

## BRACKISH WATER AS AN ENVIRONMENT FOR ALGAE

C. DEN HARTOG

### 1. THE CONCEPT 'BRACKISH WATER'

The term 'brackish water' is used in several senses and, therefore, I want at first to explain what I consider to be brackish water and what not. Redeke (1933) defined brackish water as a mixture of fresh water and sea water *sensu stricto*. This definition excludes the continental salt waters which have a different origin. There exist, however, salt waters which have lost long ago their contact with the sea and have now a chemical composition completely aberrant from sea water, due to the joint effect of continual inflow of new electrolytes with river water, evaporation, and precipitation. As examples the Caspian and the Aral Sea may be mentioned.

Other investigators prefer to include on grounds of hydrological and hydrochemical similarities also the continental salt waters which at no time in their history have been in contact with the sea, e.g. the Great Salt Lake in Utah, U.S.A. They regard as brackish all salt waters which have a lower salinity than the sea. According to Schmitz (1959) the differences between the continental and marine salt waters are only of a relative value as both categories have the following four hydrological characters in common:

1. The total salinity is generally between that of fresh and sea water.
2. The waters show often salinity stratification.
3. Horizontal differences in salinity occur e.g. where a river discharges in a salt lake.
4. Large seasonal fluctuations in salinity occur.

These characters stress the unstable conditions which govern the salt waters. They have to be regarded as *poikilohaline* in contrast to the *homoiohaline* environments: the sea and the fresh water (Dahl, 1956).

From a hydrochemical point of view the marine brackish waters and the continental salt waters form a series without clearly separated categories. Where sea water is diluted with fresh water poor in electrolytes the Knudsen tables can be applied without reserve. Where sea water mixes with fresh water rich in electrolytes, these tables cannot be used without corrections. For NaCl the deviation amounts to 0.1‰, but for ions that occur in small quantities in sea water, e.g.  $\text{Ca}^{++}$ , the Knudsen tables cannot be applied any longer. The deviations increase with the decrease of the marine influence. In the relict brackish waters which have lost their contact with the sea in former geological periods, the Knudsen principle cannot be used for the NaCl either, and it is evident that it cannot be used for the continental salt waters in which often other salts than NaCl predominate.

On grounds of hydrological and hydrochemical characters it seems difficult to separate the continental and marine salt waters, especially as there are so many intermediate cases. From the biological point of view, however, the separation between the two categories is very evident. The marine salt waters are characterized by a marine element in their flora and fauna, which is absent in the continental salt waters. Even in the relict marine waters the marine element is still very pronounced (see e.g. Zenkevitch, 1963).

If we regard as brackish only the waters of marine origin, the definition that brackish water is in fact diluted sea water has, nevertheless, to be reconsidered. There are several waters with a salinity higher than the sea, the so-called *hyperhaline* or *metahaline* waters. These hyperhaline waters have also to be regarded as brackish, as their flora and fauna are in fact an impoverished reflection of those of the diluted sea water (Hedgpeth 1959). There are many transitions between the hyperhaline and *mixohaline* waters. Often the situation is found that a water has in the dry period a salinity higher than the sea, while in the wet period the salt-content decreases to an amount below that of the sea.

The waters can thus be subdivided according to the degree of stability of their salt-content in:

- A. Homoiohaline waters which have a practically constant salinity:
  1. Sea water.
  2. Fresh water.
- B. Poikilohaline waters in which the salinity is subjected to periodical and/or occasional fluctuations:
  1. Brackish waters of marine origin, and in which NaCl is consequently the predominant salt. The flora and fauna show an important marine element:
    - a. Diluted sea water (*mixohaline*).
    - b. Concentrated sea water (*hyperhaline*).
  2. Continental salt waters which have never been in contact with the sea. The principal salt may be NaCl,  $\text{MgSO}_4$ ,  $\text{Na}_2\text{CO}_3$ , etc. The flora and fauna are derived from terrestrial and fresh-water ancestors (Hedgpeth, 1959; Schmitz, 1959).

A definition of brackish water has to be put as follows: *Brackish water is water with an unstable salinity and the salt of which originates mainly from the sea.*

## 2. THE ENVIRONMENT 'BRACKISH WATER'

The flora and fauna of the brackish water are poor in species in comparison with those of the sea and the fresh water. Most of the marine organisms are stenohaline and are unable to live permanently in water with a higher or lower salt-content than the sea. The number of fresh-water organisms that are able to tolerate a somewhat higher salinity is not great either. The set of true brackish-water species which generally do not occur in the sea or in fresh water, is small, and greatly outnumbered by the euryhaline marine and salt-tolerant fresh-water species which inhabit the brackish water.

The euryhaline marine species can tolerate a considerable dilution of the sea water and occupy the whole range between sea and fresh water. The fresh-water species, in contrast, do not penetrate far into the brackish water, and, therefore, seem less euryhaline. We have to realize, however, that a marine species which can tolerate a dilution of its medium to half the concentration, is able to live in brackish water of 8‰ Cl'. A fresh-water species which lives in slightly brackish water with a salinity of 0.6‰ Cl', has to cope with at least the double salt concentration of the fresh-water medium. Seen in this light, fresh-water species which are able to live in water of 2‰ Cl' are in fact as euryhaline as marine species which live in water of the same concentration. Therefore, the absolute species minimum in the brackish range is not situated halfway between sea and fresh water, but is shifted considerably in the direction of the fresh water (see also Remane, 1934, 1940, 1958).



