number of conceptacles per receptacle and the number of oogonia per conceptacle. He found that each plant had a potential supply of 10-20 million eggs. The discrepancy between the two estimates may be explained by the different methods used to derive them. Vernet based his estimates on the number of oogonia and receptacles present at the time of sampling, however it is possible, indeed likely, that more conceptacles would develop and mature during the reproductive season. Alternatively, if the plants were sampled late in the fertile season, it was possible that many eggs may already have been released, also producing a low estimate of the number of oogonia per conceptacle. The method employed here may over-estimate propagule production because it assumes a constant rate of release over one to two months when in

fact the rate of release may be reduced at the beginning and end of the reproductive season, and not all receptacles or conceptacles may release all the time. The release rate in culture may also be higher than occurs on the shore due to some trauma associated with introducing plants to the laboratory.

Receptacles of F. serratus ripen progressively, releasing oogonia from the proximal end of the receptacle first and then maturing acropetally so that those in the developing apex are released last (Evans 1962). This means that although a receptacle may have a potential of millions of eggs only a proportion will be mature at once and some may never reach maturation. Egg release is thus a steady dribble of several thousand eggs per day from each receptacle, unless a change in the environment stimulates the release of greater numbers. Plants appear to receive such a stimulus when introduced into the laboratory. The stimulus may be a specific change in the environment such as temperature, irradiance or culture medium or a combination of changes. Introduction to the laboratory has been reported to have the same effect on propagule production in Macrocystis (Anderson 1965), although nothing has been suggested as to the nature of the stimulus. However Anderson (1965) did find, as in the present investigation, that propagule release was not affected by excision of the reproductive structures.

Plants of Fucus serratus may release 10-100 times more eggs per day after 24 hours in the laboratory than when first collected. This means that the eggs released in one day in the laboratory

would, in nature, have been released over a longer period, perhaps several days or even weeks. Thus some of those released in culture may be immature and infertile. This could be an important factor when collecting gametes to use in the preparation of cultures and may be worthy of investigation.

It has been reported that the number of gametes released by several species of fucoids increases in response to an increased period of exposure to air (Baker 1910). After a period of exposure on the shore at low tide it is possible to observe exuded gametes on the surface of receptacles, ready for dispersal by the rising tide. However the results of present experiments indicated that drying does not promote egg release nor is there any increase in egg release associated with increasing exposure to air.

Baker (1910) investigated the effect of exposure to air on egg release in an experiment carried out on the shore. Specimens were collected as the tide ebbed and then were left in a large rock pool until required. The plants were carefully washed, and exposed to the open air, by leaving them lying on flat stones on the shore for different periods of time. Baker then covered the dried receptacles with a measured quantity of water, after trimming them so that there were 200 conceptacles in each receptacle. After 12 hours the receptacles were removed and the number of oogonia in the water was counted with the naked eye. The results Baker obtained are shown below.

Hours exposed to air	9	3	2	1
Replicates	187	67	64	28
	151	140	72	52
	171	240	-	18
Mean	169	145	68	33

TABLE 6: The number of oogonia released by pieces of receptacle, containing 200 conceptacles, in 12 hours after receiving different periods of exposure to air (Baker 1910)

Baker concluded that increased exposure to air promoted egg release. However a single-factor analysis of variance carried out on these data did not indicate a significant relationship due to the large variation between replicates.

Large variations in the number of eggs released from receptacles seems to be common-place. Baker recorded smaller variations in the rate of release than found in the present study but as she used only 200 conceptacles and not whole receptacles this would eliminate some of the variables such as the number of conceptacles per receptacle.

The results suggest that even if receptacles do release more oogonia after a period of exposure to air the natural variation in the rate of egg release is so large as to make such small changes insignificant.

The study by Baker provides a useful comparison of the rate of egg release on the shore for the present investigation. The mean number of oogonia collected by Baker from the receptacles exposed to air for up to three hours was 82 per 200 conceptacles. When this was converted to number per receptacle (assuming 334 conceptacles per receptacle, Vernet unpublished) per 24 hours and then multiplied by eight for the number of oospheres per oogonia, a figure of 2,191 was produced. This is of a similar order to the results obtained for receptacles on day 1 in the laboratory, which suggests that laboratory studies, if confined to the first 24 hours of culture may provide a realistic estimate of what is happening in the field.

CHAPTER II

DISPERSAL AND SETTLEMENT

A. INTRODUCTION

Dispersal is a vital stage in the life cycle of seaweeds. It allows annual species to colonise new areas and perennial species to maintain an established population and extend it. Short distance dispersal ensures a dense settlement of propagules in a habitat which favoured the development of the parent plant, and should therefore suit the progeny. On settlement however, the propagule must compete with both established parent plants and crowds of sibling germlings. Long-range dispersal means that a few plants will colonise suitable areas free from others of their own kind, but at a high risk of mortality due to the uncertainty of the new habitat and the long duration of the planktonic phase.

The distance propagules are dispersed before they settle on the substrata will depend on several factors, namely the size of the inoculum and height from which it is released, the direction and velocity of the current; and the motility and sinking velocity of the propagules.

Little information has been collected on how the size of the inoculum effects the dispersal of algal propagules. However one study of Macrocystis (Anderson and North 1966) showed that spore dispersal was more restricted for a single plant than for a population of plants. The maximum dispersal distance of spores from an isolated plant was only 5 m and the number of juveniles decreased inversely as the cube of the radius of dispersal, whereas from a group of plants

the propagules reached over 70 m distant, and the fall off in numbers with increasing distance was not so marked.

The height of the propagule source may range from millimetres to metres. Obviously the greater the height from which spores are released the further they are likely to travel. Many of the larger seaweeds do not bear reproductive structures on their longest laminae, Alaria esculenta, for example, has sporophylls low down on the stipe so that they are only a few centimetres above the substratum. Alaria esculenta lives in very exposed habitats and so a low height of release may compensate for the high water velocities. The sporophylls of the giant kelp, Macrocystis pyrifera, are borne on short basal shoots, usually not more than 30-60 cm in length, whereas some of the vegetative laminae have stipes of 500 cm or more in length (Delf and Levyn 1926). Nereocystis however does have its reproductive structures on the laminae many metres above the substratum, but instead of releasing zoospores individually, large pieces of tissue break away and descend rapidly through the water, only then are the spores released (Nicholson 1970). The height from which propagules are released, therefore, is quite small even for the larger species, and the potential dispersal distance is not as great as might be inferred from the size of the plants.

The direction of the prevailing current will determine the direction of dispersal, but it is common for the direction of the current to change with the ebb and flow of the tide. Therefore dispersal, although always down current, could actually be in more than one direction. However, if propagules are released so that they are dispersed on first immersion, for example, then the direction of the incoming tide may be the more important.

In Japan, where Monostroma is grown commercially, it was noticed that the location of the Monostroma growing areas changed from year to year and was closely correlated with the main surface current of the Spring tide (Segi and Kida 1960). Similarly an area of shore colonised by Fucus zygotes was found to have received its inoculum from zygotes dispersed on the rising tide, (Burrows and Lodge 1950). The dispersal of juveniles from an adult plant of Gelidium cartilagineum was also found to follow a specific direction, presumably determined by the direction of the major current (Guzmán del Prío and de la Campa de Guzmán 1969).

The power of movement of motile zoospores is very small compared to the movement of water currents. Current velocities of up to 14 ms^{-1} have been reported by Jones and Demetropoulis (1968) and Vogel (1981) suggested these may actually have been as great as 16 ms^{-1} . Even for a very sheltered bay Muus (1968), using dissolving plaster balls, recorded current velocities of 0.2 ms^{-1} . Zoospores of Macrocystis have been estimated to swim at a rate of 0.33 mh^{-1} and under the microscope they frequently changed direction and showed no tactic responses (North 1972). It would seem therefore that the motility of zoospores plays only a minor role in their dispersal, however it may play a more important part in the settlement of spores once they have reached the calm water of the boundary layer, close to the rock surface.

The sinking velocity of a propagule may also influence how far it will be carried by the tide before it reaches the rock surface. The sinking rates of eleven species of red algae have been studied

by allowing the propagules to fall through the field of view of a horizontally-positioned inverted phase microscope. In general it was found that the sinking velocities of the spores increased with increasing size (Okuda and Neushul 1981). However the actual size of the red algal spores was considerably under-estimated as the authors did not include the thickness of the substantial mucilage sheath in their measurements.. In Sargassum muticum the sinking velocity of the propagules also increased as they increased in size, until the development of protruding rhizoids increased their form drag and slowed the rate of descent. However the stage of development of the majority of the germlings, when released from the parent plant, was that which sank most rapidly (Norton and Fetter 1981).

The greatest sinking velocity of 0.68 mm s^{-1} for Sargassum (Norton and Fetter 1981) is small compared to the velocity of water currents. Spores are much more likely to be flung against the rock surface by the turbulent structure of the water flow passing over the substratum. The importance of turbulent deposition in relation to sedimentation obviously increases with current speed and so is likely to be of over-riding importance in most situations in the sea (Norton and Fetter 1981). Sedimentation may be important in areas of still or slowly flowing water, for example in dense algal stands in sheltered bays or in the boundary layer of water close to the substratum. The sinking velocity of an algal propagule may also become more important in long distance dispersal. The vertical distribution of seaweed spores in a 20 m water column 30 km off the coast of North Carolina

was documented by Amsler and Searles (1980). The small spores of green algae and bangiophycidean red algae were found throughout the water column, whereas the larger propagules of brown algae and florideophycidean red algae were found near to the bottom of the water column. This reflects the greater sinking velocity of the larger spores. Interestingly, in this example the algae with small spores and hence a greater dispersal shadow were the opportunistic species and those species with large spores and consequently shorter dispersal distances were the typically secondary colonisers. However this may be simply because most opportunists tend to be green seaweeds. In an analogous situation of tiny, slow-falling fungal spores in the atmosphere, Hirst and Hurst (1967) found that spores of different sizes drifted in large discrete clouds with larger spores at lower altitudes. This was interpreted as reflecting the gradual sedimentation of the spores during their lateral drift, with larger spores sinking faster.

Several species liberate propagules in association with a slime secretion so that the spores are held together in groups by the mucilage and thus may have increased sinking velocities. However this effect will depend very much on the density of the slime secretion, if the mucilage is very much less dense than seawater then it may help the spores to remain afloat and could in fact increase their potential dispersal distance. Mucilage secretion is associated with propagule release in many red algae Grinnellia americana (Brannon 1897), Gracilaria verrucosa (Oza and Krishnamurthy 1969); Rhodymenia pertusa (Boney 1978) and Hypnea (Mshigeni 1976a).

Liberation of carpospores and tetraspores from Dumontia incrassata involves the sloughing of surface plant tissue (Kilar and Mathieson 1978) which again may mean an increased sedimentation rate as the spores are released in groups. Norton and Fetter (1981) noted however, that groups of Sargassum muticum propagules sank faster than individuals only if they were in tight clusters, and that loose rafts of propagules sank more slowly than did isolated individuals.

The possible significance of differential dispersal by having propagules with different sedimentation rates has yet to be appreciated. For example the carpospores in most red algae are larger than the tetraspores (Mshigeni 1976b; Ngan and Price 1979) and have greater sinking velocities (Okuda and Neushul 1981). Also in Hypnea mucilage secretion is only associated with carpospore release which again suggests that carpospores may be better adapted for sinking than tetraspores. Why this should be so is not fully understood. What is really needed is an investigation into the type of spores settling at different distances from the parent plants.

For the sexually reproducing seaweeds, where the male and female organs are borne on different plants, there must be a critical dispersal distance. This occurs where the distance separating the gametophytes exceeds the distance an antherozoid could traverse. However, the distance an antherozoid can cover will be aided, or even impeded, by water currents. Experimental attempts to determine the critical distance for Macrocystis were unsuccessful (North 1972).

In the sexually reproducing seaweeds there exists some doubt as to whether the dispersal phase is primarily the zygote or the gametes.

There would be a greater fertilisation success rate if fertilisation occurred immediately after gamete release and the zygotes were dispersed, as in Sargassum muticum (Fletcher 1980). A study by Pollock (1970) on Fucus distichus also suggested that here too fertilisation occurred very soon after gamete release, within less than 20 minutes. However, this study was carried out in calm water in the laboratory, in the sea where the water is turbulent the sperm suspension would be diluted and the eggs dispersed, making the chance of fertilisation less likely.

If gametes are the main dispersal phase the chances of fertilisation would be greatly reduced by the effects of dilution. It is likely that both zygote and gamete dispersal occur to some extent, although the evidence suggests that it is primarily the zygote that is dispersed as the seaweeds have adopted a variety of methods by which the chance of immediate fertilisation is increased.

Gamete release has been shown to exhibit a regular periodicity related to the lunar and tidal cycles for several species, thus ensuring a synchronous availability of large numbers of male and female gametes. This has been reported for the green algae Cladophora (Fritsch 1945), Enteromorpha intestinalis (Christie and Evans 1962), Monostroma (Ohno 1972), and Ulva (Smith 1947); the brown algae Dictyota dichotoma (Williams 1905), Himanthalia elongata (Gibb 1938) Pelvetia canaliculata (Subrahmanyam 1957) and Sargassum (Tahara 1909; Fletcher 1980; Norton 1981) and for the red algae Gloiopeltis and Hijikia fusiforme (Boney 1965).

Other species respond to different stimuli. In Zonaria (Liddle 1968) and Dictyota binghamiae (Foster et al. 1972) egg release is

triggered by light. Pelvetia fastigiata (Jaffe 1954), Sargassum muticum and the gametophytes of Laminaria japonica do not release gametes under continuous illumination but can be stimulated by a single dark period (Norton 1981).

As mentioned earlier, intertidal plants may be stimulated to release by slight drying out, as occurs during low tide, so that freshly released gametes would be intermingled by the rising tide. In some species the male and female gametes are found in the same conceptacle. Of the fucoids common to the British Isle it is only Fucus spiralis and Pelvetia canaliculata that are monoecious. These two species occupy the highest levels of the intertidal and are less frequently covered by the sea and for shorter periods of time than other intertidal fucoids. In contrast the inhabitants of the lower shore F. vesiculosus and F. serratus are both dioecious but they are regularly submerged and so have greater opportunity for release of gametes and subsequent fertilisation.

The chance of fertilisation occurring can also be increased if instead of both male and female gametes being released into the sea one is retained on the parent plant. In several monoecious species of Sargassum the ova are retained by a stalk on the outside of the conceptacle so that they are not dispersed (Fletcher and Fletcher 1975). The oogonia of Hijikia fusiforme (Boney 1965) and Laminaria hyperborea (Bisalputra et al. 1971) gametophytes are also retained in this way.

Oospheres are dense, spherical objects and so sink quite rapidly once released (Fritsch 1945), the antherozoids on the contrary are motile, not very dense and therefore more buoyant. However, they are known

to be negatively phototactic and negatively aerotactic, but positively geotactic (Fritsch 1945) presumably therefore they will sink and follow the ova, thus again increasing the chance of fertilisation. In the red algae, Tiffaniella snyderae, the spermatia are exuded and retained in slime strands containing 8-21 spermatia. The strand remains attached to the male plant and is contracted or extended by water movement so that it is brushed over the female trichogyne (Fetter and Neushul 1981). It is also postulated that the sticky strands of spermatia may become detached and subsequently adhere to a female thallus, thus bringing male and female into even closer contact.

There is a certain amount of chemotactic attraction between ova and antheridia as a result of pheromones excreted from the ova. These substances have been isolated for Ectocarpus, Cutleria and Fucus and are termed Ectocarpen, Multifiden and Fucoserraten respectively. A similar chemical is thought to stimulate release of male gametes and attract them to oogonia in some of the laminarians but has not yet been identified (Müller 1980). These chemicals appear not to be effective more than 0.5 mm distant from female cells. This would suggest that chemotactic attraction is only a very short-distance phenomenon (Müller 1981).

The ratio of male and female gametes is also an important factor in successful fertilisation, the greater the proportion of male gametes the better the chance of the oogonia being fertilised. In the fucoids each oogonium emitted from a conceptacle may contain one, two, four or eight oospheres depending on the species, but there are always sixty-four spermatozooids per antheridium. The ratio of spermatozooids

to oospheres is also of course influenced by the number of conceptacles per receptacle on male and female plants and the ratio of male to female plants in the population. For most Fucus populations however the ratio of male to female appears to be close to one to one (Vernet and Harper 1980; Kangas et al. 1982). This also seems to be true for Furcellaria fastigiata (Boney 1965), Dictyota binghamiae (Foster et al. 1972) and Dumontia (Kilar and Mathieson 1978).

Thus a variety of factors may increase the likelihood of a successful union of gametes. However, the fecundity of the seaweeds, as discussed in Chapter I, is probably their greatest aid to sexual reproduction. The large number of gametes released compensates for the inevitable wastage of some gametes dispersed far and wide by the tide.

A large inoculum of propagules might be expected to produce either a significant long distance dispersal pattern (because the dilution effect would be reduced) or a very dense close settlement, depending on how quickly the propagules fell to the ground. Of the species for which dispersal distances have been recorded most appear to have very restricted dispersal patterns for both single plants and for groups. Postelsia palmaeformis was found to have a dispersal distance of less than 3 m (Dayton 1973; Paine 1979) even though it inhabits wave swept shores, likewise Ecklonia radiata and Sargassum sinclairii (Schiel 1980). In recent work on Sargassum muticum (Deysher and Norton 1982) fertile adult plants were transplanted into areas distant from natural populations and the subsequent colonisation of the adjacent substratum was followed. Colonisation was very dense

within 3 m of the parent plant but diminished abruptly with increasing distance. A second experiment on a natural population again showed a high density of germlings within 1 m of the parent plants and not insignificant settlement up to 3 m away, but beyond this densities were very low, although a few plantlets arose up to 30 m from the parents. Similar results have also been obtained for Sargassum muticum by Critchley (1981). Data for Alaria esculenta (Sundene 1962) also showed that spore dispersal was restricted to 10-12 m from the parent plant. Burrows and Lodge (1950) reported that zygotes from a population of Fucus in the course of a year colonised a strip along the shore extending up to 70 m distant from the parent plants. No details of the number and distribution of the plantlets were presented nor the size of the inoculum, although it was noted that the inoculum was from a dense band of plants, 10 m wide, that fruited copiously. Colonisation by Laminaria longicruris was reported to occur up to 40 m distant from experimentally placed parent plants and up to 600 m from a mature forest (Chapman 1981).

