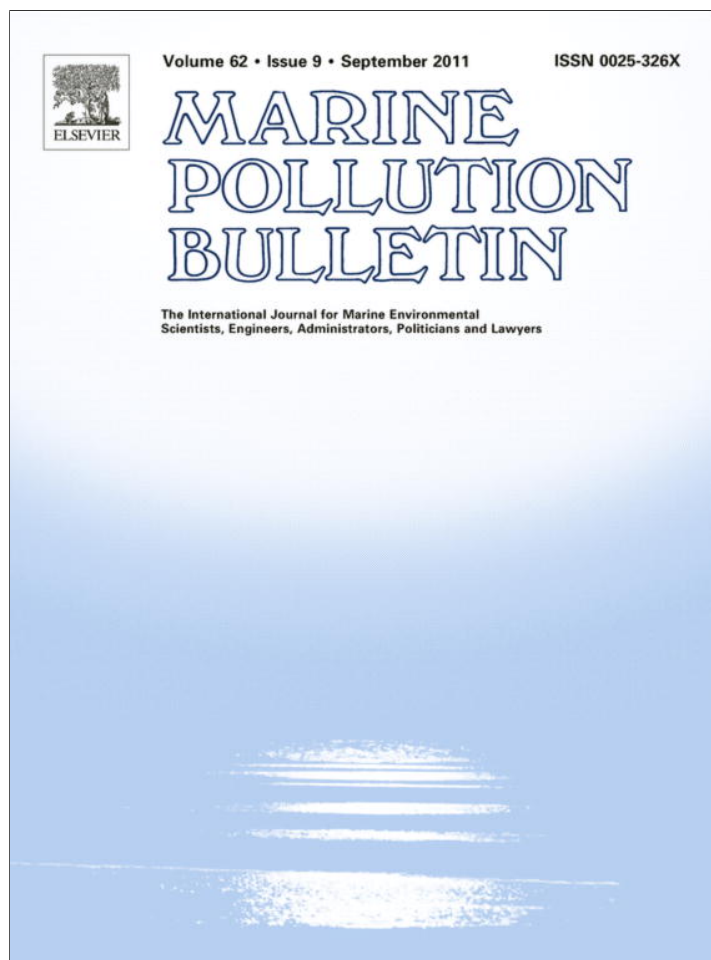




This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept

Hendrik Schubert^a, Peter Feuerpfeil^a, Ronny Marquardt^a, Irena Telesh^{b,*}, Sergei Skarlato^c

^a University of Rostock, Institute of Biological Sciences, Department of Ecology, Albert-Einstein-Str. 3, D-18051 Rostock, Germany

^b Zoological Institute, Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia

^c Institute of Cytology, Russian Academy of Sciences, Tikhoretsky Ave. 4, 194064 Saint Petersburg, Russia

ARTICLE INFO

Keywords:

Baltic Sea
Horohalinity
Macroalgae
Salinity gradient
Species diversity

ABSTRACT

Remane's species-minimum concept, which states that the lowest number of taxa occurs at the horohalinity (5–8 psu), was tested by investigating macroalgal diversity on hard substrates along the natural salinity gradient in the Baltic Sea. Field data on species occurrence and abundance were collected by SCUBA diving along 10 transects of the Finnish, Swedish and German coasts, covering a salinity range from 3.9 to 27 psu. Macroalgal species numbers declined steadily with salinity, decreasing until 7.2 psu was reached, but in the horohalinity, a marked reduction of species number and a change in diversity were indicated by the Shannon index and evenness values. The non-linear decrease in macroalgal diversity at 5–8 psu and the lack of increase in species numbers at salinities below 5 psu imply a restricted applicability of Remane's species-minimum concept to macroalgae.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

The explosive accumulation of biodiversity data over the past few decades has brought into question the general applicability of Remane's *Artenminimum* (species-minimum) concept (Remane, 1934), which had been an accepted textbook model for brackish water ecosystems for decades (e.g., Kinne, 1971; Remmert, 1989; Lalli and Parsons, 1997). This concept argues that taxonomic diversity in organisms is lowest in the salinity range between 5 and 8 psu, i.e., within the horohalinity (Kinne, 1971). The concept was originally developed from data on macrozoobenthos in the Baltic Sea (Remane, 1934) and was widely applied to the overall diversity of other brackish water bodies, such as the Caspian Sea (Zenkevitch, 1959), and even tidal estuaries (McLusky and Elliott, 2004). However, new evidence shows that the earlier idea of low overall species diversity in brackish waters has resulted largely from insufficient knowledge of the taxonomic composition of the plankton (Telesh et al., 2011a,b). Reconsideration of biodiversity data on pelagic communities, especially protists in the Baltic Sea, has led to the conclusion that the diversity of plankton in brackish waters may be strikingly high and that this diversity may provide a basis for a new 'protistan species-maximum concept' (Telesh et al., 2011a).

Data on macrophytes were hardly considered in the debates on biodiversity within the horohalinity, although information on

this important benthic constituent can shed additional light on general biodiversity patterns in brackish waters. In the Baltic Sea, the first survey of macrophytobenthos diversity in the salinity gradient along the Swedish west coast (Kylin, 1907) revealed a steady decline in species numbers with decreasing salinity. Later, Hoffmann (1932) completed the picture begun by Kylin (1907) with data from the southern Swedish coast, and he confirmed the trend of a continuous decline in species numbers of macrophytes with decreasing salinity. Remane (1940) referred to this result and came to the conclusion that the slope of decrease in species numbers of plants with decreasing salinity, as shown by Hoffmann (1932), was similar to that for macrozoobenthos. However, the data of Hoffmann (1932, 1943) showed the continuous decline in macroalgal species numbers down to a salinity of 3 psu, without any sign of further increase of the diversity in green, brown or red algae at the lowest salinities, which was a remarkable departure from Remane's species-minimum concept. Therefore, the overall distribution of macrophytobenthos within the salinity gradient of the Baltic Sea remained to be tested by field observations.

It has also been recognized that the most pressing need is for an evaluation of species diversity of macroalgae identified with the help of modern taxonomic treatments and collected at sites with environmental characteristics defined largely by the salinity gradient minimizing the effects of other stressors (e.g., eutrophication, pollution, and climate variability). Application of this approach could contribute to research on the ecosystem–economy level through up-to-date knowledge of biological components and their biodiversity and function, which support the evaluation of aquatic

* Corresponding author. Tel.: +7 (812) 328 1311; fax: +7 (812) 328 2941.

E-mail addresses: itelesh@yahoo.com, itelesh@zin.ru (I. Telesh).

ecosystem health (Golubkov and Alimov, 2010; Telesh et al., 2010, 2011a). Macrophytes have been included in the list of important ecosystem quality indicators by the European Water Framework Directive (WFD, 2000/60/EC), which makes knowledge on their diversity, speciation and distribution an essential component of Baltic Sea environmental health assessment.

The Baltic is a relatively young basin that has undergone several changes from freshwater to marine phases since its deglaciation 9000–15,000 years ago. These changes occurred due to geological uplifting phenomena and changes in sea level. The present brackish-water 'Mya period' is approximately 2000 years old (Lass and Matthäus, 2008), which is a relatively short period in evolutionary history. Therefore, the Baltic Sea is believed to be an "unsaturated" ecosystem, in which most of the species have invaded from neighboring habitats without being fully acclimated, and some have even claimed that no macroalgal species are endemic there (Russell, 1985). Later, however, Bergström et al. (2005) described an endemic lineage of *Fucus vesiculosus* as *Fucus radicans* L. Bergström et al. L. Kautsky, which can be classified as its own species based on morphological, molecular genetic and life history data.

