The ecological niche of invasive gobies at the Lower Rhine in intra- and interspecific competitive and predatory interactions

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«Bei einem Fluss ist das Wasser das man berührt das letzte von dem was
vorübergeströmt ist und das erste von dem was kommt.
So ist es auch mit der Gegenwart.»

Leonardo da Vinci (1452 – 1519)

«Es gibt Menschen, die Fische fangen und solche, die nur das Wasser trüben.»

Chinesische Weisheit

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Inhaltsverzeichnis

Abbreviations and terms

0+	description of an age class, same as YOY, fishes that had hatched within that year
ANOVA	analysis of variance
ANCOVA	analysis of covariance
ISF	index of stomach fullness [%]
Nf	monkey goby *Neogobius fluviatilis*
Nm	round goby *Neogobius melanostomus*
Pk	bighead goby *Ponticola kessleri*
PPR	prey predator ratio
SD	standard deviation
SE	standard error
TL	total length [mm]
YOY	young of the year, fishes that had hatched within that year

Species list (species, English, German)

Aspius aspius	asp	Rapfen
Barbus barbus	barbel	Barbe
Neogobius fluviatilis	monkey goby	Flussgrundel
Neogobius melanostomus	round goby	Schwarzmaulgrundel
Perca fluviatilis	Eurasian perch	Flussbarsch
Ponticola kessleri	bighead goby	Kesslergrundel
Rutilus rutilus	roach	Rotauge
Sander lucioperca	pikeperch	Zander

Teilpublikationen

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Submitted manuscripts

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- Gertzen, S., Borcherding, J. (submitted). Measuring dietary competition from field data – Dietary competition between native and invasive juvenile fish species at the Lower Rhine (Germany). **Chapter IV**

Abstract

Biological invasions represent a fascinating process with potentially severe consequences, as the displacement of native species. Therefore, determining the impact on natives and the whole ecosystem is inevitable to protect the endemic biodiversity. At the Lower Rhine a special situation has arisen from three congeneric fish species of the family Gobiidae establishing populations with high densities in a strongly anthropogenic altered habitat, which is additionally limited in dietary resources. Mechanisms of niche separation for the three goby species could be shown on a spatial and temporal axis. Although high dietary overlaps were obtained between the three goby species, ontogenetic dietary shifts in combination with habitat shifts reduced levels of competition. Fine-tuned niche differentiation was also displayed in reproductive traits by temporal separation of spawning onset and intensity, as well as in drifting patterns. Drifting strategy differed within the three species not only to their temporal occurrence in the drift, but also regarding the sizes of drifting individuals. These mechanisms of niche partitioning were suggested to allow for the co-existence of the three Gobiidae and to enforce the impact on native species. The system seemed to have reached its capacities, as already decreasing densities of bighead goby and high levels of dietary competition indicate. Competitive and predatory interactions emerged between the single goby species, as well as with the native fish community. A temporal scaled bottom-up top-down system could be obtained for invasive gobies and two native Percidae. Native piscivores were forced into a dietary juvenile competitive bottleneck, while later on preying on gobies. Adaptation to this novel prey has just started, thus up to now detrimental effects of the competitive interactions prevail. Additionally, population development of the three invasive species is still in progress, revealing a highly dynamic system, where the next years will determine the outcome of this invasion.

Keywords: invasion * niche differentiation * reproduction * dispersal * competition * predation

Introduction

Biological invasions

Due to increasing global trade and human mediated alterations of transport networks, the amount of biological invasions is steadily increasing and the spread of non-native species has accelerated (Vitousek et al., 1996; Ricciardi and MacIsaac, 2000; Ricciardi, 2006; Banks et al., 2015). Invasion biology has gained a lot of attraction in the past decades, as it represents a global problem and additionally affects several disciplines besides ecology (Vitousek et al., 1996; Simberloff et al., 2013). Estimates for the economic costs are missing for most regions or are too hard to predict (Born et al., 2005; Lovell et al., 2006), but may reach as colossal scales as $120 billion per year just in the United States (Pimentel et al., 2005). High importance for this topic also arises by the fact that even human health can be concerned, as seen for the invasion of the Asian tiger mosquito, a vector for dengue fever (Medley, 2010). Although such severe consequences do not emerge with every invasion process, ecological impacts might be as detrimental as they could lead to the displacement or extinction of endemic species (e.g., Rodda et al., 1997; Mooney and Cleland, 2001).

To find ecological generalities for invaders or their traits, and thus being able to predict invasiveness of species before introduction is a great aim for the flora as well as for the fauna (Ricciardi and Rasmussen, 1998; Kolar and Lodge, 2001; Cadotte et al., 2006). Although there seems to be no typical set of characteristics being valid for all taxa, high adaptability was of importance for successful colonizers (summarized in Sakai et al., 2001). Particularly plasticity in life-history traits appeared to have promotional effects (Buczkowski, 2010; Davidson et al., 2011), as well as a broad tolerance towards environmental factors and pollution, which seems to be especially true for aquatic invasions (Bij de Vaate et al., 2002; Karatayev et al., 2009).

In the same way vulnerability of habitats was examined, leading to the conclusion that anthropogenic habitat degradations facilitate invasion success (Byers, 2002; Didham et al., 2007). Indeed, for several successful invasions previous ecosystem disruptions, going along with the decline of native species biodiversity, seemed to enable population establishment of the invader (Bauer, 2012).

In the early phase after introduction, quite often a lag phase concerning population growth of the invader can be obtained. Such lag times might be due to evolutionary processes and the adaptation to the new environmental conditions experienced (Sakai et al., 2001). Afterwards, growth rate of the invasive population can be very rapid, due to the lack of co-evolved predators, parasites or diseases (Colautti et al., 2004). Once the introduced species has established a self-sustaining population, impact of invasive species might increase, acting directly via competition or predation (see sections below), but might also result in indirect effects, as ecosystem transformations (Simberloff et al., 2013), affecting species on several trophic levels and leading to whole food web disruptions (Vander Zanden et al., 1999; Roemer et al., 2002; Geiger et al., 2005).

However, due to such interactions with natives several cases of introductions where invaders have become hyper abundant resulted later on in decreased densities displaying relatively stable states (e.g., Moore et al., 2012). This so called “boom and bust” phenomenon (Williamson and Fitter, 1996) acts through depleted or adapted prey populations, exploited resources, or the increase/adaptation of enemies (predators and pathogens) and might even be reversed ending up in a cycle of boom and bust (Salonen et al., 2007). Therefore invasions are highly dynamic processes affecting the whole ecosystem on huge spatial as well as temporal axes.

Niche differentiation

As stated in the competitive exclusion principle “complete competitors cannot coexist” (Hardin, 1960). Thus, a high niche overlap will either lead to the exclusion of one species, or to resource partitioning going along with niche separation. Defining the limits of such niche separations at which species can stably coexist is the major aim and challenge of studies dealing with resource partitioning (Schoener, 1974).

Niche differentiation and resource partitioning attend a special position in invasion biology. An introduced species may occupy a present vacant niche, resulting in co-existence with native species without any niche restraints being required (Cornell and Lawton, 1992). However, in most cases, invaders overlap at least to some extent in resource use with natives and are often shown to be the superior competitor (Sakai et al., 2001). Thereby, increased levels of niche overlap do not have to result in competition followed by resource partitioning mandatorily. If shared resources are not limited, species can co-exist without shrinking their niche width (Colwell and Futuyma, 1971). Admittedly, during invasion processes several invading species reach high densities resulting in strongly exploited resources (e.g., Holway, 1999; Carlsson et al., 2004) or high levels of interference (e.g., Hansen et al., 2002). This might be especially severe, if two or more invasive species sharing the same resources try to establish in the new habitat simultaneously. For co-existence, niche separation has to arise not only between invasive and native species, but also within the group of invasive species.

An interesting case was observed in the UK, where an invasive mink had established at a point of time when abundances of two native mustelids were relatively low. With recovering densities if the two native species, invasive mink populations underwent a temporal shift of foraging from nocturnal to diurnal, as well as a dietary shift

(Harrington et al., 2009). Although these niche shifts first resulted in lower body conditions of invasive minks, this resource partitioning with two native mustelids is assumed to account for the co-existence of the three species (Harrington et al., 2009).

Resource partitioning in fish assemblages mainly occurs on the axis of diet (57 %), followed by habitat (32 %) and temporal separation (11 %, Ross, 1986). Also for other taxa, dietary and habitat usage studies seem to be an important component to detect niche breadth, degree of overlap and going along with this, levels of competition (e.g., Schwartz and Ellis, 1981; de Almeida Jácomo et al., 2004). Partitioning not only occurs between species, but can also act within one species by changing ecological niches during ontogeny (ontogenetic niche), as seen in several size-structured populations (Werner and Gilliam, 1984). Thus, mechanisms of niche separation can be very fine-tuned, requiring a detailed analysis, but deliver important information on future population development if invasive species are concerned.

Reproduction

Across the animal kingdom a wide range of more or less peculiar reproductive systems has evolved (Bull, 1983). All of them have one thing in common: to ensure population maintenance by passing on the own genes. Thereby natural selection favors traits which improve probability of survival and reproduction success, both determining population growth (Campbell et al., 2003).

Reproductive effort is the result of environmental conditions and physiological constraints (Schaffer, 1974; Aldridge, 1982), often representing a trade-off between somatic growth and gonadal investment (Hirshfield and Tinkle, 1975; Cohen, 1976). Timing of reproduction may be an important local adaptation across geographic range (Griffith and Watson, 2005), a determinant for the availability of suitable food resources for the offspring (Wright and Bailey, 1996), as well as of major intra- or interspecific relevance, assessing the impact of competition and predation on the offspring (James and Shine, 1985).

In fishes, reproductive strategies encompass a variety of techniques. From unisexual species, hermaphrodites up to sexual reproduction, which can occur within the female or as in most cases exteriorly, everything is represented (Fiedler, 1991). Mating choice and sexual selection, including alternative reproduction techniques bear their own peculiarities and the base for several interesting studies (e.g., Sargent et al., 1986; Dugatkin, 1992; Kvarnemo and Ahnesjo, 1996; Smith and Jurajda, 2002; Stauffer Jr et al., 2002; Andersson and Simmons, 2006), yet, were not the focus in this thesis and will thus not further be explained. Behavior following fertilization includes several guarding strategies of eggs, like ovovivipary (e.g., Poecilidae, Plath et al., 2007), mouthbreeding (e.g., *Tilapia galilaea,* Cichlidae, Oppenheimer, 1970), nest building (e.g., *Gasterosteus aculeatus*, Van Iersel, 1953) and plenty more forms of parental care (Migdalski et al., 1976; Gross and Sargent, 1985). Further, frequency and timing of spawning can vary from one single spawning event in life up to multiple spawning within one season (Migdalski et al., 1976). Thus, reproduction is highly versatile in fishes, and thereby a diversified range of life-history traits and phenotypic plasticity within those traits can be displayed.

Besides dietary and habitat dependent annidations of invasive species, life-history traits potentially bear the highest predictive power concerning future population development or the expanding range (Sakai et al., 2001; Van Kleunen et al., 2010; Angert et al., 2011). Especially reproductive traits have been used to assess the nuisance character of invasive species, as those are an important prerequisite for management strategies (e.g., Cucherousset et al., 2009; Guo et al., 2013). Plasticity in those life-history traits seems to promote invasion success (Kolar and Lodge, 2001; Amundsen et al., 2012). Further, the reproduction mode influences the spread of invasive species (Sakai et al., 2001), as for instance, large clutch sizes and multiple breeding per season are related to range expansion in birds (O'Connor et al., 1986). Thereby reproduction and dispersal jointly determine the rate of colonization at invasion fronts (Angert et al., 2011).

Dispersal

Dispersal is a spatial dynamic event, which can depend on ecological or evolutionary processes. It is used across a wide range of taxa, mostly occurs for juveniles and for some organisms implicate an additional sex difference (Greenwood, 1980); e.g., while in birds it is mostly the female which disperses, in mammals dispersal is clearly male-biased (Greenwood, 1980). In general, dispersal is regarded advantageous if the costs of moving are outweighed by the fitness benefits gained in the new habitat (Bowler and Benton, 2005). Thereby, unfavorable conditions exhibited in the origin like competitive interactions, which are often due to increased densities, as well as uneven sex ratios and inbreeding are considered as trigger (reviewed in Bowler and Benton, 2005).

Dispersal relying on density-dependent effects of prey and predator could also be validated for fishes (e.g., Hauzy et al., 2007). Particularly drift as a dispersal mechanism is a common phenomenon for early life stages of fishes (Gale and Mohr, 1978; Jurajda, 1998; Lucas and Baras, 2002; Reichard et al., 2002; Zitek et al., 2004a; 2004b). While for some species it represents an essential stage during ontogeny (Pavlov, 1994), for others it might further result in favorable conditions as decreased levels of competition (Humphries, 2005). Thereby, drift initiation can either be passively as washing downstream of disorientated juveniles (Brown and

Armstrong, 1985), or actively triggered by abiotic or biotic conditions (Reichard et al., 2002).

Studies on dispersal mechanisms are of special importance for invasive species, as species with greater dispersal ability are more likely to expand their natural range (Angert et al., 2011). Factors constraining a further distribution of an organism can be of abiotic origin as climatic conditions, or biotic as the occurrence of facilitators or competitors (Gaston, 2003). Defining the spatial spread of biological invasions thereby represents a vital determinant for management purposes and protection of uninvaded habitats (Arim et al., 2006).

Interactions with invasive species: Competition and Predation

Competition

Niche separation as one consequence of competitive interactions with invasive species was already explained in the referring section (see above). As niche differentiation allows for the co-existence of species, this section focusses on a general description of competition, as well as on more harmful impacts of invasive species.

Competition is a strong structuring force in communities (Sih et al., 1985), acting through exploitation of resources or interference with other individuals. Exploitative competition affects each individual of the community as resources are depleted (Begon et al., 2005). Thereby, resources can be as apparent as food (Hart, 1987), water and nutrients (Nambiar and Sands, 1993), or more context-dependent like light for plants (Schmitt and Wulff, 1993), space for nesting bird colonies or sessile animals (Duffy, 1983), or even females for taxa with harem structures (Le Boeuf, 1974; Clapham, 1996). In contrast, interference is a direct interaction between two individuals, as defense of territories like fighting in cervids (Veiberg et al., 2004).

Competitive interactions between native and invasive species are highly potential to result in detrimental effects via several axes. Invasive Argentine ants had better interference and exploitative competitive abilities than natives, resulting in the displacement of the latter (Holway, 1999). Indeed, displacement seems to be the most occurring consequence of competitive interactions with invasive species. Competition for shelter (Gherardi and Daniels, 2004), pollination services (Brown et al., 2002), nesting sites (Strubbe and Matthysen, 2009) and several other resources have led to the displacement of natives across a wide range of taxa, often going along with an aggressive behavior of the native, leading to additional mechanisms of interference (Kiesecker et al., 2001).

Nevertheless, competitive interactions with invasive species might also result in the facilitation of other native species (Rodriguez, 2006). An invasive mussel was shown to facilitate survival of a native mussel by protecting those from exposure to waves (Rius and McQuaid, 2009). Similarly, the invasion of the aquatic plant *Hydrilla ventricilliata* led to increased growth and survival of benthic invertebrates (Posey et al., 1993). However, those facilitations mostly rely on the expense of other species.

A special form of competitive interactions might arise between juveniles of future prey and predator species, the so called "juvenile competitive bottleneck" (Persson and Greenberg, 1990a; Byström et al., 1998). Predatory species often undergo dramatic dietary niche shifts during early ontogeny, restricting those species to behavioral and morphological limits concerning feeding efficiency on different prey categories, and thus being potentially inferior to their future prey species (Werner and Gilliam, 1984; Persson, 1988). Although the predatory species might prey on the inflected species in future and thereby benefit from this species, development and recruitment is hampered by the superior competitor in juvenile stages. Such size-structured interactions of competition and predation seem to be a common phenomenon in fishes (Persson and Greenberg, 1990a; Hegge et al., 1993; Olson et al., 1995; Byström et al., 1998), but could also be validated for copepod populations (Neill, 1975). Recent studies have proved the juvenile competitive bottleneck to also occur between invasive and native species, as in case of the invasive round goby *Neogobius melanostomus* forcing the yellow perch *Perca flavescens* into the competitive bottleneck (Houghton, 2015).

Predation

Predation like competition is a structuring force in communities (Sih et al., 1985), yet, in contrast to competition, predation is a clear defined interaction between two species, leading to the death by consumption of the concerned individual. Nevertheless, predation as well implies far-reaching consequences, affecting species from several trophic positions.

As interaction with invasive species, predation can occur on both sides with the invader either being the prey or the predator. The main cause of invasive predators is the decline of native species by direct predation. Here, a prey-predator naivety might require adaptations before effective predatory acts will be recognizable, whereby a pattern of community similarity as obtained in native habitats should accelerate this process (Sih et al., 2010). Introduced rats have led to heavily reduced prey populations, what was especially severe as endangered sea birds and water turtles were concerned (Caut et al., 2008). Intraguild predation in two Coleoptera species could be shown to be more aggressive and effective from the invasive part, leading to asymmetries in competition (Michaud, 2002).

Effects of invasive predators might also result in non-lethal responses, like behavioral shifts of the prey concomitant with reduced growth rates (Pangle and Peacor, 2006). Sweeping effects could also be identified after the introduction of foxes to Australia, with the demise of native fauna, impacts on agricultural production, as well as transmission of diseases (Saunders et al., 2010). Invasive predators might even affect other (invasive) predators by preying more efficiently on the same prey resource, thereby decreasing consumption rates of the first predator (Griffen et al., 2008). However, effects might vary in course of time, as the prey may also evolve predator avoidance mechanisms, thereby reducing the invaders impact. For instance, in native mussels shell-thickening could be observed following predation of the invasive Asian shore crab *Hemigrapsus sanguineus* (Freeman and Byers, 2006).

Invasive species can in turn also act as prey for native predators (Carlsson et al., 2009), especially if the invasive prey represents a limiting resource (Rodriguez, 2006). Invasive zebra mussels have become an important prey for native fishes (Magoulick and Lewis, 2002) and crayfishes (Perry et al., 1997). Similarly, invasive topmouth gudgeon was the main prey item for three piscivorous fish species (Musil and Adamek, 2007). Due to their high densities, invasive species can strongly promote the referring native predator, as seen for increasing densities of two cuckoo species preying on invasive moths (Barber et al., 2008). As known for invasive predators, also for invasive prey the extent of predation can depend on adaptations and co-evolution with a similar predator. Predation on an invasive ant species by an endemic toad facilitated native ant species due to an invasive-naivety effect with the invasive ants not being familiar to this predator (Wanger et al., 2011). Yet, it is not always the case that invasive species are included in the diet of native predators. The potential benefits have to outweigh the costs of adaptation to this novel prey item, which can be already achieved due to its high abundance, but might be permitted by morphological constraints (Carlsson et al., 2009). Another reason to deny an invasive highly abundant species can be toxins of the invasive prey. This pattern could be observed for native keelback snakes, which clearly avoided invasive, toxic cane toads (Llewelyn et al., 2010). Contrary, for native black snakes resistance to the toxin developed within just 26 generations and thereby predation on cane toads increased (Phillips and Shine, 2006). Scavenging raptors, being less vulnerable to bufotoxins, preyed on cane toads by only consuming the toad's tongue, thereby minimizing the uptake of the toxin, but still preferred native prey if available (Beckmann and Shine, 2011). Clear preference for an invasive species could for instance be shown for a native crab species picking an invasive mussel species over the native (Mistri, 2004).

Thus, predators respond in several ways to invasive prey ranging from rejection to preference, whereby the latter might in some cases lead to biotic resistance, decreasing the abundances effectively and hindering the further spread of invasive species (deRivera et al., 2005). European eel *Anguilla anguilla* is suggested as control of invasive crayfish populations in Italy (Aquiloni et al., 2010). In the same way, intraguild predation is regarded as a biological control concerning invasive species (Bampfylde and Lewis, 2007).

Altogether, invasions might be the most fascinating processes in nature, as they bear evolutionary proceedings on several levels and the whole community structure is concerned probably for decades, displaying a steadily ongoing process of interactions and cascades. Yet, this intriguing process has detrimental impacts on native biota, economics and even human welfare, thereby being everyone's concern.

Objectives

The purpose of this thesis was to define the impact of the invasion of three congeneric goby species in the Lower Rhine. Therefore, in a first step, the ecological niches that were occupied by the invasive gobies had to be defined (Fig. 1). Resource partitioning is generally expected to be higher in closely related species experiencing a similar life cycle going along with high niche overlaps (Gregory, 1978). As the three Gobiidae co-existed in alarmingly high abundances in this new habitat, niche separations between the three species were assumed to arise on several axes, including diet, habitat usage, and temporal aspects like life-history traits of reproduction (Ross, 1986). As a logical consequence, high impact on co-occurring native species was expected. Thus, competitive and predatory interactions with natives including all ontogenetic stages were examined (Fig. 1), representing the two strongest structuring forces in communities (Sih et al., 1985). The specific objectives for the following chapters were as follows:

Chapter I	**Diet**: Defining the dietary niche of all three Gobiidae concerning niche differentiation on an ontogenetic and spatial axis
Chapter II	**Reproduction**: Determining the onset of spawning and temporal separation of reproduction of all three invasive species, as well as the density development and growth of 0+ gobies across the season
Chapter III	**Dispersal**: Defining the drifting activity of 0+ gobies and comparing it to drifting behavior of native 0+ fishes before and after the goby invasion
Chapter IV	**Competition**: Evaluating the extent of dietary competition with juvenile native species during their first growing season

Chapter V **Predation**: Estimating the proportion of gobies in the diet of native predators during all ontogenetic stages and in course of the years

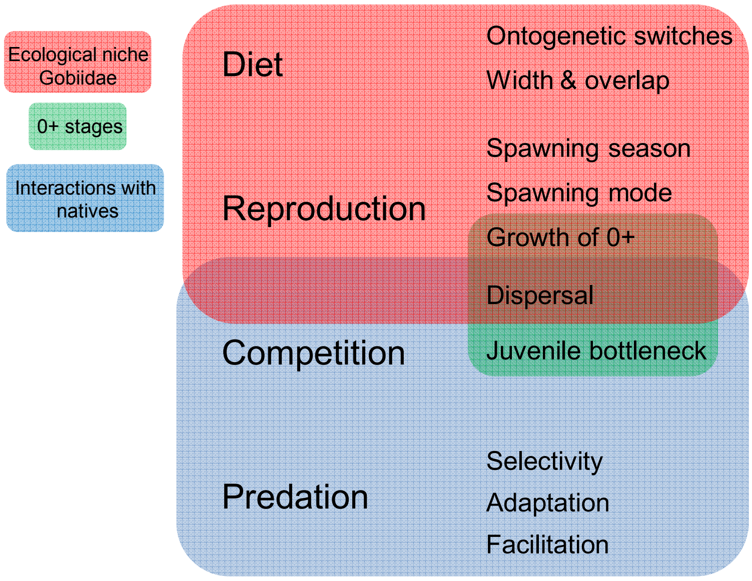

Figure 1. Overview of issues of the thesis and the referring arrangement in defining the ecological niche of Gobiidae (red), studies dealing with 0+ stages (green) and interactions with native species (blue).

Material and Methods

Gobiidae

All three invasive gobies belong to the family of Gobiidae and originate from the Ponto-Caspian area, but have invaded habitats far beyond their natural range (e.g., Gozlan et al., 2010; Semenchenko et al., 2011; Kornis et al., 2012). The most prominent representative is the round goby *Neogobius melanostomus*, which not only invaded several parts of Europe, but also reached and spread immediately within the Great Lake system (Jude et al., 1992; Bronnenhuber et al., 2011). The most important vector for range expansion of gobies seemed to be shipping via ballast waters (Ricciardi and Rasmussen, 1998; Holeck et al., 2004). After the opening of the Rhine-Main-Danube Canal in 1992, a new corridor for introductions from the Ponto-Caspian area was generated, connecting the Danube with the Rhine basin and allowing several species, including gobies, to enter the Lower Rhine (Bij de Vaate et al., 2002; Leuven et al., 2009). Ahead of the goby invasion, Ponto-Caspian macroinvertebrates like the amphipod *Dikerogammarus villosus,* already established great populations in this region, now representing an important food source for the invasive fishes (Bij de Vaate and Klink, 1995; Polacik et al., 2009; Chapter I; IV).

The first goby species, which appeared at the Lower Rhine, was the tubenose goby, *Proterorhinus semilunaris,* in 1999 (Fig. 2). However, this species is primarily found in the lentic backwaters and never reached graving densities (Scharbert and Borcherding, 2013). In 2006 first individuals of bighead goby, *Ponticola kessleri,* were found, followed by round goby, *Neogobius melanostomus,* and monkey goby, *N. fluviatilis,* in 2008 (Fig. 2). Within just a few years, the three species contributed the major part of local fish communities (Borcherding et al., 2011).

All of them have a sedentary lifestyle and are supposed to be rather bad swimmers, as they lack a swim bladder (Charlebois et al., 1997), yet, swimming power against currents seems to be quite mighty at least for round gobies (Tierney et al., 2011). As a morphological characteristic, their pelvic fins are fused, acting as a suction disk in strong currents (Charlebois et al., 1997). Diet spectrum is broad and rather opportunistic with some ontogenetic shifts (Adamek et al., 2007; Polacik et al., 2009, Chapter I). The males perform parental care in cave-like structures by guarding the eggs and fry, which can originate from various females (Miller, 1984; Corkum et al., 1998). Thereby, nest defense can include chasing and biting of possible intruders (Wickett and Corkum, 1998). Most gobiids are iteroparous, thus spawn several times per season (Corkum et al., 1998), yet reproduction modes and traits of the three concerned species seem to vary across regions (see Chapter II and references therein). Gobies undergo a direct development, missing a clear larval phase (Kovac and Siryova, 2005; Capova et al., 2008). Diel vertical migration of freshly hatched round goby could be shown to occur in the Great Lakes and was expected to act as a dispersal mechanism (Hensler and Jude, 2007b; Hayden and Miner, 2009).

Due to its world-wide spread a lot of studies are dealing with round goby as an invasive species. In comparison, literature is pretty scarce on bighead and monkey goby and even more seldom comprising all three species. Adamek et al. (2007) analyzed the diets of all three species in invaded habitats of south Slovakia, showing similar dietary preferences for crustaceans and chironomid larvae. Competition for shelter was analyzed for all four invasive goby species and two native benthic species, resulting in competitive displacement of at least one native species in co-occurrence of bighead goby (van Kessel et al., 2011). Competitive interactions with native species could also be shown for round gobies, as spawning interference with mottled sculpins resulting in recruitment failure of the latter (Janssen and Jude, 2001), or competition for food between round goby and flounder (Karlson et al., 2007). Additionally, the territorial aggressiveness of this species is assumed to eventuate in displacement events (Dubs and Corkum, 1996).

Besides competitive interactions, gobies may also serve as prey for natives. In the Great Lakes round gobies made up < 5 % to 65 % of diet of native piscivores species specifically (Reyjol et al., 2010). Facilitation of natives was observed for grey heron populations, showing increasing densities after intensive predation on round gobies in Poland (Jakubas, 2004). Further, invasive gobies could be shown to serve as prey for nestlings of cormorants shortly after introduction (Somers et al., 2003). In a recent study, condition also improved for pikeperch as round gobies increased in its diet (Hempel et al., 2016). Even predatory control of invasive gobiids was suggested by predation of burbot (Madenjian et al., 2011).

Figure 2. Portraits of invasive gobies in chronological order of introduction: tubenose goby *Proterorhinus semilunaris* (upper left), bighead goby *Ponticola kessleri* (upper right), round goby *Neogobius melanostomus* (bottom left), and monkey goby *N. fluviatilis* (bottom right). All photos: S. Gertzen.

Native species

Besides invasive gobies, this study includes a number of native species, almost representing the entire fish fauna occurring at the Lower Rhine (Chapter III). The focus, however, lies strongly on two native Percidae, the Eurasian perch *Perca fluviatilis* and the pikeperch *Sander lucioperca* (Chapter IV, V), as well as on a piscivorous cyprinid species, the asp *Aspius aspius* (Chapter IV).

Eurasian perch – Perca fluviatilis

Perch is a eurytopic species, described as a generalist feeder, which can also effectively hunt on fish prey (Turesson and Brönmark, 2004, Fig. 3). During ontogeny, it usually switches from a pelagic to a benthivorous diet, followed by a shift to piscivory (Persson, 1988; Persson and Greenberg, 1990b). However, diet shifts in perch are seldom absolute and strongly depend on prey availability (Van Densen et al., 1996). For instance, for perch (and also for pikeperch) the availability of zooplankton early during ontogeny and suitable sized prey fishes coincided with the ontogenetic diet shift towards piscivory (Mehner et al., 1996). As perch is a sight-dependent, actively searching predator, foraging takes place during daytime (cf. Turesson and Brönmark, 2004). Further, this species showed co-operatively hunting (Eklöv, 1992) and the capability of social learning (Magnhagen and Staffan, 2003).

Perch was not only included in this study due to its high abundances at the Lower Rhine (Staas, 1996b), but also as it served as model organism for the juvenile competitive bottleneck in other areas interacting with roach *Rutilus rutilus* (Persson and Greenberg, 1990a; Byström et al., 1998). Thus, perch was held under suspicion for such interactions also to occur at the Lower Rhine, especially, as round gobies could be shown to serve as important prey for perch in the Baltic (Almqvist et al., 2010).

Pikeperch – Sander lucioperca

Pikeperch, as the second piscivorous Percidae has a more slender morphology than perch and reaches larger sizes within the first year of growth (Mehner et al., 1996, Fig. 3). In contrast to perch, it is a nocturnal predator, which is not as dependent on sight and thus, can also hunt in turbid water (Popova and Sytina, 1977). As this species is also preying on zooplankton during early ontogeny, at a size of 100 mm TL diet is quoted as exclusively piscivorous (Van Densen, 1985; Buijse and Houthuijzen, 1992). Active prey choice could be shown for pikeperch preying on smaller-sized prey (Turesson et al., 2002), as well as preference of single species (Greenberg et al., 1995).

In contrast to perch, pikeperch forages solitary, hampering social learning for this species (Nilsson et al., 2006). For pikeperch, diel habitat shifts with movement to inshore habitats at night possibly for hunting were detected (Wolter and Freyhof, 2004). At the Lower Rhine pikeperch is an important fish for angling, thus, it´s population development is not only of ecological interest but implies an economic value. Additionally, an increase in condition after predation of pikeperch on round goby could be shown in northern Germany (Hempel et al., 2016), suggesting that predation on gobies might occur here as well.

Asp - Aspius aspius

Asp is a member of the family Cyprinidae (Fig. 3), but contradictory to other cyprinids, asp displays an ontogenetic switch to a piscivorous diet in its first year of life (Krpo-Cetkovic et al., 2010). Insects could be validated as prey category for juvenile asp in Poland (Kujawa et al., 1998), indicating that this might be an intermediate ontogenetic step before switching to piscivory. Asp was included in these studies, as it was abundant in 0+ stages in groin fields at the Lower Rhine and thus, both, competitive interactions in juvenile stages, as well as predatory acts in adult stages were expected to arise. Further, levels of competition and predation were assumed to differ considerably from those of the two piscivorous percids, by preying also on other food sources.

Figure 3. Native species included for competitive and predatory interactions: Eurasian perch *Perca fluviatilis* (upper left, photo: J. Lindner), pikeperch *Sander lucioperca* (upper right, photo: S. Gertzen), and asp *Aspius aspius* (bottom, photo: K. Gertzen).

Study place

The River Rhine is one of the major navigable waterways of Europe, starting in the Alps and opening out in the North Sea (1,320 km). Due to increasing canalization and the connection of different waterbodies, it is strongly affected by invasive species and even described as the global highway for aquatic invasions (Leuven et al., 2009). In 1986 a chemical accident at Basel resulted in a great pollution event, extinguishing a great share of aquatic life (Van Dijk et al., 1995). Since then, water quality strongly enhanced, also due to the improvement of sewage plants, as well as reductions of phosphates in washing agents (Bij de Vaate et al., 2006). Yet, this has led to a severe decrease in primary productivity (decline of chlorophyll a by 90 % from 1990-2009), further influencing higher trophic levels (Vohmann et al., 2010; Hardenbicker et al., 2014). Therefore, the River Rhine can be seen as food limited system, which is still afflicted by anthropogenic environmental constraints, hampering the complete recovery of its biodiversity and allowing the establishment of neozoan populations (Kureck, 1992; Bij de Vaate et al., 2006).

The Lower Rhine in particular, is characterized by artificial river banks displayed by exclusively riprap embankments, as well as large sandy groin fields (Fig. 4). Groin fields represent beach like structures adjacent to one another and are separated by artificial stony embankments (groins), which ensure navigability of ships in the main channel (Kalweit, 1993; Leuven et al., 2009). Vegetation is sparse and water level fluctuates, covering areas of strongly varying sizes in those groin fields. Due to the ongoing disappearance of connected floodplain areas (Buijse et al., 2002), which normally serve as spawning and nursery areas for native species (Scharbert and Borcherding, 2013), the importance of groin fields as recruitment habitats for juvenile fishes has strongly increased.

Sampling places were all located at the Lower Rhine close to the city of Rees (Rhine-km 831-845, Chapter I, II, IV, V) and added by a sampling station at the Ecological Rhine Station of the University of Cologne for drifting studies (Rhine km 684.5, Vohmann *et al.*, 2010, Chapter II).

Figure 4. Artificial banks at the Lower Rhine: exclusively riprap (left, photo: S. Gertzen), and large groin fields (right, photo: J. Borcherding).

Fishing

Beach seining

Most study organisms were caught via beach seining (Chapter I, II, IV, V), which was applied in the sandy groin fields of the River Rhine (Fig. 5). Two different net types (further referred to as small and big net) were used with varying mesh sizes to allow catchability of different length classes of fishes (small net: 10 m x 1.5 m, mesh size 1 mm; big net: 15 m x 1.5 m, mesh size 4 mm). Both nets were hand-dragged against the current and were prepared with a weighted bottom line and integrated swimmers at the upper line, ensuring sampling of the whole water column. Two wooden sticks were used for dragging at which ropes were fixed to aid pulling the net against the strong current. The big net further possessed a pouch in its middle, where fishes accumulated after seining. Both nets were dragged parallel to the shore ending up in a half-circle towards the beach.

For analyses of reproductive activity and the development of goby densities and growth across the season (Chapter II), a narrow, well designed sampling scheme had to be applied. Studies on competitive and predatory interactions further required the necessity of inclusion of different day times (Chapter IV and V). Whereas for studies dealing with larval and juvenile stages only the small net was used, predatory interactions (Chapter V) implied the usage of the big net as well. As part of the sampling program, the small net was always dragged for a specific distance to obtain density estimates (usually approximating 20 m, width 5 m, yielding ca. 100 m²). The big net in contrast was just used to get access to large predators, which were only seldom caught with the small net.

Sampling scheme in general encompassed 27 stretches per month from April to October in 2011 to 2013. Those were divided in three succeeding campaigns (à 9 stretches) each starting at one of three daytimes (3 stretches). Morning samplings were performed at 9 am, afternoon samplings at 3 pm and night samplings were taken directly after civil twilight, thus ranging from ca. 8 pm (October) to 10.30 pm (June). Between two campaigns at least 24 hours laid in between. Additional samplings were applied during peaks of 0+ goby densities, as well as for the catch of predators (big net). However, some campaigns could not be fulfilled due to thunder storms, or strong increases in water level, diminishing catching rate substantially.

In 2014 beach seining was performed irregularly across the season with both nets and also at varying daytimes, as in that year only fishes for predatory analyses were required (Chapter V).

Drift nets

Studies of drifting fish were performed in the years 2000 and 2012-2014 at the Ecological Rhine Station in Cologne (Rhine-km 684.5, Chapter III, Fig. 5). The net had an opening of 1 m x 0.5 m (500 µm mesh size) and was fixed on a steel frame that could be positioned in the current via a crane. Additional weights at the frame ensured the right position in the current, ca. 20 cm below the water surface. Distance to the riprap bank was approximately 8 m. Current velocity was measured by the use of flow meters of Schiltknecht (Schweiz, MiniAir2) or Höntzsch (Germany IP-ASDI), respectively. Except for the year 2000, when some samples were also taken during daytime, the drift net was exposed during dusk and/or early night. In addition, on five occasions evenly distributed over the season in 2013, eight samples were gathered in a sequence from dusk and early to late night and dawn (cf. Janac *et al.*, 2013). The duration of net exposure lasted between 15 and 60 min, where sampling duration was dependent on the quantity of the latest catch. Sampling was more often at the beginning of the season when abundances of larvae were high, but was evenly distributed over the rest of the season.

Electro-Fishing

Electro-fishing was applied to get access to adult gobies (Chapter I) and medium-sized perch (Chapter V). It was performed in the riprap areas surrounding the groin fields with a portable backpack gear (maximum output 225-300 V, frequency 55–75 Hz, dip net anode 40 x 20 cm, mesh size 4 mm, SEN f.Bednar, Czech Republic, Fig. 5) and added with a second dip net to increase catching success within the stones. Electro-fishing was performed at least twice a year from 2011 to 2014 and also included different day and nighttime samples.

Angling

Angling was applied to sample large, adult perch and pikeperch, as access via electro-fishing or beach seining was not feasible. It was executed at several sites at the Lower Rhine (Rhine-km 831-845) in irregular intensities for the years 2011 to 2014. Thereby, mainly baits and equipment for spin fishing were used (Fig. 5).

Figure 5. Fishing techniques used: beach seining (upper left, photo: L. Barthel), drift net sampling (upper right, photo: K. Brenner), electro-fishing (bottom left, photo: M. Ondračkovà) and angling (bottom right, photo: S. Gertzen).

Post-capture handling of fishes

Regardless of fishing technique, all gobies smaller than 50 mm TL and native species being too small to be determined on site, were directly transferred into 96 % ethanol. Species of special interest for the thesis (perch, pikeperch, asp, maximum 15 individuals per species and trial) were also fixed in ethanol up to a size limit of 50 mm TL. All gobies and species of interest exceeding this size were placed on ice and directly after sampling stored at -18 °C. Huge individuals of perch and pikeperch caught during angling were expertly killed on site, measured, and their innards transferred into a vessel with ethanol containing the corresponding fish data (date, location, time, angler, species, TL, weight), while the rest of the fish served as dinner. All fishes, including their larval stages were determined to species level and their TL (nearest 1 mm) was measured. In case of Gobiidae, sex was additionally checked by the shape of the urogenital papillae. Surplus and other native species which were not used for analyses were carefully released after measuring. Larval determination occurred in the laboratory using keys for larval fish identification (Koblickaya, 1981; Mooij, 1989; Urho, 1996; Staas, 1996a; Pinder, 2001).

Stomach content analyses

For dietary analyses of gobies (Chapter I), as well as for competitive (Chapter IV) and predatory (Chapter V) interactions, stomach content analyses were required. Although, the data could always be used for more than one study, in total 5,928 stomach content analyses were performed. Gobies and asp lack a real stomach (Jaroszewska et al., 2008; Warren Jr et al., 2014), therefore, the whole digestive tract from esophagus to rectal sphincter was analyzed, whereas analyses for perch and pikeperch proceeded with the stomach. The stomachs and tracts were freed from other organs and weighted to the nearest 0.0001 g. Afterwards contents were removed by flushing and/or scraping with a scalpel before the empty tracts were weighted again. Items were classified to lowest possible taxonomic unit (Olympus SZX 9) and their proportion to the whole content was visually estimated (Polacik et al., 2009). In case of piscivory and an early digestive state, total lengths of prey fishes were also measured to the nearest 1 mm.

Data proceedings

Dietary analyses

For quantitative objectives the wet weight of the whole stomach/digestive tract content, as well as the index of stomach fullness (ISF, Hyslop, 1980) were determined. Further, the adjusted condition factor was calculated (Chapter I, V), based on the Fulton’s condition factor (Bagenal and Tesch, 1978).

Prey taxa were grouped in major categories for gobies of all sizes (zooplankton, Mollusca, Crustacea, Chironomidae, fish, rest, undefined mass, Chapter I), juvenile gobies, perch, pikeperch and asp (zooplankton, Mollusca, Crustacea, Chironomidae, fish, rest, Insecta, undefined mass, Chapter IV) and predatory analyses of perch and pikeperch (zooplankton, Mollusca, Crustacea, rest, Insecta, undefined fish, native fishes, Gobiidae, undefined mass, Chapter IV). For all species of the regarded length class a mean value per category was calculated, wherefore individuals with an empty stomach were excluded, thus all mean values of the categories in the end yielding a sum of 100 %.

Feeding strategy and importance of certain prey taxa were further visualized using modified Costello plots (Amundsen et al., 1996). Therefore, the prey-specific abundance is plotted against the frequency of occurrence of prey in the diet of the predator for major food categories. Major food categories of gobies (Chapter I) revealed to be zooplankton, Mollusca, Crustacea, Chironomidae, fish and further include the category “rest”. For predatory analyses (Chapter V) the categories were chosen as zooplankton, Gobiidae, native fishes, Crustacea and Insecta.

For competitive analyses (Chapter IV) a row of complex calculations were applied (please see the referring section in Chapter IV for all formulas). First, individual consumption rates were determined. Then an estimate of maximum food intake, the ISF_{MAX}, was defined as the median of the highest 10 % of all ISF values species specifically. The median was chosen, as this value is robust against outliers, which naturally occur due to piscivory, yielding temporarily very high indices of stomach fullness. For every individual the proportion of the individual ISF in relation to the species specific ISF_{MAX} was calculated and served as the measurement of individual *strength of dietary competition SDC*. As dietary competition can only occur if the species are feeding on the same resources, the *diet overlap* O_D was calculated between all species, and this for all months and years following Schoener (1970) using all 83 types of food items observed in this study. As we aimed to include densities of all other fish within one month and year into the estimation of the diet overlap, we also had to calculate the intraspecific diet overlap to facilitate the inclusion of densities of conspecifics as competitors. In contrast to the interspecific diet overlap, for which the mean diets of species are compared on a monthly basis, the diets of the single individuals of one species were compared with each other. In those cases where more than 50 individuals per month were dissected, 50 individuals were randomly chosen from the subset. For each individual the diet overlap to all other conspecifics within the sample was calculated and the intraspecific diet overlap was then calculated as the mean of all these values. This allowed an estimation of the intraspecific diet overlap based on the same calculation scheme as for interspecific comparisons. Finally, the *weighted diet overlap* O_{Dw} was established species specifically, which integrated the density of the particular species, all other occurring species (also those which were not analyzed), as well as the intraspecific diet overlap.

For predatory analyses (Chapter V) the prey-predator ratio was calculated for those perch and pikeperch which had measurable prey fishes in their stomach.

Reproduction

For densities of 0+ gobiids in course of the season (April to October, Chapter II), densities were pooled per month (mean of 27 stretches), as dial aspects were not in focus of the study.

Growth rates were calculated as daily growth by comparing the mean total length of the first cohort of every sampling date with the mean total length of the following sampling event (Heermann and Borcherding, 2013). Thereby one mean growth rate per year and species was generated.

For determining hatching and spawning dates, growth rates were only applied to individuals in their first three month of life to avoid inaccuracies as growth naturally slows down during ontogeny. Assuming a hatching size of about 5.5 mm TL (Pk & Nf: personal observation; Nm: Logachev and Mordvinov, 1979), a hatching date could be calculated for every goby caught, up to a certain size limit (TL), which was determined by the mean size of gobies that was reached within the first three months after hatching. Calculation of spawning dates was also done species specifically and on an individual level. For back-calculating from hatching to spawning events 350 day degrees (water temperature data: monitoring station of Lobith) were subtracted, matching personal observations for monkey goby, as well as literature indications for round goby (Moiseyeva, 1983; Moskalkova, 1989; Krönke, 2008). To eliminate unreliable values, a control was applied by subtracting 20 days from the calculated hatching date, as this was the highest mentioned time for egg development quoted in literature (Moiseyeva, 1983; Moskalkova, 1989; Krönke, 2008). When spawning dates calculated by those two methods (day degrees and by subtracting 20 days) differed by 10 or more days, these dates were eliminated from further analysis. Examples for calculations are given in the referring section of Chapter II.

The standard gonadosomatic index (GSI) was determined for female adult gobies of all three species per month, which is defined as the relation of gonadal fresh weight to total body mass (Ricker, 1975).

Drifting

To obtain densities from drifting data, abundances of larvae and juveniles were calculated as number of fishes per filtered water, whereby the amount of filtered water was defined as the drift net influx surface multiplied with the current velocity and the sampling duration. Using these data on species level, the dominance (percentage of a species within the total catch per year), as well as the frequency of occurrence was calculated, which is an estimate of the percentage on how many sampling days of a year the species was caught.

