KLAIPĖDA UNIVERSITY

COASTAL RESEARCH AND PLANNING INSTITUTE

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DIVERSITY AND FUNCTIONAL ROLE OF PLANKTON CILIATES IN A EUTROPHIC COASTAL LAGOON

Doctoral dissertation

Biomedical sciences, ecology and environmental sciences (03B), hydrobiology, marine biology, aquatic ecology, limnology (B260)

Klaipėda, 2012

Dissertation was prepared in 2006–2011 at the Klaipėda University, Coastal Research and Planning Institute.

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KLAIPĖDOS UNIVERSITETAS
BALTIJOS PAJŪRIO APLINKOS TYRIMŲ IR PLANAVIMO INSTITUTAS

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PLANKTONO INFUZORIJŲ ĮVAIROVĖ IR FUNKCINIS VAIDMUO EUTROFINĖJE PRIEKRANTĖS LAGŪNOJE

Daktaro disertacija
Biomedicinos mokslai, ekologija ir aplinkotyra (03B), hidrobiologija, jūrų biologija, vandenų ekologija, limnologija (B260)

Klaipėda, 2012

Disertacija rengta 2006 – 2010 metais Klaipėdos universiteto Baltijos pajūrio aplinkos tyrimų ir planavimo institute.

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1. INTRODUCTION

Scope of the study. Ciliates are an important component of the pelagic microbial food webs, both in the freshwater and marine systems. Numerous studies have reported ciliate feeding on bacteria, picoplankton and nanoplankton (Stoecker and Evans, 1985; Porter *et al.,* 1985; Bernard and Rassoulzadegan, 1990; Šimek *et al.,* 1998), making them a likely link in the transfer of energy from the microbial components to higher trophic levels (Azam *et al.,* 1983; Sherr *et al.,* 1986). Due to the high metabolic rates and short generation time, ciliates may play a pivotal role in determining the overall rates of grazing, nutrient regeneration and secondary production, especially during periods when they are most abundant (Weisse *et al.,* 1990). Our understanding of the processes determining the size and taxonomic structure of the microbial community and subsequent alterations in the trophic transfers has become increasingly important under condition of climate change and increasing eutrophication.

The plankton ciliate studies in the Baltic Sea region cover a wide range of habitats from the open sea to the closed coastal areas (Smetacek, 1981; Boikova, 1984; Arndt, 1991; Kivi and Setala, 1995; Uitto *et al*. 1997; Witek, 1998; Setala and Kivi 2003; Johansson *et al.* 2004; Samuelsson *et al.* 2006; Beusekom *et al.* 2007), however the knowledge of ciliate taxonomic composition, seasonal dynamics and their trophic role in the transitory ecosystems with changing riverine discharges and salinity regimes are still scarce (Boikova, 1989; Mironova *et al.,* 2009; Telesh *et al.,* 2009; Mironova *et al.,* 2011). The Curonian lagoon is transitory ecosystem and one of the most heavily eutrophicated coastal areas of the Baltic Sea. The trophic role of ciliate grazers is largely unknown in such coastal eutrophic habitats characterized by high spatial and seasonal variability in taxonomic and size structure of phytoplankton. Dilution experiments combined with size fractionation is one of the best methods to investigate ciliate grazing within these ecosystems (Reckermann, 1996).

The detailed freshwater ciliate taxonomical composition of the Curonian Lagoon described by Mažeikaitė (1978a, 2003), missed the brackishwater ciliate assemblage. Also, the previous studies included only fragmentary data on seasonality of the ciliate community (Mažeikaitė, 1978b) and were based only on live material counts, missing small nano-ciliates, which can contribute to a large part of the total abundance and biomass of ciliate community.

Aim and objectives of the study. The principle aim of this study is to reveal the species diversity and patterns of plankton ciliate seasonal dynamics and to evaluate their grazing role in the eutrophic oligohaline lagoon ecosystem.

To achieve this aim the following objectives were proposed:

1. to describe the taxonomic composition of planktonic ciliates, providing a revised species list for the entire estuarine gradient;
2. to compare the suitability of living and Lugol fixed material counting methods for the determination of ciliate abundance and species composition;
3. to investigate structural differences of ciliate assemblage in oligohaline and freshwater parts of the lagoon;
4. to reveal the patterns of the seasonal changes in the freshwater ciliate assemblage;
5. to estimate the influence of ciliates on pico- and nanophytoplankton in the oligohaline and freshwater parts of the lagoon.

Novelty of the study. This study is intended to contribute to the knowledge of the biodiversity of ciliate communities in eutrophic coastal waters. Seasonal groups of planktonic ciliates were distinguished and the factors governing ciliate seasonal dynamics in the Curonian Lagoon were evaluated. For the first time, dilution technique with size-fractionation of phytoplankton was applied in the

coastal waters of the Baltic Sea to estimate microzooplankton grazing on different phytoplankton size fractions.

Scientific and practical significance of the results. The results of this study could be used to improve existing ecosystem models by incorporating the microbial components, for better understanding how eutrophication processes may be controlled by micrograzers in eutrophic coastal waters. Data from this study could be used to develop the bioindicators for environmental quality assesment.

Defensive statements

1. The total number of taxa increases from the river inflow areas towards oligohaline part of the lagoon.
2. Combination of live and Lugol fixed material counts increases taxonomic resolution of the analysis, however for the quantitative characteristics preserved samples should be used.
3. Ciliate species diversity decreases with the increasing salinity and community structure changes towards larger sized species.
4. Seasonal dynamics of plankton ciliates in the freshwater part of the lagoon is typical for the eutrophic water bodies with grazers dominated during spring and mixed community of grazers and omnivores during the rest of vegetation season.
5. Due to the dominance of the large sized ciliates in the brackishwater community, significant grazing on nanophytoplankton fraction is expected, while in the freshwater community pico-fraction of phytoplankton should be affected by numerically dominant nano-ciliates.

Scientific approval

The results of this study were presented at 8 international and 2 reagional conferences and seminars:

- 42nd International Symposium: „Estuarine Ecosystems: Structure, Function And Management“, Kaliningrad-Svetlogorsk, Russia, September 2007;
- 1st Congress of LaguNet and 3rd European Conference on Lagoon Research, Naples, Italy, November 2007;
- ASLO Aquatic Sciences Meeting, Nica, France, January 2009;
- International conference „Research and Management for the Conservation of Coastal Lagoon Ecosystems, South - North comparisons”, Montpellier, France, December 2010;
- International BONUS conference, Vilnius, Lithuania, January 2010;
- 1st international symposium on “Viruses of Microbes”, Paris, France, June 2010;
- International Workshop "Climate Change Impacts on Estuarine and Coastal Ecosystems: a Zooplankton Perspective", Boulogne surMer, France, June 2010;
- 3rd international student conference “Biodiversity and functioning of aquatic ecosystems in the Baltic Sea region”, Klaipėda, Lithuania, October 2008;
- Regional practical scientific conference “Marine and coastal research-2008”, Palanga, Lithuania, April 2008;
- Regional practical scientific conference “Marine and coastal research-2010”, Palanga, Lithuania, April 2010.

Three publications were published on the dissertation topic.

Volume and structure of the thesis. The dissertation is presented in the following chapters: Introduction, Literature Review, Study Area, Material and Methods, Results, Discussion, Conclusions and References. References include 191 sources. The dissertation contains 12 tables and 29 figures. The size of the dissertation is 123 pages.

Acknowledgements

Firstly, I would like to thank my supervisor dr. Zita Gasiūnaitė for special patience, support, constructive criticism and care during the whole PhD thesis preparation time.

I am especially gratefull to dr. Jūratė Lesutienė for a help in preparation of the thesis manuscript and scientific papers, nice company during the field work, long lasting friendship and encouragment during the most diffucult moments of my life. I am very gratefull to dr. Stasė Mažeikaitė for valuable knowledge on taxonomy of plankton ciliates and for care and warmness through all PhD years. Special thanks to dr. Ričardas Paškauskas for supporting me while choosing to study plankton ciliates and variuos help during field trips and experimental work. I would like to tank my colleague Sigitas Šulčius for bacteria sample analysis, as well for a help during dilution experiments and interesting scientific discusions. I am gratefull to dr. Kęstutis Arbačiauskas (Nature Research Center) for lending filtration equipment, dr. Elmira Boikova (University of Latvia) for consultancy on identification of ciliates from Lugol fixed samples.

I largely appreciate the contribution of all my collegues at CORPI: prof. Artūras Razinkovas, prof. Sergej Olenin and dr. Saulius Gulbinskas for involment into scientific projects, dr. Diana Vaičiūtė for assistance during dilution experiments, dr. Renata Pilkaitytė for chlorophyll *a* analysis, dr. Mindaugas Žilius for dissolved oxygen analyses, Viačeslav Jurkin – for preparation of maps and all others for friendship and support.

I thank my collegues from Leibniz Baltic Sea Research Institute (IOW) for the possibility to use laboratory facilities using HPLC for pigment analysis, Frederike Korth for help during nutrient analysis, and prof. Maren Voss for financial support of pigment sample analysis.

I greatly appreciate Environmental Protection Agency, Marine Research Department for providing monitoring data.

I thank my mother for care of my daughter. My daughter Luka for undestanding and patience during PhD thesis writing period. Special

thanks to my sister Vilija, my friends K. and V. Didžiuliai, E. Grine, M. Lesutis, Jack O'Sullivan and Dalia Smelsoriūtė for the support.
This study was partially funded by EU BONUS project AMBER (Assessment and Modelling of Baltic Ecosystem Response, Nr. 31V-1) and EU FP7 Project MEECE (Marine Ecosystem Evolution in a Changing Environment, 212085).

2. LITERATURE REVIEW
2.1 General characteristics of the ciliates

The kingdom Protozoa (Cavalier-Smith, 1998) "is compromised by predominantly unicellular, plasmodial or colonial protists (eukaryotic microorganisms) that are mostly phagotrophic, colorless, lacking cellulosic cell walls, and microscopic in body size" (after Corliss, 1994; 2001). The Protozoa kingdom is divided in to 14 phyla: the phylum Ciliophora (ciliates) is among the top five phyla of protists in terms of species number (Corliss, 2001; 2004). 8000 species of ciliates are described, including about 200 fossil forms, 2600 symbiotic forms and 5200 free-living forms (Corliss, 2001; Lynn, 2008). According to Foissner *et al.* (2008), number of free-living ciliates is higher, seeks up to 5600 species and the described ciliate biodiversity compose only around 20%, while the rest are undiscovered. About 170 species of freshwater planktonic ciliates have been described worldwide (Berger *et al*., 2000).

Functionally, the term protozoa can be defined as unicellular, heterotrophic protists, mainly including these free-living groups: ciliates, flagellates and sarcodina (Fenchel, 1987; Laybourn-Parry, 1992; Finlay and Esteban, 1989).

The ciliates are distinguished from other protists by three major features: 1) the presence of cilia or ciliary structures, such as cirri and membranelles, distributed over the body surface and around the mouth (cytostome) and functioning in locomotion and feeding processes; 2) nuclear dimorphism: two types of nucleus – macronucleus, which is normally one per cell and responsible for regulation of physiological and biochemical processes, while micronuclei (may have many) – concerned with replication of genetic material during the reproduction 3) conjugation as a sexual process – a reproduction mode in which partners fuse temporarily to exchange gametic nuclei (Raikov, 1972; Laybourn-Parry, 1992; Lynn, 2008).

Shapes of ciliate vary from simple geometric ones – spheres, cones, spheroids, cylinders, which may be flattened dorsoventrally to colonial species that have unusual forms (Lynn, 2008). In general, ciliate size ranges from 10 to 4500 μm (Lynn, 2008). Planktonic forms of ciliates belong to microzooplankton (20 – 200 μm in size; Sieburth et al. 1978). Although the smallest ciliate species are <20 μm, or even <10 μm, in their largest diameter, and do not actually fit the definition of micro-sized protists (Setälä, 2004).

The small size of ciliates defines short generation time, which may span a few hours to several days (Laybourn-Parry, 1992). Generally, growth rates to over 1 d^{-1} and more have been found in ciliates (Verity, 1985; Dolan, 1991; Strom and Morello, 1998).The growth rates depends on environmental conditions (temperature) and prey concentration (Verity, 1985).

Ciliates could be found in all types of aquatic habitats: planktonic, benthic, epiphytic etc. Many ciliates can attach themselves to various surfaces among the plankton such as suspended particles, phytoplankton and zooplankton (Christensen-Dalsgaard and Fenchel, 2003; Šimek *et al.,* 2004). Peritrichs are predominant between attached forms (Fig. 1b). Planktonic ciliate species are dominated by oligotrichs and tintinnids (both having lorica and naked forms) (Fig. 1c, e) in freshwater and marine ecosystems (Fenchel, 1987; Laybourn-Parry, 1992).

According to Finlay and Esteban (1998), three trophic groups of ciliates can be distinguished based on feeding mechanism:

1) Raptorial (interceptor) feeders catching relatively large food items individually, may have simple apical mouth (e. g. *Prorodon, Loxodes, Askenasia*); some (*Lacrymaria, Monodinium, Didinium, Dileptus*) may kill the prey (Fig. 1a); others (*Nassula*, *Chilodonella*) 'hoover' diatoms and other food particles. Dead organic matter feeder *Coleps hirtus* belongs to raptorial feeders (Fig. 1d).

2) Filter feeders use a filter to remove microbial food from suspension (*Cyclidium, Glaucoma, Vorticella*). Many filter feeders are

specialized to feed on very small particles (~0.3 μm) (Fenchel, 1987). However, to this trophic group belonging tintinnids can prey on larger particle sizes, the maximum size of food particle ingested is usually up to 40–45% of the oral diameter of the lorica (Splitter, 1973; Heinbokel, 1978) or even 100% of the oral diameter of lorica (Capriulo, 1982).

3) Diffusion feeders collide swimming prey with their sticky tentacles, through which the prey contents are sucked; they are common benthic species. Among the ciliates, mainly suctorians use this type of feeding and their prey is almost exclusively other ciliates (Fenchel, 1987).

Five trophic groups of ciliates can be distinguished according to the food particle size-classes grazed and feeding mechanism (Gaedke and Wickham, 2004; Mironova *et al*., 2012): 1) pico-filterers (mainly bacterivorous); 2) nano-filterers (mainly algivourus); 3) pico-nano filterers (both types of food: bacteria and algae); 4) omnivores feeding on nano-micro size particles (heterotrophic flagellates, algae, ciliates); 5) predators feeding on nano-micro size particles (other ciliates).

First tree groups belong to true filterers; the last two are raptorial feeders. Exception is pico-nano filterers, because very small (<15 μm) prostomatid taxa such as *Urotricha* sp. is raptorial feeder, feeding on both bacteria and algae (Šimek *et al*., 1986).

Some planktonic ciliates (especially oligotrichids) are mixotrophs, which combine both heterotrophy and photosynthesis. Wide spread brackish marine haptorid *Myrionecta rubra* is noted for obligate autotrophy: it contains cryptophycean endosymbionts, which are capable of photosynthesis (Telesh *et al*., 2009).

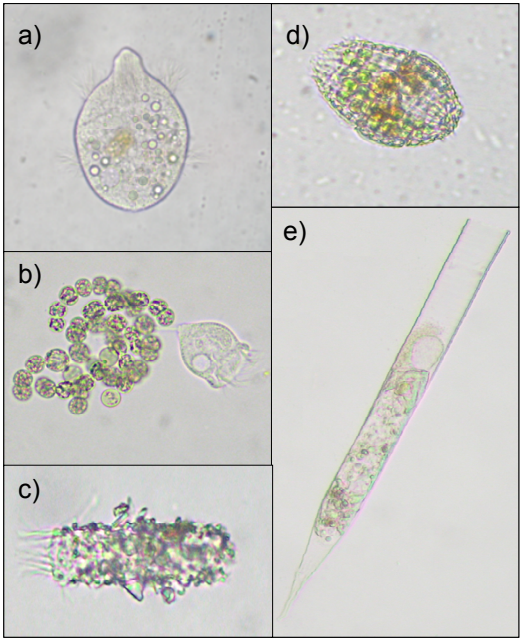

Fig. 1. Some ciliate species found in the Curonian Lagoon: a) haptorid: *Didinium nasutum*; b) peritrich attached to *Anabaena* sp.: *Vorticella microstoma*; c) tintinnid: *Tintinnidium pusillum*; d) prostomatid: *Coleps hirtus*; e) tintinnid: *Helicostomella subulatum.*

2.2. Diversity of the planktonic ciliates in the Baltic Sea

The latest annotated checklist, which includes most important previous studies of Baltic sea ciliate taxonomic composition, comprises 814 species of ciliates from the open and coastal areas of the Baltic Sea (Telesh *et al*., 2009), 160 of them are typically planktonic (Mironova *et al*., 2009). The non-typical brackish-water biodiversity pattern, i.e. protistan diversity maximum at salinity 5 to 8 PSU (critical salinity or horohalinicum) was observed in the Baltic Sea by Telesh *et al*. (2011a) and proposed as a novel opposite to the

Remane's Artenminimum (species minimum) concept which was originally based on macrozoobenthos data (Remane, 1934). Authors explain this phenomenon by better adaptability and advanced osmoregulation strategy of protists, than it could occur in macrozoobenthos species. The hypothesis was criticized by Ptacnik *et al.* (2011) suggesting that the pattern might be an artifact of incorrect pooling of species lists within salinity bands, thereby obtaining patterns that reflect sampling effort rather than species richness. Ptacnik *et al*. (2011) also noted that the data used to describe the pattern to a large extent come from coastal sites which are not representative of the open Baltic Sea. In a replay to the critics, Telesh *et al.* (2011b) remained robust about the conclusion that protistan species richness peaks in the horohalinicum, arguing, that re-fitting algorithm to the available data sets did not alter the shape of the plankton diversity trends. However, the suggestion by Ptacnik *et al*. (2011) to use a more detailed statistical analysis for describing the patterns of overall plankton diversity was accepted in this reply.

Within this context the Curonian Lagoon represents an oligohaline coastal habitat (salinity range 0–8 PSU) where the species richness hypotheses could be tested.

So far planktonic ciliate studies in the Curonian Lagoon were undertaken only in the freshwater part. The studies began with the description of 9 taxa by the German scientist Schmidt-Ries (1940). The detailed freshwater ciliate taxonomical composition was described by Mažeikaitė (1978a; 2003). Recently upgraded planktonic ciliate list covering both freshwater and oligohaline parts of the lagoon (Grinienė *et al*., 2011) is given and discussed in this dissertation.

2.3. Seasonal succession of the ciliate communities

The descriptions of successional sequences and possible mechanisms of seasonal succession of plankton communities were integrated by Sommer *et al.* (1986) in PEG (Plankton Ecology Group) model. This is 24 steps verbal model, describing the seasonal events

occurring in the phytoplankton and zooplankton of idealized temperate lake, based on long term plankton data of the lakes, reservoirs, fish ponds representing different trophic, climatological and stratification types of the water body. It emphasized the role of physical factors, grazing and nutrient limitation for phytoplankton and the role of food limitation and fish predation for zooplankton.

"Microbial loop" components initially were not included into the PEG model. The attempt to incorporate bacteria to this model was done later by Güde (1989); ciliates were included by Müller *et al*. (1991) and Nõges *et al*. (1998).

The PEG model was re-evaluated and extended by Sommer *et al*. in 2012. Heterotrophic protists, namely ciliates and flagellates, were added, the mechanism of seasonal dynamics of protists was explained by "top-down" and "bottom-up" control continuum. Ciliates are dependent on the phytoplankton as a resource directly or indirectly via bacterivory and follow the same seasonal pattern as phytoplankton with some delay during the growth phases. Ciliates become food limited during winter and clear water phase, while the predator (metazooplankton) control is strongest during clear water phase; the consequence is bimodal ciliate seasonal distribution with high biomass during spring and summer and low during winter and clear water phase.

In the brackish water ecosystems seasonal cycles of ciliates differs from the freshwater systems, due to the more expressed "top-down" control of metazooplankton (plankton crustaceans), especially during the summer (Smetacek, 1981; Witek, 1998).

Two-phase seasonal succession scheme was described in open northern Baltic sea proper (Johansson *et al*., 2004). Shortly after the first diatom bloom in spring, ciliate biomass peaks. The main representatives of this peak – large (40 μm) sized ciliates (Oligotricida and Haptorida) benefit from late spring bloom conditions, when nano-sized food is readily available and predation by copepods is low. During the second phase in the summer, the shift from larger to

smaller ciliates coincides with the increase of mesozooplankton biomass and occurrence of small sized phytoplankton.

In the Neva estuary two ciliate associations were distinguished with a shift at water temperature from 5 to 12 ^{o}C. During the warm season (April-October) ciliate community was dominated by algivorous pico- and nano- filterers, while in the cold season (October-early April) large benthic predatory species and small bacterivores occurred. The shift of these ciliate associations could be related to seasonal phytoplankton dynamics (Mironova *et al*., 2012).

This hampered the complete application of the PEG model and to delineate the seasonal succession of the plankton community in the Neva estuary.

2.4. Role of plankton ciliates in the pelagic food web

Ciliates having great variability of feeding modes and size structure are very important component of pelagic food web. According to Haris *et al.* (2000) they are (Fig. 2):

1) consumers of bacteria, heterotrophic flagellates; grazers on various sizes of phytoplankton (mainly pico- and nanophytoplankton);

2) food for larger metazooplankton (copepods, cladocerans and rotifers);

3) remineralizers of essential nutrients (phosphorus and nitrogen).

Ciliates as grazers. Ciliates feed on both autotrophic and heterotrophic pico- (0.2–2 μm) and nano- (2–20 μm) plankton fractions. The pico fraction mainly is made up by prokaryotes (bacteria) and coccoid Cyanobacteria (Laybourn-Parry, 1992).

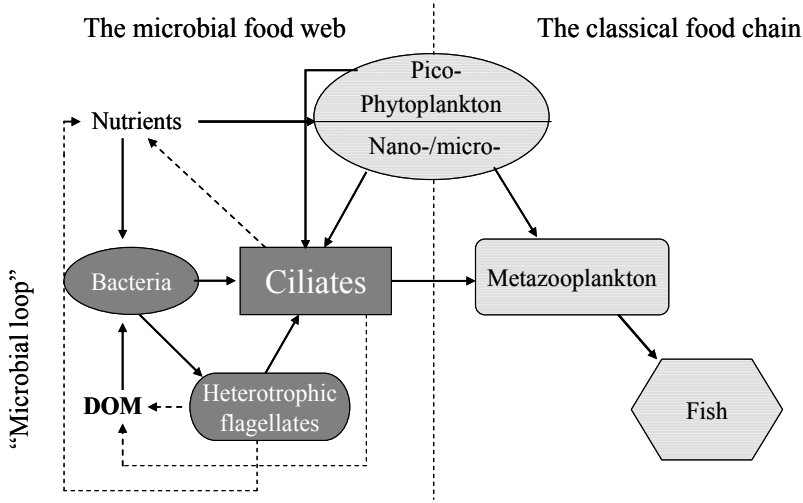

Fig. 2. Schematic representation of a pelagic food web showing the microbial food web (left panel) and the classical food chain (right panel) modified from Pomeroy and Weibe (1988). Continuous arrows represent uptakes of matter and dashed arrows represent release of chemical compounds. DOM – dissolved organic matter.