Being the largest stable brackish water habitat of the world, the Baltic Sea is characterized by pronounced gradients of climatic and hydrological factors, both of which affect the occurrence and distribution of aquatic plant species. Several studies have shown the influence of, for example, temperature regime, length of the vegetation period, duration of ice cover, availability of substrates, or eutrophication on macrophytes in the Baltic Sea (Lindgren, 1964; Breeman, 1988; Kautsky and Kautsky, 1989; Middelboe, 2000). The importance of these factors varies with the spatial scale of the analysis. Physical dispersal barriers act as a controlling factor on a regional scale, whereas suitability of the substrate is important on a local scale (Middelboe and Sand-Jensen, 2004). In addition, anthropogenic eutrophication has been shown to strongly influence the presence of macroalgal species, leading to lower species diversity at eutrophied sites (Munda, 1982; Middelboe and Sand-Jensen, 2004).

The salinity gradient in the Baltic Sea is uniquely smooth because the horohalinicum occupies the major area of the Baltic proper and a great part of the vast coastal zone (Schiewer, 2008; Feistel et al., 2010). On the sea-size scale, however, salinity decreases throughout the Baltic, from fully marine values near the narrow connection with the North Sea to almost freshwater conditions in the Bothnian Bay and the Neva Bay in the eastern Gulf of Finland. A similar salinity gradient exists in the Danish fjords and some estuaries, although on a much smaller spatial scale (Kalvestad, 1978; Munda, 1978; Middelboe et al., 1998), which reduces the influence of effects caused by climatic gradients. However, the fjords and estuaries of northern Europe often show strong eutrophication gradients that are caused by nutrient-rich freshwater runoff, whereas the latter confounds results on the occurrence and distribution of the macrophytes species (Diaz and Rosenberg, 1995).

In the Baltic Sea, earlier studies often focused on the distribution of macroalgae within certain ranges of the salinity gradient. Hoffmann (1932, 1943) found decreasing numbers of macroalgal species in areas with lower salinity. Wallentinus (1991) reported a reduction in both thallus size and species numbers with decreasing salinity, based on observations in the area around Askö and existing literature data. The same trend was observed in the most comprehensive study on the distribution of benthic macrophytes in the Baltic Sea by Nielsen et al. (1995), which included essentially all available data on the occurrence of macrophytes at that time. These works, however, were largely based on literature data that were collected before effective sampling techniques and reliable taxonomic identifications of many macroalgal groups were available. Moreover, the comprehensive region-based compilation of

Nielsen et al. (1995) is a survey without site-specific salinity data, and therefore, it is of limited value for assessing the application range of Remane's *Artenminimum* concept. Thus, the overall distribution of macroalgae within the salinity gradient of the Baltic Sea remained to be tested by field observations. This approach has gained special interest in the light of the recent reconsideration of Remane's concept as it relates to plankton (Telesh et al., 2011a,b) and bacteria (Herlemann et al., 2011).

In this study, we investigated species numbers, species diversity and depth zonation of macroalgae along the salinity gradient of the Baltic Sea. The aim of the study was to assess the role of salinity in controlling macroalgal distribution and to test the applicability of Remane's species-minimum concept to macrophytes. Field investigations were conducted by SCUBA diving along the line transects at 10 sampling sites in Finland, Sweden and Germany, with salinity ranging from 3.9 to 27 psu. All localities were not eutrophied by terrestrial runoff. Only exposed sites with prevailing hard substrates were considered to ensure comparability between sites and to minimize the influence of factors other than salinity. Transects in the salinity range 5–8 psu, the main focus of this study, were located at the same geographic latitude to minimize the effects of climate on the vegetation.

2. Materials and methods

2.1. Study sites and sampling

Ten exposed, non-eutrophied sites with hard substrates and differing salinity levels were chosen along the Baltic coast (Fig. 1). These sites were investigated during four field trips in May 2001, October 2001, May 2002 and June 2002.

The vegetation was documented down to a maximum depth of 15 m by SCUBA diving along the transect lines perpendicular to the coastline. One transect was investigated at each locality. The occurrence of species and their degree of cover were noted in randomly placed quadrates. Each transect was divided into four vertical sections, referred to as 'splash zone', 'filamentous algal zone', 'brown algal belt' and 'red algal zone'. Three quadrates were placed in each horizon. The size of the quadrates differed for each horizon: 0.25 × 0.25 m (splash zone), 0.8 × 0.8 m (filamentous algal zone), 1 × 1 m (brown algal belt) and 2 × 2 m (red algal zone), representing the minimum necessary area according to A. Ruuskanen (personal communication). All plant specimens larger than 2 cm were considered to be macroalgae and included in the study; unattached species were excluded.

The percentage cover was estimated *in situ*, according to a 9-level numerical scale (5%, 10%, 15%, 20%, 30%, 40%, 55%, 75% and 100%). The mean coverage was calculated for each species from the 3 individual frames.

While still alive, species were identified in the laboratory using the 'field keys' of Hiscock (1979a,b) and Snoeijs and Johansson (1999), except for the following taxa. *Ceramiales* were identified using Maggs and Hommersand (1993), *Gigartinales* were identified using Dixon and Irvine (1977), *Ectocarpales* were identified using Kornmann (1964), and *Cladophorales* and *Ulva* were identified using Burrows (1991). In the case of nomenclature changes (e.g., *Enteromorpha*) published after appearance of these guides, the Latin names used in the respective keys were maintained in this paper to allow readers to refer to the original sources.

2.2. Data analysis

Biodiversity, which was expressed by Shannon index and evenness values, was calculated with the following equations (Sneath and Sokal, 1973):

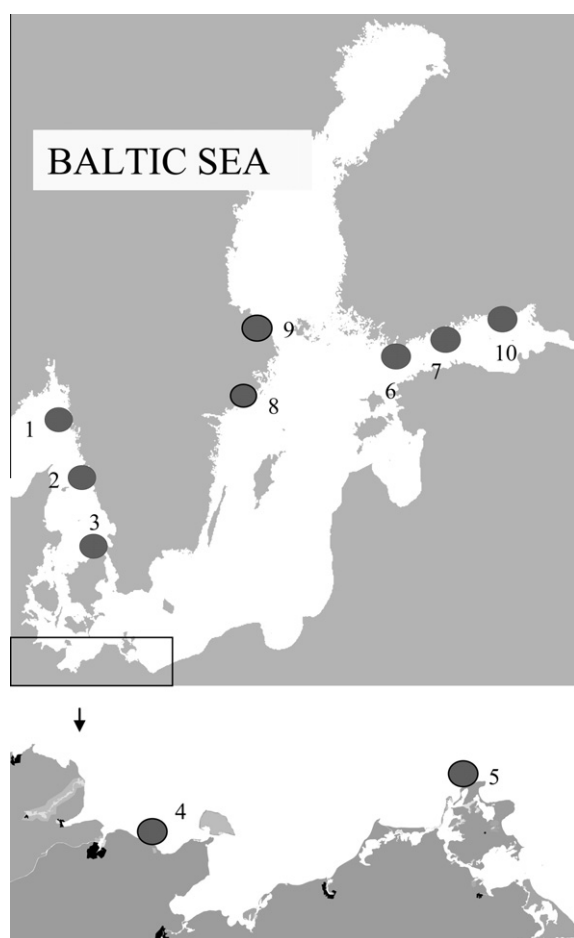


Fig. 1. Map of study area and the locations of investigation sites along the salinity gradient in the Baltic Sea: 1 – Smögen (Sweden), 2 – Lerkil (Sweden), 3 – Arild (Sweden), 4 – Hohwachter Bucht (Germany), 5 – Varnkevit (Germany), 6 – Tvärminne (Finland), 7 – Pokala (Finland), 8 – Nothamn (Sweden), 9 – Svartklubben (Sweden), 10 – Hanski (Finland).

$$H_s = - \sum p_i (\ln p_i), \quad (1)$$

where H_s is Shannon index, $p_i = n_i/N$, n_i – coverage of one taxon, and N – coverage of all taxa;

$$E = H_s/H_{\max}, \quad (2)$$

where E is evenness and $H_{\max}$ – maximum value of the Shannon index.

