KLAIPĖDA UNIVERSITY

Rasa MORKŪNĖ

FOOD WEB OF THE LITHUANIAN BALTIC SEA COASTAL ZONE: STRUCTURE AND ORGANIC MATTER FLOWS

DOCTORAL DISSERTATION

Biomedical sciences, ecology and environmental sciences (03B)

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KLAIPĖDOS UNIVERSITETAS

Rasa MORKŪNĖ

MITYBOS TINKLAS BALTIJOS JŪROS LIETUVOS PRIEKRANTĖJE: STRUKTŪRA IR ORGANINĖS MEDŽIAGOS SRAUTAI

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Abstract

This study is based on a reconstruction of the coastal food web in the southeastern Baltic Sea. The combination of stable isotope analysis and ECOPATH modeling approaches was used to deal with the complexity of the Lithuanian coastal ecosystem which is partially sustained by passive organic matter flow from the nearby lagoon system and active migration of animals. Analysis of stable carbon and nitrogen isotope ratios revealed the contribution of the Curonian lagoon outflow to the food web compartments along the coastal zone. Stable isotope ratios in fishes reflected their seasonal migrations across the ecosystems of the coastal zone, the Curonian lagoon and the open Baltic Sea. Moreover, stable sulfur isotope ratios were proved to serve as an effective supplement to stable carbon and nitrogen isotope ratios for trophic studies in the coastal Baltic ecosystem. Using triple stable isotope mixing models, the proportions of different fishes and benthic organisms in the diet of wintering marine bird species were estimated.

The trophic structure of the Lithuanian coastal zone was reconstructed using ECOPATH modelling approach. The model incorporated 41 compartments representing the period of 2000-2010. The overall pedigree index of the model was relatively high (0.66) as many of the input parameters were obtained directly in the study area. The results indicated net heterotrophy of the coastal ecosystem and allowed to estimate organic matter flows. Analysis of direct and indirect trophic impacts revealed the compartments with the strongest total impact to other compartments within the food web. The most important functional groups (featuring both high trophic impacts and keystones values) are piscivorous birds, pike-perch, nectobenthos and mesozooplankton. Fishery is found affecting the food web negatively both directly and indirectly. Relationship between stable nitrogen isotope ratios of consumers and trophic levels estimated by the ECOPATH model confirmed the relevance of both methods applied to the analysis of the Baltic Sea coastal zones.

Key words

ECOPATH model; stable isotope analysis; fish migrations; diet of marine birds.

Reziumė

Disertacijoje atlikta pietryčių Baltijos priekrantės ekosistemos mitybos tinklo rekonstrukcija. Stabiliųjų izotopų analizė ir ECOPATH modeliavimas buvo taikyti kompleksinėje Lietuvos priekrantės ekosistemoje, kurią veikia pasyvus organinės medžiagos srautas iš gretimos lagūninės ekosistemos ir aktyvi gyvūnų migracija. Stabiliųjų anglies ir azoto izotopų santykiai atskleidė Kuršių marių gėlo vandens prietakos poveikį mitybos tinklo komponentams skirtinguose priekrantės taškuose. Įvairioms migracinėms gildijoms priklausančių žuvų izotopiniai skirtumai atspindėjo jų migracijos pobūdį tarp priekrantės, Kuršių marių ir atviros Baltijos jūros ekosistemų. Stabiliųjų sieros izotopų metodas efektyviai papildė stabiliųjų anglies ir azoto izotopų santykių analizės panaudojimą Baltijos jūros priekrantės ekosistemoje. Trijų stabiliųjų izotopų maišymosi modeliais buvo įvertintos skirtingų žuvų ir dugno bestuburių proporcijos žiemojančių jūros paukščių racionuose.

Sudarytas ECOPATH Lietuvos priekrantės mitybos tinklo modelis apėmė 41 komponentą, reprezentuojantį 2000–2010 m. laikotarpį. Aukštas modelio kilmės indeksas (0,66) parodė, kad dauguma naudotų duomenų buvo surinkti tiriamoje priekrantėje. Rezultatai atskleidė priekrantės mitybos tinklo heterotrofiškumą ir padėjo įvertinti organinės medžiagos srautus. Darbe taip pat analizuojami tiesioginis ir netiesioginis mitybos poveikis bei išskirti stipriausiai kitus mitybos komponentus veikiantys organizmai. Svarbiausiais mitybos tinklo komponentais, kuriems būdingi ir stiprus trofinis poveikis, ir aukšti svarbumo indeksai, buvo žuvlesiai paukščiai, starkiai, nektobentoso ir mesozooplanktono organizmai. Palyginus vartotojų stabiliųjų azoto izotopų santykius su ECOPATH modeliu įvertintais mitybos lygmenimis, buvo patvirtintas abiejų metodų tinkamumas Baltijos jūros priekrantės tyrimams.

Reikšmingi žodžiai

ECOPATH modelis; stabiliųjų izotopų analizė; žuvų migracijos, jūros paukščių mityba.

Contents

1

Introduction

1.1. Relevance of the thesis

Characterization of a food web is an initial step in understanding interrelationships between dynamics and stability of community and ecosystem functioning (Link, 2002; de Ruiter et al., 2005; Heymans et al., 2014). Increasing anthropogenic activity and its pressure to species interactions and ecosystem functioning have become important issues in marine environment, and ecosystem-based approach is suggested to understand this entirety. In the Baltic Sea, ecosystem-based management is still missing approach and a majority of environmental problems are still treated separately due to a lack of understanding of ecosystem processes (Elmgren et al., 2015).

Coastal ecosystems in the Baltic Sea are convenient for the food web research and ecosystem-based analysis due to extensive sampling reaching historical times, and availability of results coming from social to hydrodynamic studies (Christian et al., 2005). Coastal zones usually represent a set of gradients originating from the transitional nature of these ecosystems. Organic matter flow from freshwater basins to marine ecosystems influences production and consumption balance in coastal ecosystems (Heip et al., 2011). Moreover, coastal food web structures are complex due to passively transported organic matter and active migration of organisms (Deegan, 1993; Heip et al., 2011; Hyndes et al., 2014). Though their presence is well documented, the organic matter flows from adjacent ecosystems and migratory species are often not taken into account in studies on ecosystem functioning (Willson and

Halupka, 1995; Winemiller and Jepsen, 1998). This leads to inaccurate depictions of trophic structure and limits ability to estimate coastal ecosystem functions.

In the Lithuanian coastal zone of the Baltic Sea, the majority of fish and waterbird species are present on a seasonal basis. These active migrants together with freshwater flow from the adjacent Curonian Lagoon contribute to trophic structure and characteristics of the coastal ecosystem. While previous studies covered only the distinct trophic relationships or discrete food webs of the transitional waters (e.g. Razinkovas and Zemlys, 2000; Ertürk et al., 2008; Tomczak et al., 2009), there is still a need for reconstruction of the complete coastal food web. Stable isotope analysis (hereinafter – SIA) might be used describing trophic relationships for various organisms, including migratory fish and wintering marine birds (e.g. Hansson et al., 1997; Vaslet el al., 2012). A food web model, based on ecosystem approach (Christensen et al., 2005), might present roles of main compartments and organic matter flow. This work is based on application of the above mentioned approaches in order to reconstruct the Lithuanian coastal food web and improve understanding of ecosystem functioning.

1.2. Objectives and main tasks of the study

This study aims to reconstruct the food web and quantify organic matter flows in the Lithuanian Baltic Sea coastal zone ecosystem.

The work could be divided in the following tasks:

1. To evaluate the stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) ratios of main food web compartments, including ecological guilds of fish, in the Lithuanian coastal zone during vegetative season;
2. To quantify the contribution of different food sources in the diet of wintering marine birds highlighting the application of stable sulfur isotopes ($\delta^{34}S$) for trophic studies;
3. Using ECOPATH modelling approach, to evaluate trophic network structure and characteristics, trophic impacts within the community and to calculate the keystoneness of individual compartments;
4. To compare the measured $\delta^{15}N$ ratios in consumers and tropic levels estimated using the ECOPATH model.

1.3. Novelty of the study

In this study, the most detailed food web model in the Baltic Sea was constructed using ECOPATH. For the first time such food web structure and characteristics were assessed for the entire Lithuanian coastal zone. The model allowed to evaluate the contribution of main compartments, including migratory organisms, to the biomass balance in the coastal zone and to calculate keystone compartments and trophic impacts within community.

For the first time in the studied coastal zone, the stable isotope (hereinafter – SI) values of main food web compartments and the contribution of the organic matter originated from the neighboring lagoon were estimated. For the first time in the Baltic Sea, $\delta^{34}S$ ratios together with $\delta^{13}C$ and $\delta^{15}N$ ratios were applied for the quantification of the food sources for wintering marine birds.

1.4. Scientific and applied significance of the results

In absence of holistic studies of the open sandy coast ecosystems, this study is a significant advance in understanding the functioning of coastal ecosystems in general (so far only some communities like benthic invertebrates or fishes were investigated in depth in this type of environment).

Reconstructed food web of the entire Lithuanian coastal zone provides a possibility to evaluate the role of separate species and organism groups, including seasonally present fishes and waterbirds, on the ecosystem functioning in general. The model is a base for further investigations of the coastal food web that is under influence of invasive species, climate change and increasing anthropogenic activities as fishery, wind energy development, increasing shipping, water pollution, etc. The network model might be used as a tool planning environmental protection, managing the ecosystem resources, evaluating the ecosystem effects of external pressures, guiding the management policy in combination with economic, social and ecological considerations.

This study provides a solid foundation for future research based on SIA in the Lithuanian coastal zone. It also proves that the $\delta^{34}S$ values effectively supplement the dual $\delta^{13}C$ and $\delta^{15}N$ values assessing the diet of consumers, including threatened marine birds.

1.5. Statements to be defended

1. During the vegetative season, the SI ratios in food web compartments of the Lithuanian coastal zone are the derivatives of a mixture of organic sources originating in the Curonian Lagoon and the open Baltic Sea.
2. The Lithuanian coastal food web is heterotrophic. The balance is sustained by the organic matter import from adjacent ecosystems.
3. The SI ratios in wintering waterbird blood reflect their feeding preferences during their stay in the Lithuanian coastal zone: diet of piscivorous birds consists of different proportions of pelagic, benthic and benthopelagic fishes; diet of benthivorous ducks depends on their feeding grounds – macrozoobenthos and marine fish dominates diet in sandy habitats, while anadromous fish are the most important prey in the stony bottom habitat. The $\delta^{34}S$ ratios supplements the $\delta^{13}C$, $\delta^{15}N$ ratios for diet assessment for wintering waterbirds.

4. Despite their low biomass, the top predators and fishery have strong negative impacts, while mesozooplankton and nectobenthos have strong positive trophic impacts on compartments of the coastal food web.

5. Trophic levels (TLs) of consumers, estimated by ECOPATH model, correspond well to the δ^{15}N ratios measured for same groups.

1.6. Scientific approval

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

The 8th Conference of the European Ornithologists' Union, Riga, Latvia, August 2011;

The 52nd International ECSA Symposium *Research and Management of Transitional Waters*, Klaipėda, Lithuania, September 2012;

The 9th Baltic Sea Science Congress, Klaipėda, Lithuania, August 2013;

World Conference on Natural Resource Modeling *Modeling Our Way Back to the Future*, Vilnius, Lithuania, July 2014;

The 5th International Sea Duck Conference, Reykjavik, Iceland, September 2014;

The 10th Baltic Sea Science Congress 2015, Riga, Latvia, June 2015;

The 7th European Coastal Lagoons Symposium, Murcia, Spain, March 2016.

1.7. Papers published

Three publications were published on the dissertation topics:

Morkūnė R., 2011. Trophic Peculiarities of the Great Cormorant, Grey Heron and Long-Tailed Duck on the Baltic Sea Lithuanian Coast: a Stable Isotope Approach. *Ekologija* 57 (4), 173-178.

Morkūnė R., Lesutienė J., Barisevičiūtė R., Morkūnas J., Gasiūnaitė Z. R., 2016. Food Sources of Wintering Piscivorous Waterbirds in Coastal Waters: A Triple Stable Isotope Approach for the Southeastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 171, 41-50.

Razinkovas-Baziukas A., Morkūnė R., Bacevičius E., Gasiūnaitė Z. R. Trophic Network Model of Exposed Sandy Coast: Linking Continental and Marine Water Ecosystems. *Estuarine, Coastal and Shelf Science (accepted).*

Methodical manual: Morkūnas J., Morkūnė R., Raudonikis L., 2015. An Identification Guide to Diving Waterbirds. - Kaunas: Lututė, 46 p. ISBN 978-9955-37-175-5 (in Lithuanian).

1.8. Dissertation structure

The dissertation includes eight chapters: introduction, literature review, material and methods, results, discussion, conclusions, references and technical annex. It comprises 168 pages, 33 figures and 19 tables. The dissertation refers to 253 literature sources. Dissertation is written in English with an extended summary in Lithuanian.

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1.10. Abbreviations

Abbreviation	**Explanation**
SI	Stable isotopes
SIA	Stable isotope analysis
$\delta^{13}C$	Stable carbon isotope ratio
$\delta^{15}N$	Stable nitrogen isotope ratio
$\delta^{34}S$	Stable sulfur isotope ratio
TEF	Trophic enrichment/ fractionation factor
TE	Transfer efficiency is a fraction of total flows of each TL that are either transferred to higher trophic levels through consumption or exported out if the system.
POM	Particulate organic matter
TL	Trophic level
TST	Total system throughput is the total amount of flow within a system
P/B	Production/ biomass ratio
Q/B	Consumption/ biomass ratio
R/A	Respiration/ assimilation ratio
P/R	Production/ respiration ratio
TPP/TR	Total primary production/total respiration
R/B	Respiration/ biomass ratio
EE	Ecotrophic efficiency of a group is that proportion of the production that is utilized in the system
AFDR	Ash free dry weight assumed is a measurement of the weight of organic material
WW	Wet weight
FO	Frequency of occurrence

2

Literature review

2.1. Organic matter flows in coastal ecosystems

Food web studies cover the organic matter flows in ecosystems and prey-predator interactions as one of the main regulators of population dynamics through the availability of resources and mortality due to predation. Characterization of a food web is an initial step in understanding interrelationships between dynamics and stability of community and ecosystem functioning, which are continuously affected by natural and anthropogenic perturbations (Link, 2002; de Ruiter et al., 2005; Heymans et al., 2014).

Being transitional systems, coastal zone ecosystems need to be described by the importance of passive and active transport types. Passively transported forms of nutrients, organic matter, planktonic organisms and active migratory organisms influence the structure of coastal food webs and ecosystem productivity (Deegan, 1993; Heip et al., 2011; Hyndes et al., 2014). Therefore, biomass exchange between freshwater and marine ecosystems influences production and consumption balance, which characterizes the functioning of coastal ecosystems (Heip et al., 2011).

In a coastal zone, bottom habitats and benthic communities play a principal role for ecosystem productivity. Bottoms covered by submerse macrophytes usually mean high primary production (Schiewer, 2008), that follows classical theories as coastal zones serve as organic matter source for the open sea (Wollast, 1998). Conversely, sandy bottom habitats, characterized by little amount of organic matter and low primary biomass, depend on organic matter flows from areas with higher productivity, i.e. from the sea (Vassallo et al., 2012 and references in it) or from freshwater (Lundberg and Moberg, 2003). Both exposed sandy beaches (up to 5 m depth) and deeper habitats, comprising exposed coastal systems up to 20 m, have been defined as physically stressful environments where communities are regulated mainly by physical factors as wave action, resuspension and sediment transport, while biological interactions are minimal (Defeo and McLachlan, 2005; Myrberg et al., 2010).

The Baltic Sea is characterized by high variety of coastal types (Schiewer, 2008), physical and biological factors which determine primary productivity and contribute to the structures of coastal food webs. Only 9% of the Baltic is shallower than 10 m and might potentially be suitable for benthic macrophytes and microalgae. Otherwise, large sandy areas comprising the southeastern Baltic coasts are characterized by low productivity (Schiewer, 2008). Low primary production in the coastal zones suggests an importance of riverine organic inflows to the Baltic plankton food webs, especially in areas with higher zooplankton diversity and more complex trophic interactions (Rolff and Elmgren, 2000). In the majority of Baltic Sea sub-areas, pelagic production is the dominant energy source, while benthic primary production has only local importance (Elmgren, 1984).

Importance of migratory organisms and their roles in coastal food webs have not been well studied from an ecosystem perspective (Willson and Halupka, 1995; Winemiller and Jepsen, 1998). It is especially important in coastal ecosystems with a significant proportion of seasonally present fish and waterbird species. Therefore, methods as SIA and food web models, could be used to deal with feeding and seasonal migrations and to evaluate the organic matter flows and trophic relationships in coastal food webs.

2.2. Stable isotope analysis in coastal food web studies

2.2.1. Background of applications in coastal studies

Isotope tracer studies have been used widely during the past decades to understand sources and pathways of organic matter flow in aquatic ecosystems (Fry and Sherr, 1989; Mancinelli and Vizzini, 2015). SI methods are among the most powerful tools for the studies of trophic relationships, animal diets, and construction of food webs (Caut et al., 2009; Boecklen et al., 2011; Hoffman, 2016). Moreover, SIA is used to track the organic matter transport and movements of active migrants across isotopic gradients and distinct food webs (Forero and Hobson, 2002). It is important to mention that isotopic studies might be used in more ethical (non-lethal) and practical way (less expensive and less time consuming) than traditional methods (Boecklen et al., 2011). The SIA method might help to solve difficult questions as reconstruction diets of long-extinct species or studies on winter diet of waterbirds those spend whole wintering period in marine waters (Bearhop et al., 2002; Cherel et al., 2005).

In aquatic environment, trophic studies might be problematic due to limited opportunities for direct observations (Duffy and Jackson, 1986; Barrett et al., 2007), high degree of spatial and temporal complexity (Antonio et al., 2012) and diverse potential sources of nutrients and organic matter (Finlay and Kendall, 2007; Lesutienė, 2009). Therefore, ecological studies based on SIA might be effective to estimate temporally and spatially integrated information in various organisms. The isotopic ratios in organisms reflect feeding conditions during a period when particular tissues were synthesized. However, there is some period of time needed for integration of SI of diet objects to consumer tissues. Isotopic half-life is defined as the time required to reach 50% of equilibration with the consumer diet (while complete equilibrium takes much longer). Although there are still much unexplained SI variations within different consumers or their tissues, isotopic half-life period for fish muscle tissue is at least a month and highly depends on body mass; while the period for bird blood is approximately two weeks (Finlay and Kendall, 2007; Vander Zanden et al., 2015).

All applications of natural SI abundance methods depend on variation in isotope ratios in organisms and their environment (Finlay and Kendall, 2007). The $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ ratios are widely used to reconstruct diets and characterize trophic relationships in food webs because SI signatures of consumers predictably reflect the signatures of organic matter assimilated. The $\delta^{13}C$ and $\delta^{34}S$ ratios are strong for source identification, while the $\delta^{15}N$ ratios record trophic information. Moreover, SI values can be used to trace the flow of organic matter through food webs if SI values of different food sources might be distinguished among each other (Fry, 1988; Boecklen et al., 2011). Accurate assessments of extent in source variation are especially critical for studies of energy flow in food webs and use of SIA for migratory animals as well as their trophic position estimation (Finlay and Kendall, 2007).

The wide range of $\delta^{13}C$ ratios in algae at the base of food webs allows inferring different baseline sources, as primary producers in discrete ecosystems may have dissimilar $\delta^{13}C$ values. There are several processes contributing to these differences: preferential loss of ^{12}C during respiration, preferential uptake of ^{13}C enriched compounds during digestion or assimilation, or metabolic fractionation during synthesis of different tissues (review of Michener and Kaufman, 2007). As the $\delta^{13}C$ ratios of consumer reflects their diet within less than 1‰, this ratio is useful in analyzing food webs in systems where food sources are different isotopically, such as C_3 vs C_4 plans, terrestrial vs marine systems, offshore vs coastal systems (Fry and Sherr, 1989; Peterson and Fry, 1987; Michener and Kaufman, 2007). For example, freshwater POM from the Curonian Lagoon is characterized by low $\delta^{13}C$ ratios (to -33.3‰; Lesutienė, 2009), while marine POM vary from -18.6 to -23.5‰ in the Baltic Proper (Rolff and Elmgren, 2000).

The $\delta^{15}N$ ratio is a tracer of the nitrogen cycle and food web interactions. It may be used to estimate trophic position because there is a consistent increase in $\delta^{15}N$ ratios of consumers from food sources (Vander Zanden et al. 1997; Post, 2002). Averaged ^{15}N enrichment is 3.4±1.1‰ per TL (hereinafter - TL), but many authors provide evidences about differences in trophic enrichment factors (hereinafter – TEF) depending on characteristics of consumers and sampled tissues, diet, habitats, seasons. The $\delta^{15}N$ ratios can also allow determination of spatial variation if few distinct food sources are available for particular consumer (Michener and Kaufman, 2007).

The main use of $\delta^{34}S$ ratios in coastal food web studies is differentiation of terrestrial and marine sources of organic matter due to large contrast in $\delta^{34}S$ values between the environments (Connolly et al. 2003; Finlay and Kendall, 2007). Moreover, sulfides from benthic bacteria and microphytobenthos lead to low $\delta^{34}S$ values in benthic organisms (Fry and Sherr, 1989; Fry and Chumchal, 2011). Strong discrimination against heavy (^{34}S) isotope in sulfate-reducing bacteria of anoxic sediments leads to lower $\delta^{34}S$ values in infaunal benthic organisms than in organisms inhabiting oxic sediments or a water column (Fry and Chumchal, 2011; Karube et al., 2012; Proulx and Hare, 2014). This difference is expected to propagate to upper TLs. Therefore, $\delta^{34}S$ might be useful to distinguish different food sources for consumers (Connolly et al., 2004; Croisetière et al., 2009). Although $\delta^{34}S$ allows a great improvement for trophic studies, the number of studies using $\delta^{34}S$ analysis or all three SI remains limited in coastal marine ecosystems (Mancinelli and Vizzini, 2015).

Use of SIA depends on the extent of temporal and spatial isotopic variation at the base of the particular food web (review of Finlay and Kendall, 2007). Previous analysis of $\delta^{13}C$ and $\delta^{15}N$ in the Baltic Sea revealed that isotopic differentiation between the food web compartments might be complicated because of large variation in SI values in the primary sources of organic matter due to riverine discharge and nitrogen-fixing cyanobacteria blooms (Rolff, 2000; Rolff and Elmgren, 2000; Antonio et al., 2012; Lesutienė et al., 2014a). Using of additional SI such as $\delta^{34}S$, it might be possible to distinguish food sources of consumers in complex ecosystems where endpoints have not been identified unambiguously by $\delta^{13}C$ and $\delta^{15}N$ (e.g. Fry, 2013). However, the applicability of $\delta^{34}S$ has not been widely tested in food webs of the Baltic Sea. A single study using $\delta^{34}S$ combined with $\delta^{13}C$, $\delta^{15}N$, which has been carried out by Mittermayr et al. (2014), provided a differentiation of primary sources in the food web of a seagrass *Zostera marina* system, while identical $\delta^{13}C$ values of seagrass and epiphytes did not provide a distinction between them. The distinct values among sources were determined by different producer capability to obtain sulphur, i.e. epiphytes obtain sulphur from seawater sulfate, while seagrass at least partially obtain their sulphur from the interstitial waters of the sediment. Application of $\delta^{34}S$ as addition to $\delta^{13}C$ and $\delta^{15}N$ for upper TL organisms and its possibilities to differentiate them to the consumer diet assessment is still missing for the Baltic Sea.

2.2.2. Assumptions and limitations

The general interpretation of isotopic data demands information on the rate at which isotopes are incorporated into different tissues and species (Del Rio and Carleton, 2012; Vander Zander et al., 2015). Animal tissue does not immediately reflect the isotopic composition of the diet objects, but integrates information over some period. Therefore, interpreting food webs needs to assume that the isotopic composition of animal tissues is in equilibrium with diet. For ectotherms, isotopic turnover rate generally increases with body size. For birds, the relationship with body mass involved different allometric slopes and intercepts for different tissues (Vander Zander et al., 2015). Despite some empirical patterns, there are still unexplained variation in evaluation of SI turnover rates, indicating that there are more uncertainty and important unmeasured factors.

Variations of lipid content within and among tissues of organisms might influence $\delta^{13}C$ values significantly and result in a misguided interpretation of trophic interactions. Therefore, standardizing lipid content using either chemical lipid extraction or mathematical normalization technique has been encouraged by various authors (e.g. McConnaughey and McRoy, 1979; Post et al., 2007; Sweeting et al., 2006). During chemical lipid extraction, polar organic solvent mixtures of chloroform and methanol are used to reducing lipids to uniformly low level in a sample; however, that results in the loss of some non-lipid compounds and affects $\delta^{15}N$ value in the sample. On purpose to have correct SI values, a more expensive separate $\delta^{13}C$ and $\delta^{15}N$ analysis of untreated and lipid-extracted samples should be provided (Sweeting et al., 2006). Therefore, mathematical lipid correction is considered efficient method to eliminate bias in comparisons of consumers and prey objects (Post et al., 2007; Smyntek et al., 2007). Although there is still no consensus of the most effective mathematical normalization technique (Post et al., 2007 and references in it), it is important to integrate lipid correction into analysis, especially for interpretation of trophic interactions (Sweeting et al., 2006) and comparison of results to other studies (Smyntek et al., 2007).

The TEF reflects differences in isotopic composition between a consumer and its diet (Del Rio and Carleton, 2012; Vander Zander et al., 2015). For carbon, TEF is estimated about 1‰, while for nitrogen it is 3-4‰. TEF for sulfur is considered nearly zero (Peterson and Fry, 1987; McCutchan et al., 2003). However, TEF may vary depending on a consumer’s nutritional status, diet quality, size, age, dietary ontogeny, tissue, elemental composition, and isotopic value of diet objects. Caut et al. (2009) proposed a method to calculate TEF for carbon and nitrogen from diet isotopic ratios for each animal consumer class and type of tissue. Similar estimations for sulfur are still missing. Therefore, understanding and estimating TEF factors remains problematic and sustain the assumptions for further analysis of SI data, especially assessment of the TLs of consumers.

The SI mixing models are used to quantify source contributions to a diet of consumers (Fry 2006; Layman et al. 2012). Isotopic signatures of consumers and their food sources, values of TEF are needed for SI mixing models. However, some optional external information about gut content compositions, prey abundance or etc. also might help to incorporate data to Bayesian mixing models and to create realistic models (Parnell et al. 2010; Layman et al. 2012). However, the Bayesian mixing approach allows calculation of source contributions even when a model is very unlikely to satisfy point-in-polygon for every consumer (Parnell et al. 2010). Therefore, only potential preys should be used for the evaluation of consumer diet. Moreover, consumers being outside the mixing polygon should be omitted from mixing models using a quantitative tool for point-in-polygon. This tool allows an *a priori* evaluation of mixing models, by indicating when the data are unlikely to create the mixing geometry needed for a logical model (e.g. Monte Carlo simulation) (Smith et al., 2013).

Greater exploration of isotopic variation in the environment lead to many new applications in ecological studies. Moreover, increased knowledge of isotopic variability at the base of food webs, especially in aquatic ecosystems, provides an opportunity to re-evaluate poorly tested assumptions and improve ordinary, established methods. It is important to mention, that SI techniques are always the best in a combination with other methods (Finlay and Kendall, 2007).

2.3. Ecosystem-based modeling approach

Increasing anthropogenic activity and its pressure to ecosystem functioning and species interactions have become important issues in marine ecosystem. Food web models are used as simplified representations of natural systems and might help understand how biodiversity and ecosystems respond to various impacts and changes (Heymans et al., 2014). Assessments made using single-species models are not usually sufficient to ensure a sustainable use of marine environment because usually they ignore the larger ecosystem context and cannot take into account openness for immigrations, trophic cascade effects, etc. (Möllmann et al., 2014).

Elmgren et al. (2015) has overviewed Baltic environmental management and stated that, although there were many effective solutions of environmental problems in the following 40 years in the Baltic Sea, ecosystem-based management is still missing approach. Majority of environmental problems are still treated separately due to a lack of understanding of ecosystem processes and a strategy for combined environmental problems and solutions. Meanwhile, the ecosystem-based approach requires that the interactions of all ecosystem compartments, including humans, should be considered in the analysis and management process (Mölllmann et al., 2014; Elmgren et al., 2015).

ECOPATH with ECOSIM (Polovina, 1984; Christensen and Walters, 2004) is a suitable tool to investigate aquatic ecosystem functioning and analyze properties that are not readily measured. It is among the most powerful multi-species considerations included in the stock assessment approaches for the major fisheries resources globally. Moreover, it has the user-friendly interface, constant improvements to the software and is currently the most widely utilized approach worldwide. Other methods available for assessing the impacts of interactions between species and fisheries cannot represent full trophic spectrum of a network (an extensive overview of approaches to modelling multispecies/ ecosystem effects is given in Plagányi, 2007).

The descriptive mass balance food web module ECOPATH is the key initialization step in the modelling process, from which further temporal and spatial predictions can be simulated with ECOSIM and ECOSPACE modules for policy scenario testing (Christensen and Walters, 2004). ECOPATH has been the widely applied to represent food webs in estuaries (Sandberg et al., 2000; Tecchio et al., 2015), lagoons (Pranovi et al., 2003), coastal areas (Xu et al., 2011), ocean ecosystems (Shannon et al., 2009), and inland water ecosystems (Angelini et al., 2010). In the Baltic region, the ECOPATH with ECOSIM approach has been used describing the structure of the food webs of the Baltic Sea and its sub-basins (Elmgren, 1984; Elmgren and Hill, 1997; Sandberg et al., 2000; Harvey et al., 2003). The model for the central Baltic Sea has revealed long-term dynamics forced by fisheries and environmental drivers and promoted the holistic approach for ecosystem-based management (Tomczak et al., 2013).

Five geographically different coastal ecosystems across the southeastern Baltic, including the Curonian Lagoon and a part of the Lithuanian coastal waters, have been compared by Tomczak et al. (2009). Unified model structure of twelve functional groups in each network allowed comparing the trophic interactions in the ecosystems with different species diversity and abundance. All ecosystems were highly productive and channel a major part of primary production into detritus. The Lithuanian coastal systems were characterized with the highest phytoplankton primary production among other studied systems because high primary production of the lagoon is partly transported to the coastal zone.

2.4. Food web studies in the Lithuanian coastal waters

Numerous ecological studies have been focused on trophic aspects of organisms and their role in the food web in the Lithuanian coastal zone. Research on plankton and benthos has been mostly based on taxonomical diversity, spatial and temporal distribution patterns, and factors contributing to mentioned peculiarities (Gasiūnaitė et al., 2005; Olenin and Daunys, 2004; Bučas et al., 2009; Vaičiūtė, 2012). Although that information usually does not directly reveal the significance of mentioned compartment as lower TLs to the food web, it might be used for the food web reconstruction and analysis.

Residency periods and trophic peculiarities of migratory species, including fishes and waterbirds, are well characterized. The research on them relies mostly on scientific or commercial fish catches, visual bird census and specific data such as gut content analysis. Studies based on fish gut content analysis reveal diet variability between different fish species as well as pronounced ontogenetic differences (Bubinas and Vaitonis, 2003; Stankus, 2003; Skabeikis and Lesutienė, 2015; Bacevičius, unpubl. data). Some of these data were used for the quantitative assessment of the most important feeding grounds of selected benthic fish species in the Lithuanian Economic Zone (Šiaulys et al., 2012).

Dietary studies of waterbirds have been mostly based on the gut contents of bycaught specimens during wintering season in the Lithuanian coastal zone (Žydelis, 2002) or collecting pellets during breeding period in a cormorant colony in the Curonian Spit (Pūtys and Zarankaitė, 2010). In winter, benthivorous ducks mostly feed on macrozoobenthos, mostly bivalves. Long-tailed duck *Changula hyemalis* is present within entire Lithuanian coastal zone but prefers feeding in the hard-bottom habitat (Švažas, 1993; Žydelis and Ruškytė, 2005), while velvet scoter feeds almost exceptionally in the sand bottom habitat in the southern part of the Lithuanian coastal zone (Žydelis, 2002). Piscivorous divers and grebes mostly feed on smelt and pelagic fish (Žydelis, 2002). Breeding great cormorant forages on freshwater fishes, but approximately 7-13 % of their diet is obtained from marine environment; in total at least 25 fish taxa are used as prey. The impact of cormorants to fishery was studied in the Curonian Lagoon (Žydelis and Kontautas, 2008; Pūtys and Zarankaitė, 2010; Pūtys, 2012).

Food sources for various organisms and their trophic positions were evaluated using the SI technique. Majority of SI studies have been performed in the Curonian Lagoon; therefore, the general knowledge of isotopic variability in the lagoon is much broader, compared to that for the coastal zone of the Baltic Sea. Lesutienė J. (2009) determined SI variability in particulate organic matter (POM) within the lagoon, which was generated by autochthonous phytoplankton and riverine runoff. SI values in primary consumers as mesozooplankton, mysids and chironomids showed much stronger response to POM isotopic fluctuations than those in mollusks. The study also demonstrated that in the macrophytes-detritus food chain transfer efficiency (hereinafter – TE) of organic matter in mysids increased after their diet shifted from herbivorous to carnivorous.

Lesutienė et al. (2014a) determined seasonal patterns in δ^{13}C and δ^{15}N values of POM and consumers in the Curonian Lagoon. Seasonal variation of external sources in isotopic contents of POM entering and leaving the Curonian Lagoon was estimated also by Razinkovas-Baziukas et al. (2015). The δ^{13}C values in POM decrease during March-April period, reaching minimum -33‰ and coinciding with large discharges of Nemunas River. During summer, δ^{13}C values in POM is approx. -30‰, while high variation in the POM values is observed in September. During further months until the development of ice cover, the $\delta^{13}C$ values remain relatively stable. Moreover, autochthonous POM is isotopically indistinguishable from riverine POM in spring and autumn due to high river discharge, great proportional contribution of riverine POM and mixing processes among riverine, estuarine and marine sources. Only in summer, POM from the Nemunas River and Curonian Lagoon might be differentiated using $\delta^{13}C$ analysis (Lesutienė et al., 2014a; Razinkovas-Baziukas et al., 2015). The influence of riverine water on the Lithuanian coastal zone was evident by the low $\delta^{13}C$ values in particulate organic carbon, which indicated a strong terrestrial influence given that terrigenous matter is relatively depleted in ^{13}C ($\delta^{13}C > -25‰$) compared to marine organic matter released from phytoplankton ($\delta^{13}C \sim -20‰$) (Fry and Sherr, 1989; Korth et al., 2013).

Isotopic ratios of primary consumers in the lagoon, especially among fast-growing planktonic and nectobenthic crustaceans and chironomids, reflect seasonal changes of POM SI values. The cyanobacteria blooms account for 50-80% of secondary production of benthic and pelagic consumers illustrating the utility of SI for tracking the cyanobacteria signal (Lesutienė et al., 2014a). Pūtys (2012) used SIA for differentiation of freshwater and marine fishes as food sources for great cormorant breeding between the lagoon and the Baltic Sea. The mixing model results were comparable to those obtained by pellet analysis method showing that the contribution of marine fishes to cormorant diet composition was approximately six times lower than contribution of freshwater and diadromous fishes. Rakauskas et al. (2012) determined a significant contribution of invader round goby *Neogobius melanostomus* in the diet of predatory fishes and great cormorant.

SI studies performed in the Baltic Sea along the Lithuanian coast were mostly designed to answer specific questions. Lesutienė et al. (2014b) used the SI mixing model of food sources of non-indigenous prawns *Palaemon elegans* and estimated that more than 60% of assimilated carbon derives from the pelagic food chain, while the remaining portion of assimilated carbon originates from macroalgae. Lujanienė et al. (2015) measured $\delta^{13}C$ values in sediments, which varied between the stations in the coastal zone and open sea confirming impacts of terrestrial and freshwater on organic carbon.

The first Lithuanian coastal food web model, which included compartments from primary producers to the top predators, was compiled for the stony bottom area. It estimated the pelagic primary production as twice higher than one of benthic algae. However, this study mostly was used for the evaluation of an ecological role of *Furcellaria lumbricalis* in a part in rocky bottom habitats and did not provide estimates for the entire coastal zone (Tomczak et al., 2009).

Several models of a food web were constructed for the Curonian Lagoon. The first ECOPATH model consisting of nine compartments revealed qualitative analysis of the food web (Razinkovas and Zemlys, 2000). It was used to investigate the food web structure and organic matter flows in the littoral zone of the Curonian Lagoon (Jankauskienė, 2001; Razinkovas et al., 2005). Ertürk et al. (2008) developed an integrated model linking a nutrient flow and the trophic network of the Curonian Lagoon. The Nutrient Phytoplankton Zooplankton Detritus (NPZD) model consisted of a transport module (ESTAS) and ecological module that represented the biogeochemical cycles (ALUKAS). The combination complemented ECOPATH model with 23 compartments and provided the possibility to analyze the system using characteristics of both models. This approach demonstrated a variation in flow of nutrients and plankton and revealed bottom-up control approach for the ecosystem.

Reviewed trophic models for the Lithuanian coastal ecosystems have not implemented organic matter flows between the riverine, lagoon and open Baltic ecosystems, although passive and active organism migrations are important characteristics of coastal transitional systems (Deegan, 1993; Heip et al., 2011). While the previous studies of the Lithuanian coastal zone food web have covered only the distinct trophic relationships or discrete food webs of the transitional waters (e.g. Razinkovas and Zemlys, 2000; Ertürk et al., 2008; Tomczak et al., 2009), there is still a need for research covering the complete trophic network of the Lithuanian coastal zone.

3

Study area

3.1. Characterization of location, hydrological and physical parameters

The study area covers a stretch of 90.6 km along the Lithuanian coast in the south-eastern part of the Baltic Sea (Fig. 3.1) (Gudelis, 1967). In the Baltic Sea, the complexity of physical and biological processes result in clear gradients of biological and chemical parameters between the coastal zone and the open sea (Lessin and Raudsepp, 2007; Lessin et al., 2009). A width of the Lithuanian coastal zone might be limited to depths of 20 meters reaching 2 to 9 km from the coastline (Olenin and Daunys, 2004; Leppäranta and Myrberg, 2009). It is defined by the zone of influence of wind-generated waves on the sea bottom (Leppäranta and Myrberg, 2009), the depth of summer thermocline (Olenin and Daunys, 2004), distribution of macrophytes, variety of bottom substrates and the highest benthic species diversity (Olenin, 1997; Bučas, 2009). Thus, the coastal zone covers area of 335 km^2 (Gelumbauskaitė, 1998), including hydrodynamically active zone covering the mobile sands at depths 0.5-6 m (Olenin and Daunys, 2004).

Dominated northwardly currents spread the outflow waters along the coastline, thus the northern part (Palanga) of the coastal zone is more influenced by the estuarine plume than the southern part (Juodkrantė) (Fig. 3.2). The highest frequency of occur-

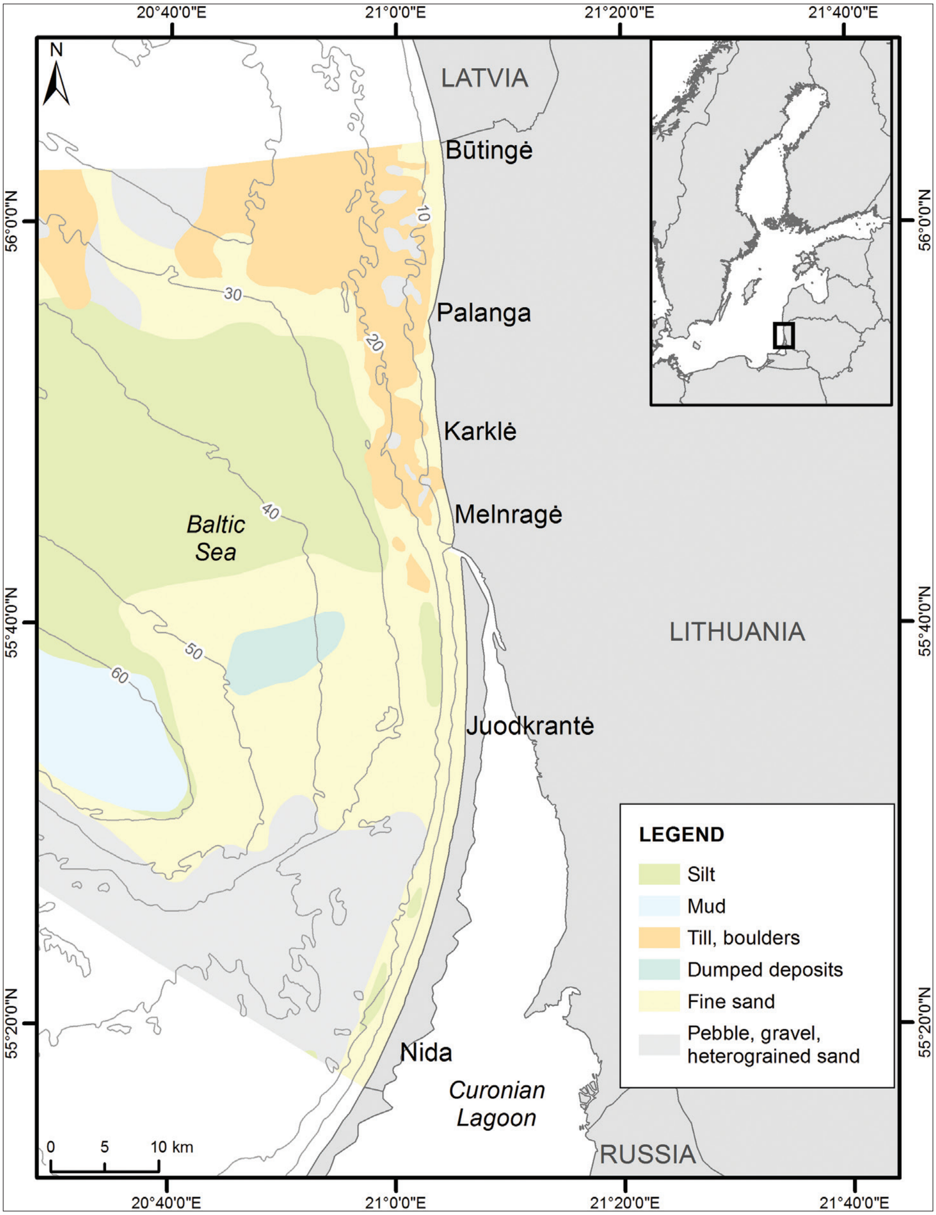

Figure 3.1. The Lithuanian coastal zone of the Baltic Sea

rence (70-100%) of the plume is observed 10 km northwards, 6 km westwards and 4 km southwards from the outflow of the lagoon, while other part of the Lithuanian Economic Zone is affected much less (frequency of occurrence of the plume <10%; Vaičiūtė, 2012).

