COASTAL RESEARCH AND PLANNING INSTITUTE
KLAIPĖDA UNIVERSITY

JŪRATĖ LESUTIENĖ

FOOD WEB OF THE CURONIAN LAGOON: ORGANIC MATTER SOURCES AND FEEDING OF MYSIDS

Doctoral Dissertation
Biomedical Sciences: Ecology and Environmental Sciences (03B)

Klaipėda, 2009

Dissertation research was carried out at the Coastal Research and Planning Institute, Klaipeda University, in 2003-2009

Research Supervisor:
doc. dr. **Zita Rasuolė Gasiūnaitė** (Coastal Research and Planning Institute, Klaipėda University, biomedical sciences, ecology and environmental science (03B))

Research Advisor:
prof. dr. **Elena Gorokhova** (Department of Systems Ecology, Stockholm University, biomedical sciences, ecology and environmental science (03B))

BALTIJOS PAJŪRIO APLINKOS TYRIMŲ IR PLANAVIMO
INSTITUTAS
KLAIPĖDOS UNIVERSITETAS

JŪRATĖ LESUTIENĖ

ORGANINĖS MEDŽIAGOS ŠALTINIAI IR MIZIDŽIŲ VAIDMUO KURŠIŲ MARIŲ MITYBINIAME TINKLE

Daktaro disertacija
Biomedicinos mokslai, ekologija ir aplinkotyra (03B)

Klaipėda, 2009

Disertacija rengta 2003-2009 metais Klaipėdos universiteto Baltijos pajūrio aplinkos tyrimų ir planavimo institute

Vadovė:
doc. dr. **Zita Rasuolė Gasiūnaitė** (Baltijos pajūrio aplinkos tyrimų ir planavimo institu-tas, Klaipėdos universitetas, biomedicinos mokslai, ekologija ir aplinkotyra (03B))

Konsultantė:
prof. dr. **Elena Gorokhova** (Sistemų ekologijos katedra, Stokholmo universitetas, biomedicinos mokslai, ekologija ir aplinkotyra (03B))

TABLE OF CONTENTS

1. INTRODUCTION

Scope of the study. Trophic connections and energy flows within ecological communities are organized in to food webs, that are used further to explore and predict community and ecosystem functioning, e.g. productivity and stability processes. These processes are contemporary affected by forces, directly or indirectly associated with human activities, such as biodiversity loss, exotic species invasions, climate change, nutrients loads, overharvesting, etc (Mills et al., 2003, Loreau, 2005, Woodward et al., 2005). The realistic representation of the basic structure of the food web is principal issue in such studies. Different approaches, starting with traditional gut content analysis and ending up with more modern techniques of molecular markers, could be used to investigate the trophic linkages of the species in aquatic communities, that will provide different and complementary information, which eventually should be synthesized and used to build the food web (Pasquaud et al., 2007, Gorokhova and Lehtiniemi, 2007).

Analysis of natural abundances of stable isotopes (e.g. $\delta^{13}C$ and $\delta^{15}N$) is particularly useful identifying primary sources of organic matter and analyzing the vertical structure of the aquatic food webs (Michener and Shell, 1994). Stable isotopes have been frequently used to estimate sources of organic matter and its incorporation in to secondary production of coastal areas and estuaries that are among most complex ecosystems in the sense of variability of primary organic matter sources (Fry and Sherr, 1984, Peterson and Howarth, 1987, Canuel et al., 1995, Vizzini and Mazzola, 2003, Carlier et al., 2007, Riera et al., 2009). Seasonality of riverine inputs, importance of macrophytes and taxonomic changes in phytoplankton populations result in high spatial and temporal variability of SI composition in primary organic matter sources, which should be investigated, otherwise understanding of trophic linkages at the base of estuarine and coastal food webs remains obscured (Peterson, 1999, Bouillon et al., 2000, Beaudoin et al., 2001). Curonian Lagoon (SE Baltic Sea) is mainly freshwater eutrophic transitory ecosystem influenced by river runoff from agricultural basin, frequent and irregular brackish water intrusions and heavy

cyanobacteria blooms in summer (Gasiūnaitė et al., 2008). The use of allochthonous and autochthonous organic matter in the food web of the lagoon is still poorly understood.

To support commercial fishery, the Ponto-Caspian mysids of genus *Paramysis* were extensively introduced into many inland water reservoirs of Russia (Komarova, 1991 and the references therein) as well as of former Soviet countries, including Lithuania (Arbačiauskas, 2002). *P. lacustris* was expected to improve the efficiency of detritus and primary production utilization in the eutrophic Curonian Lagoon (Razinkov, 1990), however there is still no evidence of the nutritional importance of detritus in mysid feeding. Moreover, questionable trophic role of *P. lacustris* as primary consumers emerged after significant proportion of animal food, particularly plankton crustaceans was observed in their gut contents (Jankauskienė, 2003).

Aim and objectives of the study. This study was performed to estimate sources of organic matter that sustain secondary production and to ascertain the role of introduced mysid *Paramysis lacustris* in the food web of Curonian Lagoon.

The main objectives:

1. to analyze spatial and temporal patterns of carbon and nitrogen stable isotope composition in the particulate organic matter of the Curonian Lagoon;
2. to identify food sources of primary consumers, evaluating contributions of allochthonous particulate organic matter from the Nemunas River and Baltic Sea;
3. to evaluate nitrogen stable isotopes variability in primary consumers generating baselines for trophic levels calculations;
4. to calculate relative contributions of different food sources to mysid diet and to identify their role in pelagic and littoral food chains, using carbon and nitrogen stable isotope analysis.

Novelty of the study. For the first time the food web of Curonian Lagoon was described using stable isotope analysis (SIA). This is the firs detailed food web description based on SIA including temporal and spatial variation in the Baltic Sea. Substantial contribution of swarming mysid in remineralization of macrophytal detritus was revealed and new approach- whole stomach content SIA was applied to detect pelagic prey.

Scientific and practical significance. This study is a basis for understanding of spatial and temporal dynamic of carbon and nitrogen stable isotopes in the organic matter of the Curonian Lagoon. It can serve as point of reference for the future SIA based research, such as trophic relationships of invasive species, fish migrations, point and non-point source pollution, evaluation of increased/decreased river runoff due to climate change etc. Suggested criteria for selection of $\delta^{15}N$ baseline species could be important for comparative studies of food chains among eutrophic aquatic ecosystems, characterized by high $\delta^{15}N$ variability due to atmospheric N_2 fixation.

Defensive statements

1. Stable isotope variability in particulate organic matter of Curonian Lagoon is mainly determined by autochthonous phytoplankton and Nemunas river runoff.

2. In the summer, primary consumers of the Curonian Lagoon are sustained by phytoplankton or phytodetritus, whereas submersed macrophytes is not important food source.

3. Atmospheric N_2 fixation induced $\delta^{15}N$ decrease in summer phytoplankton is transferred to primary consumers with different rate. This should be considered while choosing baseline for trophic level calculations.

4. During the ontogenetic development, mysid diet changes towards increasing carnivory, in particular on zooplankton in summer.

5. Submersed macrophyte detritus is important mysid food source during the autumn swarming in the littoral.

Scientific approval

The results of this study were presented at 8 international conferences:

- 4th European Crustaceans Conference, University of Lodz, Poland July 22-26, 2002;
- 38th European Marine Biology Symposium, Aveiro, Portugal September 8-12, 2003;
- "Baltic the Sea of Aliens". Gdynia, Poland August 25-27, 2004;
- Plankton Symposium III. Figueira da Foz, Portugal March 20-22, 2005;
- 42th European Marine Biologist Symposium. Kiel, August 26-31 2007;
- 1st , 2nd and 3rd regional student conference on "Biodiversity and functioning of aquatic ecosystems in the Baltic Sea region", Klaipeda, Lithuania, in 2004, 2006 and 2008.

Three publications were published on the dissertation topic:

1. Lesutienė J., Gasiūnaitė Z.R., Grinienė E. Habitat induced heterogeneity in the Curonian lagoon littoral assemblages: mysids, juvenile fish and plankton crustaceans. Acta Zoologica Lituanica, 2005, Vol. 15 (4): 312-323.

2. Lesutiene J., Gorokhova E., Gasiunaite Z.R., Razinkovas, R. 2007. Isotopic evidence for zooplankton as an important food source for the mysid *Paramysis lacustris* in the Curonian Lagoon, the South-Eastern Baltic Sea. Estuarine, Coastal and Shelf Science, 73: 73-80.

3. Lesutiene, J., Gorokhova, E., Gasiunaite, Z., Razinkovas, A. 2008. Role of mysid seasonal migrations in the organic matter transfer in the Curonian Lagoon, south-eastern Baltic Sea. Estuarine, Coastal and Shelf Science 80: 225–234.

Volume and structure of the theses. The dissertation is presented in the following chapters: Introduction, Study Area, Literature Review, Materials and Methods, Results, Discussion, Conclusions, References and Appendixes. The volume of the dissertation is 140 pages. References include 220 sources.

Acknowledgements

Firstly, I would like to thank my supervisor dr. Zita Gasiūnaitė for trust, tolerance and care during whole my scientific carrier. I am especially grateful to my scientific advisor prof. Elena Gorokhova for essential input in preparation of this theses and scientific papers, valuable comments and explanations, as well as encouragement and warmness. I largely appreciate the contributions of all my colleagues at CORPI to this work and my activities during the PhD studies: dr. Artūras Razinkovas for encouragement to apply SIA in this study and involvement in to scientific projects; prof. Sergej Olenin and dr. Darius Daunys for organizing PhD studies and reviews; dr. Renata Pilkaitytė for chlorophyll and phytoplankton samples analysis and valuable advises on data interpretation; Evelina Grinienė for zooplankton analysis, field and laboratory assistance; Aleksej Šaškov- my champion in academic rowing, for his help in taking mysid samples; dr. Anastasija Zaiko for field and laboratory assistance; dr. Saulius Gulbinskas for sediment analysis; Nerijus Nika for fish samples; Viačeslav Jurkin for preparation of maps; Aistė Paldavičienė for explaining cyanotoxicity; Simona Mačiukaitė for administrative help; to all PhD students for their support and friendship. I appreciate Vita Jušienė (KU Science Department) help in preparation for the defense.

I thank A. Sjösten (Systems Ecology, Stockholm University) for his kind permission to use laboratory facilities, and Dr. David Harris (University of California at Davis, Stable Isotope Facility) for stable isotope analyses. Lithuanian Hydrometeorological Service and Marine Research Center for data.

Many thanks goes to prof. E. Gorokhova family for warm home in Stokholm also Lisa for help in the lab. I thank my parents, brother

Aurimas, sisters Eglė and Žaneta and all family friends for care and support; our daughters Marija and Sofija for being far from what has involved me that much recently. My particular thanks go to my husband Mindaugas for his understanding, patience and help.

Three mobility grants provided to me by Nordic Marine Academy are particularly appreciated. This research was supported by Coastal Research and Planning Institute, EU funded projects (FW6 505446 MARBEF, Marine Biodiversity and Ecosystem Functioning, and EU FW 6 506675 ALARM, Assessing Large Scale Risks for Biodiversity with tested Methods). I was also granted by Lithuanian State Science and Studies Foundation.

Abbreviations used in the theses: BPOM- bottom surface particulate organic matter, EPOM- estuarine particulate organic matter, MPOM- marine particulate organic matter, POM –particulate organic matter, RPOM- riverine particulate organic matter, SI- stable isotopes, SIA- stable isotope analysis, TL- trophic level.

2. LITERATURE REVIEW

2.1. Food web research in the transitional coastal ecosystems

Transitional coastal ecosystems encompass wide spectrum of habitats from tidal estuaries to non-tidal brackish lagoons with common feature – substantial influence by riverine freshwater flows (McLusky and Elliot, 2007). Estuaries and lagoons are among the most productive ecosystems that have been intensively exploited by human population for centuries (Breber et al., 2008). However, recent human activities such as land use, mobilization of nutrients and overfishing induced critical changes in structure and functioning of these ecosystems over past 50 years which lead to loss of goods and services important for local socio-economy (Cloern, 2001, McLusky and Elliot, 2004, Breber et al., 2008). Restoration and management of resources

should be based on better knowledge of natural processes at the ecosystem-level, e.g. responses of the functioning of the food webs to various external forcing (Kremer et al., 2000, Pasquaud et al., 2007, Winemiller, 2007, Ertürk et al., 2008). Among other ecosystems, estuarine food webs are characterized by large spatial and temporal variability under the influence of multiple abiotic and biotic factors, such as rapid and intense fluctuations of the physicochemical factors redistributing and transforming primary organic matter sources, community structural changes along salinity gradients, ontogenetical and seasonal migrations of fish, biological invasions etc. (Mann, 2000, Winemiller, 2007, Pasquaud et al., 2007 and the references therein). Therefore analysis of estuarine food web might be complicated; on the other hand, it can provide opportunities for evaluating controls of natural and anthropogenic stress on trophic structure (Kremer et al., 2000, Christian et al., 2005). More network analysis have been conduced on estuaries than on any other kind of ecosystems, partially because of extensive sampling and good data availability, these analysis can serve as object of comparative ecosystem ecology linked to human impacts (Christian et al., 2005).

The sustainable environmental management and protection of lagoons and estuaries is particularly difficult because of hydrologic connectivity that transmits disturbances outside the boundaries of the system, which are often beyond the direct control of managers (Pringle, 2003). Therefore, coastal lagoons and estuaries, as typical representatives of transitional waters, are classified as particularly vulnerable, and needs specific attention in water policy and management strategies (EC, 2000). One of the stringent issues to enhance the understanding of functioning of coastal ecosystems and improve their management is to estimate the allochthonous and autochthonous sources of organic matter that sustain the food webs (Cloern et al., 2002, Pedersen et al., 2004). Estuaries receive high amounts of fluviogenic material, vascular plant detritus from adjacent wetlands and marshes, marine phytoplankton, POM of domestic and industrial wastewaters etc (Cloern et al., 2002). Increasing nutrients loads to coastal lagoons and estuaries enhance primary production of microalgae, macroalgae and vascular

plants, representing the main sources of autochthonous POM (Pedersen et al., 2004). All types of POM intermix and are potentially available for secondary production. Therefore the identification and quantification of primary source of organic matter is a challenging issue that needs advanced techniques, such as SIA, biochemical markers etc. (Cloern et al., 2002, Pasquaud et al., 2007).

Curonian Lagoon is the largest lagoon in Europe, influenced by the Nemunas River discharge and brackish water from the Baltic Sea (Breber et al., 2008, Gasiūnaitė et al., 2008). Togethor with other lagoons of the Balthic Sea (Vistula and Oder) it is classified as a transitional ecosystem (McLusky and Elliot, 2007). The food web interactions and role of POM in the secondary production of Curonian Lagoon is still poorly understood. The field studies of trophic interactions are based on gut content analysis, which was applied for investigation of feeding of Ponto-Caspian mysids and amphipods, fish larvae, juvenile and adult benthofagous and predatory fish, birds (Bubinas and Ložys, 2000, Bubinas and Vaitonis, 2003, Jankauskienė, 2003, Ložys, 2003, Lesutienė et al., 2005, Žydelis and Kontautas, 2008).

Modelling approaches were used to estimate assimilation and biodeposition of POM by *Dreissena polymorha* (Daunys et al., 2006), consumption of phytoplankton primary production by herbivorous zooplankton and mysid (Razinkovas and Gasiūnaitė, 1999). Utilization of phytoplankton, bacteria, particulate detritus in the food web and trophic levels were calculated using ECOPATH by Razinkovas and Zemlys, 2000 and later updated by Ertürk, 2008. The estimated upper trophic levels equaled: 4.35 of piscivorous birds, 4.05 of predatory fish, 3.18 of planktivorous fish and 3.2 of demersal fish. Most of macrozoobenthos species were assigned to 2-2.3 TL, mysids 2.44 TL, grazing zooplankton 2 TL, carnivorous zooplankton 2.9 TL (Ertürk, 2008). Typically quantitative diet compositions are among the most uncertain parameters needed to balance the trophic model (Pasquaud et al., 2007 and the references therein). Therefore modeling and SIA could serve as complementary methods for food web analysis.

2.2. Tracing of primary organic matter sources by stable isotopes

Natural concentrations of carbon and nitrogen stable isotopes (^{13}C, ^{12}C and ^{15}N, ^{14}N) are among the most frequently used tracers determining the origin of suspended and sedimentary organic matter, its composition in assimilated diet of primary consumers and further transfer along the food chains (Cloern et al., 2002). Stable isotope (SI) ratios are expressed as δ notation of deviation from standards following the equation: $\delta^{15}N$ or $\delta^{13}C = \left[\left(R_{sample} / R_{standard}\right) - 1\right] \times 10^3$, where R is the ratio of heavy isotope to the light isotope $^{15}N/^{14}N$ and $^{13}C/^{12}C$.

Stable isotope, particularly $\delta^{13}C$, composition of organic material is primarily determined during the photosynthesis because of carbon isotope fractionation (Peterson and Fry, 1987). Dominating terrestrial C_3 plants derive CO_2 directly from the atmosphere ($\delta^{13}C$ = -7.4 –8 ‰), discriminating strongly against heavier $^{13}CO_2$ molecules, which result in their average $\delta^{13}C$ value of -27.8 ‰ (Peterson and Fry, 1987, Lajtha and Marshall, 1994). In aquatic environments three main factors are responsible for $\delta^{13}C$ value in autotrophes: isotopic composition of dissolved inorganic carbon (DIC) pool, the isotopic discrimination of the enzyme responsible for carbon fixation, concentration of CO_2 and HCO_3^-. All together these factors results in much wider range of isotopic variation in aquatic plants and algae (Fry and Sherr, 1984).

Terrestrial or aquatic vascular plant organic matter undergoes minor changes in $\delta^{13}C$ during the decomposition and sedimentation, therefore plant detritus inputs in POM pool of coastal ecosystems could be successfully traced using $\delta^{13}C$ (Fry and Sherr, 1984). The riverine particulate organic matter (RPOM) in the lower reaches of the European rivers usually has three main contributors: riverine phytoplankton, particulate organic matter from terrestrial vegetation litter and POM from industrial and domestic waters (Hellings et al., 1999, Maksymowska et al., 2000). All these sources of riverine particulate organic matter (RPOM) could be differentiated by C and N stable isotopes and C/N ratio. Riverine phytoplankton is slightly more depleted

in ^{13}C than terrestrial vegetation and has lower C/N ratio close to Redfield ratio 6.6. (Fry and Sher, 1984, Cloern et al., 2002). Terrestrial detritus has C/N ratio of >10 or higher >15 (Hellings et al., 1999, Matson and Brinson, 1990). Frequently, a positive linear relationship between $\delta^{13}C$ values and C/N is found in RPOM, i.e. higher $\delta^{13}C$ and C/N values indicate the increased proportion of detritus in RPOM (Hein et al., 2003, Maksymowska et al., 2000).

Terrigenous organic matter originating from terrestrial vegetation is more refractory than autochthonous phytoplankton, therefore, as revealed by SIA, has weaker nutritional impact in estuarine food webs, whereas phytoplankton is selected or assimilated preferentially by the consumers, even its contribution to the total POM is low (Sobczak et al., 2002, Martineau et al., 2004, Kasai et al., 2004, but see Rolff and Elmgren, 2000). In contrast, detritus of mangrove, aquatic macrophytes, such as seagrass or macroalgae, and salt marsh material has been shown as important contributors in the diet of pelagic and benthic consumers in the lagoons and estuaries (Peterson and Howarth, 1987, Vizzini and Mazzola, 2003, Abrantes and Sheaves, 2008, Vonk et al., 2008, Riera et al., 2009). However, phytoplankton tends to prevail in the diet of primary consumers over macrophyte detritus. For example, as indicated by $\delta^{13}C$, macrophytes contributed 77 % to sinking particles, whereas only <10% in the diet of suspension and deposit feeders in the coastal ecosystem (Bode et al., 2006). SI also revealed contradictory findings of no importance of macrophytes or their detritus in the consumers feeding; epiphytes and/or microbes that colonize the decaying plants are suggested as more important food source for primary consumers (Hamilton et al., 1992, Abreu et al., 2006).

Autochthonous phytoplankton primary production, enhanced by the land derived nutrients, is among the most important sources that sustain secondary production in coastal ecosystems (Cloern, 2001). Freshwater and marine phytoplankton could be discriminated by $\delta^{13}C$, because dissolved inorganiv carbon (DIC) in the open ocean is fairly uniform and equal to 0 ‰ whereas in freshwater ranges from -5 to -10 ‰ (Michener and Shell, 1994). There is a common estuarine gradient

from more ^{13}C-depleted POM, originating from terrestrial detritus and freshwater phytoplankton, in the upper estuary, to more ^{13}C-enriched POM at the mouth of the estuary (Canuel et al., 1995). The $\delta^{13}C$ in consumers also increases with salinity from upper to lower regions along estuaries (Deegan and Garritt, 1997, Kasai and Nakata, 2005, Bucci et al., 2007, Garcia et al., 2007). This SI phenomenon promoted many attempts to evaluate the relative importance of terrestrial vs. marine organic matter sources to POM pool, tissues of primary consumers and fish (Nikolova Eddins, 2001, Fry, 2002, Darnaude, 2005). However usually these studies encounter difficulties in estimating end-members, because of high temporal variability and overlap of SI values in riverine and marine POM, as well as importance of other POM sources, such as macrophyte detritus etc., that prevents of application of simple two-end-members mixing model to explain the relative importance of riverine and marine end-members in the mixture of POM and estuarine secondary production (Cifuentes et al., 1988, Peterson, 1999). The investigations of the food webs in highly dynamic estuaries and lagoons primarily should be focused on seasonal variability of SI composition in POM sources prior to estimating the sources contribution to secondary production.

The $\delta^{15}N$ in most of the biosphere components varies from -10 to 10 ‰ with little deviations from the constant value in the atmosphere set at 0 ‰, as standard for natural ^{15}N abundance measurements (Peterson and Fry, 1987). Low fractionation of nitrogen isotopes in plant growth and bacterial mineralization appears because often nitrogen is a limiting nutrient (Peterson and Fry, 1987). The variability of $\delta^{15}N$ in phytoplankton is determined by the three forms of inorganic nitrogen: N_2 gas, ammonia and nitrate (Michener and Schell, 1994). Low molecular weight ammonia (amino acids and urea) is primarily released by aquatic organisms, whereas nitrate has high $\delta^{15}N$ value left after denitrification, which has a high fractionation factor (Michener and Schell, 1994). Atmospheric N_2 fixation by diazotrophic cyanobacteria results in low nitrogen isotopic signal in phytoplankton, which than propagates through all size-classes of plankton, indicating direct or

secondary utilization of fixed nitrogen form cyanobacteria (Rolff, 2000).

Management of eutrophication and wastewater pollution in the coastal zone has been hampered by the lack of direct method to trace nitrogen sources from land into coastal food webs (Mc Clelland et al., 1997). The treated domestic and agricultural wastewaters, after loss of light nitrogen during denitrification, have high $\delta^{15}N$ value that differs from other natural sources of nitrogen in coastal ecosystems (Mc Clelland et al., 1997, McClelland and Valiela, 1998). Nowadays $\delta^{15}N$ is becoming a suitable indicator of wastewater-N propagation in coastal food webs, often suggested as conventional monitoring method (Costanzo et al., 2001, Costanzo et al., 2005, Schlacher et al., 2005). A distinct gradient in $\delta^{15}N$ values in sedimentary POM from eutrophic coastal areas to open more oligotrophic waters was reported from the Baltic Sea as well (Voss et al., 2000). The increased $\delta^{15}N$ values in sedimentary POM is primarily a result of increased antrophogenic nutrient loads in the rivers (Voss et al., 2000). High spatio-temporal variability of $\delta^{15}N$ values in the POM is very likely in eutrophic coastal lagoons, such as the Curonian Lagoon, because of N_2 fixation by diazotrophic cyanobacteria and antropogenic nitrogen loads with riverine discharge to the lagoon.

There are isotopic food web researches built on the single field sampling of food web components (Beaudoin et al., 2001, Jones and Waldron, 2003, Riera et al., 2009). However, high spatial and temporal variability of SI composition in primary organic matter sources obscured understanding of trophic linkages at the base of food web (Peterson, 1999, Bouillon et al., 2000, Beaudoin et al., 2001). Therefore, several seasonal surveys of primary producers and consumers are suggested instead of single sampling to reconstruct the food webs using SIA in highly variable coastal ecosystems (Carlier et al., 2007).

However, it should be pointed out, that isotopic information alone, cannot definitively reveal or measure the dominant sources of organic matter or the food supply to primary consumers in ecosystems having multiple and time-varying sources of autochthonous and exogenous

organic matter (Cloern et al., 2002). Many alternative or supplementary methods to identify and measure these sources could be used in parallel to SI measurements at natural concentrations, such as isotope additions, compound specific SIA (Fantle et al., 1999, Raikow and Hamilton, 2001, Hadven and Bunn, 2005, Pond, 2006), as well as other molecular biomarkers, bioassays, etc. (Cloern et al., 2002, Perga et al., 2006). Ecologists should also consider the need for interdisciplinary approach to fully understand the SI processes in biota, that are ecological, physiological and biochemical (Gannes et al. in 1997). The general methodological strategy, formulated for the hydrologists known as Fretwells' Law, could be valid for ecologists also (Fry, 2006).

Fretwell's Law: "Warning! Stable isotope data may cause severe and contagious stomach upset if taken alone. To prevent upsetting reviewers' stomachs and your own, take stable isotope data with a healthy dose of other hydrologic, geologic, and geochemical information. Then, you will find stable isotope data very beneficial." (Marvin O. Fretwell, pers. comm. 1983, according to Kendall and Caldwell, 1998).

2.3. Stable isotope analysis approach in feeding studies: advantages and limitations

Interest in application of SIA in ecological research rose over last few decades because of rapid advances, greater accessibility and affordability of the technology (Grey, 2006). Gannes et al. in 1997 have foreseen this explosion of SI use by field ecologists and stressed the need of more controlled (experimental) research to examine the assumptions of the method and set the limits to what can be deduced from SI field data. Since than many researches in the field of aquatic ecology were conduced to validate the method that could be classified in to (1) gut content and SIA data comparisons, (2) estimation of variability of trophic enrichment factors, (3) consumers SI composition equilibration to the diet. Still many questions remain about the use of SIA in

animal ecology, in particular, investigations of stable isotope incorporation, routing in to different tissues, factors that determine fractionation are still in progress (del Rio et al., 2009).

Most of the studies that have combined the SIA and gut content analysis involved fish, few of them targeted invertebrates (Beaudoin et al., 2001, Hart and Lovvorn, 2001, Perga and Gerdeaux, 2005, Winemiller et al., 2007, Pasquaud et al., 2008). The main advantages of SIA over direct observations of gut contents are (1) SI show the assimilated diet not just ingested; (2) they integrate the diet over time, whereas gut contents analysis is a snapshot of diet composition of the short period; (3) unidentifiable macerated matter in the animal gut could be identified by SIA; (4) gut content analysis of small organisms is simply impossible (review of Grey, 2006 and the references therein). SIA is obviously limited in taxonomic resolution of food components in contrast to gut content analysis, which can provide accurate species composition of the diet, if the expertise of the researcher is sufficient (Winemiller et al., 2007). Combined SIA and gut content analysis conduced by Perga and Gerdeaux (2005) revealed that SI in fish muscle does not show the diet during the September-March period, when nutrients are allocated to basal metabolism and to gonadic growth. In general the SI data should not be interpreted without prior or simultaneous independent evidence such as gut contents or other feeding investigations (Hart and Lovvorn, 2001). Therefore SIA can not replace gut content analysis (if it is doable) in trophological investigations but could be used successfully as complementary approach (Lin et al., 2007, Pasquaud et al., 2008). When applied together, stable isotope and dietary analyses reveal a more detailed and accurate trophic structure of the community, including greater taxonomic, temporal, and spatial resolution (Winemiller et al., 2007).

Relative contribution of different food items to the consumers diet is calculated using linear mixing models by the assumption, that the isotopic composition of consumers tissues equals the weighted average of the isotopic composition of the constituents of its diet (Gannes et al., 1997). Proportions of two sources are estimated using isotopic signa-

tures of a single element (e.g. $\delta^{15}N$ or $\delta^{13}C$), three sources need SI ratios of two elements (e.g. $\delta^{15}N$ and $\delta^{13}C$) (Phillips and Gregg, 2001). If there is more than n+1 source in the diet (1) the range of feasible solutions could be estimated, (2) sources could be combined if they are not significantly different and if grouping has functional or ecological meaning (Phillips and Gregg, 2003, Phillips et al., 2005). One of the limitations of this method is that it depends on isotopically distinct sources (e.g. algae vs. macrophytes) and for some questions and systems these will not be present (Winemiller et al., 2007). The SI signatures in the dietary components should be corrected by fractionation factor (Phillips and Gregg, 2001). On average $\delta^{15}N$ in the consumer is enriched by 3.4 ‰ relative to the diet, whereas $\delta^{13}C$ changes only slightly by <1 ‰ as it is transferred from the diet to the consumer (Minagawa and Wada, 1984, Michener and Shell, 1994). However lots of experimental and field research revealed variability of $\delta^{15}N$ and $\delta^{13}C$ fractionation in the consumers, that depend on species taxa, food type (herbivores vs. carnivores), food quality (Adams and Sterner, 2000, Vander Zanden and Rasmussen, 2001, McCutchan et al., 2003, Vanderklift and Ponsard, 2003).

Another problem in diet calculations: mixing model method assumes that consumer is in isotopic equilibrium with its diet, which is rarely truth (Harvey et al., 2002). The length of time, over which isotope ratios of different tissues or whole body indicate an animal's diet, has been investigated under laboratory conditions for various species of invertebrates and fish (Frazer et al., 1997, Gorokhova and Hansson, 1999, Logan et al., 2006, Dubois, 2007). Equilibration depends on tissue isotopic turnover (Fig. 1), which is a function of both tissue growth and metabolic tissue replacement (Fry and Arnold, 1982, Hesslein et al., 1993). The isotopic change after diet shift follows exponential model $C = C_n + (C_0 - C_n) \times e^{-(k+m)t}$, where C is observed animal isotopic signature at time t after diet shift; C_0 and C_n animal signatures in equilibrium with the old and new diet, respectively; k and m are the instantaneous rate constants for growth and metabolic turnover that could be estimated only experimentally (Hesslein et al.,

1993). The relative importance of each process varies with growth rate and tissue type. Tissue growth is responsible for isotopic turnover in rapidly growing species and young individuals, whereas metabolism is more important to isotopes turnover in the adult individuals with no growth or during the seasonal slowdown of the growth rates (Bosley et al., 2002, Dattagupta et al., 2004, Perga and Gerdeaux, 2005). Muscles usually have slower tissue turnover than liver of fish or molts of crustaceans (Gorokhova and Hansson, 1999, Perga and Gerdeaux, 2005, Logan et al., 2006). Growth and tissue turnover rates are still relatively rarely accounted in the aquatic field studies interpreting SI data (Hart and Lovvorn, 2001, Herzka et al., 2002, Schmidt et al., 2003, Perga and Gerdeaux, 2005, Gustafson et al., 2007, Guelinckx et al., 2008).

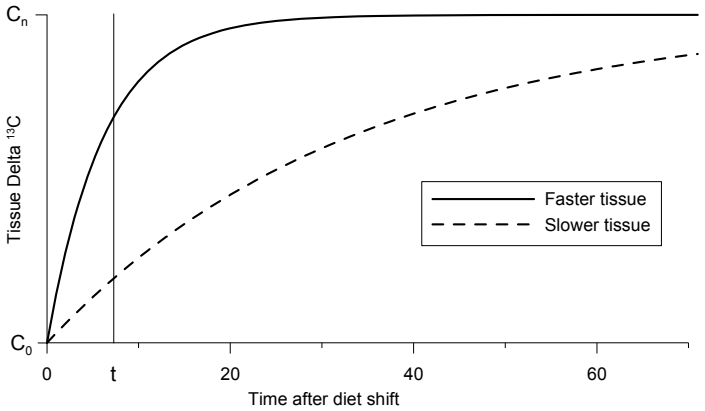

Fig. 1. Hypothetical isotopic changes in two tissues with faster and slower turnover after diet shift at time 0. Redrawn with modifications from Phillips and Eldridge, 2006, using Hesslein et al.'s (1993) exponential model of isotopic change following a diet shift in animal tissue. C_0 and C_n are the isotopic composition of animal tissue under the old and new diet, respectively.

The temporal variation of SI composition in the dietary components as well as the time over which consumer integrates the diet should be considered not only in the mixing models but also reconstructing the

food chains and calculating the trophic levels using SI field data. Usually, there is a strong linear relationship between $\delta^{15}N$ values in consumers and their trophic position in the aquatic food chains (Cabana and Rasmussen, 1994, Yoshii et al., 1999). Because of relatively constant step-wise 3.4 ‰ enrichement of consumer relative to diet, the trophic level of the consumers could be calculated knowing the $\delta^{15}N$ value of basal food source (Minagawa and Wada, 1984). However, if food chain components are collected once without any knowledge of temporal variations of SI ratios within the system, the $\delta^{15}N$ gives a misleading information on food chain structure. E.g., phytoplankton and zooplankton can have higher $\delta^{15}N$ than planktivorous fish due to quick assimilation of upwelled ^{15}N-enriched nitrate immediately prior to sampling for SIA (O'Reilly et al., 2002). Therefore, due to rapid stable isotope fluctuations at the level of inorganic nutrients, dissolved organic matter and particulate organic matter, long living primary consumers, such as mussels, are suggested as base-line organisms for $\delta^{15}N$ while analyzing the food web at upper trophic levels (Cabana and Rasmussen, 1996, Vander Zanden et al., 1999, Post, 2002). The establishment of base-line however should be specified for particular community, habitat and the time-scale over which it should integrate the SI variations at the basal food source. E.g. littoral gastropods are more appropriate to represent SI compositions of littoral primary producers, whereas zebra mussel and zooplankton represent pelagic primary production in lakes (Post, 2002). It should be considered also, that long living mussels will not capture acute fluctuations in basal food source (Gustafson, 2007). The ideal scenario is to select the baseline and the consumer that are biologically related and likely had similar temporal and spatial integration of food source isotopic signatures (Matthews and Mazumder, 2003). The task becomes more difficult, because in the natural conditions consumers usually feed upon multiple items with potentially varying turnover rates (Hart and Lavvorn, 2001). The estimation of most appropriate baseline to calculate the trophic levels, considering the different turnovers among primary consumers and high variability of $\delta^{15}N$ due to N_2 fixing, in the Curonian Lagoon food

web will contribute to understanding how the baseline $\delta^{15}N$ affects the reconstructed food chain length.

2.4. Trophic role of mysids

Mysids (Crustacea: Mysidacea) are common in the coastal and estuarine environments, however are often overlooked using conventional benthic and pelagic samplers (Mauchline, 1980). In coastal and estuarine ecosystems, mysids contribute considerably to secondary production (Fockedey and Mees 1999) and are an important food source for demersal fish (Hostens and Mees 1999) as well as for juveniles of predatory fish (Ložys 2003). They are opportunistic omnivores, feeding on the most abundant food sources (Fockedey and Mees 1999, Viherluoto et al. 2000), or selective feeders (Viherluoto and Viitasalo 2001), with seasonal and ontogenetic (Branstrator et al. 2000, Viherluoto et al. 2000) diet changes. There are also numerous observations that the composition of the mysid diet changes during their ontogeny (life-history omnivory), with herbivory dominating among juveniles and carnivory among adults (Viherluoto et al., 2000; Branstrator et al., 2000; Viherluoto and Viitasalo, 2001). The broad diet implies a variety of possible functional roles in the ecosystem food webs and difficulties in predicting their trophic linkages and extrapolating from one ecosystem to another. In particular, mysids are important in consumption of suspended matter in the detritus-based estuarine food webs (Fockedey and Mees, 1999), bentho-pelagic coupling by diel vertical migrations (Lasenby and Shi, 2004) and regulation of zooplankton community structure (Rudstam et al., 1989, Jane et al., 1996; Ketelaars et al., 1999; Spencer et al., 1999). An attention on mysid feeding investigations was particularly enhanced after their intentional introduction and uncontrolled spread in the inland waters of Europe and North America which affected local communities and functioning of the food webs (Grossnickle, 1982, Cabana and Rasmussen, 1994, Ketelaars et al., 1999, Spencer et al., 1999). The interest on the topic has also emerged in the coastal ecology, as long as broad tolerance of

mysids to environmental factors enables their spread from freshwater inland to brackish coastal habitats (Arbačiauskas, 2002, Ojaveer et al., 2002, Ovčarenko et al., 2006).

Three species of the Order Mysidacea are common in the Lithuanian part of Curonian lagoon: *Neomysis integer* (Leach, 1814) – the most widespread species in the Baltic (Köhn, 1992), and two species of Ponto-Caspian origin *Paramysis lacustris* (Czerniavsky, 1882) and *Limnomysis benedeni* (Czerniavsky, 1882). The Ponto-Caspian mysids were originally introduced in to Kaunas water reservoir and other lakes in 1960, and reached Curonian lagoon via Nemunas River (Gasiunas, 1963). One of the three introduced mysid species, *Hemimysis anomala,* was never detected in the northern part of the lagoon (Razinkovas, 1996, this investigation) but was occasionally captured in the central part (Razinkov, 1989). Another typical Baltic mysid of the genus *Praunus* occurs occasionally in Klaipeda strait area (Razinkov, 1990; Daunys and Zettler, 2006). Ponto – Caspian mysids became an essential food source for juvenile >1 to 2 years age group of perch and pikeperch in the Curonian Lagoon, mysids share in their diet is 62 and 98 % respectively (Ložys, 2003). *Neomysis integer* spreads in the lagoon along with brackish water mass (Razinkovas, 1996), their abundances of about 10 indv. m^{-2} can still be found in the 20 km distance to the sea inlet in the lagoon (Lesutienė, unpublished data). Its trophic role in the Curonian Lagoon is unknown. In other European coastal and estuarine environment *N. integer* behaves as opportunistic omnivore, feeding on most available food source or prefers carnivorous feeding (Köhn, 1992, Fockedey and Mees, 1999). *Limnomysis benedeni* is smallest among the mysids of Curonian Lagoon. Its food items largely include detritus and phytoplankton, occasionally - rotifers (Jankauskienė, 2003). However, decline in zooplankton was recorded after *L. benedeni* invasion (Ketelaars et al., 1999) which probably implies its wider diet spectrum. *L. benedeni* is restricted to submersed vegetation zone in the Curonian Lagoon (Razinkovas, 1996) and occurs rarely at the depths of >2 m (Lesutienė, unpublished data). As shown by mysid trapping in the vegetation dur-

ing vertical nocturnal migrations *P. lacustris* prevailes in the littoral mysid assamblages, however in highly vegetated study sites, *L. benedeni* numbers could be as high as *P. lacustris* (Lesutienė et al., 2005).

