NON-NATIVE GOBY SPECIES IN SWITZERLAND

IMPACTS AND MANAGEMENT

Inauguraldissertation
zur
Erlangung der Würde eines Doktors der Philosophie
vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

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Basel, 2017

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät
auf Antrag von Prof. Dr. Patricia Holm und PD Dr. Jost Borcherding

Basel, den 13. Dezember 2016

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ABSTRACT

Non-native invasive species are one of the main reasons for biodiversity decline. They can disrupt ecosystem functioning and cause enormous ecological and economic damage. To manage non-native invasive species is a challenge asking for the cooperation of practice and research. In my thesis, I focus on two recent invaders in the High Rhine, bighead goby *Ponticola kessleri* and round goby *Neogobius melanostomus*. These two small bottom-living fish species belong to a group of Ponto-Caspian gobiid species that were introduced probably by ballast water to Europe and North America in the last few decades. In the High Rhine in Basel, they were first detected 2011 and immediately caught the attention of decision makers. Throughout my thesis, I highlight the importance of a transdisciplinary process that can guide researchers in collaboration with decision makers to co-produce measures for an effective and efficient invasive species management. The first step in this transdisciplinary process is to objectively assess priorities and contributions of both scientists and decision makers, followed by an open communication about these priorities and contributions. After such a clarification, ideally, a joint research paradigm for invasive species management can be developed.

By applying this process to invasive gobies, several research priorities have emerged in the first step during a workshop together with decision makers: both scientists and decision makers agree that research on management measures such as prevention is of highest priority. A systematic literature review showed that this priority is met by a lack of scientific knowledge on management measures and by an abundance of scientific knowledge on impacts.

Scrutinising the scientific knowledge on impacts revealed that the strength and the direction of the impacts strongly depend on local conditions. Thus, the knowledge on impacts in other systems is of limited use if stakeholders want to base their management decisions on expected impacts in their ecosystem of concern, because invasive species' impacts are ecosystem- and time-dependent. More important is knowledge on preventive management such as e.g. cleaning of boats. If such preventive measures are intended, rapid action should be initiated despite incomplete knowledge about an approaching invader's impacts.

If the preventive approach failed, as is already the case for at least part of the High Rhine, eradication or containment by removing goby eggs and adults can be management alternatives. Using a field study and a population model, I found that eradication is only feasible if started immediately after the introduction of the population and if inflow of new propagules can be stopped. Because measures to control an already established population need an extremely high amount of effort, prevention should be favoured and eradication should only be attempted in very valuable habitats. The findings from my thesis form the basis of a "Goby Action Plan" to implement management measures along the lines of decision makers' valuation and scientific advice.

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LIST OF PAPERS

This thesis is based on five papers, which are referred to in the text by their roman numerals (Paper I-V).

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II P.E. Hirsch*, A. N'Guyen*, I. Adrian-Kalchhauser, P. Burkhardt-Holm. 2016. What do we really know about the impacts of one of the worst invaders in Europe? A reality check. *Ambio* 45(3): 267-279. doi:10.1007/s13280-015-0718-9

III I. Adrian-Kalchhauser, P.E. Hirsch, J. Behrmann-Godel, A. N'Guyen, S. Watzlawczyk, S. Gertzen, J. Borcherding, P. Burkhardt-Holm. 2016. The invasive bighead goby *Ponticola kessleri* displays large-scale genetic similarities and small-scale genetic differentiation in relation to shipping patterns. *Molecular Ecology* 25(9): 1925-1943. doi:10.1111/mec.13595

IV P.E. Hirsch, I. Adrian-Kalchhauser, S. Flämig, A. N'Guyen, R. Defila, A. Di Giulio, P. Burkhardt-Holm. 2016. A tough egg to crack: recreational boats as vectors for invasive goby eggs and transdisciplinary management approaches. *Ecology and Evolution* 6(3): 707-715. doi:10.1002/ece3.1892

V A. N'Guyen, P.E. Hirsch, C. Bozzuto, I. Adrian-Kalchhauser, K. Hôrková, P. Burkhardt-Holm. 2017. A dynamical model for invasive round goby populations reveals efficient and effective management options. *Journal of Applied Ecology.* doi:10.1111/1365-2664.12934

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PROLOGUE

Once upon a time…
It was a happy place, the Rhine

Salmon and trout abound,
No goby was ever found

With no gobies that compete –
For perches and bullheads, there was plenty to eat

It was the year 2011, they say
When the first goby came on its way

In ballast water they came over the sea
In the Ponto-Caspian region they started their spree

Nothing in the new environment caused their decline
And that is how they became invasive in the Rhine

Arrived in the harbour they began to spread fast
And for the fishermen the flourishing days were long past

More than half of their catch consists of this ground-dwelling fish
Which, with its small size, does not yield a whole dish

The stakeholders and politicians, they started to worry
For without any guidelines, the future seemed blurry

So scientists and decision makers worked together
And this proved to be for the better

They co-produced two options to control the population:
Removing eggs and removing adults, this was the situation

Effective the solution shall be
But also the effort matters, the parties agree

Not removing eggs, but adult females and their mate
was found to be most efficient to eradicate

A model can help to provide the know-how
To deal with this invasive species right now

So what do you say to sceptics that ask:
"Can we stop the invasion and solve this difficult task?"

Fear not, because: Yes, we can!
Born is the Goby Action Plan

INTRODUCTION

Why should we care about non-native invasive species?

Non-native invasive species are one of the most important threats to biodiversity worldwide and can disrupt ecosystem functioning (Sala et al. 2000, Clavero and García-Berthou 2005, Pejchar and Mooney 2009). They are estimated to cause yearly annual costs of 120 billion USD in the United States (Pimentel et al. 2005), at least 12.5 billion EUR but probably over 20 billion EUR in Europe (Kettunen et al. 2009) and 1.7 billion GBP in Great Britain (Williams et al. 2010). The Convention on Biological Diversity states that "Each Contracting Party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (Secretariat of the Convention on Biological Diversity 2005, Article 8h).

A species is called "non-native" (used as synonyms: alien, introduced, exotic, novel, non-indigenous, see e.g. Colautti and MacIsaac 2004, Heger et al. 2013 for a discussion of definitions) when it is introduced outside its natural range, e.g. in an ecosystem that is separated from the species' native habitat by dispersal barriers such as oceans or mountains. The year 1492 when Columbus reached North America is widely accepted as a somewhat arbitrary time point for the distinction between native and non-native flora and fauna (Nentwig 2007). The rate at which humans move organisms both intentionally, e.g. as pets, for food, agriculture, recreational or ornamental purposes, and un-intentionally, e.g. attached to ship hulls, in ballast water or in packaging, has strongly increased over the years due to human activities such as trade and travelling (Ricciardi 2007, Touza et al. 2007). For aquatic species, the main vectors are global trade, opening of canals, transport of ballast water and recreational boating activities (Wonham et al. 2000, Galil et al. 2007, Gollasch 2007, Horvath 2008).

A non-native species is called "invasive" (used as synonyms: nuisance, noxious, pest) when it maintains a self-sustaining population, spreads and causes negative impacts to the recipient ecosystem (Colautti and MacIsaac 2004). To evaluate these negative impacts, many established methods are available, e.g. risk assessment instruments that are usually applied before a species is introduced (e.g. Andersen et al. 2004, Keller et al. 2007, Campbell 2011, Puntila et al. 2013, Snyder et al. 2014), bio-economic modelling to measure economic damage (e.g. Settle and Shogren 2002, Knowler 2007), schemes to assess ecological impact (e.g. Jeschke et al. 2014, Cucherousset and Olden 2011) and impacts to ecosystems and their services (e.g. Pejchar and Mooney 2009, Rothlisberger et al. 2012). A clear-cut distinction between ecological and (socio-)economic impact is hard to identify and may not even be needed, since ecological and economic impacts tend to be highly correlated (Vilà et al. 2010). At any case, assessing impacts, be they ecological or economic, is a challenging task (Simberloff et al. 2013).

Before a species can cause impacts, it has to overcome a series of transitions – first, it has to be picked-up by a transport vector, survive transport and introduction, establish in the wild and be able to spread (Kolar and Lodge 2001). The "tens-rule" states that 1 in 10 of all introduced species appears in the wild, 1 in 10 of those becomes established and 1 in 10 of those becomes invasive (Williamson and Fitter 1996). Which species are more successful invaders than others is of great interest to many scientists. Suggested traits facilitating invasion success include, among others, high number of seeds or offspring, prolonged lengths of flowering or breeding season, multiple reproductive events, faster growth rate, high phenotypic plasticity, or some form of "novel weapon" (e.g. Callaway and Ridenour 2004, van Kleunen et al. 2010, Davidson et al. 2011). Another approach is to focus on the characteristic of the invaded ecosystem. For example, the "biotic resistance hypothesis" suggests that ecosystems with high biodiversity are more resistant than ecosystems with low biodiversity, and the "enemy release hypothesis" suggests that invaders are successful because they do not encounter enemies such as predators or parasites in the invaded ecosystem (see Jeschke et al. 2012 for a discussion of major invasion hypotheses).

Connecting research and practice to manage non-native invasive species

The role of invasion scientists is not only to generate more ecological knowledge, but also to enhance the transdisciplinary dialogue between research and practice (Kueffer 2010). Importantly, transdisciplinarity is not a linear one-way process of "demand and deliver"; rather, scientists co-create knowledge with stakeholders, decision makers, environmental managers and other practitioners on an equal footing to solve "real-world problems" (Hirsch Hadorn et al. 2008, Lang et al. 2012, Defila and Di Giulio 2016). The "real-world problem", in this case, is the challenge of managing invasive species. Management actions include, among others, prevention, eradication, containment and long-term population control (e.g. Horan et al. 2002, Hulme 2006, Genovesi 2007, Simberloff 2009, Liu and Cook 2016). These approaches are discussed in detail below.

Regardless of which management approach is chosen – the inclusion of stakeholders is crucial for management success, as numerous studies show (see e.g. McNeely 2001, García-Llorente et al. 2008, Selge et al. 2011, Sharp et al. 2011, Estévez et al. 2015, Moon et al. 2015, Novoa et al. 2016). A prominent example is the eradication of *Caulerpa taxifolia* in California, where one of the success factors was the strong commitment by stakeholders leading to immediate management after the first detection of the algae (Anderson 2005). Also in Hawaii, informal multi-partner committees were successful in rapidly eradicating 26 plants and vertebrates from islands (Kraus and Duffy 2010). In contrast, when the interests of the public are not included, management measures are difficult to implement. In Italy, civil resistance delayed an eradication program of the grey squirrel *Sciurus carolinensis* for several years, so that eradication would no longer be feasible because the grey squirrel population was too wide-spread (Bertolino and Genovesi 2003). Additionally, local ecological knowledge of stakeholders, e.g. anglers reporting catches of non-native fish species, can be essential to a successful management (Reed 2008, Schüttler et al. 2011).

The preventive approach

Invasive species can cause potentially costly and irreversible impacts. Following the precautionary principle, the establishment of non-native species should be prevented even in the absence of full scientific evidence on its impacts (Simberloff 2003, Vitule et al. 2009, Edelaar and Tella 2012). Thus, the gold standard in dealing with non-native invasive species is to prevent their introduction in the first place (Leung et al. 2002, Secretariat of the Convention on Biological Diversity 2005, Cook et al. 2007). By definition, preventive measures have to be implemented *before* an invasive species invades the ecosystem under consideration. Therefore, as mentioned above, installing a preventive management will always be designed with incomplete knowledge about species' impacts in the ecosystem under consideration, because one cannot wait with prevention until scientific knowledge about the invaders' impacts is "complete" (Horan et al. 2002, Edelaar and Tella 2012). But even if few information is available in the early stages of an invasion, this information may be sufficient to support a preventive management (Keller et al. 2008).

The control approach

The control approach includes containment, defined as “limiting the spread of a species by containing its presence within defined geographical boundaries”, and eradication, defined as “the complete and permanent removal of all wild populations of an invasive species from a defined area in a time-limited campaign” (Genovesi 2007). Eradications of invasive plants and animals, including invertebrates, fish, birds and mammals, have been successfully carried out on islands, in aquatic habitats and also on contiguous land masses (Veitch and Clout 2002, Britton et al. 2008, Russell and Holmes 2015, Jones et al. 2016, Robertson et al. 2017). For population control to be successful, it has to be well-planned from a financial and technical point of view; in this process, scientists can provide valuable species-specific knowledge about e.g. which life stage should be targeted (Myers et al. 2000, Pluess et al. 2012). However, one of the most important prerequisites for successful control approaches is stakeholder and decision maker support (Schüttler et al. 2011, Sharp et al. 2011, Vane and Runhaar 2016). Thus, as mentioned above, the inclusion of decision makers is a guiding principle throughout this thesis.

Study case: Non-native invasive gobies in the High Rhine

The High Rhine has a long history of invasions (Baur and Schmidlin 2007). Most recently, two non-native invasive fish species from the Ponto-Caspian region have been detected (Figure 1): bighead goby *Ponticola kessleri* (Günther 1861) and round goby *Neogobius melanostomus* (Pallas 1814) (Kalchhauser et al. 2013). Both bighead goby and round goby are generalist or opportunistic feeders (Carman et al. 2006, Borcherding et al. 2013, Brandner et al. 2013*a*), show phenotypic plasticity in life-history traits (Brandner et al. 2013*b,* Hôrková and Kováč 2014, Gertzen et al. 2016) and are able to cope with environmental stress (Hempel and Thiel 2015, Hôrková and Kováč 2015). While bighead goby was initially more abundant than round goby in the High Rhine, round goby now reaches extremely high densities with more than 12 adults m^{-2} (personal observation, summer 2015) and non-native invasive gobies (species not defined) constitute the majority of all reported catches by anglers (Figure 2). This change in abundance might reflect a typical “boom-and-bust” cycle often showed by invasive species (Borcherding et al. 2016).

Round goby is declared to be one of “Europe’s worst 100 invasive species” in the Delivering Alien Invasive Species In Europe (DAISIE) database (DAISIE 2016). It is the most widely introduced Ponto-Caspian gobiid species. In the last 30 years, it has spread presumably in ballast water of cargo ships to the American Great Lakes (Jude et al. 1992) and to most European water bodies such as the Baltic Sea (Sapota and Skóra 2005), Danube (Stránai and Andreji 2004, Jurajda et al. 2005, Wiesner 2005), Oder (Schomaker and Wolter 2014), Elbe (Hempel and Thiel 2013), Rhine (Borcherding et al. 2011), and multiple rivers in the Netherlands (van Beek 2006), Belgium (Verreycken et al. 2011) and France (Manné et al. 2013). Three other Ponto-Caspian goby species currently expanding their range in Europe (Roche et al. 2013) will probably follow in the High Rhine: Western tubenose goby *Proterorhinus semilunaris* (Heckel 1837), monkey goby *Neogobius fluviatilis* (Pallas 1814) and racer goby *Babka gymnotrachelus* (Kessler 1857).

However, the High Rhine at the border of Switzerland and Germany provides a unique opportunity to prevent further dispersal of non-native gobiid species. Several hydropower dams upstream of the current range expansion might be able to slow further dispersal by swimming. Even more importantly, cargo shipping stops at the dam in Rheinfelden, coinciding with the current upper edge of goby range expansion. This dam also provides an exceptional opportunity to clean recreational boats, and regular surveys in the newly constructed fish passage would allow to monitor goby dispersal closely. Thus, management measures can be aimed at human vector activities as well as on the dispersal and control of the non-native invasive species itself.

Figure 1: Bighead goby *Ponticola kessleri* (left) and round goby *Neogobius melanostomus* (right) caught in the harbour Kleinhueningen in Basel, Switzerland, with minnow traps in April 2014. (Source: own pictures)

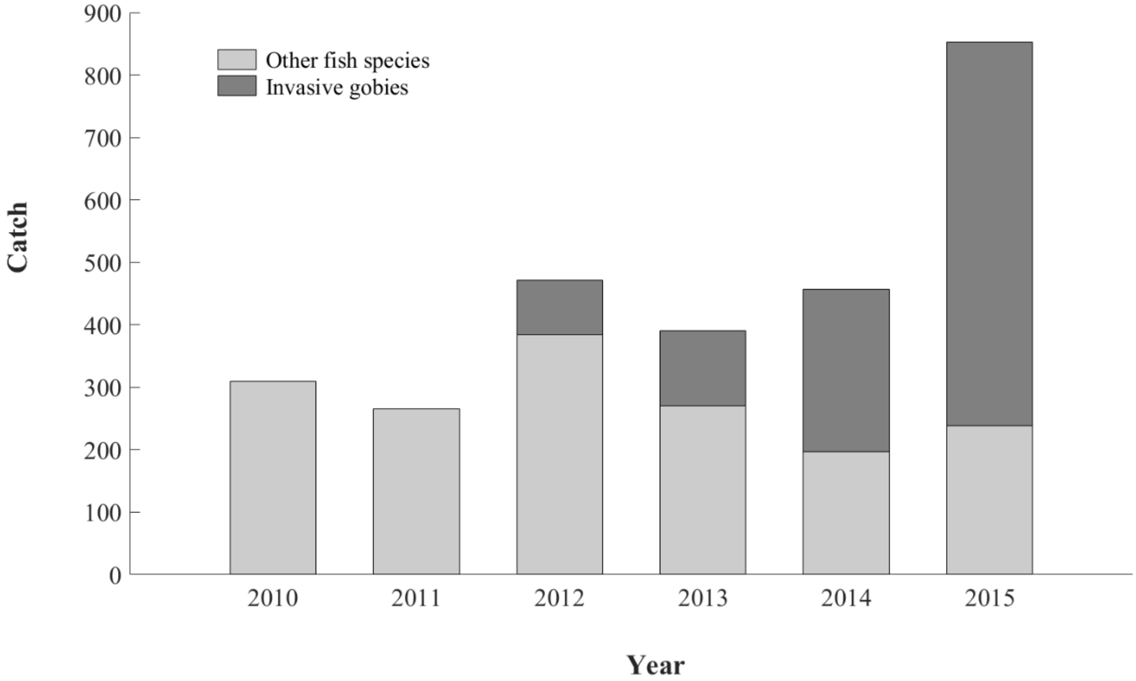

Figure 2: Official catch numbers reported by anglers in the Canton Basel-Stadt show an increase in invasive goby catch numbers. Other fish species include barbel *Barbus barbus,* chub *Squalius cephalus*, asp *Leuciscus aspius*, brown trout *Salmo trutta*, perch *Perca fluviatilis*, zander *Sander lucioperca*, pike *Esox lucius*, rainbow trout *Oncorhynchus mykiss*, bream *Abramis brama*, grayling *Thymallus thymallus,* roach *Rutilus rutilus*, wels *Silurus glanis*, eel *Anguilla anguilla*, carp *Cyprinus carpio* and undefined other fish species. (Source: Canton Basel-Stadt)

MAIN OBJECTIVES

What are ecological impacts of non-native invasive gobies?

How can non-native invasive gobies be managed using preventive measures and population control methods?

How can decision makers and scientists collaborate to tackle the challenges posed by non-native invasive gobies?

SUMMARY OF METHODS AND RESULTS

A transdisciplinary approach to manage non-native invasive gobies

The introduced goby species in the High Rhine immediately caught the attention of stakeholders, including decision makers from cantonal authorities, fishery associations and non-governmental organisations (**Paper I**). To engage in a transdisciplinary dialogue and to co-produce knowledge with decision makers, I co-organised regular workshops to exchange knowledge, set priorities and assess contributions of all involved parties. The kick-off workshop revealed that research output (represented by peer-reviewed papers identified in a literature review) does neither represent scientists' nor decision makers' most pressing research priority – both scientists and decision makers stated that they prioritise research on preventing the spread, whereas most of the research output is on impacts. In general, my assessment of the scientific contribution to these priorities showed that there is a clear lack of knowledge about goby management approaches in the published literature.

Assessing impacts of non-native invasive gobies

Scientists' primary contribution is scientific knowledge on impacts (**Paper I**). To further scrutinise this contribution, I conducted a systematic quantitative literature review on the ecological impacts of round goby on native species in different ecosystems through interactions such as predation or competition (**Paper II**). A systematic quantitative literature review allows identifying the current state of scientific knowledge and locating knowledge gaps in a transparent way (Moher et al. 2009, Pickering and Byrne 2014). The review is focused on round goby and not on other invasive gobies, because round goby impacts are well-studied in different spatial and temporal scales on both sides of the Atlantic, thus allowing a comparison of impacts in different ecosystem contexts and time scales.

The review showed that round goby can profoundly alter ecosystems through predation, competition for food, competition for habitat and spawning grounds, and by providing a new link in the food web. It is striking that round goby has different impacts on native fish species depending on whether it interacts with eggs, juveniles or adults of a species. For example, round goby can act as predator of eggs, compete with juveniles, and represent a novel prey for adults of one and the same species. In addition, round goby impacts depend on the characteristics of the ecosystem under consideration, e.g. due to plastic foraging strategies in different ecosystems (Borza et al. 2009, Borcherding et al. 2013, Brandner et al. 2013*a*), and on the observed time frame, e.g. because predators need to learn about new prey (Carlsson et al. 2009, Pothoven and Madenjian 2013).

A broad range of methods has been applied in the reviewed studies, including laboratory experiments, manipulative studies under semi-natural conditions, before/after studies in the field, stomach content analysis and stable isotope analysis. The breadth of the published studies and the quantitative approach used to explore all available studies indicate that it is neither a lack of studies nor methodological shortcomings that lead to incomplete knowledge. Therefore, one of the most important take-home messages from this study is that we, as scientists, need to be aware of the fact that our knowledge on potential future impacts of an invasive species in a new ecosystem will always be incomplete, regardless of how many studies we perform.

When decision makers ask for detailed knowledge on the impacts of invasive species in their ecosystem of concern before they decide on any action, scientists' incomplete knowledge might hinder a rapid installation of management measures to prevent further spread and establishment of an invasive species. However, in the context of invasions, there is not enough time to wait until scientists can provide complete knowledge about future impacts in the newly invaded ecosystem (Edelaar and Tella 2012). An important step is thus to feed back the state of current knowledge to decision makers in a timely manner, e.g. by workshops, presentations or fact sheets. A central task thereby is to communicate that incomplete knowledge on negative impacts is no reason to neglect possible future impacts, i.e. absence of evidence for negative impacts is not evidence for the absence of negative impacts (Ojaveer and Kotta 2015).

Managing non-native invasive gobies

Several options to manage non-native invasive species exist, e.g. prevention, eradication, containment and long-term population control (see INTRODUCTION above). In the kick-off workshop, scientists and decision makers identified some of these management options as research priorities: research on prevention and research on population control of invasive gobies (**Paper I**).

The preventive approach

In the case of non-native gobies in the High Rhine, ballast water management may still be an option for future invading Ponto-Caspian gobies such as tubenose goby, monkey goby and racer goby. For bighead goby and round goby, prevention is no longer possible for at least parts of the High Rhine. However, given the unique hydrogeographic situation, preventing further spread is a promising option. Commercial ships, probably responsible for the introduction to the High Rhine as has been shown by genetic analyses (**Paper III**), cannot cross the dam in Rheinfelden, which is currently limiting goby range expansion.

This dam also limits recreational boating activities. All boats need to be taken out of the water when they want to cross the dam or relocate from the High Rhine to other water bodies. This provides an ideal opportunity to inspect and clean boats which are proposed to be a vector for secondary dispersal when gobies attach their eggs to boat structures (**Paper IV**). We tested the survival abilities of goby eggs and found high resistance to drag force and desiccation, thus highlighting the importance of a thorough "check – clean – dry" procedure. In the North American Great Lakes, this method may have prevented the spread of new aquatic invasive species (Horvath 2008). Additional preventive measures could be focused on anglers, aquarists, divers and other water sport enthusiasts (Drake and Mandrak 2014, Anderson et al. 2014).

The control approach

To contribute scientific knowledge to the decision making process, I assessed the effectiveness and efficiency of management options to control round goby populations (**Paper V**). First, I identified together with practitioners two control options: removing eggs with spawning traps and removing adults with minnow traps. Then, I tested these options in the field under real conditions to examine their performance.

To assess the control options' effectiveness, i.e., is an option suitable to accomplish the goal, I co-designed a population model simulating different control options under different population scenarios: managing a newly detected population vs. an established population, and managing a population with vs. without propagule flow. To assess the control options' efficiency, i.e., how is an option's relation between effect and effort, the model incorporates a measure of effort for each option under each scenario in units of time. The model was parametrised using life history data and effort data collected in a field study 2012-2016 in the Harbour Kleinhueningen in Basel, Switzerland, and in an extensive literature review.

Parallel to the field study and modelling process, preliminary results were fed back to decision makers in a transdisciplinary process with regular workshops.

Managing a population early after detection needs substantially less effort for eradication than managing an established population. In addition, although removing eggs and adults combined leads to earlier eradication success than removing adults only, total effort for the combined removal of eggs and adults is much higher. Thus, early removal of adults was identified to be the most efficient strategy to reach eradication, highlighting the need for monitoring and early detection. Nonetheless, considerable effort is required: when removing less than 57% of the adult population, eradication is not feasible, even if assuming low survival and fecundity rates for the population. In this case, the goal of the management could be containment with the aim to minimise ecosystem impacts and to prevent further secondary dispersal. Additionally, the inflow of new propagules makes eradication efforts ineffective. Thus, I propose to install such expensive population control measures only in key habitats where inflow can be stopped with a preventive management.

PAPER I

Ambio 2016, 45:280–289
DOI 10.1007/s13280-015-0723-z

PERSPECTIVE

Improving invasive species management by integrating priorities and contributions of scientists and decision makers

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Received: 5 July 2015 / Revised: 12 October 2015 / Accepted: 13 October 2015 / Published online: 5 November 2015

Abstract Managing invasive species is a major challenge for society. In the case of newly established invaders, rapid action is key for a successful management. Here, we develop, describe and recommend a three-step transdisciplinary process (the "butterfly model") to rapidly initiate action for invasion management. In the framing of a case study, we present results from the first of these steps: assessing priorities and contributions of both scientists and decision makers. Both scientists and decision makers prioritise research on prevention. The available scientific knowledge contributions, however, are publications on impacts rather than prevention of the invasive species. The contribution of scientific knowledge does thus not reflect scientists' perception of what is essentially needed. We argue that a more objective assessment and transparent communication of not only decision makers' but also scientists' priorities is an essential basis for a successful cooperation. Our three-step model can help achieve objectivity via transdisciplinary communication.

Keywords Conservation managers · Decision makers · Invasive species · Round goby · Strong objectivity · Transdisciplinary

INTRODUCTION

Invasive species are a major global threat to biodiversity (Sala et al. 2000), and their economic costs have been estimated to be almost 120 billion $/year in the USA (Pimentel et al. 2005) and 12.5 billion EUR/year in Europe (Kettunen et al. 2009). Managing invasive species remains a major challenge because it requires the close cooperation of two key players (Seidl et al. 2013): scientists and decision makers. Traditionally, the scientific community provides a scientifically sound basis for management measures, while decision makers are responsible for the decision about and implementation of management measures. Thus, the main task of scientists is to find causal relationships and publish the results in peer-reviewed papers (Byers et al. 2002), and the main task of decision makers is to decide about management strategies and their implementation (Simberloff 2009). However, for a successful invasive species management strategy, it is necessary to cross these disciplinary boundaries (Heger et al. 2013). A transdisciplinary process allows to reach such a cooperation between scientists and decision makers and "to overcome the mismatch between knowledge production in academia, on the one hand, and knowledge requests for solving societal problems, on the other" (Hirsch Hadorn et al. 2008).

This paper aims to evoke a more objective view of scientists' contributions to a transdisciplinary process. Our perspective of a transdisciplinary process is based on the systems perspective. Put forward by Seidl et al. (2013), the systems perspective aims to facilitate a thorough transdisciplinary interaction between science and society by acknowledging and combining different groups' priorities and decision spaces. We adopt this perspective and formulate a practical three-step approach which we term the "butterfly model". The goal of our model is to combine the priorities and decision spaces of scientists and decision makers into a joint research paradigm for managing invasive species. Our model's three steps are as follows: firstly an objective assessment of decision makers' and our own (scientists') priorities and contributions to the co-production of knowledge (Step 1); secondly a communication of this assessment's results to gain mutual understanding

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between players (Step 2); and finally the establishment of a joint research paradigm based on the mutual appreciation of contributions (Step 3). Following Chalmers (2013), we define a paradigm in the practical sense as such that it coordinates and directs the “puzzle-solving” activity of a group.

We specifically emphasize the need to include ourselves in our roles as scientists. Recent applications of the concept of “strong objectivity” suggest that a transdisciplinary process greatly benefits from such a reflexivity of scientists about their own standpoint (Rosendahl et al. 2015). Importantly, the objectivity here does not mean a fact-based approach as a characteristic of the scientific method. Rather, it is the process of scrutinising our own standpoint as scientists that needs to be more facts-based and more objective. We argue that one major step towards improved objectivity is to achieve more transparency in the communication of our contributions. More directly put, we as scientists should disclose on what basis and priorities our knowledge is built on. In this paper, we exemplify how exactly our three-step approach will play out in reality by means of a topical case study.

Using a case study to demonstrate the first step of a transdisciplinary process

Our case study is a recent fish invasion in the River Rhine (RR) in Switzerland. The RR plays a paramount role socio-economically in Switzerland. It is the largest river of Switzerland and its catchment comprises 88 % of the country’s total area (Fig. 1). Countless restoration efforts have been instated to restore its previously compromised ecosystem health (IKSR 2015, accessed June 24th). Recently, the non-native round goby (*Neogobius melanostomus*) was detected in a Swiss harbour of the RR (Kalchhauser et al. 2013). Round goby is a small (mean total body length around 10 cm) bottom-living fish species native to the Ponto–Caspian region. It is listed as one of Europe’s 100 worst invaders and is believed to be a potential threat to native ecosystems (DAISIE 2015, accessed June 24th). An account of its possible impacts on native species can be found in Hirsch et al. (2015). Because iconic freshwater fish species such as the salmon (*Salmo salar*) could potentially be affected, the round goby invasion is a concern amongst societal groups interested in the RR. This is further elaborated upon in Hirsch et al. (2015). In an unpublished survey, we found that a majority of surveyed societal groups associated to the RR, either as hobbyists or professionally, want to preserve the river ecosystem with its variety of ecological functions. An invasive round goby population is a possible threat to this natural value. We therefore assume that the invasion underway actually is a concern to a relevant part of society. Exploring whether and how a round goby invasion management would be in line with the public opinion at large, and whether and how the European strategy on invasive alien species (Genovesi and Shine 2004) or signed conventions such as the Convention on Biodiversity (Secretariat of the Convention on Biological Diversity 2005) make such a management imperative, is beyond the scope of this article.

Because of the special geographic situation, the restricted range of the population, and because round gobies are unlikely to substantially expand their range through natural dispersal (Fig. 1), the chances for success of a rapid management are high. Therefore, in the framing of our case study, we apply our proposed three steps towards a transdisciplinary process for a management of round goby. We follow all three steps as follows:

Step 1: Objective assessment. To assess our own priorities and contributions to the co-production of knowledge as scientists in practice, we asked the following questions:

(a) What are decision makers’ and scientists’ research priorities concerning the management of round goby in the River Rhine, and do they match?
(b) Are decision makers’ and scientists’ research priorities reflected in the existing body of scientific knowledge?

We answered these two questions using two approaches: a workshop survey and a quantitative literature review. While surveying decision makers’ priorities at a transdisciplinary workshop, we also surveyed scientists’ own priorities concerning round goby research. The research priorities of both groups were then compared to scientists’ main contribution to the process, i.e. scientific knowledge represented in peer-reviewed papers.

Step 2: Communication. Based on the results of this assessment, we review existing recommendations and conditions that favour a successful communication within a transdisciplinary project. We give specific hints on how a transparent communication in our case study and in general could be implemented.

Step 3: Joint research paradigm. To outline the final step in our model, we combine the results and insights from the first two steps. We propose how the establishment of a joint research paradigm can proceed based on the first two steps. Finally, we discuss how joint research paradigms can be put into practice in the context of species invasions.

METHODS

Workshop survey

Following the human–environment system approach to a transdisciplinary process (Seidl et al. 2013), we started by transparently assessing decision makers’ and scientists’

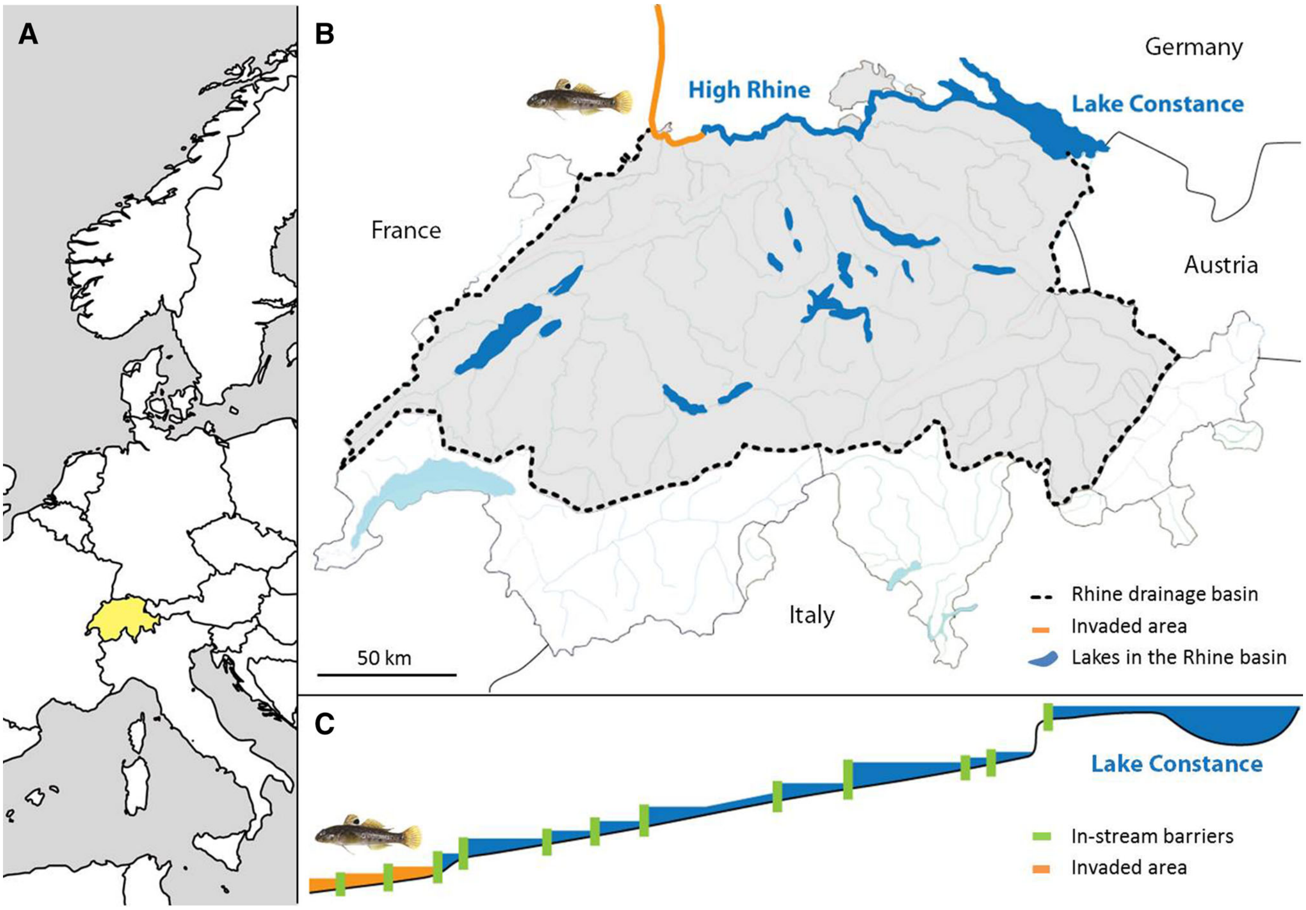

Fig. 1 The geographical situation of the recently established round goby population in Switzerland makes a management probable. **A**, **B** Round goby (*Neogobius melanostomus*) was first detected in Switzerland 2012 in the Rhine harbour in Basel. **C** Gobies are bad swimmers and a series of 12 in-stream barriers (hydropower dams) in the River Rhine (RR) upstream of Basel may prevent the natural dispersal of round gobies further into the RR. However, human recreational activities can aid natural dispersal by translocating invasive species. For example, each of the in-stream barriers is crossed by recreational boats that could provide means of transport for round gobies and allow them to disperse further (own manuscript, in review). Further upstream the RR lies Lake Constance, a pre-alpine lake which features socio-economically important recreational and commercial fisheries (Hirsch et al. 2013). Because round gobies are unlikely to naturally disperse into the lake, preventive management is a real possibility, provided that measures to halt the translocation of round gobies are implemented rapidly. If the localised population is not rapidly managed, it will most likely spread and increase its range, making a management less feasible and more expensive (Vander Zanden and Olden 2008)

contributions to the process. Decision makers, in our context, are not limited to political decision makers, but also include societal decision makers (Secretariat of the Convention on Biological Diversity 2005; Nentwig 2007; Hirsch Hadorn et al. 2008). Thus, decision makers include relevant stakeholders that both hold a stake and have technical experience in the topic, and non-certified so-called "experience-based experts". These stakeholders and non-certified experts have a specialist expertise in a field relevant to the case study of round goby and could be divided into two groups: representatives of recreational fisheries and conservation managers. Representatives of recreational fisheries are e.g. fisheries wardens or opinion leaders of local fishing clubs. Conservation managers are local environmental authorities or non-governmental environmental agencies. In contrast to these non-certified "experience-based experts", we defined invited scientists from other institutions and ourselves as "certified experts" with a specialist expertise in a field relevant to the research. For a detailed discussion of different demarcations between such groups, please refer to Collins and Evans (2002) and Defila and Di Giulio (2015).

The policy and decision-making processes on invasive species in Switzerland can be separated into two levels, the federal level and the cantonal level. At the federal level, there are over-arching policies issued such as the "Strategy on Invasive Alien Species" (Federal Office for the Environment Switzerland 2015). At the cantonal level, there are more specific regulations in place (such as the "Ordinance on the Release of Organisms into the Environment", Swiss

Federal Council 2008) which are followed and enforced by local authorities. In appreciation of this complex decision-making structure, we had representatives from both authorities joining the group of decision makers (see above).

Shortly after round goby arrival, we installed yearly decision maker workshops to share the current state of scientific knowledge and to discuss management methods. For the kick-off workshop, we chose a three-phase approach. In the first phase, the participants were informed about the round goby case in the plenum. In the second phase, the participants were allocated to five brainstorming groups consisting of maximum five persons with different backgrounds. In each group, at least one scientist was present. To reach “strong objectivity” (sensu Rosendahl et al. 2015), scientists need to openly communicate their role and their standpoint in transdisciplinary research. During the brainstorming process about future round goby management, a set of research priorities evolved. In the last phase, the participants joined again in the plenum and the research priorities from all groups were presented. Following the multi-voting variant, a form of cumulative voting, each participant could allocate five votes to the research areas (Bens 2012). It was possible to allocate several votes to the same area, but not more than three votes. Votes were cast during a workshop break and could be assigned to groups (decision makers and scientists) via group-specific colour codes, but not to individuals.

Literature review

To evaluate how decision makers’ and scientists’ priorities are reflected in the contributions (i.e. peer-reviewed papers) of the broader scientific community, we performed a systematic quantitative literature review following the PRISMA statement (Moher et al. 2009). This method allows to objectively identify the current state of scientific knowledge (Pickering and Byrne 2014). Because invasive round gobies are well studied in different spatial and temporal scales on both sides of the Atlantic, they provide an ideal case study to assess the traditional contributions of scientists to a transdisciplinary process in the context of invasions.

We carried out four literature searches covering four research priorities that emerged in the workshop: impacts on native species, early detection methods, preventing the spread and control measures. The fifth priority “costs of management measures” was covered within the results of prevention and control measures. The literature searches were carried out in the web of knowledge database (http://webofknowledge.com) using the search terms ‘round goby’ and ‘*Neogobius melanostomus*’, combined with search terms for one of the four priorities. The search terms were separated by Boolean operators ‘AND’ or ‘OR’.

For all four searches, we followed the steps outlined in the PRISMA statement (Moher et al. 2009). In a first step, duplicates were removed. In a second step, papers were screened to identify relevant primary research articles. Only peer-reviewed studies in English were considered. All review articles, books, book chapters and grey literature such as reports were excluded. We acknowledge that non-peer reviewed publications can be a useful source of information for invasive species management. However, we were primarily interested in an assessment of the role of scientists as a hub for scientific knowledge. In particular, we wanted to make the scientific knowledge contribution to the transdisciplinary process more transparent by scrutinising scientists’ prime sources of knowledge: peer-reviewed papers. Despite substantial shortcomings of the peer-review process, it is still the highest standard in science and peer-reviewed papers are compiled in databases that can be mined in a transparent way.

The full text of the remaining peer-reviewed papers was assessed for eligibility (see Table 1 for inclusion criteria). For a paper to be deemed relevant in the category “impact on native species”, it must provide a quantitative analysis of round goby interactions with other species. These impacts must be measurable, but not necessarily significant (Davidson and Hewitt 2014; Ojaveer and Kotta 2015). Impacts must be based on results from a field study or laboratory experiments, including e.g. stomach content analysis, stable isotope analysis or behavioural experiments. For a paper to be deemed relevant in the categories “early detection”, “prevention” or “control”, it must provide basic research towards the measure, including modelling, or a practical application of the measure, either in the laboratory or in the field. Basic research is defined as research towards understanding fundamental processes without the goal of applying the results in a practical context; applied research is conducted with the clear goal of applying the results in a practical context.

The reference lists of relevant papers were screened for additional papers, which entered the same process as papers found in the database. The information of relevant papers in each research area was entered in a personal spreadsheet database (Pickering and Byrne 2014).

RESULTS

Workshop survey: Decision makers’ and scientists’ research priorities match

The workshop survey revealed a match of priorities between decision makers and scientists; both prioritise research towards preventing the spread of an establishing invader. The multi-voting process with 13 decision makers

Table 1 Inclusion criteria for papers in each research area and resulting search terms

Research area	Inclusion criteria	Search term used	Last search carried out on
Impacts on native species	Quantitative analysis of round goby interactions with other species such as predation, competition for food or shelter and availability of a new prey. Impacts are based on data from field studies or laboratory experiments, including, e.g. stomach content analysis, stable isotope analysis or behavioural experiments	('round goby' OR 'neogobius melanostomus') AND ('diet' OR 'predation' OR 'prey' OR 'competition' OR 'impact' OR 'effect')	08/04/2015
Preventing the spread	Basic or applied research on how to prevent the spread of round goby, e.g. modelling of vectors, risk assessments with policy implications	('round goby' OR 'neogobius melanostomus') AND ('prevention' OR 'preventive' OR 'management' OR 'spread')	05/06/2015
Early detection methods	Basic or applied research on how to detect round goby early, e.g. eDNA, monitoring by anglers	('round goby' OR 'neogobius melanostomus') AND ('eDNA' OR 'e-DNA' OR 'environmental DNA' OR 'early detection' OR 'monitoring')	05/06/2015
Control measures	Basic or applied research on how to control round goby, e.g. predatory control, piscicides, physical removal, population modelling	('round goby' OR 'neogobius melanostomus') AND ('control' OR 'eradication' OR 'management')	05/06/2015
Costs of measures	Reference to the costs of methods or measures	Directly located in papers of the other four areas	

and 9 scientists showed that both groups' first priority is research on preventing the spread of round goby (23.4 and 24.5 % of cast votes, respectively; Fig. 2). Scientists' next priorities are research about impacts on native species (8.5 %), early detection methods (6.4 %) and control measures (5.3 %). Decision makers' next priorities are research about control measures (16 %), impacts on native species (7.4 %), early detection methods and costs of management measures (both 4.3 %).

When priorities of the two decision maker groups (recreational fisheries and conservation managers) are analysed separately, some differences between the two groups become apparent: conservation managers are more interested in impacts' research, early detection and cost of management. However, both groups almost equally prioritise research on the prevention of spread and control measures (Fig. 2).

