# A STUDY OF THE ENVIRONMENTAL FACTORS GOVERNING THE VERTICAL DISTRIBUTION OF INTERTIDAL FUCOIDS

Mark W. Schonbeck, A.B.

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Department of Botany,
University of Glasgow.

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*To my parents and my elder brother Niels*

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## SUMMARY

The aim of this investigation was to determine the environmental factors that control the limits of vertical distribution of five intertidal species of fucoid algae which form a characteristic sequence of zones on the shore.

The death of algae transplanted above their normal limits, together with field observations of the seasonal truncation of the uppermost plants in natural stands, clearly indicated that the upper limits of Pelvetia, Fucus spiralis and Ascophyllum are determined by their ability to survive the prolonged desiccation occasioned by warm dry weather during neap tides.

Measurements made under controlled laboratory conditions showed that the upshore species Pelvetia and F. spiralis do not avoid tissue dehydration more effectively than the lower shore species F. serratus. Plants of all three species evaporated water at similar rates, with Pelvetia marginally the fastest owing to its peculiar thallus shape. All three species also retained similar amounts of residual water when air-dried to a low water potential.

In nature, mutual protection from desiccation appears to be less in mature stands of Pelvetia and F. spiralis than in those of the larger midshore species. However, the vulnerable zygotes and young germlings of the upshore species enjoy protection from extremely rapid dehydration by settling in sheltered microhabitats and growing in dense carpet-like stands.

Drought tolerance was assessed in the laboratory by comparing oxygen evolution rates before drying and on resubmersion after drying, and by measuring growth in culture over a 10 to 15 day period after an experimental stress. All except the low-shore species F. serratus survived dehydration to air-dryness, but the maximum duration for which each species tolerated this stress correlated precisely with its position in the zonation sequence: Pelvetia > F. spiralis > Ascophyllum > F. vesiculosus > F. serratus. Pelvetia demonstrated great drought tolerance all year round, and could be air-dried at any

temperature and relative humidity which occurs on British shores without immediate harm. F. spiralis often suffered sublethal damage upon being air-dried, and its drought tolerance showed a pronounced seasonal variation. It was found that substantial drought hardening could be induced in this species by daily exposures to a warm dry atmosphere.

Other physical conditions during tidal exposure can modify the physiological effects of dehydration. High temperature and high humidity accelerated time-dependent injury in experimentally dried plants, possibly by increasing the rate of adverse metabolic changes. Hence it is actually advantageous for Pelvetia and F. spiralis to dry quickly during exposure to hot weather. Sudden simulated rainfall upon air-dry plants also aggravated drought damage, although rain by itself seemed to exert little effect on fucoids, either in the laboratory or on the shore.

With regard to lower limits, both Pelvetia and F. spiralis survived and grew when transplanted to levels below their normal zones. However, Pelvetia, unlike other fucoids, seems to have a physiologically determined lower limit on the shore, as it decayed in winter when transferred to the midshore, and became necrotic when kept constantly submerged in culture.

F. spiralis grows much more rapidly in length than Pelvetia and forms a shading canopy beneath which Pelvetia apparently cannot grow. Pelvetia zygotes settled, germinated and grew normally within the F. spiralis zone when the latter species was experimentally weeded out. However, Pelvetia was never observed to develop into macroscopic plants within natural stands of F. spiralis even where the canopy was broken. There is no evidence that F. spiralis could directly eliminate Pelvetia by either whiplash effect or by shading. Indeed, in culture, the germlings of all intertidal fucoids including Pelvetia could remain viable for long periods of time in total darkness. However, in the light, the embryos of Pelvetia were found to grow much more slowly than those of Fucus species. They would therefore be prone to overshadowing by Fucus, which would further retard their growth, leaving them vulnerable to grazing by molluscs over an extended period.

The growth rates of the embryos of the three Fucus species correlated with their relative positions on the shore: F. spiralis < F. vesiculosus < F. serratus, which might explain the scarcity of F. spiralis within the ranges of the other two species which can outgrow it.

Ascophyllum resembles Pelvetia in the very slow growth of its embryos and young plants, but, unlike Pelvetia, its young plants were found to survive beneath a Fucus canopy. This ability, combined with the great longevity of Ascophyllum contribute to its ability to dominate the midshore under certain conditons.

# 1. INTRODUCTION

One of the primary tasks of the ecologist is to relate species distribution to conditions in the natural environment. The limits of distribution of each species in any ecosystem may be influenced by a large number of physical, chemical and biological factors. Each species is excluded from those habitats in which extremes of temperature, water deficit or any other physical or chemical stress exceeds its limits of tolerance. Competition, predation and other biotic influences may further exclude it from some habitats which it would otherwise occupy. The total range of habitats in which the physical conditions would permit the species to survive is defined as its "fundamental niche", and the range of habitats it actually occupies as its "realized niche" (Colwell and Fuentes 1975). Since only the realized niche can be observed in nature, it is often not immediately apparent whether the species' distributional limits are determined by physical stresses or by biotic interactions.

In many ecosystems, these factors interact to produce a mosaic of habitats in which the primary causes of each species' distribution pattern are extremely difficult to identify. However, in some natural environments, species distribution can be related to a well-defined environmental gradient of increasing intensity of one or several physical stresses. The shore is one such environmental gradient which is of special interest for two reasons. Firstly, it is a transition zone between the two fundamentally different habitats of land and sea. Therefore the vertical distributions of shore species may be controlled by a large number of physical environmental parameters which change radically in intensity from low to high water mark. Secondly, the shore is one of the steepest environmental gradients in nature. The entire transition takes place over a distance of a few to a few hundred metres, within which a striking series of species zones or belts can often be observed. On such a gradient, the role of the physical factors in determining the realized niche of each species can be conveniently assessed by experiment.

Theoretically, an unchanging sea level would demarcate a fixed boundary between the marine and terrestrial environments with little

or no transition region. However, most shores are characterized by the daily ebb and flow of tides which generate the observed shore gradient. The term "shore gradient" as used in this dissertation is specifically defined as the complex physical environmental gradient extending from the marine habitat at low water mark to the terrestrial habitat above the reach of wave splash and spray.

## 1.1 Tides and tidal exposure

On most European shores, sea level rises and falls as a roughly sinusoidal function of time with a period of a little more than twelve hours. Therefore, the duration of each submersion decreases progressively up the shore gradient. Also the levels of high and low tides vary in a fortnightly rhythm, with a regular alternation of spring and neap tides. During the spring tides, tidal amplitude reaches its maximum, producing the highest high-water and lowest low-water levels. During the neap tides, tidal amplitude is smallest, and the highest low-water and lowest high-water levels occur. Above the high water level of neap tides, the frequency as well as the duration of submersion decreases with distance upshore. Therefore, the shore gradient can be described in terms of two parameters of tidal exposure. The first is percent tidal exposure, i.e.

$$\frac{\text{(total hours exposed)}}{\text{(total hours exposed) + (total hours submerged)}} \times 100\% ,$$

which is calculated over several fortnight-long periods at different times of the year to obtain an unbiased sample of spring and neap tides (Colman 1933). The second parameter is the longest tidal exposure, which is the maximum possible duration of a single uninterrupted period of exposure to the atmosphere. Analogous parameters can be calculated for tidal submersion. The position of an organism relative to the high and low water marks of spring and neap tides determines the percent tidal exposure and longest tidal exposures and submersions it must endure, and will hereafter be referred to as its tidal level.

Because it is generated by the tides, the shore gradient is unique in that intermediate levels are characterized not by intermediate conditions, but by an alternation of the two extremes. Therefore

severe physical stresses operate at all levels of the shore. Any organism which invades the intertidal zone must be capable of surviving in an entirely alien physical environment for part of the time, during tidal submersion for a terrestrial organism and during tidal exposure for a marine organism.

## 1.2 Stresses associated with the shore gradient

Intertidal seaweeds and invertebrates are generally regarded as marine organisms which have become adapted to a greater or lesser degree of tidal exposure (Lewis 1964; den Hartog 1968). This would suggest that conditions are most favourable to these organisms during tidal submersion. The sea provides mineral nutrients, oxygen and carbon dioxide in solution and protects shore organisms from the violent environmental fluctuations which take place in the air. However there are stresses associated with tidal submersion. The mechanical action of the waves exerts a decisive influence on the shore's biota (Lewis 1964) and submersion to a depth of a few metres may greatly reduce the amount of radiation available for photosynthesis.

The most severe physiological stresses upon shore organisms take place during tidal exposure. For example, even at 90% relative humidity, the atmosphere can remove more than three quarters of the tissue water from fucoid algae (personal observation). Intense insolation during low tide on a warm day may increase the temperature of intertidal seaweeds to 30°C or more (Schramm 1968), causing both a heat stress and accelerated dehydration. The shore may also be affected by severe frost during the winter, and intertidal algae have been found frozen solid in ice on shores at high latitudes (Kanwisher 1957). Finally, heavy rainfall during low tide exposes them to fresh water. The resulting osmotic shock may be especially pronounced if a sudden shower falls upon desiccated seaweeds.

Since tidal exposure is an "all or nothing" event at all levels on the shore, it is the duration rather than the intensity of these stresses which increases most markedly up the shore gradient. The effect upon an organism of a physiological stress is often directly related to how long it continues without relief (Levitt 1972). The maximum possible

duration of continuous dessication, freezing, high temperature or rainfall at a given level on the shore is determined by the longest tidal exposure at that level. This tidal parameter increases gradually from zero at the extreme lowest water level of spring tides (ELWS) to about twelve hours at extreme high water of neap tides (EHWN, i.e. the lowest high water), then rises abruptly to twenty-four hours just above this level. It increases rapidly with further distance upshore, and organisms living at the mean high water level of spring tides (MHWS) may be continuously exposed for several weeks. Colman (1933) reported that a large number of species reach their upper limits near EHWN. Therefore, this level appears to be a physiologically critical one, below which the shore gradient is relatively gradual and above which it becomes very steep.

During tidal exposure, seaweeds are also cut off from their mineral nutrient supply, and must utilize gaseous carbon dioxide for photosynthesis. Unless an intertidal alga can fix carbon under these conditions, it can grow only during periods of tidal submersion. Theoretically, the upper limits of hardy species which can tolerate the prolonged stress above EHWN may be determined in part by these nutritional factors.

The shore gradient may be modified by waves which effectively extend the marine influence above the actual sea level. On shores exposed to heavy surf, species zones lie much higher with respect to theoretical tide levels, than they do in shelter. Lewis (1964) redefined the main ecological zones of the sea to land transition in terms of observed species distributions. He set the upper limit of the "sublittoral zone" at the highest level attained by Laminaria spp., which normally grow subtidally in the absence of wave action. He defined the "littoral zone" as extending from the upper limit of Laminaria to the upper limit of the marine lichen Verrucaria. This zone extends from ELWS to mean high water level (MHW) on very sheltered shores. However on very wave-exposed coasts, these limits may be raised to mean tide level (MTL) and up to ten metres above EHWS, respectively.

The littoral zone corresponds roughly to the shore gradient as defined in the present discussion. Many ecological studies of species zonation have been conducted on sheltered or mildly wave-exposed shores where zonal uplift is less dramatic and the shore gradient extends

essentially from ELWS to EHWS. Nevertheless, wave splash may reach a few tenths of a metre above the actual tide level, and the parameter of "longest tidal exposure" must be interpreted with caution. Seaweeds attached above EHWN may not remain completely dry during a long "tidal exposure" as indicated by tide gauge records, but may be wetted briefly by wave splash at high tide. This may explain why midshore species commonly extend to the mean high water of neap tides (MHWN) or slightly higher, rather than to the theoretically critical level of EHWN.

## 1.3 The vertical distribution of intertidal fucoids

In the present study of species distribution on the shore, attention was focussed on several intertidal species of the marine algal family Fucaceae for two reasons. Firstly, different species inhabit different levels and form a characteristic, well-defined series of zones or belts up the shore. Secondly, the intertidal fucoids are very abundant and constitute the dominant feature of sheltered rocky shores of northern and western Europe.

The fucoid zones of most British shores are composed largely of five common and widespread species. Listed in order of occurrence from high to low shore, they are:

*Pelvetia canaliculata* (L.) Decne. et Thur.
*Fucus spiralis* L.
*Ascophyllum nodosum* (L.) Le Jol.
*Fucus vesiculosus* L.
*Fucus serratus* L.

Details of the morphology and the life cycle of these five species are summarized in Table 1.

The vertical distribution of the five species at many British and European shores has been described, and a recurrent pattern has emerged (Fig.1). *Pelvetia* consistently occupies the highest level on the shore, with *F. spiralis* occurring immediately below it. *F. spiralis* occasionally extends down to MTL, but *Pelvetia* appears to be strictly confined to the upper shore, i.e. above EHWN. With one exception (den Hartog, 1968) *Pelvetia* has never been reported to occur below EHWN.

Table 1 Features of growth form and life cycle of the five common intertidal fucoids.

Common Features

Apical growth.
Life cycle of single diploid generation. Meiosis produces motile antherozoids and non motile eggs.
Gametes formed in reproductive receptacles differentiated at tips of branches with determinate growth.

Specific Features

| Species | Usual length at maturity | Branching | Shape of Axes | Vesicles | Midrib | Stipe | Receptacles | Reproduction |
|---|---|---|---|---|---|---|---|---|
| Pelvetia canaliculata | 80 - 200 mm | Dichotomous | Narrow lamina inrolled to form channel | Absent | Absent | Not distinct from rest of axis | Somewhat swollen sometimes forked | Hermaphroditi |
| Ascophyllum nodosum | 500 - 2000 mm | Dichotomous and lateral | Compressed-cylindrical to flattened | Large, single, at 100 to 200 mm intervals along axes | Absent | | Swollen, rounded borne on short lateral branches | Dioecious |
| Fucus spiralis | 150 - 350 mm | Dichotomous | Broad flattened lamina, wavy or spirally twisted | Absent | Pronounced | Formed by secondary thickening of midrib in older parts of plant, from which rest of lamina erodes away | Swollen, rounded with distinct flattened sterile margin | Hermaphroditi |
| Fucus vesiculosus | 400 - 1000 mm | Dichotomous | Broad flattened lamina | In pairs on either side of midrib | Pronounced | | Swollen, pointed sometimes forked | Dioecious |
| Fucus serratus | 400 - 1000 mm | Dichotomous | Broad flattened lamina with serrated edge | Absent | Pronounced | | Flat, once or twice forked | Dioecious |

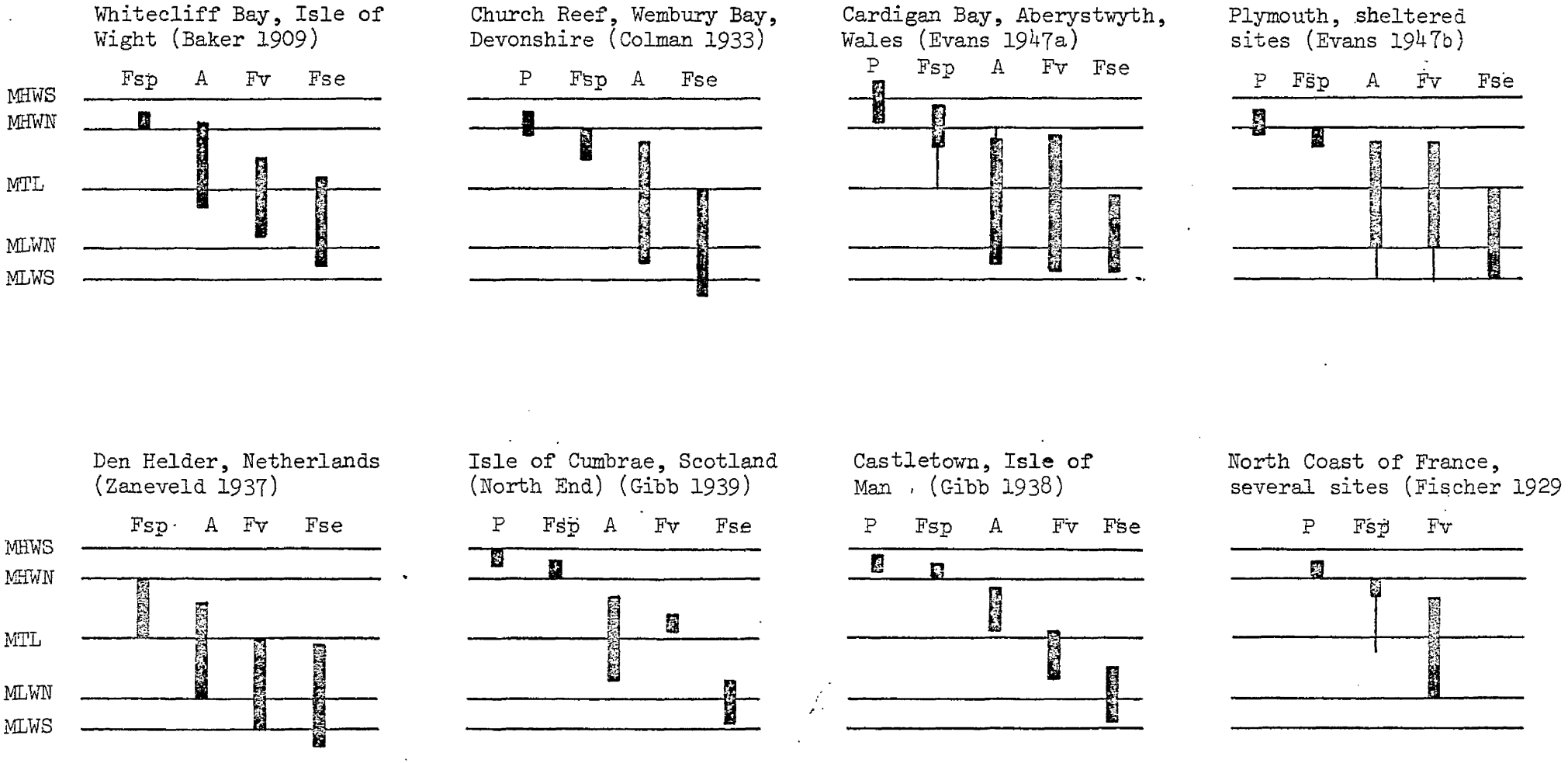



Figure 1. Vertical distributions of five common intertidal fucoids at various European shores. P = Pelvetia canaliculata Fsp = Fucus spiralis Fv = Fucus vesiculosus A = Ascophyllum Fse = Fucus serratus Bar indicates species abundant; line indicates species present but not abundant.

Ascophyllum and F. vesiculosus dominate the middle shore, with upper limits near or below MHWN. F. serratus consistently occupies the lowest vertical range, beginning near MTL and reaching its greatest abundance near mean low water of neap tides (MLWN). The five species can be conveniently divided into two categories: the "upshore fucoids" (Pelvetia and F. spiralis) and the "midshore fucoids" (Ascophyllum, F. vesiculosus and F. serratus).

On shores bearing a dense cover of fucoids, the boundaries between Pelvetia and F. spiralis, and between F. spiralis and Ascophyllum are usually quite clearly defined (Colman 1933; Lewis 1964; Evans 1947a, 1947b). Conversely, the ranges of Pelvetia and F. spiralis may overlap considerably on shores where the fucoid cover is thin and broken due to wave action or a loose, unstable substratum (Evans 1947b). Similarly, F. spiralis often appears near MTL amid open stands of F. vesiculosus, F. serratus and Ascophyllum (Lewis, 1964; Fischer 1929).

Lewis has also observed that species zonation is most distinct on relatively steep rock slopes, on which the direction of the shore's environmental gradient is well defined. By contrast, Pelvetia and F. spiralis often intermingle on gently sloping, irregular surfaces where local variations in aspect and drainage may produce a mosaic of microenvironments rather than a clearly defined directional gradient.

Boundaries between the three midshore fucoids are typically ill-defined. Ascophyllum and F. vesiculosus generally occur together, although strong wave action or loose substrata may exclude the former leaving F. vesiculosus as the dominant species (Evans 1947b). F. serratus may either form a distinct low-shore zone or may overlap the lower half of the F. vesiculosus - Ascophyllum zone (Lewis 1964).

A typical pattern of fucoid species zonation prevails on the shores of Isle of Cumbrae, Scotland, where the field work for the present investigation was undertaken. The distributions of the five species relative to tide levels, which are shown in Fig.2, correspond to those reported elsewhere in Britain.

The sequence of Pelvetia, F. spiralis and Ascophyllum is well-defined on the steeper rock slopes (Plate 1), and the boundary between Pelvetia and F. spiralis zones is very distinct (Plate 2). In flat areas with loose stones, the zones become less well-defined, and all

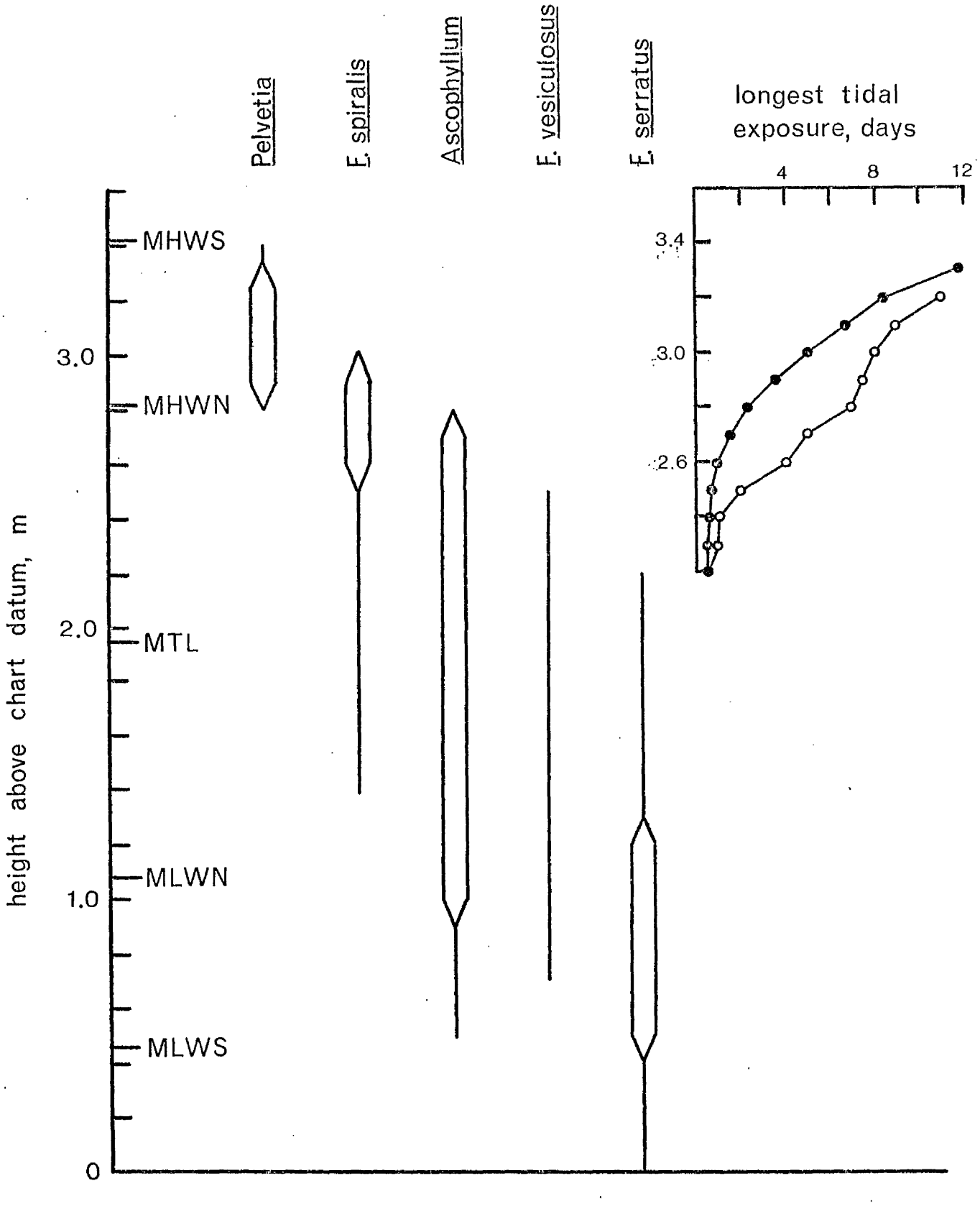



Figure 2. Vertical distribution of five common intertidal fucoids at Isle of Cumbrae. Levels of MHWS, MHWN, MTL, MLWN and MLWS shown represent means for the period January 1965 to December 1975 given by Harry T. Powell (personal communication). Inset graph shows mean (●) and maximum (○) of longest tidal exposure during fornightly neap tides between May 1 and August 31 of 1975 and 1976.

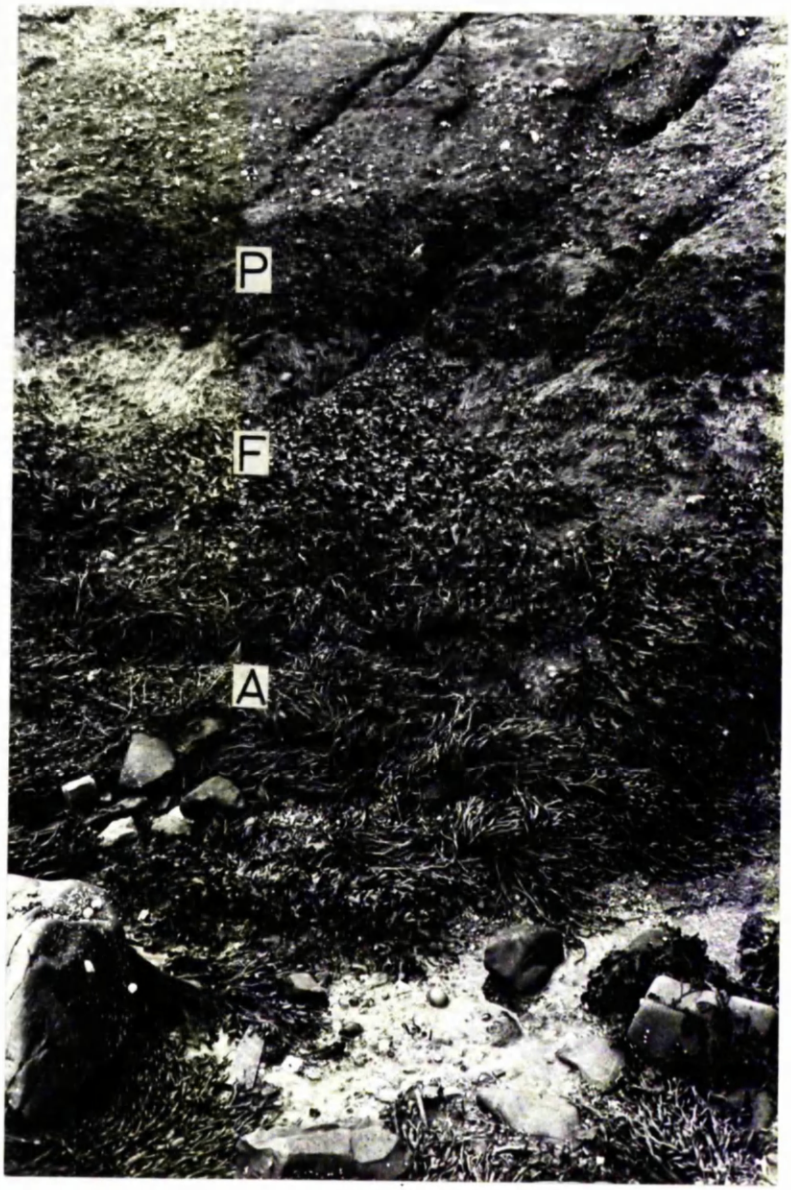



Plate 1: Distinct belts of Pelvetia (P), Fucus spiralis (F) and Ascophyllum (A) on a moderately steep rock slope at the North Slip. Note the F. spiralis plants in the foreground well within the Ascophyllum zone.


Plate 2: Very distinct boundary between Pelvetia (P) and Fucus Spiralis (F) on a nearly vertical rock face at the North Slip.

three species have been found growing together near MHWN (Plate 3). Mature Pelvetia never occurs below this level, except as occasional plants on small loose stones which may be transported downshore by wave action. However, F. spiralis frequently occurs near MTL mingled with the other Fucus species (Plate 4), or in open stands of Ascophyllum (Plate 1, foreground). Although F. spiralis is not abundant at this level, the individual plants are large and healthy, and produce many receptacles.*

Ascophyllum tends to dominate the upper part of the midshore, and gives way gradually to F. serratus on the lower shore. F. vesiculosus is a less abundant species at Isle of Cumbrae, and it broadly overlaps F. serratus and Ascophyllum, so that all three species commonly occur together below MTL.

* In discussing the species zones, these midshore plants will not be considered as part of the "F. spiralis zone", which will be defined as "the range over which F. spiralis is the dominant fucoid".

## 1.4 Physical and biological factors influencing fucoid zonation

Although the zonation of intertidal fucoids has been amply described, much less is known about the physical and biological factors which create the observed patterns. The purpose of this investigation is to identify the primary causal factors, and to examine in detail their roles in determining upper and lower limits of species zones.

A group of closely related and ecologically similar species may show any of several distributional patterns with respect to an environmental gradient (Colwell and Fuentes 1975). In many cases, different species inhabit different but overlapping niches delimited largely by physical variables associated with the gradient. On the other hand, two species may occupy adjacent but non-overlapping ranges, as do Pelvetia and F. spiralis on many shores. In numerous well-documented examples, this pattern appears to result partly from a difference in the two species' capacities to endure stress, and partly from interspecific competition. Each species extends up the gradient to its tolerance limit, and the more hardy organism therefore occupies habitats in which the other, more sensitive species cannot survive.


Plate 3: Pelvetia (P), Fucus spiralis (F) and Ascophyllum (A) growing together near MHWN on a nearly level beach with loose stones and boulders.

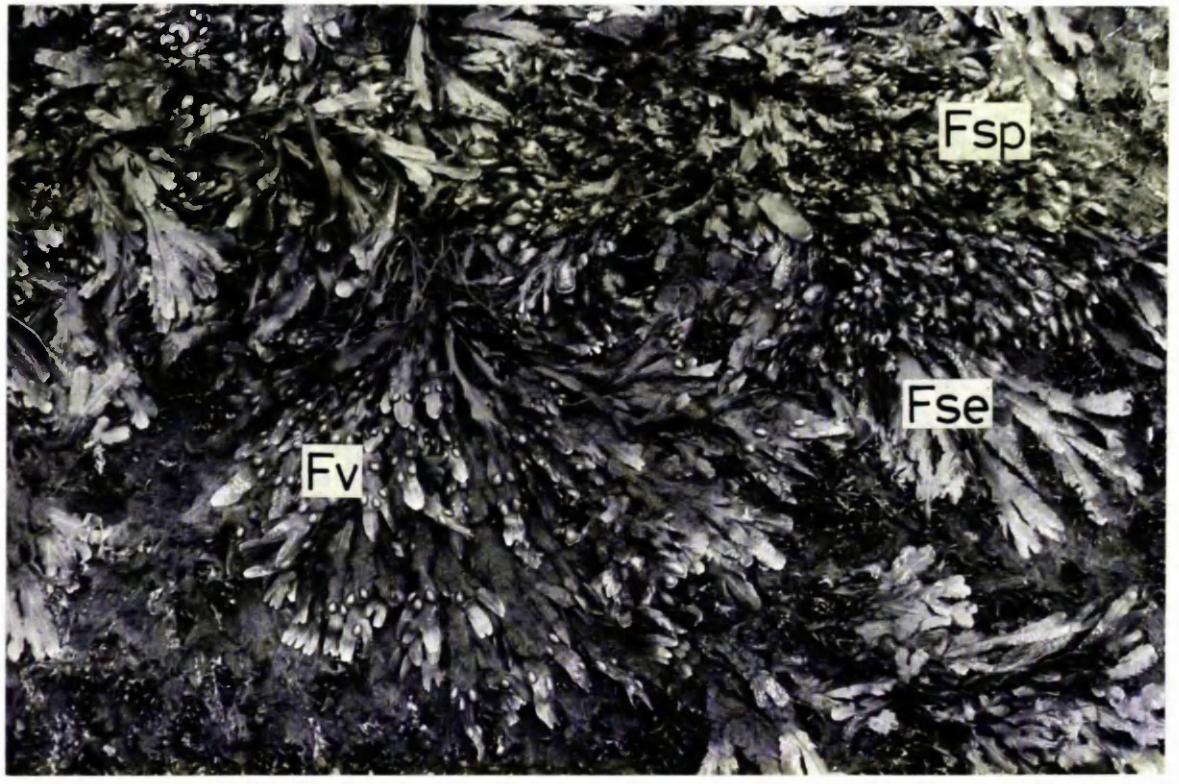



Plate 4: Three species of Fucus occurring together on the middle shore.
Fsp = Fucus spiralis Fv = Fucus vesiculosus Fse = Fucus serratus

However, the former cannot invade the niche of the latter because it cannot compete successfully for light, primary space or some other essential resource. This competitive pressure may exclude the hardy species from its physiologically optimum habitat, and restrict it to that part of the gradient near to its tolerance limit. In such cases, experimental removal of the sensitive species permits the hardy species to invade the habitat of the former, and to grow as well or better than it does within its own normally realized niche. This has been successfully demonstrated for intertidal barnacles (Connell 1961), seaweeds (Hruby 1976; Menge 1975), and for many species living in terrestrial and freshwater habitats (Colwell and Fuentes 1975). Predation and grazing have also been found to restrict some stress-tolerant species to the upper shore in some intertidal communities (Dayton 1971, 1975; Paine 1971, 1974).

An underlying principle of biologically determined lower limits and physically determined upper limits is demonstrated in all the examples cited. In the two main sections of this dissertation, the applicability of this principle to the upper and lower limits of the intertidal fucoids will be examined.

### 1.4.1 Upper limits

Several investigators have stated that the upper limits of the intertidal fucoids are governed by the physical factors associated with tidal exposure (Lewis 1964; den Hartog 1968; Zaneveld 1937), and there is some experimental evidence to support this viewpoint (Baker 1909; Hatton 1938). This would suggest that each species extends upshore to the limit of its tolerance to a particular stress or combination of stresses. Therefore, the relative capacities of the five species to tolerate the critical factors should be:

*Pelvetia* > *F. spiralis* > *Ascophyllum* ∿ *F. vesiculosus* > *F. serratus*.

The present investigation of the upper limits was designed to test this hypothesis.

The specific aims of the experimental work were:

(1) to determine by interzonal transplantation whether fucoids can survive at levels above their upper limits of distribution on the shore.

(2) to identify, in the event that they cannot survive this transfer, the critical stress factor or combination of factors involved.

(3) to demonstrate that the maximum intensity and duration of this stress each species can tolerate corresponds with the maximum intensity and duration realized in nature at its upper limit.

(4) to elucidate the mechanisms by which Pelvetia and F. spiralis tolerate prolonged and severe stress without damage.

(5) to study the nutritional implications of low percent tidal submersion on the upper shore, and the ability of the fucoids to utilize gaseous carbon dioxide for photosynthesis.

### 1.4.2 Lower limits

The lower limits of fucoids and other intertidal seaweeds have often been attributed to interspecific competition and other biotic factors (Baker 1909; den Hartog 1968; Dayton 1971; Chapman 1973; Menge 1975). Evans (1947a, 1947b) and Lewis (1964) suggested that fucoid zones are much more clearly defined in dense stands than in thin, open stands because competition is much more intense in the former. This suggests that Pelvetia is restricted to the upper shore because it cannot compete successfully with other fucoids for some essential resource, or because they interfere directly with its growth in some way. In the present investigation, the role of competition in determining the lower limit of Pelvetia was examined in detail.

The aims of the experimental work were:

(1) to study by means of interzonal transplants the ability of Pelvetia and F. spiralis to survive and grow at levels below their normal zones.

(2) to determine whether Pelvetia zygotes will settle and grow in the F. spiralis zone if the latter species is removed.

(3) to demonstrate the process of competitive exclusion of Pelvetia by F. spiralis, if it occurs.

(4) to elucidate the mechanism of resource exploitation and/or interference by which F. spiralis excludes Pelvetia.

(5) to clarify the competitive relationships between F. spiralis and the midshore fucoids, and to determine why F. spiralis is much less strictly confined to the upper shore than is Pelvetia.

# 2. MATERIALS AND METHODS

In the laboratory and field work, several relatively simple methods were used in a large number of experiments. These basic procedures will be described in this section, and any variations will be detailed with the relevant experiments. Other procedures which were used only for one specific experiment will also be described in the appropriate sections.

## 2.1 Study sites

All field work was carried out on the Isle of Cumbrae located in the Firth of Clyde, Argyll, Scotland. Fig.3 is a map of the Isle of Cumbrae showing the location of the main experimental shores. Most of the field work was carried out on two shores, one at Port Loy and the other just north of Cumbrae Ferry Slip, which are indicated on the map. Port Loy is a small, fairly sheltered bay at which the five major fucoid species occur abundantly and show a more or less typical zonation. The substratum is mostly solid rock and large boulders composed of red sandstone, although there are also some patches of shingle and gravel. The experimental area located a short distance north of the Cumbrae Ferry Slip is slightly more exposed to wave action. The upper shore is a solid rock slope of red sandstone and sandstone-conglomerate interrupted by basaltic dikes, and bears well-developed belts of *Pelvetia* and *Fucus spiralis*. The middle and lower shore is composed largely of boulders and shingle, although the solid rock slope extends to about MTL in some places. The cover of *Ascophyllum* and *Fucus* spp. is less dense and more patchy than at Port Loy, probably because of the loose stones and the slightly greater wave action. This shore will be referred to hereafter as the "North Slip" shore, although all experiments were done on the natural rocky slope, not on the ferry slip itself.

## 2.2 Algal material

Most of the algal material used in culture and other laboratory work was collected from the Isle of Cumbrae. However, on a few

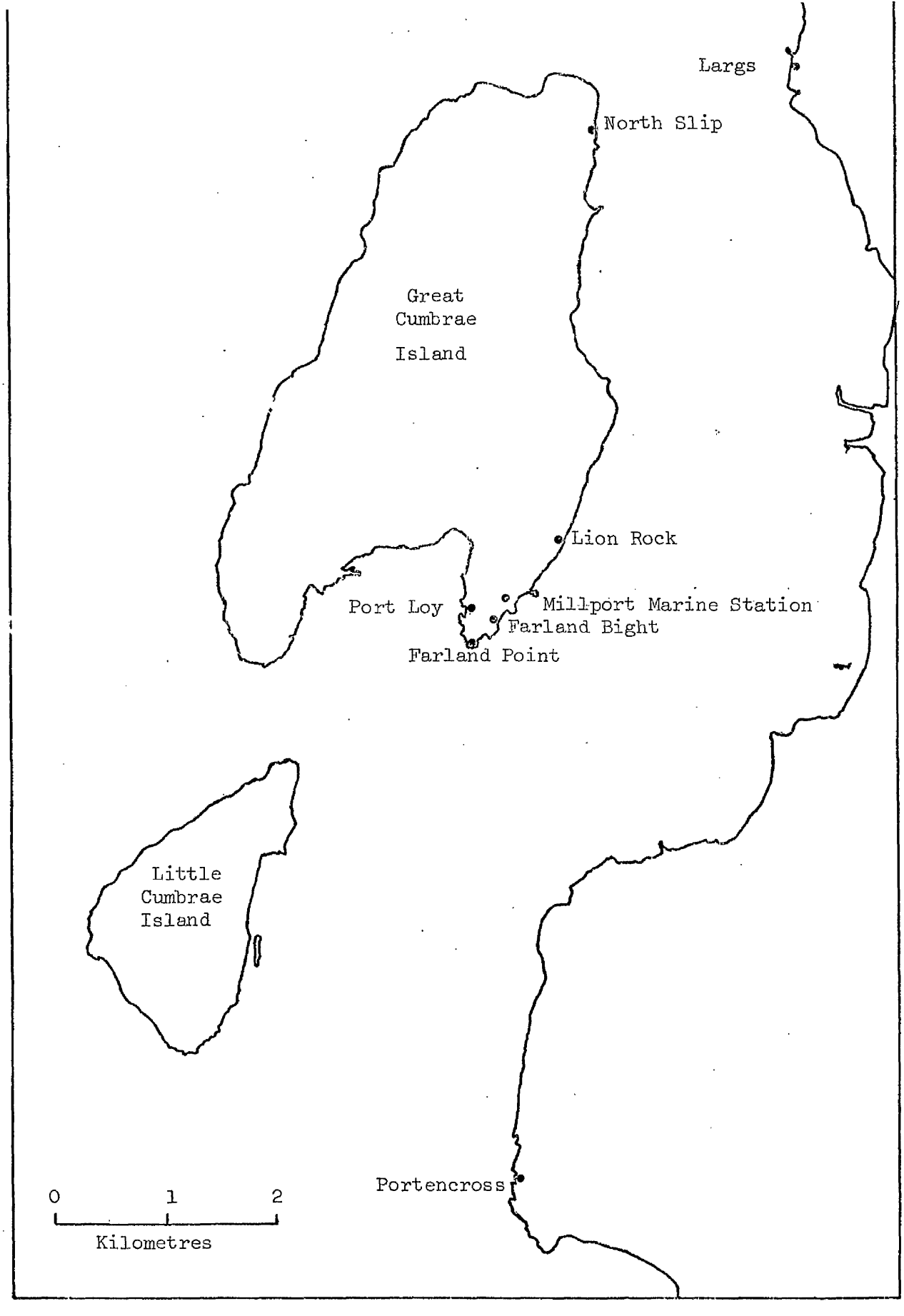



Figure 3. Map of Great Cumbrae Island and environs showing study sites.

occasions when gales prevented access to the island, algae were collected from the mainland just north of Largs, or at Portencross (Fig.3).

The algae were kept damp but not submerged, in polythene bags and stored under refrigeration (0-5°C) until use. It was found that vegetative material could be stored for up to five days under these conditions without damage, and algae stored for longer than this were not used in culture work. Receptacles gave a poor release of gametes if they were stored for longer than two days; hence these were used as promptly after collection as possible.

## 2.3 Field work

### 2.3.1 Determination of tidal levels

The tidal levels of experimental sites and points of observation were determined as follows. During a very calm day, the time was noted when each site was just being submerged or exposed by the tide. The tidal level at each of these times was then obtained from continuous records maintained by the tidal gauge at the Millport Marine Biological Station. Tide levels of the major experimental sites at Port Loy were determined on three occasions: 16 April 1975, 11 June 1975 and 27 February 1976. The levels found on the three days agreed to within 0.05 m. Replicate observations were also taken for experimental sites at the North Slip. Discrepancies up to 0.10m were found, possible because this shore is about three miles from the tide gauge, and significant differences in sea level frequently occur over such distances.

### 2.3.2 Interzonal transplants

The algae to be transplanted were collected without separating their holdfasts from the substratum. Initially, small pieces of sandstone bearing single young plants were chipped loose from the shore using a geological hammer. However, the chips of sandstone thus obtained often crumbled, and many plants attached to such chips were lost shortly after being transferred. Therefore, small loose stones with groups of young plants attached were collected from a shingle

beach near Lion Rock on the east shore of Isle of Cumbrae (Fig.3). The plants were either transferred immediately or were stored overnight in a seawater tank at the marine station and transplanted the next day. All plants in a given experiment received the same treatment between the time of collection and time of transplantation.

At each site to which the plants were transferred, an area of rock about 0.5 $m^2$ was cleared of macroalgae. The stones and rock chips were attached to the cleared rock surface with quick-setting cement and numbers were drawn in the wet cement for identification.

For each species, fifteen to thirty plants were transferred to a site above or below its normal distributional range. Simultaneously, fifteen to thirty control plants were transferred to a site at the same tidal level from which they were collected. The number of samples fluctuated during the course of the experiments due to the loss of individual plants, and to the subsequent appearance of other plants which were so small as to escape notice at the time of transfer.

The lengths of the plants were measured to the nearest 0.5mm, initially and at intervals of several weeks using a millimetre ruler. Since each of the stones collected from the shingle beach bore a number of plants, the relative positions of these plants on the stone were carefully mapped when measurements were taken. Mean net growth of each species at each site during a given interval was calculated from the changes in length of those plants which were successfully located and measured at the beginning and the end of that interval.

## 2.4 Cultures

The majority of the laboratory investigations was based on the culture of the various fucoid species. The early embryonic stages were grown from gametes released and fertilized in culture. Also, complete plants weighing 30-1000 mg were collected from the shore and grown in culture. Such plants are here always called "young plants" as distinct from the very early stages obtained from zygotes called "embryos".

### 2.4.1 Culture conditions

#### 2.4.1.1 Medium

The embryos and young plants were cultured in an enriched seawater medium, which was changed every seven to fourteen days. The formula of the medium and the procedure of heat-sterilization used are given in Appendix A. For reasons detailed in Section 2.4.2, the medium was diluted ten times in filtered seawater before heat-sterilization.

#### 2.4.1.2 Illumination

The cultures were illuminated from above either with two six-foot Atlas Daylight 85 watt fluorescent tubes at a distance of 230 mm, or with two five-foot Philips Daylight 65-80 watt tubes at 230 mm, or with three Philips Daylight tubes at 280 mm. The glass shelves upon which the culture vessels were placed were covered with opaque construction paper to eliminate illumination from the tubes over the shelf below.

The illuminance was measured with an EEL Portable Photoelectric Photometer Serial No. 18.1132. In order to obtain irradiance values, this instrument was calibrated against a Kipp and Zonen Solarimeter and Kipp and Zonen Type AL4-Microva Galvanometer. The solarimeter, serial no. CM5-711251, had been calibrated to the International Pyrheliometer Scale 1956.

The calibration was carried out as follows: The solarimeter and photometer were placed at a distance of 230 mm from two five-foot Philips Daylight tubes in a room free from extraneous illumination, and the readings of both meters taken. It was found that after the fluorescent tubes were turned off, the solarimeter recorded a small residual irradiance due to a slight warming of the tubes while they were on. Therefore a series of ten readings with the tubes on were taken, each followed by a solarimeter reading with the tubes off. This last reading was then subtracted from the solarimeter's reading while illuminated, in order to obtain that proportion of the irradiance not due to the heating.

A conversion factor of 58.4 mg-cal/$cm^2$-min = 1000 footcandles (range 58.0-58.9) was obtained. The procedure was repeated with three tubes at 280 mm distance, and the conversion factor was similar:

59.5 mg-cal/cm$^2$ -min = 1000 footcandles (range 59.1-59.8).

The cultures received an illuminance of 280-400 footcandles, and an irradiance of 16.5 to 23.6 mg-cal/cm$^2$-min from the daylight fluorescent tubes. The exact light level varied according to the age of the tubes and the degree of reflection from the walls of the cabinet, which varied between different shelves. However, all cultures in any one experiment were grown simultaneously on the same shelf, and therefore received the same irradiance.

Although the irradiance delivered by the daylight fluorescent tubes was only a small fraction of full sunlight, (roughly 1000 mg-cal/cm$^2$-min), light limitation was not evident. Linear growth rates of Fucus and Pelvetia in culture were comparable to and sometimes exceeded growth rates on the shore observed at Isle of Cumbrae and also those reported from nature by Subrahmanyan (1960, 1961) and Knight and Parke (1950).

### 2.4.1.3 Aeration

Most of the cultures of young thalli were aerated by an air pump, but a few experiments were not aerated owing to a limited supply of pumps. The culture of zygotes was carried out in dishes too small to be aerated.

### 2.4.1.4 Temperature

All cultures were grown in a theromastatically controlled culture cabinet at 10°C ± 1°C. However, some parts of the culture room were found to be considerably cooler, and air pockets as cold as 6°C often formed at one end of a shelf while the other end was 9-10°C. In those experiments which included a large number of culture vessels extending along more than half of a shelf, the positions of these vessels was rotated at intervals during the experiment to equalize the effects of these temperature differences on the growth of the plants.

## 2.4.2 Control of contamination

In nature, the spores of many species of algae settle upon the surface of intertidal fucoids, and some germinate and grow as epiphytes.

Since these spores are abundant over the entire surface of the thallus, they were inevitably present in the cultures of young plants and in the suspensions of gametes obtained from receptacles. They germinated and developed rapidly during constant submersion in enriched medium, and became a serious problem within two or three weeks.

The epiphytes which developed on the young plants in culture could not be removed without damaging the fucoids because they were firmly attached to their hosts. Also, an attempt to surface-sterilize the young plants and the receptacles by submerging them briefly in a 0.1% sodium hypochlorite solution failed. This treatment severely damaged the young plants without killing all the algal contaminants. Also the growth rate of zygotes obtained from surface-sterilized receptacles was slower than that of untreated controls.

Contamination was reduced significantly by diluting the medium five to forty times with filtered seawater before heat-sterilization. Fortunately, fucoid embryos grew at maximal rates in dilutions down to twenty times (Table 2) and the same was true for the young plants. Therefore, a ten times dilution was used for all further culture work to ensure an ample nutrient supply for the fucoids yet limit the growth of algal contaminants.

Table 2 Mean length of pigmented portion of thirty *F. spiralis* embryos after 28 days, and intensity of algal contamination in duplicate cultures at each of five different dilutions of culture medium.

\+ light contamination ++ moderate contamination +++ heavy contamination

| Concentration of Medium. | First replicate Mean length | contamination | Second replicate mean length | contamination |
|---|---|---|---|---|
| 1/40 | 647 µm | ++ | 913 µm | + |
| 1/20 | 954 µm | + | 1156 µm | + |
| 1/10 | 1066 µm | + | 1026 µm | ++ |
| 1/5 | 1032 µm | ++ | 1090 µm | ++ |
| 1/2 | 950 µm | +++ | 638 µm | +++ |

Considerable epiphytic growth sometimes appeared on the young plants after several weeks even in the diluted medium. When this occurred, the epiphytes were carefully scraped off with a razor blade just before the final weight was taken.

Fucus spp. consistently grew well in the diluted medium, but Pelvetia often began to decay toward the end of the longer experiments. For this reason, young plants of Pelvetia could be successfully cultured only for about four weeks. Also, one or two plants occasionally broke into several pieces even during the first four weeks, and were lost. Sample sizes given with the results of each experiment indicate the number of plants grown successfully during the entire experiment.

In the cultures of embryos, the most troublesome contaminants that persisted in the 1/10 strength medium were small green algae and diatoms. In preliminary experiments, these organisms showed a strong but inconsistent tendency to inhibit the growth of the embryos. Therefore the following procedure was used to further reduce the number of extraneous spores in the suspension of fucoid zygotes. Immediately after fertilization, the zygotes were swirled into suspension in a flask and allowed to stand just long enough to settle. Then the liquid was decanted and replaced with filtered seawater. This was repeated several times with fresh portions of filtered seawater before the zygote suspension was used to inoculate the cultures. The zygotes of Fucus and Ascophyllum are very dense and settle much more quickly than diatoms and green algal spores, most of which could therefore be decanted away. However, the oogonial mesochiton in which Pelvetia zygotes remain for several days after fertilization are not as dense as the zygotes of the other two genera, and are not as effectively separated from contaminants by decantation. It was therefore difficult to obtain Pelvetia zygote cultures without contamination.

Since unialgal embryo cultures could not be obtained for any of the fucoids, and the contaminants exert unpredictable effects on growth, each treatment in each experiment was run in duplicate or triplicate. A difference between growth obtained with two different treatments was considered significant only in those cases in which all replicates of one treatment gave significantly greater growth rates than all replicates

of the other treatment.

### 2.4.3 Culture of fucoids from gametes

#### 2.4.3.1 Release, fertilization and inoculation of cultures

Plants bearing mature receptacles were selected and, in the case of the diocious species Fucus vesiculosus, F. serratus and Ascophyllum, the sex was determined by microscopic examination of material from the receptacles. The receptacles were then excised from the plants and either stored overnight at 0-5°C in the refrigerator, or laid out on paper towels in the laboratory until partially dehydrated. They were then washed for about 5 to 15 seconds in ice-cold distilled water and then placed in culture dishes containing filtered pasteurized sea water at 10°C ± 2°C in the culture cabinet. Release of gametes required from six to forty-eight hours. This procedure for obtaining gametes was derived from those given by Gail (1918), Pollock (1970) and McLachlan et al (1971).

The male and female gametes were then pipetted out of the culture dishes, swirled together in a 100 ml or 250 ml conical flask and permitted to stand for one to three hours to fertilize the eggs. In the case of the hermaphroditic species Pelvetia and F. spiralis, most of the eggs were fertilized during the six to forty-eight hour release period and could be used directly. The zygotes were washed as described in Section 2.4.2, and then pipetted over glass slides submerged in filtered pasteurized seawater. They were allowed to attach for six to twenty-four hours, and transferred to the culture vessels containing medium.

Each slide of attached zygotes was cultured in 40 ml of medium in a 100 mm diameter petri dish. In some experiments deeper dishes containing 100-200 ml medium were used, and either one or two slides were placed in each dish.

#### 2.4.3.2 Assessment of growth of embryos

The fucoid embryo consists of a roughly cylindrical, pigmented "head" which develops into the upright thallus, and an unpigmented

rhizoid which becomes a much branched, entwined mass and ultimately forms the plant's holdfast. Since the thallus is often fairly regular in form while the rhizoids are irregular and vary greatly in total length, the length and maximum width of the thallus were used to assess growth of the embryos. Measurements were taken at the end of a three to five week growing period, and, in some experiments, at weekly intervals during that time. The embryos were measured to the nearest 5 μm with a calibrated ocular micrometer at 100 x total magnification under a Nikon binocular compound microscope.

The embryos were measured directly on the slide on which they were grown whenever possible. At the final measurement, a second slide was placed over the first in order to press the embryos into a horizontal position, thus obtaining a more accurate measurement. This was somewhat damaging to the embryos and was not done for measurements taken during the course of the culture period. Twenty to thirty embryos on each slide were selected for measurement by means of random coordinates obtained from random number tables.

When the embryos exceeded 1 to 1.5 mm in length, it was not possible to obtain an accurate measurement while they were attached, and they were removed from the slide and suspended in a dish of seawater. A "random" sample of twenty to thirty embryos was then obtained by nonselectively drawing embryos out of the suspension with a pipette.

### 2.4.4 Culture of young plants

#### 2.4.4.1 Vessels and mounting plates

The young plants were cultured in rectangular glass tanks, which measured 180 x 250 x 170 mm high, and had a capacity of a little more than five litres. The tanks were covered with glass plates cut to fit the tops of the tanks. The plants were mounted on 160 x 230 mm plates of 6.5mm thick clear Perspex, in which a 5 x 5 array of holes about 4 mm in diameter were drilled. Short lengths of thread with slip knot loops at either end were used to secure the plants, as illustrated in Figure 4 for one row of five plants. Terylene thread was used, since cotton thread was found to decay rapidly in the enriched seawater medium. In this way, twenty five plants could be cultured in

each tank and the identity of each plant known from its position. In a few experiments, thirty or thirty five plants were cultured in each tank. In this case, the loops of one or two rows held a second thread with two plants attached. Two plants that differed considerably in size were attached at each hole so that they could not be confused in subsequent measurements.

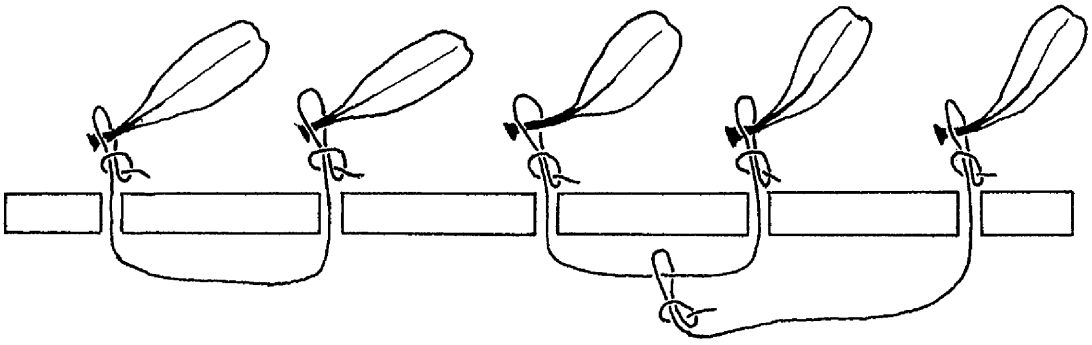


Figure 4: Method of attaching plants to Perspex plates

The Perspex plates appeared to exert no adverse effects upon the growth or morphology of the fucoid plants, and Bernhard, Zattera and Filesi (1966) reported that Perspex is entirely safe for use in algal cultures.

Each plate of plants was cultured in three to five litres of medium in a glass tank. On a few occasions, all available tanks were in use, and other vessels were used, the details of which will be presented with the description and results of those investigations.

2.4.4.2 Assessment of growth

Growth was assessed in two ways. Linear growth was measured as the increase in length taken from holdfast to the tip of the longest branch. Since length could be measured without detaching the plants from the plates, this was done initially and at 10 to 15 day intervals during the culture period. The plants were measured to the nearest

0.5 mm with a millimetre ruler. In order to facilitate comparison, growth rates are expressed in some experiments as millimetres per thirty day month, regardless of the actual duration of the experiment.

Increase in mass was assessed by taking a fresh weight of each plant at the beginning and at the end of the culture period. The plants were soaked in seawater at 8 to 12°C for at least eight hours before use. They were then blotted with paper towels and weighed immediately to the nearest 0.1 mg on a Mettler Type H6 single pan balance.

Experimental error in fresh weight was assessed by weighing, resubmerging briefly and reweighing a series of 50 F. spiralis and 50 Pelvetia plants. The two weights differed by two percent in only four of these 100 plants, and by less than one percent in seventy-four. A more detailed analysis of error in fresh weight measurements is given in Appendix B.

Weight change was found to be a sensitive and very useful indicator of growth since the plant's weight typically increased by 10 to 40% over a ten day period. Weight changes were expressed on a relative basis as follows:

$$\frac{(\text{Final Wt}) - (\text{Initial Wt})}{(\text{Initial Wt})} \times 100\%$$

The relative rather than the absolute weight gain was selected as a growth parameter because the relative weight gains of the plants of a given species in a given treatment were fairly similar despite large differences in the sizes of plants used.

Weight change was also expressed as a percent gain per day to facilitate comparison of rates between different experiments. The percent weight gain per day was calculated using logarithms from the following formula, in which n is the time in days between initial and final weighings:

$$\left( \sqrt[n]{\frac{\text{Final Weight}}{\text{Initial Weight}}} - 1 \right) \times 100\%$$

Accurate surface area measurements could not be obtained for all the sample plants because of the irregularities of the thallus and

overlap of branches, especially in Pelvetia. An accurate surface area measurement of the larger Pelvetia could only be taken destructively, i.e. by dividing the thallus into several pieces. However, surface area and weight were found to bear a fairly constant relationship to one another, so that the relative rate of weight gain is approximately equal to the relative rate of increase in surface area. Therefore surface area measurements were not taken in subsequent experiments.

In some experiments, the number of branch apices on each plant was counted each time the length was measured, so that the rate of initiation of new apices could be determined.

### 2.4.5 Simulation of tides in culture

A tidal simulator was designed and constructed to provide the alternating submersion and exposure which characterises the shore habitat. The apparatus consists of three large culture tanks, in which plants can be cultured under three different semidiurnal "tidal" regimes. Details of the design of the tidal simulator are given in Appendix C.

Each of the three plastic materials used in the construction of the apparatus was tested for possible toxic effects on the fucoids. Some slight effects were observed, but they were not great enough to be considered serious. The results of these tests are presented in detail in Appendix D.

There were numerous mechanical problems with the tidal simulator, and the tanks often did not drain and fill reliably. Owing to these difficulties, only one six-week run was completed successfully, and all other tide-simulation work was carried out manually.

A semidiurnal tide could not be conveniently simulated manually, since this would require two visits to the culture cabinet each night for the duration of the experiment. Therefore two diurnal "tide" regimes of four and twenty hours submersion were simulated manually as follows. Two plates of young plants weighing between 50 and 1000 milligrams were cultured as described in section 2.4.4 except that one plate of algae was placed in an empty tank and the other in an aerated tank containing 5 litres of medium. Each morning, the two plates were interchanged between the empty and full tanks, and they were interchanged

again four hours later. In this way, one plate of algae received four hours submersion in medium and the other plate twenty hours, each day. The plate which spent only four hours per day in the medium received this four hour submersion during the light period of the culture cabinet's day/night cycle.

An occasional error was made in the timing of the exchanges, the most serious of which led to a $6\frac{1}{2}/17\frac{1}{2}$ hour cycle on two occasions. Since this still gave a very long submersion to the 20-hour plate as compared to the 4-hour plate, and since the mean times of submergence over the duration of the experiment were near 20 and 4 hours per day, the results were probably not seriously affected by these errors.

## 2.5 Measurement of desiccation rates and "colloidal water"

### 2.5.1 Rate of desiccation

#### 2.5.1.1 Experimental

Desiccation rates of algal samples were measured as follows: After the wet weight was determined, the samples were dried simultaneously and reweighed after various intervals of time. In most determinations each algal sample was suspended by a thread or paper clip during drying so that all surfaces of the plant were equally exposed to the air. Laying the plant on a flat surface would better duplicate natural circumstances during low tide on the shore, but would also complicate interpretation of results because part of the plant is protected by being in contact with the surface. The degree of protection would depend on the shape of the plant and would be very difficult to assess.

After the course of desiccation was thus recorded, the dry weights of the samples were determined. At first dry weight was obtained by drying the samples for two to four days in a 105°C oven. However, since the heating could drive off small amounts of other substances as well as water, the samples in later experiments were taken to dryness for four days over silica gel in a desiccator. All weights were taken to the nearest 0.1 mg on a Mettler Type H6 single pan balance.

Initially the samples were dried in the laboratory, in which temperature and relative humidity varied somewhat, and were therefore monitored using a wet bulb-dry bulb hygrometer. Later determinations

were carried out under more stringently controlled conditions. Both drying and weighing of samples were performed within the closed chambers of six Stanton Model A48 balances. This model has a precision of about 0.5-1 mg and the balance beam is equipped with hooks over the pans from which objects up to one gram can be suspended and weighed directly. The volume of the chamber is about 40 litres. Humidity within the chamber was regulated by means of a 3 molar magnesium chloride solution. Fifty millitres of fresh solution was divided between four open ten-centimetre petri dishes, placed in each balance a few hours before the sample was introduced, and left in the closed chamber for the duration of the desiccation rate measurements. Preliminary experiments with a wet bulb-dry bulb hygrometer included in the system showed that an essentially constant relative humidity of about 75% was maintained by the solution, either with or without an algal sample weighing 0.3 g drying in the balance. Since the area of the hygrometer wick was similar to that of an 0.3 gram algal sample, water evaporation from it probably did not seriously affect the observed relative humidity. In the actual determination of desiccation rate, the hygrometer was not included in the balance chamber, and the relative humidity was assumed to be 75%.

A second advantage of drying the samples in the closed balance chambers is that extraneous air currents were excluded. The determinations were carried out in a thermostat-controlled room; nevertheless temperature did vary somewhat and was therefore carefully monitored.

The disadvantage of this method is that only a few samples could be processed simultaneously. It is for this reason that I report the results of other determinations done under less controlled conditions, since they provide accessory data to support the conclusions drawn from the results of this method.

For each determination, vapour pressure deficit and atmospheric water potential were calculated from the temperature and relative humidity. The atmospheric water potential is a thermodynamic parameter which reflects the free energy or chemical potential of the water vapour in the atmosphere. It is determined from this formula:

$$\psi_w = \frac{R\,T}{\bar{V}} \log_e \left( \frac{\text{relative humidity, \%}}{100\%} \right),$$

where R is the gas constant, T is the absolute temperature, $\bar{V}$ is the partial molal volume of water, and $RT/\bar{V}$ = 1375 bars at 298°K. The vapour pressure deficit is the difference between the actual atmospheric water vapour pressure and that of an atmosphere of the same temperature and at 100% relative humidity. The water potential of the atmosphere governs how much water remains in the plant tissue when it has come into water equilibrium with the atmosphere, while the vapour pressure deficit governs how rapidly water is lost. Thus a cold and a warm atmosphere may have the same water potential so that tissues will eventually become equally dry in both, but they will dry out much more quickly in the warm atmosphere which has the greater vapour pressure deficit. Thus initial desiccation rates are related to vapour pressure deficit, while the equilibrium water content of the air-dry plant is related to the water potential.

2.5.1.2 Calculation of rate parameters

The original water content of each sample was determined by subtracting the dry weight from the wet weight. The dry weight was then subtracted from each of the weights taken during the course of desiccation to obtain remaining water contents. It was found that water loss proceeds in a roughly log-linear pattern with time over the first few hours, but becomes quite slow later when the plant has lost most of its water. Therefore the rate of desiccation over the first one or two hours was expressed as a relative tissue dehydration rate:

$$r = \frac{-\log_e \left[ \left( \begin{matrix}\text{water content after} \\ \text{t hours drying}\end{matrix} \right) \Big/ \left( \begin{matrix}\text{water content} \\ \text{before drying}\end{matrix} \right) \right]}{t}.$$

In some of the determinations, plant surface area was obtained and evaporation flux was measured during the initial, most rapid water loss:

$$D = \frac{\text{(weight after drying } t \text{ hours)} - \text{(wet weight)}}{(t)\ (\text{surface area})}.$$

The surface area measurements were also used to obtain the ratios of surface area to fresh weight for each sample. This ratio determines how fast the tissue becomes dry (r) at a given evaporation flux (D).

Surface areas of the samples were determined by gently flattening the thalli between glass plates and photocopying them twice. The duplicate images were then carefully cut out and weighed. The area to weight ratio of the photocopy paper was determined by weighing ten to twenty pieces cut to a known area. From this ratio and the mean weight of the two cut-out photocopies of the sample, the sample's surface area was determined. The result was multiplied by two to obtain the surface area of both sides of the thallus. However, this method does not take into account the surfaces of the edges of the thallus which are oriented perpendicular to the xerox plate, and therefore not photocopied. In the broad, flattened Fucus, the edge surface is negligible, but Pelvetia and Ascophyllum thalli are only two to four times as wide as thick, and omission of the edge constitutes a serious underestimate. Therefore a series of measurements were made on cross sections of these two species to obtain a correction factor of 1.36 for Pelvetia and 1.15 for Ascophyllum. For details on the derivation of these factors, see Appendix E.

Photocopy paper from the same package was used for all surface area measurements in any one experiment, and the area to weight ratio of the paper was re-determined whenever a new package was opened for a new experiment.

### 2.5.2 Colloidal Water Content

When a plant tissue has come to water equilibrium with the surrounding atmosphere, it is said to be "air-dry". It still contains some water, but does not contain any water which can be lost to the atmosphere. The term "colloidal water" is sometimes used to refer to

this water which is so tightly bound in the cells and intercellular mucilage that its chemical potential is equal to or lower (ie. more negative) than that of the water vapour in the air. The quantity of colloidal water is related to the atmospheric water potential. Therefore, when the terms "colloidal water" and "air-dry" are used, they must be qualified by stating the atmospheric water potential at which they are measured. That proportion of the plant's tissue water which is at a higher (less negative) potential than the atmosphere's water vapour will hereafter be referred to as "volatile water". This term will also be qualified by stating the water potential at which it is determined.

The capacity of the different fucoid species to retain "colloidal water" at a given water potential was determined from the fresh weight, the "air-dry weight" and the dry weight obtained by drying in the oven or over silica gel. Two parameters of the colloidal water content were calculated:

$$\text{Percent of total water content retained as colloidal water} = \frac{\text{air-dry weight} - \text{dry weight}}{\text{wet weight} - \text{dry weight}} \times 100\%$$

$$\text{colloidal water retained per 100 g dry matter} = \frac{\text{air-dry weight} - \text{dry weight}}{\text{dry weight}} \times 100 \text{ g.}$$

## 2.6 Assessment of effects of environmental stresses

In order to compare the effects of desiccation and other physical environmental factors, intact young plants between 30 and 1000 mg were subjected to experimental stresses under known conditions. After the stress period, either the photosynthetic rate was measured and compared to the rate obtained before the stress, or growth rate was measured and compared to that of control plants which did not receive the stress.

### 2.6.1 Experimental stress conditions

The effects of desiccation at various temperatures and atmospheric

water potentials were investigated as follows. The samples were placed in desiccators or airtight jars over aqueous solutions of $H_2SO_4$, which maintained a constant relative humidity in the enclosed space. The concentrations were selected to obtain the desired relative humidities using data from McLean and Cook (1941).

The algae in the airtight containers were placed either in the culture cabinet (8-12°C), or in a warm culture cabinet at 25-27°C under constant illumination from fluorescent tubes. When the effects of the two different temperatures on the samples were compared, the desiccators or jars in both culture cabinets were covered in the evening with black polythene or an opaque box, and uncovered in the morning in order to obtain identical day/night cycles.

The atmospheric water potential was calculated from the temperature and relative humidity over the sulfuric acid solution, using the formula given in section 2.5.1.1.