In feeding experiments conducted prior to the introduction, *Paramysis lacustris* showed a preferential feeding on detritus and phytoplankton (Komarova, 1991 and references therein) and, therefore, it was expected to improve the efficiency of detritus and primary production utilization in the eutrophic Curonian Lagoon (Razinkov, 1990). Contrary to the expectations, mentioned in Komarova, 1991, the stomach content analysis of field-collected *P. lacustris* revealed a significant proportion of planktonic crustaceans, especially during nocturnal vertical migrations, suggesting that mysids feed actively on mesozooplankton (Jankauskienė, 2003). Owing to their ability to forage on larger prey, adult *P. lacustris* are supposed to be more important feeders on zooplankton than juveniles. Food particle size selected by juveniles can reach up to 350 μm, while adults ingest prey ranging from 100 to 1700 μm (Jankauskienė, 2001). Therefore, during their nocturnal migrations, adult mysids are capable of foraging on many zooplankton species of Curonian Lagoon excluding large *Daphnia* and *Leptodora*. However there was no evident influence of mysids on zooplankton abundance and distribution in the littoral of Curonian Lagoon: zooplankton density and homogeneity increased at night, although mysids showed a clear tendency to aggregate in littoral vegetation during their nocturnal migrations (Lesutienė et al., 2005).

Microscopic analysis of mysid gut contents is rather difficult and could be misleading, because mysids macerate their food, which result in large proportion of unidentifiable particulate matter in their stomach contents (Mauchline, 1980, Grossnickle, 1982). Whereas SIA approach has been successfully applied to evaluate feeding of mysids (Toda and Wada, 1990; Gorokhova and Hansson, 1999; Branstrator et al., 2000). Therefore SIA is expected to give more insights in feeding ecology of Ponto-Caspian mysids in the Curonian Lagoon.

3. STUDY AREA

3.1. Water circulation, salinity and temperature

This study was performed in the northern part and the Nemunas River inflow area of the Curonian Lagoon (SE Baltic Sea). Each year, 23.1 km^3 of riverine water is discharged in to the lagoon (Žaromskis, 1996). The main field sampling of POM and consumers took place in 2006. In 2006, according to the Lithuanian Hydrometeorological Service, the average monthly river discharge differed slightly from the typical annual cycle (Fig. 2).

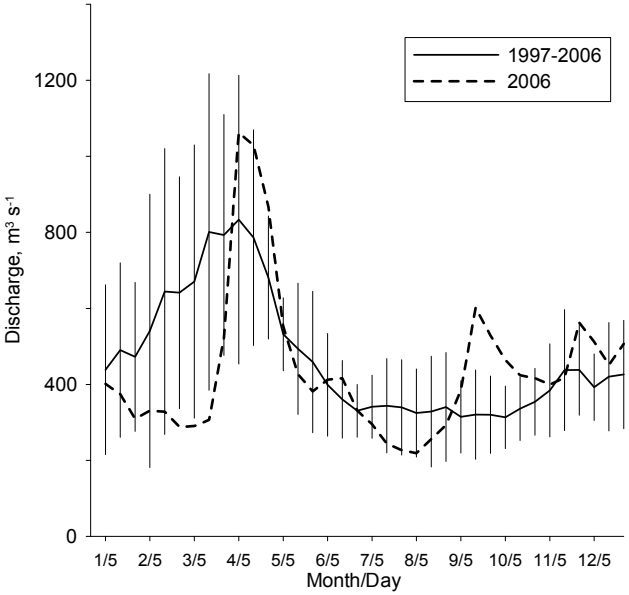

Fig. 2. Seasonal dynamics of the Nemunas River discharge; Lithuanian Hydrometeorological Service data, monitoring station *Smalininkai*, data presented as means ± SD of 5 days periods.

From May to November, 2006, river discharge peaked twice: in the mid of June (up to 469 m^3 s^{-1}) and in September (up to 664 m^3 s^{-1}),

whereas it was particularly low in July-August, with total seasonal minimum of 216 $m^3 s^{-1}$.

In terms of hydraulic zonation, the northern part of the Curonian Lagoon is classified as transitory and intermediate between transitory and stagnant (Ferrarin et al., 2008). In spring and autumn, whole northern part of the lagoon is essentially transitional, while in the summer, most of the lagoon areas are stagnant (Ferrarin et al., 2008).

About 5 km^3 of brackish Baltic water is carried in to the Curonian Lagoon annually (Žaromskis, 1996). The irregular sea water intrusions happen more frequently in autumn, most of them last 1-6 days (Gasiūnaitė, 2001). This water differs considerably from the fresh Curonian Lagoon water in its physical, chemical as well as biological properties (Žaromskis, 1996, Jokšas et al., 2005, Gasiūnaitė et al., 2008). The mixing of fresh and brackish water masses creates spatially and temporally unstable salinity gradient in a range of 0-8 in the northern part of the lagoon (Gasiūnaitė, 2001). The mean annual salinity, decreases from the Klaipeda Strait towards the central part of the lagoon (Dailidienė and Davulienė, 2007). Baltic Sea water influences mainly the area in a distance up to 20 km from the sea entrance (Ferrarin et al., 2008).

In May-October, 2006, there were 3 marine water intrusions that increased salinity at the monitoring station *Vente* to >0.5 (Fig. 3). Low river discharge (Fig. 1) and the substantial water level decrease after hot and dry period, caused the particularly intense marine water intrusion on 11 July, 2006 in to the lagoon (Galkus, 2007). Thereafter maximal salinity values of >7, typical for the brackish water, were measured at Juodkrante station (Fig. 3).

Water temperature in 2006 was on average 1.8°C higher than in 2004, September–October period the mean difference was 2.6 °C (Fig. 4).

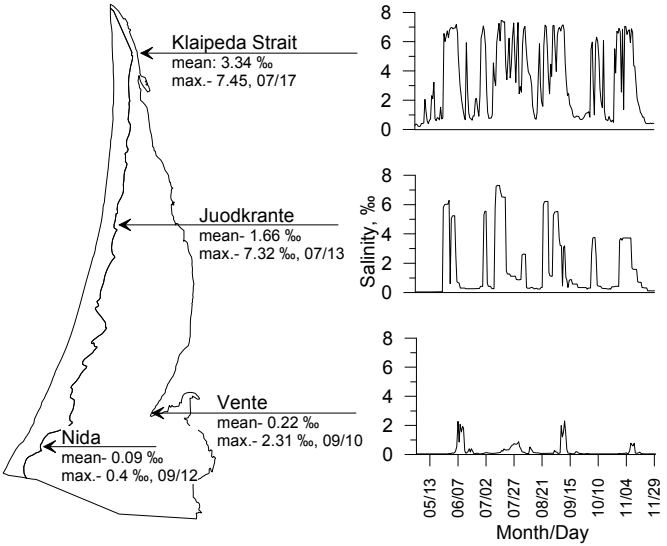

Fig. 3. Salinity in the Curonian Lagoon in 2006, Marine Research Centre monitoring data.

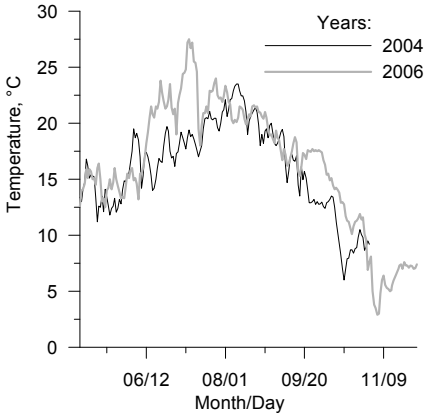

Fig. 4. Seasonal dynamics of water temperature in the Curonian Lagoon at monitoring station *Vente* (VL, see Fig. 5); Marine Research Centre data.

3.2. Suspended particulate matter

Annually, the Curonian Lagoon receives 170000 t of particulate organic material from 100500 km^2 catchment area, 98 % of which belongs to the Nemunas River (Žaromskis, 1996, Galkus and Jokšas, 1997). The greatest concentrations of particulate sedimentary material in lower reaches of the Nemunas River occur during spring spate ~30 and summer ~25 mg l^{-1}, the lowest – in winter (Jokšas et al., 2005). In summer, during the lowest discharge period (Fig. 2) the river water at the lower reaches is characterized by highest relative contribution of organic matter ~50 % to the total particulate matter (Jokšas et al., 2005).

Marine water mass is characterizd by 3-6 fold lower concentration of suspended particulate matter than in the Curonian Lagoon or the Nemunas River; it varies in the range of 5-7 mg l^{-1} and contains 50-60 % of organic matter during the spring-autumn period (Jokšas et al., 2005).

The major source of organic matter in the Curonian Lagoon is autochthonous phytoplankton, ~610 000 t particulate matter is produced annually in the lagoon, with a half of it produced during the summer (Table 1, Galkus and Jokšas, 1997). Freshwater phytoplankton assemblage in the lagoon follows a seasonal cycle typical for eutrophic basins: the succession starts with prevalence of diatoms in spring, biomass peak is reached in August-September by the highest contribution of Cyanobacteria, whereas diatoms dominate again at the end of vegetation season (Olenina, 1997). The potentially toxic *Microcystis* spp. and N_2-fixing *Aphanisomenon flos-aquae* prevail in the cyanobacteria assemblage during the summer peak (Olenina, 1997, Pilkaitytė and Razinkovas, 2006). The total abundance of phytoplankton decreases with increasing salinity (Gasiūnaitė et al., 2008). Diatoms dominate phytoplankton community in the lower reaches of Nemunas River from April to July, green algae are also abundant during May-September, whereas cyanobacteria prevail only in August (Gasiūnaitė et al., 2008).

The relative contribution of different sources to the annual balance of POM in the lagoon could be outlined as follows: the major source is lagoon phytoplankton (69 %), riverine phytoplankton (16 %), riverine allochthonous matter (mainly humic substances, 3 %), other allochthonous organics (rain, dust, etc., 10 %), marine POM- 2 %, with some seasonal variation (Galkus and Jokšas, 1997; Table 1). Relatively large part of riverine and lagoon phytoplankton (i. e., autochthonous organic matter) is outflowed to the sea, whereas allochthonous detritus tends to accumulate in the lagoon (Table 1). Most of suspended sedimentary material outflowed from the Curonian Lagoon deposits in the close proximity or is transported along the coast by dominant water stream of northern direction (Galkus and Jokšas, 1997).

Table 1. The sources (amount thous. t) of the particulate organic matter (POM) in the Curonian Lagoon; modified from Galkus and Jokšas, 1997.

Source of POM	**Income sources**					**Out-flow**	**Stay in the lagoon**
	Rivers	**Primary production in the lagoon**	**Sea**	**Other**	**Total**		
Spring							
Autochthonous	75.0	97.6	2.16		174.8	106.4	**68.4**
Allochthonous	3.85		0.49	40.35	44.7	0.5	**44.2**
Summer							
Autochthonous	44.1	296.6	3.6		344.3	59.2	**285.1**
Allochthonous	4.9		1.45	18.05	24.4	2.5	**21.9**
Autumn							
Autochthonous	20.1	198.9	6.3		225.3	49.6	**175.7**
Allochthonous	5.1		0.5	21.9	27.5	3.5	**24.0**
Winter							
Autochthonous	3.6	17.1	1.3		22.0	5.75	**16.3**
Allochthonous	13.4		1.2	9	23.6	5.65	**18**
Year							
Autochthonous	**142.8**	**610.2**	**13.4**		**766.4**	**220.9**	**545.5**
Allochthonous	**27.25**		**3.6**	**89.3**	**120.2**	**12.2**	**108.1**

3.3. Mesozooplankton, macrozoobenthos and fish

The fresh water mesozooplankton community is composed of cladocerans and copepods (*Daphnia*, *Bosmina*, *Diaphanosoma*, *Chydorus*, *Cyclops* and *Eudiaptomus* species), whereas brackish water assemblage is mainly contributed by calanoids *Acartia*, *Temora* and *Eurytemora* (Gasiūnaitė, 2000). The detailed composition and seasonal dynamic of mesozooplankton community are described elsewhere (Gasiūnaitė and Razinkovas, 2004).

The mean annual salinity is a main factor determining the distribution of the benthic species in the northern part of Curonian Lagoon (Daunys, 2001). The sandy bottoms in the sea water inflow area are mainly occupied by Oligochaeta, Chironomidae, *Valvata* spp., *Marenzelleria neglecta* (Olenin 1996, Daunys, 2001). The biomass and biodiversity of macrozoobenthic community is higher in the area exposed to the Nemunas River delta (Daunys, 2001). The mussel beds of *Dreissena polymorpha* create a stable substrate and sheltering structures which are inhabited by various benthic species: chironomids, oligochaetes, leeches, gastropods and crustaceans (Olenin 1996, Daunys, 2001, Zaiko, 2009). Littoral open and vegetated habitats are characterized by benthic communities, with the significant contribution of Ponto-Caspian amphipods during the vegetation season (Daunys and Oleninas, 1999). Species contribution to the amphipod assemblages differs in the freshwater and brackish areas (Daunys and Zettler, 2006, Arbačiauskas, 2008).

The fish assemblage in the Lithuanian part of the Curonian Lagoon is dominated by demersal species: bream (*Abramis brama*, 22 % of total fish biomass), roach (*Rutilus rutilus*, 33 %), ruffe (*Gymnocephalus cernuus*, 13 %) and silver bream (*Blicca bjoerkna*, 10 %). Predatory species in the community are represented by perch (*Perca fluviatilis*, 15 %) and pikeperch (*Stizostedion lucioperca*, 3 %) (Repečka, 1997 cited by Žydelis and Kontautas, 2008).

4. MATERIAL AND METHODS

4.1. Sampling sites

All field sampling was conducted by the author, with a help from the colleagues from Coastal Research and Planning Institute, Klaipeda University, during years 2003 to 2006 (Table 2). The food web studies included two sites (JO-JL and VO-VL, Fig. 5) in the northern part of the Curonian Lagoon. POM was collected at several sites in the lagoon (VL, SL, VO, JO Fig. 5), the Nemunas River and the Baltic Sea. Mysids for feeding and population dynamic investigations were collected at the littoral (VL) and offshore (VO_4) stations (Fig. 5).

The principal difference between the sites **VL-VO** and **JL-JO** are in salinity, sediment type, and zoobenthic community structure (Table 3). Three types of bottom habitats that differ in number and abundance of benthic species could be found in an area VO: 1) **VO_1**- bottom sediments dominated by zebra mussel shell deposits; 2) **VO_2**- living zebra mussel community; 3) **VO_3**- no zebra mussel in the zoobenthos community and no zebra mussel shells in the sediments (Zaiko, 2009). They were sampled in order to collect more diverse zoobenthos assemblages for stable isotope analysis (SIA) and to consider the spatial heterogeneity within an area. At the mysid monitoring station **VO_4** (Fig. 4), bottom is also cowered with living mussels or shell deposits. VL and JL stations have slightly different sediment types and vegetation cower pattern, whereas salinity conditions correspond to that in offshore stations VO and JO respectively (Table 1). **SL** station (Fig. 4) is located in the eastern littoral of the lagoon at the moderate distance from the sea inlet (~30 km), submersed vegetation here is relatively scarce, represented mainly by charophytes (pers. observations). The riverine sampling site **NR** is located 14 km upstream the Nemunas River entry to the Curonian Lagoon in one of tributaries - Atmata of the delta (Fig. 5). Baltic Sea (**BS**) station is located at 6 km distance to the Curonian Lagoon outflow, to shore- 1 km, depth - 7-8 m (Fig. 5).

Table 2. Set of sample material used in the thesis; sampling sites and time. VO, JO - offshore, VL, JL, SL- littoral sites in the Curonian Lagoon, NR - Nemunas River and BS - Baltic Sea.

Study object	Sampled material	Date, period/Sites
Mysid spatial distribution and abundance	Quantitative samples of mysid	2003 July 15/ 11 stations 2004 August 18/ 10 stations 2006 August 3/ 14 stations
Mysid population dynamic and growth rate analysis		2004 June - October /VO, VL 2006 June – November/ VL
Mysid feeding on zooplankton in the pelagial	1) Quantitative samples: phytoplankton and zooplankton; 2) Samples for SIA: mysids, mysid stomachs and zooplankton	2004 June – October/VO
Mysid feeding in littoral	1) Quantitative samples: phytoplankton and zooplankton; 2) Samples for SIA: mysids, zooplankton, EPOM, BPOM, macrophytes	2006 August – November/VL
Structure of the food web	Samples for SIA: EPOM, macrophytes, zooplankton, macrozoobentos, fish	2006 May-August-October/VO, VL, JO, JL
Temporal and spatial variation of SI composition in POM	1) quantitative samples: chlorophyll a, POM concentration, phytoplankton 2) POM samples for SIA	2006 May – November/ NR, VL, BS, SL, JL

4.2. Quantitative sampling

4.2.1. Phytoplankton and zooplankton

Quantitative samples of phytoplankton and EPOM samples for SIA were collected simultaneously at VL in 2006. Mesozooplankton and phytoplankton samples were collected in concert with mysid sampling at VO and VL in 2004 and 2006, respectively. Quantitative samples of mesozooplankton were also taken during the food web sampling surveys at JO and VO sampling sites in May, August and October, 2006.

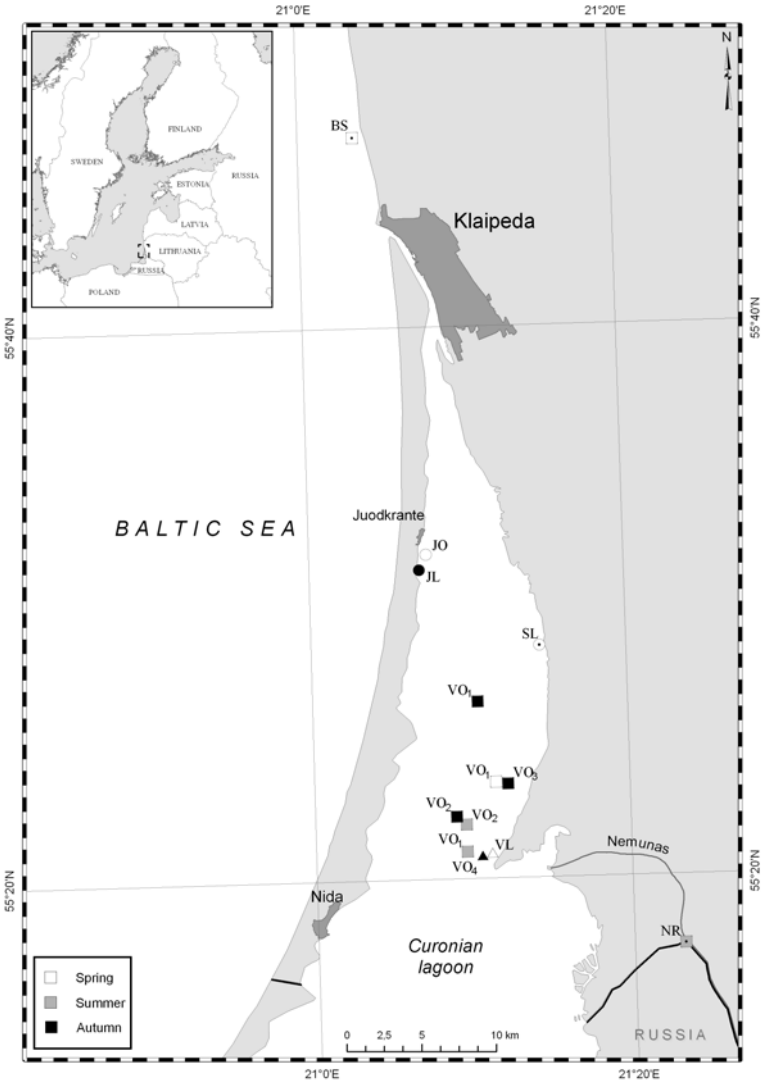

Fig. 5. Location of the study sites in the Curonian Lagoon, the Nemunas River and the Baltic Sea.

Table 3. Abiotic and biotic characteristics of the study sites.

	River inflow area	Sea water inflow area
Offshore sampling sites	**VO**	**JO**
Depth[a,c], m	3-4	1-2
Distance to the sea inlet, km	~40	~20
Distance to the river mouth (Atmata)	~10 km	~30 km
Salinity[b]		
Annual Max – Annual Min	2.43 – 0.03	7.24 – 0.04
Spring Mean ± SD	0.04 ± 0.05	0.54 ± 1.32
Summer Mean ± SD	0.05 ± 0.08	1.44 ±1.92
Autumn Mean ± SD	0.12 ± 0.18	1.9 ± 2.15
Residence time, days[f]	40-100	80-100
Sediments[c]	Mussel beds, shell deposits with silt and sand	fine sand
Macrozoobenthos[d, e]		
Biomass, g m^{-2}	880-11 000	~100
Dominant species, contribution by biomass %	*Dreissena polymorpha*, 83 %	*Valvata* spp., 60 %
Total number of species	75	51
Littoral sampling sites	**VL**	**JL, SL**
Depth[c], m	0.7 – 1	0.7 – 1
Sediments[c]	Sand, stones and shells deposits	sand
Submersed vegetation		
Species	*Potamogeton perfoliatus, P. pectinatus, Cladophora spp.*	*P. perfoliatus, P. pectinatus, Cladophora spp.*
Coverage in summer	75-100%	<50%
Amphipods[g,h]		
Dominant species	*Pontogammarus robustoides*	*Obessogammarus crassus, Gammarus tigrinus*

[a]Žaromskis, 1996; [b]Dailidienė and Davulienė, 2007; [c]Gulbinskas et al., 2002; [d]Olenin, 1996; [e]Daunys 2001; [f]Ferrarin et al., 2008, [g]Daunys and Zettler, 2006, [h]Arbačiauskas, 2008.

Phytoplankton and zooplankton samples were taken with a 10-L Niskin sampling bottle. For phytoplankton community analysis, 200 ml of water were fixed with acid Lugol solution. Phytoplankton taxonomic composition (identified to species, genus or higher taxa, picoplankton not included), abundance and biovolume were estimated using inverted microscope (200× and 400×) according to HELCOM recommendations (HELCOM, 1988). In 2006 (VL), the biovolume was calculated according to HELCOM, 1988 recommendations. The biovolume of two cell/filament/colony length groups, <70 and >70 μm was calculated separatelly. In 2004 (VO), only cyanobacteria (100-μm units of filaments and colonies of coccoids considered as a counting unit) were counted.

For zooplankton community analysis, 3 × 10 L subsamples were taken (at the offshore stations from 0.5, 1, and 2 m depths) and pooled together. Sample water was filtered through a 70-μm net and zooplankton was preserved with 4% formaldehyde. Mesozooplankton organisms (0.2-2 mm; HELCOM, 1988) were identified to species or genus level, measured and counted under an Olympus SZ40 stereomicroscope equipped with an ocular micrometer. The biomass, expressed as dry weight (DW mg L^{-1}), was calculated using length measurements and allometric regressions (Rumohr et al., 1987; Jorgensen et al., 1995).

4.2.2. Mysids

Samples for mysid spatial distribution analysis were taken during 3 field trips in July-August of 2003, 2004 and 2006 in the northern part of the Curonian Lagoon. The depth and sediment type, including the fraction of *Dreissena polymorpha* shells during the survey in 2003, were estimated. Mysids were collected with an epibenthic sledge net (opening 20 × 60 cm, mesh size – 500 μm) at 32 sampling sites located at the depths ranging from 0.7 to 3.8 m. Three replicate samples, each covering 4 – 15 m^2 were taken at the sampling site and preserved in 4% formaldehyde. All mysids were identified and counted in the sample. Body lengths (BL, mm) from the tip of the rostrum to the end

of the telson were measured using ocular micrometer (±0.1mm) under the stereomicroscope; if possible all individuals were measured, otherwise 120 specimens in each replicate sample were randomly selected and measured. The length- dry weight relationship of *P. lacustris* was established, excluding the females caring embryos in their marsupium. Each individual was measured, dried individually at 60 ºC for 48 h and weighted using a Sartorius M3P microbalance (±0.002 mg). The biomass (B, DW mg/m^2) of *P. lacustris* population was estimated as $B=\Sigma B_i \times N_i$, where N_i - abundance (indv m^{-2}) and B_i - dry weight (DW, mg) of i^{th} size group (each 1 mm length interval).

Samples for mysid population dynamics and growth rate analysis were collected at two stations: offshore - VO_4, at 2.5 m depth and littoral – VL, at 0.8 m depth (Fig. 5). Samples were taken weekly at both stations in June-October, 2004, and with 1 to 3 week interval at VL station in July-November, 2006. The trawling area was 45 m^2 in the open-water station but was limited to 15 m^2 in the littoral because of the submersed vegetation clogging the net. Samples were collected in triplicate and preserved with 4% formaldehyde. In each replicate, all specimens were identified, counted and measured. If available, 100 individuals were measured; otherwise, all individuals were measured.

4.3. Sample collection and preparation for stable isotope analysis

4.3.1. Particulate organic matter and macrophyte

Routine sampling of estuarine particulate organic matter (EPOM) and riverine particulate organic matter (RPOM) was performed at VL station in the lagoon (Fig. 5) and in the Nemunas River (NR) from May to November, 2006, with 3-4 wk interval. Littoral station SL (Fig. 5) was sampled simultaneously with VL on July 31, to trace the salinity effect on stable isotope composition in the EPOM. EPOM was also collected occasionally at the offshore stations (VO and JO), jointly with other food web components (in May, August and October, Table

4). Marine particulate organic matter (MPOM) was sampled in the Baltic Sea (Fig. 5) on two occasions: July 11 and August 8, 2006.

Samples for POM stable isotope analysis were taken using a 10-L Niskin sampling bottle and transported to the laboratory in 3-5 L acid pre-washed plastic vessels each replicate sample separately. Chlorophyll-a content (μg L^{-1}) in the POM <70μm fraction, POM <70μm concentration (mg DW L^{-1}) as well as salinity and water temperature were measured on each sampling occasion (the data are given in the Appendix 2). At the littoral stations, all EPOM samples were taken in calm weather to avoid resuspension of bottom sediments, except for November 9, when strong winds of ~16 m s^{-1} (according to MRC data) caused a substantial mixing.

Sampled water was prefiltered through 70 μm mesh to remove zooplankton and concentrated onto glass fibre filters (Whatman, GF/F, 0.7μm pore size). On several sampling occasions, including those for food web sampling, EPOM was separated into <70 μm and 100-200 μm fractions. The Curonian Lagoon phytoplankton is frequently dominated by large cyanobacteria colonies, such as *Microcystis* spp. and *Aphanizomenon* spp. (Pilkaityte, 2003). Therefore total phytoplankton could not be precisely separated from zooplankton. However, small zooplankton that was not possible to remove from the samples and colonies of N_2-fixing *Aphanizomenon* spp. could have contributed to the SI signatures, with opposite effects on $\delta^{15}N$ values in larger fraction of EPOM. Indeed, atmospheric N_2 fixation has a small fractionation factor, diazotrophs have lower $\delta^{15}N$ than other phytoplankton (Michener and Schell, 1994), while zooplankton $\delta^{15}N$ are usually higher than those of their diet (Vincent et al., 2007). Its contribution to the EPOM stable isotope composition therefore should be considered.

Samples on GF/F filters were dried for 48 h at 60 ˚C and weighted. From each filter, three subsamples were prepared by cutting a 4-8 mm diameter circle using a puncher, packed into the tin capsules, weighted and used as analytical replicates. For each filter, 10 to 20% of the filtering area was analyzed.

Potamogeton perfoliatus and filamentous littoral algae *Cladophora* spp. were collected manually on food web sampling surveys in spring and summer at VL and JL stations (Table 4). Samples were cleaned with a tap water, washed with 1M HCl to remove carbonates and rinsed with distilled water (Cloern et al., 2002). Macrophyte material was placed in to the aluminium foil cups, dried at 60˚C for 48 h, grind to fine powder using mortar and pestle and weighted in to tin capsules for SIA.

4.3.2. Invertebrate and fish

Animal samples for the SIA were collected at two sites in the northern part of the Curonian Lagoon (VO-VL and JO-JL, Fig. 5) on three occasions: in spring - May 24-31, summer - July 31/ August 1-8 and autumn - October 10-11, 2006. The set of samples taken for SIA included zooplankton, nectobenthos, macrozoobenthos and fish (Table 4). Depth, water temperature and salinity were measured on each sampling occasion.

Mesozooplankton samples were taken with 10 L Niskin water sampler by filtering 30-500 L water from the different water column layers (0, 1, 2 m depth) through 200 μm zooplankton net. Samples were transported to the laboratory in 3-5 L acid pre-washed plastic bottles. Visible debris, large filaments of cyanobacteria and specimens of *Leptodora kindtii* were removed from the samples with forceps using a dissecting microscope. Than mesozooplankton was concentrated onto glass fibre filters (Whatman, GF/F, 0.7μm pore size). *Leptodora kindtii* was sampled with the large plankton net (50cm diameter, 500μm mesh size). Specimens were cleaned from visible debris and collected in on to the GF/F filters. The further treatment of zooplankton samples same as for POM filter samples (Section 4.3.1).

Amphipods were collected with the hand-net at the shallow littoral stations VL and JL. Mysids were collected using epibenthic sledge. Ekman or Van Veen bottom grab samplers were used to collect macrozoobenthos. The sediments were sieved through 500 μm sieve, specimens collected with the forceps and placed alive in to the prefil-

Table 4. Salinity, temperature (T), wind speed, at the stable isotope sampling stations VL, VO, JL and JO. EPOM<70, EPOM 100-200- suspended particulate organic matter of <70µm and 100-200 µm particle size, ab- *Abramis brama*, ch- Chironomidae, cl- *Cladophora* spp., dp- *Dreissena polymorpha*, e- Erpobdellidae, et- *Eiseniella tetraedra*, g- Glossiphoniidae, gm- Gammaridae, gc- *Gymnocephalus cernuus*, lb- *Limnomysis benedeni*, lk- *Leptodora kindtii*, lm- Lymnaeidae, mn- *Marenzelleria neglecta*, o- Oligochaeta, pc- *Pelecus cultratus*, pf- *Perca fluviatilis*, pl- *Paramysis lacustris*, pp- *Potamogeton perfoliatus*, rr- *Rutilus rutilus*, sl- *Stizostedion lucioperca*, u- Unionidae, va- *Valvata* spp., vi- *Viviparus* spp., z- mesozooplankton (>200µm). Subscript juv- juveniles, ad- adults. Asterisks denote fish samples collected from fisherman. nd- no data.

Study site	Salinity, psu T, ˚C Wind speed, m s^{-1}			Samples collected		
	Spr	Sum	Aut	Spring	Summer	Autumn
VL	0.06 14.06	0.88 25.12	0.04 13.74	SPOM<70, cl, pl_{ad}, pp	EPOM<70, cl, gm, lb_{ad}, pl_{ad}, pl_{juv}, pp	EPOM<70, EPOM100-200, pl_{ad}, pl_{juv}, z
VO	0.04 13.98	0.3 21.53	0.04 14.25	SPOM<70, ch, dp, e, et, g, o	EPOM<70, EPOM100-200, ch, dp, e, et, g, lk, lm, o, pc*, pf*, pl_{ad}, pl_{juv}, rr*, u, va, vi, z	EPOM<70, EPOM100-200, ch, dp, e, et, o, pl_{ad}, pl_{juv}, va, vi, z
JL	- - -	0.4 22.9 nd	- - -	-	gm, gc_{juv}, pf_{juv}, pp, rr_{juv}	-
JO	0.05 14.1 nd	0.9 22.3 nd	0.45 14.3 nd	EPOM<70, EPOM100-200, lk, mn, o, pl_{ad}, va, z	EPOM<70, EPOM100-200, ab*, ch, lk, o, pl_{ad}, pl_{juv}, sl*, va, z	EPOM<70, EPOM100-200, ab*, ch, gc*, mn, pf_{juv}*, pf_{ad}*, pl_{ad}, pl_{juv}, rr*, va, z

tered water for gut content evacuation and transported in the coolers for further treatment in the laboratory. All specimens were sorted and

identified to species or genus level (except chironomids and oligochaetes) under dissecting microscope. Details of mysid sample preparation are in Section 4.3.3. The shell length (SL) of the bivalves, shell height (SH) of the gastropods, amphipod body length (BL) were measured to the nearest millimetre. Two size groups of amphipods: 5-10 mm and > 10 mm and *Dreissena polymorpha* SL~1 cm and ~2 cm were considered. The whole body of amphipods, chironomids, oligochaetes, polychaetes, leaches, and soft tissues of molluscs (mantle muscle if possible) were taken for SIA. Sample material was washed in the distilled water and placed in the aluminium foil cups using forceps. Each specimen of mysid and large molluscs was sorted individually, whereas 10-20 spesimens of other macrofauna (chironomids, oligochaetes, amphipods and small molluscs) were pooled.

Littoral juvenile fish were caught using modified Breder-trap (Lesutiene et al., 2005). In summer, adult fish were collected from the local fisherman fishing in the VO and JO sampling areas, whereas in the autumn (November 28) fish samples were collected in the southern part of the Klaipeda Channel, at the Kiaules Nugara Island, during the survey within the "Klaipeda state seaport environmental monitoring program". The specimens were determined to species level; the total length (TL, cm) of each individual was measured. The white muscle of fish were dissected from the dorsal part and placed individually into the foil cups.

All samples were dried at 60°C for 48 h, grinded to fine powder in an agate mortar, and assigned to 2-5 analytical replicates (3-10 individuals of each taxonomic/size group per replicate if available). See Appendix 1 for sample types, specimen's description (taxonomy, BL, L of fish or SH and SL of molluscs) as well as number of replicates.

4.3.3. Mysid and their food sources

Mysids, collected at the offshore station (VO_4) in 2004 and preserved in 4% formaldehyde were used for body tissue and stomach content $\delta^{15}N$ analysis. To compare mysid bolus $\delta^{15}N$ to that of ambient zoo-

plankton, the formaldehyde preserved zooplankton samples were used. To derive isotopic composition of the bolus at the time of collection, stomachs of adult mysids were dissected from the dorsal side, transferred to tin capsules (2-3 analytical replicates per size group, 6-7 stomachs per replicate), and processed separately from the bodies. In preparation for SIA, mysids were rinsed with distilled water and measured. The specimens were classified into 4 size groups: juveniles (<5 mm; grand mean±SD: 4.2±0.5mm), subadults (5-7 mm; 6.3±0.4 mm), small adults (7-10 mm; 8.7±0.7mm), and large adults (>10 mm; 11.2±0.8mm). From each collection, 10 to 20 randomly selected individuals per group were used, depending on availability. Whole shrimps (juveniles and subadults) or abdominal tissue (adults) were used to derive body isotopic signatures; mysid abdomen was assumed to represent muscle tissue of the animal. All samples were dried at 60 °C for 48 h, grinded in an agate mortar, and assigned to 5 analytical replicates, 3-4 individuals per replicate. The dry mass of the samples was determined to the nearest microgram using a Sartorius M3P microbalance. Zooplankton samples were filtered trough a 200-µm nylon mesh and rinsed with tap water. Using a dissecting microscope, specimens of *Leptodora kindtii*, visible debris occasionally found in zooplankton samples as well as large filaments of cyanobacteria were removed with forceps. Residual water was removed from underneath the sieve with paper tissue. Bulk samples of crustaceans were then transferred to pre-weighed tin capsules (1 to 5 replicates for each sampling occasion), dried at 60 °C for 24 h and stored desiccated until the analysis.

To calculate the diet composition of *P. lacustris* using mixing models, the dual isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ was performed. Fresh material of mysids and their potential food sources (i.e., zooplankton, detritus, submersed vegetation, EPOM and BPOM) were sampled for SIA on four occasions: August 30, September 19, October 10 and November 9, in the littoral station VL in 2006. EPOM samples taken at VL station for the seasonal dynamics analysis (Section 4.3.1.) were used in the mysid diet investigations. All samples were transported to the

Table 5. Sampling dates, number of replicates (n) and sample preparation procedures for SIA of mysids and their potential food sources in the littoral (VL) in 2006.

Sample type		Sampling dates and number of replicates (n)	Sample preparation
Submersed macrophytes		Aug 30 (5)	Dead foliage and green leaves of *Potamogeton perfoliatus*
POM	EPOM <70 µm	Aug 30(3), Sept 19(3), Oct 10(3), Nov 9(5)	Water sample (300-1200 ml) filtered through 70µm net and concentrated onto GFF.
	RPOM	Aug 30(5), Oct 10(5)	
	EPOM 100-200 µm	Aug 30(3), Oct 10(3)	Water sample filtered through 200µm, collected on 100µm net, cleaned from mesozooplankton and debris, and transferred to GFF.
BPOM		Aug 30(4), Sept 19(5), Oct 10(5)	Sediments sucked from a surface with a syringe, cleaned from coarse plant debris and zoobenthos, and transferred to GFF
Mesozooplankton		Aug 30(3), Sept 19(3), Oct 10(2)	Collected on 200µm net, cleaned from phytoplankton, using dissecting microscope, forceps and pipette, concentrated onto GFF
Mysids	subadults BL 5-7 mm	Aug 30(5), Sept 19(3), Oct 10(3)	*P. lacustris* dried for 48h at 60˚C; abdominal tissues pulverized and weighted into the tin capsules. Each replicate sample contained up to 6 pooled specimens, if available, to reduce the individual variation.
	adults BL >7 mm	Aug 30(5), Sept 19(3), Oct 10(5), Nov 9(4)	

laboratory in coolers for sorting and sample preparation (Table 5). The leaves of *P. perfoliatus,* both decomposing and fresh, were collected manually and treated as described in Section 4.3.1. Mesozooplankton for SIA was concentrated by filtering 200-300 L of water through 200 µm mesh. BPOM was carefully sucked from the sediment surface of approximately 0.1 m^2 with a syringe and transferred to glass vessels; the total amount of 0.5 L of the suspension was collected for each rep-

licate. The samples were sedimented for 2 h in cold to allow sand particles to settle down. The suspension was carefully transferred to a Petri dish and the large pieces of plants as well as benthos (small amphipods, oligochaetes, nematodes and harpacticoids) were removed with forceps under the dissecting microscope. The remaining suspension was concentrated on glassfiber filters. Further sample treatment is described in Section 4.3.1.

4.4. Stable isotope analysis

Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ as well as %C and %N in the samples were determined using continuous-flow isotope mass spectrometry provided in Automated NC Analysis (ANCA) SL 20-20, PDZ Europa at the Stable Isotope Facility, UC Davis, USA. The standard reference materials were Vienna PDB and atmospheric N_2. Isotope ratios were expressed as parts-per-thousands (‰) differences from the standard reference material (Peterson and Fry, 1987). Repeated analyses of homogeneous material yielded standard deviations of less than 0.05 %.

