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U. MESSNER[1], *J.A. VON OERTZEN*[2]

LONG-TERM CHANGES IN THE VERTICAL DISTRIBUTION OF MACROPHYTOBENTHIC COMMUNITIES IN THE GREIFSWALDER BODDEN

[1] Waren
Federal Republic of Germany
and
[2] Department of Biology, University of Rostock
Rostock, Federal Republic of Germany

Species diversity among the submerged vegetation of Greifswalder Bodden (Southern Baltic, Island of Rügen, Germany), which exhibits a distinct vertical zonation, is low. The vegetation grows at depths down to 3–4 m. Corresponding to the depth variations, aerial photographs show up to 3% of the bottom to have a plant canopy. Distribution of the phytal fauna depends greatly on the structure of the different plant species, the life cycles of both plants and animals, and on movements of the water and sediment. The literature reports plants growing at depths down to 8 m 50 years ago, over 90% of the bottom having a plant canopy then. The magnitude and ecological consequences of the drastic loss of vegetation due to eutrophication are discussed.

INTRODUCTION

The purposes that our waters have to serve are continuing to multiply and are often mutually exclusive. The coastal waters bear the brunt of the waste water load from large catchment areas, the effects being particularly grave in semi-enclosed inlets such as the German boddens. It is therefore hardly surprising that eutrophication presents a drastic problem in the boddens. Its primary consequence is a deterioration of underwater light conditions leading to restriction of the phytal zone to shallower regions. The consequences of this for the matter and energy balance of the ecosystem vary. Important functions of the phytal zone, such as the "nursery function" for commercially important fish species and coastal protection are also adversely affected.

AREA OF STUDY

The Greifswalder Bodden (Fig.1) occupies an area of 514 km^2 and is thus the Germany's largest inland sea area. It is bordered by the south coast of Rügen in the north and the mainland in the south. The water exchange with the Baltic Sea and the areas west of Rügen is relatively good through the Strelasund in the west and a broad opening to the open sea (limited by an underwater ridge) in the east. Owing to the mean depth of 5.6 m, the water body is always well mixed, and oxygen deficiency near the bottom is therefore rare (Schmidt unpubl.). The mean salinity is about 7 ‰ the water being therefore classified as b-mixo-mesohaline.