Table 1
Location of the investigation sites, salinity and numbers of macroalgal species.

Station number	Station name (country)	Latitude	Longitude	Salinity (psu)	Number of taxa			
					Rhodophyta	Phaeophyceae	Chlorophyta	Total
1	Smögen (Sweden)	58.35N	11.21E	27.0	23	12	7	42
2	Lerkil (Sweden)	57.27N	11.55E	22.1	22	11	7	40
3	Arild (Sweden)	56.28N	12.55E	16.0	15	7	5	27
4	Hohwachter Bucht (Germany)	54.36N	10.58E	13.1	15	6	6	27
5	Varnkevit (Germany)	54.32N	13.41E	7.2	6	6	5	17
6	Tvärminne (Finland)	59.84N	23.20E	5.7	9	4	4	17
7	Pokala (Finland)	59.93N	24.38E	5.4	5	4	3	12
8	Nothamn (Sweden)	60.02N	18.51E	4.9	4	3	2	9
9	Svartklubben (Sweden)	60.11N	18.80E	4.8	4	2	4	10
10	Hanski (Finland)	59.93N	24.38E	3.9	3	4	3	10
Total					41	18	17	76

To identify possible patterns of species distribution along the salinity gradient, the Jaccard index was used (Jaccard, 1912). It is calculated as follows:

$$S_j = c/(a + b + c), \quad (3)$$

where S_j is Jaccard index, 'c' is the number of species occurring at both stations that are compared, and 'a' and 'b' are the numbers of species only occurring at one of the stations. These indices then served as the basis for a hierarchical clustering analysis using the complete linkage algorithm and Euclidean distances with the program NCSS 2001 (NCSS Kaysville, Utah) according to Sneath and Sokal (1973).

3. Results

Table 1 shows the investigation sites with their geographic position, the respective salinity and macroalgal species richness. Salinity ranged from 3.9 psu (Hanski, Finland) to 27 psu (Smögen, Sweden). The total number of macroalgae larger than 2 cm amounted to 76 taxa, with the majority belonging to the Rhodophyta (41 species). Chlorophyta and Phaeophyceae displayed nearly equal numbers (17 and 18 species, respectively).

Within all groups, species numbers declined with decreasing salinity (Table 1). The strongest reduction of species was observed in the Rhodophyta, for which numbers dropped along the salinity gradient from 23 to 3 species, a reduction of 87%. Chlorophyta displayed a 57% decrease in species number and Phaeophyceae was reduced by 67%. Total numbers of macroalgae decreased from 42 to 10 species. The decline in species number was strongest at salinities of 5–6 psu, where the total number of species was reduced by

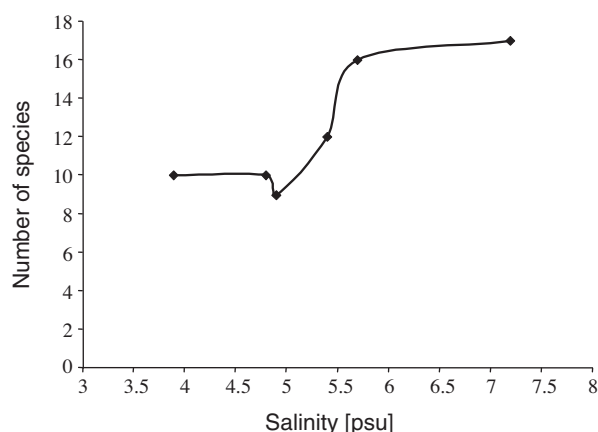


Fig. 2. Number of macroalgal species found in the salinity range 3.9–7.2 psu; each dot corresponds to one investigation site.

	Station	Värnkevit	Tvärminne	Pokala	Nothamn	Svartklubben	Hanski
	Salinity	7,2	5,7	5,4	4,9	4,8	3,9
Species							
<i>Cladophora glomerata</i>							
<i>Cladophora rupestris</i>							
<i>Enteromorpha</i> sp.							
<i>Enteromorpha intestinalis</i>							
<i>Spongomorpha lanulosum</i>							
<i>Chorda filum</i>							
<i>Ectocarpus siliculosus</i>							
<i>Elachista fucicola</i>							
<i>Fucus serratus</i>							
<i>Fucus vesiculosus</i>							
<i>Pilayella littoralis</i>							
<i>Sphacelaria arctica</i>							
<i>Ceramium tenuicorne</i>							
<i>Ceramium</i> sp. (corticate)							
<i>Furcellaria lumbricalis</i>							
<i>Hildenbrandia rubra</i>							
<i>Phyllophora pseudoceranoides</i>							
<i>Phyllophora truncata</i>							
<i>Polysiphonia fibrillosa</i>							
<i>Polysiphonia fucoides</i>							
<i>Polysiphonia stricta</i>							
<i>Rhodomela confervoides</i>							

Fig. 3. Species that have their lower distribution limit in the salinity range 3.9–7.2 psu. Distribution ranges were complemented (indicated by light grey areas) if a species was absent from a particular site, but occurred again at a lower salinity.

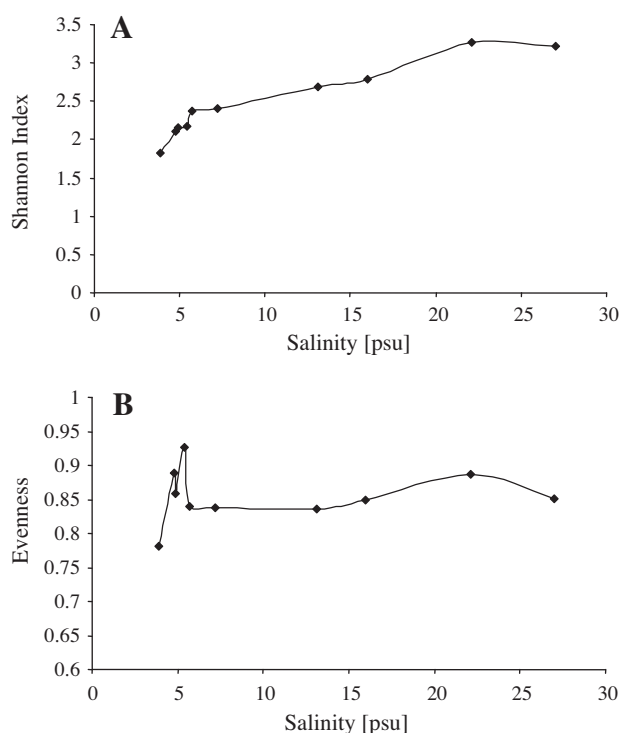


Fig. 4. Shannon index of species diversity (A) and evenness values (B), calculated from the number of macroalgal species and their degree of coverage at each of the ten investigation sites along the salinity gradient in the Baltic Sea.

nearly 50% within the range of 1 psu (Fig. 2). Within this narrow salinity span, species numbers declined abruptly from 17 species at 7.2 psu to 9 species at 4.9 psu. A list of species that occurred within the salinity range of 3.9–7.2 psu is shown in Fig. 3. Twelve species seem to have the lowest limit of their distribution within this range, and this produces the steep decline in overall species

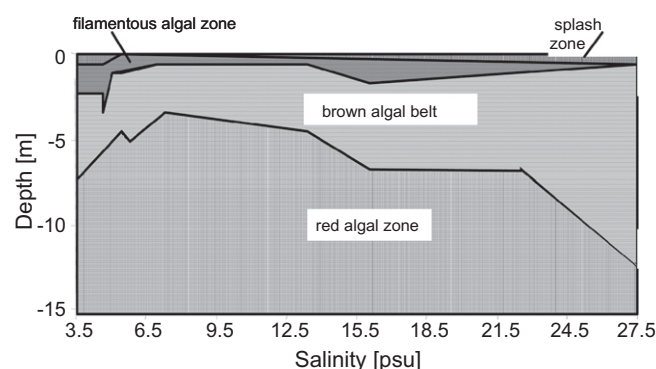


Fig. 5. Changes in depth range of the horizons designated as splash zone, filamentous algal zone, brown algal belt and red algal zone along the salinity gradient in the Baltic Sea.

numbers. All major macroalgal groups contributed to these 12 species, but the decrease was most pronounced in the Rhodophyta (7 species).

