

**The seaweed flora of a young semi-enclosed sea:
The Baltic.
Salinity as a possible agent of flora divergence***

G. Russell

Department of Botany, The University, Liverpool L69 3BX, England

ABSTRACT: The salinity tolerances of Baltic and Atlantic populations of *Fucus vesiculosus* and *Chorda filum* have been measured using net photosynthesis as an index of tissue damage. Atlantic *Fucus* proved to have a broader salinity tolerance than Atlantic *Chorda*, a result which is consistent with others published on the tolerances of intertidal and sublittoral marine species. The optimum salinity for all Atlantic plants was 11 or 34‰, but that of all Baltic plants was 6‰. Baltic *Fucus* and *Chorda* were different in breadth of tolerance, in spite of the fact that they inhabit the same sublittoral habitat. This difference is interpreted in relation to their respective life-forms, *Fucus* being perennial and *Chorda* annual. *Fucus* is therefore present as a macrothallus at all times of year, including the critical low-salinity period of the spring ice-melt. *Chorda* evades damage by existing as a resistant microthallus at this time. It is concluded that the distinctive character of Baltic marine algae deserves nomenclatural recognition at some level below that of the species. The rank of subspecies would appear the most appropriate of those listed in the Code, but none of those available is able adequately to express the patterns of variation now being reported.

INTRODUCTION

The Baltic Sea, like the Mediterranean, has a very narrow exit to the Atlantic Ocean, and the fact that the flow of its seawater is almost always in an outward direction, serves only to increase its isolation. Inward movement of water from the North Sea, which doubtless conveys algal diaspores, does occur from time to time but these "pulses" are evidently infrequent and of short duration (Jansson, 1980; Ehlin, 1981). The geographical isolation of the Baltic has inevitably invited comparison with the Mediterranean (Segerstråle, 1957) and has encouraged a search for endemism and other manifestations of the evolutionary process. However, the spatial similarity of these seas is accompanied by some major differences which have equally important evolutionary implications. As a habitat for marine plants, the Baltic is undoubtedly extremely young. Its marine flora was most probably recruited at the beginning of the Littorina Sea episode (ca 7500 BP), the preceding Ancylus Lake period having been one of freshwater, when any marine plants present were almost certainly killed. The end of the Littorina Sea (ca 3000 BP) was accompanied by a cooling and desalination of Baltic waters to their present rather low values (Ignatius et al., 1981). Thus, if the Baltic flora has diverged at all from its N Atlantic

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progenitor, then it has done so with great rapidity and under strong selection pressure from changes in its physical and chemical environment (Russell, 1985a). The peculiar features of the Baltic environment may therefore make it an unsatisfactory model for estimations of rates of evolutionary change in fully marine seas.

The evolutionary status of Baltic marine algae has been a matter of some controversy. Some phycologists have evidently concluded that major evolutionary changes, up to and including speciation, have occurred. Lakowitz (1929), for example, has identified over 40 endemic taxa in the Baltic flora. However, this conclusion has been disputed by Hoffmann (1950) and others, partly on the basis of more critical floristic and morphological studies and partly from experimental evidence. Modern phycologists seem to be in fairly strong agreement that Baltic algae are members of N Atlantic species, but they seem also to recognise that they are, in some respects at least, a little different. This problem of interpretation has been expressed succinctly by Powell (1963) in his review of speciation in *Fucus* and related genera. Writing about Baltic populations of *F. vesiculosus* L., living in waters of very low salinity, he remarks (p. 74): "... Surely such physiological adaptation as this deserves nomenclatural recognition." This comment in fact conceals three separate questions: Is Baltic *F. vesiculosus* indeed different physiologically from W European populations; if so, does it deserve nomenclatural recognition; and, if so, at which taxonomic rank?

