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LIFE-HISTORY TRAITS, FUNCTIONAL ROLE AND GENETIC VARIABILITY OF *POTAMOPYRGUS ANTIPODARUM* (J. E. GRAY, 1853) IN LITHUANIAN MESOTROPHIC LAKE ECOSYSTEMS

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VILNIAUS UNIVERSITETAS

GAMTOS TYRIMŲ CENTRAS

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NAUJAZELANDINĖS VIJASRAIGĖS *POTAMOPYRGUS ANTIPODARUM* (J. E. GRAY, 1853) GYVENIMO CIKLO RODIKLIAI, FUNKCINIS VAIDMUO IR GENETINĖ ĮVAIROVĖ LIETUVOS MEZOTROFINIŲ EŽERŲ EKOSISTEMOSE

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CONTENTS

DEFINITIONS

Accidential introduction is an unconscious species translocation to new area due to various human activity (NOBANIS 2015).

Genetic diversity is the variety of alleles and genotypes present in a population.

Haplotype is a group of genes, which is inherited together by an organism from a single parent.

Introduction is the movement by human agency, indirect or direct, of an alien species outside of its natural range (past or present) (NOBANIS 2015)

Intentional introduction is the deliberate movement and/or release by humans of an alien species outside its natural range

Invasive species is organisms that are introduced accidently or deliberately into where they are not normally found, with serious negative consequences not only for their new environment, but also causing economical damage.

Life-history traits are characteristics that affect the life table of an organism, and can be imagined as various investments in growth, reproduction, and survivorship.

Macroinvertebrates are aquatic invertebrate animals larger than 2−3 mm, living on, under, and around rocks and sediments on the bottoms of various aquatic ecosystems.

Non-indigenous species is a species, subspecies or lower taxon (such as a variety, race, provenance or stock), introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce (NOBANIS 2015).

Native species is a species, subspecies or lower taxon, occurring within its natural range (past and present) and dispersal potential (i.e. within the range it occupies naturally or could occupy without direct or indirect introduction or care by humans) (NOBANIS 2015).

Recent invasion is the invasion of a non-indigenous species, that occured in past 5-7 years (in the context of current study).

Stable isotopes are variants of a particular chemical element which differ in neutron number, although all isotopes of a given element have the same number of protons in each atom.

***d*13C** means the ration of stable carbon isotope ratio (13C/12C) in animal tissues with stable isotope ratio found in fossil belemnite (*Belemnita americana*) (Fry 2006).

***d*15N** means the ratio of stable nitrogen isotope ratio ($^{15}N/^{14}N$) in animal tissues with stable isotope ratio found in atmospheric nitrogen (N2) (Fry 2006).

INTRODUCTION

The worldwide rapid decline of biodiversity is observed in recent decades. Biodiversity is the main key to ecosystem functioning and stability, which in turn provide services for people (Isbell 2010). Human activity is though to be the main factor in multiple changes on a global scale that resulted in biodiversity decline. In particular, land use changes, non-indigenous species invasions, nutrient enrichment, and climate change are often considered some of the most ubiquitous and influential global ecosystem changes (Vitousek *et al*. 1997, Chapin *et al*. 2000, Isbell 2010, Butchart *et al*. 2010).

Biological invasion is a rapid spread and successful establishment of certain species in ecosystems outside the native range resulting in biodiversity decline, ecological and economical losses or threat to human welfare. Human activities are though to be the main variable in species ability to overcome natural barriers and establish outside the native range. Though only minor portion of introduced species becomes invasive, they reach enormously hight densities and has both direct and indirect impacts to native community members. Biological properties, such as wide ecological tolerance, hight demographic potential, absence of parasites and predator avoidance mechanisms enable the species to become a successful invader in various ecosystems.

The New Zealand mudsnail *Potamopyrgus antipodarum* (J. E. Gray, 1853) is one of the most widespread invasive species in the world. The snail is described as typical invader, characterised by the properties of invasive species. First, it become well established in many various fresh- and brackish-water ecosystems in North and South America, Australia, Asia and Europe. Second, obligate parthenogenetic reproduction mode is typical for *P. antipodarum* in an invasive range, where adult females produce numerous clonal daughters. Third, besides the absence of parasites, *operculum,* small hard shell and low nutritional value also enabled the species to escape native predators. Such biological properties allowed the snail to colonise various ecosystems in five continents and reach enormously hight densities (200.000, 500.000 or even 800.000 ind. m^{-2} has been recorded) in an invasive range causing drastic changes in both, community and ecosystem, levels (Hall *et al*. 2003, Riley *et al*. 2008, Arango *et al*. 2009, Moore *et al*. 2012, Kerans *et al*. 2005).

In recent decades, *P. antipodarum* become very popular study object in a variety of long and short term field and laboratory studies. Increasing number of community surveys report new invaded ecosystems by *P. antipodarum*, indicating not only hight dispersion rates of the snail, but also the possible lack of studies associated with dispersion history and vectors. Recently invaded communities, due to hight density of this invasive species are under the most severe impact. Studies of such communities can reveal not only life-history traits of the invader during initial colonisation, but also the ecological interactions between invader and native macroinvertebrates. Such studies can also reveal colonisation patterns, such as dispersion history and vectors, genetic structuring caused by rapid spread across the broad environmental range. Overall, current information on recent distribution, genetic diversity, life-history traits and functional role in invaded ecosystems is clearly insufficient, and sometimes contradictory.

The objective and tasks of the study.

The main objective of this study was to examine the present distribution in Lithuanian inland waters, genetic variability, main population and life-history traits and functional role of *P. antipodarum* in Lithuanian mesotrophic lake ecosystems. The following tasks were set to achieve this objective:

1. To evaluate the recent distribution of *P. antipodarum* in Lithuanian inland waters.
2. To determine the genetic variability of the snail, using the microsatellite DNA and mitochondrial DNA markers.
3. To examine basic population characteristics and life-history traits of *P. antipodarum* in Lithuanian mesotrophic lakes.
4. To assess the functional role of *P. antipodarum* in lake macroinvertebrate communities using stable isotope analysis (SIA).
5. To estimate the role of *P. antipodarum* in the diet of benthivorous fish.

The novelty of the study.

1. Recent distribution of *P. antipodarum* in Lithuanian inland waters was defined.
2. Genetic variability of *P. antipodarum* individuals in eight Lithuanian and one Polish population was evaluated using mitochondrial and microsatellite molecular markers.
3. Basic life-history traits and population characteristics were estimated and compared between recently invaded Lithuanian mesotrophic lake ecosystems.
4. For the first time, somatic growth curves of *P. antipodarum* were estimated.
5. For the first time, fish species capable of consuming the snail *P. antipodarum* were identified.
6. The proportion of *P. antipodarum* in various benthivorous fish diet in recently invaded mesotrophic lakes was quantified.

Scientific and practical significanse of the study.

1. The results of current study contribute to invasion history of *P. antipodarum* and can be applied for modelling the further species spread.
2. Estimated patterns of life-history traits, population characteristics and functional role in recently invaded lake ecosystems contribute to understanding and prediction of dynamics of *P. antipodarum* populations and potential impacts of the invader on native communities and ecosystems.
3. The study provides an evidence of rapid colonisation of invaded habitats and severe alteration of resident macroinvertebrate communities; such information demonstrantes the threat of invasive species and can be used for education and increase of public awareness.

Propositions of the thesis.

1. The New Zealand mudsnail *P. antipodarum* is a recent and rapidly spreading invasive species in Lithuanian fresh waters.
2. There is no genetic variability in populations of *P. antipodarum* inhabiting Lithuanian inland waters.
3. The New Zealand mudsnail *P. antipodarum* can attain hight densities and can compete for resources with native macroinvertebrates in recently invaded mesotrophic lake ecosystems.
4. Although some benthivorous fish species were capable to consume the mudsnail *P. antipodarum* under laboratory conditions, the field data suggests that benthivorous fishes avoids feeding on the snail in recently invaded lakes.
5. The mudsnail *P. antipodarum* is capable of surviving the pasage of gastrointestinal tract of various benthivorous fish species; this may increase the species potential to rapidly colonise invaded ecosystems.

The approval of the results.

The results of the thesis were presented in 3 publications, and 3 international and 1 national conference.

Publications:

Butkus R, Šidagytė E, Arbačiauskas K (2012) Two morphotypes of the New Zealand mud snail *Potamopyrgus antipodarum* (J.E. Gray, 1843) (Mollusca: Hydrobiidae) invade Lithuanian lakes. *Aquatic invasions* 7 (2): 211-218

Butkus R, Šidagytė E, Rakauskas V, Arbačiauskas K (2014) Distribution and current status of non-indigenous mollusc species in Lithuanian inland waters. *Aquatic invasions* 9(1): 95-103

Rakauskas V, **Butkus R**, Merkytė E (2016) Consumption of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) by benthivorous predators in temperate lakes: a case study from Lithuania. *Hydrobiologia* (775): 213-230.

Conferencies:

Butkus R (2012) First results of *Potamopyrgus antipodarum* (J.E. Gray, 1843) in Lithuanian lakes. 6th International conference „*Aquatic environmental research*“. Palanga, Lithuania.

Butkus R (2013) Baltijos baseino gėlųjų vandenų invaziniai moliuskai: kurie ateiviai, o kurie sugrįžėliai?National conference „*Bioateits: gamtos ir gyvybės mokslų perspektyvos*“. Vilnius, Lithuania.

Butkus R (2014) Past, present and future: the case of highly invasive snail *Potamopyrgus antipodarum.* International conference „*Vital nature sign 2014*“. Kaunas, Lithuania.

Butkus R, Arbačiauskas K (2014) Modelling the somatic growth of invasive snail *Potamopyrgus antipodarum* in a mesotrophic lake. International conference „*World conference on natural resource modeling 2014*“.Vilnius, Lithuania.

THE REVIEW OF THE LITERATURE

Main aspects of *P. antipodarum* biology

Potamopyrgus antipodarum (J. E. Gray, 1853) is a small hydrobiid snail, with elongate shell consisting of 5 to 8 dextral whorls separated with deep grooves. In an invasive range, average snail shell length is usually about 4-6 mm, but may reach 12 mm in its native location (Zaranko *et al*. 1997, Levri *et al*. 2007). The aperture is oval and its hight is less than the hight of the spire. Thin and corneus operculum with an off-centre nucleus is characteristic to the species. The most frequent morphological shell form is smooth, though keeled or spined morphs can also be present in some populations (Warwick 1952, Warwick 1969, Zaranko *et al.* 1997, Richards *et al.* 2002, Holomuzki and Biggs 2006, Levri *et al*. 2007, Butkus *et al*. 2012) (Fig. 1). The snails with hair keel can be exceptionaly dominant in some populations (Warwick 1952, Warwick 1969), but usually it constitutes a minor portion of all *P. antipodarum* individuals (Warwick 1952, Warwick 1969, Butkus *et al.* 2012). Though the nature and purpose of the keel are unclear, it is believed to be the result of increased amounts of thannins in the water or food (Warwick 1969). Moreover, some authors state that the function of the keel can be assocated with a resistance to the predators (Holomuzki and Biggs 2006, Levri *et al*. 2007, Zaranko *et al*. 1997).

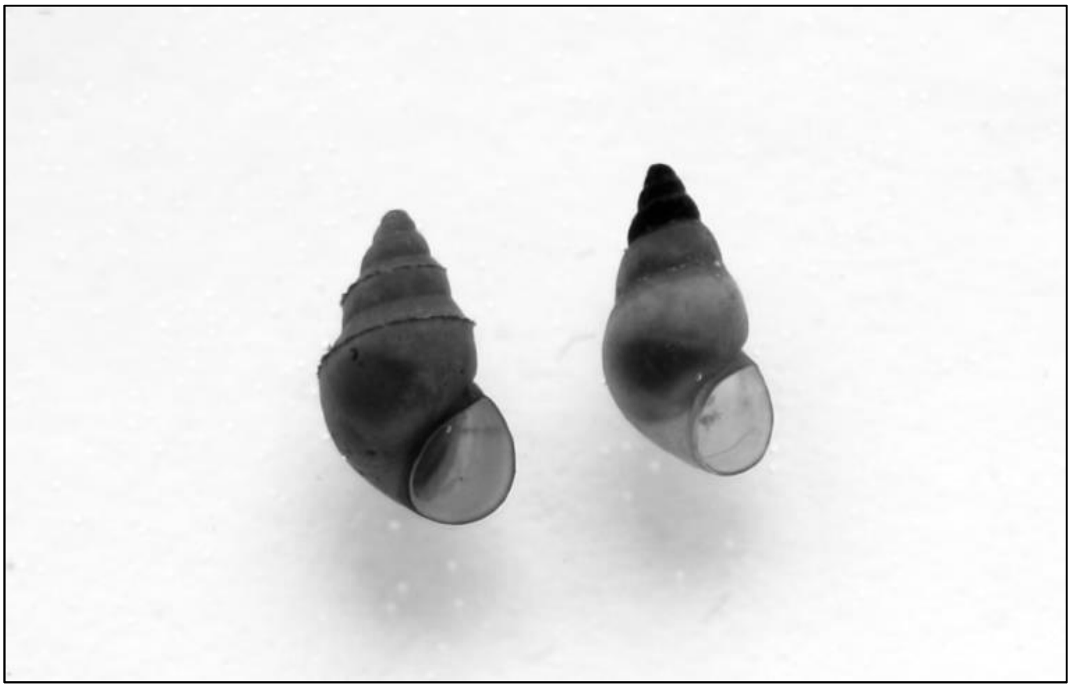

Fig. 1. Two morphological forms of *P. antipodarum*, left – keeled, right – smooth.

Extremely wide ecological tolerance limits allowed *P. antipodarum* to inhabit various aquatic ecosystems. It can colonise various habitats, such as lakes, ponds, rivers, canals, estuaries, lagoons and ditches (Brown *et al*. 2008). The optimal salinity for *P. antipodarum* is near 5 ppt, but it is capable of feeding, growing and reproducing in ecosystems with salinity of 0-15 ppt, and can survive even 30-35 ppt for short time periods (Duncan and Klekowski 1967, Costil *et al*. 2001, Gerard *et al*. 2003, Cejka *et al*. 2008). The highest individual densities have been observed in ecosystems with hight primary production, cobble substrate, constant temperature and flow (Richards *et al.* 2002, Holomuzki and Biggs 2007). The biggest proportion of individuals usually is aggregated in the littoral zone (up to 25 m depth) of the water body. The maximal depth of 45 m, where *P. antipodarum* was recorded, has been reported (Zaranko *et al*. 1997, Grigorovich *et al*. 2003, Cejka *et al*. 2008). The prevalence of the snail in littoral zone is probably associated with food concentration, as *P. antipodarum* is a grazer, feeding on epiphytic and periphytic algae, sediments, diatoms, plant and animal detritus (Broekhuizen *et* *al*. 2001, James *et al*. 2000a, Kelly and Hawes 2005, Parkyn *et al*. 2005). Besides, *P. antipodarum* is capable of consuming the food that is mixed with inedible particles. In this case, the snails consume this mix, srap off the algae following by spewing out the uneatable particles (Matthaei *et al*. 2010, Wagenhoff *et al*. 2011).

Potamopyrgus antipodarum exhibits both obligate asexual parthenogenetic and sexual ovoviviparous reproduction modes (Wallace 1992, Neiman *et al*. 2006, Hamada *et al*. 2013). Both reproduction modes are common only in the native range, where diploid sexual males and females, and asexual polyploid females are found (Dybdahl and Lively 1995). Asexual reproduction is typical in invasive populations, which consists mainly of parthenogeneticaly derived females (Zaranko *et al*. 1997, Dybdahl and Drown 2011, Hamada *et al*. 2013). Males are very rare and have been recorded only in several studies (Wallace 1992, Neiman *et al*. 2011, Hamada *et al*. 2013, Soper *et al*. 2013, Tatara *et al*. 2014). Although embryos are year round produced, the main reproduction occurs in spring and summer (Schreiber *et al*. 1998, Lively and Jokela 2002, Gerard *et al*. 2005, Hall *et al*. 2003).

P. antipodarum can establish extremely dense populations; densities reaching up to 500 000 or 800 000 ind. m^{-2} in an invasive range (Ponder 1988, Schrieber *et al.* 1998, Hall *et al.* 2003, Levri *et al.* 2007, Davidson *et al.* 2008). Such dense and large populations may have a significant effect not only on macroinvertebrate communities, but also on whole ecosystems. These snails can consume up to 75% of gross primary production and dominate secondary production by composing up to 95% of invertebrate biomass thereby affecting N and C cycles (Hall *et al*. 2006, Lewin and Smolski 2006). Its secondary production can be from 7 to 40 times higher than that of any other macroinvertebrate, and reach up to 194 g ash-free dry mass (AFDM) m^{-2} y^{-1} (Hall *et al*. 2003, Hall *et al*. 2006, Richards *et al*. 2002). Abundant *P. antipodarum* individuals can displace, compete or inhibit growth of native macroinvertebrates, causing significant community level changes (Richards *et* *al*. 2002, Kerans *et al*. 2005, Alonso and Castro-Diaz 2008, Brown *et al*. 2008, Davidson *et al*. 2008, Cowie *et al*. 2009). Such changes in macroinvertebrate community structure may also have a substantial direct effect on the fishes. As *P. antipodarum* is a poor and mostly un-digestible food source, it can lock the energy in lower levels of the food web. Consequently, invader induced changes in macroinvertebrate community composition and functions are likely to result in changes in the food web (Davidson *et al*. 2008, Alonso and Castro-Diaz 2008).

Invasion history, dispersion vectors and current distribution of *P. antipodarum*

P. antipodarum is a snail native to New Zealand. Due to human activities it become one of the most widespread invasive species in the world. There are three main types of dispersion vectors, which operate at different distances. First, seafreight and ballast waters, are believed to be the main distant dispersion vectors, which allowed the snail to invade ecosystems in different continents (Ponder 1988, Zaranko *et al*. 1997). Seafreight, possibly drinking water barrels are though to be responsible for the first introduction of *P. antipodarum* to Australia in about the middle of the last century (Ponder 1988). Second, ballast waters possibly played a major role in further spread to N. America, Europe, Asia and Africa (Zaranko *et al*. 1997). Besides the seafreight and ballast waters, there are several other important dispersion vectors which play a major role in dispersion between the catchment basins (intra-continentinal). These include water birds, water transport, ornamental organisms, fish stocking and sport fishing (Loo *et al*. 2007, Van Leeuven and Van der Velde 2012). Finally, water birds, fishes, floating materials (like a clump of moss, wood debris, etc.) can accelerate the spread of *P. antipodarum* inside the water body (Jensen 2010, Alonso and Castro-Diaz 2008, Cejka *et al*. 2008, Davidson *et al*. 2008).

The worldwide expansion of *P. antipodarum* was relatively rapid. Firstly it was introduced to Australia, in seafreight, possibly drinking water barrels and earliest records were made in 1872 (Ponder 1988). *P. antipodarum* rapidly spread in Australia inland waters and in 1963 it was already recorded in Sydney area (Ponder 1988).The first intercontinentinal „jump“ was made to Europe, where the snail is thought to be introduced from Australia (Winterborn 1970, Ponder 1988). First records of *P. antipodarum* individuals were made in River Thames, England in 1889 (Smith 1889), though it could be introduced as early as 1859 (Ponder 1988) or even earlier (Hubendick 1950). The first confirmed record from Ireland is from 1893 (Hubendick 1950). *P. antipodarum* reached the European mainland by about 1900, where it was recorded in the Baltic coast of Germany (Hubendick 1950, Lassen 1978). In later years it rapidly spread to various freshwater and brackishwater ecosystems. Recent distribution of *P. antipodarum* in Europe is presented in Figure 2. In Lithuanian inland waters it was first recorded in 1959 in the Curonian lagoon in vicinity of the Klaipėda port (Gasiūnas 1959). Only in 2005 its occurence was reported for the delta of the Nemunas River (Zettler *et al*. 2005, Zettler *et al*. 2007).

The second intercontinentinal introduction was made to N. America where *P. antipodarum* was first recorded in 1987 (Bowler 1991) and rapidly spread to various inland waters. Recent molecular studies indicate multiple separate introduction events as three different clones are found in USA – two in western USA and one in the Great Lakes basin (Zaranko *et al*. 1997, Levry and Jacoby 2008). Ballast waters of ships and fish stocking were the most probable introduction vectors (Bowler 1991, Bowler and Frest 1992).

Though there are no doubt that *P. antipodarum* was introduced to South America via the shipping, the date of introduction is still unclear. The misidentification probably was the reason, as snails from the Chalinga river and Estero Consuelo (Chile) based on morphology were assigned to the genus *Heleobia* Stimpson, 1865 by Collado (2011) following Biese (1944, 1947).

Later comprehensive phylogenetic analysis based on molecular markers revieled that the populations surveyed in central Chile belong to the highly invasive clonal snail *P. antipodarum* (Collado 2014).

The most recent intercontinentinal introduction of *P. antipodarum* was recorded in Asia. Possibly due to the lack of scientific research the snails was recorded only in several countries. Despite it was discovered as early as 1990 in the northern and central Japan (Habe 1990), only in 1998 it was reported as introduced species (Masuda *et al*. 1998). By 2010, *P. antipodarum* was recorded in many water bodies of northern and central parts and Shikoku and Kyushu islands of Japan (Urabe 2007, Masuda 2010). Other countries where *P. antipodarum* was introduced recently include Turkey, Iraq and Lebanon (Demir 2003, Yildirim *et al*. 2006, Naser and Son 2009). There are two most possible different ways of *P. antipodarum* introduction to Japan and other countries in Asia. The shipping could be the main introduction vector to Japan, due to low possibilities of introduction by water birds. Meanwhile water bird migration could play a major role in an introduction to Turkey, Iraq and Lebanon (Naser and Son 2009), as Azov-Black Sea Basins, are connected to bird migration corridors and the snail can survive gut passage or be transported on feathers of water birds (Ribi 1986, Aarnio and Bonsdorff 1997, Alonso and Castro-Diez 2008, Van Leeuven and Van der Velde 2012). Recent worldwide and European distribution of *P. antipodarum* is presented in Figure 2.

Literature data indicate hight potential of invasive New Zealand mudsnail *P. antipodarum* to overcome natural barriers, colonise various habitats and become dominant macroinvertebrate species in non-indigenous region. In recent years the number of colonised ecosystems is rapidly increasing. This suggests possible dispersion vectors, such as water birds or human activities which may accelerate the spread of the invasive snail between water basins (Butkus *et al*. 2012). Thus, data on recent species distribution is particularly imporant for identification of dispersion patterns, probable dispersion vectors and modeling further spread.

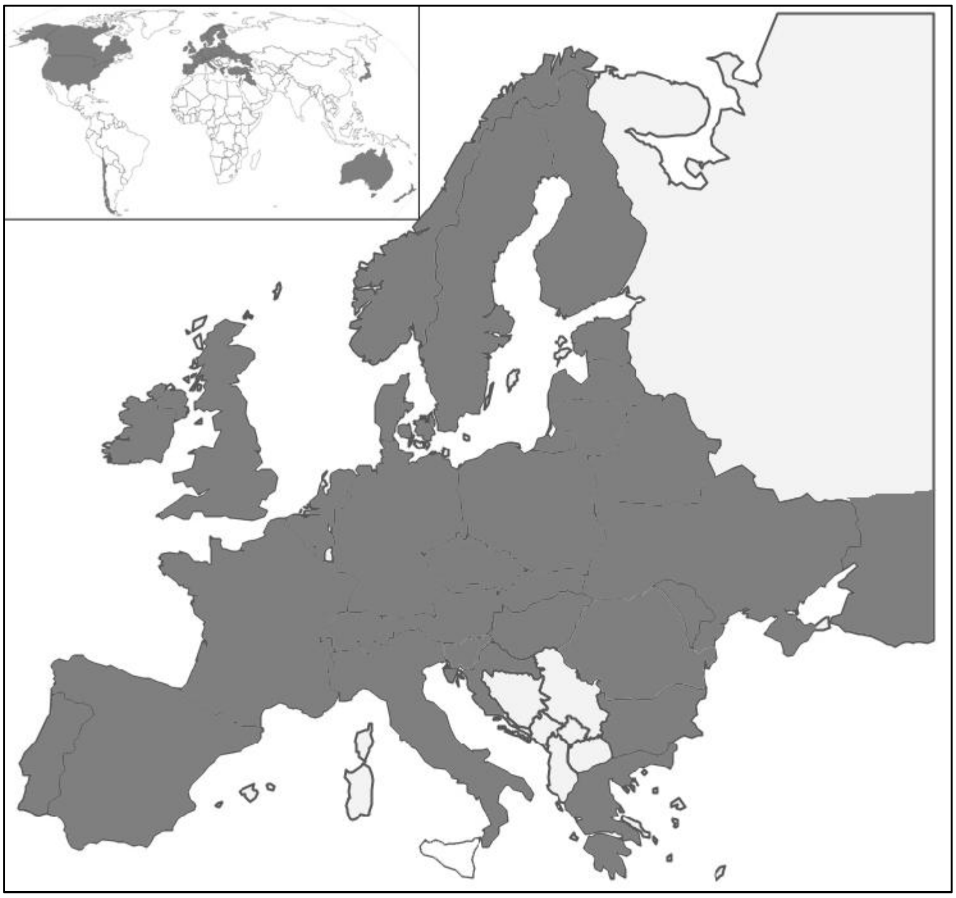

Fig. 2. Recent distribution of *P. antipodarum* in worldwide scale and Europe. Data used for Europe map: UK (Ponder 1988), Norway (Gederaas *et al*. 2007), Sweden and Findland (Carlsson 2000), Estonia (Kalinkina and Berezina 2010), Latvia (Mudite *et al*. 2010), Lithuania (Gasiūnas 1959), Denmark (Thomsen *et al*. 2009), Russia (Kaliningrad) (Filippenko and Son 2008), Russia (Azov-Black sea basins) (Son *et al*. 2008), Belarus (Semenchenko *et al*. 2009), Poland (Brzezinski and Kolodziejczyk 2001), Germany (Wagner 2000), Ukraine and Moldova (Son 2008), Slovakia and Romania (Cejka *et al*. 2008), Portugal (Sousa *et al*. 2005), Spain (Múrria *et al*. 2008), Italy (Cianfanelli *et al*. 2007), France (Zettler and Richard 2004), Greece (Radea *et al*. 2008), Belgium (Städler *et al*. 2005), Netherlands (Berg *et al*. 1997), Switzerland (Schmidlin *et al*. 2012), Austria (Zieritz and Waringer 2008), Czech republic (Zounkova *et al*. 2014), Bulgaria (Irikov and Georgiev 2008), Slovenia and Hungary (Bodis *et al*. 2012).

Genetic diversity of *P. antipodarum* populations

Clonal reproduction via apomictic parthenogenesis is an important life history trait of invasive *P. antipodarum* populations. Moreover, it was a first documented case of mollusc apomictic parthenogenesis in Europe (Boycott 1919, Robson 1923). Due to such reproductive mode invasive *P. antipodarum* populations consists mainly of females while males may be produced only occasionaly by asexual females (Wallace 1992, Neiman *et al*. 2012). Such males can produce sperm (Soper *et al*. 2013), however, the sexual reproduction mode was never evidenced. Besides some variation on female and male ratio was observed between invasive populations (Wallace 1992, Tatara *et al* 2014), possibly indicating different production of males. New Zeland populations often harbour both diploid sexuals and triploid, all-female parthenogens, with population sex ratios varying from almost exclusively female to moderately female based (Lively 1987, Lively 1992, Wallace 1992, Dybdahl and Lively 1996, Fox *et al*. 1996, Negovetic and Jokela 2001, Lively and Jokela 2002, Städler *et al*. 2005). As these snails undergo both sexual and clonal reproduction in their native range, genotypic diversity is very hight in New Zealand (Dybdahl and Lively 1995). Further detailed studies in native range also indicated broad diversity of ecologically distinct multilocus genotypes associated with the occupation of certain habitats (Fox *et al*. 1996, Jokela *et al*. 1999, Jokela *et al*. 2003). Overal, these studies suggest, that a wide range of habitats might be colonised by *P. antipodarum* in an invasive range, if sufficient number of genetically different clones were present.

Previous studies indicated a low genetic variation in *P. antipodarum* populations outside the native range. Surveyed British and Danish populations of *P. antipodarum* using nuclear DNA markers to assess clonal population structure and divergence (Hauser *et al*. 1992, Jacobsen *et al*. 1996, Weetman *et al*. 2002), indicated the possibility of a very limited number of successfully spreading clonal lineages. This assumption suggests, that population structure in Europe is significantly different from that in New Zealand, where single lake may harbour hundreds of distinct clonal genotypes as well as a genetically diverse sexual subpopulation (Dybdahl and Lively 1995, Fox *et al*. 1996, Städler *et al*. 2005).

Mitochondrial DNA of *P. antipodarum* studies also indicate a low genetic diversity in an invasive range. In UK, where the snail was recorded for the first time in Europe, four clonal lines were recognised by Weetman *et al* (2002). While other authors reported only two clones (Städler *et al*. 2005) colonising areas across the Europe. Higher number of mitochondrial DNA haplotypes was found across the USA. Totally, based on several genetic markers, there are four recorded clones, the three observed in the western USA (US1, US1a, US3) and one clone recorded in the Great Lakes region (US2) (Dybdahl and Drown 2011). The mtDNA haplotype of US2 (Dybdahl and Drown 2011) is identical to that of the EU A clone that is widespread across continentinal Europe (Städler *et al*. 2005). Several mtDNA haplotypes of *P. antipodarum* were also found in Japan, they include JA, JB-I, JB-II (Hamada *et al*. 2013). The haplotype JA is identical to haplotype from Denmark, Lake Superior (USA) and Lake Alexandrina (South Island, New Zealand), indicating a possible pathways of *P. antipodarum* to Japan (Hamada *et al*. 2013). However Lake Alexandrina is not the only possible origin of this haplotype, as large regions of New Zealand remain unsampled (Städler *et al*. 2005).

Studies of microsatellite allelic variation and their mutational processes in populations of *P. antipodarum* outside the native range revealed higher genetic variation than nuclear and mitochodrial DNA. The study of eight geographically isolated clonal populations across the Great Britain showed a pattern consistent with the existence of a small number of highly divergent clonal lineages within which minor variation has been possibly generated by mutations since the introduction of *P. antipodarum* to Britain in the late 19th century (Weetman *et al*. 2002). Consistent with this hypothesis, the most widespread genotype in Great Britain was likely the ancesor of 16 multilocus genotypes (MLG‘s) that differ only by few mutational steps (Weetman *et al*.

