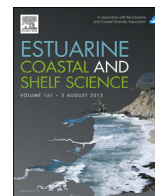




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Size, seasonality, or salinity: What drives the protistan species maximum in the horohalinicum?

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ABSTRACT

The protistan species maximum concept for the challenging zone of critical salinity 5–8 (the horohalinicum) where the large benthic organisms experience the destructive osmotic stress has developed smoothly into the understanding that in the environment with sharp salinity fluctuations community regulations and life strategies of small unicellular planktonic organisms differ substantially from those of large multicellular bottom-dwellers. This inductive supposition has initiated efforts to define the major organismal traits and environmental factors that might be responsible for the new biodiversity pattern. There also emerged a need to better relate the novel conceptual assertions with the ‘field/pooled data paradox’ – a controversy when the pooled long-term large-scale datasets provide results which seem to contradict the field observations. This paper uses a long-term (1972–2006) phytoplankton dataset from the Baltic Sea for testing three new compatible research hypotheses by means of correlation analysis, non-metric multi-dimensional scaling using a Bray–Curtis dissimilarity matrix, and the rarefaction analysis. Hypothesis 1 argues that the smaller and therefore the faster evolving unicellular organisms are taxonomically more diverse in the horohalinicum than in the other sectors of the salinity gradient. Hypothesis 2 suggests that the recently discovered biodiversity pattern may be caused by a pronounced seasonality within the horohalinicum which might promote the shift in plankton community composition towards dominance of small-sized species in the critical salinity regions. Hypothesis 3 proposes that the protistan species maximum in the horohalinicum is largely backed up by the significant between-sample variation in highly changeable brackish-water environment rather than by within-sample species richness. Our results provided statistical proof that algal cell size minimum underpins the protistan species maximum in the horohalinicum, and supported all three research hypotheses.

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1. Introduction

Like panic at the peak of financial crisis, scientific knowledge has an implacable tendency to ramify as it grows and this ramification often causes radical changes in the underlying theory. The challenging issue of biodiversity paradigm shifts has been repeatedly emerging in the focus of the increasing research interest since the last three decades (Bruno et al., 2003; Whitfield et al., 2012). This was largely due to growing concern about the effects of species extinction and invasions on the functioning and sustainable

development of ecosystems, or search for signs of climate change and elaboration of the reliable methods for their evaluation, development of biological indication of the anthropogenic impacts on ecosystems, and other indispensable reasons (Elliott and Whitfield, 2011; Telesh et al., 2011a, 2013; Hooper et al., 2012; Reich et al., 2012; Cardinale, 2012; Basset et al., 2013; Pinto et al., 2014; Rajasilta et al., 2014; Vuorinen et al., 2015). However, whereas many general biodiversity patterns have been described for the terrestrial plant communities, for example, such as the increase of the community-average specific leaf area with the increasing soil water content (Cornwell and Ackerly, 2009), only a few such patterns have been developed for aquatic environments.

Body size of organisms is recognized as a pivotal component of evolutionary fitness which provides a beneficial contribution to the understanding of certain biodiversity distribution patterns (Hart and

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Bychek, 2011). Life cycle strategies are known to have strong relation to body size of plankton (Allan, 1976). The small zooplankton: rotifers and cladocerans – the “r-selectors” according to MacArthur (1972), possess high intrinsic rates of the population increase and short life cycles; they are well adapted to seasonal or unpredictable changes of the environment. These organisms form large, highly variable populations and react to habitat changes nearly without time lags. The larger zooplankters – the ‘k-selectors’ such as copepods, reproduce at lower rates and have longer life cycles; consequently, they respond to environmental changes with relatively larger time lags. However, these issues are far more complex than one can imagine, and zooming into size distribution patterns of aquatic organisms often reveals unexpected results, for example, such as the multimodal large time scale frequency distribution of the average size of the phytoplankton species weighted by biovolume being the product of the unimodal short-term patterns (Downing et al., 2014).

Seasonality in plankton species composition is clearly related to the size of the organisms which controls their fundamental physiological traits and thereby determines many attributes of the species ecology and community structure in ecosystems, performing as a convenient surrogate for variables linked to evolutionary and ecological patterns (Blackburn and Gaston, 1994). It is possible even to make inferences about the distribution of eco-physiological organismal traits based on variations in the size spectra, or the relative abundance of different size classes in plankton (Cermeño et al., 2006), as many of those traits are constrained by the cell or body size (Barton et al., 2013).