4.5. Mathematical and statistical methods

4.5.1. Stable isotope data analysis

Spearman's rank correlation coefficients were calculated to assess the relationship between: (1) POM concentration, phytoplankton biomass, and chlorophyll a content; (2) $\delta^{15}N$ and $\delta^{13}C$ values in POM and river discharge, phytoplankton biomass, biomass of diazotrophic cyanobacteria and C/N ratio in POM.

One-way ANOVA was applied for (1) spatial effect on stable isotope composition ($\delta^{15}N$ and $\delta^{13}C$) in POM followed by Bonferroni post-hoc procedure, and (2) for all consumers species effect on $\delta^{15}N$ and $\delta^{13}C$ values in summer, followed by Fishers LSD post hoc comparisons for grouping by similar $\delta^{13}C$ and $\delta^{15}N$ values.

Two-way ANOVA was used to evaluate effects of (1) sampling site (NR vs. VL) and time (7 sampling occasions from May to October in 2006) on the $\delta^{15}N$ and $\delta^{13}C$ in POM, (2) species and season (spring, summer, autumn) on the $\delta^{15}N$ and $\delta^{13}C$ in consumer (3) species and sampling site (VO-VL vs. JO-JL) on the $\delta^{15}N$ and $\delta^{13}C$ in consumers. Bonferroni or Tukey post-hoc comparisons were applied to investigate the differences between individual groups. T-test and paired t test were also applied to compare the means.

4.5.2. Trophic level and mixing model calculations

Trophic levels (TL) were calculated for the first and second order predators: leeches, benthivorous and predatory fish in summer using single and combined baselines of primary consumers. Single baseline TL were calculated by the equation (1):

$TL = \left(\delta^{15}N_{sc} - \delta^{15}N_{baseline}\right)/3.4 + 2$ (Post 2002) (1), where $\delta^{15}N_{sc}$ nitrogen isotope ratio in secondary consumer of interest, $\delta^{15}N_{baseline}$ is nitrogen isotopic baseline of primary consumer, corresponding TL 2. The $\delta^{15}N$ values of *Valvata* spp., Chironomidae and Bivalvia (large ~2 cm *Dreissena polymorpha* and *Unio* spp.) were averaged between the sampling stations to generate the baselines.

The combined baseline method, proposed by Post (2002) to calculate the trophic position of the predators that use ultimate food source from different food webs: pelagic- base1, and littoral- base2, was applied in this study to calculate TL of the predators that are based on two isotopically distinct groups of primary consumers (base1, base2), that reflect old signal of ultimate source of organic matter and recent signal of dietary organic matter, produced in the summer:

$TL = 2 + \left(\delta^{15}N_{sc} - \left[\delta^{15}N_{base1} \times \alpha + \delta^{15}N_{base2} \times (1-\alpha)\right]\right)/3.4$, (Post 2002) (2), where α is the proportion of nitrogen in the secondary consumer ultimately derived from the base1. Assuming the same flow rate of nitrogen and carbon from the diet to the predator, α is estimated using $\delta^{13}C$ by the equation (3):

$$\alpha = \left[\delta^{13}C_{base2} - \left(\delta^{13}C_{sc} + \Delta_c t_{sc}\right)\right] / \left(\delta^{13}C_{base2} - \delta^{13}C_{base1}\right) \text{ (Post 2002)}_{(3)},$$

where Δ_c is the trophic fractionation, t_{sc} trophic position of the secondary consumer of interest.

Dual-isotope mixing model IsoError (Phillips and Gregg, 2001) was applied to calculate the assimilated diet composition by biomass for the primary consumers (suspension and deposit feeders) in summer, using $\delta^{15}N$ and $\delta^{13}C$ values of the consumers and potential POM sources (EPOM, RPOM and MPOM). EPOM stable isotope composition shifted substantially from spring to summer, but the new diet was reflected in consumers only with certain time lags, therefore old signatures of EPOM were also included in to mixing models as end-points. If the POM sources were isotopically indistinguishable (t-test, $p>0.05$) or the difference between sources was <2 ‰, the combined end-member isotopic signatures were calculated (Phillips and Gregg, 2001, Phillips et al., 2005), averaging the $\delta^{15}N$ and $\delta^{13}C$ values between (1) the sampling sites (i.e., riverine and estuarine, marine and estuarine), (2) sampling dates, to reflect assimilation of the POM during the sertain period in the past: a) in spring and preceding halph of the year (RPOM/EPOM May – September - October), during previous two months (EPOM/MPOM June - July) or week (EPOM July 31 and August 2-4). Standard deviations (SD) of the combined end-members in the mixing models were determined by first-order error propagation of uncertainties: $SD_{combined} = \sqrt{\left(SD_1^{\,2} + SD_2^{\,2}\right)}$. Trophic enrichment factors of 3.4 and 1 ‰ were used in the models for $\delta^{15}N$ and $\delta^{13}C$, respectively (Post, 2002).

To determine the contribution of littoral macrophytes to the diet of juvenile, mainly herbivorous, amphipods and mysids IsoSource two isotopes-five sources mixing model was applied (Phillips and Gregg, 2003). Littoral macrophytes (*Potamogeton perfoliatus* and *Cladophora* spp.) and 3 wk old as well as most recent EPOM isotopic signatures were taken as end-points, as older signal of EPOM was not expected in the tissues of fast growing juvenile crustaceans. All possible

combinations of each source contribution (0-100 %) were examined in 1 % increments.

For adult mysids, caught at VO_4 in 2004, we calculated δ^{15}N of the bolus using isotopic signatures of mysid stomachs and muscle tissue and assuming stomach tissue having the same isotopic composition as muscle tissue from the abdomen. The mass of the stomach tissue in the full mysid stomach was assumed to be 25% of the stomach mass as was experimentally determined for *Mysis mixta* in the same size range (Gorokhova, 2009). As the stomach fullness would affect the proportion of the stomach tissue N in the bulk (i.e., stomach + bolus), we investigated two possible scenarios: (1) $\delta^{15}N_{bolus} = \left(\delta^{15}N_{stomach} - 0.25 \times \delta^{15}N_{tissue}\right) / 0.75$, assuming the 100% gut fullness and (2) $\delta^{15}N_{bolus} = \left(\delta^{15}N_{stomach} - 0.4 \times \delta^{15}N_{tissue}\right) / 0.6$, assuming 50% gut fullness. In these calculations, SE were determined by first-order error propagation of uncertainties.

Based on the previous findings (Komarova, 1991; Lesutiene et al., 2007), mesozooplankton, EPOM and BPOM were selected as plausible food sources of the mysids in the littoral (VL station, data of 2006). As C and N elemental concentrations differed considerably between mesozooplankton, EPOM and BPOM, the concentration-weighted, dual-isotope mixing model (Phillips and Koch, 2002) was applied to calculate the diet composition by biomass for subadult and adult mysids on the three sampling dates (September, October, and November, 2006) using δ^{15}N, δ^{13}C values and C and N concentrations of the consumers and their potential food sources. To obtain prey isotopic composition which is representative of the consumer signature, delta values of the food sources (i.e., mesozooplankton, EPOM and BPOM) were averaged between the adjacent sampling dates; growth estimates obtained by cohort analysis corroborate this assumption. Since food sources are required to be significantly different to be used in the mixing model; their isotopic signatures were compared using a t-test for each pair of sources and each isotope prior to their use as end-members in the mixing model calculations. Trophic enrichment

factors of 3.4 and 0.5 ‰ were used for $\delta^{15}N$ and $\delta^{13}C$, respectively (Post, 2002).

To quantify relative proportions of EPOM, RPOM and macrophyte detritus in the BPOM according to their $\delta^{15}N$ and $\delta^{13}C$ values, we used the IsoError model (Phillips and Gregg, 2001). We assumed constant $\delta^{13}C$ values of decomposing macrophyte detritus (estimated in August) for these calculations, referring to the previous findings of little change in $\delta^{13}C$ values of decomposing litter of aquatic plants with low initial lignin concentrations (Machás et al., 2006), that are characteristic for freshwater submerged plants, such as *P. perfoliatus* (Webster and Benfield, 1986).

4.5.3. Mysid growth, spatial distribution and stable isotope data analysis

For cohort analysis, length-frequency histograms of mysids sampled on different occasions were analyzed by the Rmix package – the version of MIX (Macdonald and Green, 1988) for the R environment (Du, pers. comm.). A gamma distribution was assumed for the distribution. The goodness-of-fit Chi-square test indicated how well the mixture distribution fit the histogram overall. In case of extensive overlap of distribution components, the test is not very sensitive (Macdonald and Green, 1988). In such cases, we relied on visual examination of the distribution curve fit to the histogram. The mean BL for each mysid cohort on consequent sampling dates was estimated and used for the growth rate calculation. The results of cohort analysis from 2004 and 2006 were pooled for growth-rate analysis. Specific growth rate (SGR, %DW d^{-1}) of mysids was calculated as $SGR = 100 \times (\ln W_t - \ln W_0)/t$, where $\ln W_t$ and $\ln W_0$ are the natural logs of two subsequent individual weights and t is the time (days) between the dates. The weight estimates (DW, mg) were based on length measurements (BL, mm) and allometric regression $W = 0.004 \times BL^{2.73}$, $R^2 = 0.985$, n = 88 (Lesutiene, unpublished data). The relationship between SGR and mysid BL was estimated by nonlinear regression using the Gauss-Newton method to determine best fit. As the

calculation of total mysid population production was hampered by abundance changes due to migration, we calculated the somatic production of the *P. lacustris* population. Somatic production (P_s, mg DW m^{-2}) was computed for each of the 6 sampling intervals from August 30 to November 30, 2006 and then for the entire period as $P_s = \sum SGR_i \times B_i \times t$, where i– number of size group (12 size groups in total), SGR_i (%DW d^{-1}) – specific growth rate and B_i (mg DW m^{-2}) – biomass of i^{th} size group, t – time (days).

Two-way ANOVA was applied to evaluate effects of (1) habitat (littoral vs. offshore) and time (sampling occasion) on the abundance of *P. lacustris*, and (2) mysid size (subadults vs. adult) and time (sampling occasion) on $\delta^{15}N$ and $\delta^{13}C$ in 2006 and (3) sampling date and mysid BL on the $\delta^{15}N$ values in 2004. A post-hoc Tukey HSD test for unequal sample size was applied. Bartlett's and/or Levene's tests were performed to investigate homogeneity of variances and normality was checked by visual exploration of probability plots; if needed data were $\sqrt{x}$ transformed. A one-way ANOVA was used to test the effect of sampling date on $\delta^{15}N$ values in 2004. The Fisher's least significant difference (LSD) procedure was applied as an ANOVA post-hoc test.

5. RESULTS

5.1. Seasonal dynamic of POM concentration, chlorophyll a content and phytoplankton

In 2006, the concentration of RPOM<70 μm varied from 4 to 14 mgDW L^{-1} , with an exception of June 21, when the extremely high concentration of RPOM<70 μm coincided with the river discharge peak (Fig. 2, 6). The RPOM<70 μm concentration and chlorophyll a content did not correlate significantly (Spearman correlation r=-0.37, p>0.1, Fig. 6). Assuming chlorophyll a to contribute 1% to phytoplankton DW (Reynolds, 2006), average phytoplankton contribution to RPOM <70 μm was 37 % (Appendix 2).

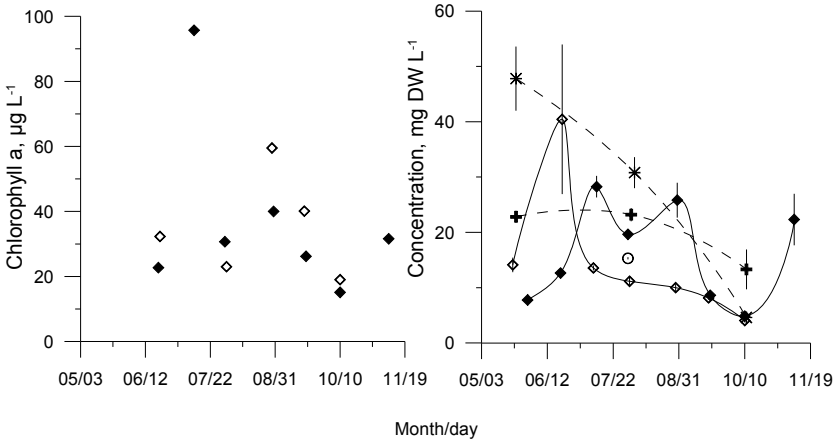

Fig. 6. Seasonal dynamic of concentration of chlorophyll a (left) and POM <70 µm (mg DW L^{-1}) (right) in Nemunas River (open rhombs) and Curonian Lagoon (filled rhombs- VL, circles- SL, crosses- JO, asterisks- VO stations) in 2006.

The seasonal pattern of EPOM<70 µm concentration at VL station, with low values in spring and autumn and maximal in summer, was significantly related to chlorophyll a content (Spearman r=0.94. p<0.05; Fig. 6) and river discharge (Spearman r=-0.74, p=0.05). The substantial deviations from this pattern at VL and other stations could be attributed to salinity and wind resuspension effects, although there was no significant correlations between EPOM<70 µm and these variables. Salinity varied in the narrow range from 0.04 to 1.5 on sampling occasions, but in between of sampling dates there were three brackish water intrusions that increased salinity to >6 in the lagoon (Fig. 3). The temporal decrease of EPOM concentration on July 31 at VL and SL stations to ~19.6 and 15.3 mg DW L^{-1}, respectively coincided with the salinity of >0.5 for at least one week before sampling (Fig. 3). The low wind velocity of 2 - 6 m s^{-1} on most of sampling occasions is an artefact of sampling planning, however high EPOM<70 µm concentrations on May 24 at VO and JO and on November 9 at VL obviously were caused by strong wind (10 - 16 m s^{-1}) resuspension of sediments (Table 3, Appendix 2, Fig. 6).

As estimated from chlorophyll a content, average phytoplankton contribution to EPOM <70 μm was 24 % (Appendix 2). The highest total phytoplankton biomass was recorded on July 12 and 31 (21.3 and 19 mg L^{-1} respectively), it peaked again in September to 14.3 mg L^{-1} (Fig. 7). Average relative contributions of small (<70 μm) and large (>70 μm) fractions to the total phytoplankton biomass were 35 ± 13 and 65 ± 13 %, respectively. The first phytoplankton <70 μm biomass peak in July, contributed largely by cyanobacteria, coincided with the EPOM<70 μm and chlorophyll a peaks, however the second peak in September, dominated by diatoms, was not reflected in EPOM<70 μm and chlorophyll a concentration (Fig. 6, 7). Probably because diatoms have lower chlorophyll a content than cyanobacteria (Reynolds, 2006). There was no significant correlations between EPOM<70 μm concentration and biomass of phytoplankton <70 μm (Spearman $r=0.48$, $p>0.05$) and between chlorophyll a and biomass of phytoplankton <70 μm (Spearman $r=0.43$, $p>0.05$).

Phytoplankton community was dominated by freshwater species, with small contribution of brackishwater species, such as *Thalassiosira* spp., whereas marine species were never found in the samples at VL station. Cyanobacteria contributed most to the large phytoplankton >70 μm throughout the season, whereas small phytoplankton <70 μm underwent seasonal succession with dominance of diatoms in May, cyanobacteria – in June-July, green algae in the end of August and diatoms in autumn (Fig. 7).

Diazotrophs *Anabaena* spp. and *Aphanizomenon* spp. dominated cyanobacteria community in >70 μm size group in June and July, whereas *Microcystis* spp. and *Planktothrix* sp. were main contributors in August and September, respectively (Fig. 8). Small cyanobacteria (<70 μm) were dominated by *Anabaena* spp. in June-July and *Microcystis* spp. in August (Fig. 8). The rough observation of large fraction of EPOM 100-200 μm collected at VO and JO stations on three sampling occasions in spring, summer and autumn revealed dominance of *Microcystis* spp., whereas diazotrophic cyanobacteria, such as *Apha-*

nizomenon spp., were observed only in October at JO station (Appendix 1).

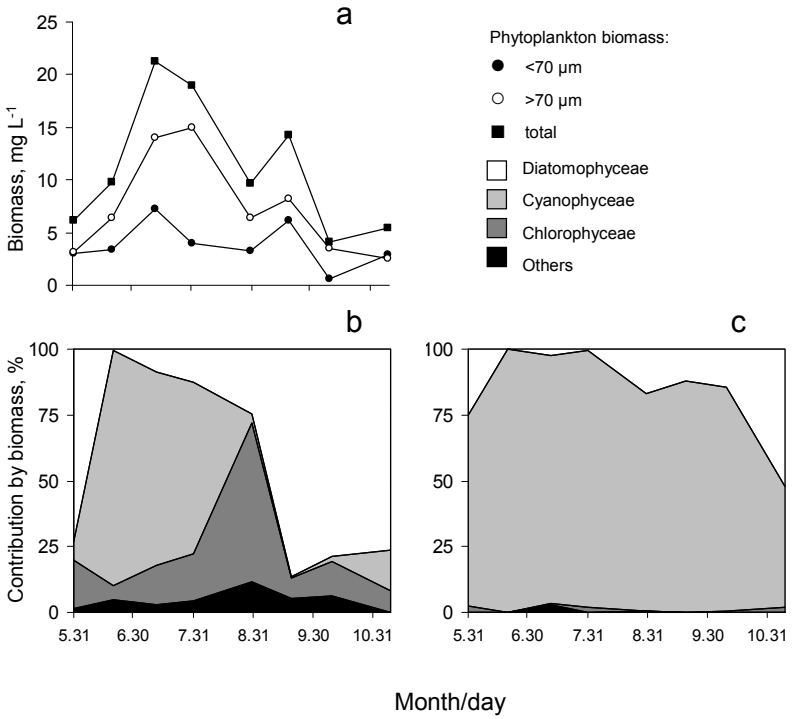

Fig. 7. Biomass (mg L^{-1}) (a) and composition (%, by biomass) of two size groups: <70 µm (b) and >70 µm (c) of Curonian Lagoon phytoplankton at VL sampling station in 2006.

The abundance of total cyanobacteria was also investigated in 2004 at VO site as important ultimate source of $\delta^{15}N$ variability at mysid trophic level. The assemblage of cyanobacteria was dominated by the *Aphanizomenon flos-aquae*, *Microcystis aeruginosa* and *Anabaena flos-aquae* in 2004. The timing of cyanobacteria blooms differed slightly between two years 2004 and 2006 (Fig. 9).

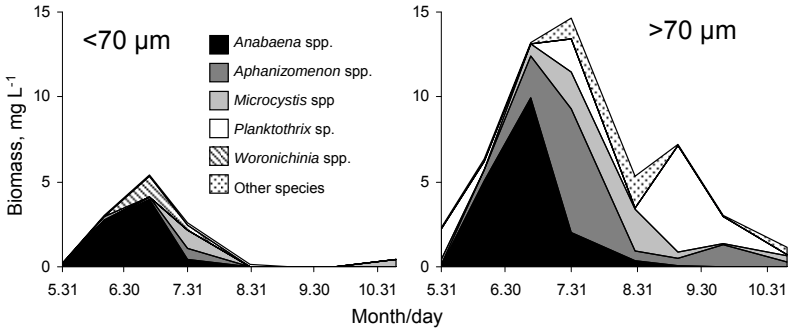

Fig. 8. Seasonal dynamic of cyanobacteria in the Curonian Lagoon at VL sampling station in 2006.

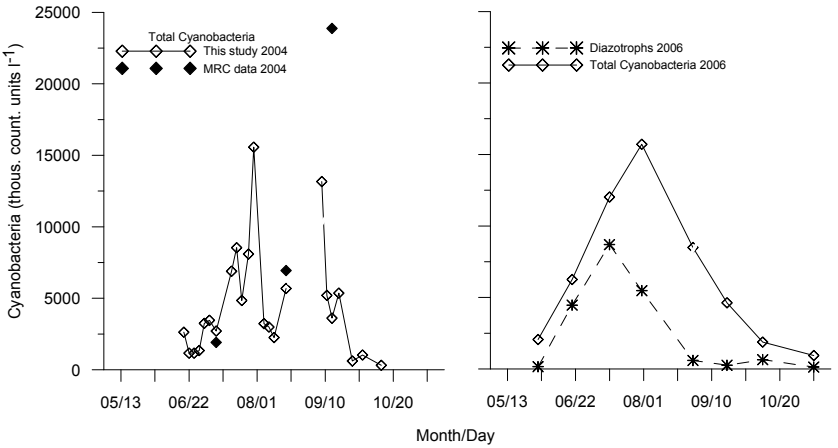

Fig. 9. The seasonal dynamics of cyanobacteria in the study area VL-VO. The monitoring data of 2004 were obtained by MRC from the station located in 2 km distance from the sampling station VO.

The cyanobacteria abundance peaked twice – in the end of July and beginning of September 2004 (Fig. 9). From August 18 to September 8, the sampling was interrupted, which might have resulted in the underestimated magnitude of the second peak. The national monitoring

in the area reported the cyanobacteria density considerably higher than what we observed in the late September (Fig. 9). Whereas there was a single peak of diazotrophic cyanobacteria in July, 2006.

5.2. Isotopic and elemental composition of riverine and estuarine POM

The RPOM was most enriched in ^{13}C in June and depleted towards autumn, with seasonal mean of -32.91 ± 2.38 ‰. On most sampling dates, the EPOM<70 µm $\delta^{13}C$ values were more enriched in ^{13}C compared to those of RPOM<70 µm (two-way ANOVA, Table 6). The difference between the $\delta^{13}C$ in EPOM<70 µm and RPOM<70 µm was lowest in spring (not significant, post-hoc Bonferroni tests, $p>0.05$), increasing to 9.1‰ in the mid-summer and returning to low values in the autumn (Fig. 10). Both RPOM<70 µm and EPOM<70 µm were most depleted in ^{13}C in September (-35.9 and -33.3‰, respectively).

Table 6. The two-way ANOVA for $\delta^{13}C$ and $\delta^{15}N$ values in RPOM<70 µm and EPOM<70 µm.

Variables and source of variation	Df	SS	MS	F	P
$\delta^{13}C$ (‰)					
Interaction	6	139.2	23.2	285.5	< 0.0001
Station	1	114.9	114.9	1414.0	< 0.0001
Time	6	227.2	37.9	466.0	< 0.0001
Residual	28	2.3	0.1		
$\delta^{15}N$ (‰)					
Interaction	6	50.3	8.4	62.5	< 0.0001
Station	1	86.9	86.9	647.6	< 0.0001
Time	6	105.8	17.6	131.4	< 0.0001
Residual	28	3.8	0.1		

The $\delta^{15}N$ values in RPOM<70 µm varied in the narrower range than in EPOM<70 µm 7.5-10.1 and 2.1-9.6 ‰, respectively (Fig. 10). Seasonal mean $\delta^{15}N$ was 8.4 ± 0.97 in RPOM<70 µm and 6.1 ± 3 ‰ in

EPOM<70 μm. The largest difference (5 ‰) between $\delta^{15}N$ values in RPOM<70 μm and EPOM<70 μm was in June and July, when $\delta^{15}N$ in EPOM<70 μm reached its lowest value of 2 ‰. There were no significant differences between $\delta^{15}N$ in EPOM<70 μm and RPOM<70 μm in the end of May and September (post-hoc Bonferroni tests, $p>0.05$).

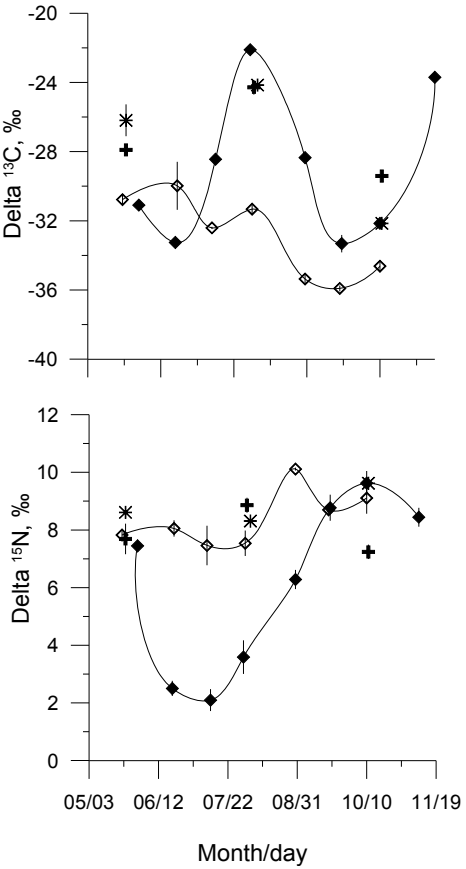

Fig. 10. Seasonal dynamic of stable isotope composition ($\delta^{13}C$, $\delta^{15}N$, ‰) in EPOM<70 μm (filled rhombs- VL, crosses- JO, asterisks- VO stations) and RPOM<70 μm (open rhombs).

Stable isotope composition of EPOM on November 9 was obviously affected by resuspended BPOM, largely originated from decaying macrophyte detritus in the littoral (see more results Section 5.7.3). Excluding this measurement, the $\delta^{13}C$ of EPOM<70 μm correlated negatively and $\delta^{15}N$ – positively to river discharge at VL station (Spearman r=-0.86 and 0.78 respectively, $p<0.05$). No significant correlations were observed for river discharge and either $\delta^{13}C$ or $\delta^{15}N$ in the RPOM<70 μm. Stable isotope composition in EPOM<70 μm was not related significantly to neither total phytoplankton <70μm biomass nor chlorophyll a. However the $\delta^{15}N$ in EPOM<70 μm correlated negatively with the biomass of diazotrophic cyanobacteria <70μm (Spearman r=-0.88, $p<0.05$).

The average concentrations of elemental C and N were 20 ± 6 and 3 ± 1%, respectively, in EPOM<70 μm; and 21 ± 13 and 4 ± 3%, respectively, in RPOM<70 μm. The 100-200μm fraction of EPOM contained more elemental C and N than EPOM<70μm, 35 ± 8 and 6 ± 2 % vs. 19 ± 7 and 3 ± 1 % of carbon and nitrogen respectively (paired t tests, $p<0.05$, on pooled data from VL, SL, VO and JO stations). This implies larger contribution of inorganic compounds in EPOM<70 μm fraction, whereas EPOM 100-200 μm elemental content is similar to typical phytoplankton elemental composition 40-50 % of C and 3.8-9 % of N (Jorgensen et. al., 1991).

There was significant correlation between $\delta^{13}C$ composition in EPOM<70 μm and EPOM 100-200 μm (Pearson r=0.8, $p<0.05$) which implies, that common factors determine $\delta^{13}C$ variability in both EPOM fractions. On average, carbon in EPOM<70 μm was 0.7 ‰ more enriched in ^{13}C than in EPOM 100-200 μm (Table 7). This was most probably caused by larger concentration of carbonates in the EPOM<70 μm.

Particle size (100-200 μm and <70 μm) effect on $\delta^{15}N$ values in EPOM was inconsistent among the sampling occasions (Table 7), and there was no significant correlation between $\delta^{15}N$ composition in EPOM<70 μm and EPOM 100-200 μm (Pearson r=0.58, $p>0.05$). The $\delta^{15}N$ values were significantly more depleted in EPOM 100-200 μm at

VL and JO stations in October, probably due to *Aphanizomenon* spp. contribution to large phytoplankton (Table 7, Fig. 8., Appendix 1). Whereas EPOM 100-200 μm was more enriched in ^{15}N at JO station in May and VL station on July 12 because of contribution of copepodites and nauplii (Table 7, Appendix 1). Non significant differences of $\delta^{15}N$ in two EPOM fractions (Table 7) coincide with the dominance of *Microcystis* spp. in phytoplankton community, probably because of its ability to form the broad size range of flocks, that could be retained on the 100 μm mesh or penetrate in to the filtrate (pers. observations).

Table 7. The stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, ‰) in two size fractions of suspended particulate matter EPOM 100- 200 μm and <70 μm. Signifficant (t tests) differences in isotope ratios ($\Delta^{13}C$ and $\Delta^{15}N$, ‰) between the fractions are indicated with asterisks ***p < 0.001 **p < 0.01 *p < 0.05; ns – p > 0.05.

Date/Station	$\delta^{13}C$		$\Delta^{13}C$	p	$\delta^{15}N$		$\Delta^{15}N$	p
	EPOM 100-200	EPOM <70			EPOM 100-200	EPOM <70		
May 24/ JO	-31.28	-27.90	3.38	***	10.70	7.69	-3.01	***
July 12/ VL	-26.19	-28.44	-2.25	***	5.91	2.10	-3.82	***
July 31/ SL	-24.38	-21.70	2.68	***	2.91	2.74	-0.17	ns
August 4/ VO	-24.03	-24.15	-0.12	ns	8.31	8.31	0.00	ns
August 4/ JO	-23.84	-24.28	-0.43	ns	8.32	8.86	0.54	ns
August 30/ VL	-28.94	-28.35	0.59	***	7.55	6.28	-1.26	**
October 10/ VL	-32.95	-31.75	1.19	**	4.42	8.14	3.72	***
October 10/ JO	-30.16	-29.41	0.74	**	5.47	7.25	1.77	***
October 10/ VO	-32.67	-32.15	0.52	ns	9.10	9.62	0.43	ns

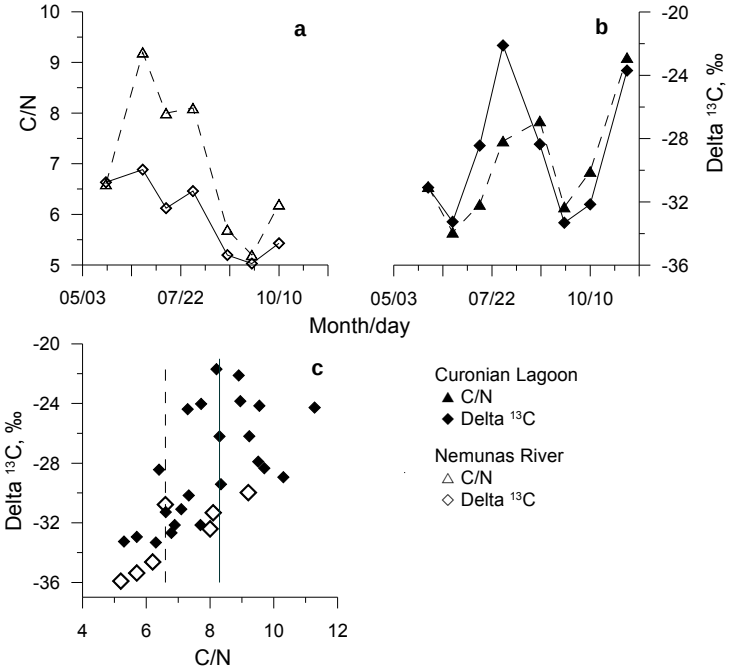

Fig. 11. Seasonal variation of carbon isotopic composition ($\delta^{13}C$, ‰) and molar C/N ratio in RPOM<70μm (a) and EPOM<70μm at VL station (b), and relationship between molar C/N ratio and stable carbon isotope composition ($\delta^{13}C$, ‰) in EPOM (pooled data from all stations and fractions) and RPOM<70 μm (c). The dashed line in the panel c indicates the Redfield ratio C/N=6.6 in phytoplankton; solid line indicates nitrogen deficiency level C/N>8.3 for phytoplankton (Hecky et al., 1993).

The mean seasonal atomic C/N ratios in RPOM<70 μm and EPOM<70 μm at VL station did not differed significantly 7 ± 1.5 and 7.3 ± 1.5 respectively (Mann-Whitney test, $p>0.05$). The C/N molar ratio in RPOM<70 μm and EPOM<70 μm varied in concert with $\delta^{13}C$ (Spearman $r=0.89$ and 0.79, respectively; $p<0.05$, Fig. 11). The highest values of C/N, ranging from 9 to 9.6, were observed at offshore stations JO and VO in May and August, whereas the overall maximum 11.3 was observed in EPOM<70 μm at JO station on August 2 (Ap-

pendix 2). There was positive linear relationship between C/N and $\delta^{13}C$ in EPOM for pooled data from all stations and fractions ($\delta^{13}C$ = -40.6 + 1.55 C/N, $p<0.05$, R^2 = 38.98, n = 23). However, higher C/N values in EPOM corresponded to more scattered $\delta^{13}C$ values, which imply an existence of non-common sources of variation of C/N and $\delta^{13}C$ in EPOM (Fig. 11c).

5.3. Spatial variability of the stable isotope composition in estuarine POM

There was a significant spatial effect on stable isotope composition in POM<70 μm collected at different stations in the lagoon and the Baltic Sea (one-way ANOVA's for different months, Table 8).

Table 8. The one-way ANOVA's for $\delta^{13}C$ and $\delta^{15}N$ values in POM<70μm. Significant effects are indicated with asterisks (*p<0.05, **p<0.001); sampling stations in the lagoon (VL, VO, JO, SL) and the Baltic Sea (BS).

Sampling time and source of variation	$\delta^{13}C$				$\delta^{15}N$			
	SS	df	MS	p	SS	df	MS	p
May 24-31								
Stations (VL, VO, JO)	37.2	2	18.6	**	2.2	2	1.1	*
Residual	2	6	0.3		0.7	6	0.1	
Total	39.2	8			2.9	8		
July 31 – August 8								
Stations (BS, SL, VL, VO, JO)	48.8	4	12.2	**	96.5	4	24.1	**
Residual	0.4	9	0.1		2	9	0.2	
Total	49.2	13			98.5	13		
October 10-11								
Stations (VL, VO, JO)	13.2	2	6.6	**	8.7	2	4.3	**
Residual	0.3	6	0.0		0.2	6	0.0	
Total	13.4	8			8.9	8		

In spring and summer, isotopic composition of EPOM<70 μm was similar in the offshore areas located in close proximity to the river mouth (station VO) and in a 20-30 km distance to it (and JO) (Fig.

12). In October, SI in EPOM <70 μm at VO station were closer to that in RPOM (-34.6 and 9.1 ‰), whereas EPOM <70 μm sampled in the brackish water inflow area (JO) was more enriched in ^{13}C and depleted in ^{15}N. The largest difference in SI composition, particularly in $\delta^{15}N$ values, between offshore (VO and JO) and littoral stations (VL and SL) was observed in the summer, due to different composition of cyanobacteria assemblage (Fig. 7, 11).

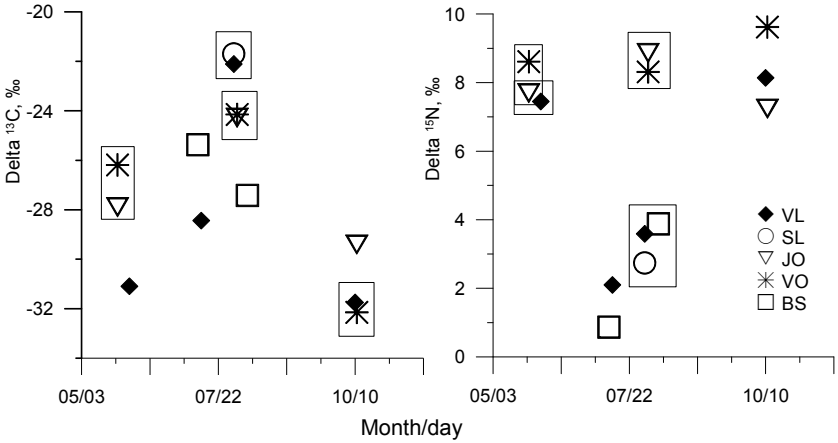

Fig. 12. Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of the POM <70 μm at different sampling stations in the lagoon (VL, VO, JO, SL) and the Baltic Sea (BS) in May, August and October. The values that are not significantly different (according to the Tukey post-hoc test for each month separately, $p>0.05$) are in the boxes.

The isotopic composition of MPOM varied between the two sampling dates, July 10 and August 8. On July 10-12, the coastal MPOM <70 μm had slightly more enriched $\delta^{13}C$ value than EPOM (t test, $p>0.05$, Fig. 12), whereas in the beginning of August, MPOM was significantly more depleted in ^{13}C than EPOM (-27.42 ± 0.05 ‰ vs. -24-22 ‰, Fig. 12). The $\delta^{15}N$ values were similar in EPOM<70 μm and MPOM on July 10-12 (t test, $p>0.05$), whereas in the end of July - beginning of August the differences were inconsistent due to spatial heterogeneity of $\delta^{15}N$ composition in the EPOM (Fig. 12).

5.4. Stable isotope ratios in macrophytes

There were temporal, spatial and species specific differences in stable isotope composition of littoral macrophytes (Table 9). The $\delta^{13}C$ values in *Cladophora* spp. were more negative than in *P. perfoliatus* (t tests, $p<0.05$), whereas $\delta^{15}N$ was similar between the species in May (t test, $p>0.05$) but differed significantly in August (t test, $p<0.05$). *P. perfoliatus* had slightly different isotopic composition at two stations VL and JL in the summer (1.3 ‰ and 1.9 ‰ difference of $\delta^{15}N$ and $\delta^{13}C$ respectively, t tests $p<0.05$, Table 9). Values of $\delta^{13}C$ were significantly more depleted in May than in August in both *P. perfoliatus* (one-way ANOVA Bonferroni post-hoc test, $p<0.05$) and filamentous algae (t-test, $p<0.05$). $\delta^{15}N$ values did not differed between sampling dates in *P. perfoliatus* (one-way ANOVA for $\delta^{15}N$, $F=3.07$, $p>0.05$), whereas $\delta^{15}N$ values in *Cladophora* spp. decreased significantly from May towards August (t test, $p<0.05$). Decaying leaves of *P. perfoliatus* were slightly more depleted in ^{13}C and ^{15}N (t tests, $p<0.05$).

Table 9. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, ‰) of littoral macrophytes at two littoral stations VL and JL. *PP- Potamogeton perfoliatus*, *C- Cladophora* spp.

Species		VL			JL
		May 31	August 1	August 30	August 5
PP	leaves	-22.1 ± 0.7 10.8 ± 1.3	-15.1 ± 1.1 9.3 ± 0.5	-16.0 ± 1.3 9.0 ± 0.4	-13.2 ± 0.7 7.9 ± 0.5
	foliage			-18.5 ± 0.5 8.0 ± 0.3	
C		-28.9 ± 0.9 11.6 ± 0.2	-19.7 ± 0.4 5.1 ± 0.2		

5.5. Temporal and spatial variation of stable isotope ratios in consumers

There were significant effects of the season and species on $\delta^{13}C$ and $\delta^{15}N$ values in the consumers (Table 10). The seasonal variation of the $\delta^{13}C$ in the consumers had the same temporal dynamics as in EPOM<70 μm - *i.e.* significant enrichment in ^{13}C from the spring to

the summer followed by depletion towards the autumn (Fig. 10, 13). The $\delta^{15}N$ values in mesozooplankton, mysids and chironomids responded to the depletion of ^{15}N in EPOM<70 μm in summer (Fig. 10, 13), whereas $\delta^{15}N$ values of *D. polymorpha* and leeches did not change significantly (Bonferroni post-hoc test, $p>0.05$).