2002). In contrast, a microsatellite survey of USA populations, scored less microsatellite alleles and MLGs, though the number of microsatellite MLGs was variable between the studies (Hershler *et al*. 2010, Dybdahl and Drown 2011). As *P. antipodarum* was first recorded only in 1987 (Bowler 1991), the shorter time in USA populations for the mutational input could be the reason for much lower microsatellite variation. Besides there are several different studies of clonal variation in USA and the exact number of clones is still controversial between the studies with regard to the differencies in applied methodology (Hershler *et al*. 2009, Dybdahl and Drown 2011, Hershler *et al*.2012, Dybdahl and Drown 2011). Overal data on genetic diversity of *P. antipodarum* populations in eastern Europe is very limited, and the additional studies would greatly increase the understanding of clonal *P. antipodarum* structure and invasion history.

Population and life history characteristics of *P. antipodarum*

Non-indigenous species, that become invasive can reach exceptionally high densities in their introduced range, threatening both biodiversity and ecosystem functioning (Strayer *et al*. 1999, Hall *et al*. 2003, Hall *et al*. 2006). Obligate parthenogenetic reproduction mode, hight production rates, low predator and parasite pressure and hight ecological plasticity enabled the *P. antipodarum* to become successful invasive species in the introduced range (Alonso *et al*. 2012). *P. antipodarum* density rarely exceeds 1000 ind. m^{-2} in its native range (Holomuzki and Biggs 1999), with occasional densities up to 180.000 ind. m^{-2} (Mjchaelis 1977). In introduced environments, *P. antipodarum* can establish extremely hight population densities, tens to hundreds of thousands of individuals per square meter. In Australia, densities of 120.000 ind. m^{-2} have been recorded (Ponder 1988, Schreiber *et al*. 1998). Meanwhile in N. America densities of 200 000, 500 000 and 800 000 ind. m^{-2} were observed in highly productive streams (Davidson *et al*. 2008, Brown *et al*. 2008, Hall *et al*. 2003, Levri *et al*. 2007). Despite extreme densities in Australia and N. America, *P.*

antipodarum densities in Europe are comparitively low and rarely exceed 30 000 ind. m^{-2} (Zbikowski and Zbikowska 2009). Such differencies may imply biotic and/or abiotic factors controlling the density of *P. antipodarum*.

Biotic factors

Main biotic factors infuencing population densities besides the food quality and quantity, include parasitism, predation and competition. The food quality can affect population dynamics by affecting life history traits. It is shown, that *P. antipodarum* fed low-P algae grew slower, maturated later and at smaller body size, and produced smaller offspring than snails reared on algae with hight levels of P (Bowman *et al*. 2005, Cross *et al*. 2005, Tibbets *et al*. 2010, Neiman *et al*. 2013). As food levels and quality can highly differ within the habitat, it is a possible explanation for an aggregated spatial distribution which is typically seen in species populations (Dorgelo 1987). Hight density of *P. antipodarum* on hard surfaces was observed in several studies (Dorgelo 1987, Son 2008). This suggests higher food particle (periphyton) concentration on hard surfaces, such as boulders, than on the sand (Cattaneo *et al*. 1997).

When the food is sufficient and hight in quality, population increases. In this case the limitation can be expected only from biotic interactions such as parasitism, predation and competition. Parasitism is probably the most important factor in population regulation. In native range, New Zealand, 14 trematode species are known to use *P. antipodarum* as intermediate host and the prevalence of parasites in some snail populations exceed 80% (Winterbourn 1970). Though, despite the worldwide distribution and hight abundance of *P. antipodarum*, there are only few documented cases of parasites in these snails in the invasive range. In Europe, two cases of *Sanguinicola* sp. cercaria were found - one in France (Mont Saint Michel Bay) (Gerard and Le Lannic 2003) and one in Poland (Bory Tucholskie National Park) (Zbikowski and Zbikowska 2009). Such a low number of documented cases of *P. antipodarum* invasion by native flukes is unusual as there are several dozen species of trematods, using snails as intermediate hosts (Morley 2008, Zbikowski and Zbikowska 2009). Moreover, the results of laboratory experiment showed that three out of six native trematode parasite species were able to settle as metacercariae in *P. antipodarum* (Zbikowski and Zbikowska 2009). However, the high mortality of *P. antipodarum* was observed during this experiment, which indicates a low co-adaptation between the host and the parasites (Zbikowski and Zbikowska 2009). In N. America, six individuals of *P. antipodarum* were found harboring trematodes (Adema *et al*. 2009). Moreover, snails (designated as genotype US1) were susceptible to a New Zealand isolate of *Microphallus* sp. (Fromme and Dybdahl, 2006), indicating that snails have not evolved the resistance to trematodes, but rather that local digenean parasites have only recently started to acquire *P. antipodarum* as a novel first intermediate host (Adema *et al*. 2009).

Another biotic factor controlling the density of organisms is predation. In the case of *P. antipodarum*, predation together with parasitism play a minor role in population density regulation in an invasive range. Though there are potential predators in an invasive range, there is a lack of studies indicating these snails as a food source. This can be associated with a resistance to predators, a low nutrition value or too short invasion time for local predators to adapt to this prey. Broader literature analysis on *P. antipodarum* in the fish diet is presented in section „The role of *P. antipodarum* in the diet of dominant freshwater fish“. The third biotic factor affecting and controlling population size is competition. Though both forms, inter- and intra-specific competition exists in non-native *P. antipodarum* populations, it differs in result. In the case of inter-specific competition, invasive snails outcompete or inhibit the growth and reproduction of native snails (Richards 2004, Lysne and Koetsier 2008, Riley *et al*. 2008). Though some *in situ* experiments indicate positive relationship between *P. antipodarum* density and native macroinvertebrates at temporal and spatial scales, where the coprofagy was suggested as a possible mechanism of native fauna facilitation (Schreiber *et al*. 2002). Meanwhile the intra-specific competition plays a major role, where populations grow to extreme densities and exhaust the food resources (Krist and Dybdahl 2005, Neiman *et al*. 2013). This type of competition is evidenced to act through reduced reproduction and decreased individual growth rates which in turn increases time until maturity and together reduces population growth rates (Cope and Winterbourn 2004, Zachar and Neiman 2013).

Abiotic factors

Abiotic factors affecting population size of *P. antipodarum* in an invasive range are mainly associated with environmental variables, such as temperature, trophic status of ecosystem, habitat structure, pollution. Temperature as a factor influencing *P. antipodarum* density acts both directly and indirectly. It has a direct effect on reproductive output and individual growth together with maturation time (Quinn *et al*. 1994, Arbačiauskas 1998, Dillon 2004). *P. antipodarum* can survive a wide range of temperatures (4-32°C) (Quinn *et al*. 1994), but also exhibits winter population crashes (Talbot and Ward 1987, Zaranko *et al*. 1997, Schreiber *et al*. 1998, Kerans *et al*. 2005). Indirectly, temperature can influence snail density through the effect on food quality and quantity. The type of water body can also highly influence the individual density. In most cases, extremely abundant populations of *P. antipodarum* were found in rivers (Dorgelo 1987, Kerans *et al*. 2005, Hall *et al*. 2006), where density can be sustained by hight rates of primary production, stable hydrology and temperature of the water (Kerans *et al*. 2005, Hall *et al*. 2006). Eventually, water pollution is another important variable which can also have a negative effect to *P. antipodarum* density through the physiological stress which in turn leads to reduced reproduction output and decreased individual growth rates (Alonso and Camargo 2013, Coulaud *et al*. 2013).

Overal, both biotic and abiotic factors can highly influence the density of *P. antipodarum* through the reduced growth rates, increased time to maturity, decreased reproductive output, size at maturity or offspring size and viability.

These life-history traits have the effect on population size structure, which may indicate a viability of a population of the studied species. Hight number of young individuals, with a hight growth rates and together fast maturation, has a potential to increase its population size unless death rates increase rapidly. On the other hand, the larger proportion of old individuals indicate low fecundity rates or hight mortality after birth as a consequence of environmental changes, leading to population decline.

Reproduction is one of the key events for succesful invasion. Individuals of *P. antipodarum* are asexuals and reproduces parthenogenetically in an invasive range. Though the production of embryos is being observed throughout the year, the main reproduction occurs in the late spring and summer (Richards *et al*. 2002). Reproduction characteristics, such as size at first reproduction, development time and number of embryos, neonate size can be strongly influenced by both biotic and abiotic environmental variables which were reviewed previously. Predation and parasitism can play only a minor role for reproduction characteristics, due to low number of predators and parasites in an invasive range. Though there are several predator species (Cadwallader 1975, Jellyman 1989) and 14 documented trematode parasite species (Winterbourn 1973) in different ways influencing the reproduction of *P. antipodarum* in New Zealand. The individuals of genus *Microphallus* are tigthly associated with reproduction of *P. antipodarum*. The parasites exclusively use *P. antipodarum* as a host and has castrating effect (Winterbourn 1973). Besides, the infestation differs highly between the clones, habitats and depth, and is believed to be one of the main causes of maintenance of sexual reproduction mode (Lively 1987, Levri *et al*. 1996, Jokela *et al*. 1999, Lively and Jokela 2002). Another important variable, competition, can also play a significant role on traits associated with the reproduction (Zachar and Neiman 2013, Neiman *et al*. 2013). It possibly acts though the depletion of hight quality food (hight in P), which is essential for individual growth and reproduction (Tibbets *et al*. 2010, Krist *et al*. 2014). Temperature as a factor can not only prolong maturation time, but also may have a strong effect on clutch size and duration of embryonic development (Gust *et al*. 2011, Macken *et al*. 2012). Though the data on life-history traits of *P. antipodarum* is available for various ecosystems (Dorgelo 1987, Schreiber *et al*. 1998, Tibbets *et al*. 2009, Bennet *et al*. 2014, Dorgelo *et al*. 2014), it is still limited for recently invaded mesotrophic lakes. Recent invasion is associated with highest population growth rates, caused by maximised resource allocation to reproduction and individual growth rates, which in turn leads to hight secondary production of the invader.

The functional role of *P. antipodarum* in lake littoral community

The role in macroinvertebrate communities

Competition for limited food sources or space frequently occurs between native and invasive macroinvertebrate species (Lysne *et al*. 2008, Riley *et al*. 2008). Invasive gastropods and native periphyton grazers can experience exploitative competition when hight population densities result in food resource depletion (Larson *et al*. 2016). Experiments indicate negative relationship between gastropod abundance and periphyton biomass (Brown *et al*. 1994, King-Lotufo *et al*. 2002).

P. antipodarum frequently reach enormously hight densities in non-native range, which result in changes of nitrogen and carbon cycling (Hall *et al*. 2003, Arango *et al*. 2009), consumption of large amounts of primary production (Riley *et al*. 2008) and changes in native macroinvertebrate communities (Kerans *et al*. 2005, Moore *et al*. 2012). Though the experimental studies indicate contradictory results on the effects to individuals of particular species. Several investigations found, that as a result of intensive competition with *P. antipodarum*, the growth rates of native snails were reduced (Riley *et al*. 2008, Thon *et al*. 2010), but the presence of native snails facilitated the growth rates of *P. antipodarum* (Riley *et al*. 2008, Thon *et al*. 2010). However, other studies indicate opposite results. Lysne and Koetsier (2008) found that *P. antipodarum* did not impose competitive pressure to the native snail, *Valvata utahensis*. In fact, at low densities, the presence of *P. antipodarum* increased the growth rates of *V. utahensis* (Lysne and Koetsier 2008). Moreover, Brenneis *et al*. 2011 performed combination of field surveys, stable isotope analysis and short term laboratory experiments and did not find any evidence of a negative competitive influence of invasive *P. antipodarum* on native benthic macroinvertebrates in the estuarine system. Although the competetive interactions between *P. antipodarum* and native grazers are weak or absent in estuarine ecosystem, freshwater ecosystems can undergo the overgrazing of diatoms by *P. antipodarum*, leading to significant shifts of algae community, which was observed by Moore *et al*. (2012) in the long term study. As a consequence of alteration of algae community structure, the drastic changes are expected in macroinvertebrate community (Moore *et al*. 2012). Particularly, hight abundance and high grazing rates of invasive snail leads to decrease of native grazers as a result of overgrazing. Epiphytes are the most important contributors to the nutrition of *P. antipodarum*, which has $d^{13}C$ values closest to epiphytes (Jaschinski *et al*. 2011). Other studies also indicate *P. antipodarum* to be a generalist feeder, consuming sand microflora, fungi, periphyton, bacteria and detritus (James *et al*. 2000b, Aberle *et al*. 2005). Food sources of *P. antipodarum* in an invasive range are similar to those in native region, New Zealand, where stable isotope signatures and gut analyses indicate epiphytes as the predominant carbon source for this species (James *et al*. 2000a).

Studies indicate, that during the growing period, with the highest density of individuals, the proportional contribution of epiphyte carbon to the nutrition of *P. antipodarum* can be reduced by half when compared with other periods of the year (Jaschinski *et al*. 2011). The overgrazing of epiphytes, which strongly decrease in biomass, could be main possible reason. As a consequence, the contributions of sand microflora and alder leafs increased accordingly in *P. antipodarum* diet (Jaschinski *et al*. 2011). This indicates the reduction in the quantity of the preferred food which induce a switch in nutrition to less attractive food items (Jaschinski *et al*. 2011). Furthermore, these results support the hypothesis that grazing invertebrates can control the density of epiphytes and thus the competition between epiphytes and macrophytes for light and nutrients (Jones *et al*. 2002).

P. antipodarum can consume large amounts of periphyton but the reduction of chlorophyll *a* is similar or near similar levels as native macroinvertebrate grazers, including native snails (Riley *et al*. 2008, Krist and Charles 2012). It suggests that despite the *P. antipodarum* competition with native grazers for periphyton, it does not account for the dominance of *P. antipodarum* in an invaded ecosystems (Riley *et al*. 2008, Larson *et al*. 2016). Thus, as consumed periphyton amount does not account for *P. antipodarum* dominance in macroinvertebrate communities, the higher grazing and assimilation rates, lower metabolic maintenance costs, or changes in the periphyton community structure (not suitable for native grazers) could be possible explanation (Riley 2008, Broekhuizen *et al*. 2002, Krist and Charles 2012, Moore *et al*. 2012, Larson *et al*. 2016). Long term study of Moore *et al*. (2012) found, that highly abundant *P. antipodarum* can sequester periphyton production, driving other benthic invertebrates from a variety of functional feeding groups to shift towards other sources of energy. The same study found changes in benthic macroinvertebrate stable isotope levels in *P. antipodarum* invaded area. In this area, the native invertebrates showed a decreased reliance on periphyton compared to non-invaded site (Moore *et al*. 2012). Further, after *P. antipodarum* populations crashed in an invaded site, native consumers showed a shift back to periphyton food sources (as a 2.28 % increase in d^{13}C; Moore *et al*. 2012). Previous study also indicated a negative relationship between native benthic herbivore abundance and *P. antipodarum* density (Moore *et al*. 2012). Such results agree with previous small-scale experiments which showed that *P. antipodarum* competition can be detrimental to native grazing invertebrates (Riley *et al*. 2008). The positive relation between *P. antipodarum* density and piercing herbivorous caddisflies abundance was also found. Moore *et al*. (2012) indicated that highly abundant *P. antipodarum* individuals overgrazed and caused a shift in composition of benthic algae, from diatoms to filamentous algae, which in turn led to changes in benthic herbivore community structure. Such species displacement not only negatively affects native macroinvertebrate communities, but may also affect local fisheries. Local benthic macroinvertebrates are important source for benthivorous fish diet (Bubinas 1994) and have higher nutritional value than tiny, hard-shelled *P. antipodarum* (Sagar and Glova 1995, Duffy 2003).

The role in diet of dominant benthivorous fishes

Invasive species, reaching extremely hight densities can possibly become a new additional food source to the secondary consumers. In some cases, native predators can inhibit the establishment and expansion of introduced species (Ricciardi and MacIsaac 2011, Montserrat *et al*. 2012, Twardochleb *et al*. 2012). However, if an invader has the ability to bypass the predator, it cannot be easily included in to predator‘s diet (Lasenby *et al*. 1986, Spencer 1991). *P. antipodarum* individuals having small hard shell, operculum and low nutritional value are unattractive food for fishes and can even survive the passage through their digestive tract (Vinson and Baker 2008, Brenneis *et al*. 2011, Bruce *et al*. 2009). Consequently, invaders consume a certain portion of primary production but are not consumed by local predators and the energy flow to higher trophic levels can be reduced. Such effect is more likely to occur, where the local macroinvertebrate abundance and diversity decline due to invader, which in turn do not take their role as prey for fish (Lasenby 1986, Spencer *et al*. 1991, Spencer *et al*. 1999).

Though there are several predator species consuming reasonable amount of these snails in New Zealand (Cadwallader 1975, Jellyman 1989), there are limited records on predators outside the native range. Previous studies indicate several marine and brackish water fish species, such as the Pacific staghorn sculpin (*Leptocottus armatus* (Girard, 1854)), the Starry flounder (*Platichthys stellatus* (Pallas, 1787)) (Brenneis *et al*. 2011) and the round goby (*Neogobius melanostomus* (Pallas 1811)) (Azour 2011, Rakauskas *et al*. 2013), consuming *P. antipodarum* in an invasive range. Despite there are documented cases of rainbow trout (*Onchorynchus mykiss* (Walbaum, 1792)) and brown trout (*Salmo trutta* (Linnaeus, 1758)) feeding on *P. antipodarum*, about 80% of those consumed passed through their digestive system undigested indicating *P. antipodarum* to be poor and mostly undigestible food source (Bersine *et al*. 2008, Vinson and Baker 2008). It has been shown that *P. antipodarum* not only replace valuable food sources, but also inflict poor health and reduce survivorship of fishes that consume it (Vinson and Baker 2008).

Additionally to the fishes, crayfishes can also predate on these snails. Performed experiments proved two crayfish species the signal crayfish (*Pacifastacus leniusculus* (Dana, 1852)) (Brenneis *et al*. 2011, Twardochleb *et al*. 2012) and the red swamp crayfish (*Procambarus clarkii* (Girard, 1852)) (Bennett *et al*. 2015) to consume *P. antipodarum* individuals in an experimental conditions. Moreover several fish species, the three-spined stickleback (*Gasterosteus aculeatus* (Linnaeus, 1758)) (Brenneis *et al*. 2011), rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) (Vinson and Baker 2008), sea trout (*Salmo trutta* (Linnaeus, 1758)) (Vinson and Baker 2008) and the chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)) (Bersine *et al*. 2008) consumed the snails during experiments.

Changes in community structure can have negative consequences to whole food chain. Decreased amount and diversity of preffered energetically valuable food items together with increased number of *P. antipodarum* individuals can significally impact secondary consumers (Lasenby 1986, Spencer *et al*. 1991, Spencer *et al*. 1999). So the data on potential *P. antipodarum* predators and their ability to digest these snails is limited. Such knowledge would greatly increase the understanding of predator-prey interactions, particularly *P. antipodarum* and native benthivorous fish species.

MATERIALS AND METHODS

Distribution assessment of *P. antipodarum*

The initial data on *P. antipodarum* distribution in Lithuanian freshwater ecosystems was collected in September and October of 2010. Two surveys, a study of littoral macroinvertebrate communities of 16 lakes and a study of molluscan assemblages in five rivers outflowing from lakes (including one lake, Lake Vilkokšnis) were performed. Both surveys included quantitative sampling by a stovepipe sampler (lakes, cross-sectional area 0.1 m^2) and a frame (rivers, area 1 m^2), respectively. Similar as possible littoral habitats in the lakes (sandy or stony bottom fragmentally (≤10%) overgrown with macrophytes: *Potamogeton* sp., *Chara* sp. or *Phragmites australis* (Cav.) Trin. ex Steudel were sampled. In rivers, quantitative samples were collected from sandy or stony substrates occasionally with some macrophytes present. Three replicates were taken at each study site.

An additional semi-quantitative sampling procedure, similar to that described by O'Hare *et al*. (2007), was applied in the lake study. Using a standard dip-net, two samples were collected from two core eulittoral mesohabitats of each lake: a bottom (preferably hard) kick sample and a vegetation (preferably submerged) sweep sample. Within a stand of each mesohabitat, a stretch of about 15-20 meters long was sampled while moving along the shore in a trajectory of a zigzag curve (from the shoreline to a depth of 1 m) within a period resulting in a 3 minute (actual) sampling time (O'Hare *et al*. 2007). The same methodics were applied for river survey. These data sets provided species relative abundance estimated as catch per timed sampling effort.

The current distribution of *P. antipodarum* in Lithuanian inland waters was determined using both data from the literature and results of surveys conducted during 2010–2015 occasional investigations of various water bodies. Samples were collected using a standard dip net or a dredge. The number of sampling sites per water body and the number of samples collected from one site varied from one to several. During this study, geographic coordinates were measured at sampling sites. The majority of literature data had only approximate sampling site information. In such cases, where possible, the coordinates of the most probable sampling location according to descriptions were given, or reference was made to the coordinates of the geographic centre of the water body.

Molecular analysis of *P. antipodarum* populations

Sample collection

Samples were collected in 8 populations of Lithuania: Curonian Lagoon, the Strėva River, lakes Plateliai, Vilkokšnis, Daugai, Dusia, Metelys and Obelija, and one population of Poland, in Lake Wigry. Samples were collected using standard dip net in as many biotopes as possible. Sampled individuals were fixed using 96% ethanol and transported to laboratory. After 24h the ethanol was changed and samples were placed into the fridge until DNA extraction.

DNA extraction

Genomic DNA was isolated from the entire body (without shell) of preserved snails using ammonium acetate protocol (Richardson *et al*. 2001, Sambrook & Russell 2001). DNA extractions were used for either mitochondrial DNA sequencing, microsatellite DNA genotyping, or both. DNA concentrations were measured using a spectrophotometer.

Cytochrome b analysis

The polymerase chain reaction (PCR) was used to amplify the mitochondrial Cytochrome b gene. The previously published primers were used (Neiman *et al*. 2011). PCR was performed in a reaction mixture of 25 µl containing *Phusion* DNA polymerase (0.15 µL), 3.1 µl PCR buffer solution, 1.0 µl template DNA (25 ng/µl), 1.6 µl dNTP, 0.8 µl primers (0.4 µM each), and 18.35 µl distilled water. Following initial denaturation for 30 s at 98°C, denaturation was at 98°C for 10 s, annealing at 54°C for 20 s, and extension at 72 °C for 30 s (40 cycles), followed by final extension for 10 min at 72 °C. The verification of successful PCR amplification was assessed by agarose gel electrophoresis. The PCR products of the part Cytb were purified and directly sequenced using the PCR primers. All specimens were sequenced on an Applied Biosystems 3500 DNA sequencer in the Open Access centre. The DNA sequences were processed, aligned by means of the BioEdit software and checked visually.

16S rRNA analysis

The polymerase chain reaction (PCR) was used to amplify the mitochondrial part 16S rRNA fragment. The previously published primers were used (Städler *et al.* 2005) was used for the amplification. Polymerase chain reaction (PCR) amplifications were performed in 25 µL volumes consisting a mix of 1 µL genomic DNA (25 ng/µl), 2.5 µL PCR buffer solution, 3.0 µL dNTP, 2 µL primers (1.0 µM each), *Dream Taq* DNA polymerase and 16.37 µl distilled water. Following initial denaturation for 5 min at 92°C, denaturation was at 92°C for 30 s, annealing at 55°C for 60 s, and extension at 72 °C for 90 s (40 cycles), followed by final extension for 5 min at 72 °C. The verification of successful PCR amplification was assessed by agarose gel electrophoresis. The PCR products of the part 16S rRNA were purified and directly sequenced using the PCR primers. All specimens were sequenced on an Applied Biosystems 3500 DNA sequencer in the Open Access centre. The DNA sequences were processed, aligned by means of the BioEdit software and checked visually.

Microsatellite analysis

Individual snails were screened with a panel of four microsatellite markers (Pa217, Pa254, Pa56 and Pa112) (Weetman *et al.* 2001). A forward primer dye-labelled with Applied Biosystems HEX was used in PCRs for locus Pa254 and Applied Biosystems FAM for Pa56, Pa112 and 217. Each 10.0 µL reaction contained 5.1 µL distilled water, 2 µL buffer, 1.0 µL of dNTPs, 0.4 µL dyelabelled forward primer, 0.4 µL of reverse primer, 0.1 µL of Phusion Hot Start II polymerase (F-549S) and 1.0 µL of template DNA. The thermal profile for reactions was as follows: the PCR consisted of an initial 30 s denaturation step at 98°C, followed by 35 cycles of denaturation for 5 s at 98°C, annealing at 58°C temperature for 5 s, extention 10 s at 72°C and a final extension step at 72°C for 1 min. Microsatellites were genotyped in the DNA Core Sequencing Facility of University of Illinois. Microsatellite peak data was analysed using Peak Scanner Software v1.0

Number of individuals used for molecular analysis from studied ecosystems is presented in Table 1.

Table 1. Number of individuals used in analysis.

	Cytochrome b	16S rRNA	Microsatellites
Curonian lagoon	6	4	35
Strėva river	8	5	30
Lake Plateliai	2	-	12
Lake Dusia	5	5	30
Lake Daugai	16	4	25
Lake Metelys	7	4	28
Lake Obelija	2	-	12
Lake Vilkokšnis	11	4	32
Lake Wigry (PL)	6	6	26

Population characteristic and life-history trait of *P. antipodarum* analysis

Sampling technique selection

Due to relatively large sampling area and representative data cylinder is widely used in field sampling. Though usage of the cylinder is complicated during ice-coverage period. One of more comfortable ways to sample *P. antipodarum* in all seasons is using Eckman grabber. To check whether there are any significant differencies between two sampling devices, samples were collected in three depths (0.25, 0.5, 0.75 m) in lake Vilkokšnis using cylinder (0.10 m^{-2}) and Eckman grabber (0.02 m^{-2}). Three replicate samples were taken in all cases. The field samples were transported in plastic containers to the laboratory, where snails were counted. The density was estimated as individuals per square meter (m^{-2}). Due to the small number of samples, non-parametric Kruskal-Wallis ANOVA test was used to compare the densities. All statistical calculations were made using statsoft Statistica v10.

Sample collection

Populations of *P. antipodarum* were sampled in the littoral zone of mesotrophic lakes Vilkokšnis, Dusia, Metelys and Obelija. To estimate population characteristics and life-history traits, such as size specific growth rates in the field, size at maturity and monthly dynamics of individual density, size structure, biomass, reproduction and secondary production, quantitative samples of snails were taken monthly from October 2012 through November 2013 in lake Vilkokšnis. To compare the population characteristics and life-history traits, samples were collected in other three additional mesotrophic lakes Dusia, Obelija and Metelys in May, August and November months of 2013. All samples were taken in depth of 1.0 m using Eckman grabber (sampling area 0.02 m^2). During the sampling 10 replicate samples were taken. The field samples were transported in plastic containers to the laboratory, where snails were sorted, counted, measured and preserved in 96% ethanol for further analysis.

Spatial distribution assessment

The dispersion of *P. antipodarum* in studied lakes was estimated using Morisita‘s dispersion index (Morisita 1971):

$$I_d = n\left(\frac{\sum X^2 - N}{N(N-1)}\right),$$

where n = total number of plots; X = number of individuals of one species in a single plot; N = total number of individuals in all plots. Values of I_d correspond to three different interpretations of a distribution: $I_d < 1$ indicates a uniform, $I_d = 1$ a random, and $I_d > 1$ an aggregated distribution.

Density, biomass and size structure analysis

Prior to analysis, density data was log transformed to remove mean to variance relationship. ANOVA was used to estimate the effect of month in Lake Vilkokšnis. To analyse density between the studied lakes nested ANOVA was used. In order to evaluate the effect of lake to average density, the effect of season was eliminated by nesting lakes in seasons, following the post hoc comparisons between the lakes. The same procedure was applied analysing the effect of season, where the effect of lake was eliminated by nesting seasons in lakes. Additionally, post hoc test was applied.

For biomass analysis, the length-mass regression was used to calculate the ash-free dry mass (AFDM) of an individuals. The regression from Hall *et al.* (2006) for *P. antipodarum* was:

Mass = 0.0199 x length^$^{2.375}$ (n = 46, $r^2 = 0.96$),

where mass was measured in miligrams (AFDM) and shell length in milimeters. This mass includes organic matter in the shell, but not the inorganic shell itself. The effect of month to average log transformed biomass in Lake Vilkokšnis was estimated using ANOVA. To analyse biomass between the studied lakes nested ANOVA was used. In order to evaluate the effect of lake to average biomass, the effect of season was eliminated by nesting lakes in seasons, following the post hoc comparisons between the lakes. The same procedure was applied analysing the effect of season, where the effect of lake was eliminated by nesting seasons in lakes. Additionally, post hoc test was applied.

To check the effect of sampling month to average individual size in Lake Vilkokšnis, ANOVA was used. The relationship of average density on average size of individuals was assessed applying linear regression analysis, where the density was log transformed. To check the effect of studied lakes and seasons, two-way ANOVA was used, followed by multiple post hoc unequal HSD comparison test.

A pairwise Kolmogorov-Smirnov test was used to compare size structure of *P. antipodarum* between the studied lakes and seasons. All statistical calculations were made using statsoft Statistica v10.

Reproduction analysis

Reproduction analysis was performed by dissecting snails under the stereo microscope. During the dissection, snail shell was crashed, embryos collected and counted. Size at first reproduction was assessed by dissecting various shell length snails under the microscope searching for embryos. The size of smallest embryos bearing females were considered to be the size at maturity.

Statistical analysis

The effect of sampling month on fecundity in Lake Vilkokšnis was estimated using ANOVA. The linear regression analysis was applied to estimate the relationship between female shell length and cluch size, where the data from all lakes and seasons was pooled. To estimate the effect of lake on fecundity with respect to seasons nested design ANOVA was used, where seasons were nested in lakes, following post hoc unequal HSD test. To estimate the effect of season on fecundity with respect to lakes nested design ANOVA was used, where lakes were nested in seasons, following post hoc unequal HSD test. All statistical calculations were made using statsoft Statistica v10.