Literature review: Research contributions and research priorities do not match

The quantitative literature review revealed a mismatch between scientists' priorities and the current state of published scientific knowledge. The systematic quantitative literature review focussing on the five priority areas showed that most published research results are about impacts of round goby on native species. There seems to be a lack of publications on preventive management options that have received the highest standard of scientific quality control, i.e. peer review (Fig. 2). The systematic quantitative literature review showed that the large majority of peer-reviewed papers (76 %, $n = 113$) is about round goby impacts on native species. Research results on control measures are presented in 4 % of papers ($n = 6$), on preventing the spread in 14 % ($n = 21$) and on early detection methods in 1 % ($n = 2$). Six papers (4 %) refer in some way to costs of measures.

DISCUSSION

Our study aimed to evoke an objective view of scientists' research priorities and contributions to the management of an invasive species. To this end, we proposed the butterfly model consisting of three steps, the first of which we tested "in the field" by analysing data from a transdisciplinary workshop (Fig. 2). Taking the first step, we objectively assessed scientists' and decision makers' research priorities concerning the management of an invasive species. An objective literature review revealed that the knowledge scientists actually contribute to the process does not match the research they prioritise, whereas both groups' research priorities match. We discuss these findings in detail and present an outlook for steps 2 and 3 in the transdisciplinary process (Fig. 3).

Step 1: Objective assessment

To identify the gap between research priorities and research contributions among or within groups is a fundamental first step of a transdisciplinary process under the concept of strong objectivity. The concept posits that

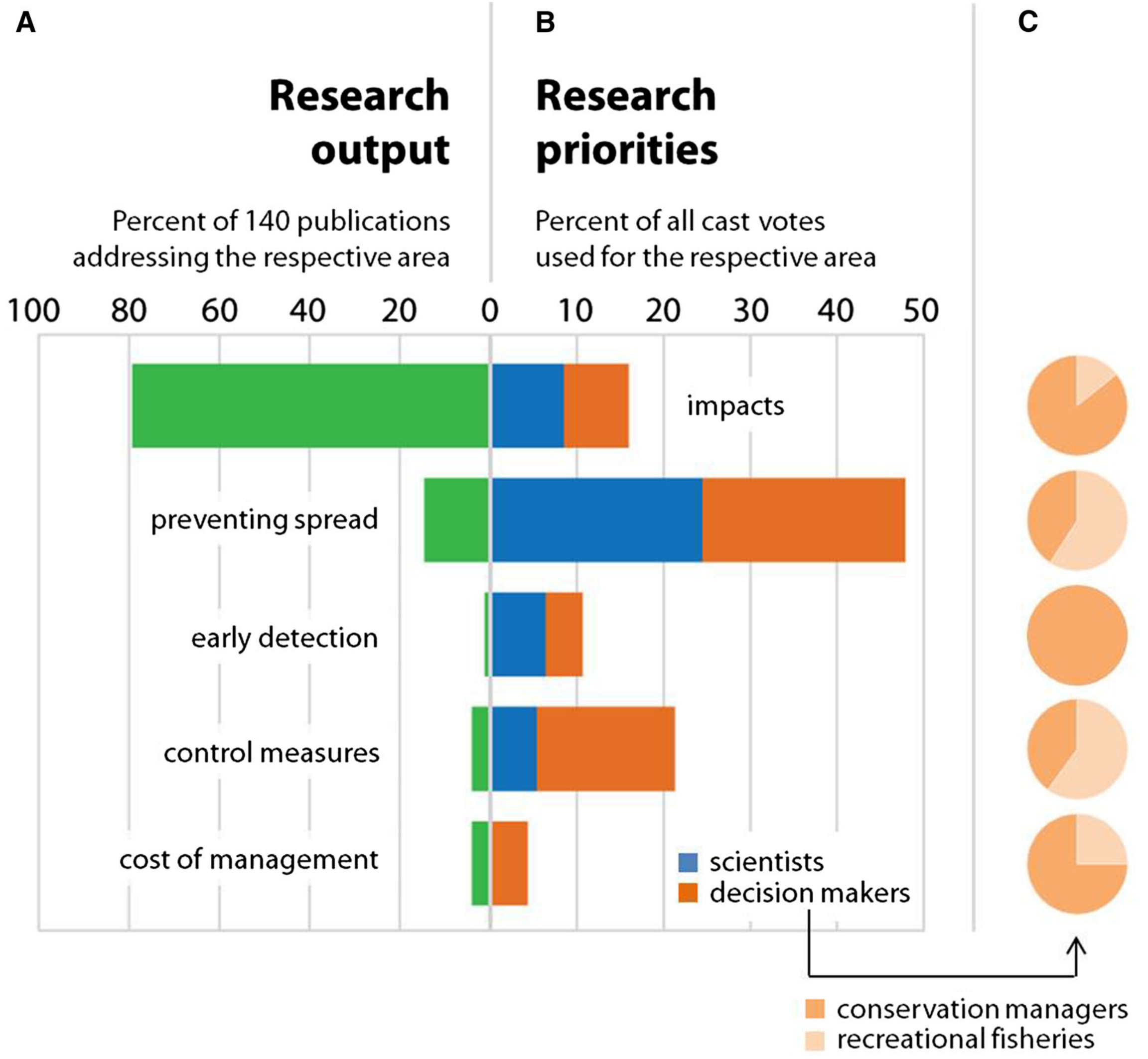

Fig. 2 Research contributions and research priorities. **A** Research contributions represented by peer-reviewed papers identified in the literature review ($n = 140$) do not match the research priorities of either decision makers or scientists: most research covers impacts of round goby on native species. **B** Research priorities of decision makers ($n = 13$) and scientists ($n = 9$) identified in the workshop survey match: both groups prioritise research towards preventing the spread of round goby. **C** Detailed presentation of votes cast by subgroups of decision makers: conservation managers and representatives from the recreational fisheries

strong objectivity is needed to instigate a fruitful communication between players in and outside academia (Rosendahl et al. 2015). Our literature review revealed that scientists' primary contributions in the form of peer-reviewed papers are insufficient as a knowledge basis for invasive species management: most knowledge is on impacts of round goby and not on its management. We deemed it relevant to further scrutinise the knowledge that scientists actually can contribute to the process, which is knowledge on round goby impacts. To accomplish this, we conducted an in-depth review of publications dealing with round goby impacts alongside our transdisciplinary project. The results are presented and discussed in detail in Hirsch et al. (2015).

From an objective standpoint, the mismatch between priorities and existing knowledge is especially interesting. As evidenced by numerous conventions and statements, the international scientific community views prevention as the "gold standard" in invasive species management (Leung et al. 2002; Cook et al. 2007; Keller et al. 2008; Vander Zanden and Olden 2008; Vitule et al. 2009; Simberloff et al. 2013). Within the scientific community, there is a solid knowledge on the fact that acting timely is necessary to prevent the spread of an invasive species. This knowledge is based on empirical studies which have repeatedly shown how effective early action against invasive species can be (Horan et al. 2002; Lockwood et al. 2005; Keller et al. 2008; Vander Zanden et al. 2010; Edelaar and Tella

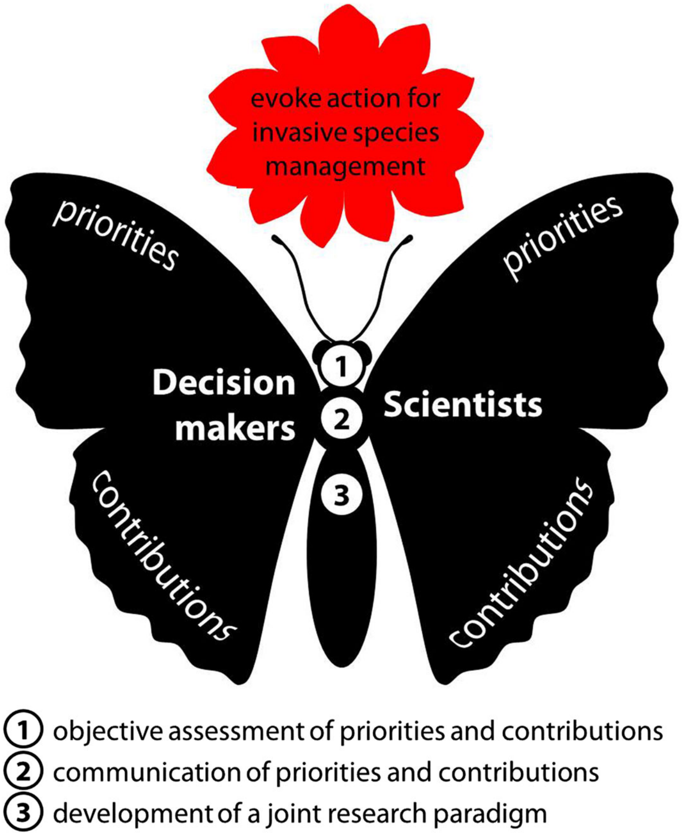

Fig. 3 The butterfly model. Decision makers and scientists need to engage in a three-step transdisciplinary process to evoke action for invasive species management

2012). Despite this agreement on the importance of prevention, there seems to be a lack of studies about scientifically tested, specific and practical prevention measures. The underlying mechanisms behind this discrepancy might be explained by the fact that scientists do not get credit for publishing papers on successful preventive management or even research towards it; vice versa, decision makers are rewarded for managing, not for publishing (Simberloff 2009).

Our finding of a mismatch between scientists' priorities and scientists' contributions to the process of knowledge co-productions has implications for the way we interact with decision makers. One often-mentioned reason why decision makers feel uninformed on management of invasive species is that the available knowledge is system and location specific (Walsh et al. 2015). So should scientists devote more time and resources to publish peer-reviewed papers on specific management measures? We argue that they should not. More specific knowledge on management options, even if published as peer-reviewed papers, will inevitably be even more system specific. Specific measures need to be tailored solutions to be successfully implemented.

While we focus in this article on scientists' contributions to the process, it will also be necessary to acknowledge in all three steps the different contributions of different decision makers (Barreteau et al. 2010). As our results show, priorities of the two groups of decision makers, i.e. recreational fisheries and conservation managers, differ to some extent (Fig. 2), and so will their contributions to the transdisciplinary process. Conservation managers, for example, can provide knowledge on the practical aspects of management implementation and enforcement; recreational fisheries, for example, can provide local knowledge on the invasion front through community-based monitoring (see Conrad and Hilchey 2011 for a review on citizen science and community-based monitoring). Again, we argue that a full disclosure of the underlying motivations for these priorities will improve the objective assessment of all contributions.

In any case, there is no substitute to a transdisciplinary process towards a joint research on and implementation of management. In the second step within this process, the fact that scientists cannot deliver the knowledge they themselves deemed as their essential contribution needs to be understood and communicated. The discrepancy between what the scientific community has in store and what is needed in the field needs to be openly discussed and solutions need to be found together.

Step 2: Communication

The second step is to openly communicate how priorities and knowledge match or mismatch by and among both groups (Fig. 3). Based on the concept of "strong objectivity", we expect that information on our own and others' priorities and knowledge facilitates reflexivity on each groups' contributions to the process. In this paper and in Hirsch et al. (2015), we aimed at disclosing the scientific basis of such priorities to facilitate reflexivity among us as scientists. This approach of an objective assessment and subsequent reflexivity can be the fundament of communication leading to rapid management action for two reasons. Firstly, neither player is left in the dark about where other players' contributions come from. Secondly, as sources of contributions are transparent, it is less likely that either player is waiting for knowledge or decisions the other player cannot and will not deliver. For example, our literature review indicates that impacts of a specific species can indeed be profound, but there is almost no scientific (i.e. peer-reviewed) knowledge on e.g. the relative effectiveness of different management measures.

Making scientific knowledge on invaders easily available to decision makers can improve the chances of a successful management (Drolet et al. 2014). There has been a great deal of attention devoted to what decision makers want from scientists and what scientists deliver. For example, decision makers want to receive more specific information on management measures (Walsh et al. 2015). In such a context, it is easy to simply aim for an improved unidirectional process of "order and delivery" such that decision makers request information and that scientists produce knowledge to eventually satisfy this request, without any feedback amongst these two groups involved.

Our study suggests that, in the current situation, scientists do not hold the primary knowledge monopoly on management of invasive species. Scientists do not possess a body of knowledge within their community that can simply be transferred to decision makers. Also here, there is no substitute to a transdisciplinary process. Scientists and decision makers need to co-produce the knowledge that is most needed for invasive species management. It has to be avoided that decision makers wait for "secured scientific facts", while in the meantime the invader can establish and spread. Thus, scientists need to communicate that they do not have a tool box of tried-and-true management options from which the decision makers can pick. Instead, scientists and decision makers together have to appreciate their own and the other groups' contributions to a joint research paradigm towards invasive species management (Fig. 3). Rather than playing the part of delivering knowledge, scientists can co-create knowledge together with decision makers if both groups follow a joint research paradigm. This process matches the transdisciplinary ideal of "science with" rather than "science for" society (Seidl et al. 2013).

Step 3: Joint research paradigm

The third and final step towards invasive species management will be to establish a joint research paradigm (Fig. 3). In the context of a transdisciplinary process, a research paradigm needs to be controlled by both decision makers and scientists (Seidl et al. 2013). The ultimate outcome of the joint research paradigm needs to be co-produced knowledge about which measures are efficient and effective. Also in other cases of environmental management, the timely involvement of decision makers allowed a co-production of knowledge about successful management measures (Burkhardt-Holm et al. 2005; Cowling et al. 2008; Reed 2008; García-Llorente et al. 2011). The scientific output in the form of efficient management measures would then also be implemented faster, more smoothly and with better compliance when both players will have planned it together. Scientists and decision makers have sought together to "maximize the trade-off between accuracy and utility" of a management from the beginning (Kornis et al. 2013).

These joint efforts are often published in technical reports addressing a specific situation such as the "Summary of the Rapid Response to Round Goby (*Neogobius melanostomus*) in Pefferlaw Brook" by Dimond et al. (2010). The existence of such local solutions has implications for the objective assessment of scientists' contribution to invasive species management. Specific management recommendations are typically not published as peer-reviewed papers, suggesting that epistemic knowledge of scientists is not something that is created within the scientific community and can then be "transferred" to decision makers where it is awaiting application. In general, the power and applicability of local solutions jointly established with local decision makers is an important reason why transdisciplinary research can lead to successful management measures (Hirsch Hadorn et al. 2008). Yet, the acknowledgement of how well such local solutions work and the appreciation of research towards them have been found to be under-represented within the scientific community (Simberloff 2009).

We suggest that our butterfly model can facilitate research towards such local and specific management solutions for three reasons: firstly invasion biologists who objectively assess their own priorities and contributions will realise that the existing knowledge within their community might not match the priorities needed for a rapid management. Secondly, if scientist disclose the basis of their knowledge contributions and communicate this to decision makers, both groups are more likely to appreciate the need for a joint research paradigm (Seidl et al. 2013). Thirdly, if both groups have disclosed the sources or the knowledge basis of their own priorities and contributions, it will be easier to collaborate on an equal footing (Bayliss et al. 2013; Rosendahl et al. 2015).

CONCLUSIONS

Our study aimed to evoke an objective view of scientists' role within a transdisciplinary process. Importantly, we found that a "strong objectivity" that includes us as scientists in the assessment of priorities can reveal relevant and unexpected results. Our three steps towards the installation of a joint research paradigm demonstrate how an objective assessment of whether priorities and contributions match can be a solid basis for further communication. By realising what scientists prioritise and what they deliver, they can become an integral rather than auxiliary part of the transdisciplinary process. On a broader scale, our butterfly model gives clues how a mutual learning between science and society can be put into practice. In the context of invasive species, we conclude that more objectively assessing contributions to a co-production of knowledge, i.e. disclosing priorities and knowledge sources, can allow for a more efficient and timely installation of management measures.

Acknowledgements We thank all workshop participants and organisers, Catherine Cornaz for assistance with the literature review, Hannes Weigt, Philipp Mayer and an anonymous reviewer for helpful comments on an earlier version of this manuscript. This project was funded by a special grant from the Federal Office for the Environment, Switzerland, the Research Centre for Sustainable Energy and Water Supply (FoNEW), the canton BS, plus cantonal lottery funds of AG, BL, SO. The authors declare no conflict of interest.

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PAPER II

Ambio 2016, 45:267–279
DOI 10.1007/s13280-015-0718-9

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REVIEW

What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check

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Patricia Burkhardt-Holm

Received: 5 July 2015 / Revised: 12 September 2015 / Accepted: 24 September 2015 / Published online: 5 November 2015

Abstract Invasive species are one of the greatest threats to biodiversity worldwide, and to successfully manage their introductions is a major challenge for society. Knowledge on the impacts of an invasive species is essential for motivating decision makers and optimally allocating management resources. We use a prominent invasive fish species, the round goby (*Neogobius melanostomus*) to objectively quantify the state of scientific knowledge on its impacts. Focusing on how native fish species are affected by round goby invasions, we analyzed 113 peer-reviewed papers and found that impacts are highly ecosystem and time scale dependent. We discovered round goby impacts to be profound, but surprisingly complex. Even if identical native species were affected, the impacts remained less comparable across ecosystems than expected. Acknowledging the breadth but also limitations in scientific knowledge on round goby impacts would greatly improve scientists' ability to conduct further research and inform management measures.

Keywords Invasive species impact · Management · Prevention · Round goby · *Neogobius melanostomus*

INTRODUCTION

Invasive species pose one of the most serious threats to ecosystems in general and aquatic ecosystems in particular (Strayer 2010). For example, the number of introduced fish species still continues to grow (Blanchett et al. 2009; Ellender and Weyl 2014). Introductions occur either intentionally, e.g., by releasing aquarium fishes or by stocking, or unintentionally, e.g., in ballast water of cargo ships (García-Berthou et al. 2005). Some of these numerous fish introductions are a risk to native ecosystems and, if ecosystem services are compromised, eventually to humans (Gozlan 2008). The increasing number of introductions and the uncertainty about whether introductions will lead to an invasion with ecological impacts poses a challenge to decision makers. Decision makers prioritize management efforts on those species that are expected to have the most adverse impact (Simberloff 2003). Because not all potentially harmful introductions can be simultaneously managed, decision makers have to "maximize the trade-off between accuracy and utility" of a management (Kornis et al. 2013).

The process of a successful management is multidisciplinary and requires at least three main players to efficiently interact on an equal footing: decision makers (in our context especially ecosystem managers), scientists, and the general public (Bayliss et al. 2013; Seidl et al. 2013). The ontology of these interactions has received much scientific attention (Lawrence 2015). In this paper, we focus on the primary contribution of scientists to the process: providing scientific knowledge (Walsh et al. 2015; N'Guyen et al. 2015). One key aspect of scientific knowledge that is relevant to decision makers is the information on how harmful a recently detected non-native species can become. For fish invasions, tools such as the fish invasiveness scoring kit (FISK) have been developed to allow decision makers a risk assessment and to ensure that management actions are commensurate with the level of risk posed by an invader (Copp et al. 2009). FISK assesses the risk of a non-native fish becoming invasive in a certain ecosystem based on 49

Philipp E. Hirsch and Anouk N'Guyen shared first authorship.

Electronic supplementary material The online version of this article (doi:10.1007/s13280-015-0718-9) contains supplementary material, which is available to authorized users.

questions about the species' biogeography, invasion history, biology, and ecology.

These tools should help prevent the introduction of potentially harmful species that have had demonstrable ecological impacts elsewhere. Countries such as New Zealand or Australia use risk-assessment tools as basis for the customs authorities to implement import bans of certain species (Keller et al. 2007, 2008; Campbell 2011). These tools, however, are of limited use if a non-native species has already established a localized population and decision makers need to decide whether and how such a potential source population should be managed (Gozlan et al. 2010). For example, in Europe alone, more than one non-native species per year becomes established (EU 2009). Decision makers cannot simultaneously instigate a preventive management against the spread of all non-native species. Rather, they want to know which one will have the most severe impacts, because the most important reason to manage a localized non-native population is to prevent its impacts. The safest way to know whether a non-native species will have impacts in a new ecosystem is knowledge about its impacts in already invaded ecosystems (Daehler and Gordon 1997; Simberloff 2003; Bayliss et al. 2013). Scientists' primary contribution to a prospective preventive management is knowledge about the impacts a potential invasive species has had elsewhere.

Scientifically, there has long been a call for more structured reviews providing an objective account of invasion processes (Heger et al. 2013). There have been several new approaches put forward that might improve the predictive capabilities of invasion biologists. For example, the analysis and comparison of functional responses of invaders and native species could improve impact assessments because invasive species that are more efficient resource consumers than native species should have more severe impacts (Dick et al. 2014).

Whether any impacts of non-native species become detected is a matter of time. Biological invasions are characterized by time lags: the introduction lags behind vector activity, the population growth lags behind establishment, and so on (see Crooks 2005 for a review on time lags in invasion biology). Eventually, also the impacts of an invasive species lag behind its population increase and its areal distribution. Even the per-capita impact of an invader can change over time. For example, over time, the invader might evolve aggressive behavior or native species might evolve to better cope with the new predator or prey. Thus, an objective analysis of any invaders' impacts needs to consider temporal aspects of its invasion. Decision makers need to be informed about time lags, too. For example, the decision to spend a lot of resources to contain an invasion in its early stages is informed by the knowledge that population growth lags behind establishment and a population is best managed when it is still in its post-establishment lag phase (Crooks 2005).

Our aim here is to use a topical case study to objectively analyze scientists' knowledge contribution in the form of peer-reviewed papers to inform a preventive management. Our study species is the round goby (*Neogobius melanostomus*; Fig. 1). The round goby is a small bottom-living fish native to the Ponto-Caspian region. This species is listed among the 100 worst invasive species in Europe (DAISIE 2015). In 1990, it was found both in the Baltic Sea and in the Laurentian Great Lakes, probably after being introduced by ballast water (Corkum et al. 2004). Since then, it has been spreading rapidly (Kornis et al. 2012). The building of waterways and the increased commercial and recreational shipping across Europe and North America is believed to have accelerated the spread of round goby by providing pathways and vectors for active and passive dispersal (Britton and Gozlan 2013; Roche et al. 2013).

Round goby was discovered 2012 in the Rhine in Switzerland (Kalchhauser et al. 2013). The Swiss population is currently rather localized to some 15 km of river, but it might spread further into Swiss and German waters such as the River Aare or Lake Constance. This secondary spread concerns scientists and decision makers. It also bothers the general public when, e.g., iconic native fish species are negatively affected by round goby. Therefore, we instigated a transdisciplinary project to prevent the further spread of round goby into Switzerland. A first joint workshop of scientists and decision makers within this project revealed that scientific knowledge on round goby prevention and control would be needed, but is sparse. The vast majority of published knowledge on round goby is about its ecological impacts (N'Guyen et al. 2015). This review aims at objectively quantifying the scientific state of knowledge on round goby impacts. We consider such an objective assessment of scientists' knowledge contribution as an important basis for a successful management. This successful management includes the prevention of further spread and the control of an established population. To reach any of these goals, a cooperative process bridging disciplines is needed. An objective assessment of each players' contribution, in our case, scientific knowledge, facilitates such a successful cooperative management across disciplines (Rosendahl et al. 2015).

Given the fact that most scientific papers on round goby are about its impacts on native species, we expected to find clearly demonstrable impacts across invaded ecosystems. We were especially interested whether different studies found similar impacts of round goby on native fish. Therefore, we expect that, ultimately, the knowledge on impacts that round goby had in other ecosystems will improve the chances of a successful preventive management of their secondary spread.

Fig. 1 **a** Round goby (*Neogobius melanostomus*) displaying the characteristic black spot on the first dorsal fin and its fused pelvic fin. **b** Gobies amassing on an unhooking mat during a recreational fishing event by the Mosel, a river in Germany where round gobies have established and spread. **c** Study case: the Harbour Kleinhüningen, Switzerland, where round gobies have been first detected in 2012. Photo credits: **a** Magnus Thorlacius, **b** Guido Eberhardt, **c** Philipp E. Hirsch

MATERIALS AND METHODS

We aimed to explore the known impacts of non-native round goby on native species. To this end, we conducted a systematic quantitative literature review. This method allows us to objectively identify overlaps and gaps in current scientific knowledge (Pickering and Byrne 2014). Following the PRISMA statement (Moher et al. 2009), we analyzed the published literature on the ecological impacts of round goby on native species in different ecosystems. We define ecological impact as measurable outcomes of interactions that include any of the following: predation, competition for food or shelter, and availability of a new prey. These interactions must lead to quantitatively measurable changes, but the changes do not have to reach a certain significance level to be considered in our review (Davidson and Hewitt 2014; Ojaveer and Kotta 2015). The literature search was carried out in the web of knowledge database (http://webofknowledge.com) using the search terms 'round goby,' '*Neogobius melanostomus,*' 'diet,' 'predation,' 'prey,' 'competition,' separated by Boolean operators 'AND' or 'OR': ('round goby' OR 'neogobius melanostomus') AND ('diet' OR 'predation' OR 'prey' OR 'competition'). The last search was conducted on April 8, 2015.

The resulting list of publications was first screened for duplicates, which were removed. In a second step, papers were screened to identify relevant primary research articles. We included only peer-reviewed studies in English providing a quantitative analysis of round goby interactions with other species based on results from a field study or laboratory experiments, including, e.g., stomach content analysis, stable isotope analysis, or behavioral experiments. All review articles that did not present original research, books, book chapters, and gray literature such as reports were excluded. We acknowledge that these forms of publications might also contain information on round goby impacts. However, our aim was to objectively quantify the scientific knowledge on impacts. Because scientific papers are filed in web of knowledge in a structured and accessible way and because peer review is, despite substantial shortcomings, the highest standard in science, we feel our focus is justified. Reference lists of all papers were screened for additional papers, which entered the same process as the papers found in the web of knowledge.

The information on impacts was extracted from the paper and entered in a personal spreadsheet database (Pickering and Byrne 2014). Studies and species were then structured and grouped with Excel®'s built-in filter function in three categories: impacts on invertebrates, impacts on a specific vertebrate described in one study, and impacts on a specific vertebrate described in more than one study. Here, we focus on round goby impacts on native fish as predator, competitor, or prey. From a management perspective, the impact on native fish is likely to receive the most attention. Fish directly or indirectly provide a variety of important ecosystem services and are of socioeconomic value (Holmlund and Hammer 1999). For example, native brown trout (*Salmo trutta*) are the most popular game fish in Switzerland, and expensive restoration programs supported by the public have been installed to conserve the native Atlantic salmon (*Salmo salar*) in the Rhine (Anonymous 1998; Burkhardt-Holm et al. 2002). Because the above-mentioned attractiveness of fish species applies in other countries as well, most of the papers published on round goby impacts in other ecosystems focus on fish. This review is therefore also driven by the concern that iconic freshwater fish species will be affected by round goby invasion and that this effect deserves particular attention when communicating with decision makers and the general public.

RESULTS

We screened 168 papers according to our criteria to identify relevant primary research articles (Fig. 2). After excluding reviews, theses, reports, and studies not meeting the inclusion criteria (e.g., to provide a quantitative assessment of round goby impact on native species), the results of 113 relevant papers were entered in the personal spreadsheet database. Finally, to analyze whether different studies found the same round goby impacts on the same native species, papers and species were grouped as described above. We show and discuss here only impacts on fish species that are represented in more than one study, to allow a comparison of the impacts between different ecosystems. For full disclosure and to facilitate future data mining, we provide the spreadsheet as electronic supplementary material (Table S1). An exemplary presentation of how this detailed information allows comparing impacts across ecosystems can be found in Table 1, where we present the available information about impacts of round goby on Eurasian perch (*Perca fluviatilis*) in a structured and comprehensive way. Supplementary Table S2 provides the same information for yellow perch (*Perca flavescens*).

A broad range of methods have been applied in the reviewed papers, including laboratory experiments, manipulative studies under semi-natural conditions, before/after studies in the field, stomach content analysis, and stable isotope analysis. The literature review showed some profound, but ambiguous impacts of round goby on native fish species (Table 2). We summarize and structure these based on a taxonomic grouping of the affected species: native benthic fish, predatory percid fish, predatory gadid fish, and predatory salmonid fish.

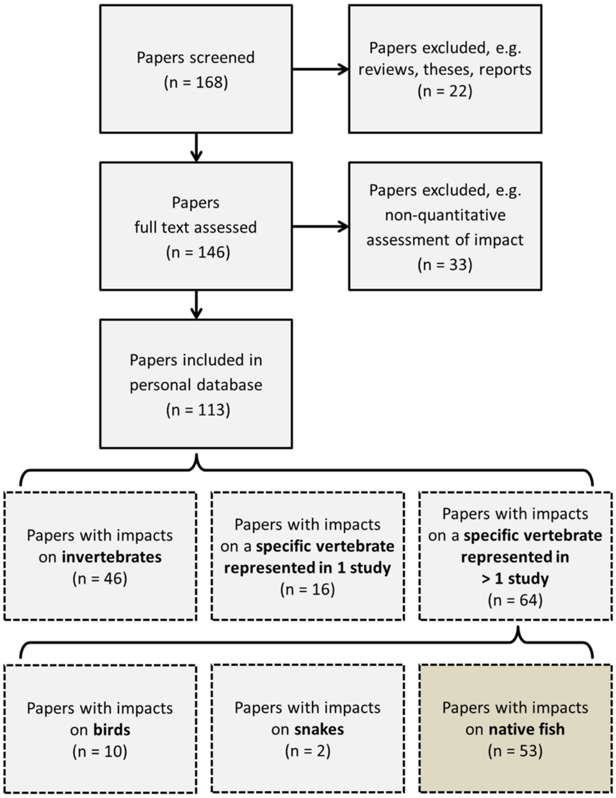


Fig. 2 Numbers of screened and included papers for the literature review. Papers can enter several categories in the personal database, e.g., when a paper studied goby diet and goby as prey item, it is included in the category “invertebrates” as well as “vertebrates.”

Impacts on native benthic fish

The impacts of round goby on benthic fish have been investigated in 13 of the 53 papers. Logperch (*Percina caprodes*) and round goby compete for food and shelter under laboratory conditions (Balshine et al. 2005; Bergstrom and Mensinger 2009) and show high diet overlap in the St. Clair River (French and Jude 2001). However, the impact of round goby abundance on logperch abundance in Hamilton Harbour, Lake Ontario remains elusive (Balshine et al. 2005). No impact on logperch abundance has been found in catchments of Lake Michigan (Kornis et al. 2013).

Johnny darter (*Etheostoma nigrum*) abundance decreased in southern Lake Michigan following round goby invasion. No specific interaction is established as the causal link for the decline (Lauer et al. 2004). In contrast, no change in johnny darter abundance has been found in catchments of Lake Michigan (Kornis et al. 2013). In a tributary river of Lake Michigan, round gobies have invader-density-dependent impacts on growth rates of johnny darter: johnny darter growth rates decreased in an in situ experiment with presence of a few gobies (2.7 individuals m^{-2}), but not with the presence of many gobies

Table 1 Round goby interactions with Eurasian perch (*Perca fluviatilis*) are context dependent (n.a. = not available, TL = total length, SL = standard length)

Species	Eurasian perch (*Perca fluviatilis*)		
Water body	Baltic Sea		Middle Danube
Sampling site	Bay of Gdansk, Poland	Curonian Lagoon, Lithuania	Near Bratislava, Slovakia
Abiotic factors			
Salinity	Brackish water	Brackish water	Fresh water
Depth (m)	n.a.	n.a.	0.5–2.5
Min./max./mean temp. (°C)	n.a.	n.a.	n.a.
Year(s) of study	2004	2007–2012	2004
Season of study	May–August	n.a.	30 Aug. and 1 Sept.
First record round goby	Late 1980s	2002	2003
Age of round goby population	Approx. 15 years	5–7 years	1 year
Round goby population density	n.a. (“one of the dominant species”)	1–251 ind./1000 m^3	n.a.
Life stage or length of round goby	n.a.	n.a.	1–4 years
Life stage or length of native species	113–293 mm TL	Small: 8.9 ± 0.3 cm TL Medium: 13.1 ± 1.0 cm TL Large: 27.2 ± 1.4 cm TL	Age 1: 56.8–63.7 mm SL Age 2: 89.2–109 mm SL Age 3: 78.5–138.3 mm SL Age 4: 104.1–178.1 mm SL
Primary data acquisition method	Stomach content and stable isotopes from field samples; comparison between invaded and uninvaded area (around island of Öland)	Stomach content and stable isotopes from field samples	Stomach content and stable isotopes from field samples
Sample size of perch	100	9	56
	Predation on round goby		Competition with round goby
Primary interaction	Perch almost exclusively feed on round goby; importance as food organism increases with increasing perch size	Round goby constitutes 17.4 ± 14.3% of large perch diet (estimated from stable isotopes); no isotopic niche overlap with benthivorous perch (small and medium length classes), thus no competition suspected	High diet overlap (except for age 2 or 3 perch [unclear]), due to preference for gammarids
Resulting impact on native species	Changes in trophic links; round goby is an energy pathway from mussels to top predators	Change in top predator diets	Potential for competition with small perch
Anticipated future effects	Bioaccumulation of toxins via mussels and round goby possible; may contribute to a new link in the energy pathway from bivalves to higher human exploited trophic levels (i.e., fish)	Stabilization of round goby population density due to predation	n.a.
Authors	Almqvist et al. (2010)	Rakauskas et al. (2013)	Copp et al. (2008)

Table 2 Variations of round goby interactions with native species (see text for references). (A) The general type of interactions between round goby and native species varies with interactor life stage. (B) The intensity of the interaction differs between ecosystems and studies. (C) The impact resulting from the interaction differs between ecosystems and studies

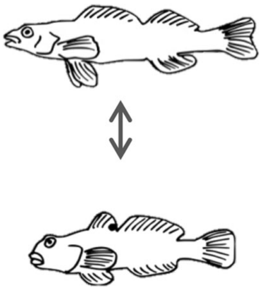
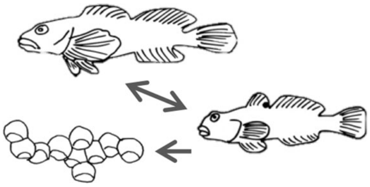
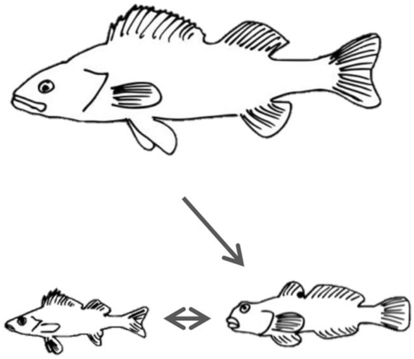
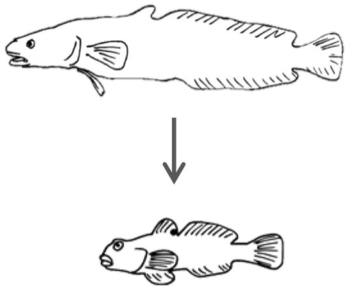
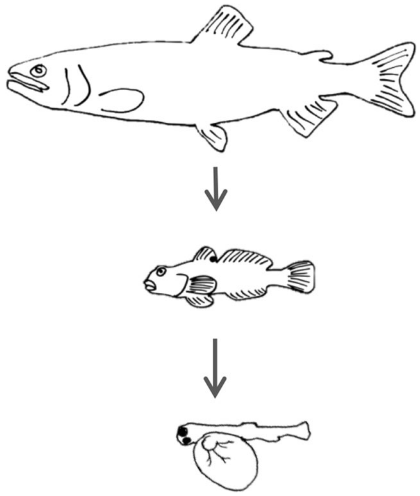
(A) General type of interaction	Studied native species	(B) Differences in interaction intensity with native species	(C) Differences in impacts on native species
Competition			
	Logperch (*Percina caprodes*)	Non-ambiguous (i.e., competition was found in all studies)	Inter-study differences in round goby impact on logperch abundance
	Johnny darter (*Etheostoma nigrum*) and other darter species	Ambiguous: inter-study differences in round goby competition with darter species	Inter-study differences in round goby impact on darter abundance Inter-study differences in round goby impact on darter growth rates
Competition and predation			
	Mottled sculpin (*Cottus bairdii*) and other sculpin species	Ambiguous: inter-study differences in round goby competition with sculpin species	Inter-study differences in round goby impact on sculpin abundance
	Yellow perch (*Perca flavescens*)	Ambiguous: inter-study differences in round goby competition with juvenile yellow perch Ambiguous: Inter-study differences in yellow perch predation on round goby	Inter-study differences in round goby impact on yellow perch body condition
	Eurasian perch (*Perca fluviatilis*)	Ambiguous: inter-study differences in round goby competition with juvenile Eurasian perch Ambiguous: Inter-study differences in Eurasian perch predation on round goby	Not assessed in studies
Predation			
	Burbot (*Lota lota*)	Ambiguous: Inter-study differences in predation on round goby	Inter-study differences in round goby impact on burbot body condition
	Lake whitefish (*Coregonus clupeaformis*)	Ambiguous: Inter-study differences in predation on round goby	Inter-study differences in round goby impact on lake whitefish body condition

Table 2 continued

(A) General type of interaction	Studied native species	(B) Differences in interaction intensity with native species	(C) Differences in impacts on native species
	Lake trout (*Salvelinus namaycush*)	Ambiguous: Inter-study differences in predation on round goby	Inter-study differences in round goby impact on lake trout reproduction
	Smallmouth bass (*Micropterus dolomieu*) and other bass species	Ambiguous: Inter-study differences in predation on round goby	Inter-study differences in round goby impact on bass growth and body condition
	Walleye (*Sander vitreus*)	Ambiguous: Inter-study differences in predation on round goby	Inter-study differences in round goby impact on walleye growth and body condition

(10.7 individuals m^{-2}; Kornis et al. 2014). Other darters such as blackside darter (*Percina maculate*), fantail darter (*Etheostoma flabellare*), and rainbow darter (*E. caeruleum*) are suspected to have diet or habitat overlap with round goby (French and Jude 2001; Poos et al. 2010; Abbett et al. 2013). In tributaries of Lake Erie, no rainbow darters and johnny darters were found in any of the streams containing round goby, whereas they were present in all of the goby-absent streams (Krakowiak and Pennuto 2008).

Mottled sculpins (*Cottus bairdii*) interact with round gobies in three ways: they compete for food and shelter (Dubs and Corkum 1996), mottled sculpins prey on round goby young-of-the-year (YOY; French and Jude 2001), and round goby prey on mottled sculpin eggs and YOY (French and Jude 2001; Mychek-Londer et al. 2013). These interactions have different impacts on mottled sculpin abundance in different ecosystems. In southern Lake Michigan, mottled sculpin populations were displaced, and their abundance decreased within less than 4 years after the first round goby was caught (4 years: Janssen and Jude 2001; 2–3 years: Lauer et al. 2004). On the other hand, no short-term change or temporal trend in mottled sculpin abundance was observed in Lake Michigan catchments despite increases in round goby abundance (Kornis et al. 2013). Other sculpin species did not show clear-cut responses to round gobies when investigated: round gobies gained more weight during a feeding experiment than slimy sculpins (*C. cognatus*) or spoonhead sculpins (*C. ricei*), but the non-native and native species had little physical contact (Bergstrom and Mensinger 2009). In the field, round gobies show no significant diet overlap with deepwater sculpins (*Myoxocephalus thompsonii*) and slimy sculpins (Mychek-Londer et al. 2013).

Impacts on percid fish

The impact of round goby on native percids have been investigated in 23 out of 53 papers. Round goby impacts on yellow perch (*P. flavescens*) have been extensively studied in the Great Lakes area (9/53; Table S2). Impacts are life stage dependent and include competition for food in the juvenile stages (Duncan et al. 2011; Crane et al. 2015) or one-sided predation by adult yellow perch on round gobies (Johnson et al. 2005; Lee and Johnson 2005; Truemper and Lauer 2005; Truemper et al. 2006; Campbell et al. 2009; Reyjol et al. 2010; Taraborelli et al. 2010; Crane et al. 2015). The strengths of both interactions depend on the complexity of habitat structure, biotic factors, and round goby density (Reyjol et al. 2010). If predation occurs in the adult stages, round goby as novel food item can be beneficial for yellow perch. Round gobies may provide an energetic advantage over traditional prey: foraging costs should be lower when predators feed on abundant goby prey than on less-abundant and presumably harder-to-catch native prey (Johnson et al. 2005), thus leading to a higher mass-at-length for larger yellow perch (> 27.5 cm total length TL, Crane et al. 2015).

Round goby impacts on Eurasian perch (*P. fluviatilis*) are known from several sites in Europe and are life stage dependent (3/53; Table 1). Round goby compete with juvenile benthivorous perch not only for food (Copp et al. 2008), but also serve as a prey for larger piscivorous perch, albeit with varying importance (Almqvist et al. 2010; Rakauskas et al. 2013).

Adult smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), rock bass (*Ambloplites rupestris*), and white bass (*Morone chrysops*) prey on round goby (Johnson et al. 2005; Dietrich et al. 2006; Hogan et al. 2007; Campbell et al. 2009; Taraborelli et al. 2010; Brownscombe and Fox 2013; Crane et al. 2015). Smallmouth bass predation on round gobies is higher in areas with earlier goby invasion, which can be explained by predator-learning ability (Brownscombe and Fox 2013). In Lake Erie and Lake Ontario, increases in smallmouth bass growth and condition following round goby invasion have been found (Steinhart et al. 2004b; Reyjol et al. 2010; Crane et al. 2015). For white bass, there has been no consistent trend in increased growth after round goby invasion (Johnson et al. 2005). However, round goby impacts on bass are life stage specific. Round gobies have been described as egg predators of smallmouth bass in Lake Erie, where they ate the complete offspring of an unguarded smallmouth bass nest within 15 min in an experiment in the field, in which nest-guarding bass were caught from the nest and later released again (Steinhart et al. 2004a).

Round goby impacts on walleye (*Sander vitreus*) are predominantly manifested in round goby becoming a prey, but impacts are partly life stage dependent, and inconsistent impacts on predator growth and condition are found. In Lake Ontario, the largest walleye length class benefitted from improved condition, but not the smaller-length classes (pre-invasion period 1993–2004 compared with post-invasion period 2005–2012, Crane et al. 2015). In Lake Erie, walleye condition did not change after round goby invasion (pre-invasion period 1993–1998 compared with post-invasion period 1999–2012, Crane et al. 2015). Some walleye eggs were found in Lake Erie round goby stomachs, but the authors suggest that these eggs were ingested by accident by round gobies foraging on dreissenids (Roseman et al. 2006). The contribution of round goby to walleye diet ranges from around 10% of diet in Lake Erie (Johnson et al. 2005), 30% frequency of occurrence in Lake Ontario (Taraborelli et al. 2010) and Lake Huron (Roseman et al. 2014), to around 50% frequency of occurrence in Lake St. Pierre in the St. Lawrence River (Reyjol et al. 2010).

Impacts on gadid fish

Round goby is an important diet item for burbot (*Lota lota*) in the Great Lakes area (Johnson et al. 2005; Stapanian et al. 2007; Hensler et al. 2008; Jacobs et al. 2010; Madenjian et al. 2011; Stapanian et al. 2011; Crane et al. 2015). However, the impact of round goby on burbot is life stage and ecosystem dependent. Round goby contribution to burbot diet varies across different ecosystems, and not all burbot size classes benefit from this novel prey. In Lake Erie, round goby is the most important food organism for particularly older burbot by wet weight (Madenjian et al. 2011), and by dry mass (Johnson et al. 2005). A significant improvement in condition of burbot feeding on round goby has recently been detected only for individuals of the smallest length class (375 mm TL), which were in poor-to-median condition prior to round goby invasion. For individuals in the greatest length class (743 mm TL), a significant decrease in condition has been found (pre-invasion period 1993–1998 compared with post-invasion period 1999–2012, Crane et al. 2015). In Lakes Michigan and Huron, burbot with a high amount of round gobies in their diets showed lower growth than those with a lower amount of round goby. The authors suggest that “burbot have not eaten round gobies long enough to affect increases in growth” without further specifying the underlying mechanisms (Hensler et al. 2008).