From this evidence it would seem that where plants appear many kilometres away from a possible source then the inocula was probably other than spores. Moss et al. (1981) have examined the colonisation of the North Sea Oil platforms by Laminaria and Alaria where the source for colonisation is some 100 miles distant. They suggest that this is too great a distance for the zoospores to have dispersed and propose that fertilised female gametophytes made the journey, but provide no evidence to support this contention. It seems more probable, however, that colonisation occurred by fertile drift seaweed becoming entangled

in the platform. A similar example is that of Sargassum muticum which migrated 1100 km down the entire coast of California in a single step (Deysher and Norton 1982). This appears to have occurred by the dispersal of floating vegetative branches which later became fertile en route.

Algae may also be dispersed as a result of the activities of man. Ship hulls have long been available for colonisation and subsequent travel round the world. Importations of shell fish are also a means by which algal spores can cross the globe. In fact it is suggested that this is how Sargassum arrived in the west from Japan (Farnham 1980) and how many species of exotic algae reached Hawaii (Russell 1980). Algal spores may also be dispersed over very much shorter distances by the activity of grazers, where spores are ingested and then deposited, still viable, several centimetres away (Santelices et al. 1982).

Propagules dispersed by the tide eventually come to rest on the substratum. The exact site where settlement and attachment occurs may be determined by several factors for example microtopography, water velocity, algal cover and whiplash of the thalli of neighbouring adult plants. Two of these factors, microtopography and water velocity, have been considered in detail in relation to the settlement and survival of Sargassum muticum propagules (Norton and Fetter 1981; Norton 1983). In flowing water it was found that smooth substratum was the least favourable for settlement and that settlement density increased with substratum roughness until an optimum roughness was reached. Far fewer propagules settled on the tops of the sand grains constituting the synthesized rock surface

than in depressions. With increasing water velocity there was a progressive reduction in the percentage of propagules settling on the tops of the grains and a corresponding increase in the proportion accumulating in the depressions. Germlings showed increased survival with increasing substratum roughness up to an optimum where the depressions were deeper than the height of the germlings. However, when germlings settled in large depressions there was a possibility that they may be removed by the scouring action of the water. It was found that propagule settlement increased monotonically with decreasing water velocity until a maximum value was reached. In stationary water the topography of the substratum was unimportant and equal numbers of propagules were found to attach on the tops of the grains as on the sides or in depressions.

The effect of microtopography and water velocity on settlement is an area of propagule ecology which has only recently been seriously investigated. Earlier workers investigating the effect of substratum on settlement failed to differentiate between initial settlement and subsequent survival. This was because 'settlement' was only noted when the plantlets became large enough to count, meanwhile many may have settled successfully but subsequently died off without ever having been recorded by the researcher.

Very little is known about the settlement and dispersal pattern of Fucus propagules, but the work of Burrows and Lodge (1950), unlike the results of investigations on most other species, showed that Fucus propagules can have quite a large dispersal range. It was decided

to investigate this further and also the effect of microtopography on the settlement of Fucus propagules.

B. METHODS

It was decided to investigate the dispersal distance of Fucus propagules by transplanting fertile adult plants into an area naturally devoid of fucoids. This presented many problems, as the fucoids are the most common of British seaweeds and occur on almost every stretch of shore. However, the alternative was to denude an area of shore of existing fucoids, which would have been a very time-consuming task as the minimum area required was the width of the intertidal zone over a distance of 20 m.

A suitable site was eventually found at Portencross, Ayrshire (Figure 1). It is a fairly exposed shore which has a dense barnacle cover and an abundant limpet population. There were no fucoids for a distance of several hundred metres although most other common algal species were present.

F. spiralis was the obvious choice of experimental plant because both male and female gametes are found on one plant and as an inhabitant of the upper shore it was conveniently accessible to the investigator.

Fertile F. spiralis plants, collected from Millport, were transplanted into the experimental area and the subsequent colonisation of adjacent test substratum was followed.

Between 60 and 80 plants were fixed to the shore in a net bag 0.5 m square with a mesh size of 1 cm^2 which was attached by wires at each corner and at intervals along the sides to nails embedded in the rock

(Plate 1). The plants were arranged in the bag to form a canopy and secured by threading holdfast and stipe through the net. Other plants from the same sample were returned to the laboratory and their propagule output monitored to ensure that gametes were being released.

The test substrata used to follow colonisation were glass 25 x 75 mm microscope slides placed in groups of three at increasing distances from the parent plants. The slides were held on the shore in slide carriers (Figure 2, Plate 2) which had been cemented down using Purimacho's 'Jetcem', a quick-drying cement. The use of slide carriers meant slides could easily be removed and replaced.

Plain glass is known to be an unfavourable surface for algal colonisation so a layer of quartz sandgrains were stuck on to the slides using quick-setting Araldite. When the glue had hardened the slides were soaked for 48 hours in fresh water as this is known to leach out many substances toxic to algae (Schonbeck and Norton 1980c). The rugosity of the slides was then measured and compared with that of the natural local sandstone to ensure that they were similar. This was done by examining the surface beneath a microscope and measuring the roughness by focusing from the tip of each peak to the base of the adjacent trough as the objective was moved along the length of the slide. The depth of each trough was calculated from the movement of the focusing knob of the microscope. This was facilitated by a rotary potentiometer fixed to the knob and giving an output displayed on a meter calibrated in μm (Norton and Fetter 1981).

The dispersal experiment was repeated on three occasions, 16th



PLATE 1: Fertile plants of *F. spiralis* placed on the shore in a net bag, 0.5 m square, attached by wire to nails embedded in the rocks. On either side slide carriers are visible, awaiting colonisation.

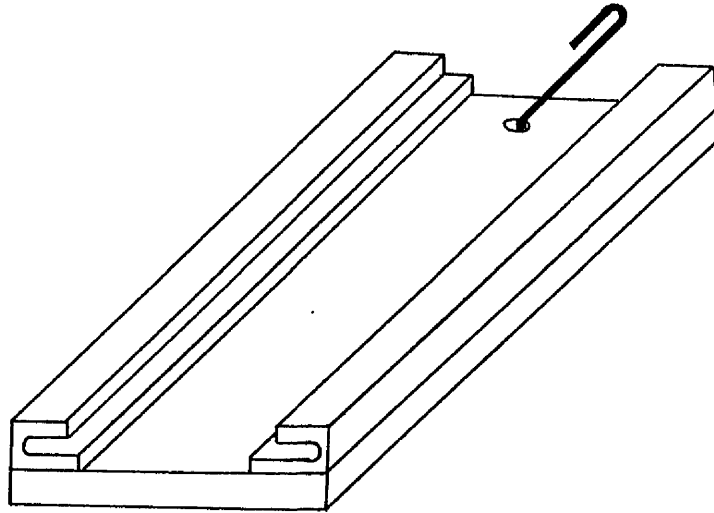


FIGURE 2: Diagram of the slide carrier used for holding microscope slides to the shore. The base is a piece of Perspex 85 mm x 37 mm x 4 mm with a central hole 10 mm from one end. The slides are held in place with two strips of plastic curtain railing. The railing was melted down at the end opposite to the hole to keep the slide in place on a sloping shore. A piece of wire was looped through the hole at the other end to prevent the slide being removed by the tide.

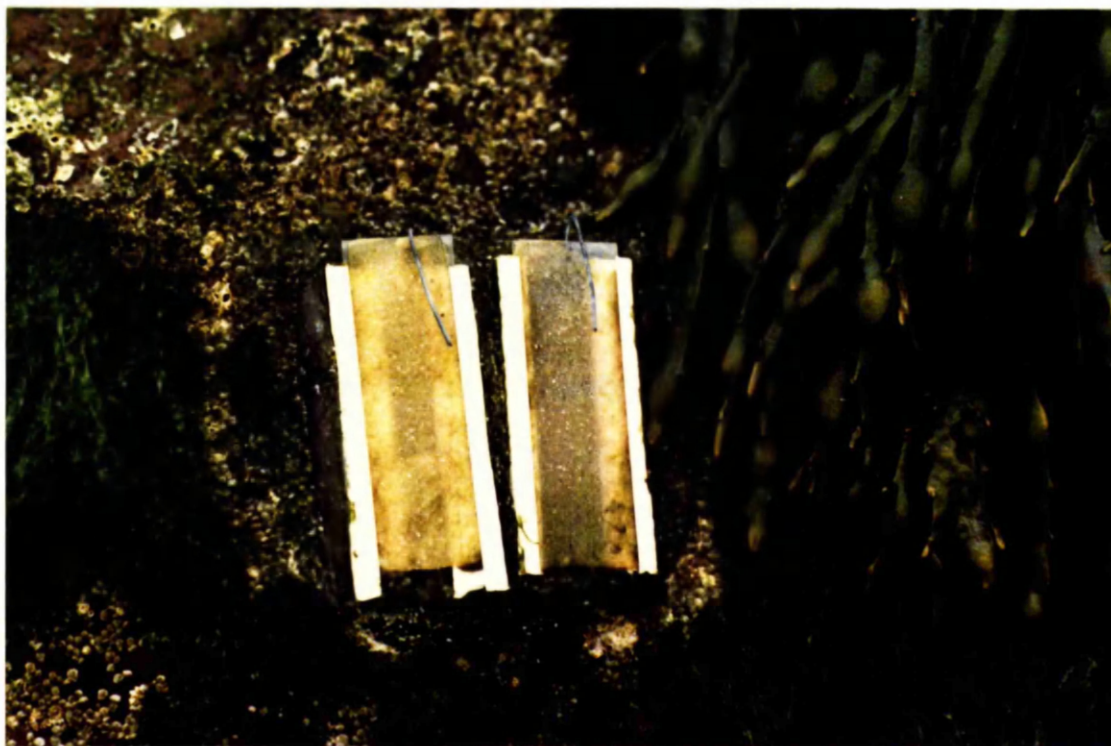


PLATE 2: Two slide carriers each containing one glass 25 x 75 mm microscope slide specially prepared with a layer of sand grains stuck on the upper surface.

August, 1982, 6th June, 1983 and 15th June, 1983. On each occasion slides were placed at 0.5, 3.0, 5.0 and 10.0 m from the parent plants, both up and down the shore (Plate 3). The slides were left in place for a period of 5-7 days and then returned to the laboratory. The entire surface of each slide was systematically examined beneath a dissecting microscope at a magnification of x 24.5, and the number of zygotes counted. Where zygotes were successfully collected in the field, their distribution in relation to slide microtopography was also recorded. For each microscope field the numbers of germlings found on the top, sides and depressions of sand grains was noted. This was then compared with the data from zygotes settled on similar slides in still water in the laboratory. Other slides settled in the laboratory, were transferred to the shore for 17 days and the distribution of the germlings that remained after the period on the shore was noted.

The proportion of a slide surface area composed of sides, peaks and depressions was calculated from 'contour maps'. A slide was examined under the binocular microscope at x 70 total magnification. The peaks were mapped on to graph paper, then the depressions were brought into focus and mapped. The total surface area for each map was known from the microscope field and so an estimate of the side area was obtained by subtraction. This however provides a slightly low estimate of the surface area of the sides as no compensation was made for surface relief. It was calculated that this method underestimated the surface area of the sides by approximately 30% but could be as much as 80% for the steepest slopes and as little as 15% for the lower slopes.



PLATE 3: The slide carriers were placed at 0.5 m (a);
1.0 m (b); 3.0 m (c); 5.0 m (d) and 10.0 m (e)
distances, both up and down the shore, from the
parent plants.

C. RESULTS

Although the test plants were invariably found to release gametes, F. spiralis zygotes colonised the experimental slides on only one occasion and that was in the experiment set up on 16th August, 1982. The zygotes collected were on the three slides positioned 0.5 m downshore from the parent plants, and had settled at a mean density of 15.37 zygotes per cm² (± 1.4 S.E.).

These data are inadequate to provide an indication of the dispersal pattern and effective dispersal range of F. spiralis propagules.

The zygotes that successfully colonised slides in the dispersal experiment were found to be distributed between the tops, sides and bottoms of the sand grains on the slides as shown in Table 7. The percentage of the total surface area provided by the three types of surface are also given, together with data for the distribution of zygotes settled in the laboratory.

	TYPE OF SURFACE			n
	TOPS	SIDES	BOTTOMS	
Surface area %	8	60	32	-
Zygotes collected on the shore %	2.8	14.7	82.6	286
Zygotes settled in still water%	18	35	47	689
Zygotes settled in still water and transferred to the shore for 17 days %	0	0.16	99.8	1223

TABLE 7: The distribution of zygotes between the tops, sides and bottoms of sand grains when settled under different conditions, shown as a percentage of total number counted (n)

The zygotes settled in still water showed a fairly even distribution over the three types of surface. However a larger proportion of zygotes settled in depressions and on peaks than expected and fewer on the sides of grains (Chi-squared, $0.001 > p < 0.01$). The slides collected from the shore had far more zygotes in depressions but fewer on both sides and tops. Likewise for the slides settled in the laboratory and then placed on the shore, where all but the zygotes settled in depressions were eliminated.

D. DISCUSSION

There are many possible reasons why few zygotes were collected in the dispersal experiment. On the occasion when zygotes were collected they were found on slides beneath the net bag, which had become detached in several places and the fertile, plants trailed over the adjacent slides by the tide. This suggests that dispersal might be restricted to the substratum immediately beneath the adult plants, but this is very unlikely in view of the wide dispersal documented by Burrows and Lodge (1950). It is more probable that the zygotes collected on these slides were covered by the blanket of algae in the net bag and thus were not dispersed.

Few zygotes may have been collected due to an inadequacy in the experimental technique, although similar methods have been successfully used by other workers for other plant species. However the procedure could be improved by increasing the sampling area by either using larger slides or more of them or by clearing areas of rock and

monitoring subsequent colonisation over a longer period of time. The main problem was in selecting a suitable site, as those areas devoid of Fucus also tended to be quite exposed. This may have meant few zygotes were able to settle for Norton and Fetter (1981) showed in the laboratory that settlement rate decreased with increasing water velocity. The exposure of the site also meant that the bag containing the algae was damaged on one occasion and a large proportion of the fertile algae were subsequently lost. It is also possible that propagule release and dispersal may have been affected by the plants being contained in a net bag.

F. spiralis is quite a small plant, 15-30 cm in length, and as in the other species, the receptacles are borne on the ends of the thalli. The maximum height of propagule release therefore is 30 cm above the substratum. If, as Baker (1910) suggested, the plants release their gametes on the rising tide, after a period of exposure to air, then the height of the inoculum may be much less than 30 cm because at the time of propagule release the plants would not be upright. Containment of plants in a bag therefore is unlikely to affect the height of release and hence dispersal distance.

However, the closeness of the plants in the bag may have reduced the degree of drying out at low tide and hence affected propagule output. The lack of zygotes colonising the experimental slides was not due to the fact that there were few gametes in the conceptacles of the plants as plants collected from the same sample as those used in the experiments contained many gametes and readily released them in the laboratory.

Species for which the dispersal pattern has been successfully investigated release large numbers of propagules over a short fertile season. Sargassum for example releases the majority of its propagules in discrete pulses over a period of two months (Fletcher and Fletcher 1975). Fucus which is not known to exhibit monthly or bimonthly periodicity probably releases a small number of eggs over a long period of time. Therefore at any one time it is unlikely that many eggs will be available to colonise the surrounding rock. Hruby and Norton (1979) collected surface water from the Firth of Clyde and found very few furoid propagules in their samples. The maximum was 12 in one 400 ml sample whereas species such as Blidingia and Enteromorpha were collected in large numbers of up to 675 and 917 spores respectively per 400 ml of water. However it must be remembered that these data were from surface waters and as Fucus has relatively large propagules they may have been more abundant lower in the water column.

Hruby and Norton (1979) also noted that seaweed spores were patchily distributed in the sea and this was reflected in a patchy colonisation of the shore. They proposed that propagules released by seaweed on immersion would be mixed into a fairly uniform suspension by the water turbulence, but that this suspension would be dispersed as a batch by water currents. Furthermore, any patchiness in the distribution of the parent species on the shore may accentuate the patchiness of their propagules in the water. The experimental plants were an isolated patch and so may have released small discrete 'clouds' of propagules into the sea with each tide. These could have settled

as localised patches so that a small area sampled on the shore may not have been colonised even though an adjacent area of rock may have been densely settled. This again suggests the need for a larger sampling area in an investigation of dispersal and settlement.

Fucus is obviously capable of efficient colonisation as evidenced by the work of Burrows and Lodge (1950) and its obvious success on so many shores, but its steady rate of egg release means that the dispersal pattern may only become apparent over a long period of time when sufficient numbers of propagules have settled. This may also be true for another member of the Fucales, Himanthalia elongata, as a dispersal experiment, similar to that described for F. spiralis was carried out on fertile plants of H. elongata and again few propagules were collected.

Alternatively Fucus zygotes may not have been collected because they disperse a distance greater than 10 m before settling. This is extremely unlikely in view of the evidence collected from other species with similar-sized propagules. It is much more likely that the lack of colonisation is a consequence of the chronic pattern of propagule release in Fucus which means few zygotes are available for colonisation at any one time.

Although the dispersal experiments were unsuccessful in providing information about the dispersal pattern of Fucus propagules they did provide some information about the effect of microtopography on settlement. On the occasion when zygotes were successfully collected in the field (16th August, 1982) they were found to have settled mostly in the minute depressions between the sand grains on the test substratum.