Individual growth analysis

Size-specific growth rates of *P. antipodarum* were estimated by two methods, direct measurement of snail growth and size-frequency distribution analysis. The latter method was applied for natural population in Lake Vilkokšnis. Snails were sorted into 10 size classes, with shell length interval of 0.5 mm. Two models, non-seasonal and seasonal were applied to estimate growth curve parameters. The analysis of size-frequency dynamics was made using FISAT II software (FAO-ICLARM FishStock Assessment Tools, Version 1.2.2; Food and Agriculture Organisation of the United Nations—International Center for Living Aquatic Resources Management, Rome). The *K* scan routine in Electronic Length Frequency Analysis I (ELEFAN I) in FiSAT II was conducted to assess a reliable estimate of the von Bertalanffy growth coefficient *K* (asymptotic growth rate at the maximum size L_∞) (Pauly and David 1984).

As seasonal oscillations in growth rates are typical for most of aquatic organisms living in temperate climate zone, biseasonal model, incorporated in Fisat II software, was applied and the parameters of seasonality were evaluated. Seasonality parameters C and WP refer to the intensity of the (sinusoid) growth oscillations of the growth curve and the onset of the first oscillation relative to t = 0, respectively.

The specific growth rates of the snail were also measured during laboratory experiment, which was conducted at two temperatures (15°C and 20°C). For the growth experiment individuals collected in the littoral zone of Lake Vilkokšnis were measured and transferred to 0.9 L glass containers (3 specimens of different shell length per container) with a 16-h light cycle. Each container was filled with filtered lake water. Stones (from 4 to 7 depending on size) covered with periphyton and a lump of fontinalis moss (*Fontinalis* *antipyretica* Ren. and Card.) were used as food source for snails. Additionaly, a solution of dried *Spirulina* algae was fed two times per week. Water in each container was changed every week. Snail shell length and wet weight were measured every second week.

The growth of *P. antipodarum* was described by von Bertalanffy‘s equation:

$L_t = L_\infty \text{ x } (1-e^{-kt})$,

where L_t is shell length at time t, L_∞ is theoretical maximum (asymptotic) length, and k is the growth coefficient. Parameters L_∞ and k were estimated from linear regression of shell length increment per time unit ($v_{\Delta t}$) on shell length at time t (L_t), using equations:

$L_\infty = A/B$

and

$–k = 1/\Delta t \text{ x } \ln(1-B)$,

where A and B are the intercept and slope of this regression (Arbačiauskas, 1998).

Life-history characteristics, shell length at maturity, maximal animal size and fecundity in lake for different seasons were estimated from quantitative samples. Shell length at birth was measured during growth experiments. The smallest, embryos bearing females were deemed to be individuals with a body length at maturity.

Specific growth rates of *P. antipodarum* (G_s) were estimated from the expression:

$G_s = \text{Ln}(L_2/L_1)/(t_2-t_1)$,

where L_1 and L_2 are shell length of the snail at times t_1 and t_2, and t_2-t_1 is the time in days elapsed between sampling dates.

The temperature coefficient (Q_{10}), a measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by 10 °C was calculated according to equation (Bayne and Newell 1983, Saucedo *et al.* 2004):

$$Q10 = \left(\frac{R2}{R1}\right)^{\frac{10}{T2-T1}},$$

Where R_1 is the measured reaction rate at temperature T_1 (where $T_1 < T_2$), R_2 is the measured reaction rate at temperature T_2 (where $T_2 > T_1$), T_1 is the temperature at which the reaction rate R_1 is measured (where $T_1 < T_2$), T_2 is the temperature at which the reaction rate R_2 is measured (where $T_2 > T_1$).

Statistical analysis

To compare the specific growth rates in laboratory and field, temperature corrections were applied for growth curves estimated from size frequency distributions. The corrections were applied to estimated growth curve parameter *k*. First, temperature differencies between laboratory and field were evaluated. Second, Q_{10} value for parameter *k* between estimated temperatures was calculated. Third, field curve parameter *k* was multiplied (for field winter curve) or divided (for field summer curve) by estimated Q_{10} value. Besides, as different asymptotic lengths were estimated for laboratory and field growth curves, the asymptotic lengths from laboratory estimates were asssigned to temperature corrected field growth curves. Finally, growth curves were drawn using temperature corrected parameter *k* and assigned asymptotic lengths estimated from laboratory experiments. These temperature corrected and asymptotic length assigned growth curves were used to estimate specific growth rates.

To compare the specific growth rates of *P. antipodarum* under different temperatures in laboratory and field, GLM Homogeneity of slopes model was firstly applied to check possible interaction effect of temperature and individual size. As there were nointeraction effect, GLM ANCOVA model was applied, where specific growth rates were dependent variable, growth conditions (laboratory or field) categorical and temperature continous predictor. Specific growth rates, used in analysis were obtained from direct measurements (laboratory) and calculated from growth curve (field).

To compare specific growth rates under different temperatures in laboratory conditions and to check possible interaction effect of temperature and individual size, GLM Homogeneity of slopes model was applied. Specific growth rates were dependent variable, temperature – categorical predictor and shell length was set to continous predictor. Additionally, snails were grouped to 4 size groups with the interval of 1.5 mm, and the specific growth rates within groups compared between the temperatures using two-way ANOVA, following post hoc test. Besides, Q_{10} values were calculated for specific growth rates of previously mentioned size groups. All statistical calculations were made using statsoft Statistica v10.

Secondary production analysis

The production of *P. antipodarum* was estimated with respect to water temperature and individual size. The production was assessed by several steps. Firstly, shell length of the sampled snails was converted to ash-free dry mass (AFDM) using previously mentioned regression. Secondly, daily weight-specific growth rate of i – size individuals, was assessed using data from laboratory experiments:

$$G_i = \ln(W_{t+\Delta t}/W_t)/\Delta t,$$

where W_t = mean AFDM of an individual at time t, $W_{t+\Delta t}$ = mean AFDM of an individual at time $t+\Delta t$; Δt = length of time interval, in days. Thirdly, as the growth rates are highly influenced by temperature and individual size, multiple linear regression of weight-specific growth rates (d^{-1}) on temperature (°C) and initial individual size (mg) was assessed. This equation allowed to estimate temperature and size dependent specific growth rates of *P. antipodarum*. To estimate the contribution of fecundity to biomass growth, number of embryos per reproducing female was multiplied by average AFDM of one embryo (0.0033 mg AFDM (Hall *et al.* 2006)). If fecundity data was not available, average number of embryos per reproducing female in particular month was applied, following multiplication by AFDM of one embryo. Ash-free dry mass of females and embryos, they carried, were summed. Finally, the secondary production was estimated using a noncohort technique - instantaneous growth method. Daily production ($P_{d,}$) in units of mg AFDM m^{-2} d^{-1} was calculated as:

$P_d = G_i$ x B_M,

where B_M = mean population biomass for two consecutive dates in units of mg AFDM m^{-2} (Benke and Jacobi 1994, Benke and Huryn 2007).

In the case of monthly dynamics in Lake Vilkokšnis, daily production during particular month was multiplied by number of days between two consecutive dates. Such monthly estimates were summed to obtain the production per year. Meanwhile production per growing season in Lakes Obelija, Dusia, Metelys and Vilkokšnis was estimated by averaging spring-summer and summer-autumn production values per day^{-1} and multiplying obtained value by day number in growing season.

Functional role of *P. antipodarum* in mesotrophic lake ecosystems

The role in macroinvertebrate communities

Data collection

Samples for stable isotope analysis (SIA) were taken in Lakes Daugai, Dusia and Metelys in September of 2011. Stable isotopes of particulate organic matter (POM), macrophytes, periphyton, sand organics and common macrozoobenthic organisms were analysed in this study. Several typical and abundant for all studied lakes potential competitor species such as *P. antipodarum*, R*adix. auricularia* (Linnaeus, 1758) and *Chaetogammarus warpachowskyi* (G.O. Sars, 1894) were selected for the study. The snail *R. auricularia* was selected as a native primary consumer, feeding on algae, periphyton, and detritus (Dillon 2000). Meanwhile *C. warpachovskyi* is non-indigenous omnivorous species in Lithuanian ecosystems. Though due to the absence of native amphipods, it was selected for analysis, representing possibly similar feeding habits. The samples of macrophytes, periphyton and sand organics were collected from 50-70 cm depth. Submerged leafs of *Potamogeton* sp. were collected by hand. In each of the studied lake the attached periphyton was carefully scraped from the stones and rinsed with a distilled water in to the three plastic buckets. Samples of sand organic were collected with 20 ml syringe by sucking the top layer of sediment at the sandy bottom of the lake. Totally 200 ml of the top sand sediments was sucked per replicate into plastic bucket. Water samples for determination of SIA of particulate organic material (POM) were collected in the opened part of the lake surface and screened through 200 µm Nitex to remove mesozooplankton. All collected samples were transported to laboratory where the plant material was rinsed carefully in distilled water to remove fine detritus and attached animals. Macrophyte samples were assigned to 3 analytical replicates per lake (10 leafs per replicate). Samples of periphyton, sand organics and seston were concentrated on pre-weighted glass fibre filters (Whatmann GF/F, 47 mm diameter), dried for 48 h at 60ºC and weighted. From each filter, two subsamples were prepared by cutting a circle with a puncher, and packed into tin capsules. In total 6 replicates of attached periphyton, sand organic and POM per lake were set.

Benthic macroinvertebrates were collected by a standard dip net (25 x 25 cm opening, 0.5 mm mesh size) from the lake littoral up to 1.5 m depth. All collected specimens of the macroinvertebrates were placed alive into the pre-filtered lake water and transported to the laboratory for further treatment. In laboratory, invertebrates were maintained alive in filtered water overnight to allow for gut content evacuation. The whole body of the amphipods and only the soft tissues of molluscs were taken for stable isotope analysis. All macroinvertebrate samples were assigned to 5 analytical replicates per lake, 3-15 individuals of each taxonomic group per replicate if available. Each sample was dried to constant weight at 60ºC for 48 h and ground to fine powder in an agate mortar and placed into the foil capsules. Samples were analysed at the Mass spectrometry laboratory, Centre for Physical Science and Technology, Vilnius, Lithuania. An elemental analyzer coupled to the isotope ratio mass spectrometer (EA-IRMS, Flash EA1112—Thermo V Advantage) via ConFlo III interface was used for the d13C and d14N analysis. Carbon isotopic ratio measurements presented here are expressed relative to the Pee Dee Belemnite (PDB) standard using the following formula: d (‰) = [(Rsample/Rstandard) – 1] × 1000, where Rsample and Rstandard are the ratios of 13C to 12C in the sample and the standard (referred to as PDB), respectively. Analytical precision and calibration of reference gas CO2 (for d13C measurements) to PDB was evaluated by repeated analysis of certified reference material caffeine IAEA-600, which gave an average d13C: mean ± SD = -27.77 ± 0.08% (certified value: mean ± SD = -27.771 ± 0.043‰ VPDB), and oil (NBS 22, d13C= -30.031 ± 0.043‰ VPDB). For calibration of reference gases N2 (d15N measurements) to air the IAEA-600 standard was used and had an average d15N: mean ± SD = 1 ± 0.2%.

Statistical analysis

To compare mean d13C and d15N values between primary producers and between primary consumers ANOVA was applied, following post hoc Unequal N HSD test. Calculations were performed using Statistica 10.0 software.

Mixing models

$d^{13}C$ and $d^{15}N$ - based stable isotope analysis in R (SIAR) mixing model (Parnell *et al*. 2010) was used to calculate the contribution of littoral primary production to studied consumer diet in all three lakes. The SIAR models were focused on carbon sources that were available for studied consumers: *Potamogeton* sp., periphyton, sand organics and particulate organic matter (POM). The trophic enrichment factors (TEFs) were set to 0.39‰ ± 1.30‰ for $d^{13}C$ and 3.4‰ ± 0.98‰ for $d^{15}N$ (Post 2002).

The role in a diet of dominant benthivorous fishes

Analysis of littoral benthic macroinvertebrate communities

The abundance and the biomass of littoral macroinvertebrates were studied in lakes Dusia, Vilkokšnis and Spindžius in September, 2014. Macroinvertebrate samples were collected using Eckman grabber sampler, with a cross-sectional area of 0.02 m^2. All macroinvertebrate samples were collected at the depth of 0.5–1.0 m, with a three replicates per lake. Collected samples were preserved in 70% ethanol. In the laboratory, samples were examined for the presence of macroinvertebrates which were sorted according to their taxonomic dependence. All macroinvertebrate specimens (except Oligochaeta and Chironomidae, which were not identified further) were identified to the species taxonomic level and specimens of each taxon were counted and weighed (wet weight). When identification to species level was not possible (young developmental stage or injury during sampling), a higher taxon was identified. Three replicate samples were averaged to obtain an estimate of the mean abundance, biomass, and proportion of particular taxon in a total macroinvertebrate community in each lake.

Analysis of littoral fish communities

Fish community analysis in lakes Dusia, Spindžius and Vilkokšnis was performed in September, 2014. The composition of fish species was investigated at 2.0-5.0 m depths using multi-mesh bottom gillnets of a mesh size of 14–18–22–25–30–40–50–60 mm, with each section 5 m long and 3 m height (Thoresson 1993). Eight nets were used per lake. All specimens were identified to the species taxonomic level, measured to the nearest 1.0 mm (TL) and weighed to the nearest 0.1 g immediately after capture. Obtained results allowed assessing the dominance of different fish species in a lake littoral fish community.

Feeding experiments

Feeding experiments were conducted to determine which of the main local benthivorous fish and crayfish species from temperate lakes recognize *P. antipodarum* as a potential prey and may consume it under experimental conditions. The test fishes such as the European perch, *Perca fluviatilis* (Linnaeus, 1758), ruffe, *Gymnocephalus cernua* (Linnaeus, 1758), roach, *Rutilus rutilus* (Linnaeus, 1758), tench, *Tinca tinca* (Linnaeus, 1758), common rudd, *Scardinius erythrophthalmus* (Linnaeus, 1758) were chosen as they are dominant benthivorous fish species in Lithuanian lakes (Arbačiauskas *et al*. 2011, Virbickas 2012, Virbickas 2013, Virbickas 2014). Additionally the spiny-cheek crayfish, *Orconectes limosus* (Rafinesque, 1817) was used in experiment. The hypothesis that fish feeding mode (crush the prey or swallow it whole) can affect the consumption of this invasive snail was also tested. Additionally, round goby *N. melanostomus* (Pallas 1811), and Chinese sleeper *Perccottus glenii* (Dybowski, 1877) were chosen as a benthivorous test fishes with a different feeding mode for this collation. *N. melanostomus* was chosen as molluscivorous fish that possess pharyngeal teeth and can crush their prey

(Raby *et al*. 2010, Barton *et al*. 2005, Kipp *et al*. 2012). While *P. glenii* as an omnivorous benthic fish that lack of the pharyngeal teeth and swallows their prey whole (Reshetnikov 2003, Reshetnikov 2008, Grabowska *et al*. 2009).

Main experimental local fish and crayfish material was collected from lake Balsys using electro fishing device in August, 2014. Invasive fish species, such as *P. glenii* and *N. melanostomus* were collected respectively from lake Beržuvis and Curonian lagoon in August, 2014. The electro fishing device was used to catch *P. glenii* and crayfish traps to catch the *N. melanostomus*. The *P. antipodarum* individuals, used in experiments were collected from lake Vilkokšnis in August, 2014. Standart dip net (25x25 cm) was used to catch the individuals. All experimental material, snails, fishes and crayfishes was acclimated to laboratory conditions for one week. Fish and crayfish acclimation was performed in closed recirculating system consisting of six 92.4 L rectangular (49.0 x 38.5 cm) tanks at the 17°C water temperature and natural photoperiod. During this period frozen midge larvaes were fed twice a day. Snail acclimation was performed in plastic 1 L buckets at 17°C water temperature and natural photoperiod. Every second day, 25% of the water was changed. The clump of *Fontinalis antipyretica* Hedw. moss was added as a food source for the snails. Only large snails (shell length >3 mm) were used in experiments. All experiments were performed in closed recirculating system made of eight 10.6 L aquaria (22.5 x 21 cm) and one 92.4 L circulation tank. All aquariums were filled with tap water for a total volume of 9.5 L and water depth of 20 cm.

Totally 134 fish and 14 crayfish individuals were used in the experiment and the same individuals were not used twice in any treatment. Before the experiment predators were not fed for 48 h. After this period, fishes and crayfishes were transfered to experimental aquaria. For each experimental trial, single fish or crayfish individual was placed in to each of eight 10.6 L experimental aquaria and acclimated for 24 h before experiment. After the acclimation period a number of 100 *P. antipodarum* individuals was spread in each aquaria and allowed the predators to forage for 24h. Some fish species used in survival experiments, such as *S. erythropthalmus* or *P. glenii* do not consume snails in natural environment, but have a hight possibility to eat it accidentally with other food sources, such as filamentous algae or detritus particles. In this case *P. antipodarum* individuals were served inserted in earth worms. After 24h fish and crayfish were removed from tanks and rinsed carefuly to remove the stacked snails on the fish. Remaining *P. antipodarum* individuals were collected from experimental aquaria and counted. The number of consumed snails was used as a proxy of fish feeding intensity on the invasive snails.

Analysis of fish diet in field

The diet of the main benthivorous fish species (*P. fluviatilis, R. rutilus, G. cernua, T. tinca,* white bream, *Blicca bjoerkna* (Linnaeus, 1758), and freshwater bream, *A. brama* (Linnaeus, 1758)) from *P. antipodarum* invaded lakes was assessed to determine whether field data support the evidence for *P. antipodarum* consumption in experimental environment. *Perca fluviatilis* individuals were divided into two length groups as it is known to undergo ontogenetic niche shifts (Hjelm *et al*. 2000, Horppila *et al*. 2000, Svanbäck and Eklöv 2002). Fish specimens for diet analysis were collected from lakes Vilkokšnis, Dusia and Spindžius in September of 2014. The multi-mesh bottom gillnets of a mesh size of 14-18-22-25-30-40-50-60 mm, with each section 5 m long and 3 m hight (Thoresson 1993) were used. All captured specimens were identified to species taxonomic level, measured to the nearest 1.0 mm (TL) and weighed to the nearest 0.1 g immediately after capture. After initial fish composition analysis, up to 30 individuals (if possible) of different benthivorous fish species were euthanized and retained for diet analysis. Stomachs of the fish retained for diet analysis were immediately removed and preserved in 10% formaldehide solution for at least two weeks until analysis in the laboratory. Fish with empty stomachs were excluded from the analysis. In total, food content of 333 specimens of various fish species was included in the analysis.

Fish gut content was dissected out and food items were identified to the lowest possible taxa under a stereomicroscope. Grouped items were counted and weighed by individual taxonomic groups, and their proportions in the total gut content biomass was assessed. Digested and thus unidentifiable particles were classified as “various stomach content” and in further analysis their volume (biomass) was proportionally divided among identified food items. For fish diet illustration identified items were grouped into seven categories: molluscs, zooplankton, macrocrustaceans, insects, fish, macrophytes and other.

Fish feeding selectivity for *P. antipodarum* was calculated as the Ivlev selectivity index (E) (Ivlev 1955):

$E_i = (r_i - p_i)/(r_i + p_i)$,

where r_i and p_ii are proportions of *P. antipodarum* biomass in fish diet and environment, correspondingly. E_i selectivity is expressed on a scale from -1 to 1. When $E_i = 0$, there is no selective feeding on *P. antipodarum*, whereas $E_i > 0$ or $E_i < 0$ indicates positive or negative selectivity, respectively.

The experiments on P. antipodarum survivorship the gastrointestinal tract of fishes

The survival experiments of *P. antipodarum* were conducted in order to determine if this invasive snail can survive gastrointestinal passage of the main local benthivorous fish. The same aquaria, experiment conditions and fish species were used as in previous feeding experiments. We also tested initial hypothesis that feeding mode could affect *P. antipodarum* survival through the gastrointestinal tract of benthivorous fishes. The first group was represented by fishes that possess pharyngeal teeth and thus are known as molluscivorous fish species: *N. melanostomus, T. tinca* and *R. rutilus*. Second group was represented by omnivorous fishes that lack of the pharyngeal teeth, but have well expressed stomach: *P. fluviatilis* and *P. glenii*.

A total of 73 fish individuals were used in the survival experiments and the same individual were not used twice in any treatment. The size of fishes and crayfishes are presented in table 3. After the acclimation period a number of 100 individuals of *P. antipodarum* were spread in each aquarium. Fish were allowed to forage for 18 hours. The leftovers of the *P. antipodarum* in each experimental aquarium were carefully pumped and sieved on the 50 µm mesh size sieve and unharmed snails were counted in order to estimate the exact number of consumed snails. For fish species (*P. fluviatilis, R. rutilus, P. glenii* and *S. erythrophthalmus*) that did not significantly consumed *P. antipodarum* during feeding experiments, but were revealed to consume *P. antipodarum* naturally, snail individuals were served by inserting them in the common earthworm, *Lumbricus terrestris* (Linnaeus, 1758). Thereafter, fish were put individually into empty experimental aquaria, in which a net (5 mm mesh) was placed about 3 cm above the bottom. The net was placed in the bottom of experimental aquaria to avoid the re-consumption of faecal pellets. Experimental fishes were left to defecate for 48 h at 17ºC. For each experiment the faecal material was siphoned and sieved (50 µm mesh) in experimental aquaria at 8 h time interval. All unharmed and undigested snails were rinsed with water and put from each experimental aquaria in separate Petri dishes filled with tap water for 12 hours. The snails were sorted in to 3 groups – digested (only the remains of the shell), undigested (shell ir snail intact, but not alive) and alive. The number and condition of all unharmed snails in each Petri dish were recorded using a dissecting microscope. Assessment of snail condition was based on snail appearance and movement, as dead snails either remained deep within their shells or if exposed outside their shells exhibited no movement when probed. Survived prey specimens generally were crawling around in Petri dishes. Number of alive and dead *P. antipodarum* was counted. The proportion of undigested and survived snails was calculated for each individual of experimental fish.

Statistical analysis

As data did not satisfied requirements of parametric statistical methods (Shapiro-Wilk‘s W test, $p < 0.05$), Kruskal-Wallis ANOVA test was applied to check the effect of different predators on numbers of consumed and survived *P. antipodarum* individuals. Mann-Whitney U test was applied to compare the number of consumed, digested or survived snails between two different predator groups or species. Calculations were performed using Statistica V10 software.

RESULTS

Current distribution of *P. antipodarum* in Lithuanian inland waters

For the first time, *P. antipodarum* individuals were found in 4 lakes and river (Butkus *et al*. 2012). In the study of lake littoral macroinvertebrate communities, *P. antipodarum* was detected in three of 16 lakes, lakes Daugai, Dusia and Metelys. Among investigated rivers, the species was recorded in the Verknė River, at two of five study sites, which were the closest to the source-lake. Further investigation also revealed the presence of *P. antipodarum* in the source-lake Vilkokšnis. Overal, during the 2010-2016 year surveys, *P. antipodarum* was found in 19 study sites. In 2012, it was found in the Spernia River (outflowing from Lake Dusia), the Strėva River and in the closely linked lakes Spindžius and Spindžiukas. Later, in 2013 it was recorded in lakes Obelija and Plateliai and in 2014 in lake Lūšiai. In 2015 *P. antipodarum* individuals were found in Šventoji river besides the port (western Lithuania) and in lake Prūtas (northeastern part of Lithuania). Finally, in 2016 the species was recorded in Elektrėnai water reservoir and lake Talša. In total, recently species occurs in 42 sites, where 18 were evaluated during the study period (Figure 3, Table 1) (Butkus *et al*. 2014). Besides, during the period of 2010 – 2016, 41 different ecosystem was sampled, but the species was not found (Figure 4). Such results indicate rapid *P. antipodarum* spread across Lithuanian inland waters in recent years. Besides, further expansion of *P. antipodarum* can be expected in Lithuanian inland waters.

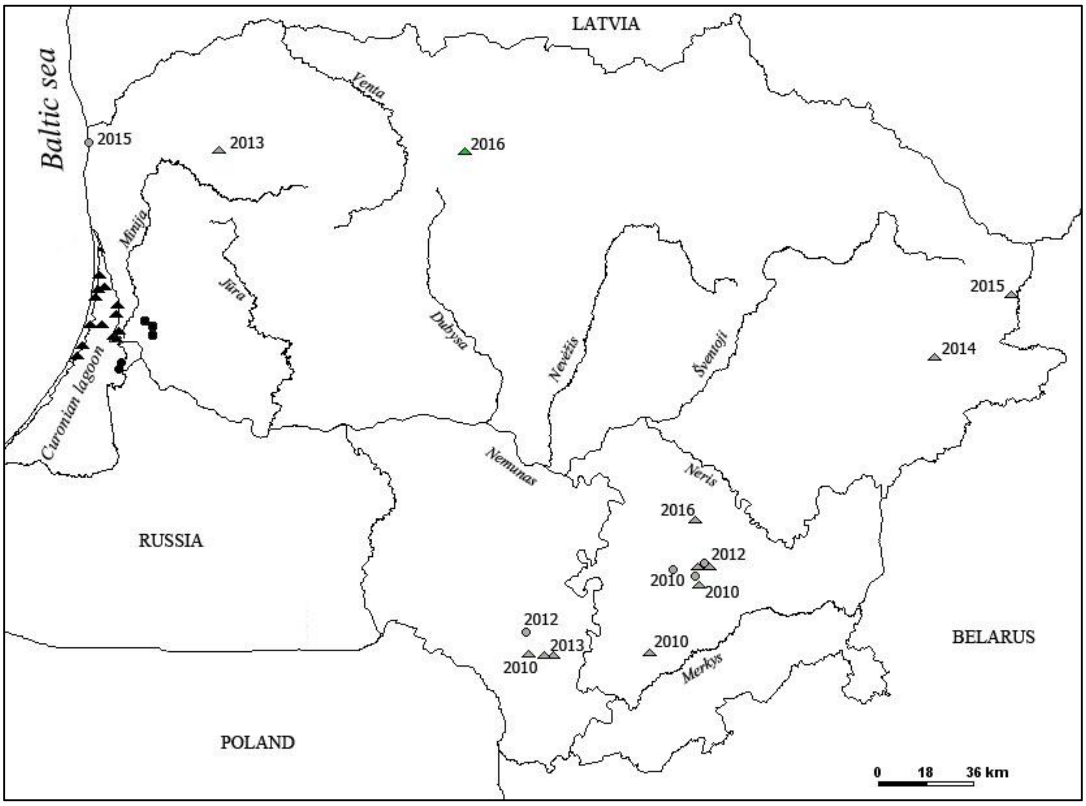

Fig. 3. Distribution of the New Zealand mudsnail *P. antipodarum* in Lithuanian inland waters. Circles and triangles indicate localities in lotic and lentic waters, respectively. Colours indicate source of data: from literature (black), current study (gray). Literature sources presented in Table 2.

Table 2. Records of the mud snail *Potamopyrgus antipodarum* in Lithuanian inland waters. References: Gasiūnas 1959 (1), Šivickis 1960 (2), Bubinas and Vaitonis 2005 (3), Zettler *et al*. 2005 (4), Zettler and Daunys 2007 (5), Butkus *et al*. 2012 (6), data from current study (2012–2015) (7).

No.	Water body	Latitude, N	Longitude, E	References
1	Curonian Lagoon	55°33’40.38"	21°09’15.66"	4, 5
2	Curonian Lagoon	55°38’57.42"	21°09’07.68"	4, 5
3	Curonian Lagoon	55°39’13.80"	21°09’19.44"	4, 5
4	Curonian Lagoon	55°38’19.98"	21°07’58.80”	4, 5
5	Curonian Lagoon	55°29’46.92"	21°14’50.52"	4, 5
6	Curonian Lagoon	55°33’12.00"	21°07’42.00"	4, 5
7	Curonian Lagoon	55°31’40.02"	21°07’06.00"	4, 5
8	Curonian Lagoon	55°39’38.08"	21°08’26.59"	1
9	Curonian Lagoon	55°28’13.62"	21°15’15.72"	4, 5
10	Curonian Lagoon	55°19’11.70"	21°01’28.68"	4, 5
11	Curonian Lagoon	55°25’05.88"	21°06’18.60"	4, 5
12	Curonian Lagoon	55°22’07.98"	21°03’35.82”	4, 5
13	Curonian Lagoon	55°35’22.80"	21°08’00.78"	4, 5
14	Curonian Lagoon	55°22’51.96"	21°14’50.52"	4, 5
15	Curonian Lagoon	55°20’51.96"	21°11’50.82"	4, 5
16	Curonian Lagoon	55°20’34.44"	21°11’48.60"	4, 5
17	Curonian Lagoon	55°38’29.16"	21°09’02.41"	7
18	Curonian Lagoon	55°25’16.68"	21°09’48.91"	2, 3
19	Nemunas Delta (Rinda)	55°16’36.90"	21°15’48.96"	4, 5
20	Nemunas Delta (Skatulė)	55°17’46.50"	21°17’20.40"	4, 5
21	Nemunas Delta (Rumbas)	55°21’11.88"	21°16’19.62"	4, 5
22	Nemunas Delta (Upaitis)	55°21’04.44"	21°14’46.26"	4, 5
23	Nemunas Delta (Kniaupas)	55°21’52.92"	21°15’00.36"	4, 5
24	Elektrėnai water reservoir	54°45’20.89"	24°40’16.91"	7
25	Spernia river	54°20’18.23"	23°39’52.62"	7
26	Strėva river	54°34’18.74"	24°40’05.92"	7
27	Verknė river	54°32’24.83"	24°38’23.50"	6
28	Verknė river	54°33’14.89"	24°30’56.99"	6
29	Šventoji river	56°01’46.48"	21°04’25.15"	7
30	Šventoji river	56°01’51.40"	21°05’16.00"	7
31	Šventoji river	56°02’49.02"	21°07’49.70"	7
32	Lake Daugai	54°18’53.69"	24°22’51.61"	6
33	Lake Dusia	54°19’32.85"	23°40’36.75"	6
34	Lake Metelys	54°18’18.00"	23°44’53.68"	6
35	Lake Obelija	54°17’36.16"	23°49’14.91"	7
36	Lake Plateliai	56°02’50.02"	21°50’02.61"	7
37	Lake Spindžiukas	54°34’13.92"	24°39’52.18"	7
38	Lake Spindžius	54°34’11.67"	24°40’49.96"	7

Table 2 (continued)

No.	Water body	Latitude, N	Longitude, E	References
39	Lake Vilkokšnis	54°30’21.35"	24°40’40.61"	6
40	Lake Prūtas	55°28’49.28"	26°32’29.34"	7
41	Lake Lūšiai	55°19’54.53"	26°04’18.47"	7
42	Lake Talša	55°56’11.21"	23°20’05.52"	7

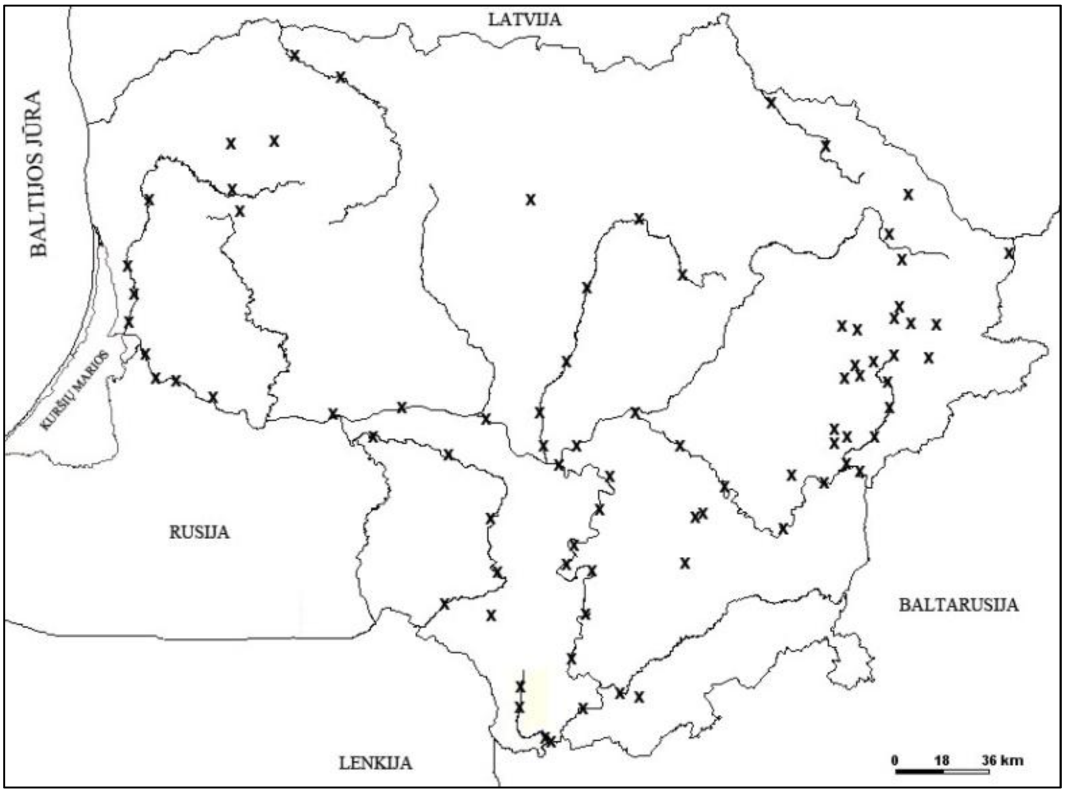

Fig. 4. The study sites, where macroinvertebrates were sampled, but *P. antipodarum* was not found.