Impacts on salmonid fish

Round goby impacts on lake trout (*Salvelinus namaycush*) are life stage and ecosystem dependent: round goby prey on lake trout eggs and fry, thus negatively affecting lake trout reproduction (Chotkowski and Marsden 1999). Adult lake trout prey on round gobies, but their importance as food item varies across ecosystems. Round goby is not an important food item for lake trout in Lake Michigan, although consumed in small numbers (Jacobs et al. 2010). In contrast, round goby is the most important lake trout food organism in Lake Huron (Roseman et al. 2014), and the second most important food item for large lake trout in Lake Ontario in 2004 (Dietrich et al. 2006). Another study in Lake Ontario, conducted four years later, found that round goby contributed substantially to the diet of all length classes of adult lake trout (Rush et al. 2012). Predation on round goby has potentially positive impacts on lake trout reproduction, because round gobies contain relatively high concentrations of thiamine (vitamin B1). High consumption rates of round goby by lake trout could mitigate the thiamine deficiency that might otherwise impair reproduction in trout (Fitzsimons et al. 2009). However, negative impacts of round goby predation on lake trout eggs in the Great Lakes are speculated to overweigh these positive impacts: when round goby overwinter on spawning reefs or forage along river banks, they are believed to decrease recruitment by interstitial predation on lake trout eggs (Chotkowski and Marsden 1999; Fitzsimons et al. 2006, 2009).

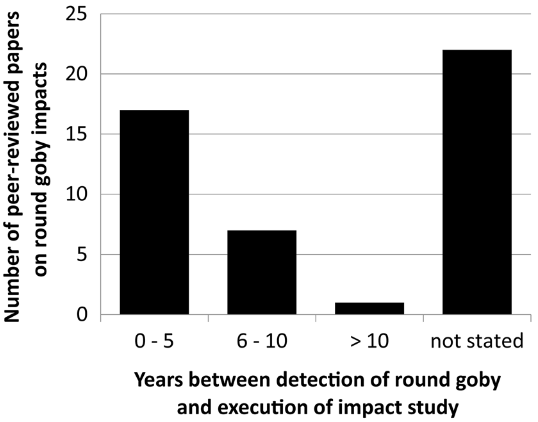


Fig. 3 Most peer-reviewed papers about round goby impacts on native fish species do not state the years between detection of round goby and execution of the impact study

Lake whitefish (*Coregonus clupeaformis*) have been found to use round goby as a new prey item. In Lake Michigan, round gobies are the most important food organisms for lake whitefish in winter (Lehrer-Brey and Kornis 2014). In Lake Huron, their importance during the whole year ranges from low to high depending on the region of the lake (Pothoven and Madenjian 2013). However, despite increased piscivory, the condition of whitefish foraging on round goby did not clearly improve (Pothoven and Madenjian 2013). Our literature review did not find any articles investigating the effects of round goby on the European trout (*Salmo trutta*) or whitefish (*Coregonus lavaretus*) species flock.

Temporal aspects are usually not addressed

When assessing the time since first detection across studies analyzing the impacts of round goby on native fish species, we found that many studies give no information at all (Fig. 3). The majority of studies are undertaken within 5 years after detection of round goby as an invasive species, and only one study assessed the long-term impacts (more than 10 years).

DISCUSSION

Round goby impacts are profound, but variable across ecosystems, life stages, and time scales

In our literature review, we found 53 papers demonstrating that round gobies interact with native fish species (Fig. 2). Affected species respond in a variety of ways to this new predator, competitor, or prey. The directions, i.e., whether native species individuals or populations showed positive or negative responses, frequently differed across studies (Table 2). We did not find that round goby had the same clearly demonstrable, comparable impacts on a specific native species across all studies.

We identified three main explanations for why the literature did not reveal a more straightforward picture: First, round goby interactions with the same native species vary with the life stage of the interactor (Table 2A). For example, round gobies act as predators of eggs, compete with juveniles, or act as novel prey for adults of the same species (e.g., mottled sculpin or smallmouth bass). Second, the intensity of the interactions (e.g., intensity of competition or predation) differs across ecosystems (Table 2B). In some ecosystems, the interaction is very strong; in other ecosystems, the interaction between round goby and the same native species is not observed at all. For example, the intensity of competition, e.g., measured as diet overlap between native species and round gobies, varies in different ecosystems (e.g., logperch and Eurasian perch). Similarly, round goby contribution to predator diet is different for the same predatory species in different ecosystems (e.g., burbot). Third, not only the intensity of the interaction, but also how round goby impacts are reflected in native species' growth rate and abundance differ across studies (Table 2C). For example, although competition with round goby can lead to a decreased abundance of the native species in some ecosystems, no change in the abundance of the same native species has been observed in other ecosystems (e.g., johnny darter). Similarly, predation on round gobies can lead to better condition factor or growth rate in predators in one ecosystem, whereas in another ecosystem no change in predator condition or growth can be observed (e.g., yellow perch).

Reasons for impact variations across ecosystems, life stages, and time scales

Species invasions are natural processes. The impacts of an invasive species can therefore be as complex as the impacts of any other species in the ecosystem (Crooks 2005). Against this background, it is not surprising that round goby impacts vary across ecosystems.

To further complicate things, finding impacts of invasive species depends on the temporal scale that is applied in searching for them (Strayer et al. 2006). Investigating impacts of a recently established population can reveal entirely different results from those obtained when investigating impacts of a longer established population. Unfortunately, despite our efforts to explore the time dependency of impacts, we could not investigate this question; too few studies did even state the age of the round goby population investigated (Fig. 3). The remaining studies did not allow for a quantification of impacts across population age. Scaling impacts from severe to weak or positive to negative alone would be a daunting task, so that a relationship between invasion time and impact scale would be rather arbitrary. We can say, however, that scientists should be better aware of the time dependency in biological invasions. If scientists appreciate frequently occurring lag phases in invasion research, then we can eventually arrive at a more thorough understanding of the relationship between time and impact.

This is all the more important as evolutionary processes can influence biological invasions on timescales that were previously not appreciated—the so-called contemporary time scales (Stockwell et al. 2003). Some traits which cause a non-native species to become invasive have evolved in a new system on timescales less than ten years (Whitney and Gabler 2008). This also holds good for the native species responding to invasive species. If, for example, native predators adapt to invasive species as a new prey, then native predator populations can increase over time, whereas invasive species populations decrease (Sheehy and Lawton 2014). In the case of round goby, Brownscombe and Fox (2013) tested for how readily native predators forage upon this newly available prey species: predation rates on round gobies were lower in the recently invaded systems compared to systems in which predators had time to learn to capture and consume this novel prey species.

Eventually, biological invasions can even result in entirely new species (Lee 2002; Lee et al. 2007). Processes such as hybridization with native or other invasive species can tremendously alter the ecological interactions and congruent impacts in any invaded ecosystem. In lower stretches of the River Rhine, for example, the round goby has been found to hybridize with monkey goby (*Neogobius fluviatilis*), a confamilial invasive goby species (Lindner et al. 2013). Which impacts are in store when invasive goby species hybridize will be even harder to predict than when clearly defined species boundaries exist.

The state of the scientific knowledge needs to be communicated to decision makers

It becomes clear that, if we want to inform a preventive management, we cannot wait until conclusive evidence for comparable impacts of round goby is available. We propose to communicate the knowledge on impacts scientists already have accrued, despite our inabilities to predict and generalize. On the onset of our project, we expected that impacts on specific native species, which re-occur across different studies, could help decision makers to prioritize if and how to instigate management measures against round goby. To this end, our focus was to scrutinize the broadest body of knowledge that scientists possess concerning round goby: knowledge on impacts. We believe the available scientific information on round goby impacts, albeit ecosystem dependent, can still be relevant to inform decision makers about potential threats. Paradoxically, the chances for successful management of a non-native species are best when we know least about its impacts: at the time when it has just established (Kriticos et al. 2003). We argue that the lack of comparable impacts of round goby on native species is no reason to conclude that there will be no impacts of round goby in a newly invaded ecosystem.

Decision makers want timely and relevant information if and how a potentially invasive non-native species should be managed (Walsh et al. 2015). Therefore, in a management context, it is more important to rapidly disseminate the current knowledge than to improve our epistemic knowledge and ability to predict round goby impacts in a particular system. In the context of preventing an approaching invader, a central task for scientists is to communicate that incomplete knowledge on negative impacts is no reason to neglect possible future impacts, i.e., the absence of evidence for negative impacts is not an evidence for the absence of negative impacts (Ojaveer and Kotta 2015). Importantly, the appreciation of time lags will improve the decision making at different stages of the invasion to more effectively make the right management choices. Along these lines, it also needs to be appreciated that an approaching invader can cross the country-borders in the course of its spread. In the case of round goby, this means that if the High Rhine and adjoining Lake Constance are invaded, three or more Central European countries will be affected. Managing such an invasion requires cooperation across borders. Institutions such as the International Commission for the Protection of the Rhine or the International Commission for the Protection of Lake Constance (ICPR 2015; IGKB 2015) provide an existing framework for this kind of cooperation. This literature review advances our ability to objectively assess what we as scientists can contribute to this cooperation and how to more effectively instigate an effective management of one of the 100 worst invaders in Europe.

Acknowledgments The authors thank Catherine Cornaz for her help with the literature review and two anonymous reviewers for helpful comments on an earlier version of this manuscript. This project was funded by a special grant from the Federal Office for the Environment, Switzerland, the Research Centre for Sustainable Energy and Water Supply (FoNEW), the canton BS, plus cantonal lottery funds of AG, BL, SO.

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AMBIO

Electronic Supplementary Material
This supplementary material has not been peer reviewed.

Title: **What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check**

Authors: Philipp E. Hirsch, Anouk N'Guyen, Irene Adrian-Kalchhauser, Patricia Holm

Excel file of supplementary Table S1 can be requested by E-Mail:
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Supplementary Table S1: Literature review
Supplementary Table S2: Impacts on Yellow perch *Perca flavescens*

Table S2: Round goby interactions with Yellow perch (*Perca flavescens*) are context dependent. (n.a. = not available, TL = total length, SL = standard length)

Species		**Yellow perch (*Perca flavescens*) (1/2)**								
Water body		**Lake Ontario**				**Lake Erie**				
Sampling site		Eastern part		Lower Bay of Quinte	Upper Bay of Quinte	Eastern part			Central part	Hatchery Bay, Western Lake Erie
Abiotic factors	Salinity	Fresh water		Fresh water		Fresh water			Fresh water	Fresh water
	Depth [m]	n.a.	n.a.	Transects: 1.5-3 m, 3-5 m, 5-7m Traps, seining, angling: 1-5 m		n.a.	n.a.	n.a.	Bottom trawl at 5-9.9 m, 10-14.9 m, 15-19.9 m, and > 20 m	1-3 m
	Temp.	See Fig. 1				See Fig. 1		n.a.	See Fig. 3	n.a. for field, 23.6 °C ± 1.13 SD and 20.8 °C ± 1.1 SD in lab experiments
Year(s) of study		Pre-invasion: 1993-2004 Post-invasion: 2005-2012		2004/2005		Pre-invasion: 1993-1998 Post-invasion: 1999-2012		2002/2003	1995-2002, data from 2002	2002
Season of study		Late summer		May-Oct./Nov.		Early autumn		July-August	May-Oct	June-Aug.
First record round goby		2005		1999	2001	1999		n.a.	1994	Early 1990s
Age of round goby population		0-7 years		6 years	4 years	0-13 years		n.a.	8 years	Approx. 10 years
Round goby population density		n.a.		11.2 t/km^2 ; see table 1	5 t/km^2 ; see table 1	n.a.		n.a.	Standing stock 203-4803 t/y, peak at 4.2 ± 1.5 billion ind. (1999), since then rel. stable probably due to predators, see table 2	n.a.
Life stage or length of round goby		n.a.		Populations were dominated by age 0 to age 2; especially 2.3-13.6 cm TL, see table 2		n.a.	n.a.	Small: < 11.2.cm Large: ≥11.2 cm	0-4 years, see table 3	< 6 cm TL Lab: overall mean sizes of round goby 63.5 ± 2.8 SD (dreissenid habitat) and 62.2 ± 4.0 SD (macrophyte habitat)
Life stage or length of native species		16.5-22.5 cm TL	27.5-34 cm TL	12.6-29 cm TL		16.5-22.5 cm TL	27.5-34 cm TL	average 19.53 ± 5.68 cm TL	n.a.	Field: < 95mm: n=29; 95–150 mm: n=38; > 150 mm TL: n=32 Lab: overall mean sizes of yellow perch 63.5 ± 0.6 SD (dreissenid habitat) and 63.1 ± 1.9 SD (macrophyte habitat)
Primary data acquisition method		Mass-at-length from field samples		Stomach content from field samples, bioenergetics modelling		Mass-at-length from field samples		Stomach content and stable isotopes from field samples	Stomach content from field samples	Stomach content from field samples and lab experiments
Sample size of perch		Pre-invasion: 1154 Post-invasion: 1608		123	88	Pre-invasion: 593 Post-invasion: 8972		33	n.a.	99

Primary interaction and indices	Predation on round goby								Competition with round goby
	n.a.		Mean percent composition by weight of round goby in perch stomach: spring 93%, summer 82%, fall 92%, table 5	Mean percent composition by weight of round goby in perch stomach: spring 89%, summer 20%, fall 100%, table 5	n.a.		Round gobies are part of yellow perch diet, see figure 5	Yellow perch derived approximately 30% of their diet from round gobies	Significant diet overlap between juvenile perch (< 95 mm TL) and gobies (< 60 mm TL) in August, large yellow perch displayed very little diet overlap with any round goby size class, see figure 1
Resulting impact on native species	Mass-at-length partly deteriorated, see table 4	Mass-at-length generally improved, see table 4	Change in top predator diets		Mass-at-length partly deteriorated, see table 4	Mass-at-length generally improved, see table 4			Low to strong aggression depending on the amount of food present; differing habitat preference and food resource use allow coexistence
Anticipated future effects	Changes in body condition may have implications for additional population and life history characteristics		n.a.		Changes in body condition may have implications for additional population and life history characteristics		Changes in energy flows between profundal, pelagic and littoral environments due to round goby	Round goby may provide energetic advantage over traditional prey (reduction in foraging cost); round goby transfer energy from benthos to higher trophic levels	Heterogeneous habitat structure may avoid negative effects
Authors	Crane et al. (2015)		Taraborelli et al. (2010)		Crane et al. (2015)		Campbell et al. (2009)	Johnson et al. (2005)	Duncan et al. (2011) (Duncanetal.É

Species		Yellow perch (*Perca flavescens*) (2/2)					
Water body		St. Lawrence river	Lake Michigan				
Sampling site		Lake St. Pierre	Southern part				
Abiotic factors	Salinity	Fresh water	Fresh water				
	Depth [m]	1.5-3.9, average 3.2 m, navigation channel 11.3 m	Max. depth of Lake 265 m, mean 99 m Sampling at 5 / 10 / 15 m				
	Temp.	Around 20° C	n.a.				
Year(s) of study		2007	2002				
Season of study		Aug.-Oct.	June-Aug.				
First record round goby		2006	1998				
Age of round goby population		1 year	4 years Diet 2002 compared to other studies from 1984 and 1992/93 (pre-invasion)				
Round goby population density		n.a.	n.a.				
Life stage or length classes of round goby		n.a.	21–170 mm TL				
Life stage or length classes of native species		92-319 mm TL, mean 177 ± 39 mm TL	10-11.9 cm TL	12-15.9 mm TL	16-18.9 mm TL	> 18.9 cm TL	< 10 cm TL

Primary data acquisition method	Stomach content from field samples	Stomach content from field samples				
Sample size of perch	245	1984: 365 1992/93: 68 This study 2002: 365	1984: 127 1992/93: 167 This study 2002: 127	1984: 9 1992/93: 208 This study 2002: 9	1984: 5 1992/93: 401 This study 2002: 184	2212 total captured, out of them 1293 randomly sub-sampled for stomach analysis, out of them 268 contained alewife or round goby and were used for subsequent diet analysis
Primary interaction	**Predation on round goby**					**No predation on round goby**
	21.9% frequency of occurrence; 16.4% perch consume exclusively round goby; 4.4-100% of weight of consumed food organisms, table 1	10.2% of stomach content	33.3% of stomach content	68.9% of stomach content; yellow perch ≥ 150 mm LT consumed round goby as a major prey item	38.8% of stomach content	Perch < 10 cm TL were collected, but were found not to consume round goby
Resulting impact on native species	Goby preference mainly governed by biotic (assemblage of predators) and geographic factors (round goby density)	Energetic link between zebra mussels and yellow perch; new food source for yellow perch; diet shift from mottled sculpin and johnny darter as prey items in 1984 to a diet with round goby in 2002				n.a.
Anticipated future effects	Changes in nutrient and contaminant transfers	It appears that yellow perch has the capability to successfully adapt to diet changes caused by environmental features and influences, specifically those enhanced by anthropogenic activity				n.a.
Authors	Reyjol et al. (2010)	Truemper and Lauer (2005) and Truemper et al. (2006)				Truemper and Lauer (2005)

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PAPER III

MOLECULAR ECOLOGY

Molecular Ecology (2016) **25**, 1925–1943 doi: 10.1111/mec.13595

The invasive bighead goby *Ponticola kessleri* displays large-scale genetic similarities and small-scale genetic differentiation in relation to shipping patterns

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Abstract

Colonization events, range expansions and species invasions leave genetic signatures in the genomes of invasive organisms and produce intricate special patterns. Predictions have been made as to how those patterns arise, but only very rarely, genetic processes can be monitored in real time during range expansions. In an attempt to change that, we track a very recently established invasive population of a fish species, the bighead goby *Ponticola kessleri*, with high temporal and spatial resolution through 2 years to identify patterns over time. We then compare Swiss and German samples of bighead goby along the river Rhine using microsatellites, mitochondrial D-loop sequences and geometric morphometrics to investigate geographic patterns. We detect weak temporal and strong geographic patterns in the data, which are inconsistent with isolation by distance and indicate long range transport. In search of an explanation for our observations, we analyse the vector properties and travel patterns of commercial vessels on the river Rhine. We present evidence that freshwater cargo ships and tankers are plausible vectors for larvae of invasive goby species. We also present indications that cargo ships and tankers act as differential vectors for this species. In summary, we present genetic data at unique temporal resolution from a vertebrate invasion front and substantiate the paramount role of commercial shipping in freshwater fish translocations.

Keywords: ballast water, invasion genetics, microsatellite, Ponto–Caspian goby, vector

Received 7 July 2015; revision received 12 February 2016; accepted 17 February 2016

Introduction

Colonization events, range expansions and biological invasions are predicted to leave certain signatures in the genome of a population (Excoffier *et al.* 2009). On the one hand, these signatures are helpful to track the geographic source regions and the pathways that an expanding species has taken. On the other hand, these signatures can be used to identify genetic challenges arising during range expansions. For example, an invasive population may be founded by just a few individuals that contain only a fraction of the source population's genetic variation (Williamson & Fitter 1996). Also, dispersal from the range margin may be under strong selective forces. For example, dispersal may favour certain traits such as flight capacities, directed movement behaviour, leg length or early flowering (Phillips *et al.* 2006; Hughes *et al.* 2007; Alford *et al.* 2009; Colautti *et al.* 2010). Expanding populations may also be subject to deleterious allele surfing events of

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non-neutral mutations, which can reach unexpectedly high densities at the expanding wave front (Travis *et al.* 2007; Peischl & Excoffier 2015). Such genetic challenges are thought to limit an expanding species' adaptive potential and, thus, its success of establishment in the newly colonized area by reducing genetic diversity, favouring inbreeding, counteracting environmental adaptations or by producing unfavourable allele combinations (Briskie & Mackintosh 2004; Frankham 2005; Dlugosch & Parker 2008; Dlugosch *et al.* 2015).

In some cases, however, species seem to have bypassed those challenges. Invasive species have been found to harbour significant levels of standing variation in the invasive range (Kolbe *et al.* 2004, 2007, 2008; Stepien & Tumeo 2006; Hochkirch & Damerau 2009). In some instances, invasive populations are genetically not diverse or even clonal, but nonetheless highly successful (Dlugosch & Parker 2008; Zhang *et al.* 2010; Carvalho *et al.* 2014; Lobos *et al.* 2014; Pigneur *et al.* 2014; Hagenblad *et al.* 2015; Ray *et al.* 2015). Dependent on the species specific situation, these unexpected observations have been explained by a variety of biological and/or evolutionary genetics mechanisms: large numbers of founding propagules (Simberloff 2009), parallel introduction events from diverse source populations (Durka *et al.* 2005; Henshaw *et al.* 2005; Brown & Stepien 2009; Zalewski *et al.* 2010), clonal reproduction strategies (Chapman *et al.* 2004), introgression events (Choler *et al.* 2004; Suehs *et al.* 2004), fast drift at the wave front of expanding populations (Edmonds *et al.* 2004; Miller 2010), fast adaptation and selection processes in the very early establishment phases (Phillips *et al.* 2006; Kelehear *et al.* 2012) or intraspecific admixture (Kolbe *et al.* 2008).

Most of these assumptions on genetic processes at invasion fronts of wild species, however, are inferential. Genetic data taken at high temporal and spatial resolution from colonizing populations in their early establishment phase are scarce. Observations and genetic investigations on invasive populations usually start many years or generations after the actual introduction event. By that time, secondary introductions and gene flow among introduced populations may have had ample opportunity to obscure early population scale processes (Colautti *et al.* 2005). Also, stratified-dispersal strategies, in which different vector activities blend with natural dispersal in space and time, may yield genetic patterns which no longer contain the genetic signatures of the original introduction events (Bronnenhuber *et al.* 2011). Therefore, many aspects about genetic processes during early invasion stages remain unknown (Bock *et al.* 2014).

Invasive Ponto–Caspian gobies are benthic fish species which present an excellent case study to fill some of these knowledge gaps in vertebrates. As vigorous and adaptive invaders with high reproductive capacities, five species of Ponto–Caspian gobies (*Neogobius melanostomus, Ponticola kessleri, Neogobius fluviatilis, Proterorhinus semilunaris* and *Babka gymnotrachelus*) are presently colonizing European freshwaters, European coasts and the Great Lakes and its tributaries. They are expected to colonize the majority of freshwater and brackish temperate water bodies worldwide (Puntila *et al.* 2013; Snyder *et al.* 2014; Hempel & Thiel 2015). Ponto–Caspian goby invasions have been attributed to shipping traffic (Roche *et al.* 2013). Importantly, however, there are no records of Ponto–Caspian larvae or adults found aboard ships in the scientific literature, and speculations on egg attachment can be traced to a single anecdotal source (Tsepkin *et al.* 1992; Sokolov *et al.* 1994; Moskal'kova 1996; Ahnelt *et al.* 1998). In Europe, several invasion corridors have been proposed (Ricciardi & MacIsaac 2000), but the relative contribution of these pathways to the spread of Ponto–Caspian gobies has not yet been analysed on a molecular level. Importantly, Ponto–Caspian gobies are easy to sample, and it is possible to install extensive passive monitoring schemes to detect very early invasion stages.

We chose one Ponto–Caspian goby species, the bighead goby *Ponticola kessleri*, to evaluate population genetic structure during a vertebrate range expansion in time and in space and to identify processes, such as vector activities, which may have an impact on the genetic structure. We chose this particular species for two reasons. First, very little is known about the phylogeographic and genetic structure of this successful pan-European invader, as the only two existing studies could not detect genetic differentiation between the sampled populations (Ondrackova *et al.* 2012; Cerwenka *et al.* 2014a). Ondrackova *et al.* (2012) compared the genetic diversity of one bighead goby population from the native range with an introduced population from the invasive range using 16 microsatellites. They found those populations to be similar in diversity and attributed this to high propagule pressure during the invasion, which would promote the transfer of a wide spectrum of alleles from the native range to the invasive range. Cerwenka *et al.* (2014a) sampled bighead goby *Ponticola kessleri* and round goby *Neogobius melanostomus* subpopulations at several sites along the Upper Danube for AFLP and mtDNA cytochrome B analysis. They could identify genetic patterns in round, but not in bighead goby and suggested that a genetically impoverished source population or a genetic bottleneck in the bighead goby may be the reason for this low genetic variability. This is, actually, a vivid example on how similar genetic data can be interpreted in very different ways with regard to the unobserved processes that may have caused the observed patterns.

A second reason why the bighead goby is attractive for the study of genetic processes during invasion is that bighead goby usually invades Central European sites before other Ponto–Caspian goby species (Seifert & Hartmann 2000; Paintner & Seifert 2006; Borcherding *et al.* 2011). The bighead goby invaded the Upper Danube River area before the round goby (Seifert & Hartmann 2000; Paintner & Seifert 2006) and developed high population densities, which then decreased after the arrival of the round goby (Cerwenka *et al.* 2014b). In this case, genetic data indicate that the bighead goby may be genetically less diverse and therefore less able to adapt to novel environments than the round goby. The same dynamic pattern of the two species is also visible in the Lower Rhine and, in this location, may be attributable to lower competitive strength on food resources in the bighead goby (S. Gertzen, J. Borcherding, pers. observations). The bighead goby may thus be more revealing with regard to the introduction pathways of Ponto–Caspian gobies in Europe than other invasive goby species because its early establishment is least affected by competitive interactions with sister species.

For this study, bighead goby samplings were initiated at an invasion hotspot, the commercial harbour in the river Rhine at Basel (Switzerland), immediately after fishermen first recorded the species (Kalchhauser *et al.* 2013), and were continued weekly for 2 years. These samples were complemented with samples taken along 16 km of upstream river in the High Rhine in Switzerland, and with samples from the Lower Rhine in Western Germany, taken >600 km downstream. All sampled individuals were genotyped for 15 microsatellites. A subset of individuals, chosen on the basis of microsatellite results, was additionally subjected to mitochondrial haplotype analysis and body morphology quantifications. With the ambition to provide explanations for the observed genetic patterns, information on the use and on the specifications of freshwater ballast water tanks was recovered from locally relevant shipping companies, and the travel patterns and mooring patterns of all ships arriving in Basel in 2012 were analysed.

We considered the river Rhine, which is the second largest river in Central Europe and heavily impacted by shipping traffic, a uniform introduction route, and commercial shipping a homogeneous vector, and thus expected the samples from the invasion front in Switzerland to be genetically homogeneous. We also expected to identify time-dependent patterns from the genetic markers in the Swiss harbour population, based on the idea that ships would continuously supply new propagules and thus add new alleles to the recently established population. We figured that the samples from Western Germany would likely differ genetically from the Swiss samples, based on the notion that geographically separated populations are usually genetically more distant than geographically close populations ('isolation by distance'). We further expected that maternally inherited mitochondrial haplotypes and nuclear markers would give comparable results, because to date, there is no record of sex-specific invasion behaviour in Ponto–Caspian gobies.

Body morphology was expected to be independent of either genetic markers. In fish, and also in several goby species, body morphology is an ecologically relevant phenotypic trait that reflects how an individual interacts with its environment (Smith & Skulason 1996; Hirsch *et al.* 2013). Ecological theory predicts that invasive species should be highly plastic because this would enable a faster adaptation to new environmental conditions such as novel food sources (Agrawal 2001; Davidson *et al.* 2011). However, morphology is of course not completely independent from genetic features. Aspects of morphology may be encoded by loci that are linked to microsatellites, and may therefore differ between genotypes, as has been seen for the lateral plate phenotype in sticklebacks (Colosimo *et al.* 2004). Finally, we expected that patterns in vector behaviour and genetic patterns at the invasion front would match and thus confirm previous notions on the vector activities responsible for the introduction of the species.

Materials and methods

Sampling and geography

Bighead gobies were sampled at several sites in the Lower Rhine in Western Germany, where the bighead goby established before 2006, and at several sites in the High Rhine in Switzerland, where the bighead goby established just before 2012 (Kalchhauser *et al.* 2013; Lower Rhine: km 660 to 1.033 of the river Rhine; High Rhine: km 0 to 165 of the river Rhine). Sampling sites were named from 1 to 16 and are indicated in Fig. 1. Sites 1–5 are situated in the commercial harbour of Basel, Switzerland, and were probed biweekly between 2012 and 2014. Sites 6–11 are situated within 16 km upstream from the commercial harbour in the High Rhine in Switzerland, and were probed at varying time points between 2012 and 2013. Sites 12–16 are situated in Western Germany in the Lower Rhine and surrounding channels and were probed at varying time points between 2013 and 2014. Site coordinates as well as geographic distances between sites are indicated in Table 1. Catch methods included minnow traps, spawning traps (Hirsch *et al.* 2015), angling and electro fishing in accordance with national legal requirements. All fish were

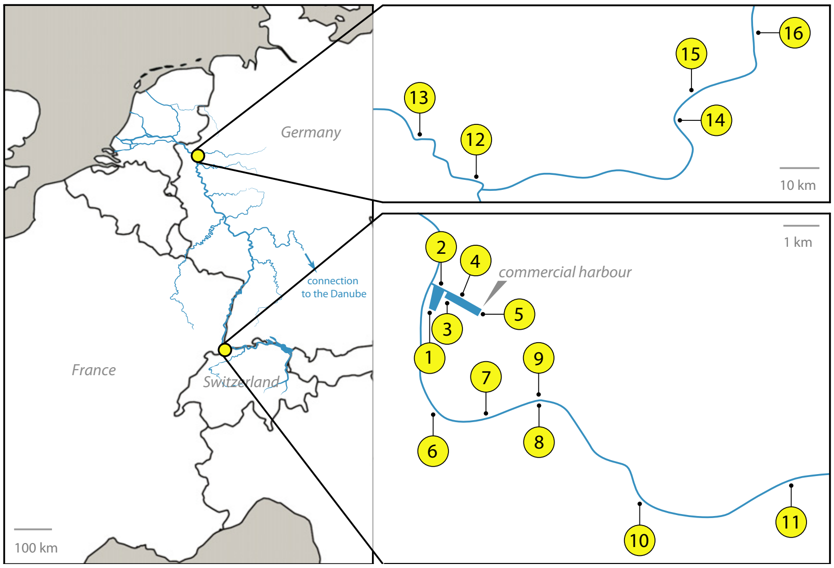

Fig. 1 Map of sampling sites. Sampling sites are situated in Switzerland in the river Rhine (1–11) and in Western Germany (12–16) in the river Rhine and surrounding channels. Swiss sampling sites are spread along 16 km and are separated from German sites, which are spread across 100 km, by 640 km. Site coordinates and distances between individual sites are given in Table 1. At sites 1–11, bighead gobies were first reported between 2012 (site 6) and 2014 (site 11). At sites 12–16, bighead gobies were first reported in 2006. The town Basel (lower yellow dot in the left panel) is situated at 47° 33′28.1″N 7°35′17.2″E.

Table 1 Sampling site coordinates

Sampling site	Latitude	Longitude	Region	Sampling site name	*n*
1	47°34′58.8″N	7°35′18.3″E	Switzerland	Commercial harbour, site A	74
2	47°35′20.2″N	7°35′32.7″E	Switzerland	Commercial harbour, site B	73
3	47°35′14.9″N	7°35′36.4″E	Switzerland	Commercial harbour, site C	73
4	47°35′07.4″N	7°35′55.0″E	Switzerland	Commercial harbour, site D	74
5	47°35′05.0″N	7°36′06.1″E	Switzerland	Commercial harbour, site E	74
6	47°33′25.9″N	7°35′32.8″E	Switzerland	Münstergalgen	1
7	47°33′29.9″N	7°36′39.0″E	Switzerland	Galgen 30	6
8	47°33′45.5″N	7°37′47.2″E	Switzerland	Galgen 8	4
9	47°33′33.2″N	7°38′10.9″E	Switzerland	Birsfelden	32
10	47°31′59.2″N	7°40′25.8″E	Switzerland	Schweizerhalle	1
11	47°32′27.8″N	7°43′16.5″E	Switzerland	Kaiseraugst	5
12	51°45′50.4″N	6°20′13.2″E	Germany	Rhein km 842	2
13	51°39′28.9″N	6°35′38.1″E	Germany	Rhein Wesel	5
14	51°47′17.5″N	7°23′39.6″E	Germany	DEK Abfahrt Lüdinghausen	32
15	51°50′42.5″N	7°28′08.0″E	Germany	DEK Abfahrt Senden	1
16	51°59′05.5″N	7°39′37.8″E	Germany	DEK Schleuse Münster	17

n, number of individuals sampled at the respective site.

frozen at −20 °C after catch, later thawed on ice and weighed, measured, sexed and photographed in a standardized manner. All details on the samples, such as sampling time points, catch methods, weight, length and sex of each individual are indicated in Table S1 (Supporting information).

Microsatellite analysis

We tested 46 published goby microsatellites (Dufour *et al.* 2007; Vyskocilova *et al.* 2007; Feldheim *et al.* 2009; Ruggeri *et al.* 2012) for amplification from bighead goby DNA in single amplicon PCRs at annealing temperatures between 54 and 64 °C with FastStart Taq DNA Polymerase from Roche [amplification protocol: 4′ 94 °C; 30″ 94 °C, 30″ 54–64 °C, 1′ 72 °C (35 cycles); 7′ 72 °C; 4°C ∞]. For reactions which failed, alternative oligos were designed, renamed (f.ex., Nme3.1 fw is the redesigned Nme3 fw), and amplification was retested. In total, 36 of 46 microsatellites could be amplified, cloned and sequenced for bighead goby using this procedure.

All 46 microsatellites were also tested and, if they could be amplified successfully, cloned in round goby to serve as a resource for similar studies in this species. Microsatellite sequences from both species are compiled in Appendix S1 (Supporting information). All oligos used in this study are listed in Table S2 (Supporting information).

Multiplex sets were compiled and amplified with the Qiagen Multiplex PCR Kit (amplification protocol: 15′ 95 °C; 30″ 94 °C, 90″ 56 °C, 1′ 72 °C (35 cycles); 30′ 60 °C; 4 °C ∞) according to the manufacturers' instructions. A total of 200 bighead goby individuals from sites 1–5 were initially genotyped to identify polymorphic, reliably amplifying microsatellites among the 36 cloned microsatellites. A total of 20 microsatellites were polymorphic, and 15 amplified reliably in multiplex PCR. The oligo sets that worked reliably were: Set 1: Ame10, NG92, NG150, NG195, NG70, Nme3.1; Set 2: NG71, NG111, NG135, NG184; and Set 3: NG132, NG167, NG236, NG28, Nme6. Oligos were fluorescently labelled with the dyes TAMRA, ROX, 6-FAM and JOE as indicated in Table S2 (Supporting information). An overview of the microsatellite selection process is presented in Table S3 (Supporting information).

Between May 2012 and April 2014, more than 1000 bighead gobies were caught in the harbour at sites 1–5. To reduce the size of the harbour sample, while preserving the ability to identify genetic changes over time, we decided to use the first and the last fish caught at each site in the commercial harbour for microsatellite analysis. For the '2012' group, we chose the first 37 individuals caught at each site, starting May 2012. For the '2014' group, we chose the last 37 individuals caught at each site, up to April 2014. An overview of the samples chosen is given in Fig. S1 (Supporting information). From all sites outside the commercial harbour, all available individuals entered microsatellite analysis. In total, 474 individuals were genotyped: 368 from the Swiss harbour (sites 1–5), 49 from the High Rhine (sites 6–11) and 57 from the Lower Rhine and surrounding channels (sites 12–16).

DNA was isolated from muscle samples using the DNeasy Blood and Tissue 96 well Kit from Qiagen. Microsatellites were amplified from 1 microlitre of eluate in PCR plates using the oligo sets indicated above and the Qiagen multiplex PCR Kit. Amplified samples were spiked with GeneScan – 500 LIZ Size Standard from Applied Biosystems and analysed on an ABI sequencer. Microsatellite traces were scored using Peak Scanner 2. Fragment lengths were rounded in Excel after manual inspection of the length value distributions of each microsatellite. Population structure was determined for all samples including females, males, juveniles and nonsexable individuals together ($n = 474$), as well as for females ($n = 239$) and males ($n = 214$) separately, and for harbour samples (sites 1–5, $n = 368$) and all nonharbour samples (sites 6–16) separately, using STRUCTURE 2.3.4 (Pritchard *et al.* 2000), under the admixture model with 10^5 burnings and 10^6 iterations. Structure Harvester 0.6.8 (Earl & vonHoldt 2012) was used to implement the Evanno method (Evanno *et al.* 2005) to find the most probable number of genetic clusters K. Runs were performed to $K = 8$ (all samples), $K = 5$ (males and females), $K = 5$ (harbour samples only) and $K = 7$ (all samples except harbour samples). Based on a first Bayesian cluster analysis including the complete data set, three groups were determined. These groups largely correspond to the different localities of catchment and were accordingly named Swiss harbour SH, Swiss Rhine SR and German Rhine GR (see results part for details). Based on this finding, all loci were checked group-wise for genotyping errors such as large allele dropout and stuttering and the presence of null alleles using the software MICROCHECKER (van Oosterhout *et al.* 2004). Indications for stuttering were found in two loci (Ame10 and NG150), null alleles were indicated for three loci (Ame 10, NG150 and NG111) in one cluster and for NG071 in another group (Table S4, Supporting information). However, none of the loci showed a consistent pattern of genotyping errors occurring in more than one group and exclusion of the four loci did not alter the results for the pairwise F_{ST} comparisons. Therefore, all 15 loci were used in further analysis.

Possible deviations from the Hardy–Weinberg equilibrium (HWE) were calculated by comparing the number of observed and expected heterozygotes and tests for locus by locus linkage disequilibrium using Arlequin 3.5 (Excoffier & Lischer 2010). Arlequin 3.5 was also used to calculate pairwise F_{ST} comparisons between all localities sampled and between the three groups found by the Structure program. To look for a pattern of isolation by distance, a Mantel test (10 000 permutations) was conducted in Arlequin 3.5 correlating pairwise F_{ST} comparisons between sampling locations with geographic distance (km). To adjust for strongly unequal sample sizes, the disproportionally large harbour sample was reduced using only a random subset from harbour locations (sampling site 1 from 2012, sampling site 2 from 2012, sampling site 4 from 2014 and sampling site 5 from 2014, $n = 148$). Allelic counts, richness and prevalence were calculated using the hierfstat package in R [Version 2.13.1; R Core Team (2014)]. Data not presented in the results part are summarized in Table S4 (Supporting information).

Analysis of mitochondrial haplotypes

To complement the nuclear microsatellite data, we established and analysed mitochondrial markers. The mitochondrial D-loop contains the replication origin and regulatory sequences and is considered the most variable region in the mitochondrial genome. Therefore, the D-loop is considered a suitable mitochondrial sequence to discriminate populations that are suspected to be closely related. It has been previously used to infer on-site evolutionary divergence in North American invasive goby populations (Dillon & Stepien 2001). We first identified polymorphic nucleotides by sequencing the entire mitochondrial D-loop (Kalchhauser *et al.* 2014; D-loop: nucleotide 15961–16890 and 0–527 from GenBank accession no. KM583832, 2029 bp in total) of a subsample of 37 individuals chosen randomly from the sample set to represent all major sampling sites (choice of individuals indicated in Table S1, Supporting information). We identified four deviations from the published mitochondrial genome in 14 of 37 individuals [nt 239 A->G (1×), nt 16038 G->A (5×), nt 16249 G->A (10×) and nt16393 G->A (1×)]. We then developed a PCR-based SNP-genotyping assay for the two more frequent polymorphisms, nt 16038 G/A and nt 16249 G/A. In this assay, the 3′ nucleotide of the forward primer of the PCR assay binds to the polymorphic site, which results in differential amplification behaviours of the two alleles and differential band patterns of the PCR products after separation on an agarose gel. Oligos SL_F16024_pmA and SL_R16367 were used at an annealing temperature of 49 °C to genotype nt 16038 G/A. SL_F16231_pmG and SL_R16503 were used at an annealing temperature of 60 °C to genotype nt 16249 G/A. Illustra PuReTaq Ready-To-Go PCR Beads were used to amplify the fragments according to the manufacturers' instructions. The assay was then performed on 147 additional individuals that were carefully chosen to represent individuals from all microsatellite clusters and from all major sampling sites. Chosen individuals are indicated in Table S1 (Supporting information). Individuals were genotyped and assigned to one of the four D-loop haplotypes, GG, GA, AG or AA. We then tested whether populations and clusters as defined from microsatellite analysis would differ in mitochondrial haplotype proportions with the prop.test function from the stats package in R [Version 2.13.1; R Core Team (2014)].

Analysis of phenotypic differentiation

Geometric morphometrics are an established way to assess body shape differences independently of body size. For geometric morphometrics, each individual was photographed with its fins spread and fixed to the surface of a polystyrene bed. We chose 22 landmarks on the left side of each specimen following general guidelines for placement of landmarks (Zelditch *et al.* 2012). We also digitized five semilandmarks to account for shape differences in regions of the fish body that do not naturally contain landmarks, such as fin insertions (see Fig. S2, Supporting information). To quantify morphological variation in body shape among individuals, we performed multivariate geometric shape analysis. After digitizing the landmarks using TPSDIG (all pictures clicked by one person), we analysed each landmark's relative position and hence overall variation in body shape using TPSRW [Thin-Plate Spline Relative Warp (Rohlf & Marcus 1993), all TPS-software and information available for download at http://life.bio.sunysb.edu/morph/index.html]. TPSRW allowed calculation of the partial warp and uniform scores that denote the differences in body shape among the individuals. To account for differences in size among specimens, the geometric morphometrics analysis includes a scaling procedure. During this scaling procedure both partial warps and uniform scores are scaled to centroid size as part of a generalized procrustes analysis (GPA; please refer to Rohlf & Slice (1990) for details of the method). We then analysed the partial warps and uniform scores using a multivariate discriminant function analysis (DFA using Statistica version 11) based on the classification of individuals into genetic clusters. Following a significant DFA, we calculated a canonical variance analysis (CVA). The CVA combined all partial warp and uniform scores for each individual into a single score that maximally discriminates between the previously chosen classifications. The CVA scores were used solely for visualization of the differences in morphology because they represent single values for an individual that are easy to use in software designed to visualize shape differences. For visualization of the body shape differences between classifications, we manually connected the landmarks of two extreme (5× the observed range of scores) individuals that lie on opposite ends of the morphology spectrum. Body shape depictions were created using the software TPSREGR that regresses the variation in body shape with independent variables such as CVA scores.

Analysis of vector plausibility

Many species invasions depend on a vector, which picks up individuals in the native range, transports them across a distance, which they would not be able to cover on their own, and releases them alive at a location where the species is not native. A transport vehicle can be considered a plausible vector for a certain species when it has properties that allow the pickup and release of individuals of this species, and when the species displays features that promote pick-up by the vehicle, such as attachment organs or a small life stage. To investigate whether commercial freshwater vessels were a plausible vector for Ponto–Caspian gobies, we gathered information on vessel properties from shipping companies operating in Basel. We contacted all shipping companies listed by the Ports of Switzerland per March 2014 (http://www.port-of-switzerland.ch/) and asked for an opportunity to interview a representative with expertise in ship construction. A total of 11 out of 42 officially listed companies could be reached and were willing to get involved. Phone conversations with company representatives were conducted in a flexible, situation-dependent manner, but followed guideline questions. Guideline questions focused on (i) whether the company's vessels would use ballast water, in which situations, and how much, (ii) what kind of filters were used to prevent particulate material from entering ballast water tanks and (iii) whether the interviewee could imagine any other transport opportunities for small sticky items such as eggs (Hirsch *et al.* 2015), small floating items such as larvae (Hensler & Jude 2007; Janac *et al.* 2013), or items of the size of an adult goby on board the company's vessels. To investigate whether freshly hatched goby juveniles could be taken up through ballast water filters with the obtained specifications, we collected clutches from the wild, hatched larvae in the laboratory (Hirsch *et al.* 2015) and measured their size.

Analysis of commercial vessels' mooring patterns in Switzerland

Patterns of genetic differentiation among members of a very recently introduced population are an indication for differential introduction pathways. In search of an explanation for the genetic structure observed among Swiss samples (sites 1–11), we analysed port call data provided by the Ports of Switzerland. These data contain information on the accurate mooring position(s), as well as exact arrival and departure times, of all vessels that use infrastructure of the Ports of Switzerland. We chose to analyse data from the year 2012, when the bighead goby was first recorded in Switzerland (Kalchhauser *et al.* 2013). As we were interested in incoming voyages with long distance vector potential, we excluded local ferry services and local small-scale cargo shipping among local ports from the data set. We did this by filtering for newly incoming cargo ships and tankers that had been absent from Basel for at least 20 days before in R [Version 2.13.1; R Core Team (2014)] and Excel. A total of 4419 arrivals passed this filter and were grouped by mooring site and ship type.