Statistics

Except for Chapter I, where SPSS (Ver. 19.0, SPSS Corp.) was utilized, all statistics were performed using the software R (Ver. 3.1.1, R Development Core Team, 2009). Statistical analyses followed a standardized procedure for all data. Data displayed as percentages (e.g., ISF) were log transformed prior to analyses to achieve homogenous variances. Data were checked for normal distribution via Shapiro-Wilk tests, followed by a Levene-test to validate homogeneity of variances. If one of these assumptions was violated, non-parametric tests were used. Non-parametric tests started with Kruskal-Wallis tests if more than two groups of interest were concerned, followed by Wilcoxon tests to specify significant differences between single groups. In case of normal distribution and homogenous variances, parametric tests could be applied. This was in most cases the use of an ANOVA followed by *post-hoc* analyses.

For the competitive interactions between juvenile gobies and native species (Chapter IV) a linear mixed model was applied to assess the seasonal development of competitive strength. To account for the nested structure and temporal correlation of “month” within “year”, “year” was integrated as random factor, whereas “month” and “species” determined the fixed effects. Model structure was ensured by determining the significance of the single fixed effects and their interactions via an ANOVA of the referring model and by comparison with simpler models using Akaike information criterion based model selection.

Results and Discussion

Dietary and spatial niche separation Gobiidae

Decreasing condition values with concomitant increasing densities for all three species in course of the years supported the idea of the Lower Rhine being a resource limited system, and thus potential high levels of dietary competition between the three species. All gobies showed an opportunistic feeding behavior, consistent with findings in other areas (Adamek et al., 2007; Polacik et al., 2009; Grabowska et al., 2009), with 90 % of all consumed prey referring to only three categories: Crustacea (56 %), chironomid larvae (21 %) and Mollusca (11 %). For all gobies Crustacea (mainly the invasive *D. villosus*) gained importance during ontogeny going along with decreasing intake of chironomids. For monkey and bighead goby this shift was rather abrupt at a size of 50 mm TL, whereas for round goby the change occurred more steadily. A distinct dietary shift followed for large individuals (> 125 mm) of monkey and bighead goby to fish and for round goby to a molluscivorous diet (Fig. 6).

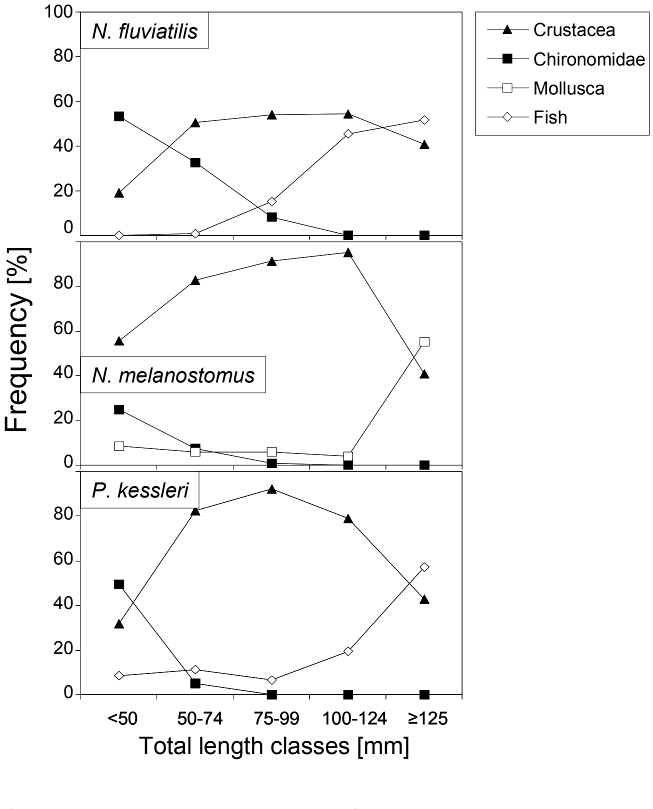

Figure 6. Frequency of the three most important food categories in dependence to the size of the three gobiid species (separated in 25 mm size classes) at the Lower Rhine between 2009 and 2011. From Chapter I.

The shift to Crustacea in bighead goby was consistent with a habitat shift from the sandy groin fields, which could be validated as nursery habitat for all three species (Chapter II), to the surrounding riprap structures. In contrast, monkey goby preferred to stay in the sandy groin fields, thus displaying no ontogenetic habitat shift. Habitat occupation in round goby was more flexible, presenting a ubiquitous distribution. Thus, dietary and spatial resources were used via fine-tuned resource partitioning, allowing for the co-existence of the three species (Hardin, 1960).

The overall dietary overlap was significant between 0+ stages of all Gobiidae. High dietary overlap between the juveniles could further be validated in Chapter IV throughout the season. In the riprap structures, where only large round and bighead goby occurred, dietary overlap was strongly dependent on the season, with highest values gained in summer. Species specific predation on mollusks (Nm) and fish (Pk) decreased overlaps in this length group for the rest of the season. This shift to other prey categories which are not included in the diet of heterospecifics decreased the level of interspecific dietary competition by niche differentiation (Werner and Gilliam, 1984). That this shift was most pronounced in autumn reflects the abundances of other major food items, which usually decrease before winter (Borcherding and Sturm, 2002). Further, competition in general might be decreased in those adult individuals, as gape size limitations decrease with size and the potential to use more diverse prey items regularly increases (Beeck et al., 2002; De Roos et al., 2003; Borcherding et al., 2010).

The three species showed fine-tuned differences in ontogenetic habitat and diet usage, thereby niche differentiation occurred on the three major axes for resource partitioning in fish assemblages (Ross, 1986). Additionally, intra-specific competition was reduced by varying ontogenetic niches (Werner and Gilliam, 1984).

The co-occurrence of 0+ Gobiidae on the sandy beaches together with significant dietary overlaps for this stage, led us to the assumption of niche separation during spawning onset and intensity to spread the dietary competition between freshly hatched gobies across the season. Thus, Chapter II focused on the reproductive traits of the three Gobiidae and the densities of 0+ gobies in course of the season.

Reproductive traits

Gobiidae at the Lower Rhine showed differing reproduction modes, presented by single versus multiple spawning events, spawning season length and intensity across the season.

Monkey and round goby displayed multiple spawning events, as also seen in their native habitats (Kalinina, 1976; Konecna and Jurajda, 2012), whereas for bighead goby only one spawning event could be detected, also being in accordance to native habitats (Kalinina, 1976), but contrary to other invaded areas (Kovac et al., 2009).

Spawning seasons were extended from mid-March to mid-September for monkey and round goby, and restricted from mid-March to mid-July, with 50 % of all spawning activity being already accomplished at the end of April for bighead goby. Spawning intensity for round gobies was highest at the beginning of the season, whereas spawning of monkey gobies peaked later, in the middle of the season. Therefore, a temporal separation of spawning was displayed, resulting in varying hatching frequencies of the three species (Fig. 7). Successive spawning events could also be validated to occur in other congeneric fish species to spread competition for spawning sites and resources (Tsikliras et al., 2010).

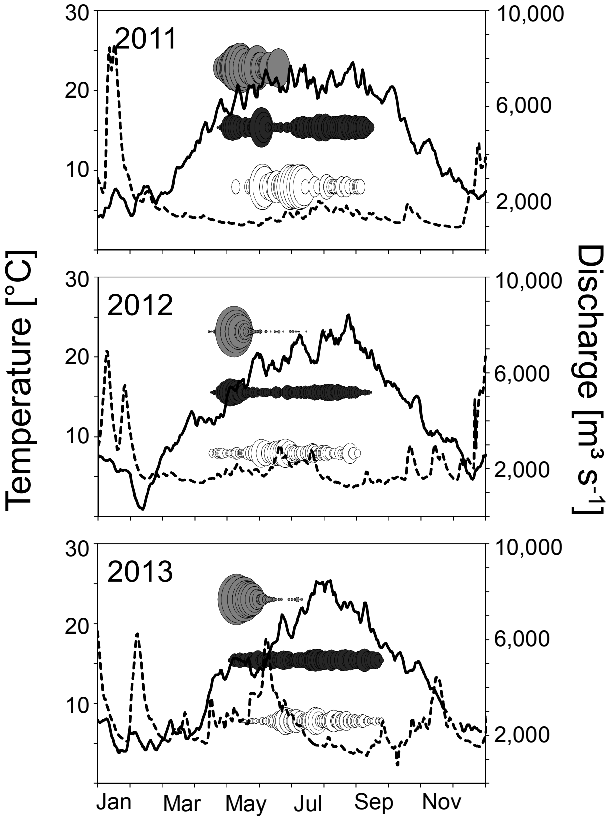

Figure 7. Water temperature (black line), discharge (dotted line), and relative abundances of all calculated hatching events per year and species. With *P. kessleri* (grey), *N. melanostomus* (black), *N. fluviatilis* (white) for the years 2011 (above), 2012 (middle), and 2013 (bottom). From Chapter II.

Continuous spawning in general has several advantages over a single spawning event, as e.g., the risk of predation or unfavorable conditions is spread over a longer period (summarized by Mcevoy and Mcevoy, 1992). Hence, multiple spawning usually assures that at least some portion of the total offspring will survive to recruitment (Goodman, 1984). The most risky reproductive characteristics were therefore obtained for bighead goby and, indeed, a reproductive failure of this species was obvious in 2011, which was most probably associated to a phase of extremely low water level right after spawning, consequently desiccating the batches.

Our results could further indicate spawning onset being independent of temperature and photoperiod for all three species, contrary to findings for several other fishes (Munro et al., 1990; Reichard et al., 2004; Dahl et al., 2004; Chernyaev, 2007). Thus, factors like endogenous rhythms, hormone levels (Liley and Stacey, 1983; Woods and Sullivan, 1993), male behavior and/or plasticity to avoid significant niche overlaps might be more determinative to initiate spawning.

The capability of phenotypic plasticity in reproductive traits surely promoted the success of the Ponto-Caspian gobies and resulted in fine-tuned niche partitioning on a temporal axis (Hardin, 1960; Schoener, 1974). Growth rates for the 0+ individuals of the three species were most stable for round goby, showed prospering trends for monkey goby, whereas it decreased in course of the years for bighead goby, indicating that invasion and population development is still in progress at the Lower Rhine. In accordance with those findings, bighead goby seems to be less threatening than round and monkey goby by showing already decreasing densities and lower recruitment rates. Strongest increase in population development is expected for monkey gobies, as growth rates and densities for this species show prospering trends. Round goby in contrast displayed the most stable values, probably indicating the peak of invasion.

Dispersal by drifting

The four years of drift sampling within a period of 15 years yielded more than 26,500 caught fishes. This was the first study dealing with drifting activity of fishes in the Lower Rhine so far. Further, it was the first time that drifting activity of all three goby species living in sympatry outside their native range could be documented. As niche separation was apparent on the dietary axis (Chapter I), as well as it could be seen for reproductive traits of the three gobies (Chapter II), differences in the drifting pattern were also assumed to exist between the three species.

Drifting activity could be found highest in the first part of the night, being in accordance to several other studies on drifting behavior of fishes (Pavlov, 1994; Johnston et al., 1995; Jurajda, 1998; Gadomski and Barfoot, 1998; Copp et al., 2002; Oesmann, 2003; White and Harvey, 2003; Zitek et al., 2004a; Reichard and Jurajda, 2007; Schludermann et al., 2012; Janac et al., 2013). Such diel drifting patterns are giving evidence for an active entering of the current, as a result of stage- and species-specific adaptations and behavioral responses to the light levels as ultimate factor (Reichard and Jurajda, 2007). This is supported by the fact that neither temperature, nor discharge could be identified to correlate to drifting activity.

Two different drifting techniques were obvious, performed by representatives of the invasive gobies, as well as by native species. Exemplified was this varying behavior by the natives roach *Rutilus rutilus* and barbel *Barbus barbus,* two abundant cyprinid species at the Lower Rhine. Long drifting periods were obtained for all species except bighead goby, which only occurred in April and May. Roach and bighead goby showed an increase in size of drifting over the season, whereas barbel, monkey and round goby drifted always at similar sizes.

For monkey and round goby a narrow size window of drifting fishes was obtained (Fig. 8), which could also be shown for round goby to occur in other regions (Hensler and Jude, 2007a; Hayden and Miner, 2009). This led to the assumption that drifting is restricted to this specific ontogenetic stage, representing only a few days (Janac *et al.*, 2013). The same pattern was displayed by barbel, drifting at a size of about 14 mm TL, which is in accordance with sizes obtained in other studies (Copp *et al.*, 2002; Zitek *et al.*, 2004b). Contrary, size of bighead goby increased in the period of drifting from 8 mm up to 23 mm TL. A pattern that was also obvious in roach, though this species drifted much longer over the season, reaching sizes of more than 60 mm TL. While an increase in size of roach could also be found in other rivers to occur for drifting individuals (Pavlov, 1994; Jurajda, 1998; Zitek et al., 2004a; Speierl, 2007), such large sizes have not been observed before.

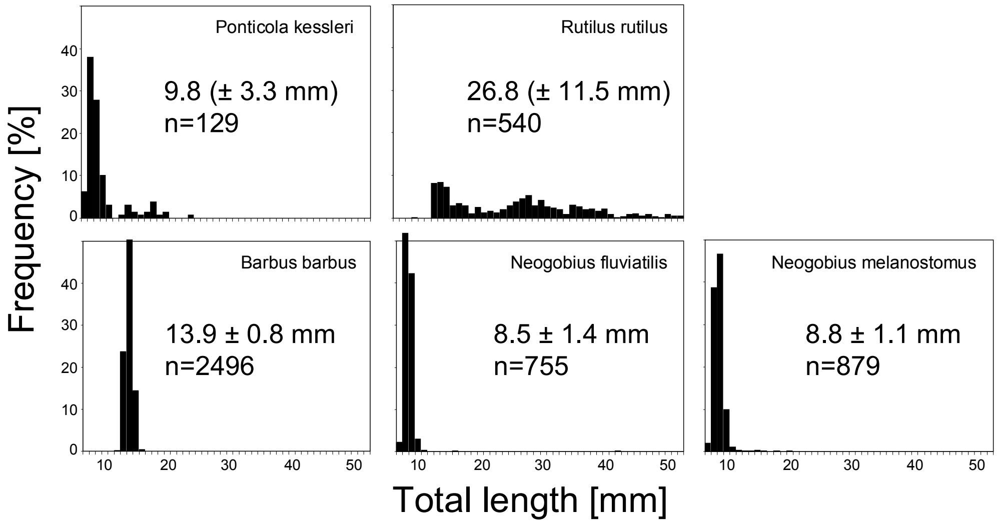

Figure 8. Length-frequency distributions of all *R. rutilus*, *P. kessleri* (upper panels), *B. barbus*, *N. fluviatilis* and *N. melanostomus* (lower panels) caught in drift nets over the sampling season 2013 at the Rhine station in Cologne. Indicated at each panel are the overall mean (mm TL ± SD) and the number of individuals (n), respectively. From Chapter III.

Thus, for barbel, round and monkey goby for which drifting is restricted to a certain developmental stage, the initiation of drifting seemed to refer to morphological constraints (Pavlov, 1994; Reichard and Jurajda, 2007), whereas for bighead goby and roach further factors might determine the extension of the drifting window. Such optional drift patterns resulting in plasticity in drifting behavior might be related to density dependent effects like competition or decreased resources (Reichard and Jurajda, 2007).

Species diversity, total numbers and abundance of fish did not change from 2000 to 2012-2014 (Tab. 1), dominant species like barbel and roach occurred in same numbers in the drift before and after goby invasion. However, some changes were apparent in the dominance of certain species, as the clear decrease in drifting bream *Abramis brama* individuals. Albeit, this might rather be related to long lasting changes within the spawner population of potamodromous bream, due to the loss of connectivity with lateral waters and thus spawning grounds, as with the occurrence of invasive gobies (Molls, 1999; Grift et al., 2003; Borcherding and Staas, 2008; Scharbert and Borcherding, 2013).

This study revealed a first indication that the detrimental effects of gobies on native species seemed not to act on the reproductive output and drifting behavior of native species, but rather occurred during later ontogenetic stages. Further, the results underpin the trend of decreasing densities of bighead goby from 2012 to 2014, as also seen in our other studies (Chapter I, II, IV).

Table 1. Species-specific data for all sampling campaigns on the frequency of occurrence (F, on how many sampling days of a year the species was caught) and the dominance (D, amount of a species within the total catch per year) of all drift catches. Dominance values above 10 % are printed in bold.

	2000		2012		2013		2014	
	F	D	F	D	F	D	F	D
Abramis brama	40	**41.8**	24	0.40	11	0.50	6	0.17
Alburnus alburnus	47	7.16	21	0.41	42	4.74	11	0.24
Aspius aspius	27	0.60	31	0.64	5	0.18	11	0.10
Barbus barbus	60	**32.6**	76	**31.4**	66	**41.3**	61	**27.5**
Blicca bjoerkna	20	0.13			13	0.22	6	0.04
Chondrostoma nasus	20	0.61	7	0.11			22	0.59
Cyprinus carpio	7	0.04			3	0.07		
Gobio gobio	33	2.25						
Leuciscus idus	13	0.10	17	0.16	8	0.10	33	2.00
Leuciscus leuciscus	13	0.12			8	0.16	17	0.43
Rutilus rutilus	60	4.30	62	9.00	66	7.67	44	3.99
Squalius cephalus	60	7.04			21	0.62		
Perca fluviatilis	7	0.03	31	2.46	26	2.29	28	2.00
Sander lucioperca	40	1.96	14	0.32	18	0.35	17	0.37
Coregonus sp.	40	0.12						
Cottus gobio	60	0.04						
Esox lucius	7	0.09						
Gasterosteus aculeatus	7	0.09			3	0.05		
Lampetra fluviatilis	33	0.86						
Neogobius fluviatilis			62	**18.7**	68	**18.4**	61	**15.4**
Neogobius melanostomus			62	**21.8**	89	**20.5**	72	**46.4**
Ponticola kessleri			31	**14.6**	24	2.82	11	0.79
Number of species	19		12		16		14	

Competition

Based on the findings of dietary niche separation between the three goby species (Chapter I), levels of dietary competition were expected to be also very high between goby species and native fishes. Further the levels of competition were expected to be highest during early ontogeny, thus for 0+ individuals, as it could already be shown for the three goby species (Chapter I).

For the evaluation of dietary competition between gobies and natives, first an estimate of dietary overlap had to be established. The “weighted diet overlap” incorporated not only the diet overlap with every other occurring species (Schoener, 1970), but also the intraspecific diet overlap, as well as densities of the referring species. Further, an estimate to assess the “dietary competitive strength” of the single species in course of the season was applied (see Chapter IV for formulas and explanation).

Weighted diet overlap values were found to be high throughout the whole season for natives, as well as for the three goby species (Fig. 9), revealing high levels of resource competition in this limited system. Although weighted diet overlap values were even higher for the invasive gobies as for the native species analyzed, their competitive strength was considerably better (Fig. 10). Round goby displayed the best dietary competitive strength, followed by monkey goby. Bighead goby had by far the highest individual consumption rates, indicating high energy demands for this species (Mehner, 2013), but failed in competitive strength when compared to the other two goby species.

Best competitive ability concerning food utilization for the native species was obtained for the piscivorous cyprinid asp, due to an additional prey source (insect imagos picked from the surface), which was not integrated in any of the other species diets. Contrary, the diet of perch and pikeperch overlaped to some extent with the gobies; mainly by consumption of the amphipod *D. villosus* (see also Chapter V). Both Percidae ranked last in competitive ability, clearly suffering by food shortage imposed by the invasive gobies.

Levels of dietary competition followed a clear seasonal pattern, as suggested in Chapter I, which was less pronounced in the strong competitors round goby and asp. Dietary competitive strength peaked in the mid-season, reflecting the food abundance in the River Rhine (Van Riel et al., 2011). Competition was therefore highest at the beginning of the season in a critical phase of early development, which may result in reduced growth or mortality (Tonn et al., 1992). Additionally, competition increased again at the end of the season, another critical point of time, as energy storages needed to be built up before winter (Post and Parkinson, 2001).

The low competitive strength of perch and pikeperch together with the seasonality led to the assumption of those two Percidae being forced into a juvenile competitive bottleneck by food depletion and superior competitive ability of the invasive gobies (Persson and Greenberg, 1990a). By being faced with three instead of just one invasive species, the impact on the native species was enforced (Strayer, 2012). Pikeperch suffered even more than perch by reaching only about 20 % of desired food uptake. However, this species included fish earlier in its diet than perch, leading to the assumption that predation on gobies might occur and reduce the effects of the juvenile competitive bottleneck (Chapter V and section below).

Native species were strongly affected by invasive gobies, leading to high levels of dietary competition during critical phases of development. Also within the invasive gobies clear differences could be obtained with bighead goby, which additionally had the highest energy demands, being inferior to the other two Gobiidae. This further supported the impression of decreasing population densities of bighead goby, whereas again for round goby the most stable values were obtained. As round goby had the highest 0+ densities and the best competitive strength of all analyzed species, most detrimental effects can be referred to this species.

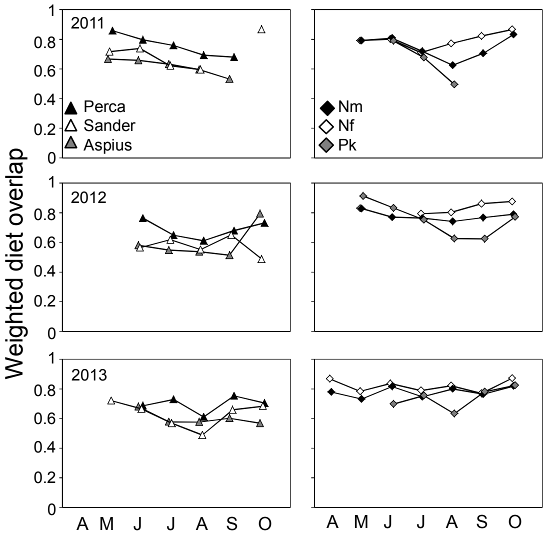

Figure 9. Weighted diet overlap O_{DW} (incorporating the density, intra- and interspecific overlaps) of native (left) and invasive species (right) for the three years in course of the season. From Chapter IV.

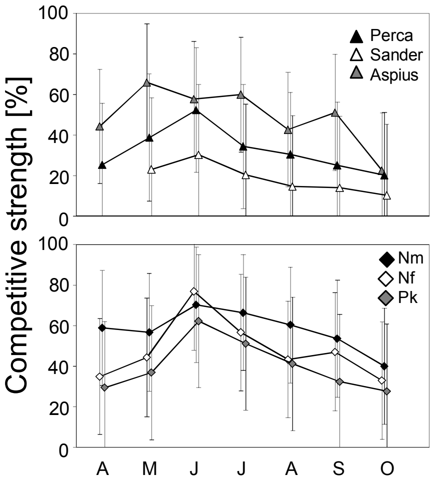

Figure 10. Competitive strength, defined as the proportion of the ISF_{MAX} (%, fitted values ± SE), indicating the dietary competitive ability, that is yielded per species in course of the season. From Chapter IV.

Predation

As detrimental effects were obtained on 0+ perch and pikeperch by being forced into a juvenile competitive bottleneck (Chapter IV), levels of predation on invasive gobies were of interest which might possibly outweigh the competitive outcome. Both Percidae included invasive gobies in their diet but in varying extent and pace.

Onset of piscivory was comparable to other regions for both species (Van Densen, 1985; Mehner et al., 1996), yet switch to an exclusively piscivory for perch was earlier than for pikeperch at a size of > 150 mm TL, whereas predation on fish for the smaller length classes was negligible. Contrary, for pikeperch piscivory already occurred for the smallest individuals, but the switch to an exclusively piscivorous diet was somewhat delayed (Van Densen, 1985; Buijse and Houthuijzen, 1992).

Early onset of piscivory is assumed to reduce intra- and interspecific competition by intraguild predation (Polis et al., 1989; Polis and Holt, 1992; Borcherding et al., 2010). Intraguild predation acted on gobies with juvenile Percidae as predators at the Lower Rhine, yet, predation of small individuals on gobies, or fish in general was still modest.

With increasing size, at clearly piscivorous stages, gobies were included in the diet of both Percidae to varying extent. Perch preyed almost exclusively on gobies and thereby picked nearly solely round gobies. Pikeperch in contrast showed no preference at all; neither between gobies or native species, nor for a single species or habitus. Selectivity in perch might be a potential adaptation to the hyper abundance of this species (Carlsson et al., 2009) combined with habitat-dependent encounter rate. Habitat usage during foraging might also explain prey choice of pikeperch, as this species hunts in nearshore habitats (Wolter and Freyhof, 2004), where juveniles of several species including invasive gobies co-occur (Chapter I, II).

For the first four length classes (up to 200 mm TL), increases in condition went along with increasing predation on gobies in course of the years (Fig. 11). A strong increase of gobies in the diet of both predators was obtained in the last year analyzed (2014), thus 8 years after the first occurrence of bighead gobies. For perch invasive gobies seemed to be a facilitation step to switch to piscivory, as gobies were abundant in small sizes all over the season (Chapter II). A similar pattern could be observed for juvenile smallmouth bass (*Micropterus dolomieu*) in Lake Erie due to high densities of gobies (Steinhart et al., 2004).

It remained unclear, why gobies were not included earlier (or to a greater extent) in the diet of perch and pikeperch, especially as it seems to be an advantageous prey item for both. In the brackish waters of northern Germany (Kiel Canal), round goby made up the most important fish prey for pikeperch leading to increased growth rates, biomass and condition of the predator within the same timespan after introduction as in this study, yet, contrary to the Lower Rhine, dietary competition seemed to be negligible between juvenile gobies and pikeperch (Hempel et al., 2016).

Although first signs of adaptation were obvious for both Percidae, this process has apparently just started and might yet not diminish the negative competitive effects of invasive gobies on juvenile perch and pikeperch (Chapter IV).

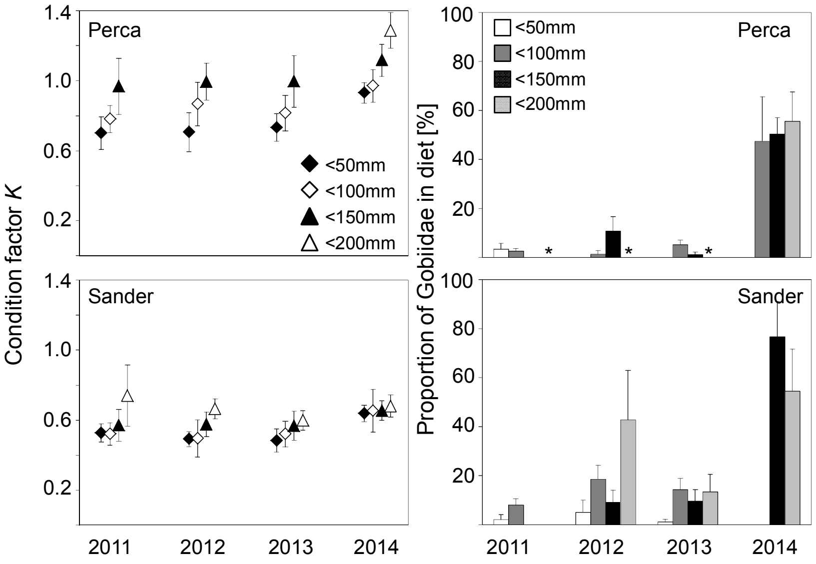

Figure 11. Condition factor *K* (mean ± SD, left) and proportion of Gobiidae in the diet (right) of the first four length classes of perch (above) and pikeperch (bottom) for the four analyzed years 2011 – 2014. *= Less than four individuals of this size class, thus data are not shown. Modified from Chapter V.

Population development Gobiidae

Work on invasive gobies started in summer 2009 at the Lower Rhine with the help of Dr. Ing. Pavel Jurajda (Institute of Vertebrate Biology, Head of the Research Facility Brno, Czech Republic) and his team, who was experienced with gobies, leading to a still ongoing, fruitful cooperation.

In 2009 bighead goby was the main representative of the three goby species making up 52.5 % of the total catch, followed by round goby with 25 %, while all other fishes (including a few individuals of monkey goby) represented less than 20 % (Borcherding et al., 2011). Since then, the pattern has strongly changed over the years; with bighead goby showing decreasing densities, whereas monkey goby showed prospering trends and round goby now displaying the highest densities.

Decreasing densities of bighead goby were not only visible within the adult community (Chapter I), but also for 0+ individuals (Chapter II). Although reproductive output was high in some years, recruitment seemed to fail for this species, probably due to competitive effects with the other gobies and its high energy demands (Chapter IV). Thus, for bighead goby I expect populations further to decrease up to a stable level, diminishing nuisance character of this species.

Although monkey goby is strongly habitat restricted, increasing population densities are assumed for this species. Due to its high competitive ability concerning resource use (Chapter IV) and its other traits like multiple spawning (Chapter II), or (yet) missing predation by perch (summarized in Tab. 2), prospering population development is expected. Indeed, increasing growth rates in course of the years for 0+ stages and increasing densities of 0+ individuals support this assumption.

As it has by far the highest densities of the three species, impact of round goby can be referred to as being the most detrimental on native biodiversity. Regardless of the objective of the study, round goby always revealed to have the most stable values, probably indicating the peak of invasion. Significantly decreasing conditions for bighead and round goby in course of the years already revealed the system to be at an edge of its capacities. While in bighead goby population decimation is just yet obvious, it is suggested to arise in round goby within the next years.

Predation on gobies might be an additional factor regulating the population densities, at least for round gobies (Chapter V). Nevertheless, invasiveness of round and monkey is extremely high and native species needed to be monitored and protected. Things will get even worse, when further hybrids, as discovered between monkey and round goby at the Lower Rhine will emerge, possibly bearing even more detrimental traits (Lindner et al., 2013).

Table 2. Profile of the ecological niche of invasive Gobiidae at the Lower Rhine. * = goby species in comparison with each other.

Species	Monkey goby (Nf)	Round goby (Nm)	Bighead goby (Pk)
Maximum size (TL)	160 mm	190 mm	190 mm
Reproduction mode	multiple	multiple	single
Parental care	paternal	paternal	paternal
Spawning season	mid-March to mid-September	mid-March to mid-September	mid-March to mid-July
Spawning habitat	unknown	stony caves in riprap	stony caves in riprap
Habitat (adult)	shallow groin fields (preference for sandy substrate)	shallow groin fields, deep waters, riprap	riprap
Habitat (0+)	shallow groin fields	shallow groin fields	shallow groin fields
Ontogenetic habitat shift	no shift	continuous sizes	ca. 60 mm TL
Drifting acitivity	May to September	April to September	April to June
Size at drifting (TL)	8.5 (± 1.4) mm	8.8 (± 1.1) mm	9.3 (± 3.3) mm
Sexual dimorphism	pronounced (spawning)	pronounced (spawning)	minimal (spawning)
Piscivory	>100 mm TL	no	>100 mm TL
Dietary competitive strength	high	high	intermediate
Metabolism*	low	intermediate	high
Activity*	low	high	intermediate
Individual consumption [$g\ g^{-1}\ d^{-1}$]	0.076 (± 0.03)	0.097 (± 0.02)	0.152 (± 0.05)
Prey for perch	little	yes	no
Prey for pikeperch	yes	yes	little
Invasion status	extremely high	extremely high	high

General findings

By intensive sampling in nursery habitats across four years not only knowledge on the population development of invasive gobies was gained. An enormous data set of densities, recruitment success, and growth rates of several native species was obtained. Distinct seasonal and diel differences in occurrence and frequency could be seen for 30 species in total (Tab. 3). Those results are of special importance for fishery management and allow the recommendation for a rational monitoring program at the Lower Rhine. The densities of gudgeon *Gobio gobio* for instance have dramatically decreased in the last years and dietary overlap revealed to be very high between gobies and this species (data not shown). However, if this trend is due to competition with the invasive gobies or just a reflection of the high variable system needs further research. Similar, competition was expected to be very high with ruffe *Gymnocephalus cernua,* but as this species only occurred in October in high abundances in those sandy groyne fields, evaluation was hindered. However, in other areas, due to their shared habitat, high dietary competition with ruffe could already be validated to occur with round goby (Rakauskas et al., 2013).

Table 3. List of species and seasonal occurrence for the years 2010-2013. ● species was present in this month every year, ◌ species was caught up to three years in this month, ○* species was present up to three years in that month, but less than 5 individuals per year, SF = single find. %* frequency of occurrence of all seinings (N=488).

Species	Apr	May	Jun	Jul	Aug	Sep	Oct	%*
Abramis brama		○	○	○	○	○	○*	13.9
Alburnus alburnus	○	○	●	●	●	○	●	27.8
Anguilla anguilla		SF		SF				0.37
Aspius aspius	○*	○	○	●	●	●	○	35.1
Barbus barbus	○*	○	○	●	○*	○*		14.8
Blicca bjoerkna		○	○	○	○*	○	○*	7.8
Chondrostoma nasus		○	○	○	●	○*	○	11.1
Cobitis taenia	○*	○*	○*	○*	○*	○*		3
Coregonus sp.	○*	○						2.8
Cyprinus carpio			SF	○*				0.6
Esox lucius				○*				0.6
Gasterosteus aculeatus	○*	○	●	●	○	○	○	16.1
Gobio sp.	○*	○	○	○	○*			12.1
Gymnocephalus cernua		○*	○	●	●	●	●	14.1
Squalius cephalus					SF			0.2
Leuciscus idus		○	○	●	○	●	●	51.6
Leuciscus leuciscus	○*	○	○	●	○	○	●	23.4
Neogobius fluviatilis	●	●	●	●	●	●	●	78.7
Neogobius melanostomus	●	●	●	●	●	●	●	90.4
Perca fluviatilis	○	○	●	●	●	●	●	64.2
Ponticola kessleri	●	●	●	●	●	●	●	59.9
Platichthys flesus	SF	○*	SF	○*				1.1
Proterorhinus semilunaris		○*	○*	○*				1.5
Pseudorasbora parva		○*	SF	SF				0.7
Rhodeus amarus				SF				0.2
Rutilus rutilus	○*	○	○	●	●	●	●	46
Sander lucioperca	○*	●	●	●	●	●	●	50.5
Scardinius erythrophtalmus		SF						0.2
Tinca tinca			SF					0.2
Vimba vimba			○	○				1.5

Conclusions

In the first chapter, we could show fine-tuned dietary niche separation on a spatial and temporal axis between the three goby species. The second paper revealed additional distinct separations in reproductive traits apparent in onset and intensity of spawning. Further resource partitioning occurred by temporal separation of drifting and drifting of different sized gobies (Chapter III). All those niche differentiations and resource partitioning allowed the co-occurrence of the three congeneric goby species at the Lower Rhine. However, differences in dietary competitive ability (Chapter IV), as well as the occurrence of reproductive failures and low recruitment rates, have already led to a decline in bighead goby densities. The bighead goby population is expected to further decrease, whereas for monkey goby prospering trends are assumed and round goby might have reached the peak of invasion (see section “Population development Gobiidae”).

Interactions with native species were obtained in the last two chapters represented as competition and predation and revealing a bottom-up – top-down system acting on a temporal axis. Dietary competition was shown to be dramatically high in this food limited system (Chapter IV). Especially perch and pikeperch, two native Percidae, are clearly suffering by the food shortage induced by the invasive gobies and are forced into a juvenile competitive bottleneck. Chapter V showed how two piscivorous predators of the same family adapted to the novel prey of Gobiidae in varying extent and pace. Although levels of predation on gobies increased in the last year (2014) and went along with an improvement in the condition of perch and pikeperch, by now predation cannot outweigh effects of the juvenile competitive bottleneck. However, if youngest 0+ individuals of perch and pikeperch would also adapt to this novel prey and adult specimens would keep on preying to a great extent on gobies, this could counteract the hyper abundance of invasive Gobiidae and reduce levels of competition effectively.

Management plans

With the establishment of invasive gobies, severe consequences for the native fauna developed. Complete eradication of an invasive species might work on an isolated island, e.g., by the use of poison (Taylor and Thomas, 1989), but will surely not be applicable to a freshwater stream that is used as major transport route for Europe (Leuven et al., 2009). As a complete removal of the invasive gobies is utopian, management strategies have to focus on the recovery and protection of native diversity. The River Rhine as a degraded, strongly anthropogenic altered habitat represents a non-suitable area for spawning and recruitment of native species. As several fishes prefer the backwaters for spawning and usage as nursery habitat (Scharbert and Borcherding, 2013), their connectivity needs to be improved. Due to soil erosion of the main channel lateral connectivity, and thus, floodplain area has strongly decreased in the past decades (Buijse et al., 2002). Therefore, a lowering of the surrounding area is required to regenerate floodplain functioning.

Intensive fishing of gobies for commercial purposes could additionally support native species. In their native range, Gobiidae are a delicate food. I have tried them myself and can absolutely recommend it, as it is easy to catch in huge amounts by angling and simple to prepare. A commercial use as ingredient for dog or cat food is likewise conceivable. In general, anglers have to be better informed and enlightened how to use gobies as bait (and food) and to not further spread them via bait buckets.

Lastly, a well-organized monitoring program needs to be applied to follow population development of the invasive Gobiidae and to early detect the occurrence of potential new invaders.

Future Studies

Our studies on invasive gobies at the Lower Rhine could almost gapless unveil the ecological niche of three invasive Gobiidae occupied at the Lower Rhine. Yet, this is a highly variable system and several processes have just started or are still in progress. Thus, future studies should include the monitoring of goby population densities with special emphasis on the development of competitive and predatory interactions. In addition, a comparison with native populations is absolutely necessary, as here even basic data are missing. Studying native populations might give important hints why those invasive gobies have become such a pest beyond their native distribution and might therefore deliver important information for management.

Up to now it could not be clarified in the field, where adult monkey gobies spawn. In laboratory studies this species preferred cave like structures with a curved ceiling for placement of eggs and the male also guarded those eggs (personal observation), supposing that the riprap structure which is used by the other two species might also be suitable for monkey goby. However, no monkey goby at all could ever be caught with electro-fishing in those habitats. Additionally, angling data also obtained no catches of this species in either the riprap or deeper sandy areas (data not shown).

As mentioned in the thesis, studies on drifting gobies should focus on the trigger of dispersal. What initiates drifting and which individuals are going into the drift? Are there differences in condition and how far can 0+ individuals drift? Answering those questions might shed light on invasion spread and dispersal ability.

Competitive interactions with natives focused on perch and pikeperch at the Lower Rhine, manifesting detrimental effects on those two species. The occurrence and consequences of the juvenile competitive bottleneck should be compared with other invaded regions, which also host at least a subset of those species. Why is the impact on perch and pikeperch here so substantial, but did not seem to arise in other areas (Hempel et al., 2016)? As these interactions should be further examined, other native species might also be affected by competitive interactions. One example could be the potential dietary competition with ruffe or gudgeon, two benthic orientated species. Competition might also act on other axes like habitat usage. Although the artificial riprap structure is avoided by several native species, some natives like eel *Anguilla anguilla* (or again ruffe) are dependent on those structures and might be displaced by the aggressive gobies.

Predation has just started on gobies by perch and pikeperch. This adaptation to novel prey should definitely be further investigated. Laboratory studies on preference for single species could be added, or studies to see if the increase in condition is related to goby prey per se or just reflected the decreased encounter rate with native prey. Energy content of fishes varies species specifically (Ball et al., 2007), whereby demersal fish in general have intermediate energy densities compared to pelagic fishes, which have been shown to have either very high or low values (Anthony et al., 2000). Thus, a determination of the energy content of the three goby species in comparison with natives would help to assess the value of gobies as prey.

Predation of asp on gobies might arise, which could not be determined in this study due to missing large individuals. As there is no competitive bottleneck on juvenile asp, this species could be an effective predator on gobies. Indeed, communications with anglers in this region reveal more and more catches of asp close to the ground and not, as it used to be, in surface waters, indicating a possible switch in habitat and thus potentially dietary usage. This would include a great adaptive plasticity, surely requiring further studies. Dietary analyses on a piscivorous bird the cormorant *Phalacrocorax carbo sinensis* have just started in our working group, revealing this species to prey on gobies, but yet it is unknown to which extent it is included in the diet (personal communication S. Wantia).

References

Adamek, Z., Andreji, J., Gallardo, J. M., 2007. Food habits of four bottom-dwelling Gobiid species at the confluence of the Danube and Hron Rivers (South Slovakia). Internat. Rev. Hydrobiol. 92, 554-563.

Aldridge, D. W., 1982. Reproductive tactics in relation to life-cycle bioenergetics in three natural populations of the freshwater snail, *Leptoxis carinata*. Ecology 63, 196-208.

Almqvist, G., Strandmark, A. K., Appelberg, M., 2010. Has the invasive round goby caused new links in Baltic food webs? Env. Biol. Fish. 89, 79-93.

Amundsen, P. A., Gabler, H. M., Staldvik, F. J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data - Modification of the Costello (1990) method. J. Fish Biol. 48, 607-614.

Amundsen, P. A., Salonen, E., Niva, T., Gjelland, K. O., Praebel, K., Sandlund, O. T., Knudsen, R., Bohn, T., 2012. Invader population speeds up life history during colonization. Biol. Invasions 14, 1501-1513.

Andersson, M., Simmons, L. W., 2006. Sexual selection and mate choice. Trends Ecol. Evol. 21, 296-302.

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., Chunco, A. J., 2011. Do species traits predict recent shifts at expanding range edges? Ecol. Lett. 14, 677-689.

Anthony, J. A., Roby, D. D., Turco, K. R., 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. exp. mar. Biol. Ecol. 248, 53-78.

Aquiloni, L., Brusconi, S., Cecchinelli, E., Tricarico, E., Mazza, G., Paglianti, A., Gherardi, F., 2010. Biological control of invasive populations of crayfish: the European eel (*Anguilla anguilla*) as a predator of *Procambarus clarkii*. Biol. Invasions 12, 3817-3824.

Arim, M., Abades, S. R., Neill, P. E., Lima, M., Marquet, P. A., 2006. Spread dynamics of invasive species. Proc. Natl. Acad. Sci. U. S. A. 103, 374-378.

Bagenal, T. B., Tesch, F. W., 1978. Age and growth. In: Ed: T. B. Bagenal, Methods for assessment of fish production in fresh waters. Blackwell Scientific Pub., Oxford, London, Edinburgh, Melbourne, pp. 101-136.

Ball, J. R., Esler, D., Schmutz, J. A., 2007. Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators. Polar Biol. 30, 699-708.

Bampfylde, C. J., Lewis, M. A., 2007. Biological control through intraguild predation: Case studies in pest control, invasive species and range expansion. Bull. Math. Biol. 69, 1031-1066.

Banks, N. C., Paini, D. R., Bayliss, K. L., Hodda, M., 2015. The role of global trade and transport network topology in the human-mediated dispersal of alien species. Ecol. Lett. 18, 188-199.

Barber, N. A., Marquis, R. J., Tori, W. P., 2008. Invasive prey impacts the abundance and distribution of native predators. Ecology 89, 2678-2683.

Bauer, J. T., 2012. Invasive species: "back-seat drivers" of ecosystem change? Biol. Invasions 14, 1295-1304.

Beckmann, C., Shine, R., 2011. Toads tongue for breakfast: exploitation of a novel prey type, the invasive cane toad, by scavenging raptors in tropical Australia. Biol. Invasions 13, 1447-1455.

Beeck, P., Tauber, S., Kiel, S., Borcherding, J., 2002. 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. Freshwat. Biol. 47, 2359-2369.

Begon, M., Townsend, C. R., Harper, J. L., 2005. Ecology - From Individuals to Ecosystems. 4th edition. Blackwell Publishing, Oxford.

Bij de Vaate, A., Breukel, R., van der Velde, G., 2006. Long-term developments in ecological rehabilitation of the main distributaries in the Rhine delta: fish and macroinvertebrates. Hydrobiologia 565, 229-242.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Can. J. Fish. Aquat. Sci. 59, 1159-1174.

Bij de Vaate, A., Klink, A. G., 1995. *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae) a new immigrant in the Dutch part of the Lower Rhine. Lauterbornia 20, 51-54.

Borcherding, J., Beeck, P., DeAngelis, D. L., Scharf, W. R., 2010. Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. J. Anim. Ecol. 79, 1101-1112.

Borcherding, J., Staas, S., 2008. Local riverine fish communities as promoters for habitat restoration in the floodplain area of the lower Rhine. Am. Fish. Soc. Symp. 49, 835-843.

Borcherding, J., Staas, S., Krüger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Borcherding, J., Sturm, W., 2002. The seasonal succession of macroinvertebrates, in particular the zebra mussel (*Dreissena polymorpha*), in the River Rhine and two neighbouring gravel-pit lakes monitored using artificial substrates. Internat. Rev. Hydrobiol. 87, 165-181.

Born, W., Rauschmayer, F., Bräuer, I., 2005. Economic evaluation of biological invasions–a survey. Ecol. Econ. 55, 321-336.

Bowler, D. E., Benton, T. G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol. Rev. 80, 205-225.

Bronnenhuber, J. E., Dufour, B. A., Higgs, D. M., Heath, D. D., 2011. Dispersal strategies, secondary range expansion and invasion genetics of the nonindigenous round goby, *Neogobius melanostomus*, in Great Lakes tributaries. Mol. Ecol. 20, 1845-1859.

