BALTIC COASTAL ZONE
Journal of Ecology and Protection of the Coastline

Vol. 21 pp. 233-244 2017

ISSN 1643-0115

Original research paper

Received: 23/05/2017
Accepted: 23/10/2017

IMPORTANCE OF TINTINNIDS AND *MESODINIUM RUBRUM* IN COMMUNITIES OF PLANKTONIC CILIATES IN THE SHALLOW BRACKISH LAKES GARDNO AND ŁEBSKO (NORTHERN POLAND)

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Abstract

Ciliates constitute an important trophic link in aquatic environments, because they are essential food sources for zooplankton and fish. In this study, the spatial differences in abundance and composition of ciliate communities in relation to varying water salinity were investigated. The study was conducted in the large, brackish, eutrophic lakes Gardno and Łebsko. In the studied lakes, no significant differences among ciliate communities were identified among sampling sites. Ciliate communities in Lake Łebsko were characterized by a high contribution of tintinnids, with mean values at particular sites between 32% and 36%. In Lake Gardno, where salinity was lower, the importance of tintinnid ciliates increased after a marine water intrusion into the lake. In both lakes, the importance of tintinnids in ciliate communities was higher than in adjacent fresh and marine waters. Shortly after wind-driven intrusions of marine waters (backwaters), the marine and brackish mixotrophic ciliate *Mesodinium rubrum* was observed in both lakes. Once, in the eastern part of Lake Łebsko, *Mesodinium major* (= *Mesodinium rubrum forma major*) was observed after a strong backwater when salinity reached 5.4 PSU.

Key words: protozoa, protists, *Myrionecta rubra*, *Mesodinium major*, distribution, salinity, eutrophic

INTRODUCTION

Ciliates are protists that are common in aquatic environments. They graze on bacteria and other protists (protozoa and algae) and are an important food source for zooplankton and fish (recent review in Rakshit et al. 2014, Rychert et al. 2016). Thus, ciliates constitute an important trophic link in aquatic environments. Their abundance corresponds to the trophic status of a water body (Beaver and Crisman 1982, Pfister et al. 2002, Rychert et al. 2016), whereas their community composition depends on both trophic status and the type of the water body, e.g. freshwater lake, brackish lake, peat pond, etc. (Beaver and Crisman 1982, Pfister et al. 2002). In brackish waters, both freshwater and marine ciliates are observed, and their abundance might be elevated, because, in comparison to freshwater lakes of the same trophic status, the grazing pressure of mesozooplankton in these lakes might be reduced (Pfister et al. 2002, Urrutxurtu et al. 2003, Rakshit et al. 2014). In large water bodies, the salinity gradient can result in differences among ciliate communities observed in different parts of water body (e.g., Urrutxurtu et al. 2003).

The aim of this study was to assess the spatial distribution of abundance and composition of ciliate communities in the brackish lakes Gardno and Łebsko. Both lakes are large (Lake Gardno – 25 km^2, Lake Łebsko – 71 km^2, Jańczak 1997), shallow (Lake Gardno – 1.2 m, Wielgat-Rychert and Rychert 2017; Lake Łebsko – 1.6 m, Jańczak 1997), and eutrophic (Jarosiewicz 2009). Salinity in these lakes changes frequently depending on freshwater inflows from rivers and intrusions of marine water into the lakes (Cieśliński 2011). Seasonal changes in the abundance and composition of ciliate communities were described previously in both lakes, but they were studied at only one sampling site at each lake (Rychert et al. 2012). In the present study we investigated spatial differences in abundance and composition of ciliate communities, driven by the salinity gradient, at six sites in Lake Gardno and three in Lake Łebsko. Special attention was paid to tintinnid ciliates, which are believed to be estuarine and coastal organisms (McManus and Santoferrara 2013). Attention was also focused on the widespread marine species complex *Mesodinium rubrum* (Lohmann), also known as *Myrionecta rubra* Jankowski (synonym), which is an important primary producer in marine and brackish environments because of its mixotrophy (Esteban et al. 2010, Qiu et al. 2016), and it can occur in waters with a salinity as low as 1.5‰ (Lindholm 1978, Breckenridge et al. 2015). *M. rubrum* was long divided into two size classes: *forma minor* and *f. major* (Leegaard 1920). This eventually resulted in the species being divided into the larger *M. major* and the smaller *M. rubrum* (Garcia-Cuetos et al. 2012). In this study, both forms, or species, were investigated. It was hypothesized that tintinnids would be of elevated importance in the planktonic communities in more saline parts of the lakes studied. Water salinity in some parts of both lakes regularly exceeds 1.5‰, thus, it was expected that *M. rubrum* and *M. major* would be important components of the ciliate communities in the more saline parts of the two lakes.

