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Zooplankton monitoring of the Darß-Zingst lagoon – long-term changes and inter-annual variability

Zooplankton Monitoring der Darß-Zingster Boddenkette – Langzeitänderungen und interannuale Variabilität

Abstract

We studied a long time series, dating from 1969-2004, of zooplankton biomass in the shallow and wind-exposed Darß-Zingst lagoon (Northern Germany). Our aim was to investigate long-term changes and inter-annual variability. Copepods and rotifers occurred over the total time of investigation. Other groups, phyllopods and the larvae of an invaded polychaete, developed considerable biomass values only during restricted periods. All groups showed a stable pattern of seasonal change with a dominance of copepods in spring and late summer, the phyllopods during early summer, the rotifers in mid-summer and the poychaete larvae during late autumn and winter. Besides these tendencies, a considerable inter-annual variability of the biomass level was observed. This resulted mainly from climatic differences between the years. Deterministic chaos as a source of variability could not be identified in the data sets.

In the long-term run, two cases of change were observed in the dominance structure and overall biomass level during a rather short period of a few years. (1) In the beginning of the 1980s, a pronounced decrease of copepod biomass occurred. This resulted from a shift in food quality, which probably was caused by a switch of the Darß-Zingst lagoon from a macrophyte dominated system to a system dominated by phytoplankton. The phyllopods disappeared completely in connection with this event. (2) In the beginning of the 1990s, a clear decrease of the rotifer biomass was observed at the same time as the alien polychaete species Marezellaeria neglecta invaded the Darß-Zingst lagoon. Whether or not the decline of rotifers is causally linked to the polychaete invasion is not yet clear.

Keywords: Zooplankton, coastal lagoon, long-term time series, seasonal changes

1 Introduction

The German coastal waters of the Baltic Sea consist of several inlets and bays which belong to type 1 and 2 according to the classification of SCHIEWER (2006). These landlocked waters are considered possible sources of water for human use, i.e. fishery, recreation, agriculture, and disposal of waste waters. Connected with a

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complex program for maintaining the coastal water resources, the University of Rostock has been entrusted with the task of the elucidation of basic hydrographical and biological characteristics of these waters. Especially the semi-enclosed chain of lake-like waters south of the Darß-Zingst peninsula (Type 1) and Greifswald Bay (Type 2) were selected as case examples for investigation. Since its implementation by Werner Schnese, a continuous monitoring program for hydrographical and biological parameters was realized as a contribution to the worldwide activities within the framework of the International Biological Program (SCHIEWER 1990). The program resembled the investigation of the system of the Naroch Lakes, which was initiated by G. G. Vinberg already a decade earlier (VINBERG 1986). In this paper, we analyze monthly means of zooplankton data from the Darß-Zingst lagoon for a period of 35 years. Differences between the years and long-term trends are considered.

2 Material and methods

2.1 Description of the area of investigation

The Darß-Zingst Lagoon (54˚ 26' N, 12˚ 42' E, Fig. 1) has a length of 55 km, an area of 196.8 km^2 and a catchment area of 1600 km^2. The inflow of freshwater is supplied to 61 % by the rivers Recknitz and Barthe (SCHLUNGBAUM et al. 1994a).

The annual water balance expressed in million m^3 is characterized as follows (BROSIN 1965): Total volume of 342, river run off 322, precipitation 115, evaporation 112, input from the sea 1021, output to the sea 1346. The considerable input from the sea during episodes of flood is important for the reduction of the trophic state. While mixing with the water of the lagoon during the inflow, the Baltic Sea loads the lagoon water with nutrients, and removes nutrients from the lagoon when flowing back. This “ventilation“ supports the capacity of the lagoon for self-purification (SCHNESE 1975). Because the basins are connected with narrow channels, the exchange of water takes place slowly. The river water entering the Saaler and the Barther Bodden mixes with the water coming from the Baltic Sea. Therefore, the chain of basins does not act as a uniform water body, but the annual water turnover rate differs between the basins: Grabow 32, Barther Bodden 55, Bodstedter Bodden 33, Saaler Bodden 7 (SCHLUNGBAUM et al. 1994b). Each basin has its own typical salinity, ranging from almost freshwater in the west to nearly 14 psu in the east. The increase in salinity is accompanied by decreases in nutrient concentrations, turbidity, algal biomass and primary production. According to data compiled by WASMUND (1990) for the period 1969-1980, the increase from east to west amounts from 3.6 to 27.9 mm^3 /l for the annual mean of the phytoplankton biomass and from 109 to 611 g C m^{-2} a^{-1} for the annual net primary production of phytoplankton. These numbers show that the degree of trophy varies from slightly eutrophic to polytrophic conditions. The Chlorophyta and Cyanobacteria dominate the phytoplankton (WASMUND 1990). A constant relationship for the phytoplankton-zooplankton biomass ratio was observed in a horizontal scale. Both phytoplankton and zooplankton increased in biomass and production from east to west. SCHNESE (1973) estimated a biomass ratio of ca. 10 : 1 for all basins of the lagoon, whereas the less eutrophic sites at the outlet of the estuary have a relation of 5 : 1.