Brown, A. V., Armstrong, M. L., 1985. Propensity to drift downstream among various species of fish. J. Freshwater Ecol. 3, 3-17.

Brown, B. J., Mitchell, R. J., Graham, S. A., 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83, 2328-2336.

Buczkowski, G., 2010. Extreme life history plasticity and the evolution of invasive characteristics in a native ant. Biol. Invasions 12, 3343-3349.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., Van Geest, G. J., Grift, R. E., Ibelings, B. W., Oosterberg, W., Roozen, F. C. J. M., 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwat. Biol. 47, 889-907.

Buijse, A. D., Houthuijzen, R. P., 1992. Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Can. J. Fish. Aquat. Sci. 49, 894-902.

Bull, J. J., 1983. Evolution of sex determining mechanisms. The Benjamin/Cummings Publishing Company, Inc..

Byers, J. E., 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97, 449-458.

Byström, P., Persson, L., Wahlström, E., 1998. Competing predators and prey: Juvenile bottlenecks in whole-lake experiments. Ecology 79, 2153-2167.

Cadotte, M. W., Murray, B. R., Lovett-Doust, J., 2006. Ecological patterns and biological invasions: using regional species inventories in macroecology. Biol. Invasions 8, 809-821.

Campbell, N. A., Reece, J. B., Markl, J., 2003. Biologie. 6. Aufl. Heidelberg: Spektrum.

Capova, M., Zlatnicka, I., Kovac, V., Katina, S., 2008. Ontogenetic variability in the external morphology of monkey goby, *Neogobius fluviatilis* (Pallas, 1814) and its relevance to invasion potential. Hydrobiologia 607, 17-26.

Carlsson, N. O., Brönmark, C., Hansson, L. A., 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. Ecology 85, 1575-1580.

Carlsson, N. O., Sarnelle, O., Strayer, D. L., 2009. Native predators and exotic prey-an acquired taste? Front. Ecol. Environ. 7, 525-532.

Caut, S., Angulo, E., Courchamp, F., 2008. Dietary shift of an invasive predator: rats, seabirds and sea turtles. J. Appl. Ecol. 45, 428-437.

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J., Rudinka, S., 1997. The round goby *Neogobius melanostomus* (Pallas). A review of European and North American Literature, 96 ed. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey, INHS Special Publication No. 20.

Chernyaev, Z., 2007. Factors and possible mechanisms causing changes in the rate of embryonic development of bony fish (with reference to Coregonidae). J. Ichthyol. 47, 494-503.

Clapham, P. J., 1996. The social and reproductive biology of humpback whales: an ecological perspective. Mammal Rev. 26, 27-49.

Cohen, D., 1976. The optimal timing of reproduction. Am. Nat., 801-807.

Colautti, R. I., Ricciardi, A., Grigorovich, I. A., MacIsaac, H. J., 2004. Is invasion success explained by the enemy release hypothesis? Ecol. Lett. 7, 721-733.

Colwell, R. K., Futuyma, D. J., 1971. On the measurement of niche breadth and overlap. Ecology, 567-576.

Copp, G. H., Faulkner, H., Doherty, S., Watkins, M. S., Majecki, J., 2002. Diel drift behaviour of fish eggs and larvae, in particular barbel, *Barbus barbus* (L.), in an English chalk stream. Fisheries Manag. Ecol. 9, 95-103.

Corkum, L. D., MacInnis, A. J., Wickett, R. G., 1998. Reproductive habits of round goby. Gt. Lakes Res. Rev. 3, 13-20.

Cornell, H. V., Lawton, J. H., 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities - A theoretical perspective. J. Anim. Ecol. 61, 1-12.

Cucherousset, J., Copp, G., Fox, M., Sterud, E., van Kleef, H., Verreycken, H., Zahorskí, E., 2009. Life-history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. Biol Invasions 11, 2171-2180.

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A., Ragnarsson, B., 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. Can. J. Zool. 82, 1864-1870.

Davidson, A. M., Jennions, M., Nicotra, A. B., 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecol. Lett. 14, 419-431.

de Almeida Jácomo, A. T., Silveira, L., Diniz-Filho, J. A. F., 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. J. Zool. 262, 99-106.

De Roos, A. M., Persson, L., McCauley, E., 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecol. Lett. 6, 473-487.

deRivera, C. E., Ruiz, G. M., Hines, A. H., Jivoff, P., 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. Ecology 86, 3364-3376.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., Ewers, R. M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol. Evol. 22, 489-496.

Dubs, D. O. L., Corkum, L. D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. 22, 838-844.

Duffy, D. C., 1983. Competition for nesting space among Peruvian guano birds. Auk, 680-688.

Dugatkin, L. A., 1992. Sexual selection and imitation: females copy the mate choice of others. Am. Nat., 1384-1389.

Eklöv, P., 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. Anim. Behav. 44, 313-326.

Fiedler, K., 1991. Lehrbuch der Speziellen Zoologie, Band II, Teil 2: Fische. Gustav Fischer Verlag, Jena.

Freeman, A. S., Byers, J. E., 2006. Divergent induced responses to an invasive predator in marine mussel populations. Science 313, 831-833.

Gadomski, D. M., Barfoot, C. A., 1998. Diel and distributional abundance patterns of fish embryos and larvae in the lower Columbia and Deschutes rivers. Env. Biol. Fish. 51, 353-368.

Gale, W. F., Mohr, J. R. H. W., 1978. Larval fish drift in a large river with a comparison of sampling methods. T. Am. Fish Soc. 107, 46-55.

Gaston, K. J., 2003. The structure and dynamics of geographic ranges. Oxford University Press.

Geiger, W., Alcorlo, P., Baltanas, A., Montes, C., 2005. Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands. Issues in Bioinvasion Science. Springer, pp. 49-73.

Gherardi, F., Daniels, W. H., 2004. Agonism and shelter competition between invasive and indigenous crayfish species. Can. J. Zool. 82, 1923-1932.

Goodman, D., 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theor. Popul. Biol. 25, 1-20.

Gozlan, R. E., Britton, J. R., Cowx, I., Copp, G. H., 2010. Current knowledge on non-native freshwater fish introductions. J. Fish Biol. 76, 751-786.

Grabowska, J., Grabowski, M., Kostecka, A., 2009. Diet and feeding habits of monkey goby (*Neogobius fluviatilis*) in a newly invaded area. Biol. Invasions 11, 2161-2170.

Greenberg, L. A., Paszkowski, C. A., Tonn, W. M., 1995. Effects of prey species composition and habitat structure on foraging by two functionally distinct piscivores. Oikos 74, 522-532.

Greenwood, P. J., 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28, 1140-1162.

Gregory, P. T., 1978. Feeding habits and diet overlap of three species of garter snakes (Thamnophis) on Vancouver Island. Can. J. Zool. 56, 1967-1974.

Griffen, B. D., Guy, T., Buck, J. C., 2008. Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. Journal of Animal Ecology 77, 32-40.

Griffith, T. M., Watson, M. A., 2005. Stress avoidance in a common annual: reproductive timing is important for local adaptation and geographic distribution. J. Evol. Biol. 18, 1601-1612.

Grift, R. E., Buijse, A. D., Van Densen, W. L. T., Machiels, M. A. M., Kranenbarg, J., Breteler, J. P. K., Backx, J. J. G. M., 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Res. Applic. 19, 353-374.

Gross, M. R., Sargent, R. C., 1985. The evolution of male and female parental care in fishes. Am. Zool. 25, 807-822.

Guo, Z., Cucherousset, J., Lek, S., Li, Z., Zhu, F., Tang, J., Liu, J., 2013. Comparative study of the reproductive biology of two congeneric and introduced goby species: implications for management strategies. Hydrobiologia 709, 89-99.

Hansen, D. M., Olesen, J. M., Jones, C. G., 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? J. Biogeogr. 29, 721-734.

Hardenbicker, P., Rolinski, S., Weitere, M., Fischer, H., 2014. Contrasting long-term trends and shifts in phytoplankton dynamics in two large rivers. Int. Rev. Hydrobiol. 99, 287-299.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Harrington, L. A., Harrington, A. L., Yamaguchi, N., Thom, M. D., Ferreras, P., Windham, T. R., Macdonald, D. W., 2009. The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression. Ecology 90, 1207-1216.

Hart, D. D., 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia 73, 41-47.

Hauzy, C., Huloz, F. D., Gins, A., Loreau, M., 2007. Intra- and interspecific density-dependent dispersal in an aquatic prey-predator system. J. Anim. Ecol. 76, 552-558.

Hayden, T. A., Miner, J. G., 2009. Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: diel vertical migration of early juvenile round goby. Biol. Invasions 11, 1767-1776.

Heermann, L., Borcherding, J., 2013. Competition, predation, cannibalism: the development of young of the year perch populations in ponds with bream or roach. J. Appl. Ichthyol. 29, 549-554.

Hegge, O., Hesthagen, T., Skurdal, J., 1993. Juvenile competitive bottleneck in the production of brown trout in hydroelectric reservoirs due to intraspecific habitat segregation. Regul. Rivers 8, 41-48.

Hempel, M., Neukamm, R., Thiel, R., 2016. Effects of introduced round goby (*Neogobius melanostomus*) on diet composition, growth and biomass of zander (*Sander lucioperca*), a main predator in Northern European brackish waters. Aquat. Invasions (accepted).

Hensler, S. R., Jude, D. J., 2007a. Diel vertical migration of round goby larvae in the great lakes. J. Great Lakes Res. 33, 295-302.

Hensler, S. R., Jude, D. J., 2007b. Diel vertical migration of round goby larvae in the great lakes. J. Great Lakes Res. 33, 295-302.

Hirshfield, M. F., Tinkle, D. W., 1975. Natural selection and the evolution of reproductive effort. Proc. Natl. Acad. Sci. U. S. A. 72, 2227-2231.

Holeck, K. T., Mills, E. L., MacIsaac, H. J., Dochoda, M. R., Colautti, R. I., Ricciardi, A., 2004. Bridging troubled waters: Biological invasions, transoceanic shipping, and the Laurentian Great Lakes. BioScience 54, 919-929.

Holway, D. A., 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology 80, 238-251.

Houghton, C. J., 2015. Round goby-induced changes in young-of-year yellow perch diet and habitat selection.PhD thesis. University of Wisconsin Milwaukee, 81 pp.

Humphries, P., 2005. Spawning time and early life history of Murray cod, *Maccullochella peelii* (Mitchell) in an Australian river. Environ. Biol. Fish. 72, 393-407.

Hyslop, E. J., 1980. Stomach content analysis - a review of methods and their application. J. Fish Biol. 17, 411-429.

Jakubas, D., 2004. The response of the grey heron to a rapid increase of the round goby. Waterbirds 27, 304-307.

James, C., Shine, R., 1985. The seasonal timing of reproduction. Oecologia 67, 464-474.

Janac, M., Slapansky, L., Valova, Z., Jurajda, P., 2013. Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. Ecology of Freshwater Fish 22, 430-438.

Janssen, J., Jude, D. J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27, 319-328.

Jaroszewska, M., Dabrowski, K., Wilczynska, B., Kakarekok, T., 2008. Structure of the gut of the racer goby *Neogobius gymnotrachelus* (Kessler, 1857). J. Fish Biol. 72, 1773-1786.

Johnston, T. A., Gaboury, M. N., Janusz, R. A., Janusz, L. R., 1995. Larval fish drift in the Valley River, Manitoba - influence of abiotic and biotic factors, and relationships with future year class strengths. Can. J. Fish. Aquat. Sci. 52, 2423-2431.

Jude, D. J., Reider, R. H., Smith, G. R., 1992. Establishment of Gobiidae in the Great-Lakes Basin. Can. J. Fish. Aquat. Sci. 49, 416-421.

Jurajda, P., 1998. Drift of larval and juvenile fishes, especially *Rhodeus sericeus* and *Rutilus rutilus*, in the River Morava (Danube basin). Arch. Hydrobiol. 141, 231-241.

Kalinina, E., 1976. Reproduction and development of Azov-Black Sea gobies. Naukova Dumka, Kiev.

Kalweit, H., 1993. Der Rhein unter der Einwirkung des Menschen. Ausbau, Schiffahrt, Wasserwirtschaft. Internationale Kommission für die Hydrologie des Rheingebietes, Lelystad.

Karatayev, A., Burlakova, L., Padilla, D., Mastitsky, S., Olenin, S., 2009. Invaders are not a random selection of species. Biol. Invasions 11, 2009-2019.

Karlson, A. M. L., Almqvist, G., Skora, K. E., Appelberg, M., 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64, 479-486.

Kiesecker, J. M., Blaustein, A. R., Miller, C. L., 2001. Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. Ecology 82, 1964-1970.

Koblickaya, A. P., 1981. Key for identifying young freshwater fishes (in Russian). Light and Food Industrial House, Moskau.

Kolar, C. S., Lodge, D. M., 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16, 199-204.

Konecna, M., Jurajda, P., 2012. Population structure, condition, and reproduction characteristics of native monkey goby, *Neogobius fluviatilis* (Actinopterygii: Perciformes: Gobiidae), in the Bulgarian Danube. Acta Ichthyol. Piscat. 42, 321-327.

Kornis, M. S., Mercado-Silva, N., Van der Zanden, M. J., 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. J. Fish Biol. 80, 235-285.

Kovac, V., Copp, G. H., Sousa, R. P., 2009. Life-history traits of invasive bighead goby *Neogobius kessleri* (Gunther, 1861) from the middle Danube River, with a reflection on which goby species may win the competition. J. Appl. Ichthyol. 25, 33-37.

Kovac, V., Siryova, S., 2005. Ontogenetic variability in external morphology of bighead goby *Neogobius kessleri* from the Middle Danube, Slovakia. J. Appl. Ichthyol. 21, 312-315.

Krönke, F., 2008. Ein ambivalenter Immigrant im Aquarium: *Neogobius melanostomus*, die Schwarzmaulgrundel. AKFS-aktuell 21, 9-14.

Krpo-Cetkovic, J., Hegedis, A., Lenhardt, M., 2010. Diet and growth of asp, *Aspius aspius* (Linnaeus, 1758), in the Danube River near the confluence with the Sava River (Serbia). J. Appl. Ichthyol. 26, 513-521.

Kujawa, R., Mamcarz, A., Skrzypczak, A., Kucharczyk, D., 1998. Feeding habits of asp *Aspius aspius* larvae (Cyprinidae) in Lake Maroz, Poland. Ital. J. Zool. 65, Suppl., 235-236.

Kureck, A., 1992. Neue Tiere im Rhein - Die Wiederbesiedlung des Stroms und die Ausbreitung der Neozoen. Naturwiss. 79, 533-540.

Kvarnemo, C., Ahnesjo, I., 1996. The dynamics of operational sex ratios and competition for mates. Trends Ecol. Evol. 11, 404-408.

Le Boeuf, B. J., 1974. Male-male competition and reproductive success in elephant seals. Am. Zool. 14, 163-176.

Leuven, R. S. E. W., Van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. J. R., de Vaate, A. B., 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. Biol. Invasions 11, 1989-2008.

Liley, N. R., Stacey, N. E., 1983. Hormones, pheromones, and reproductive behavior in fish. Fish Physiol. 9.

Lindner, K., Cerwenka, A. F., Brandner, J., Gertzen, S., Borcherding, J., Geist, J., Schliewen, U. K., 2013. First evidence for interspecific hybridisation between invasive goby species *Neogobius fluviatilis* and *N. melanostomus* (Teleostei: Gobiidae: Benthophilinae). J. Fish Biol. 82, 2128-2134.

Llewelyn, J., Schwarzkopf, L., Alford, R., Shine, R., 2010. Something different for dinner? Responses of a native Australian predator (the keelback snake) to an invasive prey species (the cane toad). Biol. Invasions 12, 1045-1051.

Logachev, V. S., Mordvinov, Y. E., 1979. Swimming speed and activity of larvae of round goby and some predatory crustaceans of the Black Sea. Biol. Morya, pp. 77-80.

Lovell, S. J., Stone, S. F., Fernandez, L., 2006. The economic impacts of aquatic invasive species: a review of the literature. Agric. Resour. Econ. Rev. 35, 195.

Lucas, M. C., Baras, E., 2002. Migration of Freshwater Fishes. Blackwell Science, Oxford.

Madenjian, C. P., Stapanian, M. A., Witzel, L. D., Einhouse, D. W., Pothoven, S. A., Whitford, H. L., 2011. Evidence for predatory control of the invasive round goby. Biol. Invasions 13, 987-1002.

Magnhagen, C., Staffan, F., 2003. Social learning in young-of-the-year perch encountering a novel food type. J. Fish Biol. 63, 824-829.

Magoulick, D. D., Lewis, L. C., 2002. Predation on exotic zebra mussels by native fishes: effects on predator and prey. Freshwat. Biol. 47, 1908-1918.

Mcevoy, L. A., Mcevoy, J., 1992. Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. J. Fish Biol. 41, 125-136.

Medley, K. A., 2010. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. Glob. Ecol. Biogeogr. 19, 122-133.

Mehner, L., 2013. Metabolic rates of three invasive Gobiidae in the Lower Rhine - Oxygen consumption under varying conditions. Bachelor Thesis, University of Cologne, 90 pp.

Mehner, T., Schultz, H., Bauer, D., Herbst, R., Voigt, H., Benndorf, J., 1996. Intraguild predation and cannibalism in age 0 perch (*Perca fluviatilis*) and age 0 zander (*Stizostedion lucioperca*): interactions with zooplankton succession, prey fish availability and temperature. Ann. Zool. Fennici 33, 353-361.

Michaud, J. P., 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environ. Entomol. 31, 827-835.

Migdalski, E. C., Fichter, G. S., Weaver, N., 1976. The fresh and salt water fishes of the world. Random House Value Publishing.

Miller, P. J., 1984. The tokology of gobioid fishes. In: Potts,G.W., Wooton,R.J. (Eds.), Fish reproduction strategies and tactics. Academic Press, London UK, pp. 119-153.

Mistri, M., 2004. Prey preference of *Carcinus aestuarii*: possible implications with the control of an invasive mytilid and Manila clam culture in a northern Adriatic lagoon. Aquaculture 230, 261-272.

Moiseyeva, Y. B., 1983. The development of the gonads of the round goby *Neogobius melanostomus* (Gobiidae), during the embryonic period. J. Ichthyol. 23, 64-74.

Molls, F., 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. J. Fish Biol. 55, 1187-1200.

Mooij, W. M., 1989. A key to the identification of larval bream, *Abramis brama*, white bream, *Blicca bjoerkna*, and roach, *Rutilus rutilus*. J. Fish Biol. 34, 111-118.

Mooney, H. A., Cleland, E. E., 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the United States of America 98, 5446-5451.

Moore, J. W., Herbst, D. B., Heady, W. N., Carlson, S. M., 2012. Stream community and ecosystem responses to the boom and bust of an invading snail. Biol. Invasions 14, 2435-2446.

Moskalkova, K. I., 1989. Anatomical histological and functional peculiarities of development of the intestine in round goby, *Neogobius melanostomus*, a species with direct type of development. J. Ichthyol. 29, 108-122.

Munro, A. D., Scott, A. P., Lam, T. J., 1990. Reproductive seasonality in teleosts : environmental influences. CRC Press, Boca Raton (Florida).

Musil, J., Adamek, Z., 2007. Piscivorous fishes diet dominated by the Asian cyprinid invader, topmouth gudgeon (*Pseudorasbora parva*). Biologia 62, 488-490.

Nambiar, E. S., Sands, R., 1993. Competition for water and nutrients in forests. Can. J. For. Res. 23, 1955-1968.

Neill, W. E., 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology 56, 809-826.

Nilsson, P. A., Turesson, H., Brönmark, C., 2006. Friends and foes in foraging: intraspecific interactions act on foraging-cycle stages. Behaviour 143, 733-745.

O'Connor, R. J., Usher, M. B., Gibbs, A., Brown, K. C., 1986. Biological characteristics of invaders among bird species in Britain [and discussion]. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 314, 583-598.

Oesmann, S., 2003. Vertical, lateral and diurnal drift patterns of fish larvae in a large lowland river, the Elbe. J. Appl. Ichthyol. 19, 284-293.

Olson, M. H., Mittelbach, G. G., Osenberg, C. W., 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76, 1758-1771.

Oppenheimer, J. R., 1970. Mouthbreeding in fishes. Anim. Behav. 18, 493-503.

Pangle, K. L., Peacor, S. D., 2006. Non–lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. Freshw. Biol. 51, 1070-1078.

Pavlov, D. S., 1994. The downstream migration of young fishes in rivers - mechanisms and distribution. Folia Zool. 43, 193-208.

Perry, W. L., Lodge, D. M., Lamberti, G. A., 1997. Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake-outlet stream. Can. J. Fish. Aquat. Sci. 54, 120-125.

Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations. In: Eds: B. Ebenman, L. Persson, Size-Structured Populations. Springer-Verlag, Berlin, Heidelberg, pp. 203-218.

Persson, L., Greenberg, L. A., 1990a. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. Ecology 71, 44-56.

Persson, L., Greenberg, L. A., 1990b. Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a resource gradient. Ecology 71, 1699-1713.

Phillips, B. L., Shine, R., 2006. An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. Proc. R. Soc. Lond. B. Biol. Sci. 273, 1545-1550.

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52, 273-288.

Pinder, A. C., 2001. Keys to larval and juvenile stages of coarse fishes from freshwaters in the British Isles. Freshwater Biological Association, Ambleside.

Plath, M., Makowicz, A. M., Schlupp, I., Tobler, M., 2007. Sexual harassment in live-bearing fishes (Poeciliidae): comparing courting and noncourting species. Behav. Ecol. 18, 680-688.

Polacik, M., Janac, M., Jurajda, P., Adamek, Z., Ondrackova, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecol. Freshwat. Fish 18, 640-649.

Polis, G. A., Holt, R. D., 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. 7, 151-155.

Polis, G. A., Myers, C. A., Holt, R. D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. System., 297-330.

Popova, O. A., Sytina, L. A., 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish Res. Board Can. 34, 1559-1570.

Posey, M. H., Wigand, C., Stevenson, J. C., 1993. Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the upper Chesapeake Bay. Estuar. Coast. Shelf S. 37, 539-555.

Post, J. R., Parkinson, E. A., 2001. Energy allocation strategy in young fish: Allometry and survival. Ecology 82, 1040-1051.

R Development Core Team, 2009. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. (ISBN 3-900051-07-0).

Rakauskas, V., Putys, Z., Dainys, J., Lesutiene, J., Lozys, L., Arbaciauskas, K., 2013. Increasing population of the invader round goby, *Neogobius melanostomus* (Actinopterygii: Perciformes: Gobiidae), and its trophic role in the Curonian Lagoon, SE Baltic Sea. Acta Ichthyol. Piscat. 43, 95-108.

Reichard, M., Jurajda, P., 2007. Seasonal dynamics and age structure of drifting cyprinid fishes: an interspecific comparison. Ecol. Freshwat. Fish 16, 482-492.

Reichard, M., Jurajda, P., Ondrackova, M., 2002. The effect of light intensity on the drift of young-of-the-year cyprinid fishes. J. Fish Biol. 61, 1063-1066.

Reichard, M., Jurajda, P., Smith, C., 2004. Male-male interference competition decreases spawning rate in the European bitterling (*Rhodeus sericeus*). Behav. Ecol. Sociobiol. 56, 34-41.

Reyjol, Y., Brodeur, P., Mailhot, Y., Mingelbier, M., Dumont, P., 2010. Do native predators feed on non-native prey? The case of round goby in a fluvial piscivorous fish assemblage. J. Great Lakes Res. 36, 618-624.

Ricciardi, A., MacIsaac, H. J., 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. 15, 62-65.

Ricciardi, A., Rasmussen, J. B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can. J. Fish. Aquat. Sci. 55, 1759-1765.

Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Divers. Distrib. 12, 425-433.

Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries and Marine Service, Canada.

Rius, M., McQuaid, C. D., 2009. Facilitation and competition between invasive and indigenous mussels over a gradient of physical stress. Basic Appl. Ecol. 10, 607-613.

Rodda, G. H., Fritts, T. H., Chiszar, D., 1997. The disappearance of Guam's wildlife - New insights for herpetology, evolutionary ecology, and conservation. BioScience 47, 565-574.

Rodriguez, L. F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol. Invasions 8, 927-939.

Roemer, G. W., Donlan, C. J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Natl. Acad. Sci. U. S. A. 99, 791-796.

Ross, S. T., 1986. Resource partitioning in fish assemblages - A review of field studies. Copeia 1986(2), 352-388.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., Weller, S. G., 2001. The population biology of invasive species. Ann. Rev. Ecol. System. 32, 305-332.

Salonen, E., Amundsen, P. A., Bohn, T., Jankun, M., Brzuzan, P., Hliwa, P., Luczynski, M., 2007. Boom and bust development by invading vendace *Coregonus albula* in the subarctic Inari-Pasvik watershed (Finland, Norway and Russia). Adv. Limnol. 60, 331-342.

Sargent, R. C., Gross, M. R., Van Den Berghe, E. P., 1986. Male mate choice in fishes. Anim. Behav. 34, 545-550.

Saunders, G. R., Gentle, M. N., Dickman, C. R., 2010. The impacts and management of foxes *Vulpes vulpes* in Australia. Mammal Rev. 40, 181-211.

Schaffer, W. M., 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108, 783-790.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348-360.

Schludermann, E., Tritthart, M., Humphries, P., Keckeis, H., 2012. Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study. Can. J. Fish. Aquat. Sci. 69, 1302-1315.

Schmitt, J., Wulff, R. D., 1993. Light spectral quality, phytochrome and plant competition. Trends Ecol. Evol. 8, 47-51.

Schoener, T. W., 1974. Resource Partitioning in Ecological Communities. Science 185, 27-39.

Schoener, T. W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51, 408-418.

Schwartz, C. C., Ellis, J. E., 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol., 343-353.

Semenchenko, V., Grabowska, J., Grabowski, M., Rizevsky, V., Pluta, M., 2011. Non-native fish in Belarusian and Polish areas of the European central invasion corridor. Oceanol. Hydrobiol. Stud. 40, 57-67.

Sih, A., Bolnick, D. I., Luttbeg, B., Orrock, J. L., Peacor, S. D., Pintor, L. M., Preisser, E., Rehage, J. S., Vonesh, J. R., 2010. Predator–prey naiveté, antipredator behavior, and the ecology of predator invasions. Oikos 119, 610-621.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. Ann. Rev. Ecol. System., 269-311.

Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol. Evol. 28, 58-66.

Smith, D. A., Jurajda, P., 2002. Sexual conflict, sexual selection and sperm competition in the spawning decisions of bitterling, *Rhodeus sericeus*. Behav. Ecol. Sociobiol. 51, 433-439.

Somers, C. M., Lozer, M. N., Kjoss, V. A., Quinn, J. S., 2003. The invasive round goby (*Neogobius melanostomus*) in the diet of nestling double-crested cormorants (*Phalacrocorax auritus*) in Hamilton Harbour, Lake Ontario. J. Great Lakes Res. 29, 392-399.

Speierl, T., 2007. Fischökologische Funktionalität von Fließgewässerrenaturierungen im oberfränkischen Mainsystem. PhD Thesis, University Bayreuth, 324 pp.

Staas, S., 1996a. Anleitung zur Bestimmung von 0+ - Jungfischen aus dem Rhein.Report Ecological Field Station Rees-Grietherbusch. University of Cologne, 14 pp.

Staas, S., 1996b. Das Jungfischaufkommen im Niederrhein und in angrenzenden Nebengewässern unter Berücksichtigung der Uferstrukturen. PhD Thesis, Universität zu Köln, 144 pp.

Stauffer Jr, J. R., McKaye, K. R., Konings, A. F., 2002. Behaviour: an important diagnostic tool for Lake Malawi cichlids. Fish Fish. 3, 213-224.

Steinhart, G. B., Stein, R. A., Marschall, E. A., 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? J. Great Lakes Res. 30, 381-389.

Strayer, D. L., 2012. Eight questions about invasions and ecosystem functioning. Ecol. Lett. 15, 1199-1210.

Strubbe, D., Matthysen, E., 2009. Experimental evidence for nest-site competition between invasive ring-necked parakeets (*Psittacula krameri*) and native nuthatches (*Sitta europaea*). Biol. Cons. 142, 1588-1594.

Taylor, R. H., Thomas, B. W., 1989. Eradication of Norway rats (*Rattus norvegicus*) from Hawea Island, Fiordland, using brodifacoum. N. Z. J. Ecol., 23-32.

Tierney, K. B., Kasurak, A. V., Zielinski, B. S., Higgs, D. M., 2011. Swimming performance and invasion potential of the round goby. Env. Biol. Fish. 92, 491-502.

Tonn, W. M., Paszkowski, C. A., Holopainen, I. J., 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. Ecology, 951-958.

Tsikliras, A. C., Antonopoulou, E., Stergiou, K. I., 2010. Spawning period of Mediterranean marine fishes. Rev. Fish Biol. Fish. 20, 499-538.

Turesson, H., Brönmark, C., 2004. Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. J. Fish Biol. 65, 363-375.

Turesson, H., Persson, A., Brönmark, C., 2002. Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. Ecol. Freshwat. Fish 11, 223-233.

Urho, L., 1996. Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. Ann. Zool. Fennici 33, 659-667.

Van Densen, W. L. T., 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). J. Appl. Ichthyol. 3, 119-131.

Van Densen, W. L. T., Ligtvoet, W., Roozen, R. W. M., 1996. Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Ann. Zool. Fennici 33, 495-506.

Van Dijk, G. M., Marteijn, E. C. L., Schulte-Wülwer–Leidig, A., 1995. Ecological rehabilitation of the River Rhine: plans, progress and perspectives. Regul. Rivers 11, 377-388.

Van Iersel, J. J. A., 1953. An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour. Supplement, III-159.

van Kessel, N., Dorenbosch, M., De Boer, M. R. M., Leuven, R. S. E. W., Van der Velde, G., 2011. Competition for shelter between four invasive gobiids and two native benthic fish species. Curr. Zool. 57, 844-851.

Van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13, 235-245.

Van Riel, M. C., Van der Velde, G., Bij de Vaate, A., 2011. Dispersal of invasive species by drifting. Curr. Zool. 57, 818-827.

Vander Zanden, M. J., Casselman, J. M., Rasmussen, J. B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401, 464-467.

Veiberg, V. r., Loe, L. E., Mysterud, A., Langvatn, R., Stenseth, N. C., 2004. Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? Oecologia 138, 135-142.

Vitousek, P. M., D`Antonio, C. M., Loope, L. L., Westbrooks, R., 1996. Biological invasions as global environmental change. Am. Sci. 84, 468-478.

Vohmann, A., Borcherding, J., Kureck, A., Bij de Vaate, A., Arndt, H., Weitere, M., 2010. Strong body mass decrease of the invasive clam *Corbicula fluminea* during summer. Biol. Invasions 12, 53-65.

Wanger, T. C., Wielgoss, A. C., Motzke, I., Clough, Y., Brook, B. W., Sodhi, N. S., Tscharntke, T., 2011. Endemic predators, invasive prey and native diversity. Proc. R. Soc. Lond. B. Biol. Sci. 278, 690-694.

Warren Jr, M. L., Burr, B. M., Tomelleri, J. R., 2014. Freshwater Fishes of North America: Volume 1: Petromyzontidae to Catostomidae, 1 ed. JHU Press.

Werner, E. E., Gilliam, J. F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. System. 15, 393-425.

White, J. L., Harvey, B. C., 2003. Basin-scale patterns in the drift of embryonic and larval fishes and lamprey ammocoetes in two coastal rivers. Env. Biol. Fish. 67, 369-378.

Wickett, R. G., Corkum, L. D., 1998. Nest defense by the non-indigenous fish, the round goby, *Neogobius melanostomus* (Gobiidae), on a shipwreck in western Lake Erie. Can. Field Nat. 112, 653-656.

Williamson, M. H., Fitter, A., 1996. The characters of successful invaders. Biol. Cons. 78, 163-170.

Wolter, C., Freyhof, J., 2004. Diel distribution patterns of fishes in a temperate large lowland river. J. Fish Biol. 64, 632-642.

Woods, L. C. I., Sullivan, C. V., 1993. Reproduction of striped bass, *Morone saxatilis* (Walbaum), broodstock: monitoring maturation and hormonal induction of spawning. Aquac. Res. 24, 211-222.

Wright, P. J., Bailey, M. C., 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. Mar. Biol. 126, 143-152.

Zitek, A., Schmutz, S., Ploner, A., 2004a. Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. J. Fish Biol. 65, 1339-1357.

Zitek, A., Schmutz, S., Unfer, G., Ploner, A., 2004b. Fish drift in a Danube sidearm-system: I. Site-, inter- and intraspecific patterns. J. Fish Biol. 65, 1319-1338.

CHAPTER I

Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany

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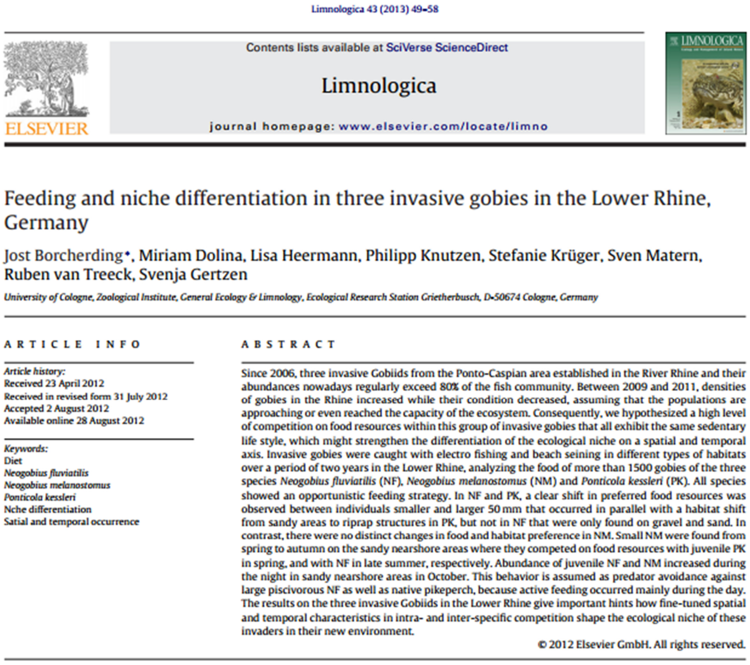

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ABSTRACT

Since 2006, three invasive Gobiids from the Ponto-Caspian area established in the River Rhine and their abundances nowadays regularly exceed 80% of the fish community. Between 2009 and 2011, densities of gobies in the Rhine increased while their condition decreased, assuming that the populations are approaching or even reached the capacity of the ecosystem. Consequently, we hypothesized a high level of competition on food resources within this group of invasive gobies that all exhibit the same sedentary life style, which might strengthen the differentiation of the ecological niche on a spatial and temporal axis. Invasive gobies were caught with electro fishing and beach seining in different types of habitats over a period of two years in the Lower Rhine, analyzing the food of more than 1500 gobies of the three species *Neogobius fluviatilis* (NF), *Neogobius melanostomus* (NM) and *Ponticola kessleri* (PK). All species showed an opportunistic feeding strategy. In NF and PK, a clear shift in preferred food resources was observed between individuals smaller and larger 50 mm that occurred in parallel with a habitat shift from sandy areas to riprap structures in PK, but not in NF that were only found on gravel and sand. In contrast, there were no distinct changes in food and habitat preference in NM. Small NM were found from spring to autumn on the sandy nearshore areas where they competed on food resources with juvenile PK in spring, and with NF in late summer, respectively. Abundance of juvenile NF and NM increased during the night in sandy nearshore areas in October. This behavior is assumed as predator avoidance against large piscivorous NF as well as native pikeperch, because active feeding occurred mainly during the day. The results on the three invasive Gobiids in the Lower Rhine give important hints how fine-tuned spatial and temporal characteristics in intra- and inter-specific competition shape the ecological niche of these invaders in their new environment.

Abstract

Since 2006, three invasive gobiids from the Ponto-Caspian area established in the River Rhine and their abundances nowadays regularly exceed 80 % of the fish community. Between 2009 and 2011, densities of gobies in the Rhine increased while their condition decreased, assuming that the populations are approaching or even reached the capacity of the ecosystem. Consequently, we hypothesized a high level of competition on food resources within this group of invasive gobies that all exhibit the same sedentary life style, which might strengthen the differentiation of the ecological niche on a spatial and temporal axis. Invasive gobies were caught with electro fishing and beach seining in different types of habitats over a period of two years in the Lower Rhine, analyzing the food of more than 1,500 gobies of the three species *Neogobius fluviatilis* (Nf), *N. melanostomus* (Nm) and *Ponticola kessleri* (Pk). All species showed an opportunistic feeding strategy. In Nf and Pk, a clear shift in preferred food resources was observed between individuals smaller and larger 50 mm that occurred in parallel with a habitat shift from sandy areas to riprap structures in Pk, but not in Nf that was only found on gravel and sand. In contrast, there were no distinct changes in food and habitat preference in Nm. Small Nm were found from spring to autumn on the sandy nearshore areas where they competed on food resources with juvenile Pk in spring, and with Nf in late summer, respectively. Abundance of juvenile Nf and Nm increased during the night in sandy nearshore areas in October. This behavior is assumed as predator avoidance against large piscivorous Nf as well as native pikeperch, because active feeding occurred mainly during the day. The results on the three invasive gobiids in the Lower Rhine give important hints how fine-tuned spatial and temporal characteristics in intra- and inter-specific competition shape the ecological niche of these invaders in their new environment.

Keywords: Diet * *Neogobius fluviatilis* * *Neogobius melanostomus* * *Ponticola kessleri* * niche differentiation * spatial and temporal occurrence

Introduction

The diet of fishes as an important part of the ecological niche has widely been analyzed, whereby many factors were documented to influence resource use on a spatial and temporal axis (e.g., Ross, 1986 for a review). The diet choice of individuals can be connected to ontogenetic (Mittelbach and Persson, 1998), behavioral or morphological aspects (Skúlason and Smith, 1995 for review). In addition and most important, various aspects of food intake are connected to size-dependent morphological (e.g., gape size, Mittelbach and Persson, 1998; Nilsson and Brönmark, 2000), physiological (e.g., vision: Hairston and Li, 1982, reactive distance: Breck and Gitter, 1983, digestion: Persson *et al.*, 2004) or behavioral traits (e.g., Magnhagen and Borcherding, 2008; Nakayama and Fuiman, 2010). Thereby, changes of foraging ability or growth rates with size (Wilson, 1975can cause discrete ontogenetic diet shifts, executed both towards lower (Benavides et al., 1994; Durtsche, 2000) and higher trophic positions (Mittelbach and Persson, 1998; Cereghino, 2006). As fish assemblages are often strongly size-structured, not only different species but also different size- or age-cohorts of one species (often named ecological species) interact with each other, such that resource partitioning (Ross, 1986) can be related to the avoidance of intra- (Persson and Greenberg, 1990a; 1990b) and inter-cohort competition (Werner and Hall, 1977; Persson, 1986) or predation pressure (Werner *et al.*, 1983).

Neozoans have to successfully meet new environmental conditions, such as climate, predators, diseases or parasites (deRivera *et al.*, 2005). Besides environmental conditions and predators, also competition experienced in non-native areas determines invasive success of neozoans (see Sakai *et al.*, 2001 for a review). In almost all cases reported, the invader was shown to be competitively superior to native species in both, interference and exploitative competition, leading to reduced survival, growth (Sakai *et al.*, 2001) and even competitive displacement of native species (Williamson, 1997). For multiple invasions Simberloff and Von Holle (1999) suggested the term ‘invasional meltdown’ to describe “the process by which a group of nonindigenous species facilitate one another’s invasion in various ways, increasing the likelihood of survival and/or of ecological impact”. This hypothesis was tentatively supported for the ecosystem of the Great Lakes, where “direct positive (mutualistic and commensal) interactions among introduced species are more common than purely negative (competitive and amensal) interactions” (Ricciardi, 2001).

Strong interspecific competition might also be found in Ponto-Caspian gobies invading Europe and North America (Grabowska and Grabowski, 2005; Gozlan et al., 2010), when negatively interacting with the native fauna (Jude et al., 1992; Corkum et al., 2004) as competitors for habitats (Bauer et al., 2007) and food (Bergstrom and

Mensinger, 2009), and as predators on eggs of other species (Chotkowski and Marsden, 1999) and small fishes (Grabowska and Grabowski, 2005). At this point four species are documented in the River Rhine, Germany, namely tubenose goby (*Proterorhinus seminularis*), bighead goby (*Ponticola kessleri*), round goby (*Neogobius melanostomus*) and monkey goby (*Neogobius fluviatilis*) (in chronological order, c.f., Borcherding et al., 2011). Thereby, gobies not only interact with native species but might also be affected by each other, as all invasive gobies have the same sedentary life style. Although interaction between invasive gobies has not yet been studied in detail, data on pairs of other closely related fish species revealed high dietary overlap (Copp and Kovac, 2003; Salgado et al., 2004; Specziar, 2005), hence also suggesting strong interspecific competition on food between invasive Ponto-Caspian gobies.

Assuming a high level of differentiation for species competing on a similar ecological niche, we studied invasive gobies in the Lower Rhine to disentangle factors influencing diet, and related to this, performance of invasive species. In this sense the present study focussed on the most abundant three invasive goby species in the River Rhine, Germany, analyzing (1) size-dependent (ontogenetic) differences in diet, (2) habitat-specific diet use, and (3) seasonal as well as (4) dial aspects in the usage of food resources. Such results are essential to understand the different spatial and temporal characteristics of the ecological niche of these invaders and to estimate their future potential impact on the ecosystem.

Material and Methods

Fish sampling

All gobies in this study were caught at the Lower Rhine (Rhine km 832-846) using varying methods at the different types of habitat (for details on the sampling sites and habitat description cf. Borcherding et al., 2011). At riprap structures, fishes were caught at daytime by electro-fishing with portable backpack units (maximum output 225/300 V, frequency: 75–85 Hz; fitted with a 40/20 cm, elliptical, anode of stainless-steel with netting of 4 mm mesh size, Lena f. Bednář, Czech Republic, cf. Borcherding et al., 2011). In areas of gravel and sand at the groin fields samples were taken with a beach seining net (10 x 1.5 meters, mesh size 1 mm) that was regularly dragged 20 meters against the current (all sampling dates are given in Tab. A1, Supporting Information).

Based on preliminary studies that indicated rapid re-colonization of freshly sampled areas, beach seining in October 2010 was repeatedly conducted in the morning (directly after sunrise), the afternoon and at night (about 2 hours after sunset) with always 3 replicate samples at fixed locations (Rhine km 842; 20 m length, around 5 m width, thus approx. 100 m²). This sampling procedure was repeated three times within 10 days, only changing the starting time of each consecutive sampling series (first series start in the afternoon, second series start at night, third series start in the morning), resulting in a full factorial design and a total of 27 samples. For all samples, smaller individuals were directly fixed in ethanol (approx. < 50 mm total length (TL)), while larger fish were stored in a cooling bag on ice and subsequently conserved at a temperature of minus 18°C.

Gastrointestinal analysis

With the gastrointestinal analysis of fish information on the food uptake during the last approximately 8 hours can be obtained (cf. Hyslop, 1980). After sex was noticed of at least all invasive gobies ≥ 70 mm TL (roughly 25 %), total length was measured to the nearest 1 mm and the fish was weighted to the nearest 0.001 g. In the next step the stomach was removed from the fish following the instructions of Gertzen (2010) and weighted to the nearest 0.0001 g. Afterwards the digestive tract content was removed and finally the empty digestive tract was re-weighted. In 23 out of the more than 1,500 dissected individuals the alimentary tracts were empty and not considered in further analysis. The volumetric amount of each prey taxon was visually estimated as percentage of the total sample volume (Polacik *et al.*, 2009).

For each fish the weight of the consumed prey, the index of stomach fullness (ISF) (Hyslop, 1980) and the adjusted condition factor (ACF), based on Fulton's condition factor (Bagenal and Tesch, 1978) were calculated by using the following formulas:

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

with W_{prey} = weight of the prey items [g], $W_{stomach\ full}$ = weight of the full stomach [g] and $W_{stomach\ empty}$ = weight of the stomach without prey items [g].

ISF = $(W_{prey}/W)*100$, with W = weight of the fish [g]

ACF = $10^5 * (W-W_{prey})/TL^{-3}$, with TL = total length of the fish [mm]

Although we did not eviscerate body cavity prior to analysis (e.g., potential differences of testis and gonads that may affect results), regularly no sex-dependent differences in condition and stomach fullness were observed (Knutzen & Krüger, University of Cologne, pers. comm.). Further, no consistent differences in the sex ratio occurred in our samples. This allowed analyzing condition and stomach fullness independently of the factor gender.

