KLAIPĖDA UNIVERSITY

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ROLE OF THE ROUND GOBY (*NEOGOBIUS MELANOSTOMUS*) IN THE FOOD WEB OF THE SOUTH-EASTERN BALTIC SEA COASTAL WATERS

DOCTORAL DISSERTATION

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ecology and environmental sciences (N 012)

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KLAIPĖDOS UNIVERSITETAS

Artūras SKABEIKIS

JUODAŽIOČIO GRUNDALO (*NEOGOBIUS MELANOSTOMUS*) VAIDMUO PIETRYTINĖS BALTIJOS JŪROS PRIEKRANTĖS MITYBOS TINKLE

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Abstract

This study provides the first comprehensive research on the functional role of the invasive round goby in the food web of the SE Baltic Sea coastal ecosystem. The round goby invasion success was determined by evaluating its abundance, morphometric/biological parameters and contribution in the fish communities from the stony and sandy biotope types. The diet composition of the round goby and its feeding niche overlap with the native benthophagous flounder, eelpout and vimba bream was evaluated by applying the gut content and stable isotope analyses. The round goby vulnerability to the piscivorous fish was determined by performing the stomach content analysis of the cod, turbot, shorthorn sculpin and perch. The ECOPATH model was employed to reveal the trophic position of differently sized round gobies and their effects to other food web compartments. The results of the present study suggested that the round goby became a key component of the coastal food web. It posed a detrimental impact on the blue mussel population and the wintering site quality of the benthophagous long-tailed ducks, but positively affected piscivorous fish/waterbirds and coastal fishery as an important forage/commercial catch species.

Key words

Biotope type, invasive species, food competition, predation, ECOPATH model.

Reziumė

Šios studijos metu buvo pirmą kartą atlikti išsamūs invazinio juodažiočio grundalo funkcinio vaidmens pietrytinės Baltijos jūros priekrantės ekosistemos mitybos tinkle tyrimai. Juodažiočio grundalo invazijos sėkmė buvo nustatyta vertinant gausumą, morfometrinius/biologinius parametrus ir svarbą priekrantės moreninio ir smėlėto dugno buveinių žuvų bendrijose. Juodažiočio grundalo raciono sudėtis ir mitybinės nišos persidengimas su vietinėmis bentofagėmis upine plekšne, gyvavede vėgėle ir žiobriu buvo vertinamas taikant skrandžio turinio ir stabiliųjų izotopų analizes. Juodažiočio grundalo pažeidžiamumas plėšrių žuvų poveikiui buvo nustatomas atliekant menkės, oto, builio ir ešerio skrandžio turinio analizę. ECOPATH modelis buvo panaudotas siekiant įvertinti skirtingų dydžių juodažiočių grundalų trofinę padėtį ir poveikį kitiems mitybos tinklo komponentams. Tyrimo rezultatai parodė, kad juodažiotis grundalas tapo vienu pagrindinių priekrantės mitybos tinklo komponentų. Juodažiotis grundalas sukėlė žalingą poveikį midijų populiacijai ir bentofagių ledinių ančių žiemavietės kokybei, tačiau teigiamai paveikė plėšrias žuvis/vandens paukščius ir priekrantės zonos žvejybą kaip svarbi mitybos/komercinė rūšis.

Reikšmingi žodžiai

Buveinės tipas, invazinės rūšys, mitybos konkurencija, plėšrūnizmas, ECOPATH modelis.

Contents

1

Introduction

1.1 Relevance of the thesis

The round goby (*Neogobius melanostomus*, Pallas 1814), a small bottom-dwelling fish, originating from the Ponto-Caspian region: the Black Sea, the Caspian Sea, the Sea of Azov and the Sea of Marmara (Charlebois et al. 1997) is a particularly successful invasive species, which established viable populations in a wide variety of water body types distributed throughout the North America and Eurasia. Since 1990 the round goby colonized many freshwater ecosystems, including Laurentian Great Lakes (Jude et al. 1992), their tributaries (Carman et al. 2006; Bronnenhuber et al. 2011), Eurasian rivers (Copp et al. 2005), estuaries (Czugała and Woźniczka 2010; Rakauskas et al. 2013) and the brackish Baltic Sea (Kotta et al. 2016). Abundant round goby populations pose negative effects to the native fauna by reducing quantity and species richness of benthic invertebrates (Krakowiak and Pennuto 2008), outcompeting benthic fish in the resource competition (Balshine et al. 2005) and facilitating the transfer of pollutants (Kwon et al. 2006) and diseases (Herbert et al. 2014) to higher trophic levels. On the other hand, piscivorous predators (Almqvist et al. 2010; Madenjian et al. 2011), commercial (Ojaveer et al. 2015; Järv et al. 2017) and recreational (Gutowsky et al. 2011) fishery highly benefit from dense, easily accessible invasive fish. Because of the rapid population growth, opportunistic diet and weak resistance to the predation pressure, the round goby has a great potential to change energy, nutrient and contaminant pathways within the invaded ecosystems (Johnson et al. 2005).

At present time, the round goby is widespread in the Baltic Sea coastal waters and alters functioning of invaded ecosystem through the direct and indirect trophic interactions with native organisms, belonging to different trophic levels of the food web (Kotta et al. 2016; Oesterwind et al. 2017; Herlevi et al. 2018; Christoffersen et al. 2019). The round goby in the Lithuanian coastal waters is present since 2002 (Zolubas 2003), and mostly concentrates in the stony bottom areas. Large-scale stony habitat forms Lithuanian coastal reefs that are located in a territory of NATURA 2000 and the Seaside Regional Park marine protected areas (MPA). Before the round goby invasion, this area provided favorable living environment for many invertebrate species associated with the blue mussels and macrophytes (Bučas 2009; Šiaulys et al. 2012; Šaškov et al. 2014) and ensured a rich forage base for the benthivorous fish (Bubinas and Ložys 2000; Bubinas and Vaitonis 2003) and wintering waterfowl (Žydelis 2002). Therefore it is important to determine the impact of the round goby invasion, particularly in the coastal areas, characterized by the heterogeneous stony seabed. The current study is the first attempt to evaluate the round goby invasion success and functional role in the space limited stony and prevailing sandy biotope types of the Lithuanian coastal waters by applying the combination of stomach/gut content analysis, stable isotope analysis and ECOPATH modelling.

1.2 Aim and objectives

The aim of this study was to determine the functional role of the invasive round goby in the stony and sandy biotopes of the SE Baltic Sea coastal ecosystem.

The following objectives were raised:

1. To estimate the round goby abundance and importance in fish communities in the stony and sandy biotopes;
2. To evaluate the morphometrical, age, body condition and fecundity parameters of the round goby in the stony and sandy biotopes;
3. To determine the feeding patterns of the round goby and its feeding niche overlap with the native benthophagous fish;
4. To determine the impact of the round goby predation on the blue mussel biomass and long-term dietary changes of the wintering long-tailed duck in the stony biotope;
5. To assess the importance of the round goby in the diet of piscivorous fish;
6. To estimate the food web level effects of the round goby expansion using the updated ECOPATH model (2000-2010) of the Lithuanian Baltic Sea coastal ecosystem.

1.3 Novelty

This study is the first attempt to present the habitat specific round goby invasion effects at the levels of population, community and ecosystem. This study presents new results on the round goby population size/age structure, body condition, diet composition and feeding niche overlap with native benthophagous fish, as well as piscivorous fish predation efficiency on the round goby in the coastal stony and sandy biotopes of the SE Baltic Sea. For the first time, the round goby predation induced cascading effects (depletion of blue mussels induced dietary and trophic level shifts of wintering long-tailed duck) were detected. This study also provides the first ECOPATH model results, presenting positive and negative food web effects of the round goby in the Baltic Sea.

1.4 Scientific and applied significance of the results

The current study has increased the scientific knowledge regarding the round goby invasion success and impact on the ecosystem functioning in different biotope types. The accumulation of the round goby in the stony bottom areas is an important aspect to be considered by the environmental managers of marine protected areas as well as the assessment of newly emerged commercial round goby targeted fishery. The results of the study could be used to create the indicators of non-indigenous species impact evaluation in Marine Strategy Framework Directive. The results of stomach/gut content, stable isotope analyses and ECOPATH modelling provided insights on how different techniques could be applied to the investigation of invasive species effects on the food web.

1.5 Scientific approval

The results of the study were presented in 8 international and 3 national conferences and seminars:

1. EUAC Congress 2014. Genoa, Italy, November 2014;
2. BONUS BIO-C3/BAMBI/INSPIRE 2015 Summer School "The Baltic Sea: a model for the global future ocean?". Glücksburg, Germany, July 2015;
3. 1st Hjort Summer School "Fishing and physics as drivers of marine ecosystem dynamics". Bergen, Norway, August-September 2015;
4. XV European Congress of Ichthyology. Porto, Portugal, September 2015;
5. Course for PhD students "Fish and Fisheries Evolutionary Ecology". Kristineberg, Sweden, September-October 2015;
6. Baltic Sea round goby workshop. Tallinn, Estonia, June 2016;
7. NEOBIOTA 2016. Vianden, Luxembourg, September 2016;
8. ICES Annual Science Conference 2016. Riga, Latvia, September 2016;
9. 9th national conference "Marine and coastal research". Klaipėda, Lithuania, April, 2016;
10. 10th national conference "Marine and coastal research". Palanga, Lithuania, April, 2017;

11. 11th national conference “Marine and coastal research”. Klaipėda, Lithuania, May, 2018.

The material of this study was presented in 2 original publications, published in peer-reviewed scientific journals:

1. Skabeikis A., Lesutienė J. (2015) Feeding activity and diet composition of round goby (*Neogobius melanostomus*, Pallas 1814) in the coastal waters of SE Baltic Sea. Oceanological and Hydrobiological Studies 44(4): 508-519;
2. Skabeikis A., Morkūnė R., Bacevičius E., Lesutienė J., Morkūnas J., Poškienė A., Šiaulys A. (2019) Effect of the round goby (*Neogobius melanostomus*) invasion on the blue mussel (*Mytilus edulis trossulus*) population and winter diet of the long-tailed duck (*Clangula hyemalis*). Biological Invasions 21(3): 911-923.

1.6 Thesis structure

The dissertation includes eight chapters: introduction, literature review, material and methods, results, discussion, conclusions, references and technical annex. The material is presented in 168 pages, 33 figures and 17 tables. The dissertation refers to 317 literature sources. Dissertation is written in English with an extended summary in Lithuanian language.

1.7 Acknowledgements

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1.8 Abbreviations

Abbreviation	**Explanation**
CPUE	Catch per unit effort
EELP	Eelpout
FL L	Large flounder (>250 mm)
FL M	Intermediately sized flounder (200-250 mm)
FL S	Small flounder (100-120 mm)
RG L	Large round goby (>140 mm)
RG M	Intermediately sized round goby (120-140 mm)
RG S	Small round goby (60-120 mm)
SE	South-eastern
SEA	Standard ellipse area
SEA_C	Transformed version, providing unbiased correction of standard ellipse area
SI	Stable isotopes
SIA	Stable isotope analysis
TL	Trophic level
VIM	Vimba bream
$\delta^{13}C$	Stable carbon isotope ratio
$\delta^{15}N$	Stable nitrogen isotope ratio
$\delta^{34}S$	Stable sulfur isotope ratio

2

Literature review

2.1 Taxonomy, morphology, age and reproduction of the round goby

The round goby (Fig. 1) belongs to the Gobiidae family, the second largest teleost family after Cyprinidae, containing more than 2000 species in more than 200 genera (Patzner et al. 2011). Gobiids are widely distributed throughout the globe and inhabit fresh, brackish and marine water ecosystems (Froese and Pauly 2007). Scientific classification of the round goby is as follows:

Kingdom: Animalia
Phylum: Chordata
Class: Actinopterygii
Order: Perciformes
Suborder: Gobioidei
Family: Gobiidae
Subfamily: Benthophilinae
Genus: *Neogobius*
Species: *N. melanostomus*

Figure 1. Male (upper) and female (lower) individuals of the round goby. © J. Fedotova.

1 pav. Juodažiočio grundalo patinas (viršuje) ir patelė (apačioje). © J. Fedotova.

The round goby is a relatively small fish, normally reaching 215 mm in total length, but is capable of growing up to 290 mm (Berg 1949). It has a soft cylindrical elongated body with a large wide head, terminal mouth, thick lips and a slightly notched tongue. Other morphological features, characterizing the round goby are: fused pelvic fins (which form a suction disk on the ventral surface), frog-like raised eyes, pharyngeal teeth, a large oblong black spot on the anterior end of the first dorsal fin and the lack of swimming gas bladder (Crossman et al. 1992; Ghedotti et al. 1995; Charlebois et al. 1997). Juvenile round gobies are slate grey, whereas adults exhibit variable pigmentation with grey, brown or yellow-green bodies, dappled with large dark brown lateral spots. The head is darker than the rest of the body and fins are dark grey (Miller 1984; Kornis et al. 2012). Sexual dimorphism of the round goby is common, as the males are larger at age and have enlarged cheeks and darker coloration (almost completely black) during the spawning (Belanger et al. 2007); although some males do not reproduce and lack secondary sexual characteristics (MacInnis and Corkum 2000). Both sexes have an erectile urogenital papilla, situated between the anus and the base of the anal fin. The female papilla is broad and blunt (0.3-0.5 mm wide, 0.2-0.4 mm long), whereas the male papilla is longer (0.3-0.6 mm), pointed and has a terminal slit (Charlebois et al. 1997; Kornis et al. 2012).

Lifespan of the round goby is short, because its annual mortality based on age-class comparisons for adults range from 22 to 90% (1-2 years) and to near 100% for 0 year age fish (Johnson et al. 2005; Taraborelli et al. 2010; Vélez-Espino et al. 2010). In the native Ponto-Caspian region, the round goby typically lives up to 4 years (Berg 1949), while in invaded water bodies maximum round goby age varies from 2 years in the Detroit River (MacInnis and Corkum 2000) to 4 years in the Danube River (Grul'a et al. 2012), 5-7 years in the Lake Huron (French and Black 2009; Duan et al. 2016) and 6-7 years in the Baltic Sea (Sokołowska and Fey 2011; Azour et al. 2015). The maximum size of the round goby in freshwater ecosystems tends to be smaller (MacInnis and Corkum 2000; Lavrinčíková and Kováč 2007; French and Black 2009; Duan et al. 2016) compared to the native range (Berg 1949; Gümüş and Kurt 2009) or invaded Baltic Sea (Sokołowska and Fey 2011), which is potentially related to the salinity effect (Corkum et al. 2004; Stepien and Tumeo 2006). Males are also reported to grow faster and attain larger maximum size at age than females (Kornis et al. 2012). The observed differences in mortality rates and maximum age of the round goby may result from density-dependent processes, relating to the time period passed since establishment, and saturation densities (Vélez-Espino et al. 2010).

The age of the round goby maturity depends on its sex and inhabited environment. Male round gobies mature at 3-4 years and females at 2-3 years in the native range (Miller 1984; Roşca et. al. 2010) and the Baltic Sea (Tomczak and Sapota 2006), while in the Great Lakes region males and females mature earlier, at the age of 1-2 and 2-3 years, respectively (Corkum et al. 1998; MacInnis and Corkum 2000; Phillips et al. 2003). Within a cohort, individual round gobies may exhibit different growth rate strategies, with some specimens growing faster and maturing earlier, and others growing slower and maturing later (Bil'ko and Vybornaya 1971).

The round goby is a batch spawner, which means that females do not spawn all their eggs at once, but release them in portions throughout the reproductive season (Tomczak and Sapota 2006). The spawning cycle might be repeated 5-6 times throughout the year, however in the Baltic Sea (Gulf of Gdańsk) female round gobies usually exhibit 2-4 separate breeding events (Sapota 2004). Spawning is cued by water temperature (9-26ºC) and intervals between the spawnings are approximately 17-28 days at 15-17ºC temperature (Corkum et al. 1998); higher water temperature (20ºC) shortens the intervals to 15-17 days (Charlebois et al. 1997). Spawning takes place during April-September in the Ponto-Caspian region (Charlebois et al. 1997), from the beginning of May to the end of September in the Baltic Sea (Sapota 2004), and during May-November in the Laurentian Great Lakes and their tributaries (MacInnis and Corkum 2000). Moreover, if temperature is >10ºC, the endocrine system of round gobies remains active, which allows them to spawn throughout the entire year (Charlebois et al. 1997).

Gobiids have a very specific reproduction period, constituting of 5 stages: the establishment of a territory, nest preparation, courtship behavior, spawning and parental care of the eggs (Reese 1964). The fecundity of fish using this reproductive strategy is generally lower, but offspring are larger at hatching and suffer lower mortality rates compared to other fish (MacInnis and Corkum 2000).

Establishment of a teritory. Round gobies become active after wintering period when the temperature of near-bottom water layers rises to 4.5-6ºC. At this time male round gobies massively migrate from the deep wintering sites to the shallower spawning grounds and set up territories before the females arrive (Shemonaev and Kirilenko 2009); the females show up later, after the water temperature increases to 10ºC (Shemonaev and Kirilenko 2009). Depending on the inhabited water body and its characteristics, a spwaning site could be located at depths from 0.2-1.5 m (Leslie and Timmins 2004; Sapota et al. 2014) to up to 11 m (Wickett and Corkum 1998). The male occupies the spawning site and aggressively protects it from the intruders, including other fish species or counterparts (Johnson et al. 2005). Stammler and Corkum (2005) also found, that large male round gobies are able to force smaller males to abandon their nest sites and establish there themselves.

Nest preparation. Any solid element on the bottom, such as stones, rocks, gravel, parts of wood, shipwrecks, submersed plants, roots of vascular plants and dumped waste as well as crevices in various solid objects could be used as a basis for a round goby nest (Wickett and Corkum 1998; Sapota 2006). In the sandy bottom areas, males dig under a solid substrate and use adhesive secretions from an accessory gonadal gland to create a nest out of sand (Berg 1949). In preparation for spawning, the resident male modifies the interior of the nest by picking up gravel particles from the bottom of the nest and spitting them out at the nest entrance (Meunier et al. 2009). The general requirements for prepared nest are: a hard, immobile overhead surface and a single opening to the cavity (Miller 1984). Number and density of the nests depend on the availability of suitable nesting places within the habitat. In spawning grounds with limited suitable reproduction area, the distances between the nests are much shorter compared to the areas with a high habitat complexity (Wickett and Corkum 1998; Sapota 2006; Sapota et al. 2014). The established male defends the nest by spitting sand, flaring gills, lunging and biting at intruders or producing a growling sound (Charlebois et al. 1997). It is also recorded, that males from adjacent nests avoid interacting with one another as long as each male remains within its own nest (Yavno and Corkum 2011).

Courtship behavior. The round goby courtship is initiated at the nest entrance. According to the visual attraction strategy, females spend more time near the nests occupied by large darkly pigmented males (Yavno and Corkum 2010) that defend their nests and exhibit swollen cheeks (Marentette and Corkum 2008), compared to small mottled males, that usually are sneakers, lack secondary sexual characteristics and avoid parental care (Marentette et al. 2009; Yavno and Corkum 2010, 2011). If the male is not prepared for the spawning, it prevents females from entering the nest by blocking the entrance. During the laboratory experiment, females either faced the entrance or aligned themselves perpendicular to the male within a body length of the nest entrance, advertising their swollen bellies, and erect dorsal fins to the male (Meunier et al. 2009).

Another way to exchange information between reproducing male and female round gobies is the dispersion of sex pheromones. Chemical communication using steroidal pheromones is very important, as dark nest-guarding males are difficult to detect in the spawning grounds with poor lighting conditions (Corkum et al. 2006). Reproductively matured males release pheromones that attract ripe females (Arbuckle et al. 2005; Gammon et al. 2005) and respond by increased ventilation to gonadal extracts and the putative pheromone estrone excreted by gravid females which indicates that reproductive males can recognize potential mates based on olfactory cues produced by females (Belanger et al. 2007).

Male and female round gobies also attract each other by producing "barking calls" before, during and after the egg deposition (Meunier et al. 2009). Sounds produced by the males are relatively loud and can be apparently heard in a distance of 5-10 m, while females make a quieter sound in response to the males (Charlebois et al. 1997).

Spawning. Results of laboratory experiment demonstrated, that the reproductive male began fanning within the nest and rubbing the ceiling surface with its genital papilla in order to lay sperm trails on the nest surfaces before the females enter the nest and deposit the eggs (Meunier et al. 2009). These sperm trails contain viscous material in which sperm is contained, explaining the prolonged release (up to 80 min) of sperm into the surrounding water. This early sperm trail production enables the male to defend the nest and female from intruders when females deposit eggs. The males repeatedly fertilize eggs despite the deposition of secretions on the nest surfaces before the female enters the nest (Meunier et al. 2009).

Males appear to be selective about which females will enter the nest and about the timing of spawning events (Meunier et al. 2009). Eggs clutch per nest is usually deposited by 4-6 females (Charlebois et al. 1997), however in some occasions more than 15 females might spawn in the same nest cavity (MacInnis and Corkum 2000). Female gobies have developed the strategy, in which they mate with males that already have eggs in their nests (Forsgren et al. 1996; Kraak and Weissing 1996; Jones and Reynolds 1999). Since males of many goby species are known to eat eggs or offspring in their nests (Kraak and Weissing 1996), this strategy may dilute the risk of fillial cannibalism. Thus, the chances of eggs surviving in a nest are greater if several females lay eggs in the same nest than if only one female lays eggs in a nest (Corkum et al. 1998). The deposition of eggs from more than one female is often apparent by the presence of eggs at different stages of development in the same nest (Charlebois et al. 1997; Sapota 2004). The number of eggs in different nests varies and depends on the size of the guarding male, nest structure, water temperature and duration of the reproduction period (Corkum et al. 1998).

The spawning event starts once a reproductive female enters the nest and both male and female alternately flip over upside down to deposit their gametes on the surfaces of the nest. Whenever the female deposits eggs, it performs small, rapid, undulating movements, pressing urogenital papilla against the surfaces of the nest (Meunier et al. 2009). MacInnis and Corkum (2000) recorded that in the nests containing round goby eggs, the eggs were deposited in a single layer (very small area of double eggs layer was also found) on the overhead surface, sides and bottom of nests. In all nests, the egg layer was essentially continuous; irregularities occurred only at the edges of the egg mass. After the spawning female leaves the nest, whereas male fertilizes the clutch by making similar undulating movements as female and exhibits parental care (Meunier et al. 2009). A portion of fertilized eggs might reach up to 95% (Charlebois et al. 1997); the eggs are large (3.4-3.8 mm in diameter) and their development period varies in the range of 14-20 days depending on water temperature (Moskal'kova 1996).

Parental care of the eggs. The male guards nest until the deposited eggs hatch (Kornis et al. 2012). Under laboratory conditions the nest-guarding male raised pectoral and dorsal fins upon the approach of an intruder, possibly to increase the body size and better block the access to the nest. At the next level of aggression, the male initiated vocalizations and erected its pectoral and dorsal fins in response to the intruder, and at the highest aggression level, the male darted out of the nest to chase the intruder. Once the intruders left, the male returned immediately to the nest (Meunier et al. 2009), as the egg clutch might be rapidly consumed by various aquatic animals, including round gobies, other fish species and crayfish (Wickett and Corkum 1998). Large males are able to defend larger nests with the clutches exceeding 10,000 eggs (Charlebois et al. 1997); however, predation induced mortality in large nests (8,000-10,000 eggs) is very high (50-70% of the clutch), compared to slight mortality in small nests (2,000-3,000 eggs) (Kovtun 1979). The increase in mortality is caused by the combination of higher exposure to predation and insufficient aeration at the periphery of the large nest (Corkum et al. 1998).

The male fans deposited eggs using pectoral and caudal fins in order to prevent sediment build-up inside the nest, maintain oxygenation and reduce fungal spread. Pectoral fanning appears to stir up particles in the nest and caudal fanning (with the tail at the nest entrance) may pump odours and waste out of the cavity (Meunier et al. 2009). Time and energy investement for oxygenation of the nest increases with increasing size of the eggs clutch (Jones and Reynolds 1999). Usually fanning activity intensifies during the late development stages of the eggs, and declines when the male spawns or chases intruders from the nest (Bjelvenmark and Forsgren 2002). Male round gobies also constantly inspect the clutch and eat all unfertilized, fungally-infected or dead eggs to prevent the spread of diseases (Yavno and Corkum 2011). Males also might consume the entire brood under stress conditions (Charlebois et al. 1997), as a result of energy deficiency or to gain access to necessary nutrients (Belles-Isles and FitzGerald 1991).

When larvae hatch and leave the nest after the successful incubation period, parental care of the male round goby ends. Low mortality rates of eggs and relatively high larvae/juvenile survivorship is directly related to the effectiveness in the nest defence and parental care of the male (Kornis et al. 2012). Another reason for high juvenile survivorship is that round gobies produce large eggs (Moskal'kova 1996; Leslie and Timmins 2004) and hatched larvae have food reserves in the yolk sac for an extended period of time until the external food resources are found (MacInnis and Corkum 2000).

Males do not feed during egg incubation which leads to emaciation, skin ulceration and possibly death after a single reproductive season (Shemonaev and Kirilenko 2009), whereas females have greater possibility to achieve reproduction in the year following the first spawning (MacInnis and Corkum 2000; Sapota 2006).

2.2 Predation of the round goby

The round goby is a typical benthophagous species, feeding on a wide variety of epibenthic and endobenthic macroinvertebrates (Barton et al. 2005; Walsh et al. 2007), small demersal fish (Janssen and Jude 2001; French and Jude 2001) and eggs, larvae or juveniles of large, economically valuable fish species (Nichols et al. 2003; Steinhart et al. 2004; Fitzsimons et al. 2006). The feeding activity and diet composition of the round goby are flexible and highly depend on the body size (Kuhns and Berg 1999; Vašek et al. 2014), type of inhabited biotope (Diggins et al. 2002; Borza et al. 2009), time of the day (Carman et al. 2006; Johnson et al. 2008), season (Bănaru and Harmelin-Vivien 2009) and abiotic environmental conditions (Dopazo et al. 2008; Coulter et al. 2015).

Pelagic early juvenile round gobies (~20 mm) are planktivorous and feed predominantly on mollusk eggs and veligers, copepods, their nauplii, cladocerans, ostracods, rotifers and other miscellaneous taxa (Hayden and Minor 2009; Jůza et al. 2016; Olson and Janssen 2017), while larger juveniles (~50 mm) shift their diet from zooplankton to soft-bodied benthic preys: isopods, decapods, amphipods, aquatic insects and their larvae, mysids, oligochaetes and polychaetes with a negligible contribution of small mollusks (Cooper et al. 2009; Duncan et al. 2011; Thompson and Simon 2014). The diet of the round goby tends to shift from soft-bodied invertebrates to mollusks at the body lengths of 75-100 mm (Ray and Corkum 1997; French and Jude 2001), after the complete development of pharyngeal apparatus (Andraso et al. 2011). Large (>100 mm) round gobies feed mainly on mollusks (Bunnel et al. 2005; Campbell et al. 2009; Brush et al. 2012), however in the areas where they are absent or scarce, the species easily adapts to forage on other prey types (Carman et al. 2006; Števove and Kováč 2013). The round goby prefers mussels of 8-11 mm in total length (Djuricich and Janssen 2001; Andraso et al. 2011), but is also able to consume larger shelled preys by crushing them with strong molariform pharyngeal teeth (Ghedotti et al. 1995; Weimar and Keppner 2000). Despite the fact that large round gobies feed heavily on bivalves, the laboratory experiments showed that mussels are not preferred food item when easily digestible soft-bodied organisms, such as crustaceans or aquatic insects, containing higher energetic value are available (Diggins et al. 2002; Bauer et al. 2007; Polačik et al. 2009).

Specific environmental conditions e.g. water temperature, salinity, depth, wave exposure, flow velocity, type of substrate and coverage of aquatic vegetation, combined with forage base diversity and productivity, observed in different water body types determine feeding habits of the species. In its natural range, the round goby prefers bivalve mollusks (*Dreissena polymorpha*, *Lentidium mediterraneum*, *Mytilaster lineatus*, *Mytilus galloprovincialis*, *Cerastoderma edule*), but also feeds on a wide range of other preys, including gastropods (*Rissoa* sp., *Hydrobia* sp., *Setia* sp., *Bittium* sp.), decapods (*Xantho poressa*), amphipods (*Amphithoe* sp., *Ampelisca diadema*), isopods (*Idotea balthica*), chironomid larvae, shrimps, various small fish and green algae (*Ulva* sp.) (Bănaru and Harmelin-Vivien 2009; Roşca and Surugiu 2010). The primary diet component for the round goby in the invaded Laurentian Great Lakes are bivalve mollusks (*D. polymorpha*, *D. bugensis*, *D. rostriformis*), while other prey items, including gastropods (*Viviparus viviparus*), ephemeropterans (Caenidae, Heptageniidae, Siphlonuridae, Leptophlebiidae), trichopterans (Phryganeidae, Rhyacophilidae), oligochaetes, isopods, hydracarinians, turbellarias, fish eggs and larvae are used as additional food sources (Barton et al. 2005; Walsh et al. 2007; Kornis et al. 2014). In the Baltic Sea, the round goby consumes bivalve mollusks (*M. edulis trossulus*, *Limecola balthica*, *Mya arenaria*, *C. lamarcki*), gastropods (*Hydrobia* sp., *Theodoxus fluviatilis*), amphipods (*Gammarus fasciatus*, *G. salinus*, *G. tigrinus*, *G. Zaddachi*, *Bathyporeia pilosa*, *Cyathura carinata*, *Corophium volutator*, *Diastylis rathkei*), mysids (*Mysis relicta*, *Neomysis integer*), polychaetes (*Hediste diversicolor*, *Pygospio elegans*) and fish prey (Wandzel 2003). Contrary to the lentic water bodies and the Baltic Sea, the diet of the round goby in the majority of invaded lotic systems (Eurasian rivers and tributary streams of the Great Lakes) is dominated by soft-bodied invertebrates, however in some cases mollusks remain the most important food source (Simonović et al. 2001; Raby et al. 2010; Kipp et al. 2012). In the Danube river the round goby feeds mainly on amphipods (*Dikerogammarus villosus*, *Obesogammarus obesus*, *Jaera istri*, *J. sarsi*, *Chelicorophium curvispinum*), while bivalves

(*D. polymorpha*, *Corbicula fluminea*) and gastropods (*T. fluviatilis*, *Potamopyrgus antipodarum*) represent a minor share of the diet (Borza et al. 2009; Brandner et al. 2013). In the Great Lakes tributary streams, the main food items for the round goby are *Chironomidae* larvae and pupae, mayflies (*Caenidae*, *Tricorythidae*, *Potamanthidae*, *Ephemeridae*, *Heptageniidae, Baetidae*), caddisflies (*Hydropsychidae*, *Hydroptilidae*, *Limnephilidae*) and stoneflies (*Perlidae*, *Nemouridae*), whereas various zooplanktonic organisms (Calanoida, Cyclopoida, *Daphnia*, *Eubosmina*, *Leptodora*), water mites and some other soft-bodied preys are less important (Phillips et al. 2003; Carman et al. 2006; Lederer et al. 2006; Pennuto et al. 2010).

The round goby feeds at all times of the day, with the diet changing on a diel basis (Kornis et al. 2012), because it uses several strategies for prey detection: during the day, fish searches for food visually and feeds on abundant or exposed preys (Barton et al. 2005), while at night it forages on conspicuously active organisms, suggesting, that the round goby is attracted by the prey movement (Carman et al. 2006) and detects it using a well-developed sensitive lateral line system (Charlebois et al. 1997; Bergstrom and Mensinger 2009). In the Flint River, the round goby ration is dominated by hydropsychid caddisfly and chironomid larvae during the day, chironomid pupae during the evening and heptageniid mayflies at night (Carman et al. 2006). Similarly, diel dietary shifts were recorded in the Lake Ontario, where the round goby preferred chironomids, dreissenids and amphipods during the day, chironomids and copepods in the evening, while chironomids and cladocerans comprised the major part of the diet during the dark period (Johnson et al. 2008).

Several researches, conducted in different water bodies confirmed that the feeding habits of the round goby strongly depend on the time of the year. Bănaru and Harmelin-Vivien (2009) found, that the round goby diet in the Black Sea changes depending on the season: in spring, the ration was mostly composed of polychaetes and fish prey, while in autumn it shifted to *M. galloprovincialis* and *M. lineatus*. In the Danube River, the round goby preferred chironomids with a secondary importance of *Dikerogammarus* spp., *C. curvispinum* and bryozoans during the spring; in summer dominant food items were not clearly expressed, resulting that *Dikerogammarus* spp., *C. fluminea*, *C. curvispinum*, *O. obesus*, *T. fluviatilis* and chironomids had similar importance in the diet, while in autumn *Dikerogammarus* spp., *C. curvispinum*, and *J. istri* gave the bulk of consumed preys in similar proportions (Borza et al. 2009). The investigations from the middle section of the Danube River revealed that chironomid larvae dominated the diet in all seasons, followed by Copepoda, Cladocera and *Corophium* sp. in spring and *Corophium* sp., Cladocera, *Dikerogammarus* sp. and ostracods during the summer and autumn (Števove and Kováč 2013). Another study from the Danube River revealed, that diet of the round goby differs even between the early and late summer: in the first period of the research the round goby consumed mainly chironomids and amphipods, whereas in the second period it preferred *Dikerogammarus* spp., bivalves and gastropods (Brandner et al. 2013).

Many dietary studies conducted in different invaded water body types suggested that the round goby opportunistically forages on the most abundant components of benthic community, which may change seasonally (Skóra and Rzeznik 2001; Bănaru and Harmelin-Vivien 2009). Such diet plasticity and diversity among geographically separated populations demonstrate the round goby capability to adapt to the locally abundant food sources (Kornis et al. 2012), therefore it is important to determine seasonal shifts in feeding patterns of differently sized round gobies from the coastal stony and sandy biotopes of the Baltic Sea.

2.3 Resource competition posed by the round goby

The invasive round goby poses various threats for many native fish species that have similar diet, habitat and spawning site preferences. The round goby usually outcompetes other small bottom-dwelling fish in the resource competition, because of its broad opportunistic diet, ability to adapt to the changing forage base structure (Vašek et al. 2014) and more aggressive behavior (Dubs and Corkum 1996), resulting in native fish loss of feeding or spawning sites and their displacement to the sub-optimal habitats (Kornis et al. 2012).

The results of laboratory experiments from the Laurentian Great Lakes region showed the round goby dominance in the food competition against the native slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*C. ricei*), logperch (*Percina caprodes*) (Bergstrom and Mensinger 2009) and invasive ruffe (*Gymnocephalus cernuus*) (Bauer et al. 2007; Savino et al. 2007). This finding was supported by the field experiment, which revealed significantly reduced growth rates of the native common shiner (*Luxilus cornutus*), creek chub (*Semotilus atromaculatus*), hornyhead chub (*Nocomis biguttatus*), Johnny darter (*Etheostoma nigrum*), longnose dace (*Rhinichthys cataractae*) and white sucker (*Catostomus commersonii*) after certain time period spent with round gobies in the space limited enclosure (Kornis et al. 2014). The round goby also competes for food resources with the fantail darter (*E. flabellare*) (Abbett et al. 2013), rainbow darter (*E. caeruleum*) (Poos et al. 2010), mottled sculpin (*C. bairdi*) (French and Jude 2001), rock bass (*Ambloplites rupestris*) and trout-perch (*Percopsis omiscomaycus*) (Burkett and Jude 2015) suggesting that many native fish species in the Great Lakes region suffer from the dietary competition posed by the round goby. In the Baltic Sea, the round goby competes for food and habitat with several native demersal fish species, including the flounder (*Platichthys flesus*) (Wandzel 2003; Karlson et al. 2007), perch (*Perca fluvitilis*) (Järv et al. 2011; Herlevi et al. 2018), eelpout (*Zoarces viviparus*), common goby (*Pomatoschistus microps*), sand goby (*P. minutus*), black goby (*Gobius niger*) (Corkum et al. 2004), roach (*Rutilus rutilus*), vimba bream (*Vimba vimba*) (Skóra and Rzeznik 2001), white bream (*Blicca bjoerkna*) (Herlevi et al. 2018) and juvenile turbot (*Scopthalmus maximus*) (Ustups et al. 2016).

The spawning interference was illustrated by the laboratory experiment, in which the round goby attacked nest-guarding mottled sculpins, occupied their nests and caused the loss of almost entire egg clutches (Janssen and Jude 2001). The round goby ability to displace native fish and occupy optimal habitat was also supported by several laboratory experiments, where aggressive gobies successfully expelled resident mottled sculpins (Dubs and Corkum 1996), logperches (Balshine et al. 2005; Leino and Mensinger 2015) and ruffes (Savino et al. 2007) from preferred sheltered areas. In contrast, research conducted in the Meuse and Rhine Rivers revealed, that the presence of the round goby did not affect the habitat choice for the native Chabot bullhead (*C. perifretum*) and stone loach (*Barbatula barbatula*) (van Kessel et al. 2011).

Food, shelter and spawning site competition, combined with predation effect posed by the invasive round goby, resulted in the significant abundance reduction or even extinction of some native benthic fish species in the Laurentian Great Lakes (French and Jude 2001; Janssen and Jude 2001; Lauer et al. 2004; Reid and Mandrak 2008; Burkett and Jude 2015), the Baltic Sea (Karlson et al. 2007; Ustups et al. 2016) and Eurasian rivers (Juraida et al. 2005; van Kessel et al. 2016). The study, conducted in the Lake Erie tributaries showed that species richness, Shannon diversity index, abundance per unit effort and biomass per unit effort of native fish populations were lower in round goby colonized streams, indicating the intensified rates of intra- and interspecific competition and reduced food resources (Krakowiak and Pennuto 2008).

The magnitude of competitive interactions between the round goby and native fish varies depending on the water body, its characteristics e.g. habitat heterogeneity, water temperature, forage base quality, favorable habitat availability and population densities of native and invasive fish (Kornis et al. 2012). Studies from the Lake Huron (Riley et al. 2008) and Wisconsin streams (Kornis et al. 2012) demonstrated, that in some locations native demersal mottled sculpin, fantail darter, Johny darter, blackside darter (*P. maculata*) and spottail shiner (*Notropis hudsonius*) are able to resist a significant extirpation after the round goby expansion. Native ichthyofauna in Eurasian riverine round goby invaded systems also avoided a significant abundance decline and severe interspecific resource competition (Copp et al. 2008; Piria et al. 2016; Janáč et al. 2016, 2018). Due to the absence of the detailed studies on the importance of the round goby in coastal fish communities as well as on the magnitude of food competition posed to the native benthivorous fish inhabiting homogeneous and heterogeneous habitats in the Baltic Sea, such investigations are necessary in order to determine the impact of the round goby on native ichthyofauna in different biotope types.

2.4 Predation on the round goby

Despite the lower energy density and nutritional value compared to some other forage fish species (Ruetz and Strouze 2009), the round goby seems to be very profitable prey, because it is slowly swimming, small, soft-bodied, lacking sharp spines fish containing elongated body shape (Charlebois et al. 1997), which makes it easy to catch and swallow by the gape limited predators (Płąchocki et al. 2012). Due to the previously mentioned reasons and ability to reach higher densities than native forage fish (Lauer et al. 2004; Steinhart et al. 2004; Johnson et al. 2008; Cooper et al. 2007; Campbell and Tiegs 2012), the round goby became an important food item for many piscivorous predators in the majority of invaded ecosystems.

The Laurentian Great Lakes contain a wide variety of piscivorous fish, waterbird and reptile species, feeding on the round goby and contributing to the stabilization of its rapidly increasing populations at local (Jones et al. 2009) or larger (Madenjian et al. 2011) scale. Predatory fish foraging on the round goby include the burbot (*Lota lota*) (Madenjian et al. 2011; Hares et al. 2015), lake whitefish (*Coregonus clupeaformis*) (Lehrer-Brey and Kornis 2013; Pothoven and Madenjian 2013), smallmouth bass (*Micropterus dolomieu*) (Carter et al. 2010), yellow perch (*Perca flavescens*) (Truemper et al. 2006; Webber et al. 2011), walleye (*Sander vitreus*) (Crane et al. 2015), lake trout (*Salvelinus namaycush*) (Dietrich et al. 2006; Jacobs et al. 2010; Rush et al. 2012), American eel (*Anguilla rostrata*) (Fitzsimons et al. 2013), muskellunge (*Esox masquinongy*) (Kapuscinski et al. 2012), white bass (*Morone chrysops*) (Johnson et al. 2005), brown bullhead (*Ameiurus nebulosus*), channel catfish (*Ictalurus punctatus*), sauger (*S. canadensis*) and the northern pike (*E. lucius*) (Reyjol et al. 2010). The results of the study, conducted by Johnson et al. (2005) demonstrated, that predatory fish with a high reliance on the round goby were larger at certain age, comparing to the predators that consumed low amounts of the round goby. This finding indicates an advantage of the round goby dominated diet, possibly due to the high abundance and reduced energetic costs of pursuing and capturing invasive gobies compared to alternative actively swimming pelagic prey (Johnson et al. 2005).

The most important avian round goby predator in the Great Lakes is the double-crested cormorant (*Phalacrocorax auritus*) (Somers et al. 2003; Andrews et al. 2012). After the round goby expansion, cormorants shifted their diet from native fish to the energetically less valuable round goby, which resulted in increased daily fish consumption (Johnson et al. 2015) and reduced breeding success, as the juvenile survivorship rates declined significantly (Van Guilder and Seefelt 2013). The intensified double-crested cormorant predation on the round goby positively affected populations of economically important sport fish: yellow perch and smallmouth bass, because the cormorant predation pressure on those fish species was considerably reduced (Johnson et al. 2010, 2015). Other piscivorous birds, preying on the round goby include the red-breasted merganser (*Mergus serrator*) (Bur et al. 2008), common loon (*Gavia immer*) (Kenow et al. 2018), ring-billed gull (*Larus delewarensis*), horned and red-necked grebes (*Podiceps auritus* and *P. grisegena*) and white-winged scoter (*Melanitta deglandi*) (Essian et al. 2016).

The northern water snake (*Nerodia sipedon*) and Lake Erie water snake (*N. sipedon insularum*) also shifted their diet towards the invasive round goby (King et al. 2006; Jones et al. 2009), which positively affected the snakes by influencing faster growth rates and larger body sizes (King et al. 2006).

In the Baltic Sea region the round goby is consumed by the grey seal (*Halichoerus grypus*) (Lundström et al. 2010), Baltic cod (*Gadus morhua callarias*) (Almqvist et al. 2010; Gruszka and Więcaszek 2011), perch (*P. fluvitilis*) (Liversage et al. 2017), pike-perch (*S. lucioperca*) (Hempel et al. 2016), turbot (*S. maximus*) (Sapota and Skóra 2005), wintering black-throated and red-throated loons (*G. arctica* and *G. stellata*), great crested grebe (*P. cristatus*), goosander (*M. merganser*), velvet scoter (*M. fusca*) (Saulius Karalius, Lithuanian Ornithological Society, pers. comm.), great cormorant (*P. crabro*) (Pūtys and Zarankaitė 2010; Oesterwind et al. 2017) and grey heron (*Ardea cinerea*) (Jakubas 2004; Jakubas and Mioduszewska 2005; Jakubas and Manikowska 2011). High round goby consumption rates caused relaxation of the predation pressure on several native forage fish species, including the greater (*Hyperoplus lanceolatus*) and lesser (*Ammodytes tobianus*) sandeels and Baltic sprat (*Sprattus sprattus balticus*) (Ojaveer et al. 2002).