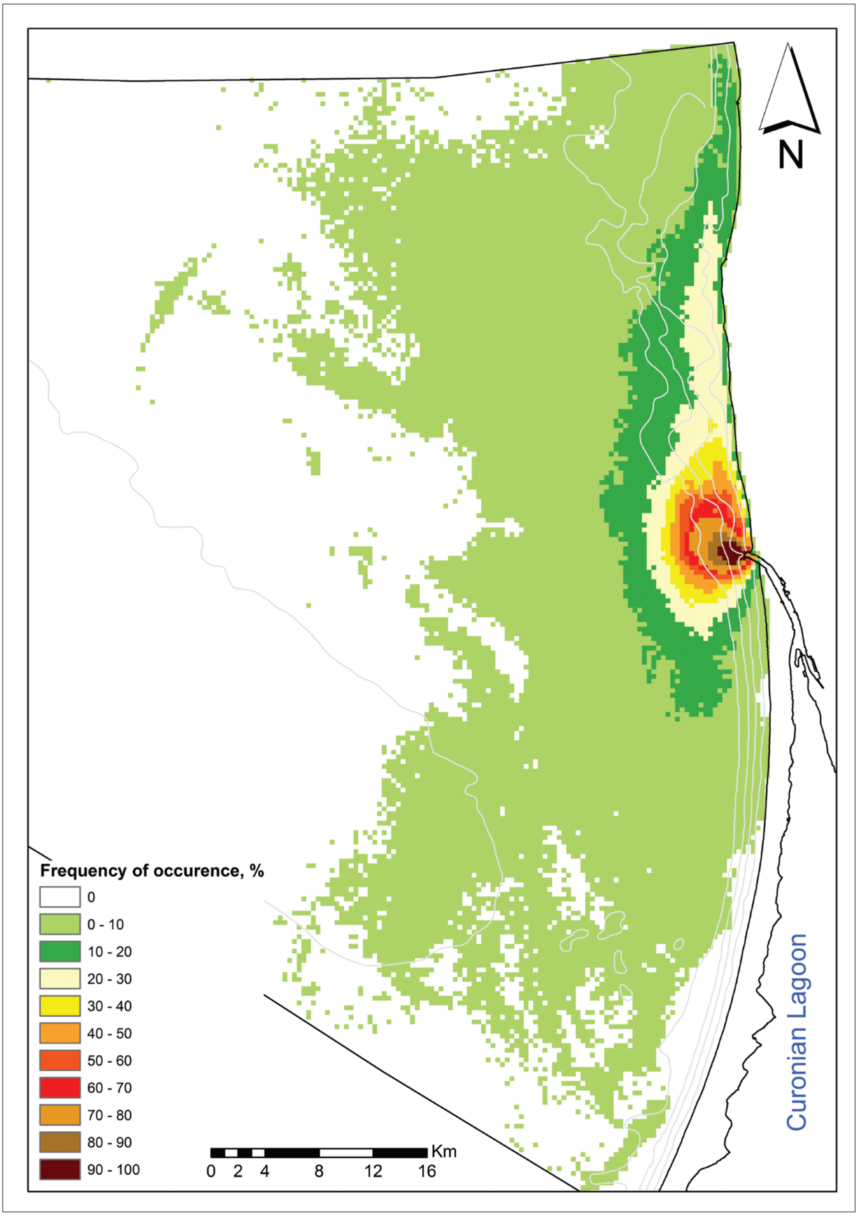

Figure 3.2. Spatial distribution and frequency of occurrence of the estuarine plume during the summer period of 2005-2011 in the Lithuanian Economic Zone (Vaičiūtė, 2012)

The high-energy open Lithuanian coast influenced by the interaction between the mesohaline (7-8‰) waters of the Baltic Proper and oligohaline-to-freshwater (0-3‰) of the hypereutrophic Curonian Lagoon (Olenin and Daunys, 2004; Schiewer, 2008). Therefore, the salinity in the area is variable and could be attributed to the alfa-oligo-

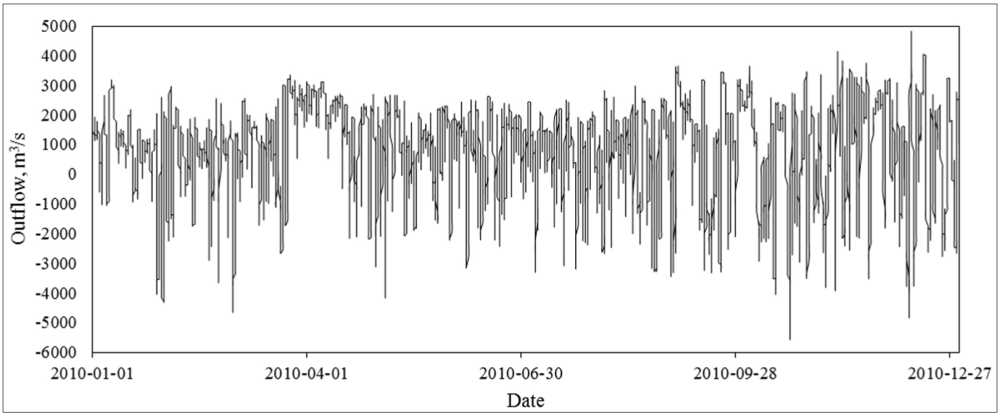

Figure 3.3. Outflow in 2010 through the Klaipeda strait from the Curonian Lagoon to the Baltic Sea, estimated by hydrodynamic model (according to Umgiesser et al., 2016)

haline type (PSU < 7‰) (Olenin and Daunys, 2004; Schernewski and Wielgat, 2004). The freshwater Curonian Lagoon, impacted by the Nemunas River discharge, influences the coastal zone of the Baltic Sea (Fig. 3.3). The positive outflow from the lagoon means transport of freshwater and organic material to the coastal zone, while the negative outflow values show irregular inflows to the lagoon from the Baltic Sea. Annual outflow from the lagoon to the coastal zone is positive meaning that freshwater and organic material is transported to the coastal zone; it reached 759 m^3/s in 2010 (Umgiesser et al., 2016), the year when a majority of samples for this study was collected.

The northern and southern parts of the Lithuanian coastal zone differ by the bottom types. Sandy bottoms dominate in the southern part of the coastal zone, while the northern part is more heterogeneous with patches of boulders and pebble scattered across the sandy habitats. In total, sandy and mixed bottom types occupy approximately 80 and 20 % of the total area accordingly (Bitinas et al., 2004).

3.2. Description of communities

3.2.1. Plankton community

In the Lithuanian coastal zone, the plankton food web compartments as phytoplankton, zooplankton and protozoans have a strongly expressed seasonal dynamics, typical for boreal areas. They also include freshwater taxa passively brought from the rivers and the Curonian Lagoon, which make a significant part of the total number of plankton species in the coastal zone (Gasiūnaitė et al., 2005).

Total phytoplankton biomass and proportions of different taxa vary seasonally in the community of the coastal zone. The lowest phytoplankton biomass (up to 1 mg/L) with the dominance of diatoms is in late autumn and winter. The biomass peak (10 mg/L) in April coincides with dominance of dinophytes. In summer phytoplankton biomass reaches approx. 2 mg/L; cyanophytes dominate within the community in July-August (Gasiūnaitė et al., 2005; Vaičiūtė, 2012).

Mesozooplankton (copepods, cladocerans, ostracods, rotifers) is the dominant group in the Baltic Sea in terms of zooplankton biomass, In the Lithuanian coastal zone, rotifer biomass (0.17 µgC/L) is higher than other zooplankton groups (less than 0.06 µgC/L) (Biodiversity in the Baltic Sea, 2009 and references therein, Strake et al., 2000). Biomass of protozoans (ciliates) is higher than mesozooplankton and reaches 5.5 µgC/L in the Lithuanian coastal zone (in April and July; Grinienė et al., 2015).

3.2.2. Benthic habitats and communities

Different bottom types determine the distribution of benthic communities in the Lithuanian coastal zone. In total, seven main benthic habitats with typical benthic communities could be outlined. The northern zone is characterized by five benthic habitats and communities which biomasses are indicated for the period of 1980-2003 (Olenin and Daunys, 2004; Bučas, 2009):

- The mobile sand habitat occupying the uppermost sublittoral from the shoreline to approximately 6 m depth. Regarding permanent sand transfer due to wave and current action and absence of macrophytes, benthic species diversity and biomass is low (from 3 to 93 g/m^2); burrowing infaunal (*Marenzelleria viridis, Pygospio elegans, Macoma balthica*) and actively swimming nectobenthic (*Bathyporeia pilosa, Crangon crangon*) forms are present.
- Soft bottom habitat from 5 to 30 m depth are occupied by about 20 species with the biomass dominanted by bivalve *M. balthica and/ or Saduria entomon*. Other characteristic species are typical coastal infaunal dwellers: polychaetes, bivalves *Mya arenaria*, crustacean *Corophium volutator*. Total biomass ranges from 0.5 to 123 g/m^2.
- Stony bottom habitat within the euphotic zone (the depth ranges from 5 to 16 m). The dense colonies of macroalgae, mainly *F. lumbricalis,* create microhabitats for diverse macrofauna community, especially for phytophagous *Idotea balthica* and nectobenthic species such as gammarids and mysids. Other characteristic species are *Mytilus* sp*., Amphibalanus improvisus, Hediste diversicolor, Hydrobia* sp*., Gammarus salinus, Jaera albifrons, C. volutator* and oligochaetes. The total benthic community biomass varies from 47 to 5735 g/m^2.
- Stony bottom habitat in the aphotic zone (15-20 m depth) is characterised by *Mytilus* sp. and *A. improvisus*. Besides these two species other characteristic

invertebrates are *J. albifrons, H. diversicolor, Gammarus* sp. Total biomass ranges from 3515 to 5530 g/m^2.
- Habitat of mixed bottoms within approximately 5 to 25 m depth range. Species composition and dominant species vary depending on the character of the bottom sediments. The blue mussels and barnacles form dense colonies on boulders and stones, attracting associated fauna as *H. diversicolor, G. salinus, J. albifrons* and *C. volutator*. The patches of gravel and pebbles are inhabited by polychaetes. The larger pebbles are suitable for *A. improvisus* and *Mytilus* sp., however, the total species richness is lower than on boulders. Sandy patches are occupied by *M. balthica* and *M. viridis*. The total biomass varies from 0 to 6060 g/m^2.

The southern zone situated along the Curonian Spit is defined by two habitats with particular benthic communities:

- The mobile sand habitat (characteristics are the same as in the northern zone);
- The soft bottom habitat within the depth range 10 – 30 m. It is more monotonous than the same habitat in the northern area. Dominant species is bivalve *M. balthica*. Other benthic macrofauna are polychaetes, *Mya arenaria, Cerastoderma glaucum*. The total biomass varies within 5 – 314 g/m^2.

Benthic communities of the coastal zone are changing continuously. There were changes in bivalve species diversity and biomasses in the soft bottom habitat where proportion of dominant *M. balthica* decreased from 56-96% to 21-63% of total benthos biomass from period of 1996-2002 to 2012-2016 within the depth range 13-15 m in the southern part (Juodkrantė). Other bivalve species have become more abundant: biomass of *M. arenaria* changed from 2-18% to 5-57%, while biomass of *C. glaucum* increased from 0-17% to 2-48% of the total benthos biomass between these two periods accordingly (State monitoring database of the Marine Research Department under the Environmental Protection Agency; Solovjova, unpubl.). Moreover, biomass and coverage of *Mytilus* sp. in the stony bottom habitat sharply decreased after 2010 (Stupelytė and Šiaulys, 2015).

3.2.3. Fish community

There are 63 fish species found in the Lithuanian Baltic Sea coastal zone (Repečka, 2003b), which could be grouped into five ecological fish guilds contrasting by different movement characteristics and residency periods in the coastal zone (classification adopted from Elliott et al., 2007):

- marine migrants entering coastal area regularly for foraging purposes,
- semi-residents spending their entire life cycle locally but capable of movement along the coastal zone,

- freshwater stragglers entering coastal area regularly for foraging purposes during warm season,
- anadromous fish species passing the coastal zone during migration from the sea into rivers to spawn,
- catadromous fish species passing the coastal zone during migration from freshwater to the sea to spawn.

In spring, marine pelagic species make up the bulk of the coastal fish community. From the end of spring to the middle of autumn, freshwater fish species from the Curonian Lagoon compose a substantial part of the coastal community that also are comprised of benthic marine migrants (Repečka et al., 2003). In winter, marine migrants, semi-resident fishes, and anadromous European smelt *Osmerus eperlanus* dominate in the coastal fish community (database of Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania).

Distribution of planktivorous fishes mostly depends on hydrographical conditions (e.g. freshwater plume extent) and zooplankton community (Rudstam et al., 1992), while the feeding and distribution of benthophagous fishes is related to benthic habitats (Statkus, 2000). The highest fish abundance and biomass was identified in the northern part of the coastal zone, which is important due to the high quality feeding grounds for marine and anadromic benthic and benthopelagic fishes (Repečka et al., 2003; Šiaulys et al., 2012), and for freshwater fishes in summer (Piščikas, 2000), as well for the reproduction of marine fishes (Repečka et al., 2003; Šaškov, 2014). However, regarding sharply decreased biomass of *Mytilus* sp. (Stupelytė and Šiaulys, 2015), the availability of food for benthivorous fishes might have been decreased recently.

3.2.4. Waterbirds

As the Baltic Sea is one of the most important wintering sites for waterbird populations within the Western Palearctic area, from November to April the Lithuanian coastal zone serves as a wintering area for internationally significant concentrations of benthivorous ducks and piscivorous waterbirds (Durinck et al., 1994; Vaitkus, 1999; Žydelis, 2002). However, over the last two decades, long-tailed duck *Clangula hyemalis* experienced decline from 30.000 to 400 wintering individuals, while velvet scoter *Melanitta fusca* declined from 40.000 to 8.000 individuals in the Lithuanian coastal zone (Švažas, 2001; database of Lithuanian Ornithological Society). Abundance of wintering piscivorous divers (black-throated diver *Gavia arctica* and red throated diver *Gavia stellata*); species ratio estimated as 1:10, respectively) was fluctuating from 40 to 900 individuals with a decreasing tendency during the last two decades. Abundance of great crested grebe *Podiceps cristatus* fluctuates from 500 to 3.300 individuals; the total number is considered stable (Sorokaitė et al., 2007;

Raudonikis and Sorokaitė, 2011). Common guillemot *Uria aalge* is a regular but not numerous wintering species in the coastal zone, though solitary individuals or small flocks are recorded frequently (Švažas, 1993; DENOFLIT, 2012).

The big colony comprising 3000 pairs of piscivorous great cormorant *Phalacrocorax carbo sinensis* and 290 pairs of grey heron *Ardea cinerea* is located in a forest between the Curonian Lagoon and the Baltic Sea (Žydelis and Kontautas, 2008; Pūtys and Zarankaitė, 2010). Breeding birds are present within and around the colony from late February until the middle of October (Švažas et al., 2011; Žydelis et al., 2002a).

3.3. Fishery

Fish stocks of the Lithuanian economic zone (LEZ), including the coastal zone, are the ones of the largest in the southeastern Baltic Sea (Repečka, 2003b). In the coastal zone, annual catches varied from 270 to 590 between 2002 and 2011. Atlantic cod *Gadus morhua*, European smelt and Baltic herring *Clupea harengus membrus* dominate the coastal catch, while marine benthic fishes and freshwater fishes were less numerous (Fig. 3.4; database of Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania).

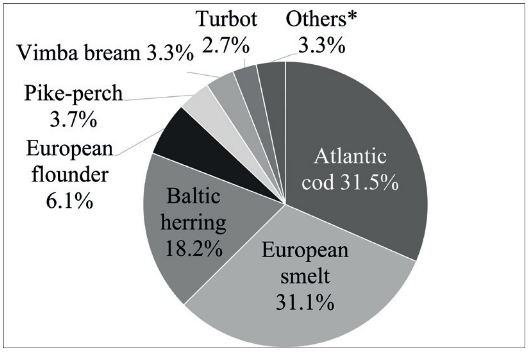

Figure 3.4. Mean fish catch composition during 2002-2010 in the Lithuanian coastal zone (data from Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania). Others* include twaite shad, Atlantic salmon, bream, European perch, garfish, and European whitefish.

Atlantic cod dominates the catches in the Lithuanian coastal zone (31.5 % of total fish catches; Fig. 3.4). It is known that cod prefers open marine areas with higher salinity, thus the distribution in different depths of the Lithuanian LEZ depends on seasonal variability of temperature and salinity (Bacevičius, unpubl.). The highest species abundance is between 30 and 59 meters all year round, while in the coastal zone (<20 meters depth), mainly young cods (2-3 y) are present during the period of August-November due to disruption of thermocline. Regarding to the gut content analysis, the species diet consists mainly of marine pelagic fish species as Baltic herring and Baltic sprat *Sprattus sprattus*, crustaceans *S. entomon*, gammarideans, etc. (Bubinas, 1994; Šiaulys et al., 2013; Bacevičius, unpubl.). However, the cod impact on the coastal food web is difficult to evaluate due to several reasons. First, the species is highly mobile, therefore, even the diet (based on stomach analysis) of individuals caught in the <20 m isobate area does not necessary correspond to the invertebrate community found in these locations (Šiaulys, 2013). Secondly, this zone is not suitable habitat for longer foraging of this species due to the low salinity. Thirdly, the main diet objects are more abundant offshore than in the coastal zone, that complicates evaluation of the proportions of different prey objects foraged either in the coastal zone or offshore. For these reasons, this species was excluded from the further analysis.

European smelt commercial catches contribute to 31 % of cumulative annual landings. However, due to the variation in spawning success, climate related hydrological factors and status of predatory fish populations in the southeastern Baltic Sea (Švagždys, 2010), the catches have fluctuated sharply from 18 to 280 tons on annual basis over two last decades. However, the smelt catches are highly seasonal (making up to 90 % of all fish catches in winter) (Fishery Service under the Ministry of Agriculture of the Republic of Lithuania).

4

Material and Methods

Two main approaches were used to study the food web of the Lithuanian coastal zone: measurements of SI ratios in food web compartments and ECOPATH modelling (Fig. 4.1).

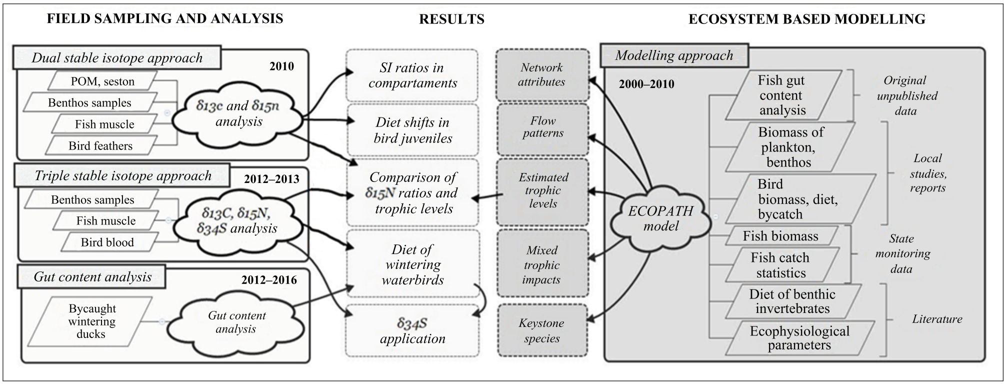

Figure 4.1. General scheme of methods used for the reconstruction the food web structure and quantification of trophic flows. Numbers indicate years for field sampling (SIA) and the period represented by data used in the ECOPATH model.

Analyses of gut contents of wintering benthivorous ducks were performed to compare diet compositions with those evaluated by SIA mixing models. The approaches of SI and modelling were combined when comparing the δ^{15}N ratios of consumers and their tropic levels estimated using the ECOPATH model. (Fig. 4.1).

4.1. Stable isotope analysis

4.1.1. Sample collection and preparation

Samples for SIA were collected during two periods at three sites along the Lithuanian Baltic Sea coast. Biological materials from particulate organic matter (POM) to bird tissues were analysed for δ^{13}C & δ^{15}N ratios and δ^{13}C & δ^{15}N & δ^{34}S ratios (in total 429 and 163 samples, accordingly) (Table 4.1, Fig. 4.2).

Table 4.1. **Types and number of samples, sampling dates, applied SIA.**

Sample type	Number of samples	Sampling period	Method
Plankton	83	Apr–Oct 2010	Measurements of δ^{13}C and δ^{15}N ratios
Benthos	109*		
Fish muscle	228		
Bird feathers	9**		
Benthos	98*	Nov 2012–Mar 2013	Measurements of δ^{13}C, δ^{15}N, and δ^{34}S ratios
Fish muscle	33*		
Bird blood	32		

*Each sample represents several pooled individuals.
**Represents a number of individuals used for multiple sampling, i.e. few samples were taken from different feather part of each individual.

Samples collected during April-October 2010 in different coastal sites were analyzed for dual SIA. Detailed sampling information is given in Table 4.2 and Fig. 4.2.

Samples collected during November 2012 – March 2013 were analyzed for triple SIA. Detailed sampling information is in Table 4.3 and Figure 4.2.

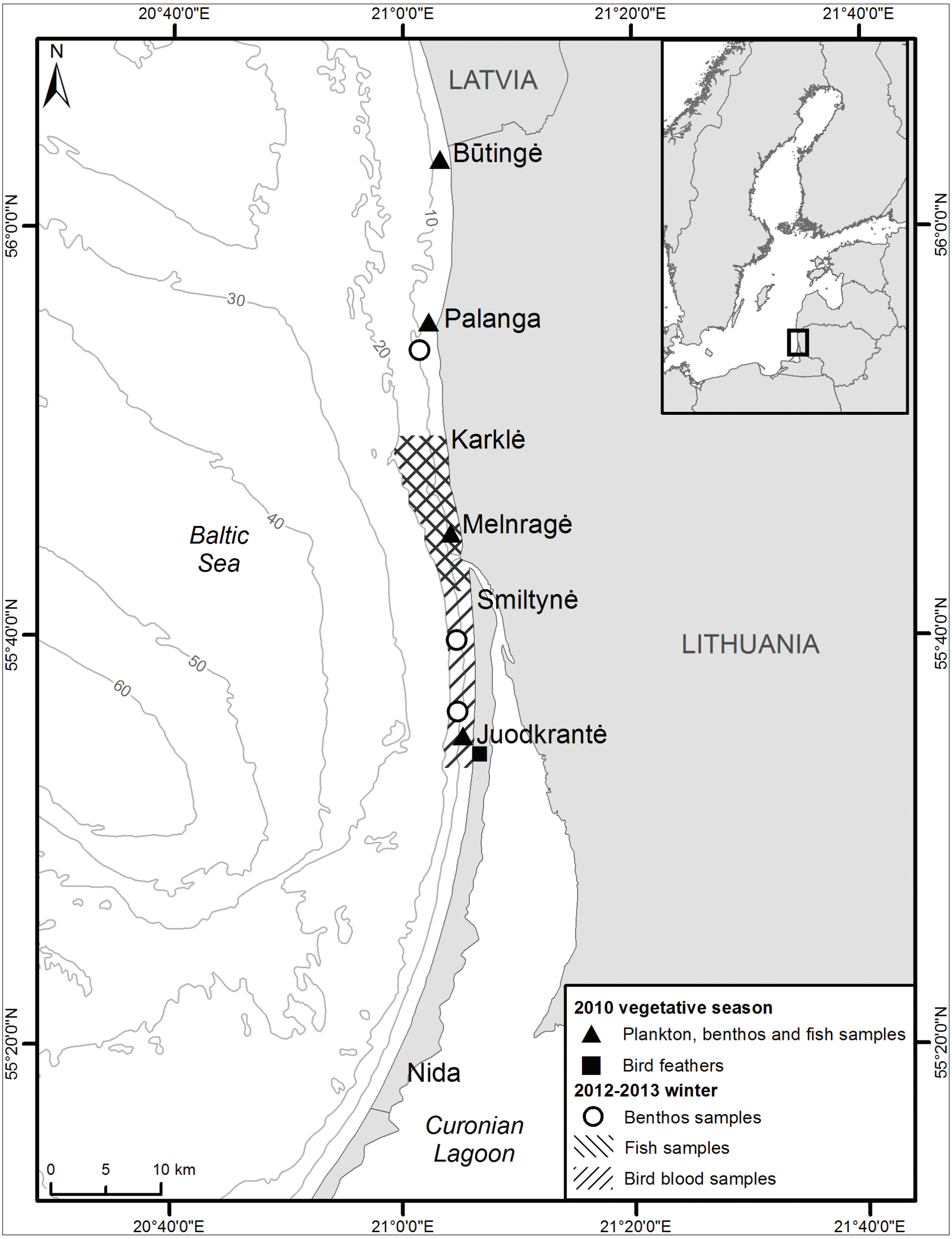

Figure 4.2. Sampling locations in the Lithuanian coastal zone.

Table 4.2. **Information on plankton, benthos, fish and bird samples taken during April – October 2010 for measurements of δ^{13}C and δ^{15}N ratios in the Lithuanian coastal zone.**

Cra – *Crangon crangon*, Amh – *Amphibalanus improvisus*, Gam – *Gammarus* sp., Ido – *Idotea balthica*, Myt – *Mytilus* sp., Neo – *Neomysis integer*, Pal – *Palaemon elegans*, Byl – *Bylgides sarsi*, Pyg – *Pygospio elegans*, Pp – pike-perch, Vb – vimba bream, Amm – Ammodytidae, Bh – Baltic herring, Bs – Baltic sprat, Ea – European anchovy, Bre – bream, Ac – Atlantic cod, Rg – round goby, Sb – silver bream, Ef – European flounder, Ep – European perch, Tss – three spined stickleback, Es – European smelt, Tur – turbot, Gh – grey heron, Gc – great cormorant.

Date	Site	Samples (numerals in brackets are the number of samples for δ^{13}C &δ^{15}N ratios analysis)
Apr 2010	Melnragė	Ef (6), Ep (4)
May 2010	Melnragė	Ef (3), Ep (5), Es(3)
Jun 2010	Juodkrantė	Gc (3), Gh (3)
	Melnragė	Ef (3), Tur (6)
	Palanga	Ef (6)
Jul 2010	Juodkrantė	Cra (3), Gc (3)
	Melnragė	Total POM (2), <70µm (2), 100-200µm (3), >200µm (2), Ep (6), Es (3),
	Palanga	Total POM (5), <70µm (6), 100-200µm (6), >200µm (6), Amh (3), Cra(6), Gam (3), Ido (3), Myt (7), Neo (9), Pal (3), Tss (2)
	Būtingė	Byl (2), Gam (9), Pyg (1)
Aug 2010	Juodkrantė	Ef (3)
	Melnragė	Total POM (3), <70µm (3), 100-200µm (3), >200µm (3), Ef (6), Pp(10), Vb (6)
	Palanga	Total POM (3), <70µm (3), 100-200µm (2), >200µm (3), Amm (2), Bh (3), Ef (6), Ep (15), Es (3), Rg (5), Sb (3), Tur (3), Vb (6)
Sep 2010	Juodkrantė	Total POM (3), <70µm (3), 100-200µm (3), >200µm (3), Amm (6), Ac (3), Bh (3), Bs (3), Cra (6), Ef (12), Ep (3), Es (3), Pp (3), Tur (3), Vb (6)
	Melnragė	Total POM (3), <70µm (3), 100-200µm (3), >200µm (3), Amm (3), Bre (2), Cra (3), Ef (6), Es (5), Gam (3), Myt (3), Neo (3), Pal(3), Pp (1)
	Palanga	Total POM (3), <70µm (3), 100-200µm (2), >200µm (3), Amm (3), Bs (3), Cra (3), Ef (2), Es (3), Gam (3), Myt (3)
	Būtingė	Amm (6), Bs (3), Es (3)
Oct 2010	Melnragė	Ea (3), Ef (9), Es (3), Pp (7), Vb (3)

Table 4.3. **Information on benthos, fish and bird samples taken during winter 2012-2013 for measurements of δ^{13}C, δ^{15}N, and δ^{34}S ratios in the Lithuanian coastal zone.**

Hed - *Hediste diversicolor*, Cor - *Corophium volutator*, Cra – *Crangon crangon*, Mys – mysids, Amh – Amphibalanus improvisus, Myt – Mytilus sp., Mya - *Mya arenaria*, Cer - *Cerastoderma glaucum*, Mac - *Macoma balthica*, Ac – Atlantic cod, Sg- round goby, Bh – Baltic herring, Bs – Baltic sprat, Ef – European flounder, Epl – European plaice, Es – European smelt, Vs – velvet scoter, Cg - common guillemot, RtD - red-throated diver, BtD - black-throated diver, Raz – razorbill, GCG - great crested grebe, LtD – long-tailed duck.

Date	Site	Samples (numerals in brackets are the number of samples for δ^{13}C &δ^{15}N ratios analysis)
Nov 2012	Smiltynė	Vs (1/1)
Dec 2012	Karklė-Melnragė	Sad (6/6), Bs (6/6), Ac (3/3), Bh (6/6), Sg (3/3)
	Karklė-Juodkrantė	Cg (1), Vs (2/2), RtD (5/5), BtD (1/1)
	Alksnynė-Juodkrantė	10 m depth: Cra (3/3), Hed (3/3), Mys (3/2), Cer (3/3), Mya (3/3)
		15 m depth: Cra (3/3), Hed (6/4), Cor (6/6), Cer (6/6), Mac (6/6), Mya (6/2)
Jan 2013	Karklė-Melnragė	Es (6/6), Ef (3/3)
	Karklė- Juodkrantė	Raz (1/1), Vs (2/2), RtD (1/1), GCG (3/3)
Feb 2013	Palanga	10 m depth: Cor (6/4), Amp (3/3), Myt (3/3)
	Karklė-Melnragė	Ef (3/3), Ac (3/3), Epl (3/3)
	Karklė- Juodkrantė	GCG (3/3), Vs (3/3), LtD (3/3)
Mar 2013	Karklė- Juodkrantė	Cg (2/2), RtD (1/1), GCG (3/3)

Surface water samples were collected for total particulate organic matter (POM) and seston analysis. Phytoplankton is considered difficult to discriminate from other living or nonliving suspended materials, thus total POM and small sizes plankton (<70 µm) were collected from the water surface, with the implicit assumption that most of this material is algal in composition. Together two types of seston as a mixture of autotrophic, heterotrophic and detrital material were collected (100-200 µm and >200 µm). Taxonomic composition in the samples was not determined, thus literature data on sizes of plankton organisms were used for SI data interpretation: size class of <70 µm representing phytoflagellates, flagellates, bacteria, cyanobacteria, 100-200 µm – ciliates, nauplii, rotifers, diatoms, >200 µm – copepodites, cladocerans, rotifers, and total POM – all groups combined (according to Rolff, 2000; Zeng et al., 2010).

Subsamples of water were prefiltered through 70, 100 or 200 µm mesh separating POM into four size-fraction classes later used for SI analysis separately. Samples were filtered on glass microfibre Whatman GF/F filters to concentrate material. Filters with samples were dried (48 h at 60°C) and then were stored frozen until analysis

(Jardine et al., 2003). Unfrozen samples were re-dried. Pieces of filters were cut by scissors and loaded into tin capsules. The water prefiltered through Nuclepore filters (0.22 µm pore size) was used to clean particles from the meshes.

Macroalgae were collected by scuba divers or picked manually from the stones in the shallow zone near Palanga and Melnragė. In total six macroalgae species were collected for SIA. Some parts of *Cladophora rupestris* were covered by protozoans *Vorticella* sp., diatoms *(Bacillariophyta*) of *Meridion* and *Pennales* orders, rarely *Diatoma vulgaris*. *Polysiphonia fucoides* were mostly covered by *Meridion* sp. diatoms and protozoan *Vorticella* sp. Some parts among branches of *Ceramium* sp. were covered by diatoms *Meridion sp.* and protozoans; there were also thin filaments with attached diatoms and protozoans. Some parts of *Coccotylus truncatus* were covered by mucus. *Ulva intestinalis* and *Furcellaria lumbricalis* were not covered by other organisms or mucus. All macroalgae samples were dried (48 h at 60°C) and then were stored frozen (Jardine et al., 2003). Unfrozen samples were re-dried and grounded into a fine powder in an agate mortar, weighed and placed into tin capsules (2.5-2.7 mg for δ^{13}C and δ^{15}N analysis).

The soft bottom macrofauna were collected using Van Veen sampler in the depth range from 10 to 15 m. Hard bottom macrofauna were sampled by scuba divers using 0.20 × 0.20 m rectangular frame between the 5 to 10 m depth. The whole body of smaller crustaceans, polychaetes, muscle tissue of large crustaceans and soft tissues of bivalves were taken for the analysis. Several specimens (2-10) of the same species and size were pooled to obtain 3 analytical replicates for each taxonomic/size group. Sampled material was dried at 60°C for 48 hours and then was stored frozen until analysis (Jardine et al., 2003). Unfrozen samples were ground into a fine powder in an agate mortar and weighed and placed into tin capsules (0.5-0.7 mg for δ^{13}C and δ^{15}N analysis and 1.1-2.3 mg for δ^{34}S analysis).

Fish specimens were collected from coastal commercial and scientific fishery catches collected by gill nets, beach seine nets and trawls. Fish tissue samples consisted of white dorsal muscle from one to three specimens (pooled to obtain three replicates for each taxonomic/size group). Collected samples were frozen until further preparation. Unfrozen samples were dried at 60°C for 48 hours and ground into a fine powder in an agate mortar (Jardine et al., 2003). Approximately 0.4-0.8 mg for δ^{13}C and δ^{15}N analysis and 1.5-2.0 mg for δ^{34}S analysis of fish material were weighed and placed into tin capsules.

Primary feathers of the juveniles of great cormorant and grey heron were taken during their breeding season in the colony situated between the Baltic Sea and the Curonian Lagoon. Samples were collected from carcasses of flightless heron juveniles found at the colony. Flying juveniles of cormorants were caught by the bird ringers in the vicinity of the colony. Covert feathers were taken from live birds; birds were released. Collected feathers were cleaned of surface contamination using detergent, rinsed with distilled water, dried and cut by scissors into small pieces. Vane tips and mid-vanes of each feather were analyzed separately. Approximately 0.5-0.6 mg of feather material was loaded into a tin capsule for $\delta^{13}C$ and $\delta^{15}N$ analysis.

Wintering marine birds were captured[1] using the night lighting technique (according to Whitworth et al., 1997). Blood (0.5–1 ml) was obtained from the medial metatarsal vein of live birds (Arora, 2010). The blood samples were stored frozen at -20°C in cryogenic vials. Before SIA samples were freeze-dried for 48 hours, weighed, and placed in tin capsules (0.5–0.7 mg for C and N; 1.7–2.0 mg for S).

4.1.2. Sample measurements

Isotope-ratio analysis involved precise measurement by mass spectrometry of the less abundant heavy isotope relative to the more abundant light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$, and $^{34}S/^{32}S$) of carbon dioxide (CO_2), nitrogen gas (N_2), or sulfur dioxide gas (SO_2) generated from combustion of the sample material. Samples of POM, seston, macrozoobenthos, fish muscle and bird feathers, collected in spring – autumn 2010, were analyzed for $\delta^{13}C$ and $\delta^{15}N$ ratios using the Carlo-Erba elemental analyzer coupled to an Isotope ratio mass spectrometer at the Leibniz Institute for Baltic Sea Research, Germany.

Samples of macrozoobenthos, fish muscle and bird blood from winter 2012-2013 were analysed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$. The $\delta^{13}C$ and $\delta^{15}N$ ratios in the samples were determined using a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Flash EA 1112 elemental analyzer at the State Research Institute Center for Physical Sciences and Technology, Lithuania. The $\delta^{34}S$ values were determined using a SerCon elemental analyzer and custom cryofocusing system interfaced to a SerCon 20-22 IRMS (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility, University of California, USA.

Results of isotopic ratios were compared to conventional standards, i.e., Vienna Peedee Belemnite (VPDB), for carbon, atmospheric N_2 for nitrogen, and Vienna Canyon Diablo troilite (VCDT) for sulfur, defined as δ values: $\delta X =[(R_{sample}/R_{standard})- 1)]\times 10^3$ (‰), where $X={}^{13}C$, ^{15}N or ^{34}S, and $R={}^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$ (Jardine et al., 2003). For calibration of reference gases CO_2 and N_2, the international standards from the International Atomic Energy Agency (Vienna) were used: IAEA-600 (Caffeine, $\delta^{13}C= -27.771 \pm 0.043‰_{VPDB}$) and NBS-22 (Oil $\delta^{13}C= -30.031 \pm 0.043‰_{VPDB}$) were used for ^{13}C and IAEA-600 (Caffeine, $\delta^{15}N= +1 \pm 0.2‰_{air\,N^2}$) for ^{15}N. Repeated analyses of homogeneous material yielded standard deviations of less than 0.08‰ for carbon and 0.2‰ for nitrogen. For calibration of reference gases SO_2, three laboratory

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[1] Permits to capture birds were obtained from the Environmental Protection Agency of Lithuania (EPA: permit 2012 No. 7 and 2013 No. 1).

standards calibrated directly against IAEA-S-1 (Silver Sulfide, $\delta^{34}S$= -0.30‰$_{VCDT}$), IAEA-S-2 (Silver Sulfide, $\delta^{34}S$= 22.7± 0.2‰$_{VCDT}$), and IAEA-S-3 (Silver Sulfide, $\delta^{34}S$= -32.3± 0.2‰$_{VCDT}$) were used. Repeated analysis of three laboratory standards yielded standard deviations of less than 0.3‰. The long-term reproducibility of $\delta^{34}S$ measurements is ± 0.4‰.

4.1.3. Analysis of isotopic data

Lipid removal was not performed in order to keep the $\delta^{15}N$ values in the samples unaffected by treatment. The mean C:N ratios in invertebrates and fishes (4.26 ± 0.64 for 2010 and 3.74 ± 0.71 for 2012-2013) were higher than the recommended limit for aquatic organisms (C:N>3.5), at which lipid correction should be performed. Therefore, we corrected the $\delta^{13}C$ values in invertebrates and fishes using an arithmetic lipid normalization equation proposed by Post et al. (2007): $\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C:N$. Lipid correction for bird blood and feathers was not applied (Cherel et al., 2005).

Carbon trophic enrichment factor (TEF) was calculated for each food source individually applying a function $TEF = -0.199 \times \delta^{13}C_{source} - 3.986$ as suggested by Caut et al. (2009). Calculated carbon TEF values ranged from 0.07 to 0.62‰ for food sources of piscivorous waterbirds and from -0.2 to 0.76‰ for sources of benthivorous ducks. The standard error for carbon TEF was determined by first-order error propagation of uncertainties. Nitrogen TEF for bird blood was set at 2.25 ± 0.20 (Caut et al., 2009). The mean reported trophic shift for sulfur (0.5 ± 0.56‰) was not significantly different from zero, similarly as reported in earlier studies (Peterson and Fry, 1987; McCutchan et al., 2003). Thus, we did not apply any TEF for sulfur when estimating diet of waterbirds.

Considering the prey size limitations for piscivorous waterbirds, isotopic values of fishes with a total length of <20 cm were included in mixing models for common guillemot and great crested grebe (Sonntag and Hüppop, 2005), and fishes <30 cm were used for red-throated diver (Guse et al., 2009).

The SPSS statistical software (SPSS/7.0) and R were used for the calculations and presentations of the results. A hierarchical agglomerative cluster analysis based on the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values of bird blood was performed using Ward's method. The differences of SI ratios among species was compared using MANOVA and subsequent univariate ANOVA (or *t* – test for individual isotopes). Tukey's Honestly Significant Difference (HSD) test was used to detect significantly different means. Non-parametric Kruskal–Wallis and Mann–Whitney *U* tests were performed if variances among groups were significantly different. Levene's test was used to test the homogeneity of variances.

For mixing modeling, the package SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) in R software (R Core Team, 2013) was used. SI mixing models using single $\delta^{34}S$, dual $\delta^{34}S$&$\delta^{15}N$, and triple $\delta^{34}S$&$\delta^{15}N$&$\delta^{13}C$ values were applied to estimate multiple food source contributions to waterbird diet. The sources were defined when having significantly different isotopic composition of at least one isotope. Otherwise, different species were aggregated into combined sources by functional significance (e.g., pelagic fishes, benthic fishes), taxonomy (e.g. crustaceans) or by similar isotopic composition within a cluster as suggested by Phillips et al. (2005). Mixing model results were compared to determine the optimal set of isotopes capable to differentiate the maximum number of sources at the study site. The mean percentage with standard deviation (SD) and the 95% credibility interval (CI_{95}) were the outputs of isotopic mixing models.

A Monte Carlo simulation of mixing polygons was used to apply the point-in-polygon assumption to the models for velvet scoter and long-tailed duck. Convex hulls (*mixing polygons*) are iterated using the distributions of the proposed dietary sources and TEFs, and the proportion of polygons that have a solution (i.e. that satisfy point-in-polygon) is calculated. It provided a quantitate basis for consumer exclusion (those outside 95% mixing region). The mixing polygon simulations were visualized with mixing regions, which were calculated by testing a grid of values for point-in-polygon (Smith et al., 2013).

Spearman-rank correlation was used to estimate a relationship between $\delta^{15}N$ ratios of 29 consumer groups and their TLs estimated by the ECOPATH model. Majority of SI studies aim to calculate TLs using $\delta^{15}N$ values of baseline organisms and fixed TEF (Cabana and Rasmussen, 1996). However, in this study, strong contribution of organic matter flow from adjacent marine and lagoon ecosystems may have affected selection of baseline organisms. Identifying species on the first or second TL is highly challenging and leads to errors of estimation. Therefore, the idea to calculate TLs using the fixed TEF is likely to be misleading due to the variety of organisms and tissues used for SIA in this study. We implied that the TEFs for different tissues and organisms should be theoretically different (e.g. Caut et al., 2009). Therefore, we have not aimed to calculate the TLs using $\delta^{15}N$ values but rather estimate an agreement between $\delta^{15}N$ ratios and TLs estimated by the ECOPATH model.

4.2. Gut content analysis of bycaught waterbirds

The diet composition was estimated for 35 individuals of velvet scoter and 61 individuals of long-tailed duck accidentally drowned in fisherman gillnets in March-November of 2012 and January-April 2012-2016, accordingly. All ducks were caught along Lithuanian coast at depths ranging from 2 to 15 m. Velvet scoters were bycaught in the soft bottom habitat along the Curonian spit (Nida – Juodkrantė), while long-tailed ducks were collected in both soft (Nida – Juodkrantė) and stony bottom habitats (Karklė – Palanga). In the laboratory, body fat score was assessed by examining the subcutaneous fat deposit ranging in the scale from 0 (no fat) to 5 (very fat).

Contents of gizzard and esophagus were treated by sorting material, and identifying each object to the lowest possible taxonomic level. Each prey taxon was weighed separately. Pebbles were not considered as prey items and together with unidentified material were excluded from the further calculations. Diet composition was assessed according to wet weight of prey in grams and proportion from total wet weight (%), including mollusk shells. Ash-free dry weight (AFDW) of prey in grams and % represented a measurement of the weight of organic material (calculations are provided in Annex Table 2). Frequency of occurrence of prey items in waterbirds was expressed in numbers of bird specimens and proportion (%) from total bird number used for the diet analysis.

4.3. ECOPATH modeling

4.3.1. The modelling approach

The static trophic network model of the Baltic Sea coastal zone of Lithuania was constructed using ECOPATH software version 6.5 The ECOPATH was selected as a tool allowing the integration of both spatial and seasonal variability of biotic compartments on an annual basis, capable to produce cumulative balances for the system as a whole and for separate trophic compartments. EwE models are based on mass-balance principles represented as master equations. The first ECOPATH equation describes how the production term for each group (i) can be split in compartments. This is implemented with the mass-balance equation:

$$P_i = Y_i + B_i M2_i + E_i + M0_i + BA_i \quad (1)$$

where P_i is the production rate of a group i, Y_i is a sum of fishery catches of a group i, $B_i M2_i$ is predated biomass, E_i is the net migration (emigration-immigration), $M0_i$ is other mortality, and BA_i is the biomass accumulation for a group i.

