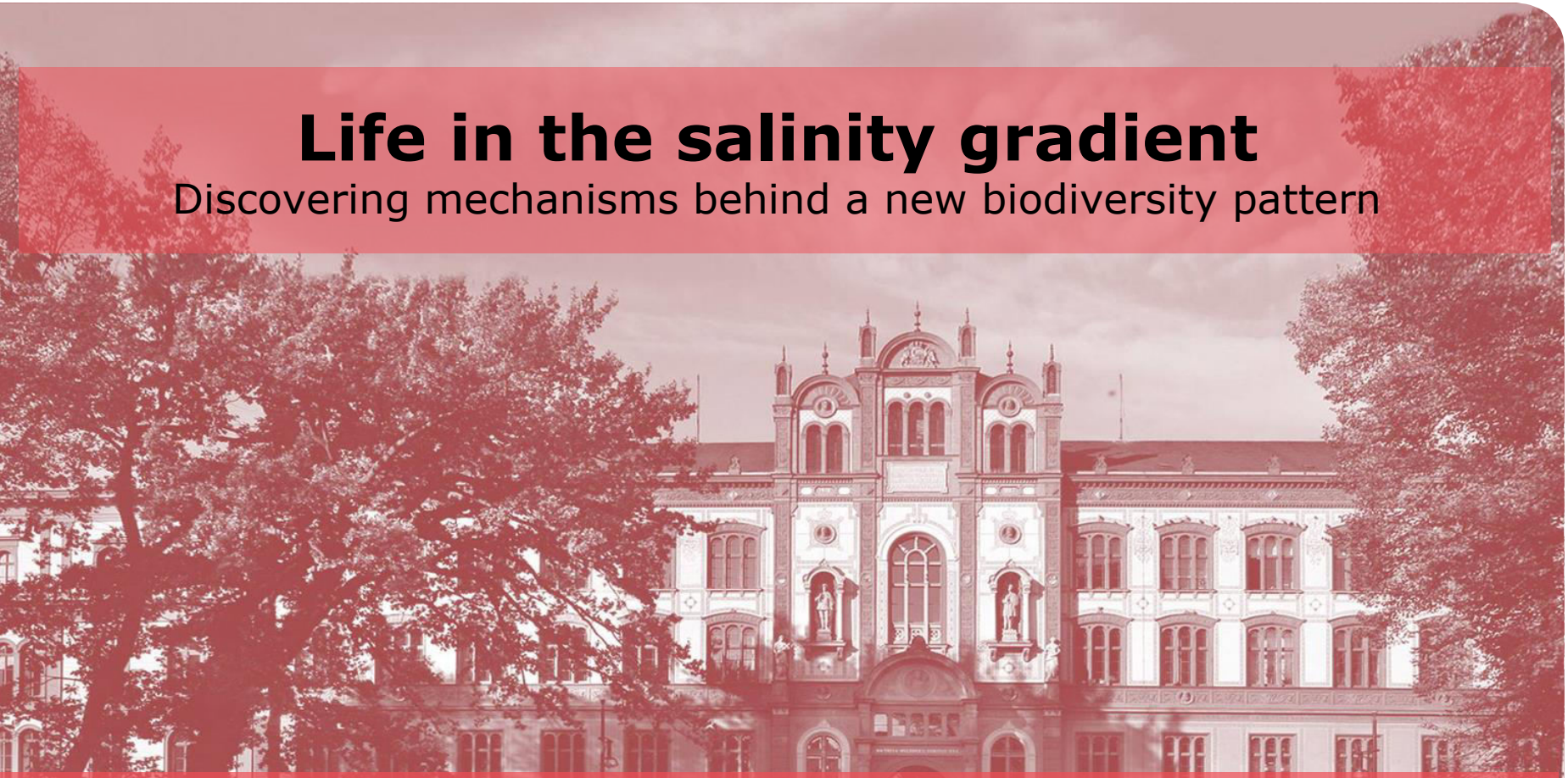
Universität Rostock Traditio et Innovatio

USE Laboratory

Life in the salinity gradient

Discovering mechanisms behind a new biodiversity pattern

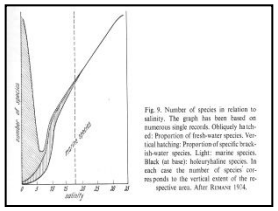


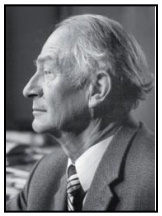
Hendrik SCHUBERT - **Inst. Biol. Sci., University of Rostock, Germany**
Sergei O. SKARLATO - **Institute of Cytology, RAS, St. Petersburg, Russia**
Irena V. TELESH - **Zoological Institute, RAS, St. Petersburg, Russia**

Contents

Remane's concept





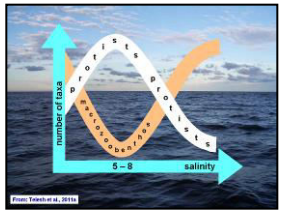


Database analysed





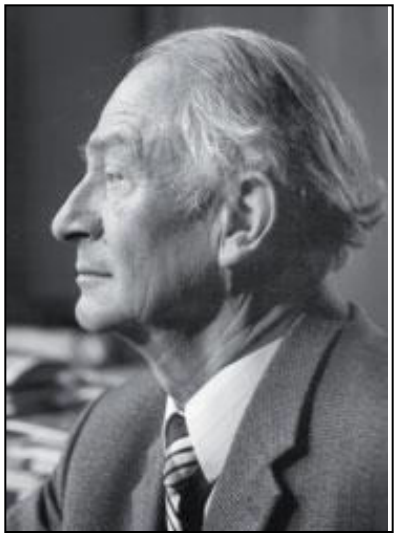
Results & conclusions for planktonic protists



Synthesis and outlook for other taxa




- ***Spatial heterogeneity in species richness is an obvious feature of the natural world. The reasons for this are numerous, but in any case site-specific (e.g. climatic long-term stability, ressource availability, area…..)***
- ***For brackish water ecosystems, Remane's Artenminimum ("species minimum") concept is probably the best known description of biodiversity pattern. This concept argues that taxonomic diversity of organisms is the lowest at salinities 5-8 PSU ("horohalinicum" or "critical salinity").***



Adolf Remane
1898-1976

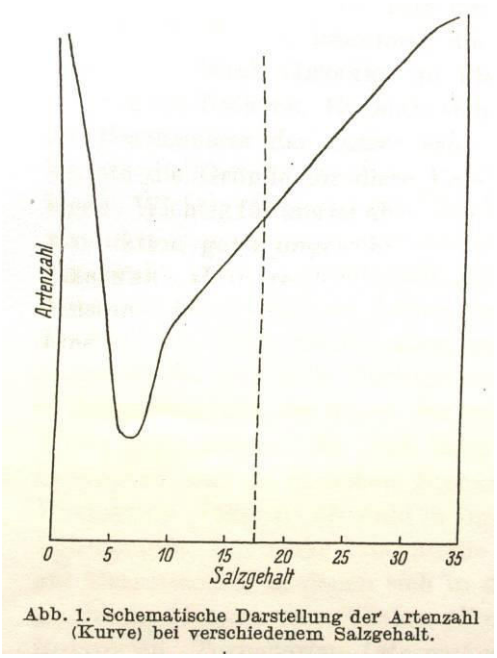


Abb. 1. Schematische Darstellung der Artenzahl (Kurve) bei verschiedenem Salzgehalt.

From: Remane, 1934

- ***Revisiting in 1934 the applicability of a small-scale study of Johannsen (1918) conducted in the Randersfjord for larger salinity gradients he came to the conclusion, that for macrozoobenthos a general minimum in species richness exist between 5-8 psu***
- ***Combining his own data with the ones of Johannsen, he constructed the conceptual drawing best known in it's 1971 version***

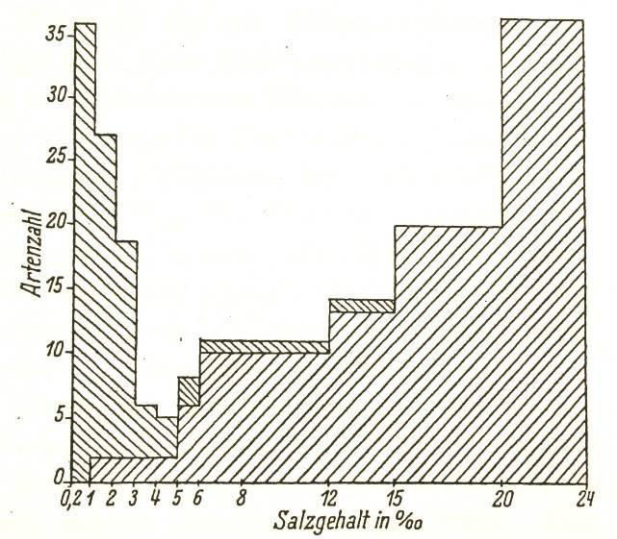


Abb. 2. Artenzahl der Mollusken im Randersfjord bei verschiedenem Salzgehalt. Der Anteil der limnischen und marinen Arten ist durch verschiedene Schraffierung gekennzeichnet. Nach JOHANNSEN, 1918; in der Darstellungsart etwas abgeändert.

Tabelle 1.
Abnahme der marinen und Brackwasserarten einiger Tiergruppen von der Nordsee zur Ostsee.

	I	II	III	IV
Porifera	15	13	0	0
Hydroidpolypen	49	26	7	3
Scyphozoa	8	5	2	1
Anthozoa	12	5	2	0
Ctenophora	3	2	1	1
Nemertini	?	ca. 25	3	2
Archianneliden	12	7	1	0
Polychaeta	> 100	66	13	5
Cumacea	19	5	2	0
Mysidacea	9	7	5	4
Amphipoda	?	36	13	8
Decapoda	49	13	5	0
Amphineura	3	1	0	0
Lamellibranchia	69	34	7	5
Opisthobranchia	—	23	6	4
Echinodermata	27	8	1	0
Ascidiae	16	6	1	0

- ***Combining his own data with the ones of Johannsen, he constructed the conceptual drawing best known in it's 1971 version***