MATERIALS AND METHODS

Subsurface water was sampled with a bucket from aboard a motor boat at each sampling station. Because of the shallow mean depth of both lakes (Lake Gardno – 1.2 m, Lake Łebsko – 1.6 m) and strong wind-induced mixing, the waters are not stratified in either lake (Ficek and Wielgat-Rychert 2009). The locations of the sampling sites are indicated in Fig. 1. Sampling was accompanied by measurements of temperature, salinity, chlorophyll *a* concentration, total suspended matter, water transparency, and other parameters. However in this study, we concentrated on salinity, which was measured using a conductometer (Lake Gardno – Elmetron CPC-401, Lake Łebsko – Elmetron CC-401). Ciliate communities were analysed in samples fixed with Lugol's solution with the standard Utermöhl method (HELCOM 2001). Samples were fixed with strong acid Lugol's solution (5% iodine, 10% potassium iodide, 10% v/v glacial acetic acid) of which 1 ml was added to 200 ml sample. Because of high abundance, organisms were observed in base plate (volume: 2.4 ml, Utermöhl-type chamber) without settling cylinders. Ciliates were identified according to Marshall (1969), Foissner and Berger (1996), a web-based guide (Strüder-Kypke and Montagnes 2002), and other keys.

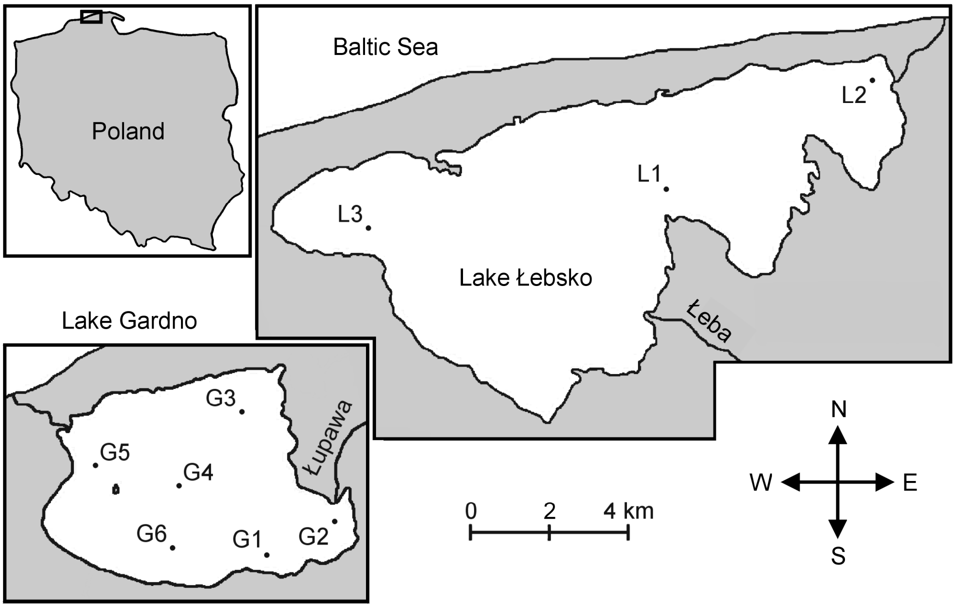

Fig. 1. Location of sampling sites in Lake Gardno (left, studied once in October 2009) and Lake Łebsko (right, studied once a month between April and December 2007). Both lakes are supplied by rivers (Lake Gardno – the Łupawa River, Lake Łebsko – the Łeba River) and are connected to the Baltic Sea. Both lakes are located in central Pomerania (northern Poland)