$M2_i$ is the predation mortality rate. Other mortality describes all mortality not elsewhere included, e.g., mortality due to diseases or old ages, and it is given by,

$$M0_i = P_i (1 - EE_i) \quad (2)$$

where the ecotrophic efficiency (EE_i) is the fraction of the production of a group that is accounted for in the models, through predation, fishing and other export, or biomass accumulation.

The second important equation for the modelling approach describes what fraction of production of ecological group i is used by predator j:

$$B_i M2_i = \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \quad (3)$$

where the summation of all predator groups (j) feeding on a group *i*, DC_{ij} is the fraction of predator *(j)* diet contributed by prey (*i*). B_j is biomass of group *j* and is consumption/biomass ratio for group *j*.

Equation 1 can be re-expressed as:

$$B \cdot \left(\frac{Q}{B}\right)_i = \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + BA_j + B_i \left(\frac{P}{B}\right)_j \cdot (1 - EE_i) \quad (4)$$

where $(P/B)_i$ indicates the production of *i* per unit of biomass and its equivalent to total mortality *(Z)*, $(Q/B)_i$ is the consumption of *i* per unit of biomass. The model is considered balanced when all previous equations have been solved.

Unit of the model were expressed in $g \cdot m^{-2}$ wet weight organic matter for biomasses and $g \cdot m^{-2} \cdot y^{-1}$ for flows. All biomasses and rates were averaged over a one year period as usual for an ECOPATH model.

4.3.2. Model construction: functional groups and parameterization

The model for Lithuanian Baltic coastal zone incorporated 41 functional groups representing 60 taxa (Table 5.4). There were 40 groups of living organisms grouped according to similarities in ecological and biological features and their importance in the study area: 28 fish groups, three bird groups, six invertebrate groups, two plankton groups, and one benthic primary producer group. Different life stages of most fish species were treated as separate compartments because of their presumably different food niches and positions in the food web. One *detritus* compartment was included in the model to represent all forms of dead organic material. Bacteria and meiofauna, which are important components in the ecosystem, were represented within the *detritus* compartment. ECOPATH is not a tool to deal with both microscopic and macroscopic components of the food web. General suggestion for this type of the model is to focus either on the macrofaunal or on the microbial food web (Heymans et al., 2016). Therefore, this work was focused on the macrofaunal food web, where the microbial part is coupled to the detritus compartment.

The model was constructed to represent the coastal zone during 2000-2010. However, when data for this period were unavailable, earlier measurements from available published sources (including databases and reports) were used. Original local data were used for fish biomass and diet parameter estimation. Fish biomass data and catch statistics were taken from the state monitoring programme carried out by the Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania and were adjusted according to the period for each species spent in the modeled coastal system. A fish diet composition matrix was derived from unpublished data (Bacevičius, unpubl.; methodology was described in Šiaulys et al., 2012). Waterbird abundance information were taken from national bird census, their diets were described according to the local study carried out by Žydelis (2002). Wintering bird bycatch discards assumed being 10 percent of the total bird abundance according to the local estimates (Žydelis et al., 2009).

Inputs of phytoplankton, zooplankton and detritus from the Curonian Lagoon were calculated by integrating daily discharges and concentrations over the year period (Ertürk et al., 2008). Other data for the model came from the literature references.

Table 4.4. **Overview of compartments and main organisms used in the ECOPATH model for the Lithuanian coastal zone.**

No	Compartment name	Representative species	Length, mm	Fish guilds
1	Phytoplankton	Bacillariophyta, Dinophyta, Cyanophyta		
2	Mesozooplankton	Copepoda, Cladocera, Ostracoda		
3	Nectobenthos	*Neomysis integer, Mysis mixta, Praunus inermis*		
4	Macrophytobenthos	*Enteromorpha intestinalis, Furcellaria lumbricalis, Coccotylus truncates, Ceramium tenuicorne, Polysiphonia fucoides, Cladophora rupestris*		
5	Macrozoobenthos filtrators	*Amphibalanus improvisus, Mytilus* sp., *Mya arenaria, Macoma balthica, Cerastoderma glaucum*		
6	Macrozoobenthos omnivorous (<9.9 mm)	*Saduria entomon, Gammarus zaddachi, Gammarus salinus, Gammarus duebeni, Idotea balthica, Crangon crangon, Palaemon elegans, Monoporeia affinis, Corophium volutator*	<9.9	
7	Macrozoobenthos omnivorous (10-20 mm)	*S. entomon, C. crangon, P. elegans*	20-Spl	
8	Macrozoobenthos omnivorous (>20 mm)	*S. entomon, C. crangon, P. elegans*	>20	
9	Polychaetes	*Hediste diversicolor, Marenzelleria viridis, Pygospio elegans*		
10	Baltic herring (juvenile)	*Clupea harengus membrus*	<70	MM
11	Baltic herring (adult)		70-260	MM
12	Baltic sprat (juvenile/adult)	*Sprattus sprattus balticus*	<120	MM
13	Lesser sand-eel (juvenile, adult), Greater sand-eel (juvenile/sub-adult)	*Ammodytes tobianus, Hyperoplus lanceolatus*	<140	SR
14	Greater sand-eel (adult)	*Hyperoplus lanceolatus*	140-250	SR
15	Common and Sand gobies (juvenile, adult)	*Pomatoschistus microps, Pomatoschistus minutus*	30-60	SR

No	Compartment name	Representative species	Length, mm	Fish guilds
16	Twaite shad (juvenile)	*Alosa fallax*	<100	AN
17	Twaite shad (adult)		100-450	AN
18	Eelpout (juvenile)	*Zoarces viviparus*	<150	SR
19	Eelpout (adult)		150-350	SR
20	European flounder (juvenile/sub-adult)	*Platichthys flesus*	<150	MM
21	European flounder (adult)		150-350	MM
22	Silver bream (adult)	*Blicca bjoerkna*	150-300	FS
23	Bream (adult)	*Abramis brama*	150-450	FS
24	Vimba bream (juvenile)	*Vimba vimba*	<150	AN
25	Vimba bream (adult)		150-450	AN
26	Three-spined stickleback (adult)	*Gasterosteus aculeatus*	40-75	FS
27	Ruffe (adult)	*Gymnocephalus cernuus*	65-160	FS
28	European perch (juvenile)	*Perca fluviatilis*	<50	FS
29	European perch (sub-adult/adult)		50-450	FS
30	Atlantic salmon (adult)	*Salmo salar*	>700	AN
31	Pike-perch (juvenile/ sub-adult)	*Sander lucioperca*	100-250	FS
32	Pike-perch (adult)		>250	FS
33	Turbot (juvenile)	*Scophthalmus maximus*	<100	MM
34	Turbot (sub-adult/adult)		>100	MM
35	European smelt (juvenile)	*Osmerus eperlanus*	<100	AN
36	European smelt (adult)		100-250	AN
37	European eel (adult)	*Anguilla anguilla*	300-800	CA
38	Great cormorant	*Phalacrocorax carbo*		
39	Wintering diving ducks	*Bucephala clangula, Melanitta fusca, Melanitta nigra, Clangula hyemalis, Polysticta stelleri*		
40	Wintering piscivorous birds	*Podiceps cristatus, Gavia arctica, Gavia stellata, Mergus merganser*		
41	Detritus			

* Guilds: MM – marine migrant; SR – semi-resident fish; FS – freshwater straggler; AN – anadromous fish; CA – catadromous fish.

Table 4.5. **Model inputs and data pedigree.**

B – biomass (ww(gm^{-2})); P/B – production/biomass ratio (y^{-1}); Q/B – consumption/biomass ratio (y^{-1}); catch representing landings for fishes and discards for birds (ww(gm^{-2})); Immigration (ww(gm^{-2}y^{-1})); EE – ecotrophic efficiency. Diet column is for pedigree only. Color scale represents the level of confidence in input data.

Scale

Worse Better

No	Group name	B	P/B	Q/B	Diet	Catch	Immigr.	EE
1	Phytoplankton	5.1990	206.00				2.770	
2	Mesozooplankton	3.9400	13.00	300.00	▓		0.210	
3	Nectobenthos	1.7918	6.04	25.00	▓			
4	Macrophytobenthos	0.0520	10.95					
5	Macrozoobenthos filtrators	71.3000	1.82	13.00	▓			
6	Macrozoobenthos omnivorous (<9.9 mm)	59.1120	2.54	13.00	▒			
7	Macrozoobenthos omnivorous (10-20 mm)	11.0835	4.94	13.00	▒			
8	Macrozoobenthos omnivorous (>20 mm)	3.6945	4.94	13.00	▒			
9	Polychaetes	48.5000	2.54	31.17	▒			
10	Baltic herring (juvenile)	0.0197	0.82	14.71	▓		0.226	
11	Baltic herring (adult)	0.0327	0.55	7.96	▓	0.232	0.622	
12	Baltic sprat (juvenile/adult)	0.0453	0.68	9.13	▓		0.236	
13	Lesser sand-eel, Greater sand-eel	0.2636	0.82	6.00	▓			
14	Greater sand-eel (adult)		0.37	4.80	▓			1.00
15	Common and Sand gobies (juvenile, adult)		0.46	3.21	▓			1.00
16	Twaite shad (juvenile)	0.0007	0.82	9.13	▓			
17	Twaite shad (adult)	0.2509	0.55	7.96	▓	0.006		
18	Eelpout (juvenile)	0.0017	0.55	2.97	▓		0.007	
19	Eelpout (adult)	0.0020	0.37	2.44	▓	0.00002	0.003	
20	European flounder (juvenile/sub-adult)	0.0172	0.55	2.97	▓		0.002	
21	European flounder (adult)	1.0964	0.37	2.44	▓	0.065		
22	Silver bream (adult)	0.0852	0.37	2.68	▓	0.002		
23	Bream (adult)	0.8517	0.37	4.00	▓	0.004		
24	Vimba bream (juvenile)	0.0336	0.55	2.97	▓		0.048	
25	Vimba bream (adult)	0.0041	0.37	4.00	▓	0.044	0.051	
26	Three-spined stickleback (adult)	0.0004	0.68	3.85	▓		0.017	
27	Ruffe (adult)	0.0008	0.46	6.00	▓		0.002	
28	European perch (juvenile)	0.00004	0.82	6.00	▓		0.007	
29	European perch (sub-adult/adult)	0.0811	0.80	3.68	▓	0.003		
30	Atlantic salmon (adult)	0.0261	0.84	6.20	▓	0.004		
31	Pike-perch (juvenile/sub-adult)	0.0042	0.84	4.57	▓		0.006	
32	Pike-perch (adult)	0.1853	0.84	1.71	▓	0.027		
33	Turbot (juvenile)	0.0139	0.55	2.97	▓			
34	Turbot (sub-adult/adult)	0.0195	0.37	2.44	▓	0.031	0.042	
35	European smelt (juvenile)	0.0514	0.82	6.00	▓		1.542	
36	European smelt (adult)	0.0021	0.55	4.80	▓	0.291	0.414	
37	European eel (adult)	0.0075	0.37	2.44	▓	0.000		
38	Great cormorant	0.0408	0.16	120.00	▓			
39	Wintering diving ducks	0.0297	0.51	120.00	▓	0.0003		
40	Wintering piscivorous birds	0.0140	0.16	120.00	▓	0.00001		
41	Detritus	1.8029						

Ecophysiological parameters such as P/B values for fish groups were calculated following Zaika (1983) according to the ecological groups (benthic, pelagic or predatory); juveniles were assumed to have 1.5 times higher P/B than adults. Q/B values for fishes and all input values for invertebrates and birds were obtained from the literature.

The pedigree index calculation was applied to quantify the uncertainty related to the sources of input parameters and the quality of the model. We have assigned a pedigree index to each of the input data values varying from 0 (guess estimated) to 1 (locally obtained data). The cumulative scores provided an overall pedigree index describing the model data quality (Christensen and Walters, 2004).

Parameterization procedure was manual and reiterative mostly using the estimated ecotrophic efficiency (EE) as a main criteria for the model validation (estimates were considered realistic at EE<1) (Table 4.5). EE of a group is the proportion of the production that is utilized in the system. As the bulk of the fish species are migratory and stay in the area only for some periods (Gaigalas and Mištautaitė, 1980; Ložys, 2003; Repečka, 2003a; Repečka et al., 2003; Stankus, 2003; Švagždys, 2009) we used the model to assess the migration rates, when balancing EE of the relevant species.

4.3.3. Model analyses and indices

Ecosystem structure and trophic flows were analyzed assessing the ecological indices and flow indicators within ECOPATH. Several indices originally derived from thermodynamic and information theories were used to estimate state of the system by evaluating the trophic status and development.

The trophic levels (TL) of each group was estimated as:

$$\mathrm{TL_j} = 1 + \sum_{j=1}^{n} DC_{ji} \cdot TL_i \quad (5)$$

where j is the predator of prey i, DC_{ji} is the fraction of prey j in the diet of predator j and TL_i is the level of prey i. As usual, the first TL was attributed to primary producers and detritus.

Values of consumption (Q), production (P), respiration (R), assimilation (A), exports, imports and flows to detritus were estimated for each compartment and for the ecosystem as a whole. Total system throughput (TST) denoted the sum of all flows in the model is calculated as:

$$\mathrm{TST} = \sum_{i=1,j=1}^{n} T_{ij} \quad (6)$$

where T_{ij} is the flow between any two compartments and includes respiration and export flows (Heymans et al., 2014).

A common measure of the trophic status of a system is the ratio of total primary production to total community respiration (TPP/TR) (Kirschbaum et al., 2001):

TPP/TR ratio is >1, the system is autotrophic producing more organic matter through photosynthesis than consumed through respiration;

TPP/TR ratio is <1, the system is heterotrophic consuming more organic matter through respiration than produced through photosynthesis. If the system is continuously heterotrophic, it requires an external supply of organic matter from neighboring systems.

Net primary production refers to the production of organic matter by plants minus the amount of organic matter respired by plants themselves and measured over a period of a year (Kirschbaum et al., 2001).

Net system production refers to the net primary production minus the organic matter losses in heterotrophic respiration. If the produced organic matter is higher than an equivalent amount of organic matter lost in respiration, the measured net system production is positive. Otherwise, the system would use all of its organic matter in respiration and requires import of organic matter from other systems (Kirschbaum et al., 2001).

Linear trophic chain of Lindeman energy flow represented the simplification of the trophic network and its trophic efficiency. It revealed the sum of energy flows that each TL receives from other as the losses, by respiration, excretion, egestion and other natural mortality. The TE of a TL was calculated as the sum of the flow transferred from any given TL to the next higher TL, plus exports or catches from the given TL relative to the input of the given TL. The mean TE for the coastal food web was calculated as the mean of TE for each of the TL 2 to 4 (Lindeman, 1942, Ulanowicz, 1986, Wulff et al., 1989, Libralato et al., 2002).

The estimation of mixed trophic impacts revealed the relative direct or indirect impact of a change in the biomass of one group on all other compartments in the coastal ecosystem with the assumption that their diet composition remains constant. Mixed trophic impact was used to calculate total mixed trophic impact showing an impact of each compartment on the other groups by adding all its impacts weighted by the inverse of the biomass of impacted groups (Libralato et al., 2004).

Keystoneness is an index of the ability of a compartment with low biomass to influence other compartments within a food web. Therefore, keystoneness analysis allowed identifying compartments with high overall effects in the food web. The index is calculated as $KS_i = \log [\varepsilon_i (1-p_i)]$, where ε_i is a measure of overall effect of each group, and p_i is a biomass component representing the contribution of the compartment to the total biomass of the food web. Important species have keystoneness values over or close to zero, while less important species have negative values (Libralato et al., 2006).

5

Results

5.1. Stable isotope ratios in food web compartments during a vegetative period

5.1.1. Stable isotope ratios in size-fractionated plankton

The $\delta^{13}C$ values in POM and seston fractions in Juodkrantė significantly differed from those at Melnragė and Palanga sites (Kruskal-Wallis test: H (2, N=83)=31.0, p<0.001; Fig. 5.1). The SI values in all plankton fractions were lower in Juodkrantė than in Palanga and Melnragė sites (Mann-Whitney U tests, p<0.05). The fractions >200 µm and <70µm significantly differed by $\delta^{13}C$ values (Kruskal-Wallis test: H (3, N=83) = 13.5, P=0.004), but other fractions had similar $\delta^{13}C$ values during study period across all sampling sites. The $\delta^{13}C$ values in plankton were lowest in July at Palanga site for the fractions >200 µm, total POM, and <70µm (-32.2, -31.4, -30.1‰, accordingly) and in Melnragė for the fraction 100-200µm (-30.9‰). The highest $\delta^{13}C$ values were in September in Juodkrantė (from -25.6‰ to -23.5‰ for all fractions).

There were no significant difference in $\delta^{15}N$ values among POM and seston fractions during the whole study period across three coastal sites (Kruskal-Wallis test: H (2, N=83) = 4.8, P=0.093). The lowest $\delta^{15}N$ values were measured in July: -0.1‰

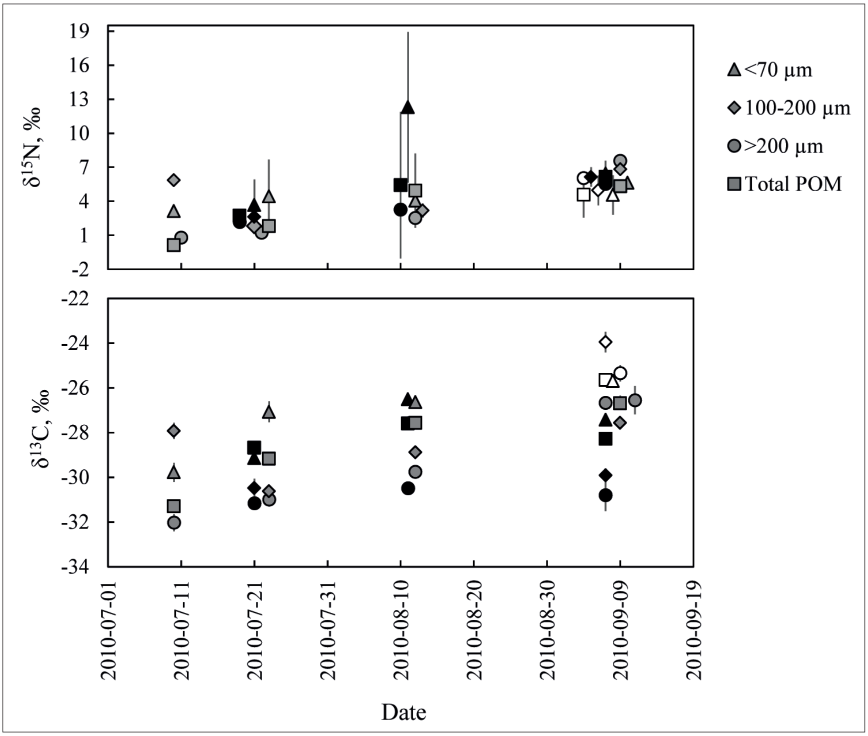

Figure 5.1. The $\delta^{13}C$ and $\delta^{15}N$ ratios in size-fractioned plankton during vegetation season in the coastal zone.

Different colors of figures indicate sampling sites: white – Juodkrantė, black – Melnragė, grey – Palanga.

for total POM, 0.4‰ for the fraction >200µm and 1.5‰ for the fraction 100-200µm were in Palanga and 2.1‰ for the fraction <70µm were in Melnragė. The highest $\delta^{15}N$ values and the largest variations were in the fraction <70µm and total POM in August in Melnragė site (16.6 and 12.8‰, accordingly), for >200µm and 100-200µm in September in Palanga (8.1 and 6.9‰) (Fig. 5.1).

5.1.2. Stable isotope ratios in benthic organisms

According to $\delta^{13}C$ and $\delta^{15}N$ values, benthic organisms fell into several clusters (Fig. 5.2). Macroalgae had the lowest $\delta^{15}N$ values, partly overlapping with crustaceans and bivalves. Most of the macroalgae species had $\delta^{13}C$ values between -18 and -27‰, except for the *C. trunkatus* which had lower $\delta^{13}C$ ratios of -36.3±0.1‰ (as the mean for samples of July and September. Small omnivorous and suspension filter

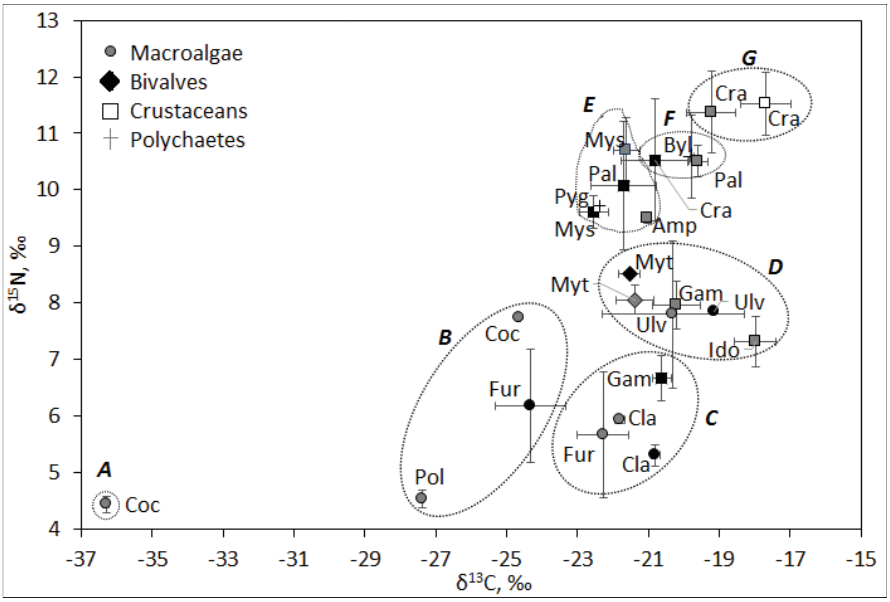

Figure 5.2. The $\boldsymbol{\delta}^{13}$C and δ^{15}N ratios in benthos organisms during vegetation season in the coastal zone (N=85).

Different colors of figures indicate sampling sites: white – Juodkrantė, black – Melnragė, grey – Palanga. Circles mark macroalgae: Coc – *Coccotylus trunkatus*, Ulv – *Ulva intestinalis*, Fur – *Furcellaria lumbricalis*, Cla – *Cladophora* sp., Pol – *Polysiphonia fucoides*. Rhombus denotes bivalve: Myt - *Mytilus* sp. Squares mark crustaceans: Mys – Mysidae, Sad – *Saduria entomon*, Cra – *Crangon crangon*, Gam – *Gammarus* sp., Amp – *Amphibalanus improvisus*, Pal – *Palaemon elegans*, Ido – *Idotea balthica*. Crosses denote polychaetes: Byl – *Bylgides sarsi*, Pyg – *Pygospio elegans*. The groups (circled) are chosen from the cluster analysis: A, B – producers; C – producers and omnivorous; D – macroalgae, omnivorous and suspension filter feeders; E – subsurface and surface deposit feeders, suspension filter feeders, omnivorous; F – omnivorous, subsurface deposit feeders, predators; G – omnivorous (according to Olenin, 1997).

feeders had the lowest δ^{15}N values, while deposit feeders, predators, and large omnivorous had higher δ^{15}N values.

There were some spatial differences in SI content in some macrozoobenthos groups (Table 5.1). *C. crangon* had the same δ^{13}C values in both Palanga and Melnragė (Mann Whitney U test, $p>0.05$), while the values in Juodkrantė were higher ($p<0.05$). The δ^{13}C values of *Palaemon elegans* in Palanga were higher than those in Melnragė ($p<0.05$). The δ^{15}N values of *Gammarus* sp. varied across the sites: values in Palanga and Būtingė significantly differed from those in Melnragė ($p<0.05$).

Table 5.1. **Comparison of $\delta^{13}C$ and $\delta^{15}N$ values of selected taxa of macrozoobenthos across the coastal sites (Juodkrantė (J), Melnragė (M), Palanga (P), Būtingė (B)) in July-September 2010. Probability values resulting from the Kruskal-Wallis test; N_{sample} – sample size; N_{site} – number of sites used for particular comparison.**

Taxon	N_{sample}	$\delta^{13}C$		$\delta^{15}N$		N_{site}
Crangon crangon[1]	12	0.01*	P=M<J	0.63	NS	3
Gammarus sp.[2]	18	0.14	NS	0.03*	P=B>>M	3
Palaemon elegans[1]	12	0.01*	P>M	0.78	NS	2

*Significant differences with $p<0.05$; NS – no significant difference; = comparisons were not significant; > the difference of samples from just one site was significant; >> all comparisons are significant. [1, 2] indicate significant differences in $\delta^{13}C$ (=1) and $\delta^{15}N$ (=2) values across the coastal sites within given species. Species caught at least at two sites were tested for spatial differences in SI ratios.

5.1.3. Stable isotope ratios in coastal fishes

Majority of studied fish species also had site-specific differences in SI values (Table 5.2). The values of $\delta^{13}C$ and $\delta^{15}N$ in pike-perch and European smelt did not differ across the coastal sites. The $\delta^{13}C$ values in European perch, European flounder, and vimba bream sampled in Juodkrantė and Palanga did not differ between each other but were higher than those from Melnragė. Baltic herring in Juodkrantė had higher $\delta^{13}C$ values than herring from Palanga.

Table 5.2. **Comparison of $\delta^{13}C$ and $\delta^{15}N$ values of fish species among coastal sites (Juodkrantė (J), Melnragė (M), Palanga (P)), in August-September 2010. Probability values according to the Kruskal-Wallis test; N_{sample} – sample size; N_{site} – number of sites used for particular comparison.**

Taxon	N_{sample}	$\delta^{13}C$		$\delta^{15}N$		N_{site}
Ammodytidae[2]	19	0.40	NS	0.02*	P=M>>J	3
European perch[1]	18	0.02*	J=P>>M	0.08	NS	3
Pike-perch	14	0.24	NS	0.14	NS	2
Turbot[2]	6	0.51	NS	0.05*	P<J	2
Baltic herring[1]	6	0.05*	J>P	0.51	NS	2
Baltic sprat[2]	9	0.18	NS	0.04*	P=M>J	3
European flounder[1]	35	<0.01*	P=J>M	0.36	NS	3
European smelt	14	0.96	NS	0.53	NS	3
Vimba bream[1,2]	18	0.02*	P=J>M	0.003*	P=M>>J	3

*Significant differences with $p<0.05$; NS – no significant difference; = comparisons were not significant; > the difference of samples from just one site was significant; >> all comparisons are significant. [1, 2] indicate significant differences in $\delta^{13}C$ (=1) and $\delta^{15}N$ (=2) values among coastal sites within given species. Species caught at least at two sites were tested for spatial differences in SI ratios.

Values of $\delta^{15}N$ in Ammodytidae, Baltic sprat, and vimba bream did not differ between coastal sites of Palanga and Melnragė, where they all had significantly higher in $\delta^{15}N$ values than those from Juodkrantė. On the contrary, the $\delta^{15}N$ values in turbot in Juodkrantė were significantly higher than those in Palanga (Table 5.2).

The $\delta^{13}C$ values in fishes belonging to different migratory guilds increased by the same pattern at all coastal sites: anadromous fishes < freshwater stragglers < marine migrants < semi-resident fishes; however, not all these differences were significant. The $\delta^{13}C$ values in anadromous and freshwater fishes did not vary significantly across the different locations. There were more pronounced differences across the locations for marine migrants and semi-resident fish guilds (Table 5.3, Fig. 5.3), while the differences between these two guilds themselves were not significant (ANOVA, $F_{1,82}$=0.3, P=0.6).

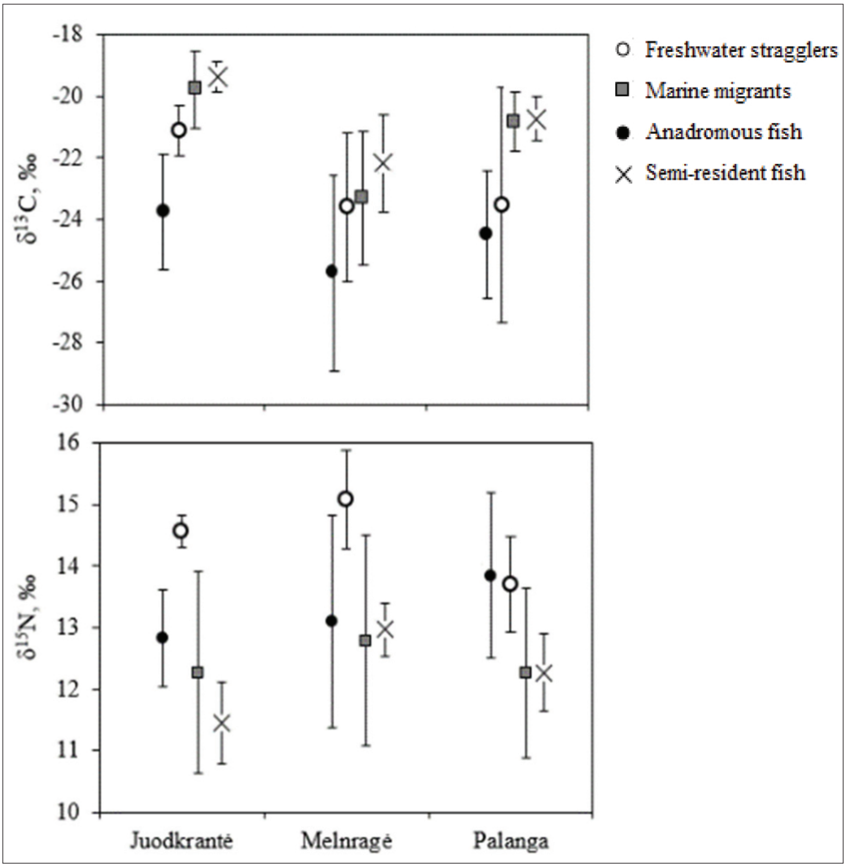

Figure 5.3. The $\delta^{13}C$ and $\delta^{15}N$ ratios for fish guilds during among the coastal sites (August-September, N=156).

Table 5.3. **ANOVAs testing for differences among coastal sites of Juodkrantė, Melnragė and Palanga of δ^{13}C and δ^{15}N values of fish guilds.**

Fish guilds	**Degr. of freedom**	**δ^{13}C**		**$\delta1^{5}$N**	
		F	**P**	**F**	**P**
Freshwater stragglers	2, 36	2.04	0.15	12.9	0.00
Marine migrants	2, 56	27.51	0.00	0.31	0.73
Anadromous fishes	2, 21	1.73	0.19	1.23	0.31
Semi-resident fishes	2, 22	13.13	0.00	5.39	0.01

In Melnragė, all guilds had homogenous δ^{13}C values (HSD, $p>0.05$), except anadromous fishes which had lower δ^{13}C values (HSD, $p<0.05$; Fig. 5.3). The δ^{15}N values of different fish guilds followed similar pattern relative to the influence of freshwater inputs except for the anadromous fishes (Fig. 5.3); however, statistically only freshwater and semi-resident fishes were different in δ^{15}N values across different sites (Table 5.3).

5.1.4. Variation of stable isotope ratios in feathers of waterbird juveniles

The δ^{13}C and δ^{15}N values in different parts of great cormorant and grey heron juveniles feathers did not show species-specific differences (MANOVA, $F_{4,\,28} = 0.44$, P=0.78) (Fig. 5.4). However, δ^{15}N values of separate feather parts of cormorant were increasing during the feather growth period (*t-test*, *t* =-4.3, df = 5, P=0.008), while δ^{13}C values were homogenous for the entire period (*t-test*, *t* = -0.4, df = 5, P = 0.72). The SI values in vane tips of individual grey herons showed a high variation, while the values in mid-vanes were much more consistent. However, SIA of grey heron feathers did not show changes in both δ^{13}C and δ^{15}N values during the feather growth period (*t-test*, *t* = -0.9 and -1.3, accordingly, df = 2, $p>0.05$) (Fig. 5.4).

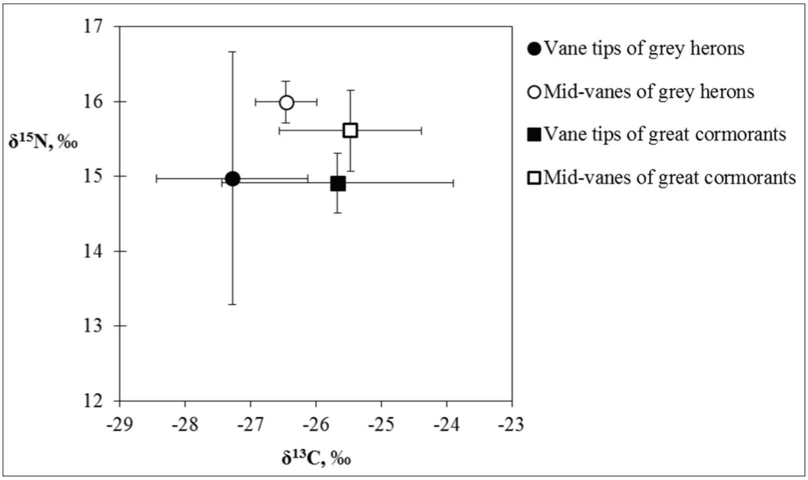

Figure 5.4. The $\delta^{13}C$ ir $\delta^{15}N$ values for vane tips and mid-vanes of juveniles of great cormorant and grey heron.

5.1.5. Isotopic differences in selected food web compartments at different coastal sites

Both $\delta^{13}C$ and $\delta^{15}N$ ratios in selected food web compartments showed a variety of values across and within species and across the coastal sites (Fig. 5.5, 5.6). The $\delta^{13}C$ values in majority of studied compartments at Melnragė site were lower than at Palanga/ Būtingė, while the most enriched $\delta^{13}C$ values were at Juodkrantė. As an exception, European smelt had higher $\delta^{13}C$ values in Melnragė site while $\delta^{13}C$ values of turbot were homogenous across all coastal sites (Fig. 5.5). The $\delta^{15}N$ values in majority of studied compartments at Melnragė site were higher than at other sites (Fig. 5.6). Only European smelt had similar $\delta^{15}N$ values across the coastal sites.

5.1.6. Structure of the food web, based on stable carbon and nitrogen isotope ratios

Across the Lithuanian coastal zone, the food web spanned broad range of $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 5.7). The $\delta^{13}C$ values ranged from -36.4 to -16.8‰, while the $\delta^{15}N$ values varied from -0.08 to 17.8‰. There were significant differences of SI values among studied organism groups (waterbirds, fishes, macrozoobenthos, macroalgae and POM/seston): Kruskal-Wallis test: H (4, N=441)=315.9 for $\delta^{13}C$ and 209.4 for $\delta^{15}N$, $p<0.001$. However, the SI values of different groups overlapped with each

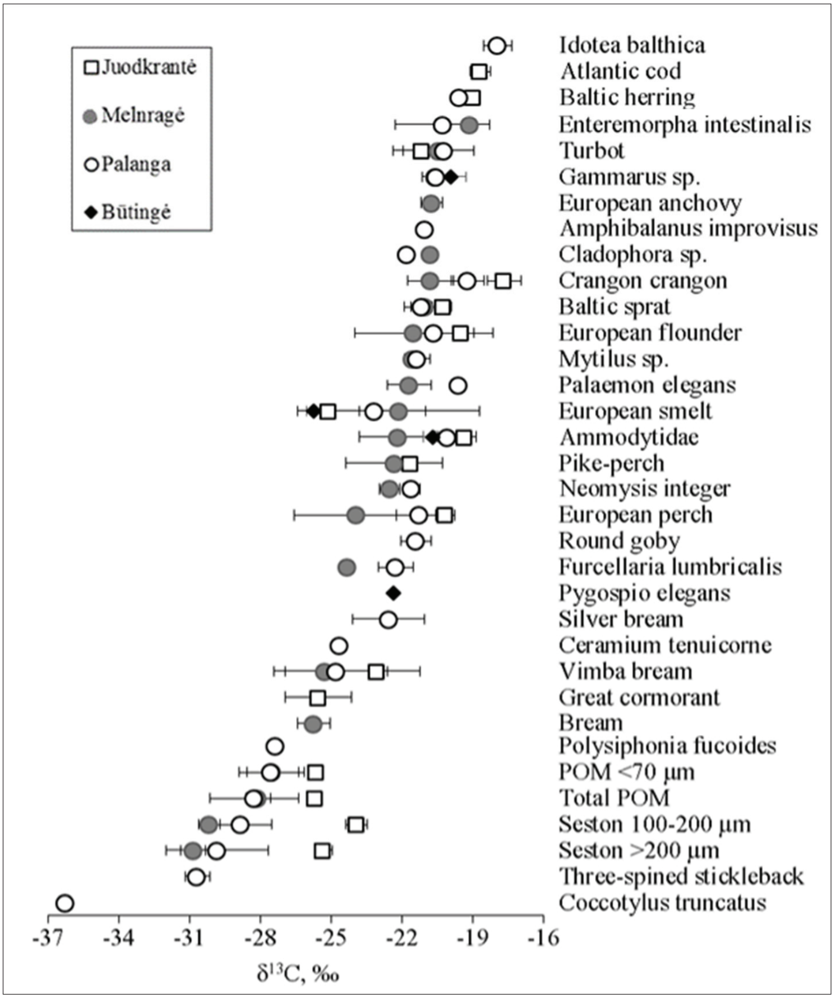

Figure 5.5. The $\delta^{13}C$ values of selected food web compartments* at different coastal sites.

*Values of $\delta^{13}C$ were sorted in order of decreasing depletion mostly based on Melnragė site.

other. Overlap in $\delta^{15}N$ values was evident between different macroalgae species and POM/seston (Mann-Whitney U-test, $p>0.05$), while they were different by $\delta^{13}C$ values ($p<0.05$). SI values of of some macrozoobenthos species overlapped with those of small pelagic fish species as Baltic sprat and European anchovy. A group of other fish species and cormorants had their distinct positions in the integrated SI biplot (Fig. 5.7).

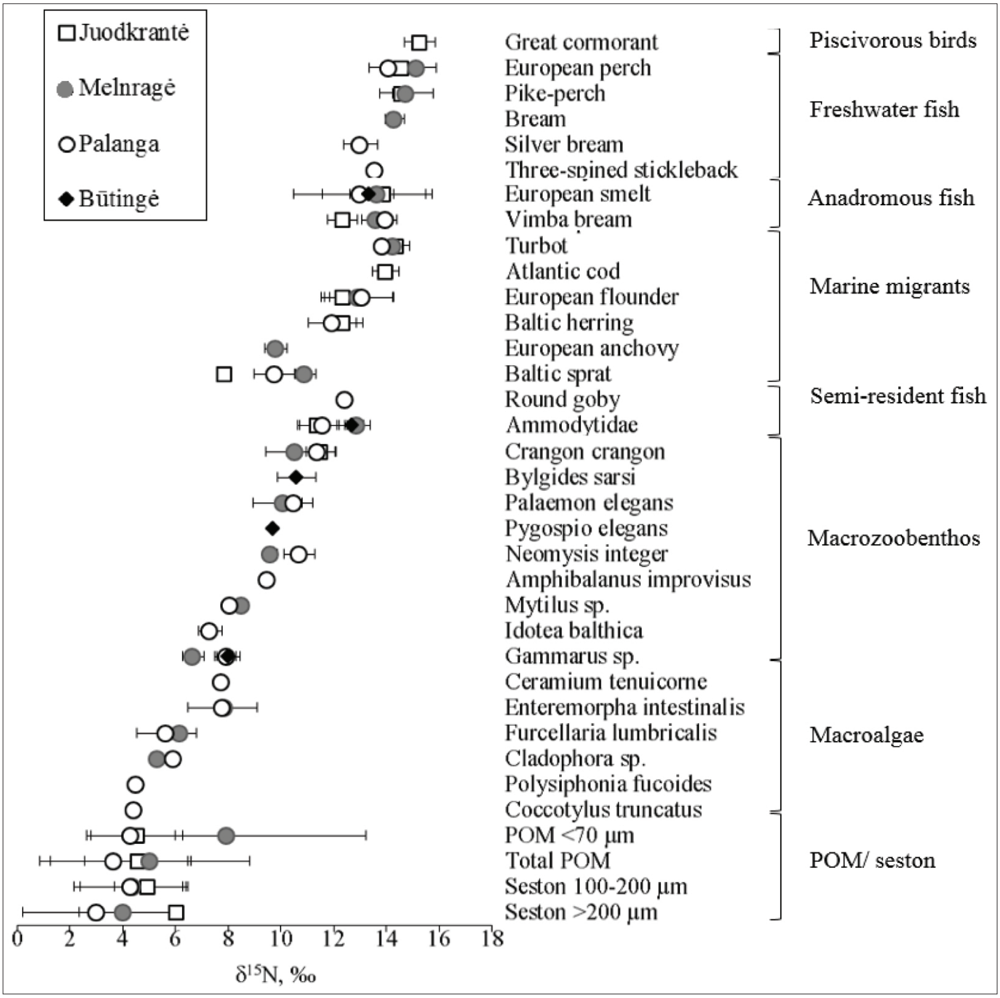

Figure 5.6. The δ^{15}N values of selected food web compartments* at different coastal sites.

*Values of δ^{15}N were sorted in order of increasing enrichment.

The ranges of δ^{13}C of POM and seston were relatively narrow compared to macroalgae (Fig. 5.7). Low δ^{13}C values were estimated in tissues of freshwater three-spined stickleback and cormorant juveniles. Intermediate δ^{13}C values were estimated in the rest of freshwater and anadromous fish species, and majority of studied macrozoobenthos species. Most enriched δ^{13}C values were in marine fishes and macrozoobenthos organisms as *C. crangon* and *I. balthica*.

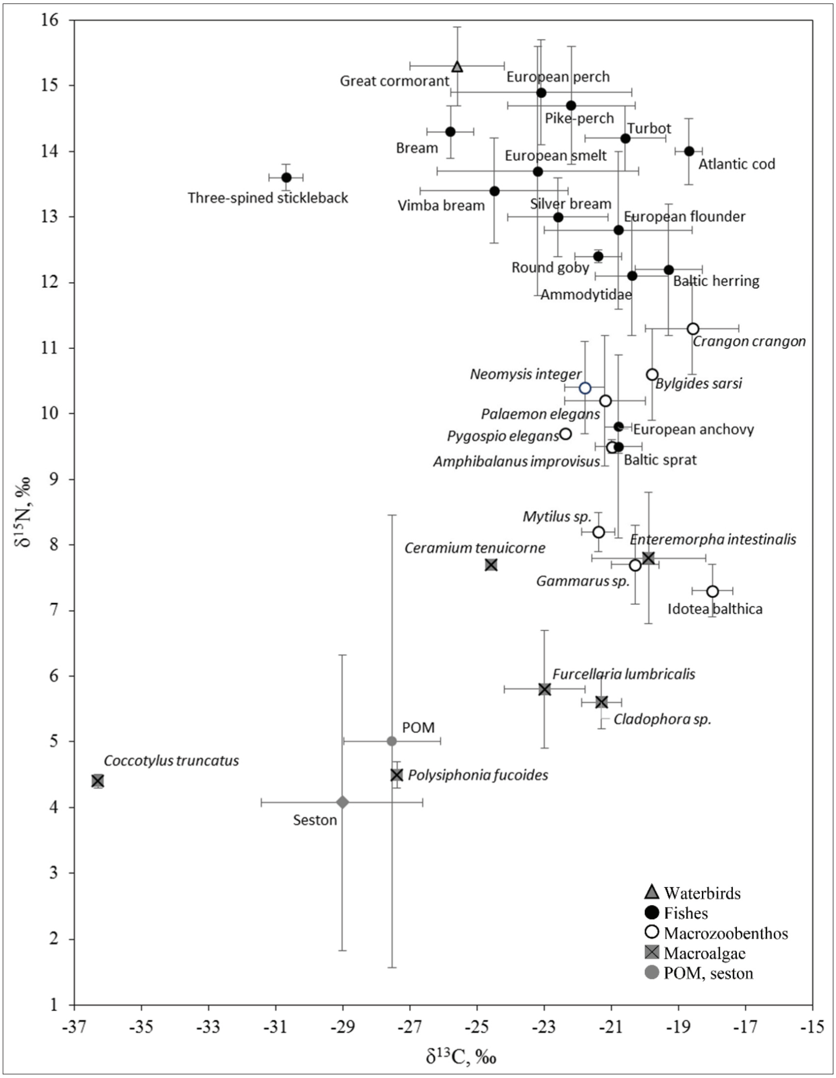

Figure 5.7. Summary of δ^{13}C and δ^{15}N values (mean ± SD) of POM, seston, macrozoobenthos, fish, and waterbirds (N=429) during a period of April-October 2010 across Lithuanian coastal sites in the Baltic Sea.