The samples were allowed to dry in the culture room or the laboratory until they lost at least three quarters of their tissue water before being introduced into the closed containers. This was done so that the acid solution would not absorb a large quantity of water from the plants, thus considerably changing in concentration. At least 50 g of solution and five partly dried plants containing a maximum of 0.3 g of volatile water were introduced into each airtight jar so that the concentration of the solution could not change by more than 0.6% during the equilibration.

The influence of the duration of exposure and of other factors upon the effect of a drought stress was also investigated. In many of these determinations, the plants were dried in the warm room whose temperature and relative humidity were monitored with wet and dry bulb thermometers.

In a few experiments, the algae were dried in the laboratory, and temperature and relative humidity were monitored. Details of the stress conditions and procedures are given with the relevant experiments.

### 2.6.2 Assessment of effects of stress upon Photosynthesis

The photosynthesis rates of sample plants were measured by

determining the rate of oxygen evolution. About twelve hours before the determination, a stoppered ten litre glass bottle equipped with a tap near the bottom was filled with seawater, placed in the 8-12°C culture cabinet and allowed to equilibrate to this temperature. Then a series of 275 ml glass bottles equipped with ground glass stoppers were carefully filled from the large bottle via a short length of plastic tubing connected to the tap. Care was taken to avoid turbulence, and an excess of 100-200 ml of seawater was allowed to overflow from each bottle to assure that the seawater inside was homogenous in oxygen concentration. The first and last bottles filled were used as controls to determine the initial oxygen concentration of the seawater. One algal sample was introduced into each of the remaining bottles which were then incubated in the light for one to two hours. In the early experiments, they were illuminated from above and below by four or six Philips Warm White Fluorescent tubes giving an irradiance of 50-80 mg-cal/$cm^2$-min., while in later experiments, they were illuminated only from above by three Philips Daylight tubes yielding 25mg-cal/$cm^2$-min. The warm white tubes were used in the early experiments because the daylight tubes were not available at the time. The plants photosynthesized at similar rates under the two different regimes.

In initial experiments, the plant was left in the bottle at the time of fixation, but this was found to reduce somewhat the measured oxygen concentration. Therefore, in subsequent experiments, the plant was fastened to a thread, the end of which was allowed to extend out of the stoppered bottle, so that the plant could be removed easily at the end of the incubation period. The thread passing through the ground glass connection between the bottle neck and stopper was found not to cause any leakage or intake of air into the bottle during incubation.

Immediately after incubation, the samples were withdrawn and the oxygen concentration of the seawater in each bottle was determined by the Winkler method detailed by Strickland and Parsons (1968).

The oxygen concentration found in the control bottles was subtracted from that found in each sample bottle to obtain the net

change due to the combined photosynthesis and respiration of the algal sample. Net photosynthetic rate in μmoles $O_2$/g fresh wt-hour was calculated as follows:

$$\text{Rate} = \frac{\left[\begin{array}{c}\text{net change in } O_2 \text{ concentration} \\ \text{in } \mu\text{moles/litre}\end{array}\right] \quad (\text{bottle volume in litres})}{(\text{plant wet weight in grams}) \qquad \left[\begin{array}{c}\text{length of incubation} \\ \text{period in hours}\end{array}\right]}$$

The volume of each bottle was measured to the nearest 0.1 ml by weighing the dry, empty bottle, and reweighing after filling with distilled water, and this volume was written directly on the bottle with a diamond pen.

It was found in preliminary determinations that bubbles of oxygen accumulated on the plant during the incubation and were lost when the plant was withdrawn from the bottle. Therefore, the 10 litre jar of seawater was partially deoxygenated to 50-75% saturation before being placed in the culture cabinet to cool. This was done by bubbling nitrogen through the seawater for 20-40 seconds, and then inverting the bottle ten to twenty times to mix thoroughly. Also the sample bottles were agitated periodically during the incubation in order to prevent a "shell" of static, oxygen-saturated seawater from accumulating around the plants. This eliminated most of the bubble formation.

The effect of a drought stress upon subsequent oxygen evolution rates of the different fucoids was compared using this method to measure photosynthetic rate before and after drying. In some determinations, the different species' ability to resume photosynthesis immediately after being resubmerged was investigated. In others, the seaweeds were resoaked in seawater for a period of time and their photosynthetic rate after this recovery period was measured.

### 2.6.3 Assessment of effects of stresses upon subsequent survival and growth.

From five to fifteen young plants of each species were selected for each experimental treatment, and their fresh weights and lengths were measured. They were then subjected to desiccation or other

experimental stress, resubmerged in seawater at 10°C ± 2°C for 12 to 24 hours, and reweighed. This second weight differed from, and was usually lower than the pre-stress weights. The magnitude of this discrepancy was found to reflect the severity of damage suffered, and this initial weight change was calculated in each experiment as follows:

$$\frac{\left[\begin{array}{l}\text{fresh weight after stress and} \\ \text{12-24 hours recovery in seawater}\end{array}\right] - \left[\begin{array}{l}\text{fresh weight} \\ \text{before stress}\end{array}\right]}{\left(\text{fresh weight before stress}\right) - \left[\begin{array}{l}\text{fresh weight after stress and} \\ \text{12-24 hours recovery in seawater}\end{array}\right]} \times 100\%$$

The length of recovery period used was the same for all plants in a given experiment.

The plants were then cultured for a period of ten to fifteen days and their growth monitored by the methods described in section 2.4.4. In some experiments, five or ten control plants of each species were cultured over the same period without being subjected to an experimental stress beforehand.

The weight and length taken before the stress was administered were used as the initial measurements from which to calculate growth rates. The weight taken after 12 to 24 hours recovery in seawater reflects the short term effects of the stress, and therefore is not truly an "initial" measurement. The plant was assumed not to be growing during the period of stress, and this was not considered part of the growth period. For example, if the plants were weighed on Day 1, dried until Day 4, and then cultured until Day 14, the length and weight changes were calculated from measurements taken Day 1 and Day 14, and the growth rate was expressed on the basis of the ten day culture period.

Tissue damage due to the experimental stress became evident as reddish, decomposing patches or areas on the thallus. It was found in preliminary experiments that many plants which showed considerable damage and decreased slightly in weight and length during the first ten to fifteen days after the stress subsequently regenerated at the apices and resumed growth. Only those plants whose apices were completely destroyed and which decreased greatly in weight were actually dead. Therefore, the condition of the plants was judged on the basis of both appearance and growth, and was quantified in some experiments

using the sixteen point "survival index" detailed in Table 3. Control plants generally scored 0 to 3, so that values between 4 and 12 indicate varying degrees of sublethal damage.

Table 3: Survival Index used to assess impact of experimental stress upon young plants. Since control plants of Pelvetia grew more slowly than those of Fucus spp, and growth rates of Fucus controls varied considerably between different experiments, points for growth were assigned on different scales for Pelvetia and for slow and fast growing Fucus.

| | Linear growth in 10 days, mm | | |
|---|---|---|---|
| Points | Pelvetia | Fucus - controls growing slowly | Fucus - controls growing rapidly |
| 4 | ≥ 2.5 | ≥4.0 | ≥ 4.0 |
| 3 | 1.5 to 2.0 | 2.5 to 3.5 | 3.0 to 4.5 |
| 2 | 0.5 to 1.0 | 1.0 to 2.0 | 1.0 to 2.5 |
| 1 | -0.5 to 0 | -0.5 to 0.5 | -0.5 to 0.5 |
| 0 | ≤-1.0 | ≤-1.0 | ≤-1.0 |

| | % wt change in 10 days | | |
|---|---|---|---|
| Points | Pelvetia | Fucus - controls growing slowly | Fucus - controls growing rapidly |
| 4 | ≥30.1% | ≥20.1% | ≥30.1% |
| 3 | 15.1 to 30% | 10.1 to 20% | 15.1 to 30% |
| 2 | 0.1 to 15% | 0.1 to 10% | 0.1 to 15% |
| 1 | -14.9 to 0% | -14.9 to 0% | -14.9 to 0% |
| 0 | ≤-15% | ≤-15% | ≤-15% |

| Points | Approximate Percent of Thallus area damaged |
|---|---|
| 4 | <5 |
| 3 | 5 - 25 |
| 2 | 25 - 50 |
| 1 | 50 - 95 |
| 0 | 100 |

| Points | Condition of Apices |
|---|---|
| 4 | Normal |
| 3 | Slightly narrowed and/or damaged |
| 2 | Damaged and/or narrowed to less than half of normal width, but clearly regenerating |
| 1 | Severely damaged, some live tissue present |
| 0 | Completely destroyed |

16 Maximum possible total

Initial weight change, percent weight change in ten days and the survival index were found to correlate very well (Table 4) and were therefore considered equally reliable parameters of the effect of an experimental treatment upon the plants.

Table 4: Correlation coefficients between initial weight change, relative weight change in ten days, and survival index in fifty samples of Fucus spiralis dried for 42 hours at 25.6 - 27.1°C, 49 to 54% relative humidity. The observed correlations were all significant at the 0.1% level.

| Parameters | Correlation coefficient |
|---|---|
| survival index and initial weight change | 0.806 |
| survival index and relative weight change in ten days | 0.948 |
| initial weight change and relative weight change in ten days | 0.915 |

# 3. FACTORS CONTROLLING UPPER LIMITS

## 3.1 Survival of Fucus spiralis and F. serratus transplanted to levels above their upper limits

The role of physical environmental factors in determining the upper limits of Fucus spiralis and F. serratus was initially investigated by transplanting these species to levels above their upper limits on a moderately steep, southwest-facing rock slope at Port Loy. Samples of Fucus spiralis were transferred into the Pelvetia zone at about 3.00 m above chart datum, and the control plants were placed in the F. spiralis zone at about 2.75 m. Samples of F. serratus were transplanted to the F. spiralis zone, and the control samples to about MTL, which is about 0.3 m below the upper limit of F. serratus at Port Loy. All samples were transferred on 15-17 February 1974, and their survival and growth were observed at roughly monthly intervals until 1 August 1974.

Fucus spiralis was obtained both as individual plants on rock chips and as groups on small stones. However, no F. serratus attached to small stones could be obtained, and this species was transferred only on rock chips. Therefore the following supplementary observation was undertaken. Two boulders, each bearing about fifty F. serratus plants, were found near the midshore transplant site and one boulder was carried to a stable position just above the F. spiralis zone transplant site. The survival and condition of the F. serratus on the two boulders was then compared over a period of several months.

Some of the early measurements of the transplants were taken during dry weather, and partial desiccation caused the plants to shrivel slightly before the measurements could be completed. From April onward, the plants were measured in wet weather to avoid this source of error. The F. spiralis on small stones, and the F. serratus control plants were fully wet when their initial lengths were taken in February, so that accurate growth rates could be calculated for these. Unfortunately, the F. serratus transferred upshore were somewhat shrivelled when their initial length was measured, and only an approximate growth rate could be obtained.

Both Fucus spiralis and F. serratus grew poorly, and eventually died when transferred to levels above their upper limits (Table 5). The plants developed a reddish colour characteristic of dead or damaged fucoid tissue before being washed away altogether. By contrast, the control plants remained healthy and grew rapidly.

No competing algae grew with the transplants during the experiment, and there was no evidence of grazing on any of the samples, with the possible exception of the F. serratus control plants. Therefore it was concluded that the plants transferred above their upper limits died because of physical conditions exceeding their limits of tolerance.

## 3.2 Critical physical factors: field observations

The control of upper limits by physical factors was readily observed in natural populations of Pelvetia, Fucus spiralis and Ascophyllum. In May 1974, the uppermost plants of Pelvetia and F. spiralis developed the reddish, "burned" colour of dying fucoid tissue (Plate 5) and Ascophyllum attached near to its boundary with the F. spiralis zone sustained similar damage to a few branches. Apparently these plants had been growing at the top of their normal distributional ranges, when some physical stress suddenly exceeded their limits of tolerance. The upper limit of Pelvetia remained stable thereafter, and only a few "burned" plants of this species were observed during the remaining two years of the present study. By contrast, the upper limit of F. spiralis fluctuated in a seasonal pattern. During the hot dry summer of 1975, the top of the F. spiralis zone was so severely truncated that a distinct gap was formed below the Pelvetia zone (Plate 6). During the following winter, F. spiralis germlings not only recolonized this gap but also appeared throughout the lower half of the Pelvetia zone. Within the latter zone, zygotes of F. spiralis settled, grew rapidly into macroscopic plants, became "burned", and ultimately disappeared in an annual cycle (Plate 7). Apparently, desiccation, heating or intense insolation associated with spring and summer weather plays a critical role in determining upper limits of fucoids.

Table 5: Survival and growth of Fucus Spiralis and F. serratus transplanted to levels above their upper limits

| Species | Level | | Initial number of sample plants | Survival | Average growth rate during period of survival, mm/month |
|---|---|---|---|---|---|
| F. spiralis (transplants) | Control: | F. spiralis zone (2.75 m) | 19 | Alive and healthy at end of $5\frac{1}{2}$ months | 5.4 |
| | Experimental: | Pelvetia zone (3.00 m) | 17 | Survived 8 weeks, then died | 3.8 |
| F. serratus (transplants) | Control: | Midshore (1.90 m) | 12 | Healthy after 8 weeks, lost thereafter* | 12.6 |
| | Experimental: | F. spiralis zone (2.75 m) | 26 | Survived 3 weeks, then died | 3.3 ** |
| F. serratus (on boulders) | Control: | Midshore (1.90 m) | ~ 50 | Alive and healthy at end of $5\frac{1}{2}$ months; healthy population of F. serratus still present on this boulder two years later | |
| | Experimental: | Upper F. spiralis zone (2.85 m) | ~ 50 | All plants dead after 8 weeks | |

* These plants disappeared after the April measurements, owing either to grazing or to crumbling of the rock chips on which they were transferred.

** This value is approximate, as the plants were somewhat dehydrated at the time of measurement.

Plate 5: Appearance of Pelvetia and F. spiralis zones at Port Loy on May 17th 1974. The reddish colour of the highest-growing plants of each species indicates severe tissue damage resulting from physiological stress.

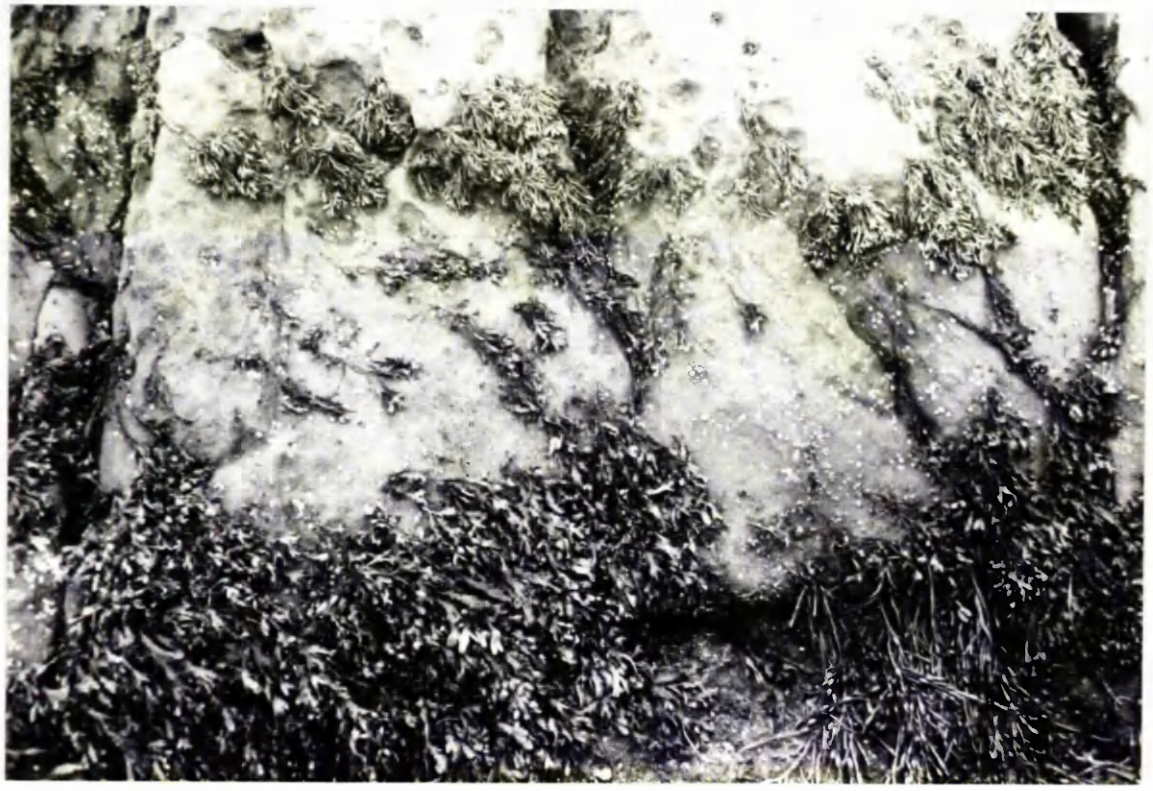
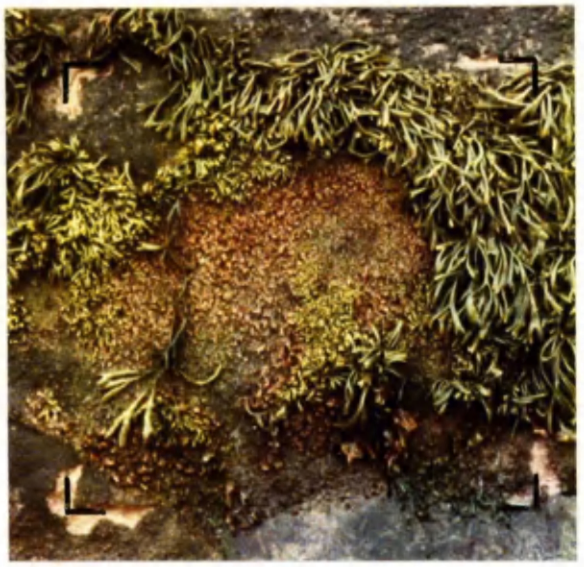
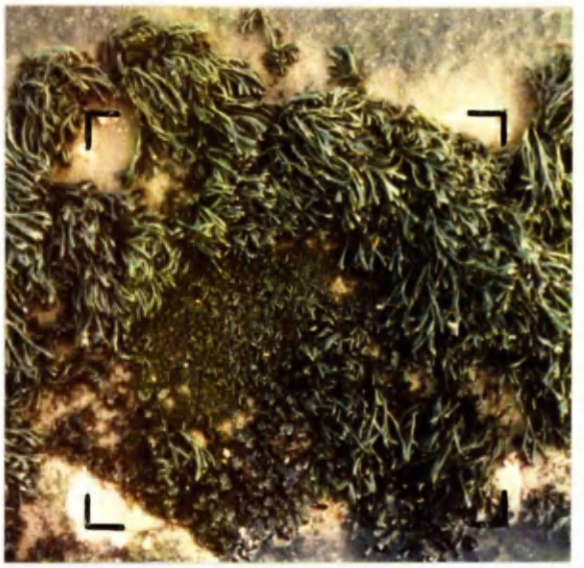


Plate 6: Appearance of Pelvetia and F. spiralis zones at Port Loy in September 1975, showing wide gap within which few F. spiralis remain.



A



B

C

D

Plate 7: Seasonal occurrence of F. spiralis in a 25 x 25 cm quadrat located at about 3.00 m above chart datum.

A. May 17th 1974. The turf of young F. spiralis has been "burned" and contrast sharply in colour with the healthy Pelvetia germlings.

B. December 10th, 1974. A new population of F. spiralis has become established in the lower part of the quadrat.

C. June 23rd 1975. The F. spiralis again shows signs of damage.

D. July 29th 1975. Most of the F. spiralis has disappeared from the quadrat.

In order to verify or refute this hypothesis, the fluctuations in the upper limit of F. spiralis between December 1975 and September 1976 were monitored by careful monthly observations on several south-west-facing rock slops at Port Loy. The changes noted during this period, and earlier observations at the same shore were then related to temperatures, weather conditions and maximum daily tide levels (Figures 5-9). Several salient points emerge from these data:

(1) In all three years, dramatic truncation of the top of the F. spiralis zone was first observed two to four weeks after the first extended period of clear dry weather in spring (Figures 5,7,9). These early dry spells were not especially hot, but each included a period of small neap tides which left the upper part of the F. spiralis zone exposed continuously for several days. Since the weather was calm most of the time during these dry spells, wave splash was minimised, and tide gauge records probably reflect the actual duration of tidal exposure. Therefore, prolonged desiccation appears to be the primary critical factor.

(2) Intense insolation accelerates tissue dehydration by heating the plant to a temperature above that of the atmosphere (Levitt 1972), and the abundant sunshine during the spring dry spells may have increased the stress in this way.

(3) During the cool summer of 1974, F. spiralis was eliminated only from the Pelvetia zone, and remained healthy below its 'usual' upper limit of 2.90 m. However, during the unusually hot summers of 1975 and 1976, considerable damage occurred below this level, and was observed throughout the summer. Therefore, high temperature appears to be an important aggravating factor, possibly because it accelerates the rate of dehydration.

(4) In summer 1975, F. spiralis remained severely damaged and was ultimately lost above the 2.75 m level on southwest-facing slopes, while during most of summer 1976, it made a slow, steady recovery from the initial damage observed in May. Hot days and small tides occurred with similar frequency during the two summers, but they

Figures 5-9. Observed changes in the upper limit of Fucus spiralis on several southwest-facing rock slipes at Port Loy, related to weather conditions and tidal heights as recorded at the Millport Marine Biological Station, Isle of Cumbrae.

Daily maximum and minimum temperatures are indicated, except for the early parts of summer 1975 and 1976, for which only maximum temperatures are given. An arbitrary "critical" level of 20°C serves as the horizontal axis in the summer graphs, while 0°C is the axis for winter graphs.

The amount of sunshine on each day is classified into three categories based on qualitative descriptions given in the weather records:


mainly sunny, or sunny after morning mist

partly cloudy

mainly dull

Rainfall is given in millimetres for each day.

The maximum height to which the flood tide rose each day is given in metres above chart datum. Horizontal lines are drawn at two "critical" levels: the usual upper limits of F. spiralis (2.90m) and Pelvetia (3.25m).

Days on which prolonged tidal exposure of the upper shore coincided with temperature extremes are indicated as follows:

* = "critical day" (max.temp. $\geq$ 20.0°C, max.tidal height < 2.90 m).

• = "semi-critical day" (max.temp. $\geq$ 20.0°C, 2.90 m level covered only by nighttime tide)

\+ = "frost day" (min. temp. $\leq$ 0.0°C, and upper shore not submerged during the predawn hours when the daily minimum temperature normally occurs).

Changes in F. spiralis are represented as follows: Downward arrow represents visible damage down to the tidal level indicated by the arrowhead. Double arrow shaft indicates that most of the F. spiralis had disappeared. An asterisk near a downward arrow indicates that damaged fucoid material was collected from just below 2.90 m, examined carefully, and found to contain small live plants capable of growth. Upward arrow below the 2.90 m line signifies partial (single shaft) or complete (double shaft) recovery from earlier damage. Upward arrow above the 2.90 m level shows the invasion of the Pelvetia zone by F. spiralis germlings. The maximum lengths of these germlings at 2.95 and 3.00 m on two short transects at Port Loy are also given in millimetres.

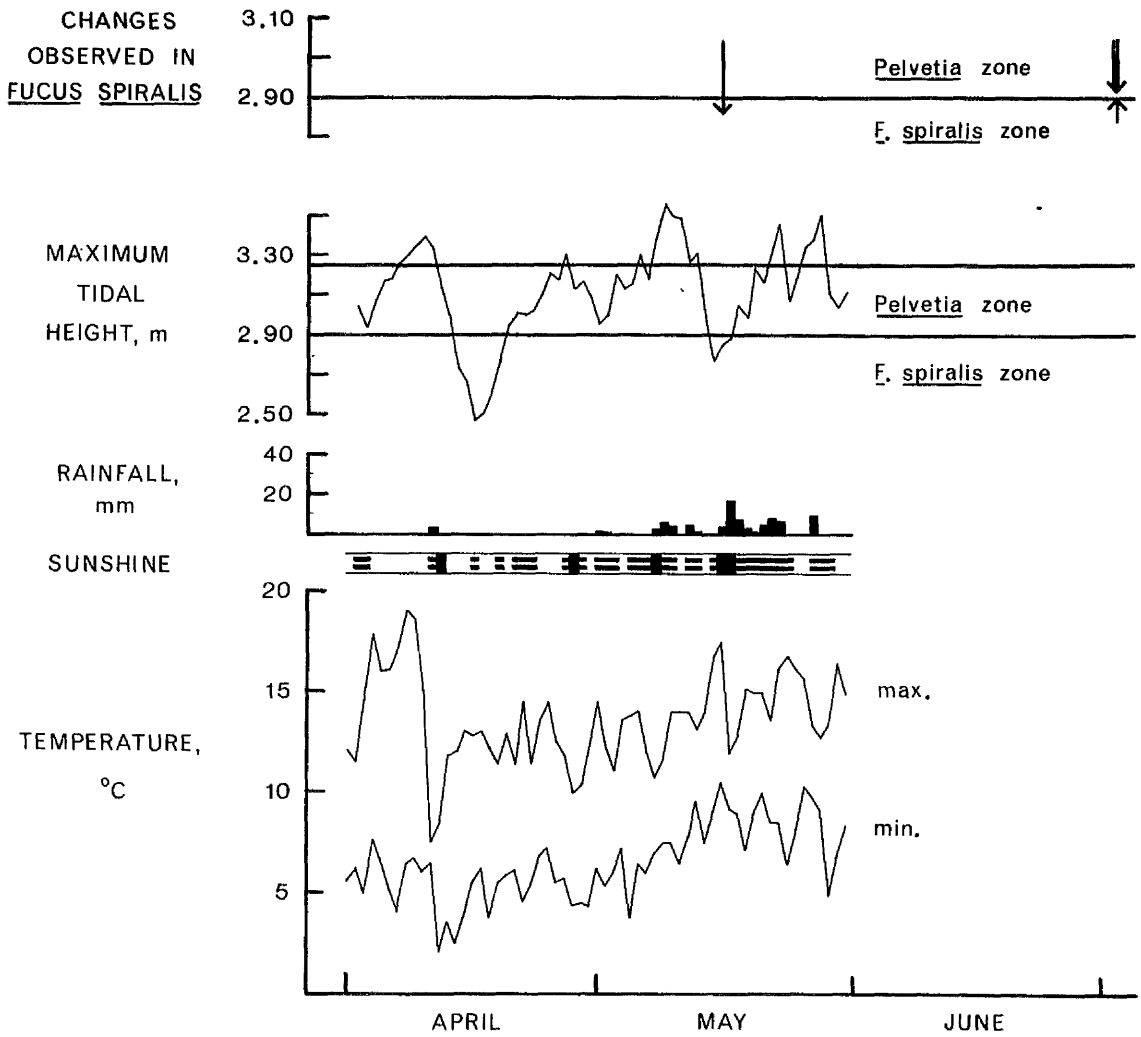



Figure 5: Spring 1974. Brief hot spell 21-25 June (maximum temperatures 20° - 25.1°C) occurred during spring tides; temperatures remained below 20°C for the remainder of the summer

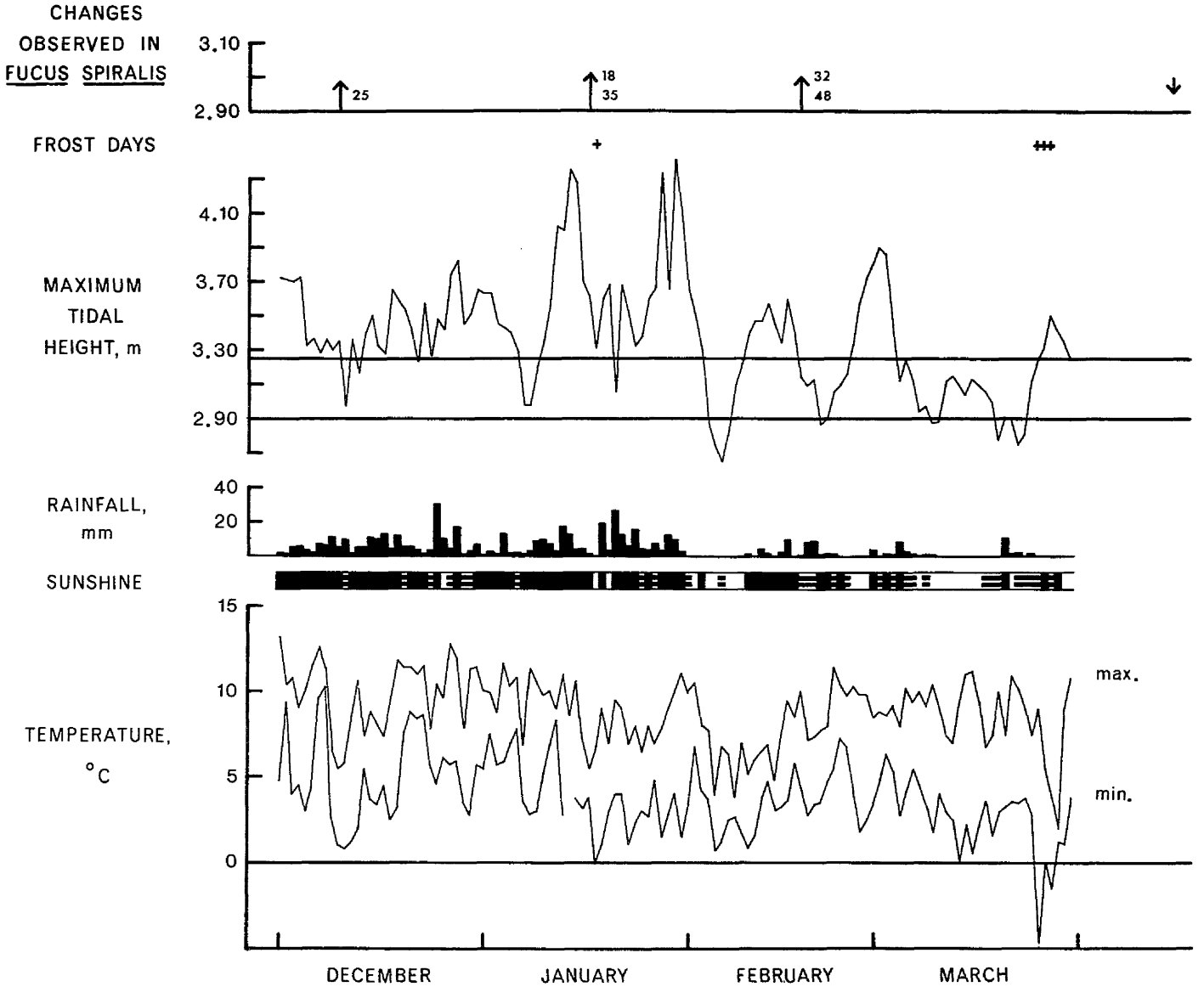



Figure 6: Winter 1974-1975

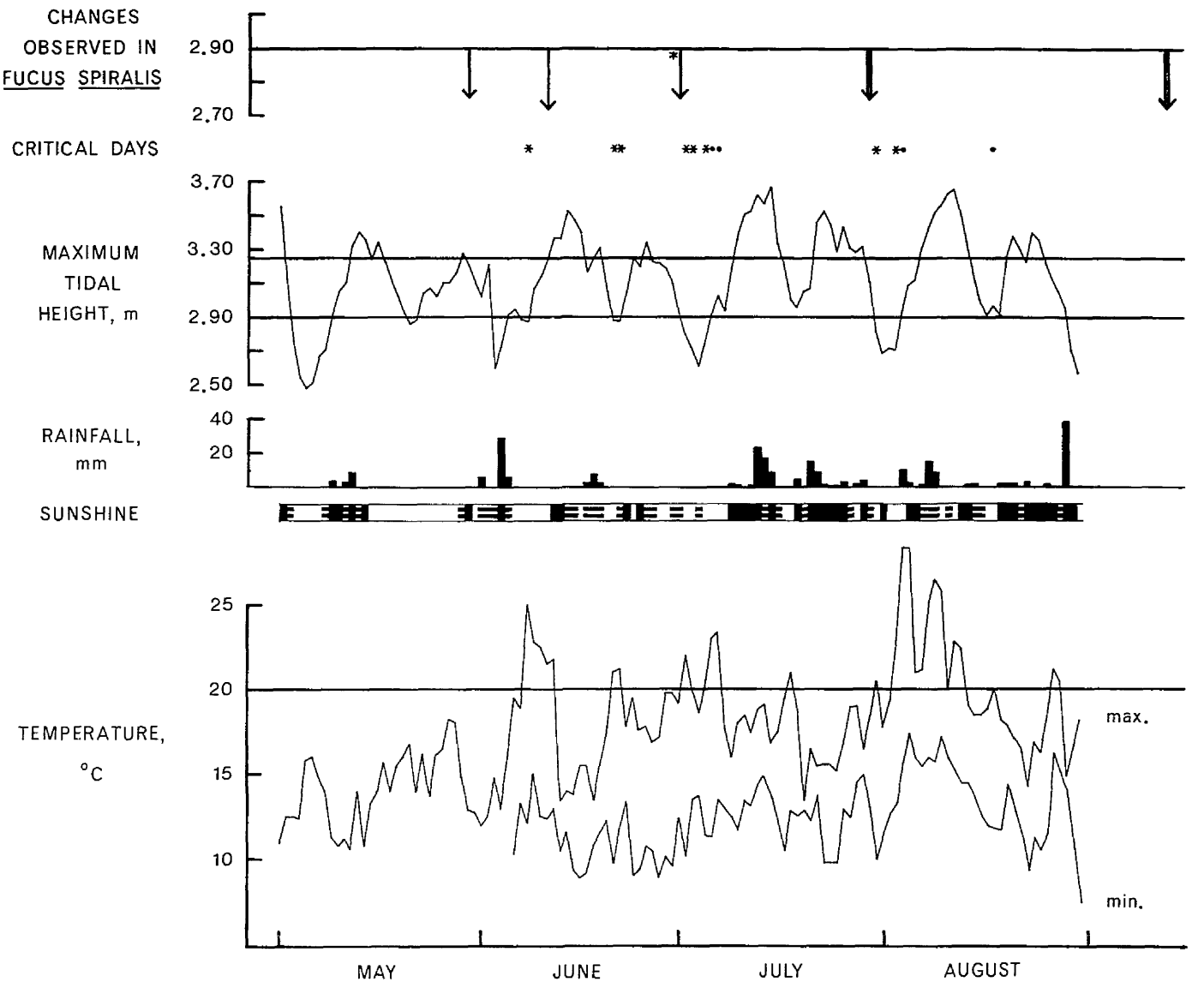



Figure 7: Summer 1975

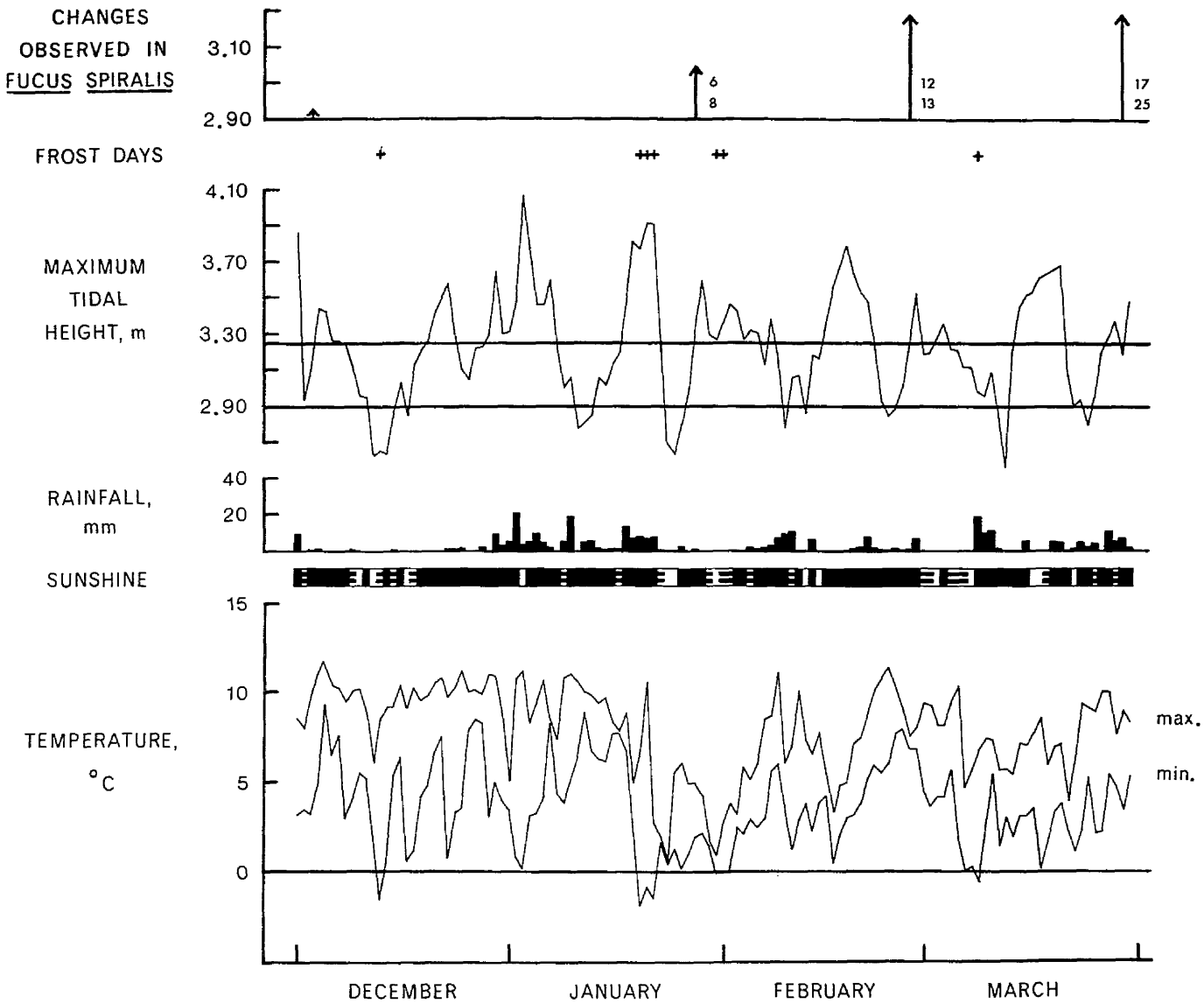



Figure 8: Winter 1975-1976

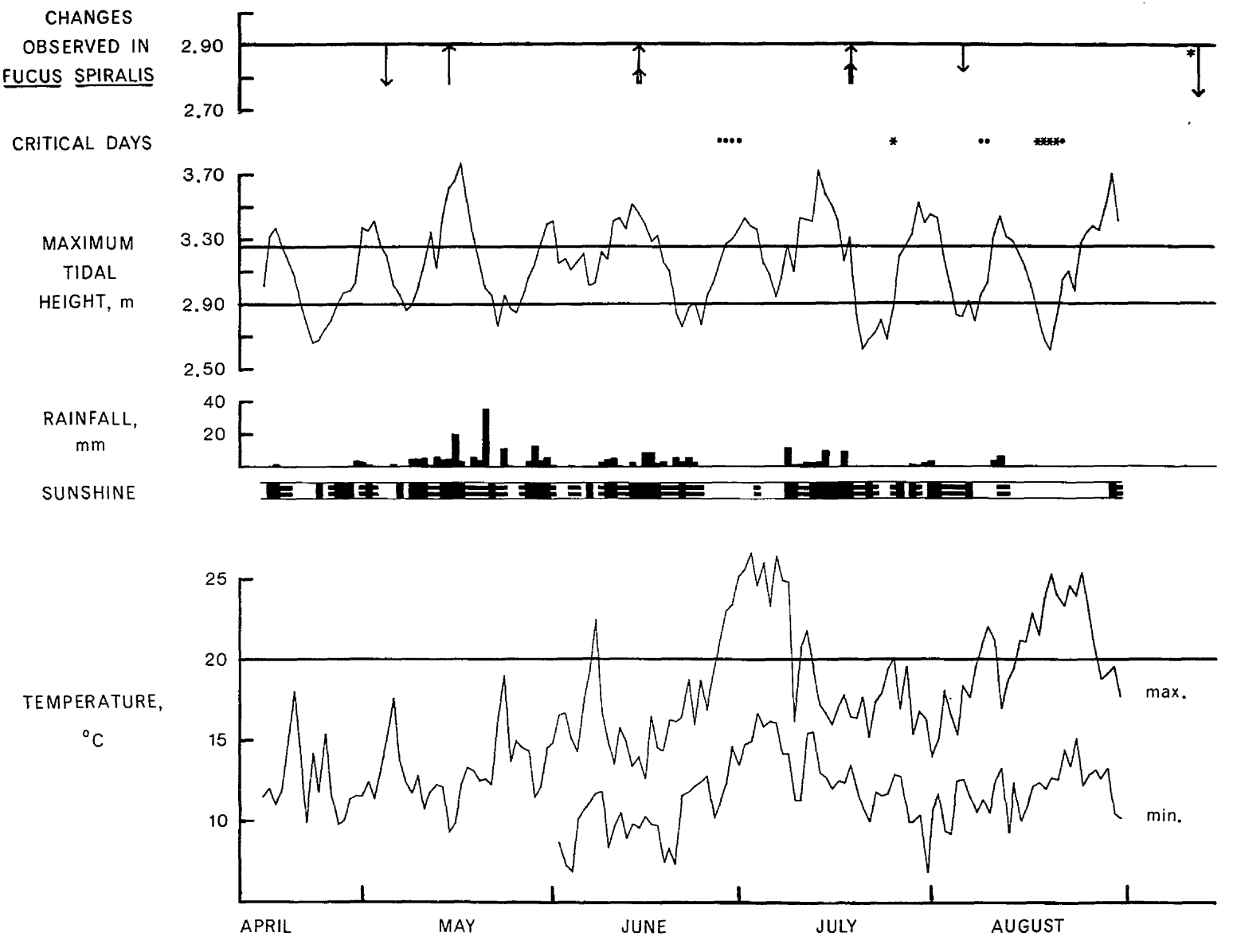



Figure 9: Summer 1976

differed in two possibly important aspects (Table 6). Firstly, in 1975 there were more "critical" days on which high temperature and small tides coincided, and they occurred earlier in the summer (Figure 7). Secondly, the hottest days of 1976 were quite dry while those of 1975 were more humid, sometimes with thunderstorms or drizzle. High humidity and sudden showers may have significantly aggravated the stress upon the exposed algae.

(5) The gradual recovery of F. spiralis in 1976 continued through most of July despite a prolonged hot spell near the beginning of that month, but was sharply reversed by a second heat wave of similar duration and intensity in late August (Figure 9). During the first, the entire F. spiralis zone was submerged each day, at least by the nighttime high tide, while four consecutive "critical" days occurred during the August heat wave. This demonstrates the importance of duration of continuous tidal exposure, and confirms the hypothesis that it is the combination of neap tides and severely desiccating weather conditions which are most damaging. In this context, the slight reversal observed on 6 August may also be related to neap tides occurring during dry though cooler weather (20-26 July, Figure 9).

(6) Germlings of F. spiralis became established in the Pelvetia zone and grew steadily both during the very wet winter of 1974-1975 (Figure 6), and the dry winter of 1975-1976 (Figure 8). The difference in highest tide level at which F. spiralis was found is probably an artefact, since tiny germlings were discovered at 3.1 to 3.2 m as a result of a careful search in 1975-1976 which was not conducted the previous winter. Clearly, neither the heavy rains of the first winter nor the cold spells and light frosts of the second caused much damage to these plants. Winter physical conditions do not appear to play a significant role in determining upper limits of fucoids at Isle of Cumbrae.

(7) Tides tend to rise very high in winter, particularly during wet stormy weather. As a result, heavy rain rarely coincides with a maximum tidal height less than 2.90, and the entire Pelvetia zone

Table 6: Comparison of the frequency of extreme weather conditions, small tides and critical days in May through August of 1975 and 1976.

| | Number of days with maximum temperature of 20.0°C or more | Number of days with maximum temperature of 25.0°C or more | Number of days ≥ 25.0°C during which rain fell | Mean and range of relative humidity at 1400 hrs on day ≥ 25.0°C * |
|---|---|---|---|---|
| 1975 | 28 | 6 | 4 | 60% (31-94%) |
| 1976 | 32 | 7 | 0 | 41% (22-51%) |

| | Number of days with maximum tidal height less than 2.90 m | Number of "critical" days (maximum temp. ≥ 20.0°C, maximum tidal height < 2.90 m) | Mean maximum temperature on "critical" days |
|---|---|---|---|
| 1975 | 24 | 8 | 21.6° |
| 1976 | 22 | 5 | 23.0° |

* as recorded by the Meteorological Office at Prestwick Airport, Ayrshire, which is located on the Firth of Clyde about 22 miles southeast of Isle of Cumbrae.

is often submerged at high tide on wet days (Figures 6,8). Furthermore, wave splash during winter storms may extend the marine influence still higher. Therefore, prolonged tidal exposure of the upper shore rarely coincides with heavy rain, and periodic submersion in seawater probably mitigates the effect of fresh water falling as rain on the seaweed.

(8) The slight damage to F. spiralis growing in the Pelvetia zone that was observed in April 1975 might be related either to the clear dry weather and fairly low maximum tidal heights in March, or to the severe frost on the twenty-sixth of that month. The latter is unlikely, since fucoids collected from temperate coasts demonstrate great frost tolerance (Parker 1960, Feldman and Lutova 1963, Edelstein and McLachlan 1975).

The next task of the present study is to verify the hypothesis that desiccation is the primary critical factor in fucoid zonation. This would imply either that the upshore fucoids can tolerate a greater degree of desiccation than the midshore species, or that they actually dry out more slowly during tidal exposure. The latter possibility has received considerable attention, and several investigators have compared rates of tissue desiccation in different species. Results have been inconclusive and conflicting (Zaneveld 1937, Kristensen 1968, Sandgren 1973, Bérard-Therriault and Cardinal 1973a), and the phenomenon of drought avoidance in fucoids was not satisfactorily established. Therefore, experiments were undertaken to assess and compare mechanisms of drought avoidance in Pelvetia, Fucus spiralis and F. serratus.

## 3.3 Avoidance of tissue desiccation by fucoids

True drought avoidance consists of a plant's ability to maintain a steady state in which the tissue water potential is much higher than that of the environment, (Levitt 1972). However, on the shore where resubmersion occurs at more or less regular intervals, a plant which simply retards its rate of tissue drying could avoid reaching air-dryness during periods of tidal exposure. Such an ability might arise

from any of several thallus properties:

(1) Intrinsic biochemical properties which enable the tissue to dry out more slowly or to store large quantities of water in a "colloidal" form.

(2) A barrier to water loss through the surface, analogous to a leaf cuticle.

(3) A lower ratio of surface area to mass, as is observed in the water-conserving cacti and desert succulents.

(4) A thallus shape which conserves water by creating a "shell" of humid air around the fronds, and therefore a less steep gradient of water vapour concentration.

(5) A bushy or gregarious habit of growth which protects much of the thallus from direct exposure to drying winds.

Theoretically, the total capacity of each species to postpone tissue dehydration during low tide would be assessed most satisfactorily by a direct comparison of desiccation rates of individual plants within natural stands. However such an assessment is fraught with complications. In addition to fluctuations of atmospheric conditions, subtle differences in shelter by the shore topography or adjacent plants may seriously affect the results. Also the plants would have to be carefully matched in terms of surface area and bushiness, which is not practicable in the field. For this reason a direct comparison of desiccation rates in the different species was not undertaken in the field, but was performed in the laboratory.

### 3.3.1 Rates of water loss by individual plants under laboratory conditions.

The ability of Pelvetia, Fucus spiralis and F. serratus to postpone the onset of tissue dehydration was initially assessed by measuring desiccation rates in individual young plants using the procedures outlined in section 2.5.1.

In a preliminary determination, the course of water loss over a ten hour period was recorded in thirty complete young plants each of Pelvetia, F. spiralis and F. serratus. The procedure in this determination differed from that described in section 2.5.1.1 in that the samples were laid on

paper towels during the experimental drying rather than being suspended. Also a slightly less sensitive balance was used and the plants were weighed to the nearest milligram. The samples were weighed at the end of the first, second, third, fourth, sixth, eighth and tenth hours of drying. Drying was carried out in the laboratory in which temperature and relative humidity fluctuated somewhat. However, since the samples were dried over roughly the same period of time, they underwent the same variations of atmospheric conditions, and a direct comparison is valid.

Unexpectedly, the Fucus serratus samples dried considerably more slowly than those of Pelvetia and F. spiralis (Figure 10). The remaining water content in the F. serratus samples significantly exceeded that in the other two species from the first hour ($t_{29} > 7$, $p << 0.001$) through the eighth hour ($t_{29} = 2.76$, $p < 0.01$). The only significant difference between Pelvetia and F. spiralis occurred in the tenth hour ($t_{29} = 2.13$, $p < 0.05$) and probably reflects a slight difference in the colloidal water content. The figure also shows the roughly log-linear pattern of tissue dehydration in all-three species.

The Fucus serratus plants used in this experiment were much larger (268-2691 mg, mean 1079 mg) than the Pelvetia plants (37-393 mg, mean 157 mg) and the F. spiralis plants (35-454 mg, mean 157 mg), and this has apparently influenced the results. When relative tissue dehydration rate (r) over the first two hours is plotted against plant wet weight, a clear inverse relationship between r and weight emerges for all species (Figure 11). The slower mean drying rate of the F. serratus samples as compared to the other species thus appears to be related to their larger mass.

The importance of the sample's size in determining its relative dehydration rate was demonstrated in a trial using large and small segments of Fucus serratus blade. Nine segments 20 to 30 mm in length were taken from adult plants and each was divided into a large (16-25 mm) and a small (5-10 mm) piece. The small piece was taken from the proximal end of five of the samples, and from the distal end of the other four, in order to avoid a sample bias resulting from chemical and structural differences in the tissue related to distance from the apex.

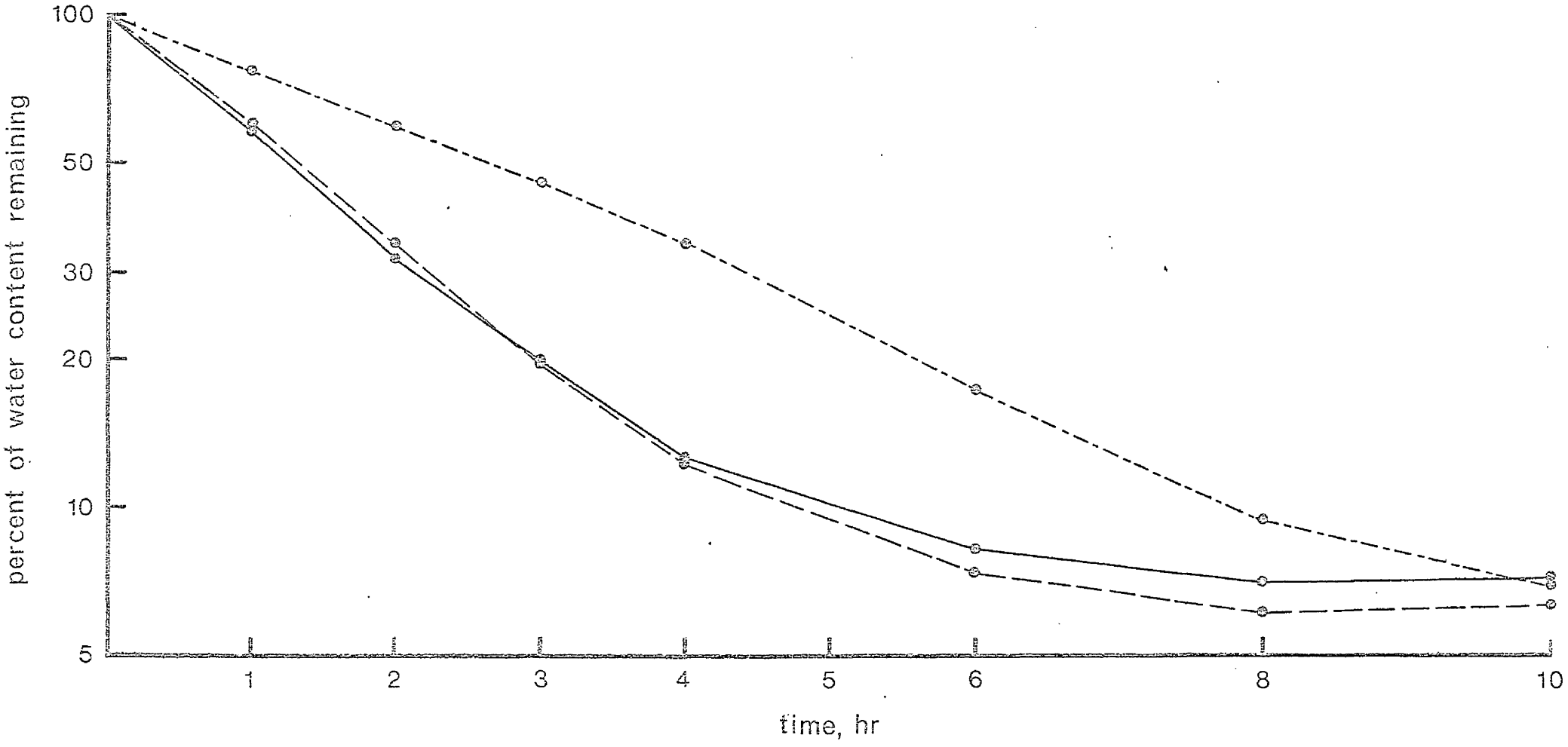



Figure 10. Course of desiccation in young plants of Pelvetia (——), Fucus spiralis (---) and F. serratus (-·--·). Mean remaining water contents of thirty plants of each species while drying at 18.6° - 19.4°C, 71-81% relative humidity, vapour pressure deficit 4.02 - 6.44 millibars, and water potential -285 to -460 bars.

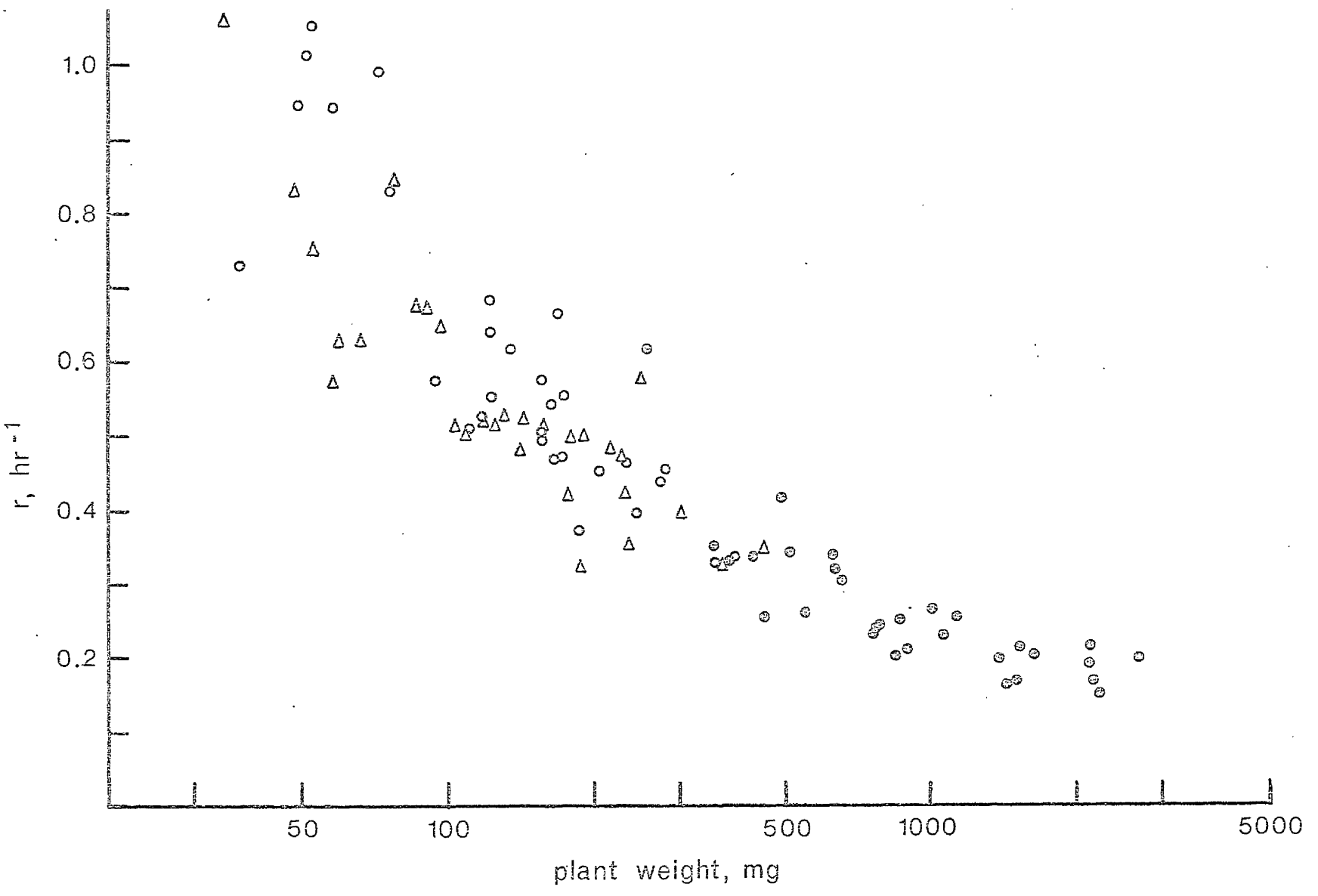



Figure 11. Relationship between relative tissue dehydration rate and fresh weight in thirty plants each of Pelvetia (o), Fucus spiralis (Δ) and F. serratus (⊙), dried at 18.6 - 19.4°C, 71-81% relative humidity, 4.02 - 6.44 millibars vapour pressure deficit.

Relative tissue dehydration rate (r) was then determined over the first hour of drying at 18.8 - 19.1°C, 76-78% relative humidity, vapour pressure deficit of 4.8-5.3 millibars, water potential -334 to - 367 bars. The large pieces dried more slowly ($r = 0.571 \pm 0.069$) than the small pieces ($r = 0.876 \pm 0.115$) and the difference was significant at the 0.1% level. Therefore further comparisons of desiccation rates of the different species were drawn only between plants of roughly similar size.

The course of desiccation was compared in a few sets of plants, each set consisting of one Pelvetia, one F. spiralis and one F. serratus, all similar in weight. These determinations were carried out in an atmosphere with a water potential of about -395 bars using the Stanton balances as described in section 2.5.1.1. The three plants of each set were run simultaneously, and were weighed at intervals over a four hour drying period. Finally, they were equilibrated overnight in the balances (23.5°C, relative humidity 75%, water potential -395 bars), and their air-dry weight was taken.

The water content at each time t was calculated as percent of volatile water remaining

$$= \frac{(\text{wt. at time t}) - (\text{air-dry wt.})}{(\text{wet wt.}) - (\text{air-dry wt.})} \times 100\%,$$

where "volatile water" refers to all the water which is lost to an atmosphere of -395 bars water potential. This percentage was used rather than total water content because it is not affected by the possibly different colloidal water contents of the different species. Air dryness corresponds to 0% volatile water content regardless of species, while it may correspond to different percentages of total water content. Therefore the use of volatile water as the basis for the percentages facilitates a direct comparison of the course of desiccation of the different species.

Samples of Pelvetia lost their volatile water a little more quickly than did Fucus spiralis and F. serratus samples of similar size. Figure 12 shows the course of desiccation over four hours of two sets of samples. Although the F. spiralis in the second set is actually smaller than the Pelvetia, it dried a little more slowly than the Pelvetia.

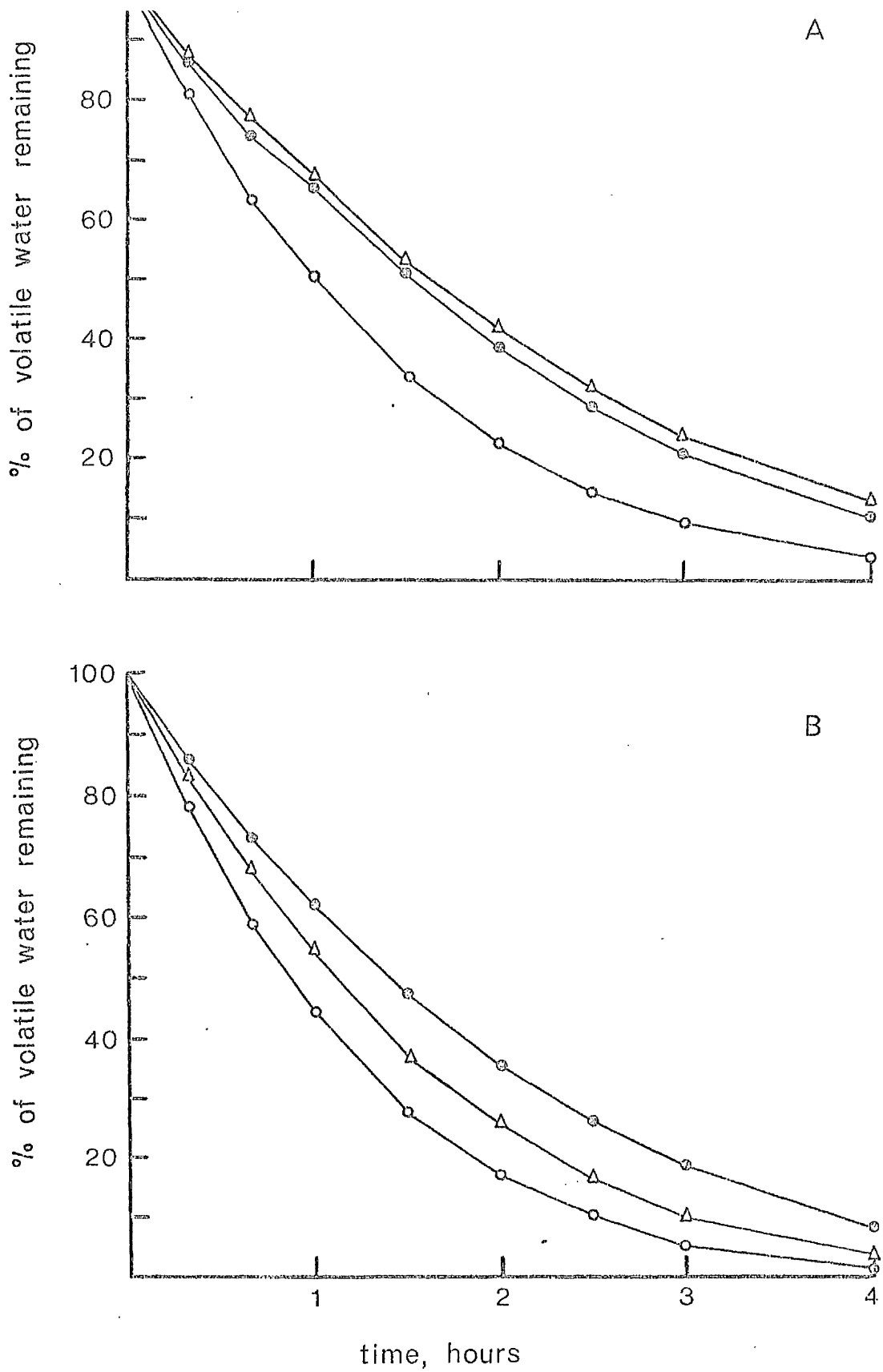



Figure 12. Course of desiccation in plants of Pelvetia (o), F. spiralis (Δ) and F. serratus (●) at 22.7 - 25.9°C, 74-76% relative humidity. Each line represents a single plant.

Initial weights of plants: A Pelvetia 242.5 mg, F. spiralis 296.5mg, F.serratus 251.0 mg.
B Pelvetia 160.5mg, F. spiralis 108.0mg F. serratus 163.0 mg.

Finally desiccation rates during the first hour were compared in eight sets of complete young plants, each set consisting of one Pelvetia, one F. spiralis and one F. serratus. The three plants of each set were selected so that their weights matched to within ± 10%. Pelvetia plants whose branches did not overlap were selected in order to avoid the complication of mutual protection of the axes from the drying atmosphere.

Before the experimental drying, the surface area of each sample was measured. Desiccation rates were then measured in the Stanton balances under the same conditions as in the previous experiment. Six balances were used, so that four separate one hour runs of two sets each were carried out. One Pelvetia and one F. serratus from the first run were resoaked and re-run after the last two sets to observe the effects upon desiccation rate of a slight, gradual rise in temperature which occurred during the course of the experiment.

Relative tissue dehydration rate ($r$), and water evaporation flux ($D$) were calculated for each sample for the first and second half hours. $r$ was calculated on the basis of volatile water in order to eliminate the effect of different colloidal water contents in the different species. The surface to wet weight ratio was also calculated for each sample.

Room temperature increased from 22.8°C to 24.3°C during the course of the experiment, causing the vapour pressure deficit at 75% humidity to increase from 6.85 to 7.5 millibars, about a 9.5% increase. The Pelvetia and F. serratus plants re-run at the end showed relative rates of tissue dehydration 9 and 10.5% higher than in the first run. Desiccation rate was therefore assumed to increase linearly with vapour pressure deficit over this small range, and both $r$ and $D$ were calculated for a vapour pressure deficit of 6.85 millibars as follows:

$$\text{rate at 6.85 mb} = (\text{rate observed}) \left( \frac{6.85 \text{ mb}}{\text{vapour pressure deficit during run}} \right)$$

The desiccation rates of the three samples of each set were compared with one another so that a series of eight paired comparisons was obtained for each of the three combinations of two species. Two statistical

analyses were used in order to check the validity of the conclusions drawn from these data: the Paired Sample t-test and the Wilcoxon Signed Rank test given by Bailey (1959). The results showed conclusively that tissues of Pelvetia and F. spiralis have no intrinsic tendency to dry out more slowly than that of the low-shore species Fucus serratus (Table 7). The surfaces of the Pelvetia samples lost water at a somewhat higher flux (D) than the surfaces of either Fucus species (Table 7, Figure 13). This difference was found significant at the 5% level when tested with the Wilcoxon Signed Rank test, and at the 1% level according to the Paired Sample t-test. The relative tissue dehydration rate (r) was significantly lower in F. spiralis than in F. serratus and Pelvetia (5% level by Wilcoxon test, 1% level by the Paired Sample t-test). However, the actual fluxes of water vapour from the two Fucus species were essentially identical, and F. serratus

Table 7: Mean values of surface to mass ratio and desiccation rates in eight samples each of Pelvetia, Fucus spiralis and F. serratus

| | | Pelvetia | F. spiralis | F. serratus |
|---|---|---|---|---|
| Surface, mass | $mm^2$/mg fresh wt. | 4.10 | 4.44 | 5.02 |
| r, $hr^{-1}$ | first half hour | 0.56 | 0.48 | 0.54 |
| | second half hour | 0.66 | 0.52 | 0.58* |
| D, $\mu g/mm^2$-hr | first half hour | 77.8 | 69.8 | 70.3 |
| | second half hour | 65.8 | 58.5 | 56.7 * |

*The data for one Fucus serratus plant during the second half hour was lost, so that this figure represents an average for seven plants. Also the statistics for this species for the second half hour refer to seven paired comparisons.

tissue became dry faster than that of F. spiralis because of its higher surface to mass ratio. Pelvetia, with a somewhat lower surface to mass ratio and a higher flux dried at a slightly faster rate, measured as r, than F. serratus, although this difference was not statistically

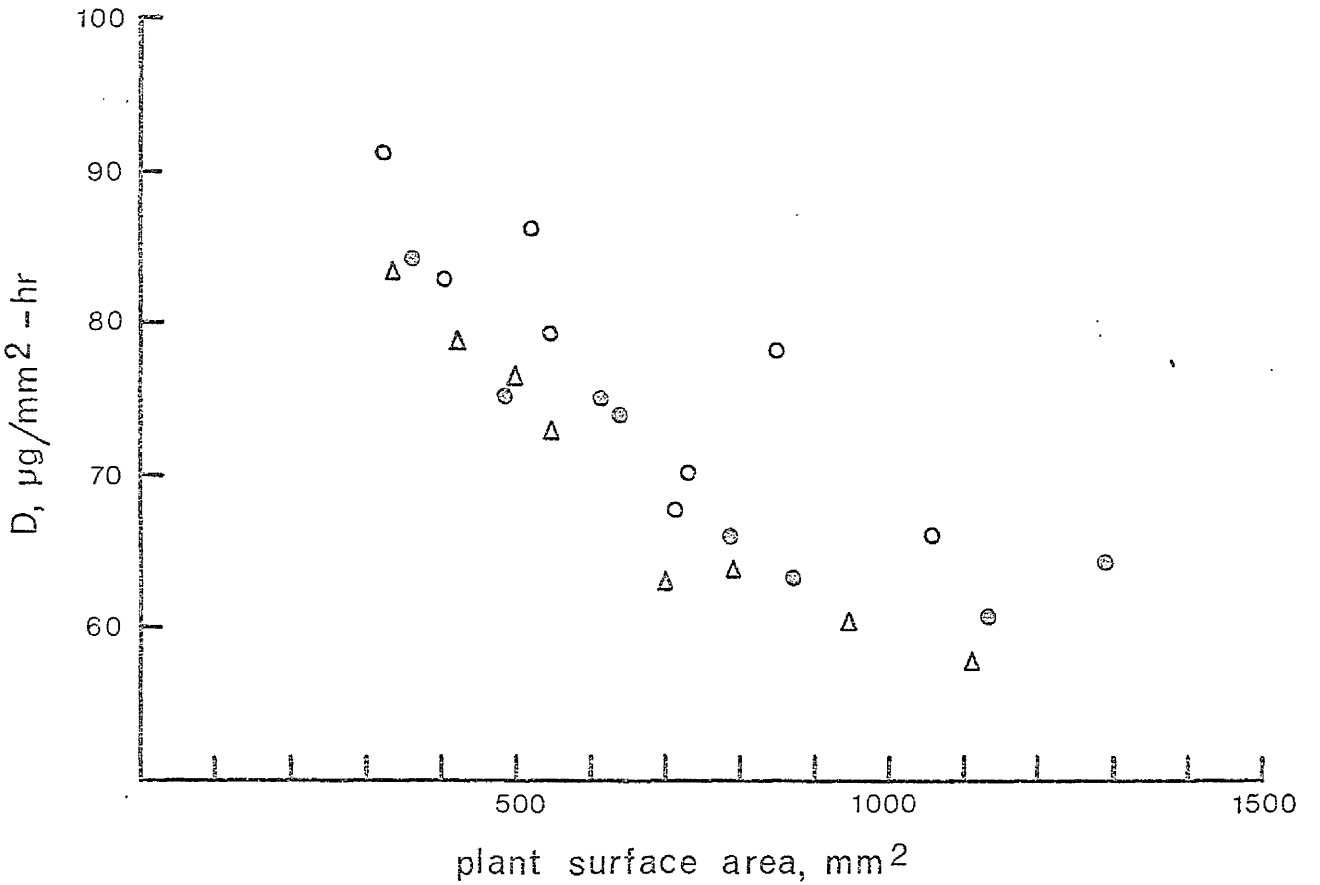



Figure 13. Relationship between evaporation flux and surface area in eight plants each of Pelvetia (o), Fucus spiralis (Δ) and F. serratus (⊙), dried at 22.8-24.3°C, 75% relative humidity, water potential -395 bars.

significant. These results indicate clearly that the tissues of Pelvetia and Fucus spiralis are no less susceptible to dehydration than those of the low shore species F. serratus when exposed to the air under controlled laboratory conditions.