Plate 1. The vegetation of fresh-water trickles which cross the intertidal belt is subjected during each tidal period to enormous and sudden salinity fluctuations. During the period of emergence the vegetation is exposed to fresh water flowing off from the shore, but when it is reached again by the rising tide it becomes covered with almost pure sea water. *Fucus ceranoides* inhabits this shock habitat, especially when silt is deposited, together with various *Enteromorpha* species. Roscoff, September 1959.



Plate 2. The Terluchtse Weel near Goes (Netherlands) lost its contact with the sea in 1831. It is now a brackish-water pond with an annual salinity fluctuation between 5 and 15 ‰ Cl'. Its algal vegetation is extremely poor and consists of a few euryhaline *Chlorophyceae* and *Cyanophyceae*. The muddy bottom is predominantly covered by *Ruppia spiralis* and reef formations of the bryozoan *Electra crustulenta*. July 1959.



Plate 3. *Pelvetia canaliculata* and *Fucus spiralis* form conspicuous belts in the upper part of the eulittoral along the Atlantic coast of Europe. Although exposed to large fluctuations in salinity, as a consequence of weather conditions during the period of emergence, the two species do not penetrate into other brackish-water habitats. Roscoff, August 1959.



Plate 4. On the exposed and sand-swept boulder beach near Le Havre the vegetation does not pass through the pioneer stage. It is mainly composed of *Enteromorpha compressa* and *Porphyra umbilicalis*, while coenoses of the barnacles *Balanus balanoides* and *Elminius modestus* cover the spaces left free by the algae. September 1959.

It appears from this point of view that marine species are in a much more favourable position for colonization of the brackish water than fresh-water species. Indeed the brackish-water communities have a pronounced marine character.

The most important factor which controls the composition of the flora and fauna of the brackish water is the instability of the salt-content. The fluctuations in salinity, their amplitude, and their period are limiting factors for many species. This may be illustrated by the following examples.

In an estuary the benthic algae and animals are subjected to considerable daily fluctuations in salinity due to the tidal rhythm, and to an as important seasonal fluctuation which depends on the discharge of river water. Particularly in the mid-estuarine section the fluctuations are enormous, and form an effective barrier for many euryhaline marine species and for all fresh-water organisms. The fresh-water element is hardly represented in the benthos of an estuary. The boundaries of the species in an estuary are obviously determined by their more or less developed ability to adapt themselves to the rhythm of the salinity fluctuations.

In the Baltic, where salinity is rather stable and is subjected only to a relatively small, annual fluctuation, the boundaries of the species, so far as they are determined by salinity, coincide more or less with their absolute salt tolerance (Den Hartog, 1964). The effect of the salinity fluctuations on the distribution of organisms appears clearly from table 1, in which the lowest average salinity values are given at which some euryhaline species have been found in the Dutch estuaries and in the Baltic.

TABLE 1: Lowest average Cl'-content in ‰, at which some euryhaline marine algae have been found in Dutch estuaries and the Baltic.

|  | estuary          | Baltic Sea |
|--|------------------|------------|
| <i>Chlorophyceae:</i>                                    |                  |            |
| <i>Blidingia minima</i> (Näg.) Kylin                     | into fresh water | 3          |
| <i>Cladophora rupestris</i> (L.) Kütz.                   | 14               | 3          |
| <i>Rhizoclonium riparium</i> (Roth) Harv.                | into fresh water | 1.1        |
| <i>Phaeophyceae:</i>                                     |                  |            |
| <i>Fucus vesiculosus</i> L.                              | 2                | 2          |
| <i>Elachista fucicola</i> (Vellay) Aresch.               | 14               | 2          |
| <i>Sphacelaria plumigera</i> Holmes                      | 16.5             | 3          |
| <i>Sphacelaria britannica</i> Sauv.                      | 16.5             | 3          |
| <i>Chorda filum</i> (L.) Stackh.                         | 14               | 1.6        |
| <i>Rhodophyceae:</i>                                     |                  |            |
| <i>Bangia fuscopurpurea</i> (Dillw.) Lyngb.              | into fresh water | < 1        |
| <i>Rhodochorton purpureum</i> (Lightf.) Rosenv.          | 13               | < 1        |
| <i>Phyllophora membranifolia</i> (Good. & Woodw.) J. Ag. | 14               | 3          |
| <i>Callithamnion roseum</i> (Roth) Lyngb.                | 7                | 3          |
| <i>Polysiphonia nigrescens</i> (Huds.) Grev.             | 14               | 2          |
| <i>Hildenbrandtia prototypus</i> Nardo                   | 2                | < 1        |

Among the species, given in table 1, *Fucus vesiculosus* is the only one which has the same salinity boundary in the estuaries and in the Baltic. In the estuaries the species is in winter often subjected to pure fresh water, sometimes for several weeks. With decreasing salinity the plants become smaller in size and also the number of air-bladders becomes reduced. Near the salinity boundary the air-bladders are completely absent. The plants maintain, however, the characteristic habit of the species and form even receptacles except in the immediate neighbourhood of the salinity boundary. In spring the plants mostly look very poorly developed, but in the course of summer, when the salt-content of the water is higher, the plants recover markedly (Draayer, unpubl.). It is noteworthy that these estuarine pessimum forms of *F. vesiculosus* are strictly intertidal. In the Baltic *F. vesiculosus* shows a similar morphological plasticity, but there the species becomes sublittoral and occurs at depths between 4 and 15 m (Waern, 1952).