Ciliates are generally less important than flagellates as bacterial consumers in natural aquatic environments (Weisse, 2003). This conclusion is supported by some empirical evidence from lakes (Beaver and Crisman, 1989). In eutrophic lakes bacterivorous ciliate can consume during spring and summer up to 18 % (Sanders *et al*., 1989), in the late summer 20% of bacterial production (Šimek *et al*., 1995). Although, at particular time and localities, ciliate bacterivory may contribute significant part of bacterial losses in freshwater lakes (Šimek *et al*., 1990; Müller *et al*., 1991) and estuaries (Sherr, 1986; Sherr and Sherr, 1987).

Sherr *et al*. (1986) pointed that ciliates can compose large fraction of the nanoplankton in estuaries and thus can be significant grazers of

bacteria and are able to remove 100% of bacterial production (Sherr *et al.,* 1987). Ciliate bacterivory may "short-circuit" the microbial loop in aquatic ecosystems by making bacterioplankton production available to metazoan grazers via simple, two-step food chain. Small ciliates, particularly oligotrichs (<30 μm) can be significant picoplankton grazers. Autotrophic picoplankton can constitute up to 48–60% of the total carbon in the diet of bacterivorous species (Šimek *et al.,* 1996).

Not only nanociliates, but larger species such *Strombidium, Laboea* and *Lohmaniella* also feed on bacteria; over 50% of naked oligotrichs were found to be able to ingest bacteria (Laybourn-Parry, 1992). It is known, that bacterivorous ciliate can feed selectively on bacteria (prefer cocci, squat rod and long rod shaped bacteria), thus may change the bacterial assemblage structure (Turley *et al.,* 1986).

Ciliates may also control efficiently heterotrophic nanoflagellates, especially during spring season (Weisse, 1990; Jürgens *et al*., 1996), although heterotrophic nanoflagellates contribute relatively little to the total food uptake by ciliate community (Müller *et al*., 1991).

Microzooplankton grazers, usually dominated by protists, are considered as one of the most important phytoplankton mortality factors in aquatic systems (Weisse, 2003). Ciliate could remove up to 60–75 % of daily primary production (Landry and Calbet, 2004). Grazing impact of microzooplankton could prevent phytoplankton accumulation in marine systems, minimize problems associated to increased eutrophication and reduce the occurrence of harmful phytoplankton blooms (Chicharo *et al*., 2009).

Sun *et al*. (2007) tested "higher grazing rates on faster-growing cells" hypothesis proposed by Strom (2002). The main idea is that in the coastal areas the microzooplankton graze on faster growing and minor biomass phytoplankton (pico-fraction), which can provide plenty of food over long time. Sun *et al*. (2007) found that in the Chesapeake and Delaware Bays picophytoplankton is mostly controlled by microzooplankton grazing, whereas the predominant

bloom-forming phytoplankton species are not picophytoplankton. The microzooplankton has a strong effect on phytoplankton biomass control and the development pathways of the phytoplankton community in these regions (Sun *et al*., 2007).

Metazooplankton predation on ciliates. Large cladoceran *Daphnia* affect all components of microbial food web: from bacteria to large ciliates (Porter *et al*., 1988; Jürgens, 1994). In general, cladocerans are the major grazers of particles in the size range of 2–8 μm; they can feed on ciliates up to 200 μm size, but with reduced efficiency (Porter *et al*., 1979). Cyclopoid and calanoid copepods are known to be efficient selective grazers on planktonic ciliates (Burns and Gilbert, 1993; Wiackowski *et al*., 1994; Wickham, 1995). According to Calbet (2008) the relative importance of ciliate consumption by copepods depends on the trophic status of the system: in oligotrophic ecosystems ciliate compose around half of the diet by copepods (the rest phytoplankton), while in more productive ecosystems they account around 20% of the diet. Laboratory experiments indicate that marine calanoids: *Centropages typicus* and *Acartia* spp. had 2–10× greater clearance rates on ciliates than on algal species and they feed selectively on oligotrichs (Sticker and Capuzzo, 1990; Wiadnyana and Rassoulzadagen, 1989). In freshwater lakes cyclopoid *Cyclops* is an efficient predator of planktonic ciliates, it generally feeds on larger ciliate species; smaller species, such as *Halteria,* are also consumed at rates of up to 20–30 ciliates copepod^{-1}h^{-1} (Wickham, 1995). Adrian and Schneider-Olt (1999) shows that calanoid *Eudiaptomus graciloides* had the strong negative impact on larger size (20–55 μm) ciliates and adult *E. graciloides* exhibited higher ingestion rates for ciliates than their juvenile stages, cyclopoid copepods and *Daphnia*.

The nature of the cyclopoid–ciliate interaction is taxon specific and the presence of alternative prey influences the impact of cyclopoid copepods on ciliates (Wickham, 1998).

Both experimental and field studies show that rotifers can feed on ciliates (Arndt, 1993). Rotifer predation on ciliates may be significant

at certain times in the annual cycle; in Lake Dalnee the decrease in the ciliate community in the end of July was attributed to predation by *Asplanchna priododonta*, it consumed 72% of protozoan production (Sorokin and Paveljeva, 1972). Field studies by Ejsmont-Karabin (1974) and Garreau *et al*. (1988) revealed that tintinnid *Codonella* can be dominant food source for *Asplanchna*.

Ciliate role in nutrient cycling. As a consequence of feeding activity, ciliates release undigested components of their ingested preys in the form of dissolved organic matter (Nagata and Kirchman, 1991; 1992; Strom *et al*., 1997; Nagata, 2000; Ward and Bronk, 2001). Dissolved inorganic nutrients, mostly ammonium and phosphate (Caron and Goldman, 1990; Neuer and Franks, 1993; Dolan, 1997; Gaul *et al*., 1999) are other final products of the feeding activity of ciliates. Therefore, protistan feeding activities provide substrates for further growth of their preys, particularly heterotrophic bacteria (Jumars *et al*., 1989) and phytoplankton (Dolan, 1997).

Due to smaller size and higher metabolic rates ciliate excretion rate of phosphorus is much higher comparing to larger plankton crustaceans. According to Buechler and Dillon (1974), if ciliates compose only 1% of total zooplankton biomass, they could be responsible for almost 50% of the total phosphorus being regenerated by the zooplankton community.

Ciliates may be an important alternative food source for metazooplankton in most eutrophic water bodies with scarce edible phytoplankton (Nakano et al. 1998).

Although toxic cyanobacteria blooms substantially reduce mesozooplankton grazing rates, these events do not have the negative impact on protistan grazing (Kim et al., 2006; Gobler et al., 2007). Therefore, ciliates, being less sensitive to cyanobacteria toxins, can graze substantial part of smaller cyanobacteria fractions (Davis and Gobler, 2011).

3. STUDY AREA
3.1. Abiotic factors

The Curonian Lagoon (SE Baltic Sea) is a shallow (the mean depth is 3.8 m) eutrophic water basin connected to the Baltic Sea by a narrow Klaipeda strait. The southern and central parts of the lagoon contain fresh water due to discharge from the Nemunas River, while the salinity in the northern part varies from 0 till 7 PSU. Seawater inflows with a residence time of 1–6 days are most common (Gasiūnaitė, 2000); the seawater intrusions are usually restricted to the northern part of the lagoon, rarely propagating more than 40 km (Dailidienė & Davulienė 2008). In terms of hydraulic zonation, the northern part of the lagoon and Nemunas River avandelta are classified as transitory, while the central part – as stagnant and intermediate (Ferrarin *et al.,* 2008). Consequently, three areas important for plankton communities could be distinguished in the lagoon, according to the level of physical forcing: 1) a spatially and temporally unstable salinity gradient; 2) the least hydrodynamically active limnetic part of the lagoon; 3) the Nemunas river-lagoon transition with abrupt changes in current velocity (Gasiūnaitė *et al*., 2008).

Water temperature shows a characteristic temperate seasonality ranging from 0.1–0.2°C in winter to 5–15°C in spring and reaching the highest values (up to 19.1–19.3°C) in July-August (Žaromskis, 1996; Pustelnikovas, 1998). The Klaipeda strait is always ice free, while in the rest of the lagoon ice cover is present for 110 days on average (Žaromskis, 1996).

Dissolved oxygen saturation of the water column fluctuates spatially and temporally (both diurnally and seasonally) and generally varies between 20 and 115 % (Pilkaitytė, 2003). Oxygen concentrations decrease during the ice cover period as well as during calm weather days in summer, when elevated water temperatures and intensive microalgae vegetation facilitate the transient establishment of hypoxia or anoxia particularly during night hours (Žilius, 2011).

Nutrient concentration dynamics is typical for temperate and boreal transitional waters with strong riverine inputs. The highest concentrations of nutrients are observed in winter and early spring. The concentration of phosphates decreases rapidly in April and starts to increase in early summer due to decomposition of organic material. The nitrogen concentration can decrease to analytical zero in May; nitrate concentration tends to increase from midsummer. The silica concentration is lowest during the spring after diatom bloom. It remains low throughout the summer and starts to increase again in early autumn (Gasiūnaitė *et al*., 2008). The seasonal range of nitrates, nitrites, phosphates and silicates in 2007–2008 is shown in Table 1.

Table 1. Average seasonal nutrients concentration (±SD) at northern (N) and central (C) parts of the lagoon in 2007–2008 (Environmental Protection Agency, Department of Marine Research, unpublished monitoring data)

Season	Station	NO_3	NO_2	PO_4-	Si
Spring	N	1.25±0.84	0.010±0.006	0.007±0.008	1.88±2.01
	C	1.36±0.46	0.010±0.006	0.011±0.012	2.34±2.00
Summer	N	0.06±0.01	0.003±0.002	0.004±0.001	0.50±0.64
	C	0.07±0.03	0.002±0.001	0.006±0.005	0.29±0.10
Autumn	N	0.05±0.02	0.005±0.003	0.020±0.019	0.39±0.18
	C	0.19±0.20	0.002±0.001	0.007±0.002	0.99±0.59
Winter	N	1.43±0.14	0.009±0.003	0.029±0.007	3.10±0.18
	C	0.53±0.30	0.003±0.000	0.017±0.005	1.89±0.84

3.2. Plankton communities

Abundance of bacteria ranged from 0.9 to 5.1 ($\times 10^6$ cells ml^{-1}) and did not differed significantly between research sites. Maximum of bacteria abundance was observed in the end of August at Smiltyne site (Šulčius, unpublished data) (Fig. 3).

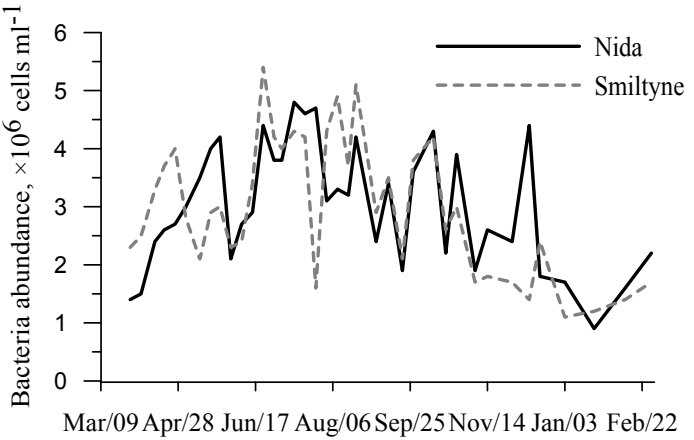

Fig. 3. Seasonal changes of bacteria abundance (×10^6 cells ml^{-1}) at the research sites

The Curonian Lagoon could be classified as eutrophic to hypertrophic water body. During the summer, the maximal chlorophyll *a* concentrations range from 117 μg L^{-1} in the northern part (Pilkaitytė and Razinkovas, 2007) to 219 μg L^{-1} in the southern stagnant part (Semenova and Aleksandrov, 2009).

In total, 438 phytoplankton species are found in the lagoon (Olenina, 1997; Gasiūnaitė *et al*., 2005). Freshwater phytoplankton assemblage follows a seasonal cycle typical for eutrophic water basins: the dynamics starts with prevalence of diatoms during winter and spring; biomass peak is reached in August-September by the highest contribution of cyanobacteria, whereas diatoms again dominate in late autumn (Olenina, 1998; Gasiūnaitė *et al*., 2008). During the spring bloom small diatoms, *Stephanodiscus* spp. and cryptophytes (*Chroomonas acuta*) dominate in phytoplankton assemblage (Gasiūnaitė and Olenina, 1998). Potentially toxic, large filamentous cyanobacteria: *Microcystis* spp. and *Aphanizomenon flos-*

aquae are responsible for the biomass peak in summer (Olenina, 1998; Gasiūnaitė *et al*., 2005; Pilkaitytė and Razinkovas, 2006). Chlorophyta (*Scenedesmus* spp., *Planktonema lauterbornii, Pediastrum boryanum*) are less important in the lagoon phytoplankton assemblage, only at the end of May they contribute 38% of total phytoplankton biomass (Gasiūnaitė and Olenina, 1998).

Diatoms dominate phytoplankton assemblage in the avandelta of Nemunas River from April to mid of July; green algae are abundant during May-September, whereas cyanobacteria prevail only in August. Quantitative phytoplankton assemblage differences along the River-Lagoon gradient are clearly pronounced throughout the year, while structural differences are well expressed during the cyanobacteria dominated period (June-October) (Gasiūnaitė *et al*., 2012).

Two distinct assemblages of crustacean zooplankton were found in the Curonian Lagoon. The limnetic (freshwater) assemblage is permanently present in the lagoon and is associated with fresh water, whereas the brackishwater assemblage enters to the lagoon only during sea water intrusions. A brackish-water zooplankton assemblage is dominated by *Acartia bifilosa, Temora longicornis, Eurytemora hirundoides, Podon polyphemoides* and *Evadne nordmanni* (Gasiūnaitė, 2000). *Bosmina spp., Chydorus sphaericus, Cyclops strenuus, Daphnia spp., Diaphanosoma brachyurum, Leptodora kindti, Eudiapthomus graciloides* and *Mesocyclops leuckarti* is dominated in freshwater assemblage (Gasiūnaitė and Razinkovas, 2004).

The seasonal crustacean zooplankton dynamics in the lagoon appears to be the consistent six-stage sequence. Cyclopoids dominate in the zooplankton assemblage until May, while large *Daphnia* specimens appear only at the beginning of the summer. The shift to small-bodied *Chydorus* is observed later at midsummer and coincides with the dominance of cyanobacteria in phytoplankton. Cyclopoida usually dominate in September-October (Gasiūnaitė *et al*., 2008).

Seasonal changes of predatory cladoceran *Leptodora kindtii* in the Lagoon are characterised by two peaks: first peak occurs in the end of May – beginning of June and the second peak in the middle of August (Lesutienė *et al*., 2011). The calculated *L. kindtii* daily consumption during the population peak was as high as 100% of the daily zooplankton production, which implies high potential of this predator to shape the grazing zooplankton assemblage in the lagoon (Lesutienė *et al*., 2011).

Nemunas River zooplankton in the low reach is dominated by copepods over the year. The total zooplankton abundance increase significantly toward the Lagoon, while structural changes of zooplankton assemblage along the River-Lagoon gradient occur during June-September only (Gasiūnaitė *et al*., 2012).

4. MATERIAL AND METHODS
4.1 Sampling and sample treatment

Qualitative and quantitative samples of the plankton ciliates and metazooplankton were collected weekly from March to November 2007 and twice a month from December 2007 to February 2008 at two sampling sites: Smiltyne and Nida, representing respectively the transitory northern oligohaline and the stagnant central freshwater parts of the Curonian Lagoon (Fig. 4; Table 2).

Table 2. General information on plankton ciliate and metazooplankton surveys.

Sampling time	Sites	Parameter	Method	Total sample number
July 29–30 (2007); June 16–17, July 29-30, October7–8, (2008)	12 stations	Ciliate taxonomic composition	Live material examination	46
2007–2008 weekly (during winter twice a month)	Nida, Smiltyne	Ciliate taxonomic composition	Live material examination	74
		Ciliate taxonomic composition, abundance, biomass	Lugol fixed samples	74
		Metazooplankton taxonomic composition, abundance, biomass	Formaldehyde preserved samples	74

Qualitative samples (live material) were also collected from 12 stations situated along the river-lagoon gradient during four cruises (Fig. 4, Table 2).

Ciliate samples were taken with a 1 l sampling bottle from the near surface layer. For quantitative analysis of ciliates and phytoplankton the 250–300 ml subsample was preserved with acidified Lugol solution till 2% final concentration and stored at 4°C in the dark. 700–750 ml of a subsample was poured into a thermos bottle for live material examination and transported to the laboratory within 6 h.

Metazooplankton was sampled using a 5 L Niskin bottle from the top 1 m of the water column; 10–15 L of water were filtered through plankton net with 80 μm mesh size. Samples were fixed in 4% formaldehyde solution.

Secchi depth, temperature, dissolved oxygen, salinity and chlorophyll *a* as well as abundance of cyanobacteria, green algae, cryptophytes and diatoms was measured simultaneously on each sampling occasion. Temperature and salinity were measured with a portable temperature and conductivity meter (WTW MultiLine F/Set-3). Dissolved oxygen was estimated by Winkler titration method. Chlorophyll *a* concentration and abundance of cyanobacteria, green algae, cryptophytes and diatoms was estimated fluorimetrically using FluorProbe II (Beutler *et al*., 2002).

Ciliates were identified to the species or genera level consulting several works (Kahl, 1930-1935; Small and Lynn 1985; Foissner and Berger 1996; Mažeikaitė, 2003).

For qualitative analysis of ciliates live material was examined. 50–500 ml of water from a thermos bottle was concentrated on a membrane filter (pore size 0.7 μm) till 10 ml volume above the filter surface by gravity filtration. The concentrated samples were analyzed in Bogorov's chamber in two or three portions under a stereomicroscope equipped with the bottom light source at 40× magnification. Individual ciliate cells were identified till the species or genus level with a microscope at 200× or 400× magnification.

Ciliate counts were performed in Lugol fixed samples by Utermöhl's (1958) method. Volumes of 10–50 ml were settled for at least 24 h in Utermöhl's chambers. Ciliates were counted and identified with an inverted microscope at 200× magnification. The entire content of each Utermöhl's chamber was surveyed and an additional subsample was counted if the total number was <150 organisms.

Ciliate biomass was estimated as ciliate biovolume, which was calculated by approximation to the nearest geometric shape from measurements of cell length and width of at least 20 ciliate cells per sample. Mixotrophy of ciliates was not measured, and all ciliates were considered heterotrophic, except *Myrionecta rubra* was considered autotrophic. To convert cell volume into biomass, the carbon:volume relationships of pg (pictogram) C $cell^{-1}=0.216\times volume^{0,939}$ for aloricated ciliates were used (Menden-Deuer and Lessard, 2000). Carbon of the tintinnids was estimated using the experimentally derived factor of 0.053 pg C pm^{-3} lorica volume (Verity and Langdon, 1984).

Metazooplankton was identified to genus or species level, measured (total length of crustaceans and rotifers excluding spines) and counted using a microscope at 40× magnification. Counts were converted to biomass (mg/l) according to the allometric body length-weight relations (Salazkin *et al*., 1984; Jorgensen *et al*., 1995).

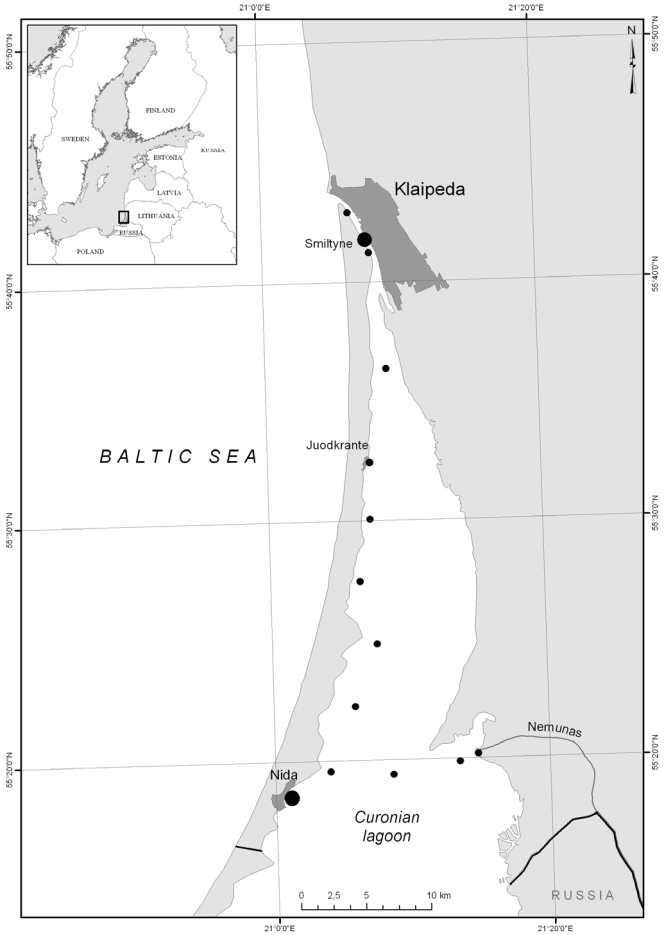

Fig. 4. Sampling sites. Large circles denote stations for seasonal sampling, small circles – spatial surveys on July 29–30, 2007; June 16–17, July 29–30 and October 7–8, 2008.

4.2. Data analysis and calculations

4.2.1. Taxonomic composition

T-test for dependent samples and correlation analysis (Pearson r) was applied in order to compare the results obtained by the two different methods: live material counts and Lugol fixed samples, where a probability of <0.05 was considered as significant.

The taxonomic list of ciliates provided in this work is based on compiled data of live and Lugol fixed samples within each month for freshwater and oligohaline site separately (Table 2).

Table 3. General information on plankton ciliate surveys used for the taxonomic analysis.