In all three species, the flux seemed to be inversely related to the total surface area (Figure 13). The high flux in Pelvetia suggests that its peculiar channelled thallus form is less rather than more effective in retarding water loss than is the Fucus blade.

### 3.3.2 Evaporation fluxes : compared with evaporation rate from a free seawater surface.

The results obtained in the preceding section suggest that Pelvetia does not possess a more effective surface barrier to water loss than do the Fucus species. However, no direct comparison could be drawn between these results and evaporation rate from a free water surface. Since the area and shape of the water surface greatly influences its evaporation rate (Steward 1959), a valid comparison would require the design of a free water surface of the same size and shape as the suspended fucoid sample. The obvious practical difficulty involved was circumvented in the following experiment.

A large number of small (10 to 50 mm long) thalli were fully soaked, lightly blotted to remove excess water, and carefully packed into an open 50 mm diameter petri dish (area 1964 $mm^2$) so that the surface of the seaweed was as nearly level with the brim of the dish as possible. Rate of water loss from the dish of seaweed was measured in the Stanton balance system at 28.3 ± 0.1°C and 75% relative humidity. The dish full of seaweed was equilibrated in the balance for fifteen to twenty minutes after which the weight loss over a thirty minute period was measured. This measurement was taken for a total of ten dishes of Pelvetia and ten dishes of Fucus spiralis. The flux (D) obtained for these samples was then compared directly with that of an open dish filled to the brim with seawater.

Since evaporation cools the body of water from which the vapour escapes, the steady state temperature of the body of water or seaweed is lower than that of the surrounding atmosphere, and it is important

to ensure that this equilibrium temperature is attained before the flux is measured. It was found in a preliminary test that a dish full of either algal species reached the equilibrium temperature within a fifteen to twenty minute equilibration period, but that the dish of sea water required about one hour. Therefore flux from a dish of seawater was measured after a one-hour equilibration in the Stanton balance and the determination was carried out over six successive thirty-minute intervals.

The ten dishes of Fucus lost an average of 79.6 ± 4.2 µg water per $mm^2$ per hour, and the value for the ten dishes of Pelvetia was essentially identical: 79.5 ± 5.2 $\mu g/mm^2$-hr. These rates are about 84% as fast as that of the free seawater surface (94.4 ± 1.6 $\mu g/mm^2$-hr.), which shows that the moist epidermis of these upshore fucoids functions only to a very slight extent as a cuticle. Since evaporation fluxes from F. spiralis samples and F. serratus samples of similar size were essentially the same (Table 7), it can be inferred that a surface composed of Pelvetia would dry no more slowly than one composed of F. serratus.

A second determination was performed to find out whether the epidermis forms a more effective barrier after becoming partially dehydrated. Two dishes of each species were dried at 28.3°C ± 0.3°C, 75% relative humidity for five hours, during which the surface of seaweed became quite dry to the touch. However, the rate of evaporation was only about 15% slower at the end of the five-hour period than that during the first half hour. This shows that no cuticle-like barrier to water loss forms upon partial drying.

One advantage of measuring water loss from the dishes of seaweed is that they more closely approximate the natural situation of seaweed lying in heaps on the shore with only the upper surface exposed than do the individual plants suspended in the atmosphere. It is interesting to note, therefore, that the more "natural" experiment showed virtually identical evaporation fluxes in Pelvetia and F. spiralis, in contrast to the earlier method which yielded somewhat higher rates for Pelvetia than for Fucus spp. A possible reason for the difference between desiccation rates of suspended samples of these two different genera will be discussed in section 3.3.5.

### 3.3.3 Colloidal water content

The colloidal water contents of Pelvetia, Fucus spiralis and F. serratus were compared in order to determine whether upshore fucoids are more hygroscopic than F. serratus. Five determinations were performed at a wide range of water potentials and at different times of the year. Two supplementary comparisons were also drawn between Pelvetia and F. spiralis. The samples were soaked, weighed, equilibrated at the desired water potential, and reweighed. Finally, their dry weights were taken, and two parameters of "colloidal water" content were calculated as described in section 2.5.2. The first parameter, water retained as a percentage of the total original water content, reflects the degree to which the cells avoid complete dehydration and resulting collapse at a given water potential. Pelvetia retained the greatest percentage of its tissue water and F. serratus the least, regardless of the water potential and the time of year (Table 8). Thus avoidance of cell dehydration and collapse appears to correlate with distributional range on the shore.

Retention of a greater percentage of the total water content at a given water potential can be attributed either to a higher percent dry matter content in the fully hydrated tissue, or to a greater hygroscopic (water-binding) capacity of the dry matter. The latter is expressed by the second parameter of colloidal water content: grams of water retained per 100 grams dry matter.

At the less negative water potentials, Fucus spiralis retained significantly more water per 100 grams dry matter than either Pelvetia or F. serratus, while at -665 bars and below, the three species retained similar amounts (Table 8). Pelvetia consistently had the greatest percent dry matter, but was not found to be the most hygroscopic in any of the seven comparisons with Fucus spp.

In order to further investigate the relationship between percent dry matter, colloidal water content, and distributional range on the shore, colloidal water contents of different regions of the thallus of four fucoids were compared. The samples were air-dried to constant weight in the laboratory, whose water potential was -440 bars (19°C, 72% humidity)

Table 8: Mean ± standard deviation of percent dry matter and colloidal water contents of Pelvetia, Fucus spiralis and F. serratus measured at different water potentials and at different times of year.

| ater otential | Date of Determination | Species | n | % dry matter | % of total original water content | grams water retained per 100 grams dry matter |
|---|---|---|---|---|---|---|
| -1374 bars | 30 March 1976 | Pelvetia | 5 | 22.6 ±1.0 | 2.8 ± 0.2 | 9.5 ± 0.8 |
| | | F. spiralis | 5 | 18.7 ±1.0 | 2.3 ± 0.2 | 9.8 ± 1.1 |
| - 950 bars | 21 Feb. 1976 | Pelvetia | 10 | 21.1 ±0.8 | 3.5 ± 0.2 | 13.2 ± 0.6 |
| | | F. spiralis | 10 | 19.6 ±1.0 | 3.2 ± 0.2 | 13.3 ± 0.4 |
| | | F. serratus | 8 | 18.4 ±1.3 | 2.9 ± 0.3 | 13.1 ± 1.8 |
| - 900 bars | 19 May 1976 | Pelvetia | 5 | 26.1 ±0.2 | 4.2 ± 0.3 | 12.0 ± 0.8 |
| | | F. spiralis | 5 | 23.7 ±0.4 | 3.7 ± 0.2 | 12.1 ± 0.3 |
| - 665 bars* | 30 May 1974 | Pelvetia | 20 | 27.4 ±1.3 | 6.6 ± 0.4 | 17.4 ± 0.4 |
| | | F.spiralis | 18 | 22.6 ±2.1 | 5.2 ± 0.6 | 17.7 ± 0.2 |
| | | F.serratus | 21 | 22.2 ±2.2 | 4.9 ± 0.6 | 17.1 ± 0.4 |
| - 395 bars | 29 Aug. 1975 | Pelvetia | 8 | 28.1 ±0.8 | 9.8 ± 0.4 | 25.0 ± 1.0 |
| | | F.spiralis | 8 | 21.0 ±1.0 | 7.8 ± 0.5 | 29.4 ± 2.2 |
| | | F.serratus | 8 | 21.5 ±2.3 | 6.4 ± 0.6 | 23.7 ± 3.1 |
| - 395 bars | 13 Sept. 1975 | Pelvetia | 10 | 30.0 ±1.2 | 8.9 ± 0.4 | 20.8 ± 1.1 |
| | | F.spiralis | 10 | 22.5 ±1.2 | 6.8 ± 0.5 | 23.2 ± 1.2 |
| | | F.serratus | 10 | 20.6 ±1.1 | 5.7 ± 0.4 | 21.9 ± 1.4 |
| pproximately - 150 to 200 bars * | 31 May 1974 | Pelvetia | 20 | 27.4 ±1.3 | 21.5 ± 1.4 | 57.0 ± 2.9 |
| | | F.spiralis | 18 | 22.6 ±2.2 | 19.0 ± 2.6 | 64.8 ± 2.8 |
| | | F.serratus | 21 | 22.2 ±2.2 | 15.3 ± 1.7 | 54.1 ± 6.0 |

* These two sets of data were obtained from the same sets of algal samples which were equilibrated firstly in the laboratory (-665 bars) and then in the 10°C culture room. An exact value of relative humidity was unfortunately not obtained in the latter, but it generally ranged between 85 and 90% ($\Psi_w$ = - 150 to - 200 bars). Since the samples were equilibrated simultaneously, a meaningful comparison of the samples' "colloidal" water content was possible.

when the air-dry weight was taken. The tissues used were: vegetative tissue and receptacles of Pelvetia, vegetative tissue and receptacles of Ascophyllum, and stipe, blade and receptacles of Fucus spiralis and F. serratus. Ten to thirty-one samples of each thallus region of each species were used.

Colloidal water content was simultaneously determined in the vegetative parts of the intertidal red alga Gigartina stellata, and in stipes and blades of the sublittoral fringe alga Laminaria digitata. These two species were included in order to compare the colloidal water contents of the four fucoids with that of an unrelated intertidal alga, and with that of an alga whose habitat is not subjected to severe desiccation. Seven to ten samples of each tissue were used.

The results of the determination show conclusively that the dry matter of Pelvetia and F. spiralis is not more hygroscopic than that of the midshore species Ascophyllum and Gigartina stellata. In fact, the colloidal water content per 100 grams dry matter is very similar in all four species (Figure 14, top). It is also similar in the different thallus regions, despite great differences in dry matter content. F. serratus retained slightly less water per 100 grams dry matter, while Laminaria retained much less, than did the mid- and high shore species. Laminaria has a higher ash and laminarin content than the Fucaceae (Black 1948a, 1948b, 1949b), and rather lower alginate content, which might explain the lower water binding capacity of its dry matter.

The most striking feature of the data is the very close correlation between percent dry matter and percent of total water content retained (Figure 14, bottom). This relationship is also evident among the samples of a single thallus region, as is illustrated in Figure 15 for F. serratus blades. Thus it is those tissues with a high percent dry matter which retain a larger portion of their water during exposure to the atmosphere. It is interesting to note in this context that the dry matter content of Pelvetia in this determination (24%) was exceeded by those of Fucus stipes and Gigartina blades (27-30%). The importance of the dry matter content in drought tolerance is investigated further in section 3.8.

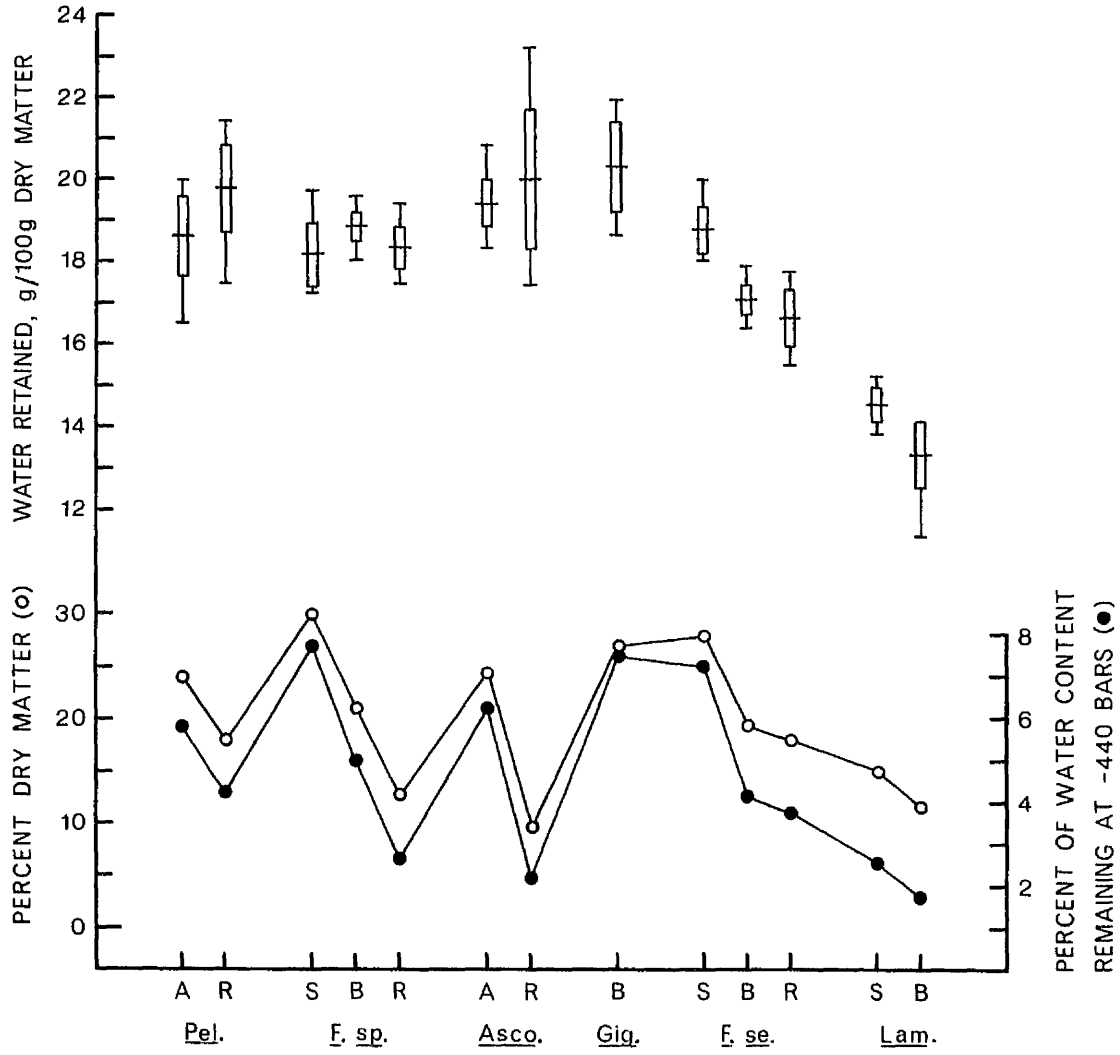



Figure 14: Dry matter content, and colloidal water content at -440 bars in different thallus regions of six algal species. Graph shows means of percent dry matter, mean percent of water retained, and mean, standard deviation and range of grams water retained per 100 grams dry matter. A = vegetative axes; B = blades; S = stipes; R = receptacles.

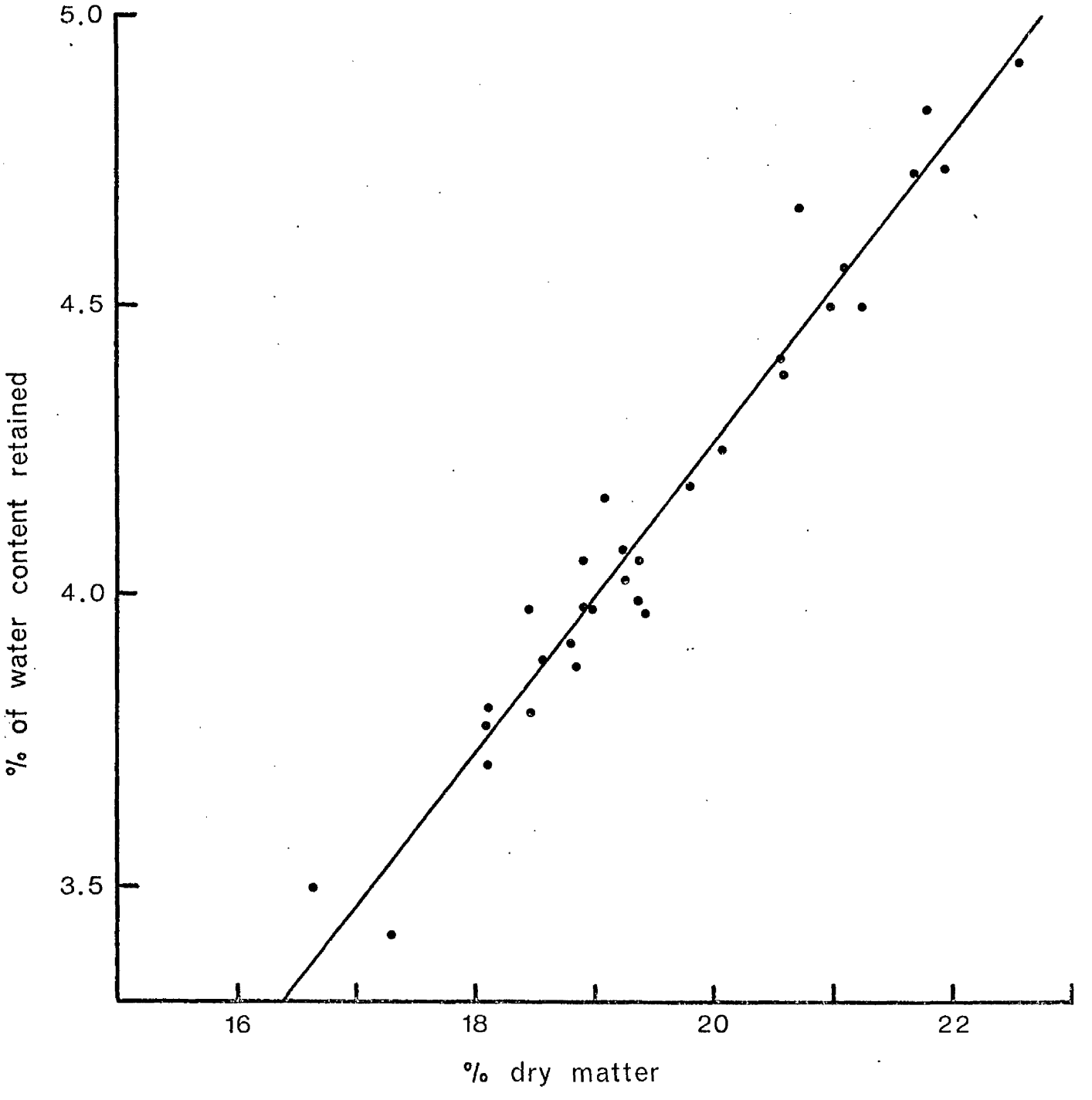



Figure 15. Relationship between percent dry matter and percent of water content retained at -440 bars water potential in Fucus serratus blades. Correlation coefficient = 0.978, $p << 0.001$. Linear regression equation: $y = 0.263x - 1.01$, where y = percent of water retained and x = percent dry matter.

### 3.3.4 Surface to mass ratio

The relative dehydration rate of a plant exposed to a drying environment is directly related to the amount of surface area per unit of plant mass, as well as to the rate of water loss per unit surface area. Therefore, since evaporation fluxes are similar in Pelvetia and Fucus spp., Pelvetia would dry out more slowly than the others if it has a lower surface to mass ratio than the other species. This value does appear a little lower in the Pelvetia samples than in the Fucus samples used in the desiccation determination (Table 7). To supplement these data, I measured this ratio in both smaller and larger juvenile plants as well as in segments of vegetative tissue taken from adult plants of Pelvetia, Fucus spp. and Ascophyllum. The samples from adult Fucus spp. were taken from the distal portions of healthy branches where the blade tissue was intact. The "stipe" portion of the Fucus plant from which the blade had eroded was excluded so that the adult Fucus samples would be more comparable with the juvenile plants which have little or no stipe region.

Surface area and wet weights were measured to obtain the surface to mass ratio of each sample. Mean surface to mass ratios of five size classes of each species are given in Table 9.

Table 9: Mean ± standard deviation of surface to mass ratio in $mm^2/mg$ wet weight in young plants and blade samples of adult plants of Pelvetia, Fucus spiralis and F. serratus, and adult samples of Ascophyllum. The sample size is also given for each size class of each species.

| Samples of adult plants | complete young plants 250–1000 mg | 100 – 250 mg | 50 – 100 mg | 6 – 50 mg |
|---|---|---|---|---|
| Pel. | 4.15 ± 0.31 n=25 | 4.01 ± 0.18 n=5 | 4.10 ± 0.22 n=16 | 4.22 ± 0.21 n=8 | 5.36 ± 0.84 n=4 |
| F.sp. | 3.19 ± 0.24 n=26 | 4.03 ± 0.22 n=6 | 4.25 ± 0.38 n=13 | 4.59 ± 0.33 n=8 | 5.62 ± 0.30 n=4 |
| F.se. | 2.73 ± 0.34 n=23 | 4.09 ± 0.24 n=6 | 4.77 ± 0.44 n=12 | 4.89 ± 0.28 n=5 | 6.21 ± 0.74 n=4 |
| Asco. | 1.52 ± 0.14 n=28 | | | | |

### 3.3.5 Effect of thallus shape on rate of desiccation

The effect of thallus shape upon desiccation rate was investigated in *Ascophyllum*, *Fucus* spp. and *Pelvetia* in order to determine whether the peculiar channel shape of the latter confers any advantage in water conservation. Three basic shapes were considered: the elliptical-cylindrical *Ascophyllum* thallus and *Fucus* stipes, the *Fucus* blade which is a flat lamina with a thickened midrib, and the channelled *Pelvetia* thallus.

In investigating the effect of thallus shape upon rate of drying, several complications were encountered. Firstly, the effect of the shape of the individual axis of the thallus must be distinguished from that of the close juxtaposition and mutual protection of thallus branches. In this investigation, single unbranched segments excised from the thallus were used in order to assess the effect of shape alone.

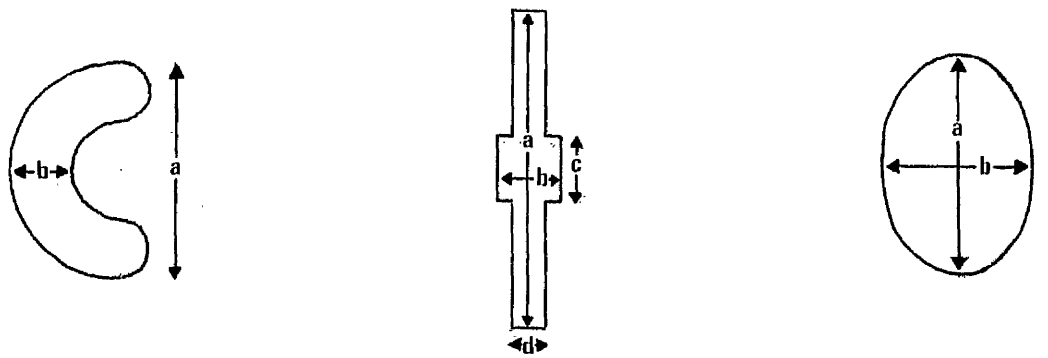
Secondly, the effect of shape must be distinguished from that of surface area to mass relationship. Ideally, this would be done by comparing samples which differ in shape but have identical surface to mass ratios. As this was not practicable, a number of samples of each species were taken and the relative dehydration rate (r) was determined and plotted against surface to mass ratio.

Thirdly, the relative dehydration rate of the segment will clearly depend upon whether it is suspended in the air or whether it is laid on a flat surface. This difference cannot be assumed to be of the same magnitude in segments of different shapes. Half of the surface area of a flat blade segment is in contact with a flat surface on which it lies, and thus effectively protected from the drying atmosphere. A cylindrical stipe has much less of its surface area in contact with and protected by the surface on which it lies. Therefore, while stipe and blade segments of the same surface to mass relationship may dry equally fast while suspended, the blade may dry more slowly than the stipe while lying on a surface. For this reason, the determination was carried out twice, once with the samples suspended, and once with the samples laid on paper towels on the laboratory bench.

Finally, owing to the very small size of the segments used, the

surface area could not be accurately assessed with the photocopy method. Therefore surface to volume ratio was estimated by dividing the perimeter of the segment's cross section by the cross sectional area. Surface to mass ratio was derived directly from surface to volume ratio assuming a specific gravity of one in the fucoids, which are observed to be of roughly neutral buoyancy.

The cross sectional perimeter and area were derived from the dimensions shown in Figure 16 which were measured with a millimeter ruler and a micrometer caliper. A mathematical approximation was used to obtain the perimeter of the elliptical cross section.




Pelvetia | Fucus blade | Ascophyllum, Fucus stipe

Figure 16: Dimensions of thallus cross sections from which surface to volume ratio was estimated.

This estimation of surface to volume ratio neglects the cut end surfaces. However, the segments were quite long relative to their thicknesses, and the end area comprised only a small fraction of the total area. Since undamaged surfaces of fucoids evaporate water 84% as fast as a free seawater surface, the error introduced by neglecting the cut ends was not large even if they lost water fully as fast as a free seawater surface.

A second disadvantage resulting from the use of small segments is that they became dry very rapidly, often losing more than half their

water content within one hour. For this reason, the evaporation flux D could not be determined accurately from the data, since it declines progressively as the tissue dries up. Therefore, only the relative dehydration rate was calculated.

The surface to mass ratio was estimated for ten segments each of Pelvetia frond, Ascophyllum frond, F. spiralis stipe, F. spiralis blade, F. serratus stipe and F. serratus blade, and the relative dehydration rate was then determined during a one hour drying period. One Pelvetia sample fell from its suspended position during the drying period; therefore this result was lost and only nine are reported for this species. The results for all four species are shown in Figure 17, which reveals the occurrence of two widely separated groups. Desiccation rates increased rapidly with surface to mass ratio in the elliptical-cylindrical Ascophyllum samples and Fucus stipes.

By contrast, the Fucus blades and Pelvetia channels presented 3.3 to 4.8 $mm^2$ surface per milligram, yet none dried more than one and one-half times as fast as the smallest stipe which had a surface to mass ratio of 1.3 $mm^2/mg$. In particular, the Fucus blade samples dried at about the same rate as the smaller Fucus stipes which had only one quarter to one third as much surface area per unit mass. Therefore the actual evaporation fluxes from the stipes must be three times those from the blades.

The Pelvetia fronds dried considerably faster than the Fucus blades of similar surface to mass ratio. Therefore the channel shape appears to confer less of an advantage than the flat blade shape in retarding water loss. This is confirmed by the observation that individual Pelvetia plants suspended in the Stanton balance system dried a little faster than did Fucus plants of the same size and a slightly greater surface to mass ratio.

In the present determination, the Pelvetia segments used were much smaller in mass than the Fucus blade segments, and the large difference in relative dehydration rates shown in Figure 17 is partially an artefact of this difference in mass.

In the second determination in which the segments were dried while

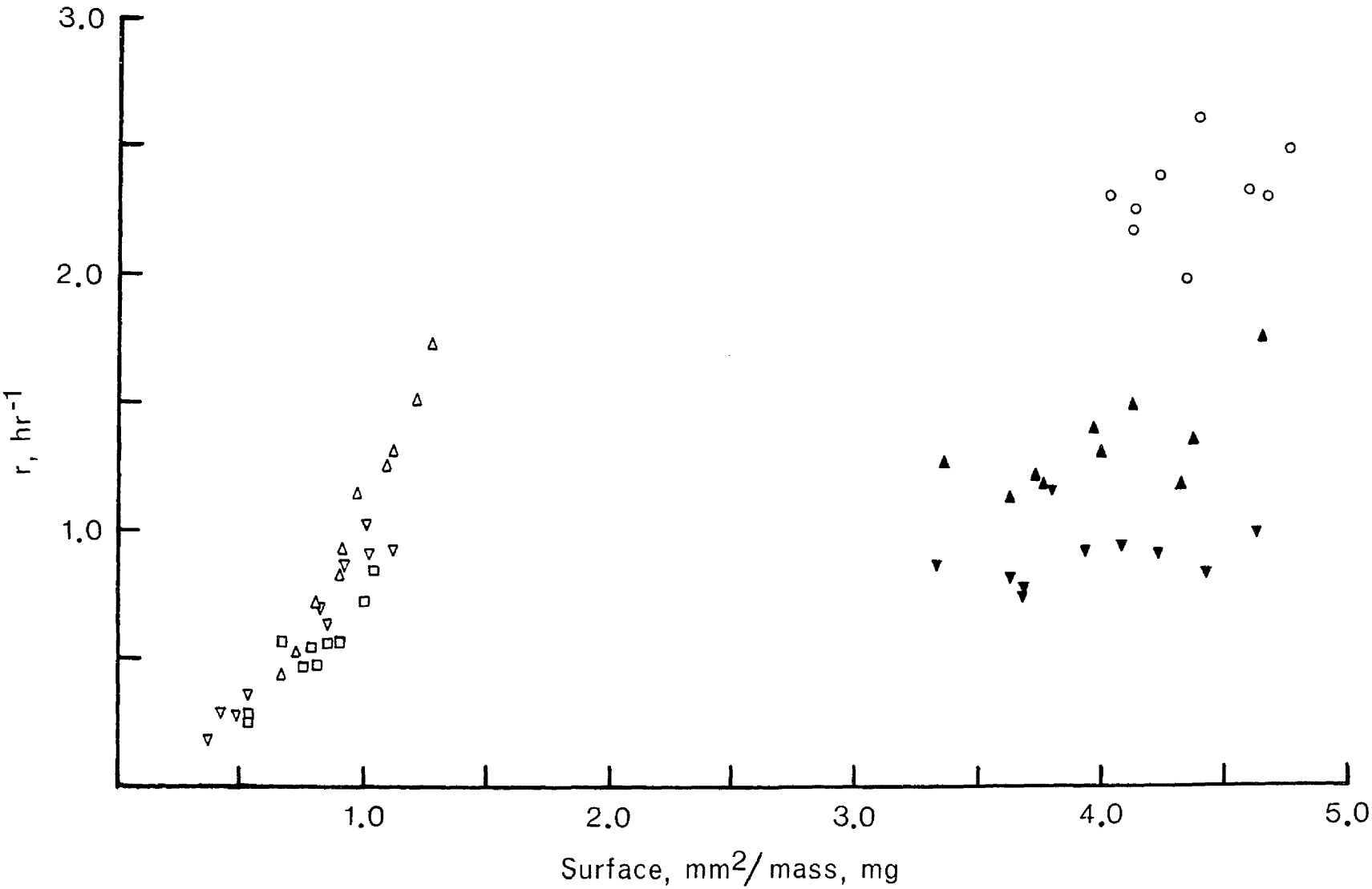



Figure 17: Relationship between relative tissue dehydration rate and surface to mass ratio in segments of Pelvetia (o), Ascophyllum (□), F. spiralis stipes (△), F. spiralis blades (▲), F. serratus stipes(▽) and F. serratus blades (▼). Samples were dried at 20.8-21.5°C, 69-71% relative humidity, vapour pressure deficit 7.4 - 7.8 millibars.

lying on a flat surface, fifteen samples each of Pelvetia, Ascophyllum and blade and stipe of each of the three Fucus species were used. Relative dehydration rates were much lower than in the suspended samples, as expected. The pattern, however, was roughly the same as that shown in Figure 17. Blades of Fucus (3.4 - 4.4 $mm^2/mg$) dried about as fast as small Fucus stipes (11 - 19 $mm^2/mg$) and Ascophyllum fronds (14 - 23 $mm^2/mg$). Pelvetia samples again dried considerably faster than Fucus blades of a similar surface to mass ratio, owing partly to the very small size of the Pelvetia segments compared to the Fucus segments, and partly to the difference in shape.

Stipes of the three species of Fucus showed very similar rates of desiccation, and the pronounced difference between stipes and blades was observed in each species. Blades of F. spiralis dried slightly more slowly than those of F. serratus in the determination with samples lying on a flat surface, but this difference was reversed in the other determination, and the evaporation fluxes from the two species were equal in the Stanton balance system (Section 3.3.1). From these results, one can conclude that F. spiralis has no greater intrinsic ability to retard tissue water loss than the other two Fucus species.

In order to determine whether or not the difference between stipe and blade is peculiar to the intertidal genus Fucus, relative dehydration rates were measured in nine stipe samples and nine blade samples of the sublittoral fringe inhabitant Laminaria digitata. The results show the same pattern as did blades and stipes of Fucus (Figure 18) and the difference between the regressions of r upon surface to mass for stipe and blade is significant at the 0.1% level. Also the actual desiccation rates of Laminaria tissues are roughly similar to those of fucoids. Since adaptation to drought would not be expected in the blades of this sublittoral fringe species, these data strongly suggest that the flat expanded blade shape itself creates a less steep water vapour diffusion gradient which compensates for the high surface to volume ratio of blades.

The effects of both total area and shape upon desiccation rates can be understood by examining what happens to water molecules evaporating from the flat surface of the blade and from the edge. Collisions

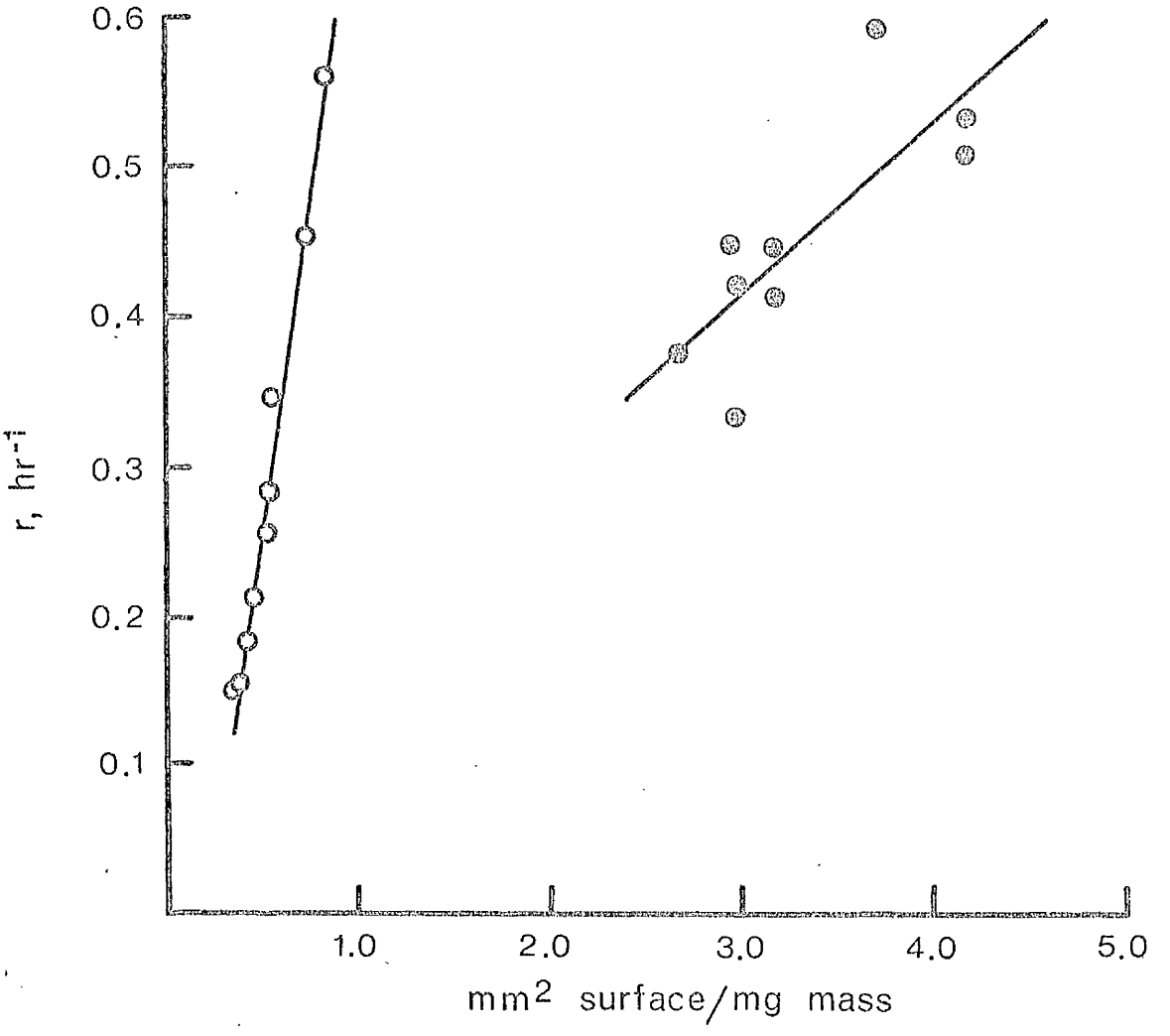



Figure 18. Relationship between relative dehydration rate and surface to mass ratio in stipes (o) and blades (●) of Laminaria digitata. Regression lines:

blades: $r = 0.114$ (surf./mass ratio) + 0.074
stipes: $r = 0.911$ (surf./mass ratio) − 0.196

The difference between the regression coefficients for blades and stipes is highly significant ($t = 13.9$, $p < 0.001$)

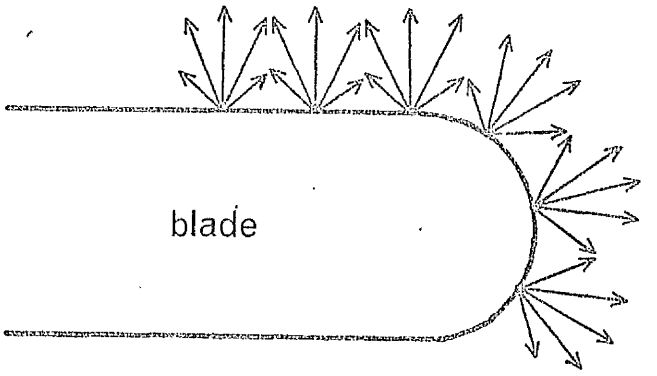
between evaporating molecules may deflect some molecules back towards the evaporating surface and thus hinder their ultimate escape. Such collisions are much more frequent over a flat surface than over a sharply curved surface such as the blade edge or the stipe (Figure 19). Thus flat surfaces set up less steep vapour gradients between themselves and the surrounding atmosphere than do the edges, and hence lose water more slowly. The larger plants present less total edge relative to flat surface, and therefore dry out more slowly.

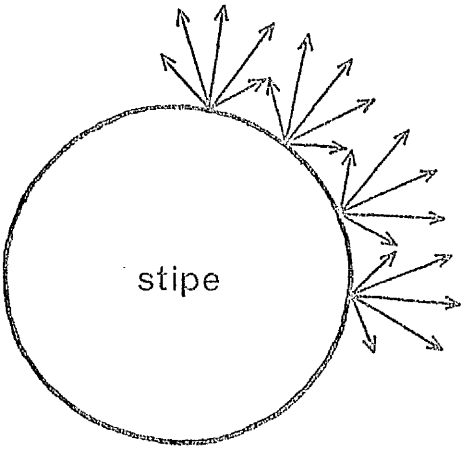
A slender stipe, with no flat surfaces is in effect "all edge" and this may explain why these stipes dry out as fast as blade samples which have three times as much surface per unit mass. The inside of the channel of Pelvetia forms a very effective water vapour trap, while the outside surface, being strongly curved like a stipe surface, must lose water at a high flux rate (Figure 19). As a result, the channel is more effective than a stipe but less so than a blade in retarding water loss.

### 3.3.6 Vulnerability to desiccation in nature: role of habit of growth and aggregation

Shape and surface to mass ratio of individual axes or blades do not alone determine how vulnerable to tissue desiccation the different fucoid species are in nature. The habit of growth of the individual plant and the degree of aggregation of the individuals into groups or extended stands may play a critical role in protecting at least some individuals from drying. The centre of a bushy, much branched plant will remain moist long after a little-branched plant becomes air-dry, even if the two plants are equal in surface to mass ratio and desiccation rate. Also an extended, densely packed stand of algae covering the substratum to a depth of several centimetres will become dry very slowly even if the individual plants are composed of uniseriate filaments with no cuticle or other defence against tissue water loss.

The degree of aggregation in natural populations of fucoids is very variable. All three genera of fucoids have been observed to occur as isolated juvenile or adult plants, small groups or clumps, and in extensive stands of mature plants completely covering the substrate.



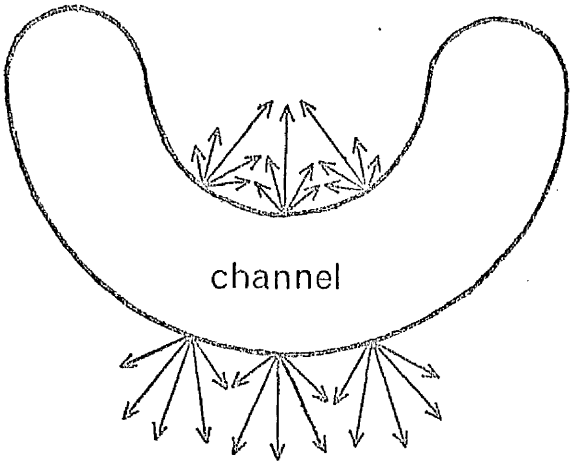




Figure 19. Diagrammatic illustration of evaporation from blade and stipe of Fucus and channelled thallus of Pelvetia, showing lower frequency of collisions between molecules evaporating from a convexly curved surface than from a plane or concave surface.

Near and above MHWN, countless thousands of juvenile Pelvetia and Fucus spiralis plants one to thirty millimetres long appear annually in large patches completely covering the rock.

In the case of the isolated juvenile plant which has not yet branched enough for the branches to overlap, rate of tissue dehydration will be determined by surface to mass ratio and thallus shape, and the results of the preceding sections become directly relevant. Laying the samples on the bench top roughly approximates the position in which the plant lies on the shore at low tide, and the results of the determination done with the samples in this positon generally confirmed those obtained with the samples suspended. Since the Pelvetia shape was shown by both methods to be somewhat less advantageous in retarding evaporation than the Fucus blade, and the surface to mass ratio was only slightly lower in very small Pelvetia than in Fucus of the same weight, the isolated juvenile Pelvetia would not be expected to dry more slowly in nature than the isolated juvenile Fucus. In fact such Pelvetia plants are often found in a brittle dry condition at low tide (personal observation).

In the isolated adult plant, habit of growth will determine the degree to which the plant's branches mutually protect each other from the drying atmosphere. The bushy, profusely branched growth form of Pelvetia contrasts with the more open growth form of the flat-bladed Fucus species, and has been cited by Isaac (1933) as an adaptation for conserving water. In the present investigation, the difference in the growth form of the two genera was quantified by measuring, weighing and assessing mutual protection by the branches in 160 plants of Pelvetia and 200 of Fucus spiralis. Plants of a wide range of sizes (5 to 167 mm in length) were collected, and care was taken to select complete thalli including the holdfasts. Mutual protection by the branches was assessed by laying the plant on a flat surface and viewing it from above. The degree of branch overlap was assessed subjectively on the following scale:

0 = no branches lying directly above or below other branches.

1 = parts of some branches lying directly below or above others, such overlap involving less than one quarter of total thallus area.

2 = one quarter to one half of the thallus area lying below or above other branches.

3 = over one half of the thallus area lying below or above other branches.

The data for each species was divided into fourteen classes according to length, and the mean weight and mean branch overlap value were calculated for each length class. In all the length classes, Pelvetia was about twice as heavy as Fucus spiralis because of its much more profuse branching (Table 10). The differences between the sample means were significant at the 5% level by the t-test for all except the 70-99.5 mm length class. Overlap of branches is also consistently more marked in Pelvetia than in Fucus spiralis, which often does not form its first dichotomy until it is over 50 mm in length.

The more "bushy" habit of growth of Pelvetia could confer a considerable advantage in water conservation, particularly in plants over 60 mm in length, in which branch overlap is quite extensive. However, Pelvetia takes a longer time to attain a given length than does F. spiralis. Pelvetia requires three to four years to become mature and fertile (Subrahmanyan 1960) by which time it is 80 to 180 mm long, while Fucus spiralis grows to a larger size (150-350 mm) at maturity at an age of two to four years. F. vesiculosus and F. serratus become mature and reach a length of 400 to 1000 mm in a similar time period. At these lengths, the Fucus species usually have many overlapping branches and may be as "bushy" as an adult Pelvetia. Therefore, while isolated adult Pelvetia are much better protected against rapid drying than Fucus of the same size, they are not necessarily better protected than Fucus of the same age. Also the young Pelvetia plant does not develop an effective degree of "bushiness" rapidly. The germling requires about 18 months to reach a length of 30 mm at which point branch overlap is still rather slight. Therefore, a Pelvetia germling growing in an isolated position on the shore is vulnerable to rapid drying throughout at least one entire summer before it becomes "bushy" enough for self-protection to become effective.

Rate of dehydration in a large clump or continuous stand of seaweeds

Table 10: Mean ± standard deviation of weight, and mean branch overlap value of Pelvetia and F. spiralis in fourteen length classes.

| Length class | Pelvetia n | Pelvetia weight, mg | Pelvetia Mean branch overlap | Fucus spiralis n | Fucus spiralis weight, mg | Fucus spiralis Mean branch overlap |
|---|---|---|---|---|---|---|
| 5 - 9.5mm | 14 | 9.4 ± 5.4 | 0.1 | 11 | 4.6 ± 1.8 | 0 |
| 10 - 14.5mm | 11 | 27.3 ± 11.3 | 0.4 | 13 | 11.8 ± 3.4 | 0 |
| 15 - 19.5mm | 17 | 59.0 ± 33.5 | 0.6 | 9 | 21.1 ± 4.4 | 0 |
| 20 - 24.5mm | 17 | 102 ± 48 | 1.2 | 8 | 45 ± 15 | 0 |
| 25 - 29.5mm | 10 | 145 ± 48 | 1.0 | 20 | 63 ± 17 | 0 |
| 30 - 34.5mm | 12 | 192 ± 85 | 1.2 | 12 | 85 ± 18 | 0 |
| 35 - 39.5mm | 17 | 215 ± 61 | 1.4 | 16 | 114 ± 23 | 0 |
| 40 - 44.5mm | 13 | 350 ± 104 | 1.5 | 15 | 171 ± 42 | 0.1 |
| 45 - 49.5mm | 7 | 487 ± 166 | 1.8 | 11 | 184 ± 22 | 0 |
| 50 - 59.5mm | 15 | 604 ± 266 | 1.9 | 18 | 300 ± 58 | 0.3 |
| 60 - 69.5mm | 7 | 998 ± 257 | 2.6 | 21 | 431 ± 162 | 0.3 |
| 70 - 99.5mm | 5 | 1728 ± 990 | 2.0 | 22 | 908 ± 402 | 1.0 |
| 100 -119.5mm | 9 | 4251 ± 2366 | 2.7 | 16 | 1613 ± 569 | 1.2 |
| 120 -167 mm | 6 | 6241 ± 2874 | 2.8 | 8 | 2492 ± 596 | 1.1 |

depends on the amount of plant surface exposed to the air per unit biomass, and the evaporation flux from that surface. The laboratory experiments showed that fluxes from surfaces of Pelvetia and Fucus spp. are essentially identical. Therefore, the rapidity with which a continuous stand of Pelvetia or Fucus will become dry throughout during low tide will depend upon the quantity of seaweed per unit surface area of the stand, i.e. its biomass density.

Mean biomass densities reported for Pelvetia are generally equalled or exceeded by those of Fucus spp., and are greatly exceeded by values reported for Ascophyllum (Table 11). However, these values do not

necessarily reflect the extent to which the different species avoid desiccation through aggregation. Two algal stands of the same mean biomass density may differ in the amount of surface area they expose. If one stand consists of a continuous 100% cover and the other consists of dense clumps with much unoccupied primary space between, the latter would expose less surface to the air per unit biomass (Table 11) and would be expected to become dry more slowly. A comparison of biomass density of those stands of the different species which do cover 100% of the substrate would be more informative than a comparison of mean biomass densities. However, if Pelvetia is shown to have the densest 100%-cover stands this alone does not indicate a more effective aggregation strategy. Firstly, the rate of development of these stands is important. If young Fucus populations more rapidly attain a biomass density at which

Table 11: Reported biomass densities of intertidal fucoids, and inferred ratio of exposed surface to biomass.

| Source | Species | Biomass density $kg/m^2$ | Surface exposed per unit biomass ($m^2/kg = mm^2/mg$): Assuming stand is continuous (100% cover | Assuming stand consist of discontinuous clumps covering 50% of substratum |
|---|---|---|---|---|
| Boney 1966 | Pelvetia | 4.2 | 0.24 | 0.12 |
| | Fucus spp | 2.1 | 0.48 | 0.24 |
| Subrahmanyan 1960 | Pelvetia | 3 | 0.33 | 0.17 |
| | F.spiralis | 2.2 to 15 | 0.45 to 0.067 | 0.23 to 0.033 |
| Moore (personal communication) | Pelvetia | 4.5* | 0.22 | |
| Chapman 1970 | Fucus spp | 3 to 8.8 | 0.33 to 0.114 | 0.17 to 0.057 |
| | Ascophyllum | 8 to 18.2 | 0.125 to 0.055 | 0.062 to 0.028 |

* mean value for sixteen quadrats taken in dense 100% cover stands.

mutual protection is effective than do young Pelvetia, then Fucus may have the more effective aggregation strategy even if its mature stands are ultimately less dense than those of Pelvetia. Secondly,

a species may form a dense cover only occasionally, and more frequently cover the substratum with only one or two layers of blades or branches. In this case, the majority of individuals would be directly exposed to the atmosphere. Therefore it is necessary to assess the average degree of mutual protection by aggregation as well as the maximum degree attained in dense stands.

At Isle of Cumbrae, Ascophyllum lies in visibly deeper layers than does Pelvetia at low tide, but the difference between Pelvetia and F. spiralis is too slight to assess qualitatively. A preliminary quantitative comparison of the density of these three species was drawn on a rocky slope at the North Slip. A series of ten short transects were laid out parallel to the slope of the shore, running through the Pelvetia, F. spiralis and upper Ascophyllum belts, and observations were made at points at 10 cm intervals along the transects. At each point along five of the transects, the thickness of the algal cover was measured. In the other five transects, the number of layers of branches lying directly below each transect point was counted. No data was taken for those points along the transect at which two or more fucoid species were present in a mixed stand, or at which there was no fucoid cover.

Ascophyllum and Pelvetia were both found to lie in fairly densely packed layers, with a mean of about five thallus layers lying over a point (Table 12). However the thickness of the Ascophyllum cover

Table 12: Mean ± standard deviation of thickness of cover and number of thallus layers covering a point on the shore for Ascophyllum, F. spiralis and Pelvetia at the North Slip. n = number of observations.

| | n | thickness, mm | n | number of thallus layers |
|---|---|---|---|---|
| Ascophyllum | 41 | 38.5 ± 20.9 | 46 | 4.8 ± 3.2 |
| F. spiralis | 41 | 17.0 ± 10.6 | 42 | 2.7 ± 1.4 |
| Pelvetia | 43 | 15.5 ± 11.0 | 40 | 5.0 ± 3.2 |

averaged more than twice that of either Pelvetia or F. spiralis because the individual fronds of Ascophyllum are much thicker than those of the other two genera. The thicknesses of Pelvetia and F. spiralis covers were similar, but Fucus had significantly fewer layers of blades lying

on the shore. Because of their spiral twisting, the blades of F. spiralis lie more loosely packed, with more space between them, and these spaces contributed to the measured thickness.

From this preliminary assessment, the density of algal cover appears to decrease in the order Ascophyllum > Pelvetia > F. spiralis. However, an important age difference between the F. spiralis and Pelvetia has affected the results. The Pelvetia stand included many mature plants 80-100 mm long bearing receptacles, while the F. spiralis, although of similar size, consisted almost entirely of juvenile plants without receptacles. Therefore, a second comparison was drawn between reproductively mature stands of these two species growing near Farland Bight (Figure 3). Thickness of cover and number of thallus layers were determined as before, except that the transects were laid horizontally through the middle of the Pelvetia and F. spiralis zones. Mean number of thallus layers was about the same in the two species, and thickness was a little greater in F. spiralis (Table 13).

Table 13: Mean ± standard deviation of thickness and number of thallus layers in mature stands of Pelvetia and F. spiralis at Farland Bight. n = number of observations.

| | n | thickness, mm | n | number of thallus layers |
|---|---|---|---|---|
| F. spiralis | 53 | 26.4 ± 11.0 | 40 | 4.7 ± 2.5 |
| Pelvetia | 53 | 21.6 ± 10.8 | 40 | 5.0 ± 2.7 |

However, the relationship between the number of thallus layers and the actual biomass density must be known for each species before any conclusion can be drawn from these results. This relationship was investigated in dense stands of mature and juvenile F. spiralis and Pelvetia at Port Loy. Three 25 x 25 cm quadrats of juvenile F. spiralis and three of fertile Pelvetia were selected. Large patches of continuous 100% cover by juvenile Pelvetia were difficult to find;

therefore four 10 x 10 cm quadrats were taken from young stands and one 25 x 25 cm quadrat from a somewhat older but not fertile stand. The quadrats of fertile plants were located in the densest stands of these two species which could be found at Port Loy. The number of thallus layers was counted under twenty-five points in each of the 25 x 25 cm quadrats, and under eight points for each 10 x 10 cm quadrat. Then the total fresh weight of the plants attached within each quadrat was taken. Finally, the lengths of the ten longest plants were taken to obtain a rough index of the age of the stand.

The results are summarised in Table 14. The estimates of ages are based on numerous observations of growth and development of these two species. Young F. spiralis develops rapidly, growing 5-20 mm/month in culture and in the field, in contrast with Pelvetia which rarely exceeds 10 mm at one year of age. The quadrats were taken on 1 June 1976, and while the young Fucus probably grew from a gamete release which began in March 1975, the young Pelvetia most likely arose from a gamete release in June-September 1974.

Table 14: Thickness in number of thallus layers, biomass density, and ratio of exposed surface area to biomass in juvenile and mature populations of Pelvetia and F. spiralis

| | Length of ten largest plants | Probable age of stand | Mean number of thallus layers | Biomass density kg fresh wt / $m^2$ | Ratio of exposed surface to biomass ($m^2$/kg = $mm^2$/mg) | Biomass density per thallus layer |
|---|---|---|---|---|---|---|
| Pelvetia: | | | | | | |
| Mature | 150-240mm | 4 years | 6.7 | 10.2 | 0.098 | 1.53 |
| Mature | 100-170mm | 3- 4 years | 5.7 | 9.0 | 0.111 | 1.58 |
| Mature | 120-160mm | 3- 4 years | 5.4 | 8.6 | 0.116 | 1.57 |
| Late-Juvenile | 85-115mm | 2- 3 years | 4.9 | 5.0 | 0.20 | 1.01 |
| Juvenile | 40-70mm | 20-24 months | 3.6 | 3.0 | 0.33 | 0.83 |
| Juvenile | 55-75mm | 20-24 months | 4.0 | 3.5 | 0.29 | 0.80 |
| Juvenile | 35-45mm | 20-24 months | 3.6 | 3.0 | 0.33 | 0.83 |
| Juvenile | 30-40mm | 20-24 months | 3.2 | 4.0 | 0.25 | 1.25 |
| F. spiralis | | | | | | |
| Mature | 170-275mm | 2- 3 years | 5.4 | 7.2 | 0.14 | 1.34 |
| Mature | 200-280mm | 2- 3 years | 4.9 | 11.2 | 0.089 | 2.28 |
| Mature | 200-250mm | 2- 3 years | 6.3 | 12.6 | 0.079 | 2.01 |
| Juvenile | 65- 90mm | 15 months | 3.4 | 2.6 | 0.38 | 0.76 |
| Juvenile | 80- 95mm | 15 months | 3.7 | 2.9 | 0.35 | 0.78 |
| Juvenile | 85-115mm | 15 months | 3.4 | 3.8 | 0.26 | 1.11 |

The estimate of fifteen months for the age of the young Fucus stands may be somewhat high, as shown by observations of recolonization of the Millport Marine Biological Station boat slip. The boat slip was cleared of macroalgae in February 1974, and F. spiralis zygotes settled on the upper part in June of that year. The longest F. spiralis plants reached a length of 92-176 mm by July 1975, at an age of 13 months (J.J.P. Clokie personal communication).

Considerable mutual protection through aggregation was apparent in all stands of both species. The ratio of exposed surface to biomass in the juvenile stands was less than one tenth as great as in the suspended individual plants (compare Tables 14 and 7), and therefore less than one fifth as great as that of individual plants lying on a flat surface.

The biomass density and the number of thallus layers of the 20-24 month old stands of Pelvetia were very similar to those of the 15 month old F. spiralis stands. The fertile stands of the two species were also roughly equal in these two parameters. The fertile Pelvetia quadrats contained some of the largest Pelvetia plants I have observed at Isle of Cumbrae, and their biomass density exceeded those found by Subrahmanyan (1960) and G. Moore (personal communication). Thus they probably represent a maximal density of stand for this species.

The quadrats containing fertile F. spiralis did not include the largest individuals of F. spiralis observed at Port Loy, where specimens up to 600 mm long have been found. The quadrats yielded biomass densities within the range given by Subrahmanyan (1961) and may not represent the maximum attained by this species. Therefore, the maximum density in Pelvetia stands is at most equal to that in Fucus spiralis stands, and mutual protection from desiccation is no greater in continuous stands of Pelvetia than in those of F. spiralis. Also since the fifteen month old stands of Fucus had nearly as high a biomass density as did the 20-24 month old stands of Pelvetia, it is clear that young F. spiralis reach a "refuge in high density" more rapidly than young Pelvetia.

The biomass per thallus layer was greater in adult stands than in juvenile stands, but was similar in adults of the two species, and

in juveniles of both species. Therefore, the number of thallus layers constitutes a valid basis of comparison for the densities of F. spiralis and Pelvetia although it is less precise than biomass.

The average degree of mutual protection through bushiness and aggregation was assessed by running a series of transects through the Pelvetia and F. spiralis bands, including both mature and young plants, and areas of dense and thin cover. At five centimetre intervals, the number of thallus layers was counted as before. Transect points over bare rock and over mixed Fucus and Pelvetia were excluded. Several transects were taken between Farland Point and Port Loy, and several more at the North Slip (see Figure 3 ). The mean number of thallus layers was calculated for each species at each site, and the frequency with which only one or two layers occurred was noted.

There was no statistically significant difference between Pelvetia and F. spiralis in mean number of thallus layers at either site (Table 15), which supports the conclusion drawn from the biomass measurements. One or two thallus layers occurred about as often in Pelvetia as in F. spiralis, indicating that a similar percentage of fronds of each species lies directly exposed to the drying atmosphere with little or no protection from other fronds.

Table 15: Number of thallus layers in Pelvetia and F. spiralis at two shores on Isle of Cumbrae

| | North Slip | | Farland Point | |
|---|---|---|---|---|
| | Pelvetia | F. spiralis | Pelvetia | F. spiralis |
| number of observations | 80 | 105 | 51 | 70 |
| number of observations with: | | | | |
| one layer: | 14 (17.5%) | 16 (15.2%) | 10 (19.6%) | 16 (22.1%) |
| two layers: | 14 (17.5%) | 11 (10.5%) | 13 (25.5%) | 13 (18.6%) |
| three or more layers: | 52 (65.0%) | 78 (74.3%) | 28 (54.9%) | 41 (58.5%) |
| Number of thallus layers: (Mean ± standard deviation) | 4.22 ± 2.86 | 4.15 ± 2.24 | 3.08 ± 1.76 | 3.80 ± 2.48 |

The top layer of blades or branches in any stand, no matter how thick, is directly exposed to the atmosphere, and must be considered vulnerable to damage during hot dry weather. This uppermost layer may be composed either of the tips of the longest branches of many plants, or of a few large plants which lie over and completely protect a large number of smaller plants. Observations of the fucoids on the shore revealed an intermediate situation, with the top layer consisting of the upper portions of the larger plants, and a few branch tips of smaller ones. Fucus plants tend to lie over one another to a somewhat greater extent than Pelvetia, and therefore Fucus stands include more completely exposed 'top' plants and more thoroughly protected smaller plants.

In either case, destruction and removal of the top layer will expose the next layer, and a long enough series of severe drought stresses during successive low tides will destroy the stand altogether. However, severely drought-damaged blades are often observed to persist for several weeks, and even to regenerate and resume growth. This is observed particularly frequently in F. spiralis and the top layer continues to function as a protective layer for some time after being badly affected by a hot spell.

From these observations on the thickness and layering of fucoid stands, it can be concluded that the upshore species have not evolved a greater degree of mutual protection than the midshore fucoids. In fact, the combined protective effects of habit of growth, aggregation and biomass density of mature stands appear to be of similar magnitude in Pelvetia and F. spiralis, and considerably greater in Ascophyllum. Although quantitative data were not obtained for F. vesiculosus and F. serratus, these are also large plants, and lie in visibly thicker layers than the upshore fucoids, although not as thick as Ascophyllum.

### 3.3.7 Vulnerability to desiccation in nature: some observations on first year plants

Most of the first-year plants of Pelvetia and F. spiralis appear annually in late winter as large patches of densely packed germlings

near and above MHWN, as shown in Plate 8. The tiny plants in these patches dry much more slowly than isolated plants of a similar size, and therefore employ a strategy of mutual protection. This is not observed in midshore fucoid germlings which often appear singly or in small groups (Plate 9). Since the crowded patches of tiny fucoids have a much smaller biomass density than mature stands, they would be expected to dry out much more quickly than the adult stands. However, the reverse is often observed. The first year plants are often found in locations where they are partly protected from the sun and wind by the aspect of topography of the rock, or by neighbouring clumps of adult plants. This is observed especially in Pelvetia, whose patches of first year plants often remain damp long after the top layers of older plants have become quite dry. The clumps of adult plants project several centimetres above the surface of the rock and may effectively break the wind so that pockets of static humid air can accumulate over the juvenile plants thus reducing the vapour pressure deficit in their vicinity.

A well developed "turf" of first year Pelvetia is never found directly beneath large plants where the protection from drying would be far greater. However, microscopic examination of scrapings taken from the rock directly beneath the distal portions of such large Pelvetia revealed numerous, dark-coloured Pelvetia embryos 200 to 600 µm long. Since these scrapings were taken in May and Pelvetia gametes are released between June and September, these embryos had persisted and grown very slowly beneath the adult plants for at least eight months. Their slow growth may be related to the reduced availability of light under the larger plants. When the canopy of adult plants was experimentally removed, the embryos were observed to become lighter in colour and to grow noticeably larger over a two month period. Greatly protected by the large overlying plants, these tiny plants may act as a reserve in case extreme conditions kill off the "turf" of first year plants growing elsewhere in the Pelvetia zone.

A "reserve" strategy of a slightly different type is observed in the first-year stands of F. spiralis. The first severe desiccation in spring usually occurs in April. At this time the largest germlings of F. spiralis derived from the previous summer's gamete release generally


Plate 8: Dense stands of young Pelvetia and F. spiralis on the upper shore at the North Slip, photographed June 15th, 1976. P1 = Pelvetia from 1975 gamete release, P2 = Pelvetia probably from 1974 gamete release, F1 = Fucus spiralis from 1975 gamete release.

Plate 9: Young *Fucus* spp. growing singly and in small groups in turf of the red alga *Gigartina stellata* on the middle shore. Photograph was taken June 15th, 1976 at the North Slip.

exceed 20 mm and can effectively lie over and protect the smaller individuals during low tide. The top layer of plants in first year stands of F. spiralis are often severely damaged or killed by spring dry spells. However, I have examined a number of such badly damaged young stands and have invariably found many unharmed F. spiralis plants beneath those which had been killed. These plants are smaller and much darker in colour than those in the top layer, but they grow and replace the plants lost during the drought (Plate 10). Viable germlings are often present in stands more severly burned than that in the photograph. Careful examination of a sample of apparently dead F. spiralis collected at about 2.85m above chart datum in summer 1975 revealed some very small plants with live tissue near the midrib and apex. The tips of these plants regenerated and grew several millimetres during thirty days in culture. The number of these small "reserve" plants decreases as the stand grows larger and older, but a few plants 5 to 50 mm long are sometimes found even beneath mature fertile populations of F. spiralis.

These strategies cannot protect the tiny plants from tissue desiccation at all times, since the entire stand of Pelvetia or F. spiralis sometimes becomes air-dry in nature. However, the rate at which the young plants lose their water is effectively reduced by the protection. Rapidity of water loss as well as total percentage of tissue water lost may determine whether drought injury occurs in many lower and higher plants (Levitt 1972), and may be critical in the case of young fucoids.

### 3.3.8 Maximum tissue dehydration in nature

Since Pelvetia and F. spiralis appear to lose their "volatile water" as readily as most other lower plants, their tissues must reach (ie. very negative) value of a very low water potential during lengthy exposure to warm dry weather. In order to determine how dry Pelvetia and F. spiralis can become in nature, ten samples of each were collected during a hot spell in August 1976 which coincided with neap tides. They were transported to the laboratory in airtight plastic bags, and weighed immediately. They were then dried for four days over silica gel and reweighed to determine how much water per 100 grams dry matter the plants had

A

B

C

Plate 10: "Reserve" strategy in young Fucus spiralis.

A. Stand of young F. spiralis at the North Slip shore showing persistence of a severely drought-damaged top layer of plants. The photograph was taken May 31st 1976, about four weeks after damage first became evident.

B. The same stand, photographed the same day after the top layer was removed, revealing smaller, healthy plants underneath.

C. The same stand photographed July 19th. The "reserve" plants have remained healthy and have grown somewhat despite severe drought in late June and early July.

contained at the time of collection. This water content was compared with the colloidal water contents found in laboratory determinations at different water potentials (Table 8) in order to estimate the water potential the plants had reached in nature. Other samples collected from the same place at the same time were cultured for about ten days in order to determine whether the naturally dried material was still alive. A similar determination was performed for Pelvetia during a dry but cooler spell in June 1976.

The results show that these plants may lose 90-95% of their water under natural conditions, reaching very low water potentials, yet can tolerate this stress (Table 16). The tissue water potentials attained on 9 June and 20 August compared roughly to "air-dryness" at relative humidities of 75 and 40-50% respectively, values which are frequently realized in the atmosphere under normal conditions. Clearly, the main adaptation of Fucus spiralis and Pelvetia to their difficult upshore habitat is one of drought tolerance, i.e. the ability to survive in a state of air-dryness during prolonged exposure.

