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Affecting the ecosystem and being affected by it: the case of the non-indigenous round goby, *N. melanostomus*, in the Baltic Sea

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Front cover: Round goby male. Photo: Jens Hedlund
Back cover: Round goby male in bottle. Photo: Jens Hedlund

Abstract

Increased human trade and transport in the last decades has increased the number of non-indigenous species, NIS, being distributed around the globe. Some NIS establish in new areas, and of these some give rise to negative environmental, economic and/or social consequences. Low native species richness in an ecosystem is associated with a high degree of invasibility, defined as the susceptibility of a habitat and the associated biological community to invasion. Between 1970 and 2013 the number of detected NIS in the Baltic Sea increased by 86%. One of them is *Neogobius melanostomus*, round goby, of which the first specimen in the Baltic Sea was found in 1990 in the Gulf of Gdansk. *N. melanostomus* in the Baltic Sea seems to display a variation in life-history strategies within the area and in comparison to populations in other areas. It is also an opportunistic predator, but with some prey preferences, and displays ontogenetic shifts during its course of life. It shows dietary adaptation to local conditions with the most pronounced deviation in the westernmost and northernmost parts of the Baltic Sea, where mussel-feeding is lower compared to other areas. *N. melanostomus* is an important prey to some predator species in the Baltic Sea, like cod and perch. However, also other species may benefit of *N. melanostomus* as prey. When resources (i.e. food or space) are limited, *N. melanostomus* appears to be the stronger competitor to a wide range of species, but also intraspecific competition occurs and could be a driver for *N. melanostomus* to spread to new areas. It appears as if *N. melanostomus*, despite the relatively short time since the establishment, has already made its mark on the Baltic Sea ecosystem acting as predator, competitor and prey, and also been marked by it, as the species to some extent has adapted to local conditions in the Baltic Sea. However, *N. melanostomus*' role as predator, competitor and prey needs to be investigated further in order to clarify its ecological position in the Baltic Sea ecosystem. In the future, this knowledge should be incorporated to achieve an ecosystem-based management and sustainable commercial and recreational fisheries.

Keywords: Distribution, life-history strategy, diet, predators, competition, coastal zone ecology, ecosystem-specific effects

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Abbreviations

aquaNIS	Aquatic non-indigenous species
CBD	Convention on Biological Diversity
GNP	Gross National Product
IAS	Invasive alien species
ICES	International Council for the Exploration of the Sea
IUCN	International Union for Conservation of Nature and Natural Resources
NIS	Non-indigenous species
PSU	Practical salinity units
SL	Standard length
TL	Total length

1 Introduction

In this essay I provide an overview of the consequences of introductions of non-indigenous species, with special emphasis on the Baltic Sea area. I have in particular investigated the ecological impacts of the introduction of *N. melanostomus* in the Baltic Sea. The aspects I have looked into are 1) variation in life-history strategies in areas/populations where the species is well established *vs.* areas of recent introduction, 2) the role of *N. melanostomus* in the food web, and 3) other ecosystem effects of *N. melanostomus* introduction. This includes events like trophic cascades, transmission of diseases and parasites, potential hybridization and biomagnification of pollutants. The purpose has been to identify knowledge gaps and establish a knowledge base for the scope of my PhD-studies.

The literature survey is based on scientific articles found mainly with help of the SLU library resources, including Web of Science, and Google Scholar. Also books have been important components in the literature survey. Additionally, I have used information found on webpages and in grey literature (reports etc.), but only to a limited extent as such literature rarely provides new information but rather synthesizes information produced by others. Webpages and reports may also have a targeted aim, which in some cases make them unsuitable as non-biased information sources. The search terms included, but were not restricted to, different combinations of the phrases "*Neogobius melanostomus*", "round goby", "invasive species", "Baltic Sea", "biodiversity", "phenotypic plasticity", "life-history strategies", "predation" and "diet".

Non-indigenous species (NIS): an overview

The Earth's ecosystems are under anthropogenic pressure, and the major drivers pointed out are habitat change (both terrestrial and aquatic), overexploitation, non-indigenous species, pollution and climate change (Millennium Ecosystem Assessment, 2005). Increased human trade and transport has increased the number of NIS being distributed around the globe. Some of these species establish in new areas, and of these some give rise to negative environmental, economic and/or social consequences (Millennium Ecosystem Assessment, 2005, Keller et al., 2011). Among the environmental consequences biodiversity loss is particularly denoted as a serious threat, and one that is likely to increase with climate change (Bailey, 2015).

Terminology

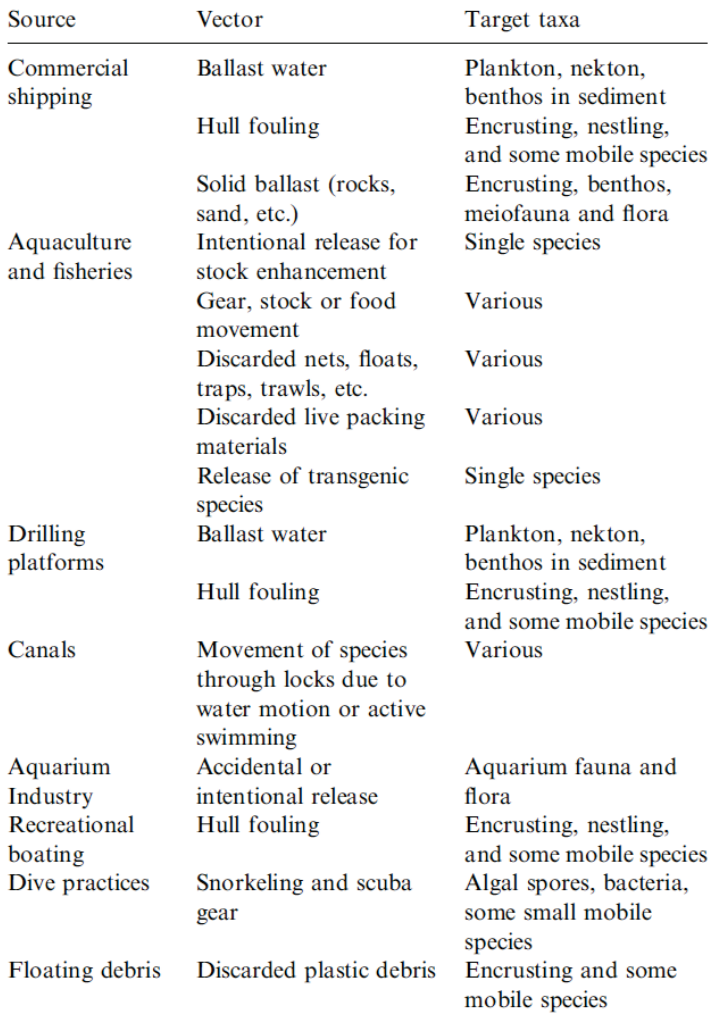
There are a number of ways to describe species new to an area. As the field of invasion biology is rather new and rapidly developing, the terminology is diverse and also changes over time (Olenin et al., 2017). A native species is categorized as having evolved in a certain region, or evolved elsewhere but arrived in the region by its own means. An "introduced species" is any species that arrives somewhere with human help, while an "invasive species" is a species that arrives with human assistance, establishes a population and spreads (Simberloff, 2013). The term "invasive" also means, according to the Convention on Biological Diversity (CBD) that the species "must successfully out-compete native organisms […] increase in population density and harm ecosystems in its introduced range" (United Nations Environmental Program, n.d.) or, according to Keller et al. (2011), adversely affect economy or human health. A "non-indigenous", "nonnative", "alien" or "exotic" species is present in a region but not native to it, i.e. transferred there by human activities (Simberloff, 2013). Also the word "xenodiversity" is occasionally used for biological diversity of foreign origin (Leppäkoski and Olenin, 2000). A "transplant" is a species moved within a country, while "feral species" is the term for cultured species that have escaped and established outside the cultures. After some time the new species may have become an integrated part of the invaded ecosystem to such a degree that it is mistaken for being native, and at that point it is referred to as “naturalized” (Hill, 2008). A “cryptogenic species”, on the other hand, is a species which status as native or nonnative is unknown (Simberloff, 2013). The abbreviation “IAS”, standing for “invasive alien species”, is reserved for species with profound negative consequences for the ecosystem, human health and/or socio-economic values (Olenin et al., 2017).

In this review, I will use the terms “non-indigenous species”, NIS, and “aquatic non-indigenous species”, aquaNIS. These are commonly used by the International Council for the Exploration of the Sea (ICES, 2017) and are neutral in the sense that they do not imply whether the consequences of the species introduced are positive or negative, thus not being subjective in any way. For names of species, I first give both the Latin and the common name, and in all following places only the Latin name.

General mechanisms of spread of NIS

Species have been transferred to new areas by humans for thousands of years. Some species that we consider indigenous to certain areas are actually introduced and subsequently naturalized (Carlton, 1999, Simberloff, 2013). However, due to increased levels of global trade, transport and tourism following population growth and globalization (United Nations Environmental Program, n.d.), the annual rate of first records of NIS is increasing for most taxa in both terrestrial and aquatic ecosystems, despite a number of mitigation strategies (Seebens et al., 2017). The increase in detection of NIS over time is also partly explained by better identification and surveillance tools (Ojaveer et al., 2018). In aquatic ecosystems potential ways of spread of NIS include, but are not restricted to, commercial shipping, aquaculture and fisheries (Table 1). AquaNIS can be transported on ship hulls, although this was more common in times when wooden ships were standard. Due to antifouling paint, increased ship speed and shorter harbor residencies the degree of hull fouling has decreased, and aquaNIS are now mainly transported in ballast water (Carlton, 1999).

Table 1. Pathways of introduction of aquaNIS (Bax et al., 2003, modified from Carlton 2001; reprinted with permission from the author).



