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Review

Small but Mighty: The Round Goby (*Neogobius melanostomus*) as a Model Species of Biological Invasions

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Abstract: Invasive "game-changer" species cause severe ecological impacts such as "phase shifts" in recipient ecosystems all over the world. Since the early 1990s, the ongoing global spread of the small but highly invasive Ponto-Caspian round goby *Neogobius melanostomus* into diverse freshwater and marine ecosystems has been observed. We postulate that this species is an ideal model to better understand and mitigate aquatic invasions. Its wide invaded range, as well as its diverse impacts on native species, have triggered a large body of research worldwide concerning its spread, ecology, and traits facilitating invasion. Several hypotheses related to invasiveness have been tested for the round goby, which are also applicable to other invasive species and for understanding general principles in invasion biology. However, a common theory explaining invasion success, especially in round goby, is still lacking. Many case studies do not consider time since invasion and use different sampling protocols and methodologies, hampering the comparability of results and conclusions. We thus propose strengthening the network of goby researchers and establishing long-term databases based on continuous and harmonized monitoring covering all stages of the invasion process as crucial requirements to better understand and manage aquatic invasions. In many cases, such monitoring can easily be integrated into existing survey schemes.

Keywords: alien species; aquatic invasion; fish; hypothesis-driven research; invasion biology; invasion theory; invasion success; invasive traits

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1. The Round Goby as a Model Species

Human-triggered environmental changes such as the invasion of different "game-changer" species are reported from all over the world, even in remote environments such as deserts invaded by the Buffel grass *Cenchrus ciliaris* [1] or the deep-sea invaded by the Crocodile toothfish *Champsodon nudivittis* [2]. Species movements and translocations associated with human activities have occurred ever since people were on the move [3]. However, contemporary human-supported dislocation of species exceeds all previous natural migration activities, both in terms of the number of translocated species as well as the distances bridged by these translocations. Invasive alien species (IAS) can have severe ecological impacts on the recipient ecosystems resulting in "phase shifts". The main interactions with native species include competition, predation, hybridization, spread of pathogens and parasites, and bio-fouling, which can even cause local population extinctions of species [4]. Notably, invasions of aquatic ecosystems have received less attention in this respect than terrestrial ones [5], although such impacts may even be more intense and long-lasting in aquatic ecosystems, particularly in freshwaters [6]. Perceivably, IAS are globally considered as one of the major threats to freshwater ecosystems and their biodiversity [7].

Most translocated invasive fish species are linked to stocking, accidental or intentional pet and bait release, and ballast water transport [8]. Such a human-mediated translocation often is a basic requirement for a species to establish and eventually become invasive. Understanding invasion processes is not only interesting from a scientific point of view, but also essential for their management, particularly since introduction rates and potential subsequent invasions still increase [7].

Prominent IAS examples from freshwater ecosystems are the Ponto-Caspian gobies of the benthophiline fish subfamily (Gobiidae: Benthophilinae), and in particular, the highly invasive round goby *Neogobius melanostomus* (Figure 1). This species is a small benthic fish, native to the Ponto-Caspian Basin (Black Sea, Caspian Sea, Sea of Azov and adjacent nearshore habitats), which is considered invasive in more than 20 countries [9] of Central and Western Europe as well as North America (Figure 2). The round goby started to gain visibility following its ballast-water-mediated invasions during the 1990s into the North American Great Lake basin [10] and the Baltic Sea [11]. Soon after, it was noticed that the species was rapidly colonizing the artificially connected Danube-Rhine river corridor in Europe [12–14] as well as the large Eastern European rivers like Volga, Don and Dnieper where the species has naturally expanded its distribution range [15]. By now, this small bottom-dwelling fish has been recorded in several watersheds along the northern hemisphere (e.g., [16]), and has become listed as one of the worst (aquatic) IAS in the world [17]. Furthermore, its eradication is thought to be impossible [18], therefore requiring ways of adaptation management and mitigation.

Interestingly, invasion success as well as the progression of round goby invasions have not been uniform, but highly site-specific. This fish species shows the same exploratory and fast expanding trend like most IAS, but on a global scale it causes strong ecosystem effects, which makes it an outstanding model species for the study of aquatic invasions in general [19]. Other attributes that make it a highly interesting model species in invasion, evolutionary and adaptation biology are its fast life cycle, short life span, small home range, high abundance in a large variety of different water bodies, as well as its easy accessibility and observability in nature and under laboratory conditions. In addition, the species has diverse effects on the recipient ecosystems and its invasive impacts are strongly case-specific [17,20]. This has triggered a wealth of research related to its invasions, management and impact mitigation. Hence, a great diversity of researchers and institutions across all of the round goby's distribution range and beyond are working on different aspects of the species' biology (Table S1).

Figure 1. The round goby and its habitat; (**a**) Photograph of a round goby (*Neogobius melanostomus*) specimen from the Danube River in Germany; (**b**) Computerized tomography (CT) scan of the round goby's skeleton; (**c**) Coastal habitat near Kamen bryag, Bulgaria (Black Sea, native range), (**d**) River Osam near Musalievo village, Bulgaria (right tributary of the Danube, invaded range); (**e**) Rip-rap habitat below Regensburg, Germany (Danube River, invaded range)—a man-made habitat structure preferred by gobies; (**f**) Groins above Mariaposching, Germany (Danube River, invaded range).

1.1. Origin and Invasion Prerequisites

At present, the round goby occurs in a large variety of habitats in both its invaded and native range, including freshwater, brackish and marine water bodies with salinities up to 30‰ [21] (Figure 1). Native marine populations of the round goby can be found in the

Black Sea, the Caspian Sea and the Sea of Azov. It is also found in near-shore lakes and reservoirs adjacent to the Ponto-Caspian marine basin [22,23].