### 3.4 Relationship between drought tolerance and vertical distribution on the shore

The ability of different fucoid species to tolerate tissue desiccation was initially compared by means of photosynthesis measurements before and after drying, as described in section 2.6.2. Three or four samples each of Pelvetia, F. spiralis, Ascophyllum and F. serratus were dried in the laboratory for twenty-six hours, then placed directly in sample bottles and incubated for two hours to determine their oxygen evolution rates. These were compared with oxygen evolution rates by other samples of the same four species which had not been dried. The ability of the four species to photosynthesize immediately after desiccation differed greatly, and the differences related precisely to their order of occurrence on the shore: Pelvetia > F. spiralis > Ascophyllum > F. serratus (Table 17). In particular, Pelvetia and F. spiralis, which are often exposed for longer than twenty-six hours in nature, showed a net positive oxygen evolution, while Ascophyllum and F. serratus which are normally submerged twice daily, remained below

Table 16: Colloidal water content, approximate percent water loss, and approximate tissue water potential of fucoid samples collected after prolonged desiccation in nature. Mean ± standard deviation is given for colloidal water content.

| Species and Date collected | n | Approximate level from which samples were collected | No. of days the algae had been continuously exposed | Weather conditions on day algae were collected | "colloidal" water content grams/100g dry matter | Approximate tissue water potential | Approximate percent of tissue water lost* | Condition of naturally dried plants after 10 days in culture |
|---|---|---|---|---|---|---|---|---|
| F. spiralis | | | | | | | | |
| 20 Aug 1976 | 10 | 2.8m | 2 | clear, maximum temperature 25.4°C | 12.6 ± 1.0 | -900 to -1200 bars | 95.8 | Damaged but regenerating |
| Pelvetia | | | | | | | | |
| 20 Aug 1976 | 10 | 3.1m | 4 | | 10.3 ± 0.7 | -1200 to -1300 bars | 95.6 | Some plants slightly damaged, all surviving |
| Pelvetia | | | | | | | | |
| 9 June 1976 | 10 | 3.2m | 3 | Cloudy, maximum temperature 16.8°C | 24.0 ± 1.3 | -350 to -400 bars | 89.7 | Little damage |

*Calculated by assuming fully hydrated Pelvetia is about 30% dry matter and F. spiralis about 25%, which are typical summer values for these species.

the compensation point. The oxygen concentrations measured in the sample bottles in this determination may have been somewhat low because the algal samples were left in the bottle when the chemical reagents were added. However, the large differences between the four species after desiccation were not found in the controls, and were therefore not an artefact of this source of error.

Table 17: Oxygen evolution rate in μmoles $O_2$/g.wet wt. - hour of Pelvetia, Fucus spiralis, Ascophyllum and F.serratus with and without drying immediately before incubation. The experimental plants were dried for 26 hours at 19-21°C, 66-73% relative humidity, water potential -425 to -565 bars.

| | Without drying | | After drying | |
|---|---|---|---|---|
| | Rates for individual samples | Mean | Rates for individual samples | Mean |
| Pelvetia | 13.7, 13.4, 13.1, 13.0 | 13.3 | 10.9, 9.0, 8.9, 6.8 | 8.9 |
| F.spiralis | 10.8, 9.2, 8.9 | 9.6 | 3.8, 2.1,-0.2 | 1.9 |
| Ascophyllum | 11.3, 8.0, 7.0, 6.8 | 8.3 | 0.6,-1.0,-2.6,-4.9 | -2.0 |
| F.serratus | 10.8, 8.6, 8.4, 8.1 | 9.0 | -3.3,-7.7,-7.8,-9.2 | -7.0 |

The large difference between Pelvetia and F. spiralis in ability to evolve oxygen immediately after desiccation was reinvestigated as follows. Oxygen evolution of three plants of each species was measured and the plants were then desiccated for three hours in the warm culture room. Five other plants of each species were dried over the same period of time and their remaining water content measured to determine whether the two species had become equally dry in three hours. Pelvetia lost 96.4 ± 0.2% of its water, and F. spiralis 96.3 ± 0.4%, indicating that their tissues had been subjected to similar degrees of dehydration.

The three plants of each species whose photosynthetic rates had been measured before drying were incubated again for three one-hour intervals beginning immediately after resubmergence. The oxygen

evolution rates of each plant during each hour was expressed as a percentage of its rate before drying (Figure 20). Pelvetia recovered a little more rapidly than F. spiralis during the first two hours after drying, but the difference was less pronounced than in the first determination. Also, the two species were similar in the third hour, during which photosynthesis rates in the Pelvetia samples were slightly lower than in the preceding hour for reasons which are not known.

These results pertain only to the immediate effect of the drying upon photosynthetic rate. The midshore species might still be capable of recovery after a longer period in seawater, or, conversely, the upshore species may suffer damage despite an initial positive rate of oxygen evolution. In order to determine whether a delayed recovery occurs, samples of Pelvetia, F. spiralis and Ascophyllum were dried for twenty-four hours, and allowed to recover for four hours in seawater before their oxygen evolution rates were measured. Considerable recovery was evident in all three species, and Ascophyllum showed a net positive oxygen evolution (Table 18). The large difference between Pelvetia and F. spiralis shown in Table 17 was abolished by the recovery period during which both species returned fully to their normal rates. Apparently, neither species is damaged by twenty-four hours drying under moderate conditions, although Pelvetia may resume normal photosynthetic rates more promptly after resubmergence.

Table 18: Mean ± standard deviation of oxygen evolution rate in μmoles $O_2$/gram wet wt. - hour of Pelvetia, Fucus spiralis, and Ascophyllum with and without twenty-four hours drying and four hours recovery in seawater. The experimental plants were dried at 19-21°C, 65-70% relative humidity, water potential -480 to -580 bars.

| | Without drying | | After drying | |
|---|---|---|---|---|
| | n | Oxygen evolution rate | n | Oxygen evolution rate |
| Pelvetia | 5 | 13.7 ± 2.6 | 8 | 14.3 ± 1.6 |
| F. spiralis | 5 | 9.6 ± 2.3 | 8 | 11.8 ± 0.9 |
| Ascophyllum | 5 | 8.2 ± 1.5 | 8 | 3.7 ± 1.8 |

This finding is not surprising since natural populations of both upshore species endure exposures longer than this during neap tides. The higher-growing plants of F. spiralis are often exposed for two or

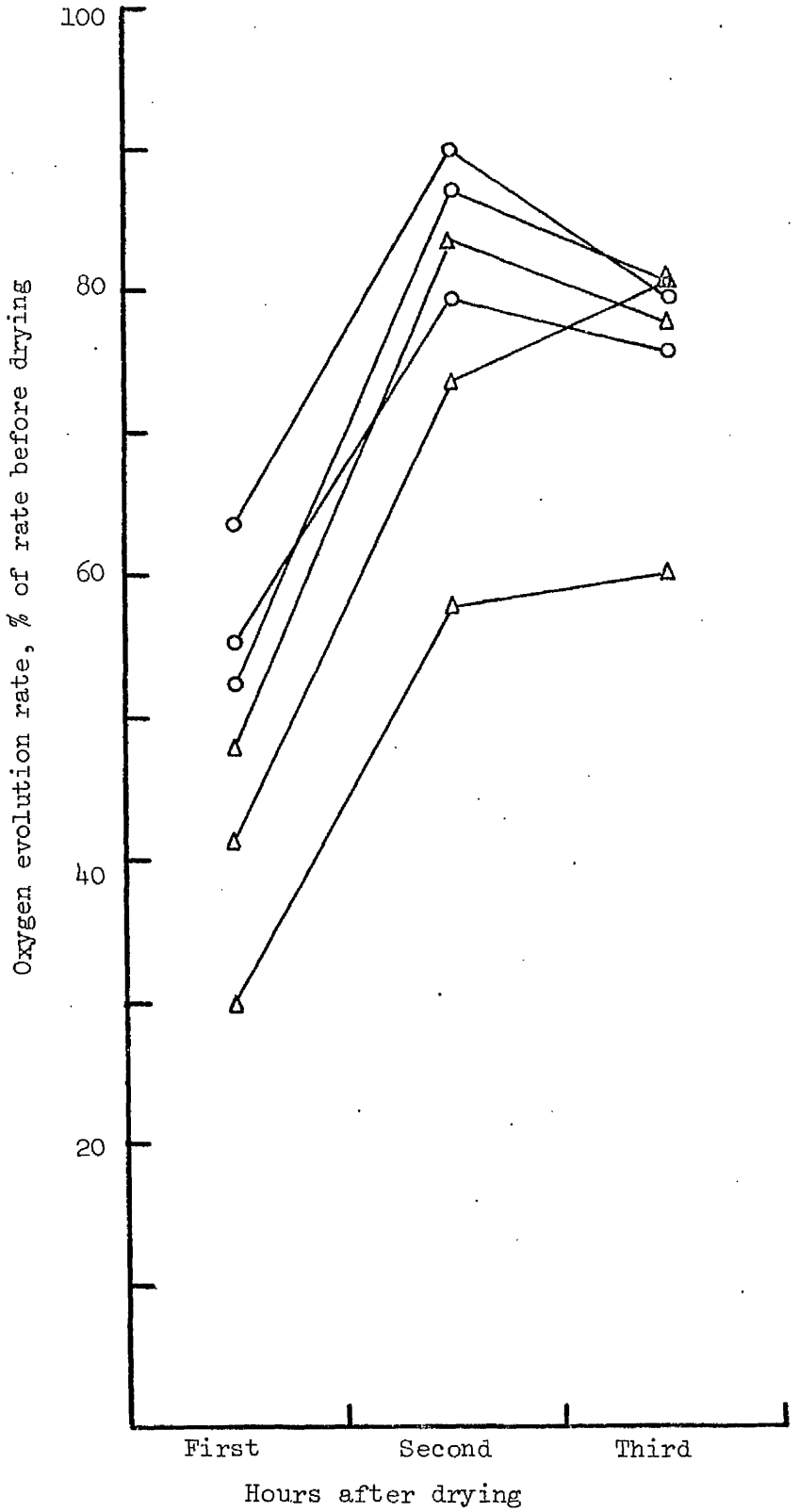



Figure 20. Recovery of photosynthetic rate in three plants each of Pelvetia (o) and Fucus spiralis (Δ) after three hours drying at 24.9 - 26.1°C, 44-50% relative humidity, water potential -950 to -1135 bars.

three days, while Pelvetia may be exposed for a week or longer. Therefore, a difference between these two species in degree of recovery might be expected after desiccation for about four days. An experiment was undertaken to test this hypothesis. Ten plants of each species were selected and their photosynthetic rates measured. They were then dried in the laboratory for ninety hours and resubmerged for ten hours before their photosynthetic rates were remeasured. In this determination, the algal samples were withdrawn from the bottles just before the chemical solutions were added, so that the actual values for oxygen evolution are more accurate than those given in Tables 17 and 18.

Pelvetia recovered most of its photosynthetic capacity during the ten hour resubmersion, while F. spiralis recovered only about one third, and the difference between the two species was highly significant. (Table 19). Rates of photosynthesis measured even after ten hours recovery may not reflect the long term effects of desiccation. A plant which can evolve much oxygen after a given stress may yet be unable to simultaneously fix carbon, or might have suffered damage to other metabolic pathways. Hence rate of oxygen evolution may not be a reliable index of survival unless it is correlated with the plants' subsequent survival and growth rate. To determine whether this correlation

Table 19: Oxygen evolution rate in μmoles $O_2$/gram wet wt.-hour of Pelvetia and F. spiralis before and after ninety hours drying and ten hours recovery in seawater. Figures represent mean ± standard deviation. The plants were dried at 20 to 27°C, relative humidity not recorded.

| | n | Rate before drying | Rate after drying | Percent of original rate |
|---|---|---|---|---|
| Pelvetia | 10 | 23.3 ± 2.2 | 19.8 ± 1.6 | 86 ± 7 |
| F. spiralis | 10 | 19.8 ± 4.6 | 6.4 ± 4.6 | 34 ±26 |
| t | | 2.17 | 8.58 | 5.99 |
| p | | ∿ 0.06 | < 0.001 | < 0.001 |

exists, the effects of desiccation on Pelvetia, F. spiralis and F. serratus were assessed by oxygen evolution rates and by three other criteria: initial weight change, condition of the thallus after ten

days in culture, and relative weight gain during that period. After their initial oxygen evolution rates were determined, five plants of each species were dried for five hours at 25.5 - 27°C in the warm culture room. A second set of samples were dried simultaneously and their remaining water content measured. This measurement showed that the three species underwent similar degrees of dehydration during the five hour exposure (Table 20).

The second photosynthesis measurement was taken after eighteen hours recovery in seawater following the experimental stress. Then the plants were reweighed to calculate the initial weight change, and cultured for ten days.

Recovery of photosynthetic capacity correlated well with all three other criteria of survival (Table 21), and therefore appears to be a reliable test of the effects of drought stress on fucoids. Furthermore, all four assessments indicated once again that drought tolerance of these three species correlates with their vertical distribution on the shore. The occurrence of sublethal damage in F. spiralis after only five hours drying conflicts somewhat with earlier results. This determination was performed on material collected in

Table 20: Remaining water content in Pelvetia, Fucus spiralis and F. serratus after five hours drying at 25.5 - 27°C, 48-52% relative humidity, water potential -900 to -1015 bars. Figures represent mean ± 1 standard deviation.

| | n | Percent of water content retained | Grams water per 100 grams dry matter |
|---|---|---|---|
| Pelvetia | 10 | 3.5 ± 0.2 | 13.2 ± 0.6 |
| F. spiralis | 10 | 3.2 ± 0.2 | 13.3 ± 0.4 |
| F. serratus | 8 | 2.9 ± 0.3 | 13.1 ± 1.8 |

February, while those summarized in Tables 17 - 19 were done in June - July, which suggests that drought tolerance may vary seasonally. This possibility will be examined in greater detail in section 3.8

Table 21: Effects of desiccation on Pelvetia, Fucus spiralis and F. serratus assessed by oxygen evolution rates, survival and growth rates (mean ± standard deviation). Oxygen evolution rate μmoles $O_2$/gram wet wt. - hour

| | n | before drying | After 5 hrs drying α and 18 hrs recovery in seawater | Percent of original rate | Initial weight change, % | relative weight gain in 10 days % | condition of thalli at end of 10 days in culture |
|---|---|---|---|---|---|---|---|
| Pel. | 5 | 23.3 ± 2.7 | 20.6 ± 2.1 | 90 ± 18 | -3.8 ± 1.3 | 31.7 ± 11.8 | Good |
| F.sp. | 5 | 29.0 ± 7.2 | 13.5 ± 4.5 | 45 ± 18 | -10.9 ± 3.1 | 2.6 ± 15.3 | damaged, especially near tip: |
| F.se. | 5 | 24.7 ± 2.6 | 0.0 ± 2.4 | 0 ± 10 | -22.7 ± 3.2 | - | dead |

α plants dried at 25.5 - 27°C, 48-52% relative humidity

It was stated in the introduction that the shore gradient is characterized mainly by increasing duration of stress with distance upshore rather than increasing intensity. If this statement is interpreted strictly, one might infer that all fucoids can tolerate being dehydrated to air-dryness, but that different species can survive in this condition for different periods of time. This hypothesis was tested by experiment. Seventeen to eighteen samples each of Pelvetia, Fucus spiralis and the midshore species F. vesiculosus were dried in the warm culture room whose temperature (24-27°C) and relative humidity (40-60%) are very similar to those attained during the hottest summer weather at Isle of Cumbrae (Table 6, section 3.2). Two or three plants of each species were left exposed in the warm room for seventy hours and weighed at intervals in order to determine how quickly they became air-dry. The weights of these plants showed only minor fluctuations after five hours with no consistent downward trend, indicating that the samples had become essentially air-dry within that time (Table 22).

Table 22: Changes in weight of samples of Pelvetia, F. spiralis and F. vesiculosus during exposure at 23.8 - 26.7°C, 50-59% relative humidity, water potential - 720 to -970 bars.

Weight in milligrams

| hours exposed | Pelvetia | | Fucus spiralis | | | F. vesiculosus | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 1 | 2 | 3 | 1 | 2 | 3 |
| 5 | 104.3 | 35.2 | 103.0 | 74.0 | 52.3 | 84.7 | 90.9 | 42.5 |
| 6.5 | 104.2 | 35.4 | 102.8 | 73.9 | 52.4 | 84.6 | 90.8 | 42.4 |
| 13 | 103.3 | 35.2 | 102.0 | 73.5 | 52.0 | 83.7 | 90.0 | 42.0 |
| 23 | 102.8 | 34.8 | 101.5 | 73.0 | 51.5 | 83.1 | 89.3 | 41.5 |
| 35 | 105.0 | 35.5 | 103.4 | 74.3 | 52.5 | 84.4 | 90.6 | 42.2 |
| 49 | 105.3 | 35.7 | 103.9 | 74.8 | 52.9 | 84.4 | 90.7 | 42.0 |
| 70 | 104.8 | 35.5 | 103.0 | 74.3 | 52.5 | 83.5 | 89.5 | 41.7 |

Groups of five F. vesiculosus plants were removed from the warm room and placed in culture after six, twelve and twenty-four hours exposure, i.e. roughly one, seven and nineteen hours after becoming air-dry. Five plants each of Pelvetia and F. spiralis were taken after twelve, twenty-four and forty-eight hours. The two Pelvetia and three F. spiralis used to monitor weight changes over seventy hours were also placed in culture, and all plants were grown for nine days thereafter. Since the plants that were dried for shorter periods spent correspondingly longer times in culture, mean linear growth and percent weight gain of each group of samples was calculated as follows:

$$\text{Mean growth in 10 days} = (\text{mean growth})(^{10}/\text{number of days in culture})$$

Both Pelvetia and F. spiralis survived desiccation to air-dryness, but they differed greatly in the duration for which they could tolerate this stress (Table 23). F. spiralis was killed by a forty-eight hour exposure which did not affect Pelvetia. F. vesiculosus was severely damaged but survived when exposed just long enough to become air-dry, and was killed when it remained dry for an additional six hours. In a separate

determination, Ascophyllum also survived being air-dried briefly in the warm room, and was only slightly affected by a similar drying at a somewhat lower temperature (Table 24). The Ascophyllum plants were grown in culture dishes without aeration; hence observed growth rates may be somewhat slower than they would have been in aerated culture.

Table 23: Survival and growth of Pelvetia, Fucus spiralis and F. vesiculosus (mean ± standard deviation) after drying for varous periods of time at 23.8 - 26.7°C, 50-59% relative humidity, water potential -720 to -970 bars.

| Species | duration of exposure | n | Initial weight change | Linear growth mm/10 days | Relative weight gain, %/10 days | Condition of thalli at end of ten days |
|---|---|---|---|---|---|---|
| Pel. | 12 hrs | 5 | - 4.1 ± 0.4 | 3.0 ± 0.7 | 25.0 ± 2.3 | excellent |
| | 24 hrs | 5 | - 3.2 ± 0.7 | 3.2 ± 0.5 | 28.7 ± 3.2 | excellent |
| | 48 hrs | 5 | - 5.1 ± 0.7 | 2.5 ± 0.7 | 22.4 ± 1.7 | excellent |
| | 70 hrs | 2 | - 9.2 | not measured | - 6.1 | damaged, but alive |
| F.sp. | 12 hrs | 5 | -13.4 ± 1.1 | 4.3 ± 1.3 | 16.2 ± 6.9 | slightly damaged |
| | 24 hrs | 5 | -16.8 ± 4.4 | -0.9 ± 2.8 | -14.9 ± 9.6 | damaged, but alive |
| | 48 hrs | 5 | -24.2 ± 2.8 | - | - | dead |
| | 70 hrs | 3 | -23.7 | - | - | dead |
| F.ves. | 6 hrs | 5 | -14.2 ± 5.3 | 0 ± 2.2 | - 6.3 ±10.6 | damaged, 4 definitely alive |
| | 12 hrs | 5 | -26.4 ± 6.0 | - | - | dead |
| | 24 hrs | 5 | -22.0 ± 7.0 | - | - | dead |

Table 24: Remaining water content, survival and growth of Ascophyllum (mean ± standard deviation) after seven hours drying at two different temperatures and water potentials.

| | Remaining water content | | | Survival and growth | | | | |
|---|---|---|---|---|---|---|---|---|
| Treatment | n | % of original water content | Grams per 100 grams dry matter | n | Initial weight change | Linear growth mm/10 days | Relative weight gain %/10 days | Conditions of Thalli at end of ten days |
| Dry 7 hrs at 25.5-26.5°C, 54-56% relative humidity, water potential -800 to -850 bars | 5 | 5.0 ± 0.5 | 16.3 ± 2.0 | 10 | -7.0 ± 1.3 | 0.3 ± 0.5 | 0.7 ± 5.9 | 6 plants somewhat damaged, 4 pl good |
| Dry 7 hrs at 19-19.5°C, 62-66% relative humidity, water potential -560 to -645 bars | 5 | 6.2 ± 0.5 | 19.4 ± 1.9 | 10 | -5.5 ± 2.1 | 1.3 ± 1.1 | 8.1 ± 3.7 | good |
| Controls (not dried) | | | | 10 | | 1.4 ± 0.5 | 12.3 ± 3.6 | good |

Apparently, extreme dehydration is not immediately lethal to fucoids with the possible exception of F. serratus. However, some physiological change occurs in the air-dry thallus which results in cumulative damage with time. This process takes place rapidly in midshore fucoids, fairly slowly in F. spiralis and very slowly in Pelvetia.

The maximum durations of exposure which Pelvetia and F. spiralis tolerated in this experiment were shorter than the longest tidal exposures at their upper limits on the shore. The highest growing F. spiralis may be exposed for up to seven days (Figures 5.7.9, section 3.2), yet this species survived only twenty-four hours when exposed in the warm culture room. Also Pelvetia, which may be exposed for several weeks in nature, was somewhat damaged after seventy hours in the experiment. However, both species were clearly distinguished from F.vesiculosus in that the former survived a twenty-four hour exposure under severe conditions while the latter, which is normally submerged twice daily in nature, did not.

Fucoids appear to suffer less when exposed under slightly cooler and more humid conditions (Tables 18, 19, 24). Therefore, an experiment was undertaken to determine whether they could survive very long tidal exposures in a mildly desiccating atmosphere. Samples of Pelvetia, F. spiralis and F. serratus were exposed for seven days in a cool culture room (6-9°C, 79-81% relative humidity). F. serratus was killed, but F. spiralis suffered only moderate damage and Pelvetia was unharmed by this exposure (Table 25).

Table 25: Survival and growth of Pelvetia, Fucus spiralis and F.serratus (mean ± standard deviation) after seven days exposure at 6-9°C, 79-81% relative humidity, water potential -275 to -305 bars.

| | Initial weight change, % | Linear growth, mm in 13 days | Relative weight gain,% in 13 days | Conditions of thalli at end of 13 days |
|---|---|---|---|---|
| Pelvetia | -1.5 ±1.2 | 4.5 ± 0.7 | 46.2 ± 4.6 | Good |
| F.spiralis | -11.7 ± 2.9 | 4.1 ± 1.7 | 13.7 ±12.1 | somewhat damaged near ti |
| F.serratus | -26.7 ± 2.3 | - | - | dead |

Clearly, temperature and water potential influence the rate at which adverse physiological change occurs in the air-dry thallus. The effects of these two parameters will be considered in greater detail in the following two sections.

## 3.5 Effect of temperature during exposure on survival

In order to determine whether high temperatures might aggravate the effect of desiccation, samples of Pelvetia and F. spiralis were dehydrated for twenty-four hours at two different temperatures but at the same water potential. Since the vapour pressure deficit at a given water potential is related to temperature, fully hydrated samples would require much longer to become air-dry at the lower temperature than at the higher. Therefore, the plants were weighed and left exposed in the laboratory for about two hours in order to remove the majority of their tissue water. Then ten plants of each species were placed in a desiccator in the cool culture room ($9^{\circ} \pm 1^{\circ}C$) over a sulphuric acid solution which gave a humidity of 73.8% at this temperature, and a water potential of -395 bars. At the same time ten more samples of each were placed in a second desiccator in the warm culture room ($25^{\circ} \pm 1^{\circ}C$) and maintained at 75% relative humidity, water potential -395 bars. The two desiccators were positioned so as to receive roughly the same illumination, and were covered with opaque black polythene in the evening and uncovered the next morning so as to provide identical light regimes.

After the desiccation, the plants were soaked for 20 hours, weighed and cultured for ten days. Dehydration to -395 bars exerted a greater effect upon F. spiralis at $25^{\circ}C$ than at $9^{\circ}C$ (Table 26). Pelvetia grew well after drying at both temperatures, but it showed a significant initial weight loss only at the higher temperature.

Since Pelvetia was quite resistant to drying for twenty-four hours, samples were dried for fourteen days at -950 bars water potential to determine whether temperature affects their ability to survive such a long exposure. The plants survived this stress at $9^{\circ}C$ and underwent

only a small initial weight change (-4.0 ± 2.7%, n=5). At 25°C the plants were killed (initial weight change -22.6 ± 3.5%, n=4). Apparently, the higher temperature accelerates damaging physiological change in air-dried seaweeds.

Table 26: Survival and growth of Pelvetia and Fucus spiralis (mean ± standard deviation) after drying for twenty-four hours at a water potential of -395 bars at temperatures of 9°C and 25°C. Table includes t test for significance in differences between the two treatments. * = $p < 0.05$ *** = $p < 0.001$

| | n | Initial weight change, % | Linear growth, mm in 10 days | Relative weight gain, % in 10 days | Condition of thalli at end of 10 days |
|---|---|---|---|---|---|
| Pelvetia | | | | | |
| 9°C | 10 | +0.3 ± 1.7 | 4.0 ± 0.8 | 37.1 ± 7.0 | Generally good |
| 25°C | 10 | -7.4 ± 1.9 | 3.3 ± 0.8 | 31.4 ± 7.1 | Generally good |
| t | | 3.01* | 1.95 | 1.80 | |
| Fucus spiralis | | | | | |
| 9°C | 10 | -3.4 ± 1.6 | 7.2 ± 1.5 | 51.0 ± 9.8 | Good |
| 25°C | 10 | -13.4 ± 3.0 | 3.7 ± 1.4 | 20.1 ± 11.7 | Tips narrowed 4 plants damaged |
| t | | 9.26*** | 5.38*** | 6.41*** | |

It was initially assumed that the plants would contain the same amount of tissue water when air-dried at different temperatures to the same water potential. In order to test this assumption, colloidal water content was measured at 25° and 9°C at a series of four different water potentials. Three samples each of Pelvetia and F. spiralis were used for each combination of temperature and water potential. Colloidal water content was found to be greater at 9°C than at 25°C at intermediate potentials, while this difference was much smaller at -1100 bars, and was apparently reversed at -395 bars (Table 27). Therefore, one of the effects of the higher temperature is to change the hygroscopic properties of the algal tissues, thus altering tissue water content at a given water potential.

Table 27: Colloidal water in grams per 100 grams dry matter in samples of Pelvetia and F. spiralis air-dried at 9°C and 25°C at four different water potentials. Each value listed represents a single sample.

| Water Potential | Pelvetia | | Fucus spiralis | |
|---|---|---|---|---|
| | 25°C | 9°C | 25°C | 9°C |
| -395 bars | 37.7 | 35.4 | 39.7 | 35.2 |
| | 36.1 | 32.3 | 37.6 | 33.5 |
| | 34.8 | 31.2 | 34.0 | 31.6 |
| -595 bars | 21.9 | 22.7 | 21.6 | 24.0 |
| | 21.0 | 22.6 | 20.6 | 23.1 |
| | 20.7 | 22.3 | 19.9 | 22.6 |
| -820 bars | 15.2 | 18.2 | 16.0 | 18.3 |
| | 15.2 | 17.4 | 16.0 | 17.7 |
| | 15.0 | 17.4 | 13.9 | 17.7 |
| -1100 bars | 12.1 | 12.3 | 11.8 | 12.2 |
| | 11.9 | 12.1 | 11.5 | 12.1 |
| | 11.8 | 12.0 | 11.3 | 11.8 |

In order to determine whether high temperature accelerates harmful physiological changes at a given tissue water content, the experiment was repeated with the following modification. The samples at 9°C were maintained at a potential of -960 bars and those at 25°C at -775 bars, since the data in Table 27 suggest that these two regimes would give approximately equal tissue water contents. All samples were first equilibrated for eight hours in the laboratory (20.5 - 22.0°C, water potential -940 to -945 bars) and weighed. Ten plants of each species were then put into each treatment for a further eleven hours, and weighed again. Since it is safe to assume that the samples had reached their equilibrium water contents after eight hours in the laboratory, any difference in tissue water content between the samples after the 9°C and the 25°C treatments could be detected by comparing final air-dry weights of the plants in each treatment with their weights after drying in the laboratory. The amounts by which the plants' weights did change while in the desiccators were similar for the two treatments

(Table 28), and the samples had therefore reached similar tissue water contents.

Table 28: Mean standard deviation of percent weight change in samples of Pelvetia and F. spiralis during eleven hours in two experimental desiccation treatments. Plants had been air-dried at 20.5 - 22.0°C, -940 to -945 bars water potential before being introduced into the separate treatments. Table also gives t test for differences observed.

| Conditions | n | Pelvetia weight change, % | n | F. spiralis weight change, % |
|---|---|---|---|---|
| 25°C, $\Psi_w$ = -775 bars | 10 | 5.0 ± 1.0 | 10 | 4.2 ± 1.0 |
| 9°C, $\psi_w$ = -960 bars | 10 | 4.8 ± 1.0 | 10 | 3.7 ± 0.5 |
| t | | 0.45 | | 1.42 |
| p | | >0.60 | | >0.10 |

After the experimental stress, the samples were cultured for eleven days, and ten control plants of each species were grown for the same period. Once again, initial weight loss was significantly greater in both species at 25°C than at 9°C. (Table 29). Pelvetia grew normally after both treatments, but F. spiralis was adversely affected, and damage was significantly more severe after drying at 25°C than at 9°C. This shows that high temperature does not increase stress solely through increasing the degree of dehydration. Furthermore, the effect observed in this experiment cannot be attributed to an accelerated rate of dehydration since all the samples were pre-dried under identical conditions to a slightly lower water content than that at which they were equilibrated in the experimental treatments. Therefore, an increase in temperature directly accelerates the rate of adverse physiological change in fucoid tissues dried to a given water potential. Since the higher temperature used in the experiments is similar tothe highest reached at Isle of Cumbrae, and since exposed fucoids can become significantly warmer than the surrounding air on a sunny day (Schramm 1968), high temperature may be considered an ecologically important aggravating factor.

Table 29: Survival and growth of Pelvetia and Fucus spiralis (mean ± standard deviation) after drying to the same tissue water contents at two different temperatures. Table also gives t test of observed differences between the 9°C and 25°C drying treatments.
** = $p < 0.01$ *** = $p < 0.001$

| | n | Initial weight change, % | Linear growth, mm in 11 days | Relative weight gain, % in 11 days | condition of thalli at end of 11 days |
|---|---|---|---|---|---|
| Pelvetia | | | | | |
| Control | 10 | - | 2.8 ± 1.0 | 28.1 ± 3.7 | Good |
| 9°C, $\psi_w$ = -960 bars | 10 | -2.1 ± 1.3 | 2.8 ± 0.8 | 28.6 ± 6.6 | Good |
| 25°, $\psi_w$ = -775 bars | 10 | -4.7 ± 1.0 | 2.2 ± 0.8 | 27.0 ± 6.4 | Good |
| t | | 5.01*** | 1.40 | 0.48 | |
| Fucus spiralis | | | | | |
| Control | 10 | - | 8.3 ± 1.6 | 52.2 ± 11.0 | Good |
| 9°C, $\psi_w$ = -960 bars | 10 | -15.0 ± 4.1 | 0.5 ± 1.9 | -10.9 ± 15.6 | Damaged but regenerating[α] |
| 25°, $\psi_w$ = -775 bars | 10 | -21.8 ± 5.1 | -3.2 ± 1.0 | -35.8 ± 3.1 | Dead |
| t | | 3.29** | 5.44*** | 4.94*** | |

α five of these plants grew in length and gained weight when cultured for another eight days.

## 3.6 Survival after dehydration at various water potentials

Since the degree of tissue dehydration is directly related to the water potential of the surrounding atmosphere, this parameter would be expected to exert a profound influence on the alga's ability to survive during tidal exposure. The possibility that a higher relative humidity might mitigate the effects of exposure was tested by experiment. Five samples each of Fucus spiralis and Pelvetia were dried at 9° ± 1°C at each of four different water potentials. The Pelvetia was dried for forty-eight hours and the F. spiralis for twenty-four so that each species was subjected to a sublethal but possibly damaging stress. After drying, the plants were resubmerged and cultured for ten days, and five control plants of each species were also cultured for the same period. The experiment was repeated at 25° ± 1°C to determine whether the effect of water potential was similar at the higher temperature. Survival was assessed by four criteria: initial weight change (as defined on page 31 ), linear growth, relative weight gain and condition of the thalli at the end of the culture period.

Surprisingly, stress injury at 25°C became progressively less severe with decreasing water potential (Table 30, Figures 21, 22, 23). This was especially pronounced in Pelvetia which was unaffected after two days at -1375 bars, but severely damaged after two days at -100 bars. At 9°C, Pelvetia was unaffected at all water potentials, while damage to F. spiralis appeared to increase slightly with decreasing water potential, which was the expected trend.

Table 30: Condition of Pelvetia and F. spiralis dried to different water potentials at 9°C and at 25°C, and cultured for ten days. 0 = no damage, † = some or all plants slightly damaged, †† = moderate damage, ††† = severe damage.

| | | Water potential, bars | | | | |
|---|---|---|---|---|---|---|
| | | -100 | -395 | -775 | -1370 | Control |
| Pelvetia | 9°C | 0 | 0 | 0 | 0 | 0 |
| | 25°C | ††† | ††† | †† | 0 | 0 |
| F.spiralis | 9°C | 0 | † | † | † | 0 |
| | 25°C | ††† | †† | ††† | † | 0 |

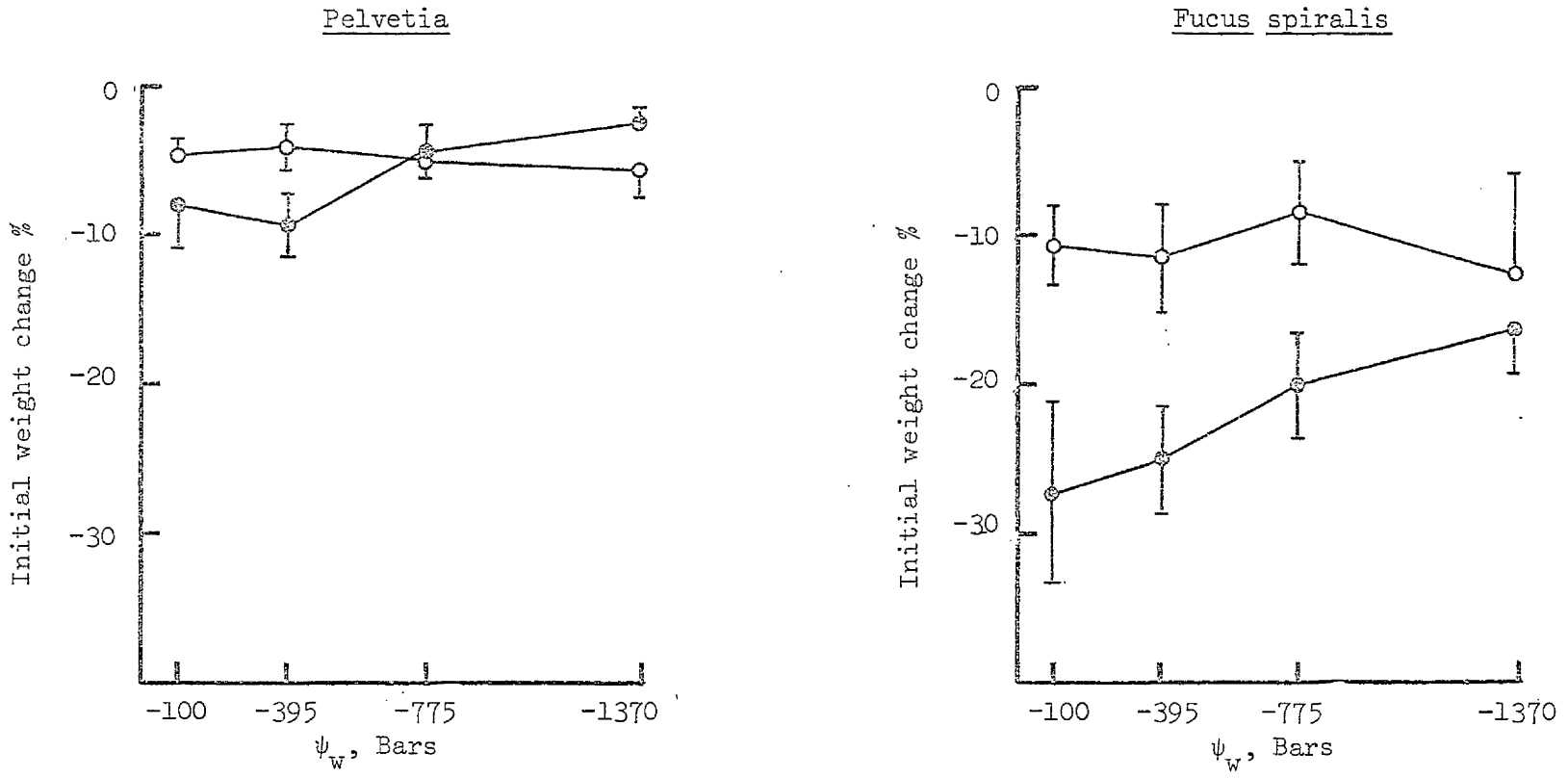



Figure 21. Mean ± standard deviation of initial weight change in Pelvetia and F. spiralis dried at various water potentials at 9°C (o) and at 25°C (●) n=5 for each treatment. Pelvetia dried for 48 hours; F. spiralis dried for 24 hours in each treatment.

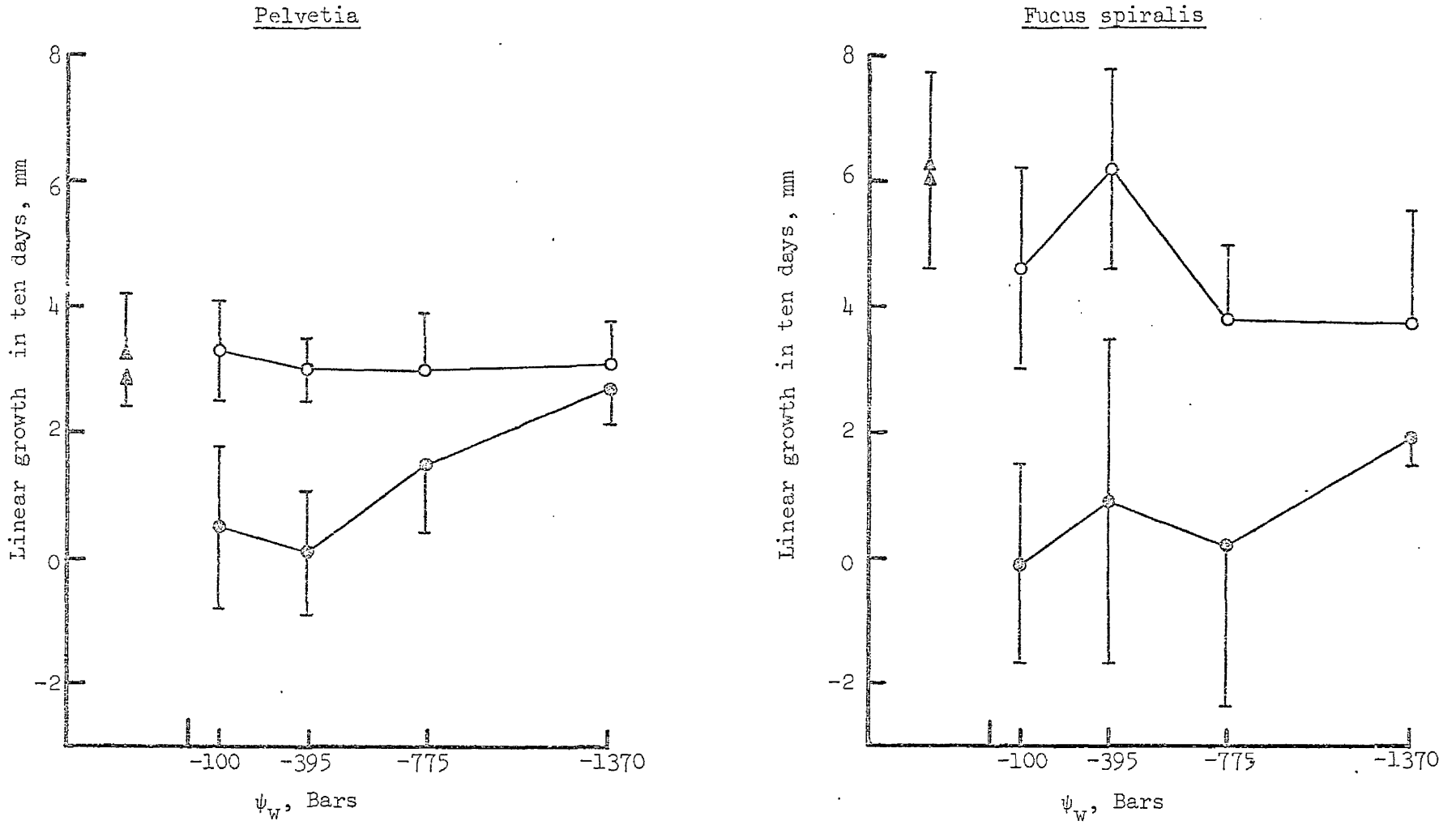



Figure 22. Mean ± standard deviation of linear growth in Pelvetia and F. spiralis after drying at various water potentials at 9°C (o) and at 25°C (●), compared with controls (▲). n=5 for each treatment and each set of controls. Pelvetia dried for 48 hours; F. spiralis for 24 hours in each treatment.

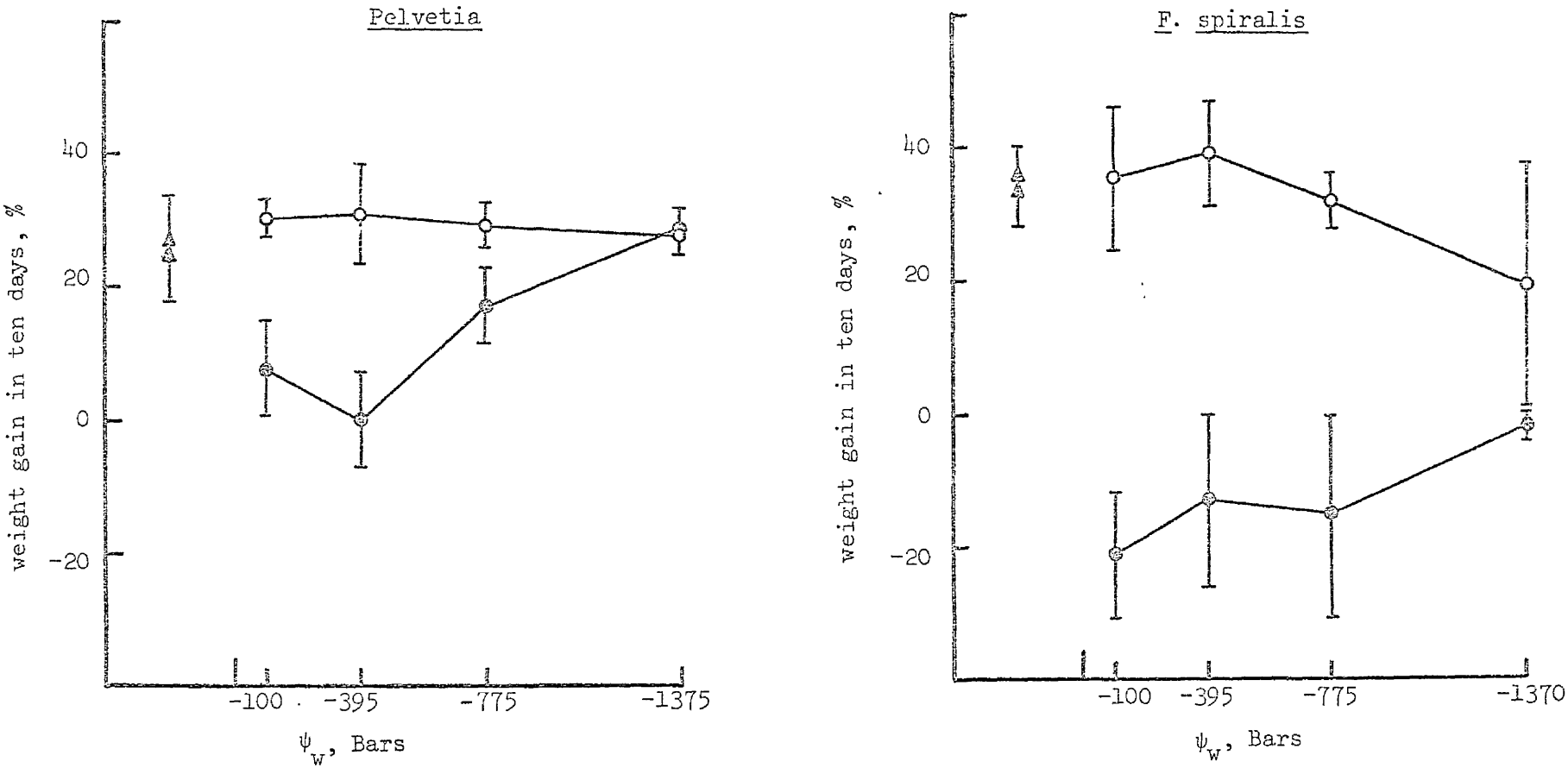



Figure 23. Mean ± standard deviation of relative weight gain in Pelvetia and F. spiralis after drying at various water potentials at 9°C (o) and at 25°C (●), compared with controls (▲). n=5 for each treatment and each set of controls. Pelvetia dried for 48 hours; F. spiralis for 24 hours in each treatment.

These trends were subjected to two different statistical analyses. Firstly, initial weight loss, linear growth and percent weight gain after drying at -100 and at -1370 bars were compared for each species at each temperature by means of a simple t-test. Secondly, a single-factor analysis of variance was performed on each parameter to compare the variance resulting from the different treatments to the variance attributed to replicates and error. These tests show that the unexpected "reversed" trend in Pelvetia at 25°C is highly significant (Table 31). The significances of the trends in F. spiralis at both temperatures are uncertain. However, the convergence of the 9°C and 25°C curves with decreasing water potential is evident in all three parameters measured. Therefore, initial weight loss and growth rates of F. spiralis exposed at the two temperatures were compared at each water potential using the t-test. The effect of temperature was most pronounced at -100 bars and least so at -1370 bars, at which the differences between the 9°C and 25°C sets were statistically insignificant (Table 32).

Table 31: Statistical tests of significance of trends in survival and growth related to water potential during exposure. $t_4$ = t value of difference between effects of drying at -100 and at -1375 bars. F(3,16) = ratio of variance resulting from different water potentials to variance resulting from all other causes * = $p < 0.05$ ** = $p < 0.01$

| | $t_4$ | F(3,16) |
|---|---|---|
| Pelvetia 9°C | | |
| initial weight change | 0.58 | 0.52 |
| linear growth | 0.42 | 0.18 |
| relative weight gain | 1.57 | 0.47 |
| F.spiralis 9°C | | |
| initial weight change | 0.55 | 0.73 |
| linear growth | 0.83 | 2.81 |
| relative weight gain | 1.70 | 2.83 |
| Pelvetia 25°C | | |
| initial weight change | 4.10* | 12.47** |
| linear growth | 3.61* | 6.73** |
| relative weight gain | 5.37** | 18.58** |
| F.spiralis 25°C | | |
| initial weight change | 3.83* | 7.19** |
| linear growth | 2.68 | 1.30 |
| relative weight gain | 4.01* | 2.56 |

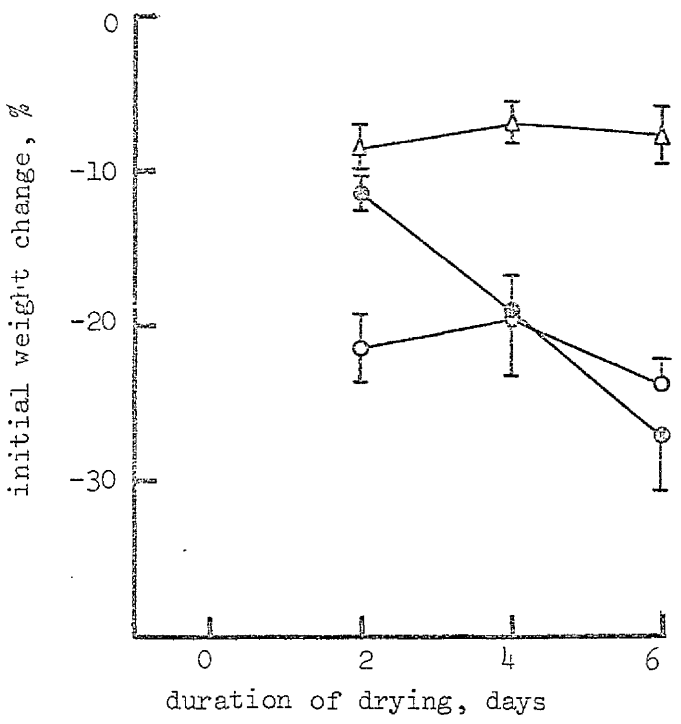
Table 32: t values for difference between effects of drying at 9°C and 25°C on Fucus spiralis at four different water potentials. * = $p < 0.05$ ** = $p < 0.01$

| $\psi_{w_{ci}}$ bars | initial weight change | Linear growth | relative weight gain |
|---|---|---|---|
| -100 | 5.54** | 4.64** | 8.74** |
| -395 | 5.79** | 3.88** | 7.57** |
| -775 | 5.09** | 2.82* | 6.63** |
| -1375 | 1.20 | 2.13 | 2.57 |

A second experiment was undertaken with Pelvetia to determine whether the results obtained at 25°C are reproducible, and whether the observed trend extends to much lower relative humidities. Samples of Pelvetia were dried at 75% and at 37% humidity, and other samples were dried over silica gel, giving a relative humidity near zero percent. Groups of five plants were subjected to each treatment for two, four and six days and then cultured. They were grown in unaerated culture dishes, and the growth rate of the five control plants was relatively slow as a result. However, a very distinct pattern emerged (Figures 24, 25). Exposure at 75% relative humidity (water potential -395 bars) caused a progressive injury, with slight damage after two days and lethal effects after six. By contrast, drying at 37% humidity (-1370 bars) caused only a very slight effect which did not increase with time during the six day experiment. However, complete dehydration over silica gel proved fatal even after only two days. In a separate determination at 9°C, drying at 0% relative humidity damaged the plants almost as severely as at 25°C, but exposure at high humidity caused no visible injury and curtailed growth somewhat only after six days (Table 33).

Table 33: Survival and growth of Pelvetia (mean ± standard deviation) after exposure at 9°C at high humidity and at 0% humidity. n = 5 for each treatment.

| relative humidity | duration | initial weight change | linear growth mm/10 days | relative weight gain in 10 days | condition of thallus after 10 days |
|---|---|---|---|---|---|
| 0% | 2 days | -10.4 ± 4.1 | -1.1 ± 0.5 | -9.4 ± 5.1 | severely damaged |
| | 6 days | -17.5 ± 1.3 | not measured | not measured | dead |
| 78-93% | 2 days | +1.0 ± 1.5 | 2.1 ± 0.5 | 19.2 ± 5.1 | good |
| | 6 days | -0.1 ± 0.8 | 1.0 ± 0.7 | 10.3 ± 1.9 | good |



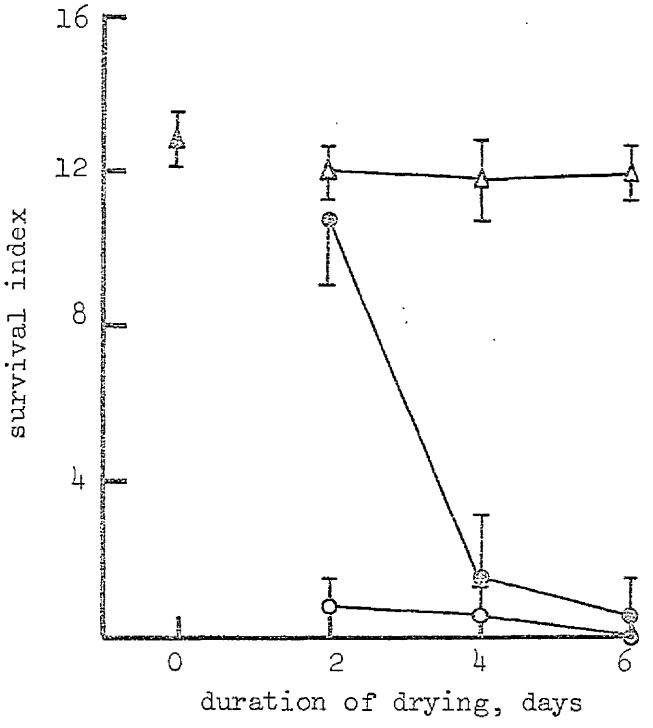




Figure 24. Mean ± standard deviation of initial weight change and survival index in Pelvetia dried for different periods of time at 25-27°C and at relative humidities of 75% (●) 37% (Δ) and 0% (○). Survival index also given for controls (▲) n=5 for each treatment.

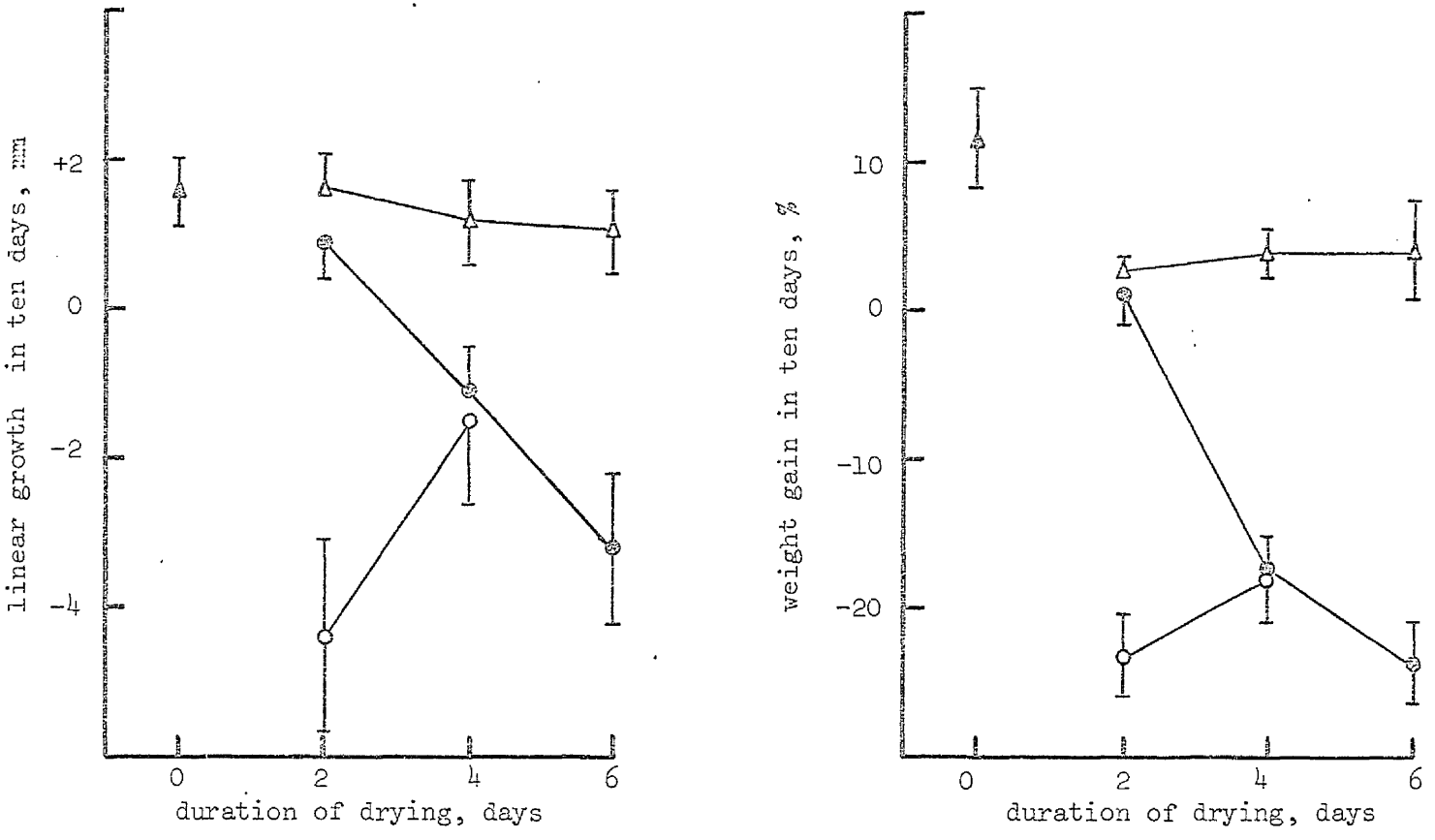



Figure 25. Mean ± 1 standard deviation of linear growth and relative weight gain in Pelvetia dried for different periods of time at 25-27°C and at relative humidities of 75% (●) 37% (Δ) and 0% (o), compared with controls (▲). The plants maintained for six days at 0% humidity were too decayed to measure at the end of ten days. n=5 for each treatment.

Because the samples were equilibrated over $H_2SO_4$ solutions in small jars during the desiccation period, only a very limited amount of oxygen was available to them. Since more respiration might occur at -395 bars than at potentials near -1000 bars, the progressive deterioration of the samples at -395 bars and 25°C may have resulted directly from oxygen depletion. Therefore, the effect of high water potential was tested in an open system. The plants were placed over a solution of magnesium chloride in a 5 litre tank covered with clear polythene in which two small holes had been cut. An air stream was passed through a closed bottle of magnesium chloride solution of the same concentration as that in the tank, and then delivered to the tank via a length of plastic tubing inserted through the intake hole. Three sets of samples were dried: one over 1.0 M $MgCl_2$, a second over 2.5 M $MgCl_2$, and a third in an open tray in the same room.

Fifteen samples of F. spiralis were exposed for 28 hours, and fifteen Pelvetia for 90 hours, to each treatment. Remaining water content was determined using five samples from each set, and the other ten were grown in unaerated culture dishes for ten days. Relative humidity could not be determined accurately in these open systems, but the approximate water potentials were estimated by comparison of remaining water contents with the data in Table 8, section 3.3

Once again, Pelvetia suffered much more damage at higher water potentials than at lower potentials (Table 34).

Table 34: Remaining water content, survival and growth of Pelvetia (mean ± standard deviation for ten samples) after exposure at 24.4 - 29.4°C for 90 hours at three different water potentials. Air constantly replenished to prevent oxygen depletion.

| rying onditions | g water retained per 100g dry matter | estimated water potential | initial weight change | percent weight gain in 10 days | condition of thalli after 10 days |
|---|---|---|---|---|---|
| room | 6.9 ± 1.1 | -1500 | -4.6 ±1.7 | -1.1 ± 4.8 | slightly damaged, most tips in good condition. |
| over 2.5M $MgCl_2$ | 22.3 ± 2.0 | -400 | -9.1 ±2.9 | -8.6 ± 4.1 | moderate to severe damage, most tips affected |
| over 1.0M $MgCl_2$ | 47.6 ± 5.1 | -200 | -20.7±2.5 | -21.2± 2.2 | dead |

F. spiralis suffered severe damage after exposure at all three water potentials (Table 35). The plants used in this determination were collected 20 August 1976, at which time they were undergoing a prolonged, intense drought stress (Figure 9, following page 37 ). F. spiralis samples collected at this time for other culture work showed slight damage resulting from the natural stress, and the experimental exposure applied immediately afterward apparently exceeded the tolerance limit of this species. Initial weight loss was slightly greater, and the thalli became more discoloured, at the higher water potentials.

In conclusion, the results of these experiments suggest that during exposure at temperatures near 25°C, harmful physiological changes occur most rapidly at relatively high water potentials. Therefore, high humidity may be considered an ecologically important aggravating factor during summer hot spells.

Table 35: Remaining water content, survival and growth of Fucus spiralis (mean ± standard deviation for ten samples) after exposure at 24.4 - 29.4°C for 28 hours at three different water potentials. Air constantly replenished to prevent oxygen depletion.

| drying conditions | grams water retained per 100g dry matter | estimated water potential | initial weight change | percent weight gain in 10 days | condition of thalli after 10 days |
|---|---|---|---|---|---|
| room | 8.7 ± 0.5 | -1500 | -11.0 ± 1.8 | -14.2 ± 3.3 | most of thallus somewhat discoloured |
| over 2.5 M $MgCl_2$ | 23.4 ± 3.3 | -400 | -12.5 ± 2.8 | -12.5 ± 3.5 | most of thallus discoloured |
| over 1.0 M $MgCl_2$ | 53.9 ± 2.5 | -200 | -16.1 ± 5.1 | -14.8 ± 7.5 | most of thallus very discoloure |

## 3.7 The effect of rainfall during low tide upon fucoids

The combination of high temperature and humidity is realized in the extreme during very warm rains, such as those which occurred in August 1975 (Figure 7, following page 37 ). The effect of such unusually warm rains upon exposed fucoids was investigated by simulating these conditions in the

laboratory. Ten plants each of F. spiralis and Pelvetia were subjected to each of two treatments. One set was attached to a Perspex plate and placed in an empty five-litre tank that was maintained at 9°C under a 16-8 hour light/dark cycle in the culture room. The plants were sprayed twenty times over a forty-eight hour period with distilled water from an atomizer. The plate was supported on large test tubes laid in the tank so that the plants did not become submerged as the water accumulated in the bottom of the tank. In this way, the plants were kept fully hydrated by contact with fresh water only, as they are in nature when small tides coincide with wet weather. A second set received the same treatment at 25°C. This was done by placing both the tank and the atomizer in a water bath resting on the same shelf as the first tank. In the evening, the water bath temperature was lowered to 16 to 17°C which is close to the highest nighttime minima observed at Isle of Cumbrae (Figures 7 and 9, following page 37 ). All twenty sprayings were done in the day with the water bath at 25°C. The total amount of water sprayed on each set of plants was about 1.37 litres, equivalent to a rainfall of 30.4mm when applied over the area of the bottom of the tank. This is a realistic amount of rain over a two day period for Isle of Cumbrae (Figures 5-9).

The experimental plants and ten control plants of each species were cultured for ten days in aerated tanks. At the end of the culture period percent dry matter was measured as well as fresh weight. The simulated rain had little effect on Pelvetia at either temperature (Table 36). The control plants showed slight damage owing to severe desiccation in nature just prior to collection of the samples.

Table 36: Percent dry matter, survival and growth of Pelvetia (mean ± standard deviation) after exposure to simulated rainfall at 9°C and at 25°C. n= 10 for each treatment.

| treatment | % weight change in 10 days | linear growth in 10 days | condition of thalli after 10 days | % dry matter |
|---|---|---|---|---|
| "rain" at 25°C | 13.8 ± 3.8 | 1.3 ± 0.8 | slight damage | 31.1 ± 1.3 |
| "rain" at 9°C | 19.8 ± 4.0 | 1.7 ± 0.5 | very slight damage | 30.4 ± 1.4 |
| control | 9.9 ± 2.2 | 1.3 ± 0.6 | very slight damage | 32.0 ± 0.6 |

The simulated rain caused large, gas-filled swellings to form on the thalli of Fucus spiralis. Such swellings often occur in Fucus spp. growing on shores which are exposed to fresh or brackish water. On the experimental plants, they persisted and became waterlogged during the ten day culture period. This caused a considerably lower percent dry matter compared with controls, and a spuriously high relative weight gain (Table 37). Judging from the linear growth and the extent of damage to the thalli, the "rain" was at most slightly harmful to F. spiralis even at 25°C. Apparently, exposure to high summertime temperatures is much less harmful when the thallus is wet than when it is equilibrated at -100 to -400 bars water potential. It is also clear that exposure of fully hydrated plants to rainfall does not constitute an ecologically critical stress, either in winter or in summer.

Table 37: Percent dry matter, survival and growth of Fucus spiralis (mean ± standard deviation) after exposure to simulated rainfall at 9°C and at 25°C. n = 10 for each treatment.

| treatment | % weight change in 10 days | linear growth in 10 days | condition of thalli after 10 days | % dry matter | no. of plants with watery swellings at end of culture perio |
|---|---|---|---|---|---|
| "rain" at 25°C | 40.2 ± 19.8 | 2.6 ± 1.1 | slightly damaged. tips slightly burned in 7 plants. | 23.8 ± 3.4 | 7 |
| "rain" at 9°C | 55.7 ± 18.2 | 3.2 ± 1.6 | slightly damaged. tips slightly burned in 4 plants | 22.8 ± 2.2 | 9 |
| Control | 15.5 ± 5.6 | 3.6 ± 1.7 | slightly damaged. tips slightly burned in 1 plant | 28.0 ± 1.4 | 0 |

The effect of sudden rainfall upon desiccated seaweeds was investigated in F. spiralis. Ten plants were subjected to each of five treatments:

(1) Dried for eight hours twenty minutes, then immediately doused for thirty minutes with fresh water delivered via a watering can rose connected to a tap..
(2) Dried for one hour five minutes, then watered for thirty minutes, as above.
(3) Dried for eight hours thirty-five minutes.
(4) Watered for thirty minutes.
(5) Controls, kept in sea water at 9°C.

The drying was carried out at 24.5 - 26.7°C, water potential -950 to -1070 bars. Other samples of F. spiralis were dried simultaneously to measure remaining water content. The plants were air-dry after eight hours twenty minutes (3.3% ± 0.4% of water content remaining, 11.6 ± 0.4 g water/100 g dry matter), but contained a considerable amount of "volatile water" after one hour five minutes (16.3 ± 1.1% of total water content, 58.6 ± 18.6 g water/100 g dry matter).

The tap water was about 14°C. The rate at which it was sprayed on the plants by the watering can rose was much too great to realistically simulate normal rainfall. However, this experiment roughly simulated the conditions produced if a sudden heavy shower occurs immediately after a hot sunny period.

Drying for eight hours caused a slight but significant decrease in growth rate, and this effect was much more pronounced when the algae were watered for thirty minutes immediately after drying (Table 38). Watering alone or following partial desiccation had little effect. Therefore, rainfall is an ecologically important aggravating factor when it falls upon the fucoids when they are very dry.

Table 38: Growth of F. spiralis (mean ± standard deviation) after desiccation, simulated heavy rain, or both. Plants dried at 24.5 - 26.7°C, water potential -950 to -1070 bars. t-values for comparison between each treatment and the controls; * = $p < 0.05$ *** = $p < 0.001$.

| Treatment | n | linear growth mm in 12 days | relative weight gain, % in 12 days | condition of thalli after 12 days |
|---|---|---|---|---|
| dried 8 hrs 20mins then watered 30 mins | 10 | 4.7 ± 1.6 t = 5.12*** | 23.7 ± 9.3 t = 5.97*** | moderate damage, tips in good condition |
| dried 1 hr 5 mins then watered 30 mins | 10 | 6.9 ± 1.1 t = 2.55* | 45.2 ± 5.8 t = 0.73 | very slight damage |
| dried 8 hrs 35 mins | 10 | 6.7 ± 1.1 t = 2.88* | 37.6 ± 5.7 t = 3.06* | slight damage |
| watered 30 mins. | 10 | 6.9 ± 1.2 t = 2.49* | 41.3 ± 4.5 t = 1.98 | good |
| controls | 10 | 8.6 ± 1.8 | 47.6 ± 8.6 | good |

## 3.8 Aspects of drought tolerance and drought hardening in upshore fucoids.

In the preceding sections, duration of exposure to a desiccating atmosphere has been identified as the primary critical factor in determining upper limits of fucoids, and high temperature together with high humidity and sudden showers as secondary factors. Further experiments were undertaken to learn more about the mechanisms by which the upshore fucoids have adapted to the prolonged exposures they must endure.

### 3.8.1 Rate of reimbibition of water after resubmersion

The upshore fucoids not only endure severe dehydration, but also are submerged only for brief periods of time. Since metabolic processes necessary to growth normally take place only when the tissues are fully hydrated, the ability to reabsorb water rapidly upon resubmergence is an

important aspect of drought tolerance in upshore fucoids. As submersions are particularly brief in the Pelvetia zone this species' rate of reimbibition was compared with that of Fucus spiralis. Five plants of each species were dried in the warm culture room for one hour, five for two and one-half hours, and fifteen for about twenty hours. Each set was weighed before and after drying, and again precisely thirty minutes after resubmersion in seawater at 8-10°C. The percentage of the water loss regained was calculated as follows:

$$\frac{(\text{weight thirty minutes after resubmersion}) - (\text{weight after drying})}{(\text{wet weight}) - (\text{weight after drying})} \times 100\%$$

After one hour drying, both species regained close to two thirds of their tissue water loss during thirty minutes resubmergence. F. spiralis reimbibed a progressively smaller fraction of its tissue water deficit as the length of exposure was increased, while Pelvetia reabsorbed the same proportion regardless of the duration of exposure (Table 39).

