Review

Life in the salinity gradient: Discovering mechanisms behind a new biodiversity pattern

Irena Telesh [a,c,*], Hendrik Schubert [b], Sergei Skarlato [c]

[a] Zoological Institute, Russian Academy of Sciences, Universitetskaya Embankment, 1, Saint Petersburg 199034, Russia
[b] Institute of Biological Sciences, University of Rostock, Rostock 18059, Germany
[c] Institute of Cytology, Russian Academy of Sciences, Saint Petersburg 194064, Russia

A B S T R A C T

A recently discovered paradoxical maximum of planktonic protistan species in the salinity gradient of the Baltic Sea revealed an inverse trend of species number/salinity relation in comparison to the previously accepted species-minimum model for macrozoobenthos. Here, we review long-term data on organisms of different size classes and ecological groups to show that eukaryotic and prokaryotic microbes in plankton demonstrate a maximum species richness in the challenging zone of the critical salinity 5–8, where the large-bodied bottom dwellers (macrozoobenthos, macroalgae and aquatic higher plants) experience large-scale salinity stress which leads to an impoverished diversity. We propose a new conceptual model to explain why the diversity of small, fast-developing, rapidly evolving unicellular plankton organisms benefits from relative vacancy of brackish-water ecological niches and impaired competitiveness therein. The ecotone theory, Hutchinson's Ecological Niche Concept, species–area relationships and the Intermediate Disturbance Hypothesis are considered as a theoretical framework for understanding extinctions, speciation and variations in the evolution rates of different aquatic species in ecosystems with the pronounced salinity gradient.

1. Introduction

Biological and environmental gradients are common attributes of all aquatic ecosystems worldwide, from an ephemeral pool to ocean depths. In ecology, the gradient can be specified as the rate at which one set of parameters or traits changes in relation to the others. The fitness of aquatic organisms for certain abiotic conditions emerges from the interaction of multiple fine-level traits and the environment the organism encounters, which varies along numerous gradients producing its characteristic temporal and spatial distribution (Barton et al., 2013). Ultimately, ecological changes in populations and communities of organisms generally track environmental gradients, ecosystem variability and climate change which drive biodiversity and large-scale biogeographical patterns.

A synthesis of global published data reveals that biodiversity loss is becoming a major driver of ecosystem change as extinctions are altering key processes important to the productivity and sustainability of ecosystems (Hooper et al., 2012). A suit of data meta-analyses show that the impacts of diversity loss on ecological processes might be sufficiently large to rival the impacts of many other global drivers of environmental change such as drought, ultraviolet radiation, climate warming, ozone, acidification, elevated CO_2, herbivory, fire and certain forms of nutrient pollution (Cardinale, 2012). Given worldwide declines in species and the increasing role of species invasions in structuring natural communities, there is much evidence that biodiversity may thus control but not just respond to ecological processes (Reich et al., 2012), although its impact differs as interrelated ecosystem structure and functions vary across a wide range of environmental conditions (Palmer and Febria, 2012).

Whereas the biological processes underlying biogeochemical ones are generally well characterized, understanding the relationship of biodiversity to ecosystem functioning poses a number of fundamental challenges: e.g. developing an ability to integrate across relatively unexplored dimensions of biodiversity, such as microbial diversity, to explain ecosystem responses to key global

* Corresponding author. Zoological Institute, Russian Academy of Sciences, Universitetskaya Embankment, 1, Saint Petersburg 199034, Russia, Institute of Cytology, Russian Academy of Sciences, Saint Petersburg 194064, Russia.
E-mail addresses: itelesh@zin.ru, itelesh@yahoo.com (I. Telesh), hendrik.schubert@uni-rostock.de (H. Schubert), s_skarlato@yahoo.com (S. Skarlato).

change factors including biodiversity loss (Naeem et al., 2012), or shifting conventional viewpoints by providing novel insights into how much diversity is needed to maintain the productivity of ecosystems (Cardinale, 2012). In the light of new information and understanding, there is a constant need to test and review established paradigms that are generally structured around some fundamental aspects of science (Elliott and Whitfield, 2011; Telesh et al., 2011a). Specifically, the nonlinear interactions observed in nature are often responsible for existence of principal discontinuities and thresholds that challenge the usual linear way of thinking and contrast with traditional explanations of ecological complexity (Solé and Bascompte, 2006).

Fluctuating salinity is one of the major natural stress factors for aquatic biota in coastal waters of seas, estuaries, other brackish environments, hyperhaline water bodies, etc. It is known that alterations in salinity regime and other chemical and physical conditions, together with nutrient input and grazing pressure strongly affect the diversity, community structure and temporal dynamics of phytoplankton (Winder and Sommer, 2012), as well as the fauna (de Jonge, 1974). Phytoplankton constitutes a major portion of microscopically-small, unicellular eukaryotic microbes (protists), and plankton in general. These microbial components of pelagic biota, which occupy the base of aquatic food webs, as well as their multicellular consumers are vulnerable to environmental alterations and climate change and can cause serious repercussions for the entire ecosystem (Winder and Sommer, 2012). Hence we question how (if ever) species diversity impacts ecosystem functionality, productivity, and vulnerability to alien species invasions in aquatic environments?

Robust linkages between biodiversity, productivity, and stability across trophic levels in marine ecosystems were indicated by a number of original studies, and identified mechanisms behind those linkages include complementary resource use, positive interactions, and increased selection of highly performing species at high diversity (Worm et al., 2006; Loreau and de Mazancourt, 2013, and references therein). For example, ciliate diversity, community structure and dynamics in a solar saltern (a system of interconnected hypersaline evaporating ponds) in the coastal area of the Yellow Sea may influence salt production (Lei et al., 2009).

Moreover, bacterial genetic diversity measured in operational taxonomic units (OTUs) demonstrates unusual distribution patterns. This can be exemplified by data from the 2000 km long salinity gradient within a large brackish-water Baltic Sea (Herlemann et al., 2011). The results from the conventional, discontinued "gradient" composed of the data from separate water bodies with different salinity (e.g., the case study of 32 Tibetan lakes described by Wang et al., 2011) also conform to the above conclusion. This latter case, however, represents a dataset of independent water salinity values from distinct water bodies rather than a real, natural salinity gradient. Therefore, we suggest terming such case a 'ruptured gradient' in order to differentiate it from environmental gradients that naturally develop and evolve within an ecosystem.

At the same time, microbial diversity in the broad sense, i.e. diversity of both prokaryotic and eukaryotic unicellular organisms, and its functional role in aquatic ecosystems is a very large field of knowledge which is traditionally underestimated unless focused studies are performed. In particular, recent investigations have begun to elucidate how environmental factors influence microbial communities at different scales, and estimate the traits of poorly known microbial species which sometimes number in the millions of taxonomic units when genetic diversity is considered (Naeem et al., 2012). Moreover, new data and a re-analyses of historical knowledge on microbial diversity are transforming the traditional view of biodiversity in certain environments, e.g. in large brackish

water bodies (Schubert et al., 2011; Herlemann et al., 2011; Telesh et al., 2011a,b), small isolated brackish-water systems (as shown by de Jonge, 1974), small isolated lakes (Wang et al., 2011), and transitional estuarine waters; this new knowledge underpins novel biodiversity concepts and generates paradigm shifts (Elliott and Whitfield, 2011). The very large increase of data on microbial biodiversity over the past few decades has radically changed the basic brackish-water concepts putting forward a question whether biodiversity distribution patterns of planktonic microbes in the salinity gradient differ from those of multicellular large bottom-dwelling organisms (Schubert et al., 2011; Wang et al., 2011; Telesh et al., 2011a,b), and if so, what might be the reasons of this phenomenon.

Here, we advocate the idea that salinity gradient provides a subsidy for the small-bodied, fast-developing and rapidly evolving unicellular planktonic microbes, and develop conceptual basics for discrimination between microbial plankton biodiversity patterns versus distribution of benthic macroorganisms, macroalgae and higher plants in the salinity gradient in natural aquatic ecosystems. We further discuss possible reasons of this paradoxical discrepancy of life within the salinity gradient and the perspectives for unraveling the evolutionary, ecological, physiological and molecular mechanisms responsible for the recently discovered excitingly high microbial diversity in the conditions of salinity stress. We highlight the impact of climate on the performance of environmental gradients and outline their role in extinction, speciation and evolution of aquatic species.

2. Salinity gradient: stress or subsidy?

Salinity of natural waters is one of the main environmental factors which define structural and functional characteristics of aquatic biota. Effects of salinity fluctuations are most striking in estuaries and other brackish coastal waters that are generally characterized by a more or less pronounced salinity gradient. It may even be postulated that an 'estuarine' ecosystem develops everywhere in the conditions of the salinity gradient, as one of the recent definitions of an estuary generalizes (Telesh and Khlebovich, 2010, and references therein). The flora and fauna of these ecosystems is rather specific (Telesh, 2004). Internal fluxes such as remineralization and resuspension of organic material (de Jonge and van Beusekom, 1995), input of external organic materials (de Jonge, 1995), and the continuous flow-through of allochthonous organic matters (Van Beusekom and de Jonge, 1994) support high productivity in these environments (de Jonge and de Jong, 2002; de Jonge et al., 2002; Telesh and Khlebovich, 2010).