Very few studies on the round goby consumption by ichthyophagous predators in the Eurasian riverine systems were performed, however information concerning the round goby importance in the diet of the northern pike (*E. lucius*), pike-perch (*S. lucioperca*), perch (*P. fluvitilis*), burbot (*L. lota*), European catfish (*Silurus glanis*) and Volga zander (*S.volgensis*) is available (Płąchocki et al. 2012; Mikl et al. 2017).

Natural predation on the rapidly increasing and spreading round goby populations in various different localities is very important in order to reduce the round goby abundance and magnitude of its impact on the invaded ecosystems (Madenjian et al. 2011; Crane et al. 2015; Hempel et al. 2016). No comparative studies of the round goby vulnerability to the predation of piscivorous fish in the structurally diverse and bare biotopes of the Baltic Sea have been conducted yet, therefore it is a need to determine the diet composition of native predatory fish and their potential to control the round goby populations in the coastal stony and sandy habitats.

2.5 Round goby invasion to the Baltic Sea

The intentional and unintentional human mediated transfer of non-native species beyond the range of their natural occurrence is a very old phenomenon, dating back to pre-historical time, however the rates of aquatic invasions increased significantly during several last decades because of changes in factors e.g. the duration of the voyages or anthropogenic disturbance in donor and recipient areas that used to prevent ecosystems from biological introductions (Leppäkoski et al. 2002). Successfully established non-native (alien, exotic, foreign, introduced, non-indigenous) species are capable to reproduce, increase in abundance, form self-sustaining populations and turn to invasive species, constantly spreading their range and causing serious ecological and economic threats across the globe (Occhipinti-Ambrogi 2007). Negative effects of invasive species include displacement of native species, reduction of genetic variation, dispersion of novel parasites and diseases, alteration of food web structure, loss of ecosystem functions, biological homogenization and climate change (Galil 2007; Molnar et al. 2008; Golzan et al. 2010). The disturbed aquatic systems, characterized by low species richness (e.g. the Baltic Sea), are especially vulnerable to invasiveness due to a wide range of unoccupied niches, reduced competition rates, high resource availability and few natural predators (Paavola et al. 2005). Because of more expressed anthropogenic pressure, such as extensive shipping activities, artificial substrates, over-fishing, habitat degradation and susceptible environment (variety of habitats, salinity gradient and nutrient enrichment), the highest magnitude of invasive species impact on native communities, habitats and ecosystem functioning occurs in the coastal waters (Zaiko et al. 2011).

At present time there are 118 non-indigenous species observed and approximately 90 established in the Baltic Sea, including 13 exotic fish (HELCOM 2018). The most successful vertebrate invasive species in the coastal zone of this water body is the round goby. Most probably eggs, juveniles or adult specimens of the round goby were unintentionally transported to the Baltic Sea in ballast water tanks of foreign vessels, operating in the Ponto-Caspian region (Corkum et al. 2004; Sapota 2004). Theoretically, the round goby might also have migrated to the Baltic Sea naturally through the northern Ponto-Caspian species migration corridor, connecting the Gulf of Gdańsk with the Black Sea through the Dnieper, Pripyat, Pina, Kanal Krolewski, Bug and Vistula Rivers or the Gulf of Finland with the Caspian Sea through the Volga River, Rybinskoe water reservoir and the Onega and Ladoga Lakes (Skóra and Stolarski 1993; Bij de Vaate et al. 2002).

In the Baltic Sea, the round goby was first reported in 1990, from the Gulf of Gdańsk, in the vicinity of Hel and Gdynia harbors. Several years later the population significantly increased in numbers, began to spread to the mouth of Vistula River, adjacent canals, Vistula Lagoon (Sapota and Skóra 2005), Szczecin Lagoon (Czerniejewski and Brysiewicz 2018), Odra River estuary (Czugała and Woźniczka 2010) and naturally or through commercial shipping expanded over the entire Baltic Sea coastal area (Kotta et al. 2016). First specimen of the round goby in the Lithuanian coastal waters was captured near the southern pier of Klaipeda harbour in 2002 (Zolubas 2003). Within a decade after the first observation, the abundance of the round goby increased dramatically, allowing this fish to become a key component of ichthyofauna in the Lithuanian coastal aquatory (Ložys et al. 2016) and occupy nearby located Klaipeda strait and Curonian Lagoon (Rakauskas et al. 2008, 2013).

A number of studies, focused on the round goby range expansion (Sapota and Skóra 2005; Kotta et al. 2016; Azour et al. 2015), feeding preferences (Skóra and Rzeznik 2001; Wandzel 2003; Nurkse et al. 2016; Schrandt et al. 2016; Oesterwind et al. 2017), food competition with native fish (Karlson et al. 2007; Järv et al. 2011; Herlevi et al. 2018), importance in the diet of piscivorous predators (Jakubas 2004; Almqvist et al. 2010; Pūtys and Zarankaitė 2010; Gruszka and Więcaszek 2011; Hempel et al. 2016; Liversage et al. 2017) and biological parameters (Wandzel 2000; Tomczak and Sapota 2006; Sokołowska and Fey 2011) were previously conducted in the Baltic Sea. Despite this, it is still unknown how the habitat heterogeneity (stony *vs*. sandy) affects the round goby abundance, its contribution in the fish communities, morphometry, fecundity, diet, magnitude of resource competition posed to the native fish/wintering ducks and vulnerability to the predators, therefore detailed investigations on the round goby functional role in different biotope types were performed in the course of the present study.

2.6. Commercial round goby fishery in the Lithuanian coastal waters

The abundance of the round goby in the Lithuanian Baltic Sea coastal waters increased considerably in 2011 (Fig. 6), which was reflected in long-term coastal commercial fishery catch and sale statistics (Fig. 2). Before 2010, the round goby was considered as a bycatch species, comprising a negligible proportion of the total fish catches, and therefore had no commercial value. The amount of captured round gobies and its economic value grew consistently during 2010-2016 and remained high in 2017-2018 (Fig. 2). An extreme increment of the round goby catches recorded in 2016 was influenced by the significantly increased round goby abundance in the stony biotope (Fig. 7) and highly intensified usage of benthic fish traps (Ložys et al. 2016). It should be noted, that the majority of total round goby catches (>90%) originated from the mainland segment of the Lithuanian coastal zone (Fisheries service under the Ministry of Agriculture of the Republic of Lithuania, unpublished data).

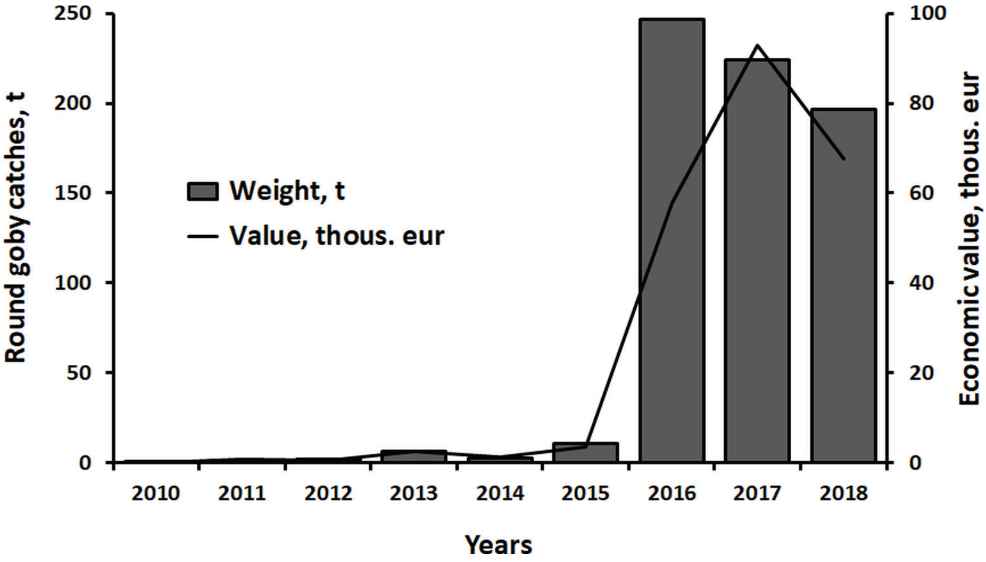

Figure 2. Long-term round goby catch and sale statistics of commercial fishery in the Lithuanian coastal waters. Data derived from the Fisheries service under the Ministry of Agriculture of the Republic of Lithuania.

2 pav. Ilgalaikės verslinės juodažiočio grundalo žvejybos sugavimų ir pardavimų statistika Baltijos jūros Lietuvos priekrantėje. Duomenys gauti iš Žuvininkystės tarnybos prie Lietuvos Respublikos žemės ūkio ministerijos.

During 2010-2018, the mean round goby market price was 0.36 Euro/kg and varied from 0.1 to 4.0 Euro/kg (Fisheries service under the Ministry of Agriculture of the Republic of Lithuania, unpublished data) depending on the body size of captured fish (price increases with increasing length) and market demand. At present time three round goby market size classes are distinguished: small (<120 mm), intermediately sized (120-180 mm) and large (>180 mm). <120 mm specimens are used as animal food or soil fertilizers, while larger individuals are used for human consumption (Taurūnas Areškevičius, commercial fishermen, pers. comm.). According to the round goby body size distribution determined in the course of the current study, the population is highly dominated by the intermediately sized specimens (71%), followed by small (23%) and large (7%) individuals (Fig. 28), which combined with high fishery supply results at medium market price.

3

Material and Methods

3.1 Biotope and community structure of the study site

The study was performed in the SE Baltic Sea, the Lithuanian coastal waters of Karklė (55°47’34”N; 21°02’96”E) and Juodkrantė (55°32’37”N; 21°05’26”E), representing stony and sandy biotopes, respectively (Fig. 3). The coastal waters zone is delineated by the 20 m depth bathymetric boundary, which extends 2-9 km from the coastline and comprises an area of 335 km^2 along the Lithuanian Baltic Sea coast (Gelumbauskaitė 1998). The outflow from the Curonian Lagoon (at Klaipeda port gates) divides the Lithuanian coastal area into the southern (Curonian spit) and the northern (mainland) parts. The southern segment is predominated by the sandy seabed, while the northern part contains very diverse bottom types, including morainic clay, boulders, cobble, pebble and coarse, medium and fine sands (Olenin and Daunys 2004; Fig. 3). As the Lithuanian coastal waters comprise two different benthic habitats: sandy and mixed (sand mixed with boulders), it is assumed, that the mixed habitat occupies approximately 20% of the total coastal area (Razinkovas-Baziukas et al. 2017).

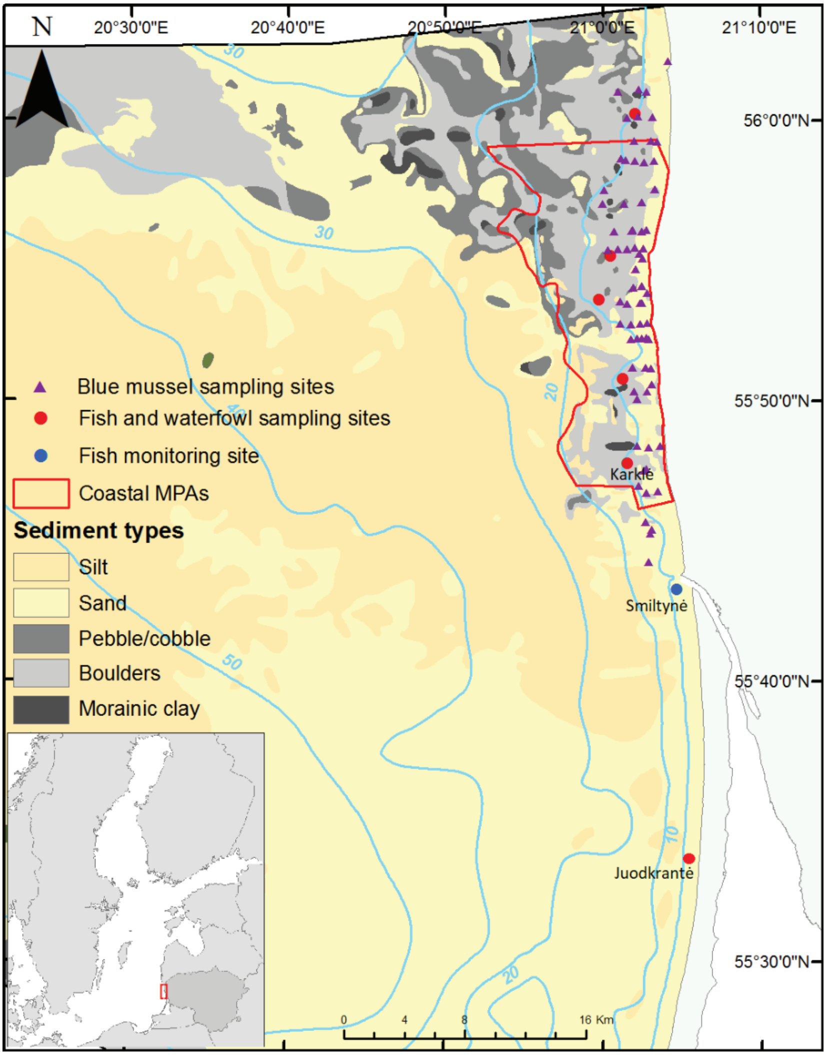

Figure 3. Locations of fish monitoring site, round goby, long-tailed duck and blue mussel sampling sites, coastal MPAs borders and bottom types in the study area (designed by dr. A. Šiaulys).

3 pav. Žuvų monitoringo, juodažiočio grundalo, ledinės anties ir midijų mėginių ėmimo vietos, saugomų jūrinių teritorijų ribos bei tyrimo vietoje išsidėstę dugno buveinių tipai (sudarė dr. A. Šiaulys).

The biotope structure and benthic biodiversity in the Karklė sampling site change depending on the depth and gradient of the hydrodynamic activity. The mobile sand biotope, characterized by burrowing infaunal (*Marenzelleria viridis*, *Pygospio elegans* and *Limecola balthica*) and actively swimming nectobenthic (*Crangon crangon* and *Bathyporeia pilosa*) invertebrates, occupies the uppermost sublittoral from the shore line to 1-2 m depth, where sand is permanently transferred due to wave and current action. The seabed at 2-3 m depth is composed of sand, gravel, pebble and large sporadic boulders, overgrown by annual filamentous green algae *Cladophora glomerata*, *C. rupestris* and *Enteromorpha intestinalis*, providing habitat for mobile *Gammarus* sp. amphipods, fish fry and other associated animals; epifauna at this depth is scarce due to constant effect of waves and abrasive sediment movement (Oleninas et al. 1996).

The bottom structure at 4-5 m depth is very patchy, composed of the mixture of boulders, gravel and coarse sand, inhabited mainly by epibenthic barnacles (*Amphibalanus improvisus*) and small crustaceans (Oleninas et al. 1996; Olenin and Daunys 2004). The deepest part of the stony study site (5-25m) is characterized by boulders with small patches of sand, gravel and pebble. Hard substrates are covered by the colonies of barnacles and blue mussels (*Mytilus edulis trossulus*), creating a shelter for other benthic invertebrates e.g. *Fabricia sabella*, *Jaera albifrons*, *B. pilosa*, gammarids and oligochaetes. Soft sediments at this depth are occupied by infaunal bivalves (*L. balthica* and *Mya arenaria*), crustaceans (*Corophium volutator*) and polychaetes (*Hediste diversicolor*, *Pygospio elegans* and *M. viridis*) (Bubinas and Vaitonis 2003; Olenin and Daunys 2004). The zoobenthic community at 5-25 m depth is the most diverse, represented by ~50 macrofaunal species (Oleninas et al. 1996), which was highly productive and contained biomass up to 5 kg m^2 before the round goby invasion (Olenin and Daunys 2004). After the round goby expansion, biomass of benthic invertebrates declined ~ 15-fold and is highly dominated by the cirripeds (barnacles) (Fig. 4).

A heterogeneous biotope composed of hard geological substrates forms coastal reefs occupied mainly by the blue mussels, barnacles (Olenin and Daunys 2004) and perennial red algae (*Furcellaria lumbricalis*) (Bučas et al. 2007). These coastal reefs are within the territories of the Seaside Regional Park and NATURA 2000 MPAs (Fig. 3), that are important for wintering birds (EC Birds Directive, Special Protection Areas for the protection of the wintering Steller's eider (*Polysticta stelleri*), common goldeneye (*Bucephala clangula*), goosander (*Mergus merganser*) and concentrations of the migratory little gull (*Larus minutus*)) and marine habitats protection (EC Habitat Directive).

In contrast to Karklė sampling site, Juodkrantė area has a monotonous sandy biotope and less pronounced benthic community structure change along the depth gradient. Detailed benthic environment investigations have not been performed in <10 m depth of this coastal area yet (Olenin and Daunys 2004), while in the deeper

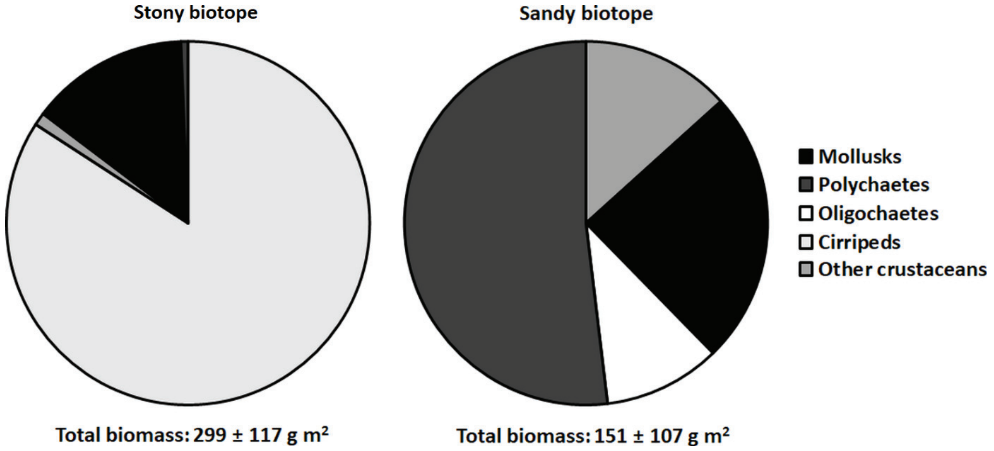

Figure 4. Biomass frequency of the main benthic invertebrate groups in the coastal stony (2013-2017) and sandy (2005-2017) biotopes. Zoobenthos data from the stony and sandy biotopes were derived from Marine Research Institute (unpublished data) and Marine Research Department (unpublished data), respectively.

4 pav. Pagrindinių dugno bestuburių gyvūnų grupių biomasės dažnio pasiskirstymas priekrantės moreninio (2013–2017 m.) ir smėlėto (2005–2017 m.) dugno buveinėse. Neskelbti zoobentoso biomasės duomenys gauti iš Jūros tyrimų instituto ir Jūrinių tyrimų departamento.

(10-30 m) zone the zoobenthic community is dominated by *L. balthica*, *M. arenaria*, *Cerastoderma lamarcki*, *Pygospio elegans*, *H. diversicolor*, *M. viridis*, *Saduria entomon*, *Pontoporeia affinis* and oligochaetes (Bubinas and Vaitonis 2003, 2007) and accumulates lower biomass compared to the stony biotope (Olenin and Daunys 2004; Fig. 4).

3.2 Sampling methods

Fish sampling took place during April-October 2014-2016. Fish were captured by using 3 sets of multi mesh gill nets (120 m length, 3 m depth, divided into 8 sections with mesh sizes of 14, 18, 22, 25, 30, 40, 50, 60 mm) (Fig. 5), at depths ranging from 5 to 12 m.

The gill nets were set in the water overnight for about 12 hours, including both dusk and dawn periods. The catch per unit effort was calculated as the annual mean number and biomass of fish caught per net (CPUE, ind. net 12 h and CPUE, kg net 12 h) (Karlson et al. 2007; Coulter et al. 2012). In total, 9 sampling events at each research station were conducted (Table 1). The abundance (ind.) and biomass (kg) of all

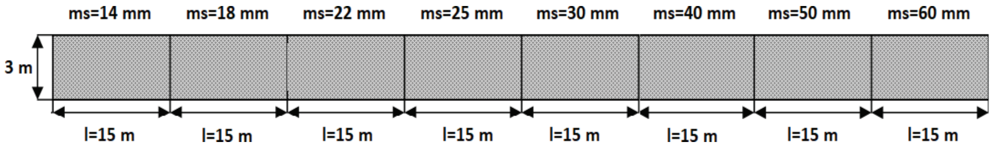

Figure 5. Characteristics of the sampling gill nets (ms - mesh size; l - length).

5 pav. Statomųjų tinklaičių charakteristikos (ms – tinklo akies dydis; l – ilgis).

captured fish species were expressed as CPUE of fish caught in the set of multi mesh gill nets (360 m^2) during 12 hours. Later on, the abundance and biomass of the round goby per m^2 were calculated by dividing the total abundance and biomass captured in the set of gill nets from 360 m^2.

The long-term round goby abundance dynamics were determined by analyzing coastal ichthyological monitoring data, collected during 2002-2016 period from the Smiltynė sampling site (Fig. 3). Surveys were performed repeatedly during April-September and the number of annual sampling events varied from 8 to 17. Fish samples were collected by using a multi mesh gill net at 5-12 m depth (for the detailed gill net characteristics see Kregždys et al. 2018a). The abundance of the round goby was expressed as CPUE of individuals captured in 75 m of the 20 mm mesh size gill net (the highest round goby capture efficiency) during the time period of 24 hours (CPUE, ind. 75 m 24 h).

For dietary analysis in different round goby invasion phases, round gobies were collected during June-October in three periods: (1) 2008-2009 (data collected by E. Bacevičius), (2) 2012 and (3) 2014-2015 in sampling sites, distributed throughout 20 km of mainland coastal stretch characterized by the stony bottom area (Fig. 3). Immediately after capture, fish were stored frozen at a temperature of -20°C.

Zoobenthos data were provided by the Benthic Habitat Ecology group (Klaipėda University, Marine Research Institute). For the estimation of blue mussel biomass, 275 benthic samples from 72 locations were collected in 2003-2014 on various scientific projects sampling occasions (Fig. 3). The samples were taken by SCUBA divers from hard substrates at the depths of 2-20 m, using a 0.2×0.2 m frame. All samples were fixed in 4% formaldehyde solution and the biomass (wet weight with shells) was estimated by the gravimetric method. For the analysis of blue mussel size structure, length measurements of 11,866 individuals were performed in 39 samples from 2006 and 14 samples from 2014. All laboratory analyses of the blue mussels were performed by A. Poškienė.

Table 1. **Sampling date and site, total abundance (mean ± SD, ind.) and biomass (mean ± SD, kg) of fish, captured in the set of gill nets (360 m²) during 2014-2016.**

1 lentelė. **Mėginių rinkimo data ir vieta, bendras žuvų, sugautų įvairiaakių statomųjų tinklaičių komplektu, gausumas (vidurkis ± SN, ind.) ir biomasė (vidurkis ± SN, kg) 2014–2016 m.**

Date	Sampling site	Total abundance, ind. net	Total biomass, kg. net
01-10-2014	Karklė	107.7 ± 10.8	9.4 ± 2.2
04-10-2014	Karklė	70.1 ± 2.5	10.5 ± 2.0
06-10-2014	Juodkrantė	108.3 ± 17.9	9.0 ± 1.4
05-12-2015	Karklė	41.3 ± 4.9	4.0 ± 1.7
24-05-2015	Juodkrantė	89.3 ± 20.8	13.3 ± 2.5
29-06-2015	Karklė	85.0 ± 14.5	6.1 ± 1.5
01-07-2015	Karklė	95.3 ± 16.7	4.6 ± 1.4
24-07-2015	Juodkrantė	66.3 ± 10.6	9.5 ± 2.1
16-08-2015	Juodkrantė	93.7 ± 10.4	13.3 ± 1.9
22-08-2015	Juodkrantė	87.3 ± 16.0	13.5 ± 3.0
12-09-2015	Juodkrantė	67.0 ± 4.0	6.6 ± 1.6
29-09-2015	Karklė	84.7 ± 5.8	8.1 ± 3.4
03-04-2016	Juodkrantė	95.3 ± 28.6	13.3 ± 5.4
25-04-2016	Karklė	541.0 ± 347.7	45.2 ± 21.8
13-07-2016	Karklė	398.0 ± 95.5	29.1 ± 5.2
19-07-2016	Juodkrantė	71.3 ± 11.7	11.7 ± 2.1
20-09-2016	Juodkrantė	70.3 ± 29.0	7.2 ± 3.4
05-10-2016	Karklė	387.7 ± 52.3	34.8 ± 2.9

Wintering long-tailed ducks were obtained from the coastal fishermen as a bycatch captured with the gill nets at 2-15 m depth in several localities, distributed throughout the coastal stony biotope (Fig. 3). Samples were collected during three wintering periods (January-March): (1) 2002-2004 (samples collected by dr. A. Petraitis), (2) 2011-2012 and (3) 2014-2016 (samples collected by J. Morkūnas). Collected birds were stored frozen at -20°C for further analysis.

3.3 Biological round goby analyses

Otolith preparation and age determination. Otoliths for the round goby age determination were extracted from the fish captured during July-September 2015 in Karklė (213 specimens) and Juodkrantė (146 specimens) sites. Both sagittal otoliths (left and right) were removed from each fish, cleaned with ethyl alcohol, dried and lightened with xylol solution. Otoliths with unclear patterns (~15%) were prepared for age reading by grinding and polishing, following the method suggested by Stevenson and Campana (1992). Then the age of the round goby was assigned according to the counts of annual rings (alternating opaque and translucent zones) along the axis from the core to the rostral tip of the otolith by using 2-5× Olympus stereomicroscope. Two age readings with 1-2 month intervals were performed by two readers without the reference to fish lengths. The left or right sagitta was used for the age estimation depending on the clarity of the increment pattern. If the ages obtained from different readers or reading events were different, the otolith was re-examined. The otoliths with excessive vateritic growth, deformation or indistinct annulus character were excluded from the age analysis (6 and 2 pairs of otoliths from Karklė and Juodkrantė sites, respectively).

Sex and fecundity determination. Sex of the round goby was determined visually according to the shape of urogenital papilae (Charlebois et al. 1997) and dissected gonads, while small individuals with indeterminable sex were considered as juveniles. Since female round gobies are batch spawners and their gonads contain eggs at higher and earlier developmental stages, their maturity was determined according to the fraction of eggs at a higher developmental stage. The evaluation of female eggs' maturity was performed using classification suggested by Tomczak and Sapota (2006). The fecundity was estimated only for the females containing fully riped gonads (IV maturity stage). In the process, 1 g of the gonads was weighed (± 0.001 g), eggs were accurately calculated and the absolute fecundity of the female was then evaluated by multiplying the number of eggs in 1 g of the gonads to the whole gonad weight (earlier weighed to the nearest 0.001 g). The absolute fecundity was estimated for 95 female round gobies from Karklė and 55 from Juodkrantė sites.

3.4 Stomach/gut content analysis

Benthophagous fish. For a dietary analysis benthivorous fish (the round goby, flounder, eelpout and vimba bream) were randomly selected by taking 20-30 individuals of each species and size group (if possible) from the catches of all sampling events conducted during 2014-2016 period (Table 1). Seasonal feeding patterns of benthophagous fish were determined by evaluating dietary shifts during spring (April-May), summer (June-August) and autumn (September-October) 2014-2016. In the laboratory frozen fish were thawed, measured to a total length (± mm) and weighed with the accuracy of ± 0.1 g. The round goby (RG) and flounder (FL) were sorted into small (S), intermediately sized (M) and large (L) individuals according to Karlson et al. (2007). The lengths of distinguished different round goby and flounder size groups were as follows: RG S = 60-120 mm, RG M = 120-140 mm, RG L = >140 mm, FL S = 100-120 mm, FL M = 200-250 mm, FL L = >250 mm (Karlson et al. 2007).

The total length of captured eelpouts and vimba breams varied in a relatively narrow range: from 201 mm to 283 mm and from 253 to 263 mm, respectively, therefore individuals of these species were not divided in different size groups. Small flounders from the stony bottom area were not included in the dietary analysis, because only 1 specimen with food remains in the guts was captured. In total, the gut content analysis was performed in 572 round gobies, 258 flounders, 23 eelpouts and 72 vimba breams.

The alimentary tract from esophagus to anus of each examined specimen was removed, weighed full and empty (± 0.001 g) to obtain wet weight of the gut content. Feeding objects were identified to the lowest possible taxa, measured and counted under a 2-5× Olympus stereomicroscope. Crushed mollusk shells and hulls of crustaceans were reconstructed from the particles whenever possible to gather taxonomically identifiable and measurable parts of the ingested prey. In case of high digestion level, the number of consumed soft-bodied organisms, found in posterior guts was determined based on characteristic structural elements, such as mandibles and chaetae of polychaetes, or telsons, legs and eyes of crustaceans (Skóra and Rzeznik 2001), considering their body length as an average length from all measured individuals of certain prey taxa found in the gut contents of dissected fish. Wet weight of each feeding object was determined using length-weight regressions (Rumohr et al. 1987). Rarely consumed feeding objects, such as macroalgae, gastropods *Theodoxus fluviatilis* and *Hydrobia* sp., bivalves *C. lamarcki*, mysids *Neomysis integer* and isopods *S. entomon* were pooled and considered as other prey. Unidentified preys were excluded from further calculations.

Predatory fish. For a dietary analysis piscivorous fish (cod, turbot, shorthorn sculpin and perch) were randomly selected by taking 20-30 individuals of each species and size group (if possible) from the catches of all sampling events conducted in 2014-2016 (Table 1). The majority specimens of coldwater species: cod and shorthorn sculpin were captured in spring and autumn, when water temperature was <10°C; perch - in summer, during migration from the Curonian Lagoon (Ložys 2003) and turbot - in late spring-early summer, during the spawning (Stankus 2003). Piscivorous fish were measured to the nearest cm (total length) and weighed to the nearest g. According to the recommendations provided by previous studies and determined body size distributions during the current research, predatory fish were divided into 2 size groups (small and large): cod - <400 mm and >400 mm (Dziaduch 2011), perch <150 mm and >150 mm (Płąchocki et al. 2012), shorthorn sculpin <200 mm and >200 mm and turbot <200 mm and >200 mm. The turbot from the coastal stony biotope was excluded from the dietary study, because only 2 specimens with food remains in the stomach contents were caught. In total, the diet of 240 cods, 191 perches, 122 shorthorn scuplins and 37 turbots was evaluated.

For the dietary analysis, anterior part of alimentary tracts (oesophagus and stomach) were removed, placed in plastic bags, labeled and frozen (-20°C) for further investigations. Later on stomachs were thawed, their contents were removed to place on the Petri dish and washed with water. Ingested preys were sorted, counted and identified to the lowest possible taxa. For biomass calculations, total length of each consumed invertebrate prey was measured to the nearest mm. All fish preys found in the stomach contents were measured to the nearest 0.5 cm, determining either total length (TL) or standard length (SL, defined as the length from the tip of the upper jaw to caudal fin base). In case of broken tails, total length was determined from the TL-SL relation (Pachur and Horbowy 2013). Partly digested fish preys were recognized according to the fish identification keys (Muus and Nielsen 1999). Non-digested weights of consumed fish were restored using the data from the *Fishbase* (Froese and Pauly 2007) or from the relation between the otolith size and fish prey size (Härkönen 1986). The length-weight relationships of ingested invertebrate food items were obtained from Rumohr et al. (1987). Unidentified preys were excluded from further calculations.

Long-tailed duck. All laboratory analyses of the waterfowl were performed by dr. A. Petraitis, dr. R. Morkūnė, J. Morkūnas and A. Karlonė. A more detailed description of the applied methods could be found in Skabeikis et al. (2019).

3.5 Stable isotope analysis

3.5.1 Sample collection, preparation and measurements

To obtain markers for the middle-to-long term diet composition and trophic niche overlap, $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ stable isotope analyses (SIA) of small, intermediately sized and large round gobies and flounders were conducted in samples, collected at Juodkrantė site during September-October 2015. The round goby and flounder were captured using multi mesh gill nets at the depth of 5-12 m. Benthic invertebrates (*L. balthica*, *C. lamarcki*, *M. arenaria*, *C. crangon*, polychaetes and amphipods) for SIA were collected at 5, 10, 15 and 20 m depths using a Van Veen grab sampler at Juodkrantė sampling site during 9th October 2015. At each depth, 3 samples (12 samples in total) were taken, flushed and fixed in 4% formaldehyde solution. It should be noted, that the isotopic values of benthic invertebrates were not affected by the depth horizon, as samples of all analyzed species collected at 5, 10, 15 and 20 m depths did not differ in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ compositions (ANOVA; $p > 0.05$ for all cases). Small (<15 mm) and large (>15 mm) individuals of *L. balthica* also had similar isotopic compositions (*t*-test; $p > 0.05$ in all three SI spaces), therefore all samples from different depths and size groups were pooled during the stable isotope analysis of selected benthic invertebrates (Figs. 20 and 21). 15 individuals of small (31-58 mm, preferred prey size range) sand gobies (*P. minutus*), as representatives of fish prey for the round goby and flounder, were captured in the sandy bottom site (56°43’34”N; 21°04’37”E) during May 2018, using the landing net at 1-1.5 m depth.

Pieces of a dorsal muscle (0.5-1 cm^3) were sampled individually from 15 specimens in each round goby and flounder size group (45 samples for each species). Muscle tissues of 3 *P. minutus* individuals were combined in one sample (15 specimens constituted 5 samples for SIA) in order to evaluate isotopic composition of the fish prey. Soft muscle tissue of mollusks and whole bodies of polychaetes and amphipods (in some cases several small specimens of the same species/higher taxa were pooled in one sample) were used for SIA. All prepared samples were dried at 60°C temperature for 48 hour period and ground to a fine powder in an agate mortar (Jardine et al. 2003). Approximately 0.8-1.0 mg material for $\delta^{13}C$ and $\delta^{15}N$ analyses and 1.5-2.0 mg for $\delta^{34}S$ analysis were weighed (±0.0002 mg) and placed into tin capsules. The isotopic composition was determined at the “UC Davis Stable Isotope Facility”, USA.

The isotope ratio analysis was conducted by applying mass spectrometry in order to measure 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) and sulfur dioxide gas (SO_2) generated during combustion of the sample material. $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ ratios were calculated according to Peterson and Fry (1987):

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000\ (‰) \qquad (1)$$

where: $X = {}^{13}C$, ^{15}N or ^{34}S; R = the ratio of heavy and light isotopes, where standards were considered as Vienna-PeeDee Belemnite (V-PDB) in the case of carbon, atmospheric N_2 in the case of nitrogen and Vienna Canyon Diablo troilite (VCDT) in the case of sulfur.

3.5.2 Stable isotope data analysis

Lipid removal was not performed in this study, therefore mean C:N ratios in the round goby, flounder and their preys were calculated (Annex 5). Evaluated C:N ratios of intermediately sized flounders (3.55 ± 0.37) and benthic invertebrates (5.03 ± 0.79) were higher than recommended limit for aquatic fauna (C:N > 3.5), at which lipid correction should be performed; therefore the $\delta^{13}C$ values in the mentioned organism groups were corrected by applying lipid normalization equation (Post et al. 2007):

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N \qquad (2)$$

To compare isotopic niche breadth of differently sized round gobies and flounders, ellipses of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ biplots were constructed using a multivariate SIBER (Stable Isotope Bayesian Ellipses in R) package in R (Jackson et al. 2011). Standard Ellipse Area (SEA) demonstrates mean isotope variability in x and y values of the stable isotope biplot. The SEA represents approximately 40% of the spread of data, reveals the core niche and is expected to be insensitive to sample size. In the cases of small (<30) sample sizes, the transformed version (SEA_C), providing unbiased correction of SEA is used (Jackson et al. 2011, 2012):

$$SEA_C = SEA \times \frac{n-1}{n-2} \tag{3}$$

The application of SEA_C results in a slightly larger ellipse for small sample sizes, which allows calculating the isotopic niche overlap at the confidence level, which can be used as a quantitative measure of dietary similarity among the studied groups (Jackson et al. 2012).

Triple ($\delta^{13}C$ and $\delta^{15}N$ and $\delta^{34}S$) SIA mixing models were built using the SIAR (Stable Isotope Analysis in R) package in R (Parnell et al. 2010). Biplots of SI mixing models were constructed in order to determine the contribution of different food sources to the diet of native and invasive benthophagous fish. Food sources were defined as different when they had significantly different isotopic composition of one or more isotopes; otherwise, different species or higher taxa (amphipods, polychaetes, fish prey) were pooled in combined food sources by the similarity in isotopic compositions within the groups (Phillips et al. 2005).

Values of carbon (0.4 ± 1.3‰) and nitrogen (3.4 ± 1.0‰) trophic enrichment factors (TEF) were obtained from Post (2002). TEF of sulfur was not used in the current study, because its trophic shifts do not differ from 0 (McCutchan et al. 2003). The mixing model results were presented as median, 25% and 75% quartiles of the contribution of food sources in the diet.

3.6 Calculations and data analysis

3.6.1 Diversity metrics

Species richness and other metrics for alpha diversity analysis (species number, Shannon-Wiener biodiversity index, Simpson's biodiversity index and Rényi diversity profiles) were calculated in order to compare biodiversity of fish communities between the stony and sandy biotope types and the periods, when abundance of round goby was low and high.

Shannon-Wiener biodiversity index *H'* was calculated using function of Shannon and Weaver (1949):

$$H = -\sum_{i=1}^{n} pi \ln pi \tag{4}$$

where: p_i = proportion of individuals found in species *i*.

The Rényi diversity profile values (H_α) were calculated according to Rényi (1961):

$$H_\alpha = \frac{\ln(\sum p_i^\alpha)}{1 - \alpha} \tag{5}$$

where: H_α = Rényi diversity profile; p_i = abundance of taxa *i* divided by the total abundance; α = a scale parameter, ranging from zero to infinity.

The Rényi diversity profile values for α = 0, 1 and 2 are related to the species richness, Shannon-Wiener diversity index and logarithm of the reciprocal Simpson's diversity index, respectively. The shape of the curves shows the extent of dominance within the community: a smoothed line indicates high evenness, because diversity values on the *y*-axis are negligibly affected by the alpha values, while the community with a high degree of dominance has a diversity profile that drops steeply with increasing α values. A community is considered as more diverse when its profile is consistently higher compared to other community; the crossing profile lines indicate that the communities cannot be ranked. The Rényi diversity profiles were generated for each fish community for 2014-2015 and 2016 periods separately by using the PAST 3.12 software (Hammer et al. 2001).

3.6.2 Calculation of the diet composition and feeding niche metrics

The index of stomach fullness (ISF), reflecting the feeding activity of the fish was calculated by using the following formulas (Hyslop 1980):

$$W_{prey} = W_{stomach\,full} - W_{stomach\,empty} \tag{6}$$

where: W_{prey} = weight of the prey items (g); $W_{stomach\,full}$ = weight of the full stomach (g), $W_{stomach\,empty}$ = weight of the stomach without prey items (g):

$$ISF = \frac{W_{prey}}{W} \times 100 \qquad (7)$$

where: W = weight of the fish (g).

Relative weight contribution of each prey taxa in the diet of the round goby, benthivorous/predatory fish and wintering long-tailed duck was assessed with reference to Hyslop (1980):

$$W(\%) = \frac{W_x}{W} \times 100 \qquad (8)$$

where: $W(\%)$ = weight percentage of prey x; W_x = reconstructed weight of prey x (g); W = total weight of all consumed preys (g).

The condition factor for benthivorous fish was determined by calculating values of Fulton's body condition index (Froese 2006):

$$K = 100\frac{M_T - M_G}{L^3} \qquad (9)$$

where: K = Fulton's body condition index; L= total length of the fish (mm); M_T = total fish body mass (g); M_G = gut content mass (g).

Feeding niche overlap between the round goby, native benthophagous fish and wintering long-tailed duck was determined via the equation proposed by Schoener (1970):

$$D_{x,y} = 1 - 0.5\left(\sum_{i=1}^{n} \left|P_{ix} - P_{iy}\right|\right) \qquad (10)$$

where: $D_{x,y}$ = Schoener's dietary overlap index between species x and species y; P_{ix} = proportion of prey category i in the diet of species x; P_{iy} = proportion of prey category i in the diet of species y. The index ranges from 0 (no dietary overlap) to 1 (complete dietary overlap), considering that values of 0.6 or higher indicate significant dietary overlap and possible food competition (Linton et al. 1981; Martin 1984).

Feeding strategy and prey importance of the round goby were graphically presented using the modified Costello (1990) method (Amundsen et al. 1996) in order to demonstrate differences in the round goby feeding strategy from the stony and sandy biotopes. For the data analysis and graphical presentation, 8 major prey categories: *L. balthica*, *M. arenaria*, *M. edulis trossulus*, *A. improvisus*, Amphipoda, Polychaeta, Pisces and other prey (*C. crangon*, *S. entomon* and *T. fluviatilis* combined) were used. Prey specific abundance (P_i) of each prey category was plotted against the frequency of occurrence of each prey category ($\%F_i$) (Amundsen et al. 1996):

$$\%F_i = \frac{N_i}{N} \times 100 \qquad (11)$$

where: N_i = the number of fish with prey *i* in their guts; N = the number of all analyzed fish.

$$P_i = \frac{\sum s_i}{\sum s_{ti}} \times 100 \qquad (12)$$

where S_i = the summarized number of prey *i*; S_{ti} = the total number of preys in the gut contents of fish, which consumed prey *i*.

The vertical axis represents feeding strategy in terms of specialization or generalization, where specialization increases with increasing height (specialization in the upper part and generalization in the lower part of the diagram). A fictive axis from the lower left to the upper right describes the importance of each prey category. A marker in the upper right represents a dominant prey, while in the lower left indicates low importance of the food source (Amundsen et al. 1996).

The feeding niche breadth of benthivorous round goby, flounder, eelpout and vimba bream was calculated according Levins (1968):

$$B = \frac{1}{\sum p_{i2}} \qquad (13)$$

where: B = feeding niche breadth; p_i = the weight proportion of fish diet comprised of prey category *i*. The index values vary between 1 and *n*, with *n* corresponding to the number of prey categories consumed. Low values indicate specialized feeding strategy (diet dominated by few preys), while higher values indicate generalized feeding strategy (diet comprised of diverse food sources).

Trophic level of the long-tailed duck before and after the round goby expansion was estimated according to Christensen and Pauly (1992):

$$TL_j = 1 + \sum_{i=1}^{n} DC_{ji} \cdot TL_i \qquad (14)$$

where: j = predator of prey i; DC_{ji} = fraction of prey i in the diet of predator j and TL_i = trophic level of prey i.