Genetic diversity of *P. antipodarum*

Cytochrome b diversity

Analysis of the 63 individuals across the 9 sites in Lithuania and Lake Wigry in Poland, returned one cytochrome b haplotype. This haplotype was identical to cytochrome b haplotype, recorded in clones Duluth (genbank: GQ996433.1), 7 (genbank: GQ996432.1) and DenmarkA (genbank: GQ996424.1) (Neiman *et al*. 2010).

16S rRNA diversity

Analysis of the 32 individuals across the 9 sites in Lithuania and Lake Wigry in Poland returned one 16S rRNR haplotype, which is described as t haplotype in literature.

Microsatellite DNA MLG diversity

Analysis of the 230 individuals across the 9 sites in Lithuania and Lake Wigry in Poland returned 1 msDNA MLG indicating monomorphic *P. antipodarum* populations. Single alleles, 149 and 168 were found at loci Pa56 and Pa217, respectively (Figure 5). Meanwhile two alleles were found at loci Pa112 (216 and 217) and Pa254 (128 and 146) (Figure 5).

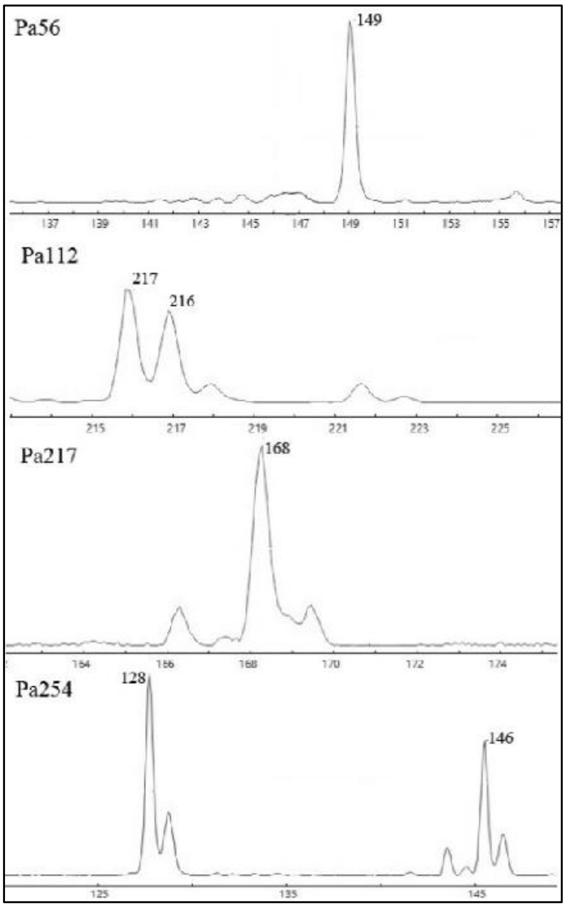

Fig. 5. Microsatellite peak patterns at four studied loci.

The analysis of 8 Lithuanian and one Poland *P. antipodarum* populations, using three different molecular markers, indicated absence of genetic diversity within and among the populations.

Population characteristics and life-history traits of *P. antipodarum*

Optimal sampling technique selection

Samples, collected in different depths were compared to check whether there are any significant differencies in *P. antipodarum* densities. As there was no significant difference between depths for both cylinder (Kruskal-Wallis ANOVA test, $H_{2, 9}$ = 1.70, p = 0.52) and Eckamn grabber (Kruskal-Wallis ANOVA test, $H_{2, 9}$ = 0.07, p = 0.99), density data was pooled and compared between sampling devices. There was no significant difference between the mean density of *P. antipodarum* assessed using different sampling devices (Kruskal-Wallis ANOVA test, $H_{1, 18}$ = 1.03, p = 0.31) (Fig. 6). Eckman grabber was considered to be the optimal sampling technique due its ease of use in all seasons.

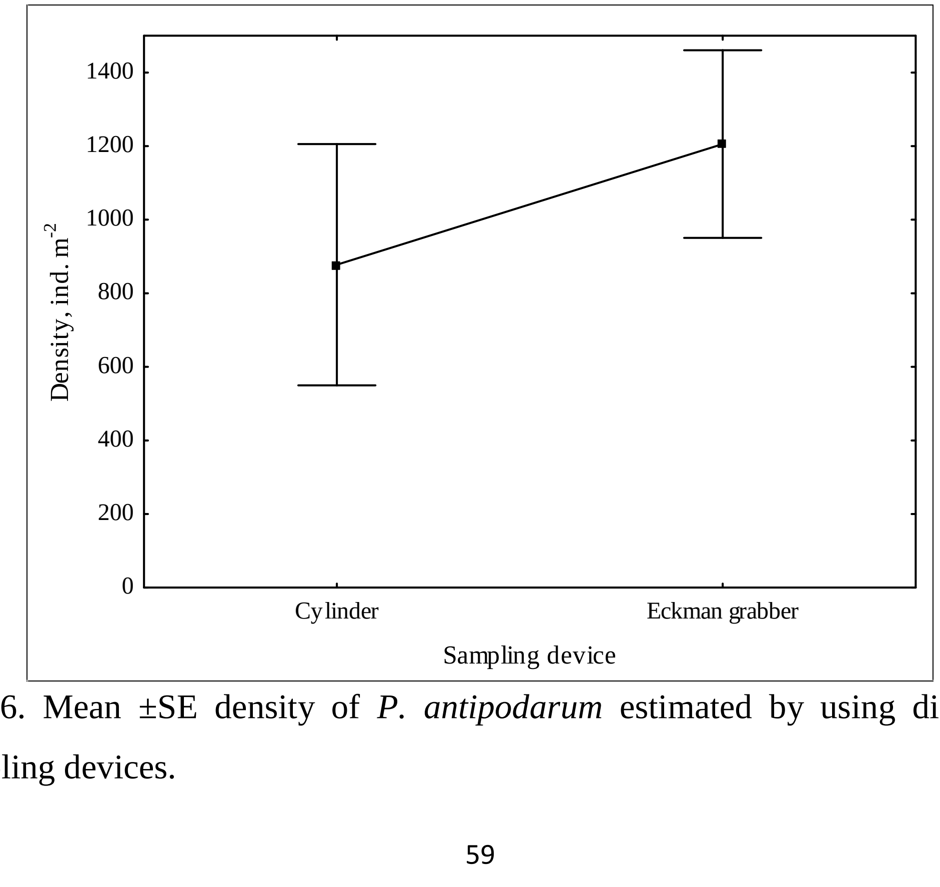

Fig. 6. Mean ±SE density of *P. antipodarum* estimated by using different sampling devices.

Pattern of spatial distribution was evaluated for *P. antipodarum* in studied lakes. The Morisita's spatial distribution index ($I\alpha$) values indicated hight spatial aggregation ($I\alpha > 1$) of *P. antipodarum* individuals in all studied lakes and all studied periods. The values varied between 1.8 and 2.1 in lake Vilkokšnis, 1.4 and 2.1 in lake Obelija, 2.4 and 2.8 in lake Dusia and 1.3 and 1.8 in lake Metelys.

Lake Vilkokšnis

The dynamics of *P. antipodarum* density during the one year period was estimated in Lake Vilkokšnis. It varied significantly throughout the year (ANOVA, $H_{14,\ 135} = 3.47$, $p < 0.001$) (Fig. 7). Applied post-hoc Tukey HSD test indicated lowest densities of *P. antipodarum* during cold season months, when average density decreased below 100 ind. m^{-2}. Meanwhile highest (Tukey HSD test, $p < 0.05$) density was estimated in the end of the growing season, when the highest average density of 1490.0 ind. m^{-2} was recorded.

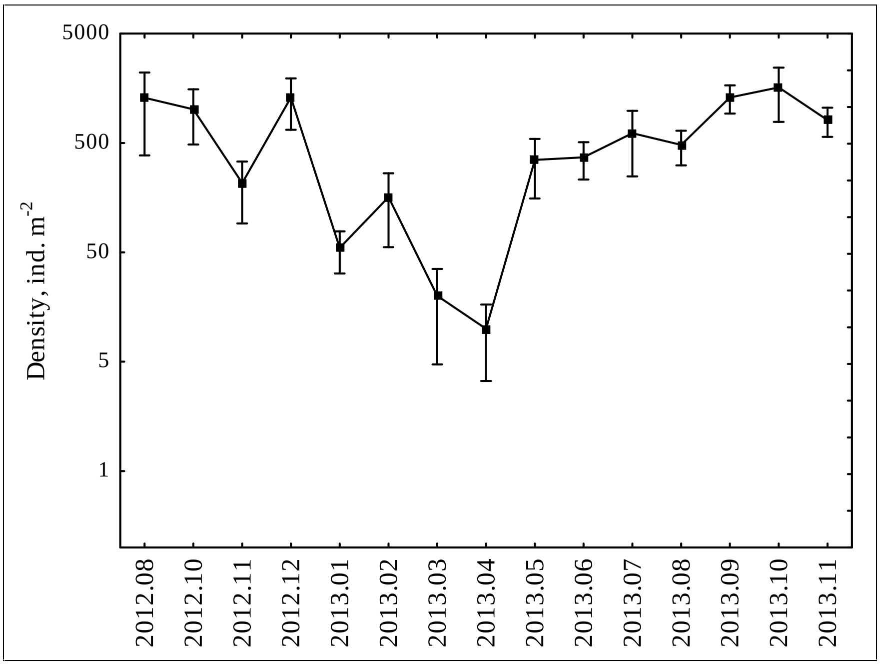

Fig. 7. Mean ±SE density of P. antipodarum in Lake Vilkokšnis. Note logarithmic scale.

The dynamics of average *P. antipodarum* biomass throughout the study period is presented in Figure 8. Hight variation was observed in average biomass values between different months. It ranged from 9.18±6.43 in April to 676.49±315.67 mg AFDM m^{-2} in October of 2013. Overal, biomass tracked the dynamics of density .

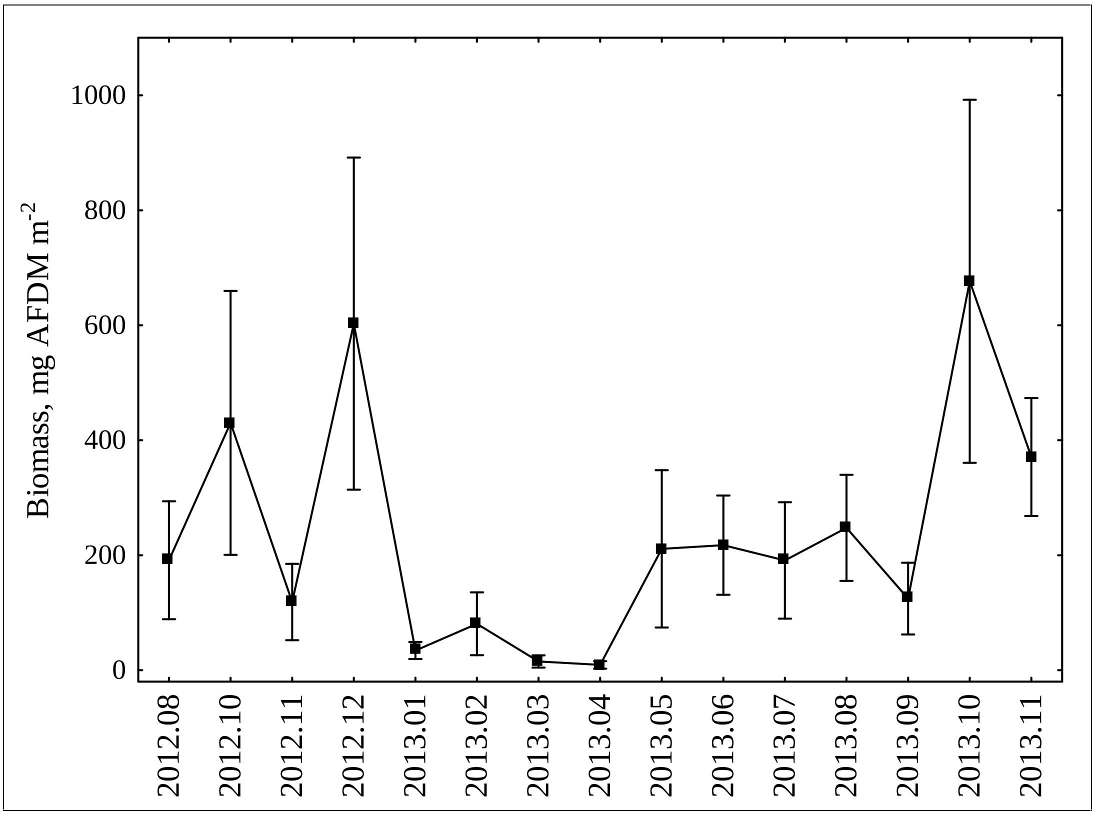

Fig. 8. Mean ±SE biomass of *P. antipodarum* in Lake Vilkokšnis.

To estimate the effect of month to average log-transformed biomass, analysis of variance (ANOVA) was applied. The analysis resulted in statistically significant ($F_{14, 135} = 4.10$, $p < 0.001$) effect of sampling month.

The shell length of all sampled individual was measured. The recorded shell length ranged between 1 mm to 5.7 mm in lake Vilkokšnis. The significant variation (ANOVA, $F_{13, 1726} = 45.92$, $p = 0.001$) in average shell length was observed in lake Vilkokšnis throughout the year, where average values ranged from 2.1 mm in August of 2012 to 4.9 mm in April of 2013 (Fig. 9).

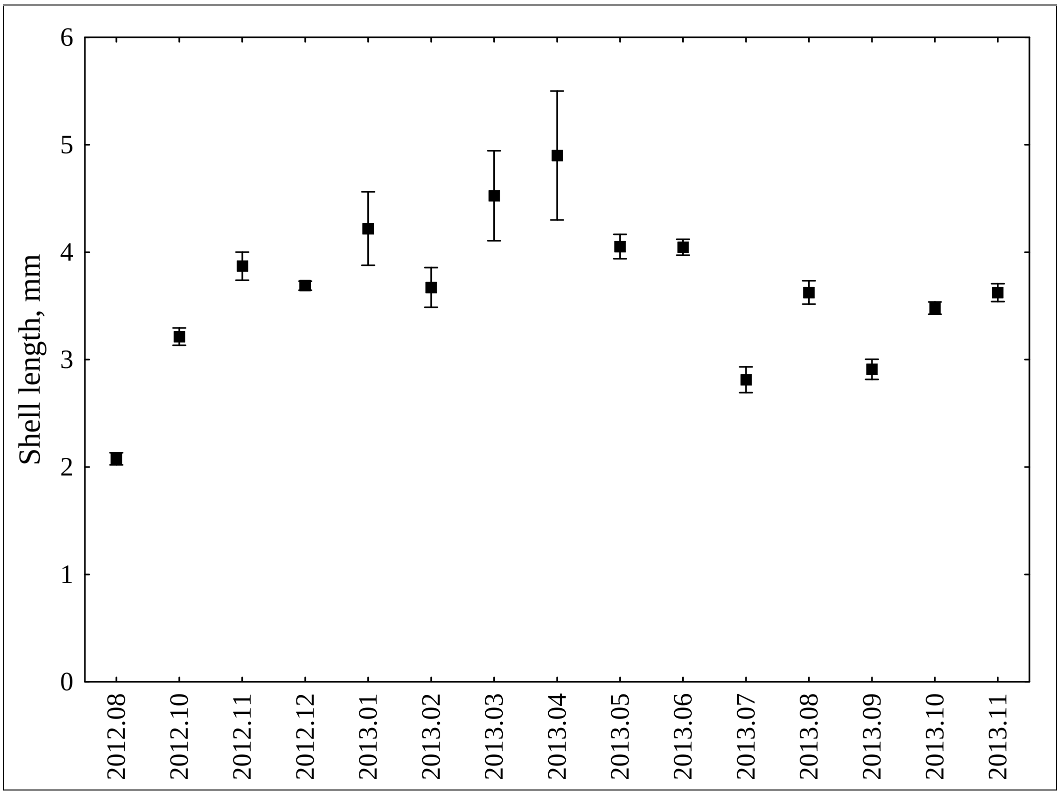

Fig. 9. Mean ±SE shell length of *P. antipodarum* in lake Vilkokšnis.

The density of organisms substantially depends on average individual size in population, i.e. highest densities are being observed after reproduction, when young individuals emerge in the population. To estimate the relationship of mean shell length on log-transformed *P. antipodarum* density linear regresion analysis was applied for data from Lake Vilkokšnis. Results indicated weak, though significant negative relationship ($L = 4.10 – 0.22 * Log(N)$; $r^2 = -0.145$; $p < 0.001$), indicating higher density of juvenile *P. antipodarum* individuals in comparison to adults, what can be expected in natural populations (Fig. 10).

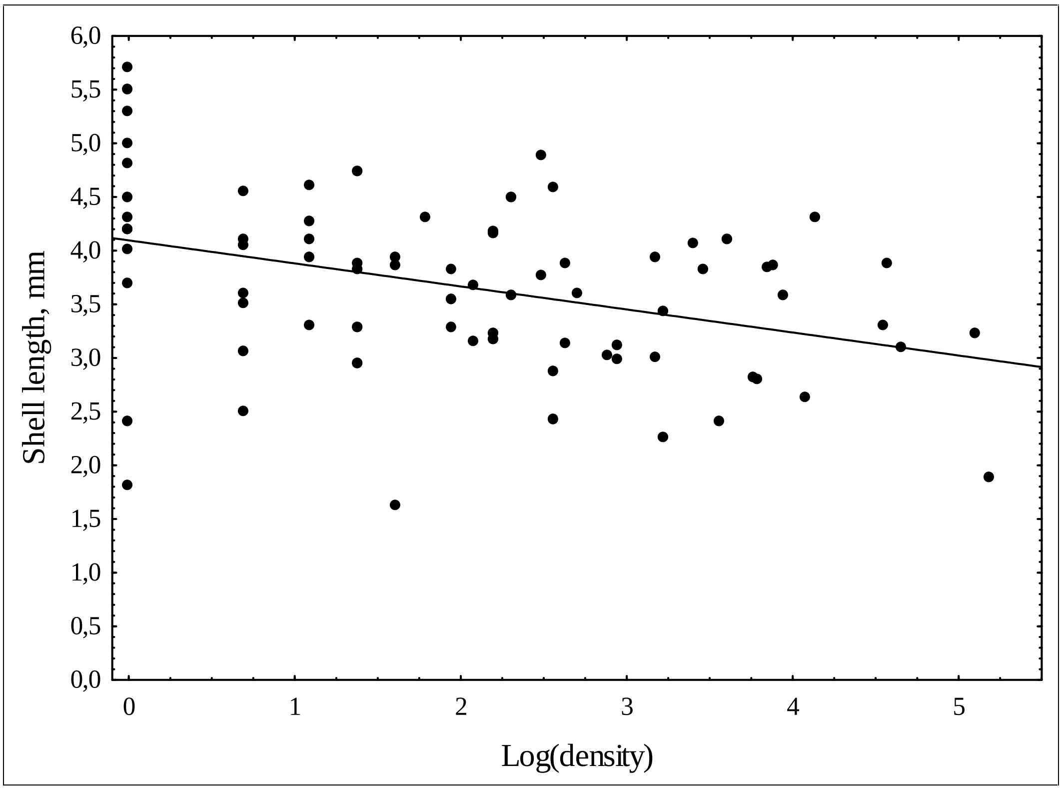

Fig. 10. Relationship between mean shell length and density of *P. antipodarum* in lake Vilkokšnis.

Comparison between lakes

Nested Anova indicated significant effect of lake on average snail density ($F_{3, 108}$ = 45.80, p < 0.001). Post hoc Tukey HSD test indicated lowest densities in Lake Dusia in comparison to other lakes, and significant (p < 0.001) difference between lakes Vilkokšnis and Metelys. Though there were no significant differencies between lakes Metelys and Obelija (p = 0.34), and between lakes Vilkokšnis and Obelija (p = 0.07) (Fig. 11). Also, there was a significant effect of season ($F_{2, 108}$ = 15.37, p < 0.001), where the lowest (Tukey HSD test, p < 0.05) densities were observed in spring and generally increased to highest densities in autumn (Fig. 11).

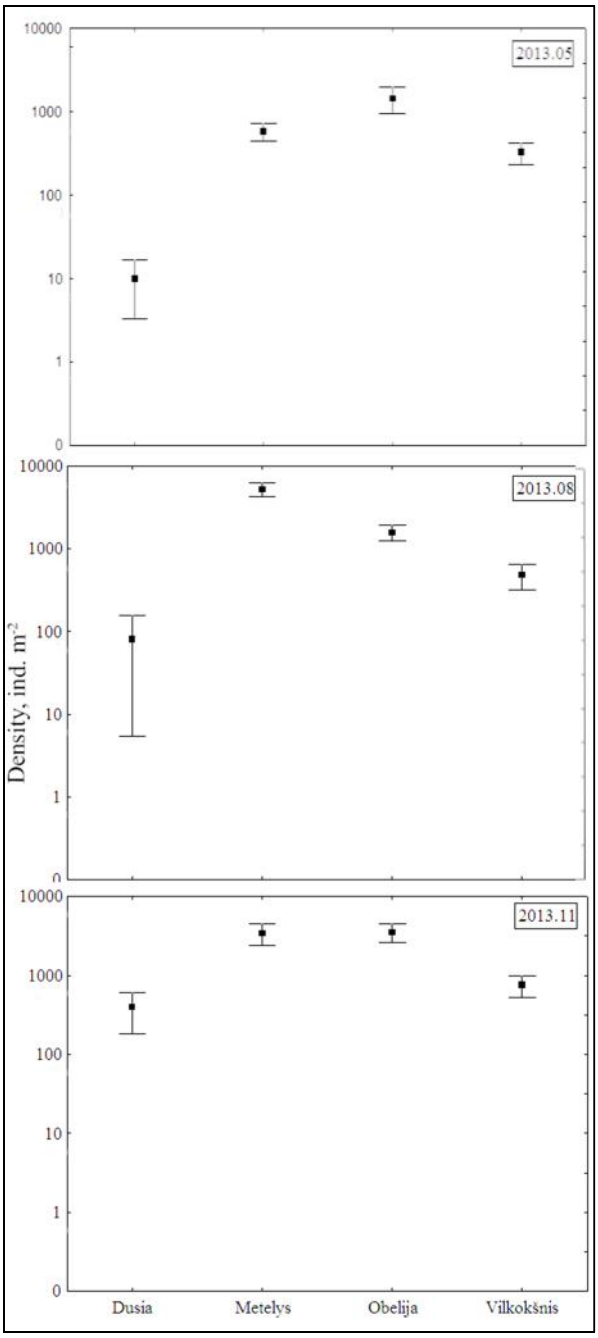

Fig. 11. Mean ±SE *P. antipodarum* density in lakes Dusia, Metelys, Obelija and Vilkokšnis in May, August and November of 2013. Note the logarithmic scale.

The effect of the season and lake on mean log-transformed biomass was estimated using nested ANOVA‘s. The analysis indicated significant effect of lake ($F_{3,\ 106}$ = 37.67, p < 0.001). Applied post hoc Tukey HSD test indicated lowest biomass in Lake Dusia (Fig. 12). Meanwhile average biomass in Lake

Vilkokšnis was significantly ($p < 0.05$) lower than in Lakes Metelys and Obelija. Also, there was a significant effect of season ($F_{2,\ 106} = 13.21$, $p < 0.001$), where significantly (Tukey HSD test, $p < 0.05$) lower biomass were observed in spring than in summer and autumn seasons (Fig. 12).

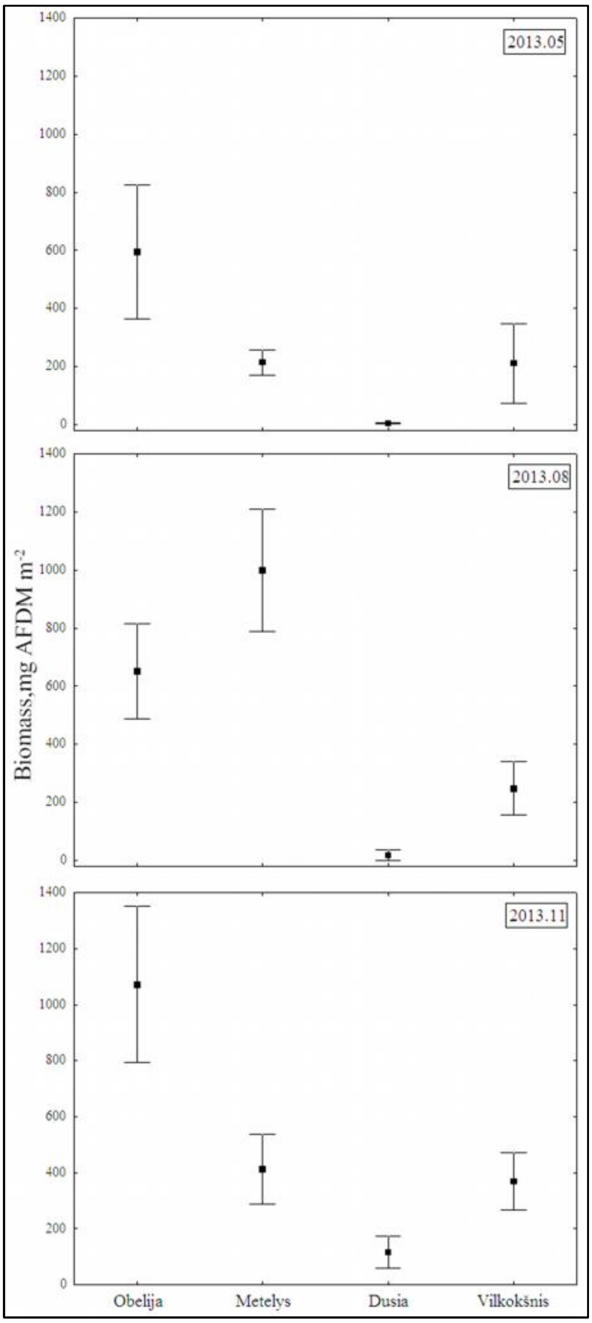

Fig. 12. Mean ±SE biomass during different seasons in studied lakes.

Estimated average (±SE) biomass varied not only between the studied lakes, but also between different seasons (Fig. 12). In spring, average biomass in

Lake Obelija was 594.39±231.75 mg AFDM m^{-2} and it was more than 130 times highter than that estimated in Lake Dusia (4.56±3.13 mg AFDM m^{-2}). Meanwhile average biomass in Lakes Metelys and Vilkokšnis were 214.54±43.26 and 211.06±136.86 mg AFDM m^{-2}, respectively. In summer, average biomass increased in most of the lakes. In Lake Metelys it increased to 998.57±210.55 mg AFDM m^{-2} and it was 54.5 and 4 times highter than in respectively Lakes Dusia (18.31±17.99 mg AFDM m^{-2}) and Vilkokšnis (247.6±92.22 mg AFDM m^{-2}). Average biomass in Lake Obelija was 652.25±164.52 mg AFDM m^{-2}. In autumn, average biomass in Lake Obelija increased more than 1.6 times to 1072.55± 278.99 mg AFDM m^{-2}, which was 9.1 times highter than estimated in Lake Dusia (117.53±58.16 mg AFDM m^{-2}). In Lakes Metelys and Vilkokšnis, estimated average biomass was 413.61±124.20 and 370.81±102.64 mg AFDM m^{-2}, respectively.