Table 39: Mean ± standard deviation of percent of water loss regained by Pelvetia and F. spiralis during thirty minutes resubmergence after drying at 25-26°C, water potential -940 to -1100 bars, for different lengths of time.

| duration of exposure | n | percent of water loss reimbibed | |
|---|---|---|---|
| | | Pelvetia | F. spiralis |
| 1 hour | 5 | 65.5 ± 2.6 | 61.4 ± 4.4 |
| 2½ hours | 5 | 66.6 ± 2.9 | 55.3 ± 4.8 |
| 20 hours (plants air-dry) | 15 | 64.9 ± 2.7 | 50.8 ± 4.4 |

In a second experiment, five samples each of Pelvetia, F. spiralis and F. serratus were dried for five hours, resubmerged and weighed after one-half, one, two and four hours' recovery, and again the next morning. In all three species most of the total reimbibition occurred within thirty minutes. However, while Pelvetia replaced almost its entire water loss within only four hours, neither Fucus species exceeded 70 percent replacement within twenty-four hours, nor gave any indication

that they would do so subsequently (Figure 26). This weight loss in Fucus foretold the severe damage which became evident after ten days in culture, whereas Pelvetia remained healthy and grew rapidly within the same period. The question of whether the entire weight loss can be attributed to incomplete reabsorption of water will be considered in the following section.

### 3.8.2 Causes of the initial weight loss

When a desiccated alga is resubmerged, it may not return to its original weight either because it does not reabsorb all the water it has lost, or because it loses other substances from its tissues into the surrounding sea water. In order to determine which of these processes causes most of the initial weight loss, dry weights before and after reimbibition following desiccation were compared. Twenty plants each of Pelvetia and F. spiralis were weighed and divided into two groups of ten plants each. The plants in group A were dried over silica gel to obtain the percent dry matter (parameter A in Table 40). The plants in group B were air-dried for twenty-four hours, soaked overnight in sea water, reweighed, dried over silica gel, and weighed again. The percent dry matter in the resoaked plants (parameter B, Table 40) was calculated as follows:

$$\frac{(\text{weight after drying and resoaking})}{(\text{dry weight})} \times 100\%.$$

The ratio of the dry weight to the fresh weight before air-drying was also calculated as a percentage (parameter C, Table 40). This determination was carried out three times at different temperatures and water potentials.

Incomplete reabsorption of water during resoaking would produce a higher percent dry matter after recovery (parameter B) than before air-drying (parameter A). Such incomplete reabsorption would cause an initial weight change equal to $\left(\frac{A}{B} - 1\right) \times 100\%$. Loss of some of the dry matter itself during resoaking after air-drying would be revealed by a value of parameter C lower than parameter A, since C is the ratio of dry matter remaining in the plant after air-drying and resubmersion to the original wet weight. Loss of substances from the tissue would cause

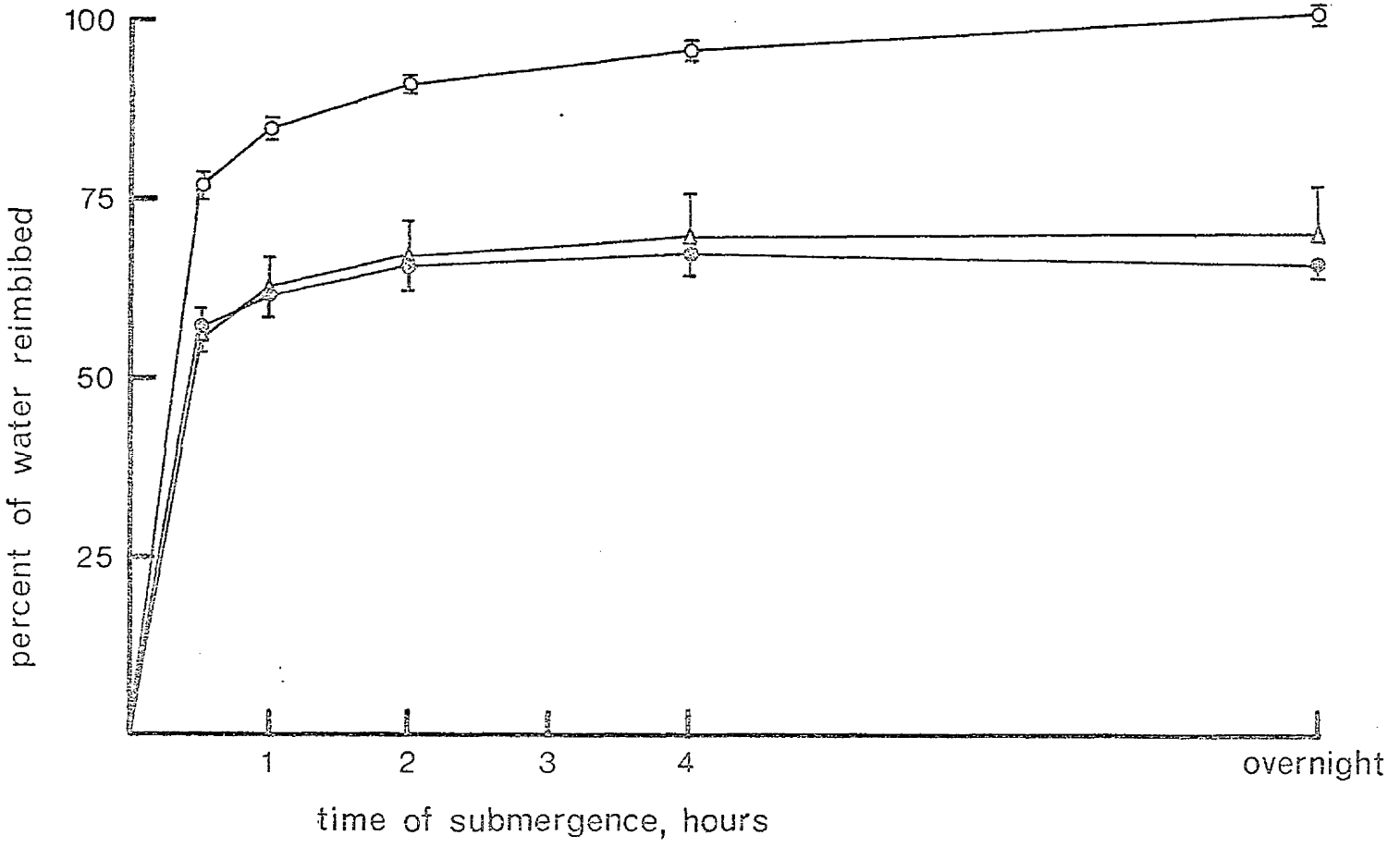



Figure 26. Course of reimbibition of water (mean ± standard deviation) after five hours desiccation at 26-26.5°C, 48-49% relative humidity, water potential -980 to -1015 bars, in Pelvetia (o), Fucus spiralis (Δ) and F. serratus (⊙).

Table 40: Contribution of incomplete reimbibition and loss of tissue substances to initial weight loss in Pelvetia and Fucus spiralis, estimated from mean values of A, B and C.

A = percent dry matter before air-drying (Group A)

B = percent dry matter after air-drying for twenty-four hours and resoaking (Group B)

C = ratio of dry weight after air-drying and resoaking to fresh weight before air-drying (Group B)

Mean ± standard deviation for A,B and C; * adjacent to B or C value indicates significant difference from A ($t > 2.26$, $p < 0.05$).

| Species | Drying conditions | n | initial weight change,% | A | B | C | initial weight change attributed to incomplete reimbibition: $(\frac{A}{B} - 1) \times 100\%$ | initial weight change attributed to loss of tissue substances $(\frac{C}{A} - 1) \times 100\%$ |
|---|---|---|---|---|---|---|---|---|
| Pelvetia | 17.2 - 20.3° C $\psi_w$ = -680 to -810 bars | 10 | -1.9 ± 0.9 | 22.8 ± 1.9 | 23.8 ± 1.6 | 23.3 ± 1.7 | -4.2 | +2.2 |
| | 8°C $\psi_w$ = -960 bars | 10 | -2.1 ± 1.5 | 22.1 ± 1.6 | 22.2 ± 0.7 | 21.7 ± 1.0 | -0.5 | -2.3 |
| | 25°C $\psi_w$ = -822 bars | 10 | -6.1 ± 3.5 | 21.5 ± 2.2 | 21.9 ± 0.7 | 20.6 ± 0.8 | -1.9 | -4.2 |
| Fucus spiralis | 17.2 - 20.3°C $\psi_w$ = -680 to -810 bars | 10 | -10.9± 4.6 | 20.9 ± 2.6 | 22.1 ± 1.4 | 19.8 ± 1.9 | -5.5 | -5.3 |
| | 8°C $\psi_w$ = -960 bars | 10 | -13.1± 3.8 | 18.2 ± 1.0 | 19.1 ± 1.4 | 16.6 ± 1.4* | -4.7 | -8.8 |
| | 25°C $\psi_w$ = -822 bars | 10 | -21.9± 4.0 | 17.8 ± 1.2 | 19.3 ± 1.1* | 15.0 ± 1.2* | -7.8 | -15.7 |

an initial weight change equal to $(\frac{C}{A} - 1) \times 100\%$. The derivation of these formulae are given in Appendix F.

The total initial weight change in Pelvetia was too small in all three determinations for either parameter B or C to differ significantly from A. However, both incomplete reimbibition and loss of tissue dry matter during resoaking apparently contributed to the larger initial weight losses observed in F. spiralis (Table 40). Loss of tissue substance was particularly important after the most severely damaging exposure.

Collapse of the cells during dehydration causes mechanical stress in cell membranes which may lead to damage and increased permeability (Levitt 1972). Such membrane damage results in both incomplete reabsorption of water and the loss of intracellular solutes. Since a high dry matter content lessens the degree of collapse during dehydration, it may significantly reduce the damage. Therefore, the role of dry matter content in drought resistance of fucoids was investigated in greater detail.

### 3.8.3 The relationship between percent dry matter and drought tolerance

Fifty plants of Fucus spiralis were weighed, dried for forty-two hours in the warm culture room, and reweighed. They were then grown for ten days in aerated culture to observe the effects of the lengthy exposure. The initial weight loss, percent weight gain over ten days, and the survival index were calculated for each plant. The plants' initial percent dry matter could not be determined because they were resoaked and cultured after being air-dried in the warm room. Therefore, the parameters of survival were related to the ratio of air-dry weight to original wet weight. Since the variance of colloidal water content measured at low water potentials is generally quite small (Table 8, page 49 ), the ratio of air-dry weight to wet weight bears a roughly constant relationship to the percent dry matter, and can be considered a reliable index of dry matter content.

A very strong correlation was observed between the air-dry to wet weight ratio and all three parameters of survival (Figures 27-29). Plants in which the air-dry to wet weight ratio was near 20% were killed,

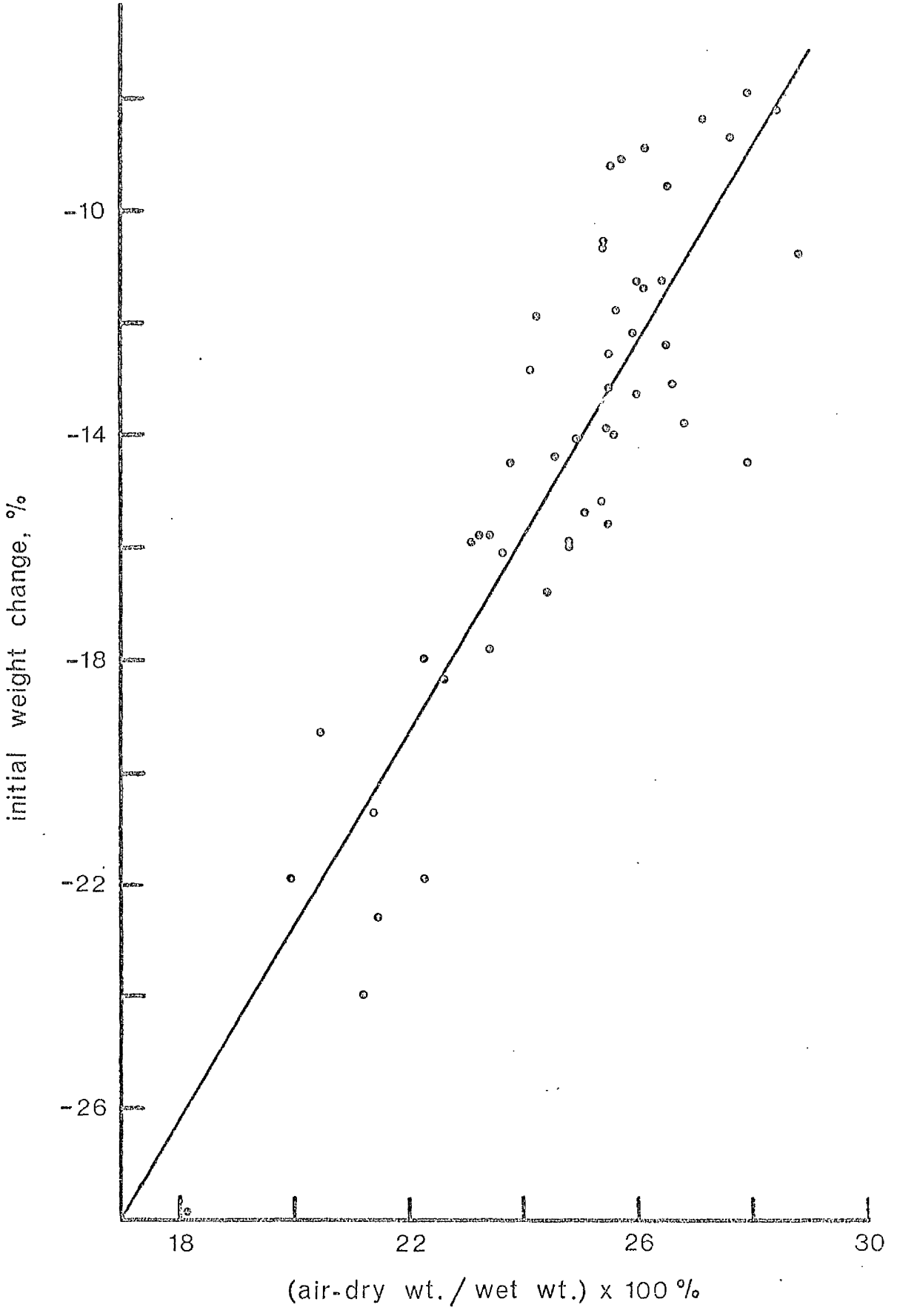



Figure 27. Relationship between initial weight loss and ratio of air-dry weight to wet weight in fifty plants of F. spiralis dried forty-two hours at 25.6-27.1°C, water potential -0.5 to -990 bars. Correlation coefficient 0.881, $p << 0.001$.

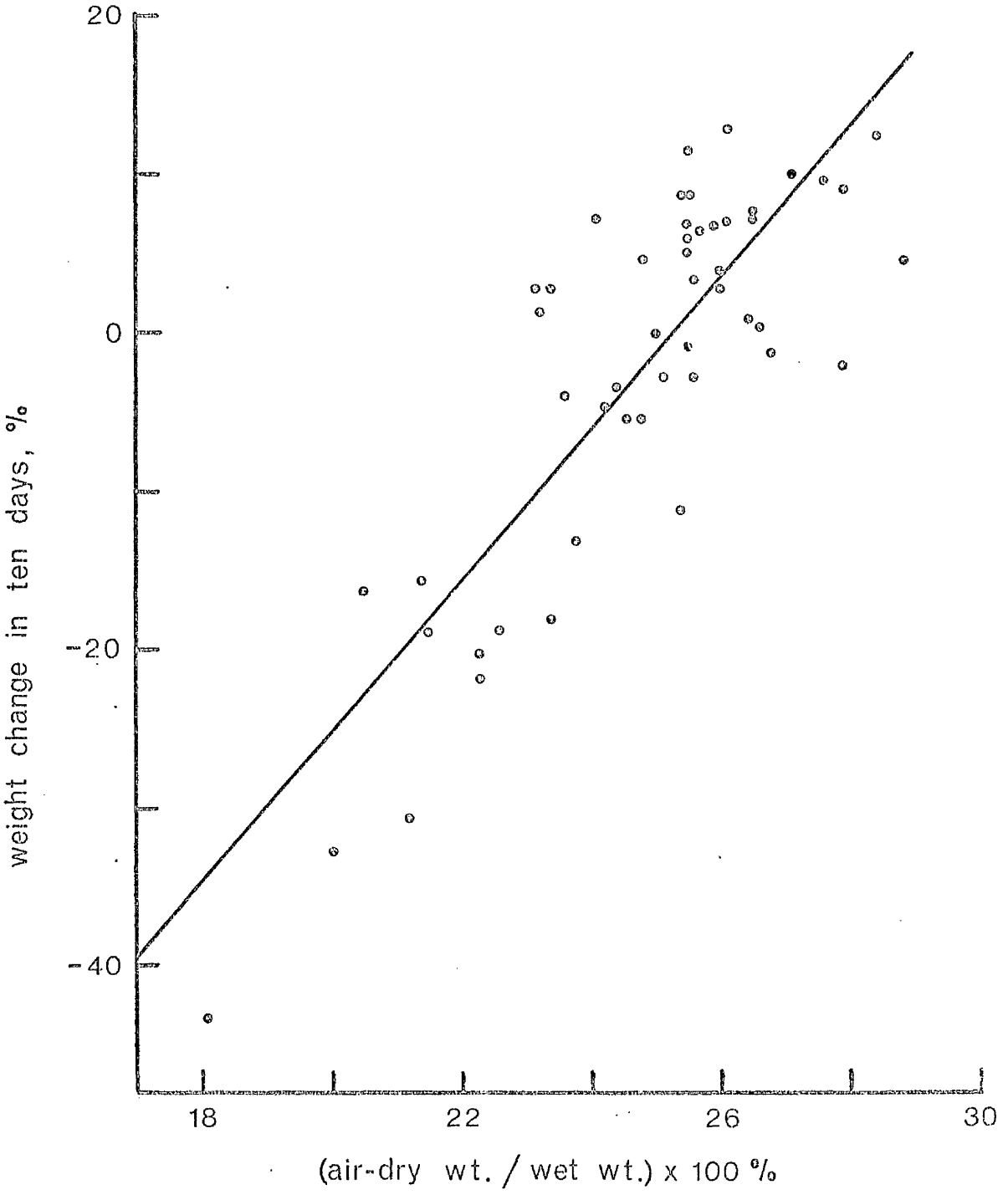



Figure 28. Relationship between relative weight gain and ratio of air-dry weight to wet weight in fifty plants of F. spiralis dried forty-two hours at 25.6-27.1°C, water potential -5-5 to -990 bars. Correlation coefficient 0.839 $p << 0.001$

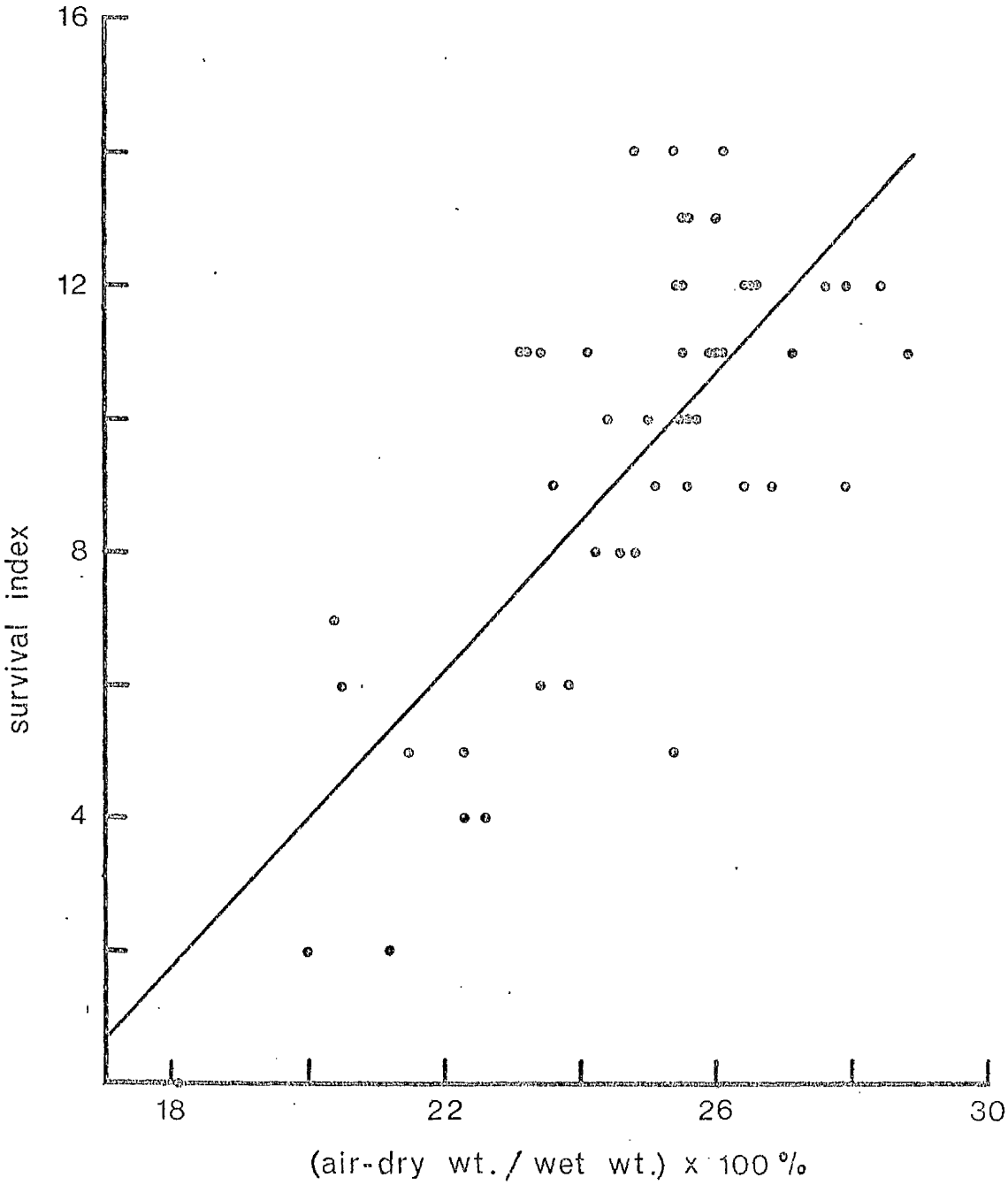



Figure 29. Relationship between survival index and ratio of air-dry to wet weight in fifty plants of F. spiralis dried forty-two hours at 25.6 - 27.1°C, water potential -645 to -990 bars. Correlation coefficient 0.744, $p << 0.001$.

while those near 28% were only slightly affected by the experimental drying. Since dry matter content appears to play an important role in drought tolerance, the factors influencing the observed variation in this parameter were investigated further.

In several culture experiments, young plants were grown under different culture conditions which produced very different growth rates. In each experiment, both Pelvetia and F. spiralis showed a strong inverse relationship between percent dry matter at the end of the culture period and growth rate during that culture period (Table 41). Rapid growth appears to produce tissue with a low dry matter content, and possibly a low drought tolerance as well.

Table 41: Relationship between percent dry matter and relative weight gain per day in Pelvetia and Fucus spiralis (mean ± standard deviation).

| | Pelvetia | | | Fucus spiralis | | |
|---|---|---|---|---|---|---|
| Experiment and conditions | n | % dry matter | % weight gain per day | n | % dry matter | % weight gain per day |
| Simulated rainfall[α] | | | | | | |
| controls | 10 | 32.0 ± 0.6 | 0.95 ± 0.20 | 10 | 28.0 ± 1.4 | 1.44 ± 0.5 |
| "rain", 25°C | 10 | 31.1 ± 1.3 | 1.29 ± 0.34 | 10 | 23.8 ± 3.4 | 3.36 ± 1.41 |
| "rain", 8-10°C | 10 | 30.4 ± 1.4 | 1.82 ± 0.35 | 10 | 22.8 ± 2.2 | 4.47 ± 1.17 |
| Submersion vs exposure during light period. /12 hour manual tide[b] | | | | | | |
| exposed during illumination | 15[c] | 26.9 ± 0.8 | 1.16 ± 0.20 | 15[c] | 25.6 ± 1.5 | 1.15 ± 0.20 |
| submerged during illumination | 15[c] | 25.3 ± 0.6 | 2.31 ± 0.27 | 15[c] | 22.1 ± 1.6 | 2.62 ± 0.35 |
| Length of submersion and strength of medium[b] | | | | | | |
| unenriched, 4hrs/day | 10 | 30.3 ± 0.8 | 0.16 ± 0.06 | 10 | 31.1 ± 1.0 | -0.32 ± 0.26 |
| /20 strength, 4hrs/day | 10 | 29.4 ± 0.9 | 0.66 ± 0.41 | 9 | 28.1 ± 0.5 | 1.27 ± 0.33 |
| /5 strength, 4hrs/day | 10 | 28.4 ± 1.5 | 1.23 ± 0.31 | 10 | 24.3 ± 1.6 | 2.14 ± 0.61 |
| unenriched, 20hrs/day | 10 | 27.1 ± 1.2 | 1.13 ± 0.38 | 10 | 25.4 ± 1.6 | 2.22 ± 0.42 |
| /20 strength, 20hrs/day | 9 | 25.1 ± 2.4 | 2.19 ± 0.61 | 9 | 21.4 ± 1.1 | 2.76 ± 0.44 |
| /5 strength, 20hrs/day | | - | - | 9 | 19.7 ± 0.9 | 2.86 ± 0.55 |

α experiment detailed in section 3.7
b experiments detailed in section 3.9
c n=5 for percent dry matter determination.

Seasonal variation has been reported in growth rates (Knight & Parke 1950, Subrahmanyan 1960, 1961) and in dry matter content (Bérard-Therriault & Cardinal, 1973a, Black 1948a, 1949a), which suggests that drought resistance might also vary seasonally. Although monthly measurements of percent dry matter and desiccation tolerances were not taken, the results from a large number of other experiments yielded some information on changes in these parameters between January and September. Unforunately, no measurements were taken during the last quarter of the year. Dry matter content was lowest in January-March, and highest in summer. This difference was most pronounced in Pelvetia, which reached 28-30% dry matter in June-September (Fig.30). Drought tolerance also increased during summer months; however this trend was most evident in Fucus spiralis (Table 42).

Table 42: Seasonal variation in drought resistance in Pelvetia and Fucus spiralis. 0 = plants not affected † = plants slightly damaged †† = plants quite damaged but surviving ††† = plants killed. Percent dry matter contents indicated in parentheses represent means of five to ten samples collected from same place on same day as test plants.

| | Duration of exposure at 24-29°C, 30-60% relative humidity | | | | | |
|---|---|---|---|---|---|---|
| | 4-6 hours | 10-20 hours | 24-30 hours | 40-50 hours | 3-4 days | 6 days |
| **Pelvetia** | | | | | | |
| January | 0 | | 0 | | | |
| February | 0 | | | | | |
| March | | 0 | † | | | |
| April | | | | † | | |
| May | | | | 0 | | |
| June | | | | † | † | †(23-25% |
| | | | | 0 | | †(29%) |
| August | | | | 0 | | |
| | | | | †† | | |
| September | | 0 | 0 | 0 | †† | |
| **Fucus spiralis** | | | | | | |
| January | †† | | ††† | | | |
| February | †† | | | | | |
| March | | †††(20.7%) | ††† | | | |
| April | | | †† | | | |
| May | 0 | | | †† | | |
| | | | | † | | |
| June | | | | ††(20.9%) | | |
| | | | | †† | | |
| August | | | | †† | | |
| | | | | †††(26.6-27.3%) | | |
| | | | | †† | | |
| September | | † | †† | ††† | ††† | |

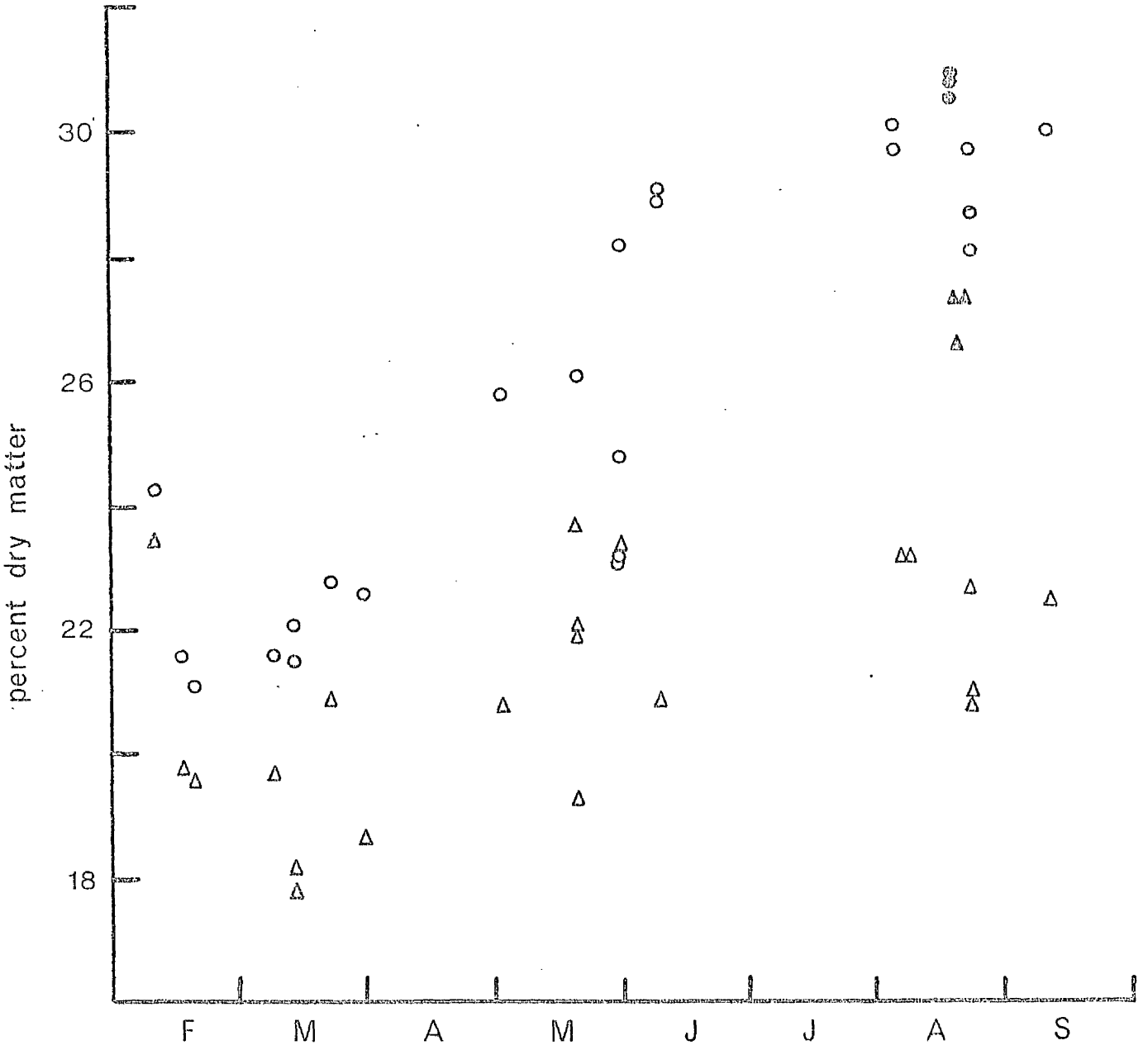



Figure 30. Mean percent dry matter in samples of 4 to 25 plants of Pelvetia (o) and F. spiralis (Δ) collected at different times of year. Standard deviations (not shown on graph) varied between ±0.5 and ±2.5% dry matter. Solid symbol represents sample collected during severe natural desiccation.

This species was killed by twelve to twenty hours exposure in the warm room in January-March, but survived up to forty-two hours during the summer months. This suggests that tidal exposure during progressively warmer weather in spring and early summer causes a drought-hardening process to occur in the fucoid tissues.

The dry matter content does not correlate consistently with drought resistance (Table 42). Samples of Pelvetia collected in June 1976 which had only 23-25% dry matter were found nearly as drought tolerant as other samples collected in the same month which contained 29% dry matter. Also, a June sample of Fucus spiralis was far more drought tolerant than a March sample of similar dry matter content, and slightly more hardy than an August sample which had a much higher dry matter content. Apparently some environmental conditions may cause an increase or decrease in dry matter content without causing a corresponding change in drought tolerance. This was readily demonstrated in culture. Young plants of Pelvetia and F. spiralis which were grown in a diurnal tidal cycle of twelve hours submersion per day grew much faster when this submersion coincided with the light period than when it coincided with the dark period (Table 49, page 113). Percent dry matter was significantly lower in the faster growing group, but drought tolerance was similar after the two treatments (Table 50, page 114). Apparently, an increase in dry matter content does not necessarily protect the tissue from the damaging effects of dehydration.

This observation conflicts with the earlier result which showed a strong correlation between dry matter content and drought tolerance in natural populations of F. spiralis (Figures 27-29, page 97). Therefore samples of this species were exposed to a series of subcritical desiccation stresses in order to determine whether drought hardening occurs and whether it is accompanied by an increase in percent dry matter. Seventy plants were collected from a 100 x 100 mm patch in a dense continuous stand of first-year plants, and divided into two groups of thirty-five. The "unhardened" group was kept in seawater in the 9°C culture room, and the hardened group was dried briefly on each of five successive days in the warm room (25-27°C, water potential -820 to -1080 bars). The duration of exposure was gradually increased from two hours on the first day to four hours on the fifth. On the sixth day, thirty plants of each group

were placed in the warm room to dry for a total of forty-four hours. The five remaining plants of each group were kept in seawater as controls in order to determine whether the hardening procedure itself significantly affected the plants. After the forty-four hour drying, five plants in each group were used to determine percent dry matter and colloidal water content, and the other twenty-five were soaked in seawater for twenty-one hours to determine the initial weight loss. Finally, the five control plants and ten of the experimental plants of each group were cultured for twenty-five days.

The hardening procedure did not significantly affect the plants, and brought about a dramatic increase in drought resistance (Table 43). The hardened set underwent a very small initial weight loss and their growth was almost unaffected, while the unhardened set suffered moderate damage. A comparison of colloidal water contents showed that the hardened tissue had not become more hygroscopic, but percent dry matter was significantly elevated by the hardening process (Table 43). These results show clearly that fucoid tissues can be effectively drought-hardened by exposure to subcritical dehydration stresses, and that part of the hardening process is an accumulation of dry matter in the tissues. Apparently, this change acts in conjunction with other physiological processes to increase drought resistance.

The increase in dry matter content is rapidly reversed during a period of rapid growth. After twenty-five days in culture, the dry matter content of all hardened F. spiralis had decreased to the pre-hardening level (Table 43). Only the unhardened plants whose growth had been curtailed by the forty-four hour desiccation contained a higher percent dry matter at the end of the culture period. This suggests that a few weeks of rapid growth under favourable conditons may reverse the drought-hardening process.

Further experiments were undertaken to determine whether drought resistence in natural populations varies according to local environmental conditions. Samples of F. spiralis were collected from both the upper and lower part of its zone. Five plants from each level were dried for two days in the laboratory, and five control plants for each level were retained in seawater in the 9°C culture room. After the drying period,

Table 43: Percent dry matter, colloidal water content, and survival after forty-four hour exposure at 25-27°C water potential -900 to -960 bars measured in unhardened and hardened plants of Fucus spiralis. Figures represent mean ± standard deviation.

| | percent dry matter (n=5) | percent of water retained (n=5) | grams water retained per 100g. dry matter (n=5) | initial weight loss (n=25) | ratio of air-dry weight to wet weight, % (n=25) |
|---|---|---|---|---|---|
| hardened | 25.0 ± 2.7 | 5.1 ± 0.8 | 15.2 ± 0.8 | 2.4 ± 1.1 | 27.0 ± 1.2 |
| unhardened | 20.9 ± 1.2 | 4.0 ± 0.2 | 15.0 ± 0.9 | 13.5 ± 3.2 | 24.4 ± 1.7 |

| | n | linear growth mm in 25 days | relative weight gain %in 25 days | condition of thallus after 25 days | mean survival index | percent dry matter at end of 25 days in culture |
|---|---|---|---|---|---|---|
| hardened and dried 44 hrs. | 10 | 14.2 ± 1.8 | 129.4 ± 31.9 | slight damage on blade near base | 15.0 | 21.4 ± 1.4 |
| unhardened and dried 44 hrs. | 10 | 4.6 ± 3.8 | 15.9 ± 21.5 | moderate damage some "burning" near tips | 8.6 | 24.3 ± 1.9 |
| hardened controls | 5 | 16.2 ± 3.0 | 131.0 ± 20.2 | very slight damage on blade near base | 16.0 | 21.1 ± 0.7 |
| unhardened controls | 5 | 19.5 ± 2.8 | 130.8 ± 6.9 | no damage | 16.0 | 21.0 ± 0.5 |

the experimental and control plants were grown for fifteen days in culture. The plants collected from the lower part of the zone were affected a little more by the experimental stress than those collected from the upper part (Table 44). This suggests that the more severe conditions in the upper zone had somewhat hardened the F. spiralis growing at that level. An attempt was made to demonstrate a similar effect in Pelvetia. Young plants were collected from a dry, exposed site in the upper half of the Pelvetia zone, and from a second site lower in the zone which was protected from the wind. They were dried for four days in the warm room, and resubmerged overnight to compare the initial weight change. The experimental stress did not seem to affect the plants, and initial weight change was as small in

the plants from the sheltered site (-4.1 ± 0.6%) as in those from the exposed site (-4.0 ± 1.0%).

Table 44: Drought tolerance in samples of Fucus spiralis collected from the upper and lower parts of its zone. Mean ± standard deviation of growth rates after forty-eight hours exposure at 15-22°C, relative humidity not recorded.

| | n | linear growth mm in 15 days | relative weight gain, % in 15 days | condition of thalli after 15 days in culture |
|---|---|---|---|---|
| Plants from upper part of zone | | | | |
| desiccated | 5 | 0.8 ± 1.4 | 6.5 ± 8.1 | severely damaged, but tips alive |
| control | 5 | 5.6 ± 0.8 | 32.3 ± 7.6 | good |
| Plants from lower part of zone | | | | |
| desiccated | 5 | -0.3 ± 0.9 | -3.8 ± 4.8 | severely damaged, tips appear to be dead |
| control | 5 | 6.3 ± 1.1 | 42.7 ± 7.2 | good |

The effects of local environmental conditions upon drought tolerance were also investigated by means of transplantation. Young plants of Pelvetia and F. spiralis were transplanted to a site near MTL (1.9m above chart datum) at Port Loy (Figure 3), and allowed to grow for five and one-half months to determine whether the natural drought-hardiness of these two species would diminish under midshore conditions. A second set was simultaneously transferred to the F. spiralis zone (2.75 m above chart datum) and grown for the same five and one-half month period. Then the plants were collected from both levels and their drought tolerance was compared. Photosynthesis of four or five samples of each species from each level was measured before and three hours after the end of an experimental exposure in the laboratory. Dry matter content was also determined, using six to ten samples of each species from each level. Oxygen evolution rate of the F. spiralis transferred to the midshore was

much more severely affected by the experimental drying than that of the F. spiralis transferred into its own zone (Table 45). Also, the midshore plants grew considerably faster during the five and one-half months after transplantation, and ultimately contained a lower percent dry matter than the plants transferred to the upper shore. Apparently, a "dehardening" process accompanied by a decrease in dry matter content was induced by transfer to the favourable midshore habitat. Dehardening was less pronounced in Pelvetia, although still statistically significant (Table 45). Drought tolerance appears to be more readily influenced by environmental conditions in F. spiralis than it is in Pelvetia.

Table 45: Percent dry matter, and effect of desiccation upon photosynthesis in Pelvetia and F. spiralis (mean ± standard deviation) transplanted to the upper shore and to the middle shore five and one-half months prior to the determination. Plants were dried at 20-23°C, -485 to -305 bars water potential. F. spiralis was exposed for 42 hours, Pelvetia for 92 hours. t values are given for difference between upshore and midshore plants. * = $p < 0.05$ ** = $p < 0.01$

Oxygen evolution, μ moles/g wet wt-hr

| | n | rate before drying | rate after drying and 3 hrs recovery in seawater | percent of original rate | n | percent dry matter |
|---|---|---|---|---|---|---|
| Pelvetia | | | | | | |
| 2.75m above chart datum | 5 | 24.2 ± 1.8 | 19.9 ± 1.8 | 82 ± 6 | 10 | 28.7 ± 0.9 |
| 1.90m above chart datum | 5 | 27.6 ± 2.9 | 18.7 ± 0.7 | 68 ± 3 | 10 | 29.8 ± 2.0 |
| t | | 2.22 | 1.39 | 5.13** | | 1.58 |
| Fucus spiralis | | | | | | |
| 2.75m above chart datum | 5 | 21.7 ± 5.3 | 16.1 ± 2.3 | 76 ± 13 | 6 | 27.1 ± 1.6 |
| 1.90m above chart datum | 4 | 25.8 ± 4.6 | 9.8 ± 2.6 | 38 ± 7 | 10 | 24.4 ± 1.8 |
| t | | 1.30 | 3.89* | 5.77* | | 2.92* |

### 3.8.4 The effect of plant size on drought tolerance

Field observations indicate that very small F. spiralis plants are sometimes more severely affected by desiccation than larger plants, possibly because they are more sensitive, and possibly because they dry out much more rapidly than the larger plants. An experiment was carried out to determine whether very young plants are intrinsically less drought tolerant than older plants. Fifteen small plants and fifteen larger plants each of Pelvetia and F. spiralis were collected and subjected to a thirty-nine hour exposure. During the initial phase of drying, the plants were exposed in the laboratory, and the small plants of each species were sheltered under petri dishes to prevent excessively rapid drying. The tiny Pelvetia samples became dehydrated faster than the larger plants despite this precaution, but the smaller and larger F. spiralis plants dried at similar rates. When all the plants were nearly air-dry, they were transferred to the warm room for thirty-nine hours, resubmerged and cultured for ten days. The small and large Pelvetia plants were equally resistant to the experimental stress (Table 46). Since small Pelvetia plants normally grow very slowly, the difference in linear growth rate between the two groups is probably not related to drought stress. Small plants of F. spiralis were much more severely affected than larger plants, although they had not dried more quickly (Table 46). Also, the dry matter content of these small plants was lower than that of the larger plants.

The relationship between plant size and drought tolerance was investigated further, using the data obtained from the fifty F. spiralis plants whose drought tolerance and dry matter content were correlated in Figures 27-29. The correlation was much less pronounced for plant size than for dry matter content, but was still significant at the 5% level (Figure 31). Some of the small plants were as drought-hardy as the largest ones, while others were very sensitive. This variability is understandable, for some small plants grow in exposed positions while others grow under the protection of larger plants. The former may have undergone a greater degree of natural hardening than the latter.

Table 46: Percent dry matter, and survival and growth after desiccation in small and large plants of Pelvetia and F. spiralis (mean ± standard deviation) plants were dried for thirty-nine hours at 25-27°C, water potential -815 to -1015 bars.

| Species | n | initial wet weight, mg | initial weight change | linear growth mm in 10 days | relative weight gain, % in 10 days | survival index | percent dry matter (n=5) |
|---|---|---|---|---|---|---|---|
| Pelvetia | 15 | 3-19 | -6.0 ± 5.0 | 0.8 ± 0.5 | 22.2 ± 6.3 | 12.8 ± 0.9 | not determined |
| | 14 | 192-723 | -2.0 ± 1.2 | 2.3 ± 0.8 | 19.0 ± 3.7 | 13.9 ± 1.0 | 26.1 ± 0.2 |
| F.spiralis | 15 | 36-80 | -20.0 ± 6.0 | -0.9 ± 1.4 | -20.2 ± 9.8 | 2.9 ± 2.3 | 19.3 ± 1.9 |
| | 15 | 342-710 | -9.5 ± 3.6 | 2.2 ± 2.2 | 7.1 ± 10.6 | 9.3 ± 2.9 | 23.7 ± 0.4 |

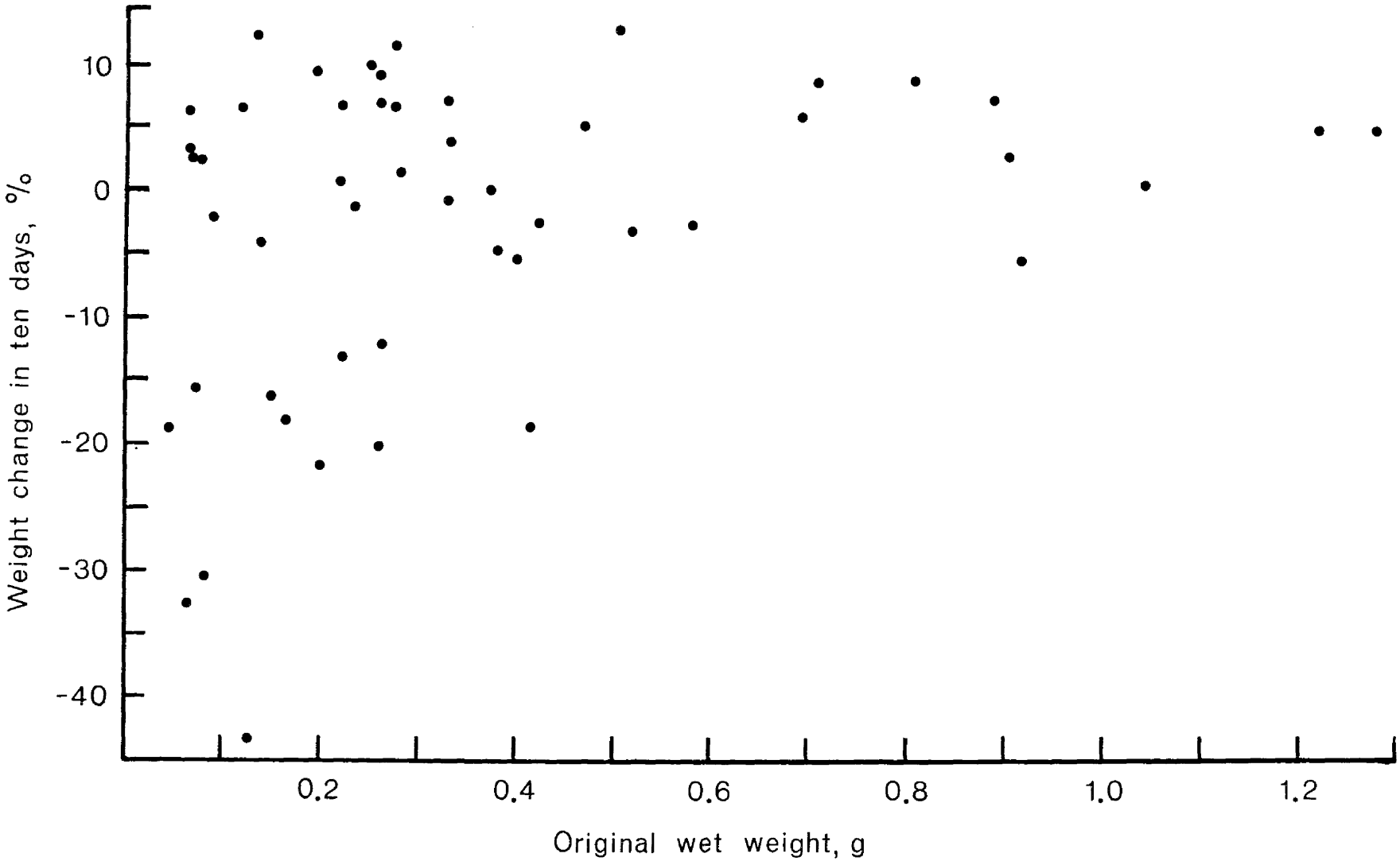



Figure 31: Relationship between relative weight gain in ten days and initial wet weight in fifty plants of Fucus spiralis dried forty-two hours at 25.6 - 27.1 °C, water potential -845 to -990 bars. Correlation coefficient 0.309, $p < 0.05$.

## 3.9 Effects of limited availability of nutrients and dissolved carbon dioxide upon growth of upshore fucoids

In the previous sections, the relationship between drought resistance and upper distributional limits of the different fucoids was clearly established. However, in order to grow and mature on the upper shore, Pelvetia and F. spiralis must also obtain an adequate supply of mineral nutrients, carbon dioxide and oxygen. Marine organisms obtain these substances in dissolved form from the sea, but upshore species are exposed most of the time, and must be capable of absorbing an adequate supply during brief submersions. Therefore upshore fucoids might be expected to possess special physiological adaptations by which they can absorb nutrients rapidly, and possibly utilize carbon dioxide directly from the atmosphere for photosynthesis. These possibilities were investigated in culture by means of simulated tidal cycles, as described in section 2.4.5. Since the plants were placed in a tank covered with a glass plate and kept in the 8-10°C culture room during simulated tidal exposure, they underwent little desiccation and were not subjected to other physical stresses. Therefore, the effects of limited availability of dissolved nutrients and respiratory gases upon survival and growth could be studied in the absence of these complicating factors.

### 3.9.1 Comparison of growth rates in Pelvetia, Fucus spiralis and F. serratus under three different tidal regimes

The tidal simulation apparatus described in Appendix C was used to produce three different semidiurnal tidal cycles: one, six and eleven hours submersion in every twelve hours. Fifteen plants each of Pelvetia, Fucus spiralis and F. serratus were cultured in each tidal cycle, in culture medium diluted ten times in seawater. Linear growth, relative weight gain and rate of initiation of new apices were measured over a period of forty-two days.

All three species survived and grew under all three tidal regimes. Pelvetia and F. spiralis grew almost as rapidly in length and weight when submerged only one hour in every twelve as they did when submerged eleven hours (Table 47). F. spiralis remained healthy and the apices maintained a normal appearance in all three cycles. However, the apices of Pelvetia

became abnormally narrow and developed small brown necrotic spots near the apical pit, particularly when submerged six or eleven hours per twelve. The possibility that prolonged submersion may have an adverse effect upon Pelvetia will be discussed in chapter 4.

F. serratus grew progressively faster with increasing duration of submersion, and the differences between the growth rates of the plants in the one-hour and eleven-hour cycles were highly significant (Table 47).

Table 47: Linear growth, relative weight gain (mean ± standard deviation) and increase in mean number of apices of Pelvetia, F. spiralis and F. serratus in three tidal cycles. n=15 for each species in each cycle. t values for difference between one hour and eleven hour cycles
* = $p < 0.05$ *** = $p < 0.001$.

| | Tidal cycle, hours submerged per twelve | | | |
|---|---|---|---|---|
| | One | Six | Eleven | t |
| **Pelvetia** | | | | |
| linear growth, mm/month | 4.4 ±0.9 | 3.7 ±1.1 | 4.5 ±1.1 | 0.28 |
| percent wt.gain per day | 1.75 ± 0.23 | 1.81 ± 0.27 | 2.05 ± 0.36 | 2.73* |
| initial number of apices | 8.4 | 8.7 | 8.8 | |
| no.of apices after 42 days | 11.7 | 11.9 | 12.9 | |
| percent increase | 39 | 37 | 47 | |
| **F. spiralis** | | | | |
| linear growth, mm/month | 11.1 ±± 2.0 | 11.4 ± 2.4 | 12.9 ± 2.9 | 1.97 |
| percent wt.gain per day | 2.29 ± 0.20 | 2.14 ± 0.33 | 2.41 ± 0.22 | 1.57 |
| initial number of apices | 2.5 | 2.7 | 2.4 | |
| no.of apices after 42 days | 3.7 | 4.5 | 4.4 | |
| percent increase | 48 | 67 | 91 | |
| **F. serratus** | | | | |
| linear growth, mm/month | 8.9 ± 2.5 | 13.6 ± 1.2 | 16.6 ± 1.5 | 10.1*** |
| percent wt.gain per day | 1.57 ± 0.46 | 2.26 ± 0.22 | 2.59 ± 0.24 | 7.58*** |
| initial number of apices | 1.8 | 1.8 | 1.7 | |
| no.of apices after 42 days | 2.5 | 3.0 | 3.3 | |
| percent increase | 39 | 67 | 94 | |

The plants remained healthy in the six and eleven-hour submersions, and the apices became noticeably wider in the latter, which reflects the vigorous growth of the plants. In the one-hour submersion, the tips became distinctly narrowed, and linear growth tended to decrease toward the end of the forty-two day period.

These results show that Pelvetia and F. spiralis are both well adapted to the limited availability of dissolved nutrients on the upper shore, and that F. serratus is somewhat less so. Furthermore, the two upshore species either can utilize carbon dioxide from the atmosphere, or can absorb and store large quantities of dissolved inorganic carbon during brief submersions and utilize this supply for photosynthesis while exposed.

### 3.9.2 Adaptations of upshore fucoids to nutrient scarcity associated with tidal exposure

Since percent tidal submersion is considerably less in the Pelvetia zone than in the F. spiralis zone, the former species is subjected to a greater degree of nutrient scarcity. Therefore, experiments were designed to compare the abilities of these two species to grow despite a limited supply of dissolved mineral nutrients. The growth rates of these two species were compared under two different tidal regimes and in culture media containing different concentrations of added nutrients. Diurnal tidal cycles of four hours submersion and twenty hours submersion per day were simulated manually. In the first experiment, twenty-five plants of each species were grown in each tidal regime in the fully enriched medium detailed in Appendix A. Linear growth was measured over a forty-two day period. Relative weight gain could not be determined because the plants became heavily contaminated and tended to decay, especially in the twenty-hour submersion.

The experiment was repeated three times using 1/5 concentration and 1/20 concentration media, and unenriched seawater. The initial sample size in these three determinations was ten plants of each species in each treatment but in some cases one or two plants broke and were lost. Linear growth and relative weight gain were measured over a thirty-nine day period in the unenriched seawater, and over a fifty-six day period in the 1/5 and 1/20 concentration media. In the latter two, the plants were measured after twenty-eight days and again after fifty-six days to determine whether they became adapted to the culture conditions and grew faster during the latter part of the experiment.

Pelvetia gradually decayed when submerged twenty hours per day in

1/5 concentration medium, and only linear growth over the first half of the culture period could be measured. F. spiralis developed a heavy cover of epiphytes when submerged twenty hours per day, and these epiphytes were scraped off before the final weighing. They were not removed before the weighing after twenty-eight days in the 1/5 and 1/20 concentration media because scraping would have damaged the plants' epidermis; hence the observed weights of the plants after twenty-eight days were a little higher than the true weights. Therefore, the relative weight gains determined for the first twenty-eight days were a little higher than the true values, and those determined for the second twenty-eight days a little lower than the true values.

The effects of nutrient scarcity associated with short tidal submersions was clearly demonstrated in both Pelvetia and F. spiralis (Table 48). When submerged twenty hours per day, both species grew rapidly in 1/20 concentration medium, and seemed to be somewhat nutrient-limited only in the unenriched seawater. Growth rates were slower in F. spiralis in full concentration, and in Pelvetia in 1/5 concentration because these enriched media seemed to promote decay of the thalli. Nutrient limitation was much more pronounced when the plants were submerged only four hours per day. Their growth rates decreased progressively with decreasing concentration of the medium (Table 48). Initially, Pelvetia seemed to be more capable of growing on a limited nutrient supply than F. spiralis. When submerged four hours per day in unenriched seawater, Pelvetia gained weight very slowly, while F. spiralis lost a small but statistically significant amount of weight, and grew in length at the expense of its own reserves (Table 48). Also, during the first twenty-eight days, relative weight gain was much lower in F. spiralis than in Pelvetia when submerged four hours per day in the 1/20 and 1/5 concentration media. However, F. spiralis quickly adapted to the limited nutrient supply, and grew much more rapidly during the second twenty-eight days. Pelvetia also adapted, but to a lesser degree, so that its relative weight gain during the second half of the culture period was considerably less than that of F. spiralis.

The large difference in growth rates between the four- and twenty-hour submersions in 1/5 and 1/20 concentration media were surprising, since both Pelvetia and F. spiralis grew almost as rapidly in the one-hour semi-

Table 48: Mean ± standard deviation of linear growth and relative weight gain of Pelvetia and Fucus spiralis grown in four different culture media under two different tidal cycles.
(n = number of plants measured at beginning and end of culture period)

| concentration of medium | culture period | Pelvetia submerged 4 hours per day n | linear growth mm/month | relative weight gain %/day | Pelvetia submerged 20 hours per day n | linear growth mm/month | relative weight gain %/day |
|---|---|---|---|---|---|---|---|
| 1 | 42 days | 25 | 5.6 ± 2.4 | not measured | 25 | 7.8 ± 2.4[b] | not measured |
| 1/5 | first 28 days | 10 | 5.0 ± 1.5 | 0.82 ± 0.29 | 10 | 5.1 ± 2.8 | not measured |
| | second 28 days | 10 | 4.8 ± 1.4 | 1.23 ± 0.31 | | decayed | decayed |
| 1/20 | first 28 days | 10 | 3.3 ± 1.6 | 0.29 ± 0.22 | 9 | 8.6 ± 2.4 | 2.27 ± 0.38 |
| | second 28 days | 10 | 2.3 ± 1.7 | 0.66 ± 0.41 | 8 | 5.8 ± 1.0 | 2.19 ± 0.61 |
| unenriched | 39 days | 10 | 1.7 ± 0.6 | 0.16 ± 0.06 | 10 | 5.3 ± 0.9 | 1.13 ± 0.38 |

| concentration of medium | culture period | Fucus spiralis submerged 4 hours per day n | linear growth mm/month | relative weight gain %/day | Fucus spiralis submerged 20 hours per d n | linear growth mm/month | relative weight gain %/day |
|---|---|---|---|---|---|---|---|
| 1 | 42 days | 25 | 15.1 ± 3.7[α] | not measured | 25 | 12.2 ± 4.4[c] | not measured |
| 1/5 | first 28 days | 10 | 3.9 ± 1.3 | 0.30 ± 0.47 | 10 | 18.6 ± 2.8 | 3.88 ± 0.58 |
| | second 28 days | 10 | 5.0 ± 1.4 | 2.14 ± 0.61 | 10 | 22.8 ± 6.3 | 2.86 ± 0.55 |
| 1/20 | first 28 days | 10 | 3.4 ± 1.5 | 0.19 ± 0.47 | 10 | 18.2 ± 3.8 | 4.21 ± 0.55 |
| | second 28 days | 10 | 5.5 ± 1.8 | 1.27 ± 0.33 | 9 | 24.9 ± 5.0 | 2.76 ± 0.44 |
| unenriched | 39 days | 10 | 1.5 ± 0.9 | -0.32 ± 0.26 | 10 | 10.9 ± 1.5 | 2.22 ± 0.42 |

α 12.2 mm/month during first fifteen days, increasing to about 17mm/month during final fourteen days.
b growth rate during first fifteen days only; plants decayed rapidly thereafter.
c 17.4 mm/month during first fifteen days. Plants grew more slowly and decayed somewhat thereafter.

diurnal cycle as in the eleven-hour cycle in the tidal simulator, in which 1/10 concentration medium was used (Table 47). The different results of these two experiments may reflect a seasonal physiological change in the plants. The experiments with the 1/5 and 1/20 concentration media were carried out on material collected in January, when nitrate and phosphate concentrations in the Firth of Clyde are at a maximum (Hinton 1974). The automatic simulation was done on plants collected in June, at which time these nutrients are at their minimum concentrations. Therefore, the plants cultured in the automatic apparatus may have been so well adapted to low nutrient concentrations that they could absorb an adequate supply during only two hours daily submersion in 1/10 concentration medium.

### 3.9.3 Utilization of atmospheric carbon dioxide by upshore fucoids

The utilization of atmospheric carbon dioxide by exposed fucoids has been investigated by means of $^{14}CO_2$ uptake, manometry and other standard photosynthetic measurements (Bidwell and Craigie 1963, Kremer & Schmitz 1973, Johnson et al 1974, Brinkhuis and Tempel 1975). The results have been very inconsistent, and the question of whether upshore fucoids can fix atmospheric carbon dioxide and form new tissue while exposed remains unanswered. Therefore, I compared the rate of growth based entirely upon photosynthesis in a damp atmosphere with that based entirely on photosynthesis while submerged. This was done in the following manner. Two plates, each bearing fifteen F. spiralis and fifteen Pelvetia were cultured in a twelve hour exposed/twelve hour submerged diurnal tide cycle. Each day, the plates were exchanged at 1100 and at 2300 hours between an empty tank and a tank containing five litres of 1/10 concentration culture medium. At 2300 hours an opaque box was placed over both tanks, and the aeration tubes were inserted through small, tight-fitting holes in the box. At 1100 hours the box was removed. In this way, each plate received twelve hours light and twelve hours darkness, and twelve hours submersion per day. One plate was submerged and the other exposed during the entire light period.

A stream of air was passed through the dry tank to prevent depletion of carbon dioxide during the day, and of oxygen at night. The air was pumped through a closed bottle of water to humidify it to near saturation before being delivered to the tank via a length of plastic tubing.

Table 49: Comparison of growth rates (mean ± 1 standard deviation) in Pelvetia and F. spiralis exposed during light period with growth rates in plants submerged during light period. n=15 for each species in each treatment.

| | Submerged and illuminated 1100 - 2300 hours; Exposed and dark 2300 - 1100 hours. | | Exposed and illuminated 1100 - 2300 hours; Submerged and dark 2300 - 1100 hours | |
|---|---|---|---|---|
| | Linear growth mm/month | Percent weight gain per day | Linear growth mm/month | Percent weigh gain per day |
| Pelvetia | | | | |
| 25 July-7 August | 8.3 ± 2.4 | 2.18 ± 0.27 | 5.3 ± 1.2 | 1.16 ± 0.22 |
| 7 - 18 August | 8.2 ± 1.9 | 2.47 ± 0.47 | 5.2 ± 1.2 | 1.15 ± 0.31 |
| 25 July-18 August | 8.1 ± 1.8 | 2.31 ± 0.27 | 5.1 ± 0.9 | 1.15 ± 0.20 |
| Fucus spiralis | | | | |
| 25 July-7 August | 16.6 ± 2.8 | 2.34 ± 0.38 | 10.6 ± 2.5 | 1.01 ± 0.49 |
| 7-18 August | 18.8 ± 2.7 | 2.95 ± 0.41 | 9.3 ± 2.5 | 1.29 ± 0.28 |
| 25 July-18 August | 17.6 ± 2.5 | 2.62 ± 0.35 | 10.0 ± 2.2 | 1.15 ± 0.20 |

Length and weight were measured initially, after thirteen days and twenty-four days to determine whether the plants could maintain steady growth rates when exposed during the light period. Steady growth in length and weight was observed in both species in this regime, as well as when submerged during the light period. Therefore the plants were fixing atmospheric carbon dioxide and utilizing it to form new tissue, and were not growing in length at the expense of tissue reserves. However, both species grew much more slowly when exposed during the light period than when submerged during the light period (Table 49). Also the two species grew equally slowly in weight when exposed during the light period. Therefore Pelvetia does not appear to utilize atmospheric carbon dioxide more efficiently than does F. spiralis, and both species utilize carbon dioxide more efficiently from seawater.

This result contrasts with that obtained with the tidal simulator, in which Pelvetia and F. spiralis grew rapidly when submerged only one hour per twelve (Table 47). In this regime, the plants were submerged only

one hour per day while illuminated. In this case, the differences cannot be attributed to seasonal physiological changes, since both experiments were performed on summer-collected material. The results therefore suggest that the plants can absorb and accumulate large quantities of dissolved inorganic carbon during brief submersions, and utilize this store to supplement the slow absorption of gaseous carbon dioxide during exposure. Such rapid absorption must be a light-dependent phenomenon, since it does not seem to occur during nighttime submersion in culture.

Another possible explanation is that the products of photosynthesis during exposure are chemically different, or are utilized differently, from those formed during submersion. The latter may contribute to a rapid growth of new tissue with a low dry matter content, while the former may tend to accumulate in the cells as solutes, or may be converted into specific substances which increase resistance to dehydration or other stresses. In order to test this possibility, the dry matter content of five plants from each treatment was determined, and another ten were used to estimate drought tolerance. The latter were weighed, air-dried in the warm room, soaked for twelve hours, and reweighed to determine the initial weight loss.

Table 50: Mean ± standard deviation of percent dry matter, colloidal water content and initial weight change after drying at 27.8 - 29.4°C, 34-38% relative humidity, in Pelvetia and F. spiralis, measured after 24 days in two tidal regimes. Pelvetia dried for 48 hours; F. spiralis for 36 hours.

| | submerged and illuminated 1100-2300 hours; exposed and dark 2300-1100 hours | exposed and illuminated 1100-2300 hours; submerged and dark 2300-1100 hours |
|---|---|---|
| Pelvetia | | |
| percent dry matter (n=5) | 25.3 ± 1.9 | 26.9 ± 0.8 |
| colloidal water at end of drying period; grams/100g dry matter (n=5) | 8.1 ± 0.6 | 9.2 ± 0.9 |
| initial weight change (n=10) | -7.3 ± 3.2 | -5.3 ± 3.4 |
| Fucus spiralis | | |
| percent dry matter (n=5) | 22.1 ± 1.6 | 25.6 ± 1.5 |
| colloidal water at end of drying period; grams/100g dry matter (n=5) | 7.4 ± 0.2 | 7.5 ± 0.3 |
| initial weight change (n=10) | -19.1 ± 3.20 | -22.2 ± 4.0 |

In both species, percent dry matter was somewhat higher in the plants that had been exposed during the light cycle than in those which had been submerged during the light cycle. However, drought resistance in plants grown in the two regimes was similar (Table 50). Therefore, some photosynthates may have accumulated in the cells of the plants that were exposed during illumination, but there was no apparent increase in drought tolerance associated with the increased dry matter content.

## 3.10 Discussion

Intertidal organisms commonly have well defined upper limits on the shore, which appear to be determined by exposure to atmospheric conditions. This is confirmed by the observation that many species reach their upper limits near MHWN (Colman 1933, Lewis 1964), above which the duration of tidal exposure increases abruptly. Critical tide levels are even more marked on the Pacific shores of the northwest United States (Doty 1946). The mixed semidiurnal-diurnal tides of these shores produce several critical levels at which the longest tidal exposure increases by a factor of two or three, and the upper limits of many organisms correspond with these levels.

Experiments have shown that intertidal fucoids cannot survive at levels above those which they occupy. Fucus spiralis and F. serratus died when transplanted above their upper limits (Table 5), and Hatton (1938) reported the same result with F. vesiculosus and Ascophyllum. The upper limits of these seaweeds are apparently controlled by the gradient of increasing exposure to atmospheric conditions.

Desiccation seems to be the most critical stress to which seaweeds are subjected during tidal exposure. Many species extend further upshore wherever they are protected from desiccation by repeated wave splash (Burrows et al. 1954; Lewis 1964), or by an overlying canopy of larger algae (Fischer 1929; Menge 1975), or by inhabiting shady crevices or north-facing slopes (Johnson & Skutch 1928; Fischer 1929; Zaneveld 1937; Hatton 1938). Hatton also found that the survival of his transplants of F. vesiculosus and Ascophyllum could be prolonged by transferring them in dense clumps which dry more slowly than single plants, or by placing them beneath large Pelvetia plants.

Desiccation was also observed to regulate the seasonal fluctuation in the upper limit of Fucus spiralis on the Isle of Cumbrae. Germlings of this species which became established in the lower Pelvetia zone during the winter were invariably killed by the first prolonged exposure to dry weather in the spring. Fluctuations in the upper limits of Pelvetia and Ascophyllum are less readily observed largely because their early stages develop very slowly. Embryos which settle during autumn at levels above their upper limits would be killed by drought the following summer before they become conspicuous. Nevertheless, "burning" was observed in a few of the highest Ascophyllum at those times when the uppermost F. spiralis were similarly affected, and the entire upper third of the Pelvetia zone was killed by drought in spring 1974. Recolonization of the upper Pelvetia zone did not occur during the present study probably because the prolonged dry spells of 1975 and 1976 removed the first-year plants while they were still microscopic.

Laboratory experiments confirmed that desiccation is the primary critical factor governing the upper limits of fucoids. Firstly, experimental plants showed reduced photosynthesis rates and developed tissue damage after being dried for five hours at a temperature and relative humidity similar to those found during summer at Isle of Cumbrae (Table 21). Secondly, in a large number of experiments (summarized in Table 51), the extent to which the different fucoids were affected by desiccation correlated consistently with their relative positions on the shore gradient. The same correlation was observed by Baker 1909, 1910) in cultures of Ascophyllum and Fucus in which the plants were subjected to a semidiurnal "tidal" exposure in a drying atmosphere. Montfort (1937) and Sandgren (1973) also found that F. spiralis resumed photosynthesis more rapidly and completely after an experimental desiccation than did midshore Fucus species. Similar correlations between desiccation tolerance and distributional ranges have been reported for other algal species (Biebl 1952), intertidal limpets (Branch 1975) and barnacles (Connell 1961).