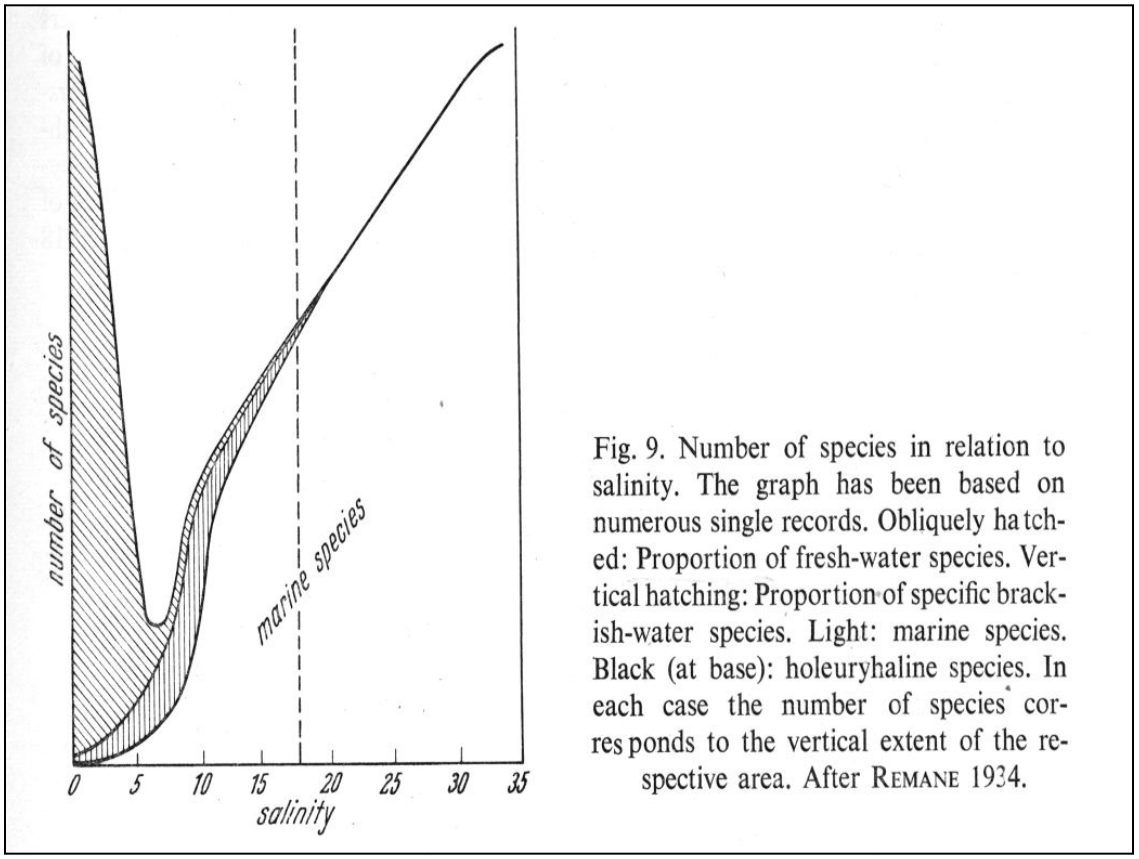


Fig. 9. Number of species in relation to salinity. The graph has been based on numerous single records. Obliquely hatched: Proportion of fresh-water species. Vertical hatching: Proportion of specific brackish-water species. Light: marine species. Black (at base): holeuryhaline species. In each case the number of species corresponds to the vertical extent of the respective area. After REMANE 1934.

- ***For brackish water ecosystems, Remane's Artenminimum ("species minimum") concept is probably the best known description of biodiversity pattern. This concept argues that taxonomic diversity of organisms is the lowest at salinities 5-8 PSU ("horohalinicum" or "critical salinity").***

- ***Combining his own data with the ones of Johannsen, he constructed the conceptual drawing best known in it's 1971 version***

- ***This concept was of such a striking plausibility and, moreover, supported by several later investigations that it went soon into the textbooks***

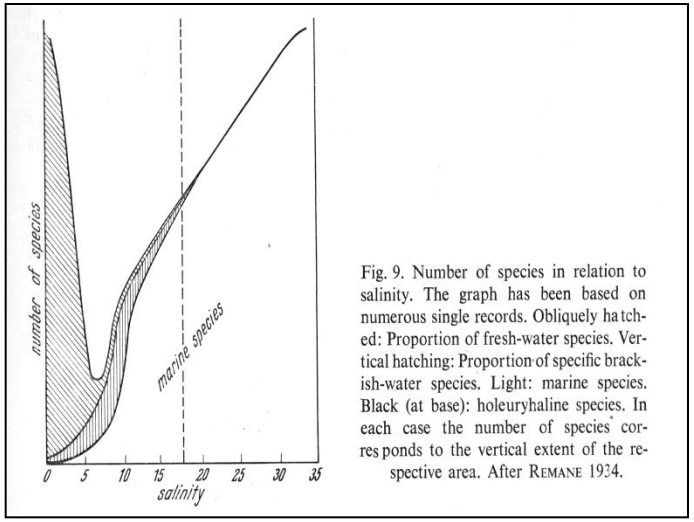


Fig. 9. Number of species in relation to salinity. The graph has been based on numerous single records. Obliquely hatched: Proportion of fresh-water species. Vertical hatching: Proportion of specific brackish-water species. Light: marine species. Black (at base): holeuryhaline species. In each case the number of species corresponds to the vertical extent of the respective area. After REMANE 1934.

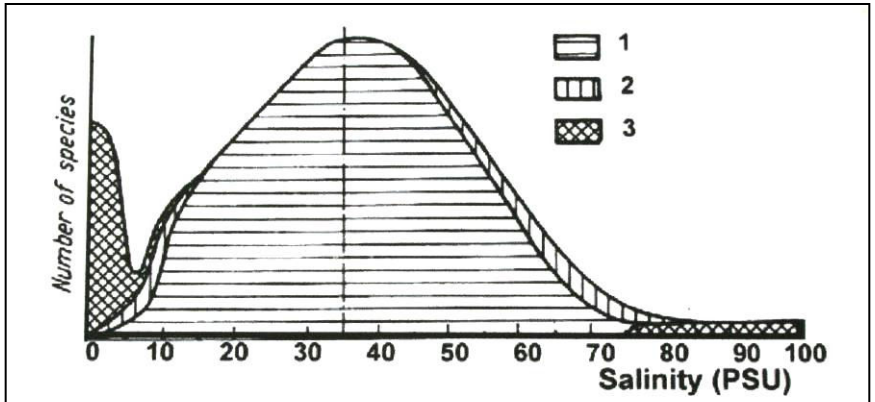


Fig. 1. Number of marine animal species (1), brackish water and euryhaline animal species of marine origin (2), and freshwater species (of freshwater origin, 3) (after Khlebovich (1962, 1969)).

Explanations for the species minimum:

- ***First, the Baltic Sea is a geologically young water body (Lass & Matthäus, 2008) where the niche-occupation process is still going on. This process is particularly well illustrated by the high rate of unintentional biological invasions (Paavola et al., 2005; Schiewer, 2008; Telesh et al., 2008b; Telesh et al., 2009).***

- ***Second, the average surface water salinity in the Baltic Sea proper is 5-8 PSU which corresponds to the critical salinity level (Khlebovich, 1969), or the horohalinicum (Kinne, 1971). This salinity range provides unfavorable osmotic conditions for aquatic organisms of both freshwater and marine origin. It is impeding high species diversity since hypo- and hyperosmotic adjustments are required within this zone (Telesh & Khlebovich, 2010).***

Amphipoda – 36 spp
Amphineura – 3
Anthozoa – 12
Archiannelida – 12
Ascidiae – 16
Cumacea – 19
Decapoda – 49
Echinodermata – 27
Hydropolyps – 49
Lamellibranchia – 69
Mysidacea – 9
Nemertini – 25
Ophistobranchia – 23
Polychaeta > 100
Porifera – 15
Scyphozoa – 8
Ctenophora – 3

TOTAL: ca. 400 spp

- ***But even in it's latest version, only a few planktonic groups are represented in the database.....***

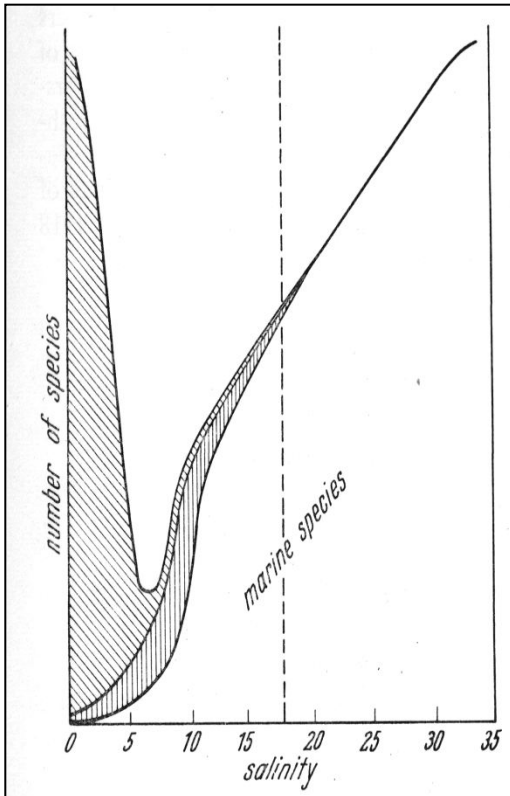


Fig. 9. Number of species in relation to salinity. The graph has been based on numerous single records. Obliquely hatched: Proportion of fresh-water species. Vertical hatching: Proportion of specific brackish-water species. Light: marine species. Black (at base): holeuryhaline species. In each case the number of species corresponds to the vertical extent of the respective area. After REMANE 1934.

for example ZOOPLANKTON:

- ***The Baltic zooplankton in Remane' times was poorly studied, just ca. 40 species were known (Remane, 1934; Hernroth & Ackefors, 1979), and this number fitted well to the species-minimum notion developed for macrozoobenthos.***
- ***Checklists for the Baltic zooplankton were lacking in the Remane' time.***
- ***So already in 1950-ies Baltic biologists assumed that the real diversity of the Baltic Sea might be higher if the smallest, microscopic organisms of plankton and meiobenthos are taken into account (Remane, 1958; Ackefors, 1969; Jansson, 1972).***
- ***In 1986-2009, we revised the zooplankton diversity in the Baltic Sea and gained new vast knowledge, also on microzooplankton.***









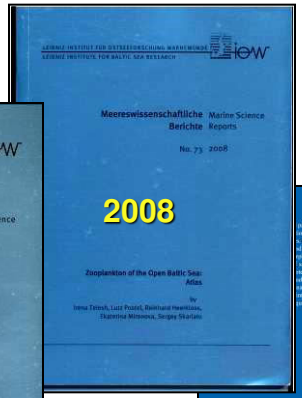


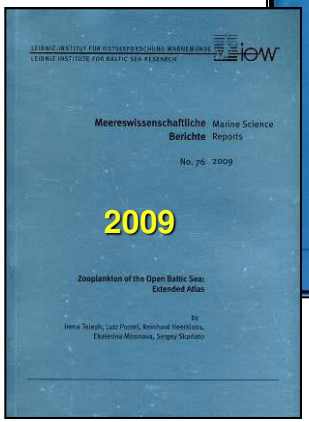


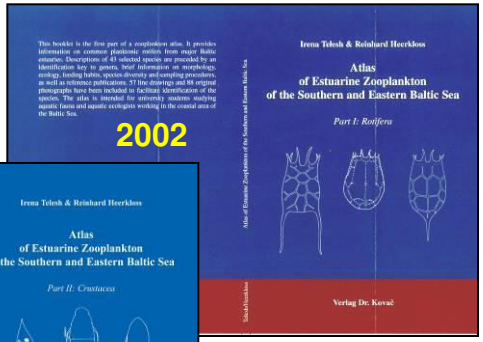


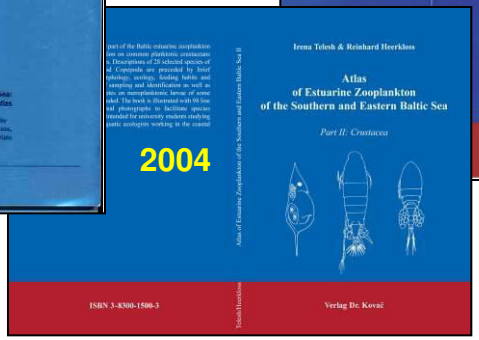





Meereswissenschaftliche Berichte
Marine Science Reports
2008
Zooplankton of the Open Baltic Sea: Atlas

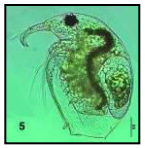

Meereswissenschaftliche Berichte
Marine Science Reports
No. 76 2009
2009
Zooplankton of the Open Baltic Sea: Extended Atlas


Irena Telesh & Reinhard Heerkloss
Atlas of Estuarine Zooplankton of the Southern and Eastern Baltic Sea
Part I: Rotifera
2002