*Bangia fuscopurpurea* and *Rhizoclonium riparium* penetrate in the Dutch estuaries not only into the fresh-water tidal section but occur also in polluted stations in the tideless rivers. In the northern Baltic these species do not invade the fresh water; this may be ascribed to the poverty in electrolytes of the latter. For *Blidingia minima*, which belongs to the same ecological group, the innermost occurrence in the Baltic is not yet known, but anyway it occurs below 3 ‰ Cl'. Although *Rhodochorton purpureum* has not been found in the estuaries at an average salinity below 13 ‰ Cl', it occurs in the Baltic even in water with an average salinity below 1 ‰ Cl'. It tolerates submersion in fresh water for a considerable period.

In most cases the algal species disappear in the estuaries after a rather slight decrease of the average salinity, while in the Baltic the same species are normal constituents of the brackish-water vegetation.

In inland brackish waters, such as pools and ponds, which are permanently or temporarily isolated from the sea, the annual salinity fluctuations are mostly considerable, but the daily fluctuations are negligible (plate 2). Here the salinity changes depend on precipitation, evaporation, depth, seepage, and human interference (e.g. the maintenance of a certain water level). The minimum and maximum salinities determine which species

TABLE 2: Lowest average Cl'-content in ‰ Cl' at which some euryhaline marine algae have been found in estuaries and coastal inland brackish waters in the Netherlands.

|  | estuary | coastal inland water |
|--|---------|----------------------|
| <i>Chlorophyceae:</i>                          |         |                      |
| <i>Ulva lactuca</i> L.                         | 10      | 9.5                  |
| <i>Chaetomorpha linum</i> (O. F. Müll.) Kütz.  | 10      | 7.7                  |
| <i>Bryopsis plumosa</i> (Huds.) Ag.            | 12      | 8                    |
| <i>Rhodophyceae:</i>                           |         |                      |
| <i>Ceramium rubrum</i> (Huds.) J. Ag.          | 14      | 9.5                  |
| <i>Polysiphonia urceolata</i> (Lighthf.) Grev. | 10      | 3                    |
| <i>Polysiphonia nigrescens</i> (Huds.) Grev.   | 14      | 10                   |
| <i>Callithamnion roseum</i> (Roth) Lyngb.      | 7       | 10                   |
| <i>Chondrus crispus</i> Stackh.                | 14      | 10                   |

can occur and which not. In this connection the duration of extreme circumstances and the time of the year in which they take place are of great importance. Other factors may be involved as well in the limitation of the flora and fauna of isolated brackish waters, e.g. deficit in oxygen, development of  $H_2S$ , and fluctuations in temperature. Generally speaking the ecological conditions are more extreme than in estuaries, except for the fact that the daily salinity fluctuations are small. The vegetation consists mainly of euryhaline species of the genera *Ulva*, *Enteromorpha*, *Monostroma*, *Chaetomorpha*, and *Cladophora*. Where some exchange with sea water can take place the vegetation is much richer in species than in completely isolated waters with corresponding salinity values. The salinity boundaries of a number of organisms are different in estuaries and in isolated brackish waters. In the latter they can occur generally at lower average salinity than in the estuaries (see table 2).

### 3. MAIN BRACKISH HABITATS

It appears that in each of the main brackish habitats discussed the instability of the salt-content follows its own pattern, and thus exercises its influence on plants and animals in its own way. Two factors are of importance for the degree of instability: 1) the continuity or discontinuity of the transition between sea and fresh water; 2) the periodicity of the salinity fluctuations.

With help of these two factors, it is possible to recognize 9 main brackish habitats, which are found in nature (Den Hartog, 1964):

- A. A continuous and gradual transition between the sea and the fresh water.
  1. A very gradual transition, with very slight annual fluctuations in salinity occurs in brackish seas, e.g. in the Baltic.
  2. A continuous transition between sea and fresh water, but with considerable annual salinity fluctuations occurs in river mouths, not subjected to the tides.
  3. In estuaries daily salinity fluctuations occur of which the period depends on the tidal rhythm, and annual fluctuations, caused by the seasonal change of the fresh-water discharge. The same conditions, although less pronounced, prevail in sheltered bays and shallow coastal waters, e.g. in the Dutch Waddenzee. Although these are not estuaries in the strict sense, I regard them as estuarine habitats as their flora and fauna are very similar.
- B. A continuous but sudden transition between the sea and the fresh water.
  4. Small fresh-water streams and trickles which discharge into the sea are subjected in the intertidal belt during each tidal cycle twice to a sudden salinity shock from a minimum to a maximum and vice versa. Between this 'shock biotope' and the estuaries occur transitional cases. The main difference is that in the shock biotope the quantity of fresh water may be almost neglected as soon as it mixes with the sea water (plate 1).
- C. Temporary or permanent blocking of the transition between sea and fresh water.
  5. Supralittoral pools which are within the reach of spring tides. In these waters salinity is determined by precipitation, evaporation, and salt spray water, but during the periodic or episodic submersion salinity is adjusted again to the marine salinity level. Many pools are not reached by the sea in summer and it is completely dependent on the climate whether they get a fresh-water character (e.g. along the northern Atlantic coasts) or a hyperhaline character (e.g. along the Mediterranean coast) or dry out.