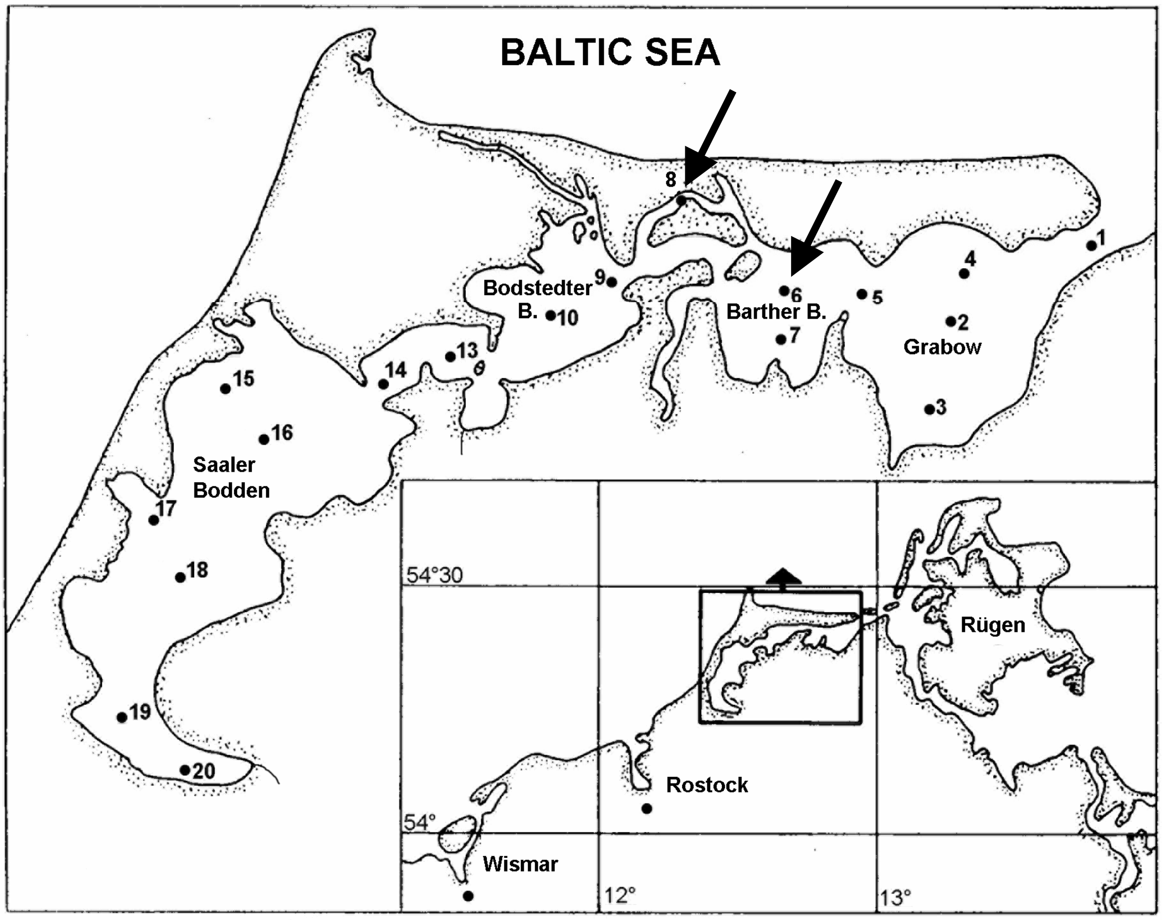

Fig. 1 Map of the Darß-Zingst lagoon. Numbers indicate the stations of monitoring. The arrows show to Station 8 (Zingster Strom) and station 6 (Barther Bodden), which are the sampling points of this investigation.

2.2 Long-term Zooplankton monitoring

Samples were taken at stations located in the central part of the lagoon (Fig. 1). The sampling method during the first 12 years of observation differed slightly from later times with respect to two points:

(1) From 1969-1980 a Ruttner sampler was used. 1 litre was taken from a depth of 0.5 m, poured into a bottle and fixed with neutralized formaldehyde to a final concentration of 3 %. A Fridinger sampler (Hydrobios, Kiel) has been used since 1981 to avoid losses of fast-moving large animals due to the turbulence, which is induced by the horizontal folds of the Ruttner sampler. Although no significant difference in catching efficiency was found for the species occurring in the Darß-Zingst Lagoon, an underestimation of the larger copepod items cannot be fully excluded. However, the decline of copepods reported in this paper since the beginning of the 1980s is not to be considered as an artefact produced by changing

the type of sampler. In the case of a methodical artefact, the result would be an increase of the copepods, not a decrease as was observed.

(2) An integrated mode of sampling was introduced in 1981 to make the sampling more representative. 5 x 5 liters were taken from both 0.5 m depth and above the bottom. The samplers were emptied into a 50 l vessel. The content of 1 l was poured into a bottle after mixing (full sample for small animals). Another 3 l were sieved through gauze with a mesh size of 50 µm. The animals were then washed from it into a small volume of 0.45 µm filtered biotop water (net sample for large animals). Neutralized formaldehyde was added to both bottles to a final concentration of 3 %. To make the results of the non-integrated sampling from the period before 1981 more representative and comparable to the integrated sampling, the mean biomass values from 3 locations were used for the period 1969-1980. These were two stations from the basin Barther Bodden and one from the basin Zingster Strom, the connection between Barther Bodden and Grabow (see Fig. 1). The data since 1981 are all from the location Zingster Strom. The inclusion of the sampling stations from the Barther Bodden could have had a depressing influence on the biomass values used for our investigation. SCHNESE (1973) found that zooplankton biomass decreased from the western to the eastern parts of the lagoon. However, if there is an effect, it was rather slight in comparison to changes which were observed in the long-term trend. A comparison between both locations for biomass values from April to September in 1981-1985 resulted in an arithmetic mean of 1.27 mm^3 l^{-1} and 1.11 mm^3 l^{-1} for the Barther Bodden and Zingster Strom respectively. No significant difference was found between the medians.