Irena Telesh & Reinhard Heerkloss
Atlas of Estuarine Zooplankton of the Southern and Eastern Baltic Sea
Part II: Crustacea
2004
ISBN 3-8300-1500-3
Verlag Dr. Kovač



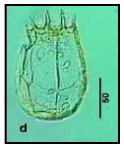




















Main Questions:

1. Is plankton of the Baltic Sea really poor in species?

2. Is the 'species-minimum concept' applicable to other groups of organisms in the Baltic Sea?

To answer this, in addition to the above mentioned Zooplankton data the following databases were included in the reviews:

- 15-years long data base on phytoplankton of the Baltic Sea (Sagert et al., 2008);
- Annotated check-list of phytoplankton species in the Baltic Sea (Hällfors, 2004);
- Check-lists from long-term studies of zooplankton in the Baltic estuaries (Telesh & Heerkloss, 2002, 2004; Telesh, 2004; Telesh et al., 2008a);
- Revision of zooplankton species richness in the open Baltic Sea (Mironova et al., 2009) and the North Sea (Lindley & Batten, 2002).
- Distributional index of the benthic macroalgae of the Baltic Sea area (Nielsen et al. 1995)
- Species and synonym list of German marine macroalgae (Schories et al. 2009)

Life in the salinity gradient

Baltic Sea PLANKTON	Number of species	Data source
CYANOBACTERIA	*190*	*Hällfors, 2004*
PHYTOPLANKTON	2666	Hällfors, 2004
Heterokontophyta	1904	*ibid.*
Chlorophyta	383	*ibid.*
Dinophyta	232	*ibid.*
Haptophyta	72	*ibid.*
Euglenophyta	46	*ibid.*
Cryptophyta	29	*ibid.*
ZOOPLANKTON	1200	Telesh et al., 2011a
Ciliophora	814	Mironova et al., 2009; Telesh et al., 2009
Rotifera	178	Telesh & Heerkloss, 2002; Telesh et al., 2009
Cladocera	108	Telesh & Heerkloss, 2004; Telesh et al., 2009
Copepoda	65	Telesh & Heerkloss, 2004; Telesh et al., 2009
Cnidaria, Ctenophora, Copelata, Chaetognatha, Turbellaria	35	Telesh et al., 2009
PLANKTON TOTAL	**4056**	Telesh et al., 2011a

So with respect to the first question:

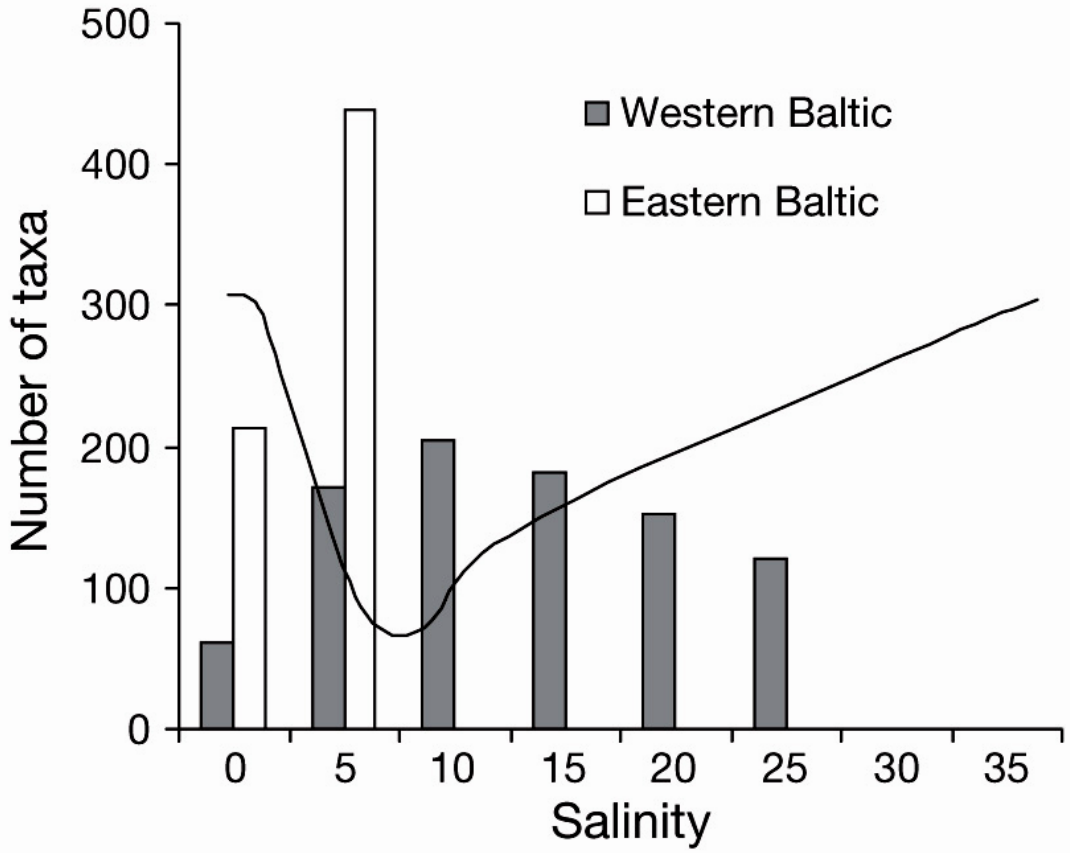
Is plankton of the Baltic Sea really poor in species?

The answer clearly is NO!

- *the number of taxa known to exist in the Baltic Sea area is comparable to numbers known from other Seas as, e.g. North Sea (1500 phytoplankton species; Hoppenrath 2004) or Australian coastal water bodies etc……the same held true for small Zooplankton species*

- *However, this finding even underlines the importance of the question about possible salinity patterns because "species richness" might be due to addition of freshwater taxa naturally not present in regular Seas….*
- *In the Baltic for example phytoplankton species richness have been shown to be highest in the Bay of Finland – which is most probably an effect of taxonomic skills or sample processing rather than biodiversity pattern*

Life in the salinity gradient



Number of PHYTOPLANKTON taxa in the Western and Eastern Baltic Sea

Data for 0 PSU Eastern Baltic: Telesh et al., 2008a,

Data for 5 PSU Eastern Baltic: Olenina & Olenin, 2002

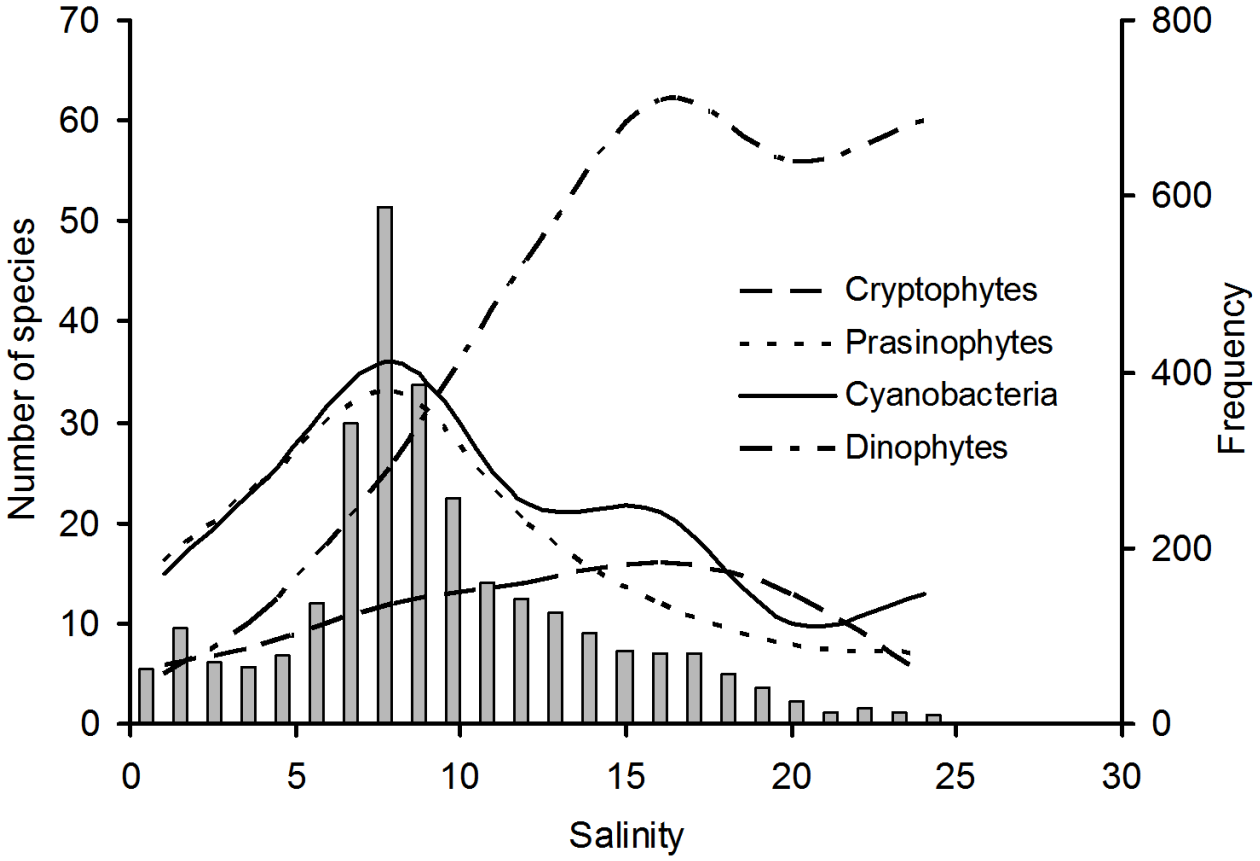
Western Baltic (0-29 PSU): Sagert et al., 2008

Solid line: reconstructed cumulative Remane curve

All columns are mainly (> 85%) species-based but still contain genera and family data in cases of difficult and problematic groups

From: Telesh et al., 2011a

Life in the salinity gradient

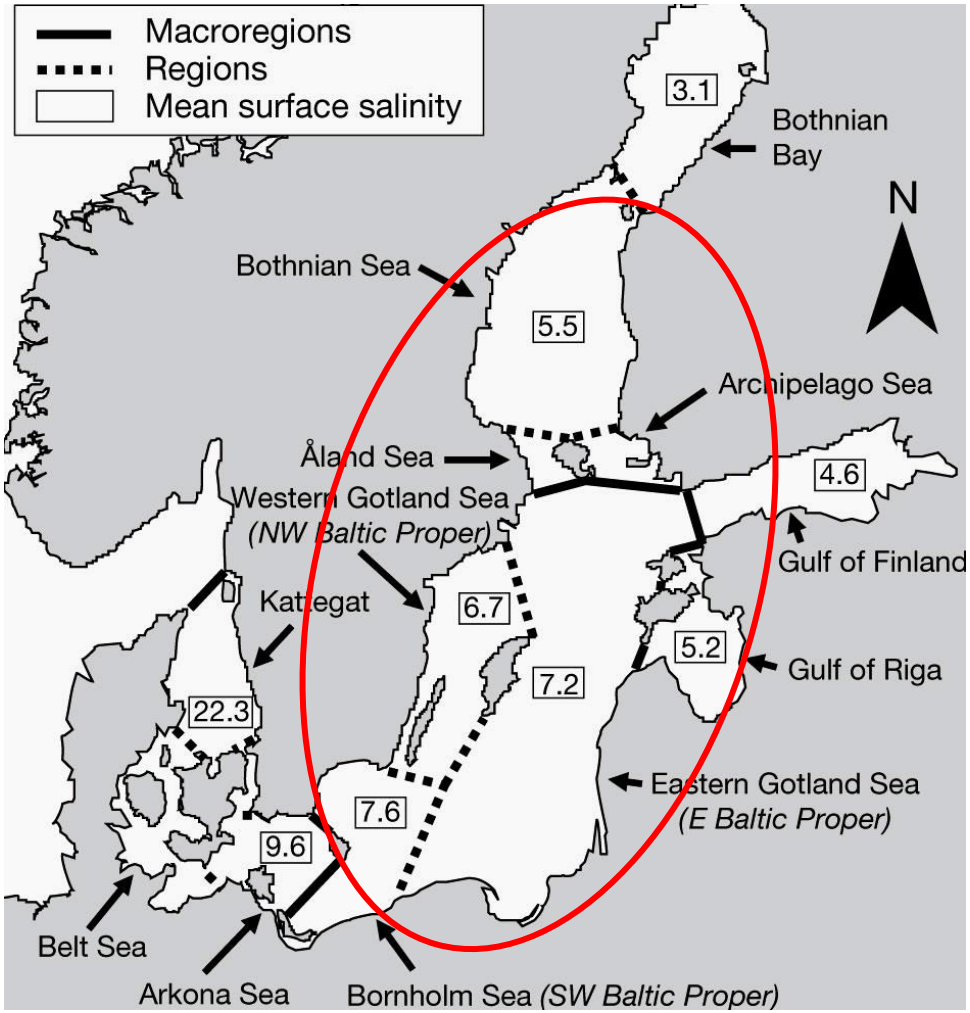


Species numbers of common phytoplankton groups at different salinities along the German Baltic coast