Trophic level values of recognized invertebrate and fish prey species in the ration of the long-tailed duck were obtained from Razinkovas-Baziukas et al. (2017) and the references therein, while trophic level of unidentified fish prey was assumed as the average 3.3 trophic level value of all recognized fish species.

3.6.3. Statistical analysis methods

Permutational one- and two-factorial ANOVAs (PERMANOVAs) (Anderson 2001) with a random subset of 999 permutations were used to test the effects of sampling years on fish community abundance structure in the coastal stony and sandy biotopes, season effect on the diet of vimba bream and flounder, and the season and biotope type influence on the diet of differently sized round gobies. Prior to the statistical analyses, the data were standardized and square root-transformed to reduce the effects of outliers. Similarity matrices were conducted using the Bray-Curtis similarity coefficient. Non-metric multi-dimensional scaling (nMDS) analysis, based on the Bray-Curtis similarity coefficient was employed to demonstrate the differences in fish community abundance composition and magnitude of the round goby expansion impact on its structure in the stony and sandy biotope types. The analysis of similarity (SIMPER) was employed to determine the contribution of different preys in the diet of the round goby and flounder. The principal component analysis (PCA) was applied to test the diet composition data of the analyzed predatory fish species in both studied habitat types. Multivariate analyses were performed using PRIMER v. 6 software (Clarke and Gorley 2006).

Statistical comparisons between 2 or more groups were performed by using *t*-test, one-way ANOVA, two-way ANOVA and MANOVA for multivariate dependent variables. Before the analysis, the data was tested for normality using Kolmogorov-Smirnov test. Levene's test was used to evaluate homogeneity of variances. In cases where data distribution was not normal or variances differed significantly, square root or logarithmic transformations were applied. Non-parametric Mann-Whitney *U*, Median and Krusal-Wallis tests were used if variances among the studied groups were significantly different. Post-hoc Tukey's Honestly Significant Difference (HSD) (following ANOVA) and Dunn's (following Kruskal-Wallis) tests were employed to find significantly different means. The significance level for all used tests was considered as $p < 0.05$. The statistical analyses were performed using R 3.4.1., SPSS 7.0 and PRIMER v. 6 software.

3.7 ECOPATH modelling

3.7.1 The modelling approach, model analyses and indices

The static trophic network model of the Lithuanian Baltic Sea coastal waters was built using ECOPATH software version 6.4 (Christensen and Pauly 1992). ECOPATH model is based on mass-balance principles, represented by several master equations. The production of each group (i) is described by the mass-balance equation:

$$P_i = Y_i + B_i M2_i + E_i + MO_i + BA_i \tag{15}$$

where: P_i = production rate of the group i; Y_i = sum of fishery catches for the group i; B_iM2_i = predated biomass; E_i = net migration (emigration-immigration); $M0_i$ = other mortality; BA_i = biomass accumulation of the group i.

Term “other mortality” describes all cases of natural mortality (e.g. due to the lack of food, parasites, diseases or old age) and excludes predation induced mortality ($M2_i$). $M0_i$ is presented by the equation:

$$MO_i = P_i\,(1 - EE_i) \tag{16}$$

where: P_i = production rate of the group i; (EE_i) = ecotrophic efficiency - fraction of the production of the group i, that is accounted in the model through biomass accumulation or predation, fishing and other exports.

Another important equation describes what fraction of group i production is used by predator j:

$$B_i M2_i = \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \tag{17}$$

where: j = summation of all predator groups, consuming the group i; DC_{ij} = fraction of predators (j) diet, contributed by prey (i); B_j = biomass of group j and Q/B = consumption/biomass ratio of group j.

Equation, calculating P_i can be re-expressed as:

$$B \cdot \left(\frac{Q}{B}\right)_i = \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + E_i + BA_j + B_i \left(\frac{P}{B}\right)_j \cdot (1 - EE_i) \qquad (18)$$

where: $(P/B)_i$ = production of group i per biomass unit (equivalent to the total mortality (Z)); $(Q/B)_i$ = consumption of group i per unit of biomass.

The model is considered as balanced when all previous equations are solved. The model results are expressed in g m^{-2} wet weight of organic matter for biomass and g m^{-2} year^{-1} for flows. All biomasses and rates were averaged over a one year period.

The ecosystem structure and functioning analysis was based on ecological indices and flow indicators. The trophic level (TL) of each food web compartment was expressed according to Christensen and Pauly (1992) (see equation 14).

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

$$TST = \sum_{i=1,j=1}^{n} T_{ij} \qquad (19)$$

where: T_{ij} = flow between any two compartments, including respiration and export flows.

The evaluation of mixed trophic impacts revealed the direct or indirect impact of biomass changes in one functional group on all other compartments in the system, following the assumption that their diet composition remains the same. The total mixed trophic impact, revealing an impact of each functional group on all other groups was calculated by summing all impacts weighed by the inverse biomass of the impacted groups (Libralato et al. 2004).

The keystoneness index showed the overall effect of each functional group within a food web; the relatively important food web compartments had keystoneness values greater or close to 0, while the index values of compartments with negligible overall effect were considerably lower (Libralato et al. 2006).

3.7.2 Model construction and updates

Two ECOPATH model setups of the Lithuanian Baltic Sea coastal ecosystem were built from the periods before (2000-2010) and after (2011-2015) the round goby expansion on the basis of Razinkovas-Baziukas et al. (2017) model. For the construction of both models, the entire Lithuanian coastal zone up to 20 m depth was considered as a single ecosystem. The spatial habitat heterogeneity was addressed by defining proportion of areas, covered by the sandy (80%) and mixed (20%) seabed; in further calculations, 5% of the mixed bottom area was considered as the stony biotope. The model from 2000-2010 incorporated 41 functional groups, including 28 fish groups, 3 bird groups, 6 invertebrate groups, 2 plankton groups, 1 primary producer group and detritus (Razinkovas-Baziukas et al. 2017) and did not include the round goby in the compartment list. The model from 2011-2015, representing the round goby expansion and adjustment phases, was expanded to 47 compartments by adding 6 fish groups: 2 groups of the round goby, cod and shorthorn sculpin (Annex 1). Different life stages of most fish species were treated as separate compartments because of their presumably different feeding niches and positions in the food web (Razinkovas-Baziukas et al. 2017; Annex 1).

Most of the 2011-2015 model input data were obtained from the 2000-2010 model (Razinkovas-Baziukas et al. 2017), although following changes in the input data of certain compartments biomass, diet matrix and fisheries catch statistics were made:

1. The biomass data of the adult Baltic herring, smelt, ruffe, eelpout, flounder, bream, vimba bream, turbot and both functional groups of the round goby, pike-perch, cod and shorthorn sculpin were collected during the gill net sampling in both studied biotopes and recalculated for the whole coastal zone by taking into account the habitat heterogeneity; the biomass values of wintering diving ducks and piscivorous birds were derived from the counts of wintering birds, unpublished data of the Lithuanian Ornithological society (Annex 1);
2. The diet composition of the adult eelpout, vimba bream, perch, turbot and both functional groups of the round goby, flounder, cod and shorthorn sculpin were determined in the course of the present study. The dietary data of both pike-perch groups were taken from Narvilas (2013), wintering diving ducks and piscivorous birds - from Morkūnė et al. (2016, 2018) and Skabeikis et al. (2019), whereas the diet data of the great cormorant were obtained from Oesterwind et al. (2017) (Annex 1);
3. Fisheries catch statistics for the 2011-2015 period was derived from the Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania.

P/B and Q/B values of the round goby, cod and shorthorn sculpin, added to the 2011-2015 model were obtained from Langseth et al. (2012), Harvey et al. (2003) and

Zaika (1983), respectively. P/B and Q/B values for other fish, invertebrates and waterbirds remained the same as in the original model designed by Razinkovas-Baziukas et al. (2017).

The parameterization procedure was manual and reiterative, using the estimated ecotrophic efficiency (EE) as the main criteria for the model validation (the estimates were considered realistic at $EE < 1$). Instead of calibrating fish diet matrix and biomasses, the adjustments in migration rates were used to balance the EE of migratory species as suggested by Razinkovas-Baziukas et al. (2017).

4

Results

4.1 Round goby invasion pattern, abundance and contribution in the fish communities from the coastal stony and sandy biotopes

According to the monitoring data, the abundance of the round goby was low during the nine years period after the first observation. A rapid increase occurred during 2011-2012; thereafter the population abundance fluctuated, but remained relatively high (Fig. 6). Based on the general description of the invasion stages (Reise et al. 2006; Olenin et al. 2017), four stages of the round goby invasion were distinguished: arrival (approximately 2002), establishment (2002-2010, mean abundance 10 ± 11 CPUE), expansion (2011-2012, 234 ± 152 CPUE) and adjustment (2013-2016, 140 ± 141 CPUE) (Fig. 6). The increasing round goby population expanded and occupied different biotope types in other localities of the Lithuanian Baltic Sea coastal waters (Fig. 7).

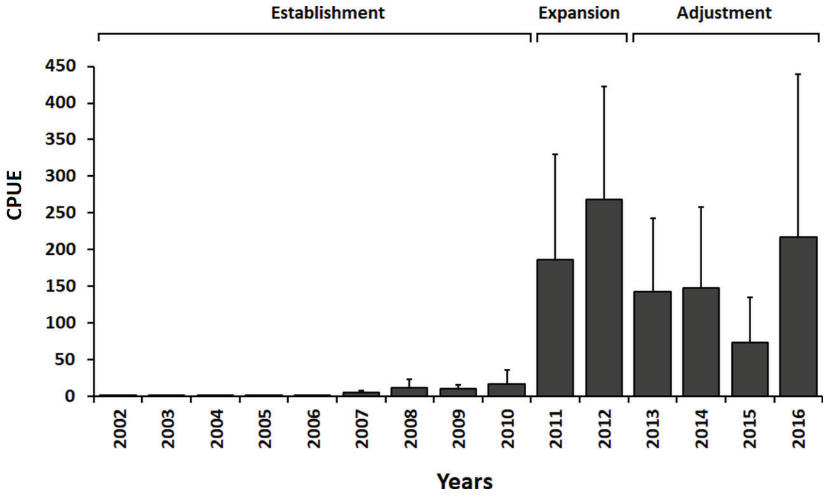

Figure 6. Long-term (2002-2016) abundance dynamics of the round goby (CPUE) in the Lithuanian Baltic Sea coastal waters of Smiltynė (site of the first observation).

6 pav. Ilgalaikė (2002–2016 m.) juodažiočio grundalo gausumo dinamika (CPUE, kasmetinis vidurkis ± SN) Baltijos jūros Lietuvos priekrantėje ties Smiltyne (pirmojo rūšies pastebėjimo vieta).

The annual mean abundance and biomass of the round goby were significantly higher in the stony habitat compared to the sandy biotope (1.36 ± 1.74 *vs.* 0.08 ± 0.05 ind. m^2 and 0.09 ± 0.12 *vs.* 0.005 ± 0.004 kg m^2; Mann-Whitney U; $p < 0.05$ for both cases) (Fig. 7). The abundance (Kruskal-Wallis; $H = 16.99$; $df = 2$; $p < 0.05$) and biomass (Kruskal-Wallis; $H = 16.98$; $df = 2$; $p < 0.05$) of the round goby in the coastal stony biotope changed significantly during different years of the study, while in the sandy bottom area these parameters remained stable throughout the time (ANOVA; abundance: $F = 0.48$; $df = 2$; $p = 0.63$ and biomass: $F = 2.28$; $df = 2$; $p = 0.12$; Fig. 7). The abundance and biomass of the round goby from the stony habitat increased significantly in 2016 compared to 2014 and 2015 (Dunn's test; $p < 0.05$ for both cases).

The stony bottom area was also characterized by the significantly higher abundance and biomass of total fish catches during 2014-2016 (Mann-Whitney U; $p < 0.05$ for both cases) (Annex 3). The fish communities from the coastal stony and sandy biotopes comprised 17 and 14 species, respectively (Annex 3). The nMDS plot revealed that the structure of the fish communities in the stony and sandy bottom areas was considerably different (Fig. 8). The community structure in the sandy biotope was monotonous during all three years of the study, whereas the round goby abundance increment in 2016 caused significant structural shifts of the fish community in the stony habitat (Fig. 8).

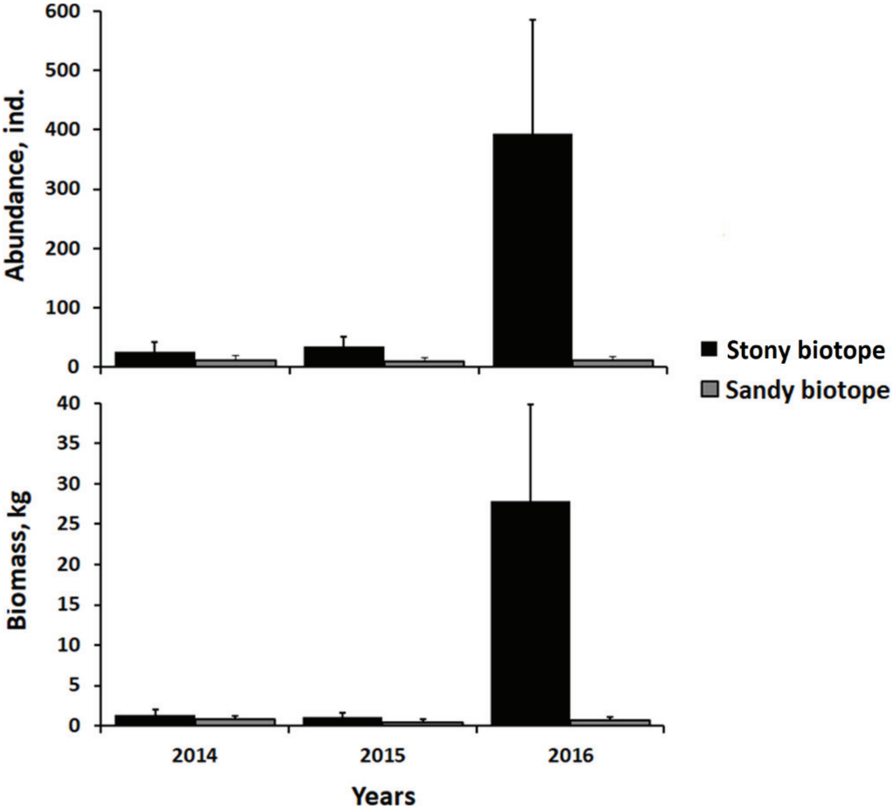

Figure 7. Abundance (annual mean ± SD, ind.) and biomass (annual mean ± SD, kg) dynamics (CPUE per set of multi mesh gill nets (360 m^2)) of the round goby in the coastal stony and sandy biotopes during 2014-2016.

7 pav. Juodažiočio grundalo metinio gausumo (vidurkis ± SN, ind.) ir biomasės (vidurkis ± SN, kg) dinamika (CPUE žiauninių tinklaičių komplekte (360 m^2)) priekrantės moreninio ir smėlėto dugno buveinėse 2014–2016 m.

PERMANOVA analysis showed, that the fish community structure in the coastal stony biotope varied during different years of the study, while the fish composition in the sandy habitat remained stable (Table 2). The results of nMDS analysis were supported by the pairwise post-hoc test, which also revealed the differences in the stony biotope fish community structure in 2016 (Table 2).

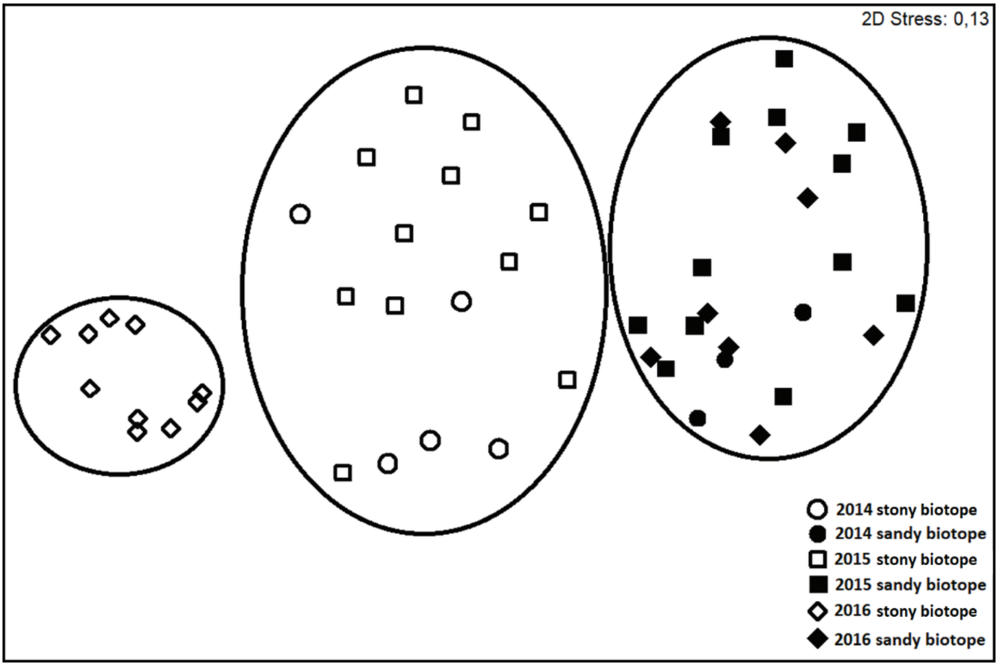

Figure 8. The nMDS plot for the Lithuanian Baltic Sea fish community abundance structure in the coastal stony and sandy biotopes during 2014-2016.

8 pav. nMDS grafikas, vaizduojantis Baltijos jūros priekrantės žuvų bendrijos gausumo sudėtį moreninio ir smėlėto dugno buveinėse 2014–2016 m.

During 2014-2015, the bulk of the fish community from the stony bottom area was represented by the the round goby (47% of total fish abundance), perch (13%), Baltic herring (11%) and flounder (9%), and became highly predominated by the round goby (89%) in 2016. Fish community from the sandy biotope was dominated by the flounder (42%), Baltic herring (24%) and round goby (12%) (Annex 4).

The number of fish species in each habitat type did not change over time. The abundance of most fish species from the stony biotope had marginal positive or negative fluctuations among 2014-2015 and 2016 periods (Mann-Whitney U; $p > 0.05$ for all cases) (Fig. 10; Annex 3). Comparing “low” *vs.* “high” round goby abundance years in the stony habitat, the significant abundance reduction of perch and roach was recorded (Mann-Whitney U; $p < 0.05$ for both cases), whereas abundance of cod and shorthorn sculpin increased (Mann-Whitney U; $p < 0.05$ for both cases). In contrast, the abundance of all fish species from the sandy bottom area was stable over time (Mann-Whitney U; $p > 0.05$ for all cases) (Fig. 10; Annex 3).

Table 2. **PERMANOVA output for (A) testing effects of sampling years (2014, 2015 and 2016) on fish community abundance structure in the coastal stony and sandy biotopes; and (B) Pairwise test of groups within the factor sampling years.**

2 lentelė. **PERMANOVOS rezultatai, gauti analizuojant (A) tyrimo metų (2014, 2015 ir 2016) poveikį žuvų bendrijos gausumo struktūrai priekrantės moreninio ir smėlėto dugno buveinėse; ir (B) grupių porinio testo rezultatai, gauti vertinant tyrimo metų faktorių.**

Size group	Source	df	SS	MS	Pseudo-F	p
A						
Stony biotope	Years	2	33496	16748	17.57	**0.001**
	Residual	22	20973	953.3		
	Total	24	54470			
Sandy biotope	Years	2	3672.3	1836.2	1.53	0.12
	Residual	20	24023	1201.1		
	Total	22	27695			
B						
Stony biotope	2014, 2015				23.92	0.77
	2014, 2016					**0.01**
	2015, 2016					**0.01**
Sandy biotope	2014, 2015				6.29	0.23
	2014, 2016					0.56
	2015, 2016					0.42

Shannon-Wiener biodiversity index and Rényi diversity profiles revealed, that the round goby abundance increment in 2016 substantially reduced fish biodiversity in the stony habitat, whereas fish biodiversity in the sandy biotope changed negligibly (Fig. 9; Table 3).

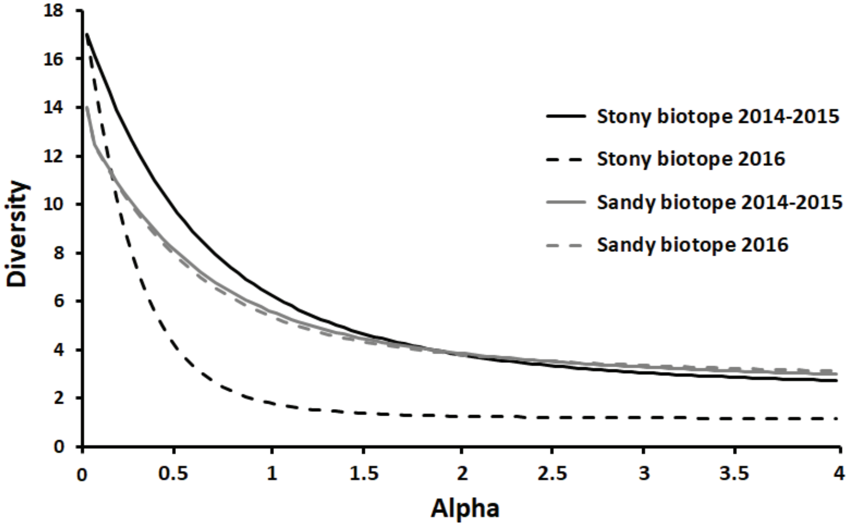

Figure 9. Rényi diversity profile (H_α) of fish communities in the coastal stony and sandy biotopes during 2014-2015 and 2016 periods.

9 pav. Priekrantės moreninio ir smėlėto dugno buveinių žuvų bendrijų Rényi įvairovės profiliai (H_α) 2014–2015 m. ir 2016 m. periodais.

***Table 3.* Species number and values of Shannon-Wiener (H’) biodiversity index of fish communities in the coastal stony and sandy biotopes during 2014-2015 and 2016 periods.**

***3 lentelė.* Moreninio ir smėlėto dugno buveinių žuvų bendrijų rūšių skaičius ir Šenono ir Vynerio (Shannon-Wiener) bioįvairovės indekso (H‘) vertės 2014–2015 m. ir 2016 m. periodų metu.**

Biotope type	Stony		Sandy	
Period	2014-2015	2016	2014-2015	2016
Species number	17	17	14	14
H’	1.76	0.57	1.70	1.69

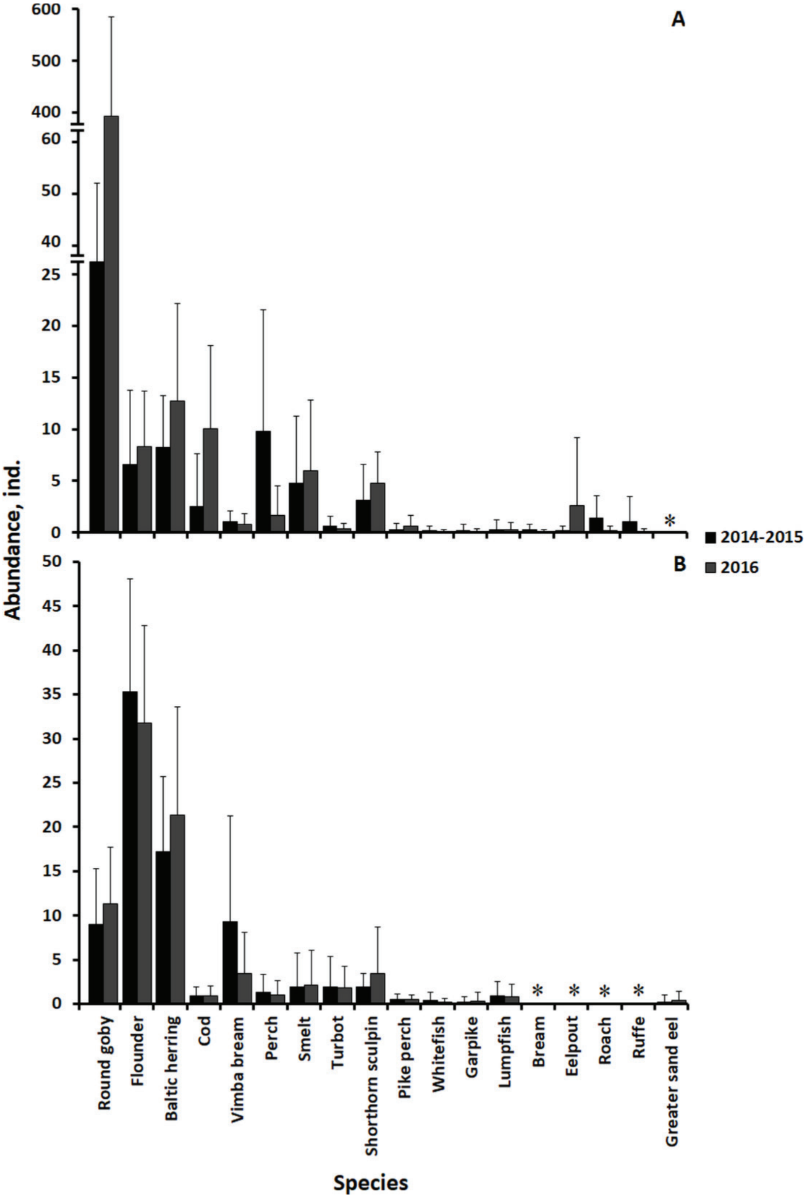

Figure 10. Abundance (mean ± SD, ind.) dynamics (CPUE per per set of multi mesh gill nets (360 m^2)) of all fish species captured in the coastal stony (A) and sandy (B) biotopes during 2014-2016. * - absence of the species.

10 pav. Visų žuvų rūšių, sugautų priekrantės moreninio (A) ir smėlėto (B) dugno buveinėse gausumo (vidurkis ± SN, ind.) kaita (CPUE žiauninių tinklaičių komplekte (360 m^2)) 2014–2016 m. * – rūšies nebuvimas.

4.2 Size and age structure, body condition and fecundity of the round goby

Round gobies inhabiting coastal stony and sandy biotopes had different length and weight distributions (Table 4).

Table 4. **Number of analyzed fish, total length (TL, range and mean ± SD, mm) and weight (W, range and mean ± SD, g) of the round goby in the coastal stony and sandy biotopes.**

4 lentelė. **Tirtų juodažiočių grundalų skaičius, absoliutinis kūno ilgis (TL, intervalas ir vidurkis ± SN, mm) ir svoris (W, intervalas ir vidurkis ± SN, g) priekrantės moreninio ir smėlėtoto dugno buveinėse.**

Biotope type	Sample size	TL, mm		W, g	
		Min - Max	Mean	Min - Max	Mean
Stony	374	81 - 211	138 ± 26	10.5 - 149.9	43.0 ± 26.2
Sandy	162	98 - 214	141 ± 24	12.4 - 185.3	48.7 ± 31.3

The age of analyzed round gobies varied from 2 to 6 years. At both sampling locations the round goby populations were dominated by 3+ and 4+ individuals, however the median age of specimens from the stony bottom area (4+) was significantly higher compared to the sandy biotope (3+) (Median test; $p < 0.05$) (Fig. 11).

The 5+ specimens in the stony habitat were relatively common (16% of the analyzed fish), while in the sandy bottom area only <1% of individuals were recorded within this age group. Very few round gobies (1%) from the stony biotope were classified as 6+, whereas the fish of this age were absent in the sandy habitat. The 5+ and 6+ specimens were excluded from further statistical analyses because of the absence or very low numbers of individuals from those year classes recorded in the sandy biotope (Fig. 11).

The total length and weight of the round goby differed significantly between the age groups and biotopes (two-way ANOVA; Table 5). The 2+ and 3+ round gobies were larger in the sandy habitat (HSD; $p < 0.05$ for both cases), whereas the total length of 4+ individuals did not differ among the stony and sandy biotope types (HSD; $p = 0.41$) (Fig. 12; Table 5). The total weight of round gobies from all tested age groups was significantly higher (HSD; $p < 0.05$ for all cases) in the sandy bottom area (Fig. 12; Table 5).

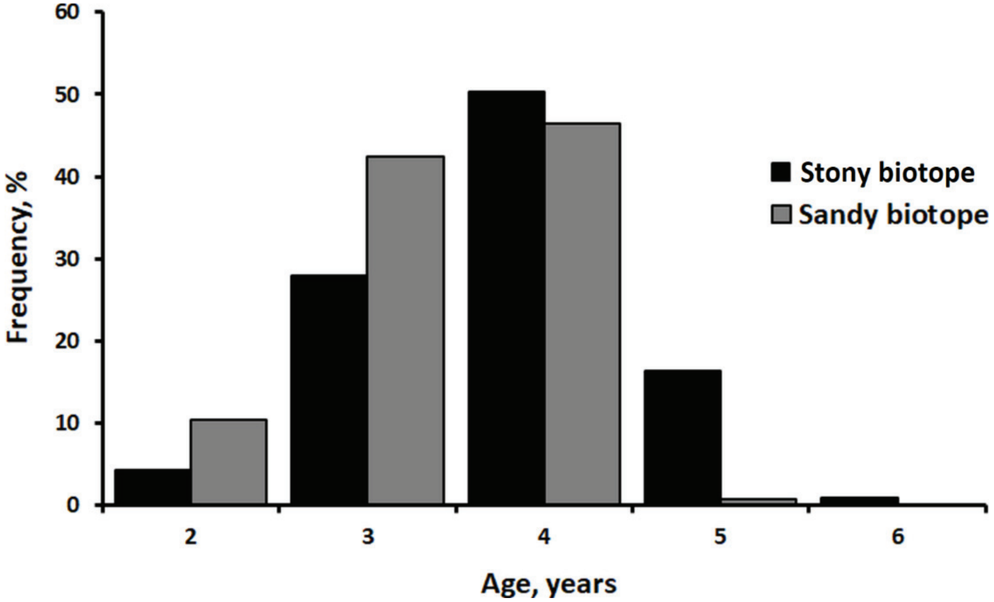

Figure 11. Age frequency distribution of the round goby in the coastal stony and sandy biotopes.

11 pav. Juodažiočio grundalo amžiaus grupių dažnio pasiskirstymas priekrantės moreninio ir smėlėto dugno buveinėse.

The habitat type and age had a significant effect on the values of the round goby body condition index (two-way ANOVA; Fig. 13; Table 5). Fish from the 3+ and 4+ age groups had better physiological condition in the sandy habitat (HSD; $p < 0.05$ for both cases), while the body condition values of 2+ round gobies did not differ among the studied biotopes (HSD; $p = 0.43$) (Fig. 13).

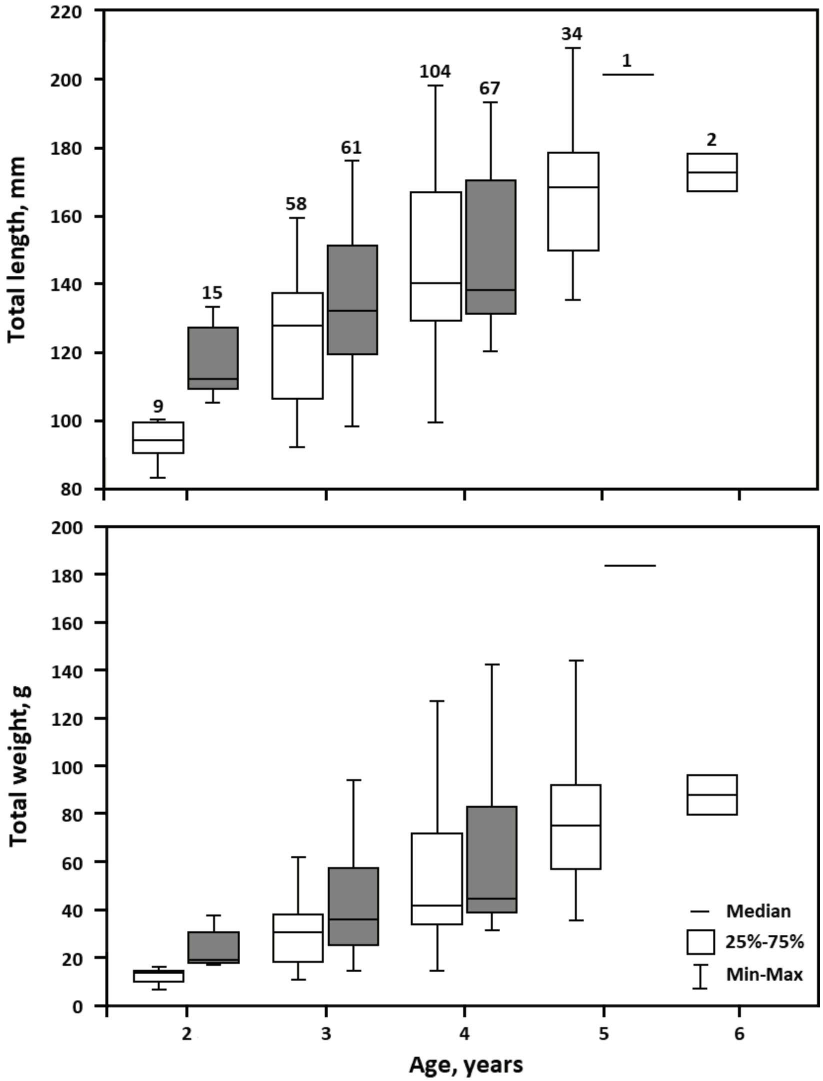

Figure 12. The total length and weight at age of the round goby in the coastal stony (open boxes) and sandy (filled boxes) biotopes. Numbers above the boxes indicate sample size.

12 pav. Absoliutinis juodažiočio grundalo kūno ilgis ir svoris amžiaus grupėse priekrantės moreninio (tuščiaviduriai stulpeliai) ir smėlėto (pilnaviduriai stulpeliai) dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį.

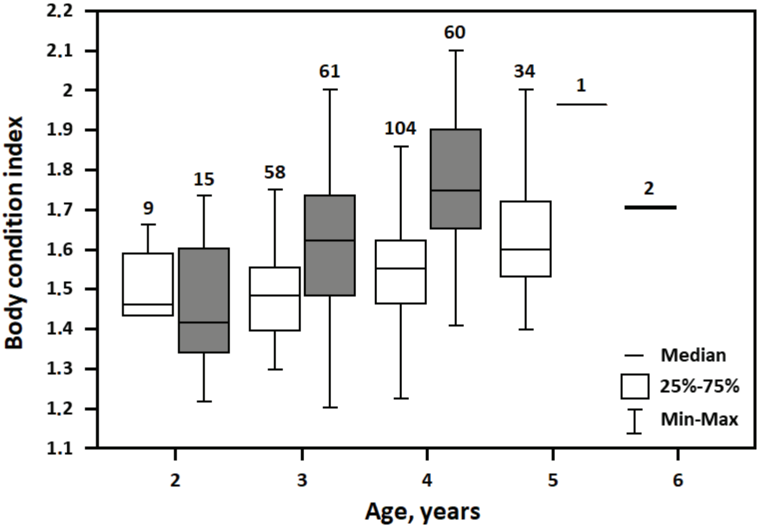

Figure 13. The body condition index at age of the round goby in the coastal stony (open boxes) and sandy (filled boxes) biotopes. Numbers above the boxes indicate sample size.

13 pav. Juodažiočio grundalo kūno būklės indekso vertės amžiaus grupėse priekrantės moreninio (tuščiaviduriai stulpeliai) ir smėlėto (pilnaviduriai stulpeliai) dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį.

***Table 5.* Two-way ANOVA for the round goby total length, total weight, body condition index and absolute fecundity at age in the coastal stony and sandy biotopes.**

***5 lentelė.* Dvifaktorinės ANOVOS rezultatai, gauti tiriant juodažiočio grundalo absoliutinį kūno ilgį, svorį, kūno būklę bei absoliutinį vislumą amžiaus grupėse priekrantės moreninio ir smėlėto dugno buveinėse.**

Source	SS	*df*	MS	F	p
Total length					
Age	2.77	2	1.38	63.22	<0.001
Biotope type	0.45	1	0.45	20.68	<0.001
Age × Biotope type	0.22	2	0.11	5.07	<0.05
Residual	6.74	308	0.02		
Total	9.67	313	0.03		
Total weight					
Age	5.46	2	2.73	48.65	<0.001
Biotope type	0.97	1	0.97	17.21	<0.001
Age × Biotope type	0.36	2	0.17	2.98	0.052
Residual	17.29	308	0.06		
Total	23.29	313	0.07		

Source	SS	*df*	MS	F	p
Body condition index					
Age	0.02	2	0.007	4.90	<0.05
Biotope type	0.11	1	0.11	76.32	<0.001
Age × Biotope type	0.003	2	0.001	0.96	0.38
Residual	0.45	301	0.002		
Total	0.70	306	0.002		
Absolute fecundity					
Age	4.30	2	2.15	49.83	<0.001
Biotope type	6.26	1	6.26	144.83	<0.001
Age × Biotope type	0.17	2	0.08	1.93	0.15
Residual	5.27	122	0.04		
Total	14.30	127	0.11		

The absolute fecundity of reproducing female round gobies varied from 106 to 5511 eggs. The fecundity was significantly affected by the age group and type of inhabited biotope (two-way ANOVA; Table 5). Females from each age group were more fecund in the sandy biotope (HSD; $p < 0.05$ for all cases) and the fecundity increased with increasing age at both habitat types (Fig. 14).

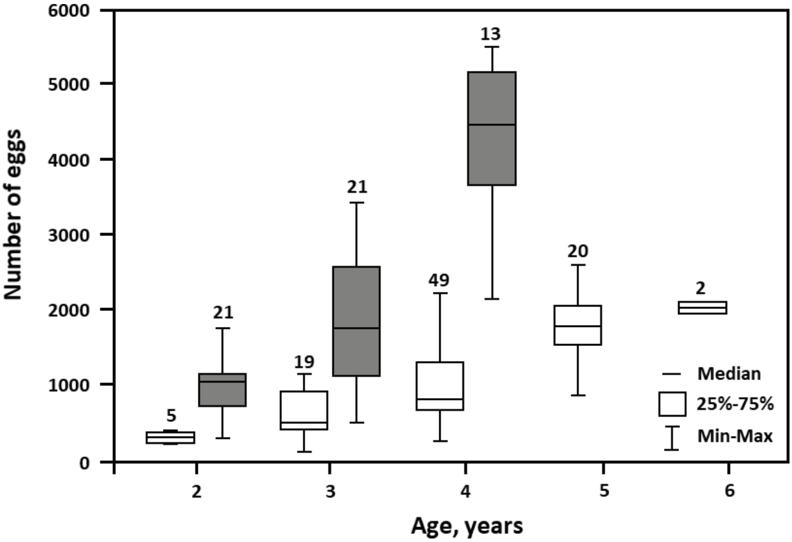

Figure 14. Absolute fecundity at age of female round gobies in the coastal stony (open boxes) and sandy (filled boxes) biotopes. Numbers above the boxes indicate sample size.

14 pav. Juodažiočio grundalo patelių absoliutinis vislumas amžiaus grupėse priekrantės moreninio (tuščiaviduriai stulpeliai) ir smėlėto (pilnaviduriai stulpeliai) dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį.

4.3 Feeding patterns of the round goby and its diet overlap with native benthophagous fish

4.3.1 Diet composition of the round goby

The diet composition of the round goby varied depending on the type of inhabited biotope, body size and time of the year (Fig. 15). In the stony biotope, the round goby consumed mainly blue mussels (<4 mm specimens), barnacles, *L. balthica* and fish prey during spring and autumn seasons and shifted their diet towards polychaetes in summer. Weight contribution of blue mussels and polychaetes in the ration of the round goby declined with increasing body size, as larger specimens preferred fish prey, infaunal mollusks and other feeding objects over small epibenthic bivalves. In summer season, epibenthic organisms, including barnacles and large (>10 mm) blue mussels were relatively important food sources only for the largest fish (Fig 15).

In the sandy habitat small round gobies (RG S) fed mainly on polychaetes and brown shrimps, whereas the diet of intermediately sized (RG M) and large (RG L) specimens was dominated by relatively equal portions of polychaetes and *M. arenaria* in spring. During summer, the diet of all round goby size groups was based on *M. arenaria* and polychaetes. In autumn, RG S preferred polychaetes, RG M - *M. arenaria* and RG L - brown shrimps (Fig 15).

PERMANOVA analysis indicated that small and intermediately sized round gobies had variable diet, which changed depending on the season, biotope type and interaction of presented factors (Table 6). The season effect on the diet of large round goby was insignificant (Table 6). The pairwise post-hoc test demonstrated that the diet composition of RG S changed significantly from summer to autumn, whereas RG M diet differed significantly between the spring and summer seasons (Table 6).

The Costello plots showed different round goby feeding strategies, related to the seasonal changes of available food sources in the stony and sandy bottom areas. Round gobies from the stony habitat had a specialized feeding strategy (indicated by the presence of data points in the upper part of the Costello plots), with a diet based on 4 major prey types: blue mussels, barnacles, amphipods and polychaetes, which were consumed in different proportions across the seasons (Fig. 16). Contrary to the stony biotope, round gobies from the sandy habitat utilized various food resource types simultaneously with the prey-specific abundance entirely below 25% throughout the year, which indicates a generalistic feeding strategy (Fig. 16).