Study year	Dates	Number of stations	Geographic range	Sampling method
1975[a]	From end of May till 12-13 September (every 10 days)	5	Northern part of the lagoon	1L bathometer, integrated sample
1991[b]	June 7, July 14 and October 1	7	Northern (port area) and central parts including Nemunas river avandelta	1L bathometer, integrated sample
2001[c]	July	1	Nemunas river avandelta	1L bathometer, integrated sample

[a]Mažeikaitė (1978 a)
[b]Antanynienė *et al.* (1994)
[c]Mažeikaitė (2003)

The Shannon-Wiener diversity index (Krebs, 1989) was calculated using species/taxa abundance in Lugol fixed samples. Nonparametric

Spearman correlation coefficients between the environmental parameters and Shannon-Wiener diversity indices were calculated.

The species list published by Mažeikaitė (2003) was used as a long term data set, which includes results from the earliest studies (Mažeikaitė, 1978 a; Antanynienė *et al*., 1994).

The taxonomic nomenclature was standardized following Corliss (1979). The data from previous studies are described in Table 3, data from this study – in the Table 2.

4.2.2. Seasonal dynamics

Seasonal groups of the ciliates in the freshwater site of the lagoon were distinguished by hierarchical clustering procedure (Bray-Curtis similarity) with group-average linking. Analysis was based on the relative abundances of dominant and common ciliate spiecies/taxa (*Askenasia* spp., *Cyclidium* spp., *Coleps hirtus*, *Epystylis rotans*, *Halteria* sp., *Lohmaniella* spp., *Lohmaniela spiralis*, *Mesodinium pulex*, *Monodinium* sp., *Strombidium* spp., *Strobilidium* spp., *Tintinnidium pusillum*, *Tintinnopsis* sp., *Tintinnopsis tubulosa*, *Vorticella* spp., *Urotricha* spp. and the rest as one group ‘others’).

Plankton ciliates were divided into three groups by their relative abundance in the samples: rare (up to 1% from total abundance), common (1 to 10%) and dominant (more than 10%) according to Gasiūnaitė and Razinkovas (2004); Walseng *et al.* (2006).

Ciliate size groups (<20 µm, 20–30 µm, 30–60 µm and >60 µm) and trophic groups (pico-filterers (bacterivorous), nano-filterers (algivorous), pico-nano (bacterio/algivorous), predators (feeding on ciliates), omnivores (feeding on algae, heterotrophic flagellates and ciliates) were distinguished according to Mironova et al. (2011) and using literature references (Chorik, 1968; Maeda and Carey, 1985; Foissner and Berger, 1996; Montagnes, 1996; Gaedke and Wickham, 2004).

Multi-dimensional scaling (MDS) based on Bray-Curtis similarity coefficient used to evaluate the pattern of ciliate assemblage structural changes along the salinity gradient at oligohaline site. Relative abundance of the same common and dominant species/taxa was used as in the freshwater site plus one brackishwater species *Myrionecta rubra*.

The dissimilarity between seasonal/salinity groups was tested using ANOSIM analysis. The SIMPER (similarity percentage) procedure was used to examine the contribution of each species/higher taxa to the average similarity inside the seasonal/salinity groups.

Multivariate redundancy analysis (RDA) based on correlation calculations was used to identify relationships between environmental factors (explanatory variables: temperature, oxygen concentration, chlorophyll *a* concentration of four phytoplankton groups: diatoms, cyanobacteria, green algae and cryptophytes, metazooplankton taxonomic groups and bacteria abundance) and abundances of different trophic groups (pico-filterers, nano-filterers, pico-nano filterers, predators, omnivores) as response variables. According to seasonal groups, derived by hierarchical clustering procedure (winter, early spring, late spring and summer-autumn), four nominal (dummy) variables were defined. Statistical procedure followed recommendations described by Zuur et al. (2007).

Brodgar (2.6.6.) and R (2.13.1) (Highland Statistics Ltd.) packages were used for RDA analysis. MDS and cluster analysis was performed using PRIMER 6 (PRIMER-E Ltd.).

4.2.3. Production and grazing rates of the ciliates and metazooplankton

Daily production for metazooplankton was calculated using a physiological model $K_2 = P/(P+R)$, where K_2 is the growth efficiency coefficient estimated as 0.4–0.5 for rotifers, 0.3–0.4 for cladocerans and 0.2–0.3 for copepods, P is the daily production, and R

is respiration (Salazkin *et al*., 1984). The individual respiration (R_{ind}, cal d^{-1}) was calculated using equation: $R_{ind} = (24 \times Q \times OK)/q$, where OK is oxy-calorific coefficient equal 4.86 cal ml^{-1} O_2; $Q = 0.106W^{0.796}$ for rotifers $Q = 0.143W^{0.803}$ for cladocerans, $Q = 0.2W^{0.777}$ for copepods. The data were divided by the temperature correction factor q if the water temperature (T) differed more than ± 2 °C, $q = 2.3^{0.1(20-T)}$. Individual body mass W (mg) was calculated from body length using allometric equations (Salazkin *et al*., 1984). Conversion from wet weight (WW) to dry weight (DW) was performed using formula: $DW = 0.13 \times WW$ (Mullin, 1969).

The potential maximum production of ciliates was estimated by multiplying the biomass (µg C L^{-1}) by maximum growth rate (day^{-1}) that was estimated from empirical formula proposed by Müller and Geller (1993): $\ln \mu = 1.52 \ln T - 0.27 \ln V - 1.44$, where μ is the maximal growth rate (day^{-1}), T is the temperature (^oC) and V is the mean cell volume (μm^3).

Maximum carbon consumption was calculated from the net production using a growth efficiency of 30% for ciliates and metazooplankton (Downing and Rigler, 1984).

4.3 Dilution experiment

The dilution technique is based on a series of dilution treatments, creating a gradient of grazer abundance. The treatments are incubated under *in situ* light and temperature conditions. Under reduced grazing pressure, the phytoplankton assemblage in each treatment grows at a rate which is a linear function of grazer density (Harris *et al*., 2000). For each dilution treatment, 'apparent phytoplankton growth rate' (*AGR*) is estimated based on change in chlorophyll *a* concentration over time of incubation. The apparent phytoplankton growth rate is plotted as a function of dilution factor (decimal fraction unfiltered sea or other investigated water) by statistical linear regression method.

The y-intercept of this relationship is the 'true' (synonyms: theoretical, specific) phytoplankton growth rate (k), in the absence of grazing and the negative slope of the line is the grazing coefficient (g). The hypothesis g=0 is tested (Harris *et al*., 2000).

The advantage of this method is that it requires little manipulation of the assemblage and estimates both the specific growth rate of the phytoplankton and specific grazing rate of the microzooplankton at the same time. The dilution technique has three necessary assumptions that may be difficult to be achieved in practice: 1) prey specific growth rate is independent of prey density, wich means that nutrient conditions must be equal across dilution gradient, non-limiting the phytoplankton growth; 2) predation is a direct linear function of prey abundance (i.e. increased dilution will cause a proportional reduction in microzooplankton grazing pressure); 3) prey growth rate can be adequately represented by the exponential growth model (Landry and Hassett, 1982; Gallegos, 1996).

Water samples for the experiment were collected from two sites: Nida on 29 August and Smiltyne on 10 October, 2009. Water was collected from 0.5 m depth using 5 l water sampler, transferred gently into two 50 l carboys, and transported to the laboratory.

The particle free water (**FW**) was prepared by filtering lagoon water through 20 µm pore size mesh, intermediate 2 and 0.7 µm GF/F filters and the last 0.2 µm Millipore filters under slight air pressure (Fig. 5). The filtration process depends on the concentration of phytoplankton and suspended solids and took 20 and 5 hours in Nida and Smiltyne site respectively. The whole lagoon water (**WW**) was collected the next day in Nida and the same day in Smiltyne case and was size-fractionated to remove mesozooplankton by gently pouring it through a 150 µm mesh. The **WW** was diluted by **FW** to four target dilutions in ratios of 1:0, 3:1, 1:1 and 1:3 (dilution factor or decimal fraction of of **WW**: 1; 0.75; 0.5; 0.25, respectively) in 3 l transparent plastic bottles (Fig. 5). No nutrients were added to the experimental bottles. The incubation volume was 3 l and treatments were carried out in triplicates. All bottles were incubated *in situ* at 0.5 m depth for

24 h. During the experiment on 10 October 2009, 7 bottles from 15 were lost during the night time storm.

At the start and at the end of both experiments, 500 ml of each dilution mixture from each experimental bottle were sampled for nutrient (nitrate, nitrite, ammonium, phosphate and silicate) analysis, 25-30 ml for nano- and pico- fractions of chlorophyll *a* and 300 ml for microzooplankton counts.

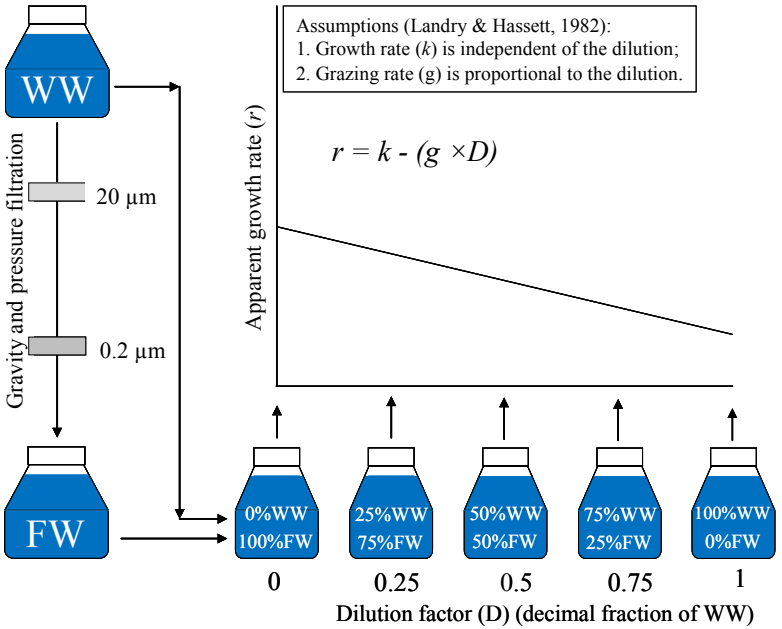

Fig. 5. Scheme of the dilution experiment, based on Landry and Hassett (1982). WW – whole lagoon water, FW – particle free water.

Samples for nanophytoplankton (2–20 µm) chlorophyll *a* were filtered through 20 µm mesh and concentrated on 2 µm Millipore polycarbonate filter. The remaining filtrate was concentrated on 0.2

μm Millipore polycarbonate filter for picophytoplankton (0–2 μm) chlorophyll *a*. Total chlorophyll *a* concentration was measured only in **WW** at the beginning of the experiments. All filters were maintained frozen at -20 ^{o}C and analyzed within two months.

The chlorophyll *a* fraction >20 μm was not measured in the experimental treatments, because microzooplankton assemblage was composed mainly by ciliates (>99% of total abundance) and the preferred size-feeding spectrum of many ciliate species is about 3–20 μm (Weisse, 2003). Pre-experiment based on visual observation before dilution experiments was done to assure that 150 μm size mesh effectively remove the mesozooplankton species and the filtration trough the mesh doesn't have negative effect on the vitality of ciliates, especially aloricated forms.

Total chlorophyll *a* concentration in the initial water samples was determined fluorimetrically (FluorProbe II).

Pigments of nano and pico-fractions were measured by high-performance liquid chromatography (HPLC) at the Baltic Sea Research Institute, Warnemünde, Germany.

Samples were analyzed according to Barlow *et al*. (1997). Pigments were detected by absorbance at 440 nm using a Biotek (545V) diode array detector and identified by retention time and online visible spectra (350 to 750 nm) obtained from scans by the diode array detector. Chlorophylls were further detected by Jasco (FP-1520) fluorescence detector (440 and 660 nm excitation and detection wavelengths respectively). The chromatograms are processed using the Biotek Kroma 3000 software. Pigment concentrations were calculated by peak area. The response factors were obtained by calibrating the system with known concentrations of external standards of chlorophylls and carotenoids obtained from DHI Bioproducts-The International Agency for ^{14}C Determination, Denmark.

Nutrients were analyzed at the Baltic Sea Research Institute (Warnemünde, Germany) using the following methods: 1. Manual

salicylate and hypochlorite method for NH_4^+ using nitroprusiate as catalyst (Bower and Holm-Hansen, 1980); 2. Standard colorimetric method using flow injection analyzer for NO_x^-, NO_2^- and SRP (Grashoff, 1983); 3. NO_3^- was calculated as a difference between NOx- and NO_2^-; 4. Calorimetric method for SiO_3^- (Karoleff, 1976); 5. Calorimetric method for PO_4^- described by Murphy and Riley (1962).

Microzooplankton was counted as described in section 4.1. *Myrionecta rubra* was observed in Smiltyne site experiment, but not included to the total ciliate abundance and biomass counts, because it appears to function mostly as an autotroph (Dolan *et al*., 2000). Rotifers and copepod nauplii counted using a microscope at 40× magnification in Bogorov chamber.

Dilution experiment data analysis was performed according to Landry and Hasset (1982). The prey apparent growth rate (*AGR*) was estimated using function: $AGR(d^{-1}) = (\ln(Chla_t / Chla_o)/t)$; $Chla_t$, $Chla_o$ are final and initial concentrations of pico- and nano- size fractions of chlorophyll *a* (μg L^{-1}), *t*- time of incubation (d).

The rates of prey growth and grazing mortality were calculated by the linear regression of *AGR* versus actual dilution factor. The absolute value of the slope of the regression is the grazing rate by microzooplankton (*g*, d^{-1}) and ordinal intercept (y-intercept) of the regression is the growth rate of phytoplankton in the absence of grazing (*k*, d^{-1}).

Significant negative slope (one-tailed t-test, $P<0.05$) suggests a measurable grazer effect on phytoplankton growth. In the cases of a statistically non-significant regression or significant positive slope (theoretically impossible), grazing rates were not determined. In the cases of statistically non-significant regression or significant positive slope, the phytoplankton growth rates can be obtained from averaged AGR among all dilution treatments, rather than using the intercept to predict the "true" growth rate (Twiss and Smith, 2011).

Standing stock of phytoplankton biomass (as a chlorophyll *a*, μg L^{-1}) removed daily ($P_{i,}$ % d^{-1}) and phytoplankton potential production grazed daily ($P_{p,}$ % d^{-1}) were calculated using equations presented in James and Hall (1998):

$P_i = 1 - e^{-g}$; $P_p = (e^k - e^{k-g})/(e^k - 1)$, where: *k*- growth rate of phytoplankton and *g*- grazing rate of microzooplankton estimated from the linear regression.

5. RESULTS
5.1. Environmental conditions

Water temperature ranged from 0.1 to 22.7 ˚C during the studied period. No significant differences were found between Nida and Smiltyne sites (Table 4). The highest temperature was observed in the beginning of June and August (22.7 ˚C) at Nida site (Fig. 6 a). The temperature decreased to <15˚C in the end of September, the lowest temperature was measured in the beginning of January (0.1˚C) at Nida.

Water transparency varied from 0.6 to 1.8 m at Smiltyne in positive relation to the salinity (Pearson r=0.6, N=36, p<0.05) and was significantly lower at freshwater station throughout all seasons (Table 4). Dissolved oxygen concentration was inversely related to seasonal fluctuations of water temperature (Pearson r=-0.8, -0.9, N=36 at Nida and Smiltyne sites respectively, p<0.05) (Fig. 6 b).

Table 4. Comparison of the sites according to the environmental variables: results of the paired *t*-test. N – Nida, S – Smiltynė.

Parameter	t	p	Station	Mean ± SD
Temperature (˚C)	-0.78	0.44	N	11.9 ± 7.2
			S	12 ± 7.1
Dissolved oxygen (mg L^{-1})	-1.63	0.11	N	11.6 ± 2.8
			S	11.9 ± 2.5
Secchi depth (cm)	-4.81	0.00	N	68 ± 20
			S	97 ± 34

The brackish water never occurred at freshwater site Nida, whereas the salinity varied from 0 to 6.9 PSU at oligohaline site Smiltyne. Brackish water (>0.5 PSU) intrusions occurred at 68% of all sampling cases. Around half of these cases are short duration (1–4 days) intrusions prior to sampling date; in the remaining sampling cases brackish water residence time was longer and varied from 7 to 28 days, indicating outflow or mixing of water masses (Fig. 7).

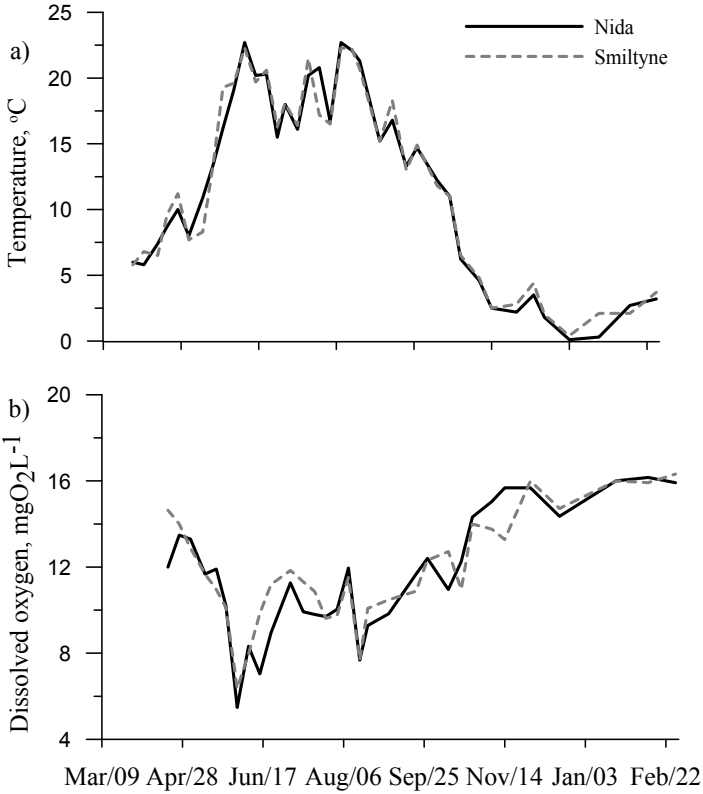

Fig. 6. Seasonal changes of the temperature (a, °C) and dissolved oxygen (b, mg O_2 L^{-1}) in the research sites

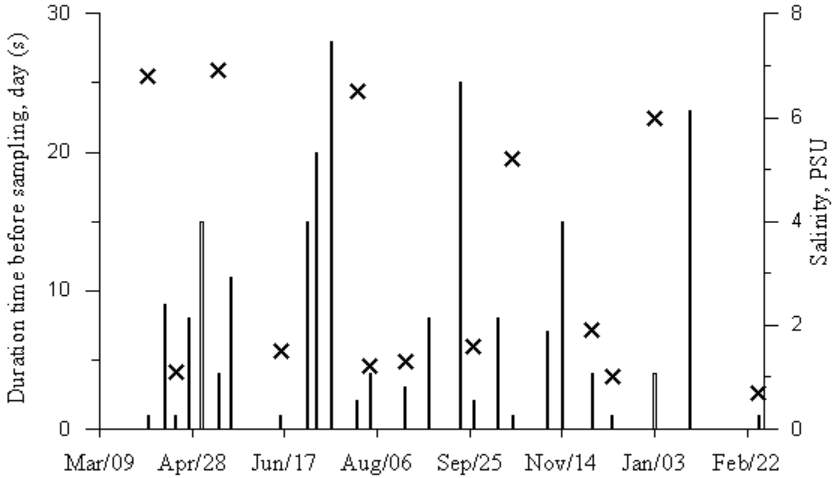

Fig. 7. Brackish water (>0.5 PSU) residence time prior to sampling, denoted as bars (Environmental Protection Agency, Department of Marine Research, unpublished monitoring data) and salinity (asterisks) during each sampling occasion at Smiltyne site.

The chlorophyll *a* concentration was significantly higher at freshwater Nida site (paired *t*-test, N=34, t=6.1, $p<0.001$). Phytoplankton assemblage was dominated by diatoms and green algae (52 and 22% of total chlorophyll *a* respectively) in early spring (March-April). The chlorophyll *a* concentration peaked to 62 μg L^{-1} in the beginning of May simultaneously with the dominance of diatoms (65% of total chlorophyll *a*) (Fig. 8). The phytoplankton assemblage shifted to prevalence of Cyanobacteria during summer and autumn, with highest total chlorophyll *a* concentration in the beginning of September (73 μg L^{-1}). Cyanobacteria composed 64% of total chlorophyll *a* on average during summer and autumn. Cryptophytes were less important for phytoplankton assemblage; they shared up to 29% of total chlorophyll *a* only in the beginning of the June. Codominance of Cyanobacteria and diatoms was observed in late

autumn and winter (Fig. 8); chlorophyll *a* concentrations were below 15 µg L^{-1} in winter time.

The lower chlorophyll *a* concentrations were related to brackish water intrusions in the oligohaline Smiltyne site (Pearson r=-0.6, N=34, p<0.05).

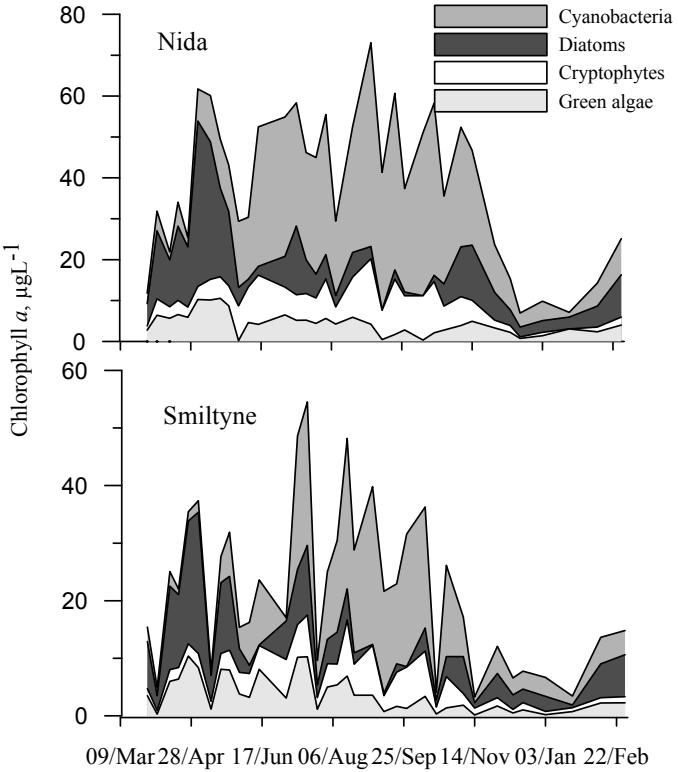

Fig. 8. Seasonal dynamics of the chlorophyll *a* concentration (µgL^{-1}) at research sites

In this site phytoplankton dynamics followed the same pattern: diatoms dominated in phytoplankton assemblage in the spring, while Cyanobacteria prevailed in the summer and autumn. The highest chlorophyll *a* concentration (55 μg L^{-1}) was determined in the middle of July (Fig. 8).