The shell length of all sampled individuals was measured and compared. Overal, the recorded shell length ranged from 0.8 mm in lake Obelija to 5.7 mm in lake Vilkokšnis. The two-way ANOVA analysis was applied to check the effect of lake and season on average size of *P. antipodarum* individuals. Results indicated statistically significant effect of both lake ($F_{3,\ 3406} = 223.84$, $p < 0.001$), and season ($F_{2,\ 3406} = 10.72$, $p < 0.001$). Applied post-hoc unequal HSD test ($p < 0.05$) indicated largest mean individual size in Lake Vilkokšnis, and lowest in Lake Metelys. Also the test indicated significantly ($p < 0.05$) larger individuals in spring than summer and autumn, indicating dominance of large individuals before reproduction in the begining of growing season.

Overal, the decrease of mean shell length from spring to autumn was observed in all studied lakes. The largest decrease, from 3.3 ± 0.1 mm to 1.9 ± 0.1 mm was observed in Lake Metelys. Meanwhile in other studied lakes, it decreased from 4.1 ± 0.1 to 3.6 ± 0.1 mm in Lake Vilkokšnis, from 3.4 ± 0.1 to 2.8 ± 0.1 mm in Lake Obelija and from 3.7 ± 0.3 to 2.8 ± 0.1 mm in Lake Dusia. Such decrease in average shell length indicated increasing number of young individuals toward the end of growing season.

A pairwise Kolmogorov-Smirnov test was applied to compare the size frequency distributions of *P. antipodarum* between the studied lakes and seasons. The results indicated significant differencies in size frequency distribution between Lake Vilkokšnis and Lakes Metelys ($p > 0.001$), Obelija ($p > 0.001$) during the spring season. In other lakes there were no significant ($p > 0.1$) differencies. Meanwhile in summer, the statisticaly significant ($p < 0.005$) differencies were found between all studied lakes. The significant differencies in size structure between most of the studied lakes were also found in autumn. The only exception was found for lakes Obelija and Dusia, where size structure did not differed significantly ($p > 0.1$). The size frequency distribution was also compared between the seasons for separate lakes. The analysis indicated significant variation in size structure between the seasons. In Lake Vilkokšnis significantly different size structure was estimated between spring and summer ($p < 0.01$), autumn ($p < 0.01$) seasons. Meanwhile in lakes Obelija and Metelys significant ($p < 0.001$) differencies in size structure were estimated between all seasons. Though there were no significant variation in size structure between the seasons in Lake Dusia. Overal the analysis indicated significant variation in size structure of *P. antipodarum* not only between the seasons, but also between the studied lakes (Fig. 13).

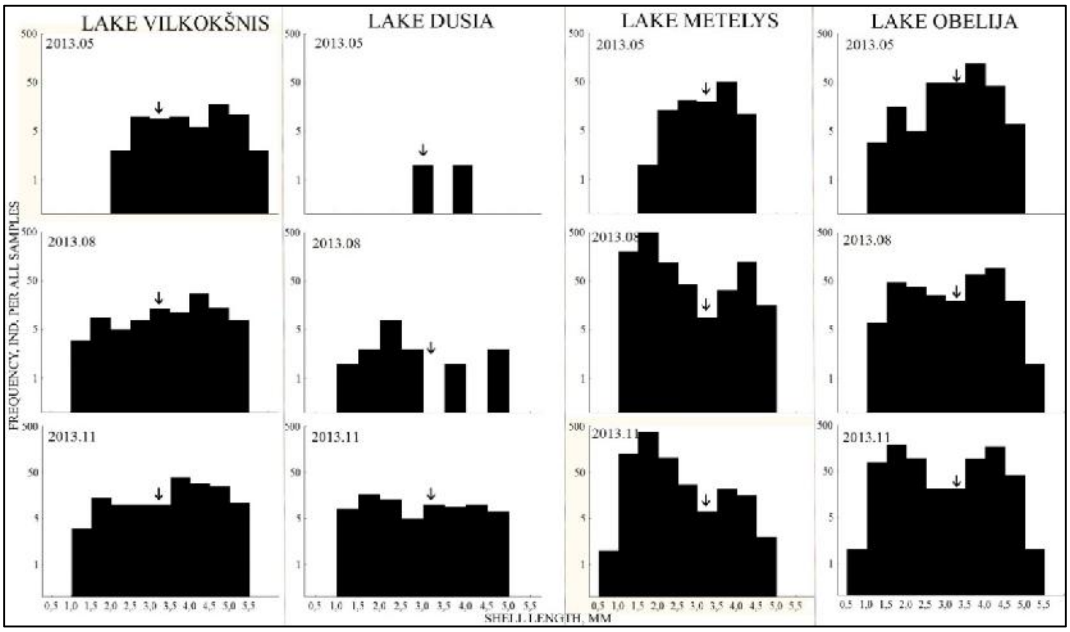

Fig. 13. Variation in size structure of *P. antipodarum* in lakes at different seasons. Arrows indicate size at first reproduction (3.4 mm).

Reproductive traits

Lake Vilkokšnis

Ovigerous females (with embryos) were found year-round in lake Vilkokšnis. However, the percentage of females carrying embryos varied throughout the year. The highest proportion of adult females with embryos was recorded in May (100%) and June (100%) months. The lowest proportion was observed during the winter, when less than 20% of dissected females of reproductive size were bearing embryos (Fig. 14A).

Significant variation in fecundity (ANOVA, $F_{14,\ 477} = 5.10$, $p < 0.001$) was observed throughout the year (Fig. 14). Fecundity varied from 4.8 in March to 19.5 embryos per adult female in July. In April - July period fecundity and average cluch size were equal or nearly equal, indicating the most intense reproduction, i.e. the highest precentage of adult females with embryos (Fig. 14B).

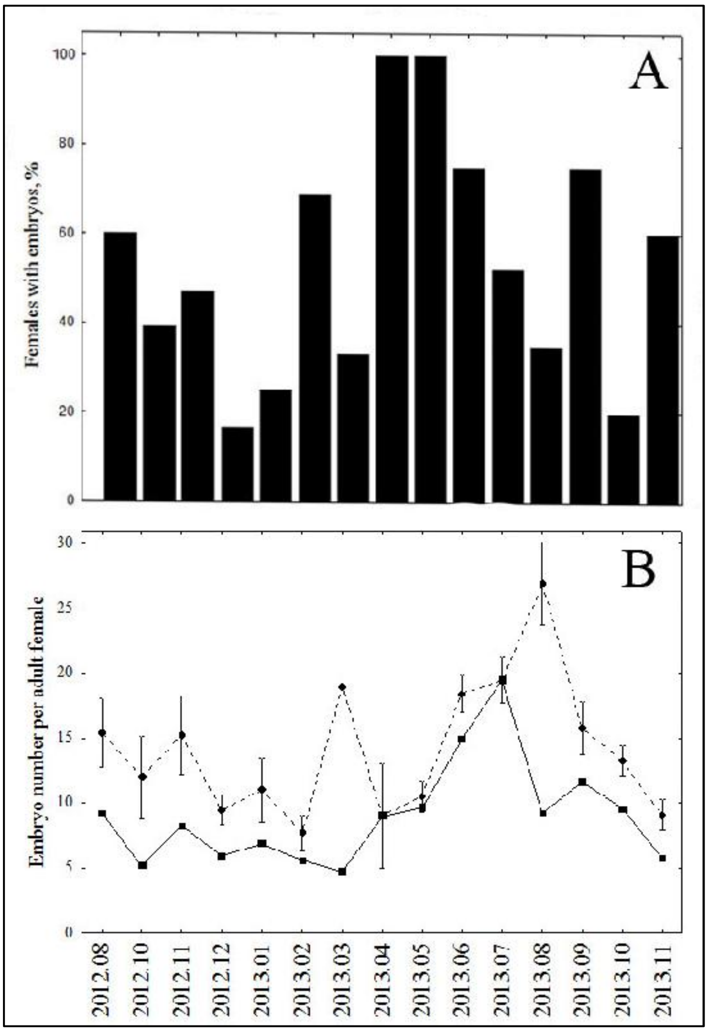

Fig. 14. The dynamics of percentage of females with embryos (A); Fecundity as average embryo number per adult female (black) and average cluch size (±SE) (grey) of *P. antipodarum* in lake Vilkokšnis (B). There are no whiskers on the cluch size in march due to only one recorded female with embryos.

To estimate the effect of female shell length on clutch size, data from all studied lakes was pooled and linear regression analysis was applied. Significant regression (Clutch size = $-22.58 + 8.22*L_{shell}$, $r^2 = 0.20$, $p < 0.001$) between female shell length (L_{shell}) and clutch size (embryo number) was found (Fig. 15). In general, besides other less important factors, body size of the female mainly controls for clutch size. The results indicated, that smaller females had less embryos than the larger females, i.e. clutch size increased together with female size. Though the model explained only about 20%

variation. It was possibly determined by asynchronous and continous throughout the growing period release of embryos, which resulted in hight variance.

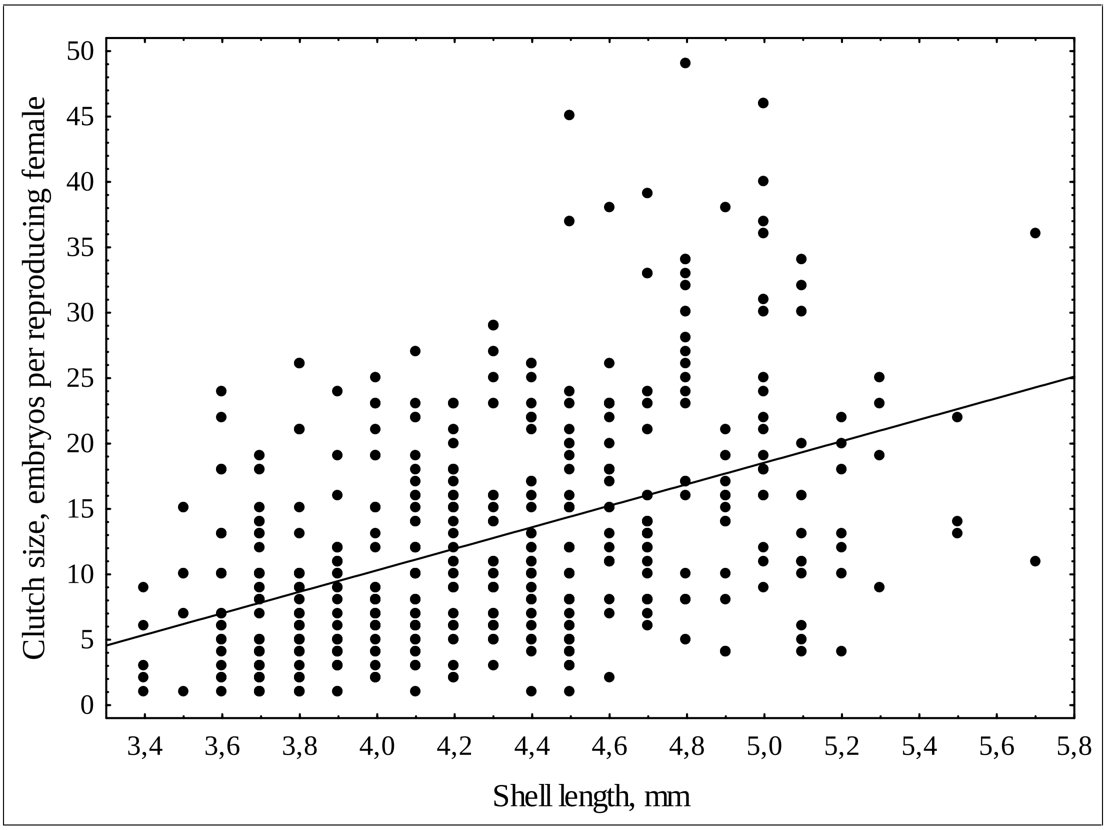

Fig. 15. Relationship between shell length and clutch size of *P. antipodarum*.

The comparison between studied lakes

In lakes Metelys and Obelija ovigerous females were found in all seasons and brood size ranged from 1 to 17 and from 1 to 26 embryos per reproducing female, respectively. Due to the absence (in May) or very low number (in August) of dissected females, Lake Dusia was excluded from reproductive trait analysis.

The effect of lake on fecundity in different seasons was estimated using nested design ANOVA, where seasons were nested in lakes. Applied model indicated significant effect of the lake and season in lake on fecundity (Table 3), indicating significant differencies in fecundity between lakes in different seasons. Applied post-hoc unequal N HSD test indicated significantly lower fecundity in Lake Metelys than in lakes Vilkokšnis ($p < 0.001$) and Obelija ($p = 0.03$) during spring sampling (Fig. 16).

Table 3. Nested analysis of variance (ANOVA) for fecundity (no. embryos carried per adult female) of *P. antipodarum* in studied lakes with respect to different seasons.

Source of variation	No. embryos adult female^{-1}		
	df	*F*	p
Lake	2	4.56	0.011
Season (lake)	6	5.53	< 0.001
Error	289		

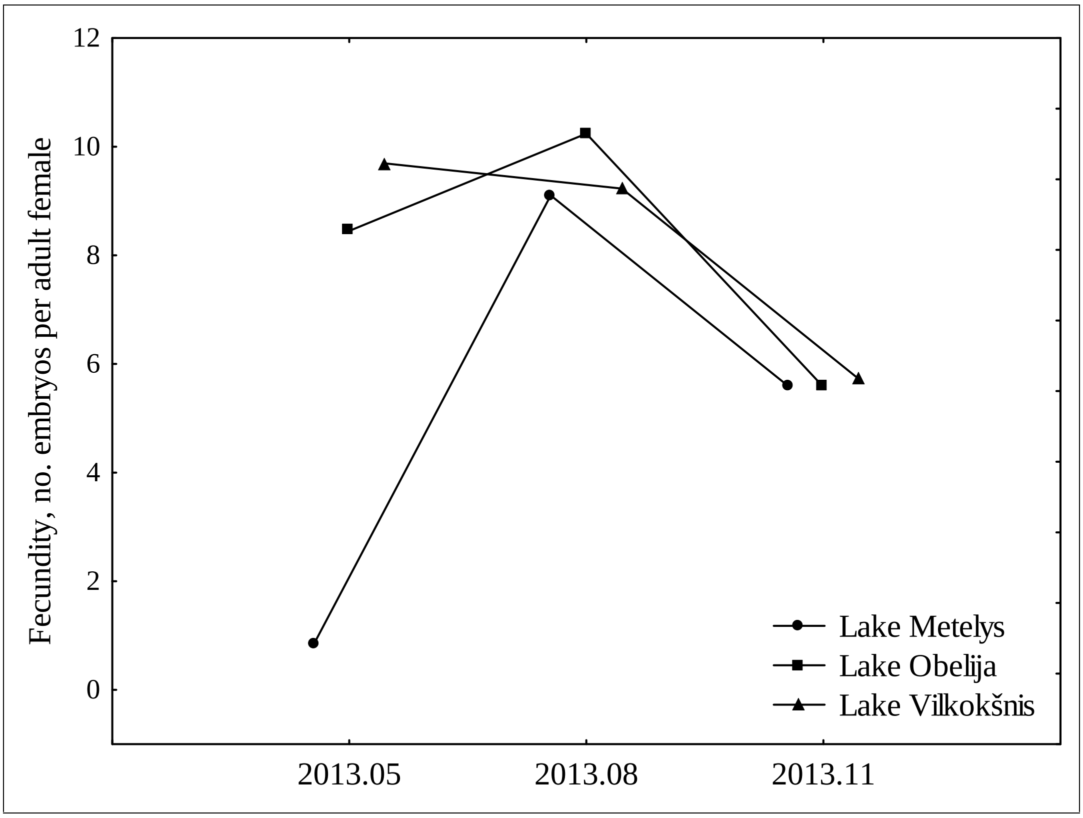

Fig. 16. Fecundity of *P. antipodarum* in different seasons of studied lakes.

Individual growth in field and laboratory conditions

Specific growth rates of *P. antipodarum* were estimated in two ways – laboratory experiments and from the dynamics of size frequency distribution in the field. Growth curve parameters from laboratory experiments were estimated using linear regression of v_{dt} on L_t equations: $v_{dt} = 0.103 – 0.019*L_t$; $r^2 = 0.72$; $p < 0.001$ for 20ºC and $v_{dt} = 0.068 – 0.012*L_t$; $r^2 = 0.54$; $p < 0.001$ for 15ºC. Growth curves in field were estimated from size frequency distribution data – one integrated for whole year period with two seasons (Fig. 17, parameters presented in Table 4) and two for separate, „winter“ and „growing“ seasons. Only seasonal field growth curves were used for further analysis.

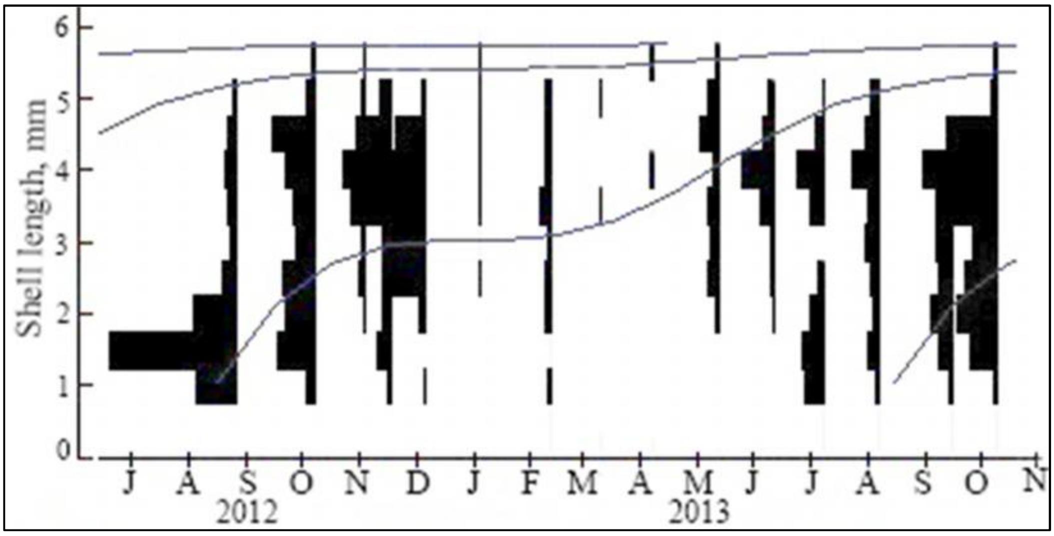

Fig. 17. Growth curves based on size frequency distributions in lake Vilkokšnis during 2012 – 2013 year.

Table 4. Growth conditions, growth curve parameters L_∞ and k, starting point (C) and seasonality (WP) parameters of annual biseasonal growth curve, maximal recorded length (L_{max}), length at maturity (L_m), length at birth (L_0) for *P. antipodarum*.

Conditions	L_∞	k	L_{max}	L_m	L_o	WP	C
Field: year	5.78	0.0055	5.7	3.4	0.59	1	1

The parameters characterizing growth curve parameters, growth conditions and life-history characteristics for *P. antipodarum* during laboratory experiment and field observations are presented in Table 5. Different intercept and slope of shell length increment on shell length regressions resulted in different asymptotic length estimated for laboratory growth curves. Both size at maturity and size at birth were set to be the same for all conditions as all individuals used in this study were sampled in the same lake so these traits may be considered to be similar.

Table 5. Growth conditions in the laboratory growth experiment and lake, growth curve parameters L_∞ and k, maximal recorded length (L_{max}), length at maturity (L_m), length at birth (L_0) for *P. antipodarum*. Temperature and length are in °C, mm, correspondingly.

No	Conditions	L_∞	k	L_{max}	L_m	L_o
1	Laboratory: 15°C	5.23	0.0130	4.6	3.4	0.59
2	Laboratory: 20°C	6.00	0.0200	5.1	3.4	0.59
3	Field: winter	5.78	0.0030	5.7	3.4	0.59
4	Field: summer	5.78	0.0192	5.2	3.4	0.59

In order to compare specific growth rates in field and laboratory, specific growth rates in field were adjusted to laboratory temperatures by applying temperature corrections for field growth curves. Growth curve in cold period was corrected for 15°C and growth curve in growth period for 20°C. Additionally, to make laboratory and field growth data comparable, the same asymptotic length value was assigned. Obtained growth curve parameters and conditions are presented in Table 6.

Table 6. Temperature-corrected growth curve parameters and conditions. Letters indicate - real temperature (T_r), corrected temperature (T_c), assigned asymptotic length (L_∞) and growth curve parameter k.

No	Conditions	T_r	T_c	L_∞	k
5	"Field growth curve$_{15°C}$"	4.0	15	5.23	0.0094
6	"Field growth curve$_{20°C}$"	21.1	20	6.00	0.0179

Overal six growth curves were estimated – two from laboratory experiments under the 15°C and 20°C (Fig. 18, number 1 and 2), two from the dynamics of size frequency distribution of *P. antipodarum* in Lake Vilkokšnis (for winter and summer periods) (Fig. 18, number 3 and 4), and two from field data with applied corrections, which were used for further analysis (Fig. 18, number 6 and 7).

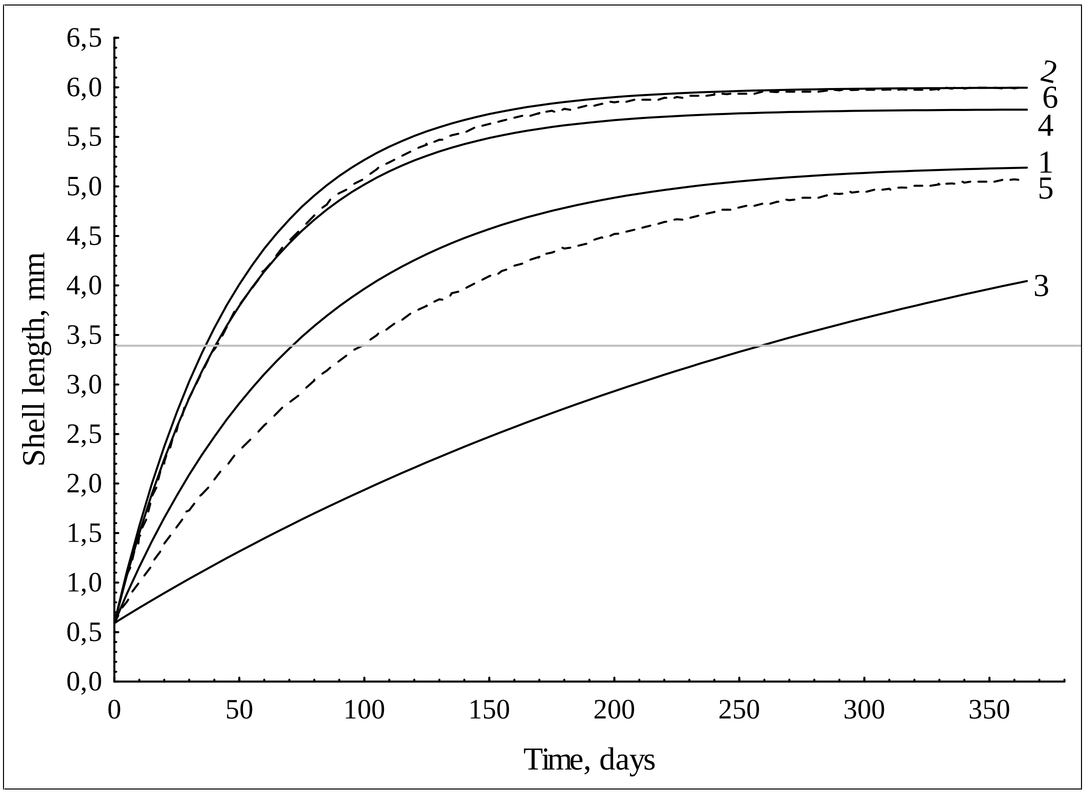

Fig. 18. Growth curves for *P. antipodarum* in laboratory and field. For numbers of curves see Tables 4 and 5 which indicates temperature conditions and growth curve parameters. Doted lines indicate temperature corrected growth curves in field. Horizontal gray line indicate size at maturity.

Size specific growth rates obtained from laboratory experiments and specific growth rates estimated from field growth curves (temperature corrected) were compared to check whether there is any effect of growth conditions (field and laboratory) and together how well the obtained growth curves describe the individual growth in field. As the interaction effect between initial shell length and growth conditions was not significant (Homogeneity of slopes model, for 20ºC: $F_{1,\,92} = 2.38$, p = 0.13, for 15ºC: $F_{1,\,84} = 7.8$, p = 0.10), ANCOVA model was used. The analysis indicated significant effect of shell length and growth conditions for both temperatures (Tables 7 and 8). The effect of growth conditions indicate highter specific growth in laboratory than in the field.

Table 7. Summary of ANCOVA results for specific growth rates of *P. antipodarum* under 20ºC with growth conditions as categorical and shell length as continous predictors.

Effect	*df*	*F*	p
Shell length	1	561.71	<0.001
Growth conditions (field or laboratory)	1	5.74	0.019
Error	93		

Table 8. Summary of ANCOVA results for specific growth rates of *P. antipodarum* under 15ºC with growth conditions as categorical and shell length as continous predictors.

Effect	*df*	*F*	p
Shell length	1	319.82	<0.001
Growth conditions (field or laboratory)	1	25.96	<0.001
Error	85		

The comparative analysis of specific growth rates under different temperatures in laboratory indicated not only statistically significant (Homogeneity of slopes model, $p < 0.05$) effect of water temperature and initial size of snails, but also significant interaction effect (Table 9). This interaction indicates that relationship between specific growth rate and body length differ between temperatures (Fig. 19).

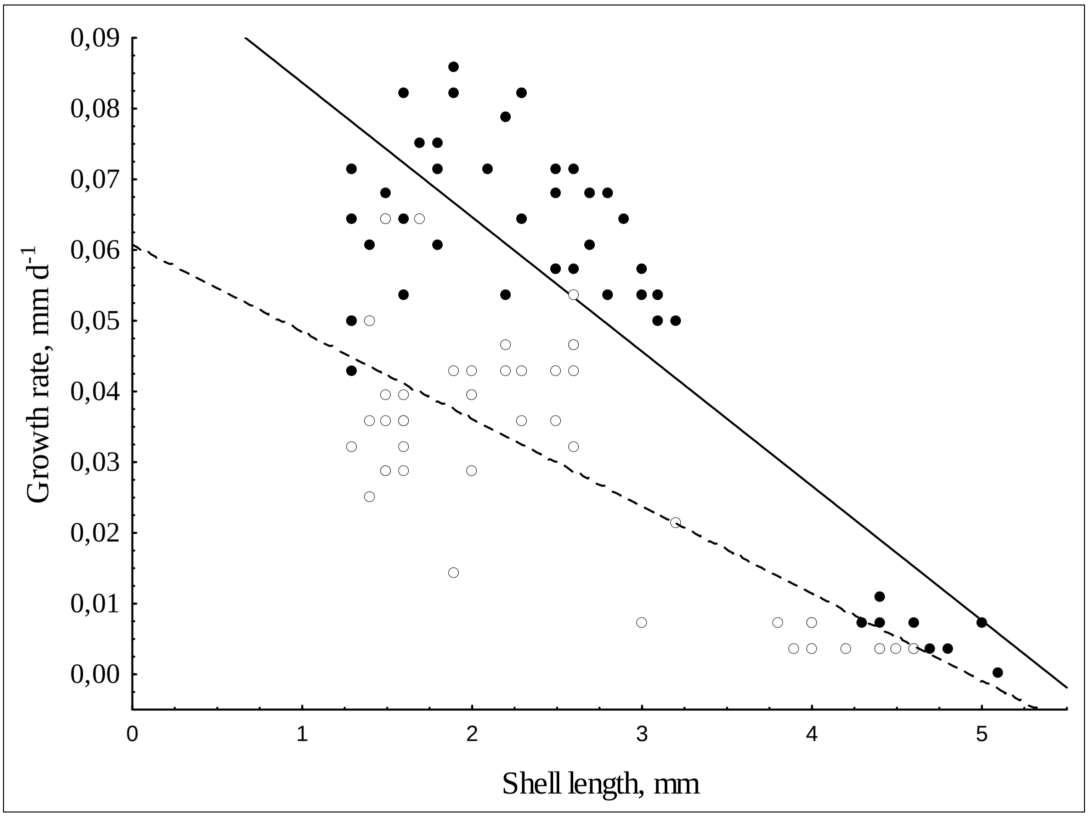

Fig. 19. The relationship of *P. antipodarum* shell length on specific growth rates under different temperatures (black circles under 20°C and empty circles under 15°C)

Table 9. Summary of homogeneity of slopes model results for specific growth rates of *P. antipodarum* in laboratory with temperature as categorical and initial length as continous predictors.

Effect	*df*	*F*	p
Temperature	1	61.52	<0.001
Shell length	1	690.90	<0.001
Temperature*Shell length	1	12.01	<0.001
Error	88		

Besides, average specific growth rates in different size groups between 15°C and 20°C temperature threatments were compared using two-way ANOVA. In addition to the significant effect of temperature ($F_{1,\ 82} = 20.64$, $p < 0.001$) and size group ($F_{4,\ 82} = 97.01$, $p < 0.001$) to specific growth rates, the analysis also indicated significant interaction of temperature and size group effect ($F_{4, 82}$ = 4.20, p = 0.003). Applied post hoc unequal N HSD test indicated significantly different specific growth rates under different temperatures in 1 (p < 0.001) and 2 (p < 0.001) size groups. Though there were no significant differencies in growth rates for 3 (p = 0.11) and 4 (p = 1) size groups (Fig. 20). These results indicated highter sensitivity of young immature individuals to water temperature than pre-adult and adult size individuals.

