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**Seasonal variability in plankton community structure,
productivity and food web transfer along the salinity
gradient of the Baltic Sea**

by

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Abstract

The brackish water environment in the semi-enclosed Baltic Sea causes changes in plankton community structure in close relation to large-scale circulation patterns. In addition, seasonal changes in nutrients levels and stoichiometric ratios, light and stratification successively modified it. The analysis of comprehensive data sets on environmental properties, micro and meso-plankton communities, their metabolic activity and productivity basing on classical and enzymatic methods allows verifying the interplay between community structure and food web transfer from Kattegat to the Gulf of Finland in the ninety nineties. Aspects, like the ratio between new and regenerated production, the percentage of primary productivity utilized by heterotrophs of different size, and the stoichiometry in nutrient regeneration by mesozooplankton were investigated. Regions where new (primary) production was detectable were restricted to areas with river discharge after the spring bloom, but did never exceed some percentages of gross

production. Nitrogen and phosphorous were excreted by mesozooplankton in N/P=6 in May and N/P=10 in August in the same region because of the larger percentage of parthenogenetically reproducing cladocerans in summer. Herbivorous plankton <100 μ utilized one magnitude more matter of autotrophic origin, than larger plankton. Although there was a marked variability along the zonal gradient, overall seasonality exceeded regional salinity driven differences in food web transfer and in the community structure.

Introduction

Biochemical, especially enzymatic methods for measuring proxies of physiological rates were developed in the nineteen seventies for example for respiration (Electron transport system [ETS] activity by Packard, 1969; Owens and King, 1975), ammonia excretion (Glutamate dehydrogenase [GDH] activity by Bidigare and King, 1981), and growth (e.g. Aspartat transcarbamylase [ATC] activity by Bergeron and Buestel, 1979). The use of these methods became more and more practicable (c.f. in Harris et al., 2000). In contrast to classical incubation methods, analyses were less time consuming and dislocated from ship to land based laboratories. The reduction of initial volumes for various determinations permitted diverse measurements from the same source material. This allowed a multidimensional mapping of various physiological rates (e.g. Packard, 1985) in parallel with the quasi-synoptic hydrographical measurements.

Results of enzymatic methods need to be calibrated by classical approaches mostly basing on incubations. Both types of methods have their special restrictions and discussions on their accuracies are not fully completed. On the other hand, the parallel use has also potentials for testing hypothesis of fundamental relevance, for example the meaning of allometric relationships in planktology (Packard and Gómez, 2008).

Twenty years ago, we used the enthusiasm during the process of European reunification and associated funding to exchange ideas, to share knowledge, and to deepen partly existing research co-operations. It resulted in a larger data set mainly on plankton respiration, ammonia excretion, and growth collected during cruises when the Leibniz Institute of Baltic Sea Research, Warnemünde, Germany and partly the Marine Science Faculty of the University of Las Palmas, G.C., Spain, were involved. The activities started in 1989 in the central part of the Atlantic Ocean (Hernández-León et al., 1999), intensively continued in the Baltic Sea (Postel et al., 1992, 1995) and covered regions in Indian Ocean, a Norwegian Fjord, and the Angola- Benguela-Frontal Region (Fig.1). Currently, the material will be viewed, data experiments performed in order to use it for complex solutions. The space-temporal resolution of data is highest in the Baltic Sea. On the other hand, combined studies on interactions in community structure and matter transfer in the Baltic Sea are rather rare (Sandberg, 2007). Therefore, we started in this

region with our analysis. Later we will focus our efforts also in the deep sea areas and on methodological aspects.

Methods

In principle, plankton of the Baltic Sea was collected during ordinary monitoring cruises between Belt Sea and Gulf of Finland in 1990 (Fig.2). Phytoplankton fraction was collected by bottle samples while WP2 net tows of 55 and 200 μm mesh sizes were used for zooplankton. The metabolic balance in oxygen has been measured in micro-plankton ($<100\mu\text{m}$) from standard depths down to 20m using an automated version of the micro Winkler method (Aristegui and Montero, 2005). Calculations of new production base on a conceptual model. It considers the idea that the physiological uptake of nitrate by the phytoplankton is controlled by the nitrate reductase reaction which was measured. Zooplankton samples were sieved into size classes, splitted for biomass determinations, species analyses and measuring metabolism by enzymatic methods and by classical incubation methods on selected stations (Postel et al., 1995; Hernández-León and Torres, 1997; Hernández-León et al., 1995). Phytoplankton data were used from IOW data base. Methods on sampling and analysis are described in Wasmund et al. (2008).

Searching for reasonable geographical differences in phytoplankton and zooplankton community structures in the upper layer, we conducted similarity and cluster analyses applying Bray Curtis similarity analysis, square root transformation and complete linkage as the cluster mode by PRIMER software (cf., Clarke and Warwick, 1994).

Results and Discussion

The actual salinity pattern in the one meter level (Figure 3) seems to be the result of the large-scale counter-clockwise circulation in the Baltic proper. Plankton communities followed this structure. Four clusters were found at the 50% similarity level using zooplankton abundance and species composition in the upper layer (Figure 4a). They show an analogous distribution when using the 30% similarity level (Figure 4b). The result recurred for phytoplankton. After the same analysis, the stations grouped in five different categories at the 50% level (Figure 5a) and showed a sequence of stations like zooplankton when using the 30% similarity level (Figure 5b).

In this stage of the analysis, we haven't looked for the detailed influence of different community structures on matter transfer.

The investigations were done after the phytoplankton spring bloom. Therefore, new primary productivity calculated from nitrate reductase showed significant higher values in areas of external nutrient supplies only like in the Odra river plume and in the Gulf of Finland (Figure 6). In general, new production was clearly smaller in comparison to gross production (see units).

Consequently, the percentage of new production did not exceed 5% of gross production, i.e. regenerated production dominated at this stage of seasonal development already.

Converting respiration to carbon and related to primary productivity as described in Postel et al. (1995), up to 80% of primary productivity was utilized by plankton <100µm, and about 6% by plankton > 100µm (Figure 7). This percentage exceptionally increased up to 38% in summer when zooplankton was more abundant.

Generally, *in situ* (Arrhenius corrected) respiration of plankton between 100 and 200µm was in turn with excretion except at some stations (Figure 8). This was not generally the case, which might be of special interest. Figure 9 reflects the situation off Odra River in autumn. The situation was characterized by a salinity front in about 10 nautical miles distance to the river mouth (Fig.9a). Plant pigments decreased drastically on the sea side of the plume. It fitted with the specific growth rate in terms of ATC activity units (substrate utilization), while the specific respiration reached maximum values in the frontal area (stress?). In contrast to Figure 8, excretion activity (GDH) did not spatially correlate with respiration. It increased downstream the frontal area when respiration was low (Figure 9b).

The stoichiometry in nutrient regeneration by mesozooplankton was not investigated in detail in our first attempt. Averages of N and P regenerated by zooplankton <200µm showed differences in May and in August according to Postel et al. (1995). The ratio was smaller in May (N/P=6) than in August (N/P=10). It could be explained by different plankton composition and potential differences in energy requirements for reproduction (Gismervik, 1997). In August, the proportion of cladocerans was much higher than in May (Figure 10) which may cause larger P requirements for energy rich ATP compounds due to their parthenogenetic reproduction mode. By all means, this should become clearer when dealing with the annual time series (Table 1). For the future, we also see potentials for answering the question: Do changes in communities change the transfer of matter - to which extent - and *vice versa*?