The impressive tolerance to salinity and water temperature (ranging from −1 to 30 °C, see Corkum et al. [24]) of the round goby and of many other Ponto-Caspian species enables them to colonize a multitude of new habitats and regions, which was noticed as early as the 1960s. A few decades later, Ponto-Caspian mussels, crustaceans and gobies are considered among the most problematic invaders in Central Europe, the Baltic Sea area and the North American Laurentian Great Lakes [25–28]. Many of these organisms are known to have preceding or parallel invasions alongside the round goby (e.g., *Dreissena polymorpha*, *Dreissena bugensis*, *Dikerogammarus villosus*, as well as several other goby species), potentially contributing to biological homogenization and invasional meltdown of recipient ecosystems (e.g., [29]).

According to Stepien and Neilson [30], the genus *Neogobius* is not monophyletic, but consists of several lineages. The same authors conclude that there are six goby species from three lineages, which are likely to invade further regions outside their native range in the near future: *Neogobius melanostomus*, *Neogobius fluviatilis*, *Ponticola kessleri*, *Ponticola gorlap*, *Babka gymnotrachelus*, and *Proterorhinus semilunaris*. Recently, Adrian-Kalchhauser et al. [31] emphasized that the exceptionally large mitochondrial genome (19 kb) of *N. melanostomus* may bear yet unknown features, which can facilitate adaptation to novel environments. This is particularly interesting, since the round goby has an exceptionally low metabolic rate, especially under high water temperatures. Further, Adrian-Kalchhauser et al. [9] postulate that both their innate immune system and their osmoregulatory genes facilitate invasion success in round goby.

A round goby invasion can happen extremely fast and the species can become dominant within less than two years after its initial introduction [32]. This can be explained by its very high embryo survival (>90%) in both fresh and saltwater [33] and the subsequent tremendous population increase, especially in the first three years. Length-at-age back calculations show divergent results in different invaded regions and they depend heavily upon the used aging structure and model [33,34]. In freshwater ecosystems, round gobies are typically smaller and growth is slower than in marine ones (Table 1). In freshwater conditions, they may reach a size of about 50 mm in their first year and ca. 90 mm in their second one [33]. In the first two years, males grow faster than females, thereafter growth declines in every further year: annual growth is ca. 30 mm in 2+, 20 mm in 3+ and 15 mm in 4+ individuals, which are mostly females as they have a longer lifespan than males [33]. Most studies report higher growth rates in invaded regions than in ecosystems within the native geographical range, postulating a "bigger is better" mechanism. This also holds true for recently colonized areas where population density is still lower and growth greater than in established areas [35,36]. However, observations from the Laurentian Great Lakes where growth seems to be lower [37] suggest that such patterns also strongly depend on local conditions. Karsiotis et al. [38] showed highest round goby growth at salinities between 5 and 15 ppt, whereas survival was highest at 20 ppt.

Salinity tolerance is a critical and strongly discussed topic in the context of round goby invasion success. Behrens et al. [39] showed that more than 60% of analysed individuals survived salinities of 30 PSU in an experimental setup. However, there is no documented established population at oceanic salinity conditions [40–42]. In addition, increased salinity values may reduce physiological performance (e.g., feeding [39,41]), competition success, migration distance and individual growth in round goby. Recorded size differences may occur due to different reasons than salinity, e.g., available food resources, time of hatching (due to multiple spawning events across the year; Table 1), sex and competition. Furthermore, founder effects and the age of the invasive population also affect population dynamics, trends and development.

Once (successfully) introduced and before spreading, a non-native species often passes through the so-called "lag phase", having little or no impact on native species and ecosystems [20]. This phase can last between two and five years in round goby, at least in the

Baltic Sea [43]. During this phase, adaptive changes can take place [44,45], while its duration depends on factors associated with the novel environment. IAS population size and factors related to the invaders' fitness such as genetic constitution [46] and phenotypic plasticity [45,47] also determine the duration of this lag phase. Similarly, during the course of an invasion, different traits and characters may become crucial and determine long-term invasion success. According to Thomaz [48], the persistence of an established population over time, at least in fish, seems to depend mainly on the species' dispersal ability and anthropogenic habitat disturbance as well as on the presence of competitors and predators (quantity of empty niches). However, a boom-bust dynamic has been observed in many invasive species [49] since factors influencing population size and success are never static. Being a trophic generalist in combination with possessing high environmental tolerance seem to be important prerequisites in determining long-term invasion success [7]. This is exemplified in the round goby [50], which is known to reach densities of up to 100 individuals per square meter [51], despite being described to be highly aggressive and territorial [52].

1.2. Invaded Regions

The spread of the round goby is heavily mediated via anthropogenic translocations (e.g., ship ballast water transport) and facilitated by human activities such as connection of formerly separate river systems as well as channelization and habitat modification [14,53]. Several of the above-mentioned factors interact in a synergistic way [54]. Despite its small size and limited movement ability [55], the round goby has a high potential for self-sustained dispersal, allowing it to spread quickly after initial introductions [50,56]. Žak et al. [57] describe round goby activity to be size- and sex-dependent, with males having a higher locomotion activity than females.

According to invasion theory, multiple introductions from different source populations can enhance species invasiveness [45]. However, this was not confirmed in round goby and it is unknown whether mixing fish from different sources would further enhance the species' ability to expand. Brown and Stepien [58] indicate that populations from the River Dnieper are likely the source for the invasion of the Laurentian Great Lakes. Here, a secondary spread had started from the St. Lawrence River [10] and five years later, the round goby was detected in all five Laurentian Great Lakes [59] and several of their large tributaries including the Rivers Detroit, Trent, Illinois, St. Clear, Maumee (e.g., [60], Figure 2). In the Gulf of Gdansk (Baltic Sea), Björklund et al. [61] assigned the sole origin of this invasive population to the River Dnieper, indicating that the round goby can be a successful invader even when introduced from a single source. Comparably, Cerwenka et al. [62] found no admixture of source populations along the upper Danube River, where small-scale genetic differentiation was instead explained by adaptation processes. Several examples illustrate the species' ability for habitat switches, irrespective of their origin. For instance, the invasion of nearshore habitats in the North Sea and Baltic Sea was likely driven by secondary invasions from originally invaded river habitats in Belgium, the Netherlands, Denmark, Sweden, Finland, Latvia, Lithuania and Estonia [63–67].