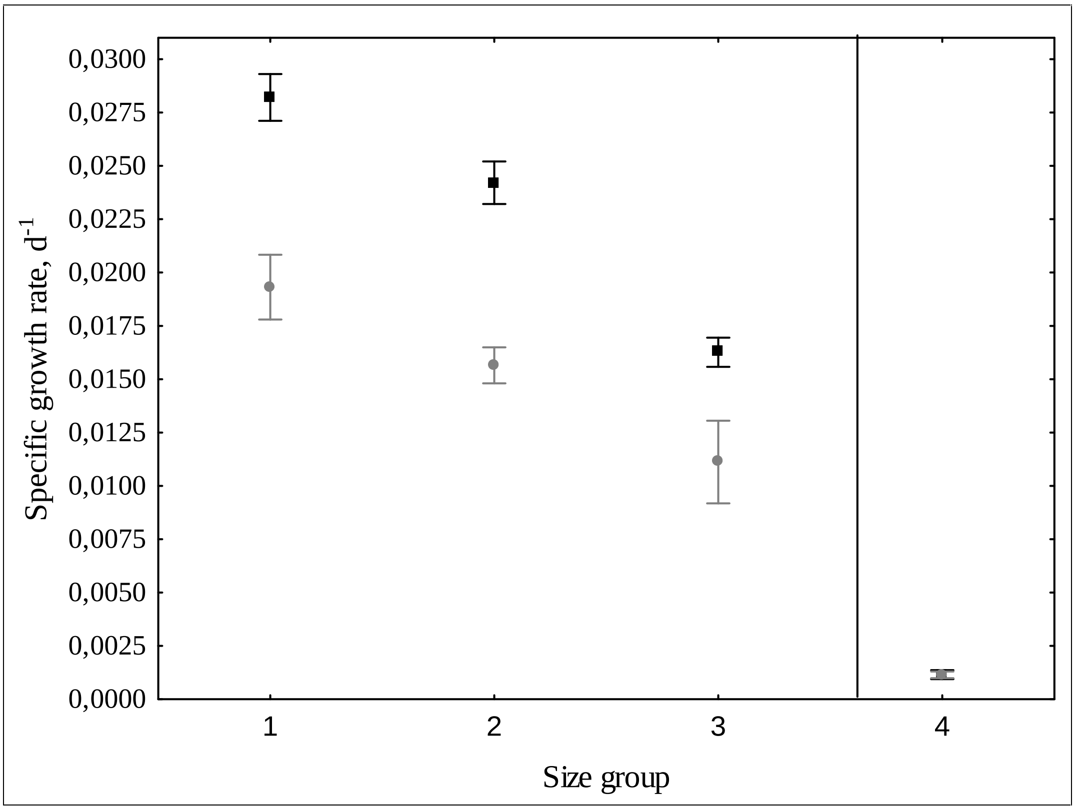

Fig. 20. Mean±SE specific growth rates of different *P. antipodarum* size groups under 15ºC (grey color) and 20ºC (black color). Vertical line separates immature and mature individuals.

The estimated Q_{10} values indicated highter sensitivity of young rather than mature individuals (Table 10). The Q_{10} value of smallest size individuals (≤ 1.5 mm) was 2.3 and decreased gradually toward increasing size. For pre-mature individuals it was 2.1 and 1.8, for ≤ 2.5 mm and ≤ 3.5 mm size groups, respectively. Meanwhile for adults the Q_{10} value was 1.2, suggesting very low temperature impact on growth rates of mature individuals at studied temperatures.

Table 10. Estimated Q_{10} values for different size groups.

Size group	Q_{10} value
≤ 1.5 mm	2.3
≤ 2.5 mm	2.1
≤ 3.5 mm	1.8
> 3.5 mm	1.2

Secondary *P. antipodarum* production

Lake Vilkokšnis

To estimate the daily production of *P. antipodarum* weight-specific growth rates were calculated. Growth rates were high, and strongly varied as a function of snail weight and average water temperature (multiple regression, growth rate, d^{-1} = -0.0058 + 0.0035 * temperature – 0.0805 * shell size, with size in milligrams AFDM and temperature in °C, $n = 92$, $r^2 = 0.86$, $p < 0.001$).

The dynamics of *P. antipodarum* production throughout the study period is presented in Figure 21. The results indicated variation of production during different study periods. As the temperature droped down to about 4ºC and large individuals dominated in population, there was no production during winter period. Together with increasing average water temperature and changes in population size structure (young individuals with hight growth rates become abundant), secondary production of *P. antipodarum* increased to its maximum during growing season. The annual production of *P. antipodarum* was 544.93 mg AFDM m^{-2} y^{-1}.

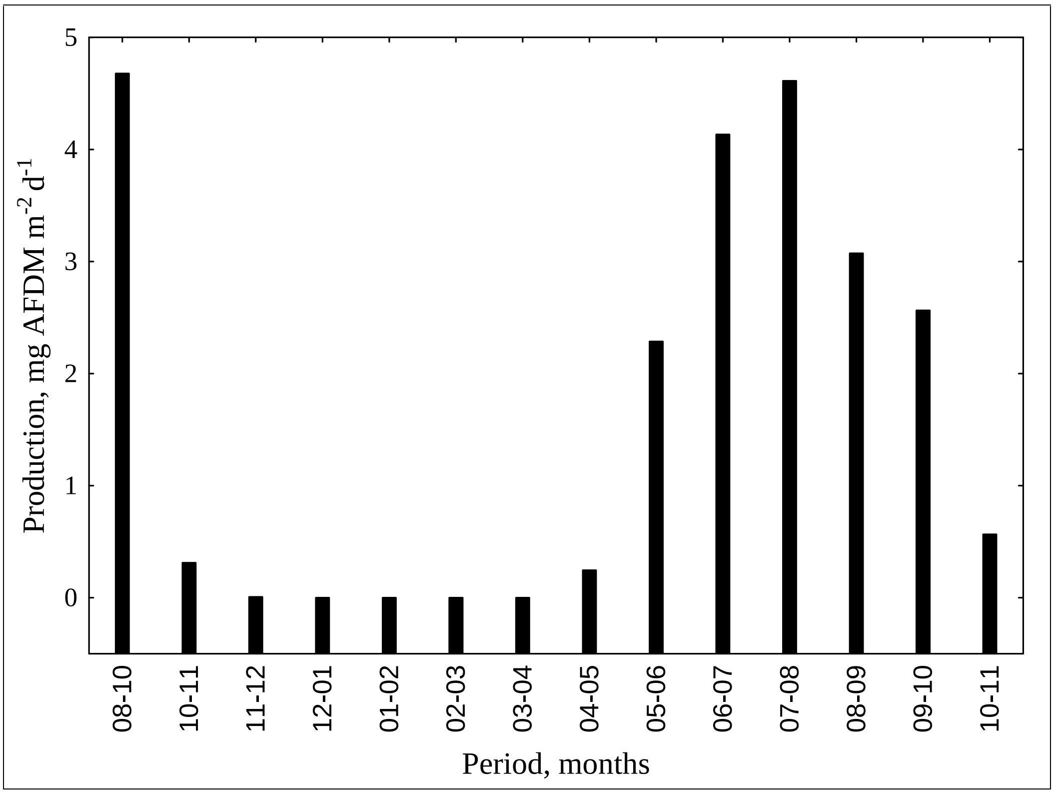

Fig. 21. The dynamics of *P. antipodarum* production during 2012-2013 period in lake Vilkokšnis.

The comparison between studied lakes.

Secondary production of *P. antipodarum* in studied lakes was estimated for whole growing season. It varied between the studied lakes (Fig. 22). Several times highter production was estimated in Lakes Metelys and Obelija, than in Lakes Vilkokšnis and Dusia. In latter lakes the production was respectively 5.5 times and 25.6 times lower than that estimated in Lake Metelys. Meanwhile in Lake Obelija the production of *P. antipodarum* was only 1.2 times lower than in Lake Metelys. Such great differencies in *P. antipodarum* production were determined by hight differencies in individual abundance, size structure and together biomass between studied lakes.

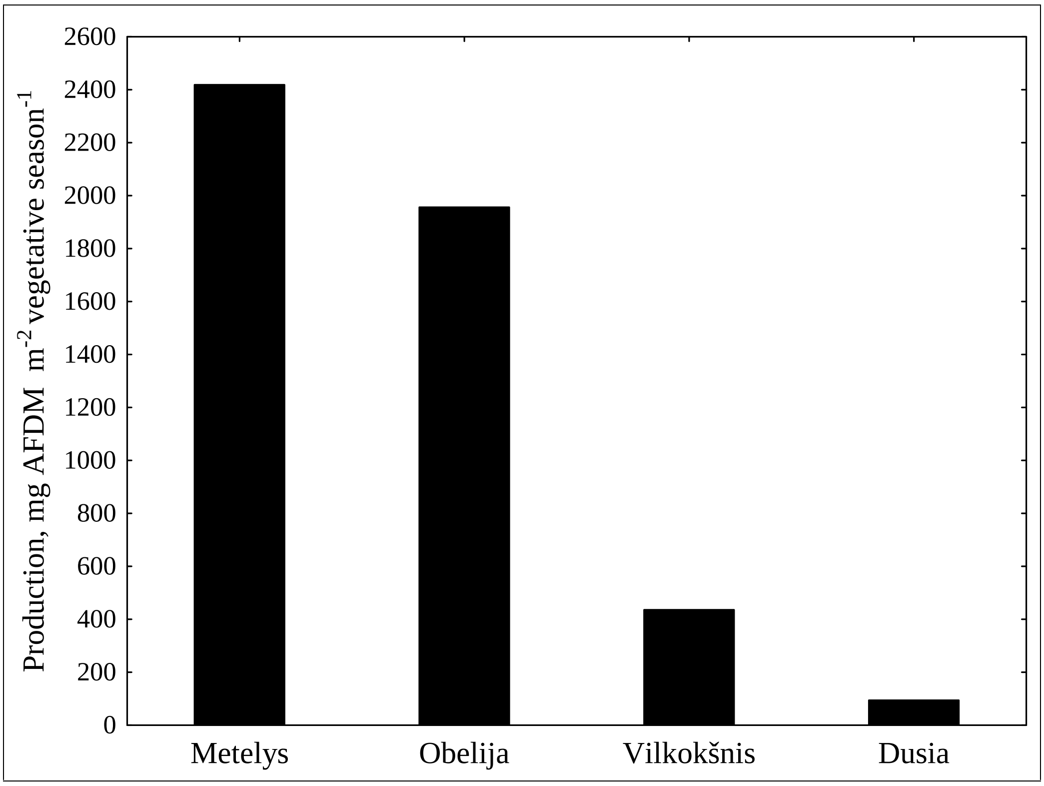

Fig. 22. Secondary production of *P. antipodarum* in studied lakes during whole growing season (April – November months).

In summary, life-history traits together with population characteristics of *P. antipodarum* varied significantly not only between the seasons, but also between the lakes. As expected, lowest density, biomass, fecundity and together secondary production were estimated in winter period. Meanwhile highest - in growing season. The significant variation in density, biomass, size structure, fecundity and together secondary production of *P. antipodarum* was also observed between the studied mesotrophic lakes. Average density of *P. antipodarum* differed ~476 times between some of the studied lakes. Meanwhile biomass in some lakes was 238 times highter than others. There was also significant differencies in size structure and average individual size. The analysis of *P. antipodartum* reproduction showed that the size at first reproduction is 3.4 mm in all studied lakes. The hightest number of adult females with embryos, and nearly equal fecundity and clutch size (which significantly depended on female size) indicated most intense embryo production in April-July period. The fecundity in studied lakes was similar in most of studied seasons. Hightly variable biomass and size structure between the lakes led to ~26 times highter secondary production estimates in some of the studied lakes. For the first time, integrated growth curves for *P. antipodarum* were estimated. The analysis of specific growth rates indicated highter growth rates in laboratory than field. Besides, the analysis also indicated highter sensitivity of young rather than mature individual growth rates to temperature.

The functional role of *P. antipodarum* in mesotrophic lake ecosystems

The role in macroinvertebrate communities

Stable isotope signatures for studied primary consumers and possible carbon sources sampled in Lakes Daugai, Dusia and Metelys are presented in Figure 22. Possible basal carbon sources fall into two categories based on d^{13}C values in all studied lakes: (1) an enriched autochthonous littoral source of *Potamogeton* sp., periphyton, sand organics; (2) depleted pelagic carbon source consisting of particulate organic matter (POM). The most depleted d^{13}C values were in POM and ranged between -32 and -28‰ in studied lakes meanwhile for autochthonous littoral sources it ranged between -22 and -13‰, providing a characteristic differentiation between pelagic and benthic basal carbon sources. The comparative analysis indicated significant differencies in isotopic composition (d^{13}C and d^{15}N) of studied primary producers in all studied lakes: Daugai (ANOVA. For d^{13}C, $F_{3, 14} = 54.72$, $p < 0.001$ and d^{15}N, $F_{3, 14} = 4.99$, $p = 0.015$), Dusia (ANOVA. For d^{13}C, $F_{3, 12} = 7.99$, $p = 0.003$ and d^{15}N, $F_{3, 12} = 6.84$, $p = 0.006$) and Metelys (ANOVA. For d^{13}C, $F_{3, 13} = 20.86$, $p < 0.001$ and d^{15}N, $F_{3, 13} = 22.32$, $p < 0.001$). Besides, applied unequal HSD test indicated statistically significant ($p < 0.05$) differencies between mean d^{13}C values of POM and littoral producers (periphyton, *Potamogeton* sp. and sand organics) in most of the studied lakes. The only exception was found for sand organics and POM values in lake Dusia, which did not differed significantly ($p > 0.05$). Periphyton always had the most depleted average d^{15}N values ranging from 1 to 2.2‰ in studied lakes, whilst average d^{15}N values of POM were the most enriched (3.3 – 4.8 ‰).

There were also significant differencies in d^{13}C and d^{15}N isotopic composition of studied primary consumer species in all studied lakes: Daugai (ANOVA. For d^{13}C, $F_{3,\ 8}$ = 81.87, p < 0.001 and d^{15}N, $F_{3,\ 8}$ = 8.48, p = 0.007), Dusia (ANOVA. for d^{13}C, $F_{3,\ 9}$= 78.45, p < 0.001; for d^{15}N, $F_{3,\ 9}$ = 34.87, p < 0.001) and Metelys (ANOVA. For d^{13}C, $F_{3,\ 11}$ = 13.29, p < 0.001 and d^{15}N, $F_{3,\ 11}$ = 6.4, p = 0.009) (Fig. 23). To check whether there are any significant differencies between average stable isotope values of *P. antipodarum* and other studied macroinvertebrates, post hoc Unequal HSD test was applied. There were significant (p < 0.05) differencies in d^{13}C between *P. antipodarum*, a typical grazer and *D. polymorpha*, a typical pelagic filter-feeder, in Lakes Daugai and Metelys. Though it did not differed significantly in Lake Dusia. As there were no significant differencies between the average d^{13}C values between POM and sand organics, the sedimented POM possibly is more important carbon source for *P. antipodarum* in Lake Dusia, than other studied lakes. Meanwhile, average d^{15}N values of *P. antipodarum* and *D. polymorpha* differed significantly in Lake Dusia, where the d^{15}N was more enriched in the latter. Also, significantly highter average d^{15}N values were estimated for *R. auricularia* than for *P. antipodarum* and in Lake Metelys. The mean d^{13}C and d^{15}N values of *P. antipodarum* overlapped mainly with *C. warpachowskyi* and *R. auricularia* in most of studied lakes, indicating the exploitation of similar carbon sources (Fig. 23).

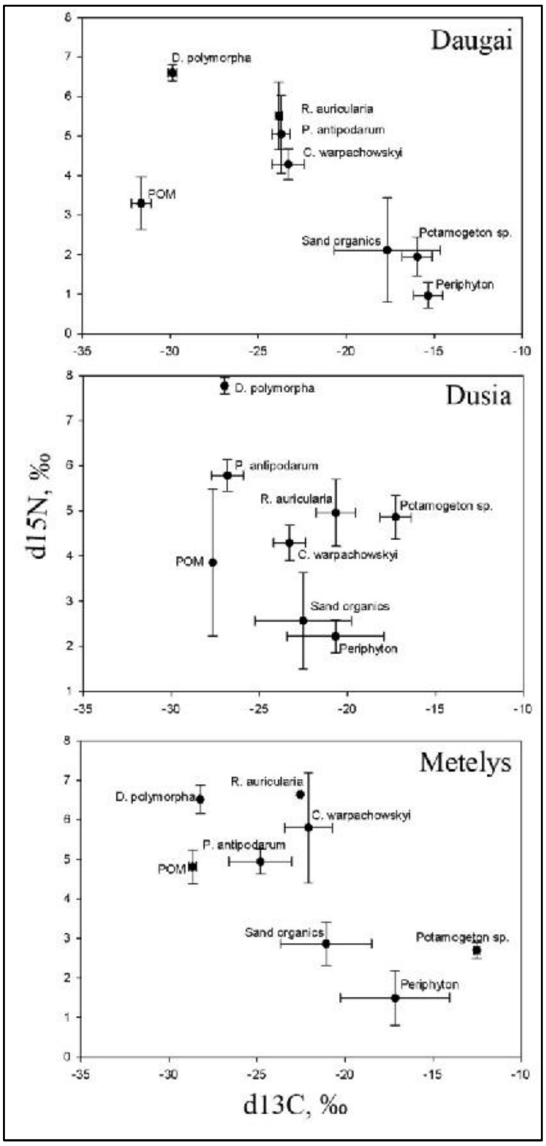

Fig. 23. Isotopic bi-plots showing the mean (±SD) d^{13}C and d^{15}N values for different basal carbon sources and primary consumers of the studied lakes.

The contribution of littoral primary production i.e. macrophytes (*Potamogeton* sp.), periphyton, sand organics to the diet of *P. antipodarum* was evaluated by applying the feasible mixture model, which incorporates two, d^{13}C and d^{15}N, isotopes into analysis. The results showed that autochthonous littoral production was the most likely food source for *P. antipodarum* in all studied lakes, though the percentage varied between the lakes. Highest contribution of littoral primary production was found in Lake Dusia (77.4 %). Meanwhile in Lakes Daugai and Metelys the contribution was respectively 65.7 and 63.1%.

In summary, results indicate that P. antipodarum is primary consumer exploitating mainly littoral carbon sources. Highly abundant P. antipodarum definitely consume a significant portion of primary production, implying potential exploitative competition with native macroinvertebrate species, which occupy similar trophic nische.

The role in a diet of dominant benthivorous fishes

Littoral macroinvertebrates communities

Analysis of lake littoral macroinvertebrate communities was performed in order to reveal *P. antipodarum* density and its share in these communities. Performed analysis revealed the chironomids, bivalves and *P. antipodarum* to be the dominant benthic macroinvertebrates in the littoral zone of studied lakes (Figure 24). The highest share of *P. antipodarum* in a total biomass of the littoral benthic macroinvertebrate community was in Lake Dusia and constituted more than 40% (Table 10). *P. antipodarum* proportion by biomass in a total macroinvertebrate samples was similar in lakes Spindžius and Vilkokšnis and comprised 33 and 38%, respectively. However, *P. antipodarum* proportion by numbers was different in studied lakes and ranged from 22% in Lake Spindžius to 60% in Lake Vilkokšnis (Table 10). The average *P. antipodarum* densities were even more variable and ranged from 67 in Lake Spindžius to 5650 ind. m^{-2} in Lake Dusia (Table 10).

Among recorded bivalves the most common species in collected samples were *Dreissena polymorpha* (Pallas, 1771), *Pisidium amnicum* (O. F. Müller, 1774) and *Sphaerium corneum* (Linnæus, 1758). Meanwhile *Bithynia tentaculata* (Linnaeus, 1758), *Radix balthica* (Linnaeus, 1758) and *Lymnaea stagnalis* (Linnaeus, 1758) were dominant species among gastropods in studied lakes (Figure 24).

Table 10. The mean abundance (A), biomass (B), and proportion by individuals (P_A) and by biomass (P_B) of *P. antipodarum* in macroinvertebrate community. Values are mean ± SD.

Lake	A (ind./m^2)	P_A (%)	B (g/m^2)	P_B (%)
Dusia	5650 ± 7522	37.7 ± 36	41.4 ± 53.4	40.6 ± 27.1
Spindžius	67 ± 115	22.2 ± 38	0.7 ± 1.2	33.2 ± 57.4
Vilkokšnis	3767 ± 1998	59.5 ± 10	29.8 ± 13.6	38.0 ± 43.2

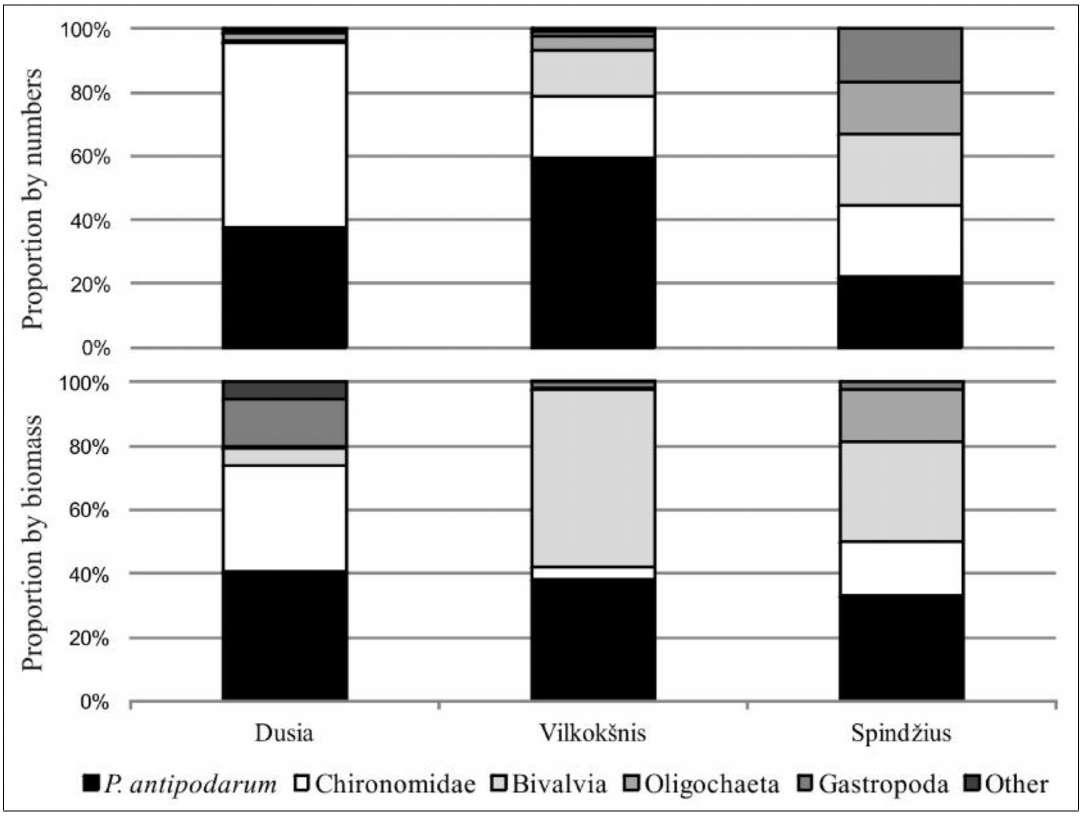

Fig. 24. Proportions by numbers and biomass of various benthic littoral macroinvertebrates in studied lakes.

Littoral fish community composition

In total, 13 different fish species were recorded in studied lakes during this investigation. Seven of them, *R. rutilus* (Linnaeus, 1758), *P. fluviatilis* Linnaeus, 1758, *G. cernua* (Linnaeus, 1758), *T. tinca* (Linnaeus, 1758), *A. brama* (Linnaeus, 1758), *S. erythrophthalmus* (Linnaeus, 1758) and *B. bjoerkna* (Linnaeus, 1758), can be distinguished as benthivorous fishes, as these species forage near the bottom and benthic invertebrates constitutes significant share of their diet content (Kublickas 1959, Virbickas 2000). Results showed that *P. fluviatilis* and *R. rutilus* were dominant species among all recorded benthivorous fish species by the proportion of their number and biomass in a total fish catch in all studied lakes. *G. cernua* was among the dominant fish species by their number and reached 19% of a total fish number catch in Lake Dusia. *B. bjoerkna* and *T. tinca* were among the common fishes in the gill net catches from Lake Spindžius. The share of *B. bjoerkna* in the total catches was 24% by number. Meanwhile *T. tinca* was not so abundant and reached only 2% in a total fish catch in Lake Spindžius.

Feeding experiments

Performed feeding experiments showed that all tested predator species consumed *P. antipodarum* individuals, however the consumption of this invasive snail was different for different tested predator species (Kruskal-Wallis ANOVA test: $H_{7,\ 148} = 32.44$, $p < 0.001$) (Table 11). *N. melanostomus* showed the highest *P. antipodarum* consumption prevalence. Almost each *N. melanostomus* specimen consumed *P. antipodarum* individuals during experiments. However, on average they consumed only 15% of available snails in experimental aquaria. Those individuals that consumed *P. antipodarum*, on average ate 16 snails per specimen (Table 11). From all tested predators the highest consumption of *P. antipodarum* was recorded for *T. tinca* and *O. limosus*. These species consumed 31 and 27% of available snails in aquaria, respectively. Those *T. tinca* and *O. limosus* specimens that consumed *P. antipodarum* on average ate more than 40 snails per specimen (Table 11). Consumption of *P. antipodarum* by the remaining tested predator species (*R. rutilus*, *P. fluviatilis*, *G. cernua*, *S. erythrophthalmus* and *P. glenii*) was significantly lower compared with that of *T. tinca*, *N. melanostomus* and *O. limosus* (Mann-Whitney U test: $Z = -5.23$, $p < 0.001$). On average they consumed less than 2% of all available snails in aquaria and never consumed more than 4 snails per specimen (Table 11). Overall, only *T. tinca*, *O. limosus* and *N. melanostomus* showed significant consumption of the available *P. antipodarum* under the experiment condition. While other fish species showed accidental consumption of the served *P. antipodarum*.

Table 11. Experimental consumption of *P. antipodarum* by seven predator species: number of investigated predators (n); total length of predators (TL); percent of predator individuals that consumed *P. antipodarum* (P); proportion of consumed *P. antipodarum* from all available snail in experimental tank (C); number of consumed *P. antipodarum* individuals per specimen (I). Values are mean ± standard deviation.

Species	n	TL (cm)	P (%)	C (%)	I (ind.)
Perccottus glenii	11	12.1 ± 1.3	27.3	0.4 ± 0.7	1.3 ± 0.6
Rutilus rutilus	22	14.7 ± 1.4	50.0	0.8 ± 0.9	1.5 ± 0.7
Scardinius erythropthalmus	13	14.9 ± 1.7	46.2	0.7 ± 0.9	1.5 ± 0.8
Gymnocephalus cernua	42	12.5 ± 0.9	59.5	1.1 ± 1.2	1.9 ± 1.1
Perca fluviatilis	14	13.2 ± 4.3	28.6	0.9 ± 1.6	3.3 ± 1.0
Neogobius melanostomus	16	15.2 ± 2.8	93.8	14.8 ± 18.2	15.8 ± 18.4
Orconectes limosus	14	8.4 ± 1.3	64.3	27.1 ± 35.2	42.2 ± 36.0
Tinca tinca	16	15.9 ± 4.7	62.5	31.4 ± 38.3	50.2 ± 37.3

Fish diet in the field

Fish field diet analysis revealed high variation of the dominant prey species in different fish diet (Figure 24). The diet of small *P. fluviatilis* was clearly dominated by zooplankton, while larger *P. fluviatilis* preferred fish fry in all studied lakes. Insects were dominant prey type in the diet of *A. brama* and *G. cernua*. Insects comprised more than 65% of *A. brama* diet in all studied lakes and more than 77% of *G. cernua* diet in lakes Vilkokšnis and Spindžius. Macrophytes formed significant share of *B. bjoerkna*, *R, rutilus* and *T. tinca* diet. The share of macrophytes in these fish diet varied from 12 to 70% in studied lakes. Molluscs formed a significant part in a diet of *B. bjoerkna*, *T. tinca*, *G. cernua* and *R. rutilus*. However, molluscs as a dominant prey type was found only in *T. tinca* diet in lakes Dusia and Spindžius, in *R. rutilus* diet in lakes Dusia and Vilkokšnis and in diet of *B. bjoerkna* in Lake Vilkokšnis (Figure 25). Moreover, *D. polymorpha*, *Bithynia* sp., *Pisidium* sp. and

Sphaerium sp. were the dominant molluscs in studied fish diet while contribution of *P. antipodarum* to total fish of certain species diet was very low in all studied lakes and comprised up to 6.7 %.

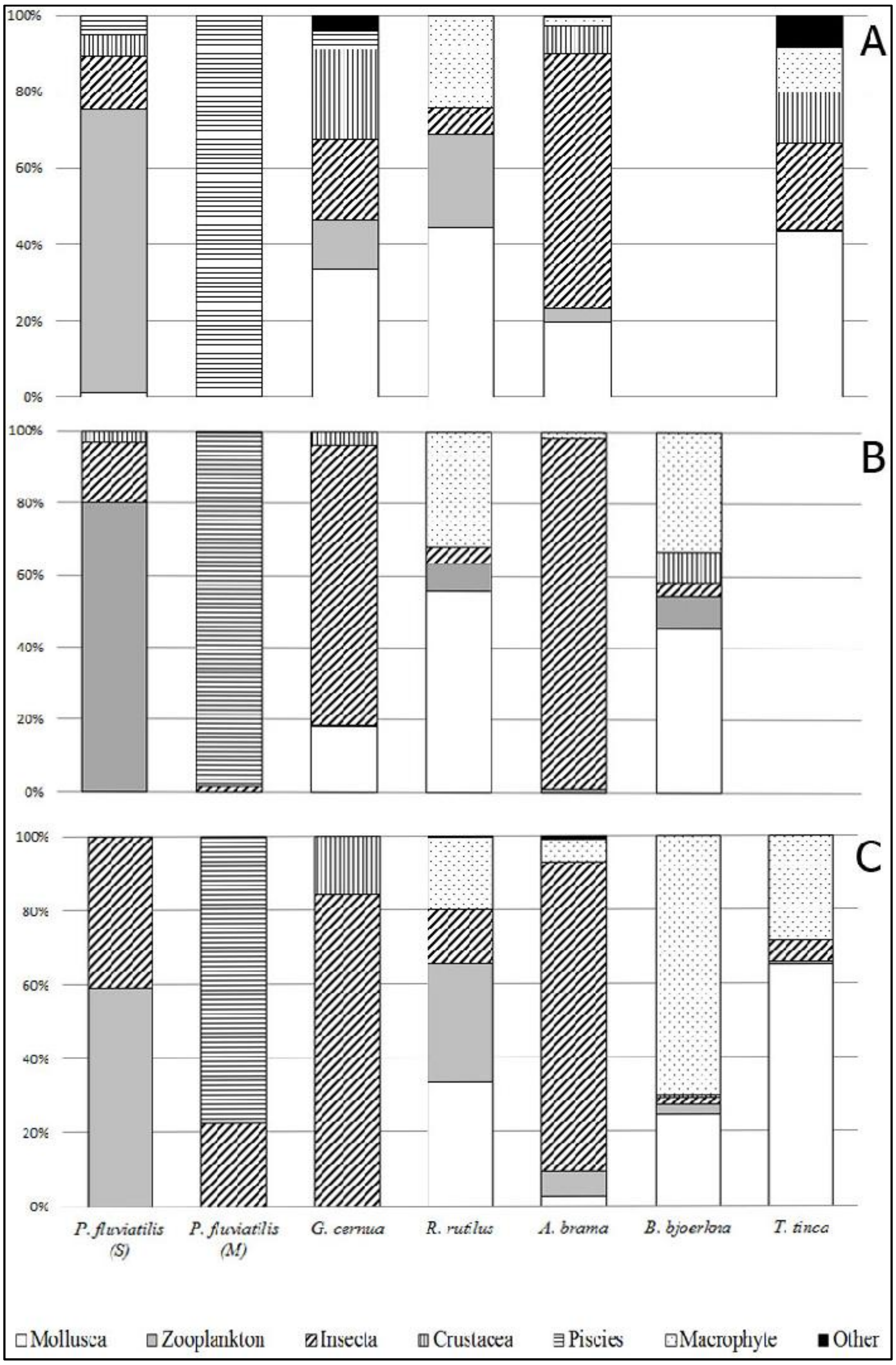

Fig. 25. Diet composition of different benthivorous fish species in studied lakes: Dusia (A), Vilkokšnis (B) and Spindžius (C). Analysed fish size and numbers are the same as in Table 12.