In aquatic ecosystems, salinity is the environmental factor of extreme importance which fluctuations define the heterogeneity of habitats and species diversity. One bright example of the impact of salinity variations on the heterogeneity of habitats and species richness of aquatic communities is the correlation between the benthic species number and stability of the salinity regime, described by de Jonge (1974) for approx. 20 inland brackish water bodies in the Netherlands. Among other salinity-explicable biodiversity patterns, the benthic species-minimum conception for brackish waters is probably not only the first but also the best known one (Remane, 1934). It shows that marine and freshwater benthic macroinvertebrates demonstrate the reduction of taxonomic diversity with gradual salinity change from both, freshwater and marine habitats towards the minimum number of species (*Artenminimum*) at salinities 5–8. The latter range was termed the ‘critical salinity zone’ (Khlebovich, 1968), or the horohalimum (Kinne, 1971). This pattern was best described by the conceptual diagram of Remane (1934), which allows concluding that for sedentary or slowly moving bottom-dwelling forms sharp fluctuations around the salinity 5–8 are particularly stressful. Recently, the *Artenminimum* concept was verified by new data on macrozoobenthos diversity in the salinity gradient of the Baltic Sea, demonstrating the applicability of Remane's concept to benthic invertebrates (Josefson and Hansen, 2004; Josefson, 2009; Bleich et al., 2011; Filippenko, 2013; Zettler et al., 2014).

However, the large-scale long-term datasets which characterise the pelagic diversity of the Baltic Sea coastal and open waters do not support the validity of Remane's concept for plankton, especially when its smallest size fraction is considered (Herlemann et al., 2011; Telesh et al., 2011a). On the contrary, it was shown that the diversity of microplankton (presumably, the protists, i.e. all autotrophic, heterotrophic and mixotrophic unicellular eukaryotic organisms, and also some prokaryotes, e.g. the cyanobacteria) demonstrate maximum number of species in the zone of critical salinity 5–8. These data served the basis for the discovery of a new biodiversity pattern: the protistan species maximum in the horohalimum, which underpins a new concept named correspondingly (Telesh et al., 2011a, 2011b).

The protistan species maximum pattern may be explained by high adaptability of these unicellular eukaryotes to the environmental stresses which leads to their unprecedented cosmopolitanism (Fenchel and Finlay, 2004; Fuhrman, 2009; Matantseva and Skarlato, 2013). Protists are among the first organisms which invade relatively free niches after the catastrophic events; their diversity is high in the large, comparatively stable brackish water basins like the Baltic Sea (Telesh et al., 2011a); and they use effectively the subsidy of the moderately stressed environment, drifting with water masses within the salinity gradients and thus being less affected by the environmental instability (Telesh et al., 2013). Therefore, the theoretical basics of this peculiar distribution trait of microorganisms in plankton, with maximum diversity in the horohalimum, fit well with Hutchinson's ecological niche concept (Hutchinson, 1957), the Species-area relationship (Kratochwil, 1999; Gaston, 2000), the Intermediate disturbance hypothesis (Connell, 1978) which explains in part the ‘paradox of plankton’ (Hutchinson, 1967), and the ecotone concept extended to entire ecosystems rather than applied to the contact zone between two ecosystems only (Basset et al., 2013). Indeed, the horohalimum in the Baltic Sea is an evident example of the exceptionally large, multi-dimensional pelagic ecotone ecosystem where the marine and freshwater microplankton communities mix and demonstrate the increased biodiversity. This can be achieved due to wide salinity tolerance range of many planktonic protists and their effective physiological adaptations to subsidy of the brackish environment (Telesh et al., 2013, and references therein).

Moreover, it was revealed recently that macroalgae also do not exhibit a species minimum in the horohalimum (Schubert et al., 2011), while the genetic diversity of the planktonic bacteria measured as the number of the operational taxonomic units (OTUs) fluctuated irregularly around the relatively high average values, likewise not showing any minimum diversity at the critical salinities (Herlemann et al., 2011).

Further search for mechanisms behind the newest biodiversity pattern – the species maximum of planktonic protists in the critical salinity zone where the large macrozoobenthic organisms experience the destructive osmotic stress – has smoothly developed into an assumption that in the environment with sharp salinity fluctuations the community regulations and life strategies of small unicellular protists and the cyanobacteria inhabiting the microscopic world of the pelagial differ substantially from those in the assemblages of large, multicellular bottom-dwelling organisms (Telesh et al., 2013). For the latter, Dahl (1956) showed that the number of marine benthic species in the transition area between the North Sea and the Baltic Sea was about halved between salinity 30 and 17; moreover, in the salinity interval between 34 and 30 a reduction in species number by 75% had already taken place. For the freshwater planktonic rotifers, on the contrary, an approx. 70% reduction in species number was observed with the salinity increase from 0 to 8 in the eastern Baltic Sea (see Fig. 3 in Telesh et al., 2011a).

However, so far one could only hypothesise on the mechanisms behind this remarkable discrepancy between the biodiversity patterns of various groups of plankton and benthos by considering the peculiarities of their physiological adaptations, osmoregulation, and differences in the evolution rate, modes of life and body size, or cell size in the case of unicellular organisms as the basic traits which determine the relative fitness of aquatic organisms in the environmental gradients. Meanwhile, the discovery of the protistan species maximum in the horohalimum and the convincing proof of this biodiversity pattern by the analysis of the long-term dataset (described in Sagert et al., 2008) and the meta-analysis of the large sets of the original and published data on the Baltic plankton (Telesh et al., 2011a; references therein; Mironova et al., 2009, 2012, 2013, 2014) have initiated the efforts to define both the organismal

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