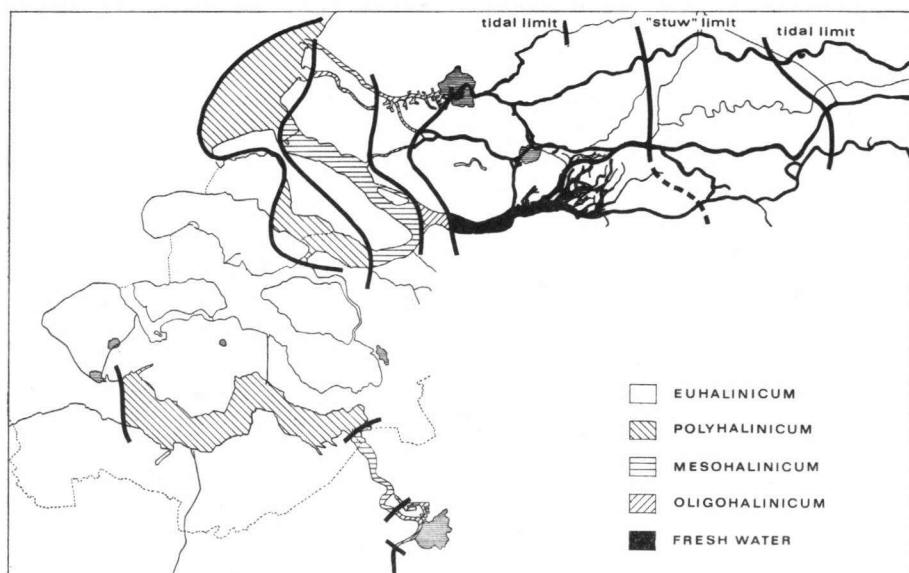


Fig. 1. The deltaic region of the rivers Rhine, Meuse, and Scheldt, subdivided according to the composition of the biocoenoses.

6. In lagoons, 'étangs', and ponds, ditches and former creeks now situated within the dikes, the direct influence of the sea is completely blocked or the exchange of water is limited or regulated by sluices, culverts, etc. (plate 2). The salinity cycle in these waters is annual, but may be very different even in adjacent waters. The effect of such climatic factors as precipitation and evaporation is in a high degree dependent on topographical factors as depth and exposure to the prevailing wind direction. In shallow ponds the salinity may rise far above that of the sea during dry summers (D'Ancona, 1959; Petit & Schachter, 1959).
7. Relict brackish waters, e.g. Caspian, Aral Sea (Zenkevitch, 1963).
- D. Other brackish situations.
  8. The intertidal belt (plate 3) in which the flora and fauna are subjected to precipitation and evaporation during the emersion period has to be considered a brackish habitat (Dahl, 1956, 1959).
  9. The coastal ground water.

It has to be stressed that transitional cases between the defined main habitats and also complex situations (e.g. shallow pools in the eulittoral belt of an estuary) are not rare features in nature.

Although these main habitats are very unequally proportioned it appears that most of them are well-characterized by faithful indicator species which do not or hardly occur in the other habitats. The smaller-sized habitats which are at the same time the most extreme ones, show in this respect the most pronounced specialization.

In the supralittoral pools many highly characteristic *Chlorophyceae* occur, e.g. species of the genera *Brachiomonas*, *Platymonas*, *Asteromonas*, and *Dunaliella*. In the estuarine waters some diatoms, e.g. *Coscinodiscus commutatus* and *Chaetoceros radians* are good



indicator species. From the sessile algae *Fucus ceranoides* is limited to a very special habitat viz. small estuaries and transitions of these to the shock biotope.

Of course there are also true brackish-water taxa which occur in more than one main habitat. *Ectocarpus confervoides* f. *fluviatilis* is not uncommon in the northern part of the Baltic Sea, but it is also present in the canals and ports of Amsterdam and in the mid-estuarine section of the mouths of the rivers Rhine, Scheldt, Weser, and Severn. *Capsosiphon fulvescens* occurs in the upper part of the intertidal belt of estuaries and the open sea coast, but also in the shock biotope.

Several of the main habitats can be subdivided into finer units, according to the composition of the biocoenoses, which are correlated with the average salinity (Redeke, 1922, 1933; Välikangas, 1933; D'Ancona, 1954; Hedgpeth, 1957; Remane & Schlieper, 1958; Venice System, 1959; Den Hartog, 1960, 1961).

This will be demonstrated by means of the distribution of the algae in the estuaries of the south-western part of the Netherlands.

#### 4. DISTRIBUTION OF ALGAE IN DUTCH ESTUARIES

In the estuaries of the Dutch Deltaic area a gradual transition occurs between the sea and the fresh water over a distance of 40 to 70 km (Den Hartog, 1961, 1963; fig. 1). In the most seaward situated part the water is fully marine, although sometimes a short-lasting decrease in salinity occurs when the amount of discharged river water is very large. The marine biocoenoses are of the normal composition, with a well-developed fucoid zonation and a sublittoral zone with *Codium fragile*, *Hypoglossum woodwardii* (fig. 2), *Dictyota dichotoma*, *Giffordia mitchellae*, *Sphacelaria plumigera*, *Antithamnion cruciatum*, *A. plumula*, *Griffithsia devoniensis*, *Callithamnion byssoides*, *Polysiphonia nigrescens*, *P. elongata*, *P. denudata*, etc. In more exposed stations *Petalonia zosterifolia*, *Polysiphonia urceolata*, and *Ceramium deslongchampsii* are more frequent species. According to Dutch standards the vegetation is 'rich' in species (Den Hartog, 1959, 1962). In comparison with other coasts it is, however, poor. This may be ascribed to the absence of rocky and stony bottoms. The only available substrates for epilithic algae are the dikes and shells of oysters, mussels, and other lamellibranchiates. As a result of the small depth and the partial exchange of sea water in the Eastern Scheldt, the difference between the water temperatures in summer and winter is extremely large: c. 20° C. In this connection it is interesting that the many species with southern distribution, which occur in the Deltaic region, are without exception summer annuals.