It was found that Pelvetia, F. spiralis, Ascophyllum and F. vesiculosus can all survive dehydration to air-dryness, and differ

Table 51: Relationship between severity of effects of dehydration stresses upon different fucoids and their relative positions on the shore. Species are listed from high to low shore.

| Experimental stress | Duration | Method of assessment | Relative severity of effect of stress |
|---|---|---|---|
| 19-21°C, $\psi_w$ = -425 to -565 bars | 26 hours | oxygen evolution | Pelvetia < F. spiralis < Ascophyllum < F. serratus |
| 19-21°C, $\psi_w$ = -480 to -580 bars | 24 hours | oxygen evolution | Pelvetia$^{\alpha}$ ~ F. spiralis$^{\alpha}$ < Ascophyllum |
| 20-27°C, $\Psi_w$ not recorded | 90 hours | oxygen evolution | Pelvetia < F. spiralis |
| 25.5 - 27°C, $\psi_w$ - 900 to -1015 bars | 5 hours | oxygen evolution, survival and growth | Pelvetia$^{\alpha}$ < F. spiralis < F. serratus |
| 23.8 - 26.7°C, $\psi_w$ = -720 to -970 bars | 12 hours | survival and growth | Pelvetia$^{\alpha}$ < F. spiralis < F. vesiculosus |
| | 24 hours | survival and growth | Pelvetia$^{\alpha}$ < F. spiralis < F. vesiculosus |
| 6-9°C, $\psi_w$ = - 275 to -305 bars | 7 days | survival and growth | Pelvetia$^{\alpha}$ < F. spiralis < F. serratus |

$\alpha$ no adverse effects observed

largely in the duration for which they can tolerate this stress. This reflects the nature of the shore gradient, since different levels are exposed to the same atmospheric conditions but for different lengths of time. The duration of experimental stress each species could tolerate was actually shorter than the longest tidal exposures occurring at its upper distributional limit (Table 52). This discrepancy probably arose because the plants were subjected to a more severe stress in the laboratory than they are in nature. For example, the experimental plants dried much more quickly than individuals in natural stands, in which they are protected by their neighbours. Also, the test plants were maintained constantly at 24-29°C, but in nature, relatively cool and humid conditions at night may provide partial relief during a prolonged exposure.

Although the upper limits of fucoids are determined largely by desiccation, other physical factors may play an important role by modifying the physiological effects of dehydration. This appears to be particularly true of temperature, as fucoids survived experimental exposure for longer periods when dried at lower temperatures (Table 52). One possible explanation of the observed temperature effect is that the rate of desiccation, being proportional to water vapour pressure deficit, increases rapidly with temperature at any given relative humidity. Rapidity of dehydration influences the degree of damage in many plants (Levitt 1972), and may also do so in fucoids. Moreover, the hygroscopic (water-binding) capacity of fucoid tissues is lower at 25°C than at 9°C (Table 27); hence dehydration becomes more severe at a given water potential as temperature rises. However, when these two possibilities were eliminated by experimental design, more severe drought damage was still observed in plants kept air-dry at 25°C than at 9°C. This temperature effect is undoubtedly important in nature, since summertime air temperatures often reach 25°C, and intense insolation may heat intertidal fucoids to 30-40°C (Schramm 1968). Schramm found that F. vesiculosus was more severely affected by desiccation at 30-40°C than at 20°C, and concluded that heat stress rather than dehydration is the most important cause of damage to natural populations of this species. However, prolonged exposure during spring dry spells resulted

Table 52: Comparison between longest tidal exposure at the upper limits of the fucoid species and their drought tolerances as measured in the laboratory. Mean and extreme longest tidal exposures defined as in Figure 2.

| species | upper limit on sunny exposures, m above chart datum | longest tidal exposure at upper limit, days mean | extreme | maximum observed duration of survival at 24-29°C, 30-60% relative humidity | maximum observed duration of survival at lower temperatures |
|---|---|---|---|---|---|
| Pelvetia | 3.3 | 11.8 | 27 | 6 days[α] | 14 days[α] (9°C, 50% relative humidi |
| F. spiralis | 2.9 | 3.6 | 7.5 | 2 days[b] | 4 days[b] (20-24°C, relative humidit not recorded) |
| | | | | | 7 days[b] (9°C, 79-81% relative humidity) |
| Ascophyllum | 2.7 | 1.5 | 5 | 7 hours[b] | 1 day[b] (20-24°C, relative humidit not recorded) |
| F. vesiculosus | 2.5 | 0.7 | 2 | 6 hours[c] | |
| F. serratus | 2.2 | submerged twice daily even during smallest neap tides | | died after 5 hours | |

α Healthy. Plants died after 14 days at 25°C, 50% relative humidity in separate experiment.

b Slightly to moderately damaged.

c Severely damaged.

in widespread damage to F. spiralis at Isle of Cumbrae although daily maximum temperatures during these exposures were only 10-18°C. Since it is unlikely that the seaweeds were heated to critical temperatures during these exposures, the damage probably resulted from drought.

In order to study heat tolerance in the absence of other stresses, Kanwisher (1966), Biebl (1972), and Feldman & Lutova (1963) performed experiments on submerged algae. Unfortunately, such tests are of doubtful relevance to the present study, for within the geographic ranges of Fucus spp, Pelvetia and Ascophyllum, seawater temperatures never reach critical levels. Therefore, these seaweeds are subjected to heat stress in nature only while exposed and undergoing dehydration. Such dehydration may be important to their survival, as it enhances their heat tolerance by several degrees Celsius (Schramm 1968, Biebl 1972). Moreover, high temperature during exposure causes the most severe injury when the plants are only partially dehydrated owing to high atmospheric humidity. This damaging combination of hot and humid conditions may be of critical importance during the summer, since relative humidity is often high in the immediate vicinity of the sea.

Seaweeds may also be exposed to extremely low temperatures during low tide, and arctic fucoids are often frozen solid in ice. However, they resume normal photosynthesis immediately upon thawing (Kanwisher 1957), and even temperate populations of midshore fucoids demonstrate frost tolerances of -20° to -35°C (Parker 1960; Feldman & Lutova 1963; Biebl 1972; Bird & McLachlan 1974). Since the lowest temperature recorded on British coasts is about -16°C (Lewis 1964), freezing is not an important factor on these shores.

Another modifying factor is rainfall during tidal exposure. This might mitigate stress by preventing or interrupting desiccation, but, being fresh water, it may also cause an osmotic shock. Rainfall has been reported to damage some intertidal seaweeds (den Hartog 1968; Edelstein & McLachlan 1975), and to retard the growth rate of Pelvetia (Hatton 1938). Den Hartog (1968) stated that exposure to fresh water, rather than desiccation, is the primary critical factor of the shore gradient. He cited as evidence the lowering of the upper limits of

intertidal organisms in estuaries in which a surface layer of very low salinity lies over a deeper layer of higher salinity. However, tidal submersion in brackish water is qualitatively different from exposure to rain. Such exposure in itself does not appear to be an important stress, as F. spiralis germlings continued to grow within the Pelvetia zone during the wet winter of 1974-75, and simulated rainfall exerted only a mild effect on fucoids in culture. However, simulated rainfall upon air-dry plants compounded drought injury. Sudden rehydration by fresh water might create a damaging osmotic shock, which may explain the adverse effects of rainfall reported by other investigators.

Since desiccation has clearly emerged as the primary critical factor associated with the shore gradient, it is logical to consider what adaptations the upshore fucoids have evolved to survive prolonged drying. Higher plants avoid tissue desiccation by means of stomata which regulate transpiration rates, and roots which absorb water from the soil, but lower plants lack these structures, and do not often show true drought avoidance (Levitt 1972). Nevertheless, several workers have tried to determine whether the upshore fucoids can retard their tissue water loss and thus avoid complete dehydration during tidal exposure. Zaneveld (1937) found that relative rates of water loss during an experimental exposure decreased in the order F. serratus > F. vesiculosus > Ascophyllum > F. spiralis, and concluded that the slower desiccation rate of the higher-growing species was of ecological significance. However, when Kristensen (1968) measured desiccation rates in all five intertidal fucoids, the differences did not coincide with their shore zonation: F. spiralis > F. vesiculosus > F. serratus > Pelvetia > Ascophyllum. Sandgren (1973) measured relative dehydration rates in F. spiralis and the midshore species F. distichus, and found no significant difference between these two species.

The trends reported by Kristensen and Zaneveld may have arisen from differences in size, habit of growth and surface to mass ratio between the test plants of the different species. After these factors were taken into account in the present study, the tissues of Pelvetia and F. spiralis did not exhibit a greater intrinsic ability to retard water loss than those of F. serratus. Furthermore, the surfaces of

fucoids evaporate water almost as fast as a free seawater surface, and do not form a barrier to further water loss after partial dehydration, as was suggested by Bérard-Therriault & Cardinal (1973a). Therefore, any postulated drought avoidance by upshore fucoids must be based on some other strategy such as thallus shape, surface to mass ratio, habit of growth or aggregation of individuals. With regard to thallus shape, the channelled Pelvetia thallus actually permits a more rapid water loss than the Fucus blade. Black (1949a) suggested that upshore fucoids may dry more slowly than midshore species owing to a lower surface to mass ratio, but this trend was found only in the very young plants, and was reversed in vegetative adult plants (Table 9). Pelvetia's bushy habit of growth has also been cited as a strategy to avoid dehydration during exposure (Isaac 1933). However, when the combined effects of habit of growth, aggregation and biomass density were considered, the degree of mutual protection was found to be similar in mature stands of F. spiralis and Pelvetia, and greater in Ascophyllum (Tables 12-15).

During exposure to hot weather, rapid water loss is probably advantageous, since damage during such exposure is most severe when the tissues are maintained at a relatively high water potential. Therefore it might be argued that the lack of drought avoidance in upshore fucoids represents an adaptation to prolonged tidal exposure. In this context it seems paradoxical that the young stages of Pelvetia and F. spiralis should exhibit drought avoidance strategies such as dense aggregation, unless these young plants are less able to tolerate dehydration than are the adult plants. This appears to be true in culture, where zygotes of Pelvetia and F. spiralis showed poor germination and growth when exposed four hours per day to an atmosphere at 8-12°C, 80-90% relative humidity. Indeed, cultured zygotes of F. spiralis require nearly constant submersion to develop (T. Hruby personal communication). How, then, are fucoids recruited on the shore if the zygotes are so sensitive to desiccation? The answer may lie in the nature of the substratum. In the laboratory, the zygotes were cultured on glass slides which became quite dry during simulated tidal exposure. On the shore, the zygotes settle in tiny cracks and crevices which may afford protection from desiccation. Pelvetia zygotes sometimes settle

and germinate in the channel of the adult plant, which curls around them during drying conditions (Moss 1974). The germlings may either develop epiphytically on the adult plant, or fall out and attach themselves to the rock. Fucoid zygotes may also be protected by small green algae such as Enteromorpha. The presence of these algae has been shown to enhance the establishment and growth of F. vesiculosus germlings on the shore (Hatton 1932; Jones 1948; Knight & Parke 1950; Southward 1962), and of F. spiralis germlings in simulated tidal cultures (T. Hruby, personal communication).

When the upper shore is subjected to a prolonged exposure during warm dry weather, all these strategies would be expected to fail, since entire algal stands and the rocky substratum itself may become thoroughly dry. As a result the fucoid germlings must also become air-dry, which they could not tolerate in culture. However, it is possible that fucoid embryos seem drought sensitive only because they are prone to extremely rapid dehydration owing to their small size and high surface to mass ratio. The embryos cultured on glass slides became dry within the first hour of exposure, as they might on a smooth, exposed rock surface on the shore. On the other hand, embryos located in sheltered microhabitats undoubtedly dry much more gradually. Plants often tolerate dehydration to a given water potential much better when dried slowly than when dried rapidly (Levitt 1972). Therefore any shelter which simply retards water loss without preventing ultimate air-dryness might be sufficient to ensure the survival of fucoid embryos. The aggregation of macroscopic first-year plants probably has a similar function. Since the greatest danger to the adult plant may be failure to become thoroughly dry during hot weather, rather than excessively rapid dehydration, it is not surprising that drought avoidance strategies are exhibited only by the early stages of upshore fucoids.

A size-related difference in drought tolerance was observed in macroscopic first-year F. spiralis which cannot be attributed to different desiccation rates alone, since this factor was eliminated in the experiment (Table 46). This result might be explained by the observation that the larger plants in a dense stand are more directly exposed to the atmosphere than the smaller plants growing between them.

A drought stress sufficient to induce hardening of the larger, more exposed plants might not induce such hardening in the smaller, protected plants. However, the understorey of smaller plants sometimes shows remarkable drought resistance. When the understorey in a small patch of F. spiralis was experimentally exposed in May 1976 by removing a severely damaged top layer, the small plants remained healthy and grew despite subsequent abnormally hot weather (Plate 10). Apparently, the dry spell in April of that year which damaged the top layer, simultaneously induced drought hardening in the understorey.

These observations suggest that, in order to survive on the upper shore, the very young plants must be partially but not completely protected from desiccation. They must not undergo a fatally rapid dehydration, but they must be subjected to sufficient drying to induce drought hardening, so that they can tolerate increasingly severe exposure as they grow larger and become more exposed to the weather. The drought avoidance strategies of the zygotes and germlings seem to function exactly in this way.

Clearly, drought resistance of upshore fucoids is based largely on biochemical and physiological properties which render their tissues capable of becoming air-dry without harm. An investigation of these adaptations is beyond the scope of the present study, but several features of drought injury and tolerance in fucoids reflect some of the biochemical aspects of stress discussed in detail by Levitt (1972). Critical intensities of drought, freezing and heat stress all cause a similar sequence of events which begins with a reversible denaturation, or unfolding of the cell's proteins. This exposes the -SH and -SS groups of the proteins which may then participate in oxidative reactions or exchange reactions resulting in intermolecular disulfide bonds. The normal function of protein molecules thus aggregated is permanently destroyed since they can no longer resume their native configuration when the stress is relieved. Commonly, these changes occur quickly at the onset of stress, but may develop slowly in resistant tissues.

When a tissue undergoes dehydration, mechanical stress develops in the cell membranes which forcibly unfolds some of the molecules in the inner and outer protein layers. Simultaneously, the intervening

lipid layer may be disrupted, causing points of direct contact between the two protein layers, at which denatured molecules may form disulfide bonds. This creates "holes", resulting in a dramatic rise in membrane permeability. Such membrane damage is indicated by a loss of cell solutes and an inability to reimbibe enough water to re-establish cell turgor, both common features of drought and frost injuries (Levitt 1972). The initial weight loss after drying in fucoid algae, which results from incomplete reimbibition and loss of tissue substances, presumably reflects similar membrane damage.

This theory also explains why fucoids are very tolerant of frost. Freezing causes the same stress as drying, since water diffuses out of the cells and freezes in the intercellular spaces. At -15°C, Ascophyllum loses only 76%, and F. vesiculosus 82% of their intracellular water (Kanwisher 1957). Since these species survived brief dehydration to a water loss of more than 90%, it is not surprising that fucoids can tolerate freezing to temperatures much lower than -15°C.

When stress is not sufficiently severe to damage membranes, but is prolonged, harmful metabolic imbalances may gradually develop over a period of time. Some vital biochemical reactions are inhibited more than others by a subcritical stress, with the result that some essential substances may become depleted or toxic substances may accumulate. For instance, in the leaves of higher plants, photosynthate may become depleted during drought. As the leaves begin to lose water, the stomata close and curtail photosynthesis long before respiration is arrested. However, since lower plants lack stomata, their photosynthetic rates may remain faster than their respiration until dehydration is severe enough to inhibit both processes. This has been demonstrated in lichens (Brock 1975), fucoids of salt marshes (Brinkhuis & Tempel 1975) and other intertidal seaweeds (Johnson et al. 1974). Other forms of metabolic injury have been reported, notably a net breakdown of proteins which arises because the complex pathways of protein synthesis are easily disrupted by stress (Levitt 1972).

Drought injury in fucoids shows three features which indicate that metabolic injury may be involved. Firstly, severity of damage is dependent upon the duration of stress which suggests that gradual

metabolic changes occur in the air-dry thallus. Secondly, damage becomes more severe as temperature is increased. Since the rates of biochemical reactions are directly related to temperature, metabolic stress injury is generally accelerated by high temperature (Levitt 1972). Thirdly, the effects on Pelvetia and F. spiralis of exposure at high temperature are mitigated by low relative humidity. As a plant tissue becomes more and more dehydrated, all biochemical reactions are eventually inhibited so that metabolic imbalances accrue very slowly if at all. It appears likely that the secondary factors of temperature and humidity modify the effects of drought stress through their influence on the rate of metabolic changes in the air-dry plant.

It might seem paradoxical that time-dependent drought damage in fucoids is characterized by an initial weight loss, which suggests membrane damage rather than metabolic imbalance. However, intermolecular disulfide bonding sometimes occurs gradually and may depend on temperature or water potential as do other biochemical reactions (Levitt 1972). Also, protein breakdown or other metabolic changes might gradually erode the plant's defences against membrane injury, so that both types of damage ultimately occur.

In addition to time-dependent drought injury, some immediate membrane damage appears to occur in Fucus spp. exposed under severe conditions (Tables 21, 23). This effect is least pronounced in F. spiralis, although it was observed in all except experimentally hardened plants. It is interesting to note that an immediate injury can be demonstrated in Pelvetia only when it is dehydrated to near 0% humidity. Since the humidity never approaches 0% on the shore, Pelvetia can be considered immune to immediate injury under any condition to which it is likely to be subjected in nature.

Immunity to membrane damage during stress may be based on any biochemical adaptation which impedes either protein denaturation or reaction between exposed -SH or -SS- groups. One of the simplest strategies is the conversion of starches to sugars observed in drought and frost hardening, which results in an increased osmotic potential (Levitt 1972). This decreases the percent water loss during dehydration to a given water potential, so that the cell shrinks less, and suffers less mechanical stress in its membranes.

A high dry matter content might be expected to confer the same advantage; in fact, a very strong correlation between drought tolerance and percent dry matter was observed in Fucus spiralis (Figures 27-29). In natural populations of this species, dry matter content and drought tolerance both rise to a seasonal maximum in late summer. This suggests that progressively warmer and drier conditions in spring and summer induce a drought hardening process, part of which might be accumulation of dry matter. Experimental evidence supports this hypothesis. Firstly, F. spiralis plants collected from the upper shore contained more dry matter and were more drought hardy than plants simultaneously collected from the middle shore where exposure is less severe. Secondly, when exposed daily to subcritical desiccation, F. spiralis showed a dramatic increase in drought tolerance within six days, which was accompanied by an increase in dry matter content (Figure 32).

However, it would be incautious to conclude from these results that dry matter content determines drought tolerance, especially since the correlation was not always consistent. For example, under experimental culture conditions, the dry matter content of F. spiralis increased in comparison with controls without a corresponding decrease in initial weight loss after drying (Figure 32). Further more, samples of F. spiralis which were collected in August 1976 after two days' severe desiccation on the shore and tested immediately in the laboratory had very high dry matter contents but were no more drought tolerant than other summer collected material (Table 42). The dry matter content of these plants may have been elevated by incomplete reimbibition of water after drying. It is possible that this increase in dry matter is incidental to drought hardening. Alternatively, the increase in dry matter content may be the first event in a complex hardening process which had not been completed when the experimental plants were tested in the laboratory. It is unlikely that the natural desiccation was so severe that the plants could not recover sufficiently to become hardened, since other plants collected the same day and used in other culture experiments showed only slight tissue damage.

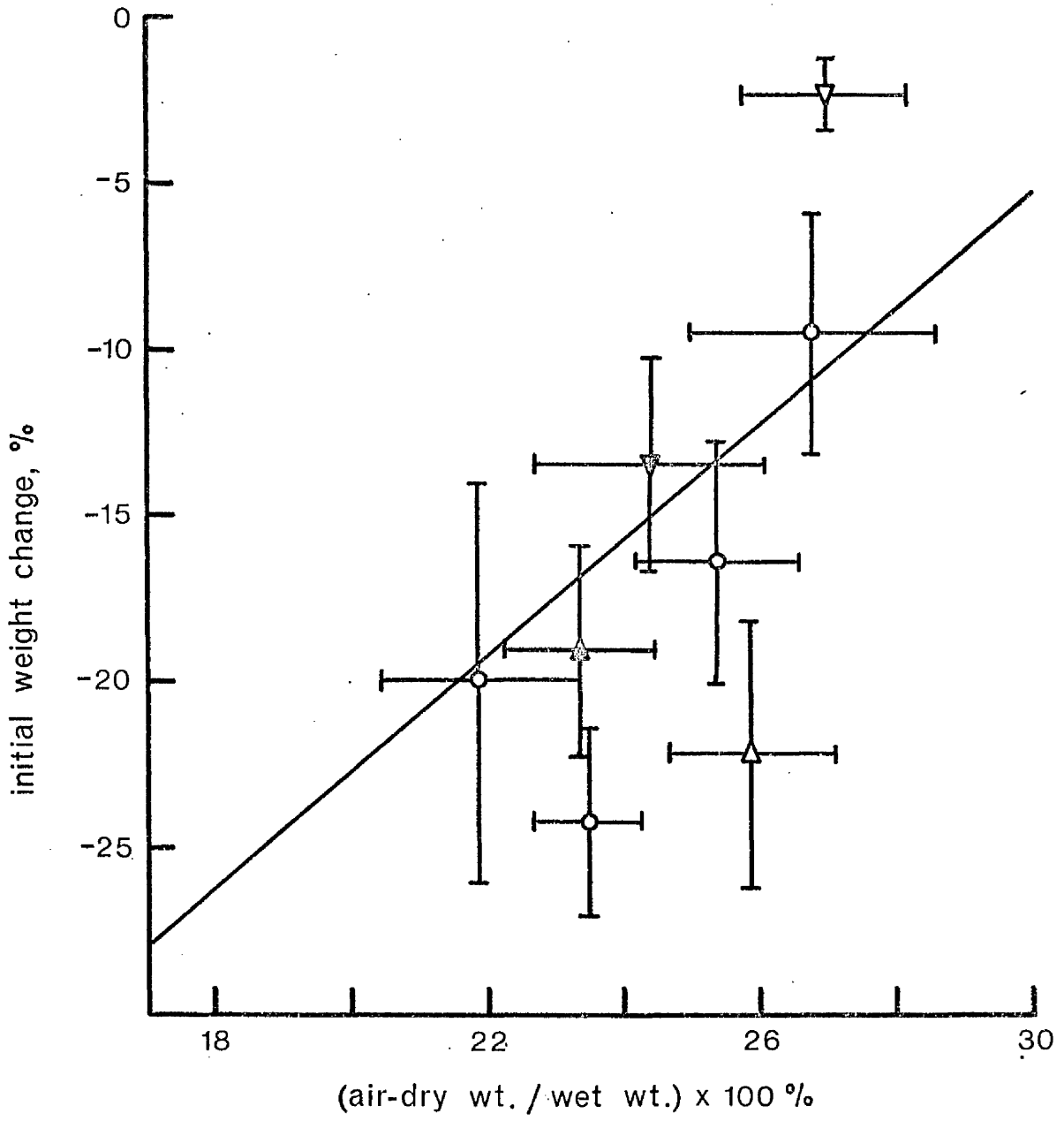



Figure 32. Relationship between initial weight loss after drying and ratio of air-dry weight to wet weight (Mean ± standard deviation) in samples of 5 to 25 Fucus spiralis, tested immediately after collection and after various pre-treatments in the laboratory. All plants were dried for 36 to 44 hours at 24-29°C, 30-60% relative humidity.

- ▽ plants hardened before experimental drying
- ▼ not hardened
- △ cultured for 24 days in 12 hour daily illumination and 12 hour daily submersion during dark period
- ▲ cultured for 24 days in 12 hour daily illumination and 12 hour daily submersion during light period
- o as collected; no pre-treatment

The regression line shown in Figure 27 is reproduced here for comparison.

In Pelvetia, dry matter content again was not consistently correlated with drought tolerance. The dry matter content of this species rises to a very high seasonal maximum in summer, and falls to a value little higher than that of F. spiralis in winter, but drought tolerance in Pelvetia remains high year round. Clearly, the drought tolerance of both species is based in part on other biochemical adaptations.

The large quantity of alginate and fucoidan in fucoid tissues has been cited as an important adaptation to desiccation (Zaneveld 1937; Bérard-Therriault & Cardinal 1973a, 1973b; Lestang & Quillet, in press). One of the properties of these polysaccharides is to retain a large amount of "colloidal water" when dried, which may reduce cell shrinkage during dehydration in the same way as would an elevated dry matter content. Alginate is characteristically quite hygroscopic at very low water potentials (Lestang & Quillet in press), but does not appear to be involved in the special drought adaptations of upshore fucoids. Alginate is not more abundant in Pelvetia and F. spiralis than in midshore fucoids and the content in all species falls to a seasonal minimum in late summer when drought tolerance would be most important (Black 1948a, 1949a). Furthermore, the air-dry tissues of Pelvetia, Fucus spiralis and F. serratus have equal hygroscopic capacities at water potentials of -665 bars and below (Table 8).

Fucoidan, which becomes very hygroscopic only at high relative humidity, is most abundant in Pelvetia and progressively less so in F. spiralis, Ascophyllum, F. vesiculosus and F. serratus (Lestang & Quillet, in press). Therefore, at relatively high water potentials, upshore fucoids would be expected to retain more water than midshore species. This was observed in F. spiralis but not in Pelvetia (Table 8), which suggests that the latter actually contains a less hygroscopic form of this polysaccharide. The most important property of fucoidan may be its ion exchange capacity rather than its water retention. Lestang & Quillet (1973) presented considerable evidence that the polymerized sulfate esters which comprise fucoidan function to remove excess sodium from the cell. Since one effect of dehydration is a drastic rise in salt concentration in the cells, and high salt

concentration often promote protein aggregation, excretion of sodium ion may be an important factor in drought adaptation. The sulfate fraction of the fucoidan of Pelvetia shows a turnover rate of 16% per hour (Lestang & Quillet 1973) compared to 10% per hour in F. vesiculosus reported by Bidwell & Ghosh (1963), which suggests that Pelvetia might possess a form of fucoidan which is unusually effective in eliminating excess intracellular sodium.

There is some evidence that the composition of the lipids in fucoids also play a role in their stress tolerance. Haas & Hill (1933) and Liem & Laur (1976) found that the lipids of Pelvetia are more saturated than those of other fucoids, and related this difference to the greater exposure to hot weather this species must endure. The degree of saturation of membrane lipids may determine how these membranes react to stress at different temperatures (Levitt 1972). A saturated lipid layer in the membrane may become stiff and "crack" at very low temperatures, causing greater contact between the protein layers, while an unsaturated lipid layer would remain intact. However, at high temperatures unsaturated lipids "melt" and a saturated lipid layer would more effectively keep the protein layers separate. In fucoids, seasonal variations in lipid saturation and tolerances to extremes of temperature support this hypothesis. Lipid saturation in Fucus vesiculosus and F. serratus reaches a maximum in summer and a minimum in winter (Liem & Laur 1976), and the same species reach their greatest heat tolerance in summer and their greatest frost tolerance in winter (Feldman & Lutova 1963). This suggests that the greater saturation of the lipids of Pelvetia enhance this species' ability to tolerate exposure to hot weather. Liem & Laur (1975, 1976) also reported that Pelvetia contains more sulfolipids than other fucoids. Since sulfolipids are an integral part of pigment-bearing membranes in chloroplasts (Collier & Kennedy 1963, Kennedy & Collier 1963, Hitchcock & Nichols 1971), they might play an important role in the stability of these structures during dehydration or other stress. Aside from these few findings and speculations, the biochemical aspects of stress resistance in fucoids remain largely unexplored.

In addition to tolerating desiccation, upshore fucoids must obtain an adequate supply of dissolved mineral nutrients for growth during brief and infrequent tidal submersions. Logically, for each algal species, there must be some point on the shore gradient above which it cannot grow owing to nutrient scarcity. Since the upper limit of F. spiralis is often exposed 90% of the time, and that of Pelvetia may only be wetted by wavesplash (Colman 1933; Evans 1947a, 1947b), nutrient scarcity might be expected to play a role in determining these upper limits. Baker & Bohling (1916) ascribed the dwarfing of salt-marsh fucoids at high levels to this factor, since the salt marsh habitat is not characterized by severe desiccation.

In tidal-simulation cultures, slow growth of Pelvetia and F. spiralis in four hours daily submersion was clearly related to nutrient limitation since this effect was largely eliminated by using a sufficiently enriched medium. However, growth rates of natural populations of these species in their usual zones were similar to those obtained in constant submersion in culture (Table 53). It should be noted here that sea temperatures and mean daily total visible radiation during the months of October to February are roughly similar to those realized in culture, but that nutrient conditions in nature and in culture cannot be adequately compared. During submersion in nature, the seaweeds have access to an essentially unrestricted volume of seawater, while in culture the volume is quite small. This may explain why the fucoids are much more nutrient-limited by short tidal submersion in culture than they seem to be on the shore.

The growth rate of F. spiralis in nature became slightly slower toward the top of its zone, and markedly slower at the 3.05 m level, at which Pelvetia grew at its maximum rate (Table 53). Brinkhuis & Jones (1976) reported that Ascophyllum in salt marshes grows more slowly near the top of its zone than it does further down, and attributed this partly to nutrient limitation. However, several results and observations in the present study indicate that nutrient limitation does not contribute to the differentiation of the upper limits of F. spiralis and Pelvetia. Firstly, Pelvetia was not clearly

Table 53: Comparison of linear growth rates (mean ± standard deviation) of Pelvetia and Fucus spiralis in culture with growth rates observed in natural populations. Data for natural populations are the same as those which appear in Table 61.

| species | height above chart datum | growth rates in natural populations mm/month: early Sept - end Oct. | end Oct - mid Feb. | mid Feb - mid May | growth rates in constant submersion in culture mm/month |
|---|---|---|---|---|---|
| Pelvetia | 2.95 | 4.9 ± 2.4 | 5.8 ± 1.8 | 7.0 ± 1.5 | 3.9-9.9 |
| | 3.05 | 7.0 ± 3.0 | 6.8 ± 1.1 | 9.0 ± 1.6 | |
| | | 7.1 ± 2.3 | 6.2 ± 1.4 | 7.6 ± 1.1 | |
| Fucus spiralis | 2.65 | 22.1 ± 2.7 | 15.3 ± 2.7 | 21.9 ± 2.3 | 10.8-22.6 |
| | 2.75 | 23.1 ± 3.1 | 15.2 ± 2.9 | 18.0 ± 5.6 | |
| | 2.85 | 10.5 ± 3.1 | 11.1 ± 1.7 | 18.7 ± 3.6 | |
| | 3.05 | 6.0 ± 2.0 | 5.5 ± 2.2 | 7.3 ± 1.4 | |

more efficient in exploiting a limited supply of nutrients in culture than was F. spiralis. Although F. spiralis initially grew more slowly than Pelvetia when submerged four hours per day in dilute media, it became adapted to the short nutrient supply and ultimately grew faster than Pelvetia. Secondly, summer-collected material of both species grew almost as fast when submerged only two hours per day in a dilute medium as when submerged twenty-two hours per day. This strongly suggests that both species had become adapted to summer-time minimum nutrient concentrations in the sea. Thirdly, the reduction in the growth of F. spiralis with distance upshore was no less marked during autumn and winter when nutrients were most abundant in the sea than during spring, when the annual phytoplankton increase began to deplete the supply. Desiccation rather than nutrient scarcity probably restricted the growth of F. spiralis in the Pelvetia zone. This has been demonstrated for F. vesiculosus and Ascophyllum growing near the tops of their zones

(Hatton 1938). Isolated plants at this level grew slowly, but plants in mutually protected clumps grew as rapidly as downshore plants of the same species. When Hatton thinned these clumps to single plants, the growth rates of the remaining individuals decreased significantly.

While Pelvetia and F. spiralis were equally efficient in utilizing a limited nutrient supply in culture, F. serratus was distinctly less efficient (Table 47). However, this species still grew more than half as fast in a one hour semidiurnal submersion as in an eleven hour submersion. Therefore, its upper limit near MTL is probably determined not by nutrient limitation but by other factors.

Short and infrequent tidal submersion also restricts the availability of dissolved inorganic carbon, and Pelvetia and F. spiralis must be capable either of very rapid absorption of carbon dioxide during submersion or of using atmospheric carbon dioxide directly. Several investigators have assessed by means of photosynthesis measurements the efficiency with which seaweeds can utilize atmospheric carbon dioxide, and the results have been very variable. Bidwell & Craigie (1963) measured the uptake of $^{14}CO_2$ by F. vesiculosus from a damp atmosphere containing 1% $CO_2$. They found that although the plants suffered no desiccation, their assimilation rates in this atmosphere were less than one quarter of those of submerged plants under the same conditions of light and temperature. Using similar methods, Kremer and Schmitz (1973) found much greater fixation of $CO_2$ from the atmosphere by three species of Fucus. F. spiralis photosynthesized 100%, F. vesiculosus 75% and F. serratus 54% as fast in the atmosphere as they did in seawater, which relates logically to their order of occurrence on the shore. Kremer (1976) found that Pelvetia photosynthesizes at similar rates when exposed and when submerged, and reported that the distribution of $^{14}C$ label among photosynthates was also similar during exposure and submersion. Brinkhuis, Tempel & Jones (1976) measured $CO_2$ uptake of salt-marsh ecads of Ascophyllum and Fucus vesiculosus while exposed to a drying atmosphere not enriched with added $CO_2$. They found that photosynthesis rates of these species actually increased somewhat as the plants lost the first 30% of their tissue water, followed by only a gradual decrease up to 50-60% loss, and a very rapid

decline to zero thereafter. E.C. Oliviera (personal communication) found that Pelvetia also photosynthesizes best when slightly dehydrated, and remains above the compensation point until it has lost 70% of its tissue water. The most dramatic rise in photosynthesis rates with exposure and partial desiccation was reported by Johnson et al (1974) for the midshore species Fucus distichus. Exposed to the atmosphere and slightly dehydrated, this species fixed carbon at over six times the rate it achieved in seawater, and the rate was still half of this maximum value when the tissues had lost 60% of their water. Three other intertidal species showed the same pattern, although to a somewhat lesser degree. They attributed this remarkable finding to an enhanced diffusion of $Co_2$ into the cells of the partly dried thallus.

One difficulty with these measurements is that one cannot use the same method for determining photosynthetic rates in seawater and in the air. Results obtained by different methods may contain different inherent sources of error, and may not be strictly comparable. A further problem is that release of oxygen or consumption of carbon dioxide does not prove that growth is taking place. For example, Gail (1922) reported that samples of F. vesiculosus evolved some oxygen when submerged to depths of up to 35 metres, but did not grow when submerged more than a metre. For these reasons, utilization of atmospheric carbon dioxide by upshore fucoids was investigated by means of growth rate measurements rather than measurements of gas exchange. Pelvetia and F. spiralis definitely utilized atmospheric carbon dioxide, although only 30-40% as efficiently as inorganic carbon dissolved in seawater (Table 49). This result corroborates evidence presented by Strömgren (1976) that fucoids can grow while exposed. Strömgren used laser diffraction to measure length decrease of apices of Pelvetia, Fucus spp., and Ascophyllum during fifteen to sixty minutes exposure to a drying atmosphere. Rates of shrinkage were much lower in algae desiccated in bright light than in algae dried under subdued light and otherwise similar conditions. He attributed this to light-dependent growth occurring simultaneously with dehydration, and this was substantiated when the apices were resoaked and found to recover within eight minutes to lengths exceeding their original lengths.

In the present investigation, Pelvetia and F. spiralis both grew much more slowly when illuminated during the twelve hours' exposure of a 12/12 diurnal tidal cycle than when illuminated during the twelve hours' submersion (Table 49). This result was considered surprising for two reasons. Firstly, these species grew quickly when submerged only one hour per twelve in the tidal simulator, and secondly they grow as rapidly in their upshore zones as they do in constant submersion in culture. It was initially supposed that some of the photosynthate produced by exposed seaweeds is diverted toward building up specific drought-tolerance mechanisms. However, this is apparently not the case, as the plants exposed during the light cycle underwent no drought-hardening (Table 50).

Clearly, one of the metabolic steps between the primary light reaction and synthesis of new tissue cannot occur efficiently unless the alga is submerged while illuminated. If carbon dioxide absorption is the critical step, then the plant must be capable of accumulating, during a one-hour submersion, as much inorganic carbon as it normally absorbs during an entire day. Furthermore, it must be capable of doing so only while illuminated; otherwise the plants exposed during illumination in the experiment would have obtained their supply during their nighttime submersion. It might also be argued that cells cannot elongate during exposure owing to a lack of turgor pressure. This would certainly be true of the partially desiccated plants in which Johnson et al (1974) found high photosynthetic rates. In my experiment, the exposed plants were kept in a humid atmosphere in which little desiccation occurred; however sufficient loss of turgor might have occurred to inhibit cell elongation. This would imply not only that the cells of submerged plants undergo most of their elongation while illuminated, but also that they can accomplish enough elongation during one hour illuminated submersion per day to achieve a normal growth rate. This is not as unlikely as it seems. Burrows (1956) found that Fucus zygotes cultured in the dark undergo cell divisions without increasing in size, with the result that such embryos are composed of a large number of small cells. When transferred from very dim light to bright light, Laminaria saccharina showed a very rapid expansion of the blade near the meristem

(Burrows 1964). This suggests that many small cells were produced by repeated divisions in the dim light and underwent rapid enlargement when adequate light was suddenly provided. It is possible that cell division can occur in exposed, illuminated fucoids but that cell enlargement occurs primarily during submersion in the light.

Although the reason for the slow growth of fucoids during exposure was not elucidated, the results have shown that Pelvetia and F. spiralis both require at least brief submersion in the light in order to grow rapidly. The two species do not differ in their ability to grow without such submersion, hence this factor does not contribute to the difference between their upper distributional limits.

# 4. FACTORS CONTROLLING LOWER LIMITS

## 4.1 Survival and growth of Pelvetia and F. spiralis transferred to levels below their normal zones

The role of physical environmental factors in determining the lower limits of Pelvetia and Fucus spiralis was explored by transplanting these species to levels below their usual distributional ranges. The transfers were carried out on the same south-west-facing slope at Port Loy (Figure 3) as were the transfers of Fucus spp. above their upper limits. One set of Pelvetia samples was placed in the F. spiralis zone, a second set near MTL, and the control set was placed in the Pelvetia zone. Samples of F. spiralis were transplanted to the mid-shore and controls were placed in the F. spiralis zone. For both species, individual plants attached to rock chips, and small stones bearing groups of young plants were cemented at each level. The samples were transferred on 15-17 February 1974, and their survival and growth was observed at roughly monthly intervals until 1 August 1974, at which time they were collected and their drought tolerance tested in the laboratory (Table 45).

Competition from other seaweeds was initially eliminated in this experiment since all macro-algae were cleared from the rock surface to which the transferred plants were fixed. Biotic factors operating against embryonic phases were also bypassed since plants 10-80 mm long were transferred. However, grazing upon these plants was not eliminated and the possible role of grazers was therefore considered in the interpretation of the results.

The February and March measurements of the plants attached to rock chips were not considered reliable because, owing to dry weather conditions, the plants shrivelled somewhat before they could all be measured. To avoid this problem, the plants were subsequently measured only when wet. The mean growth rate of each species at each level over the five and one-half month period was calculated from the length increase of the plants attached to stones between February and April, and the monthly length increases of all the plants thereafter.

A number of very small individuals were present on the stones bearing Pelvetia, some of which were measured only during the latter part of the five month period because they were initially small enough to escape notice. Pelvetia plants less than 15 mm long commonly grow much more slowly in length than larger plants, and their inclusion in the data from which mean growth rates are calculated would affect these means. Therefore, the transplanted Pelvetia were divided into two classes for which separate means were calculated: those 15 mm or more in length at the initial measurement, and those initially shorter than this.

Both Pelvetia and F. spiralis grew much more rapidly when transplanted below their normal lower limits than when transferred into their own zones (Table 54). The samples transferred to MTL remained quite healthy throughout the five and one-half month period (Plate 11), although Pelvetia developed a peculiar curling of the branches which is characteristic of its salt marsh form (Baker & Bohling 1916). This was much less pronounced in the Pelvetia transferred to the F. spiralis zone.

The slow growth rates of the controls suggest that Pelvetia and F. spiralis inhabit levels on the shore well above those at which they would grow most rapidly. It was concluded in the previous chapter that these species do in fact grow near to their upper limits of tolerance to physical stress. However, growth rates in natural populations of young Pelvetia and F. spiralis greatly exceeded those of the control transplants, and sometimes equalled those of the MTL transplants (Table 61 ). These natural stands were fairly dense, and the plants enjoyed considerable mutual protection from drying. The transplants were much less densely clumped, and those on the stones were particularly exposed to drying winds because these stones projected above the surrounding rock slope. Since the growth rates of fucoids attached near their upper limits are strongly influenced by the degree of mutual protection (Hatton 1938), it was concluded that the control transplants grew so slowly because they lacked such protection.


Plate 11: Pelvetia (P) and Fucus spiralis (F) transplanted to the midshore February 15th, 1974, photographed August 1st.

Table 54: Growth rates of Pelvetia and Fucus spiralis transplanted to levels below their usual lower limits

| species | size class | level | initial number of sample plants [α] | average growth rate over five month period mm/month |
|---|---|---|---|---|
| Pelvetia | < 15 mm | Control: Pelvetia zone (3.00m) | 8 | 1.0 |
| | | Experimental: F.spiralis zone (2.75m) | 4 | 2.3 |
| | | Experimental: Midshore (1.90m) | 9 | 1.8 |
| | ≥ 15 mm | Control: Pelvetia zone (3.00m) | 12 | 1.5 |
| | | Experimental: F.spiralis zone (2.75m) | 13 | 4.3 |
| | | Experimental: Midshore (1.90m) | 20 | 4.1 |
| F. spiralis | all sizes | Control: F.spiralis zone (2.75m) | 11 | 5.4 |
| | | Experimental: Midshore (1.90m) | 9 | 13.8 |

α excluding plants attached to rock chips, whose initial measurements were not reliable owing to shrivelling, and were therefore excluded from the calculations of growth rate between February and April

In order to further investigate the effect of increased submersion time upon the two upshore species, a second transfer of stones bearing them was carried out in July 1974. For each species, four stones bearing four to ten plants each were transplanted to the midshore at Port Loy. Control transfers were carried out as before, except that they were placed a few centimetres lower than the February transplants in order to compensate for the greater exposure they suffer compared to the surrounding natural stands. Mean growth was estimated as before, except that data was taken only for plants that were measured initially, and smaller plants

that were noticed only later in the course of the experiment were ignored. The plants were measured periodically for one year, and observed qualitatively thereafter.

Plants of Fucus spiralis grew much more rapidly when transferred to MTL than when placed in their own zone (Figure 33). Although the growth rate of the midshore transplants decreased noticeably in winter, the plants remained healthy, resumed rapid growth in the spring, and developed into a dense stand of large, fertile plants by the end of July 1975 (Plate 12). The growing apices of the F. spiralis control transplants were heavily damaged by grazing in January-March 1975, but they survived and produced a few small receptacles by midsummer (Plate 13). Their growth would doubtless have been more vigorous had grazing not occurred, but would probably not have equalled that attained by the midshore transplants. Both sets of transplants persisted and grew through their second winter, and produced another set of receptacles in summer 1976.

During the first few months after transfer, Pelvetia also grew faster at MTL than within its own zone (Figure 34). However, the growth of the midshore transplants became much slower as winter approached, and ceased altogether after 10 December. At this time, the plants were visibly beginning to decay. Their condition deteriorated steadily through the winter, and they were colonized by numerous epiphytes including both Elachista fucicola and Polysiphonia lanosa. There was also evidence of grazing by snails on a few plants in January, which may have accelerated the removal of Pelvetia from the midshore. Four plants persisted until spring and appeared to be reviving somewhat. However by June 1975, they were completely overgrown and hidden from view by a vigorous growth of young Fucus spiralis plants which had first appeared on the Pelvetia stones in February. The four surviving Pelvetia were collected at this time so that a colleague could study the unusual occurrence of Elachista fucicola on Pelvetia.

Many of the Pelvetia control transplants were lost during the first year so that the total biomass on the stones visibly decreased, but some plants persisted and became fertile in summer 1976. As before, the relatively poor performance of the controls was attributed to the

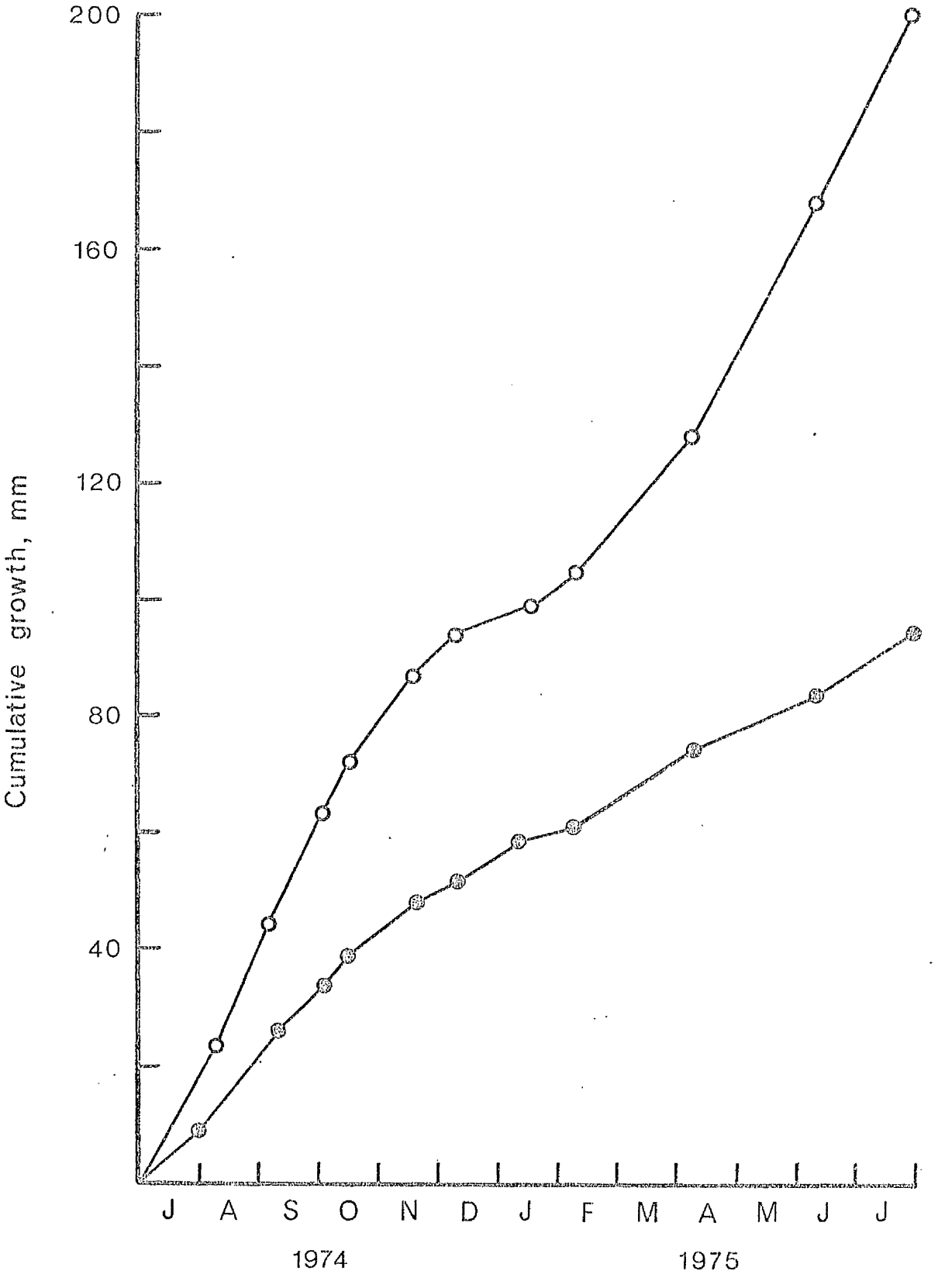



Figure 33. Course of growth of Fucus spiralis plants transplanted into their own zone at 2.75 m above chart datum (•) and to the midshore, 1.90 m above chart datum (o).

A


B

Plate 12:

A. Pelvetia and Fucus spiralis immediately after transfer to the midshore July 3rd, 1974. The stones are fixed to the shore by means of quick-setting cement.

B. The same F. spiralis (F) as those shown in Plate 12 A photographed July 29th, 1975.

A


B

Plate 13: A. Fucus spiralis control transplants immediately after transfer July 3rd, 1974.

B. The same plants, photographed July 29th, 1975, showing receptacles (R).

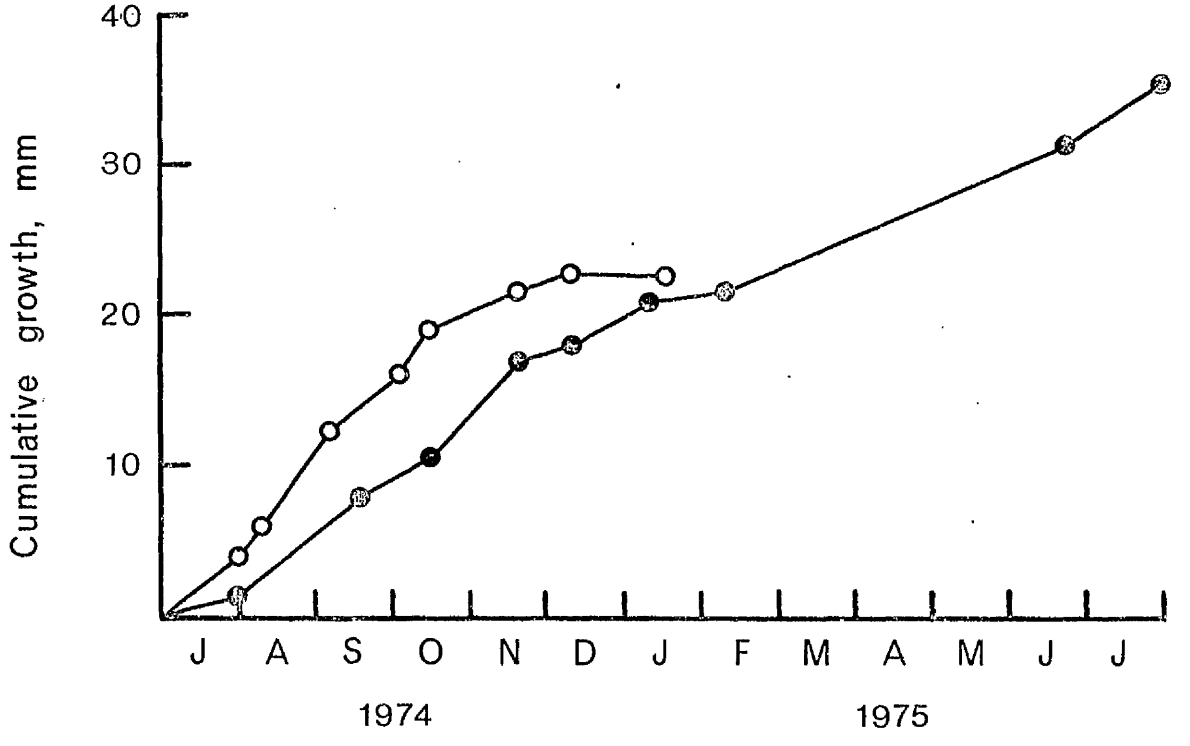



Figure 34. Course of growth of Pelvetia plants transplanted into their own zone at 3.0m above chart datum (●) and to the midshore, 1.90m above chart datum(o).

greater exposure they suffered in comparison to natural stands at the same level. However, in the long term they fared far better than did the midshore transplants.

Clearly, some environmental factor - either physical or biotic- adversely affected the midshore Pelvetia transplants during the winter. However, the actual lower limit of this species does not appear to be determined by physical factors. When the February 1974 transplants were collected in August of that year, a few small Pelvetia in the F. spiralis zone were overlooked. These plants persisted and grew normally for two years, and produced receptacles in summer 1976.

However, no new Pelvetia appeared naturally at this level during the entire two and one-half year period. Therefore, some biotic factor appears to operate against the very early stages of Pelvetia to exclude it from the Fucus spiralis zone. A series of field experiments were designed to determine whether this factor is interspecific competition with Fucus spiralis itself.

## 4.2 The establishment of Pelvetia in the Fucus spiralis zone after the removal of Fucus spiralis.

A Fucus spiralis removal experiment was undertaken to determine whether Pelvetia zygotes can settle, germinate and grow under the physical conditions within the F. spiralis zone. All F. spiralis were removed from a patch of shore 1 metre long lying between 2.95 and 2.65m above chart datum on a steep, protected, south-west facing slope at Port Loy (Figure 3). Fucus holdfasts, barnacles and the majority of crustose algae were removed with a geology hammer. The patch was cleared on June 10th 1974, at the beginning of Pelvetia's gamete release season, and a well-developed belt of fertile Pelvetia was left intact immediately above the cleared area. Nearby plants of F. spiralis were also fruiting at this time, so that zygotes of the two species undoubtedly settled on the denuded rock at roughly the same time. The patch remained apparently bare until September 1974, when a cover of ephemeral green algae appeared. Microscopic examination of scrapings taken from the rock on 10 December revealed numerous fucoid embryos. At this time, a quadrat 0.25 x 0.25m was marked out between 2.90 and 2.75m

within the cleared area. The quadrat was subdivided into twenty-five 50 x 50 mm subsquares, within each of which the growth of the fucoids was subsequently monitored.

The fucoid germlings remained too small to identify or measure in the field until spring 1975; therefore small samples were scraped from the rock and examined microscopically. On January 11th all sporelings were scraped from a 10 x 20 mm area of rock at about 2.90 m above chart datum, just outside the quadrat, and a similar sample was taken at about 2.75m. The embryos were counted under the microscope, and an attempt was made to identify all embryos 1mm or more in length. Pelvetia was found in all these scrapings, but were less numerous than F. spiralis and seemed to be developing more slowly (Table 55).

From April 1975 onward, the development of the fucoids was monitored as follows. In each subsquare of the quadrat, the presence or absence of identifiable Pelvetia and F. spiralis was noted, and the longest plant of each species was measured. In April 1975, the entire quadrat was dominated by a cover of F. spiralis germlings (Plate 14). although tiny Pelvetia were also identified in nineteen subsquares. Fortuitously, warm dry weather combined with neap tides in May and June selectively killed most of the F. spiralis within the quadrat, thus bringing the small Pelvetia into view (Plate 15). This natural event effected a much more thorough selective removal of F. spiralis than could have been done experimentally, and permitted the Pelvetia germlings to continue growing in the absence of competition. With the exception of three subsquares in the lower left corner of the quadrat in which many F. spiralis survived, only a few badly damaged individuals of this species persisted through the summer. Healthy Pelvetia germlings were observed in all but the lowermost left-hand subsquare, but they grew very slowly, while the F. spiralis in the three least drought-damaged squares began to grow rapidly (Table 56).

By mid-September many of the subsquares contained F. spiralis plants which were recovering from drought damage and resuming growth. In order to determine whether these F. spiralis would inhibit further development of Pelvetia, the F. spiralis was permitted to grow only in alternate subsquares. Beginning on 12 September, and every few weeks

Plate 14: Quadrat within area cleared of Fucus spiralis June 10th, 1974, photographed April 16th, 1975 showing a carpet of young F. spiralis.

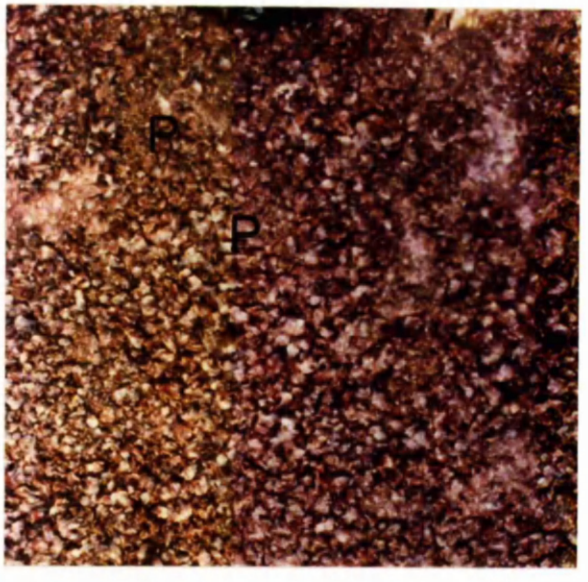



Plate 15: Close-up photograph of experimental quadrat taken June 11th, 1975. Severe desiccation has killed the F. spiralis, and small, healthy Pelvetia germlings (P) can be seen in contrast with the damaged Fucus thalli.

Table 55: Abundance and length of *Pelvetia* and *Fucus spiralis* germlings in samples taken at two different levels within *Fucus spiralis* zone seven and eight months after removal of macro-algae and barnacles.

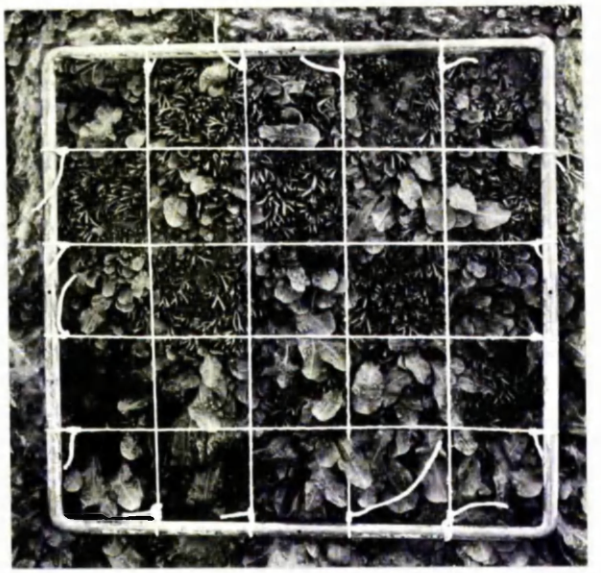
| Date | Level | number of germlings | number of germlings 1 mm or more in length | percent of germlings ≥ 1 mm long identified as Pelvetia | maximum length mm | percent of germlings ≥ 1mm long identified as Fucus | maximum length mm | percent of germlings ≥ 1 mm long not identified |
|---|---|---|---|---|---|---|---|---|
| 11 Jan | 2.90m | 455 | 57 | 12 | 1.2 | 49 | 2.3 | 39 |
| | 2.75m | 650 | 125 | 7 | 1.4 | 42 | 3.5 | 51 |
| 10 Feb | 2.90m | 376 | 106 | 14 | 1.5 | 50 | 3.5 | 36 |
| | 2.75m | 516 | 153 | 12 | 1.9 | 55 | 3.3 | 33 |

Table 56: Survival and growth of first-year Fucus spiralis and Pelvetia during summer 1975 in quadrat cleared of F. spiralis in June 1974. Mean ± standard deviation of maximum lengths measured in each of the subsquares.

| | Fucus spiralis | | | Pelvetia | |
|---|---|---|---|---|---|
| Date | number of subsquares with live plants | mean maximum length, mm | Maximum lengths in three subsquares least affected by drought, mm | number of subsquares with live plants | mean maximum length, mm |
| 16 April 1975 | 25 | 10.4 ± 1.8 | 12.0, 9.5, 9.0 | 19 | ∿ 1.5[α] |
| 11 June 1975 | 16 | 10.6 ± 2.6 | 14.0, 12.0, 12.0 | 24 | 2.1 ± 0.5 |
| 12 Sept. 1975 | 15 | 13.8 ± 7.8 | 31.0, 27.0, 21.0 | 24 | 2.7 ± 0.7 |

α too small to measure accurately

thereafter, all F. spiralis large enough to handle with forceps were removed from twelve of the subsquares (hereafter called the "weeded subsquares"). The lengths of the longest Pelvetia in each subsquare, and of the longest F. spiralis in each unweeded subsquare were measured at intervals of four to ten weeks until May 1976. During this time Pelvetia developed far more rapidly than it did during its first year in the quadrat, and grew equally fast in subsquares with and without F. spiralis (Table 57). However, F. spiralis grew four times as fast as Pelvetia (Table 57), forming a closed canopy in the unweeded subsquares and lying over the adjacent weeded subsquares in the lower part of the quadrat (Plate 16). The Pelvetia was noticeably darker in colour and formed a less dense cover in these squares than in those not covered by F. spiralis blades. From mid-May onward, the large F. spiralis were trimmed with a pair of scissors so that the canopy was restricted to the unweeded squares, and growth rate measurements were therefore terminated.



| | | | | |
|---|---|---|---|---|
| | * | | * | |
| * | | * | | * |
| | * | | * | |
| * | | * | | * |
| | * | | * | |

* = weeded

Plate 16: Experimental quadrat, photographed February 28th, 1976. F. spiralis was periodically removed from alternate subsquares from September 12th, 1975 onward, as shown in the diagram. Large F. spiralis in some of the unweeded subsquares are lying over the weeded subsquares in the next lower row.

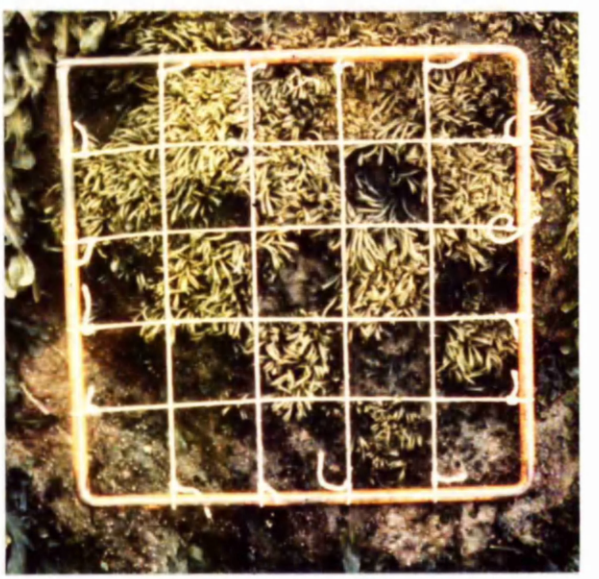


Plate 17: Experimental quadrat photographed July 19th, 1976, immediately after removing F. spiralis from all subsquares.

By late July 1976, the effect of the F. spiralis canopy on Pelvetia became much more distinct. When all F. spiralis were removed from the quadrat, many of the subsquares in which it had been permitted to grow were found to contain a rather patchy cover of Pelvetia, some of which were very dark in colour (Plate 17). The two weeded squares in the lower left part of the quadrat which contain little Pelvetia had been shaded considerably by overhanging F. spiralis from adjacent squares before the first trimming in May. The photograph shows clearly that Pelvetia spores can settle, germinate and grow normally under the physical conditions within the F. spiralis zone provided that the much more rapidly growing F. spiralis is constantly removed.

The area to the right of the quadrat was cleared of F. spiralis by drought in summer 1975 which provided an opportunity to observe recolonization after removal of F. spiralis by natural causes.

Table 57: Course of growth of Fucus spiralis, and of Pelvetia in subsquares with and without F. spiralis. Mean ± standard deviation of length of longest plant in subsquare, measured on six occasions over an eight month period.

| | Fucus spiralis | | Pelvetia (F.spiralis excluded) | | Pelvetia (F.spiralis present | |
|---|---|---|---|---|---|---|
| Date | number of subsquares | mean maximum length, mm | number of subsquares | mean maximum length, mm | number of subsquares | mean max. length, mm |
| 12 Sept. 1975 | 13 | 7.9 ± 9.1[α] | 12 | 2.6 ± 0.7 | 12 | 2.8 ± 0.7 |
| 26 Nov. 1975 | 13 | 18.0 ±14.8 | 12 | 6.5 ± 0.5 | 12 | 6.9 ± 1.5 |
| 24 Jan. 1976 | 13 | 36.4 ±23.5 | 12 | 10.3 ± 1.5 | 12 | 10.4 ± 2.3 |
| 27 Feb. 1976 | 13 | 48.2 ±25.5 | 12 | 12.2 ± 2.6 | 12 | 11.3 ± 3.1 |
| 30 March 1976 | 13 | 65.9 ±27.8 | 12 | 17.2 ± 3.4 | 12 | 16.8 ± 4.0 |
| 15 May 1976 | 12[b] | 84.4 ±34.9 | 12 | 22.0 ± 4.7 | 12 | 20.8 ± 6.2 |

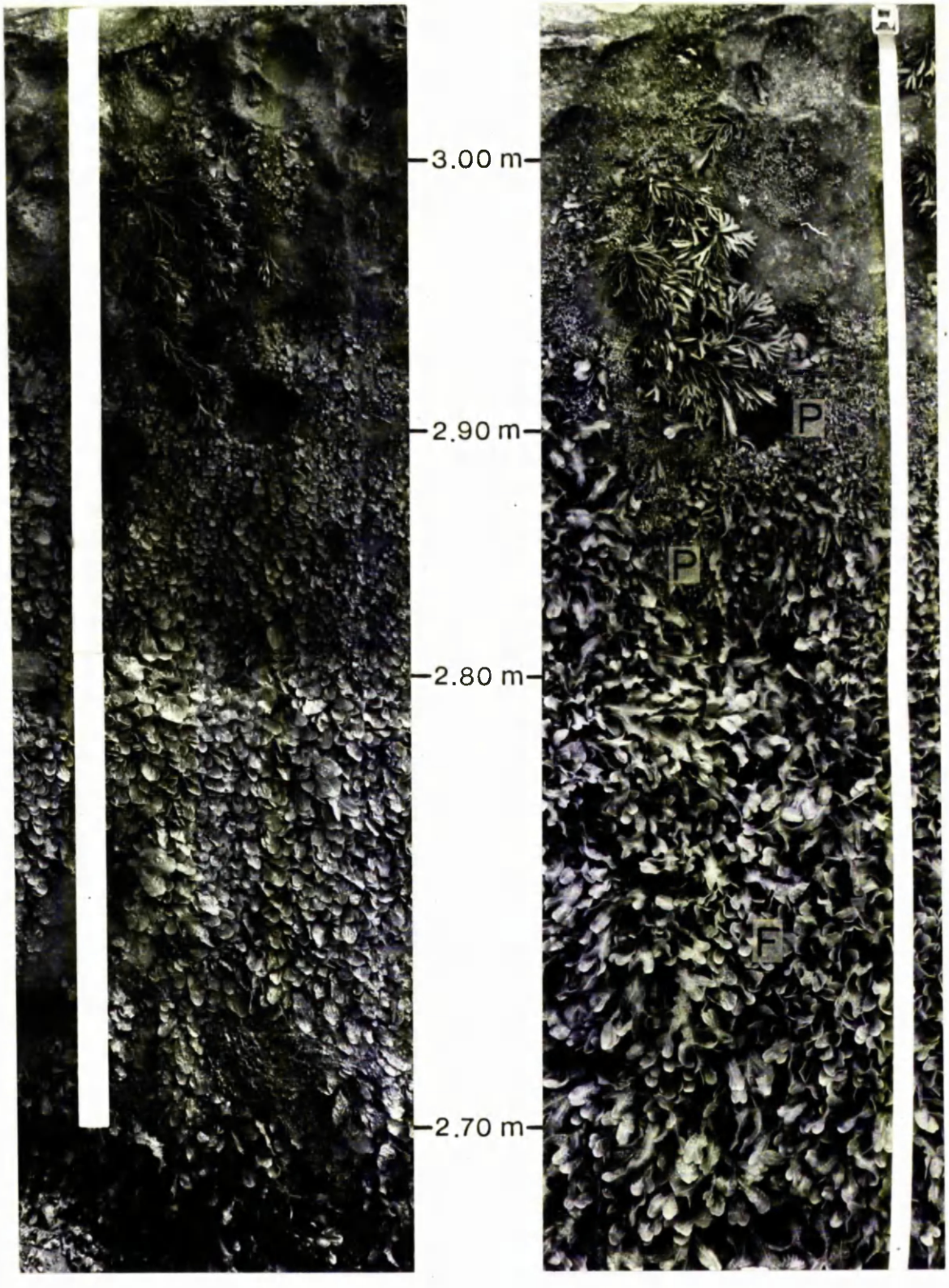
α includes five squares without live macroscopic F.spiralis which were assigned a length of zero. F. spiralis appeared in all five by 26 November.

b data for one square was lost.

A 0.2 m wide transect was marked out between 3.00 and 2.65 m above chart datum on this rock slope and observed from September 1975 until August 1976. Initially, adult Pelvetia were present down to 2.90 m on this transect, and the rock was essentially barren from that point to about 2.72 m, with only a few small F. spiralis. Below 2.72 m, the rock was covered by large fertile F. spiralis and other algae.

In October 1975, small samples were scraped from the rock at eight levels between 3.00 and 2.70 m and examined microscopically for the presence of fucoid zygotes and germlings. Pelvetia zygotes are readily distinguishable from those of F. spiralis because they are larger and they remain in pairs surrounded by the oogonial sheath. Zygotes and embryos of both species were found in scrapings taken at all levels between 2.70 and 3.00 m, and those of Pelvetia were numerous between 2.75 and 2.90 m. However, in March 1976, relatively few macroscopic Pelvetia germlings were found at levels below 2.87 m, and these were hidden from view by the much faster-growing F. spiralis germlings (Plate 18A). Severe desiccation in late spring and summer 1976 killed many of the F. spiralis above 2.80 m, and curtailed the growth of those that survived. Pelvetia grew and became more conspicuous above this level (Plate 18B), but no Pelvetia could be found in the dense stand of F. spiralis which covered the shore from 2.80 m down.