The purpose of this paper is to explore these questions using *F. vesiculosus* and *Chorda filum* (L.) Stackh. as experimental materials. The latter has been included

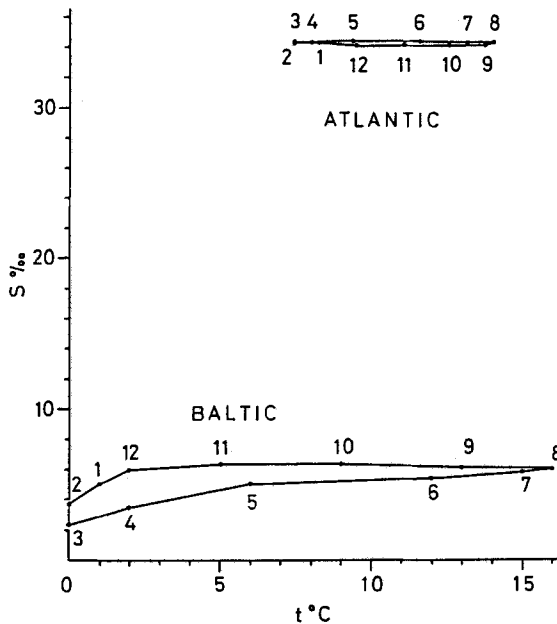


Fig. 1. Temperature-salinity polygons based upon monthly mean data for surface seawater at Port Erin, Isle of Man and Tvärminne, SW Finland. Numbers 1–12 denote months January–December. Values for the Baltic water were taken from Luther et al. (1975) and those for the Atlantic site are from Slinn & Eastham (1984)

because it shares the upper sublittoral zone of the Baltic with *F. vesiculosus* and is therefore liable to experience very similar hydrographic conditions. On Atlantic coasts, however, these two species do not as a rule occur together. *Chorda* is normally a sublittoral plant and, when intertidal, is almost always submerged in pools. *F. vesiculosus*, on the other hand, is almost always intertidal and emergent.

MATERIALS AND METHODS

Baltic plants of *Fucus vesiculosus* and *Chorda filum* were collected from two skerries (Brännskär and Joskär) near Tvärminne Zoological Station in SW Finland. The plants were growing in the sublittoral zone at depths of approximately 1.0 m. Two Atlantic populations of the same species were sampled; *F. vesiculosus* from Hilbre Island at the mouth of the R. Dee, NW England, and *C. filum* from Derbyhaven, Isle of Man. The monthly mean surface seawater temperatures and salinities for Tvärminne and the Isle of Man are given in Figure 1.

After collection, plant material was returned to the laboratory in buckets of seawater or in polythene bags. It was then transferred to tanks of aerated seawater of the particular locality, and maintained at 10°C until required for experiments. All experiments were begun within 36 h of collection.

Clean, epiphyte-free portions of thallus were removed from the plants and placed in waters of different salinities. The *Fucus* tissues were excised vegetative apices (mean dry weight 0.126 g; S.D. 0.036 g) while those of *Chorda* (mean dry weight 0.059 g; S.D. 0.021 g) were cut from the midthallus region. The media were based upon seawater ($S = 34\text{‰}$) obtained from the Marine Sciences Laboratory, Menai Bridge, N Wales and they were prepared either by dilution with distilled water or by evaporation over gentle heat (80–90°C). The following saline treatments were applied (0, 6, 11, 34, 68, 102‰), and each in triplicate. Thallus tissues were incubated for 48 h at selected temperatures and under artificial light of approximately $70 \mu\text{E m}^{-2} \text{sec}^{-1}$ (range 30–120) in 8 : 16 h photoperiods. The material was then transferred to ground-glass stoppered bottles (125cm^3