Analysis of commercial vessels' travel patterns

If the localities of certain vector types, such as cargo ships and tankers in our case, overlap with the localities of certain genotypes, differential properties of these vector types may represent the underlying cause for the observed genetic pattern. We tested whether cargo ships and tankers arriving in Switzerland displayed such differences with respect to their travel patterns. Travel data of all vessels arriving in Basel in 2012 were procured from the FleetMon database (https://www.fleetmon.com/en/). These data contain information on all stops (location and time) which a vessel travelling towards Switzerland in 2012 had made in a 14-day interval before arrival. Unreasonable and faulty data were excluded from the set by removing those voyages that contained stop records outside of Europe as well as those voyages that exceeded 40 km/h. For the remaining 4469 voyages, the locations of source and stopover ports were plotted with the packages 'maps', 'mapdata', 'mapproj' and 'gpclib' of the software R [Version 2.13.1; R Core Team (2014)].

Results

Genetic processes in the Swiss harbour population

We first examined samples from the commercial harbour (sites 1–5) in detail. From 2012 to 2014, the bighead goby population displayed a short phase of gradual growth, followed by exponential population growth and a population peak in 2013. This was followed by a retrogression phase, in which catch per unit effort decreased substantially. The retrogression phase coincided with the arrival and establishment of the round goby in the harbour (Fig. 2A). Structure analysis (Fig. 2B) suggested the presence of two major genetic clusters in the commercial harbour. Increasing the most probable number of clusters K did not reveal any further substructure (Fig. S3, Supporting information). Admixed individuals could be identified, as only 51% of all individuals showed $q < 90\%$ for either cluster. Both the Structure plot as well as pairwise population F_{ST} values close to zero (Table 2) indicated a high degree of homogeneity among samples. However, we found evidence for subtle temporal changes. At site 5, where population growth and crash were most pronounced (Fig. S4, Supporting information), both Structure and F_{ST} value indicated that the '2012' and the '2014' samples differed to some degree. Also, when inspecting loci individually, we found that two loci experienced allele frequency changes. The 192 nt allele of NG167 was present in the beginning but disappeared towards 2014, while the 165 nt allele of Ame10 was absent in 2012 and appeared towards the end of the sampling period (Fig. 2C).

Microsatellite population structure

A first Structure run including all individuals from all samples indicated a most probable number of $K = 2$

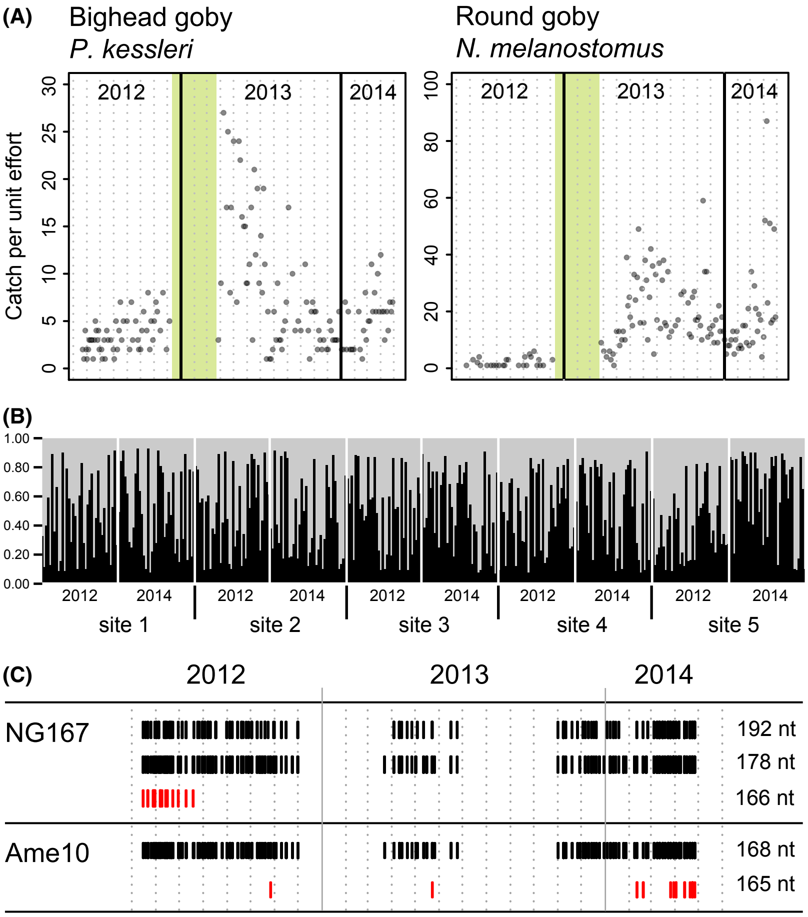

Fig. 2 Genetic processes in the harbour population. (A) Catch data from sites 1–5 in the commercial harbour from 2012 until 2014. Each dot indicates how many individuals of bighead goby or round goby were cumulatively caught in the commercial harbour on the respective field day. Vertical dotted lines indicate the first day of a new month. Vertical straight lines indicate the first day of a new year. No sampling took place from December 2012 to March 2013 (green bar). (B) Structure plot of '2012' and '2014' bighead goby samples from the indicated sites in the commercial harbour. Each vertical line represents one individual. The grey and black colour, respectively, indicates the degree of affiliation of the individual with the respective genetic cluster. (C) Allele occurrence of the microsatellites NG167 and Ame10 between 2012 and 2014. Each vertical bar represents an individual carrying the respective allele. Bars of alleles that experience frequency changes over time are drawn in red. The 166 nt allele of NG167 disappears in 2012, the 165 nt allele of Ame10 increases in incidence towards 2014.

genetic clusters (Fig. 3A, Fig. S5, Supporting information). Close inspection of Structure plots revealed two main groups or populations. The first group included individuals from the commercial harbour (sites 1–5) and the two most upstream locations in Switzerland, sites 10 and 11. These are hereafter referred to as 'population SH'. The second group included sites 6 to 9 in the Swiss Rhine, and the German sites 12 to 16, which are situated more than 600 km downstream (Fig. 1). An additional peak in the Delta K distribution at $K = 7$ however indicated further substructure in the entire data set (Fig. S5, Supporting information). Based on these findings, we confirmed substructuring in the second group, between gobies from the Swiss Rhine (hereafter called 'population SR') and the German sites (hereafter called 'population GR'). While gobies from population SR showed no further structure, additional substructuring was indicated for the German sites (Fig. S3, Supporting information).

We used the population structuring as indicated by the Structure runs to calculate the classical genetic diversity indices and pairwise F_{ST} comparisons population-wise. For eight of the 15 loci, we found deviations from the HWE for population SH, while only one locus deviated from HWE for population SR and none for population GR. The tests for deviations from linkage disequilibrium were significant in four of 315 comparisons at $P < 0.001$. However, because the significant linkage tests involved different pairs of loci in different populations, we concluded that they were more likely effects of type I errors than physical linkage between loci. The population substructure as indicated in the Structure runs was supported by significant pairwise F_{ST} comparisons (Table 2). Mantel tests were weakly significant (correlation coefficient: $r = 0.37$, $P = 0.025$) when all samples were included, and hardly significant when the dominating harbour sample was reduced in size (correlation coefficient: $r = 0.304$, $P = 0.049$).

Mitochondrial haplotypes and phenotypic differentiation

In a next step, we tested whether mitochondrial markers and body shape would mirror the microsatellite population structure. One-hundred fifteen individuals from population SH, 36 individuals from population SR

Table 2 Pairwise F_{ST} values between sampling sites. Sites with $n = 1$ were excluded from analysis. Top and bottom panel are identical except for the colour coding. F_{ST} values are indicated below, P-values above the diagonal. Green colour indicates P-values below 0.05. (A) F_{ST} values are heat-map colour coded from blue (lowest values) to red (highes values). (B) F_{ST} values are coloured yellow if they were significant after sequential Bonferroni correction

n	site	1 (2012)	1 (2014)	2 (2012)	2 (2014)	3 (2012)	3 (2014)	4 (2012)	4 (2014)	5 (2012)	5 (2014)	7	8	9	11	12	13	14	16
(A)																			
37	1 (2012)		0.41511	0.75596	0.75992	0.42026	0.27364	0.14385	0.16622	0.05613	0.49906	0.00792	0.00000	0.00000	0.04435	0.05445	0.07544	0.00000	0.00000
37	1 (2014)	0.00049		0.37046	0.21641	0.12840	0.67746	0.01455	0.19137	0.00000	0.53480	0.00139	0.00000	0.00000	0.05594	0.05168	0.12019	0.00000	0.00000
36	2 (2012)	−0.00360	0.00109		0.75220	0.65904	0.37303	0.54341	0.17434	0.01841	0.72191	0.00545	0.00010	0.00000	0.07455	0.09761	0.28769	0.00000	0.00000
37	2 (2014)	−0.00363	0.00338	−0.00351		0.63291	0.58578	0.56767	0.56153	0.14999	0.54331	0.01337	0.00010	0.00000	0.10445	0.13593	0.31225	0.00000	0.00000
36	3 (2012)	−0.00048	0.00469	−0.00303	−0.00279		0.35175	0.95921	0.44392	0.22136	0.61350	0.00495	0.00000	0.00000	0.02604	0.05079	0.11316	0.00000	0.00000
37	3 (2014)	0.00209	−0.00269	0.00078	−0.00181	0.00018		0.24116	0.96753	0.02267	0.52510	0.00238	0.00000	0.00000	0.08534	0.10702	0.20919	0.00000	0.00000
37	4 (2012)	0.00430	0.01203	−0.00152	−0.00167	−0.00792	0.00233		0.47906	0.13306	0.09336	0.00139	0.00000	0.00000	0.02792	0.10167	0.26552	0.00000	0.00000
37	4 (2014)	0.00495	0.00461	0.00507	−0.00110	−0.00034	−0.00763	−0.00061		0.21523	0.48659	0.00317	0.00000	0.00000	0.13692	0.10484	0.27512	0.00000	0.00000
37	5 (2012)	0.00793	0.02470	0.01246	0.00464	0.00243	0.01046	0.00470	0.00385		0.00673	0.00079	0.00000	0.00000	0.01762	0.09266	0.08039	0.00000	0.00000
37	5 (2014)	−0.00072	−0.00105	−0.00343	−0.00132	−0.00268	−0.00127	0.00644	−0.00031	0.01654		0.00327	0.00010	0.00000	0.22552	0.04168	0.08118	0.00000	0.00000
6	7	0.05286	0.07148	0.05727	0.04922	0.05220	0.06372	0.06230	0.07211	0.07080	0.06896		0.57945	0.92030	0.03218	0.72488	0.14484	0.00000	0.00129
4	8	0.13733	0.14847	0.12859	0.11254	0.12842	0.13333	0.14233	0.14833	0.15398	0.13848	−0.00445		0.29482	0.04970	0.06514	0.00762	0.00000	0.00020
32	9	0.05972	0.06979	0.06768	0.05484	0.05955	0.06569	0.07293	0.06901	0.06949	0.07073	−0.02172	0.01333		0.00050	0.30749	0.03703	0.00000	0.00000
5	11	0.03871	0.03775	0.03551	0.02820	0.04214	0.03119	0.04597	0.02828	0.05321	0.01685	0.15883	0.16219	0.12899		0.17860	0.19543	0.00000	0.00129
2	12	0.07617	0.08089	0.06262	0.04801	0.06130	0.05538	0.05224	0.06591	0.05589	0.09377	0.02055	0.05986	0.03166	0.17501		0.61994	0.01287	0.17434
5	13	0.02626	0.02193	0.00840	0.00617	0.01694	0.01192	0.00525	0.01190	0.02658	0.02958	0.04101	0.08779	0.04968	0.04631	−0.04070		0.00040	0.20374
32	14	0.12861	0.11317	0.13236	0.10842	0.10880	0.11257	0.12619	0.12453	0.11704	0.13485	0.14422	0.17393	0.13020	0.15977	0.11129	0.08819		0.00000
17	16	0.08020	0.09691	0.08527	0.07837	0.09727	0.09786	0.08631	0.10612	0.09055	0.11880	0.09854	0.16478	0.09735	0.14343	0.04869	0.01476	0.13154	
(B)																			
37	1 (2012)		0.41511	0.75596	0.75992	0.42026	0.27364	0.14385	0.16622	0.05613	0.49906	0.00792	0.00000	0.00000	0.04435	0.05445	0.07544	0.00000	0.00000
37	1 (2014)	0.00049		0.37046	0.21641	0.12840	0.67746	0.01455	0.19137	0.00000	0.53480	0.00139	0.00000	0.00000	0.05594	0.05168	0.12019	0.00000	0.00000
36	2 (2012)	−0.00360	0.00109		0.75220	0.65904	0.37303	0.54341	0.17434	0.01841	0.72191	0.00545	0.00010	0.00000	0.07455	0.09761	0.28769	0.00000	0.00000
37	2 (2014)	−0.00363	0.00338	−0.00351		0.63291	0.58578	0.56767	0.56153	0.14999	0.54331	0.01337	0.00010	0.00000	0.10445	0.13593	0.31225	0.00000	0.00000
36	3 (2012)	−0.00048	0.00469	−0.00303	−0.00279		0.35175	0.95921	0.44392	0.22136	0.61350	0.00495	0.00000	0.00000	0.02604	0.05079	0.11316	0.00000	0.00000
37	3 (2014)	0.00209	−0.00269	0.00078	−0.00181	0.00018		0.24116	0.96753	0.02267	0.52510	0.00238	0.00000	0.00000	0.08534	0.10702	0.20919	0.00000	0.00000
37	4 (2012)	0.00430	0.01203	−0.00152	−0.00167	−0.00792	0.00233		0.47906	0.13306	0.09336	0.00139	0.00000	0.00000	0.02792	0.10167	0.26552	0.00000	0.00000
37	4 (2014)	0.00495	0.00461	0.00507	−0.00110	−0 00034	−0.00763	−0.00061		0.21523	0.48659	0.00317	0.00000	0.00000	0.13692	0.10484	0.27512	0.00000	0.00000
37	5 (2012)	0.00793	0.02470	0.01246	0.00464	0.00243	0.01046	0.00470	0.00385		0.00673	0.00079	0.00000	0.00000	0.01762	0.09266	0.08039	0.00000	0.00000
37	5 (2014)	−0.00072	−0.00105	−0.00343	−0.00132	−0.00268	−0.00127	0.00644	−0.00031	0.01654		0.00327	0.00010	0.00000	0.22552	0.04168	0.08118	0.00000	0.00000
6	7	0.05286	0.07148	0.05727	0.04922	0.05220	0.06372	0.06230	0.07211	0.07080	0.06896		0.57945	0.92030	0.03218	0.72488	0.14484	0.00000	0.00129
4	8	0.13733	0.14847	0.12859	0.11254	0.12842	0.13333	0.14233	0.14833	0.15398	0.13848	−0.00445		0.29482	0.04970	0.06514	0.00762	0.00000	0.00020
32	9	0.05972	0.06979	0.06768	0.05484	0.05955	0.06569	0.07293	0.06901	0.06949	0.07073	−0.02172	0.01333		0.00050	0.30749	0.03703	0.00000	0.00000
5	11	0.03871	0.03775	0.03551	0.02820	0.04214	0.03119	0.04597	0.02828	0.05321	0.01685	0.15883	0.16219	0.12899		0.17860	0.19543	0.00000	0.00129
2	12	0.07617	0.08089	0.06262	0.04801	0.06130	0.05538	0.05224	0.06591	0.05589	0.09377	0.02055	0.05986	0.03166	0.17501		0.61994	0.01287	0.17434
5	13	0.02626	0.02193	0.00840	0.00617	0.01694	0.01192	0.00525	0.01190	0.02658	0.02958	0.04101	0.08779	0.04968	0.04631	−0.04070		0.00040	0.20374
32	14	0.12861	0.11317	0.13236	0.10842	0.10880	0.11257	0.12619	0.12453	0.11704	0.13485	0.14422	0.17393	0.13020	0.15977	0.11129	0.08819		0.00000
17	16	0.08020	0.09691	0.08527	0.07837	0.09727	0.09786	0.08631	0.10612	0.09055	0.11880	0.09854	0.16478	0.09735	0.14343	0.04869	0.01476	0.13154	

and 32 individuals from population GR (individuals indicated in Table S1, Supporting information) that could unambiguously be assigned to a certain microsatellite genotype were genotyped for their D-loop haplotype. We could distinguish four D-loop haplotypes GG, GA, AG and AA, which we found to occur in a site-specific manner. GG occurred preferentially in the commercial harbour, GA occurred preferentially in the Swiss Rhine and AA occurred preferentially in the German Rhine. This site-dependent distribution was statistically significant, also when we restricted our analysis to individuals associated with the same microsatellite cluster (Fig. 3B, Table 3). The same was true for body shape. Individuals from the German Rhine and from the Swiss Rhine differed significantly in body shape, even when only individuals affiliated with the same microsatellite genotype were analysed. At the same time, we could not identify a significant difference in body shape between individuals caught in the same location, the commercial harbour, but affiliated with different genetic clusters (Fig. 3C, Table 4).

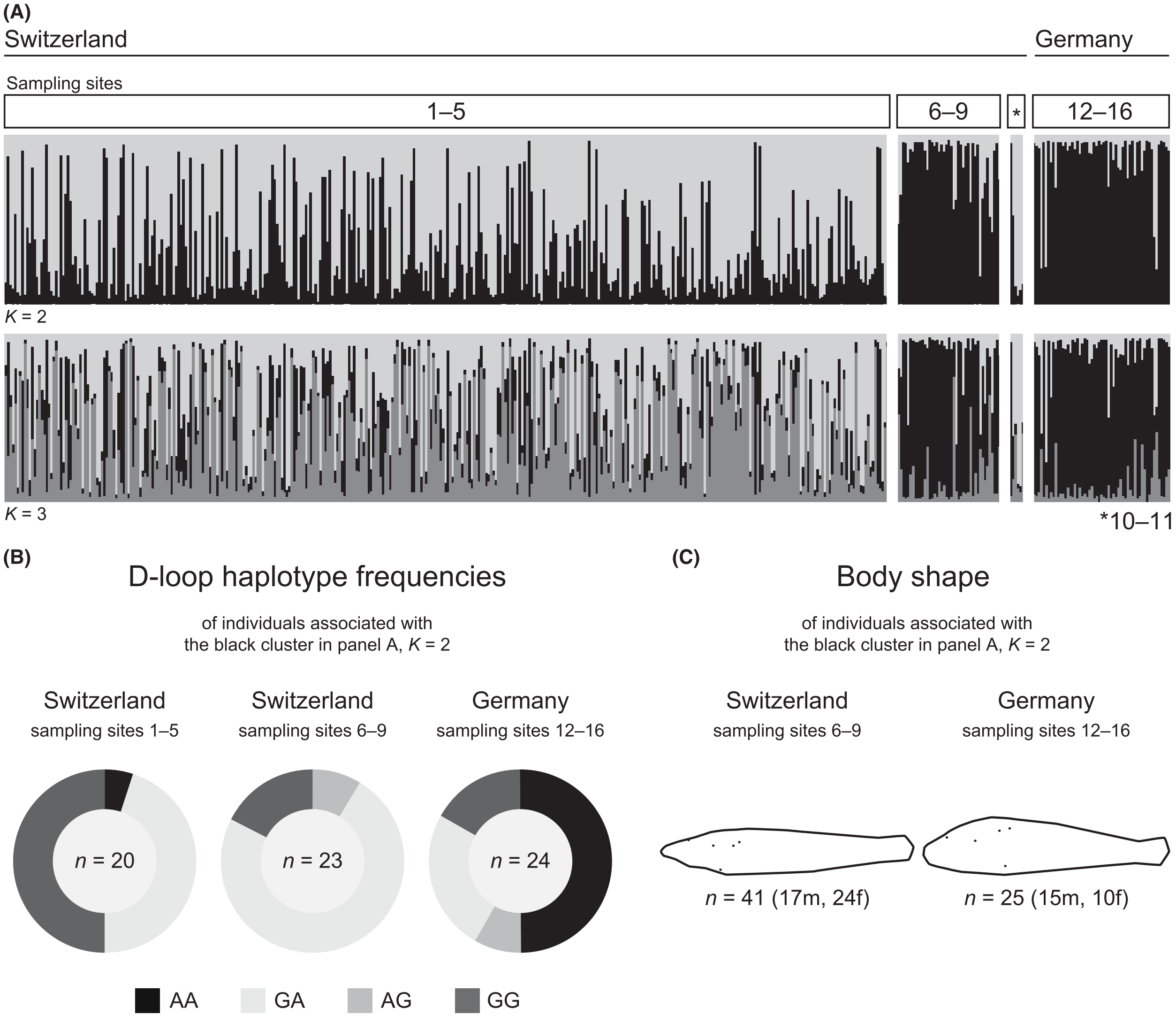

Fig. 3 Comparison of microsatellite structure, D-loop haplotypes and body shape. (A) Structure plot of all samples. Each individual is represented by a vertical line. The grey and black colour, respectively, indicates the degree of affiliation with the respective genetic cluster. Sampling sites and geographical region of origin of individuals are indicated above the plot. (B) Mitochondrial haplotype frequencies. The indicated numbers (*n*) of selected individuals from the indicated sites that were affiliated with the black cluster in panel A, $K = 2$ were genotyped for their D-loop haplotypes. (C) Body shape. The indicated numbers (*n*) of selected individuals from the indicated sites that were affiliated with the black cluster in panel A, $K = 2$ were analysed for their body shape using geometric morphometrics. m, males. f, females. Body outlines represent the connected landmarks of two extreme (5× the observed range of scores) individuals that lie on opposite ends of the morphology spectrum.

Table 3 D-loop haplotype affiliations. (A) Numbers of individuals affiliated with the respective haplotype are given for all genotyped individuals (top) and for genotyped individuals affiliated with the black cluster in Fig. 3A, $K = 2$ (bottom). (B) Pairwise comparisons of haplotype proportions between indicated groups of individuals. P-values below 0.05 indicate that haplotype distributions are significantly different between the groups compared

(A) Haplotype counts			
Country	Switzerland		Germany
Pop	SH	SR	GR
Sampling site	1–5	6–9	12–16
Data set: all individuals	$n = 184$		
Haplotype AA	1	0	15
Haplotype AG	4	2	3
Haplotype GA	45	30	9
Haplotype GG	65	4	6
Data set: black cluster ($K = 2$)	$n = 67$		
Haplotype AA	1	0	12
Haplotype AG	0	2	2
Haplotype GA	9	17	6
Haplotype GG	10	4	4

(B) Pairwise comparisons of haplotype proportions		
First data set	Second data set	P-value
Pop SH	Pop SR	0.00002791*
Pop SH	Pop GR	0.00000000000182*
Pop SR	Pop GR	0.000006397*
POP SH, black cluster only	Pop SR, black cluster only	0.04895*
Pop SH, black cluster only	Pop GR, black cluster only	0.002604*
Pop SR, black cluster only	Pop GR, black cluster only	0.0006286*
Pop SH	Pop SH, black cluster only	0.4018
Pop SR	Pop SR, black cluster only	0.6809
Pop GR	Pop GR, black cluster only	0.99

*$P < 0.05$.

Evidence for commercial vessels as vectors for the bighead goby

Structure runs suggested that fish from the Swiss Rhine may be more similar to fish from Germany than to fish from the commercial harbour. Such a pattern would imply some kind of connection between the geographically widely separated populations SR and GR. When we interviewed ship inspectors, captains, executive directors and fleet inspectors on the vector potential of their company's vessels, eight of eleven interviewees confirmed the use of ballast water. They indicated that all commercial ship types travelling on the Rhine towards Switzerland – tankers, cargo vessels and passenger boats – use large amounts of ballast water to stabilize empty vessels and to pass below bridges. The mesh sizes of ballast water tank filters were specified as ranging from 3 to 8 mm. Ponto–Caspian goby larvae that were hatched from eggs (Hirsch *et al.* 2015) for comparison with mesh sizes were found to be approximately 2 × 2 × 7 mm in size (Fig. 4A). In addition to ballast water tanks, company representatives pointed at the ships' cooling systems as a potential hideaway for adult individuals. They indicated that these so-called sea chests were continually flushed with fresh river water through entry slits that were 3–8 cm wide. Adult bighead gobies in Switzerland reach about 3–4 cm in head width and no more than 3 cm body height, and can be much smaller than that (own observation, data not shown).

Structure runs and pairwise FST comparisons revealed genetic structuring among Swiss sampling sites, in particular between the harbour population SH and the adjacent river population SR. The genetic differences observed between population SH and population SR may be caused by differential introductions. When analysing mooring patterns of cargo ships and tankers in Switzerland, we found that these two ship types use available anchoring sites in a nonuniform manner. The major mooring sites for cargo ships overlap with sites associated with population SH (sites 1–5 and sites 10 and 11). Tanker mooring sites on the other hand overlap with sites associated with population SR (sites 6–9) (Fig. 4B).

When analysing travel patterns of vessels heading towards Switzerland to test whether these ship types may potentially pick up propagules from different source populations, we found that cargo ships and tankers used different harbours before their arrival. Tankers almost exclusively called at harbours along the river Rhine, while cargo ships also used ports along the Danube and Rhine–Main–Danube channel, as well as ports in Northern Germany, before they arrived in Switzerland (Fig. 4C).

Discussion

In this study, we have for the first time identified genetic structuring among invasive populations of the bighead goby *Ponticola kessleri*. The observed structure carries a number of signatures of a recent and ongoing range expansion. Also, the genetic structure is informative with respect to introduction routes. Observed genetic patterns relate well to vessel anchoring and vessel travel patterns. In accordance with these findings, we describe that ballast water use and ballast water tank specifications in the freshwater environment are permissive for the introduction of invasive gobies by commercial vessels.

Table 4 Geometric morphometrics

	Group 1						Group 2					Results					
		n	m	f	j	NA		*n*	m	f	j	Eigenvalue	Canon R	Wilk's Lambda	Chi-Square	df	*P*-value
All individuals	Male	**216**	216	0	0	0	Female	**240**	0	240	0	1.683008	0.792013	0.372716	418.4619	50	**<0.001**
harbour population	Grey cluster (*K* = 2)	**35**	13	18	3	1	Black cluster (*K* = 2)	**168**	85	75	8	0.406310	0.537512	0.711081	60.01064	50	**0.1570**
Black cluster (*K* = 2)	German Rhine	**41**	17	24	0	0	Swiss Rhine	**25**	15	10	0	2976.009	0.999832	0.000336	159.9735	40	**<0.001**

The body shapes of indicated groups with the indicated affiliation were compared. *n*, total number of individuals entering analysis from the indicated group. m, f, j, NA, number of male, female, juvenile and not sexed individuals, respectively. *P*-values below 0.05 indicate that the body shapes of the compared groups are significantly different.

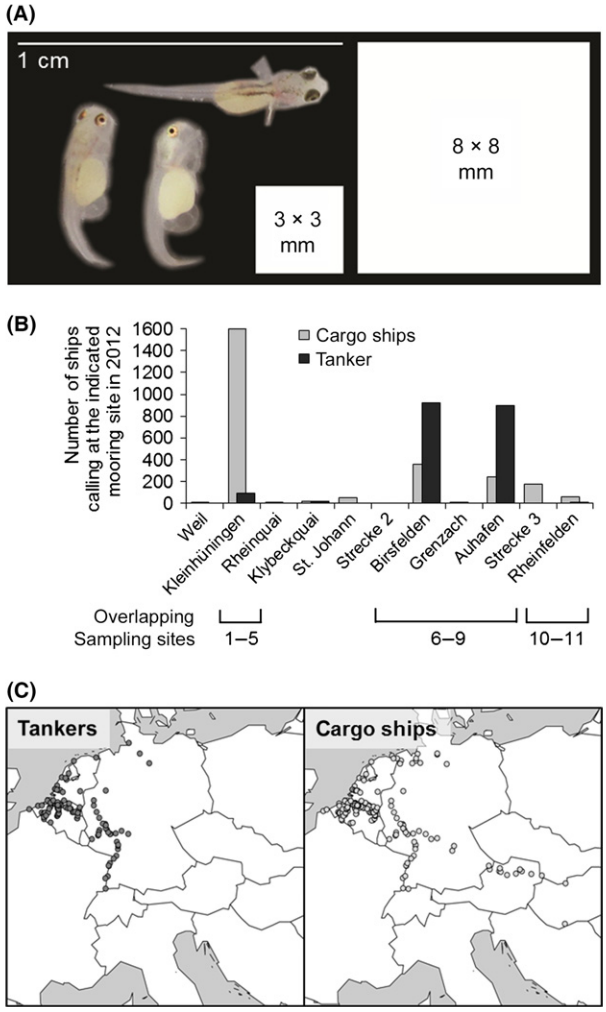

Fig. 4 Evidence for commercial shipping as vector for non-native gobies. (A) Freshly hatched goby larvae displayed at scale next to drawings of ballast water tank filter pores. (B) Bar plot of the numbers of cargo ships and tankers calling at the indicated mooring sites in Switzerland. Goby sampling sites closest to these mooring sites are indicated below the plot. Sites 1–5, 10 and 11 affiliate with one genetic cluster, sites 6–9 affiliate with a different genetic cluster (Fig. 3A). (C) Source harbours of cargo ships and tankers arriving in Basel, Switzerland. Each dot on the map indicates a harbour where a ship of the indicated type that arrived in Basel in 2012 had stopped within 14 days prior to arrival.

Invasive bighead goby populations are genetically differentiated

Previous studies (Ondrackova *et al.* 2012; Cerwenka *et al.* 2014b) could not observe any structuring on small or large scales for invasive bighead goby populations. This may reflect a low overall genetic diversity in this species, at least in the invasive range. In contrast to these reports, we detected genetic structuring among bighead goby populations and could even resolve temporal turnover in a densely sampled harbour population. This difference between studies may be attributable to the marker types and sampling schemes used. Microsatellites and D-loop sequences as used in this study are fast evolving sequences and therefore may yield higher resolution than AFLP markers and Cytochrome B sequences as used by Cerwenka *et al.* (2014a). Also, our data suggest that the sampling scheme may have an impact on the ability to detect structuring. If we would have sampled less sites (e.g. only sites 6–9, or only sites 1–5, 10 and 11), we would not have been able to detect genetic differences between sites and would have come to similar conclusions as Ondrackova *et al.* (2012) and Cerwenka *et al.* (2014b).

Genetic signatures of an ongoing invasion

Our catch data suggest that the goby population in the commercial harbour has arrived recently and was going through an establishment period during our sampling interval. The relative dynamics of round and bighead goby catches, with the bighead goby being present in low numbers from the beginning of monitoring and with the round goby arriving during the monitoring, represents a typical pattern for the establishment period of Ponto–Caspian gobies in Central Europe. In the Upper Danube River, the bighead goby invaded shortly before the round goby (Seifert & Hartmann 2000; Paintner & Seifert 2006) and decreased in abundance after the arrival of the round goby. A similar pattern was also observed in the Lower Rhine (Borcherding *et al.* 2011; J. Borcherding, S. Gertzen, P. Jurajda, pers. communication). Also, fishermen at the Rhine at Basel did not register non-native gobies before 2012, although they were informed about their expected arrival (Dönni 2002).

Our genetic results support the idea that the bighead goby arrived in Switzerland very recently. We identify deviations from HWE specifically in the harbour population, indicating that this population is either substructured or subjected to selection and/or drift processes. As we could exclude geographic, temporal or sex-dependent substructuring, we propose that the population is currently subject to genetic processes. Indeed, we could detect turnover of individual microsatellite alleles in the commercial harbour. At site 5, genetic turnover may also be ongoing at the population level, as suggested by Structure analysis. This turnover may be linked to the population growth and crash that was suggested by catch data from this site. In summary, these observations validate our approach to monitor genetic processes at an invasion front in real time. We look forward to similar experiments on the round goby, which started invading the harbour during our sampling timeline and thus also represents an excellent case of an ongoing invasion.

Genetic evidence for vector activities of cargo ships and tankers

Swiss populations were introduced recently, are closely spaced, and are likely linked through larval drift. Based on our understanding of commercial shipping as a single and homogeneous vector, we expected samples from Switzerland to be genetically homogeneous. Based on the fact that German populations established in 2004, and invasive gobies arrived in Switzerland not before 2011, we expected German and Swiss samples to differ pronouncedly. Yet, the invasion front in Switzerland is genetically fragmented, and German and a subset of Swiss samples do seem to bear some kind of similarity. As Swiss populations are young, the genetic differences among them cannot be attributed to evolutionary divergence.

Our results suggest that shipping travel behaviour may underlie the observed pattern. While round goby translocations to and within the Great Lakes have been attributed to shipping traffic (LaRue *et al.* 2011), the potential of commercial river shipping to transport fish propagules is to date unresolved. Here, we demonstrate that commercial freshwater vessels may present excellent vectors for upstream transport of invasive goby species. Freshwater vessels do indeed use ballast water on their way to Switzerland, and larvae are without any doubt small enough for uptake in freshwater ballast tanks. Ponto–Caspian goby larvae are present in the water column in massive amounts (Hensler & Jude 2007; Janac *et al.* 2013) and drift downstream in rivers from March/April to August (Janac *et al.* 2013). During this time, they can easily be taken up with ballast water by commercial vessels in harbours or during shipping, and released with the ballast water upon discharge.

In addition, our observations and our data suggest that eggs may also serve as propagules. Ponto–Caspian gobies readily accept any kind of narrow cave-like structure, such as PVC tubes, as shelter and spawning substrate, both in the laboratory and in the field (Hirsch *et al.* 2015). Adult invasive gobies may thus seek shelter in the cooling systems of commercial vessels while these are anchored in a harbour. The openings of those systems are large enough to accommodate Ponto–Caspian gobies. While it is unlikely that individual adults would be able to hold on to the cooling systems during transport, goby eggs are highly resistant to dragging forces and other stressors (Hirsch *et al.* 2015). Eggs deposited in the cooling system or on any other crevice of the ship may be transported with the ship to the next destination and would eventually hatch.

Our genetic data suggest that individuals may have been introduced to Switzerland from different source populations. Shipping data support this interpretation. The mooring sites of cargo ships and tankers, two ship types that we find to come to Basel from different source regions, mirror the geographic occurrence of populations. Also, we observe four unique alleles in the harbour population, but none in the Swiss Rhine population and only one in the German Rhine population (Table S4, Supporting information), indicating that the harbour population receives input from somewhere else – putatively, from populations in the Danube. It seems like bighead goby population genetics may accurately mirror the introduction pathways. This could be further investigated in the future using mtDNA haplotype data, as these were found to differ between all three investigated populations in this study. Source regions were not sampled in this study, and it is important to note in this context that very little is known about the genetic structure of Ponto–Caspian goby species in the native area. An elaborate phylogeographic analysis investigating mtDNA haplotypes of Ponto–Caspian gobies in their native range, combined with common shipping travel routes, would eventually provide detailed information about the source of goby introductions for all sites investigated. Comparing these patterns for different invasive goby species would be highly interesting.

We are not aware of any alternative variable such as habitat structure or water temperature that would covary with the genetic patterns observed. Also, we can exclude that bait-bucket transfers play a major role in setting up the observed structure. Bait-bucket transfers have been shown to be relevant in Northern America (Drake *et al.* 2014). However, fishermen in Switzerland were not yet routinely catching invasive gobies when sample collections started. Also, the use of live bait is generally forbidden in the area. In such a situation, the propagule pressure exerted by bait-bucket transfers would be, if present at all, minuscule.

Mitochondrial markers and body shape

As there is no evidence for bottlenecks during Ponto–Caspian goby invasions (Stepien & Tumeo 2006), and propagule numbers are therefore assumed to be high, we expected that maternally inherited mitochondrial haplotypes would yield similar patterns as nuclear markers. Body morphology was expected to be independent of either genetic marker, as fish are known to be morphologically plastic, particularly during development (Langerhans & Reznick 2010).

We found that individuals associated with the same microsatellite cluster would differ in both mitochondrial haplotype and in body shape when they came from different sites. While this is an interesting observation, it is important to note that these analyses were all based on the result of the Structure run at $K = 2$. At $K > 3$, the cluster uniting population SR and population GR splits up. Differences in morphology and in mitochondrial markers may therefore not be surprising when comparing population SR and GR individuals.

For both markers, we also found that individuals associated with different microsatellite clusters would be similar if they came from the same site. In the case of morphology, these results add to recent studies on phenotypic differentiation in goby species, which assume that morphological differences among subpopulations arise from plasticity rather than rapid genetic adaptation (Simonovic *et al.* 2001; Polacik *et al.* 2012; Cerwenka *et al.* 2014b). However, as microsatellites are generally considered to be neutral genetic markers because they rarely occur in coding regions (Li *et al.* 2002), we may have missed an association between body shape and genotype due to our choice of markers.

For mitochondrial haplotypes, the observation indicates that maternally inherited mitochondrial genotypes and nuclear genotypes have the potential to yield divergent patterns for this species. Similar diverging patterns of nuclear and mitochondrial markers have been observed, for example in brown and polar bears (Hailer *et al.* 2012; Bidon *et al.* 2014) and have been attributed to male-biased introgression due to migratory males (Bidon *et al.* 2014). In the case of invasive gobies, a sex-specific bottleneck would provide an explanation for diverging patterns. Invasive goby males and females do indeed differ in traits that might be relevant to dispersal. Sexual dimorphism in size is common in gobiids and might lead to different swimming and range expansion performance between larger male individuals and smaller female individuals. Also, behaviour can differ fundamentally between sexes. In the round goby, males were found to be more active and more prone to explore novel environments than females. Consequently, in the field males move larger distances than females (Marentette *et al.* 2011). Conversely, recent research in the Danube suggested that migrating adult females (and not males) were mainly driving a range expansion (Brandner *et al.* 2013). However, sexual dimorphisms themselves can change as an invasive population expands its range. For example, size differences between males and females increased as a population of the round goby expanded its range (Brandner *et al.* 2013). In general, sex-biased dispersal is well described in mammals and birds, and mounting evidence from studies with fish suggests that differences between the sexes can create complex range expansion dynamics. Alternatively, a sex-specific bottleneck may be independent from differential behaviour of males and females and arise simply through the reduced population size of males/females in relation to the entire population. Together, our observations advertise caution when inferring population structures from one marker type only. Even when not expected, sex-specific processes may be at work, and may affect the results. In this context, it is important to note that the observed microsatellite-based population structure was sex-insensitive. The population structure was equally supported by males and females (Fig. S6, Supporting information). Our data also indicate that invasive Ponto–Caspian gobies may be well suited as models for research addressing the differential contribution of sexes to a range expansion (Prugnolle & de Meeus 2002).

Implications for biological invasions and invasion genetics

Our results provide important insights into population genetics of recently invasive species and propose relevant conclusions on how to study invasive populations.

First, our data support the notion that isolation by distance applies only weakly to invasive gobies, and very likely, to most invasive species in general. In fact, our observation of very low levels of isolation by distance may be attributable to the unequal numbers of fish sampled at individual sites. In our data set, 75% of all samples originate from within <2 km. Indeed, Mantel tests become less significant when we reduce the harbour data set by arbitrarily removing a fraction of individuals from the analysis. Isolation by distance thus actually may not apply to our data set. Our results therefore support the idea that invasive organisms experience a distorted distance landscape in which vector activity complements, or possibly even replaces, geographic separation as distance measure (LaRue *et al.* 2011; Darling *et al.* 2012; Ghabooli *et al.* 2013a,b; Schrey *et al.* 2014).

In addition, our observations indicate that human actions may promote spatial differentiation of invasive species through cryptic diversity in vector behaviour. Our data indicate that hidden variations among closely spaced sampling sites, such as the slightly shifted travel patterns of cargo and tank ships in our case, may be sufficient to generate a signature in population genetics. Consequently, our observations suggest that, if one wants to investigate population structures and invasion pathways with restricted resources, sampling more sites less intensely may be better than sampling few sites more intensely. Temporally widely stretched and geographically very restricted sampling schemes, such as those used by Stepien & Tumeo (2006) or Brown & Stepien (2009) for the round goby, sometimes cannot be avoided, but are problematic because such schemes do neither take temporal turnover into account nor do they subsample potentially fragmented source populations.

Invasive populations are expected to lose diversity and fitness at the range margin during expansion processes (Peischl & Excoffier 2015). Frequently, however, invasive populations are highly successful. Importantly, current models of expanding populations are linear and do not deal with multiple sources (Peischl *et al.* 2015). Successful invasions, however, are often associated with multiple introductions and subsequent mixing (Bock *et al.* 2014). Our data provide further evidence that invasive populations integrate input from diverse sources. Linear expansion models, although highly relevant for cancerous tissue expansion processes or for slow post-glacial species expansion processes, may not be able to properly recapitulate genetic processes during species invasions.

Our data indicate that the genetic clusters of bighead goby have started to interbreed where they meet. The harbour population contains a low fraction of admixed individuals. Accordingly, interbreeding has either not been going on for very long or 'true type' individuals keep arriving and maintain a relevant proportion of nonadmixed individuals. Depending on the mechanism at work, genetic structuring will disappear in the future through continuous interbreeding in combination with larval drift and local migration or will be maintained by continued input of true type individuals. In this context, it is interesting to note that subpopulations in Western Germany, which established around 2006 (Borcherding *et al.* 2011), show some degree of substructuring. Whether they started off that way, or whether this substructure resulted from selection and adaptation processes since 2006, is unclear. Future research will show whether the Swiss subpopulations will be able to maintain the existing genetic differences, homogenize or establish novel genetic differences.

Finally, we propose that vector-induced genetic fragmentation of the invasion front may explain the lag phase frequently observed during species invasions. It has been proposed previously that introduction sites may serve as melting pots when different genotypes from different sources are introduced to the same site (Brown & Stepien 2009). We do observe such a phenomenon in the harbour population. Additionally, our data suggest that subtle differences in vector behaviour may result in a geographically–genetically structured invasion front. In such a scenario, geographically separated and genetically discrete subpopulations may have to go through a phase of natural migration and small-scale translocations before they would be able to mix. In such a model, a lag phase preceding exponential population growth may not just represent the time needed for reshuffling of alleles between two genotypes introduced at the same spot to yield novel beneficial allele combinations, but may rather represent the time needed for different genotypes to get to the same spot (and mix afterwards).

Implications for ballast water management

Ballast water in the marine sector contains a diverse community of organisms and taxa (Gollasch *et al.* 2002). As freshwater vessels take smaller volumes of ballast water compared to marine vessels, their potential to transport reasonable amounts of organisms is not fully acknowledged, and freshwater ballast water is thus not managed. Our data substantiate the relevance of freshwater vessels for the translocation of non-native vertebrate species. With this study, we hope to contribute to the establishment of freshwater ballast water management procedures such as proposed by Briski *et al.* (2015) and also hope to provide decision makers in the freshwater sector with the evidence they need to promote ballast water hygiene measures.

Acknowledgements

Gobies from sites 14, 15 and 16 were collected by personnel of the Landesfischereiverband Westfalen und Lippe e.V., which is greatly acknowledged. Gobies from sites 6, 7, 8 and 9 were collected by local Swiss fishermen, who have displayed extraordinary support for our work. We are further grateful to Pascal Blarer, Lilian Röllin, Heidi Schiffer, Nicole Seiler, Stefan Leiser and Catherine Cornaz for technical assistance, to Sebastian Adrian-Kalchhauser (http://s-a.cc) for graphic and conceptual support during data visualization and to local fishing authorities for continuous support of our work. This project was funded by a special grant from the Federal Office for the Environment, Switzerland, the canton BS and cantonal lottery funds of AG, BL, SO. We confirm that we do not have a conflict of interest to declare.

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I.A.K. designed the project. I.A.K., P.E.H., J.B.G., A.N., S.W., S.L. and S.G. collected data. I.A.K. and J.B.G. analysed genetic data. I.A.K. analysed shipping data. P.E.H. analysed morphometric data. I.A.K., P.E.H., J.B.G., A.N., J.B. and P.H. wrote the study.

Data accessibility

All data are accessible in the Supplementary Material provided with this article.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Sample information including sampling date, site, catch method, weight, length, sex, microsatellite genotype, D-loop haplotype and cluster affiliation for $K = 2$.