The salinity gradient plays an important role promoting sinks of organic matter and nutrients, dissolved and particulate matter as well as their associated compounds (de Jonge and de Jong, 2002). The execution of filtering capacity by an ecosystem depends on the intensity of various environmental gradients, primarily on the decrease rate of water flow velocity from the river mouth to the outer estuary which, in turn, influences the magnitude of the salinity gradient. Thus, the salinity gradient is a decisive environmental feature whose presence or absence distinguishes different types of water bodies. Since recently, this feature has been included in the definition of estuaries as trans-boundary regions between river and sea where the fresh and saline waters mix and which ecosystems are characterized by a variety of inter-related biotic and abiotic structural components naturally undergoing change in space and time along with intensive chemical, physical and biological processes exposed against a salinity gradient (Telesh and Khlebovich, 2010). Other definitions of estuaries are reviewed in the above mentioned paper (Telesh and Khlebovich, 2010, and references therein), and the major paradigms in estuarine ecology

are extensively discussed elsewhere (Elliott and Whitfield, 2011; Whitfield et al., 2012).

Usually, the salinity gradient is unstable, depending on freshwater inflow rate and tidal regime; however, it can also be rather stable or even permanent in the cases of tideless estuaries or large brackish water bodies such as the Baltic Sea, the Caspian Sea, or the Chesapeake Bay. As hypothesized earlier (Elliott and Quintino, 2007), the high natural variability in estuaries may confer an ability to withstand stress, both natural and anthropogenic – a supposition which logically supports the idea that in estuaries salinity decrease may not be a stress (with only negative effect on biota) but subsidy – a perturbation with a positive effect on the system (Costanza et al., 1992).

This viewpoint can be best exemplified by plankton of the semi-closed, brackish, tideless Baltic Sea which is a large 'estuary-like' water body due to significant freshwater inflow from the Neva Estuary in the east and fully saline water intrusions from the North Sea in the west. Being the largest stable brackish water habitat of the world, the Baltic Sea is a suitable model of a generally non-tidal water basin characterized by the pronounced gradients of climatic and hydrological factors affecting the occurrence and distribution of aquatic plant and animal species. The salinity gradient in this sea is uniquely smooth and stable, and the horohalinicum zone of 'critical' salinities 5–8[1] (Khlebovich, 1968; Kinne, 1971) occupies the major area of the Baltic proper as well as a great part of the extensive coastal zone of the sea (Schiewer, 2008). 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 in the north and the Neva Bay of the Gulf of Finland in the north-east (Feistel et al., 2010).

Biodiversity data from this specific sea allow distinguishing between groups of aquatic organisms for which the salinity gradient within the horohalinicum can act either as stressor or as subsidy. Recent investigations document the difference in a species richness distribution mode of macrozoobenthos, macrophytes and plankton within the salinity gradient, with an emphasis on horohalinicum where the salinity changes and biotic alterations are the sharpest (Bleich et al., 2011; Herlemann et al., 2011; Schubert et al., 2011; Telesh et al., 2011a). Specifically, it was shown that in case of variable or abrupt salinity gradient, the adverse environmental conditions provide significant stress to bottom-dwelling aquatic organisms and the effect is greatest for sessile macro-fauna and macrophytes while plankton, especially their smallest fractions react differently to salinity fluctuations (Schubert et al., 2011; Telesh et al., 2011a,b).

2.1. Macrozoobenthos

Marine and freshwater benthic macroinvertebrates demonstrate reduced taxonomic diversity with gradual salinity change towards the minimum number of species (*Artenminimum*) at the 'critical' salinities 5 to 8 *sensu* Khlebovich (1968), i.e. within the horohalinicum *sensu* Kinne (1971) (Fig. 1A, broken line). This rule was best described by the conceptual diagram of Remane (1934). Thus, it can be postulated that for sedentary or slowly moving bottom-dwelling forms sharp salinity fluctuations around 5–8 are stressful.

Zenkewitch (1959) described the similar *Artenminimum* zones in the Azov and Caspian seas. For the Baltic Sea, recent studies
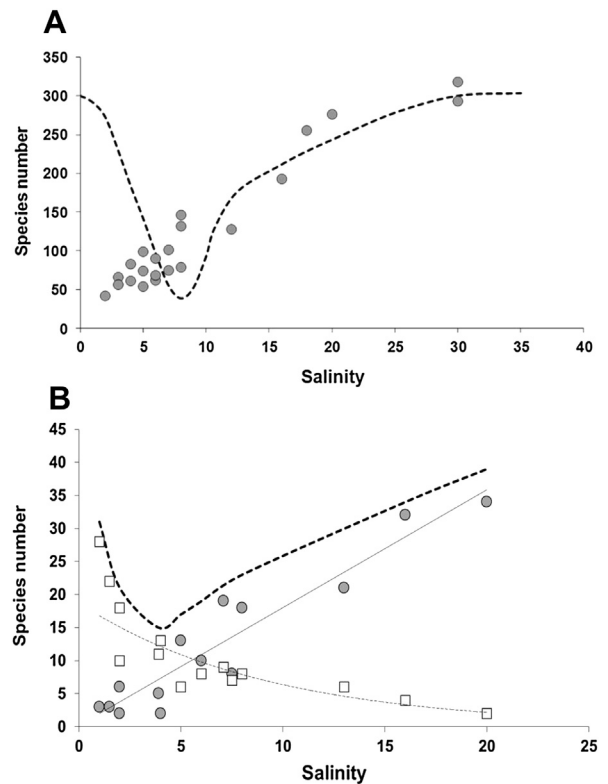

Fig. 1. A: Distribution of species number of macroalgae at different salinities in the Baltic Sea (filled circles; data from Nielsen et al., 1995) versus the reconstructed Remane curve (broken line). B: Distribution of species number of macroalgae (filled circles) and aquatic higher plants (empty squares) at different salinities during long-term field studies along the German Baltic coast in 2000 through 2006; the broken line shows the sum curve for combined species number of macroalgae and higher plants; trend lines for macroalgae (thin solid line) and higher plants (thin dotted line) are indicated; each dot – average for at least 20 transects.

showed that the number of marine invertebrate taxa decreased 10-fold between the Kattegat (ca. 850 macroscopic animal species) and the Baltic proper (ca. 80), the Bothnian Sea (ca. 50) and the innermost Bothnian Bay (<10) (Leppäkoski and Olenin, 2000). Josefson (2009) also established that the species number increased by a factor of 10 between salinities of 10 and 33. In the Pomeranian Bay, where salinity ranges between 6 and 10, Powilleit et al. (1995) found 20 taxa in 1993 through 1994. Bleich et al. (2011) agreed with other findings (e.g. Josefson and Hansen, 2004; Josefson, 2009) and showed that the decline in salinity down to the horohalinicum level is the main factor in the decreasing species richness across the Baltic Sea. These authors did not investigate macrozoobenthic diversity in the oligohaline regions of the sea; however, they found strong evidence that species richness increased significantly below salinity 3, mainly through intervening/accessory freshwater taxa such as insects (i.e. chironomids and trichoptera) and oligochaetes (Perus and Bonsdorff, 2004; Piscart et al., 2005). Thus, recent studies of the macrozoobenthos of the Baltic Sea, albeit still disembodied and lacking generalization for the entire sea, indirectly support Remane's conceptual assertions for benthic macro-invertebrates.

2.2. Macroalgae and higher plants

Macroalgae on different substrata in the Baltic Sea show a stable linear decrease of species number with the salinity decrease from fully marine in the Danish Straits to oligohaline conditions in the Gulf of Bothnia (Fig. 1A). Macroalgae on hard substrata also

---

[1] Salinity is reported using the Practical Salinity Scale approved by the Joint Panel of Oceanographic Tables and Standards, according to which salinity is defined as a pure ratio, and has no dimensions or units.

decrease in species richness linearly until salinity reaches the value of approximately 1.0 (Fig. 1B, circles), below which practically no macroalgae can be found, mainly due to the negligible availability of hard substrata in the freshwater reaches of the Baltic estuaries (Schubert et al., 2011). This trend, shown by different researchers and reviewed by us recently (e.g., Fig. 7 in Schubert et al., 2011), is clearly different from Remane's curve for macrozoobenthos (Remane, 1934).