RESULTS AND DISCUSSION

Water salinity

Samples were taken in Lake Gardno in October 2009, about a week after a wind-driven backwater. At sampling, the water level was still elevated by 0.4-0.5 m above the typical level and water salinity was high ranging from 1.7 PSU in the eastern part of the lake, close to the mouth of the Łupawa River to 2.2 PSU in the western part of the lake where it is connected with the Baltic Sea (Fig. 1). At sampling site G1 salinity was 1.9 PSU and was high compared to values reported from long-term studies performed at this sampling site – range: 0.1 to 1.9 PSU, typical values of 0.6-0.7 PSU (Wielgat-Rychert et al. 2010, Rychert et al. 2012, Wielgat-Rychert et al. 2015, Wielgat-Rychert and Rychert 2017, unpubl. obs.). The study by Cieśliński (2011) also confirmed that water salinity at this study site was elevated after intrusion of marine water into the lake. Cieśliński (2011) reported mean water salinity in Lake Gardno of 0.6 PSU close to the sampling site G1 and 1.1 PSU close to the lake's connection with the Baltic Sea (the northwestern most part of the lake).

Samples were taken in Lake Łebsko at three sampling sites (Fig. 1). They were collected once per month between April and December 2007 (nine sampling occasions). Water salinity ranged from 1.1 to 1.8 PSU (mean: 1.6 PSU) at site L1, from 1.5 to 5.4 PSU (mean: 2.7 PSU) at site L2, and from 1.2 to 1.9 PSU (mean: 1.6 PSU) at site L3 (Fig. 1). Such differences in salinity are influenced by the location of freshwater inflows; the mouth of the Łeba River is located between sampling sites L1 and L3 (Fig. 1) and the connection with the Baltic Sea is situated close to sampling site L2 (Fig. 1). The water salinity ranges corresponded to those published by Cieśliński (2011), who reports a mean salinity of 2.2 PSU close to the connection with the Baltic Sea (L2) and a mean salinity of 1.6 PSU in the southern part of the lake.

Ciliate abundance

In October 2009, ciliate abundances at particular sampling sites in Lake Gardno ranged from 63.3 to 93.3 cells ml^{-1} and no considerable spatial pattern was observed (Fig. 2). Seasonal changes in ciliate abundance at sampling site G1 were studied in previous years (Rychert et al. 2012), and the values noted in October (48.3-153.3 cells ml^{-1}) corresponded to those observed in this study. Ciliate abundances observed in Lake Gardno (mean value of 80.0 cells ml^{-1}) were slightly lower than the mean annual abundance of about 100 cells ml^{-1} (Rychert et al. 2012, Rychert 2016) and fell within the mean annual ciliate abundances observed in eutrophic (55.5 ±7.6 cells ml^{-1}, mean ±standard deviation) and hypertrophic lakes (155.0 ±60.9 cells ml^{-1}) that were determined for a considerable number of subtropical lakes (Beaver and Crisman 1982). Ciliate abundances in Lake Gardno were also higher than those reported for eutrophic lakes in the temperate zone (annual mean of about 60 cell ml^{-1}; Pfister et al. 2002).

Ciliates were studied at three sampling sites in Lake Łebsko between April and December 2007 (Fig. 2). Ciliate abundances were high between June and September (Fig. 2) with the highest abundance (86.7 cells ml^{-1}) observed at station L3 in August (Fig. 2). During spring and fall, ciliate abundances were lower (Fig. 2) with mean values at sampling sites of 36.8 cells ml^{-1} (L1, Fig. 2.), 39.3 cells ml^{-1} (L2), and 41.5 cells ml^{-1} (L3). The ranges of ciliate abundance observed at sites L1 and L3 were wider than those observed at site L2 (Fig. 2), but mean values at all sampling sites were quite similar. Statistical analysis did not demonstrate significant differences among ciliate abundances observed at sampling stations (ANOVA, $p = 0.9$, non-significant). Ciliate abundances in Lake Łebsko (mean values for sampling sites between 36.8 and 41.5 cells ml^{-1}) were slightly lower than those reported in eutrophic lakes (55.5 ±7.6 cells ml^{-1}, mean ±standard deviation, Beaver and Crisman 1982).