Regarding the δ^{15}N values, piscivorous waterbirds and predatory fish species as European perch and pikeperch had the highest values (Fig. 5.7). Majority of fish species had intermediate δ^{15}N values, while those in small pelagic marine fishes as Baltic sprat and European anchovy were relatively low and overlapped with values in omnivorous macrozoobenthos (mostly crustaceans). The lowest δ^{15}N values were estimated for other macroalgae species and POM/seston.

5.2. Food sources of wintering waterbirds

5.2.1. Grouping of wintering waterbirds, based on triple stable isotope ratios

There was a significant differentiation in isotopic composition among the waterbird species (MANOVA, $F_{6,25}=5.78$, $p<0.001$, Table 5.4). Univariate analysis showed significant differences in δ^{34}S ($F_{6,\ 25}=4.06$, $P=0.006$) and δ^{15}N values ($F_{6,25}=10.70$, $p>0.001$), while there were no differences in δ^{13}C values among studied birds species ($F_{6,25}=2.21$, $P=0.07$). The δ^{34}S analysis revealed differences between great crested grebe and other piscivorous birds as common guillemot and red-throated diver (HSD, $p<0.05$). The δ^{15}N values significantly differed between benthivorous ducks and piscivorous birds (HSD, $p<0.05$). The highest variation in all three SI values were observed in samples of long-tailed duck (Table 5.4). Regarding the blood SI values, two strong clusters have been defined in the cluster dendrogram (Fig 5.8A).

Table 5.4. **The species and number of analysed waterbirds (N), their mean body weights, mean (± SD), lowest (Min) and highest (Max) values of δ^{13}C, δ^{15}N and δ^{34}S in blood samples.**

Species	**N**	**C:N mass ratio**	**δ^{13}C, ‰**		**δ^{15}N, ‰**		**δ^{34}S, ‰**	
			Min-Max	**Mean**	**Min-Max**	**Mean**	**Min-Max**	**Mean**
Red-throated diver	7	3.5±0.05	-22.6-(-21.3)	-22.0±0.6	13.9-17.0	15.4±1.1	16.1-18.3	17.0±0.9
Black-throated diver	1	3.5		-23.3		14.9		18.6
Great crested grebe	9	3.4±0.04	-22.6-(-20.9)	-21.4±0.5	14.1-16.9	15.8±0.9	11.1-16.8	14.7±1.7
Common guillemot	3	3.5±0.05	-21.5-(-21.3)	-21.4±0.1	12.9-15.0	13.9±1.0	17.3-18.9	18.0±0.8
Razorbill	1	3.5		-21.4		13.6		17.5
Velvet scoter	8	3.5±0.04	-21.6-(-21.2)	-21.4±0.2	10.4-13.0	11.5±0.8	14.9-18.8	16.3±1.3
Long-tailed duck	3	3.4±0.09	-22.4-(-19.0)	-21.0±1.8	10.4-6.2	13.1±2.9	15.3-19.6	17.5±2.2

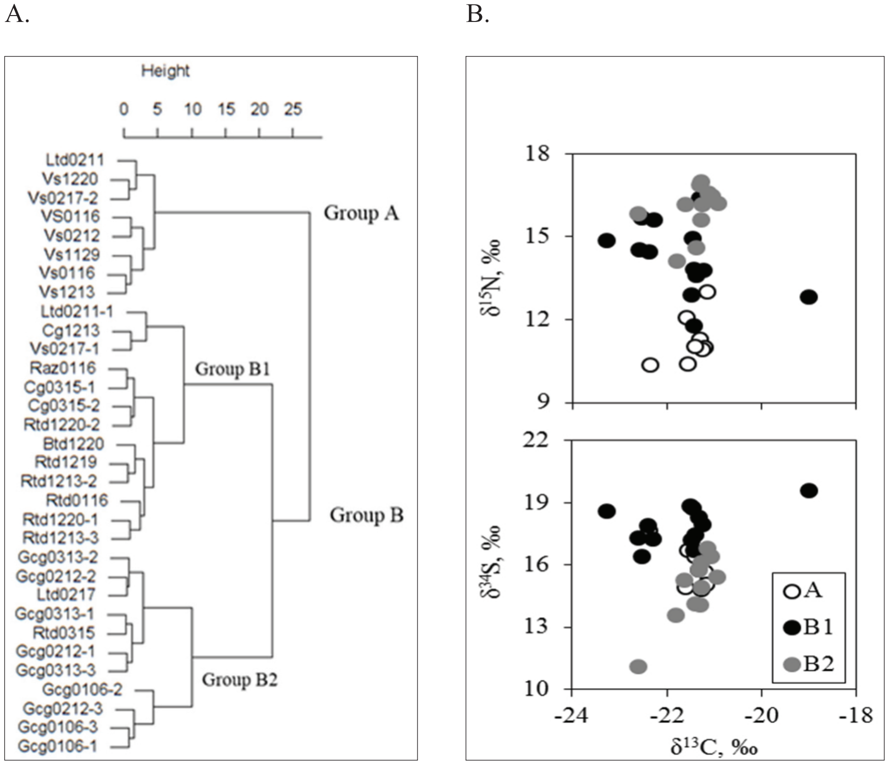

Figure 5.8. A. Ward's cluster analysis of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values in blood samples* of birds. B. Scatter plots of the clusters (A, B1, and B2) determined by Ward's linkage hierarchical clustering.

*Rtd – red-throated diver, Btd – black-throated diver, Gcg – great crested grebe, Cg – common guillemot, Raz – razorbill, Vs – velvet scoter, Ltd – long-tailed duck. Numbers in the labels represent sampling month and day in 2012-2013. Additional number after the hyphen represents sample number.

The first clear group consisted of seven individuals of benthivorous velvet scoter with and single long-tailed duck (Fig. 5.8A; Cluster A). The second cluster (Fig. 5.8A, Cluster B) contained the remaining completely or partly piscivorous birds and has two weaker, second-order sub-groups. The B1 group was composed of piscivorous birds as red-throated diver, common guillemot, razorbill, and two individuals of benthivorous ducks – velvet scoter and long-tailed duck. The B2 group was composed of all nine individuals of great-created grebe, single red-throated diver, and single long-tailed duck. However, due to overlapping SI values (Fig. 5.8B) interpretation of these sub-groups should be made with caution.

5.2.2. Food sources of piscivorous waterbirds

Stable isotope ratios of piscivorous waterbirds

Using triple isotope approach, the diets of great crested grebe, red-throated diver and common guillemot were estimated. There was a significant difference in isotopic compositions among these three species of wintering piscivorous birds (MANOVA, $F_{6,28}$=7.01, p<0.001). Univariate analysis revealed significant differences in mean δ^{34}S ($F_{2,16}$=10.07, p=0.002) and δ^{15}N values ($F_{2,16}$=4.16, p=0.035). Specifically, great crested grebe had a significantly lower δ^{34}S values relative to the values for red-throated diver (HSD, p<0.01) and common guillemot (HSD, p<0.01) (Fig. 5.9).

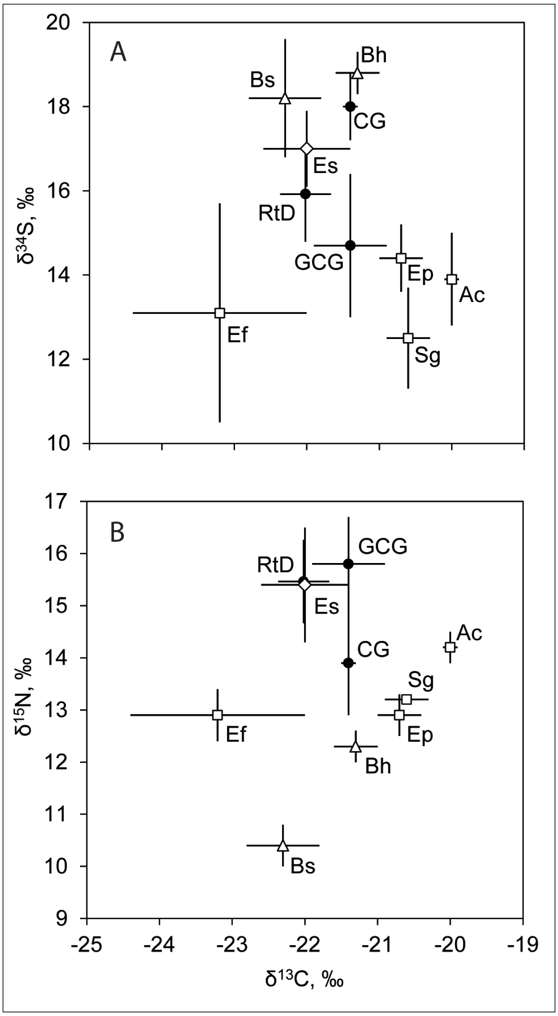

Figure 5.9. The mean δ^{34}S, δ^{15}N, and δ^{13}C values (± SD) in piscivorous waterbirds (blood samples) and fishes (white dorsal muscle). A. δ^{34}S versus δ^{13}C. B. δ^{15}N versus δ^{13}C.

Circles denote birds: RtD – red-throated diver, GCG – great crested grebe, and CG – common guillemot. Triangles denote pelagic fish species: Baltic herring (Bh) and Baltic sprat (Bs). Squares indicate benthic fish species: Atlantic cod (Ac), European flounder (Ef), European plaice (Ep), and sand goby (Sg). Rhombus marks benthopelagic European smelt (Es).

A noticeable variation of bird SI values was discovered over the study period (6.10).

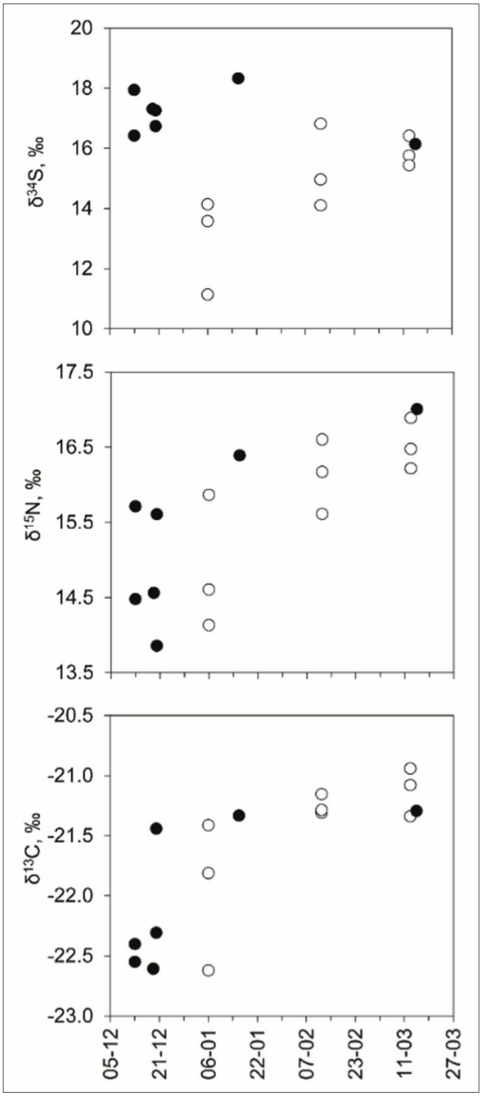

Figure 5.10. Variation of $\delta^{34}S$, $\delta^{15}N$, and $\delta^{13}C$ values in the blood of great crested grebe (open symbols) and red-throated diver (closed symbols) during the wintering season.

The 4‰ difference between the $\delta^{34}S$ values in great crested grebe and red-throated diver was observed in the beginning of the wintering season but it was not present in spring. There was also a shift towards higher $\delta^{13}C$ and $\delta^{15}N$ values in great crested grebe and red-throated diver at the end of the wintering season (Fig. 5.10).

Stable isotope ratios of piscivorous waterbirds food sources

There was a significant difference of $\delta^{34}S$ values among pelagic fishes and benthic fishes, as well as benthopelagic European smelt (ANOVA, $F_{2,30}=40.34$, $p<0.001$). The sulfur isotopic distance between pelagic fishes and benthic fishes equaled to 5.1‰ ($\delta^{34}S=18.49\pm1.01$ and 13.39±1.83‰, respectively). Smelt had an intermediate position and differed significantly from both pelagic fishes and benthic fishes in $\delta^{34}S$ values (15.92±1.13‰, HSD, $p=0.014$ and $p=0.015$, respectively). The $\delta^{15}N$ values differed significantly among the three groups (Kruskal–Wallis test: H [2, N=33]=25.38, $p<0.01$) and ranged from 11.34 ± 1.01‰ in pelagic fishes to 15.46±0.79‰ in smelt. The $\delta^{13}C$ values was similar among pelagic fishes and benthic fishes, as well as smelt (-21.19±0.57‰, -21.11±1.46‰, and -22.00±0.36‰, respectively, Kruskal–Wallis test: H [2, N=33]=4.11, $p=0.13$, Table 5.5).

There were significant differences in the individual SI content among species within the benthic and pelagic fish groups, which enabled us to separate sources in the mixing model at species level. Within the pelagic fish group, sprat differentiated from herring, displaying lower $\delta^{15}N$ values (1.9‰ difference, *t*-test, $t=-10.6$, df=10.6, $p<0.001$). Two benthic fish groups could be distinguished by $\delta^{13}C$ values: European flounder displayed the lowest values in the assemblage, whereas the other benthic fishes, including Atlantic cod, European plaice, and sand goby, had similar values (MANOVA, $F_{6,8}=5.4$, $p=0.06$). The $\delta^{13}C$ value of European flounder was 2.8‰ lower than those for other benthic fishes (Mann–Whitney *U*-test, $p<0.001$). There were no differences in $\delta^{34}S$ and $\delta^{15}N$ values between the two benthic fish groups ($P=0.77$ for $\delta^{34}S$ and $P=0.11$ for $\delta^{15}N$).

***Table 5.5.* The number of analysed individuals (N), body length (total length TL, Min – Max, cm), C:N mass ratios and mean (±SD) values for stable carbon ($\delta^{13}C$ and $\delta^{13}C$norm, ‰), nitrogen ($\delta^{15}N$, ‰), and sulfur ($\delta^{34}S$, ‰) isotopes in the white dorsal muscle of fishes.**

Species	N	TL, cm	C:N mass ratio	$\delta^{13}C$, ‰	$\delta^{13}C_{norm}$, ‰	$\delta^{15}N$, ‰	$\delta^{34}S$, ‰
Pelagic fishes							
Baltic sprat	6	7-12	4.8 ± 1.1	23.0 ± 0.7	21.5 ± 0.6	10.4 ± 0.4	18.2 ± 1.4
Baltic herring	6	15-26	3.8 ± 0.2	21.4 ± 0.4	20.9 ± 0.4	12.3 ± 0.3	18.8 ± 0.5
Benthic fishes							
European plaice	3	18-25	3.4 ± 0.03	-20.7 ± 0.3	20.6 ± 0.3	12.9 ± 0.4	14.4 ± 0.8
Sand goby	3	<5	3.6 ± 0.1	-20.6 ± 0.3	20.4 ± 0.3	13.2 ± 0.1	12.5 ± 1.2
European flounder	6	10-16	3.4 ± 0.1	-23.2 ± 1.2	23.1 ± 1.2	12.9 ± 0.5	13.1 ± 2.6
Atlantic cod	3	15-25	3.3 ± 0.04	-20.0 ± 0.1	20.1 ± 0.2	14.2 ± 0.3	13.9 ± 1.1
Benthopelagic fish							
European smelt (small)	3	10-15	3.4 ± 0.04	-22.0 ± 0.5	22.0 ± 0.5	14.8 ± 0.4	16.9 ± 0.6
European smelt (large)	3	20-25	3.4 ± 0.1	-22.0 ± 0.3	-22.0 ± 0.3	16.2 ± 0.1	15.0 ± 0.5

Mixing model results of the piscivorous waterbird diet

The isotopic values of the waterbird blood samples overlapped with the corrected values of their potential prey tissues (Fig. 5.11). The models revealed the diet composition differences for the waterbird species. Diets of common guillemot and red-throated diver were mainly composed of pelagic fishes (50–70% and 51–56%, respectively), whereas benthic fishes dominated in the diet of great crested grebe (48–53%) (Table 5.6). The average proportion of smelt in the diets of great crested grebe and red-throated diver was estimated within the range of 27–37%, whereas estimates for common guillemot varied from 19 to 34%, depending on the mixing model setup.

Table 5.6. **Contributions of food sources (mean ± SD and CI_{95}, %) to the diet of piscivorous birds, calculated by three, four, and five sources mixing models using mean $\delta^{34}S$, $\delta^{15}N$, $\delta^{13}C$ values of fishes.**

Mixing Model	Sources	Great crested grebe	Red-throated diver	Common guillemot
$\delta^{34}S$	Pelagic fishes*	20 ± 13 (0-42)	54 ± 12 (33-77)	50 ± 19 (11-88)
	European smelt	27 ± 16 (0-53)	32 ± 16 (0-58)	34 ± 18 (0-65)
	Benthic fishes**	53 ± 12 (30-77)	14 ± 9 (0-31)	16 ± 14 (0-44)
$\delta^{34}S$ & $\delta^{15}N$	Pelagic fishes*	12 ± 8 (0-27)	52 ± 8 (36-69)	65 ± 17 (32-94)
	European smelt	37 ± 11 (15-58)	36 ± 11 (13-56)	21 ± 15 (0-49)
	Benthic fishes**	51 ± 11 (29-73)	12 ± 8 (0-28)	14 ± 12 (0-39)
$\delta^{34}S$ & $\delta^{15}N$	Baltic sprat	7 ± 6 (0-19)	25 ± 11 (1-45)	37 ± 14 (6-64)
	Baltic herring	11 ± 9 (0-27)	31 ± 13 (4-54)	33 ± 15 (1-59)
	European smelt	34 ± 11 (12-56)	31 ± 11 (8-51)	19 ± 12 (0-40)
	Benthic fishes**	48 ± 12 (25-70)	14 ± 9 (0-30)	12 ± 10 (0-32)
$\delta^{34}S$ & $\delta^{15}N$ & $\delta^{13}C$	Baltic sprat	8 ± 6 (0-19)	25 ± 11 (2-44)	32 ± 13 (5-57)
	Baltic herring	11 ± 8 (0-26)	26 ± 11 (2-48)	26 ± 12 (1-47)
	European smelt	29 ± 10 (8-48)	27 ± 11 (6-48)	19 ± 11 (0-38)
	European flounder	28 ± 8 (11-44)	15 ± 10 (0-33)	14 ± 9 (0-30)
	Other benthic fishes	25 ± 9 (8-41)	7 ± 6 (0-19)	9 ± 8.1 (0-26)

*The combined pelagic fish source included Baltic sprat and Baltic herring. **The benthic fish source included only small benthic sand goby and European flounder in the models for great crested grebe and common guillemot, whereas benthic sand goby, European flounder, European plaice, and Atlantic cod were combined in the models for red-throated diver.

The single $\delta^{34}S$, dual $\delta^{34}S$&$\delta^{15}N$, and triple $\delta^{34}S$&$\delta^{15}N$&$\delta^{13}C$ isotope mixing models provided comparable mean values for proportions of main fish groups in bird diet (Table 5.6). The mixing model of a single $\delta^{34}S$ isotope predicted the proportions with the highest scores of CI_{95}, whereas the dual $\delta^{34}S$&$\delta^{15}N$ model allowed to estimate for precisely the share of benthic and pelagic fish groups and smelt (Fig. 5.11 and 5.12). The advantage of dual $\delta^{34}S$&$\delta^{15}N$ modeling approach is the possibility to analyze sprat and herring contributions as sources separately (Table 5.6). The triple isotope mixing model with five sources provided the lowest variability of different fish group contributions. Moreover, adding δ^{13}C to the model allowed us to differentiate the contribution of European flounder from other benthic fish species, while the proportions of other main groups remained close to those estimated by a four source δ^{34}S&δ^{15}N model (Table 5.6). These combinations suggest that dual δ^{34}S&δ^{15}N analysis is applicable to estimate smelt, herring, and sprat contributions to the diet, while δ^{13}C is only useful to resolve some heterogeneity within benthic fish assemblage.

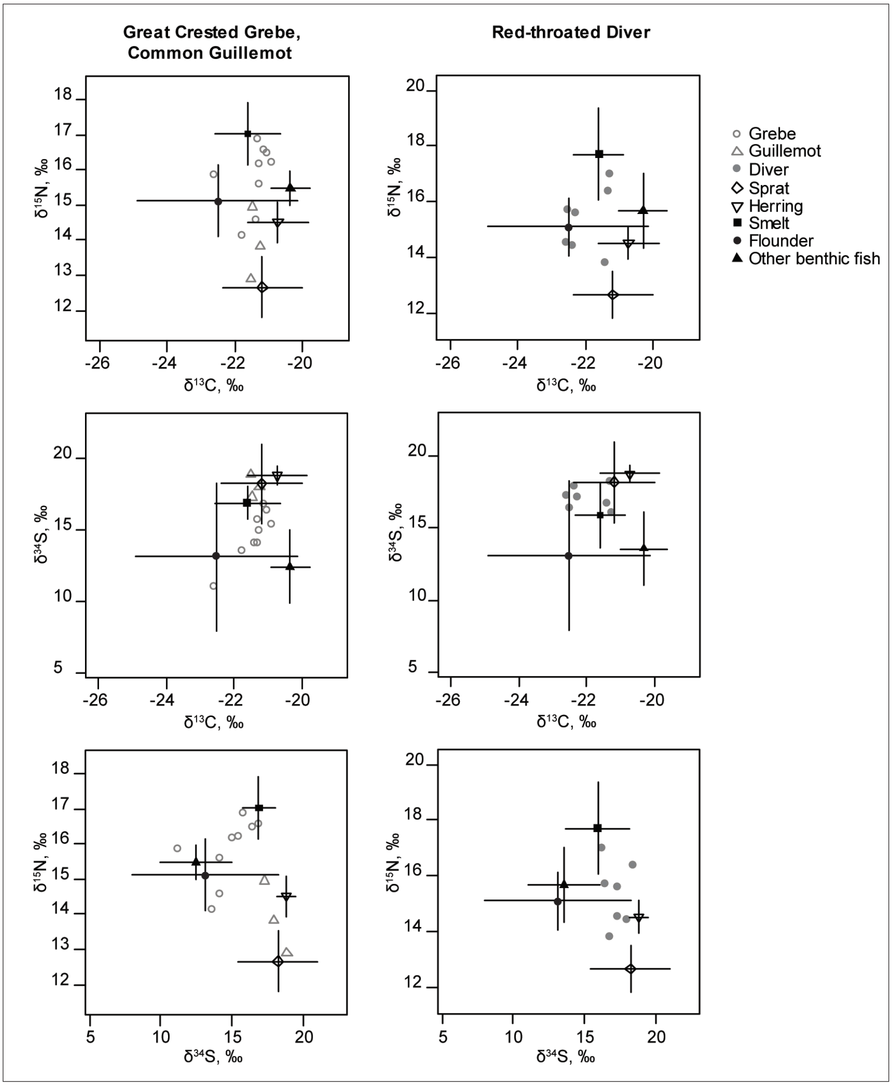

Figure 5.11. The five-sources mixing model biplots showing δ^{34}S, δ^{15}N, and δ^{13}C values in waterbirds (blood samples) and their potential food sources, incorporating the TEF correction.

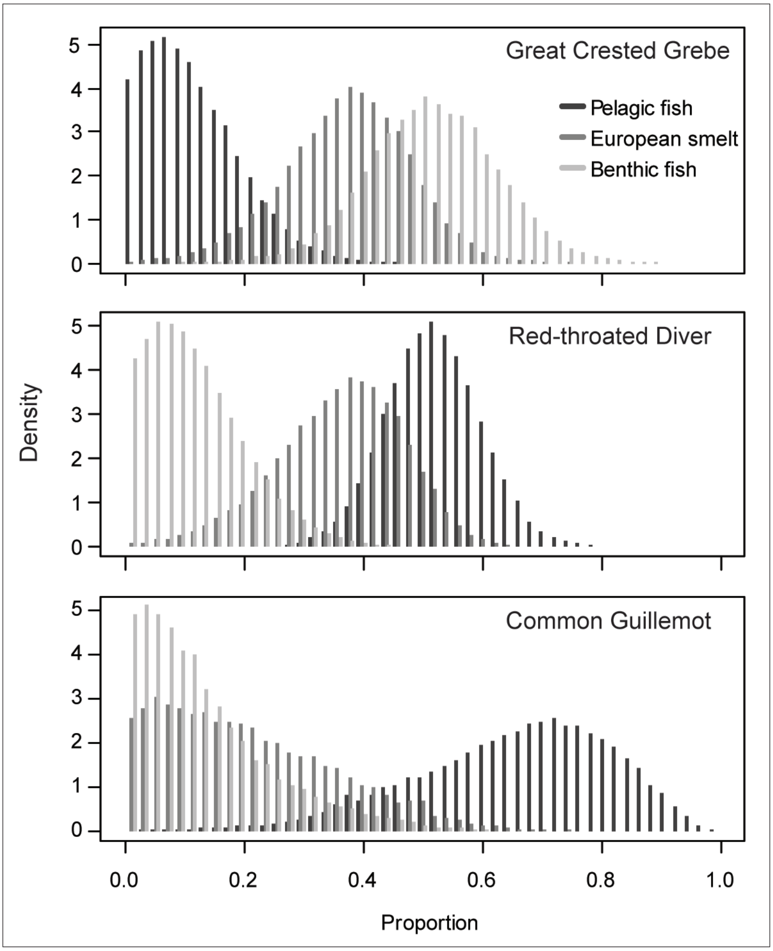

Figure 5.12. Probability density histograms showing the distribution of possible contributions from three fish groups (pelagic fishes, benthic fishes, and benthopelagic smelt) to the diet of great crested grebe, red-throated diver, and common guillemot calculated using $\delta^{34}S$ and $\delta^{15}N$ values from blood samples pooled over the whole season.

The triple isotope mixing models were also applied using SI values in birds for each sampling month to delineate the possible temporal changes in food source composition (Fig. 5.13).

The proportion of smelt increased by 1.7-fold in the diet of great crested grebe and three times in the diet of red-throated diver (Fig. 5.13). Grebes' consumption of European flounder declined by 2.4-fold across the study period. In turn, the share of pelagic fishes in the diet of divers decreased, while the contribution of sprat and

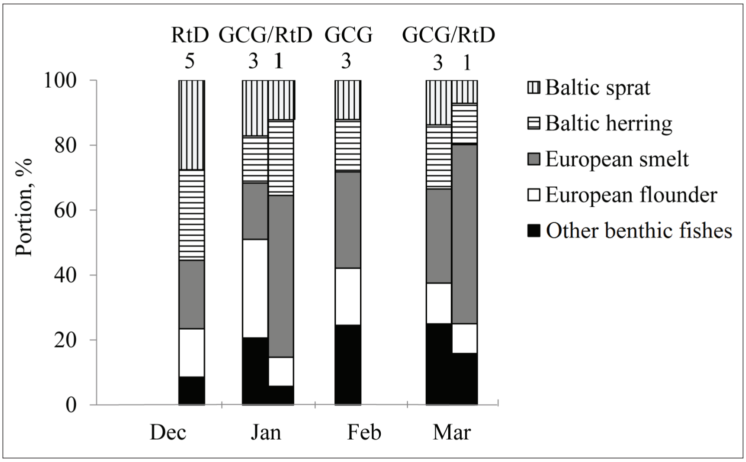

Figure 5.13. Monthly mean contribution of food sources to the diet of wintering great crested grebe (GCG) and red-throated diver (RtD) , calculated by triple stable isotope ($\delta^{34}S$, $\delta^{15}N$, and $\delta^{13}C$) five-source mixing models.

herring decreased by 3.9-fold and 2.2-fold, respectively. However, for more reliable results of seasonal variation, larger sample sizes should be used.

5.2.3. Food sources of benthivorous ducks

Stable isotope ratios of benthivorous ducks

We did find the isotopic composition of individuals of velvet scoter constant without any significant seasonal variations (regression analysis of the date effect, $p = 0.28$, 0.26 and 0.29 for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$). In contrast, the three measured individuals of long-tailed duck differed in isotopic composition (Fig. 5.14).

In general, the isotopic content of long-tailed duck was more variable than one of velvet scoters. The ranges for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were 0.4, 1.7 and 3.9‰ for velvet scoter and 3.4, 2.4 and 4.3‰ for long-tailed duck, respectively.

Stable isotope ratios of velvet scoter food sources

Analysis of diet composition of velvet scoter was estimated applying MANOVA to SI values of soft bottom macrozoobenthos, including crustaceans, collected at depth of 10-15 meters (Fig. 5.15; Table 5.7). Bivalves *C. glaucum* and *M. arenaria* were pooled into one homogeneous group by all three SI values (HSD, $p>0.05$). Polychaetes and *M. balthica* had similar $\delta^{34}S$ values (HSD test, $p>0.05$), but these two groups could still be separated by $\delta^{15}N$ values (HSD, $p<0.001$).

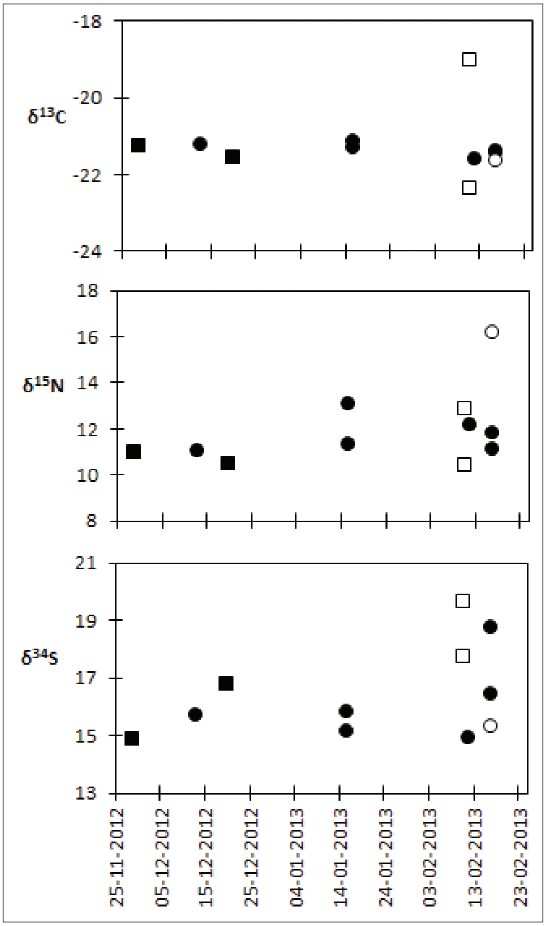

Figure 5.14. SI ratios in blood of velvet scoter (closed symbols) (N=8) and long-tailed duck (open symbols) (N=3) wintering in the Lithuanian coastal zone. Squares denote females, circles mark males.

According to the homogeneous groups defined by $\delta^{34}S$ and $\delta^{15}N$ values, five benthic food sources could be distinguished: 1) crustaceans *S. entomon*, 2) crustaceans *C. crangon,* 3) a mixed group of *M. arenaria* and *C. glaucum*, 4) polychaetes, and 5) *M. balthica.* These groups could be included as separate end-points in to the mixing model. The homogeneous group distinguished by $\delta^{13}C$ values included large crustaceans *C. crangon* and *S. entomon* with the most enriched $\delta^{13}C$ values, which differed significantly between each other (-20.1± 0.1‰ and -18.8± 0.3‰; HSD, $p<0.05$).

Table 5.7. **The number of individuals (N), C:N mass ratios and mean (±SD) values for stable carbon (δ^{13}C and $\delta^{13}C_{norm}$, ‰), nitrogen (δ^{15}N, ‰), and sulfur (δ^{34}S, ‰) isotopes in macrozoobenthos organisms as food sources for velvet scoter. N represents sample sizes for combined δ^{13}C and δ^{15}N/ separate δ^{34}S analysis.**

Sources	N	C:N	δ^{13}C, ‰	$\delta^{13}C_{norm}$, ‰	δ^{15}N, ‰	δ^{34}S, ‰
Saduria entomon	6/6	6.1±0.4	-21.5±0.3	-18.8± 0.3	13.1±0.3	15.1±0.9
Crangon crangon	6/6	3.4±0.0	-20.1±0.1	-20.1± 0.1	12.4±0.2	13.5±0.9
Macoma balthica	6/6	4.8±0.1	-22.8±0.1	-21.5±0.2	7.8±0.2	10.7±0.2
Mya arenaria	9/5	4.1±0.1	-22.6±0.3	-21.9±0.2	6.6±0.2	16.6±0.6
Cerastoderma glaucum	12/12	5.0±0.2	-23.6± 0.7	-22.0±0.8	5.7±0.4	17.4±0.7
Polychaetes	9/4	4.3±0.2	-23.1±0.4	-22.2±0.5	11.0±0.6	10.7±1.0

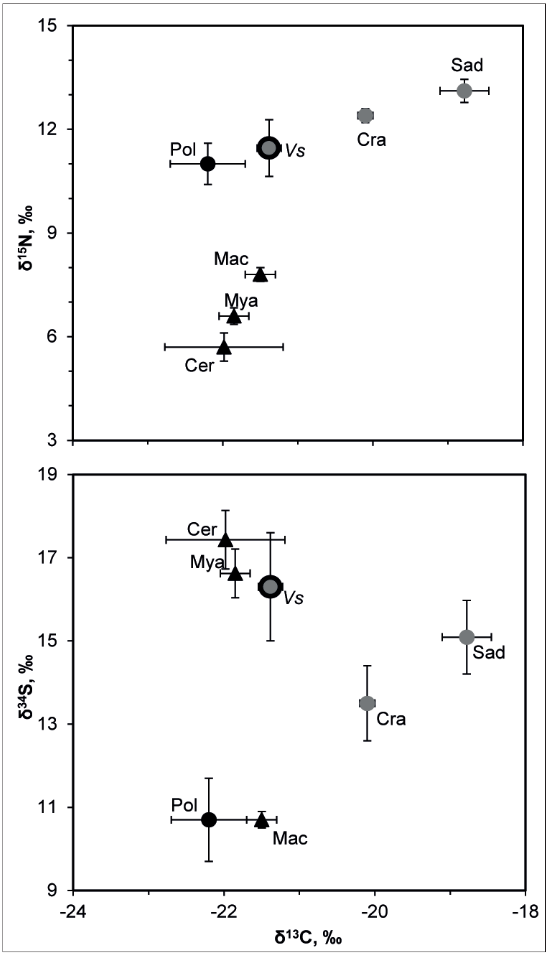

Figure 5.15. The mean δ^{34}S, δ^{15}N, and δ^{13}C values (± SD) in velvet scoter and potential food sources. A. δ^{15}N versus δ^{13}C. B. δ^{34}S versus δ^{13}C. Large circle denotes velvet scoter (Vs). Triangles denote bivalves: Mac – *Macoma balthica*, Mya – *Mya arenaria*, Cer – *Cerastoderma glaucum*. Grey circles mark crustaceans: Sad – *Saduria entomon*, Cra – *Crangon crangon*. Black circle denotes polychaetes.

Mixing model results of the velvet scoter diet

The Bayesian mixing models were calculated only for consumers being in the 95% mixing region of the sources. However, the positions of individuals of velvet scoter in the biplots and suitability of proposed model was difficult to inspect visually (Fig. 5.16A). Therefore, mixing polygon simulation approach was used to indicate the suitability of the proposed mixing model for velvet scoter. One of the eight individuals of velvet scoter occurred outside the 95% mixing region (Fig. 5.16B), which requires an alternative model to explain its isotopic signatures and was excluded from further analysis and mixing models calculation.

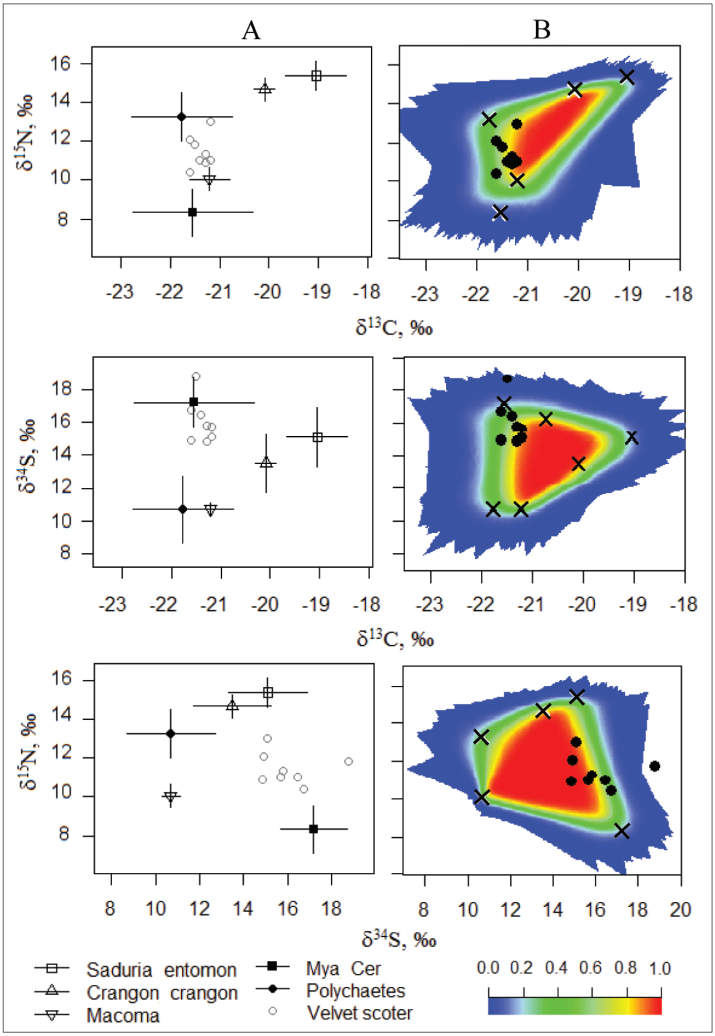

Figure 5.16. A. The five-source mixing model biplots showing δ34S, δ15N, and δ13C values in velvet scoter and potential food sources, incorporating the TEF corrections. B. The simulated mixing polygon for the biplots in A. The positions of velvet scoter (black dots) and mean source values (black crosses) are shown. Probability levels (at 20% step) were shown as color scale classes.

The mixing models for the remaining seven individuals showed that the main food source is derived from the mixed group of bivalves *M. arenaria, C. glaucum* (Table 5.8) contributing from 51 to 56% depending on different model setups. The single $\delta^{34}S$, dual $\delta^{34}S$&$\delta^{15}N$, and triple $\delta^{34}S$&$\delta^{15}N$&$\delta^{13}C$ isotope mixing models provided comparable mean values for proportions of the main source groups in the diet of velvet scoter. However, contribution of other groups varied with different model setups. Proportion of large crustaceans in the diet composition derived using the five-source mixing model was lower than using three- or two-sources mixing model. The share of combined *M. balthica* and polychaetes group was larger in five-source model than in models with fewer number of sources.

We did find that even $\delta^{34}S$ values alone could characterize main sources quite accurately. Dual mixing models allowed the discrimination of *M. balthica* and polychaetes. Adding $\delta^{13}C$ values to the model, further differentiation of *S. entomon* and *C. crangon* as separate groups was possible (Table 5.8).

Table 5.8. **Contributions of food sources (mean ± SD and CI_{95}, %) to the diet of velvet scoter, calculated by three, four, and five sources mixing models using mean $\delta^{34}S$, $\delta^{15}N$, $\delta^{13}C$ values of macrozoobenthos.**

Mixing model setup	Sources	Proportions
$\delta^{34}S$	Large crustaceans*	33 ± 16 (0-58)
	Mya arenaria & Cerastoderma glaucum	56 ± 11 (35-78)
	Macoma balthica, Polychaetes	11 ± 7 (0-24)
$\delta^{34}S$ & $\delta^{15}N$	Large crustaceans*	37 ± 8 (21-51)
	Mya arenaria & Cerastoderma glaucum	51 ± 6 (38-63)
	Macoma balthica	6 ± 5 (0-15)
	Polychaetes	7 ± 5 (0-18)
$\delta^{34}S$ & $\delta^{15}N$ & $\delta^{13}C$	*Saduria entomon*	9 ± 7 (0-21)
	Crangon crangon	13 ± 9 (0-30)
	Mya arenaria & Cerastoderma glaucum	52 ± 9 (32-68)
	Macoma balthica	7 ± 6 (0-21)
	Polychaetes	18 ± 10 (0-36)

*include *S. entomon* and *C. crangon*.

Stable isotope ratios of long-tailed duck food sources

Analysis of diet composition of long-tailed duck involved macrozoobenthos species from both soft and hard bottom types and fishes (Fig. 5.17 and Table 5.9). Isotopic values in the potential food sources of long-tailed duck differed statistically (MANOVA, $F_{3,36} = 74.2$, $p<0.001$). However, bivalves (*C. glaucum*, *M. arenaria)*, Corophiidae, and mysids composed a homogeneous group by $\delta^{34}S$ values (*Mixed sand*; HSD, $p>0.05$). Hard bottom macrozoobenthos species as *Mytilus* sp. and Corophiidae were also separated into a distinct group (*Mixed hard*) using $\delta^{13}C$ values ((HSD, $p>0.05$).

***Table 5.9.* The number of individuals (N), body length (total length TL, Min – Max, mm), C:N mass ratios and mean (±SD) values for δ^{13}C, δ^{13}C$_{norm}$, δ^{15}N, and δ^{34}S in organisms as food sources for long-tailed duck. N represents sample sizes for combined δ^{13}C and δ^{15}N / separate δ^{34}S analysis.**

Sources	N	δ^{13}C$_{norm}$, ‰	δ^{15}N, ‰	δ^{34}S, ‰
European flounder	6/6	-23.1±1.2	12.9±0.5	13.1±2.6
European smelt	6/6	-22.0±0.4	15.5±0.8	15.9±1.1
Large crustaceans*&Sand goby	20/20	-19.9 ± 0.8	12.7±0.5	13.7±1.3
Macoma balthica	12/12	-21.0±0.5	8.1±0.4	10.0±0.9
Mixed hard**	13/11	-23.8±1.2	7.9±0.6	14.4±1.1
Mixed sand***	38/27	-21.3±1.0	6.2±1.0	16.9±0.7
Polychaetes	15/8	-22.0±0.6	11.0±0.5	9.8±1.2

* Large crustaceans include C. crangon and S. entomon.