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Table and Figures

Table 1: Review on zooplankton data collection (Project, when, where, parameter measured, related aspects)

Figure 1: Locations of zooplankton studies on community structure, metabolism and growth by enzymatic and classical methods by Leibniz Institute of Baltic Sea Research, Warnemünde, Germany, and partly by Marine Science Faculty of the University of Las Palmas, G.C., Spain

Figure 2: Sampling locations in the Baltic Sea in May 1990

Figure 3: Salinity pattern in the one meter level during May 1990

Figure 4: (a) Similarity plot basing on abundance and species composition of zooplankton > 100µm in the upper layer in May 1990 and (b) distribution of stations related on the 30% similarity level

Figure 5: (a) Individual dominance (relative abundance) within five phytoplankton clusters during May 1990 in the upper 20 m and (b) distribution of station related on the 30% similarity level

Figure 6: New versus regenerated production of plankton <100µm in the upper 20m in May 1990: Gross production, new production calculated from nitrate reductase activity, and the percentage of new production at gross production

Figure 7: Percentage of primary productivity utilized by plankton <100µm and by plankton > 100µm (PB Pomeranian Bay, AS Arkona Sea, BS Bornholm Sea, S&C GS Southern and central Gotland Sea, NBP Northern Baltic proper, GoF Gulf of Finland, WGS Western Gotland Sea, BS2 Bornholm Sea 2nd survey, AS2 Arkona Sea 2nd survey)

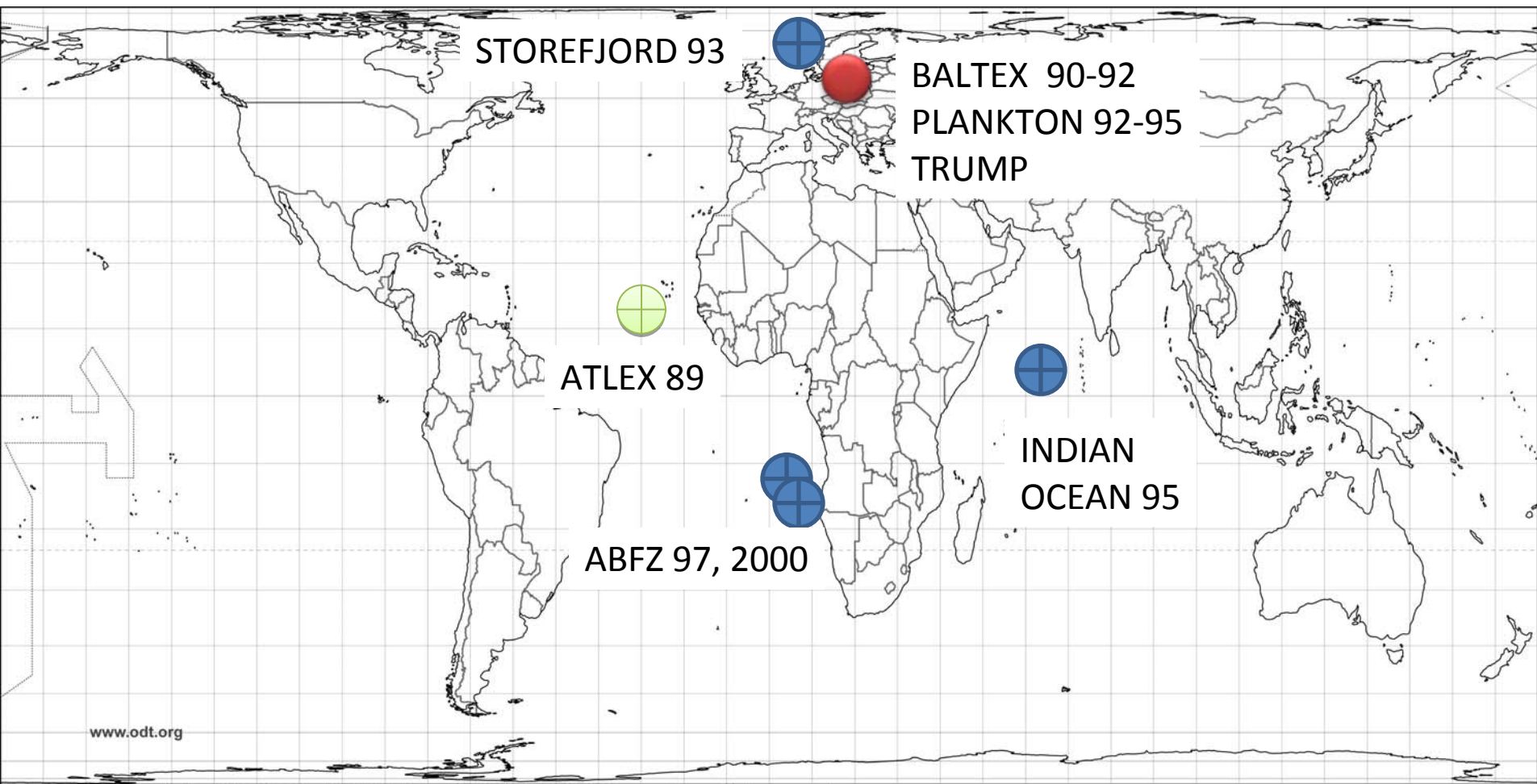
Figure 8: Comparison of the course of in situ specific ETS- and GDH activity of the fraction 100 to 200µm between the western Baltic Sea (station 12) and the Gulf of Finland (station 305) and return to Arkona Sea (station 113) in May, 1990

Figure 9: Course of the in situ specific metabolic rates and growth off then Odra River mouth in fall 1993: (a) salinity and plant pigments, (b) specific rates of ETS, GDH, and ATC

Figure 10: Comparison of average taxonomic composition of zooplankton >200µm in May and August in relation to the average N: P ratio in the Baltic Sea (according to Postel et al., 1992)

			ETS	GDH	ATC	EggProd	Remi	Respi	Abundance	Aspect
BALTEX	05,1990	Open Baltic	x	x	x	x	x	x	x	spring, summer, (autumn) Salinity gradient
HELCOM	08,1990	Sea,					x	x	x	
BALTEX	05,1991	Pomeranian	x	x	x		x	x	x	
BALTEX	08,1991	Bay	x	x	x		x	x	x	
BALTEX	11,1991		x	x	x		x	x	x	
BALTEX	05,1992		x	x	x		x	x	x	
PLANKTON	08,1992		x	x	x		x	x	x	
PLANKTON	10,1993	Near coastal	x	x	x	x	x	x	x	
PLANKTON	09,1995	& open Baltic	x	x	x	x	x	x	x	
PLANKTON	04,1996	Sea	x	x	x	x	x	x	x	
STORE-FJORD	06,1993	Norway	x	x	x	x	x	x	x	Vertical profile to 400 (?) m
Annual coastal Station	1999 2000	Warne- münde, Rugen Island	x	x	x		x	x	x	Seasonal cycle, weekly sampling
TRUMP	09,1993	Near coastal	x	x	x		x	x	x	Salinity gradient
TRUMP	06,1994	(Pomeranian	x	x	x		x	x	x	
TRUMP	01,1995	Bay)	x	x	x		x	x	x	
TRUMP	04,1995		x	x	x		x	x	x	
TRUMP	07,1995		x	x	x		x	x	x	
TRUMP	09,1995		x	x	x		x	x	x	
TRUMP	10,1995		x	x	x		x	x	x	
TRUMP	09,1993		x	x	x		x	x	x	
ABFZ 97	1997	ABFZ	x	x	x		x	x	x	Frontal zone, Zonation
ABFZ 2000 (M48-3)	2000	ABFZ	x	x	x				x	
Indik	1995	Meridional section	x	x	x		x	x	x	Open ocean
ATLEX 89	1989	Latitudinal section	x	x	x		x	x	x	Open ocean