This was in accordance with work on Sargassum by Norton and Fetter (1981) who found that between 37.5% and 64.0% of total settlement in flowing water was in depressions, the exact proportion depending on the water velocity and mean depth of depressions. The slides used in the present experiment had a wide range of depths of depressions to simulate the natural substrata, but the mean was 217.67 μm (± 18.47 S.E.). This is almost three times the size of a Fucus zygote and is approximately the ratio between the size of Sargassum propagules and the depth of depression where maximum settlement was found to occur. 82.6% of the total settlement of Fucus was on the bottom of depressions which is considerably greater than the maximum percentage found for Sargassum. All other factors being equal, this difference is most likely to be a result of the greater water velocities found on the shore than those tested in the laboratory. However this study does not differentiate between the initial settlement pattern and subsequent survival, unlike Norton and Fetter (1981) who deal only with initial settlement. It is possible therefore that during the few days on the shore before the slides were examined there may have been differential survival of the zygotes between the three surfaces. Certainly slides settled in the laboratory and moved to the shore lost all the zygotes that had settled on the tops and most of those on the sides of grains. Far fewer of those in depressions were lost and the ones that survived were almost entirely confined to depressions. Depressions probably offer some protection not only from water motion but also from desiccation and grazing animals.

Zygotes settled in stationary water in the laboratory showed a

more even distribution between the three surfaces although there were fewer on the sides than would have been expected from the proportion of the total surface area provided by each of the three surfaces. Possibly few zygotes were found on the sides of grains because although zygotes are adhesive, few are sticky enough to adhere on the sides of grains and so roll down into a depression.

Restriction of zygotes to depressions, whether caused by differential settlement or by differential survival, may have long lasting repercussions for observations on the shore revealed that a large proportion of the juvenile F. spiralis population have their holdfast lodged in cracks and crevices.

CHAPTER III

INTRASPECIFIC COMPETITION AMONGST FUCUS GERMLINGS

A. INTRODUCTION

The development and survival of zygotes, once they have become firmly attached to the substratum, may be affected by many factors, such as exposure to air (Townsend and Lawson 1972; Allender 1977; Hruby and Norton 1979), salinity (Gessner and Schramm 1971), temperature (Gessner 1971) and silting (Moss, Mercer and Sheader 1973; Norton 1978) but one factor which will effect all developing germlings is their interaction with each other, particularly, as it appears that large numbers of propagules are released and the majority settle in close proximity to the parent plant. The density of zygote settlement is an important influence on subsequent development because the degree of crowding effects competition for light, space and nutrients.

Very little information is available on intraspecific competition in the seaweeds, particularly at the germling stage. This area of research is much more advanced in higher plant ecology and it is from there that the theory behind intraspecific competition is drawn. Competition can be defined as 'the tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, volume of space or molecule of water' (Grime 1973). The three points listed below summarize the consequences of competitive plant interaction and are fundamental to the competition--density theory,

- a) under competitive conditions the form or size of a plant may be modified without leading to the death of the plant, these modifications are known as 'plastic responses'.
- b) death will occur if the capacity of a plant to withstand competition by means of its plastic responses is exceeded.
- c) when the carrying capacity of a habitat has been reached further growth can only occur at the expense of some of the biomass already present.

Bearing these points in mind we can consider the development of monospecific even-aged stands over time. At the seedling stage mean plant biomass is independent of stand density, but as the plants increase in size they begin to interfere with each other's growth by competing for the same essential resources. This can occur even when all factors are favourable for growth. At higher densities, where competition is more intense plants grow on average more slowly so that over time mean plant biomass becomes density-dependent. This is illustrated in Figure 3.

Competing populations at different densities can all be fitted to a hyperbolic curve that relates mean plant weight and density of survivors (Kira et al. 1953).

$$\bar{w} = Kd^{-a} \quad (1)$$

$$\text{or } \log_{10} \bar{w} = \log_{10} K - a \log_{10} d \quad (2)$$

where \bar{w} = mean above ground plant biomass (g)

d = density, number of plants per m^2

K = constant

a = the competition - density
index ranging between 0 and 1

At very low densities most individuals are sufficiently widely spaced not to compete for resources. At such densities a small increase in the number of plants has little or no effect on their mean biomass. Therefore the slope of the line relating mean dry weight per plant to density is always zero (i.e. $a = 0$) and there is a direct linear increase in yield per unit area with increasing density. This part of the relationship is denoted as phase 1 in Figure 3.

At intermediate densities however, plants may compete and this can result in reduced growth rate and modifications of plant form. For example in higher plants there may be a reduction in the size and number of branches, leaves, flowers and seeds (Watkinson 1981). Under these circumstances, with increasing density, the decrease in the mean biomass per plant counteracts the greater number of plants. As a result the yield per unit area approaches a constant value for a range of densities and is equivalent to the carrying capacity of the environment. This is described by the expression:

$$\bar{w} = Kd^{-1} \quad (3)$$

when $a = 1$.

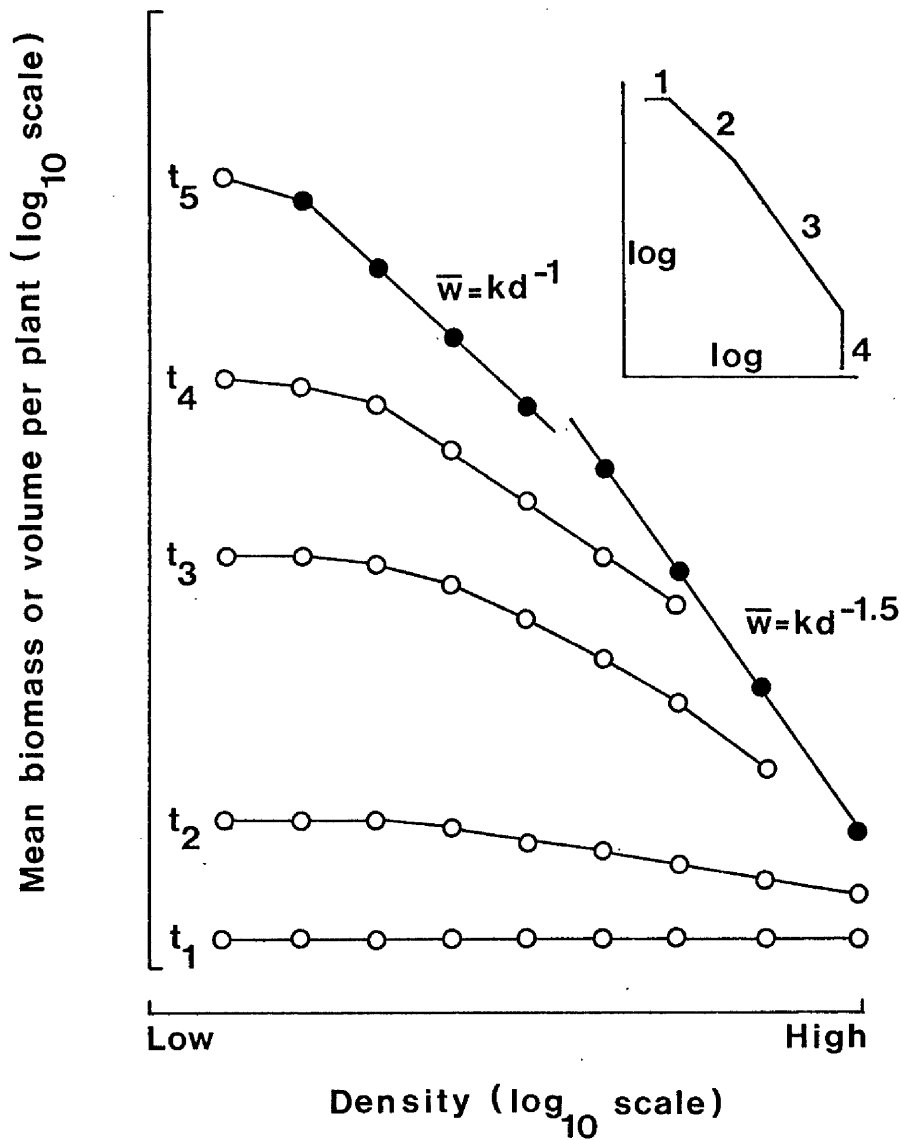


FIGURE 3: A generalised graphical scheme for representing competition-density effects, (after White 1980). Subscripted t indicates successive time periods. At high densities plants grow on average more slowly so that over time mean plant biomass becomes density-dependent illustrated by the increase in slope of the line between t_2 and t_5 . Inset shows the four main phases of the competition-density effect, described in the text.

This is shown in phase 2 of Figure 3. As yield is constant over a range of densities the expression has been termed 'the law of constant final yield'.

At high densities the ability of a plant to compensate for competitive stress by plasticity of form may be exceeded and so mortality may occur. Mortality due to density effects within a pure stand is termed 'self-thinning'. The rate at which plants die because of competition in crowded even-aged stands is determined by the equation:

$$\bar{w} = Kd^{-3/2} \text{ or } \bar{w} = Kd^{-1.5} \quad (4)$$

This is known as the $-3/2$ power law (Yoda et al. 1963). It describes a boundary line of slope 56° which designates the maximum permissible combination of density and mean plant biomass it is theoretically possible to achieve. Stands in the region of the boundary line lose individuals as they accumulate biomass and so travel along the line, but cannot extend beyond it. Thus over time a stand progressively comes to be composed of fewer larger individuals as shown in Figure 4.

The $-3/2$ power law' has been fitted to over one hundred plant species ranging from herbs to trees (Westoby 1977) and $\log_{10} K$ is typically between 3.5 and 4.3 (White 1980). The biomass at a given density can vary six-fold between different species depending on plant size, but this is small compared to the 10^{16} fold variation in biomass as a function of density (Hutchings 1983). Environmental factors may affect the rate of accumulation of biomass but not the

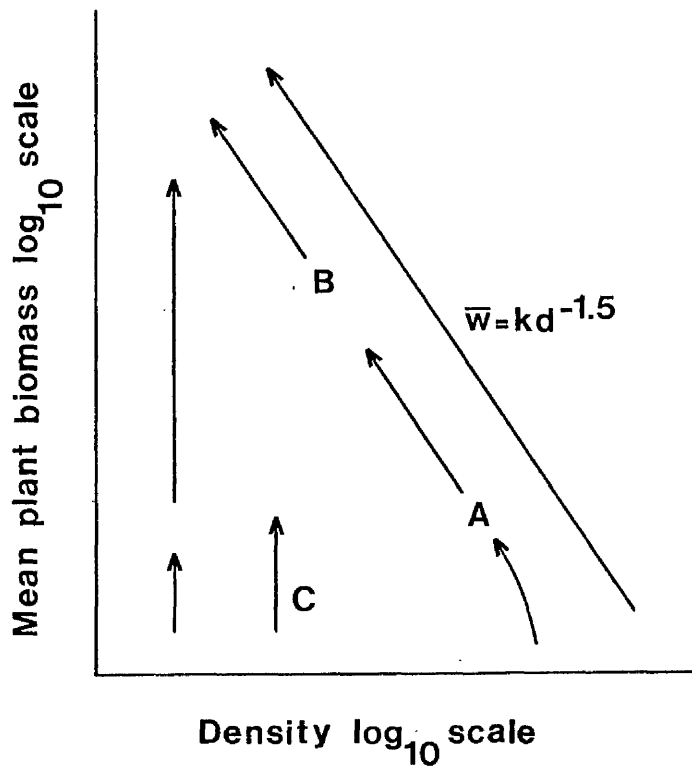


FIGURE 4: The slope of $-3/2$ is the boundary condition. Arrows indicate the trajectories that stands of plants theoretically follow at different biomass-density combinations (Westoby 1981). In the region of the thinning line (A,B) even-aged stands low individuals as they accumulate biomass in such a way as to travel along the line. Even-aged stands well below the line (C) accumulate biomass without mortality and rise to the line. Stands do not enter the area beyond the thinning line from below (but see Westoby and Howell 1981).

slope of the thinning line.

Even-aged monospecific stands of seaweeds, also appear to conform to the ' $3/2$ power law'. The relationship between \log_{10} mean frond weight and \log_{10} frond density has been determined for several species of algae including F. vesiculosus (Cousens and Hutchings 1983) and in all except one case it was along or below the thinning line described by the equation $\log_{10} \bar{w} = 4.3 - 1.5 \log_{10} d$. The exception was a stand of Ascophyllum which had an extremely positively skewed frond weight frequency distribution. In such a case an arithmetic mean was a poor descriptor of the population and when the geometric mean was used the relationship fell below the thinning line (Cousens and Hutchings 1983).

The 'law of constant final yield' has also been applied to the algae. The relationship between density and final yield was investigated for Porphyra tenera growing on hibi nets (Yoshida 1972). During the early stage of growth a larger yield was obtained from high density stands, but at maturity the yield reached a maximum value of 2g per 10 cm of hibi string independent of density which ranged from 400-2000 plants per 10 cm of hibi string.

Accounts of individual plant weights and stand densities of seaweeds are generally uncommon in the literature. There is abundant evidence on the general effects of density, although often in relation to other environmental variables. A reduction in plant size with increasing density has been reported for Chondrus crispus (Simpson et al. 1978), Chordaria (Rice and Chapman 1982), Durvillea (Hay and South 1979), Fucus distichus (McLachlan et al. 1971), Iridaea cordata

(Adams and Austen 1979), Laminaria (Fang and Jiang 1963; Jupp and Drew 1974; Gerard and Mann 1979); and Nereocystis leutkana sporophytes (Vadas 1972). An increase in mortality with an increase in density has also been reported for Egregia laevigata (Black 1974) and Leathesia difformis (Chapman and Goudey 1983).

Only Schiel and Choat (1980) have suggested that seaweeds differ from higher plants in their response to density. They reported the Ecklonia radiata and Sargassum sinclairii both grew larger at high densities than low. However this work has been criticised on several points (Brawley and Adey 1980; Cousens and Hutchings 1983). Schiel and Choat assumed that the only difference between their stands was in plant density. There may also have been differences in abiotic factors so that the dense stands were growing in more favourable conditions and therefore produced larger individuals in spite of crowding. Furthermore, stands were not studied over time, so that the final densities recorded may not have been representative of the density during the growth period, particularly as the adverse conditions of the marine environment may cause drastic changes in population structure in a short period of time.

Density appears to be an important factor in the population biology of adult seaweeds and so it also may be important in the establishment and growth of the very early juvenile stages. The effects of intra-specific competition on germling growth were investigated for F. serratus, F. vesiculosus and F. spiralis germlings up to a maximum age of 50 days by which time the germlings were upright cylindrical bodies attached to

the substratum by several rhizoids. To assess the broader ecological significance of density on growth, exposure to air and grazing were selected as two important factors whose effects might be influenced by the density of a germling lawn.

B. METHODS

B.1 Laboratory Studies

a) Collection of gametes and treatment of zygotes

Plants bearing mature receptacles were selected and in the case of the dioecious species, F. serratus and F. vesiculosus, the sex was determined by microscopic examination of sections of receptacle. Receptacles were excised and rinsed in cold running tapwater for one minute, blotted with absorbant paper and left in the laboratory to dry for approximately 30 minutes. They were then transferred to 250 ml beakers containing filtered seawater, and placed in the constant temperature room in the light at 12°C for 12-48 hours. This method was based on that used by Callow, Coughlan and Evans (1978). After they had released, the receptacles were removed from the beakers and the excess water poured off. The gametes were then mixed and allowed to stand for 45-60 minutes for fertilisation to occur. In the case of the monoecious species, F. spiralis, most of the eggs were fertilised during the 12-48 hour release period and could be used directly. The zygotes were washed with several changes of pasteurized seawater, each time allowing most of the zygotes to sediment before removing the excess water. The aim of rinsing the zygotes was to remove debris and algal contaminants. The latter

were largely species of green algae with spores that are considerably smaller than Fucus zygotes, consequently they sink more slowly and most can be decanted off with the seawater. Green algal contamination was only a problem in cultures set up during the summer months and even then only after a period of several weeks, by which time most measurements of growth had been made.

b) Culture of germlings

Culture slides were 25 x 75 mm glass microscope slides covered by a layer of nylon gauze, mesh size c 50 μ m, secured on the underside with nylon thread. This provided a better surface for attachment than a smooth glass slide, as the rhizoids were able to become entwined in the gauze (Moss 1975). Zygotes were pipetted over slides submerged in filtered pasteurized seawater, to ensure an even distribution of zygotes on the slide. To obtain a range of settlement densities the inoculating suspension of zygotes was diluted several times. Replicate slides were inoculated simultaneously by placing them side by side in blocks of up to twelve. The zygotes were allowed to attach for 24-48 hours, before being transferred to the culture vessel. There were twelve slides per culture vessel initially, reducing to eight by the end of the experiment. The culture vessels were 25 cm x 12 cm x 8 cm perspex tanks containing 1000 ml of medium and were kept in the constant temperature room. The culture conditions are detailed in Appendix A.

c) Assessment of density (number cm^{-2}) and growth

The density of surviving germlings was estimated at each harvest using a Vickers dissecting microscope at x 24.5 total magnification. The number of germlings in fifteen randomly selected fields was counted for each slide and converted to the number per cm^2 . For the greater densities x 70 total magnification was used so as to reduce the number of zygotes counted in each field. However more fields were counted to compensate for the smaller surface area sampled.

Length, dry weight and plant volume were recorded as parameters of germling growth. To measure length a microscope slide was placed over the germlings to press them into a horizontal position thus allowing a more accurate measurement. Twenty-five embryos were measured on each slide. They were selected by means of random co-ordinates obtained from random number tables. The germlings were measured at either 100 x or 40 x total magnification under a Nikon binocular compound microscope.

Yield per slide was assessed in two ways, firstly as the volume occupied by the germlings and secondly as total dry weight. Volume was measured in a graduated centrifuge tube, the germlings were carefully scraped off into a tube, washed down to the bottom and centrifuged at number 5 for 5 minutes in an MSE Minor Centrifuge.

Dry weight was obtained by removing the germlings from the centrifuge tube after rinsing several times in distilled water and placing them in pre-weighed aluminium foil cups. They were then dried at 96°C for 7 hours.