**Mixed hard bottom group includes Mytilus sp. and Corophiidae.

***Mixed sand group involves M. arenaria, C. glaucum, Corophiidae, and mysids.

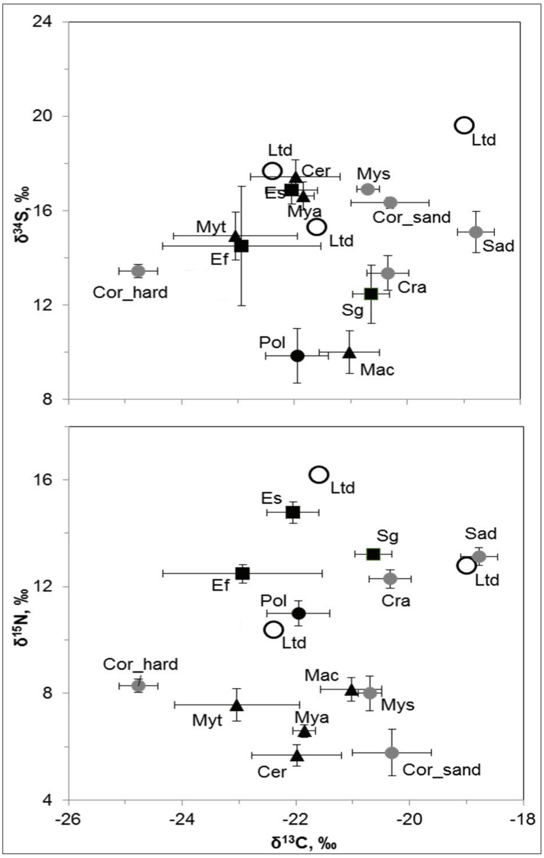

Figure 5.17. The mean δ^{34}S, δ^{15}N, and δ^{13}C values (± SD) in long-tailed duck and their potential food sources. A. δ^{34}S versus δ^{13}C. B. δ^{15}N versus δ^{13}C. Large open circles denote ducks (Ltd). Triangles denote bivalves: Myt - *Mytilus* sp., Mac – *Macoma balthica*, Mya – *Mya arenaria*, Cer – *Cerastoderma glaucum*. Grey circles mark crustaceans: Cor – Corophiidae from hard and sandy bottom, Mys – mysids, Sad – *Saduria entomon*, Cra – *Crangon crangon*. Squares indicate fish species: Ef - European flounder, Sg - Sand goby, Es – European smelt.

Mixing model results of the long-tailed duck diet

Applied mixing polygon simulation suggested that only one of three individuals of long-tailed duck occurred inside the 95% mixing region with analyzed food sources (Fig. 5.18). Therefore, the mixing model was applied only for single individual. The model output showed that the main food source was European smelt (45% of the total diet). Lesser contributions came from European flounder and the group of large crustaceans and sand goby (18 and 12%, respectively). Contributions of other groups were less than 8% (Table 5.10).

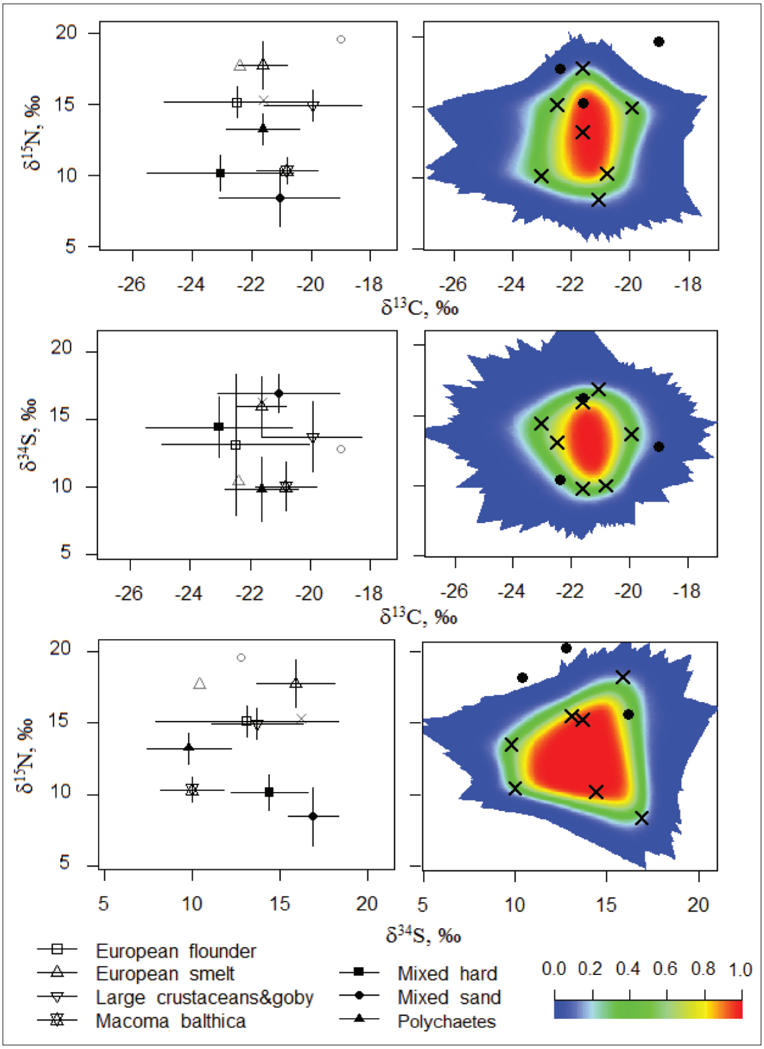

Figure 5.18. A. The seven-source mixing model biplots showing $\delta^{34}S$, $\delta^{15}N$, and $\delta^{13}C$ values in long-tailed duck (grey symbols) and food sources (explained symbols), incorporating the TEF corrections. B. The simulated mixing polygon for the biplots in A. The positions of long-tailed duck (black dots) and the average source values (black crosses) are shown. Probability levels (at 20% step) were shown as color scale classes.

Table 5.10. **Seven source contributions (mean ± SD and CI$_{95}$, %) to the diet of single long-tailed duck, calculated by mixing model using mean δ^{34}S, δ^{15}N, δ^{13}C values of fishes and macrozoobenthos.**

Model setup	Sources	Proportions
δ^{34}S & $\delta 1^{5}$N & δ^{13}C	European flounder	18 ± 13 (0-44)
	European smelt	45 ± 12 (21-67)
	Large crustaceans&Sand goby	12 ± 9 (0-31)
	Macoma balthica	4 ± 3 (0-11)
	Mixed hard	7 ± 5 (0-18)
	Mixed sand	8 ± 6 (0-20)
	Polychaetes	5 ± 4 (0-13)

Diet composition of benthivorous ducks by the gut content analysis

As the both median fat scores for velvet scoters and long-tailed ducks were 4, we consider that all individuals were healthy and actively foraging birds. A total of 35 velvet scoters were collected from fisherman nets located in the soft bottom habitats. Proportion of velvet scoters with full esophagi and gizzards was 89 %. Majority of collected individuals contained some pebbles and at least one species of bivalves. Three bivalve species living in soft substrate were the most important food sources for the velvet scoter (Table 5.11).

Table 5.11. **Diet composition of velvet scoter (N=31) in the soft bottom habitats. Wet weights (WW) and organic matter weight (AFDW) of different food objects are presented in grams (g) and percentage (%). Frequency of occurrence (FO) of prey objects is presented by number (n) and percentage (%) of duck specimens which consumed particular prey.**

Taxa of prey objects	WW, g	WW, %	AFDW, g	AFDW, %	FO, n	FO, %
Bivalvia	188.84	99.76	21.13	99.45	31	100.00
Mya arenaria	51.43	27.17	7.44	35.01	28	90.32
Macoma balthica	51.46	27.19	6.59	31.01	27	87.10
Cerastoderma glaucum	85.95	45.41	7.10	33.43	30	96.77
Crustacea	0.45	0.24	0.12	0.55	1	3.23
Crangon crangon	0.45	0.24	0.12	0.55	1	3.23
Total	189.29	100.00	21.24	100.00	31	

A total of 61 long-tailed ducks were collected from fisherman nets located in the hard and soft bottom habitats. Proportions of ducks with full esophagi and gizzards was 39 % in the hard bottom habitat and 72 % in the soft bottom habitat. In the hard bottom habitat, the fishes, particularly the European smelt, were the most important prey item, the bivalves were found in more than a half of all ducks but they constituted only 2% of the organic matter content of the total diet, while crustaceans were found in the guts of one third of analysed birds and contributed to the approx. 3% organic matter content (Table 5.12).

***Table 5.12.* Diet composition of long-tailed ducks in the stony and soft bottom habitats. N means number of ducks used for the diet analysis. Wet weights (WW) and organic matter weight (AFDW) of different prey objects are presented in grams (g) and percent (%). Frequency of occurrence (FO) of prey objects is presented by number (n) and percent (%) of duck specimens what consumed particular prey.**

Taxa of prey objects	**Hard bottom (N=24)**						**Soft bottom (N=13)**					
	WW, g	**WW, %**	**AFDW, g**	**AFDW, %**	**FO, n**	**FO, %**	**WW, g**	**WW, %**	**AFDW, g**	**AFDW, %**	**FO, n**	**FO, %**
Algae	0.04	0.03			2	8.3	-	-			-	-
Bivalvia	16.33	13.02	2.12	2.15	14	58.3	3.26	3.16	0.37	0.60	9	69.2
Mya arenaria	0.59	0.47	0.09	0.09	4	16.7	1.24	1.20	0.18	0.29	4	30.8
Macoma balthica	6.15	4.90	0.79	0.80	6	25.0	0.19	0.18	0.02	0.04	3	23.1
Mytilus sp.	9.52	7.58	1.24	1.26	9	37.5	0.14	0.14	0.02	0.03	3	23.1
Cerastoderma glaucum	0.07	0.06	0.01	0.01	2	8.3	1.69	1.64	0.14	0.24	6	46.2
Crustacea	12.52	9.98	2.85	2.88	8	33.3	46.90	45.46	9.52	15.52	9	69.2
Mysids	1.05	0.84	0.28	0.29	1	4.2	-	-		0.00	-	-
Saduria entomon	6.29	5.02	1.23	1.24	4	16.7	35.71	34.61	6.95	11.34	5	38.5
Crangon crangon	4.94	3.94	1.28	1.30	3	12.5	0.83	0.80	0.22	0.35	1	7.7
Unident. crustacea	0.24	0.19	0.05	0.06	2	8.3	10.36	10.04	2.35	3.84	5	38.5
Pisces	96.57	76.97	93.67	94.96	13	54.2	53.01	51.38	51.42	83.88	6	46.2
Osmerus eperlanus	80.92	64.50	78.49	79.58	8	33.3	3.69	3.58	3.58	5.84	1	7.7
Gasterosteus aculeatus	1.29	1.03	1.25	1.27	1	4.2	-	-	0.00	0.00	-	-
Ammodytes tobianus	5.30	4.22	5.14	5.21	2	8.3	37.72	36.56	36.59	59.68	3	23.1
Platichthys flesus	0.17	0.14	0.16	0.17	1	4.2	-	-	0.00	0.00	-	-
Pomatoschystus minutus	5.44	4.34	5.28	5.35	2	8.3	-	-	0.00	0.00	-	-
Unident. fishes	3.45	2.75	3.34	3.39	4	16.7	11.60	11.24	11.25	18.35	4	30.8
Total	125.46	100.0	98.64	100.00			103.17	100.0	61.30	100.00		

In the soft bottom habitats, fishes and crustaceans were the most important food objects (84 and 15 % of the organic matter content, accordingly) (Table 5.12). Lesser sand-eel as the most important fish species contributed to 37% of the total wet weight and 60% of organic matter content of the total diet. Contribution of *S. entomon* was 11% of the organic matter weight and this crustacean was taken by 39% of birds. Bivalves were frequently consumed by birds (69%) but their contribution to the total wet or organic matter weight was negligible.

5.3. ECOPATH model for the coastal food web

5.3.1. Structure and characteristics of the food web

The food web model of the Baltic Sea Lithuanian coastal zone estimates the TLs in the range of 1 to 4.2 (Table 5.13; Fig. 5.19). Overview of TLs together with other estimates and ecophysiological parameters by group is presented in Table 5.13.

Table 5.13. **Model estimates for the coastal food web.**

TL - trophic level; EE – ecotrophic efficiency (ww(gm^{-2})); B – estimated biomass (ww(gm^{-2})); P/Q – production/consumption ratio (y^{-1}); R/A - respiration/ assimilation (y^{-1}); P/R - production/ respiration (y^{-1}); R/B - respiration/ biomass (y^{-1}).

No	Group name	TL	EE	B	P/Q	R/A	P/R	R/B
1	Phytoplankton	1.0	0.65	5.1990				
2	Mesozooplankton	2.0	0.50	3.9400	0.043	0.95	0.057	227.0
3	Nectobenthos	2.5	0.25	1.7918	0.242	0.70	0.433	13.96
4	Macrophytobenthos	1.0	0.07	0.0520				
5	Macrozoobenthos filtrators	2.0	0.50	71.3000	0.140	0.83	0.212	8.58
6	Macrozoobenthos omnivorous (<9.9 mm)	2.0	0.31	59.1120	0.195	0.76	0.323	7.86
7	Macrozoobenthos omnivorous (10-20 mm)	2.2	0.27	11.0835	0.380	0.53	0.905	5.46
8	Macrozoobenthos omnivorous (>20-50 mm)	2.4	0.23	3.6945	0.380	0.53	0.905	5.46
9	Polychaetes	2.0	0.36	48.5000	0.081	0.90	0.113	22.40
10	Baltic herring (juvenile)	3.1	0.99	0.0197	0.056	0.93	0.075	10.95
11	Baltic herring (adult)	3.2	0.99	0.0327	0.069	0.91	0.095	5.82
12	Baltic sprat (juvenile/adult)	3.0	0.99	0.0453	0.074	0.91	0.103	6.62

No	Group name	TL	EE	B	P/Q	R/A	P/R	R/B
13	Lesser sand-eel, Greater sand-eel juvenile/sub-adult)	3.2	0.49	0.2636	0.137	0.83	0.206	3.98
14	Greater sand-eel (adult)	3.3	1.00	0.104	0.077	0.90	0.107	3.47
15	Common and sand gobies (juvenile. adult)	3.1	1.00	4.573	0.143	0.82	0.218	2.11
16	Twaite shad (juvenile)	3.8	0.11	0.0007	0.090	0.89	0.126	6.48
17	Twaite shad (adult)	3.6	0.37	0.2509	0.069	0.91	0.095	5.82
18	Eelpout (juvenile)	3.0	0.999	0.0017	0.185	0.77	0.301	1.82
19	Eelpout (adult)	3.2	1.00	0.0020	0.151	0.81	0.233	1.59
20	European flounder (juvenile/sub-adult)	3.3	0.999	0.0172	0.185	0.77	0.301	1.82
21	European flounder (adult)	3.3	0.47	1.0964	0.151	0.81	0.233	1.59
22	Silver bream (adult)	3.0	0.06	0.0852	0.138	0.83	0.209	1.77
23	Bream (adult)	3.2	0.01	0.8517	0.093	0.88	0.131	2.83
24	Vimba bream (juvenile)	2.7	1.00	0.0336	0.185	0.77	0.301	1.82
25	Vimba bream (adult)	2.8	1.00	0.0041	0.093	0.88	0.131	2.83
26	Three-spined stickleback (adult)	3.4	0.99	0.0004	0.177	0.78	0.283	2.40
27	Ruffe (adult)	3.2	0.99	0.0008	0.077	0.90	0.106	4.34
28	European perch (juvenile)	3.0	0.99	0.00004	0.137	0.83	0.206	3.98
29	European perch (sub-adult/adult)	3.8	0.09	0.0811	0.216	0.73	0.371	2.15
30	Atlantic salmon (adult)	4.0	0.18	0.0261	0.135	0.83	0.204	4.12
31	Pike-perch (juvenile/sub-adult)	4.0	0.99	0.0042	0.184	0.77	0.298	2.82
32	Pike-perch (adult)	4.2	0.17	0.1853	0.491	0.39	1.591	0.53
33	Turbot (juvenile)	3.5	0.94	0.0139	0.185	0.77	0.301	1.84
34	Turbot (sub-adult/adult)	3.9	1.00	0.0195	0.151	0.81	0.233	1.59
35	European smelt (juvenile)	3.2	0.99	0.0514	0.137	0.83	0.206	3.98
36	European smelt (adult)	3.7	1.00	0.0021	0.115	0.86	0.167	3.29
37	European eel (adult)	4.1	0.06	0.0075	0.151	0.81	0.233	1.59
38	Great cormorant	4.2	0.00	0.0408	0.001	0.99	0.002	95.84
39	Wintering diving ducks	3.0	0.02	0.0297	0.004	0.99	0.005	95.49
40	Wintering piscivorous birds	4.2	0.01	0.0140	0.001	0.99	0.002	95.84
41	Detritus	1.0	0.99	1.8029				

Invertebrates occupy TLs lower than 2.5. TLs of fishes vary from 2.7 to 4.2, showing no significant differences among different guilds, except for the semi-resident species being in a quite narrow range (TL 3.0-3.3) (Table 5.13, Fig. 5.20). Both size groups of vimba bream are at the lowest TLs of 2.7 and 2.8. Small pelagic and benthic fishes including juveniles of larger fish species are at TLs from 3 to 3.4. Higher TLs from 3.5 to 3.9 are assigned to fishes that are at least partially piscivorous. All groups of pike-perch, adults of Atlantic salmon and European eel occupy the TLs higher than 4.0. Moreover, there are large differences between waterbird groups: benthivorous ducks are on TL 3, while the TLs of piscivorous waterbirds, including great cormorant, are higher than 4.

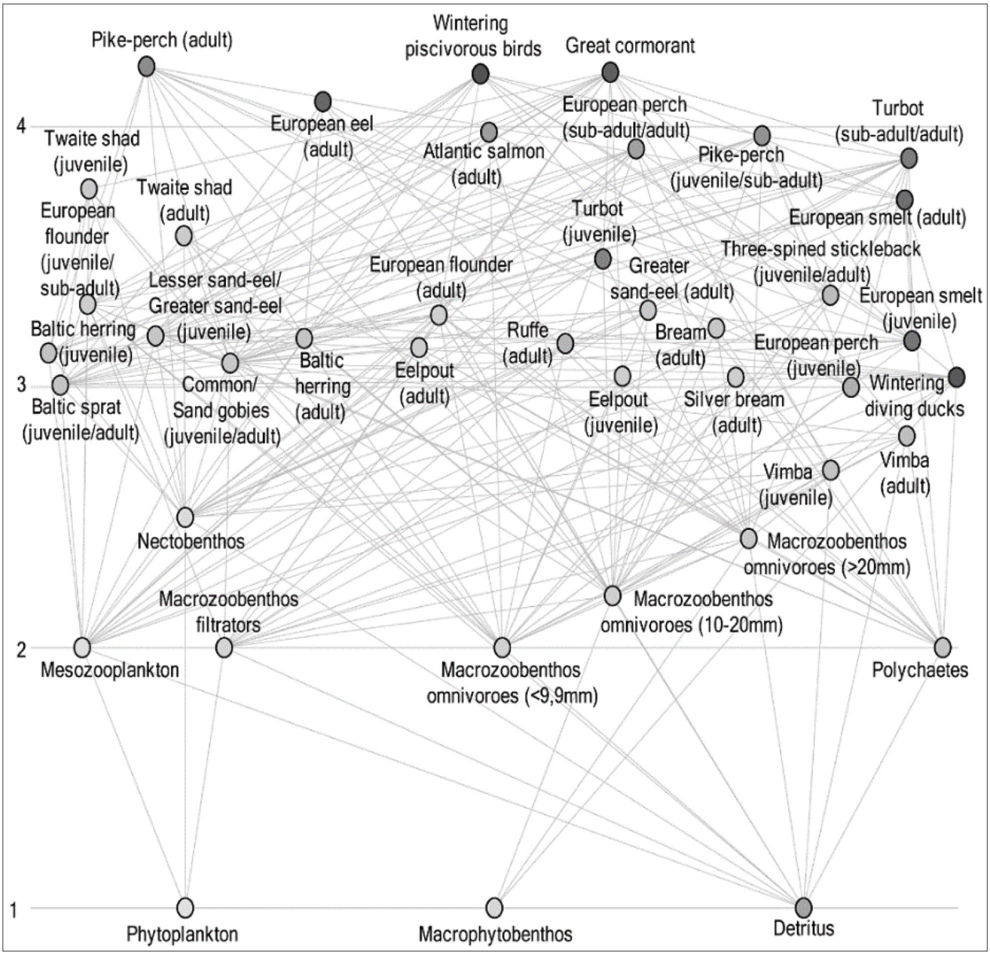

Figure 5.19. A food web of the Lithuanian coastal zone in the Baltic Sea (numbers on the left indicates trophic levels) (modified from Razinkovas-Baziukas et al., accepted).

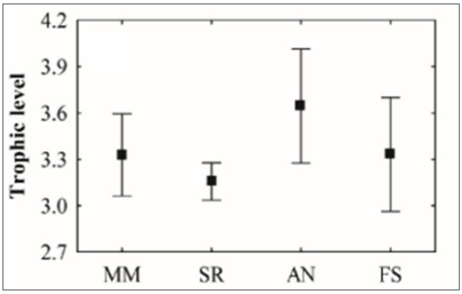

Figure 5.20. Differences among fish guilds in trophic levels (modified from Razinkovas-Baziukas et al., accepted).

Planktonic organisms dominate the biomass of primary producers while benthic invertebrates constitute the bulk of secondary producers and 93% of the total biomass (Table 5.13). Fishes, being mostly at the upper part of trophic pyramid, comprise 3.6% of all biomass in the studied system. Fish guilds differ in their biomass estimated over a one-year period. Biomass of semi-resident fishes comprises 63.6% of the total fish biomass, while freshwater stragglers and marine migrants compose the rest (15.5 and 16.0%). Biomass of anadromous and catadromous fishes is very low (4.7% and 0.1% accordingly). However, marine migrants and anadromous fish species are the most abundant in fishery catches (both comprise 95% of catches), while freshwater stragglers compose the rest of the catch.

The parameter values estimated by the ECOPATH are reasonable and indicate well compiled and balanced model (Christensen et al., 2008; Heymans et al., 2016):

- The model was balanced, thus estimated EE < 1 for all compartments.
- Estimated P/Q values for anadromous and catadromous fish groups, marine migrants, and semi-residents vary from 0.06 to 0.19, while those for freshwater stragglers are from 0.08 to 0.49; birds have the lowest P/Q values (<0.004); invertebrates have a relatively broad range of P/Q – from 0.04 till 0.38 (Table 5.13).
- The R/A ratio for all groups were less than 1. Pike-perch adults had the highest P/R ratio (1.6), while this parameter for all other groups did not exceed 1.
- The ratios of R/B are between 0.5 and 11 for fishes and higher for invertebrates and birds.

5.3.2. Summary statistics for the network

Summary statistics and flows for the modelled food web are shown in Table 5.14. In the overall balance of the system, the consumption flows dominated the total system throughput, making 43.8% of the overall ecosystem flow, while respiratory flows and flows to detritus followed (31.4% and 24.9%, respectively).

Export flows were negative, indicating the studied system as a sink. Total primary production/total respiration (TPP/TR) was 0.83 (less than 1) and net system production was negative designating the system as heterotrophic. The mean TL of commercial fishery catch was 3.47.

Table 5.14. **Statistics (in g m^{-2} y^{-1}, but g m^{-2} for biomass) (modified from Razinkovas-Baziukas et al., accepted).**

Parameter	Value
Sum of all consumption	1793.04
Sum of all exports	-4.81
Sum of all respiratory flows	1285.81
Sum of all flows into detritus	1021.84
Total system throughput	4095.87
Sum of all production	1220.19
Mean trophic level of the catch	3.47
Calculated total net primary production	1071.56
Total primary production/total respiration (TPP/TR)	0.83
Net system production	-214.24
Total primary production/total biomass	20.32
Total biomass/total throughput	0.01
Total biomass (excluding detritus)	52.73
Total catches	0.71
Pedigree index	0.66

Pedigree index of 0.66 represents a proportion of all input data obtained in the ecosystem, while only one-third of the information used for the model compilation was derived from published studies (Table 5.14).

5.3.3. Trophic flows

The Lindeman chain represents the origin of energy flows and their distribution among discrete TL at which the particular modeled group received energy (Fig. 5.21). About 42% of the total system throughput of the model flows out from the TL2 that contains 72% of the total living biomass and the highest respiration in the system. Detritus and primary producers are involved into 26 and 30% of flows accordingly, while the share of other TLs is negligible.

From 1071.6 gC m^{-2} y^{-1} of net primary production 66% is used by TL2 (705.0 gC m^{-2} y^{-1}) and that constitutes 41% of all TL2 incoming matter. The higher amount of organic matter (59%) consumed by the TL2 is obtained from the detritus compartment. Similar proportion of total flow originates from detritus (56%). Flows to detritus mainly come from primary producers and TL2, while imports are also relevant (Fig. 5.21).

Values of trophic efficiency (TE) for flows through TL3 and TL4 are the highest (11.8 and 9.8, accordingly), that is coincidental with the highest catches at TL3 and mean TL of the catch (Fig. 5.21, Table 5.14). The largest amount of imported material

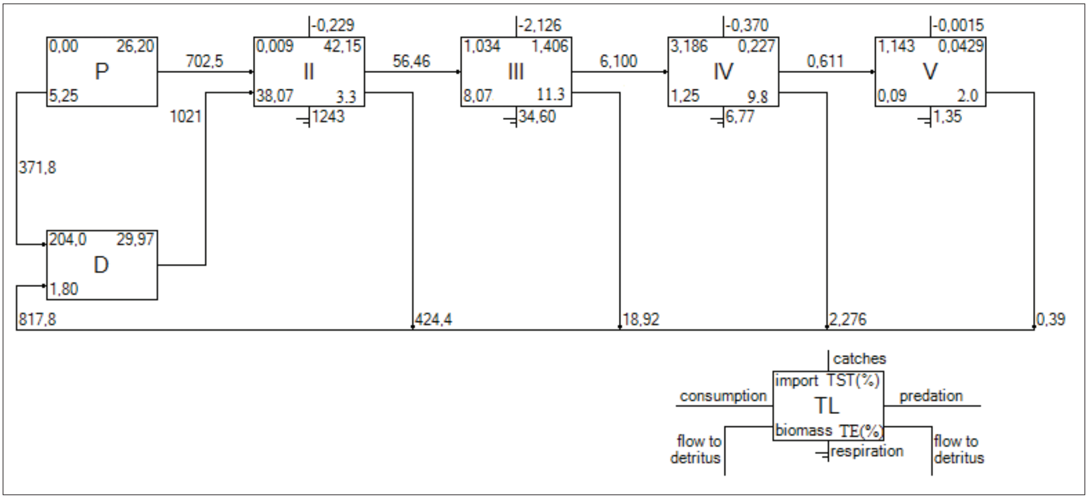

Figure 5.21. Representation of trophic flows by integer trophic levels (TLs) in the form of Lindeman Spine (in ww(g/m^2), otherwise indicated). TST (%) represents the percentage of total system throughput flowing through the trophic level. Primary producers (P) and detritus (D) were separated to clarify the representation (both on TL1), while >TL5 were not considered due to their minor overall contribution.

(in this case migratory fishes) is for TL4, while the absolute values of imported material reaching TL3 and TL5 are threefold lower. Total TE is equal to 7.1%.

5.3.4. Trophic impacts in the community

The estimation of mixed trophic impacts revealed interactions among all living compartments, detritus and fishery (Fig. 5.22). Organisms of lower TLs are involved in many trophic relationships. Phytoplankton has positive impacts to various groups in the trophic network, especially to nectobenthos, filtrators, three-spined stickleback and turbot juveniles. Mesozooplankton negatively affects majority of compartments, but has positive impacts on small pelagic fishes and adults of Atlantic salmon. Nectobenthos has positive impacts on phytoplankton, turbot juveniles and adults of ruffe, twaite shad, and European smelt, while negative impacts were indicated for Baltic sprat and mesozooplankton. Macrozoobenthos filtrators negatively affect all invertebrate compartments, while positive impacts were indicated for wintering benthivorous ducks and adults of some benthivorous fish species. Three macrozoobenthos omnivorous groups have different impacts on a wide range of compartments. Intermediate sized omnivorous group negatively affects macrophytobenthos, the smallest omnivorous macrozoobenthos, and several groups of small Perciformes.

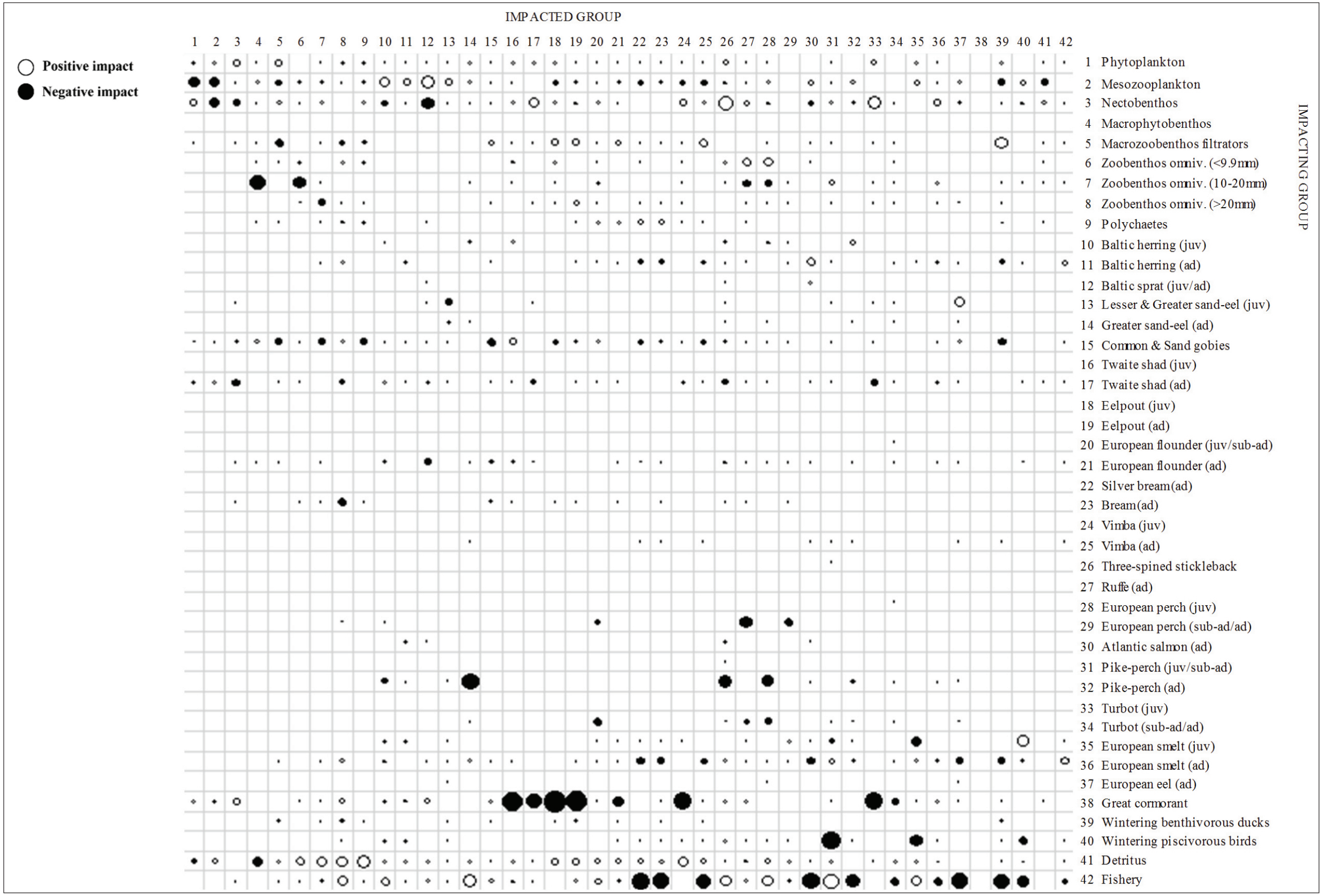

Figure 5.22. Mixed trophic impact plot of living compartments, detritus and fishery in the Lithuanian coastal zone (modified from Razinkovas-Baziukas et al., accepted).

The freshwater straggler predators appeared to have negative impacts on both smaller freshwater straggler species (ruffe, three-spined stickleback and juveniles of perch) and several semi-resident fishes as greater sand-eel. Piscivorous birds have multiple negative impacts on several fish species. Great cormorant negatively affects such fish groups as twaite shad, eelpout, vimba bream and turbot juveniles. Wintering piscivorous birds influence many fish groups, but the strongest impacts are on pike-perch juveniles and smelt adults. The fishery has both negative and positive impacts on analyzed groups. Negative impact of the fishery on both diving ducks and piscivorous birds are caused mostly by the bycatch that included substantial numbers of wintering waterbirds. The fishery has strong negative impacts on large fishes that are otherwise not much predated; averaged catch TL was 3.4. This could be an explanation of the positive impact to some smaller fishes such as greater sand-eel, juveniles of pike-perch, herring and perch, three-spined stickleback (Fig. 5.22).

Regarding the grouped impacts of fish guilds (Fig. 5.23), macrozoobenthos, detritus, and phytoplankton positively impact fish guilds, while fish guilds and piscivorous birds

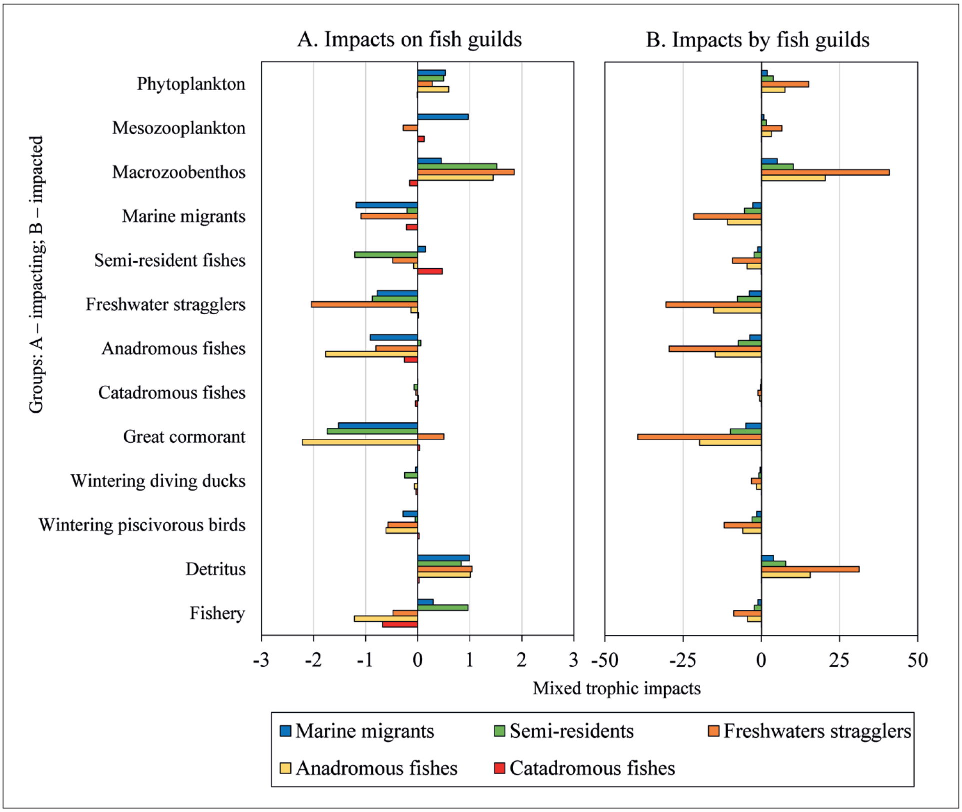

Figure 5.23. Mixed trophic impacts by fish guilds:
A. Impacts of living groups, detritus and fisheries on different fish guilds;
B. Impacts of fish guilds on other living groups, detritus and fisheries.

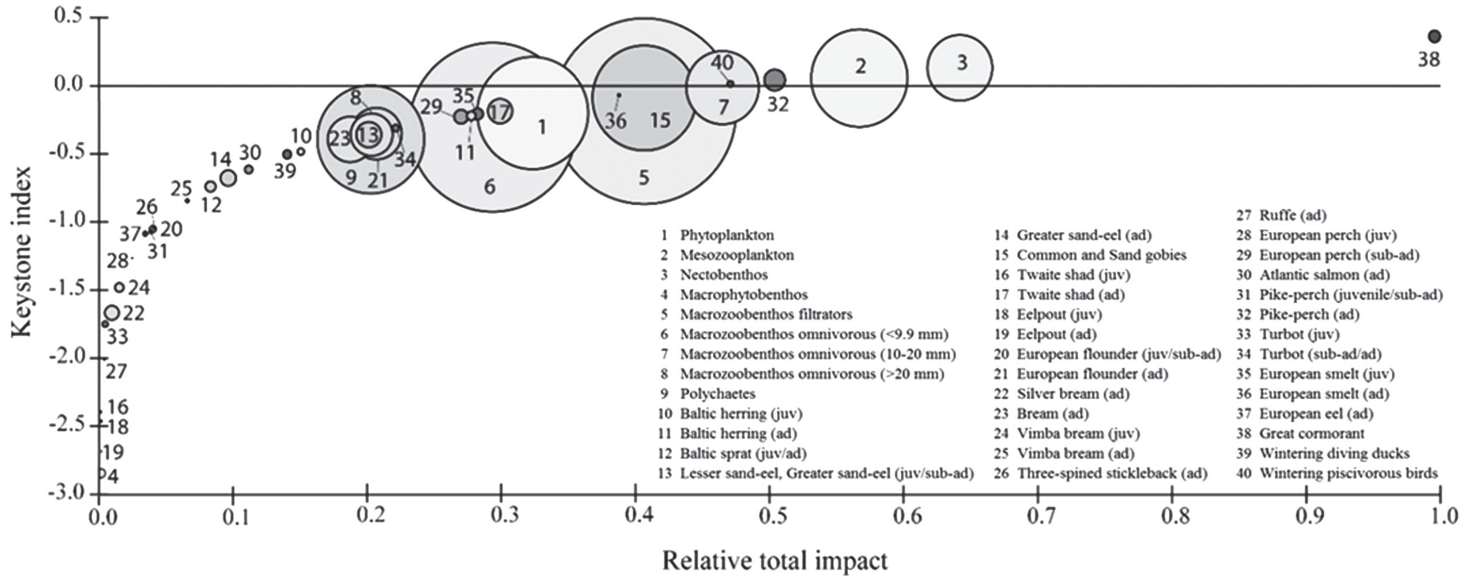

Figure 5.24. Keystoneness index of compartments of the Lithuanian coastal zone model. Radius of nodes represent biomass of each group. Index at 0 indicates the importance (modified from Razinkovas-Baziukas et al., accepted).

cause negative impacts on fishes. Fishery negatively affects freshwater, anadromous and catadromous fishes and positively affects marine and semi-resident fishes (Fig. 5.23A). Looking at the role of fishes (Fig. 5.23B), freshwater and anadromous fishes have the strongest positive impacts on macrozoobenthos, phytoplankton and detritus, while their negative impacts are estimated for piscivorous birds, marine, freshwater and anadromous fishes. Other fish guilds have much weaker mixed trophic impacts.

The highest keystoneness indices (greater than zero) were calculated for cormorant, nectobenthos, mesozooplankton, pike-perch adults and wintering piscivorous birds (Fig. 5.24). Values close to zero were estimated for omnivorous macrozoobenthos (10-20 mm), European smelt, common and sand gobies.

6

Discussion

6.1. Trophic network structure and flows

The reconstructed food web of the Lithuanian Baltic Sea coastal zone represents basic information about the ecosystem structure and the organic matter flows. The trophic model integrated both spatial and seasonal variability of biotic compartments on an annual basis, to produce cumulative balances for separate trophic compartments and for the system as a whole. Despite the model complexity, the calculated overall pedigree index was relatively high – 0.66, as much of the input data originated exactly from the study area. It is among about 10% of published ECOPATH models which have a pedigree index higher than 0.60 (Morissette et al., 2006; Morissette, 2007).

The coastal food web of the Baltic Sea Lithuanian coastal zone comprises compartments of the TLs in the range of 1 to 4.2 (Fig. 5.19). While invertebrates occupy TLs lower than 2.5, various fish species occupied TLs from 2.7 to 4.2, birds occupied TL 3 (for benthivorous ducks) and TL 4.2 (for piscivorous waterbirds). The TL2 contains the largest part of all living biomass combining mesozooplankton and macrozoobenthos compartments. Moreover, organisms at TL2 consume the largest proportion of organic matter and provide the largest share of total systems throughput. Dominance of benthic compartments is a common feature of coastal ecosystems (e.g. Milessi et al., 2010).

The trophic efficiency (TE) for the discrete TLs may be determined largely by the quality of food. Flow from detritus to TL2 is the highest in the food web, however, poor assimilation of detritus (Pechen-Finenko, 1984) and cyanobacteria (Bednarska et al., 2014) might result in low TE for TL2. High TE at TL3 and TL4 is a result of high-quality food consumed by carnivores. The total TE of 7.1% is lower than the theoretical value of 10% which is often assumed in ecosystems, but it is within the range of values attributed to aquatic ecosystems in general (according to Christensen and Pauly, 1993). That might be a result of heterotrophy and importance of detritus in the overall metabolism of the ecosystem.

Low autochthonous productivity and physical stress predominantly control the functioning of the Lithuanian coastal zone. The ratio between total primary productivity and total ecosystem respiration (0.83) characterize the studied zone as heterotrophic. It is consistent with results of other ECOPATH models described by Christensen and Pauly (1993) and is the lowest among other coastal systems in the southeastern Baltic (Tomczak et al. 2009). Tomczak et al. (2009) evaluated a part of the Lithuanian coastal zone as autotrophic (TPP/TR=3.4), however, this paper focused on the most productive area covering hard bottom habitats with rich benthic communities (Olenin, 1997). The heterotrophy is a common feature of other river dominated coastal environments in the Baltic Sea (Stepanauskas et al., 2002; Korth et al., 2013). However, the heterotrophy is in contrast to the majority of coastal ecosystems that in general are known to be very productive and autotrophic (Wollast, 1998; McLachlan and Brown, 2006).

Passive transport of organic matter and organisms actively migrating from adjacent freshwater and marine water areas might contribute to the heterotrophic status of the food web. The SIA approach allowed to describe main food web compartments from plankton to marine birds and revealed their isotopic differences depending on characteristics of feeding, transfer, or migrations. The obtained $\delta^{13}C$ ratios allow identification of utilized food sources representing a high variation in $\delta^{13}C$ values across different food web compartments. The $\delta^{13}C$ values from -32.3 to -23.4 ‰ characterize coastal POM/ seston which is transported passively from the Curonian Lagoon and mixed with marine waters. Freshwater POM from the Curonian Lagoon is characterized by low $\delta^{13}C$ ratios (to -33.3‰; Lesutienė, 2009), while marine POM vary from -18.6 to -23.5‰ in the Baltic Proper (Rolff and Elmgren, 2000). Therefore, coastal POM and seston $\delta^{13}C$ values are in a range of values estimated in adjacent systems.