However, if the data on species number of aquatic higher plants (Fig. 1B, squares) are combined with macroalgal species numbers (Fig. 1B, circles), the resulting trend line (Fig. 1B, dotted line) reveals the species minimum in the horohalinicum and remarkably resembles the Remane curve for macrozoobenthos (Fig. 1A). Nevertheless, the former is underpinned by totally different mechanisms responsible for diversity distribution of aquatic vegetation if compared with the latter for zoobenthos. Indeed, a total lack or limited availability of hard substrata in the oligohaline reaches of the Baltic salinity gradient is responsible for the minimum number of macroalgae species at the critical salinities 5–8 (Schubert et al., 2011). However, field data witness that the number of freshwater higher plants is exponentially increasing below 5–8 towards lower salinities (Fig. 1B). As a result, the trend line of the combined curve resembles the Remane diagram. This conclusion is supported by the original data showing the shift in composition of macrophytes from dominance of epilithic forms at salinities above 15 to prevalence of rooted or epiphytic ones at salinities below 5 (Fig. 2).

2.3. Plankton

Contrary to bottom-dwellers, small-sized motile plankton organisms, presumably prokaryotes and eukaryotic microbes, or protists, i.e. practically all eukaryotic unicellular organisms irrespective of whether they are heterotrophs (protozoa), phototrophs (protophytes), or mixotrophs, demonstrate the opposite distribution mode, with maximum species richness in the horohalinicum; these findings have recently served the basics for the novel 'protistan species-maximum concept' (Telesh et al., 2011a).

To provide new insights into the role of salinity gradients and microbial diversity in maintaining ecosystem stability, we
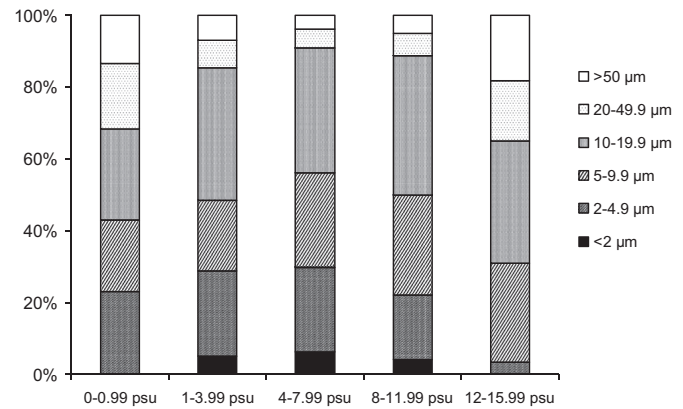
Fig. 3. Percentage of phytoplankton size classes at different salinities in the Baltic Sea. A dataset of approximately 3000 samples collected during the long-term monitoring studies along the German Baltic coast, including the inner coastal water bodies, was analyzed for the relative distribution of algae of different size classes within a salinity gradient. Each salinity class is represented by data from at least 200 samples. The total number of data analyzed exceeds 10,000 data points with respect to cell size information (for details about the database see Sagert et al., 2008).

performed size-group composition analysis (Fig. 3) which evaluates the shifts in the plankton community structure towards dominance of small, fast-evolving organisms in the salinity-stressed environment. A dataset of approximately 3000 phytoplankton samples taken along the German Baltic coast, including the inner coastal water bodies, was analyzed for the relative size class distribution. Each salinity class is represented by data from at least 200 samples; the total number of data analyzed exceeds 10,000 data points with respect to the size of algal cells (for details about the database see Sagert et al., 2008). The results of the analyses clearly demonstrate that the total species richness of algae with cell size below 20 μm is highest at the salinities ranging between 4 and 12, while outside this range the share of larger algae tends to increase (Fig. 3).

The size of phytoplankton cells constrains many of their physiological rates, biotic interactions and behavior within the fluid environment (e.g. sinking speed); therefore, cell size might play a key role in determining the diversity and relative abundance of
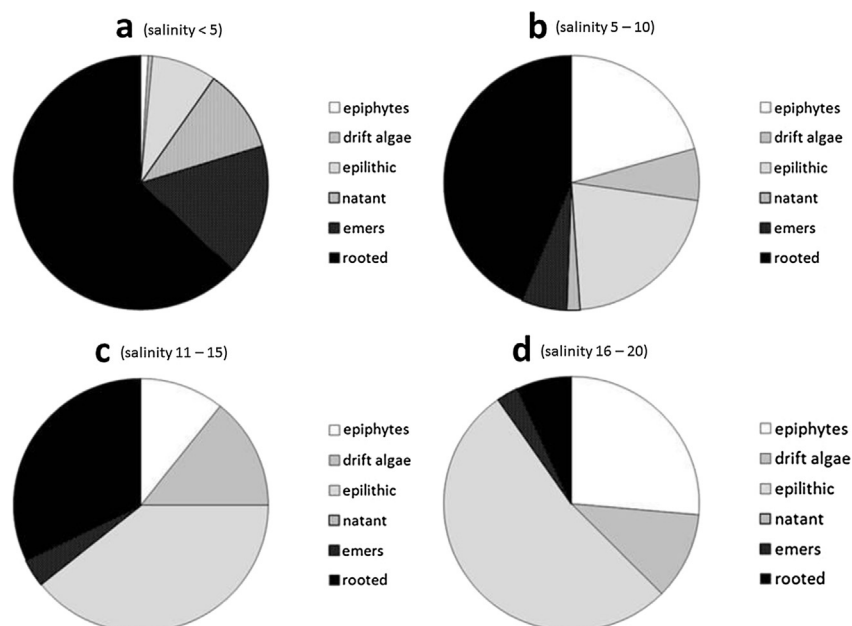
Fig. 2. Dominance (% of total species number) of macrophyte groups at different salinities in the Baltic Sea. Shift from prevalence of rooted forms at salinities below 5 to dominance of epiphytes at salinities above 15 is demonstrated.

competing phytoplankton species (Barton et al., 2013). Meanwhile, for the entire plankton community the species richness of major plankton groups and their contributions to the overall pelagic diversity in the Baltic Sea account for dominance of protists *sensu lato*, Heterokontophyta and Ciliophora in particular (Telesh et al., 2011a). Thus, the horohalinicum most likely provides subsidy rather than stressful environment for the smallest planktonic protists as they demonstrate high physiological adaptability to fluctuating salinity (Stock et al., 2002) which allows them to prosper in the conditions of variable environment within the salinity gradient. The positive effect here is expressed by the maximum species richness of eukaryotic microbes and prokaryotic cyanobacteria in the horohalinicum that can capitalize on the lack of inter-specific competition and thus achieve not only high population densities (e.g. Herlemann et al., 2011) but also reach the exceptionally high taxonomic diversity (Telesh et al., 2011a); the latter ensures the ecosystem is maintained as a benefit for those species adapted to the inherently variable conditions (Elliott and Quintino, 2007).

3. Horohalinicum or ecotone: minimum or maximum of species?

The recently discovered high protistan species richness and its specific distribution with maximum in the horohalinicum at salinities 5–8 (Telesh et al., 2011a) is in accordance with one of the classical patterns: the increased biodiversity within a border zone, an ecotone, due to the mixing of biota from two adjacent systems, marine and freshwater. Paradoxically, this phenomenon has hardly been documented in estuarine ecotones (Attrill, 2002; Elliott and Whitfield, 2011; Basset et al., 2013). Meanwhile, the Baltic horohalinicum is evidently an example of the exceptionally large-scale pelagic ecotone system where the microplankton communities demonstrate the increased biodiversity (Fig. 4), as it would be expected in a classical ecotone, due to high degree of cosmopolitanism of many planktonic protists and their effective physiological adaptations to subsidy of brackish environment.

Not actually supporting the extreme idea of considering the entire Baltic Sea as a giant estuary which has been repeatedly debated in the literature (e.g. Schubel and Pritchard, 1990; McLusky and Elliott, 2004, and references therein), we nevertheless cannot ignore the fact that the protistan species maximum (Fig. 4) and the recently discovered high overall plankton diversity in the Baltic Sea (Telesh et al., 2011a) are among the major characteristic features of
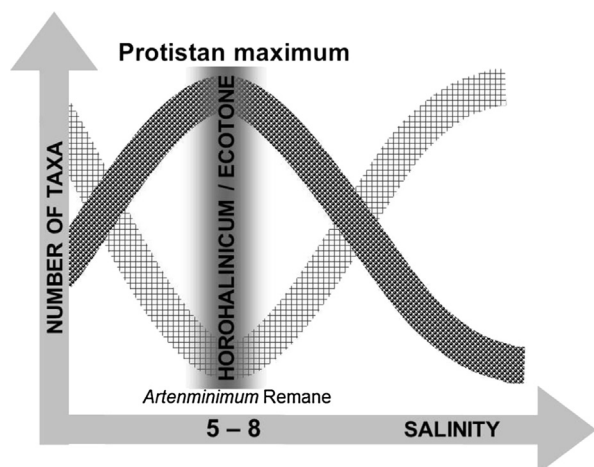

Fig. 4. The protistan species maximum versus Remane's *Artenminimum* in the horohalinicum as an ecotone.

an ecotone pointing indirectly at the optional estuarine quality of this peculiar sea.