However analysis indicated that *P. antipodarum* was consumed to some extent by all studied fish species. The highest prevalence of *P. antipodarum* was found in *A. brama* and *T. tinca* stomachs in lakes Dusia and Spindžius respectively, and reached 50% of all studied fish specimens. Meanwhile the prevalence of *P. antipodarum* in other fish gastrointestinal tracts was low (Table 12). The numbers of ingested *P. antipodarum* were similar throughout all fish species and did not yield statistically significant differences in data from lakes Dusia or Vilkokšnis (Kruskal–Wallis ANOVA test for Lake Dusia: $H_{5,\ 109} = 8.60$, $p = 0.13$; for Lake Vilkokšnis: $\mathrm{H}_{5,127} = 1.69$, $P = 0.89$). Though there was significant species effect on the number of *P. antipodarum* in the stomachs of the fish from Lake Spindžius (Kruskal-Wallis ANOVA test: $H_{6,\ 97} = 24.62$, $p < 0.001$). This was mainly determined by the *T. tinca* which consumed significantly more *P. antipodarum* per fish compared with other fish species in this lake (Mann-Whitney U test: $Z = –4.74$, $p < 0.01$). However, the average number of *P. antipodarum* per fish was very low and never exceeded 10 individuals for all fish species in any of studied lake. Thus the relative abundance of *P. antipodarum* in the total fish diet was also very low and did not exceeded 7% in any investigated fish species (Table 12). Assessing relative macroinvertebrate abundances allowed estimating feeding selectivity for *P. antipodarum*, however none of the fish species turned out to have positive selectivity for it (Table 12). Moreover, more than 80% of *P. antipodarum* individuals found in dissected fish were hidden deep within their intact shells and thus were assumed to have remained undigested.

Table 12. Prevalence of *P. antipodarum* in field diet of fish from the studied lakes and its load per fish specimen: investigated fish number (n); total fish body length (TL); percentage of fish containing *P. antipodarum* (P); number of *P. antipodarum* per fish containing the snail in gastrointestinal tract (I); *P. antipodarum* share in total fish species diet (S); and feeding selectivity (E_i). Values are mean ± SE. Fish size categories: S small, M medium.

Fish species	n	TL (cm)	P (%)	I (ind.)	S (%)	E_i
Lake Dusia						
Abramis brama	8	35.0 ± 4.9	50.0	8.0 ± 10.4	1.8	-0.95
Gymnocephalus cernua	24	12.6 ± 1.9	16.7	2.3 ± 1.3	6.7	-0.72
Perca fluviatilis M	10	17.9 ± 2.1	0	0	0	-1.00
Perca fluviatilis S	18	13.3 ± 1.3	5.6	3.0	1.0	-0.94
Rutilus rutilus	43	18.6 ± 2.8	25.6	6.5 ± 3.3	6.4	-0.73
Tinca tinca	6	28.9 ± 11.6	0	0	0	-1.00
Lake Vilkokšnis						
Abramis brama	5	39.8 ± 2.9	0	0	0	-1.00
Blicca bjoerkna	12	15.0 ± 1.9	0	0	0	-1.00
Gymnocephalus cernua	19	11.1 ± 0.3	0	0	0	-1.00
Perca fluviatilis M	10	17.7 ± 1.7	0	0	0	-1.00
Perca fluviatilis S	12	11.4 ± 0.4	0	0	0	-1.00
Rutilus rutilus	69	23.3 ± 6.9	2.9	10.0 ± 9.0	1.3	- 0.94
Lake Spindžius						
Abramis brama	5	42.4 ± 9.0	0	0	0	-1.00
Blicca bjoerkna	9	16.1 ± 3.2	11.1	1.0	3.3	-0.82
Gymnocephalus cernua	11	11.2 ± 1.3	0	0	0	-1.00
Perca fluviatilis M	10	18.5 ± 1.2	0	0	0	-1.00
Perca fluviatilis S	7	14.7 ± 2.7	0	0	0	-1.00
Rutilus rutilus	51	20.6 ± 7.4	2.0	1.0	0.02	-1.00
Tinca tinca	4	41.8 ± 1.7	50.0	4.0 ± 3.0	3.3	-0.92

Assessment of P. antipodarum survival in fish gastrointestinal tract

Survival tests indicated that the fate of ingested *P. antipodarum* was significantly different between studied benthivorous fish species (Kruskal-Wallis ANOVA test: $H_{5,\,73} = 43.26$, $p < 0.001$). Performed experiments showed that some individuals of *P. antipodarum* survived gut passage in at least several specimens of each analysed fish species except *T. tinca* (Table 13). Experiments also showed, that only 1% of all eaten snails passed the gastrointestinal tract of *T. tinca* unharmed, however, none of them remained alive (Table 13). Meanwhile, more than 90% of consumed *P. antipodarum* individuals passed through the gastrointestinal tracts of *P. fluviatilis* and *P. glenii* unharmed. However, the survival of the *P. antipodarum* was different for these species (Mann-Whitney U test: $Z = -3.5$, $p < 0.001$). Only 15% of all eaten *P. antipodarum* passed alive through *P. fluviatilis* gastrointestinal tracts, while even 45% of eaten snail survived the gastrointestinal tracts of *P. glenii* (Table 13). Among the molluscivorous fishes that possess pharyngeal teeth and can crush their prey, highest survivorship of *P. antipodarum* was shown for *R. rutilus*. 76% of all eaten snails passed its gut intact and around 15% survived it. Interestingly, more than 95% of ingested snails passed through the gut intact and more than 80% survived it in the case of *S. erythrophthalmus*, a fish that also possesses the pharyngeal teeth.

Overall, performed survival experiments suggested that feeding mode is important factor when predicting the fate of consumed *P. antipodarum* by different fish species. Results indicated that molluscivorous predators that can crush their prey, such as *R. rutilus*, *N. melanostomus* and *T. tinca*, consumed significantly more *P. antipodarum* than omnivorous fishes that lack the pharyngeal teeth and swallows their prey whole such as *P. fluviatilis* and *P. glenii* (Mann-Whitney U test, $Z = 5.90$, $p < 0.001$). Experimental trials also revealed significantly lower survival percentage of *P. antipodarum* through the gastrointestinal tracts of molluscivorous comparing to the omnivorous fishes (Mann-Whitney U test, $Z = -4.70$, $p < 0.001$).

Table 13. Fate of *P. antipodarum* shown as percentages of individuals ingested by various predators: number of investigated fish individuals (n); total fish body length (TL); number of ingested P. antipodarum per fish (I). Values are mean ± standard deviation.

Species	n	TL (cm)	I (ind.)	Undigested (%)	Survived (%)
Perca fluviatilis	12	16.8 ± 0.7	12.6 ± 5.1	99.6 ± 1.4	14.6 ± 15.1
Rutilus rutilus	12	15.5 ± 0.8	13.7 ± 4.2	76.1 ± 31.0	14.6 ± 21.4
Perccottus glenii	24	16.1 ± 1.5	8.6 ± 1.3	94.6 ± 13.4	44.6 ± 25.9
Scardinius erythropthalmus	6	16.5 ± 0.4	13.0 ± 5.6	95.8 ± 6.5	80.8 ± 20.8
Neogobius melanostomus	10	16.2 ± 2.9	22.7 ± 19.1	56.5 ± 33.7	7.9 ± 10.8
Tinca tinca	9	18.5 ± 3.6	55.4 ± 35.5	1.1 ± 1.5	0 ± 0

In summary the results of this study indicate that some local predator species have the potential to prey effectively upon the invasive snail under experimental conditions, though field data did not support this expectation. In general, results showed that the main benthivorous fish species did not consume *P. antipodarum* substantially even after several years of this snail presence in a lakes. This suggests that local fishes probably have no potential to regulate density of *P. antipodarum* populations in Lithuanian lakes. In addition, this study also showed that some fish species may act as a local dispersion vector for *P. antipodarum*. Experiments indicated that the snail survived the gastrointestinal tract of the main benthivorous fish species. This could reduce colonization time of new suitable habitats by *P. antipodarum* in invaded lakes.

DISSCUSION

The distribution of *P. antipodarum* in Lithuanian inland waters

There are 3 non-indigenous freshwater mollusc species recorded in Lithuanian inland waters. Two of them, *D. polymorpha* and *P. antipodarum* are considered as invasive species. Though the *D. polymorpha* is most widely distributed in Lithuanian freshwater ecosystems, *P. antipodarum* is being recorded in more new sites (Butkus *et al*. 2012, Butkus *et al*. 2014). The invasion history of *P. antipodarum* in Lithuanian inland waters begins in 1954, when it was recorded in Curonian lagoon for the first time (Gasiūnas 1959). The ballast waters are though to be a possible introduction vector, as *P. antipodarum* was recorded besides the port. It took several decades for *P. antipodarum* to spread across the Curonian lagoon and reach the Nemunas delta (Rinda, Skatulė, Rumbas, Upaitis, Kniaupas) (Zettler *et al*. 2005, Zettler and Daunys 2007). This relatively slow spread rate implies natural dispersion to play a major role in Curonian lagoon. However, in 2010, individuals of *P. antipodarum* were recorded in several lakes and river in southern part of Lithuania (Butkus *et al*. 2012) and during later 2011-2015 surveys it was found in 9 additional water bodies. Such invasion history implies that *P. antipodarum* may already be widely established in Lithuanian inland waters and continues to spread across the uninvaded water bodies. The case of lake Dusia, where *P. antipodarum* was not found in 2003-2006 surveys (Gumuliauskaite 2007) and was recorded in 2010 (Butkus *et al*. 2012) illustrates it well. Moreover, the samples of littoral macroinvertebrates collected at the same study site in Lake Daugai during 2009 and 2010 showed that the species was absent in the first year, but was recorded in considerable numbers in the second year (Butkus *et al*. 2012), as an exponential growth of invasive species following its invasion is to be expected (Arim *et al*. 2006).

Not only the exact time of the invasion, but also the dispersion vectors and routes of *P. antipodarum* are undefined. It is supposed that there could be two possible invasion routes to lakes and river, where *P. antipodarum* was recorded for the first time. As the positive rheotactic behavior (Zaranko *et al.* 1997) is typical to *P. antipodarum* individuals, the upstream dispersion through Nemunas River could be possible explanation. Though the species was not recorded in Nemunas River above the delta. On the other hand, as *P. antipodarum* individuals can survive the gastrointestinal tract of the fishes, migratory fishes (Aarnio and Bonsdorff 1997, Vinson and Baker 2008) could facilitate the upstream dispersion. Second, *P. antipodarum* individual spread with water birds from Curonian lagoon or more likely from Lake Wigry (Poland), which is located relatively nearly the lakes, where it was firstly recorded. The latter invasion route is more possible, as *P. antipodarum* individuals were not recorded during the surveys in Nemunas and its main tributaries in 2008 and 2015 (Arbačiauskas *et al.* 2011, personal observation). If this hypothesis is correct, *P. antipodarum* was firstly introduced from Curonian lagoon to Lake Wigry and later it dispersed to Lithuanian lakes. First records of *P. antipodarum* in the lakes, located in southern part of Lithuania, where the distance from Lake Wigry is relatively small support this assumption. Overall, in addition to marine shipping (the vector of primary invasion into the Curonian Lagoon), secondary dispersion of this species by water birds, water recreation activities and natural dispersion may be involved in the species spread across Lithuanian inland waters (Butkus *et al.* 2012). The exceptional attention should be payed to water recreation activities, such as boating, which is possibly responsible for several introductions of *P. antipodarum*. The port in Šventoji river, Lake Plateliai besides the yacht-club, the site of Lake Daugai, intensively used by local commercial fisherman – the sites where *P. antipodarum* was recorded for the first time.

The invasive New Zealand mudsnail *P. antipodarum* is well established in an invaded regions and is rapidly expanding its range. Racent rapid spread of the snail is recorded in Europe (Lewin and Smolinski 2006), N. America (Levri *et al.* 2007) and Australia (Schreiber 2003). Besides the dispersion vectors, the relatively active motion of the snail can also increase dipersion rates. It was shown, that *P. antipodarum* can move 60 m upstream in 3 months through positive rheotactic behavior (Zaranko *et al*. 1997). Though such dispersion mainly operates in very local scale. In recently invaded ecosystems fishes can accelerate the establishment of the snail. It was shown that snails can survive passage through the guts of fish and may be transported by these animals (Bruce 2005, Rakauskas *et al*. 2016). *P. antipodarum* can also be spread anthropogenically through movement of gear such as waders, boots, angling equipment, and boats or by the translocation of aquaculture materials (live fish or eggs; Haynes *et al*. 1985, Bowler 1991, Hosea and Finlayson 2005, Bothwell *et al*. 2009, Gates *et al*. 2009). Secondary introductions may occur on birds that carry the snails among their feathers or by fish that consume but are unable to digest snails (Bondesen and Kaiser 1949, Haynes *et al*. 1985). Besides dispersion on floating material was also documented (Gaino *et al*. 2008) and can be particularly important dispersion vector in places where river outflows from the lake. In some circumstances, the invasive species can escape the awareness of wildlife services. Such situation was observed in S. America, where *P. antipodarum* was misidentified as local hydrobiid species (Collado 2014).

In summary, in recent years *P. antipodarum* is being recorded in new, previously uninvaded water bodies of Lithuania. It is highly possible, that marine shipping (ballast waters) was the primary introduction vector for *P. antipodarum* to Curonian lagoon. Rapid dispersion among the lakes indicate certain dispersion vectors to play a major role in spread of *P. antipodarum* across Lithuanian water bodies. The population of *P. antipodarum* in Curonian lagoon was probably the source population to Lake Wigry, where water birds could be main dispersion vector. In later years, the snail was introduced to nearby lakes in Lithuania. In this case, both local movement of water birds between the lakes and anthropogenic activities could play a major role in *P. antipodarum* dispersion. For several lakes, where the snail was firstly recorded in sites with intensive recreational boating and fisherman gear transportation, these can be suspected as dispersion vectors. Meanwhile *P. antipodarum* introduction to more distant ecosystems from already invaded lakes, such as Lake Prūtas, water birds can be suspected. Undoubtedly, the dispersion of *P. antipodarum* will proceed across the Lithuanian inland waters, and the identification of probable dispersion vectors remains relevant question for further studies.

Genetic diversity of *P. antipodarum* populations

Three types of genetic markers were used in several Lithuanian and one Poland populations of *P. antipodarum* to determine the genotypic diversity of a highly invasive clonal species. The combined genetic marker (16S rRNR, cytochrome b and microsatellite) data showed the absence of genotypic variation within and among the populations of *P. antipodarum*.

Our studied populations of *P. antipodarum* were monomorphic in both studied cytochrome b and 16S rRNA mtDNA haplotypes. Such results may be attributed to the founder effect, in which the decrease of genetic diversity is being observed along the geographic distance from the source population, resulting in reduced genetic diversity in newly established populations (Kawamura *et al*. 2006, Hamada *et al*. 2013). Though other authors claims, that the much reduced haplotype diversity across Europe, compared to the native range, can be associated with population bottlenecks during the colonisation (Städler *et al*. 2005). However, despite the recent low genetic variability, none of the molecular studies on genetic diversity can eliminate the possibility of much more higher clonal diversity among the initially released propagules during the introduction. Besides, the more extensive studies could also give a new insight to genetic heterogenity of *P. antipodarum* populations, particularly for poorly studied cytochrome b haplotypes across the Europe.

The data on the distribution of cytochrome b haplotypes in Europe is limited only to one population in Denmark. The majority of the data is from studies evaluated in New Zealand (Neiman *et al*. 2010, Paczesniak *et al*. 2013). During this study obtained cytochrome b haplotype is identical to the sequence from Danish population (the populations indicated in Hamada *et al*. 2013) (Neiman *et al*. 2010, genbank: GQ996424). The sequences from the Duluth (lake Superior) (Neiman *et al*. 2010, genbank: GQ996433) and clone 7 from the lake Aleksandrina (South island, New Zealand) (Neiman *et al*. 2010, genbank: GQ996432) are also identical to haplotype estimated in this study. The same tendency was found for COI and 16S rRNA sequences, probably indicating common source population in New Zealand (Städler *et al*. 2005, Hamada *et al*. 2013). Conversely, the data on 16S rRNA haplotype distribution in Europe (Fig. 25) is much more extensive. Städler *et al*. (2005) found two haplotypes t and z differing at 5 bp, which is well above the average of pairwise differencies among all 17 New Zealand haplotypes. Other study found haplotype z in the sea besides Estonia (Stanevičiūtė *et al*., GenBank: JQ346706.1). As most of the individuals of the haplotype z are recorded in in UK, France and Belgium, the record in northern Europe is exceptional. The main explanation for haplotype z presence in Baltic sea is possibly the lack of *P. antipodarum* genetic studies in northern Europe, particularly in brackish water ecosystems. Generally accepted three European morphotypes, which were described by Warwick (1952), exhibit ecophysiological differencies. Two strains are associated with haplotype z and are found exclusively in coastal, brackish-water habitats, whereas the haplotype t characterizes mainly freshwater sites (Städler *et al*. 2005). This explains well the record of haplotype z in Baltic sea. Thus such distribution of haplotypes t and z in Europe indicate different invasion routes of separate haplotypes. As haplotype z is mainly associated with coastal and brackish waters, its ability to become widespread in mainland is possibly limited and related to shipping as the main dispersion vector. Meanwhile widely distributed in freshwater ecosystems, haplotype t possibly has „generalist“ qualities (Städler *et al*. 2005) and this clone-habitat association appears to have been stable for many decades (Bondensen and Kaiser 1949, Warwick 1952, Hughes 1996, Jacobsen *et al*. 1996, Weetman *et al*. 2002, Städler *et al*. 2005). Mitochondrial data together with ecological and life-history differencies between the clonal lineages indicate divergence predating the colonization of Europe (Hughes 1996, Städler *et al*. 2005).

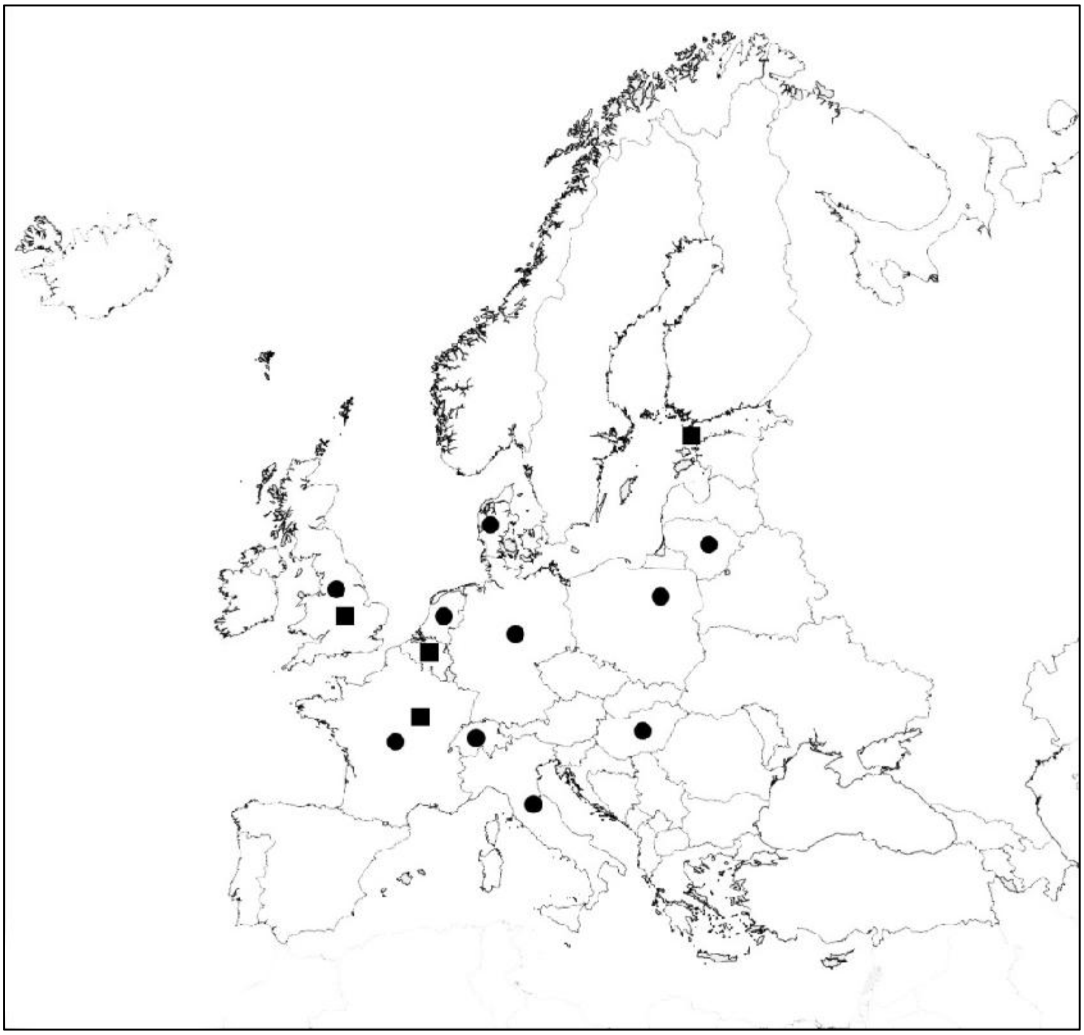

Fig. 26. The distribution of the 16S rRNA haplotypes of *P. antipodarum* in Europe. Symbols indicate t (circles) and z (squares) haplotypes. Data from recent study, Städler *et al*. 2005, Stanevičiūtė *et al*. 2013 (GenBank: JQ346706.1, JQ346709.1, JQ346708.1, JQ346707.1, JQ346705.1).

Microsatellites are though to be much more variable than mtDNA. Studies, based on direct estimates derived from individuals with known parentage (Leopoldino and Pena 2003, Henke and Henke 2006, Seyfert *et al.* 2008) and indirect estimates applicating the microsatellite mutation models (Chakraborty *et al.* 1997) indicate microsatellite mutation rates as high as 10^3 and 10^4/locus/generation in animals. Most studies show that the spectrum of microsatellite mutations is heavily dependent on particular loci (Weetman *et al.* 2002), variation in the numbers of germline cell divisions per generation of study organism (Seyfert *et al.* 2008) and allele size (Xu *et al.* 2000, Lai and Sun 2003). The evolution of microsatellites is a complex, nondirectional process, which includes a change in the repeat unit number, point mutations, and long insertions/deletions, leading both to the formation of the new repeat types and to possible microsatellite loss, as well as to its possible restoration (Shaikhaev and Zhivotovsky 2014). Though many studies directly recording the direction of microsatellite mutations report a bias toward addition of repeats, indicating microsatellites to expand (Cooper *et al.* 1999, Zhu *et al.* 2000, Neff and Gross 2001), several studies also reported a deletion bias. Examples of microsatellites exhibiting a deletion bias are rare and appear to be limited to a few loci in multilocus studies (Udupa and Baum 2001, Weetman *et al.* 2002) or to very long alleles at a particular locus (Ellegren 2000b, Xu *et al.* 2000, Huang *et al.* 2002). Some authors state that microsatellite allele size changes can be associated with mechanism which prevents infinite expansion by mutational balance (Ellegren 2000a, Ellegren 2000b, Xu *et al.* 2000, Huang *et al.* 2002, Whittaker *et al.* 2003). The reconstruction of *P. antipodarum* microsatelite mutation history revealed consistent deletion bias, particularly in Pa217 and Pa254 loci of a triploid individuals of particular clone lineage (Weetman *et al.* 2002). Weetman *et al.* (2002) made two assumptions for this deletion bias. First, that a ploidy level may be associated with microsatellite size reduction. However, this explanation would rely on a relatively recent conversion to triploidy. Second that a deletion bias might also be favored by selection for reduced genome size. As the inverse correlation between genome size and development rate is characteristic for opportunistic organisms (Charlesworth *et al*. 1996), selection would be predicted to act against the accumulation of large amount of „junk“ DNA (Weetman *et al*. 2005).

As the invasion time of several studied Lithuanian and Poland populations is long enough and several generations per year are produced, mutational input should be hight enough, variation in msDNA to appear, despite the obligate parthenogenesis. Despite the hight possibility of microsatellite diversification, this study found no variation in microsatellites of studied *P. antipodarum* populations. Even in highly variable Pa217 and Pa254 loci, microsatellites were identical in studied populations. The recorded multilocus msDNA genotype differs from genotypes reported in UK and USA. Besides, previous studies indicate hight microsatellite diversity differencies not only between the continents but also between the studies, performed in the same water bodies. Hershler *et al*. (2010) reported 75 MLGs (among the 812 snails) from single Snake river basin, Idaho, USA, while Dybdahl and Drown (2011) found only 4 microsatellite MLGs (among the 372 snails) across 20 sites, including Snake river. Such discrepancy between the studies could arise due to methodological issues, such as range of allele sizes and number of markers used in the study (Dybdahl and Drown 2011). Study of microsatellite mutational processes and allelic variation also showed a large number of microsatellite MLGs in an introduced populations of Great Britain. A survey of several populations across the Great Britain revealed 34 MLGs based on four microsatellite loci (Weetman *et al*. 2002). If compare the invasion time, the invasive snail *P. antipodarum* was found as early as 1954 (Gasiūnas 1959) in Curonian lagoon, and only in 2010 (Butkus *et al*. 2012, Butkus *et al*. 2014) in southeastern lakes and river of Lithuania. In Poland, snails of this species were first noted by Urbanski (1938) in Trilag Lake (northern Poland) and by Lewandowski (1992) in Wigry lake system. In N. America it was firstly recorded in 1987 in the Snake river and tributary springs near Hagerman (Bowler 1991), while in UK, the invader was introduced to the river Thames in the late 19th century (Smith

1889). Thus the invasion time time differs greatly between the sites of different studies, but the variation of msDNA seems not to be related with time as the only diversifying factor. It rises an assumption of different msDNA mutation rates possibly due to clonal, environmental or both differencies. Moreover it can not be rejected, that several individuals of distinct genotypes (msDNA) were introduced to USA and UK, and only minor variation arose after the invasion.

In summary, three types of genetic markers were surveyed in several Lithuanian and one Poland populations of *P. antipodarum* to determine the genotypic diversity of a highly invasive clonal species. The results indicate the absence of genotypic diversity within and between the studied populations, in other words studied populations are monomorphic. As obligate parthenogenesis is typical for *P. antipodarum* outside the native range, the main genetic variation may arises due to mutational input. Despite the environmental and invasion time differencies of studied populations, mutation rates seems to be minimal, as no genetic variation was observed. Though there are no genetic variation between and within recent Lithuanian and one Poland *P. antipodarum* populations, the possibility of genetically diverse individuals during initial introduction can not be rejected. The studies performed in USA and UK indicate much more variable populations of *P. antipodarum*. It rises the assumption of the initial introduction of single genotype individuals to Curonian lagoon and further rapid spread across the lakes, which could be possible explanation for absence of genetic variation between studied ecosystems. However this assumption still needs verification and the formation of genetic structure, particularly msDNA, in asexual populations remains relevant question for further studies.

Life-history traits and population characteristics in mesotrophic lakes

Hight spatial aggregation of *P. antipodarum* individuals was observed in all studied lakes, where the density varied from absence to 11 850 ind. m^{-2}. The degree of aggregation varied between and within the lakes. In August and November months, individual spatial aggregation in lake Dusia was highest among all studied lakes, which could be the effect of higher individual concentration on hard surfaces, particularly stones. Higher density of *P. antipodarum* on hard surfaces was already observed in other studies (Dorgelo 1987, Son 2008). This indicates higher food particle (periphyton) concentration on hard surfaces, such as boulders or stones, than on a sand (Cattaneo *et al*. 1997).