Mean dry weight per plant and mean volume per plant were calculated from the total values by dividing by the estimated number of germlings per slide.

d) Growth of germlings in a simulated tide regime

It was hypothesized that crowding may offer mutual protection from the effects of desiccation experienced by germlings during the tidal cycle. Therefore it was decided to investigate the effect of density on growth at a range of exposures to air.

The apparatus employed to simulate a tidal regime was based on that used by Townsend and Lawson (1972). Four large glass plates, each 39 mm x 157 mm and ground on one side were placed on a rack which was lowered and raised on a 12 hour sinusoidal cycle within a glass tank containing five litres of enriched seawater (formula in Appendix B). One motor was used to operate two or four racks which acted as counter-weights to each other, the apparatus is shown in Figure 5. The tanks were aerated and the culture medium was changed weekly. The apparatus was used in the constant temperature room (relative humidity 70-72%).

Plates were inoculated using the method described above and were left submerged for 24-48 hours, to allow the zygotes to attach before being transferred to the apparatus. The level on the plate occupied by a germling determined the period of submergence that was experienced during each tidal cycle. Those at the bottom of the plate were continuously submerged whereas those at the top were submerged for less than one hour per cycle. The density of the zygotes was

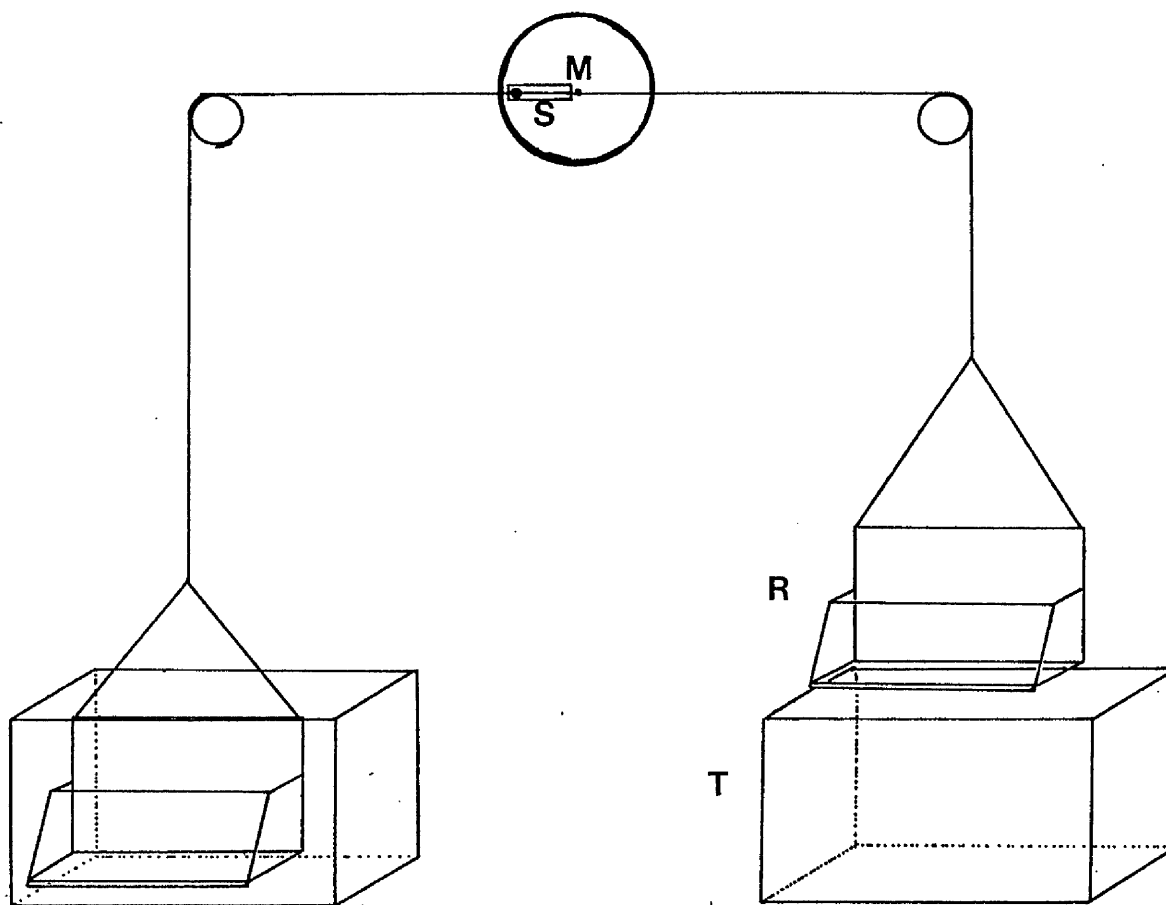


FIGURE 5: Diagram of the tide simulator showing placement of tank (T), rack (R) and motor (M) (Crouzet type 82-344, 1 rev/12 hrs.) The distance between the maximum and minimum elevation on a cycle was adjusted by a movable belt held in Slot (S)

estimated by counting the number in each of ten microscope fields at x 24.5 total magnification for five levels on each plate. Germling length was measured for a random sample of 100 germlings, 20 from each of the five different sampling levels.

To calculate the time during which each level was submerged per cycle the following algorithm (after Hruby and Norton 1979) was used.

$$T = \frac{12 \times \cos^{-1}(2^{D/m}-1)}{\pi}$$

where T = time submerged in hours

m = maximum distance on the slide between the lowest level which was out of the water and the highest level which was submerged.

D = distance between the lowest level of emersion and the level at which the plants were measured.

e) The affect of germling density on the activity of grazers

Grazers may exert a considerable influence on seaweed abundance and biomass (see Vadas and Norton 1982) and therefore seemed to be ideal for investigating the broader ecological significance of germling density. For example, do Littorinid snails, known to graze juvenile fucoids (Knight and Parke 1950; Menge 1975), exhibit a preference for grazing sparse or dense germling lawns.

The effect of germling density on grazing by Littorina littorea was investigated in a choice experiment. Two slides were placed side by side in a petri-dish of filtered seawater, one slide had a dense lawn of F. serratus germlings and the other a sparse lawn.

The slides were left in the petri-dish for 30 minutes before a snail was added so that there was some opportunity for a concentration gradient of exudates to develop. The snails had been kept without food for 4-6 days prior to the experiments in an attempt to standardise their degree of hunger. One snail was added to the petri-dish at a point equi-distant from the neighbouring slides and which slide was grazed first was recorded. The position of the snail was then recorded every five minutes over a period of one hour. The density of the germling lawn was estimated before and after grazing to determine the number of germlings consumed. The number of germlings dislodged but not eaten by a grazing snail was determined by counting the number of loose lying germlings in the petri-dish at the end of the experiment. The experiment was repeated eight times with different snails and germling lawns. Care was taken to thoroughly clean the petri-dishes between experiments as snails will follow the trails left by others. To ensure that the snails were not responding to some gradient other than density the relative positions of the densely 'seeded' slide and the sparsely 'seeded' one were varied from dish to dish.

B.2 Field studies

a) Density of natural stands on the shore

The density of natural stands of juvenile plants in the field was determined to ensure that realistic densities were being used in culture. The mean density of F. spiralis juveniles was determined by taking ten random samples with a 0.5 m^2 quadrat. The quadrat was subdivided into 10 cm squares and the number of plants less than 3 cm

in length was recorded for each square. Densities were recorded for F. spiralis since this species could be found in monospecific stands. F. spiralis and Pelvetia canaliculata are the only fucoids inhabiting the upper shore and they can be easily distinguished at an early stage.

b) The effect of settlement density on germlings transferred to the shore

To establish that any density-dependent growth that might be observed in the laboratory was not just a phenomenon associated with culture, the effect of crowding on germling growth was also investigated in the field. Two levels on the shore were selected at the study site near Lion Rock on the Isle of Great Cumbrae, Firth of Clyde (Figure 1). The upper level, at the top of the F. vesiculosus zone was exposed to air for 6.5 hours per tidal cycle and the lower one, at the bottom of the F. vesiculosus zone, was exposed to air for 3.2 hours per tidal cycle determined for a Spring tide (25.4.83). This allowed the effect of density to be investigated with two different periods of exposure to air. Roughened slides were prepared in the laboratory as described in Chapter II and inoculated with F. vesiculosus zygotes. The slides were retained in the laboratory for 24 hours to allow the germlings to become well-attached. At both levels 16 slide carriers (described in Chapter II) were attached to the rock so that they formed eight pairs. One densely settled slide and one sparsely settled slide were placed in adjacent slide carriers and were left for a period of 17 days. The density of the germlings was estimated before the period on the shore and afterwards when germling length was also measured.

C. RESULTS

C.1 The effect of density on germling growth

Germling growth was found to be significantly affected by the density of a germling stand (Plate 4). Germlings of all three species of Fucus responded to density by changes in length, mean plant biomass and mean plant volume.

Germling length was found to decrease in response to increasing stand density, shown in Figures 6, 7 and 8. For both F. spiralis and F. vesiculosus the relationship between length and density was found to be linear, but for F. serratus it was curvilinear, (analysis of variance using Fisher's orthogonal coefficients). The relationship between length and density changed with time so that the difference in length between plants in a sparse stand and those in a dense stand became progressively more pronounced (Figure 8). After 29 days of growth F. vesiculosus germlings at low densities were 32.5% longer than those at high density but by 50 days they were nearly 69% longer. This was shown by an increase in slope of the relationship between length and density. Data for germling length after 43 days (not shown) fell into an intermediate position.

Mean dry weight per plant has a negative linear relationship with density when plotted on a logarithmic scale (Figure 9). Thus as density increases mean dry weight per plant decreases. The relationships are very similar and extend beyond the thinning line for all three species. The relationship is highly significant for F. serratus and F. vesiculosus (Regression analysis of variance) but is not significant for F. spiralis (although the correlation



A

B

PLATE 4: Fucus germlings grown in a sparse lawn (651.03 plants per $\text{cm}^2 \pm 29.08$ S.E.) (A) are generally larger than those grown in a dense lawn (1772.08 plants per $\text{cm}^2 \pm 147.08$ S.E.) (B) (x 5 magnification)

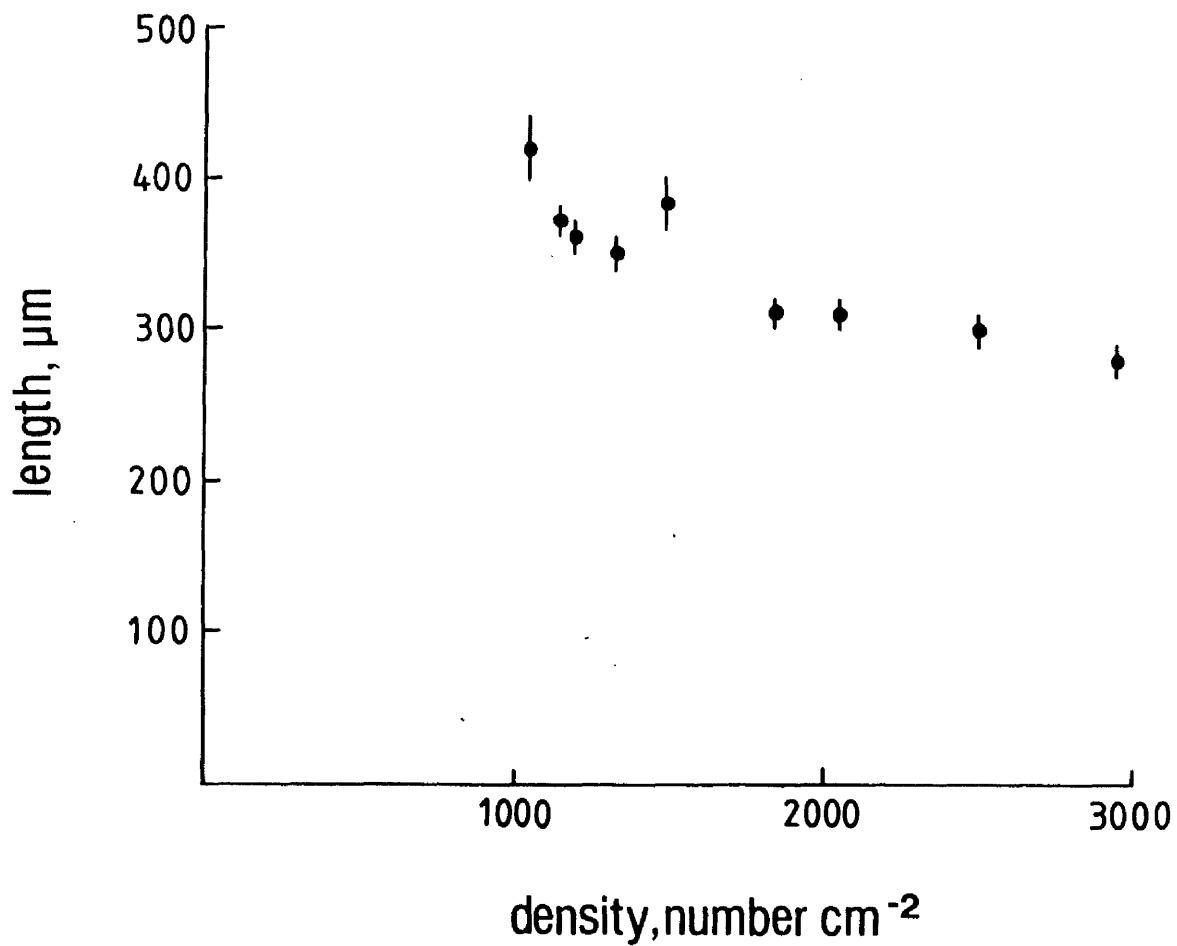


FIGURE 6: Relationship between length and density of surviving germlings for F. spiralis after 26 days of growth: each point is the mean of 25 values \pm S.E.

$$y = -0.059 (\pm 0.022)^{N.S.} x + 446.15$$

where y is length and x is density, linear regression fitted by least squares method.

(N.S. = not significant at 5% level)

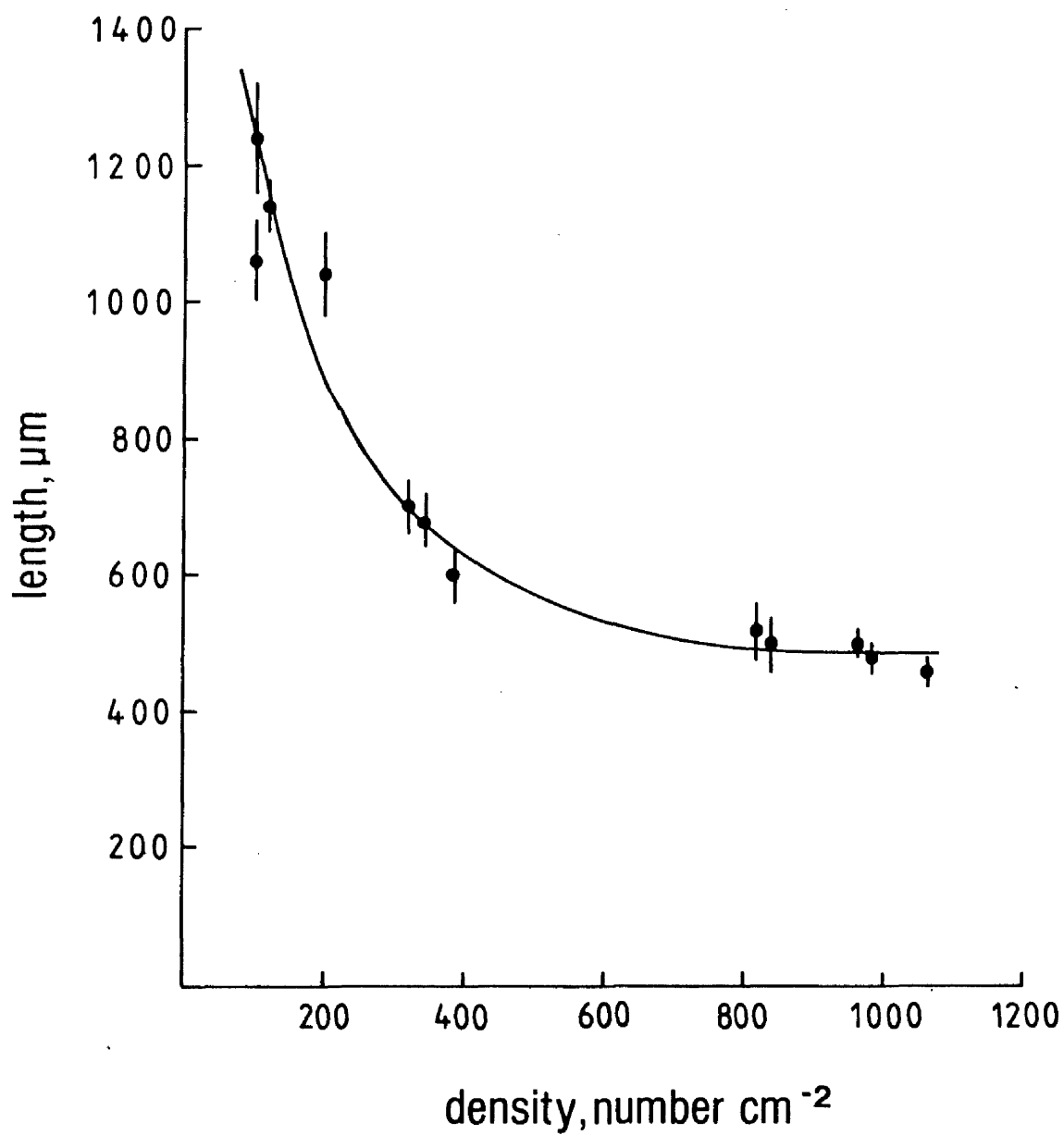


FIGURE 7: Relationship between length and density of surviving germlings for F. serratus after 26 days of growth: each point is the mean of 25 values \pm S.E. Curve fitted by eye.