The mechanisms behind the phenomenon of protistan species maximum in the horohalinicum as an ecotone are still to be investigated. On the one hand, the impact of salinity gradient on different aquatic communities is not yet fully understood; similarly, the net effect of environmental fluctuations on the overall biological diversity is still largely unknown (Huisman and Weissing, 1999; Roelke et al., 2003; de Jonge, 2007; Benincà et al., 2008). On the other hand, it is already an established fact that the Remane minimum of macrozoobenthic species within the horohalinicum (Remane, 1934) and the similar pattern for macroalgal and higher plant diversity change (Fig. 1) undoubtedly confront the peculiarity of spatial dynamics of plankton diversity in the salinity gradient (Fig. 4). This contradiction denotes significant differences in reaction to salinity fluctuations between assemblages of large sessile or attached organisms versus small motile plankton-dwellers that are driven by water masses to considerable distances (Telesh et al., 2011a).

Using the data from the recent findings, we described the differences mentioned above by simple mathematical formulae (Table 1) and proposed a conceptual model for spatial dynamics of the species number of micro- and macro-organisms in the salinity gradient of a large estuary-like brackish water body (Fig. 5).

As seen in Fig. 5, the diversity of planktonic bacteria, measured in operational taxonomic units and therefore reflecting the molecular diversity, differs notably from other trend lines which reflect the dynamics of the morphological species diversity, and demonstrates a steady line for the bacteria within the studied salinity range, with variation around the relatively constant average values of approximately 350 OTUs per sampling site. Measured for the first time within the entire 2000 km long Baltic Sea salinity gradient (Herlemann et al., 2011), this remarkable molecular bacterial diversity accounts for a large variety of favorable environmental conditions for these microbes in the study area; their distribution trend line reflects only a small impact of salinity fluctuations on the number of bacterial OTUs. Reduced bacterial diversity in brackish conditions was not established, possibly due to the rapid adaptation rate of the bacteria which has enabled a variety of lineages to fill what for higher organisms remains a challenging and relatively unoccupied ecological niche (Herlemann et al., 2011).

Alternatively, the dynamics of species number of macrozoobenthos, macrophytes, cyanobacteria and planktonic protists in the salinity gradient can be all approximated by the polynomial (binomial) trend lines (Fig. 5). However, the curves for protists (unicellular eukaryotes) and cyanobacteria (unicellular prokaryotes) mirror the trend lines for macro-organisms, thus demonstrating maximum species numbers in the horohalinicum, contrary to the minimum of benthic species numbers in this critical salinity zone. Explanations for this amazing integrity, and at the same time discrepancy, are not evident; they require further analyses, experimenting, and certain theoretical generalizations which might contribute to understanding why species numbers of fast and small protists and cyanobacteria peak in the 'critical' zone of the salinity gradient contrary to slow-moving, sedentary or rooted, relatively large bottom inhabitants that experience dramatic osmotic stress in the same environment.

4. Fast and small versus large and slow

Additionally to the ecotonal characteristics of the critical salinity zone, which evidently subsidizes the protistan species maximum, several other solid theoretical explanations can be provided for the discovered diversity distribution trends. Among those,

Table 1
Diversity distribution trends for macro- and microorganisms in the salinity gradient.

Organisms	Equation	Description of trend	Comments
Macrozoobenthos	$y = a_1 x^2 - b_1 x + c_1$	Polynomial trend; minimum species number in the horohalinicum.	The data for analysis are taken from Remane (1934).
Macrophytes	$y = a_2 x^2 - b_2 x + c_2$	Polynomial trend; minimum species number in the horohalinicum.	Macrophytes here are macroalgae and higher plants; for reference data see: Schubert et al. (2011).
Protists	$y = -a_3 x^2 + b_3 x + c_3$	Polynomial trend; maximum species number in the horohalinicum.	Protists are all eukaryotic unicellular photo-, mixo- and heterotrophic organisms; for reference data see: Telesh et al. (2011a).
Cyanobacteria	$y = -a_4 x^2 + b_4 x + c_4$	Polynomial trend; maximum species number in the horohalinicum.	Prokaryotic unicellular organisms, commonly considered as essential part of phytoplankton; for reference data see: Telesh et al. (2011a).
Bacteria	$y = $ const.	Linear trend; variation around relatively stable mean value.	Very high molecular diversity; "taxa" – operational taxonomic units (OTUs); for reference data see: Herlemann et al. (2011).

Hutchinson's Ecological Niche Concept (Hutchinson, 1957), the species–area relationships (Kratochwil, 1999), especially those developed for protists (Gaston, 2000; Fenchel and Finlay, 2004; Fuhrman, 2009), and the Intermediate Disturbance Hypothesis (Connell, 1978) provide the most convincing arguments in favor of the new biodiversity-in-the-gradient concept for protists (Telesh et al., 2011a), thus constructing a theoretical framework for understanding extinctions, speciation, and variations in the evolution rates of aquatic organisms.

4.1. Ecological Niche Concept

According to Hutchinson (1957), the ecological niche can be defined as the n-dimensional hyper-volume where dimensions are the environmental conditions and the resources that allow a population to exist. Considering this viewpoint in combination with the Gause competitive exclusion principle (Hardin, 1960) which states that no two species can occupy the same niche in the same environment (habitat) for a long time provides an understanding that the number of species in a given habitat depends on the number of distinct niches.

If salinity effects are not taken into account and other environmental gradients are considered as having only a minor impact on determining the niches, then we generally have no arguments to expect the existence of different number of niches in freshwater and marine habitats; consequently, the number of species should also be similar in freshwater and marine habitats within one water body. This logic naturally admits that potential niches can be still left open in cases where evolution has not yet delivered the

respective specialists – e.g., in the brackish waters, and therefore the eurytopic species there are still without specialized competitors that might have been outcompeting them and disjointing the niche.

However, freshwater as well as marine habitats are known as relatively stable ones (Remmert, 1969), allowing for long evolutionary histories of organisms which are filling the niches within these habitats. Therefore, applying the assumptions given above to the data on macrozoobenthos diversity provided by Remane (1934), we can conclude that both marine and freshwater ranges of the Baltic Sea ecosystem are filled in with species, but there is still a biodiversity gap in between – i.e., in the brackish environment. This presumes that the brackish-water biodiversity gap has not yet been filled with the respective species because of the relatively short evolutionary time during which this geologically young brackish-water sea has been existing (Lass and Matthäus, 2008). Therefore, the vacant brackish water niches here are first invaded by the fastest, the smallest, rapidly evolving and the most highly adaptable organisms: the bacteria and the protists. New data on planktonic ciliates in the Neva Estuary (eastern Baltic Sea) supports this conclusion, showing, for example, that among the 111 ciliate species discovered in the area during 2007–2009, 12% of species were freshwater, 14% known from only marine and/or brackish waters, while most species were small ciliates of 20–30 μm with a broad range of salinity tolerance (Telesh et al., 2009; Mironova et al., 2012, 2013).

Moreover, the relative vacancy of brackish pelagic niches in the Baltic Sea can be proved by the intensively on-going niche-occupation process which can be well illustrated by the high rate of unintentional biological invasions of planktonic alien species through different natural and human-mediated pathways from other marine and freshwater basins (Telesh et al., 2011a, and references therein). Among the most recent multicellular plankton invaders are the ponto-caspian species: onychopod crustaceans *Cercopagis pengoi* and ctenophores *Mnemiopsis leidyi* that have successfully established permanent populations which cause a significant impact on the Baltic Sea ecosystem (Ojaveer et al., 2010).

In the microbial world, some successful invasive species, e.g. potentially toxic dinoflagellates *Prorocentrum minimum* in the Baltic Sea, and also many native organisms exploit a peculiar life strategy, mixotrophy, which allows these tiny organisms to consume both inorganic and organic substrata for their mixotrophic growth, largely depending on the environmental conditions (Matantseva and Skarlato, 2013). Due to this strategy, such microorganisms reside at different trophic levels: as primary producers and consumers. This ability ensures their competitiveness in invading empty niches, underpins a high taxonomic diversity of mixotrophs, and promotes their exclusively important role in the brackish-water ecosystem functioning. Recently, mixotrophy of
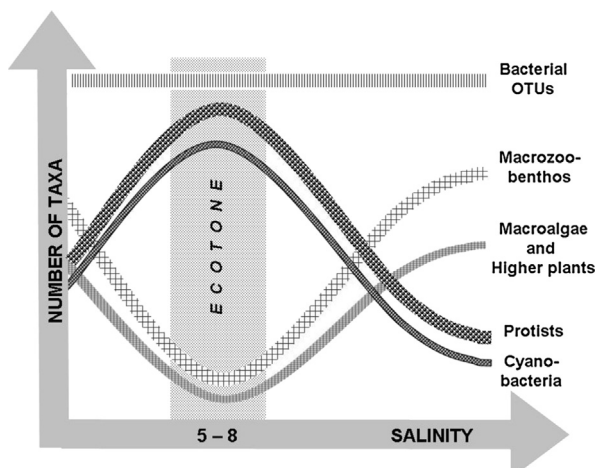

Fig. 5. Distribution of microbes and macro-organisms in the salinity gradient.

traditional autotrophs (such as dinoflagellates) and classical het-erotrophic protists (e.g. ciliates) has been proved to be very com-mon in the oceans globally rather than an exception, as thought earlier (reviewed by Matantseva and Skarlato, 2013; Barton et al., 2013). This phenomenon can cause a significant paradigm shift in the present understanding of trophic web organization and func-tioning, contributing to the development of the Ecological Niche Concept.