Source	Vector	Target taxa
Commercial shipping	Ballast water	Plankton, nekton, benthos in sediment
	Hull fouling	Encrusting, nestling, and some mobile species
	Solid ballast (rocks, sand, etc.)	Encrusting, benthos, meiofauna and flora
Aquaculture and fisheries	Intentional release for stock enhancement	Single species
	Gear, stock or food movement	Various
	Discarded nets, floats, traps, trawls, etc.	Various
	Discarded live packing materials	Various
	Release of transgenic species	Single species
Drilling platforms	Ballast water	Plankton, nekton, benthos in sediment
	Hull fouling	Encrusting, nestling, and some mobile species
Canals	Movement of species through locks due to water motion or active swimming	Various
Aquarium Industry	Accidental or intentional release	Aquarium fauna and flora
Recreational boating	Hull fouling	Encrusting, nestling, and some mobile species
Dive practices	Snorkeling and scuba gear	Algal spores, bacteria, some small mobile species
Floating debris	Discarded plastic debris	Encrusting and some mobile species

Consequences of introduction of NIS

Different ecosystems are not equally vulnerable to invasions. The level of invasibility, defined as the susceptibility of a habitat and the associated biological community to invasion (Davis et al., 2005), is affected by both biotic and abiotic conditions (Catford et al., 2012). In general, low native species richness in an ecosystem is associated with a high degree of invasibility – a pattern clearly seen in the Baltic Sea (Snoeijs-Leijonmalm, 2017).

Negative implications of NIS are diverse as they can cause both ecological, economic and social damage (Simberloff, 2013) and vary significantly both spatially and temporally (Katsanevakis et al., 2014). NIS can for example transmit diseases and predate upon native species with following ecological consequences, e.g. niche displacement or extinction (United Nations Environmental Program, n.d.). They can further act as competitors to native species (Simberloff, 2013) and cause trophic cascades (Levin, 2009). Additionally, NIS can occasionally hybridize with native or introduced species. Two or more NIS can also enhance the negative impact on the invaded ecosystem to a much greater extent than each of them could on their own, a process known as "invasional meltdown". Lastly, NIS can modify habitats and act as ecosystem engineers, i.e. species whose activities fundamentally change the physical structure of the environment (Simberloff, 2013).

Globally, the costs of NIS have been estimated to 1.4 trillion dollars every year, which is equivalent to 5% of world GNP (Simberloff, 2013). They can reduce productivity in e.g. the agricultural (Simberloff, 2013) and fishing sectors (IUCN, 2009), cause export and import trade restrictions (Government of Canada, 2017), have negative impact on tourism (IUCN, 2009) and reduce property values (Zhang and Boyle, 2010). In addition, some costs of NIS are very difficult to assess, e.g. the costs of extinctions of native species caused by NIS. However, NIS can also be economically beneficial, e.g. as crops (Simberloff, 2013).

The social consequences of introduction of NIS can include harm to human health as parasites or diseases (Simberloff, 2013), or reduction of recreational opportunities (Government of Canada, 2017). They may also be a major threat to people who rely on native species for subsistence harvesting (IUCN, 2009). Additionally, NIS can have cultural impacts (Simberloff, 2013) and decrease aesthetic and spiritual values (Chornesky et al., 2005).

Despite the evidence that NIS may exert severe impact on invaded ecosystems, there are examples of NIS with positive consequences, or a mix of positive and negative effects. In fact, positive impacts are usually underestimated as there is often a perception bias against NIS (Katsanevakis et al., 2014). It is predicted that the proportion of NIS viewed as benign or desirable will increase over time (Schlaepfer et al., 2011). In European marine ecosystems, the ecosystem services that are most positively affected by NIS are water purification, climate regulation and cognitive benefits, such as material for research and education or inspiration for art (Katsanevakis et al., 2014).

The establishment of NIS can also result in neutral effects, meaning lack of apparent effects (Levin, 2009), but such examples are difficult to find in the literature. The reason for this may be either publication bias – it is probably not considered very rewarding to publish a paper on lack of effects, or that the NIS with neutral effects more often go unnoticed for a rather long time. Nevertheless, it is important to highlight also neutral effects, since we need to look at NIS and their consequences from an objective point of view and take all aspects into consideration.

NIS occurrence and impacts on the Baltic Sea ecosystem

In the Baltic Sea the most prominent features are the lack of tides, pronounced seasonal variation in temperature and its low salinity with a marked salinity gradient. The salinity ranges between 9-10 psu in the surface waters in the south-western parts and decreases towards the north and east, reaching approximately 3 psu e.g. in the inner Gulf of Finland and 1-2 psu in the Gulf of Bothnia (Bernes, 2005). Similar gradients in temperature and salinity go from coastal areas into deeper waters (Snoeijs-Leijonmalm and Andrén, 2017).

The Baltic Sea is species poor due to its brackish water, allowing only few species of marine and limnetic origins to thrive there, and the fact that it is a young ecosystem. Approximately 8000 years have passed since the last glacial period when the Baltic Sea as we know it started to form (Snoeijs-Leijonmalm and Andrén, 2017), which means that all species are more or less new to the area (Bernes, 2005). No obligate marine or limnetic species are found in the Baltic Sea (Snoeijs-Leijonmalm, 2017), except for certain insect larvae found only in low salinity coastal areas (Radziejewska et al., 2017). Instead, all species display varying degrees of euryhalinity (Snoeijs-Leijonmalm, 2017). Further, the genetic variation of marine species in the Baltic Sea is low in comparison with their conspecifics in the north-east Atlantic. Approximately 50 and 10% in mDNA loci and nuclear loci has been lost, respectively (Johannesson and Andre, 2006). The low genetic variation in the Baltic Sea probably makes the area vulnerable to further loss of genetic variation, which could be one consequence of NIS introductions.

Shipping, stocking of fish and natural spread from other invaded areas have been the main pathways of introduction in the Baltic Sea, accounting for ~ 39, 28 and 25% of the introductions, respectively, while canals account for 5% (Ojaveer et al., 2017a). It can be comparatively easy for NIS to establish in the Baltic Sea, since the low number of native species lowers the risk of newcomers to be outcompeted or predated upon (Bernes, 2005). In the Baltic Sea, 95 multicellular aquaNIS (out of a total of 879 investigated species) have been reported until 2013, and the number of detected NIS is estimated to have increased by 86% between 1970 and 2013 (Fig. 1; Galil et al., 2014).

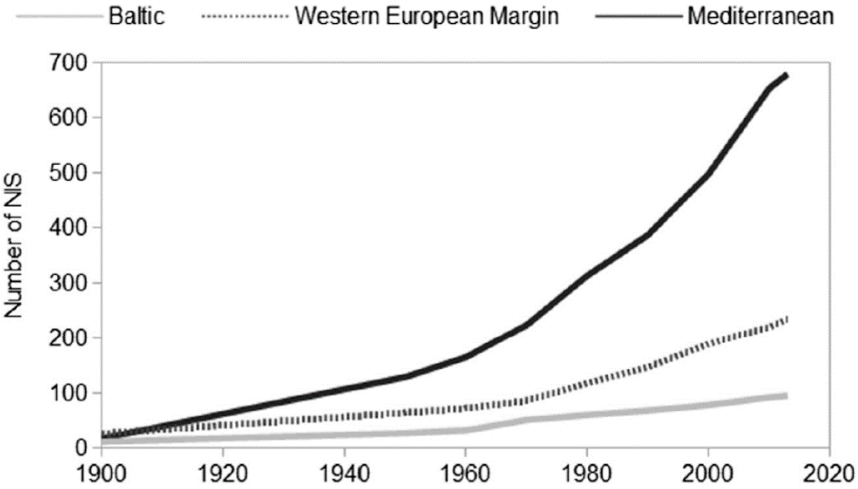


Fig. 1. The increasing number of aquaNIS between 1900-2013 in the Baltic Sea, the Western European margin and the Mediterranean (reprinted with permission from Galil et al., 2014).

Two benthic invertebrate invaders in the Baltic Sea, the polychaete *Marenzelleria* spp. and *Dreissena polymorpha*, zebra mussel, act as ecosystem engineers, affect nutrient flows and cause new food web interactions, mostly as competitors to native species. The consequences can be both positive and negative. For example, bioturbation by *Marenzelleria* spp. can release hazardous substances but also improve oxygen conditions on the sea floor and thus enhance phosphorus retention (Olenin et al., 2017). In the Archipelago Sea and along the Finnish coast *Rhithropanopeus harrisii*, North American white-fingered mud crab, could potentially cause trophic cascades by predating upon the snail *Theodoxus fluviatilis*, which under normal conditions graze on filamentous algae on *Fucus vesiculosus* (Forsström et al., 2015). *R. harrisii* could potentially also feed on other grazers. *Cercopagis pengoi*, fishhook waterflea, has deleterious effects on native cladocerans and enhances eutrophication due to predation on phytoplankton-grazing zooplankton. It also clogs fish nets and trawls, which causes economic losses. Further, it competes with small planktivorous fish, but at the same time serves as prey for larger planktivorous fish. The non-indigenous amphipods *Gammarus tigrinus*, *Obesogammarus crassus* and *Pontogammarus robustoides* almost entirely outcompete their native relatives in some areas. This is probably because they are more opportunistic feeders, which changes community composition in the phytobenthic zone. Together with *Neogobius melanostomus,* round goby, the amphipods are categorized as the NIS with the most profound impacts on the Baltic Sea ecosystem (Olenin et al., 2017). The impact of *N. melanostomus* on aquatic ecosystems is explored below.

2 The round goby, *Neogobius melanostomus*

Ecology

N. melanostomus, of the family Gobiidae, originates from the Black Sea (subspecies *N. melanostomus melanostomus*) and the Caspian Sea (subspecies *N. melanostomus affinis*). *N. melanostomus* found in the Baltic Sea belongs to the Black Sea subspecies (Brown and Stepien, 2008).

N. melanostomus coloration varies between grey, brown and yellow-green with darker lateral spots. *N. melanostomus* also has a characteristic black spot on the hind part of the first dorsal fin. The head is large and the body is elongated and almost round in cross section. Two pelvic fins have evolved into a suction plate (Kornis et al., 2012), which allows the fish to adhere to a substrate in a streaming water environment (Nellbring, 2014). Males display greater body size (Kornis et al., 2012) but growth rates appear to be similar for both sexes (Sokolowska and Fey, 2011). *N. melanostomus* has a benthic lifestyle and lacks a swim bladder (Leslie and Timmins, 2004), but is a surprisingly good swimmer. It can move up to 14 m/h and in still water exhibits startle bursts at up to 163 cm/s, equaling 587 m/h (Tierney et al., 2011). The dispersal rate under natural conditions can be up to 30 km yr^{-1} (Azour et al., 2015).