Table 10. Two-way ANOVA's for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, ‰) of consumer species (ch- Chironomidae, dp1 and dp2- *D. polymorpha* with shell length of ~1 cm and ~2 cm, respectively, e- Erpobdellidae, pl- *Paramysis lacustris* (adults), va- *Valvata* spp., z- mesozooplankton) and season (spring, summer, autumn) in the sampling stations VO and JO. Significant effects are indicated with asterisks ***$p < 0.001$ **$p < 0.01$ *$p < 0.05$; ns – $p > 0.05$.

Variables and source of variation	Df	SS	MS	F	p
VO-$\delta^{13}C$					
Interaction	8	17.33	2.17	17.33	***
Season	2	177.90	88.93	711.70	***
Species (ch, dp1, dp2, e, pl)	4	63.74	15.94	127.50	***
Residual	29	3.62	0.13		
VO- $\delta^{15}N$					
Interaction	8	40.68	5.09	39.73	***
Season	2	38.75	19.38	151.40	***
Species (ch, dp1, dp2,e, pl)	4	69.80	17.45	136.30	***
Residual	29	3.71	0.13		
JO-$\delta^{13}C$					
Interaction	4	45.52	11.38	23.67	*
Season	2	110.50	55.25	114.90	***
Species (va, z, pl)	2	47.08	23.54	48.97	***
Residual	18	8.65	0.48		
JO- $\delta^{15}N$					
Interaction	4	8.16	2.04	19.37	**
Season	2	43.68	21.84	207.30	***
Species (va, z, pl)	2	18.46	9.23	87.62	***
Residual	18	1.90	0.11		

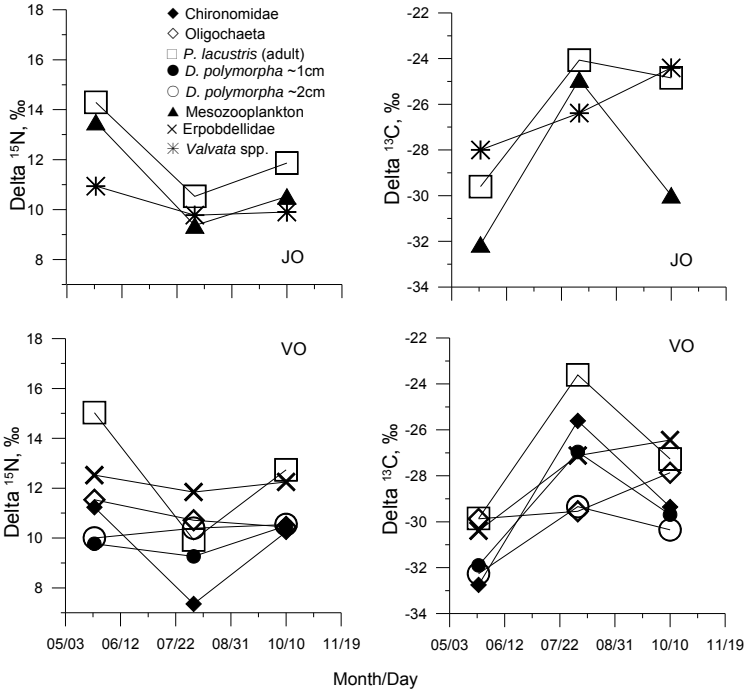

Fig. 13. Seasonal variation of stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$ ‰) in various consumers at sampling stations VO and JO.

Given that, body length (BL) in most of the investigated fish species differed between seasons (Appendix 1), the seasonal changes in their stable isotope signatures cannot be estimated independently from the ontogenetic diet shifts and changes of the position in the food chain. The $\delta^{13}C$ and $\delta^{15}N$ values in bream of the same size (BL 34.9 ± 3 and 35 ± 0 cm in the summer and autumn, respectively) did not differed significantly (t-tests, $p>0.05$) between seasons.

In stable isotope signatures of mysids, there were no significant differences between samples collected at VO and JO stations in spring (t-tests for $\delta^{13}C$ and $\delta^{15}N$, $p>0.05$), while oligochets had 2 ‰ lower $\delta^{15}N$ value at JO (Fig. 14). Significant species specific spatial effect on the stable isotope ratios in consumers was detected in summer and autumn

by two-way ANOVA (Table 11). In summer, gastropods, gammarids and juvenile mysids had on average 1.4 ‰ higher $\delta^{15}N$ at JO-JL than at VO-VL, while $\delta^{13}C$ of most consumers did not differed significantly between the sites (Fig. 14). There was an opposite pattern in the autumn: higher $\delta^{15}N$ values of the consumers at VO than at JO and significantly lower $\delta^{13}C$ signatures at VO (Fig. 14, Table 11). $\delta^{13}C$ values in roach and perch did not differed considerably between the sites (VO-VL and JO-JL) in summer, whereas $\delta^{15}N$ had lower values at JO-JL site (Fig. 14, Table 11), which is probably related to differences in BL (roach: 11 and 25 cm; perch: 11 and 30 cm, at JL and VO, respectively) *i. e.* ultimate differences in trophic level.

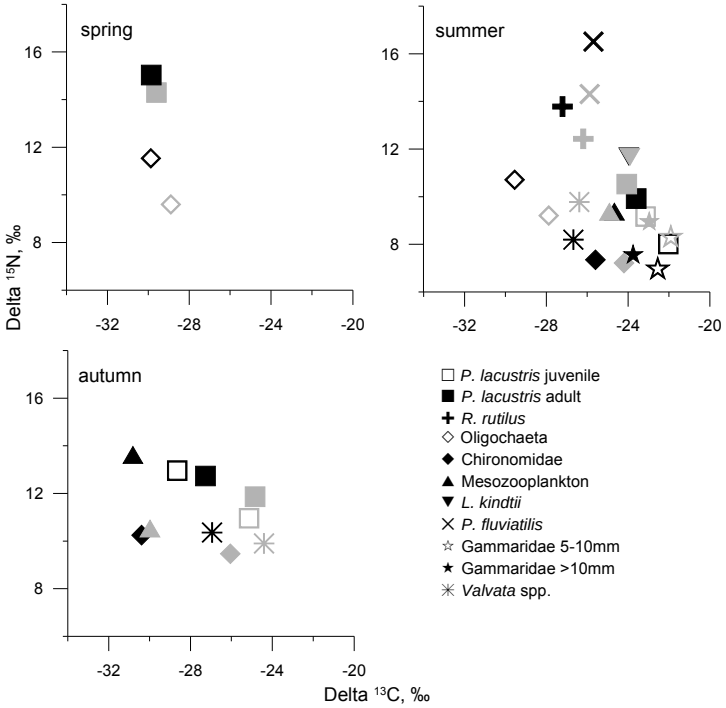

Fig. 14. Temporal and spatial variability of stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, ‰) in the consumers. Sampling sites: VO and VL (black symbols) and JO and JL (grey symbols).

Table 11. Two-way ANOVA for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$, ‰) of consumer species (see explanation of abreviations in Table 3) at different stations (VO-VL and. JO-JL) in the summer and autumn. Bonferroni post-hoc comparisons were carried out to compare $\delta^{13}C$ and $\delta^{15}N$ values in the species analyzed between the stations (VO-VL vs. JO-JL). Significant effects are indicated with asterisks ***p < 0.001 **p < 0.01 *p < 0.05; ns – p > 0.05.

Variables and source of variation	Df	SS	MS	F	p
Summer-$\delta^{13}C$					
Interaction	9	12.10	1.35	9.24	***
Station	1	2.55	2.55	17.53	***
Species (ch, $gm_{5\text{-}10}$, $gm_{>10}$, lk, pl_{ad}, pl_{juv}, pf, rr, va, z)	9	127.8	14.20	97.52	***
Residual	38	5.53	0.146		
Summer- $\delta^{15}N$					
Interaction	9	20.48	2.28	18.78	***
Station	1	1.46	1.46	12.08	**
Species (ch, $gm_{5\text{-}10}$, $gm_{>10}$, lk, pl_{ad}, pl_{juv}, pf, rr, va, z)	9	368.3	40.92	337.9	***
Residual	38	4.60	0.12		
Autumn-$\delta^{13}C$					
Interaction	4	10.57	2.64	4.61	**
Station	1	55.67	55.67	97.06	***
Species (ch, pl_{ad}, pl_{juv} va, z)	4	88.61	22.15	38.62	***
Residual	20	11.47	0.57		
Autumn- $\delta^{15}N$					
Interaction	4	5.95	1.49	7.47	***
Station	1	18.55	18.55	93.08	***
Species (ch, pl_{ad}, pl_{juv}, va, z)	4	28.44	7.11	35.69	***
Residual	20	3.99	0.2		

		Post-hoc comparisons VO vs. JO, VL vs. JL			
		Summer		Autumn	
Species		$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Valvata spp.		ns	***	**	ns
Mesozooplankton		ns	ns	ns	***
Paramysis lacustris	adults	ns	ns	**	ns
	juveniles	*	**	***	***
Chironomidae		***	ns	***	ns
Rutilus rutilus		*	***		
Perca fluviatilis (adults)		ns	***		
Gammaridae	>10mm	ns	***		
	5-10mm	ns	**		
Leptodora kindtii		ns	ns		

5.6. Structure of the Curonian Lagoon food web

5.6.1. Primary organic matter sources in the summer

The distribution of consumers in the $\delta^{15}N$ vs. $\delta^{13}C$ biplot is pyramid shaped, with the most variable SI values at the base and the least variable in the top consumers (Fig. 15). In the summer, consumer's $\delta^{13}C$ varied from -30.3 to -21.9 ‰ (Table 12, Fig. 15), with significant species-specific differences (one-way ANOVA, $F=48.8$, $p<0.05$). Different trophic guilds i.e. suspension and deposit feeders as well as predators are represented throughout the whole $\delta^{13}C$ spectrum (Table 12). The most ^{13}C-depleted group ("a-c", Table 12), includes oligochaetes, mussels (unionids and large specimens of *D. polymorpha*), large oligochaetes *Eiseniella tetraedra* and leeches of the family Glossiphoniidae (block A, Fig. 15). The second group – "d-i" includes most of the macrozoobenthic species (Table 12), such as chironomids (VO_1), gastropods (block B, Fig. 15), leeches of the family Erpobdellidae and benthophagous fish (roach, bream, and ruff). Predatory perch and pickeperch as well as planktivorous *P. cultratus* occupy the intermediate position in the $\delta^{13}C$ spectrum. The most enriched in ^{13}C group "l-t" includes zooplankton, chironomids, nectobenthic crustaceans (block C, Fig. 15), *Leptodora* and juvenile perch.

Assuming low or no ^{13}C fractionation, primary consumers in block A are on the line that connects the food chain with the RPOM as a most potential primary source of organic matter (Fig. 15). In addition, the BPOM at 5-10 cm sediment depth, that has low $\delta^{13}C$ value, fits as a primary source for the consumers in block A, which is quite plausible for sub-surface deposit feeders, such as oligochaetes. Primary consumers in block B and fish are on the line indicating, that the EPOM of the preceding 2 months is a primary source of organic matter (Fig. 15). All mysids and juvenile perch in block C are close to the line that suggests the EPOM of previous 3 weeks, and/or MPOM as primary sources of organic matter. Macrophytes are relatively distant to littoral consumers, therefore are not likely to be an important food source for investigated species such as amphipods and mysids (Fig. 15).

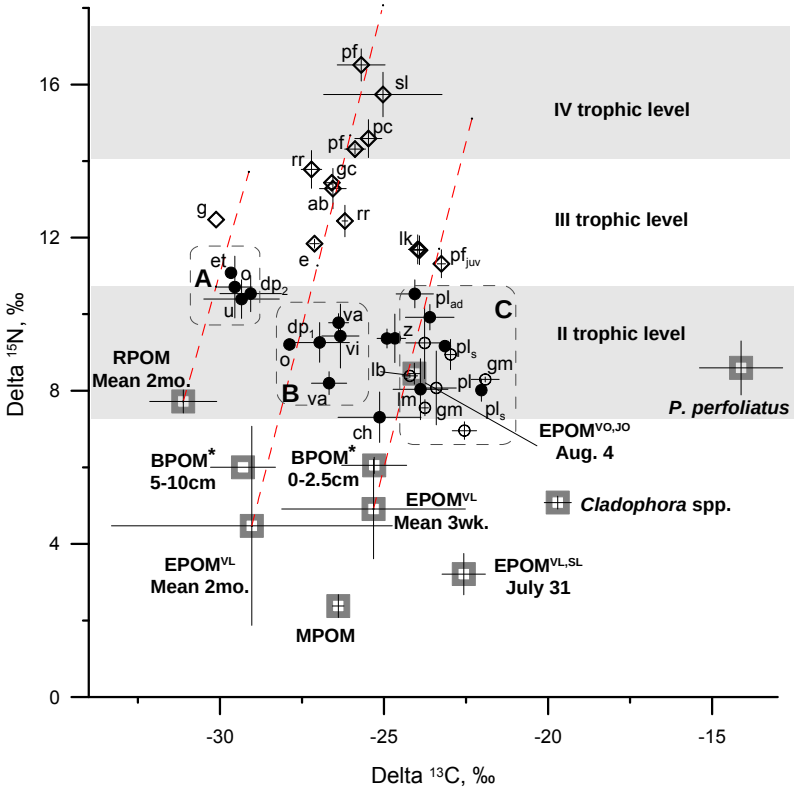

Fig. 15. The structure of the Curonian Lagoon food web in summer revealed by stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$, ‰). Squares denote primary sources of organic matter: marine (MPOM), riverine (RPOM) and estuarine (EPOM) particulate organic matter, littoral macrophytes and BPOM at upper (0-2.5 cm) and deeper (5-10 cm) of sediment layers (starred values from Voss et al., 2000, measured on sand bottom in the northern part of the lagoon). EPOM sampling stations are denoted by superscript. Open circles - littoral primary consumers and omnivores, filled circles - offshore consumers and omnivores; rhombs - predators. Species abbreviations as in Table 2. Dashed lines show the hypothetical food chain for RPOM and EPOM as primary source of organic matter, 3.4 and 1 ‰ enrichment per trophic level for $\delta^{15}N$ and $\delta^{13}C$ respectively. Shaded bars indicate trophic levels calculated for $\delta^{15}N_{chyronomid}$ baseline.

Table. 12. Stable carbon isotopes ratios (mean±SD $\delta^{13}C$, ‰) in the consumers of the Curonian Lagoon in summer. Significantly different $\delta^{13}C$ values between the species (LSD, $p < 0.05$) are denoted with non-matching letters. Feeding guilds: grazers (G), suspension feeders: epifaunal (ESF), infaunal (ISF), nectobenthic (NSF), pelagic (PSF); deposit feeders: epifaunal (EDF), infaunal sub-surface (SSDF), infaunal (IDF), nectobenthic (NDF); predators (P). * Classification modified from Olenin, 1996.

Species	Station	$\delta^{13}C$	N	Consumers grouping by means of $\delta^{13}C$	Feeding guilds*
D. polymorpha SL~2cm	VO_2	-30.3±0.7	3	a	ESF
Oligochaeta	$VO_{1,2}$	-29.6±0.5	3	ab	SSDF
Unio spp.	VO_2	-29.1±0.9	4	bc	ISF
D. polymorpha SL~2cm	VO_1	-28.4±0.3	3	c	ESF
D. polymorpha SL~1cm	VO_2	-27.2±1.3	3	d	ESF
Rutilus rutilus	VO	-27.2±0.3	3	de	P
Erpobdellidae	VO_2	-27.1±0.2	3	de	P
Chironomidae	VO_1	-26.7±0.8	3	def	IDF
D. polymorpha SL~1cm	VO_1	-26.7±0.4	3	def	ESF
Valvata spp.	VO_1	-26.7±0.5	3	def	ESF
Gymnocephalus cernuus	JL	-26.6±0.2	3	defg	P
Viviparus spp.	VO_2	-26.6±0.5	3	defg	EDF
Abramis brama	JO	-26.6±0.4	3	defg	P
Valvata spp.	JO	-26.4±0.3	3	efgh	ESF
Rutilus rutilus	JO	-26.2±0.1	3	fghi	P
Viviparus spp.	VO_1	-26.1±0.7	3	fghi	EDF
Perca fluviatilis	JO	-25.9±0.3	4	ghi	P
	VO	-25.7±0.7	5	hi	
Pelecus cultratus	VO	-25.5±0.4	3	ij	P
Mesozooplankton	JO	-24.9±0.2	3	jk	PSF
	VO_1	-24.7±0.3	3	jkl	
Chironomidae	VO_2	-24.5±0.3	3	klm	IDF
	JO	-24.2±0.2	3	klmn	
Paramysis lacustris adults	JO	-24.1±0.6	3	lmno	NSF, P
Limnomysis benedeni	VL	-24.0±0.5	4	lmno	NSF
Leptodora kindtii	VO_1	-24.0±0.3	3	lmnop	P
	JO	-23.9±0.1	3	lmnop	
Limnaeidae	$VO_{1,2}$	-23.8±1.4	4	lmnop	EDF
Gammaridae >10mm	VL	-23.8±0.1	3	mnopr	NDF, G
Paramysis lacustris adults	VL	-24.0±0.6	5	mnopr	NSF, P
P. lacustris subadults	VL	-23.4±0.4	3	nopr	NSF
P. fluviatilis juv.	JL	-23.3±0.1	3	oprs	P
P. lacustris subadults	JL	-23.1±0.1	3	prs	NSF
Gammaridae >10mm	JL	-23.0±0.2	2	rs	NDF, G
Gammaridae 5-10mm	VL	-22.6±0.4	3	st	NDF, G
P. lacustris subadults	VO_1	-22.0±0.1	3	st	NSF
Gammaridae 5-10mm	JL	-21.9±0.4	2	t	NDF, G

Scattering of the primary consumers in the stable isotope biplot from spring values towards more depleted $\delta^{15}N$ and enriched $\delta^{13}C$ in summer indicates the continuous replacement of "older" isotopes with the "new" ones from the freshly assimilated material (Fig. 15). Mixing triangles A and B (Fig. 15) connect the EPOM values averaged over different period in time considering contribution of riverine and marine sources. Mixing triangle A includes the "oldest" end-member spring/autumn mixture of EPOM/RPOM and more recent EPOM/$MPOM_{coastal,\ offshore}$ mixture and encloses species that are little or moderately moved from the spring starting positions i.e. most of the molusc. Mixing triangle B, connecting the most recent EPOM values, is built for offshore species that are most equilibrated to the summer EPOM diet, such as mysids, zooplankton, limneids. Whereas chironomids could be attributed to both mixing triangles (Fig. 15). Mixing polygon C, generated for IsoSource mixing model to calculate the diet of littoral consumers, involves the same end-points as mixing triangle B and littoral macrophytes.

Time-related sources contributions to the assimilated diet, calculated by three-end-member mixing models, differed between species considerably (Table 13). Large specimens of *Dreissena polymorpha* and unionids relied for 62 – 71 % of their diet on ^{13}C- depleted mixture of EPOM/RPOM, which was available 3 or more months ago, indicating their long term isotopic memory of more than 3 months (Table 13). Whereas smaller specimens of *D. polymorpha* and gastropods (*Valvata* and *Viviparus*) contained about 30 % of tissues, generated from the older EPOM/RPOM mixture, and 40-60 % from the more recent EPOM/MPOM mixture, which implies about 2 mo time lag over which the stable isotope ratios of food are reflected in their tissues (Table 13). A and B mixing models showed, that assimilation of the EPOM was reflected in the diet of chironomids with a lag from 2 months to 3 weeks (Table 13). Subadults of *Paramysis lacustris* relied mainly on the EPOM of recent origin (one week old) (Table 13). Mesozooplankton contained only 45 % of ambient EPOM, other assimilated material was isotopically close to that of EPOM originated 3 weeks earlier (Table 13).

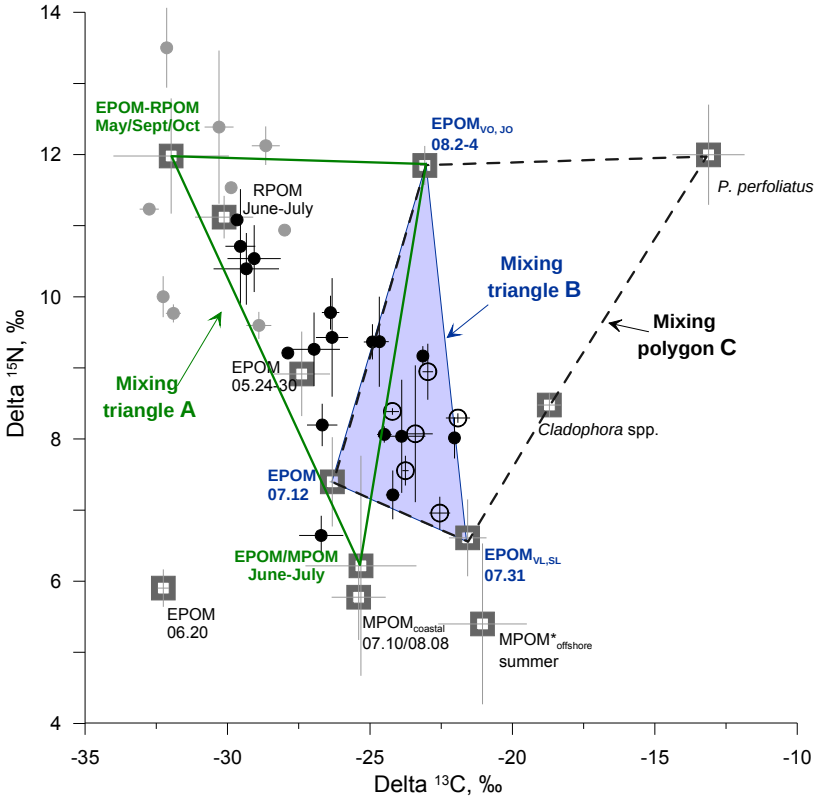

Fig. 15. Mean isotopic (δ^{15}N and δ^{13}C, ‰; mean ± SD) composition of organic matter sources (squares; EPOM- estuarine, RPOM- riverine, MPOM- marine suspended particulate matter, starred value from Maksymowska et al., 2000 and Rolff and Elmgren, 2000) used in the mixing models to calculate the assimilated diet composition of primary consumers in the summer. Filled and open circles denote the offshore and littoral specimens respectively; black circles- summer SI values, grey - spring values; see explanations in the text. The end-member POM values in the vertices of the mixing triangles A, B and mixing polygon C are averaged between indicated sampling dates/locations. The stable isotope values of all end-members are calculated using fractionation factors +3.4‰ and +1‰ for δ^{15}N and δ^{13}C, respectively.

Table 13. The relative contributions (%; mean ± SE, upper and lower limits of the 95% confidence interval) of the POM to the assimilated diet of suspension and deposit feeders. The diet contributions were calculated by the three-end-member mixing models using $\delta^{13}C$ and $\delta^{15}N$ signatures of the consumers and sources. See explanations in the text and Fig. 16 for mixing models A and B end-members.

Species/ Station	**Mixing model A**					
	$RPOM/EPOM_{VL}$ May, Sept, Oct -32.98± 2.03; 8.58 ± 0.81		$EPOM_{VL,SL}$ /MPOM June – July -26.11 ± 1.95; 2.52 ± 1.55		$EPOM_{VO,JO}$ Aug 2-4 -24.07 ± 0.18; 8.45 ± 0.27	
	Lag >3mo		**Lag 2mo**		**Lag 1wk**	
	95% conf. interv.	Mean ± SE	95% conf. interv.	Mean ± SE	95% conf. interv.	Mean ± SE
Dreissena 2cm/$VO_{1,2}$	42 - 87	64 ± 9	12 - 43	27 ± 8	0 - 32	8 ± 11
Dreissena 1cm/$VO_{1,2}$	17 - 50	34 ± 7	30 - 63	47 ± 7	0 - 39	20 ± 9
Unio /VO_2	37 - 87	62 ± 10	7 - 42	25 ± 7	0 - 39	13 ± 11
Viviparus/$VO_{1,2}$	12 - 42	27 ± 7	11 - 76	44 ± 10	6 - 53	29 ± 10
Valvata/VO_1	8 - 45	26 ± 8	43 - 88	65 ± 9	0 - 31	8 ± 11
Valvata/JO	17 - 41	29 ± 5	24 - 51	37 ± 6	19 - 48	33 ± 7
Chironomidae/VO_2	0 - 19	1 ± 7	44 - 90	67 ± 8	9 - 53	31 ± 9
Chironomidae/JO	0 - 17	-5 ± 8	53 - 100	82 ± 11	0 - 50	23 ± 12
	Mixing model B					
	$EPOM_{VL}$ July12 -27.32±0.10; 4±0.63		$EPOM_{VL, SL}$ July31 -22.57±0.66; 3.21±0.54		$EPOM_{VO, JO}$ Aug 2-4 -24.07 ± 0.18; 8.45 ± 0.27	
	Lag 3wk		**Lag 1wk**		**Lag 1wk**	
Chironomidae/VO_2	43 - 68	55 ± 4	16 - 35	25 ± 4	16 - 27	19 ± 3
Chironomidae/JO	44 -65	54 ± 4	31 - 53	42 ± 5	0 - 17	3 ± 5
Limnaeidae/$VO_{1,2}$	11 - 74	42 ± 10	12 - 61	37 ± 10	0 - 48	21 ± 9
Paramysis subad./VO_1	0 - 13	1 ± 5	61 - 83	72 ± 5	15 - 39	27 ± 5
Paramysis subad./JO	12 - 25	18 ± 3	29 - 42	35 ± 3	40 - 52	46 ± 3
Mesozooplankton/VO, JO	43 - 65	54 ± 5	0 - 14	2 ± 6	30 - 60	45 ± 6

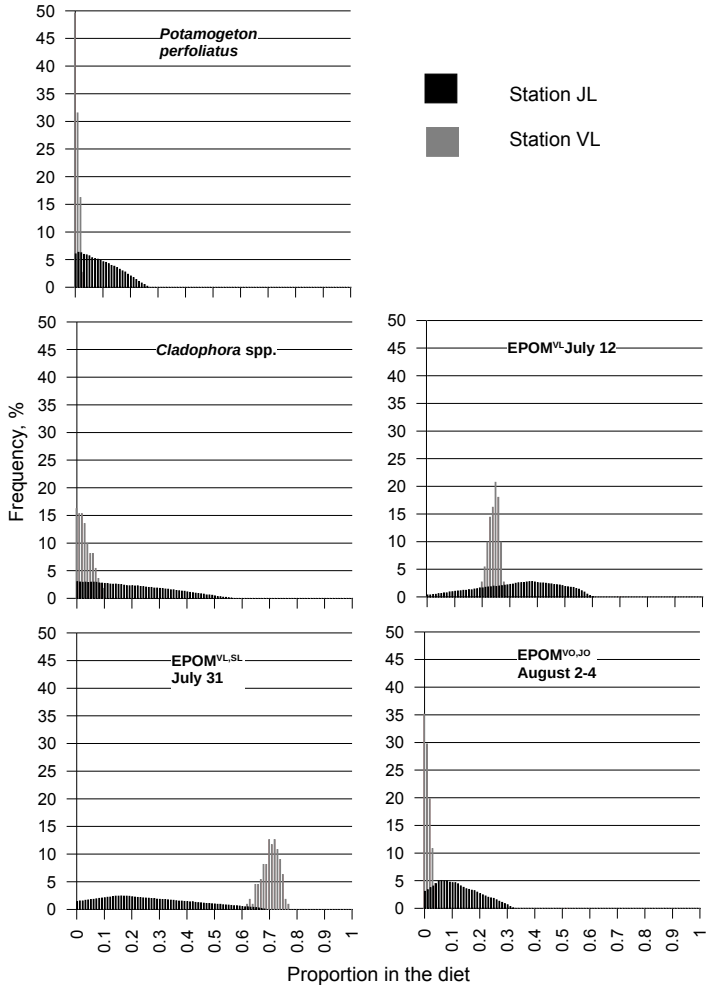

Fig. 17. Frequency distributions of the biomass contribution of estuarine particulate organic matter (EPOM) and littoral macrophytes (*Cladophora* spp. and *Potamogeton perfoliatus*) to the diet of littoral gammarids (BL 5 – 10 mm). Distributions shown reflect 111 and 5155 dietary solutions found by the IsoSource mixing model for the specimens collected at VL and JL stations respectively.

As revealed by the IsoSource two isotopes-five sources mixing model (mixing polygon C, Fig. 16), biomass contribution of the littoral macrophytes to the diet of subadult *Paramysis lacustris* was low, 13.4 ± 9 % and 5.6 ± 4 % for *Cladophora* and *Potamogeton perfoliatus*, respectively, whereas percentage of EPOM was higher 53 ± 8 % and 20 ± 11 %, for July 12 and July 31, respectively. Diet contributions in *L. benedeni* were similar: 8 ± 6 % and 6.2 ± 4.7 % for *Cladophora* spp. and *P. perfoliatus*, respectively, and 61 ± 8, 10 ± 7.4 and 15 ± 6 % of EPOM collected on July 12, July 31 and August 2-4, respectively.

The macrophyte share in the diet of littoral gammarids was negligible at VL station: 3.2 ± 2.6 % and 0.7 ± 0.8% for *Cladophora* and *P. perfoliatus*, respectively, and slightly higher at JL station, with 19.6 ± 13.6 and 9.1 ± 6.4 %, respectively. EPOM (July 12 and July 31) was the main contributor in the diet of gammarids (Fig. 17).

5.6.2. Consumer trophic positions in summer

There were significant $\delta^{15}N$ differences between consumers in the summer (one-way ANOVA $F=82.7$, $p<0.05$). Chironomid larvae and gammarids had the most depleted $\delta^{15}N$ values, whereas piscivorous fish were most enriched (Table 14). The $\delta^{15}N$ of primary consumers varied in the range of 6.6 - 10.7 ‰. Secondary consumers (benthic predatory leeches Erpobdellidae and Glossiphoniidae, benthivorous fish, such as roach and bream, as well as plankton predators *L. kindtii* and juvenile fish) had $\delta^{15}N$ values in the range of 11.3 - 13.8 ‰ (Table 14, Fig. 15). Large piscivorous fish, such as *P. fluviatilis* and *S. lucioperca*, and planktivorous *P. cultratus* have the highest $\delta^{15}N$ values, >14.5 ‰ (Table 14).

Two combined baselines were calculated: (1) by grouping more ^{15}N-enriched primary consumers in block A, collected in spring ("j-k" group, post-hoc LSD test, $p>0.05$, Table 13), with that collected in spring (oligochaetes, chironomids, *Valvata*, *Dreissena* and mesozooplankton), (2) by pooling offshore and littoral primary consumers in B

Table 14. Stable nitrogen isotope ratios ($\delta^{15}N$, ‰) of consumers in summer. Significant differences between the $\delta^{15}N$ values of species (LSD, $p < 0.05$) are denoted with non-matching letters.

Species	Station	$\delta^{15}N$, mean ± SD	Post-hoc comparisons
Gammaridae 5-10mm	VL	7.0 ± 0.2	ab
Chironomidae	JO	7.2 ±0.3	abc
Gammaridae >10mm	VL	7.6 ± 0.2	bcd
P. lacustris subadults	VO_1	8.0± 0.3	cd
Limnaeidae	$VO_{1,2}$	8.0 ± 0.8	d
Chironomidae	VO_2	8.1 ± 0.1	de
P. lacustris subadults	VL	8.1 ± 1.0	de
Valvata spp.	VO_1	8.2 ± 0.3	de
Gammaridae 5-10mm	JL	8.3 ± 0.1	def
Gammaridae >10mm	JL	9.0 ± 0.4	efg
Viviparus spp.	VO_1	9.1 ± 0.7	fg
D. polymorpha L~1cm	VO_2	9.1 ± 0.7	fg
P. lacustris subadults	JL	9.2 ± 0.1	fg
P. lacustris adults	VL	9.3 ± 0.9	g
Mesozooplankton	JO	9.4 ± 0.1	gh
Mesozooplankton	VO_1	9.4 ± 0.4	gh
D. polymorpha L~1cm	VO_1	9.4 ± 0.3	gh
Valvata spp.	JO	9.8 ± 0.2	ghi
Viviparus spp.	VO_2	9.8 ± 0.9	ghij
P. lacustris adults	VO_1	9.9 ± 0.3	ghijk
D. polymorpha L~2cm	VO_1	10.0 ± 0.5	hijk
P. lacustris adults	JO	10.5 ± 0.4	ijkl
Unio spp.	VO_2	10.5 ± 0.5	jk
Oligochaeta	$VO_{1,2}$	10.7 ± 0.8	kl
D. polymorpha L~2cm	VO_2	10.8 ± 0.2	kl
P. fluviatilis juv.	JL	11.3 ± 0.4	lm
Leptodora kindtii	JO	11.7 ± 0.2	mn
	VO_1	11.7 ± 0.2	mn
Erpobdellidae	VO_2	11.8 ± 0.1	mn
Rutilus rutilus	JL	12.4 ± 0.4	n
Abramis brama	JO	13.3 ± 0.5	o
G. cernuus	JL	13.4 ± 0.1	o
Rutilus rutilus	VO	13.8 ± 0.5	op
Perca fluviatilis	JL	14.3 ± 0.1	pr
Pelecus cultratus	VO	14.6 ± 0.5	r
S. lucioperca	JO	15.7 ± 0.6	s
P. fluviatilis	VO	16.5 ± 0.4	s

and C blocks (Fig. 15). Pooled consumers in block A and in spring (A+spring consumers) represent the food source that has seasonally stable SI composition and are depleted in $\delta^{13}C$ (mean -30.2 ‰) and enriched in $\delta^{15}N$ (10.7 ‰). Pooled consumers, such as gastropods, chironomids, mysids, mesozooplankton and all littoral consumers, from B and C blocks (BC consumers) represent the summer secondary producers, which are more enriched in $\delta^{13}C$ (-24.6 ‰) and depleted in $\delta^{15}N$ (8.4 ‰). The average $\delta^{13}C$ and $\delta^{15}N$ values in A+spring and BC consumers differed by 5.6 and 2.3 ‰, respectively. The relative contribution of A and BC primary consumers to secondary consumers diet differed between the species: largest contribution of ^{13}C-depleted A+spring source was in the leeches and roach at VO site, whereas smaller individuals of perch, roach and planktivorous *P. cultratus* relied slightly more on the ^{13}C-enriched sources (Fig. 18).

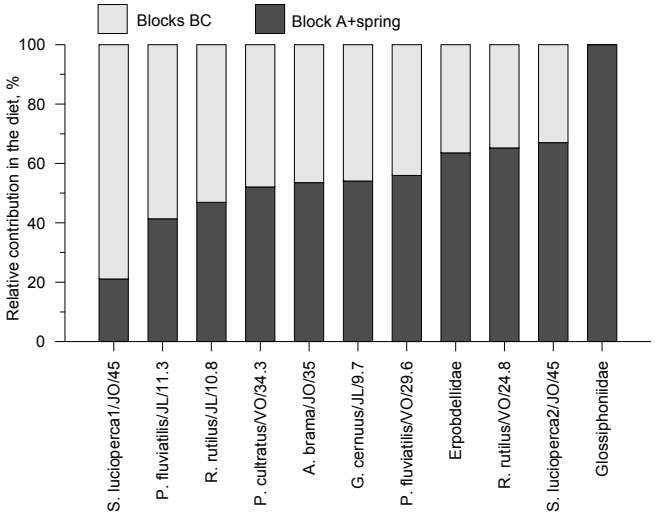

Fig. 18. Relative contribution of primary consumers with more depleted $\delta^{13}C$ = -30.2 ‰ (block A+spring) and more enriched $\delta^{13}C$ = -24.6 ‰ (blocks BC) values in the diet of fish and leeches, calculated by two-end-member mixing model. The models were calculated using $\delta^{13}C$ fractionation factors of +1 and +2 ‰ for secondary and tertiary consumers, respectively.

There was, however, substantial between individual variations in some cases. For example, two similarly sized individuals of pikeperch showed opposite proportions of ^{13}C-depleted and ^{13}C-enriched source in their diet.

The TL of secondary and tertiary consumers estimated using single baseline approach varied in the range of 0.9 TL, with the highest estimates obtained using $\delta^{15}N_{Chironomidae}$ baseline and the lowest using $\delta^{15}N_{Bivalvia}$ baseline, while $\delta^{15}N_{Valvata}$ baseline resulted in intermediate TL values (Fig. 19). The maximal trophic position was calculated for perch (L 30 cm) 3.8-4.7 TL. Estimated TL based on weighted source contributions differed from that calculated using single baselines, most of them were between the TL values estimated using $\delta^{15}N_{Bivalvia}$ and $\delta^{15}N_{Valvata}$ (Fig. 19).

5.6.3. Organic matter sources and trophic levels in autumn

In the autumn, consumers' $\delta^{13}C$ values decreased slightly compared to those in the summer, varying from -31 to -23 ‰ (Fig. 20). At VO sampling site, many species lowered their $\delta^{13}C$ values, whereas, at JO site, consumer $\delta^{13}C$ remained relatively enriched, similar to their summer levels (Fig. 20). At VO site, a clear association was evident between the $\delta^{13}C$ values in the consumers and EPOM and RPOM, particularly in October. At JO site, stable isotope composition of the consumers suggests that their primary source of organic matter was more ^{13}C-enriched and ^{15}N-depleted, which could be the EPOM originated from August-September as well as coastal or offshore MPOM. The most ^{13}C-enriched consumers (-25 to –23 ‰) were fish and mysids at JO sampling site.

In the autumn, $\delta^{15}N$ values in primary and secondary consumers varied in narrower interval than in the summer (9.46 - 13.92 ‰, Fig. 20), with little but significant differences between the species (one-way ANOVA, $F=29.81$, $p<0.05$). Most of benthic primary consumers fell into one group, with depleted $\delta^{15}N$ values from 10 to 11 ‰ (post-hoc LSD test, $p>0.05$), while *Marenzelleria neglecta*, mysids, leeches and fish had slightly more enriched $\delta^{15}N$ values (~12-13 ‰). Assuming

$\delta^{15}N_{Chironomidae}$ baseline for second trophic level, most of other consumers were assigned to 2-3 TL (Fig. 20).