The spring maximum of the metazooplankton assemblage was mainly contributed by increase of rotifers *Conochilus unicornis* and *Keratella quadrata.* In Nida the maximum abundance of rotifers was observed in the middle of May (855 ind. L^{-1}) and in the beginning of October (86 ind. L^{-1}). However, in Smiltyne site the spring peak of rotifers was less pronounced (395 ind. L^{-1}) (Fig. 9).

The abundance of cladocerans was low in spring at both sites. The significant increase was recorded in the middle of June and end of July in Smiltyne and Nida respectively. Cladocerans were represented by *Chydorus sphaericus, Diaphanosoma*, *brachyurum* and *Daphnia* spp. during the peak (Fig. 9).

Copepods *Mesocyclops leuckarti* and *Eudyapthomus graciloides* dominated in zooplankton assemblage during late autumn-winter time in Nida site and all the year round in Smiltyne site. (Fig. 9).

Metazooplankton had the highest production and consumption during the summer/autumn. During the winter the metazooplankton production and consumption were low. (Fig. 9,; Appendix, Table A.2).

In the midsummer metazooplankton potential production reached maximum, at this time cladocerans made up 64% of total metazooplankton production (Fig. 9). The production of copepods (including nauplii and younger copepodite stages) contributed the most to total annual metazooplankton production (on average 69%) during all seasons (Appendix, Table A.2). Rotifer production was low, comparing to cladocerans and copepods and increased during the late spring only (Appendix, Table A.2).

The metazooplankton production correlated with temperature ($r=0.5$, $p<0.05$). Metazooplankton production was tightly related with biomass ($r=0.94$, $p<0.05$).

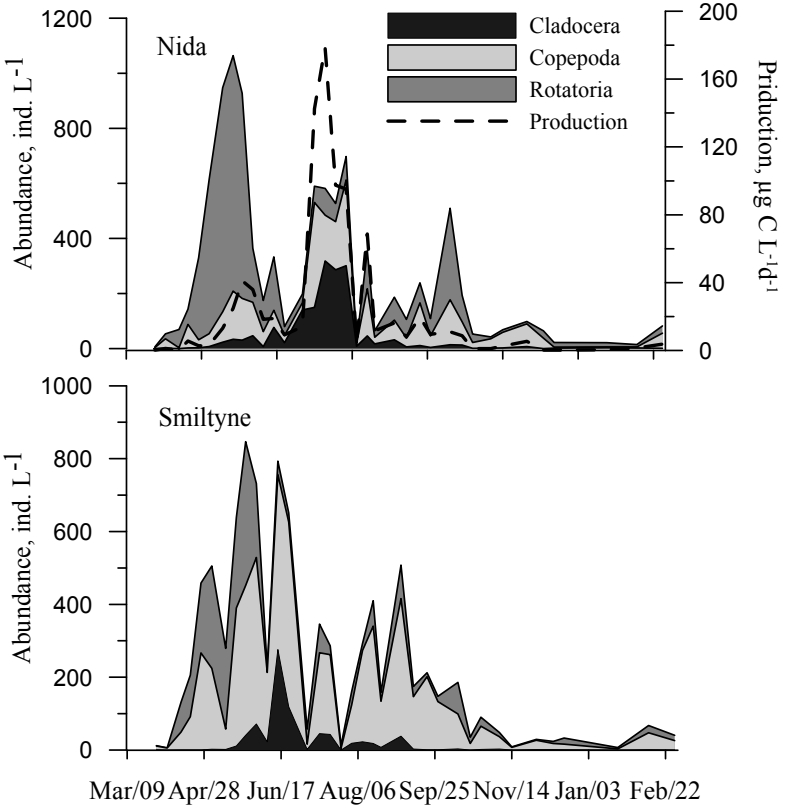

Fig. 9. Seasonal dynamics of the metazooplankton abundance (ind. L^{-1}) at research sites and production (µg C $L^{-1}d^{-1}$) at Nida site

5.2. Methodology and main characteristics of the plankton ciliate assemblage

5.2.1. Comparison of the live and Lugol fixed counts

Prior to the comparison of two sampling methods, paired *t*-test was applied to test the differences of the ciliate abundance between Nida and Smiltyne sites. No significant differences were found between sites (t=1.27, t=0.17; N=36, N=34; p>0.05 for live and Lugol fixed counts, respectively), therefore, data from both sites were pooled. Nano-ciliates *Cyclidium* spp., *Halteria* sp., *Strobilidium* spp., *Urotricha* sp., *Lohmaniella* sp. and *Mesodinium pulex* were missed in the live material and thus removed from the further method comparison procedure.

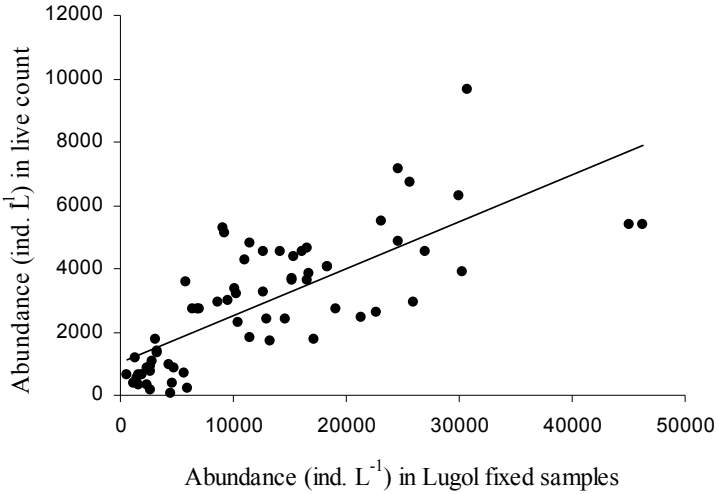

Fig. 10. Total ciliate abundance (ind. L^{-1}) in live material counts *versus* Lugol fixed samples

There was strong significant relationship between the total abundance of ciliates in live material counts and Lugol fixed samples (r=0.75, N=68, p<0.05, Fig. 10). However, the average abundance was 4 times higher in Lugol fixed samples, than in the live material counts *(*paired *t*- test, t=9, N=68, p<0.0001, Fig. 11).

The difference of abundance in fixed samples and live counts correlated with temperature (r=0.6, N=68, p<0.05). During cold season (late autumn-winter) the difference was less pronounced, than during the warm season.

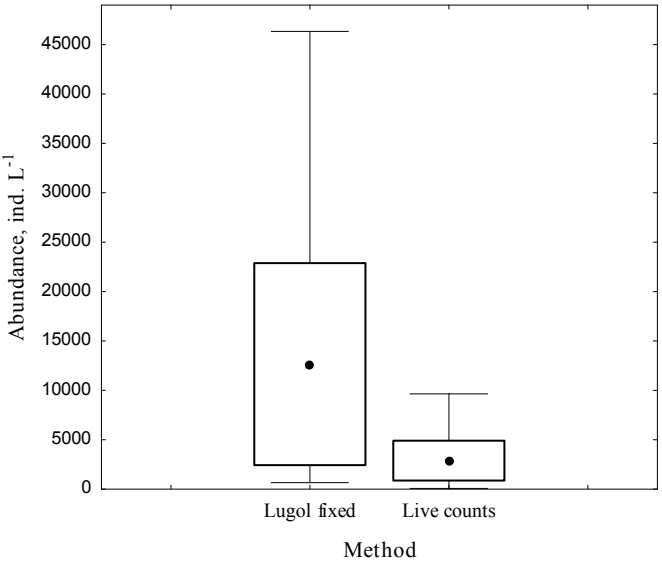

Fig. 11. Mean values of total ciliate abundance (±SD and min-max range as whiskers) in Lugol fixed and live material counts

There were significant differences in the assemblage structure estimated by two methods. Relative abundance of haptorids and peritrichids was significantly higher in Lugol fixed samples than in the live material counts (paired *t*-test, t=5.45, t=3.37, N=68, p<0.001), while naked oligotricids and prostomatids *vice versa* (paired *t*-test, t=-

5.17, t=-7.51, N=68, p<0.001) (Fig. 12). However, no statistically significant differences were revealed for relative abundance of tintinnids (paired *t*-test, t=1.06, N=68, p>0.05) (Fig.12).

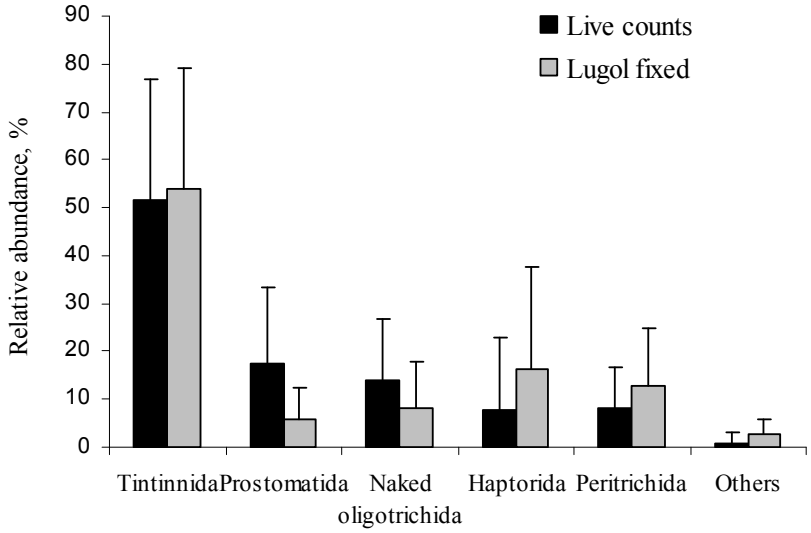

Fig. 12. Relative abundance of main taxonomic groups in Lugol fixed and live material counts ±SD

5.2.2. Taxonomical composition

In total 100 ciliate species/higher taxa were identified, 81 species/higher taxa were found in Nida and Smiltyne sites during the seasonal studies and 19 new species/higher taxa were added to the list from the cruises investigations at other lagoon stations (Apendix Table A.1). During seasonal studies in oligohaline site (Smiltyne) 76 taxa were identified, whereas 63 taxa – in freshwater (Nida) site. During spatial studies 66 taxa were identified: 12 in Nemunas river avandelta and 54 – in other lagoon stations (Table 5).

All registered taxa/species were assigned to 13 orders: Oligotrichida, Haptorida, Prostomatida, Peritrichida, Hymenostomatida, Heterotrichida, Pleurostomatida, Cyrtophorida, Scuticociliatida, Hypotrichida, Suctorida, Colpodida and Nassulida (Apendix, Table A.1; Table 5).

Oligotrichida (including tintinnids and naked oligotrichs), prostomatids, haptorids and peritrichs dominated in the ciliate assemblage in terms of the species number in both seasonal and spatial studies and occurred in almost all samples (92 to 100%) (Table 5). These groups were present in all sites throughout the sampling period, contributing up to 85–90% to all recorded taxa. Tintinnids *Tintinidium pusillum, Tintinnopsis tubulosa, Tintinnopsis* sp. and naked oligotrichs *Stobilidium velox, Halteria grandinela*, *Strombidium viride,* haptorids *Askenasia* spp., *Monodinium* sp., peritrich *Vorticella microstoma* and prostomatid *Coleps hirtus* occurred in the samples most frequently.

The species number of the orders Hymenostomatida, Heterotrichida, Pleurostomatida, Cyrtophorida, Scuticociliatida, Hypotrichida and Suctorida were much lower. Nevertheless, occurrence of the representatives of Scuticociliatida, Cyrtophorida and Hypotrichida were comparatively high. Scuticociliatida (*Cyclidium* spp.) occurred in all Nida and Smiltyne samples, but were missed in the spatial studies because only live material was analyzed (Table 5). High occurrence of Cyrtophorida and Hypotrichida (75 and 100% respectively) were registered in the Nemunas River avandelta.

During the study 12 brackish/marine ciliate species were found; 9 of them (*Myrionecta rubra, Codonella relicta, Strombidium conicum, Strombidium styliferum, Tintinnopsis baltica, Tintinnopsis kofoidi, Cothurnia maritima, Frontonia marina* and *Helicostomella subulatum*) – in the Smiltyne site and the other 3 (*Lohmaniella spiralis, L. oviformis, Lohmaniella* sp.) were common in both sites: Nida and Smiltyne (Apendix Table A.1).

Spatial studies added 19 species/taxa to the list, the most of them (12 taxa: *Paradileptus conicus, Hypotrichidium conicum, Holophryra atra*, *H. hexatricha*, *Litonotus lamelata, Nassula* sp., *Cyclotrichium limneticum, Staurophrya elegans, Paruroleptus piscis, Frontonia leucas, Paramecium* sp., *Phascolodon vorticella*) were observed only in the Nemunas River avandelta area. (Table 5; Apendix Table A.1). The rest 2 taxa (*Strongilydium lanceolatum* and *Uroleptus* sp.) were found only in Nemunas river and other lagoon stations, while 5 taxa (*Condylostoma vorticella, Rhabdostyla cyclopis, Rhabdostyla pyriformis, Litonotus fasciola and Colpoda steinii*) only in other lagoon stations, but never found during seasonal studies, also they were absent in Nemunas avandelta samples.

Table 5. The number of species/ higher taxa (N. taxa) of main ciliate groups and its occurrence in the samples (Oc., %) in Nida, Smiltyne, Nemunas River avandelta and other stations during the study period of 2007-2008.

Order	Seasonal studies				Spatial studies			
	Nida		Smiltyne		Other stations		Nemunas r. avandelta	
	N. taxa	Oc. (%)	N. taxa	Oc. (%)	N. taxa	Oc. (%)	N. taxa	Oc. (%)
Oligotrichida	17	100	23	100	16	100	11	100
Haptorida	11	100	14	100	10	100	9	100
Prostomatida	11	100	12	92	8	100	8	100
Peritrichida	10	92	11	92	11	100	7	100
Hymenostomatida	4	33	5	25	1	25	3	50
Heterotrichida	2	17	4	17	2	25	-	-
Pleurostomatida	3	58	2	42	1	25	1	25
Cyrtophorida	2	17	1	8	1	25	2	75
Scuticociliatida	2	100	2	100	-	-	-	-
Hypotrichida	-	-	1	8	2	50	4	100
Suctorida	1	8	1	17	1	25	1	25
Colpodida	-	-	-	-	1	25	-	-
Nassulida	-	-	-	-	-	-	1	25
Total	63		76		54		47	

The Shannon–Wiener species diversity index (H') ranged from 0.96 to 2.65, and from 0.18 to 2.52 at Nida and Smiltyne sites respectively. The highest H' values were recorded during spring and summer, the lowest – during late autumn and winter. Biodiversity was significantly related to temperature (ρ=0.43, $p<0.05$ for Nida; ρ=0.55, $p<0.05$ for Smiltyne) and chlorophyll *a* concentration (ρ=0.67, $p<0.05$ for Nida; ρ=0.68, $p<0.05$ for Smiltyne).

In Smiltyne site the significant negative relation was found between Shannon–Wiener species diversity and salinity (ρ=-0.45, $p<0.05$, Fig. 13). H' reached the maximum values at 0–2 PSU, and tended to decrease at >4 PSU. The minimum value of H' index was estimated for the ciliate assemblage at 7 PSU (Fig. 13). The same pattern was observed for the average number of taxa: it dropped from 18 at the salinity of <2 PSU to 11 at the salinity of >2 PSU (ρ=-0.46, $p<0.05$). Shannon-Wiener species diversity index in 0–2 PSU salinity group was significantly higher than in >2 PSU group (Mann-Whitney test for independent groups, Rank group 1=543, Rank group 2=87, Z=2.8, $p<0.01$).

The complete list of the plankton ciliates of the Curonian Lagoon including historical data comprises 152 species/higher taxa (Appendix Table A.1). About one third of taxa (58) were the same in the present and past inventories, 52 were not identified in the present study (Fig. 13).

Representatives of 42 taxa were found for the first time during the present survey; 25 of them were identified to the level of genera and 17 – to the species level (*Enchelys pupa, Spirostomum minus, Helicostomella subulatum, Lohmaniella oviformis, L. spiralis*, *Tintinnopsis baltica, T. kofoidi, Cothurnia maritima, Paruroleptus piscis, Coleps hirtus subsp. viridis, C. spetai, Holophrya atra, H. hexatricha, Prorodon discolor, Frontonia leucas, Marituja pelagica* and *Chilodonella cucullus*).

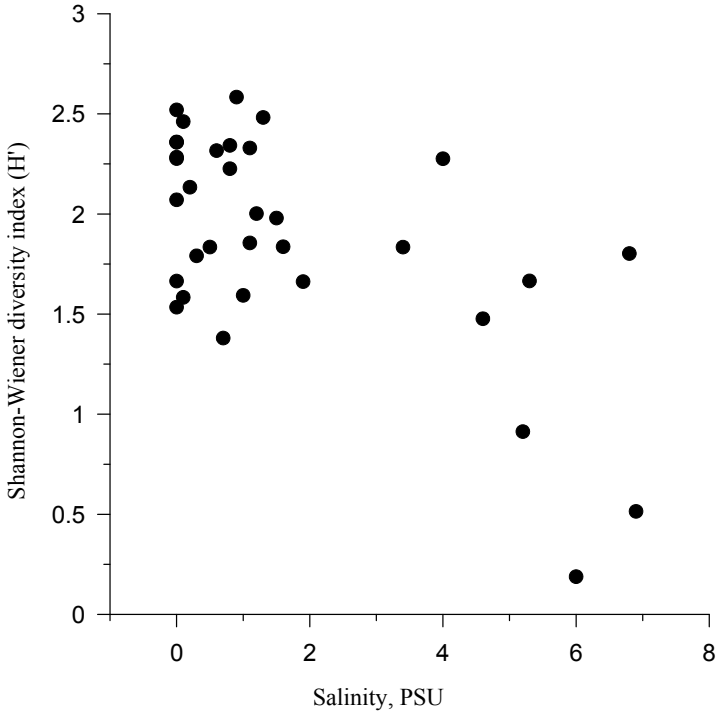

Fig. 13. Species diversity of ciliates (H', Shannon-Wiener diversity index) versus salinity

The present list of species comprises representatives of all orders, found in earlier studies, except for the species-poor order Odontostomatida (1 species) (Fig. 14). The highest overlapping of both species lists was found for Peritrichida, Heterotrichida and Cyrtophorida (61, 63 and 67% of common taxa respectively). The hypotrichids and haptorids were better represented in Mažeikaite's (2003) list, whereas Oligotrichida has more representatives in this study than in the previous species list (Fig.14).

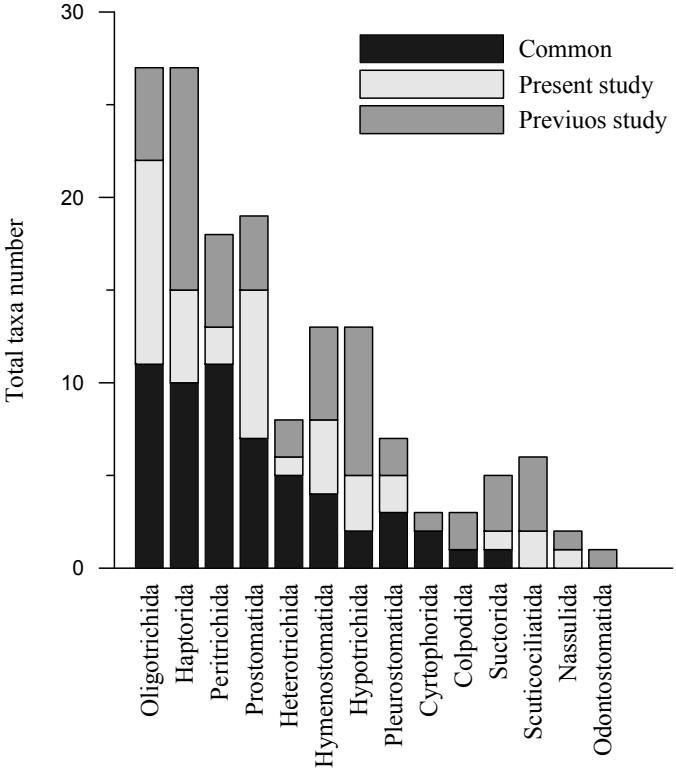

Fig. 14. Number of taxa found in the present and previous (Mažeikaitė, 1978–2001) studies

5.3. Seasonal dynamics of plankton ciliates

5.3.1. Seasonal dynamics of plankton ciliates in the oligohaline part of the lagoon

Total abundance and biomass of ciliates varied within the range of 0.9 - 91.7×10^3 ind. L^{-1} and 0.9–88.3 µg C L^{-1} at Smiltyne site (Fig. 15).

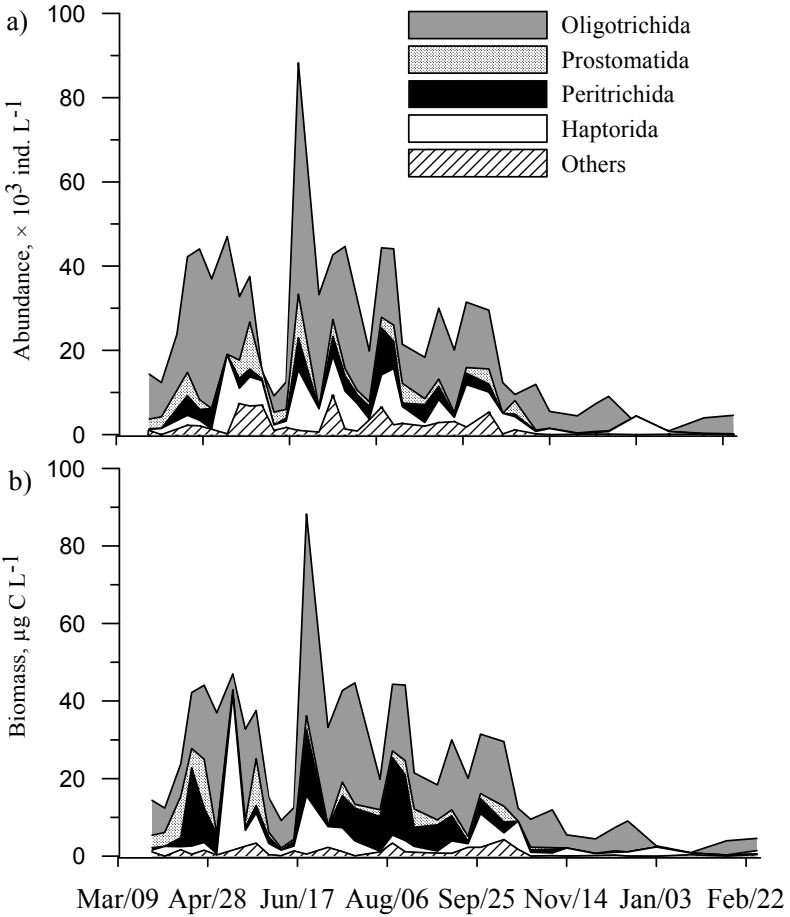

Fig. 15. Seasonal dynamics of ciliate abundance (a, ind. L^{-1}) and biomass (b, µg C L^{-1}) at Smiltyne site

The highest abundance and biomass was observed in the end of June. Spring abundance and biomass maximum was less pronounced than summer. Sharp decrease of ciliate quantitative characteristics in the first half of June was also characterized for this site (Fig. 15).