FIGURE 8: Relationship between length and density of surviving germlings for

F. vesiculosus after 29 days (o) and after 50 days (●) of growth. Each point is the mean of 20 values \pm S.E.

$$o \quad y = -0.12 (\pm 8.84 \times 10^{-3})^{**} x + 475.93$$

$$\bullet \quad y = -0.48 (\pm 0.03)^{***} x + 916.56$$

where y is length and x is density. Linear regression fitted by least squares method. Significance levels were calculated using a regression analysis of variance.

N.S. = not significant at 5% level,

* $p = 0.05$, ** $p = 0.01$, *** $p = 0.001$

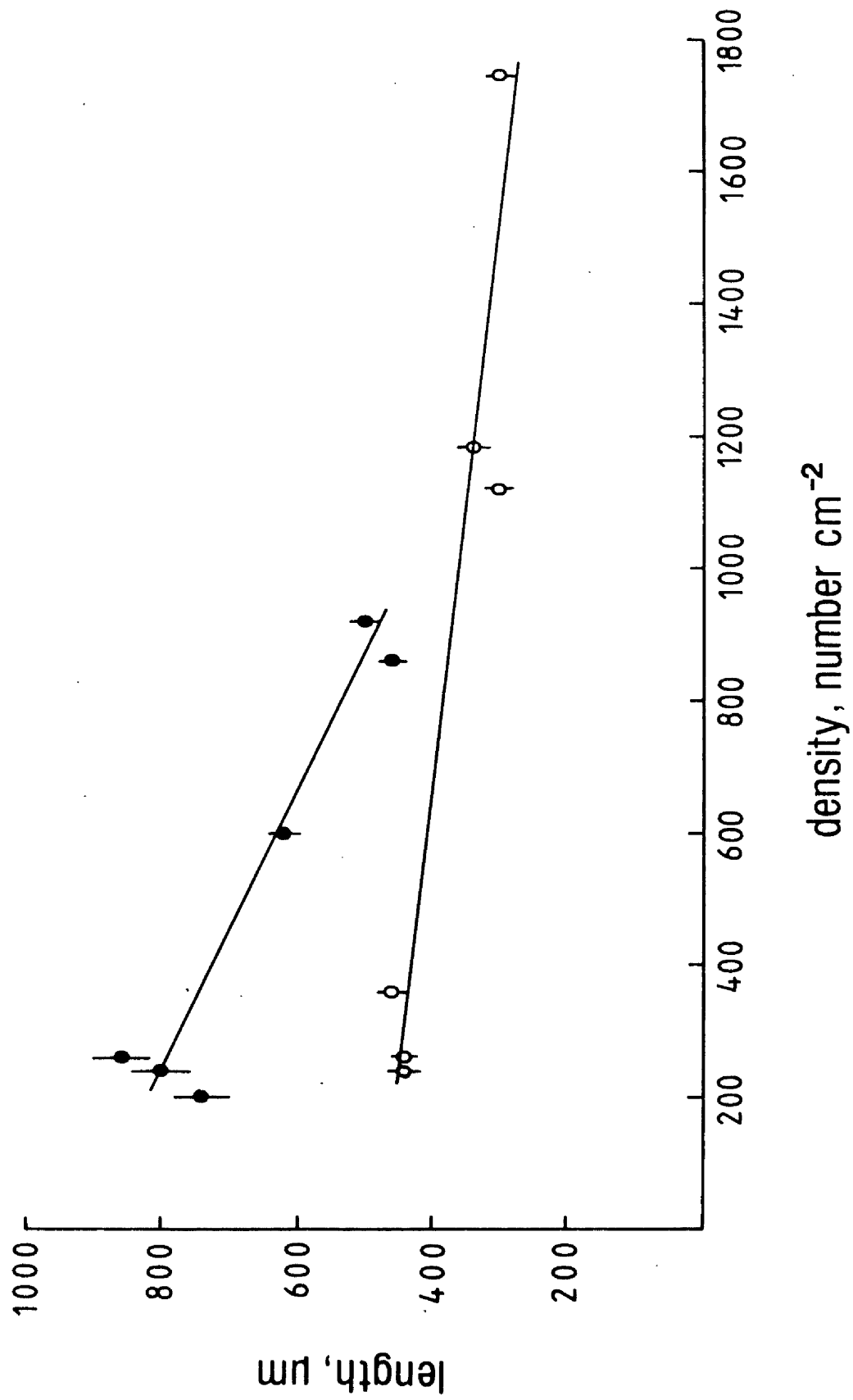
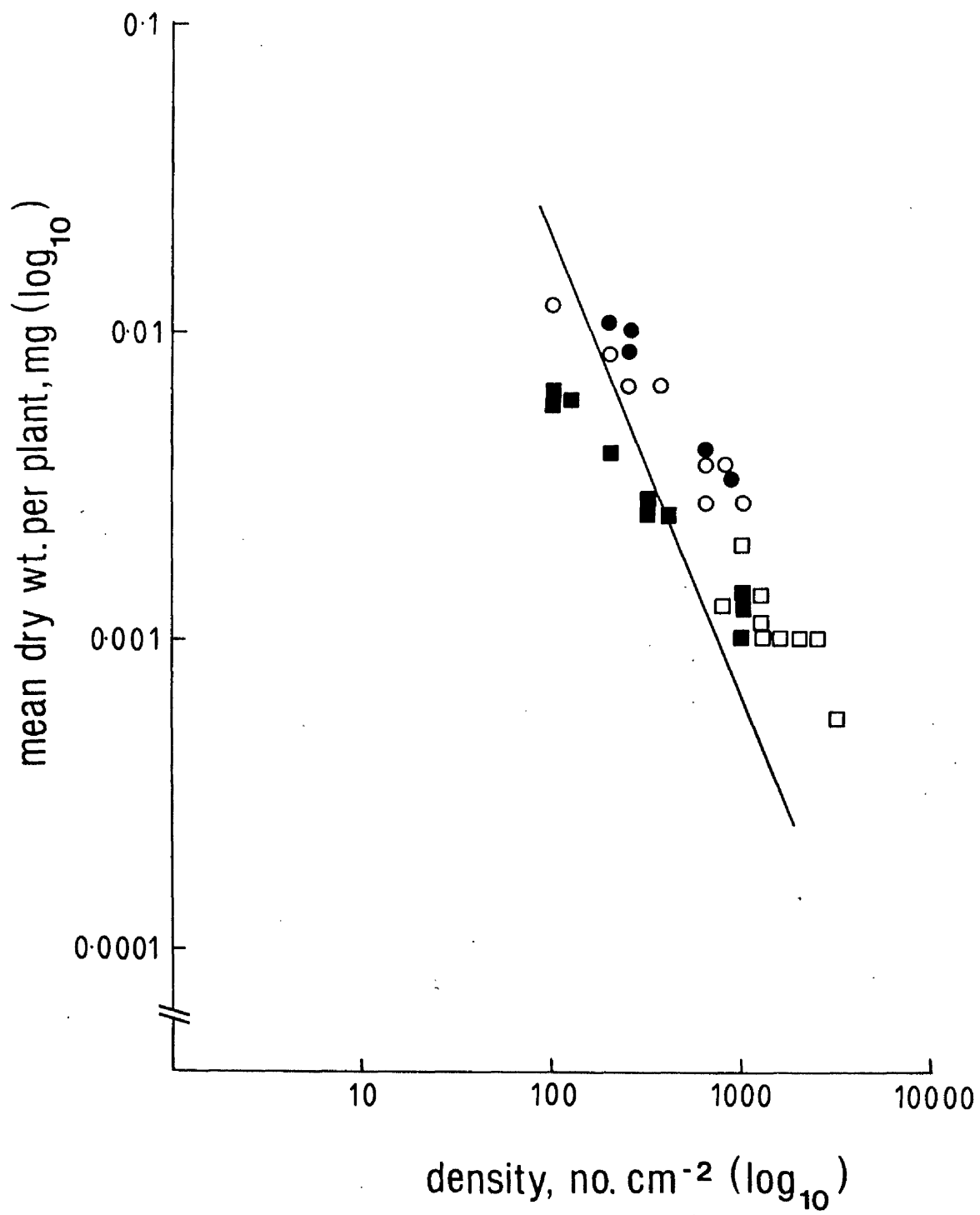


FIGURE 9: Relationship between mean dry weight per plant (\log_{10}) and the density of surviving germlings (\log_{10}) for F. spiralis after 26 days (\square); for F. serratus after 43 days (\blacksquare); and for F. vesiculosus after 43 days (\circ) and after 50 days (\bullet) of growth

$$\begin{aligned} (\square) \quad & \log_{10} y = -0.77 (\pm 0.35)^{\text{N.S.}} \log_{10} x - 0.50 \\ (\blacksquare) \quad & \log_{10} y = -0.73 (\pm 0.004)^{***} \log_{10} x - 0.75 \\ (\circ) \quad & \log_{10} y = -0.70 (\pm 0.029)^{***} \log_{10} x - 0.49 \\ (\bullet) \quad & \log_{10} y = -0.79 (\pm 0.069)^{**} \log_{10} x - 0.16 \end{aligned}$$

where y is mean dry weight per plant and x is density. Linear regression fitted by least squares method. The line is the boundary condition, $\log_{10} y = 4.3 - 1.5 \log_{10} x$



coefficient is significant at the 0.1% level). The slope of the relationship increased between 43 and 50 days for F. vesiculosus as the difference in size between high and low density plants became more apparent. Unfortunately the results for 29 days had to be discarded due to a change in technique when it was realized that unless the germlings were thoroughly rinsed in distilled water prior to determination of dry weight the results may be distorted by salt contamination.

Yield increased linearly with an increase in density despite the reduction in mean plant size with increasing density. The relationship between yield and density shown in Figures 10, 11 and 12 was highly significant for F. serratus and very significant for F. vesiculosus (Regression analysis of variance). There is some evidence for a similar trend for F. spiralis (Figure 10), but it is not significant at the 5% level. The relationship between yield and density appears to change with time. The difference in yield between low density stands and high density stands is progressively reduced so that the slope of the line tends to zero (Figure 12).

The data for mean volume per plant and yield, in terms of volume, produced very similar relationships with density as did mean plant biomass and yield (mg). Mean plant volume decreased with increasing density but total yield (cm^3) increased (Tables 8 and 9).

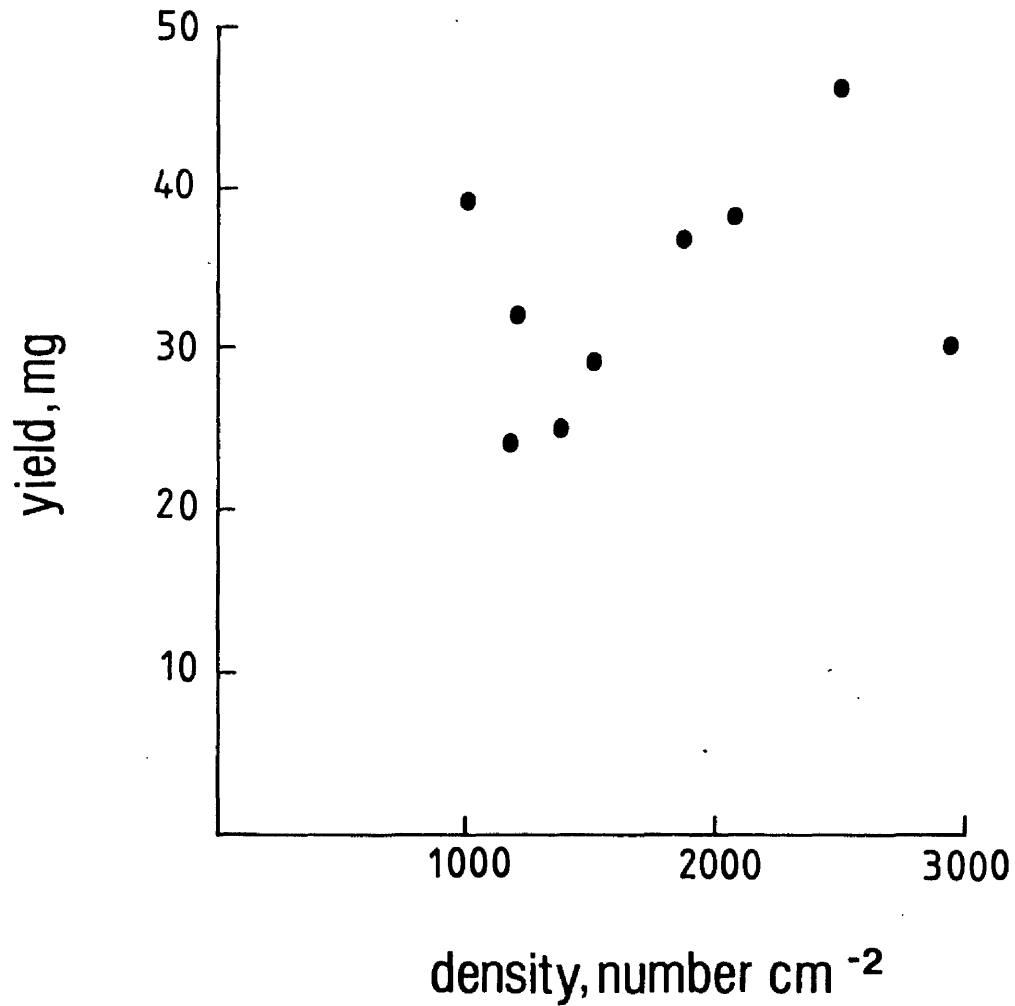


FIGURE 10: Relationship between yield (mg) and density of surviving germlings for F. spiralis after 26 days of growth:

$$y = 4.17 \times 10^{-3} (\pm 1.29 \times 10^{-3})^{N.S.} x + 11.7$$

where y is yield and x is density. Linear regression fitted by least squares method.

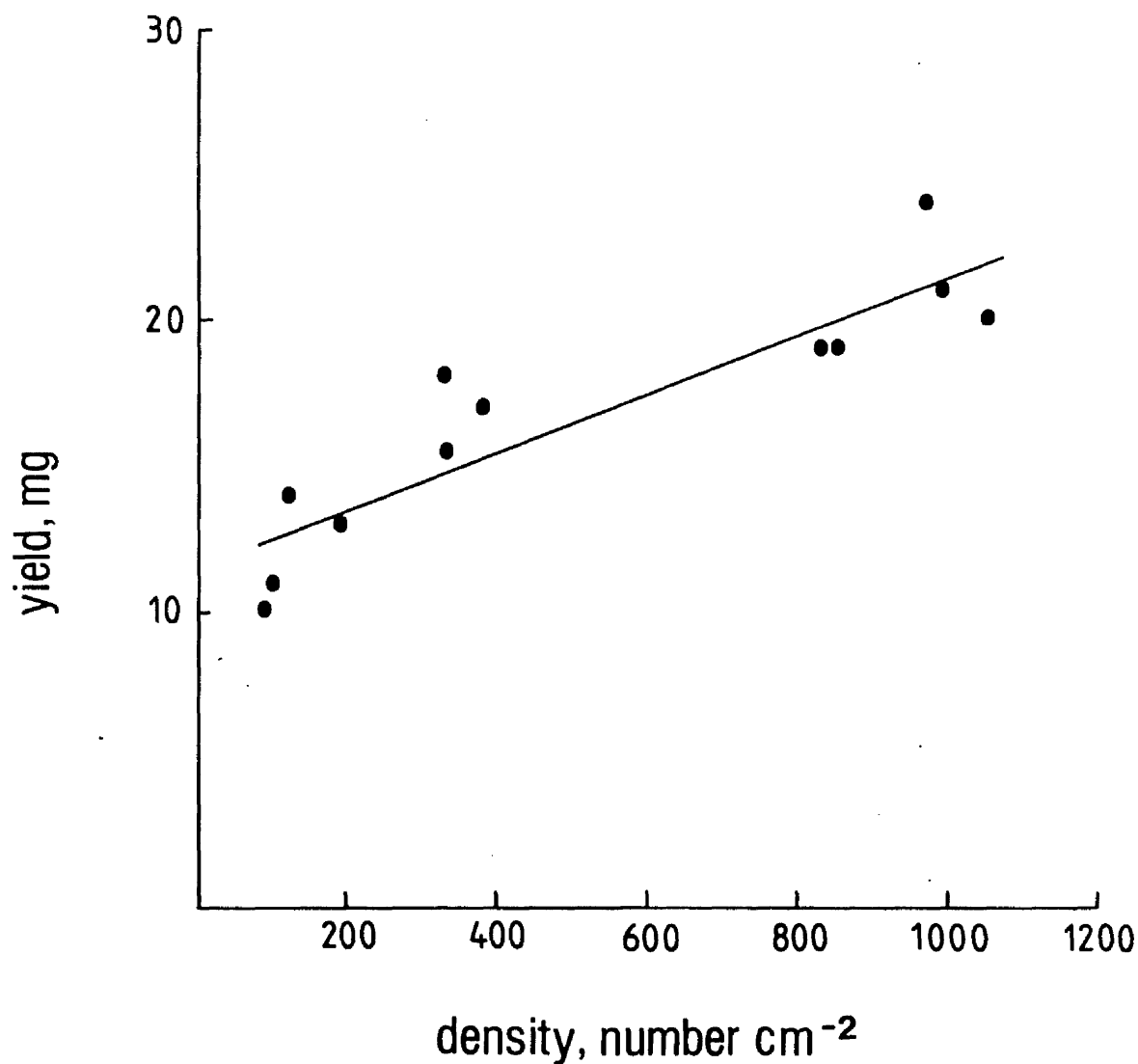


FIGURE 11: Relationship between yield (mg) and density of surviving germlings for *F. serratus* after 43 days of growth.

$$y = 9.90 \times 10^{-3} (\pm 4.38 \times 10^{-4})^{***} x + 11.7$$

where y is yield and x is density. Regression fitted by least squares method.