Fig. 4A shows the decline of diversity with lower salinity, expressed by means of the Shannon index. The shape of the distribution curve here is partly similar to the one depicted by the decrease in species numbers (Fig. 2), with biodiversity values dropping more rapidly below 7.2 psu. Biodiversity in the area with the lowest salinity (3.9 psu, eastern Gulf of Finland) is estimated to be about half as high as in the nearly fully marine areas (27 psu, Skagerrak). The corresponding evenness values are displayed in Fig. 4B. The evenness remained nearly constant for a broad range of salinity (5.7–27 psu) but became very ‘noisy’ at salinities below 5.4 psu. At 5.4 psu, the evenness reached a value of almost 1, reflecting the fact that all species present in this area have an equal distribution, excluding the dominant species, before evenness steeply declines to its lowest value at 3.9 psu.

Fig. 5 summarizes the results with respect to depth zonation. The splash zone, which is poor in species and not well developed in the Baltic Sea due to the absence of tides, did not change much

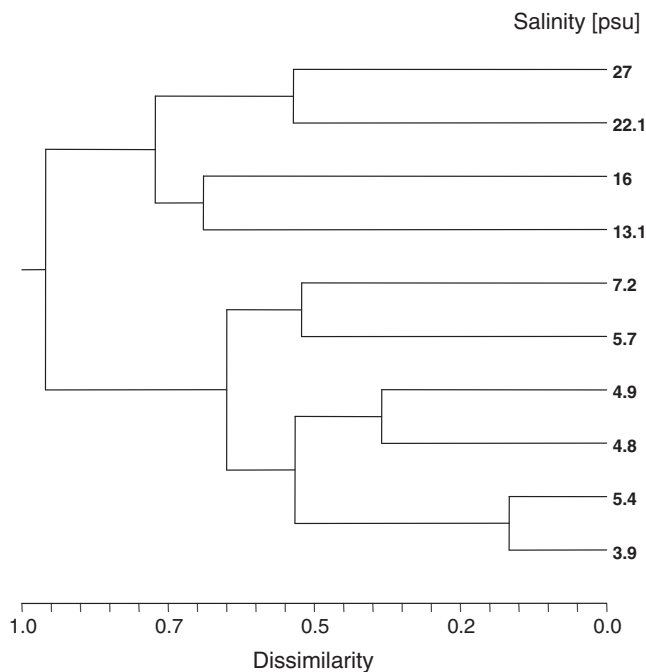


Fig. 6. Dendrogram from hierarchical clustering analysis using Jaccard's index shows the dissimilarity in the macroalgae community composition at sites with different salinities. Clustering was performed using Euclidean distances and the single linkage algorithm.

between stations; it had a depth range of 0–0.3 m. The depth limit of the subsequent filamentous algal zone, mainly consisting of filamentous green algae, increased from 0.5 m at 27 psu to a maximum depth of 1.7 m at 16 psu. The range subsequently narrowed again to a lower depth limit of 0.4 m before the deepest example was reached, with a lower depth limit of 3 m at 4.9 psu. The brown algae belt consisted mainly of large Phaeophyceae such as *F. vesiculosus*, *F. serratus*, *Laminaria saccharina* and *L. digitata*. The maximum depth of 12 m was reached at the highest salinity (27 psu). The reduction in depth distribution was caused by stepwise loss of the former dominant species: *L. digitata* at 22 psu, *L. saccharina* at 16 psu and *F. serratus* at 7.2 psu. The submergence of the brown algal belt in areas below 7 psu was an effect caused by *F. vesiculosus* as the last large habitat-structuring Phaeophyceae species. The upper limit of the red algal zone, dominated by Rhodophyta that have adapted to low-light conditions, seemed to be controlled by the depth range of the brown algal belt.

Fig. 6 shows the result of a hierarchical cluster analysis based on Jaccard index values as a characteristic for determining the similarity of the sites. The dendrogram is divided into two main clades, one of which consists of all sites located within the critical salinity zone (below 7.2 psu).

4. Discussion

The Baltic Sea is the world's largest brackish water ecosystem, and it is very young from a geological and evolutionary point of view; therefore, almost all organisms living there must have originated from neighboring marine and freshwater habitats, and very few truly endemic species exist (e.g., Hoffmann, 1950; Russell, 1985; Bergström et al., 2005). One of the unique features of the Baltic Sea is the natural salinity gradient that runs from fully marine environments near the connection with the North Sea to almost freshwater conditions in the North-Eastern parts, with a concomitant change in species occurrence and distribution, which was first described in detail by Remane (1934). This author investigated the decline of the benthic macrofauna species' numbers with decreas-

ing salinity and discovered a species minimum between 5 and 8 psu (Fig. 7A). At lower salinities, species numbers of macrozoobenthos increased again due to organisms invading from adjacent freshwater ecosystems.

As shown further by Remane (1955) and a number of other researchers (Khlebovich, 1968, 1969, 1974; de Jonge, 1974; Deaton and Greenberg, 1986; Michaelis et al., 1992; Telesh and Khlebovich, 2010, etc.), the brackish environments place high physiological demands on all organisms, as both hypo- and hyperosmotic adjustment are required in this zone. The salinity range of 5–8 psu is characterized by the occurrence of very few marine and freshwater species but co-dominance of brackish water-dwelling species (Remane and Schlieper, 1958). This peculiar 'critical salinity zone' (*sensu* Khlebovich, 1968, 1969, 1974), later referred to as the 'horohalimum' (Kinne, 1971), usually forms the 'nucleus' or core part of an estuary where the major chemical, physical and biological characteristics and processes demonstrate non-linear dynamics (Telesh and Khlebovich, 2010; Telesh et al., 2011a). Some hydro-chemical parameters related to nutrient concentrations show the alterations within the salinity gradient that are linked to the processes of mineralization and consumption by biota. For example, at salinities close to 5 psu in coastal waters of the Caspian Sea, the silicon consumption/excretion ratio reverses due to the substitution of freshwater diatoms by marine species of these algae (Khlebovich, 1989). The change in the charge of particles drawn by water occurs in the horohalimum, which is one of the most prominent physical phenomena in the salinity gradient (Pravdič et al., 1981). This effect results in alteration of the sediment formation mode on either side of the critical salinity barrier due to increased flocculation, which, in turn, influences other physical characteristics of waters, e.g., transparency (Gordeev, 1983; Khlebovich, 1990). The latter statement was proven by Van Beusekom and de Jonge (1994), who showed that the dynamics of suspended matter concentration in the Ems Estuary (North Sea) exposed maximum fluctuations at the critical salinity level.