Analysis of the dietary overlap (O_D) was calculated according to Schoener (1970) using all 55 types of food items observed in this study:

$O_D = 1-0.5*\sum |(p_{ix} - p_{iy})|$

where p_{ix} is the percentage of a food item i in species or size class x, and p_{iy} is the percentage of a food item i in species and or size class y. The dietary overlap varies between 0 and 1 with the value 0 as no overlap and 1 as a total overlap. Wallace (1981) considered the overlap to be biologically significant when the index value exceeds 0.6 (i.e. 60 % similarity).

Feeding strategy and prey importance are graphically presented using the modified Costello method (Amundsen et al., 1996) to point out differences between species and size classes. For this analysis as well as the graphical presentations the prey categories were computed for different categories (e.g., zooplankton, crustacean, insects), including the category “Rest” (e.g., fish spawn, annelida, plant material) and indeterminable compounds. The prey specific abundance (P_i) of every prey category was plotted against the frequency of occurrence of the prey category (% F_i), with:

% $F_i = (N_i/N)*100$,

with N_i = the number of fish with prey i in their stomachs and N = the number of all analyzed fish, and

$P_i = (\sum S_i/\sum S_{ti})*100$,

where S_i = the summarized amount of prey i and S_{ti} = the stomach content weight of those fish who consumed prey i.

The feeding strategy is constituted along the vertical axis with specialization in the upper part and generalization in the lower part of the diagram. A fictive axis from the lower left to the upper right describes the importance of every prey category. A point in the upper right represents a dominant prey, while in the lower left the prey is rare. Information about the niche width contribution is shown from the upper left (high between-phenotype component) to the lower right (high within-phenotype component; Amundsen *et al.*, 1996).

Statistical analysis

To achieve homogenous variances when Levene-tests revealed inequality, statistical analysis of the ACF was performed on log transformed data. The log transformed ACF for each species was used as dependent variable in an ANCOVA, with ‘Year’ (2009, 2010, 2011) as independent factors and ‘TL’ as covariate, followed by a *post-hoc* analysis, in which the ACF was described with a linear regression in relationship to the TL. Also based on log transformed data, the ISF as dependent variable was analyzed with an ANOVA using ‘Species’ (*N. fluviatilis*, *N. melanostomus*, *P. kessleri*) and ‘Season’ (spring, summer autumn) as independent factors. This analysis was performed separately for gobies < 50 mm TL caught on gravel and sand, and for fish ≥ 50 mm TL that were caught in the riprap structures.

Goby densities in the sampling experiment on gravel and sand in October 2010 were compared on a dial basis using Kruskal-Wallis tests. For this sampling, the Levene test revealed equal variances of the ISF between the different samples, allowing an ANOVA on the ISF as dependent variable using ‘Species’ (*N. fluviatilis*, *N. melanostomus*), ‘Size-class’ (gobies smaller and larger 50 mm TL) and ‘Daytime’ (morning, afternoon, night) as independent factors. For the interaction term ‘Species x Daytime’, different groups were compared using a t-test. All statistics were computed using SPSS (Ver. 19.0, SPSS Corp.).

Results

Condition

In total more than 1,500 gobies of the three species *Neogobius fluviatilis*, *N. melanostomus* and *P. kessleri* were analyzed (Table A1, supporting information). For all three species the adjusted condition factor (ACF) increased significantly with increasing size of the fish (as covariate within the ANCOVA model: $F_{1,\,1554} = 2001.4$, $p < 0.0001$; *N. fluviatilis*: ACF = 0.368 + 0.0058 TL, $n = 258$, $r^2 = 0.417$; *N. melanostomus*: ACF = 0.430 + 0.0117 TL, $n = 675$, $r^2 = 0.702$; *P. kessleri*: ACF = 0.423 + 0.0079 TL, $n = 629$, $r^2 = 0.636$). In parallel to increasing densities of gobies in the riprap structures of the Lower Rhine, condition significantly decreased between 2009 and 2011 (ANCOVA: $F_{2,\,1554} = 16.1$, $p < 0.0001$), at least for *N. melanostomus* and *P. kessleri* (Fig. 1).

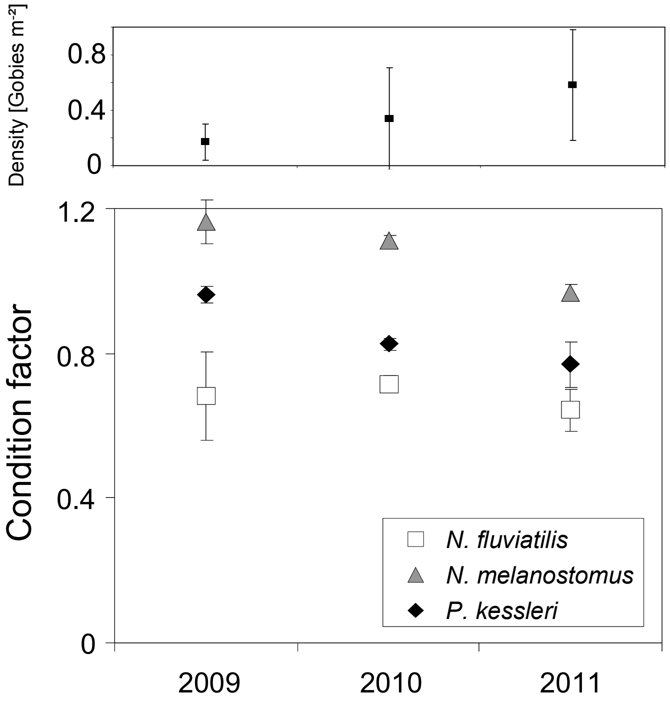

Figure 1. Density (mean ± SD) of invasive gobies in the Lower Rhine (km 832-846) based on electro-fishing data from riprap structures between 2009 and 2011 (top), and adjusted condition factor (mean ± 95 % conf. limits) of three gobiid species, presented as result from the ANCOVA (r^2=74.1 %) and calculated for a mean goby size of 56.3 mm TL (bottom).

Size dependent feeding

Averaging all analyzed fish, nearly 90 % of the ingested and identified food items belonged to only three categories, Crustacea (approximately 56 %, mainly invasive *Dikerogammarus villosus*), Chironomid larvae (approximately 21 %) and Mollusca (approximately 11 %, mainly invasive *Dreissena* sp. and *Corbicula* sp.). The three most important food items for each species showed considerable variation with the size of the gobies. Chironomid larvae and Crustacea were most important for the smallest individuals in all three species. While in *N. melanostomus* the importance of these food items changed more steadily with increasing size, there was a distinct switch between the smallest and the second smallest size class in *N. fluviatilis* and especially in *P. kessleri*, from chironomid larvae to Crustacea as most important food resource (Fig. 2). With increasing size of the fish the importance of chironomid larvae decreased for all three species close to zero and Crustacea was then the most important food resource. Although only based on low numbers of the largest individuals (> 125 mm TL) of all three species (*N. fluviatilis* and *N. melanostomus* each *n* = 3, *P. kessleri* *n* = 9), a second switch of the most important food item loomed, revealing Mollusca for *N. melanostomus*, and fish for *N. fluviatilis* and *P. kessleri* as dominant resource in the diet, respectively.

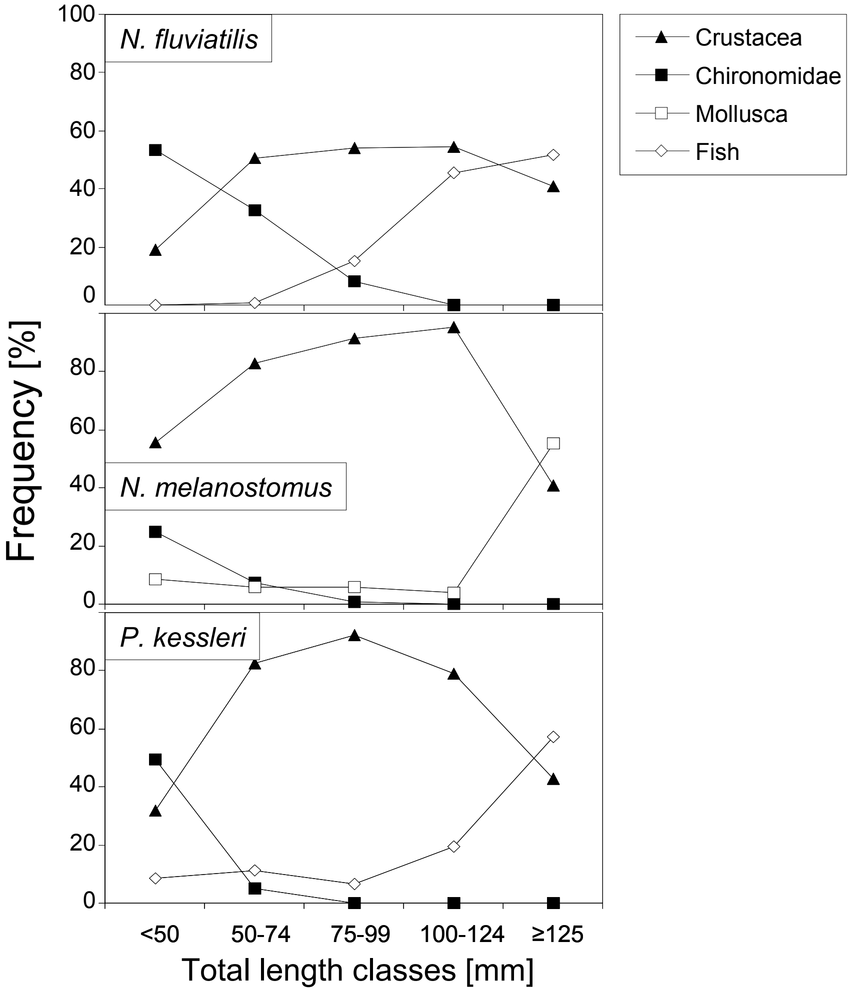

Figure 2. Frequency of the three most important food categories in dependence to the size of the three gobiid species (separated in 25 mm size classes) at the Lower Rhine between 2009 and 2011.

With respect to the first distinct switch in food items between the smallest and the second smallest size class in *N. fluviatilis* and *P. kessleri* and less fundamental changes with further increasing size (also only low numbers of individuals in the largest size class), the following analysis of the feeding and niche differentiation was performed for two size classes, individuals smaller and larger than 50 mm TL (Tab. A1). There were no clear hints of individual specialization for both size classes (i.e. no data points in the upper left corner of the Costello plots) demonstrating a more mixed and opportunistic feeding strategy of the three Gobiid species in the Lower Rhine, with varying degrees to use different prey types (Fig. 3). With the change of the feeding strategy between both size classes in *P. kessleri*, this species also changed the habitat from gravel and sand when being small, to the riprap structures when increasing in size. Although a comparable change of the feeding strategy between the two size classes occurred in *N. fluviatilis,* this species was found on gravel and sand only, independently of its size. In *N. melanostomus* no clear change of the feeding strategy became obvious with increasing size and larger individuals were found in nearly every catch in both habitats, the riprap structures of the banks and the gravel and sand areas of the groin fields (Fig. 3).

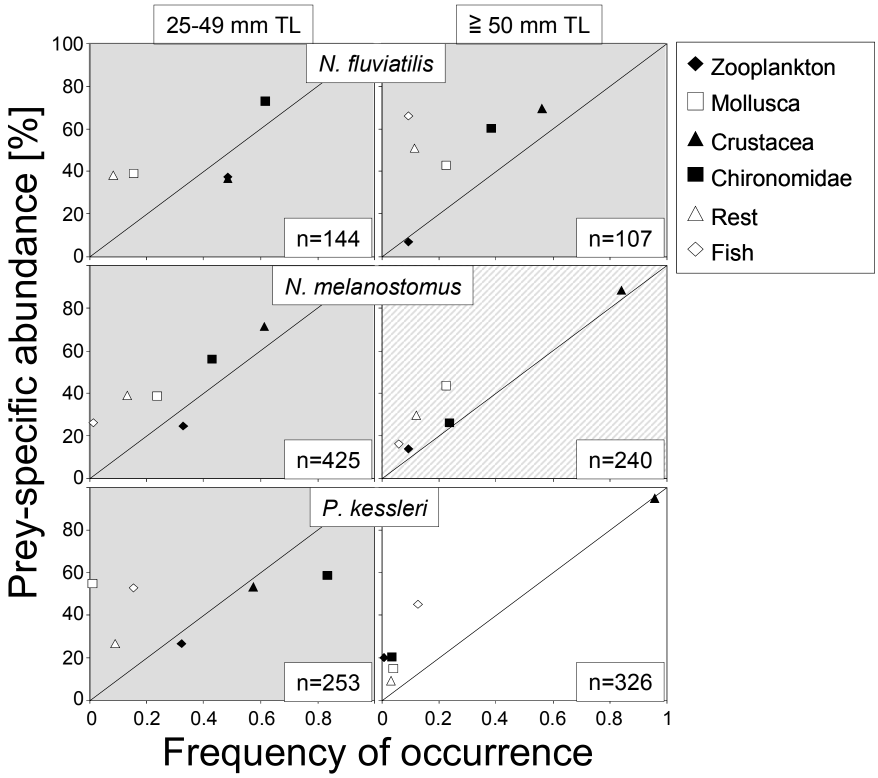

Figure 3. Feeding strategy (prey-specific abundance plotted against frequency of occurrence of prey in the diet of the predator for the major food items) of two size classes of the three gobiid species at the Lower Rhine described with the modified Costello diagram (Amundsen et al., 1996). Plots are based on catches of fish < 50 mm TL (left) and ≧ 50 mm TL (right) of each species originating from gravel and sand (highlighted in grey), from riprap structures (highlighted in white) or from both habitats (grey-white striped), respectively.

Seasonal feeding of small gobies on gravel and sand

Gobies of all species < 50 mm TL (i.e. young-of-the-year, YOY) were only caught in areas of gravel and sand, indicating this habitat as rearing area of all three species in the Lower Rhine. While small *N. melanostomus* were found here at any time, juveniles of both other species occurred in abundance on gravel and sand seasonally, thus, creating inter-specific competitive situations only during distinct periods. The index of stomach fullness (ISF) gives a solid estimation on the quantities of ingested food. For juvenile gobies < 50 mm TL the ISF differed significantly between the species (ANOVA: $F_{2,\ 799} = 75.0$, $p < 0.0001$, *P. kessleri* >> *N. melanostomus* > *N. fluviatilis*) and the season (ANOVA: $F_{2,\ 799} = 17.7$, $p < 0.0001$), as all three species had significantly more food ingested in spring and summer compared to autumn (Fig. 4).

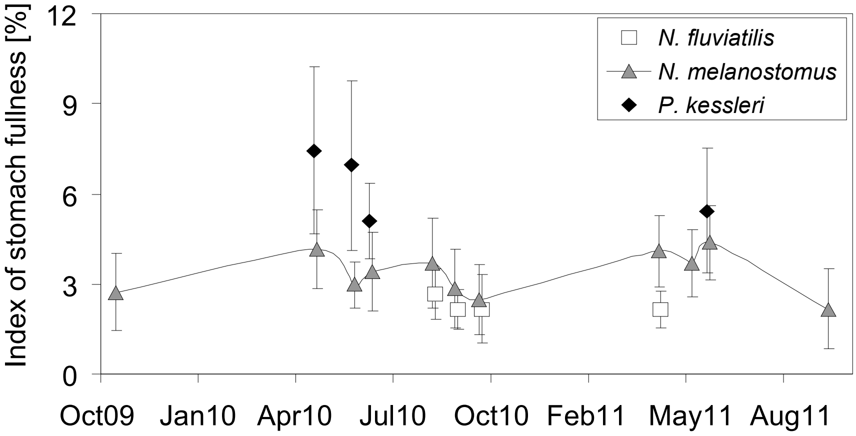

Figure 4. Index of stomach fullness (mean ± SD) of fish < 50 mm TL of the three Gobiid species caught on gravel and sand in the Lower Rhine between October 2009 and October 2011.

As already indicated by the Costello plots, chironomid larvae and Crustacea were most important food items for all three species also over the course of the season (Fig. 5). For the small individuals zooplankton occasionally became an important food resource (e.g., at the end of June 2010). In contrast to both *Neogobius* species, juvenile *P. kessleri* < 50 mm TL preyed also on fish to a small amount (on average about 8 % of the intestine content). On the other hand, *N. melanostomus* used more Mollusca than both other species, especially in autumn (on average about 10 % of the intestine content). Despite such small differences in the usage of different food resources, the overall dietary overlap between the species was always above 60 % (cf. Fig. 5), indicating an important criterion for significant interspecific competition when species occur simultaneously on areas of gravel and sand.

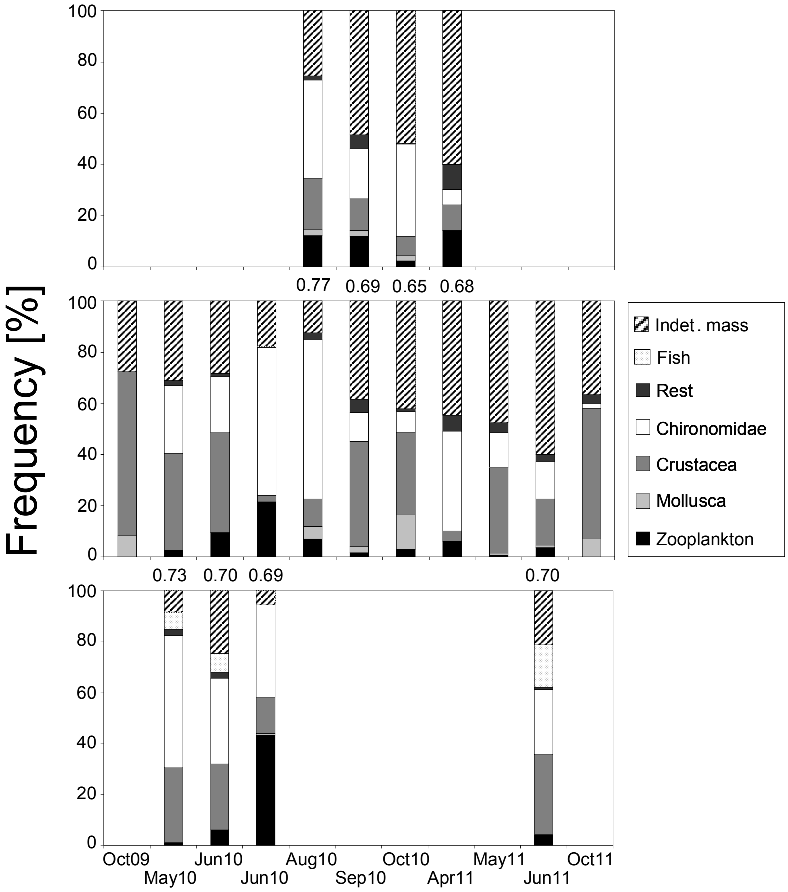

Figure 5. Frequency of major food categories found in the intestine of fish < 50 mm TL of the three gobiid species (top: *N. fluviatilis*; middle: *N. melanostomus*; bottom: *P. kessleri*) caught on gravel and sand in the Lower Rhine between October 2009 and October 2011. Indef. mass: food items not identifiable; Rest: mainly mites, annelids etc.. The dietary overlap between species when occurring together is indicated between the single columns.

Seasonal feeding of large gobies in riprap structures

Only *P. kessleri* and *N. melanostomus* were caught in the riprap structures of the banks at the Lower Rhine which were never < 57 mm TL. Mean size of *P. kessleri* was 89 ± 13.8 mm TL and the majority of *N. melanostomus* was even larger (102 ± 29.3 mm TL). Quantitative analysis of food uptake of these large individuals in the riprap structures revealed comparable results as obtained for small individuals on gravel and sand, with a significantly higher ISF for *P. kessleri* than *N. melanostomus* (ANOVA: $F_{1,\ 384}$ = 13.1, $p < 0.0001$), and significantly lowest ISF values in autumn compared with spring and summer samples (ANOVA: $F_{2,\ 384}$ = 26.1, $p < 0.0001$; Fig. 6). Regularly Crustacea were the main food resource for both species, except for *N. melanostomus* mainly in the solely riprap structures (compared to riprap structures at the groin fields), where Mollusca dominated the diet in autumn (Fig. 7). Similar to small *P. kessleri* on gravel and sand and in contrast to all size classes of *N. melanostomus*, large *P. kessleri* added a certain amount of fish to its diet, especially in the riprap at the groin fields. While in autumn and spring fish prey consisted mainly of gobiids, it changed in early summer to small cyprinids (detailed data not shown). The dietary overlap between both species occurring in the same habitat was much higher in spring and early summer than in autumn (Fig. 7).

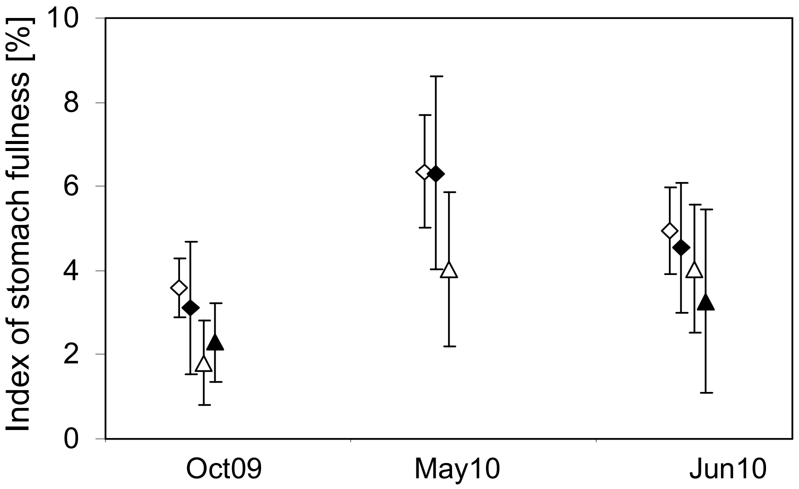

Figure 6. Index of stomach fullness (mean ± SD) of *Neogobius melanostomus* (triangles) and *Ponticola kessleri* (diamonds) ≧ 50 mm TL caught in riprap structures at a groin field (white) or at solely riprap structures (black) in the Lower Rhine between October 2009 and June 2010.

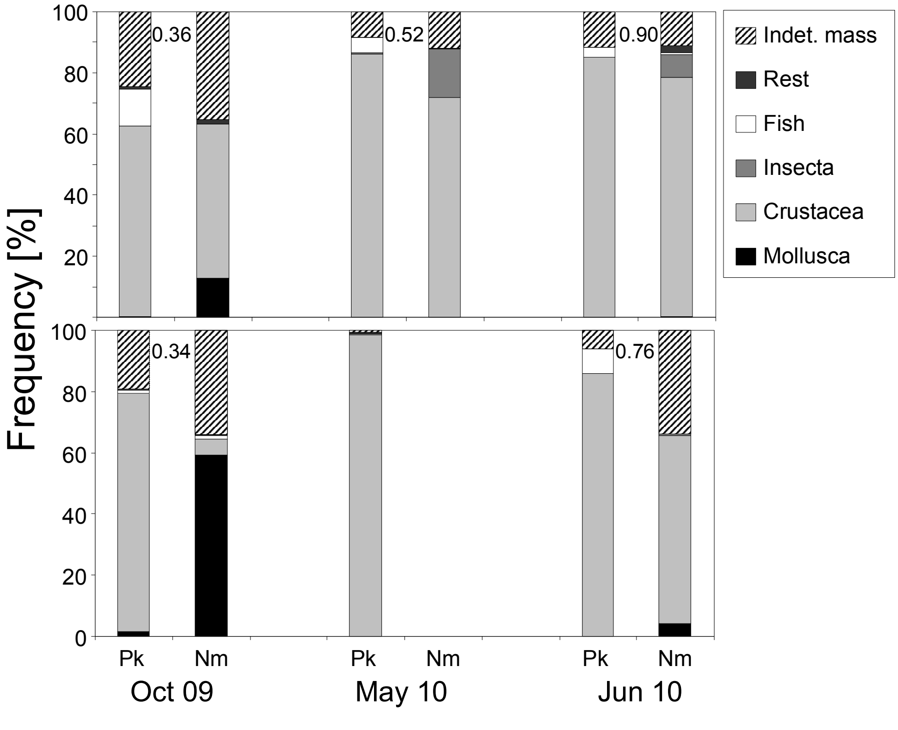

Figure 7. Frequency of major food categories found in the intestine of *Neogobius melanostomus* (Nm) and *Ponticola kessleri* (Pk) ≧ 50 mm TL caught in riprap structures at a groin field (top) or at solely riprap structures (bottom) in the Lower Rhine between October 2009 and June 2010. Indef. mass: food items not identifiable; Rest: mainly mites, annelids etc.. The dietary overlap between species when occurring together is indicated between the single columns.

Dial feeding of small and large gobies on gravel and sand

In October 2010, beach seining during the daytime and early night caught nearly 1,200 fishes. More than 87 % of these fishes were gobies, including few *P. kessleri* (6 %) not further analyzed here. Some small cyprinids (about 6 % of the total catch) were mainly caught during daytime and the percids ruffe (*Gymnocephalus cernua*, about 2 %) and pikeperch (*Sander lucioperca*, about 2 %) occurred only during the night. The length-frequency distribution of *N. fluviatilis* and *N. melanostomus* (Fig. A1) revealed a distinct increase in small individuals during the night for both species (Kruskal-Wallis-Test: *df* = 2, *N. fluviatilis* *p* = 0.002; *N. melanostomus* *df* = 2, *p* = 0.011, Fig. 8). For the individuals ≥ 50 mm TL a significant increase in abundance during the night was only proven for *N. fluviatilis* (Kruskal-Wallis-Test: *df* = 2, *p* = 0.011), but not for *N. melanostomus* (Kruskal-Wallis-Test: *df* = 2, *p* = 0.823, Fig. 8).

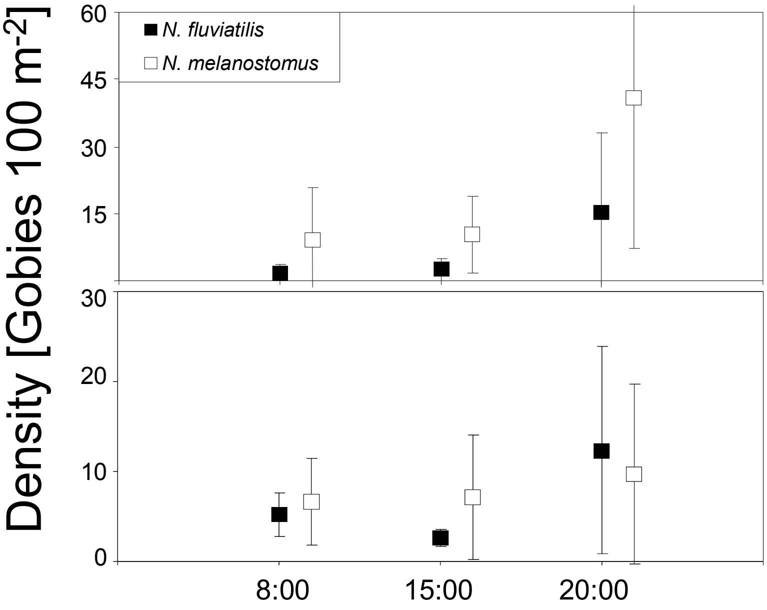

Figure 8. Density of *N. fluviatilis* (black) and *N. melanostomus* (white) (mean gobies 100 m^{-2} ± SD) caught at three sampling times (8:00 directly after sunrise, 15:00 daytime; 20:00 two hours after sunset) during the sampling experiment on gravel and sand at the Lower Rhine in October 2010, separately for fish < 50 mm TL (top) and ≧ 50 mm TL (bottom).

Dial feeding periods of both species in October 2010 were estimated with the ISF, again revealing the significantly higher gastrointestinal content in *N. melanostomus* than in *N. fluviatilis* (ANOVA *p* < 0.001, Tab. 1). For both species and independently of size, lowest values of the ISF were observed for individuals that were directly caught after sunrise, evincing lowest food uptake during the preceding night (Fig. 9). Beneath the independent factors ‘Species’ and ‘Daytime’ also the interaction term ‘Species x Daytime’ was significant in the statistical analysis (Tab. 1).

Table 1. Three-factor ANOVA on the ISF (index of stomach fullness) of gobies sampled on gravel and sand in the River Rhine in October 2010. Independent factors: Species (*N. fluviatilis* and *N. melanostomus*), Size class (< 50 mm TL and ≥ 50 mm TL) and Daytime (morning, afternoon, night). Significant effects are printed in bold.

Source	d.f.	*F*	*P*
Species	1	16.07	**<0.001**
SizeClass	1	0.42	0.519
Daytime	2	18.46	**<0.001**
Species X SizeClass	2	2.65	0.156
Species X Daytime	2	3.12	**0.045**
SizeClass X Daytime	2	0.70	0.586
Species X SizeClass X Daytime	2	0.02	0.989
Error	355		

Post-hoc comparisons of the ISF revealed a significant increase from the morning till the afternoon for both species (t-test: *N. fluviatilis* *df* = 67, *p* < 0.001; *N. melanostomus* *df* = 112, *p* = 0.012). While a further significant increase of the ISF until the early night was found in *N. melanostomus* (t-test: *df* = 157, *p* = 0.012). There was a slight tendency in *N. fluviatilis* that the ISF decreased until the night; this change, however, was not significant (t-test: *df* = 121, *p* = 0.089). *N. melanostomus* preyed mainly on Crustacea in both size classes, while YOY *N. fluviatilis* fed predominately on Insecta (mainly Chironomid larvae). Larger individuals of *N. fluviatilis* preferred to feed also on Crustacea, but added a certain amount of fish to its diet, especially during the early night (Fig. 10). Except for the diet of individuals from the morning samples (with significantly less feeding activity in the preceding period, cf. Fig. 9), inter-specific dietary overlap was always higher than the intraspecific dietary overlap between size classes of both species.

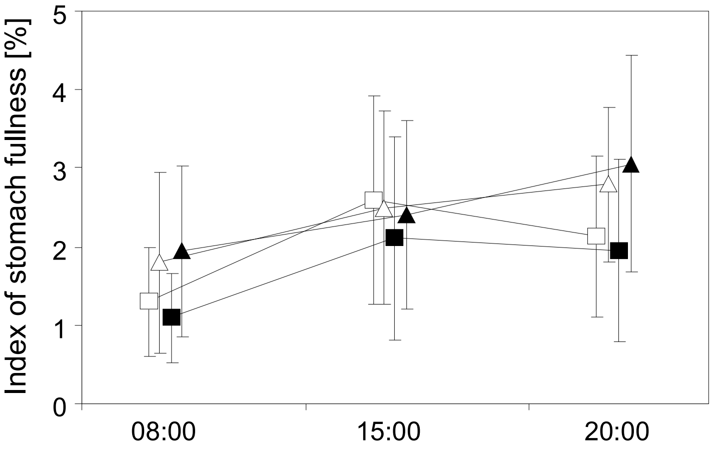

Figure 9. Index of stomach fullness (mean ± SD) of *N. fluviatilis* (squares) and *N. melanostomus* (triangles) caught at three sampling times (8:00 directly after sunrise, 15:00 daytime; 20:00 two hours after sunset) during the sampling experiment on gravel and sand at the Lower Rhine in October 2010, separately for fish < 50 mm TL (white) and ≧ 50 mm TL (black), respectively.

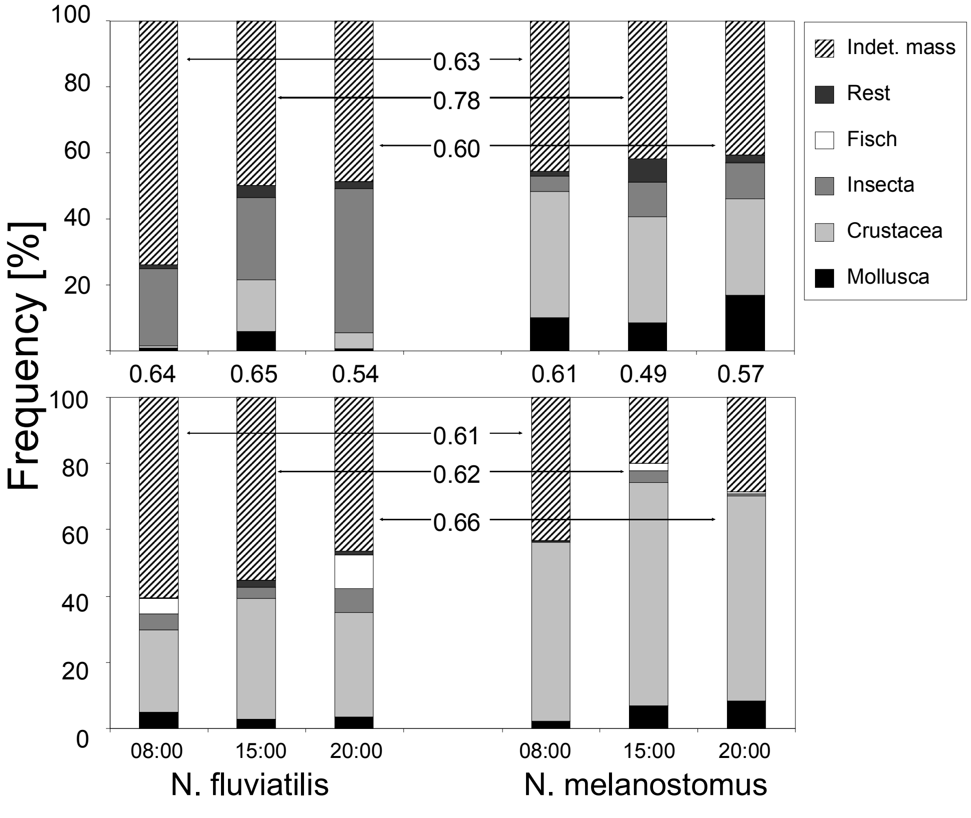

Figure 10. Frequency of major food categories found in the intestine of *N. fluviatilis* (left) and *N. melanostomus* (right) caught at three sampling times (8:00 directly after sunrise, 15:00 daytime; 20:00 two hours after sunset) during the sampling experiment on gravel and sand at the Lower Rhine in October 2010, separately for fish < 50 mm TL (top) and ≧ 50 mm TL (bottom), respectively. Indef. mass: food items not identifiable; Rest: mainly mites, annelids etc.. The intraspecific dietary overlap between both size classes is indicated between the single columns, and the interspecific dietary overlap between both species is given within the connecting arrows.

Discussion

Based on the analysis of more than 1,500 gobies, we found a significant and isometric increase of the condition with size for all three invasive gobiid species that is in good agreement to morphological studies on these species (Kovac and Siryova, 2005; L'avrincikova et al., 2005; Capova et al., 2008). Particularly our results revealed, however that condition, at least in *N. melanostomus* and *P. kessleri* significantly decreased between 2009 and 2011 (Fig. 1). As this decrease was in correlation to increasing densities of gobies, we assume our condition data on invasive gobies as a hint that food capacity for fishes in the Lower Rhine is actually at its limits. Especially in a limited environment “ecological differentiation is the necessary condition for coexistence” (competitive exclusion principle, Hardin, 1960), thus, a high level of differentiation is to expect for species competing on a similar ecological niche. In the following, we focussed on spatial and temporal characteristics of interspecific food consumption that may shape the ecological niche of the three invasive gobiid species at the Lower Rhine. However, prior to the analysis of inter-specific interactions, knowledge of intraspecific aspects must be obtained, as different size- or age-cohorts of one species may act as ecological species also competing on limited resources.

Size dependent feeding

The most important food items of the gobies in our study (Crustacea, mainly invasive *D. villosus*, chironomid larvae and Mollusca, mainly invasive *Dreissena* sp. and *Corbicula* sp.) are to a comparable extend also the most abundant macroinvertebrates in the River Rhine (e.g., Borcherding and Sturm, 2002; Bij de Vaate et al., 2002), clearly demonstrating the opportunistic feeding strategy of the three invasive gobiid species in the Lower Rhine. Within this diet spectrum, chironomid larvae were obviously preferred by smaller individuals of all species (Fig. 2). In contrast, Mollusca were increasingly preyed on with increasing size, which became obvious, however, mainly in the round goby *Neogobius melanostomus*, while larger individuals of the bighead goby *Ponticola kessleri* and the monkey goby *N. fluviatilis* increasingly used fish as most important resource, besides Crustacea. The observed diets of the invasive gobiids in the Lower Rhine are in good agreement to results from different freshwater habitats through Europe (e.g., *N. fluviatilis*: Grabowska et al., 2009; *N. melanostomus*: Polacik *et al.*, 2009; *P. kessleri*: Borza et al., 2009) and North America (here only *N. melanostomus*: Barton *et al.*, 2005) that always exhibited a generalistic and highly flexible feeding strategy. While feeding in competition between the adults of different invasive gobies was analyzed in some occasions (and will be discussed later), size specific differences in resource use of the different species are hardly to obtain in literature.

In *N. fluviatilis* and *P. kessleri* a clear shift in diet was observed between individuals smaller and larger than 50 mm TL (Fig. 3), resembling an ontogenetic diet shift as described for several fish species (e.g., Post and McQueen, 1988; Olson, 1996; Hjelm et al., 2000; Amundsen et al., 2003). In *P. kessleri* this observed dietary shift occurred in parallel with a strict habitat shift (similar to observations e.g., in *Perca fluviatilis*, Persson and Greenberg, 1990c), while all size classes of *N. fluviatilis* were always found on gravel and sand only. In contrast to *N. fluviatilis* and *P. kessleri*, no distinct changes in diet of *N. melanostomus* < 125 mm TL were found in our samples from the Lower Rhine. Additionally, all size classes of this species also occurred simultaneously on gravel and sand, not proving a size-specific habitat shift like in *P. kessleri*. To represent true ontogenetic thresholds or transitions changes in the ontogeny of a population, such shifts should occur to some extent simultaneously, e.g., in ecological interactions, feeding, physiological process, behavioral patterns, and/or shifts in morphology (Werner and Gilliam, 1984; Kovac et al., 1999). Consequently, our results on size-specific feeding and habitat preference give a preliminary systematic order based on ontogenetic transitions, with (1) clear changes in habitat preference and feeding in *P. kessleri*, (2) a clear shift in the use of food resources in *N. fluviatilis* but no changes in habitat preference, and (3) obviously neither a dramatic change in the usage of food resources, nor in habitat preference in *N. melanostomus*.

Seasonal aspects of feeding

Species-specific ontogenetic transitions give the overall framework to analyze and evaluate interspecific interactions, as e.g., distinct habitat shifts may limit the periods of competition. *N. melanostomus* was the only gobiid species in the Lower Rhine that was found at small sizes in every catch in the areas of gravel and sand. In late spring and early summer the juveniles of *N. melanostomus* (fish that hatched in the previous spawning season) mainly co-occurred with YOY *P. kessleri* that left this area with their habitat shift to the riprap structures in July (Gertzen, 2010). During the period of co-occurrence, high values of dietary overlap were found (mean above 70 %, Fig. 5), indicating high levels of interspecific competition on food resources of juvenile *N. melanostomus* and *P. kessleri* on gravel and sand. This high interspecific competition was accompanied by significant differences in the index of stomach fullness (ISF) revealing juvenile *P. kessleri* to feed on average more than twice as much as *N. melanostomus* (Fig. 4). These observations raise the question whether one of the species is the better competitor or if there are for instance physiological constraints for either species that are expressed in, or are the reason for the differentiated usage of food resources. Although we have no answer to this question until now, there are, however, some observations during recent behavioral experiments that may give first hints: (1) In single species experiments on behavioral reactions towards food and shelter as well as during periods of acclimatization in the laboratory, *P. kessleri* showed always much higher interest in food than *N. melanostomus* (Borcherding, Hertel, Breiden, unpublished data). (2) Observations revealed that *P. kessleri* clearly lost more weight over longer periods in the laboratory although being fed the same amount of food as were *N. melanostomus* (S. Gertzen, personal communication). These observations may lead to a first hypothesis that metabolic constraints may force *P. kessleri* to feed more than *N. melanostomus* or has to use food with higher energetic value (fish versus Crustacea, cf. Borcherding et al., 2007). However, to prove such a hypothesis on an increased metabolic rate in *P. kessleri* compared to *N. melanostomus*, either daily increments in otoliths have to be analyzed in detail (e.g., Morales-Nin, 2000) or appropriate experiments and measurements have to be conducted.

Whenever juvenile gobies occurred together on gravel and sand there was a high dietary overlap averaging to about 70 % (Fig. 5). Competition for food resources between juveniles of invasive gobiid species were, to the best of our knowledge, never studied in detail until now. Studying a pair of marine gobies (sand goby *Pomatoschistus minutus* and common goby *Pomatoschistus microps*) Salgado *et al.* (2004) revealed also high dietary overlaps over the season between both species of similar size. Comparable results were shown for stickleback species in English lowland streams (Copp and Kovac, 2003), and the dietary overlap of two species of Sander in Lake Balaton were also high at small sizes, however, rapidly decreased with increasing size (Specziar, 2005).

With increasing size and, thus, decreasing gape size limitations, the potential to use more diverse prey items regularly increases, and consequently, competition on food resources may be reduced (Beeck et al., 2002; De Roos et al., 2003; Borcherding et al., 2010). Similar as for the juveniles, the adults of *P. kessleri* had a significantly higher ISF than *N. melanostomus* while co-occurring in the riprap structures (Fig. 6). The dietary overlap between the larger individuals of both species, however, clearly differed over the season, with high values that indicated biological significant overlaps in summer and only a low dietary overlap in autumn (Fig. 7). High dietary overlaps between the two species were also reported by Copp *et al.* (2008), without further differentiating between sizes and season. High overlap values may evolve in the absence of competition if shared resources are not limiting, but they can also reflect competition for shared resources (Borza *et al.*, 2009). Studying three-spined sticklebacks (*Gasterosteus aculeatus*), Svanbäck and Bolnick (2007) demonstrated that increased population density led to reduced prey availability, causing individuals to add alternative prey types to their diet, and confirming that resource competition promotes niche variation within populations. We interpret our diet data in the same sense, assuming increased competition in autumn on lowered food resources that forced differential feeding between *N. melanostomus* and *P. kessleri* in the riprap structures of the Lower Rhine (cf. Borcherding and Sturm, 2002 for seasonal abundance of macroinvertebrates in the Lower Rhine). In contrast to our results, *N. melanostomus* and *P. kessleri* in the riprap structures of the River Danube, Hungary, showed highest dietary overlap in summer and autumn and lowest in spring (Borza *et al.*, 2009). The authors suggested a combination of varying seasonal abundances of macroinvertebrates in combination with morphological constraints between both species as most important to shape the food usage in the River Danube (Borza *et al.*, 2009), however, without addressing changing levels of food abundance.

Dial aspects of feeding

While levels of food abundance and composition of the macroinvertebrate community are known to change seasonally (e.g., Borcherding and Sturm, 2002), occurrence and feeding of fish was shown in many instances to depend also on dial aspects (e.g., Borcherding *et al.*, 2002; Jacobsen *et al.*, 2002). Dial dynamics of YOY chub (*Squalius cephalus*) and dace (*Leuciscus leuciscus*) at the River Ourthe, Belgium, essentially emerge as a size specific trade-off between feeding and hiding (Baras and Nindaba, 1999), and the authors recommended that future studies should focus on spatial and temporal occurrence and feeding of fish. The results of our fishing campaign in the nearshore areas on gravel and sand in October clearly revealed: (1) juveniles of *N. fluviatilis* and *N. melanostomus* migrated into this habitat during the night (Fig. 8); (2) the main feeding time of both species was directly after sunrise but not during the night (Fig. 9). From these results a first hypothesis on the mechanistic relationships can be drawn, with the juveniles of both species that primarily hide during the night in nearshore areas on gravel and sand.

Conducting a similar fishing campaign in late spring in the Vistula River system, Poland, Grabowska *et al.* (2009) found neither differences in the consumption of food categories among three size-groups of *N. fluviatilis* nor differences in their gut fullness coefficient over the 24-h period. These results were in contrast to similar studies on the invasive racer goby in the same reservoir that revealed this species to be primarily a nocturnal feeder (Grabowska and Grabowski, 2005). Similar to our results, however, Grabowska *et al.* (2009) also observed that *N. fluviatilis* were more numerous during sunset and night, and the authors suggested that they migrate into shallower waters at this time (without any assumptions on the reasons). A higher abundance of four different invasive gobiid species during the night was also observed in the littoral zone of the River Danube, Hungary (Erös *et al.*, 2005). Nevertheless, the present results give clear evidence that, beside seasonal characteristics, also dial aspects have to be considered when describing the ecological niche of the different gobiids at the Lower Rhine.

Conclusions

The extremely high amounts of gobies within the fish community of the Rhine (actual values are always in the range of 80 % or even more of all fish) together with decreasing condition of the invasive gobies are a clear hint that populations/communities are approaching or even have reached the capacity of the ecosystem. Our results further give important hints how fine-tuned spatial and temporal characteristics in intra- and interspecific competition shape the ecological niche of these invaders, providing some essential and conclusive correlations that allow specifying certain hypotheses to be experimentally tested in the future.