Table 6. **PERMANOVA output for (A) testing effects of season (spring, summer and autumn), biotope type (stony and sandy) and season × biotope type on the round goby diet composition within each size group; and (B) Pairwise test of groups within the factor season.**

6 lentelė. **PERMANOVOS rezultatai (A), gauti tiriant sezono (pavasaris, vasara, ruduo), buveinės tipo (moreninis ir smėlėtas) bei sezono ir buveinės tipo sąveikos poveikį juodažiočio grundalo mitybos sudėčiai; (B) grupių porinio testo rezultatai, gauti vertinant tyrimo metų faktorių.**

Size group	Source	*df*	SS	MS	Pseudo-F	p
A						
RG S	Season	2	22772	11386	3.70	<0.01
	Biotope type	1	34148	34148	11.10	<0.01
	Season × Biotope type	2	18804	9401.9	3.06	<0.05
	Residual	124	3.82	3076.7		
	Total	129	4.86			
RG M	Season	2	12826	6413.1	1.98	<0.05
	Biotope type	1	63179	63179	19.56	<0.01
	Season × Biotope type	2	18180	9090.1	2.81	<0.05
	Residual	200	6.46	3230.1		
	Total	205	8.12			
RG L	Season	2	15869	7934.5	2.30	0.08
	Biotope type	1	68221	68221	19.80	<0.01
	Season × Biotope type	2	15675	7837.4	2.27	<0.05
	Residual	180	6.20	3446.2		
	Total	185	7.64			
B						
RG S	Spring, summer				2.24	0.11
	Spring, autumn					0.89
	Summer, autumn					**0.01**
RG M	Spring, summer				5.68	**0.03**
	Spring, autumn					0.79
	Summer, autumn					0.07
RG L	Spring, summer				0.98	0.23
	Spring, autumn					0.47
	Summer, autumn					0.43

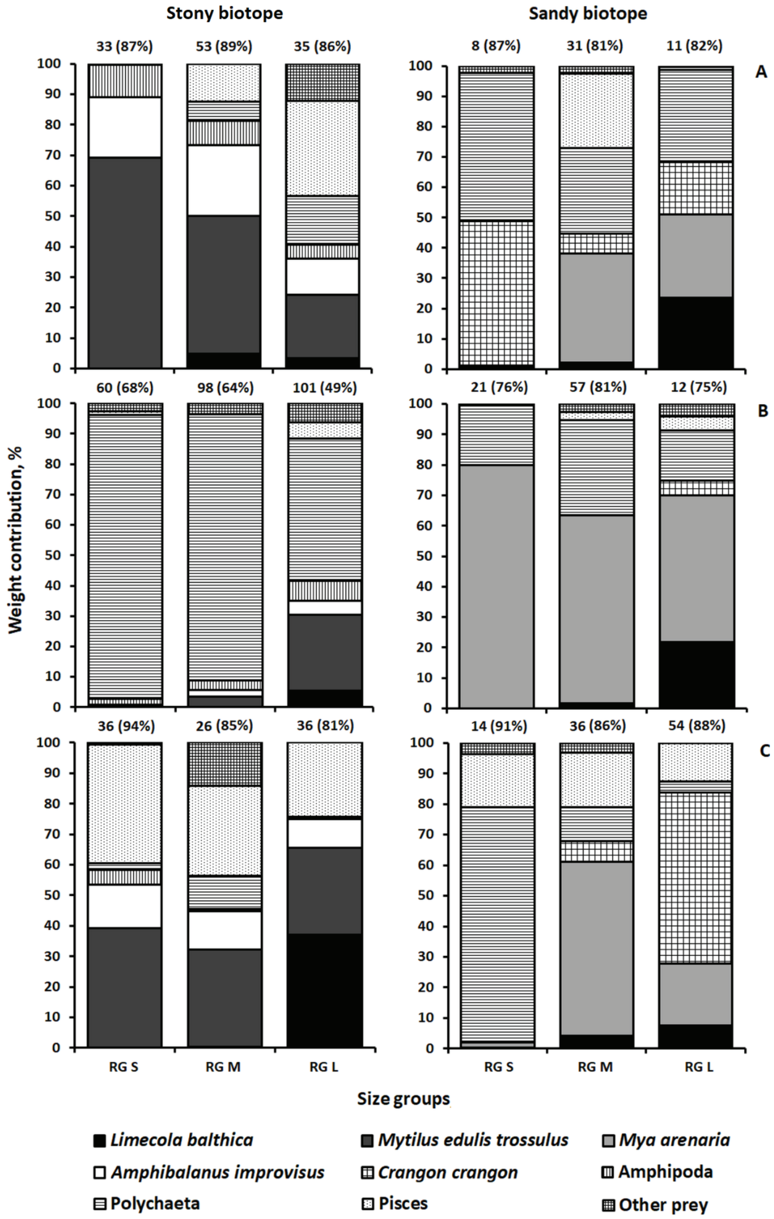

Figure 15. Mass percentage diet composition of the round goby during spring (A), summer (B) and autumn (C) 2014 - 2016. Numbers above the columns indicate sample size and feeding efficiency (percentage of full guts).

15 pav. Juodažiočio grundalo procentinės masės dalies mityba 2014–2016 m. pavasarį (A), vasarą (B) ir rudenį (C) priekrantės moreninio ir smėlėto dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį ir mitybos efektyvumą (procentinę pilnų virškinimo traktų išraišką).

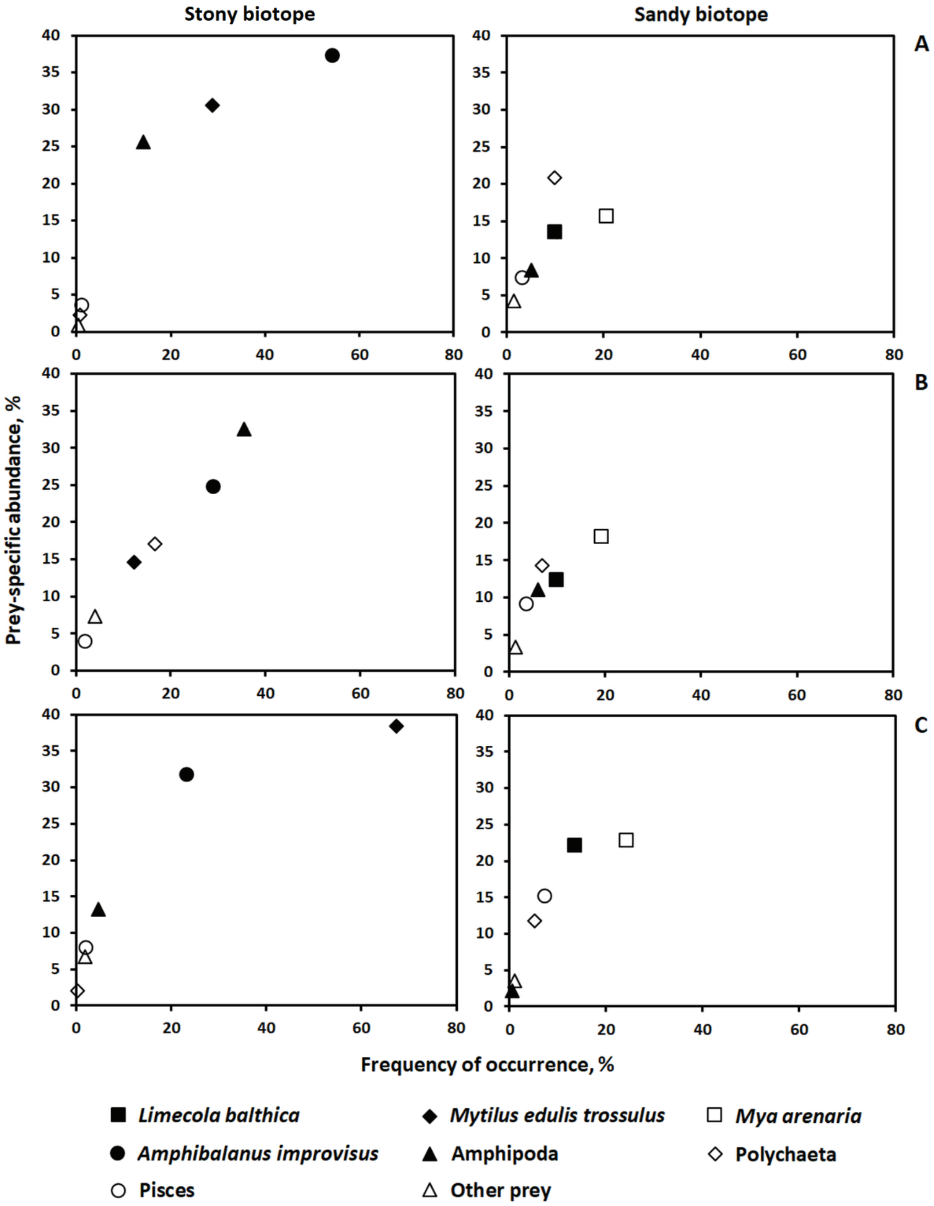

Figure 16. Electivity plot, displaying seasonal dietary preferences of the round goby (all size groups combined) from the stony and sandy biotope types during spring (A), summer (B) and autumn (C) 2014-2016.

16 pav. Grafikas, vaizduojantis sezoninį juodažiočio grundalo (visos dydžio grupės sujungtos) mitybos pasirinkimą 2014–2016 m. pavasarį (A), vasarą (B) ir rudenį (C) priekrantės moreninio ir smėlėto dugno buveinėse.

4.3.2 Feeding niche overlap between the round goby and native benthophagous fish

The values of feeding efficiency, stomach fullness and body condition indexes of analyzed benthivorous fish varied depending on the species and type of inhabited biotope. The round goby and flounder had a slightly higher stomach fullness index in the stony bottom area (*t*-test; $p > 0.05$ for both cases), however the body condition of both species was significantly better in the sandy biotope (*t*-test; $p < 0.05$ for both cases). The eelpout from the stony habitat had the relatively high feeding activity and body condition, while the vimba bream from the sandy biotope had the lowest values of the feeding efficiency, stomach fullness index and body condition (Table 7).

Table 7. **Overall feeding efficiency (FE, % (percentage of full guts)), stomach fullness index (SFI, mean ± SD) and Fulton's body condition index (K, mean ± SD) of the round goby (all size groups combined), flounder (all size groups combined), eelpout and vimba bream in the coastal stony and sandy biotopes during spring-autumn 2014-2016.**

7 lentelė. **Bendras juodažiočio grundalo (vìsos dydžio grupės sujungtos), upinės plekšnės (vìsos dydžio grupės sujungtos), gyvavedės vėgėlės ir žiobrio mitybos efektyvumas (FE, %), skrandžio užpildymo indeksas (SFI) (vidurkis ± SN) ir Fultono kūno būklės indeksas (K, vidurkis ± SN) priekrantės moreninio ir smėlėto dugno buveinėse 2014–2016 m. pavasario–rudens sezonais.**

Species	Stony biotope			Sandy biotope		
	FE, %	SFI	K	FE, %	SFI	K
Round goby	73	1.3 ± 0.2	1.2 ± 1.0	83	1.0 ± 0.8	1.5 ± 0.2
Flounder	79	3.5 ± 1.6	1.1 ± 0.3	63	3.3 ± 2.5	1.4 ± 0.2
Eelpout	96	2.7 ± 1.4	1.5 ± 0.1	-	-	-
Vimba bream	-	-	-	56	0.9 ± 0.7	1.0 ± 0.1

In the stony habitat, intermediately sized (FL M) and large (FL L) flounders preferred bivalve mollusks *L. balthica*, *M. arenaria* and polychaetes throughout the year (season effect for FL M: PERMANOVA; *df* = 2; Pseudo F = 2.13; p = 0.10) and FL L (PERMANOVA; *df* = 2; Pseudo F = 0.28; p = 0.19). The diet of small flounders (FL S) from the sandy biotope comprised mainly *M. arenaria*, polychaetes and *C. lamarcki* during spring, summer and autumn, whereas FL M and FL L consumed mainly *M. arenaria*, *L. balthica*, polychaetes and *C. crangon* (Fig. 17). The ration of FL S (PERMANOVA; *df* = 2; Pseudo F = 0.63; p = 0.18), FL M (PERMANOVA; *df* = 2; Pseudo F = 2.30; p = 0.10) and FL L (PERMANOVA; *df* = 2; Pseudo F = 1.69; p = 0.12) also did not differ across the studied seasons. The diet of the vimba bream in the sandy biotope, dominated by *M. arenaria*, brown shrimps, polychaetes and green macroalgae (*Cladophora* sp.) did not vary significantly between the summer and autumn seasons (PERMANOVA; *df* = 1; Pseudo F = 0.86; p = 0.51). The ration of the eelpout in the stony habitat was based on amphipods, polychaetes and blue mussels (Fig. 17).

Small and intermediately sized round gobies had wider feeding niches in the sandy biotope, while feeding niche breadth of the largest specimens was higher in the stony habitat. Flounder from all size groups had wider feeding niches in the stony biotope. The feeding niche breadth of the round goby increased with increasing body size, while the feeding niche breadth of the flounder declined with increasing total length in both biotope types (Table 8). The feeding niche breadth of the native vimba bream was the highest among the studied benthivorous fish, whereas the feeding niche of the eelpout was relatively narrow (Table 8).

Table 8. **Feeding niche breadth of the round goby (RG), flounder (FL), eelpout (EELP) and vimba bream (VIM) in the coastal stony and sandy biotopes during spring-autumn 2014-2016. Size groups are denoted in letters S – small, M – intermediately sized, L – large.**

8 lentelė. **Juodažiočio grundalo (RG), upinės plekšnės (FL), gyvavedės vėgėlės (EELP) ir žiobrio (VIM) mitybinės nišos plotis priekrantės moreninio ir smėlėto dugno buveinėse 2014–2016 m. pavasario-rudens sezonais. Dydžių grupės pažymėtos raidėmis: S – mažas, M – vidutinio dydžio, L – didelis.**

	Species/Size group							
Biotope type	**RG S**	**RG M**	**RG L**	**FL S**	**FL M**	**FL L**	**EELP**	**VIM**
Stony	2.0	3.0	4.7	-	3.4	2.4	2.5	-
Sandy	3.6	3.8	4.2	3.1	2.5	1.9	-	4.8

The feeding niche overlap was not significant (Schoener's index < 0.6) between the round goby and native benthivorous flounder and eelpout in the coastal stony habitat (Table 9).

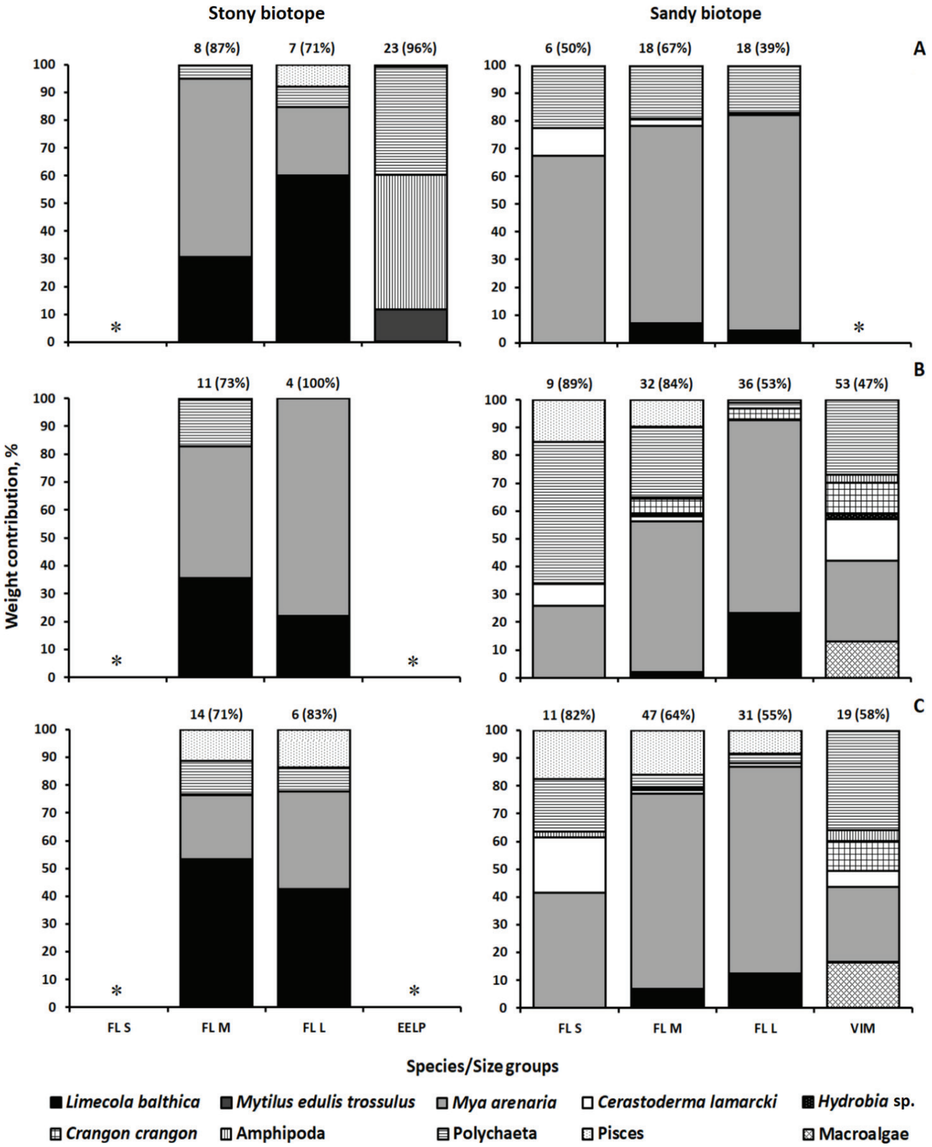

Figure 17. Mass percentage diet composition of the flounder, eelpout and vimba bream in the coastal stony and sandy biotopes during spring (A), summer (B) and autumn (C) 2014-2016. Numbers above the columns indicate sample size and feeding efficiency (percentage of full guts). * - no data.

17 pav. Upinės plekšnės, gyvavedės vėgėlės ir žiobrio procentinės masės dalies mityba 2014–2016 m. pavasarį (A), vasarą (B) ir rudenį (C) priekrantės moreninio ir smėlėto dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį ir mitybos efektyvumą (procentinę pilnų virškinimo traktų išraišką). * – duomenų nebuvimas.

Table 9. **Values of the feeding niche overlap (Schoener's index) between the round goby (RG), flounder (FL), eelpout (EELP) and vimba bream (VIM) in the coastal stony and sandy biotopes during spring, summer and autumn 2014-2016. Size groups are denoted in letters S - small, M intermediately sized, L - large. Cells fonted in grey color mark have significant feeding niche overlap.**

9 lentėlė. **Mitybos nišų (Schoner'io indeksas) persidengimo vertės tarp juodažiočio grundalo (RG), upinės plekšnės (FL), gyvavedės vėgėlės (EELP) ir žiobrio (VIM) priekrantės moreninio ir smėlėto dugno buveinėse 2014–2016 m. pavasarį, vasarą ir rudenį. Dydžių grupės pažymėtos raidėmis: S – mažas, M – vidutinio dydžio, L – didelis. Pilka spalva pažymėti langeliai nurodo reikšmingą mitybinių nišų persidengimą.**

	Stony biotope						Sandy biotope					
Spring												
	RG S	RG M	RG L	FL S	FL M	FL L	RG S	RG M	RG L	FL S	FL M	FL L
RG S												
RG M	**0.73**						0.38					
RG L	**0.63**	**0.88**					0.49	**0.66**				
FL S	-	-	-				0.24	**0.61**	0.50			
FL M	<0.10	<0.10	<0.10	-			0.21	0.59	0.53	**0.89**		
FL L	<0.10	<0.10	<0.10	-	**0.61**		0.18	0.55	0.49	**0.84**	**0.93**	
EELP/VIM	0.22	0.20	0.26	-	<0.10	<0.10	-	-	-	-	-	-
Summer												
RG S												
RG M	**0.96**						**0.81**					
RG L	0.53	**0.60**					**0.65**	**0.72**				
FL S	-	-	-				0.45	**0.62**	0.49			
FL M	0.17	0.17	0.23	-			**0.74**	**0.86**	**0.78**	**0.63**		
FL L	<0.10	<0.10	<0.10	-	**0.69**		**0.72**	**0.67**	**0.77**	0.29	**0.64**	
EELP/VIM	-	-	-	-	-	-	0.55	0.58	0.59	**0.67**	**0.70**	0.42
Autumn												
RG S												
RG M	**0.77**						0.34					
RG L	**0.63**	**0.63**					0.18	0.47				
FL S	-	-	-				0.41	**0.73**	0.36			
FL M	0.14	0.23	0.49	-			0.24	**0.84**	0.44	**0.63**		
FL L	0.16	0.23	0.51	-	**0.85**		0.15	**0.74**	0.40	0.55	**0.90**	
EELP/VIM	-	-	-	-	-	-	0.49	0.55	0.43	**0.62**	0.42	0.40

Contrary to the stony bottom area, a significant interspecific food competition (Schoener's index > 0.6) between differently sized flounders and round gobies from the coastal sandy habitat was detected during all studied seasons (Table 9). The highest overlap was estimated between the intermediately sized and large individuals of both species during the summer season. No significant feeding niche overlap between the native vimba bream and invasive round goby was found (Table 9).

SIMPER analysis revealed that the similarity in the diet of different round goby and flounder size groups during the summer season was determined by the high contribution of polychaetes and infaunal bivalve mollusks *M. arenaria* and *L. balthica* in their diet (Table 10). This result shows that the highest feeding niche overlap of differently sized round gobies and flounders detected in summer season (Table 9), was caused by the preference of the mentioned preys.

Table 10. **Contribution (%) of the main feeding objects to the diet similarity between the round goby (RG) and flounder (FL) during summer 2015-2016. Cells fonted in grey color mark preys contributing >10% to the diet similarity.**

10 lentelė. **Pagrindinių mitybos objektų reikšmė (%) skirtingo dydžio juodažiočių grundalų (RG) ir upinių plekšnių (FL) raciono sudėties panašumui 2015 ir 2016 m. vasaros sezonais. Pilka spalva pažymėti langeliai nurodo mitybos objektus, kurių reikšmė dietos panašumui buvo >10 %.**

Feeding objects	**Species/Size groups**					
	RG S	**RG M**	**RG L**	**FL S**	**FL M**	**FL L**
Limecola balthica			**40**			**37**
Mya arenaria	**94**	**58**	**36**	**51**	**66**	**56**
Cerastoderma lamarcki		6			5	
Polychaeta		**27**	**12**	**42**	**23**	
Pisces			5			
Other preys	6	9	7	7	6	7

4.3.3 The isotopic niches overlap between the round goby and flounder in the sandy biotope

The standard ellipse areas (SEAs) of small, intermediately sized and large round gobies overlapped in all three stable isotope spaces (Fig. 18), and the highest level of the overlap (0.65) was estimated for the RG S and RG M in $\boldsymbol{\delta}^{34}$S & δ^{15}N space (Table 11). There was a remarkable divergence between the SEAs of differently sized flounders. The differentiation of the flounder isotopic niches was based on higher δ^{15}N values found in the intermediately sized and large specimens (Fig. 20). FL M and FL L as well as FL S and FL M had considerably overlapping isotopic niches in all isotopic biplots, while SEAs of FL S and FL L overlapped in δ^{13}C & $\boldsymbol{\delta}^{34}$S and $\boldsymbol{\delta}^{34}$S & δ^{15}N spaces (Table 11).

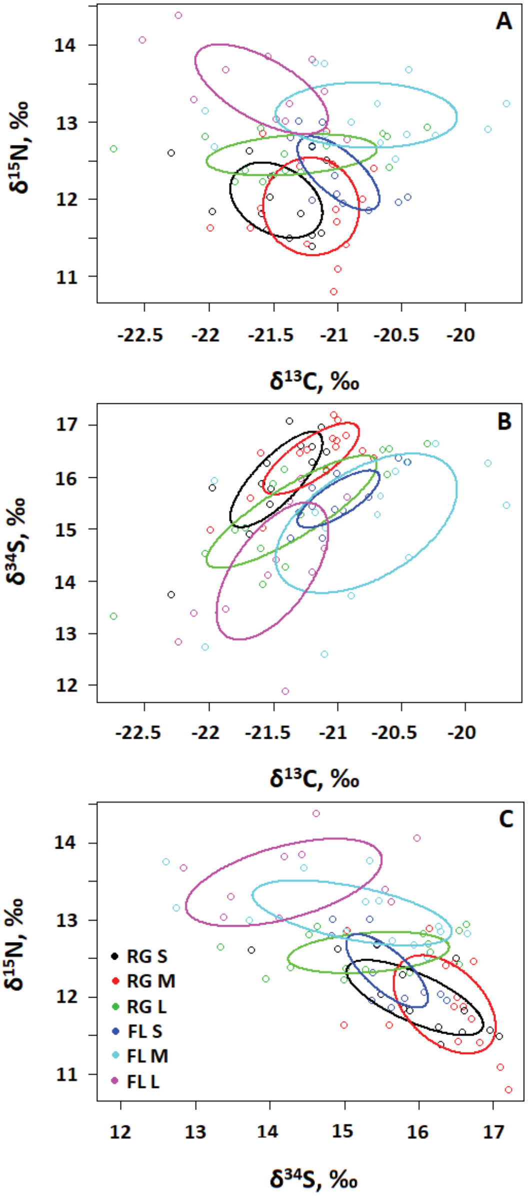

Figure 18. Stable isotope biplots with the standard ellipse areas (SEAs), indicating the isotopic niche width of differently sized round gobies (RG) and flounders (FL) in $\delta^{13}C$ & $\delta^{15}N$ (A), $\delta^{13}C$ & $\boldsymbol{\delta}^{34}S$ (B) and $\boldsymbol{\delta}^{34}S$ & $\delta^{15}N$ (C) spaces.

18 pav. Stabiliųjų izotopų grafikai su standartinių elipsių plotais, vaizduojantys skirtingo dydžio juodažiočių grundalų (RG) ir upinių plekšnių (FL) izotopinių nišų plotį $\delta^{13}C$ & $\delta^{15}N$ (A), $\delta^{13}C$ & $\delta^{34}S$ (B) ir $\delta^{34}S$ & $\delta^{15}N$ (C) aplinkose.

SEAs of RG L, FL S and FL M overlapped in all three stable isotope spaces. Overlap between RG M and FL S was detected in δ^{13}C & δ^{15}N and **δ^{34}**S & δ^{15}N environments, while niches of FL S and RG S as well as FL L and RG L overlapped in **δ^{34}**S & δ^{15}N and δ^{13}C & **δ^{34}**S isotopic spaces, respectively (Table 11). It could be concluded that RG S and RG M had minor probability of dietary overlap with FL S, whereas RG L potentially have more severe feeding niche overlap with FL S and FL M. For FL L, occupying considerably higher trophic position (Fig. 20), the dietary overlap with all size groups of the round goby is minor (Table 11).

Table 11. **Values of the standard ellipse areas (SEAs) overlap between differently sized round gobies (RG) and flounders (FL) in δ^{13}C & δ^{15}N, δ^{13}C & δ^{34}S and δ^{34}S & δ^{15}N stable isotope spaces. Cells fonted with dark, lighter and the lightest grey color mark SEAs overlap in three, two and one isotopic spaces, respectively; no shading indicates no SEAs overlap.**

11 lentelė. **Standartinių elipsių plotų persidengimo tarp skirtingo dydžio juodažiočių grundalų (RG) ir upinių plekšnių (FL) reikšmės δ^{13}C & δ^{15}N, δ^{13}C & δ^{34}S ir δ^{34}S & δ^{15}N stabiliųjų izotopų aplinkose. Langeliai, pažymėti tamsia, šviesesne ir šviesiausia pilka spalva, atitinkamai nurodo standartinių elipsių plotų persidengimą trijose, dviejose ir vienoje stabiliųjų izotopų aplinkose; nepažymėti langeliai nurodo nepersidengiančius standartinių elipsių plotus.**

δ^{13}C & δ^{15}N					
	RG S	RG M	RG L	FL S	FL M
RG S					
RG M	0.32				
RG L	0.07	0.07			
FL S	< 0.01	0.15	0.15		
FL M	< 0.01	< 0.01	0.06	0.01	
FL L	< 0.01	< 0.01	< 0.01	< 0.01	0.18
δ^{13}C & δ^{34}S					
RG S					
RG M	0.30				
RG L	0.16	0.07			
FL S	< 0.01	< 0.01	0.27		
FL M	< 0.01	< 0.01	0.40	0.36	
FL L	< 0.01	< 0.01	0.38	0.08	0.49
δ^{34}S & δ^{15}N					
RG S					
RG M	0.65				
RG L	0.09	0.05			
FL S	0.35	0.20	0.27		
FL M	< 0.01	< 0.01	0.17	0.03	
FL L	< 0.01	< 0.01	< 0.01	0.30	0.48

FL M and FL L had wider isotopic niches than all size groups of round goby; this difference was particularly evident in $\delta^{13}C$ & $\delta^{34}S$ and $\delta^{34}S$ & $\delta^{15}N$ isotopic spaces (Fig. 19).

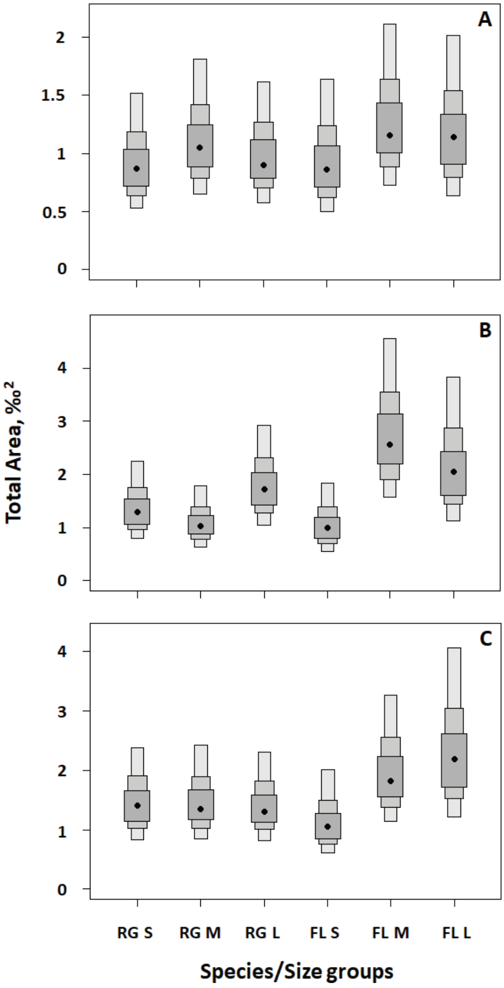

Figure 19. Density box-plots of the corrected standard elipse area (SEA_C) for muscle tissue of small (S), intermediately sized (M) and large (L) round gobies (RG) and flounders (FL) in $\delta^{13}C$ & $\delta^{15}N$ (A), $\delta^{13}C$ & $\boldsymbol{\delta}^{34}S$ (B) and $\boldsymbol{\delta}^{34}S$ & $\delta^{15}N$ (C) isotopic spaces. Black circles correspond to the mean standard ellipse area for each group and grey boxes represent 50%, 75% and 95% confidence intervals.

19 pav. Pakoreguotų standartinių elipsių plotų (SEA_C) tankio skirstiniai, gauti tiriant mažų (S), vidutinio dydžio (M) ir didelių (L) juodažiočių grundalų (RG) ir upinių plekšnių (FL) raumens audinius $\delta^{13}C$ & $\delta^{15}N$ (A), $\delta^{13}C$ & $\delta^{34}S$ (B) ir $\delta^{34}S$ & $\delta^{15}N$ (C) aplinkose. Juodi apskritimai vaizduoja kiekvienos tirtos grupės standartinės elipsės ploto vidurkį, o pilki stačiakampiai – 50 %, 75 % ir 95 % pasikliautinius intervalus.

4.3.4 Stable isotope dietary mixing model of the round goby and flounder in the sandy biotope

Seven potential food sources: *L. balthica*, *M. arenaria*, *C. lamarcki*, *C. crangon*, Amphipoda, Polychaeta and Pisces were selected to represent the isotopic diets of the round goby and flounder (Fig. 20). Bivalve mollusks *C. lamarcki* and amphipods were pooled in one homogeneous group, because their values did not differ significantly in all three SI spaces (*t*-test; $p > 0.05$ for all cases). *M. arenaria* was also included into this group, although statistical testing was not possible, because its isotopic compositions were estimated only in one sample (Figs. 20 and 21; Annex 5). Fish prey and *C. crangon* had similar $\boldsymbol{\delta}^{34}$S values (*t*-test; $p = 0.09$), but significantly differed in δ^{13}C and δ^{15}N (*t*-test; $p < 0.05$ for both cases), therefore these preys were not combined in one food source. Later on five food sources: 1) *L. balthica*, 2) combined *M. arenaria*, *C. lamarcki* and Amphipoda (*Mya_Cer_*Amph), 3) *C. crangon*, 4) Polychaeta and 5) Pisces were distinguished and used in the SI mixing models (Fig. 21; Table 12). The differences in isotopic compositions between distinguished food sources were significant (MANOVA; $F = 7.82$; $p < 0.05$). Univariate analyses also showed significant differences in δ^{13}C (ANOVA; $F = 42.33$; $df = 5$; $p < 0.05$), δ^{15}N (ANOVA; $F = 225.42$; $df = 5$; $p < 0.05$) and $\boldsymbol{\delta}^{34}$S (ANOVA; $F = 104.91$; $df = 5$; $p < 0.05$) values. The post-hoc tests revealed that *C. lamarcki* and amphipods had significantly lower δ^{13}C, δ^{15}N and $\boldsymbol{\delta}^{34}$S values (HSD; $p < 0.05$ for all cases) compared to other potential preys (Fig. 20; Annex 5).

The SI mixing model output revealed that polychaetes was the most important food source for RG S (65% of the diet), RG M (52%) and RG L (67%), followed by the *Mya_Cer_*Amph group (25%, 35% and 20%, respectively), whereas the contribution of *L. balthica*, brown shrimps and fish prey was considerably lower (Fig. 21; Table 12).

Polychaetes and *Mya_Cer_*Amph group dominated the diet of FL S (33% and 34%, respectively), FL M (43% and 37%) and FL L (63% and 10%). Contrary to the round goby ration, *C. crangon* was relatively important prey for differently sized flounders (21%, 6% and 13%) (Table 12).

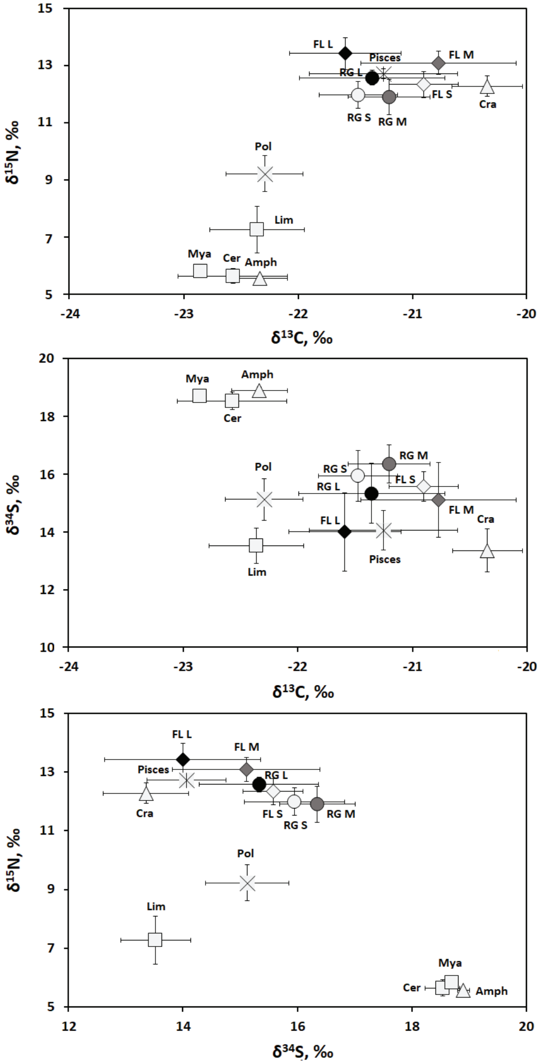

Figure 20. The mean $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values (± SD) in round gobies, flounders and their potential food sources. Circles denote differently sized round gobies, diamonds - differently sized flounders. Squares mark bivalves: Lim - *Limecola balthica*, Mya - *Mya arenaria*, Cer - *Cerastoderma lamarcki*; triangles denote crustaceans: Cra - *Crangon crangon*, Amph - amphipoda, crossed square denotes polychaetes (Pol) and square with an asterix marks fish (Pisces).

20 pav. Vidutinės juodažiočių grundalų, upinių plekšnių ir jų potencialių mitybos šaltinių $\delta^{13}C$, $\delta^{15}N$ ir ^{34}S vertės (± SN). Apskritimai vaizduoja skirtingo dydžio juodažiočius grundalus, rombai – skirtingo dydžio upines plekšnes. Kvadratai žymi dvigeldžius moliuskus: Lim – *Limecola balthica*, Mya – *Mya arenaria*, Cer – *Cerastoderma lamarcki*; trikampiai – vėžiagyvius: Cra – *Crangon crangon*, Amph – šoniplaukas; kvadratas su kryžiumi – daugiašeres kirmėles (Pol), kvadratas su žvaigžde – žuvis (Pisces).

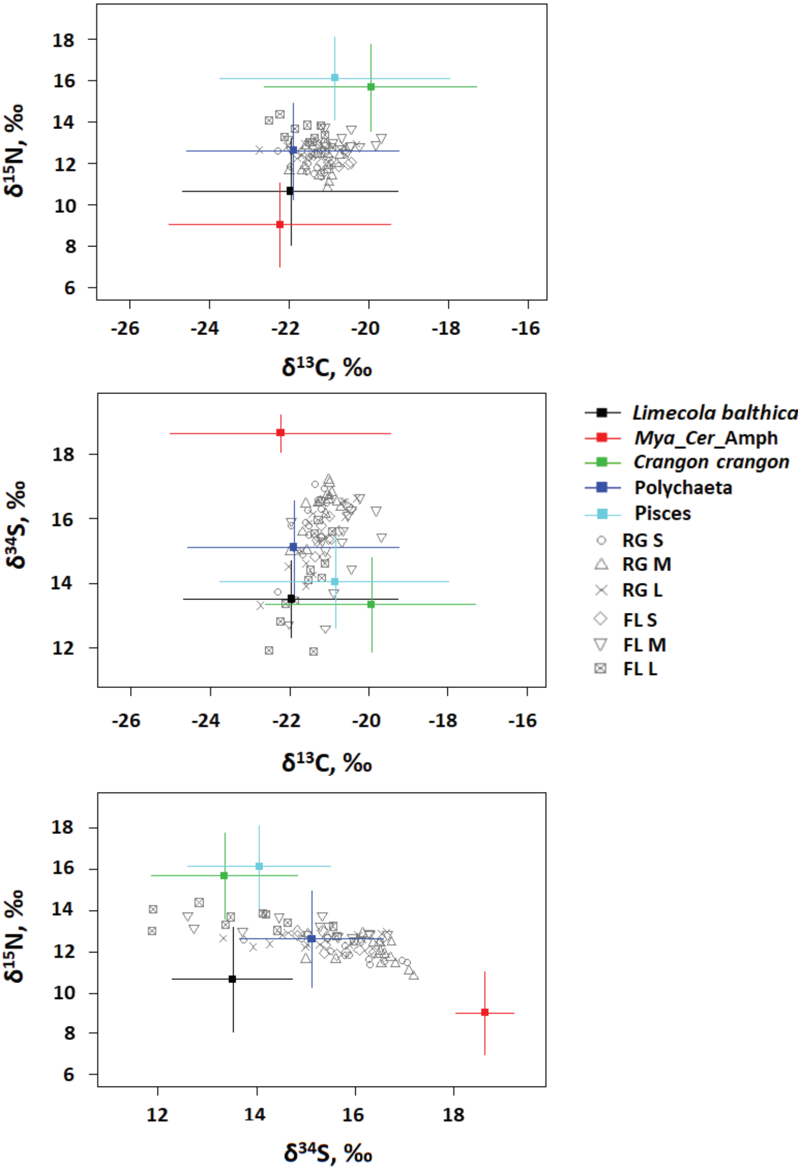

Figure 21. The five source mixing model biplots, showing δ^{13}C, δ^{15}N and δ^{34}S values in differently sized round gobies, flounders and their potential food sources, incorporating the trophic enrichment factor (TEF) corrections.

21 pav. Penkių šaltinių maišymosi modelio grafikai, vaizduojantys skirtingo dydžio juodažiočių grundalų, upinių plekšnių ir jų potencialių mitybos šaltinių δ^{13}C, δ^{15}N ir δ^{34}S vertes, pakoreguotas pritaikius frakcionacijos koeficientą.

Table 12. **Contribution of food sources (median, 25% and 75% quartiles) in the diet of differently sized round gobies and flounders, calculated by the five source ($\delta^{13}C$ & $\delta^{15}N$ & $\delta^{34}S$) mixing model setup, using mean $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values of potential benthic invertebrate and fish preys.**

12 lentelė. **Mitybos šaltinių svarba (mediana, 25% ir 75% kvartiliai) skirtingo dydžio juodažiočių grundalų ir upinių plekšnių mityboje, apskaičiuota penkių šaltinių ($\delta^{13}C$ & $\delta^{15}N$ & $\delta^{34}S$) maišymosi modeliu, naudojant vidutines potencialių dugno bestuburių ir žuvų aukų $\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$ vertes.**

	Size groups of round goby and flounder								
	Small			Intermediately sized			Large		
Food sources	Median	25%	75%	Median	25%	75%	Median	25%	75%
Round goby									
Limecola balthica	2	1	3	2	1	2	3	1	5
*Mya_Cer_*Amph	25	22	27	35	33	37	20	17	22
Crangon crangon	4	2	6	5	2	8	5	3	9
Polychaeta	65	61	68	52	48	57	67	62	71
Pisces	4	2	6	6	2	8	5	2	8
Flounder									
Limecola balthica	7	5	10	2	1	3	6	2	9
*Mya_Cer_*Amph	34	29	37	19	9	33	10	4	12
Crangon crangon	21	15	28	6	3	9	13	9	23
Polychaeta	33	11	43	69	66	73	63	28	72
Pisces	5	2	9	4	2	7	8	1	8

4.4 Round goby predation induced shifts in the blue mussel population and the diet of the wintering long-tailed duck in the stony biotope

The biomass of the blue mussel declined from 2.3 ± 1.5 kg m^{-2} in 2003 to 0.001 ± 0.001 kg m^{-2} in 2012 and remained low at 0.03 ± 0.004 kg m^{-2} during 2013-2014 (Fig. 22) in response to the increasing abundance of the invasive molluscivorous round goby (Fig. 7).

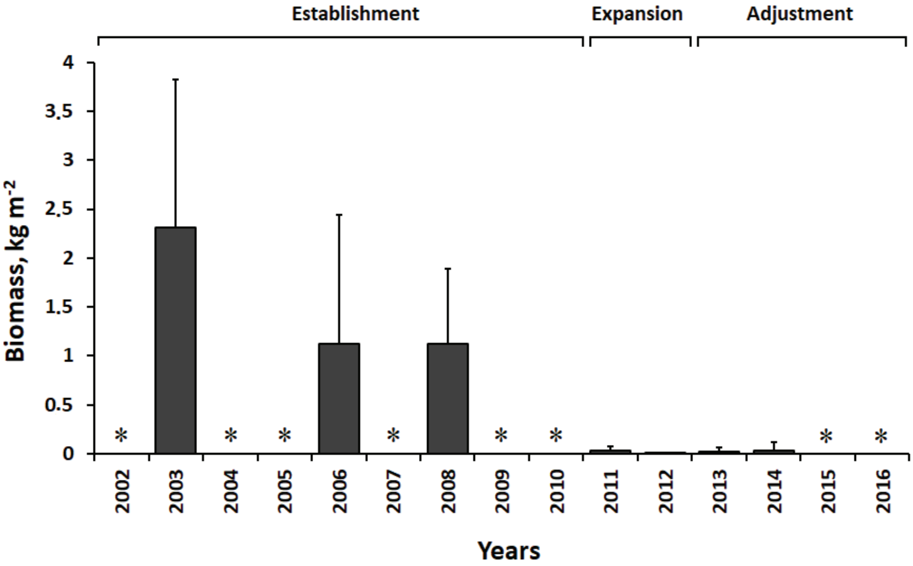

Figure 22. Biomass dynamics of the blue mussel (kgWW m^{-2}, mean ± SD) during different round goby invasion phases in the coastal stony biotope. * - no data.