Prior to spawning, *N. melanostomus* migrates from deeper areas into shallower and warmer waters. In the Baltic Sea spawning takes place in temperatures of 17-18 °C (Tomczak and Sapota, 2006 and references therein). *N. melanostomus* is a multiple batch spawner, meaning that the female ovulates several times during the spawning season (Tomczak and Sapota, 2006). The interval between the released batches is reported to be 17-28 days, depending on temperature (Tomczak and Sapota, 2006 and references therein). Eggs are deposited on hard surfaces, e.g. in cavities and under rocks (Strake et al., 2013) in a favored male's nest, which he then guards during egg development (Corkum et al., 1998). The males do not feed during spawning and nest-guarding (Corkum et al., 1998, Kornis et al., 2012) and are believed to die when the spawning period is over (e.g. Almqvist, 2008). Egg survival rates are highly dependent on the care exhibited by the males (Kornis et al., 2012 and references therein). However, the eggs may be predated upon by conspecifics (Meunier et al., 2009). The larvae are fully developed at hatching, meaning that the eyes, fins and digestive system are functioning (Leslie and Timmins, 2004). They undertake diel vertical migration in the water column (Hensler and Jude, 2007, Hayden and Miner, 2009), a behavior potentially developed as a dispersal strategy and/or to escape predators (Hensler and Jude, 2007).

Sex ratios differ over time and between populations (Table 2). Male-biased sex ratios dominate in non-native populations in the Great Lakes and the Baltic Sea. At the same time, female-biased sex ratios are the most common in non-native populations in European rivers and canals. The male biased sex ratios seen in the Great Lakes and the Baltic Sea could be influenced by male nest guarding, as females move away to deeper waters, or sampling bias, if males are more active and curious and thus experience more encounters with passive sampling gear (Kornis et al., 2012). These theories might explain the differences between native and newly established populations, if more active and curious males more readily disperse and explore new environments.

Table 2. *N. melanostomus* sex ratios in its area of origin and in non-native populations of different age.

Area	**Population age**	**Sex ratio**	**Reference**
Area of origin	N.A.	1.6-1.9:1 (F:M)	(Kornis et al., 2012 and references therein)
Area of origin	N.A.	1:1	(Tomczak and Sapota, 2006 and references therein)
Danube River	Not specified (core population)	1:0.9 (F:M)	(Brandner et al., 2013)
Danube River	Not specified (front population)	1:0.7 (F:M)	(Brandner et al., 2013)
Danube River	Not specified (front population)	1:0.77 (F:M)	(Brandner et al., 2013)
Danube River	>4-8 years	1:0.88 (F:M)	(Brandner et al., 2018)
Danube River	Not specified (front population)	1:0.56 (F:M)	(Brandner et al., 2018)
Danube River	Not specified (front population)	1.2:1 (M:F)	(Brandner et al., 2018)
Kiel Canal	5-6 years	1.3:1 (F:M)	(Hempel, 2017)
Baltic Sea (Danish waters)	1 year	2.5:1 (M:F)	(Azour et al., 2015)
Baltic Sea (Danish waters)	2-5 years	1:1	(Azour et al., 2015)
Baltic Sea (Gulf of Gdansk)	5-6 years	2:1-4:1 (M:F)	(Skora and Rzeznik, 2001)
Baltic Sea (Gulf of Gdansk)	~11 years	3:1 (M:F)	(Corkum et al., 2004)
Baltic Sea (Gulf of Gdansk)	13-16 years	1.8:1-6.6:1 (M:F)	(Almqvist, 2008)
Great Lakes	<11 years	6:1 (M:F)	(Corkum et al., 2004)
Great Lakes (Lake Ontario)	12-18 years	~2:1 (M:F)	(Young et al., 2010)
Great Lakes (Lake Ontario)	Not specified (core population)	1.4:1 (M:F)	(Gutowsky and Fox, 2011)
Great Lakes (Lake Ontario)	Not specified (front population)	2.2:1 (M:F)	(Gutowsky and Fox, 2011)

N. melanostomus salinity tolerance covers a span between 0 and 40.5 psu (Ellis and Macisaac, 2009 and references therein). Individuals from newly established fresh water populations do not survive salinities ≥ 30 psu (Ellis and Macisaac, 2009, Karsiotis et al., 2012). The upper limit in salinity tolerance may inhibit or at least decrease the pace of spread to fully marine areas. Salinity scope for reproduction is narrower. In its area of origin, egg development decreases in salinities ≥ 19 psu (Karsiotis et al., 2012 and references therein). In the Baltic Sea salinities of 8-9 psu are reported as required for spawning (Tomczak and Sapota, 2006 and references therein). However, the salinity scope has to be broader than that, since viable populations are found in the central and northern parts with salinities < 8 psu.

N. melanostomus has a wide temperature tolerance range of -1 to 30 ˚C (Pinchuk et al., 2003). It can withstand rapid temperature changes (Pinchuk et al., 2003) but prefers water temperatures in the upper range (Kornis et al., 2012). The energetic optimum temperature is reported to be 26 ˚C. The species is further tolerant to low oxygen levels. It can endure hypoxic conditions down to levels of 0.4-1.3 mg O^{-1}, but tends to migrate from areas of ca 4 mg O^{-1} (Kornis et al., 2012). However, *N. melanostomus* prefers conditions where oxygen levels are at least 60% (Pinchuk et al., 2003), which corresponds to 5.68 mg O^{-1} at 18˚ C (calculated by http://www.waterontheweb.org/under/waterquality/DOSatCalc.html).

N. melanostomus prefers hard bottoms with rocks for shelter, probably because of lower risk of predation (Kornis et al., 2012) and high densities of mollusc prey (Strake et al., 2013). Still, the species is found under a broad range of environmental conditions (Kotta et al., 2016), from soft substrata in open habitats (Kornis et al., 2012) to shallow sandy habitats (Ustups et al., 2016). The depth distribution varies during summer between 3-20 m depth (Strake et al., 2013, Florin and Jonsson, 2016) but winter depth distribution is not known.

Global dispersal: mechanisms, timeline and geography

Outside its native range, *N. melanostomus* was first observed in 1990 both in St. Clair River in the Great Lakes system in North America (Jude et al., 1992) and in the Gulf of Gdansk in the Baltic Sea (Skora and Stolarski, 1993). Both in the Baltic

Sea and in the Great Lakes the first introduction was followed by an unknown number of subsequent introductions (Brown and Stepien, 2009, Björklund and Almqvist, 2009). In the Great Lakes the species has spread at an unprecedented rate (Charlebois et al., 2001), whereas the Baltic Sea invasion has been slower (Fig. 2).

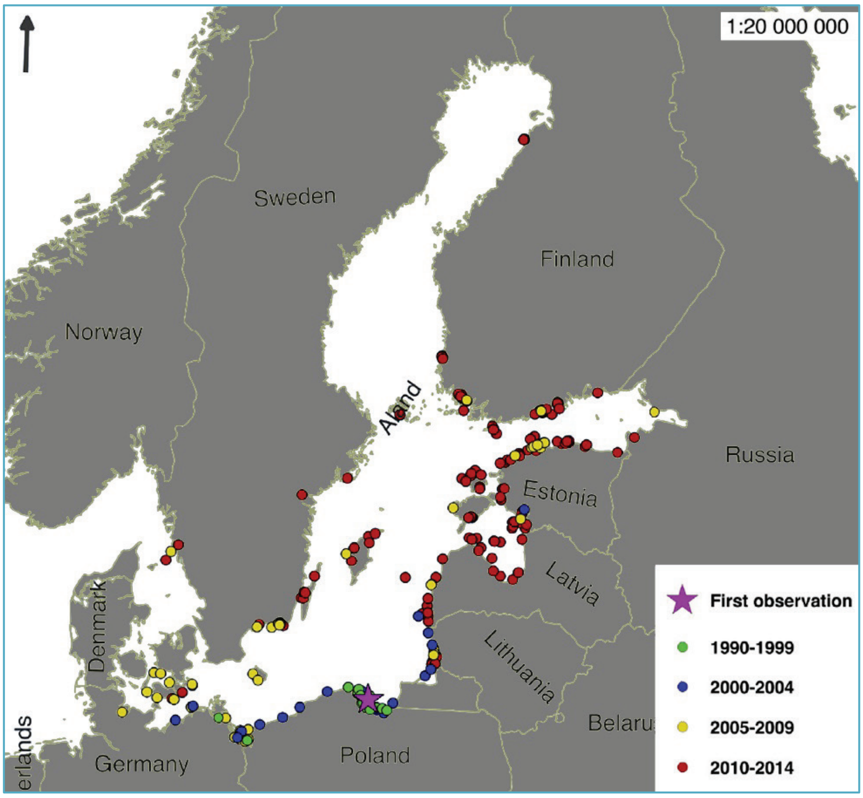


Fig. 2. Dispersal of *N. melanostomus* in the Baltic Sea 1990-2014 (modified from Kotta et al., 2016).

The first *N. melanostomus* specimen found in the Baltic Sea was an adult, implying that the species might have reached the Baltic in the mid- or late 1980's (Skora and Stolarski, 1993, Almqvist, 2008). It was most probably transported to the Baltic Sea and the Great Lakes system as larvae in ballast water (Kornis et al., 2012). This is supported by the high probability of *N. melanostomus* prevalence in areas close to large cargo ports (Kotta et al., 2016) as well as ship traffic in general (Florin et al., 2018). Egg deposits on ship hulls are also believed to be a transport vector, although there is no scientific evidence to support this (Adrian-Kalchhauser et al., 2017). Individuals from the Black Sea can also spread via rivers and canals in Europe (Brown and Stepien, 2008). Longitudinal movement is probably facilitated by human-made rock armor structures along river banks that provides food and shelter (Brandner et al., 2015). By 2014, presence of *N. melanostomus* had been reported from 16 European countries, with no signs of the invasion slowing down (Hôrková and Kováč, 2014).

In Sweden *N. melanostomus* was first found in 2008 in Karlskrona in the south-east, with subsequent findings in Gothenburg and Visby in 2010, 2013 in Muskö south of Stockholm, and 2014 in Kalmarsund. Year 2017 occurrence was reported from Ystad in Skåne (Florin, 2017). The same year it was also found in Kvädöfjärden on the mid-/central Baltic coast (A.-B. Florin, Swedish University of Agricultural Sciences, pers. comm.). In 2016 the first Swedish observation of *N. melanostomus* in freshwater was reported from northern Gotland (Hellström, 2016) and in 2017 one specimen was found in a stream outside Kalmar in south-eastern Sweden (Månsson, 2017).