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References

Amundsen, P. A., Bohn, T., Popova, O. A., Staldvik, F. J., Reshetnikov, Y. S., Kashulin, N. A., Lukin, A. A., 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. Hydrobiologia 497, 109-119.

Amundsen, P. A., Gabler, H. M., Staldvik, F. J., 1996. A new approach to graphical analysis of feeding strategy from stomach contents data - Modification of the Costello (1990) method. J. Fish Biol. 48, 607-614.

Bagenal, T. B., Tesch, F. W., 1978. Age and growth. In: Ed: T. B. Bagenal, Methods for assessment of fish production in fresh waters. Blackwell Scientific Pub., Oxford, London, Edinburgh, Melbourne, pp. 101-136.

Baras, E., Nindaba, J., 1999. Seasonal and diel utilisation of inshore microhabitats by larvae and juveniles of *Leuciscus cephalus* and *Leuciscus leuciscus*. Env. Biol. Fish. 56, 183-197.

Barton, D. R., Johnson, R. A., Campbell, L., Petruniak, J., Patterson, M., 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002-2004. J. Great Lakes Res. 31, 252-261.

Bauer, C. R., Bobeldyk, A. M., Lamberti, G. A., 2007. Predicting habitat use and trophic interactions of Eurasian ruffe, round gobies, and zebra mussels in nearshore areas of the Great Lakes. Biol. Invasions 9, 667-678.

Beeck, P., Tauber, S., Kiel, S., Borcherding, J., 2002. 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. Freshwat. Biol. 47, 2359-2369.

Benavides, A. G., Cancino, J. M., Ojeda, F. P., 1994. Ontogenic changes in gut dimensions and macroalgal digestibility in the marine herbivorous fish, *Aplodactylus punctatus*. Funct. Ecol. 8, 46-51.

Bergstrom, M. A., Mensinger, A. F., 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. Trans. Am. Fish. Soc. 138, 1009-1017.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Can. J. Fish. Aquat. Sci. 59, 1159-1174.

Borcherding, J., Bauerfeld, M., Hintzen, D., Neumann, D., 2002. Lateral migrations of fishes between floodplain lakes and their drainage channels at the Lower Rhine: diel and seasonal aspects. J. Fish Biol. 61, 1154-1170.

Borcherding, J., Beeck, P., DeAngelis, D. L., Scharf, W. R., 2010. Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. J. Anim. Ecol. 79, 1101-1112.

Borcherding, J., Hermasch, B., Murawski, P., 2007. Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. Ecol. Freshwat. Fish 16, 198-209.

Borcherding, J., Staas, S., Krüger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Borcherding, J., Sturm, W., 2002. The seasonal succession of macroinvertebrates, in particular the zebra mussel (*Dreissena polymorpha*), in the River Rhine and two neighbouring gravel-pit lakes monitored using artificial substrates. Internat. Rev. Hydrobiol. 87, 165-181.

Borza, P., Erös, T., Oertel, N., 2009. Food resource partitioning between two invasive Gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. Internat. Rev. Hydrobiol. 94, 609-621.

Breck, J. E., Gitter, M. J., 1983. Effect of fish size on the reactive distance of Bluegill (*Lepomis macrochirus*) Sunfish. Can. J. Fish. Aquat. Sci. 40, 162-167.

Capova, M., Zlatnicka, I., Kovac, V., Katina, S., 2008. Ontogenetic variability in the external morphology of monkey goby, *Neogobius fluviatilis* (Pallas, 1814) and its relevance to invasion potential. Hydrobiologia 607, 17-26.

Cereghino, R., 2006. Ontogenetic diet shifts and their incidence on ecological processes: a case study using two morphologically similar stoneflies (Plecoptera). Acta Oecol. 30, 33-38.

Chotkowski, M. A., Marsden, J. E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. J. Great Lakes Res. 25, 26-35.

Copp, G. H., Kovac, V., 2003. Sympatry between threespine *Gasterosteus aculeatus* and ninespine *Pungitius pungitius* sticklebacks in English lowland streams. Ann. Zool. Fennici 40, 341-355.

Copp, G. H., Kovac, V., Zweimüller, I., Dias, A., Nascimento, M., Balazova, M., 2008. Preliminary study of dietary interactions between invading Ponto-Caspian gobies and some native fish species in the River Danube near Bratislava (Slovakia). Aquat. Invas. 3, 193-200.

Corkum, L. D., Sapota, M. R., Skora, K. E., 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. Biol. Invasions 6, 173-181.

De Roos, A. M., Persson, L., McCauley, E., 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecol. Lett. 6, 473-487.

deRivera, C. E., Ruiz, G. M., Hines, A. H., Jivoff, P., 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. Ecology 86, 3364-3376.

Durtsche, R. D., 2000. Ontogenetic plasticity of food habits in the Mexican spiny-tailed iguana, *Ctenosaura pectinata*. Oecologia 124, 185-195.

Erös, T., Sevcsik, A., Toth, B., 2005. Abundance and night-time habitat use patterns of Ponto-Caspian Gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. J. Appl. Ichthyol. 21, 350-357.

Gertzen, S., 2010. Co-occurrence of three invasive Gobiidae in the Lower Rhine - Niche separation by habitat partitioning on a seasonal and diel basis. Master Thesis, University of Cologne, 149 pp.

Gozlan, R. E., Britton, J. R., Cowx, I., Copp, G. H., 2010. Current knowledge on non-native freshwater fish introductions. J. Fish Biol. 76, 751-786.

Grabowska, J., Grabowski, M., 2005. Diel-feeding activity in early summer of racer goby *Neogobius gymnotrachelus* (Gobiidae): a new invader in the Baltic basin. J. Appl. Ichthyol. 21, 282-286.

Grabowska, J., Grabowski, M., Kostecka, A., 2009. Diet and feeding habits of monkey goby (*Neogobius fluviatilis*) in a newly invaded area. Biol. Invasions 11, 2161-2170.

Hairston, N. G., Li, K. T., 1982. Fish vision and the detection of planktonic prey. Science 218, 1240-1242.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Hjelm, J., Persson, L., Christensen, B., 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122, 190-199.

Hyslop, E. J., 1980. Stomach content analysis - a review of methods and their application. J. Fish Biol. 17, 411-429.

Jacobsen, L., Berg, S., Broberg, M., Jepsen, N., Skov, C., 2002. Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study. Freshwat. Biol. 47, 2370-2379.

Jude, D. J., Reider, R. H., Smith, G. R., 1992. Establishment of Gobiidae in the Great-Lakes Basin. Can. J. Fish. Aquat. Sci. 49, 416-421.

Kovac, V., Copp, G. H., Francis, M. P., 1999. Morphometry of the stone loach, *Barbatula barbatula*: do mensural characters reflect the species' life history thresholds? Env. Biol. Fish. 56, 105-115.

Kovac, V., Siryova, S., 2005. Ontogenetic variability in external morphology of bighead goby *Neogobius kessleri* from the Middle Danube, Slovakia. J. Appl. Ichthyol. 21, 312-315.

L'avrincikova, M., Kovac, V., Katina, S., 2005. Ontogenetic variability in external morphology of round goby *Neogobius melanostomus* from Middle Danube, Slovakia. J. Appl. Ichthyol. 21, 328-334.

Magnhagen, C., Borcherding, J., 2008. Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness? Anim. Behav. 75, 509-517.

Mittelbach, G. G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences [Review]. Can. J. Fish. Aquat. Sci. 55, 1454-1465.

Morales-Nin, B., 2000. Review of the growth regulation processes of otolith daily increment formation. Fish. Res. 46, 53-67.

Nakayama, S., Fuiman, L. A., 2010. Body size and vigilance mediate asymmetric interference competition for food in fish larvae. Behav. Ecol. 21, 708-713.

Nilsson, P. A., Brönmark, C., 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos 88, 539-546.

Olson, M. H., 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. Ecology 77, 179-190.

Persson, L., 1986. Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). Ecology 67, 355-364.

Persson, L., Claessen, D., De Roos, A. M., Byström, P., Sjörgren, S., Svanbäck, R., Wahlström, E., Westman, E., 2004. Cannibalism in a size-structured population: Energy extraction and control. Ecol. Monogr. 74, 135-157.

Persson, L., Greenberg, L. A., 1990a. Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca fluviatilis*. Oikos 59, 97-106.

Persson, L., Greenberg, L. A., 1990b. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. Ecology 71, 44-56.

Persson, L., Greenberg, L. A., 1990c. Optimal foraging and habitat shift in perch (*Perca fluviatilis*) in a resource gradient. Ecology 71, 1699-1713.

Polacik, M., Janac, M., Jurajda, P., Adamek, Z., Ondrackova, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecol. Freshwat. Fish 18, 640-649.

Post, J. R., McQueen, D. J., 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): A response to prey and predators ? Can. J. Fish. Aquat. Sci. 45, 1820-1826.

Ricciardi, A., 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Can. J. Fish. Aquat. Sci. 58, 2513-2525.

Ross, S. T., 1986. Resource Partitioning in Fish Assemblages - A Review of Field Studies. Copeia 1986(2), 352-388.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., Weller, S. G., 2001. The population biology of invasive species. Ann. Rev. Ecol. System. 32, 305-332.

Salgado, J. P., Cabral, H. N., Costa, M. J., 2004. Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Kroyer, 1838) in the upper Tagus estuary, Portugal. Sci. Mar. 68, 425-434.

Schoener, T. W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51, 408-418.

Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1, 21-32.

Skúlason, S., Smith, T. B., 1995. Resource polymorphisms in vertebrates. Trends Ecol. Evol. 10, 366-370.

Specziar, A., 2005. First year ontogenetic diet patterns in two coexisting Sander species, *S. lucioperca* and *S. volgensis* in Lake Balaton. Hydrobiologia 549, 115-130.

Svanbäck, R., Bolnick, D. I., 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc. R. Soc. Lond. B 274, 839-844.

Wallace, R. K., 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110, 72-76.

Werner, E. E., Gilliam, J. F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. System. 15, 393-425.

Werner, E. E., Gilliam, J. F., Hall, D. J., Mittelbach, G. G., 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64, 1540-1548.

Werner, E. E., Hall, D. J., 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58, 869-876.

Williamson, M., 1997. Biological invasions, First edition ed. Chapman & Hall, London.

Wilson, D. S., 1975. Adequacy of body size as a niche difference. Am. Nat. 109, 769-784.

Appendix Chapter I

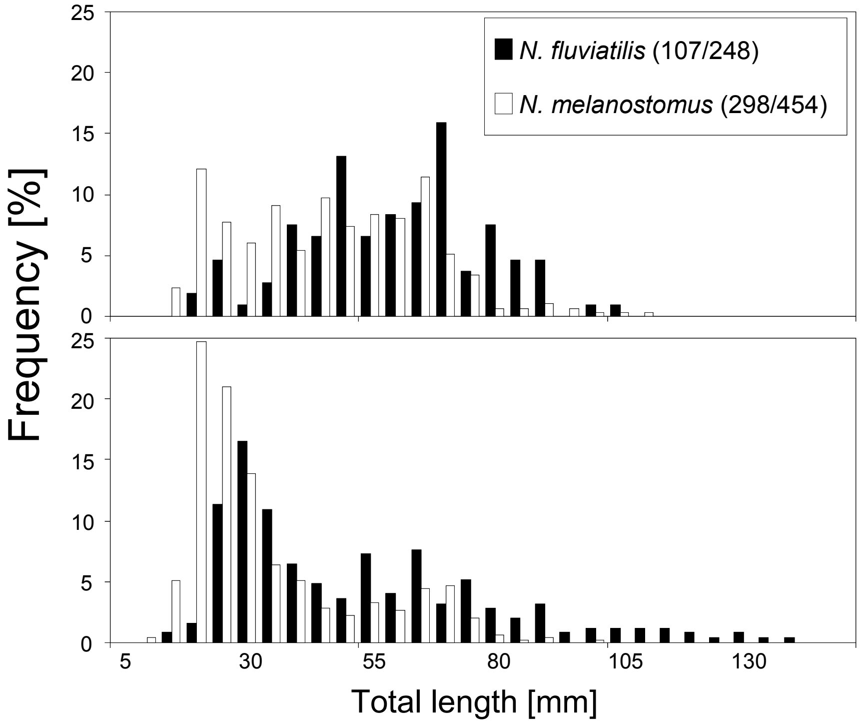

Figure A1. Length-frequency distributions of *Neogobius fluviatilis* (black) and *Neogobius melanostomus* (white) caught on gravel and sand in October 2010 during the day (top) and during the night (bottom). For further details of this sampling experiment see text. In parentheses the total number of fish caught at day/night is given.

Table A1. Samples of gobies from different habitats (G&S= gravel and sand; RrGF= riprap at groin field; SRr= solely riprap) at the Lower Rhine between October 2009 and October 2011, for which the content of intestine were analyzed. Beside the number of analyzed gobies per sample (n), the mean size (TL ± SD) and the mean condition (ACF ± SD) are given for two size classes.

			Size 25-49 mm Total Length					Size ≥ 50 mm Total Length				
Species	Date	Habitat	n	TL	± S.D.	ACF	± S.D.	n	TL	± S.D.	ACF	± S.D.
N. fluviatilis	29. Aug 10	G&S	14	40.5	± 7.4	0.58	± 0.11					
	21. Sep 10	G&S	35	37.0	± 7.3	0.55	± 0.04					
	11.-21. Oct 10	G&S	87	36.2	± 7.0	0.60	± 0.19	78	75.0	± 23.3	0.86	± 0.17
	14.-18. Apr 11	G&S	23	39.0	± 5.7	0.54	± 0.07					
N. melanostomus	6.-13.Oct 09	G&S	7	37.0	± 4.6	1.05	± 0.13					
		SRr						7	120.1	± 18.6	1.66	± 0.15
		RrGF						15	103.1	± 25.4	1.49	± 0.11
	3.-5.May 10	G&S	11	41.9	± 3.9	0.73	± 0.07					
		RrGF						7	56.3	± 3.4	1.09	± 0.29
	7.-18.Jun 10	G&S	6	46.3	± 2.0	1.13	± 0.09					
		SRr						4	71.6	± 12.8	1.36	± 0.14
		RrGF						67	68.5	± 15.9	1.29	± 0.18
	29. Jun 10	G&S	22	27.9	± 4.7	0.68	± 0.06					
	29. Aug 10	G&S	4	36.0	± 4.5	0.81	± 0.05					
	21. Sep 10	G&S	22	38.0	± 7.9	0.77	± 0.11					
	11.-21. Oct 10	G&S	83	34.7	± 7.0	0.83	± 0.17	129	63.8	± 10.1	1.30	± 0.12
	14.-18. Apr 11	G&S	24	38.5	± 6.7	0.90	± 0.24					
	23. May 11	G&S	63	41.3	± 4.8	0.83	± 0.09					
	7.-16. Jun 11	G&S	86	37.6	± 8.4	0.79	± 0.09					
	10-11. Oct 11	G&S	97	32.7	± 7.3	0.81	± 0.11					
P. kessleri	6.-13.Oct 09	SRr						104	84.0	± 14.0	1.18	± 0.19
		RrGF						124	86.1	± 20.0	1.20	± 0.23
	3.-5.May 10	G&S	118	30.8	± 4.0	0.60	± 0.07					
		SRr						20	82.8	± 9.4	1.20	± 0.25
		RrGF						20	91.6	± 27.7	1.12	± 0.22
	7.-18.Jun 10	G&S	73	29.0	± 3.3	0.61	± 0.06					
		SRr						69	99.0	± 8.0	1.16	± 0.09
		RrGF						34	101.1	± 10.8	1.18	± 0.10
	29. Jun 10	G&S	21	37.1	± 4.5	0.64	± 0.05					
	7.-16. Jun 11	G&S	22	35.0	± 6.1	0.64	± 0.08					

CHAPTER II

Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany)

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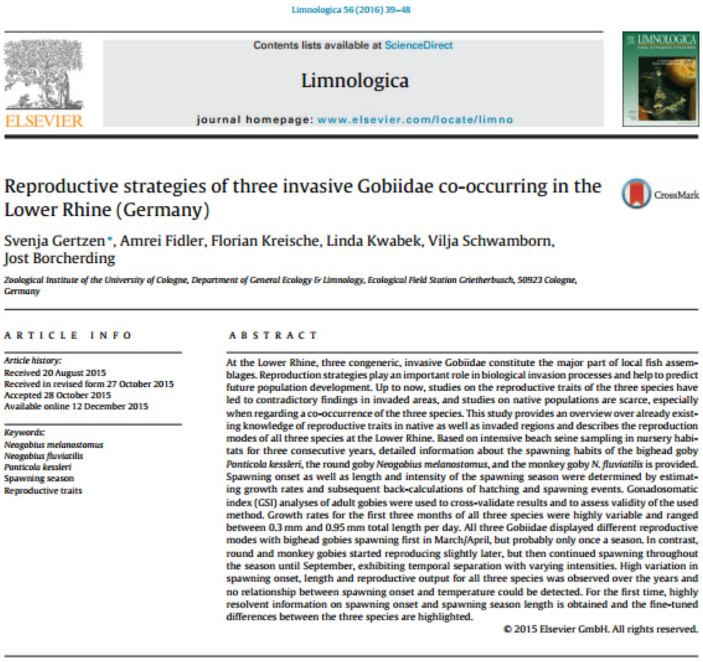

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ABSTRACT

At the Lower Rhine, three congeneric, invasive Gobiidae constitute the major part of local fish assemblages. Reproduction strategies play an important role in biological invasion processes and help to predict future population development. Up to now, studies on the reproductive traits of the three species have led to contradictory findings in invaded areas, and studies on native populations are scarce, especially when regarding a co-occurrence of the three species. This study provides an overview over already existing knowledge of reproductive traits in native as well as invaded regions and describes the reproduction modes of all three species at the Lower Rhine. Based on intensive beach seine sampling in nursery habitats for three consecutive years, detailed information about the spawning habits of the bighead goby *Ponticola kessleri*, the round goby *Neogobius melanostomus*, and the monkey goby *N. fluviatilis* is provided. Spawning onset as well as length and intensity of the spawning season were determined by estimating growth rates and subsequent back-calculations of hatching and spawning events. Gonadosomatic index (GSI) analyses of adult gobies were used to cross-validate results and to assess validity of the used method. Growth rates for the first three months of all three species were highly variable and ranged between 0.3 mm and 0.95 mm total length per day. All three Gobiidae displayed different reproductive modes with bighead gobies spawning first in March/April, but probably only once a season. In contrast, round and monkey gobies started reproducing slightly later, but then continued spawning throughout the season until September, exhibiting temporal separation with varying intensities. High variation in spawning onset, length and reproductive output for all three species was observed over the years and no relationship between spawning onset and temperature could be detected. For the first time, highly resolvent information on spawning onset and spawning season length is obtained and the fine-tuned differences between the three species are highlighted.

Abstract

At the Lower Rhine, three congeneric, invasive Gobiidae constitute the major part of local fish assemblages. Reproduction strategies play an important role in biological invasion processes and help to predict future population development. Up to now, studies on the reproductive traits of the three species have led to contradictory findings in invaded areas, and studies on native populations are scarce, especially when regarding a co-occurrence of the three species. This study provides an overview over already existing knowledge of reproductive traits in native as well as invaded regions and describes the reproduction modes of all three species at the Lower Rhine. Based on intensive beach seine sampling in nursery habitats for three consecutive years, detailed information about the spawning habits of the bighead goby *Ponticola kessleri,* the round goby *Neogobius melanostomus*, and the monkey goby *N. fluviatilis* is provided. Spawning onset as well as length and intensity of the spawning season were determined by estimating growth rates and subsequent back-calculations of hatching and spawning events. Gonadosomatic index (GSI) analyses of adult gobies were used to cross-validate results and to assess validity of the used method. Growth rates for the first three months of all three species were highly variable and ranged between 0.3 mm and 0.95 mm total length per day. All three Gobiidae displayed different reproductive modes with bighead gobies spawning first in March/April, but probably only once a season. In contrast, round and monkey gobies started reproducing slightly later, but then continued spawning throughout the season until September, exhibiting temporal separation with varying intensities. High variation in spawning onset, length and reproductive output for all three species was observed over the years and no relationship between spawning onset and temperature could be detected. For the first time, highly resolvent information on spawning onset and spawning season length is obtained and the fine-tuned differences between the three species are highlighted.

Keywords: *Neogobius melanostomus* * *Neogobius fluviatilis* * *Ponticola kessleri* * spawning season * reproductive traits

Introduction

Invasion processes are a world-wide phenomenon which have increased due to globalization and the concomitant establishment of new pathways and links between geographical regions (Ricciardi and MacIsaac, 2000; Hulme, 2009; Banks et al., 2015). Numbers of studies concerning biological invasions have dramatically increased since 1990 (Kolar and Lodge, 2001; Gurevitch et al., 2011), revealing serious impacts of invasive species on the local environment, economy and even human health across several systems (Ricciardi and MacIsaac, 2000; Pimentel et al., 2005; Pejchar and Mooney, 2009; Keller et al., 2011). The River Rhine, one of the most important European waterways, has experienced a sharp increase of non-native aquatic species in the last decades, with the Ponto-Caspian area being a main donor region (Leuven et al., 2009). Besides several macroinvertebrate species like the amphipod *Dikerogammerus villosus* (Bij de Vaate et al., 2002), fishes of the family Gobiidae have entered the Lower Rhine and now constitute the major part of the local fish community (Borcherding et al., 2011; 2013) In this region, the bighead goby *Ponticola kessleri* (all names referring to Neilson and Stepien, 2009) was first found in 2006, followed by the round goby *Neogobius melanostomus* and the monkey goby *N. fluviatilis*, both in 2008 (Borcherding et al., 2011; 2013).

As invasions are assumed to be a leading cause of faunal extinctions (Clavero and Garcia-Berthou, 2005), it is an important issue in ecological and conservation research to detect the mechanisms allowing the success of invasive species and thereby the resulting consequences for the native fauna (Byers et al., 2002). High invasive potential and negative impact on native species have already been shown for Ponto-Caspian gobiids for several regions across Europe and the Great Lakes of North America (Dubs and Corkum, 1996; Jude, 1997; Chotkowski and Marsden, 1999; Janssen and Jude, 2001; Steinhart et al., 2004; Grabowska and Grabowski, 2005; Karlson et al., 2007; Adamek et al., 2007).

Studying life-history traits provides valuable insights, as they bear potential predictive power concerning future population development or the expanding range (Sakai et al., 2001; Van Kleunen et al., 2010; Angert et al., 2011). Especially reproductive traits have been used to assess the nuisance character of invasive species (e.g., Cucherousset et al., 2009; Guo et al., 2013). However, besides a number of studies on round goby, knowledge about reproductive modes of Ponto-Caspian Gobiidae, particularly in their native habitats, is scarce (see Tab. 1). Bighead gobies appear to undergo a single spawning event in native ranges (Kalinina, 1976; cited by Kovac et al., 2009), but invest in at least two batches per season in invaded regions with an extended spawning season from May to August (Kovac et al., 2009). The spawning season of monkey gobies in their native ranges also takes place from May to August with multiple spawning events (Charlebois et al., 1997; Konecna and Jurajda, 2012). In invaded areas, a higher allocation in reproduction rather than in somatic growth could be observed, indicating plasticity in these traits (Placha et al., 2010). Reproduction habits of round gobies are well described in the literature (e.g., reviewed in Charlebois et al., 1997, Kornis et al., 2012), yet, an overview of reproductive traits in native compared to invaded areas is missing.

Shifts in reproductive traits in invaded habitats have been observed, displayed by e.g., smaller sizes at maturity (MacInnis and Corkum, 2000; Balazova-L'avrinìkova and Kovac, 2007; Horkova and Kovac, 2014). Furthermore, even intra-population differences were found by comparing round gobies of early and newly invaded sites of the Trent River (Canada, Gutowsky and Fox, 2012). Invasive species often show a higher phenotypic plasticity (Davidson et al., 2011) and are usually characterized as highly adaptable species that are generally more successful when facing new environments (Kolar and Lodge, 2002). Plasticity in life-history traits can strongly promote invasion success (Claridge and Franklin, 2002) and even support the evolution of invasive characteristics (Buczkowski, 2010). Additionally, phenotypic plasticity in life-history regarding reproductive strategies seems a distinctive trait for a successful invasion (Olden et al., 2006), as reproductive success and the recruitment into the next generation are important values to determine future development and fitness of the population (Zeug and Winemiller, 2007; Scharbert and Borcherding, 2013).

Defining the impact of fish introductions is quite delicate (Leprieur et al., 2009) and impact evaluation becomes even more crucial when the ecosystem is facing several invasive species simultaneously. Under such conditions interactive effects as a result of niche separation between two or more non-natives might even be more detrimental (Ross et al., 2004). Comparative studies on the reproductive cycle of more than one of these invasive species in the same habitat are currently lacking. Consequently, the main aim of this study was to create a precise description of the onset, intensity and length of the spawning season of three congeneric gobiid species in an invaded area, thereby highlighting the interspecific differences. For this purpose, we sampled nursery habitats of invasive gobies at the Lower Rhine throughout three sequenced years, analyzing occurrence and density of early hatched juveniles, as well as growth rates of their first months of life. The samples on the juveniles were added to a gonadosomatic index analysis of the adults for cross-validation. The second aim was to compare these results with already existing literature on reproductive traits observed in native as well as other invaded regions to evaluate levels of phenotypic plasticity.

Methods

Fish sampling

Fishing campaigns were carried out for three consecutive years (2011 – 2013) in three fixed large sandy groin fields at the Lower Rhine (Rhine km 842, cf. Borcherding et al., 2013). Groin fields were bay-like structures of the main river and were adjacent to another, only separated by the groin heads. Substrate varied from sand to sand and gravel within a groin field, whereas other structures as macrophytes were completely absent. Samples were taken with a beach seining net (10 m x 1.5 m, mesh size 1 mm) that was hand-dragged against the current and which allowed for effective sampling of fish larvae and early juveniles due to the small mesh size. Campaigns were conducted monthly from April to October to ensure samples from the whole reproductive season (pre- and post-spawning) were gathered. This was validated by no occurrence of early hatched juveniles in April and absence of 0+ individuals beneath 15 mm total length (TL) during the latest sampling dates. Sampling regularly consisted of 3 replicate stretches each 20 m in length and about 5 m in width (yielding roughly 100 m²). This sampling was repeated three times a day (morning, afternoon, night) to cover potential dial aspects of goby occurrence (Borcherding et al., 2013). However, dial differences were not in the focus of this paper and are, thus, not further considered here. Therefore, we rely in this study on a regular number of 9 replicates per sampling date (only single exceptions e.g., due to thunderstorms), resulting in a total of 487 beach seinings (48,700 m^2) (Tab. 2, Fig. A1 and Tab. A2).

Every fish caught was identified to species level, total length was measured to the nearest 1 mm and in the case of Gobiidae sex was determined. Gobies exceeding 50 mm TL were measured directly, stored on ice and shortly later conserved at a temperature of -18 °C for further analyses. Native species transcending the larval phase could be determined in the field and were released carefully after sampling. All gobies smaller than 50 mm and indigenous species being too small to be determined on site were fixed in 96 % ethanol and were shortly afterwards measured and identified to species level in the laboratory using available keys for larval fish identification (Koblickaya, 1981; Mooij, 1989; Staas, 1996; Urho, 1996; Pinder, 2001).

Growth, hatching and spawning

Based on the high quantity of caught fish over the whole season, length frequency distributions allowed to differ between 0+ and older stages and also to follow the first cohort in case of multiple spawning events. Growth rates (G) for the three goby species could be calculated by comparing the mean total length of the first cohort of every sampling date with the mean total length of the following sampling event (Heermann and Borcherding, 2013).

$G = (TL\ t_2 – TL\ t_1) * \Delta d_{t1t2}^{-1}$

With TL t_2 = mean TL of first cohort at sampling date 2, TL t_1 = mean TL of first cohort at sampling date 1 and Δd_{t1t2} = difference of days between sampling date 1 and 2.

As an example, during samplings on the 11th of June 2012 bighead gobies had a mean total length of 30.67 mm. On the 20th of June, 9 days later, the mean total length was 32.64 mm, resulting in G = (32.64 mm – 30.67 mm) / 9 days = 0.219 mm per day. For growth rate calculations, only data with at least 5 days in between sampling events were considered, since growth could not be measured for smaller time intervals. As we sampled for several days per month (usually 7-9 days for one campaign), we determined several growth rates per species and year. Thus, a mean species specific value was calculated for those growth rates (G). Therefor only growth rates up to the end of July (the first three months after hatching) were considered, as the process of growth naturally slows down during ontogeny. By taking these mean values and assuming a hatching size of about 5.5 mm TL (Pk & Nf: personal observation; Nm: Logachev and Mordvinov, 1979), a hatching date could be calculated for every goby caught. This was only done up to a certain size limit (TL), which was determined by the mean size of gobies that was reached within the first three months after hatching. Bighead gobies in 2012 had a mean total length of 55.1 mm at the end of July, thus only hatching dates for individuals being smaller than 55.1 mm TL were calculated. As an example, imagine a bighead goby that was caught on 14th of June 2012 with a TL of 28 mm. From that we have to subtract the hatching size of 5.5 mm, resulting in 22.5 mm of pure growth. Mean growth rate G for that species and year was calculated as 0.725 mm per day. Dividing 22.5 mm by this growth rate results in 31.04 days of growth, revealing the 14th of May 2012 as the day of hatching. For larger individuals no back-calculations were made since approximations got inaccurate even if taking two or more growth rates, showing a decrease over the season for those individuals. Based on calculated hatching dates, spawning dates were defined. This was also done species specifically and on an individual level. For back-calculating from hatching to spawning events 350 day degrees (water temperature data: monitoring station of Lobith, http://live.waterbase.nl/waterbase_wns.cfm?taal=nl) were subtracted, matching personal observations for monkey goby as well as literature indications for round goby (Moiseyeva, 1983; Moskalkova, 1989; Krönke, 2008). To eliminate unreliable values a control was applied by subtracting 20 days from the calculated hatching dates, as this was the highest mentioned time for egg development quoted in literature (Moiseyeva, 1983; Moskalkova, 1989; Krönke, 2008). When spawning dates calculated by those two methods (day degrees and by subtracting 20 days) differed by 10 or more days, these dates were eliminated from further analysis. For our bighead goby example this would mean to subtract 350 day degrees from the hatching date (14th of May 2012), this results in the 21st of April 2012 as spawning date. Subtracting 20 days from the 14th of May ends up at the 24th of April, differing only by three days from the result of the day degree calculation. So the 21st of April would have been accepted as spawning date. As back-calculations always bear inaccuracies, this approach allowed for receiving trustable results without losing a high percentage of the field data.

Gonadosomatic index

To cross-validate results of spawning calculations, a total of 350 female gobies, 110 monkey gobies (71.2 ± 20.2 mm TL), 168 round gobies (71.2 ± 18.2 mm TL), and 72 bighead gobies (65.1 ± 18.4 mm TL), were dissected for gonadal analyses. Fish originated from above mentioned beach seining catches of mid-September 2012 up to mid-October 2013. Sex was first determined externally by the shape of the urogenital papillae, which is pointed and narrow in males but broad and blunt-ended in females (Miller, 1984). Total body mass and gonads were weighted to 0.0001 g accuracy for assigning the standard gonadosomatic index (GSI; Ricker, 1975):

$$GSI = \frac{B}{W} \times 100$$

with B = weight of the ovaries [g], W = wet weight of fish [g].

Statistics

To obtain densities of young of the year gobies data were pooled and analyzed per month. Density data of 0+ gobies were neither normal distributed (Shapiro-Wilk test), nor revealed homogenous variances (Levene-test). Thus, non-parametric Kruskal-Wallis tests were applied to check for significant differences between the species, years and months. Afterwards, significant differences were further specified by the use of Wilcoxon rank sum tests between the single groups. Growth rate data of the three species for the first three months met the requirements for parametric tests and were analyzed with a multifactorial ANOVA with “species” and “year” used as independent factors. GSI data were analyzed species specific with non-parametric Kruskal-Wallis tests followed by Wilcoxon rank sum tests, if significant differences were revealed. All statistics were performed using the software R (Ver. 3.1.1,R Development Core Team, 2009).

Table 1 Reproductive traits of *N. fluviatilis* (Nf), *N. melanostomus* (Nm) and *P. kessleri* (Pk) in native and non-native regions. An extended version of this table is given in the supplementary (Tab. A1). SL: standard length; TL: total length; f: female; m: male; NS: not specified. Values in brackets are mean values ± SD.

Species	Region	Status	Smallest size at maturity [mm]	Relative fecundity [eggs/g]	Absolute fecundity [eggs/female]	Max. GSI (f) [%]	Max. GSI (m) [%]	Date max. GSI	Spawning season	Spawning mode	Reference
Nf	Bulgarian Danube	native	41.65 SL (f)	NS	NS	~ 4% (mean Jun)	~ 0.21% (mean Apr)	Jun (f), Apr (m)	May-Aug	multiple	Konecna and Jurajda, 2012
Nf	Lower Rhine, Germany	invasive	78 TL (f)	0-18,755 (2,617±3,188)	0-10,600 (3,305±3,158) all stages	17.39%	2.05%	18th Jun (f,m)	Mid-Mar-mid-Sep	multiple	this study + unpublished data
Nm	native range	native							Apr-Sep (Bulgaria) + May-Aug (Romania)		Miller, 1986 (cf. Kornis et al., 2012, Wandzel, 2000)
Nm	native range	native							Apr-Aug		Lindberg et al., 1980 (cf. Tomczak and Sapota, 2006)
Nm	native range	native			one batch: 543 eggs					multiple	Kalinina, 1976 (cf. Wandzel, 2000, Simonovic et al., 2001)
Nm	Sea of Azov	native			328-5,221						Kovtun, 1978 (cf. Kornis et al., 2012)
Nm	Danube Bulgaria	native	49 SL (f)	101.5-3,158.5	419-7,865 (all stages)	22.7%	NS	NS	Apr-Jun	multiple	Horkova and Kovac, 2014
Nm	Literature summary	native/invasive	NS	NS	200-9,771 (spawned/f)	NS	NS	NS	Apr-Jun (Romania), Apr-Jul (Sea of Azov), Apr-Sep (Varna, Bulgaria, Azerbaijan)	multiple	Charlebois et al., 1997
Nm	Danube River, Slovakia	invasive	mean: 57.57 SL (2004/2005), 50.58 SL (2008/2010)	NS	NS	NS	NS	NS	NS	multiple	Grula et al., 2012
Nm	Danube River, Slovakia	invasive	46 SL (f)	224.7-3,568.9	1,578-10,605 (all stages)	22.84%	NS	NS	Mar-Jul	multiple	Horkova and Kovac, 2014
Nm	Danube River, Slovakia	invasive	NS	NS	bef.: 928-3,245 (1,724), aft.: 548-10,605 (3,412)	bef.: 17.33%, aft.: 21.51%	NS	NS	Apr-Jun (bef.), Apr-mid-Jul (aft.)	multiple	Horkova and Kovac, 2015b
Nm	Danube River, Cunovo + Bratislava, Slovakia	invasive	45.1 SL (f)	25.7 - 96.3	103.5 -1938.2	NS	NS	NS	NS	multiple	L'avrincikova and Kovac, 2007
Nm	Gulf of Gdansk	invasive	NS	9-143 (34 +-24)	94-2,190 (645±433) (stages 2,3,4)	32%	11%	NS	Mar-Sep (pause in Jun)	multiple	Tomczak and Sapota, 2006
Nm	Puck Bay, Gulf of Gdansk	invasive	74 TL (f), 70 TL (m)	17-109	89 - 3,841 (1,739)	13.4%	NS	May	Apr-Aug/Sep	multiple	Wandzel, 2000
Nm	St.Clair River, Great Lakes	invasive	NS	NS	NS	NS	NS	NS	Apr/May-late summer	multiple	Leslie and Timmins, 2004
Nm	Hamilton Harbour, Great Lakes	invasive	NS	NS	NS	NS	NS	NS	May-Aug	multiple	Young et al., 2010
Nm	Upper Detroit River	invasive	42.5 SL (f)	NS	84-606	~9%	NS	29th May + 8th Jul	May-Jul	multiple	MacInnis and Corkum, 2000
Nm	Trent River, Canada	invasive	mean:62-83 TL (f)	NS	NS	14%	NS	Jun	Jun-Aug	multiple	Gutowsky and Fox, 2012
Nm	Lower Rhine, Germany	invasive	37 TL (f), 45 TL (m)	4.74 - 29,910.04	32 -14,300	18.6%	9.36%	29th Apr (f), 22nd Apr (m)	Mid-March-mid-Sep	multiple	this study + unpublished data
Pk	native region	native								single	Kalinina, 1976 (cf. Kovac et al., 2009)
Pk	Danube River, Bulgaria	native	NS	NS	NS	~19%	~2%	Apr	NS	NS	Ondrackova et al., 2010
Pk	Danube River, Slovakia	invasive	42.8 SL	61.6-174.0 (119.6)	669-5,646 (2,109)	NS	NS	NS	May-Aug	multiple	Kovac et al., 2009
Pk	Danube River, Slovakia	invasive	NS	NS	NS	NS	NS	NS	NS	NS	Ondrackova et al., 2010
Pk	Lower Rhine, Germany	invasive	67 TL (f)	112-4,416	360 – 10,000	15.27%	5.02%	2nd May (f), 9th Oct (m)	Mid-Mar-mid-Jul	single	this study + unpublished data

Results

Fish assemblages of beach seining hauls

A total of 63,684 fishes represented by 30 different species were caught with beach seining, whereof gobies comprised 73.8 % (Tab. 2). 48.839 fishes (22 species) of the total catch were of the stage 0+, from which 16,851 individuals could be identified as round gobies (34.5 %), 3,261 as monkey gobies (6.7 %), 10,696 as bighead gobies (21.9 %) and 1,826 individuals were declared as gobies, being too small or partially damaged to be designated to species level (3.7 %). Other fish species were represented by 16,205 0+ individuals, with Eurasian perch *Perca fluviatilis* being the most abundant native species (6,495 individuals, 13.3 %), followed by pikeperch *Sander lucioperca* (2,195 individuals, 4.4 %) and ide *Leuciscus idus* (1,738 individuals, 3.6 %).

Table 2. Absolute numbers of caught fish by beach seining.

N	Species	2011	2012	2013
0+ Gobies	Nf	243	604	2,414
	Nm	6,957	5,707	4,187
	Pk	103	7,419	3,174
	Goby	1,473	352	1
>0+ Gobies	Nf	445	709	1,061
	Nm	1,648	4,775	5,630
	Pk	12	5	53
0+ Others		2,898	6,701	6,606
>0+ Others		188	111	208
Total		13,967	26,383	23,334
Seinings (N)		109	174	204

Occurrence of freshly hatched gobies

In total, 8,187 freshly hatched gobies (≤ 15 mm TL) were found in the samplings. Allocation of the single species varied greatly between the three years (Tab. 3), with round goby making up 93.1 % of all caught freshly hatched gobies in 2011, 6.9 % in 2012 and 47.1% in 2013. The low value in 2012 was due to a great amount of bighead gobies, making up 89.1 % in that year, whereas in 2011 there were almost no freshly hatched bighead gobies (1.1 %). In 2013 also only low amounts of this species (15.2 %) were caught. Monkey goby had the greatest share in 2013 with 37.7 % of all freshly hatched gobies, while the other year’s values stayed below 6 %.

Table 3. Number of freshly hatched gobies (≤ 15 mm TL) caught by beach seining and percentages of the single species per year (Nf: monkey goby, Nm: round goby, Pk: bighead goby).

Year	Σ Gobies ≤15mm	Nf [%]	Nm [%]	Pk [%]
2011	1,172	5.8	93.1	1.1
2012	5,616	4.0	6.9	89.1
2013	1,399	37.7	47.1	15.2

Density of 0+ gobies

Densities of 0+ gobies varied greatly between the years, within the season and between species. Altogether, round gobies had the highest densities, followed by bighead and finally monkey gobies (Kruskal-Wallis test: $\chi^2=72.39$, $df=2$, $p<0.0001$). Monkey gobies reached the highest densities in October 2013 with 0.26 individuals per m², round gobies in September 2011 with 1.6 individuals per m², and bighead gobies in May 2012 resembled by 2.46 individuals per m² (Fig. 1). For monkey gobies densities were relatively stable throughout the season with peaks in August and July in 2011 and 2012, respectively. 2013 differed significantly from the preceding years (Wilcoxon rank sum test, 2011: $W=7{,}602.5$, $p=0.0004$, 2012: $W=14{,}049.5$, $p=0.0006$), with densities being at least twice as high as the years before representing the best reproductive success of this species. Round gobies showed increasing densities towards the end of the season in the first year, fluctuating densities in the second year (peak in September) and stable values in the last year (peak in July), with 2011 being the most reproductive year and differing significantly from the other years (Wilcoxon rank sum test, 2012: $W=10{,}634$, $p=0.0002$, 2013: $W=13{,}591$, $p<0.0001$). 0+ densities of bighead gobies showed a clear seasonal pattern in 2012 and 2013 with peaks at the beginning of the season (May 2012: Wilcoxon rank sum test, April: $W=0$, $p<0.0001$, June: $W=153$, $p=0.0004$, July: $W=56.5$, $p<0.0001$, August: $W=19$, $p<0.0001$, September: $W=611.5$, $p<0.0001$, October: $W=234$, $p<0.0001$; June 2013: Wilcoxon rank sum test, April: $W=0$, $p<0.0001$, May: $W=1034.5$, $p<0.0001$, July: $W=107.5$, $p<0.0001$, August: $W=4.5$, $p<0.0001$, September: $W=725$, $p<0.0001$, October: $W=729$, $p<0.0001$), where densities were more than 100 times higher than at the end of the season. Reproductive output was highest in 2012 for bighead gobies, whereas 2011 could be declared as reproductive failure, as no peak for this species could be detected and densities stayed low the whole season, never exceeding 0.02 individuals per m².

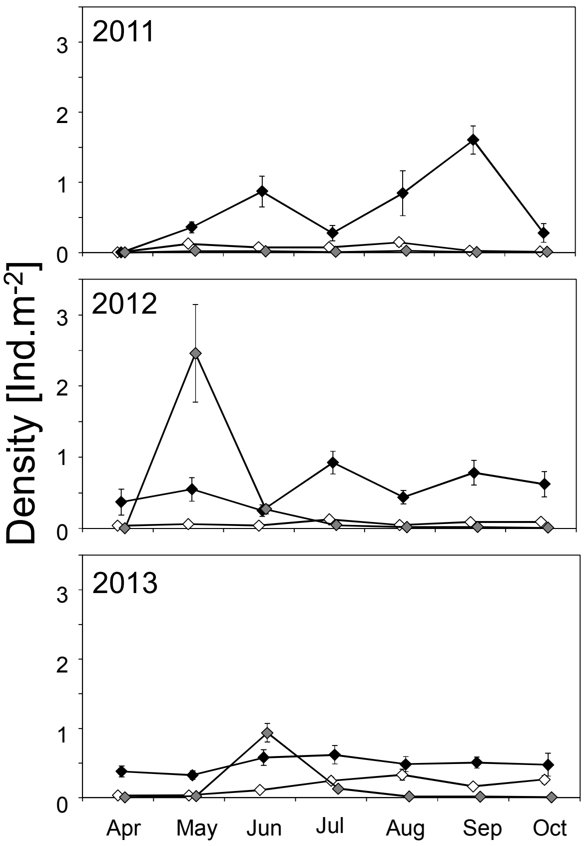

Figure 1. Densities (Ind.m^{-2} ± SE) of 0+ monkey gobies (white), round goby (black), and bighead goby (grey) for the years 2011, 2012, and 2013 in course of the season.

Hatching

First hatching occurred for bighead gobies from 15th of April (2012) to 5th of May (2013) and ended on 19th of June (2011) up to 4th of August (2013) (Tab. 4), representing a regularly short period of intensive hatching resulting in one cohort of bighead gobies per year (Fig. 2). In contrast, hatching of round gobies lasted from 17th of April (2012) up to 25th of September (2013) revealing several spawning events per season. In 2011 and 2012 hatching intensity of round gobies was more pronounced at the beginning of the season, while in 2013 it was in a continuous state for the breeding season. However, no clear batches or breeding pauses could be detected for all years. Hatching of monkey goby also lasted from 17th of April (2012) up to 25th of September (2013), providing evidence of multiple spawning. Unlike round gobies, hatching rates of monkey gobies peaked in the middle of the season.