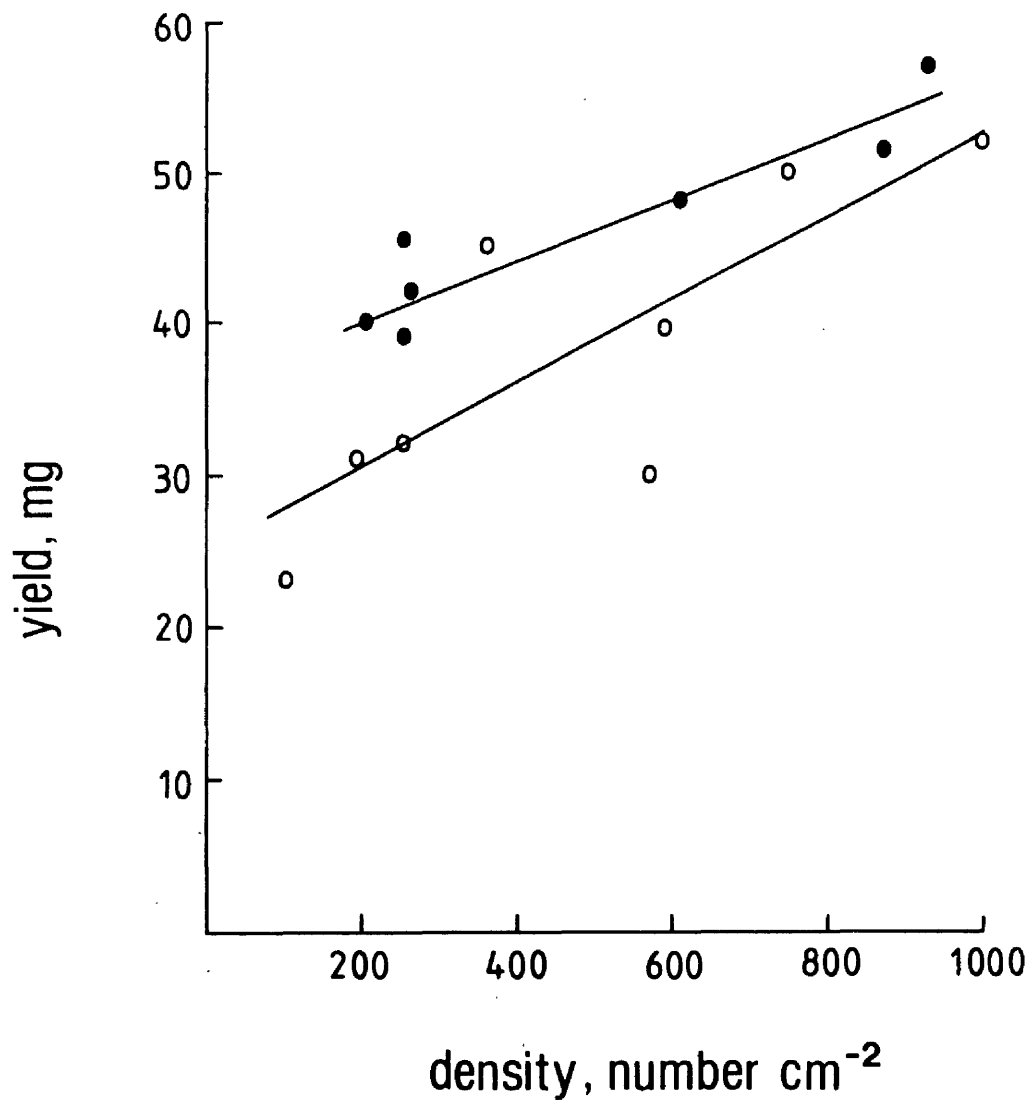


FIGURE 12: Relationship between yield (mg) and density of surviving germlings for F. vesiculosus after 43 days (○) and after 50 days (●) of growth.

(○) $y = 2.75 \times 10^{-2} (\pm 2.89 \times 10^{-3}) x^{**} + 24.6$

(●) $y = 2.01 \times 10^{-2} (\pm 1.13 \times 10^{-3}) x^{**} + 36.4$

where y is yield and x is density. Linear regression fitted by least squares method.

Species	Days of growth	Regression equation
<u>F. serratus</u>	43	$y = 2.64 \times 10^{-3} (\pm 2.11 \times 10^{-4})^{**} x + 2.63$
<u>F. vesiculosus</u>	43	$y = 3.02 \times 10^{-4} (\pm 4.34 \times 10^{-5})^{NS} x + 0.40$
<u>F. spiralis</u>	26	$y = 1.35 \times 10^{-4} (\pm 3.30 \times 10^{-5})^{NS} x + 0.30$

TABLE 8: The relationship between yield (y) in terms of total plant volume (cm³) and density of surviving germlings (x). Significance levels were calculated using a regression analysis of variance. N.S. not significant at 5% levels,
 * p = 0.05, ** p = 0.01 *** p = 0.001

Species	Days of growth	Regression equation
<u>F. serratus</u>	43	$\log_{10} y = -0.69 (\pm 0.02)^{***} \log_{10} x - 2.49$
<u>F. vesiculosus</u>	43	$\log_{10} y = -0.78 (\pm 0.02)^{***} \log_{10} x - 2.13$
<u>F. spiralis</u>	43	$\log_{10} y = -0.38 (\pm 0.10)^{NS} \log_{10} x - 3.57$

TABLE 9: The relationship between log₁₀ mean volume per plant (y) and log₁₀ density of surviving germlings (x). Significance levels were calculated using a regression analysis of variance. N.S. = not significant at 5% level, * p = 0.05, ** p = 0.01, *** p = 0.001

C.2 The effect of density on germlings growing in a simulated tide regime

The effects of density and time submerged per tidal cycle on germling length are shown in Figures 13, 14 and 15. In all three species for both high and low density settlements germling length decreased with increased periods of exposure to air (analysis of variance significant at the 0.1% level). At upper levels on the plates, where germlings were exposed to air for more than 9 hours per 12 hour tidal cycle, there was no development of the zygote. For all species maximum growth occurred at levels which were continuously submerged.

The relationship between length and period of submergence appears to be more or less sigmoid in form for all species.

Germlings did not differ significantly in length between the two density treatments when examined over the full range of submergence. However the interaction between density and period of submergence was highly significant (analysis of variance). Germlings in a sparse stand exposed to air for between 3 and 4 hours per 12 hour cycle were larger than those in a dense stand (Plate 5). However germlings that were exposed to air for more than 4 hours per cycle were larger when growing in a dense stand than when in a sparse stand (Plate 6). Plants in dense stands were also found to survive at higher levels on the plates than those in sparse stands (Plate 7).

The exact vertical level at which the disadvantages of crowding

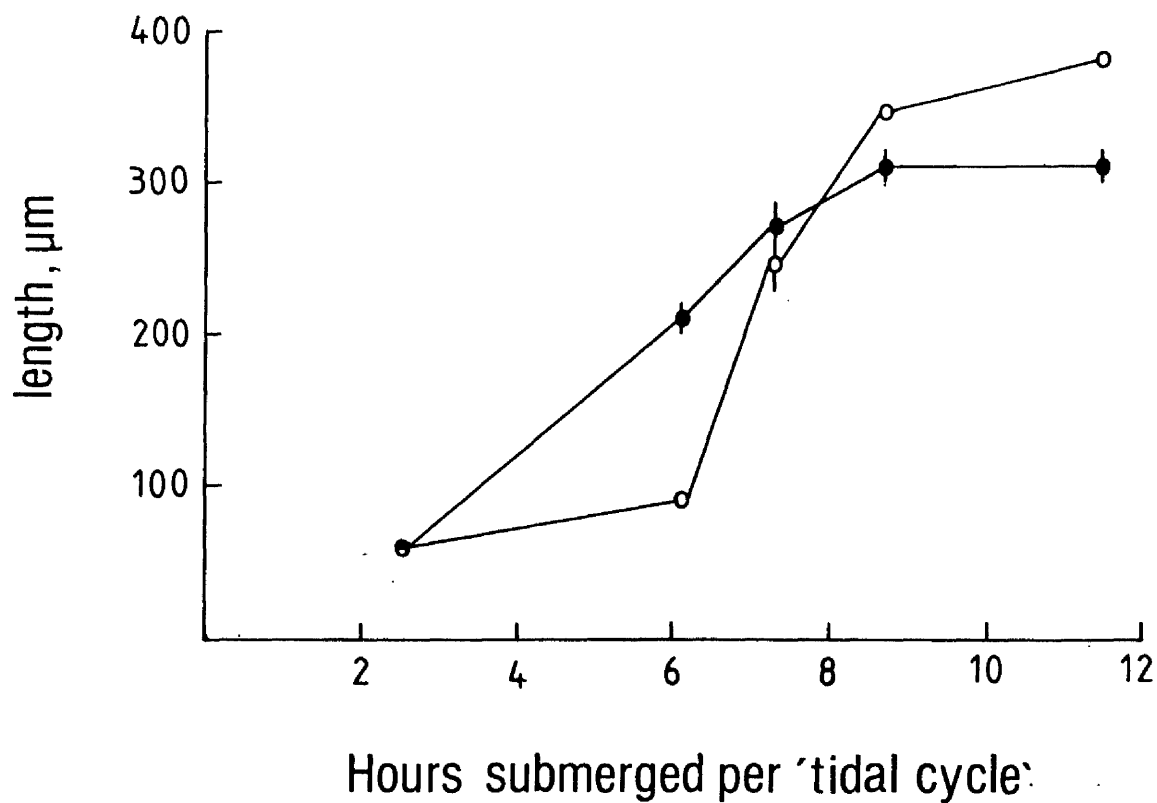


FIGURE 13: Length of *F. spiralis* germlings after 35 days of growth at high (●) and low (○) densities in a simulated tide regime. Each point is a mean of 20 values \pm S.E.

(●) 1376.2 plants $\text{cm}^{-2} \pm 125.9$ S.E.

(○) 519.6 plants $\text{cm}^{-2} \pm 48.86$ S.E.

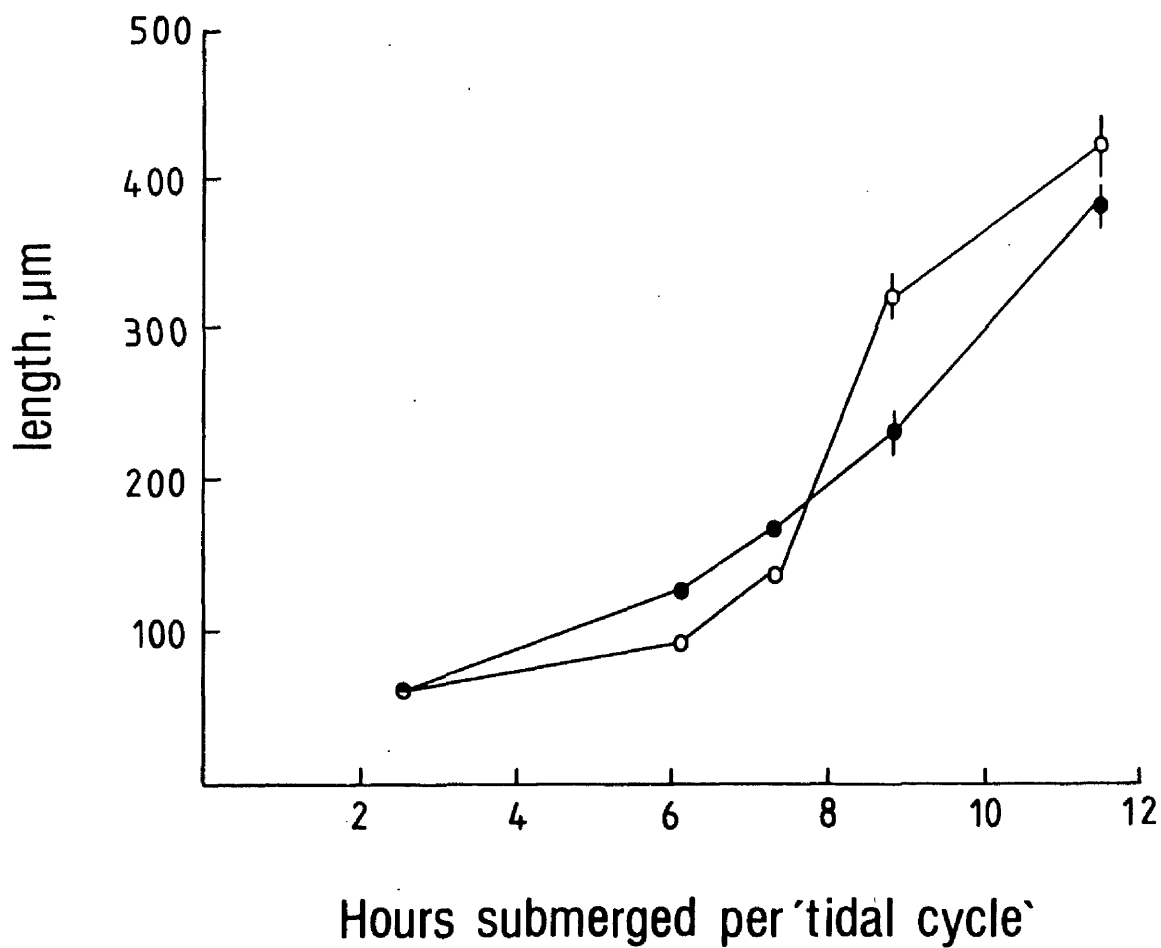


FIGURE 14: Length of *F. vesiculosus* germlings after 38 days of growth at high (●) and low (○) densities in a simulated tide regime. Each point is a mean of 20 values \pm S.E.

(●) 681.00 plants $\text{cm}^{-2} \pm 39.06$ (S.E.)

(○) 519.60 plants $\text{cm}^{-2} \pm 21.23$ (S.E.)

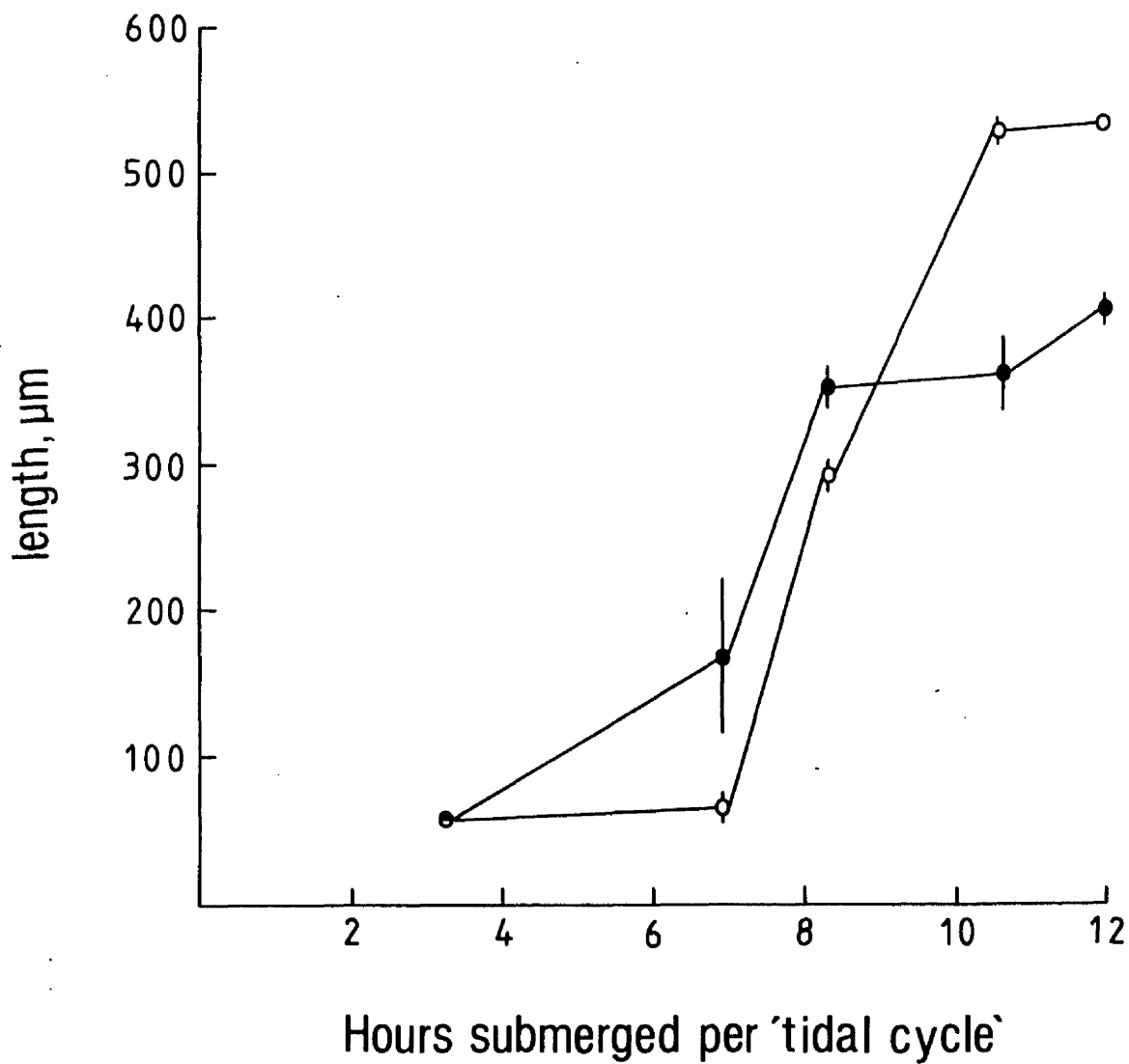
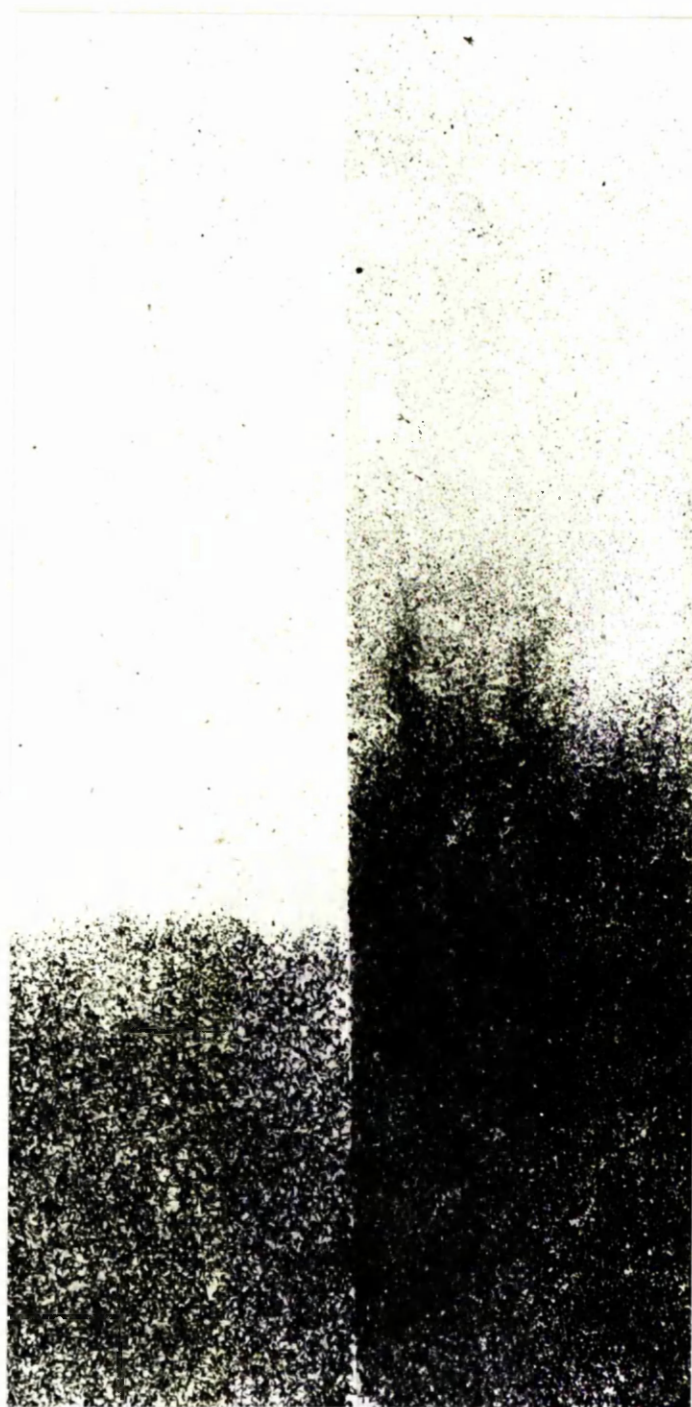