Standard methods were used for microscopic counting and biomass calculation. Samples were counted under an inverted microscope or in Kolkwitz chambers. In total, ca. 1150 samples were investigated. Equivalents of the body volume of individuals were used for the calculation of the biomass from abundance. A list of them is given in HEERKLOSS et al. (1991a). 2 - 3 samples were taken per month. A more comprehensive list of biomass equivalents is given in Appendix 1-3. It was compiled from several publications on the zooplankton of the Baltic Sea and its coastal waters (SCHWARZ 1966, ARNDT & HEIDECKE 1973, RASMUSSEN et al. 1981, CHOJNACKI 1983, HERNROTH 1985, ARNDT 1985, MACKENZIE et al. 1990, BUSCH 1993).

2.3 Data analysis for chaos

To study the inter-annual variability of the zooplankton data, we analyzed the copepods and rotifers, which constitute more than 90 % of the total biomass. In addition to a multivariate analysis which was performed by FEIKE et al. (in press), the possibility of chaotic processes as a source of inter-annual variability was studied. LJAPUNOV exponents for the data series of copepods and rotifers were calculated by Frank HILKER (pers. communication) for the period 1993-2004, the period which was without any gaps in the monthly means.

3 Results

3.1 Seasonal pattern of biomass variation and species composition

The sequence of monthly biomass values of copepods and rotifers from 1969-2004 (Fig. 2 and 3) showed a stable shape of the curve of seasonal changes for the whole period. The copepods dominated in spring and autumn and the rotifers in summer. The biomass of the copepods was composed mainly of two species of calanoids, *Eurytemora affinis* (Poppe) and *Acartia tonsa* Dana. The spring peak was composed mainly of *E. affinis,* but in late summer both species were present. The biomass of cyclopoid copepods was negligible. The dominating species during the time of the summer peak of rotifers were *Keratella cochlearis* (Gosse), *Filinia longiseta* (Ehrenberg), *Brachionus quadridentatus* (Hermann) and *Trichocerca* spp. *K.cochlearis* consisted almost completely of *K. cochlearis* f. *tecta* (Gosse). *B. quadidentatus* appeared, as a rule, later than the others, contemporary with the second peak of the copepods.

3.2 Long-term changes

In the long-term run, two cases of change were observed with respect to dominance relationships as well as the overall biomass level. These changes occurred during rather short periods of a few years. The first case was connected with a change of the crustacean biomass in the beginning of the 1980s. A pronounced decrease of copepod biomass occurred (Figure 2). At the same time, the phyllopods disappeared completely (Figure 4). In the beginning of the 1990s another case of change occurred. A clear decrease of the rotifer biomass was observed, connected with a change in dominance structure within this group. *Keratella cochlearis* f. *tecta* (Gosse) became the most dominant species, constituting up to more than 95 % of the total biomass of the rotifers. The share of *F. longiseta* in the rotifer biomass became smaller and *B. quadridentatus* disappeared almost completely from the plankton. The index of species diversity fell in these years (FEIKE et al. in press). However, a return of *B. quadridentatus* was observed in recent years, especially in 2004 and 2005.

At the same time asthe rotifer biomass decreased, an alien polychaete, the species *Marezellaeria neglecta* Sikorski & Bick[1], invaded the Darß-Zingst lagoon (Figure 5). It's filter-feeding meroplanktic larvae developed considerable biomass values during November and December 1989 – 1999.

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[1] We designated this species in an earlier paper (HEERKLOSS & SCHNESE 1999) as *Marenzelleria viridis* (VERRILL, 1873). However, after a revision of the genus *Marenzelleria* by SIKORSKI & BICK (2004) it is now described as a new species.