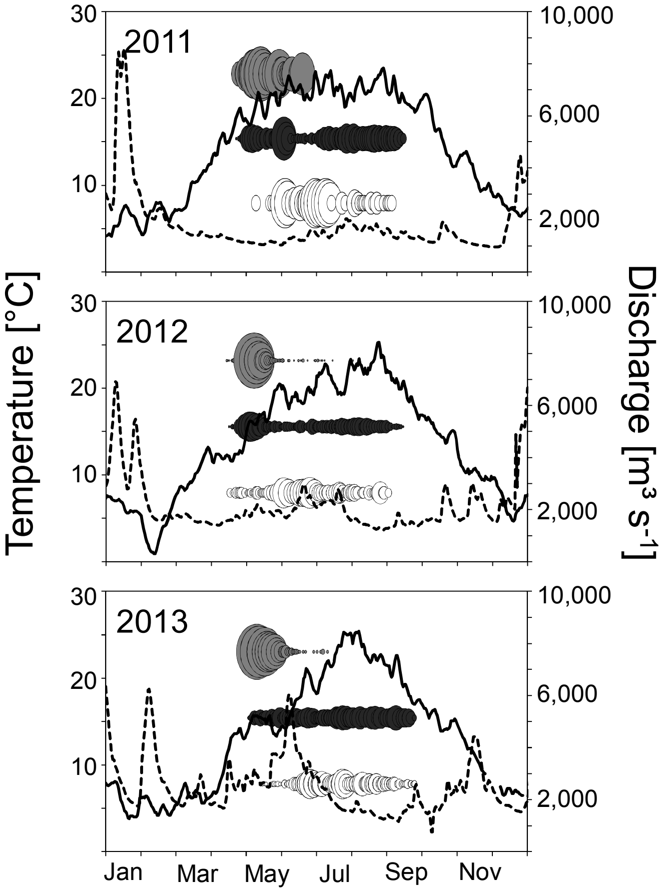

Figure 2. Water temperature (black line), discharge (dotted line), and relative abundances of all calculated hatching events per year and species. With bighead goby (grey), round goby (black), and monkey goby (white) for the years 2011 (above), 2012 (middle), and 2013 (bottom).

Spawning

Spawning was earliest in 2012 for all three species with bighead gobies starting on the 17th of March followed by monkey and round gobies, both on 19th of March. In this year breeding season was also longest ranging from 124 days (bighead goby) to 170 days (round goby) (Tab. 4). Latest spawning was calculated for all species in 2013 lasting up to 25th of June in case of bighead gobies, and up to 11th and 12th September for round and monkey gobies, respectively. In general, breeding season of bighead gobies lasted from mid-March to mid-July with a mean duration of 88 ± 32 days. However, the relatively long spawning season of 124 days in 2012 was due to some single specimens (< 1 %) that were caught later in the season. 50 % of spawning was already achieved by the end of April in all years, showing a clear pattern of only one spawning event per season. Round goby spawned from mid-March to mid-September with a mean period length of 161 ± 8 days. 50 % of spawning activity was already achieved by 7th of May in 2012, while in 2011 and 2013 it lasted up to 6th of July. Breeding season of monkey gobies also continued from mid-March to mid-September, lasting 140 ± 17 days with 50 % of spawning events being accomplished from 6th of June (2012) to 4th of July (2013).

Table 4. Spawning length of gobies, given is 1st date of spawning, the date where 50% of spawning activity was accomplished, and the last day of spawning. Additionally, length of breeding season [d] and first and last day of hatching is shown.

Species	Year	1st day of spawning	50% spawning	last day spawning	Breeding season[d]	1st day of hatching	last day hatching
Nf	2011	21st Apr	14th Jun	20th Aug	121	10th May	04th Sep
	2012	19th Mar	06th Jun	20th Aug	154	17th Apr	04th Sep
	2013	21st Apr	04th Jul	12th Sep	144	15th May	25th Sep
Nm	2011	31st Mar	06th Jul	03rd Sep	156	23rd Apr	20th Sep
	2012	19th Mar	07th May	05th Sep	170	17th Apr	22nd Sep
	2013	06th Apr	06th Jul	11th Sep	158	05th May	25th Sep
Pk	2011	03rd Apr	29th Apr	03rd Jun	61	25thApr	19th Jun
	2012	17th Mar	14th Apr	19th Jul	124	15th Apr	04th Aug
	2013	06th Apr	24th Apr	25th Jun	80	05th May	12th Jul

Spawning onset showed no dependency on water temperature or photoperiod for all species, as it varied greatly between the years (Fig. 3). This variability could not only be found for temperatures at the defined spawning dates, but also for day-degrees from 10 up to 30 days before the very first spawning events and for the whole year, respectively. Monkey gobies spawned at temperatures ranging from 10.3 - 25.2 °C, round gobies from 6.9 – 21.9 °C, and bighead gobies from 6.9 – 20.8 °C. Interestingly, 2011, which was the warmest year, showed the shortest spawning season for all species.

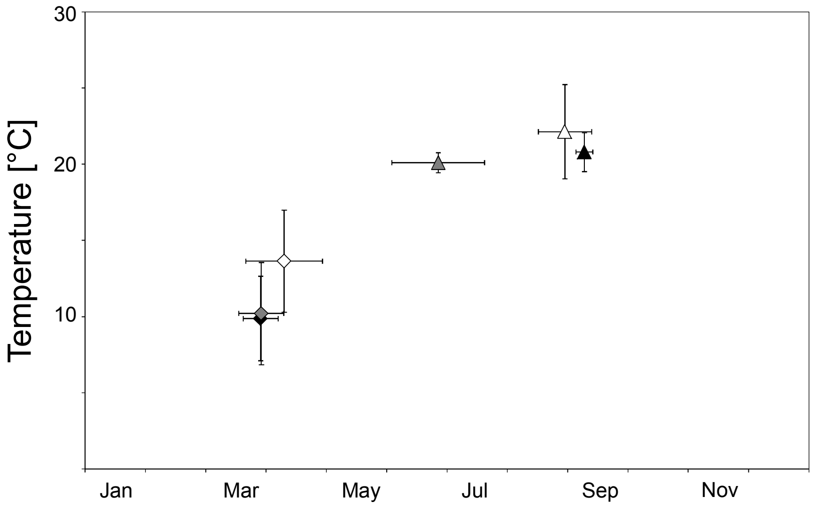

Figure 3. Water temperature (°C ± SD) during onset (diamond) and end (triangle) of spawning activity of monkey goby (white), round goby (black), and bighead goby (grey) for the three years.

Growth rates

Growth rates for the first three months were highly variable and alternated between 0.3 mm (2012) and 0.71 mm per day (2013) for monkey gobies, 0.38 mm (2013) and 0.51 mm per day (2011) for round gobies, and between 0.48 mm (2013) and 0.95 mm per day (2011) for bighead gobies, respectively (Fig. 4). While bighead gobies showed decreasing growth rates during the course of the three years, round gobies had almost stable growth rates, with a small decreasing trend, whereas monkey goby was the only species with an increasing trend of growth rates, however due to high variability in the growth rates this trend was not significant (ANOVA, species: *df*= 2, *F*=0.542, *p*=0.588, year: *df*=2, *F*=0.4009, *p*=0.6738).

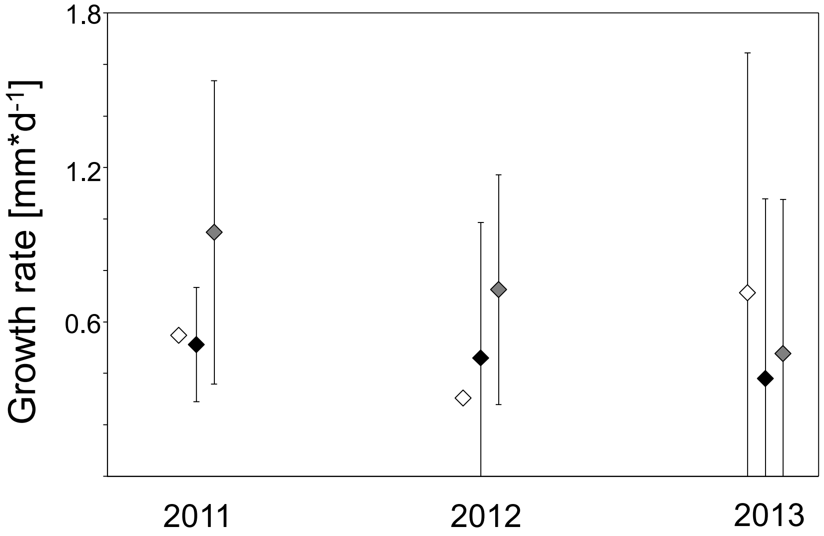

Figure 4. Growth rates (mm*d^{-1} ± SD) of juvenile (freshly hatched – 3 months) monkey (white), round (black), and bighead (grey) gobies. Growth rates were determined for the first cohort of each year followed up to the end of July / beginning of August, respectively.

Gonadosomatic index

GSI values of female bighead gobies peaked at the beginning of May with 6.8 % ± 6.5 %, whereas it stayed low (< 0.85 %) the rest of the season. A slight, yet significant increase from September to October (1.2 % ± 0.5 %; Fig. 5) could be observed, indicating starting gonadal investment already before the winter (begin September to mid-October: Wilcoxon rank sum test, *W*=10, *p*=0.003). High standard deviation at the beginning of May was due to a high amount of females which had already spawned in combination with females that were ready to spawn at that time. Highest GSI values for round goby were obtained from the beginning of May until the end of July, peaking at the end of June (5.3 % ± 4.8 %), significantly differing from the end of the season (end of June: Wilcoxon rank sum test, end August: *W*=92, *p*=0.008, begin September: *W*=119, *p*=0.0005, mid-October: *W*=162, *p*=0.0037). The same pattern could be observed for female monkey gobies, where GSI values from beginning of May until the end of July stayed high and also peaked at the end of June (9.0 % ± 5.5 %), with June varying significantly from August (Wilcoxon rank sum test: *W*=232, *p*<0.0001), September (Wilcoxon rank sum test: *W*=160, *p*=0.0004) and October (Wilcoxon rank sum test: *W*=192, *p*=0.0002).

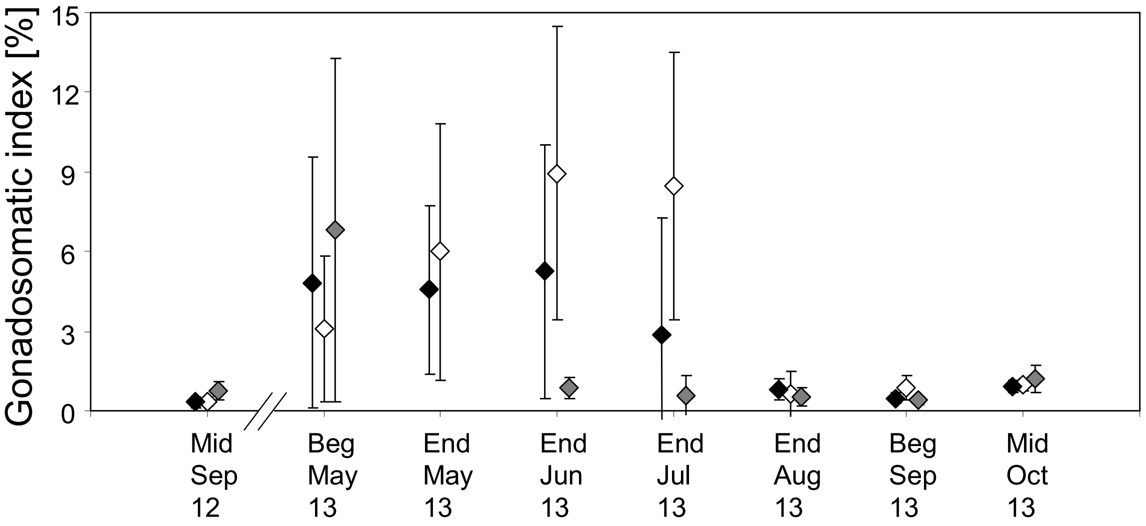

Figure 5. Gonadosomatic index (GSI; % ± SD) of female monkey (white), round (black), and bighead gobies (grey) in the course of the year (mid-September 2012 – mid-October 2013).

Discussion

The invasive gobiid species at the Lower Rhine showed differing reproduction modes, presented by single versus multiple spawning events, spawning season length and intensity across the season. To understand and define the impact of our results, the data were compared with reproductive traits obtained from native populations, as well as from other invaded areas ranging from Slovakia to the Great Lakes (Tab. 1). Spawning season length and spawning mode were the traits that could be found in a high share of the investigated literature and which seem to be less affected by methodological issues than other traits. For monkey gobies multiple spawning events could be validated at the Lower Rhine, as it is in their native habitats (Konecna and Jurajda, 2012). In their native area, spawning took place between May and August, but was prolonged in the invaded habitat from mid-March to mid-September. Round gobies were also quoted in all studies as multiple spawning species (see Tab. 1). Longest spawning season was reported for the Gulf of Gdansk, where it lasted from March to September with a pause in June (Tomczak and Sapota, 2006). We also saw an extended spawning period from mid-March to mid-September, yet no pauses were detected. Bighead gobies at the Lower Rhine showed a restricted spawning season (mid-March to mid-July, with 50 % of all spawning activity being already accomplished at the end of April), whereas in other invaded ranges a multiple spawning habit was observed (Kovac et al., 2009). Besides spawning season length and spawning mode, the smallest size at maturity seems to be the most reliable trait to examine, as it was used in several studies to determine status of invasion (L'avrincikova and Kovac, 2007; Horkova and Kovac, 2014). Despite not being in the focus of this study, in our area, females of *N. melanostomus* matured at much smaller sizes compared to other regions. For monkey and bighead goby, data were scarce. Whilst female monkey gobies mature at 41.65 mm SL in native habitats (Konecna and Jurajda, 2012), the smallest size at maturity was much larger (78 mm TL, female) in the Lower Rhine. Invasive bighead goby females in the Slovakian Danube matured at 42.8 mm SL (Kovac et al., 2009), contrasting smallest sizes of 67 mm TL at the Lower Rhine. Data of relative and absolute fecundities varied strongly, mainly due to methodological issues (counting eggs of all stages vs. counting only stage 4 eggs). Maximum detected GSI values also need to be interpreted with caution, as they were sometimes calculated as percentage of eviscerated body weight and sometimes of whole body weight. Additionally, no study sampled fishes in a perfect year-round cycle, thus potentially missing the highest values.

Though some studies at least report distinct batches for round gobies, no clear batches could be distinguished at the Lower Rhine for round and monkey gobies. In captivity, female round gobies can produce new batches every 18–20 days up to six times a season (Rashcheperin, 1964; Kovtun, 1978). Hence breeding seasons of 156 – 170 days, as observed at the Lower Rhine would potentially generate 8 to 9 batches. Spawning intensity for round gobies was highest at the beginning of the season, whereas spawning of monkey gobies peaked later, in the middle of the season, but was also continuous. Spawning season of bighead gobies was clearly shorter, only represented by a single batch. Consequently, calculated hatching intensities and time of spawning revealed distinctive reproduction modes for all three species.

The annual reproductive cycle was confirmed by GSI analyses of female gobies, which showed the rapid decline of the GSI values of *P. kessleri,* in contrast to *N. melanostomus* and *N. fluviatilis*, where the GSI decreased progressively over the season, as it is typical for multiple spawning species (Rinchard and Kestemont, 1996). In contrast to GSI analyses, by following the abundances of early hatched individuals over the whole season, starting at a point of no occurrence, spawning onset cannot be dismissed and additional information on spawning intensity can be obtained.

The general advantages of multiple, or continuous spawning for the duration of the season, are (1) an increased fecundity as there is more space in the ovary if oocytes do not hydrate all at the same time; (2) the risk of predation on larvae and eggs is spread over a longer period; (3) the impact on prey items is allocated over the season; and (4) the risk of spawning the eggs at a time of unfavorable conditions is also spread (summarized by Mcevoy and Mcevoy, 1992). Additionally, prolonged breeding periods are regarded as key factor for successful recruitment in streams with high extremes in temperature and flow (Humphries et al., 2002). Thus, multiple spawning will assure that at least some portion of the total offspring may survive to recruitment, if changes in temperature, discharge, predatory pressure or food availability occur at some point in the season that could extinguish the whole batch (Goodman, 1984). Bighead goby therefore showed the most risky reproductive characteristics, as a complete failure of reproduction could, and indeed did occur at the Lower Rhine in 2011. To our opinion, this was most probably associated to a phase of extremely low water level right after spawning, consequently desiccating the batches.

The spawning season of many fish species is determined by water temperature and/or photoperiod (e.g., Munro et al., 1990; bitterling *Rhodeus sericeus*, Reichard et al., 2004; pikeperch *Sander lucioperca,* reviewed by Lappalainen et al., 2003; salmon *Salmo salar* Dahl et al., 2004; whitefish *Coregonus lavaretus* Chernyaev, 2007). Although some studies included temperature in their description of the spawning season (Charlebois et al., 1997; Leslie and Timmins, 2004), no dependency was detected so far, probably due to the fact that round goby is described as eurythermal species with an endocrine system being active all year (Charlebois et al., 1997). In our study, temperature did not seem to trigger spawning, as it greatly varied between the years. Additionally, there was no fixed date of spawning onset, thus photoperiod seems to be also of minor importance to affect breeding. Other factors like endogenous rhythms, hormone levels (Liley and Stacey, 1983; Woods and Sullivan, 1993), male behavior and/or plasticity to avoid significant niche overlaps might be more determinative to initiate spawning.

For round gobies spawning is reported to occur at temperatures between 9 °C and 26 °C (Charlebois et al., 1997), slightly higher temperatures as observed in our study (6.9 °C - 21.9 °C), but resembling conditions seen for monkey gobies in our area (10.3 °C - 25.2 °C). Though a small temperature range described the end of spawning season in bighead gobies, it remains doubtful, if the spawning season of this species was restricted by high temperatures in the mid-season. Yet, bighead gobies seem to be more sensitive to warm temperatures than the other two species (Mehner, 2013), which might limit spawning to temperatures below 20.8 °C. Indeed, for three co-occurring goby species of the genus *Pomatoschistus* 25 °C was the critical temperature for goby egg survival of two species, whereas eggs of the third species showed minor affection at this temperature (Fonds and Van Buurt, 1974).

Besides a possible temperature restriction of bighead goby, it is noticeable that although this species had very good reproductive success in two years (Tab. 3, Fig. 1), recruitment seemed to fail, as year-class strength declined dramatically for the rest of the season. It is known, that this species undergoes an ontogenetic habitat shift to riprap structures at a size of about 60 mm TL (Borcherding et al., 2013), yet this size was not reached before August-September, where the decline was already clearly obvious.

Juvenile growth rates, reflecting energy allocation of the individual, have been used for other invasive fishes as a predictor for species invasiveness (Copp and Fox, 2007). Altogether round gobies had the highest densities of 0+ specimens and the most stable growth rates, likely having the highest impact on native fishes. Nevertheless, monkey gobies showed increasing densities and growth rates in the course of the years, giving some evidence for a still prospering population development. However, as growth rates were highly variable, further studies are needed to really define invasion status and impact on native fishes.

Overall, the detected reproductive traits were mainly within the range of traits observed in native habitats or other invaded ranges (Tab. 1). Phenotypic plasticity in reproductive traits has been shown across a wide range of taxa, e.g., great tits (Husby et al., 2010) or lacertid lizards (Du, 2006). Some invasive populations of gobies across a wide geographical distribution showed a higher allocation in reproduction, represented by an extended spawning season, smaller sizes at maturity and higher fecundity (see References in Tab. 1). Spawning season of bighead goby was restricted, resembling traits of native habitats (Kalinina, 1976, cited from Kovac et al., 2009). However, our results also support plasticity in reproductive traits, as spawning seasons of monkey and round gobies were extended and at least round gobies had smaller sizes at maturity in this region compared to other habitats. Higher potential of phenotypic plasticity concerning body shape could be observed for invasive round gobies at the Danube compared to bighead gobies (Cerwenka et al., 2014). However, observed shifts can just depend on biotic and abiotic factors differing from the situation exhibited in the native range (Strayer et al., 2006). Further, shifts in life-history traits can be based on large-scale factors like evolutionary or geographical responses (Mann et al., 1984; Arnett and Gotelli, 1999; Blanck and Lamouroux, 2007), or as a consequence of fine-scale exhibited conditions, e.g., chemical release (Burks et al., 2000), predator occurrence (Crowl and Covich, 1990; Claessen et al., 2002), or fluctuations of resource accessibility leading to changes in levels of competition (Boggs and Ross, 1993). Additionally, invasion is a gradually advancing process. Therefore, different biological traits may be favorable during different stages of invasion, depending on density-dependent aspects, e.g., decreasing food availability or access to spawning sites (Hänfling and Kollmann, 2002; Ribeiro et al., 2008) Further, besides changes based on invasional processes and geographical adaptations, fishes are also known to react to annual variations of environmental conditions, like productivity or summer droughts with differences in spawning modes and intensities (Lobon-Cervia et al., 1991; Mazzoni and Iglesias-Rios, 2002).

At the Lower Rhine the special situation arises, that three congeneric and morphologically similar goby species have invaded an anthropogenic modified environment (Leuven et al., 2009) and still co-occur in high densities 7 – 9 years after initial introduction (Borcherding et al., 2013; this study). This exacerbates the problem of trustable risk assessment on the one hand and, on the other hand, may lead to fine-tuned niche partitioning on several axes (Hardin, 1960; Schoener, 1974). Tsikliras et al. (2010), who studied the spawning season of 168 Mediterranean fishes, found that congeneric species occupying the same habitats showed successive, non-overlapping spawning events. Size and accessibility of breeding sites are also known to affect reproductive rates of fish (Oliveira et al., 1999; Reichard et al., 2004). Therefore, in habitats where spawning sites are limited, multiple spawning may spread the interference competition for this resource on a temporal axis. At the River Rhine, artificial stony embankments present plenty suitable spawning sites, which might have facilitated early invasion success, as anthropogenic alterations are known to favor non-native species and increase their impact on native fauna (Byers, 2002). Yet, the Ponto-Caspian gobiids occur in very high abundances at the Lower Rhine and are known for their aggressive and territorial behavior (Dubs and Corkum, 1996). Therefore, altogether, it is difficult to tell if the differences in reproduction modes of the three species are based on phylogenetic, invasional processes, niche separation, varying geographical and environmental conditions or a mixture of those factors.

The importance of reliable growth and reproductive data in combination with the interaction between life-history traits and invasiveness for other introduced species has been stressed before (Cucherousset et al., 2009). The capability of phenotypic plasticity in reproductive traits surely promotes the success of the Ponto-Caspian gobies. We tried to summarize important reproductive traits from different regions, however, methodological issues constraint the usefulness of such an overview. Here, the application of standardized methods is absolutely necessary. Spawning season length and spawning mode seem to be reliable and important traits to look at. With our study we showed a new method of determining the spawning season with a high resolution and detailed information on spawning intensity. Yet, further studies are needed comparing reproductive traits of the three species co-occurring in their native habitats. Additionally, studies on reproductive traits of monkey and bighead gobies in invaded areas are required to set these results into a better context. The here presented data reflect a highly variable system, indicating that invasion and population development is still in process at the Lower Rhine. To conclude, invasiveness of bighead gobies seemed to be of a lower level compared to round and monkey gobies, as this species showed no strong year-class strength and lower recruitment at the end of the season, even if reproduction success was obvious. We assume strongest increases in population development for monkey gobies, as growth rates and densities for this species show prospering trends. Round goby in contrast displayed the most stable values, probably indicating the peak of invasion.

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References

Adamek, Z., Andreji, J., Gallardo, J. M., 2007. Food habits of four bottom-dwelling gobiid species at the confluence of the Danube and Hron rivers (South Slovakia). Int. Rev. Hydrobiol. 92, 554-563.

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., Chunco, A. J., 2011. Do species traits predict recent shifts at expanding range edges? Ecol. Lett. 14, 677-689.

Arnett, A. E., Gotelli, N. J., 1999. Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. Evolution, 1180-1188.

Balazova-L'avrinìkova, M., Kovac, V., 2007. Epigenetic context in the life history traits of the round goby, *Neogobius melanostomus*. In: Ed: F. Gherardi, Biological invaders in inland waters: Profiles, distribution, and threats. Springer Netherlands, pp. 275-287.

Banks, N. C., Paini, D. R., Bayliss, K. L., Hodda, M., 2015. The role of global trade and transport network topology in the human-mediated dispersal of alien species. Ecol. Lett. 18, 188-199.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Can. J. Fish. Aquat. Sci. 59, 1159-1174.

Bil´ko, V. P., 1971. Comparative description of the growth of gobies (Gobiidae) and Lee´s phenomenon. J. Ichthyol. 11, 543-555.

Blanck, A., Lamouroux, N., 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. J. Biogeogr. 34, 862-875.

Boggs, C. L., Ross, C. L., 1993. The effect of adult food limitation on life history traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology, 433-441.

Borcherding, J., Staas, S., Kruger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Borcherding, J., Dolina, M., Heermann, L., Knutzen, P., Krüger, S., Matern, S., van Treeck, R., Gertzen, S., 2013. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. Limnologica - Ecology and Management of Inland Waters 43, 49-58.

Buczkowski, G., 2010. Extreme life history plasticity and the evolution of invasive characteristics in a native ant. Biol. Invasions 12, 3343-3349.

Burks, R. L., Jeppesen, E., Lodge, D. M., 2000. Macrophyte and fish chemicals suppress Daphnia growth and alter life-history traits. Oikos 88, 139-147.

Byers, J. E., 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97, 449-458.

Byers, J. E., Reichard, S., Randall, J. M., Parker, I. M., Smith, C. S., Lonsdale, W. M., Atkinson, I. A. E., Seastedt, T. R., Williamson, M., Chornesky, E., 2002. Directing research to reduce the impacts of nonindigenous species. Conserv. Biol. 16, 630-640.

Cerwenka, A. F., Alibert, P., Brandner, J., Geist, J., Schliewen, U. K., 2014. Phenotypic differentiation of Ponto-Caspian gobies during a contemporary invasion of the upper Danube River. Hydrobiologia 721, 269-284.

Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J., Rudinka, S., 1997. The round goby *Neogobius melanostomus* (Pallas). A review of European and North American Literature, 96 ed. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey, INHS Special Publication No. 20.

Chernyaev, Z., 2007. Factors and possible mechanisms causing changes in the rate of embryonic development of bony fish (with reference to Coregonidae). J. Ichthyol. 47, 494-503.

Chotkowski, M. A., Marsden, J. E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. J. Great Lakes Res. 25, 26-35.

Claessen, D., Van Oss, C., De Roos, A. M., Persson, L., 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology 83, 1660-1675.

Claridge, K., Franklin, S. B., 2002. Compensation and plasticity in an invasive plant species. Biol. Invasions 4, 339-347.

Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20, 110.

Copp, G., Fox, M., 2007. Growth and life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in Europe, and the relevance to its potential invasiveness. In: Ed: F. Gherardi, Biological invaders in inland waters: Profiles, distribution, and threats. Springer Netherlands, pp. 289-306.

Crowl, T. A., Covich, A. P., 1990. Predator-induced life-history shifts in a freshwater snail. Science 247, 949-951.

Cucherousset, J., Copp, G., Fox, M., Sterud, E., van Kleef, H., Verreycken, H., Zahorskí, E., 2009. Life-history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. Biol Invasions 11, 2171-2180.

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A., Ragnarsson, B., 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. Can. J. Zool. 82, 1864-1870.

Davidson, A. M., Jennions, M., Nicotra, A. B., 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecol. Lett. 14, 419-431.

Du, W.-G., 2006. Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. Oikos 112, 363-369.

Dubs, D. O. L., Corkum, L. D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. 22, 838-844.

Fonds, M., Van Buurt, G., 1974. The influence of temperature and salinity on development and survival of goby eggs (Pisces, Gobiidae). Hydrobiol. Bull. 8, 110-116.

Goodman, D., 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theor. Popul. Biol. 25, 1-20.

Grabowska, J., Grabowski, M., 2005. Diel-feeding activity in early summer of racer goby *Neogobius gymnotrachelus* (Gobiidae): a new invader in the Baltic basin. J. Appl. Ichthyol. 21, 282-286.

Grula, D., Balazova, M., Copp, G., Kovac, V., 2012. Age and growth of invasive round goby *Neogobius melanostomus* from middle Danube. Cent. Europ. J. Biol. 7, 448-459.

Guo, Z., Cucherousset, J., Lek, S., Li, Z., Zhu, F., Tang, J., Liu, J., 2013. Comparative study of the reproductive biology of two congeneric and introduced goby species: implications for management strategies. Hydrobiologia 709, 89-99.

Gurevitch, J., Fox, G. A., Wardle, G. M., Inderjit, Taub, D., 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecol. Lett. 14, 407-418.

Gutowsky, L. F. G., Fox, M. G., 2012. Intra-population variability of life-history traits and growth during range expansion of the invasive round goby, *Neogobius melanostomus*. Fisheries Manag. Ecol. 19, 78-88.

Hänfling, B., Kollmann, J., 2002. An evolutionary perspective of biological invasions. Trends Ecol. Evol. 17, 545-546.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Heermann, L., Borcherding, J., 2013. Competition, predation, cannibalism: the development of young of the year perch populations in ponds with bream or roach. J. Appl. Ichthyol. 29, 549-554.

Horkova, K., Kovac, V., 2015a. Ontogenetic phenomena, temporal aspect, and ecological factors in the successful invasion of round goby *Neogobius melanostomus* in the River Danube. Aquat. Invasions 10, 227-235.

Horkova, K., Kovac, V., 2015b. Rapid response of invasive round goby (*Neogobius melanostomus*) (Pallas, 1814) to an environmental perturbation demonstrated in reproductive parameters of females. J. Appl. Ichthyol. 31, 328-332.

Horkova, K., Kovac, V., 2014. Different life-histories of native and invasive *Neogobius melanostomus* and the possible role of phenotypic plasticity in the species invasion success. Knowl. Manag. Aquat. Ec. 412, 1-11.

Hulme, P. E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10-18.

Humphries, P., Serafini, L. G., King, A. J., 2002. River regulation and fish larvae: variation through space and time. Freshwat. Biol. 47, 1307-1331.

Husby, A., Nussey, D. H., Visser, M. E., Wilson, A. J., Sheldon, B. C., Kruuk, L. E., 2010. Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. Evolution 64, 2221-2237.

Janssen, J., Jude, D. J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27, 319-328.

Jude, D. J., 1997. Round gobies: cyberfish of the third millennium. Gt. Lakes Res. Rev. 3, 27-34.

Kalinina, E., 1976. Reproduction and development of Azov-Black Sea gobies. Naukova Dumka, Kiev.

Karlson, A. M. L., Almqvist, G., Skora, K. E., Appelberg, M., 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES J. Mar. Sci. 64, 479-486.

Keller, R. P., Geist, J., Jeschke, J. M., Kühn, I., 2011. Invasive species in Europe: ecology, status, and policy. Environ. Sci. Eur. 23, 1-17.

Koblickaya, A. P., 1981. Key for identifying young freshwater fishes (in Russian). Light and Food Industrial House, Moskau.

Kolar, C. S., Lodge, D. M., 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298, 1233-1236.

Kolar, C. S., Lodge, D. M., 2001. Progress in invasion biology: predicting invaders. Trends Ecol. Evol. 16, 199-204.

Konecna, M., Jurajda, P., 2012. Population structure, condition, and reproduction characteristics of native monkey goby, *Neogobius fluviatilis* (Actinopterygii: Perciformes: Gobiidae), in the Bulgarian Danube. Acta Ichthyol. Piscat. 42, 321-327.

Kornis, M. S., Mercado-Silva, N., Van der Zanden, M. J., 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. J. Fish Biol. 80, 235-285.

Kovac, V., Copp, G. H., Sousa, R. P., 2009. Life-history traits of invasive bighead goby *Neogobius kessleri* (Gunther, 1861) from the middle Danube River, with a reflection on which goby species may win the competition. J. Appl. Ichthyol. 25, 33-37.

Kovtun, I. F., 1978. On the fecundity of the round goby, *Gobius melanostomus*, from the Sea of Azov. J. Ichthyol. 17, 566-573.

Krönke, F., 2008. Ein ambivalenter Immigrant im Aquarium: *Neogobius melanostomus*, die Schwarzmaulgrundel. AKFS-aktuell 21, 9-14.

Kulikova, N. I., 1985. Effect of chorionic gonadotropin on the growth and maturation of oocytes in the Caspian round goby, *Neogobius melanostomus* (Gobiidae). J. Ichthyol. 25, 86-98.

L'avrincikova, M., Kovac, V., 2007. Invasive round goby *Neogobius melanostomus* from the Danube mature at small size. J. Appl. Ichthyol. 23, 276-278.

Lappalainen, J., Dörner, H., Wysujack, K., 2003. Reproduction biology of pikeperch (*Sander lucioperca* (L.)) - a review. Ecol. Freshwat. Fish 12, 95-106.

Leprieur, F., Brosse, S., Garcia-Berthou, E., Oberdorff, T., Olden, J. D., Townsend, C. R., 2009. Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes. Fish Fish. 10, 88-97.

Leslie, J. K., Timmins, C. A., 2004. Description of age-0 round goby, *Neogobius melanostomus* Pallas (Gobiidae), and ecotone utilisation in St. Clair Lowland Waters, Ontario. Can. Field Nat. 118, 318-325.

Leuven, R. S. E. W., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. J. R., de Vaate, A. B., 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. Biol. Invasions 11, 1989-2008.

Liley, N. R., Stacey, N. E., 1983. Hormones, pheromones, and reproductive behavior in fish. Fish Physiol. 9.

Lindberg, G. U., Heard, A. S., Rass, T. S., 1980. Multilingual dictionary of names of marine food-fishes of World fauna. Nauka, Leningrad.

Lobon-Cervia, J., Montanges, C., De Sostoa, A., 1991. Influence of environment upon the life history of gudgeon, *Gobio gobio* (L.): a recent and successful colonizer of the Iberian Peninsula. J. Fish Biol. 39, 285-300.

Logachev, V. S., Mordvinov, Y. E., 1979. Swimming speed and activity of larvae of round goby and some predatory crustaceans of the Black Sea. Biol. Morya, pp. 77-80.

MacInnis, A. J., Corkum, L. D., 2000. Fecundity and reproductive season of the round goby *Neogobius melanostomus* in the upper Detroit River. Trans. Am. Fish. Soc. 129, 136-144.

Mann, R. H. K., Mills, C. A., Crisp, D. T., 1984. Geographical variation in the life-history tactics of some species of freshwater fish. Fish reproduction: strategies and tactics, 171-186.

Mazzoni, R., Iglesias-Rios, R., 2002. Environmentally related life history variations in *Geophagus brasiliensis*. J. Fish Biol. 61, 1606-1618.

Mcevoy, L. A., Mcevoy, J., 1992. Multiple Spawning in Several Commercial Fish Species and Its Consequences for Fisheries Management, Cultivation and Experimentation. J. Fish Biol. 41, 125-136.

Mehner, L., 2013. Metabolic rates of three invasive Gobiidae in the Lower Rhine - Oxygen consumption under varying conditions. Bachelor Thesis, University of Cologne, 90 pp.

Meunier, B., Yavno, S., Ahmed, S., Corkum, L. D., 2009. First documentation of spawning and nest guarding in the laboratory by the invasive fish, the round goby (*Neogobius melanostomus*). J. Great Lakes Res. 35, 608-612.

Miller, P. J., 1984. The tokology of gobioid fishes. In: Potts,G.W., Wooton,R.J. (Eds.), Fish reproduction strategies and tactics. Academic Press, London UK, pp. 119-153.

Miller, P. J., 1986. Fishes of the North-East Atlantic and the Mediterranean, Gobiidae. ed Paris: UNESCO.

Moiseyeva, Y. B., 1983. The development of the gonads of the round goby *Neogobius melanostomus* (Gobiidae), during the embryonic period. J. Ichthyol. 23, 64-74.

Mooij, W. M., 1989. A key to the identification of larval bream, *Abramis brama*, white bream, *Blicca bjoerkna*, and roach, *Rutilus rutilus*. J. Fish Biol. 34, 111-118.

Moskalkova, K. I., 1989. Anatomical histological and functional peculiarities of development of the intestine in round goby, *Neogobius melanostomus*, a species with direct type of development. J. Ichthyol. 29, 108-122.

Munro, A. D., Scott, A. P., Lam, T. J., 1990. Reproductive seasonality in teleosts : environmental influences. CRC Press, Boca Raton (Florida).

Neilson, M. E., Stepien, C. A., 2009. Escape from the Ponto-Caspian: Evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). Mol. Phylogenet. Evol. 52, 84-102.

Olden, J. D., Poff, N. L., Bestgen, K. R., 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. Ecol. Monogr. 76, 25-40.

Oliveira, R. F., Almada, V. C., Forsgren, E., Goncalves, E. J., 1999. Temporal variation in male traits, nesting aggregations and mating success in the peacock blenny. J. Fish Biol. 54, 499-512.

Ondrackova, M., Francova, K., Davidova, M., Polacik, M., Jurajda, P., 2010. Condition status and parasite infection of *Neogobius kessleri* and *N. melanostomus* (Gobiidae) in their native and non-native area of distribution of the Danube River. Ecol. Res. 25, 857-866.

Pejchar, L., Mooney, H. A., 2009. Invasive species, ecosystem services and human well-being. Trends Ecol. Evol. 24, 497-504.

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52, 273-288.

Pinder, A. C., 2001. Keys to larval and juvenile stages of coarse fishes from freshwaters in the British Isles. Freshwater Biological Association, Ambleside.

Placha, M., Balazova, M., Kovac, V., Katina, S., 2010. Age and growth of non-native monkey goby *Neogobius fluviatilis* (Teleostei, Gobiidae) in the River Ipel, Slovakia. Folia Zool. 59, 332-340.

R Development Core Team, 2009. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. (ISBN 3-900051-07-0).

Rashcheperin, V. K., 1964. Osobennosti portsionnogo ikrometaniya bycka-kruglyaka Azovskogo moray i chislennost´yego molodi. Tr. molodykh uchenykh. Features of the intermittent spawning of the round goby from the Azov Sea and the abundance of its young. Works by young scientists. Pishchepromizdat, Moscow.

Reichard, M., Jurajda, P., Smith, C., 2004. Male-male interference competition decreases spawning rate in the European bitterling (*Rhodeus sericeus*). Behav. Ecol. Sociobiol. 56, 34-41.

Ribeiro, F., Elvira, B., Collares-Pereira, M. J., Moyle, P. B., 2008. Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. Biol. Invasions 10, 89-102.

Ricciardi, A., MacIsaac, H. J., 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. 15, 62-65.

Ricker, W. E., 1975. Computation and interpretation of biological statistics of fish populations. Department of the Environment, Fisheries and Marine Service, Canada.

Rinchard, J., Kestemont, P., 1996. Comparative study of reproductive biology in single- and multiple-spawner cyprinid fish .1. Morphological and histological features. J. Fish Biol. 49, 883-894.

Ross, D. J., Johnson, C. R., Hewitt, C. L., Ruiz, G. M., 2004. Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Mar. Biol. 144, 747-756.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., Weller, S. G., 2001. The population biology of invasive species. Ann. Rev. Ecol. System. 32, 305-332.

Sapota, M., Balazy, P., Mirny, Z., 2014. Modification in the nest guarding strategy – one of the reasons of the round goby (*Neogobius melanostomus*) invasion success in the Gulf of Gdansk? Oceanol. Hydrobiol. Stud. 43, 21.

Sasi, H., Berber, S., 2010. Some biological characteristics of the monkey goby in Anatolia. Asian J. Anim. Vet. Adv. 5, 229-233.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348-360.

Schoener, T. W., 1974. Resource partitioning in ecological communities. Science 185, 27-39.

Simonovic, P., Paunoviç, M., Popoviç, S., 2001. Morphology, feeding, and reproduction of the round goby, *Neogobius melanostomus* (Pallas), in the Danube River Basin, Yugoslavia. J. Great Lakes Res. 27, 281-289.

Smirnov, A. N., 1986. Fauna Ukrainy 8, Ryby (5): Okuneobraznye (byckovidnyje), skorpenoobraznyje, kambaloobraznyje, udiljšcikoobraznyje. ed Naukova Dumka, Kiev. (in Russian).

Staas, S., 1996. Anleitung zur Bestimmung von 0+ - Jungfischen aus dem Rhein. Report Ecological Field Station Rees-Grietherbusch.

Steinhart, G. B., Stein, R. A., Marschall, E. A., 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? J. Great Lakes Res. 30, 381-389.

Strayer, D. L., Eviner, V. T., Jeschke, J. M., Pace, M. L., 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. 21, 645-651.

Tomczak, M. T., Sapota, M. R., 2006. The fecundity and gonad development cycle of the round goby (*Neogobius melanostomus* Pallas 1811) from the Gulf of Gdansk. Oceanol. Hydrobiol. Stud. 35, 353-367.

Tsikliras, A. C., Antonopoulou, E., Stergiou, K. I., 2010. Spawning period of Mediterranean marine fishes. Rev. Fish Biol. Fish. 20, 499-538.

Urho, L., 1996. Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. Ann. Zool. Fennici 33, 659-667.

Van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13, 235-245.

Wandzel, T., 2000. The fecundity and reproduction of round goby *Neogobius melanostomus* (Pallas, 1811) in the Puck Bay (Baltic Sea). Bull. Sea Fish. Inst. 2, 43-51.

Woods, L. C. I., Sullivan, C. V., 1993. Reproduction of striped bass, *Morone saxatilis* (Walbaum), broodstock: monitoring maturation and hormonal induction of spawning. Aquac. Res. 24, 211-222.

Young, J. A. M., Marentette, J. R., Gross, C., McDonald, J. I., Verma, A., Marsh-Rollo, S. E., Macdonald, P. D. M., Earn, D. J. D., Balshine, S., 2010. Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. J. Great Lakes Res. 36, 115-122.

Zeug, S. C., Winemiller, K. O., 2007. Ecological correlates of fish reproductive activity in floodplain rivers: a life-history-based approach. Can. J. Fish. Aquat. Sci. 64, 1291-1301.

Appendix Chapter II

Table A1. Reproductive traits of Nf, Nm, and Pk in native and invaded areas (extended version of Tab. 1). SL: standard length; TL: total length; f: female; m: male; NS: not specified. Values in brackets are mean values ± SD. Table continues on next page.