However, irrespective of numerous supportive findings, the horohalimum concept and its basic tenets have been thoughtfully debated in the literature for several decades (e.g., Deaton and Greenberg, 1986; Attrill, 2002). Remane's *Artemninimum* (species-minimum) model, which gave credence to the horohalimum concept, described the distribution of benthic macroinvertebrate diversity along a marine–freshwater salinity gradient in the Baltic Sea (Remane, 1934). Meanwhile, some zoobenthos studies in estuaries have demonstrated a marked departure from the Remane model (Boesch et al., 1976; Attrill, 2002). Moreover, it has been shown that, for zooplankton and bacteria, Remane's model is inapplicable, as plankton organisms often do not exhibit minimum species diversity in the intermediate zone between marine and freshwater environments (Laprise and Dodson, 1994; Crump et al., 1999; Dolan and Gallegos, 2001; Hewson and Fuhrman, 2004; Telesh, 2004; Mironova et al., 2009; Herlemann et al., 2011; Telesh et al., 2011a,b). Species diversity in phytoplankton likewise did not display a minimum within the marine–freshwater salinity gradient of the estuary of the Schelde River (Muylaert et al., 2009), although this observation may be largely due to the density-driven accumulation of suspended material that contributes to the estuarine turbidity maximum in meso- and macrotidal estuaries.

Additionally, various opinions on whether genuine brackish-water species exist (e.g., Remane, 1958 but Remane, 1969; Barnes, 1989; Attrill, 2002) challenge Remane's curve. Finally, the concept of low species diversity in the brackish-water Baltic Sea (the model sea for Remane's *Artemninimum* assertions) was shown to result largely from insufficient knowledge of the taxonomic composition of the zooplankton and phytoplankton, especially their microscopic fractions (Telesh et al., 2011a,b). Unlike the relatively low brackish-water species diversity among bottom-dwelling animals

(Remane, 1934; Zenkewitch, 1959) and macroalgae (Schubert and Schories, 2008; this study), the pelagic diversity in the Baltic Sea was shown to be strikingly high (>4000 taxa), defined mainly by protists whose species richness peaks in the horohalinicum, thus providing the basis for the novel 'protistan species-maximum concept' (Telesh et al., 2011a).

Contrary to Remane's concept, the earlier and the contemporary phycological studies do not show any pronounced species minimum around the horohalinicum or at any other given salinity (Fig. 7). This can at least partially be explained by the fact that intact plant cells are always hyperosmotic (Kirst, 1990), and thus, hypoosmotic regulation is not required, which eliminates one of the arguments for the *Artenminimum* concept (see above). Hoffmann (1932, 1943) divided the Baltic Sea into four areas with different average salinities, compared the number of macroalgal species to numbers from the North Sea and found a continuous decline in species number (Fig. 7B). Wallentinus (1979) worked in the area of the Askö laboratory in Sweden and compared the number of macroalgal species larger than 1 cm from that area with literature data from the Baltic Sea regions with different salinities; again, a constant decline in species number was observed (Fig. 7C). The most comprehensive floristic study so far is the one by Nielsen et al. (1995), which is based mainly on previous litera-

ture data and lists the distribution of nearly all multicellular algae in the Baltic Sea. All habitats and available records were included in the distribution curve, and, as a result, a constant decline in species numbers of benthic macroalgae can be clearly seen (Fig. 7D). These studies differ from the work presented here by their inclusion of soft-bottom macroalgae in the analysis, their definition of a 'macroalga' and their inclusion of data from areas with different substrates and hydrological conditions.

Comparison of the studies mentioned above (Fig. 7B–E) with the work undertaken here (Fig. 7F) reveals that all diversity curves show the same general trend: the decline of marine species numbers of macroalgae with salinity decreasing to very low values. The biggest difference is in the actual number of species, depending on the sampling methods and on the definition of what had been regarded as a 'macroalga'. The graphs differ slightly in their steepness depending partly on the macroalgal groups included in the analyses.

The distribution of benthic algal species along the salinity gradient was also studied in the fjords and estuaries of other seas (Middelboe et al., 1998; Munda, 1978; Bergström and Bergström, 1999). It became apparent that eutrophication strongly influences macroalgal distribution (Kalvestad, 1978). However, Icelandic fjords, for example, span only small spatial scales and do not show

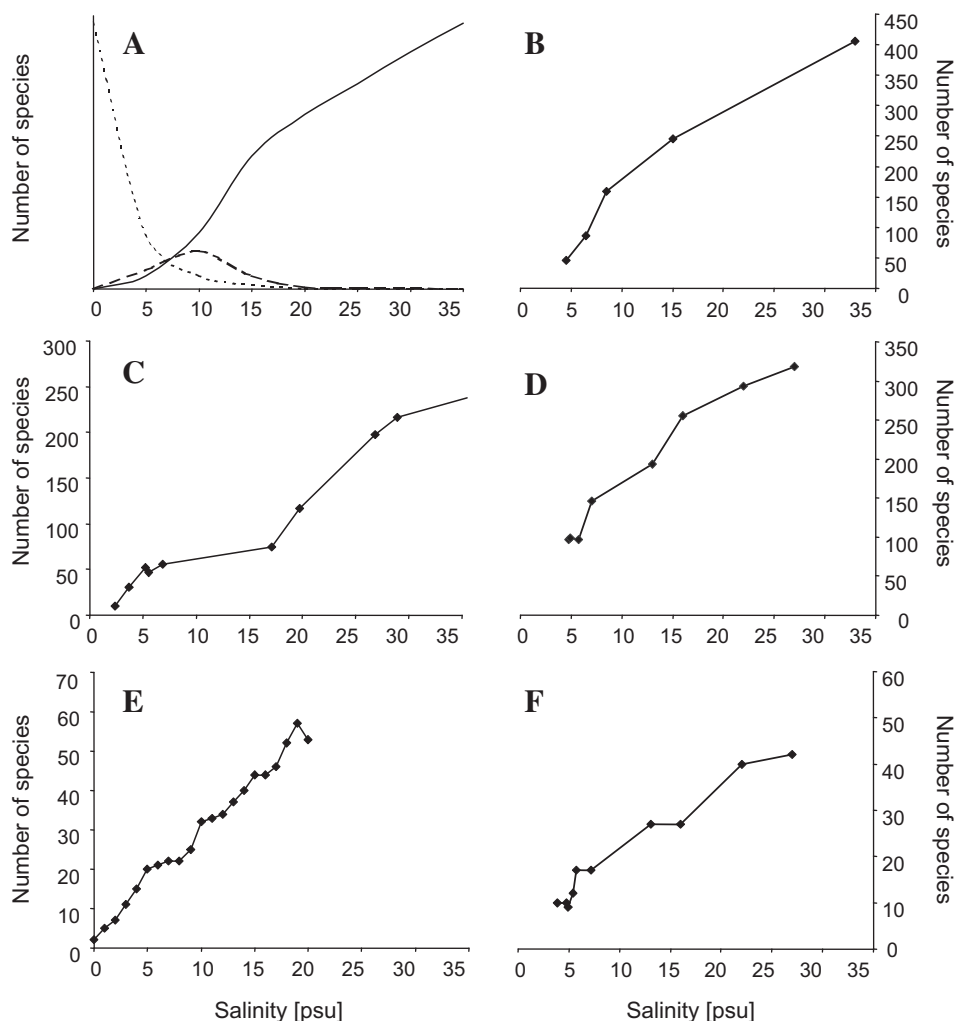


Fig. 7. Comparison of species numbers along salinity gradients. (A) Macrozoobenthos in the Baltic Sea; solid line = marine species; broken line = brackish-water species; dotted line = freshwater species; modified after Remane (1934). (B) Macroalgae along the salinity gradient from the North Sea into the Baltic Sea; modified after Hoffmann (1932). (C) Macroalgae in the Baltic Sea, modified after Wallentinus (1979). (D) Macroalgae in the Baltic Sea, modified after Nielsen et al. (1995). (E) Macroalgae in the Dyrafiord (Iceland), modified after Munda (1978). (F) Macroalgae in the Baltic Sea, this study.

any signs of eutrophication; therefore, they allow the study of species occurrence and distribution of macroalgae without the interfering effects of climate or nutrient load (Munda, 1978). Fig. 7E shows the decline of macroalgal species numbers in the Dyrafjord (North-Western Iceland), a pattern similar to those of the other graphs in Fig. 7, except for being somewhat steeper. From all results, except for Fig. 7E, it can be seen that the decline of species numbers becomes steeper below 8 psu; i.e., many macroalgal species reach their lower distribution limit in that salinity level.