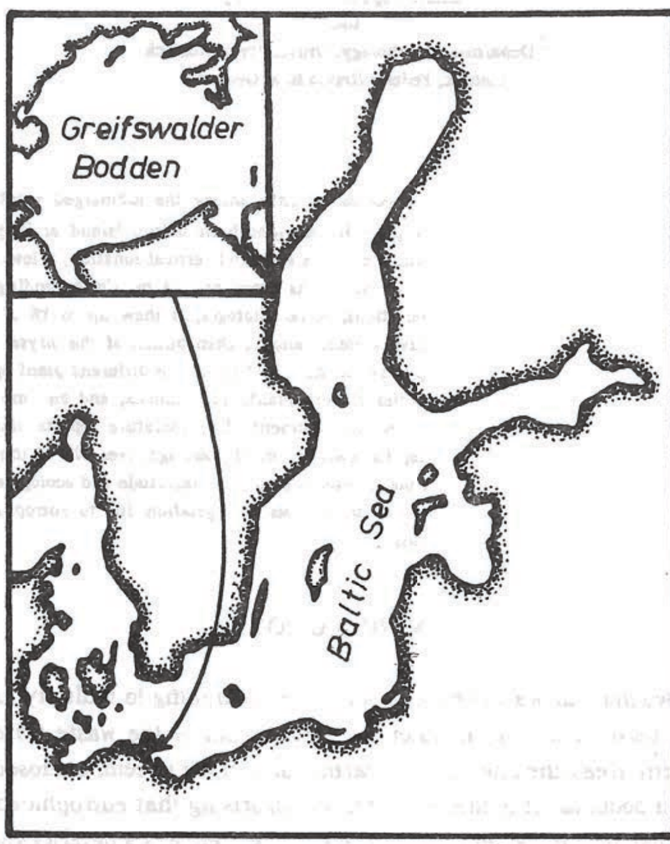

Fig. 1. Area of study – location in the Baltic Sea

MATERIALS AND METHODS

The results presented are based on field studies performed by skin diving and analyses of aerial photographs taken from April 1985 until 1989. Quantitative plant samples were obtained by harvesting the standing crop from within an area cut off by a steel frame. The wet weight was determined after manual centrifugation to remove the water Faunistic samples were collected by towing a closing net over the plants before these were harvested. The plant wet weight served as a reference parameter. Aerial photography analysis was used mainly to estimate the standing crop in the phytal zone (cf. Lindner 1978).

RESULTS AND DISCUSSION

Macrophytobenthos

Substrate conditions. The coastal morphology in the Greifswalder Bodden varies greatly. For the purpose of our considerations, it can be broken down into an abrasion coast with numerous boulders and a more or less sandy accumulation coast. The vegetation along the cliffs is enriched by algal species colonizing hard bottom, whereas vegetation of the sandy bottoms is uniform and contains few higher plants. The main factor governing colonization by benthic plants is the mobility of the substrate, which can be considerable in areas exposed to the wind. Rauch (1986) estimated the wave energy input along the Greifswalder Bodden coast, his estimates corresponding closely to the macrophytobenthos distribution. The mobility of the sand forming the southeastern shore, for instance, is so high that the area contains absolutely no benthic plants.

Vertical and horizontal distribution. Since the salinity of the Greifswalder Bodden, a brackish water ecosystem, lies roughly in the range of the species minimum, the species diversity in the submersed vegetation is low. The few species present form almost pure stands that exhibit a distinct zonation:

0–1.5 m:	green algae zone	2–4 m:	*Zostera marina* zone
1–3 m:	*Potamogeton pectinatus* zone	3–4 m:	red algae zone

The green and red algae zones are restricted to hard bottom coastal areas, in many places there being no red algae zone.

The species dominating the stands are *Potamogeton pectinatus* and *Zostera marina*. In a few shallow areas, small groups of *Ruppia cirrhosa* occur, and *Ranunculus baudotti* and *Myriophyllus spicatum* are seen occasionally. *Zanichellia palustris* colonizes the margins of the eelgrass meadows at the borders of the vegetated zone. *Fucus vesiculosus* grows in sparse stands at depths down to 1 m, but avoids greatly exposed regions. A detailed list of species is given in Geisel (1986).

The horizontal distribution of the plant canopy cannot be accurately analyzed from aerial photographs. Fig. 2 shows a map of a region (45.000 m^2) on the NE coast of Zickersches Höft (SE-Rugen). This kind of colonization can be regarded as typical. The movement of the water and substrate permits only isolated colonies to become esta-