Further upstream in the estuaries the vegetation changes gradually, as the species disappear in sequence of their degree of euryhalinity. The fucoids, except *Fucus vesiculosus*, disappear already before the 10‰ Cl' isohaline at high tide.

Instead of the fucoids *Chlorophyceae*, as *Ulothrix* and *Enteromorpha* species, become more important, but a new positive element could not be ascertained as far as the algal vegetation concerns. This section of the estuary, in which the decrease of marine species takes place, has been indicated as the *polyhalinicum*. The upstream border of this section has been established as being c. 10‰ Cl'. Most algae do not reach this border because there is also an edaphic barrier caused by increase of silt deposition.

The *mesohalinicum* is the section of the estuary between the isohalines of 10‰ and 1.8‰ Cl' at high tide. Only the very euryhaline marine species are left: *Hildenbrandtia prototypus*, *Callithamnion roseum*, *Fucus vesiculosus*, *Ulothrix flacca*, *Rhizoclonium riparium*, *Enteromorpha* species, *Blidingia minima*, *Monostroma oxyspermum*, and a few others. They are able to stand the enormous daily salinity fluctuations which prevail in this section.

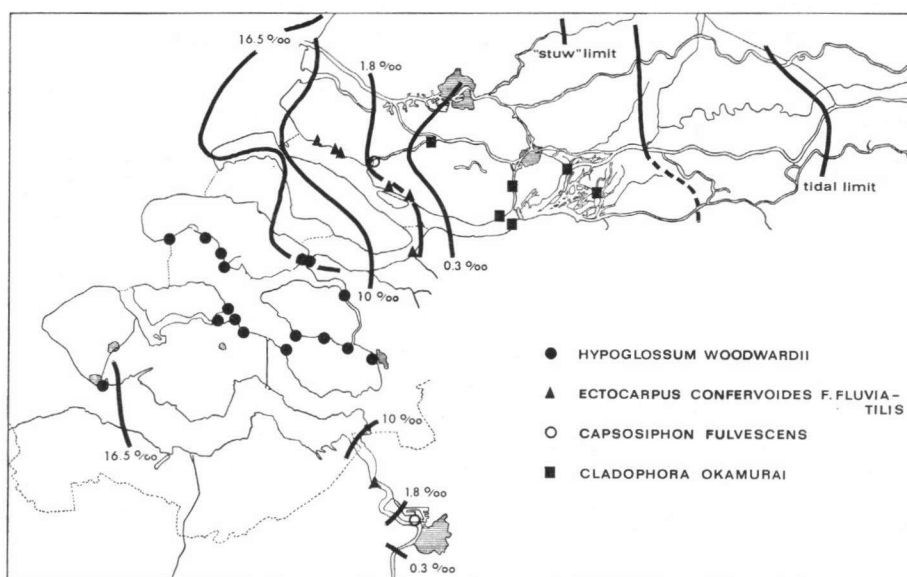


Fig. 2. Distribution of *Hypoglossum woodwardii*, *Ectocarpus confervoides* f. *fluviatilis*, *Capsosiphon fulvescens*, and *Cladophora okamurai* in the deltaic region of the rivers Rhine, Meuse, and Scheldt. Under the estuarine conditions of this area *Hypoglossum woodwardii* is an indicator species for the euhalinicum, *Ectocarpus confervoides* f. *fluviatilis* is limited to the mesohalinicum, *Capsosiphon fulvescens* is faithful to the oligohalinicum, and *Cladophora okamurai* to the fresh-water tidal area. The average annual isohalines at high tide of 0.3 ‰, 1.8 ‰, and 10 ‰ Cl' are given.

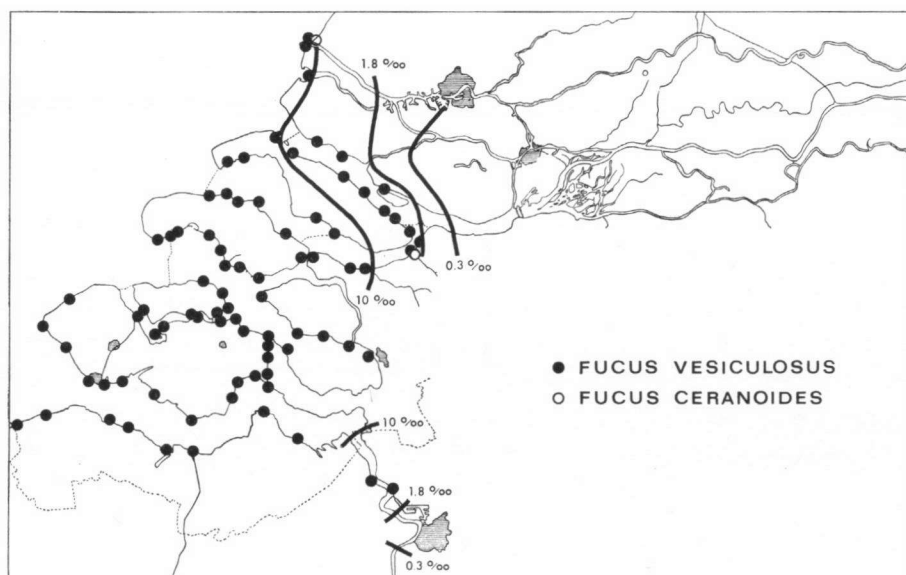


Fig. 3. Distribution of *Fucus vesiculosus* and *Fucus ceranoides* in the deltaic area of the rivers Rhine, Meuse, and Scheldt. *F. ceranoides* is restricted to the localities where the largest salinity fluctuations during one tidal cycle occur. The average annual isohalines at high tide of 0.3 ‰, 1.8 ‰, and 10 ‰ Cl' are given.