Total abundance of ciliates correlated negatively with salinity in Smiltyne site (r=-0.42, N=34, p<0.05). MDS plot revealed two ciliate assemblages according to salinity intervals 0–2 PSU and ≥4 PSU (Fig. 16). The global R statistics from ANOSIM of these assemblages demonstrated that the overall differences between them were statistically significant (Global R=0.939, p<0.01).

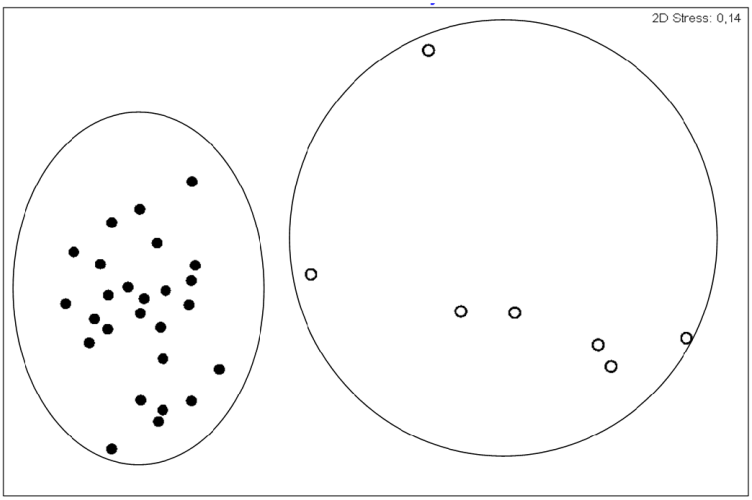

Fig. 16. The MDS plot for Smiltyne site ciliate samples (filed circles – samples with salinity interval 0–2 PSU, open circles – samples with salinity ≥4 PSU)

Assemblage at salinity ≥4 PSU was more structurally homogeneous than 0–2 PSU group. *Myrionecta rubra* dominated in the assemblage at ≥4 PSU and contributed 77% to similarity inside the group (Fig. 17). Another characteristic representative is *Strombidium* spp., contributing 7% to the similarity.

Assemblage at salinity range 0–2 PSU is characterized by the dominance of *Strobilidium* spp. (40% to similarity inside the group)

and *Tintinnidium pusillum* (14%). *Cyclidium* spp., *Urotricha* spp., *Vorticella* spp. and *Tintinnopsis* sp. contribute from 5 to 7% of similarity inside the group (Fig. 17).

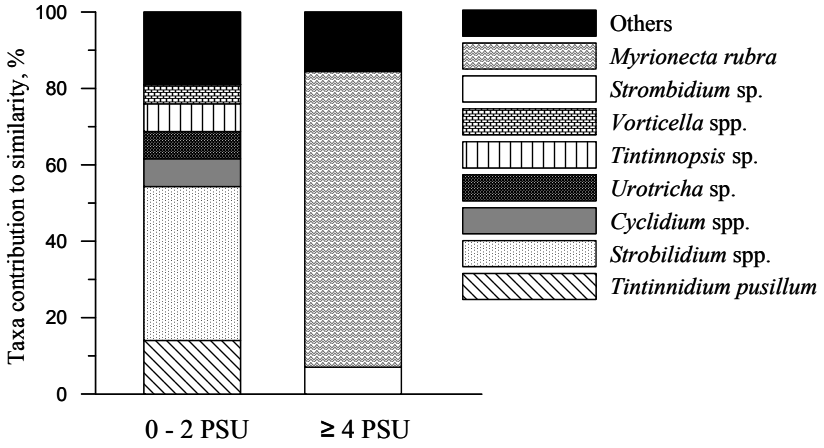

Fig. 17. Results of the SIMPER analysis, representing the contribution of dominant ciliate species/ higher taxa to the average similarity inside two different salinity assemblages

Size structure of ciliates differs between salinity assemblages: at 0–2 PSU it dominates by nano-ciliates (<20 μm size), while at ≥4 PSU is mainly composed by size fractions of 20–30 and 30–60 μm; nano-ciliates share only 15 % of total abundance in this group (Fig. 18 a).

Functionally these two ciliate assemblages are different as well. In the ≥4 PSU group mixotroph *Myrionecta rubra* share 45% of total abundance, pico-filterers and omnivores compose only 5% of total abundance, predators are absent. Pico-nano feeders dominate (47% of total abundance) in the group of 0–2 PSU, omnivores and pico-

filterers compose 12 and 14% of total ciliate abundance respectively, predators share 3% of total abundance (Fig. 18 b).

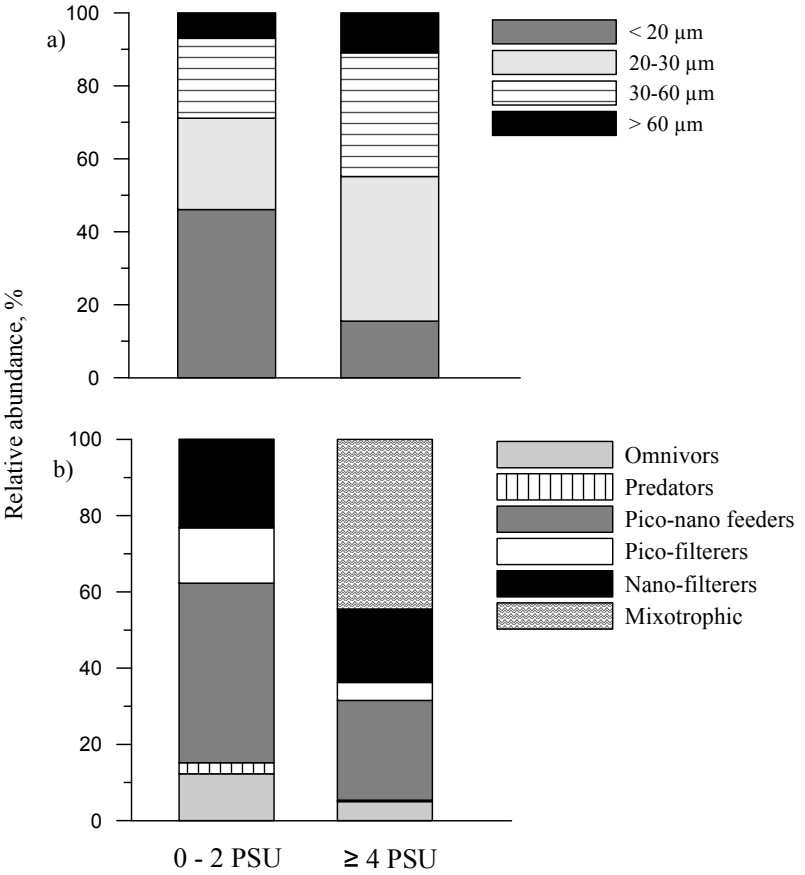

Fig. 18. Relative abundance of ciliate size fractions (a) and different trophic groups (b): pico-filterers (bacterivorous), nano-filterers (algivorous), pico-nano (bacterio/algivorous) feeders, predators (feeding on ciliates), omnivores (feeding on algae, heterotrophic flagellates and ciliates) and mixotrophs (*Myrionecta rubra*) in two salinity assemblages: 0–2 PSU and ≥4 PSU.

5.3.2. Seasonal dynamics of plankton ciliates in the freshwater part of the lagoon

Total abundance and biomass of ciliates varied within the range of 2.4–74×10^3 ind. L^{-1} and 4.1–52.7 µg C L^{-1} at Nida site (Fig. 19). Ciliate abundance and biomass peak observed at Nida site in late spring was followed by sharp decrease in the first half of June. In the end of June-July the abundance and biomass were high again (52×10^3 ind. L^{-1}) and followed by gradual decrease towards the end of autumn. During the winter ciliate abundance and biomass was low.

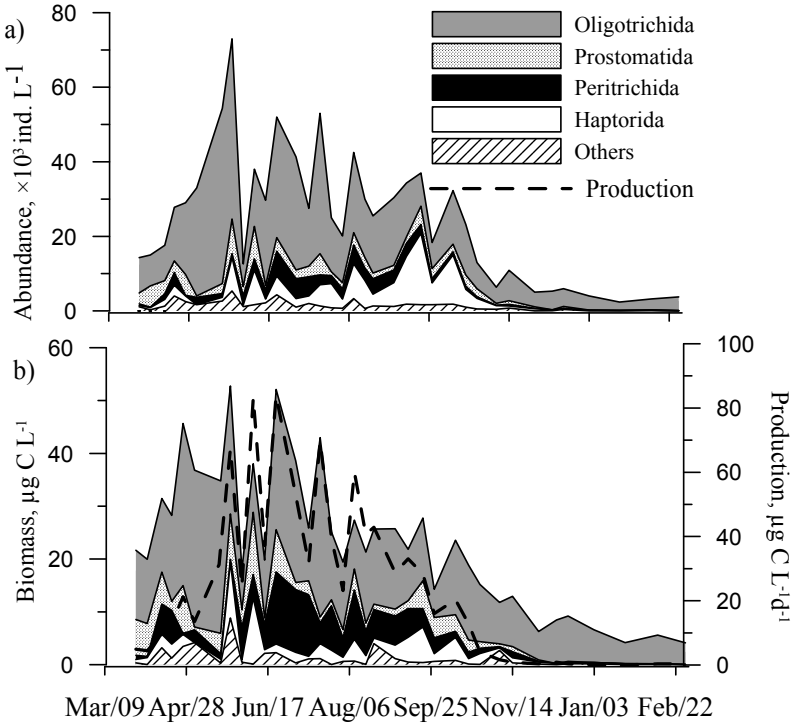

Fig. 19. Seasonal dynamics of ciliate abundance (a, ind. L^{-1}), biomass (b, µg C L^{-1}) and production (b, µg C L^{-1}d^{-1}) at Nida site

The potential maximum production of the ciliates was highest in the late spring and in the beginning of the summer, tintinnids contributed the most to the total production of ciliates (Fig.19b, Appendix, Table A.2). The maximal production of ciliates correlated with temperature ($r=0.86$, $p<0.05$) and biomass ($r=0.77$, $p<0.05$).

The dendrogram of sample similarity calculated on the basis of abundances of sixteen dominant and common species/taxa and one pooled group for rare species, shows a clear separation of all seasonal samples into 4 clusters at 55% similarity (Fig. 20). Therefore, four seasonal ciliate assemblages were derived: winter, early spring, late spring and summer/autumn.

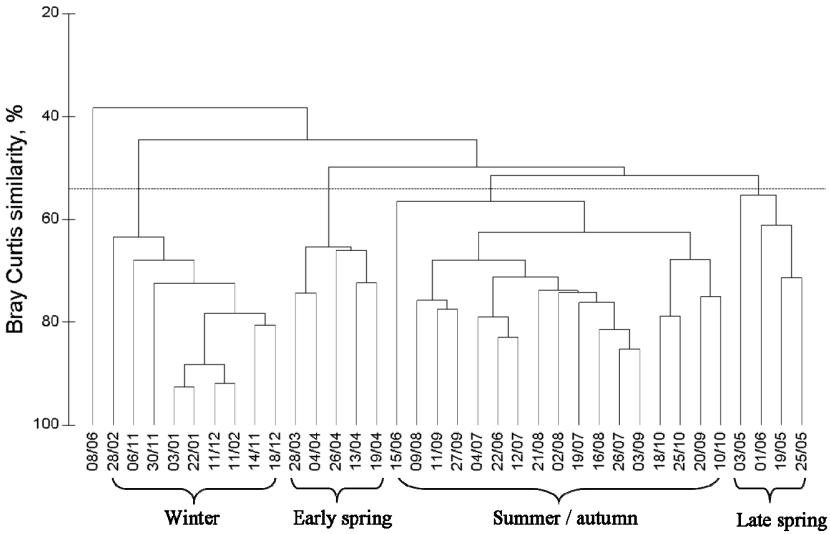

Fig. 20. Dendrogram for hierarchical clustering (group average linking) of Nida site samples based on Bray-Curtis similarity

As revealed by SIMPER analysis, winter assemblage is most structurally homogeneous; *Tintinnidium pusillum* and *Strobilidium*

spp. are dominant species contributing 88% to similarity inside the assemblage (Fig. 21).

Early spring assemblage is characterized by co-dominance of *Tintinnidium pusillum*, *Strobilidium* spp. and *Urotricha* spp. each contributing ~20% to the similarity. *Lohmaniella* spp. and *Halteria* become an important component in ciliate assemblage contributing by ~9% each to the similarity among spring samples.

Late spring assemblage is characterized by largest (39%) contribution of *Tintinnopsis* sp. to the similarity. *Tintinnidium pusillum, Halteria* sp.*, Strobilidium* spp., *Urotricha* spp., *Cyclidium* spp. and *Vorticella* spp. shared 4–15% to cluster similarity (Fig. 21).

Summer/autumn cluster is characterized by relatively high abundance of *Mesodinium pulex*, contributing 15% to similarity inside cluster (Fig. 21).

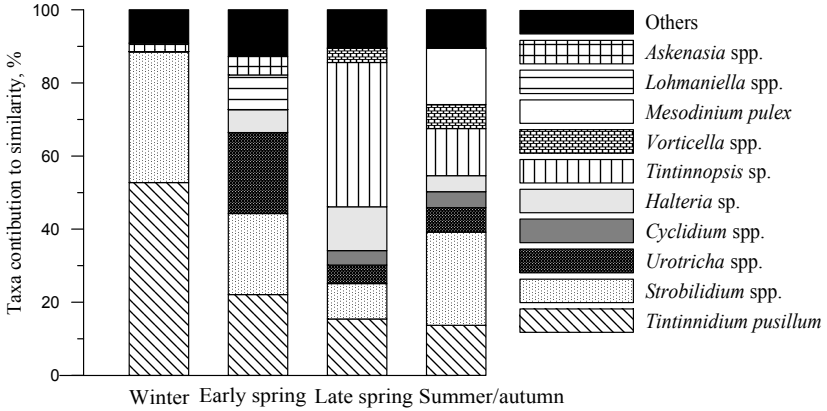

Fig. 21. SIMPER results, representing the contribution of dominant ciliate species/ taxa to the average similarity inside seasonal ciliate assemblages.

The structural differences between the seasonal clusters were significant. As shown by ANOSIM global R statistics approaching 1, the highest differences were observed between spring and winter assemblages, also between two spring assemblages (Table 6).

The quantitative characteristics of seasonal assemblages are shown in the Table 7. The highest total abundance and biomass values were estimated for late spring, the lowest – for winter assemblage.

Table 6. Analysis of similarity (ANOSIM) of the four seasonal assemblages.

Assemblages	R statistics	Significance level
Winter, Early spring	0.96	$p<0.01$
Early spring, Late spring	0.91	$p<0.01$
Late spring, Summer/autumn	0.74	$p<0.01$
Summer/autumn, Winter	0.88	$p<0.01$

Table 7. The abundance and biomass of seasonal assemblages (mean±SD).

Assemblages	Abundance ($\times 10^3$ ind. L^{-1})	Biomass (μg C L^{-1})
Winter	5.2±2.5	7.7±3.2
Early spring	20.7±7.1	29.4±10.2
Late spring	43.2±26.1	35.5±14.2
Summer/autumn	31.5±11.1	26.2±9.9

Dominant ciliate taxa/species cell size range and average size is presented in the Table 8. Small sized organisms (<20 μm and 20–30 μm) dominated in the Curonian Lagoon ciliate assemblage throughout spring, the clear increase of these fractions was registered during

summer/autumn season, when they composed more than 70% of total abundance (Fig. 22a). Nano-ciliates (<20 μm) are represented by naked oligotrichs (*Halteria* sp., *Strobilidium* spp., *Lohmaniella* spp.), scuticociliates (*Cyclidium* spp.), haptorid *Mesodinium pulex* and prostomatid *Urotricha* sp. Size fraction of 20–30 μm was composed by haptorids *Askenasia volvox* and *Monodinium* sp.

Medium sized ciliates (30–60 μm) were less abundant; they contributed up to 38% of total abundance during late spring only. During the rest of the season their contribution ranged from 23 to 26% (Fig. 22a). This size fraction was composed by *Askenasia faurei*, *Coleps hirtus*, *Lohmaniella spiralis*, *Strombidium viridae, Urotricha pelagica* and *Tintinnopsis* sp.

The proportion of large ciliates (>60 μm) was low during the spring and summer/autumn seasons, but increased significantly during the winter time (27% of total abundance, Fig. 22a). Large ciliates were represented primarily by tintinnids (*Tintinnidium pusillum*, *Codonella cratera*, *Tintinnopsis tubulosa*), haptorid *Lacrymaria* sp. and peritrich *Epystilis rotans*.

Functional groups of the ciliates in the Curonian lagoon are filterers (nano-, pico- and pico/nano- fractions) and interceptors (pico/nano- and nano/micro- fractions, the last one group divided to omnivores and predators). (Table 8). These groups are related to size structure of ciliate assemblage.

Nano-filterers feeding on nano- sized phytoplankton were dominated by large and medium sized ciliates, mainly tintinnids and large naked oligotrich *Lohmaniella spiralis*. This fraction was most numerous in the winter and late spring (49% of total abundance), while in early spring and summer-autumn they composed 27% of total abundance (Fig 22 b).

Abundance of pico-fraction filterers (*Cyclidium* spp. and *Vorticella* spp.) was low in winter (3% of total), increased to 10% in spring and summer. Pico/nano- feeders are most taxonomically diverse and include ciliates with different feeding strategies (small naked

oligotrichs *Strobilidium* spp., *Halteria* sp., *Lohmaniella* sp., *Strombidium* spp. and large peritrich *Epystlis rotans* are filterers whereas *Urotricha* spp. are interceptors). Pico/nano- feeders composed 40% of total abundance during late autumn-winter and summer seasons, and 53% and 32% during early and late spring, respectively.

Table 8. The cell size range (min-max, and mean in the brackets) and feeding mode of dominant ciliate species in the Curonian Lagoon. O – omnivorous, P – predators, Al – algae, Ba – bacteria, HFl – heterotrophic flagellates, interceptor=raptorial feeder.

Species/higher taxa	Cell size range (mean); μm	Feeding type
Askenasia spp.	23–40 (28)	Nano-interceptor (O)
Mesodinium pulex	3–30 (18)	Nano/micro-interceptor (O)
Monodinium sp.	23–30 (25)	Nano/micro-interceptor (P)
Coleps hirtus	30–56 (45)	Nano/micro-interceptor (O)
Urotricha spp.	15–51 (24)	Pico-nano-interceptor (Ba, Al, HFl)
Lohmaniella sp.	18–25 (22)	Pico/nano-filterer (Ba, Al)
Halteria sp.	15–25 (19)	Pico/nano-filterer (Ba, Al)
Strobilidium spp.	10–40 (20)	Pico/nano-filterer
Strombidium spp.	22–70 (46)	Pico/nano-filterer (Ba, Al)
Epystilis rotans	48–75 (70)	Pico/nano-filterer (Ba, HFl)
Vorticella spp.	18–50 (29)	Pico-filterer (Ba)
Cyclidium spp.	13–25 (17)	Pico-filterer (Ba)
Tintinnidium pusillum	25–126 (62)	Nano-filterer (Al)
Tintinnopsis sp.	23–63 (39)	Nano-filterer (Al)
Tintinnopsis tubulosa	51–101 (72)	Nano-filterer (Al)
Lohmaniella spiralis	48–71 (55)	Nano-filterer (Al)

Omnivorous ciliates (*Mesonidium pulex*, *Askenasia* spp. and *Coleps hirtus*) occurred constantly in the assemblage; their relative abundance was around 7% during winter and early spring, decreased to 3% in late spring and increased during the summer-autumn to the 21% of total abundance. Predatory ciliates (*Monodinium* sp.) were rare during all seasons (≤1% of total abundance), with slight increase to 5% in late spring (Fig. 22b).