Species	Region	Status	Methods used	Catching Time	Size at maturity [mm]	Age at maturity	Relative fecundity (eggs/g)	Absolute fecundity (eggs/female)	Maturity stages of eggs	Mean GSI	Max. GSI	Date of max GSI	Egg sizes [mm]	Clutch sizes	Spawning season length	Start hatching	Co-occurrence with other gobies	Batches per season	Spawning mode	Spawning trigger	Degree-days for incubation	Sneaker males	Sex ratio (f:m)	Sexual dimorphism	Reference
Nf	Ukraine	native				age 2																			Smirnov, 1986 (cf. Placha et al., 2010)
Nf	Anatolia, Turkey	native	age determination (scales)	Apr 2006-Mar 2007	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	1:1.4	NS	Sasi and Berber, 2010
Nf	Danube, Bulgaria	native	GSI + histological analyses of ovaries	Apr, Jun, Jul, Oct 2006	41.65SL (f)	age 1	NS	NS	1,2,3,4	NS	~4% (f, Jun),~0.21% (m, Apr)	Jun (f), Apr (m)	>1.2 (ripe oocytes)	NS	May-Aug	NS	NS	2-3	multiple	NS	NS	NS	~1:1	NS	Konecna and Jurajda, 2012
Nf	Lower Rhine, Germany	invasive	GSI + gonadal analyses	Sep 2012, Apr-Oct 2013	78TL(f)	age 1	0-18,755 (2,617±3,188)	0-10,600 (3,305±3,158) all stages	1,2,3,4	NS	17.39% (f),2.05 % (m)	18th Jun	0.03-1.5	433 - 2,419	Mid-Mar-mid-Sep	17th Apr-15th May	Nm, Pk	NS	multiple	NS	380 - 550	NS	NS	yes	this study + unpublished data
Nm	native range	native				age 2-3 (f), 3-4 (m)																			Bil´ko, 1971 (cf.MacInnis and Corkum, 2000)
Nm	native range	native						one batch:543										4	multiple						Kalinina, 1976 (cf. Wandzel, 2000,Simonovic et al., 2001)
Nm	Sea of Azov	native						328-5,221																	Kovtun, 1978 (cf.Kornis et al., 2012)
Nm	native range	native													Apr-Aug										Lindberg et al., 1980 (cf. Tomczak and Sapota, 2006)
Nm	native range	native				age 2-3 (f), 3-4 (m)									Apr-Sep (Bulgaria) + May-Aug (Romania)										Miller, 1986 (cf.Kornis et al., 2012, Wandzel, 2000)
Nm	Danube, Bulgaria	native	GSI (eviscerated body mass, only f)	Mar-Oct 2010	49SL (f)		101.5-3,158.5	419-7,865 (all stages)	2-3 oocyte size classes	5.34% (f)	22.7% (f)	NS	1.72-2.75 (ripe oocytes)	NS	Apr-Jun	NS	NS	2-3	multiple	NS	NS	NS	NS	NS	Horkova and Kovac, 2014
Nm	Literature summary	native/ invasive	Review	NS	NS	age 2 (f), age 3 (m)*	NS	200-9,771 (spawned per f)**	NS	NS	NS	NS	3.4-3.8 (laid eggs)	up to 10,000	Apr-Jun (Romania), Apr-Jul (Azov), Apr-Sep(Bulgaria)	NS	NS	5-6 (in captivity)**	multiple	NS	300-340 (~20°C); 420-476 (~15-17°C)***	NS	NS	yes	Charlebois et al., 1997 (*Nikols´kii1961,**Kovtun, 1978, ***Kulikova, 1985
Nm	Puck Bay, Gulf of Gdansk	invasive	GSI (gutted weight)	Mar-Sep 1999	74TL(f), 70TL(m)		17-109	89 - 3,841 (1,739)	I - V (Maier 1906)	NS	13.4% (f)	May	NS	NS	Apr-Aug/Sep	NS	NS	NS	multiple	NS	NS	NS	NS	NS	Wandzel, 2000
Nm	Upper Detroit River	invasive	GSI, age analyses otoliths, artificial nest experiments (only f)	spring-fall 1996	42.5SL(f)	age 1 (f)	NS	84-606	NS	NS	~9% (f)	29th May + 8th Jul	~3	644-9,462	May-Jul	23rd May-5th Aug	NS	at least 3	multiple	NS	NS	NS	NS	yes	MacInnis and Corkum, 2000
Nm	Danube River basin, Yugoslavia	invasive	maturity stages of eggs	Sep 1998	NS		NS	NS	4, in Sep only stage 2	NS	NS	NS	NS	NS	NS	NS	Nf,Pk,Ps,Bg	NS	NS	NS	NS	NS	NS	no	Simonovic et al., 2001
Nm	St.Clair River/Great Lakes	invasive	collection of larvae and eggs from the field	1994-2000	NS		NS	NS	NS	NS	NS	NS	3.1-3.5 x 1.8-2.0 (laid eggs)	200-300	Apr/May-late summer	NS	Ps	NS	multiple	NS	NS	NS	NS	NS	Leslie and Timmins, 2004
Nm	Gulf of Gdansk	invasive	GSI (per egg developmental stage)	Jul,Aug,Oct 1999, Mar-Aug 2000	NS	age 1 (f)	9-143 (34±24)	94-2,190 (645±433) stage 2,3,4	1,2,3,4	NS	32% (f), 11% (m)	NS	NS	NS	Mar-May, Jun-Aug/Sep	NS	NS	NS	multiple	NS	NS	NS	3:5	NS	Tomczak and Sapota, 2006
Nm	Danube, Cunovo + Bratislava, Slovakia	invasive	maturity stages of eggs	Apr-Nov 2004/2005	45.1SL (f)		25.7 - 96.3	103.5 - 1,938.2	2 size classes	NS	NS	NS	0.5-1.12 (group I), 0.78-2.35 (group II)	NS	NS	NS	NS	NS	multiple	NS	NS	NS	NS	NS	L'avrincikova and Kovac, 2007
Nm	Great Lakes	invasive	laboratory studies, video recording	Aug 2007 + 2008	NS	NS	NS	NS	NS	NS	NS	NS	NS	683 (by 3 f)	NS	NS	NS	NS	NS	artificial spring conditions water temp. 20°C, 16L:8D	NS	NS	NS	yes	Meunier et al., 2009

Species	Region	Status	Methods used	Catching Time	Size at maturity [mm]	Age at maturity	Relative fecundity (eggs/g)	Absolute fecundity (eggs/female)	Maturity stages of eggs	Mean GSI	Max. GSI	Date of max GSI	Egg sizes [mm]	Clutch sizes	Spawning season length	Start hatching	Co-occurrence with other gobies	Batches per season	Spawning mode	Spawning trigger	Degree-days for incubation	Sneaker males	Sex ratio (f:m)	Sexual dimorphism	Reference
Nm	Hamilton Harbour/ Great Lakes	invasive	GSI (reproductive condition assumed if GSI >8% (f), or >1% (m))	2002-2008	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	Jun-Aug (peak of reproduction)	NS	NS	NS	multiple	NS	NS	NS	~1:2	NS	Young et al., 2010
Nm	Trent River, Canada	invasive	GSI (only f)	Jun-Aug 2007+2008	62-83TL (f)	age 1.2-2.0 (f)	NS	NS	NS	1.99% - 6.33% depending on site (f)	14% (f)	8th Jun	NS	NS	Jun-Aug	NS	NS	NS	multiple	NS	NS	NS	NS	NS	Gutowsky and Fox, 2012
Nm	Danube, Slovakia	invasive	age determination (scales)	2004/2005+ 2008/2010	mean size 57.57SL (2004/2005); mean size 50.58SL	age 1.29 (04/05), 1.36 (08/10)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	multiple	NS	NS	NS	76:43; 447:93	NS	Grula et al., 2012
Nm	Lower Rhine, Germany	invasive	GSI, maturity stages of eggs	Sep 2012, Apr-Oct 2013	37TL (f), 45TL (m)	age 1	4.74 - 29,910.04	32 -14,300	1,2,3,4	NS	18.6% (f), 9.36% (m)	29th Apr (f), 22nd Apr (m)	0.02-2.88	NS	Mid-March-mid-Sep	17th Apr-5th May	Nf,Pk	NS	multiple	NS	NS	yes	NS	yes	this study + unpublished data
Nm	Puck Bay, Gulf of Gdansk	invasive	field observations	May-Sep 2006-2008	NS	NS	NS	NS	NS	NS	NS	NS	NS	2,000; max 16,000	NS	NS	NS	NS	multiple	NS	NS	NS	NS	NS	Sapota et al., 2014
Nm	Danube, Slovakia	invasive	GSI (eviscerated body mass, only f)	Mar-Oct2010	46SL (f)	NS	224.7-3,568.9	1,578-10,605 (all stages)	2-3 oocyte size classes	4.87% (f)	22.84% (f)	NS	1.5-2.73 (ripe oocytes)	NS	Mar-Jul	NS	NS	2-3	multiple	NS	NS	NS	NS	NS	Horkova and Kovac, 2014
Nm	Danube, Slovakia	invasive	GSI (eviscerated body mass, only f), data before and after environmental perturbation	2008(Oct)-2010(Jul)	NS	NS	NS	bef.: 928-3,245 (1,724), aft.: 548-10,605 (3,412)	2-3 size classes	NS	bef.: 17.33% (f) aft.: 21.51% (f)	NS	bef.: 1.37-2.56, aft.: 1.53-2.73 (last mat. stage)	NS	Apr-Jun (bef.) + Apr-mid-Jul (aft.)	NS	NS	2-3	multiple	increase in reproductive investment after envir. perturbation	NS	NS	NS	NS	Horkova and Kovac, 2015a
Pk	native region	native																	single						Kalinina, 1976 (cf.Kovac et al., 2009)
Pk	Danube, Bulgaria	native	GSI (eviscerated body weight)	Apr+Oct 2005+2006	NS	NS	NS	NS	NS	NS	~19% (f), ~2% (m)	Apr	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	Ondrackova et al., 2010
Pk	Danube, Slovakia	invasive	maturity stages of eggs	Apr-Nov 2004	42.8SL	NS	61.6-174.0 (119.6)	669-5,646 (2,109)	2 size classes	NS	NS	NS	0.06-0.85 (group I), 0.55-1.7 (group II)	NS	May-Aug	NS	Nm	at least 2	multiple	NS	NS	NS	NS	NS	Kovacet al., 2009
Pk	Danube, Slovakia	invasive	GSI (eviscerated body weight)	Apr+Oct 2005+2006	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	Ondrackova et al., 2010
Pk	Lower Rhine, Germany	invasive	GSI, maturity stages of eggs	Sep 2012, Apr-Oct 2013	67TL (f)	age 1	112-4,416	360 – 10,000	1,2,3,4	NS	15.27% (f), 5,02% (m)	2nd May (f), 9th Oct (m)	0.0298-2.18	NS	Mid-Mar-mid-Jul	15th Apr-5th May	Nf,Nm	1	single	NS	NS	NS	NS	NS	Kwabek 2014

Table A2. Number of performed beach seinings per year and month.

Stretches (N)	2011	2012	2013
April	7	9	18
May	7	26	40
June	27	27	27
July	27	40	38
August	9	36	27
September	28	27	27
October	4	9	27
Total	109	174	204

Table A3. Mean water temperature during spawning activity for the three species and years.

Species	Year	Mean Temperature [°C]	± SD [°C]
Nf	2011	20.4	1.5
	2012	17.8	4.0
	2013	19.2	3.9
Nm	2011	19.8	2.5
	2012	18.2	4.0
	2013	18.4	4.6
Pk	2011	17.8	2.2
	2012	16.6	3.7
	2013	14.6	3.0

Table A4. Number, size range [TL, mm] and mean total length [mm] of female gobies for GSI analyses.

	Nf	Nm	Pk
N	110	168	72
Size range [mm]	34-119	21-124	34-145
Mean TL ± SD [mm]	71.2 ± 20.2	71.2±18.2	65.1±18.4

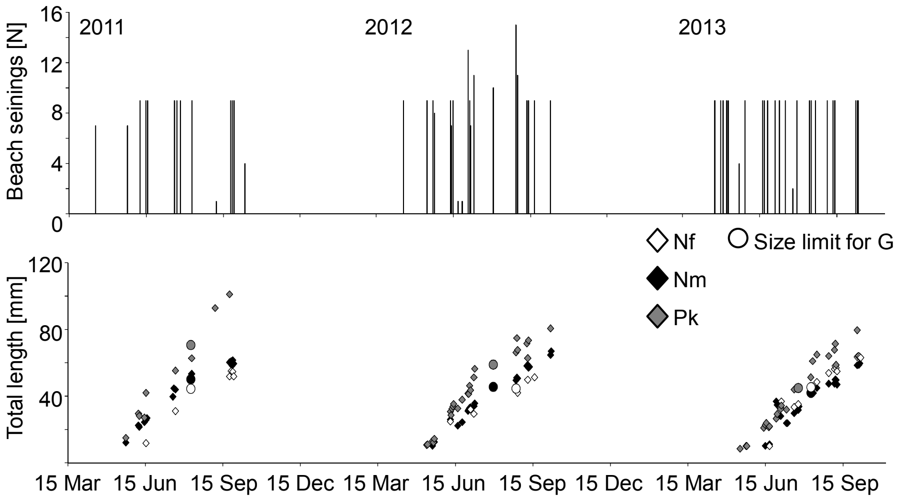

Figure A1. Number of beach seinings performed over the season in the three years 2011 – 2013 (chronological order, above) and the corresponding mean TL of the first cohorts at the different sampling dates for the three species (bottom; Nf white, Nm black, Pk grey). Circles show the date up to which growth rates G were calculated per species and year.

CHAPTER III

Drift of fish larvae and juveniles in the Rhine before and after the goby invasion

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Abstract

Drift is described as a dispersal mechanism immanent in many freshwater fish species. The main aim of this study was a comprehensive description of drift patterns of three invasive gobies living in sympatry, and to compare these results with similar sampling efforts before the occurrence of invasive gobies at the River Rhine. More than 26,500 larvae and juvenile fishes were caught with drift nets over four years within a period of 15 years. No differences were found in the drift of autochthones before and after the goby invasion, neither with respect to species numbers, abundances nor sizes. Roach and bighead goby increased in size over the season, indicating a somewhat different drift strategy than for barbel, monkey and round goby that drifted over several months, but remained at a similar size. The drift data give a first indication that the potential impact of gobies in the River Rhine should act on other stages than on the very first larvae within the life-cycle of important members of the local fish communities. However, the data also clearly reveal that bighead goby (*Ponticola kessleri*) is actually at the bust phase within typical boom-and-bust cycles of invasive species, while round (*Neogobius melanostomus*) and monkey goby (*N. fluviatilis*) have not yet left the boom phase so far at the Lower Rhine.

Keywords: Reproduction * invasive * spawning season * drift strategy * *Rutilus rutilus* * *Barbus barbus* * *Neogobius fluviatilis* * *Neogobius melanostomus* * *Ponticola kessleri*

Introduction

Drift is described as a dispersal mechanism immanent in many freshwater fish species (Lucas and Baras, 2002), which may (1) play an important role in the population and metapopulation dynamics of many species (Reichard and Jurajda, 2007), (2) enhance species diversity and gene flow (Lechner et al., 2014), (3) is assumed to reduce competition and predation (Humphries, 2005), and (4) is often described as an essential period within the ontogenetic lifecycle (Pavlov, 1994). Though drift is described mainly as a passive transport mechanism in rivers with buoyant eggs and small larvae being carried downstream, its initiation within the lifecycle can be either active or passive (Lucas and Baras, 2002). The latter is certainly true for those fishes which have (at times) pelagic eggs, such as many characins (e.g., Araujo-Lima and Oliveira, 1998) or some freshwater Clupeidae (e.g., Bilkovic et al., 2002). Passive drift initiation may further be affected by species-specific behavior with respect to hatching. For instance, migratory coregonid larvae begin to swim immediately after hatching. As they are positively phototactic, they move toward the surface (Fabricius and Lindroth, 1954; Lindroth, 1957), where they immediately start to drift in running waters (e.g., North Sea houting, *Coregonus oxyrinchus*, Borcherding *et al.*, 2014). However, there are also many species that exhibit behavioral patterns at certain life stages that are considered as “active elements” within the passive downstream migration (Pavlov, 1994).

Different drift strategies and their initiation have evolved as adaptations of the species-specific lifecycle within specific conditions of a particular environment (Pavlov, 1994), such as the European River Rhine that went through long lasting periods of river degradation and its secondary changes in biotic communities. Starting in the 19th century, engineering projects have been carried out in order to reduce bank erosion and the inundation of primary floodplains, to improve shipping traffic, and to allow the extension of cities and industries through wetland drainage (Neumann, 2002). Together with extreme water pollution after the Second World War and massive over-exploration by local fisheries, the result was a population decline of fishes from the late 19th century onwards, which ended in the extinction of several species (De Groot, 2002). The fish community of the Lower Rhine had recovered from its historically worst periods at the end of the 1960s, when water quality began to improve in the 1980s (Borcherding and Staas, 2008). Since then, most fishes from historical periods were found to be back in the Lower Rhine, though sometimes in low numbers (actual lists can be found here: http://www.rheinfischerei-nrw.de/fischerei-themen/fischfauna-des-rheins/). Even extinct migratory species like the North Sea houting were recently reintroduced and have established a self-reproducing population that has dispersed over the whole Rhine delta (Borcherding et al., 2010; Borcherding, 2011).

Morphological and hydrological alterations in the River Rhine were added by biotic changes of the ecosystem. After the opening of the Rhine–Main–Danube-Channel in 1992, the southern corridor served as an entrance door for the introduction of invasive species (Bij de Vaate et al., 2002). In 1986, 12 % of the benthic invertebrates of the 850 km of navigable Rhine were non-native (Kureck, 1992), while in 2000, 80 % of all species belonged to this group, and in terms of biomass the invasive species had even increased to more than 90 % (A. Kureck, personal communication). The first gobiid species detected in the Lower Rhine was the tubenose goby *Proterorhinus semilunaris* in 1999, followed by the bighead goby *Ponticola kessleri* in 2006 (Borcherding et al., 2011). Both, the round goby *Neogobius melanostomus* and the monkey goby *N. fluviatilis* were recorded first in the Lower Rhine in 2008 (Borcherding *et al.*, 2011), and even first hybrids of these species have already been discovered (Lindner et al., 2013). The introduction was potentially enabled through the transport on ship hulls and via ballast water (Ahnelt et al., 1998; Ricciardi and MacIsaac, 2000; Roche et al., 2013), and invasive gobiids now constitute the major part of local fish community (Borcherding et al., 2011; 2013; Gertzen et al., 2016).

As gobiids are well known to use drift as a dispersal mechanism (e.g., Hayden and Miner, 2009; Janac et al., 2013), the major aim of this study was the first comprehensive description of drift patterns of three invasive gobies living in sympatry at the Lower Rhine. As we were, however, interested to assess how far invasive gobies may affect local fish communities, recent sampling over three consecutive years was compared to a similar study conducted before the goby invasion. All results together should then give a first overview on drift patterns of the fish community under actual environmental conditions at the anthropogenically altered Lower Rhine. Finally, the results should allow a first survey on the ecological niche differentiation under constraints of the species-specific drift patterns (strategies), helping to reveal the status of the invasion process and to assess the future development of local fish communities.

Material and Methods

Sampling of fish

At the Ecological Rhine Station of the University of Cologne (Rhine km 684.5, Vohmann *et al.*, 2010) a drift net of 1 x 0.5 m net opening (500 µm mesh size) was used in the years 2000 and 2012-2014 to catch drifting fishes. The net was fixed on a steel frame and could be positioned in the current with the help of weights and a crane mounted on the ship. The net was exposed about 20 cm beneath the surface, to catch only drifting fishes, thus clearly distinguishing the catch from those fishes that are actively moving near the bottom. The distance from the sampling point to the riprap of the bank was approximately 8 m. Except for the year 2000, velocity was always measured at least three times in the beginning and at the end of the drift sampling using either flow meters of Schiltknecht (Schweiz, MiniAir2) or Höntzsch (Germany IP-ASDI). Abiotic parameters like temperature or water level (expressed as discharge) were either measured directly at the sampling station or obtained from internet sources (https://www.elwis.de/gewaesserkunde/Wasserstaende/).

Table 1. Summarized parameters of the drift catches for the years 2000, and 2012-2104, respectively. Sampling time, temperature and discharge are given as minimum and maximum values, as well as with its mean (± SD) for all days of drift fishing in the named fishing campaigns.

Year	Period	Time of Day	Samples	Sampling time Min/Max	Mean ± SD	Temperature [° C] Min / Max	Mean ± SD	Discharge [m³ sec^{-1}] Min/Max	Mean ± SD
2000	19 Apr - 23 Jul	mix of day, dusk & night	41 on 15 days	30 /30	30 ± 0	14.8 / 22.6	19.3 ± 2.1	1448 / 2566	2117 ± 266
2012	5 Apr - 20 Aug	dusk &night	48 on 29 days	15 / 60	39 ± 20	11.8 / 24.1	18.5 ± 3.5	1187 / 2823	1900 ± 415
2013	22 Apr - 14 Oct	dusk & night	84 on 44 days	15 / 30	20 ± 7	12.3 / 25.6	19.4 ± 3.8	1031 / 5940	2296 ± 1046
2014	23 Apr - 28 Aug	dusk to night	29 on 18 days	10 / 30	29 ± 5	15.5 / 23.1	19.7 ± 2.5	1037 / 2914	1854 ± 610

Except for the year 2000, when a few catches were also performed during daytime, the samples were taken regularly during dusk and/or early night (cf. Tab. 1). In addition, on five days evenly distributed over the season in 2013 (as well as in other years not reported here), eight samples were gathered in a sequence from dusk and early to late night and dawn (cf. Janac et al., 2013). The duration of net exposure lasted between 15 and 60 min (sampling duration was chosen according to the quantity of the latest catch, in order to catch at least 100 fish, if possible). Sampling dates were roughly evenly distributed over the seasonal sampling period, with somewhat higher numbers in the beginning of the season. The catch was removed immediately from the net after sampling and fixed in ethanol. All fish were measured to the nearest 0.5 mm total length (TL). Abundance of larvae and juveniles were calculated as follows:

1. Filtered water [m³ hour^{-1}] = (drift net influx surface [m²] * velocity [m s^{-1}] * sampling duration [s] * 3600
2. Abundance [Ind 1000 m^{-3}] = (number of fish / filtered water) * 1000

Using these data on the species level, the dominance (percentage of a species within the total catch per year) as well as the frequency of occurrence was calculated, which is an estimate of the percentage of how many sampling days of a year the species was caught.

All sampled larvae and juvenile fishes were identified up to the species level (whenever possible), according to keys for larval fish identification (Koblickaya, 1981; Spindler, 1988; Mooij, 1989; Urho, 1996; Staas, 1996; Pinder, 2001). Gobies have no real larval stage, the whole larval period is replaced by development in the egg (Urho, 2002), i.e. the embryo period is followed by the juvenile period directly. The newly hatched juveniles have an appearance similar to adult gobies, however, some of the characteristics to identify the different species are not developed at this stage. To find reliable characteristics to identify the species of 7-11 mm long gobies, additional characteristics were searched by individuals of size that makes the identification with actual keys like Brunken (2008) and Koblickaya (1981) possible (Urho, 2002).

Age determination of drifting gobies

In some fish species, age can be roughly estimated by the size and/or the developmental stage (e.g., Teletchea and Fontaine, 2010). However, as no comprehensive data for gobies were available, about 50 randomly selected goby juveniles of each species sampled at the station in Cologne in 2014 were used for an age-determination. First, the TL of each investigated fish was measured (± 0.05 mm). Afterwards the otoliths of each fish were removed and studied under a binocular microscope. If possible, daily increments were counted for both otoliths (counts by two persons, always left and right, means are presented) and the diameter at their widest part was measured (± 5 µm, cf. Jones, 1992). Finally, additional information about special features of each otolith was noted.

Statistical analysis

In order to analyze frequencies of fish occurring in diel drift samples in 2013, standardized samples were compared with a One-Way-ANOVA, in which the diel samples were factorized as follows: 1=sunset, 2=45' after sunset, 3=90' after sunset, 4=150' after sunset, 5=150' before sunrise, 6=90' before sunrise, 7=45' before sunrise, 8=sunrise (cf. Janac et al., 2013). Sizes of otoliths were compared between species using a Welch Two Sample t-test. For all statistics the free software R for statistical computing (R Development Core Team, 2009) was used.

Table 2. Species-specific data for all sampling campaigns on the frequency of occurrence (F, on how many sampling days of a year the species was caught) and the dominance (D, amount of a species within the total catch per year) of all drift catches. Dominance values above 10 % are printed in bold.

	2000		2012		2013		2014	
	F	D	F	D	F	D	F	D
Abramis brama	40	**41.8**	24	0.40	11	0.50	6	0.17
Alburnus alburnus	47	7.16	21	0.41	42	4.74	11	0.24
Aspius aspius	27	0.60	31	0.64	5	0.18	11	0.10
Barbus barbus	60	**32.6**	76	**31.4**	66	**41.3**	61	**27.5**
Blicca bjoerkna	20	0.13			13	0.22	6	0.04
Chondrostoma nasus	20	0.61	7	0.11			22	0.59
Cyprinus carpio	7	0.04			3	0.07		
Gobio gobio	33	2.25						
Leuciscus idus	13	0.10	17	0.16	8	0.10	33	2.00
Leuciscus leuciscus	13	0.12			8	0.16	17	0.43
Rutilus rutilus	60	4.30	62	9.00	66	7.67	44	3.99
Squalius cephalus	60	7.04			21	0.62		
Perca fluviatilis	7	0.03	31	2.46	26	2.29	28	2.00
Sander lucioperca	40	1.96	14	0.32	18	0.35	17	0.37
Coregonus sp.	40	0.12						
Cottus gobio	60	0.04						
Esox lucius	7	0.09						
Gasterosteus aculeatus	7	0.09			3	0.05		
Lampetra fluviatilis	33	0.86						
Neogobius fluviatilis			62	**18.7**	68	**18.4**	61	**15.4**
Neogobius melanostomus			62	**21.8**	89	**20.5**	72	**46.4**
Ponticola kessleri			31	**14.6**	24	2.82	11	0.79
Number of species	**19**		**12**		**16**		**14**	

Results

Larval fish community

Highest numbers of autochthonous fish species were found in 2000, when no invasive gobies occurred in the drift of the River Rhine (Tab. 2). However, five species were found with only one individual on one sampling day, of which e.g. bullhead (*Cottus gobio*) and pike (*Esox lucius*) were never caught again in the drift. After the invasion of the gobies into the Rhine, number of species was always lower, however, offering a high variability between the years (Tab. 2). What changed conspicuously was the dominance within the total catch of the year. While before the goby invasion bream (*Abramis brama*) and barbel (*Barbus barbus*) dominated the fish community with values above 30 %, this picture changed to a fish community clearly dominated in all sampling years by invasive gobies, mainly *N. fluviatilis* and *N. melanostomus*. The third goby species *P. kessleri* was also dominant in 2012, but then decreased in abundance and dominance in the following years (Tab. 2). Apart from invasive gobies, only barbel was found with high values of dominance in Cologne throughout the years. The frequency of occurrence in the catches per year revealed only barbel and roach (*Rutilus rutilus*) with values constantly over 50 %. *N. fluviatilis* and *N. melanostomus* reached similar frequencies after the goby invasion (Tab. 2). In contrast, the third species *P. kessleri* occurred in lower frequencies within the catches.

Temporal occurrence of fish larvae

The total amount of fishes varied significantly in the sequence of diel samples throughout extensive sampling in the season 2013 (ANOVA, $p<0.001$). The same tendencies were also visible on the species level of the most important fishes in Cologne 2013 (ANOVA: barbel: $p=0.0347$; roach: $p=0.0936$; monkey goby: $p=0.0434$; round goby: $p<0.0001$; bighead goby: $p<0.01$), with always highest numbers during the first part of the night, compared to periods before dusk and the second part of the night (before and while dawn and early morning, Fig. 1).

Despite some samples with unidentified cyprinids at the beginning of each sampling season (mostly in the beginning to the mid of April), drift started at the end of April up to the mid of May, predominately with either bream (3.5.2000), barbel (28.4.2012; 23.4.2014), or gobies (18.5.2013). A first peak of total abundance of drifting fishes was about 10 to 25 days later, formed by the dominating occurrence of barbel and roach (14.5.2000; 7.6.2013) or barbel and gobies (21.5.2012; 9.5.2014; Fig. 2). When comparing fish counts in the drift over the years, there was no evidence that either temperature or discharge alone was a major triggering factor initiating drift (cf. Fig. 2 and Fig. A1). Especially there was no consistent impact of discharge on the amount of drifting fishes (cf. 2012 and 2013, first major peak, Fig. A1), as would have been expected for instance due to increasing current with increasing discharges and a potential wash out of small larvae. Only low spring temperatures, like in the year 2013, seemed to hold back the onset of drifting to some extent (Fig. A1).

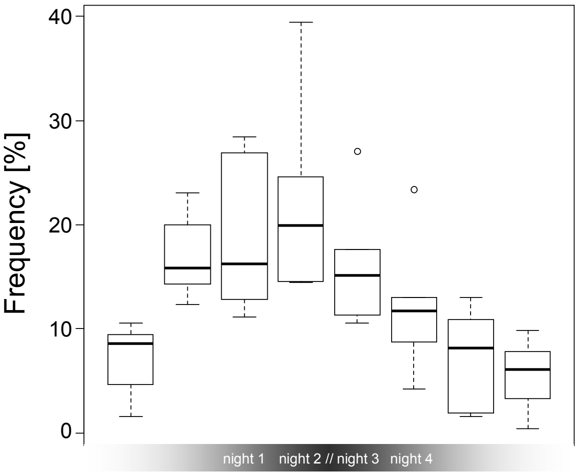

Figure 1. Frequency of drifting fish in relation to the time of day (estimates resulting from GLM) caught at 6 days between the end of May and the end of August 2013 at the Rhine station in Cologne (diel samples: sunset, 45' after sunset, 90' after sunset, 150' after sunset, 150' before sunrise, 90' before sunrise, 45' before sunrise, sunrise). Box whisker: median, box=25-75 % quartile, whisker min-max (if min or max are more than 1.5 fold larger or smaller than the inter-quartile range, these values were expected as outliers, given with circles).

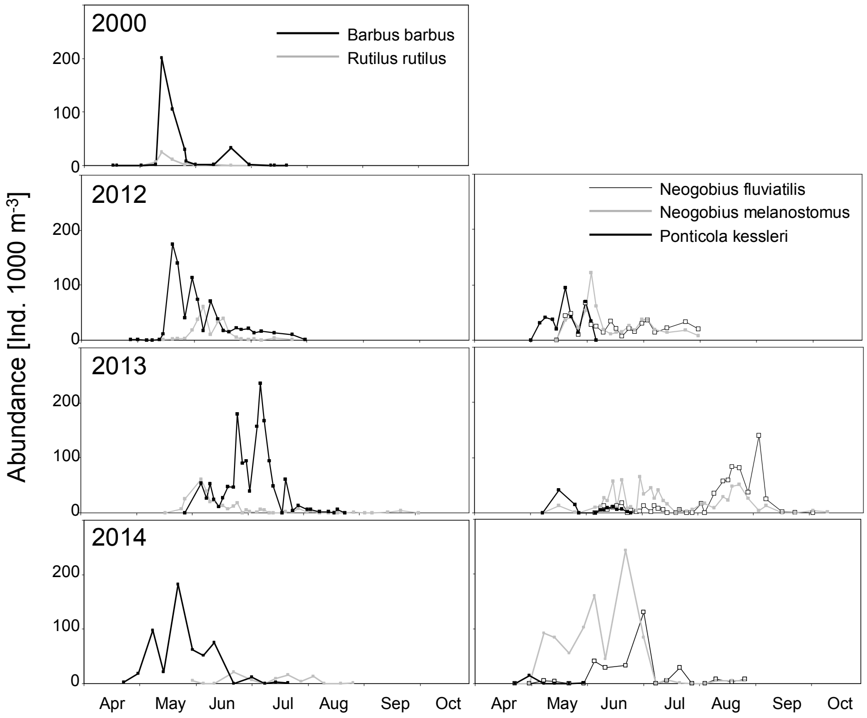

Figure 2. Seasonal patterns in drift abundance of *Barbus barbus*, *Rutilus rutilus* (left panels), *Neogobius fluviatilis*, *N. melanostomus* and *Ponticola kessleri* (right panels) over the sampling season for different years at the Rhine station in Cologne.

The more detailed analysis of the five most important species over the years (barbel, roach, gobies) revealed long drifting periods for all species except for bighead goby. For the latter, the drifting period was not longer than roughly one month, starting in the beginning (2012, 2014) or in the mid (2013) of May (Fig. 2). While round and monkey goby were found until the end of the sampling season (in 2013 even until the end of September/beginning of October), occurrence of barbel lasted until the beginning of July (2000), the end of July (2014) or to the mid of August (2012, 2013). For roach, these estimations are less descriptive because of overall lower number in the drift (Tab. 2, Fig. 2).

The cumulative numbers of larvae/juveniles per species were calculated for all years (Tab. 3), giving some evidence that total numbers did not change between the year 2000 and the sampling period 2012-2014. Though there was some variation between consecutive years, barbel and roach occurred in similar numbers before and after the goby invasion. The cumulative numbers for monkey and round goby also showed some variation, however, without any clear trend between the years. This is in contrast to bighead goby that clearly decreased to less than 10 % in cumulative abundance from 2012 to 2014 (Tab. 3).

Table 3. Mean of densities (Ind. 1000 m^{-3}) including Null-samples for days with no catches within the period of appearance, and duration of drift appearance (period of the first until the last appearance in drift samples) for selected fish species at the Lower Rhine in Cologne in 2000 and 2012-2014.

Year	*Barbus barbus*	*Rutilus rutilus*	*Neogobius fluviatilis*	*Neogobius melanostomus*	*Ponticola kessleri*	Total
2000	42.2	5.6				125.7
	52 days	52 days				97 days
2012	34.5	13.2	27.4	31.9	42.7	161.0
	96 days	71 days	73 days	73 days	28 days	96 days
2013	55.4	7.9	20.8	19.6	9.3	136.0
	76 days	122 days	108 days	149 days	38 days	175 days
2014	40.6	5.9	18.4	55.6	3.0	143.7
	91 days	89 days	111 days	111 days	30 days	127 days

Size of drifting larvae and juveniles

In all sampling years, barbel was found in the drift with a mean size of roughly 12-15 mm TL, independent of the sampling date within the year (Fig. 3). In contrast, roach size was positively correlated with time, regularly starting at around 10 mm TL in the beginning of roach drifting season and ending up in the range of 50-60 mm TL towards the end of the season (2013 and 2014, cf. Fig. 3). The same analysis for invasive gobies revealed more constant and small size patterns for round and monkey goby in the course of the season (large values of the regularly small standard deviation depended on some single larger individuals), while for bighead goby an increase was observed, starting at 8-9 mm TL and ending at sizes near 20 mm TL at the end of the drifting season (Fig. 4). Unfortunately, in 2012, species-specific length of gobies was not measured. Thus, a more stable size was documented over the season with somewhat higher variability at the mid of June, which is probably a result of the high number of larger bighead gobies within the goby samples during this time (cf. Fig. 2).

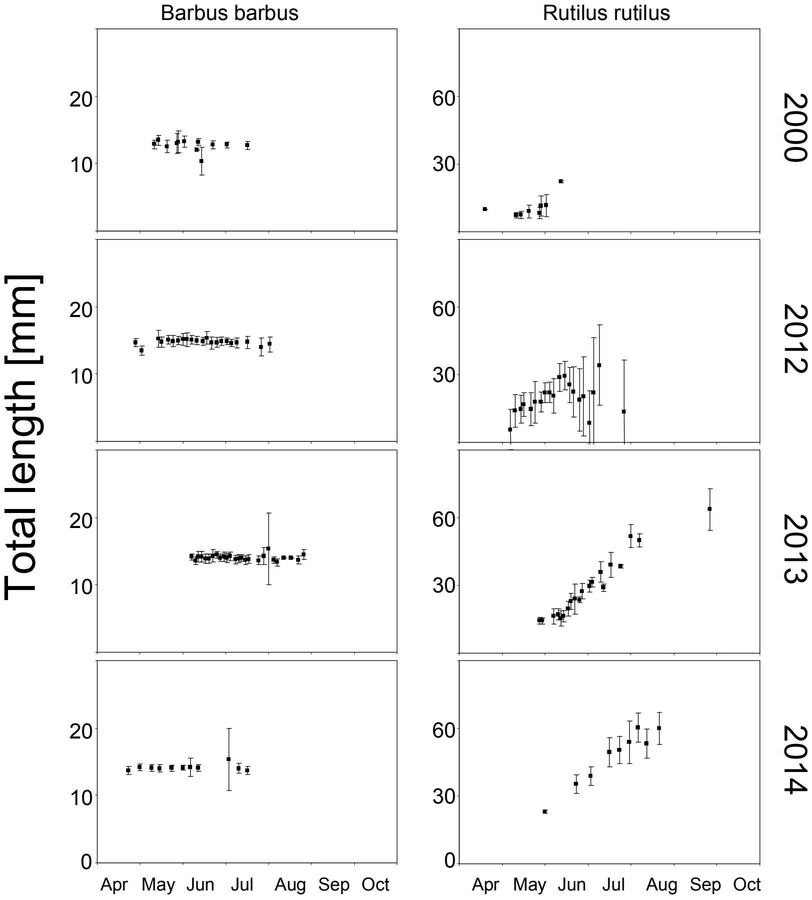

Figure 3. Size (± SD) of *Barbus barbus* (left panels) and *Rutilus rutilus* (right panels) caught in drift nets over four sampling years in relation to the sampling season at the Rhine station in Cologne.

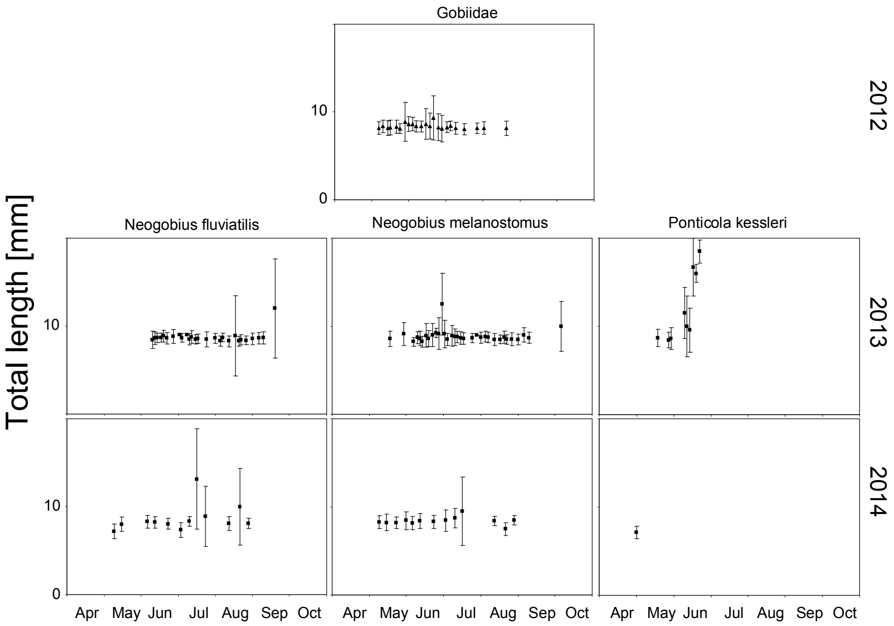

Figure 4. Size (± SD) of all gobiids in 2012, as well as *Neogobius fluviatilis* (left panels), *N. melanostomus* (mid panels) and *Ponticola kessleri* (right panels) caught in drift nets over the sampling season 2013 and 2014 at the Rhine station in Cologne.

Length-frequency distributions were drawn for 2013 data, when all five species occurred in reliable numbers (Fig. 5). While size distributions of bighead goby and roach were wider and showed higher percentages for the standard deviation in comparison to its mean (about 30 to 45 %), size distributions of barbel, round and monkey goby were extremely narrow. The standard deviation in comparison to its mean was lower than 17 % for the gobies and even less than 6 % for barbel. This gives evidence that these species drift only at a certain size, which is about 14 mm TL for barbel and 8-9 mm TL for round and monkey goby, respectively (Fig. 5).

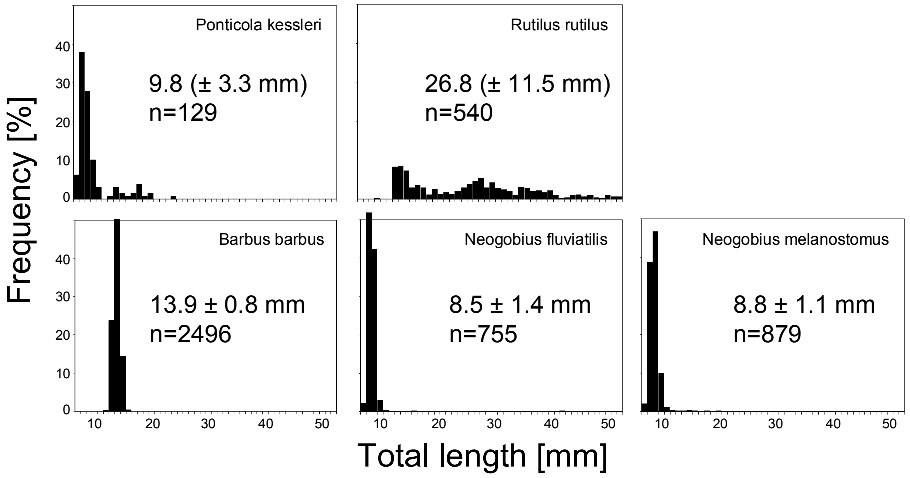

Figure 5. Length-frequency distributions of all *Rutilus rutilus*, *Ponticola kessleri* (upper panels), *Barbus barbus*, *Neogobius fluviatilis* and *N. melanostomus* (lower panels) caught in drift nets over the sampling season 2013 at the Rhine station in Cologne. Indicated at each panel are the overall mean (mm TL ± SD) and the number of individuals, respectively.

Age of drifting gobies

As no data on the age of drifting gobies were available, otoliths of randomly selected gobies of the 2014 samples were used in a comprehensive analysis to establish species-specific relationships between age and size. The otolith studies revealed a great variety in the structure of the otoliths, with large differences, not just between species, but also between individuals of the same species or even between the left and right otolith of one individual. Despite this high variability, the diameter of the otolith at its widest part was always nearly the same for the left and right otolith of one individual. The average otolith diameter was significantly lower for bighead goby compared to round and monkey goby (Welch Two Sample t-test; $p < 0.001$), while no significant differences could be found between round and monkey goby (Welch Two Sample t-test; $p > 0.05$; Tab. 4). In addition to these size differences, more than 80 % of the otoliths of *P. kessleri* showed a “tree-ring” like structures near the centre of the otolith (cf. Fig. 6, nothing like that in the *Neogobius* species), and their otoliths seemed to be a bit more roundish but had a less smooth surface.

In 2014, the size of the majority of the gobies caught in the drift varied between 6 and 10 mm TL. Mean size of bighead goby was about 7 mm TL, whereas most round and monkey goby were about 8 mm TL (Tab. 4). The youngest round gobies found in the drift were assumed to be one day old, the youngest monkey and bighead goby were found to have two day rings. For all species age-size relationships could be established (Fig. 7), revealing that gobies of about 8 mm TL were on average around four days of age, assuming one day ring per day after hatching (Tab. 4).

Table 4. Number of analyzed individuals and mean values (± SD) of the size of the three gobiid species and the count of rings and the largest diameter of their otoliths, calculated for all fishes smaller than 10 mm in total length. Analyzed fishes were randomly selected from the catch in drift nets over the sampling season 2014 at the Rhine station in Cologne.

	N	Total length [mm]	Number of rings	Otolith diameter [µm]
Neogobius fluviatilis	49	7.88 ± 0.73	4.1 ± 1.2	320 ± 32
Neogobius melanostomus	48	8.12 ± 0.84	4.3 ± 1.5	323 ± 25
Ponticola kessleri	41	7.06 ± 0.59	3.9 ± 1.3	256 ± 27

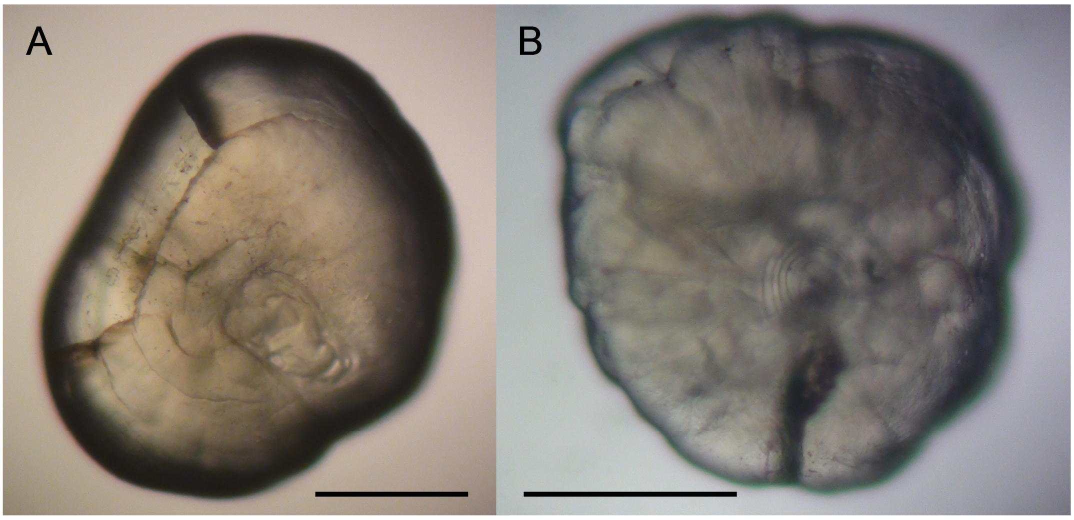

Figure 6. Otoliths of (A) *Neogobius melanostomus* (8.9 mm TL) and (B) *Ponticola kessleri* (8.6 mm TL). The bars indicate a length of 100 µm. Note, the otolith of *P. kessleri* shows the characteristic “tree-ring” like structures near the centre.

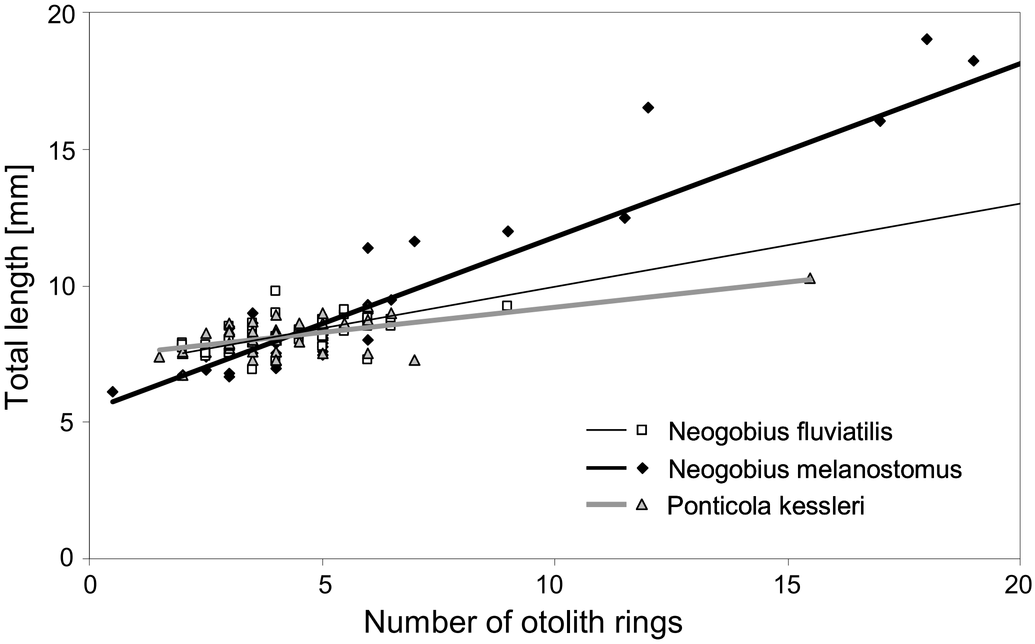

Figure 7. Total length of *Neogobius fluviatilis*, *N. melanostomus* and *Ponticola kessleri* in relation to the number of otolith rings (NOR, assumed as day rings) for randomly selected individuals that were caught in drift nets over the sampling season 2014 at the Rhine station in Cologne. Regression lines:

N. fluviatilis, TL=6.92 + 0.305*NOR; R^2=0.79
N. melanostomus TL=5.45 + 0.634*NOR; R^2=0.86
P. kessleri, TL=7.34 + 0.185*NOR; R^2=0.38

Discussion

In this study, we sampled the drift of larvae and juvenile fishes over four years within a period of 15 years, in total catching more than 26,500 individuals, of which roughly ¾ could be analyzed on the species level. To the best of our knowledge, this is not only the first comprehensive study on the drift of larvae and juvenile fishes in the Lower Rhine so far, it is also the very first study that analyses the drift of three gobiid species living in sympatry outside their native range. First of all, we could not find any major differences concerning the drift of autochthonous fishes before and after the goby invasion, neither with respect to species numbers, abundances nor sizes. For roach and bighead goby we observed an increase of size in drifting fish over the season, indicating a somewhat different drift strategy than for barbel as well as for monkey and round goby that drifted over several months always at a similar size.