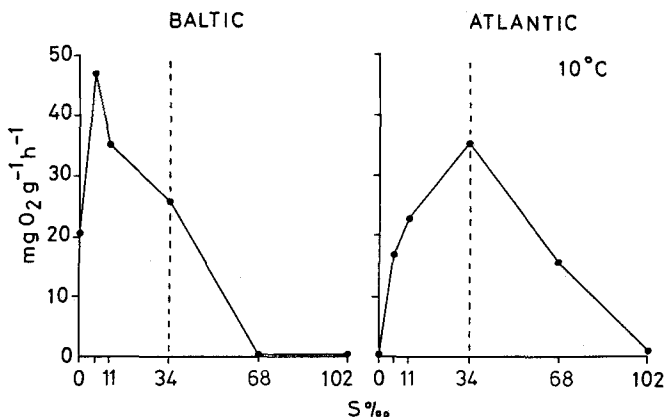


Fig. 2. Net oxygen production per g dry weight by *Chorda filum* tissues following treatment in waters of different salinities for 48 h at 10°C. The Baltic population was located at Tvärminne, SW Finland while that from the Atlantic was at Derbyhaven, Isle of Man

capacity) containing degassed seawater from the plants' natural locality, supplemented with NaHCO_3 ($5 \mu\text{mol}$). The bottles were then exposed to artificial light ($94 \mu\text{E m}^{-2} \text{sec}^{-1}$) for 2.5 h at 10°C . Finally, the tissues were removed and oven-dried while the oxygen content of the water was determined by standard Winkler technique (Strickland & Parsons, 1968), the amount of dissolved oxygen present being expressed in terms of tissue dry weight. This technique, which follows Russell (1987b) seems to register salinity damage quite effectively but may lead to artificially elevated productivity figures. The choice of photon flux densities and, to some extent, also temperatures was determined by growth-room availability at the two laboratories.

RESULTS

The responses of the two *Chorda* populations are shown in Figure 2. Maximum net production by the Atlantic plants was associated with treatment in 34‰, their natural salinity, while 0 and 102‰ were lethal. Baltic material was most productive when treated with water of its own natural salinity (6‰). The 0‰ (distilled water) medium, though harmful, was not lethal but material subject to 68‰ and 102‰ was killed. One-way ANOVA demonstrated that each population responded significantly (Atlantic, $p = 0.0002$; Baltic, $p < 0.0001$). The results of a two-way ANOVA are as follows: treatments $p < 0.0001$, populations $p = 0.007$, interaction $p < 0.0001$. It shows that the two populations differ significantly in their responses to treatment and that the interaction between these is also significant. These experiments were run at 10°C , a temperature which lies within the range of those experienced by the macrothallus in both localities.

The *Fucus* experiments were run twice, at 4°C and 18°C . The latter temperature approximates to the summer maximum at Tvärminne while the former is close to the minimum for growth of Baltic *Fucus* (Russell, 1985a). The results of these treatments are

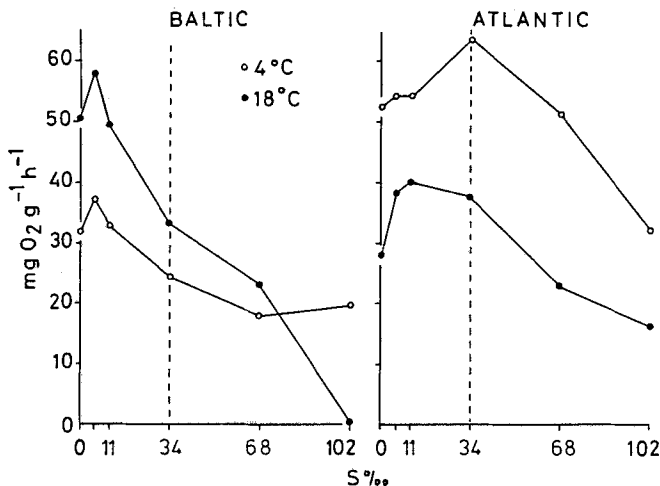


Fig. 3. Net oxygen production per g dry weight by *Fucus vesiculosus* tissues following treatment in waters of different salinities for 48 h at 4° and 18°C . The Baltic population was located at Tvärminne, SW Finland while that from the Atlantic was at Hilbre Island, NW England

