INTERTIDAL FUCOID ZONATION AND DESICCATION

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INTRODUCTION

The intertidal, fucoid flora on hard substrates, which occurs in the temperate region of the northern hemisphere, is broken into a series of subzones (STEPHENSON and STEPHENSON,(1949); see also COLMAN (1953) and CHAPMAN (1942)). From high to low shore level the subzones successively consist of the wracks *Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum, F.vesiculosus* and *F.serratus*. Lower yet *Laminaria* species occur. Factors controlling the delimitation of the algal zonation have been reviewed by ZANEVELD (1969). The rate of water loss of these large brown algae during ebb is considered to be of great importance.

PRINGSHEIM (1923) compared the water loss of *Fucus platycarpus* (=*F. spiralis*), *F.vesiculosus* and *F.serratus*. He found *F.platycarpus* to lose its water sooner than the other species, but his data do not allow statistical analysis. The same holds for the findings of ISAAC who compared *Pelvetia canaliculata* with *Fucus spiralis* (1933) and *Laminaria digitata* with *F.serratus* (1935); according to ISAAC (1935) the latter were sampled at the same shore level and not at different levels as is cited abusively by ZANEVELD (1937:457). ZANEVELD (1937) compared the desiccation of *Fucus spiralis, Ascophyllum nodosum, F.vesiculosus* and *F.serratus*. Again, statistical analysis is unreliable as only four pieces of thallus per species have been used (see his Table VI). He carelessly drew Fig. 8, for the point that indicates the water loss of *F.vesiculosus* after one hour has too low a position. His conclusion that high level fucoid species 'reach dry weight on evaporation of water later' than lower level species is ecologically irrelevant as it is based on measurements in a desiccator with sulphuric acid (in which the relative humidity fell to zero) over a period that widely exceeds the intertidal exposure time. His conclusion that the high level species have a higher water content is not correct because the means of the weight percentages of fresh weight of the species (based on six measurements; see his Table VII) after 96 hours do not differ statistically. ZANEVELD maintained his conclusions in his review (1969). PRIOU (1962) concluded, also without statistical support, that the lower level wracks lose more water than the higher level species. KRISTENSEN (1968), studying *Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum, F.vesiculosus* and *F.serratus*, confirmed ZANEVELD's (1937) conclusion that species from higher shore levels have thicker cell walls than species from lower zones. He found no correlation between cell wall thickness and desiccation and announced this conclusion as being contrary to that of ZANEVELD (1937), but both authors based their conclusion on only 2-4 thallus tips.

Therefore, the controversy in literature (PRINGSHEIM and KRISTENSEN versus ZANEVELD and PRIOU) is uncertain as long as statistically significant differences in water loss rate can either be established or not. This contribution aims to solve the problem.

MATERIAL AND METHODS

The brown algae were sampled in October in the Oosterschelde near Kattendijke (Delta area, SW-Netherlands) on a dike slope consisting of Vilvordian limestone. On this porous substrate, contrary to basalt, the upper fucoid subzone is formed by *Pelvetia canaliculata* (DEN HARTOG, 1959). The location faces the north and has no particular characteristics in terms of conditions of exposure to sun, surf and time of emersion.

The species, listed according to vertical layering, are *Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum, F.vesiculosis* and *F.serratus*. Furthermore, *Laminaria saccharina* was included to compare the water loss rate. It was obtained from the base of small walls (of former oyster ponds along the dike) which runs dry at low-water springs only. The fronds were kept immersed in sea water in the laboratory at 5° C. Continuous immersion in water of 15-20°C made the thalli very mucous after some days. The thallus tips were selected according to ZANE-VELD (1937). In case of *A.nodosum* and *F.vesiculosus* the air vesicles were excluded. Of *Laminaria saccharina* the thallus parts were taken from the base of the frond as the top was heavily divided in dying filaments. The parts were placed under room conditions (T = ca. 22°C; RH = ca. 40-45%) and weighed to the nearest 0.01 mg. After the experiments they were dried to a constant weight at 100° C. Dessication is expressed as the percentage of the initial fresh weight. Of each species pieces of 12 individuals were used.

RESULTS

In Fig. 1 the water loss rates are given of the six species of brown algae. The following conclusions can be drawn. (a) Rates of water loss are greatest during the first 2-3 hours, with the exception of *Laminaria saccharina*; *Pelvetia canaliculata* has the greatest water loss rate and *L.saccharina* the smallest. (b) The graphs of *Ascophyllum nodosum* and the three *Fucus* species are intermediate to those of *P.canaliculata* and *L.saccharina*; within this group *F.vesiculosus* loses its water significantly sooner. (c) All wrack species tested reach the maximum water loss after about 5 hours; *L.saccharina* loses more water but this takes much more time, which is of no importance, however, for a species that is almost continuously immersed.