columns (right Y-axis): number of samples with a given salinity

Telesh, Schubert & Skarlato (2011b). MEPS 432: 293-297 (OA)
Protistan diversity does peak in the horohalinicum of the Baltic Sea: Reply to Ptacnik et al. (2011)

Life in the salinity gradient

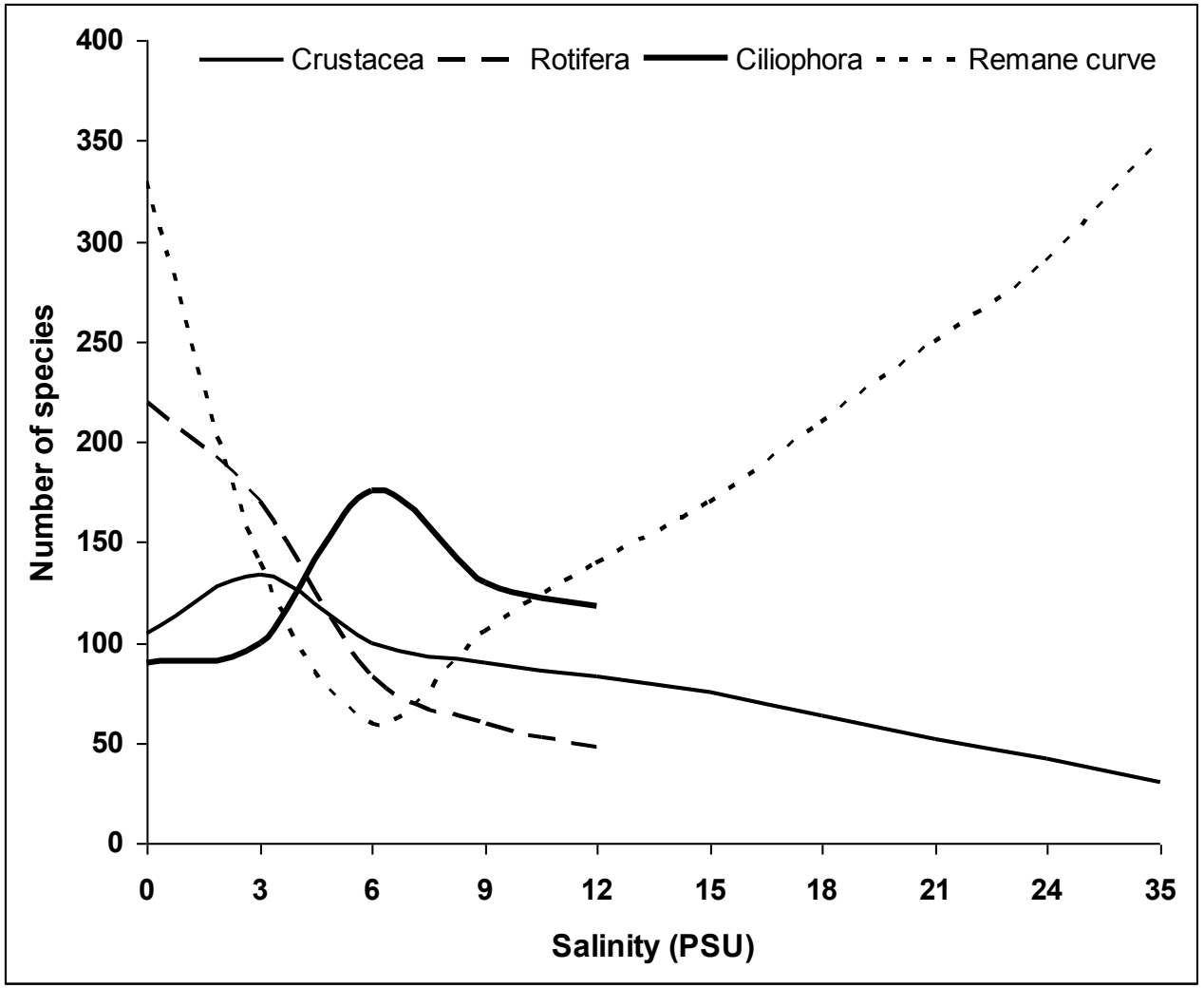


The horohalinicum occupies major area of the Baltic Sea

Salinity calculated for 2006 – 2009 (Feistel et al., 2010)

From: Telesh et al., 2011a

Life in the salinity gradient

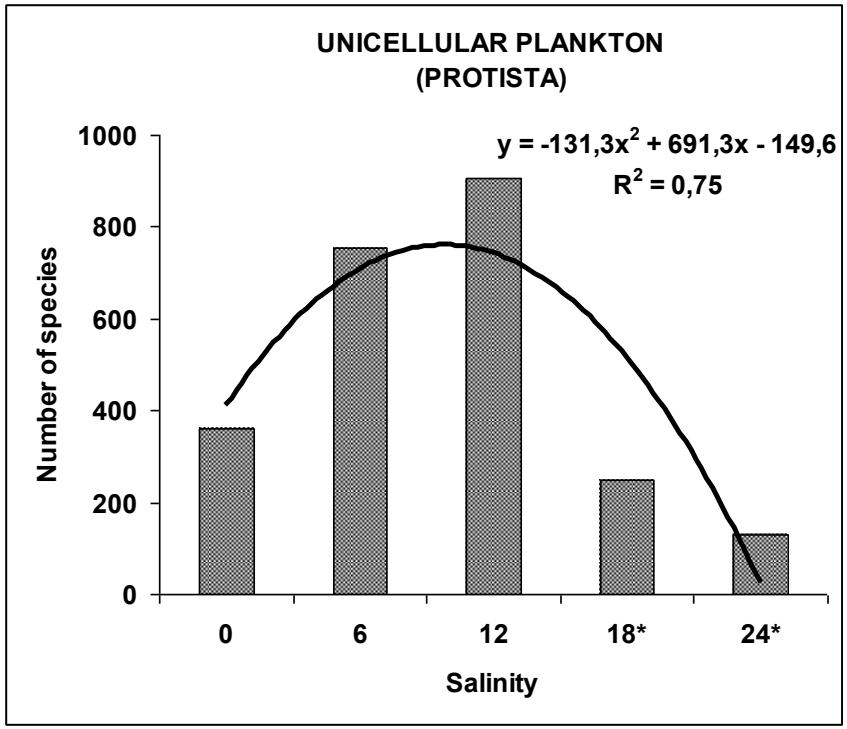


Number of ZOOPLANKTON species in the salinity gradient of the Baltic Sea

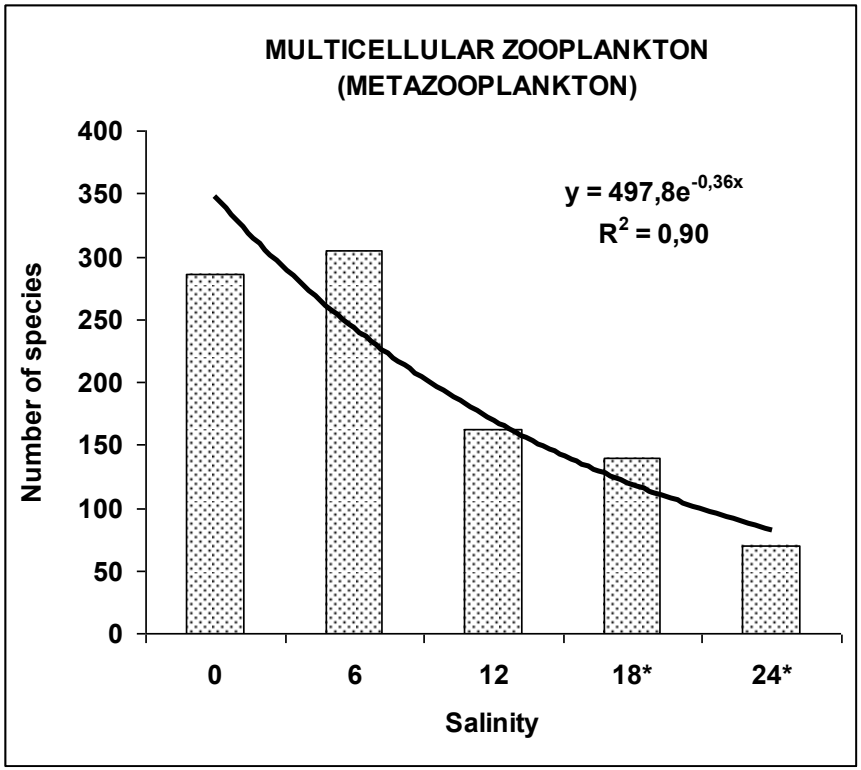
(Telesh & Heerkloss, 2002, 2004; Telesh et al., 2009)