Table 1. Two-way ANOVA of results of salinity experiments on Baltic and Atlantic populations of *Fucus vesiculosus* (see Fig. 3)

	4 °C	18 °C
Treatments	p < 0.0001	p < 0.0001
Populations	p < 0.0001	p = 0.004
Interaction	p < 0.0001	p < 0.0001

given in Figure 3. It can be seen that peak production by the Atlantic plants was associated with treatment in either 34‰ (4 °C) or 11‰ (18 °C) whereas Baltic material was consistently most productive at 6‰ and was harmed by all higher salinities. One-way ANOVA showed Atlantic material to have responded significantly at both temperatures (4 °C, $p = 0.0001$; 18 °C, $p = 0.0001$). The outcome of two-way ANOVA is given in Table 1, which shows the populations to differ significantly in their responses at both temperatures and in the interactions of these. Some differences are evident in the effects of temperatures, Atlantic thalli being more productive after treatment at 4 °C than at 18 °C, while the reverse is true of the Baltic population. Also, Baltic plants were less severely damaged by the highest salinity at 4 °C than at 18 °C.

DISCUSSION AND CONCLUSIONS

Between-species variation

It is evident that Atlantic *Fucus* is less susceptible to damage from saline extremes than Atlantic *Chorda* (Figs 2 and 3). This result is consistent with those already reported for a number of other intertidal and sublittoral species on Atlantic coasts (Biebl, 1952; Russell, 1987a). It is also a result which may be interpreted readily in terms of selection pressures, the intertidal region being one of more fluctuating salinities than the sublittoral zone (den Hartog, 1968). However, when the Baltic populations of these species are compared, it is equally clear that their responses have not been identical, despite the fact that they occupy the same habitat. In *Chorda*, net production is more seriously impaired by both fresh and strongly saline waters than is the case with *Fucus*. This anomaly is perhaps more apparent than real; the salinities of Baltic surface waters are not as uniform seasonally as those of Manx inshore waters (Fig. 1) and, during the spring ice-melt, they are liable to be very low indeed. *Fucus* as a perennial, is present as a macrophyte throughout the year but *Chorda*, an annual, passes the winter-spring period as a microthallus. Experiments on the salinity tolerance of Atlantic *Chorda* by Norton & South (1969) have shown that these microthalli may survive very low salinities. The macrothallus of Baltic *Chorda* is evidently less able to withstand 48 h of freshwater than Baltic *Fucus*, but then it occupies a seasonal niche in which the possibility of such an experience is remote.

The superior ability of Baltic *Fucus* to tolerate high salinities is an anomaly which is more real than apparent. However, it is possible that *Fucus* has a higher organic solute content which may enable it to survive both lower temperatures and higher salinities than the *Chorda* macrothallus. The fact that Baltic *Fucus* remained productive after treatment in 102‰ at 4 °C but not at 18 °C would be consistent with that.

Within-species variation

The population differences (Figs 2 and 3) have proved to be as pronounced as Powell (1963) has predicted. Atlantic *Fucus* has a broader salinity tolerance than the Baltic populations, the optimal salinities for which are skewed sharply to 6‰. The response curve of Baltic *Chorda* is similarly skewed and is strongly (negatively) correlated with the salt-tolerance curve proposed for Baltic algae by Russell (1987a). The latter was based upon observations of cell mortality in several species, all annuals. Atlantic *Chorda*, on the other hand, appears to behave like several other sublittoral algae from Atlantic coasts in showing evidence of tissue damage in salinities above and below 34‰ (Biebl, 1952; Russell, 1987a).