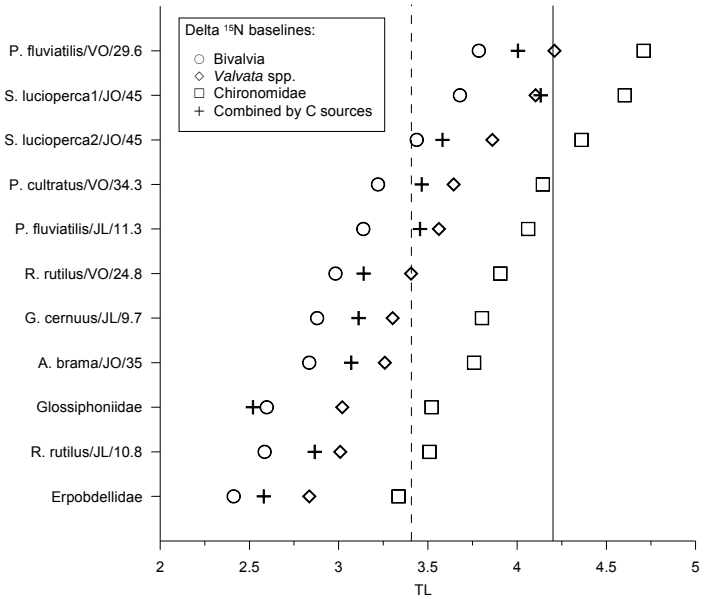

Fig. 19. The trophic levels of predators: (fish and leeches) calculated using single baseline approach with (1) $\delta^{15}N_{Bivalvia}$=10.4, (2) $\delta^{15}N_{Valvata}$=9, and (3) $\delta^{15}N_{Chironomidae}$=7.3: and combined baseline approach with A plus spring and BC consumer blocks ($\delta^{15}N_{A+spring}$=10.7 $\delta^{15}N_{BC}$=8.4, Fig. 15), weighted to the relative contribution of each block to the diet, calculated by two-end-member mixing model for $\delta^{13}C$ values (Fig. 18). Fish total lengths and sampling stations are indicated. Ecopath TL estimates of 3.4 and 4.2TL (Ertürk, 2008) for benthophagous and predatory fish are denoted with dashed and solid lines, respectively.

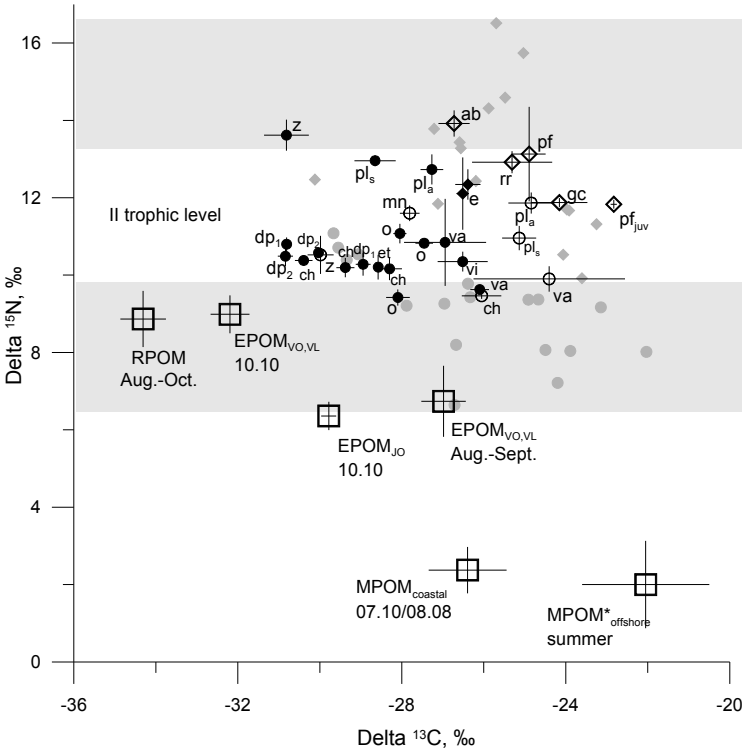

Fig. 20. Stable isotope ($\delta^{15}N$ and $\delta^{13}C$, ‰) composition of consumers and their primary sources of organic matter (squares) in the autumn. Organic matter sources were: marine (MPOM), riverine (RPOM) and estuarine (EPOM) particulate organic matter, with the sampling sites, denoted as superscript (starred value from Maksymowska et al., 2000 and Rolff and Elmgren, 2000). Herbivores and omnivores: open (JO) and filled (VO) circles; predators: open (JO) and filled (VO) rhombs. Grey symbols all consumers in the summer. Species abbreviations as in Table 2. Shaded bars indicate trophic levels calculated for $\delta^{15}N_{Chironomidae}$ baseline.

5.7. The trophic role of *P. lacustris*

5.7.1. Spatial distribution and seasonal dynamics of *P. lacustris* population

In the summer, the highest abundance of *P. lacustris* were found in the northern part of investigated area dominated by sand bottom and depths of 2 ± 0.4 m at sampling sites (Fig. 22). Assuming estimated 40 % capture efficiency of epibenthic sledge in the southern area with shell deposits and living zebra mussel communities (Lesutiene unpublished), the abundance of *P. lacustris* was slightly lower but did not differed significantly from that estimated on sand 30 ± 17 vs. 51.3 ± 28 indv/m^2 , respectively at the same 2 - 2.8 m depth range (t-test, $p>0.05$). The maximal record reached 282 ± 16 indv m^{-2} and 475 ± 91 mgDW/m^{-2} in 2003. The estimated length-weight relationship of *P. lacustris* is $DW=0.004 \times L^{2.73}$ (n=88, R^2=98.5; Fig. 21). The biomass varied among the stations the mean biomass on sand was 84.3±30.3 on sediments with shells and *Dreissena* 24.7±4.7 Mean±SE, mg DW m^{-2}, respectively.

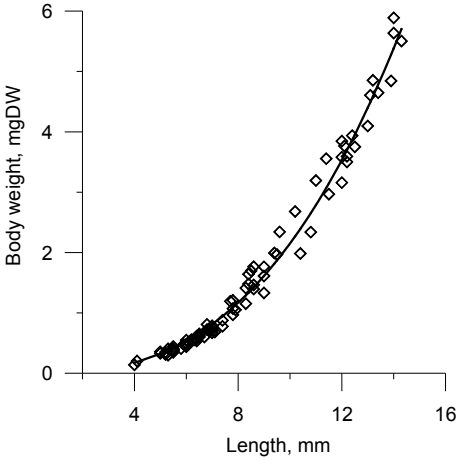

Fig. 21. *Paramysis lacustris* body dry weight (DW, mg) to length (L, mm) relationship.

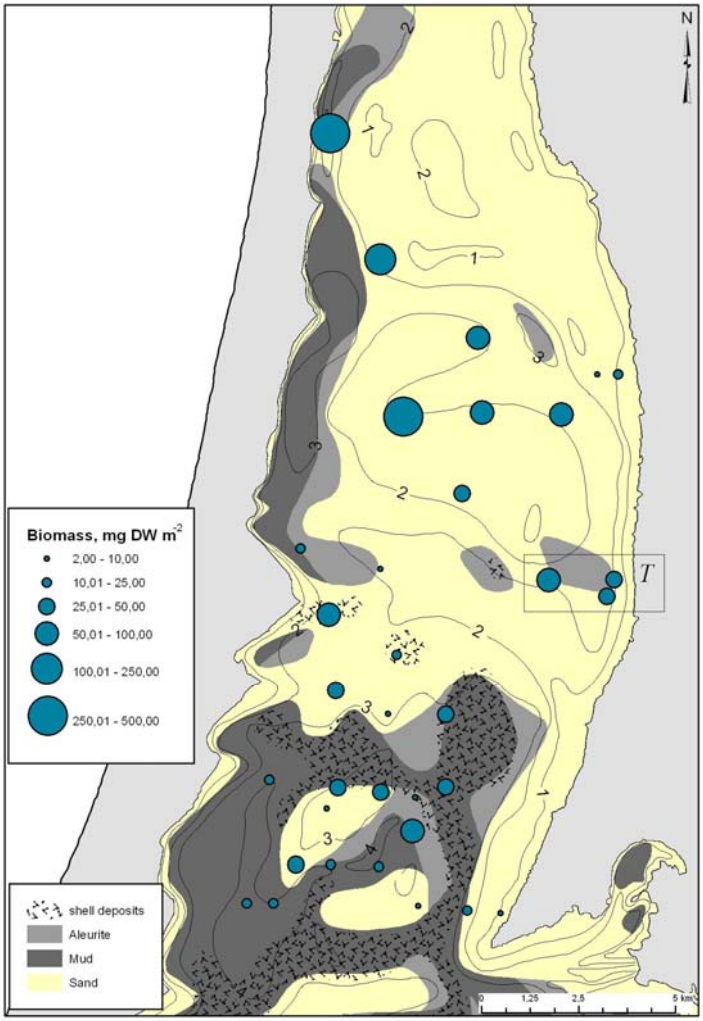

Fig. 22. The biomass (mg DW m^{-2}) of *P. lacustris* in August (data collected in 2003-2007). The biomass estimates in the areas with shell deposits or living zebra mussel communities (Gulbinskas et al., 2002, Zaiko 2009) are corrected for 40 % capture efficiency of the epibenthic sledge.

P. lacustris population was dominated by small individuals in the summer, but mean size of mysid was increasing with depth (one-way ANOVA, F=163.4, p<0.05, Fig. 23). Mean lengths of mysids were 5±1.8, 6.5±2.2 and 7.9±2.3 mm at 1.2, 2.2 and 2.7 m depths, respectively.

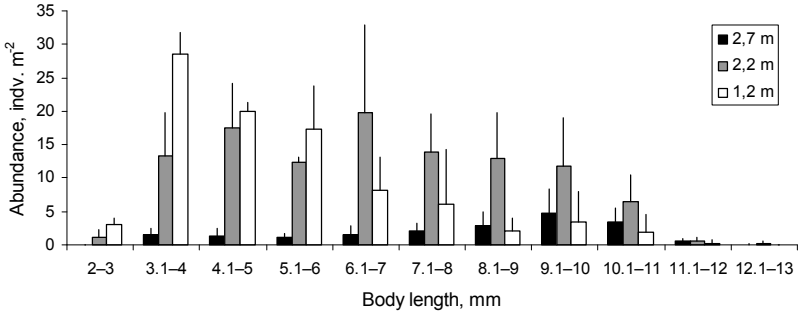

Fig. 23. Abundance (indv m^{-2}) of different *Paramysis lacustris* size groups at 2.7, 2.2 and 1.2 depths, in the ***T*** sampling transect (see Fig. 22) in August 2006.

During the summer *P. lacustris* was more abundant offshore (VO site than in the littoral (VL site), up to 13 and 4 ind. m^{-2}, respectively (Fig. 24). From mid-August to mid–October 2004, abundance increased at both stations, 4.3-fold offshore and 56-fold in the littoral (VO and VL, respectively). In 2006, the same trend was observed, with significant increase in the littoral up to 142-fold (one-way ANOVA, F=20.87, p<0.05; Fig. 24). There were no significant effects of habitat type and sampling date on mysid abundance (data for 2004; two-way ANOVA, p>0.05, in both cases), but the interaction between the two factors was significant (F=5.05, p<0.05). This result implies that the difference between the littoral and pelagic habitats is time dependant: highest in the early autumn and lowest in October. Moreover mysid preference for the deeper habitats shifts to the littoral beginning at the end of September (Fig. 24). Mysid biomass in in October 2006 0.5 - 0.7 g DW m^{-2}, was higher than any other estimate in the summer (Fig. 22).

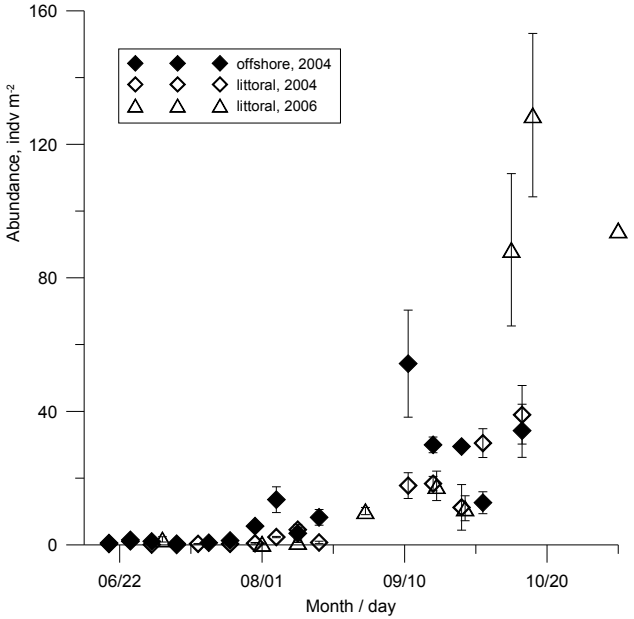

Fig. 24. Population abundance (ind m^{-2}; mean ± SE) of *P. lacustris* in the littoral (year 2004- open triangles and year 2006- open diamonds) and offshore habitats (year 2004 – filled triangles).

5.7.2. Mesozooplankton, mysid stomach and bolus $\delta^{15}N$ signatures

Mesozooplankton biomass peaked at the end of July (10.87 mg L^{-1}) and dropped to less than 0.02 mg L^{-1} in October, 2004. The mesozooplankton community was dominated by *Bosmina* spp. and small *Daphnia* spp. in the first half of July and switched to dominance by large-bodied *Daphnia* spp. towards the end of the month (Fig. 25). Large *Daphnia* spp. prevailed in the community till the middle of September, while other cladocerans and copepods contributed less (about 20 and 10%, respectively) to the total mesozooplankton biomass. The predatory cladoceran *L. kindtii* occasionally appeared in the samples but its contribution to the total biomass never exceeded 1%.

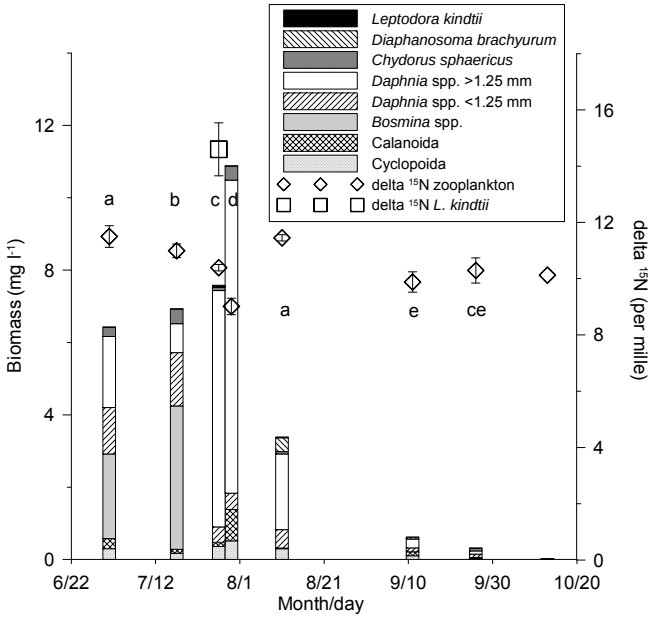

Fig. 25. Seasonal variation of mesozooplankton community composition and $\delta^{15}N$ values in 2004. Non-matching letters denote the significant differences between the sampling dates (LSD, $p<0.05$).

Mesozooplankton $\delta^{15}N$ values varied substantially during the study period. There was a significant date effect on $\delta^{15}N$ values (ANOVA: $F=49.8$, $p<0.05$) and mesozooplankton $\delta^{15}N$ values significantly and negatively correlated to the abundance of cyanobacteria ($r=-0.62$, $p<0.05$). However, lowest $\delta^{15}N$ values coincided also with the increase of mesozooplankton biomass and the shift in the community structure in the end of July (Fig. 25). In particular, the $\delta^{15}N$ increase towards the August 11 coincided with the increased contribution of cladoceran *Diaphanosoma brachyurum* to the community (11% of the total biomass) and nearly total disappearance of calanoid copepods. It is also possible that some mesozooplankton samples used for stable isotope analyses were contaminated with *L. kindtii*, which had significantly

higher δ ^{15}N than herbivorous mesozooplankton (14.6±0.9‰ vs. 10.4±0.1; t test, $p<0.05$; Fig. 25).

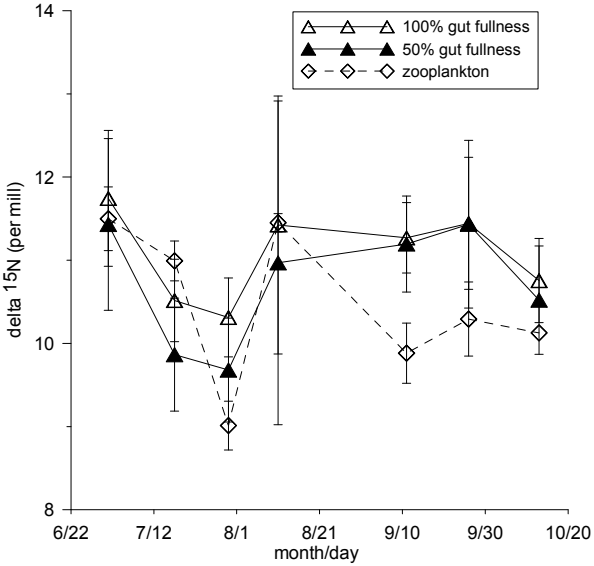

Fig. 26. The δ^{15}N signatures of *P. lacustris* bolus (pooled data for small and large adults) and mesozooplankton. The gut fullness in mysids was assumed to be either 50% or 100%.

Neither stomach δ^{15}N values nor calculated bolus δ^{15}N values differed significantly between the small and large individuals (paired t test, $p>0.05$). Therefore, the calculated δ^{15}N values of bolus were pooled together for the two size groups and compared to mesozooplankton δ^{15}N values (Fig. 26). The average seasonal differences between mysid bolus and mesozooplankton δ^{15}N were 0.6±0.9‰ and 0.3±1.1‰ for 100 and 50% stomach fullness, respectively, but the differences between the bolus values and mesozooplankton as well as between both scenarios were never significant (paired t test, $p>0.05$). The differences between δ^{15}N of mysid body and bolus were higher in the summer than in the autumn for both small (1.8±1.0 vs. -0.1±1.1,

respectively, $p<0.05$) and large (2.5±0.9 and 1.0±0.3, respectively, $p<0.05$) adults.

5.7.3. Mysid body $\delta^{15}N$ signatures as indicator of ontogenetical and seasonal diet changes

There was a significant increase in $\delta^{15}N$ values with size (Fig. 27), although the difference between mean seasonal $\delta^{15}N$ values in juveniles and subadults was negligible (11.2‰ and 11.3‰, respectively, $p>0.05$). The time effect was comparable in all size groups (Fig. 27, Table 15), with relatively invariant isotopic signatures in July-August and a significantly lower (by 1.7‰ on average) $\delta^{15}N$ values in September followed by a slight increase towards the mid-October 2004 (LSD, $p<0.05$; Fig. 27).

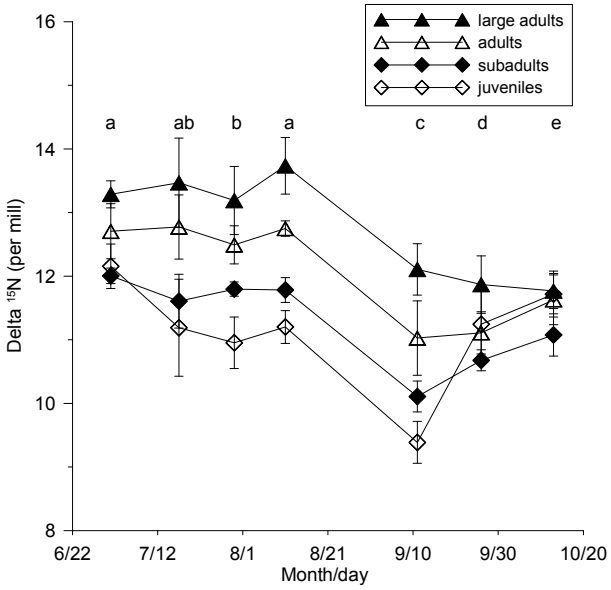

Fig. 27. Seasonal variation of $\delta^{15}N$ values in different *P. lacustris* size groups in 2004. Significant differences between the sampling dates (LSD, $p<0.05$) are denoted with non-matching letters.

Table 15. Two-way ANOVA testing effects of mysid size (BL, mm) and sampling occasion on mysid $\delta^{15}N$ (muscle tissue in adults, whole bodies in immature individuals).

Effect	df	MS	F	p
size group	3	19.9	131.24	0.0000
time	6	9.6	63.13	0.0000
size group × time	18	1.1	6.99	0.0000
Error	110	0.2		

When compared to *L. kindtii* (end of July), the adult mysids had significantly lower $\delta^{15}N$ values (t test, $p<0.05$) (Fig. 28).

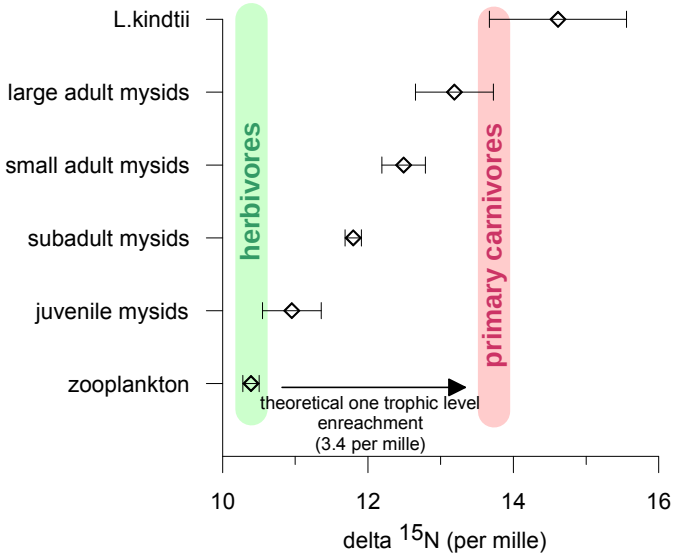

Fig. 28. The structure of the pelagic trophic chain in the summer (end of July, 2004).

On the other hand, their $\delta^{15}N$ values were significantly higher than those in mesozooplankton (paired t test, $p<0.05$), during the entire sampling season, while $\delta^{15}N$ values of juveniles and subadults were not different from mesozooplankton (paired t test, $p>0.05$). As a re-

sult, the trophic shift $\Delta^{15}N$ of mysid over mesozooplankton differed significantly between the size groups (ANOVA $F=23.4$, $p<0.05$), with no significant differences between juveniles and subadults (overall average difference is 0.8±0.9) and significant differences between small and large adults (1.6±0.9 vs. 2.3±0.9 respectively; LSD, $p<0.05$,) as well as between these groups and smaller mysids (LSD, $p<0.05$).

5.7.4. Mysid individual growth rate in the autumn

Mysid BL frequency distributions indicated that one cohort originated in August and two subsequent cohorts were born in September, with 1-2 wk difference in timing between colder 2004 and warmer 2006. The negligible (0.8-3.5% in October and 0% in November) percentage of new-born mysids (BL<4 mm) as well as the minor contribution (<3% in October - November) of ovigerous females in the population indicated that reproduction ceased after September. Each cohort became dominant approximately one month after hatching: cohort I dominated at the end of August, cohort II - at the end of September, and cohort III - in the second half of October-November (Table 16). The September cohorts grew and matured by November (Fig. 29) and represented the overwintering generation.

Table 16. The relative proportions of subsequent cohorts (I, II and III coh.; data for 2006) in the population and the results of Chi-square test for the goodness-of-fit of the mixture distribution model. Asterisks indicate significant ($p<0.05$) differences between the model and the length-frequency data; n – number of individuals measured at each sampling date.

		Aug 30	Sep 19	Sep 27	Oct 10	Oct 16	Nov 9
% in population	I coh.	98	4.3	-	-	-	-
	II coh.	-	95.7	74.4	51.2	28.2	
	III coh.	-	-	25.6	48.8	71.8	100
Chisq,		0.73	17.54	5.30	5.51	8.73	12.69
p		0.87	0.004*	0.258	0.480	0.273	0.026*
n		453	378	388	373	343	100

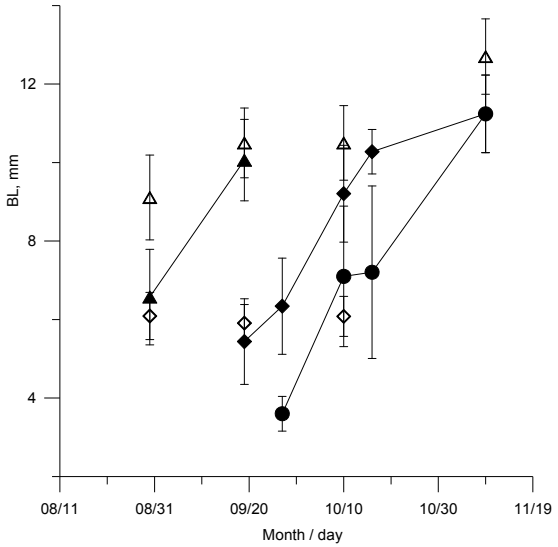

Fig. 29. Temporal changes in body length of *Paramysis lacustris* (BL, mm; mean ± SD) in 2006. Different cohorts are shown as follows: cohort I – filled triangles, cohort II – filled diamonds, and cohort III – circles. BL of individuals selected for SIA is shown with open symbols: triangles for adults and diamonds for subadults.

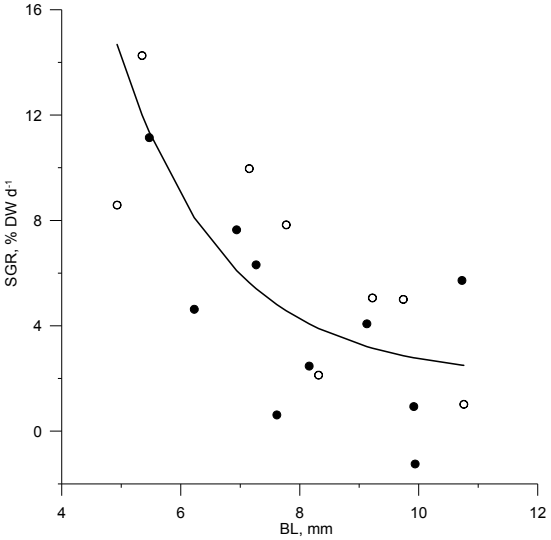

Fig. 30. Relationship between specific growth rate (SGR, % DW d^{-1}) and body length (BL, mm): closed circles- data of 2004, open circles- 2006, regression line of pooled data of 2004 and 2006.

5.7.5. Mysid food sources in the littoral in autumn

Littoral mesozooplankton biomass was dominated by copepodites and adult harpacticoids (body size 0.3-0.7 mm) and cladocerans. The species contributing most were harpacticoid *Bryocamptus* spp. (on average 30% of total zooplankton biomass) and cladoceran *Daphnia* spp. (20%), while cyclopoids *Acanthocyclops viridis* and *Mesocyclops leuckarti* made 8 and 10%, respectively. From August to October, the concentration of EPOM <70 µm decreased 6.5-fold RPOM 2.5-fold (Table 17). The high concentrations recorded on November 9 were, most probably, caused by the windy weather and re-suspension of BPOM in the shallow littoral zone. Assuming chlorophyll a to contribute 1% to phytoplankton DW (Reynolds, 2006), phytoplankton contribution to EPOM was 16, 30, 38 and 14% by DW at each successive sampling date. Cyanobacteria (*Microcystis*, *Aphanizomenon*, *Planktothrix* and *Chroococcus*) dominated large phytoplankton

(>70μm) during the study. The contribution of diazotrophic cyanobacteria (*Anabaena* spp. and *Aphanizomenon* spp.) to the total >70μm phytoplankton biovolume was 15, 6, 36 and 10% on four sampling dates, respectively. The total biovolume of phytoplankton <70 μm was variable (582-6123 μm^3 l^{-1}), with a maximum in September and minimum in October (Table 17). This fraction was dominated by green algae (*Scenedesmus* and *Pediastrum*) in August and later by diatoms (*Thalassiosira*, *Cyclotella* and other small Centrales).

Table 17. Composition and abundance of lagoon (EPOM) and riverine (RPOM) POM in 2006. Suspended POM <70μm: concentration (mgDW l^{-1}, mean±SD) and chlorophyll a (μg l^{-1}) content. Phytoplankton <70μm and >70μm: biomass (mg l^{-1}) and community structure (% by biomass; chlorophytes - CHL, cyanobacteria - CB and diatoms - DT). Mesozooplankton: biomass (mg DW l^{-1}) and community structure (% by biomass).

			Aug 30	Sept 19	Oct 10	Nov 9
EPOM	Concentration <70μm		25.8±3.2	8.6±0.9	4.0±0.3	22.3±4.7
	Chlorophyll a <70μm		40	26.2	15.1	31.6
	Phytopl. <70μm	Biomass	3.3	6.1	0.6	2.9
		CHL	60	8	13	8
		CB	4	1	2	16
		DT	24	87	79	76
	Phytopl. >70μm	Biomass	6.4	8.2	3.5	2.5
		CHL	0	0	0	2
		CB	83	88	85	46
		DT	17	12	14	52
Mesozooplankton		Biomass	0.067	0.052	0.029	0.038
		Cladocera	21	13	7	62
		Harpactic.	35	15	66	3
		Calanoida	3	2	23	14
		Cyclopoida	41	70	3	21
RPOM	Concentration <70μm		10.0±0.9	8.1±0.3	4.0±0.3	-
	Chlorophyll a <70μm		59.5	40.1	19.1	-

C and N contents were highest in zooplankton and lowest in BPOM (Table 18). The $\delta^{13}C$ and $\delta^{15}N$ isotopic composition of BPOM differed from that of RPOM and lagoon EPOM at the end of summer, but was very close to the aged dead leaves of the submerged macrophytes (Tables 9, 18), which resulted in the high (44-100%) contribution of this

source to the fine bottom detritus estimated by the mixing model (Table 19). In September and October, BPOM was still more enriched in $\delta^{13}C$ than lagoon EPOM, consisting largely of macrophyte-originated detritus (50-80%; Table 17, Table 18). Simultaneously, stable isotope ratios of riverine and lagoon POM became fairly similar (Table 18), hampering estimates of their individual contributions to BPOM. Most probably, the contribution of the RPOM to both EPOM and BPOM increased as a result of the doubled river discharge in September. As the EPOM 100-200 μm had very low $\delta^{15}N$ values in October (Table 18), due to the dominance of nitrogen-fixing *Aphanizomenon* spp., it is not likely to contribute to BPOM appreciably.

Table 18. C and N elemental composition (%, by DW) and mean C:N ratio (by atoms) of EPOM <70μm,; bottom fine suspended detritus (BPOM), and mesozooplankton. All data are presented as means±SD.

Source		August 30	September 19	October 10	November 9
EPOM	C	28±1	20±2	28±3	18±6
	N	3±0.1	4±0.4	4±0.5	2±0.4
	C:N	9.7	6.3	7.7	12.2
	$\delta^{13}C$	-28.3±0.0	-33.3±0.5	-31.8±0.2	-23.7±0.2
	$\delta^{15}N$	6.3±0.3	8.8±0.5	8.1±0.1	8.4±0.3
RPOM	C	39±7	16±1.6	42±5	–
	N	8±2	3.6±0.4	8±1	
	C:N	5.7	5.2	6.2	
	$\delta^{13}C$	-35.4±0.3	-35.9±0.2	-34.6±0.3	
	$\delta^{15}N$	10.1±0.1	8.7±0.2	9.1±0.3	
BPOM	C	7±4	17±3	18±4	–
	N	1±0.5	2±0.4	2±0.4	
	C:N	15.0	8.9	10.2	
	$\delta^{13}C$	-18.5±2.8	-25.9±1.5	-24.3±0.5	
	$\delta^{15}N$	7.2±0.7	8.2±0.5	8.6±0.1	
Mesozoo plankton	C	51±15	51±11	–	–
	N	12±4	12±2	–	
	C:N	5.2	5	5.2	
	$\delta^{13}C$	-29.3±0.2	-32.6±0.2	-29.8±0.2	
	$\delta^{15}N$	10.6±0.2	13.0±0.2	13.6±0.4	

Table 19. The relative contributions (%; upper and lower limits of 95% confidence interval; mean ± SE) of particulate organic matter EPOM- estuarine, RPOM- riverine and submersed macrophyte detritus (MACROPH) to the littoral bottom fine POM (BPOM) calculated by the mixing model using $\delta^{13}C$ and $\delta^{15}N$ values on August 30 and $\delta^{13}C$ on September 19 and October 10.

Date	Source	Relative proportion of the source	
		95% conf. int.	Mean ± SE
Aug 30	RPOM	0 – 12	-16 ± 10
	EPOM	0 – 79	27 ± 16
	MACROPH	44 – 100	89 ± 14
Sept 19	EPOM/RPOM	24 – 76	50 ± 6
	MACROPH	24 - 76	50 ± 6
Oct 10	EPOM/RPOM	36 – 52	44 ± 3
	MACROPH	48 – 64	56 ± 3

Differences between the isotopic signatures of mesozooplankton, BPOM and EPOM <70 μm were significant on all sampling dates (t-tests, $p<0.05$ in all cases), except for $\delta^{15}N$ in BPOM and EPOM in August and September and $\delta^{13}C$ in mesozooplankton and EPOM in September (t-tests, $p>0.05$ in both cases). Relative to mesozooplankton and EPOM, BPOM was enriched in C^{13} by 8‰, whereas mysids had intermediate $\delta^{13}C$ values (Fig. 31). In mesozooplankton and mysids, $\delta^{15}N$ values were on average 4.5‰ higher than in SPOM and BPOM. The $\delta^{15}N$ and $\delta^{13}C$ of mysids varied in concert with those in suspended and benthic POM, averaged over 3 weeks between consecutive sampling occasions (Spearman's correlation coefficients:SPOM, $r=0.88$ and 0.79 and BPOM, $r=0.9$ and 0.77, for $\delta^{15}N$ and $\delta^{13}C$, respectively, $p<0.05$ in all cases; Fig. 31). Between mysids and zooplankton, the correlation was significant for $\delta^{15}N$ ($r=0.91$, $p<0.05$), but not for $\delta^{13}C$ ($r=0.3$, $p>0.05$). When isotopic signatures of mysids were correlated with those in the food sources at the same sampling date, the correlations were not significant ($p>0.05$ in all cases).

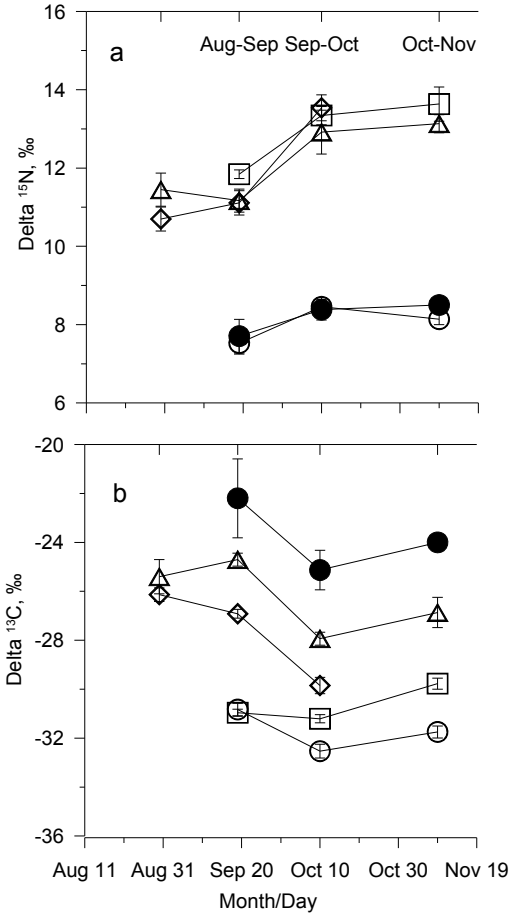

Fig. 31. Variation (mean±SD) of $\delta^{15}N$ (a) and $\delta^{13}C$ (b) in *Paramysis lacustris* (adult mysids – open triangles and subadults – open diamonds) and their food sources (EPOM –open circles, BPOM – filled circles, and zooplankton – open squares). On each panel, the lower x axis indicates the sampling dates for mysids and the upper x axis – the corresponding sampling intervals for the food sources. The food sources (i.e., end-members) were averaged between consecutive sampling occasions and matched with the consumer signatures used in the mixing model calculation.

Sources contributions, estimated by the concentration-weighted dual isotope mixing models, differed slightly between mysid size groups and sampling dates (Fig. 32). The contribution of EPOM was larger in the diet of subadult mysids, while BPOM dominated the diet of adult mysids (Fig. 32). In both size groups, the proportion of mesozooplankton was negligible in September and about 9% in October-November. On average, mysids obtained 46% of their nitrogen from EPOM, 35% from BPOM and 19% from mesozooplankton, whereas 44, 43 and 13% of carbon originated from the each source, respectively.

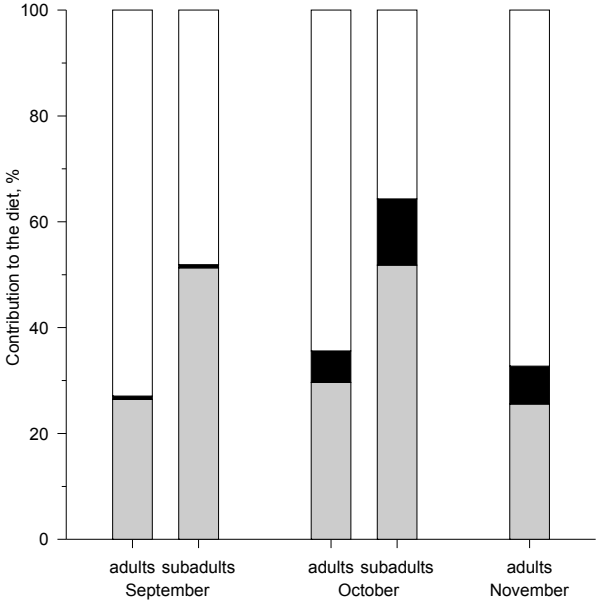

Fig. 32. Relative contribution by biomass of different food sources to the diet of *Paramysis lacustris* (adults and subadults) estimated by the concentration-weighted, dual-isotope mixing model. Color coding: EPOM - grey, mesozooplankton - black, and BPOM - white.