22 pav. Midijų biomasės kaita (kgWW m^{-2}, vidurkis ± SN) moreninio dugno priekrantėje skirtingų juodažiočio grundalo invazijos fazių metu. * – duomenų nebuvimas.

The diet composition of the round goby and long-tailed duck changed dramatically along with declining biomass of the blue mussel. During the round goby establishment period, both round goby and long-tailed duck preyed mainly on *M. edulis trossulus* (69% and 80% of the diet, respectively) (Fig. 24). The round goby fed on 4-24 mm size blue mussels (median size 7 mm) (Fig. 23B), while the long-tailed duck consumed 1-25 mm size (median size 9 mm) mollusks (Fig. 23C).

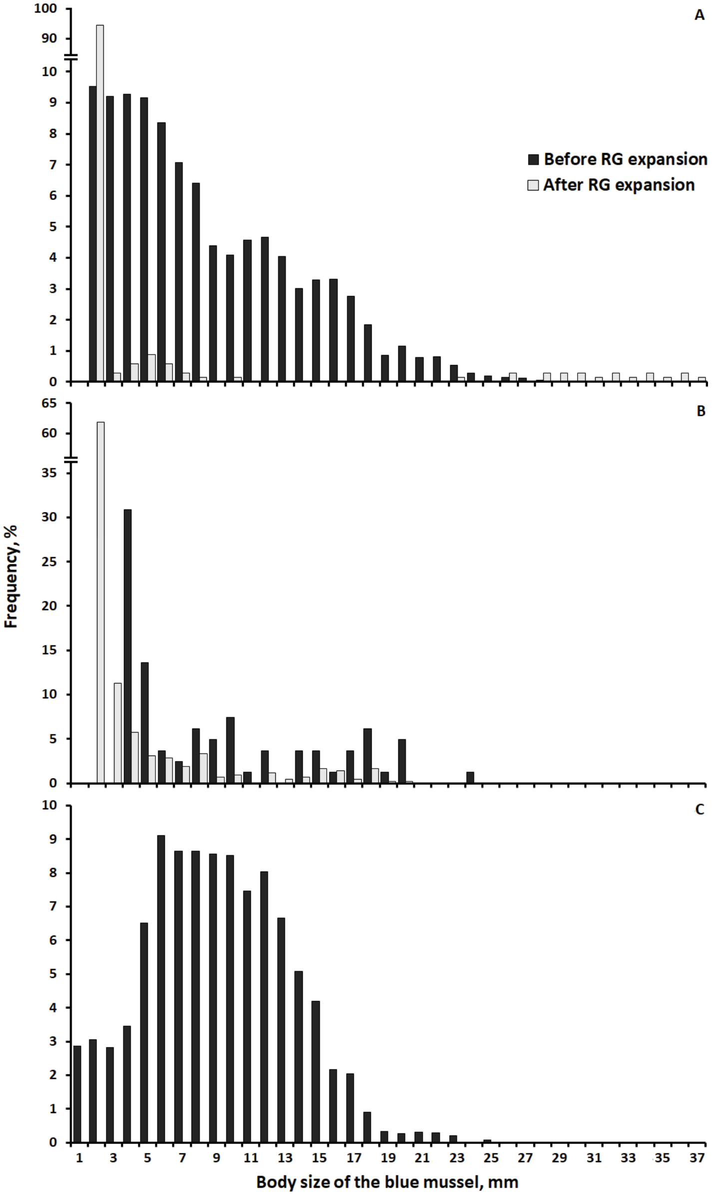

Figure 23. Changes in the blue mussel size structure in the natural environment (A), guts of the round goby (B), and gizzards/esophagi of the long-tailed duck (C) before (2002-2010) and after (2013-2016) the round goby expansion.

23 pav. Midijų dydžių struktūros pokyčiai natūralioje aplinkoje (A), juodažiočių grundalų virškinimo traktuose (B) ir ledinių ančių skilviuose/stemplėse prieš (2002–2010 m.) ir po (2013–2016 m.) juodažiočio grundalo išplitimo.

During the round goby expansion phase, the diet of the round goby was dominated by *M. edulis trossulus* (49%), *C. crangon* (27%) and *L. balthica* (16%). In the last invasion period it shifted to polychaetes (74%) and only negligible amounts (8%) of blue mussel, mainly represented by 2-3 mm sized individuals (median size 2 mm) (Fig. 23B) were found in their gut contents (Fig. 24).

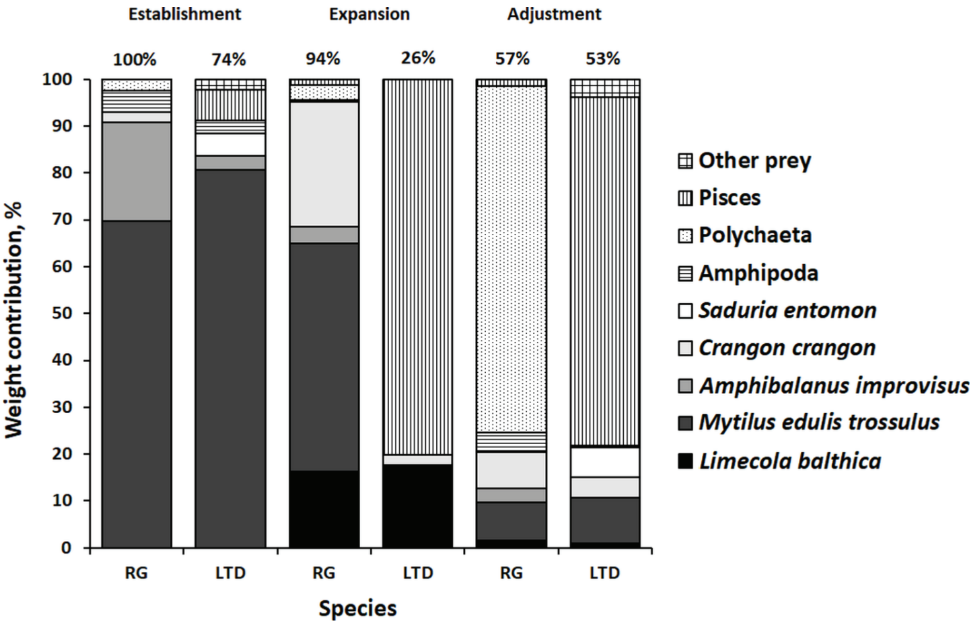

Figure 24. Mass percentage diet composition of the round goby (RG) and long-tailed duck (LTD) during different round goby invasion phases. Numbers above the columns indicate feeding efficiency (percentage of full guts/gizzards).

24 pav. Juodažiočio grundalo (RG) ir ledinės anties (LTD) procentinės masės dalies mityba skirtingų juodažiočio grundalo invazijos fazių metu. Skaičiai virš stulpelių nurodo imčių dydį ir mitybos efektyvumą (procentinę pilnų virškinimo traktų/skilvių) išraišką).

Before the round goby expansion size of the blue mussel ranged from 2 to 32 mm with dominance of 2-8 mm specimens (median size 7 mm). After the round goby expansion, blue mussel population was composed of small (2-8 mm, 97%) and large (23-37 mm, 3%) individuals (median size 2 mm), while specimens of intermediate size (9-22 mm) were absent (Fig. 23A).

The feeding efficiency of the round goby remained consistently high throughout the study period, and the number of individuals with empty guts increased considerably only after the dietary shift towards infaunal prey, mainly polychaetes (Fig. 24).

The reduced feeding efficiency resulted in a significant decline of the round goby body condition factor, when comparing the establishment and adjustment phases (Mann-Whitney U test; $p < 0.001$; Table 13).

Table 13. **Number of analyzed specimens, total length (TL, mean ± SD, cm), wet weight (W, mean ± SD, g) and Fulton's body condition index (K, mean ± SD) of round gobies captured during different invasion phases.**

13 lentelė. **Skirtingų invazijos fazių metu tirtų juodažiočių grundalų skaičius, absoliutinis kūno ilgis (vidurkis ± SN, cm), svoris (vidurkis ± SN, g) ir Fultono kūno būklės indekso vertės (K, vidurkis ± SN).**

Sampling years	Invasion phase	No. of specimens	TL, cm	W, g	K
2008 - 2009	Establishment	36	15.6 ± 3.6	78.4 ± 60.9	1.8 ± 0.2
2012	Expansion	98	16.7 ± 3.5	87.3 ± 54.5	1.6 ± 0.3
2014 - 2015	Adjustment	274	15.0 ± 2.2	56.5 ± 28.9	1.5 ± 0.2

The long-tailed duck shifted from feeding on blue mussels to fish prey during the round goby expansion and adjustment phases (80% and 75% of the diet, respectively) (Fig. 24). The percentage of empty long-tailed duck gizzards/esophagi increased from 26% in the round goby establishment phase to 74% and 50% during the expansion and adjustment phases, respectively (Fig. 24). This dietary shift did not have an adverse effect on the bird body condition (Table 14).

Table 14. **Number of investigated specimens, percentage of male (M) and female (F) individuals, median and minimum-maximum fat scores of male and female long-tailed ducks analyzed during sampling periods corresponding to different round goby invasion phases.**

14 lentelė. **Tirtų ledinių ančių skaičius, patinų (M) ir patelių (F) procentinė išraiška, mediana ir minimali ir makimali riebalingumo vertė tyrimo periodais, reprezentuojančiais skirtingas juodažiočio grundalo invazijos fazes.**

Sampling years	Invasion phase	No. of specimens	Sex, %		Median fat score (min-max)	
			M	F	M	F
2002 - 2004	Establishment	46	44.4	55.6	5 (2-7)	5.5 (3-9)
2011 - 2012	Expansion	31	35.7	64.3	7 (3-9)	7 (4-9)
2014 - 2016	Adjustment	30	36.7	63.3	6 (2-9)	6 (5-9)

The feeding niche overlap between the round goby and long-tailed duck was significant during the round goby establishment (0.76) and became considerably lower during the expansion (0.20) and adjustment (0.17) phases. The long-tailed duck dietary shift towards the fish prey, mainly smelt (~90% of identified fish) increased its trophic position from 3.1 in 2002-2004 to 4.3 in 2015-2016 (Fig. 33).

4.5 The importance of the round goby in the diet of piscivorous fish

The round goby has become an important food source for native piscivorous fish in both biotope types (Table 15). The overall feeding efficiency of predatory fish species was relatively similar in the stony and sandy biotopes (81% and 87% of all analyzed predators, respectively), but the percentage of individuals containing the round goby in their stomachs was considerably higher in the sandy biotope (46% and 73%) (Table 15).

Table 15. **Total length (TL, mean ± SD, mm), number and percentage of predatory fish, containing food remains in the stomach contents and proportion of piscivores preying on the round goby (RG) in the coastal stony and sandy biotopes. Mean values of piscivorous fish diet composition and feeding efficiency from the coastal stony and sandy biotopes were calculated using the data collected during all sampling events during 2014-2016 period.**

15 lentelė. **Tirtų plėšrių žuvų rūšių kūno ilgis (vidurkis ± SN), individų, turėjusių maisto liekanų skrandžio turinyje, skaičius ir procentinė išraiška bei žuvų, mitusių juodažiočiais grundalais (RG) priekrantės moreninio ir smėlėto dugno buveinėse, skaičius ir procentinė išraiška. Ichtiofagių žuvų dietos sudėtis ir mitybos efektyvumas buvo įvertinti analizuojant 2014–2016 m. laikotarpiu visų atliktų žuvų apgaudymų metu moreninio ir smėlėto dugno buveinėse surinktus duomenis.**

Predator species	Stony biotope					Sandy biotope				
	TL	Full stomachs		Preying on RG		TL	Full stomachs		Preying on RG	
		No.	%	No.	%		No.	%	No.	%
Cod	332 ± 53	171	82	83	49	353 ± 61	26	84	18	69
Perch	144 ± 39	51	86	17	33	180 ± 65	109	81	79	73
Shorthorn sculpin	230 ± 41	36	69	19	53	216 ± 54	47	78	31	76
Turbot	-	-	-	-	-	245 ± 38	35	94	31	89

In the stony habitat the round goby dominated the diet of cod (65% and 61% in the ration of small and large specimens, respectively) and shorthorn sculpin (80% and

93%), while the perch preferred the rockpool shrimp (*Palaemon elegans*) (71% and 25%), smelt (2% and 40%) and round goby (10% and 25%) (Fig. 25).

In the sandy bottom area, the round goby was the most important prey for the small (69%) and large (79%) cod, large perch (90%) and shorthorn sculpin (52%) as well as small (92%) and large (88%) turbot. The diet of the small perch consisted of the round goby (26%), smelt (29%) and Baltic sprat (31%) at similar proportions with a mixture of various other preys (14%); the small shorthorn sculpin consumed just 3 feeding objects, including the brown shrimp (*C. crangon*) (58%), round goby (42%) and amphipods (<1%) (Fig. 25).

The results of the principal component analysis (PCA) revealed, that the variation in the diet composition of differently sized predatory fish from the coastal stony and sandy habitats was mainly determined by the round goby contribution (Fig. 26). First two axes explained 80% of the data variability (61% and 19%, respectively). PCA biplot showed that the cod from both biotope types, the shorthorn sculpin and large perch from the stony biotope, the large shorthorn sculpin as well as the turbot from the sandy bottom area had the round goby based diets. Highly related preys included with the round goby - the Baltic herring, lesser sandeel and *S. entomon* were negatively correlated to other forage fish: Baltic sprat and smelt (Fig. 26).

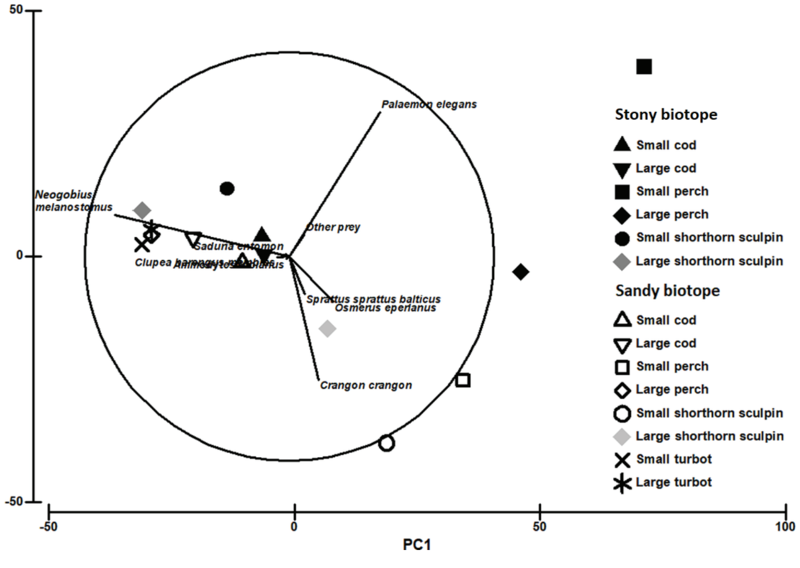

Figure 26. Principal component analysis (PCA) correlation biplot, showing the variation of piscivorous fish diet composition in terms of consumed preys in the coastal stony and sandy biotopes.

26 pav. Pagrindinių komponenčių analizės (PCA) koreliacijos grafikas, vaizduojantis ichtiofagių žuvų mitybos variaciją priklausomai nuo suvartotų mitybos objektų priekrantės moreninio ir smėlėto dugno buveinėse.

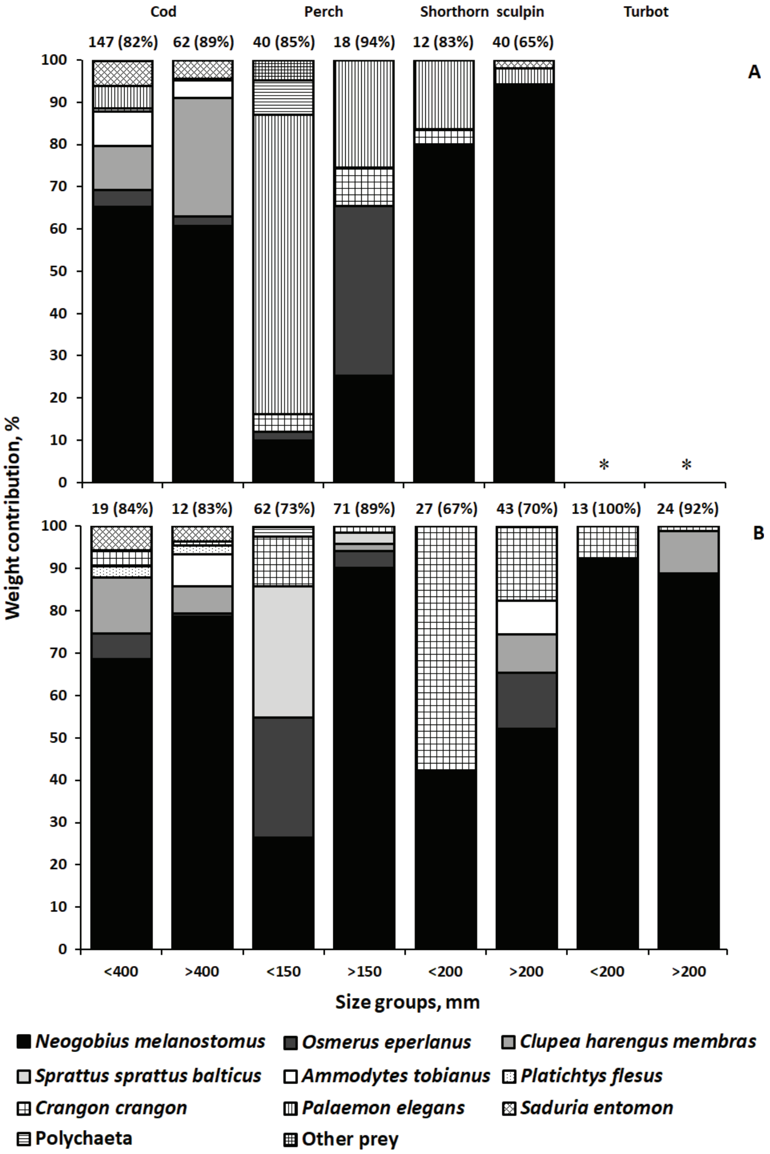

Figure 25. Mass percentage diet composition of piscivorous fish in the coastal stony (A) and sandy (B) biotopes. Numbers above the columns indicate sample size and feeding efficiency (percentage of full stomachs). * - no data.

25 pav. Ichtiofagių žuvų procentinės masės dalies mityba priekrantės moreninio (A) ir smėlėto (B) dugno buveinėse. Skaičiai virš stulpelių nurodo imčių dydį ir mitybos efektyvumą (procentinę pilnų skrandžių išraišką). * – duomenų nebuvimas.

The total length of round gobies, consumed by predatory fish ranged from 38 mm to 156 mm. The perch from the sandy habitat preyed on larger gobies than in the stony bottom area 75.0 ± 25.5 mm *vs*. 52.1 ± 14.4 mm (*t*-test; $p < 0.05$), whereas the total length of round gobies, eaten by the cod (95.8 ± 32.7 mm *vs*. 94.1 ± 27.2 mm) and shorthorn sculpin (96.8 ± 23.7 mm *vs*. 87.7 ± 27.1 mm) did not differ significantly among the habitat types (*t*-test; $p = 0.80$ and $p = 0.17$, respectively). The turbot from the sandy bottom area preferred 84.6 ± 14.9 mm round gobies (Fig. 27).

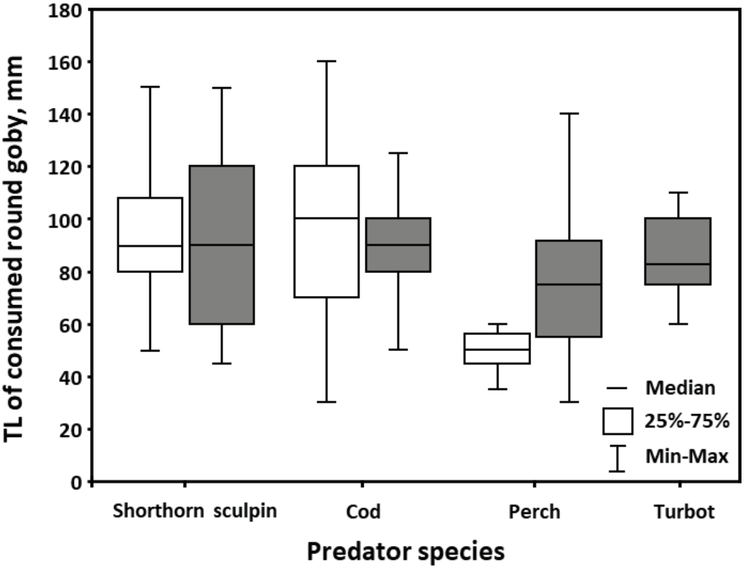

Figure 27. Total length (TL) of round goby, consumed by piscivorous fish in the coastal stony (open boxes) and sandy (filled boxes) biotopes.

27 pav. Absoliutinis ichtiofagių žuvų suvartotų juodažiočių grundalų kūno ilgis (vidurkis ± SN, mm) priekrantės moreninio (tuščiaviduriai stulpeliai) ir smėlėto (pilnaviduriai stulpeliai) dugno buveinėse.

Piscivorous fish preyed mainly on 40-100 mm round gobies, whereas the gill net catches were dominated by larger, 100-160 mm individuals (Fig. 28).

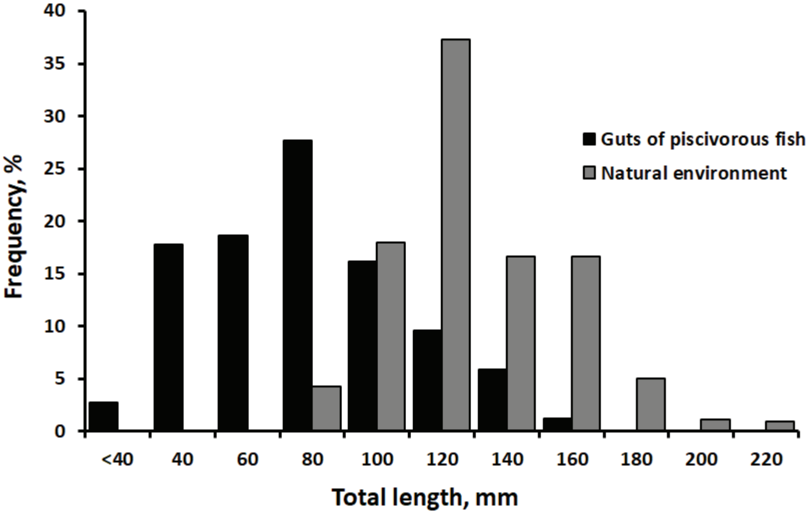

Figure 28. Body size frequency of round gobies caught with gill nets in natural environment and found in the stomach contents of piscivorous fish (all analyzed species and size groups combined) in the coastal stony and sandy biotopes.

28 pav. Natūralioje aplinkoje žiauniniais tinklaičiais sugautų ir ichtiofagių žuvų skrandžiuose (visos tirtos rūšys ir dydžio grupės sujungtos) rastų juodažiočių grundalų kūno ilgio pasiskirstymo dažnis priekrantės moreninio ir smėlėto dugno buveinėse.

The perch consumed significantly higher amount of round gobies in the sandy bottom area compared to the stony habitat (1.2 ± 0.4 *vs*. 1.5 ± 0.9; *t*-test; $p < 0.05$), whereas the number of round gobies per stomach content of the cod (1.1 ± 0.4 *vs*. 1.3 ± 0.5) and shorthorn sculpin (1.2 ± 0.4 *vs*. 1.2 ± 0.3) did not differ among the biotope types (*t*-test; $p = 0.13$ and $p = 0.72$, respectively). The turbot from the coastal sandy bottom area contained 1.8 ± 1.0 round gobies per stomach content.

4.6 ECOPATH model of the coastal food web

The current model of the Lithuanian Baltic Sea coastal waters was constructed using data from 2011-2015 period, representing the expansion and adjustment phases of the round goby population (Fig. 6). Juvenile and sub-adult/adult round gobies occupied 3.0 and 3.2 trophic levels of the food web, respectively (Fig. 29; Annex 6).

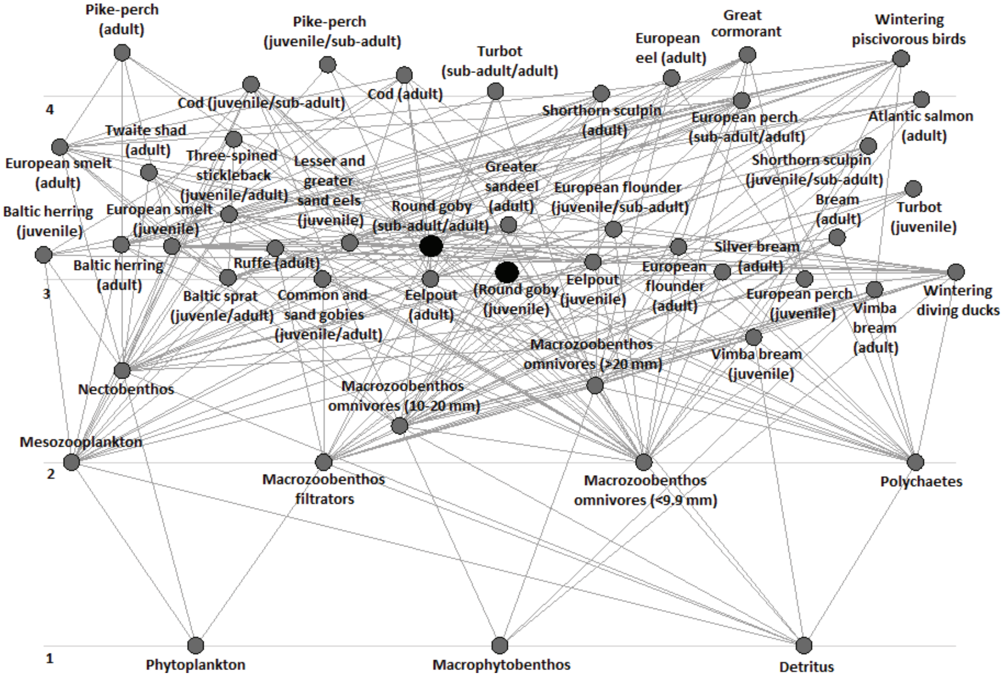

Figure 29. Food web structure of the Lithuanian Baltic Sea coastal waters (numbers on the left indicate trophic levels).

29 pav. Baltijos jūros Lietuvos priekrantės mitybos tinklo struktūra (skaičiai karėje grafiko pusėje žymi trofinius lygmenis).

Both round goby groups positively impacted piscivorous fish (the highest positive effect), waterbirds and fishery, while polychaetes and benthivorous fish suffered negative effect (Fig. 30; Annex 7). Sub-adult/adult round gobies posed a negative effect on benthic filtrators, omnivores and wintering diving ducks (the latter suffering from the most negative effect) (Fig. 30; Annex 7). It could be counted, that both round goby groups had 14 positive effects and 10 negative effects on different food web compartment groups. Juvenile and sub-adult/adult round gobies were positively influenced by producers, filtrators, polychaetes and fishery, but suffered from piscivorous fish and waterbirds (Fig. 30).

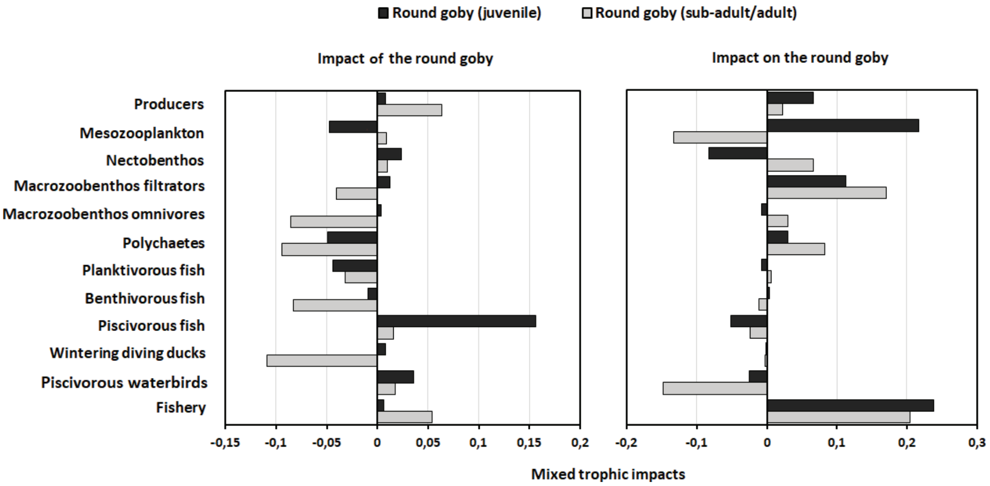

Figure 30. Mixed trophic impact of/on the round goby by different food web compartments and fishery (for food web compartment group composition see Annex 1).

30 pav. Mišrus trofinis juodažiočio grundalo poveikis skirtingiems mitybos tinklo komponentams ir žvejybai bei skirtingų mitybos tinklo komponentų ir žvejybos poveikis juodažiočiam grundalui (mitybos tinklo komponentų grupių sudėtis nurodyta 1 priede).

The results of total mixed trophic impact analysis revealed, that the most negative effect for all food web compartments was induced by the fishery (-6.9), adult specimens of Baltic herring (-2.2), sub-adult/ adult round goby (-2.1), wintering piscivorous birds (-2.1) and the great cormorant (-2.0). Nectobenthos (2.3), phytoplankton (2.1), <9.9 mm macrozoobenthos omnivores (1.9) and juvenile round gobies (0.74) had the most positive effect (Fig. 31).

The highest values of keystoneness index were determined for the great cormorant (0.21), wintering piscivorous birds (0.15), mesozooplankton (0.09), nectobenthos (0.09), juvenile smelt (0.03) and adult Baltic herring (0.02). Juvenile and sub-adult/ adult round gobies were also important components of the food web, because values of their keystoneness index were close to 0 (-0.12 and -0.07, respectively) (Fig. 32).

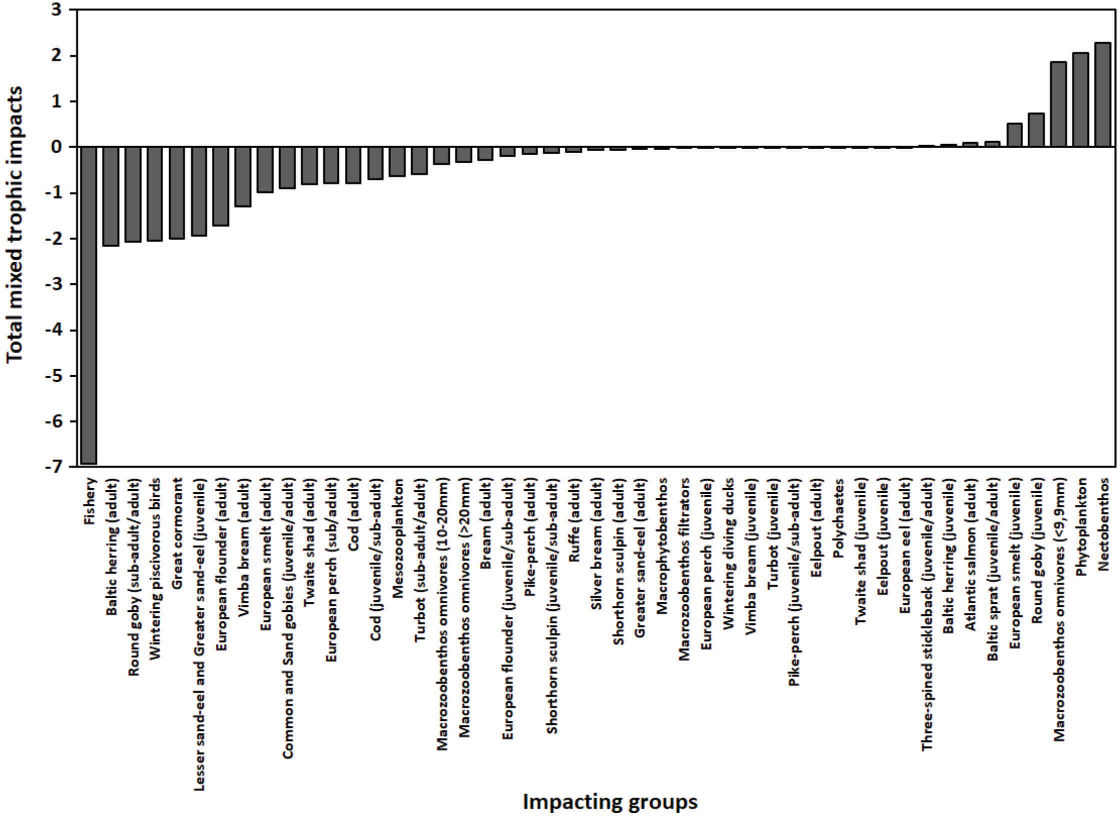

Figure 31. Total mixed trophic impact of each impacting food web group on all impacted groups.

31 pav. Absoliutus mišrus kiekvienos darančios poveikį mitybos tinklo grupės poveikis visoms paveiktoms grupėms.

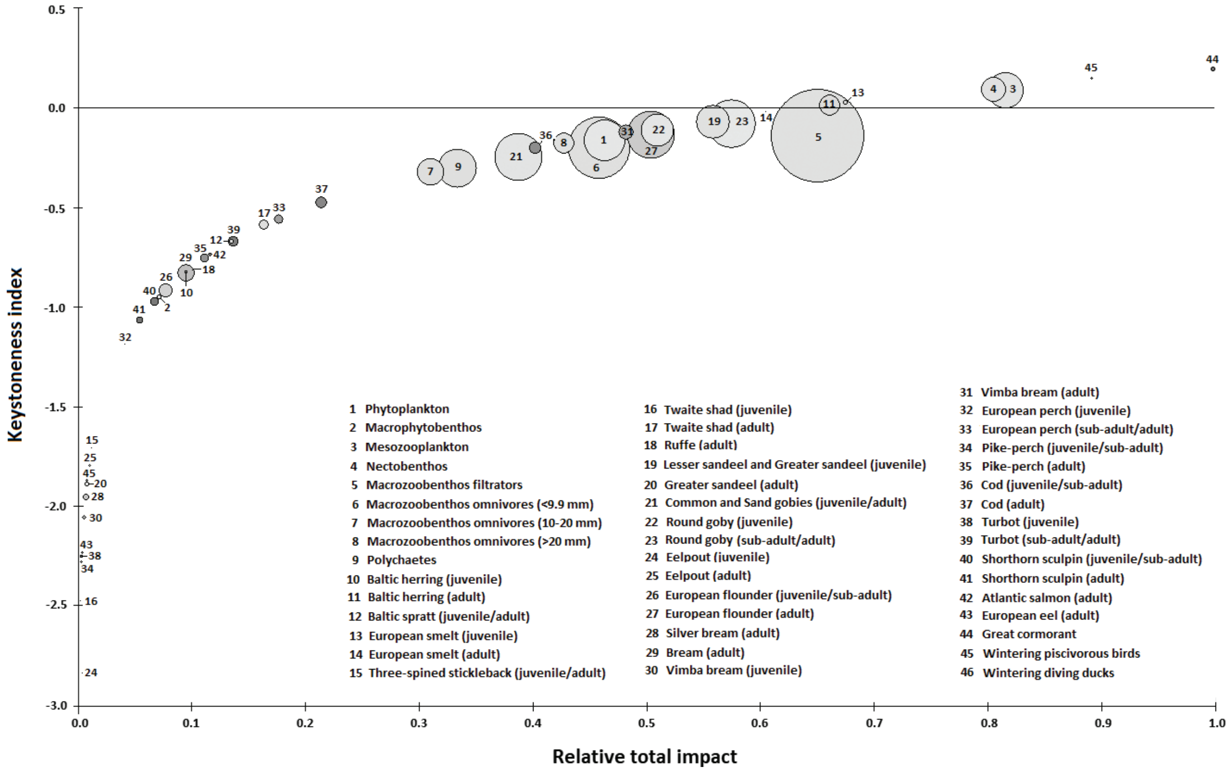

Figure 32. Keystoneness index of all Lithuanian coastal zone food web model compartments after the round goby expansion. Radius of the nodes represent biomass of each compartment.

32 pav. Visų Lietuvos priekrantės modelio komponentų svarbumo indeksai po juodažiočio grundalo išplitimo. Apskritimų skersmenys reprezentuoja kiekvieno mitybos tinklo komponento biomasę.

5

Discussion

5.1 Round goby invasion success and role in fish communities from the stony and sandy biotopes

The results of this study demonstrated, that the round goby established viable populations in the coastal stony and sandy biotopes of the SE Baltic Sea successfully. Lithuanian coastal waters provided a favorable environment for the round goby abundance increment because of its suitable abiotic conditions, variety of complex natural and human-made (e.g. piers and port constructions) habitats and rich forage base. It is also suggested, that low species richness in the brackish water communities facilitate the invasion success of alien species in the Baltic Sea (Ojaveer et al. 2010).

The initial round goby occurrence in the Lithuanian Baltic Sea coastal waters was recorded in 2002 at Smiltynė site, located in a close proximity to the entry of Klaipėda harbor (Zolubas 2003). Several years later the species began to increase in abundance and spread to other coastal localities. The first observations of the round goby in Karklė, situated northwards at a distance of ~10 km and Juodkrantė, situated ~20 km southwards, were recorded in 2006 (Taurūnas Areškevičius, commercial fisherman, pers. comm.) and 2008 (Arūnas Grigaitis, commercial fisherman, pers. comm.), respectively. The dispersal rate of the round goby in the Lithuanian coastal waters was ~3 km per year, which is lower compared to the nearby located Latvian coastal waters (7 km per year) (Ustups et al. 2016) and the Curonian Lagoon (6 km per year) (Rakauskas et al. 2013). Slower dispersion rates were most likely determined by the high mortality due to the predation on solitary round gobies migrating through the shelterless sandy habitat prevailing from Smiltynė to Karklė and Juodkrantė sites. In the Baltic Sea coastal waters containing complex stony seabed, the round goby is able to disperse up to 30 km per year (Azour et al. 2015).

The commercial round goby gill net catches in the stony habitat peaked during 2011-2013 (Taurūnas Areškevičius, commercial fisherman, pers. comm.), while in the sandy biotope it remained sparse since the initial introduction (Arūnas Grigaitis, commercial fisherman, pers. comm.). The expansion of the round goby population in the stony habitat began 4-6 years after the first observation. This time lag is typical in many invaded areas, including the Great Lakes (Clapp et al. 2001; Bunnel et al. 2005; Bergstrom et al. 2008) and other localities of the Baltic Sea (Sapota and Skóra 2005; Ustups et al. 2016; Hempel et al. 2016). The round goby expansion in less suitable Smiltynė site covered by the sandy seabed with the space limited artificial hard substrates began 10 years after the first observation and has not occurred in the sandy Juodkrantė site yet, which suggests that the habitat heterogeneity is a key factor determining the round goby invasion success. It was found, that under favorable conditions round goby populations increase in density at the early stages of invasion and show major declines later due to overexploited carrying capacity and predation effect (Young et al. 2010; Brownscombe and Fox 2012). The round goby density in the coastal stony and sandy biotopes was comparable to other invaded areas (Sapota and Skóra 2005; Taraborelli et al. 2009; Azour et al. 2015). Different sampling techniques might result in different estimated abundance of the species. Passive sampling methods (gill nets, traps) are not the best tools to estimate the round goby abundance, particularly in the heterogeneous environment (Diana et al. 2006). Records of the scuba divers or underwater video transects are considered as the most efficient sampling methods, allowing to evaluate spatial distribution, abundance and biomass of round gobies across different substrates (Johnson et al. 2005). It suggests that the abundance of the round goby could be underestimated in the course of the current study.

This study revealed, that the abundance and biomass of the round goby were significantly higher in the stony habitat, which is in agreement with previously conducted studies, showing the round goby preference to the heterogeneous bottom areas covered by rocks, ripraps, boulders, cobbles, pebbles, gravel or aquatic vegetation (Ray and Corkum 2001; Johnson et al. 2005; Taraborelli et al. 2009; Young et al. 2010). The round goby dominance in the stony biotope fish community was influenced by the combination of favorable biotope type and negligible resource competition and predation pressure, resulting from the low abundance of bottom-dwelling fish living in association with hard substrates and a minor spatio-temporal overlap with migrating predatory fish (Ložys 2003; Florin and Franzén 2010; Olsson et al. 2012). Contrary to the stony habitat, the round goby failed to expand in the sandy biotope due to high vulnerability to the predators in a shelter-free environment (Belanger and Corkum 2003) and abundant populations of demersal fish (Annex 3), increasing the rates of interspecific resource competition. Predation by the flounder (the most abundant species in the sandy biotope) also diminished the success of the round goby proliferation, because small (40-60 mm) gobies comprise ~10% in the diet of >200 mm flounders (Skabeikis, unpublished data). Despite the lack of high-quality nesting and hiding places, the round goby population from the sandy biotope was self-sustaining and contained juveniles, reproducing females and black colored males. The round goby populations in both habitat types have also possibly been replenished by specimens from other localities, as their planktonic larvae are able to disperse long distances from initial spawning grounds (Leslie and Timmins 2004; Hayden and Miner 2009).

After the rapid round goby abundance increment in 2016 the biodiversity of ichthyofauna decreased ~ three-fold in the coastal stony biotope. Despite this, the abundance of native fish species did not decline in the stony habitat, except of freshwater perch and roach. These species perform feeding migrations from the Curonian Lagoon during the summer season (Repečka 2003), therefore the variation of their abundance might not be related to the round goby abundance increment and rather it has been induced by population dynamics or migration efficiency from the lagoon. Such a result suggests that the round goby expansion did not trigger detrimental effects to the fish communities in the Lithuanian Baltic Sea coastal stony and sandy habitats.

Small sized species like the sand goby, juvenile smelt and three-spined stickleback are known to decline in density and biomass with increasing round goby abundance (Corkum et al. 2004). The smelt, dominating juvenile fish community in the Baltic Sea coastal waters (Ustups et al. 2003) and three-spined stickleback, migrating from the Curonian Lagoon, accumulate mostly in the areas characterized by the heterogeneous seabed (Repečka et al. 1996) where abundance of the round goby is very high. The sand goby is also known to coexist with the round goby in the shallow sandy habitats (Horackiewicz and Skóra 1998), which suggests a potential resource competition and predation posed by the round goby. The listed species are frequently encountered in the guts of large round gobies (Skabeikis 2013; Skabeikis and Lesutienė 2015; this study), therefore the round goby has a great potential to reduce their abundance. Further, more comprehensive studies are necessary to determine the round goby impact on small forage fish and juveniles of the commercially valuable smelt in the Baltic Sea coastal waters.