In Europe, the species is invasive in major rivers such as the Danube, the Rhine, the Elbe and some of their adjacent tributaries (e.g., [19,68,69]). Throughout Europe, the round goby has shown an impressive range expansion along the larger central and northern rivers. The main river corridors facilitating this spread are: (1) Northern corridor—along the Volga River watershed connecting the Caspian and Azov Seas to the Northern Baltic Sea; (2) Central corridor—along the Dnieper River watershed connecting the Black Sea to the Central Baltic Sea; (3) Southern corridor—along the Danube River watershed; (4) Western corridor—along the Rhine watershed ([70]). Within these corridors, canals and man-made shipping routes connect formerly separate drainage systems, presenting newly available migration routes which provide access to distant and formerly separated ecosystems.

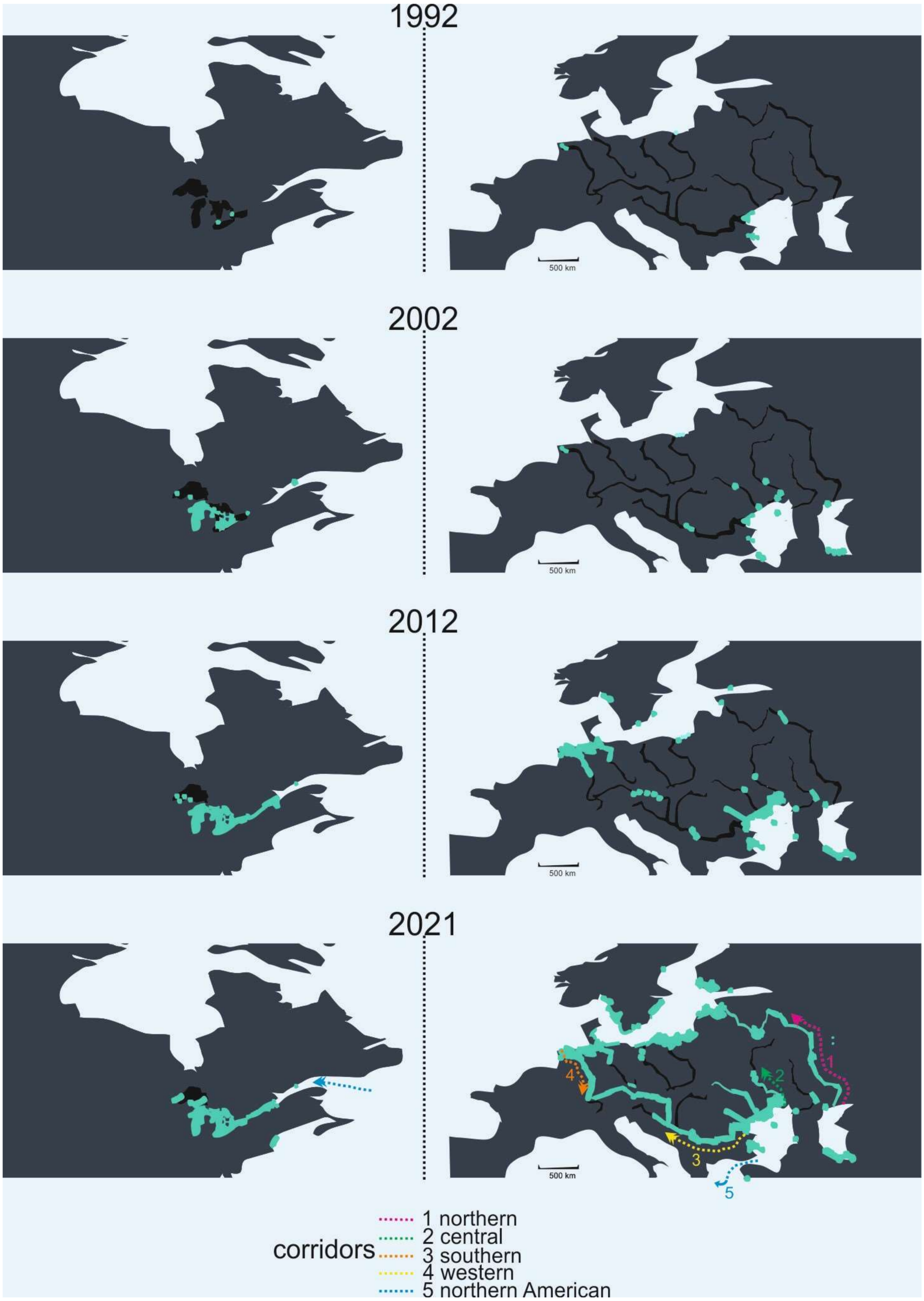

Figure 2. Range expansion of the round goby (*Neogobius melanostomus*) in North America (left panels) and Europe (right panels) along major corridors (2021: 1–5, marked in different colors) over the last 30 years. The green dots indicate reported round goby occurrences compiled from multiple sources; distribution patterns are presented in 10-year sequences from 1992 through 2021.

In contrast to the range expansion to the north, there are only few records of round goby invasions in Europe south of the Danube basin. Round goby spread into several Bulgarian Danube tributaries via upstream dispersal [71]. It was also recently found in a reservoir in southern Bulgaria (probably as a result from stocking or bait bucket transfer), being the first invasive record for the Aegean (Mediterranean) basin [72]. Manne et al. [73], detected a self-sustaining population in the Moselle and Scheldt basins in France.