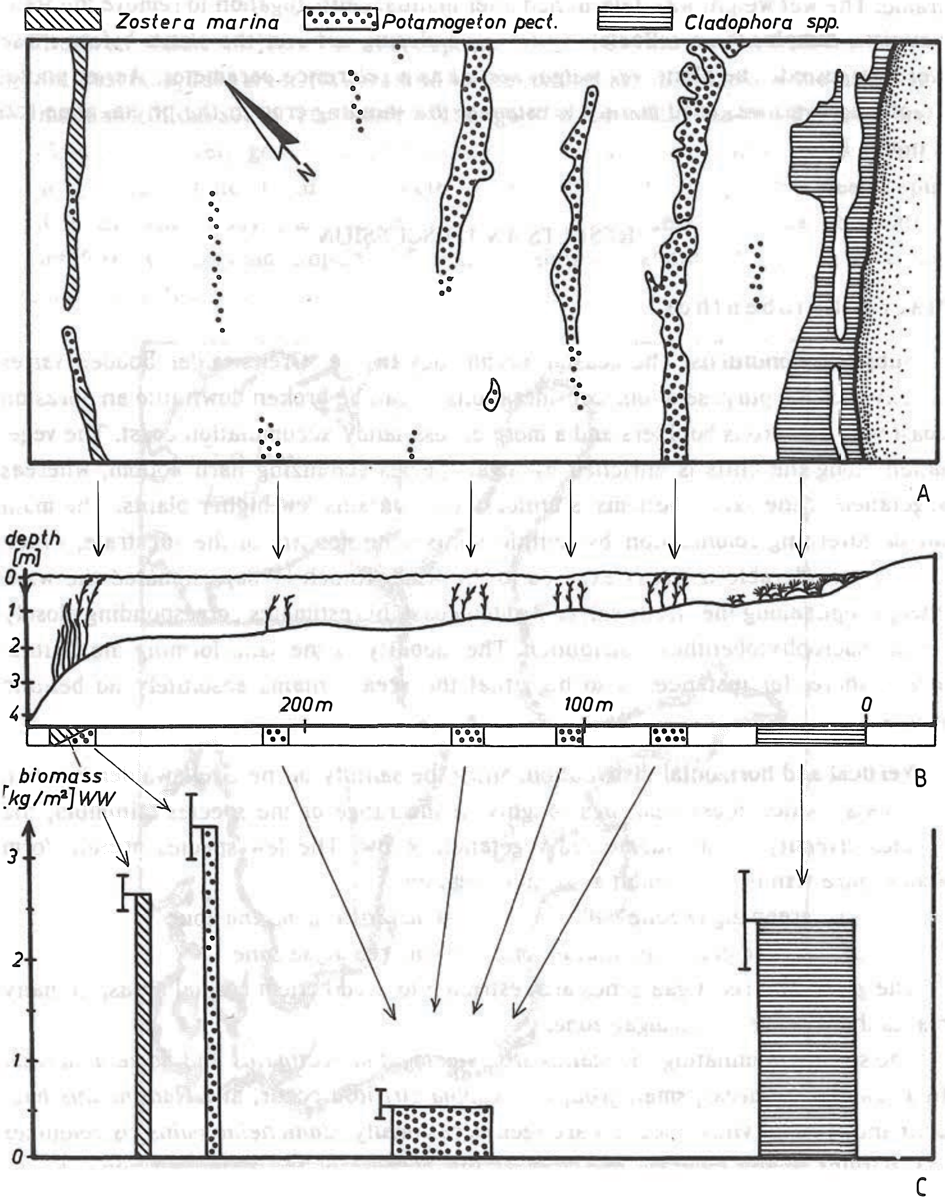

Fig. 2. A: Plant canopy mapped with aerial photography (area of 45.000 m^2)
B: Vegetation profile; C: Wet weight biomass (kg/m^2) on colonized areas

blished parallel to the sand banks. Variability of these plant stands is very considerable (cf. Grundel 1982, 1984). Density of the plants remains low and they fail to grow to their maximum height. The standing crop remains therefore low. In the deeper littoral zone where the substrate mobility is lower, detritus sedimentation is higher and competition for light is intensive, the stands are extremely dense and high. In these areas, *Potamogeton pectinatus* achieves heights of 3 m, but the depths are dominated by *Zostera marina* growing to heights of up to 2 m! These examples are sufficient to show that the areas where plant growth is possible are most exposed to wave action and currents, which greatly restricts colonization by macrophytobenthos.

Historical aspects. To judge from previous descriptions of the macrophytobenthos, eutrophication and the resultant deterioration of light conditions on the bottom led to