The distributions of macroalgae described in our study and in the literature differ from the classic Remane curve for benthic macrofauna in their lack of an increase in algal species numbers at low salinities. This can be explained by the nearly complete absence of freshwater macroalgal species on hard substrates in the Baltic Sea. All species found in this study, except for *Cladophora glomerata* and *Ulothrix zonata*, originated from marine systems. If soft bottom substrates are included in the analysis, the number of species occurring in the Baltic Sea increases slightly but not dramatically due to the presence of some charophytes (Nielsen et al., 1995; Schubert et al., 2003). Only a few freshwater macroalgae occur on hard substrates, and areas with soft bottoms were not included in this study. The present-day flora of the Baltic Sea is merely a subset of the cold-temperate flora of the North Atlantic (Lüning, 1985), even though adaptation of macroalgal species to brackish environments can be observed (e.g., Russell, 1985; Rietema, 1991; Rueness and Kornfeldt, 1992; Nygard and Dring, 2008). However, no specific brackish algal flora exists, and this leads to the continuous decrease of species numbers observed in all studies of macroalgal distribution along the salinity gradient in the Baltic Sea (Fig. 7B–F). For the marine algae, the general trend and the slope of declining numbers of species match the classic trend curve published for the benthic macrofauna (Remane, 1934). However, our results clearly show the pronounced non-linear decrease in macroalgal species diversity within the horohaliniacum (i.e., at salinities of 5–8 psu), which was not the case for macrozoobenthos (Remane, 1934); moreover, this trend differs significantly from Remane's curve.

Thus, the horohaliniacum has been interpreted as a 'threshold region' for macroalgae, where species composition changes drastically (Wallentinus, 1991). In the present study, the similarity of the floristic composition of the ten investigation sites was analyzed using Jaccard's index and subsequent cluster analysis (Sneath and Sokal, 1973). As shown in Fig. 6, two distinct groups are detected; one includes all sites with salinity above 7.2 psu, and another includes all sites within and below the horohaliniacum (3.9–7.2 psu). This result is not an indicator of species turnover, as it might be interpreted at first sight; the dissimilarity between the two distinguished salinity ranges simply stems from the number of species shared with adjacent areas. Because there is a rapid decline in species numbers between 5 and 8 psu, only half of the species are shared between 4.9 and 7.2 psu, whereas sites at higher salinities have many more species in common.

An analysis like this is important when comparing stations with similar species numbers (i.e., Bergström and Bergström, 1999), but it is less valuable for a large spatial gradient with a strong and rapid reduction in species numbers. The dendrogram in Fig. 6 shows the mentioned loss of species and indicates that habitats in low salinity areas are quite uniform and consist of only a few species of macroalgae. This can also be inferred from the drop in the Shannon index values (Fig. 4A), illustrating an abrupt reduction in biodiversity. The evenness values reflect the distribution and dominance of species at a particular site (Fig. 4B). The drop in the evenness at 5.4 psu indicates that some of the species present become dominant, which is typical for fast-growing opportunistic annuals. The fact that some species become dominant is also shown by the extension of the lower depth limit of the filamentous algal zone below 7 psu (Fig. 5). This coincides with the downward

spread of the brown algal belt, represented solely by *F. vesiculosus* in this salinity range.

Assessment of the relative roles of natural processes and anthropogenic influences on aquatic communities is one of the key problems for ecosystem evaluation and management, especially in estuarine and coastal environments (Golubkov et al., 2003; Elliott and Quintino, 2007; Alimov and Golubkov, 2008). In this study, the observed effects can be attributed to the decrease in salinity because the impacts of eutrophication, exposure, substratum, or the combination of different sampling methods and data sources have been minimized as much as possible by selecting only medium-exposed sampling sites with hard substrates. Even the impact of climatic differences was kept low by locating all study sites at nearly the same geographic latitude. The effectiveness of this approach to the selection of study sites was additionally demonstrated by the similarity in the curves showing dynamics of the macroalgal species numbers in this study and in the previous works. The latter fact implies that salinity is a superior driver for macroalgal diversity and distribution, and therefore, the trends in these characteristics of macroalgae communities are practically not affected by (minor) differences in research methodology and choice of taxonomic groups or by dissimilarity of the study sites.

Our results clearly demonstrate the pronounced non-linearity in the distribution of macroalgal species diversity within the horohaliniacum. This fact supports the horohaliniacum concept (Khlebovich, 1969, 1974; Kinne, 1971) and backs up the universal nature of this barrier salinity zone that separates the main flora and fauna complexes and ecological groups of aquatic organisms that represent various modes of life (i.e., drifting plankton, sedentary benthos, or attached macroalgae) and different cellular and biochemical types of homeostasis (Telesh and Khlebovich, 2010). Meanwhile, the net effect of the salinity gradient and environmental variability in general on the overall biological diversity is still largely unknown (Huisman and Weissing, 1999; Roelke et al., 2003; de Jonge, 2007; Benincá et al., 2008). Nevertheless, as the recent findings that show that the distribution of planktonic protists challenges the classic *Artenminimum* concept (Telesh et al., 2011a,b), our data on macroalgal diversity in the Baltic Sea is likewise inconsistent with the major brackish-water biodiversity rule of Remane (1934).

New ideas often take time to be recognized and adopted. Our field data on macroalgal diversity in the salinity gradient of the Baltic Sea has now risen in importance due to a modern reassessment of the application range of Remane's concept (Telesh et al., 2011a,b). As a result, the updated knowledge on the macroalgal and planktonic diversity in the brackish-water Baltic Sea, derived from the field experimental studies and meta-analyses of large-scale long-term biodiversity data sets, reduces the applicability of Remane's model to macrozoobenthos only. Further development of ecological concepts and high quality integral models based on both modern biodiversity data and an understanding of the economic aspects of their utilization is essential for increasing the predictive power of our ecosystem-health forecasts and for improving environmental management for our large brackish-water ecosystems.

Acknowledgements

This study was financed by the DFG – project Schu 983/5-1 and partly supported by Grants RFBR 10-04-00943, 10-04-90420, 11-04-00053, LSS 3276.2010.4, Program "Biodiversity" of the Presidium of the Russian Academy of Sciences and the German Federal Ministry of Education and Research (project RUS 09/038). Christian Boedeker, Phillip Riel and Sven Ihnken supported the fieldwork by diving and mapping algae on two field trips. The help of Pauli

Snoeijs (Stockholm University), Gustav Johannson (Uppsala University) and Ari Ruuskanen (Helsinki University) in identifying suitable investigation sites in Sweden and Finland is gratefully acknowledged.