Mixotrophy is common in the Baltic protists (Mironova et al., 2012, 2013; Matantseva and Skarlato, 2013, and references therein); however, the knowledge of physiological and molecular grounds of this phenomenon is insufficient. Further investigations of the microorganism molecular and functional traits and the implication of this new knowledge to mechanically define ecolog-ical niches for plankton (Litchman et al., 2012) may provide addi-tional proof of relative vacancy of brackish-water niches in the Baltic Sea.

4.2. Species—area relationship

Another supportive argument is the species—area relationship, which on a global scale restricts the number of species within a habitat to the size of a given habitat (Kratochwil, 1999). In the case of brackish water habitats (e.g., in estuaries), that are relatively narrow and usually not interconnected, the taxonomic diversity is generally low, limiting the evolution of specialized forms, as shown for other fragmented ecosystems (Templeton et al., 2001). More-over, the size of a habitat must also be considered in relation to the individual size of organisms — the larger an average organism, the smaller is the relative size of a habitat and, consequently, the slower is the evolution rate because of lower generation frequency within a population of larger organisms if compared to smaller ones (Schaefer, 1999).

However, the dimensions of the salinity gradient and, conse-quently, of its most stressful zone — the horohalinicum may be considerable, accounting for the major part of the entire area of the sea (as shown in Fig. 1 in Telesh et al., 2011a). Therefore, high protistan diversity, calculated as a result of large-scale spatial data meta-analysis (Telesh et al., 2011a), agrees relatively well with the general species—area relationships: the larger the studied area, the more species of organisms can be found there.

4.3. Environmental variability and the Intermediate Disturbance Hypothesis

Not less important is the variability of abiotic factors in the environment which sets limits to specialization rate (Whittaker, 1965). As postulated by the Intermediate Disturbance Hypothesis (Connell, 1978; Reinolds et al., 1993), the variability of external stress must be related to generation time of organisms; in case the environmental factor fluctuates more frequently, the period during which an organism lives under the optimum conditions may not be sufficient enough to support the population maintenance during the sub-optimum conditions.

For example, the large-scale salinity gradient may be sur-prisingly stable both in space and time, and this can be well-illustrated by the highly constant average salinity within a long-term cycle (Fig. 6A). However, the inter-annual variations as well as the average salinity fluctuations at smaller time scales (months and days) usually demonstrate remarkable amplitudes. Particularly, the data for August 1985 in the Zingster Strom (Darss-Zingst bodden chain, German Baltic coast) show that the daily average salinity values can fluctuate in a range from 3.4 to 7.6 within a decade, and the amplitude of this variation may be even larger during the winter months (Fig. 6B). This high
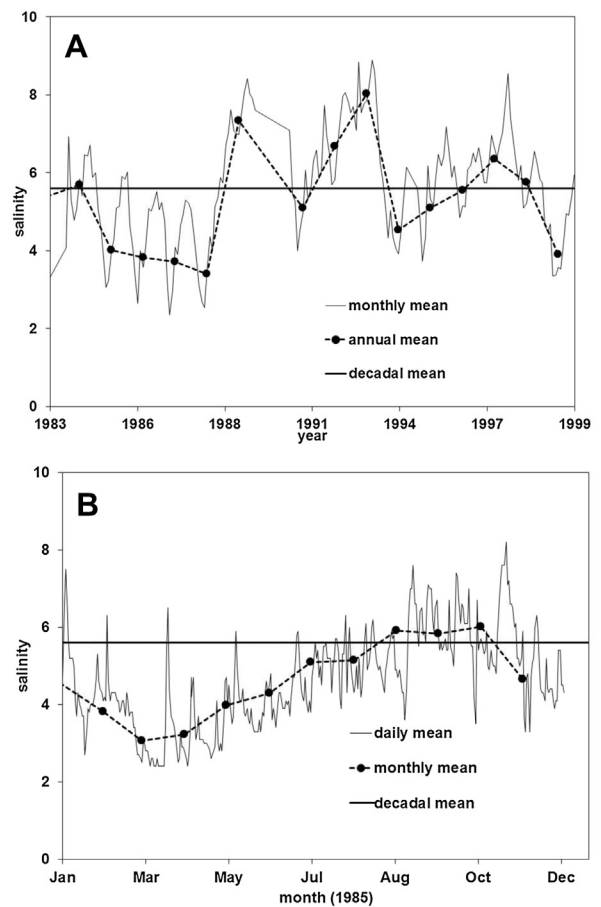

Fig. 6. Long-term (A) and short-term (B) salinity fluctuations around a stable decadal mean value (thick solid line) demonstrate comparable amplitudes in the Zingster Strom (Darss-Zingst bodden chain, German Baltic coast).

variability of salinity and the subsequently high frequency of stress events is far shorter than the generation times of benthic organisms and macrophytes that are measured in months. However, this frequency of salinity stress is quite comparable to the generation turnover times of planktonic organisms that ac-count for several weeks (e.g., pelagic crustaceans) or days (e.g., rotifers), and especially of the protists whose generation times are measured in hours.

Therefore, the environmental variability has different critical stress levels for planktonic and benthic organisms: benthos is exposed to the adverse effects of moving waters of different salinity, whereas plankton are moving within these water masses, thus avoiding large-scale salinity fluctuations. It is of note that the average salinity ranges taken as a measure in the Remane con-ceptual model for macrozoobenthos (Remane, 1934) grade though imply large variability of this stress factor which reaches the lethal limits of individual salinity tolerance of many benthic invertebrates in the critical zone within the horohalinicum.

Meanwhile, for many planktonic organisms, high salinity tolerance might still provide sub-optimal conditions under salinity stress, and this reduces the strength of resource competition, allowing co-existence of species which otherwise might have been outcompeted. Moreover, the short generation times of planktonic organisms, especially the smallest of them — the protists, might have allowed evolution of more brackish-water specialists, or rather provide benefit to the organisms us-ing a subsidy of just being cosmopolitans, as many protists are (Fenchel and Finlay, 2004). At least, many ciliate species certainly

tend to have much broader geographic ranges and occur more widely than is typically observed for most multicellular taxa (Azovsky and Mazei, 2013).

Assuming similar physiological salinity tolerance ranges for freshwater and marine plankton and zoobenthos, respectively, the higher stability of the salinity regime for the planktonic ones (due to their transfer within water masses) allows for a less sharp decline of species number with changing salinity from both sides: from fresh to brackish waters, as well as from marine to brackish environment, if compared to the same trend for macrobenthos (Fig. 7). As a result of this differentiated reaction to salinity fluctuations, the sum curve for benthic species demonstrates the minimum at critical salinities (Fig. 7A), while the sum curve for plankton species numbers peaks in the same zone (Fig. 7B).

Thus, the higher stability of the environmental regime for plankton drifting within water masses and being therefore less affected by salinity fluctuations provides another simple, mechanistic explanation of the protistan species maximum in the salinity gradient. Consequently, the high plankton/protistan species diversity may have buffering impact on the ecosystem resistance to and recovery after external or natural stresses, which generates an insurance value that is worth being incorporated into future economic valuations and management decisions (Worm et al., 2006) concerning large brackish water ecosystems with pronounced environmental gradients.
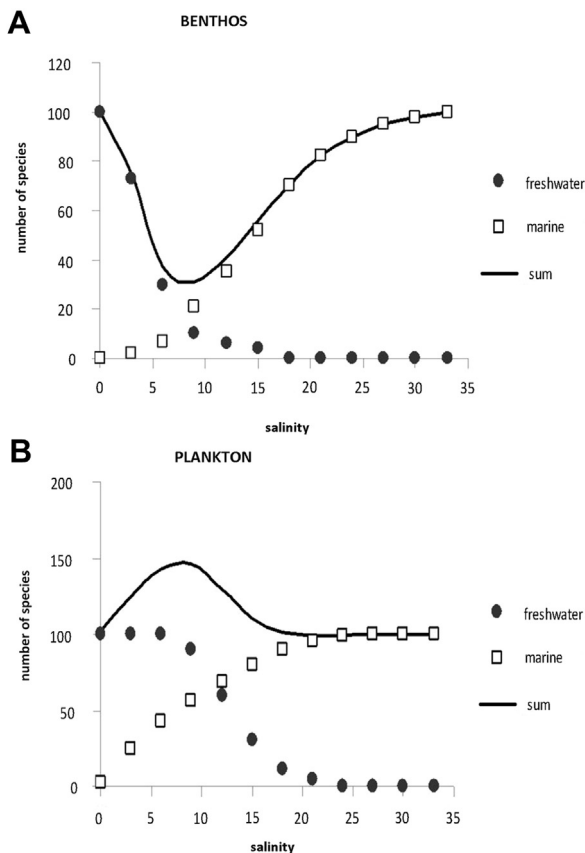

Fig. 7. Mechanistic explanation of the planktonic protistan species maximum and the benthic species minimum in the horohalinicum. A sharper decline of benthic species number with changing salinity from freshwater and marine sites towards the horohalinicum result in species minimum (A), while a less sharp decline of plankton species numbers is responsible for the sum curve with maximum species number in the same zone (B), due to different salinity tolerance ranges of benthic and planktonic organisms.