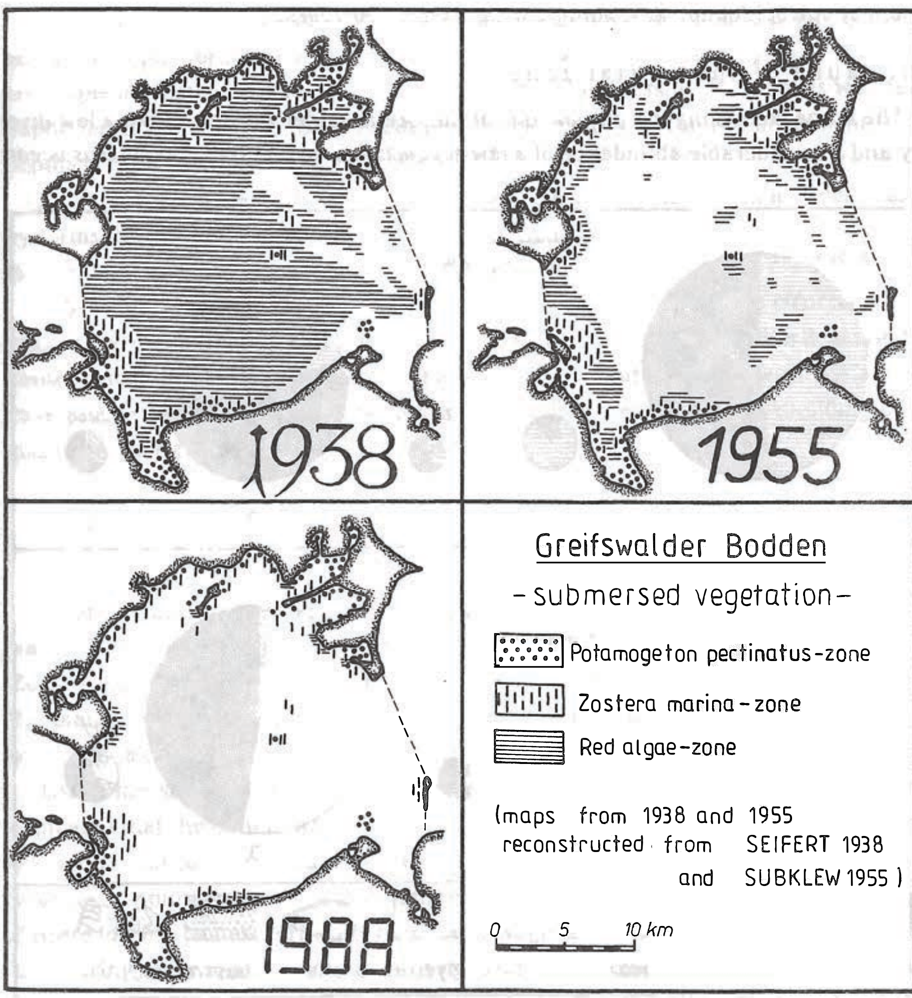

Fig. 3. Historical and present state of submerged vegetation in Greifswalder Bodden

a rapid decline of the submerged vegetation to its present state. Data of Seifert (1938) regarding the plant canopy on the Greifswalder Bodden bottom allow to reconstruct the situation as shown in Fig. 3. Reibisch (1904) and Henking (1904) published similar impressive descriptions. The red algae, dominated mainly by *Furcellaria fastigiata* in those days, formed mostly loose-lying stands at depths down to about 8 m where there was still sufficient light, but no wave action. Subklew (1955) stated that, during his study, the vegetation extended down to only 6 m (Fig. 3). The current situation is shown in Fig. 3 in which the phytal zone is assumed to be restricted to the depth of 4 m.

Secchi depths reported during the summer algal blooms: 2.5 m (Seifert 1938); 1–1.5 m (Subklew 1955); 0.2 m (Schmidt unpubl. manuscript) provide indications of the extent of eutrophication advancing during the past 50 years.