FIGURE 15: Length of *F. serratus* germlings after 27 days of growth at high (●) and low (○) densities in a simulated tide regime. Each point is a mean of 20 values \pm S.E.

(●) $1772.08 \text{ cm}^{-2} \pm 147.08 \text{ (S.E.)}$

(○) $651.03 \text{ cm}^{-2} \pm 29.08 \text{ (S.E.)}$



A

B

PLATE 5: Densely settled Fucus germlings (1772.08 plants per $\text{cm}^2 \pm 147.08$ SE) slide B, survive longer periods of exposure to air in the tidal simulator than do sparsely settled germlings (651.03 plants per $\text{cm}^2 \pm 29.08$ SE) Slide A

PLATE 6: Fucus germlings cultured continuously submerged
are larger if sparsely settled (A) than if
densely settled (B) (x 30 magnification)

PLATE 7: Germlings exposed to air for more than four
hours per tidal cycle are larger when grown
in a dense stand (B) than when in a sparse
stand (A) (x 30 magnification)

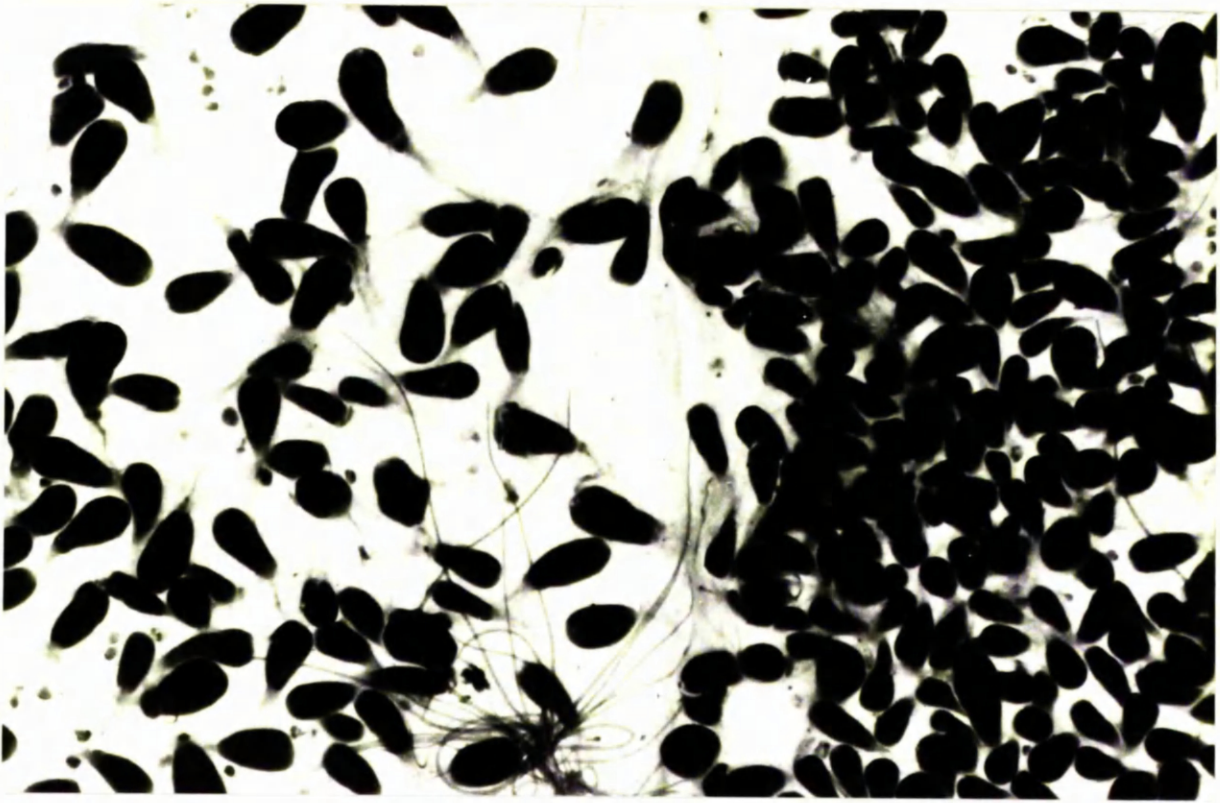


Plate 6

A

B

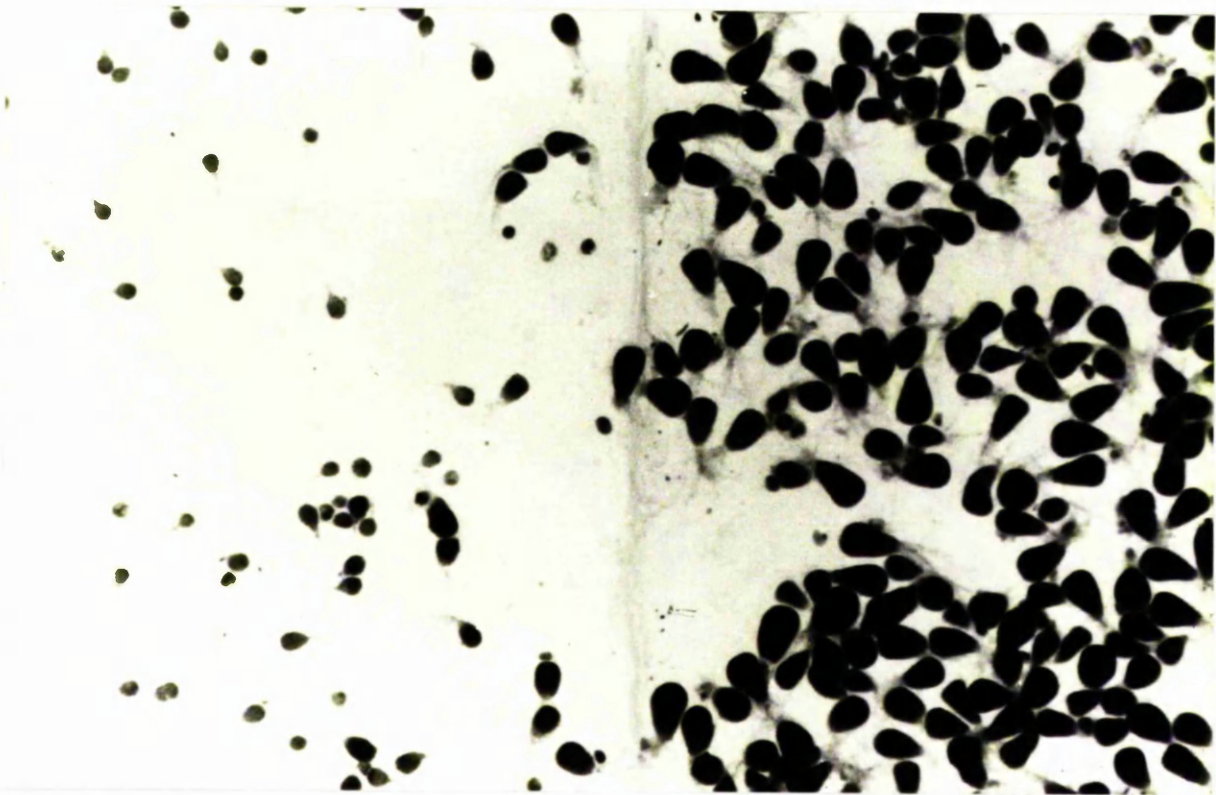


Plate 7

A

B

whilst submerged, were compensated by its advantages when out of water (shown by the cross over point in Figures 13, 14 and 15) varied slightly between species. This point was at 3.1 hours of exposure to air for F. serratus, 4.3 hours for F. vesiculosus and 4.7 hours for F. spiralis. The exact point cannot be determined for F. spiralis because there is an area of overlap between 4.2 and 4.7 hours exposure to air per 12 hour cycle where no significant difference in germling length was found for the two density treatments.

C.3 The effect of germling density on grazing by Littorina

The effect of germling density on grazing of F. serratus by Littorina littorea was investigated and the results are presented in Table 10. The snails did not preferentially graze dense or sparse germling lawns. Equal numbers of snails grazed each density first and the time spent on each was not significantly different at the 5% level (Signed - rank test). The snails did however graze 1.5 times more germlings per minute when on the dense lawn than when on the sparse, but as the dense lawn had over twice as many germlings per cm^2 than the sparse lawn it suffered marginally less grazing damage in terms of the proportion of germlings grazed per minute (Table 10). The snails did not appear to become satiated during the period of grazing and few germlings were dislodged by the snails whilst grazing that were not consumed, this number varied little between the two densities.

Initial density of germling lawn Number cm ⁻² ± SE	Number of germlings grazed cm ⁻² min ⁻¹ ± SE	Proportion of germlings grazed per minute, %	Proportion of time spent on each lawn %	Mean number of germlings dislodged snail ⁻¹ ± SE
899.12 ± 38.94	134.50 ± 24.03	14.1	42.5	0.51 ± 0.05
393.03 ± 18.19	84.04 ± 11.75	21.4	57.5	0.37 ± 0.03

TABLE 10: The grazing behaviour of Littorina littorea (n = 8) when presented with a choice of both densely and sparsely settled lawns of F. serratus germlings

C.4 The effect of density on germlings transferred to the shore

The investigation to determine the effect of density and period of exposure to air on the growth of F. vesiculosus germlings in the field produced some interesting results (Table 11). After a period of 17 days on the shore all the germlings had been removed from the upper shore slides and over 93% from those at the lower level, representing loss rates of up to $70.6 \text{ germlings cm}^{-2} \text{ day}^{-1}$ from the dense stands and $29.4 \text{ germlings cm}^{-2} \text{ day}^{-1}$ from the sparse stands.

As all the germlings had been lost from the upper shore slides it was not possible to tell whether the density of the germlings had significantly affected plant size, however for the lower shore slides there was no apparent difference in length between the germlings grown in dense and sparse stands. It should also be noted that because all the germlings were lost from the upper shore slides the loss rates presented in Table 10 are minimum rates. It is possible that all the germlings could have been killed within several days.

C.5 Density of natural stands of juvenile Fucus

The mean density of natural stands of juvenile F. spiralis plants, less than 3 cm in length, was recorded to provide a comparison for the densities used in the laboratory studies. The natural density averaged 0.77 cm^{-2} and ranged between 0 and $2.69 \text{ plants cm}^{-2}$.

Initial density Number cm ⁻²	UPPER SHORE			LOWER SHORE		
	Final density-2 number cm	Proportion lost %cm ⁻² day ⁻¹	Length of germlings μm S.E.	Final density-2 number cm	Proportion lost %cm ⁻² day ⁻¹	Length of germlings μm S.E.
c 1200	0	5.88	-	24.26	5.76	108.0(± 3.5)
c 1200	0	5.88	-	40.38	5.68	141.5(± 5.4)
c 500	0	5.89	-	15.78	5.70	119.3(± 3.8)
c 500	0	5.89	-	31.02	5.52	102.3(± 2.3)

TABLE 11: Results from the field experiment where densely and sparsely settled slides of

F. vesiculosus zygotes were placed at two levels on the shore for 17 days.

The upper shore slides were exposed to air for 6.5 hours per tidal cycle

and the lower shore slides for 3.2 hours per tidal cycle.

D. DISCUSSION

On the shore the average density of juvenile F. spiralis plants, less than 3 cm in length, was approximately 0.8 cm^{-2} . This is similar to the densities of 0.39 cm^{-2} for F. serratus and of 0.14 cm^{-2} for F. vesiculosus calculated from the data presented by Knight and Parke 1950. As in the Firth of Clyde F. spiralis plants 3 cm in length are at least four months old (Schonbeck and Norton 1980a), it is not unreasonable to suggest that the stands may initially have been at considerably greater densities, especially if natural stands of Fucus experience loss rates approaching those recorded for F. vesiculosus germlings on artificial substrata. Thus the densities of up to 3000 germlings per cm^2 used in laboratory cultures probably approximate to natural initial settlement densities on the shore.

The density of germling settlement significantly affected plant size. Germling length showed a very obvious negative relationship with increasing density, however it was not clear whether the relationship was linear or curvilinear. Although indisputably linear for F. spiralis and F. vesiculosus it appeared to be curvilinear for F. serratus, although for this species the poor scatter of the data along the x-axis means the possibility of a linear relationship with a break in slope at a density of $350 \text{ plants cm}^{-2}$ cannot be dismissed. At densities of less than $350 \text{ plants cm}^{-2}$ a decrease in number per cm^2 produces a much greater increase in plant length than changes in density above $350 \text{ plants cm}^{-2}$. Unfortunately the range of low densities over which F. spiralis and F. vesiculosus

were grown was insufficient to determine whether they too may have a curvilinear relationship.

Vadas (1972) working on young Nereocystis leutkana sporophytes also found there was a significant decrease in sporophyte length at densities above 10,000 per 100 ml of culture medium. At this density the mean length of the ten largest sporophytes from three experiments was 6.19 mm, but at four times the density the mean length was 3.60 mm and at eight times was 1.1 mm. Hruby (1977) however reported that spore density had no effect on the size of Blidingia minima sporelings when measured by the ten largest plants. From personal observation density may not be found to affect plant size if measured by the largest individuals, because even in the most dense Fucus stands some individuals were noticeably larger than the average size of the majority. Plant populations growing under stress may have a skewed distribution of plant weight (Harper 1977). Obeid et al. (1967) working on the Fiber flax, Linum usitatissimum, noted that a hierarchy of individuals developed in a stand with a few large dominants and a large number of suppressed plants. Similar observations have been made for dense forests of Laminaria hyperborea where populations of plants were found to have predominantly long or short stipes with few intermediates (Kain 1971). Hruby (1977) and Vadas (1972) may have reached different conclusions if mean plant size had been calculated from a randomly selected group of individuals rather than from the largest individuals.

With increasing density Fucus germlings also became smaller in volume per plant and mean biomass per plant. The relationships

relating mean dry weight and density on a logarithmic plot appears to extend beyond the boundary condition described by the equation $\log_{10} \bar{w} = 4.3 - 1.5 \log_{10} d$ derived from higher plant studies. Plant populations do not normally extend beyond this line because it describes the theoretical maximum combination of biomass and density that can occur. However in very exceptional cases some populations do transgress the line. In an example described by Westoby and Howell (1981) seeds were sown at such high densities that on germination the plot of the mean dry weight of the deployed cotyledons extended above the line, however this was followed by rapid mortality. The deviation of Fucus germlings from the rule cannot be explained by growth due to seed reserves as in Westoby and Howell's (1981) experiment. The results from all three species of Fucus are very similar which suggests that it is not the data that are in doubt but possibly the applicability of the ' $-3/2$ power law' where $k = 4.3$. The value of $k = 4.3$ is taken from mature higher plants and although applicable to adult seaweeds (Cousens and Hutchings 1983) may not be appropriate to seaweed germlings. It has already been reported that coniferous trees generally have higher intercepts than deciduous trees and that grasses have higher intercepts than dicotyledons (Lonsdale and Watkinson 1983). Since the intercept of the ' $-3/2$ power law' may vary between species due to variations in plant geometry and canopy shape (Lonsdale and Watkinson 1983) and with growing conditions (Lonsdale and Watkinson 1982; Westoby and Howell 1981) it is possible that the seaweeds may also have a different intercept. A boundary line of slope - 1.5

with an intercept of 5.14 would encompass all the points on Figure 9. A value of 5.14 is not abnormally large, as intercepts of 5.64, 5.82 and 6.67 have been reported for Agrostemma, Cichorium and Festuca respectively (Lonsdale and Watkinson 1983).