References

- Alimov, A.F., Golubkov, S.M., 2008. Changes in the ecosystems of the eastern Gulf of Finland. *Herald of Russian Academy of Sciences* 3, 223–230.
- Attrill, M.J., 2002. A testable linear model for diversity trends in estuaries. *Journal of Animal Ecology* 71, 262–269.
- Barnes, R.S.K., 1989. What, if anything, is a brackish water fauna? *Transactions of the Royal Society of Edinburgh Earth Science* 80, 235–240.
- Benincá, E., Huisman, J., Heerkloss, R., Johnk, K.D., Branco, P., Van Nes, E.H., Scheffer, M., Ellner, S.P., 2008. Chaos in a long-term experiment with a plankton community. *Nature* 451, 822–827.
- Bergström, L., Bergström, U., 1999. Species diversity and distribution of aquatic macroalgae in the Northern Quark, Baltic Sea. *Nordic Journal of Botany* 19 (3), 375–383.
- Bergström, L., Tatarenkov, A., Johannesson, K., Jönsson, R.B., Kautsky, L., 2005. Genetic and morphological identification of *Fucus radicans* sp. Nov. (Fucales, Phaeophyceae) in the brackish Baltic Sea. *Journal of Phycology* 41, 1025–1038.
- Boesch, D.F., Diaz, R.J., Virnstein, R.W., 1976. Effects of tropical storm Agnes on soft-bottom macrobenthic communities of the James and York estuaries and the lower Chesapeake Bay. *Chesapeake Science* 17, 246–259.
- Breeman, A.M., 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds – Experimental and phenological evidence. *Helgoländer Meeresuntersuchungen* 42, 199–241.
- Burrows, E.M., 1991. Seaweeds of the British Isles, vol. 2 (Chlorophyta). The Natural History Museum, HMSO, London.
- Crump, B.C., Armbrust, E.V., Baross, J.A., 1999. Phylogenetic analysis of particle-attached and free-living bacterial communities in the Columbia river, its estuary, and the adjacent coastal ocean. *Applied and Environmental Microbiology* 65, 3192–3204.
- Deaton, L.E., Greenberg, M.J., 1986. There is no horohalinicum. *Estuaries* 9, 20–30.
- De Jonge, V.N., 1974. Classification of brackish coastal inland waters. *Hydrobiological Bulletin* 8, 29–39.
- De Jonge, V.N., 2007. Toward the application of ecological concepts in EU coastal water management. *Marine Pollution Bulletin* 55, 407–414.
- Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review* 33, 245–303.
- Dixon, P.S., Irvine, L.M., 1977. Seaweeds of the British Isles, vol. 1 (Rhodophyta), Part 1 – Introduction, Nemaliales, Gigartinales. British Museum (Natural History), Publ. 781, London.
- Dolan, J.R., Gallegos, C.L., 2001. Estuarine diversity of tintinnids (planktonic ciliates). *Journal of Plankton Research* 23, 1009–1027.
- Elliott, M., Quintino, V., 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* 54, 640–645.
- Feistel, R., Weinreb, S., Wolf, H., Seitz, S., Spitzer, P., Adel, B., Nausch, G., Schneider, B., Wright, D.G., 2010. Density and absolute salinity of the Baltic Sea 2006–2009. *Ocean Science* 6, 3–24.
- Golubkov, S.M., Alimov, A.F., 2010. Ecosystem changes in the Neva Estuary (Baltic Sea): natural dynamics or response to anthropogenic impacts? *Marine Pollution Bulletin* 61, 198–204.
- Golubkov, S.M., Alimov, A.F., Telesh, I.V., Anokhina, L.E., Maximov, A.A., Nikulina, V.N., Pavel'eva, E.B., Panov, V.E., 2003. Functional response of midsummer planktonic and benthic communities in the Neva Estuary (eastern Gulf of Finland) to anthropogenic stress. *Oceanologia* 45 (1), 53–66.
- Gordeev, V.V., 1983. River Drainage to the Ocean and Its Hydrochemical Features (in Russian). Nauka, Moscow, p. 160.
- Herlemann, D.P.R., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J.J., Andersson, A.F., 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME Journal*, doi:10.1038/ismej.2011.41.
- Hewson, I., Fuhrman, J.A., 2004. Richness and diversity of bacterioplankton species along an estuarine gradient in Moreton Bay. *Australian Applied and Environment Microbiology* 70, 3425–3433.
- Hiscock, S., 1979a. A field key to the British brown seaweeds (Phaeophyta). *Field Studies Council Occasional Publication* 5 (1). Dorset Press, Dorchester, p. 44.
- Hiscock, S., 1979b. A field key to the British red seaweeds (Rhodophyta). *Field Studies Council Occasional Publication* 13. Dorset Press, Dorchester, p. 101.
- Hoffmann, C., 1932. Zur Frage der osmotischen Zustandsgrößen bei Meeressalgen. *Planta* 17, 805–809.
- Hoffmann, C., 1943. Der Salzgehalt des Seewassers als Lebensfaktor mariner Pflanzen. *Kieler Blätter: Veröffentlichungen der Wissenschaftlichen Akademie des NSD* 3, 160–176.
- Hoffmann, C., 1950. Ueber das Vorkommen endemischer Algen in der Ostsee. *Kieler Meeresforschungen* 7, 24–34.
- Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402, 407–410.
- Jaccard, P., 1912. The distribution of the flora of the alpine zone. *New Phytologist* 11, 37–50.
- Kalvestad, N., 1978. The marine algae of the polluted inner part of the Oslofjord. *Botanica Marina* 21, 71–97.
- Kautsky, L., Kautsky, H., 1989. Algal species diversity and dominance along gradients of stress and disturbance in marine environments. *Vegetatio* 83, 259–267.
- Khlebovich, V.V., 1968. Some peculiar features of the hydrochemical regime and the fauna of mesohaline waters. *Marine Biology* 2, 47–49.
- Khlebovich, V.V., 1969. Aspects of animal evolution related to critical salinity and internal state. *Marine Biology* 2, 338–345.
- Khlebovich, V.V., 1974. The Critical Salinity of Biological Processes (in Russian). Nauka, Leningrad, p. 236.
- Khlebovich, V.V., 1989. Critical salinity and horohalinicum: modern analysis of concepts. *Proceedings of Zoological Institute* 196, 5–11 (in Russian).
- Khlebovich, V.V., 1990. Some physico-chemical and biological phenomena in the salinity gradient. *Limnologia (Berlin)* 20 (1), 5–8.
- Kinne, O., 1971. *Marine Ecology*. Wiley Interscience, London.
- Kirst, G.O., 1990. Salinity tolerance of eukaryotic marine algae. *Annual Review of Plant Physiology and Plant Molecular Biology* 41, 21–53.
- Kornmann, P., 1964. Ectocarpaceen-Studien von Paul Kuckuck. *Biologische Anstalt Helgoland*, 1–239.
- Kylin, H., 1907. Studien über die Algenflora der schwedischen Westküste. *Akademische Abhandlungen Uppsala (Dissertation)*, Uppsala, p. 285.
- Lalli, C.M., Parsons, T.R., 1997. *Biological Oceanography – An Introduction*. Butterworth-Heinemann, Oxford, pp. 314.
- Laprise, R., Dodson, J.J., 1994. Environmental variability as a factor controlling spatial patterns in distribution and species-diversity of zooplankton in the St-Lawrence Estuary. *Marine Ecology Progress Series* 107, 67–81.
- Lass, H.-U., Matthäus, W., 2008. General Oceanography of the Baltic Sea. In: Feistel, R., Nausch, G., Wasmund, N. (Eds.), *State and Evolution of the Baltic Sea 1952–2005*. John Wiley & Sons Inc., Hoboken, NJ, pp. 5–44.
- Lindgren, P.E., 1964. Coastal algae off Göteborg in relation to gradients in salinity and pollution. *Acta Phytogeographica Suecica* 50, 92–98.
- Lüning, K., 1985. Meeresbotanik, Verbreitung, Ökophysiologie und Nutzung der marinen Makroalgen. Thieme-Verlag, Stuttgart.
- Maggs, C., Hommersand, M.H., 1993. Seaweeds of the British Isles, vol. 1 (Rhodophyta), Part 3A (Ceramiales). The Natural History Museum, HMSO, London.
- McLusky, D.S., Elliott, M., 2004. *The Estuarine Ecosystem: Ecology Threats and Management*, third ed. University Press, Oxford, p. 214.
- Michaelis, H., Fock, H., Grotjahn, M., Post, D., 1992. The status of the intertidal zoobenthic brackish-water species in estuaries of the German Bight. *Netherlands Journal of Sea Research* 30, 201–207.
- Middelboe, A.L., 2000. Species diversity, distribution and abundance of marine macroalgae. Ph.D. thesis, University of Copenhagen, Copenhagen.
- Middelboe, A.L., Sand-Jensen, K., Krause-Jensen, D., 1998. Patterns of macroalgal species diversity in Danish estuaries. *Journal of Phycology* 34, 457–466.
- Middelboe, A.L., Sand-Jensen, K., 2004. Patterns of species number and abundance in macroalgal communities in coastal waters. *Hydrobiologia* 511, 173–183.
- Mironova, E.I., Telesh, I.V., Skarlato, S.O., 2009. Planktonic ciliates of the Baltic Sea. *Inland Water Biology* 2, 13–24.
- Munda, I., 1978. Salinity dependent distribution of benthic algae in estuarine areas of Icelandic fjords. *Botanica Marina* 21, 451–468.
- Munda, I., 1982. The effects of organic pollution on the distribution of fucoid algae from the Istrian coast (vicinity of Rovinj). *Acta Adriatica* 23 (1/2), 329–337.
- Muylaert, K., Sabbe, K., Vyverman, W., 2009. Changes in phytoplankton diversity and community composition along the salinity gradient of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal and Shelf Science* 82, 335–340.
- Nielsen, R., Kristiansen, A., Mathiesen, L., Mathiesen, H., 1995. Distributional index of the benthic macroalgae of the Baltic Sea area. *Acta Botanica Fennica* 155, 1–50.
- Nygard, C.A., Dring, M.J., 2008. Influence of salinity, temperature, dissolved inorganic carbon and nutrient concentration on the photosynthesis and growth of *Fucus vesiculosus* from the Baltic and Irish Seas. *European Journal of Phycology* 43 (3), 253–262.
- Pravdič, V., Jednačák-Biscan, J., Juráček, M., 1981. Physico-Chemical Parameters Describing the Role of Particulate Material in Estuarine Waters. *River Inputs to Ocean System*. UNEP and UNESCO, Switzerland, pp. 188–196.
- Remane, A., 1934. Die Brackwasserfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft, Greifswald*, 34–74.
- Remane, A., 1940. Einführung in die zoologische ökologie der Nord- und Ostsee. In: Grimpe, G., Wagler, E. (Eds.), *Die Tierwelt der Nord- und Ostsee*. vol. 1 (1a) Akad. Verlagsgesellschaft. Leipzig, pp. 1–238.
- Remane, A., 1955. Die Brackwasser-Submergenz und die Umkomposition der Coenosen in Belt- und Ostsee. *Kieler Meeresforschungen* 11, 59–73.
- Remane, A., 1958. Ökologie des Brackwassers. In: Remane, A., Schlieper, C. (Eds.), *Die Biologie des Brackwassers. Binnengewässer*, 22, pp. 1–216.
- Remane, A., 1969. Wie erkennt man eine genuine Brackwasser art? *Limnologia* 7, 9–21.
- Remane, A., Schlieper, C., 1958. Die Biologie des Brackwassers. In: Thienemann, A. (Ed.), *Die Binnengewässer, Schweizerbart'sche Verlagsbuchhandlung*, Stuttgart.
- Remmert, H., 1989. Ökologie – Ein Lehrbuch. Springer-Verlag, Berlin.
- Rietema, H., 1991. Evidence for ecotypic divergence between *Phycodrys rubens* populations from the Baltic Sea and North Sea. *Botanical Marina* 34, 375–381.
- Roelke, D., Augustine, S., Buyukates, Y., 2003. Fundamental predictability of multispecies competition: the influence of large disturbance. *American Naturalist* 162, 615–623.