Although in this study, the SI values in POM and seston represent a mixture of primary production coming from different sources, other organisms are able to integrate organic matter over the certain periods of time. The SI values in consumers vary across the sites along the Lithuanian coastal zone; therefore, SIA might be further used to study the migratory behavior of fish compartments. Only individuals inhabiting area for a considerable period might equilibrate their body isotopic composition to a degree that is possible to discriminate them among individuals from other sites (Hansson et al., 1997). In this study, significant intra-specific differences in $\delta^{13}C$ values of macrozoobenthos and fishes were found across the coastal sites: the most depleted samples were collected at Melnragė, while values in organisms from Palanga site lay between those in Melnragė and Juodkrantė. These patterns are consistent with the information provided by the estuarine plume maps based on satellite images and in situ phytoplankton measurements (Vaičiūtė, 2012) as well as to spatial differences in $\delta^{13}C$ values of sedimentary organic matter in the lagoon-sea system (Remeikaitė-Nikienė et al., 2016), which in turn represent the spatial coverage of freshwater impact on the Lithuanian coastal zone. The ECOPATH model also suggests that terrestrial inputs from the Nemunas River – Curonian Lagoon system are important for the Lithuanian coastal system providing nearly 20% of the total organic matter inputs to the system (regarding to the TPP/TR in Table 5.14).

Macroalgae usually display a high interspecific variability in $\delta^{13}C$ and a low $\delta^{15}N$ ratios (review of Fry and Sherr, 1989; Briand et al., 2015). In the Lithuanian coastal zone, this variability in SI ratios is high among taxons belonging to the same phylum (Rhodophyta) or is low ($\delta^{13}C$ in Chlorophyta). Therefore, red macroalgae (Rhodophyta) might be distinguished by $\delta^{13}C$ ratios because some species in the phylum have low $\delta^{13}C$ values compared to other algae species or organisms in a food web (e.g. Fredriksen, 2003; Briand et al., 2015). In this study, the single red algae *Coccotylus truncatus* were distinguished by low $\delta^{13}C$ values (-36.3±0.1‰), while ratios of other red algae species were in the range of green algae species (Chlorophyta). This species exhibited very low $\delta^{13}C$ values contrasting to the rest of organisms in the food web in both in summer and winter (-36.4‰ own unpubl. data). The range magnitude of $\delta^{15}N$ values of macroalgae is 4.7‰ representing a mixture of different taxa. The SI ratios of macrophytes are related to their phylogeny, particularly to the biochemical processes involved in the dissolved inorganic carbon uptake during photosynthesis and to environmental parameters (Briand et al., 2015).

Macrozoobenthos organisms generally are sessile or move insignificantly along the coast; therefore, their tissues represent SI values representing the individual coastal sites. Generally, the tissues of all coastal macrozoobenthos species had $\delta^{13}C$ ratios from -23.5 to -16.8‰ which are more enriched in $\delta^{13}C$ than macrozoobenthos in the Curonian Lagoon (Lesutienė, 2009). Moreover, $\delta^{13}C$ ratios in *C. crangon* and *Palaemon elegans* were significantly different across coastal sites and reflected a pattern of freshwater contribution to $\delta^{13}C$ ratios: samples from Melnragė were the most depleted, while samples from Juodkrantė and Palanga were more enriched. The SI values of small omnivorous *Gammarus* sp., mostly herbivorous *Idotea balthica,* and suspension feeder *Mytilus* sp. overlapped with those in macroalgae. Other groups containing deposit and suspension feeders and large omnivorous animals had higher the $\delta^{15}N$ values than previously mentioned groups. Omnivorous *C. crangon* had the highest $\delta^{15}N$ ratios which likely represents their predatory feeding habits(according to Olenin, 1997). Therefore, the different macrozoobenthos feeding groups could be separated by their $\delta^{15}N$ ratios, while $\delta^{13}C$ ratios are not so helpful (Fig. 5.2).

The majority of fish species are present in the coastal system on a seasonal basis and the positive balance of active migrations contributes to the heterotrophy of this exposed coastal system. Considering that the migrations of freshwater fish species from the lagoon to the coastal zone in late spring, it could be assumed that by the end of summer these individuals should be well adjusted to the coastal isotopic signatures. However, at the end of vegetative season freshwater fishes still have lower $\delta^{13}C$ values than marine and semi-resident fish species. Though, there are pronounced isotopic differences between individuals migrating to the coastal zone or staying in the lagoon for summer. Pūtys (2012) demonstrated sharp differences between $\delta^{13}C$ signatures of European perch caught in the Curonian lagoon (-27.8‰) to the individuals from the coastal zone (-21.3‰), given the $\delta^{15}N$ values are the same in both environments (approx. 14.8‰). The three-spined stickleback $\delta^{13}C$ values (-31‰) were the most depleted and represent freshwater since they were sampled just at the mouth of small river at Palanga site. These findings contribute to a qualitative and quantitate evidence of the migratory habits of freshwater fishes in the lagoon-coastal zone system.

The ECOPATH model estimated biomass of groups required to keep the overall food web balance, while fish migrations were assessed indirectly preventing the values of EE being higher than 1. EE values estimated for most of the invertebrate compartments, including planktonic species, were considerably lower when compared to values measured in the Baltic Sea (Sandberg et al., 2000), but higher than estimated in the sandy beach environment (Lercari et al., 2010) or the Curonian Lagoon (Ertürk et al., 2008). This corresponds well to the general paradigm of exposed beaches as predominantly physically controlled environments, where biological interactions are of lower importance than environmentally driven mortality (Defeo and McLauchlan, 2005; Lercari et al., 2010). However, in the analysed system, comprising wider habitat range than exposed beach habitats, higher TLs including fishes are much better represented. Low EE values of large freshwater stragglers such as adults of silver bream, bream, pikeperch, and perch (0.06-0.17) indicate not only the low overall consumption of these species (Fig. 6.1) but also point towards their migration back to the lagoon and contribution to the reversal of flow in biomass and energy from the coastal zone to the river-lagoon system. This is consistent with other studies on fish feeding migrations between the coastal zone and the Curonian Lagoon (e.g. Ložys, 2003; Ložys, 2004; SI values in this study). Nevertheless, the EE values for the migratory fish species were fitted rather than calculated by the model itself and no reliable conclusions on the trophic interaction strength and no quantitative estimation of these migrations could be made.

Semi-resident fish species, common for the sandy habitats (gobies, sand-eels), are consumed by marine benthic predators (mostly turbot), freshwater stragglers (pike-perch, perch) and anadromous species (salmonids) (Fig. 6.1). The biomass of semi-resident sand and common gobies was mostly derived from the trawling data in the model area and does not match their share in stomachs of the predators caught in the same environment, resulting unrealistic EE values calculated by the model (EE>300). Therefore, we have assumed that the biomass of semi-resident fishes was heavily underestimated and this is supported by evidence from other studies (e.g. Repečka et al., 2003a; Ehrenberg et al., 2005). In this case, the ECOPATH model estimate the minimum biomass of gobies and sand-eels necessary in the coastal ecosystem to sustain total mortality of these compartments.

6.2. Passive flow of organic matter

Passive input of organic matter from adjacent ecosystems is presented by mixture of organic sources in coastal POM and seston those isotopic values differed among the coastal sites and months. Significant differences among the $\delta^{13}C$ values in POM and seston at different coastal sites were detected at the beginning of September: the most depleted samples were in Melnragė (-31.5 to -27.4‰), samples from Palanga were similar but more enriched (-27.7 to -26.1‰), while the most enriched samples were in Juodkrantė (-25.8 to -23.5‰). Differences could be explained by the source of organic matter because marine waters mixes with freshwater plume from the lagoon at Melnragė (Lesutienė, 2009). Palanga and Juodkrantė sites receive lower amounts of freshwater outflow, therefore, their POM and seston samples reflect $\delta^{13}C$ values of the marine POM (Rolff and Elmgren, 2000). In regard to dominant northwardly currents spreading the freshwater outflow water along the coastline, Palanga site is more influenced by the freshwater plume than Juodkrantė in the southern part of the area (e.g. Vaičiūtė, 2012). A high outflow from the lagoon, which lasted for five-seven days before sampling in September as during the sampling time, might contribute to the similar $\delta^{13}C$ values both in Melnragė and Palanga (Umgiesser et al., 2016). The same tendency of spatial patterns in $\delta^{13}C$ values of sediments had been already demonstrated (Lujanienė et al., 2015; Remeikaitė-Nikienė et al., 2016).

Other POM and seston samplings for this study were carried out in July and August, when the outflow from the lagoon could be characterized as varying (Umgiesser et al., 2016). Due to rapid changes in outflow patterns, $\delta^{13}C$ ratios in samples, taken even at adjacent dates at both Melnragė and Palanga sites, did not exhibit spatial differences. Similar $\delta^{13}C$ values in POM and seston between the sites together with high variability among replicates and different size classes might be explained also by mixing of water from different areas. High $\delta^{13}C$ values of the smallest plankton class (total POM and <70) might represent large respiration losses of light carbon (^{12}C) because organisms of these small size classes might contribute to carbon consumption rather than provide a carbon source for larger plankton organisms (Rolff and Elmgren, 2000 and references in it). Moreover, a mixture of representative taxa in each size fraction might explain $\delta^{13}C$ and $\delta^{15}N$ ratios variability among size-fractioned plankton samples without indication of size-dependent consumption within the plankton community (according to Rolff, 2000 and references therein). Rolff (2000) stated that size-dependent enrichment of $\delta^{15}N$ ratios is clearer in spring and autumn than in the summer, reflecting time lags and diversity in the Baltic zooplankton community. However, the size-dependent consumption in plankton community were partly indicated in the large shallow lake in China (Zeng, et al., 2010) and in marine plankton food webs of the coastal Baltic Sea (Rolff, 2000).

Considering published studies, variability of plankton SI values could depend on changes in diversity and dominant taxa of plankton community during the study period from July to September. The phytoplankton constitutes the largest part of total organic present in the plankton community; however, coexistence of seston groups having different SI values had been found in the Curonian Lagoon (Lesutienė, 2009). We speculate that water fluxes transport the plankton community from the lagoon to the coastal zone and contribute greatly to coastal plankton community structure and their SI ratios.

Although $\delta^{15}N$ ratios usually are used to determine trophic positions, complexity of plankton communities in coastal systems and the inability to fractionate effectively plankton size groups make the assignment of trophic status in plankton communities very difficult. However, the variability of $\delta^{15}N$ values attributed to the presence of allochtonous organic matter also might provide insights for freshwater contribution to the coastal ecosystem. High $\delta^{15}N$ ratios in plankton (up to 16.6‰ in Melnragė) might indicate uptake of ^{15}N-enriched inorganic nitrogen due to eutrophication (Zeng et al., 2010) or sewage inputs and fertilizers (Costanzo et al., 2000). Low $\delta^{15}N$ values in POM and seston (from -0.08‰) were registered in July at Melnragė and Palanga sites which are the most affected by estuarine flow. It could be attributed to the massive presence of N_2 fixing cyanobacteria in the plankton community as it was reported previously in the Curonian Lagoon (Lesutienė, 2009). Nitrogen-fixing cyanobacteria are ecologically more important than instantaneous nitrogen sources in the Baltic Sea (Voss et al., 2000). Cyanobacteria blooms account for 50-80% of secondary production of benthic and pelagic consumers in the Curonian Lagoon (Lesutienė et al., 2014a), which in turn contribute to blooms in the Lithuanian coastal zone. Cyanobacteria fix atmospheric nitrogen and might contribute to the considerably low $\delta^{15}N$ values ($\delta^{15}N = -2$‰ in the Baltic Sea; Rolff, 2000; Karlson et al., 2014) in comparison to other plankton taxa. Thus, low $\delta^{15}N$ ratios in different size-classes of plankton illustrate direct or secondary utilization of fixed nitrogen from cyanobacteria in the Baltic Sea (Rolff, 2000). This process might constitute a significant pathway for fixed nitrogen to the non-cyanobacterial plankton community. Therefore, depleted $\delta^{15}N$ values in nitrogen-fixing cyanobacteria have been mirrored in zooplankton and littoral consumers, and could be used as a tracer of dietary nitrogen (Karlson et al., 2014 and references in it). For the studied coastal zone, however, variability in SI values of POM and seston at coastal sites reflects differences in contribution of allochtonous organic matter. That complicates differentiation of organic matter sources consumed by living food web compartments.

Unfortunately the monthly POM and seston sampling scheme during single vegetative period did not provide conclusive information about an influence of estuarine plume and marine waters to the coastal food web. Therefore, these data should be interpreted with caution. More frequent water samplings at sites along the entire coast stretch might help to determine the variation of SI values in POM and seston. Plankton taxa identification and measurements of water parameters might improve the interpretation of the SIA results.

6.3. Migratory fish guilds

Coastal fishes are an important resource for commercial and recreational fisheries in many ecosystems, including the Lithuanian coastal zone in the southeastern Baltic Sea (Bergström et al., 2016; Repečka et al., 2003a; Repečka, 2003c). The compositions of coastal fish communities vary spatially and seasonally in relation to the different habitats, hydrological parameters, and biological species characteristics (Razinkovas et al., accepted). Therefore, the introduction of the migratory fish guild concept contributes to the understanding of resources used by fish, their impact on food webs and connectivity with other ecosystems (Elliott et al., 2007).

The isotopic part of this study reveals that migratory fish guilds differed among each other by SI values reflecting the origin of assimilated organic material and migration patterns. The $\delta^{13}C$ and $\delta^{15}N$ values in semi-resident fishes differed across the coastal sites. This group contains small benthic fishes that are usually sedentary; therefore, the $\delta^{13}C$ ratios in their tissues might represent an integration of organic matter typical for the certain coastal areas, while relatively low $\delta^{15}N$ ratios denote their intermediate trophic position in the studied food web.

The SI ratios in freshwater and marine fishes represent group-specific migratory patterns. Differences in $\delta^{15}N$ ratios of marine fishes from small pelagic Baltic sprat to large benthic turbot reflected quite wide range of trophic positions. SI ratios in marine fishes were similar to those found in semi-resident gobies and Ammodytidae because both groups live only in marine environment. Accordingly, freshwater and anadromous fishes had lower $\delta^{13}C$ values than marine and semi-resident species.

Anadromous fishes had similar $\delta^{13}C$ and $\delta^{15}N$ values at all studied coastal sites, but their low $\delta^{13}C$ values during vegetative period could be contributed to the recent movement from the freshwater environment as well. Their SI values overlapped with those in freshwater fishes. Due to movements between the adjacent ecosystems, tissues of freshwater and anadromous fishes represent mixed and spatially homogenous $\delta^{13}C$ values reflecting their seasonal movements within the lagoon-sea system. Other studies report that the $\delta^{15}N$ values might be unique for anadromous trout (Salmonidae) within the different populations, while $\delta^{13}C$ values do not contrast radically (Ciancio et al., 2008).

Commercial catches of fishes, especially freshwater species, are much lower in Juodkrantė than those in Melnragė – Palanga zone (Repečka et al., 2003a). Juodkrantė is characterized by higher salinity and monotonous soft bottom habitat with low benthic diversity and biomass (Olenin and Daunys, 2004). Moreover, high $\delta^{13}C$ values in freshwater fishes caught in Juodkrantė site demonstrated that they had spent enough time to integrate at some extent the marine signatures into their tissues. Spatial differences in marine migrants were evident in $\delta^{13}C$ values because individuals from Juodkrantė and Palanga sites were isotopically different from the individuals of the same species sampled in Melnragė. In similar study performed in the Mediterranean region, the SI approach has been used to differentiate two populations of common sole (*Solea solea*) staying in the coastal zone or facultatively using the lagoons as nurseries. The lagoon soles had low $\delta^{13}C$ ratios indicating a higher importance of freshwater POM in the lagoon compared to coastal nurseries. However, the lagoon individuals showed a strong enrichment in muscle tissue ^{15}N compared to their coastal relatives, likely linked to sewage inputs (Dierking et al., 2012). Contribution of sewage discharges to increase $\delta^{15}N$ values in an entire food web from producers to predators had been presented by other studies too (e.g. Hansson et al., 1997). In the Lithuanian coastal waters, higher $\delta^{15}N$ values were detected in the sedimentary organic matter from the Curonian Lagoon comparing to those in the coastal zone. This could reflect the contribution of Nemunas River and the anthropogenic input in the basin area (Remeikaitė-Nikienė et al., 2016). The $\delta^{15}N$ ratios in freshwater and semi-resident fishes reflected the freshwater input only in Melnragė site, while values at other sites did not follow this pattern. High $\delta^{15}N$ values in freshwater fishes were found also at Juodkrantė site, but that could be related to individual tolerance to higher salinity and lower water temperature.

6.4. Diet composition of wintering waterbirds applying the $\delta^{34}S$ as supplement to $\delta^{13}C$ and $\delta^{15}N$ ratios

6.4.1. Advantages of triple stable isotope approach in the trophic studies

Triple SI approach ($\delta^{13}C$&$\delta^{15}N$&$\delta^{34}S$) provided an evidence of interspecific trophic segregation among waterbird species wintering in the southeastern Baltic Sea. Firstly, the $\delta^{15}N$ values show significant differences in trophic positions between benthivorous ducks and piscivorous birds, which is in agreement with the gut content analysis based diet estimates (Stempniewicz, 1994; Žydelis, 2002). Secondly, the results allowed discriminating piscivorous birds according to their foraging preferences into pelagic or benthic fishes consumers, because low $\delta^{34}S$ values of piscivorous great-crested grebe allow the species separation from other piscivorous birds. Trophic segregation of waterbirds using $\delta^{13}C$ and $\delta^{15}N$ ratios have been done in many studies covering water ecosystems of temperate and polar areas (e.g. Hobson et al. 1994, 2002; Weiss et al., 2009). However, the application of the dual analysis of $\delta^{13}C$ and $\delta^{15}N$ ratios in the coastal food web studies is difficult due to frequent overlap of these SI ratios among the food sources (this study; Mittermayr et al., 2014). Therefore, $\delta^{34}S$ ratios complementary to $\delta^{13}C$ and $\delta^{15}N$ ratios could be a valuable approach in trophic ecology in the coastal areas of the Baltic Sea.

This study proves that $\delta^{34}S$ values can be used as a tracer of benthic production in the coastal food web of the Baltic Sea because this method has a higher discriminatory capacity in comparison to dual $\delta^{13}C$ and $\delta^{15}N$ approach. The $\delta^{34}S$ values allow discrimination between facultative and obligatory suspension feeding bivalves as well pelagic and benthic fishes, whereas $\delta^{13}C$ and $\delta^{15}N$ values do not discriminate between these two groups. Triple isotope approach is consistent with studies of Moreno et al. (2008) and Conolly et al. (2004) which demonstrated that $\delta^{34}S$ ratios allow to discriminate main food sources indistinguishable by other isotopes.

The values of inorganic sulfur might be used to predict the possible range of variation of $\delta^{34}S$ values in the primary sources sustaining the food web (Connolly et al., 2004). The $\delta^{34}S$ ratios in seawater sulfate of the western Baltic Sea is +20‰ (Hartmann and Nielsen, 2012 are similar to the World Ocean mean $\delta^{34}S$ ratio +20.3‰ (Nehlich, 2015). Comparable are $\delta^{34}S$ values in dissolved organic matter in the Baltic proper (17.8‰) (Alling et al., 2008), zooplankton in Kiel Bight (~19‰; Mittermayr et al., 2014), and pelagic fishes in coastal waters of the southeastern Baltic Sea (18.5‰; this study). In contrast to the uniformness of $\delta^{34}S$ values in the water column, there is a higher variability of sedimentary $\delta^{34}S$ values related to oxygen depletion (Karube et al., 2012; Proulx and Hare; 2014), mixing of freshly settled POM and heterotrophic production by sulfate-reducing bacteria within sediments (Fry and Chumchal, 2011). For example, the $\delta^{34}S$ values range between -15 and -35‰ in the sediments of the western Baltic Sea (Hartmann and Nielsen, 2012), while rhizomes of *Zostera marina* in Kiel Bight have -0.44 ‰ of $\delta^{34}S$ (Mittermayr et al., 2014).

Benthic invertebrates obtain their sulfur from either the sediments, below sediment-water interface, or the water column; this could be the reason for taxa-specific $\delta^{34}S$ values (this study; Croisetière et al., 2009; Karube et al., 2012). Facultative suspension feeders *M. balthica* and polychaetes have approximately 5.5‰ lower $\delta^{34}S$ values than obligatory suspension feeders *C. glaucum* and *M. arenaria*. Although mentioned organisms at least seasonally rely on different food sources, $\delta^{13}C$ and $\delta^{15}N$ ratios in previous studies presented an overlap of their trophic niches (Rossi et al., 2004). Comparable $\delta^{34}S$ values of *M. balthica* and polychaetes in this study might show a contribution of sedimentary sulfides to diets of these deposit feeders (according to Fry, 2008). Moreover, polychaetes had much higher $\delta^{15}N$ values than *M. balthica* ($\Delta\delta^{15}N = 3.5‰$) reflecting their higher trophic position in the food web. The $\delta^{34}S$ and $\delta^{15}N$ ratios of *M. balthica* might be attributed to switches between suspension- and deposit-feeding (Zwarts and Wanink, 1989; Lin and Hines, 1994).

In the Lithuanian coastal zone, benthic fishes have significantly lower and more variable $\delta^{34}S$ values than pelagic fishes ($\Delta\delta^{34}S = 5‰$). The variability of $\delta^{34}S$ ratios in benthophagous organisms increases uncertainty in determining the proportion of consumers' diets derived from a benthic source. Potential uncertainty could be reduced with larger sample sizes and knowledge of the temporal and spatial variation of $\delta^{34}S$ in benthic fauna of coastal and offshore waters of the Baltic Sea, or with the addition of other SI to the analysis. It should be noted, that coastal areas might be under strong influence of freshwater derived materials that are potentially depleted in ^{34}S, relative to marine-derived material (Peterson and Howard 1987; MacAvoy et al., 2000; Fry and Chumchal, 2011).

An important finding of this study is the capacity of $\delta^{34}S$ and $\delta^{15}N$ ratios to discriminate European smelt from other coastal fish species in the Baltic Sea. Smelt was found to have values of $\delta^{34}S$ which are intermediate between pelagic and benthic fish species. Moreover, the $\delta^{15}N$ values of smelt tissues were 4.1 and 2.2‰ higher comparing to pelagic and benthic fishes, respectively. These differences may occur due to the anadromous migration pattern (Ciancio et al., 2008), predatory and cannibalistic feeding habits (Taal et al., 2014), starvation during the spawning period, and allocation of nutrients into the reproductive tissues during winter; all these factors together might induce a higher fractionation of ^{15}N in tissues (Jenkins et al., 2001; Vander Zanden and Rasmussen, 2001; Jardine et al., 2005). In many studies over the World, anadromous fish species were found to be isotopically district from freshwater residents (MacAvoy et al., 2008).

Marine birds might be considered as the most mobile consumers in the coastal zone, which are able to change their feeding habitats or use several habitats at the same time (Cherel et al., 2008). Even when foraging only in marine environment, diving birds might move large distances within shifts of hydrological conditions. Tissues of newly arrived migrants are isotopically acquired in previous feeding habitats. Local food sources and mixing models based on them cannot be used to explain the diets in the new habitat (Phillips and Gregg, 2001). Therefore, the SIA results should be interpreted with an assumption that tissues of waterbirds have reached an isotopic equilibrium before sampling at the wintering sites. In this study, the complete isotopic equilibrium in some bird blood samples might not be reached on first sampling occasions. Isotopic half-life of bird blood is estimated being approximately two weeks, while complete equilibrium takes much longer (according to Vander Zanden et al., 2015). Moreover, difficulties to collect blood from live waterbirds in marine waters determined the relatively small number of samples and their uneven distribution during the study period. However, this study demonstrates that triple isotope mixing models based on blood analysis might provide insights in the feeding ecology of piscivorous waterbirds and benthivorous ducks at their wintering grounds.

6.4.2. Diet of piscivorous waterbirds

It is widely accepted that piscivorous birds tend to feed opportunistically on the most abundant and easy-to-catch fishes and that their diet composition reflects the structure of the local fish community (Jakubas and Mioduszewska, 2005; Guse et al., 2009; Žydelis and Kontautas, 2008). As shown by mixing model calculations in this study, common guillemot and red-throated diver mostly forages on pelagic fishes, while great crested grebe prefers benthic fishes. These results supplement the previous knowledge on the investigated bird feeding behavior and habitat preferences. Divers are mostly distributed in the offshore sites and are less abundant in the coastal zone (Švažas, 1993). They have specialized foraging on shoaling pelagic fishes occurring in higher numbers offshore or smelt in the coastal zone, with benthic fishes being rare in the diet (Žydelis, 2002; Guse et al., 2009). Whereas, great crested grebe winters in shallow coastal zones after freshwater lagoons and inland lakes freeze (Žalakevičius, 1995; Žydelis, 2002; Skov et al., 2011). At this time the visibility of benthic fishes in coastal waters is particularly high (Hunt et al., 1999), causing suitable conditions for feeding on benthic fishes.

The estimated diet composition of common guillemot consisted mainly of clupeids; however, there was also a contribution of benthic fishes and smelt. Guillemots are limited by fish size and Baltic sprat is the only suitable fish in pelagic areas of the Baltic Sea (Lyngs and Durinck, 1998; Kadin et al., 2012). It was previously shown that guillemots mainly feed in offshore waters and forage at depths of up to 100 meters, although shallower horizontal dives are more efficient, allowing them to feed mostly on pelagic fishes (Benvenuti et al., 2001; Sonntag and Hüppop, 2005). Similarly to this study, a partly benthic diet was reported for common guillemot at the Gannets Islands (Labrador) (Bryant et al., 1999) and in the southeastern North Sea (Helgoland) (Sonntag and Hüppop, 2005).

Smelt is a very likely food source for wintering birds but its share in bird diets varies in time. Regarding to SI mixing models, the proportions of smelt in the diet of grebes and divers increased from 17 and 21% to 29 and 55%, respectively, during the winter (Fig. 5.13). It could be related to the variability of smelt abundance in the coastal area. According to fishery reports for the winter 2012–2013, smelt catches consisted of 9.3 tons in December, 48.4 tons in January, 26.9 tons in February, and 16.2 tons in March (data from Fisheries Service). Diver, which is specialized in feeding on pelagic fishes, seems to be more responsive to the change in smelt availability than grebe. Unfortunately, the absence of scientific data on truly available fish resources and smelt dynamics in the coastal area limits evaluation of the reliability of modeling output. More than a two-fold higher proportion of smelt (75–79%) was found in the stomachs a decade ago (Žydelis, 2002), although smelt commercial catches were comparable during both periods: 101 tons in 2013 and 102–175 tons annually during the period 1998–2001 (data from Fisheries Service). Stomach content analysis of birds collected from smelt gillnets may hold an artifact and possibly cause the overestimation of smelt proportion. Since a SI signal of bird blood provides dietary information integrated for approximately two weeks (Vander Zander et al., 2015), the tissue analysis might respond to fluctuations in certain fish consumption changes.

This work demonstrated the capacity of triple isotope approach to differentiate clupeids at the species level and discriminate smelt, which is an important contribution to the trophodynamic studies of the top predator level. According to dual and triple SI calculations, the herring to sprat ratio was 1.4–1.5, 1.1–1.2, and 0.8–0.9 in the diet of great crested grebe, red-throated diver, and common guillemot, respectively. These numbers are in line with those reported for cod diet (herring to sprat ratio between 0.2 and 1.8) in the Baltic Sea (Neuenfeldt and Beyer, 2006).

6.4.3. Diet of benthivorous ducks

The triple SI approach and the gut content analysis allowed to asses diet compositions of velvet scoter and long-tailed duck wintering in the Lithuanian coastal zone. Both SI approach and gut content analysis revealed velvet scoter preference for soft bottom bivalves *M. arenaria* and *C. glaucum*, while proportions of other food sources (crustaceans and polychaetes) varied. Homogenous SI values in *M. arenaria* and *C. glaucum* did not allow discriminating these food items; therefore, they were aggregated and used together in the SI mixing models. The SI mixing models revealed the joint contribution of *C. glaucum* and *M. arenaria* to the scoter diet – 51-56% (Table 5.8). Regarding the gut content analysis, *M. arenaria* was found in twice less amounts than *C. glaucum* (27 and 45% of total weight respectively in 2012; present study), although *M. arenaria* had dominated in scoter diet previously (82% of total weight in 1996-2002; Žydelis, 2002). Regarding the organic matter contributions (Table 5.12), all bivalve species, including *M. balthica*, were found to be at the same proportions (1/3 of total AFDW) in guts of velvet scoter.

Bivalve *C. glaucum* and crustacean *C. crangon* were found in the guts of velvet scoter this study, although previously they had not been reported as prey items for scoters in the Lithuanian coastal zone (Žydelis, 2002). In this study, *C. crangon* was rare, but *C. glaucum* was consumed almost by each velvet scoter individual and contributed to 33% of total organic matter weight (Table 5.8). Other studies report

C. glaucum as one of the dominant prey items in scoter diet in the Danish, English, Polish, and German Baltic coasts (review by Fox, 2003).

As abundance of certain prey species vary spatially and temporally, diet composition of scoters could also vary among the areas and particular periods (Fox, 2003). According to benthos monitoring data, total benthos biomass in sandy bottom habitats within the depth range of 13-15 m at Juodkrantė site has not changed. However, differences in diet compositions of velvet scoter between periods of 1996-2002 (by Žydelis, 2002) and 2012 (present study) could be still explained by shifts in proportions of three main bivalve species. *M. balthica* was dominating species comprising 56-96% of total benthos biomass during 1996-2002 but its proportion markedly decreased during 2012-2016 (21-63%). Other bivalve species have become more abundant: *M. arenaria* composed 2-18% and 5-57%, while *C. glaucum* composed 0-17% and 2-48% of total benthos biomass during 1996-2002 and 2012-2016, accordingly (State monitoring database of the Marine Research Department under the Environmental Protection Agency; Solovjova, unpubl.). Therefore, diet composition of benthivorous velvet scoter corresponds well to the composition of benthic community for the reported periods.

The SI mixing model results revealed large proportion of crustaceans in the diet of velvet scoter. It might be appropriate for individuals foraging on *S. entomon* in deeper areas (Denoflit, 2012). However, the gut content analysis of ducks bycaught only in the coastal zone which represent, the momentary diet and might reflect feeding on coastal organisms rather than offshore prey. High variability among $\delta^{13}C$ ratios in individual crustaceans and polychaetes increased their proportions and uncertainty in the diet estimates. Therefore, single $\delta^{34}S$ and dual $\delta^{34}S$&$\delta^{15}N$ models likely provide more accurate estimates for scoter diet than triple $\delta^{34}S$ & $\delta^{15}N$ & $\delta^{13}C$ mixing model.

There were also changes in long-tailed duck diet between 1997-2001 and 2012-2016 in the Lithuanian coastal zone. Although long-tailed duck is considered as ecologically plastic species, diet shift from *Mytilus* sp. (1997-2001; Žydelis, 2002) to fishes (2012-2016; present study) was unexpected. Rich beds of *Mytilus* sp. (Olenin, 1996), characterized by low energetic value, were predictable food resources and maintained stable lipid reserves in birds (Žydelis and Ruškytė, 2005; review of Žydelis and Richman, 2015). *Mytilus* sp. has been referred as the most important prey item for long-tailed duck across the coastal zones in the Baltic, while soft-bottom organisms and mobile prey as sand goby and sand-eel consisted lesser proportion in the diet (Nilsson, 1972; Peterson and Ellarson, 1977; FEBI, 2013). In this study, feeding differences of long-tailed duck are obvious due to a sharp decline of *Mytilus* sp. in the hard bottom habitats (Stupelytė and Šiaulys, 2015). Anadromous European smelt and large crustaceans are the dominant prey for long-tailed duck in the stony bottom habitats. That could be also related to redistribution of ducks (number over hard bottom depleted) and optimization of feeding effectiveness (Nilsson et al., 2016). Changes in diet composition should be taken into account when analyzing strong decline in abundance of wintering long-tailed ducks in the entire Baltic Sea (Skov et al., 2011; database of Lithuanian Ornithological Society).

Bird gut content analysis is based on wet weight and organic matter weights of objects found in the gizzard and esophagus. It is common to find nondigestible items which could contribute to the total weight but are excreted nondigested (e. g. shells of bivalves). Conversely, such soft-bodied prey as polychaetes are often underestimated because of rapid digestion in the foregut and rare detection (review of Žydelis and Richman, 2015). In this study, we did not find polychaetes in analyzed scoter guts, but SIA mixing models estimated their contribution to the diet (7-18% according to different model setups). Moreover, polychaetes have been mentioned as food items for marine benthivorous ducks, e.g. Žydelis (2002) reports that polychaetes are taken by 83% of studied scoters but their contribution to the total weight was low (3%). Regarding this information, the SIA provides information on assimilated (not only ingested) food items, it is possible that it is not only bivalves which are important for scoter diet. The contribution of other soft bottom macrofauna as soft-bodied prey could be important but underestimated.

Food items of benthivorous ducks differ by energetic values. The bivalves as the most dominant prey are of low caloric value with high inorganic nondigestible content; moreover, shell crushing increases energetic costs (Fox, 2003). Digestion of crustaceans is relatively tough but energetically important. Scarcer but easily digestible polychaetes and fishes could provide twice, three- or even four-fold higher energetic value than bivalves (review of Žydelis and Richman, 2015). Therefore, diversity of diet objects might ensure a good body condition and high fat reserves for wintering ducks. Considering strategy to store more fat reserves when food is scarcer (Schummer 2005), we could speculate that present decreased number of ducks overwinters without energy stress in the Lithuanian coastal zone. However, true reasons of changes in macrozoobenthos community and their effects on marine bird diet are still unclear and require more detailed studies.

Long-term studies on diet or feeding conditions may help to interpret ongoing changes in marine duck abundance in general; however, this question is still not well addressed. Peterson and Ellarson (1977) did not find changes in food habits of wintering waterfowl during 1951-1972 in the Lake Michigan; but changes in waterfowl diet were reported in the Great Lakes after invasion of *Dreissena polymorpha* that become the main prey items for waterfowl (Custer and Custer, 1996). However, despite high numbers of dreissenid mussels in macroinvertebrate community (approx. 85%) in the Lake Ontario, wintering waterfowl mostly fed on high energy-density prey objects such as Amphipoda and Chironomidae (Schummer et al., 2002). However, the trophic impacts of wintering waterbirds on benthic communities have been assessed in coastal areas of the Baltic Sea (Stempniewicz, 1994, Žydelis, 2002). Long-tailed ducks, even when in high numbers, consumed only 1-2% of total biomass of *Mytilus* sp. when their stocks were considered abundant and stable around 2000s in the Lithuanian coastal zone (Olenin, 1997; Žydelis, 2002). However, the predation pressure has reached 40% of the total benthic biomass on the Oder bank and the consumption by ducks might be much higher locally (Nilsson, 1980; Kube, 1996; Žydelis, 2002). Moreover, natural fluctuations of macrozoobenthos biomass are present between years and might depend mostly on differential recruitment, mortality during winter, nutrient stress, etc. (Strasser et al., 2001). There are hypotheses that biomass of *Mytilus* sp. could be reduced by invasive round goby (Skabeikis et al., in prep.), while long-tailed duck might contribute to further *resource degradation*.

The above discussion demonstrates how new information on the ecology of marine birds can be obtained using both isotopic and conventional dietary techniques. Triple SI mixing models provide diet estimates for marine birds being consistent with the results derived from gut content analysis. Gut content analysis is essential for the interpretation of isotopic results and *vice versa* (e.g. Hobson et al., 1994). Therefore, in this study, the consistency of both approaches allows more detailed bird diet investigation and detection of temporal changes. Detected prey switching in duck feeding may affect their population dynamics.

6.5. Trophic position of consumers

Despite the widespread use of both mass-balance models and SI methods, studies including both approaches are still rare (e.g. Navarro et al., 2011). However, the simple comparison of trophic positions obtained by both methods could useful for the validation of modelling approach. Moreover, most of published research results present comparisons of trophic positions for macrozoobenthos and fishes, while waterbirds are mentioned only in few studies (according to Navarro et al., 2011). In this study, high and positive correlation ($R=0.83$, $p<0.05$; Spearman-rank correlation) between $\delta^{15}N$ ratios in fishes, macrozoobenthos, and waterbirds and their TLs calculated by ECOPATH revealed a good agreement (Fig. 6.1). A similar study in the northwestern Mediterranean Sea reported a good correlation between trophic positions estimated by ECOPATH model and $\delta^{15}N$ ratios for fishes, cephalopods, cetaceans, turtles, and marine birds as well (Navarro et al., 2011).

This study confirms that $\delta^{15}N$ ratio and mass-balanced modelling estimates are both comparable and suitable methods to delineate the trophic positions of consumer groups in the coastal ecosystem. However these two methods differ a lot in their requirements for the labor costs, expertise, and time. The ECOPATH model setup was mostly based on the original monitoring and trophology data resulting in time and expertise consuming model construction, parameterization efforts. The SIA could be relatively inexpensive and quick as no elaborate sampling procedures are required.

Therefore, the approach to use δ^{15}N ratios for estimation of trophic positions could be a kind of *express* assessment of coastal food webs, while mass balance modelling approach delivers much more detailed information, which cannot be measured directly. On the other hand, the good agreement of the results produced by both approaches confirms that the input information used in the mass-balanced model was relevant and accurate (Navarro et al., 2011).

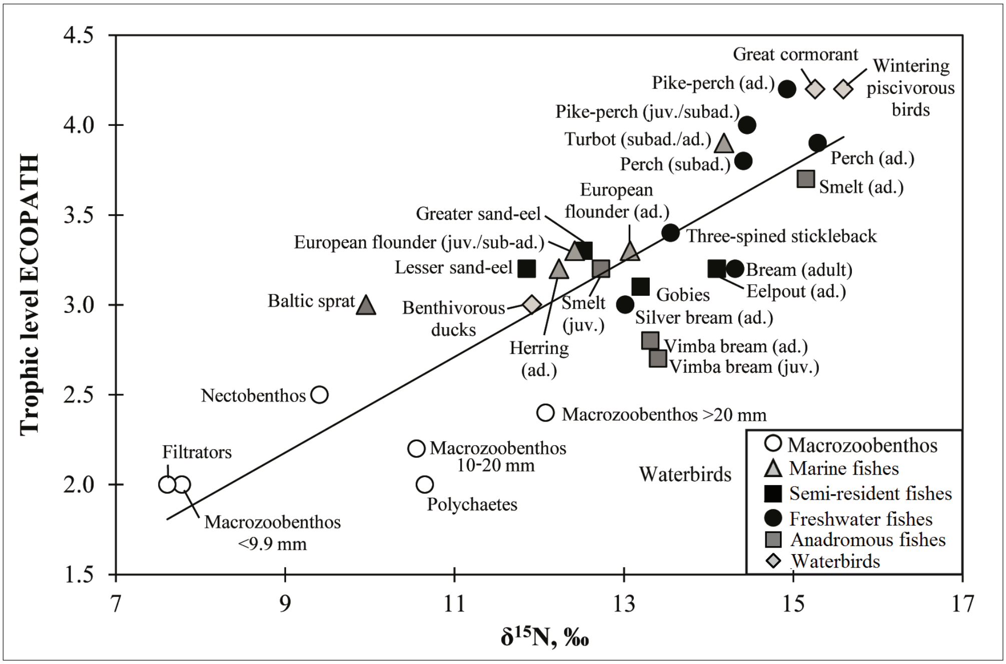

Figure 6.1. Relationship between δ^{15}N ratios of consumers and trophic levels estimated by the ECOPATH model (N=29, R=0.83, p<0.001).

Although trophic positions of consumers evaluated by two methods are comparable, some disagreements appear. Differences in δ^{15}N ratios and outputs of the ECOPATH model might be attributed to the ecological characteristics of species and the accuracy of certain assumptions used for each method. The lower trophic position calculated by ECOPATH in comparison to isotopic evidence for the partly detritivorous vimba bream could be explained by the assumption of detritus being of the TL 1 in the model. It is known, however, that detritivorous fishes have higher δ^{15}N ratios than primary consumers (Navarro et al., 2011). The same interpretation might be used for polychaetes and other omnivorous macrozoobenthos (10-20 and >20 mm length), which are also at least partly detritivorous. Trophic positions of invertebrates were more scattered than those of fishes and birds (Fig. 6.1). That could be attributed to inconsistencies of the diet estimates, which were mostly compiled from the literature data originated from different ecosystems. Moreover, some groups as omnivorous macrozoobenthos comprised species that were very different in size and as a result both their diet and attraction for predators might have been very different. Polychaetes, which were pooled into the single group in the model vary in their feeding characteristics between detritovorous and predatory, which in turn could have contributed to higher TL in the ECOPATH model. The group of nectobenthic organisms could include some crustaceans which are attributed to macrozoobenthos groups and *vice versa*. Therefore, comparison of the δ^{15}N ratios and TL estimated by the ECOPATH suggests changes in grouping compartments, especially of those, which diets were difficult to estimate or assumptions were taken from other ecosystems. In this case SIA could clearly improve the selection and grouping of macrozoobenthic organisms (Nordström et al., 2015).

Comparison of trophic positions of large predatory fishes as pikeperch and piscivorous waterbirds also provided some clues. Based on δ^{15}N ratios, interpretations of predator trophic-level suggest that lower trophic-level organisms might be more important to predators than it was recognized previously using conventional dietary studies. The same tendency was observed for TL estimates for some seabird species in the coastal waters of the northeast Pacific Ocean (Hobson et al., 1994).

Migratory freshwater fishes might contain higher δ^{15}N values because of their at least partial residency in the Curonian Lagoon and exposure to the freshwater originated food sources. Individuals used for this analysis were sampled in August-September with the aim to detect SI signatures which are already at least partly adjusted to the coastal environment. However, part of the coastal population could have migrated from the lagoon more recently than other individuals, which could also lead to the discrepancies of trophic positions when comparing TL estimated by ECOPATH and δ^{15}N ratios. There were also comparative studies analyzing trophic networks of the Baltic sub-areas and the Chesapeake Bay ecosystem where seasonal changes in fish diet compositions contributed to variation of fish trophic positions (Wulff and Ulanowicz, 1989). Vander Zanden et al. (1997) indicated that trophic position of freshwater fishes might vary by one position among populations, but the mean dietary positions corresponded closely to δ^{15}N ratios.

Majority of published models do not include birds or have only single bird compartment, which might lead to the underestimation of bird importance. In the Lithuanian coastal zone, benthivorous ducks feed mainly on macrozoobenthos and have intermediate trophic position, whereas two groups of piscivorous waterbirds have top positions (estimated by both ECOPATH model and δ^{15}N ratios). Therefore, it is more correct to have multiple groups of waterbirds differing in their diets and residency periods in the study area.

Furthermore, in this study, the good correlation between trophic positions evaluated using the two methods could be explained by relatively high number of compartments. The introduction of compartments representing different ontogenetic stages of fish species contributed to the improvement of the entire model as well, because changes in their dietary preferences and importance for predators are expected as fish grow (Nilsen et al., 2008).

6.6. Trophic impacts in the community

Waterbirds were the major fish consumers (35%) followed by freshwater stragglers (18%), while the coastal fishery was only the 5th among the important biomass consumers (12%) (Fig. 6.2). However, the main prey items of waterbirds are the non-resident anadromous fishes, mostly smelt. Great cormorant, the most important species according to the keystones index (Fig. 5.24), has attained local attention from the fishing community (e.g. Žydelis and Kontautas, 2008). However, our results did not show strong direct and indirect impacts of the cormorant on the fishery. It was shown that the composition of fish catches and the diet of cormorants overlap very little in the Curonian Lagoon (Pūtys, 2012; Troynikov et al., 2013). This bird species is assumed to be an important consumer of smaller fishes, so rather competing with larger fish species than fishermen (Mous et al., 2003; Pūtys, 2012).