6. DISCUSSION

6.1. Composition of riverine POM

Depleted $\delta^{13}C$ in the Nemunas RPOM (mean: -32.9 ± 2.3 ‰, minimum: -35.9 ± 0.2 ‰) and low C/N ratio of 7.1, close to the Redfield ratio 6.6, indicates prevalence of phytoplankton in RPOM during the study. However, the positive correlation between $\delta^{13}C$ and C/N in the Nemunas RPOM indicates that variation in terrestrial organic matter input is detectable in Nemunas River (Fig. 11). These results corroborate earlier findings reporting low (5-20 %) contribution of terrestrial organic substances to the RPOM during the vegetation season (Table 1, Galkus and Jokšas, 1997). This also suggested that dominance of algal and bacterial cells in Nemunas RPOM in the summer implies its high bioavailability for microbial food web and direct mixing into EPOM of Curonian Lagoon (Stepanauskas et al., 2002).

Similar seasonality of most negative RPOM $\delta^{13}C$ values in spring-summer and least negative values in winter are found in Sheldt and Vistula Rivers (NW and NE Europe, respectively) (Hellings et al., 1999, Maksymowska et al., 2000, De Brabandere et al., 2002). This indicates that phytoplankton dominates the RPOM in growth season (March-November), whereas terrigenous detritus is a main contributor in winter (December-February). RPOM $\delta^{13}C$ values range from -26.5 to -27.6 ‰ in Sheldt and -27.5 to -28 ‰ in Vistula in winter (Hellings et al., 1999, Maksymowska et al., 2000). As there were no such measurements of Nemunas RPOM from winter, there is no true reference value for the terrestrial material in the Nemunas River as it known that in winter its share reaches 80 % of RPOM (Table 1, Galkus and Jokšas, 1997). However, terrestrial organic matter runoff could also be enhanced by heavy rainfall during the warm season. For instance, during flood events in the Danube River (Central Europe), the increased C/N (>10) and $\delta^{13}C$ values (>-25 ‰) corresponded to >80 % detrital carbon in the total POM pool (Hein et al., 2003). The maximal $\delta^{13}C$ (-30.0 ± 1.4 ‰) and C/N (9.2) values of the Nemunas RPOM, also cor-

responded to the flood event and increased concentration of total suspended matter on June 21, 2006 (Fig. 2, 6).

The northern pristine tributaries in the Gulf of Bothnia (the Baltic Sea) have a much lower $\delta^{15}N$ signal (Ångermanälven River, Table 20) compared to south-eastern eutrophied rivers that enter the Baltic Sea from the densely inhabited basins (Rolff and Elmgren, 2000, Voss et al., 2005). The mean $\delta^{15}N$ value in the Nemunas RPOM (8.4 ± 1.0 ‰) is close to that reported for most of the European eutrophied rivers (Table 20, Vistula: 8.7 ± 3.2 ‰ and Oder: 8.9 ± 1.9 ‰; Voss et al., 2005) but is higher than in other reports (4.0 ± 2.5, Maksymowska, 2000). Elevated $\delta^{15}N$ signature in riverine nitrogen is a result of municipal and agricultural wastewater loads, complex transformations of fertilizers in soils and bacterial activity (McClelland et al., 1997, Voss et al., 2000, Costanzo et al., 2001).

6.2. Composition of estuarine POM

POM samples for SIA usually include a mix of phytoplankton, detritus, microzooplankton and bacteria, separation of these constituents is difficult and still open for innovations (Michener and Shell, 1994, Hamilton et al., 2005). The estimated C/N ratios and stable isotope ratios in EPOM evidence that largest proportion of organic matter in it comes from autochthonous phytoplankton.

Strong correlation of the chlorophyll a concentration with the concentration of EPOM<70 μm suggested that phytoplankton constitute significant part of EPOM<70 μm, on average 24 % of the EPOM<70 μm DW (Appendix 2) as estimated from chlorophyll-a content. Composition of the remaining matter in EPOM <70 μm was not investigated, obviously it contained more inorganic sediments, reflected in low C and N concentrations, 20 and 3 %, respectively.

Table 20. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$, ‰) composition in the suspended (POM) and sedimentary (BPOM) organic matter in the Baltic Sea and coastal waters.

Data collection areas	Organic matter source/particle size	Data collection time	$\delta^{13}C$, Mean ± SD; or Min – Max (‰)	$\delta^{15}N$, Mean ± SD ; or Min – Max (‰)
		Riverine		
Nemunas River[a]	POM GF/F - 70µm	10 July 2006	-32.4 ± 0.1	7.5 ± 0.7
Vistula River[b]	POM total	Annual mean,1996	-28.5 ± 1.2	4 ± 2.5
Vistula River[d]	POM	Annual mean, 2003	–	8.7 ± 3.2
Vistula River[f]	POM	February-March, 2001 and 2002	-27.8 – -26.2	4.2 – 11.6
Oder River[d]	POM	Annual mean, 2003	–	8.9 ± 1.9
Ångermanälven River[c]	POM GF/F - 5µm	July, 1994	-31 ± 0.2	2 ± 0.5
		Baltic coastal		
Curonian Lagoon[a]	POM GF/F-70µm	4 August 2006	-24.1 ± 0.1	8.3 ± 0.4
	POM GF/F - 70µm	12 July 2006	-28.4 ± 0.1	2.1 ± 0.4
Curonian lagoon, fine sandy silt-rich mud area[e]	BPOM surface	1993-1997	-24.8	6.5
	BPOM at 20 cm sedimeth dept	Sediment age corre-sponds to 1950	-30.3	4.8
Baltic Proper Coastal Areas/Gulfs of Riga and Finland[d]	BPOM surface	1993-2003	-25.4 ± 2.2	7.3 ± 2.1
Baltic Sea Lithua-nian coast[a]	POM GF/F - 70µm	11 July 2006	-25.4 ± 0.3	0.9 ± 0.5
	POM GF/F - 70µm	8 August 2006	-27.4 ± 0.0	3.9 ± 0.3
Gulf of Gdansk[b]	POM total	Summer, 1996	-22.3 ± 0.4	1.5 ± 0.8
		Baltic offshore		
Central Baltic Prop-er[c]	POM 50-100 µm	July, 1994	-21.8 ± 1.5	2.5 ± 1.5
Central Baltic Proper/Gulf of Bothnia[d]	BPOM surface	1993-2003	-25.2 ± 1.1	3.5 ± 0.6

[a]This study; [b]Maksymowska et al., 2000; [c]Rolff and Elmgren, 2000; [d]Voss et al., 2005a; [e]Voss et al., 2000, [f]Voss et al., 2005b.

Whereas EPOM 100-200 μm has higher C and N concentrations (35 and 6 %, respectively) similar to those in phytoplankton (40-50 and 3.8-9 %, respectively; Jorgensen et al., 1995). The concentration of EPOM<70 μm increased and elemental concentrations decreased to ~11 % and ~1-2 % of C and N, respectively on the sampling occasions, when strong wind induced inorganic sediments resuspension (Fig. 6, Appendixes 1, 2). It is known, that inorganic sediments in the EPOM contain carbonaceous matter about 10% of total DW during the growth season (Jokšas et al., 2005). Carbonates have near zero $\delta^{13}C$, therefore must be removed by acidification (Cloern et al., 2002). In this study no carbonate removal from POM filter samples was chosen as a compromise between accuracies for $\delta^{13}C$ and $\delta^{15}N$ estimates, because neutralization of carbonates by acid wash decrease $\delta^{15}N$ values in the organic matter (Lorrain et al., 2003, Jacob et al., 2005). Indeed, $\delta^{13}C$ composition differed only slightly (0.7 ‰) and correlated well between EPOM<70 μm and 100-200 μm, therefore it could be assumed that $\delta^{13}C$ EPOM<70 μm mirrors well that of the whole EPOM.

The allochthonous detritus is not expected to contribute substantially to the EPOM (Table 1, Galkus and Jokšas, 1997). Although, most of the EPOM C/N values were above Redfield ratio (6.6; Fig. 10), high C/N ratios observed in concert with elevated $\delta^{13}C$ values cannot be interpreted as an unambiguous indicator of terrestrial detritus in EPOM. It could also indicate that in the time of sampling non-diazotrophic phytoplankton was N limited, because C/N ratio in freshwater phytoplankton is sensitive to nitrogen limitation, with C/N values of 8.3-14.6 usually corresponding to moderate nitrogen deficiency (Hecky et al., 1993). In cyanobacteria dominating summer phytoplankton community in the Curonian Lagoon, N-limitation promotes growth of the N_2-fixing species (Pilkaitytė and Razinkovas, 2007). In this study, C/N values > 9 coincided with the dominance of non-N_2-fixing *Microcystis* spp. in phytoplankton community, which is most likely more nitrogen limited than *Aphanizomenon* spp. or *Anabaena* spp. (Appendix 1).

The largest differences in $\delta^{15}N$ values between EPOM<70 μm and 100-200 μm were at VL and JO stations in October, due to *Aphanizomenon* spp. contribution to the phytoplankton (Table 7, Fig. 8., Appendix 1), and at JO station in May, due to contribution of copepodites and nauplii in EPOM 100-200 μm (Table 7, Appendix 1). These results imply, that $\delta^{15}N$ varies among EPOM fractions, therefore should not be interpreted without knowledge of phytoplankton community structure and careful observations of presence of zooplankton, if its physical removal is not feasible.

6.3. Seasonal and spatial dynamic of stable isotope composition in estuarine POM

RPOM and EPOM were well differentiated by their $\delta^{13}C$ and $\delta^{15}N$ in summer but not in spring and autumn (Fig. 10). The largest differences in $\delta^{13}C$ and $\delta^{15}N$ values between EPOM and RPOM coincided with the lowest river discharge (Fig. 2), maximal phytoplankton biomass in the lagoon, with high contribution of diazotrophic cyanobacteria (Fig. 7, 8). Mixing with MPOM also created spatial variability of EPOM isotopic composition in the sea water inflow area (Fig. 12). These relationships suggest coupling between hydrodinamic and biologic control mechanisms, when lentic conditions ensure dominance of in situ biological processes (Matson and Brinson, 1990). Seasonal and spatial changes of stable isotope ratios in POM of Curonian Lagoon could be described by following scheme: in spring, the whole river-lagoon system is isotopically homogeneous, due to river-induced water mixing and prevalence of riverine organic matter and inorganic nutrients (e.g. $\delta^{15}N$ enriched nitrates) in the lagoon; in summer- stable isotope composition in the EPOM is mainly determined by development and structure of the autochthonous phytoplankton; in autumn-central part of the lagoon is influenced by the river runoff, northern part- by brackish water mass, which result in pronounced riverine-estuarine gradient of SI composition in EPOM. Hydrodinamical and biological control mechanisms are coupled in estuarine environments: lentic conditions ensure dominance of in situ biological processes

(Matson and Brinson, 1990). Essentially these findings corroborate the hydraulic regime based zonation of the Curonian Lagoon, which demonstrates that in the summer transitional zones in the lagoon shrink, turning most of the lagoon in to stagnant water body (Ferrarin et al., 2008).

In May, at the end of spring spate, and in September-October, during the increased river runoff, RPOM and EPOM had a very close isotopic composition with depleted $\delta^{13}C$ and enriched $\delta^{15}N$; this was most pronounced in the permanently freshwater area (VL-VO; Fig. 10). This indicates increased proportion of RPOM to the EPOM in spring and towards autumn, while local phytoplankton production was decreasing. Another mechanism of homogenization of $\delta^{13}C$ in POM is the ^{13}C-depletion in dissolved inorganic carbon pool caused by the microbial respiration of the ^{13}C-depleted riverine organic matter, which also could have contributed to the decrease of autochthonous phytoplankton $\delta^{13}C$ (Bouillon et al., 2000), making the two sources of POM isotopicaly indistinguishable.

The difference in both $\delta^{13}C$ and $\delta^{15}N$ between EPOM and RPOM was considerable in June-August (Fig. 8). The rapid decrease in the EPOM $\delta^{15}N$ resulted in ~ 6 ‰ difference from RPOM $\delta^{15}N$ values, coinciding with the near 90% contribution of diazotrophic cyanobacteria *Anabaena* spp. and *Aphanizomenon* spp. to the phytoplankton community in the lagoon (Fig. 7, 8). Contribution of cyanobacteria in the lower reaches of the Nemunas River is usually lower than in the lagoon during the same period (Gasiūnaitė et al., 2008). In the Baltic Sea, ^{15}N depleted phytoplankton was also dominated by diazotrophic *Aphanizomenon* sp. (Rolff, 2000). When the cyanobacteria assemblage shifted to the dominance of non-N_2 fixing species, such as *Microcystis* spp. and *Planktothrix* sp., at the offshore stations (VO, JO) in the beginning of August and at the VL station in the end of August, the $\delta^{15}N$ values of EPOM rose to 7-8 ‰ again (Fig 8, 10, Appendix 1). The heterogeneous distribution of different cyanobacteria assemblages is also a source of $\delta^{15}N$ spatial variability in the lagoon, the ~5 ‰ difference in EPOM $\delta^{15}N$ was observed between samples collected within

3-5 days in the end of July and the beginning of August at VL, SL, JO and VO (Fig. 12). This suggests seston with different isotopic ratios can coexist and circulate with water masses in the lagoon, becoming available for the sessile consumers in different locations, which should be considered in the mixing models.

In summer, $\delta^{13}C$ was more enriched in EPOM than in RPOM. The $\delta^{13}C$ values in EPOM start to increase in June along with phytoplankton biomass rise (Fig. 7, 10). In the end of July – beginning of August, the maximal values of -22 ‰ and -24 ‰ were recorded at SL-VL and VO-JO stations, respectively (Fig. 10). The $\delta^{13}C$ signatures of freshwater phytoplankton vary widely depending on the source and concentration of dissolved CO_2 in the waters (Quay, 1986, Peterson and Fry, 1987, Fogel et al., 1992). In summer, intense photosynthesis exhausts the CO_2 pool in the water, which leads to 1) less discrimination of ^{13}C during the diffusive transport through the algal cell membrane and enzymatic CO_2 fixation, and (2) active bicarbonate (HCO_3^-) transport in to the algal cells, which altogether results in higher $\delta^{13}C$ signature in phytoplankton (Fogel et al., 1992, France, 1995). Situations of low CO_2 caused by high phytoplankton biomass and subsequent ^{13}C enrichment in POM were demonstrated in eutrophic and hypertrophic lakes, and in highly nutrient polluted estuaries (Quay, 1986, Gu and Schelske, 1996, Hellings et al., 2001). The uptake of bicarbonates by phytoplankton, while the CO_2 concentrations are limiting for photosynthesis, is a known process in the eutrophic Curonian Lagoon (Žaromskis, 1996). Enhanced primary production fuelled by the nutrient inputs to the lagoon causes less fractionation of the inorganic carbon that is reflected in the increased ^{13}C isotopes in the Curonian Lagoon sediments over the last 50 years (Voss et al., 2000, Table 20).

In spring (end of May), there was a 0 salinity at all stations (VL, VO and JO) at least for 3-4 weeks prior EPOM sampling and there were virtually no spatial variation in SI composition (Fig. 3, 10), apart from the higher $\delta^{13}C$ EPOM values at VO station, which was probably caused by the increased resuspension of the ^{13}C-enriched sediments (Fig. 6). In summer and autumn, higher salinities were frequently ob-

served in the lagoon, which could have effect on the SI composition in EPOM i.e. increase $\delta^{13}C$ and lower $\delta^{15}N$ (Fig. 11).

In the Baltic Sea (Central Baltic Proper, Gulf of Gdansk), the offshore MPOM has about $\delta^{13}C$ of -22 ‰ and δ^{15} of N 2 ‰ in the summer (Table 20, Maksymowska et al., 2000, Rolff and Elmgren, 2000). The EPOM stable isotope ratios at VL (salinity 0.88) and SL (salinity 1.5) on July 31 were very close to these values in offshore MPOM (Fig. 12). However, MPOM collected at the coastal station (BS, salinity 6.8) on July 10 has distinct signature, with more depleted $\delta^{13}C$ (Fig. 11), which indicates prevalence of terrestrial-freshwater organic matter. Northward coastal area from the lagoon outflow is under strong influence of freshwater, with mean salinity of 6.8 (Gasiūnaitė et al., 2005). Similarly, runoff from the Vistula River also affects the SI composition of the organic matter, particularly in coastal areas (Voss et al., 2005b). As indicated by enriched $\delta^{13}C$, offshore marine water masses have a potential to enter the Curonian Lagoon. Indeed, salinity of >7, which is more typical for the offshore Baltic Sea proper (Galkus, 2007), was recorded on July 11 at JO station in the lagoon, indicating marine water intrusion (Fig. 3). As marine water stayed in the lagoon for 3 weeks before the consumers sampling in August, MPOM was considered as a potential food source for primary consumers in the mixing model calculations (Fig. 16). In the coastal areas, stable isotope variability in surface POM subjected to riverine inputs is a particularly high, making determination of end-point values in mixing models and baselines in food web analysis difficult (Cloern et al., 2002, Sugimoto et al., 2006, Harmelin-Vivien et al., 2008).

6.4. Organic matter sources of primary consumers

Stable isotope ratios in primary consumers followed the same spatial and temporal patterns as in EPOM (Fig. 13, 16, 20), which identifies EPOM and allochthonous POM sources that mix in it, as a main diet source. In the summer, both guilds of suspension feeders that filter POM from the water column (zooplankton) and deposit feeders that filter or collect POM at sediment surface (chironomids, *Valvata* spp.)

had close $\delta^{13}C$ (Table 12). This indicates the common primary source of organic matter and suggests similar POM SI composition in water column and at the sediment surface, which is plausible, as long as lentic conditions dominate in the Curonian Lagoon. The overlap between the pelagic (zooplankton) and benthic (chironomids) primary consumers in late spring and summer, over the periods of high production, was also reported from Lake Geneva (Perga and Gerdeaux, 2005).

In the estuarine systems, stable isotope ratios in sedimentary organic matter usually also mirror those in water column POM, especially in weakly flushed estuaries (Matson and Brinson, 1990, Cifuentes et al., 1988, Andrews et al., 1998), but can differ slightly because of microbial processes, greater influence of refractory detritus in sedimentary material as compared to POM, as well as site specific sedimentation conditions (Fry and Sherr, 1984). In the eutrophic Curonian Lagoon, herbivorous zooplankton is unable to consume most of phytoplankton production that is exposed to microbial respiration or sinks to the bottom (Razinkovas and Gasiūnaitė, 1999). In midsummer, during the phytoplankton peak, water column production to decomposition ratio varies in the range of 2.7 – 5.4 in the central area of the Curonian Lagoon (corresponding to site VO), which leads to accumulation of organic matter (Krevs, 2007). Shallow depth and frequent resuspension back to the water column (Daunys et al., 2006) are also a reason why EPOM deposits are poorly decomposed (Galkus and Jokšas, 1997). Altogether these processes imply that both sources are interrelated and mixed to some extent, therefore the stable isotope ratios of carbon and nitrogen in EPOM and surface BPOM are not likely to differ strongly. The $\delta^{13}C$ and $\delta^{15}N$ values in surface BPOM, -24.8 and 6.5 ‰, respectively, are in the range of SI values in EPOM estimated during the summer 2006 (Voss et al., 2000, Table 20).

The physical sedimentation in the *D. polymorpha* distribution area (VO site) is accelerated by biodeposition. Appreciable amounts (higher than of physical sedimentation) of POM in the form of faeces and pseudofaeces enter the mussel bed and fuel benthic community, the richest in diversity and biomass in the lagoon (Daunys et al.,

2006). Biodeposits can differ from suspended organic matter by physical properties, organic matter and chlorophyll a content after mussel gut passage and due to selective feeding upon certain phytoplankton taxa (Baken et al., 1998, Orlova et al., 2004). To my knowledge, it is unknown, whether production of faces or pseudofaeces by *Dreissena* transform SI ratios in seston organic matter. Fecal pellets of other species, e.g. some marine copepods, are known to be depleted in both $\delta^{13}C$ and $\delta^{15}N$ relative to the diet (Tamelander et al., 2006), but mirror unchanged SI composition of the most recent diet of mysids, when fed unispecies food source with high organic content (Gorokhova and Hansson, 1999). Therefore this process might be related to food quality and metabolic rates in mussels, which needs to be studied experimentally. This study did not show constant differences of SI composition in benthic deposit feeders (e.g. Chironomidae) and suspension feeders (e.g. *Valvata*) between the sites dominated by *Dreissena* community (VO) and bare sediments (JO).

Benthic microalgae have more enriched $\delta^{13}C$ values than their planktonic counterparts and can contribute significantly to benthic primary production and fuel secondary production in the estuaries (France, 1995, Kibirige et al., 2002). However, they are not likely to contribute considerably to BPOM in the highly turbid Curonian Lagoon, where Secchi depth ranges from 0.3 to 2.2 m, with mean value in July being 0.7 m (Krevs, 2007, Gasiūnaitė et al., 2008).

Oligochaetes had different SI composition than other surface deposit feeders, uncoupled from EPOM variations (Fig. 10. 13). The samples dominated by Tubificidae and Lumbriculidae that ingest sediments below the surface at depth of 4-5 cm (Monakov, 1998, Ciutat et al., 2006). The sedimentary $\delta^{13}C$ in this feeding zone was reported earlier to be around -29 ‰ in the Curonian Lagoon (Voss et al., 2000), corresponding well to the average seasonal oligochaete $\delta^{13}C$ signature of -29 ± 1 ‰. This implies that sediments in the feeding zone of oligochaetes are not mixed by resuspension and probably contain significant fraction of terrestrial detritus, as its value of -29 ‰ is close to -28 ‰, reported from Sheldt and Vistula in winter (Hellings et al., 1999,

Maksymowska et al., 2000). Refractory terrestrial organic matter seams to be relatively important in the sedimentary pool despite its low contribution in the suspended POM, which is dominated by marine, riverine and estuarine autochthonous matter in the estuarine systems (Middelburg and Nieuwenhuize, 1998). As shown by this study, refractory organic matter is below sediment surface and can be available only for subsurface deposits feeders.

Mixing models with the mixtures of the EPOM/RPOM and EPOM/MPOM as end-points help revealing the role of allochthonous organic matter in the secondary production in the summer, when source SI signatures are clearly differentiated (Table 13). In the summer, consumers that reflect the most recent changes in POM, i.e. mysids, chironomids and mesozooplankton, have $\delta^{13}C$ values (-25 to -22 ‰), which are far from those in RPOM (-31 ± 1 ‰, spring-early summer) (Table 13, Fig. 10). Therefore, RPOM share in their summer diets estimated by the mixing models is fairly undetectable in neither of the study sites, located in a 10 km and 30 km distance from the river mouth (Table 13). Although, algal and bacterial cells, dominating the Nemunas River RPOM in the summer, have high nutritional value and were suggested to contribute significantly to secondary production (Stepanauskas et al., 2002). However the significant contribution of RPOM in the secondary consumers in the summer is probably restricted to near proximity of the river delta.

In contrast, MPOM which was mixed with EPOM and circulated over 3 wk in the investigated area prior to consumers sampling in July, has great potential to become incorporated into the consumer tissues (Table 13). Although, the relative contribution of MPOM to the annual POM balance in the lagoon is low (2 %, Galkus and Jokšas, 1997), it seems like contribution of MPOM in the secondary production could be important locally during continued sea water intrusions. This is well supported by the gradient in the carbon SI composition of the consumers that was more evident during the autumn: ^{13}C-depleted in the river inflow area and ^{13}C-enriched in the sea water inflow area (Fig. 20). Numerous studies demonstrate the same pattern of $\delta^{13}C$ spa-

tial variability in the estuarine consumers (Canuel et al., 1995, Deegan and Garritt, 1997, Kasai and Nakata, 2005). However, quantitative contribution of MPOM in the consumer diets needs more detailed investigations of variable marine end-point.

Macrophytes represent isotopically very distinct source of organic matter in the littoral (Fig. 16), however, there is little support from isotopic analysis for a substantial reliance of littoral consumer on macrophyte primary production in the summer. In the assimilated diet of amphipods and herbivorous mysids, average contributions of filamentous algae and *Potamogeton perfoliatus* varied 3-20 % and 1-9 %, respectively. These results contrast to previous findings suggesting successive grazing of alien amphipod species on macrophytes in other coastal regions of the Baltic Sea (Berezina et al., 2005, Orav-Kotta et al., 2009). Omnivorous/carnivorous feeding mode has been reported for investigated amphipod species (Berezina et al., 2005, Gumuliauskaitė and Arbačiauskas, 2008), however, the observed $\delta^{15}N$ values of gammarids were among the lowest, which translates to low trophic level (Table 14). More careful sampling of potential organic matter sources in the littoral is needed to evaluate diet composition of gammarids in detail.

The fate of littoral macrophyte detritus is poorly understood in the Curonian lagoon. Littoral macrophytes with enriched $\delta^{13}C$ values produce significantly ^{13}C-heavier particulate detritus than other POM sources (this study Table 8, Fig. 14., Bode et al., 2006, Cloern et al., 2002). In the offshore areas of the Curonian Lagoon, particularly in the summer, their relative contribution to the total pool of BPOM is probably negligible. But in the autumn macrophyte detritus contribute to BPOM in the littoral significantly and seems to be more readily available for mysids, and perhaps other benthic grazers (see more discussion Section 6.10).

6.5. Variability of stable isotope ratios at primary consumer level

The spatio-temporal variation of SI composition in EPOM is a main source of stable isotope fluctuations at the base of food web. Another source of stable isotope variability in primary consumers is a species specific response to the isotopic fluctuations in the EPOM, which depends on tissue turnover rates. It was most well pronounced in mesozooplankton, mysids and chironomids, whereas molluscs demonstrate moderate seasonal response to the stable isotope composition variation in EPOM (Fig. 13). The mixing models in this study demonstrate different ability of primary consumers to capture the most recent isotopic signal of EPOM (Table 13).

The tissue isotopic turnover in growing organism is a function of both tissue growth and metabolic replacement (Fry and Arnold, 1982). Therefore the time over which isotope ratios of different tissues or whole body indicate an animal's diet varies a lot in dependence on growth rates and species, animal age and temperature specific metabolic rates (Gorokhova and Hansson, 1999, Harvey et al., 2002, Dattagupta et al., 2004). It could be estimated precisely only by experimental approach, which is not feasible in multispecies research.

The more frequently known biomass turnover rate of the population, expressed as P/B yr^{-1} ratio, is variable among ecosystems but could be ranked among taxonomic groups of primary consumers (Wetzel, 2001). In bivalves, the P/B yr^{-1} is 0.36, whereas other benthic consumers have higher values of around 8.7 in the Curonian Lagoon (Krylova, 1985, Razinkovas and Zemlys, 2000). Although most annual P/B ratios of benthic consumers fall in the range of 1 to 10, extremely high (50- >100) values can occur in chironomids (Benke, 1998, Wetzel and Likens, 2000). The highest average annual P/B coefficients (~16) among aquatic metazoans are reported for herbivorous mesozooplankton (Wetzel, 2001). In the absence of empirical data for SI turnover, P/B coefficients could be used as a proxy for SI turnover rates.

Species ranking by biomass turnover rates corresponds well to the observed temporal SI variation: it is best pronounced in mesozooplankton, mysids and chironomids, whereas molluscs demonstrate moderate seasonal response to the stable isotope composition variation in EPOM (Fig. 13). The $\delta^{13}C$ and $\delta^{15}N$ values in chironomids, mysids and zooplankton changed from May to August by around 6 and 4 ‰, respectively (Fig. 13); these changes were of the same magnitude as those in EPOM (Fig. 10), reflecting rapid response of the consumers to alterations in the food. In the same time, $\delta^{15}N$ of large *D. polymorpha* (L = 2cm) did not change appreciably, whereas $\delta^{13}C$ increased by only 2 % (Fig. 13). The response of the isotopic signal in younger *D. polymorpha* (L = 1 cm) and *Valvata* spp. was weaker than that in zooplankton or mysids but relevant to the seasonal trend in EPOM.

The considerable SI shift in EPOM from spring to summer, provides a good opportunity to demonstrate how far different species are equilibrated to the new diet and to reveal approximate time lag, over which animal tissues integrate the stable isotope composition in the diet. According to the mixing model calculations, mussels collected in the mid summer, carried on spring or earlier EPOM isotopic signal from the previous growth season, in particular autumn (Table 13). Chironomids contained material assimilated over preceding 6 weeks (mixing model A, Table 13) or 3 weeks (mixing model B) but had also significant contribution of EPOM from the recent days before the sampling. The 3-weeks old EPOM stable isotope signal is hardly detectable in herbivorous juvenile mysids due to their rapid growth, estimated as 200 % over 3 weeks period (see more discussion in Section 6.9). Contrary to the predictions of most rapid biomass turnover and equilibration rate to ambient diet, zooplankton contained about a half of the assimilated material that was isotopically close to the EPOM sampled 3 weeks ago (Table 13). The $\delta^{13}C$ of bulk POM provides only a simplified view of organic matter diversity and complexity of trophic links in the pelagic food webs (Zohary et al., 1994). The more plausible explanation of discrepancy between ambient bulk EPOM and potential diet, predicted by mesozooplankton SI values, is the selective feeding of zooplankton crustaceans upon different phytoplankton taxa or reli-

ance on non-algal C sources (Grey et al., 2001, Matthews and Mazumder, 2003). For example, they could avoid the toxic *Microcystis* spp. that was dominating the EPOM samples in the beginning of August 2006 (Paldavičienė et al., submitted manuscript). Another explanation could be that older life stages of crustaceans, that have low or no (like copepods) somatic growth channeled all newly assimilated material into offsprings. In this case, they could have reflected food that was assimilated when they were juveniles, which is ~1-3 weeks back.

6.6. Estimating trophic levels of predators

Consumers $\delta^{15}N$ values reflected adequately to their position in the food chain in the summer: lowest values in suspension and deposit feeders, highest in predatory fish (Table 14). Several approaches for trophiv level (TL) calculation based on different $\delta^{15}N$ baselines, demonstrated that the values of TL, calculated on most depleted and most ^{15}N-enriched baseline consumer, can differ in more than one TL within the same system (Fig. 19). This study suggests that baseline consumers should primarily integrate the SI composition during the most intense fish growth period spring-summer. During that period $\delta^{15}N$ composition can differ significantly in basal source of organic matter from the rest of year (Fig. 10). Baseline consumers having moderate isotopic tissue turnover rates, such as *Valvata* are more appropriate than species with slow isotopic turnover rate, e.g. *Dreissena* or Unionidae, in comparative studies of food chains between eutrophic ecosystems that have pronounced seasonal isotopic variability at the base of food web.

Bivalves are among the most frequently used organisms for baseline calculations in marine and freshwater food web studies, particularly estimating the trophic position of fish (Vander Zanden et al., 1997, Post, 2002, Fukumori et al., 2008). Mussels are relatively long living, essentially non-selective suspension feeders that can integrate the suspended POM fluctuations over several months or years (Cabana and Rasmussen, 1996, Dattagupta et al., 2004). On the other hand, slow

growth and metabolic tissue replacement of mussels also result in slow rates of $\delta^{15}N$ turnover, which in turn obscures the estimation of trophic relationships (Tieszen et al., 1983, Gustafson et al., 2007). Large specimens of *D. polymorpha* in this study, showed low seasonal variation in $\delta^{15}N$ signatures (10.3 ± 0.3 ‰; Fig. 13), however the TL calculated using $\delta^{15}N_{Bivalvia}$ were too low for the most of the secondary consumers. The TL of perch and pikeperch did not reached TL=4 (Fig. 19), although European perch (larger than 20 cm) and pikeperch are entirely piscivorous in the coastal Baltic Sea regions, including the Curonian Lagoon (HELCOM, 2006). The estimated TL<3 for benthivorous bream and ruff is also unrealistically low. These findings suggest that the $\delta^{15}N_{Bivalvia}$ does not represent the actual signature of the food source that fish community is based on. Mussels do not equilibrate to ^{15}N-depleted summer primary production of diazotrophic cyanobacteria, that sustain largely new biomass of other benthic and planktonic primary consumers in the summer (Table 13). Fish produce most of their muscle tissues in the spring-summer period, whereas in the autumn and winter the assimilated food is allocated to gonad growth or is used to sustain basal metabolic requirements, therefore is reflected only in the liver (Perga and Gerdeaux, 2005). Therefore, low $\delta^{15}N$ signal of cyanobacteria is likely to be transferred to fish, even it persists in the system for only 2 months, as it was in 2006.

The most plausible results were obtained using *Valvata* spp. as baseline. TL estimates based on *Valvata* spp. baseline resulted in TL closest to that reported from ECOPATH model of the Curonian Lagoon food web: 3.2 vs. 3.4 TL, respectively, for benthivorous fish and 4.1 vs. 4.2 for predators (Ertürk, 2008). The TL values calculated using $\delta^{15}N_{Chironomidae}$ are certainly overestimated, all demersal fish have the TL >3.5, predatory fish >4.5 TL. Chironomids have fastest tissue turnover rate therefore could represent the SI signal of primary consumers, derived from ^{15}N- depleted cyanobacteria in summer. However, better match of TL estimated on moderately ^{15}N-depleted *Valvata* spp. baseline, indicates that fish obtain their basal isotopic signal from both: depleted in ^{15}N sources which are typical in the summer

and more enriched in ^{15}N sources, characteristic for the rest of the season.

It was shown previously, that $\delta^{13}C$ and $\delta^{15}N$ of fish muscle tissue for whole year retained the signal the food consumed during the spring and summer period (Perga and Gerdeaux, 2005). As revealed by the two-end-member mixing model, in the summer 40-50 % of the assimilated carbon in fish muscle is derived from ^{13}C- enriched consumers (chironomids, mysids, gastropods, amphipods and zooplankton), essentially representing the summer secondary production (Fig. 18). Whereas another 50-60 % of the assimilated diet comes from either mussels or oligochetes, which have lower $\delta^{13}C$; and/or tissues still reflect the old spring diet. The highest proportion of ^{13}C-depleted source in leeches and roach at VO site, could confirm their close relationship to *D. polymorha* as a food source, as it is known that leeches of the genus Glossiphonia feed exclusively on mollusks (Monakov, 1998), whereas roach is the main consumer of zebra mussel in the lagoon (Virbickas, 2000). Two individuals of pikeperch with completely different contribution of ^{13}C-depleted and ^{13}C-enriched sources in the diet (Fig. 18), probably are representatives of two different subpopulations: one of them migrates to the sea and forage on ^{13}C-enriched food during the summer, while another stays in the lagoon and uses local ^{13}C-depleted food sources (Ložys, 2003).

The TL calculated using combined $\delta^{15}N_{A+spring}$ and $\delta^{15}N_{BC}$ baselines, weighted to relative contribution of corresponding food source in the diet, were close to that estimated using $\delta^{15}N_{Valvata}$ baseline (Fig. 19), and did not differed notably from that calculated by ECOPATH: 3.1 vs. 3.4 for benthivorous fish and 4.1 vs. 4.2 for predators using $\delta^{15}N_{combined}$ baseline and estimated in ECOPATH, respectively. The TL of planktivorous pelagic *P. cultratus* in the food chain was 3.5, estimated using $\delta^{15}N_{combined}$ baseline, whereas ECOPATH gaves 3.3. The 3.5 TL means that roughly half of the diet is derived from TL 2 (i.e. zooplankton), while another half from higher TL (i.e., omnivorous and/or carnivorous zooplankton, fish eggs, etc.). According to some sources, *P. cultratus* is a strong selective feeder upon large sized

zooplankton such as *Diaphanosoma* and *Leptodora* (Liu and Herzig, 1996) or even fish larvae (Virbickas, 2000).

6.7. Spatial distribution of *P. lacustris* population and horizontal migrations

Mysid abundance and biomass was low in midsummer. Even the maximal estimate of 0.5 g DW m^{-2} (Fig. 22) could hardly equal the biomass of other benthic species, such as, for instance, 1.1 and 0.7 mg DW m^{-2} of Chironomidae and Oligochaeta, respectively (Olenin, 1996). The population of *P. lacustris* reaches its highest abundance during the autumn and becomes the key species in the littoral food web. From the first half of October, *Paramysis lacustris* exhibited pronounced horizontal migrations from deeper areas to the littoral (Fig. 24). During this time, there was no significant reproduction, which implies that immigration from the offshore areas was the only source of the mysid abundance increase in the littoral.

Various external forces could be responsible for this habitat shift. In summer, submersed vegetation provides a refuge for small predatory fishes, e.g., juvenile perch. However, through breakdown of the macrophytes in early autumn, their relative abundance in the littoral decreases from 30% in August–September to 0% in October (Žiliukas, 2003), making the littoral a predator-free area for the mysids. This is particularly beneficial for the mysids, because during the same time pikeperch and perch migrate from the Baltic Sea to the inner part of the lagoon to overwinter (Ložys, 2003). These fish at the age of 1 to 3 yr feed particularly extensively on mysids (Ložys, 2003) and thus impose increased predation pressure on *P. lacustris* in the offshore areas, which may cause their inshore migration. Similarly, dense aggregations of *Neomysis integer* in the littoral zone have been suggested to be an antipredatory behavioral strategy (Lindén, 2007). Other studies suggested selection of low-flow environments as a main force of *N. integer* migratory behavior, although an upshore food gradient were also highlighted as a potential factor for mysid migrations, which are site- and species-specific (Speirs et al., 2002). Indeed, changes in food

availability could be another possible factor triggering migrations of *P. lacustris*. Webb and Wooldridge (1990) described a very similar pattern of diel horizontal migrations in *Mesopodopsis slabberi*: inshore - towards more abundant phytoplankton at night, and offshore - to the deep waters free from predators. Albertsson (2004) also indicated importance of near-bottom zooplankton as an alternative food source for mysids during periods with low pelagic food availability. In the Curonian Lagoon, zooplankton biomass is highest in the midsummer and is mainly composed by cladocerans (Gasiūnaitė et al., 2008), which are an important food source for *P. lacustris* (Lesutienė et al., 2007). From July to October, total zooplankton biomass decreases more than 7-fold, shifting dominance to copepods (Gasiūnaitė et al., 2008), which have better escape abilities than cladocerans (Lampert and Sommer, 1997). Therefore, in the autumn, *P. lacustris* is likely to become food limited and search for alternative food sources. Ample supply of decaying organic matter in the littoral together with induced development of microplankton may attract mysids and cause their inshore migrations. Chemical cues from primary producers have been implicated in regulating migrations in other zooplankton species (Van Donk, 2007).

6.8. Zooplanktivory and trophic position of *P. lacustris* in summer pelagic food chain

The zooplankton based food chain is distinguishable on the $\delta^{15}N$ to $\delta^{13}C$ biplot (Fig. 14). The SI signatures of *Leptodora*, juvenile perch and adult *Paramysis lacustris* are associated along the trophic pathway originating from the most recent EPOM. However, *P. lacustris* is less enriched in ^{15}N relative to zooplankton, than *Leptodora* and perch, which implies its intermediate position between the herbivores and true carnivores in the plankton food chain.