Variation in life-history strategy in native and non-native *N. melanostomus* populations

Life-history strategy refers to combinations of life-history traits related to growth and reproduction in a population, and the way these are combined to optimize fitness (Jennings et al., 2001). Age or size at maturity linked to growth rate and natural mortality are the main life-history traits that define population dynamics. Further, these traits determine population responses to environmental effects (Domínguez-Petit et al., 2017). Trade-offs between traits affect whether non-indigenous populations can evolve towards being better dispersers, more fast-growing or producing more off-spring in comparison to older, conspecific NIS populations as well as native populations (Phillips et al., 2010 and references therein).

There are two generalized life-history strategies: K-selected and r-selected species. K-selected species fluctuate around the carrying capacity in a usually rather stable environment. Such species are slow-growing, long-lived, and start reproducing relatively late. Ultimately, they produce few, large offspring and are likely to having evolved parental care (Rafferty, 2011a). The r-selected species, on the other hand, are governed by their biotic potential. They are usually found in variable environments where they grow quickly and have short life-spans. They typically start reproducing early and produce off-spring in high numbers in which mortality might be high (Rafferty, 2011b). A species can also display a mix of r- and K-selected traits (Reynolds et al., 2001).

In a population undergoing expansion and invading new areas individuals at the invasion front will encounter more r-selective environments compared to the individuals at the core of the population. Therefore, the invasion front is r-selective and will favor life-history strategies with high reproductive rates (Phillips et al., 2010) as well as short generation times and high growth rates (Sokolowska and Fey, 2011 and references therein). When a population expands its range, it is restricted by its dispersal ability at the edge of the distribution range. This means that only the supreme dispersers of each generation make it to the distribution edge. In addition, the number of conspecifics at the distribution front is lower than in the area of the founding population, and the number of specialist enemies is expected to be low at the distribution front as well. These factors have, in turn, three effects on life-history traits on the invasion front: they promote the evolution of traits that favor increased dispersal and reproductive rates, and, as a trade-off, traits that favor defense against specialized enemies are down-regulated (Phillips et al., 2010). However, divergent life-history strategies leading to successful establishment of NIS may also be the result of genetic diversity or, more likely, phenotypic plasticity and alternative ontogenies (Kovác, 2010). Individuals at early stages of an invasion display more opportunistic life-history strategies (Masson et al., 2016) while individuals at later stages of the invasion process display more specialized life-history strategies, usually resembling those in its area of origin (Kovác, 2010). As shown below, *N. melanostomus* life-history strategy varies in space and time.

Size and age distribution

In the Black Sea specimens can reach 250 mm SL (Pinchuk et al., 2003), while sizes of ~290 mm have been reported but not confirmed (Brown and Stepien, 2008, Gruľa et al., 2012 and references therein). For *N. melanostomus* inhabiting the fresh water of the Great Lakes (<0.5 psu; Casties et al., 2016), maximum length is 180 mm TL (Pinchuk et al., 2003). In the central-European river Danube recorded maximum lengths are 140-160 mm, which is claimed to be typical for non-native *N. melanostomus* populations in freshwater (Gruľa et al., 2012). In the Baltic Sea *N. melanostomus* maximum length is ~250 mm (Skora and Stolarski, 1993, Sokolowska and Fey, 2011), i.e. resembles that in its area of origin (Pinchuk et al., 2003). Growth rates for *N. melanostomus* in its area of origin appear to be slightly lower in comparison to *N. melanostomus* in the Baltic Sea (Skora and Stolarski, 1993). Within the Great Lakes system, higher growth rates in front populations compared to core populations are indicated (Kornis et al., 2016). Most teleost fish have a blood osmolality of ~10.5 psu (Karsiotis et al., 2012). Euryhaline fish have lower energetic costs for metabolic processes and thus display greater somatic growth at intermediate salinities (5-18 psu), i.e. iso-osmotic conditions (Bœuf and Payan, 2001). Accordingly, the highest growth rates for *N. melanostomus* occur in salinities of 5-10 psu in laboratory experiments (Karsiotis et al., 2012, Hempel and Thiel, 2015). Such salinities correlate with natural conditions in the Baltic and Black Sea, where *N. melanostomus* displays its largest maximum size.

Age distribution also varies between populations. In the species native range, maximum age is 5 years (Gruľa et al., 2012 and references therein) while longevity in the Great Lakes has been found to be 5 years in a core population and 2 years in a front population (Kornis et al., 2016). In the Baltic Sea the oldest individuals recorded are 6 (Sokolowska and Fey, 2011) and 7 years old (Azour et al., 2015) and stem from core populations. The maximum age differs potentially because of differences between core/front populations, but differences in age reading cannot be ruled out (Florin et al., 2017). Pronounced differences in size-at-age exist between populations (Table 3).

Table 3. Length (mm) at age in different *N. melanostomus* populations. SL is standard length and TL is total length. a = range of maximum values, b = non-specified values, c = maximum values, d = mean values, e = mean values in two different locations, f = mean values for males and females separated.

Length at age										
		Year								
Area	**Population age**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**SL/TL**	**Reference**
Area of origin (Sea of Azov) (a)	N.A.	50/70	99/120	116/140	123				SL	(Simonovic et al., 2001 and references therein)
Area of origin (Caspian Sea) (b)	N.A.		45	95					SL	(Simonovic et al., 2001 and references therein)
Danube River (c)	Not defined	42	77	93					SL	(Simonovic et al., 2001)
Danube River (d)	1-2 years	33	62	73	105				SL	(Gruľa et al., 2012)
Danube River (d)	5-7 years	26	53	67	82				SL	(Gruľa et al., 2012)
Great Lakes (Lake Huron) (d)	8 years	31.4/41.5	49.9/61.4	63.3/74.9	80.9/87.6				SL	(French and Black, 2009)
Baltic Sea (Gulf of Gdansk) (e)	16-17 years			119/94	136/125	146/133	155/144	209/175	TL	(Sokolowska and Fey, 2011)

N. melanostomus in the Gulf of Gdansk displays greater size-at-age than fish from newly established populations in fresh water (Table 3). This can however be influenced by the method, as measurements of TL yields larger sizes than SL. Age estimations can also vary greatly depending on age reading method and reader (Florin et al., 2017), thus potentially over- or underestimating the ages shown in Table 3. In the Danube River, sampled twice, *N. melanostomus* size had decreased with time since establishment. Instead the allometric growth was positive in the second sampling occasion, indicating that there was in fact a re-allocation of resources from reproduction to somatic growth in the longer established population (Gruľa et al., 2012).

In conclusion, reports of maximum size, growth rates, age and size-at-age differ for the areas studied. Contradictory reports can most likely often be ascribed to differences in methodology; see section "Outlining of hypotheses, knowledge gaps and future outlook" below.

Reproductive features

In their native range *N. melanostomus* females reach maturity at age 2-3 years, while males mature at age 3-4 years (MacInnis and Corkum, 2000 and references therein). In front populations in the Great Lakes females mature at age 1-2 years (MacInnis and Corkum, 2000, Kornis et al., 2016), while in a core population maturity-at-age for females is 2.4 years (Kornis et al., 2016). This differs slightly from the Danube River, with maturity-at-age of 1.29 in a front population and 1.36 in a core population (both sexes pooled; Gruľa et al., 2012). However, discrepancies in life-history traits can possibly be ascribed to differences in environmental conditions between sites rather than invasion-front effects (Kornis et al., 2016) or to differences in age reading methodology (Florin et al., 2017). No information about *N. melanostomus* maturity-at-age in the Baltic Sea has been found in the literature.

In the Black and Caspian Seas *N. melanostomus* spawns from 2-3 to 5-6 times per season (Marsden et al., 1997 and references therein, Hôrková and Kováč, 2014). In non-native populations, two spawning events per season is the most common (Almqvist, 2008, Hôrková and Kováč, 2014, Hempel, 2017) although 3 to 4 spawning events have also been recorded (MacInnis and Corkum, 2000, Leslie and Timmins, 2004). The onset of spawning is temperature-regulated (Almqvist, 2008 and references therein). It starts during spring (Marsden et al., 1997 and references therein, MacInnis and Corkum, 2000, Hôrková and Kováč, 2014) and can in the Baltic Sea go on until September (Tomczak and Sapota, 2006) with peaks in May and July (Almqvist, 2008).

Baltic Sea *N. melanostomus* produces more eggs compared to in the Great Lakes and conspecifics in the area of origin (Table 4). Since egg production is size dependent (MacInnis and Corkum, 2000, Tomczak and Sapota, 2006, Almqvist, 2008), the higher egg production in the Baltic Sea is in line with the higher maximum lengths recorded in this area (Table 3). No information has been found in the literature about whether *N. melanostomus* is a determinate or indeterminate spawner, and thus the estimated egg production in Table 3 is not recommended for calculations of total or relative fecundity.

Table 4. *N. melanostomus* egg production in different areas.

Area	**Population age**	**Egg production (min-max)**	**Reference**
Area of origin	N.A.	328-5221*	(MacInnis and Corkum, 2000 and references therein)
Kiel Canal	5-6 years	457-3203*	(Hempel, 2017)
Great Lakes (St. Clair River)	4-10 years	800-1200**	(Leslie and Timmins, 2004)
Great Lakes (Detroit River)	6 years	252-1818**	(MacInnis and Corkum, 2000)
Baltic Sea (Gulf of Gdansk)	<5 years	2700-3000*	(Leslie and Timmins, 2004 and references therein)
Baltic Sea (Gulf of Gdansk)	9-10 years	94-2190**	(Tomczak and Sapota, 2006)
Baltic Sea (Gulf of Gdansk)	13-16 years	448-3123**	(Almqvist, 2008)

*Unknown if values are estimated or factual

**Estimated, several batches

Females at the invasion front have been shown to display smaller oocytes, overall higher fecundity and smaller size at maturity in comparison to native populations. Additionally, prolonged spawning periods have been recorded in new populations, potentially in order to compensate for lower offspring fitness and thus maximizing the chances of reproductive success. Since newly established populations display low genetic variation due to a founder/bottleneck effect, the differences in life-history strategy are presumably related to phenotypic plasticity (Hôrková and Kováč, 2014).

N. melanostomus in the food web

N. melanostomus *as predator*

N. melanostomus is an opportunistic predator feeding on several taxa (Kornis et al., 2012). This strategy is probably advantageous for successful establishment, since introduced species often encounter novel prey species composition and abundance patterns compared to in their native ranges (Grosholtz and Ruiz, 1996). *N. melanostomus* is morphologically predisposed to feed on molluscs. Its muscular jaw and gullet are used for biting off molluscs attached to a substrate, and the pharyngeal teeth are used for crushing shells (Pinchuk et al., 2003). Consequently, *N. melanostomus* feeds to a large extent on bivalves, as shown below.