From: Telesh et al., 2011a

Life in the salinity gradient



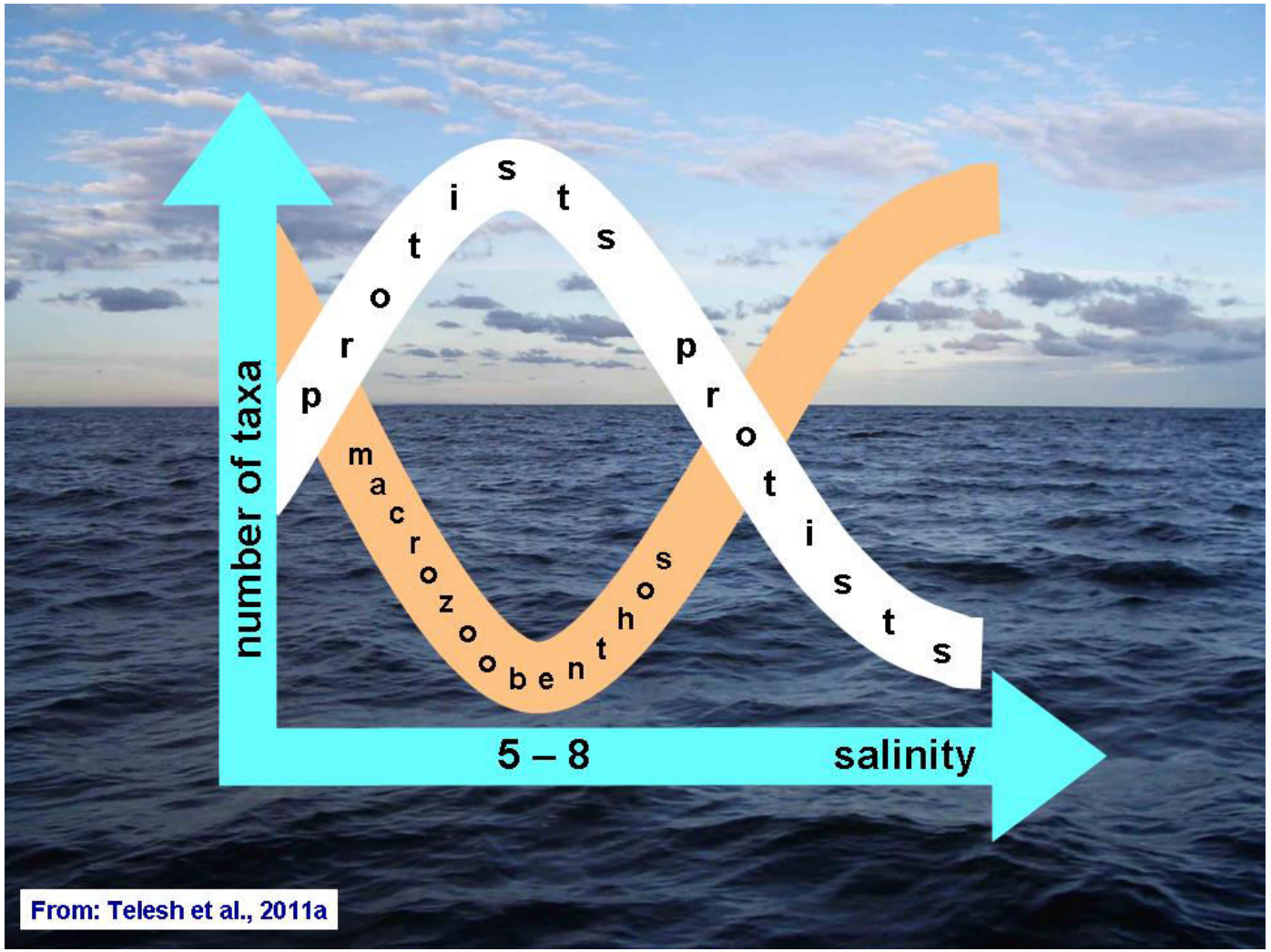
Unicellular protists:
phytoplankton, heterotrophic nanoflagellates, planktonic and bentho-pelagic ciliates
(* - regions where data on ciliates were lacking)



Multicellular zooplankton

From: Telesh et al., 2011a

Life in the salinity gradient

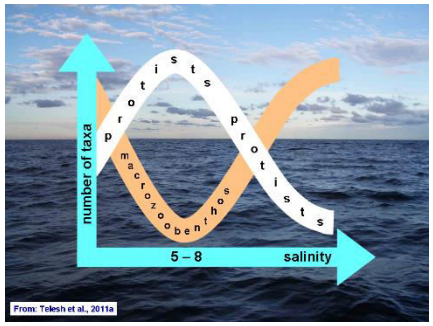


Life in the salinity gradient

CHARACTERISTICS OF PROTISTS → ESTABLISHED HYPOTHESES

CHARACTERISTICS OF PROTISTS	ESTABLISHED HYPOTHESES
Planktonic mode of life => Transfer with water masses => Low stress in salinity gradient	The Intermediate Disturbance Hypothesis (Grime, 1973; Connell, 1978) Moderate disturbance by low salinity => highest protistan diversity
Broad range of salinity tolerance, fast recovery after stress	
Specific osmoregulation mode (e.g. contractile vacuole)	Taxa-area relationship (Fenchel & Finlay, 2004; Fuhrman, 2009) Large area of the Baltic Sea => high protistan diversity
Ability to form cysts in unfavorable conditions	
Fast reproduction, large genetic diversity, high adaptability => cosmopolitanism	The body-size dependency of the evolution rate (Fenchel & Finlay, 2004) Small body size of protists => fast evolution

Life in the salinity gradient



But working with field samples you would immediately protest! Counting a marine sample is much more time-consuming than a central Baltic Sea one!

Now we have to follow two different directions:

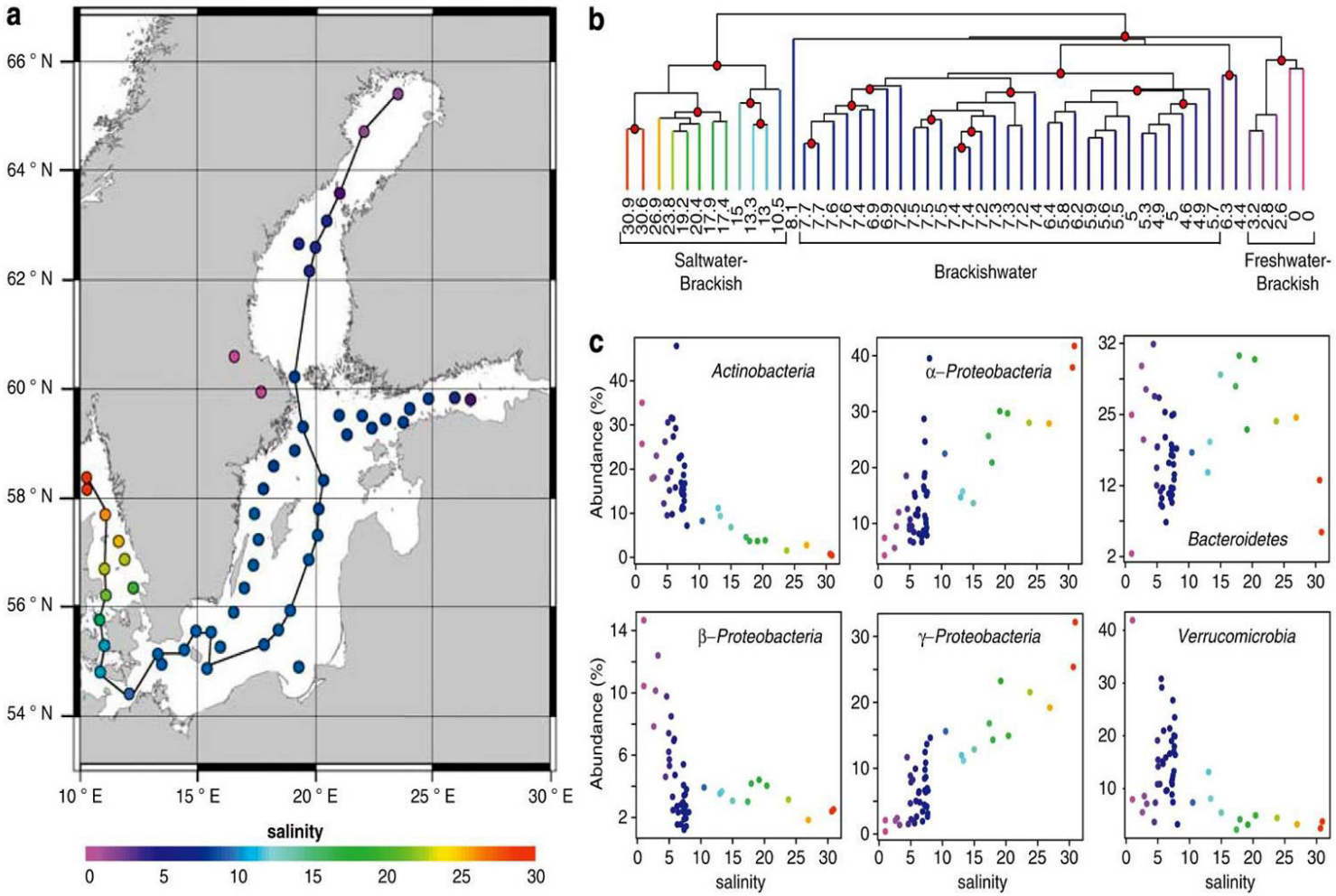
First to follow the trail – looking for species minima in other groups of organisms

For this, we'll look for even smaller and faster ones – Bacterioplankton

And for the other group of sessile and slow ones - Makrophytobenthos

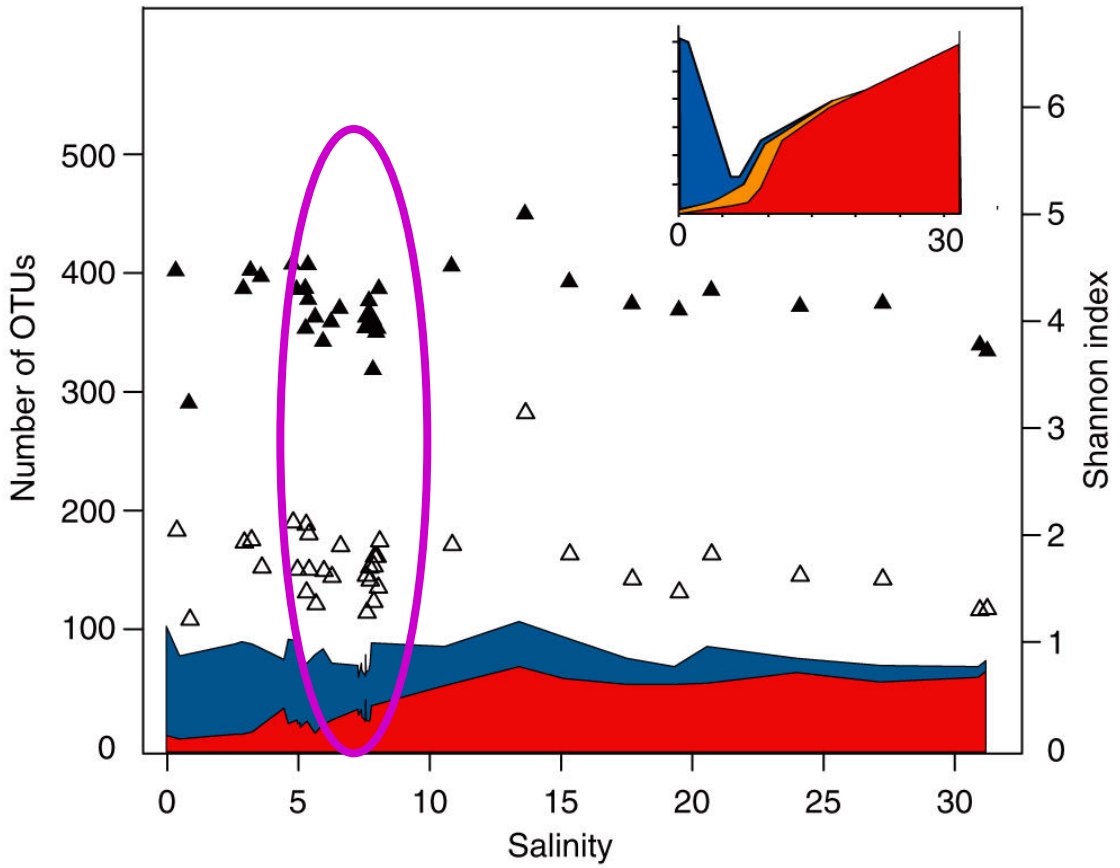
After this, we'll continue trying to solve the field vs. pooled data problem above

Life in the salinity gradient



Herlemann et al., 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. The ISME J.