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Hobo-Dyer Equal area projection, © 2002, ODT, Inc., PO Box 134, Amherst MA 01004, 800-736-1293; Email: seeingmaps@aol.com; www.odt.org

Figure 1: Locations of zooplankton studies on community structure, metabolism and growth by enzymatic and classical methods by Leibniz Institute of Baltic Sea Research, Warnemünde, Germany, and partly by Marine Science Faculty of the University of Las Palmas, G.C., Spain

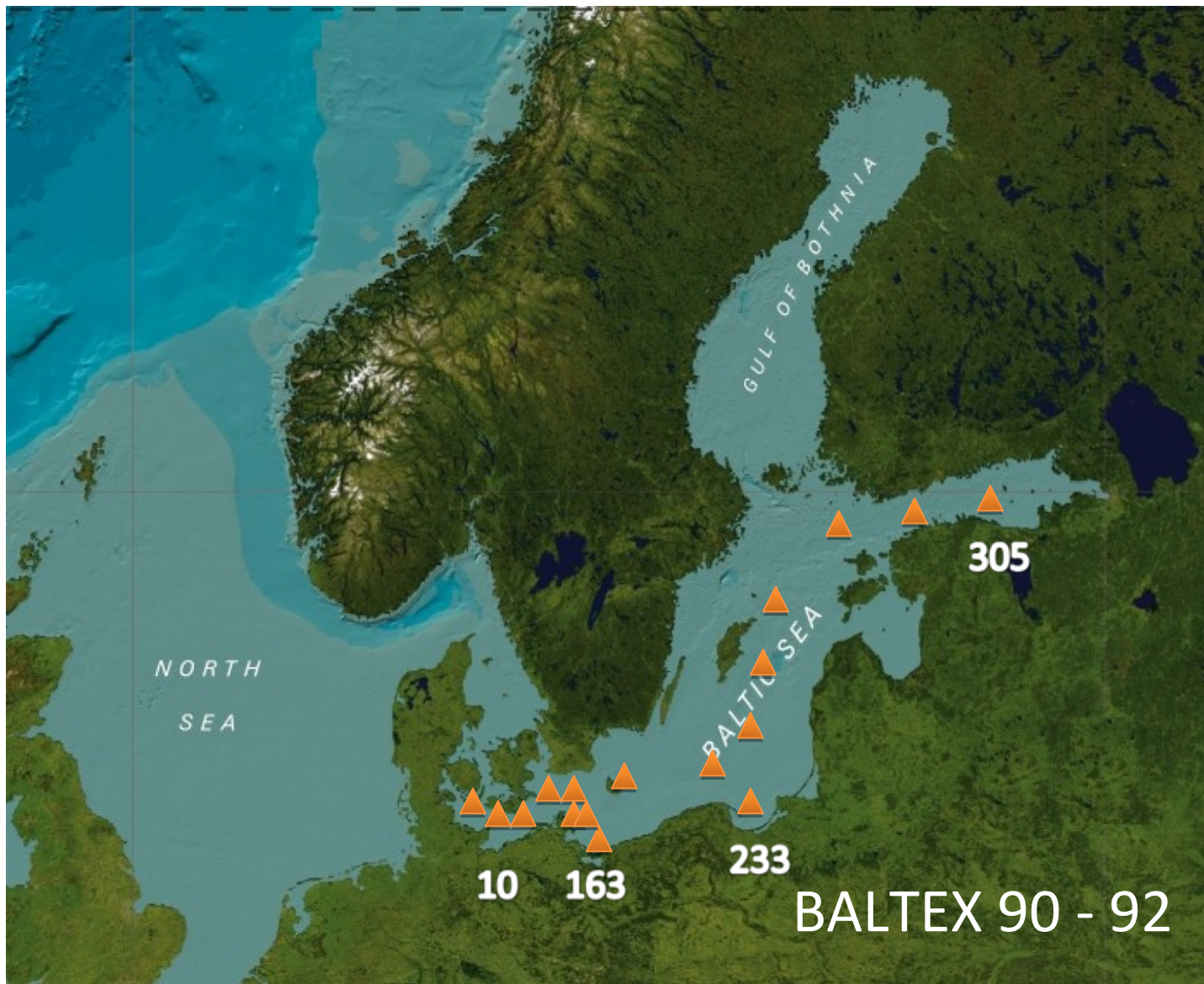