Diet choice of *N. melanostomus* has been shown to vary with substrate, water clarity and prey motility (Diggins et al., 2002) as well as habitat (Ustups et al., 2016). This means that local conditions are probably important for structuring of *N. melanostomus* diet (Foley et al., 2016). There is also evidence that *N. melanostomus* diet varies over the season (Skora and Rzeznik, 2001, Skabeikis and Lesutienė, 2015, Hempel, 2017). Further, feeding activity partly depends on sex. Adult females feed the least prior to and during spawning, while males feed the least during spawning. Both sexes then feed actively post spawning (Skabeikis and Lesutienė, 2015). Gobies in general show peaks in feeding intensity at dusk and dawn (Zander, 2011). However, time of the day has no significant influence on *N. melanostomus* feeding intensity (Vsetickova et al., 2015).

Ponto-Caspian area

In its area of origin *N. melanostomus* feeds primarily on molluscs, mainly dreissenids (Nellbring, 2014) such as *Dreissena polymorpha*, and then in descending order on polychaetes, crustaceans and fish (Skora and Rzeznik, 2001 and references therein). Also worms, insects and detritus can make up part of the diet (Nurkse et al., 2016 and references therein).

Great Lakes

In the Great Lakes, non-indigenous dreissenids are common prey for *N. melanostomus* (e.g. Ray and Corkum, 1997, Corkum et al., 2004), but the picture of dreissenids as the main food source has become more nuanced since the 1990's. Stable isotope analyses reveal that the importance of dreissenids is lower than what can be expected from stomach content analyses. Instead, *N. melanostomus* may exert a heavy predation pressure on the soft-bodied benthic community in the Great Lakes (Brush et al., 2012). However, large *N. melanostomus* feeds to a great extent on dreissenids, meaning that it is dependent on energy from pelagic pathways. *N. melanostomus* can also exploit different production pathways in different areas (Foley et al., 2016). Other prey ingested by *N. melanostomus* are snails, mayflies, soft-shelled crayfish and zooplankton. Also chironomids, dragonflies, amphipods, isopods, fish eggs and fish larvae can be part of *N. melanostomus* diet in this area (Ray and Corkum, 1997, Corkum et al., 2004).

Laboratory studies from the Great Lakes show that *N. melanostomus* readily consumes novel food types (Chotkowski and Marsden, 1999) and confirm *N. melanostomus'* preference for bivalves (e.g. Ray and Corkum, 1997, Naddafi and Rudstam, 2014). *N. melanostomus* also feeds on fish eggs, which provide a lipid-rich, high-energy food resource, particularly during winter when *N. melanostomus*' reserves are depleted after spawning and nest-guarding (Chotkowski and Marsden, 1999). *N. melanostomus* has been found to predate on *Salvelinus namaycush* (lake trout) eggs in aquaria experiments (Fitzsimons et al., 2006), and efficiently so in competition with *Cottus bairdi*, mottled sculpin (Chotkowski and Marsden, 1999). Also eggs of other commercially important species are being predated upon: under natural conditions eggs from *Acipenser fulvescens* (lake sturgeon) and *Micropterus dolomieu* (smallmouth bass) (Kornis et al., 2012) and under experimental conditions eggs from *Pimephales promelas* (fathead minnow) (Almeida et al., 2016). For *P. flavescens* (yellow perch) eggs under experimental conditions, *N. melanostomus* is deterred by the skein, i.e. the gelatinous skin enclosing the eggs, but readily feeds on eggs without the skein. This could indicate that actual *N. melanostomus* predation on *P. flavescens* eggs in the field, where the eggs are usually found in skeins, is low (Almeida et al., 2016). Additionally, *N. melanostomus* males feed on eggs from conspecifics, including their own eggs when brood size is small (Meunier et al., 2009).

Baltic Sea

In the Baltic Sea, *N. melanostomus* diet is diverse and seems to vary according to prey availability. Zooplankton (i.e. copepods) and meiobenthic organisms are the dominating prey in *N. melanostomus* < 50 mm (Skabeikis and Lesutienė, 2015, Ustups et al., 2016). In bigger fish, gastropods and mussels are popular prey (Azour, 2011, Puntila, 2016, Herlevi et al., 2017). Crustaceans such as mysids, amphipods and decapods are regularly ingested by *N. melanostomus* (Skabeikis and Lesutienė, 2015, Ustups et al., 2016, Hempel, 2017) and also isopods can contribute significantly to the food base (Sapota, 2004, Almqvist, 2008). Further, aquatic insects such as chironomids can from time to time be a very common prey (Rakauskas et al., 2013).

An ontogenetic shift from soft-bodied benthic organisms to larger shelled prey occurs at around 100-150 mm length (Puntila, 2016, Ustups et al., 2016, Oesterwind et al., 2017). This is in contrast with many other fish species, which often feed on small and immobile prey as juveniles and switch to larger, mobile prey as they grow older. The increase in feeding on larger shelled prey with age is probably the result of the ability of larger gobies to pick and break the shells of molluscs and a more sedentary life-style of adult fish (Skora and Rzeznik, 2001). Also increased gape width and height is important as it otherwise limits prey size (Skabeikis and Lesutienė, 2015).

All four native mussel species in the Baltic Sea, *Mytilus* spp., *M. balthica*, *Mya arenaria* (sand gaper) and *Parvicardium* spp., are common prey for *N. melanostomus* (Skora and Rzeznik, 2001). In some areas *Mytilus* spp. and *M. balthica* make up the major proportion of its diet (Skora and Rzeznik, 2001, Sapota, 2004, Almqvist, 2008, Skabeikis and Lesutienė, 2015, Puntila, 2016). The introduction of *N. melanostomus* has been linked to decreasing numbers of *Mytilus* spp. in Latvian and

Lithuanian waters (Skabeikis and Lesutienė, 2015 and references therein, Larsson, 2016 and references therein). Interestingly, in contrast to in its native area and in the Great Lakes, only one study reports *D. polymorpha* in *N. melanostomus* stomach content (Skabeikis and Lesutienė, 2015). The distribution of *D. polymorpha*, which is also an invasive species, overlaps to a large extent with *N. melanostomus* distribution (Werner et al., 2012, Kotta et al., 2016), and it thus seems that *N. melanostomus* prefers to prey upon native mussel species.

Prey species preference varies between studies. *N. melanostomus* has been reported to prefer small *Mytilus* spp. over large *M. balthica* (Schrandt et al. 2016). However, Karlson et al. (2007) found no preference for either *Mytilus* spp. or *M. balthica*. Furthermore, *N. melanostomus* displays no clear preference for a particular taxon when given the opportunity to choose between bivalves and one amphipod species (Nurkse et al. (2016). However, juveniles in the Gulf of Gdansk prefer *M. arenaria.* The discrepancy in diet between juveniles and adults has been linked to habitat preferences. Adults are mainly found in complex environments with large stones and concrete structures that can be used as nests or hiding places. In these environments *Mytilus* spp. can occur in large numbers. Juveniles, on the other hand, prefer habitats with loose stones and gravel where *M. arenaria* is common (Skora and Rzeznik, 2001).

Mussels dominate *N. melanostomus* diet in many areas, but there are exceptions. The most pronounced deviations from the mussel-feeding pattern are reported from the western and northernmost parts of the Baltic Sea (Puntila, 2016, Herlevi et al., 2017). Gastropods are particularly common in the diet in areas where mussel-feeding is less pronounced (Azour, 2011, Puntila, 2016, Herlevi et al., 2017). In the western-most parts of the Baltic Sea also *Palaemon* spp., shrimp, is frequently found in the diet, and *N. melanostomus* in this area may compete with the local shrimp fishery (Azour, 2011). In the northernmost part of the Baltic Sea, barnacles are actively selected for by *N. melanostomus* of all size classes (Puntila, 2016). The reason for the lower consumption of bivalves is unknown, but as salinities are higher in the western parts of the Baltic Sea the *Mytilus* spp. specimens there are of intermediate sizes, compared to the smaller specimens with thin shells found further to the north-east (Kautsky et al., 1990). The more robust *Mytilus* spp. in the west may be more challenging for *N. melanostomus* to chew, digest and dispose, and thus constitute a less desirable food item. However, this explanation is not valid for the northernmost parts of the Baltic Sea. Salinities in the northern Baltic Proper are 5-6 psu (Bernes, 2005) and as a result, *Mytilus* spp. displays a dwarf form and low growth down to its absolute minimum of salinity requirements (4.5 psu; Riisgård et al., 2014). Therefore, it is possible that these small mussels contain too little energy for being consumed.

The presence of polychaetes in stomach content varies. Polychaetes are actively deselected for by *N. melanostomus* in some areas (Puntila, 2016) but very popular prey in other places (Skora and Rzeznik, 2001, Ustups et al., 2016, Bublys et al., 2017, Oesterwind et al., 2017). Barnacles are occasionally found in *N. melanostomus* stomach content. They may either be ingested by mistake, growing on the shells of *Mytilus* spp. (Skora and Rzeznik, 2001), or actively selected for (Puntila, 2016).

N. melanostomus also preys on fish, both conspecifics (Azour, 2011, Skabeikis and Lesutienė, 2015, Herlevi et al., 2017) and other species such as *Osmerus eperlanus* (smelt), *Pomatoschistus minutus* (sand goby) and 0-gr *Clupea harengus* (herring; Skabeikis and Lesutienė, 2015, Bublys et al., 2017, Hempel, 2017). However, Oesterwind et al. (2017) concluded that *N. melanostomus* predation pressure on native fish is negligible, and it has also been suggested that *N. melanostomus* may scavenge on dead fish rather than actively prey upon it (Bublys et al., 2017). Under experimental conditions *N. melanostomus* predates upon juvenile *P. flesus/P. solemdali* (Schrandt et al., 2016), but whether this is the case also in the field is not clear.

Stable isotope analyses reveal that the mean trophic level of *N. melanostomus* decreases with size in the Baltic Sea, which is uncommon in fish. This is ascribed to the fact that polychaetes, on a higher trophic level, are common prey for small *N. melanostomus*, while *Mytilus* spp., on a lower trophic level, are more important prey for large *N. melanostomus* (Karlson et al., 2007, Almqvist, 2008). Isotope analyses further show that nitrogen isotope levels are similar for *N. melanostomus* and *P. flesus/P. solemdali* of the same sizes (Karlson et al., 2007). Trophic position may also vary with time since *N. melanostomus* establishment or merely the prey community available. In a more recently established population, ontogenetic shifts and potential availability of more nutritious prey may explain higher trophic position compared to in an older population (Herlevi et al., 2018).