Life in the salinity gradient

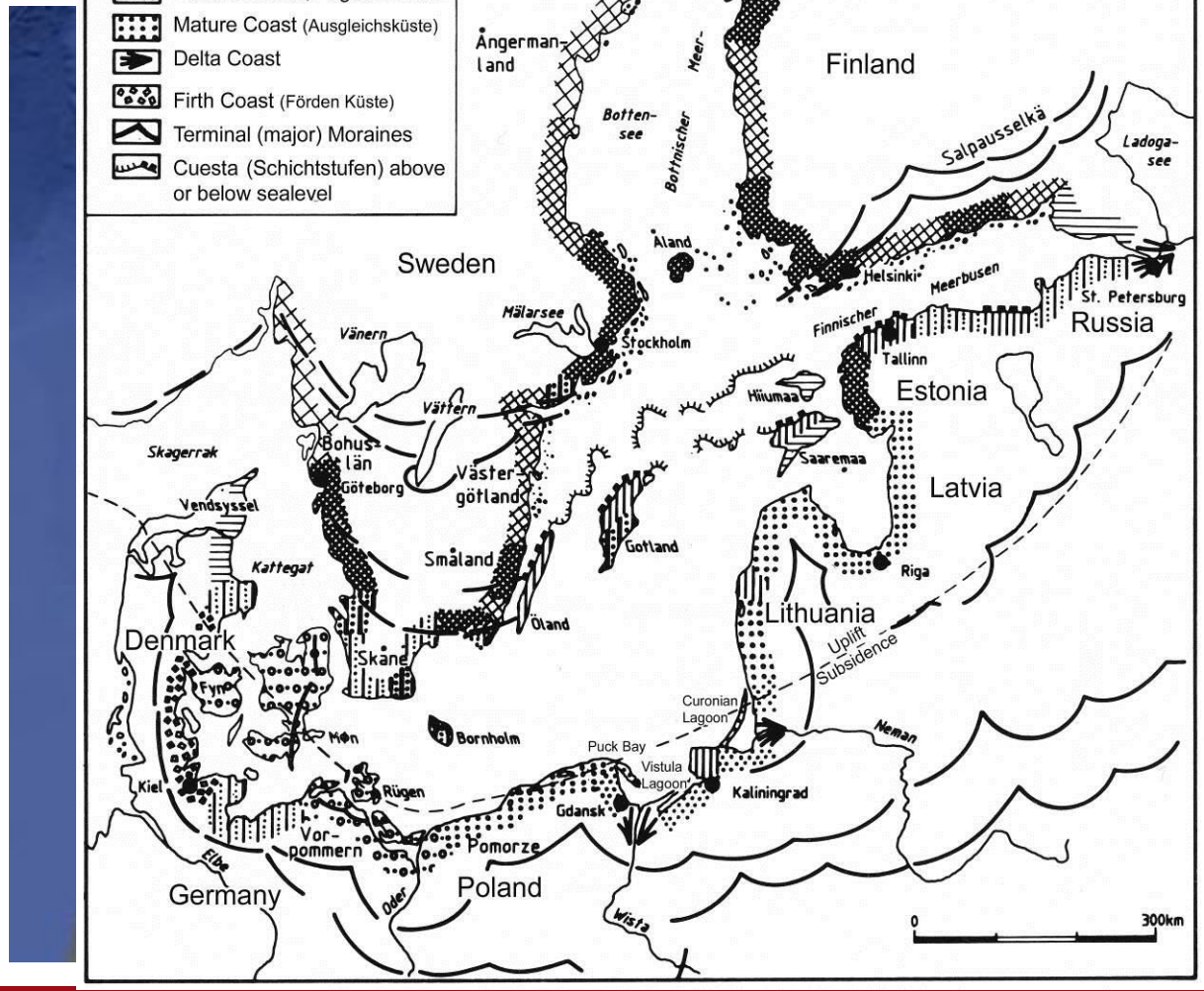


No decrease in BACTERIAL DIVERSITY (OTUs) in the Baltic horohalinicum was observed, nor did the Shannon diversity index change markedly (Herlemann et al., 2011).

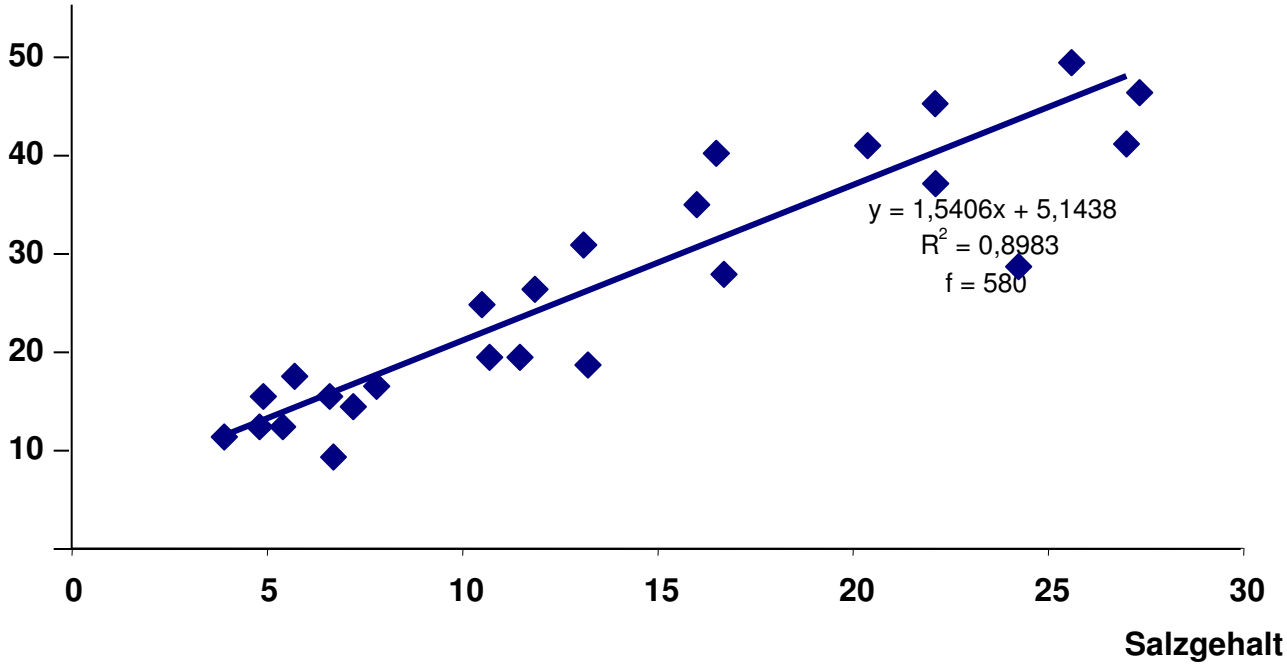
Empty triangles are observed number of OTUs; black triangles are Shannon index values.