5.2. Morphometric and biological parameters of the round goby

The round goby populations in both habitat types were predominated by 3+ and 4+ specimens, which was also found in other invaded ecosystems (Sokołowska and Fey

2011; Huo et al. 2014; Duan et al. 2016). The population from the stony habitat was characterized by the significant contribution of 5+ specimens that were almost absent in the sandy habitat. Such an age distribution pattern was caused by the different degree of predation, because the excess of hiding places available in the stony biotope allowed round gobies avoiding the predation more efficiently and survive longer compared to the shelter-free sandy bottom area (Belanger and Corkum 2003; Taraborelli et al. 2010; Liversage et al. 2017). Very few individuals were able to survive to the age 5+ in the sandy biotope, possibly due to their ability to burrow in the soft bottom (Ray and Corkum 2001). The oldest round gobies caught in different biotope types of the Lithuanian coastal waters were 5+ and 6+, which is similar to the results previously reported from other Baltic Sea areas (Sokołowska and Fey 2011; Azour et al. 2015) and Laurentian Great Lakes (French and Black 2009; Huo et al. 2014; Duan et al. 2016), whereas the maximum age of round gobies from Detroit (MacInnis and Corkum 2000) and Danube (Grul'a et al. 2012) Rivers was lower. Shorter lifespan in the invaded freshwater ecosystems is influenced mostly by the earlier age of maturation (at 1+ and 2+ age) (MacInnis and Corkum 2000), while in marine ecosystems (including the study area) majority of round gobies mature older, at age 2+ and 3+ (Berg 1949; Roşca et. al. 2010; Tomczak and Sapota 2006; this study).

The spatial variation of the round goby morphometric and biological parameters depend mainly on the quality and quantity of available food resources (Duan et al. 2016) and population density (Kornis et al. 2014). The total biomass of zoobenthic organisms was considerably higher in the stony biotope, however their nutritional value was low due to the dominance of *A. improvisus* and mollusks (mostly blue mussels) (Fig. 4). The diet based on barnacles and epibenthic mollusks is poor, because it has low nutritional value (Brey et al. 1988; Thiyagarajan et al. 2003) and requires high energy expenditure as preys are strongly attached to the substrates and have thick shells, which makes them hard to remove from the surfaces, crush and digest. The forage base in the coastal sandy biotope was dominated by the soft-bodied polychaetes, amphipods and oligochaetes (Fig. 4), that contain much higher energetic value compared to the shelled preys (Brey et al. 1988) and are easily available and digestible for the benthivorous fish (Bubinas and Vaitonis 2003).

The abundance of the round goby in the coastal stony biotope was ~15-fold higher compared to the sandy bottom area, which indicates more intense intraspecific resource competition. Higher population density combined with poor forage base resulted in significantly lower values of the total length, weight and body condition in the stony habitat, suggesting that the population is reaching or even exceeding its carrying capacity (Young et al. 2010; Thompson and Simon 2015). Contrary to the stony biotope, better morphometric and biological parameters of the sparse round goby population from the sandy biotope were sustained by the low intraspecific food competition and availability of energetically more valuable feeding objects.

Table 16. **Range (min-max) of the round goby total length (TL), weight (W) and fecundity (F) in the Lithuanian Baltic Sea coastal stony and sandy biotopes and other invaded localities.**

16 lentelė. **Juodažiočio grundalo absoliutinio kūno ilgio (TL), svorio (W) ir vislumo (F) intervalas (nuo minimalaus iki maksimalaus) Baltijos jūros Lietuvos priekrantės moreninio ir smėlėto dugno buveinėse bei kitose kolonizuotose vietose.**

Water body	TL, mm	W, g	F, number of eggs	Reference
Stony biotope	81 - 211	10.5 - 149.9	106 - 2862	Present study
Sandy biotope	98 - 214	12.4 - 185.3	283 - 5511	Present study
Gulf of Gdańsk	29 - 215	-	-	Skóra and Rzeznik 2001
Gulf of Gdańsk	-	-	94 - 2190	Tomczak and Sapota 2006
Hel	59-216	-	-	Herlevi et al. 2018
Åland Islands	52-182	-	-	Herlevi et al. 2018
Puck Bay	74 - 166	-	89 - 3841	Wandzel 2000
Lake Erie	22 - 112	0.2 - 17.6	-	Phillips et al. 2003
Lake Erie	17 - 198	0.2 - 11.3	-	Johnson et al. 2005
Lake Erie	17 - 113	-	-	Thompson and Simon 2014
Lake Ontario	61 - 152	-	-	Walsh et al. 2007
Lake Ontario	28 - 90	-	-	Johnson et al. 2008
Lake Ontario	-	-	134 - 618	Vélez-Espino et al. 2010
Lake Ontario	14 - 118	-	-	Pennuto et al. 2012
Danube River	21 - 183	-	-	Lavrinčíková et al. 2005
Danube River	45 - 134	2.7 - 48.3	104 - 1938	Lavrinčíková and Kováč 2007
Danube River	60 - 130	2.9 - 37.1	-	Hôrková and Kováč 2015
Detroit River	58 - 83	-	259 - 1818	MacInnis and Corkum 2000
Flint River	54 - 82	-	-	Carman et al. 2006
Rhine River	18 - 157	-	-	Borcherding et al. 2011
Rhine River	22 - 123	0.1 - 30.1	-	Ghomi et al. 2014
Sava River	45 - 97	0.9 - 12.5	-	Piria et al. 2011
St. Lawrence River	47 - 104	-	-	Kipp et al. 2012

The absolute fecundity at age of the analyzed round gobies was also higher in the sandy bottom area and this pattern was most likely related to the lower population density and better body condition factor that allowed females to produce more eggs. The fecundity increased with increasing age and body size in both biotope types, which was previously recorded in other marine (Wandzel 2000; Tomczak and Sapota 2006) and freshwater (MacInnis and Corkum 2000; Lavrinčíková and Kováč 2007; Vélez-Espino et al. 2010) ecosystems. The absolute fecundity, total length and weight of round gobies from both habitats of the Lithuanian coastal waters was higher compared to other Baltic Sea areas and invaded lentic and lotic North American and Eurasian water bodies (Table 16). Most probably this result was initiated by more suitable environmental conditions (i.e. salinity, temperature, habitat type) and better forage base compared to other invaded ecosystems.

5.3 Feeding niche overlap with native benthophagous fish: gut content *vs.* stable isotope analyses

The round goby is known to forage on the most dominant components of benthic community (Skóra and Rzeznik 2001; Bănaru and Harmelin-Vivien 2009; Brandner et al. 2013), which highly differ in the coastal stony and sandy biotopes. The diet of the round goby in the stony bottom area comprised various epibenthic, infaunal, nectobenthic invertebrates and fish prey, whereas in the sandy habitat it foraged mainly on infaunal bivalves and polychaetes. Before the round goby expansion phase, when forage base in the stony biotope was very productive and contained large biomass of the blue mussel, the diet of the round goby was based on easily accessible epibenthic mussels throughout the year (E. Bacevičius, Klaipėda University Marine Research Institute, pers. comm.). After the depletion of the blue mussel population the round goby became a feeding specialist and adapted to shift its diet in response to the seasonally changing abundance of available food resources. For example, the abundance of scarce blue mussel population reaches the peak during autumn season, the period after the recruitment of mussel spat (Kautsky 1982). The increment of juvenile blue mussel abundance in autumn was particularly reflected in the diet of small and intermediately sized round gobies that prefer this food item whenever possible (Nurkse et al. 2016; Schrandt et al. 2016). The contribution of the blue mussel in the ration of large round gobies remained relatively stable throughout the seasons, as they are not limited to feeding on small mussels and are capable of ingesting specimens of a wider size range by swallowing whole mollusks or crushing them with pharyngeal teeth (Ghedotti et al. 1995; Andraso et al. 2011). In spring round gobies fed mainly on blue mussels from the previous autumn generation and shifted their diet towards polychaetes in summer. The highest contribution of polychaetes in the guts of analyzed round gobies was recorded in midsummer, when small newly hatched polychaetes stay close to the sediment surface (Marty and Retiere 1999) and represent easily accessible prey for the benthivorous fish.

The diet of differently sized round gobies from the sandy biotope was predominated by polychaetes and *M. arenaria* throughout the year, although slight seasonal dietary shifts were also detected. In spring season a large portion of *C. crangon* was found in their gut contents, because brown shrimps migrate from deeper areas and accumulate in the coastal waters at that time (Łapińska and Szaniawska 2006). In summer the diet of all round goby size groups was dominated by juvenile (2-4 mm) *M.*

arenaria. *M. arenaria* reaches the highest abundance during July-August (Möller and Rosenberg 1983; Günther 1992) and inhabit the upper 2 cm of the substrate (Zwarts and Wanink 1989), which makes them easily available for the gape limited fish. In autumn juvenile *M. arenaria* became larger (Günther 1992) and burrowed deeper into the sediments (Zwarts and Wanink 1989) inducing the dietary shift of small round gobies towards the polychaetes. The majority of *L. balthica* specimens ingested by the round goby were much larger (>10 mm) and comprised a substantial part of the diet only for the largest fish, that were capable of reaching and swallowing large deeply burrowed preys (Zwarts and Wanink 1989). During September-October round gobies from both biotope types foraged on fish more frequently compared to the spring or summer, and their main fish prey was juvenile smelts, concentrating in the coastal waters of the Baltic Sea in autumn (Ustups et al. 2003). Small juvenile round gobies were also consumed by large counterparts, which confirmed cannibalistic feeding habits of the species, previously determined by French and Jude (2001), Carman et al. (2006), Skabeikis and Lesutienė (2015) and Ustups et al. (2016).

No significant dietary overlap was detected between the round goby and native benthivorous fish in the stony habitat, which implies that a heterogeneous environment provides more opportunities for the species to specialize and share available resources. It is also highly possible that due to the interference competition the round goby prevents the flounder from using the stony habitat and epibenthic fauna as a food source, because the diet of flounder in the stony study site shifted from the epibenthic blue mussel to infaunal *L. balthica* and *M. arenaria* when comparing periods before (Bubinas and Ložys 2003) and after (this study) the round goby invasion. Contrary to the stony habitat, the ration of the flounder in the sandy bottom area did not change substantially throughout the time (Bubinas and Vaitonis 2003; this study). A significant dietary overlap (based on the gut content analysis) was determined between round gobies and flounders in the sandy bottom area, particularly during summer season, when the diet of both species was mainly composed of bivalve mollusks and polychaetes.

The stable isotope analysis (conducted during the autumn season) provided contrasting information on the feeding sources compared to the gut content analysis from the same time. The diet equilibration rate is a slow process. In large individuals of the round goby and flounder, 50% of diet equilibration can take ~ 2 and ~3 months, respectively (calculated according to Vander Zanden et al. 2015). The full equilibration takes even longer, thus the isotopic values in the individuals collected in autumn could be integrated from the diet of the whole summer period. Schoner's dietary overlap index showed that intermediately sized and large round gobies had highly similar diet composition with all size groups of the flounder, however SEAs revealed less overlapping feeding niches. According to the results of the gut content analysis, the flounder had narrower feeding niche compared to the opportunistically foraging round goby, although the stable isotope analysis revealed that intermediately sized and large flounders had wider feeding niches than round gobies from all size groups. The stable isotope analysis showed that large and intermediately sized flounders had higher $\delta^{15}N$ values compared to all round goby size groups. Larger body size presumably allowed the flounder to feed higher up in the food chain, i.e. consume larger feeding objects, more enriched in $\delta^{15}N$, such as fish prey and brown shrimps. Based on the mixing model results, polychaetes was the most likely forage source for intermediately sized and large flounders in autumn, although their proportion in the guts was relatively low at that time. The differentiation between the $\delta^{34}S$ values of both analyzed species might also be induced by the consumption of infaunal invertebrates inhabiting different soft sediment depths (Kharlamenko et al. 2001).

It should be acknowledged that stable isotope analysis provides quantitative information on both resource (preys) and habitat (Newsome et al. 2007). Therefore wider isotopic niche of the flounder could be related to its wider habitat use or long distance migrations (Raffaelli et al. 1990; Karlson et al. 2007; Dando 2011) and incorporation of elements from isotopically distinct areas, whereas round gobies feeding in a limited home range (Ray and Corkum 2001) potentially have less variable isotopic composition. It is known that the round goby performs long distance migrations from and to the wintering areas in the Baltic Sea (Christoffersen et al. 2019). The seasonal migration could only negligibly affect the isotopic signal in the analyzed individuals, because the time period from the round goby arrival to the coastal waters and the sampling for the stable isotope analysis was ~5 months (April-September) i.e. two times longer than the half of equilibration period (calculated according to Vander Zanden et al. 2015).

5.4 Importance of the round goby in the diet of piscivorous fish

The invasive round goby became a very important food source for the piscivorous cod, turbot, shorthorn sculpin and perch in the coastal stony and sandy habitats. All analyzed predatory fish species are opportunistic feeders, capable of shifting their diet composition in response to the changing environmental conditions and abundance of available preys (Moore and Moore 1974; Aarnio et al. 1996; Almqvist et al. 2010). According to the optimal foraging theory, predators prefer the most abundant and easily capturable preys, which ensures high efficiency of energy intake (Werner and Hall 1974). Higher round goby abundance compared to other potential forage fish (Annex 3), combined with oblong body shape and poor swimming ability, increasing prey capture and ingestion success for gape limited predators (Płąchocki et al. 2012) induced ichthyophagous fish dietary shifts towards the round goby in both studied biotopes. Despite lower abundance, piscivorous fish preyed on the round goby more efficiently and contained more round gobies per stomach content in the sandy biotope. This pattern was caused by the limited round goby swimming speed (Charlebois et al. 1997), which resulted in much higher vulnerability to the predation pressure in a shelter-free sandy habitat (Belanger and Corkum 2003). In contrast, round gobies from the stony biotope had significantly reduced predation rates due to the variety of shelters available in a heterogeneous seabed.

In the Baltic Sea offshore areas lacking the round goby, fish prey of the cod is predominated by the pelagic Baltic sprat and Baltic herring (Załachowski 1985; Sparholt 1994; Uzars 1994; Pachur and Horbowy 2013). The study conducted in the Lithuanian coastal waters before the round goby invasion also revealed the dominance of clupeids in the diet of the cod, with a secondary importance of the benthic lesser sand eel (*A. tobianus*) and crustaceans: *S. entomon*, amphipods and mysids (Bubinas and Vaitonis 2003). After the round goby establishment differently sized cods from both biotope types based their diet on the round goby, which resulted in considerably reduced consumption of pelagic fish and benthic invertebrates. This finding was supported by the studies from other Baltic Sea areas, where the round goby also began to prevail in the ration of >250 mm cod (Almqvist et al. 2010; Gruszka and Więcaszek 2011).

Before the round goby invasion the most common preys for >200 mm turbot in the studied area were the pelagic Baltic herring and sprat with a minor share of the benthic flounder and brown shrimp (Stankus 2003). At present time the turbot from the sandy bottom area shifted completely towards benthic food sources, highly dominated by the round goby. Results of the study, conducted in the sandy habitat with the adjacent Klaipeda harbor pier demonstrated lower round goby contribution in the diet of >200 mm turbot (Narvilas 2013), which was induced by the differences in available forage base, as the diet of the turbot is highly site specific (Bubinas and Ložys 2000). No other studies on the turbot dietary changes after the round goby expansion in the Baltic Sea region have been conducted yet, although Sapota and Skóra (2005) proposed that importance of the round goby in the diet of the turbot from the Gulf of Gdańsk is constantly increasing, which is in agreement with the results of the present study. Ustups et al. (2016) found that the increasing round goby abundance in the coastal waters of the eastern Baltic Sea induced dietary shifts and abundance reduction of the juvenile turbot as a result of intense food competition, posed by the round goby. The long-term juvenile fish monitoring from the Lithuanian coastal waters did not record substantial decline in the juvenile turbot abundance (Kregždys et al. 2018 b), which suggests that the round goby invasion has not harmed juvenile and positively affected adult turbots as a novel profitable prey.

It was found that the shorthorn sculpin is an opportunistic feeder and has a highly variable, site specific diet, which might be dominated by planktonic organisms (Moore and Moore 1974), crabs (Cui et al. 2012), amphipods (Dick et al. 2009) or a mixture of crabs, shrimps and crustaceans (Gray et al. 2017). In the Baltic Sea dietary investigations on the shorthorn sculpin are very scarce; the study conducted in the south-western Baltic Sea revealed that <200 mm sculpins fed exclusively on crustaceans, while larger individuals shifted towards fish prey, mainly the Baltic herring (Cardinale 2000). The results from the research performed in the Lithuanian coastal waters showed that the diet of differently sized shorthorn sculpins is highly fish-based and dominated by the round goby (Narvilas 2013). The present study supported this pattern, however the importance of shrimps was also substantial in both biotope types, especially in the diet of <200 mm specimens.

From all analyzed piscivorous fish the perch had the lowest reliance on the round goby and preferred other food items, particularly in the stony bottom area. In the stony biotope the small and large perch actively consumed the invasive rockpool shrimp (*Palaemon elegans*), which successfully established and reached high abundance in the Karklė site (Lesutienė et al. 2014). Other studies from the Baltic Sea region also revealed that <150 mm perch forages mainly on invertebrate preys and shifts to the fish dominated diet with the increasing body size (Lappalainen et al. 2001; Mustamäki et al. 2014). Before the round goby invasion the small perch in the Lithuanian coastal waters preyed mainly on mysids, while larger specimens preferred the juvenile smelt, common goby and brown shrimp (Bubinas and Ložys 2000). After the round goby expansion the perch incorporated the round goby in its ration, particularly in the sandy bottom area, where it became the most important food item for large individuals. In other Baltic Sea areas >150 mm perch shifted the diet towards the round goby (Almqvist et al. 2010; Liversage et al. 2017) and its vulnerability to the perch consumption increased with decreasing degree of habitat heterogeneity (Liversage et al. 2017), which was also found in the course of the current study. In the Laurentian Great Lakes the round goby became the major prey for >150 mm yellow perch (*P. flavescens*) (Truemper et al. 2006; Reyjol et al. 2010; Taraborelli et al. 2010; Webber et al. 2011). Most probably, the pike-perch, another member of the perch family, also consumes substantial amounts of the round goby in the stony and sandy study sites, because it forages on the round goby in other Baltic Sea coastal areas (Hempel et al. 2016; Oesterwind et al. 2017) and Eurasian rivers (Płąchocki et al. 2012). The diet composition of the pike-perch was not presented in this study due to the very low amount of the captured individuals (Annex 3).

The total length of the round goby consumed by the cod and shorthorn sculpin did not vary among the coastal stony and sandy biotopes and was higher compared to the round gobies ingested by the perch and turbot. Such a pattern was recorded because both cod and shorthorn sculpin have larger gape size compared to the perch and turbot (Skabeikis, pers. obs.) and therefore preferred larger preys, containing higher amount of energy (Reyjol et al. 2010). The total length of the round goby consumed by cod and perch were comparable to the size of gobies ingested by these predators in other ecosystems (Truemper and Lauer 2005; Almqvist et al. 2010; Webber et al. 2011; Płąchocki et al. 2012).

The predation on the invasive round goby in a species-poor brackish Baltic Sea ecosystem is very important in order to control its density and impact on the ecosystem functioning, particularly in the space limited stony biotope. The results of this study suggest that the current population size of the piscivorous cod, shorthorn sculpin and perch is not capable of reducing the round goby abundance substantially in the stony habitat. Despite this, the dietary shift towards the round goby reduced predation pressure on native fish and benthic invertebrates, which ensures better forage base for various local fish (Bubinas and Ložys 2000; Bubinas and Vaitonis 2003; Razinkovas-Baziukas et al. 2017) and waterbird (Žydelis 2002; Morkūnė et al. 2016, 2018) species. Contrary to the stony habitat, the abundance of the round goby in the sandy biotope was low, which most probably was caused by the more efficient predation of piscivorous fish (Table 15) and great cormorants from the nearby located nesting colony (Pūtys and Zarankaitė 2010). This hypothesis was supported by Madenjian et al. (2011), who found that the predation of the burbot (*L. lota*) successfully controls the round goby population size in the Lake Erie.

5.5 Did the round goby cause changes in the coastal food web?

Juvenile and sub-adult/adult round gobies successfully established in the Lithuanian coastal food web and completed direct connections with 15 food web compartments, which resulted in formation of novel energy transfer pathways (benthic invertebrates-round goby-piscivorous fish/waterbirds) within the studied ecosystem. Juvenile and sub-adult/adult round gobies occupied TL = 3.0 and TL = 3.2, respectively along with other secondary consumers: wintering diving ducks and planktophagous/benthophagous fish. A similar round goby trophic position was determined by Hossain et al. (2012) and Yu-Chun et al. (2014), which indicates the comparable contribution of the species in the food webs of other invaded ecosystems.

A substantial round goby contribution in the food web of the invaded coastal ecosystem was indicated by the relatively high keystoneness index values of juvenile (-0.12) and sub-adult/adult (-0.07) individuals. A significant round goby role in the food web was determined by the consumption of planktonic, benthic and fish preys (Skabeikis and Lesutienė 2015), trophic interaction with benthivorous fish (Herlevi et al. 2018) and wintering diving ducks (Skabeikis et al. 2019), high contribution in the diet of predatory fish (Narvilas 2013), great cormorant (Pūtys and Zarankaitė 2010; Pūtys 2012) and commercial fishery (Ložys et al. 2016; Fig. 2).

The results of the mixed trophic impact analysis showed that both round goby groups made a substantially positive impact on producers, piscivorous fish/waterbirds and fishery, but negatively affected polychaetes and planktivorous fish. A considerably high negative impact on macrozoobenthos filtrators/omnivores, benthivorous fish and wintering diving ducks posed by the sub-adult/adult round gobies was also detected. Predatory fish (Narvilas 2013; this study) and waterbirds (Pūtys and Zarankaitė 2010; Pūtys 2012) highly benefited from the round goby by incorporating it in their diet (Annex 8). As the Lithuanian coastal food web is based on imports and local planktonic production (Annex 2) and the most abundant benthivorous fish (flounder) is not consumed or comprises negligible portion in the diet of piscivorous fish (Bubinas and Ložys 2000; Bubinas and Vaitonis 2003; Narvilas 2013; this study) and waterbirds (Pūtys 2012), the active round goby consumption by various predators allowed transferring the benthic organic matter to the higher trophic levels much efficiently. The coastal fishery received a positive impact, because in 2016-2018 period the round goby became the most important commercial (in terms of landings) fish species (Fisheries Service under the Ministry of Agriculture of the Republic of Lithuania, unpublished data), generating sufficient economic value (Fig. 2). Polychaetes suffered a negative effect due to the intense round goby predation (Annex 8), while the Baltic herring and sprat, preying mainly on zooplankton and nectobenthos (Arrhernius and Hansson 1993; Casini et al. 2004) were presumably negatively influenced by the food competition with the juvenile round goby, having similar ration in the study site (Skabeikis 2013; Skabeikis and Lesutienė 2015). Benthophagous fish and wintering diving ducks were negatively impacted by the round goby due to the competition for benthic invertebrate and fish preys (Bubinas and Ložys 2000; Žydelis 2002; Morkūnė 2017; Morkūnė et al. 2018; Skabeikis et al. 2019). The shifts of the epibenthic community structure and functional role after a dramatic blue mussel decline in the stony bottom area were not determined by the newly balanced ECOPATH model, because it was constructed by using the biomass data of already depleted blue mussel population. Therefore, ECOPATH model, representing food web structure during the round goby expansion and adjustment phases cannot be used to demonstrate the changes in the energy flows related to the blue mussel decline.

Both round goby groups were positively affected by producers, providing a forage base for their pelagic and benthic preys (Dolmer 2000; Berezina et al. 2005), filtrators and polychaetes, comprising the bulk of their ration, and fishery, eliminating large predatory fish (Jørgensen et al. 2009) and waterbirds (Žydelis et al. 2009 and references therein) from the system, but suffered from piscivorous fish and waterbirds predation. The effects induced by the planktivorous fish had a negligible impact on juvenile and sub-adult/adult round gobies, as phytoplankton and zooplankton comprise ~80% of the total production/biomass ratio of the coastal food web (Annex 2), therefore the limitation of planktonic prey and interspecific food competition is not likely. The results of ECOPATH modelling supported a negligible magnitude of interactions among the round goby and native benthivorous fish (based on the gut content analysis), which showed that benthophagous fish in the stony biotope had distinct diets, while a significant feeding niche overlap between round gobies and flounders in the sandy habitat had no negative effect for the latter.

The total mixed trophic impact analysis demonstrated different juvenile and sub-adult/adult round goby effects on all food web compartments. Juvenile round round gobies had the fourth most positive impact on other food web compartments, because they were actively consumed by the piscivorous fish and had negligible predation induced impact on zooplankton, which resulted in a weak interspecific resource competition with planktivorous consumers. Contrary to the juveniles, sub-adult/adult specimens posed the third most negative impact on other food web compartments, presumably due to the intense predation on benthic invertebrates and juvenile fish, which declined the abundance of the feeding objects and directly or indirectly induced resource competition with the majority of benthivorous fish and wintering ducks. The large sub-adult/adult round goby contribution in the diet of ichthyophagous fish did not reduce its negative value of the total mixed trophic impact, because predatory fish and great cormorants are known to prefer <100 mm round gobies and other fish species in the Lithuanian coastal waters (Pūtys 2012; Narvilas 2013; this study).

The comparison of the main ECOPATH model statistics from 2000-2010 (Razinkovas-Baziukas et al. 2017) and 2011-2015 models (present study) were conducted in order to determine the impact of the round goby invasion on the coastal food web functioning (Table 17). The total biomass of the newly balanced model was 73% higher compared to the basal model, which subsequently increased the total flow into detritus and total system throughput. More negative net system production (72%) indicated a substantial decline of the net system production, most probably caused by the high round goby exports from the coastal ecosystem performed by the commercial fishery (Fig. 2) and intense predation of migratory piscivorous fish and waterbirds (Annex 8). The value of the pedigree index slightly declined during 2011-2015 due to more frequent usage of data sources originating outside of the study area (Christensen and Wolters 2004).

In conclusion, the round goby posed no detrimental effects on the Lithuanian Baltic Sea coastal food web, dominated by the pelagic food chain. The ecosystem was positively affected by the piscivorous fish and waterbird dietary shift towards the invasive round goby, which resulted in the reduced predation pressure on native hydrobionts. The highly abundant round goby population in the stony bottom area resulted in significantly increased abundance of predatory fish (cod and shorthorn sculpin), which was also detected in other invaded ecosystems (Morissette et al. 2018).

Table 17. **Summary of the main ECOPATH model statistics, expressed in g m^{-2} year^{-1}.**

17 lentelė. **Pagrindinių ECOPATH modelio statistikų suvestinė, išreikšta g m^{-2} metai^{-1}.**

Parameter	2000-2010	2011-2015	Change (%)
	Value	Value	
Sum of all consumption	1793.04	2036.25	14
Sum of all respiratory flows	1285.81	1440.55	12
Sum of all flows into detritus	1021.84	1942.981	90
Total system throughput	4095.87	6255.49	53
Sum of all production	1220.19	1260.11	3
Mean trophic level of the catch	3.47	3.56	3
Calculated total net primary production	1071.56	1071.56	0
Total primary production/total respiration	0.83	0.74	-11
Net system production	-214.24	-368.99	72
Total primary production/total biomass	20.32	21.75	7
Total biomass/total throughput	0.01	0.02	100
Total biomass (excluding detritus)	52.73	91.22	73
Total catches	0.71	0.88	24
Pedigree index	0.66	0.62	-6

5.6 Implications for vulnerable duck populations and management of MPAs

The predation of the round goby induced a dramatic decline of the blue mussel biomass and altered its size structure, which highly affected feeding efficiency and diet composition of the globally vulnerable (IUCN 2016) wintering long-tailed duck (Fig. 24). Before the round goby expansion, the long-tailed duck foraged mainly on the blue mussels with a negligible proportion of fish, infaunal mollusks, amphipods and polychaetes (Žydelis 2002) and shifted towards the fish prey after the depletion of the blue mussel biomass, which considerably elevated its trophic level (Fig. 33).

The abundance of the long-tailed duck wintering in the Lithuanian coastal waters was at the peak from 1995-1999; however it sharply declined in 2002 and has remained low until present (Skabeikis et al. 2019). The establishment of the round goby has not been the main factor causing the recent decline of the number of wintering long-tailed ducks in the Baltic Sea (the decline has been observed since 1990s), however significantly reduced resources of preferred food at wintering sites could be a future important additional factor limiting the recovery of the vulnerable long-tailed duck in whole Baltic Sea basin.

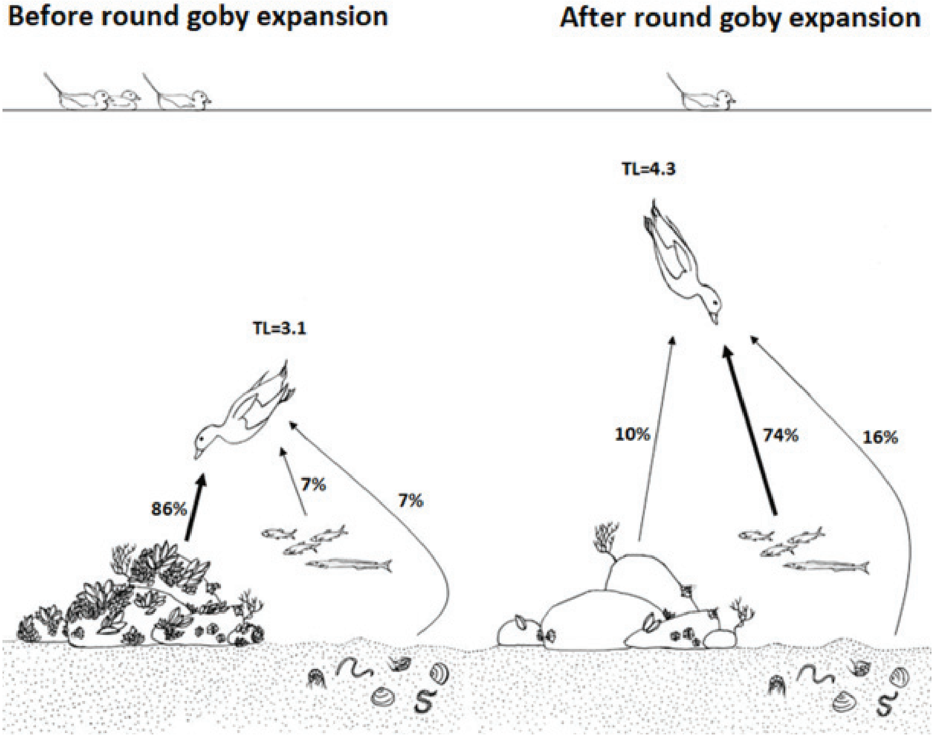

Figure 33. Scheme, demonstrating shifts of the food web links and long-tailed duck trophic levels (TL) before and after the round goby expansion in the coastal stony habitat (scheme drawn by S. Karalius).

33 pav. Schema, vaizduojanti mitybos tinklo jungčių ir ledinės anties trofinio lygmens (TL) pokyčius prieš juodažiočio grundalo išplitimą ir po jo moreninio dugno priekrantėje (schemą piešė S. Karalius).

The recovery of the blue mussel population depends on two major factors: the recruitment success and effect of predation. Currently, the recruitment of blue mussel is supported by local large individuals (>25 mm), which are out of the size range for both predator species (Taraborelli and Schaner 2002; Žydelis 2002; Andraso et al. 2011) and those on offshore reefs (Samuolivienė et al. in prep.) not depleted by the round goby predation. Offshore reefs are situated 30-50 km from the coast, at 30-45 m depths, and are below the summer thermocline of the Baltic Sea, which forms at ~20 m depth and contains water layer of 3-6°C temperature (Møller and Hansen 1994). Such water temperature is lower than the energetic optimum (26°C) (Lee and Johnson 2005) and spawning (9-26°C) (Charlebois et al. 1997) temperature for the round goby, which limits its expansion and foraging in deeper areas. Despite the successful recruitment of blue mussel juveniles, they do not reach maturity in the coastal waters due to high vulnerability to the round goby predation. As long as newly settled blue mussels are efficiently removed by the round goby, the population recruitment is halted.

The results of the present study suggest that the heterogeneous wintering site with depleted blue mussel beds became less attractive for the vulnerable long-tailed duck (Žydelis and Ruškytė 2005) and other benthophagous seaducks. Two decades ago, Lithuanian coastal reefs used to be the second most important Steller's Eider (*Polysticta stelleri*) wintering site in the Baltic Sea (Žydelis 1997), however the last observation of single individual of this species in the Lithuanian coastal waters was recorded in 2012 (Saulius Karalius, Lithuanian Ornithology Society, pers. comm.), when the biomass of the blue mussel was already very low. The extinction of Steller's Eider in the Lithuanian coastal waters is highly related to the dramatically reduced availability of epibenthic mollusks, as the species has low flexibility in feeding ecology and forages mainly on 4-8 mm blue mussels (Bustnes and Systad 2001) that are absent in our study site. On the other hand, the declined numbers of seaducks wintering in the Lithuanian coastal waters might be caused by the global warming, as since the mid-2000s waterfowl are known to spend winters in the areas far to the north and east of their former wintering range (Fox et al. 2018).

Conservation issues in the coastal stony biotope, highly invaded by the round goby, should be addressed by the intensive commercial round goby targeted fishery before and during the reproduction period in order to reduce its recruitment success, abundance and mitigate its impact on the native ecosystem functioning. The fishery should be conducted by using benthic fish traps that are the most efficient gear to catch the round goby in the stony bottom areas (Diana et al. 2006) and cause lower mortality of vulnerable wintering diving ducks (Julius Morkūnas, Marine Research Institute, pers. comm.) and seals (Westerberg et al. 2007). Another indirect round goby population control method could be reduced fishery quotas for economically valuable piscivorous fish (Ojaveer et al. 2015), which in turn could potentially reduce the round goby density. The expanding colony of the great cormorant in nearby located Plazė natural reserve, currently composed of ~700 breeding pairs (Erlandas Paplauskis, Seaside Regional Park, pers. comm.) has a great potential to reduce the round goby population, therefore it is recommended not to control the size of the cormorant population by disturbing the colony during breeding and nesting periods. Gremillet et al. (1995) found that an adult cormorant raising chicks consumes 423 g of fish on a daily basis, therefore the whole colony is capable of consuming ~125 t of round gobies annually, and thus the cormorant colony is of high importance for the natural control of the round goby population in the Seaside Regional Park MPA. It should be acknowledged that despite the application of all possible management methods, the eradication of the round goby population is not likely.

In the homogeneous sandy habitat, containing a stably sparse round goby population, no management tools are necessary and the further round goby abundance control should be left as a natural, self-sustaining process, mainly based on the predator effect.

6

Conclusions

1. The overall round goby abundance was significantly higher in the stony biotope, where it became the dominant component of ichthyofauna (47-89% of all captured) compared to the sandy habitat (11-14%). The fish biodiversity (H') declined ~ three-fold in the stony habitat when comparing the years with the low and high round goby abundance, although the total number of captured fish species and abundance of majority species did not change significantly;
2. The round goby population from the stony biotope contained older fish, however the total length, weight, body condition and fecundity at age were higher in the sandy bottom area, indicating better forage base and/or lower rates of resource competition;
3. In the stony habitat the round goby consumed mainly blue mussels, barnacles, *L. balthica* and fish prey during spring/autumn seasons and polychaetes in summer. The ration of the round goby in the sandy bottom area had lower seasonal variability and was dominated by the polychaetes, *M. arenaria*, *L. balthica* and brown shrimps. A significant feeding niche overlap (Schoener's index >0.6) between the round goby and flounder recorded in the sandy biotope was not supported by the triple SIA ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$). The isotopic differentiation between the round goby and flounder was determined by the higher $\delta^{15}N$ values of the latter, which indicates its feeding at higher trophic level. Stable

isotope mixing model showed that the diet of all round goby and flounder size groups was based on polychaetes;

4. During the expansion phase the round goby depleted biomass and changed the size structure of the blue mussel in the stony biotope. Reduced availability of blue mussels caused the dietary shift of wintering long-tailed duck from the blue mussel to fish prey. Although the body condition of the analyzed long-tailed ducks did not deteriorate, foraging on motile food source at higher trophic level presumably resulted in overall decline of the wintering site quality for the species;
5. The round goby became the most important prey for the piscivorous cod, perch, shorthorn sculpin and turbot. Ichthyophagous fish preyed on the round goby more efficiently in the sandy habitat;
6. The round goby had relatively high values of the total mixed trophic impact and keystoneness indexes in the coastal food web; however, the pelagic components such as zooplankton/nectobenthos-Baltic herring-piscivorous waterbirds prevailed. The results of the mixed trophic impact analysis revealed that juvenile and sub-adult/adult round gobies had positive effects on piscivorous fish/waterbirds and fishery and posed negative effects to the mesozooplankton, macrozoobenthos filtrators/omnivores, polychaetes, planktivorous and benthivorous fish and wintering diving ducks.

7

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8

Santrauka

ĮVADAS

Temos aktualumas

Juodažiotis grundalas (*Neogobius melanostomus*, Pallas 1814) – smulki, dugninė žuvis, kilusi iš Ponto – Kaspijos regiono: Juodosios, Kaspijos, Azovo ir Marmuro jūrų, yra itin sėkminga invazinė rūšis, įsitvirtinusi įvairiuose Šiaurės Amerikos ir Eurazijos vandens telkiniuose (Charlebois ir kt. 1997). Nuo 1990 m. juodažiotis grundalas aptinkamas Šiaurės Amerikos Didžiuosiuose ežeruose (Jude et al. 1992), jų intakuose (Carman ir kt. 2006; Bronnenhuber ir kt. 2011), Eurazijos upėse (Copp ir kt. 2005), estuarijose (Czugała ir Woźniczka 2010; Rakauskas ir kt. 2013) ir druskėtoje Baltijos jūroje (Kotta ir kt. 2016). Gausios juodažiočių grundalų populiacijos neigiamai paveikia vietinę fauną, sumažindamos dugno bestuburių gyvūnų kiekį ir rūšinę įvairovę (Krakowiak ir Pennuto 2008), nugalėdamos dugnines žuvis konkurencijoje dėl išteklių (Balshine ir kt. 2005) ir palengvindamos teršalų (Kwon ir kt. 2006) bei ligų (Herbert ir kt. 2014) perdavimą į aukštesnius trofinius lygmenis. Iš kitos pusės, ichtiofagiai plėšrūnai (Almqvist ir kt. 2010; Madenjian ir kt. 2011), komercinė (Ojaveer ir kt. 2015; Järv ir kt. 2017) ir rekreacinė (Gutowsky ir kt. 2011) žvejyba gauna nemažą naudą iš gausių, lengvai sugaunamų invazinių žuvų. Dėl spartaus populiacijos augimo, oportunistinės mitybos bei silpno atsparumo plėšrūnizmo poveikiui, juodažiotis grundalas turi didelį potencialą pakeisti apgyventos ekosistemos energijos, maistmedžiagių ir teršalų srautus (Johnson et al. 2005).

Šiuo metu juodažiotis grundalas yra plačiai paplitęs Baltijos jūros priekrantėje ir per tiesiogines ar netiesiogines trofines sąveikas su skirtingiems mitybos tinklo lygmenims priklausančiais organizmais keičia kolonizuotos ekosistemos funkcionavimą (Kotta ir kt. 2016; Oesterwind et al. 2017; Herlevi et al. 2018; Christoffersen et al. 2019). Baltijos jūros Lietuvos priekrantėje juodažiotis grundalas aptinkamas nuo 2002 m. (Zolubas 2003) ir daugiausia telkiasi moreninio dugno buveinėse. Didelio ploto riedulynai Lietuvos priekrantėje formuoja rifus, esančius NATURA 2000 ir Pajūrio regioninio parko (PRP) jūrinėse saugomose teritorijose (JST). Prieš juodažiočio grundalo invaziją riedulynai teikė palankią gyvenamąją aplinką daugeliui su midijomis ir makrofitais susijusių bestuburių gyvūnų rūšių (Bučas 2009; Šiaulys ir kt. 2012; Šaškov ir kt. 2014) ir užtikrino vertingą pašarinę bazę bentofagėms žuvims (Bubinas ir Ložys 2000; Bubinas ir Vaitonis 2003) bei žiemojantiems vandens paukščiams (Žydelis 2002). Dėl šios priežasties yra svarbu įvertinti juodažiočio grundalo invazijos poveikį priekrantės akvatorijoje, ypač heterogenišku moreniniu dugnu pasižyminčiose teritorijose. Šis tyrimas yra pirmas bandymas įvertinti juodažiočio grundalo invazijos sėkmę ir funkcinį vaidmenį ribotos erdvės moreninio bei vyraujančioje smėlėto dugno buveinėse, taikant skrandžio (žarnyno) turinio analizę, stabiliųjų izotopų analizę ir ECOPATH modeliavimą.

Tyrimo tikslas ir pagrindiniai uždaviniai

Tyrimo tikslas – įvertinti invazinio juodažiočio grundalo funkcinį vaidmenį Baltijos jūros priekrantės moreninio ir smėlėto dugno buveinėse.

Pagrindiniai uždaviniai:

1. Nustatyti juodažiočio grundalo gausumą ir reikšmę įvairovei moreninio ir smėlėto dugno buveinių žuvų bendrijose;
2. Įvertinti juodažiočio grundalo morfometrinius, amžiaus, kūno būklės ir vislumo parametrus moreninio ir smėlėto dugno buveinėse;
3. Įvertinti juodažiočio grundalo mitybos ypatumus ir mitybinės nišos persidengimą su vietinėmis bentofagėmis žuvimis;
4. Nustatyti juodažiočio grundalo plėšrūnizmo poveikį midijų biomasei ir ilgalaikiams ledinės anties mitybos pokyčiams moreninio dugno buveinėje;
5. Įvertinti juodažiočio grundalo reikšmę plėšrių žuvų mityboje;
6. Įvertinti juodažiočio grundalo išplitimo sukeltą Baltijos jūros Lietuvos priekrantės ekosistemos mitybos tinklo lygmens poveikį atnaujinant 2000–2010 metų ECOPATH modelį.

Darbo naujumas

Šio darbo metu buvo pirmą kartą pristatomi juodažiočio grundalo invazijos skirtingų tipų buveinėse sukelti padariniai populiacijos, bendrijos ir ekosistemos lygmenyse. Šiame darbe pateikiami nauji rezultatai apie invazinio juodažiočio grundalo populiacijos ūgio ir amžiaus struktūrą, kūno būklę, mitybą bei pažeidžiamumą plėšrūnų poveikiui pietrytinės Baltijos jūros moreninio ir smėlėto dugno buveinėse. Tyrimo metu pirmą kartą buvo nustatyti juodažiočio grundalo plėšrūnizmo sukelti kaskadiniai efektai (ryškus midijų populiacijos sumažėjimas sąlygojo žiemojančių ledinių ančių mitybos ir trofinės padėties pokyčius). Šiame tyrime, naudojant ECOPATH modelį, buvo pirmą kartą įvertinti teigiamas ir neigiamas juodažiočio grundalo poveikiai Baltijos jūros mitybos tinklui.