Figure 2: Sampling locations in the Baltic Sea in May 1990

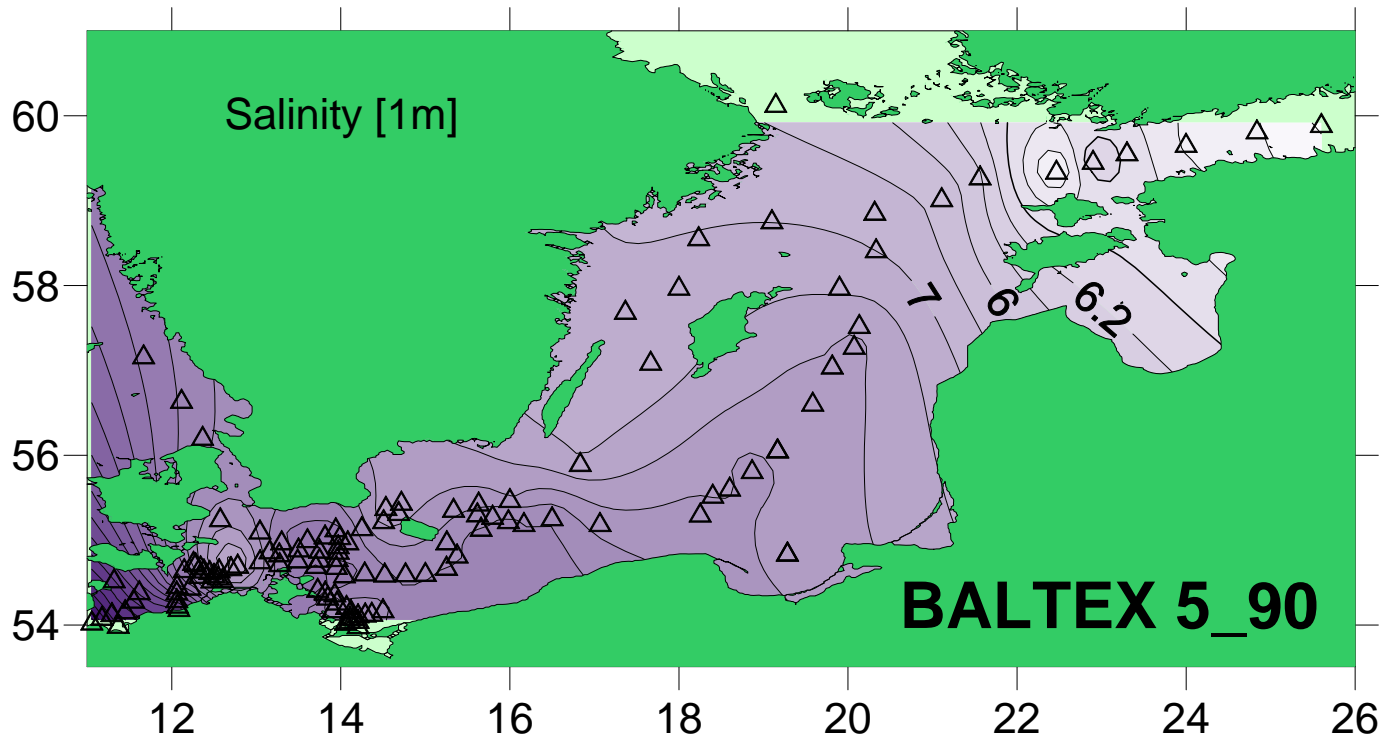
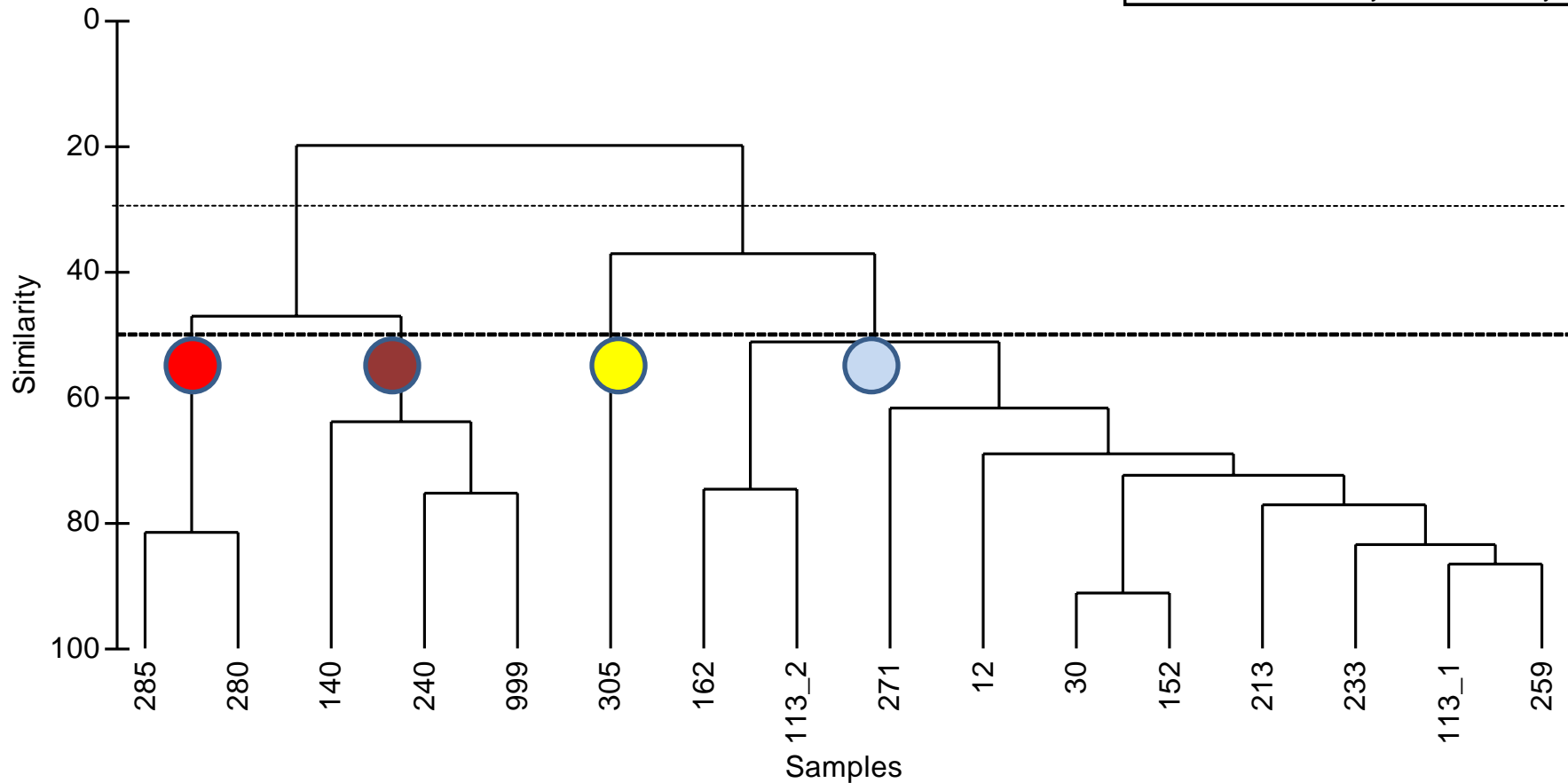


Figure 3: Salinity pattern in the one meter level during May 1990

BALTEX 5_90 Zooplankton Abundance >100 μ m

Complete linkage

Transform: Square root
Resemblance: S17 Bray Curtis similarity



Upper layer

Figure 4: (a) Similarity plot basing on abundance and species composition of zooplankton > 100 μ m in the upper layer in May 1990