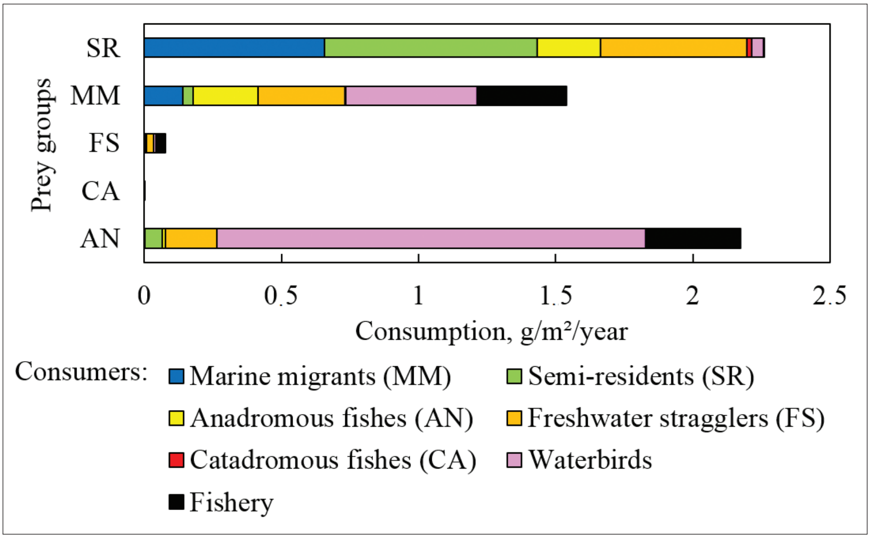

Figure 6.2. Estimated consumption of fish by different consumer groups as fishes, waterbirds and fishery (modified from Razinkovas-Baziukas et al., accepted).

The great cormorant has been identified as the key species in the Lithuanian coastal ecosystem. The analysis of SI ratios in feathers revealed temporal diet changes of cormorant and grey heron juveniles (Fig. 5.4). The interpretation of SI results was based on knowledge that the vane tips of bird feathers are synthesized earlier than the middle feather parts, thus isotopic difference between these two parts provides information on diet changes. An increase of $\delta^{15}N$ values in different parts of feathers indicates diet changes for cormorant juveniles during the fledging period. Therefore, it could be assumed that adults feed juveniles by smaller fishes at the beginning of fledging, switching later to larger prey. Pūtys (2012) provided seasonal differences in diet composition of cormorant juveniles at the same colony, mostly corresponding to seasonal changes in fish community. Lehikoinen (2005) and Čech et al. (2008) proved that great cormorant might switch size and species of prey fishes during fledging period.

This study did not indicate a statistically significant diet shift for juveniles of grey heron during a fledging period. This could be a result of a high variation in the $\delta^{15}N$ values in vane tips, while the SI values in mid-vanes were more homogenous. Other studies report that grey heron opportunistically feed on a broad range of prey from insects to small mammals (Navasaitis, 1983; Jakubas and Mioduszewska, 2005). In mixed colonies of herons and cormorants, the diet of heron juveniles might be supplemented by fishes regurgitated by cormorant juveniles (Wojczslanis et al., 2005; observations at the studied colony). Regarding SIA results of this study, the earlier diet of heron juveniles might be composed of prey objects varying in their $\delta^{15}N$ values. At the later phase of fledging, when cormorant adults intensively feed their juveniles, heron adults might collect fishes dropped from cormorant nests and feed them to juveniles. Dominant prey for cormorant are medium size ruffe, European perch, and roach (body length 5-17 cm, Pūtys, 2012), those are suitable prey for the heron juveniles too. Moreover, larger fishes brought by cormorant adults might be difficult to swallow for their own juveniles, therefore, there is a higher possibility for them to be dropped down and collected by herons (Čech et al., 2008; Pūtys, 2012). Herons might choose to feed their juveniles on this easily available resource rather than search for prey in adjacent territories. Therefore, we speculate that this food type could contribute to the quite high and constant $\delta^{15}N$ values in mid-vanes of heron juveniles.

According to the ECOPATH estimates, freshwater predatory fishes, breeding and wintering piscivorous birds along with the coastal fishery have the strongest direct and indirect impacts on the majority of analyzed groups in the studied coastal ecosystem (Fig. 6.3). Representing the highest keystoneness values, pike-perch adults and wintering piscivorous waterbirds were important groups contributing to overall fish consumption. The high keystoneness values of nectobenthos, mesozooplankton, and omnivorous makrozoobenthos (10-20 mm) are mostly due to their strong importance to the diet of fish groups. Waterbirds, predatory fish, zooplankton and nectobenthic invertebrate species have been identified as keystone compartments in many modelled food webs, especially in the shallow coastal systems (Libralato et al., 2006; Coll et al., 2007; Pedersen et al., 2008). However, their role is not obvious and could be derived from the indirect trophic effects (Libralato et al., 2006). Considerably high keystoneness indices for both adults and juveniles of anadromous smelt could be attributed to their high proportion in the diets of waterbirds and predatory fish species and commercial fishery, similarly as was found in other areas, e.g. the shallow eutrophic Ijsselmeer lake (the Netherlands) (Buijse et al., 1993). Therefore, this study confirms the importance of non-resident fish species in both internal (prey and consumer) and external (migrations) transfers of organic matter (Deegan, 1993; Willson and Halupka, 1995; Holmlund and Hammer, 1999 and references in it).

In this study, the ECOPATH model of the Lithuanian coastal zone did not include Atlantic cod, although this species is very important for the marine fishery in the Baltic (e.g. Harvey et al., 2003). There are a number of studies presenting abundance and diet changes in the Baltic fish community, trophic cascades, and potential causes of changes and effects. This species prefers open marine areas with higher salinity rather than the coastal zone habitats, where cod is present irregularly and in low abundance to feed on clupeids and macrozoobenthos (Österblom et al., 2007). Moreover, inconsistencies in the estimation of cod diet in the coastal zone, forced us to exclude this species from the coastal model (more detailed explanation in Section 3.3). In the present model, the predation and fishing mortality of clupeids (Baltic sprat and Baltic herring) is high enough even without cod, thus the balance of biomass is maintained by supply from the open Sea. The inclusion of cod as a compartment in the model would only increase clupeid immigration figures in terms of biomass leaving the overall structure of the model unchanged. As macrozoobenthos compartments are not much consumed in this coastal food web (EE is less than 0.3; Table 5.13), consumption by cod would also not make much difference here as well. Obviously, given the cod would be included to fishery landings, the only significant change would be some increase of the mean TL value of catches.

Fishery was the single anthropogenic activity included to the model. Although non-resident fishes as marine migrants, freshwater stragglers and anadromous fishes dominate the coastal catches, fishery represents one of the most negative impact factors on the food web compartments. The recent invasion of the round goby in the Lithuanian coastal was not included as most of the data used in the model were collected before this event. However, there is clear evidence that both fishery and the food web itself might have changed significantly since the invasion (Almqvist et al., 2010).

This thesis represents a complex reconstruction of the coastal food web as the result of combined application of different techniques involving literature data, field samples and SIA. The analysis revealed the structural complexity of the ecosystem both on spatial and temporal scale. Our findings, especially relevant to the transitional environment, emphasized the importance of both active migration and passive organic matter transport from the freshwater Curonian Lagoon-Nemunas River system resulting in the net heterotrophic status of this coastal ecosystem. Although heterotrophy is

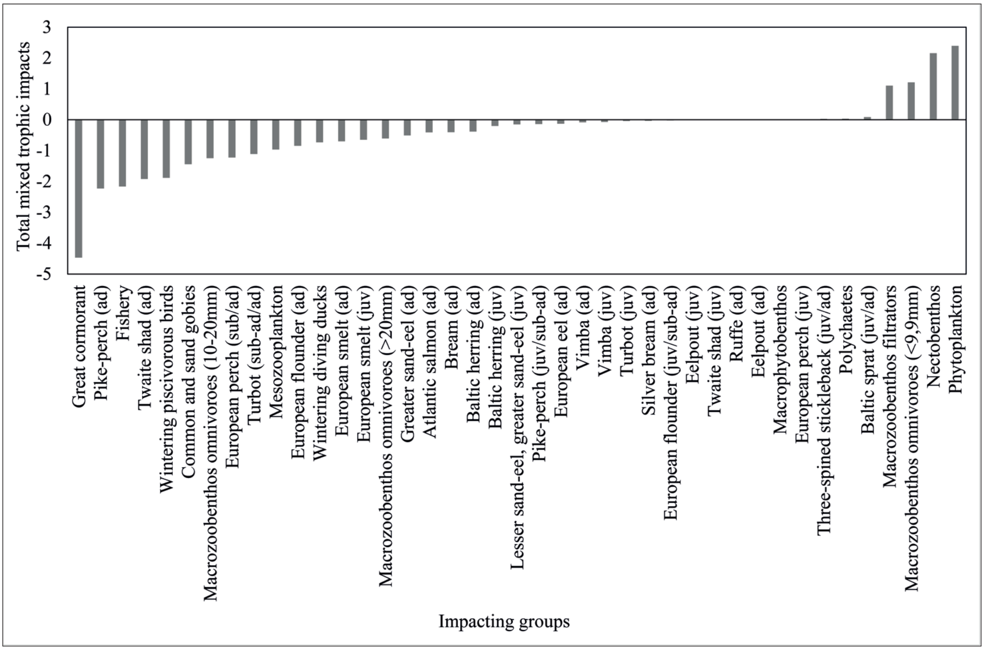

Figure 6.3. Total predicted impact of each impacting compartment on all the impacted compartments of the coastal food web.

not uncommon in other river dominated coastal environments in the Baltic Sea (Stepanauskas et al., 2002; Korth et al., 2013), this study is the first one demonstrating it using the complete food web mass-balance. approach..

Calculated keystoneness demonstrated that even only seasonally present summer resident top predators as great cormorant and pike-perch adults, and wintering piscivorous birds are important in regulation of pelagic fish species and the whole coastal food web. Furthermore, nectobenthos and mesozooplankton are important food sources for small fishes and contribute to organic matter transfer to higher TL; these groups make bottom-up control whole year round in the coastal ecosystem. Bottom-up control is the major mechanism for various ecosystems in the Northeast Atlantic (e.g. Lassalle et al., 2013). Although bottom-up control could be quite stable in the Lithuanian coastal ecosystem, at least temporary top-down control is also relevant.

The reconstructed coastal food web with characterization of web structure and trophic flows allows further analysis of the ecosystem functioning. Moreover, it serves a baseline for ecosystem-based management that is already needed as one of the best approaches for determination of driving factors, effective environmental protection, resource management and guidance to combination with economic, social and ecological considerations.

7

Conclusions

1. Variability of SI ratios in food web compartments reflects the uneven contribution of the freshwater outflow from the Curonian Lagoon to different coastal sites: the lowest $\delta^{13}C$ ratios in the food web compartments were found in Melnragė site, the highest – at Juodkrantė, intermediate – at Palanga. Different ecological fish guilds demonstrated the spatial heterogeneity across the coastal sites in SI values: both $\delta^{13}C$ and $\delta^{15}N$ ratios in semi-resident fishes, $\delta^{13}C$ ratios in marine migrants and $\delta^{15}N$ ratios in freshwater stragglers were spatially variable; however, anadromous fishes have homogenous SI values across all the studied sites.

2. The food web of the Lithuanian coastal zone was net heterotrophic (TPP/TR=0.83) because of large inputs of organic matter supplied from the neighboring Curonian Lagoon and actively migrating fish species.

3. The triple SIA approach ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) revealed that wintering red-throated diver and common guillemot mostly foraged pelagic fishes, whereas great crested grebe preferred benthic fishes; European smelt comprised a quarter of the diet of studied birds. The triple SIA approach revealed that prey items of velvet scoter mainly consisted of sandy bottom bivalves, mostly *Cerastoderma glaucum* and *Mya arenaria*, while the gut content analysis also indicated the contribution of *Macoma balthica* to the diet . Long-tailed duck foraged mostly on European smelt in the stony bottom habitats, while lesser sand-eel and crustacean *S. entomon* dominated the diet in the soft bottom habitats.

4. According to the ECOPATH model of the Lithuanian coastal zone, fishery and such keystone compartments as piscivorous birds and adult pike-perch had the strongest overall negative impacts, while nectobenthos and mesozooplankton had positive impacts on other food web compartments.

5. Statistically significant and strong relationship between $\delta^{15}N$ ratios of consumers and trophic levels estimated by the ECOPATH model revealed the high relevance of the both methods applied to the analysis of the Baltic Sea coastal zone.

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Annex

Table 1. **The SI values for invertebrates, fish and birds during April-October 2010 across Lithuanian coastal sites. N – number of samples.**

Group	Species	N	C:N mass ratio		δ^{13}C, ‰		$\delta^{13}C_{norm}$, ‰		δ^{15}N, ‰	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
POM	<70	23	7.3	1.0	-27.3	1.3			5.6	3.7
	Total	21	6.3	1.4	-29.5	2.4			3.8	2.5
Seston	100-200	19	6.5	0.4	-28.5	2.3			4.4	1.9
	>200	20	7.0	0.9	-27.8	1.6			4.3	3.1
Algae	*Ceramium tenuicorne*	2	11.6	0.3	-24.6	0.0			7.7	0.0
	Cladophora sp.	4	9.8	0.1	-21.3	0.6			5.6	0.4
	Coccotylus truncatus	4	9.3	0.8	-36.3	0.1			4.4	0.1
	Ulva intestinalis	6	13.0	4.5	-19.9	1.7			7.8	1.0
	Furcellaria lumbricalis	6	10.1	0.5	-23.0	1.2			5.8	0.9
	Polysiphonia fuciodes	2	8.7	0.0	-27.4	0.0			4.5	0.2
Macrozoo-benthos	*Amphibalanus improvisus*	3a	5.4	0.1	-23.0	0.1	-21.0	0.0	9.5	0.1
	Crangon crangon	21	4.3	0.3	-19.5	1.5	-18.6	1.4	11.3	0.7
	Gammarus sp.	18 a	5.6	0.4	-22.5	0.8	-20.3	0.7	7.7	0.6
	Bylgides sarsi	2	5.3	0.0	-21.7	0.1	-19.8	0.1	10.6	0.7
	Idotea balthica	3 a	6.2	0.3	-20.8	0.6	-18.0	0.6	7.3	0.4
	Mytilus sp.	13 a	5.8	0.6	-23.8	0.6	-21.4	0.5	8.2	0.3
	Neomysis integer	12 a	4.4	0.2	-22.9	0.8	-21.8	0.6	10.4	0.7
	Palaemon elegans	12	4.5	0.3	-22.4	1.4	-21.2	1.2	10.2	1.0
	Pygospio elegans	1 a	5.0		-24.0		-22.4		9.7	
Fish	Ammodytidae SR	20	4.2	0.3	-21.2	1.2	-20.4	1.1	12.1	0.9
	Atlantic cod MM	3	3.8	0.1	-19.2	0.4	-18.7	0.4	14.0	0.5
	Baltic herring MM	6	4.1	0.2	-20.1	0.5	-19.3	0.4	12.2	0.8
	Baltic sprat MM	9	4.2	0.2	-21.7	0.8	-20.8	0.7	9.5	1.4
	Bream FS	2	4.1	0.2	-26.5	0.9	-25.8	0.7	14.3	0.4
	European anchovy MM	3	3.8	0.0	-21.2	0.4	-20.8	0.4	9.8	0.4
	European flounder MM	62	4.0	0.2	-21.4	2.2	-20.8	2.2	12.8	1.2
	European perch FS	33	3.9	0.1	-23.6	2.7	-23.1	2.7	14.9	0.8

Group	Species	N	C:N mass ratio		$\delta^{13}C$, ‰		$\delta^{13}C_{norm}$, ‰		$\delta^{15}N$, ‰	
	European smelt AN	26	4.0	0.1	-23.8	3.0	-23.2	3.0	13.7	1.9
	Pike-perch FS	21	3.9	0.1	-22.7	1.9	-22.2	1.9	14.7	0.9
	Round goby SR	5	3.9	0.1	-21.9	0.6	-21.4	0.7	12.4	0.1
	Silver bream FS	3	3.8	0.1	-23.1	1.5	-22.6	1.5	13.0	0.6
	Three-spined stickleback FS	2	4.2	0.1	-31.6	0.5	-30.7	0.5	13.6	0.2
	Turbot MM	12	3.8	0.1	-21.1	1.3	-20.6	1.2	14.2	0.5
	Vimba bream AN	21	4.3	0.6	-25.4	2.1	-24.5	2.2	13.4	0.8
Birds	Great cormorant	6b					-25.6	1.4	15.3	0.6
	Grey heron	3b					-26.9	0.9	15.5	1.1

[a] Each sample represents several pooled individuals; [b] Represents a number of individuals used for several sampling, i.e. few samples were taken from different feather part of each individual. SR, FS, MM, AN indicate fish guilds: semi-resident, freshwater, marine migrants or anadromous fish.

Table 2. **Calculations of organic matter content (AFDW) for food items of wintering ducks.**

It was assumed that bivalves biomass comprised approx. 15% of soft tissues, crustacean biomass - 50% of soft tissues of and entire biomass of fish specimens in gizzard and esophagus of ducks. WW – wet weight, SFWW – shelf free wet weight, DW – dry weight, AFDW – ash free dry weight.

Food items	Used calculations	Source
Macoma balthica	WW=40.2% SFWW; DW=48.% WW; AFDW=18.5% DW	Rumohr et al., 1987
Mya arenaria	WW=51.3% SFWW; DW=53.8% WW; AFDW=15.4% DW	
Cerastoderma glaucum	WW=36% SFWW; DW=54.1% WW; AFDW=11.5% DW	
Mytilus sp.	DW=43.6% WW; AFDW=20% DW	
Crangon crangon	DW=19.1% WW; AFDW=90,7% DW	
Saduria entomon	DW=19.9% WW; AFDW=65,2% DW	
Unidentified crustacea	DW=19.5% WW; AFDW=77,6% DW	
Mysids	DW=19.9% WW; AFDW=90% DW	
Fish	AFDW=3% WW	Timberg et al., 2001

Table 3. Input data and references for the Lithuanian coastal model

Group name and parameters	Reference	Observations
Phytoplankton		
Biomass	Gasiūnaitė et al., 2005	Used mean value multiplied by mean photic depth. An haft of mean depth of the coastal zone was assumed as mean photic depht (Bučas, 2009)
P/B	Kudryavtseva et al., 2011; Gasiūnaitė et al., 2005	Used conversion factor from gC to wet weight of 0.1 (Matthews and Heimdal, 1980)
Mesozooplankton		
Biomass	Aleksandrov et al., 2009	Used mean value multiplied by mean depth of the coastal zone
P/B	Witek, 1995	
Q/B	Harvey et al., 2003	The value was used from a food web model for the Baltic Sea proper
Diet	Wasmund et al., 2001	The diet depends on particle composition in the water, so detritus and phytoplankton were in the diet
Nectobenthos		
Biomass	Aaser et al., 1995	
P/B	Aaser et al., 1995	
Q/B	Harvey et al., 2003	Taken as for pelagic macrofauna
Diet	Viherluoto et al., 2000	
Macrophytobenthos		
Biomass, P/B	Bučas, 2009	
Macrozoobenthos filtrators		
Biomass	Bubinas and Vaitonis, 2003; Bubinas and Repečka, 2003	Used median
P/B	Cusson and Bourget, 2005	Used value for filter feeders
Q/B	Harvey et al., 2003	
Diet	Arapov et al., 2010	

Group name and parameters	Reference	Observations
Macrozoobenthos omnivorous (<9,9mm)		
Biomass	Bubinas and Vaitonis, 2003; Bubinas and Repečka, 2003	The value for the group calculated according to Oh et al., 2001
P/B	Cusson and Bourget, 2005	Used value for deposit feeders
Q/B	Harvey et al., 2003	
Diet	Monakov, 1998	
Macrozoobenthos omnivorous (10-20mm)		
Biomass	Bubinas and Vaitonis, 2003; Bubinas and Repečka, 2003	The value for the group calculated according to Oh et al., 2001
P/B	Cusson and Bourget, 2005	Used value for omnivorous
Q/B	Harvey et al., 2003	
Diet	Monakov, 1998	
Macrozoobenthos omnivorous (>20mm)		
Biomass	Bubinas and Vaitonis, 2003; Bubinas and Repečka, 2003	The value for the group calculated according to Oh et al., 2001
P/B	Cusson and Bourget, 2005	Used value for omnivorous
Q/B	Harvey et al., 2003	
Diet	Oh et al., 2001; Monakov, 1998; MarLIN, 2005	
Polychaetes		
Biomass	Bubinas and Vaitonis, 2003; Bubinas and Repečka, 2003	Used median of biomasses
P/B	Cusson and Bourget, 2005	Used value for deposit feeders
Q/B	Harvey et al., 2003	
Diet	Monakov, 1998	
Baltic herring (juvenile)		
Biomass	Database of Fishery Research Laboratory, 2010	

Group name and parameters	**Reference**	**Observations**
P/B	Zaika, 1983	
Q/B	Harvey et al., 2003	
Diet	Bacevičius E., unpubl. data	
Baltic herring (adult)		
Biomass	Database of Fishery Research Laboratory, 2000-2010	
P/B	Zaika, 1983	
Q/B	Harvey et al., 2003	
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Baltic sprat (juvenile/adult)		
Biomass	Database of Fishery Research Laboratory, 2000-2010	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Used value for European anchovy
Diet	Bacevičius E., unpubl. data	
Lesser sand-eel and Greater sand-eel (juvenile)		
Biomass	Database of Fishery Research Laboratory, 2000- 2010	
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	Regarding to Q/B value used for Greater sand-eel
Diet	Bacevičius E., unpubl. data	
Greater sand-eel (adult)		
Biomass	Estimated by Ecopath	Ecotrophic efficiency was assumed to be 1
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	

Group name and parameters	**Reference**	**Observations**
Diet	Bacevičius E., unpubl. data	
Common and Sand gobies (juvenile/adult)		
Biomass	Estimated by Ecopath	Ecotrophic efficiency was assumed to be 1
P/B	Zaika, 1983	
Q/B	Pauly, 1989	
Diet	Bacevičius E., unpubl. data	
Twaite shad (juvenile)		
Biomass	Database of Fishery Research Laboratory, 2000-2010	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Taken as for Baltic sprat which assumed to be as European anchovy
Diet	Bacevičius E., unpubl. data	
Twaite shad (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Harvey et al., 2003	Taken as for Baltic herring adult
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Eelpout (juvenile)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for small flatfish
Diet	Bacevičius E., unpubl. data	
Eelpout (adult)		

Group name and parameters	Reference	Observations
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for large flatfish
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
European flounder (juvenile/sub-adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for small flatfish
Diet	Bacevičius E., unpubl. data	
European flounder (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for large flatfish
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Silver bream (adult)		
Biomass	Piščikas, 2000	Calculated as 1/5 of bream biomass. According to Ložys L. (pers. comm.), silver bream biomass approximately is equal 1/4 bream biomass in the Curonian lagoon. Silver bream is more termofilic than bream, therefore, less individuals migrate to the coastal water.
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	

Group name and parameters	**Reference**	**Observations**
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Bream (adult)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Vimba bream (juvenile)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for small flatfish
Diet	Bacevičius E., unpubl. data	
Vimba bream (adult)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	Used value for other fish being benthic carnivores
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania 2000-2010	
Three-spined stickleback (juvenile/adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	
Diet	Bacevičius E., unpubl. data	

Group name and parameters	Reference	Observations
Ruffe (adult)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Taken as for juvenile of European perch according to sub-adult and adult of the species
Diet	Bacevičius E., unpubl. data	
European perch (juvenile)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Taken according to sub-adult and adult of European perch
Diet	Bacevičius E., unpubl. data	
European perch (sub-adult/ adult)		
Biomass	Piščikas, 2000; Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Used value for European perch (17.9 cm in body length) and yellow perch (33.6 cm in body length)
Diet Landings	Bacevičius E., unpubl. data Official Government Statistics for Lithuania, 2000-2010	
Atlantic salmon (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Jarre-Teichmann, 1995	Used mean value of different seasons
Diet	Bacevičius E., unpubl. data	

Group name and parameters	Reference	Observations
Landings	Official Government Statistics for Lithuania, 2000-2010	
Pike-perch (juvenile/sub-adult)		
Biomass	Piščikas, 2000	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Taken according to sub-adult of European perch
Diet	Bacevičius E., unpubl. data	
Pike-perch (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Palomares and Pauly, 1998	Used mean value for northern pikes
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Turbot (juvenile)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Taken as for small flatfish
Diet	Bacevičius E., unpubl. data	
Turbot (sub-adult/adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Used value for large flatfish
Diet	Bacevičius E., unpubl. data	

Group name and parameters	Reference	Observations
Landings	Official Government Statistics for Lithuania, 2000-2010	
European smelt (juvenile)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	Used value for greater sand-eel
Diet	Bacevičius E., unpubl. data	
European smelt (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Pauly et al., 1990	Taken as for sandeel
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
European eel (adult)		
Biomass	Database of Fishery Research Laboratory, 2010	
P/B	Zaika, 1983	
Q/B	Trites et al., 1999	Taken as for eelpout what was assumed to be as large flatfish
Diet	Bacevičius E., unpubl. data	
Landings	Official Government Statistics for Lithuania, 2000-2010	
Great cormorant		
Biomass	Žydelis et al., 2002a; Švažas et al., 2011	Estimated by median abundance, individual weight, residency time and study area. Abundance was estimated not only by breeding pairs but also by non-breeding specimens accounting for 20-25% of nesting bird numbers

Group name and parameters	**Reference**	**Observations**
P/B	Christensen et al., 2009	
Q/B	Christensen et al., 2009	
Diet	Pūtys and Zarankaitė, 2010; Žydelis et al., 2002a	
Wintering diving ducks		
Biomass	Sorokaitė et al., 2007; Europos..., 2007; 2009; 2010; Žydelis, 2002; Švažas, 2001; Dagys et al., 2004	Estimated by median abundance, individual weight, residency periods and study area
P/B	Christensen et al., 2009	
Q/B	Christensen et al., 2009	
Diet	Žydelis et al., 2002b	
Discards	Žydelis et al., 2009	
Wintering piscivorous birds		
Biomass	Sorokaitė et al., 2007; Lietuvos fauna, 1990; Žydelis, 2002; Europos..., 2006; 2007; 2009; Švažas et al., 1998; Švažas, 2001; Žydelis et al., 2002a; Dagys et al., 2003; 2004	Estimated by median abundance, individual weight, present time and study area
P/B	Christensen et al., 2009	
Q/B	Christensen et al., 2009	
Diet	Žydelis et al., 2002a, b	
Detritus		
Biomass	Used empirical equation from Pauly et al., 1993	Primary productivity (Kudryavtseva et al., 2011) and photic depth (Bučas, 2009) were required for the equation. Used conversion factor from gC to wet weight of 0,1 (Matthews and Heimdal, 1980)

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Santrauka

ĮVADAS

Temos aktualumas

Mitybos tinklo aprašymas yra vienas pirmųjų žingsnių siekiant suprasti ryšius tarp bendrijos kaitos ir stabilumo bei ekosistemos funkcionavimo (Link, 2002; de Ruiter et al., 2005; Heymans et al., 2014). Stiprėjantis antropogeninės veiklos poveikis rūšių sąveikai ir jūrų ekosistemų funkcionavimui tampa vis svarbesnis. Baltijos jūros regione vis dar trūksta ekosisteminiu požiūriu paremto valdymo, todėl daugelis aplinkos problemų sprendžiamos atskirai (Elmgren et al., 2015).

Ekosisteminiu požiūriu grįstus Baltijos jūros priekrantės ekosistemų mitybos tinklų tyrimus palengvina tai, kad ekstensyvus mėginių rinkimas siekia istorinius laikus, o tyrimų įvairovė apima visą spektrą klausimų – nuo socialinių iki hidrodinaminių (Christian et al., 2005). Priekrantės ekosistemoms būdinga aibė gradientų, kurių kilmė yra susijusi su tarpinių vandenų bruožais. Organinės medžiagos srautas iš gėlavandenių baseinų į jūrines ekosistemas lemia priekrantės ekosistemų produkcijos ir suvartojimo balansą (Heip et al., 2011). Be to, dėl pasyviai transportuojamos organinės medžiagos ir aktyviai migruojančių organizmų priekrantės mitybos tinklai yra labai kompleksiški (Deegan, 1993; Heip et al., 2011; Hyndes et al., 2014). Todėl, norint supaprastinti užduotį, organinės medžiagos srautai iš gretimų ekosistemų ir migruojančios rūšys dažnai nėra įtraukiamos į priekrantės ekosistemų funkcionavimo tyrimus

(Willson and Halupka, 1995; Winemiller and Jepsen, 1998). Tai lemia nepilną trofinės struktūros aprašymą ir apriboja priekrantės ekosistemų funkcijų įvertinimą.

Baltijos jūros Lietuvos priekrantės ekosistemos struktūrai ir funkcionavimui įtakos turi gėlo vandens prietaka iš gretimų Kuršių marių ir didelis skaičius sezoninių migrantų. Ankstesnės Lietuvos tranzitinių vandens ekosistemų studijos apėmė tik atskirų rūšių sąveiką arba tam tikrų akvatorijų mitybos tinklų tyrimus (pavyzdžiui, Razinkovas and Zemlys, 2000; Ertürk et al., 2008; Tomczak et al., 2009), o viso priekrantės mitybos tinklo rekonstrukcija iki šiol atlikta nebuvo. Mitybos tyrimams taikoma stabiliųjų izotopų analizė (toliau – SIA) gali atspindėti sąveiką tarp įvairių organizmų, įskaitant migruojančias žuvis ir žiemojančius vandens paukščius (e.g. Hansson et al., 1997; Vaslet el al., 2012). Naudojantis mitybos tinklo modeliu (Christensen et al., 2005), galima įvertinti pagrindinių komponentų vaidmenis bei organinės medžiagos srautus. Šis darbas remiasi minėtų metodų taikymu rekonstruojant Lietuvos priekrantės mitybos tinklą ir siekiant geriau suprasti šios ekosistemos funkcionavimą.

Tyrimo tikslai ir pagrindiniai uždaviniai

Tyrimo tikslas – rekonstruoti mitybos tinklą ir kiekybiškai įvertinti organinės medžiagos srautus Lietuvos Baltijos jūros priekrantės ekosistemoje.

Pagrindiniai uždaviniai:

1. Įvertinti pagrindinių Lietuvos priekrantės mitybos tinklo komponentų, įskaitant žuvų ekologines gildijas, stabiliųjų anglies ($\delta^{13}C$) ir azoto ($\delta^{15}N$) izotopų santykius vegetacijos periodu.
2. Įvertinti skirtingų mitybos šaltinių proporcijas žiemojančių jūros paukščių racionuose, pritaikant stabiliųjų sieros izotopų ($\delta^{34}S$) naudojimą mitybos tyrimams.
3. Naudojantis ECOPATH modeliu, rekonstruoti priekrantės mitybos tinklą, įvertinti jo struktūrą ir charakteristikas bei trofinį poveikį bendrijoje.
4. Palyginti vartotojų $\delta^{15}N$ vertes ir jų trofinius lygmenis, įvertintus ECOPATH modeliu.

Darbo naujumas

Sudarytas šiuo metu detaliausias Baltijos jūroje mitybos tinklo ECOPATH modelis. Pirmą kartą įvertintos visos Lietuvos priekrantės mitybos tinklo charakteristikos, įskaitant sezoninių žuvų migracijos įtaką biomasės balanso palaikymui priekrantės mitybos tinkle, kertinius komponentus bei mitybos poveikį bendrijoje. Pirmą kartą buvo įvertinta iš Kuršių marių atneštos organinės medžiagos įtaka Lietuvos priekrantės mitybos tinklui. Pirmą kartą kiekybiškai įvertinant Baltijos jūroje žiemojančių jūros paukščių mitybos šaltinius kartu su $\delta^{13}C$ ir $\delta^{15}N$ buvo panaudotas $\delta^{34}S$.

Darbo mokslinė ir praktinė reikšmė

Dėl holistinio šio darbo pobūdžio reikšmingai pagerėjo žinios apie priekrantės ekosistemų funkcionavimą.

Rekonstruotas visos Lietuvos priekrantės mitybos tinklas suteikia galimybę įvertinti įvairių organizmų, tarp jų ir sezoniškai migruojančių žuvų ir vandens paukščių, vaidmenis ekosistemoje bei bendrą ekosistemos funkcionavimą. Mitybos tinklo modelis gali būti naudojamas tolimesniems mitybos tinklo tyrimams, vertinant invazinių rūšių, klimato kaitos, stiprėjančių antropogeninių veiklų kaip žvejybos, vėjo energetikos, laivybos, vandens užterštumo poveikį. Šis modelis gali būti naudingas planuojant aplinkos apsaugą, valdant išteklius bei derinant įvairius ekonominius, socialinius ir ekologinius aspektus.

Šis darbas suteikia pagrindus tolimesniems SIA tyrimams Lietuvos priekrantėje. Jis patvirtina $\delta^{34}S$ analizės naudojimo efektyvumą mitybos tyrimams, papildant $\delta^{13}C$ ir $\delta^{15}N$ analizę, ir pagerina nykstančių jūros paukščių rūšių mitybos įvertinimą.

Ginamieji teiginiai

1. Vegetacijos sezonu Lietuvos priekrantės mitybos tinklo komponentų $\delta^{13}C$ ir $\delta^{15}N$ santykiai atspindi Kuršių marių ir atviros Baltijos jūros organinės medžiagos derinius.

2. Lietuvos priekrantės mitybos tinklas yra heterotrofinis. Balansą palaiko organinės medžiagos importas iš gretimų Kuršių marių ir atviros Baltijos jūros ekosistemų.

3. Žiemojančių vandens paukščių kraujo SI santykiai atspindi jų pasirenkamus mitybos šaltinius Lietuvos priekrantėje: žuvimi mintančių paukščių racionas sudarytas iš skirtingų pelaginių, dugninių ir bentopelaginių žuvų proporcijų; dugniniais organizmais besimaitinančių ančių racionas priklauso nuo jų mitybos vietų: makrozoobentoso organizmai ir jūrinės žuvys dominuoja racione virš smėlėto dugno buveinių, anadrominės žuvys – virš akmenuoto dugno. $\delta^{34}S$ papildo $\delta^{13}C$ ir $\delta^{15}N$ galimybes vertinant žiemojančių vandens paukščių mitybą.

4. Nepaisant mažos biomasės, plėšrūnai bei žvejyba turi stiprų neigiamą poveikį, mesozooplantono ir nektobentoso grupės stipriai teigiamai veikia kitus priekrantės mitybos tinklo komponentus.

5. Vartotojų trofiniai lygmenys, įvertinti naudojantis ECOPATH modeliu, gerai sutampa su tų pačių grupių $\delta^{15}N$ vertėmis.

Darbo rezultatų aprobavimas

Šio darbo rezultatai buvo pristatyti septyniose tarptautinėse konferencijose:

8-oje Europos ornitologų konferencijoje 2011 m. rugpjūčio mėn. Rygoje, Latvijoje;

52-oje tarptautiniame ECSA simpoziume „Research and management of transitional waters“ 2012 m. rugsėjo mėn. Klaipėdoje, Lietuvoje;

9-ajame Baltijos jūros mokslų kongrese 2013 m. rugpjūčio mėn. Klaipėdoje, Lietuvoje;

Pasaulinėje gamtinių išteklių modeliavimo konferencijoje „Modeling our way back to the future“ 2014 m. liepos mėnesį Vilniuje, Lietuvoje;

5-oje tarptautinėje Jūros ančių konferencijoje 2014 m. rugsėjo mėn Reikjavike, Islandijoje;

10-ame Baltijos jūros mokslų kongrese 2015 m. birželio mėn. Rygoje, Latvijoje;

7-ame Europos priekrantės lagūnų simpoziume 2016 m. kovo mėn. Murzijoje, Ispanijoje.

Publikacijos

Šios disertacijos rezultatai buvo paskelbti mokslinėse publikacijose:

Morkūnė R., 2011. Trophic peculiarities of the great cormorant, grey heron and long-tailed duck on the Baltic Sea Lithuanian coast: a stable isotope approach. Ekologija 57 (4), 173–178.

Morkūnė R., Lesutienė J., Barisevičiūtė R., Morkūnas J., Gasiūnaitė Z. R., 2016. Food sources of wintering piscivorous waterbirds in coastal waters: A triple stable isotope approach for the southeastern Baltic Sea. Estuarine, Coastal and Shelf Science 171, 41–50.

Razinkovas-Baziukas A., Morkūnė R., Bacevičius E., Gasiūnaitė Z. R. Trophic network model of exposed sandy coast: linking continental and marine water ecosystems. Estuarine, Coastal and Shelf Science (priimtas publikuoti).

Išleistas žinynas: Morkūnas J., Morkūnė R., Raudonikis L., 2015. Nardančių vandens paukščių atžinimo žinynas. – Kaunas: Lututė, 46 p. ISBN 978-9955-37-175-5.

Disertacijos struktūra

Disertaciją sudaro šie skyriai: Įvadas, Literatūros apžvalga, Tyrimų vietos apžvalga, Medžiaga ir metodai, Rezultatai, Diskusija, Išvados, Literatūros sąrašas, Priedai, Santrauka. Disertacijos apimtis – 168 puslapiai. Joje panaudoti 253 literatūros šaltiniai. Disertacija parašyta anglų kalba su išplėstine santrauka lietuvių kalba. Lietuviškoje santraukoje pateikiami paveikslų ir lentelių pavadinimai lietuvių kalba. Iš viso darbe yra 19 lentelių ir 33 paveikslai.

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SANTRUMPŲ SĄRAŠAS

Santrumpa	Paaiškinimas
SI	Stabilieji izotopai
SIA	Stabiliųjų izotopų analizė
$\delta^{13}C$	Stabiliųjų anglies izotopų santykis
$\delta^{15}N$	Stabiliųjų azoto izotopų santykis
$\delta^{34}S$	Stabiliųjų sieros izotopų santykis
SOM	Suspenduota organinė medžiaga
TL	Trofinis lygmuo
TST	Sistemos našumas, apibūdinantis visus organinės medžiagos srautus sistemoje
EE	Ekotrofinis efektyvumas
N	Imties dydis
SN	Standartinis nuokrypis
CI_{95}	95 % reikšmių intervalas

PAVEIKSLŲ SĄRAŠAS

5.3 pav. Žuvų gildijų δ^{13}C ir δ^{15}N vertės skirtingose priekrantės vietovėse (rugpjūčios–rugsėjo mėnesiai, N=156).

5.4 pav. Didžiųjų kormoranų ir pilkųjų garnių jauniklių plunksnų galų ir vidurinių dalių δ^{13}C ir δ^{15}N vertės.

5.5 pav. Pasirinktų mitybos tinklo komponentų δ^{13}C vertės skirtingose priekrantės vietovėse.

5.6 pav. Pasirinktų mitybos tinklo komponentų δ^{15}N vertės skirtingose priekrantės vietovėse.

5.7 pav. SOM, sestono, makrozoobentoso, žuvų ir paukščių δ^{13}C ir δ^{15}N vertės 2010 m. balandžio–spalio mėnesiais Baltijos jūros Lietuvos priekrantėje.

5.8 pav. A. Paukščių kraujo mėginių* δ^{13}C, δ^{15}N ir δ^{34}S verčių klasterinė analizė. B. Ward’o klasterizacijos metodu išskirtų grupių (A, B1, and B2) reikšmių sklaidos diagramos.

5.9 pav. Žuvlesių paukščių (kraujo mėginių) ir žuvų (baltojo nugaros raumens) vidutinės δ^{13}C, δ^{15}N ir δ^{34}S vertės (±SN). A. δ^{34}S ir δ^{13}C santykiai. B. δ^{15}N ir δ^{34}S santykiai.

5.10. pav. Ausuotųjų kragų (balti apskritimai) ir rudakaklių narų (juodi apskritimai) δ^{13}C, δ^{15}N ir δ^{34}S verčių kaita žiemos sezonu.

5.11 pav. Penkių šaltinių maišymosi modelio diagrama, parodanti paukščių (kraujo mėginiai) ir jų potencialių mitybos šaltinių δ^{13}C, δ^{15}N ir δ^{34}S vertes pritaikius frakcionacijos koeficientą.

5.12 pav. Tikimybių tankumo histograma, parodanti galimas trijų žuvų grupių (pelaginių, dugninių žuvų, bentopelaginių stintų) proporcijas ausuotųjų kragų, rudakaklių narų ir laibasnapių narūnėlių racionuose, kurie buvo įvertinti naudojant viso sezono kraujo mėginių δ^{15}N ir δ^{34}S vertes.

5.13 pav. Mėnesių vidutinės šaltinių proporcijos ausuotųjų kragų (GCG) ir rudakaklių narų (RtD) racionuose, kurie buvo įvertinti trijų stabiliųjų izotopų (δ^{13}C, δ^{15}N ir δ^{34}S) penkių šaltinių maišymosi modeliais.

5.14 pav. Lietuvos priekrantėje žiemojančių nuodėgulių (juodi simboliai) (N=8) ir ledinių ančių (balti simboliai) (N=3) kraujo SI santykiai. Kvadratai žymi pateles, apskritimai – patinus.

5.15 pav. Nuodėgulių ir jų potencialių mitybos šaltinių vidutinės δ^{13}C, δ^{15}N ir δ^{34}S vertės (±SN). A. δ^{15}N ir δ^{13}C vertės. B. δ^{34}S ir δ^{13}C vertės.

5.16 pav. A. Penkių šaltinių maišymosi modelio diagramos, parodančios nuodėgulių ir jų potencialių mitybos šaltinių δ^{13}C, δ^{15}N ir δ^{34}S vertes pritaikius frakcionacijos koeficientą. B. Sudaryti maišymosi poligonai A pav. diagramoms. Pavaizduotos nuodėgulių (juodi taškai) ir vidutinės šaltinių vertės (juodi kryželiai). Spalvų skalė vaizduoja patikimumo lygmenis (kas 20%).

5.17 pav. Ledinių ančių ir jų potencialių mitybos šaltinių vidutinės δ^{13}C, δ^{15}N ir δ^{34}S vertės (±SN). A. δ^{34}S ir δ^{13}C vertės. B. δ^{15}N ir δ^{13}C vertės.

LENTELIŲ SĄRAŠAS

4.5 lentelė. Modelio įvesties duomenys ir jų kilmė.

5.1 lentelė. Pasirinktų makrozoobentoso organizmų $\delta^{13}C$ ir $\delta^{15}N$ verčių palyginimas priekrantės vietovių atžvilgiu (Juodkrantė (J), Melnragė (M), Palanga (P), Būtingė (B)) 2010 m. liepos–rugsėjo mėnesiais. Tikimybės įvertintos Kruskal'io ir Wallis'o kriterijumi; N_{sample} – mėginių skaičius; N_{site} – palygintų vietovių skaičius.

5.2 lentelė. Žuvų rūšių $\delta^{13}C$ ir $\delta^{15}N$ verčių palyginimas. Mėginiai surinkti 2010 m. rugpjūčio–rugsėjo mėnesiais skirtingose priekrantės vietovėse (Juodkrantė (J), Melnragė (M), Palanga (P)). Tikimybės įvertintos Kruskal'io ir Wallis'o kriterijumi; N_{sample} – mėginių skaičius; N_{site} – vietovių, naudotų palyginimui, skaičius.