Table S2 Primer sequences for primers used in this study.

Table S3 Microsatellite set establishment process indicating which of the published goby microsatellites passed which analysis stage.

Table S4. Information on stutter, allele dropout, null alleles, HWE, linkage disequilibrium, population F_{ST}, Mantel tests, allele frequencies, allelic richness, F_{IS} and genetic diversity.

Appendix S1 Microsatellite sequences for bighead goby and round goby as determined in this study.

Fig. S1 Weight vs. Catch Date plots, separately drawn for sites 1–5 from the commercial harbour, are illustrating which 37 first and last individuals caught at each site entered analysis.

Fig. S2 Landmarks used for Geometric Morphometrics.

Fig. S3 Structure plots for $K = 2$ to $K = 5$–8, drawn separately for all samples, the harbour samples, and all samples minus the harbour samples.

Fig. S4 Catch data for bighead goby split by sites 1–5 from 2012 to 2014. Solid lines indicate the beginning of a year, and dotted lines indicate the beginning of a month.

Fig. S5 Structure Harvester plot indicating the most probable K for all samples.

Fig. S6 Structure plots for $K = 2$–5 for all samples, all male samples and all female samples.

Supporting Information

The invasive bighead goby *Ponticola kessleri* displays large scale genetic similarities and small scale genetic differentiation in relation with shipping patterns.

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Contents:

Figure S1

Weight vs Catch Date for the samples from sites 1-5 in the harbor Basel (37 fist and 37 last individuals from each site) that were included in the study.

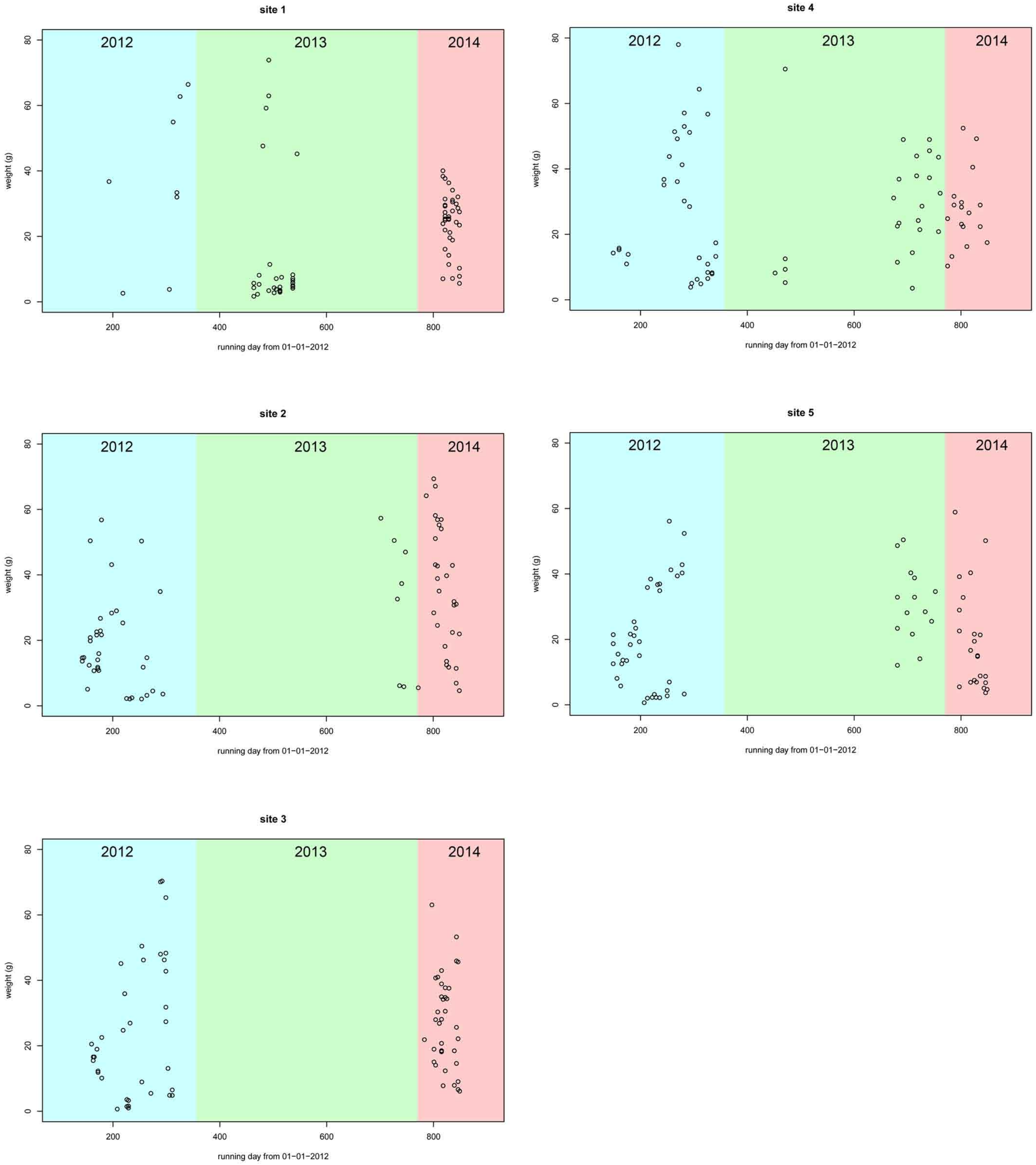


Figure S2

Landmarks used for Geometric Morphometrics.

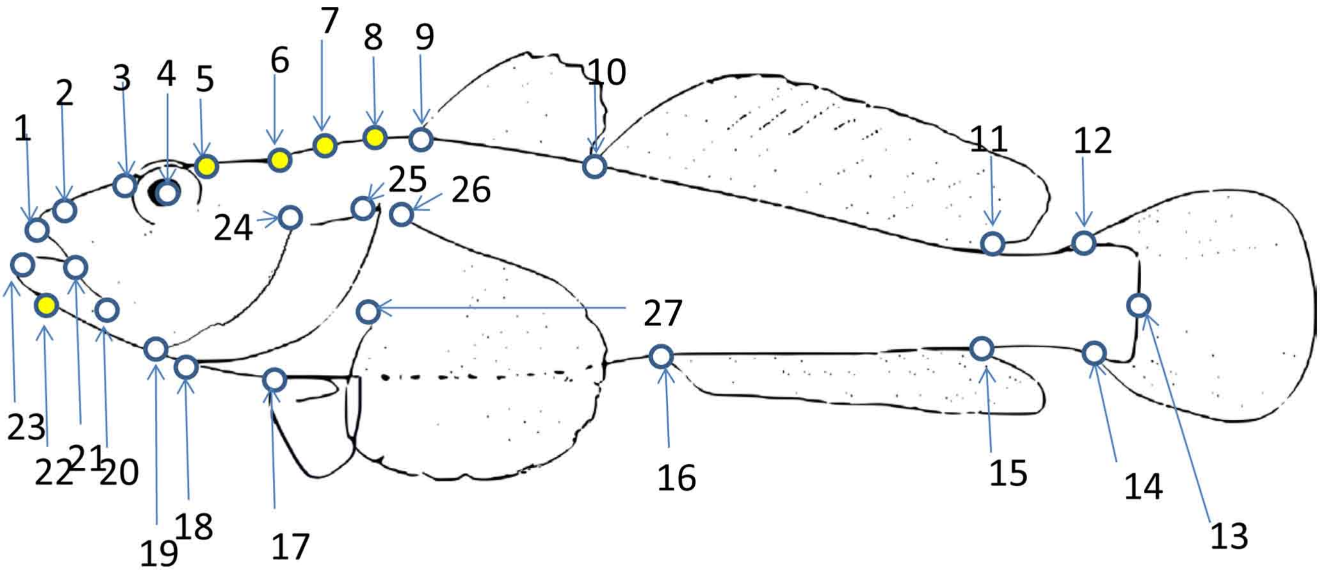


Figure S3

This part of the supplementary material can be found online:

http://onlinelibrary.wiley.com/doi/10.1111/mec.13595/full

Figure S4

Total catch data for bighead goby split by sites 1-5 from 2012 to 2014.
Solid lines indicate the beginning of a year, dotted lines indicate the beginning of a month.

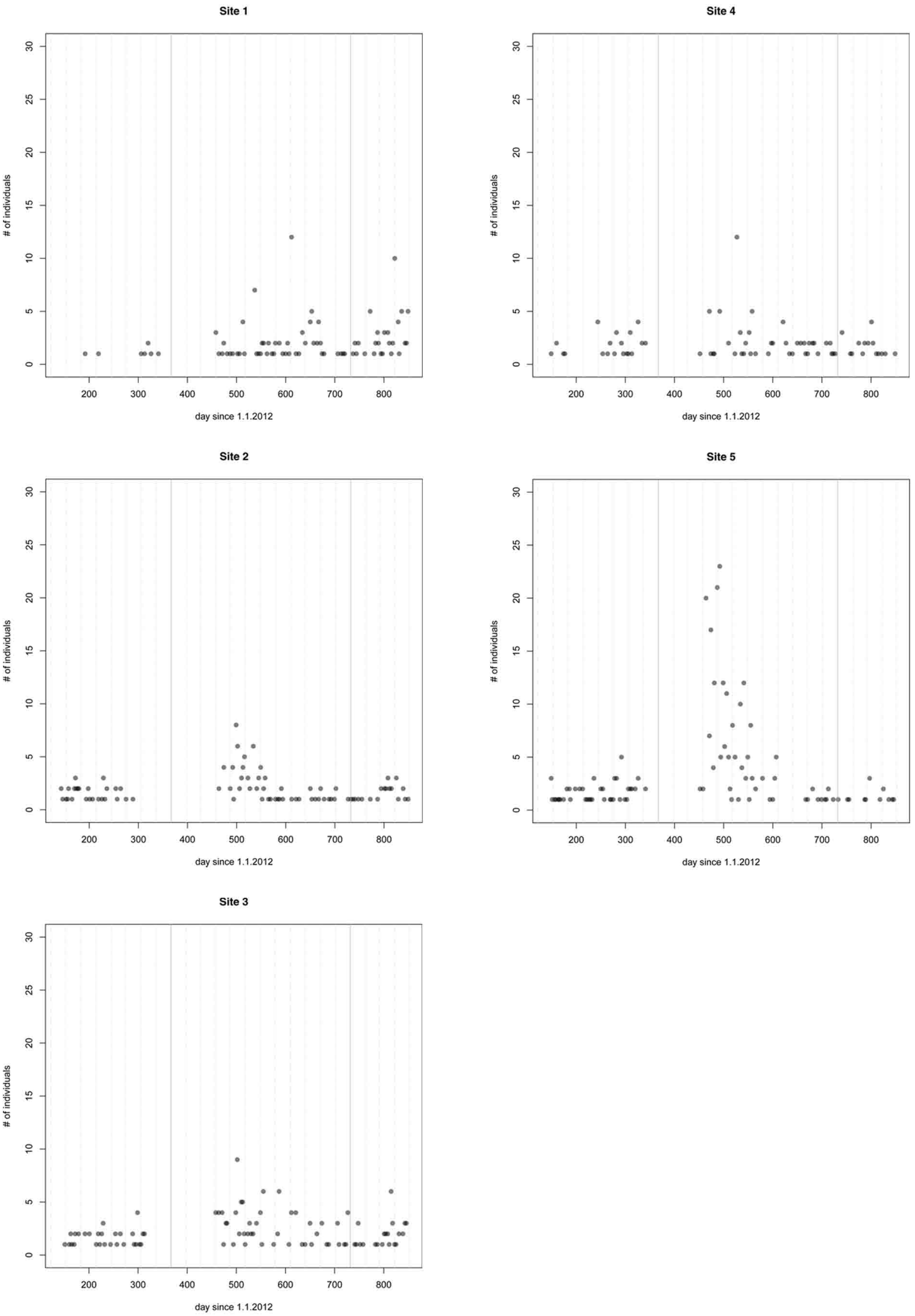


Figure S5

Structure Harvester plot indicating the most probable K for all samples.

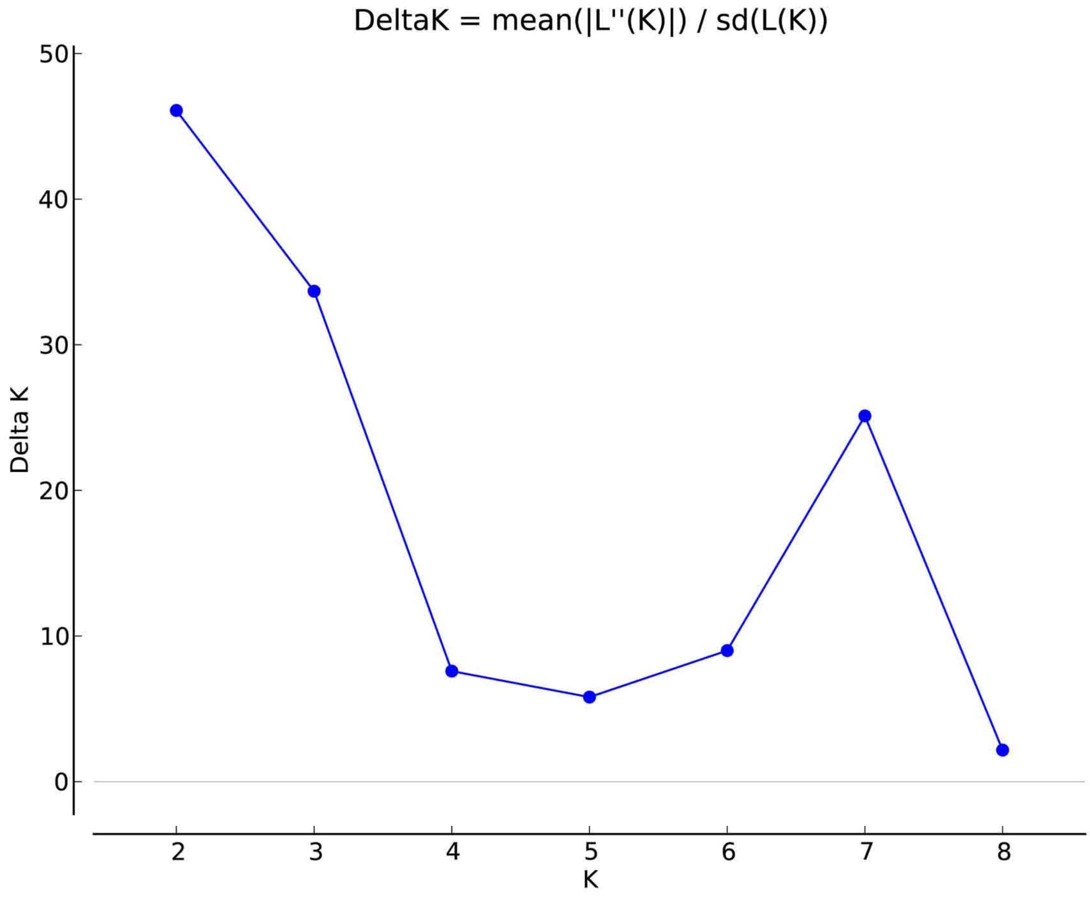
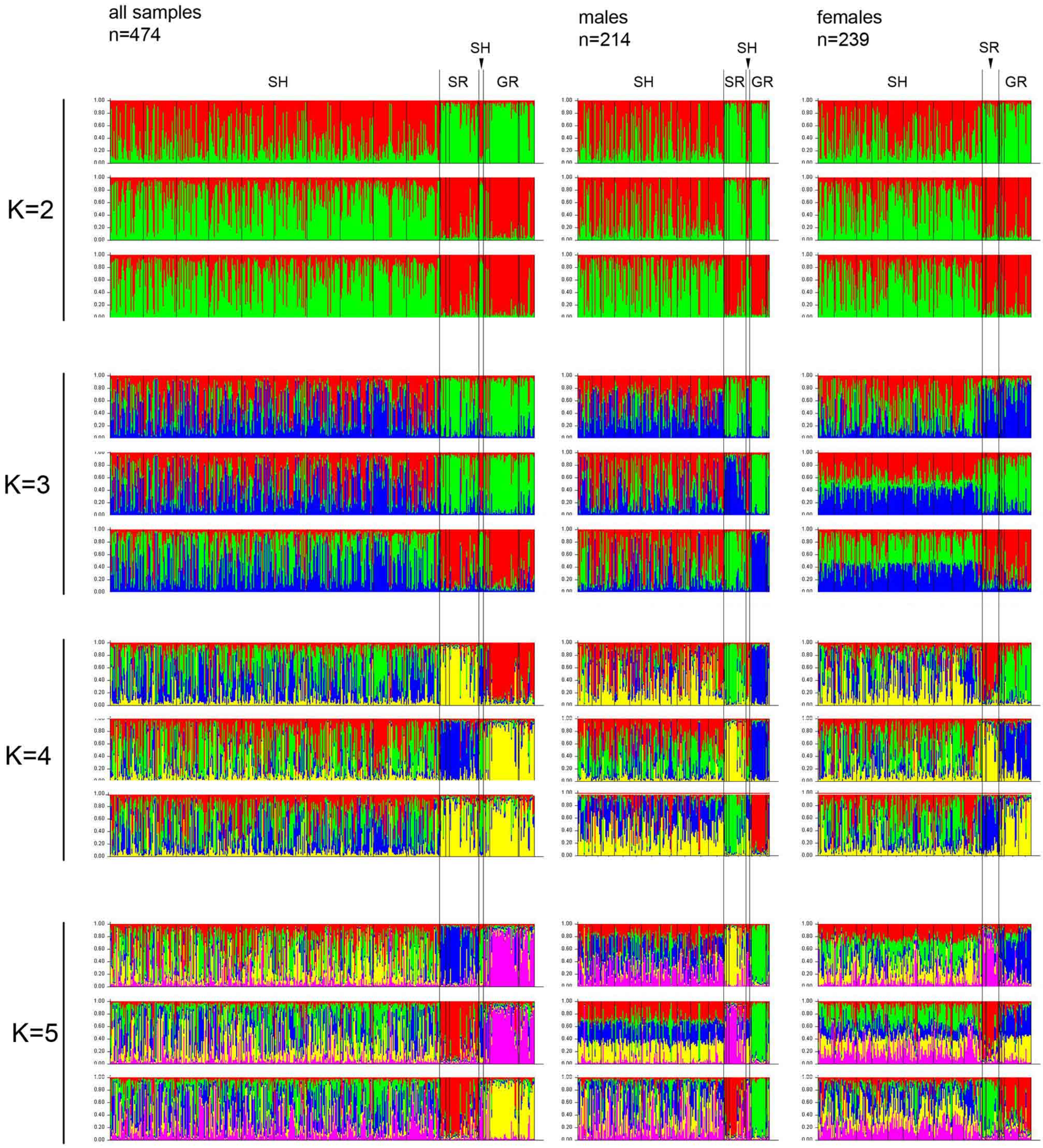


Figure S6

Structure plots for K=2 to K=5 for all sites., split by sex.

Left, all samples. Middle, male samples only. Right, female samples only.
The data set contained an additional 21 juvenile individuals that could not be associated with either sex.

SH, SR, GR - populations as defined in the manuscript.
Sampling sites run consecutively from 1 (left) to 16 (right).



Supplementary Material 1

Microsatellite sequences of *Ponticola kessleri* and *Neogobius melanostomus*

Legend:

Original primers
Redesigned primers, version .1
Redesigned primers, version .2
Microsatellite as published
Novel, alternative Microsatellite

Primer binding sites are labelled even if there are minor mismatches to the primer sequence.

Sequence labeling and order:

1. >original, published sequence
2. >*N.melanostomus*/as sequenced from a Basel specimen
3. >*P.kessleri*/as sequenced from a Basel specimen

This part of the supplementary material can be found online:
http://onlinelibrary.wiley.com/doi/10.1111/mec.13595/full

PAPER IV

Ecology and Evolution

Open Access

A tough egg to crack: recreational boats as vectors for invasive goby eggs and transdisciplinary management approaches

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Keywords
Attachment strength, biological invasions, conservation management, desiccation tolerance, *Neogobius melanostomus*, *Ponticola kessleri*, saltatorial dispersal.

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Funding Information
Research Centre for Sustainable Energy and Water Supply (FoNEW), Federal Office for the Environment, Switzerland, Canton of Basel Stadt, Lottery funds of the cantons Aargau, Basel-Land, and Solothurn.

Received: 8 October 2015; Revised: 17 November 2015; Accepted: 25 November 2015

doi: 10.1002/ece3.1892

Abstract

Non-native invasive species are a major threat to biodiversity, especially in freshwater ecosystems. Freshwater ecosystems are naturally rather isolated from one another. Nonetheless, invasive species often spread rapidly across water sheds. This spread is to a large extent realized by human activities that provide vectors. For example, recreational boats can carry invasive species propagules as "aquatic hitch-hikers" within and across water sheds. We used invasive gobies in Switzerland as a case study to test the plausibility that recreational boats can serve as vectors for invasive fish and that fish eggs can serve as propagules. We found that the peak season of boat movements across Switzerland and the goby spawning season overlap temporally. It is thus plausible that goby eggs attached to boats, anchors, or gear may be transported across watersheds. In experimental trials, we found that goby eggs show resistance to physical removal (90 mN attachment strength of individual eggs) and stay attached if exposed to rapid water flow (2.8 $\mathrm{m \cdot s^{-1}}$for 1 h). When exposing the eggs to air, we found that hatching success remained high (>95%) even after eggs had been out of water for up to 24 h. It is thus plausible that eggs survive pick up, within-water and overland transport by boats. We complemented the experimental plausibility tests with a survey on how decision makers from inside and outside academia rate the feasibility of managing recreational boats as vectors. We found consensus that an installation of a preventive boat vector management is considered an effective and urgent measure. This study advances our understanding of the potential of recreational boats to serve as vectors for invasive vertebrate species and demonstrates that preventive management of recreational boats is considered feasible by relevant decision makers inside and outside academia.

Introduction

Naturally, individuals of any purely aquatic species cannot move freely between water bodies because of the dendritic nature of watersheds and due to the isolation of catchments from one another (Thienemann 1950). It is therefore intriguing that aquatic ecosystems are disproportionally impacted by rapid range expansions of invasive species across watersheds (Rahel 2007). The most probable reasons behind this large-scale spread of invasive species are human activities. Humans break down natural barriers to dispersal in aquatic ecosystems by, for example, building shipping ways that connect major catchments (Rahel 2007). For example, the Rhine–Main–Danube channel provides a link between two major European watersheds. Humans also provide vectors which realize the uptake of propagules in one system, the translocation, and the release into another system (Johnson et al. 2001). For example, many bivalves are able to adhere to aquatic equipment and survive exposure to air during transport (Johnson et al. 2001; Clarke Murray et al. 2011). Whereas the loss of natural barriers is hard to reverse, the management of human vectors is possible. Hence, if we want to prevent the negative impacts of invasive species on native aquatic ecosystems, we have to manage human vectors (Hirsch et al. 2015; N'Guyen et al. 2015). Importantly, such a management should follow the precautionary principle. As illustrated by the proverb that an ounce of prevention is better than a pound of cure, a preventive management is the most cost-efficient strategy against the negative impacts of invasive species (Leung et al. 2002). In the case of an imminent invasion, acting timely is essential.

To be effective and successful, the management of invasive species' vectors needs to be installed as soon as an invasion is anticipated, and it needs to fulfill two prerequisites. Firstly, it needs to rest on empirical knowledge on how plausible certain propagules and certain vectors are for the invasion process (Johnson et al. 2001). Secondly, management measures have to be feasible in light of both scientific knowledge and of perceived barriers to its implementation (Tzankova and Concilio 2015). The feasibility of a measure cannot be established by scientific knowledge alone (Gozlan et al. 2013). Human vectors need to be managed by humans, and perceptions of people outside academia, including stakeholders, ultimately determine whether a measure is implemented (Gozlan et al. 2013; Tzankova and Concilio 2015).

In this study, we test for both the plausibility and the management feasibility of a vector. Our study species are invasive Ponto-Caspian gobies (round goby *Neogobius melanostomus* and bighead goby *Ponticola kessleri*). They are likely to cause economic and ecological harm and have recently established a potential source population in the river Rhine in Switzerland (Hirsch et al. 2015; N'Guyen et al. 2015). From this localized population, further invasions into previously goby-free Swiss waters can be expected (Kornis et al. 2012; Kalchhauser et al. 2013). Gobies are small benthic fish that are incapable of prolonged swimming. The invasion of gobies follows a saltatorial pattern: Instead of continuously expanding along a watercourse, new populations establish rapidly in isolated water bodies and areas far away from the presumed source population (Kalchhauser et al. 2013). This suggests that their dispersal is aided by some vector. Commercial ship traffic, transporting propagules in ballast water tanks, is assumed to be a major long-distance vector for gobies, although empirical evidence for the plausibility of this vector is still lacking. Spread into isolated and smaller water bodies is more likely to be realized by recreational rather than commercial boat traffic (Johnson et al. 2001; Poos et al. 2010). In the High Rhine, natural upstream dispersal of gobies is unlikely because of weirs and dams which pose effective in-stream barriers for similar-sized native benthic fish species (Hirsch et al. 2015; N'Guyen et al. 2015). Isolated alpine lakes in Switzerland are not connected to the Rhine via navigable waterways. However, recreational boats are frequently transported overland between lakes and also across in-stream barriers. Consequently, overland transport by recreational boats is a possible vector that requires further study. The introduction of invasive gobies in Switzerland provides a suitable case in point to empirically explore if recreational boats are plausible as a vector and how feasible a preventive management of this vector is perceived inside and outside academia.

From an invasion science point of view, the precautionary principle makes the preventive management of any vector imperative as soon as the vector's plausibility is established (Leung et al. 2002). The plausibility of a vector is given when vectors and propagules occur at the same time in the same place (hence allowing for pick up of propagules by vectors), and when propagules survive pick up, transport and release (Drake and Mandrak 2014). Eggs are one of the most frequently mentioned, yet previously unexplored, propagules of invasive fish. For invertebrate species, resting stages and eggs are well-described as propagules (Havel and Shurin 2004). However, despite much speculation in the literature about fish eggs as potential propagules, this assumption remains to be empirically tested (see Appendix S1 for a list of references that mention eggs as invasive goby propagules). In the case of invasive gobies, speculations on egg transport rely on the observation that gobies readily spawn adhesive eggs onto artificial substrates (Fig. 1, Appendix S2). Anecdotal reports suggest that goby eggs are laid onto boat hulls or gear such as anchors, and it has thus been speculated that goby eggs may stay attached to these substrates when the boats travel in water or are transported overland (Appendix S1).

In this study, we empirically address the plausibility of recreational boats as vectors and goby eggs as propagules as well as the feasibility of management based on the following questions: (1) Do vector and propagules temporally overlap in activity to make a pick up and translocation plausible? (2) Are propagules able to survive conditions during a translocation? (3) How do relevant decision makers value a preventive management of the vector? To address question (1), we examine the temporal overlap of vector movements and propagule availability using data on local boat movements and on the local goby spawning season. We consider a large temporal overlap as a necessary condition for the vector to pick up propagules. To address question (2), we experimentally test the ability of eggs to survive relevant transport conditions. We postulate (i) that eggs need to be capable of resisting drag forces as they are moved by a vector within or between water bodies, attached to boats or gear, and

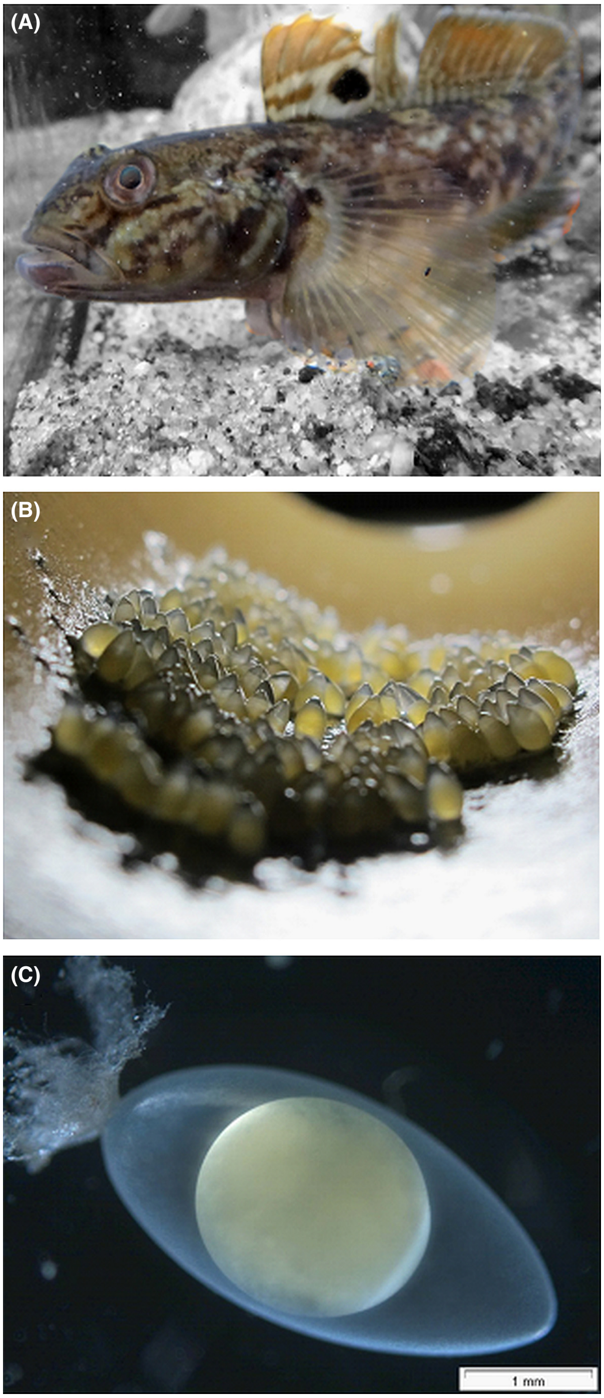

Figure 1. Invasive goby and adhesive eggs as possible propagules. (A) Round goby (*Neogobius melanostomus*) in an aquarium. (B) Adhesive eggs spawned into a PVC pipe as part of a spawning trap (see Appendix S4 for more details). (C) Microscopic picture of an egg showing the attaching filaments (scale bar = 1 mm).

(ii) that eggs need to be tolerant to desiccation as they are moved from one catchment to the other. To address question (3), we asked relevant experts inside and outside academia how efficient, difficult or urgent they would rate a preventive management of recreational boats as vectors. We argue that the combination of empirically confirmed plausibility of a specific vector and the consensus on the need for its preventive management would allow to more specifically counteract the human spread of invasive gobies (cf. N'Guyen et al. 2015).

Materials and Methods

Question (1)

To establish the plausibility of eggs serving as propagules and boats as vectors, we explored the temporal overlap of vector activity and the propagule availability. Data on recreational boat movements in Switzerland between 2009 and 2013 were obtained from a survey on boats in Switzerland carried out at the Swiss Federal Institute of Aquatic Science and Technology (EAWAG; see Weissert 2013 for details). The data (kindly provided by L. DeVentura [EAWAG]) were further analyzed to explore how many boats are moved overland during which time of the season. This analysis resulted in a subset of 684 recorded overland transports that we used in this study to demonstrate how these were distributed across one season. To investigate the temporal overlap of boat movement across in-stream barriers, we compiled data for boat passages across the dam Birsfelden which is upstream of the source population (for information on the questionnaire and data on all boat passages across all in-stream barriers upstream of the source population in the Rhine, see Appendix S3).

Goby eggs were retrieved from the recently detected source population in the local harbor at Basel, Switzerland (47.587518°N, 7.593447°E), with specifically designed spawning traps consisting of clay pots and PVC pipes as artificial spawning substrates (see Appendix S4 for details). Clutches found in the traps were transported in a bucket of aerated harbor water and photographed upon arrival in the laboratory. Digital photographs were used to count the number of eggs. Each clutch was kept in a separate 10 L overflow tank supplied by 14.8°C (±0.1°C) UV-treated tap water.

Question (2)

To experimentally test the propagules' endurance of relevant transport conditions, we measured (i) the attachment strength and (ii) the desiccation resistance of goby eggs. To measure attachment strength in the laboratory, the clutches attached to their artificial substrate (PVC pipes) were fixed to a glass dish and peak resistance force was recorded for each individual egg pulled perpendicular from the substrate using tweezers (force gauge: Model M7i, Mark-10 Corporation, Copiague, NY, USA, sensor Mark-10 via Plug TestTMTechnology). Outliers (0.1% of all data) caused by handling errors (such as tweezers slipping) were identified using the Grubb's outliers test and removed from the data set.

To measure egg attachment under flow conditions, eggs attached to artificial substrates from the spawning traps were exposed to water flow in a swim tunnel (185 L, 50 Hz, ®Loligo Systems, Tjele, Denmark). Clutches were attached in the tunnel so that flow would hit the eggs on their longitudinal side at a right angle. The tested velocity of $2.8\ \text{m}\cdot\text{s}^{-1}$ corresponds to approximated velocities occurring on the hull of a recreational boat traveling with $10\ \text{km}\cdot\text{h}^{-1}$ upstream the Rhine. Egg attachment under flow conditions was expressed as number of eggs remaining attached after 1 h of water flow exposure. We assumed that a boat with the above-mentioned cruising speed would need 1 h to travel from the harbor where gobies have established upstream to the next major in-stream barrier.

To test for survival of eggs under air exposure, four different exposure periods (0.25, 0.5, 12 h or 24 h) were applied with one half of a clutch exposed to air in an incubator (Model IPP 300, ®Memmert, Schwabach, Germany) and the other half remaining in the tank as a control. The incubator temperature was identical to the mean summer air temperature during spawning season (incubator: 18°C, field: 18°C). The incubating humidity was also similar to field conditions (incubator: 60–85% (median 80%), field 75% (median), all field data from Federal Office of Meteorology and Climatology MeteoSwiss, 2013). After exposure, the clutch halves from the incubator were placed into tanks until hatching started. The hatching rate can be different among different clutches. To account for this variation, we set the hatching rate of the untreated half of each clutch as the standard successful hatching rate for each clutch and the hatching rate in the treated half was expressed in % of this untreated clutch-specific "standard hatching rate." Hatching success was calculated as number of hatched embryos divided by the number of viable eggs for each clutch half.

Question (3)

A successful installation of preventive measures against invasive species requires the cooperation and compliance of relevant decision makers inside and outside academia. To explore the feasibility of a preventive management of recreational boats, we developed a questionnaire completed by participants of a transdisciplinary workshop which we organized (see N'Guyen et al. (2015) for background information on our transdisciplinary approach). The workshop's participants were certified experts (holding academic degrees in relevant subjects or holding professional positions in relevant areas; example: researchers, environmental authorities) and noncertified experts (expertise built on experience; example: representatives of local fishing clubs) (Defila and Di Giulio 2015). All experts were decision makers representing different groups which we classified as representatives of civil society 1 (public and private companies, $n = 6$), civil society 2 (angler associations and NGOs, $n = 4$), authorities and administration ($n = 7$), or scholars ($n = 4$). All participants received an individual handout together with the questionnaire. The handout described a check-clean-dry routine as a possible management measure to prevent recreational boats acting as vectors for invasive gobies (Appendix S5). Participants were then asked to rate effectiveness, urgency, and perceived difficulty of implementation by making crosses on a linear scale which we then recorded as numerical values by overlaying a scale from 1 to 10, with 0.1 intervals. The scale reached from very urgent, effective, and difficult to not urgent, effective or difficult (see Appendix S6 for the actual questions).

Results

Question (1)

During the spawning season, we could retrieve an estimated 350,000 goby eggs by providing and regularly clearing artificial spawning substrates in the local harbor (Fig. 2A). Testing for the temporal overlap between vector activity and propagule availability, we found that overland boat transfers and passages across in-stream barriers overlapped with the peak of the local goby spawning season (Fig. 2B and C).

Question (2)

(i) Using peak force measurements, we found that the force required to remove a naturally spawned individual egg from an artificial surface is 90 mN (±8.04 standard deviation = SD; Fig. 3). We further explored how naturally spawned eggs would adhere to the substrate under simulated field conditions in a swim tunnel and found that after one hour of simulated boat travel, on average 80% (±13.04 SD) of all eggs remained attached (Fig. 4A). (ii) To test the plausibility that eggs taken out of the water survive as propagules, we investigated egg survival under air exposure and found that eggs exposed to air for 0.15–24 h had a mean hatching rate of 94% (±12.16 SD), with all clutches synchronously hatching after air exposure (Fig. 4B, Appendix S3).

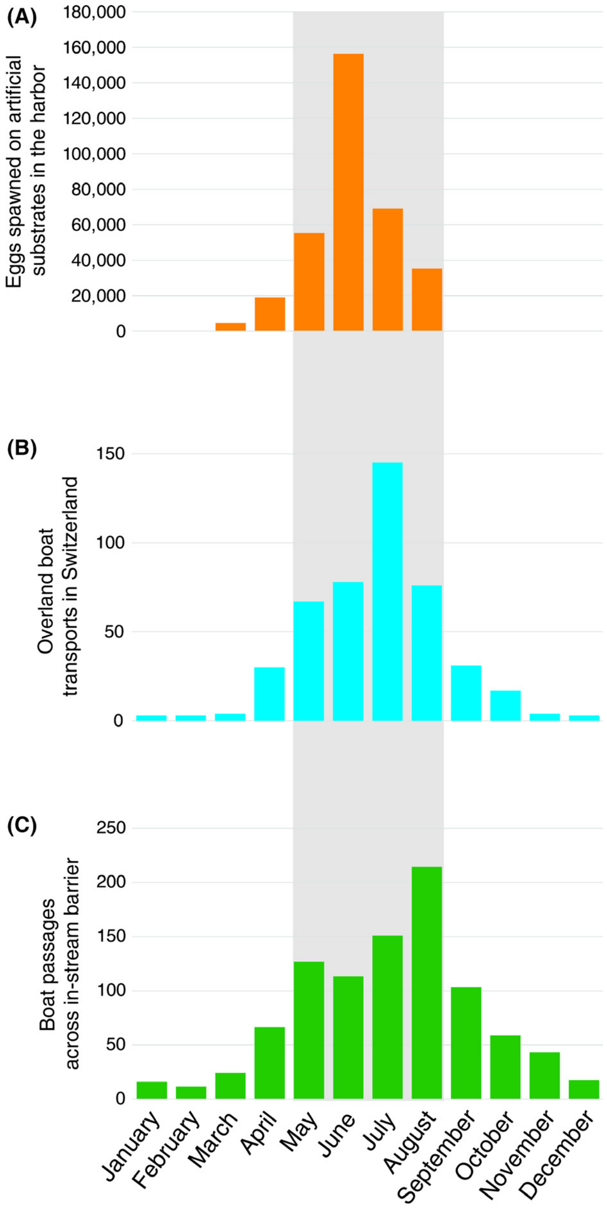

Figure 2. Goby spawning season overlaps with vector activity. (A) Number of goby eggs spawned on artificial substrates by the potential source population in 2013. (B) Number of overland recreational boat transports between 2009 and 2013 (data kindly provided by L. DeVentura). (C) Number of boat passages across the in-stream barrier adjacent to the source population (watergate Birsfelden) between 2009 and 2013 (see Appendix S5 for all in-stream barriers upstream of the source population).

Question (3)

When decision makers were asked to rate a "check–clean–dry" measure as a preventive management tool, all but one respondents found the measure urgent and effective (Fig. 5). However, the decision makers also saw barriers to the potential implementation of the measure (Fig. 5, Appendix S8).

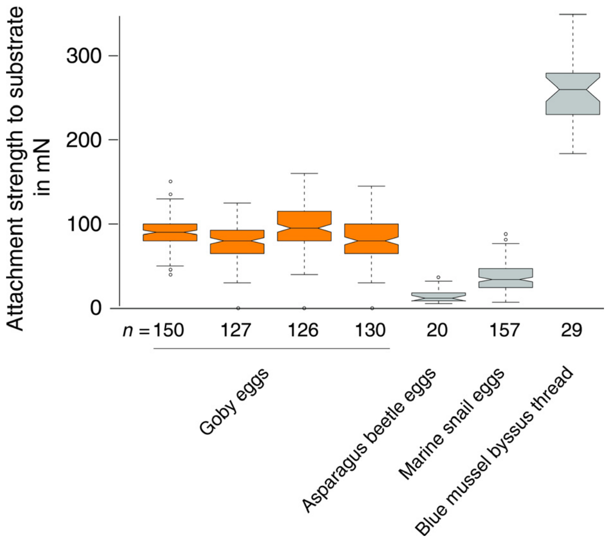

Figure 3. Force measurements reveal attachment strength of goby eggs. Data show peak resistance to perpendicular pulling force in mN. For illustration, the published attachment strengths of asparagus beetle eggs (*Crioceris asparagi*) (Voigt and Gorb 2010), marine snail eggs (*Melanochlamys diomedea*) (Castro and Podolsky 2012), and blue mussel byssus threads (*Mytilus edulis*) (Brenner and Buck 2010) are shown. Nongoby data were extracted from figures in the respective articles using the software GetDataGraphDigitizer v. 2.26 (www.getdata-graph-digitizer.com).

Discussion

Our results confirm the plausibility of recreational boats as vectors of goby eggs. Answering question (1), we could demonstrate that recreational boats are moved in high numbers during the spawning season and that gobies spawn eggs onto artificial substrates. Answering question (2), we found our experiments to reveal resistance of goby eggs to (i) physical forces and (ii) air exposure. Overall, our results provide the first empirical test for eggs attached to boats or gear as plausible propagules of invasive fish. Answering question (3), we learned that decision makers, consisting of certified and noncertified experts, consider a preventive management urgent and effective, albeit with some barriers to implementation.

Empirical evidence suggests the plausibility of recreational boats as vectors and eggs as propagules

The overlap between vector activity and propagule availability makes pick up of eggs by boats plausible. This is especially relevant since harbors and marinas have previously been found to be primary invasion hot spots of gobies and other aquatic invasive species (Kalchhauser et al. 2013). The frequent establishment of invasive goby populations in harbors and the concentration of recreational boat traffic in marinas make both a temporal and spatial co-occurrence of vectors and propagules likely (Clarke Murray et al. 2011; Drake and Mandrak 2014). Our results confirm this co-occurrence empirically. The high attachment strength of eggs on artificial surfaces suggests that the propagules can remain attached to the vector during within-water transport. The high strength of goby egg attachment becomes evident from comparing the attachment forces of goby eggs with other species' eggs or attachment organs that serve the purpose of resisting drag forces to increase survival. For example, the attachment forces of marine snail eggs *Melanochlamys diomedea* that withstand tidal and wave forces in marine systems are on average lower than those observed in goby eggs. The swim tunnel results demonstrate under more realistic conditions that the observed attachment strength of goby eggs is indeed high enough to prevent goby eggs from being washed from the surface of boats, anchors, or gear when transported within water.

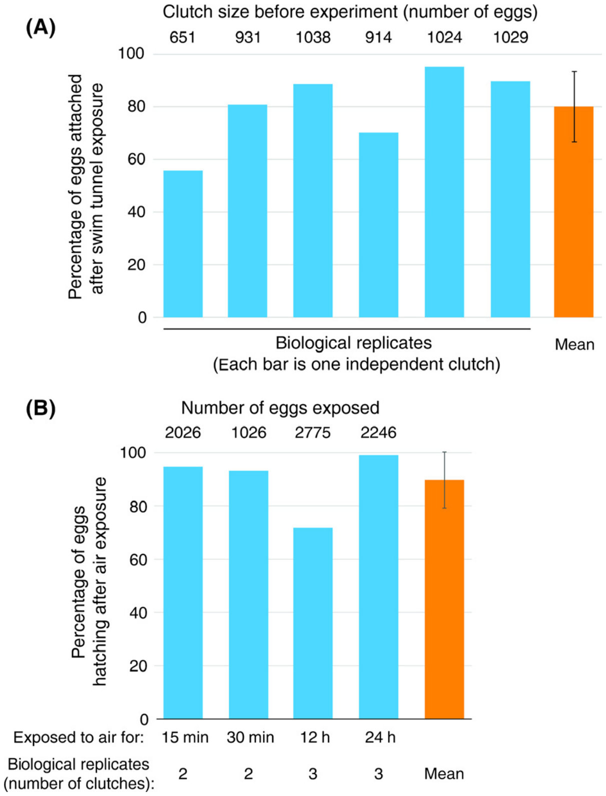

Figure 4. Eggs remain attached in water flow and air exposure does not affect hatching success. (A) Data show attachment in % of remaining eggs after exposure to a water flow of 2.8 m·s^{-1} for 1 h in a swim tunnel. (B) Data show hatching success relative to untreated control. Untreated controls consisted of eggs from the same clutch that remained in water. Error bars denote standard deviation.