In this study, we focused on three factors that can potentially influence the $\delta^{15}N$ variation of *P. lacustris* in the Curonian Lagoon: (*i*) ontogenetic changes related to possible differences in the diet preferences, (*ii*) proportion of mesozooplankton in the mysid diet, and (*iii*) enrich-

ment of consumers with ^{15}N depleted atmospheric nitrogen, which is assimilated by cyanobacteria and becomes available to other producers and consumers in the ecosystem. Moreover, to assess mesozooplankton contribution to the diet of *P. lacustris*, we compared isotopic signatures of mysid stomachs with that of ambient mesozooplankton – a technique that to the best of our knowledge has not been attempted in prior studies.

The dynamics of nitrogen isotopic composition of mysid bolus and body tissues strongly indicates zooplanktivory as very important feeding mode of adult *P. lacustris* in summer. The previous analysis underestimated the importance of mesozooplankton in the adult mysid feeding most probably because mysids for gut content analysis were collected in the littoral, where zooplankton availability is 10-fold lower than in the offshore habitats (Jankauskienė, 2003, Lesutienė et al., 2005). Moreover, the significant enrichment of mysid $\delta^{15}N$ values with the increasing size (Fig. 27, Table 15) suggests that during the ontogenetic development, mysid diet changes to include a larger proportion of mesozooplankton and mysids need to attain a threshold size of 8.7±0.7 mm (mean BL of small adult mysid) to actively feed on mesozooplankton. In July-September, the difference between the juveniles and largest mysids was 2.2‰ (Fig. 27). Assuming a trophic shift between mysids and their diet being in the range of 2.4‰ to 3.6‰ (Hansson et al., 1997; Gorokhova and Hansson, 1999), the trophic distance between the diet of the smallest and largest individuals of *P. lacustris* is nearly as high as one trophic level. This suggests that mysid diet is composed largely by phytoplankton in juveniles and by mesozooplankton in adults, whereas immature or subadult individuals have mixed diets (Froneman, 2001; this study). The similar ontogenetic changes of $\delta^{15}N$ were documented for two other Baltic mysids, *Neomysis integer* and *Mysis mixta* (Gorokhova and Hansson, 1999), as well as for *M. relicta* in the North-American Great Lakes (Branstrator et al., 2000). In the North American lakes, *M. relicta* was found to become more carnivorous in conjunction with maturation (>10 mm), however, the time of the shift varied from one lake to another, which was suggested to be related to the size spectra of phytoplankton (and

perhaps mesozooplankton) in these lakes (Branstrator et al. 2000). The lower threshold size for zooplanktivory observed in the Baltic *P. lacustris* could be explained by the high mesozooplankton prey availability in the eutrophic Curonian Lagoon and high relative abundance of microzooplankton with rotifers, nauplii and small cladocerans. As the $\delta^{15}N$ values did not differ significantly between juveniles and subadults, the immature *P. lacustris* (BL < 8.7±0.7 mm) may be considered as a homogeneous, largely herbivorous group in feeding studies.

Our approach to investigate mysid stomachs separately from the body provides a new tool to assess immediate diet isotopic composition and to compare it with that of potential prey. Indeed, analysis of dissected stomachs of *P. lacustris* revealed a good correspondence of their isotopic composition to the ambient mesozooplankton (Fig. 26). This indicates a very high contribution of mesozooplankton to the diet of adult mysids and lower contribution of other sources. Moreover, the correspondence was not distorted by variations in the stomach fullness degree (50 vs. 100%; Fig. 26). However, a more precise estimation of stomach tissue proportion as a function of the stomach fullness and an assessment of the stomach fullness in concert with stable isotope analysis are likely to improve the accuracy of the method, particularly, when multiple food sources are considered.

Interestingly, the bolus $\delta^{15}N$ values differed more from those of mesozooplankton in autumn than during summer (Fig. 26). This was likely related to seasonal changes in prey availability, which is considered to be as important factor for mysid feeding as their body size (Viherluoto et al., 2000). The opportunistic feeding causes the typical positive correlation between the proportion of the prey in mysid stomachs and its densities in the environment (Fockedey and Mees, 1999). In our study, the mesozooplankton abundance and biomass were highest in the end of July and lowest in October, the difference being 70- and 580- fold, respectively (Fig. 25). Moreover, the structure of the summer mesozooplankton community shifted from the dominance of small cladocerans in July to more abundant copepods and appearance

of *D. brachyurum* in August. Although *Daphnia* spp. did not dominated the community by number, it contributed greatly to the total mesozooplankton biomass and hence influenced the $\delta^{15}N$ values of bulk mesozooplankton (Fig. 25). The similarity of bolus $\delta^{15}N$ values with that of mesozooplankton suggests *Daphnia* spp. being the preferred mysid prey in summer. However, in autumn, when mesozooplankton becomes less abundant, mysids might shift to other food sources (e.g., benthic invertebrates), resulting in the greater discrepancy between bolus isotopic composition and that of mesozooplankton.

The seasonal development of cyanobacteria community might also have influenced the $\delta^{15}N$ values of both the mysids and mesozooplankton. The significant drop of $\delta^{15}N$ in September, pronounced in all size groups of mysids, could be attributed to the second, probably more intense, cyanobacteria bloom in the end of August-first half of September (Fig. 27). As mysid tissues reflect stable isotope composition of theIr diet with some time lag (Fig. 31), the body $\delta^{15}N$ observed in September-October are likely to reflect mysid diet in the time of the bloom. In September-October, ^{15}N depleted nitrogen was sedimented or washed out from the ecosystem thus explaining the observed levels of $\delta^{15}N$ in bolus, mesozooplankton and newly hatched juveniles in the end of September and October (Fig. 25, 26, and 27).

Summarizing our results, a trophic structure of the summer pelagic food web could be outlined as follows. Since *L. kindtii* is a true zooplanktivore mainly feeding on cladocerans (Mordukhai-Boltovskoi and Rivier, 1987), it can serve as a reference for characterizing the diet of mysids in the Curonian Lagoon. Its tissues ought to theoretically reflect the signature of a primary carnivore in the system. In our study, immature mysids ($BL<8.7\pm0.7$ mm) were generally not different from mesozooplankton, which implies that mysids within this size range are likely to be largely herbivorous. On the other hand, adults ($BL\geq8.7\pm0.7$ mm) were less enriched than the primary carnivore *L. kindtii* (Fig. 14, 28), indicating that, in addition to mesozooplankton, large mysids feed on other food sources, e.g., sediment, benthic inver-

tebrates, such as chironomids with low δ^{15}N (Fig. 15). Moreover, the contribution of these sources appears to increase towards the autumn. These estimates of the trophic position are supported by the similarity between mysid bolus δ^{15}N and that of mesozooplankton in summer and increased difference between the bolus and mesozooplankton δ^{15}N in the end of the season.

The ontogenetic and seasonal changes in *P. lacustris* feeding must be taken into account when predicting their trophic linkages in the food web. The question remains unanswered, whether *P. lacustris* is capable to make a significant effect on the zooplankton community in the Curonian lagoon in summer, as population is largely contributed by small herbivorous and omnivorous individuals (Fig. 23). However, at higher depths *P. lacustris* population contains more large specimens (this study, Fig. 23, Razinkovas, 1996). Therefore the strongest influence of mysids on mesozooplankton community is expected in summer, when the mesozooplankton is most available and at >2m depths, where carnivorous mysids (>8.7mm) prevail.

6.9. Mysid growth rate and tissue turnover – implications for stable isotope analysis

During August-September, three cohorts were produced within an approximately one month interval (Fig. 29, Table 15). The sampling frequency (i.e., 3 weeks) allowed us to use mysids of the same age (subadults) from each cohort for SIA (Fig. 29), thus eliminating possible ontogenetic differences in isotopic signatures. According to the growth curve (Fig. 30), it takes at least 20 d for a juvenile mysid to grow from 2-3 mm (i.e., when they leave the marsupium and start feeding; Komarova, 1991) to 6 mm (i.e., subadults). Therefore, isotopic signatures of mysids are representative of their feeding environment during this period. In line with this interpretation, the mysid δ^{15}N and δ^{13}C values strongly correlated with those of their potential food sources averaged over the preceding 3 weeks (Fig. 31). By contrast, Toda and Wada (1990) found an immediate response of δ^{15}N in mysid *Neomysis intermedia* to that of its food sources. This species, how-

ever, grows more rapidly than *P. lacustris*, with a generation time of about one month in *N. intermedia*, while *P. lacustris* in the Curonian Lagoon spans 50 d (Razinkovas, pers. communication). In the slow growing *Mysis mixta*, it takes 6-8 weeks and more than 3 months for $\delta^{15}N$ and $\delta^{13}C$, respectively, to come to equilibrium with a new diet (Gorokhova and Hansson, 1999). The rapid growth of juvenile *P. lacustris* with a biomass increase of about 200% between the sampling dates (Fig 30), indicates a high tissue turnover rate. This result implies that more frequent sampling of the food sources would be necessary to evaluate the diet of juveniles more precisely. The use of three-week averaging when comparing adult mysids to their food sources is more reasonable, as they perform slower, asymptotic growth and increase in weight by 50% during that period (Fig. 30). Complete turnover of N was assumed for *M. relicta*, whose growth resulted in a 33% increase in new tissues during 3 months, whereas C had zero turnover (Johannsson et al., 2001). Our results do not indicate that changes in diet are more rapidly reflected in $\delta^{15}N$ than in $\delta^{13}C$, probably due to our relatively low sampling frequency for fast growing *P. lacustris.*

6.10. Autumn diet composition of *P. lacustris* in the littoral

The littoral BPOM was largely composed of macrophyte detritus (Table 19), particularly on August 30 during the breakdown of the submersed vegetation. On average, BPOM contributed 42 to 68% to the diet of *P. lacustris,* which implies great capacity of this omnivore to consume vascular plant detritus (Fig. 32). Similarly, macrophytal detritus of a seagrass was a main food source for *N. americana* from the North American estuaries during the winter months, when phytoplankton production is low (Zagursky and Feller, 1985). Estuarine amorphous detritus, containing 3-5% of plant material, was very abundant in the stomachs of *N. integer* in European estuaries (Fockedey and Mees, 1999). Consumption and remineralization of detritus as an important trophic role of mysids was also reported from coral reef lagoons (Carleton and McKinnon, 2007). However caution should be taken while quantifying the trophic link macrophytes-detritus-mysids,

because it is important to know what fraction of detritus vs. associated microbes is actually assimilated (Moore et al., 2004).

As macrophyte detritus is usually low in organic N content (Webster and Benfield, 1986), mysids are not likely to meet their nutritional requirements by feeding only on this material, even if the ingestion rates are very high (Zagursky and Feller, 1985). According to the mixing models, mesozooplankton-derived nitrogen accounts for about 20% of mysid assimilated nitrogen, although by biomass zooplankton contributed < 13% to mysid diet. Contrary to our previous observations (Fig. 28), there was no indication of ontogenetic diet shift to greater carnivory in larger mysids. However, the earlier observed ontogenetic diet shift occurred in summer, when mysids were exposed to a several hundred times higher mesozooplankton biomass dominated by large slow-moving cladocerans (Fig. 25). In autumn (this study), biomass of the littoral mesozooplankton is low and composed mainly of small-bodied planktonic and benthic copepods, mostly by cyclopoids (Table 17) with fast escape responses (Lampert and Sommer, 1997). During this time, the zooplankton contribution to mysid diet was very low (< 1%), increasing to 9% in October-November (Fig. 32); this increase is most likely related to the increase of slower prey (i.e., cladocerans and harpacticoids) contribution to the mesozooplankton biomass. Benthic harpacticoids of the genus *Bryocamptus*, which dominated the littoral mesozooplankton, are euryphagous particle collectors from underwater surfaces (Monakov, 1998). It is very likely, that their increase was related to the increased concentration of particulate detritus in the littoral after the breakdown of the submersed macrophytes. Together, decaying plant material and thriving detritivores can build an upshore food gradient and influence mysid aggregations, similar to the proposed migration mechanism of *N. integer* (Speirs et al., 2002) and *M. slabberi* (Webb and Wooldridge, 1990).

It is likely that both predator avoidance and changes in food supply drive autumn swarming of *P. lacustris* in the littoral of the Curonian Lagoon. The use of littoral particulate organic matter, detritus from the decaying macrophytes, and meiobenthos as food sources by

mysids improves their nutritional conditions during this period. It also has at least two important ecological implications. First, it increases organic matter transfer efficiency in the macrophyte detritus food chain during the period when other important littoral consumers, such as amphipods, are scarce (pers. observations). Second, mysid horizontal migrations increase inshore-offshore habitat coupling: when these shallow waters are about to freeze, mysids move back to the deeper areas of the lagoon and become available for the fish that migrate there to overwinter (Ložys, 2003). Thus, mysids would contribute to the fish survival during the winter, when other zooplankton food is scarce. Calculated *P. lacustris* somatic production during the study period was 36 g DW m^{-2}. Assuming a 40% capture efficiency of the epibenthic sledge (Lesutiene, unpublished) and a 10% gross growth efficiency for an omnivorous shrimp (Morgan, 1980), cumulative consumption could be as high as 900 g DW m^{-2}. This is a substantial quantity of the organic material, mainly originating from the submersed vegetation, that is remineralized by mysids and becomes available to the higher trophic levels in the offshore habitats.

7. CONCLUSIONS

1. The largest differences of $\delta^{13}C$ and $\delta^{15}N$ between Nemunas River and lagoon POM coincide with the lowest river discharge, maximal phytoplankton biomass in the lagoon, and high contribution of diazotrophic cyanobacteria. The stable isotope signatures of MPOM varies in the same range as in EPOM, which hampers analysis of marine end-point impact in the sea water inflow area and consumers diets.

2. Spatial and temporal variation of SI composition in primary consumers has the same pattern as in EPOM, which identifies EPOM as a main diet source. During the stagnant phase of the lagoon, $\delta^{13}C$ composition is similar in the plankton suspension feeders and benthic deposit and suspension feeders, therefore grazing versus detrital pathways are indistinguishable on the basis of SIA. Macrophytes are not important in the diet of littoral primary consumers in summer.

3. As revealed by low $\delta^{13}C$ (mean: -32.9 ± 2.3 ‰) and low C/N ratio of 7.1, close to the Redfield ratio 6.6, phytoplankton prevails over the terrestrial detritus in Nemunas POM during investigated May-October period. Riverine POM share in the diet of primary consumers is fairly undetectable in the summer. In spring and autumn the contribution of RPOM in the diet of primary consumers could not be estimated using SIA because of similarity between the end-points.

4. Response to the isotopic fluctuations in the ambient POM was most well pronounced in mesozooplankton, mysids and chironomids, whereas molluscs (*Dreissena*, *Unio*) demonstrate moderate or small response. Several approaches for trophic level calculation demonstrated, that the values, calculated on most depleted and most ^{15}N-enriched baseline consumer, differ in more than one trophic level within the same system. The most realistic results were obtained using *Valvata* spp. as baseline, or combined baseline from primary consumers hav-

ing long term isotopic memory and consumers that reflect the recent changes of nitrogen isotopes in primary organic matter source.

5. Significant enrichment of mysid $\delta^{15}N$ values with the increasing size suggests that during the ontogenetic development, mysid diet changes from herbivory of juveniles towards increasing carnivory of adults. The dynamics of nitrogen isotopic composition of adult mysid (BL≥8.7±0.7 mm) bolus indicates zooplankton as important food source in summer.

6. The use of littoral particulate organic matter, detritus from the decaying macrophytes, and meiobenthos as food sources during autumn swarming of *P. lacustris* in the littoral, increases organic matter transfer efficiency in the macrophyte detritus food chain and inshore-offshore habitat coupling in the Curonian Lagoon.

8. REFERENCES

1. Abrantes K., Sheaves M., 2008. Incorporation of terrestrial wetland material into aquatic food webs in a tropical estuarine wetland. Estuarine, Coastal and Schelf Science 80: 401-412.
2. Abreu P.C., Costa C.S.B., Bemvenuti C., Odebrecht C., Graneli W., Anesio A. M., 2006. Eutrophication Processes and Trophic Interactions in a Shallow Estuary: Preliminary Results Based on Stable Isotope Analysis ($\delta^{13}C$ and $\delta^{15}N$). Estuaries and Coasts 29(2): 277-285.
3. Adams T.S., Sterner R.W., 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnology and Oceanography 45(3): 601-607.
4. Albertsson J., 2004. Trophic interactions involving mysid shrimps (Mysidacea) in the near-bottom habitat in the Baltic Sea. Aquatic Ecology 38: 457-469.
5. Andrews J.E., Greenaway A.M., Dennis P.F., 1998. Combined Carbon Isotope and C/N Ratios as Indicators of Source and Fate of Organic Matter in a Poorly Flushed, Tropical Estuary: Hunts Bay, Kingston Harbour, Jamaica. Estuarine, Coastal and Schelf Science 46: 743-756.
6. Arbačiauskas, K., 2002. Ponto-Caspian amphipods and mysids in the inland waters of Lithuania: history of introduction, current distribution and relations with native malacostracans. In: E. Leppakoski, S. Gollasch and S. Olenin (Editors), Invasive Aquatic Species of Europe – Distribution, Impacts and Management. Kluwer Academic Publishers, pp. 104-115.
7. Arbačiauskas K., 2008. Amphipods of the Nemunas river and the Curonian lagoon, the Baltic Sea basin: where and which native freshwater amphipods persist? Acta Zoologica Lituanica 18(1): 10-16.
8. Baker, S.M., Levinton, J.S., Kurdziel, J.P., and Shumway, S.E., 1998. Selective feeding and biodeposition by zebra mussels and their relation to changes in phytoplankton composition and seston load. Journal of Shellfish Research 17(4): 1207-13.
9. Beaudoin C.P., Prepas E.E., Tonn W.M., Wassenaar L.I., Kotak B.G., 2001. A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. Freshwater Biology 46: 465-477.
10. Benke A. C., 1998. Production dynamics of riverine chironomids: extremely high biomass turnover rates of primary consumers. Ecology 79(3): 899-910.
11. Berezina N., Golubkov S., Gubelit J., 2005. Grazing effects of alien amphipods on macroalgae in thelittoral zone of the Neva estuary (eastern Gulf of Finland, Baltic sea). Oceanological and Hydrobiological Studies 34(1): 63-82.
12. Bode A., Alvarez-Ossorio M.T., Varela M., 2006. Phytoplankton and macrophyte contributions to littoral food webs in the Galician upwelling estimated from stable isotopes. Marine Ecology Progress Series 318: 89-102.

13. Bosley K.L., Witting D.A., Chambers R.C., Wainright S.C., 2002. Estimating turnover rates of carbon and nitrogen in recently metamorphosed winter flounder Pseudopleuronectes americanus with stable isotopes. Marine Ecology Progress Series 236: 233-240.
14. Bouillon S., Chandra Mohan P., Sreenivas N., Dehairs F., 2000. Sources of suspended organic matter and selective feeding by zooplankton in an estuarine mangrove ecosystem as traced by stable isotopes. Marine Ecology Progress Series 208: 79-92.
15. Breber P., Povilanskas R., Armaitienė A., 2008. Recent evolution of fishery and land reclamation in Curonian and Lesina lagoons. Hydrobiologia 611:105-114.
16. de Brabandere L., Dehairs F., Van Damme S., Brion N., Meire P., DaroN., 2002. $\delta^{15}N$ and $\delta^{13}C$ dynamics of suspended organic matterin freshwater and brackish waters of the Scheldt estuary. Journal of Sea Research 48: 1-15.
17. Branstrator D.K., Cabana G., Mazumder A., Rasmussen J.B., 2000. Measuring life-history omnivory in the opossum shrimp, *Mysis relicta*, with stable nitrogen isotopes. Limnology and Oceanography 45, 463-467.
18. Bubinas A., Ložys L., 2000. The nutrition of fish in the Curonian Lagoon and the coastal zone of the Baltic Sea. Acta Zoologica Lituanica 10 (4): 56-67.
19. Bubinas A., Vaitonis G., 2003. The analysis of the structure, productivity, and distribution of zoobenthocenoses in the Lithuanian economic zone of the Baltic Sea and the importance of some benthos species to fish diet. Acta Zoologica Lituanica 13(2): 114-124.
20. Bucci J. P., Showers W. J., Rebach S., DeMaster D., Genna B., 2007. Stable isotope analyses ($\delta^{15}N$ and $\delta^{13}C$) of the trophic relationships of *Callinectes sapidus* in two North Carolina estuaries. Estuaries and Coasts 30: 1049-1059.
21. Cabana G., Rasmussen J.B., 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372: 255-257.
22. Cabana G., Rasmussen J.B., 1996. Comparison of aquatic food chains using nitrogen isotopes. Ecology 93: 10844-10847.
23. Canuel E.A., Cloern J.E., Ringelberg D.B., Guckert J.B., Rau G.H., 1995. Molecular and isotopic tracers used to examine sources of organic matter and its incorporation into the food webs of San Francisco Bay. Limnology, Oceanography 40(1): 67-81.
24. Carleton J.H., McKinnon A.D., 2007. Resident mysids: secondary production, consumption, and trophic role in a coral reef lagoon. Marine Ecology Progress Series 336, 89-98.
25. Carlier A., Riera P., Amouroux J-M., Bodiou J-Y., Escoubeyrou K., Desmalades M., Caparros J., Gremare A., 2007. A seasonal survey of the

food web in the Lapalme Lagoon (northwestern Mediterranean) assessed by carbon and nitrogen stable isotope analysis. Estuarine, Coastal and Shelf Science 73: 299-315.
26. Carol Kendall and Eric A. Caldwell Fundamentals of Isotope Geochemistry. In: Isotope Tracers in Catchment Hydrology (1998), C. Kendall and J. J. McDonnell (Eds.) Elsevier Science B.V., Amsterdam. pp. 51-86.
27. Christian R.R., Baird D., Luczkovich J., Johnson J.F., Scharler U.M., Ulanowicz R.E., 2005. Role of network analysis in comparative ecosystem ecology of estuaries. In. Belgrano A., Scharler U.M., Dunne J., Ulanowicz R.E. (Eds.) Aquatic Food Webs an Ecosystem Approach. Oxford University Press: 25-40.
28. Cifuentes L. A., Sharp J. H., Fogel M. L., 1988. Stable carbon and nitrogen isotope biogeochemistry in the Delaware estuary. Limnology and Oceanography 33(5): 1102-1115.
29. Ciutat A., Weber O., Gerino M., Boudou A., 2006. Stratigraphic effects of tubificids in freshwater sediments: a kinetic study based on X-ray images and grain-size analysis. Acta Oecologica 30: 228-237.
30. Cloern J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Marine Ecology Progress Series 210: 223-253.
31. Cloern J.E., Canuel E.A., Harris D., 2002. Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnology and Oceanography 47, 713-729.
32. Costanzo S.D., Udy J., Longstaff B., Jones A., 2005. Using nitrogen stable isotope ratios ($\delta^{15}N$) of macroalgae to determine the effectiveness of sewage upgrades: changes in the extent of sewage plumes over four years in Moreton Bay, Australia. Marine Pollution Bulletin 51: 212-217.
33. Costanzo S. D., O'Donohue M. J., Dennison W. C., Loneragan N. R., Thomas M., 2001. A New Approach for Detecting and Mapping Sewage Impacts. Marine Pollution Bulletin 42(2): 149-156.
34. Dailidienė I., 2007. Kuršių marių hidrologinio režimo pokyčiai. Geografija T. 43. Nr. 1. P. 36-43.
35. Darnaude A.M., 2005. Fish ecology and terrestrial carbon use in coastal areas: implications for marine fish production. Journal of Animal Ecology 74: 864-876.
36. Daunys D. and Zettler M.L., 2006. Invasion of the North American amphipod (*Gammarus tigrinus* Sexton, 1939) into the Curonian lagoon, South-Eastern Baltic Sea. Acta Zoologica Lituanica 16: 20-26.
37. Dattagupta S., Berquist D.C., Szalai E.B., Macko S.A., Fisher C.R., 2004. Tissue carbon, nitrogen, and sulphur stable isotope turnover in transplanted *Bathymodiolus childressi* mussels: relation to growth and physiological condition. Limnology and Oceanography 49: 1144-1151.
38. Daunys D., Oleninas S., 1999. Bottom macrofauna communities in the littoral zone of the Kuršių marios lagoon. Ekologija 2: 19-27. (in Lithuanian).

39. Daunys D., 2001. Patterns of the bottom macrophauna variability and its role in the shallow coastal lagoon. Doctoral theses. Klaipeda University, Klaipeda, 115p.
40. Deegan L. A., Garritt R. H., 1997. Evidence for spatial variability in estuarine food webs. Marine Ecology Progress Series 147: 31-47.
41. Dubois S., Jean-Louis B., Bertrand B., Lefebvre S., 2007. Isotope trophic-step fractionation of suspension-feeding species: implications for food partitioning in coastal ecosystems. Journal of Experimental Marine Biology and Ecology 351: 121-128.
42. European Communities, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. Official Journal of the European Communities 43 (L327), 75 pp.
43. Ertürk A., 2008. Modeling the response of an estuarine lagoon to nutrient inputs. Doctoral theses. Klaipeda University.
44. Ertürk A, Razinkovas A, Zemlys, P, Pilkaityte, R., Gasiunaite, Z. (2008) Linking NPZD and foodweb models of an estuarine lagoon ecosystem. Proceedings of the US/EU Baltic 2008 Symposium. IEEE Catalog Number:CFP08AME-CDR, Library of Congress: 2008902075.
45. Fantle M. S., Dittel A. I., Schwalm S. M., Epifanio C. E., Fogel M. L., 1999. A food web analysis of the juvenile blue crab, Callinectes sapidus, using stable isotopes in whole animals and individual amino acids. Oecologia 120: 416-426.
46. Ferrarin C., Razinkovas A., Gulbinskas S., Umgiesser G., Blindžiūtė L., 2008. Hydraulic regime-based zonation scheme of the Curonian Lagoon. Hydrobiologia 611: 133-146.
47. Fockedey N., Mees J., 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. Journal of Marine Systems 22, 207-228.
48. Fogel M. L., Cifuentes L. A., Velinsky D. J., Sharp J. H., 1992. Relationship of carbon availability in estuarine phytoplankton to isotopic composition. Marine Ecology Progress Series 82: 291-300.
49. France R. L., 1995. Carbon -13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124: 307-312.
50. Froneman P.W., 2001. Feeding ecology of the mysid, *Mesopodopsis wooldridgei*, in a temperate estuary along the eastern seaboard of South Africa. Journal of Plankton Research Vol.23 No.9: 999-1008.
51. Fry B., Arnold C.K., 1982. Rapid $^{13}C/^{12}C$ turnover during growth of brown shrimp (*Penaeus aztecus*). Oecologia 54: 200-204.
52. Fry B., Sherr E. B., 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27: 13-47.

53. Fry B., 2002. Conservative Mixing of Stable Isotopes Across Estuarine Salinity Gradients: A Conceptual Framework for Monitoring Watershed Influences on Downstream Fisheries Production
54. Fry B., Ewel, K.C., 2003. Using stable isotopes in mangrove fisheries research – a review and outlook. Isotopes in Environmental and Health Studies 39, 191-196.
55. Fry B., 2006. Stable Isotope Ecology. Springer. USA. 308 pp.
56. Fukumori K., Oi M., Doi M., Takahashi D., Okuda N., Miller T. W., Kuwae M., Miyasaka H., Genkai-Kato M., Koizumi Y., Omori K., 2008. Bivalve tissue as a carbon and nitrogen isotope baseline indicatorin coastal ecosystems. Estuarine, Coastal and Shelf Science 79: 45-50.
57. Galkus A., Jokšas K., 1997. Sedimentary material in the transitional aquasystem. Institute of Geography. Vilnius. 198 pp.
58. Galkus A. 2007. Gėlo ir Druskingo Vandens Cirkuliacijos Ypatumai Klaipėdos Sąsiauryje ir Kuršių Marių Šiaurinėje dalyje. Annales Geographicae 40(1).
59. Gannes L.Z., O'Brien D.M., Martinez del RioC., 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments.Ecology 78(4): 1271-1276.
60. Garcia A.M., Hoeinghaus D.J., Vieira J.P., Winemiller K.O., 2007. Isotopic variation of fishes in freshwater and estuarine zones of a large subtropical coastal lagoon. Estuarine, Coastal and Shelf Science73: 399-408.
61. Gasiūnaitė Z.R. 2000. Coupling of the limnetic and brackishwater plankton crustaceans in the Curonian lagoon (Baltic Sea). Internat. Rev. Hydrobiol., 85: 649-657
62. Gasiūnaitė Z.R., Cardoso A.C., Heiskanen A.-S., Henriksen P., Kauppila P., Olenina I., Plikaitytė R., Purina I., Razinkovas A., Sagert S., Schubert H., Wasmund N., 2005. Seasonality of coastal phytoplankton in the Baltic Sea: Influence of salinity and eutrophication. Estuarine, Coastal and Shelf Sciences 65: 239-252.
63. Gasiūnaitė Z.R., Daunys D., Olenin S., Razinkovas A., 2008. The Curonian Lagoon. In: U. Schiewer (Ed), Ecology of the Baltic Coastal Waters. Ecological Studies 197. Springer-Verlag, Berlin Heidelberg, pp. 197-215.
64. Gasiūnaitė Z.R., 2000. Coupling of the limnetic and brackish water plankton crustaceans in the Curonian Lagoon (Baltic Sea). International Revue of Hydrobiology 5-6: 653-662.
65. Gasiūnaitė Z.R., Razinkovas A. 2004. Temporal and spatial paatterns of crustacean zooplanktono dynamics in transitional lagoon ecosystem. Hydrobiologia 514: 139-149.
66. Gasiunas I., 1963. The acclimatization of fodder crustaceans (of the Caspian relict type) into the reservoir of Kaunas Hydroelectric power station and the possibility of their transference into other water bodies. Lietuvos TSR MA Darbai, Serija C, 1(30): 79-85 (in Russian).

67. Gorokhova E., Hansson S., 1999. An experimental study on variations in stable carbon and nitrogen isotope fractionation during growth of *Mysis mixta* and *Neomysis integer*. Canadian Journal of Fisheries and Aquatic Sciences 56: 2203-2210.
68. Gorokhova E., Lehtiniemi M., 2007. A combined approach to understand trophic interactions between Cercopagis pengoi (Cladocera: Onychopoda) and mysids in the Gulf of Finland. Limnology and Oceanography 52: 685-695.
69. Gorokhova E., 2009. Toxic cyanobacteria *Nodularia spumigena* in the diet of Baltic mysids: evidence from molecular diet analysis. Harmful Algae 8: 264-272.
70. Grey J., 2006. The use of of stable isotope analysis in freshwater ecology: current awareness. Polish Journal of Ecology 54: 563-584.
71. Grossnickle N.E., 1982. Feeding habits of *Mysis relicta* – an overview. Hydrobiologia 93, 101-107.
72. Gulbinskas S., Žaromskis R., Repečka R. 2002. Kuršių marios. Žemėlapis žvejybai. Lietuvos hidrobiologų draugija. Vilnius.
73. Grey J., Jones R.I., 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. Limnology and Oceanography 46(3): 505-513.
74. Grimvall A., Stålnacke P., 2001. Riverine inputs of nutrients to the Baltic Sea. [In:] Wulff F., Rahm L., Larsson P. [eds.] A Systems Analysis of the Baltic Sea, Ecological Studies 148. Springer.
75. Gu B., Schelske C.L., 1996. Temporal and spatial variations in phytoplankton carbon isotopes in a polymictic subtropical lake. Journal of Plankton Research Vol.18 no.11: 2081-2092.
76. Guelinckx, J. Maes J., Geysen B., Ollevier F., 2008. Estuarine recruitment of a marine goby reconstructed with an isotopic clock. Oecologia 157(1): 41-52.
77. Gumuliauskaite S., Arbaciauskas K., 2008. The impact of the invasive Ponto-Caspian amphipod *Pontogammarus robustoides* on littoral communities in Lithuanian lakes. Hydrobiologia 599: 127-134.
78. Gustafson L., Showers W., Kwak T., Levine J., Stoskopf M., 2007. Temporal and spatial variability in stable isotope compositions of a freshwater mussel: implications for biomonitoring and ecological studies. Oecologia 152: 140-150.
79. Hadwen W. L., Bunn S. E., 2005. Food web responses to low-lewel nutrient and ^{15}N-tracer additions in the littoral zone of an oligotrophic dune lake. Limnology and Oceanography 50(4): 1096-1105.
80. Hansson S., Hobbie J.E., Elmgren R., Larsson U., Fry, B., and Johansson, S. 1997. The stable nitrogen isotope ratio as a marker of food-web interactions and fish migration. Ecology 78: 2249-2257.

81. Hamilton S.K., Lewis W.M., Sippel S.J., 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia 89: 324-330.
82. Hamilton S. K., Sippel S. J., Bunn S. E., 2005. Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. Limnology and Oceanography: Methods 3: 149–157.
83. Harmelin-Vivien M., Loizeau V., Mellon C., Beker B., Arlhac D., Bodiguel X., Ferraton F., Hermand R., Philippon X., Salen-Picard C. 2008. Comparison of C and N stable isotope ratios between surface particulate organic matter and microphytoplancton in the Gulf of Lions (NW Mediterranean). Continental Shelf Research 28: 1911-1919.
84. Hart E. A., Lovvorn J.R., 2002. Interpreting stable isotopes from macroinvertebrate foodwebs in saline wetlands. Limnology and Oceanography 47(2): 580-584.
85. Harvey C. J., Hanson P. C., Essington T. E., Brown P. B., Kitchell J. F., 2002. Using bioenergetics models to predict stable isotope ratios in fishes. Canadian Journal of Fisheries and Aquatic Sciences 59: 115–124.
86. Hecky R.E., Campbell P., Hendzel L.L., 1993. The stoichiometry of carbon, nitrogen and phosphorus in particulate matter of lakes and oceans. Limnology and Oceanography 38(4): 709-724.
87. Hein T., Baranyi C., Herndl G.I., Wanek W., Schiemer F., 2003. Allochtonous and autochtonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. Freshwater Biology 48: 220-232.
88. HELCOM, 1988. Guidelines for the Baltic monitoring programme for the third stage. Baltic Sea environment proceedings No.27D, 23-86.
89. HELCOM, 2006. Assessment of Coastal Fish in the Baltic Sea. Baltic Sea environmental proceedings No. 103 A.
90. Hellings I., Dehairs F., Van Damme S., Baeyens W., 2001. Dissolved inorganic carbon in a highly polluted estuary (the Scheldt). Limnology and Oceanography 46(6): 1406-1414.
91. Hellings I., Dehairs F., Tackx M., Keppens E., Baeyens W., 1999. Origin and fate of organic carbon in the freshwater part of the Scheldt Estuary as traced by stable carbon isotope composition. Biogeochemistry 47: 167-186.
92. Herzka S.Z., Holt S.A., Holt G.J., 2002. Characterization of settlement patterns of red drum Sciaenops ocellatus larvae to estuarine nursery habitat: a stable isotope approach. Marine Ecology Progress Series 226: 143-156.
93. Hesslein R.H., Hallard K.A., Ramlal P., 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. Canadian Journal of Fisheries and Aquatic Sciences 50: 2071-2076.

94. Hostens K., Mees J., 1999. The mysid-feeding guild of demersal fishes in the brackish zone of the Westershelde estuary. Journal of Fish Biology 55, 704-719.
95. Jakob U., Mintenbeck K., Brey T., Knust R., Beyer K., 2005. Stable isotope food web studies: a case for standardized sample treatment. Marine Ecology Progress Series 287: 251-253.
96. Jane M., Almond R., Bentzen E., and Taylor W. D., 1996. Size structure and species composition of plankton communities in deep Ontario lakes with and without *Mysis relicta* and planktivorous fish. Canadian Journal of Fishery and Aquatic Sciences 53: 315-325.
97. Jankauskienė R., 2001. Trophic relations of the Ponto-Caspian higher crustaceans and fish larvae in the littoral zone of the Curonian Lagoon. Doctoral theses (in Lithuanian).
98. Jankauskienė R., 2003. Selective feeding of Ponto-Caspian higher crustaceans and fish larvae in the littoral zone of the Curonian lagoon. Ekologija 2: 19-27.
99. Johansson O.E., Leggett M.F., Rudstam L.G., Servos M.R., Mohammadian M.L., Gal G., Dermott R.M., Hesslein R.H., 2001. Diet of *Mysis relicta* in Lake Ontario as revealed by stable isotope and gut content analysis. Canadian Journal of Fisheries and Aquatic Sciences 58, 1975-1986.
100. Jokšas K., Galkus A., Stakėnienė R., 2005. Geoecological state of the lithuanian offshore of the Baltic Sea, the lower reaches of Nemunas and the Curonian Lagoon. Acta Zoologica Lituanica 15(2): 119-123.
101. Jones J.I., Waldron S., 2003. Combined stable isotope andgut contents analysis of food webs in plant-dominated, shallow lakes. Freshwater Biology 48: 1396-1407.
102. Jorgensen S.E., Nielsen S.N. and Jorgensen L. A. 1995. Handbook of ecological parameters and ecotoxicology. Elsevier, Amsterdam-London-New York-Tokyo: 1-1264.
103. Kasai A., Horie H., Sakamoto W., 2004. Selection of food sources by *Ruditapes philippinarum* and *Mactra veneriformis* (Bivalva: Mollusca) determined from stable isotope analysis. Fisheries Science 70: 11-20.
104. Kasai A., Nakata A., 2005. Utilization of terrestrial organic matter by the bivalve *Corbicula japonica* estimated from stable isotope analysis. Fisheries Science 71:151-158.
105. Ketelaars H.A.M., Lambregts-van de Clundert F.E., Carpentier C.J., Wagenvoort A.J. and Hoogenboezem W., 1999. Ecological effects of the mass occurrence of the Ponto-Caspian invader, Hemimysis anomala G.O.Sars., 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Nederlands, with notes on its autecology and new records. Hydrobiologia 394: 233-248.