Atlantic *Chorda* also seems to be less productive in water of optimal salinity than Baltic material. This is not the case in *Fucus* in which the temperature effects outweigh any differences in productivity. In SW Finland, the *Chorda* thallus is depauperate (Russell, 1985b) whereas that of *Fucus* is not (Hällfors et al., 1981). The narrowness of depauperate *Chorda* ensures that it has a greater surface area: volume ratio, which may have contributed to differences in productivity. If so, the depauperate state may be an advantageous one in a severe environment with a short growing season. Caution is required, however. The productivity of depauperate Baltic *Fucus* has been shown recently to differ very little from that of Atlantic material by Raven & Samuelsson (1988). In any event, it may be concluded that Baltic populations of *Fucus vesiculosus* and *Chorda filum* differ in their responses to these treatments from conspecific plants on Atlantic shores and that these differences imply adaptations to prevailing salinity conditions. The answer to the first of the questions raised in the Introduction should therefore be an affirmative, subject to the reservations that the results of a short-term (48 h) experiment must require. The results point chiefly to the need for a programme of long-term experiments.

Nomenclatural recognition of variation

Powell (1963) supplied his own answer to this question by awarding taxonomic status to Baltic *Fucus vesiculosus*. Baltic populations of *Ceramium strictum* Harv. (= *C. tenuicorne* Waern) have likewise received taxonomic recognition from Rueness (1978). The *C. strictum* populations differ morphologically as well as in salt tolerance and are therefore comparable with those of *Chorda filum*. However, Powell (1963) has pointed out that mid-Baltic *Fucus* is not obviously different morphologically from some Atlantic material. Baltic *Fucus* appears to have smaller oogonia than Atlantic material (Russell, 1985a) and more critical morphological study may reveal further differences. At present, however, the major difference observed in this species is that of salt tolerance. This is a cryptic character, i.e. it is not expressed morphologically, but there is no obvious reason why cryptic attributes should be excluded from the taxonomic process even if it does raise questions about the utilitarian value of the preserved type specimen. The problem has been stated and answered very succinctly by Burt (1970) who makes the point that if diversity is observed and not formally recognised then it is liable subsequently to be overlooked. These Baltic marine algae are distinctive from their Atlantic counterparts so some kind of taxonomic recognition would appear justified.

Taxonomic rank

The awkwardness of this question is illustrated by the fact that Powell (1963) considered the rank of forma appropriate for Baltic populations of *Fucus vesiculosus* and Rueness (1978) the subspecies for those of *Ceramium strictum*. Article 4 of the International Code of Botanical Nomenclature lists five infraspecific ranks, the subspecies, varietas, subvarietas, forma and subforma, but prudently does not attempt to define them. The traditional definition of the forma as a variant which occurs sporadically throughout the geographical range of a species (Stace, 1980) makes this an inappropriate rank for the Baltic algae. The customary distinction of geographical and local patterns of variation in defining the subspecies and the varietas is now questionable. Patterns of dispersion of phenotypic and genetic variation in *Fucus* (Rice et al., 1985) and *Xiphophora* (Kennington, 1987) species are too complex to be expressed clearly by these ranks when defined as above. As more becomes known about the patterns of variation present in marine macroalgae, it will inevitably become more difficult to classify variants effectively by means of spatial distribution alone. However, they are the best definitions we have, and on the basis of a rather wide geographical distribution, Baltic populations of *Fucus vesiculosus* and *Chorda filum* are probably most correctly designated as subspecies.

Article 2 of the Code affirms the hierarchical structure of plant taxonomy and, in so doing, adds considerably to the problems of classification below the species level. Infraspecific variation frequently involves small differences in a few characters, and these rarely produce a credible hierarchy. Flowering-plant systematists seem to be increasingly of the opinion that variation within species is simply not hierarchical in character (Heywood, 1986). It must follow therefore that a system of more practical value is required, which can express observed patterns of variation. It is also desirable that any such system is regularized by incorporation into the Code (Stace, 1986). Some very interesting proposals are now available to us and others may be forthcoming (see Styles, 1986). Perhaps we should be adopting a similarly positive approach to variation in algae before the volume of published information becomes too great to handle.

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