The survival of goby eggs during air exposure fulfills an important prerequisite for eggs to serve as plausible propagules on boats: The propagules are able to withstand conditions during overland transport. The high survival of fish eggs even after air exposure was unexpected: Why would fish eggs survive out of the very element they evolved in? In fact, the survival of anamniotic amphibian eggs in air has been previously acknowledged, and a recent review suggests that the ability to survive in air might also be an underappreciated ability in fish eggs (Martin and Carter 2013). For example, some mudskipper species' eggs develop out of water in an excavated air chamber (Ishimatsu et al. 2009). The resistance to air exposure in both mudskipper and goby eggs makes sense in an evolutionary context. These two fish genera are closely related, and egg adhesion is believed to be a characteristic trait within the taxonomic group of Gobioidei, of which many representatives spawn in tidal zones (Thacker 2009). Adhesive eggs that are resistant to air exposure would be conceivable to evolve as an adaptation to such habitats. In cyprinid fish species, exposure to air has been found to desynchronize hatching (Fisk et al. 2013). In our experiments, however, both control and air-exposed eggs showed synchronized hatching. This indicates that the development of goby eggs appeared to be unaffected by the desiccation treatment. Invasive goby larvae rapidly

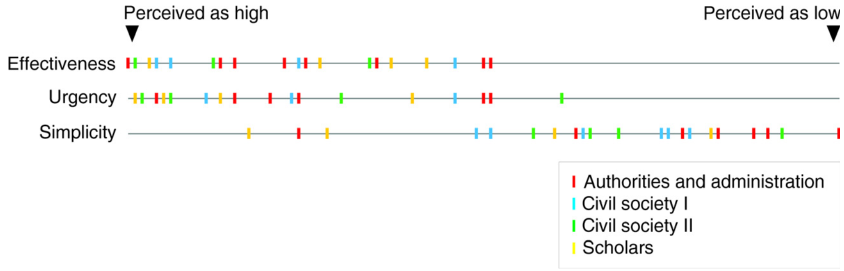

Figure 5. Certified and non-certified experts from inside and outside academia perceive vector management as effective and urgent, but see barriers to its implementation (ease of implementation is termed "simplicity"). Civil Society 1 (*n* = 6): public and private companies, civil society 2 (*n* = 4): angler associations and NGOs concerned with nature conservation, authorities and administration (*n* = 7): for example, county board, scholars (*n* = 4): scientists interested in invasive species.

start feeding externally and show a survival of over 95% in the 3 months posthatching (Bonislavskaya et al. 2014). This might further increase their chances to survive if released into a new environment. In summary, adhesive fish eggs that can survive within-water transport and air exposure might have previously underestimated capabilities to serve as propagules. Importantly, our work supports the common notion in invasion biology that a single translocation event might well suffice to establish a population if enough propagules (i.e., eggs) hatch and survive upon arrival in a new environment (Sakai et al. 2001).

Caveats on the experimental design and interpretation of results

The experiments were designed to test for the plausibility of eggs as propagules. The flow resistance and desiccation experiments were conducted under conditions that were as close to reality as possible. Drag forces in the swim tunnel approximated drag forces acting upon the eggs if they are attached to a boat cruising upstream. The conditions applied for the desiccation test were chosen to represent realistic but replicable field conditions. Naturally, other factors such as wind exposure could influence humidity and temperature and hence egg survival. However our tests were not designed to explore which kind of factors would affect hatching rates to which degree. We aimed at investigating vector plausibility through empirical tests of whether goby eggs can at all survive such conditions and thus are able serve as propagules for a translocation.

The role of human vectors in the dispersal of freshwater vertebrate species is still poorly understood although correlative data clearly hints at human factors playing a substantial role in, for example, fish invasions (Leprieur et al. 2008). For round goby in the Great Lakes, genetic data suggests a role for commercial ships as vectors. The more cargo traffic between distant harbors, the more closely are the harbor populations related to each other, suggesting an exchange of individuals between harbors realized by ships (LaRue et al. 2011). Recent reviews on aquatic invertebrate propagules increasingly acknowledge the need for more empirical studies complementing the correlative knowledge created by genetic studies (Incagnone et al. 2015). The notion that anamniotic eggs can serve as propagules for freshwater fish has long been resting on circumstantial evidence and anecdotal reports (Appendix S1). Only a few early works have explored the plausibility of fish eggs as propagules (Preusse 1924; Schiemenz 1925; but see Oulton et al. (2013) for a recent example). Our study is the first to address this question for invasive fish.

However, it is much more important to consider the need for action that is evident from the precautionary principle than to lament the past or current level of scientific evidence (Leung et al. 2002). Eggs are ubiquitously proclaimed potential propagules for the dispersal of invasive gobies, and we could empirically confirm this notion. In lieu of more conclusive evidence or quantitative knowledge on the relative importance of this vector, a preventive management should be installed based on previous experience with recreational boats as vectors for invertebrate species. For example, a preemptively installed “check–clean–dry” management measure of recreational boats originating from the goby source population would not only prevent the spread of goby propagules, but also of several other invasive species present in the local harbor such as the zebra and quagga mussels (*Dreissena* spp.) (Horvath 2008).

Management implications

To install an effective preventive management, it is important that we adopt a holistic approach: not only accruing scientific knowledge on possible vectors, but also communicating with relevant experts that serve as decision makers about the feasibility of managing such vectors. After all, it is not the researchers that actually install the management. If decision makers do not consider a management measure feasible, they are unlikely to support the installation of such measures (Hirsch et al. 2015; N’Guyen et al. 2015). Recreational boats have long been assumed to be vectors and have been considered prime management targets in marine and freshwater systems (Johnson et al. 2001; Clarke Murray et al. 2011). Despite growing evidence for the relevance of recreational boats as vectors, their management has proven difficult to implement (but see, e.g., Horvath 2008). The barriers to implementation that we identified in our study are manifold. For a successful implementation of any management measure, the barriers identified by stakeholders should be appreciated and explored by researchers (Reed 2008). We argue that a solid scientific underpinning of the plausibility of a vector can serve as an important impulse for a transdisciplinary process toward a successful implementation. Further research on the measure should be designed in cooperation with experts outside academia to deliver relevant results improving the chances of management success (Reed 2008). Our ability to successfully prevent an imminent invasion is highest when we know least about the invasion: before ubiquitous propagule traffic allows for a scientific quantification of relative vector importance. Based on our empirical data and following the precautionary principle, it becomes clear that a preventive management of invasive gobies should consider eggs as propagules. For example, our study gives clues for when the pick up of propagules by recreational boats can occur and that existing boat drying measures need to be carefully re-examined in light of the desiccation tolerance of invasive goby eggs.

Acknowledgments

We thank H. Ahnelt, F. Baertschi, C. Cornaz, L. DeVentura, R. Held, P. Reimann, M. Puffer, A. Ruegg, M. Steinacher, R. Spirig, N. Weissert, and all workshop participants. This project was funded by a special grant from the Federal Office for the Environment, Switzerland, the Research Centre for Sustainable Energy and Water Supply (FoNEW), the canton BS, plus cantonal lottery funds of AG, BL, SO.

Conflict of Interest

The authors declare no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Publications suggesting goby eggs as propagules and boats as vectors.

Appendix S2. Types of artificial substrates used by gobies for spawning in the harbor Basel.

Appendix S3. Map showing all 11 in-stream barriers upstream of the potential source population and the numbers of passages of recreational boats across them.

Appendix S4. Detailed depiction of spawning traps used to retrieve eggs for experiments and to estimate the numbers of propagules spawned onto artificial substrates in the harbor where the potential source population has established.

Appendix S5. Information provided to the participants of the transdisciplinary workshop (transferred into English by the authors, square brackets: additional explanations to improve clarity for this paper).

Appendix S6. Questions provided in the questionnaire (transferred into English by the authors).

Appendix S7. Air exposure does not affect hatching dynamics of goby larvae.

Appendix S8. Questions provided in the questionnaire (transferred into English by the authors).

S1: **Publications suggesting goby eggs as propagules and boats as vectors**

Ahnelt, Harald; Banarescu, Petru; Spolwind, Robert; Harka, Akos; Waidbacher, Herwig (1998): Occurrence and distribution of three gobiid species (Pisces, Gobiidae) in the middle and upper Danube region - examples of different dispersal patterns? Biologia 53 (5).

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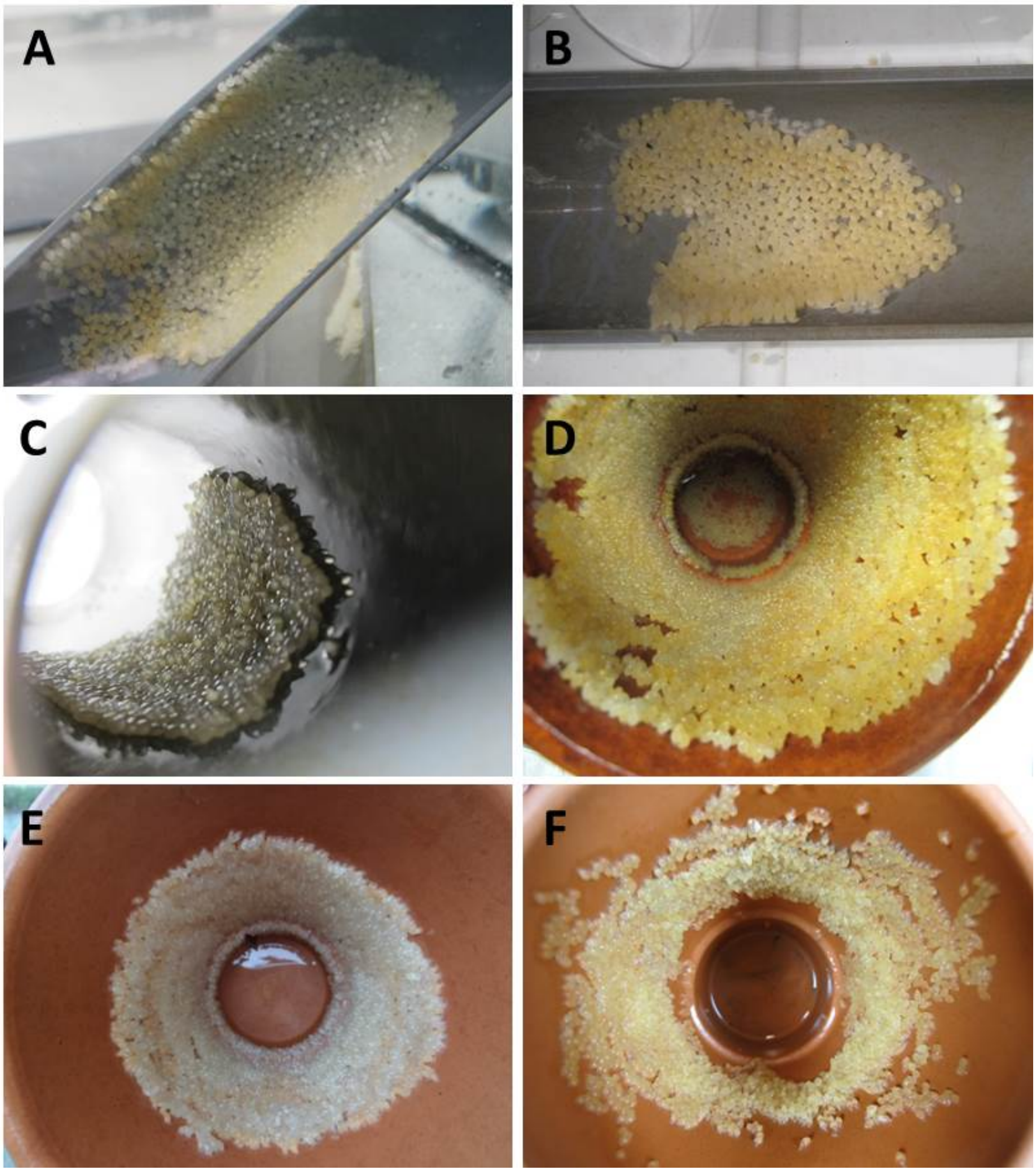
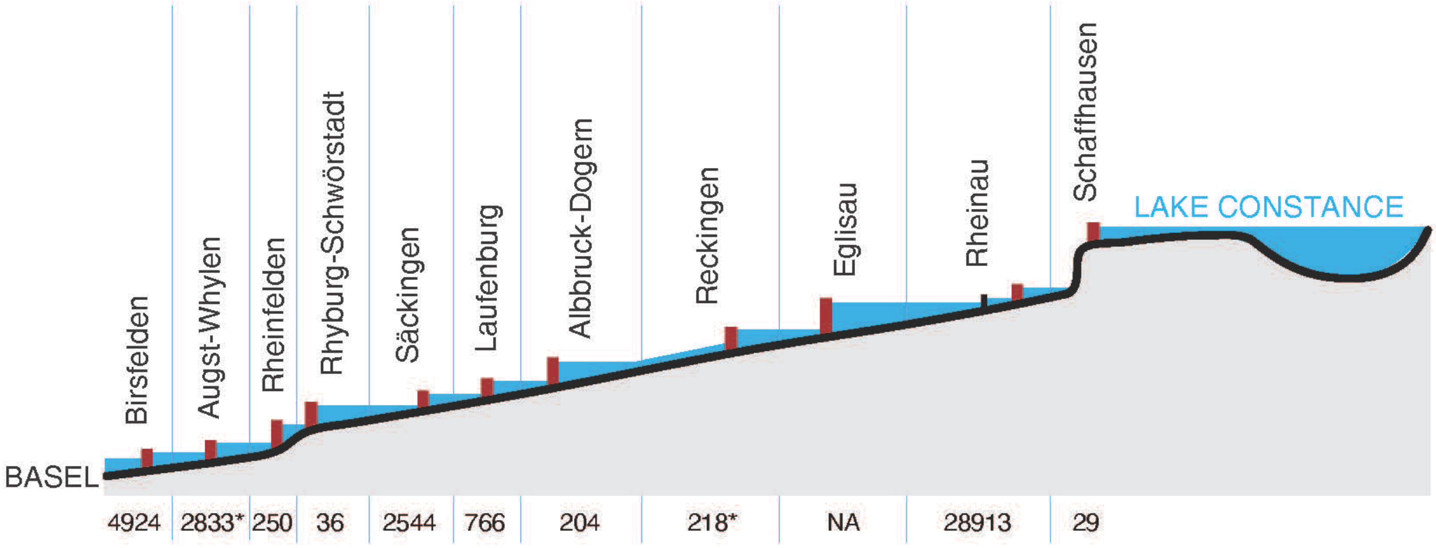


S2: **Types of artificial substrates used by gobies for spawning in the harbor Basel**. Gobies lay their eggs on PVC tubes (A, B, C) and clay pots (D, E, F).



Passages of leisure boats across the respective barrier, from 2009 to 2013
*Augst-Wyhlen: data for 4th quarter not recorded
* Reckingen: 2010-2013

S3: **Map showing all 11 in-stream barriers upstream of the potential source population and the numbers of passages of recreational boats across them.** To gather data for the years 2009 to 2013, for each year one questionnaire was sent to staff organizing upstream transfer of boats across in-stream barriers (available upon request). We then mapped the upstream migration route from the harbour where gobies first appeared to the next large alpine lake: Lake Constance. Lake Constance is free of gobies and socio-economically important due to its attraction to tourists and commercial fisheries. In total, there are 11 in-stream barriers which all are power plants except for Schaffhausen which is a natural waterfall. Transports of boats across these barriers are managed as a public service and the power plant operators also protocol this service. Only boat transports that used the facilities available are recorded, i.e. especially small boats such as canoes or rubber boats are usually not included.

S4: **Detailed depiction of spawning traps used to retrieve eggs for experiments and to estimate the numbers of propagules spawned onto artificial substrates in the harbor where the potential source population has established.**

Spawning traps consisted of the following items: a pannier filled with several ~10x5 cm stones as ballast weight, four standard clay pots (top diameter: 10.5 cm, bottom diameter: 5.5 cm, height: 13 cm), and seven grey PVC tubes (diameter: 4.5 cm, length: 20 cm). Five spawning traps were lowered to the harbour basin bottom connected to wire-cables (at approximately 4 m depth) and retrieved and checked for eggs once a week from 27th of February until no eggs were retrieved any more for two weeks which was the case in October.

S5. **Information provided to the participants of the transdisciplinary workshop (transferred into English by the authors, square brackets: additional explanations to improve clarity for this paper)**

Recommendation for management:Inspecting and cleaning of boats

A mandatory control, cleaning and drying ("check, clean, dry") of recreational boat hulls prior to transfer into another water body or another section of a water body will be implemented. This will happen together with boating clubs, organizers of water sport competitions etc. so that it becomes a broadly accepted measure.

Expected effect:

In the ideal case this management can preclude a further spread of gobies in the form of eggs attached to recreational boats. In any case, however, will the propagule pressure be strongly reduced. A lower propagule pressure will make a further spread less likely and reduce the population growth of newly introduced populations.

Possible scenario in case the management is not implemented:

Following the translocation of recreational boats, gobies will be spread across Switzerland in hard-to-predict patterns. Possibly implemented measures to halt the spread at in-stream barriers [such as e.g. impassable fish ladders] will be ineffective because these will be overcome by boats that are translocated across such barriers. A monitoring focussing on current invasion hot-spots in Switzerland will fall short of its desired effect of early detection because spread of gobies will be saltatorial and not continuous. Fishers, freshwater ecosystem managers and interested groups do not expect such a sudden [i.e. due to saltatorical spread] occurrence of gobies. They are unprepared and respond late or not at all to a detection of gobies that suddenly appear as a results of human aided long-distance dispersal.

Basis for recommendation of management:

Observations in the field indicate that gobies use boat hulls in shallow shoreline areas as spawning substrate. Trials using spawning traps have revealed that gobies accept artificial substrates for spawning. Boat hulls constitute such artifical surfaces.

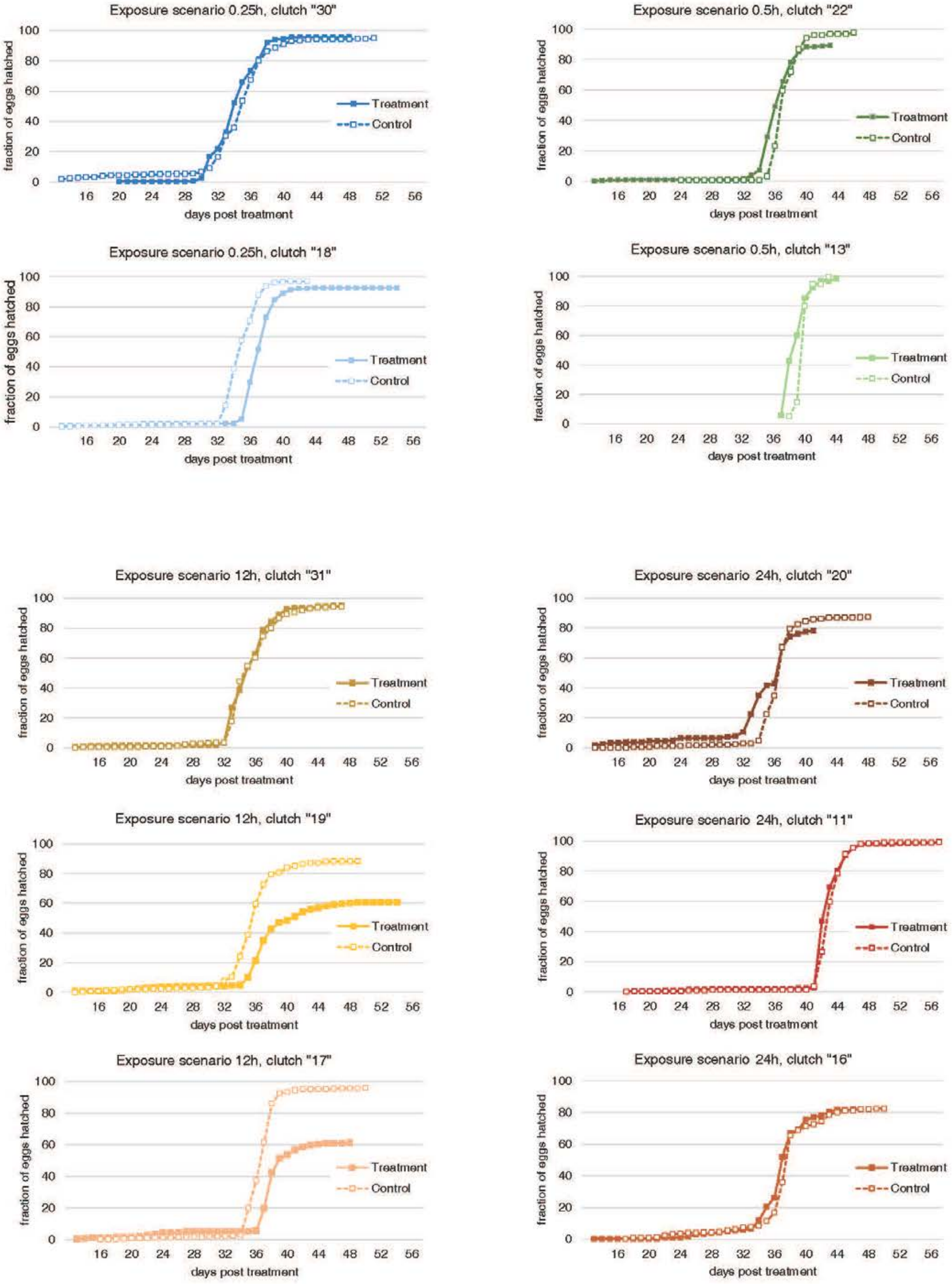
S6: Questions provided in the questionnaire (transferred into English by the authors)

1. Based on your knowledge and with respect to containing the potential source population or preventing its further spread, how effective do you consider the proposed management measure?

2. How urgent do you personally consider the implementation of the proposed measure?

3. How straightforward is the implementation, do you see hardly any or major barriers?

4. Do you have further comments concerning the proposed management measure or concerning your answers?



S7: **Air exposure does not affect hatching dynamics of goby larvae.** Cumulative hatching curves from all 10 clutches used for the air-exposure experiment. For cumulative hatching success, daily hatching success rates were summed up. Clutch numbers are for own records.

S8. **Workshop participants’ comments provided in written form (transferred into English by the authors, square brackets: additional explanations to improve clarity for this paper).**

Civil Society 1

CivSoc1.5: Reasonable also against the spread of diseases and other invasive species.

CivSoc1.6: Because this management is very sophisticated, it would only be acceptable if it is proven that gobies spread via this vector in large numbers.

Civil Society 2

CivSoc2.1: I could imagine that a control of "check, clean and dry" would be difficult.

CivSoc2.2: Efficiency: on the borderline to being effective. Barriers to implementation: enforcement and control. Important is awareness raising ++ = self-responsibility to act.

CivSoc2.3: As mentioned during the first meeting [refers to the first stakeholder workshop of our project] it is very difficult to enforce this cleaning. There are an estimated 10,000 boats per year.

Scholars

Sc.1: By all means necessary, especially in concert with the monitoring [another recommended management option]. Presumably difficult to implement and costly. In the case of Basel: rather few boats, therefore less of an effect?

Sc.2: Efficiency not yet completely clear.

Sc.3: Efficiency depends on whether this is a relevant form of spread.

Authorities/administration

Adm.1: Depends on whether this is a primary vector. Is the control of commercial ships not an issue any more?

Adm.2: We already performed a boat inspection. It became obvious that specific parts are hardly accessible and hence hardly cleanable.

Adm.3: Barriers to implementation: there probably is a complete lack of any legislative basis. Advantage: would also counteract the spread of other organisms.

Adm.4: Difficult to implement! New administrative regulations are always troublesome!

Adm.5: Enforcement requires adequate resources – are these available?

PAPER V

Received: 5 November 2016 | Accepted: 3 May 2017

DOI: 10.1111/1365-2664.12934

STANDARD PAPER

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

A dynamical model for invasive round goby populations reveals efficient and effective management options

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Funding information
Federal Office for the Environment (Switzerland); Canton Basel-Stadt; lottery funds of the Cantons Solothurn, Aargau and Basel-Landschaft

Handling Editor: Rafael Zenni

Abstract

1. When prevention of invasive species' introductions fails, society faces the challenge to manage invasive species in an effective and efficient way. The success of this depends on biological aspects and on cooperation between decision makers and scientists. Using the case of the round goby *Neogobius melanostomus*, one of Europe's "worst invasive species", we propose an approach guiding scientists to co-produce effective and efficient population control measures in collaboration with decision makers.
2. We surveyed the effectiveness, urgency and simplicity perceived by decision makers as well as the support of two population control options: removal of eggs and/or adults. Using a field study and a dynamical population model, we investigated the effectiveness and efficiency for both options in different population contexts.
3. Decision makers initially seemed to lack a clear preference for either control option. After being presented with preliminary field and modelling results, decision makers mostly approved measures being developed to implement the two control options.
4. Starting population control early after detecting the species requires in total fewer years for eradication than controlling an established population: to reach an eradication success rate of 95%, 13 years for early start vs. 18 years for late start are needed when removing eggs and adults; when removing adults only, 20 vs. 29 years are needed. Removing eggs and adults combined results in a yearly effort of 5.01 h/m^2, while removing adults only results in a yearly effort of 1.76 h/m^2. Thus, removing adults only proves to be the most efficient option to eradicate the population. Nonetheless, considerable effort is needed: when removing less than 57% of the adult population, eradication is not feasible, even assuming low survival and fecundity rates for the population. Furthermore, inflow of new propagules renders eradication efforts ineffective.
5. *Synthesis and applications*. Scientists who aim to support decision makers in finding an optimal control strategy for invasive species need to be able to provide scientific knowledge on effectiveness and efficiency of different options. For round goby and most non-native species, eradication is only feasible if started early in recently arrived populations and if inflow of new propagules can be prevented.

KEYWORDS

control, decision maker, dispersal, eradication, harvesting, matrix population model, *Neogobius melanostomus*, sensitivity analysis, stakeholder, transdisciplinary

1 | INTRODUCTION

The gold standard in coping with non-native invasive species is to prevent their introduction (Leung et al., 2002; Secretariat of the Convention on Biological Diversity 2005). When prevention fails, society faces the challenge to manage invasive species in an effective and efficient way. Two potential management strategies are eradication and containment.

The success rate of eradication, defined as "the complete and permanent removal of all wild populations of an invasive species from a defined area in a time-limited campaign" (Genovesi, 2007), has been highest on islands (Clout & Veitch, 2002; Jones et al., 2016) and in confined aquatic habitats. Successful aquatic examples include removal of topmouth gudgeon *Pseudorasbora parva* with the piscicide rotenone, de-watering and disinfection (Britton, Brazier, Davies, & Chare, 2008) or removal of rusty crayfish *Orconectes rusticus* with traps and increased fish predation (Hein, Vander Zanden, & Magnuson, 2007). In the absence of clear habitat boundaries, eradication is often deemed impossible. In such cases, containment with the goal to prohibit further dispersal of the species can be a viable alternative.

Faced with the complexity and context-dependencies of management options, decision makers require scientific information to develop explicit decision frameworks (Heger et al., 2013). Decisions on eradication or containment measures must be based on ecological aspects such as the species' life history and its susceptibility to control, and also on practical inputs such as cost, scope, time and required research (Edwards & Leung, 2009). They should also consider social dimensions (Estévez, Anderson, Pizarro, & Burgman, 2015).

The aim of our paper was to provide an approach for scientists interested in decision-making processes on population control strategies for invasive species. Throughout this paper, we use the terms "population control" or "control strategy" as a surrogate for "eradication and/or containment measures". We propose that scientists involved in such decision-making processes need to be able to provide scientific knowledge on the effectiveness, i.e. is the control strategy suitable to accomplish the goal, and on the efficiency, i.e. has the strategy the best relation between effect and effort in comparison to other available options.

To illustrate this approach, we use the case of the round goby *Neogobius melanostomus* (Pallas, 1814) (Figure 1a). This small bottom-dwelling fish species native to the Ponto-Caspian area is considered to be one of Europe's "worst 100 invasive species" (DAISIE 2016). In Switzerland, round goby were first detected in a commercial harbour in 2012 (Kalchhauser, Mutzner, Hirsch, & Burkhardt-Holm, 2013) (Figure 1b). Upon this detection of the round goby, a transdisciplinary research project was instigated, which aimed to provide information on the species' potential threats and implement evidence-based countermeasures against its further spread. Collaboration with decision makers was facilitated through a series of workshops following an introductory meeting. At this kick-off meeting, decision makers raised concerns of the species' negative effects on native ecosystems (Hirsch, N'Guyen, Adrian-Kalchhauser, & Burkhardt-Holm, 2016) and identified population control as a research priority (see N'Guyen, Hirsch, Adrian-Kalchhauser, & Burkhardt-Holm, 2016 for details on the meeting). Decision maker involvement is a fundamental success factor of invasive species management (Larson, 2007; Moon, Blackman, & Brewer, 2015). Therefore, we commenced research into population control options within a transdisciplinary project cooperating with decision makers.

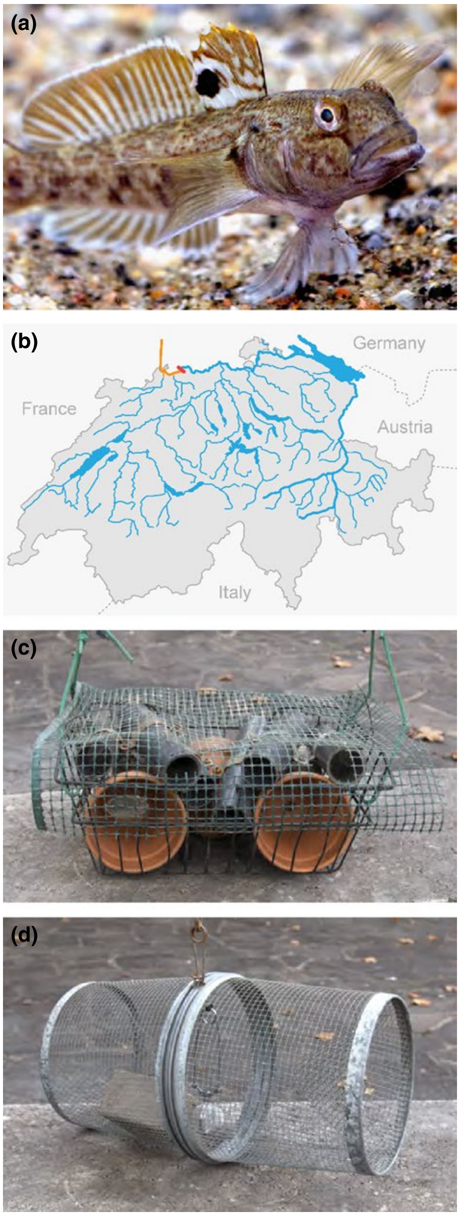

FIGURE 1 Study species and study system. (a) Round goby *Neogobius melanostomus*, one of Europe's "100 worst invasive species" (photo by Magnus Thorlacius). (b) Study system in the high Rhine and its catchment area including valuable pre-alpine streams and lakes. Current invasion area (in orange) is, among other methods, monitored in collaboration with anglers. Dams located upstream in the Rhine (red line) currently limit round goby spread. (c) Spawning trap to remove eggs. Both pots and PVC tubes are accepted as spawning substrate by round goby. (d) Baited minnow trap to remove adults [Colour figure can be viewed at wileyonlinelibrary.com]

In this paper, we provide a scientific basis for round goby population control. We first evaluated feasible population control options in a field study based on decision makers' input from previous workshops: removal of eggs with spawning traps and removal of adults with minnow traps (Figure 1c,d). Then, using a matrix population model, we analysed the effectiveness and efficiency of the identified control options. During this process, we fed back preliminary empirical and modelling results to decision makers. We discuss the process of "crafting usable knowledge" (Clark, van Kerkhoff, Lebel, & Gallopin, 2016) with scientists and decision makers collaborating on an equal footing.

2 | MATERIALS AND METHODS

2.1 | Study species: round goby *Neogobius melanostomus*

In the last decades, the round goby was introduced presumably by ballast water to the North American Great Lakes (Jude, Reider, & Smith, 1992) and to most European water bodies such as the Baltic Sea (Sapota & Skóra, 2005), Danube (Stránai & Andreji, 2004), Rhine (Borcherding et al., 2011) and multiple smaller rivers and lakes. It builds up high population densities, out-competes native species and changes food web structures (Kornis, Mercado-Silva, & Vander Zanden, 2012). Round goby adults generally show high site affinity (Lynch & Mensinger, 2012), but downstream-drift in the larval stage is common (Borcherding et al., 2016). Round goby females spawn multiple batches in nests, where males provide parental care (Meunier, Yavno, Ahmed, & Corkum, 2009).

Reproductive output and survival are crucial parameters in population control. In the case of the round goby, adult survival can be lowered using minnow traps (Diana, Jonas, Claramunt, Fitzsimons, & Marsden, 2006) and eggs can be retrieved by spawning traps (Hirsch, Adrian-Kalchhauser, et al., 2016). Because of male parental care, a potential differential control strategy with respect to sex could alter population dynamics (Kovtun, 1979). See N'Guyen et al. (2017) for a literature review on round goby life-history parameters and Appendix S3 for details on parameter estimation.

2.2 | Connecting research and practice using workshops

To integrate this biological knowledge with the knowledge of stakeholders who make decisions according to their field experience and policy prerequisites, we asked 17 decision makers in an initial workshop (1 year after the kick-off meeting) using a written survey to rate the perceived effectiveness, urgency and simplicity of two population control options: removal of eggs and removal of adults (see Hirsch, Adrian-Kalchhauser, et al., 2016 for details on the survey method). After successfully testing both options in the field from a practical point of view and generating preliminary modelling results, we then asked 20 decision makers in a subsequent workshop using another written survey to what extent they approve measures being developed to implement these options (see Appendix S1 for details on the method). Decision makers for both workshops were representatives from cantonal and federal administrations, fishery associations, non-governmental organisations or private companies. Because of e.g. personnel turnover, representatives of the decision maker groups changed between workshops. In total, 11 decision makers from the initial workshop took part in the subsequent workshop.

2.3 | Field study to test control options and to parameterise the model

Based on decision makers' initial ratings and our preliminary field data, we conducted a detailed field study to test the control options and to partially parameterise the population model. Life-history data on round goby were sampled in the High Rhine, Switzerland, in the Harbour Kleinhueningen from 2012 to 2016 using spawning traps and minnow traps (see Table 1 for parameter values, Appendices S2 and S3 for details on sampling methods, and N'Guyen et al., 2017 for literature values). This field study also allowed gathering information on control effort (see Appendix S4 for details on effort estimations).

2.4 | Dynamical population model

To investigate population control options in terms of effectiveness and efficiency, we constructed a post-breeding two-sex stage-structured and density-dependent population model. The model's state vector consists of laid eggs (at this point all hatching with success; see below), adult females and adult males (Equation 1):

$$\begin{bmatrix} x_e \\ x_f \\ x_m \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 \\ \theta s_0(\mathbf{x}_e) & s_a(\mathbf{x}_a) & 0 \\ (1-\theta)\, s_0(\mathbf{x}_e) & 0 & s_a(\mathbf{x}_a) \end{bmatrix}_t \begin{bmatrix} x_e \\ x_f \\ x_m \end{bmatrix}_t \begin{bmatrix} 1 \\ (1-p_f) \\ (1-p_m) \end{bmatrix} + \begin{bmatrix} (1-p_e)\, g(\mathbf{x},\mathbf{p}) \\ 0 \\ 0 \end{bmatrix}_t \quad (1)$$

The 3 × 3 matrix on the right-hand side of Equation 1 is a transition (survival) matrix, where θ is the primary proportion of females emerging from eggs, and s_0 and s_a are larval and adult survival, respectively, from year t to year $t + 1$. The state variable subscripts refer to eggs (e), adult females (f), adult males (m) and adults (a), the latter being the sum $f + m$; we present and discuss the stage-specific removal terms p_i (i = eggs, females or males) in section *Removal effort* below. Survival rates are assumed to be equal among sexes and density-dependent (Vélez-Espino, Koops, & Balshine, 2010). s_0, s_a and g followed by parentheses in Equation 1 indicate a function with entries in bold as the functions' arguments. We implemented density dependence of adult survival using an exponential model: $s_a(\mathbf{x}_a) = s_a \exp(-\gamma_a(x_f + x_m))$. Larval survival is defined similarly, but depending on x_e and differing in the strength of density dependence γ_e; see Appendix S3 for further details.

Our per capita fecundity estimate F is a weighted mean of all reproducing female age classes (sections *Reproduction* and *Fecundity* in Appendix S3). Given such a mean, we introduced reproduction into the model via a reproduction vector (right-most term). Since we implemented a post-breeding model, females as well as eggs

TABLE 1 Parameter values used for population model and control effort. When more than one value is reported, entries in bold are the standard set used for simulations, unless otherwise noted in the text

Symbol	Parameter	Values	Remarks
Survival			
s_0	Survival larvae from year t to year $t + 1$, density-dependent: $s_0(\mathbf{x}_e) = s_0\exp(-\gamma_e(\mathbf{x}_e))$	**0.0087** (0.0056, 0.0124)	Mean from Table 1 in Vélez-Espino et al. (2010), confidence interval calculated with CV = 0.2 using beta distribution; mean used as "standard", lower and upper bound used for simulations shown in Figure 5
s_a	Survival adults from year t to year $t + 1$, density-dependent: $s_a(\mathbf{x}_a) = s_a\exp(-\gamma_a(x_f + x_m))$	**0.6240** (0.3673, 0.8474)	Mean from Table 1 in Vélez-Espino et al. (2010), confidence interval calculated with CV = 0.2 using beta distribution; mean used as "standard", lower and upper bound used for simulations shown in Figure 5
–	Coefficient of variation survival larvae and adults	0.2	A higher CV would be unrealistic, because the lower bound of the confidence interval is already relatively low (see above)
κ	Strength of within-nest density dependence	10,000	Value estimated so that the function approximately reproduces the results reported in Kovtun (1979)
γ_e	Density dependence (DD) larvae	0.00044024	Carrying capacity eggs per m^2: weak DD 20,380, strong DD 7,972
γ_a	Density dependence (DD) adults	Weak DD: 0.0036 **Strong DD: 0.0099**	Fitted curves from Figures 2 and 3 in Vélez-Espino et al. (2010), carrying capacity adults per m^2: weak DD 15.2, strong DD 5.1; our field data better matched the values for strong DD
Reproduction			
θ	Primary sex ratio (primary proportion of female eggs)	0.5	
ϱ	Proportion of females participating in reproduction	1.00	Based on own data
F	Eggs per female = per capita fecundity estimate, weighted mean of all female age classes reproducing	**3,238** (2,673, 4,010)	Confidence interval calculated from fit log-normal distribution based on own data; mean used as "standard", lower and upper bound used for simulations shown in Figure 5
–	Coefficient of variation fecundity	**0.092** (0.0857, 0.1009)	Confidence interval calculated from fit log-normal distribution based on own data
c	Clutch size = max. eggs per nest	4,655	0.75 quantile of eggs in artificial nests based on own data
η	Max. number of nests per m^2	2	Alternatively tested values: 0.1, 1, 4 nests per m^2, source for general range Figure 2 in Sapota et al. (2014)
α_i	Proportion of eggs laid, on average, during batch i for a total of 3 batches	i = 1, 2, 3 4/10, 3/10, 3/10	Based on own data
Management (control variables)			
ε_a	Catchability coefficient adults	**0.2356** (0.0926, 0.4812)	Maximum likelihood estimation based on own data; mean used as "standard", lower and upper bound used for simulations shown in Figure 5
ε_e	Catchability coefficient eggs	0.0334	Based on own data; for a combination of all catchability coefficients and resulting removal proportions see Figure 4, Figures S7.1 and S8.1
–	Detection density	0.1 fish per m^2	Alternatively tested values: 0.5, 1 fish per m^2
–	Time per trap	0.2 h = 12 min	Time to control one minnow trap or one spawning trap based on own data
–	Max. effort eggs	3.25 h/m^2 per control period	Total time per m^2 per year during control period April, May, June, July, August, based on own data
–	Max. effort adults	1.32 h/m^2 per control period **1.76 h/m^2 per control period**	Total time per m^2 per year during control period February and March depending on the number of traps per m^2 (Vélez-Espino et al., 2010) based on own data

potentially becoming females right before spawning season first have to survive one winter in order to reproduce. We thus define $x_f^{sp} = s_0(\mathbf{x}_e)\,\theta x_e + s_a(\mathbf{x}_a)x_f$, where superscript *sp* means spawning. Since only adult males, but not juvenile males influence the number of nests, we define $x_m^{sp} = s_a(\mathbf{x}_a)x_m$. We assume that all nests are occupied during spawning season, and we define a total maximum number of potential eggs to be laid in nests per square metre as $N = \min(\eta, x_m^{sp})\,c$ (section *Nests* in Appendix S3). Reproduction is characterised by three batches with proportion α_i of eggs laid, on average, during batch *i* (section *Fecundity* in Appendix S3). The total number of eggs potentially to be laid by all females is then $E = x_f^{sp}\varrho F$, where ϱ is the proportion of females reproducing. For every batch, there might be a sex ratio induced reduction in eggs laid per female, defined as $\phi_i = \min\left(1, N/\left(\alpha_i E\right)\right)$. This means that, for every batch, the number of nests built and parental care conducted by males is a limiting reproduction factor. Finally, due to reported density-dependent within-nest mortality (Kovtun, 1979), we defined $\psi_i = \exp\left(-\left(E\alpha_i c\phi_i/\left(N\kappa\right)\right)^2\right)$, so that values near one indicate low density-dependent mortality. In sum, the first entry in the reproduction vector in Equation 1 for an unharvested population is given by $x_e\left(t+1\right) = g(\mathbf{x}) = E\sum_{i=1}^{3}\alpha_i\phi_i\psi_i$.

2.4.1 | Population control options and within-year allocation of resources

A convenient starting point to investigate the effectiveness of control options is to perform a sensitivity analysis. For example, one could be interested in gauging which model parameter, e.g. a management-related model parameter, affects a population's growth rate the most. Given our density-dependent population model, we followed the perturbation approach presented in Caswell (2009), which allows to calculate sensitivity values of equilibrium densities to model parameters (see Appendix S5 for details).

Our model consists of sequential events (Appendix S3) and mirrors population dynamics on a yearly basis. Thus, answering the question of when during a modelled year to remove specific stage classes might offer additional advantages with respect to eradication success. This is because species have variable natural (age-dependent) mortality rates throughout the year. As shown in Appendix S4, removing adults is more effective after density-dependent natural mortality and before the reproductive season. A similar reasoning can be used for the youngest stage class, i.e. eggs. Here, however, we are comparing the effect of removing eggs before natural mortality, i.e. after they are laid, to removing almost 1-year-old adults right before reproduction. Since the removal of eggs and adults differ in effort, we will show the (dis)advantage of removing eggs and adults graphically in the *Results* section.

2.4.2 | Removal effort

Instead of absolute removal, i.e. subtracting an absolute number of eggs or adults, we modelled proportional removal to state the effort dependency more clearly. Thus, p_i is the proportion of stage *i* removed, and $(1 - p_i)$ is the proportion of stage *i* surviving (avoiding removal). To calculate the proportion of adults removed (given the effort applied for our study population; section *Effort* in Appendix S4), we used a Poisson catchability model to construct a likelihood function (Seber, 1982), and inferred a 95% confidence interval (CI) for the estimated catchability coefficient ε_a by means of a likelihood ratio test. The catchability coefficient depends, among other factors, on efficiency of fishing gear. For eggs, too, we assumed a Poisson catchability model. Due to insufficient data, we indirectly inferred the proportion of eggs removed by relating our sample mean of removed eggs to the expected number of eggs at equilibrium, calculated using stochastically generated population trajectories. Here, too, we calculated a mean and 95% CI for the catchability coefficient ε_e (Appendix S4).