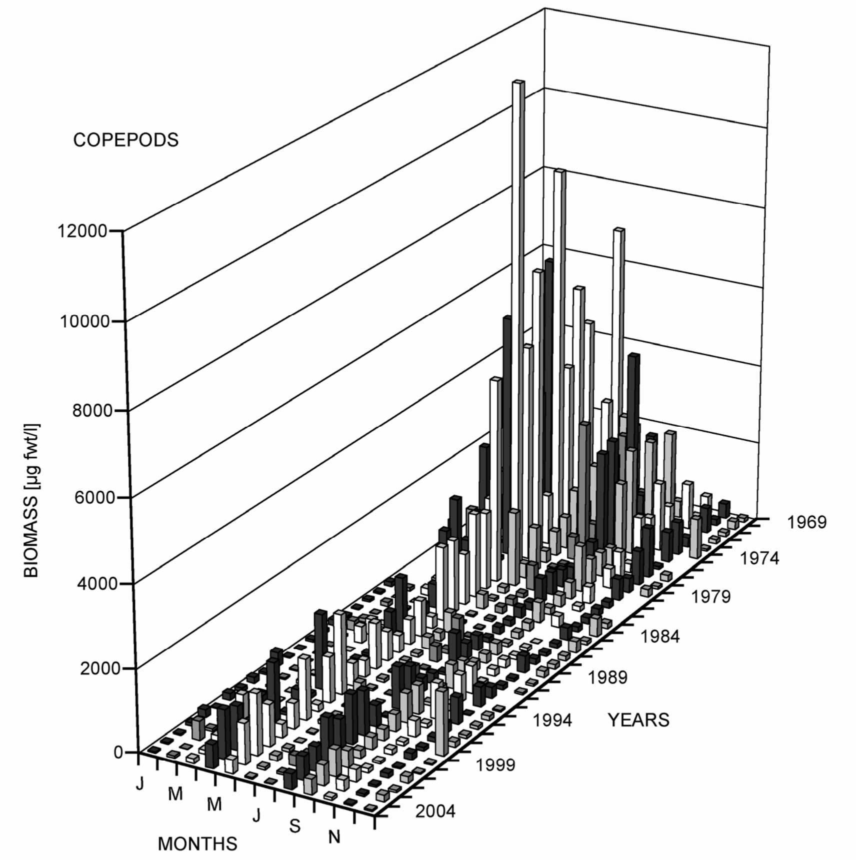


Fig. 2
Biomass of the group of "Copepods" 1969 - 2004, consisting of the two species *Eurytemora affinis* and *Acartia tonsa*. fwt = fresh weight.

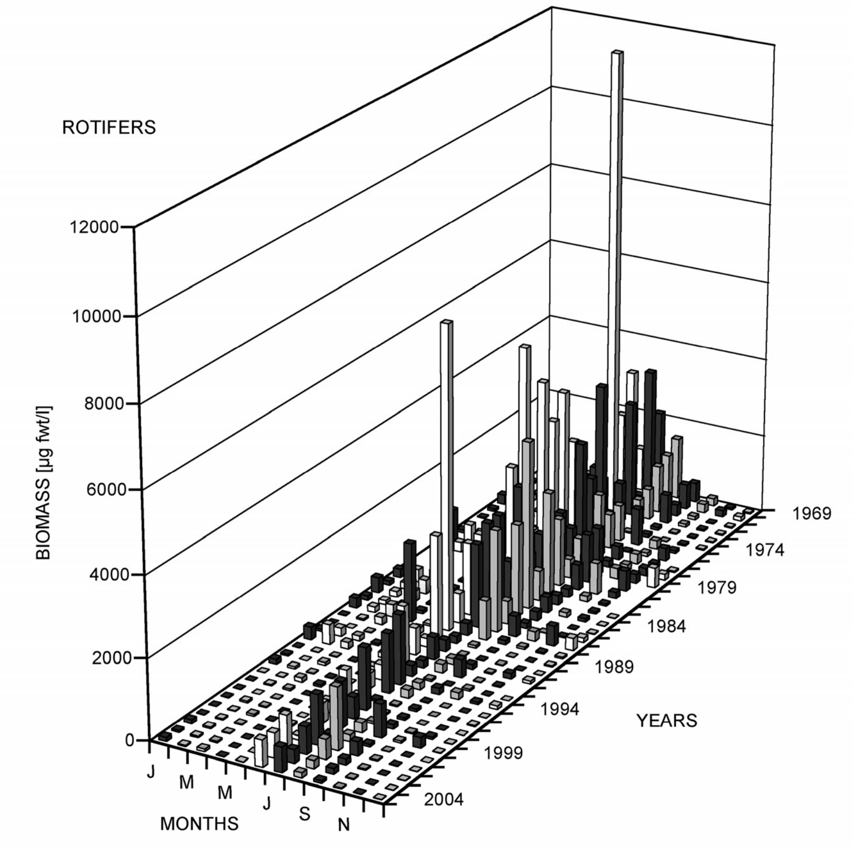


Fig. 3
Biomass of the group of "Rotifers" 1969 – 2004.

Fig. 4
Development of the biomass of the group of the remaining zooplankton species 1969 – 2004. This group consists of phyllopods, cyclopoid and harpacticoid copepods, ostracods, as well as meroplanktonic larvae except *Marenzelleria neglecta*.