1.3. Traits Facilitating Invasion

Traits facilitating invasions are neither universal at species level, nor at ecosystem rank. Instead, they vary even among invasion stages [74] and those phases can act as filters selecting for different traits. Examples are the phase of transportation (in ballast water) acting as a potential filter for heat stress, the introduction phase as a filter for the tolerance or resistance to novel pathogens, and the spread phase filtering for selected dispersal abilities [75]. Thus, the invasive phenotype of non-native species typically comprises a mix of traits needed during different invasion phases. Apart from the round goby's genetic prerequisites for invasive spread, the species has several biological and ecological traits that facilitate successful invasions (Table 1). Some traits are expressed in all known habitats, including parental care and tolerance towards pollution. For several invasive populations the presence of alternative reproductive tactics (ARTs) has been confirmed, where some males specialize in parental care, while others imitate females externally (a.k.a. sneaker males), sneaking and fertilizing the eggs in the nests guarded by other males [76,77]. So far, little is known about the relation between the different ARTs and the invasion process. The traits of some sneaker males from the upper Danube population might be further explained by the individual trait hypothesis [78].

Other invasive traits such as external morphology, growth, maturation, fecundity, and spawning period vary among different habitats. High levels of plasticity in these traits seem to be a key characteristic of round goby's overall invasion success and may in turn boost selected traits [70]. For instance, there is evidence that geographically separated invasive populations can show similar morphological traits (both in single characters and in fin allometry) [79]. In addition, it seems that the species reaches maturity at a smaller body length in invaded regions compared to native ones, while either absolute fecundity is lower or fewer egg batches are released within a season [80,81]. The role of founder effects and genetic drift is an omnipresent subject in invasion biology and intensively discussed [82]. After (first) introduction, founder effects can contribute to population differences across different sites, promoting diversification, specific local adaptation and subsequent differentiation [70]. Thus, every single (sub-)population can frame a unique mix of traits, which may result in spatial sorting. As a consequence, species expansion may be assisted or even accelerated [70]. Alternatively, single invasive population differences in trait allocation may result from divergent selection pressures.

As a generalist species, round goby has a very plastic diet, which is one of the key factors facilitating its adaptability to novel environments and its invasive spread ([48,83], Table 1). The preferred diet of the round goby includes mostly benthic macroinvertebrates such as insects, crustaceans and molluscs, and to a lesser extent fish eggs and larvae, small fish and zooplankton. The ability to feed on molluscs gives it an advantage over other co-occurring fish since very few species are adapted to utilizing hard-shelled resources. Even small round gobies may consume molluscs as part of their diet, but an ontogenetic change in the pharyngeal morphology has been linked to the feeding on molluscs when the round goby reaches a total length (TL) of about 8 to 10 cm, i.e., when the pharyngeal teeth are fully developed [50,84]. Notably, Brandner et al. [35] described a higher trophic level in round goby pioneering populations compared to longer established ones, indicating plasticity even in this trait. Invasion success is often explained by extensive feeding on mussel species such as *D. polymorpha* and *D. bugensis* [82–84], which frequently invade freshwaters at the same time, or before round goby introduction. However, the round goby is not tightly dependent on the presence of molluscs and can also invade habitats where such food resources are lacking [81]. Under laboratory conditions, the species was observed to continue feeding even at low water temperatures (5 °C) [85], which is already below the lower feeding limits of most co-occurring fishes. This is also confirmed by stomach content analyses of gobies from three tributaries of the lower Danube River, where feeding was also observed during winter months [80]. Winter-feeding may give the round goby an additional competitive advantage, particularly over native species that have a winter dormancy period. In the same population where winter-feeding was recorded, the oocytes had a diameter of about 1 mm in December and the gonadosomatic index (GSI) reached 3% in February, allowing the species to be ready for reproduction much earlier than the native fish species [80].

Table 1. Comparison of traits facilitating invasion and basic fish-biological data of round goby (*Neogobius melanostomus*) from various invaded and native regions in Europe and North America. Morphological, reproductive and feeding-specific traits are displayed separately.

Invaded Regions	Laurentian Great Lakes (Invaded)	Baltic Sea (Invaded)	Pontic Range (Native)	Rivers of Central and Western Europe	Caspian Range (Native)	References
Relevant invasion corridors		Northern and Southern corridors		Central and Western corridors		
Native origin	Southern Dnieper River	Black Sea		Lower Danube		
			Size, Morphology and Age			
Maximal recorded body size	177 mm TL	235 mm TL	260 mm TL	260 mm TL	153 mm TL	[36,86–88]
Allometric coefficient of the ventral fin width	1.21 ± 0.10	1.43 ± 0.16	1.60 ± 0.19	1.49 ± 0.28		[36,81,89]
Maximal recorded age *	7+ years	6+ years	5+ years	4+ years	4+ years	[83–85,90,91]
			Reproduction **			
Relative fecundity		9 to 143 eggs/g		225 to 3569 eggs/g		[92]
Absolute fecundity	81 to 1818 eggs	457 to 3203 eggs	1008 to 3803 eggs	419 to 3568 eggs	1665 to 5221 eggs	[24,87]
Egg batches per season	at least 3		up to 4	up to 9	up to 4	[80,87,92]
Size at maturity	42.5 mm SL (f)	37 mm TL (f) 45 mm TL (m)	50 mm SL (f)	49 mm TL (f)	50 mm SL (f)	[80,93]
Spawing period	May to August	March to September	April to September	March to July	April to September	[16,80,94]
			Feeding ecology			
Length when pharyngeal teeth are developed	80 mm TL					[84]
Minimal age when mollusc feeding occurs	50 mm TL	<50 mm TL	30 mm TL	65 mm SL	30 mm TL	[87,95,96]
Evidence of winter feeding				December to February		[97]

* Age identification is very difficult for this species (see [34]); ** traits and used methods vary in the literature (see [77] for an overview).

Recent studies revealed some of the reasons why *N. melanostomus* is such a successful invader (Table 2). Even though Adrian-Kalchhauser et al. [31] suggest that all gobiids may adapt to a variety of salinity levels, there is evidence that round goby is not only able to produce, but also to accumulate osmolytes [9]. This ability might (i) further extend its salinity tolerance by increasing water retention, (ii) make overland egg transportation possible (fertilized eggs survive dry-periods of up to 48h [98]), and (iii) result in protection at low water-temperatures. Lastly, (iv) it may enhance the immune response which can be particularly important when exposed to new and unknown pathogens as typical in any colonization event beyond the original distribution range. Further, the authors could correlate round goby invasion success to gene expansions related to salinity tolerance and to immune response.