Zooplankton abundance cluster

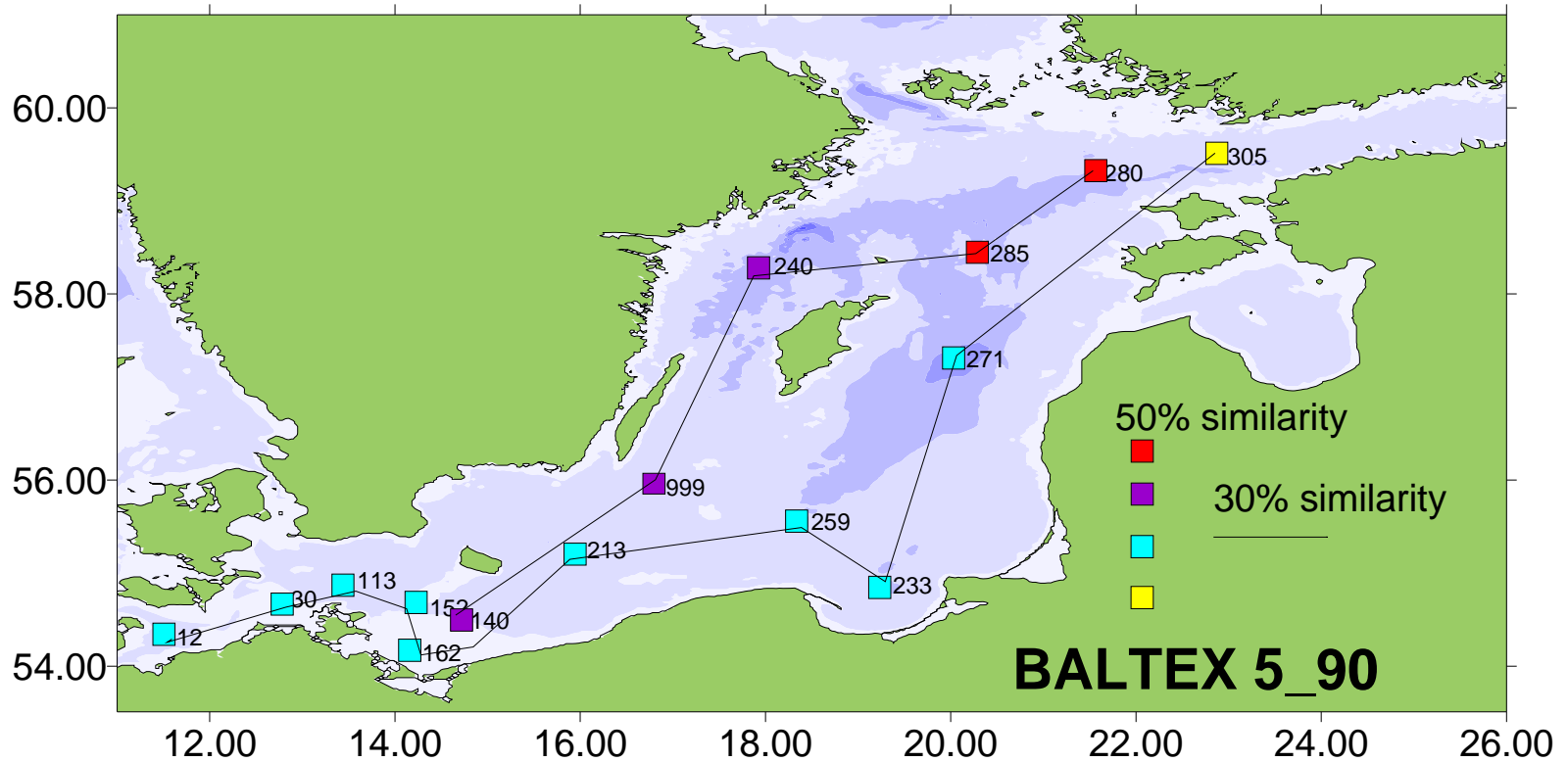


Figure 4: (b) Distribution of stations related on the 30% similarity level

Individual dominance [%] in five phytoplankton abundance cluster BALTEX_5_90

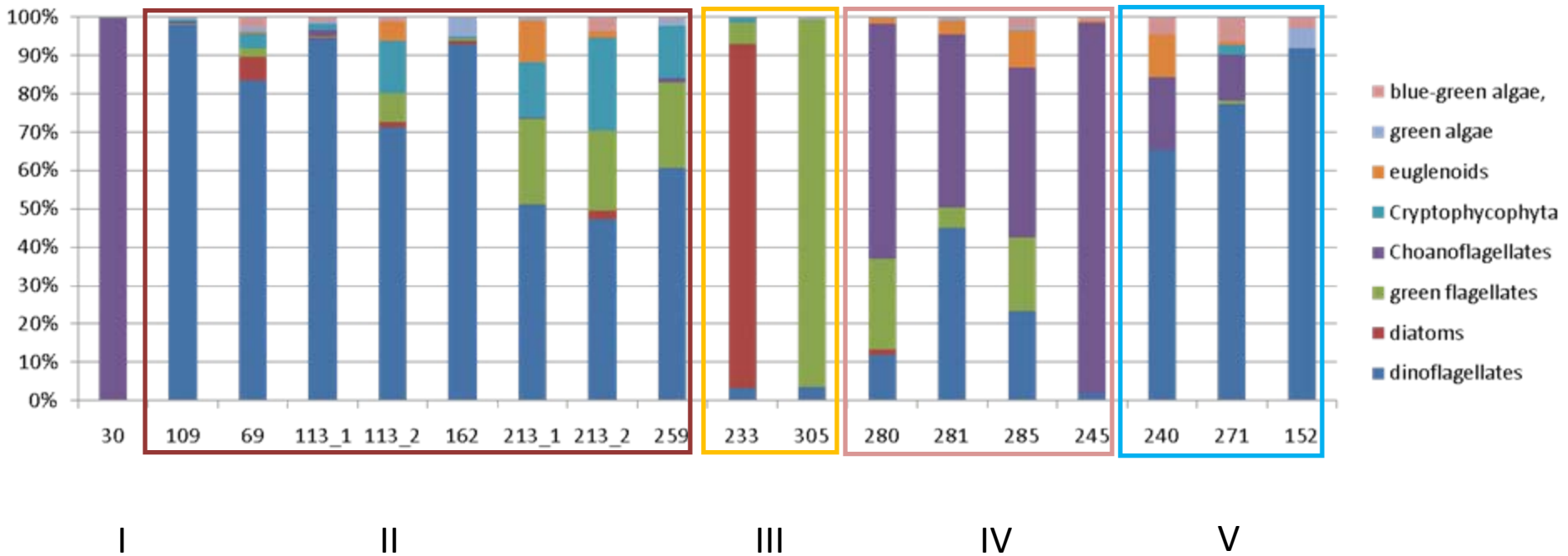
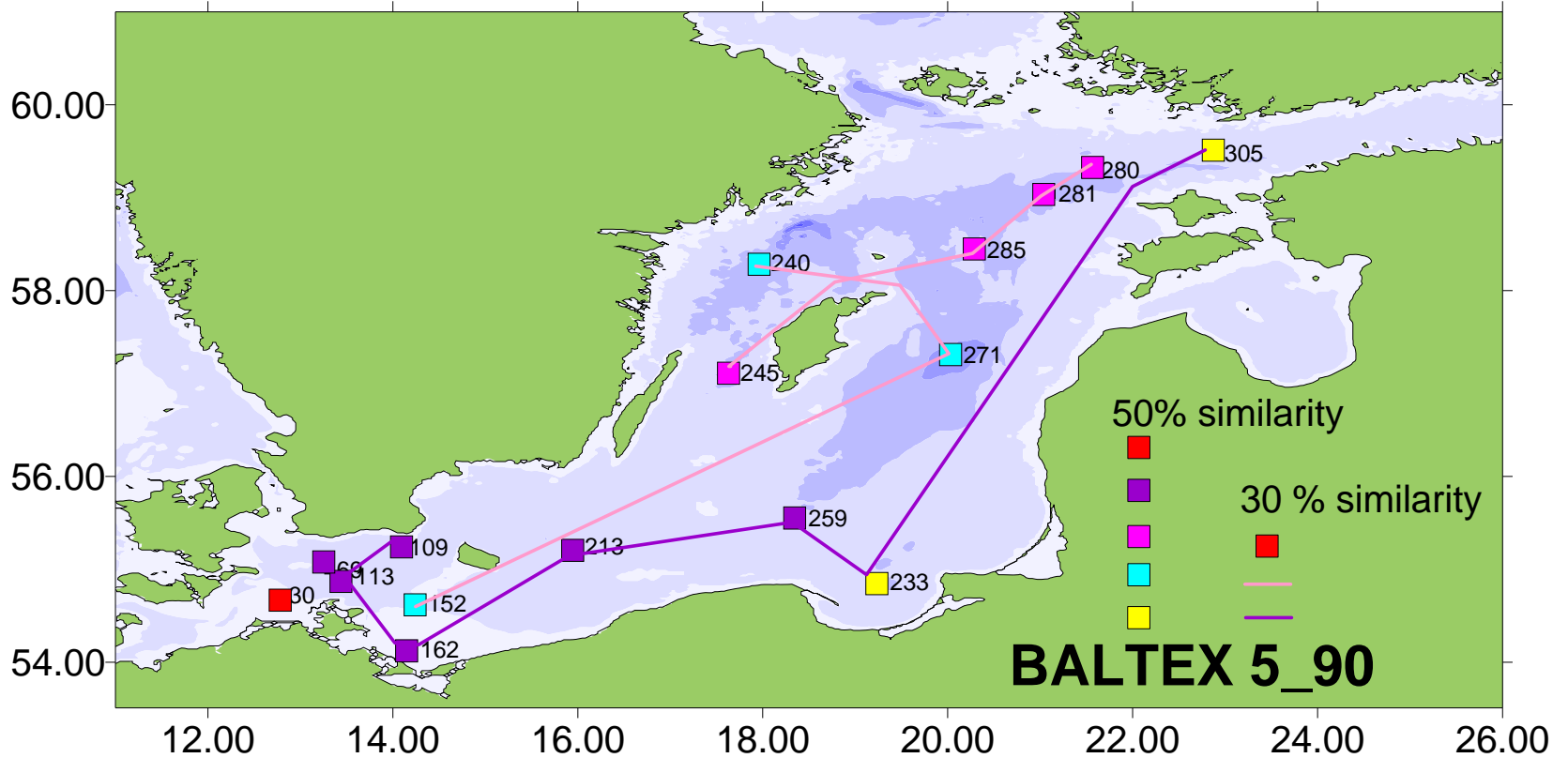