In December 1975, when the fucoid germlings first became large enough to be easily identified, a 100 x 100 mm square was marked off just outside the transect at 2.78 m. The square was divided into four 50 x 50 mm subsquares, and all F. spiralis large enough to handle were removed from two subsquares, initially and at approximately monthly intervals until July 1976. By this time numerous macroscopic Pelvetia had appeared in both of the weeded squares, but none could be found among the F. spiralis which grew in the adjacent unweeded squares (Plate 19). Those results show that Pelvetia zygotes settle and germinate in spaces cleared within the F. spiralis zone by natural causes, but they become macroscopic only if the faster-growing F. spiralis germlings are repeatedly removed.

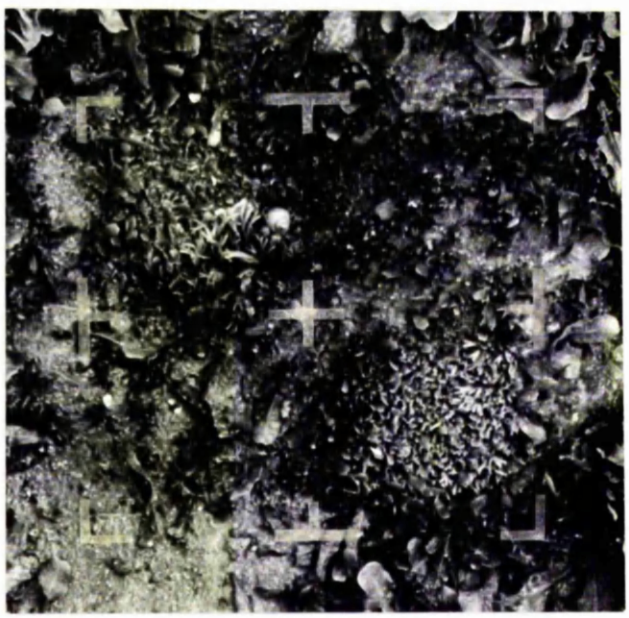



A B

Plate 18: A. Transect through upper F. spiralis zone denuded by severe desiccation in summer 1975, photographed March 30th, 1976, showing mat of young F. spiralis below 2.90m

B. The same transect photographed July 19th, 1976. Pelvetia germlings (P) were evident from 2.80m upward, but none were found in the dense F.spiralis canopy (F) occupying the lower half of the transect.


A



B

Plate 19: A. Fucus removal experiment initiated December 1975 at 2.78 m above chart datum adjacent to transect shown in Plate 18, photographed July 19th, 1976. Pelvetia (P) is visible in the two weeded squares.

B. The same squares photographed the same day after the larger F. spiralis plants were removed, showing that Pelvetia had not appeared in the

## 4.3 The process of interspecific competition in mixed stands of young plants

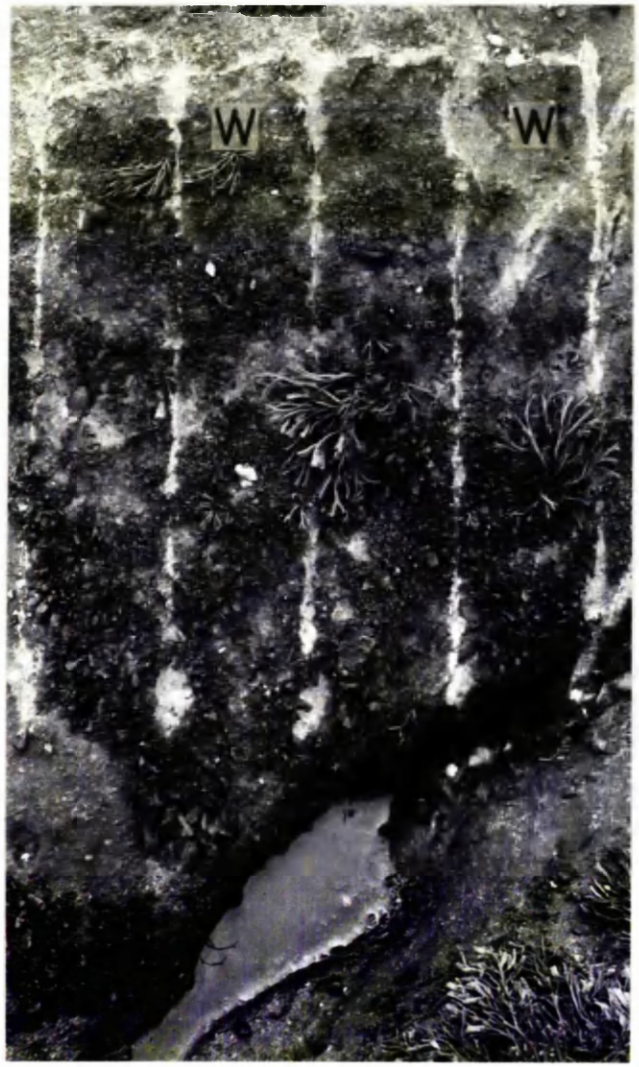
While the boundary between the F. spiralis and Pelvetia zones is usually distinct in adult stands, germlings of the two species often grow together in mixed stands. The process of interspecific competition was studied in one such mixed stand located between 2.90 and 3.05 m above chart datum on a gentle north-facing slope at the North Slip (Figure 3). On 12 September 1975, four adjacent transects 100 mm wide were drawn through the mixed stand of young fucoids (Plate 20A). All F. spiralis large enough to handle were removed from the second and fourth transects on 26 September and again at intervals of several weeks until 19 July 1976. At this time all F. spiralis were removed from all four transects and the cover of Pelvetia in each was compared.

Initially, numerous one-year-old Pelvetia plants between one and eight millimetres long were present over most of the entire length of the four transects, and many young F. spiralis were present over the lower two-thirds (Plate 20A). The Fucus were mostly 5 to 25 mm long, although a few individuals were somewhat larger. By the end of February F. spiralis up to 110 mm long dominated the lower two-thirds of the two unweeded transects. The young Pelvetia were healthy and had grown to lengths of 17 to 30 mm throughout the four transects, but they were noticeably less abundant beneath the canopy of F. spiralis. From March onward, Pelvetia developed rapidly and covered 100% of the substratum in the weeded transects. In the unweeded transects, a distinct zonal boundary formed at about 3.00 m, below which the rapidly growing Fucus formed a dense canopy several layers thick (Plate 20B). Only a few small, dark-coloured Pelvetia were found when the Fucus canopy was removed in July (Plate 20C). This clearly shows that the lower boundary of the Pelvetia zone is largely determined by competition with Fucus spiralis, and that the level of this boundary can be readily lowered by experimental exclusion of Fucus. Since Pelvetia seems to decline only after Fucus has formed a canopy over it, the critical factor appears to be light. This possibility will be examined in the following sections.

Plate 20: A. Experimental site at North Slip, photographed September 12th, 1975 showing a mixed stand of young Pelvetia and F. spiralis on the lower two thirds of the transects. Each transect is about 100 mm wide, and all F. spiralis were removed from the two transects marked "W" on September 26th, and periodically thereafter. The two large Pelvetia plants in the two right-hand transects were lost from natural causes early in the experiment and had little effect on the outcome.

B. The four experimental transects photographed July 19th, 1976, showing a sharp zonal boundary between Pelvetia and F. spiralis in the unweeded transects, and a dense cover of healthy Pelvetia throughout the weeded transects.

C. The same transects photographed the same day immediately after all F. spiralis was removed from the unweeded transects, revealing only a few small Pelvetia (P) in the understory of one of the transects.




A

B


C

## 4.4 Comparison of growth rate of Pelvetia with that of F. spiralis

The relative competitive ability of different plant species is often determined in large part by their comparative rates of growth, and this is particularly true when the critical limiting resource is light. Firstly, a good competitor must grow rapidly in height in its earliest stages in order to escape being shaded by other species, unless it is capable of growing in low light levels. Secondly, in order to eliminate competitors by casting shade, the species must not only continue to grow rapidly as it becomes older, but must also grow in such a way as to form an effective canopy. In the field experiments F. spiralis grew much more rapidly in length than Pelvetia, and formed a solid canopy before it reached the age of one year. Further data were collected in the laboratory and the field to obtain a more quantitative estimate of the difference between the growth rates of these two species.

### 4.4.1 Growth rates of embryos

Pelvetia and F. spiralis were cultured from zygotes as described in section 2.4.3, and randomly selected samples of 20 embryos of each species were measured at intervals.

The embryos of F. spiralis grew six times as fast in length as those of Pelvetia, while the difference in growth in width was less pronounced (Figure 35). The F. spiralis embryos quickly assumed a very elongated shape while the lengths of the Pelvetia embryos were still less than twice their widths after forty-nine days in culture. Clearly, the embryos of F. spiralis have a great competitive advantage over those of Pelvetia not only because they develop faster, but also because elongation is emphasized in their pattern of development.

### 4.4.2 Photosynthetic rates and growth characteristics of macroscopic plants

The rates of photosynthesis and of growth of young plants of Pelvetia and F. spiralis were compared using laboratory data already collected for other determinations. Firstly, oxygen evolution rates of the two species were measured several times without a preceding

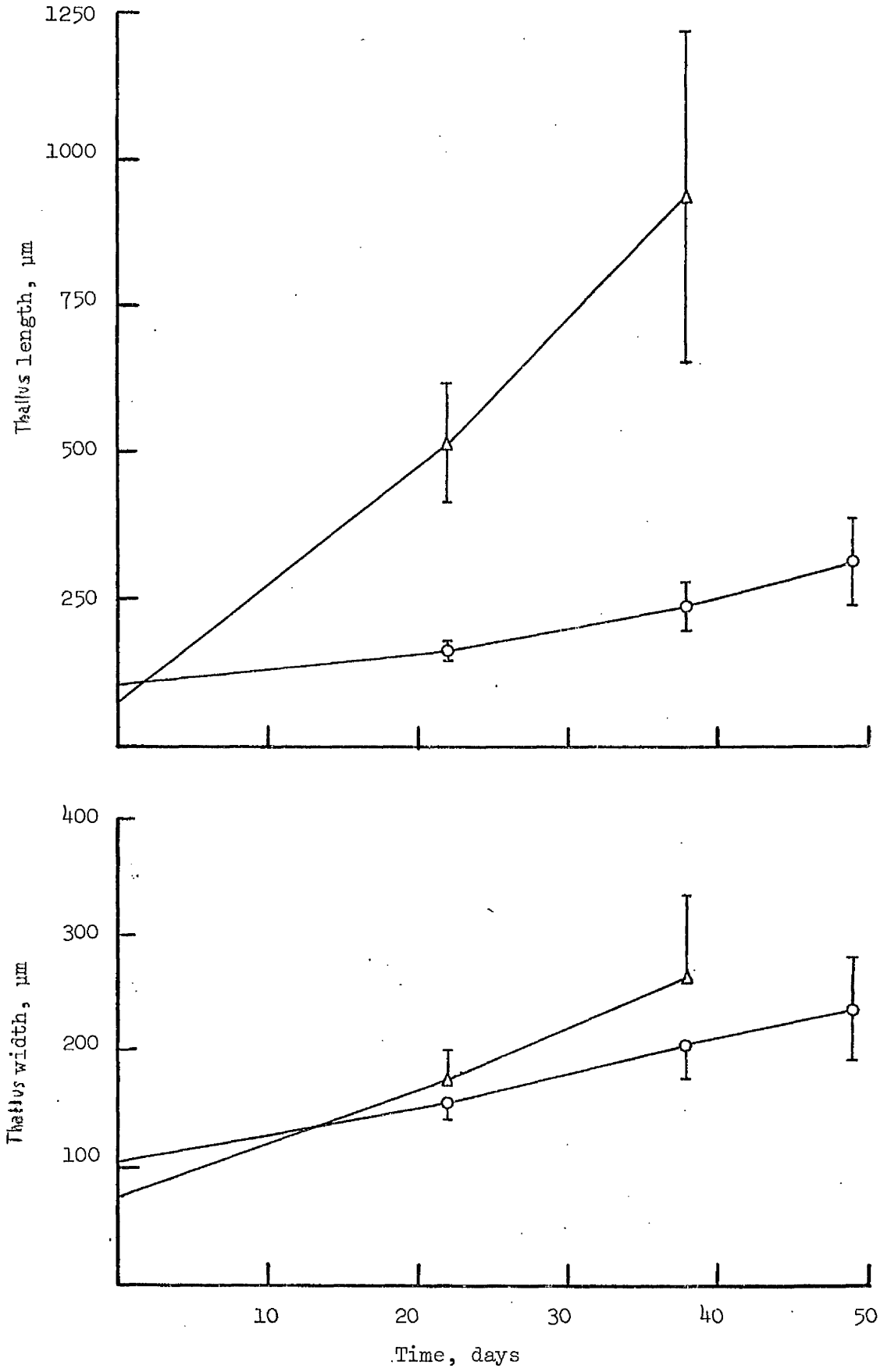



Figure 35. Course of growth in embryos of Pelvetia (o) and Fucus spiralis (Δ). Each point represents mean ± standard deviation of twenty randomly selected embryos. Initial head length and width are equal to observed diameter of zygotes.

experimental stress, and these rates were compared directly. Secondly, in many of the culture experiments, the growth rates of the two species were determined simultaneously under identical conditions. For each treatment in each experiment, the linear growth and relative weight gain of Pelvetia were expressed as a percentage of the rates observed in F. spiralis. Data for plants which were desiccated prior to the culture period or were submerged less than twelve hours per day were excluded, since the treatments affect the two species differently.

Oxygen evolution rates, calculated on a wet weight basis, were essentially similar in Pelvetia and F. spiralis (Table 58) which was a surprising result considering the much more rapid development of F. spiralis in the field experiments. However, Pelvetia has a somewhat higher percent dry matter than F. spiralis, and must fix more carbon than F. spiralis to produce a given amount of new tissue. Therefore, Pelvetia would be expected to produce somewhat less new tissue per unit existing tissue per day, and would show a slower relative weight gain. This was found to be true in all the culture work, and the difference was usually statistically significant (Table 59). However, Pelvetia and F. spiralis differed much more dramatically in their linear growth rates, (Table 60). It was shown earlier that Pelvetia plants have a more bushy habit of growth than F. spiralis plants of the same size (Table 10), which might explain the observed contrast in linear growth rates. The two species appear to differ not in photosynthetic rate, but in how they allocate their photosynthate, i.e. their growth strategy. Pelvetia produces a bushy thallus composed of tissue with a high dry matter content while F. spiralis utilizes its photosynthate to produce a rapid linear growth.

Table 58: Comparison of oxygen evolution rates of Pelvetia and Fucus spiralis * = $p < 0.05$.

| Fucus spiralis | | Pelvetia | | | |
|---|---|---|---|---|---|
| n | oxygen evolution rate μ moles/g - hour | n | oxygen evolution rate, μ moles/g -hour | percent of rate observed in F. spiralis | t value for differences |
| 10 | 18.5 ± 2.9 | 10 | 22.3 ± 2.6 | 120.5 | 3.11* |
| 10 | 19.8 ± 4.6 | 10 | 23.2 ± 2.2 | 117.2 | 2.17 |
| 5 | 21.7 ± 5.3 | 5 | 24.2 ± 1.8 | 111.4 | 0.94 |
| 5 | 25.8 ± 4.6 | 4 | 27.6 ± 2.9 | 106.9 | 0.69 |
| 3 | 28.2 ± 1.7 | 3 | 26.7 ± 1.2 | 94.7 | 1.25 |
| 5 | 29.0 ± 3.2 | 5 | 23.3 ± 2.7 | 80.4 | 1.66 |

Table 59: Comparison of relative weight gain of Pelvetia with that of F. spiralis in culture.
* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

| | Pelvetia | | Fucus spiralis | | rate in Pelvetia as percent | |
|---|---|---|---|---|---|---|
| treatment number | n | % weight gain per day | n | % weight gain per day | of rate in F.spiralis | t value for difference |
| 1 | 15 | 2.31 ± 0.27 | 15 | 2.62 ± 0.35 | 88.1 | 2.72* |
| 2 | 9 | 0.95 ± 0.20 | 10 | 1.44 ± 0.50 | 66.0 | 2.85* |
| 3 | 10 | 2.28 ± 0.27 | 10 | 3.87 ± 0.67 | 58.9 | 6.94*** |
| 4 | 5 | 2.31 ± 0.63 | 5 | 2.94 ± 0.42 | 78.5 | 1.85 |
| 5 | 5 | 2.39 ± 0.35 | 5 | 3.14 ± 0.31 | 76.1 | 3.58* |
| 6 | 10 | 4.42 ± 0.39 | 10 | 5.88 ± 0.26 | 75.2 | 9.86*** |
| 7 | 15 | 1.81 ± 0.27 | 15 | 2.14 ± 0.33 | 84.6 | 2.99** |
| 8 | 15 | 2.05 ± 0.36 | 15 | 2.41 ± 0.22 | 85.0 | 3.30** |
| 9 | 5 | 2.44 ± 0.70 | 5 | 3.24 ± 0.32 | 75.3 | 2.33 |
| 10 | 10 | 1.13 ± 0.33 | 10 | 2.22 ± 0.42 | 50.9 | 4.73** |
| 11 | 10 | 2.27 ± 0.38 | 10 | 4.21 ± 0.55 | 54.0 | 9.15*** |
| 13[α] | 5 | 1.81 ± 0.68 | 5 | 3.72 ± 0.69 | 48.7 | 4.41* |

α relative weight gain was not measured in treatment 12

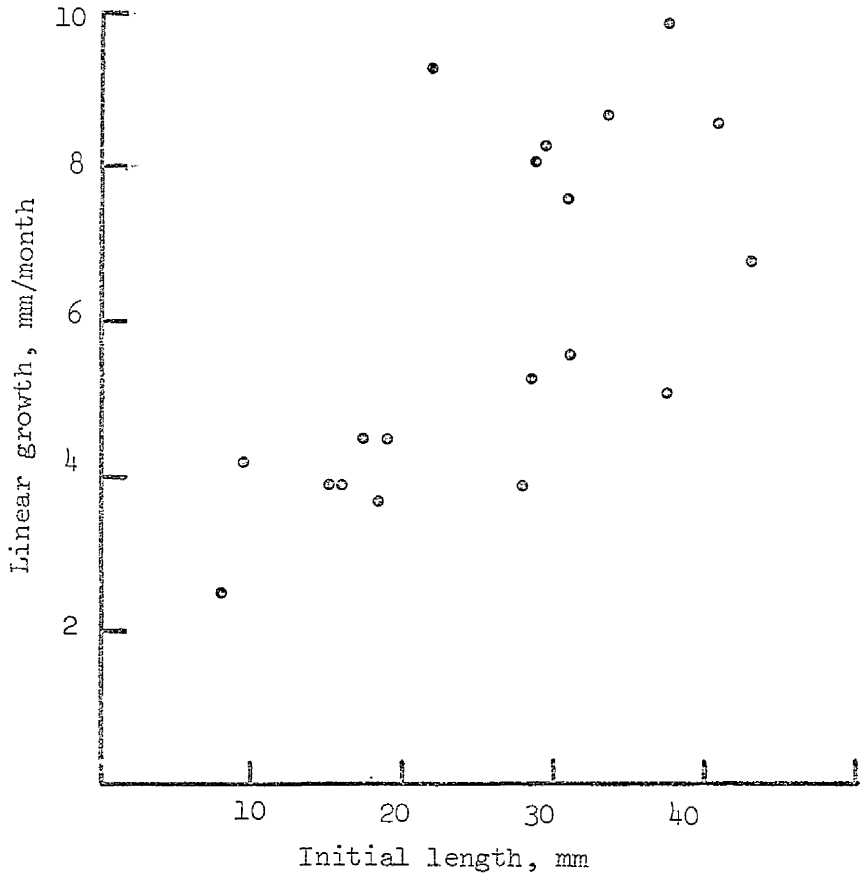
Table 60: Comparison of linear growth rate of Pelvetia with that of F. spiralis in culture.
* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

| treatment number | Pelvetia n | Pelvetia growth mm/month | Fucus spiralis n | Fucus spiralis growth mm/month | rate in Pelvetia as percent of rate in F.spiralis | t value for difference |
|---|---|---|---|---|---|---|
| 1 | 15 | 8.1 ± 1.8 | 15 | 17.6 ± 2.5 | 46.0 | 11.93** |
| 2 | 9 | 3.9 ± 1.7 | 10 | 10.8 ± 5.0 | 36.1 | 4.11** |
| 3 | 10 | 7.6 ± 2.8 | 10 | 22.6 ± 3.6 | 33.6 | 9.69*** |
| 4 | 5 | 8.7 ± 0.6 | 5 | 18.3 ± 4.5 | 47.5 | 4.72** |
| 5 | 5 | 9.9 ± 2.7 | 5 | 18.9 ± 4.2 | 52.4 | 4.48* |
| 6 | 10 | 9.3 ± 2.2 | 10 | 22.2 ± 2.9 | 41.9 | 11.55*** |
| 7 | 15 | 3.7 ± 1.1 | 15 | 11.4 ± 2.4 | 32.5 | 11.30*** |
| 8 | 15 | 4.5 ± 1.1 | 15 | 12.9 ± 2.9 | 34.9 | 10.50*** |
| 9 | 5 | 4.5 ± 2.3 | 5 | 17.6 ± 3.6 | 25.6 | 6.86** |
| 10 | 10 | 5.3 ± 0.9 | 10 | 10.9 ± 1.5 | 48.6 | 10.12*** |
| 11 | 10 | 8.6 ± 2.4 | 10 | 18.2 ± 3.8 | 47.2 | 6.75*** |
| 12 | 10 | 5.1 ± 2.8 | 10 | 18.6 ± 2.8 | 27.4 | 10.77*** |
| 13 | 5 | 8.3 ± 1.3 | 5 | 18.0 ± 1.0 | 46.1 | 13.23*** |

A second consequence of Pelvetia's bushy habit of growth is that it casts shade less effectively than F. spiralis. The branches of a Pelvetia plant overlap each other to a greater extent than do those of a F. spiralis plant of a similar weight (eg. compare the 40-44.5 mm Pelvetia length class with the 60-69.5 mm length class of F. spiralis in Table 10). Since surface to mass ratios are similar in the two species and since F. spiralis fronds tend to lie over the surrounding substratum, the F. spiralis plant can cast shade over a larger area than a Pelvetia plant of the same weight.

It was observed in the competition experiments that Pelvetia develops much more slowly during its first year than during its second. For example, plants which had reached only 1-8 mm in length at the age of one year (Plate 20A) grew to lengths of 40-70 mm during their second year (Plate 20B). In culture, a distinct positive correlation was found between the plants' initial length and their linear growth rate (Figure 36 left). However, there was no correlation between percent weight gain and initial length in the cultures (Figure 36, right), which indicates that young and older Pelvetia plants differ largely in allocation of photosynthate rather than photosynthetic rates. Apparently, the growth pattern of Pelvetia is one of particularly slow linear growth during the early stages, which was demonstrated in the extreme by the embryos (Figure 35). As a result, the first-year Pelvetia plant is particularly vulnerable to being overgrown and shaded by competitors.

Culture conditions never precisely duplicate those in nature, and might produce serious artefacts in growth rate comparisons. In order to ascertain whether culture conditions affected the present results, linear growth rates of natural populations of Pelvetia and F. spiralis were measured. On the shore, growth, loss of branches and loss of entire plants occur simultaneously, which complicates comparison between growth rates in natural stands and those of individual plants in culture. Therefore, two parameters of growth were measured as follows. Quadrats measuring 0.25 x 0.25 m were marked out in stands consisting mostly of young plants, and each quadrat was divided into twenty-five 50 x 50 mm subsquares. The longest plant present in each of the subsquares was measured initially and on three occasions over a period of nine months. For each subsquare, the change in maximum length between successive measurements was noted. No data were taken for subsquares which contained no plants at the beginning and end of a given time interval, but the loss of all plants from a subsquare, and the appearance of new plants in a previously barren subsquare was recorded as the appropriate change in maximum length. Often the plants in some subsquares showed a negative change in their maximum length, but the majority of the subsquares showed a net increase. For each



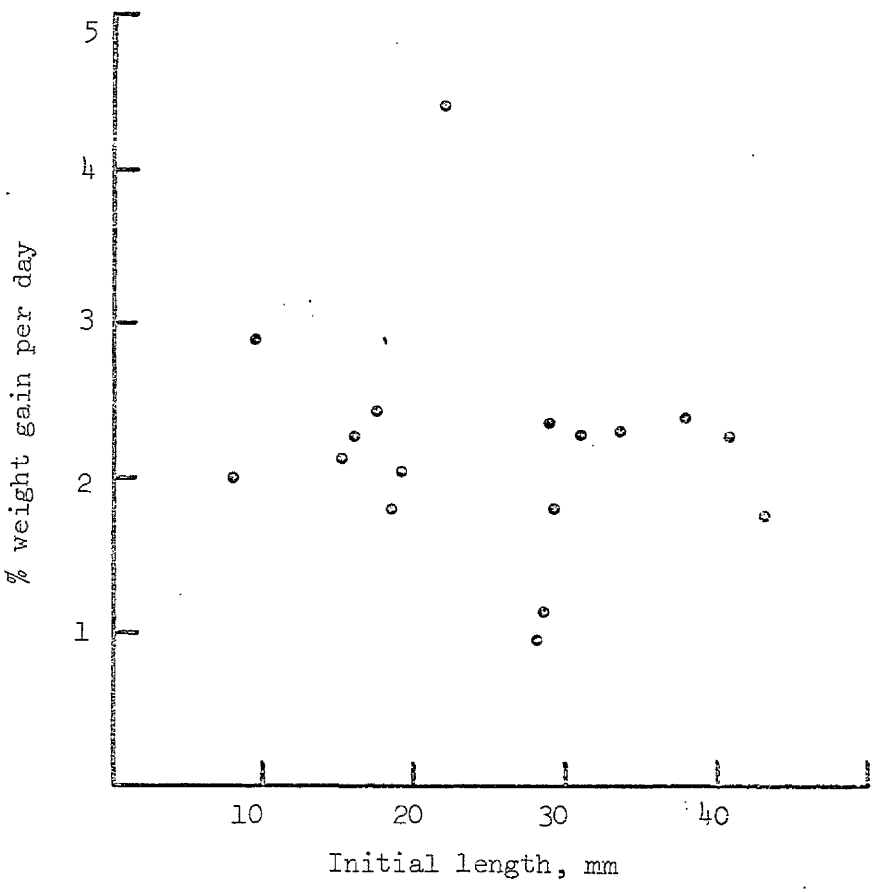



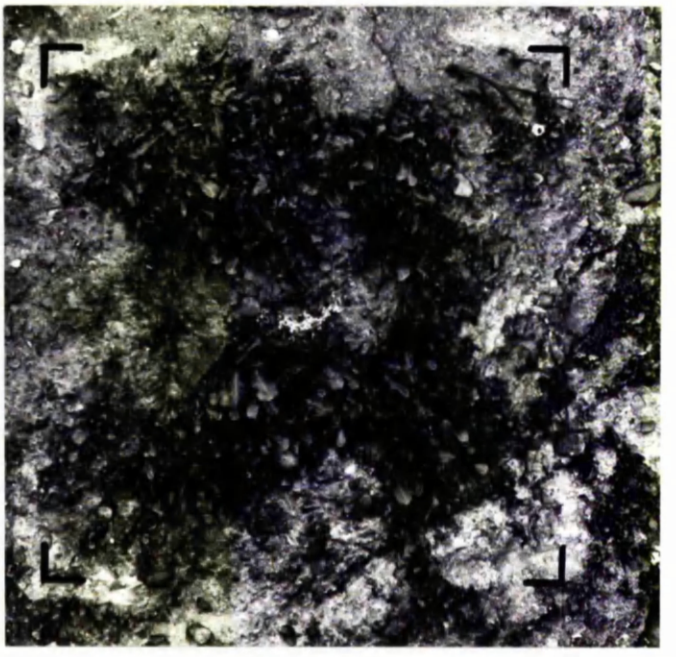

Figure 36. Relationship between initial length and growth rate of Pelvetia in culture. Each point represents mean value for five to fifteen plants.

quadrat, the "net growth rate" was calculated as the mean of the length changes in all subsquares, which reflects the combined effects of growth and attrition. The ten largest increases were averaged to obtain the second parameter "maximum growth rate", which was used as an estimate of the growth rate of individual plants not affected by attrition.

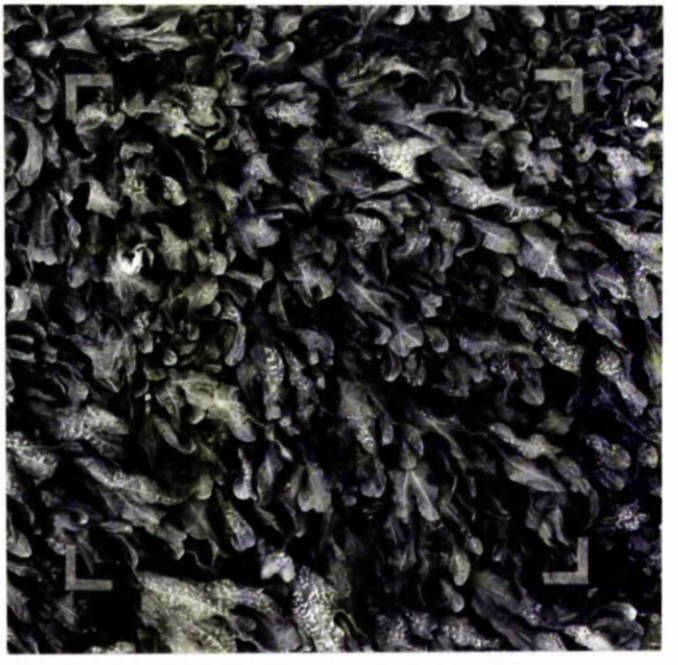
Growth was assessed by this method for two reasons. Firstly, it is the net growth rate which determines competitive ability. A population in which many plants lose branches or are removed altogether by natural causes may not form an effective canopy even if the few plants which are not thus affected grow rapidly in length. Secondly, estimating growth by measuring individual marked plants is difficult owing to the tendency to lose a large percentage of the plants.

Growth rates of F. spiralis were measured in three quadrats placed within the F. spiralis zone, and in one quadrat in the Pelvetia zone which contained a sparse stand of F. spiralis in addition to a well developed stand of young Pelvetia. Growth rates of Pelvetia were measured in the last-mentioned quadrat and in two others within the Pelvetia zone. The quadrats included mostly young plants, but a few older, larger plants were present which were lost during the first two-month period, resulting in very low or negative net growth rates during this interval.

The maximum growth rates observed in the two species were very similar to their growth rates in culture (Compare Tables 61 and 60), which suggests that culture conditions did not seriously affect the growth rate of either species. Both the net growth rate and the maximum growth rate of F. spiralis were generally two to three times those of Pelvetia (Table 61). During the nine month period, F. spiralis developed into a solid cover several thallus layers deep (Plate 21) while the Pelvetia stands remained visibly less massive (Plate 22). It is interesting to note that the F. spiralis in Quadrat 5, within the Pelvetia zone grew in length at roughly the same rate as the Pelvetia (Table 61), and remained inconspicuous at the end of nine months (Plate 21). Apparently physical conditions in the Pelvetia zone restricted the growth of the F. spiralis plants, and prevented them from outcompeting Pelvetia.



A

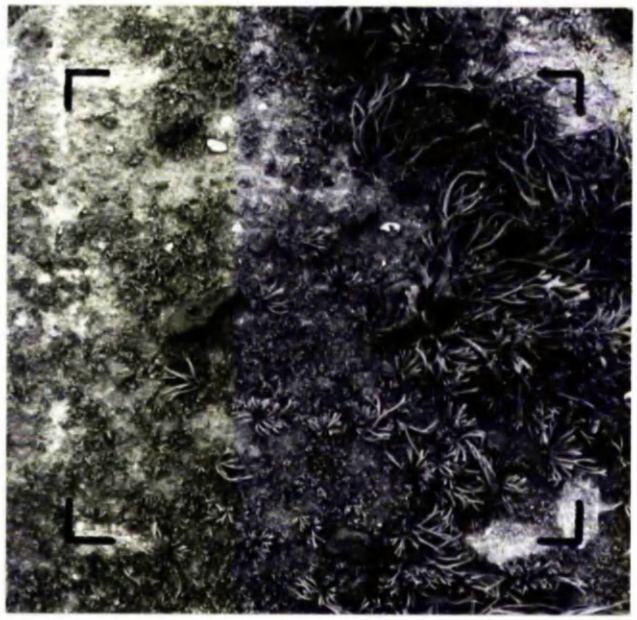


B

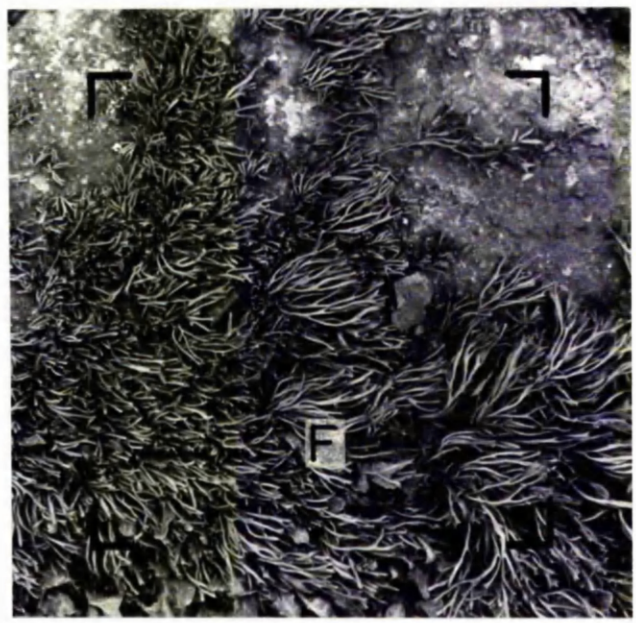
Plate 21: Quadrat 3, located within the Fucus spiralis zone, showing rapid development of dense cover of Fucus spiralis over a nine month period.

A. September 4th, 1975.

B. June 15th, 1976.



A




B

Plate 22: Quadrat 5, located within the Pelvetia zone showing development of a stand of young Pelvetia over a ten month period.

A. August 25th, 1975.

B. June 15th, 1976. Fucus (F) has grown within the quadrat but has remained inconspicuous.

Table 61: Mean ± standard deviation of net growth rate and maximum growth rate in natural populations of Pelvetia and Fucus spiralis located within their normal zones. Growth rates given in millimetres per month. n = number of subsquares for which data were obtained.

| qudrat number | height above chart datum | species | Early Sept-Early Nov.1975 n | net growth rate | maximum growth rate | Early Nov.1975-Mid Feb. 1976 n | net growth rate | maximum growth rate | Mid Feb. - Mid May 1976 n | net growth rate | maximum growth rate |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2.65 m | F. spiralis | 25 | 2.9 ± 31.0 | 22.1 ± 2.7 | 25 | 7.4 ± 9.4 | 15.3 ± 2.7 | 24 | 14.7 ± 11.6 | 21.9 ± 2.3 |
| 2 | 2.75 m | F. spiralis | 25 | 15.4 ± 8.0 | 23.1 ± 3.1 | 25 | 7.4 ± 9.0 | 15.2 ± 2.9 | 25 | 6.9 ± 11.9 | 18.0 ± 5.6 |
| 3 | 2.85 m | F. spiralis | 25 | 6.5 ± 4.4 | 10.5 ± 3.1 | 25 | 7.9 ± 3.6 | 11.1 ± 1.7 | 25 | 14.9 ± 4.3 | 18.7 ± 3.6 |
| 4 | 2.95 m | Pelvetia | 24 | -1.4 ± 15.7 | 4.9 ± 2.4 | 24 | 2.9 ± 3.5 | 5.8 ± 1.8 | 24 | 3.9 ± 3.7 | 7.0 ± 1.5 |
| 5 | 3.05 m | Pelvetia | 24 | 0.9 ± 11.2 | 7.0 ± 3.0 | 23 | 3.6 ± 5.6 | 6.8 ± 1.1 | 25 | 4.8 ± 9.2 | 9.0 ± 1.6 |
| | | F. spiralis | 20 | 2.1 ± 7.4 | 6.0 ± 2.0 | 18 | 3.4 ± 2.9 | 5.5 ± 2.2 | 21 | 4.2 ± 4.6 | 7.3 ± 1.4 |
| 6 | 3.05 m | Pelvetia | 25 | -1.1 ± 12.8 | 7.1 ± 2.3 | 25 | 3.7 ± 2.6 | 6.2 ± 1.4 | 25 | 5.0 ± 2.6 | 7.6 ± 1.1 |

Theoretically, Pelvetia might escape competition in the F. spiralis zone by releasing its zygotes at a time when F. spiralis is not reproducing. However, the observed fertile period of Pelvetia (June-September at Isle of Cumbrae) lies entirely within that of F. spiralis (April-October). Therefore, any free primary space which becomes available in the F. spiralis zone during summer would be settled by zygotes of both species at the same time, and the extremely slow-growing Pelvetia germlings would remain in the understorey beneath the developing canopy of F. spiralis. The absence of a Pelvetia understorey beneath natural stands of F. spiralis suggests that Pelvetia cannot grow in the reduced illumination beneath such stands, and this possibility was investigated in culture.

## 4.5 The effect of reduced illumination upon growth rates of young plants

Young plants of Pelvetia, Fucus spiralis and F. serratus were cultured for twenty days under two different levels of irradiance in order to determine whether Pelvetia requires a higher light intensity to grow normally than do Fucus spp. Ten plants of each species were cultured in each of two tanks, one of which was completely covered with several layers of white muslin to reduce the irradiance reaching the plants. The two tanks were placed on the same shelf under daylight fluorescent tubes and the irradiance measured with the photometer which had been calibrated as described in section 2.4.1.2. The algae in the tank covered with muslin received 8.2 - 8.5 mg-cal/$cm^2$-min., and those in the control tank received 22.2 - 23.4 mg-cal/$cm^2$-min.

All three species grew more slowly at the lower irradiance, but the difference was most pronounced in Pelvetia and least so in F. serratus (Table 62). This indicates that the light requirements of the different fucoids are related to their vertical distributions on the shore. However, the extremely high relative weight gains of the control plants suggests that the algal material used in this experiment was unusual in some way that might have affected the results.

Table 62: Mean ± standard deviation of growth rates of Pelvetia, Fucus spiralis and F. serratus cultured under two different irradiances. n=10 for each species in each treatment. t values for differences between the two treatments * = $p < 0.05$; *** = $p < 0.001$.

| | | control (22.2 - 23.4 mg.cal/cm$^2$-min) | experimental (8.2 - 8.5 mg.cal/cm$^2$-min) | % of control | t |
|---|---|---|---|---|---|
| Pelvetia | Linear growth, mm/month | 9.3 ± 2.2 | 6.6 ± 1.6 | 64 | 3.14* |
| | % weight gain per day | 4.42 ± 0.39 | 2.68 ± 0.43 | 61 | 9.56*** |
| F. spiralis | Linear growth, mm/month | 22.2 ± 2.9 | 18.0 ± 2.2 | 81 | 3.36* |
| | % weight gain per day | 5.88 ± 0.26 | 4.93 ± 0.52 | 84 | 5.16*** |
| F. serratus | Linear growth, mm/month | 21.0 ± 4.4 | 20.0 ± 2.8 | 95 | 0.61 |
| | % weight gain per day | 4.65 ± 0.89 | 4.19 ± 0.54 | 90 | 1.40 |

A second experiment was performed using a new set of samples to determine whether the observed trend is reproducible. Young plants of Pelvetia, F. spiralis and Ascophyllum were collected and cultured for twenty days under irradiances of 16.8 and 7.1 mg-cal/cm$^2$-min. Ascophyllum was included because healthy young plants were often found beneath a heavy F. spiralis canopy under which Pelvetia has proven unable to survive, which suggests that Ascophyllum is more tolerant of dim light.

The results of this determination were ambiguous. The trend observed in the preceding experiment was present to a lesser degree in linear growth, but was not evident in relative weight gain (Table 63).

Table 63: Mean ± standard deviation of growth rates of Pelvetia, F. spiralis and Ascophyllum cultured under two different irradiances. n = 10 for Pelvetia and F. spiralis, n = 15 for Ascophyllum. t values for differences between the two treatments * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

| | | control 16.8 mg-cal/ $cm^2$-min | experimental 7.1-7.6 mg-cal/$cm^2$-min | % of control | t |
|---|---|---|---|---|---|
| Pelvetia | Linear growth, mm/month | 4.2 ± 1.1 | 2.7 ± 0.5 | 64 | 3.91** |
| | % weight gain per day | 2.90 ± 0.55 | 1.90 ± 0.19 | 66 | 5.43*** |
| F. spiralis | Linear growth, mm/month | 15.3 ± 2.4 | 11.7 ± 2.9 | 77 | 2.85* |
| | % weight gain per day | 3.20 ± 0.31 | 1.84 ± 0.52 | 58 | 7.10*** |
| Ascophyllum | Linear growth, mm/month | 6.2 ± 1.5 | 4.8 ± 1.8 | 77 | 2.32* |
| | % weight gain per day | 2.57 ± 0.42 | 1.84 ± 0.39 | 72 | 4.92*** |

Furthermore, the relative weight gains of the three species at the lower light intensity were essentially the same, hence there is no clear indication that Pelvetia requires a higher light intensity than the other two species.

In both experiments, the plants grown under reduced irradiance became considerably darker and more olive-green in colour than the controls. On the shore, the same dark colour was repeatedly observed in young fucoids located under a canopy of larger plants (eg. Plate 17) which suggests that such plants may be significantly light-limited.

A third experiment was undertaken to compare the effect on Pelvetia and Ascophyllum of a more severe reduction in irradiance. Ten plants

of each species were cultured for twenty days under each of two irradiances: 10.6-12.4 mg-cal/cm$^2$-min and 2.3-3.1 mg-cal/cm$^2$-min. The higher irradiance was obtained by covering the tank completely with two layers of white muslin, and the lower irradiance by covering the sides and bottom with opqaue black paper, and the top with seven layers of muslin. Under both regimes Ascophyllum grew somewhat faster in length and weight than Pelvetia but both species appeared to be very close to their compensation points at the lower irradiance (Table 64).

Table 64: Mean ± standard deviation of growth rates of Pelvetia and Ascophyllum at two low levels of irradiance

| | 2.3-3.1 mg-cal/cm$^2$day | | | 10.6-12.4 mg-cal/cm$^2$-day | | |
|---|---|---|---|---|---|---|
| | n | linear growth mm/month | % weight gain per day | n | linear growth mm/month | % weight gain per day |
| Pelvetia | 9 | 0.9 ± 0.6 | 0.06 ± 0.09 | 9 | 4.2 ± 2.2 | 0.77 ± 0.21 |
| Ascophyllum | 10 | 1.6 ± 2.0 | 0.19 ± 0.07 | 10 | 6.9 ± 3.9 | 1.39 ± 0.33 |

Two conclusions were drawn from these results. Firstly, Pelvetia's light requirement is at most slightly higher than that of the other fucoids. Secondly, the growth compensation point in culture under a 16/8 day/night cycle is near 2-3 mg-cal/cm$^2$-min. Since growth rates in cultures maintained at 16-24 mg-cal/cm$^2$-min were close to the maximum growth rates observed on the shore, the plants were assumed to become light-saturated within this range. To determine whether light is actually limiting under a canopy of F. spiralis the expected irradiances under such a canopy were estimated and compared with these threshholds. The light attenuation by one and by two layers of F. spiralis blades was measured as follows. The EEL Photoelectric Photometer was set up in the field with the photoreceptor on a horizontal surface. A single layer of young F. spiralis plants was carefully arranged on the receptor, covering it completely with as little overlap of blades as possible, and the illumination was measured. Then the blades were quickly removed

and the illumination immediately remeasured. This was repeated ten times, and the ratio of illumination with blades to illumination without blades was calculated for each pair of readings. Five pairs of readings were also taken using two layers of blades. Transmittance by a single layer was found to be 9.0 ± 3.5%, and two layers reduced incident light to 2.1 ± 0.6%. Using these data and the monthly means for the daily global solar radiation on a horizontal surface, the amounts of radiation available for photosynthesis under one and under two layers of F. spiralis blades in June and December were calculated (Table 65). Two assumptions were made in these estimates. Firstly, since the F. spiralis zone is exposed most of the time, and rarely submerged to a depth greater than one metre, light attenuation owing to submergence was disregarded. Secondly, when the plants are submerged, water currents move the blades about and effectively reduce the number of layers shading the substratum. Since the substratum in F. spiralis stands usually remains completely hidden from view during submersion (personal observation) it was assumed to be shaded by at least one thallus layer.

The estimates show that the Fucus canopy may reduce the irradiance to subsaturating levels during the summer, and may curtail it to near or below the compensation point during the winter (Table 65). The actual amount of light available to Pelvetia growing under such a canopy would actually be somewhat less than that indicated by the table for two reasons. Firstly, during low tide, the F. spiralis blades lie several layers deep over the substratum (Tables 13 and 14). Secondly, since the absorption spectra and photosynthesis action spectra of brown algae are very similar (Steeman-Nielsen 1975), the overlying F. spiralis blades would selectively absorb those wavelengths Pelvetia could use most efficiently. Clearly, Pelvetia growing beneath a F. spiralis canopy would be severely light-limited, especially during winter.

The germlings of many brown algae can survive for long periods of time in darkness or very dim light, and resume growth when adequate light is again available (Burrows 1961, Kain 1964, Sheader & Moss 1975). An experiment was undertaken to ascertain whether Pelvetia might lack this ability. Eight glass slides were inoculated with Pelvetia zygotes and cultured for eight days under an irradiance of 16-24 mg-cal/cm$^2$-min supplied sixteen hours per day. Six of the slides were than placed in a tank

Table 65: Total global solar radiation per day and mean irradiance available to unshaded plants and to plants beneath one or two layers of F. spiralis blades. 1 mg-cal/cm$^2$-min = 0.6972 watt/m$^2$.

Total radiation available per day, watt-hrs/m$^2$

| | Mean daily global solar radiation on a horizontal surface [a] | Mean daily global solar radiation available for photosynthesis [b] | Available under one layer of blades | Available under two layers of blades |
|---|---|---|---|---|
| June | 4788 | 2250 | 203 | 47.3 |
| December | 318 | 150 | 13.5 | 3.1 |

Approximate compensation point in culture: 22.3 (2mg-cal/cm$^2$-min,16 hrs/day)[c]

Approximate saturation point in culture: 223.1 (20mg-cal/cm$^2$-min,16 hrs/day)

Mean irradiance between sunrise and sunset, mg-cal/cm$^2$-min

| | Mean day length at 56°N latitude, hours | Irradiance available for photosynthesis | Irradiance under one layer of blades | Irradiance under two layers of blades |
|---|---|---|---|---|
| June | 17.48 | 184.6 | 16.6 | 3.9 |
| December | 7.12 | 30.1 | 2.7 | 0.6 |

Approximate compensation point in culture: 2

Approximate saturation point in culture: 20

α Data for Dunstaffnage Marine Laboratory near Oban, Argyll, Scotland, supplied by Meteorological Office in Edinburgh.

b Total irradiance multiplied by 0.47, as this is the proportion of solar radiation between 350 and 700 nm and therefore available for photosynthesis (Steeman-Nielsen 1975)

c Virtually all the radiation from fluorescent tubes lies between 350 and 700 nm.

from which light was excluded by a covering of opaque polythene. The medium in the tank was changed every fourteen days, and was aerated to assure that oxygen did not become depleted. The remaining two slides were cultured in the light for another twenty-one days after which thirty embryos on each slide were selected at random and their lengths measured. Slides were withdrawn from the darkened tank at intervals and thirty embryos on each slide were measured. Each slide was then cultured in the light for twenty-one days, at the end of which thirty embryos were measured again to determine whether the embryos grew after the prolonged dark treatment.

A similar determination was carried out with Fucus spiralis to find out whether this species could survive longer in the dark than Pelvetia. Newly-fertilized zygotes and six-day embryos were cultured in the dark for 14, 30, 61, 91 and 120 days. With the exception of the slides removed after fourteen days, thirty embryos were measured immediately after the dark period. Each slide was cultured for eleven days in the light, after which thirty embryos were measured again.

During the first nineteen days in the dark, Pelvetia embryos underwent numerous cell divisions and produced several rhizoids, but did not appear to develop further thereafter. Growth during the twenty-one day illuminated culture period was slow, even in the controls, but the length increases during this period after nineteen, thirty and sixty days in the dark were statistically significant (Table 66). The embryos which had spent sixty days in the dark were recultured for a second twenty-one days to determine whether the dark period had a long-lasting effect on their growth rate. Unfortunately, the culture became heavily contaminated with green algae, which may have caused the observed inhibition of growth. After ninety days in the dark, scattered dead cells were observed in many of the embryos. No net growth was observed during twenty-one days in the light (Table 66), but a few healthy embryos were noticed which were considerably larger than the others. This suggests that at least a small percentage of Pelvetia embryos can remain viable after ninety days in the dark.

Both the zygotes and the six-day embryos of F. spiralis remained healthy during the dark period, and produced a very long primary rhizoid during the first fourteen days, after which little further development occurred.

Table 66: Growth of Pelvetia embryos after dark periods of various durations. Mean ± standard deviation of thallus length of thirty embryos. Embryos eight days old at beginning of dark period. t value for difference between length immediately after dark period and after twenty-one days in culture in the light. *** = $p < 0.001$

| | Length, µm | | | |
|---|---|---|---|---|
| duration of dark period | immediately after dark period | 21 days after dark period | 42 days after dark period | t |
| none | | 177 ± 22<br>196 ± 21 | | |
| 19 days | 141 ± 12<br>143 ± 11 | 167 ± 21<br>174 ± 25 | | 3.67***<br>6.21*** |
| 30 days | 147 ± 12 | 165 ± 22 | | 3.92*** |
| 60 days | 144 ± 13 | 162 ± 23 | 169 ± 40[α] | 3.73*** |
| 90 days | 140 ± 14<br>146 ± 11 | 138 ± 17<br>149 ± 23 | | 0.50<br>0.64 |

α Heavy contamination of culture may have affected growth

Growth during the first eleven days after the dark period seemed to become progressively slower as the length of the dark period increased (Table 67). When the embryos were maintained in illuminated culture for a longer period of time, they resumed rapid growth (Table 67), which shows that the prolonged dark period had only a temporary effect on their development. Clearly, the early F. spiralis embryos are very capable of surviving for several months in total darkness, and can resume rapid growth a short time after light again becomes available. The Pelvetia embryos seemed a little less adapted than those of F. spiralis to surviving long periods of darkness or very dim illumination.

Table 67: Growth of Fucus spiralis embryos after dark periods of various durations. Mean ± standard deviation of thallus length of thirty embryos. t values for difference between length immediately after dark period and after eleven days in culture in the light. ** = $p < 0.01$ *** = $p < 0.001$

Embryos six days old at beginning of the dark period

| dark period | Length, μm immediately after dark period | 11 days after dark period | t | 22-23 days after dark period |
|---|---|---|---|---|
| 14 days | (90-130)[α] | 236 ± 34 | | |
| 30 days | 106 ± 12 | 187 ± 24 | 16.52*** | |
| 61 days | 109 ± 11 | 155 ± 21 | 10.64*** | |
| 91 days | 109 ± 17 | 133 ± 17 | 5.47*** | 303 ± 36 |
| 120 days | 111 ± 16 | 128 ± 22 | 3.42** | 311 ± 65 |
| | 113 ± 13 | 125 ± 18 | 2.96** | 320 ± 49 |

Zygotes less than twenty-four hours old at beginning of dark period

| dark period | Length, μm immediate after dark period | 11 days after dark period | t | 22-23 days after dark period |
|---|---|---|---|---|
| 14 days | (80-100)[α] | 192 ± 24 | | |
| 30 days | 91 ± 8 | 172 ± 21 | 19.75*** | |
| 61 days | 98 ± 11 | 137 ± 20 | 9.36*** | |
| 91 days | 97 ± 8 | 123 ± 15 | 8.46*** | 299 ± 46 |
| | 94 ± 10 | 127 ± 16 | 9.38*** | 282 ± 41 |
| 120 days | 95 ± 10 | 116 ± 14 | 6.66*** | 294 ± 49 |

α Estimated range. Exact measurements not taken.

However tiny, healthy Pelvetia embryos were discovered underneath natural stands of adult plants in May 1976. Since the minimum age of these embryos was eight months, it was concluded that germlings of this species can survive for long periods under a fucoid canopy. It might be expected that such embryos would be present in the F. spiralis zone and would grow into conspicuous plants wherever the F. spiralis canopy is suddenly removed by storms or other natural causes. Since Pelvetia is rarely found in the F. spiralis zone, some other factor apparently removes small Pelvetia from the understorey of F. spiralis stands before they become macroscopic. One such factor might be the secretion of chemical substances of F. spiralis which adversely affect Pelvetia.

## 4.6 The effect of Fucus spiralis upon the survival and growth of Pelvetia in culture.

The effect of substances excreted by F. spiralis on zygotes of Pelvetia was investigated in culture. One slide bearing zygotes was placed in each of three petri dishes containing 40 ml of culture medium and small plants of F. spiralis weighing a total of 0.25 ± 0.18 g. Care was taken to ensure that the Fucus plants did not shade the slides or otherwise interfere with them physically. Simultaneously, three control cultures were set up on which the Pelvetia zygotes were grown alone. Because the F. spiralis plants might affect the Pelvetia embryos by exhausting the nutrient supply in the small volume of medium, a second set of controls was cultured with 0.25 ± 0.01 g. of Pelvetia in each petri dish. Nutrient depletion would be expected to occur in these controls to about the same extent as in the experimental set. To minimize the possibility of nutrient exhaustion by the larger plants, 1/5 concentration medium was used rather than 1/10 concentration. The zygotes were cultured for thirty-six days after which thirty embryos on each slide were measured.

There was no indication that the F. spiralis plants inhibited the growth of the Pelvetia embryos (Table 68). However, the cultures became very contaminated which probably contributed to the great variation between replicates and may have seriously affected the results.

Table 68: Effect of Fucus spiralis on the growth of Pelvetia embryos. Mean ± standard deviation of thallus length after thirty-six days in culture.

Length, µm

| replicate | cultured alone | cultured with 0.25 ± 0.01g of larger Pelvetia plants | cultured with 0.25 ± 0.01g of F. spiralis plants |
|---|---|---|---|
| 1 | 153 ± 14 | 210 ± 38 | 252 ± 52 |
| 2 | 149 ± 19 | 178 ± 19 | 181 ± 31 |
| 3 | 159 ± 21 | 138 ± 13 | 187 ± 23 |

Since contamination is very difficult to eliminate in cultures of Pelvetia embryos, a second experiment was carried out using small Pelvetia plants 9-21 mm in length. Fifteen of these were grown with several large F. spiralis plants and another fifteen small Pelvetia were cultured with several large Pelvetia. The large plants were attached securely to the opposite end of a perspex plate from the small plants to ensure that they would not shade them. The growth rates of the small plants during twenty days in culture were measured, and were found to be equal in the two treatments (Table 69). Therefore it was concluded that young stages of Pelvetia are not affected by F. spiralis any more than they are by adult plants of their own species.

Table 69: Effect of Fucus spiralis on the growth of young plants of Pelvetia (Mean ± standard deviation). t value for difference between treatments.

| treatment | n | linear growth, mm/month | % weight gain per day |
|---|---|---|---|
| grown with five Pelvetia plants total weight 4.65g | 15 | 3.9 ± 1.4 | 52.8 ± 10.2 |
| grown with five F.spiralis plants total weight 4.58g | 15 | 3.9 ± 1.1 | 57.2 ± 13.5 |
| t | | 0 | 1.01 |

## 4.7 Effect of prolonged submersion on Pelvetia

It has been shown that F. spiralis forms a shading canopy beneath which Pelvetia germlings cannot grow, but that this alone does not eliminate these germlings. Indeed, many of the Pelvetia plants transferred to the midshore decayed and were lost before other algae had started to form a canopy over them, which suggests that prolonged submersion itself may adversely affect this species. Certainly, Pelvetia, unlike F. spiralis, was difficult to culture for longer than four or five weeks, especially in constant submersion. The tips tended to become abnormally narrow and to develop small dark necrotic spots near the apical pit, and the entire plant sometimes decayed. Often they were overgrown with green and blue-green algal epiphytes. In the tidal simulation cultures, decay and epiphytic growth increased progressively with increasing submersion time and with increasing strength of the medium (Table 70). The similarity between the effects observed in culture and those observed in the midshore transplants indicates that prolonged submersion itself may have contributed to the demise of these transplants.

Table 70: Intensity of decay and epiphytic growth on Pelvetia in cultures with different media and under different tidal regimes.

0 = no decay or epiphytes
† = light
†† = moderate
††† = extensive

Decay

| tidal regime, hours submerged per day | unenriched seawater | 1/20 | 1/10 | 1/5 | fully enriched |
|---|---|---|---|---|---|
| 22 | | | †† | | |
| 20 | † | † | | ††† | ††† |
| 12 | | | †† | | |
| 4 | † | † | | † | †† |
| 2 | | | † | | |

Epiphytes

| tidal regime, hours submerged per day | unenriched seawater | 1/20 | 1/5 | fully enriched |
|---|---|---|---|---|
| 20 | † | † | ††† | ††† |
| 4 | 0 | 0 | † | ††† |

## 4.8 The role of interspecific competition in determining relative abundances of Fucus spp. and Ascophyllum at various levels on the shore

Ascophyllum and the three species of Fucus differ qualitatively from Pelvetia in that they all can grow well at midshore and occur at this level naturally. However, they are characteristically abundant at different levels. In particular, F. spiralis forms a well defined upshore zone and is not abundant near MTL, although it can grow vigorously and reproduce at this level (Plate 12 B). By contrast, Ascophyllum tends to dominate the middle shore, which suggests that it is competitively superior to Fucus spp., particularly F. spiralis with which it often forms a distinct zonal boundary. The relative competitive abilities of these four species were initially investigated by comparing the growth rates of their embryos. The zygotes were cultured as described in section 2.4.3, except that the slides were placed in a large tank of medium. The thallus lengths of fifteen to thirty randomly selected embryos of each species were measured at intervals. The thallus widths were also taken once after twenty-eight days. The embryos were transferred to aerated culture medium and grown until they were 114 days old to determine whether they would develop normally. Finally, the five largest plants of each species were taken from the slides, mounted on a perspex plate and cultured for another twenty-six days during which their growth in length and width was monitored.

During the initial twenty-eight days, F. serratus embryos grew the most rapidly by far, followed by F. vesiculosus and F. spiralis in that order (Figure 37), which corresponds to their order of occurrence on the shore. This suggests that F. spiralis is not abundant within the ranges of its two congeners because it is a somewhat inferior competitor, owing to its slower early development. Surprisingly, Ascophyllum grew only half as rapidly as F. spiralis, and thus seems to be at a severe disadvantage in its early stages. The four species differed much less in the widths attained by their embryos in twenty-eight days, and the ratio of length to width was directly related to linear growth rate (Table 71). Apparently, the

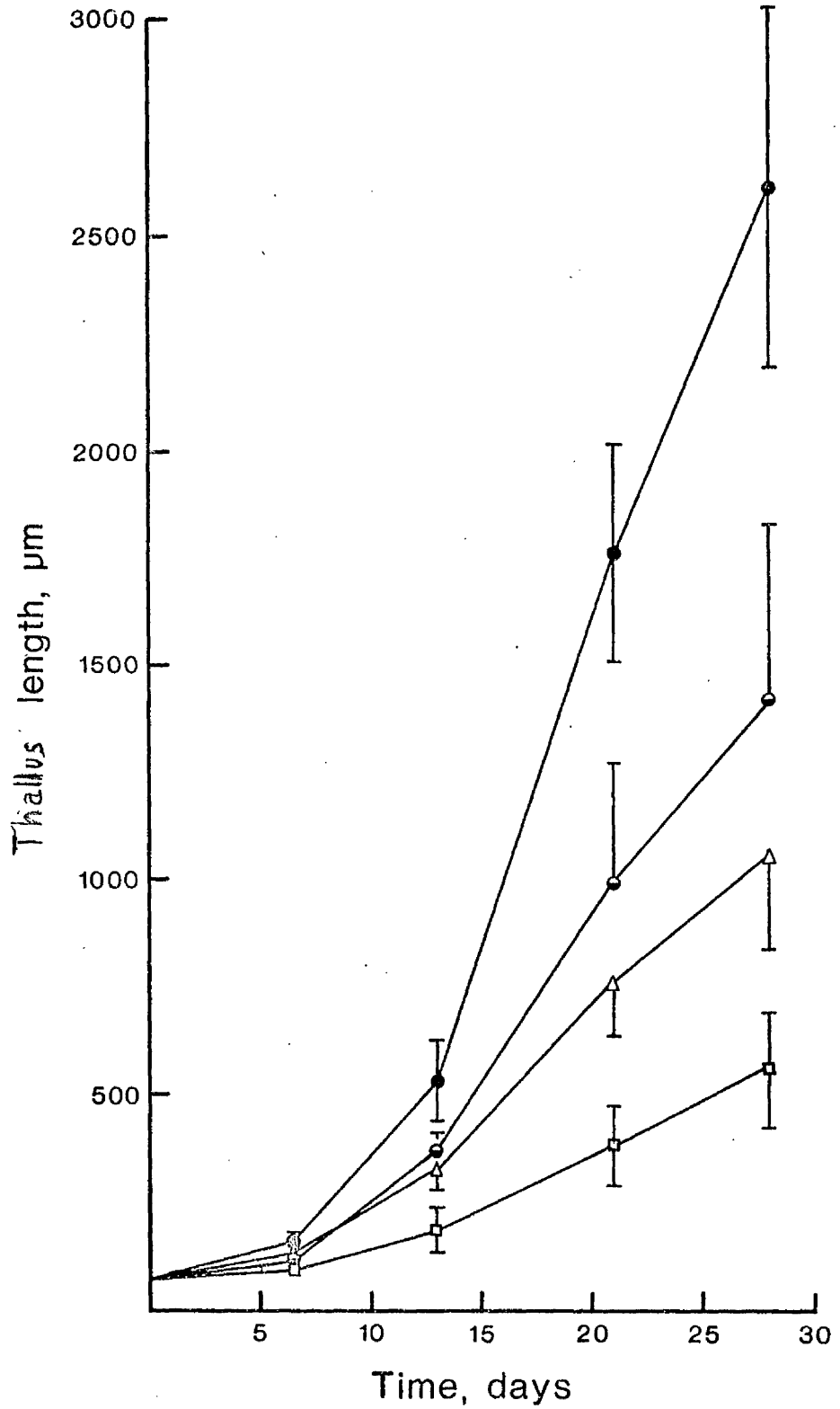



Figure 37: Course of growth of embryos of Ascophyllum (□), Fucus spiralis (Δ), F. vesiculosus (◐) and F. serratus (●) (mean ± standard deviation). n = 30 for measurement after $6\frac{1}{2}$ days, n = 15 for measurement after 13 and 21 days, n = 25-30 for measurement after 28 days.

Table 71: Length, width and ratio of mean length to mean width in twenty-eight day old embryos of Ascophyllum and three species of Fucus. Mean ± standard deviation of thirty embryos for length and width.

| | n | length, µm | width, µm | ratio of mean length to mean length |
|---|---|---|---|---|
| Ascophyllum | 30 | 558 ± 133 | 209 ± 28 | 2.67 |
| F. spiralis | 30 | 1058 ± 222 | 248 ± 47 | 4.27 |
| F. vesiculosus | 30 | 1409 ± 417 | 298 ± 65 | 4.71 |
| F. serratus | 25 | 2604 ± 414 | 383 ± 76 | 6.80 |

growth strategy of the early stages of Fucus spp. is one of rapid elongation and escape from the shade of competing algae, and this strategy is developed to the extreme in F. serratus. By contrast, Ascophyllum forms a much less elongated thallus, and its growth pattern somewhat resembles that of Pelvetia in this respect.

At the end of 114 days the largest plants of the three Fucus species had developed the characteristic midrib and blade of this genus. F. vesiculosus had overtaken F. serratus in length, and continued to grow the most rapidly, while Ascophyllum remained by far the smallest and slowest-growing of the four species (Table 72).

Table 72: Mean ± standard deviation of length and width, and mean growth rate of the five largest plants in 114 day old cultures of Ascophyllum and three species of Fucus

| | 114 days old | | 140 days old | | mean linear growth |
|---|---|---|---|---|---|
| | length, mm | width, mm | length, mm | width, mm | mm/month |
| Ascophyllum | 4.3 ± 0.4 | 0.8 ± 0.1 | 6.9 ± 0.7 | 1.4 ± 0.2 | 3.0 |
| F. spiralis | 13.2 ± 2.5 | 3.1 ± 0.7 | 20.5 ± 3.8 | 5.4 ± 1.3 | 8.4 |
| F. vesiculosus | 25.5 ± 5.6 | 4.7 ± 1.5 | 38.3 ± 7.6 | 8.5 ± 2.2 | 14.8 |
| F. serratus | 24.1 ± 5.4 | 4.2 ± 1.5 | 29.1 ± 5.8 | 6.2 ± 1.7 | 9.2 |

In a few culture experiments, the linear growth rate and relative weight gain of young plants of F. serratus were determined simultaneously with those of Pelvetia and F. spiralis, and this was also done once for Ascophyllum. The comparison revealed a striking resemblance between Ascophyllum and Pelvetia. Both species grew far more slowly in length, but only slightly more slowly in weight, than did F. spiralis (Table 73). There was also a great similarity between F. spiralis and F. serratus, especially in their linear growth rates.

Table 73: Comparison of linear growth rates and relative weight gains of Ascophyllum and Fucus serratus with those of Pelvetia and F. spiralis. Figures represent mean ± 1 standard deviation.

linear growth, mm/month

| n | Pelvetia | n | F. spiralis | n | Ascophyllum | n | F. serratus |
|---|---|---|---|---|---|---|---|
| 10 | 4.2 ± 0.7 | 10 | 15.3 ± 1.6 | 15 | 6.2 ± 1.5 | | |
| 10 | 9.3 ± 2.2 | 10 | 22.2 ± 2.9 | | | 10 | 21.0 ± 2.9 |
| 15 | 4.5 ± 1.1 | 15 | 12.9 ± 2.9 | | | 15 | 16.6 ± 1.5 |
| 5 | 8.3 ± 1.3 | 5 | 18.0 ± 1.0 | | | 5 | 12.7 ± 3.3 |

% weight gain per day

| n | Pelvetia | n | F. spiralis | n | Ascophyllum | n | F. serratus |
|---|---|---|---|---|---|---|---|
| 10 | 2.90 ± 0.55 | 10 | 3.20 ± 0.31 | 15 | 2.57 ± 0.42 | | |
| 10 | 4.42 ± 0.39 | 10 | 5.88 ± 0.26 | | | 10 | 4.65 ± 0.89 |
| 15 | 2.05 ± 0.36 | 15 | 2.41 ± 0.22 | | | 15 | 2.59 ± 0.24 |
| 5 | 1.81 ± 0.68 | 5 | 3.72 ± 0.69 | | | 5 | 2.32 ± 0.65 |

Since Fucus spiralis rapidly outgrows and shades Pelvetia in mixed stands in nature, a mixed stand of F. spiralis and Ascophyllum was observed over a period of nine months to determine whether Ascophyllum would suffer the same fate. One of the experimental quadrats in which the net growth rate of F. spiralis was measured was located at the boundary between the F. spiralis and Ascophyllum zones, at 2.65 m above chart datum, (Quadrat 1, Table 61), and contained many small plants of both species (Plate 23A). The mean net growth rate and maximum growth


A

B

C

Plate 23: Interaction between F. spiralis and Ascophyllum in Quadrat 1, located near the boundary between the two species' zones.

A. August 25th, 1975, showing young plants of Ascophyllum (A) and F. spiralis (F).

B. June 15th, 1976. The F. spiralis has formed a solid canopy over the Ascophyllum.

C. June 15th, 1976, after removal of F. spiralis, revealing that the Ascophyllum has grown considerably in length and mass despite being covered by F. spiralis.

rate of Ascophyllum was determined during the same period over which those of F. spiralis were measured.

Fucus spiralis generally grew two to three times as fast as Ascophyllum and the growth rate of the latter was similar to that of Pelvetia (Table 74). The F. spiralis in the quadrat were initially smaller than the Ascophyllum (Plate 23A) but they ultimately formed a solid canopy which hid the Ascophyllum from view (Plate 23B). However, Ascophyllum survived and grew somewhat beneath this canopy (Plate 23C), which suggests that it is immune to whatever factor removed young Pelvetia plants in the competition experiments.

In culture, young plants of Ascophyllum were only slightly more tolerant of reduced irradiance than Pelvetia (Tables 63, 64). In order to determine whether this is also true of the embryos, zygotes of Ascophyllum and Pelvetia would ideally be cultured simultaneously at different irradiances. However this was not possible since the fertile periods of the two species do not overlap. Therefore Ascophyllum was compared with Fucus spiralis and F. serratus keeping in mind that F. spiralis embryos are slightly more tolerant of prolonged dark periods than those of Pelvetia (Tables 66 and 67).