macrophytes

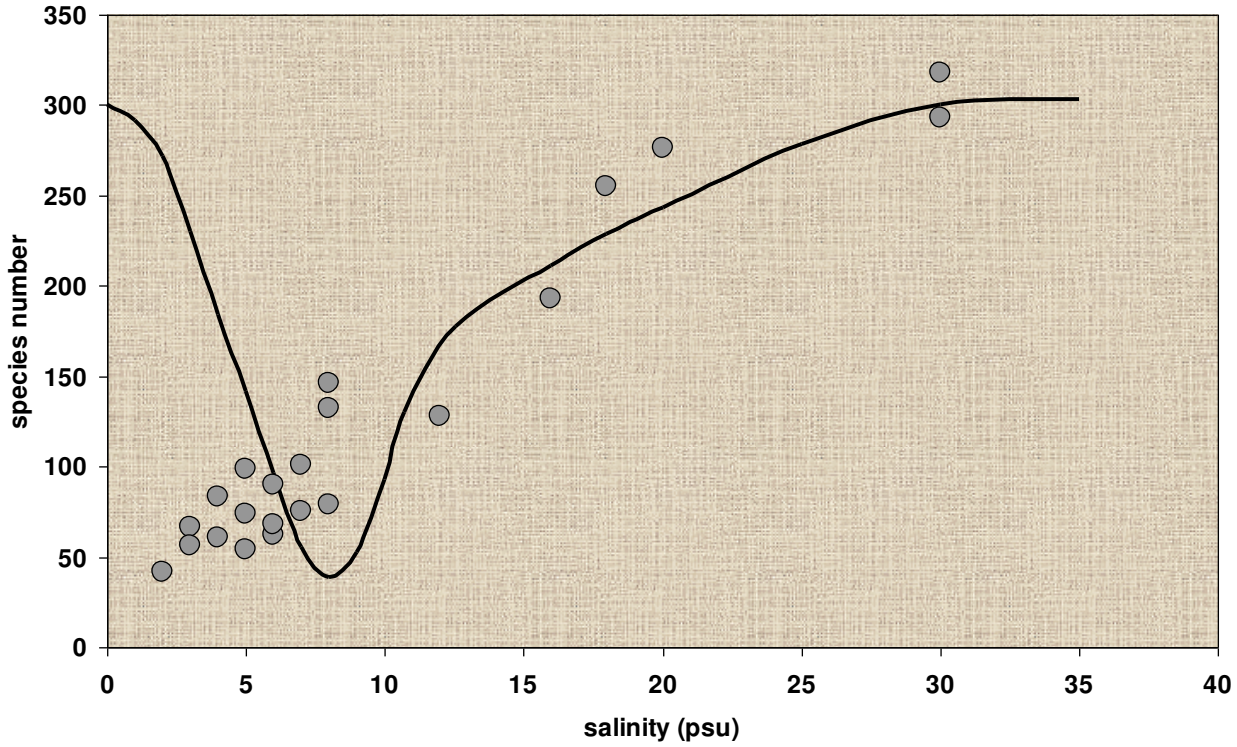
The field



Results – species number

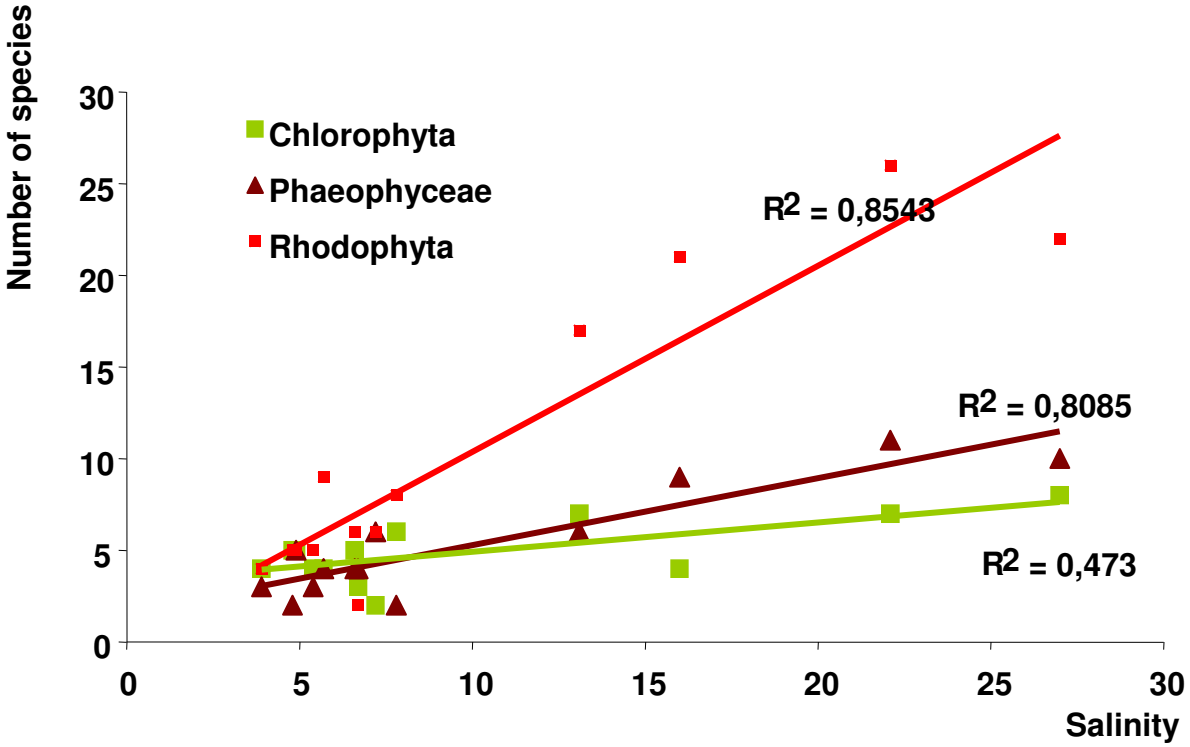


Comparison with known data



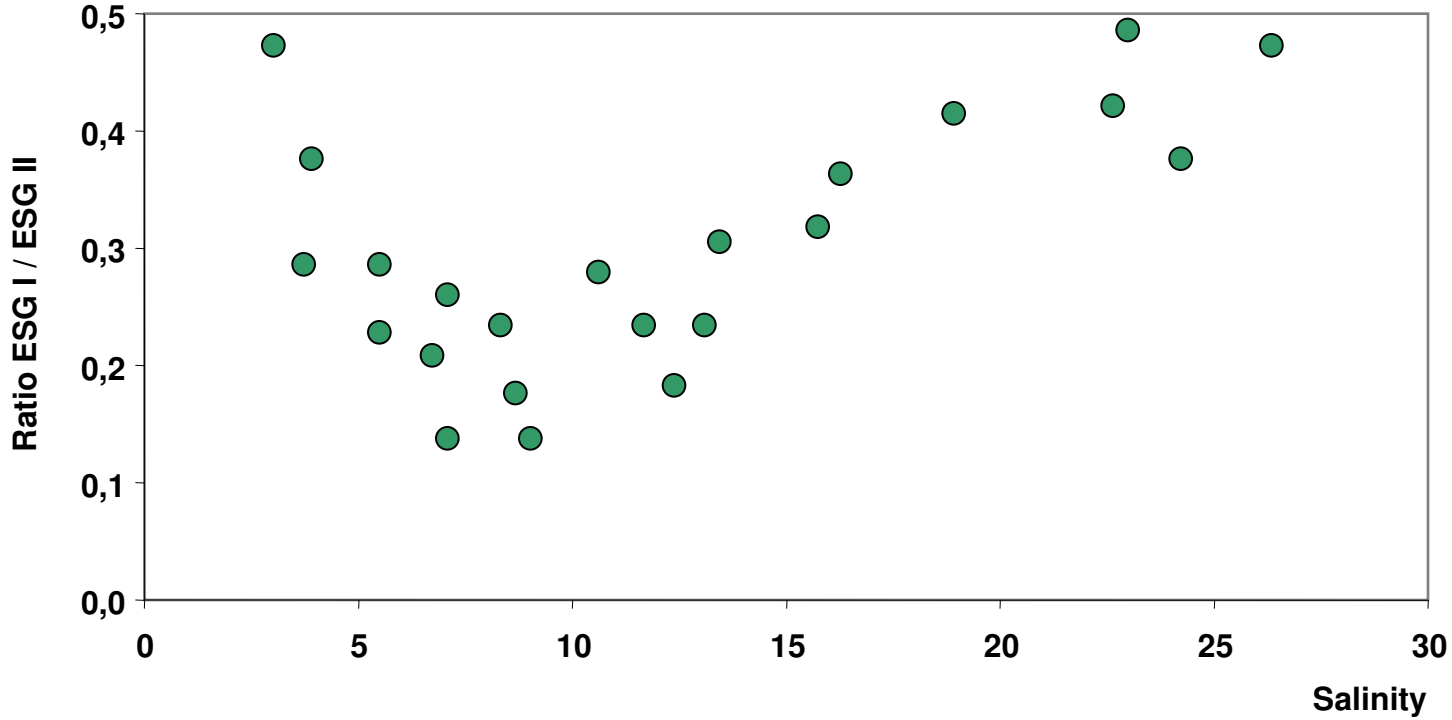
Data from REMANE (1957, Makrozoobenthon) and Nielsen et. al. (1995, Makrophytobenthon)

Functional diversity of macrophytes



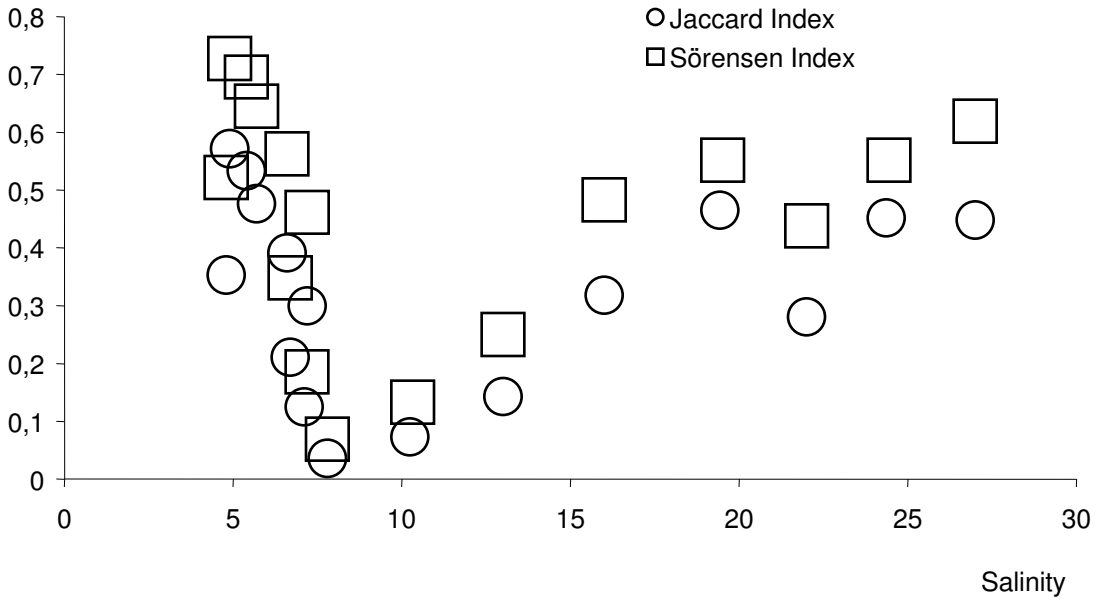
So we find another „general picture“ for Macrophytes?

Not really, because if we include higher plants, the Remane-picture comes back:



But the reason is different – osmotically higher plants are different because of their turgor, the picture above rather reflects evolutionary constraints with respect to anchoring in the habitat. Only a few algae are able to anchor in soft substrates, a kind of habitat rare under marine conditions but prevailing in the limnetic biome...

Results – *similarity of species composition of neighboured sites*



This is also reflected in community composition, where the drop around the „critical salinity“ is caused by the disappaerance of habitat builders, i.e. large perennial brown algae species („kelp“-species)

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Life in the salinity gradient

German Partners:

University of Rostock

Leibniz-Institute for Baltic Sea Research (IOW)



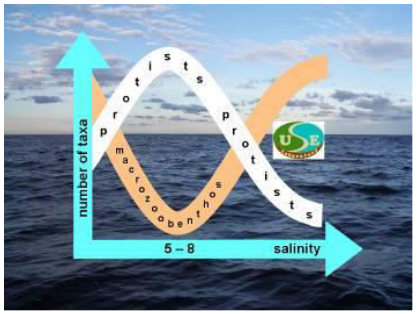
Russian Partners

Institute of Cytology, Russian Academy of Sciences

Zoological Institute, Russian Academy of Sciences

1. The Baltic Sea is not poor in plankton species (as thought earlier).

2. Remane's Artenminimum (species-minimum) concept is valid for macrozoobenthos, but cannot be extrapolated to other major ecological groups of aquatic organisms in the Baltic Sea.

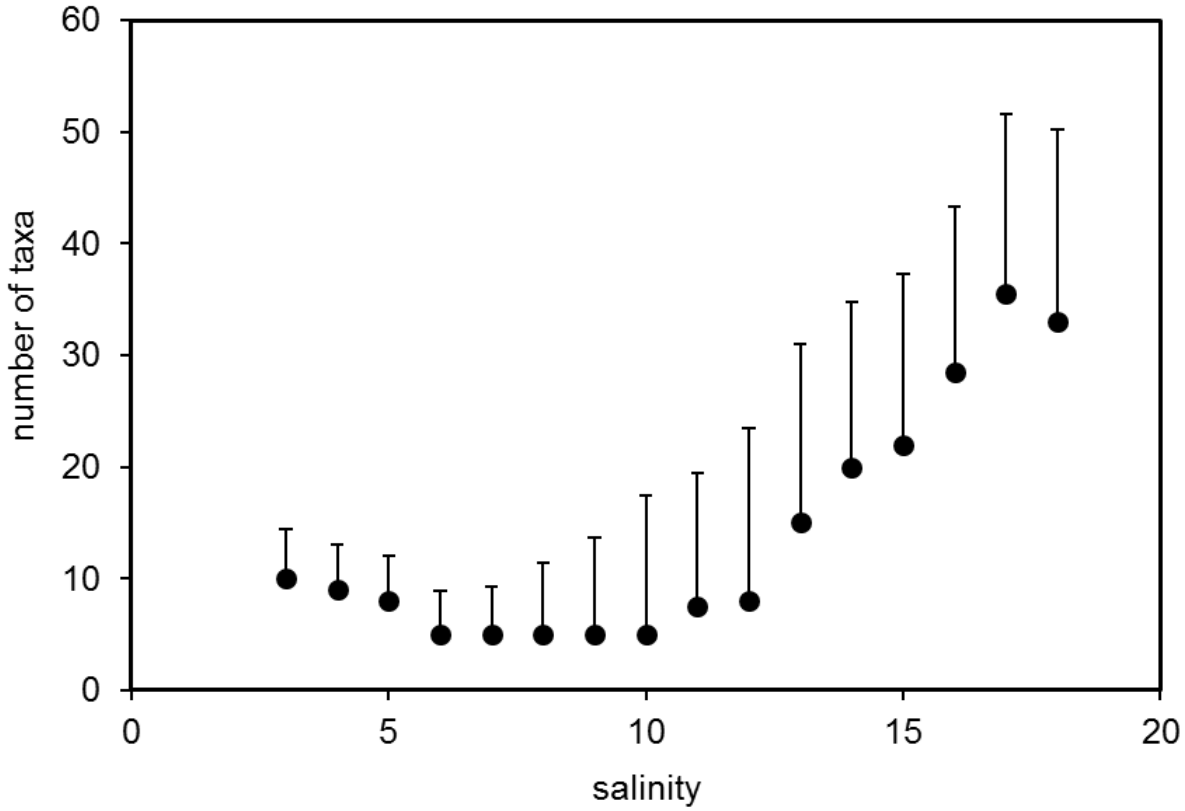


3. The protistan species richness peaks in the horohalinicum giving grounds to the novel 'protistan species-maximum concept'.

4. Field investigations proved restricted applicability of Remane's species-minimum concept to macrophytes.

But the field vs. pooled data problem?