Figure 5: (a) Individual dominance (relative abundance) within five phytoplankton clusters during May 1990 in the upper 20 m

Phytoplankton abundance cluster



Counter-clockwise surface water circulation !

Figure 5: (b) distribution of station related on the 30% similarity level

New versus regenerated production

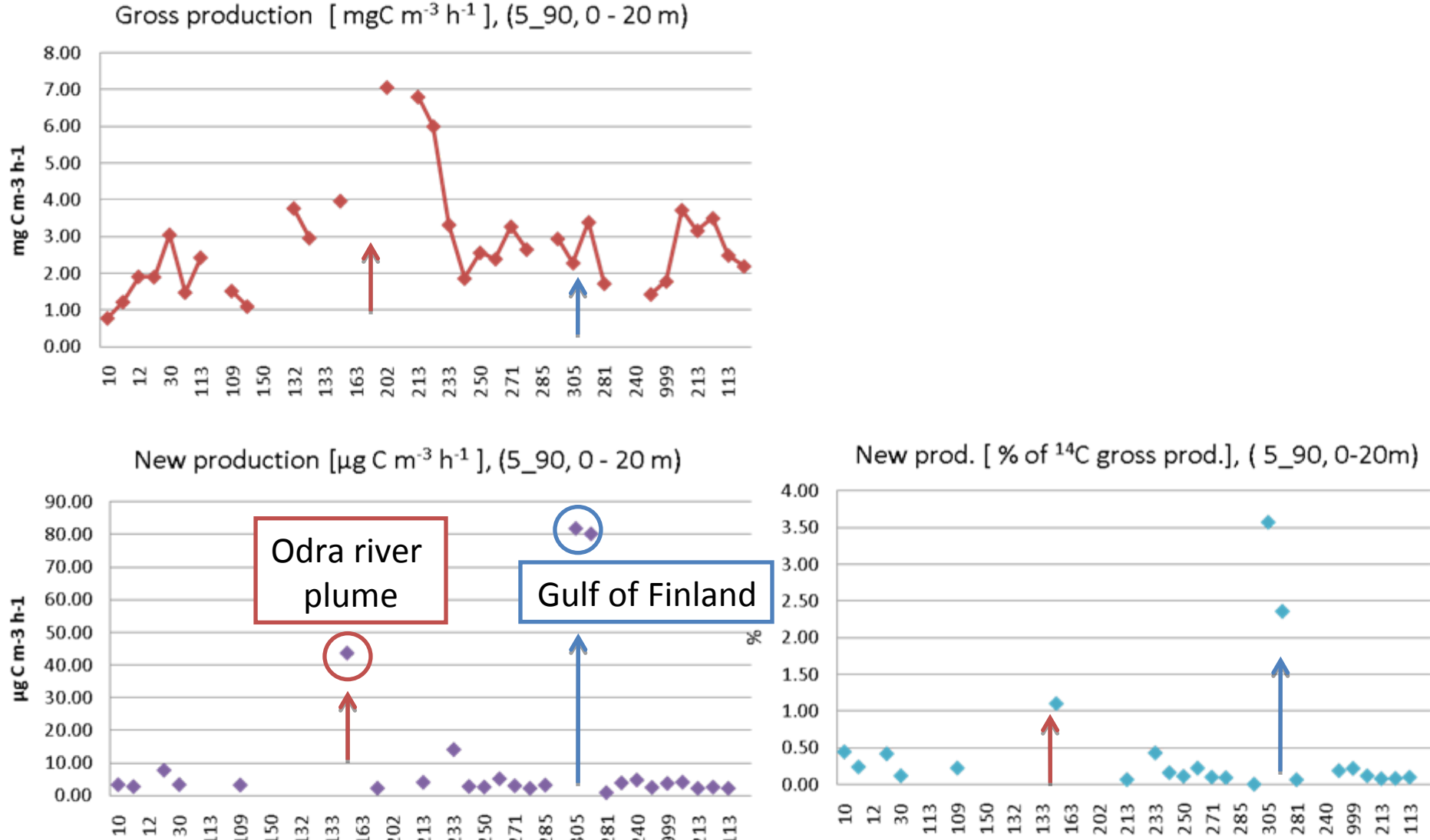
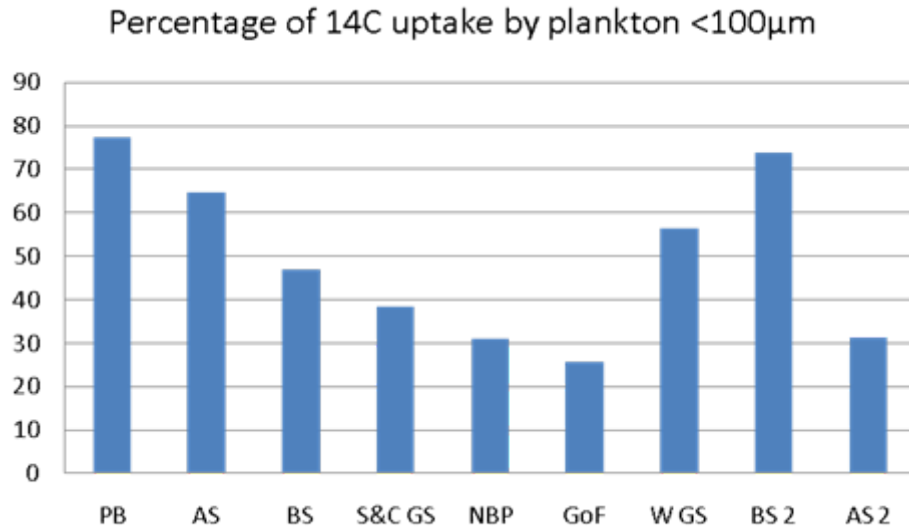


Figure 6: New versus regenerated production of plankton <100µm in the upper 20m in May 1990: Gross production, new production calculated from nitrate reductase activity, and the percentage of new production at gross production

Primary productivity utilized by heterotrophs



$<100\ \mu\text{m}$ (BALTEX 5_90)

25 - 80 %

In average: **about 6 %**

$>100\ \mu\text{m}$ (Postel et al. 1995)

→ summer, when meso-zooplankton is abundant – up to 38%!