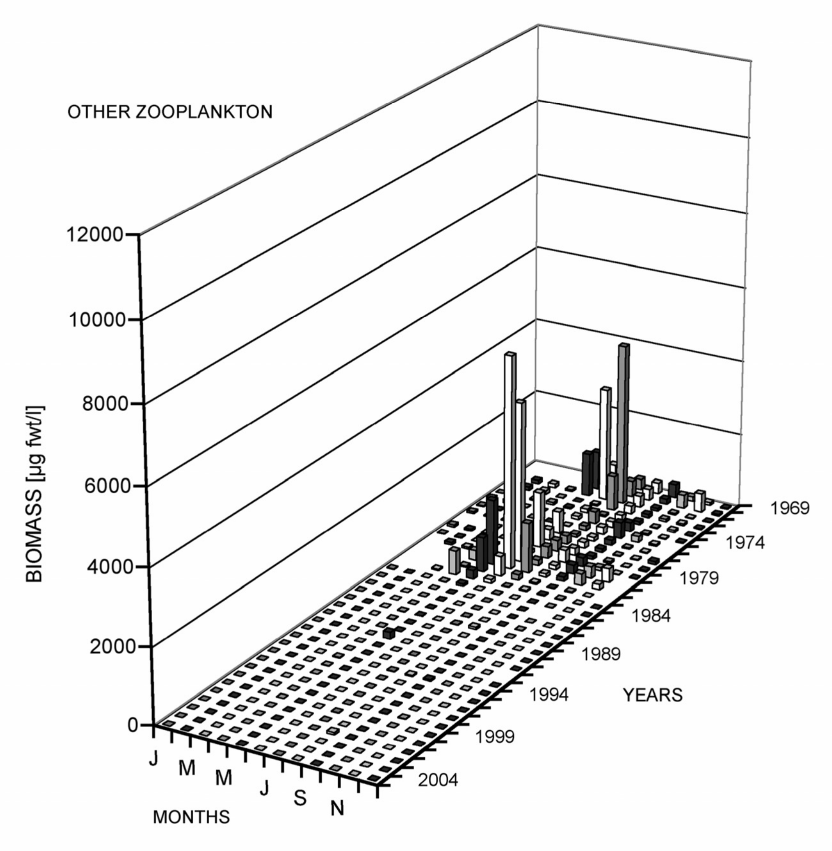
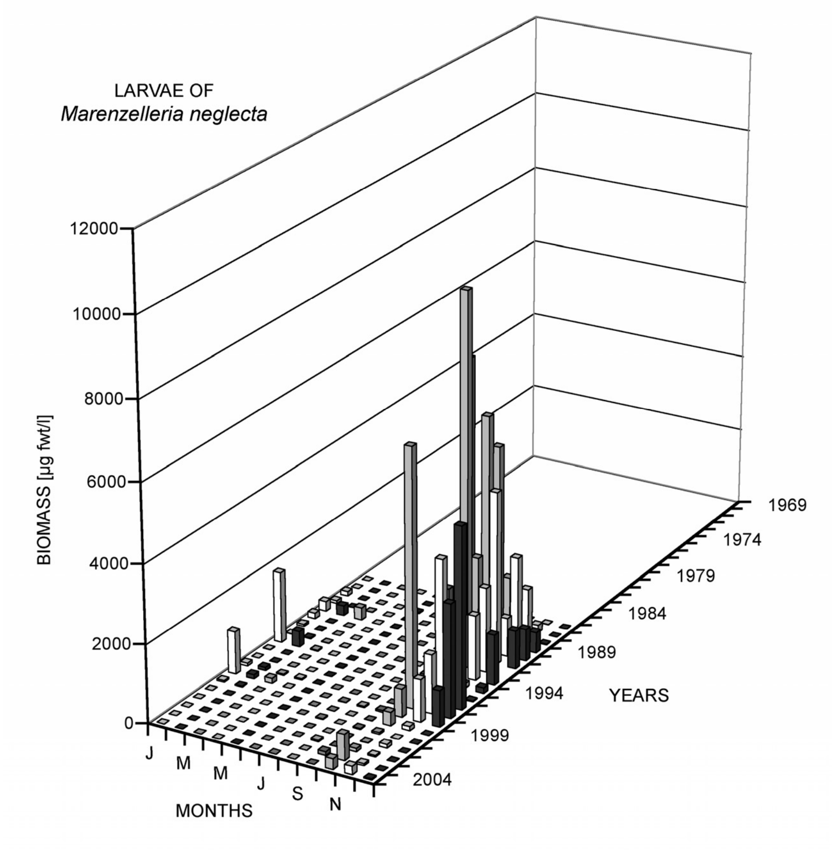


Fig. 5
Biomass of the meroplanktonic larvae of the polychaete sp. *Marenzelleria neglecta*, which invaded the Darß-Zingst lagoon in 1985.



3.3 Inter-annual variability of the data

Besides the changes described in paragraph 3.2, a considerable variability of the biomass values data was observed. These differences may be attributed to the variation in climatic and hydrologic condition of the different years. FEIKE et al. (in press) were able to show by multivariate statistics that the annual means of biomass correlate well with temperature, precipitation, and pH-value. Furthermore, a correlation was also found for the yearly duration of ice covering and the NAO[2] winter index. High values of the latter parameter indicate years which start with mild and damp winter climate. The optimum of rotifers corresponded well with higher pH-values and a longer duration of ice covering. In contrast, the copepods corresponded to higher values of temperature, precipitation and NAO index. Nevertheless, a theoretical source of variability may be connected with biotic interrelationships within the planktonic food web. This can be assumed because, under certain circumstances, mathematical and experimental food-web models with few species show chaotic properties (HASTINGS & POWELL 1991, HUISMAN & WEISSING 1999, BECKS et al., 2005), and because the species richness of the zooplankton of the Darß-Zingst lagoon is low. A part of the long-term time series of copepods and rotifers from 1993-2004, which was without gaps in the monthly means, was analyzed with respect to its exponential divergence. This is an indication for chaos. The analysis showed that it is impossible to identify a chaotic dynamic in these time series in the presence of internal and external noise.