2.4.3 | Evaluating population control success

To assess population control success, we calculated (1) a success rate (proportion of stochastically generated runs leading to eradication), given a fixed management period, (2) the mean time needed to achieve eradication and (3) a proxy for total management costs, in terms of hours per square metre (h/m^2) and years needed in situ. We defined a population to be eradicated whenever female or male density reached 10^{-6} fish per m^2. An influential variable is the management time span. We chose 15 years based on preliminary simulation results because variation in success rates can be best shown for this time span.

We set up stochastic simulations to calculate the above-mentioned measures as follows. Survival and fecundity rates were randomly generated using a beta probability distribution and a log-normal distribution, respectively. Vital rates were "sign-correlated," e.g. a good year for fecundity would also be a good year for survival. In addition, we calculated 95% CI for survival and fecundity (Appendix S6). Furthermore, we implemented removal as a binomial process with time-/sex-/stage-dependent densities and probabilities. We ran every grid-based combination of adult removal proportions 300 times. For egg removal, we fixed the removal proportion associated to the effort used for the study population. Finally, to start simulations, we emulated either a newly established population or a population at carrying capacity (5.1 fish per m^2, Table 1). For a newly established population, we introduced a detection threshold (adult density 0.1 fish per m^2) where population control starts; below the threshold, managers would not be aware of the presence of round goby. Unless otherwise noted, parameter values used for simulations are the "standard set" in Table 1 (when more than one value was tested, values in bold are the standard set). See Appendix S6 for further implementation details.

We further present some analytically derived results from our model. Here, we were interested in the stability of the system's equilibria and in studying combinations of removal proportions that would define a removal-induced extinction boundary. To this end, we simplified our model by assuming the proportion of females and males removed are equal. Thus, we rewrote our model with two stages, namely eggs and adult females. See Appendix S7 for details.

2.4.4 | Larval flow and adult dispersal

To analyse the effects of inflow and outflow on population control, we extended the model with inflowing and outflowing larvae and dispersing adults. Larval flow was included by adding or subtracting a certain number of larvae to post-reproductive densities, but before density-dependent natural mortality (section *Larval in-/outflow* in Appendix S9). Adults dispersing from the population were included by assuming different dispersal models in relation to population density (section *Adult dispersal* in Appendix S9).

3 | RESULTS

3.1 | Connecting research and practice—initial evaluation of options

During the initial workshop, decision makers seemed to lack a clear preference for one of the two control options "removal of eggs" or "removal of adults". The perceived effectiveness, urgency and simplicity of removing adults or removing eggs before modelling results were available ranged from very high to very low for both control options (Figure 2a).

3.2 | Removal of adults and eggs are feasible options in the field and in the model

We removed 3,457 round goby adults with minnow traps and 336,170 round goby eggs with spawning traps during the study period (Appendix S2). The simplified model (see Appendix S7) shows that various combinations of removal proportions of eggs and adults are possible to cross the analytically derived, removal-induced extinction boundary (i.e. to reach eradication, Figure S7.1 in Appendix S7). Note that some removal combinations (eggs, females, males) can induce irregular oscillations. However, these oscillations seemed not to influence eradication success (results not shown; see Appendix S8 for details).

3.3 | Re-connecting research and practice—re-evaluation of options

After testing the two control options in the field, we compiled field data (Appendices S2–S4) and preliminary modelling results. These preliminary modelling results showed that removal of eggs and adults can lead to population eradication when applying a certain effort (see Appendix S7 for extinction boundary). We presented these results in a subsequent workshop to decision makers and asked to what extent they approve measures being developed to implement these recommendations, i.e. removing eggs with spawning traps or removing adults with minnow traps. Most of the 20 surveyed decision makers strongly approved (30% for removing eggs and 60% for removing adults) or approved (60% for removing eggs and 30% for removing adults) measures being developed (Figure 2b).

3.4 | Early removal outperforms late removal in terms of effort

The model revealed that eradication success crucially depends on when in a population's history population control is initiated. Starting early after detecting the presence of round goby, i.e. as soon as the detection threshold of 0.1 fish per m^2 is exceeded, requires on average

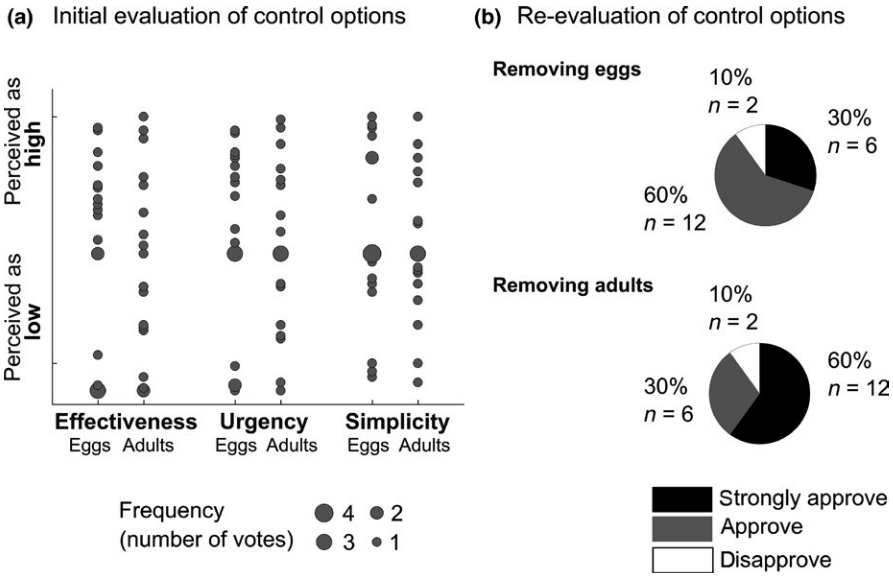

FIGURE 2 Evaluation of control options "removing eggs with spawning traps" and "removing adults with minnow traps" by decision makers before (a) and after (b) field tests and preliminary modelling results. (a) Decision makers in the initial workshop seemed to lack a clear preference for one of the two control options concerning effectiveness, urgency and simplicity before being presented with the field test and preliminary modelling results (*n* = 6 representatives from public and private companies, *n* = 4 from angler associations and NGOs, *n* = 7 from cantonal and federal administration). (b) Decision makers in the subsequent workshop mostly approved measures being developed to implement these recommendations after being presented with preliminary results (*n* = 3 representatives from public and private companies, *n* = 6 from angler associations and NGOs, *n* = 11 from cantonal and federal administration)

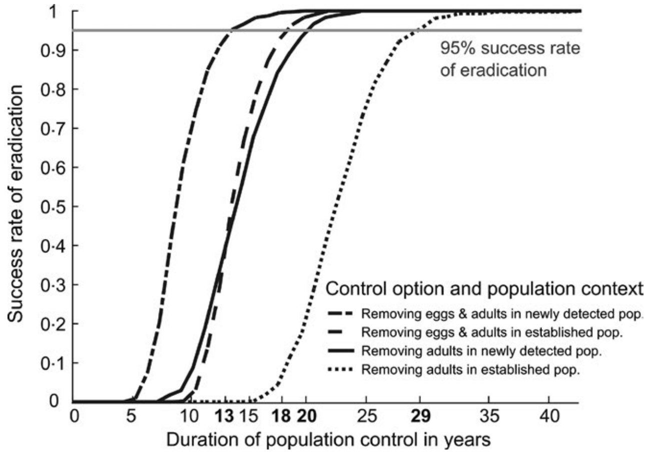

FIGURE 3 Success rates for both options show that starting population control when the population is newly detected needs less years than starting when the population is established. Success rate is defined as proportion of stochastically generated runs leading to eradication, e.g. a success rate of 0.95 (horizontal line) means that 95% of all runs led to eradication

less years than controlling an established population (Figure 3). For example, to reach a success rate of at least 95% when starting early with removing eggs and adults, 13 years are needed; when starting at carrying capacity, 18 years are needed. Furthermore, for both initial conditions, removing eggs and adults combined needs on average less control years compared to removing only adults. To reach a success rate of at least 95% when starting early with removing adults, 20 years are needed; when starting at carrying capacity, 29 years are needed.

3.5 | Adult removal outperforms egg removal in terms of effort

The combined removal of eggs and adults is successful faster than removing either only eggs or only adults. However, our perturbation analysis showed that equilibrium densities are more sensitive to removal of adults, especially females, than egg removal (Appendix S5). In addition, removing adults only proved to be the best eradication option in terms of control effort. This can be seen by comparing the yearly effort associated with the endpoints of the extinction boundary in Figure 4. All combinations on the right of the extinction boundary (white line) lead to extinction of the population. The yearly effort per square metre to remove eggs is higher than that for adults because eggs are removed for a longer period during the season (April to August for eggs vs. February and March for adults) and with a higher maximum effort (3.25 h/m^2 for eggs vs. 1.76 h/m^2 for adults; see Appendix S4).

3.6 | Removal effort must be high even if life-history parameters are low

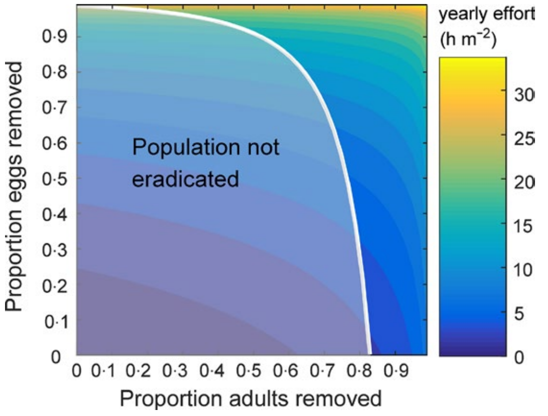

FIGURE 4 Various combinations of removal proportions of eggs and adults and associated yearly effort per square metre show that removing eggs needs more effort than removing adults. The white line shows the analytically derived, removal-induced extinction boundary and the shaded area on the left side indicates removal combinations not leading to eradication [Colour figure can be viewed at wileyonlinelibrary.com]

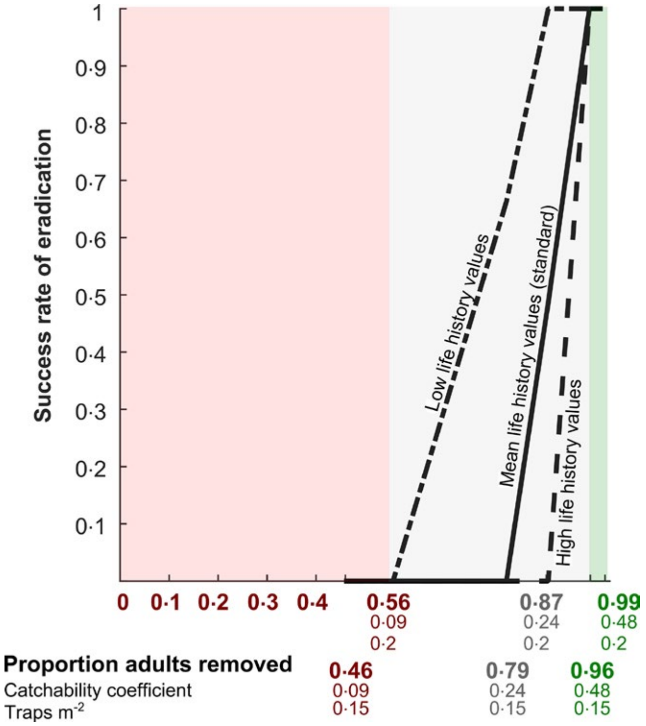

FIGURE 5 If removing up to 56% of adults, eradication is not successful; if removing between 57% and 95%, eradication success depends on life-history values; if removing more than 96%, eradication is always successful. Proportion of adults removed (numbers in bold) results from different catchability coefficients ε_a (0.09, 0.24, 0.48) and number of traps per m^2 (0.15, 0.2). See Table 1 for life-history values (mean, lower, and upper bound of 95% CI) [Colour figure can be viewed at wileyonlinelibrary.com]

Since we found that removing adults immediately after invasion is the best option in terms of total effort, we analysed the influence of control parameters, i.e. catchability coefficient and number of traps per square metre, and life-history parameters, i.e. adult and larval survival rates and fecundity rate, on these results (see Table 1 for standard values and 95% CI).

If using the catchability coefficient's lower bound, i.e. removing up to 56% of the adult population, it is not feasible to eradicate the

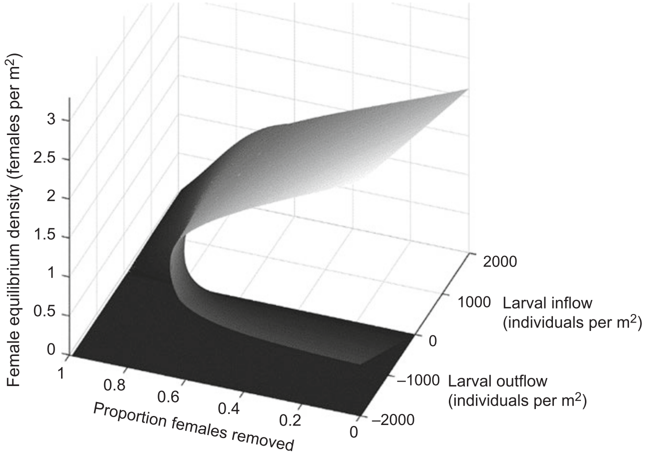

FIGURE 6 Larval flow, in combination with the proportion of females removed, qualitatively affects the system's dynamics. The bifurcation analysis shows the effect of varying in-/outflow of larvae (*x*-axis) and the proportion of females removed (*y*-axis) on adult female equilibrium density (*z*-axis); these results were generated using the simplified model (Equation S7.1 in Appendix S7). Results for larval flow in combination with egg and adult removal look qualitatively very similar

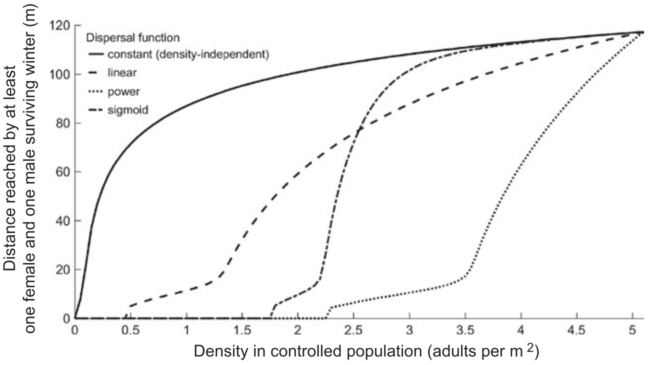

FIGURE 7 Distance (m) reached by at least one female and one male after surviving winter depends on the assumptions on density-dependent dispersal and diverges for a given density in the controlled population. Assumptions on dispersal include density-independent constant dispersal and density-dependent dispersal described by a power function and by two intermediate models using a linear or a sigmoid function

population, even with low survival and fecundity rates (red area in Figure 5). The success of removing 57%–95% of the population (mean catchability coefficient) depends on survival and fecundity rates of the population (grey area). If 96% or more of the population can be removed (catchability coefficient's upper bound), eradication is possible even with high survival and fecundity rates (green area).

3.7 | Removal effort is futile if propagule inflow exists

Our simulations indicate that inflow and outflow rates have an important effect on eradication success. If the population experiences constant larval inflow, e.g. by ballast water, eradication is almost never possible, even if the inflow is very low. Analytically, the origin is not an equilibrium anymore, since a constant amount of inflow shifts the lower equilibrium away from the origin (Figure 6).

If the population experiences constant larval outflow, e.g. by drift, less effort is needed for eradication. Analytically, three equilibria exist: the origin (stable), an intermediate- (unstable) and a high-density equilibrium (stable). By increasing removal (Figure 6, *y*-axis) with constant outflow (fixed value on *x*-axis), the intermediate and high-density equilibria coincide and annihilate each other (saddle-node bifurcation) and the origin is the only equilibrium left. Adults dispersing out of the population, in contrast, only influence eradication success if we assume the biologically unrealistic situation of constant density-independent dispersal; all other dispersal models do not appreciably influence eradication success (Figure S9.2 in Appendix S9).

If eradication is not possible, population control may lead to lower population densities, thus reducing the number of individuals that successfully disperse to new habitats (Figure 7, for densities of the focal population related to different control options see Figure S8.2 in Appendix S8). Depending on the form of density-dependent dispersal, the distance that can be overcome by at least two reproductive individuals surviving winter to potentially initiate a new population diverges for a given density (see Appendix S9 for details).

4 | DISCUSSION

4.1 | Decision maker input into a research agenda

Invasive species management requires the collaboration of scientists and decision makers from administration and civil society in a transdisciplinary process. The high level of agreement to the two population control options reported in our study could be explained by decision makers' prior knowledge on the species and its assumed negative impacts (Bremner & Park, 2007) as well as by the proposed removal methods (Olszańska, Solarz, & Najberek, 2016). In general, scientific results that are co-produced by all relevant parties in a transdisciplinary process have the potential for better social acceptance and higher compliance by decision makers (Hirsch Hadorn et al., 2008). However, the complex mechanisms in which scientific results may impact society on different levels are out of the scope of this article (see e.g. Defila & Di Giulio, 2016 for a thorough discussion).

4.2 | Early adult removal is the "best" control option

Our model showed that immediately removing adults is the best option in terms of total effort. However, still considerable effort is needed: to reach a 95% eradication success rate, the model showed that 1.76 h/m^2 would need to be invested in situ every year during 20 years (Table 1, Figure 3). With increasing size of the controlled habitat, total time increases; in contrast, additional expenses, such as driving time or costs for vehicles, decrease per unit area. Minnow traps have been suggested to be the most cost-efficient option to remove adult round goby in comparison to gill nets and trotlines (Diana et al., 2006). The catch efficiency of traps could by increased by e.g. pheromones (Corkum, Meunier, Moscicki, Zielinski, & Scott, 2008), acoustic signals (Isabella-Valenzi & Higgs, 2016; Moynan, Neumann, & Welsh, 2016), electric lead (Johnson et al., 2016) or bait selection, thus lowering control effort. For labour-intensive work, Simberloff (2009) proposed to deploy volunteers, schoolchildren, eco-tourists or convicts.

4.3 | Inflow should be integrated into management considerations

Our model showed that control effort is futile if the population experiences propagule inflow. Propagule pressure, defined by propagule size, i.e. the number of individuals arriving during an introduction event, and propagule number, i.e. the number of introduction events, is one of the most important factors for the success of an invasion (Lockwood, Cassey, & Blackburn, 2005). This highlights the importance of preventive management and early detection measures, e.g. by eDNA (Adrian-Kalchhauser & Burkhardt-Holm, 2016).

4.4 | Sex-specific removal—a control option?

The number of available nests and the sex ratio are both important factors affecting reproduction because of round goby's nest guarding strategy (Meunier et al., 2009). A challenging issue is that the observed sex ratio can be biased by the catch technique (Brandner, Pander, Mueller, Cerwenka, & Geist, 2013; Thompson & Simon, 2015) and by invasion stage. Because of a lack of own field data and unclear literature values (N'Guyen et al., 2017), in our model we assumed equal proportions of removed males and females (Figure S7.1 in Appendix S7). However, a removal-induced change in sex ratio can have important implications for eradication success because it may interrupt reproduction, e.g. if males are removed in high numbers during the reproductive season. Potential technological advances such as the above-mentioned pheromone or acoustic traps may allow tailoring removal efforts to specific populations with specific sex ratios.

4.5 | Population model parameter uncertainties

We made a number of assumptions for parameterising our model. Where field data were available, whenever possible we calculated confidence intervals. Where field data were not available, we relied on literature values. Survival rates were taken from a harbour in Lake Ontario (Vélez-Espino et al., 2010) because reported conditions are similar as in our case. In addition, this is to our knowledge the only study providing information on not only adult but also larval survival. Estimations of density, fecundity and other reproduction-related parameters from our field data are in the range of the reported values (N'Guyen et al., 2017).

4.6 | Application to other systems

The round goby is a successful invader across very different ecosystems, including brackish and freshwater systems, and shows greatly varying life-history traits (Hôrková & Kováč, 2014). Nest site availability differs between ecosystems (Sapota, Balazy, & Mirny, 2014) and environmental heterogeneity influences round goby abundance (Kornis, Sharma, & Vander Zanden, 2013). Thus, trapping efficiency most likely varies among ecosystems, and other methods than minnow traps may be more efficient, e.g. electrofishing in riprap structures (Brandner et al., 2013). Additionally, depending on species composition in a given ecosystem, population control by predators may be a promising alternative (Huo et al., 2014; Madenjian et al., 2011). Consequently, food web and whole-ecosystem effects need to be considered when removing an invasive species (Hansen, Hein, et al., 2013; Zavaleta, Hobbs, & Mooney, 2001). To make things even more complex, invasive species abundance (Hansen, Vander Zanden, et al., 2013) and their impacts vary across habitats (Latzka, Hansen, Kornis, & Vander Zanden, 2016) and time-scales (Crooks, 2005). These system-specific differences underscore the need for basic ecological knowledge combined with local decision makers' priorities to create evidence-based control options.

5 | CONCLUSIONS

In this study, we aimed to fill an existing gap between research and implementation of invasive species population control. Using an imminent invasion of an ecologically harmful fish as a case study, we combined decision makers' valuation of control options with scientific field and modelling data. We found that decision makers were initially ambiguous about the removal of adults and eggs as control options. To contribute scientific knowledge to the decision-making process, we conducted an empirical field study and constructed a population model to assess the effectiveness and efficiency of these two options. Preliminary results fed back to decision makers appeared to create comparable support for both options. More detailed modelling for both options identified removal of adults as the best option in terms of total effort. Still, enormous effort is needed to eradicate the population. The modelling also revealed strong time and context dependencies: eradication is only feasible if started early in recently arrived populations, and inflow of new propagules renders most eradication efforts ineffective.

Because the goal of any management should be to maximise its impact given scarce time and funds, round goby population control should only be applied in valuable habitats where inflow can be stopped. Valuable habitats could be water bodies that provide spawning grounds for endangered or commercially valuable native fish species such as brown trout *Salmo trutta* or Atlantic salmon *Salmo salar* (Verliin et al. 2017). The presented transdisciplinary approach is transferrable to other regions and taxa and can form the basis of a decision framework for the actual implementation of population control along the lines of decision makers' valuation and scientific advice.

ACKNOWLEDGEMENTS

Students helping in the field, participants from the workshops, Heidi Schiffer, Nicole Seiler, Sascha Gregori, Sylvie Flämig, Rico Defila, Antonietta Di Giulio, Hannes Weigt, Nina Gerber, Isobel Booksmythe, M.S. Kornis and an anonymous reviewer for helpful comments. Parts of the calculations were performed at sciCORE, University of Basel. Project funded by the Federal Office for the Environment, Switzerland, Canton Basel-Stadt, lottery funds of the Cantons Solothurn, Aargau and Basel-Landschaft. The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.N., P.E.H., I.A.K. and P.B.H. designed and conducted the field study; K.H. provided fecundity results; C.B. provided all statistical and mathematical modelling methods; A.N. and C.B. generated all results; A.N., P.E.H., C.B., I.A.K. and P.B.H. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data on round goby life history are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.84fk9 (N'Guyen et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: N'Guyen A, Hirsch PE, Bozzuto C, Adrian-Kalchhauser I, Hôrková K, Burkhardt-Holm P. A dynamical model for invasive round goby populations reveals efficient and effective management options. *J Appl Ecol*. 2017;00:1–11. https://doi.org/10.1111/1365-2664.12934

Appendix S1: Decision maker survey

Upon detection of the round goby in Switzerland 2012, a transdisciplinary research project was instigated. In the introductory kick-off meeting 2012, population control was identified as a research priority (N’Guyen, Hirsch, Adrian-Kalchhauser & Burkhardt-Holm 2016). Two options for population control were briefly discussed in the kick-off meeting: removal of eggs and removal of adults. We then commenced researching these two population control options. One year after the kick-off meeting, we surveyed the perceived effectiveness, urgency and simplicity of egg removal and adult removal during the “initial workshop” with 17 decision makers (see Hirsch *et al.* 2016 for details on the method). After finding that decision makers had no clear preference for either of the two options, we tested both options in the field (see S2) and collected life history and population control parameters (see S3 and S4). Furthermore, we generated preliminary modelling results, i.e. we showed that removal of eggs and adults can lead to eradication of a population (see S7 for extinction boundary). In the “subsequent workshop”, we fed back these results to 20 decision makers and asked in a written survey to what extent they approve measures being developed to implement these recommendations (removing eggs with spawning traps or removing adults with minnow traps; Fig. S1.1).

Decision makers were representatives of public and private companies (initial workshop n = 6, subsequent workshop n = 3), angler associations and NGOs (initial workshop n = 4, subsequent workshop n = 6) and cantonal and federal administration (initial workshop n = 7, subsequent workshop n = 11). In total, eleven decision makers from the initial workshop took part in the subsequent workshop. These workshops are part of a series of workshops that we conduct in at least yearly intervals to assess priorities and promote a dialogue between all involved parties (N’Guyen, Hirsch, Adrian-Kalchhauser & Burkhardt-Holm 2016).

To what extent would you approve measures being developed to implement this recommendation? [removing eggs with spawning traps or removing adults with minnow traps; asked in two separate questions]

Strongly approve ☐
Approve ☐
Disapprove ☐
Strongly disapprove ☐

I don’t know ☐

Reasons for your assessment: [more space provided]

Figure S1.1: Part of a questionnaire to survey 20 decision makers during the subsequent workshop. Transferred into English by the authors, original question in German: “Wie sehr sind Sie dafür, dass Massnahmen erarbeitet werden, um diese Empfehlung umzusetzen?” Additional explanations in square brackets to improve clarity for this paper.

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Hirsch, P.E., Adrian-Kalchhauser, I., Flämig, S., N'Guyen, A., Defila, R., Di Giulio, A. & Burkhardt-Holm, P. (2016) A tough egg to crack: recreational boats as vectors for invasive goby eggs and transdisciplinary management approaches. *Ecology and Evolution*, **6** (3), 707–715.

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Appendix S2: Details field study

To sample eggs, spawning traps were deployed at five sites A to E in the Rhine Harbour Kleinhueningen, Switzerland (depth range 1.7-4.0 m, Fig. S2.1) from February to October 2014 (Fig. S2.2a, see Table S2.1a for exact dates and catch numbers). Spawning traps consisted of clay pots and plastic tubes in a bike basket (Fig. 1c, see Hirsch *et al.* 2016 for a description of the spawning traps). The deployed spawning traps were controlled twice weekly, pots and tubes with eggs were removed and replaced by new ones. Pots and tubes with eggs were taken to the laboratory, photographed and counted (see Hirsch *et al.* 2016 for a description of the method). The peculiar reproductive behaviour of round goby make spawning traps a species-specific option that minimises the possibility of impacting non-target species (see section *Reproduction* in S3). However, managers in other systems with different species compositions may need to be careful not to remove native species’ eggs with the traps (e.g. sculpins or small perches). In this case, a modification of the traps would be necessary.

To sample adults, minnow traps (HRH Fishing Hebeisen, www.hebeisen.ch, Fig. 1d) were deployed at the same five sites A to E in the harbour. We used 3 pieces of dry dogfood (Frolic, www.frolic.at) in a tea strainer as bait. The entrance holes of the minnow traps were widened with a pair of pliers to obtain a diameter of approximately 7 cm. Minnow traps were installed in a standardised way from May-December 2012, March-December 2013, January-April and September-November 2014, July-September 2015 and August 2016 (Fig. S2.2b, see Table S2.1b for exact dates and catch numbers). Additional samplings were conducted in spring 2015 and spring 2016 (data not shown, but see section *Number of traps* m^2 in S4). Traps were controlled for fish twice weekly. Native fish species were identified and released. Round goby were euthanized using 150 µl of pure clove oil solved in 10 ml 70% ethanol. All samples were transported on ice to the laboratory and immediately frozen at -20 °C. Before further analysis, all samples were photographed, weighed to the nearest gram and measured (standard length SL and total length TL) to the nearest millimetre. A subset of samples was further processed to collect life history parameters. When parameters were not available, we resorted to literature values (Table S1).

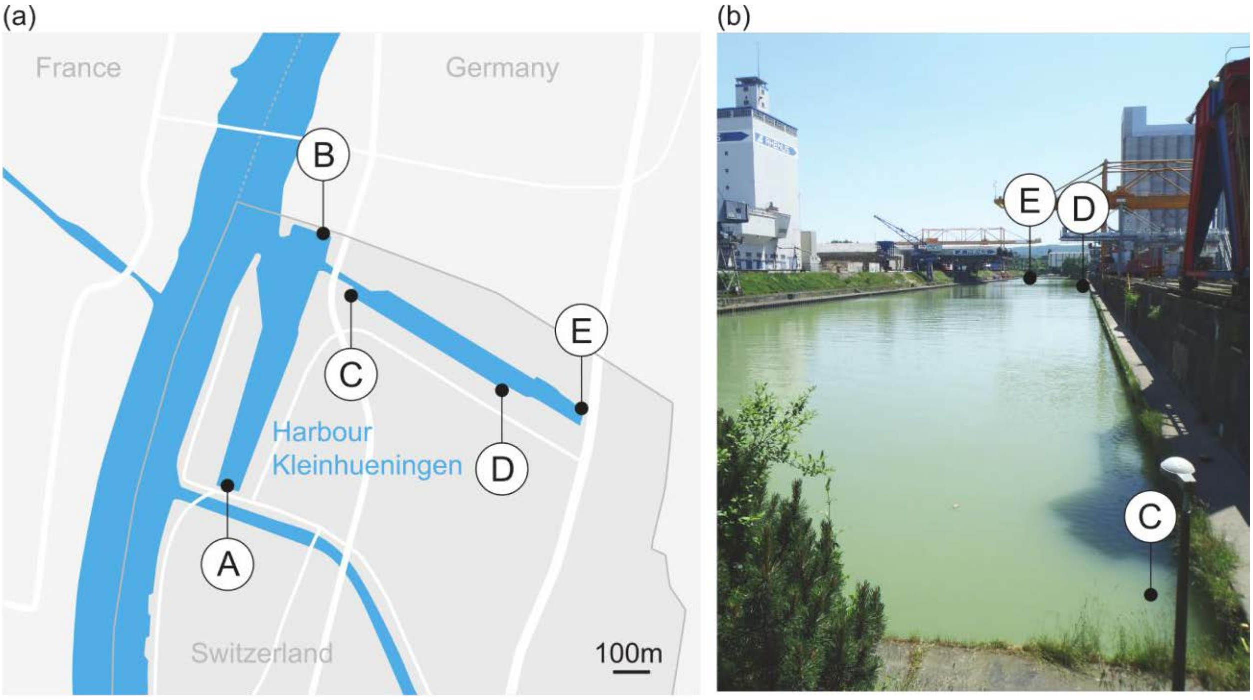

Figure S2.1: Study system harbour Kleinhueningen in Basel, Switzerland. (a) Sampling sites A to E in the harbour. (b) View of the sampling site C in the front and D and E in the back.

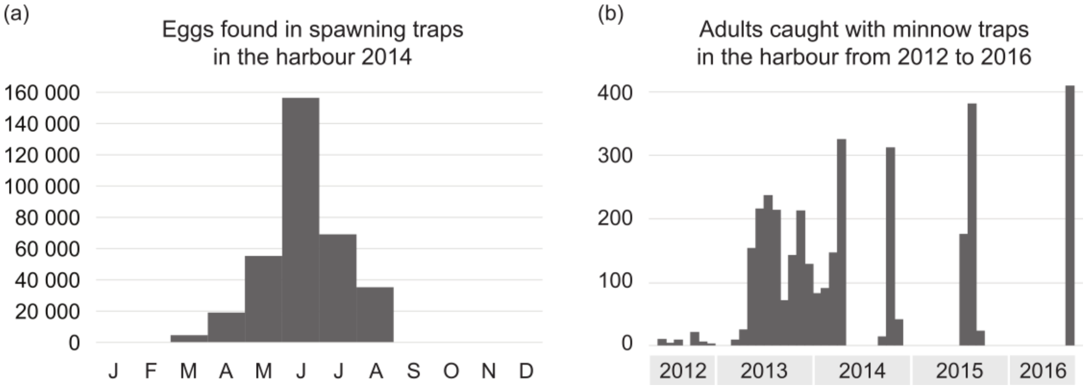

Figure S2.2: Removal of eggs and adults are feasible control options in the study system. (a) Round goby eggs found in spawning traps 2014 at sites A, B, C, D and E in the harbour (modified with permission from Hirsch *et al.* 2016). **(b)** Round goby adults caught 2012 to 2016 at sites A, B, C, D and E with minnow traps. Note that sampling was not continuous, see Table S2.1b for details on study period.

Table S2.1: Removal of eggs and adults in the study system

(a) Number of eggs and adults removed with spawning traps.

Year	Study period	Duration in weeks	# round goby eggs	# round goby adults
2014	04/03 – 25/08 *	25	336’170	311

* Spawning traps were installed from early February to late October 2014 to be sure we covered the whole spawning season; study period here refers only to the period where eggs were found, thus reflecting also the spawning season.

(b) Number of adults removed with minnow traps during the standardised sampling.

Year	Study period	Duration in weeks	# round goby adults	# round goby adults per week
2012	22/05 – 06/12	29	55	1.9
2013	27/03 – 31/12	41	1408	34.3
2014	01/01 – 28/04 22/09 – 12/11	24	1008	42
2015	29/07 – 03/09	5	578	115.6
2016	02/09 – 31/08	4	408	102
Sum		99	3457	30.8

Reference

Hirsch, P.E., Adrian-Kalchhauser, I., Flämig, S., N'Guyen, A., Defila, R., Di Giulio, A. & Burkhardt-Holm, P. (2016) A tough egg to crack: recreational boats as vectors for invasive goby eggs and transdisciplinary management approaches. *Ecology and Evolution*, **6** (3), 707–715.

Appendix S3: Life history parameter estimation for dynamical population model

Reproduction. Round goby spawn in batches repeatedly from early April to late August (Hôrková & Kováč 2015b; Pennuto, Krakowiak & Janik 2010; Sapota, Balazy & Mirny 2014; Tomczak & Sapota 2006). During this spawning season, one or more females lay their eggs in batches in cave-like nests guarded by males. After fertilising the eggs, the male round goby defends the nest during the spawning season (Meunier, Yavno, Ahmed & Corkum 2009, see section *Fecundity* for number of batches). Depending on temperature, hatching can start approximately between 8 and 28 days after egg deposition (Bonisławska *et al.* 2014; Hirsch *et al.* 2016). All round goby females and a subsample of males were examined regarding their age of first reproduction. For females, the gonad development stage was inspected during dissection (adapted from Tomczak & Sapota 2006) and we found that females start to reproduce at age 1. Additionally, the fecundity analysis to determine the number of released eggs (see section *Fecundity*) confirmed that age 1 females take part in the reproduction process. For males, we followed a different approach. Nest-guarding males turn black (Marentette, Fitzpatrick, Berger & Balshine 2009). Therefore, we analysed the pigmentation values using pictures taken for morphometric analysis. We found that age 1 males did not show the nuptial dark colour; thus, we assumed they do not yet take part in the nest-guarding.

Fecundity. A subsample of 90 females from the sampling period 2013 was analysed to estimate the number of batches, the total number of oocytes (TNO) and total number of released oocytes (NRO). The diameters of 50 randomly chosen oocytes per individual were measured using an ocular micrometer to the nearest 0.0025 mm, and/or from photographs using the AxioVision 4.8.2 software, Carl Zeiss MicroImaging GmbH. Based on the oocyte diameter and their frequency distribution, the number of spawning batches and the batches with the most developed eggs (supposed to be spawned within the season) were determined for each female. TNO was defined as the total number of oocytes present in ovaries. To calculate TNO, 90 females from June to September were used. NRO was defined as the number of oocytes spent within a spawning season (batch with the most developed eggs which was clearly distinguished from the rest of oocytes). To calculate NRO, 49 females from June to August were used. TNO and NRO were calculated from different sub-samples of ovaries and subsequently determined gravimetrically (Holčík & Hensel 1972). According to the oocyte diameter frequency distribution, two or three spawning batches per season were identified in the round goby females, which is consistent with data from other locations (Hôrková & Kováč 2015b; Hôrková & Kováč 2015a; MacInnis & Corkum 2000; Pennuto, Krakowiak & Janik 2010). To not underestimate reproductive potential, we assumed three batches per female per season with different proportions of eggs allocated to each batch. The reproduction function in our population model includes the maximum number of eggs that one female will potentially lay in one spawning season. To this end, we fit a lognormal distribution to NRO and used the estimated mean and variance to calculate a coefficient of variation (Table 1 in the main text). See S6 for details on the 95% confidence interval.

Nests. Female round goby spawn on hard substrate in cave-like nests guarded by males (Meunier, Yavno, Ahmed & Corkum 2009). A nest has a maximum number of eggs that can be fitted into it. We used the spawning trap data to estimate the maximum number of eggs laid per nest, e.g. clutch size. As has been previously reported, round goby's reproduction is characterised by within-nest density dependence: the more eggs in a nest, the less eggs will successfully hatch because of predation and lack of aeration (Kovtun 1979). Habitat conditions in our study site are similar to those reported by Sapota, Balazy & Mirny (2014) in the Baltic Sea (personal observation P.E. Hirsch), therefore we estimated the number of nests / m^2 to be in the same range as shown in Sapota, Balazy & Mirny (2014).

Age. Due to a lack of age-dependent vital rates and the pronounced difficulty in the field to target specific age classes, we used stage-classes instead of age-classes. To estimate maximum age and age of first reproduction (see section *Reproduction*), aging with scales has been conducted with a subsample of 1015 fish following the methods described by Gruľa, Balážová, Copp & Kováč (2012). The maximum observed age for both females and males was 4 years.

Density. We estimated population densities in the most recent year at the most undisturbed site D, assuming that in this year the subpopulation would fluctuate around equilibrium, i.e. would have attained a stationary distribution. To estimate density, we used a Poisson catchability model to construct a likelihood function *L*, which we then numerically maximized to obtain an initial density estimate per site (see section *Removal effort* in S4) divided by the home ranges reported in Vélez-Espino, Koops & Balshine (2010). In addition, we compared our field study density data with data obtained by snorkelling upstream of the field site. We observed population densities ranging from 3-12 individuals / m^2, which is in accordance with our density estimate from the field study catch data.

Survival. Survival rates between sexes seem not to differ despite previous assumptions that males survive only one reproductive season (Lynch & Mensinger 2013; Vélez-Espino, Koops & Balshine 2010). The model’s two-sex structure still allows to adjust survival rates for males and females later on if needed, e.g. when a control strategy is able to target a specific sex. To establish the strength of density-dependence affecting larvae as well as adult survival, we first estimated adult density-dependence by using Velez-Espino’s data (Vélez-Espino, Koops & Balshine 2010), namely by fitting our exponential survival model to densities (their Fig. 2) and survival rates (their Fig. 3a log-transformed). We chose their lower density estimates, because our estimate of an equilibrium density value for adults (see section *Density* above) matched that range. Having estimated adult density-dependence and with our equilibrium estimate as a constraint, we then iteratively solved our model for larval density-dependent survival. See S6 for details on the 95% confidence interval.

Fig. S3.1 shows all these events during a modelled year. See S4 for removal and S9 for larval flow and adult dispersal.

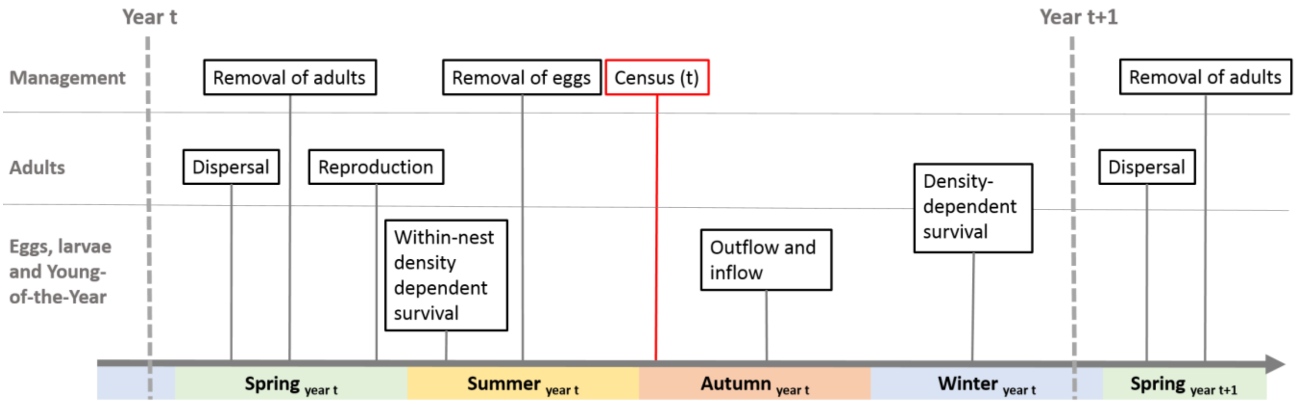

Figure S3.1: Schematic timeline showing the chronological order of all events during a modelled year in relation to the respective season. Census means the model’s iteration from the previous to the current year. Note that the order of the events is important, but not the exact dates. Adult dispersal and larval flow was only included in part of the simulations.

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Appendix S4: Population control parameter estimation and removal timing

Number of traps per m^2. The maximum effort in hours per square meter (hours / m^2) is defined by the maximum number of traps that can be installed in a given habitat without having overlapping catch areas. Thus, the maximum number of minnow traps and spawning traps and consequently the maximum effort depend on the assumptions on home ranges of round goby (Vélez-Espino, Koops & Balshine 2010). We tested whether a control strategy involving a high number of minnow traps at the same site controlled daily resulted in the same mean catch per unit effort (CPUE) as our other field data. We installed 4 minnow traps at site C in March 2016 and removed fish daily. This additional sampling revealed that mean CPUE is, given the population densities in our field site, not influenced by the number of traps per site (distance between traps approx. 5 m) and by the sampling interval (sampling daily vs. twice weekly, Fig. S4.1). To assess the catch area of a spawning trap, we calculated how many males from how many square meters must have been present to be able to occupy the number of full nests we found in the spawning traps.

In addition, bait presence or absence had minimal influence on the trap efficiency in our system. However, in other systems, different forms of bait (e.g. chicken or beef liver, personal communication M.S. Kornis) can increase catch efficiency of traps.

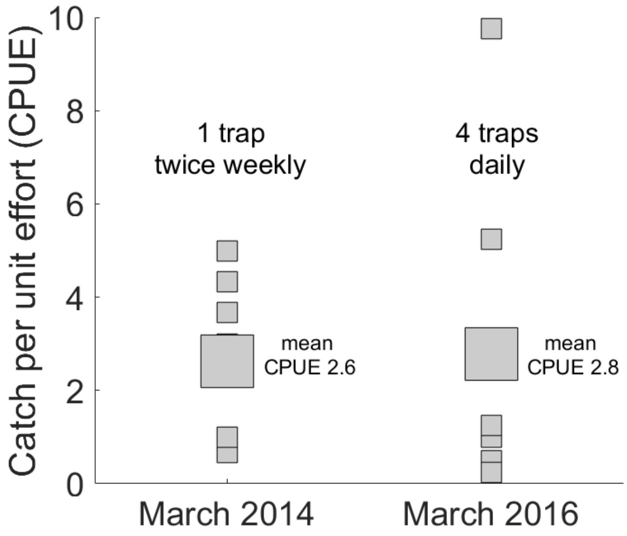

Figure S4.1: Traps for population control can be installed in close proximity and fish can be removed daily. Mean catch per unit effort (CPUE) at site C in March 2014 (sampling twice weekly with one minnow trap) and March 2016 (sampling daily with four minnow traps) is not significantly different (two-sample t-test, $p = 0.905$).

Removal effort. Based on our field experience, we set the time needed to control one minnow trap and remove adults or to control one spawning trap and remove eggs to 12 minutes. We set the maximum control effort (respecting the maximum number of traps / m^2, see section *Number of traps per m^2* above) such that minnow traps are controlled daily and spawning traps are controlled weekly. We report the effort in hours rather than monetary values, because wages differ between countries. To calculate the total number of hours, we defined the control window according to the life history of round goby. Adults are removed before the spawning season in February and March; eggs are removed during the spawning season in April, May, June, July and August (see section *Within year allocation of population control resources*). For each month, we assumed an average of 22 working days (excluding weekends). Each working day consists of 8 working hours.