Figure 7: Percentage of primary productivity utilized by plankton $<100\mu\text{m}$ and by plankton $> 100\mu\text{m}$

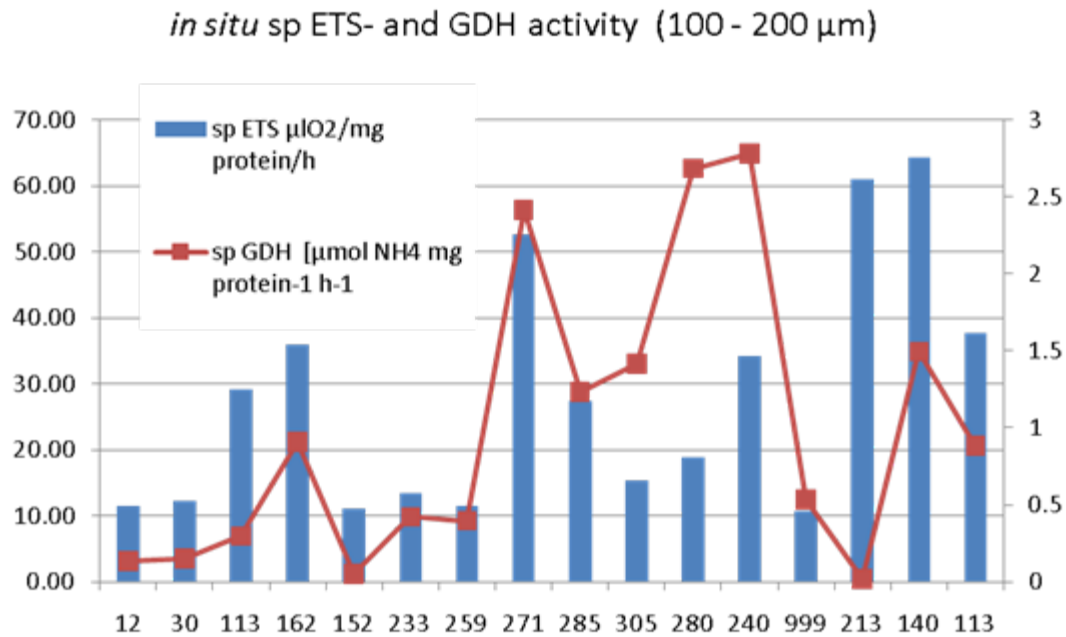
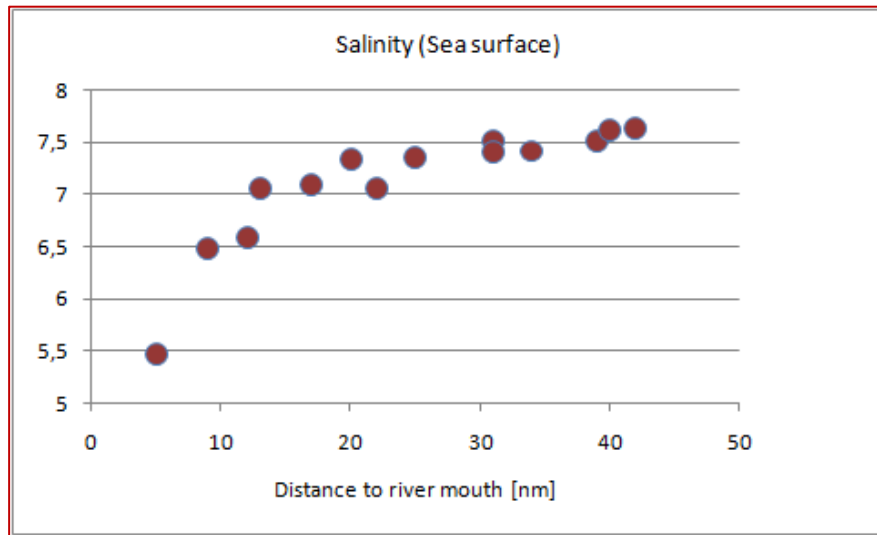
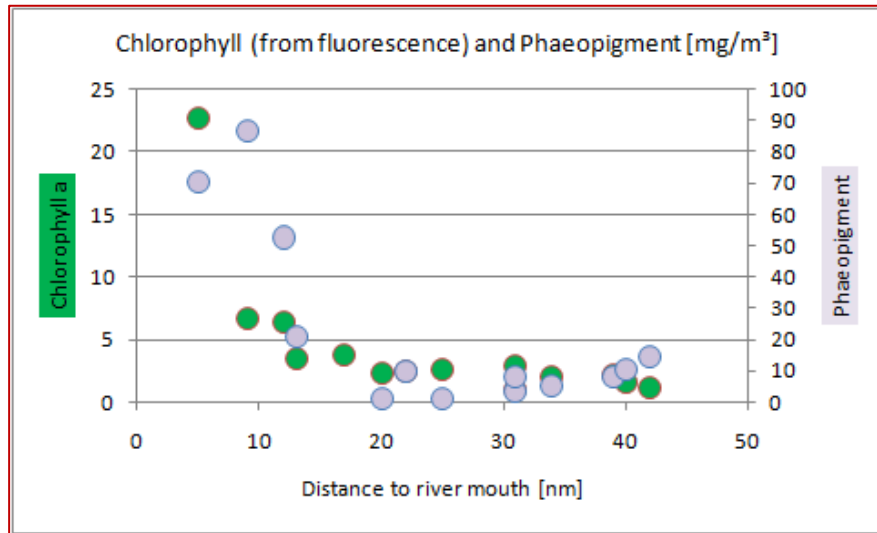


Figure 8: Comparison of the course of *in situ* specific ETS- and GDH activity of the fraction 100 to 200 μ m between the western Baltic Sea (station 12) and the Gulf of Finland (station 305) and return to Arkona Sea (station 113) in May, 1990