P. antipodarum density rarely exceeds 1000 ind. m^{-2} in its native range (Holomuzki and Biggs 1999), with occasional densities up to 180 000 ind. m^{-2} (Mjchaelis 1977). Though the snail can establish extremely dense populations in the invasive range, which varies between the invaded ecosystems – from several to several tens of thousands individuals in lake ecosystems (Dorgelo 1987, Schreiber *et al*. 1998) and to hundreds of thousands in rivers (Kerans *et al*. 2005, Bennet *et al*. 2014). Occasional densities of 200 000, 500 000 and even 800 000 ind. m^{-2} and biomass greater than 30 000 mg AFDM m^{-2} were reported in several studies (Dorgelo 1987, Hall *et al*. 2003, Kerans *et al*. 2005, Hall *et al*. 2006). During this study the density varied between and within the lakes with a maximal density of 11 850 ind. m^{-2} and a biomass of 2327.19 mg AFDM m^{-2} in Lake Metelys. As the number of parasite species, capable of using *P. antipodarum* as a host is very limited in an invasive range, there are two possibly most important variables, which can explain these differencies in density and together biomass. First, environmental differencies, such as trophic conditions, salinity, temperature or habitat structure can have a significant impact on individual growth and reproductive output, which in turn impacts density and biomass of the snails (Heywood and Edwards 1962, Jacobsen and Forbes 1997, Moffitt and James 2012, Tibbets *et al*. 2010, Neiman *et al*. 2013, Dorgelo *et al*. 2014, Krist *et al*. 2014). In most cases, extremely abundant populations of *P. antipodarum* were found in rivers (Dorgelo 1987, Kerans *et al*. 2005, Hall *et al*. 2006). Hight individual density and biomass can be sustained only by hight rates of primary production, stable hydrology or warm temperature of the water (Kerans *et al*. 2005, Hall *et al*. 2006). The significant decline of individual density during ice coverage period, which was estimated during a detailed study of *P. antipodarum* density dynamics throughout the year in lake Vilkokšnis, possibly are associated with a decrease of water temperature together with food quality and quantity decline (Liboriussen and Jeppesen 2009). A broad seasonal fluctuations of *P. antipodarum* density are also recorded in Australia (Ponder 1988, Schreiber *et al*. 1998), several parts of Europe (Siegismund and Hylleberg 1987, Dorgelo 1987, van den Berg 1997, Savage 1996) and N. America (Kerans *et al*. 2005). Second, population size of invasive species may directly depend on the stage of invasion, which relates with the age of an invasion (Krebs 2009). There are three main stages - lag, rapid growth and peak, where the highest individual abundance is observed in peak phase. As the populations of *P. antipodarum* in Lithuanian lake ecosystems were first recorded only in 2010 (Butkus *et al*. 2012), the populations are possibly in the begining of rapid growth phase. While the populations with extremely hight individual abundance in USA (Hall *et al*. 2003, Kerans *et al*. 2005, Hall *et al*. 2006) or some parts of Europe (Dorgelo 1987) possibly have already reached the peak phase.

The population size structure and average individual size in the population in most cases resemble population viability and environmental suitability to study species. Hight number of young individuals (small average size), which are characterised by hight growth rates and together fast maturation, can increase the population size in short time, unless death rates increase rapidly. Meanwhile, the highter proportion of old individuals (average size highter than size at maturity) indicate low fecundity rates or hight mortality after birth as a consequence of environmental changes, leading to population decline. The results of this study suggest different size structure in studied mesotrophic lakes. Such differencies in size structure between the lakes could possibly arise due to the differencies in studied lake properties or stage of invasion. As *P.*

antipodarum individuals were first recorded in 2010 in lake Dusia (Butkus *et al*. 2012) and investigations performed during 2003-2006 in the same lake did not detect the species (Gumuliauskaitė 2007), initial stage of invasion can be considered in this lake. Though there are no available data on the presence of this snail before 2010 in other studied lakes. It is known, that trophic status (content of total phosphorus) of the lake can also significantly influence population size structure, as hight amount of phosphorus in a diet enables higher growth rates during immaturity, leading to shortening maturation time and early reproducton (Tibbets *et al*. 2010, Liess and Lange 2011). As all studied lakes are considered to be mesotrophic, the trophic conditions (content of phosphorus and nitrogen) in these lakes are expected to be similar.

Previous studies indicated the production of embryos being observed throughout the year in parthenogenetic *P. antipodarum* females, though the main reproduction occurs in the late spring and summer (Richards *et al*. 2002). It corresponds to the results of this study, where embryos were present in females throughout the year in lake Vilkokšnis and the highest fecundity, highest number of reproducing adult females, highest population density were observed during the months of the growing season. In this period, water temperature, which is crucial factor for duration of embryonic development (Gust *et al*. 2011, Macken *et al*. 2012) increases to its maximum of the year. Moreover, the effect of photoperiod together with temperature, which influence most reproductive cycles of animals in temperate regions, could also play significant role (Bohlken and Joosse 1981, Gomot 1990, Dillon 2000). Besides other factors, such as female size (Jokela *et al*. 1997, Neiman 2006), food quality (Tibbets *et al*. 2010, Krist *et al*. 2014), parasites (Jokela *et al*. 1999), properties of habitat (Jokela *et al*. 1999, Negovetic and Jokela 2001) and individual density (Neiman 2006, Zachar and Neiman 2013, Neiman *et al*. 2013) can also play a significant role on *P. antipodarum* life-history traits associated with the reproduction, such as size at first reproduction, fecundity, embryo development time, size at birth. The results also indicated significant differencies in fecundity between the studied lakes. Besides the above mentioned factors, which can influence the fecundity, the different age of invasion can also be important. Recently established invasive populations are rapidly increasing in size and due to hight density, intraspecific effects are increasing, which can lead to prolonged maturation, changes in clutch size or embryo size at birth (Neiman 2006, Zachar and Neiman 2013, Neiman 2013).

Besides other factors, water temperature is one of the main variable affecting life-history parameters, such as density dynamics and production in most of aquatic invertebrates (Panov and McQueen 1998, Arbačiauskas 1998, Dillon 2000). Though *P.antipodarum* can survive temperatures as low as 4°C and as hight as 32°C (Quinn *et al*. 1994), temperature appears to be one of the limiting factors (Levri *et al*. 2014). The results of this study as well as other studies, analyzing dynamics of different freshwater invertebrate growth (Bayne and Worrall, 1980, Arbačiauskas 1998) indicate hight seasonal variation of growth rates in a populations of *P. antipodarum.* Estimated field and laboratory growth curves indicated comparable growth rates of *P. antipodarum* in field and laboratory conditions when accounting for temperature differencies. There were significant differencies between specific growth rates estimated in laboratory and field, with a highter growth rates in laboratory. Such differencies can be attributed to several main differencies between field and laboratory. First, differencies in food quality and quantity (Tibbets *et al*. 2010, Liess and Lange 2011, Krist *et al*. 2014). As the quality and quantity of food were probably different during laboratory experiments and field (particularly during winter season) the differencies in growth rates could arise. Second, differencies in *P. antipodarum* density between laboratory and field. Approximate density during laboratory experiments was around 266 ind. m^{-2}, meanwhile density in field varied from 10 to 1490 ind. m^{-2}. Hight densities can result in reduced growth rates due to intraspecific interactions (Neiman 2006, Zachar and Neiman 2013, Neiman *et al*. 2013). Results also indicated tendency, that temperature has stronger impact to small non-reproducing individuals and the effect decreases with increasing individual size, with the lowest effect on large reproducing individuals. The same tendency was shown for many other benthic macroinvertebrates, like *G. convexiusculus* (Parashar and Rao 1988), *H. azteca* (Panov and McQueen 1998), *A. aquaticus* (Panov 1988) and etc.

Together with density, average biomass of *P. antipodarum* in lake Vilkokšnis varied throughout the year from 9.18 mg AFDM m^{-2} in April to 676.49 mg AFDM m^{-2} in October. Highter biomass in autumn than during growing season (June, July and August) indicate the dominance of mid-sized individuals in a population. Such mid-sized individuals have relatively hight growth rates and constitute a hight proportion in population. Though estimated biomass of *P. antipodarum* is hight for Lithuanian ecosystems, it is very low when compared with biomass recorded in USA. The biomass of 36 000 mg AFDM m^{-2}, with abundance of more than 500 000 ind. m^{-2} were recorded in one USA population during the growing period (Hall *et al*. 2006).

Estimated secondary production of *P. antipodarum* varied highly throughout the year in Lake Vilkokšnis. The absence of production was evaluated during cold period, which is probably associated with large individual dominance in a population and highly decreased growth rates due to the low temperature. Meanwhile highest production (4.6 mg AFDM m^{-2} d^{-1}) was observed during growing season, when water temperature increased and young individuals with hight growth rates became abundant in a population. Overal, the annual production was 544.93 mg AFDM m^{-2} d^{-1} in this lake. The production of *P. antipodarum* was also estimated for whole growing season for other studied lakes. It varied from 94.4 in Lake Dusia to 2419.1 mg AFDM m^{-2} growing season^{-1} in Lake Metelys. Though such secondary production is hight for Lithuanian lakes, much more higher production was observed in N. America. In some USA rivers, daily and annual production were respectively 1500 mg AFDM m^{-2} day^{-1} in July and 171000 mg AFDM m^{-2} year^{-1} (Hall *et al*. 2006). Such great differencies between the production may emerge due to several differencies. First, different type ecosystems, lakes in this study and river in study of Hall *et al*. (2006), were studied. It was already shown, that higher density and together biomass are appropriate for rivers rather than lakes (Dorgelo 1987, Schreiber *et al*. 1998, Kerans *et al*. 2005, Bennet *et al*. 2014). Highest estimated density of *P. antipodarum* in Lithuanian ecosystems was ~12000 ind. m^{-2}, meanwhile densities reaching more than 500000 ind. m^{-2} (Hall *et al*. 2006) were recorded in USA. These differencies could be accounted for hight individual density variation between the studied lakes. Besides, trophic conditions in different ecosystems, affecting the fecundity and growth rates, can also affect the production.

In summary, strongly aggregated spatial distribution pattern is typical for *P. antipodarum* individuals, possibly indicating uneven prefferable food particle spatial distribution. As for most of macroinvertebrates, density of *P. antipodarum* varied throughout the year, with the lowest density during cold period and extremely hight for Lithuanian ecosystems during the growing season. Hight specific growth rates, early maturation, hight fecundity are the main traits, which enabled the *P. antipodarum* to reach hight demographic potential during growing season. Growth rates as hight as 0.048 mm d^{-1} are typical for young (up to 1.5 mm) individuals during growing season (~20ºC), which leads to fast maturation (size at maturity 3.4 mm) and together reproduction. Though clutch size significantly depends on female size, fecundity is hight (about 19.5 embryos per adult female) and continous throughout the growing season. Such intensive reproduction leads to hight population growth rates. In addition, due to the lack of predators and parasites in an invasive range, the populations of *P. antipodarum* are not limited by interspecific interactions. These characteristics enables *P. antipodarum* to reach densities of 11 850 ind. m^{-2} and biomass highter than 2327.19 mg AFDM m^{-2} in some Lithuanian lakes. Though both density and biomass and together production, varied significantly between the studied lakes. Such differencies can possibly be accounted to the differencies of particular lake properties or more probably to different age of invasion.

Functional role of *P. antipodarum* in macroinvertebrate communities

The isotopic niche of *P. antipodarum* was evaluated and compared with other primary consumers in order to reveal the probable exploitative competition. The trophic niches of the *P. antipodarum*, *R. auricularia* and *C. warpachovskyi* were described by applying stable isotope (carbon $^{13}C/^{12}C$ and nitrogen $^{15}N/^{14}N$) analysis (SIA). SIA mixing model analysis was used to evaluate the contribution of littoral primary production to the nutrition of *P. antipodarum*.

P. antipodarum in general is believed to be a generalist feeder (i.e. both grazing herbivore and detritivore) feeding on sand microflora, periphyton, fungi, bacteria, and detritus (James *et al*. 2000b, Aberle *et al*. 2005). Other studies indicated epiphytes as the most important contributors to the nutrition of *P. antipodarum*, which has $d^{13}C$ values closest to those of epiphytes (Jaschinski *et al*. 2011). Study performed in New Zealand, where stable isotope signatures and gut analyses were used, also indicated that epiphytes are the predominant food source for this species (James *et al*. 2000a). Epiphytes on submerged plants in temperate regions are generally believed to have the potential to fix more carbon than the macrophytes they grow on (Cattaneo and Kalff 1980, Jaschinski *et al*. 2008, Jaschinski *et al*. 2011). Though their biomass production is relatively low, epiphytes provide a better quality food than most macrophytes do (Jaschinski *et al*. 2011). Epiphytes usually contain more nitrogen and phosphorus compared to macrophytes and leaf litter (Jaschinski *et al*. 2011). However other studies indicated periphyton as major food source for *P. antipodarum* (Cada 2004, Moore *et al*. 2012). Such disagreement could probably arise due to differencies in studied habitat properties (type and trophic condition of water body, allochthonous material input ant etc.) especially benthic habitats, where the nutrient content of periphyton is very variable (Kahlert *et al*. 2002). As expected, SIA analysis of this study showed that *P. antipodarum* is a primary consumer which mainly exploitates littoral carbon sources. As *P. antipodarum* was mainly aggregated on sandy substrates or stones in studied lakes the assumption that littoral primary producers such as sand organics and periphyton are the main food sources was made. However, the epiphytes, indicated in previous studies as one of the main food resource, were not included in this analysis. *P. antipodarum* occupied similar to other studied macroinvertebrates, such as *R. auricularia* and *C. warpachovskyi* isotopic position in studied lakes. This suggests similar to native macroinvertebrates diet components of *P. antipodarum* in the lake littoral. The isotopic overlap between *P. antipodarum* and other macroinvertebrates was also documented in other studies and can be expected due to overlap in habitat (benthos) and resources (algae, detritus) (Brenneis *et al*. 2011, Jaschinski *et al*. 2011). The stable isotope composition of the snail differed from *D. polymorpha* (typical filter-feeder, exploitating pelagic food web) in most of the studied lakes, indicating highter importance of littoral primary production to *P. antipodarum*. This indicates typical separation between pelagic and littoral consumers. Though stable isotope composition was much more enriched in *P. antipodarum* than in other studied typical littoral consumers and similar to *D. polymorpha* in Lake Dusia. Besides the stable isotope values of sand organics and POM in this lake were similar, possibly implying hight contribution of sedimented POM to lake littoral. As sand organics is one of the main sources for *P. antipodarum*, it utilizes sand organics together with sedimented POM. Hence, although stable isotope signatures of *P. antipodarum* and other studied macroinvertebrates indicate similar food sources and exploitative competition can be expected, additional studies needs to be done on food availability, limitation, and habitat preferences, in order to confirm the hypothesis.

SIA modelling showed that autochthonous littoral production (61.6 – 78.4 % contribution) is the most important carbon source for *P. antipodarum* in studied lakes. These findings agree to the results of other studies which showed that *P. antipodarum* is primary consumer which grazes on periphyton, diatoms, and plant or animal detritus (Richards *et al*. 2002, Cada 2004, Alonso and Castro-Diaz 2008, Brown *et al*. 2008, Levri *et al*. 2008, Jaschinski *et al*. 2011).

Recent SIA analysis indicated similar isotopic position of *P. antipodarum*, *R. auricularia* and *C. warpachovskyi,* which belongs to different functional feeding groups. The similar isotopopic position of macroinvertebrates from different functional groups was also shown in other studies. Jaschinski *et al*. (2011) indicated similar contribution of epiphytes to the diet of *P. antipodarum*, *G. pulex* and *A. aquaticus*. Such similarity of isotopic position is particularly important for native species, such as *R. auricularia*. Hight density of *P. antipodarum*, which is present in most of studied lakes and similar diet can inhibit the growth and reproduction of native species with similar trophic preferencies due to exploitative competition. Though such hypothesis needs further verification.

Overall, recent study suggests *P. antipodarum* to be primary consumer, mainly exploitating littoral production sources. Isotopic position of the snail can vary and possibly depends on accessibility to certain resources. This can possibly be influenced either by habitat properties, such as trophic state, substrate type, macrophyte (together with epiphyte growing on them) abundance, or the abundance of other grazers, which can deplete preferable resources. Recent analysis also suggests that diet objects for *P. antipodarum*, *R. auricularia* and *C. warpachovskyi* may strongly overlap. Such similarity of possible food sources and hight density of *P. antipodarum* rises the assumption of possible exploitative competition with studied macroinvertebrate species. However, it needs further studies to confirm this hypothesis.

The role of *P. antipodarum* in a fish diet

The integration and impact of an invasive species on food webs in a new environment depends mainly on abilities of local predators to consume the invader. If the invader can escape the predators, it can not be easily included in to preditors diet. As the invader consume a certain portion of lake primary production, but is not used as a food source by local preditors, the energy flow to higher trophic levels is reduced. Such effect is more likely to be pronounced where invaders outcompete native species, but do not take the functional role of outcompeted local species (Lasenby *et al*. 1986, Spencer *et al*. 1991, Spencer *et al*. 1999). *P. antipodarum* is one of the most rapidly spreading invasive species in various freshwater and brackish water ecosystems, where it reaches enormously hight densities. Thus, the integration and impacts of *P. antipodarum* on the local benthivorous predator's diet in temperate lakes are largely unknown.

Littoral benthic macroinvertebrates communities

P. antipodarum is abundant species in all studied lakes. Earlier studies indicated that the snail was present and was dominating benthic macroinvertebrate community over the last several years from first records in Lake Dusia. Data about the appearance of *P. antipodarum* in Lakes Vilkokšnis and Spindžius are sparse. The species was recorded in Lakes Vilkokšnis and Spindžius, respectively in 2010 and 2012 (Butkus *et al*. 2012, Butkus *et al*. 2014). It is known that *P. antipodarum* can reach extremely high densities in particular ecosystems, dominate over the native macroinvertebrate species and alter the ecosystem functioning (Hall *et al*. 2003, Hall *et al*. 2006). Both positive and negative interactions between certain native benthic macroinvertebrate groups and *P. antipodarum* densities have been observed (Kerans *et al*. 2005, Cada 2004, Schreiber *et al*. 2002). In both cases significant changes in species composition or quantity of native invertebrates leads to community level changes, which in turn can alter the diet of local benthivorous predators by reduced number of a native prey in their diet (Vinson *et al*. 2006). Finally, it may cause a poor fish growth as *P. antipodarum* represents a low quality prey species (its shell constitutes more than 90% of a total body weight) that may displace more nutritionally valuable prey items (Vinson and Baker 2008). Therefore, the rapid spread, population growth rates, and persistence of *P. antipodarum* in temperate lakes has the potential for food web and fisheries impacts.

In general, the time period of this invasive snail presence in studied lakes is relatively short. However, it was possibly enough time for the integration of *P. antipodarum* in studied lakes food webs for several reasons. First, at least for several years, *P. antipodarum* existed at hight densities which can affect native benthic invertebrate and fish communities in most of studied lakes. Secondly, earlier performed studies proved that newly introduced macroinvertebrate species may be incorporated into fish diet in less than two years after their establishment into new ecosystems (Gasiūnas 1963, Gasiūnas 1965, Vinson and Baker 2008).

Feeding experiments

Although the conclusions of performed feeding experiments are limited due to the only one prey species used during the trials, some predictions of their ability to feed on *P. antipodarum* could be made. The initial hypothesis of this study was that if predator does not recognise *P. antipodarum* individuals as potential prey species under the experiment conditions, when only this prey is available, it also would not recognise it in natural environment. Feeding experiments suggested that crayfish may be considered as potential predators of *P. antipodarum* in temperate lakes as *O. limosus* consumed large numbers of this invasive snail. Other studies also indicated several crayfish species, such as the signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), and the red swamp crayfish, *Procambarus clarkii* (Girard, 1852), to consume significant quantities of *P. antipodarum* snails in laboratory conditions (Brenneis *et al*. 2011, Twardochleb *et al*. 2012, Bennett *et al*. 2015).

Performed feeding experiments also suggested that molluscivorous *T. tinca* can be considered as potential predator species for *P. antipodarum* in lake ecosystems. Meanwhile the consumption of *P. antipodarum* by other studied fish species was very low and they are less likely to operate as *P. antipodarum* predators. This study indicated that the presence of the pharyngeal teeth alone cannot account for high consumption of *P. antipodarum* rate, as it was not observed in the case of *R. rutilus* and *S. erythrophthalmus*. However, molluscivorous fishes, such as *T. tinca* and *N. melanostomus*, ingested comparably more *P. antipodarum* than other studied fish species. This implies possible differencies in the structure of pharyngeal teeth. According to this assumption, the pharyngeal teeth of *T. tinca* and are possibly more suitable to crush small and hard shell of *P. antipodarum* individuals. Other feeding studies indicated that omnivorous fishes, such as *Gasterosteus aculeatus* (Linnaeus, 1758), *Leptocottus armatus* (Girard, 1854) and *Platichthys stellatus* (Pallas, 1787), consumed *P. antipodarum* in very trivial numbers (Kelley 2005, Brenneis *et al*. 2011). As these fish lack well-expressed pharyngeal teeth and swallow their prey whole, they cannot crush the shell of *P. antipodarum*. This implies the snail to be resistant to their predation and to survive after passing through the digestive tracts of the fishes.

Benthivorous fish diet

Wild-caught fish diet analysis revealed that *P. antipodarum* was present in all investigated fish diet. As it was expected the highest prevalence of the snails was found in molluscivorous fishes such as *A. brama*, *R. rutilus* and *T. tinca* diet, though it varied between studied lakes. Performed laboratory feeding experiments showed, that *T. tinca* can significantly consume *P. antipodarum*, though in natural environments the share of this snail was very low. In general, the number of *P. antipodarum* per fish and its share in the total fish diet was very low for all investigated benthivorous fish species, despite that the other molluscs were abundant in several fish guts. Therefore, it can be concluded, that the main benthivorous fish species in temperate lakes avoid feeding on *P. antipodarum* individuals and hardly can influence the density of the invasive snails in studied lakes. Such conclusion is in coincidence with fish diet studies in natural environments from other regions. It was assessed that fishes such as

Cymatogaster aggregata (Gibbons, 1854), *Pleuronectes vetulus* (Girard, 1854) (Brenneis *et al*. 2011), *Salmo trutta* (Linnaeus, 1758), *Cottus bairdi* (Girard, 1850) (Cada, 2004) and *Oncorhynchus tshawytscha* (Walbaum, 1792) (Bersine *et al*. 2008) also consume *P. antipodarum* in minor quantities in natural environment. *N. melanostomus*, which according to our experiments may also significantly consume *P. antipodarum* individuals, has been shown to consume *P. antipodarum* in trivial quantities in brackish environments (Rakauskas *et al*. 2014).

On the other hand, it is also possible that due to recent invasion the consumption of *P. antipodarum* by local predators is low and it needs more time to local benthic predators to adapt to new prey species. Such case was reported for *S. trutta* in the Green River, Utah (Vinson *et al*. 2006). In that river, *P. antipodarum* initially appeared in less than 5% of all trout diets, but within 5 years was found in nearly 60% of all trouts. Therefore the increase of *P. antipodarum* share in benthivorous fish diet in studied lakes may still be expected in the future.

The *experiments on P. antipodarum survivorship throughout the gastrointestinal tract of fishes*

Feeding experiments and wild-caught fish diet analysis showed that most of the main benthivorous predators from studied lakes fed on *P. antipodarum* to some degree. However wild-caught fish diet analysis also revealed that most of the ingested *P. antipodarum* snails remained intact. Similar results were obtained in other studies, where most of ingested snails remained intact, even in fish species from New Zealand, where coevolution could be expected (McCarter 1986, Jellyman 1989). This encouraged to perform laboratory experiments on survivorship of *P. antipodarum* throughout the gastrointestinal tract of dominant benthivorous fishes. These experiments indicated that *P. antipodarum* can survive the passage of gastrointestinal track of various studied fish species. Besides the results also indicated that molluscivorous fish digest *P. antipodarum* more effectively than omnivorous fish, which swallow their prey whole.

Feeding experiments revealed that *T. tinca, N. melanostomus* and *O. limosus* showed the highest consumption rate of the invasive snail among all investigated benthivorous predators. However, the fate of consumed *P. antipodarum* was different for those predators. As it was expected none of *P. antipodarum* individuals passed unharmed the gastrointestinal tract of *O. limosus* as they crush and pulverize their prey before consumption. From other molluscivorous predators, only *T. tinca* smashed and digested all consumed snails, meanwhile some of *P. antipodarum* individuals survived the passage of the gastrointestinal tracts of *N. melanostomus*. Thus, performed experiments suggest that only *T. tinca* and *O. limosus* may be considered as potential predators for *P. antipodarum* among the main benthivorous predator species. Meanwhile the other benthivorous predator species such as *P. fluviatilis*, *R. rutilus*, *P. glenii*, *G. cernua* or *S. erythrophthalmus* are less likely to operate as a *P. antipodarum* predatory species in lakes.

On the other hand, performed survival experiments indicate that most of the tested fishes can accelerate the dispersion of *P. antipodarum* in the freshwater ecosystems. This study also proved that *S. erythrophthalmus*, *R. rutilus*, *P. fluviatilis*, *P. glenii* and *N. melanostomus* may transport *P. antipodarum* internally as these organisms can survive passage through their digestive system. Similar results were obtained with other fish species in other regions (Vinson and Baker 2008, Bruce *et al*. 2009, Brenneis *et al*. 2011). Though active dispersion by *P. antipodarum* snails is limited due to their small size (Kappes and Haase 2011), the dispersion by fishes may be an explanation for generally rapid colonization of new suitable habitat in larger lentic freshwater ecosystems by this invasive aquatic snail.

Food web impact

The integration and impact of an invasive species on food webs in a new environment depends on a local predator's ability to consume invaders. Of a particular interest from the fisheries management point of view is how introduced *P. antipodarum* individuals can alter benthic fish and crayfish diet in temperate lakes. In general, the introduction of a new species into an ecosystem can provide a new resource for secondary consumers. Sometimes predators may even inhibit the establishment and expansion of introduced species below a threshold of management concern (Ricciardi and MacIsaac 2011, Montserrat *et al*. 2012, Twardochleb *et al*. 2012). On the other hand, if invaders are somewhat resistant to predation, they cannot be easily included into predator's diet. Consequently, as invaders consume a certain portion of lake primary production, but are not consumed by local predators, direct energy flow to higher trophic levels could be reduced. Such effect is more likely to be pronounced where invaders dominate over the native species, but do not take their role as prey for fish (Lasenby *et al*. 1986, Spencer *et al*. 1991, Spencer *et al*. 1999). Though this complete chain of events has not been well studied, particularly in temperate lakes, our data prove it may be realistic in some Lithuanian lakes where *P. antipodarum* is now abundant. First, *P. antipodarum* was shown to be primary consumer which may utilize different carbon sources in freshwater ecosystems (Haynes and Taylor 1984, Winterbourn and Fegley 1989, Death 1991, Radea *et al*. 2008). This study also showed that *P. antipodarum* dominates in the littoral benthic macroinvertebrate communities of invaded lakes. Thus *P. antipodarum* definitely consume significant portion of primary production in these lakes. Second, performed diet analysis of the main benthivorous fish species from invaded lakes showed insignificant *P. antipodarum* consumption in all studied lakes. Moreover, performed survival experiments showed that *P. antipodarum* individuals, due to hard shell and operculum, are resistant to predation of most local benthivorous fishes and can survive the passage through their digestive tracts.

Overall, all these evidence together suggests that the main benthivorous fishes consume insignificant number of *P. antipodarum*, though it is one of the most abundant invertebrate species in the littoral macroinvertebrate communities of invaded lakes. If local fishes are not consuming *P. antipodarum,* a part of energy from primary production is locked and unavailable to higher trophic levels in an invaded lakes. Thus, it is possible that highly abundant *P. antipodarum* may reduce energy flow towards higher trophic levels in these lakes.

Nevertheless, predatory benthic macroinvertebrates may also contribute to the *P. antipodarum* consumption in temperate lake ecosystems. Performed feeding experiments showed, that *O. limosus* can also be considered as a potential predator for the *P. antipodarum* individuals in temperate lakes. Other studies also showed that crayfishes consume large numbers of *P. antipodarum* individuals (Brenneis *et al*. 2011, Twardochleb *et al*. 2012, Bennet *et al*. 2014). It was shown, that New Zealand crayfish, *Paranephrops planifrons* (White, 1842), consume *P. antipodarum* in their native range (Parkyn *et al*. 1997). However, crayfishes could not account for long-term snail decline in Lithuanian lakes because they are scarce in most of *P. antipodarum* invaded ecosystems (V. Rakauskas personal observation) and, as generalist predators, are possibly unlikely to provide sustained population regulation. However this hypothesis warrants further investigation of natural crayfish diet from *P. antipodarum* invaded lakes.

In summary, this study indicates direct interactions between *P. antipodarum* and their potential predators in temperate lakes. In general, it is predicted that native predators should adopt their consumption on invasive species after some period. The findings of this study do not support the hypothesis that abundant *P. antipodarum* replace native prey in the diets of local benthivorous fishes. Performed experiments indicate that some local predators have potential to prey significantly upon invasive snail under experimental conditions, though the field data do not support this expectation. In general, results indicated that the main benthivorous fish species avoid consuming *P. antipodarum*, despite the several years of this snail invasion in studied lakes. This suggests that local fishes possibly have no potential to regulate *P. antipodarum* population density in Lithuanian lakes. Consequently, as *P. antipodarum* is generally not consumed by local fishes, primary production share consumed by this invader will not directly reach higher food chain levels. Therefore the decrease of some benthivorous fish species production can be expected in *P. antipodarum* invaded lakes in future. Despite the negative consequences to energy flow, this study also revealed that fishes may act as a potential local dispersion vector for *P. antipodarum* in lake ecosystems. As this snail may pass undigested through the gastrointestinal tract of the main benthivorous fish species, it can accelerate spread in freshly invaded ecosystems.

CONCLUSIONS

1. The invasive New Zealand mudsnail *P. antipodarum* is rapidly spreading across the fresh waters of Lithuania. Recently, the species occurs in 18 water bodies among which, 16 were recorded during the current study.
2. According to mitochondrial and microsatellite DNA markers, studied populations of *P. antipodarum* were monomorphic; one microsatellite genotype, one haplotype of cytochrome b and one haplotype of 16S RNA markers were recorded.
3. In Lithuanian lakes, the New Zealand mudsnail *P. antipodarum* typically occurs spatially aggregated, can attain high densities reaching over 10^4 ind. m^{-2} and secondary production reaching 2.4 g ash-free dry mass m^{-2} per growing season.
4. Under Lithuanian natural conditions, *P. antipodarum* reproduce continously throughout the growing season. The largest estimated clutch size was 49 embryos per female and highest fecundity in Lithuanian mesotrophic lakes during the growing season was 19.5 embryos per adult female.

5. The growth rate of young individuals was stronger affected by water temperature than of adults.

6. The New Zealand mudsnail *P. antipodarum* is a primary consumer which relies mainly on the litoral primary production; under limited resources, competition with resident macroinvertebrate species with similar diet preferences is possible.

7. The survivorship of *P. antipodarum* individuals through the gastrointestinal tract depended upon fish feeding mode and the structure of pharyngeal teeth. The lowest survivorship was observed in tentch *Tinca tinca*. The considerable amount of snails was also consumed by

the crayfish *Orconectes limosus*. Both these species can potentially affect abundance of *P. antipodarum* in mesotrophic lake ecosystems.

8. Despite hight abundance of the New Zealand mudsnail *P. antipodarum,* at least during the initial stages of the invasion, the dominant benthivorous fish species in mesotrophic lakes avoid to feed on *P. antipodarum*, thus could hardly contribute to the regulation of its density.

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