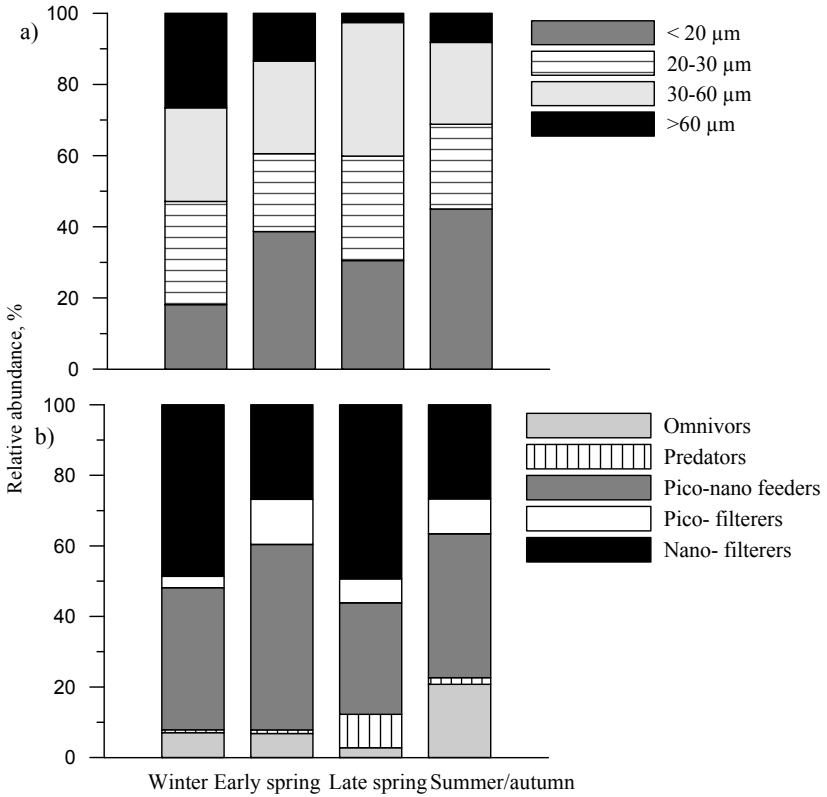

Fig. 22. Relative abundance of ciliate size fractions (a) and different trophic groups (b): pico-filterers (bacterivorous), nano-filterers (algivorous), pico-nano (bacterio/algivorous) feeders,

predators (feeding on ciliates), omnivores (feeding on algae, heterotrophic flagellates and ciliates)

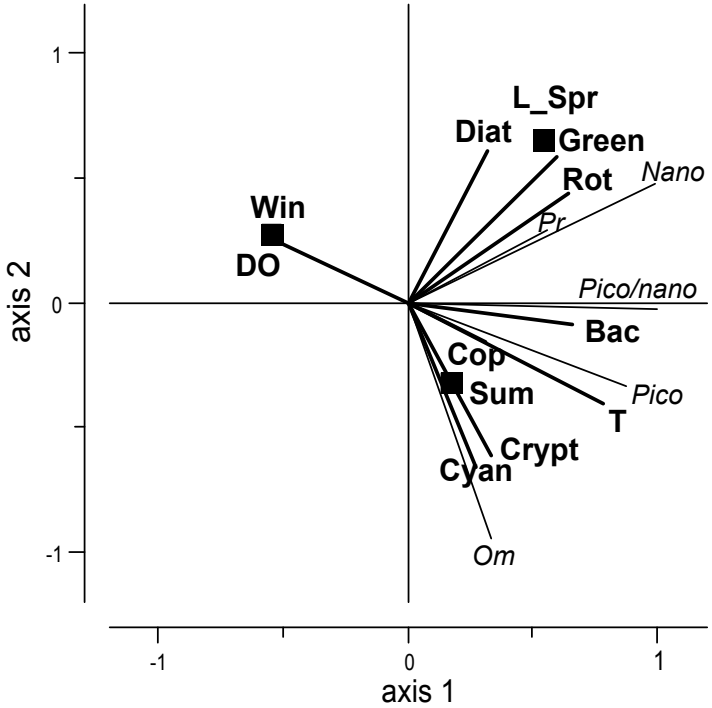

Fig 23. Redundancy analysis (RDA) biplot showing relationships between response variables (Pico – pico-filterers; Nano – nano-filterers; Pico-nano – pico-nano filterers/interceptors, Pr – predators; Om – omnivores) and explanatory variables (T– temperature; DO – dissolved oxygen concentration; Bac – bacteria; Rot – rotifers; Cop – copepods; chlorophyll *a* concentration (Green – green algae; Cyan – Cyanobacteria; Diat – diatoms; Cryp – cryptophyta); Sum – summer-autumn season; Win – winter and L_Spr – late spring)).

According to the RDA, environmental characteristics included in the analysis explain 57% of the variation of functional group abundances (Fig. 23). Permutation tests revealed that temperature (F=12.8, p=0.001), rotifer abundance (F=9.8, p=0.001) and green algae chlorophyll *a* (F=4.6, p=0.007) were significant factors. Correlation between the abundance of nano-filterers and predators was observed; both groups are most abundant during the late spring season. This season is also characterized by high concentration of green algae, diatoms and rotifers (Fig. 23). The highest abundance of omnivores co-occurred with high Cyanobacteria and Cryptophyta abundance during the summer-autumn season. Pico-filterers were positively related to temperature and pico/nano-feeders were positively related to bacteria abundance.

5.4 Grazing effects of plankton ciliates on pico- and nanophytoplankton

5.4.1. Initial abiotic and biotic conditions of dilution experiments

Dilution experiments were performed to examine the growth rates of picophytoplankton (0.2–2 μm) and nanophytoplankton (2–20 μm) and grazing rates of these fractions by microzooplankton at oligohaline and freshwater part of the Curonian Lagoon.

The initial experimental conditions and the microzooplankton abundance differed between the sites (Table 9) mainly due to the different salinity conditions.

At both sites pico-fraction of phytoplankton was represented only by chlorophyll *a* pigment, whereas nano-fraction of phytoplankton contained different pigments and varied between sites. Fucoxanthin, lutein, β carothene, divinyl chlorophyll *a* and chlorophyll *a* were found in the nano-fraction at Nida site, while at Smiltyne site fucoxanthin, 19 hexanoyloxyfucoxanthin, zeaxanthin and chlorophyll

a were recorded. In Nida site chlorophyll *a* fractions > 20 μm, nano- (2–20 μm) and pico-fraction (0–2 μm) shared respectively 47.7, 46.4 and 5.9% of total chlorophyll *a* concentration. Nano-fraction of chlorophyll *a* dominated in Smiltyne site (59.8%), >20 μm fraction shared 38.2 and pico-fraction – only 1.9 %.

Table 9. Environmental parameters and microzooplankton abundance at initial whole lagoon water (WW) at two research sites.

Parameters	Nida	Smiltyne
Temperature (^{o}C)	18.6	11
Salinity (PSU)	0	6.2
Dissolved oxygen (mg O_2 L^{-1})	16.6	10.1
Nitrates (μmol L^{-1})	0.09	7.02
Nitrites (μmol L^{-1})	0.03	0.31
Silicates (μmol L^{-1})	1.95	11.81
Amonium (μmol L^{-1})	3.37	5.15
Phosphates (μmol L^{-1})	1.88	0.98
Total chlorophyll *a* (μgL^{-1})	30.3	4.7
Pico- fraction chlorophyll *a* (μgL^{-1})	1.8	0.09
Nano- fraction chlorophyll *a* (μgL^{-1})	14.1	2.8
Microzooplankton abundance:		
Ciliates (ind. L^{-1})	30667	9800
Copepod nauplii (ind. L^{-1})	115	24
Rotifers (ind. L^{-1})	75	-

At both experimental sites microzooplankton was dominated by ciliates (99% of total abundance). Abundance of copepod nauplii was low in both sides, whereas rotifers were found in Nida site only (Table 9). Size structure of ciliates also differed between sites: nano-ciliates (<20 μm) dominated in terms of number at Nida site and there were no ciliate larger than >60μm, while medium size fraction (30–60 μm)

prevailed and nano-ciliates shared only 14% of total abundance in Smiltyne site (Fig. 24). Therefore mean size of ciliates was larger at Smiltyne site (41 µm), comparing to Nida (31 µm). In Nida site nano-ciliates were represented by *Halteria* sp.*, Strobilidium* spp.*, Cyclidium* spp., *Urotricha* sp. and *Mesodinium pulex.* Medium-sized ciliates (30–60 µm) were represented mainly by tintinnids *Tintinnidium pusillum*, *Tintinnopsis tubulosa*, *Codonella cratera* and *Tintinnopsis* sp.

In Smiltyne site medium size fraction (30–60 µm) was dominated by large brackish water naked oligotrichid species *Strombidium conicum* and *Strombidium styliferum* and tintinnid *Tintinnopsis* sp. Small fractions of ciliates (<20 and 20–30 µm) were composed by *Mesodinium* sp., *Srobilidium* spp., *Urotricha* sp. and *Lohmaniella* sp. The proportion of large ciliates (>60 µm) *Codonella relicta*, *Tintinnopsis kofoidi* was low (5% of total abundance) (Fig. 24).

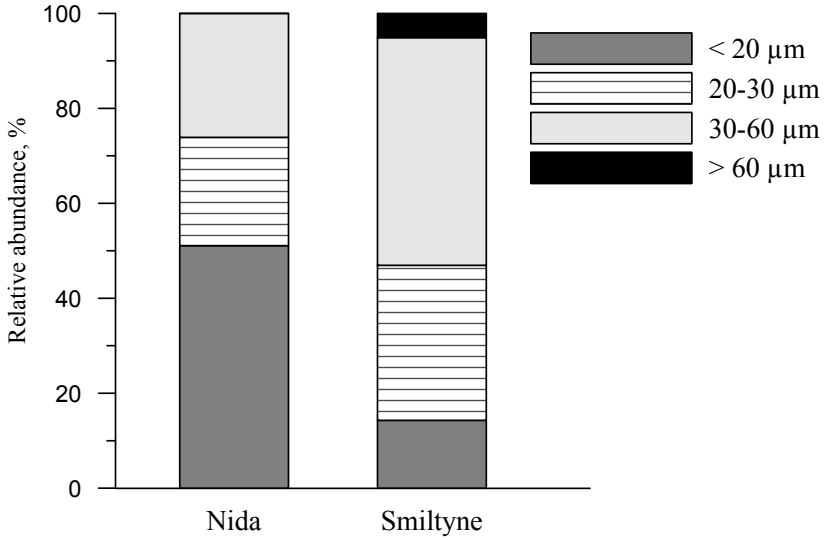

Fig. 24. Relative abundance of ciliate size classes at experimental sites

5.4.2. Nutrient fluctuation during experiments

Initial nutrient concentrations differed significantly between the particle free lagoon water (FW) and whole initial lagoon water (WW) (except nitrates+nitrites) (*t*-test, $p<0.01$), therefore, the concentration of phosphates and ammonium decreased linearly with the increasing dilution level from the lowest concentrations in FW to highest in WW at Nida site (Fig. 25).

Strong positive correlation between initial nutrient concentrations and dilution factor was found ($r=0.9$, $p<0.05$ in both cases). Initial concentrations of nitrites and nitrates correlated with dilution factor negatively ($r=-0.9$, $p<0.05$). Extreme depletion of nitrites and nitrates below detection limits occurred at the end of experiment.

No linear trend of nutrients along treatments observed in Smiltyne experiment, therefore, depletion of nutrients did not occurred during the incubation (Fig. 26).

5.4.3. Growth and grazing rates of phytoplankton

At Nida site, the growth rate (k) of pico-fraction of phytoplankton was 1.3 d^{-1}, grazing rate (g) – 1.8 d^{-1} (Table 10). Grazing rate exceeded growth rate, which indicate the high microzooplankton pressure on this phytoplankton fraction. Potential ciliate feeders on the pico-fraction of phytoplankton (*Vorticella* spp, *Cyclidium* spp., *Stobilidium* spp. and *Urotricha* sp.) were abundant in this site; they shared 60% of total ciliate abundance. The microzooplankton grazing pressure on pico-fraction of phytoplankton expressed by the percentage of grazed biomass as standing stock (P_i) and percentage of grazed potential production (P_p) was 83% and 76%, respectively.

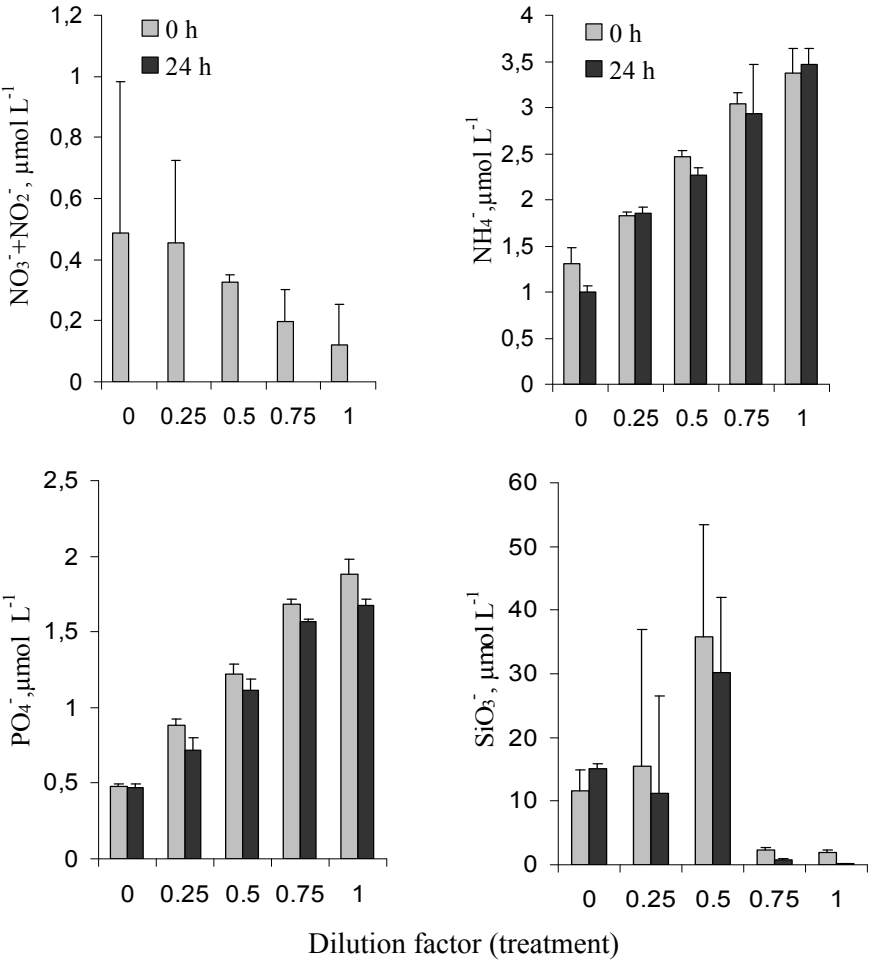

Fig. 25. Nutrient (NO_2^-+NO_3^-, NH_4^-, PO_4^- and SiO_3^-) concentration (µmol L^{-1}) ± SD in different experimental treatments (Nida site)

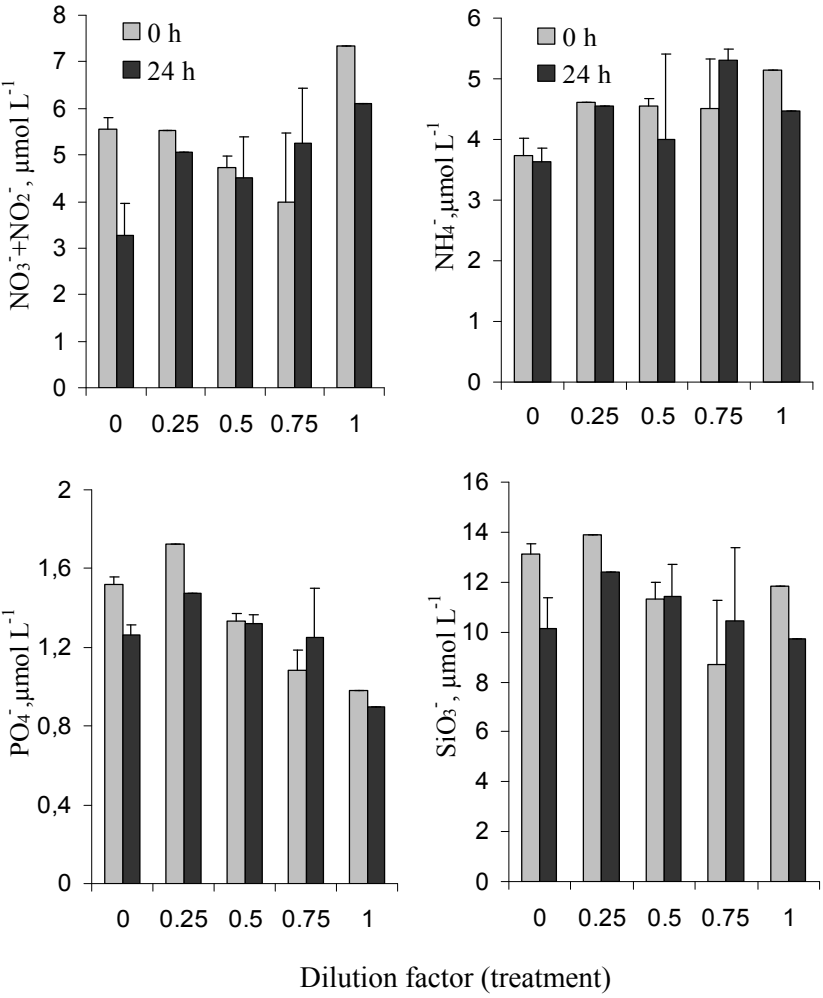

Fig. 26. Nutrient ($NO_2^-+NO_3^-$, NH_4^-, PO_4^- and SiO_3^-) concentration (µmol L^{-1}) ± SD in different experimental treatments (Smiltyne site)

The grazing rate of nanophytoplankton was not interpretable, because no significant linear relationship was observed between apparent growth rate (AGR) of this fraction and dilution factor, i. e. slope (microzooplankton grazing rate, g) was positive and did not differed significantly from zero (Fig. 27; Table 10). However, growth rate of nano-fraction of phytoplankton can be calculated as average of apparent growth rates among all dilution treatments and replicates (N=11) and it was 0.1 ± 0.12 (SE) d^{-1}.

Table 10. Growth rates of the phytoplankton pico- and nano-fractions (k±SE, day^{-1}) and microzooplankton grazing rates (g±SE, day^{-1}) based on chlorophyll *a*. R^2 – coefficient of determination; N – number of observations. The significance level of regression (i.e. slope, g, was significantly differed from zero, p<0.05) is indicated by p-value; n.s. – non significant.

Site	Fraction (μm)	k	g	R^2	p-value	N
Nida	0.2-2	1.33±0.36	-1.83±0.53	0.55	<0.01	12
	2-20	-0.03±0.34	0.19±0.49	0.02	n.s.	11
Smiltynė	0.2-2	-1.09±0.60	2.19±0.90	0.59	n.s.	6
	2-20	0.92±0.28	-1.52±0.42	0.77	<0.05	6

AGR of the pico-fraction increased linearly with dilution factor at Smiltyne site and regression analysis resulted in a positive slope, which did not differed statistically from zero (Fig. 27; Table 10), therefore the microzooplankton grazing rate (g) is not interpretable. Growth rate as in the case of Nida was calculated as average of AGR among all dilutions (N=6), it was 0.28±0.3 d^{-1}.

The growth rate of nano-fraction of phytoplankton was 0.9 d^{-1}, grazing rate was 1.5 d^{-1} (Table 10; Fig. 28). Grazing rate exceeded growth rate. Nano-filterers (tintinnid *Tintinnopsis* sp. and naked oligotrichs – *Lohmaniella spiralis*, *Strombidium styliferum* and

Strombidium sp.) dominated in ciliate assemblage; they shared 66% of total ciliate abundance. In Smiltyne site microzooplankton grazed 78% of the nanophytoplankton standing stock per day and 130% of potential daily production.

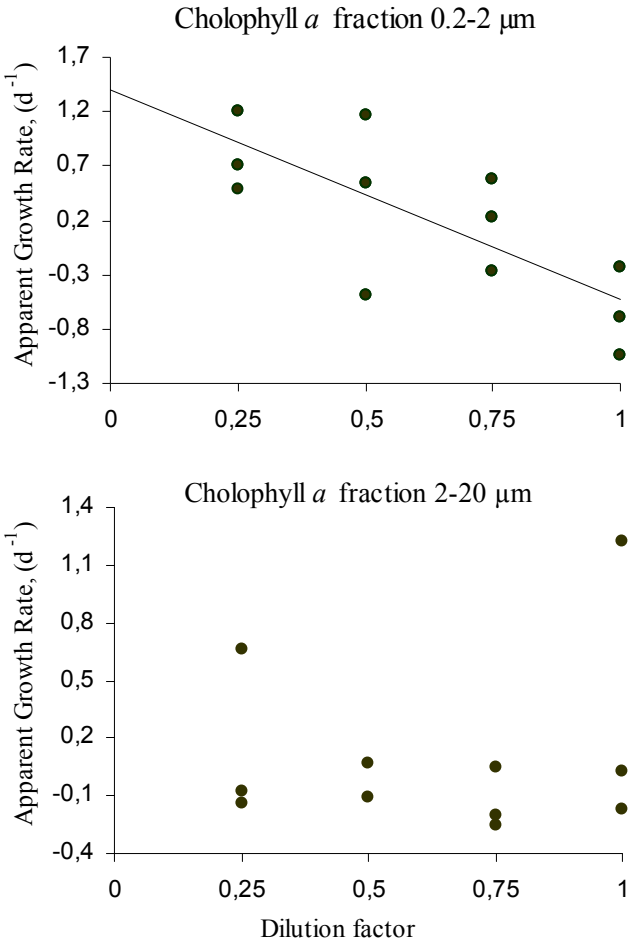

Fig. 27. Relationship between dilution factor and apparent growth rate of chlorophyll *a* of pico- and nano- fractions at Nida site

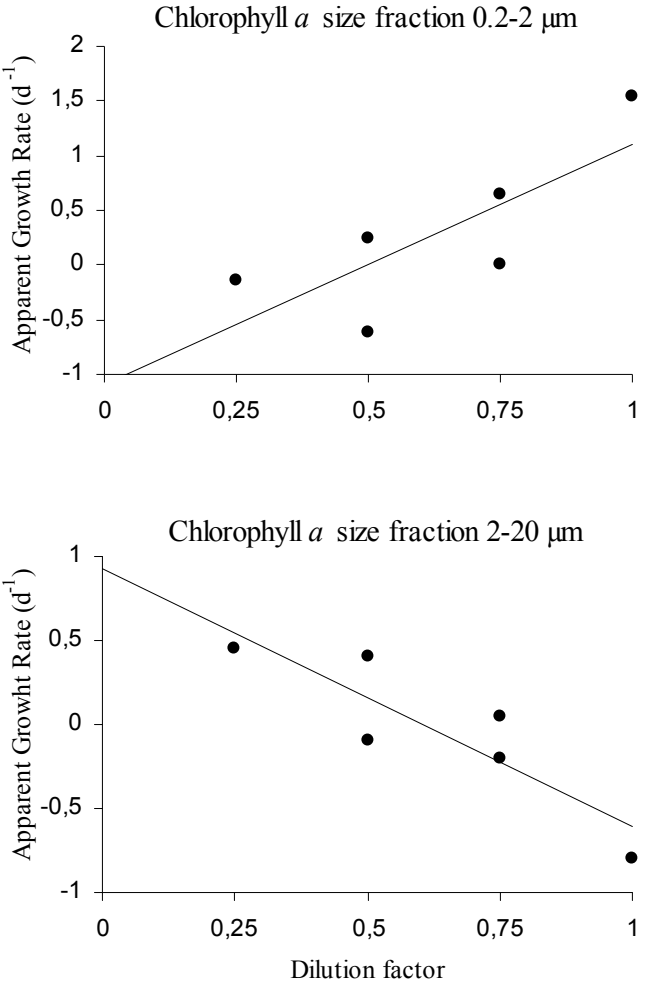

Fig. 28. Relationship between dilution factor and apparent growth rate of chlorophyll *a* of pico- and nano- fractions at Smiltyne site

6. DISCUSSION

6.1. Taxonomic composition of the ciliates and methodological considerations

This study presents one of the most completed lists of ciliates in the coastal waters of the Baltic Sea, including the salinity gradient, seasonal and long term data. To date, 152 species/higher taxa of ciliates identified in the Curonian Lagoon (Appendix; Table A.1.). This number is comparable to 155 ciliate taxa identified in the Gulf of Finland, including the freshwater Neva Bay (Telesh *et al*., 2009). It is much higher than in the Archipelago and Bothnian Sea (41 taxa; Telesh *et al*., 2009), the Gulf of Riga (33 taxa; Boikova, 1989) and the Gulf of Gdansk (40 taxa; Witek, 1998).