5.3 lentelė. Žuvų gildijų $\delta^{13}C$ ir $\delta^{15}N$ verčių skirtumai, įvertinti ANOVA testu, tarp Juodkrantės, Melnragės ir Palangos vietovių.

5.4. lentelė. Analizuotų paukščių rūšys ir skaičius (N), vidutinės kūno masės bei kraujo mėginiuose išmatuoti vidutinės (± SN), mažiausios (Min) ir didžiausios (Max) $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ vertės.

5.5 lentelė. Analizuotų žuvų individų skaičius (N), kūno ilgis (TL, Min–Max, cm), baltojo nugaros raumens C:N masių santykis ir vidutinės (±SN) stabiliųjų anglies ($\delta^{13}C$ ir $\delta^{13}C_{norm}$, ‰), azoto ($\delta^{15}N$, ‰), ir sieros ($\delta^{34}S$, ‰) izotopų vertės.

5.6 lentelė. Mitybos šaltinių proporcijos (vidurkis ± SN ir CI_{95}, %) žuvlesių paukščių racionuose, įvertintose naudojant trijų, keturių ir penkių šaltinių maišymosi modelius bei paukščių ir žuvų $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ vertes.

5.7 lentelė. Analizuotų makrozoobentoso organizmų kaip nuodėgulės mitybos šaltinių C:N masių santykis ir vidutiniai (±SN) stabiliųjų anglies ($\delta^{13}C$ ir $\delta^{13}C_{norm}$, ‰), azoto ($\delta^{15}N$, ‰), ir sieros ($\delta^{34}S$, ‰) izotopų santykiai. N žymi mėginių skaičių bendrai $\delta^{13}C$ ir $\delta^{15}N$ santykių analizei/ atskirai $\delta^{34}S$ santykių analizei.

5.8 lentelė. Mitybos šaltinių proporcijos (vidurkis ± SN ir CI_{95}, %) nuodėgulių racione, įvertintame naudojant trijų, keturių ir penkių šaltinių maišymosi modelius bei vidutines makrozoobentoso organizmų $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ vertes.

5.9 lentelė. Analizuotų organizmų kaip ledinių ančių mitybos šaltinių C:N masių santykis ir vidutiniai (±SN) stabiliųjų anglies ($\delta^{13}C$ ir δ^{13}Cnorm, ‰), azoto ($\delta^{15}N$, ‰), ir sieros ($\delta^{34}S$, ‰) izotopų santykiai. N žymi mėginių skaičių bendrai $\delta^{13}C$ ir $\delta^{15}N$ analizei/ atskirai $\delta^{34}S$ analizei.

5.10 lentelė. Mitybos šaltinių proporcijos (vidurkis ± SN ir CI_{95}, %) ledinių ančių racione, įvertintame naudojant septinių šaltinių maišymosi modelį ir vidutines makrozoobentoso organizmų ir žuvų $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ vertes.

5.11 lentelė. Nuodėgulių (N=31) raciono sudėtis virš smėlėto dugno buveinių. Skirtingų mitybos objektų šlapas svoris (WW) ir organinės medžiagos svoris (AFDW) pateiktas gramais (g) ir procentais (%). Atskirų objektų dažnumas (FO) įvertintas juos lesusių individų skaičiumi (n) ir procentais (%).

5.12 lentelė. Ledinių ančių raciono sudėtis virš akmenuoto ir smėlėto dugno buveinių. N žymi analizei naudotų ančių skaičių. Skirtingų mitybos objektų šlapas svoris (WW) ir organinės medžiagos svoris (AFDW) pateiktas gramais (g) ir procentais (%). Atskirų objektų dažnumas (FO) įvertintas juos lesusių individų skaičiumi (n) ir procentais (%).

5.13 lentelė. Priekrantės mitybos tinklo modeliu įvertinti parametrai.

5.14 lentelė. Statistinių duomenų apibendrinimas (g m^{-2} y^{-1} visiems įvertinimams, tik g m^{-2} biomasei).

TYRIMŲ MEDŽIAGA IR METODAI

Tyrimas buvo atliekamas Lietuvos priekrantėje pietrytinėje Baltijos jūros dalyje. Taikyti metodai (4.1 pav.):

- 2010 m. balandžio–spalio mėn. skirtingose priekrantės vietovėse (Juodkrantėje, Melnragėje, Palangoje) surinktuose planktono, bentoso organizmų, žuvų ir paukščių plunksnų mėginiuose išmatuotos δ^{13}C ir δ^{15}N vertės (4.1 ir 4.2 lentelės). Jų analizei taikyta vienfaktorinė analizė, Tukey'o HSD kriterijus, t-testas, neparamentriniai Kruskal'io ir Wallis'o kriterijus bei Mann'o ir Whitney'o U testas (SPSS/7.0).
- 2012 m. lapkričio mėn. – 2013 m. kovo mėn. Karklės–Juodkrantės ruože surinktuose jūros paukščių kraujo, bentoso organizmų ir žuvų mėginiuose išmatuotos δ^{13}C, δ^{15}N ir δ^{34}S vertės. Klasterinė analizė, kuri rėmėsi Ward'o metodu, buvo naudojama paukščių grupėms išskirti. Daugiafaktorė ir dvifaktorė dispersinė analizė, Tukey'o HSD kriterijus, neparamentrinis Kruskal'io ir Wallis'o kriterijus bei Mann'o irWhitney'o U testas buvo naudojami išskirant mitybos šaltinius (SPSS/7.0). Maišymosi modeliais (R programos SIAR paketas) kiekybiškai įvertintos šaltinių proporcijos paukščių mityboje (4.2 pav., 4.3 lentelė). Dugno organizmais mintančių ančių maišymosi modelių rezultatai buvo palyginti su virškinamųjų traktų analizės, kuriai 2012–2016 m. žiemomis rinktos žvejų tinkluose žuvusios antys, rezultatais.
- Naudojant ECOPATH programą (6.5 versiją), sudarytas mitybos modelis, reprezentuojantis priekrantės ekosistemą iki 20 m izobatos 2000–2010 m. laikotarpiu. Modelis apėmė 40 gyvų komponentų ir 1 detrito grupę (4.4 lentelė). Naudoti įvesties parametrai pateikti 4.5 lentelėje. Balansuojant modelį remtasi ekotrofinio efektyvumo (EE) įverčiais.
- Palyginant vartotojų δ^{15}N vertes su jų trofiniais lygmenimis (TL), įvertintais ECOPATH modeliu, naudota Spearman'o rangų koreliacija (SPSS/7.0).

REZULTATAI

Rezultatai pristatyti 3 skyriuose: 1) Mitybos tinklo komponentų stabiliųjų izotopų santykiai vegetacijos periodu, 2) Žiemojančių vandens paukščių mitybos šaltiniai, 3) Priekrantės mitybos tinklo ECOPATH modelis.

Pirmame skyriuje pateiktos pagrindinių priekrantės mitybos tinklo komponentų išmatuotos $\delta^{13}C$ ir $\delta^{15}N$ vertės bei jų analizė pagal pagrindines grupes, priekrantės vietoves ir atskirus laikotarpius (tik planktono ir paukščių mėginiams).

Keturių skirtingų planktono frakcijų (<70, 100–200, >200µm ir bendrosios suspenduotos organinės medžiagos (SOM) $\delta^{13}C$ vertės Juodkrantėje skyrėsi nuo verčių Melnragėje ir Palangoje (Kruskal'io ir Wallis'o kriterijus: H (2, N=83)=31,0 p<0,001; 5.1 pav.), nors $\delta^{15}N$ vertės vietovių atžvilgiu nesiskyrė (Kruskal'io ir Wallis'o kriterijus: H (2, N=83) = 4,8, P=0,093). Mažiausios $\delta^{13}C$ vertės buvo užregistruotos liepos mėn. Palangoje (>200 µm, bendrajai SOM ir <70µm frakcijos (atitinkamai -32,2, -31,4, -30,1‰)) ir Melnragėje (100–200µm -30,9‰). Didžiausios $\delta^{13}C$ vertės nuo -25,6‰ iki -23,5‰ būdingos visoms frakcijoms rugsėjo mėn. Juodkrantėje. Mažiausios $\delta^{15}N$ vertės buvo užfiksuotos liepos mėn.: -0,1‰ bendrajai SOM, 0,4‰ >200µm ir 1,5‰ 100–200µm Palangoje bei 2,1‰ <70µm Melnragėje. Didžiausios $\delta^{15}N$ vertės buvo būdingos <70µm frakcijai ir bendrajai SOM rugpjūčio mėn. Melnragėje (atitinkamai 16,6 ir 12,8‰) (5.1 pav.).

Remiantis išmatuotomis $\delta^{13}C$ ir $\delta^{15}N$ vertėmis, dugno organizmai buvo suskirstyti į grupes. Dalyje grupių buvo ir makrodumblių, ir vėžiagyvių, ir dvigeldžių moliuskų atstovų – tai atskleidžia SI verčių panašumą tarp skirtingų organizmų priekrantės ekosistemoje (5.2 pav.). Išsiskyrė makrodumblis *Coccotylus trunkatus*, kurio $\delta^{13}C$ vertės siekė -36,3±0,1‰, o kitų dugno organizmų $\delta^{13}C$ vertės kito nuo -18 iki -27‰. Smulkių visaėdžių bestuburių ir filtratorių $\delta^{15}N$ vertės buvo mažesnės negu detritofagų, plėšrių ar stambių visaėdžių bestuburių (pagal Olenin, 1997). Smėlinės krevetės *Crangon crangon* $\delta^{13}C$ vertės Palangoje ir Melnragėje buvo mažesnės negu Juodkrantėje (Mann'o Whitney'io U testas, p<0.05), mėlynžnyplės krevetės *Palaemon elegans* $\delta^{13}C$ vertės Palangoje buvo didesnės negu Melnragėje (p<0.05) (5.1 lentelė).

Skirtingų žuvų rūšių SI vertės atskleidė ekologinių gildijų ir priekrantės vietovių ypatumus (5.2 lentelė). Anadrominių ir gėlavandenių žuvų $\delta^{13}C$ vertės buvo statistiškai panašios visose priekrantės vietovėse, nors jūrinių ir dalinai sėslių žuvų vertės reikšmingai skyrėsi. Gėlavandenių ir dalinai sėslių žuvų $\delta^{15}N$ vertės skyrėsi erdviškai, o anadrominėms ir jūrinėms žuvims buvo būdingos homogeniškos $\delta^{15}N$ vertės visoje priekrantėje (5.3 lentelė, 5.3 pav.).

Didžiųjų kormoranų *Phalacrocorax carbo* plunksnų galų ir vidurinių dalių $\delta^{15}N$ vertės reikšmingai skyrėsi (*t-testas*, *t* =-4,3, df = 5, P=0.008). Pilkųjų garnių *Ardea cinerea* jauniklių plunksnų skirtingų dalių $\delta^{15}N$ vertės nesiskyrė (*t-testas*, *t* = -1,3, df = 2, p>0.05), išskyrus plunksnų galų vertes, kurios būdinga didelė kaita. Analizuojant $\delta^{13}C$ vertes, nenustatyta nei skirtingų plunksnų dalių, nei tarprūšinių skirtumų (*t-testai, p>0.05)* (5.4 pav.).

Daugumos tirtų priekrantės mitybos tinklo komponentų (planktono, bentoso ir žuvų) mažiausios $\delta^{13}C$ vertės buvo Melnragėje, didžiausios – Juodkrantėje, o ties Palanga rinktiems mėginiams būdingos tarpinės $\delta^{13}C$ vertės (5.5 pav.). Išskirtinės vertės buvo būdingos europinėms stintoms *Osmerus eperlanus*, kurių $\delta^{13}C$ vertės buvo didžiausios Melnragėje, ir paprastiesiems otams *Scophthalmus maximus* su homogeniškomis $\delta^{13}C$ vertėmis visoje priekrantėje. Daugumos tirtų komponentų $\delta^{15}N$ vertės Melnragėje buvo didesnės negu kitose vietovėse (5.6 pav.).

Apžvelgus visus tirtus priekrantės mitybos tinklo komponentus, teigtina, kad vegetaciniu periodu jų $\delta^{13}C$ vertės kito nuo -36,4 iki -16,8‰, $\delta^{15}N$ vertės – nuo -0,08 iki 17,8‰. Mažiausios $\delta^{13}C$ vertės buvo būdingos gėlavandenėms trispyglėms dyglėms ir kormoranų jaunikliams, vidutinės – kitoms gėlavandenėms ir anadrominėms žuvims bei daugumai makrozoobentoso organizmų, o didžiausios buvo jūrinių žuvų ir atskirų makrozoobentoso organizmų kaip smėlinių krevečių ir Baltijos lygiakojų vėžiagyvių *Idotea balthica* $\delta^{13}C$ vertės. Mažiausios $\delta^{15}N$ vertės būdingos planktonui ir makrodumbliams. Makrozoobentoso organizmams ir dalinai sėslioms žuvims buvo būdingos vidutinės $\delta^{15}N$ vertės. Jūrinių ir anadrominių žuvų vertės buvo kiek didesnės, o didžiausios $\delta^{15}N$ vertės būdingos kormoranams ir stambioms gėlavandenėms žuvims – ešeriams *Perca fluviatilis* ir starkiams *Sander lucioperca* (5.7 pav.).

Antrajame skyriuje pateikiama žiemojančių vandens paukščių kraujo mėginių $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ verčių analizė. Pirma, panaudojant septynių paukščių rūšių 32 individų (5.4 lentelė) trijų SI vertes, klasterine analize išskiriamos dvi pagrindinės grupės (5.8 pav.). Antra, naudojant paukščių ir potencialių mitybos šaltinių SI vertes (5.9 pav.), maišymosi modeliais įvertinamos įvairių šaltinių proporcijos paukščių racione. Nustatyta, kad pritaikius $\delta^{34}S$ kartu su $\delta^{13}C$ ir $\delta^{15}N$ vertėmis, galima išskirti daugiau mitybos šaltinių, negu naudojant vien tik $\delta^{13}C$ ir $\delta^{15}N$ vertes. Statistiniais metodais išskirti šaltiniai ar jų grupės (kuomet šaltinių SI vertės statistiškai nesiskyrė nei pagal vieną SI) naudojami maišymosi modeliuose (5.9, 5.12, 5.15, 5.17 pav.).

Taikant trijų, keturių ir penkių mitybos šaltinių trijų SI maišymosi modelius, nustatyta, kad ausuotieji kragai *Podiceps cristatus* daugiausiai lesė dugnines žuvis, o rudakaklių narų *Gavia stellata* ir laibasnapių narūnėlių *Uria aalge* racione dominavo pelaginės žuvys; stintos visų žuvlesių paukščių racione sudarė nuo 19 iki 34 % (5.6 lentelė).

SI maišymosi modeliai buvo pritaikyti septyniems iš aštuonių nuodėgulių *Melanitta fusca* individų bei vienam iš trijų ledinių ančių *Clangula hyemalis* individų (5.16 ir 5.18 pav.). Nuodėgulės daugiausiai lesė smėlėto dugno dvigeldžius moliuskus, būtent smėlines mijas *Mya arenaria*, ir širdutes *Cerastoderma glaucum*, mažesnę dalį jų racione sudarė vėžiagyviai jūros tarakonai *Saduria entomon* ir smėlinės krevetės *C. crangon*, moliuskai Baltijos makomos *Macoma balthica* ir daugiašerės kirmėlės (5.8 lentelė). Šiuos rezultatus lyginant su žvejų tinkluose žuvusių nuodėgulių virškinamojo trakto analize, pastebėta, kad trijų rūšių moliuskų proporcijos buvo gana panašios ir sudarė 1/3 bendrojo organinės medžiagos kiekio virškinamajame trakte (5.11 lentelė).

Septynių šaltinių maišymosi modeliu nustatyta, kad ledinės antys daugiausiai maitinosi žuvimis (stintomis ir plekšnėmis *Platichthys flesus*) ir stambiais vėžiagyviais (5.10 lentelė). Remiantis virškinamojo trakto analize, nustatyta, kad smėlėto dugno buveinėse ledinės antys daugiausiai lesė mažuosius tobius *Ammodytes tobianus*, o virš akmenuoto dugno beveik išskirtinai maitinosi stintomis (5.12 lentelė).

Trečiame skyriuje pateikti Baltijos jūros Lietuvos priekrantės mitybos tinklo rekonstrukcijos ir analizės rezultatai. Bendroje mitybos tinklo schemoje (5.19 ir 5.20 pav., 5.13 lentelė) pristatomi pagrindinių komponentų užimami TL nuo 1 iki 4,2. Modeliu įvertinti atskirų komponentų parametrai pateikiami 5.13 lentelėje, bendrieji mitybos tinklo duomenys – 5.14 lentelėje. Nustatyta, kad fitoplanktonas dominuoja tarp producentų, dugno bestuburiai sudaro 93% visos mitybos tinklo biomasės, žuvys – tik 3,6% visos biomasės. Dalinai sėslios žuvys sudaro 2/3 žuvų biomasės, gėlavandenės ir jūrinės žuvys sudaro atitinkamai 15,5% ir 16,0%, anadrominių ir katadrominių žuvų biomasė yra atitinkamai tik 4,7% ir 0,1% nuo visos žuvų biomasės tinkle. Nustatyta, kad jūrinės ir anadrominės žuvys dominuoja žvejybos laimikiuose (95% laimikių biomasės), kurių vidutinis TL siekia 3,5. Priekrantės mitybos tinklo bendrosios pirminės produkcijos ir bendrajam kvėpavimui sunaudojamos organinės medžiagos santykis yra mažesnis už 1 (0,83) – tai atspindi mitybos tinklo heterotrofiškumą. Aukštas duomenų kilmės indeksas įrodo, kad 2/3 modelyje naudotų duomenų buvo surinkta būtent tiriamoje ekosistemoje (5.13 lentelė).

Linderman'o schema vaizduoja organinės medžiagos srautus atskiruose TL (5.21 pav.). TL2 dalyvauja 42% visų tinklo srautų, detritas ir pirminiai gamintojai – atitinkamai 26 ir 30 %, kiti trofiniai lygmenys tinkle dalyvauja palyginus nežymiai. Didžioji dalis TL2 sunaudojamos organinės medžiagos (59%) yra kilusi iš detrito.

Bendrijos mišraus trofinio poveikio analizė (5.22 pav.) atskleidžia, kad žvejyba, perintys didieji kormoranai, žiemojantys žuvlesiai paukščiai, suaugę starkiai ir ešeriai bei makrozoobentoso organizmai (10–20 mm) turėjo didžiausią neigiamą poveikį kitiems tinklo komponentams, o nektobentoso ir mesozooplanktono organizmai, filtratoriai, ir daugelis kitų žemesniųjų TL organizmų teigiamai veikė kitus tinklo komponentus. Mišraus trofinio poveikio analizė pagal grupes (5.23 pav.) parodė, kad gėlavandenės ir anadrominės žuvys stipriai teigiamai veikė makrozoobentoso organizmų, fitoplanktono ir detrito komponentus bei turėjo stiprų neigiamą poveikį žuvlesiams paukščiams bei jūrinėms ir kitoms gėlavandenėms ir anadrominėms žuvims (5.23B pav.). Žvejyba neigiamai veikė gėlavandenes, anadromines ir katadromines žuvis ir turėjo stiprų teigiamą poveikį jūrinėms ir dalinai sėslioms žuvims (5.23A pav.). Apskaičiavus komponentų svarbumo indeksus (5.24 pav.), buvo išskirti kertiniai priekrantės ekosistemos komponentai: didysis kormoranas, nektobentoso ir mesozooplanktono grupės, suaugę starkiai ir žiemojantys žuvlesiai vandens paukščiai.

DISKUSIJA

Diskusija susideda iš 6 skyrių: 1) Mitybinio tinklo struktūra ir srautai, 2) Pasyvus organinės medžiagos pernešimas, 3) Migruojančių žuvų gildijos, 4) Žiemojančių vandens paukščių raciono sudėtis, naudojant $\delta^{34}S$ kaip $\delta^{13}C$ ir $\delta^{15}N$ analizės papildymą, 5) Vartotojų trofiniai lygmenys, 6) Bendrijos trofinis poveikis.

Pirmame skyriuje aptariamos Lietuvos priekrantės ekosistemos mitybinio tinklo struktūros ir organinės medžiagos srautų charakteristikos. Pažymima, kad žemas autochtoninis produktyvumas ir stresinė fizinė aplinka yra svarbūs veiksniai, kontroliuojantys priekrantės ekosistemos funkcionavimą. ECOPATH modeliu apskaičiuotas žemas bendrosios pirminės produkcijos ir bendrajam kvėpavimui sunaudojamos organinės medžiagos kiekio santykis (0.8) reiškia, kad ekosistemoje kvėpavimui sunaudojama daugiau organinės medžiagos negu jos pagaminama priekrantės zonoje (sistema yra heterotrofiška). Apytiksliai 20% priekrantės mitybos tinklui reikalingos organinės medžiagos yra atnešama iš Nemuno–Kuršių marių sistemos (pagal 5.14 lentelę). Tai iš dalies sutampa su kitų palyginamų ECOPATH modelių duomenimis (pavyzdžiui, Christensen and Pauly, 1993), be to, heterotrofinės sąlygos yra dažnos Baltijos priekrantės ekosistemose, kuriose svarbus vaidmuo tenka upių atnešamai organinei medžiagai (Stepanauskas et al., 2002; Korth et al., 2013).

Pasyviai pernešama organinė medžiaga ir aktyviai migruojantys organizmai iš gretimų gėlavandenių ir jūrinių ekosistemų gali lemti nagrinėjamo mitybos tinklo heterotrofiškumą. SIA leido įvertinti pagrindinių mitybos tinklo komponentų skirtumus, atsirandančius dėl jų mitybos, pernešimo ar migracinių charakteristikų. Išmatuotos skirtingų planktono frakcijų $\delta^{13}C$ vertės atskleidė plačias jų mitybos šaltinių ribas (nuo -32,3 iki -23,4 ‰), reprezentuojančias Kuršių marių (iki -33,3‰; Lesutienė, 2009) ir jūrinės organinės medžiagos (nuo -18,6 iki -23,5‰; Rolff and Elmgren, 2000) derinius. Kiti mitybos tinklo komponentų audiniai atspindi ilgesniais periodais integruotą organinę medžiagą. Tik individų, praleidžiančių tam tikrą laiko tarpsnį priekrantėje, audiniai gali reprezentuoti konkrečios ekosistemos SI vertes (Hansson et al., 1997). Vegetacijos pabaigoje makrozoobentoso ir žuvų $\delta^{13}C$ vertės atsiskyrė tarp Lietuvos priekrantės vietovių: mažiausios $\delta^{13}C$ vertės buvo Melnragėje, didžiausios – Juodkrantėje, tarpinės – Palangoje. Tai sutampa su estuarinės kilmės vandens masių (Vaičiūtė, 2012) bei nuosėdų $\delta^{13}C$ verčių pasiskirstymu (Remeikaitė-Nikienė et al., 2016). Taigi, gėlo vandens prietaka iš Kuršių marių ir priekrantėje dominuojanti srovės kryptis (iš pietų į šiaurę) lemia ir mitybos tinklo komponentų SI reikšmes skirtingose priekrantės vietovėse.

Antrame skyriuje aptariama pasyvaus organinės medžiagos pernešimo įtaka priekrantės planktono frakcijų SI vertėms, kurios skiriasi tirtose priekrantės vietovėse. Rugsėjo pradžioje surinktų planktono mėginių $\delta^{13}C$ vertės mažiausios buvo Melnragėje (nuo -31,5 iki -27,4‰), ties kuria Kuršių marių vanduo patenka į Baltijos jūros priekrantę, todėl šioje vietovėje gėlo vandens įtaka yra stipriausia. Didesnės planktono $\delta^{13}C$ vertės (-27,7 iki -26,1‰) užfiksuotos Palangoje, kur gėlo vandens atneša dominuojanti priekrantės srovė, tačiau patenka ir nemažai jūrinio vandens. Didžiausios planktono $\delta^{13}C$ vertės (-25,8 iki -23,5‰) būdingos Juodkrantei, kur gėlo vandens įtaka yra nedidelė, todėl stiprus jūrinio vandens poveikis (Vaičiūtė, 2012). Kitų liepos ir rugpjūčio mėn. surinktų planktono mėginių SI vertės nesiskyrė tarp priekrantės vietovių ir neatspindėjo Kuršių marių vandens įtakos – tai gali būti paaiškinama nuolatine gėlo vandens nuotėkio į Baltijos jūros priekrantę kaita (Umgiesser et al., 2016).

Vandens prietaka iš aplinkinių ekosistemų lemia ir priekrantės planktono bendrijos struktūrą, ir SI vertes. Nuo planktono frakcijų dydžio priklausančių $\delta^{15}N$ verčių šiame darbe nebuvo išskirta, tačiau jų buvo išskirta kitose ekosistemose, pažymint, kad šis reiškinys dažniau fiksuojamas pavasarį ir rudenį negu vasaros sezonu (Rolff, 2000; Zeng, et al., 2010). Planktono $\delta^{15}N$ vertės gali taip pat pateikti informacijos apie alochtoninės medžiagos naudojimą priekrantės ekosistemoje. Lietuvos priekrantėje didelės $\delta^{15}N$ vertės (iki 16,6‰ Melnragėje) gali reprezentuoti ^{15}N praturtinto neorganinio azoto panaudojimą eutrofikacijos sąlygomis (Zeng et al., 2010) arba kanalizacijos ar trąšų nuotėkį priekrantės ekosistemoje (Costanzo et al., 2000). Mažos planktono $\delta^{15}N$ vertės (nuo -0,08‰ Melnragėje ir Palangoje) gali būti siejamos su atmosferos azotą fiksuojančių cianobakterijų dominavimu planktono bendrijoje (Rolff, 2000; Lesutienė, 2009; Karlson et al., 2014). Pažymima, kad dažnesnis planktono mėginių rinkimas, fiksuojant vandens parametrus, ir taksonų identifikacija mėginiuose padėtų interpretuoti SI vertes priekrantėje.

Trečiame skyriuje aptariamos išmatuotos priekrantės žuvų SI vertės. Lietuvos priekrantės žuvų bendrijos sudėtis keičiasi sezoniškai ir erdviškai, priklausomai nuo dugno buveinių, hidrologinių parametrų ir rūšių biologinių charakteristikų (Razinkovas et al., accepted), todėl žuvų rūšių analizei pasitelktas grupavimas į ekologines gildijas (modifikuota iš Elliott et al., 2007). Tai padėjo atskleisti įvairių žuvų rūšių naudojamų resursų skirtumus, jų vaidmenis mitybos tinkle ir ryšius su kitomis ekosistemomis. SIA parodė žuvų gildijų naudojamos organinės medžiagos kilmę ir jų migracijos pobūdį. Dalinai sėslių žuvų SI vertės skyrėsi visose tirtose priekrantės vietovėse; šiai grupei priklausė smulkios dugninės žuvys, todėl jų $\delta^{13}C$ vertės reprezentuoja tam tikros vietovės SI žymes, o santykinai mažos $\delta^{15}N$ vertės atspindi vidutinę trofinę poziciją mitybos tinkle. Jūrinių žuvų grupės, apimančios įvairias žuvis nuo smulkių pelaginių Baltijos bretlingių *Sprattus sprattus* iki stambių dugninių otų, plataus diapazono $\delta^{15}N$ vertės atspindėjo įvairius TL mitybos tinkle. Jūrinėms ir dalinai sėslioms priekrantės žuvims, besilaikančioms jūriniame vandenyje, būdingos didesnės $\delta^{13}C$ vertės negu gėlavandenėms ir anadrominėms žuvims, kurių audiniai net vegetacinio sezono pabaigoje dalinai atspindi Kuršių marioms būdingas žemas $\delta^{13}C$ vertes.

Gėlavandenių žuvų $\delta^{13}C$ vertės Juodkrantėje buvo didesnės negu kitose vietovėse. Nors jūros priekrantė ties Juodkrante apibūdinama kaip didesnio druskingumo, mažesnės vandens temperatūros akvatorija su monotoniškesnėmis smėlėto dugno buveinėmis, kurioms būdinga palyginus nedidelė dugno bendrijų įvairovė ir biomasė (Olenin and Daunys, 2004), tačiau didelės gėlavandenių žuvų $\delta^{13}C$ vertės atskleidžia, kad jos praleidžia tam tikrą laiko tarpsnį būtent šioje jūrinėje priekrantės akvatorijoje.

Apibendrinus žuvų SI duomenis, nustatyta, kad erdvinis heterogeniškumas tarp skirtingų žuvų gildijų SI verčių: dalinai sėslios žuvys skyrėsi $\delta^{13}C$ ir $\delta^{15}N$ vertėmis, jūrinės žuvys – $\delta^{13}C$ vertėmis, gėlavandenės žuvys – $\delta^{15}N$ vertėmis; anadrominėms žuvims būdingos homogeniškos SI vertės tirtuose priekrantės taškuose.

Ketvirtame skyriuje aptariama žiemojančių vandens paukščių mityba bei trijų SIA pritaikymas jų tyrimams. Pirmiausia pristatomos Lietuvos priekrantėje žiemojančių vandens paukščių grupės, išskirtos pagal kraujo mėginiuose išmatuotas SI ($\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$) vertes: pirmąją grupę sudaro nuodėgulės, antrąją – žuvlesiai paukščiai, kurie dar suskirstomi į ausuotųjų kragų ir kitų žuvlesių paukščių (narai, laibasnapiai narūnėliai, alka *Alca torda)* pogrupius. Toks skirstymas sutampa su ankstesniais tyrimais, atliktais naudojant paukščių virškinamųjų traktų analizę (Stempniewicz, 1994; Žydelis, 2002), tačiau žuvlesių grupės išskyrimas į du gana aiškius pogrupius buvo galimas tik naudojant $\delta^{34}S$ vertes. Įvairių organizmų $\delta^{13}C$ ir $\delta^{15}N$ vertės priekrantės ekosistemose dažnai sutampa, todėl mitybos studijos naudojant tik šiuos du SI nėra detalios (šis darbas; Mittermayr et al., 2014). Naudojant $\delta^{34}S$ kartu su $\delta^{13}C$ ir $\delta^{15}N$ vertėmis galima išskirti daugiau mitybos šaltinių ar jų grupių. Šiame darbe tai patvirtinama atskiriant fakultatyviai ir nuolat daleline organine medžiaga besimaitinančius dvigeldžius moliuskus, taip pat pelagines ir dugnines žuvis, nors jų $\delta^{13}C$ ir $\delta^{15}N$ vertės yra vienodos. Tai sutampa su Moreno et al. (2008) ir Conolly et al. (2004) tyrimais, kuriuose pagrindinių mitybos šaltinių $\delta^{34}S$ vertės taip pat skyrėsi.

Pažymima, kad problemiškas jūros paukščių kraujo mėginių rinkimas lėmė gana nedidelį mėginių skaičių ir jų netolygų pasiskirstymą tiriamu žiemos sezonu, tačiau šis darbas patvirtina, kad kraujo mėginių SI vertės ir maišymosi modeliai suteikia svarbios informacijos apie jūrinių paukščių mitybą žiemojimo vietose. Rudakaklių narų ir laibasnapių narūnėlių racionuose dominuojančios pelaginės žuvys žiemos metu Lietuvos priekrantėje sutampa su literatūroje pateikta šių rūšių mityba (Žydelis, 2002; Lyngs and Durinck, 1998; Guse et al., 2009; Kadin et al., 2012), tik dugninių žuvų svarba šių paukščių mityboje dažniausiai yra mažesnė ir retesnė (bet Bryant et al., 1999; Sonntag and Hüppop, 2005). Didelė dugninių žuvų dalis ausuotųjų kragų racione yra tikėtina būtent dėl jų laikymosi žiemos metu arti kranto (Žalakevičius, 1995; Hunt et al., 1999; Žydelis, 2002; Skov et al., 2011). Stintų, kurios sudarė vidutiniškai 1/5 minėtų paukščių rūšių raciono, gausumas Lietuvos priekrantėje kinta atskirais žiemos mėnesiais ir skirtingais metais (Žuvininkystės tarnybos duomenys), kas gali lemti ir netolygų paukščių maitinimąsi šia rūšimi (palyginant su Žydelis, 2002).

Nustatyta, kad nuodėgulių ir ledinių ančių mitybos šaltiniai skyrėsi priklausomai nuo dugno buveinių tipų bei dugno bendrijų daugiametės kaitos. SI maišymosi modeliai atskleidė, kad virš smėlėto dugno buveinių nuodėgulės daugiausiai lesė smėlines mijas ir širdutes, nors virškinamojo trakto analizė patvirtino ir Baltijos makomų svarbą mityboje. Ankstesnėse mitybos studijose (Žydelis, 2002) nuodėgulių virškinamuosiuose traktuose nerasta širdučių, bet jų pagausėjimą dugno bendrijose patvirtina ir daugiamečio monitoringo duomenys (Aplinkos apsaugos agentūros Jūrinių tyrimų departamento duomenys; Solovjova, nepubl.).

Šiame darbe nustatyta, kad ledinės antys daugiausiai lesė stintas virš akmenuoto dugno buveinių ir mažuosius tobius virš smėlėto dugno buveinių. Akmenuotose buveinėse gausių (Olenin, 1996) ir ledinių ančių mityboje dominavusių midijų *Mytilus* sp. (Žydelis and Ruškytė, 2005) drastiškai sumažėjo (Stupelytė and Šiaulys, 2015). Nustatyta mitybos objektų gausumo kaita tinkamose dugno buveinėse ir su ja susiję jūros ančių mitybos pokyčiai Lietuvos priekrantės žiemavietėse galėtų būti naudingi analizuojant ančių gausumo mažėjimo priežastis Baltijos jūroje ir visame pasaulyje (Skov et al., 2011).

Penktame skyriuje aptariamas priekrantės mitybos tinklo vartotojų makrozoobentoso, žuvų ir vandens paukščių grupių TL, kurie šiame darbe buvo apskaičiuoti ECOPATH modeliu, palyginimas su jų δ^{15}N vertėmis (6.1 pav.). Stiprus ir patikimas ryšys (Spirmano rangų koreliacijos $R=0,83$, $p<0.05$) tarp minėtų parametrų patvirtino ECOPATH modeliavimo ir SIA tinkamumą Baltijos jūros priekrantės tyrimams. Be to, tai patvirtino, kad modelyje naudota informacija tinkamai reprezentavo Lietuvos priekrantę. Išskirti nesutapimai paaiškinami keleto komponentų mityba detritu (ECOPATH modelyje detritas priskiriamas TL1), naudota literatūrine mitybos informacija, kuri gali būti iš dalies nereprezentatyvi tiriamai priekrantei, bei makrozoobentoso organizmų grupavimu, kuomet taksonominės grupės apėmė skirtingos mitybos organizmus. Taigi, priekrantės mitybos tinklo komponentų SI vertės gali padėti sugrupuoti skirtingus organizmus sudarant mitybos tinklo modelius.

Daugelis publikuotų modelių neįtraukia vandens paukščių arba analizuoja juos bendroje paukščių grupėje (pagal Navarro et al., 2011), o tai gali trukdyti tinkamai įvertinti jų svarbą ekosistemoje, nes Lietuvos priekrantės mitybos tinkle dugno organizmais mintančios antys užima vidutinį TL, o kelios žuvlesių paukščių grupės yra plėšrūnai. Taigi, tinkamai išskirtos paukščių grupės patikslina mitybos tinklo modelius.

Šeštame skyriuje aptariami bendrijos trofinis poveikis, kuris svarbus išskiriant kertinius mitybos tinklo komponentus. Įvertintas žuvų suvartojimas pagal skirtingas vartotojų grupes (6.2 pav.) atskleidžia, kad daugiausiai žuvų (ypač stintų) suvartoja vandens paukščiai, sulesantys trečdalį visos suvartojamos žuvies. Didysis kormoranas, išskirtas kaip kertinis mitybos tinklo komponentas, turi didžiausią bendrą neigiamą įtaką kitiems mitybos tinklo komponentams (6.3 pav.), tačiau jo tiesioginė ir netiesioginė įtaka žvejybai nėra stipri. Nežymus kormoranų vartojamų žuvų ir žvejų laimikių sutapimas buvo nustatytas ir kitose studijose (Pūtys, 2012; Troynikov et al., 2013).

Šiame darbe įvertinta, kad priekrantės žvejai sugauna maždaug 12% visos mitybos tinkle suvartojamos žuvies (6.2 pav.), tačiau jie kartu su kertiniais mitybos tinklo komponentais (plėšriomis gėlavandenėmis žuvimis bei perinčiais ir žiemojančiais žuvlesiais paukščiais) stipriai neigiamai veikia kitus mitybos tinklo komponentus (6.3 pav.). Kiti kertiniai ekosistemos komponentai – mesozooplanktono ir nektobentoso grupės – kartu su fitoplanktonu ir smulkiais makrozoobentoso organizmais turi didžiausią bendrą poveikį analizuojamam mitybos tinklui (6.3 pav.). Remiantis kitų ekosistemų tyrimais, vandens paukščiai, plėšriosios žuvys, zooplanktono ir nektobentoso organizmai yra svarbiausi komponentai seklių priekrančių mitybos tinkluose (Libralato et al., 2006; Coll et al., 2007; Pedersen et al., 2008).

Nors atlantinė menkė *Gadus morhua* sudaro net trečdalį Lietuvos priekrantės žvejų sugaunamų žuvų kiekio (2002–2010 m. Žuvininkystės tarnybos duomenys), ši rūšis nebuvo įtraukta į priekrantės mitybos tinklo struktūrą. Žinoma, kad menkės laikosi didesnio druskingumo vandenyse, o į priekrantę užklysta nereguliariai ir negausiai. Jos maitinasi silkinėmis žuvimis *Clupeidae* ir stambiais makrozoobentoso organizmais, kurių atviroje jūroje yra gausiau negu priekrantės zonoje. Būtent tai apsunkina menkių mitybos įvertinimą, reikalingą priekrantės mitybos tinklo modeliui, nes neaišku, kiek ir kokių mitybos objektų yra suvartojama priekrantėje, o kiek – už jos ribų. Be to, manome, kad menkės įtraukimas į priekrantės mitybos tinklą nepakeistų modelio rezultatų. Pagrindinių mitybos objektų Baltijos bretlingių ir strimėlės *Clupea harengus membras* balansas yra neigiamas jau dabartiniame tinkle, todėl menkės, kaip dar vieno vartotojo, pridėjimas tiesiog turėtų padidinti šių silkinių žuvų imigraciją. Stambių makrozoobentoso organizmų grupė yra mažai vartojama (ekotrofinis efektyvumas tesiekia 0,3), todėl menkės, kaip dar vieno šios grupės vartotojo, pridėjimas nepakeistų modelio rezultatų. Menkės naudojimas modelyje padidintų žvejybos laimikio vidutinį TL. Apibendrinant, galima teigti, kad menkės nėra būtinos priekrantės mitybos tinklo rekonstrukcijai, tačiau reikia turėti omenyje, kad kiekvienas papildomas komponentas papildytų modelį ir suteiktų daugiau informacijos apie komponentų ryšius ir ekosistemos funkcionavimą. Darbe taip pat nepanaudota naujausia informacija apie juodažiočio grundalo *Neogobius melanostomus* gausumą ir mitybą priekrantėje, tačiau modelis gali būti naudojamas šios invazinės rūšies poveikio mitybos tinklui ir žvejybai analizei.

Šis darbas pristato pasyviai nešamos organinės medžiagos ir aktyviai migruojančių organizmų svarbą priekrantės organinių medžiagų balansui ir heterotrofiniam ekosistemos statusui. Organinės medžiagos prietaka iš Kuršių marių ir Nemuno upės lemia ir priekrantės mitybinio tinklo pagrindinių komponentų SI vertes. Vegetacinio sezono pabaigoje migruojančių žuvų SI vertės skyrėsi atskirose priekrantės vietovėse, kuriose gėlo vandens prietakos įtaka yra skirtinga skiriasi. ECOPATH modeliu apskaičiuoti rekonstruoto mitybos tinklo komponentų svarbumo indeksai atskleidė, kad sezoniškai priekrantės ekosistemą naudojantys plėšrūnai (žuvlesiai paukščiai ir suaugę starkiai) yra svarbūs reguliuojant pelaginių žuvų gausumą ir visą mitybos tinklą. Mesozooplanktono ir nektobentoso grupės visus metus yra svarbios smulkių žuvų mitybai (e.g. Lassalle et al., 2013). Kontrolė „iš apačios į viršų“ yra gana svarbi ištisus metus, bet sezoninė kontrolė „iš viršaus į apačią“ taip pat yra svarbi Lietuvos priekrantės ekosistemoje. Rekonstruotas mitybos tinklas pateikia informacijos apie priekrantės mitybos tinklo struktūrą ir organinės medžiagos srautus, o tai gali būti panaudota valdant ekosisteminiu požiūriu pagrįstą aplinkos apsaugą, derinant išteklių bei ekonominius, socialinius ir aplinkosauginius klausimus.

IŠVADOS

1. Lietuvos priekrantės mitybos tinklo komponentų erdvinė $\delta^{13}C$ verčių kaita vegetacijos periodu atspindi Kuršių marių įtaką skirtingiems priekrantės taškams: mažiausios tinklo komponentų $\delta^{13}C$ vertės buvo Melnragėje, didžiausios – Juodkrantėje, tarpinės – Palangoje. Erdvinis heterogeniškumas buvo nustatytas ir tarp skirtingų žuvų gildijų SI verčių: dalinai sėslios žuvys skyrėsi $\delta^{13}C$ ir $\delta^{15}N$ vertėmis, jūrinės žuvys – $\delta^{13}C$ vertėmis, gėlavandenės žuvys – $\delta^{15}N$ vertėmis; anadrominėms žuvims buvo būdingos homogeniškos SI vertės tirtuose priekrantės taškuose.

2. Lietuvos priekrantės mitybos tinklui būdingas heterotrofinis pagaminamos ir suvartojamos produkcijos balansas (P/R=0,83), kurį veikia organinės medžiagos atnešimas iš Kuršių marių ir aktyviai migruojantys organizmai.

3. Remiantis trijų izotopų maišymosi modeliais nustatyta, kad žiemojantys rudakakliai narai ir laibasnapiai narūnėliai daugiausiai maitinasi pelaginėmis, ausuotieji kragai – dugninėmis žuvimis; anadrominės europinės stintos sudaro vidutiniškai ketvirtadalį žuvimi mintančių paukščių raciono. Trijų izotopų maišymosi modeliai atskleidė, kad nuodėgulės maitinasi smėlėto dugno dvigeldžiais moliuskais, daugiausiai *Cerastoderma glaucum* ir *Mya arenaria,* nors virškinamojo trakto analizė patvirtino ir *Macoma balthica* reikšmę mityboje. Ledinės antys kieto dugno akvatorijose maitinasi daugiausiai stintomis, smėlėto dugno akvatorijose – mažaisiais tobiais.

4. Remiantis Lietuvos priekrantės ECOPATH modeliu, nustatyta, kad žvejyba ir mitybos tinklo kertiniai komponentai – žuvlesiai paukščiai ir suaugę starkiai – turėjo stipriausią neigiamą poveikį, nektobentoso ir mesozooplanktono grupės – stipriausią teigiamą poveikį kitiems mitybos tinklo komponentams.

5. Statistiškai patikimas stiprus ryšys tarp vartotojų stabiliųjų azoto izotopų santykių ir ECOPATH modeliu įvertintų mitybos lygmenų patvirtina abiejų metodų tinkamumą Baltijos jūros priekrantės tyrimams.

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