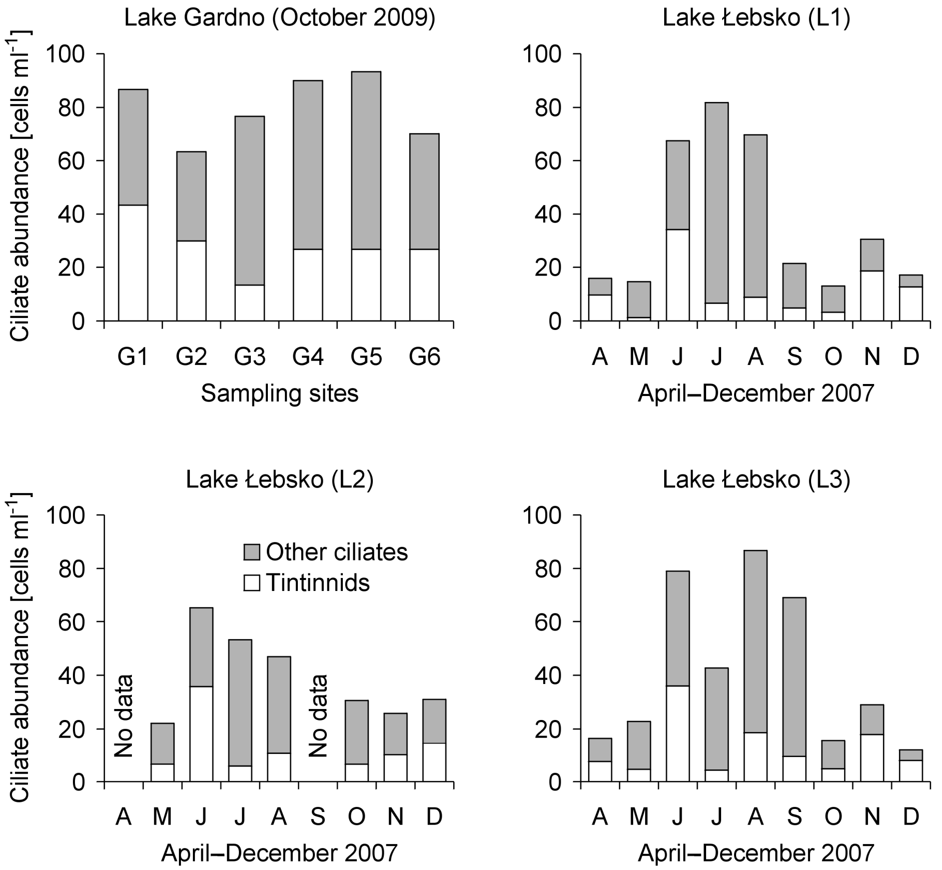

Fig. 2. Ciliate abundances observed in Lake Gardno at six sampling sites studied in October 2009 and in Lake Łebsko at three sampling sites studied between April and December 2007. Ciliates were divided into tintinnids and others. Location of sampling stations in lakes Gardno (G1-G6) and Łebsko (L1-L3) is indicated in Fig. 1

Ciliate community composition

In Lake Gardno (October 2009), ciliate communities were dominated by oligotrichs and naked choreotrichs (46-74% of abundance, depending on the study site), loricate choreotrichs (= tintinnids, 17-50%), prostomatids (up to 5%), and haptorids (up to 4% of ciliate abundance, including *Mesodinium rubrum* described below). Among oligotrichs, a few specimens of the marine ciliate *Strombidium vestitum* (Leegaard) Kahl were observed. The lowest contribution of tintinnid ciliates (17%) was observed in the northern part of the lake (site G3, Fig. 1) and their contribution to abundance at other stations ranged from 29 to 50% (Fig. 2). The organisms observed are common in Lake Gardno (Rychert et al. 2012) and other temperate, brackish lakes (Pfister et al. 2002). However, the high occurrence of tintinnids (17-50%, mean: 35%, genera: *Tintinnopsis* and *Tintinnidium*) was unusual, because their mean annual contribution to ciliate abundance in Lake Gardno was previously estimated to be 17% (Rychert et al. 2012, studies performed at site G1), and such a contribution in October was previously estimated to be 10-11% (Rychert et al. 2012, unpubl. details). The difference between typical values in October (10-11%) and those observed during the backwater (17-50%, this study) is statistically significant (test t, p = 0.04).