1.4. After Establishment

The presence of IAS can have long lasting and irreversible consequences for co-occurring species as well as ecosystem functioning [4]. For the round goby, these impacts result from its high levels of trait plasticity, but also from its adaptability, competitive ability, flexibility in diet including an ontogenetic dietary shift and successful reproduction in a wide range of salinities (e.g., [41], Table 2). Impacts vary spatially and are strongly context-dependent. They include shifts in distribution patterns of co-occurring species, which switch their preferred habitats because of goby avoidance behavior as well as the reduction of the population size [64]. Several native species have been reported as negatively affected by the round goby [17,50], with highly different trends and consequences for co-existing macroinvertebrate and fish communities. Observed negative effects are particularly strong in bottom-dwelling species that share similar habitats and niches [99]. For instance, Juza et al. [32] linked the disappearance of native ruffe (*Gymnocephalus cernua*) in the Biesbosch Lakes (the Netherlands) to the high niche overlap with *N. melanostomus*, comparable with the displacement of darters in the Laurentian Great Lakes [62]. In contrast, abundances of the larger and piscivorous European perch (*Perca fluviatilis*) and pike perch (*Sander lucioperca*) increased following goby invasion. This is in line with the hypothesis that invasive round gobies are a major threat to native fish species with a significant niche overlap and competition, e.g., for food whereas species preying upon gobies can benefit [99,100]. To date there is only one single reported case of a native population recovering after the invasion of the round goby [101].

Interaction of multiple IAS may not only influence their invasion dynamics, but may have profound effects on native species and the functioning of entire food webs. For instance, Beggel et al. [29] proposed boosted and synergistic effects of the simultaneous invasions of Ponto-Caspian amphipods (*Dikerogammarus villosus*) and round gobies on native *Gammarus pulex*, speeding up its extinction in the upper Danube River. In general, preventing biological invasions is most promising to protect ecosystems and their functioning, especially since effects may be complex and comprise interactions. Morisette et al. [18] recommend wetland restoration and a mosaic of heterogeneous habitats as best containment, particularly as they state that climatic factors are of minor importance.

2. Large Body of Hypothesis-Driven Research

Several major hypotheses have been proposed to explain and predict biological invasions (Table 2), but the general applicability of these hypotheses is largely unknown, as most of them have not been evaluated using a standard approach across taxonomic groups and habitats [102]. Many of these are highly relevant to round goby invasions (Table 2), although they might be applicable in specific scenarios only. A well-known but controversial example is the "invasional meltdown" theory [103], in which one invader is supposed to facilitate successive invasions of other IAS. Havel et al. [7] state that no reliable and documented case supports this hypothesis, at least in aquatic environments. On the other hand, most convincing proof has been found for the propagule pressure hypothesis, following Maitner et al. [101]. Simulations of de Mazancourt et al. [104] indicate that environmental change best explains species community changes. In this context, simultaneous invasions or synergistic impact may accelerate or even drive the extinction of native species [29]. Clearly, freshwater ecosystems are globally and irrevocably transformed by IAS [105], facing a homogenization of flora and fauna ([106], Table 2).

However, every invasion and every invaded system is unique, making predictions on the outcome of an invasion difficult [107]. Several theories assign non-native species properties or characteristics to attributes of invasiveness, e.g., the theory of evolution of increased competitive ability [108]. However, there is still a lack of a unified common theory explaining invasion success. The global invasion of round goby into diverse ecosystem types as well as its impacts on native species has triggered a large body of hypotheses-driven research. This comprises hypotheses related to (a) invasion theory; (b) pathways and vectors; (c) community interactions; (d) dispersal and migration; and (e) fisheries and economic impact.

Table 2. Selection of important hypotheses in invasion biology compiled from multiple literature sources with their relevance to round goby research (D = documented, P = potentially relevant, N = not relevant). The theories were sorted by the year of publication and were assigned into functional categories: (a) invasion theory, (b) pathways and vectors, (c) community interactions, (d) dispersal & migration, and (e) fisheries & economic impact.

Year	Theory	Category	Relevance for Round Goby Research	Reference	Comments
2018	Disease facilitation	a,c	D	[109]	IAS alter parasite transmission, caused by habitat alteration or physical transfer. This hypothesis extends parasite spillback assumption.
2018	Suppressive spillover	a,c	P	[109]	Native parasites limit the expansion of an introduced species (and hence hamper its invasion success).
2017	Individual trait utility	a	D	[78]	Recognition of the importance of single individuals carrying traits accountable for invasion success, such as high lipid content in round goby as observed in the Danube.
2017	Originality (phylogenetic, functional, or ecological)	a,c	P	[110]	The presence of IAS drives resident species to rapidly evolve traits to better tolerate or exploit invaders.
2014	Evolutionary imbalance	a	P	[111]	Evolution in an increasingly interconnected world suggests that invasive species continue to displace native species resulting in functional shifts in the recipient ecosystem.
2013	Bigger is better	a,d	D	[35]	Invasion success seems to be largely determined by somatic investment instead of reproductive investment. Gobies at invasion fronts at the upper Danube River [35,36] were larger than individuals from established populations.
2013	Invasive queens	a,d	P	[112]	Combining enemy release hypothesis & red queen hypotheses: Species with ability to reproduce both sexually and asexually shift towards asexual reproduction in an exotic range.
2011	Genetic admixture	a,b,d	P	[113]	Admixure / interbreeding of genetically separated populations in non-native regions, see [112]. This effect may also contribute to inbreeding depression and needs further examination.
2011	Spatial sorting	a,c,d	D	[114]	Traits are accumulated in populations according to the local requirements: dispersal abilities at the invasion edge, competitive abilities at longer established sites (e.g., [35]).
2011	Universal trade off	a	N	[115]	After interchange between formerly isolated realms, macroevolutionary patterns of differentiation and speciation constitute the movement of traits on a common tradeoff surface.