Salinity gradient



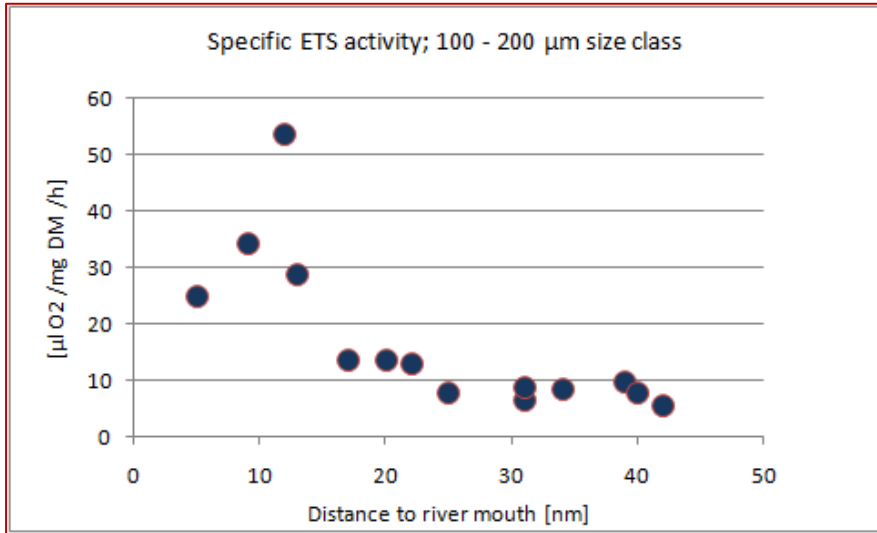
Eutrophication gradient

Pomeranian Bay,
Baltic Sea, fall 1993

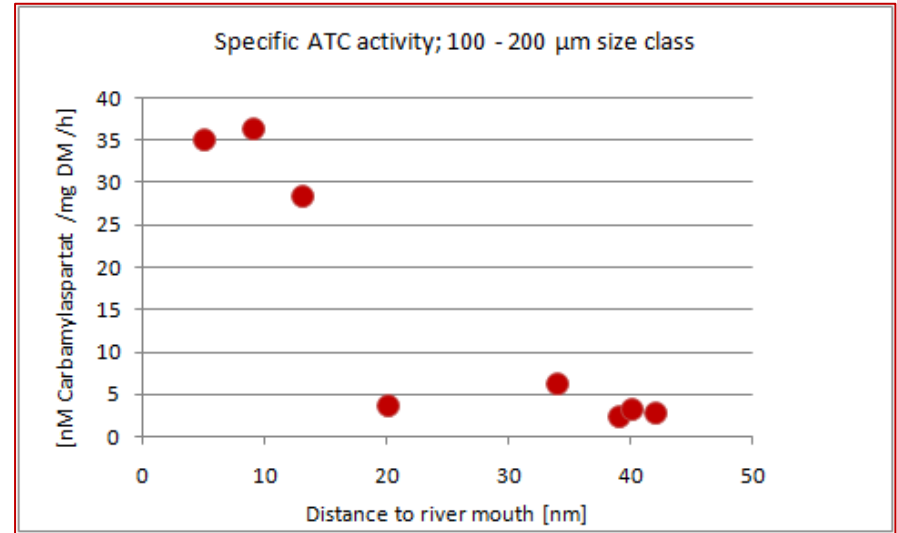
Postel et al. (1995)

Figure 9: Course of the in situ specific metabolic rates and growth off then Odra River mouth in fall 1993: (a) salinity and plant pigments

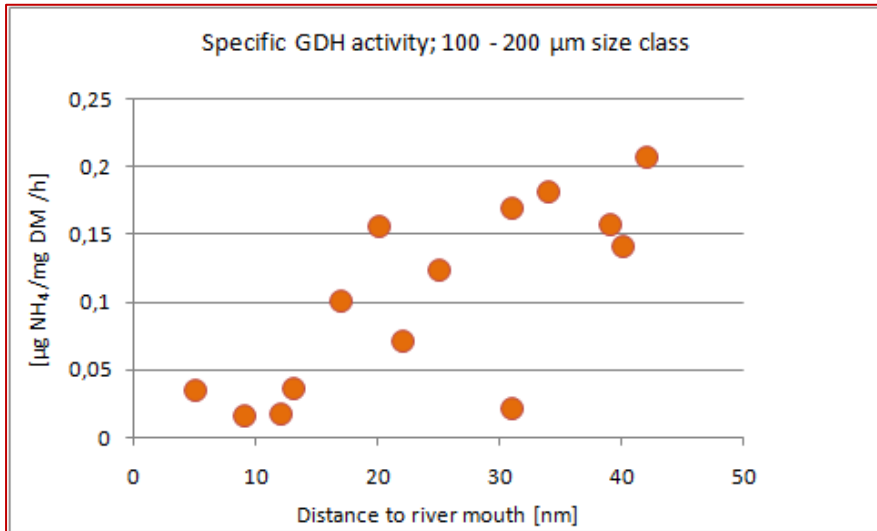
Specific respiration rate



Specific growth rate



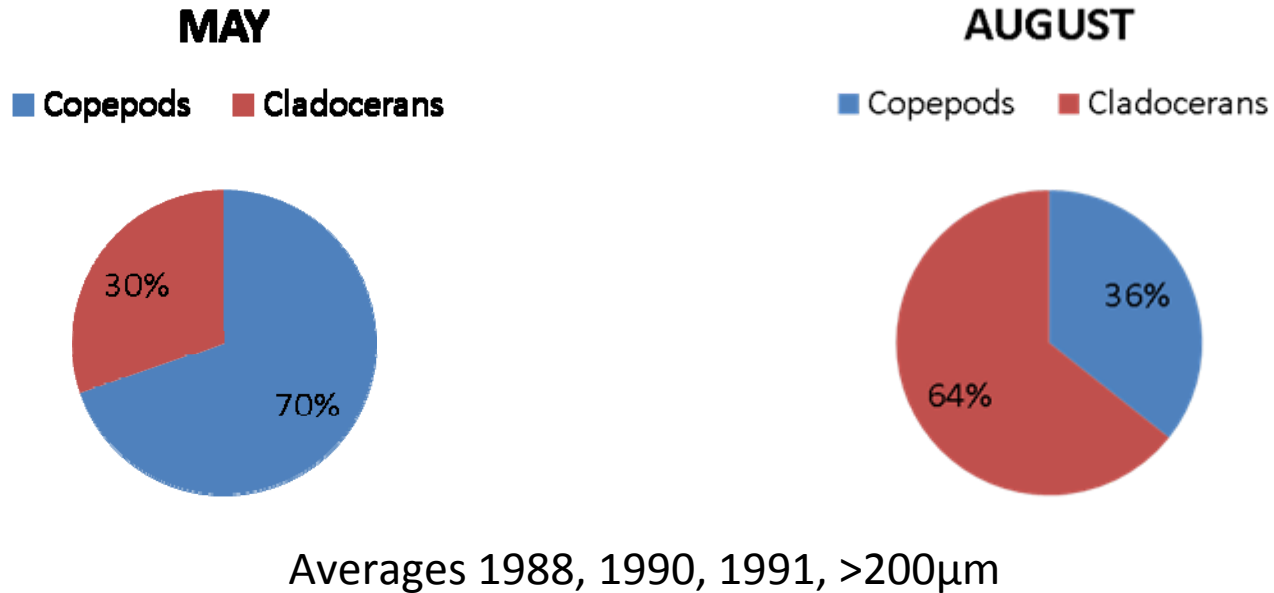
Specific excretion rate



Pomeranian Bay,
Baltic Sea, fall 1993

Figure 9: Course of the in situ specific metabolic rates and growth off then Odra River mouth in fall 1993: (b) specific rates of ETS, GDH, and ATC

Copepods ↔ Cladocerans
Parthenogenetic reproduction mode –
high short term energy requirements (ATP)



Stoichiometry in nutrient recycling

$N : P \rightarrow 6$ (in May)

$N : P \rightarrow 10$ (in August)

Figure 10: Comparison of average taxonomic composition of zooplankton >200µm in May and August in relation to the average N: P ratio in the Baltic Sea (according to Postel et al., 1992)