In Lake Łebsko, which was studied between April and December 2007, ciliate communities were dominated by oligotrichs and naked choreotrichs (mean values – L1: 37% of ciliate abundance, L2: 45%, L3: 44%, locations of stations indicated in Fig. 1) and tintinnids (mean values – L1: 36%, L2: 32%, and L3: 35%, see Fig. 2). The mean contributions of haptorids, prostomatids, and peritrichs were 8-10%, 2-8%, and 5-6%, respectively. At each sampling site, 4-5% of the ciliates remained unidentified. At all sampling sites, the composition of the ciliate communities was subjected to frequent changes and no clear seasonal trend was recorded (data not shown). Similarly, no difference in taxonomic composition was demonstrated among sampling stations. The taxonomic composition of the ciliate communities was typical of temperate lakes (Müller 1989, Pfister et al. 2002). Marine ciliates such as *Mesodinium rubrum*, *Strombidium emergens* (Leegaard) Busch, and *Strombidium vestitum* (Leegaard) Kahl were observed a few times. The contribution of tintinnids (genera *Tintinnopsis* and *Tintinnidium*) to ciliate abundance ranged from 8-11% to 55-74% at particular sampling sites (Fig. 2) with mean values at particular sites ranging from 32% to 36% (Table 1). No spatial differences in the contribution of tintinnids to ciliate abundance were detected, e.g., dependence on salinity. The highest importance of tintinnids was recorded during spring and at the end of the year (November-December), whereas their importance was the lowest between July and October (Fig. 2). Finally, in Lake Łebsko tintinnids comprised a stable, very important component of the ciliate community. This was also confirmed by further studies performed between April and September 2008 at sampling station L1 (Rychert et al. 2012, unpubl. details), which estimated an even higher contribution of tintinnids to ciliate abundance, which ranged from 31 to 67% at a mean value of 46%.

Tintinnid ciliates are considered to be estuarine and coastal organisms (reviewed by McManus and Santoferrara 2013). They typically represent less than 10% of total abundance of ciliate communities in freshwater and open marine waters, but in coastal zones and estuaries they are more important and sometimes even dominate the ciliate community (Verity 1986, Müller 1989, Dolan 2000, Pfister et al. 2002, Urrutxurtu 2004, Rychert 2009, McManus and Santoferrara 2013, Rychert et al. 2013, 2014, Sahu et al. 2016). Table 1 gathers the mean annual contribution of tintinnids to ciliate abundance determined for lakes Gardno and Łebsko and for adjacent waters. The importance of tintinnid ciliates in Lake Gardno could be considered as elevated (more than 10%), as they contributed 17% of ciliate numbers annually (Rychert et al. 2012, Table 1), and this was even more elevated during backwater episodes (mean 35%, this study). The increased importance of tintinnids in Lake Łebsko was stable at all stations studied and throughout the seasons of the year (this study, mean contribution to abundance: 32-36%). In adjacent waters, the mean annual contribution of tintinnids is typical (less than 10%). In the coastal zone of the Baltic Sea their contribution is 8%, whereas in the Słupia River it is 4% (Table 1).

Table 1

Mean contribution of tintinnids to ciliate abundance in lakes Gardno and Łebsko and also in adjacent waters

Water body (station and period studied)	Tintinnids – mean contribution to ciliate abundance calculated for period studied [%]	Reference
Słupia River (December 2005 - December 2006)	4	Rychert (2009), unpubl. details
Baltic Sea – coastal zone in Ustka (April 2003 - March 2004)	8	Rychert et al. (2013), unpubl. details
Lake Gardno (G1, April 2006 - February 2008)	17	Rychert et al. (2012), unpubl. details
Lake Gardno (G1-G6, backwater in October 2009)	35	This study
Lake Łebsko (L1-L3, April-December 2007)	32-36	This study
Lake Łebsko (L1, April-September 2008)	46	Rychert et al. (2012), unpubl. details

Location of sampling stations in lakes Gardno (G1-G6) and Łebsko (L1-L3) is indicated in Fig. 1. The Słupia River is located 10 km to the southwest of Lake Gardno, and the sampling site in the coastal zone of the Baltic Sea is located 15 km to the west of Lake Gardno

The Słupia River is located 10 km to the southwest of Lake Gardno and is generally comparable to the Łupawa River and the Łeba River (Bogdanowicz 2004), which discharge their waters into the lakes under study.