In Fig. 2 the water content per gram dry weight of the six species is compared. *L.saccharina* has the highest content. The weight differences between the maximum level of water loss during the experiments (Fig. 1) and the dry weight was very small.

Juveniles of *L.saccharina* lose their water sooner than adults (which is in accordance with the data presented by KRISTENSEN (1968) for *Fucus spiralis* and *F.serratus*), buth both reach the same maximum water loss (Fig. 3).

DISCUSSION

The course of the curves (Fig. 1) is in correspondence with that of the graphs given by others (PRINGSHEIM, 1923; ZANEVELD, 1937; PRIOU, 1962; KRISTENSEN, 1968), namely a rapid water loss during the first hours leading to cessation after about five hours. However, the sequence
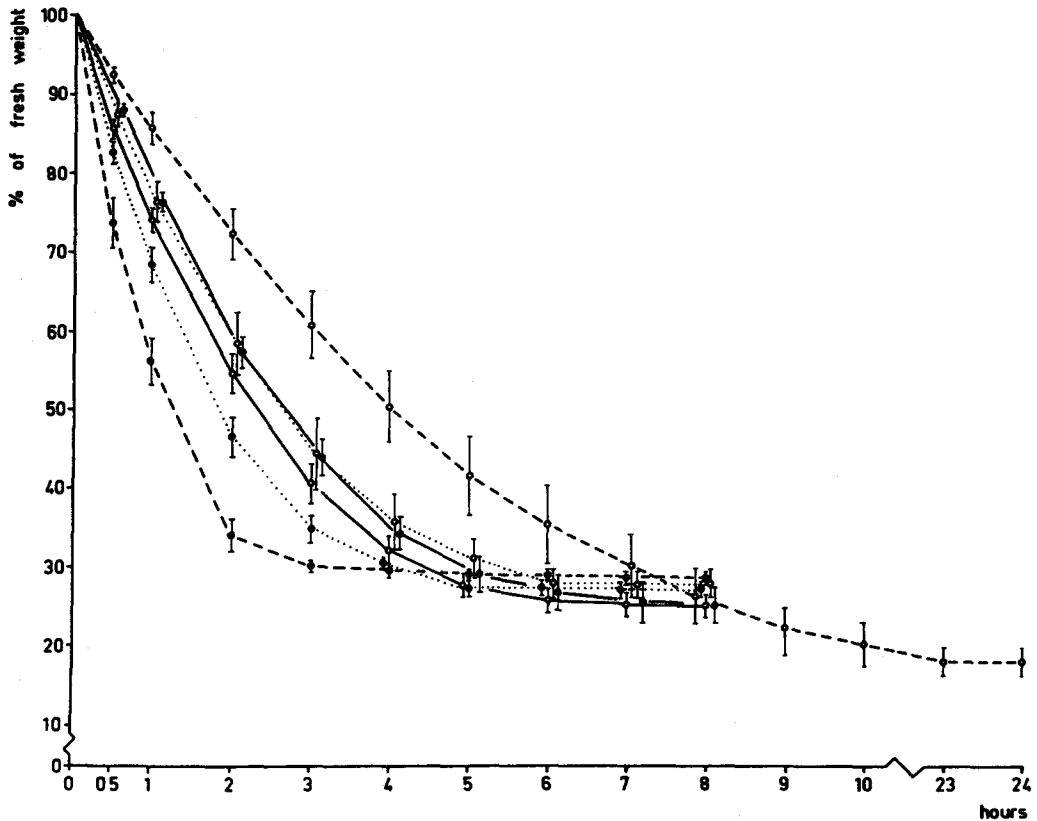
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Fig. 1. Water loss (± 2SE; n+12) of adult intertidal brown algae
under room conditions (T = ca. 22°C; RH = ca. 40-45%).