4 Discussion and conclusion

The long-term changes in the crustacean biomass are probably causally connected with changes at the level of primary producers. The Darß-Zingst lagoon consists of very shallow, unsheltered and semi-enclosed basins. The water column in such lakes is always well-mixed, and the turbulence induced by wind provides for a high content of aged and re-suspended detritus in the water column. On the other hand, the character of shallowness is connected with the phenomenon of alternative stable states, which is well known from shallow eutrophic lakes: The primary production may be realized in this case either by submerse macrophytes or by phytoplankton. A switch from the macrophyte state to the phytoplankton state can occur in a rather short time when the macrophytes are reduced due to meteorological influences, e.g. a hard winter or a strong river runoff (SCHEFFER et al. 1993). A similar mechanism might be responsible for the changes observed during our monitoring of crustacean zooplankton, because in the early 1980s a strong decline of submerse macrophytes, mainly characeans, was observed and the phytoplankton became dominant instead (SCHIEWER 1997). To explain the changing events in the early 1980s, a shift in the composition of the suspended matter is to be taken into account. The disappearance of the phyllopods and the decrease of the copepod biomass probably are both related to a degradation in food quality. A massive decline of submersed macrophytes – mainly Characea – took place in the Darß-Zingst Lagoon in 1981 (SCHIEWER 1997). The immediate reasons were a rainy spring season with

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[2] NAO = winter index of the North Atlantic Oscillation

low water salinities, high nutrient loads, and high water turbidity. The shift from macrophytes to phytoplankton resulted in increased turbidity and sediment mobility. This probably resulted in an increase of aged detritus particles from the sediment in the suspended matter by wind-induced turbulence. GEORGI (1985) measured concentrations of suspended detritus in the central part of the Darß-Zingst Estuary. He estimated a share of 80 % of detritus in the total organic seston. During summer, high C/N ratios between 10 and 15 were determined. The disappearance of the phyllopods after the beginning of the 1980s could be a result of this change in food quality, because the species which were observed in the Darß-Zingst lagoon are filtering species and non-selective feeders. Another explanation would be an increase in the top-down control by vertebrate and non-vertebrate predators. However, this alternative can be excluded because the grazing pressure of planktivorous fish on zooplankton was found to be low in the Darß-Zingst Lagoon (MEHNER & HEERKLOSS 1994). The data on the secondary production of the main non-vertebrate predator, the mysid *Neomysis integer* (Leach), also indicate a low top-down control of zooplankton by this species (JANSEN 1983). The decrease of the copepods was probably also connected with an increase in the ratio of aged detritus in the suspended particulate organic matter. Contrary to the filtering phyllopods, the herbivorous calanoid copepods are able to select food (IRIGOIEN et al. 2000), but selectivity against dead particles is less pronounced for *E. affinis* in comparison to marine calanoids. It ingests these particles along with phytoplankton because its typical estuarine habitats are strongly dominated by non-living particles. It suffers, however, from high concentrations of dead material in the food (TACKX et al. 2004). BURDLOFF et al. (2000) also observed a connection of low egg production rates of *E. affinis* with poor food quality in the Gironde estuary. A strong indication of a limitation of *E. affinis* by low food quality in the Darß-Zingst Lagoon is indicated by results on the seasonal changes of the C/N ratios of the seston and egg ratios. According to GEORGI (1985), an increase of the C/N-value from 8.8 to 10.2 is observed from May to June. At the same time the egg ratio decreases from 17 to 3 (ARNDT 1985). A strong drop of the feeding rate of *E. affinis* is also observed during this period (HEERKLOSS et al. 1990). Furthermore, changes in the composition of phytoplankton have to be taken into account as a cause of a decrease in food quality after 1981. A shift in species composition was observed. Nanoplanktonic species, which are in the preferred size class as food for *E. affinis*, were partly replaced either by picoplankton in the case of cyanobacterians or by clumped colonies of the green algae *Tetrastrum triangulare* (Chod.) (WASMUND & SCHIEWER 1994).

The mass development of rotifers in summer seems to be a sign of the high degree eutrophication of the Darß Zingst lagoon. The morphometrically similar but less eutrophicated Vistula Lagoon does not show such a rotifer peak in summer, but does show a rotifer peak in spring composed mainly of *Brachionus calyciflorus* (Pallas). (HEERKLOSS et al. 1991b). Also, the high share of *K. cochlearis* f. *tecta* among the subspecies of *K. cochlearis* is a sign for hypertrophic conditions (KARABIN 1983). To discuss the change in rotifers in the beginning of the 1990s two points are to be considered. One is the decrease of the total biomass, the other the change in the dominance relationships, which was reflected by a fall in the index of species diversity in these years. To explain this change with factors like grazing or food quality, the results from parallel investigation on ichthyofauna and phytoplankton are important. They should point to an increase in predation on rotifers or to further changes in food quality by the ongoing eutrophication, but these data give no hint of that. A decrease in the yield of planktivorous fish has beenobserved since the beginning of the 1990s (WINKLER 2006), i.e., there was obviously a bottom-up effect from the change in food quantity and quality for the fish larvae, which depend on rotifer, especially the larger species, in early summer. A further eutrophication of the Darß.Zingst lagoon was also not observed in the 1990s. A slight remesotrophication took place instead (SCHUMANN & KARSTEN 2006). Whether or not the decline of rotifers is causally linked to the polychaete invasion is not yet clear. In considering the data set 1969-2001, a hypothesis was set up by FEIKE et al. (in press) that the considerable increase of the biomass of the zoobenthos after the invasion of *M. neglecta* could be the cause of the rotifers' decline. The worms may inhibit the rotifers by feeding on their eggs and/or by promoting bioturbation and thus preventing the eggs from hatching. Assuming size-selective feeding of the worms, this influence may be more intense for larger species than for smaller ones. This would explain the shift observed to the dominance of the small sized species *K. cochlearis* f. *tecta.* The hypothesis predicts that a reverse development will take place when *M. neglecta* biomass decreases. Since 1999 *M. neglecta* has declined in the Darß-Zingst lagoon (Figure 5). Our observation that the biomass of the large-sized species *B. quadidentatus* has shown an increasing tendency since 2004 coincides with that hypothesis. At least it is an indication for a causal link between the rotifers and *M. neglecta.*