Rezultatų mokslinė ir praktinė reikšmė

Šio darbo rezultatai papildė mokslines žinias apie juodažiočio grundalo invazijos sėkmę ir poveikį ekosistemos funkcionavimui skirtingų tipų buveinėse. Juodažiočio grundalo telkimasis riedulynuose bei naujai atsiradusi komercinė juodažiočio grundalo žvejyba yra svarbūs jūrinių saugomų teritorijų valdymo aspektai. Tyrimo metu gauti rezultatai galėtų būti panaudojami kuriant Jūros strategijos pagrindų direktyvos nevietinių rūšių poveikio vertinimo rodiklius. Skrandžio (žarnyno) turinio analizės, stabiliųjų izotopų analizės ir ECOPATH modelio rezultatai parodė, kad skirtingi metodai gali būti panaudoti analizuojant invazinių rūšių poveikį mitybos tinkle.

Rezultatų aprobavimas

Šio darbo rezultatai buvo pristatyti 8 tarptautinėse ir 3 nacionalinėse konferencijose ir seminaruose:

EUAC kongrese 2014, Genuja (Italija), 2014 m. lapkritis;

BONUS BIO-C3/BAMBI/INSPIRE 2015 vasaros mokykloje „Baltijos jūra: ateities pasaulinio vandenyno modelis“, Gliuksburgas (Vokietija), 2015 m. liepa;

1-oje Hjorto vasaros mokykloje „Žvejyba ir fizika kaip varomoji jūrinės ekosistemos jėga“, Bergenas (Norvegija), 2015 m. rugsėjis;

15-ame Europos ichtiologijos kongrese, Porto, Portugalija, 2015 m. rugsėjis;

Kursuose doktorantams „Žuvų ir žvejybos evoliucinė ekologija“, Kristinebergas (Švedija), 2015 m. rugsėjis–spalis;

Baltijos jūros juodažiočio grundalo darbinėje grupėje, Talinas (Estija), 2016 m. birželis;

NEOBIOTA 2016, Viandenas (Liuksemburgas), 2016 m. rugsėjis;

Kasmetinėje ICES mokslinėje konferencijoje, Ryga (Latvija), 2016 m. rugsėjis;

9-oje nacionalinėje konferencijoje „Jūros ir krantų tyrimai“, Klaipėda (Lietuva), 2016 m. balandis;

10-oje nacionalinėje konferencijoje „Jūros ir krantų tyrimai“, Palanga (Lietuva), 2017 m. balandis;

11-oje nacionalinėje konferencijoje „Jūros ir krantų tyrimai“, Klaipėda (Lietuva), 2018 m. gegužė.

Šios disertacijos rezultatai buvo paskelbti 2 mokslinėse publikacijose:

Skabeikis A., Lesutienė J. (2015) Feeding activity and diet composition of round goby (*Neogobius melanostomus*, Pallas 1814) in the coastal waters of SE Baltic Sea. *Oceanological and Hydrobiological Studies,* 44(4): 508–519;

Skabeikis A., Morkūnė R., Bacevičius E., Lesutienė J., Morkūnas J., Poškienė A., Šiaulys A. (2019) Effect of the round goby (*Neogobius melanostomus*) invasion on the blue mussel (*Mytilus edulis trossulus*) population and winter diet of the long-tailed duck (*Clangula hyemalis*). *Biological Invasions,* 21(3): 911–923.

Disertacijos struktūra

Disertaciją sudaro tokie skyriai: įvadas, literatūros apžvalga, medžiaga ir metodai, rezultatai, diskusija, išvados, literatūros sąrašas ir priedai. Disertacijos apimtis – 168 puslapiai. Disertacijoje panaudota 317 literatūros šaltinių. Disertacija parašyta anglų kalba su išplėstine santrauka lietuvių kalba. Joje yra 17 lentelių, 33 paveikslai ir 8 priedai.

Padėka

Pirmiausia norėčiau padėkoti savo mokslinei vadovei dr. Jūratei Lesutienei už pagalbą, naudingus patarimus ir konstruktyvią kritiką. Dėkoju kolegoms iš Žuvininkystės tarnybos prie Lietuvos Respublikos žemės ūkio ministerijos, Žuvininkystės tyrimų ir mokslo skyriaus: Žilvinui Kregždžiui, Deividui Norkui, Marijui Špėgiui, Petrui Tamašauskui bei žvejams verslininkams: Taurūnui Areškevičiui ir Arūnui Grigaičiui už pagalbą renkant žuvų mėginius. Taip pat padėkoju dr. Algimantui Petraičiui, dr. Rasai Morkūnei, Juliui Morkūnui ir Agnei Karlonei už atliktą žiemojančių ledinių ančių laboratorinę analizę. Esu dėkingas dr. Jelenai Fedotovai už pagalbą analizuojant otolitus, Egidijui Bacevičiui – už supažindinimą su skrandžio turinio analizės specifika, Irenai Pivoriūnienei – už asistavimą laboratorijoje, dr. Andriui Šiauliui – už sudarytą tyrimo vietos žemėlapį bei naudingus patarimus rankraščio rengimo metu. Dėkoju prof. dr. Artūrui Razinkovui-Baziukui ir Edgarui Ivanauskui už suteiktas konsultacijas kuriant ECOPATH modelį. Esu dėkingas Jūros tyrimų institutui bei Jūrinių tyrimų departamentui už zoobentoso duomenis ir Žuvininkystės tarnybai prie Lietuvos Respublikos žemės ūkio ministerijos už ilgalaikius juodažiočio grundalo gausumo, komercinių sugavimų ir pardavimų duomenis.

Didelę padėką skiriu kolegoms iš Lietuvos jūrų muziejaus, Akvariumo ir jūrų gamtos faunos skyriaus, už teigiamą požiūrį, draugišką darbinę aplinką, toleranciją, palaikymą bei suteiktą galimybę darbo valandų metu vykdyti lauko tyrimus, laboratorinę analizę ir dalyvauti moksliniuose renginiuose. Esu itin dėkingas Sauliui Karaliui už nupieštą schemą.

Dėkoju Klaipėdos universiteto Ekologijos ir aplinkotyros doktorantūros mokyklai už suteiktą kūrybingą tarpdisciplininių tyrimų atmosferą bei daugeliui gerbiamų mokslininkų ir kolegų už gautas žinias ir su disertacija susijusius naudingus patarimus.

Esu ypač dėkingas tėvams už suteiktą galimybę sieti aukštojo mokslo ir jų nuolatinį rūpestį bei palaikymą. Didžiausią padėką skiriu savo mylimai žmonai Eglei už supratingumą, kantrybę ir visapusišką pagalbą.

Šiam darbui finansinę paramą suteikė Klaipėdos universitetas, BONUS BIO-C3 projektas (*Biodiversity changes-causes, consequences and management implications*), bendrai finansuotas septintos Europos pagrindų programos ir Lietuvos Mokslo Tarybos (Nr. BONUS-1/2014).

TYRIMŲ MEDŽIAGA IR METODAI

Tyrimų rajonas ir lauko tyrimai

Tyrimas buvo vykdomas Baltijos jūros Lietuvos priekrantės stotyse ties Karkle (55°47’34”N; 21°02’96”E) ir Juodkrante (55°32’37”N; 21°05’26”E), atitinkamai reprezentuojančiose moreninio ir smėlėto dugno buveines (3 pav.). Žuvys buvo gaudomos 2014–2016 m. balandžio–spalio mėnesiais, 5–12 m gylyje, naudojant 3 įvairiaakių dugninių statomųjų tinklaičių komplektus (5 pav.). Abiejose tyrimo vietose studijos metu buvo paimta po 9 mėginius (1 lent.).

Daugiametė juodažiočio grundalo gausumo dinamika buvo vertinta analizuojant 2002–2016 m. priekrantėje ties Smiltyne surinktus ichtiologinio monitoringo duomenis (3 pav.). Vertinant juodažiočio grundalo mitybos pokyčius skirtingų invazijos stadijų metu, mėginiai moreninio dugno buveinėje buvo renkami 3 laikotarpių birželio–spalio mėnesiais: (1) 2008–2009 m. (duomenys surinkti E. Bacevičiaus), (2) 2012 m. ir (3) 2014–2015 m. (3 pav.). Lauko tyrimų metu sugautos žuvys buvo kaip įmanoma greičiau užšaldomos -20°C temperatūroje tolimesnei laboratorinei analizei.

Juodažiočio grundalo amžiaus nustatymas

Juodažiočio grundalo amžiui nustatyti naudoti otolitai buvo paimti iš 2015 m. liepos–rugsėjo mėnesiais priekrantėje ties Karkle ir Juodkrante sugautų žuvų. Proceso metu iš juodažiočių grundalų išimti abu (kairysis ir dešinysis) otolitai buvo nuvalomi etilo alkoholiu, išdžiovinami, šviesinami ksilolo tirpikliu, o paskui pagal otolito metinių žiedų skaičių buvo įvertinamas visų tirtų žuvų amžius.

Juodažiočio grundalo lyties ir vislumo nustatymas

Juodažiočiams grundalams būdingas porcijinis nerštas, todėl jų gonadų branda buvo vertinama pagal Tomczak'ą ir Sapota'ą (2006). Absoliutinis vislumas buvo vertinamas tik patelėms, turinčioms visiškai subrendusias (IV brandos stadijos) gonadas. Siekiant įvertinti skirtingoms amžiaus grupėms priklausančių žuvų vislumo pokyčius, buvo pasveriamas 1 gramas IV brandos stadijos moteriškųjų gonadų (± 0,001 g), nustatomas tikslus jame esančių ikrų skaičius, o viename grame gonadų esantį ikrų skaičių padauginus iš visos gonadų masės (anksčiau pasvertos iki ± 0,001 g), buvo įvertinamas absoliutinis patelės vislumas.

Skrandžio (žarnyno) turinio analizė

Bentofagių juodažiočių grundalų, upinių plekšnių, gyvavedžių vėgėlių ir žiobrių dietos sudėtis buvo vertinama iki žemiausio įmanomo taksono identifikuojant žarnyne aptiktus mitybos objektus, bei atkuriant jų šlapią svorį (Rumohr ir kt. 1987). Neidentifikuojamai suvirškinti mitybos objektai nebuvo įtraukiami į tolimesnius skaičiavimus. Siekiant įvertinti skirtingų dydžių žuvų raciono sudėtį, juodažiočiai grundalai ir upinės plekšnės buvo suskirstyti į dydžio grupes (Karlson ir kt. 2007), tuo tarpu gyvavedės vėgėlės ir žiobriai, pasižymėję nedidele kūno ilgio diferenciacija, nebuvo skirstomi į atskiras grupes.

Ichtiofagių menkių, otų, builių ir ešerių mityba buvo vertinama iki žemiausio įmanomo taksono identifikuojant burnos, gerklės ir skrandžio turiniuose aptiktus maistagyvius. Plėšrūnų suvartotų žuvų ilgis buvo nustatomas išmatuojant absoliutinį ilgį (TL), santykinį ilgį (SL) arba taikant TL : SL santykį (Pachur ir Horbowy 2013). Šlapias žuvų svoris buvo nustatomas pagal *Fishbase* duomenis (Froese ir Pauly 2007) arba pagal prarytos žuvies ir otolito dydžių santykį (Härkönen 1986). Suvartotų bestuburių gyvūnų šlapias svoris buvo atkuriamas pagal Rumohr'o ir kt. (1987) metodą, o neatpažinti mitybos objektai buvo šalinami iš tolimesnės analizės. Menkės į dideles ir mažas buvo skirstomos pagal Dziaduch'o (2011), ešeriai – pagal Płąchocki ir kt. (2012) metodiką, o otai ir builiai – pagal šio tyrimo metu įvertintą populiacijų ūgio struktūrą.

Stabiliųjų izotopų analizė

Skirtingo dydžio juodažiočio grundalo ir upinės plekšnės mėginiai izotopinei analizei buvo renkami 2015 m. rugsėjo–spalio mėnesiais priekrantėje ties Juodkrante. Dugno bestuburiai (*L. balthica*, *C. lamarcki*, *M. arenaria*, *C. crangon*, daugiašerės kirmėlės ir šoniplaukos), potencialiai sudarantys bentofagių žuvų dietos pagrindą smėlėto dugno buveinėje, priekrantėje ties Juodkrante buvo surinkti 2015 m. spalio 9 d. naudojant Van Veen'o gruntotraukį 5, 10, 15 ir 20 m gylyje, kiekviename gylio horizonte imant po 3 mėginius. Smėliniai grundalai, reprezentuojantys juodažiočio grundalo ir upinės plekšnės vartojamas žuvis, buvo sugauti 2018 m. gegužę priekrantėje ties Smiltyne 1,5 m gylyje rankiniu graibštu. Surinkti mėginiai buvo 48 h džiovinami 60°C temperatūroje, sutrinami agato grūstuvėje (Jardine et al. 2003), sudedami į alavo kapsules ir išsiunčiami į Kalifornijos Daviso universiteto stabiliųjų izotopų laboratoriją (UC Davis Stable Isotope Facility), kur masės spektrometru buvo įvertinama kiekvieno mėginio izotopinė sudėtis. Skirtingo dydžio juodažiočių grundalų ir upinių plekšnių mitybinių nišų plotis ir jų persidengimas buvo vertinami naudojant R programos SIBER paketą (18 pav., 11 lent.), o kiekybinis mitybos šaltinių įvertinimas – R programos SIAR paketą (21 pav., 12 lent.).

Statistinės analizės metodai

Permutacinė vienfaktorinė ir dvifaktorinė ANOVA (PERMANOVA) (Anderson 2001) buvo taikoma vertinant tyrimo metų poveikį moreninio ir smėlėto dugno buveinių žuvų bendrijoms (2 lent.), sezono poveikį upinės plekšnės ir žiobrio dietos sudėčiai bei sezono ir buveinės tipo poveikį skirtingo dydžio juodažiočių grundalų mitybai (6 lent.). Neparametrinis daugiamačių skalių (nMDS) metodas buvo panaudotas siekiant parodyti žuvų bendrijos gausumo pokyčius po juodažiočio grundalo išplitimo moreninio ir smėlėto dugno buveinėse (8 pav.). Panašumų analizė (SIMPER) buvo naudojama vertinant juodažiočio grundalo ir upinės plekšnės skirtingų mitybos objektų reikšmę jų racione (10 lent.). Pagrindinių komponenčių analizė (PCA) naudota nustatant abiejų tipų buveinėse tirtų ichtiofagių žuvų dietos sudėtį (26 pav.). Įvairių žuvų rūšių skrandžio užpildymo indekso vertės buvo nustatomos pagal Hyslop'o (1980), kūno būklės indekso vertės – pagal Froese'o (2006) (7 lent., 15 lent.), mitybinių nišų plotis – pagal Levins'o (1968) (8 lent.), o mitybinių nišų persidengimas – pagal Schoener'io (1970) metodus (9 lent.). Juodažiočio grundalo mitybos strategija moreninio ir smėlėto dugno buveinėse buvo vertinama pagal Amundsen'o ir kt. (1996) metodą (16 pav.). Atliekant 2 ar daugiau grupių parametrinių duomenų lyginimą buvo naudojami įvairūs testai: *t* testas, vienfaktorinė ANOVA, dvifaktorinė ANOVA ir MANOVA. Prieš analizuojant duomenų normališkumas buvo tikrinamas naudojant Kolmogorov'o ir Smirnov'o, o dispersijų homogeniškumas – Levene'o testus. Tais atvejais, kai lyginamų grupių dispersijos reikšmingai skyrėsi, buvo naudojami neparametriniai Mano ir Vitnio (Mann-Whitney) *U*, Medianų ir Kruskalio ir Voliso (Kruskal-Wallis) testai. Visų atliktų testų atveju reikšmingumo lygmuo buvo laikomas $p < 0,05$.

ECOPATH modelis

Naudojant ECOPATH programinę įrangą buvo atnaujintas 2000–2010 m. laikotarpiui sukurtas mitybos tinklo modelis (2011–2015 m.), reprezentuojantis juodažiočio grundalo išplitimo poveikį Lietuvos priekrantės mitybos tinklo funkcionavimui. Naujasis modelis buvo papildytas 6 naujais komponentais: po dvi juodažiočių grundalų, menkių ir builių grupes, o jo sudėtyje buvo 46 gyvų komponentų grupės ir viena detrito grupė (1 priedas). Kuriant 2011–2015 m. modelį taip pat buvo pakeisti tam tikrų mitybos tinklo komponentų biomasės ir mitybos matricos (1 priedas) bei komercinės žvejybos sugavimo rodikliai. Balansuojant modelį buvo remiamasi ekotrofinio efektyvumo (EE) įverčiais.

REZULTATAI

Rezultatai pristatyti 6 skyriuose: 1) *Juodažiočio grundalo invazijos ypatumai, gausumas ir reikšmė priekrantės moreninio ir smėlėto dugno buveinių žuvų bendrijose*; 2) *Juodažiočio grundalo ūgio ir amžiaus struktūra, fiziologinė būklė bei vislumas*; 3) *Juodažiočio grundalo mitybos ypatumai ir mitybos persidengimas su vietinėmis bentofagėmis žuvimis*; 4) *Juodažiočio grundalo plėšrūnizmo sukelti midijų populiacijos ir žiemojančios ledinės anties mitybos pokyčiai moreninio dugno buveinėje*; 5) *Juodažiočio grundalo reikšmė plėšrių žuvų mityboje* ir 6) *Priekrantės mitybos tinklo ECOPATH modelis*.

Pirmame skyriuje pateikti rezultatai apima ilgametę (2002–2016 m.) juodažiočio grundalo gausumo dinamikos analizę Smiltynės zonoje (pirmoji rūšies registravimo vieta Lietuvos priekrantėje) bei gausumo kaitos tendencijas ir poveikį priekrantės moreninio ir smėlėto dugno buveinių žuvų bendrijoms 2014–2016 m. laikotarpiu.

Remiantis juodažiočio grundalo gausumo dinamika Smiltynės zonoje, rūšies invazijos periodas buvo suskirstytas į 4 fazes: atvykimas, įsitvirtinimas, išplitimas bei prisitaikymas (6 pav.). Juodažiočio grundalo gausumas ir biomasė 2014–2016 m. buvo statistiškai reikšmingai didesni moreninio dugno biotope (abiem atvejais pagal Kruskalio ir Voliso testą $p < 0,05$) (7 pav.). Po reikšmingo juodažiočio grundalo gausumo padidėjimo 2016 m. ši rūšis pradėjo dominuoti moreninio dugno buveinės ichtiofaunoje (89 % visų sugautų žuvų gausumo), dėl ko pasikeitė biotopo žuvų bendrijos struktūra (8 pav.; 2 lent.). Po juodažiočio grundalo gausumo padidėjimo riedulyne nustatytas statistiškai reikšmingas ešerio ir kuojos gausumo sumažėjimas bei menkės ir builio gausumo padidėjimas (visais atvejais pagal Mano ir Vitnio U testą $p < 0,05$). Skirtingai nei moreninio dugno buveinėje, smėlėtame biotope juodažiočio grundalo gausumas buvo santykinai nedidelis (12 % visų sugautų žuvų gausumo), o atskirų žuvų rūšių gausumas (visais atvejais pagal Mano ir Vitnio U testą $p > 0,05$) ir žuvų bendrijos struktūra skirtingais tyrimo periodais nekito (8 pav.; 10 pav.). Reikšmingas juodažiočio grundalo gausumo padidėjimas moreninio dugno priekrantėje ~ 3 kartus sumažino ichtiofaunos bioįvairovę (9 pav.; 3 lent.), tačiau sugaunamų žuvų rūšių skaičius biotope išliko nepakitęs (9 pav.).

Antrame skyriuje pristatomi juodažiočio grundalo morfometrinių ir biologinių parametrų skirtumai priekrantės moreninio ir smėlėto dugno buveinėse.

Tyrimo metu nustatyta, kad abiejų tipų beveinėse juodažiočių grundalų populiacijos pagrindą sudarė 3+ ir 4+ individai (11 pav.), tačiau moreninio dugno biotope buvo sugaunamos statistiškai reikšmingai vyresnės žuvys (pagal medianų testą $p < 0,05$). Juodažiočio grundalo kūno ilgis, svoris (12 pav.; 5 lent.), fiziologinės būklės indekso vertės (13 pav.; 5 lent.) ir vislumas (14 pav.; 5 lent.) amžiaus grupėse buvo statistiškai reikšmingai didesni smėlėto dugno priekrantėje.

Trečiame skyriuje pateiktas sezoninis juodažiočio grundalo, upinės plekšnės, gyvavedės vėgėlės ir žiobrio raciono sudėties ir mitybinių nišų persidengimo įvertinimas (pagal skrandžio turinio analizės rezultatus) moreninio ir smėlėto dugno buveinėse. Šiame skyriuje taip pat pristatytas stabiliųjų anglies, azoto ir sieros izotopų analizės metodu įvertintas juodažiočio grundalo ir upinės plekšnės mitybinių nišų persidengimas bei dietos sudėtis smėlėtame biotope.

Riedulyne juodažiočių grundalų raciono pagrindą pavasarį ir rudenį sudarė <10 mm midijos, jūrų gilės ir žuvys, tuo tarpu vasarą užfiksuotas ryškus daugiašerių kirmėlių dominavimas (15 pav.). Smėlėto dugno buveinėje juodažiočių grundalų racionas sezoniškai kito nedaug ir buvo daugiausia sudarytas iš daugiašerių kirmėlių, infaunos moliuskų (*L. balthica* ir *M. arenaria*) bei smėlinių krevečių (5 pav.). Skirtingo dydžio upinės plekšnės abiejų tipų buveinėse daugiausia mito infaunos moliuskais ir daugiašerėmis kirmėlėmis, gyvavedžių vėgėlių raciono pagrindą sudarė šoniplaukos, daugiašerės kirmėlės ir midijos, o žiobriai pirmenybę teikė infaunos moliuskams, daugiašerėms kirmėlėms, smėlinėms krevetėms ir žaliadumbliams (17 pav.). Mitybinių nišų persidengimo analizė (pagal Schoener'io indeksą) parodė, kad riedulyne juodažiočio grundalo ir vietinių bentofagių žuvų mitybos nepersidengia, tuo tarpu smėlėtame biotope statistiškai reikšmingas juodažiočio grundalo ir upinės plekšnės mitybinių nišų persidengimas buvo nustatytas pavasario–rudens sezonų metu (9 lent.). Mitybinė abiejų rūšių konkurencija buvo sąlygota intensyvaus infaunos moliuskų ir daugiašerių kirmėlių vartojimo (10 lent.).

Izotopinės analizės metu nustatytas žemesnio lygmens skirtingo dydžio juodažiočių grundalų ir upinių plekšnių mitybinių nišų persidengimas (18 pav.; 11 lent.). Mažų ir vidutinio dydžio juodažiočių grundalų mitybinės nišos persidengė su mažų upinių plekšnių mitybinėmis nišomis, tuo tarpu didelių grundalų mityba buvo reikšmingai panaši į mažų ir vidutinio dydžio upinių plekšnių racioną (11 lent.). Didelės upinės plekšnės pasižymėjo gerokai aukštesnėmis $\delta^{15}N$ vertėmis lyginant su visomis juodažiočio grundalo dydžių grupėmis (20 pav.), todėl jų mitybinių nišų persidengimas buvo nereikšmingas (18 pav.; 11 lent.). Stabiliųjų izotopų penkių šaltinių maišymosi modelio rezultatai parodė, kad visų juodažiočio grundalo ir upinės plekšnės dydžio grupių mityboje dominavo daugiašerės kirmėlės (21 pav.; 21 lent.).

Ketvirtame skyriuje pateikiami rezultatai, apimantys juodažiočio grundalo plėšrūnizmo sukeltų midijų biomasės ir ūgio struktūros pokyčių sąlygotus ilgalaikius žiemojančios ledinės anties raciono sudėties ir trofinio lygmens pokyčius moreninio dugno priekrantėje.

Midijų biomasė moreninio dugno buveinėje drastiškai mažėjo (22 pav.) didėjant juodažiočio grundalo gausumui (6 pav.). Prieš juodažiočio grundalo išplitimo fazę midijų populiacija buvo sudaryta iš 2–37 mm individų, tarp kurių dažniausiai randami buvo 2–20 mm moliuskai, tuo tarpu po grundalų išplitimo fiksuoti tik labai maži (<10 mm) arba labai dideli (>25 mm) individai (23 pav.). Kardinaliai sumažėjus midijų biomasei ir pasikeitus jų ūgio struktūrai, žiemojančios ledinės antys pakeitė dominuojantį dietos komponentą iš midijų į žuvis (24 pav.), dėl to gerokai padidėjo jų trofinis lygmuo (33 pav.). Ledinių ančių, pradėjusių maitintis žuvimis, mitybos efektyvumas sumažėjo, tačiau fiziologinė būklė pagerėjo palyginti su periodu, kuomet dietoje dominavo midijos (14 lent.). Itin padidėjus grundalų gausumui ir racione pradėjus dominuoti infaunos bestuburiams, jų fiziologinė būklė statistiškai reikšmingai suprastėjo (pagal Mano ir Vitnio U testą $p < 0{,}001$) (13 lent.). Juodažiočio grundalo ir ledinės anties mitybinės nišos reikšmingai persidengė įsitvirtinimo stadijos metu (Schoener'io indeksas = 0,76) (abiejų rūšių dietos pagrindą sudarė midijos), o išplitimo (0,20) ir prisitaikymo (0,17) stadijose mitybinių nišų persidengimas tapo nereikšmingas rūšims prisitaikius maitintis skirtingais mitybos objektais (24 pav.).

Penktame skyriuje pristatomi rezultatai, apimantys juodažiočio grundalo reikšmę plėšrių žuvų mityboje ir jų efektyvumą maitinantis juodažiočiais grundalais heterogeniškame riedulyne bei homogeniškoje smėlėto dugno buveinėje.

Bendras plėšrių žuvų mitybos efektyvumas buvo didesnis moreninio dugno buveinėje (atitinkamai 81 % ir 87 % tirtų ichtiofagių žuvų), tačiau analizuotų plėšrūnų dalis su skrandžio turinyje aptiktais juodažiočiais grundalais buvo gerokai didesnė smėlėtame biotope (atitinkamai 46 % ir 73 %) (15 lent.). Pagrindinių komponenčių analizės rezultatai parodė, kad abiejose tirtose buveinėse juodažiotis grundalas tapo esminiu plėšrių žuvų mitybos komponentu, o pirmos 2 komponentės paaiškino 80 % duomenų kintamumo (atitinkamai 61 % ir 19 %) (25 pav.). Invazinis juodažiotis grundalas buvo svarbiausias abiejuose biotopuose sugautų menkių, otų, builių ir ešerių mitybos objektas. Pažymėtina, kad didelę riedulyne sugautų ešerių dietos dalį sudarė mėlynžnyplės krevetės ir stintos, o smėlėto dugno buveinėje sugautų mažų (<200 mm) builių mityboje dominavo smėlinės krevetės (24 pav.). Plėšrios žuvys tyrimo metu maitinosi 38–156 mm dydžio juodažiočiais grundalais (27 pav.), pirmenybę teikdamos 40–100 mm individams (28 pav.).

Šeštame skyriuje pateikiami rezultatai, apimantys ECOPATH modeliu įvertintą skirtingo dydžio juodažiočių grundalų trofinę padėtį, reikšmingumo indekso vertes ir poveikį kitiems mitybos tinklo komponentams.

Juodažiočio grundalo jaunikliai ir suaugę individai mitybos tinkle užėmė atitinkamai 3,0 ir 3,2 trofinius lygmenis (29 pav.; 7 priedas). Abi juodažiočio grundalo grupės teigiamai paveikė 10, o neigiamai – 14 mitybos tinklo komponentų grupių. Juodažiočiai grundalai padarė teigiamą įtaką ichtiofagėms žuvims ir vandens paukščiams bei žvejybai, tačiau neigiamai paveikė daugiašeres kirmėles, filtruojančius ir visaėdžius dugno bestuburius, bentofages žuvis ir žiemojančias antis. Juodažiočius grundalus teigiamai paveikė gamintojai, filtruojantys dugno bestuburiai, daugiašerės kirmėlės ir žvejyba, tačiau buvo nustatytas neigiamas ichtiofagių žuvų ir vandens paukščių poveikis (30 pav.). Juodažiočio grundalo jaunikliai padarė teigiamą poveikį visiems mitybos tinklo komponentams, tuo tarpu suaugėliai – neigiamą (31 pav.). Juodažiočio grundalo jaunikliai ir suaugę individai tapo svarbiais priekrantės mitybos tinklo komponentais (reikšmingumo indekso vertės atitinkamai -0,12 ir -0,07) (32 pav.).

DISKUSIJA

Diskusiją sudaro šeši skyriai: 1) *Juodažiočio grundalo invazijos sėkmė bei vaidmuo moreninio ir smėlėto dugno buveinių žuvų bendrijose*; 2) *Morfometriniai ir biologiniai juodažiočio grundalo parametrai*; 3) *Mitybinės nišos persidengimas su vietinėmis bentofagėmis žuvimis: skrandžio turinio vs. stabiliųjų izotopų analizė*; 4) *Juodažiočio grundalo reikšmė plėšrių žuvų mityboje*; 5) *Ar juodažiotis grundalas sukėlė priekrantės mitybos tinklo pokyčius?* ir 6) *Poveikis nykstančių ančių populiacijoms ir jūrinių saugomų teritorijų valdymui*.

Pirmame skyriuje lyginami juodažiočio grundalo gausumas ir biomasė moreninio ir smėlėto dugno buveinėse bei jo reikšmė abiejų tirtų biotopų žuvų bendrijose. Tyrimo metu nustatyta, kad buveinės heterogeniškumas yra pagrindinis veiksnys, nulemiantis juodažiočio grundalo invazijos sėkmę. Moreninio dugno priekrantėje juodažiotis grundalas pasiekė išplitimo fazę praėjus 4–6 metams nuo pirmo rūšies registravimo, tuo tarpu homogeniškame smėlėtame biotope invazinio grundalo gausumas 2008–2018 m. periode išliko stabiliai žemas. Riedulyne juodažiočio grundalo gausumas ir biomasė buvo statistiškai reikšmingai didesni palyginti su smėlėto dugno buveine, kas patvirtina anksčiau atliktų tyrimų rezultatus (Ray ir Corkum 2001; Johnson ir kt. 2005; Taraborelli ir kt. 2009; Young ir kt. 2010). Juodažiočio grundalo dominavimą moreninio dugno priekrantės žuvų bendrijoje sąlygojo optimalus buveinės tipas (daug slėptuvių ir tinkamų nerštaviečių) bei nedidelio masto konkurencija dėl resursų ir plėšrūnizmo poveikis, nulemtas nedidelio dugninių žuvų gausumo ir nežymaus persidengimo laike ir erdvėje su migruojančiomis plėšriomis žuvimis (Ložys

2003; Florin ir Franzén 2010; Olsson ir kt. 2012). Skirtingai nei riedulyne, smėlėto dugno priekrantėje juodažiočio grundalo gausumas ir reikšmė žuvų bendrijoje buvo gerokai mažesni, kadangi homogeniškame, slėptuvių neturinčiame biotope grundalai yra labai pažeidžiami plėšrūnų (Belanger ir Corkum 2003), o gausios dugninių žuvų populiacijos (3 priedas) sąlygojo intensyvią konkurenciją dėl resursų. Didelis upinių plekšnių, efektyviai mintančių 40–60 mm dydžio juodažiočiais grundalais (Skabeikis, nepublikuoti duomenys) gausumas taip pat sumažino invazinės rūšies populiacijos augimo potencialą.

Nemažas juodažiočio grundalo gausumo padidėjimas moreninio dugno priekrantėje ~3 kartus sumažino ichtiofaunos bioįvairovę, tačiau nei sugaunamų žuvų rūšių skaičius, nei atskirų rūšių gausumas statistiškai reikšmingai nesumažėjo. Anksčiau atliktų tyrimų metu nustatyta, kad smulkių žuvų (smėlinių grundalų, trispyglių dyglių ir stintų jauniklių) gausumas ir biomasė mažėja didėjant invazinio juodažiočio grundalo gausumui (Corkum ir kt. 2004). Lietuvos priekrantėje didžiausios stintų jauniklių ir trispyglių dyglių santalkos stebimos priekrantės žemyninės dalies moreninio dugno buveinėje (Repečka ir kt. 1996), kur juodažiočio grundalo gausumas yra labai didelis. Šios smulkios žuvys yra dažnai aptinkamos didelių juodažiočių grundalų žarnyno turinyje (Skabeikis 2013; Skabeikis ir Lesutienė 2015; šis tyrimas), todėl reikalingi išsamūs tyrimai, leisiantys įvertinti juodažiočio grundalo plėšrūnizmo poveikį smulkioms pašarinėms žuvims bei komerciškai vertingų stintų jaunikliams Baltijos jūros priekrantėje.

Antrame skyriuje aptariami morfometrinių ir biologinių juodažiočio grundalo parametrų skirtumai moreninio ir smėlėto dugno buveinėse. Juodažiočio grundalo morfometrinių ir biologinių parametrų vertės daugiausia priklauso nuo pašarinės bazės kokybės (Duan ir kt. 2016) ir populiacijos tankio (Kornis ir kt. 2014). Riedulyno mitybos objektų pašarinė vertė buvo mažesnė dėl nemaistingų, sunkiai virškinamų jūrų gilių ir midijų (Brey ir kt. 1988; Thiyagarajan ir kt. 2003) dominavimo, tuo tarpu smėlėto dugno buveinės zoobentoso, sudaryto iš lengvai virškinamų daugiašerių ir mažašerių kirmėlių bei šoniplaukų, maistinė vertė buvo gerokai didesnė (Brey ir kt. 1988). Dėl didesnio (~15 kartų) gausumo ir prastesnės pašarinės bazės, juodažiočio grundalo kūno ilgis, svoris, kūno būklė ir vislumas buvo statistiškai reikšmingai mažesni moreninio dugno buveinėje, o tai rodo, kad invaziniai grundalai šio tipo biotope artėja prie aplinkos talpos arba ją net viršija (Young ir kt. 2010; Thompson ir Simon 2015). Pažymėtina, kad juodažiočio grundalo morfometrinių ir biologinių parametrų vertės abiejuose Lietuvos priekrantės biotopuose buvo gerokai didesnės palyginti su kitomis kolonizuotomis ekosistemomis (16 lent.).

Trečiame skyriuje analizuojami moreninio ir smėlėto dugno buveinėse sugautų juodažiočių grundalų ir bentofagių žuvų raciono ir mitybinių nišų persidengimai remiantis žarnyno turinio analizės metu gautais rezultatais. Šiame skyriuje taip pat aprašomi stabiliųjų izotopų analizės metu nustatyti skirtingo dydžio juodažiočių grundalų ir upinių plekšnių mitybos ypatumai smėlėtame biotope. Juodažiočio grundalo mitybos pokyčiai moreninio dugno buveinėje buvo sąlygojami sezoninių midijų gausumo svyravimų. Midijos juodažiočio grundalo racione dominavo rudenį, kai jų gausumas buvo itin didelis po naujos generacijos individų nusėdimo ant kietų substratų (Kautsky 1982), tuo tarpu vasarą, dėl grundalų plėšrūnizmo drastiškai sumažėjus pernykštės generacijos midijų gausumui, grundalai pradėjo misti dažniausia jaunomis, sedimentų paviršiuje besilaikančiomis daugiašerėmis kirmėlėmis (Marty ir Retiere 1999). Smėlėtame biotope juodažiočio grundalo mityba sezoniškai kito nedaug, o jos pagrindą sudarė daugiašerės kirmėlės ir dvigeldžiai moliuskai *M. arenaria*. Pažymėtina, kad rudenį abiejų tipų buveinėse didelę juodažiočių grundalų raciono dalį sudarė Baltijos jūros priekrantėje besitelkiantys stintų jaunikliai (Ustups ir kt. 2003).

Mitybinių nišų persidengimo analizės rezultatai parodė, kad riedulyne vietinių bentofagių žuvų ir juodažiočio grundalo dietos reikšmingai nepersidengia, nes heterogeniška buveinės aplinka rūšims suteikia daugiau galimybių specializuotis ir vartoti skirtingus mitybos objektus. Lyginant laikotarpius prieš juodažiočio grundalo invaziją ir po jos, dominuojantys upinės plekšnės mitybos komponentai riedulyne pasikeitė iš midijų į infaunos moliuskus (Bubinas and Ložys 2003; šis tyrimas). Labai tikėtina, jog dėl juodažiočio grundalo sukeltos tarprūšinės resursų konkurencijos plekšnių maitinimasis ant kietų substratų pasidarė sunkiau prieinamas. Skirtingai nei moreninio dugno buveinėje, smėlėtame biotope juodažiočio grundalo ir upinės plekšnės mitybinės nišos persidengė reikšmingai, tačiau tai nepadarė neigiamos įtakos, nes abiejų rūšių žuvys šio tipo buveinėje pasižymėjo geresne fiziologine būkle.

Stabiliųjų izotopų analizės metu gauti rezultatai parodė, kad smėlėto dugno priekrantėje juodažiočio grundalo ir upinės plekšnės mitybinių nišų persidengimo laipsnis buvo mažesnis palygti su Schoener'io indekso vertėmis. Šių skirtingais metodais įvertintų rezultatų neatitikimą greičiausiai sąlygojo tai, kad vidutinio dydžio ir didelės upinės plekšnės turėjo didesnes stabiliųjų azoto izotopų vertes, o tai rodo jų maitinimąsi aukštesniame trofiniame lygmenyje. Stabiliųjų sieros izotopų skirtumai taip pat galėjo būti nulemti skirtingame sedimentų gylyje gyvenančių dugno bestuburių vartojimo (Kharlamenko ir kt. 2001). Skrandžio turinio analizė leido nustatyti momentinę mitybos sudėtį, tuo tarpu izotopinės analizės rezultatai potencialiai parodė vasaros sezono racioną, nes juodažiočio grundalo ir upinės plekšnės organizme 50 % raumenyse esančios izotopinės mitybos sudėties pokytis įvyksta per atitinkamai ~ 2 ir 3 mėnesius (apskaičiuota pagal Vander'į Zanden'ą ir kt. 2015). Juodažiočio grundalo ir upinės plekšnės izotopinės mitybos sudėties skirtumus galėjo sukelti ir plekšnės didelio nuotolio migracijos (Raffaelli ir kt. 1990; Karlson ir kt. 2007; Dando 2011), kurių metu potencialiai buvo mintama skirtingą izotopinį signalą turinčiomis aukomis, tuo tarpu pavasarį–rudenį sėsliai gyvenantiems juodažiočiams grundalams (Ray ir Corkum 2001) buvo būdinga mažiau įvairi vietinė izotopinė sudėtis. Nepaisant juodažiočio grundalo sezoninių migracijų į dideliame gylyje esančias žiemavietes ir iš jų (Christoffersen ir kt. 2019), sezoninių migracijų poveikis jų izotopiniam signalui buvo nereikšmingas, nes laikotarpis nuo juodažiočio grundalo atvykimo į priekrantės zoną iki mėginių rinkimo izotopinei analizei buvo ~2 kartus ilgesnis nei organizmuose 50 % raumenyse esančios izotopinės mitybos sudėties pasikeitimas (apskaičiuota pagal Vander'į Zanden'ą ir kt. 2015).

Ketvirtame skyriuje apibrėžiami menkės, oto, builio ir ešerio mitybos ypatumai bei natūralaus juodažiočio grundalo išgaudymo efektyvumas moreninio ir smėlėto dugno priekrantėje. Tyrimų metu nustatyta, kad nepaisant gerokai mažesnio juodažiočio grundalo gausumo, plėšrios žuvys invaziniais grundalais efektyviau mito smėlėtame biotope, kadangi limituotas juodažiočio grundalo plaukimo greitis (Charlebois ir kt. 1997) sąlygojo mažesnį atsparumą plėšrūnizmui slėptuvių neturinčioje aplinkoje. Lyginant ichtiofagių žuvų mitybos sudėtį prieš juodažiočio grundalo invaziją (Bubinas ir Ložys 2000; Bubinas ir Vaitonis 2003; Stankus 2003) ir po jos (Narvilas 2003; šis tyrimas) nustatyta, kad plėšrios žuvys pakeitė savo racioną iš strimėlių, bretlingių, mažųjų tobių ir įvairių dugno bestuburių į juodažiočius grundalus, dėl to sumažėjo plėšrūnizmo poveikis vietiniams hidrobiontams.

Iš tyrimo rezultatų galima spręsti, kad menkės, oto ir ešerio populiacijų dydis moreninio dugno buveinėje yra nepakankamas, kad galėtų reikšmingai sumažinti juodažiočio grundalo gausumą, tačiau juodažočiai grundalai užtikrino geresnę pašarinę bazę įvairioms vietinių žuvų (Bubinas ir Ložys 2000; Bubinas ir Vaitonis 2003; Razinkovas-Baziukas ir kt. 2017) ir vandens paukščių (Žydelis 2002; Morkūnė ir kt. 2016, 2018) rūšims. Priešingai nei riedulyne, mažą juodažiočio grundalo gausumą smėlėto dugno priekrantėje tikriausiai sąlygojo efektyvus ichtiofagių žuvų (šis tyrimas) ir didžiųjų kormoranų iš gretimai esančios kolonijos (Pūtys ir Zarankaitė 2010) plėšrūnizmo poveikis.

Penktame skyriuje aptariami teigiamas ir neigiamas juodažiočio grundalo išplitimo sukeltas poveikis Baltijos jūros Lietuvos priekrantės mitybos tinklui. Juodažiočiai grundalai sėkmingai įsitvirtino Lietuvos priekrantės mitybos tinkle ir suformavo tiesioginius ryšius su 15 mitybos tinklo komponentų, dėl to atsirado naujų energijos perdavimo kelių (dugno bestuburiai – juodažiotis grundalas – plėšrios žuvys ir vandens paukščiai). Didelės juodažiočio grundalo reikšmingumo indekso vertės buvo sąlygotos jo maitinimosi įvairais planktoniniais ir dugniniais bestuburiais bei žuvimis (Skabeikis ir Lesutienė 2015), trofinių sąveikų su vietinėmis bentofagėmis žuvimis (Herlevi ir kt. 2018) ir žiemojančiomis antimis (Skabeikis ir kt. 2019) ir didelės reikšmės plėšrių žuvų (Narvilas 2013) ir didžiųjų kormoranų (Pūtys ir Zarankaitė 2010; Pūtys 2012) dietoje bei komercinėje priekrantės žvejyboje (Ložys ir kt. 2016).