●— — — —● Pelvetia canaliculata

○—————○ Fucus spiralis

○···········○ Ascophyllum nodosum

●···········● Fucus vesiculosus

●—————● Fucus serratus

○— — — —○ Laminaria saccharina

(sequence according to high - low shore levels)

of species occurrence from high to low intertidal level does not re-
flect a sequence of an increasingly higher rate and/or greater amount
of water loss (Fig. 1,2) as might be expected since ZANEVELD (1937). On
the contrary, the highest level species (P.canaliculata) reaches the max-
imum water loss first and the lowest species (L.saccharina), though
losing more water, last. Of L.saccharina (older) basal parts of the frond
instead of (young) tips were used. KREMER (1975) demonstrated that
the base of the frond of F.serratus contains less water than the top.
Therefore, when using apical parts of the thallus the initial slope of
the graph of L.saccharina may be close to that of A.nodosum and the Fu-
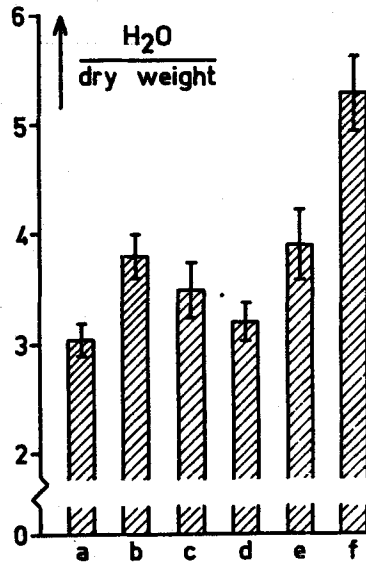cus species. Perhaps like in juveniles as can be seen in Fig. 3.

Fig. 2. The relationship between water content and dry weight expressed as g H_2O/g dry weight ($\pm$ 2SE; n=12).

a – f = sequence of species as mentioned in Fig. 1.

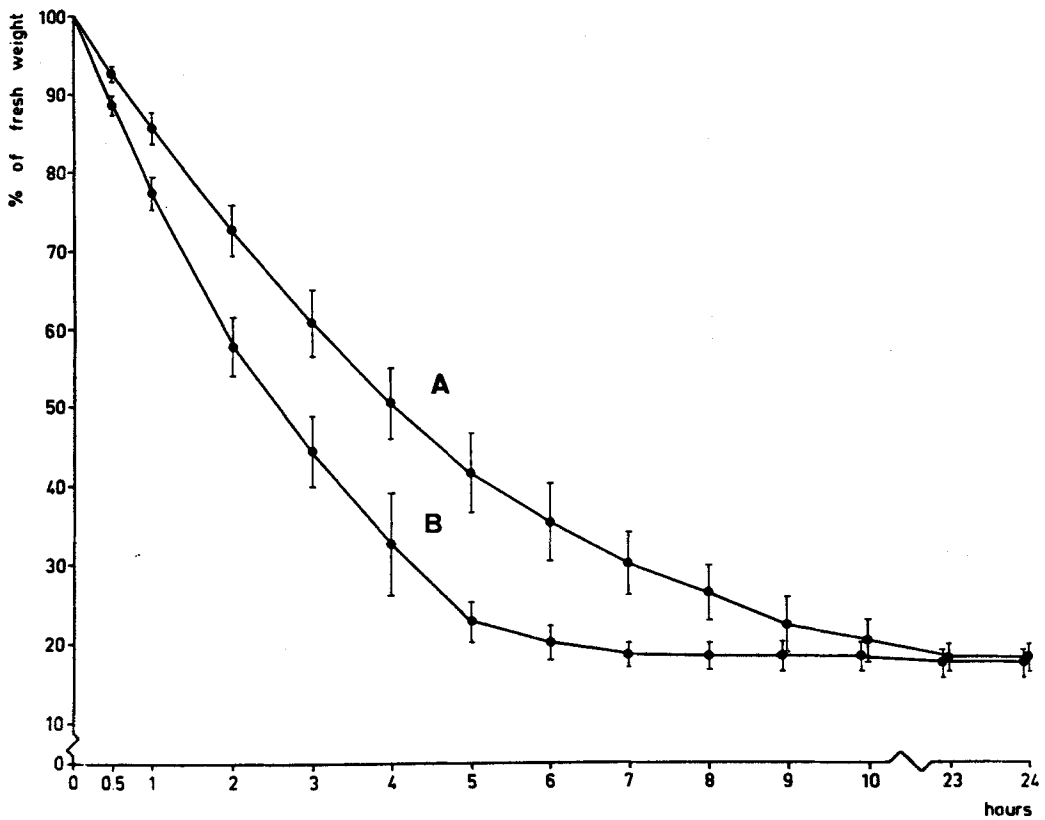

Fig. 3. Water loss ($\pm$ 2SE; n=12) of adults (A) and juveniles (B) of *Laminaria saccharina*.

Fig. 2 reveals the absence of a relationship between the water content per gram dry weight and the sequence of zonation. *L.saccharina* has the greatest water content and loses most (Fig. 1).