Table 2. *Cont.*

Year	Theory	Category	Relevance for Round Goby Research	Reference	Comments
2009	Propagule pressure (Introduction effort)	a	D	[116,117]	Propagule pressure is the combination of introduction events and number of individuals (propagules) introduced. It strongly affects invasion success.
2008	Mutualism disruption	a	N	[118]	IAS (particularly plants and fungi) may counter mutualism in non-native regions.
2007	Genetic bottlenecks	a	P	[119]	Genetic bottlenecks, i.e., genetic diversity loss as a result of small/reduced population size, are well documented in IAS and in round goby (e.g., [120]), however, they do not seem to have an effect on invasion success.
2007	Homogenization of flora and fauna, McDonaldization	a,b	P	[121,122]	Invasions lead to an increasing similarity of species assemblages, across localities, also called taxonomic homogenization.
2006	Phenotypic plasticity	a	D	[123]	Is thought to be essential in invasive species success by accelerating evolutionary adaptation processes, e.g., to different habitats (e.g., [43]).
2006	Novel ecosystems	a,b,c,d,e	D	[124]	IAS may generate new environmental conditions by eliminating and/or adding new ecosystem services.
2006	Inbreeding	a,c	N	[123]	Inbreeding may be high, when population size is low and may result in inbreeding depression or purging, e.g., [125].
2005	Driver of environmental change	a,c	D	[124]	Model illustrates native species diversity changes after invasions by claiming resources, as e.g., nesting sites in round goby (e.g., [126]).
2005	Empty niche	a,c,e	D	[127]	IAS occupy vacant niches in invaded ecosystems, e.g., Janáč et al. [128].
2005	Boom-and-bust	a	N	[129]	Reasoning for population abundance increase and subsequent breakdown patterns.
2004	Ecosystem engineers	a,c	D	[127]	The theory denominates those IAS which actively change and modify habitat quality in the invaded ecosystem, e.g., [130].
2004	Latency period after introduction (Ecological silence)	a,c	D	[131]	Explains population growth stagnancy after introduction and before (exponential) increase, also called lag-phase (e.g., [132]).
2004	New associations	a,c	P	[133]	Interactions of non-native and native species may be crucial for invasion success.
2004	Increased susceptibilityrelated to Biotic resistance	a,c,e	P	[133]	Lacking local adaptation in non-native species (e.g., temperature, pathogens) increases their enemy susceptibility in invaded communities, e.g., [134].
2004	Invasive engineers	a,c,e	P	[127]	IAS may engineer and transform environments.
2004	Shifting defense	a,c	N	[135]	Quick evolution of alternative defense mechanism, documented predominantly in plants.

Table 2. *Cont.*

Year	Theory	Category	Relevance for Round Goby Research	Reference	Comments
2002	Enemy release	a,c	D	[133,136]	Non-native populations lose up to 80% of native parasitic species when translocated. A "spillover" effect introduces new parasites to a invaded ecosystems, whereas a "spillback" effect reduces native parasites to invaders, as *Pomphorhynchus laevis* and round goby [137].
2001	Lag phase	a,c	D	[40]	see: latency period
2001	K-strategy (Secondary invasions)	a,d	P	[40]	Invasive k-strategists are thought to replace opportunistic r-strategists over the course of time. However, Cerwenka et al. [19] did not find evidence for this hypothesis in round goby.
2000	Genetic paradox	a	N	[138]	Reduced genetic diversity in non-native populations does not seem to hamper invasion success.
2000	Phylogenetic relatedness	a,c	N	[139]	Phylogenetic relatedness of an non-native species could facilitate invasion.
2000	Environmental heterogeneity	a,c	D	[140]	Habitat heterogeneity limits non-native species establishment, as exemplified in the upper St. Lawrence River and invasive round goby [141].
2000	Novel weapons	a	N	[142]	Could be seen as part of the biotic resistance hypothesis, where traits are present but not used in native populations.
1999	Invasional meltdown	a	N	[143]	Simultaneous invasions may promote non-native species success, as e.g., observed in the Danube [29] and Rhine [144].
1999	Enhanced mutualism	a	N	[145]	IAS (particularly plants and fungi) may benefit from higher mutualism rates in non-native regions.
1997	Habitat disturbance	a,d	D	[146]	(Anthropogenic) habitat disturbance facilitates invasions, as indicated for round goby in Slovakia [147,148].
1996	R-strategy (Primary invasions)	a,d	D	[149]	Species with opportunistic and generalistic traits (r-strategists) are more successful at the beginning of an invasion, when pioneering at new sites; proposed for round goby by [150].
1996	Competition relatedness Darwin's naturalization	a	P	[149]	Competitive ability/strength increases with increased phylogenetic relatedness of competitors.
1996	Tens rule	a,d	P	[151]	One out of ten species succeeds in the predefined steps introduction, establishment and spread.
1996	Integrated conceptual model	a	N	[140]	In aquatic systems, biotic resistance is less important in determining the success or failure of an invasion than the integrated environmental resistance.
1995	Evolution of increased competitive ability	a,c	P	[108]	Engineered as an explanation for the "lag-phase", where adaptive processes may take place (e.g., novel enemies and pathogens) and a species gets invasive (e.g., [132]).