Simple ecological systems can exhibit a dynamically rich behaviour, mathematically as well as experimentally (HASTINGS & POWELL 1991, BECKS et al. 2005). This recognition has made chaos an ongoing topic among ecologists, since the apparently irregular fluctuations in many time series might not necessarily be a result of internal or external noise, but might stem from intrinsic interactions. We observed from our long-term monitoring that the differences between the years in the biomass curves were considerable. However, the variability could be attributed mainly to the special climatic and hydrological conditions, especially to temperature, precipitation and the winter index of the North Atlantic Oscillation (FEIKE et al. in press). An analysis of the available data did not provide evidence of low-dimensional chaos. In particular, a LJAPUNOV exponent could not be determined, because the embedding seems to require high dimensions (Frank Hilker, pers. communication). This suggests that the system is subject to randomness and external forcing but not to deterministic chaos.

Zusammenfassung

Wir untersuchten eine Zeitreihe von 1969-2004 für die Biomasse des Zooplanktons in der flachen und windexponierten Darß-Zingster Boddenkette (Südliche Ostsee). Unser Ziel war es, die dynamischen Eigenschaften in diesem Datensatz aufzuklären, besonders in Bezug auf langfristige Änderungen sowie in Bezug auf die Variabilität zwischen den Jahren. Die beiden wichtigsten Gruppen, die Copepoden und Rotatorien traten in der gesamten Untersuchungsperiode auf. Zwei andere Gruppen, die Phyllopoden und die Larven einer eingewanderten Polychaetenart wurden nur während eines eingeschränkten Zeitraumes beobachtet.

Alle Gruppen zeigten ein stabiles Muster der jahreszeitlichen Biomasseentwicklung. Ausgeprägte Peaks wurden beobachtet bei den Copepoden im Frühjahr und Spätsommer, den Phyllopoden während des Frühsommers, den Rotatorien im Hochsommer und den Poychaeten-Larven während des Spätherbstes und Winters. Überlagert wurden diese Tendenzen aber von beträchtlichen Unterschieden zwischen den einzelnen Jahren, sowohl hinsichtlich der Form der Jahreskurve als auch in Bezug auf das durchschnittliche Niveau der Biomasse. Diese Variabilität korrelierte gut mit klimatischen Unterschieden zwischen den Jahren. Die Variabilität der Jahresmittelwerte der Copepoden und Rotatorien korrelierte größtenteils mit der Temperatur und den Niederschlagsmengen. Deterministisches Chaos als Quelle der Veränderlichkeit konnte nicht in den Datensätzen nicht nachgewiesen werden.

Während der Untersuchungsperiode traten in zwei Fällen relativ kurzfristige Veränderungen im Biomasseniveau und in der Dominanzstruktur auf. (1) Zu Anfang der achtziger Jahre gab es einen ausgeprägten Abfall der Copepodenbiomasse. Sie resultierte vermutlich aus einer Verschlechterung der Nahrungsqualität, bedingt durch die Umstrukturierung der Primärproduzenten von einem durch Makrophyten dominierten System zu einem durch Phytoplankton dominierten System. Die Phyllopoden verschwanden vollständig in diesem Zusammenhang. (2) Zu Beginn der neunziger Jahre kam es zu einer starken Abnahme der Biomasse und einer Artenverarmung bei den Rotatorien. Zur gleichen Zeit wanderte die ponto-caspische Polychaetenart *Marezellaeria neglecta* in die Darß-Zingster Boddenkette ein und dies führte dazu, dass sich im Zoobenthos die Gesamtbiomasse verzehnfachte. Die bei den Rotatorien beobachte Veränderung ist deshalb möglicherweise mit dem Eindringen dieses Polychaeten kausal verknüpft. Andere Faktoren, die für die Abnahme der Rädertiere verantwortlich sein könnten, ließen sich bisher nicht feststellen. Jedoch ist die Art der Wechselwirkung zwischen beiden Prozessen noch unklar.

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Appendix 1/1 Crustacea

Species / group	Stage	Vol. [µm³ • 10⁶/ind.]	Length [µm] (copepods without abdomen)
Nauplius stages		0.24	100
		1.10	200
		2.80	300
Acatia tonsa (summer)	N1	0.27	115
	N2	0.41	135
	N3	0.71	167
	N4	0.92	185
	N5	1.48	227
	N6	2.00	263
	C1	3.39	280
	C2	4.45	342
	C3	5.83	400
	C4	7.88	465
	C5	10.07	520
	C6-M	14.12	600
	C6-F	15.31	620
Acartia spp.		1.60	300
		4.00	400
		7.30	500
		12.60	600
		21.60	700
		32.20	800
Eurytemora affinis (winter)	N1	0.34	125
	N2	0.54	150
	N3	0.85	179
	N4	1.25	211
	N5	1.81	250
	N6	2.60	307
	C1	3.44	300
	C2	4.44	353
	C3	6.49	432
	C4	10.62	534
	C5	17.83	642
	C6-M	31.44	760
	C6-F	42.56	823