N. melanostomus ***as prey***

NIS in newly invaded areas have often left their native enemies behind. Only the most generalist predators, which are able to switch prey immediately, will exert impact on the NIS from the point of introduction (Phillips et al., 2010). More often predation on NIS becomes more pronounced after a time lag (Simberloff, 2013). Native predators benefit from NIS, both at the population level and for individual specimens, only when the novel prey species is embedded in the prey community and does not make up the entire food base. The NIS may therefore constitute a valuable supplementary food resource (Pintor and Byers, 2015).

N. melanostomus lacks defense against predation such as chemical protection or specific morphological structures, which probably makes it a rather easy target unless it seeks refuge (Almqvist et al., 2010). However, predator gape size limitation makes big *N. melanostomus*, with large heads, rather difficult to swallow (Truemper and Lauer, 2005). Therefore larger individuals find shelter in body size and form, given that smaller individuals are probably selected for. The lipid content of *N. melanostomus* is lower but protein content higher than those of e.g. *C. harengus* and *P. fluviatilis* (Melvere et al., 2017). The nutritional value of *N. melanostomus* probably varies with metabolic activity over seasons and is most likely ecosystem dependent, as *N. melanostomus* diet can vary significantly between areas.

Ponto-Caspian area

In its native area, both benthic species, such as *S. maximus* (turbot), *Acipenser* sp. (sturgeon) and *P. flesus luscus* (flounder) (Bănaru and Harmelin-Vivien, 2009), and pelagic species like *P. fluviatilis*, *S. salar* and *Sander lucioperca* (pike-perch)

(Corkum et al., 2004 and references therein) feed on *N. melanostomus*. In addition, *Tursiops truncates,* Black Sea bottlenose dolphin, and *Phocoena phocoena relicta,* harbor porpoise, utilize *N. melanostomus* as prey (Gladilina and Gol'din, 2014, Oesterwind et al., 2017 and references therein).

Great Lakes

In the Great Lakes, there is some evidence for predatory control of *N. melanostomus* (Kornis et al., 2012) as it has become an important prey to a wide range of species. The most notable ones are *Lota lota* (burbot), *P. flavescens*, *M. dolomieu* (Kornis et al., 2012), *S. namaycush* (Dietrich et al., 2006, Fitzsimons et al., 2009), *Nerodia sipedon* (watersnake; King et al., 2006) and *Phalacrocorax auritus* (double-crested cormorant). It is estimated that *L. lota* annually consumes 61% of the standing stock of *N. melanostomus* in Lake Erie. The predation has partially stabilized the *N. melanostomus* population in the area (Kornis et al., 2012). In addition, *P. flavescens* locally feeds on *N. melanostomus* to a large extent. Around 30% of *P. flavescens* diet can consist of *N. melanostomus* (Johnson et al., 2005). Gape size restricts which sizes that are chosen, although *P. flavescens* appears to choose smaller prey than what is theoretically possible (Truemper and Lauer, 2005).

Further, *M. dolomieu* in some areas relies heavily on *N. melanostomus* as prey. It can constitute almost 100% of *M. dolomieu* diet (Nelson et al., 2017). The condition of *M. dolomieu* has improved in these areas since *N. melanostomus* establishment, particularly in the smaller size classes. Habitat overlap is suggested to be one of the major mechanisms behind *M. dolomieu's* utilization of *N. melanostomus* as prey (Crane et al., 2015). In addition, *S. namaycush* feeds on *N. melanostomus*. Four to five years after detection *N. melanostomus* was one of the most common prey for *S. namaycush* in eastern Lake Ontario (Dietrich et al., 2006, Fitzsimons et al., 2009). Introduction of *N. melanostomus* has created a new energetic pathway from benthos to top predators. This has replaced the disrupted pathway *Diporeia* (amphipod)-*Cottus cognatus* (slimy sculpin)-*S. namaycush* after the decline of *Diporeia*, which was caused by the introduction of dreissenid mussels (Dietrich et al., 2006).

For the previously threatened *N. sipedon* in Lake Erie, establishment of *N. melanostomus* has led to an almost complete diet shift. Within two generations after introduction, >92% of *N. sipedon* diet consisted of *N. melanostomus*. The change in diet has had positive effects on the growth rate and body size of all size classes of *N. sipedon* (King et al., 2006). The *N. sipedon* population is now considered stable and its status as "threatened" was removed in 2011 (U.S. Fish and Wildlife Service, 2011). *N. melanostomus* further serves as important prey for *P. auritus*, which learned to feed on the species very rapidly after the introduction (Johnson et al., 2008). In northern Lake Michigan *N. melanostomus* together with two other NIS (*Alosa pseudoharengus,* alewife, and *Morone americana,* white perch) make up the major proportion of the *P. auritus* diet (Madura and Jones, 2016). Also in the Niagara River *P. auritus* predates upon *N. melanostomus* to a great extent. Prey sizes vary over seasons, but generally there is a skewedness towards bigger individuals (Coleman et al., 2012). It is noteworthy that in the Great Lakes, *P. auritus* and *S. namaycush* diets show less or no seasonal variation after *N. melanostomus* introduction (Johnson et al., 2008, Fitzsimons et al., 2009). This is probably due to all-year-round occurrence of *N. melanostomus* (Johnson et al., 2008).

Baltic Sea

In the Baltic Sea, *N. melanostomus* constitutes an abundant food source to a range of piscivores. After introduction it has in some areas become the most important prey for *P. fluviatilis* (Almqvist et al., 2010, Liversage et al., 2017, Oesterwind et al., 2017). The importance of *N. melanostomus* as prey increases with *P. fluviatilis* size (Almqvist et al., 2010, Liversage et al., 2017). Habitat structure seems to restrict *P. fluviatilis* predation on *N. melanostomus*, as predation declines in areas with high macrophyte coverage and soft sediment. They can both potentially act as refuge for *N. melanostomus*; e.g. the sediment particles can blur visibility when suspended. *N. melanostomus* density only affects *P. fluviatilis* predation rates to a limited extent. This indicates that *N. melanostomus* is over-abundant and that *P. fluviatilis* is "satiated" in some areas (Liversage et al., 2017). The conclusion contrasts with earlier results, showing that *P. fluviatilis* could potentially control the *N. melanostomus* population (Järv et al., 2011). The discrepancy between the studies, despite similar sampling area, sampling methods and time of sampling, indicates that conditions have changed over time and that *N. melanostomus*, presumably, is now more numerous.

Further, *N. melanostomus* is now locally a common (Rakauskas et al., 2013) or the most common prey species for *S. lucioperca* (Hempel et al., 2016, Oesterwind et al., 2017) in the Baltic Sea. The marked diet shift has led to higher growth rates and better condition in *S. lucioperca*, post-invasion. The predation pressure is believed to be high enough to locally affect *N. melanostomus* abundance (Hempel et al., 2016). Also *Gadus morhua* (cod) predates upon *N. melanostomus*. *G. morhua* diet has changed significantly over time. In the Gulf of Gdansk, clupeids have decreased in importance, and *N. melanostomus* and *Crangon crangon* (common shrimp) are now the most common prey (Almqvist et al., 2010). With *N. melanostomus* introduction, a shift from pelagic prey towards benthic prey occurred (Almqvist, 2008, Almqvist et al., 2010) and consequently, a new energetic pathway from mussels to *P. fluviatilis* and *G. morhua* has emerged. Since the introduction of *N. melanostomus, P. fluviatilis* and *G. morhua* share the same food resource and are thus now on the same trophic level (Almqvist et al., 2010). Also *Anguilla anguilla* (European eel) predates on *N. melanostomus* (Albrektsen, 2017, Hempel, 2017) and appears to grow faster in comparison to conspecifics from areas where *N. melanostomus* is absent (Albrektsen, 2017). *A. anguilla* is probably a very efficient predator as it is able to penetrate small interstitial spaces in e.g. rocky substrates where *N. melanostomus* is hiding (Hempel, 2017). Further, *E. lucius* (pike) feeds on *N. melanostomus* in southern Sweden (own observations). In addition, anecdotal reports exist of *Myoxocephalus scorpius* (shorthorn sculpin), *L. lota* (Puntila et al., 2018) and *S. maximus* (Sapota and Skora, 2005) feeding on *N. melanostomus*. Also *S. trutta* and *Natrix natrix* (grass snake; J. Hedlund, angler, private contact) have been observed to ingest *N. melanostomus*, which is well in line with the above reviewed studies from the Great Lakes.

Not only fish prey on *N. melanostomus* in the Baltic Sea. Both *Halichoerus grypus* (grey seal) and *Phoca vitulina* (harbour seal) predate on *N. melanostomus* in the south-western Baltic Sea (Scharff-Olsen et al., 2018). Further, *Phalacrocorax carbo* (great cormorant) and *Ardea cinerea* (grey heron) have both learned to utilize *N. melanostomus* as prey (Jakubas, 2004, Bzoma and Meissner, 2005, Jakubas and Manikowska, 2011, Rakauskas et al., 2013, Ovegård et al., 2016, Oesterwind et al., 2017). In the Gulf of Gdansk, both the *P. carbo* and *A. cinerea* populations increased rapidly in the 1990's and early 2000's. The increase coincided with the establishment and expansion of *N. melanostomus* in the area (Jakubas, 2004, Bzoma and Meissner, 2005, Jakubas and Manikowska, 2011). After stabilization of the *N. melanostomus* population the frequency in the *A. cinerea* diet has decreased. It is now partly replaced in the diet by *Gasterosteus aculeatus* (three-spined stickleback) and juvenile salmonids (Jakubas and Manikowska, 2011). During the cormorant breeding season, *N. melanostomus* is now a major prey in southern Sweden, while clupeids, *Rutilus rutilus* (roach) and *Zoarces viviparus* (eelpout) have decreased in importance. Locally, *N. melanostomus* also appears to have replaced *G. morhua* in the diet (Ovegård et al., 2016).

The proportion of *N. melanostomus* in predator diets is more pronounced in spring/summer in the Baltic Sea (Almqvist et al., 2010, Hempel et al., 2016). However, it is not clear if the higher calorific content of *N. melanostomus* during spawning in spring/summer is the primary cause for this preference or whether it is a spatial overlap that leads to increased predation (Hempel et al., 2016).