The fauna of the phytal zone

The fauna colonizing the phytal zone of the Greifswalder Bodden shows a low diversity and a considerable abundance of a few species: *Idotea chelipes, Gammarus oceani-*

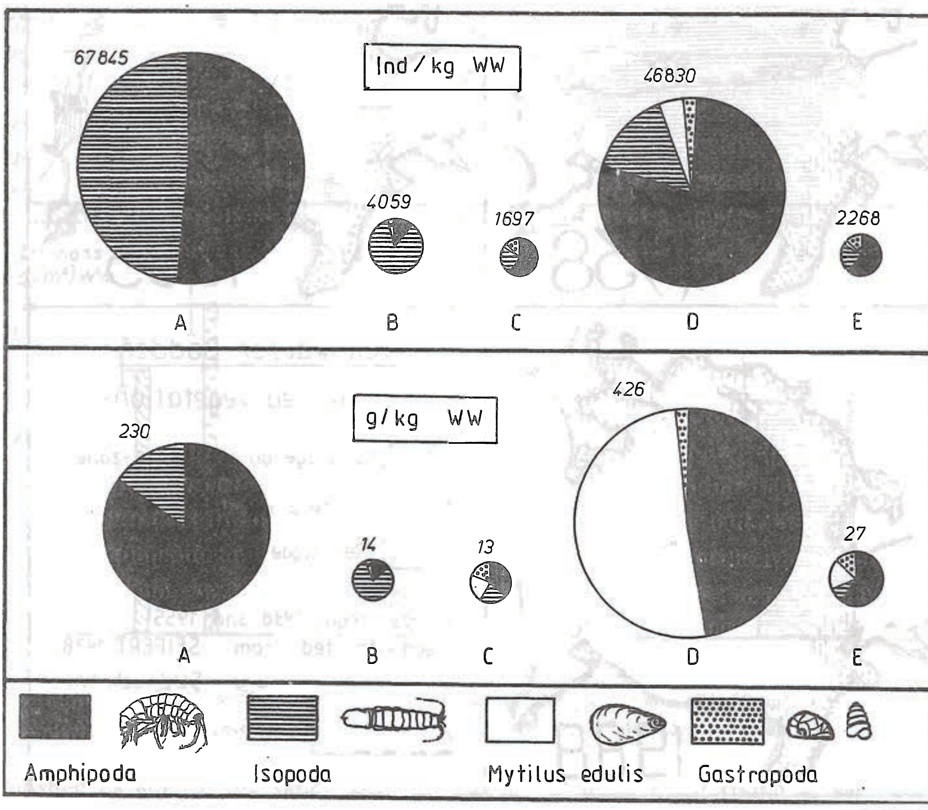

Fig. 4. Fauna colonizing the macrophytobenthos:
A: *Cladophora* sp., B: *Potamogeton pectinatus*, C: *Zostera marina*, D: *Furcellaria fastigiata*. E: *Fucus vesiculosus*

cus, G. zaddachi, Theodoxus fluviatilis, Mytilus edulis, and *Membranipora crustulenta.* An updated list of the species inhabiting the phytal zone is given in Messner (1986).

Important factors governing faunal colonization of the phytal zone include spatial structure of the substrate (plant species), water movement (wave action, depth), sediment type, and season (phase of life cycle of plants and animals).

The following conclusions can be drawn (see also Wieser 1959):

1. The widely branching plant species (*Furcellaria, Polysiphonia*) are very densely colonized and represent the "nursery" mainly for species that feed on fresh shoots (*Idotea* spp., *Gammarus* spp.). Less ramified species (*Zostera, Potamogeton*) are much less densely colonized, adult animals mainly being the inhabitants (Fig. 4).

2. Due to strong water movement (e.g. wave action), only mobile clasping species and a few haptic forms are able to persist (*Gammarus, Idotea, Theodoxus,* etc.) in the area. Species that are unable to swim (*Jaera* spp.), hemisessile (*Mytilus*) as well as most haptic forms (*Turbellaria, Gastropoda*) are found mainly in the red algae zone, i.e. at depths greater than 3 m (cf. von Oertzen 1966).

3. Thick detrital deposits, especially among filamentous algae, enable colonization by forms tha would normally inhabit muddy bottoms (e.g. *Hydrobia* spp., *Nereis diversicolor,* and various Oligochaeta).

4. Seasonal rhythms, i.e. life cycles of the species dominating the structure, determine the presence and size of the phytal regions (see the section on **Vertical and horizontal distribution**). Abundances of the animals fluctuate in tune with the reproductive phases of different plant species, substrate preferences often depending on age class (Messner and von Oertzen in press).