Two slides of embryos of each species were cultured under each of two different irradiances. Unfortunately, Ascophyllum germinated poorly, and only one slide in each treatment had enough embryos to obtain a sample of thirty for measurement.

Ascophyllum grew at almost the same rate under the two light regimes, while both Fucus species grew considerably more slowly under the lower irradiance than under the higher one (Table 75).

This result suggests that embryos of Ascophyllum can not only survive, but also grow in very dim light. This may explain in part why Ascophyllum and Pelvetia contrast so sharply in competitive ability despite their apparently similar patterns of growth.

Table 74: Net growth rate and maximum growth rate (mm/month) of young Fucus spiralis and Ascophyllum in a mixed stand (mean ± standard deviation). Data for one Pelvetia quadrat is included for comparison.

| | | Sept.-Oct.1975 | | | Nov.1975-Feb.1976 | | | Feb - May 1976 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Quadrat | n | net growth rate | maximum growth rate | n | net growth rate | maximum growth rate | n | net growth rate | maximum growth rate |
| F. spiralis | 1 | 25 | 2.9 ± 31.0 | 22.1 ± 2.7 | 25 | 7.4 ± 9.4 | 15.3 ± 2.7 | 25 | 14.7 ± 11.6 | 21.9 ± 2.3 |
| Ascophyllum | 1 | 25 | 3.0 ± 5.0 | 7.4 ± 1.8 | 25 | 1.6 ± 4.6 | 5.2 ± 2.4 | 25 | 4.7 ± 5.2 | 9.4 ± 1.7 |
| Pelvetia | 6 | 25 | -1.1 ± 12.8 | 7.1 ± 2.3 | 25 | 3.7 ± 2.6 | 6.2 ± 1.4 | 25 | 5.0 ± 2.6 | 7.6 ± 1.1 |

Table 75: Mean ± standard deviation of thallus length and width of Fucus spiralis, F. serratus and Ascophyllum embryos after twenty-seven days in culture under two levels of irradiance. n = 30 for each replicate.

| | length, μm | | length, μm | |
|---|---|---|---|---|
| | 5.9 - 6.5 mg-cal/cm$^2$-min | 22.4 - 23.0 mg-cal/cm$^2$-min | 5.9 - 6.5 mg-cal/cm$^2$-min | 22.4 - 23.0 mg-cal/cm$^2$-min |
| F. spiralis | 491 ± 67 | 615 ± 66 | 176 ± 16 | 214 ± 19 |
| | 502 ± 59 | 593 ± 130 | 168 ± 12 | 194 ± 28 |
| F. serratus | 975 ± 457 | 1187 ± 406 | 162 ± 43 | 177 ± 31 |
| | 963 ± 338 | 1574 ± 528 | 163 ± 20 | 223 ± 37 |
| Ascophyllum | 230 ± 42 | 241 ± 60 | 139 ± 15 | 152 ± 23 |

## 4.9 Discussion

Since physical conditions become progressively more severe for fucoids with distance upshore, it might be supposed that they are most favourable below ELWS. However, the gradient of decreasing illumination with increasing depth sets an ultimate lower limit for any photosynthetic organism, and this limit appears to lie just below low water mark for fucoids. F. vesiculosus and Ascophyllum were adversely affected when transplanted to the uppermost part of the subtidal zone at St. Malo, France (Hatton 1938), and F. distichus died two months after transfer to low water mark at the San Juan Islands of Washington State (Pollock 1969).

Insufficient light may contribute to the exclusion of Pelvetia from the midshore at Isle of Cumbrae. Estimates of the light reaching the Pelvetia zone and the midshore are given in Table 76. These indicate that tidal submersion can reduce light to well below saturation. This probably occurs often at Isle of Cumbrae, because winter weather is predominantly cloudy, frequent storms increase the turbidity of the water, and the very high waters of spring tides commonly occur near midday. As Pelvetia transplanted to the midshore began to decay only with the approach of winter, it seems likely that light limitation played a role in their decline. Light limitation also seemed to affect the F. spiralis plants transferred to the midshore. Their growth rate decreased to one-third of the maximum rate in November-February when daily solar radiation was least, and increased again as more light became available in spring (Figure 33). Growth rates of natural upshore populations of F. spiralis showed a much less pronounced depression in winter (Table 61), which illustrates the effect on illumination of deeper and more prolonged submersion at midshore.

Damant (1937) has demonstrated that on some shores, the observed lower limit of Ascophyllum may be determined by a combination of light limitation and hydrostatic pressure associated with deep submersion. The buoyancy of this seaweed's air bladders causes the long fronds to stand erect during submersion so that they receive more light. However, when submerged to a sufficient depth, hydrostatic pressure causes the bladders to collapse, and the fronds sink to the poorly illuminated level of the substratum. At Portishead, where the tidal amplitude is about 12 metres, Damant found many unhealthy plants with crushed bladders near the lower limit of Ascophyllum, which was only a little below MTL. The same combination of factors might similarly affect F. vesiculosus which is also equipped with air bladders. It is interesting to note that both species grow subtidally in the Baltic Sea (den Hartog 1968) and in Norwegian Fjords (C. Filion, personal communication), where tidal amplitudes are small so that pressure does not increase greatly when the tide comes in.

Table 76: Expected total irradiances between 350 and 700 mm (mg-cal/$cm^2$-min) in the Pelvetia zone and at midshore at Isle of Cumbrae, at noon on midsummer day and midwinter day under different weather conditions and different tidal heights. Calculated from incident global irradiances given by Kondratyev (1969), sea surface reflectances (Jerlov 1968), and absorbance by seawater of coastal type 3 (Steeman-Nielsen 1975) to which the waters near Isle of Cumbrae roughly correspond (Paul Tett, personal communication).

| | solar altitude | weather conditions | total incident global irradiance available for photosynthesis[α] | irradiance available in Pelvetia zone (3.00m above chart datum) when tide is at: 2.90m | 3.40m | 3.90m | irradiance available at midshore (1.90m above chart datum) when tide is at: 2.90m | 3.40m | 3.90m |
|---|---|---|---|---|---|---|---|---|---|
| Midsummer day, noon | 56° | clear | 658[b] | 658 | 562 | 472 | 460 | 383 | 313 |
| | | low overcast | 94[b] | 94 | 85 | 67 | 66 | 55 | 45 |
| Midwinter day, noon | 11° | clear | 94 | 94 | 62 | 52 | 51 | 42 | 34 |
| | | low overcast | 21 | 21 | 18 | 15 | 15 | 12 | 10 |

Saturation level observed in culture: ~20 mg cal/$cm^2$-min.

α Total global irradiance multiplied by 0.47 (Steeman-Nielson 1975)

b Since Kondratyev (1969) gave data for solar altitudes up to 50°, it was necessary to extrapolate to obtain these estimates.

Some fucoids appear to be adversely affected by constant submersion to a shallow depth at which light is reduced but slightly, and hydrostatic pressure is unimportant. Gail (1918) reported that F. distichus subsp. edentatus decayed when kept submerged only 0.3 m below the sea surface, and Fischer (1929) found that Pelvetia and F. spiralis slowly died after being submerged in an artificially constructed tide pool. The latter result must be interpreted with caution, as fluctuating temperature and salinity which might occur in such a pool are quite unlike the stable conditons in the subtidal zone. Nevertheless, Baker (1912) reported that Pelvetia decayed after four weeks in culture if kept submerged most of the time, and the same occurred in my cultures, in which temperature and salinity fluctuations were negligible. F. spiralis thrived in all cultures, and thus appears not to require tidal exposure.

Although physical factors set demonstrable lower limits of the potential ranges of fucoids, the actual lower limits often lie much higher on the shore. For example, F. spiralis is abundant only on the upper shore although it can grow well near MTL (Plate 12) and even near low water mark (Burrows & Lodge 1951). Similarly, Pelvetia transplanted to the F. spiralis zone remained healthy and produced receptacles although it almost never occurs there naturally. It has often been suggested that interspecific competition between fucoids plays an important role in their observed zonation (Baker 1909; Colman 1933; Lewis 1964) and this hypothesis is supported by the observed pattern of colonization on new substrata and experimentally cleared transects. Initially the fucoids appear in a random assortment along the shore gradient with many individuals out of their usual zones, and the normal zonation gradually reappears over a period of several years as the stands mature (Knight & Parke 1950; Burrows & Lodge 1951; den Hartog 1968). Den Hartog even found Pelvetia near MTL on a newly constructed dike slope and reported that it subsequently disappeared as the midshore fucoids formed a closed canopy. Fucoids have also been shown to colonize substrata below their lower limits after an apparently superior competitor is removed. Zygotes of Fucus spp. settle and germinate on the lower

shore of New England coasts after the dominant red alga Chondrus crispus is removed (Menge 1975), and F. serratus germlings occasionally appeared in experimentally cleared areas within subtidal Laminaria hyperborea forests (Kain 1975). In the present study, it was shown that Pelvetia can settle, germinate and grow normally in the F. spiralis zone provided that F. spiralis is weeded out.

Baker (1909) suggested that the lower limit of each fucoid species is determined by the presence of a larger and faster-growing competitor. Certainly, the midshore species are the most massive and Pelvetia the least so, and, with the possible exception of Ascophyllum, the reported growth rates of the different fucoid species correlate with their relative positions on the shore (Table 77). In the present investigation, F. spiralis seemed to eliminate Pelvetia from the F. spiralis zone by growing three to four times as fast as Pelvetia and forming a canopy over it.

This pattern has emerged in several other specific examples. For instance the F. serratus which appeared subtidally after the removal of Laminaria hyperborea was subsequently outgrown and covered by a new crop of Laminaria, and disappeared after nine months (Kain 1975). Hruby (1976) has shown that Iridaea cordata is similarly eliminated from levels below its lower limit by the faster-growing alga Laminaria saccharina.

However, competitive superiority is not always based on size and growth rates. Chondrus crispus excludes the larger and faster-growing Fucus spp. from its zone because its holdfasts fuse, forming a continuous crust on the rock, on which Fucus zygotes apparently cannot settle and germinate (Menge 1975). In this case, ability to occupy all available primary space, rather than to form a canopy seems to be the main criterion of competitive superiority. However, primary space does not seem to be the critical resource in interspecific competition between fucoids. Very young plants may be crowded in dense stands on the rock surface, but in mature stands the holdfasts occupy only a small proportion of the available primary space. In the competition experiments on Pelvetia and F. spiralis, these species coexisted in their earliest stages, and Pelvetia declined only later when considerable space was available between the Fucus holdfasts.

Table 77: Growth rates of fucoids in nature, mm/month

| Source | Location | Pelvetia | F. spiralis | Ascophyllum | F. vesiculosus | F. serrat |
|---|---|---|---|---|---|---|
| Klugh & Martin 1927 | St. Andrews, Bay of Fundy, Canada | | | | 22 | |
| Hatton 1938 | St. Malo, France | 0.3 - 1 | | 10 - 12 | 16 | |
| David 1943 | Welsh Coast | | | 15 | | |
| Pyefinch 1943 | Bardsey Island, North Wales | 1 - 1.5 | 10 | | 16-30 | |
| Knight & Parke 1950 | Argyllshire, Scotland | | | | 13-29 | 24-39 |
| Fischer-Piette 1957 | French Coast | 5 - 14[a] | | | | |
| Subrahmanyan 1960,1961 | Isle of Man | 1.5 - 4 | 6-13 | | | |
| Table 61 page 153 | Isle of Cumbrae, Scotland | 5 - 9 | 10-23 | 5-9[b] | | |

a under favourable conditions

b young plants, covered by a Fucus spiralis toward the end of period of observation

Another possible mechanism of exclusion is the sweeping action of the superior species' fronds as they are moved about by the waves. Dayton (1975) showed that the kelp Hedophyllum is excluded from very exposed coasts by the continual whiplash of the blades of another kelp Lessoniopsis. Germlings of upshore fucoids might be similarly removed from the midshore by the heavy fronds of Ascophyllum and Fucus spp. However, boundaries between fucoid zones are commonly most distinct on sheltered shores (Lewis 1964), where significant whiplash is unlikely owing to the lack of wave action.

In the competition experiment at the North Slip, most of the Pelvetia ultimately disappeared from the edges of the weeded transects (Plate 20C) which suggests at first glance that the blades of F. spiralis plants attached in the unweeded transects had swept them off. However, four months before the photograph was taken, F. spiralis had grown large enough to reach all of the Pelvetia in the weeded transects, yet Pelvetia disappeared only from the edges of the transect. This suggests that light is the critical factor, for these edges had been shaded, at least during tidal exposure, by the Fucus blades. Furthermore, the few remaining Pelvetia showed the same dark colour as the plants cultured in subsaturating irradiances, and this was also observed in other experiments in which Pelvetia had been shaded by Fucus blades (eg. Plates 16, 17). Measurements showed that a single layer of Fucus blades can reduce available light to a subsaturating level even during summer (Table 65); hence it seems likely that fucoid sporelings beneath a canopy of adult plants would suffer considerable light limitation. Therefore, the linear growth rates of the earliest stages appears to be a major determinant of competitive ability, since it controls their ability to escape from the shade of overlying algae. The exclusion of Pelvetia from the midshore might be explained by the extremely slow growth of its embryos in comparison with Fucus embryos. The scarcity of F. spiralis at and below MTL can also be understood, since its germlings grow less rapidly than those of other Fucus species, requiring about six months to reach a length of 10 mm in nature (personal observation). By contrast, germlings of Fucus vesiculosus and F. serratus may exceed 10 mm within two months after settlement (Hatton 1938; Knight & Parke 1950) and would probably rapidly form a canopy over any F. spiralis germlings growing with them.

It seems somewhat surprising in this context that Ascophyllum, whose embryos grow very slowly, often becomes dominant on the middle shore. This suggests that Ascophyllum germlings are specially adapted to survive for long periods of time in light too dim to support growth. Sheader & Moss (1975) found that Ascophyllum embryos can remain viable for up to ninety days in continuous darkness, but this ability is also demonstrated by Fucus distichus (McLachlan 1974), and F. spiralis (Table 67). Even Pelvetia embryos can survive up to ninety days in total darkness, and at least eight months under a canopy of adult Pelvetia. Apparently the formation of a canopy over the embryos does not kill them, but merely arrests their growth. They might be expected to grow and develop into visible plants wherever the shading canopy is removed by natural causes. Since Pelvetia never appears in breaks in the Fucus canopy, some other factor seems to remove any Pelvetia which germinates beneath this canopy.

One very likely factor is grazing. There is considerable evidence that gastropods exert a profound effect on fucoid populations by nonselectively scraping algal spores and germlings from the rock (Jones 1946, 1948; Newell 1958; Southward 1962; Menge 1975). Jones and Southward demonstrated that limpets can keep an entire shore free of algae. Experimental removal of the limpets allowed algal recolonization, and within a year or two the cleared areas were dominated by fucoids. The limpets eventually returned and prevented further recruitment of germlings, so that the algal cover gradually disappeared (Lodge 1948; Southward 1962).

Other shores are characterized by a F. spiralis zone above the zone containing limpets (Grubb 1936, and personal observations at Isle of Cumbrae), and the lower limit of F. spiralis zone on such shores may be determined by limpet grazing. Littorine snails also scrape algal germlings from the rock, and the largest and most voracious species reach their upper limits near MHWN (Moore 1940, Evans 1947b, Newell 1958). The observation that dense "turves" of fucoid germlings commonly occur only above this level suggests that many zygotes that settle lower down may be eaten by snails. Menge (1975) has shown that Littorine spp.

cause heavy mortality in fucoid germlings on New England coasts, and that the lower limits of fucoids are determined in part by increasing density of snails downshore. Within the normal Fucus zone, some zygotes initially escape grazing by settling in small crevices, and snails do not seriously damage germlings after they reach a length of 30-50 mm. Knight & Parke (1950) reported that grazing molluscs cause high germling mortality in British fucoids, and that the young plants reach an escape in size at about 30 mm. This alone might be sufficient to explain the absence of Pelvetia from the midshore wherever grazers are present, for its slow-growing germlings remain vulnerable for about eighteen months before they reach this size. Also, since germlings of F. spiralis grow more slowly than those of other Fucus species, relatively few F. spiralis might be expected to survive to maturity at midshore, and the observed scarcity of this species at this level is not surprising.

Germlings might also escape grazing by passing through their most vulnerable phase during the winter when the littorines are much less active owing to low sea temperatures (Newell 1958). Fucus serratus releases gametes in the winter, and the germlings grow rapidly, so that their chances of survival on the lower shore are maximized. By contrast, Pelvetia and F. spiralis both release their gametes in summer when the snails are most active and would probably eat the majority of the germlings before they become macroscopic.

Since Ascophyllum releases its gametes in spring when the snails are active, and Ascophyllum germlings grow very slowly, why is this species so successful on the middle shore? Menge (1975) reported that snails would eat Fucus but not Ascophyllum in laboratory experiments. However, it is not certain that natural populations of Ascophyllum are less vulnerable to grazing than those of Fucus, as G. Moore (personal communication) has observed grazer damage on both species at Isle of Cumbrae. Indeed, Ascophyllum establishes itself only with great difficulty on new or recently cleared substrata. Far fewer germlings of Ascophyllum than of Fucus spp. survive to a macroscopic size each year (Hatton 1938), and four to thirty years may pass before large

Ascophyllum reoccupy cleared rock surfaces within its zone (Moore & Sproston 1940; Printz 1956; Knight & Parke 1950; Baardseth 1968). It is possible that Ascophyllum germlings become established in those years when grazer populations are unusually low, and that these germlings have special adaptations for surviving and growing beneath the Fucus canopy that inevitably forms over them. The result of one culture experiment (Table 75) suggested that Ascophyllum embryos are more capable of growing in dim light than those of Fucus spp, but the data are too scanty to be considered conclusive.

One important characteristic of Ascophyllum is its longevity. Individual fronds live five to fifteen years (David 1943), and the holdfast may live for several decades, producing new basal shoots as old ones are lost (Baardseth 1968). Young plants such as those shown in Plate 23 would therefore outlive any Fucus canopy which forms over them, and would eventually form their own canopy and restrict the development of further generations of Fucus. Menge (1975) has also found small, healthy Ascophyllum plants growing beneath a canopy of Fucus, and Hatton (1938) reported a sequence of F. vesiculosus followed by Ascophyllum during recolonization of experimentally cleared areas. Competetive dominance based on longevity is also demonstrated by Laminaria hyperborea. When stands of this subtidal dominant are cleared, they are initially replaced by the faster-growing annual Sacchoriza polyschides, and L. hyperborea returns and forms a canopy after about two years beneath which further generations of Sacchoriza do not develop (Norton & Burrows 1969; Kain 1975). Unlike Ascophyllum, Pelvetia cannot outlive the fast-growing Fucus species, and this may explain why it does not appear even occasionally in breaks or openings in the Fucus canopy.

Several factors appear to contribute to the exclusion of Pelvetia from the middle shore. The competition experiments showed that it is rapidly overgrown by Fucus beneath which it cannot grow and may be vulnerable to grazing. However, the wintertime decline of Pelvetia transplanted to the midshore probably resulted neither from competition, since no canopy had formed over them, nor from grazing, since littorine snails are least active during winter (Newell 1958) and had not eaten

the transplants during the preceding summer and autumn. The transplants appeared to succumb to other causes, possibly the adverse effects of epiphytes, or some disease organism which causes decay. Observations of Pelvetia in tidal simulation cultures showed that both decay and the growth of epiphytes may be enhanced by prolonged tidal submersion and by the high wintertime nutrient concentrations in the sea. Pelvetia might depend upon prolonged tidal exposure to restrict the growth of harmful organisms; certainly, far fewer epiphytes seem to grow on Pelvetia plants in nature than on midshore Fucus plants. It is interesting to note that Ascophyllum also bears far fewer epiphytes than do Fucus spp. This may be important to the survival of the young plants which must persist for very long periods of time beneath a Fucus canopy.

## GENERAL DISCUSSION AND CONCLUSIONS

In the introduction, the problem of species zonation on the shore was discussed with regard to the fundamental and realized niches of the species involved. It was hypothesized that the upper limit of each species might be determined by its tolerance to physical stress, and its lower limit by a superior competitor. This hypothesis has been found to be largely but not wholly true. On the Isle of Cumbrae, the upper limits of Ascophyllum, F. spiralis and Pelvetia appear to be governed largely by their abilities to tolerate prolonged desiccation, as stress damage is observed in individual plants at their upper limits following a period of severe dehydration. However, no such drought-damaged individuals were observed at the more ill-defined upper limits of F. vesiculosus and F. serratus, which, at Isle of Cumbrae, lie well below the critical level of MHWN. Knight (1947) found that both of these species grow more slowly near their upper distributional limits than they do further downshore, and attributed this to the effects of tidal exposure. Similarly, Hatton (1938) has shown that Ascophyllum and F. vesiculosus grow more slowly near their upper limits than they do downshore unless they are growing in clumps which ensure some mutual protection from desiccation. In simulated tidal cultures, F. serratus grew progressively more slowly with increasing exposure time (Table 47), an effect attributable largely to nutrient limitation. It seems likely therefore that the competitive ability of each of these species decreases with distance upshore, so that better adapted fucoids might exclude them from higher levels. Certainly, Lewis (1964) has observed that dense stands of F. spiralis on the upper shore may somewhat depress the upper limit of Ascophyllum. It may also be significant that on the Isle of Cumbrae F. vesiculosus does not extend as high as it does on shores where Ascophyllum is less abundant (Evans 1947a, 1947b).

Since Pelvetia and F. spiralis are restricted to narrow zones near to their tolerance limits, it might be supposed that they are also living under suboptimal conditions. However, they grow almost as rapidly within their zones as they do when transplanted downshore or when cultured in constant submersion. Apparently, upshore conditions

are favourable to their growth most of the time; indeed it has been observed that it is occasional extremes of prolonged desiccation rather than typical day-to-day conditions which govern their upper limits.

One factor which might contribute to this difference between the midshore and the upshore fucoids is the different density of their stands. The thin covers of Pelvetia and F. spiralis dry quickly, thus avoiding the dangerous situation of being only partially dehydrated during exposure to hot weather. This is a viable strategy, as these two species can survive air-dryness for a relatively long period of time. The midshore species, which cannot survive air-dryness for more than a few hours, grow in much thicker stands which dry more slowly. Ordinarily, this would be advantageous as they are resubmerged twice daily and can avoid severe dehydration altogether simply by drying slowly. However, there might be sublethal effects of exposure which would result in slower growth rates on the upper part of the midshore where tidal exposures are longer.

The original hypothesis regarding species zonation also appears to be essentially valid with regard to lower limits. Pelvetia and the three Fucus species make up a series which demonstrates an inverse correlation between drought tolerance (Pelvetia > F. spiralis > F. vesiculosus > F. serratus), and ability to compete for light as judged by growth rates (Pelvetia < F. spiralis < F. vesiculosus < F. serratus), and this series correlates logically with their order of occurrence on the shore. The scarcity of F. spiralis downshore seems to result from its competitive inferiority while F. serratus appears to dominate the lowest levels by growing very rapidly. However, the three Fucus species do not demonstrate competitive exclusion in its strictest sense, as their ranges overlap. By contrast, F. spiralis seems to exclude Pelvetia entirely from the F. spiralis zone, possibly because the two species differ much more dramatically in growth rates than do F. spiralis and F. serratus. However, no mechanism has been demonstrated by which F. spiralis actually eliminates Pelvetia; hence other factors must also be involved.

It seems likely that grazing by intertidal molluscs reinforces the zonation pattern. The snails are larger and more numerous on the lower shore than at higher levels, and are active for much longer owing to long tidal submersion. F. serratus can cope with this grazing pressure, as it releases its gametes in winter when herbivorous littorines are least active, and the germlings grow very rapidly and soon attain an escape in size. Species growing at higher levels grow more slowly in their embryonic phases and are therefore more vulnerable to grazing, particularly because they release their gametes when the grazers are active. The extremely slow-growing germlings of Pelvetia might succumb even to very light grazing pressure, especially if a Fucus canopy forms over them and further curtails their growth.

It is interesting to note at this point that algal zonation may be profoundly influenced by higher trophic levels as well. For example, carnivores may permit the development of an algal zone by consuming grazers which might otherwise devastate algal stands, or by removing mussels which would otherwise occupy all available primary space (Paine 1971, 1974; Dayton 1975). The outcome of any of these biotic interactions depends upon the special biological characteristics of the species involved, which cannot easily be incorporated into predictive models (Dayton 1973). Dayton has shown, for instance, that the starfish Pisaster, by dispersing more prey than it eats, supplies food to the stationary anemone Anthopleura, whereas an ecological model would predict that the two carnivores would compete for their food supply. This illustrates the importance of examining carefully the biological strategy of each species in order to understand why and how it occupies its realized niche.

The fucoids segregate into two well-defined groups with regard to their biological strategies. All three Fucus species can be described as "fast-growing competitors", as their embryos and macroscopic germlings grow rapidly in length, and their broad, dichotomously branching blades form a closed canopy before the plants reach the age of one year. By contrast, Pelvetia and Ascophyllum grow much more slowly in length, especially during their embryonic stages, and their narrow fronds are less effective than Fucus blades in forming a canopy. Pelvetia avoids competition altogether by occupying a habitat

in which other fucoids cannot survive. However, Ascophyllum inhabits the middle shore, and it must employ a very different strategy from Fucus spp, as its embryos grow very slowly and very few of its germlings establish themselves successfully on the shore. Ascophyllum apparently compensates for this disadvantage by producing massive plants with a very long lifespan. Not only do the individual fronds live for at least ten years, but the large holdfast persists for several decades and initiates new fronds to replace old ones as they are lost (Baardseth 1968). For this reason, once established, Ascophyllum requires a successful recruitment of young plants only once every ten or twenty years in order to persist. In contrast, Fucus plants live for only three or four years (Knight & Parke 1950; Subrahmanyan 1961); hence these species rely on a successful annual recruitment to persist. Furthermore, it is difficult for Fucus spp. to become established within an Ascophyllum "forest" owing to the large size and long lifespan of the Ascophyllum plants.

Both the "rapid growth" and the "slow growth" strategies can be effective under adverse environmental conditions, as is exemplified by Pelvetia and F. spiralis. F. spiralis appears to be a typical "generalist" whose wide ecological amplitude allows it to occupy a habitat in which its competitors cannot survive. F. spiralis is apparently characterized by considerable physiological flexibility, as it adapts successfully to nutrient limitation in culture (Table 48), and demonstrates a seasonal drought tolerance. Not only can it become markedly drought-hardened within six days, but also it can resume rapid growth promptly upon the return of favourable condition. This flexibility permits F. spiralis to survive severe stress, yet retain sufficient competitive ability to dominate its own zone and to occur occasionally downshore. Since downshore plants commonly reach reproductive maturity, they may act as an important reserve in case extreme conditions destroy much of the usual F. spiralis zone as occurred in 1975. However, there also appears to be a disadvantage to physiological flexibility. Percent dry matter decreased considerably during the rapid growth of the drought hardened plants (Table 43), and "dehardening" might have occurred concurrently. Therefore, a sudden

prolonged desiccation following a period of rapid growth under favourable conditions might kill many plants, and this apparently happened each spring and again in August 1976 (Figures 5,7,9).

Unlike F. spiralis, Pelvetia appears to be specifically adapted to its extreme habitat. Its fundamental niche is relatively narrow, extending no lower than MTL, and it is such a poor competitor that it cannot invade the F. spiralis zone, even where there are temporary breaks in the canopy. Furthermore, Pelvetia is very well equipped to survive prolonged exposure. It demonstrates great drought tolerance all year round, and thus is less likely to be killed by a sudden stress following a period of favourable conditions. Pelvetia appears to possess special biochemical adaptations to drought, although these have not yet been elucidated, and the channelled thallus appears to serve a double function. It protects zygotes from excessively rapid dehydration, yet it dries faster than the thalli of the other fucoids, thus minimizing metabolic injury during exposure to hot weather. Clearly, Pelvetia has adopted a "specialist" strategy by which it grows almost optimally in a habitat so inhospitable that all its potential competitors, including F. spiralis, are excluded.

The study of species zonation in intertidal fucoids has been particularly instructive, as several different biological strategies have been demonstrated. On the middle shore, Fucus spp. succeed by means of rapid growth rates and a high annual sporeling recruitment, while Ascophyllum prospers by virtue of its very long lifespan and large size. On the upper shore, different forms of drought tolerance are exhibited by the generalist F. spiralis and the specialist Pelvetia.

## Appendix A. Culture medium

The following procedure for preparing enriched seawater medium was recommended by Professor A. D. Boney of University of Glasgow, and was used for all culture work:

Solution A: 905 ml filtered seawater
50 ml 0.4% $NaNO_3$ solution
2 ml of each of the following:
$MnSO_4.4H_2O$, 1.47 g/l
$CuSO_4.5H_2O$, 0.023 g/l
$CoCl_2.6H_2O$, 0.064 g/l
$Al_2(SO_4)_3.16H_2O$, 0.023 g/l
$LiCl.H_2O$, 0.005 g/l
$ZnSO_4.7H_2O$, 4.98 g/l
$Na_2MoO_4.2H_2O$, 0.25 g/l

Solution B: 15 ml of a solution containing:
2.6 g/l disodium salt of EDTA, and
0.12 g/l $FeSO_4.7H_2O$

Solution C: 15 ml of a 1.5 g/l solution of $Na_2HPO_4.12H_2O$

Vitamin solution:
1 ml of a solution containing:
cyanocobalamin 1.6 mg/l
biotin 0.8 mg/l
thiamin ·HCl 20 mg/l

Normally these four solutions are autoclaved separately, cooled and combined, but this could not conveniently be done with the large volumes of medium required in the present work. Professor A. D. Boney suggested as an alternative the following pasteurization procedure which was used for the media prepared for all culture work. The four solutions were made up, combined in three to five litre batches, and heated to 75°C over a burner. The flasks were then cooled to room temperature in a cold water bath, reheated to 75°C and cooled again before use. This method kills essentially all algal spores although it does not eliminate all bacterial contamination.

## Appendix B. Reproducibility of wet weight measurement and sources of error

The measurement of wet weight is subject to two potential sources of error. Firstly, some of the water clinging to the plant may not be removed, or some of the water in the intercellular spaces may be squeezed out, depending upon the pressure used in blotting the alga before weighing. This would produce a random error, as the pressure applied would not be absolutely constant. Secondly, the polysaccharide matrix on the thallus surface might be stripped off by each blotting, so that a progressive decrease would occur in a series of replicate weighings of a given plant. Two tests were undertaken to determine how reproducible the measured wet weight is, and to ascertain whether the removal of polysaccharides by blotting is significant. In the first test, fifty plants each of Fucus spiralis and Pelvetia were weighed, resubmerged for about 30-60 minutes, and weighed again. The percent difference between the two weighings of each plant was calculated as

$$\left( \frac{\text{second wt.} - \text{first wt.}}{\text{first wt.}} \right) \times 100\%$$

The reproducibility of the wet weight measurement was estimated from the absolute value of this percentage, the mean of which was less than 1% for both species (Table 78). The loss of surface polysaccharides in blotting was investigated by taking the mean of the percent differences and by performing a sign test, and was found to be negligible (Table 78).

Table 78: Statistical analysis of difference between two weighings taken on each of fifty Pelvetia and fifty F. spiralis. Mean ± standard deviation of differences between first weighing (A) and second weighing (B). Sign test values shown are not significant, as p = 0.05 at 1.96

| Species | Absolute value of difference between weighings $= \left\| \left( \frac{B-A}{A} \right) \times 100\% \right\|$ | Difference between weighings $= \left( \frac{B-A}{A} \right) \times 100\%$ | Sign test value |
|---|---|---|---|
| Pelvetia | 0.71 ± 0.58 | -0.10 ± 0.91 | 1.33 |
| F. spiralis | 0.58 ± 0.52 | +0.05 ± 0.78 | 1.01 |

In the second test, five plants each of F. spiralis and Pelvetia, and four of Ascophyllum were each weighed five times and resubmerged between successive weighings. An analysis of variance was used to compare the variance between successive weighings (error arising from stripping of polysaccharides by blotting) with residual variance (random error) and with the variance between different plants. There was no consistent downward trend in the observed weights in any of the species, and variance between successive weighings was significantly greater than residual variance only in F. spiralis (Table 79). Both sources of error were very small in comparison with actual differences in weight between the individual plants of the sample.

Table 79: Analysis of variance in weights of five Pelvetia plants, five F. spiralis plants and four Ascophyllum plants, each weighed five times. Significance of F. values: ** = $p < 0.01$ *** = $p << 0.001$.

Pelvetia

| Source of variance | degrees of freedom | sum of squares | mean squares | F(4,16) |
|---|---|---|---|---|
| Replicates (difference between plants) | 4 | $6.31 \times 10^{-1}$ | $1.58 \times 10^{-1}$ | 10500*** |
| Weighings (removal of polysaccharides by blotting) | 4 | $3.10 \times 10^{-5}$ | $7.75 \times 10^{-6}$ | 2.07 |
| Residual (random error) | 16 | $6.00 \times 10^{-5}$ | $3.75 \times 10^{-6}$ | |

Fucus spiralis

| Source of variance | degrees of freedom | sum of squares | mean squares | F(4,16) |
|---|---|---|---|---|
| Replicates | 4 | $9.46 \times 10^{-2}$ | $2.36 \times 10^{-2}$ | 1063*** |
| Weighings | 4 | $4.93 \times 10^{-5}$ | $1.23 \times 10^{-5}$ | 5.54** |
| Residual | 16 | $3.56 \times 10^{-5}$ | $2.23 \times 10^{-6}$ | |

Ascophyllum

| Source of variance | degrees of freedom | sum of squares | mean squares | F |
|---|---|---|---|---|
| Replicates | 3 | $2.23 \times 10^{-1}$ | $7.43 \times 10^{-2}$ | 177900*** |
| Weighings | 4 | $6.73 \times 10^{-7}$ | $1.62 \times 10^{-7}$ | 0.315 |
| Residual | 12 | $5.02 \times 10^{-6}$ | $4.18 \times 10^{-7}$ | |

It was concluded from these tests that the wet weight measurement, is of adequate accuracy for the present investigation.

## Appendix C. Design of tidal simulator

The tidal simulator is shown diagrammatically in Figure 38. Three culture tanks (a) of twenty litre capacity were constructed of glass plates sealed together in a plastic aquarium frame with Dow Corning Silicone Rubber Aquarium Sealer. Each tank was drained twice daily by a brass solenoid value (b) type 5DN416NS/1/1 by Magnetic Devices Ltd., which was opened and closed automatically by a Smith Autoset clock. When the valve was opened the water in the tank drained into a large fibreglass storage tank (c) through Portex Shore 80 plastic tubing, 15 mm internal diameter. The three culture tanks were refilled automatically twice daily by a Bedford Otter submersible pump (d), controlled by a fourth automatic clock. The pump delivered the medium to the culture tanks via a manifold (e) constructed of Portex plastic tubing and two plastic "Y" connections (f). A screw clamp (g) was placed on each inlet so that adjustments could be made to balance the inflow to the three tanks. Each inlet connected to a glass thimble (h), the closed end of which extended almost to the bottom of the tank and was perforated with a number of small holes. This design prevented excessive turbulence and splashing when the tanks were refilled.

Because of the design of the Autoset clocks, the pump could not be turned off less than one hour after being turned on, and this is much longer than the time required to fill the tanks. Therefore, each thimble was equipped with an overflow outlet (i) in order to return the excess to the storage tank. A small hole (j) in the upper surface of the outlet prevented a vacuum from developing which would otherwise disrupt the flow.

A glass wool filter (k) was included in the inlet tube before the first "Y" connection in order to remove suspended diatoms from the medium and thus reduce contamination.

Each culture tank was covered with a glass plate (l), leaving a gap of about 3 cm at one end for the inlet.

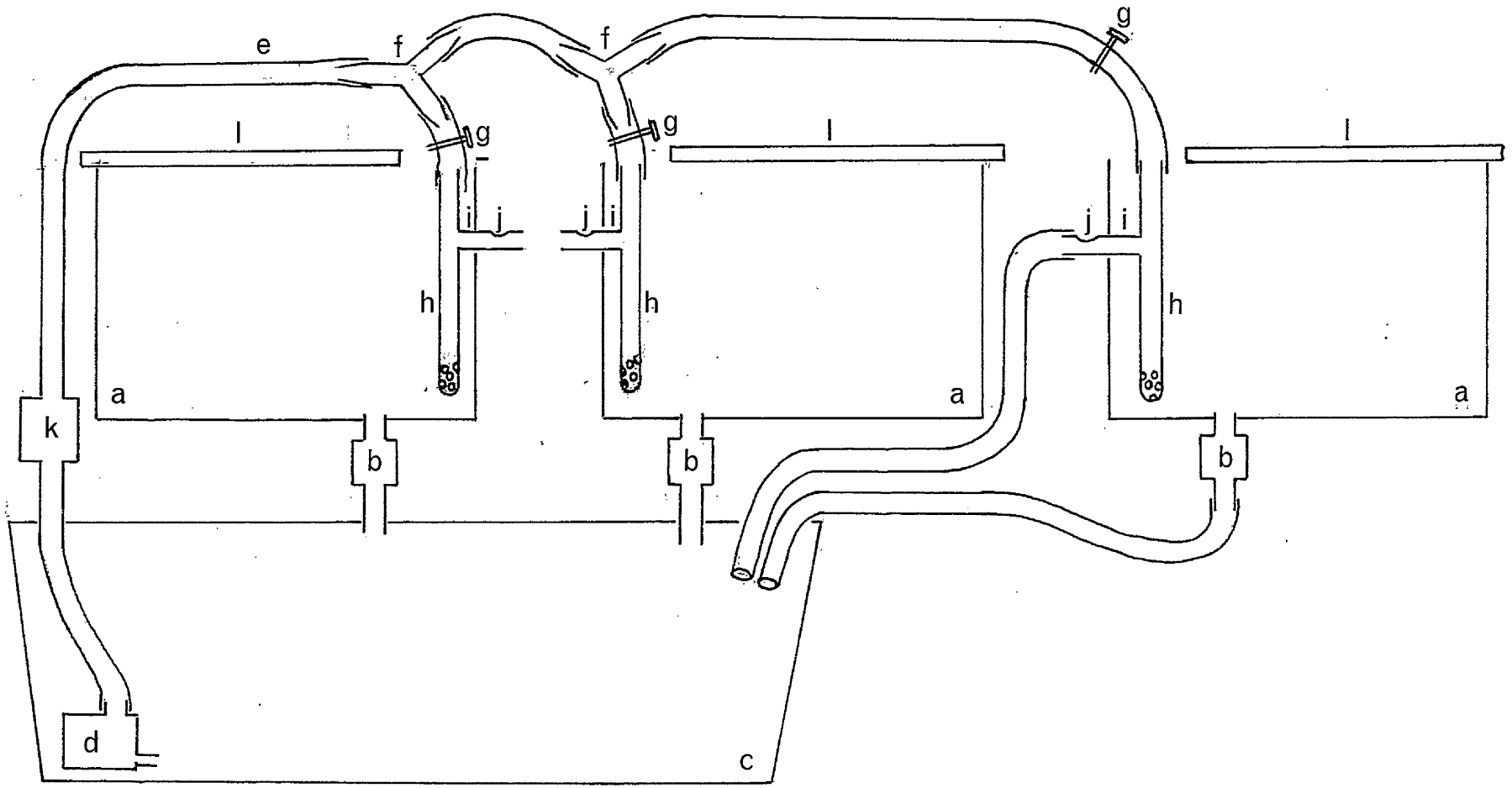



Figure 38. Diagrammatic illustration of tidal simulator

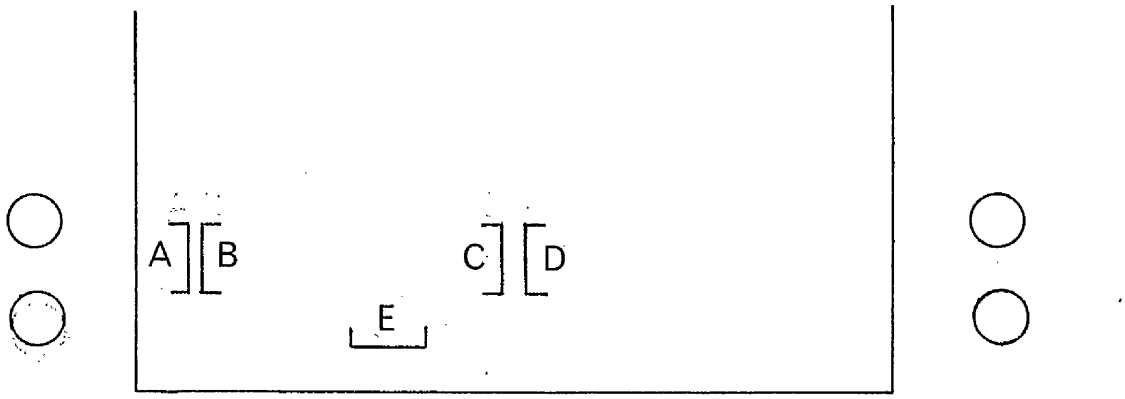



Figure 39 Positions of photoreceptor used for light measurements in tidal simulator. Figure shows first culture tank viewed end on; the other two lie directly behind it.

The clock which controlled the pump was set to refill the tanks at noon and midnight each day. The valve of each tank was then set to open twice daily for one hour. Since each valve was operated independently by a separate clock, the three tanks could be drained at different times, thus providing three different "tidal" regimes.

A total of eighty litres of 1/10 concentration medium was used, and ten litres were withdrawn from the storage tank and replaced with fresh medium every three or four days. The medium in each of the three culture tanks were aerated and agitated by air pumps.

Illumination was provided by four six-foot Atlas daylight fluorescent tubes, two on either side of the tanks. The fucoids in the tidal simulation apparatus were therefore illuminated laterally rather than from above as in other culture work. Irradiance near the front or back wall of the tank was 34 mg-cal/$cm^2$-min from the near tubes (receptor of photometer in positon A, figure 39), and 10-13 mg-cal/$cm^2$-min from the distant pair of tubes (position B). Near the centre of the tank, lateral irradiance was about 21 mg-cal/$cm^2$-min from each pair of tubes (positions C and D). Irradiance from above (position E) was much less, about 5.5 mg-cal/$cm^2$-min. Additional lighting from above could not be provided because of the presence of the somewhat bulky inlet manifold above the tanks.

## Appendix D. Toxicity test on plastics used in tidal simulator

Fucoid zygotes were cultured with each of the three plastic materials used in the construction of the tidal simulator and their growth rates were compared with those of control cultures. This was done to determine whether substances leaching out of the plastics might affect the growth of fucoids. The exposure of the medium to each plastic in the tidal apparatus was calculated as $mm^2$ plastic surface in contact with medium per litre of medium. Small samples of the plastic were added to the medium of each test culture, and the size of the sample was selected so as to give a rate of exposure greater than that realized in the tidal simulator.

The fibreglass material of which the storage tank was constructed slightly inhibited the growth of F. spiralis, which was the only species tested (Table 80). Silicone rubber slightly enhanced the growth of Ascophyllum and three species of Fucus, while the effects of Portex tubing on these four species were inconsistent (Table 80).

Table 80: Growth of fucoid embryos in presence and absence of three plastic materials used in tidal simulator. Table gives means and standard deviation of lengths of thirty to sixty embryos in each treatment.

| Material | exposure in tidal simulator $mm^2/L$ | exposure in test culture | species | culture period days | length with plastic | length without plastic |
|---|---|---|---|---|---|---|
| Fibreglass | 15,600 (24 hrs/day) | 38,000 (24 hrs/day | F.spiralis | 20 | 598 ± 140<br>538 ± 119 | 683 ± 116<br>615 ± 153 |
| Portex tubing | 4,710 ( 4 hrs/day) | 4,650 (24 hrs/day) | F.spiralis | 24 | 656 ± 95 | 605 ± 78 |
| | | | F.vesiculosus | 24 | 535 ± 100 | 759 ± 154 |
| | | | F.serratus | 24 | 1208 ± 301 | 1349 ± 227 |
| | | | Ascophyllum | 24 | 206 ± 44 | 214 ± 47 |
| Silicone rubber aquarium sealer | 2,720 (24 hrs/day) | 4,650 (24 hrs/day) | F.spiralis | 24 | 710 ± 142 | 605 ± 78 |
| | | | F.vesiculosus | 24 | 871 ± 181 | 759 ± 154 |
| | | | F.serratus | 24 | 1491 ± 333 | 1349 ± 227 |
| | | | Ascophyllum | 24 | 297 ± 66 | 214 ± 47 |

Since the test exposures were greater than those realized in the tidal simulator, and since embryonic stages are generally the most sensitive to toxins, the effect of the plastics on the plants cultured in the tidal apparatus were probably less than those shown in Table 80 , and were considered acceptable.

## Appendix E. Derivation of mean correction factors for estimating surface area in Pelvetia and Ascophyllum from photocopy.

### I. Pelvetia canaliculata

The thickness, inside width and outside width of twenty cross sections of Pelvetia axes were measured, as in Figure 40 A. Next the mean of the two widths was calculated, and a new figure constructed from the mean width and the thickness (Figure 40 B) which has the same perimeter and area as the original curved cross section. The surface to volume ratio was then calculated by dividing the perimeter by the area. The mean surface to volume ratio of the twenty axes sectioned

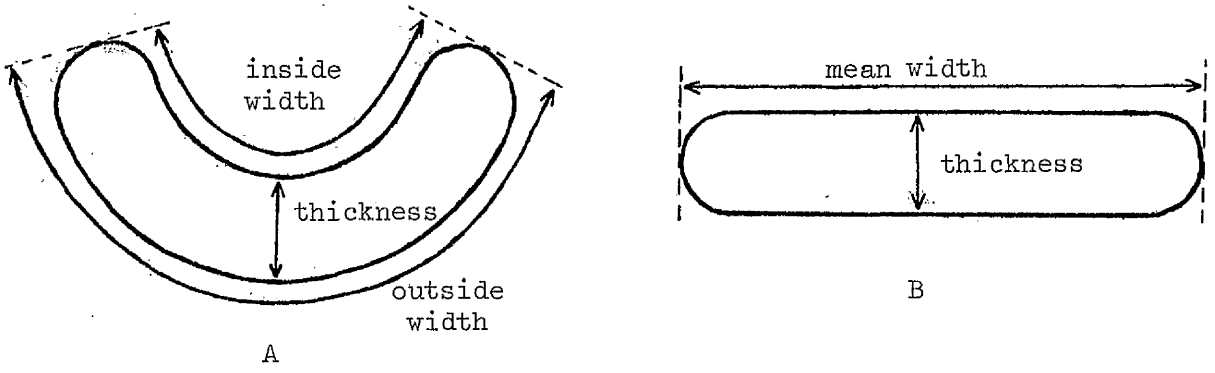



Figure 40: Dimensions used to calculate perimeter of Pelvetia cross section.

was 3.81 $mm^2/mm^3$. This value was divided by the mass density of Pelvetia (found to be 1.08g/mℓ, mean of seven determinations) to obtain a surface to mass ratio of $4.12 \pm 0.53$ $mm^2/mg$.

The mean surface to mass ratio calculated from the weights and uncorrected photocopy areas of twenty-one other Pelvetia thalli was $3.04 \pm 0.15$ $mm^2/mg$. The correction factor was calculated by dividing the mean obtained from the twenty sectioned axes by this mean, i.e. $4.12/3.04 = 1.36$.

### II. Ascophyllum nodosum

The fronds of this species are approximately elliptical-cylindrical, and the photocopy image consists of a projection of this cylinder with the major elliptical axis parallel to the photocopy sheet. Thus the

correction factor is equal to:-

(perimeter of ellipse)/(2 x length of major axis)

The major and minor axes of the elliptical cross sections of thirty Ascophyllum thalli were measured with a micrometer caliper, and the ellipse perimeter was calculated by mathematical approximation. The value of the correction factor for these thirty thalli was 1.15, with 95% confidence limits of 1.13-1.17.

## Appendix F. Calculation of initial weight change caused by incomplete reimbibition of water and by loss of tissue dry matter.

A = percent dry matter in plants as collected

B = percent dry matter in plants after air-drying and resoaking overnight.

C = ratio of dry weight measured after air-drying and resoaking to wet weight before air-drying, expressed as a percentage.

a, b c are defined as the same parameters expressed as fracitons,

i.e. $a = \frac{A}{100\%}$ .

Incomplete reimbibition acting alone would result in an initial percent weight change equal to:

$$\left[\frac{(\text{wet weight after air-drying and resoaking})-(\text{original wet weight})}{(\text{original wet weight})}\right] \times 100\%$$

$$= \left[\frac{\left(\frac{\text{wet weight after air-drying and resoaking}}{\text{dry weight}}\right) - \left(\frac{\text{original wet weight}}{\text{dry weight}}\right)}{\left(\frac{\text{original wet weight}}{\text{dry weight}}\right)}\right] \times 100\%$$

$$= \left[\frac{\left(\frac{\text{wet weight after air-drying and resoaking}}{\text{dry weight}}\right)}{\left(\frac{\text{original wet weight}}{\text{dry weight}}\right)} - 1\right] \times 100\%$$

$$= \left(\frac{1/b}{1/a} - 1\right) \times 100\% = \left(\frac{a}{b} - 1\right) \times 100\% = \left(\frac{A}{B} - 1\right) \times 100\%$$

Strictly, this formula can be derived only if loss of tissue dry matter is initially assumed not to occur; otherwise the term "dry weight" is not defined. However, the final formula remains valid regardless of whether there is loss of tissue dry matter or not during resoaking. The amount of water reimbibed per gram of remaining dry matter

$(\frac{1}{b}-1$ can be compared with the original amount of water per gram of dry matter $(\frac{1}{a}-1)$. If a = b, reimbibition is considered complete, and the initial weight loss is entirely caused by losses of tissue substance. If b >a, then incomplete reabsorption by the remaining dry matter has contributed to the initial weight loss.

Loss of tissue dry matter results in an initial percent weight change equal to:

$$\left( \frac{\left[\begin{array}{l}\text{dry weight measured}\\ \text{after air-drying and}\\ \text{resoaking}\end{array}\right] - \left[\begin{array}{c}\text{original weight}\\ \text{of dry}\\ \text{matter}\end{array}\right]}{(\text{original weight of dry matter})} \right) \times 100\%$$

$$= \left( \frac{\left[\begin{array}{l}\text{dry weight measured}\\ \text{after air-drying and}\\ \underline{\text{resoaking}}\\ \text{original wet weight}\end{array}\right] \quad \left[\begin{array}{c}\text{original weight}\\ \text{of dry}\\ \underline{\text{matter}}\\ \text{original wet weight}\end{array}\right]}{\dfrac{(\underline{\text{Original weight of dry matter}})}{(\text{original wet weight})}} \right) \times 100\%$$

$$= \left(\frac{c-a}{a}\right) \times 100\% = \left(\frac{c}{a} - 1\right) \times 100\% = \left(\frac{C}{A} - 1\right) \times 100\%$$

The main source of error is the fact that A cannot be measured with the same set of plants used to measure B and C. Plants which have been dried over silica gel to obtain parameter A have been subjected to an unnaturally severe, lethal dehydration, and the values of B and C which would be obtained by resoaking and redrying these would not be ecologically relevant. Therefore, A must be estimated using a second set of plants collected at the same time and from the same place as the set used to obtain B and C. The usefulness of this method is therefore limited by the variability of the three parameters. A difference between A and B, or A and C was considered positive evidence of incomplete rehydration and loss of cell substances respectively only when the difference was significant at the 5% level by the t-test.

## REFERENCES

Baardseth, E. (1968) Synposis of biological data on Ascophyllum nodosum. FAO Fisheries Synposis 38. Rome: Food and Agricultural Organization of the United Nations.

Bailey, N.T.J. (1959) Statistical Methods in Biology. London: English University Press Ltd.

Baker, S.M. (1909) On the causes of the zoning of the brown seaweeds on the seashore. New Phytol. 8, 196-202.

Baker, S.M. (1910) On the causes of the zoning of the brown seaweeds on the seashore. II. Effect of periodic exposure on the expulsion of gametes and on the germination of zygotes. New Phytol. 9, 54-67.

Baker, S.M. (1912) On the brown seaweeds of the salt marsh. J. Linn. Soc. 40, 275-291

Baker, S.M. & M.H. Bohling (1916) On the brown seaweeds of the salt marsh. II. Their systematic relationships, morphology and ecology. J. Linn. Soc. 43, 325-380.

Bérard-Therriault, L. & A. Cardinal (1973a) Importance de certains facteurs écologiques sur la résistance a la dessication des Fucacées (Phaeophyceae). Phycologia 12, 41-52

Bérard-Therriault, L. & A. Cardinal (1973b) Variations de la teneur en acide alginique des Fucacées de l'estuaire du Saint-Laurent (Québec) en fonction de certains facteurs écologiques. Botanica mar. 16, 96-102.

Bernhard, M.A., A. Zattera & P. Filesi, (1966) Suitability of various substances for use in the culture of marine organisms. Pubbl. Staz. zool. Napoli 35, 89-104.

Bidwell, R.G.S. & J.S. Craigie (1963) A note on the greatly reduced ability of Fucus vesiculosus to absorb or evolve $CO_2$ when not submerged. Can. J. Bot. 41, 179-182.

Bidwell, R.G.S. & N.R. Ghosh (1963) Photosynthesis and metabolism in marine algae. VI. The uptake and incorporation of $S^{35}$ -sulfate in Fucus vesiculosus. Can. J. Bot. 41, 209-220.

Biebl, R. (1952) Ecological and nonenvironmental constitutional resistance of the protoplasm of marine algae. J. mar. biol. Ass. U.K. 31, 307-315

Biebl, R. (1972) Temperature resistance of marine algae. Proc. VII Int. Seaweed Symp., ed. K. Nisizawa, 23-28.

Bird, C.J. & J. McLachlan (1974) Cold hardiness of zygotes and embryos of Fucus (Phaeophyceae, Fucales). Phycologia 13, 215-225.

Black, W.A.P. (1948a) The seasonal variation in chemical composition of some of the littoral seaweeds common to Scotland. Part I. Ascophyllum nodosum. J. Soc. chem. Ind. 67, 355-357.

Black, W.A.P. (1948b) Seasonal variation in chemical constitution of some of the sublittoral seaweeds common to Scotland. J. Soc. chem. Ind. 67, 165-176.

Black, W.A.P. (1949a) Seasonal variation in chemical composition of some of the littoral seaweeds common to Scotland. Part II. Fucus serratus, F. vesiculosus, F. spiralis, Pelvetia canaliculata. J. Soc. chem. Ind. 68, 183-189.

Black, W.A.P. (1949b) The effect of the depth of immersion on the chemical constitution of some of the sublittoral seaweeds common to Scotland. J. Soc. chem. Ind. 69, 161-165.

Branch, G.M. (1975) Ecology of Patella spp from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32, 179-188.

Brinkhuis, B.H. & R.F. Jones (1976) The ecology of temperate salt-marsh fucoids. II. In situ growth of Ascophyllum nodosum ecads. Mar. Biol. 34, 339-348.

Brinkhuis, B.H. & N.R. Tempel (1975) Photosynthesis in exposed salt-marsh macroalgae. J. Phycol. 11 supplement, 11.

Brinkhuis, B.H., N.R. Tempel & R.F. Jones (1976) Photosynthesis and respiration of exposed salt marsh fucoids. Mar. Biol. 34, 349-359.

Brock, T.D. (1975) The effect of water potential on photosynthesis in whole lichens and in their liberated algal components. Planta 124, 13-23.

Burrows, E.M. (1956) Growth control in the Fucacae. Proc. II Int. Seaweed Symp., ed. T. Braarud & N.A. Sorensen, 163-170.

Burrows, E.M. (1961) Experimental ecology with particular reference to the ecology of Laminaria saccharina (L) Lamour. in Recent Advances in Botany, U. Toronto, pp 187-189.

Burrows, E.M. (1964) An experimental assessment of some of the characteristics used for specific delimitation in the genus Laminaria. J. mar. biol. Ass. U.K. 44, 137-143.

Burrows, E.M., E. Conway, S.M. Lodge & H.T. Powell (1954) The raising of intertidal algal zones on Fair Isle. J. Ecol. 42, 283-288.

Burrows, E.M. & S.M. Lodge (1951) Autecology and the species problem in Fucus. J. mar. biol. Ass. U.K. 30, 161-176.

Chapman, A.R.O. (1973) A. critique of the prevailing attitudes toward the control of seaweed zonation of the sea shore. Botanica mar. 16, 80-82.

Collier, R. & G.Y. Kennedy (1963) The sulpholipids of plants. I. The distribution of sulpholipids and phospholipids among the major plant classes. J. mar. biol. Ass. U.K. 43 605-612.

Colman, J. (1933) The nature of the intertidal zonation of plants and animals. J. mar. biol. Ass. U.K. 18, 435-476.

Colwell, R.K. & E.R. Fuentes (1975) Experimental studies of the niche. Ann. Rev. Ecol. Syst. 6, 281-310.

Connell, J.H. (1961) The role of interspecific competition and other factors in the distribution of the barnacle Chthamalus stellatus. Ecology 42, 710-723.

Damant, G.C.C. (1937) Storage of oxygen in the bladders of the seaweed Ascophyllum nodosum. J. exp. Biol. 14, 198-209.

David, H.M. (1943) Studies in the autecology of Ascophyllum nodosum Le Jol. J. Ecol. 31, 178-198

Dayton, P.K. (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41, 351-389.

Dayton, P.K. (1973) Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. Am. Nat. 107, 662-670

Dayton, P.K. (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45, 137-159

Den Hartog, C. (1968) The littoral environment of rocky shores. Blumea 16, 374-393.

Doty, M.S. (1946) Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific Coast. Ecology 27, 314-327.

Edelstein, T. & J. McLachlan (1975) Autecology of Fucus distichus subsp distichus (Phaeophyta, Fucales ) in Nova Scotia, Canada. Mar. Biol. 30, 305-324.

Evans, R.G. (1947a) The intertidal ecology of Cardigan Bay. J. Ecol. 34, 273-309.

Evans, R.G. (1947b) The intertidal ecology of selected localities in the Plymouth neighbourhood. J. mar. biol. Ass. U.K. 27, 173-218.

Feldman, N.L. & M.I. Lutova (1963) Variations de la thermostabilité cellulaire en fonction des changements de la temperature du milieu. Cah. Biol. mar. 4, 435-458.

Fischer, E. (1929) Recherches de bionomie et de l'océanographie littorales sur la Rance et le littoral de la Manche. Annls. Inst. Océanogr., Monaco 5, 201-429.

Fischer-Piette, (1957) Pelvetia canaliculata examiné de proche en proche de la Manche au Portugal. in Écologie des Algues Marines, Paris: Centre National de la Recherche Scientifique, pp 65-74

Gail, F.W. (1918) Some experiments with Fucus to determine the factors controlling its vertical distribuiton. Publs. Puget Sound mar. biol. Stn. 2, 139-151.

Gail, F.W. (1922) Photosynthesis in some of the red and brown algae as related to light and depth. Publs. Puget Sound mar. biol. Stn. 3, 177-193.

Gibb, D.C. (1938) The marine algal communities of Castletown Bay, Isle of Man. J. Ecol. 26, 96-117.

Gibb, D.C. (1939) Some marine algal communities of Great Cumbrae. J. Ecol. 27, 364-382.

Grubb, V.M. (1936) Marine algal ecology and the exposure factor at Peveril Point, Dorset. J. Ecol. 24, 392-423.

Haas, P. & T.G. Hill (1933) Observations on the metabolism of certain seaweeds. Ann. Bot. 47, 55-67.

Hatton, H. (1932) Quelques observations sur le repeuplement en Fucus vesiculosus des surfaces rocheuses denudées. Bull. Lab. marit. Mus. His. Nat. St.Servan 9, 1-6.

Hatton, H. (1938) Essais de bionomie explicative sur quelques espèces intercotiadales d'algues et d'animaux. Annls. Inst. océanogr., Monaco 17, 241-348.

Hinton, G.C.F. (1974) Studies on the phytoplankton of the Firth of Clyde. Ph.D. thesis, University of Glasgow.

Hitchcock, C. & B.W. Nichols (1971) Plant Lipid Biochemistry. London: Academic Press.

Hruby, T. (1976) Observations of algal zonation resulting from competition. Estuar. coastal mar.Sci. 4, 231-233.

Isaac, W.E. (1933) Some observations and experiments on the drought resistance of Pelvetia canaliculata. Ann. Bot. 47, 343-348

Jerlov, N.G. (1968) Optical Oceanography. London: Elsevier Publ.Co.

Johnson, D.S. & A.F. Skutch (1928) Littoral vegetation on a headland of Mt. Desert Island, Maine. I. Submersible, or strictly littoral vegetation. Ecology 9, 188-215.

Johnson, W.S., A. Gigon, S.L. Gulman & H.A. Mooney (1974) Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. Ecology 55, 450-453

Jones, N.S. (1946) Browsing of Patella. Nature, Lond. 158, 557.

Jones, N.S. (1948) Observations and experiments on the biology of Patella vulgata at Port St. Mary, Isle of Man. Proc. Trans. Lpool. biol. Soc. 56, 60-77.

Kain, J.M. (1964) Aspects of the biology of Laminaraia hyperborea. III. Survival and growth of gametophytes. J. mar.biol. Ass. U.K.44, 415-433.

Kain, J.M. (1975) Algal recolonization of some cleared subtidal areas. J. Ecol. 63, 739-765

Kanwisher, J.W. (1957) Freezing and drying in intertidal algae. Biol. Bull. mar. biol. Lab., Woods Hole 113, 275-285.

Kanwisher, J.W. (1966) Photosynthesis and respiration in some seaweeds. in Some Contemporary Studies in Marine Science, ed. H. Barnes, London: Allen & Unwin, pp 407-420.

Kennedy, G.Y. & R. Collier (1963) The sulpholipids of plants. II. The isolation of sulpholipids from green and brown algae. J. mar. biol. Ass. U.K. 43, 613-619.

Klugh, A.B. & J.R. Martin (1927) The growth rate of certain marine algae in relation to depth of submergence. Ecology 8, 221-231.

Knight, M. (1947) A biological study of Fucus vesiculosus and Fucus serratus. Proc. Linn. Soc. London. 159, 87-90.

Knight, M. & M. Parke (1950) A biological study of Fucus vesiculosus L. and Fucus serratus L. J. mar. biol. Ass. U.K. 39, 439-514.

Kondratyev, K. Ya. (1969) Radiation in the Atmosphere. London: Academic Press.

Kremer, B.P. (1976) Distribution and biochemistry of alditols in the genus Pelvetia (Phaeophyceae, Fucales ). Br. Phycol. Bull. 11,239-243.

Kremer, B.P. & K. Schmitz (1973) $CO_2$-Fixerung und Stofftransport in benthischen marinen Algen. IV. Zur $^{14}C$-Assimilation einiger letoraler Braunalgen in submersen und emersen Zustand. Z. Pflanzenphysiol. 68, 357-363

Kristensen, I. (1968) Surf influence on the thallus of fucoids the rate of desiccation. Sarsia 34, 69-82.

Lestang, G. & M. Quillet (1973) Renouvellement rapide des esters sulfuriques de la fucoidine des frondes intactes de Pelvetia canaliculata (Decn.et Thur) pendent leur immersion en mer. C. r. hebd. Séanc. Acad. Sci., Paris, sér D 277, 2005-2008.

Lestang, G. & M. Quillet (in press) The sulfated fucoidan of Phaeophyceae as a factor of ecological adaptation. Proc. VIII Int. Seaweed Symp., ed. G.E. Fogg.

Levitt, J. (1972) Responses of Plants to Environmental Stresses. New York: Academic Press.

Lewis, J.R. (1964) Ecology of Rocky Shores. London: English University Press Ltd.

Liem, P.Q. & M.H. Laur (1975) Variations de la composition et de la teneur en lipides polaires des trois Fucacées communes des côtes bretonnes: Pelvetia canaliculata (L.) Decn. & Thur., Fucus vesiculosus L., Fucus serratus L. au cours de leur cycle annual. Botanica mar. 17, 105-113.

Liem, P.Q. & M.H. Laur (1976) Teneur, composition et répartition cytologique des lipides polaire soufrés et phosphorés de Pelvetia canaliculata (L.) Decn. et Thur., Fucus vesiculosus L. et Fucus serratus L. Phycologia 15, 367-375.

Lodge S.M. (1948) Algal growth in the absence of Patella on an expérimental strip of foreshore, Port St. Mary, Isle of Man. Trans. Proc. Lpool. bot. Soc. 56, 78-85.

McLachlan, J. (1974) Effects of temperature and light on growth and development of embryos of Fucus edentatus and Fucus distichus subsp. distichus. Can. J. Bot. 52, 943-952.

McLachlan, J., L.C.M. Chen & T. Edelstein (1971). The culture of four species of Fucus under laboratory conditions. Can. J. Bot. 49, 1463-1469.

McLean, R.C. & W.R.I. Cook (1941) Plant Science Formulae. London: MacMillan & Co. Ltd.

Menge, J.L. (1975) Effects of herbivores on community structure of the New England rocky intertidal region; distribution and diversity of algae. Ph.D. thesis, Harvard University.

Montfort, C. (1937) Die Trockenresistenz der Gezeitenpflanzen. Ber. dt. bot. Ges. 55, 85-95.

Moore, H.B. (1940) The biology of Littorina littorea. Part II. zonation in relation to other gastropods on stoney and muddy shores. J. mar. biol. Ass. U.K. 24, 227-237.

Moore, H.B. & N.G. Sproston (1940) Further observations on the colonization of a new rocky shore at Plymouth. J. Anim. Ecol. 9, 319-327.

Moss, B. (1974) Attachment and germination of the zygotes of Pelvetia canaliculata (L.) Decn. et Thur. (Phaeophyta, Fucales. Phycologia 13, 317-322.

Newell, G.E. (1958) The behaviour of Littorina littorea (L.) under natural conditions and its relation to position on the shore. J. mar. biol. Ass. U.K. 37, 229-239.

Norton, T.A. & E.M. Burrows (1969) Environmental control of the seasonal development of Sacchoriza polyschides. Proc. VI Int. Seaweed Symp., ed. R. Margalef, 287-296.

Paine, R.T. (1971) A short term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52, 1096-1106.

Paine, R.T. (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principle predator. Oecologia 15, 93-120.

Parker, J. (1960) Seasonal change in cold-hardiness of Fucus vesiculosus. Biol. Bull. mar. biol. Lab., Woods Hole 119, 474-478.

Pollock, E.G. (1969) Interzonal transplantation of embryos and mature plants of Fucus. Proc. VI Int. Seaweed Symp., ed. R. Margalef, 345-356.

Pollock, E.G. (1970) Fertilization in Fucus. Planta 92, 85-99

Printz, H. (1956) Recuperation and recolonization of Ascophyllum. Proc. II Int. Seaweed Symp., ed. T. Braarud & N.A. Sorensen, 194-197.

Pyefinch, K.A. (1943) The intertidal ecology of Bardsey Island, North Wales with special reference to the recolonization of rock surfaces and the rock pool environment. J. Anim. Ecol. 12, 82-108.

Sandgren, C.D. (1973) An investigation of desiccation and photosynthetic ability as possible factors affecting the vertical zonation of Fucus distichus and Fucus spiralis. Unpublished student project at Friday Harbour Laboratories.

Schramm, Winifrid (1968) Ökologische-physiologische Untersuchrungen zur Austroknungs und Temperaturesesteng an Fucus vesiculosus L. Int. Revue ges. Hydrobiol. Hydrogr. 53, 469-510.

Sheader, A. & B. Moss (1975) Effect of light and temperature on germination and growth of Ascophyllum nodosum (L.) Le Jol. Estuar. coastal mar. Sci. 3, 125-132.

Southward, A.J. (1962) Limpet grazing and the control of vegetation on rocky shores. in Grazing in Terrestrial and Marine Environments, ed. D.J. Crisp, Oxford: Blackwell Scientific Publications. pp. 265-274.

Steeman-Nielsen, E. (1975) Marine Photosynthesis with Special Emphasis on the Ecological Aspects. Oxford: Elsevier Scientific Publ.Co.

Steward, F.C. (1959) Plant Physiology, Volume II. Plants in relation to Water and Solutes. London: Academic Press.

Strömgren, Tor (1976) Length changes of growing apices of eulittoral Fucales during drying and soaking. Sarsia 61, 47-54.

Subrahmanyan, R. (1960) Ecological studies on the Fucales. I. *Pelvetia canaliculata* Decn. & Thur. *J. Indian. bot. Soc.* 39, 614-630.

Subrahmanyan, R. (1961) Ecological studies on the Fucales. II. *Fucus spiralis* L. *J. Indian. Bot. Soc.* 40, 335-354.

Zaneveld, J.S. (1937) The littoral zonation of some Fucaceae in relation to desiccation. *J. Ecol.* 25, 431-468.