To calculate the adults’ proportion removed, we used a Poisson catchability model to construct a likelihood function L, which we then numerically maximized to obtain an initial density estimate per site and a catchability coefficient ε_a per site (Seber 1982): $L(N,\varepsilon_a|n_i,E_i)=\prod_{i=1}^{k}[(N-x_i);n_i](1-\exp(-\varepsilon_a E_i))^{n_i}(\exp(-\varepsilon_a E_i))^{N-x_i-n_i}$, where the term in square brackets is the binomial coefficient, k the total number of removal events (k = 9), and x_i the cumulative number of animals removed. We used effort data (E_i) and numbers (densities) of animals removed (n_i) in every time step i, collected for site D in the years 2014 and 2015 (parameters in Table 1). Thus, the proportion of adults to be removed is $p=1-\exp(-\varepsilon_a E)$. Further, we inferred a 95% confidence interval (CI) for ε_a by means of a likelihood ratio test.

To calculate the proportion of eggs removed we had to resort to a different method, lacking appropriate data for a likelihood approach. Here, given our maximum effort applied for our study population to remove eggs, we stochastically simulated un-disturbed population trajectories and calculated the sought proportion as the number of eggs found in the field study divided by the number of eggs at adult equilibrium (Table 1). To calculate the latter, we proceeded as follows. First, we fit the function $f(A)=A\exp(a_0+a_1A)$ to simulated data, where A is adult density and a_0 and a_1 are parameters to be estimated. This function summarises our hypothesis that reproduction success increases with adult density; however, at intermediate densities, reproduction success starts decreasing because of the limited number of nests (see section *Nests* in S3). After fitting, we multiplied this function by A to calculate the total number of eggs as a function of density. For eggs, too, we assumed a Poisson catchability model, with a different catchability coefficient ε_e and maximum effort compared to adults (see above). We inferred a 95% CI for the (mean) proportion of eggs removed using a beta distribution, given the above mentioned sample mean and variance.

Within year allocation of population control resources. Removing adult stage classes is included in our model as $(1-p_f)$ and $(1-p_m)$ in eq. (1), where p_i (*i* = females, males) is the proportion removed. We assume that natural density-dependent mortality in round goby populations occurs predominantly during winter (Houston, Rooke, Brownscombe & Fox 2014). Further, assuming no difference in control costs per adult before and after natural mortality, we compare the following two equations: $h_1^a(x_a,p_a) = x_a(1-p_a)s_a e^{-\gamma_a x_a(1-p_a)} - x_a$, and $h_2^a(x_a,p_a) = x_a(1-p_a)s_a e^{-\gamma_a x_a} - x_a$. Thus, in both cases we are interested in the difference between an adult stage’s abundance before and after natural mortality, with removal introduced at two different points in time. As can be easily seen by reducing the equations, adult round goby should be removed – in terms of effectiveness – after density-dependent winter mortality and, here not specifically analysed, before reproduction. Note that if assuming natural and removal mortality would act simultaneously (i.e. solving an ordinary differential equation) would generate intermediate results between the above-mentioned temporal extremes.

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Appendix S5: Perturbation analysis of dynamical population model

As a starting point for implementing population control of an invasive species, a perturbation analysis can generate useful insights with regard to efficient control options. Calculating sensitivities and/or elasticities allows gauging the effect that a (small) change in parameter values has on a dependent variable. The most often studied dependent variable is the multiplicative growth rate (λ_1).

The dynamical model given by eq. 1 in the main text includes negative density-dependence, and thus for a population at carrying capacity – where the multiplicative growth rate by definition is unity – it makes more sense to ask how (small) changes in parameter values affect equilibrium densities. To this end, we followed the approach presented by Caswell (2009), and for the sensitivities of equilibrium densities to (small) changes in parameters we calculated sensitivities ($\mathrm{d}\hat{\mathbf{x}}/\mathrm{d}\boldsymbol{\theta}^T$) using eq. S5.1:

$$\frac{\mathrm{d}\hat{\mathbf{x}}}{\mathrm{d}\boldsymbol{\theta}^T} = \left(\mathbf{I}_{\mathrm{s}} - \mathbf{A} - (\hat{\mathbf{x}}^{\mathrm{T}} \otimes \mathbf{I}_{\mathrm{s}})\frac{\partial \mathrm{vec}\mathbf{A}}{\partial \mathbf{x}^{\mathrm{T}}}\right)^{-1} (\hat{\mathbf{x}}^{\mathrm{T}} \otimes \mathbf{I}_{\mathrm{s}})\frac{\partial \mathrm{vec}\mathbf{A}}{\partial \boldsymbol{\theta}^{\mathrm{T}}} \qquad \text{eq. S5.1}$$

where $^{\mathrm{T}}$ denotes the transpose, ⊗ denotes the Kronecker product, matrix **I** is an identity matrix, and matrix **A** is related to eq. 1, so that $\mathbf{x}_{t+1} = \mathbf{A}\mathbf{x}_t$. The equilibrium densities, $\hat{\mathbf{x}}$, are calculated using eq. 1 in the main text. The parameters included in the analysis, $\boldsymbol{\theta}$, are only female removal, male removal and egg removal, since we had no possibility of directly influencing fecundity or parameter κ, i.e. the strength of within-nest density-dependence. For more details, please refer to Caswell (2009), especially his equation no. 18. The results, i.e. sensitivity values, are shown in Fig. S5.1. By using these values, one can ask: How do equilibrium densities change (figure legend) if the analysed parameters are slightly changed, i.e. are in-/decreased by a small amount? The starting values for the removal parameters are zero. To see how equilibrium densities change in response to small parameter changes, say from 0 to 10% removal, one would multiply the sensitivity values (bar diagrams) associated with the analysed parameter, e.g. female removal, by 0.1. This multiplication leads to the change in density of the respective stage (eggs, females, or males).

We highlight three insights gained by this analysis. First, introducing female removal has a positive effect on male densities, and introducing male removal has a positive effect on female densities. These effects are also reproduced by simulations (see Fig. S8.2), including the asymmetric effect (compare the magnitude of density increases). Second, female removal is much more effective in controlling egg densities than egg removal itself; see also yearly control effort in Fig. 4 in the main text. Third, introducing egg removal has a positive effect on adult densities (see also Fig. S8.2).

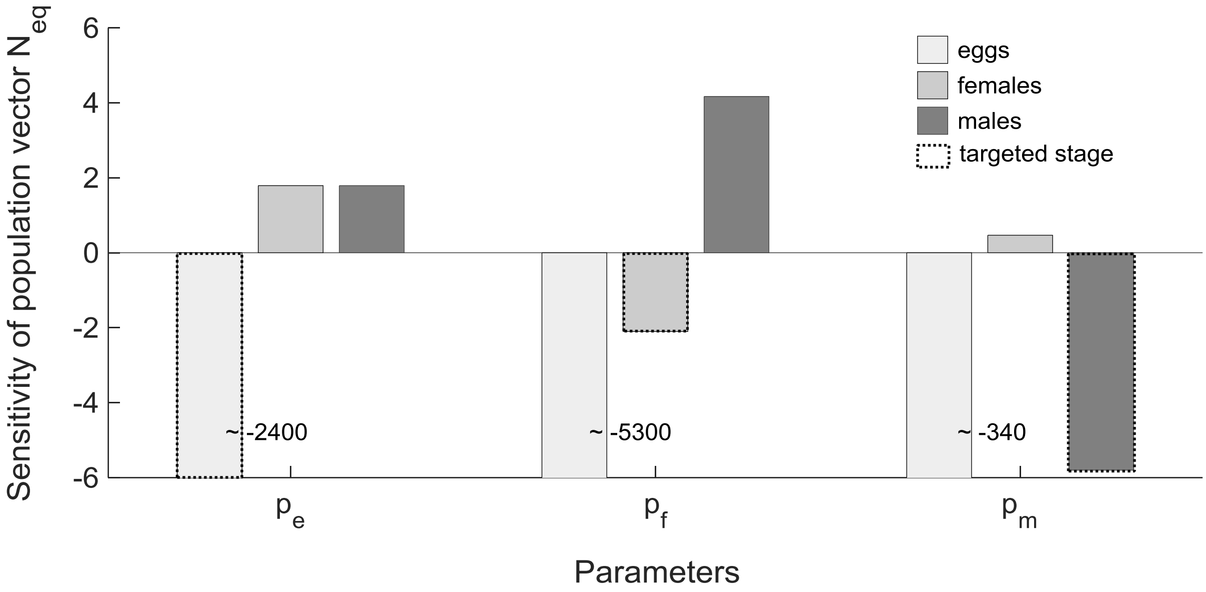

Figure S5.1: Results of sensitivity analysis for a round goby population at equilibrium (i.e. at carrying capacity *K*). The starting values for the removal parameters (p_e, p_f, p_m) are zero. To see how equilibrium densities change in response to small parameter changes, say from 0 to 10% removal, one would multiply the sensitivity values (y-axis) associated with the analysed parameter, e.g. female removal, by 0.1. This multiplication leads to the change in density of the respective stage (eggs, females, or males). Sensitivity values of egg densities are reported next to the respective bars because they are too low to show on y-axis. Targeted stage is stated in x-axis and marked with a frame (**---**).

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Appendix S6: Implementation details for stochastic simulations of population control

To evaluate eradication success, we stochastically simulated managed population trajectories. For this purpose, we simulated fecundity using a lognormal distribution, and survival rates were implemented to follow a beta distribution (e.g., Morris & Doak 2002). The variances were calculated using the respective coefficients of variation (CV): For the number of eggs per female and year, the CV was inferred from data of the study population (see section *Fecundity* in S3); for survival rates, lacking appropriate data to estimate it, we chose CV = 0.2. Given the mean survival rates reported in Table 1, this CV allowed for a substantial variation in survival. The lower 95% confidence interval (CI) bound of adult survival was 0.3673, the upper 95% CI bound led to 0.8474. In addition, we also tested CV = 0.1 and CV = 0.3 (results not shown); however, such a CV would be unrealistic, because the lower and upper bounds are already quite low and high, respectively. Further, vital rates were “sign-correlated”: a good year for survival would also be a good year for reproduction.

We implemented removal as a binomial process with time-/sex-/stage-dependent densities and probabilities. We ran every grid-based removal combination 300 times and calculated means of interesting measures (success rates, years needed, sex-dependent densities, amongst others). We set the extinction threshold density to be 10^{-6} females or males / m^2. This density closely matched the analytically derived respective extinction boundary value (see sup. information S7 below, including Fig. S7.1). Finally, to start simulations we emulated either a newly established population or a population at carrying capacity. For the former case, we also introduced a detection threshold (adult density 0.1 fish / m^2), at which population control starts; below the threshold, managers would not be aware of the presence of round goby. Simulations were performed in MATLAB R2015b (The MathWorks Inc. 2015).

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Appendix S7: Local stability analysis of a reduced dynamical model

To analytically derive the removal-induced extinction boundary mentioned in the methods section in the main text, we simplified our model as follows. We assumed that males and females have very similar adult survival probabilities (Table 1). Further, since batch proportions are rather similar (Table 1), we set all proportions $\alpha = 1/3$, and we assumed that all females reproduce, i.e. $\varrho = 1$. Finally, we focused on the case that removal is not sex-specific, i.e., the proportion of females and males removed are equal (see main text). This allowed us to reduce the original model to the following one, now only explicitly considering eggs and females:

$$\begin{bmatrix} x_e \\ x_f \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 \\ \sigma_e(\boldsymbol{x_e}) & s_a(\boldsymbol{x_f}) \end{bmatrix}_t \begin{bmatrix} x_e \\ x_f \end{bmatrix}_t \begin{bmatrix} 1 \\ (1-p_f) \end{bmatrix} + \begin{bmatrix} (1-p_e)g(\boldsymbol{x}, \boldsymbol{p_f}) \\ 0 \end{bmatrix}_t \qquad \text{eq. S7.1}$$

Since we assumed a sex ratio $\theta = 0.5$, we scaled s_e, so that $\sigma_e = s_e\theta$. The density-dependent juvenile survival function, $\sigma_e(\boldsymbol{x_e})$, is as defined in the main text. For adult females, survival depends on all adults, i.e. $s_a(\boldsymbol{x_a}) = s_a \mathrm{e}^{-\gamma_a(2x_f)}$. The reproduction function is as for the original model, except that now we define $x_m^{sp} = s_a \mathrm{e}^{-\gamma_a(2x_f)} x_f$ (before removal and reproduction).

Removal-induced extinction boundary

Instead of focusing on the biologically feasible equilibrium, given the transcendental equations we instead analysed the origin as equilibrium. Here, we were interested in parameter combinations, i.e. proportions removed, where the origin becomes a stable equilibrium. Thus, a population in the origin’s vicinity would be attracted to it and be doomed. As presented in the main text, the reproduction function contains two minimum functions, namely $N = \min(\eta, x_m^{sp})c$ and $\phi_i = \min(1, N/(\alpha_i E))$, where *i* designates the respective batch. Since here we were interested in the system’s behaviour near the origin, we set $N = x_m^{sp} c$. Further, although near the origin one could set $\phi = 1$, given the high reproductive per capita effort we set $\phi_i = N/(\alpha_i E)$; if all batch proportions are equal, then $\phi = 3x_m^{sp} c/(x_f^{sp} F)$. Finally, the original reproduction function $x_e(t+1) = E\sum_{i=1}^{3} \alpha_i \phi_i \psi_i$ can be simplified to become $x_e(t+1) = 3cx_m^{sp} \exp(-(c/\kappa)^2)$; if eggs are removed, the right-hand side of the latter equation is multiplied by $(1 - p_e)$.

The Jacobian matrix, evaluated at the origin, is given by eq. S7.2:

$$J_{\hat{x}(0,0)} = \begin{bmatrix} 0 & 3cs_a e^{-(c/\kappa)^2}(1-p_e)(1-p_f) \\ \sigma_e(1-p_f) & s_a(1-p_f) \end{bmatrix} \qquad \text{eq. S7.2}$$

For a 2 by 2 matrix, the equilibrium's stability can be conveniently inferred using the Jury criteria instead of calculating the eigenvalues of $J_{\hat{x}}$. The three Jury criteria can be summarised as $|\tau| < 1 + \Delta < 2$, where τ is the trace and Δ the determinant of $J_{\hat{x}}$, respectively. For eq. S7.2 we have $\tau = s_a(1-p_f)$ and $\Delta = -3c\sigma_e s_a e^{-(c/\kappa)^2}(1-p_e)(1-p_f)^2$. The second inequality in the above stated, summarised Jury criteria in our case is always true $(\Delta \leq 0)$. Further, $\tau \geq 0$ and the equilibrium's stability can be established using the inequality $\tau < 1 + \Delta$. Since we are interested in a removal-induced extinction boundary, we calculate the latter as $0 = 1 + \Delta - \tau$ and solve this equation for $p_e = f(p_f)$:

$$p_e = 1 + \frac{s_a(1-p_f) - 1}{3c\sigma_e s_a e^{-(c/\kappa)^2}(1-p_f)^2} \qquad \text{eq. S7.3}$$

The extinction boundary given by eq. S7.3 is depicted in Fig. S7.1. This figure shows simulated adult and egg densities (contour plot) as a function of removal proportions (axes). Note that for low adult, but high egg removal, the extinction boundary slightly overstates the proportions needed. This is because we used one specific function for the reproduction function to derive eq. S7.3 (see above). In the main text, this extinction boundary is shown in Fig. 4 together with removal-related control costs.

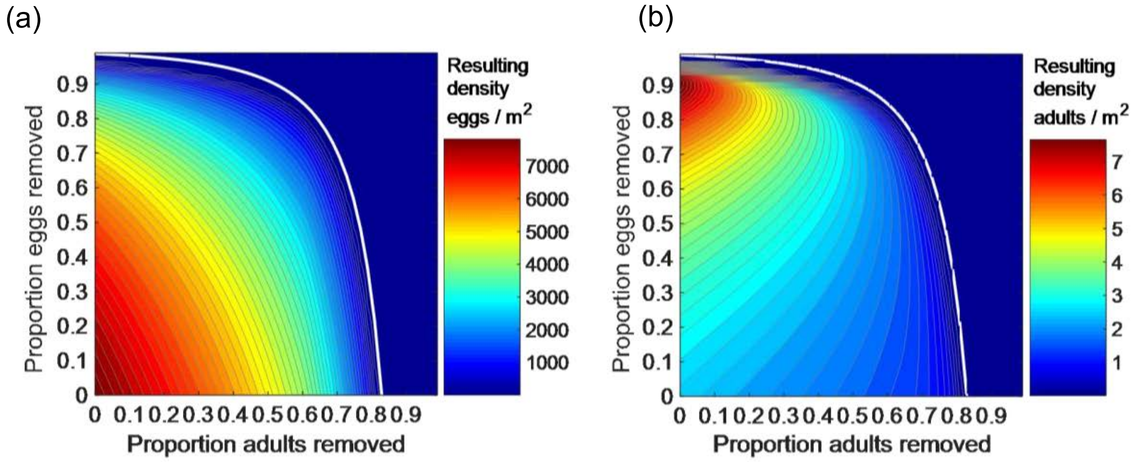

Figure S7.1: Extinction boundary (white line) and simulated egg and adult densities (contour plot). The extinction boundary corresponds to eq. S7.3. All combinations on the right side lead to extinction. Grey lines are isoclines. **(a)** Contour plot showing egg densities as a function of egg (y-axis) and adult (x-axis) removal. Red indicates high egg densities. **(b)** Contour plot showing adult densities as a function of egg (y-axis) and adult (x-axis) removal. Red indicates high adult densities.

Appendix S8: Insights from the full model

We now turn to the full model, given by eq. 1 in the main text. Instead of providing a detailed analysis, we present some salient features that may be of interest when managing a round goby population. Based on simulations we conjectured that the system has two equilibria: one is the origin, and the second is a non-trivial biologically feasible equilibrium. We first focused on the stability of the origin. In contrast to the reduced model, for the reproduction function we considered the cases $\phi = 3x_m^{sp}c/\left(x_f^{sp}F\right)$ as before (simplified model), and additionally $\phi = 1$. To infer the origin’s stability, we numerically calculated the dominant eigenvalues (λ_1) of $J_{\hat{n}(0,0)}$ – for the two cases of ϕ – as a function of the proportion of eggs, females, and males removed. Both dominant eigenvalues combined define a removal-induced extinction surface, where $|\lambda_1| = 1$ (Fig. S8.1a).

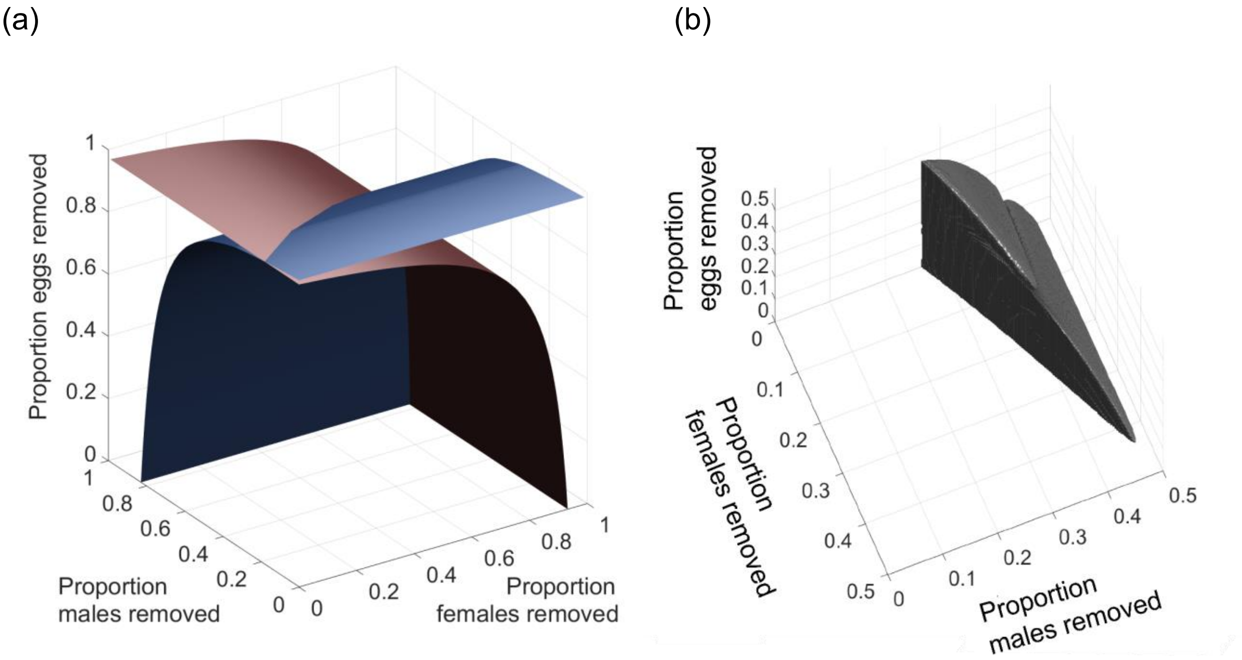

Figure S8.1: Some dynamical aspects of the full model. (a) The two different surfaces correspond to two different eigenvalues (see text S8 for more details): together they form an extinction surface, where the respective smaller value of the two eigenvalue surfaces is determining. **(b)** Connected subspace for the full model, where irregular oscillations are induced. Note the truncated axes (0.5 instead of 1.0)

Within the parameter space leading to a viable population (Fig. S8.1a), a connected subspace can be found, whose parameter combinations lead to irregular oscillations (Fig. S8.1b); for all other parameter combinations, the system attains a stable point equilibrium. We did not analyse these oscillations further. Most probably, they are quasi-periodic oscillations.

Finally, Fig. S8.2 shows simulated deterministic adult equilibrium densities when varying female and male removal. As expected after the perturbation analysis (Fig. S5.1), i.) over a certain parameter range, removing females has a positive effect on overall density (due to an increased male equilibrium density; not shown separately), and removing males has a positive effect on overall density (due to an increased female equilibrium density; not shown separately); ii.) egg removal has a positive effect on adult density (compare the origin, i.e. no adult removal, between Fig. S8.2a and b); nonetheless, to be careful, the perturbation analysis asked about density effects due to small parameter changes, here (between Fig. S8.2a and b) we change egg removal from no removal to removal at maximum effort.

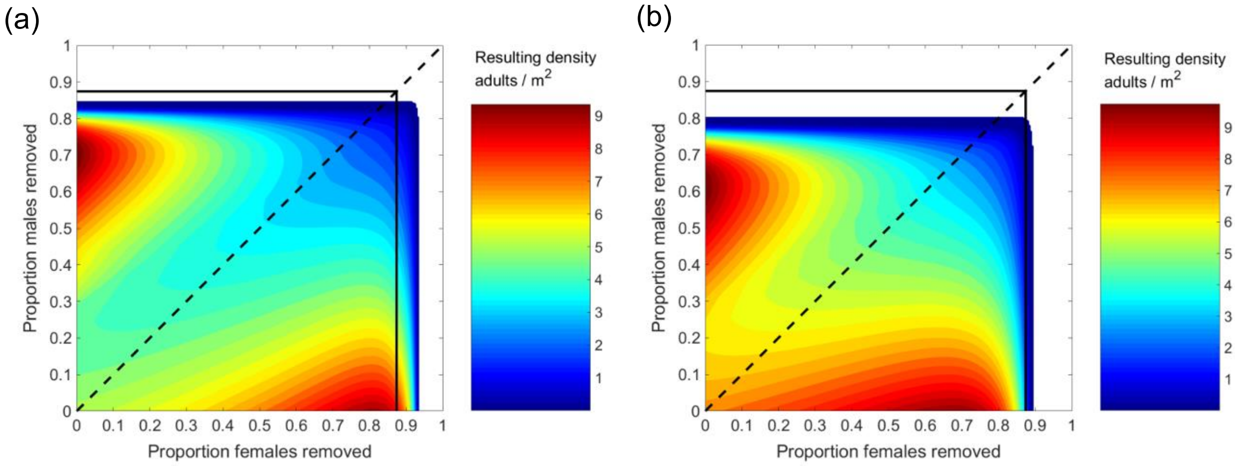

Figure S8.2: Deterministic adult equilibrium densities as a function of female, male, and egg removal. Adult equilibrium densities when only adults are removed **(a)** and when adults and eggs are removed **(b)**. Red indicates high adult densities, blue indicates low densities. The white area indicates extinction of the population. For both (a) and (b), removal proportions of adults are varied (x- and y-axis), whereas egg removal is zero in (a) and set by the maximum effort in (b). The intersection of solid black lines (—) with the diagonal dashed line (- - -) gives the removal proportions based on the effort applied for our study population.

Appendix S9: Flow and dispersal

Larval in-/outflow

To better understand the effect of in- or outflowing larvae into the system, we allowed a certain number (density) of larvae to enter or leave the system before density-dependent natural mortality occurs; see time-line in Fig. S3.1. To produce the bifurcation analysis results presented in Fig. 6 in the main text, we numerically solved the simplified model eq. S7.1 for equilibrium densities and calculated equilibrium density changes (number of equilibria and respective densities) as a function of changing net flow densities and changing removal proportions. Since removing only adults is more efficient (see main text), we only introduced and varied adult removal, i.e. setting p_e = 0 in eq. S7.1. Further, we only show the bifurcation results with respect to adult equilibrium densities because egg equilibrium densities showed a qualitatively very similar pattern.

Adult dispersal

Round goby seem to be characterised by two different dispersal abilities (or strategies), where one part of a population tends to travel much bigger distances per year than the remaining, more stationary part (Lynch & Mensinger 2012). By assuming a normally distributed dispersal kernel (symmetric about the origin), two different dispersal strategies could be modelled using two different kernels. The combination of these, i.e., a finite mixture model, produces a leptokurtic symmetric distribution about the origin. This tendency has been described for several fish species (Radinger & Wolter 2014), including round goby (Lynch & Mensinger 2012). Note that the symmetry assumption about the origin is justified for round goby since adults are actively swimming and thus less affected by river flow below a certain flow velocity (Tierney, Kasurak, Zielinski & Higgs 2011). Since the binning distances used in Lynch & Mensinger (2012) exceeded the average dispersal distance for the stationary population part, we were not able to meaningfully fit a finite mixture model to these data. Instead, we continued working with parameter estimates from a closely related taxonomic family (*Cottidae*, Table 2 in Radinger & Wolter 2014); see Fig. S9.1a for the mentioned parameters and the literature-based leptokurtic distribution.

Dispersal is known to potentially be density-dependent (Brownscombe & Fox 2012; Ray & Corkum 2001). We had no round goby-related data, nor did we find any in the literature. Thus, we tested several density-(in)dependent functions, expressing the density-(in)dependent proportion of a population that disperses per unit time. All functions include a maximum proportion μ. Given the (idealised) split between stationary and mobile population parts, we set the mobile proportion to represent μ. Thus, starting from carrying capacity and lowering densities, the mobile proportion diminishes in favour of the stationary part in a density-dependent way. Apart from a density-independent function representing a biologically unrealistic null-model with constant dispersal $f(N) = \mu$, we implemented three density-dependent dispersal functions: (i) a linear function $f(N) = \mu N$, fixing the function’s maximum value to μ for densities higher than carrying capacity (a ceiling model); (ii) a sigmoid function $f(N) = \mu N^{\delta}/(\varphi^{\delta} + N^{\delta})$, and we chose φ so that μ would be half its value when half of carrying capacity is reached; (iii) a power function (Matthysen 2005) $f(N) = \mu(N/K)^{\Delta}$, fixing the function’s maximum value to μ for densities higher than carrying capacity (a ceiling model). The graphical depiction of these functions can be found in Fig. S9.1b.

Finally, we combined both aspects of dispersing adults to gauge the yearly (natural) spreading potential. According to Brownscombe & Fox (2012), dispersal most likely takes place before or after the reproductive season. Thus, we were interested in the yearly maximum distance travelled by a certain number of adults (sex-ratio 1:1), so that after settling and surviving winter, one female and one male would be alive to reproduce next spring. To that end, given a certain local density in the controlled population, the density-(in)dependent dispersal functions, and the finite mixture probability density function, we used an inverse cumulative distribution function to calculate the maximum distance. For the simulations’ local dynamics, on the other hand, we needed a way of deciding whether an adult, after traveling a certain distance would still be part of the controlled population or would have left the system. To this end, we first “transformed” the total habitat into a circle, so that the distance between habitat centre and periphery is uniformly distributed. Then, using the approach just described for calculating the maximum distance, we calculated what part – if any – of the dispersing individuals would be kept in the population because their idealised distance would fall within the population’s habitat range.

Adults dispersing *into* the controlled population were not considered in the model, because we assumed the case of a core or founder population with no previous invasion more upstream or downstream where adults could migrate from. In addition, it is most plausible that round goby is introduced in the larval stage by e.g. ballast water (Wonham, Carlton, Ruiz & Smith 2000). Density-dependent adult dispersal *out* of the controlled population seems to have minimal influence on eradication success and average years needed for eradication, whereas the biologically unrealistic constant density-independent dispersal leads to a higher success rate and less years needed (Fig. S9.2).

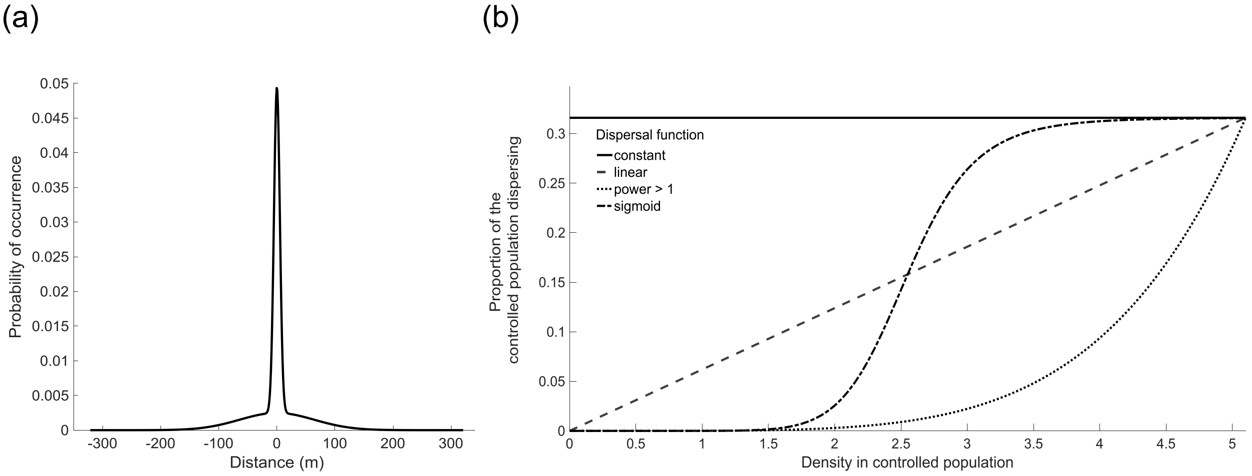

Figure S9.1: Dispersal distribution and different functions for density-dependent dispersal. (a) Leptokurtic distribution of distance using parameter values from Radinger & Wolter (2014). **(b)** Proportions of the controlled population dispersing in relation to density for different dispersal functions (Matthysen 2005).

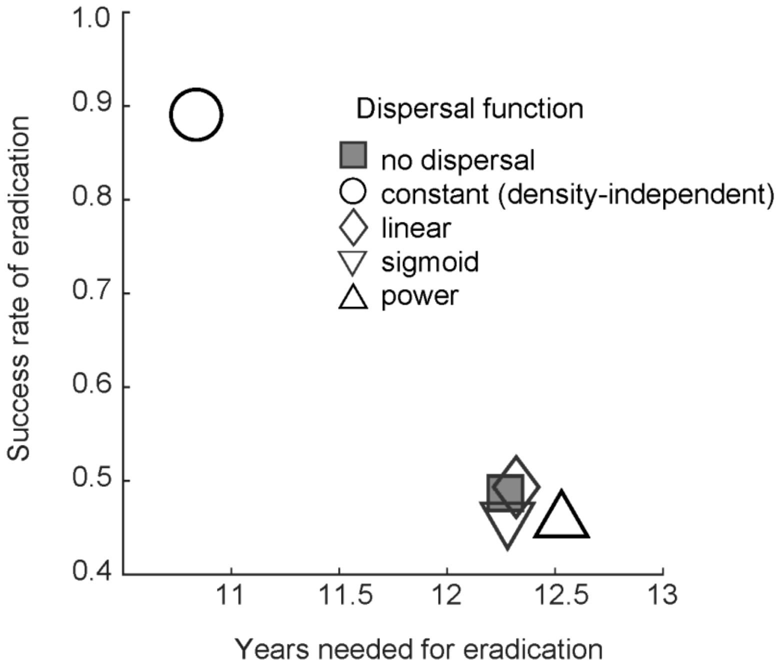

Figure S9.2: Effect of adult dispersal on success rate of eradication and years needed for eradication. The biologically unrealistic constant density-independent dispersal leads to a higher success rate of eradication and less years needed for eradication, whereas density-dependent dispersal seems to have minimal influence on eradication success and average years needed for eradication

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CONCLUSIONS

Non-native invasive gobies have an impact on ecosystems and biodiversity. However, the exact dimension of their impact in a given habitat can only be really known after they are established. This dilemma may stand in the way of an early preventive management, thus leaving no other option than expensive population control or adaptation.

A transdisciplinary process where scientists and decision makers collaborate on an equal footing has the potential to overcome this dilemma. By openly assessing priorities and contributions of all involved parties, neither party waits for actions the other cannot and will not deliver – while, in the meantime, the invader establishes and spreads unhindered.

The High Rhine below Rheinfelden may be the wrong place to install costly population control measures such as removing adult gobies, since this population is already established and propagule inflow can hardly be stopped. This highlights 1.) the importance of monitoring invasion hotspots, because population control measures need the least effort when management starts immediately after detecting a new population, and 2.) the importance of actions that prevent secondary dispersal such as informing anglers and cleaning boats to protect uninvaded water bodies that serve as spawning and rearing grounds for e.g. brown trout *Salmo trutta* or nase *Chondrostoma nasus*.

To reach this ambitious goal, scientists and decision makers from various organisations and authorities need to work together. Promising ventures such as a pilot project to clean boats, a lake declared as “neobiota-free zone” (Canton of Zurich, Department of Construction 2016) and a national “goby strategy” have been started by several cantons. Most of these projects are guided by scientific advice. Additionally, all Ponto-Caspian gobiid species are proposed to be added to Annex 3 of the Federal Law on Fisheries (Bundesamt für Umwelt BAFU 2016), making it illegal to spread and release gobies. Additionally, cantons are obliged to undertake management measures to prevent further spread. I conclude my thesis with an outlook on a Goby Action Plan summarising key findings of my thesis and providing scientific recommendations on goby management that might stimulate further policies.

OUTLOOK

Goby Action Plan

The Goby Action Plan aims at informing decision makers and outlines further research needs. The action plan (Figure 3, Table 1) is structured in four goals: preventing further passive and active dispersal, enabling rapid reaction by monitoring and early detection, controlling populations to minimise impacts and slow the spread, and, as an alternative solution, adapting to invasive species. Each goal contains several measures, their expected costs, further research needs and open questions.

Preventing further spread should be given the highest priority and be accompanied by monitoring of invasion hotspots in un-invaded habitats to enable early detection. Population control is expensive and should only be attempted immediately after detecting the population and only in habitats where inflow can be stopped. Adapting to invasive species may be an alternative approach and a last resort when prevention and control failed.

The recommendations in the action plan rest on current scientific knowledge and I refer to the papers in this thesis that either contain results or provide stimulations for further thoughts in their respective discussion parts. To successfully tackle the challenge of non-native invasive gobies, a combination of methods is required and all relevant players need to work together in a transdisciplinary process. Ideally, the process also includes the management of other aquatic invasive species.

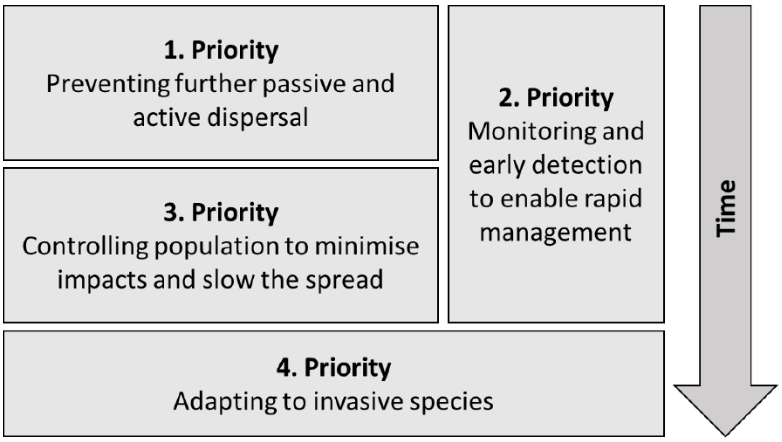

Figure 3: Schematic outline and recommended priorities of the four goals detailed in the Goby Action Plan in Table 1.

Table 1: Goby Action Plan

Goal: Preventing further passive and active dispersal

Measure	**Details**	**Expected costs** (research not included)	**Research needs and open questions**
Targeting boats as vectors	Boats that are transported from invaded water bodies to un-invaded water bodies get cleaned (“check – clean – dry”)	Low to moderate material costs: station with e.g. high-pressure cleaner, dossier for information campaign Moderate personnel costs: installation, control and maintenance, distribution and dissemination of information to relevant channels	How can knowledge be co-produced with relevant stakeholders? (**Paper I**) How can knowledge be transferred to relevant stakeholders? (**Paper I** and **Paper IV**) How is the relative importance of different dispersal vectors? (**Paper III** and **Paper IV**) How resistant are propagules such as goby eggs and what does this imply for cleaning techniques? (**Paper IV**) What kind of technical structures and incentive structures can be installed to reach compliance? What are legal frameworks?
Targeting anglers as vectors	Anglers do not move gobies and other invasive fish species between water bodies	Low material costs: dossier for information campaign Low personnel costs: distribution and dissemination of information to relevant channels	
Targeting other relevant vectors such aquarists, divers and other water sport enthusiasts	Aquarists do not import and release gobies and other invasive fish species Gear that is transported from invaded water bodies to un-invaded water bodies is cleaned (“check – clean – dry”)		
Installing dispersal barriers	Valuable streams or water bodies are protected by dispersal barriers	Low to moderate material costs: grid, ramp or other structures Low personnel costs: installation and maintenance	What are gobies’ swimming abilities under different flow velocities and riverbed structures? How can such a barrier be constructed? What are conflicting goals, e.g. dispersal of native species, and how can they be solved?

Goal: Monitoring and early detection to enable rapid management

Measure	**Details**	**Expected costs** (research not included)	**Research needs and open questions**
Monitoring with eDNA	Regular eDNA monitoring of invasion hotspots such as harbours to rapidly detect invasive gobies	Low material costs (assuming PCR machine is available): water sampler Low personnel costs: field sampling, lab analysis	Where are invasion hotspots? What are the best seasons, time intervals and environmental conditions for monitoring? What is the optimal allocation of resources to monitoring? What are next steps after a new invasive population has been detected? (**Paper V**)
Monitoring with traps, electrofishing, angling, snorkelling	Regular monitoring of invasion hotspots such as harbours to rapidly detect invasive gobies	Low material costs: traps, gear for electrofishing, angling, snorkelling Low to high personnel costs depending on intensity and regularity: controlling traps, conducting electrofishing, angling, snorkelling	
Monitoring of windows at fish ladders	Windows at relevant fish ladders at the range expansion edge are controlled for gobies, perhaps assisted by image recognition software	Low to moderate material costs: gear for sampling, software for image recognition Low to high personnel costs: monitoring, data analysis	What are the best seasons, time intervals and environmental conditions for monitoring? What are technical possibilities for image recognition software?
Monitoring involving anglers and the interested public	Anglers and the interested public participate voluntarily in monitoring activities (“citizen science”)	Low material costs: providing traps or other sampling gear as mentioned above, if needed Low personnel costs: instruction by experts	How can anglers and others be motivated to participate in monitoring? (**Paper I**) What kind of technical instruments, e.g. apps or websites, simplify data collection and reporting? What kind or parameters need to be reported and how reliable are these data sets?

Goal: Controlling populations to minimise impacts

Measure	**Details**	**Expected costs** (research not included)	**Research needs and open questions**
Eradication	Adults are removed with minnow traps, nets, electrofishing or by angling	Low material costs: traps, nets, electrofishing, angling gear Very high personnel costs: controlling traps daily before the reproductive season for at least several years	Where are sensitive areas like spawning grounds of native fishes? What are possibilities to make catch methods more efficient and how can effort be minimised? (**Paper V**) What are effects of removing non-native invasive gobies on native species, e.g. on predators adapted to this new prey? How can removed gobies be used, e.g. for human or animal consumption? (see below)
Containment	Adults are removed with minnow traps, nets, electrofishing or by angling	Low material costs: traps, nets, electrofishing, angling gear Very high personnel costs: controlling traps daily before the reproductive season for an indefinite time	What are the effects of density on dispersal? (**Paper V**) What are acceptable goby density thresholds to minimise impacts? (**Paper II**)
Restoration of aquatic habitats	Habitats are restored, which benefits native species such as predators that may naturally control invasive gobies	Moderate to high material costs: reconstruction of riverbanks and other habitats Moderate to high personnel costs: construction, monitoring	What are the causal relationships between restoration and abundance of native fish species? Which predators could naturally control gobies? (**Paper II**) What are the cascading effects on native species?

Goal: Adapting to invasive species			
Measure	**Details**	**Expected costs** (research not included)	**Research needs and open questions**
Use gobies for human consumption	Gobies are used as food or for other purposes	Low material costs: traps, nets, angling gear Low personnel costs: anglers fish gobies for own consumption If a market exists, costs and benefits should lead to an optimal allocation of resources	What are the risks for human consumption? What kind of products could be made of gobies? How is the market potential for goby products? What are legal frameworks? What kind of incentive structures exist and how can it be prevented that gobies are intentionally released?
Use gobies as pet food or as fish meal	Gobies are used as pet food or fish meal for aquaculture or animal farming	Low material costs: traps, nets, angling gear If a market exists, costs and benefits should lead to an optimal allocation of resources	How is the market potential for gobies as animal food item? What are legal frameworks? What kind of incentive structures exist and how can it be prevented that gobies are intentionally released?

ACKNOWLEDGEMENTS

Without you, my thesis would not exist. Thank you,
Patricia Holm for giving me this unique opportunity, for supporting me and pushing me,
Philipp Hirsch for inspiration and motivation – always!
Irene Adrian-Kalchhauser for teaching me how to teach (among *so many* other things),
Antonietta Di Giulio & **Rico Defila** for mind-boggling and mind-expanding discussions,
Claudio Bozzuto for endless patience and endless skype meetings.

I am grateful to the amazing **GruGru**, especially fellow PhD student **Roxane Muller** as well as current and former Master students, HiWis, visitors, collaborators and friends: **Sylvie Flämig, Catherine Cornaz, Kristína Hôrková, Ann-Kathrin Hess, Céline Mäder, Sandrine Straub, Vincent Somerville, Elisabeth Lutz, Nilgün Özdal, Michael Beister, Kristina Kraft, Giulia Pellizzato, Attila Rüegg, Hedwig Scharlipp, Hannes Weigt.**

I greatly acknowledge **fishers**, **workshop participants** and **funders** for supporting this important project.

Many thanks to the whole **MGU team**, especially sunshine **Ute Spitzer, Anneli Strobel, Camelia Chebbi, Thomas Mani, Corinne Ruesch, Heidi Schiffer** and **Nicole Seiler.**

Thank you **all** for sharing knowledge, stories, lunchbreaks, coffee, chocolate and popcorn, for helping in the lab and field, for feedback and advice.

Thank you **students** for challenging me with extravagant organisational wishes on excursions or with the most absurd papers in the "critical reading" colloquium, but also for rewarding me with much fun.

Thank you **Jost Borcherding** for reviewing my thesis. Meeting you at the goby meeting 2013 instantly made me feel welcome to the extended goby network!

Special thanks to **friends**, **family** and **Nina** – for everything.

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