As a positive element some true brackish-water taxa join this group, viz. *Ectocarpus confervoides* f. *fluviatilis* (fig. 2) and *Fucus ceranoides* (fig. 3), the latter only under very special ecological circumstances. At c. 2 ‰ Cl' *Ectocarpus confervoides* f. *fluviatilis*, *Hildenbrandtia prototypus*, and *Fucus vesiculosus* (fig. 3) reach their most upstream stations.

Here the oligohaliticum begins. The following euryhaline marine species are present in large numbers: *Blidingia minima*, *Enteromorpha* species, in particular *E. compressa*, *Ulothrix flacca*, *Rhizoclonium riparium*, and *Monostroma oxyspermum*. This group is joined by a rare brackish-water species, *Capsosiphon fulvescens* (fig. 2). The fresh-water element is not represented by any algal species, but exclusively by animals.

Although the 0.3 ‰ Cl' line, which is considered the fresh-water limit, is indeed a very abrupt boundary in the estuaries, this does not mean that it is the most upstream border reached by the marine element. *Blidingia minima* (fig. 4) and *Rhizoclonium riparium* occur plentifully in the fresh-water tidal area. The latter extends even in the tideless rivers and then is known as '*R. hieroglyphicum*'. The number of fresh-water algae in the fresh-water tidal area is yet rather limited. Among them the unbranched *Cladophora okamurai* (fig. 2) seems to be characteristic for this area.

The plankton in an estuary shows also a series of communities between the sea and the tideless river. The areas of these communities coincide under average conditions more or less with the sections which were already distinguished for the benthic algae, but under influence of the tidal currents they shift continually to and fro. During a dry spell, when the discharge of river water is small, the series can be shifted upstream for more than 20 km, while the reverse happens when the rivers are swollen. Contrary to the benthos the plankton of the estuary contains many fresh-water forms which, however, are for the larger part allochthonous. The marine element is also well-developed, but the brackish-water species occur only in the warmest period of the summer.

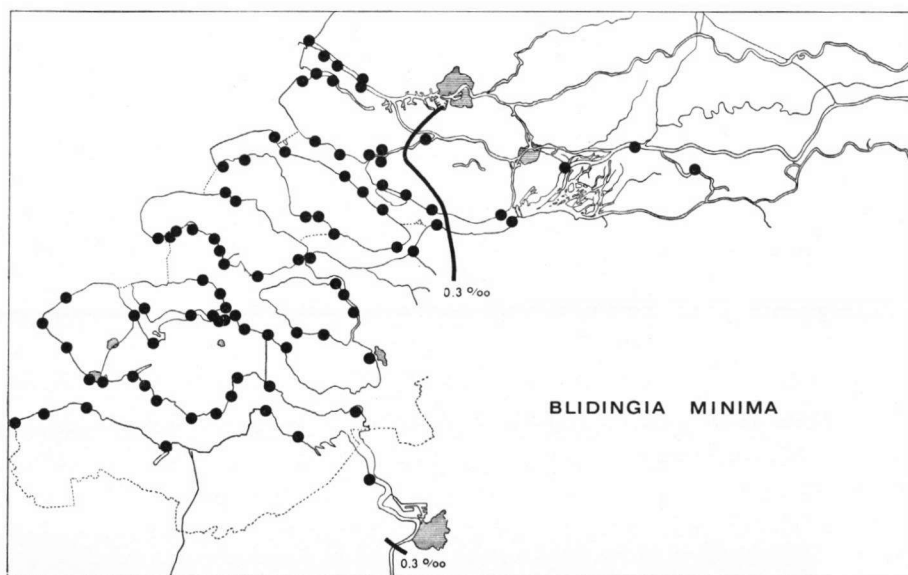


Fig. 4. Distribution of *Blidingia minima* in the deltaic area of the rivers Rhine, Meuse, and Scheldt. The average annual isohaline at high tide of 0.3 ‰ Cl', which is regarded as the boundary between fresh and brackish water, is given.

Schulz (1961) found in the river Elbe that the polyhalinicum is dominated by a community of euryhaline marine species, with a few true brackish-water organisms, e.g. *Chaetoceros radians*. The mesohalinicum is characterized by a community of euryhaline marine species and euryhaline fresh-water species, in which during the summer true brackish-water species come to dominance, e.g. *Coscinodiscus commutatus*.

A poor community of mainly euryhaline fresh-water species, in which the brackish-water element is represented by the dominance of the rotifer *Synchaeta bicornis*, is characteristic for the oligohalinicum. The decline in the quantity of algae in this section coincides more or less with the estuarine turbidity zone.

The fresh-water tidal area is characterized by a rich community of fresh-water algae, of which the centric diatom *Actinocyclus normanii* is the dominant species. This diatom has often been regarded as a brackish-water species. Indeed, there is no doubt as to its marine origin, as all its close relatives are marine. However, its sporadic and no doubt allochthonous occurrence in the brackish part of the estuary seems to me just an indication that by evolution it has become a fresh-water species which is able to maintain itself in large numbers in an unstable limnetic habitat, such as the tidal fresh water, but has not succeeded in penetrating into the more stable lacustrine habitats.