Table 2. *Cont.*

Year	Theory	Category	Relevance for Round Goby Research	Reference	Comments
1993	Community assembly	a,c,e	P	[152]	The environment influences community structure and invasion ability. Species-rich communities are thought to offer some resistance against invasion, but see [140].
1992	Hybridization	a	N	[153]	Interspecific mixing between native and invasive species.
1992	Environmental filtering	a,c	N	[154]	The environment acts as a filter removing all species lacking specified combinations of traits.
1983	Limiting similarity	a	N	[143]	IAS are more likely to establish when no native species with similar requirements are present.
1963	Purge of homozygotus deleterious genes	a	N	[155]	Deleterious alleles or mutations may be eliminated in IAS through stochastic effects of small inoculation population size.
1958	Biotic resistance = Elton's resistance = Diversity instability	a,c,e	N	[148,156]	Non-native species establishment is thought to be more difficult in species-rich communities than in species-poor ones.
1938	Allee effect	a,e	N	[156]	It is thought to decrease the speed of invasion due to decreased genetic diversity at invasion front sites (lower effective population size, population density, higher inbreeding probability). Dispersal capacity may reduce the effect.

3. Research Gaps and Future Directions

Most scientific efforts in invasion biology focus on mechanistic principles of the different phases of the invasion process or on functional interactions caused by time since invasion. Whilst selected scientific hypotheses and theories has been tested using the example of round goby, a common and integrative theory explaining its invasion success is still lacking. Are there differences between longer invaded vs. recently invaded areas concerning the invader itself or even on the scale of different invaded ecosystems? Are gobies an indicator for ecological disturbance or a driver of change themselves? Thus, from a scientific point of view, these main complex research gaps have to be named and interrelated with each other. There are at least three major challenges that we consider important for the future: (i) addressing concrete research gaps concerning the round goby biology and its invasion processes, (ii) developing standardized and comparable monitoring schemes and databases, and (iii) better linking the scientific work on the species with impact assessment and management.

3.1. Research Gaps in Round Goby Invasion Biology

In addition to the need of developing a unified framework or theory explaining invasion success of round goby, several concrete research gaps need to be filled in order to achieve this goal. There is already a wealth of data on the specific traits that constitute the round goby's invasive potential, including tolerance to salinity, temperature, turbidity, pollution, and flow conditions. Although these traits have been validated in specific case studies on a local scale, systematic analyses of these traits across different invasive populations taking into account habitat condition (e.g., temperature, habitat structure) and time since invasion are still missing. Since the round goby is easy to study under laboratory conditions, large-scale mesocosm experiments testing the performance and fitness of round gobies with different invasion origins and under different common garden conditions could be a key to better understand their adaptation processes. Applying standardized laboratory protocols at mesocosm scale and focusing on both specimen-specific traits (e.g., performance, fitness, reproduction) and population-related parameters would allow for testing round goby invasion success and allow a validation of the relevance of "invasional meltdown" [103] and of "boom and bust" concepts [49] for this species under well-defined conditions.

A further gap is a detailed and unambiguous analysis of round goby growth. This is especially important since multiple body parts (e.g., scales and otoliths) are used to determine round goby age and growth in different studies. Florin et al. [34] illustrate in detail the low reliability of different ageing methods via otoliths of the round goby, but propose no unified method of age determination. Laboratory rearing of specimens with known age could allow for a rigorous testing of the reliability and inter-calibration of different structures and methods. An alternative are mark-recapture experiments in the field which can contribute to a better understanding of age-growth relationships in various habitats under real world conditions. Reliable aging is essential for long-term monitoring of population dynamics [34], so filling this research gap will greatly improve the continuous monitoring of round goby demographics.

Some of the traits facilitating invasion as well as the interactions with co-existing species can hardly be tested under laboratory conditions. This includes assessing feeding plasticity, population structure and dynamics. The same also holds true for testing of an "invasional meltdown" [103] or a "boom and bust"-scenario [45] under realistic field conditions. In this respect, more intense collaboration and the establishment of an international goby research network may help provide datasets suitable for meta-study analyses, the scale of which would ideally comprise the entire species range and include comparisons among the native and the invaded ranges. It is encouraging that there is a sufficient number of researchers devoted to such studies and the organization of a unified effort in research seems feasible. Especially on European level, different programs such as the EU COST action may provide possibilities of establishing such exchange through networks.

3.2. Continuous Monitoring and Meta-Studies

To date, reliable data analyses of round goby population characteristics and dynamics as well as on their effects on co-occurring species are hampered by a lack of comparable survey and monitoring protocols as well as limited data accessibility. This not only holds true for scientific data, which naturally depend on the specific research question, but also for data collected during routine monitoring by state authorities. For instance, in the fish monitoring of the European Water Framework Directive, focus is placed on assessing native fishes and no standardized recordings are being made for round goby across political borderlines. Establishing harmonized sampling and standardized reporting of round goby and other invasive species, at least comprising some basic information on densities or CPUE, size distributions and other important characteristics, could be achieved with little additional effort to existing monitoring schemes.

Generally, fish populations often express more or less strong annual fluctuations and extremes over time, which is one of the reasons why multiple recordings from the same sites at different seasons are most useful in understanding real population trends. Currently, a large number of publications from nearly all invaded areas provide round goby sampling data: fish biologists in North America and Europe have gathered substantial information on densities and other population characteristics of *N. melanostomus* [18,157] for almost three decades applying different sampling methods. However, in most cases, integration of these data from different regions and habitats is hampered by the use of different sampling methods and a lack of method inter-calibration, which can largely affect the results [158], complicating or even preventing comparisons among different datasets. Although point abundance sampling (PAS) of electrofishing is commonly applied and considered the most effective and most representative catching method for *N. melanostomus* in large rivers [158], this method is not applicable in deep rivers, large lakes or marine habitats such as the Baltic Sea. However, angling or catching of gobies by using traps in these habitats may be useful if previously inter-calibrated with other methods [158]. Method harmonization and inter-calibration needs continuous updating, including the integration of novel approaches such as environmental DNA (eDNA) which may provide a powerful tool for distribution mapping of round goby (see [159]).

Since many round goby case studies do not consider time since invasion, i.e., the age of a population, identification of the current invasion phase is often impossible. Thus, long-term studies with a continuous monitoring, sequentially covering all stages of the invasion process, are crucial. These should ideally start with total absence of the round goby. Locally fixed, spatial monitoring should at least comprise community data of both fish and benthic invertebrates [60,64,160] as well as round goby specific ichthyologic standard data. Biotic and climate-change related variables driving invasion success of round goby, e.g., temperature-sensitivity, can only be analyzed by comparing reliable long-term data.