Dėl plėšrūnizmo poveikio juodažiotis grundalas padarė neigiamą įtaką įvairiems dugno bestuburiams gyvūnams (šis tyrimas), tuo tarpu planktofagės ir bentofagės žuvys ir žiemojančios antys buvo neigiamai paveiktos dėl mitybos konkurencijos (Bubinas ir Ložys 2000; Žydelis 2002; Skabeikis ir Lesutienė 2015; Morkūnė 2017; Morkūnė ir kt. 2018; Skabeikis ir kt. 2019). Plėšrios žuvys (Narvilas 2013; šis tyrimas), vandens paukščiai (Pūtys 2012) ir komercinė priekrantės žvejyba (Ložys ir kt. 2016) buvo teigiamai paveiktos juodažiočio grundalo gausumo padidėjimo, nes ši rūšis tapo svarbiu mitybos komponentu ir laimikiu (komercine prasme). Juodažiočiai grundalai buvo teigiamai paveikti gamintojų, suteikiančių pašarinę bazę jų pelaginiams ir dugniniams mitybos objektams (Dolmer 2000; Berezina ir kt. 2005), filtruojančių dugno bestuburių ir daugiašerių kirmėlių, sudarančių jų dietos pagrindą (šis tyrimas) bei komercinės žvejybos, iš ekosistemos pašalinančios jais mintančias plėšrias žuvis (Jørgensen ir kt. 2009) ir vandens paukščius (Žydelis ir kt. 2009). Pažymėtina, kad 2011–2015 m. periodo ECOPATH modelis negali būti naudojamas vertinant mitybos tinklo struktūros ir energijos srautų pokyčius po drastiško midijų populiacijos sumažėjimo moreninio dugno priekrantėje, nes kalibruojant modelį buvo naudojamos jau sunykusios midijų populiacijos biomasės vertės.

Šeštame skyriuje pristatomi juodažiočio grundalo poveikis nykstančių žiemojančių ančių populiacijoms bei rekomendacijos dėl jūrinių saugomų teritorijų valdymo. Dėl juodažiočio grundalo plėšrūnizmo drastiškai sumažėjusi midijų populiacija potencialiai pablogino ledinių ančių žiemavietės kokybę, o tai gali būti limituojantis veiksnys atsistatant rūšies gausumui Lietuvos priekrantėje (Skabeikis ir kt. 2019). Sumažėjus midijų biomasei ir pakitus jų populiacijos ūgio struktūrai, Lietuvos priekrantėje nuo 2012 metų nebeaptinkama sibirinė gaga (Saulius Karalius, LOD, asm. pran.), kuri prieš du dešimtmečius buvo gausiai žiemojanti rūšis (Žydelis 1997). Labai tikėtina, kad žiemojančių ančių populiacija Lietuvos priekrantėje nepasieks ankstesnio gausumo tol, kol neatsistatys midijų populiacija. Kita vertus, sumažėjęs žiemojančių ančių skaičius Lietuvos priekrantėje gali būti pasaulinio atšilimo padarinys, kadangi pastaruoju metu vandens paukščiai žiemoja vietovėse, nutolusiose į šiaurę bei rytus nuo jų ankstesnių žiemojimo arealų (Fox ir kt. 2018).

Juodažiočio grundalo gausumo mažinimas moreninio dugno buveinėje turėtų būti vykdomas gaudant grundalus prieš nerštinį periodą ir jo metu naudojant dugnines gaudykles, kurios yra efektyviausias gaudymo įrankis heterogeniškoje aplinkoje (Diana ir kt. 2006) bei mažiausiai kenkia žiemojančioms antims (Julius Morkūnas, Jūros tyrimų institutas, asm. pran.) ir ruoniams (Westerberg ir kt. 2007). Kitos potencialiai juodažiočio grundalo gausumą galinčios sumažinti priemonės yra plėšrių žuvų žvejybos kvotų sumažinimas (Ojaveer ir kt. 2015) ir kormoranų kolonijos netrikdymas Plazės rezervate, nes tai sąlygotų didesnį natūralų juodažiočio grundalo mirtingumą. Smėlėtame biotope, kuriame negausu juodažiočių grundalų, natūrali populiacijos dydžio kontrolė turėtų būti palikta plėšrūnams.

IŠVADOS

1. Juodažiočio grundalo gausumas buvo statistiškai reikšmingai didesnis moreninio dugno buveinėje, kur ši rūšis tapo dominuojančiu ichtiofaunos komponentu (47–89 % nuo visų sugautų žuvų), tuo tarpu smėlėtame biotope juodažiočio grundalo reikšmė buvo gerokai mažesnė (11–14 %). Žuvų bioįvairovės indeksas (H') riedulyne sumažėjo ~3 kartus lyginant periodus, kai juodažiočio grundalo gausumas buvo mažas ir didelis, tačiau sugaunamų rūšių skaičius ir bendras daugumos rūšių gausumas reikšmingai nepakito.
2. Juodažiočio grundalo populiacija moreninio dugno buveinėje buvo sudaryta iš vyresnių individų, tačiau kūno ilgis, svoris, kūno būklė ir vislumas amžiaus grupėse buvo didesni smėlėtame biotope, o tai rodo geresnę pašarinę bazę ir (ar) mažesnio laipsnio konkurenciją dėl resursų.
3. Juodažiotis grundalas riedulyne vasaros ir rudens sezonais daugiausia mito midijomis, jūrų gilėmis ir žuvimis, tuo tarpu vasarą jo racione dominavo daugiašerės kirmėlės. Juodažiočio grundalo mityba smėlėto dugno buveinėje sezonų eigoje keitėsi nedaug, o jos pagrindą sudarė daugiašerės kirmėlės, *M. arenaria*, *L. balthica* ir smėlinės krevetės. Statistiškai reikšmingas juodažiočio grundalo ir upinės plekšnės mitybinių nišų persidengimas smėlėto dugno priekrantėje (Schoener'io indeksas >0,6), nustatytas pagal skrandžio turinio analizės rezultatus, nebuvo patvirtintas stabiliųjų izotopų ($\delta^{13}C$, $\delta^{15}N$ ir $\delta^{34}S$) analizės. Izotopiniai juodažiočio grundalo ir upinės plekšnės skirtumai buvo nulemti aukštesnių pastarosios rūšies $\delta^{15}N$ verčių, o tai nurodo jos maitinimąsi aukštesniame trofiniame lygmenyje. Penkių šaltinių maišymosi modelio rezultatai parodė, kad visų juodažiočio grundalo ir upinės plekšnės dydžio grupių racione dominavo daugiašerės kirmėlės.
4. Išplitimo fazės metu juodažiotis grundalas moreninio dugno buveinėje labai sumažino pagrindinio mitybos objekto – midijos biomasę ir pakeitė jos populiacijos ūgio struktūrą. Sumažėjęs midijų prieinamumas sukėlė žiemojančios ledinės anties dietos pokytį nuo midijų į žuvis. Nors tirtų ledinių ančių kūno būklė nesuprastėjo, maitinimasis judriomis, aukštesniame trofiniame lygmenyje esančiomis aukomis tikriausiai sąlygojo ledinės anties žiemavietės kokybės suprastėjimą.
5. Juodažiotis grundalas tapo svarbiausiu plėšrių žuvų – menkės, ešerio, builio ir oto mitybos objektu. Plėšrios žuvys juodažiočiais grundalais efektyviau maitinosi smėlėto dugno buveinėje.
6. Juodažiotis grundalas priekrantės mitybos tinkle pasižymėjo santykinai aukštomis mišraus trofinio poveikio ir reikšmingumo indekso vertėmis, tačiau išliko pelaginių mitybos tinklo komponentų: zooplanktono – nektobentoso – strimėlės – žuvialesių vandens paukščių dominavimas. Mišraus trofinio povei-

kio analizės rezultatai parodė, kad juodažiočio grundalo jaunikliai ir suaugę individai teigiamai veikė ichtiofages žuvis ir vandens paukščius ir priekrantės zonos žvejybą, o neigiamai – mezozooplanktoną, makrozoobentoso filtratorius ir visaėdžius, daugiašeres kirmėles, planktofages ir bentofages žuvis bei nardančias žiemojančias antis.

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Annexes

Annex 1. Overview of organisms used in the 2011-2015 ECOPATH model of the Lithuanian Baltic Sea coastal waters. Groups: P - producers, M - mesozooplankton, N - nectobenthos, MF - macrozoobenthos filtrators, MO - macrozoobenthos omnivores, POL - polychaetes, PLF - planktivorous fish, BF - benthivorous fish, PIF - piscivorous fish, PW - piscivorous waterbirds, WDD - wintering diving ducks, DET - detritus. Reference indicates the origin of the data used in the model construction.

1 priedas. Organizmų, naudotų Baltijos jūros Lietuvos priekrantės 2011–2015 m. ECOPATH modelyje apžvalga. Grupės: P – gamintojai, M – mezozooplanktonas, N – nektobentosas, MF – makrozoobentoso filtratoriai, MO – makrozoobentoso visaėdžiai, POL – daugiašerės kirmėlės, PLF – planktofagės žuvys, BF – bentofagės žuvys, PIF – ichtiofagės žuvys, PW – ichtiofagiai vandens paukščiai, WDD – žiemojančios nardančios antys, DET – detritas. Literatūros šaltiniai nurodo modelio kūrime naudotų duomenų kilmę.

No.	Group name	Representative species	Length, mm	Group	Reference
1.	Phytoplankton	*Diatoma, Dinophyta, Cyanophyta*		P	Razinkovas-Baziukas et al. 2017
2.	Macrophytobenthos	*Enteromorpha intestinalis, Furcellaria lumbricalis, Potamogeton spp.*		P	Razinkovas-Baziukas et al. 2017
3.	Mesozooplankton	*Copepoda, Cladocera, Ostracoda*		M	Razinkovas-Baziukas et al. 2017
4.	Nectobenthos	*Neomysis integer, Mysis mixta, Praunus inermis*		N	Razinkovas-Baziukas et al. 2017
5.	Macrozoobenthos filtrators	*Amphibalanus improvisus, Mytilus edulis trossulus, Mya arenaria, Limecola balthica, Cerastoderma edule, Hydrobia ulvae*		MF	Razinkovas-Baziukas et al. 2017
6.	Macrozoobenthos omnivores (<9,9mm)	*Saduria entomon, Gammarus zaddachi, G. salinus, G. duebeni, Idotea balthica, Crangon crangon, Palaemon elegans, Monoporeia affinis, Corophium volutator*	<9.9	MO	Razinkovas-Baziukas et al. 2017
7.	Macrozoobenthos omnivores (10-20mm)	*S. entomon, C. crangon, P. elegans*	10 - 20	MO	Razinkovas-Baziukas et al. 2017
8.	Macrozoobenthos omnivores (>20mm)	*S. entomon, C. crangon, P. elegans*	>20	MO	Razinkovas-Baziukas et al. 2017
9.	Polychaetes	*Hediste diversicolor, Marenzelleria viridis, Pygospio elegans*		POL	Razinkovas-Baziukas et al. 2017

No.	Group name	Representative species	Length, mm	Group	Reference
10.	Baltic herring (juvenile)	*Clupea harengus membrus*	<70	PLF	Razinkovas-Baziukas et al. 2017
11.	Baltic herring (adult)		70 - 260	PLF	Present study
12.	Baltic sprat (juvenile/adult)	*Sprattus sprattus balticus*	<120	PLF	Razinkovas-Baziukas et al. 2017
13.	European smelt (juvenile)	*Osmerus eperlanus*	<100	PLF	Razinkovas-Baziukas et al. 2017
14.	European smelt (adult)		100 - 250	BF	Present study
15.	Three-spined stickleback (juvenile/adult)	*Gasterosteus aculeatus*	40-75	BF	Razinkovas-Baziukas et al. 2017
16.	Twaite shad (juvenile)	*Alosa fallax*	<100	BF	Razinkovas-Baziukas et al. 2017
17.	Twaite shad (adult)		100 - 450	BF	Razinkovas-Baziukas et al. 2017
18.	Ruffe (adult)	*Gymnocephalus cernuus*	65 - 160	BF	Present study
19.	Lesser sand-eel and Greater sand-eel (juvenile)	*Ammodytes tobianus, Hyperoplus lanceolatus*	<140	PLF	Razinkovas-Baziukas et al. 2017
20.	Greater sand-eel (adult)	*H. lanceolatus*	140 - 250	PLF	Razinkovas-Baziukas et al. 2017
21.	Common and Sand gobies (juvenile/adult)	*Pomatoschistus microps, P. minutus*	30 - 60	PLF	Razinkovas-Baziukas et al. 2017
22.	Round goby (juvenile)	*Neogobius melanostomus*	<60	PLF	Present study
23.	Round goby (subadult/adult)		60 - 220	BF	Present study
24.	Eelpout (juvenile)	*Zoarces viviparus*	<150	BF	Razinkovas-Baziukas et al. 2017
25.	Eelpout (adult)		150 - 350	BF	Present study
26.	European flounder (juvenile/sub-adult)	*Platichthys flesus trachurus*	<150	BF	Razinkovas-Baziukas et al. 2017
27.	European flounder (adult)		150 - 350	BF	Present study
28.	Silver bream (adult)	*Blicca bjoerkna*	150 - 300	BF	Razinkovas-Baziukas et al. 2017
29.	Bream (adult)	*Abramis brama*	150 - 450	BF	Present study
30.	Vimba bream (juvenile)	*Vimba vimba*	<150	BF	Razinkovas-Baziukas et al. 2017
31.	Vimba bream (adult)		150 - 450	BF	Present study
32.	European perch (juvenile)	*Perca fluviatilis*	<50	PLF	Razinkovas-Baziukas et al. 2017
33.	European perch (subadult/adult)		50 - 450	PIF	Present study

No.	Group name	Representative species	Length, mm	Group	Reference
34.	Pike-perch (juvenile/sub-adult)	*Sander lucioperca*	100 - 250	PIF	Present study, Narvilas 2013
35.	Pike-perch (adult)		>250	PIF	Present study, Narvilas 2013
36.	Cod (juvenile/sub-adult)	*Gadus morhua callarias*	250 - 400	PIF	Present study
37.	Cod (adult)		>400	PIF	Present study
38.	Turbot (juvenile)	*Psetta maxima*	<100	BF	Razinkovas-Baziukas et al. 2017
39.	Turbot (sub-adult/adult)		>100	PIF	Present study
40.	Shorthorn sculpin (sub-adult/adult)	*Myoxocephalus scorpius*	100 - 250	PIF	Present study
41.	Shorthorn sculpin (adult)		>250	PIF	Present study
42.	Atlantic salmon (adult)	*Salmo salar*	>700	PIF	Razinkovas-Baziukas et al. 2017
43.	European eel (adult)	*Anguilla anguilla*	300 - 800	PIF	Razinkovas-Baziukas et al. 2017
44.	Great cormorant	*Phalacrocorax carbo*		PW	Oesterwind et al. 2017
45.	Wintering piscivorous birds	*Podiceps cristatus, Gavia arctica, G. stellata, Mergus merganser*		PW	Morkūnė et al. 2016; Lithuanian Ornithological society (unpublished data)
46.	Wintering diving ducks	*Bucephala clangula, Melanitta fusca, M. nigra, Clangula hyemalis, Polysticta stelleri*		WDD	Lithuanian Ornithological society (unpublished data); Morkūnė et al. 2018; Skabeikis et al. 2019
47.	Detritus			DET	Razinkovas-Baziukas et al. 2017

Annex 2. 2011-2015 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 represents landings for fishes and discards for birds (ww(gm^{-2})); immigration (ww(gm^{-2}y^{-1})); EE - ecotrophic efficiency. Diet column indicates only pedigree assessment. Color scale represents confidence level in the input data.

2 priedas. 2011-2015 m. modelio įvesties duomenys ir jų kilmė. B – biomasė (ww(gm^{-2})); P/B - produkcijos/biomasės santykis (metai^{-1}); Q/B - suvartojimo/biomasės santykis (metai^{-1}); sugavimai reprezentuoja sužvejotų žuvų ir tinkluose žuvusių išmestų vandens paukščių kiekį (ww(gm^{-2})); imigracija (ww(gm^{-2}metai^{-1})); EE - ekotrofinis efektyvumas. Mitybos sudėties stulpelis nurodo tik modelyje naudotų duomenų kilmės įvertinimą.
Spalvų skalė nurodo modelio įvesties duomenų pasikliovimo lygį.

No.	Group name	B	P/B	Q/B	Diet	Catch	Immigr.	EE
1.	Phytoplankton	5.199	206.00				2.770	
2.	Macrophytobenthos	0.052	10.95					
3.	Mesozooplankton	3.940	13.00	300.00	▒		0.210	
4.	Nectobenthos	1.791	6.04	25.00	▒			
5.	Macrozoobenthos filtrators	134.562	1.82	13.00	▒			
6.	Macrozoobenthos omnivores (<9,9mm)	59.112	2.54	13.00	░			
7.	Macrozoobenthos omnivores (10-20mm)	11.084	4.94	13.00	░			
8.	Macrozoobenthos omnivores (>20mm)	6.155	4.94	13.00	░			
9.	Polychaetes	45.460	2.54	31.17	░			
10.	Baltic herring (juvenile)	0.019	0.82	14.71	▓		0.272	
11.	Baltic herring (adult)	1.230	0.55	7.96	█	0.086	0.107	
12.	Baltic sprat (juvenile/adult)	0.045	0.68	9.13	█	0.010	0.573	
13.	European smelt (juvenile)	0.051	0.82	6.00	█		4.320	
14.	European smelt (adult)	0.002	0.55	4.80	█	0.071	0.204	
15.	Three-spined stickleback (juvenile/adult)	0.0004	0.68	3.85	▓		0.093	
16.	Twaite shad (juvenile)	0.0007	0.82	9.13	█			
17.	Twaite shad (adult)	0.2509	0.55	7.96	█	0.005	0.001	
18.	Ruffe (adult)	0.002	0.46	6.00	█		0.553	
19.	Lesser sand eel and Greater sand eel (juv.)		0.82	6.00	▓			1.00
20.	Greater sand-eel (adult)	0.050	0.37	4.80	█			
21.	Common and Sand gobies (juvenile/adult)		0.46	3.21	█			1.00
22.	Round goby (juvenile)		1.00	2.97	█			1.00
23.	Round goby (sub-adult/adult)		0.55	2.44	█	0.026		1.00
24.	Eelpout (juvenile)	0.002	0.55	2.97	█			
25.	Eelpout (adult)	0.004	0.37	2.44	█	0.00002	0.054	

No.	Group name	B	P/B	Q/B	Diet	Catch	Immigr.	EE
26.	European flounder (juvenile/sub-adult)	0.546	0.55	2.97	■		0.002	
27.	European flounder (adult)	6.969	0.37	2.44	■	0.030		
28.	Silver bream (adult)	0.0852	0.37	2.68	▩	0.003		
29.	Bream (adult)	0.852	0.37	4.00	▩	0.004		
30.	Vimba bream (juvenile)	0.034	0.55	2.97	▩		0.001	
31.	Vimba bream (adult)	0.641	0.37	4.00	■	0.017		
32.	European perch (juvenile)	0.0004	0.82	6.00	■		0.222	
33.	European perch (sub-adult/adult)	0.234	0.80	3.68	■	0.007	0.434	
34.	Pike-perch (juvenile/sub-adult)	0.004	0.84	4.57	■		0.002	
35.	Pike-perch (adult)	0.185	0.84	1.71	■	0.011		
36.	Cod (juvenile/sub-adult)	0.417	0.45	2.71	■	0.020		
37.	Cod (adult)	0.363	1.06	2.00	■	0.040		
38.	Turbot (juvenile)	0.014	0.55	2.97	■			
39.	Turbot (sub-adult/adult)	0.325	0.37	2.44	■	0.025		
40.	Shorthorn sculpin (sub-adult/adult)	0.194	0.80	3.68	■	0.004		
41.	Shorthorn sculpin (adult)	0.121	0.80	3.68	■	0.007		
42.	Atlantic salmon (adult)	0.026	0.84	6.20	▩	0.002		
43.	European eel (adult)	0.008	0.37	2.44	■	0.0004		
44.	Great cormorant	0.046	0.16	120.00	░			
45.	Wintering piscivorous birds	0.004	0.16	120.00	■	0.00001		
46.	Wintering diving ducks	0.004	0.51	120.00	■	0.0003		
47.	Detritus	1.800						

■ **Sampled locally, high precision**
▩ **Sampled locally, low precision**
▨ **Approximate or indirect method**
░ **Guesstimate**
▢ **From other model**
□ **Estimated by ECOPATH**

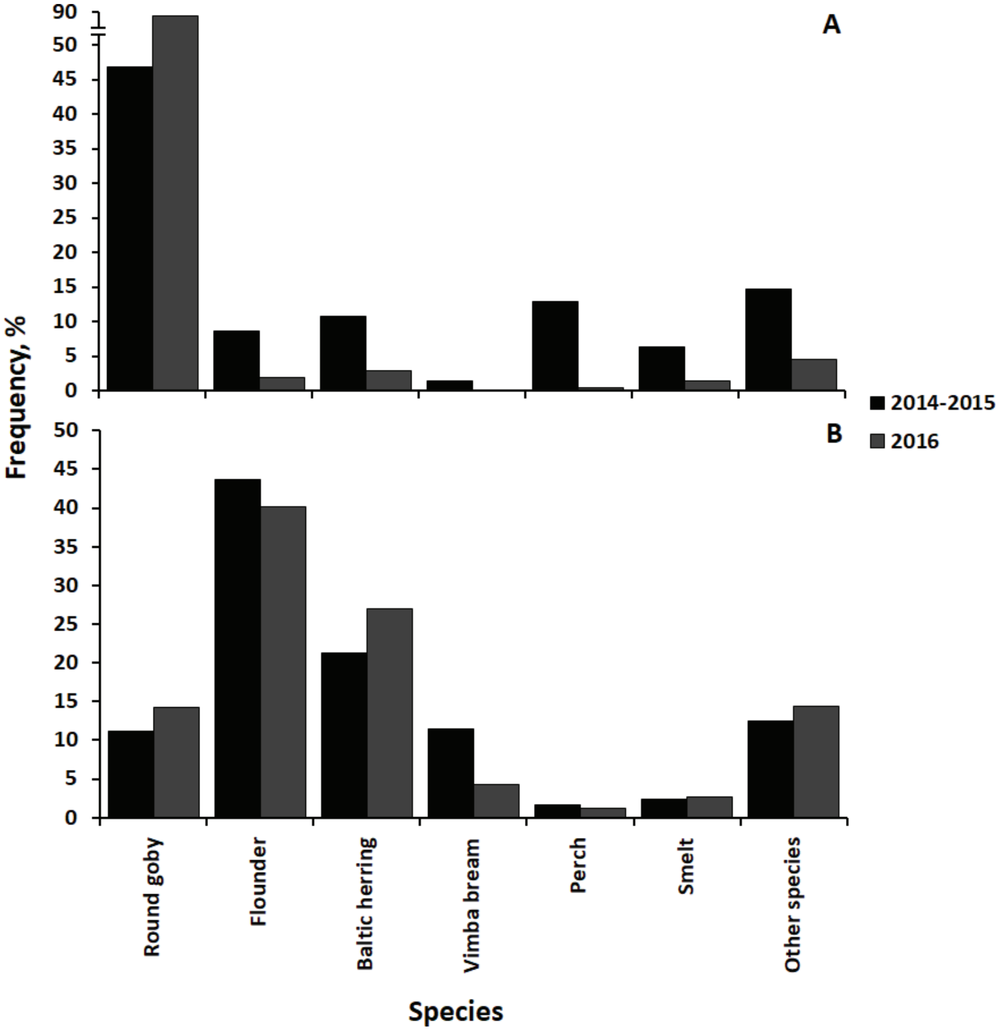
Annex 3. Mean (± SD) abundance and biomass CPUE (per set of multi mesh gill nets (360 m^2)) of fish species, captured in the coastal stony and sandy biotopes during 2014-2015 and 2016 periods.

3 priedas. Žuvų rūšių, sugautų priekrantės moreninio ir smėlėto dugno buveinėse, vidutinis (± SN) gausumas ir biomasė per žvejybos pastangą įvairiaakių žiauninių tinklaičių komplekte (360 m^2) 2014–2015 m. ir 2016 m. periodais.

Common name	Latin name	2014 - 2015				2016			
		Stony biotope		Sandy biotope		Stony biotope		Sandy biotope	
		CPUE, ind.	CPUE, kg	CPUE, ind.	CPUE, kg	CPUE, ind.	CPUE, kg	CPUE, ind.	CPUE, kg
Baltic herring	*Clupea harengus membras*	8.2 ± 5.1	0.4 ± 0.2	17.2 ± 8.5	1.0 ± 0.7	12.7 ± 9.5	0.5 ± 0.4	21.4 ± 12.2	2.0 ± 1.2
Bream	*Abramis brama*	0.3 ± 0.5	0.1 ± 0.2	-	-	0.1 ± 0.3	0.1 ± 0.1	-	-
Cod	*Gadus morhua callarias*	2.5 ± 5.1	1.3 ± 2.5	0.9 ± 1.0	0.6 ± 0.6	10.1 ± 8.0	5.5 ± 3.8	0.9 ± 1.1	0.7 ± 0.8
Eelpout	*Zoarces viviparus*	0.2 ± 0.4	0.1 ± 0.1	-	-	2.6 ± 6.6	0.3 ± 0.3	-	-
Flounder	*Platichthys flesus*	6.6 ± 7.2	0.7 ± 0.6	35.3 ± 12.8	4.5 ± 2.4	8.3 ± 5.4	0.8 ± 0.5	31.8 ± 11.0	4.4 ± 1.6
Perch	*Perca fluviatilis*	9.8 ± 11.8	0.6 ± 0.7	1.3 ± 2.0	0.2 ± 0.4	1.7 ± 2.8	0.1 ± 0.2	1.0 ± 1.6	0.2 ± 0.3
Smelt	*Osmerus eperlanus*	4.8 ± 6.5	0.2 ± 0.1	1.9 ± 3.9	0.1 ± 0.1	6.0 ± 6.8	0.2 ± 0.2	2.1 ± 4.0	0.1 ± 0.1
Whitefish	*Coregonus lavaretus*	0.2 ± 0.4	0.1 ± 0.2	0.4 ± 0.9	0.1 ± 0.2	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.4	0.1 ± 0.1
Garfish	*Belone belone*	0.2 ± 0.6	0.1 ± 0.2	0.2 ± 0.6	0.1 ± 0.3	0.1 ± 0.3	0.03 ± 0.1	0.3 ± 1.0	0.1 ± 0.3
Great sand eel	*Hyperoplus lanceolatus*	-	-	0.2 ± 0.8	0.1 ± 0.1	-	-	0.4 ± 1.0	0.1 ± 0.1
Lumpfish	*Cyclopterus lumpus*	0.3 ± 0.9	0.1 ± 0.1	0.9 ±1.6	0.1 ± 0.2	0.3 ± 0.7	0.02 ± 0.1	0.8 ± 1.4	0.1 ± 0.2
Pike-perch	*Sander lucioperca*	0.3 ± 0.6	0.1 ± 0.2	0.5 ± 0.6	0.3 ± 0.5	0.6 ± 1.1	0.1 ± 0.3	0.5 ± 0.5	0.1 ± 0.3
Roach	*Rutilus rutilus*	1.4 ± 2.2	0.2 ± 0.3	-	-	0.2 ± 0.4	0.02 ± 0.04	-	-
Round goby	*Neogobius melanostomus*	35.8 ± 16.3	1.1 ± 0.6	9.0 ± 6.3	0.4 ± 0.4	392.9 ± 191.7	28.7 ± 11.9	11.3 ± 6.4	0.6 ± 0.5
Ruffe	*Gymnocephalus cernua*	1.1 ± 2.4	0.1 ± 0.1	-	-	0.1 ± 0.3	0.06 ± 0.01	-	-
Shorthorn sculpin	*Myoxocephalus scorpius*	3.1 ± 3.5	0.4 ± 0.3	1.9 ± 1.5	0.4 ± 0.3	4.8 ± 3.0	0.8 ± 0.5	3.4 ± 5.3	0.5 ± 0.8
Turbot	*Scophthalmus maximus*	0.6 ± 1.0	0.3 ± 0.5	1.9 ± 3.5	0.9 ± 1.6	0.4 ± 0.5	0.1 ± 0.2	1.8 ± 2.5	1.1 ± 1.5
Vimba bream	*Vimba vimba*	1.1 ± 1.0	0.3 ± 0.3	9.3 ± 12.0	2.6 ± 3.4	0.8 ± 1.0	0.1 ± 0.1	3.4 ± 4.7	1.2 ± 2.0
Total catch:		**76.1 ± 23.8**	**5.7 ± 2.5**	**80.8 ± 16.7**	**11.2 ± 3.2**	**442 ± 197**	**36.4 ± 13.4**	**79.3 ± 24.4**	**11.3 ± 3.0**

Annex 4. Abundance frequency distribution of fish species captured in the coastal stony (A) and sandy (B) biotopes during 2014-2016. Fishes with a contribution of <5% from the total abundance were combined and considered as other species.

4 priedas. Priekrantės moreninio (A) ir smėlėto (B) dugno buveinėse sugautų žuvų rūšių gausumo dažnio pasiskirstymas 2014–2016 m. Žuvų rūšys, sudarančios <5% nuo bendro gausumo, buvo sujungtos ir laikomos „kitomis rūšimis“.



Annex 5. The number of analyzed samples, C:N mass ratios and mean (± SD) values of stable carbon ($\delta^{13}C$ and δ^{13}Cnorm, ‰), nitrogen ($\delta^{15}N$, ‰) and sulfur ($\delta^{34}S$, ‰) isotopes in differently sized round gobies, flounders and their main preys.

5 priedas. Tirtų mėginių skaičius, C:N masės santykis ir vidutinės (± SN) stabiliųjų anglies ($\delta^{13}C$ ir δ^{13}Cnorm, ‰), azoto ($\delta^{15}N$, ‰) ir sieros ($\delta^{34}S$, ‰) izotopų vertės skirtingo dydžio juodažiočių grundalų, upinių plekšnių bei jų mitybinių objektų organizmuose.

Species	**N**	**C:N**	**$\delta^{13}C$, ‰**	**$\delta^{13}C_{norm}$, ‰**	**$\delta^{15}N$, ‰**	**$\delta^{34}S$, ‰**
RG S	15	3.2 ± 0.02	-21.5 ± 0.3	-21.6 ± 0.4	12.0 ± 0.5	15.9 ± 0.9
RG M	15	3.3 ± 0.04	-21.2 ± 0.4	-21.3 ± 0.4	11.9 ± 0.6	16.3 ± 0.7
RG L	15	3.2 ± 0.03	-21.4 ± 0.6	-21.5 ± 0.7	12.6 ± 0.3	15.3 ± 1.0
FL S	15	3.2 ± 0.03	-21.0 ± 0.3	-21.1 ± 0.3	12.3 ± 0.5	15.6 ± 0.5
FL M	15	3.6 ± 0.4	-20.8 ± 0.7	-20.6 ± 0.6	13.1 ± 0.4	15.1 ± 1.3
FL L	15	3.4 ± 0.1	-21.6 ± 0.5	-21.6 ± 0.5	13.4 ± 0.6	14.0 ± 1.4
Limecola balthica	14	5.7 ± 0.7	-22.4 ± 0.4	-20.1 ± 0.5	5.8 ± 0.0	13.5 ± 0.6
Mya arenaria	1	4.3 ± 0.0	-22.9 ± 0.0	-22.0 ± 0.0	5.8 ± 0.0	18.7 ± 0.0
Cerastoderma lamarcki	8	5.3 ± 0.3	-22.7 ± 0.6	-20.9 ± 0.7	5.7 ± 0.3	18.5 ± 0.3
Crangon crangon	15	3.4 ± 0.1	-20.3 ± 0.3	-20.1 ± 0.1	12.3 ± 0.3	13.7 ± 0.8
Amphipoda	3	5.1 ± 0.3	-22.3 ± 0.2	-20.7 ± 0.02	5.6 ± 0.1	18.9 ± 0.1
Polychaeta	11	4.2 ± 0.3	-22.3 ± 0.3	-21.5 ± 0.3	9.2 ± 0.6	15.1 ± 0.7
Pisces	5	3.3 ± 0.1	-21.3 ± 0.6	-21.3 ± 0.7	12.7 ± 0.2	14.1 ± 0.7

Annex 6. Main model estimates of the coastal food web representing 2011-2015 period. TL - trophic level; EE - ecotrophic efficiency (ww(gm^{-2})); B - biomass (ww(gm^{-2})); P/Q - production/consumption ratio (year^{-1}); R/A - respiration/assimilation ratio (year^{-1}); P/R - production/respiration ratio (year^{-1}); R/B - respiration/biomass ratio (year^{-1}) of each food web compartment.

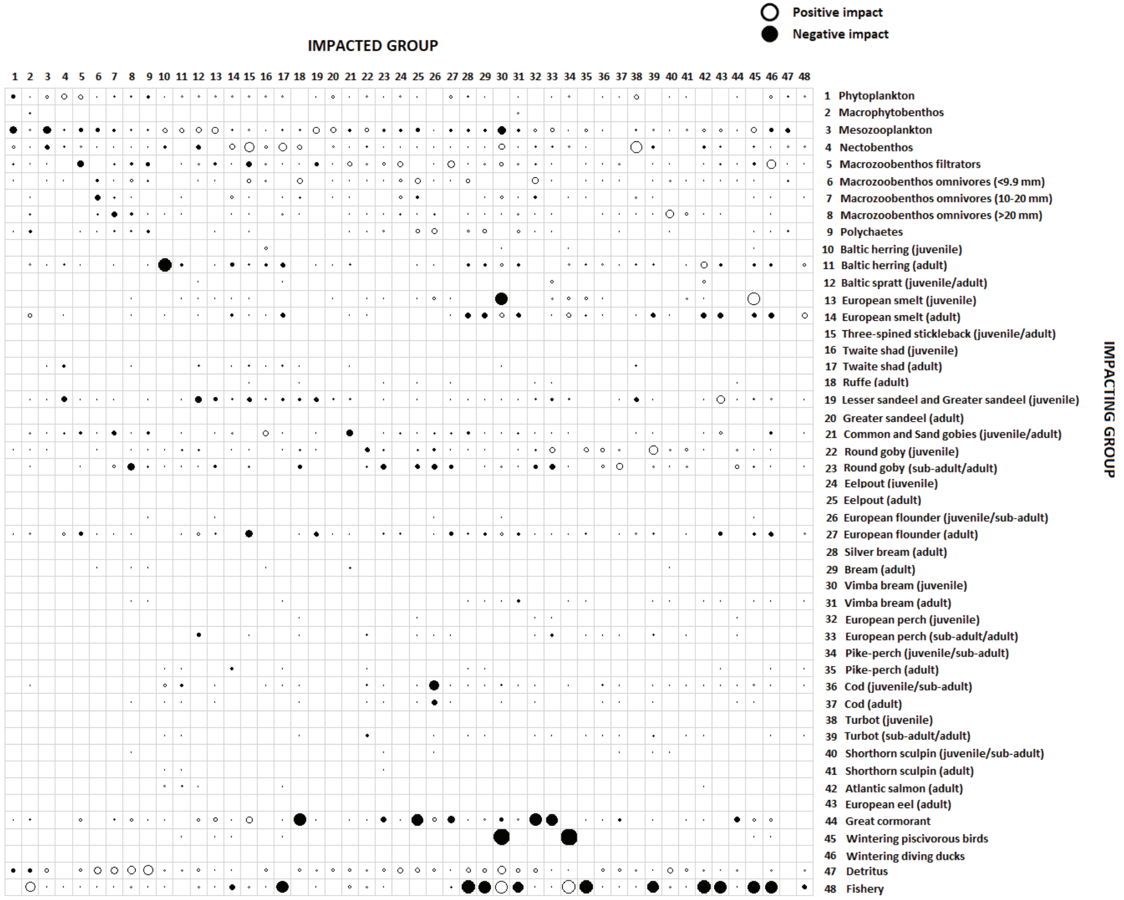
6 priedas. Pagrindiniai priekrantės mitybos tinklo, reprezentuojančio 2011–2015 m. periodą, įverčiai. Visų mitybos tinklo komponentų TL – trofinis lygmuo; EE – ekotrofinis efektyvumas (ww(gm^{-2})); B - biomasė (ww(gm^{-2})); P/Q – produkcijos/suvartojimo santykis (metai^{-1}); R/A – kvėpavimo/asimiliacijos santykis (metai^{-1}); P/R – produkcijos/kvėpavimo santykis (metai^{-1}); R/B – kvėpavimo/biomasės santykis (metai^{-1}).

No.	Group name	TL	EE	B	P/Q	R/A	P/R	R/B
1.	Phytoplankton	1.0	0.730	5.199	-	-	-	-
2.	Macrophytobenthos	1.0	0.672	0.052	-	-	-	-
3.	Mesozooplankton	2.0	0.981	3.940	0.043	0.946	0.057	227.0
4.	Nectobenthos	2.5	0.732	1.792	0.242	0.698	0.433	13.960
5.	Macrozoobenthos filtrators	2.0	0.787	134.56	0.140	0.825	0.212	8.580
6.	Macrozoobenthos omnivores (<9.9mm)	2.0	0.532	59.112	0.195	0.756	0.323	7.860
7.	Macrozoobenthos omnivores (10-20mm)	2.2	0.424	11.083	0.380	0.525	0.905	5.460
8.	Macrozoobenthos omnivores (>20mm)	2.4	0.770	6.155	0.380	0.525	0.905	5.460
9.	Polychaetes	2.0	0.966	45.460	0.081	0.898	0.113	22.40
10.	Baltic herring (juvenile)	3.1	0.883	0.020	0.056	0.930	0.075	10.948
11.	Baltic herring (adult)	3.2	0.708	1.230	0.069	0.914	0.095	5.818
12.	Baltic sprat (juvenile/adult)	3.0	0.861	0.045	0.074	0.907	0.103	6.624
13.	European smelt (juvenile)	3.2	0.799	0.051	0.137	0.829	0.206	3.980
14.	European smelt (adult)	3.7	0.756	0.002	0.115	0.857	0.167	3.290
15.	Three-spined stickleback (juvenile/adult)	3.4	0.844	0.0003	0.177	0.779	0.283	2.400
16.	Twaite shad (juvenile)	3.8	0.00	0.0007	0.090	0.888	0.126	6.484
17.	Twaite shad (adult)	3.6	0.029	0.251	0.069	0.914	0.095	5.818
18.	Ruffe (adult)	3.2	0.797	0.002	0.077	0.904	0.106	4.340
19.	Lesser sand-eel and greater sand-eel (juvenile)	3.2	0.900	3.367	0.137	0.829	0.206	3.980
20.	Greater sand-eel (adult)	3.3	0.000	0.050	0.077	0.904	0.107	3.470
21.	Common and sand gobies (juvenile/adult)	3.1	0.900	6.979	0.143	0.821	0.218	2.108
22.	Round goby (juvenile)	3.0	0.900	3.250	0.337	0.579	0.728	1.374
23.	Round goby (sub-adult/adult)	3.2	0.900	7.127	0.225	0.719	0.391	1.405
24.	Eelpout (juvenile)	3.0	0.00	0.002	0.185	0.768	0.301	1.824
25.	Eelpout (adult)	3.0	0.804	0.004	0.151	0.811	0.233	1.585

No.	Group name	TL	EE	B	P/Q	R/A	P/R	R/B
26.	European flounder (juvenile/ sub-adult)	3.3	0.137	0.546	0.185	0.768	0.301	1.824
27.	European flounder (adult)	3.2	0.121	6.970	0.151	0.811	0.233	1.585
28.	Silver bream (adult)	3.0	0.095	0.085	0.138	0.827	0.209	1.774
29.	Bream (adult)	3.2	0.013	0.851	0.093	0.844	0.131	2.830
30.	Vimba bream (juvenile)	2.7	0.058	0.033	0.185	0.768	0.301	1.824
31.	Vimba bream (adult)	2.9	0.073	0.641	0.093	0.844	0.131	2.830
32.	European perch (juvenile)	3.0	0.825	0.0004	0.137	0.829	0.206	3.980
33.	European perch (sub-adult/ adult)	4.0	0.681	0.234	0.216	0.730	0.371	2.148
34.	Pike-perch (juvenile/sub-adult)	4.2	0.036	0.004	0.184	0.770	0.298	2.816
35.	Pike-perch (adult)	4.3	0.071	0.185	0.491	0.386	1.591	0.528
36.	Cod (juvenile/sub-adult)	4.1	0.106	0.417	0.166	0.792	0.262	1.718
37.	Cod (adult)	4.1	0.104	0.363	0.530	0.338	1.963	0.540
38.	Turbot (juvenile)	3.5	0.000	0.014	0.185	0.768	0.301	1.824
39.	Turbot (sub-adult/adult)	4.0	0.208	0.325	0.151	0.811	0.233	1.568
40.	Shorthorn sculpin (sub-adult/ adult)	3.7	0.026	0.193	0.216	0.730	0.371	2.148
41.	Shorthorn sculpin (adult)	4.0	0.073	0.120	0.216	0.730	0.371	2.148
42.	Atlantic salmon (adult)	4.0	0.091	0.026	0.135	0.831	0.204	4.120
43.	European eel (adult)	4.1	0.144	0.008	0.151	0.811	0.233	1.568
44.	Great cormorant	4.2	0.000	0.046	0.001	0.998	0.002	95.840
45.	Wintering piscivorous birds	4.2	0.019	0.004	0.001	0.998	0.002	95.840
46.	Wintering diving ducks	3.0	0.131	0.004	0.004	0.995	0.005	95.490
47.	Detritus	1.0	0.565	1.800	-	-	-	-

Annex 7. Mixed trophic impact of all compartments and fishery in the Lithuanian coastal waters.

7 priedas. Mišrus visų mitybos tinklo komponentų ir žvejybos poveikis Lietuvos priekrantėje.



Annex 8. Consumption ratio (year^{-1}) of/on round goby
in the Lithuanian Baltic Sea coastal food web.

8 priedas. Juodažiočio grundalo mitybos objektų suvartojimas (metai^{-1})
ir ichtiofagių plėšrūnų sukeltas juodažiočio grundalo suvartojimas (metai^{-1})
Baltijos jūros Lietuvos priekrantės mitybos tinkle.

Preys consumed by the round goby	**Round goby compartment**	
	Juvenile	**Sub-adult/adult**
Mesozooplankton	5.944	-
Nectobenthos	-	0.000147
Macrozoobenthos filtrators	2.495	7.958
Macrozoobenthos omnivores (<9.9mm)	1.211	1.834
Macrozoobenthos omnivores (10-20mm)	-	0.133
Macrozoobenthos omnivores (>20mm)	-	2.776
Polychaetes	-	3.114
European smelt (juvenile)	-	1.570
Three-spined stickleback (juvenile/adult)	-	0.0303
Common and Sand gobies (juvenile/adult)	-	0.00326
Round goby (juvenile)	-	0.129
Total	**9.650**	**17.547**
Predators consuming the round goby		
Round goby (sub-adult/adult)	0.129	-
European perch (sub/adult)	0.470	0.0149
Pike-perch (juvenile/sub-adult)	0.000766	-
Pike-perch (adult)	0.105	0.0285
Cod (juvenile/sub-adult)	0.396	0.376
Cod (adult)	0.168	0.396
Turbot (sub-adult/adult)	0.556	0.159
Shorthorn sculpin (juvenile/sub-adult)	0.118	0.197
Shorthorn sculpin (adult)	0.0988	0.141
Great cormorant	0.886	2.216
Total	**2.928**	**3.528**

Klaipėdos universiteto leidykla

Artūras Skabeikis
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Doctoral dissertation

JUODAŽIOČIO GRUNDALO (*NEOGOBIUS MELANOSTOMUS*) VAIDMUO PIETRYTINĖS BALTIJOS JŪROS PRIEKRANTĖS MITYBOS TINKLE
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