This series of plankton communities has been found only partially in the estuaries of the Dutch Deltaic area. In the Haringvliet a well-developed oligo- and mesohaline plankton has not been found, although it could have been expected there. This probably has to be ascribed to the disturbing effect of the Volkerak flood-water (Den Hartog, 1961). The flood remainder of the Volkerak is transported back to sea via the Haringvliet, which causes the paradoxical situation that the most landward situated part of this estuary is more saline than the more seaward situated part, and that on the north-eastern coast of the island of Goeree-Overflakkee the salinity at low tide is higher than at high tide.

In the former Zuyder Zee the same series of plankton communities as in the Elbe occurred.

##### 5. EURYHALINE MARINE SPECIES OR BRACKISH-WATER SPECIES?

One of the most obvious features in the estuaries is that a number of euryhaline marine species occurs at very low average salinities, and that some of them penetrate even into the fresh water. We may wonder whether these species have to be regarded as marine or as brackish-water species. This question has been raised already by Dahl (1956) for some animals with a similar behaviour. According to him 'the essential difference between a brackish-water species and an euryhaline marine species is that the brackish-water species seems unable to establish itself successfully in a stable marine environment, even if its salinity tolerance would not prevent it from doing so. It appears as if figuratively speaking they have to pay for their great tolerance to various environmental variations by a reduced power of competition in stable habitats where more stenotopic animals are able to thrive.'

When we now consider the group of extremely euryhaline algal species which occur from the fully marine coast to the fresh water in the light of Dahl's ideas, then we can notice the following features:

1. Most of the extremely euryhaline species occur along the sea coast in the upper part of the eulittoral belt, or even in the supralittoral where, due to the long periods of emersion, the fluctuations for every ecological factor, and thus also for salinity, are large.

2. Many of them occur, often as dominants, in stations which are influenced by fresh water, e.g. in trickles on the beach, near sluices, and in estuaries.
3. Most of them are able to form closed vegetations in stations, where the original vegetation has been destroyed, and they are often the first species on new substrates. However, they are soon ousted by more specialized algae. Only in very extreme and unstable biotopes, e.g. boulder beaches (plate 4), bird-rocks, or sand-washed rocks their growths may be permanent.

It is clear that the optimum of these species in nature is certainly not in the marine environment, where they are limited to the most extreme habitats. In the brackish water where they are not subjected to competition with more specialized stenohaline forms, they are able to colonize the whole intertidal belt, and some of them grow even below low-water-mark. The fact that an euryhaline species as *Blidingia minima* is dominant in the upper part of the eulittoral belt of the fresh-water tidal area, must be ascribed to the absence of competition. Epilithic fresh-water algae which can colonize the intertidal belt and are adapted to the tidal rhythm, do not seem to exist. Between the *Blidingia minima* belt and the belt of *Cladophora okamurai* always a bare belt has been found.

The fact that many euryhaline marine species which are common in estuaries and other brackish waters along the sea coast are strictly limited to the eulittoral belt, brought Dahl to the conclusion that this belt has to be regarded as a brackish-water habitat too. Indeed the eulittoral is subjected to salinity changes under influence of precipitation and evaporation. The salinity fluctuations are at a minimum at low-water-mark, and at a maximum at high-water-mark, the average salt-content shows under our climatic conditions a slight decrease in the direction of high-water-mark. If the tidal rhythm was absolutely regular the decrease of salinity and the increase of maximum and minimum values of the salt-content between low- and high-water-mark could be expressed by very smooth curves. However, the tidal rhythm is the resultant of the attractive power of the moon and that of the sun. These powers periodically intensify and weaken each other and are expressed in the tidal cycle by the daily inequality, the neap and spring tides, and by seasonal differences in the tidal amplitude. Moreover, local conditions may exercise an important influence on the course of the tidal curve. Thus the hypothetical smooth curve, of which I spoke, appears to be somewhat vacillating, as a consequence of the daily inequality, and shows even two pronounced discontinuities at about the levels of mean high-water neap and mean low-water neap.

The part of the intertidal belt above the level of mean high-water neap, is submerged for a short time only by sea water and its salinity is highly dependent on the weather conditions. It is the belt with the largest fluctuations. The algae in this belt must be very euryhaline, and many of them have a wide distribution in all kinds of brackish waters. Others, however, are strictly intertidal and do not invade the other brackish habitats, e.g. *Pelvetia canaliculata* and *Fucus spiralis* (plate 3).

The part of the intertidal belt between the levels of mean high-water neap and mean low-water neap is covered and uncovered during every tidal period. The salinity fluctuations due to the weather conditions in the period of emersion are of short duration, and cannot become very extreme. Most algae of this belt penetrate to some extent into the polyhaline section of the estuary. The extremely euryhaline marine algae which have a wide distribution in brackish waters are limited to unstable and exposed stations in this part of the intertidal belt.

The part of the intertidal belt below the level of mean low-water neap, is only exposed for short periods and the effect of weather conditions on the salinity is only small, but

cannot be neglected. Coincidence of low water and pouring rain can have a catastrophic effect on the algal growth killing off stenohaline forms; in particular *Griffithsia*, *Cryptopleura*, *Lomentaria*, and many of the tiny *Rhodophyceae* do not tolerate a sudden dilution of their medium.