The ciliates encountered in the Curonian Lagoon have been previously identified as common to freshwater lakes or marine environments, including brackish estuaries. The ciliate assemblage of the stagnant zone of the lagoon (site Nida) was less diverse (63 species), than the estuarine assemblage in the transitory zone of the northern part of the lagoon (76 species) due to brackish ciliate species (Table 5; Appendix Table A.1.). Our findings of lower species number at the freshwater site, compared to the oligohaline site, are consistent with Pfister *et al*. (2002), who observed a significantly higher number of taxa in brackish lakes due to mixture of common freshwater species and exclusively marine species. At the Smiltyne site, we found oligothrichs *Strombidium conicum* and *Strombidium styliferum*, tintinnid species *Tintinnopsis baltica* and *Helicostomella subulatum*, as well as a unique photosynthetic haptorid − *Myrionecta rubra*, common for the brackish Baltic Sea (Smetacek, 1981; Boikova, 1984; Witek, 1998; Johansson *et al*., 2004). We identified one brackish tintinnid species *Tintinnopsis kofoidii*, which was not found previously in the Baltic Sea and is not included in the newly updated ciliate list of the Baltic Sea, provided by Telesh *et al*. (2009).

Some brackish/marine species, particularly *Lohmaniella spiralis*, *Lohmaniella* sp. and *L. oviformis* were found both in the oligohaline

and freshwater part of the lagoon. Previous observations of these species were related to higher salinities. *Lohmanniella* sp. was found in the Western Baltic Sea (Kieler Bight) and in the Southern Baltic Sea (Gdansk Basin and North-Rugian Bodden), *Lohmanniella oviformis* – in the Baltic Proper, the Western Baltic Sea (Kieler Bight) and the Eastern Baltic Sea (the Gulf of Finland, including the freshwater Neva Bay) (Telesh *et al*., 2009). *Lohmaniella spiralis* was identified in the Gulf of Riga, particularly at the mouth of the River Dauguva (at the salinity range from 1.04 to 3.94 PSU) and the River Lielupe (the salinity range from 3.14 to 6.35 PSU). *Lohmaniella* sp. was found in the mouth of the River Gauja (the salinity range from 3.14 to 6.35 PSU) (Boikova, 1989). Therefore our findings could extend the knowledge about the distribution range of these species. More detailed eco-taxonomic studies could help to clarify the remaining questions concerning the influence of salinity on the composition of ciliate communities in the future.

The lowest species richness (47 species/higher taxa) were reported from the Nemunas River avandelta. This assemblage contained ciliate taxa, typical for large European rivers: Danube, Rhine and Loire (Lair *et al*., 1999; Scherwass and Arndt, 2005; Kiss *et al*., 2009): *Paradileptus conicus, Hypotrichidium conicum, Holophryra atra, H. hexatricha, Litonotus lamelata, Nassula* sp., *Cyclotrichium limneticum, Staurophrya elegans, Paruroleptus piscis, Frontonia leucas, Paramecium* sp., *Phascolodon vorticella, Staurophrya elegans* and *Nassula* sp. Recently, *Paradileptus conicus* was identified in the River Danube as a possible invasive species (Kiss *et al*., 2009). The lentic ciliate species *Phascolodon contractilis* was not listed in any of the mentioned rivers, possibly because it can be confused with *Phascolodon vorticella* (Mažeikaitė, 2003). *Paruroleptus piscis, Frontonia leucas* and *Litonotus lamelata* were recorded in the Taro River (northern Italy) by Madoni and Zangrossi (2005).

The differences in the species lists from recent and past studies could be explained by different sampling strategy. The substantial mismatch of species from the order Hypotrichida could be explained

by a different sampling strategy (Fig. 14). Integral sampling, used in the earlier surveys by Mažeikaitė (Table 3) enables to catch benthic ciliate species from hypotrichid genera *Euplotes, Aspidisca* and *Oxytricha*. These species tend to aggregate in the near-bottom layer (Telesh *et al*., 2009) and could be hardly found in the surface samples. Additionally, all previous studies in the Curonian Lagoon were based on live ciliate counts. In contrast to fixation methods, it provides the possibility of identifying the species by some taxonomically important characteristics, visible only in live cells: locomotion pattern, shape, color, contractile vacuole. It is well known that fixation and staining of ciliates can lead to reduction of cell numbers (Sime-Ngando *et al*., 1990; Leakey *et al*., 1994) and shrinkage, swelling up to the total cell destruction (Choi and Stoecker, 1989; Dale and Burkill, 1982; Stoecker *et al*., 1994). In the live observations, rare, small and fast moving ciliate species can be overlooked or lumped with other species; moreover, longer transportation or storage time could lead to a loss of species due to changing temperature or water chemistry (Pfister *et al*., 1999). Considering all the reasons stated above, we decided to identify the ciliates by observing both the living and Lugol fixed material to provide comparable data with previous studies in the Curonian Lagoon and other parts of the Baltic Sea.

The Lugol fixation method gave a new insight into nanociliate taxonomic composition, especially to quantitative characteristics: abundance and biomass estimation. Despite comparatively low taxonomic resolution of this method (only 65% of all species were found in Lugol samples), 9 new species/higher taxa were added to the species list due to Lugol fixed samples: *Lohmaniella spiralis, L. oviformis, Lohmaniella* sp., *Strobilidium* spp. (2 species), *Cyclidium* spp. (2 species) and *Urotricha* sp, *Mesodinium pulex*. All the before mentioned species (except for *L. spiralis*), having a small size (<20 μm), were missed in the live material examination in the present and past studies in the Curonian Lagoon (Appendix Table A.1.).

As revealed by fixed material counting, the nano-ciliates (<20 μm) were the most abundant size group, sharing from 8 to 55% of overall

ciliate abundance (35% on average) in Nida site, from 1 to 75% (46% on average) in Smiltyne site, however, they were missed in live material counts. Despite that, the total abundance was significantly higher in Lugol fixed material than in live counts (Fig. 11).

Underestimation of small ciliate species (<30 μm) in live counts was previously reported by Obolkina (2006). It is known that small oligotrichs, such as *Strobilidium* spp. (10 to 45 μm in length) are very sensitive to temperature changes induced by microscope light and lose their motility once exposed for more than 10 min under the microscope light (Sime-Ngando *et al*., 1990). We used the underneath light source, which could cause some temperature increase in the counting chamber. Another reason could be the mortality of species from the genus *Strobilidium* related to the examination in the Bogorov chamber (Boikova, pers. comm.), instead of using a plate with small wells (Dale and Burkill, 1982). Therefore, the combination of live counts and fixed material is essential, since small nano-ciliates, including naked oligotrichs and scuticociliates, are the most productive and numerous in the pelagic ciliate assemblage of the Baltic Sea (Mironova *et al*., 2009).

It could be concluded, that combination of live and Lugol fixed material counts improve the reliability of ciliate taxonomic studies. If the live counting method is applied alone, small nanociliate species could be underestimated, whereas the Lugol fixed material method without live material examination provides poor taxonomic information.

6.2. Abundance and seasonal dynamics of the plankton ciliates

Abundance of ciliates recorded in the Curonian Lagoon fits within the same range as reported in other coastal areas of the Baltic Sea, but is lower comparing to the eutrophic lakes (Table 11).

Total abundance and species diversity of the ciliates tend to decrease significantly with the increasing salinity at the oligohaline part of the Curonian lagoon (Fig. 13). However, the large-scale analysis along the Baltic Sea salinity gradient revealed ciliate species richness maximum at the salinity of 5 to 8 PSU, which is a contrast to the species minimum range in classic Remanes's Artenminimum model (Telesh *et al*., 2011). According to Telesh *et al*. (2011), the possible evolutionary processes have resulted in the species adaptation in the horohalinicum (5 to 8 PSU) of the permanent salinity gradient.

Significant negative salinity effect on the ciliates in the Curonian Lagoon along the same range of salinity could be forced by the spatial and temporal variability of the gradient, which is unfavorable for the formation of stable ciliate assemblage.

Despite the local negative salinity effect, comparison of the abundance of ciliates at freshwater and oligohaline sites did not reveal significant differences during the studied period. It could be influenced by the low number of observations at the salinity of 3–7 PSU; therefore, more detailed analysis of the pattern would be questionable.

The pattern with two maxima of abundance is characteristic for the seasonal dynamics of the freshwater ciliate assemblage in the Curonian Lagoon (Fig. 19). Similar sequence is commonly referred for the eutrophic fresh water bodies (Beaver and Crisman, 1989; Carvick and Fahnenstiel, 1990; Simek and Staskrabova, 1992). The highest ciliate numbers in the lagoon were recorded during late spring peak; this is in good agreement with the data from temperate lakes across the wide trophic spectrum (Laybourn-Parry, 1992). In some eutrophic lakes the maximum of ciliate abundance was determined in

late summer (Schonberger, 1994; Zingel, 1999). In freshwater and estuarine parts of the Neva Estuary (1–5 PSU) the only autumn ciliate maximum was recorded, probably due to relatively long sampling intervals (2 weeks) enabling to miss late spring peak (Mironova *et al*., 2011).

Table 11. Published data on ciliate abundance and biomass in various regions of the Baltic Sea and freshwater lakes

Area	Salinity (PSU)	Abundance ($\times 10^3$ ind.L^1)	Biomass (μg CL^{-1})	Source
Neva Estuary (oligohaline site)	1–5	0.1–10.3	0.1–40.7	Mironova et al. (2011)
Neva Estuary (freshwater site)	0	0.1–8	0.1–53.3	
Gdansk Basin	7.5–12	0–28	0–23	Witek (1998)
Kiel Bight	13–20	2–92	0–56	Smetacek (1981)
Open Baltic Sea		0–9	0–20	Johansson et al. (2004)
Lake Pavin, France (oligo-mesotrophic)	0	5–31	-	Carrias et al. (2001)
Lake Vortsjarv, Estonia (eutrophic)	0	0.6–191	0.8–448	Noges et al. (1998)
Curonian Lagoon	0	2.4–73.0	4.1–52.7	This study
	0–7	0.9–91.7	0.9–88.3	This study

According to the relative abundance of dominant/common ciliate species four seasonal phases were distinguished in the freshwater part

of the Curonian Lagoon: winter, early spring, late spring and summer/autumn (Fig. 20). Similar seasonal phases were described in the plankton ciliate assemblage of the meso-eutrophic lake Constance (France) (Muller *et al*., 1991): spring, late spring (clear water phase), summer/autumn and winter with low ciliate abundance in the clear water phase and winter. The main difference is that clear water phase is less pronounced in the Curonian Lagoon. The details will be discussed later.

During the early spring phase the relative abundance of algivourus tintinnids decrease, comparing to the winter phase. However, abundance of pico-nano fraction feeders increase, namely, small prostomatids (*Urotricha* sp.; <25µm; raptorial feeder) and naked oligotrichs (*Halteria* sp., *Lohmaniella* sp., *Strobilidium* spp.) (Fig. 21). Consequently, the size structure of this seasonal group shifts to the dominance of smaller groups and nanociliates, which compose around 40% of total abundance (Fig. 22a). The increase of *Urotricha* sp. in early spring is common and could be related to small cryptophytes as their main food source (Müller *et al*., 1991; Weisse and Müller, 1998). Increase of cryptophytes was also registered in the Curonian lagoon during April (Olenina, unpub. monitoring data). In Lake Constance this phase is characterized by increase of small algivourus prostomatids and large or medium size oligotrichs which respond to spring phytoplankton bloom (Muller *et al*., 1991). Small numbers of large and medium size oligotrichs in the Curonian Lagoon during early spring phase could be related to the dominance of pico-nano fraction in the phytoplankton assemblage and thus better feeding conditions for smaller ciliate taxa.

Late spring phase starts with the diatom-dominated phytoplankton bloom at the beginning of May. Decrease of the chlorophyll *a* concentration follows at mid of May until beginning of June with simultaneous increase of the abundance of cyanobacteria and cryptophytes (Fig. 8). Abundance of the ciliates and rotifers increases immediately after the phytoplankton peak, while the abundance of metazooplankton (Cladocera and Copepoda) remains

low (Fig. 9). Ciliate assemblage is dominated by the medium size algivourus tintinnids *Tintinnopsis* sp.; rotifers are composed by herbivorous *Keratella quadrata* and *Conochilus unicornis*. Increasing abundance of medium size-large algivourus tintinnids following diatom bloom in late spring is observed in many mesotrophic and eutrophic temperate freshwater lakes and even brackish Baltic Sea (Johanson *et al*., 2004).

RDA plot shows clear correlation of nano-filterers (mainly *Tintinnopsis* sp.) with late spring season and green algae whereas diatoms and rotifers are less important (Fig. 23). It is known, that nano-sized green algae can serve as a food for large oligotrichs (Beaver and Crisman, 1989).

It is evident that late spring phytoplankton production is mainly utilized by small grazers (ciliates and rotifers) while plankton crustaceans become dominant grazers later in the middle of July (Fig. 9, appendix table A.2).

In Lake Constance the late spring phase (clear water phase, CWP) is characterized by the low ciliate abundance and increasing metazooplankton abundance, particularly cladocerans, consuming ciliates intensively (Muller *et al*., 1991). Zingel (1999) found ciliate collapse at the beginning of June in eutrophic Lake Vortsjarv (Estonia), this also coincide with the start of cladoceran development and increase of other metazooplankton groups.

Clear water phase is a common phenomenon in temperate meso- and eutrophic lakes and typically characterized by low algal biomass and excessive grazing of metazooplankton, in particular daphniids (Sommer *et al*., 1986). According to the long term data analysis from the Lake Constance (Tirok and Gaedke, 2006) CWP occurs regularly between mid-May and the beginning of June. The onset of the CWP in Lake Constance was defined when at least two or three of four criteria occur: high Secchi depth (≥6 m); low algal biomass (≤ 1000 $mgCm^{-2}$), low chlophyll a concentration (≤4 μgL^{-1}) and dominance of Cryptophyceae (≤50% of total algal biomass) (Tirok and Gaedke,

2006). In some years CWP was attributed to strong grazing by daphniid-dominated zooplankton assemblage, while in the rest years by a diverse assemblage of micro- and mesozooplankton (mainly ciliates and rotifers). It depended on the vertical mixing intensities in early spring. Less mixing enabled early growth of phytoplankton, ciliates and rotifers, despite low temperature and due to intense grazing of ciliates and rotifers increased non-edible phytoplankton abundance, wich in turn prevented development of daphniids (Tirok and Gaedke, 2006).

In the Curonian Lagoon CWP was described previously as a transition phase between the spring and summer phytoplankton groups (in May), characterized by low silica and phosphate concentrations, limiting diatoms and green algae groups dominating the phytoplankton assemblage at this time (Pilkaitytė and Razinkovas, 2007). Top-down interactions during this phase were not investigated. Moderate clear-water phase could be defined in this study also from beginning to mid-June, characterized by the decrease of chlorophyll *a* (half reduction comparing to the peak values), increased number of cryptophytes (from 8 to 30%) and slight increase of Secchi depth (from 60 to 80 cm). Ciliates and rotifers could be responsible for initiation of this phase, because the abundance of cladocerans was low (Fig. 9), possibly pressed by high numbers of predaceous *Leptodora kindtii* (Lesutiene *et al*., 2011). It is known that despite high grazing pressure of ciliates and rotifers on phytoplankton in spring, they alone are not capable to graze the phytoplankton to a low (clear water) level, because they feed selectively on small phytoplankton (Verity, 1991). CWP is observed only when herbivores grazing on larger forms develop as well (Tirok and Gaedke, 2006). It could explain the moderate clear water phase in the Curonian Lagoon.

The collapse of micrograzers coincide with the lowest dissolved oxygen concentration (5.48 mg O_2/l), which indirectly indicates bacterial consumption of decaying organic matter. After the collapse the sharp increase of bacterivorous ciliates in second week of June is observed. Ciliates dominate by naked oligotrichs, mainly *Halteria* sp.,

which is known as typical bacterial consumer (Sanders *et al*., 1989; Simek *et al*., 1995). This shift from dominance of grazers towards dominance of bacterivores could be defined as transition to the summer dynamics phase.

Summer/autumn phase is characterized by increased taxonomical and functional diversity of ciliates (Fig. 21, 22); it points to exploitation of wide size range of food.

Small sized naked oligotrichs (pico-nano fraction feeders) and peritrichs (mainly pico-fraction feeders) were abundant in summer. The abundance of small bacterivorous scuticociliates was low; they shared from 2 to 8% of total abundance. Prevalence of this group is related to the trophic status of the water basin, since they prefer eutrophic conditions (Beaver and Crisman, 1982). Although, Muller *et al.* (1991) found low (<2% of total) abundance of scuticociliates in the Lake Constance during all seasons. He explained that taxa belonging to this group tend to concentrate near oxycline, were bacterial productivity is high, while upper 20 m water layer of Lake Constance was fully oxygenated during all seasons and abundance of scuticociliates was low. Zingel (1999) in Lake Vortsjarv found moderate numbers of this group representatives; they shared from 4 to 22% of total abundance in different study years.

Increase of the temperature during the summer together with simultaneous bacteria peak determines predominance of small nano-ciliates (20–30 μm; pico- and pico-nano feeders). RDA plot shows clear correlation of pico-filterers with temperature and bacteria as well as correlation of pico-nano filterers with bacteria (Fig. 23). These fractions were dominant in Neva Estuary during the summer, when small ciliates (20–30 μm) composed 7–87 % of total abundance and nano-ciliates can share up to 53% (Mironova et al. 2011). Taxonomic composition of small fractions was quite similar to the Curonian Lagoon: *Strobilidium, Halteria, Lohmaniella, Mesodinium pulex* and *Cyclidium* spp.

Attached peritrichs (*Vorticella microstoma* and *V. anabaena*) were related to the cyanobacteria dominance during this phase. Omnivorous ciliates (mainly *Mesodinium pulex*) become important in autumn (Fig. 22b). *Mesodinium pulex* and cryptophyte abundance increases simultaneously. RDA plot shows omnivores correlation with summer/autumn season, as well as with cryptophytes (Fig. 23). It is known that *Mesodinium pulex* ingests a variety of prey cells including cryptophytes, dinoflagellates and ciliates (Dolan and Coats, 1991; Jakobsen *et al*., 2006).

No negative correlation was found between ciliate and metazooplankton abundance (Fig. 23) suggesting no pronounced top-down effect on ciliate seasonal dynamics. During the maximum production of plankton crustaceans in the middle of summer, ciliate production is quite high as well (Fig. 9, 19).

Winter phase is characterized by the dominance of large and medium size algivourus (nano-fraction feeders) tintinnids: *Tintinnidium pusillum* and naked oligotrichs *Strobilidium* spp. (pico-nano feeders) (Fig. 21, 22a). Metazooplankton was composed mainly by juvenile stages of copepods (nauplii, copepodits) and low number of adults of *Mesocyclops leuckarti, Eudyapthomus graciloides* and *Cyclops* sp. Phytoplankton growth is not nutrient limited during winter and early spring, but the abundance is low due to the low temperature and light (Pilkaitytė, 2003; Pilkaitytė and Razinkovas, 2007). Ciliate abundance and biomass was low due to physical conditions and decreased food recourses. Tintinnids are relatively abundant, due to their ability to feed on larger phytoplankton cells. The same winter seasonal pattern of plankton ciliates is observed in other water basins (Laybourn-Parry, 1992; Zingel, 1999; Muller *et al*., 1991; Mironova et *al*., 2011).

Summary and comparison with PEG model (Sommer et al., 2012). General scheme of the ciliate seasonal dynamics in the freshwater part of the Curonian lagoon is provided in Fig. 29. Seasonal dynamics of ciliates follows the model of temperate eutrophic water body with bimodal biomass distribution (spring and

summer peaks) predicted by Sommer *et al*. (2012). During the winter time ciliate growth is limited by low biomass of phytoplankton. In the early spring, when small size phytoplankton prevails, ciliate assemblage is dominated by small pico-nano feeders: naked oligotrichs and prostomatids, which are more vulnerable to metazooplankton predation. After the late spring diatom bloom, ciliate assemblage shifts to medium sized nano-filterers (tintinnids). At the same time rotifers increase in number; they possibly feed on the same nano-fraction of phytoplankton or/and heterotrophic flagellates (they weren't evaluated in this study) as ciliates. Phytoplankton abundance starts to decrease from end of May to the mid-June (moderate CWP). During CWP ciliate became food limited; the strongest predation by metazooplankton (especially cladocerans *Daphnia* sp.) is expected at this time according the PEG model. However, cladoceran abundance and biomass is low in the lagoon at this time and the top-down effects are hardly possible. The dominance of bacterivorous ciliates, such as *Halteria* sp. and *Lohmaniella* sp., indicates the shift from algal food to bacteria.

Functional and taxonomic diversity of ciliates increases toward the summer: they include all functional groups (grazers, bacterivores and omnivores). Metazooplankton production and consumption exceeds ciliate production and consumption; metazooplankton possibly feeds on ciliates, but the top-down interactions are moderate, as predicted in PEG model.

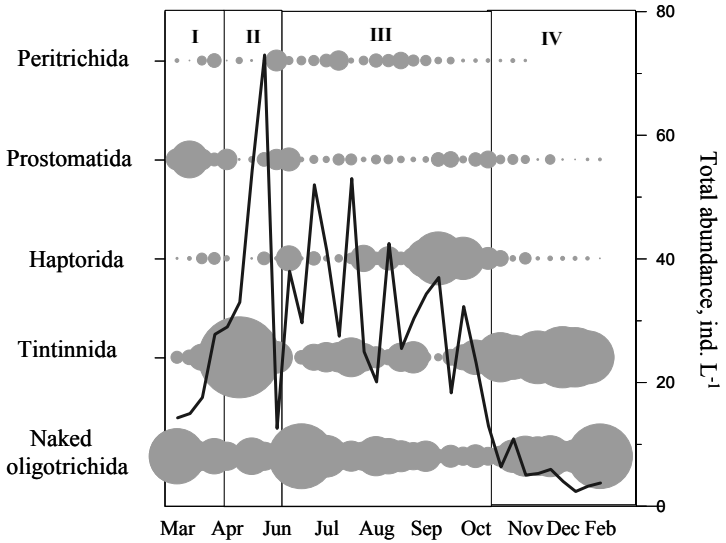

Fig. 29. Generalized scheme of the seasonal dynamics of plankton ciliates in the Curonian Lagoon (I – early spring, II – late spring, III –summer/autumn, IV – winter). The size of the spheres represents the percentage of the total abundance.