5. Role of environmental gradients in extinction, speciation and evolution of aquatic species

The above data analyses allowed us to hypothesize how evolution has formed macroecology of aquatic organisms that follow large-scale patterns in diversity and distribution within biological and abiotic gradients which provide best fitness for small planktonic fast-evolvers in the environments that are adverse for large, slowly-evolving bottom dwellers. New findings show that environmental gradients drive biodiversity patterns and functional community traits on both local and the global scales. For example, the recent survey of 1342 species of marine benthic ciliates from 17 geographical regions proved statistically that, within a global latitudinal salinity gradient, the north-east Atlantic region hosts the richest fauna of these microbes (711 species), followed by the brackish-water Baltic, Caspian and Black seas (559, 517 and 493 species, respectively); meanwhile the fully saline Kara Sea (113), southern and central Pacific (111) and the Red Sea (48 species) are the poorest (Fig. 1 in Azovsky and Mazei, 2013). These latter authors clearly demonstrate that the low-saline seas (Baltic, Caspian and Black) have the richest local diversity, contrary to the Caribbean, Mediterranean and Red seas, which have less diverse ciliate fauna than expected according to recent knowledge, albeit being well established earlier as marine biodiversity hotspots for metazoans (Myers et al., 2000). Thus, the latitudinal global diversity patterns for benthic eukaryotic microbes and metazoans also differ (Azovsky and Mazei, 2013), as already shown earlier for the regional diversity of planktonic protistan vs. benthic metazoan communities within the sea-scale salinity gradient (Telesh et al., 2011a,b).

Other environmental gradients may strongly affect species turnover and the diversity. However, recent analysis of the long-term data on phytoplankton demonstrated that the most important environmental gradients which can be expressed by eutrophication-related parameters (total and mineral nutrients) revealed low association with the phytoplankton community composition in all Baltic Sea sub-basins, thus proving that eutrophication gradients have little impact on phytoplankton community at the regional scale (Olli et al., 2011). Alternatively, marine bivalves and the entire macrozoobenthic community of the Wadden Sea clearly tended to show their maximum species richness at intermediate environmental conditions, such as sediment coarseness, speed of currents, and intertidal height (Beukema and Dekker, 2012).

At much smaller scales, strong chemical and physical gradients are created in the immediate environment of the microscopic organisms due to turbulence-driven variations in viscosity of fluids, excretions from larger organisms, cell lysis, and sloppy feeding (Stocker, 2012). These pervasive gradients at the scale relevant to microorganisms, including the bacteria, act as powerful evolutionary drivers which provide fitness advantage to motile cells, and therefore can affect species diversity and composition. Specifically for the bacteria, as spatial and temporal gradients in the nutrient landscape represent two formidable dimensions in niche space, it seems plausible that the diversity of motile forms is generally larger than the diversity of nonmotile forms because, given the high energetic cost of motility, cells might have evolved adaptive strategies to exploit gradients (Stocker, 2012). However, unlike longitudinal gradients in species abundance of marine microorganisms (Fuhrman, 2009; Azovsky and Mazei, 2013), little ecological theory has been applied at the scale of microbial microenvironments; in this realm, fitness-based models can promote evaluation of the role of specific adaptations to life in the gradients, such as high swimming speeds, hybrid locomotion, and metabolic plasticity (Stocker, 2012).

Rather than a cause of extinctions, environmental stress along gradients has been highlighted as a potential source of new species (Lexer and Fay, 2005). An unparalleled example of rapid speciation of a large, multicellular organism in the conditions of significant environmental stress imposed by the salinity gradient is the *Fucus vesiculosus–Fucus radicans* speciation event in the Baltic Sea (Pereyra et al., 2009). The salinity gradient which spans an order of magnitude (3–30) has caused strong local adaptation in most of the marine lineages that survived the marine/brackish transition of this water body (Johannesson and André, 2006). This remarkable example of two closely related species of brown algae offers opportunities to better understand the role of salinity gradients for the benthic-species-poor ecosystems, where competition is low and gene flow is expected to be high, and additionally investigate their function as peripheral extreme environments suitable for species formation (Pereyra et al., 2009).

An amazing example of a paradoxically high ciliate diversity in a hypersaline lagoon of Spain was described recently, and this unexpected diversity was not only due to a variety of halophilic and marine species, but also due to numerous brackish and freshwater species which have emerged within the adverse environment of the salinity gradient (Esteban and Finlay, 2003). Environmental gradients in the lagoon ecosystems are known to maintain differential selection favoring genetic differentiation which is expected to produce gradients in genetic polymorphism correlated with varying environmental conditions, particularly salinity and temperature (Marino et al., 2010). As exemplified by the case study of *Holothuria polii* (sea cucumber, an echinoderm) from the Man Menor lagoon, one of the largest coastal lagoons in Europe and the Mediterranean Basin (Vergara-Chen et al., 2010), high values of genetic diversity can also be recorded despite (or due to?) high instability of the lagoon environment and presence of the pronounced salinity gradient.

6. Impact of climate on the performance of environmental gradients

Model predictions postulate that the marine environment is expected to change substantially over the current century in response to greenhouse gas emissions (Barton et al., 2013), other anthropogenic impacts and global climate change (de Jonge and de Jong, 2002). Although major ecosystem patterns likely stem from fundamental principles of community organization, the evolutionary responses are generally shaped by climate (Solé and Bascompte, 2006). These large-scale climate-driven ecological alterations consequently translate into variability in performance of major environmental gradients. Specifically, it is anticipated that ocean water temperature will increase, particularly at the surface, which will cause increases in the thermal stratification of the water column while the latter pattern is imprinted on the changes in salinity regime (Barton et al., 2013, and references therein).

Moreover, we can hypothesize that an increase in air temperatures may enhance evaporation in certain sea areas which will be followed by the decreased river inflow to the estuaries and the sea coastal waters, and the consequent shifts in salinity regime towards increased salinity as well as changes in the steepness, extent and effects of the salinity gradients. Alternatively, enhanced glacial melting will probably result in ecosystem alterations attributed to lower salinities in the coastal environment. The latter event was demonstrated by shifts in the phytoplankton community composition off the Antarctic Peninsular from diatom-dominated assemblages to cryptophyte-dominated ones, and in the size structure of the community to smaller average cell size as a consequence (Moline et al., 2004).

The impact of global climate change on aquatic biodiversity is not straightforward and is translated through direct and (mainly) indirect effects on biota. A cascade of links between the large-scale climate patterns and the local climate variability synergistically govern environmental and biological gradients causing the chain of events at all levels of ecosystem organization. The consequences of these interlinked climate-driven events can bring about unusual biodiversity shifts: e.g. blooms of the newly recorded centric diatoms *Proboscia indica* and *Rhizosolenia hebetata* f. *semispina* in the English Channel in 2005 (Gómez and Souissi, 2007), or the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean where the dominant zooplankton species vary under positive and negative phases of the North-Atlantic Oscillation because each phase favors different species by imposing different hydrodynamic features (Molinero et al., 2005, 2008). These climate impacts are consequently causing a cascade amplification of effects at higher trophic levels: e.g. fluctuations in the North Sea plankton have resulted in long-term changes in cod recruitment enhanced by overfishing (Brander et al., 2004).

A general shift toward harmful algal bloom (HAB) species with global warming has been predicted by some authors (reviewed by Fu et al., 2012); however, this effect is also confounded by a number of co-varying processes such as eutrophication. For example, an increased frequency of HABs in the Chesapeake Bay is anticipated based on reviewed historical data and present understanding and prediction of how modified precipitation, nutrient inputs, etc. might act together with the direct effects of climate change (Najjar et al., 2010).

Meanwhile, an array of knowledge on what changes will take place among higher plants and animals under the global climate change is much larger than our understanding of the effects of climate on microscopic species that form the base of aquatic food webs, and this gap exists due to pronounced underestimation of the breadth and depth of microbial diversity as well as our rudimentary understanding of the factors that control the structure and function of microbial communities (Caron and Hutchins, 2013). Moreover, a possible climate impact on the salinity gradients due to shifts in chemical and physical characteristics of water is still largely unknown, contrary to broadly discussed variations in temperature, pH and irradiance under the changing climate.