When we return now to the question whether the extremely euryhaline species have to be regarded as brackish-water organisms or as marine ones, it appears that the answer has to be given for every species separately. We can regard as brackish-water species those species whose occurrence is indeed an indication for a conflict situation between the sea and the fresh water. This is the case with *Blidingia minima*, *Rhizoclonium riparium*, *Monostroma oxyspermum*, and many *Vaucheria* species. Other species occur also with great abundance in situations where other factors cause instability, e.g. where the substrate is continually moving under the influence of strong currents, and on boulder and pebble bottoms. They are always the first pioneers on new substrates. These species may be regarded as indicators for instability of the ecological circumstances. Examples are *Enteromorpha compressa* and *Ulothrix flacca* which are common in brackish water and penetrate into the estuaries up to the fresh-water limit. In the marine environment they colonize many habitats where the influence of the fresh water is negligible.

The species which normally inhabit the middle part of the intertidal belt and which penetrate into the estuaries, give no difficulties. They become impoverished with decreasing salinity, e.g. *Fucus vesiculosus*. These species are without any doubt euryhaline marine.

## 6. CONCLUSION

In this paper I have tried to demonstrate that brackish water is not really a homogeneous environment, but rather a collective name for a number of very different, well-defined habitats which have in common unstable salinity conditions. Each of these habitats represents a special conflict situation between sea and fresh water, having its own ecological features and its own biocoenoses, and being characterized by faithful indicator species. The instability of the salt-content of these habitats can be caused by changes within the same body of water by precipitation and evaporation (e.g. in stagnant waters), by periodic replacements of water masses (e.g. in estuaries), by alternate exposure to sea water and fresh water (e.g. in the 'shock habitat'), or by alternate submersion and emersion (e.g. in the intertidal belt).

## REFERENCES

- D'ANCONA, U. 1954. Fishing and fish culture in brackish-water lagoons. F.A.O. Fish. Bull. 7 (4): 1—28.
- 1959. The classification of brackish waters with reference to the North Adriatic lagoons. Archo Oceanogr. Limnol. 11 Suppl.: 93—109.
- DAHL, E. 1956. Ecological salinity boundaries in poikilohaline waters. Oikos 7: 1—31.
- 1959. Intertidal ecology in the terms of poikilohalinity. Archo Oceanogr. Limnol. 11 Suppl.: 227—237.
- HARTOG, C. DEN. 1959. The epilithic algal communities occurring along the coast of the Netherlands. Wentia 1: 1—241.
- 1960. Comments on the Venice-system for the classification of brackish waters. Int. Rev. ges. Hydrobiol. 45: 481—485.
- 1961. Die faunistische Gliederung im südwestniederländischen Deltagebiet. Int. Rev. ges. Hydrobiol. 46: 407—418.
- 1962. Fycologische Notities, 1. *Sphacelaria plumigera* in Zeeland. Gorteria 1: 81—84.
- 1963. The amphipods of the deltaic region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area, Pt 1. Introduction and hydrography. Netherl. J. Sea Res. 2: 29—39.
- 1964. Typologie des Brackwassers. Helgol. Wiss. Meeresunters. 10: 337—390.

- HEDGPETH, J. W. 1957. Biological aspects, in Chapter 23; Estuaries and Lagoons. Mem. Geol. Soc. Amer. 67 (1): 693—729.
- 1959. Some preliminary considerations of the biology of inland mineral waters. *Archo Oceanogr. Limnol.* 11 Suppl.: 111—141.
- PETIT, G., & D. SCHACHTER. 1959. Les étangs et lagunes du littoral méditerranéen français et le problème de la classification des eaux saumâtres. *Archo Oceanogr. Limnol.* 11 Suppl.: 75—91.
- REDEKE, H. C. 1922. Zur Biologie der niederländischen Brackwassertypen. (Ein Beitrag zur regionalen Limnologie). *Bijdr. Dierk.* 22: 329—335.
- 1933. Über den jetzigen Stand unserer Kenntnisse der Flora und Fauna des Brackwassers. *Verh. int. Ver. Limnol.* 6: 46—61.
- REMANE, A. 1934. Die Brackwasserfauna. *Verh. Deutsch. Zool. Ges.* 36: 34—74.
- 1940. Einführung in die zoologische Ökologie der Nord- und Ostsee. *Tierw. Nord-Ostsee* 1a: 1—238.
- REMANE, A., & C. SCHLIEPER. 1958. Die Biologie des Brackwassers. *Die Binnengewässer* 22: 1—348.
- SCHMITZ, W. 1959. Zur Frage der Klassifikation der binnenländischen Brackwässer. *Archo Oceanogr. Limnol.* 11 Suppl.: 179—226.
- SCHULZ, H. 1961. Qualitative und quantitative Planktonuntersuchungen im Elbe-Aestuar. *Arch. Hydrobiol.* 16, Suppl. 1: 5—105.
- VÄLIKANGAS, I. 1933. Über die Biologie der Ostsee als Brackwassergebiet. *Verh. int. Ver. Limnol.* 6: 62—112.
- WAERN, M. 1952. Rocky shore algae in the Öregrund Archipelago. — *Act. Phytogeogr. Suec.* 30: 1—298.
- ZENKEVITCH, L. 1963. Biology of the seas of the U.S.S.R. London. 955 pp.
- Final Resolution of the symposium on the classification of brackish waters, 1959. *Archo Oceanogr. Limnol.* 11 Suppl.: 243—245.