Appendix 1/2 Crustacea

Species / group	Stage	Vol. [µm^3 • 10^6/ind.]	Length [µm] (copepods without abdomen)
Eurytemora affinis (summer)	N1	0.21	105
	N2	0.40	133
	N3	0.69	165
	N4	0.96	188
	N5	1.46	226
	N6	2.00	263
	C1	2.94	267
	C2	4.19	341
	C3	6.01	416
	C4	7.47	461
	C5	9.59	513
	C6-M	13.10	578
	C6-F	14.71	602
		2.20	300
		5.30	400
		10.30	500
		17.80	600
		29.00	700
		42.00	800
Temora longicornis	N1-N3	1.90	
	N4-N6	3.07	
	C1	10.15	
	C2	10.65	
	C3	11.86	
	C4	24.68	
	C5	28.14	
	C6-M	59.60	
	C6-F	67.96	
		3.20	300
		7.50	400
		14.50	500
		25.00	600
		39.00	700
		59.00	800

Appendix 1/3 Crustacea

Species / group	Stage	Vol. [µm^3 • 10^6/ind.]	Length [µm] (copepods without abdomen)
Pseudocalanus elongatus	N1-N3	2.60	
	N4-N6	3.95	
	C1-C3	10.79	
	C4-C5	30.95	
	C6-M	61.50	
	C6-F	66.50	
		6.10	400
		12.00	500
		21.00	600
		33.00	700
		48.00	800
		69.00	900
Paracalanus parvus	N1-N3	1.23	
	N4-N6	2.32	
	C1-C3	6.72	
	C4-C5	14.36	
	C6	35.00	
Centropages hamatus	N1-N3	1.75	
	N4-N6	3.05	
	C1-C3	10.98	
	C4-C5	38.00	
	C6-M	61.00	
	C6-F	66.00	
		1.60	300
		4.00	400
		7.30	500
		12.60	600
		21.60	700
		32.20	800
Cyclopoidae	N	2.00	
	C1-C3	10.50	
	C4-C5	10.50	
	C6	25.00	
		3.00	300
		6.90	400
		13.50	500
		23.00	600

Appendix 1/4 Crustacea

Species / group	Stage	Vol. [µm^3 • 10^6/ind.]	Length [µm] (copepods without abdomen)
Oithona similis	N1-N3	1.08	
	N4-N6	1.81	
	C1-C3	2.85	
	C4-C5	4.00	
	C6	9.00	
		3.20	300
		8.50	400
		15.00	500
Bosmina spp.		1.50	200
		5.20	300
		9.60	400
		18.70	500
Pleopsis polyphemoides		1.10	200
		3.80	300
		9.00	400
		17.00	500
		31.00	600
		49.00	700
Daphnia longispina		3.20	400
		6.60	500
		11.00	600
		17.50	700
		26.00	800
		37.00	900
		50.00	1000
		67.00	1100
		87.00	1200
Evadne normanni		0.90	300
		2.20	400
		4.30	500
		7.40	600
		12.00	700
		17.00	800
		25.00	900
		35.00	1000

Appendix 1/5 Crustacea

Species / group	Stage	Vol. [µm^3 • 10^6/ind.]	Length [µm] (copepods without abdomen)
Diaphanosoma brachiura		5.30	400
		10.40	500
		18.00	600
		28.00	700
		42.00	800
		60.00	900
Leptodora kindtii		13.80	600
		22.00	700
		33.00	800
		47.00	900
		64.00	1000
		86.00	1100
		113.00	1200
Alona spp.		1.00	200
		3.30	300
		8.00	400
		16.00	500
Chydorus sphaericus		2.60	200
		8.70	300
		17.00	380

Appendix 2/1 Rotatoria

Species	Vol. [µm^3 • 10^6/ind.]	Length [µm] (without spines)
Synchaeta spp. (contracted)	0.052	50
	0.089	100
	0.586	200
	1.920	300
Brachionus quadridentatus	0.205	100
	0.690	150
	1.640	200
	2.840	240
Brachionus calyciflorus	0.187	100
	0.516	140
	1.090	180
	2.600	240
Brachionus angularis	0.058	60
	0.138	80
	0.269	100
	0.466	120
Brachionus plicatilis, B. urceus	0.156	100
	0.430	140
	0.910	180
	1.660	220
Keratella quadrata	0.070	70
	0.129	100
	0.290	130
	0.430	150
Keratella cochlearis f. *typica*	0.113	110
	0.146	120
	0.187	130
	0.233	140
Keratella cochlearis f. *tecta*	0.029	60
	0.046	70
	0.069	80
	0.098	90
	0.135	100

Appendix 2/2 Rotatoria

Species	Vol. [µm^3 • 10^6/ind.]	Length [µm] (without spines)
Filinia longiseta	0.110	80
	0.215	100
	0.370	120
	0.580	140
	0.870	160
Trichocerca spp.	0.018	60
	0.043	80
	0.084	100
	0.146	120
	0.231	140
Colurella spp.	0.007	40
	0.070	80
	0.180	120
	0.790	180
Collotheca spp.	0.022	120
	0.027	130
	0.034	140
	0.043	150
Notholca spp.	0.063	100
	0.170	140
	0.370	180
	0.674	220

Appendix 3 Meroplanktic larvae

Species	Vol. [µm^3 • 10^6/ind.]	Length [µm] (without spines)
Bivalvia		
	0.26	100
	2.00	200
	6.90	300
Gastropoda		
	0.16	100
	1.30	200
	4.40	300
Polychaeta	0.81	160
	1.60	200
	2.80	240
	4.30	280