CONCLUSIONS

When calculating the standing crop, only that vegetation which covered large areas was included. At present, the vegetation consist mainly of *Potamogeton pectinatus* and *Zostera marina.* In view of the disjunct nature of these stands, it must be assumed that the plant canopy currently covers only 3% of the bottom. Fig. 5 presents the results of model calculations inteded to describe the extent of the decline of the vegetation.

Using the situation described by Seifert (1938) as a baseline reference, we have estimated that the bottom was covered in 50% by red algae with a biomass (wet weight) of 5 kg/m^2 [according to data in Trei (1978) for the Kassari Bay in Estonia] and harbouring an animal biomass (wet weight) of 420 g/kg. The *Potamogeton pectinatus* and *Zostera marina* zones were considered as a single zone of a mean biomass of 1 kg/m^2, harbouring an animal biomass of 14 g/kg. This rough estimation yields a total animal biomass (wet weight) of about 514,000 tonnes in the red algae zone and about 200 tonnes for those inhabiting the *Potamogeton pectinatus* and *Zostera marine* zone 50 years ago. The phytofauna biomass, which accounted for only 0.04% of the total

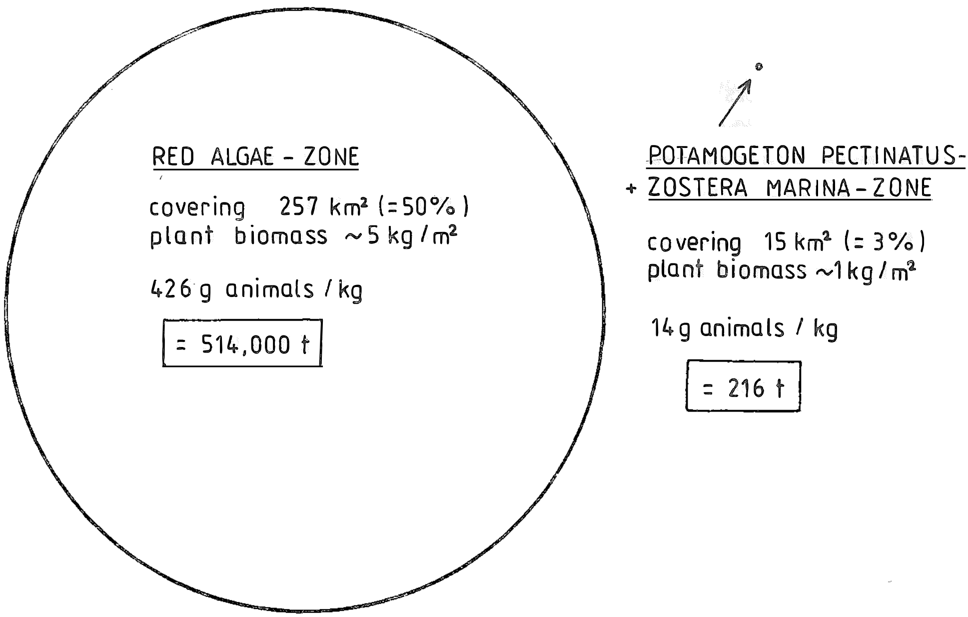

Fig. 5. Calculation of animal biomass in the phytal zone 50 years age (see text)

50 years ago, is all that remains. This represents almost the total loss of an important habitat for several fish species and a drastic change in the material and energy balance of the system.

The effects that these changes will have on productivity and stability of the ecosystem as a whole and at alternative pathways (e.g. micro- and meiofauna or soft bottom communities) the system might activate cannot be estimated until more detailed studies are carried out.

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Author's addresses:

U. Messner
Lange Str. 7
D-2060 Waren
Federal Republic of Germany

J.A. von Oertzen
Department of Biology
University of Rostock
Freiligrathstr. 7/8
D-2500 Rostock
Federal Republic of Germany