The slope of the relationships found for Fucus are approximately - 0.70, well below the slope of the boundary condition which does not alter with conditions. This suggests that the populations have not reached their limiting combination of density and biomass. As can be seen from the data on F. vesiculosus, the populations approach the slope over time. As the plants develop they will eventually reach a boundary condition with slope of - 1.5 and begin to self-thin because it would be impossible for algae to survive to maturity in stands of several hundred plants per cm^2 purely because of the physical requirement of space for holdfast development. Holdfast fusion is not uncommon in crowded individuals, but probably renders the plants more susceptible to 'uprooting' by wave action, for it reduces the ratio between area of attachment to the substratum and biomass of plant above.

Fucus also appears to conform to the law of constant final yield as the slope of the line relating yield (mg) to the density of survivors was found to approach zero over time, although very marginally. This suggests that for F. vesiculosus, and possibly for the other fucoids, yield could become more or less constant over a range of densities at the germling stage. As a consequence of density-dependent growth, plants show plasticity of form so that in dense stands plants are small and in sparse stands plants are large, hence overall yield is constant.

In the past many species have been tested to see if they conform to the law but there have been few attempts to determine why the law applies since those of Yoda et al. (1963). It is necessary to establish the theory behind the law, because without a theory there are no hypotheses to test or reject.

The algae may be a particularly useful group of plants for the investigation of the ' $-3/2$ power law' because the absence of roots simplifies any interaction between plants by confining it to above ground.

Fucus spiralis did not respond to density as dramatically as the other species. It was unlikely that F. spiralis germlings differed from those of F. serratus and F. vesiculosus in their response to density as they are similar in physiology and morphology. It was more likely that F. spiralis stands were harvested prematurely at 26 days before the effects of density were fully manifest. It was certainly apparent from the data on F. vesiculosus that the effects of density became more marked with time. Also F. spiralis was grown at considerably higher densities than the others, and it was observed from the study of F. serratus that the effects of density are more apparent at lower densities.

In the tide simulator germlings grew better when continuously submerged regardless of their natural position on the shore. Similar results were obtained for a variety of species by other workers using tidal simulators (Allender 1977; Edwards 1977; Hruby and Norton 1979). It has also been shown that F. spiralis plants on the shore will grow at levels with greater periods of submergence than normal if

relocated as mature plants, but are normally excluded as juveniles due to competitive interactions with other algal species (Schonbeck and Norton 1978).

In the tide simulator germlings growing in a dense stand appeared to benefit from mutual protection from desiccation. The vertical level at which the disadvantages of crowding whilst submerged were compensated for by its advantages when out of water varied between species. However it was not possible to draw exact comparisons between species because they were not all grown at the same densities. In general the level at which crowding became advantageous for each species fell in an order which corresponded to the vertical zonation of the species on the shore. For example F. serratus normally inhabiting the lower shore was found to have its critical level at a shorter period of exposure to air than F. vesiculosus which inhabits the middle shore.

The degree to which each species benefit from mutual protection against desiccation appeared to be related to its intrinsic resistance to desiccation. F. spiralis appeared to benefit least from a dense settlement when growing in the tide simulator. This may be because F. spiralis is an inhabitant of the upper shore known to be more resistant to desiccation than are the lower shore species.

Hruby (1977) also reported that the survival of Enteromorpha linza and Blidingia minima sporelings in a tide simulator was affected by the settlement density of the spores. However the density effect was found to be limited only to those plants that were treated with a seven day period of submerged growth prior to placement in the tide

simulator. No density effect was found on plant populations placed directly in the tide simulator.

In the present investigation density was found to effect the level of growth and hence survival of Fucus germlings on plates with only a brief 24-48 hour period of submergence. The fact that the effect of density on B. minima was modified by a pre-treatment of continuous submergence (Hruby 1977) suggests that the beneficial effects of a dense stand were a function of plant size and occur earlier in larger plants. Certainly large plants are likely to increase the water-retaining capacity of a stand and therefore reduce the rate of desiccation when exposed to air. In fucoids even the zygotes are quite large so that an initial period of submerged growth is not necessary for density-dependent effects to manifest themselves.

Although laboratory experiments clearly revealed relationships between germling growth rates, relative crowding and exposure to air, there was little evidence of such phenomenon from the field studies. However as the slides placed on the shore were colonised by large numbers of green algae this may have affected the results. This observation itself suggests that intra-specific competition at the germling stage although significant is only one of many factors influencing survival and growth.

High mortality/loss rates were recorded for the germlings on the shore, particularly at the upper shore level. Why this should be so is not clear as the highest placed slides were still within the F. vesiculosus zone and should not have experienced

excessive exposure to air. Also the slides were not covered by the thalli of surrounding algae so it is unlikely that the germlings were removed by whiplash. As the upper and lower shore sites were separated by only a few metres, differences in wave-exposure were unlikely to be sufficient to cause such a large difference in the number of germlings lost. The loss rate of germlings from both the upper and lower shore seemed extremely high compared with data collected from other species. For example the mortality amongst natural stand of Leathesia juveniles was small, only 10.8% of the population was lost in the first three weeks. In fact they exhibited a Deevey Type I survivorship curve (Deevey 1947) since mortality increased with age (Chapman and Goudey 1983). Pelvetia fastigiata germlings were depleted by 50% over 80 days and 9% survived to the first reproductive season after 1.5 years (Gunnill 1980).

It is possible that because the experimental fucoid germlings were initially settled in stationary water in the laboratory, they formed a weaker attachment to the substratum than would occur in nature and thus when transferred to the shore they were readily dislodged. However, as the loss rates for both high and low density stands were similar, it suggests that settlement density may not be important to initial survival on the shore.

A preliminary experiment on the influence of germling density on grazing suggested that germlings may be better protected from grazing when growing in a dense stand than when in a sparse stand. This requires further investigation over a wider range of densities

than tested here. Also it is unfortunate that the number of replicates was limited by the availability of Fucus zygotes for this undermines the confidence that can be invested in the results. Nonetheless, there does seem to be an important relationship between the extent of grazing damage to germling lawns and the number of plants per unit area. Hay (1981) also found that species of Halimeda, Laurencia and Dictyota when growing in a turf on the shore, lost 15-50% less biomass to the grazing urchin Diadema antillarum, than did isolated individual plants. However, the reasons proposed for the reduced susceptibility are not applicable to the dense stands of Fucus germlings grazed by Littorina.

It appears that intraspecific competition is not only an important influence on the growth of adult plants, but also in the establishment and survival of juvenile seaweed populations. The results also provide another example on which to test the applicability of the ' $-3/2$ power law'. By determining the boundary condition for a great variety of plants with different growth forms it should be possible to increase our knowledge of which factors are important in determining the position of the boundary and may eventually be able to establish why the law applies, for at present, as Hutchings (1983) so rightly states it is "ecology's law in search of a theory".

GENERAL DISCUSSION

GENERAL DISCUSSION

The growth and survival of fucoid germlings appears to be significantly affected by the density of zygote settlement. However the relevance of this finding to seaweed population biology only becomes apparent when it is considered in the broader context of shore ecology.

Fucoid germlings find themselves in a world full of potential enemies and hazards. They face the risks of desiccation, being grazed by herbivores or being out-competed in their quest for space, irradiance and nutrients. The relative importance of these stresses on a germling will depend on whether it inhabits the upper or lower shore. On the upper shore the main enemy is desiccation, but on the lower shore where desiccation rarely, if ever, prunes back fucoid zones (Schonbeck and Norton 1978) grazing is likely to be a greater threat to survival. The largest and most voracious limpets and littorinids are usually found below Mean High Water Neaps (Evans 1947a, 1947b) and may exert a profound effect on the survival of germlings by scraping them from the rock (Jones 1946, Newell 1958, Southward 1962). However, they seldom venture on to the upper shore where their grazing activity would be severely restricted by the tide as Patella and Littorina graze only when submerged. The upper shore does have its own grazers, such as Hyale, an amphipod which grazes Pelvetia (Moore 1977) and Littorina neritoides, the latter however presents little threat to fucoids as it is thought to graze mostly on lichens (Fretter and Graham 1980).

Interspecific competition is also likely to pose a greater problem to juvenile fucoids growing on the lower shore than to those growing on the upper shore where the algal cover is less and also the variety of species is fewer (Gibb 1939; Russell 1982, 1973).

Since crowding of germlings appears to offer mutual protection against the effects of desiccation (likewise for more mature plants (Hatton 1938; Schonbeck and Norton 1978)) it would be beneficial for the upper shore fucoids to recruit in dense stands. Dense settlements would mean a slower growth rate, but this is not critical as competition is low. Crowding could also provide some protection from the lesser problem of grazing damage until the germlings reached a safer size (Lubchenko 1980). On the lower shore however, where grazing is a major threat, escape requires rapid attainment of a less vulnerable size. Crowding might offer some protection from grazers but it is generally less beneficial than a sparse settlement which would allow more rapid growth. Rapid growth is also a better ploy against other competitors as larger germlings are less likely to be shaded out.

Schonbeck and Norton (1980a) have in fact reported that on the Isle of Cumbrae fucoid germlings appeared annually in dense 'turfs' on the upper shore, but only as small scattered groups lower down. This suggests that upper and lower shore fucoids may have different reproductive strategies to ensure an appropriately dense or sparse settlement. One would predict that to achieve a dense settlement, for example, upper shore fucoids might exhibit restricted dispersal of propagules; synchronized reproduction of the individuals

within a population and a short reproductive season. This would ensure that the recruitment of juveniles was concentrated in both time and space. However, the facts do not seem to support such a hypothesis. Fucus spiralis plants have slightly larger oospheres than some of the other fucoids (Vernet and Harper 1980) but this is unlikely to increase the sedimentation rate sufficiently to reduce their effective dispersal distance. The sinking rate of a seaweed propagule is thought to have relatively little influence on its dispersal distance except in the calmest of water (Norton and Fetter 1981). Thus the slight size difference between F. spiralis and F. serratus propagules, for example, would appear to be negligible in relation to water motion on the shore.

Studies on the length of the fertile period for different species of Fucus suggest that the fertile seasons are of much the same duration (Blackler 1956) and since there is no information available on the proportion of a fucoid population fertile at any one time it is impossible to comment on the degree of synchrony of reproduction. It must be concluded therefore that the differences between the 'reproductive strategies' of different Fucus species are insignificant and unlikely to have any tangible effect on germling density. It seems more likely, for both upper and lower shore species, that the propagules are scattered at random in both dense and sparse patches. Dense patches would probably be found close to the parent plants separated by sparser lawns. On the upper shore the well-spaced individuals are soon killed, leaving the crowds to become visible, but on the lower shore where the crowds are vulnerable to grazing,

because the constituent individuals grow so slowly, it is the well-spaced individuals that become obvious first. Plantlets are much less likely to be seriously damaged by molluscs once they have attained a size of 30-50 mm (Knight and Parke 1950; Menge 1975). As it could take a germling growing in a dense stand several weeks longer to reach this size than one growing in a sparse stand, crowded germlings are much more vulnerable to grazing. However, since crowds of germlings would be steadily diminished by grazing, whiplash of adult thalli and self-thinning, crowding may not be a lasting disadvantage to the lower shore germlings. Similarly on the upper shore, processes operate to reduce crowd density, but as germlings at these levels are slower-growing (Schonbeck and Norton 1980a) self-thinning operates more slowly. Therefore they will have reached the stage when crowding is less advantageous, as older plants are less vulnerable to desiccation before their numbers are diminished.

There are many dangers inherent in proposing such adaptation hypotheses, since the presumed 'strategy' may exist only in the eye of the investigator. Adaptation hypotheses are also impossible to test and therefore hardly scientific. In the words of Maynard Smith (1978), "a functional explanation through optimisation theories is a test of ingenuity rather than enquiry into truth".

The competition-density effect on algal growth has important implications not only for the shore ecologist, but also for the commercial mariculturist, for cultivation results in large mono-specific stands of seaweeds.

At present there are 493 species of economic seaweed but only four genera can be really regarded as significant crop plants (Tseng 1981), these are Porphyra, Echeuma, Laminaria and Undaria; each of which represents between 10,000 and 275,000 tonnes of dry matter per year. It is an expanding industry which has in the past been limited by the availability of raw materials, depleted as a result of over-harvesting, storm damage and other difficulties. Maximisation of yield is obviously important to the mariculturist but so too is ease of tending and harvesting and minimisation of losses due to grazers and disease.

The "law of constant final yield" is of particular relevance to the cultivation of algae. It has already been applied to the cultivation of Porphyra (Yoshida 1972) where yield was found to be constant at 2g, whether the plants were sown at 400 or 2,000 per 10 cm of hibi string. Neushul (personal communication) also found a clear density-size relationship for Macrocystis and was able to use this data to optimise yield.

If a range of densities was established where yield would not be reduced by a reduction in plant density it may be possible to avoid the detrimental effects of crowding, as crowding may affect other factors apart from plant size. For example it was noted that one of the most common physiological diseases of Laminaria, green rot, usually occurred on over-crowded fronds (Tseng 1981). The density of an algal stand may also affect the proportion of resources that a seaweed allocates to reproductive and vegetative growth. Russell (1979) found that where F. vesiculosus and Ascophyllum nodosum were competing for light and space F. vesiculosus had a

greater production of vegetative to reproductive tissues. Thus plants growing in a crowded monospecific stand competing with each other may also have a reduced reproductive output. However, as seaweeds are so fecund this might not significantly affect the supply of inoculum for the next season.

The number of grazers associated with an algal population may also vary with algal density, for example the creation of dense Durvillaea stands for harvesting increased the abundance of herbivorous isopods (Hay and South 1979). This may be because the isopods find protection from predators amongst the algal canopy. An increase in the number of herbivores is not necessarily disadvantageous as they may relieve the crop plant of its epiphytes. Where this occurred for Hypnea, its growth was increased by as much as 300% (Brawley and Adey 1981).

One advantage of a dense settlement which may compensate for any other density effects is the exclusion of 'weeds'. If spores of a crop species are settled sufficiently densely, they may overwhelm and prevent the development of the spores of competing species. This method of reducing the 'weed' problem in cultures is practised in Porphyra cultivation (Tseng 1981) and has been well-studied for higher crop plants (see Snaydon 1980).

The commercial cultivation of seaweed is in many ways similar to agronomy, it is an organized system of sowing and harvesting designed to maximise yield. There have been many studies on the effects of density on growth and yield in agricultural crops (reviewed in Snaydon 1980) the principles of which, as in the law of constant

final yield may be applicable to seaweeds. However there are several basic differences between seaweeds and higher plants notably the absence of roots, aqueous growth medium and different reproductive systems. As exemplified by this study there has been an increasing trend towards demographic studies of seaweeds using techniques developed for higher plants. However, such techniques are probably not applicable to all seaweeds, particularly crustose and mat-forming species where it is almost impossible to discern an individual from its neighbours. Studies of interspecific competition also have problems due to the similarity in colour and form of many of the juvenile stages of natural competitors on the shore, it is therefore very difficult to tell them apart. However by choosing species of different coloured algae Russell and Fielding (1974) and Enright (1979) have successfully adapted the approach developed by de Wit (1960) for the study of interspecific competition amongst higher plants. Certainly for the marine algae that grow upright as separate individuals there is much more scope for applying higher plant techniques. Demographic studies on cohorts for the production of life tables have been completed for Macrocystis pyrifera (Rosenthal et al. 1974), Pelvetia fastigiata (Gunnill 1980) and Leathesia difformis (Chapman and Goudey 1983). They have shown that this is a very profitable area of study and as noted by Russell and Fielding (1981) have established "an excellent approach to marine algal population dynamics".

APPENDIX A: CULTURE CONDITIONS

1. Medium

Receptacles and germlings were cultured in an enriched seawater medium which was changed every seven to fourteen days unless stated otherwise. The formula of the medium and the procedure of heat-sterilisation used are given in Appendix B.

2. Illumination

The cultures were illuminated from above except for the tide simulators and the spore accumulators which were illuminated from one side. In all cases the cultures were illuminated by two six-foot Phillips 'Daylight 33' 85 Watt tubes, with a 16 hour light: 8 hour dark photoperiod.

3. Aeration

All of the cultures of germlings were aerated by an air pump.

4. Temperature

All cultures were grown in a thermostatically controlled culture room at $12^{\circ}\text{C} \pm 1^{\circ}\text{C}$

APPENDIX B: PREPARATION OF ENRICHED SEAWATER MEDIUM

The culture medium was recommended by Professor A.D. Boney and was used at one quarter of the recommended concentration given below, to reduce the growth of algal contaminants (Schonbeck and Norton 1979d).

To prepare pasteurized seawater add nine parts filtered seawater to one part distilled water and heat to 65°C , cool and repeat.

To one litre of pasteurized seawater add:

60 ml Solution A which contains:

50 ml $0.4 \text{ g l}^{-1} \text{ NaNO}_3$ in distilled water

2 ml of each of the following:

- $1.47 \text{ g l}^{-1} \text{ MnSO}_4 \cdot 4\text{H}_2\text{O}$
- : $0.0023 \text{ g l}^{-1} \text{ CuSO}_4 \cdot 5\text{H}_2\text{O}$
- : $0.064 \text{ g l}^{-1} \text{ CoCl}_2 \cdot 6\text{H}_2\text{O}$
- : $0.23 \text{ g l}^{-1} \text{ Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$
- : $0.005 \text{ g l}^{-1} \text{ LiCl} \cdot \text{H}_2\text{O}$

2 ml Solution B which contains : $4.98 \text{ g l}^{-1} \text{ ZnSO}_4 \cdot 7\text{H}_2\text{O}$

15 ml Solution C which contains :

2.6 g l^{-1} tetrasodium salt of EDTA

$0.12 \text{ g l}^{-1} \text{ FeSO}_4 \cdot 7\text{H}_2\text{O}$

1.5 ml Solution D which contains: $15 \text{ g l}^{-1} \text{ Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$

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