N. melanostomus *as competitor*

Competition is an ecological interaction which benefits neither of two or more individuals or species (Levin, 2009). Interference competition is a direct interaction meaning that one part fights or intimidates the other part to secure resources. Resource competition on the other hand means that one part exploits resources to such an extent that the other part is negatively affected. For NIS in particular, resource competition with indigenous species have in many cases led to replacement of those native species (Simberloff, 2013). When competing for resources (i.e. food or space), *N. melanostomus* appears to be the stronger competitor, as reviewed below. Rather, competition appears to be negative, or at best without consequences, for the competing species. However, competitive strength varies with abiotic factors such as environmental gradients, and with biotic factors such as life stages and abundances (Cuda et al., 2015).

Ponto-Caspian area

N. melanostomus food competition in the Black Sea appears to be limited. A dietary overlap occurs with other species, but the two most common prey groups, polychaetes and *Sprattus sprattus* (sprat) are overly abundant due to high biological production. Therefore, food competition does not seem to restrict *N. melanostomus* in its native area (Bănaru and Harmelin-Vivien, 2009).

Great Lakes

In the Great Lakes *N. melanostomus* has become a successful competitor to *P. flavescens*, both in terms of food and space (Houghton, 2015). Considerable dietary overlap also occurs between *N. melanostomus* and *Etheostoma caeruleum* (rainbow darter). This may be the reason for a population decline in the St. Clair River at the time of *N. melanostomus* establishment. There is also a large dietary overlap between *N. melanostomus* and *Ambloplites rupestris* (rock bass), but no negative consequences have been detected so far. Further, *N. melanostomus* competes for food with *Percina caprodes* (logperch) and *Percopsis omiscomaycus* (trout-perch). The competition has probably increased over time, as *P. caprodes* and *P. omiscomaycus* have gradually started to consume *Dreissena bugensis* (quagga mussel), which is a favored prey item for *N. melanostomus* (Burkett, 2013). In experimental trials *N. melanostomus* is very aggressive towards *C. bairdi*, indicating that they may compete successfully under natural conditions (Dubs and Corkum, 1996).

Baltic Sea

After the introduction of *N. melanostomus,* a dietary shift has occurred for juvenile *S. maximus* and *P. flesus/solemdali*, enhancing food competition for both (Ustups et al., 2016). For adult *N. melanostomus* there is an overlap in diet with *P. flesus/P. solemdali*, as they both feed on *Mytilus* spp. and *M. balthica* to a great extent (Karlson et al., 2007). The overlap, however, varies with *P. flesus/P. solemdali* size (Karlson et al., 2007, Järv et al., 2011) and over the season (Karlson et al., 2007). *P. flesus/P. solemdali* is, at least during part of the season, forced to utilize suboptimal food resources due to *N. melanostomus* competition (Karlson et al., 2007).

In some Baltic Sea areas *N. melanostomus* dietary overlap with *P. fluviatilis* seems to be limited (Järv et al., 2011), while in other areas it may be more pronounced (Herlevi et al., 2018). Despite differences in size, *N. melanostomus* in the Baltic Sea may also compete for food with *P. minutus*, as they utilize largely the same resources: *Ostracoda*, the amphipod *Corophium volutator,* the mysid *Neomysis integer* and *M. balthica* (Aarnio and Bonsdorff, 1993, Ustups et al., 2016). *N. melanostomus* also exhibits a large dietary overlap with *Gymnocephalus cernuus* (ruffe) as indicated by stable isotope analysis, probably because they exploit the same habitat type (Rakauskas et al., 2013). *N. melanostomus* further competes for food with *Platessa platessa* (plaice), *Gobius niger* (black goby), *Z. viviparous*, *A. anguilla* (Skora and Rzeznik, 2001), *R. rutilus* and juvenile *Vimba vimba* (vimba bream; Skora and Rzeznik, 2001, Oesterwind et al., 2017). Trophic overlap may, however, be hindered due to spatial separation of the molluscs preyed upon, as suggested for missing competition between *N. melanostomus* and *R. rutilus* respective *V. vimba* (Rakauskas et al., 2013).

Further, the mussel feeding ducks *Clangula hyemalis* (long-tailed duck) and *Somateria mollissima* (common eider) (Stempniewicz, 1995, HELCOM, 2013) may compete with *N. melanostomus* for food. This assumption is supported by a decrease in *Mytilus* spp. abundance and the numbers of over-wintering *C. hyemalis* in Lithuania coinciding with the rapid increase of *N. melanostomus* in the area (Larsson, 2016).

Intraspecific competition is believed to be less pronounced in newly established populations due to greater access to prey and territory, while individual specialization is probably greater in older populations in order to reduce intraspecific competition (Herlevi et al., 2018). Under experimental conditions *N. melanostomus* intraspecific competition has been shown to reduce inter-specific competition. An important lesson learned is that NIS are not necessarily less harmful at lower densities (Kornis et al., 2014). It is also possible that intraspecific competition can be a driving force for expansion to new areas.

There can also be competition for space. Catch data from the Gulf of Gdansk shows an inverted depth distribution between *N. melanostomus* and *P. flesus/P. solemdali,* suggesting *N. melanostomus* restricting *P. flesus/P. solemdali* habitat utilization (Karlson et al., 2007). In southern Sweden competition for space between *N. melanostomus* and *P. flesus/P. solemdali* seems to occur, as *P. flesus/P. solemdali* has abandoned areas where *N. melanostomus* is now common (P. Månsson, commercial fisher, private contact). Under experimental conditions *N. melanostomus* competes for space with *P. minutus* (Kinyanjui et al., 2017). Such competition may also take place under natural conditions and likely with other gobiids such as *Pomatoschistus microps* (common goby) and *G. niger,* and/or *Z. viviparous* (Corkum et al., 2004).

Other ecosystem effects of *N. melanostomus* occurrence

Trophic cascades

The introduction of *N. melanostomus* has been hypothesized to cause trophic cascades in the Gulf of Gdansk. It could, in theory, release predator pressure on *S. sprattus* from great cormorants, leading to increased predation by sprat on zooplankton. A decrease in zooplankton levels has resulted in increasing levels of phytoplankton (Olenin et al., 2017), but the cause of the decrease is not completely understood. However, increasing levels of phytoplankton can be even more pronounced as *N. melanostomus* locally exerts a high predation pressure on molluscs (Olenin et al., 2017). In the Great Lakes *N. melanostomus* predation on invertebrate grazers increases algal biomass, and thus ultimately affects the entire ecosystem (Kipp and Ricciardi, 2012).

Parasites

The Baltic Sea *N. melanostomus* hosts rather few parasite taxa: from 21 (Ojaveer et al. 2017b) up to 34 (Herlevi et al., 2017) *vs.* 71 taxa in its native range (Herlevi et al., 2017). In general *N. melanostomus* infection rates are intermediate in the Baltic Sea, but there are exceptions. In the south-eastern Baltic Sea infection rates are low, potentially due to very low occurrence of gastropods in *N. melanostomus* diet in this area (Herlevi et al., 2017). In contrast, *N. melanostomus* from the north-eastern Baltic Sea displays infection rates close to 100%, with *Diplostomum* spp. (eye fluke) dominating the parasite assemblage (Ojaveer et al., 2017b). *Diplostomum* spp. is also very common in *N. melanostomus* from the western Baltic proper, with a prevalence of 90-100%. It appears that the parasite weakens *N. melanostomus* anti-predator behavior to increase the chances of it being eaten by an avian predator, i.e. its final host (Flink et al., 2017). No non-native parasites have been detected in *N. melanostomus* in the Baltic Sea. Instead, the parasites infesting *N. melanostomus* in the Baltic Sea are generalists usually infecting native species. It is hypothesized that part of the invasion success of *N. melanostomus* is related to enemy release (Herlevi et al., 2017).

In European inland waters *N. melanostomus* may carry the eel swim bladder parasite *Anguillicoloides crassus*. *A. anguilla* predation on *N. melanostomus* may explain higher levels of parasite infection in the Kiel Canal compared to in nearby waters where *N. melanostomus* has not yet established (Hempel, 2017). The introduction of *N. melanostomus* and *Proterorhinus semilunaris* (tubenose goby) in European rivers has also increased the transmission rates of the trematode *Bucephalus polymorphus* to *S. lucioperca* in comparison to transmission rates from the native *Abramis bjoerkna* (white bream). The growing goby populations in the area provide *S. lucioperca* with new food sources and the parasites with new intermediate hosts. However, parasites that develop in the non-native gobies display, after transmission to *S. lucioperca*, higher mortality, delayed maturity and lower egg production. This indicates that the higher transmission rates are to some degree balanced out by lower parasite fitness (Ondrackova et al., 2015).

In the Great Lakes, the introduction of *N. melanostomus* may have had a positive impact on native fauna regarding the occurrence of *Diplostomum* spp.. Within two years after *N. melanostomus* invasion in the St. Lawrence River, the prevalence of *Diplostomum* spp. in three native fish species had decreased abruptly, in one species with around 80%. Concurrently, infection rates remained the same in areas where *N. melanostomus* abundances were low. It thus seems as *N. melanostomus*, with lower infection rates than native species, has diluted the parasite load and released native species of at least some of the parasite pressure in this area (Gendron and Marcogliese, 2017).

Spawning interference

N. melanostomus has been found to have a negative impact on *C. bairdi* spawning under experimental conditions. *N. melanostomus* successfully chases away nest-guarding *C. bairdi* males, eats the eggs and displays dark coloration, indicating that *N. melanostomus* utilizes the nests for its own spawning. Most likely this also applies under natural conditions as indicated by an abrupt decrease of *C. bairdi* after *N. melanostomus* establishment in the Great Lakes, while other interference mechanisms investigated did not seem to have as profound impacts (Janssen and Jude, 2001).

Hybridization

So far, only three cases of hybridization between *N. melanostomus* and another goby species from the Ponto-Caspian region, *Neogobius fluviatilis* (monkey goby), have been reported. One hybrid was found in 1970 in the species' area of origin (Pinchuk et al. 2003), while two hybrids have later been identified in the River Rhine (Lindner et al., 2013).