Generally, the ciliate seasonal dynamics in the Curonian Lagoon correspond to the PEG model quite well, except the weak top-down effect of metazooplankton on heterotrophic protists resulting in moderate CWP.

6.4. Ciliates as phytoplankton grazers

Over the past three decades many dilution experiments have been performed to examine the grazing impact of microzooplankton in various waters all around the world, ranging from the open sea to coastal zone and estuaries (data reviewed by Landry and Calbet, 2004). However, for the freshwater environments dilution technique

was applied to the less extent (Moats, 2006; Galford and Sterner, 2000; Davis *et al*., 2012; Twiss *et al*., 2012). This relatively simple and standard technique is useful for comparative microzooplankton grazing rate studies among the geographic regions as well as time series of ecological processes (Gallegos, 1989).

The selective grazing pressure i.e. grazing of ciliates on different size fractions of phytoplankton is becoming an important issue, especially in coastal regions, where the faster grazing on small size fraction of phytoplankton, called Fast-Growing-Low-Biomass, is observed (Sun *et al*., 2007). Different size fractions of phytoplankton have specific responses to nutrient and grazing effects. Larger phytoplankton has lower maximum specific growth rates at resource (light, nutrient) saturation than do smaller phytoplankton in the same phylogenetic group (Gatham and Rhee, 1981). Therefore picophytoplankton should have an advantage under nutrient-limiting conditions due to their advantageous surface area to volume ratio (Raven, 1998). However, the phytoplankton responses to grazing in the dilution experiments is frequently masked by extremely abundant large phytoplankton fraction, not suitable for grazers, which is frequently dominant in the coastal eutrophic waters (Galegos *et al*., 1996). Therefore, the size-fractioning is suggested in coastal and estuarine areas, where major component of the total assemblage biomass is comprised by a large phytoplankton fraction, whereas small fraction is less abundant, but can have relatively higher turnover rates and contribute significantly to the secondary production of microzooplankton (Galegos *et al*., 1996).

The significant estimates of ciliate grazing rates of phytoplankton pico- and nano- fractions were obtained at Nida and Smiltynė sites. Grazing rates exceeded growth rate of phytoplankton fractions ($g>k$), suggesting that phytoplankton production and biomass accumulation is controlled by microzooplankton, as it was frequently observed by other authors (Burkill *et al*., 1987; McManus and Ederinger-Cantrell, 1992; Verity *et al*., 1993; Landry *et al*., 1995; Lehrter *et al*., 1999).

The grazing rate of pico-fraction at Nida site is in the range reported in the Cheasapeake and Delaware Bays (Table 12). Ciliates consumed 76% of potential picophytoplankton production at this freshwater site. However due to several important methodological aspects and violation of assumption on consistent nutrient concentrations during the experiment course, the obtained numbers should be interpreted with caution.

The significant difference of the nutrient concentration between the filtered and non filtered lagoon water at the start of the experiment at Nida site possibly occurred due to: 1) the time lag in water sampling and consequent differences in the nutrient concentrations in different water masses; 2) bacterial contamination and nutrient uptake could have started in the particle free water (**FW**), before the start of the experiment, because of long process of filtration (20 h). Bacterial consumption could be also responsible for complete depletion of NO_2+NO_3 concentration after 24 h incubation in all treatments (Fig. 24).

It is known that nitrates appear to be a primary limiting factor in dilution experiments (Landry and Hassett, 1982). However, despite the nutrient depletion during the incubation and different nutrient concentrations among the treatments, the changes in pico-fraction at Nida site provided statistically significant estimates of grazing rate (g) and growth rate (k). These estimates are realistic as compared to other sites (Table 12). In contrast, no reliable results were obtained for nano-fraction. This could be explained by allometry of phytoplankton metabolic and growth rates, which suggest that smaller cells are more resistant to nutrient depleted conditions than larger cells (Raven and Kübler, 2002). Moreover, the dominance of small size fractions (<20 and 20–30 μm) (Fig. 23) in the freshwater site suggests that predation on the picophytoplankton fraction can be high, but is should be tested visually by observing autotrophic pico-fraction cells via epifluorescence microscopy. In addition, as pointed by Dolan *et al.* (2000), shift in grazer assemblage can occur in favor of starvation-resistant grazers, which can feed selectively on particular fraction of

phytoplankton. Ideally, grazer assemblage structure and quantitative parameters should be checked not only at the beginning of the experiment, but after as well.

Table 12. Published results of micrzooplankton grazing in other regions. Growth rates of the phytoplankton pico- and nano-fractions (k, day^{-1}) and microzooplankton grazing rates (g, day^{-1}), P_p – potential consumption of primary production (%).

Location	Salinity (PSU)	Fraction (μm)	k	g	P_p	N	Reference
Curonian Lagoon	0	0.2–2	1.33	1.83	76	1	This study
	7	2–20	0.92	1.52	130	1	
Chesapeake Bay	20	0.2–2	2.10	1.92	97	1	Sun *et al*. (2007)
		2–20	0.61	0.41	73		
Delaware Inland Bay	15	0.2–2	2.05	0.7	58	1	
		2–20	0.81	0.77	97		
Delaware Bay	16	0.2–2	1.83	1.78	99	1	
		2–20	0.84	0.32	48		
Gulf of Alaska	?	<5	0.42	0.48 (0.02-1.07)	102 (±29)	39	Strom *et al*. (2007)
		5–20	0.34	0.39 (0.05–0.92)	102 (±32)		
Manukau estuary (New Zeland)	28–33	<5	0.2–1.8	0.3–1.3	30-230	12	Gallegos *et al*. (1996)
		5–22	0.2–1.75	0–0.8	0-98		
Upper St. Lawrence river	?	0.2–2	0.2–1.8	0–1.1	-	12–38	Twiss and Smith (2011)
		2–20	0.1–1.3	0–1.2	-		

The grazing rate of nano-fraction at Smiltyne site exceeds grazing rates in other estuarine ecosystems by 2–3 folds (Table 12). Ciliates consumed 130% of nanophytoplankton production at brackishwater site. It is not surprising as nanophytoplankton chlorophyll *a* concentration was 30 fold (Table 6) higher than picophytoplankton

chlorophyll *a* and ciliate assemblage was dominated by medium sized ciliates, composed by large naked oligotrichs *Strombidium styliferum, S. conicum* and tintinnid taxa *Tintinnopsis* sp.; all of them prefer to feed on small nano-sized algae (Stürder-Kypke *et. al.*, 2000). Potential pico-fraction feeders (nano-ciliates) shared only 14% of total abundance in this site (Fig. 23). Gallegos *et al.* (1996) used dilution technique combined with size fractioning and found, that the highest grazing rates of phytoplankton fraction of 5–22 μm coincide with tintinnid abundance increase in ciliate assemblage.

The tendency of higher consumption rates is usually reported in dilution experiments where nutrients are not added (Landry and Hassett, 1982). Adding of nutrients is recommended at the start of the experiment to keep the phytoplankton growth unlimited (Gallegos, 1998; Landry *et al*., 1995). In this study, no additional nutrient was added, assuming high rates of N and P loading in the Curonian Lagoon during autumn, when experiments were conducted (Table 1) and to avoid increased mortality of delicate protists during experiments (Landry and Hassett, 1982; Gilfford, 1988).

7. CONCLUSIONS

1. 100 species/higher taxa of the ciliates were identified in the Curonian lagoon. The lowest species richness (47 species/higher taxa) were reported from the Nemunas River avandelta. Highest species number (76 species/higher taxa) was found in the oligohaline part of the lagoon due to temporally unstable salinity and the presence of both freshwater and brackish/marine species in ciliate assemblage. Six of the brackish/marine species (*Tintinnopsis baltica, Tintinnopsis kofoidi, Cothurnia maritima, Lohmaniella oviformis, Lohmaniella spiralis* and *Helicostomella subulatum*) were recorded for the first time in the Curonian lagoon.

2. Combination of live and Lugol fixed material counts improve the reliability of ciliate taxonomical studies. In contrast to fixed material counts, the live counting method leads to the underestimation of small nanociliate species and can be applied only for qualitative analysis.

3. Salinity increase above 4 PSU leads to 1.6 fold decrease of biodiversity (H' index), 2.5 fold decrease of total abundance and 3 fold decrease in relative abundance of nano-ciliates (<20μm).

4. Seasonal dynamics of plankton ciliates in the Curonian Lagoon is typical for the meso-eutrophic and eutrophic lakes. Two maxima of the abundance and biomass were observed and four seasonal phases can be distinguished according to the structure of ciliate community: winter, early, late spring and summer/autumn.

5. Dilution experiment approach revealed significant ciliate grazing effect on nano-fraction of phytoplankton in the brackish water, and pico-fraction in the freshwater community. This pattern is related to the differences in ciliate community size structure:

larger nano-filterers dominate in the brackishwater assemblages, whereas pico-nano filterers prevail in the freshwaters.

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Apendix, Table A.1. Taxonomic list of plankton ciliates found in the Curonian Lagoon. Capital letters denote months. (N-ciliate species/taxa identified in the Nemunas River avandelta)

Taxa/Species	1975-2001[a]	2007-2008[b] Other st.	2007-2008[c] Smiltyne M	A	M	J	J	A	S	O	N	D	J	F	Nida M	A	M	J	J	A	S	O	N	D	J	F
Haptorida																										
Actinobolina vorax Wenrich, 1929	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Askenasia faurei Kahl, 1930	+	+ (N)	-	+	+	+	+	+	-	+	-	+	-	+	-	+	+	+	+	+	+	+	+	+	+	+
Askenasia volvox Eichwald, 1852	+	+ (N)	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+
Cyclotrichium gigas Fauré-Fremiet, 1924	+	-	-	-	-	-	-	+	-	+	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-
Cyclotrichium limneticum Kahl, 1935	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyclotrichium sphaericum Fauré-Fremiet, 1924	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Didinium nasutum (O. F. Müller,1773)	+	+ (N)	-	-	-	+	+	+	-	+	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-
Didinium sp.	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Dileptus cygnus (Claparède et Lachmann, 1859)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dileptus gigas (Claparède et Lachmann, 1859)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dileptus sp.	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Enchelys pupa (O. F. Müller,1786)	-	+ (N)	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-
Lacrymaria sp.	-	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	-	-	-	+	-	-	+	+	+	-
Mesodinium acarus Stein, 1863	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesodinium pulex (Claparède et Lachmann, 1859)	+	+ (N)	-	-	+	+	+	+	+	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+
Myrionecta rubra Jankowski, 1976	+	+	-	+	+	+	+	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Monodinium arnatum (Penard, 1922)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monodinium balbianii Fabré-Domergue, 1888	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	+	+	+	-	+	+	-	+	-	+
Monodinium balbianii var. nanum Kahl, 1930	+	+ (N)	-	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monodinium balbianii var. rostratum Kalh, 1926	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Monodinium sp.	-	+ (N)	-	+	+	+	-	+	+	+	-	+	-	+	-	+	+	+	+	+	+	+	+	-	-	-
Paradileptus conicus Wenrich, 1929	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paradileptus elephantinus (Sveç, 1897)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spathidium sp.	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teuthophrys trisulca Chatton et Beauchamp, 1923	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachelius ovum (Ehrenberg, 1831)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trachelophyllum sigmoides Kahl, 1926	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heterotrichida																										
Condylostoma vorticella (Ehrenberg, 1833)	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Metopus spiralis Smith, 1897	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Metopus striatus McMurrich, 1884	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spirostomum minus Roux, 1901	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spirostomum teres Claparède et Lachmann, 1858	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Stentor coeruleus (?allas, 1766)	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stentor niger (O. F. Müller,1773)	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stentor roeseli Ehrenberg, 1835	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Oligotrichida																										
Codonella cratera (Leidy, 1877)	+	+ (N)	+	+	+	+	+	+	+	+	-	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Codonella relicta Minkiewitch, 1905	+	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halteria grandinella (O. F. Müller,1773)	+	+ (N)	-	-	+	+	+	+	+	-	-	+	-	-	-	-	+	+	+	-	+	+	-	+	+	-
Halteria sp.	-	+	+	+	+	-	-	-	-	+	-	-	-	+	+	+	+	-	-	+	-	-	-	-	-	-
Helicostomella subulatum (Ehrenberg, 1833)	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lohmaniella oviformis Leegaard, 1915	-	-	-	+	+	-	+	-	+	+	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-	-
Lohmaniella sp.	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
Lohmaniella spiralis Leegaard, 1915	-	-	+	-	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
Salpingella acuminata Claparède et Lachmann, 1858	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strobilidium gyrans Stokes, 1887	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Strobilidium humile Penard, 1922	+	+ (N)	-	+	+	+	+	+	+	+	-	-	-	-	+	-	-	+	+	+	+	+	+	-	-	-
Strobilidium spp. (2 species)	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Strobilidium velox Fauré-Fremiet, 1924	+	+ (N)	+	-	+	+	+	+	+	+	+	+	-	+	-	-	+	+	+	+	+	+	+	+	+	-
Strombidium conicum Lohmann, 1908	+	+	-	+	-	+	+	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strombidium sp.	-	+ (N)	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	+	+	+	+	+	-	-	-	+
Strombidium styliferum Levander, 1894	+	+	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strombidium viride Stein, 1859	+	+ (N)	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+
Strombidium viride f. pelagica Kahl, 1932	+	+ (N)	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+
Tintinnidium fluviatile Stein, 1863	+	+ (N)	-	+	+	+	+	-	+	-	-	-	-	-	-	-	+	+	+	-	+	+	-	-	-	-
Tintinnidium fluviatile f. cylindrica Gajewskaja, 1933	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tintinnidium pusillum Entz, 1909	+	+ (N)	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tintinnopsis baltica Brandt, 1896	-	+	-	+	+	+	+	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Tintinnopsis cylindrata Kofoid et Campbell, 1892	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
*Tintinnopsis kofoid*i Hada, 1932	-	+	-	+	-	+	+	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Tintinnopsis sp.	-	+ (N)	-	+	+	+	+	+	+	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+	+	-
Tintinnopsis tubulosa Levander, 1900	+	+ (N)	-	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Peritrichida																										
Carchesium pectinatum (Zacharias, 1897)	+	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Cothurnia maritima Ehrenberg, 1838	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epistylis anastatica Linnaeus, 1767	+	+	-	-	+	-	-	+	+	-	-	-	-	-	-	-	+	+	+	-	+	+	+	-	-	+
Epistylis plicatilis Ehrenberg, 1831	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epistylis rotans Sveç, 1897	+	+ (N)	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	+	+	+	+	-	-	-	-	-
Plagiophyla nasuta Stein, 1860	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhabdostyla cyclopis Kahl, 1935	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhabdostyla pyriformis Perty, 1852	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaginicola crystallina Ehrenberg, 1830	+	+ (N)	-	-	+	-	-	-	-	-	+	-	-	-	-	+	+	-	+	+	-	+	-	-	-	-
Vaginicola ingenita (O. F. Müller,1786)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Vorticella anabaena Stiller, 1940	+	+	-	-	+	+	-	+	+	-	-	-	-	-	-	-	+	+	-	+	-	-	-	-	-	-	
Vorticella campanula Ehrenberg, 1831	+	+ (N)	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	
Vorticella mayeri Fauré-Fremiet, 1920	+	+ (N)	-	+	+	-	-	-	-	-	+	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	
Vorticella microstoma Ehrenberg, 1830	+	+ (N)	-	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	-	-	+	
Vorticella natans (Fauré-Fremiet, 1924)	+	+ (N)	+	+	-	-	+	+	+	+	-	-	-	-	-	+	-	+	+	+	+	+	-	+	-	-	
Vorticella sp.	-	+ (N)	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	
Vorticella sphaerica d'Udekem, 1864	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Zoothamnium simplex Kent, 1881	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pleurostomatida																											
Amphilepthus trachelioides (Zacharias, 1894)	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-	-	-	
Litonotus fasciola O. F. Müller,1773	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Litonotus lamelata O. F. Müller,1773	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Litonotus sp.	-	-	-	-	-	-	-	+	+	+	+	-	-	-	-	+	+	-	+	+	+	+	-	-	-	-	
Loxophyllum meleagiris O. F. Müller,1773	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Loxophyllum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	
Loxophyllum utricullariae (Penard, 1922)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Scuticociliatida																											
Cyclidium oblongum Kahl, 1831	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cyclidium spp. (2 species)	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Loxocephalus luciaus Smith, 1897	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pleuronema coronatum Kent, 1881	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Uronema marinum Dujardin, 1841	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hypotrichida																											
Aspidisca coastata (Dujardin, 1842)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Euplotes affinis (Dujardin, 1841)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Euplotes charon O. F. Müller,1786	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Euplotes patella (O. F. Müller,1773)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

Euplotes patella f. planctonicus Kahl, 1935	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypotrichidium conicum Ilowaisky, 1921	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holosticha scutellum Cohn, 1866	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paruroleptus piscis (Kowalewski, 1882)	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stichotricha aculeata Wrzesniowski, 1866	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strongylidium lanceolatum Kowalewski, 1882	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tachysoma sp.	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Uroleptus sp.	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urostyla grandis Ehrenberg, 1830	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prostomatida																											
Bursellopsis spumosa (Schmidt, 1920)	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Coleps amphacantus Ehrenberg, 1833	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleps elongatus Ehrenberg, 1830	+	+ (N)	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleps hirtus (O. F. Müller,1773)	+	+ (N)	-	+	+	+	+	+	+	+	+	+	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+
Coleps hirtus subsp. viridis Ehrenberg, 1831	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleps hirtus var. lacustris Fauré-Fremiet, 1924	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coleps hirtus var. minor Kahl, 1930	+	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Coleps spetai Foissner, 1984	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Holophrya atra Sveç, 1897	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holophrya hexatricha Savi, 1913	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Holophrya nigricans Lauterborn, 1894	+	+ (N)	+	+	+	+	+	+	+	+	-	-	-	-	+	+	+	+	+	+	+	+	-	-	-	-	-
Holophrya simplex Schewiakoff, 1893	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prorodon discolor (Ehrenberg, 1831)	+	-	+	-	-	+	-	-	-	-	-	-	-	+	+	+	-	+	-	-	+	-	-	-	-	-	-
Prorodon ovum (Ehrenberg, 1830)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Undet. (2 species)	-	+ (N)	-	+	+	+	+	+	+	+	-	-	-	-	-	+	+	+	+	+	+	+	+	+	-	-	-
Urotricha farcta Claparède et Lachmann, 1859	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urotricha pelagica Kahl, 1935	+	+ (N)	+	+	+	+	+	+	+	+	-	+	-	+	+	+	+	+	+	+	+	-	-	-	-	-	-

Urotricha sp.	-	-	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
Hymenostomatida																										
Colpidium camphylum (Stokes, 1886)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Espejoia mucicola (Penard, 1922)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frontonia leucas (Ehrenberg, 1833)	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frontonia marina Fabre-Domergue, 189	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frontonia sp.	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	+	-	-	-	-	-	+	-	-	-	-
Lembadion bullinum (O. F. Müller,1786)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lembadion lucens (Maskell, 1887)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Marituja pelagica f. minor Mažeikaitė, 1971	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marituja pelagica Gajewskaja, 1928	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Ophryoglena flava Ehrenberg, 1833	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paramecium caudatum Ehrenberg, 1833	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paramecium sp.	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stokesia vernalis Wenrich, 1929	+	+ (N)	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Cyrtophorida																										
Chilodonella cucullulus O. F. Müller,1786	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Phascolodon contractilis Kahl, 1926	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Phascolodon vorticella Stein, 1959	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Suctorida																										
Actineta papillifera Keppen, 1888	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Podophyra fixa (O. F. Müller,1773)	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphaerophrya magna Maupas, 1881	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Staurophrya elegans Zacharias, 1893	+	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tokophrya sp.	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Colpodida																										
Colpoda steinii Maupas, 1883	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Bursaria truncatella O. F. Müller,1773	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bursaridium dificile Kahl, 1927	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontostomatida[a]																											
Saprodinium dentatum Lauteborn, 1908	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nassulida																											
Nassula aurea Ehrenberg, 1833	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nassula sp.	-	+ (N)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total number	**110**	**66 (N47)**	**22**	**42**	**43**	**43**	**43**	**40**	**42**	**38**	**28**	**26**	**16**	**21**	**20**	**36**	**42**	**41**	**38**	**36**	**38**	**35**	**26**	**23**	**19**	**20**

[a] Mažeikaitė (2003)
[b,c] This study

Apendix, Table A.2. Seasonal changes of net production (μg C $L^{-1}d^{-1}$) and carbon consumption (μg C $L^{-1}d^{-1}$) of secondary consumers (ciliates and metazooplankton) in freshwater Nida site

Secondary consumers	Net production (μg C $L^{-1}d^{-1}$)				Carbon consumption (μg C $L^{-1}d^{-1}$)			
	Early spring	Late spring	Summer/ autumn	Winter	Early spring	Late spring	Summer/ autumn	Winter
Ciliates								
Tintinnida	3.2	11.6	10.5	0.3	10.7	38.8	35.1	0.96
Naked oligotrichida	3.0	7.5	8.6	0.2	10.1	25.1	28.6	0.69
Peritrichida	0.99	2.8	8.23	0.02	3.3	9.2	27.4	0.05
Prostomatida	1.9	5.0	3.4	0.03	6.3	16.6	11.2	0.09
Haptorida	0.9	4.1	4.5	0.03	2.9	13.7	14.9	0.11
Others	0.6	3.1	1.6	0.04	2.2	10.2	5.4	0.12
Total ciliates	**10.62**	**34.1**	**36.8**	**0.62**	**35.4**	**113.7**	**123.6**	**2.03**
Metazooplankton								
Rotatoria	0.3	7.5	1.3	0.02	1.0	24.9	4.4	0.06
Cladocera	0.05	1.8	17.2	0.18	0.16	6.1	57.4	0.60
Copepoda	1.7	16.9	23.5	1.7	5.5	56.2	78.4	5.7
Total metazooplankton	**2.0**	**26.2**	**42.1**	**1.9**	**6.7**	**87.2**	**140.3**	**6.3**

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Daktaro disertacija

Klaipėda, 2012

SL 1335. 2012 12 19. Apimtis 7,75 sąl. sp. l. Tiražas 15 egz.
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