Mesodinium rubrum and *Mesodinium major*

In Lake Gardno after the backwater (October 2009, this study), the marine ciliate *Mesodinium rubrum* was observed at two of six sampling sites. Its abundance at both stations (G3 and G5, Fig. 1) was 3.3 cells ml^{-1}, and *M. rubrum* comprised up to 4% of ciliate abundance at both stations. Water salinity at those stations was 1.9 and 2.2 PSU. During previous extensive studies performed between 2006 and 2009 at sampling site G1 (Rychert et al. 2012), *M. rubrum* was observed only once, a few days after an intrusion of marine water into the lake when water salinity reached 1.0 PSU. According to Lindholm (1978), *M. rubrum* requires water salinity of 1.5‰ or higher. Thus, the presence of *M. rubrum* in Lake Gardno is likely observed only after backwaters, and it is later eliminated from the community. This species was al-so rare in Lake Łebsko. In this study, *M. rubrum* was observed in 4 of 25 samples taken from Lake Łebsko. Three times its abundance ranged from 0.7 to 0.9 cells ml^{-1}, and water salinity on those occasions was 1.8-2.7 PSU. The highest abundance was observed in November 2007 at sampling station L2 (6.6 cells ml^{-1}, 26% of ciliate abundance), when water salinity was 5.4 PSU. It was the highest salinity value observed in Lake Łebsko and it indicated a strong intrusion of marine water, because salinity in this region of the Baltic Sea was 7.5 PSU (Matthäus et al. 2008). In conclusion, although salinity in Lake Łebsko often exceeds 1.5 PSU, which is the lower salinity limit of *M. rubrum* (Lindholm 1978), this species is not a permanent component of the planktonic community.

The highest abundances of *M. rubrum* observed in lakes Gardno (3.3 cells ml^{-1}) and Łebsko (6.6 cells ml^{-1}) are comparable to abundances of *M. rubrum* reported in the Baltic Sea. The mean annual abundance of *M. rubrum* at a sampling site in the coastal zone near Ustka (located 15 km westward from Lake Gardno) was 6.5 (2006) or 5.1 cells ml^{-1} (2007), and maximum abundance was 39.2 cells ml^{-1} (Rychert and Pączkowska 2012). Consequently, it is probable that *M. rubrum* is carried into lakes during backwaters, and later it does not grow despite eutrophic conditions in both lakes (Jarosiewicz 2009). Some time after being transported into lakes, specimens of *M. rubrum* succumb. According to Lindholm and Mörk (1990), *M. rubrum* is present in some Baltic Sea estuaries, fjords, and lagoons. Lindholm (1978) reports that *M. rubrum* is sometimes present in the Västra Kyrksundet basin (Åland, Baltic Sea, southwestern Finland), in which water salinity ranges from 0.3 to 3.3‰, whereas Mironova et al. (2013) report the rare occurrence of *M. rubrum* in the Neva Estuary (the Gulf of Finland, Baltic Sea), where salinity ranges from 1 to 5 PSU. Sometimes, *M. rubrum* is also observed in the Darss-Zingst estuary (western Baltic Sea), where water salinity is between 3 and 7‰ (Arndt et al. 1990). On the other hand, *M. rubrum* is reported permanently in a fjord-like inlet, Inre Verkviken (Åland, Baltic Sea, southwestern Finland), in which the salinity of the surface water is mostly between 5 and 6‰, (Lindholm and Mörk 1990, Sjöqvist and Lindholm 2011). This indicates that the occurrence of *M. rubrum* depends primarily on considerably high and stable water salinity.