ZANEVELD (1937) concluded that the thick cell walls of high(er) species 'lose water with greater rapidity than the cell walls of species growing at lower levels' but did not mention the size of the cell content. High level *Fucus* species are not larger than those from lower levels; their cell content must be smaller therefore. In that case the walls have to play a more important role in the total water loss. Besides, KRISTENSEN (1968) showed that the thickness of the cell wall is enhanced by exposure to wave action and not by the emersion time or exposure to the sun. BOADEN et al. (1975) found the size of *F.serratus* reduced under turbulent conditions. And LIDDLE (1975), comparing intertidal and subtidal populations of *Padina sanctae-crucis*, found that intertidal stress tends to dwarf this alga. Cultivation of spores of both forms under standard conditions gave no difference in growth. BIEBL 1938; 1962) mentioned that of the thin-walled intertidal algae the high level species (*Polysiphonia nigrescens, Cladophora rupestris*) lose more water during desiccation than low level species (*Plocamium coccineum*). So, wall thickness does not appear to be linked with zonation.

BÉRARD-THERRIAULT et CARDINAL (1973a,b) found a higher alginic acid (a hydrophylic polysaccharid) content of the high level *F.spiralis* as compared with the lower level *F.vesiculosus* and *A.nodosum*. *F.spiralis* also lost less water during four hours at 44°C in a stove. But *F.distichus* ssp. *distichus*, a high level form that contains more alginic acid than *F.spiralis* and *F.distichus* ssp. *evanescens* (which grows lowest of all), loses its water sooner than the two latter forms.

It is concluded that as far as differences in amount and/or velocity of water loss or in water content of the algae occur (Fig. 1, 2) they have no relationship with bathymetric layering. For animals that occupy different parts of the intertidal region the data are not decisive. A speedier water loss of lower level species has been found in limpets (ALLANSON, 1958; vide FOSTER, 1971), barnacles (FOSTER, 1971) and mussels (KENNEDY, 1976; due mainly to valve gaping), but little correlation could be demonstrated by BROEKHUYSEN (1940) and BROWN (1960; vide VERNBERG and VERNBERG, 1972) in gastropods and by DAVIES (1969) in limpets.

Apart from the rate at which water is lost there is the amount of loss that is tolerated (plasmatic resistance to desiccation). This desiccation tolerance has been expressed in the post-exposure damage to oxygen-exchange processes (e.g. MONTFORT, 1937; KALTWASSER, 1938; SCHRAMM, 1968; see also GESSNER and SCHRAMM, 1971). Though there is some controversy, high level species seem to have a greater dessication tolerance.

It is beyond doubt that the fucoid species display a successive layering but the distribution diagrams produced in literature clearly show overlap (see COLMAN, 1933; ZANEVELD, 1937; GLYNNE-WILLIAMS and HOBART, 1952). The fringe of *P.canaliculata* is in general very distinct. The gradual transition of the other species may explain that it was wrong to expect that water loss characteristics would precisely reflect the zonal differentiation. It is still impossible to explain zonation. Several authors have discussed the many factors that may locally modify the position of species adapted to intertidal life (CHAPMAN, 1942; STEPHENSON, 1942; SOUTHWARD, 1958; ZANEVELD, 1969). But the causal mechanisms involved in colonization of more aerially exposed habitats will be hard to discover.

It is worth mentioning that biotic relationships have been seriously ignored (see also DORGELO, 1976). COLMAN (1933; 1942), emphasizing the sharpness of the boundaries between the zones of *P.canaliculata* and *F. spiralis*, doubtfully suggested a reciprocal lethal influence of the two species. Nowadays we might state that exocrines could exert influence, which deserves attention.

Finally, the question arises whether only the terrestrial conditions impose the stress on all intertidal algae. According to BIEBL (1962) the supralittoral *Bangia fuscopurpurea* and *Urospora penicilliformis* require periodic desiccation to survive. OGATA and SCHRAMM (1971) found that periodic desiccation of *Porphyra umbilicalis* positively affected the rate of oxygen output but decreased growth. Thus, the aquatic environment may become harmful to intertidal species.

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SUMMARY

1. In literature a controversy exists on the relationship between the sequence in which intertidal large brown algae occur in zones between the tide-marks and their rates of water loss.
2. The water loss of six species under room conditions has been measured. These species (from upper to low shore level) are *Pelvetia canaliculata, Fucus spiralis, Ascophyllum nodosum, F.vesiculosus, F.serratus* and *Laminaria saccharina*.
3. The sequence of layering appeared to have no statistically significant correlation neither with water loss rate nor with water content. These results are discussed.

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