Number of taxa per sample



- So the feeling was right – there is a problem: brackish samples are „species poor“ – how does it comes to the „species maximum“ of pooled samples?

But the field vs. pooled data problem?

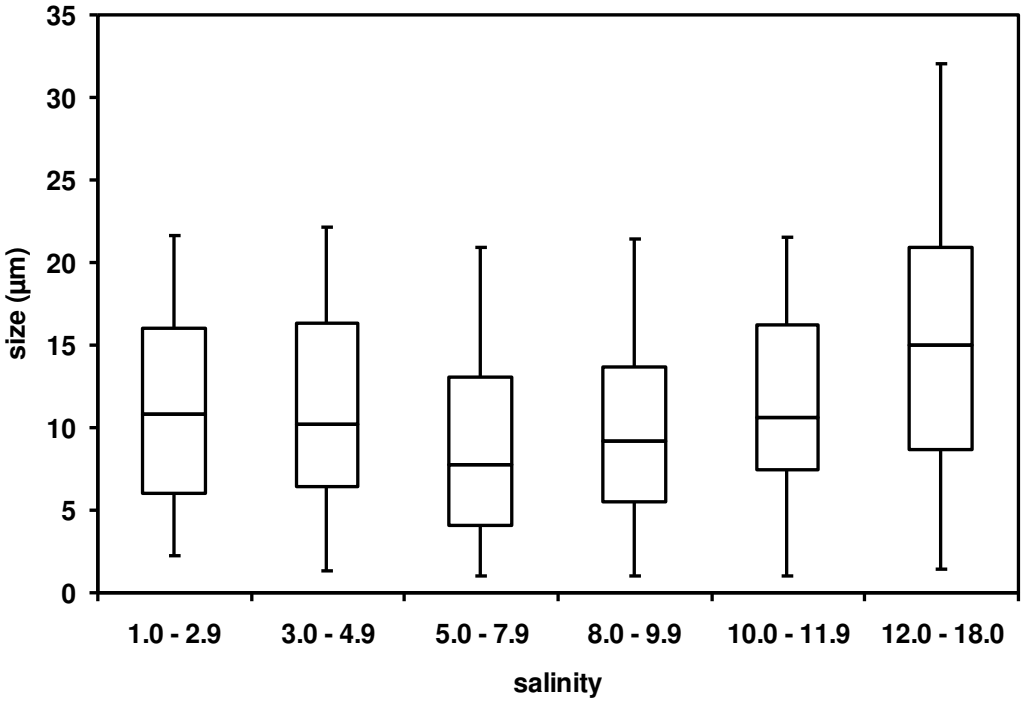
Hypotheses:

1. There is a difference in size - smaller and therefore faster evolving unicellular organisms dominate in the horohalinicum, so the observed maximum number of protistan species in the critical salinity zone is caused by a pronounced seasonality within the horohalinicum, caused by a shift in composition of phytoplankton community towards dominance of small-sized species with rather narrow optima

2. The protistan species maximum in the horohalinicum is caused by between-sample variation in highly changeable brackish waters rather than by within-sample diversity

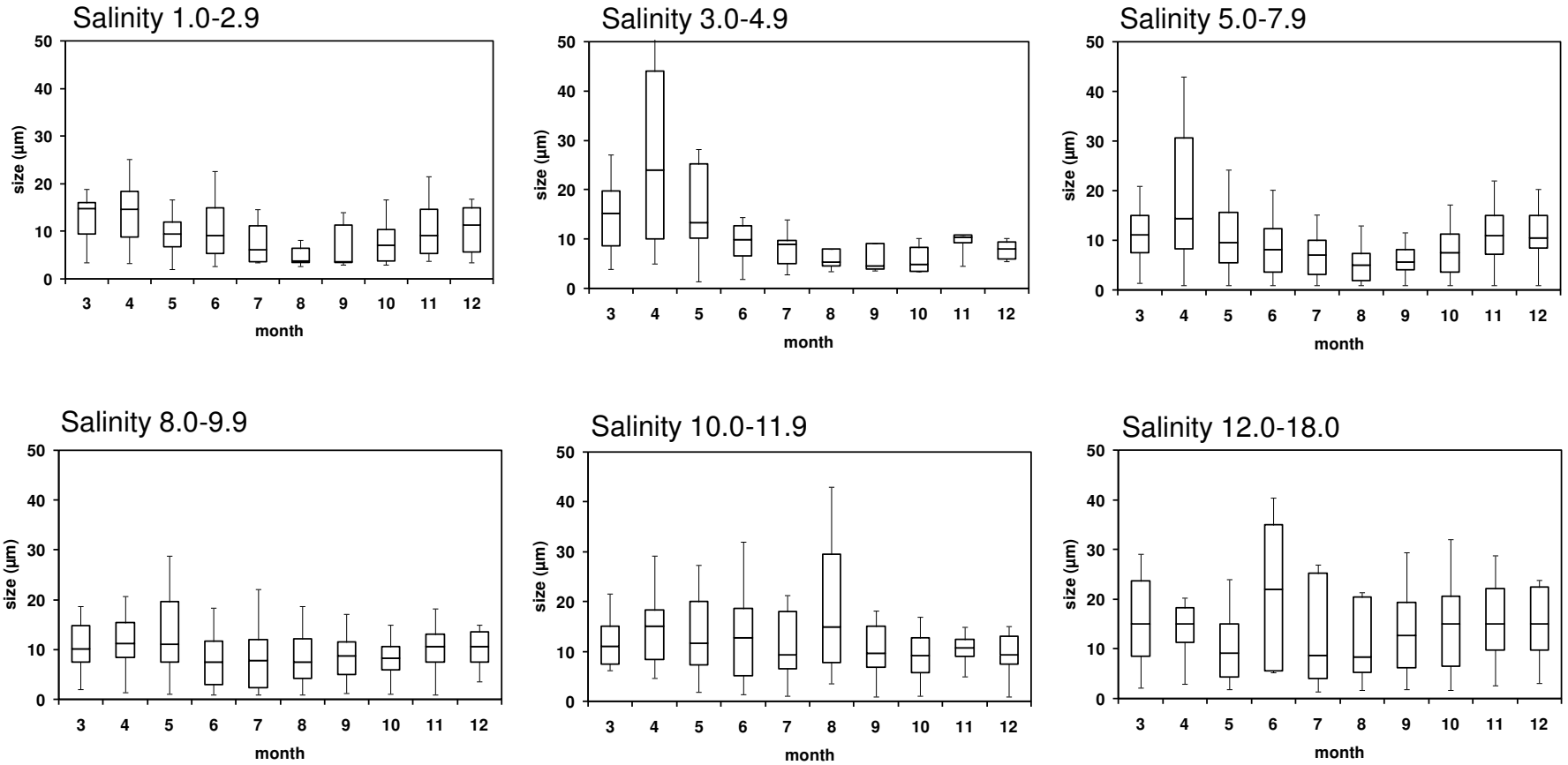
Both hypotheses are closely inter-related. Between-sample variation in plankton species richness may be caused by the regional differences in sampling sites with the same salinity due to high water mobility and the consequent heterogeneity of the pelagic environment. Alternatively, this variability may be driven by the seasonality in plankton species composition, the latter being clearly related to the size of the organisms.

Seasonality of mean size per sample



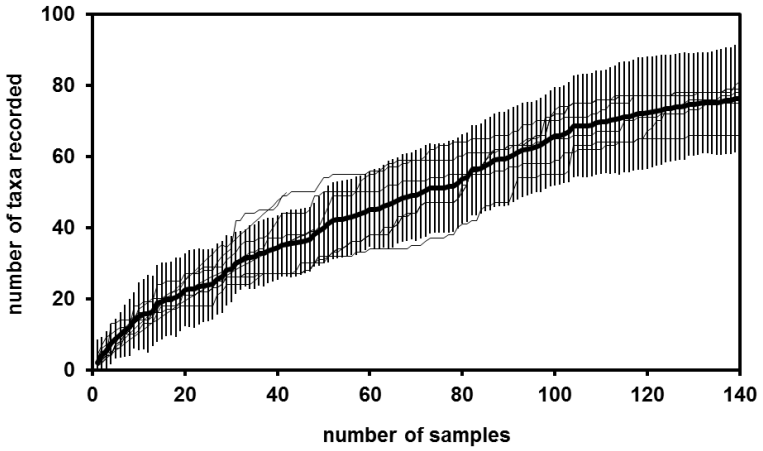
- No significant difference in mean size per sample between salinity classes
- But differences with respect to seasonality of the mean sizes?

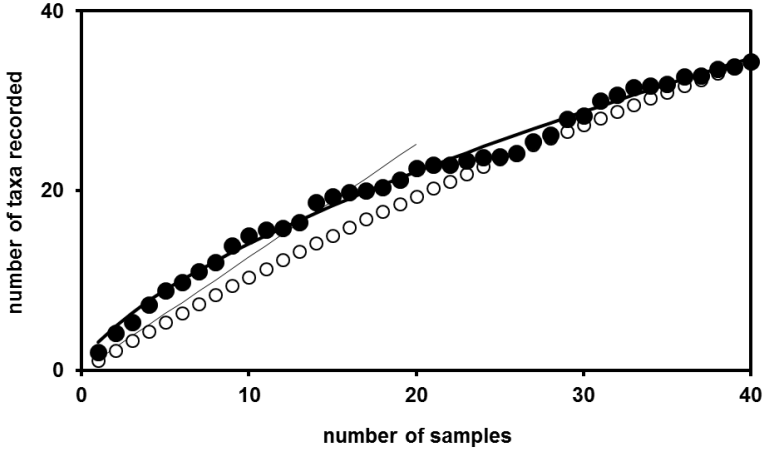
Seasonality of mean size per sample

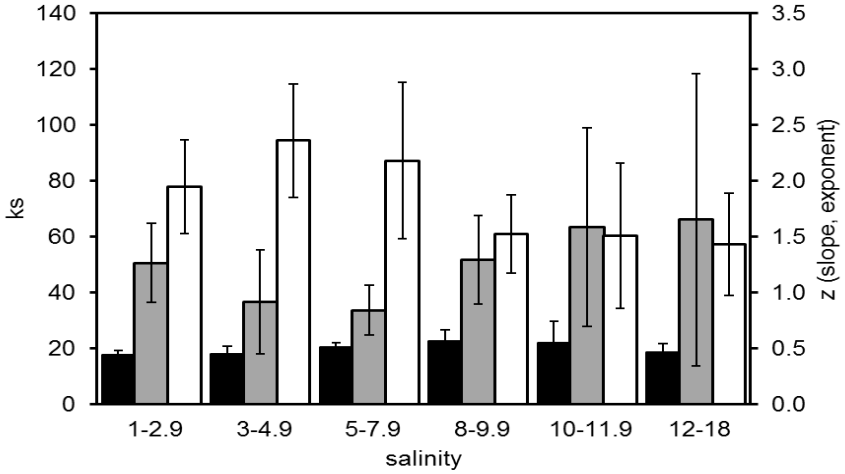


- Indeed, differences with respect to seasonality of the mean sizes between the salinity classes…

Between sample vs. within sample diversity







- Ks-values, representing the number of samples needed to detect half of the species found in the respective salinity classes are lowest at the horohalinikum (grey bars)

But the field vs. pooled data problem?

- Pronounced seasonality in the horohalinikum
- Higher between-sample diversity

There are numerous people to thank for active contributions during the field work as well by struggling trough the results:

"field workers"



"think tank"
Jochen Krause
Sigrid Sagert
Mandy Bahnwart
Uwe Selig

amendements:

Thank you for your attention

rg Martin, Irmgard Blindow,