It has long been suspected that *M. rubrum* is a species complex (Esteban et al. 2010), with small and large forms (e.g., Lindholm 1985, Rychert 2004). Eventually, Garcia-Cuetos et al. (2012) separated the species complex *Mesodinium rubrum* into two species: *M. rubrum* (sensu stricto) and *M. major* Garcia-Cuetos, Moestrup & Hansen. All the specimens examined from Lake Gardno and the majority of those from Lake Łebsko were small. In Lake Gardno, the mean diameter ranged from 15 to 20 µm (all measurements were performed on fixed, and, therefore, probably slightly shrunken specimens), whereas in Lake Łebsko the diameter of the specimens ranged from 17 to 25 µm. Once, when salinity in Lake Łebsko at sampling site L2 was 5.4 PSU, large forms were observed with a mean diameter of about 35 µm (fixed specimens, probably slightly shrunken). This corresponds with an observation by Lindholm (1985) that the large form of *M. rubrum* (*forma major* according to Leegaard 1920) is very rare in salinities below 5‰. Perhaps the large form of *M. rubrum* (most probably the species *M. major* according to Garcia-Cuetos et al. 2012) simply requires a higher water salinity than does the smaller *M. rubrum*.

CONCLUSIONS

The ciliate abundances in both eutrophic lakes were constantly high, with the highest abundances observed during summer. Despite spatial differences in water salinity, no significant differences in ciliate abundances among stations were revealed. The ciliate communities in Lake Łebsko were characterized by high contributions of tintinnids, with mean values at particular sites between 32% and 36%. In Lake Gardno, tintinnids typically contributed 17% to ciliate abundance, but during backwaters their contribution rose significantly (35%). The importance of tintinnids in the ciliate communities of both lakes studied was higher than in adjacent fresh and marine waters. This confirms the hypothesis posed in the introduction. In both lakes, the marine and brackish ciliate *Mesodinium rubrum* was observed shortly after wind-driven intrusions (backwaters) of the Baltic Sea waters into the lakes. Later, *M. rubrum* was eliminated from the community. In contrast to the hypothesis posed in the introduction, *M. rubrum* is not an important component of the ciliate communities in either of the lakes studied. Once, in the eastern part of Lake Łebsko, *Mesodinium major* (= *Mesodinium rubrum f. major* according to Leegaard 1920) was observed after a strong backwater when salinity reached 5.4 PSU.

Acknowledgments

We would like to thank Anna Jarosiewicz for salinity measurements performed in samples taken from Lake Łebsko and the Słowinski National Park rangers for their assistance during sampling. We also thank two anonymous reviewers for their comments and suggestions. The study was supported by the Polish Ministry of Science and Higher Education through the statutory activities of the Pomeranian University in Słupsk (Poland), project number 11.6.15.

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ZNACZENIE TINTINNID I *MESODINIUM RUBRUM* W ZBIOROWISKACH PLANKTONOWYCH ORZĘSKÓW W PŁYTKICH I SŁONAWYCH JEZIORACH GARDNO I ŁEBSKO (PÓŁNOCNA POLSKA)

Streszczenie

Orzęski stanowią istotne ogniwo troficzne w środowisku wodnym, ponieważ są ważnym źródłem pokarmu dla zooplanktonu i ryb. W prezentowanej pracy zbadano wpływ gradientu zasolenia na liczebność i skład zbiorowisk orzęsków. Badania prowadzono w dużych słonawych i eutroficznych jeziorach Gardno i Łebsko. Pomimo zróżnicowania przestrzennego zasolenia wody, nie wykazano istotnych różnic pomiędzy zbiorowiskami orzęsków obserwowanymi na poszczególnych stanowiskach. Zbiorowiska orzęsków w jeziorze Łebsko charakteryzowały się wysokim udziałem tintinnid, które wnosiły średnio na poszczególnych stacjach od 32% do 36% liczebności. W jeziorze Gardno, w którym zasolenie było niższe, znaczenie tintinnid wzrosło po intruzji wód morskich do jeziora. W obu badanych jeziorach znaczenie tintinnid w zbiorowiskach orzęsków było wyższe niż w przyległych wodach słodkich i morskich. Krótko po spowodowanych wiatrem intruzjach wody morskiej (cofkach) w obu jeziorach był obserwowany słono- i słonawowodny miksotroficzny orzęsek *Mesodinium rubrum*. Po silnej cofce, kiedy zasolenie we wschodniej części jeziora Łebsko sięgnęło 5,4 PSU, zaobserwowano tam *Mesodinium major* (= *Mesodinium rubrum forma major*).