Another important approach to observe spatio-temporal development of the round goby population and thus its invasion success are repeated transboundary catchment monitoring programs such as the Joint Danube Survey (JDS). This international comprehensive monitoring effort is heading towards its fifth round, covering the Danube River Basin with sampling sites in 13 countries across the whole catchment from the mouth into the Black Sea in Romania to the upper region in Germany during JDS4. It provides valuable datasets (see www.danubesurvey.org/jds4/about, accessed on 27 March 2023), but even such large-scale international sampling procedures require methodological harmonization and quality updating, which should be continued by the authorities.

In the context of transboundary studies, some publications simply combine data from previous studies with their own observations (e.g., [81]). Another approach are meta-studies within a region including several waterbodies, focusing on comparisons between core vs. edge populations, or of spreading invasive vs. native populations (e.g., [60,64,160]), or of several independent invasive populations [79]. While invasive populations have been compared with native ones, there are very few meta-studies which use a standard methodology to compare several invasive populations from different waterbodies, different habitats and with different invasion histories. Such a meta-study approach based on a rich and harmonized database from throughout the goby distribution range seems most suitable to deduce conclusions on the invasive process (invasion hypotheses), but also for the efficient management of this process in terms of environmental conservation.

3.3. Management and Mitigation

A common goal in the research on the round goby (and IAS in general) is intensifying the linkage between science, management and mitigation. Such linkage needs to consider the invasion process in light of environmental protection, ecosystem services and human well-being. This will not only be of mutual benefit (i.e., scientists addressing the most pressing management questions, managers acknowledging the usefulness of measures proposed by science on the species), but it will also increase the likelihood for more evidence-based approaches in freshwater conservation, restoration and management [161]. When managing a biological invasion, four sequential types of measures [116] may be applied:

1. Prevention of invasion in the first place;
2. Eradication if applicable;
3. Prevention of further dispersal if applicable;
4. Mitigation.

A complementary step to the four above mentioned would be to perform risk screening of potential invasions. This could increase management efficiency since eradication or spread limitations of IAS are typically only feasible during early stages of arrival. Such a screening should comprise identification of the species that are most likely to invade, i.e., becoming introduced and constituting a self-sustaining population (e.g., [162]) as well as an identification of sites and habitats that are most likely to become invaded, e.g., areas with intensive boating and recreational uses [163].

Furthermore, if a species is likely to invade, its potential presence should be monitored and an early warning system established, so that in case of detection, adequate measures could be applied in the first stage of the invasion process (the previous mentioned lag phase). The use of standard ichthyologic methods for such a preventive monitoring of not yet invaded habitats is often too time-consuming, expensive, and prone to false-negative results, whereas the use of eDNA-based monitoring of IAS is receiving increasing attention and application, e.g., [164]. Methods using eDNA may allow the monitoring of a wide range of habitat types, including the checking of introduction pathways and vectors like ballast water, bait shops, aquarium and pet trade, and of stocking material prior to actual stocking, etc. [165]. Various environmental conditions that influence detectability of eDNA have already been tested in experiments with round goby [159]. In addition, sampling and processing protocols have been developed and applied for the round goby on a local scale in Europe and North America [164,166]. Monitoring schemes using eDNA should be used in "high-risk" areas and countries, which are neighboring to the species´ current invaded range (e.g., Italy or other Mediterranean countries). The application of dispersal models predicts that round goby might invade the UK [167]. Furthermore, round goby is also considered a "door-knocker" for Norway, where the species is expected to invade [168]. In such places, monitoring of the possible occurrence of the round goby in potential high-risk areas of introduction might allow the prevention of severe impact on the native environments.

Although it is believed that an eradication of the round goby is impossible [18], this seems especially true for established populations, i.e., when round goby density is relatively high. There is yet no case study when management was applied timely on newly established populations, i.e., when eradication methods still would have had a chance of success. Hence, one of the most important aspects in management of round goby invasions (and invasions in general) is their early detection. The costs of measures applied in early stages of an invasion, if successful, significantly outweigh the cost of mitigation measures and management in already established populations (e.g., [169–171]). When a population is detected early in the course of an invasion, an elimination may still be feasible [172]. Whilst it may not always be possible to eradicate introduced populations (even if they are detected early and measures are taken immediately), prevention of further spread can always be applied for the round goby (see case study on the Mississippi River; [173]). Also Egger et al. [174] propose the possibility to design a species-specific hydraulic barrier, which may block the spread of the round goby, without affecting the migration of local fish. Generally, the application of such methods should not only be realized on a practical trial-and-error-basis. Given the wide range of round goby distribution and the amount of management efforts taken throughout its invaded range, critical scientific evaluation of management approaches and reporting of both successfully and unsuccessful measures is necessary to provide evidence-based recommendations.

4. Conclusions

Round goby has become a promising model species, often extending beyond the field of invasion biology. Strengthening the network of goby research and establishing long-term datasets based on continuous and harmonized monitoring are crucial requirements for better understanding and managing invasive round goby. Using harmonized monitoring protocols, considering time since invasion and investigating the stages of invasion is essential for improving both management of ongoing and prevention of future invasions.

Presence of the invasive round goby in diverse habitats across continents has affected a wide range of native species and aquatic communities. The characteristics of this small yet mighty fish in its genetics, biology and ecology provides a unique opportunity for researchers to understand invasion processes and effects on food webs and the functioning of aquatic ecosystems on a global scale, with important implications for understanding ecosystem phase shifts. Since the translocation and invasion of alien species is continuously increasing on an ever-larger scale, research efforts should match this scale in applying focused cross-border analysis, which would improve the management and prevention of invasions in the future.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15040528/s1, Table S1: Institutions working on round goby, type of research, the respective invasion corridor, and the scientific study systems.

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