Diseases

Outbursts of avian botulism have increased in frequency in the Great Lakes since around the year 2000. *N. melanostomus* is a probable vector. It appears to be susceptible to the *Clostridium botulinum* toxin type-E and spends its time close to the lake bottom, where the toxin is found. Infected fish display a behavior that make them easy targets for seabirds (Yule et al., 2006). Infected birds often have *N. melanostomus* in the stomach content, although water levels and temperature also seem to affect bird infection rates (Kornis et al., 2012). *N. melanostomus* is also a carrier of the viral hemorrhagic septicemia (VHS) virus in the Great Lakes. It is not known whether it passes the virus on to predators, but this cannot be ruled out (Kornis et al., 2012).

Biomagnification

The introduction of *N. melanostomus* has created new energetic pathways between benthos and top predators (Almqvist et al., 2010, Dietrich et al., 2016). It may lead contaminants from the benthic community upwards in the food web to top predators, including humans (Almqvist et al., 2010, Coleman et al., 2012). The ecosystem and the type of contaminant probably determines to which extent toxins are biomagnified. However, *N. melanostomus* itself appears to be rather tolerant to several pollutants, e.g. petroleum, mercury and radioactive calcium, in comparison to other species (Pinchuk et al., 2003). In Lake Erie, lead levels in *M. dolomieu* decreased after the introduction of *N. melanostomus*. This could be either due to *M. dolomieu* change in diet after *N. melanostomus* introduction, with lower lead levels in benthic than pelagic energetic pathways, or due to potential changes in prey lead content or decreasing lead levels in the environment over time. At the same time, methyl mercury and total mercury increased due to biomagnification, even though mercury levels in sediments have decreased. It is hypothesized that increased mercury levels in *M. dolomieu* can be attributed to increased somatic growth from predation upon *N. melanostomus,* as bioaccumulation of mercury in top predators increases with increasing size and age. As *M. dolomieu* is a very popular sport fish, especially mercury could ultimately be transferred to humans (Hogan et al., 2007).

3 Outlining of hypotheses, knowledge gaps and future outlook

In my thesis, I will investigate how life-history strategy varies between areas, i.e. with stage in the invasion process. I hypothesize that *N. melanostomus* life-history strategy differs with environmental conditions and/or stage in the invasion process. I will further look into *N. melanostomus* diet. I hypothesize that *N. melanostomus* is a quick learner that will consume both known and novel prey in accordance to availability and energy gain (i.e. being a generalist optimal feeder). This means that *N. melanostomus* should select for prey items that are abundant and/or nutritious, even though they may represent a novel food source. As prey, I hypothesize that *N. melanostomus* represents a valuable supplementary food source that predators (seals, cormorants and piscivorous fish) rapidly learn to feed on. I will further analyze the impact of *N. melanostomus* on coastal fish assemblages. The hypothesis is that impact varies with phase of the invasion process, with low impact after establishment, then increasing and ultimately stabilizing impact as *N. melanostomus* becomes an integrated part of the Baltic Sea coastal fish assemblage.

Life-history strategy

As reviewed above, there are differences in life history strategy within and between areas/populations. There are several possible explanations for such differences (Fig. 3). Differences could reflect differences in methodology, e.g. in age reading methods and/or between readers, and thus blur estimations of growth rate, age at maturity and longevity (Florin et al., 2017). They can also result from sampling at different stages in the invasion process. In these two cases the confounding factors make the populations incomparable; it is impossible to establish whether the differences exist or if they are artificial. However, if populations of similar age are compared, i.e. a certain number of generations have passed since the introduction, and similar age reading methods have been applied, the populations should be comparable. If no differences are then found between populations, it can be concluded that the stages in the invasion process largely is determined by life-history strategies. Consequently, if differences are detected between populations when the age of the population and potential methodological differences have been taken into account, they should reflect a response to various environmental conditions. I have found very little information in the literature that stage in the invasion process and differences in methodology have been accounted for (but see Hôrková and Kováč, 2014, Kornis et al., 2016). Therefore, I conclude that many previous studies most likely incorporate major flaws when comparing life-history strategy of NIS populations.

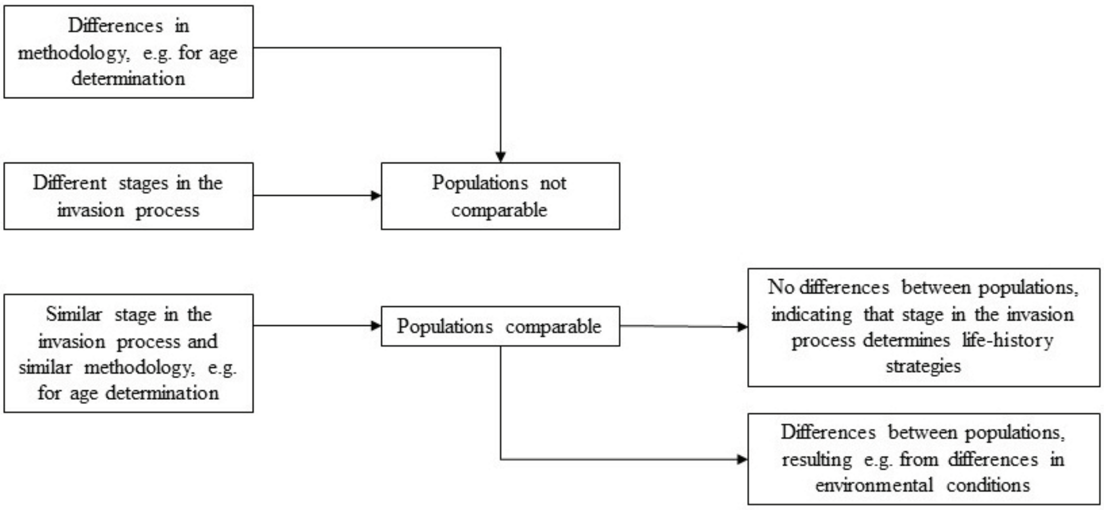


Fig. 3. Potential explanations for discrepancies between studies of life-history strategy.

I plan on studying variation of *N. melanostomus* life-history strategy by analyzing maturity-at-age and size-at-age of fish from different parts of the Baltic Sea and thus from populations of different ages. The prediction is that life-history strategy varies with stage in the invasion process, which should lead to lower maturity-at-age and size-at-age in front populations in comparison to core populations. In my own work, I aim at taking the above precautions into account. My study will provide the so far most comprehensive analysis of *N. melanostomus* life-history strategy in the Baltic Sea, paired with best-practice methods for age-reading. The outcome will be a robust assessment of *N. melanostomus* life-history strategy in the Baltic Sea and how it varies in space and time.

***N. melanostomus* in the food web**

N. melanostomus *as predator*

From my review, I conclude that *N. melanostomus* is an opportunistic predator but with certain prey preferences, which vary between ecosystems and studies and with *N. melanostomus* size. As sizes may vary between core and front populations, stage in the invasion process may indirectly influence round goby diet. To verify the position of *N. melanostomus* in the Baltic Sea food web, further studies are needed. *N. melanostomus* diet has been quite extensively studied in parts of the Baltic Sea. However, the species has not, to my knowledge, been studied from a perspective where stage in the invasion process has been taken into account. Neither, no studies so far have investigated *N. melanostomus* diet by several different methods (traditional stomach content analysis, DNA analysis and stable isotope analysis) simultaneously. I aim to do both of the above, coupled with a high spatial and temporal coverage.

Differences in *N. melanostomus* diets may reflect actual differences between areas, but they may also reflect differences between the studies themselves. A laboratory experiment might show actual preferences for different prey items, while the result of a field study may show that *N. melanostomus* feeds on the most abundant or most accessible prey item (Nurkse et al., 2016). Differences between field studies can also be related to seasonal variation in diet, if the studies have been carried out during different seasons. Further, differences can be related to long-term changes in the diet linked to time since *N. melanostomus* establishment, or to long-term changes in prey availability.

To test my hypothesis of *N. melanostomus* being a generalist optimal feeder, I will carry out aquaria experiments to study its responses to known and novel food types (e.g. eggs and larvae of fresh water species that *N. melanostomus* is unlikely to have encountered before). I will also investigate *N. melanostomus* diet in the field in different populations. Together, these approaches will contribute to a more comprehensive picture of the *N. melanostomus* position in the food web.

N. melanostomus *as prey*

Knowledge about *N. melanostomus* contribution to predator diets is somewhat limited in parts of the Baltic Sea, e.g. in Swedish coastal areas. *N. melanostomus* occurrence in avian and piscine predator diets has been investigated in some parts of the Baltic Sea, but mammalian predation is a field that needs to be explored further. Since effects of introduction of *N. melanostomus* are ecosystem specific (Hirsch et al., 2016, Hempel et al., 2016), a thorough examination of *N. melanostomus* contribution to predator diets is needed to properly assess its role in the Baltic Sea food web. I aim at doing that by investigating diets of predators from different areas both trough traditional stomach content analysis, DNA-analysis (meta-barcoding) and stable isotope analysis.

Effects of *N. melanostomus* introduction on coastal fish assemblages

Regarding impacts of *N. melanostomus* introduction on coastal fish assemblages, no large-scale studies have to my knowledge been carried out in the Baltic Sea area, although a few studies from the Great Lakes area have similar approaches (Bhagat and Ruetz, 2011, Hoyle, 2014). The impact of *N. melanostomus* establishment in the Baltic Sea may be positive for various predator populations, and at the same time lead to negative consequences for e.g. *P. flesus/P. solemdali* and *G. niger* due to predation and/or competition for food or space. Predation on eggs and juveniles by *N. melanostomus* is one particular negative aspect that could be expected to increase proportionally with *N. melanostomus* population increase. I aim to answer the question of how *N. melanostomus* introduction affected coastal fish assemblages by analyzing monitory fishing data. Such data is available from before the invasion and during different stages of the invasion process, and I will include evaluation of abiotic drivers like water temperature, salinity and nutrient loads. Fluctuations of such abiotic drivers impact species composition and abundance (Olsson et al., 2012) and thus need to be taken into account when analyzing changes in biodiversity over time.

Concluding remarks

It appears as if *N. melanostomus*, despite the relatively short time since establishment, has already made its mark on the Baltic Sea ecosystem acting as predator, competitor and prey. It has also already been marked by it, as the species to some extent has adapted to local conditions, dietary-wise, and potentially also adjusted to the special conditions by changes in life-history strategy. However, these aspects need to be investigated further in order to identify the ecological role of *N. melanostomus* in the Baltic Sea ecosystem. Such information is needed for an ecosystem-based management and sustainable commercial and recreational fisheries.

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