106. Kibirige I., Perissinotto R., Nozais C., 2002. Alternative food sources of zooplankton in a temporarily-open estuary: evidence from $\delta^{13}C$ and $\delta^{15}N$. Journal of Plankton Research 24: 1089-1095.
107. Köhn J. 1992. Mysidacea of the Baltic Sea- state of the art. In: Köhn J., Jones M.B, Moffat A. (eds). Taxonomy, biology and ecology of (Baltic) mysids (Mysidacea: Crustacea). International Expert Conference, Hiddensee, Germany, Rostock University Press, Rostock: 5-23.
108. Komarova T. I., 1991. Fauna of the Ukraine, Higher crustaceans, Mysidacea. 26(7): 1-104.
109. Kremer J. N., Kemp W. M., Giblin A. E., Valiela I., Seitzinger S. P., Hofmann E. E., 2000. Linking biogeochemical processes to higher trophic levels. In: Hobbie J.E. (ed.). Estuarine Science a synthetic approach to research and practise. Island Press. USA.: 299-341.
110. Krevs A., Koreiviene J., Paskauskas R., Sulijiene R., 2007. Phytoplankton production and community respiration in different zones of the Curonian lagoon during the midsummer vegetation period. Transitional Waters Bulletin 1: 17-26.
111. Krylova O.I., 1985. Functioning ecological differences of plankton and benthos in the Kuršių marios and Vistula Lagoons of the Baltic Sea. Atlant-NIRO. Kaliningrad (in Russian).
112. Lahjta K., Marshall J.D., 1994. Sources of variation in the stable isotopic composition of plants. In Lahjta K. and Michener R. (Eds.) Stable Isotopes in Ecology and Environmental Science: 1-21.
113. Lampert, W., Sommer, U., 1997. Limnoecology: the Ecology of Lakes and Streams. Oxford Univ. Press. New York Oxford. 382 pp.
114. Lasenby D. and Shi Y., 2004. Changes in the elemental composition of the stomach contents of the opossum shrimp *Mysis relicta* during diel vertical migration. Canadian Journal of Zoology 82: 525-528.
115. Lin H. J., Kao W. Y., WangY. T., 2007. Analyses of stomach contents and stable isotopes reveal food sources of estuarine detritivorous fish in tropical/subtropical Taiwan. Estuarine, Coastal and Shelf Science 73: 527-537.
116. Lindén E., 2007. The more the merrier: swarming as an antipredator strategy in the mysid *Neomysis integer*. Aquatic Ecology 41: 299-307.
117. Liu, Z., and A. Herzig. 1996. Food and feeding behaviour of a planktivorous cyprinid, *Pelecus cultratus* (L.), in a shallow eutrophic lake, Neusiedler See (Austria). Hydrobiologia 333: 71–77.
118. Logan J., Haas H., Deegan L., Gaines E., 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. Oecologia 147: 391-395.
119. Loreau M., 2005. Current and future perspectives on food webs. In Belgrano A., Scharler U.M., Dunne J., Ulanowicz R. (Eds.) Aquatic Food Webs and Ecosystem Approach. Oxford University Press. 262pp.

120. Lorrain A., Savoye N., Chauvaud L., Paulet Y.-M., Naulet N., 2003. Decarbonation and preservation method for the analysis of organic C and N contents and stable isotope ratios of low-carbonated suspended particulate material. Analytica Chimica Acta 491: 125-133.
121. Ložys L., 2003. Seasonal migrations of pikeperch (*Sander lucioperca* L.) from the Curonian lagoon to the Baltic Sea and advantages of the phenomenon. Acta Zoologica Lituanica 13: 188-194.
122. Macdonald, P.D.M., Green P.E.J., 1988. User's guide to programm MIX: An interactive program for fitting mixtures of distributions. Guenther printing, Ontario, Canada. 75 pp.
123. Machás R., Santos R., Peterson B., 2006. Elemental and stable isotope composition of *Zostera noltii* (Horneman) leaves during the early phases of decay in a temperate mesotidal lagoon. Estuarine, Coastal and Shelf Science 66, 21-29.
124. Maksymowska D., Richard P., Piekarek-Jankowska H., Riera P., 2000. Chemical and isotopic composition of the organic matter sources in the Gulf of Gdansk (Southern Baltic Sea). Estuarine, Coastal and Shelf Science 51, 585-598.
125. Mann K. H., 1988. Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. Limnology, Oceanography. 33: 910-930.
126. Martineau C., Vincent W.F., Frenette J-J., Dodson J. J., 2004. Primary consumers and particulate organic matter: Isotopic evidence of strong selectivity in the estuarine transition zone. Limnology, Oceanography 49(5): 1679-1686.
127. Matson E.A., Brinson M.M., 1990. Stable carbon isotopes and the C : N ratioin the estuaries of the Pamlico and Neuse Rivers, North Carolina. Limnology and Oceanography 35(6): 1290-1300.
128. Matthews B., Mazumder A., 2003. Compositional and interlake variability of zooplankton affect baseline stable isotope signatures. Limnology and Oceanography 48: 1977-1987.
129. Mauchline J., 1980. The biology of mysids and euphausids. Advances in Marine Biology 18: 81-97.
130. McClelland J.W., Valiela I., Michener R.H., 1997. Nitrogen-stableisotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnology and Oceanography 42(5): 930-937.
131. McClelland J.W., Valiela I., 1998. Linking nitrogen in estuarine producers to land-derived sources. Limnology and Oceanography 43(4): 577-585.
132. McCutchan J.H., Lewis W.M., Kendall C., McGrathc C. C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. OIKOS 102: 378-390.
133. McLusky D.S. and Elliot M., 2004. The Estuarine Ecosystem Ecology, Threats, and Management. Oxford University Press. 214 pp.

134. McLusky D.S. and Elliot M., 2007. Transitional waters: A new approach, semantics or just muddying the waters? Estuarine, Coastal and Shelf Science 71: 359-363.
135. Michener R.H., Schell D.M., 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: K. Lajhta and R. Michener (Editors), Stable Isotopes in Ecology and Environmental Science. Blackwell Scientific Publications, Oxford-Vienna, pp. 138-157.
136. Middelburg J. J., Nieuwenhuize J., 1998. Carbon and nitrogen stable isotopes in suspended matter and sediments from the Schelde Estuary. Marine Chemistry Volume 60, Issues 3-4: 217-225.
137. Mills E.L., Casselman J.M., Dermott R., Fitzsimons J.D., Gal G., Holeck K.T., Hoyle J.A., Johannsson O.E., Lantry B.F., Makarewicz J.C., Millard E.S., Munawar I.F., Munawar M., O'Gorman R., Owens R.W., Rudstam L.G., Schaner T., Stewart T.J., 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Canadian Joarnal of Fisheries and Aquatic Sciences 60: 471–490.
138. Minagawa M. and Wada E., 1984. Stepwise enreachment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta 48: 1135-1140.
139. Monakov A.V., 1998. Feeding of Freshwater Invertebrates. Russian Academy of Sciences. A.N. Severtsov Institute of Ecological and Evolutionary Problems, Moscow. 319 pp. (in Russian).
140. Moore J.C., Berlow E.L., Coleman D.C., de Ruiter P.C., Dong Q., Hastings A., Johnson N.C., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.D., Post D.M., Sabo J.L., Scow K.M., Vanni M.J., Wall D.H., 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7, 584-600.
141. Morduchai-Boltovskoi and Rivier, 1987. The predativorous cladocerans Podonidae, Polyphemidae, Cercopagidae and Leptodoridae of the world fauna. The Scientific Academy USSR. Leningrad.: 97-106 (in Russian).
142. Morgan M.D. 1980. Grazing and predation of the grass shrimp *Palaemonetes pugio*. Limnology and Oceanography 25, 896-902.
143. Nikolova Eddins S. G. 2001. Calculation of terrestrial inputsto particulate organic carbon in an anthropogenically impacted estuary in the southeastern United States. Water, Air and Soil pollution 127: 227-241.
144. Ojaveer H., Leppäkoski E., Olenin S. and Ricciardi T. 2002. Ecological Impact of Ponto-Caspian Invaders in the Baltic Sea, European Inland Waters and the Great Lakes: an Inter-ecosystem Comparison In: Invasive aquatic species of Europe - distribution, impact and management. Leppäkoski, E., S. Gollasch & S. Olenin (eds). Dordrecht, Boston, London. Kluwer Academic Publishers: 412-425.

145. Olenin S., 1996. Comparative community study of the South-Eastern Baltic coastal zone and the Curonian Lagoon bottom. Proceeding of the 13-th Symposium of the Baltic Marine Biologists: 153-161.
146. Olenina I., 1997. Phytoplankton development in the Curonian Lagoon and south-eastern Baltic Sea coastal area. Doctoral theses, Institute of Botany, Vilnius.
147. Orav-Kotta H., Kotta J., Herkul K., Kotta I., Paalme T., 2009. Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* (Amphipoda: Crustacea) in the northern Baltic Sea. Biological Invasions 11: 597-608.
148. O'Reilly C.M., Hecky R.E., Cohen A.S., Plisnier P.-D., 2002. Interpreting stable isotopes in food webs: recognizing the role of tme averaging at different trophic levels. Limnology and Oceanography 47: 306-309.
149. Orlova M., Golubkov S., Kalinina L., Ignatieva N., 2004. Dreissena polymorpha (Bivalvia: Deissenidae) in the Neva Estuary (eastern Gulf of Finland, Baltic Sea): is it a biofilter or source of pollution? Marine Pollution Bulletin 49: 196-205.
150. Ovčarenko I., Audzijonytė A., Gasiūnaitė Z. R., 2006.Tolerance of *Paramysis lacustris* and *Limnomysis benedeni* (Crustacea, Mysida) to sudden salinity changes: implications for ballast water treatment. Oceanologia 48: 231-242.
151. Pasquaud S., Lobry J., Elie P., 2007. Facing the necessity of describing estuarine ecosystems: a review of food web ecology study techniques. Hydrobiologia 588: 159-172.
152. Pasquaud S., Elie P., Jeantet C., Billy I., Martinez P., Girardin M., 2008. A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. Estuarine, Coastal and Shelf Science 78(2): 267-279.
153. Pedersen M.F., Nielsen S.L., Banta G.T., 2004. Interactions between vegetation and nutrient dynamics in coastal marine ecosystems: an introduction. In. Nielsen S.L., Banta G.T., Pedersen M.F. (Eds.) Estuarine Nutrient Cycling: the Influence of Primary Producers the Fate of Nutrients and Biomass. Kluwer academic Publishers. Dordrecht/Boston/London: 1-15.
154. Perga M.E., Gerdeaux D., 2005. Are fish what they eat' all year round. Oecologia 144: 598-606.
155. Perga M.E., Kainz M., Matthews B., Mazumder A., 2006. Carbon pathways to zooplankton: insights from the combined use of stable isotope and fatty acid biomarkers. Freshwater Bioology 51: 2041-2051.
156. Peterson B.J., 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. Acta Oecologica 20(4): 479-487.
157. Peterson B.J., Fry B., 1987. Stable isotopes in ecosystem studies. Annual Review of Ecological Systems 18, 293-320.

158. Peterson B.J., Howarth R.W., 1987. Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-march estuaries of Sapelo Island, Georgia. Limnology, Oceanography 32(6): 1195-1213.
159. Phillips D.L., Gregg J.W., 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171-179.
160. Phillips D.L., Koch P.L., 2002. Incorporating concentration dependence in stable isotope mixing models. Oecologia 130: 114-125.
161. Phillips D.L., Gregg J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.
162. Phillips D.L., Newsome S.D., Gregg J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144: 520-527.
163. Phillips D.L., Eldridge P.M., 2006. Estimating the timing of diet shifts using stable isotopes. Oecologia 147: 195-203.
164. Pilkaitytė R., 2003. Phytoplankton seasonal succession and abundance in the eutrophic estuarine lagoons. Doctoral theses. Klaipeda University. Klaipeda.
165. Pilkaitytė, R., A. Razinkovas, 2006. Factors controlling phytoplankton blooms in a temperate estuary: nutrient limitation and physical forcing, Hydrobiologia, 555 (1): 41-48.
166. Pilkaitytė, R., A. Razinkovas, 2007. Seasonal changes in phytoplankton composition and nutrient limitation in a shallow Baltic lagoon, Boreal Environmental Research, 12(5): 551-559.
167. Pond D. W., Leakey R. J. G., Fallick A. E., 2006. Monitoring microbial predator–prey interactions: an experimental study using fatty acid biomarker and compound-specific stable isotope techniques. Journal of Plankton Research 28(4): 419-427.
168. Post D., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703-718.
169. Pringle C., 2003. What is hydrologic connectivity and why is it ecologically important? Hydrological Processes 17: 2685 – 2689.
170. Quay P.D., Emerson S.R., Quay B.M., Devol A.H., 1986. The carbon cycle for Lake Wahsington – A stable isotope study. Limnology and Oceanography 31(3): 596-611.
171. Raikow D.F., Hamilton S.K., 2001. Bivalve diets in a midwestern U.S. stream: A stable isotope enrichment study. Limnology and Oceanography 46(3): 514-522.
172. Razinkov A. 1990. Production processes of mysid populations in the water bodies of the basin of the River Nemunas. Minsk, 1990. Doctoral theses (in Russian).
173. Razinkovas A. 1996. Spatial distribution and migration patterns of the mysids in the Curonian lagoon. [In:]: Andrushaitis, A. [ed.] Proceedings of the 13th Baltic Marine Biologists Symposium: 117-120.

174. Razinkovas, A., Gasiūnaitė Z.R. 1999. The potential grazing by zooplankton and nektobenthic species on phytoplankton in an estuarine system: the Kurshiu Marios (Curonian) lagoon. Finnish Environment, 263: 44-51.
175. Razinkovas A., Zemlys P., 2000. Organic matter balans in the Curonian Lagoon ecosystem. Sea and Environment 1: 32-37. (in Lithuanian)
176. Reynolds C.S., 2006. The Ecology of Phytoplankton. Cambridge University Press, New York, 535 pp.
177. Riera P., Escaravage C., Leroux C., 2009. Trophic ecology of the rocky shore community associated with the *Ascophyllum nodosum* zone (Roscoff, France): A $\delta^{13}C$ vs $\delta^{15}N$ investigation. Estuarine, Coastal and Shelf Science 81: 143-148.
178. del Rio C.M., Wolf N., Carleton S.A., Gannes L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84:91-111.
179. Rolff C., 2000. Seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ of size-fractionated plankton at a coastal station in the northern Baltic proper. Marine Ecology Progress Series 203: 47-65.
180. Rolff C., Elmgren R., 2000. Use of riverine organic matter in plankton food webs of the Baltic Sea. Marine Ecology Progress Series 197: 81-101.
181. Rudstam L.G., Danielsson K., Hansson S. and Johansson S., 1989. Diel vertical migration and feeding patterns of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. Marine Biology 101: 43-52.
182. Rumohr H., Brey T., Ankar S. 1987. A compilation of biometrics conversion factors for benthic invertebrates of the Baltic Sea. Baltic Marine Biologists Publication 9: 1-56.
183. Schlacher T.A., Liddell B., Gaston T.F., Schlacher-Hoenlinger M., 2005. Fish track wastewater pollution to estuaries. Oecologia 144: 570-584.
184. Schmidt K., Atkinson A., Stübing D., McClelland J.W., Montoya J.P., 2003. Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. Limnology and Oceanography 48: 277-289.
185. Sobczak W.V., Cloern J.E., Jassby A.D., Müller-Solger A.B., 2002. Bioavailability of organic matter in a highly disturbed estuary: the role of detrital and algal resources. PNAS 99(12): 8101-8105.
186. Speirs D., Lawrie S., Raffaelli D., Gurney W., Emes C., 2002. Why do shallow-water predators migrate? Strategic models and empirical evidence from an estuarine mysid. Experimental Marine Biology and Ecology 280: 13-31.
187. Spencer C.N., Potter D.S., Bukantis R.T., Stanford J.A., 1999. Impact of predation by Mysis relicta on zooplankton in Flathead Lake, Montana, USA. Plankton Research 21: 51-64.
188. Stepanauskas R., Jorgensen N.O.G., Eigaard O.R., Zvikas A., Tranvik L.J., Leonardson L., 2002. Summer inputs of riverine nutrients to the Baltic Sea:

bioavailability and eutrophication relevance. Ecological Monographs 72(4): 579-597.
189. Sugimoto R., Kasai A., Yamao S., Fujiwara T., Kimura T., 2006. Short-term variation in behaviour of allochthonous particulate organic matter accompanying changes of river discharge in Ise Bay, Japan. Estuarine, Coastal and Shelf Science 66: 267-279.
190. Tamelander T., Søreide J. E., Hop H., Carrol M. L., 2006. Fractionation of stable isotopes in the arctic marine copepod calanus glacialis : Effects on the isotopic composition of marine particulate organic matter. Journal of Experimental Marine Biology and Ecology 333: 231-240.
191. Tieszen L.L., Boutton T.W., Tesdahl K.G., Slade N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57: 32-37.
192. Toda H., Wada E., 1990. Use of $^{15}N/^{14}N$ rations to evaluate the food source of the mysid, *Neomysis intermedia* Czerniawsky, in a eutrophic lake in Japan. Hydrobiologia 194: 85-90.
193. Vanderklift M. A., Ponsard S., 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia 136: 169-182.
194. Vander Zanden J.M., Rasmussen J.B., 1999. Primary consumer delta^{13}C and delta^{15}N and the trophic position of aquatic consumers. Ecology 80: 1395-1404
195. Vander Zanden J.M., Rasmussen J. B., 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology, Oceanography 46(8): 2061-2066.
196. Vander Zanden J.M., Cabana G., Rasmussen J., 1996. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. Canadien Journal of Fisheries and Aquatic Sciences 54:1142-1158.
197. Van Donk, E., 2007. Chemical information transfer in freshwater plankton. Ecological Informatics 2, 112-120.
198. Viherluoto M., Kuosa H., Flinkman J., Viitasalo, M., 2000. Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. Marine Biology 136, 553-559.
199. Viherluoto M., Viitasalo M., 2001. Temporal variability in functional responses and prey selectivity of the pelagic mysid, *Mysis mixta*, in natural prey assemblages. Marine Biology 138, 575-583.
200. Vincent D., Slawyk G., L'Helguen S., Sarthou G., Gallinan M., Seuront L., Sautour B., Ragueneau O., 2007. Net and gross incorporation of nitrogen by marine copepods fed on 15N-labelled diatoms: Methodology and trophic studies. Journal of Experimental Marine Biology and Ecology 352: 295-305.
201. Virbickas J., 2000. The Fishes of Lithuania. Institute of Ecology. Vilnius.

202. Vizzini S., Mazzola A., 2003. Seasonal variations in the stable carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of primary producers and consumers in a western Mediterranean coastal lagoon. Marine Biology 142: 1009-1018.
203. Vonk J.A., Christianen M.J.A., Stapel J., 2008. Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. Estuarine, Coastal and Shelf Science. 79: 653-660.
204. Voss M., Larsen B., Leivuori M., Vallius H., 2000. Stable isotope signals of eutrophication in Baltic Sea sediments. Journal of Marine Systems 25: 287-298.
205. Voss M., Emeis K.-C., Hille S., Neumann T., Dippner J.W., 2005a. Nitrogen cycle of the Baltic Sea from an isotopic perspective. Global Biogeochemical Cycles 19, GB3001, doi:10.1029/2004GB002338.
206. Voss M., Liskow I., Pastuszak M., Rüβ D., Schulte U., Dippner J.W., 2005b. Riverine discharge into a coastal bay: A stable isotope study in the Gulf of Gdan´sk, Baltic Sea. Marine Systems 57(1-2): 127-145.
207. Webb P., Wooldridge T.H., 1990. Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea: Mysidacea) in Algoa Bay, southern Africa. Marine Ecology Progress Series 62, 73-77.
208. Webster J.R., Benfield E.F., 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17, 567-594.
209. Wetzel R.G., Likens, G.E., 2000. Limnological Analyses. Springer. 429 pp.
210. Wetzel R., 2001. Limnology: Lake and River Ecosystems. Elsevier. USA.
211. Winemiller K.O., 2007. Interplay between scale, resolution, life history and foof web properties. The Dynamics and Structure of Ecological Systems 101-126.
212. Winemiller K.O., Akin S., Zeug S.C., 2007. Production sources and food web structure of a temperate tidal estuary: integration of dietary and stable isotope data. Marine Ecology Progress Series 343: 63-76.
213. Woodward G., Thompson R., Townsend C.R., Hildrew A.G., 2005. Pattern and process in food webs: evidence from running waters. In Belgrano A., Scharler U.M., Dunne J., Ulanowicz R. (Eds.) Aquatic Food Webs and Ecosystem Approach. Oxford University Press. 262pp.
214. Yoshii K., Melnik N.G., Timoshkin O.A., Bondarenko N.A., Anoshko P.N., 1999. Stable isotope analysis of the pelagic food web in Lake Baikal. Limnology and Oceanography 44: 502-511.
215. Zagursky, G., Feller, R.J., 1985. Macrophyte detritus in the winter diet of the estuarine ysid, *Neomysis americana*. Estuaries 8, 355-362.
216. Zaiko A., 2009. Habitat engineering role of the invasive bivalve *Dreissena polymorpha* (Pallas, 1771) in the boreal lagoon ecosystem. Doctoral theses. Klaipeda University.
217. Žaromskis R. 1996. *Oceans, Seas, Estuaries*. Debesija Vilnius: 1-293.

218. Žiliukas, V., 2003. Assessment of the dynamics of main ecological parameters of the fish fry community in the coastal zone of the Curonian Lagoon near Ventė cape. Acta Zoologica Lithuanica 13, 167-175.
219. Zohary T., Erez J., Stiller M., 1994. Seasonality of stablecarbon isotopes within the pelagic web Lake Kinneret. Limnology and Oceanography 39: 1030-1043.
220. Žydelis R., Kontautas A., 2008. Piscivorous birds as top predators and fishery competitors in the lagoon ecosystem. Hydrobiologia 611: 45

APPENDIX 1. Sampling dates and sites, sample types, species composition, specimen's description (BL- body length, TL- total length of fish, SL- mussel shell length, SH- shell height), number of replicates (n), stable isotope values ($\delta^{15}N$, $\delta^{15}C$, ‰) and molar C/N ratios of the spring, summer and autumn consumer samples in the Curonian Lagoon. N – number of replicates.

Date	Site	Sample type	Sample description: species composition, specimens size	N	$\delta^{15}N$	$\delta^{15}C$	C/N
					MEAN±SD	MEAN±SD	MEAN
24.05.2006	JO	Oligochaeta		3	9.6±0.2	-28.9±0.4	5.4
24.05.2006	JO	*Valvata* spp.		3	10.9±0.8	-28.0±0.1	5.7
24.05.2006	JO	*Marenselleria neglecta*		3	12.2±0.3	-28.7±0.5	4.8
24.05.2006	JO	Mesozooplankton	Cyclopoida, Daphnia <5 %	3	13.5±0.6	-32.1±0.2	8.7
24.05.2006	JO	*Leptodora kindtii*	>500 µm	3	14.4±0.1	-31.7±0.0	5.6
24.05.2006	JO	*Paramysis lacustris*	BL 10.6 ± 1.1 mm	3	14.3±0.4	-29.6±0.2	4.3
24.05.2006	VO	Chironomidae		3	11.2±0.1	-32.8±0.3	7.3
24.05.2006	VO	Erpobdellidae		3	12.5±0.2	-30.4±0.2	5.5
24.05.2006	VO	Glossiphoniidae		3	11.4±0.2	-29.6±0.4	4.8
24.05.2006	VO	*Dreissena polymorpha*	SL 2 ± 0.3 cm	3	10.0±0.3	-32.3±0.1	5.9
24.05.2006	VO	*Dreissena polymorpha*	SL <1 cm	3	9.8±0.1	-31.9±0.3	5.8
31.05.2006	VL	*Paramysis lacustris*	BL 12.6 ± 1.2 mm	3	15.0±0.4	-29.9±0.4	4.2
02.08.2006	JO	Mesozooplankton	>200 µm, *Chydorus, Bosmina, Diaphanosoma, Daphnia, Mesocyclops*, 10 % debris and phytoplankton	3	9.4±0.1	-24.9±0.2	5.0
02.08.2006	JO	*Leptodora kindtii*	>500 µm	3	11.7±0.2	-23.9±0.1	4.9
03.08.2006	JO	*Paramysis lacustris*	BL 9.6 ± 0.9 mm	3	10.5±0.4	-24.1±0.6	3.7
03.08.2006	JO	*Paramysis lacustris*	BL 6.2 ± 0.5 mm	3	9.2±0.1	-23.1±0.1	4.0
03.08.2006	JO	*Valvata* spp.		3	9.8±0.2	-26.4±0.3	5.2
03.08.2006	JO	Oligochaeta		1	9.2	-27.9	4.8
03.08.2006	JO	Chironomidae		3	7.2±0.3	-24.2±0.2	5.2
05.08.2006	JO	*Abramis brama*	TL 35 cm	3	13.3±0.5	-26.6±0.4	3.4
05.08.2006	JO	*Stizostedion lucioperca*	TL 45 cm	2	15.7±0.6	-25.0±1.8	8.5
05.08.2006	JL	*Perca fluviatilis*	TL 6.1 ± 0.8 cm	3	11.3±0.4	-23.3±0.1	3.5
05.08.2006	JL	Gammaridae	*Pontogammarus robustoides, G. tigrinus*, BL >10 mm	2	9.0±0.4	-23.0±0.2	5.3

05.08.2006	JL	Gammaridae	*Pontogammarus robustoides, G. tigrinus* BL 5-10 mm	3	8.4±0.2	-22.1±0.5	5.0
05.08.2006	JL	*Gymnocephalus cernuus*	TL 9.7 ± 1.4 cm	3	13.4±0.1	-26.6±0.2	3.4
05.08.2006	JL	*Rutilus rutilus*	TL 10.8 ± 1.5 cm	3	12.4±0.4	-26.2±0.1	3.4
05.08.2006	JL	*Perca fluviatilis*	TL 11.3 ±0.3 cm	4	14.3±0.1	-25.9±0.3	3.3
04.08.2006	VO	*Leptodora kindtii*	>500 µm	3	11.7±0.2	-24.0±0.3	4.8
04.08.2006	VO	Mesozooplankton	>200 µm, Copepoda, Chydorus, Daphnia and Diaphanosoma <5%	3	9.4±0.4	-24.7±0.3	4.7
04.08.2006	VO	*Paramysis lacustris*	BL 5.5 ± 0.6 mm	3	8.0±0.3	-22.0±0.1	3.9
04.08.2006	VO	*Paramysis lacustris*	BL 9.2 ± 1.2 mm	2	9.9±0.3	-23.6±0.7	3.6
04.08.2006	VO	*Dreissena polymorpha*	SL, 2.4 ± 0.2 cm	6	10.4±0.5	-29.3±1.2	4.5
04.08.2006	VO	*Dreissena polymorpha*	SL, 1.1 ± 0.3 cm	6	9.3±0.5	-27.0±0.9	4.7
04.08.2006	VO	*Viviparus* spp.	SH, 2.0 ± 0.5 cm	6	9.4±0.8	-26.3±0.6	5.0
04.08.2006	VO	Limnaeaidae	SH, 0.8 ± 0.4 cm	4	8.0±0.8	-23.9±0.8	4.3
04.08.2006	VO	*Valvata* spp.		3	8.2±0.3	-26.7±0.5	4.9
04.08.2006	VO	*Unio* spp.	SL 6.5 ± 1.5 cm	4	10.5±0.5	-29.1±0.9	3.9
04.08.2006	VO	Chironomidae		6	7.4±0.8	-25.6±1.3	5.3
04.08.2006	VO	Oligochaeta		3	10.7±0.8	-29.6±0.5	5.6
04.08.2006	VO	*Eiseniella tetraedra*		1	11.1	-29.7	5.1
04.08.2006	VO	Glossiphoniidae		1	12.5	-30.1	4.4
04.08.2006	VO	Erpobdellidae		3	11.8±0.1	-27.1±0.2	4.3
09.08.2006	VO	*Rutilus rutilus*	TL 24.8 ± 1.5 cm	3	13.8±0.5	-27.2±0.3	3.3
09.08.2006	VO	*Perca fluviatilis*	TL 29.6 ± 3.9 cm	5	16.5±0.4	-25.7±0.7	3.3
09.08.2006	VO	*Pelecus cultratus*	TL 34.3 ±2.1 cm	3	14.6±0.5	-25.5±0.4	3.4
01.08.2006	VL	*Cladophora* spp.		3	5.1±0.2	-19.7±0.4	11.9
01.08.2006	VL	*Potamogeton perfoliatus*	green leaves	3	9.3±0.5	-15.1±1.1	14.8
01.08.2006	VL	*Limnomysis benedeni*	BL 6.8 ± 0.5 mm	4	8.4±0.1	-24.0±0.5	4.1
01.08.2006	VL	*Paramysis lacustris*	BL 9.1 ± 1 mm	5	9.3±0.9	-23.8±0.6	4.0
01.08.2006	VL	*Paramysis lacustris*	BL 5.9 ± 0.7 mm	3	8.1±1.0	-23.4±0.6	3.8
01.08.2006	VL	Gammaridae	*Pontogammarus robustoides, Obessogamarus crassus* BL 7.3 ± 1.3 mm	3	7.0±0.2	-22.6±0.4	5.0
01.08.2006	VL	Gammaridae	*Pontogammarus robustoides,*	3	7.6±0.2	-23.8±0.1	5.1

			Obessogamarus crassus BL 11.1 ± 1.3 mm				
11.10.2006	JO	Mesozooplankton	>500 µm *Daphnia* spp. 100 %	3	10.5±0.3	-30.0±0.3	5.2
11.10.2006	JO	*Valvata* spp.		3	9.9±0.3	-24.4±1.9	5.8
11.10.2006	JO	Chironomidae		3	9.5±0.1	-26.1±0.5	5.3
11.10.2006	JO	*Marenselleria neglecta*		2	11.6±0.2	-27.8±16.0	4.3
11.10.2006	JO	*Paramysis lacustris*	BL 6 ± 0.6 mm	3	11.0±0.3	-25.1±0.4	4.3
11.10.2006	JO	*Paramysis lacustris*	BL 9.9 ± 0.6 mm	3	11.9±0.3	-24.8±0.6	4.1
28.11.2006	JO	*Perca fluviatilis*	TL 9.3 ± 0.1 cm	3	11.8±0.1	-22.8±0.1	3.2
28.11.2006	JO	*Perca fluviatilis*	TL 15.7 ± 0.1 cm	3	13.1±1.2	-24.9±0.4	3.2
28.11.2006	JO	*Rutilus rutilus*	TL 25.1 ± 3.5 cm	2	12.9±0.3	-25.3±1.0	3.2
28.11.2006	JO	*Abramis brama*	TL 34.9 ± 3.0cm	3	13.9±0.3	-26.7±0.4	3.3
28.11.2006	JO	*Gymnocephalus cernuus*	TL≈7 cm	3	11.9±0.5	-24.2±0.7	3.4
11.10.2006	VO	Mesozooplankton	>200 µm, Daphnia 66 %, Cyclopoida 18 %, Chydorus 8 %	3	13.6±0.4	-30.8±0.4	5.7
11.10.2006	VO	*Paramysis lacustris*	BL 6 ± 0.5 mm	3	13.0±0.1	-28.7±0.5	4.1
11.10.2006	VO	*Paramysis lacustris*	BL 10.5 ± 1.3 mm	3	12.7±0.4	-27.3±0.3	4.6
11.10.2006	VO	*Valvata* spp.		5	10.4±1.0	-26.6±0.9	5.5
11.10.2006	VO	*Viviparus* spp.		3	10.4±0.3	-26.5±0.6	5.0
11.10.2006	VO	*Dreissena polymorpha*	SL 1.1 ± 0.2 cm	5	10.5±0.4	-29.7±1.0	4.8
11.10.2006	VO	*Dreissena polymorpha*	SL, 1.9 ± 0.3 cm	5	10.5±0.2	-30.4±0.5	4.7
11.10.2006	VO	*Eiseniella tetraedra*		3	10.2±0.3	-28.6±0.1	5.0
11.10.2006	VO	Chironomidae		9	10.3±0.2	-29.4±0.9	5.8
11.10.2006	VO	Oligochaeta		9	10.4±0.8	-27.9±0.4	5.3
11.10.2006	VO	Erpobdellidae		5	12.3±0.6	-26.4±0.2	4.9
10.10.2006	VL	Mesozooplankton	Harpacticoida 66%, Calanoida 23%, Daphnia 6%	2	13.6±0.4	-29.8±0.2	5.8
11.10.2006	VL	*Paramysis lacustris*	BL 6 ± 0.5 mm	3	13.5±0.3	-29.9±0.3	4.1
11.10.2006	VL	*Paramysis lacustris*	BL 10.5 ± 1 mm	5	12.9±0.6	-27.9±0.3	4.3

APPENDIX 2. Salinity (S), water temperature (T, ˚C), wind speed (W, m s^{-1}, averaged value between 6 p.m. and 6 a.m., MRC monitoring data) EPOM<70 μm chlorophyll-a content (μg L^{-1} , starred value – chlorophyl-a in total POM), concentration (mgDW L^{-1}) and phytoplankton contribution (Phytopl, % by DW), calculated from chlorophyll a content, assuming it to contribute 1 % to phytoplankton DW (Reynolds, 2006), rough composition of dominant phytoplankton species and non-algal ingredients in POM 100-200 μm fraction, estimated on visual observations under stereomicroscope Mic- Microcystis, Aph- Aphanizomenon, A- Anabaena, Au- Aulacoseira, Plan- Plankthotrix, Cop- copepodites, Rot- Rotatoria, stable isotope ($\delta^{15}N$, $\delta^{15}C$, ‰), elemental (C, N, %) composition and elemental C/N ratios (molar) in two size fractions of EPOM <70 μm and 100-200 μm on each sampling occasion. N- sample size, nd- no data.

Site/ Date	T	S	W	Size fraction	Chl a	Conc.	Species composition	Phytopl	$\delta^{15}N$	$\delta^{15}C$	C	N	C/N	N
VL/May 30	14	0.1	6	<70	nd	7.8±1.1		nd	7.4±0.2	-31.1±0.2	11±1.5	1.8±0.3	7.1	3
VL/June 20	24	0.2	4	<70	22.7	12.7±0.7		18	2.5±0.3	-33.3±0.2	19.1±1.3	4.2±0.3	5.3	3
VL/July 12				<70	95.7	28.3±1.9		34	2.1±0.4	-28.4±0.1	19.5±2.4	3.5±0.4	6.4	3
VL/July 12	27	0.1	6	100-200			*Mic*, *Aph*, *A*		5.9±0.5	-26.2±0.1	35.4±0.9	4.9±0.1	8.3	3
VL/July 31	25	0.9	2	<70	30.7	19.6±0.9		16	3.6±0.6	-22.1±0.1	15.2±0.5	2±0.1	8.9	3
VL/Aug 30				<70	40	25.8±3.2		16	6.3±0.3	-28.4±0.1	27.9±0.8	3.4±0.1	9.7	3
VL/Aug 30	21	0.1	5	100-200			*Au*, *Mic*; Rot		7.6±0.2	-28.9±0.1	31.3±8.7	3.5±0.9	10.3	3
VL/Sept 19	17	0.1	6	<70	26.2	8.6±0.9		30	8.8±0.5	-33.3±0.5	20.5±2	3.4±0.4	6.3	3
VL/Oct 10				<70	15.1	4.9±0.3		31	9.6±0.4	-32.2±0.3	28.3±3.1	4.3±0.5	7.7	3
VL/Oct 10	14	0.0	4	100-200			*Aph*, *Plan*		4.4±0.3	-33.0±0.1	47.7±2.7	9.8±0.6	5.7	3
VL/Nov 9	6	0.7	16	<70	31.6	22.3±4.7		14	8.4±0.3	-23.7±0.2	18.2±6.1	1.7±0.6	12.2	3
SL/July 31	24	1.5	nd	<70	34	15.3±0.2		22	2.7±0.7	-21.7±0.1	14.8±0.8	2.1±0.1	8.2	3

SL/July 31				100-200					2.9±0.2	-24.4±0.0	29.4±1.8	4.7±0.2	7.3	3
VO/May 24	14	0.0	8	<70	53*	47.8 ± 6		nd	8.6±0.1	-26.2±1.0	11.1±0.6	1.4±0.1	9.2	3
VO/Aug 4	22	0.3	3	<70	85*	30.8±2.8		nd	8.3±0.1	-24.2±0.1	10.3±1	1.3±0.1	9.6	3
VO/Aug 4				100-200			*Mic*		8.3±0.9	-24.0±0.2	39.1±2.7	5.9±0.5	7.7	3
VO/Oct 11	14	0.0	5	<70	17*	4.6±0.6		nd	9.6±0.2	-32.2±0.2	68.3±15	11.6±3	6.7	3
VO/Oct 11				100-200			*Mic*, *Aph*		9.2±0.1	-32.7±0.3	29.4±5.9	5.1±1.1	6.8	3
JO/May 24				<70	43*	22.8±1.1			7.7±0.5	-27.9±0.3	13.1±0.4	1.6±0.1	9.5	3
JO/May 24	14	0.0	nd	100-200			*Mic*, Cop		10.7±0.2	-31.3±0.2	24.7±2.1	4.4±0.4	6.6	3
JO/Aug 2				<70	63*	23.3±1.2			8.9±0.3	-24.3±0.4	54.6±4.5	5.6±0.3	11.3	3
JO/Aug 2	22	0.9	nd	100-200			*Mic*		8.3±0.5	-23.8±0.1	40.5±0.5	5.3±0.1	9	3
JO/Oct 11				<70	47*	13.3±3.6			7.2±0.3	-29.4±0.2	56.1±6.6	7.9±0.9	8.3	3
JO/Oct 11	14	0.5	nd	100-200			*Mic*, *Aph*		5.5±0.2	-30.2±0.1	39.2±2.8	6.2±0.4	7.3	3
NR/May 22		0.0	nd	<70	nd	14.1±1.3		nd	7.8±0.2	-30.8±0.3	14.4±0.5	2.6±0.1	6.6	3
NR/June 21		0.0	nd	<70	32.3	40.4±13.5		8	8.1±0.3	-30.0±1.4	14.3±1.8	1.8±0.4	9.2	3
NR/July 10		0.0	nd	<70	nd	13.6±0.5		nd	7.5±0.7	-32.4±0.1	14.3±0.7	2.1±0.1	8	3
NR/Aug 1	23	0.0	nd	<70	23	11.1±0.9		21	7.5±0.4	-31.3±0.3	9.2±0.4	1.3±0.1	8.1	3
NR/Aug 29		0.0	nd	<70	59.5	10±0.9		59	10±0.1	-35.4±0.3	38.7±6.8	8±1.7	5.7	3
NR/Sept 18		0.0	nd	<70	40.1	8.1±0.3		49	8.7±0.2	-35.9±0.2	16.2±1.6	3.6±0.4	5.2	3
NR/Oct 9	14	0.0	nd	<70	19	4.04±0.3		47	9.1±0.6	-34.6±0.4	41.6±4.5	7.9±0.9	6.2	3
BS/July 10	20	6.8	nd	<70	1.9	6.9±0.9		3	0.9±0.5	-25.4±0.4	10.9±1.2	1.7±0.2	7.5	5
BS/Aug 8	12	7.3	nd	<70	nd	3.4±0.0		nd	3.9±0.3	-27.4±0.1	9.5±1.6	1.5±0.2	7.6	2