- Rueness, J., Kornfeldt, R., 1992. Ecotypic differentiation in salinity responses of *Ceramium strictum* (Rhodophyta) from Scandinavian waters. *Sarsia* 77, 207–212.
- Russell, G., 1985. Recent evolutionary changes in the algae of the Baltic Sea. *British Phycology Journal* 20, 87–104.
- Schiewer, U., 2008. *Ecology of Baltic Coastal Waters*. Springer-Verlag, Berlin, Heidelberg.
- Schubert, H., Mathiesen, L., Blindow, I., 2003. The brackish environment. In: Schubert, H., Blindow, I. (Eds.), *Charophytes of the Baltic Sea*, A.R.G. Gantner Verlag Kommanditgesellschaft, Ruggell FL, pp. 15–26.
- Schubert, H., Schories, D., 2008. Macrophytobenthos. In: Feistel, R., Nausch, G., Wasmund, N. (Eds.), *State and Evolution of the Baltic Sea 1952–2005*. John Wiley & Sons Inc., Hoboken, NJ, pp. 483–542.
- Sneath, P.H.A., Sokal, R.R., 1973. *Numerical Taxonomy*. Freeman, San Francisco.
- Snoeijs, P., Johansson, G., 1999. *Swedish Marine and Brackish-Water Algae*, third ed. Uppsala University, Uppsala.
- Telesh, I.V., 2004. Plankton of the Baltic estuarine ecosystems with emphasis on Neva Estuary: a review of present knowledge and research perspectives. *Marine Pollution Bulletin* 49, 206–219.
- Telesh, I.V., Khlebovich, V.V., 2010. Principal processes within the estuarine salinity gradient: a review. *Marine Pollution Bulletin* 61, 149–155.
- Telesh, I.V., Elliott, M., de Jonge, V.N., 2010. Estuarine ecosystems: structure, function and management (ECSA-42 Symposium in Russia). *Marine Pollution Bulletin* 61, 147–148.
- Telesh, I.V., Schubert, H., Skarlato, S.O., 2011a. Revisiting Remane's concept: evidence for high plankton diversity and a protistan species maximum in the horohaliniacum of the Baltic Sea. *Marine Ecology Progress Series* 421, 1–11.
- Telesh, I.V., Schubert, H., Skarlato, S.O., 2011b. Protistan diversity does peak in the horohaliniacum of the Baltic Sea: Reply to Ptacnik et al. (2011). *Marine Ecology Progress Series* 432, 293–297.
- Van Beusekom, J.E.E., de Jonge, V.N., 1994. The role of suspended matter in the distribution of dissolved inorganic phosphate, iron and aluminium in the Ems estuary. *Netherlands Journal of Aquatic Ecology* 28 (3–4), 383–395.
- Wallentinus, I., 1979. Environmental influences on benthic macrovegetation in the Trosa – Askö area, northern Baltic Proper, II. The ecology of macroalgae and submersed phanerogams, vol. 25. Stockholm University, Stockholm.
- Wallentinus, I., 1991. The Baltic Sea gradient. In: Mathieson, A.C., Nienhus, P.H. (Eds.), *Ecosystems of the World, 24. Intertidal and Littoral Ecosystems*. Elsevier, Amsterdam.
- WFD 2000/60/EC, Directive 2000/60/EC of the European parliament, of the council of 23 October, 2000. Establishing a framework for Community action in the field of water policy. *Official Journal of the European Communities L* 327 (1), 1–72.
- Zenkewitch, L.A., 1959. The classification of brackish-water basins as exemplified by the seas of the USSR. *Archivio di Oceanografia e Limnologia* 11, 53–61.