7. Conclusions

Evolution rate, mode of life and body size, or cell size in case of unicellular microbes, are the basic traits which determine the relative fitness of aquatic organisms in the environmental gradients (Fig. 8). Our revision of the major brackish water biodiversity concepts and the analysis of new data on the protistan species maximum in the horohalinicum of a large, stable, brackish-water sea has produced the following conclusions:

1. In the unstable environment with sharp salinity fluctuations, the structural and functional community regulations and life strategies of small unicellular protists and the bacteria inhabiting the microscopic world of the plankton differ substantially from those in the assemblages of large multicellular bottom-dwelling organisms.
2. The horohalinicum, or the zone of critical salinities 5 through 8, can be considered as an ecotone where the marine and freshwater biota meet, mix, and demonstrate peculiar species distribution patterns.
3. The organisms, which are most adaptable to salinity fluctuations – the eukaryotic protists and prokaryotic microbes drifting within water masses, paradoxically develop high
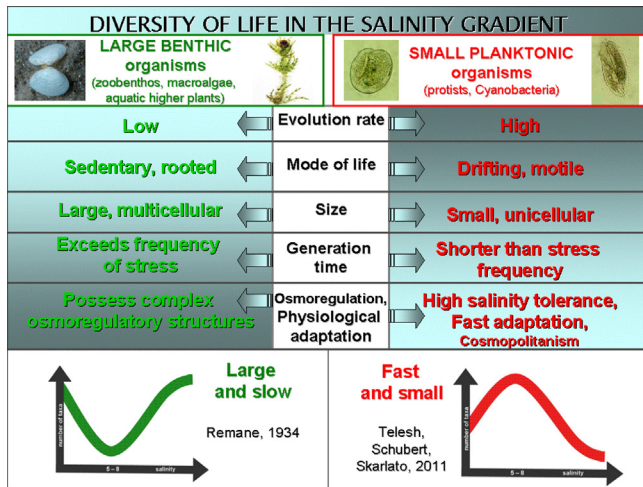
Fig. 8. Major traits underpinning macro- and microorganism diversity in the salinity gradient.

species richness in the ecotone region where the large-bodied bottom dwellers (macrozoobenthos, macroalgae and aquatic higher plants) experience a large-scale salinity stress which leads to an impoverished benthic diversity.

4. The diversity of small-bodied, fast-developing and rapidly evolving unicellular plankton benefits from the relative vacancy of brackish-water ecological niches and impaired competitiveness within the pelagic communities in the horohalinicum. These considerations may have implication for the invasive biology, as they qualify for the high rate of alien species invasions, as shown for the brackish Baltic Sea.

5. The ecotone theory, Hutchinson's Ecological Niche Concept, the species–area relationship, environmental variability rate and the Intermediate Disturbance Hypothesis provide a set of solid arguments in favor of the new conceptual model proposed in this paper. The model describes common features (i.e., polynomial distribution of species numbers) and differences (minimum vs. maximum of species) in trends for diversity distribution of large bottom-dwellers and unicellular plankton within the salinity gradient.

6. These results provide new insights into the role of environmental gradients in maintaining ecosystem stability under global climate change which have a prognostic value and significant implications for general, theoretical and applied ecology.

7. Ecological modeling and further experimental research into the fine physiological and molecular mechanisms (e.g., ability to mixotrophic growth), which underpin high adaptability of many protists to environmental instability, can provide a better understanding of biodiversity shifts, the balance between deterministic and stochastic processes and its role for niche formation in plankton, and the success of certain protistan species in the harsh conditions of environmental gradients.

Acknowledgments

References

Attrill, M.J., 2002. A testable linear model for diversity trends in estuaries. J. Anim. Ecol. 71, 262–269.

Azovsky, A., Mazei, Yu., 2013. Do microbes have macroecology? Large-scale patterns in the diversity and distribution of marine benthic ciliates. Global Ecol. Biogeogr. 22, 163–172.

Barton, A.D., Pershing, A.J., Litchman, E., Record, N.R., Edwards, K.F., Finkel, Z.V., Kiørboe, T., Ward, B.A., 2013. The biogeography of marine plankton traits. Ecol. Lett. 16, 522–534.

Basset, A., Barbone, E., Elliott, M., Li, B.-L., et al., 2013. A unifying approach to understanding transitional waters: fundamental properties emerging from ecotone ecosystems. Estuar. Coast. Shelf Sci. 132, 5–16.

Benincà, 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.

Beukema, J.J., Dekker, R., 2012. Estimating macrozoobenthic species richness along an environmental gradient: sample size matters. Estuar. Coast. Shelf Sci. 111, 67–74.

Bleich, S., Powilleit, M., Seifert, T., Graf, G., 2011. β-diversity as a measure of species turnover along the salinity gradient in the Baltic Sea, and its consistency with the Venice System. Mar. Ecol. Progr. Ser. 436, 101–118.

Brander, K.M., Lindley, J.A., Souissi, S., Reid, P.C., Beaugrand, G., 2004. Plankton effect on cod recruitment in the North Sea. Nature 426, 661–664.

Cardinale, B., 2012. Impacts of biodiversity loss. Science 336, 552–553.

Caron, D.A., Hutchins, D.A., 2013. The effects of changing climate on microzooplankton community structure: drivers, predictions and knowledge gaps. J. Plankt. Res. 35, 235–252.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1303.

Costanza, R., Norton, B.G., Haskell, B.D., 1992. Ecosystem Health: New Goals for Environmental Management. Island Press, Washington, D.C., USA.

de Jonge, V.N., 1974. Classification of brackish coastal inland waters. Hydrobiol. Bull. 8 (1/2), 29–39.

de Jonge, V.N., 1995. Wind driven tidal and annual gross transports of mud and microphytobenthos in the Ems estuary, and its importance for the ecosystem. In: Dyer, K.R., D'Elia, C.F. (Eds.), Changes in Fluxes in Estuaries, pp. 29–40.

de Jonge, V.N., 2007. Toward the application of ecological concepts in EU coastal water management. Mar. Pollut. Bull. 55, 407–414.

de Jonge, V.N., de Jong, D.J., 2002. Ecological restoration in coastal areas in the Netherlands: concepts, dilemmas and some examples. Hydrobiologia 478, 7–28.

de Jonge, V.N., Elliott, M., Orive, E., 2002. Causes, historical development, effects and future challenges of a common environmental problem: eutrophication. Hydrobiologia 475 (476), 1–19.

de Jonge, V.N., van Beusekom, J.E.E., 1995. Wind and tide induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnol. Oceanogr. 40, 766–778.

Elliott, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar. Pollut. Bull. 54, 640–645.

Elliott, M., Whitfield, A.K., 2011. Challenging paradigms in estuarine ecology and management. Estuar. Coast. Shelf Sci. 94, 306–314.

Esteban, G.F., Finlay, B.J., 2003. Cryptic freshwater ciliates in hypersaline lagoon. Protist 154, 411–418.

Feistel, R., Weinreben, 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 Sci. 6, 3–24.

Fenchel, T., Finlay, B.J., 2004. The ubiquity of small species: patterns of local and global diversity. Bioscience 54, 777–784.

Fu, F.-X., Tatters, A.O., Hutchins, D.A., 2012. Global change and the future of harmful algal blooms in the ocean. Mar. Ecol. Progr. Ser. 470, 207–233.

Fuhrman, J.A., 2009. Microbial community structure and its functional implications. Nature 459, 193–199.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227.

Gómez, F., Souissi, S., 2007. Unusual diatoms linked to climatic events in the northeastern English Channel. J. Sea Res. 58, 283–290.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

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. ISME J., 1571–1579. http://dx.doi.org/10.1038/ismej.2011.41.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105–108.

Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402, 407–410.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22 (2), 415–427. http://artifex.org/~ecoreaders/lit/Hutchinson1957.pdf.

Johannesson, K., André, C., 2006. Life on the margin – genetic isolation and loss of variation in a peripheral marine ecosystem. Mol. Ecol. 15, 2013–2030.

Josefson, A.B., 2009. Additive partitioning of estuarine benthic macroinvertebrate diversity across multiple spatial scales. Mar. Ecol. Progr. Ser. 396, 283–292.

Josefson, A.B., Hansen, J.L.S., 2004. Species richness of benthic macrofauna in Danish estuaries and coastal areas. Global Ecol. Biogeogr. 13, 273–288.

Khlebovich, V.V., 1968. Some peculiar features of the hydrochemical regime and the fauna of mesohaline waters. Mar. Biol. 2, 47–49.

Kinne, O., 1971. Marine Ecology. Wiley Interscience, London.

Kratochwil, A., 1999. Biodiversity in Ecosystems: Principles and Case Studies of Different Complexity Levels. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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.

Lei, Ya., Xu, K., Choi, J.K., Hong, H.P., Wickham, S.A., 2009. Community structure and seasonal dynamics of planktonic ciliates along salinity gradient. Eur. J. Protistol. 45, 305–319.

Leppäkoski, E., Olenin, S., 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biol. Invas. 2, 151–163.

Lexer, C., Fay, M.F., 2005. Adaptation to environmental stress: a rare or frequent driver of speciation? J. Evol. Biol. 18, 893–900.

Litchman, E., Edwards, K.F., Klausmeier, C.A., Thomas, M.K., 2012. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Mar. Ecol. Progr. Ser. 470, 235–248.

Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16, 106–115.

Marino, I.A.M., Barbisan, F., Gennari, M., Giomi, F., Beltramini, M., Bisol, P.M., Zane, L., 2010. Genetic heterogeneity in population of the Mediterranean shore crab, *Carcinus aestuarii* (Decapoda, Portunidae), from the Venice Lagoon. Estuar. Coast. Shelf Sci. 87, 135–144.

Matantseva, O.V., Skarlato, S.O., 2013. Mixotrophy in microorganisms: ecological and cytophysiological aspects. J. Evol. Biochem. Physiol. 49 (4), 245–254.

McLusky, D.S., Elliott, M., 2004. The Estuarine Ecosystem: Ecology, Threats and Management, third ed. University Press, Oxford.

Mironova, E., Telesh, I., Skarlato, S., 2012. Diversity and seasonality in structure of ciliate communities in the Neva Estuary (Baltic Sea). J. Plankt. Res. 34, 208–220.

Mironova, E., Telesh, I., Skarlato, S., 2013. Planktonic ciliates of the Neva Estuary (Baltic Sea): community structure and spatial distribution. Acta Protozool. 52, 13–23.

Moline, M.A., Claustre, H., Frazer, T.K., et al., 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. Global Chang. Biol. 10, 1973–1980.

Molinero, J.K., Ibanez, F., Nival, P., Buecher, E., Souissi, S., 2005. The north Atlantic climate and the northwestern Mediterranean plankton variability. Limnol. Oceanogr. 50, 1213–1220.

Molinero, J.K., Ibanez, F., Souissi, S., Buecher, E., Dallot, S., Nival, P., 2008. Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. Global Chang. Biol. 14, 11–26.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336, 1401–1406.

Najjar, R.G., Pyke, C.R., Adams, M.B., et al., 2010. Potential climate-change impacts on the Chesapeake Bay. Estuar. Coast. Shelf Sci. 86, 1–20.

Nielsen, R., Kristiansen, A., Mathiesen, L., Mathiesen, H., 1995. Distributional index of the benthic macroalgae of the Baltic Sea area. Acta Bot. Fenn. 155, 1–50.

Ojaveer, H., Jaanus, A., MacKenzie, B.R., Martin, G., Olenin, S., Radziejewska, T., Telesh, I., Zettler, M.L., Zaiko, A., 2010. Status of biodiversity in the Baltic Sea. PLoS ONE 5 (9), e12467. http://dx.doi.org/10.1371/journal.pone.0012467.

Olli, K., Klais, R., Tamminen, T., Ptacnik, R., Andersen, T., 2011. Long term changes in the Baltic Sea phytoplankton community. Boreal Environ. Res. 16 (Suppl. A), 3–14.

Palmer, M.A., Febria, C.M., 2012. The heartbeat of ecosystems. Science 336, 1393–1394.

Pereyra, R.T., Bergström, L., Kautsky, L., Johannesson, K., 2009. Rapid speciation in a newly opened postglacial marine environment, the Baltic Sea. BMC Evol. Biol. 9, 70. http://dx.doi.org/10.1186/1471-2148-9-70.

Perus, J., Bonsdorff, E., 2004. Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. J. Sea Res. 52, 45–56.

Piscart, C., Moreteau, J.C., Beisel, J.N., 2005. Biodiversity and structure of macro-invertebrate communities along a small permanent salinity gradient (Meurthe River, France). Hydrobiologia 551, 227–236.

Powilleit, M., Kube, J., Maslowski, J., Warzocha, J., 1995. Distribution of macro-benthic invertebrates in the Pomeranian Bay (southern Baltic) in 1993/94. Bull. Sea Fish. Inst. 136, 75–87.

Reich, P.B., Tilman, D., Isbel, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336, 589–592.

Reinolds, C.S., Padisák, J., Sommer, U., 1993. Intermediate disturbance in the ecology of phytoplankton and maintenance of species diversity: a synthesis. Hydrobiologia 249, 183–188.

Remane, A., 1934. Die Brackwasserfauna. Verhandlungen der Deutschen Zoologischen Gesellschaft. Greifswald 36, 34–74.

Remmert, H., 1969. Der Wasserhaushalt der Tiere im Spiegel ihrer ökologischen Geschichte. Naturwissenschaften 56, 120–124.

Roelke, D., Augustine, S., Buyukates, Y., 2003. Fundamental predictability of multi-species competition: the influence of large disturbance. Am. Nat. 162, 615–623.

Sagert, S., Rieling, T., Eggert, A., Schubert, H., 2008. Development of a phytoplankton indicator system for the ecological assessment of brackish coastal waters (German Baltic Sea coast). Hydrobiologia 611, 91–103.

Schaefer, M., 1999. The diversity of the fauna of two beech forests: some thoughts about possible mechanisms causing the observed patterns. In: Kratochwil, A. (Ed.), Biodiversity in Ecosystems: Principles and Case Studies of Different Complexity Levels. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 45–64.

Schiewer, U., 2008. Ecology of Baltic Coastal Waters. Springer-Verlag, Berlin, Heidelberg.

Schubel, J.R., Pritchard, D.W., 1990. Great lake estuaries – Phooey. Estuaries 13, 508–509.

Schubert, H., Feuerpfeil, P., Marquardt, R., Telesh, I., Skarlato, S., 2011. Macroalgal diversity along the Baltic Sea salinity gradient challenges Remane's species-minimum concept. Mar. Pollut. Bull. 62, 1948–1956.

Solé, R.V., Bascompte, J., 2006. Self-organization in Complex Ecosystems. Princeton Monographs in Population Biology N° 42. Princeton University Press.

Stock, C., Grønlien, H.K., Allen, R.D., Naitoh, Y., 2002. Osmoregulation in *Paramecium*: in situ ion gradients permit water to cascade through the cytosol to the contractile vacuole. J. Cell Sci. 115, 2239–2348.

Stocker, R., 2012. Marine microbes see a sea of gradients. Science 338, 628–633.

Telesh, I.V., 2004. Plankton of the Baltic estuarine ecosystems with emphasis on Neva Estuary: a review of present knowledge and research perspectives. Mar. Pollut. Bull. 49, 206–219.

Telesh, I.V., Khlebovich, V.V., 2010. Principal processes within the estuarine salinity gradient: a review. Mar. Pollut. Bull. 61, 149–155.

Telesh, I., Postel, L., Heerkloss, R., Mironova, E., Skarlato, S., 2009. Zooplankton of the open Baltic Sea: extended atlas. BMB Publ. 21. Mar. Sci. Rep. 76, 1–290.

Telesh, I.V., Schubert, H., Skarlato, S., 2011a. Revisiting Remane's concept: evidence for high plankton diversity and a protistan species maximum in the horohalinicum of the Baltic Sea. Mar. Ecol. Progr. Ser. 421, 1–11.

Telesh, I.V., Schubert, H., Skarlato, S., 2011b. Protistan diversity does peak in the horohalinicum of the Baltic Sea: reply to Ptacnik et al. (2011). Mar. Ecol. Progr. Ser. 432, 293–297.

Templeton, A.R., Robertson, R.J., Brisson, J., Strasburg, J., 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. PNAS 98, 5426–5432.

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. Neth. J. Aquat. Ecol. 28 (3–4), 383–395.

Vergara-Chen, C., González-Wangüemert, M., Marcos, C., Pérez-Ruzafa, Á., 2010. Genetic diversity and connectivity remain high in *Holothuria polii* (Delle Chiaje 1823) across a coastal lagoon-open sea environmental gradient. Genetica. http://dx.doi.org/10.1007/s10709-010-9472-x.

Wang, J., Yang, D., Zhang, Y., Shen, J., van der Gast, C., Hahn, M.W., Wu, Q., 2011. Do patterns of bacterial diversity along salinity gradient differ from those observed for macroorganisms? PLoS ONE 6 (11), e27597 http://dx.doi.org/10.1371/journal.pone.0027597.

Whitfield, A.K., Elliott, M., Basset, A., Blaber, S.J.M., West, R.J., 2012. Paradigms in estuarine ecology – a review of the Remane diagram with a suggested revised model for estuaries. Estuar. Coast. Shelf Sci. 97, 78–90.

Whittaker, R.H., 1965. Dominance and diversity in land plant communities. Science 147, 250–260.

Winder, M., Sommer, U., 2012. Phytoplankton response to a changing climate. Hydrobiologia 698, 5–16.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790.

Zenkewitch, L.A., 1959. The classification of brackish-water basins as exemplified by the seas of the U.S.S.R. Arch. Ocean. Limnol. 11, 53–61.