Our results clearly outline that all goby species appeared in the drift at the Lower Rhine with a size of roughly 8 mm TL, while barbel were found in all years with roughly 14 mm TL. Previous studies revealed similar values of drifting barbel size (e.g., Copp *et al.*, 2002; Zitek *et al.*, 2004b), which represents a developmental stage that is assigned to be about 12 days of age after hatching (Penaz, 1973; Vilizzi and Copp, 2013). This stage is morphologically quite similar to that of gobies at their first appearance in the drift (cf. Plate IIIVb in Penaz, 1973), keeping in mind that newly hatched gobies are characterized by direct development, i.e. their embryos develop directly into juveniles in possession of most of the definitive adult structures (Urho, 2002).

Hensler and Jude (2007) reported that round goby 6.5–8.9 mm in length disperse from the nest and were caught in the pelagic area of Lake Michigan. Similar in the pelagic area of Lake Erie, sizes of round goby ranged from 5.6 mm to 23 mm TL with a median length of 8.0 mm TL (Hayden and Miner, 2009). Round gobies drifted in the River Dyje in 2011 almost exclusively at sizes ranging from 6 to 8 mm SL (standard length, which is roughly 1 mm less than TL) (Janac et al., 2013), which was described as similar to that in its native range (Vassilev, 1994). All these results suggest that drift (or the occurrence in the pelagic area of lakes) of round goby is restricted to a specific ontogenetic stage defined by an interval of a few days (Janac et al., 2013). This is clearly underpinned by our results here for the Lower Rhine. In addition, the results of our otolith analyses now give conclusive evidence that round goby of this size are on average about 4 days of age (± 1.5 days, Tab. 4, Fig. 7), which is, thus, only slightly above the size (6.0–6.2 mm TL) and age (3 days after hatching) when round goby increase their levels of activity after hatching substantially (Logachev and Mordvinov, 1979).

In addition to this analysis for round goby, we are now able to present similar data also for monkey and bighead goby. Monkey goby was found in the drift for several months with a mean size of roughly 8 mm TL that equals an age of about four days (Tab. 4, Fig. 7). To the best of our knowledge these are the first detailed results on the drift of monkey goby so far (besides a rough description by Vassilev, 1994), which also holds true for bighead goby. Although the latter species also started drifting in the Lower Rhine at an age of roughly four days and at sizes around 8 mm TL (Tab. 4, Fig. 7), sizes clearly increased in subsequent samples, as shown for the year 2013, when numbers of sampled individuals were sufficient for this species and when the size of all gobies were evaluated species specifically (Fig. 4). This different appearance of seasonal sizes compared to monkey and round goby in the group of invasive species somewhat resembles the picture of autochthon fishes like barbel in comparison to roach, in which the sizes of the latter species also increased over the season. While bighead gobies were only caught for a short time period in April/May, roach were regularly sampled over several months (cf. Zitek et al., 2004a). Slight increases in size of drifting roach over the season were also found in other rivers (e.g., Pavlov, 1994; Jurajda, 1998; Zitek *et al.*, 2004a; Speierl, 2007), however, sizes of more than 60 mm TL (and that not only single individuals but more than 100 e.g., in 2013), as found in the present study at the Lower Rhine in 2013 and 2014 (Fig. 3), have usually not been observed (cf. Reichard and Jurajda, 2007 and discussion therein).

Reichard and Jurajda (2007) summarized the stage-dependence of drift in fishes and outlined that several strategies for using river current for a downstream transport have been proposed. For riverine fishes, drift strategies regularly observed during distinct developmental intervals within the larval period, are assumed as an adaptation to riverine conditions, rather than a passive dislodgement by river currents (Pavlov, 1994; Reichard and Jurajda, 2007; Pavlov et al., 2008; cf. also Fig. A1 of the present study). In addition, swimming ability at a certain developmental stage (Copp and Kovac, 1996) has to be taken into account to explain appearance in the drift (Pavlov, 1994; Reichard and Jurajda, 2007). The favored explanation for the majority of riverine (potamodromous) fishes so far is that fish enter the current actively as a result of stage- and species-specific adaptations and behavioral responses to the light levels as ultimate factor (Reichard and Jurajda, 2007). The latter is based on numerous studies in which a clear dependency of drift activity in relation to diel light conditions is described, with higher abundances of drifting fishes around dusk, dawn and during the night (Pavlov, 1994; Johnston et al., 1995; Jurajda, 1998; Gadomski and Barfoot, 1998; Copp et al., 2002; Oesmann, 2003; White and Harvey, 2003; Zitek et al., 2004a; Reichard and Jurajda, 2007; Schludermann et al., 2012; Janac et al., 2013). This also holds true for the present study (Fig. 1). Of course, there are also studies that did not find such diel drift patterns, however, these are regularly limited to species for which developmental constraints are not found to depend on diel light levels (e.g., hatching in large rivers and subsequent drifting of coregonid larvae, like North Sea houting, Borcherding *et al.*, 2014).

Once the fish had entered the current they are then transported passively downstream, and size- as well as species-specific characteristics may be important how far active behavior and/or swimming ability can affect the length of the drifting period or if small scale adjustments of direction (e.g., movement to nearshore areas) is possible (Pavlov, 1994; Schludermann *et al.*, 2012). For fishes in which drifting is clearly limited to a certain developmental stage and which is well defined over the whole season like in barbel (Copp *et al.*, 2002; Zitek *et al.*, 2004b) or round (Janac et al., 2013) and monkey goby (all species also in the present study, Fig. 3 & 4), the initiation is probably merely related to ontogenetic constraints only (Pavlov, 1994; Reichard and Jurajda, 2007). In contrast, further adjustments of drift may be postulated for species like roach or bighead goby. This could be, as an easy explanation, just the extension of an extended drifting window within the ontogenetic life cycle. Plasticity for drifting behavior of a species at different locations or at different years within one sampling area may, however, give some first clues that further factors are potentially playing important roles in the initiation of fish to enter the drift.

Reichard and Jurajda (2007) hypothesized some density dependent responses to levels of competition and outlined that such a drift pattern “is related to habitat shift from spawning to feeding areas (i.e., obligatory, performed by all fish) or is a density dependent response to high competitor density or low food abundance (i.e., optional, only some fish drift)”. The authors not only recommended some experimental studies to prove this hypothesis, but also presented some first data with differential length-frequency distributions of species-specific fish that resided in nurseries compared to those that appeared in the drift (Reichard and Jurajda, 2007). Clear differences were found for some cyprinid species (e.g., bleak, *Alburnus alburnus*) while not for others (e.g., bream, Reichard and Jurajda, 2007), which may be attributed to above named mechanism of the triggering effect of competition or low food abundance. If these hypotheses hold true, a potential way for future studies could be to measure condition of residents and drifting individuals of the same subpopulation and to search for potential differences. We will likely address this question in future in species like barbel, monkey and round goby on the one side (potential examples for obligatory *drifters* at certain developmental stage), and on the other side roach and bighead goby as potential examples for optional *drifters*, in which competitive interactions (that are assumed as triggering factor for drift) may be exhibited through condition as a first proxy (cf. Pepin et al., 1999; Voss et al., 2006; Chicharo et al., 2012).

To the best of our knowledge, sizes of more than 60 mm TL for drifting roach, as found in the present study have not been described so far. Though the comparison of drift catches of roach between the year 2000 (before the goby invasion) and those of 2012-2014 after the goby invasion displayed some differences in maximum sizes (largest roach in 2000: 28 mm TL, 2012: 56 mm TL, 2013: 74 mm TL, 2014: 70 mm TL, Fig. 3), we do not attribute these size differences to the goby invasion (although increased competition for food, as described above, could offer a potential mechanism). On the other hand, clear differences in the drifting fish community before and after the goby invasion are of course documented in the dominance structure of the total catches per year (Tab. 2). However, as (1) the most important fishes in the drift like barbel and roach were as abundant before and after the goby invasion in terms of absolute values (Tab. 3), and (2) because nearly all species were found also in the drift after the goby invasion, especially if single individuals within one year are not considered, we assume that the larval and juvenile fish community that regularly appears in the drift was apparently not affected by the goby invasion. This can be assumed as a first indication that the potential impact of gobies should act on other stages than on the very first larvae/juveniles within the life-cycle of important members of local fish communities.

Thus, are we now able to conclude that the invasion of gobies had no effect on the fish communities so far? Of course not, as the overall abundance of e.g., juvenile fish in many habitats has dropped conspicuously (Borcherding *et al.*, 2011; Borcherding *et al.*, 2013) probably because of the highly competitive gobies (Gertzen & Borcherding, unpublished data). However, studies on the drift within a system like the Lower Rhine can only give a reliable picture of one (very small) part of the life-cycle of the majority of perdurable fishes within such a system. In addition, drift may give some clues on hydraulic impact e.g., in response to anthropogenic alterations of the river system (Lechner et al., 2013; Lechner et al., 2014). It may also serve to describe fish communities between watersheds or different stretches within a river. However, long lasting alterations of communities, e.g., the decrease of bream in the Cologne area (Table 2), should depend on long lasting changes within the spawner populations, which are probably more dependent on environmental factors (Kornis et al., 2013) and then later on reflected in changing drift abundances. This is exemplified by e.g., the dramatically reduced abundance of bream, which is probably a reflection of the loss of spawning grounds for this potamodromous species (lateral migrations) in the floodplain area of the Lower Rhine (Molls, 1999; Grift et al., 2003; Borcherding and Staas, 2008; Scharbert and Borcherding, 2013).

For species with shorter lifespan, changes in their appearance in the fish community may become more obvious in shorter time intervals. This is what we assume for bullhead in the Lower Rhine, as no individuals have been recorded for more than 5 years despite intensive fishing of all habitats and with different methods (Gertzen & Borcherding, unpublished data, cf. also Dubs and Corkum, 1996; Janssen and Jude, 2001; Kakareko et al., 2013). Similar, bighead goby densities decreased obviously compared to the highest abundances around 2010/2011, reflected by electro-fishing in regular intervals at the Lower Rhine (Gertzen, Borcherding, Jurajda, Janac, unpublished data) as well as beach seining data (Gertzen et al., 2016). The same trend can also be seen in the present data on drift net fishing (Table 2), giving some evidence that bighead goby is actually at the bust phase within typical boom-and-bust cycles of invasive species (Williamson, 1997; Simberloff and Gibbons, 2004). On the other hand, there are no signs that monkey as well as round goby may leave the boom phase, giving strong evidence that these invasive species will remain important members of the fish communities at the Lower Rhine in near future.

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References

Ahnelt, H., Banarescu, P., Spolwind, R., Harka, A., Waidbacher, H., 1998. Occurrence and distribution of three gobiid species (Pisces, Gobiidae) in the middle and upper Danube region - examples of different dispersal pattern? Biologia (Bratislava) 53, 665-678.

Araujo-Lima, C. A. R. M., Oliveira, E. C., 1998. Transport of larval fish in the Amazon. J. Fish Biol. 53, 297-306.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Can. J. Fish. Aquat. Sci. 59, 1159-1174.

Bilkovic, D. M., Olney, J. E., Hershner, C. H., 2002. Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey Rivers, Virginia. Fish Bull 100, 632-640.

Borcherding, J., 2011. The successful re-introduction of North Sea houting to the River Rhine System in Europe. In: Ed: P. S. Soorae, Global Re-introduction Perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-introduction Specialist Group and Abu Dhabi, Gland, Switzerland, pp. 20-23.

Borcherding, J., Breukelaar, A., Winter, H. V., König, U., 2014. Spawning migration and larval drift of anadromous North Sea houting (*Coregonus oxyrinchus*) in the River IJssel, the Netherlands. Ecol. Freshwat. Fish 23, 161-170.

Borcherding, J., Dolina, M., Heermann, L., Knutzen, P., Krüger, S., Matern, S., van Treeck, R., Gertzen, S., 2013. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. Limnologica 43, 49-58.

Borcherding, J., Heynen, M., Jäger-Kleinicke, T., Winter, H. V., Eckmann, R., 2010. Re-establishment of the North Sea houting in the River Rhine. Fisheries Manag. Ecol. 17, 293.

Borcherding, J., Staas, S., 2008. Local riverine fish communities as promoters for habitat restoration in the floodplain area of the lower Rhine. Am. Fish. Soc. Symp. 49, 835-843.

Borcherding, J., Staas, S., Krüger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Brunken, H., 2008. Bestimmungsschlüssel deutsche Süßwasserfische, Gobiidae, Grundeln. Bearbeitungsstand: 30. November 2008.

Chicharo, M., Amaral, A., Faria, A., Morais, R., Mendes, C., Pilo, D., Ben-Hamadou, R., Chicharo, L., 2012. Are tidal lagoons ecologically relevant to larval recruitment of small pelagic fish? An approach using nutritional condition and growth rate. Estuarine Coastal and Shelf Science 112, 265-279.

Copp, G. H., Faulkner, H., Doherty, S., Watkins, M. S., Majecki, J., 2002. Diel drift behaviour of fish eggs and larvae, in particular barbel, *Barbus barbus* (L.), in an English chalk stream. Fisheries Manag. Ecol. 9, 95-103.

Copp, G. H., Kovac, V., 1996. When do fish with indirect development become juveniles. Can. J. Fish. Aquat. Sci. 53, 746-752.

De Groot, S. J., 2002. A review of the past and present status of anadromous fish species in the Netherlands: is restocking the Rhine feasible? Hydrobiologia 478, 205-218.

Dubs, D. O. L., Corkum, L. D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. 22, 838-844.

Fabricius, E., Lindroth, A., 1954. Experimental observations on the spawning of whitefish, *Coregonus lavaretus* L., in the stream aquarium of the Hölle laboratory at River Indalsälven. Rep. Inst. Freshwat. Res. Drottningholm 35, 105-112.

Gadomski, D. M., Barfoot, C. A., 1998. Diel and distributional abundance patterns of fish embryos and larvae in the lower Columbia and Deschutes rivers. Env. Biol. Fish. 51, 353-368.

Gertzen, S., Fidler, A., Kreische, F., Kwabek, L., Schwamborn, V., Borcherding, J., 2016. Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany). Limnologica - Ecology and Management of Inland Waters 56, 39-48.

Grift, R. E., Buijse, A. D., Van Densen, W. L. T., Machiels, M. A. M., Kranenbarg, J., Breteler, J. P. K., Backx, J. J. G. M., 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Res. Applic. 19, 353-374.

Hayden, T. A., Miner, J. G., 2009. Rapid dispersal and establishment of a benthic Ponto-Caspian goby in Lake Erie: diel vertical migration of early juvenile round goby. Biol. Invasions 11, 1767-1776.

Hensler, S. R., Jude, D. J., 2007. Diel vertical migration of round goby larvae in the Great Lakes. J. Great Lakes Res. 33, 295-302.

Humphries, P., 2005. Spawning time and early life history of Murray cod, *Maccullochella peelii* (Mitchell) in an Australian river. Environ. Biol. Fish. 72, 393-407.

Janac, M., Slapansky, L., Valova, Z., Jurajda, P., 2013. Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non–native area. Ecol. Fresh. Fish 22, 430-438.

Janssen, J., Jude, D. J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27, 319-328.

Johnston, T. A., Gaboury, M. N., Janusz, R. A., Janusz, L. R., 1995. Larval fish drift in the Valley River, Manitoba - influence of abiotic and biotic factors, and relationships with future year class strengths. Can. J. Fish. Aquat. Sci. 52, 2423-2431.

Jones, C. M., 1992. Development and application of the otolith increment technique. In: Eds: D. K. Stevenson, S. E. Campana, Otolith microstructures examination and analysis. pp. 1-11.

Jurajda, P., 1998. Drift of larval and juvenile fishes, especially *Rhodeus sericeus* and *Rutilus rutilus*, in the River Morava (Danube basin). Arch. Hydrobiol. 141, 231-241.

Kakareko, T., Kobak, J., Grabowska, J., Jermacz, L., Przybylski, M., Poznanska, M., Pietraszewski, D., Copp, G. H., 2013. Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*. Biol. Invasions 15, 2519-2530.

Koblickaya, A. P., 1981. Key for identifying young freshwater fishes (in Russian). Light and Food Industrial House, Moskau.

Kornis, M. S., Sharma, S., Vander Zanden, M. J., 2013. Invasion success and impact of an invasive fish, round goby, in Great Lakes tributaries. Diversity and Distributions 19, 184-198.

Kureck, A., 1992. Neue Tiere im Rhein - Die Wiederbesiedlung des Stroms und die Ausbreitung der Neozoen. Naturwiss. 79, 533-540.

Lechner, A., Keckeis, H., Schludermann, E., Humphries, P., McCasker, N., Tritthart, M., 2014. Hydraulic forces impact larval fish drift in the free flowing section of a large European river. Ecohydrology 7, 648-658.

Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M., Habersack, H., 2013. Shoreline configurations affect dispersal patterns of fish larvae in a large river. ICES J. Mar. Sci., 930-942.

Lindner, K., Cerwenka, A. F., Brandner, J., Gertzen, S., Borcherding, J., Geist, J., Schliewen, U. K., 2013. First evidence for interspecific hybridisation between invasive goby species *Neogobius fluviatilis* and *N. melanostomus* (Teleostei: Gobiidae: Benthophilinae). J. Fish Biol. 82, 2128-2134.

Lindroth, A., 1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay District. Rep. Inst. Freshwat. Res. Drottningholm 38, 70-108.

Logachev, V. S., Mordvinov, Y. E., 1979. Speed of swimming and activity of larvae of the round goby, *Neogobius melanostomus* Pall, and some predatory crustaceans of the Black Sea. Sov. J. mar. Biol. 3, 77-80.

Lucas, M. C., Baras, E., 2002. Migration of Freshwater Fishes. Blackwell Science, Oxford.

Molls, F., 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. J. Fish Biol. 55, 1187-1200.

Mooij, W. M., 1989. A key to the identification of larval bream, *Abramis brama*, white bream, *Blicca bjoerkna*, and roach, *Rutilus rutilus*. J. Fish Biol. 34, 111-118.

Neumann, D., 2002. Ecological rehabilitation of a degraded large river system - Considerations based on case studies of macrozoobenthos and fish in the Lower Rhine and its catchment area. Internat. Rev. Hydrobiol. 87, 139-150.

Oesmann, S., 2003. Vertical, lateral and diurnal drift patterns of fish larvae in a large lowland river, the Elbe. J. Appl. Ichthyol. 19, 284-293.

Pavlov, D. S., 1994. The downstream migration of young fishes in rivers - mechanisms and distribution. Folia Zool. 43, 193-208.

Pavlov, D. S., Mikheev, V. N., Lupandin, A. I., Skorobogatov, M. A., 2008. Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. Hydrobiologia 609, 125-138.

Penaz, M., 1973. Embryonic development of barbel, *Barbus barbus* (Linnaeus, 1758). Zoologicke Listy 22, 363-374.

Pepin, P., Evans, G. T., Shears, T. H., 1999. Patterns of RNA/DNA ratios in larval fish and their relationship to survival in the field. ICES Journal of Marine Science 56, 697-706.

Pinder, A. C., 2001. Keys to larval and juvenile stages of coarse fishes from freshwaters in the British Isles. Freshwater Biological Association, Ambleside.

R Development Core Team, 2009. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. (ISBN 3-900051-07-0).

Reichard, M., Jurajda, P., 2007. Seasonal dynamics and age structure of drifting cyprinid fishes: an interspecific comparison. Ecol. Freshwat. Fish 16, 482-492.

Ricciardi, A., MacIsaac, H. J., 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. 15, 62-65.

Roche, K., Janac, M., Jurajda, P., 2013. A review of Gobiid expansion along the Danube-Rhine corridor - geopolitical change as a driver for invasion. Knowledge and Management of Aquatic Ecosystems.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348-360.

Schludermann, E., Tritthart, M., Humphries, P., Keckeis, H., 2012. Dispersal and retention of larval fish in a potential nursery habitat of a large temperate river: an experimental study. Can. J. Fish. Aquat. Sci. 69, 1302-1315.

Simberloff, D., Gibbons, L., 2004. Now you see them, now you don't - population crashes of established introduced species. Biol. Invasions 6, 161-172.

Speierl, T., 2007. Fischökologische Funktionalität von Fließgewässerrenaturierungen im oberfränkischen Mainsystem. PhD Thesis, University Bayreuth, 324 pp.

Spindler, T., 1988. Determination of middle european cyprinid larvae. Österr. Fisch. 41, 75-79.

Staas, S., 1996. Anleitung zur Bestimmung von 0+ - Jungfischen aus dem Rhein.Report Ecological Field Station Rees-Grietherbusch. University of Cologne, 14 pp.

Teletchea, F., Fontaine, P., 2010. Comparison of early life-stage strategies in temperate freshwater fish species: trade-offs are directed towards first feeding of larvae in spring and early summer. J. Fish Biol. 77, 257-278.

Urho, L., 1996. Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. Ann. Zool. Fennici 33, 659-667.

Urho, L., 2002. Characters of larvae - what are they? Folia Zool. 51, 161-186.

Vassilev, M., 1994. On the downstream migration of ichthyoplankton along the Bulgarian shore oft he Danube River. Vie Milieu 44, 273-280.

Vilizzi, L., Copp, G. H., 2013. Interstitial movement and emergence of barbel *Barbus barbus* free embryos and larvae. J. Fish Biol. 82, 1057-1063.

Vohmann, A., Borcherding, J., Kureck, A., Bij de Vaate, A., Arndt, H., Weitere, M., 2010. Strong body mass decrease of the invasive clam *Corbicula fluminea* during summer. Biol. Invasions 12, 53-65.

Voss, R., Clemmesen, C., Baumann, H., Hinrichsen, H. H., 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. Mar. Ecol. Prog. Ser. 308, 243-254.

White, J. L., Harvey, B. C., 2003. Basin-scale patterns in the drift of embryonic and larval fishes and lamprey ammocoetes in two coastal rivers. Env. Biol. Fish. 67, 369-378.

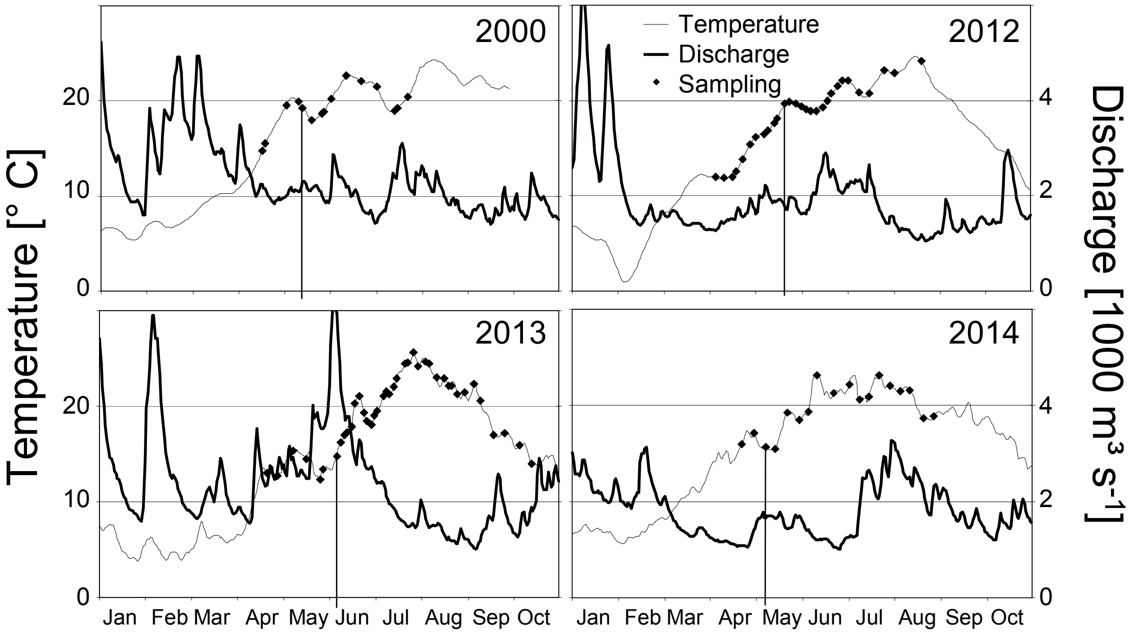
Williamson, M., 1997. Biological invasions, First edition ed. Chapman & Hall, London.

Zitek, A., Schmutz, S., Ploner, A., 2004a. Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. J. Fish Biol. 65, 1339-1357.

Zitek, A., Schmutz, S., Unfer, G., Ploner, A., 2004b. Fish drift in a Danube sidearm-system: I. Site-, inter- and intraspecific patterns. J. Fish Biol. 65, 1319-1338.

Appendix Chapter III

Figure A1: Mean daily temperature and discharge (January until October) for all sampling years at the Rhine station in Cologne. Black diamonds drawn on temperature data indicate individual sampling dates, vertical lines marked the sampling date with the first peak of fish abundance after the start of the sampling season.



CHAPTER IV

Measuring competition from field data – Dietary competition between native and invasive juvenile fish species at the Lower Rhine (Germany)

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Summary

1) In the past decades, the River Rhine has become a food limited system, which additionally has been invaded by Ponto-Caspian fishes from the family Gobiidae. This suggests dietary competition between native and invasive species.
2) As dietary competition is hard to determine from field data without the use of enclosures or removal of a species, we established a new estimate of competitive strength concerning food uptake, which allowed for a clear ranking of competitive ability of the species. The diets of three juvenile invasive and three 0+ native species were compared and analyzed concerning consumption rates and dietary overlaps. Further, intra- and interspecific levels of competition, which additionally integrated the densities of the species, were quantified.
3) Levels of competition were very high with strong differences between the individual species. Additionally, a seasonal pattern in dietary competition was observed, reflecting food abundance in the River Rhine, and revealing highest values for critical phases of fish development.
4) Highest competitive abilities were observed in the invasive round and monkey goby (*Neogobius melanostomus* and *N. fluviatilis*), whereas the third invasive species bighead goby *Ponticola kessleri* exhibited only intermediate values of competitive strength.
5) The effect of dietary competition on the native species asp *Aspius aspius* was minor, due to its use of food sources that weren´t used by any of the other species, thus showing good values of competitive strength. In contrast, juvenile stages of Eurasian perch *Perca fluviatilis* and pikeperch *Sander lucioperca* showed strong effects of dietary competitive interactions. Thereby, the potential for juvenile competitive bottlenecks posed by the invasive gobies on perch and pikeperch could be validated, revealing a high impact of the invasive gobies in this ecosystem.

Keywords: diet overlap * consumption rates * dietary competition * juvenile bottleneck * Gobiidae

Introduction

Competition as a major determinant of community structure has always been in the focus of ecological theory and the importance of competitive interactions has been stressed in numerous studies (Connell, 1983; Schoener, 1983; Tilman, 1987; Gurevitch et al., 1992). The competitive exclusion principle states that “complete competitors cannot coexist” (Hardin, 1960). Either one species will be excluded, or resource partitioning along with subsequent niche separation will be the outcome of competitive interactions. Thus, defining the limits of niche separation at which species can stably coexist is the major aim and challenge of studies dealing with resource partitioning (Schoener, 1974).

Besides spatial overlaps, dietary overlaps are the most frequently used tool to assess niche intersections across a wide range of taxa, including mammals (Biró et al., 2005), birds (Gorchov et al., 1995), reptiles (James, 1991), amphibians (Wu et al., 2005), and fishes (Pilger et al., 2010). Consumptive competition is by far the most common form of interspecific competition in freshwater systems (Schoener, 1983). Additionally, as in fishes the greatest niche partitioning occurs on the dietary axis (Ross, 1986), estimates of the dietary interaction are a common tool to investigate mechanisms of competition among them.

Efficient feeding, following optimal foraging theory (MacArthur and Pianka, 1966), is defined as the maximum energy intake per time. This includes searching, capture success and handling, thereby presuming the energy gain being greater than the loss. Efficiency is affected by phylogenetic factors, like morphological or physiological issues; by internal factors like hunger; or external factors including prey availability, predation risk and competition (reviewed by Perry and Pianka, 1997). Thus, in terms of competition the individual´s feeding rate not only depends on its own feeding efficiency, but also on the interference with competitors, as those might decrease or interfere with food availability (Nakayama and Fuiman, 2010).

Dietary interspecific competition may result in diet specialization (Winemiller, 1989), decreasing a species´ niche width, whereas intraspecific competition should expand a species´ niche (Connell, 1983). Though niche breadth and the overlap with other species can give important information on levels of competition for resources, an overlap alone does not account for competition directly, as high overlap values might also occur, if resources are not limited (Colwell and Futuyma, 1971). Hence, studies dealing with competition should not only describe the overlap of resources, but also try to include quantitative density effects of these competitive interactions. Realizing this in field studies is quite a challenge, as it often requires manipulations like the complete removal of a population or the use of enclosures (Schoener, 1983), which may result in misleading greater competitive effects than studies on free-range organisms (Gurevitch et al., 1992).

Defining the exact impact of competitive effects gets even more crucial, if invasive species are concerned. In most cases of ongoing invasion processes, the invader shows a higher competitive ability than native species (Sakai et al., 2001), which might not only affect the referring species, but may result in considerable ecological consequences, as e.g., the disruption of the native food web (Bohn and Amundsen, 2001).

In the past decade, three invasive Ponto-Caspian goby species have established high densities at the Lower Rhine, constituting around 80 % of all caught fishes (Borcherding et al., 2011; Borcherding et al., 2013). The most prominent is the round goby *Neogobius melanostomus,* which has gained a lot of attention, as it has not only invaded major parts of Europe, but also spread to the Great Lakes (Charlebois et al., 2001). The two other species, bighead goby *Ponticola kessleri* and monkey goby *N. fluviatilis,* also extended their range from the Ponto-Caspian area and are supposed to be a threat to native species (Wiesner, 2005; Jurajda et al., 2005). At the River Rhine these species invaded a habitat that is limited in food resources due to a drastic decrease in primary productivity over the last decades (up to 90 % reduction of chlorophyll a between 1990-2009, Hardenbicker et al., 2014), that was shown to result in biomass losses in major food organisms over the summer (e.g., Asian clam *Corbicula fluminea,* Vohmann et al., 2010). Thus, native fish species in the Rhine are not only facing limited food resources, but also new members within the fish community, that are assumed to further deplete food supplies (as shown e.g. for round goby competition on *Platichthys flesus*, Karlson et al., 2007; or juvenile yellow perch *Perca flavescens,* Houghton, 2015).

At the Lower Rhine the invasive gobies display an opportunistic feeding behavior (Borcherding et al., 2013), suggesting that diets may also overlap with native species, especially juvenile stages, which all share the same nursery areas. Competition in juvenile stages can influence adult performance, not only concerning recruitment, but also resource use and, along with that, morphology (Osenberg et al., 1992). Additionally, early life-history stages are more prone to mortality than adult specimens (Houde, 1997), thereby also being more vulnerable to competitive effects. Predatory species often undergo dramatic dietary niche shifts during early ontogeny, restricting those species to behavioral and morphological limits concerning feeding efficiency on different prey categories, and thus being potentially inferior to their future prey species (Werner and Gilliam, 1984; Persson, 1988). Thereby, a prey species can impose a competitive bottleneck on its predator species if resources are limited, restricting growth or recruitment of the predator to piscivorous stages as a consequence. This “juvenile competitive bottleneck” could be shown for several size-structured populations including fish (Neill, 1975; Persson and Greenberg, 1990).

To understand the ongoing invasion process and its consequences on the fish communities in the Lower Rhine, we established a new method to estimate levels of competition in the field for food uptake as the most important competitive axis in fish (Ross, 1986), without using any manipulations or enclosures. This estimate combines quantitative (e.g., consumption rates) and qualitative (e.g., intra- and interspecific diet overlaps) aspects, and is based on potentially changing densities of the studied species. As native species the two Percidae Eurasian perch *Perca fluviatilis* and pikeperch *Sander lucioperca*, and the cyprinid asp *Aspius aspius* were included. All of them switch to piscivory at different stages during ontogeny (Popova and Sytina, 1977; Kottelat and Freyhof, 2007) and showed high densities in the sampled nursery areas, being indicative of a juvenile competitive bottleneck. For the food limited Rhine we hypothesized, that the strength of competitive abilities in feeding depends (1) on the share of used food resources (differences between species), as well as (2) on temporal aspects of food availability (seasonal differences). Based on these estimates we further wanted to know for which species potential juvenile competitive bottlenecks may exist, and when crucial periods in the development of the juvenile (0+) fish communities arise. This should help to give some prognosis on the further impact of the invasive species and on the development of fish communities at the Lower Rhine.

Material and Methods

Fish sampling

For this study, a total of 487 beach seinings were conducted from 2011 to 2013 in three fixed large sandy groin fields at the Lower Rhine (Rhine km 842, cf. Borcherding et al., 2013). These bay-like groin fields have been proved to be the nursery habitat for several species, including the invasive gobies (Gertzen et al., 2016). For effective sampling of juvenile fishes a beach seining net (10 m x 1.5 m) with a very small mesh size (1 mm) was hand-dragged against the current for a stretch of 20 m in length and 5 m in width yielding approximately 100 m². Campaigns were conducted from April to October at three different daytimes to consider diel variations in density, food uptake and diet breadth (Copp, 2008). Three replicate stretches were conducted in the morning (starting 9 am), afternoon (starting 3 pm) and at night (directly after civil sunset starting at 8 pm – 11 pm). This was regularly repeated three times a month with varying starting times to avoid density dependent effects relying on sampling procedure (Borcherding et al., 2013). In general, 27 stretches were sampled per month, with two consecutive series at least having a pause of 24 h in between. However, at some dates it was not possible to create a whole campaign due to water level increases or weather conditions, which lowered catching rates substantially.

All fishes were identified to species level, total length (TL) was measured to the nearest 1 mm and sex was determined in case of Gobiidae by the shape of the urogenital papillae. In addition to all gobies, 0+ stages of native species of interest were collected (maximum of 15 individuals per trial and species) and either preserved in 96 % ethanol (individuals < 50 mm TL), or stored on ice and shortly later conserved at a temperature of -18 °C (individuals exceeding 50 mm TL). Surplus individuals and other indigenous species were released carefully after measuring. Fish larvae that could not be identified on site were also fixed in 96 % ethanol and were afterwards determined using keys for larval fish identification (Koblickaya, 1981; Mooij, 1989; Urho, 1996; Staas, 1996; Pinder, 2001).

Gastrointestinal analyses

In total, 4,243 specimens were dissected and their stomach or digestive tract content, respectively, analyzed (Tab. 1). Total length to the nearest 1 mm and wet weight (nearest 0.0001 g) was noted, before the stomach was removed. For species lacking a real stomach (gobies, Jaroszewska et al., 2008; and asp, Warren Jr et al., 2014), the whole digestive tract from esophagus to rectal sphincter was analyzed, whereas analyses for Percidae proceeded with the stomach. Therefor the stomachs and tracts were freed from other organs and weighted to the nearest 0.0001 g (stomach full S_f).

Afterwards contents were removed and the empty tracts were weighted again (stomach empty S_e). Items were classified to lowest possible taxonomic unit (Olympus SZX 9) and their proportion to the whole content was visually estimated (Polacik et al., 2009). For quantitative objectives the wet weight of the contents (S_c) [1] and the index of stomach fullness (ISF, Hyslop, 1980) [2] were determined as follows:

[1] $S_c = S_f - S_e$

with S_c = wet weight of stomach / digestive tract content [g], S_f = wet weight of full stomach / digestive tract [g], and S_e = wet weight of empty stomach / digestive tract [g].

[2] $ISF\ [\%] = \frac{Sc}{W-Sc} * 100$

with W = wet weight of the fish [g].

Table 1. Analyzed stomach/digestive tract contents per year, month and species.

Year	Month	Aspius	Nf	Nm	Perca	Pk	Sander
2011	April		3	26			
	May	23	20	68	33	3	48
	June	57	14	128	76	29	81
	July	74	33	81	106	16	32
	August	66	28	85	32	4	9
	September	12	39	81	13		1
	October	3	4	100	2	2	4
2012	April	1	2	17	5		2
	May		15	89		139	
	June	16	3	87	26	158	40
	July	9	50	76	22	30	23
	August	15	21	40	24	11	19
	September	6	65	150	14	21	10
	October	31	42	259	37	9	5
2013	April		30	44	1	3	
	May		43	72		3	16
	June	15	31	33	30	31	37
	July	30	30	48	53	59	35
	August	33	58	40	45	45	38
	September	12	30	36	29	39	22
	October	13	45	44	15	15	15
	Total	416	606	1604	563	617	437

Data Proceedings

In a first step the *individual consumption* [3] was calculated. The stomach content of juvenile fishes represents only the food uptake of the last 8 hours (c.f. Hyslop, 1980), therefore the amount of prey was multiplied with the factor 3 to yield a dial consumption rate for each individual:

[3] $\text{Consumption}_{\text{Ind}}\ [g * g^{-1} * d^{-1}] = \frac{Sc}{W-Sc} * 3$

To define the level of dietary competition from this field data, a value explaining the *desired food uptake per species* was established (ISF_{MAX}) [4]. This was done by taking the median from the upper 10 % of all ISF values species specifically (Fig. A1):

[4] $ISF_{MAX} = \tilde{x}\{x \mid x_i \geq Q_{0.9}\}$

with $\tilde{x}$ = median; $x_1, x_2, \ldots, x_i = ISF_1, ISF_2, \ldots, ISF_i$; and $Q_{0.9}$ = 90 % quantile of all species specific ISF values.

The median was chosen, as this value is robust against outliers, which naturally occur due to piscivory, yielding temporarily very high indices of stomach fullness.

For every individual the proportion of the individual ISF in relation to the species specific ISF_{MAX} was calculated and served from now on as the measurement of individual *strength of dietary competition SDC* [5]:

[5] *SDC* [%] = $\frac{100}{ISF \times ISFMax}$

As dietary competition can only occur if the species are feeding on the same resources, the *diet overlap* O_D [6] was calculated between all species, and this for all months and years following Schoener (1970) using all 83 types of food items observed in this study:

[6] $O_D = 1 - 0.5 \times \sum |(pix - piy)|$

with p_{ix} = percentage of food item *i* in species *x* and p_{iy} = percentage of food item *i* in species *y*.

As we aimed to include densities of all other fishes within one month and year into the estimation of the diet overlap, we also had to calculate the intraspecific diet overlap to facilitate also the inclusion of densities of conspecifics as competitors. In contrast to the interspecific diet overlap, for which the mean diets of species are compared on a monthly basis [6], the diets of the single individuals of one species were compared with each other. In those cases where more than 50 individuals per month were dissected, 50 individuals were randomly chosen from the subset. For each individual the diet overlap to all other conspecifics within the sample was calculated and the intraspecific diet overlap was then calculated as the mean of all these values. This allows an estimation of the intraspecific diet overlap based on the same calculation scheme as for interspecific comparisons (Fig. A2).

Lastly, the *weighted diet overlap* O_{Dw} [7] was established species specifically, which integrated the density of the particular species, all other occurring species (also those which were not analyzed), as well as the intraspecific diet overlap.

[7] $O_{DW} = \sqrt{OD1 \times D1 + \cdots + ODn - 1 \times Dn - 1 + ODi \times Di + ODm \times Dm}$

with O_{D1} = diet overlap with species 1, D_1 = density of species 1, integrated as percentage of all densities; O_{Dn-1} = diet overlap with species n-1, D_{n-1} = percentage of density of species n-1; O_{Di} = intraspecific diet overlap, D_i = density percentage of the regarded species; and O_{Dm} = mean of all calculated diet overlaps besides the intraspecific overlap (O_{Di}), D_m = sum of density percentages of all other occurring species. The last term includes all other species that were caught, but where no stomach content analyses were conducted (on average 12 ± 10 %). Taking the mean of all calculated diet overlaps (besides the intraspecific overlap) as representative for all non-analyzed fish species was justified by examining 6 different species from varying families with different feeding habits. As for the proof of significance in diet overlap, we also assume the threshold of 0.6 (Wallace, 1981) as a first estimation for the significance of the weighted diet overlap presented here.

Statistics

Densities were calculated by pooling the data of 0+ individuals per month and species. As the density data were neither normal distributed (Shapiro-Wilk test), nor showed homogenous variances (Levene test), non-parametric Kruskal-Wallis tests were applied to obtain differences between species, months and years, followed by Wilcoxon rank sum tests of the single groups. The same practice was applied to individual consumption rates and weighted diet overlap (O_{Dw}) values.

Due to the complex data structure, competitive strength data were analyzed by a linear mixed model, to account for the nested structure of “month” within “year”. Thus, year was integrated into the model as random factor, whereas “species” and “month” determined the fixed effects. Validation of effects implemented in the model was controlled by their significance (ANOVA of the mixed model, Tab. 3) and comparisons with simpler models. The shown D_C values are consequently the calculated fitted values of the model.

Results

Fish assemblage

In total, 63,684 fishes out of 30 different species were caught. 54,470 were 0+ individuals from the relevant year or from the year before, respectively, as long as no newly hatched 0+ individuals were caught. 70.1 % of all 0+ individuals were invasive gobies (Nm: 40.5 %, Nf: 6.5 %, Pk: 19.7 %, goby undefined: 3.4 %), whereas native species were mostly represented by the target species perch (12 %) and pikeperch (4 %). Asp was also caught in relatively high abundances, making up 2.1 % of all 0+ fishes. Other representative species were the cyprinids ide *Leuciscus idus* (3.2 %), roach *Rutilus rutilus* and barbel *Barbus barbus* (both 2.2 %).

Densities

Regarding the total amount of caught 0+ fishes, no differences in densities could be detected across the three years (Kruskal-Wallis $p=0.78$), with mean densities ranging from 0.9 ± 0.5 in 2011 to 1.2 ± 1.3 individuals per m² in 2013 (Fig. 1). However, densities of 0+ individuals for the single species varied greatly between months and years. While for asp, perch, pikeperch and bighead goby highest densities were reached at the beginning of the season (May – July), the multiple spawning mode of round and monkey goby resulted in higher densities towards the end of the season (July - October). Perch showed stable densities across the years (Kruskal-Wallis, $p=0.8399$) with seasonally occurring peaks in June and July, where densities differed significantly from the rest of the year (Wilcoxon, $p<0.0001$). Highest densities were obtained in June 2013 with 0.5 individuals per m². For pikeperch densities were lower and peaked a bit earlier in May and June (Wilcoxon, $p<0.005$), respectively, but also showed highest values in June 2013 (0.24 Ind./m²). In contrast, for asp 2012 was the year with the highest densities, peaking in May with 0.2 individuals per m². 2011 and 2013 differed significantly from 2012 (Wilcoxon, $p<0.05$) and from each other (Wilcoxon, $p<0.05$), with 2013 showing depressed densities.

For round goby, 2011 was the year with the highest densities, though not being significantly ahead of 2012 and 2013 (Kruskal-Wallis, $p=0.05143$). Greatest densities were reached in September 2011 with 1.6 individuals per m² (Wilcoxon, $p<0.005$). Monkey goby showed highest values in 2013 (Wilcoxon, $p<0.0001$) and comparable densities in 2011 and 2012 (Wilcoxon, $p=0.11$). Maximum values were obtained for August 2013 with 0.3 individuals per m². Bighead goby showed the most fluctuating densities of all species. 2011 could be declared as reproductive failure (Gertzen et al. 2016), clearly revealing the lowest densities (Wilcoxon, $p<0.0001$). 2012 and 2013 also differed significantly (Wilcoxon, $p=0.0289$), mostly due to a very strong peak of freshly hatched bighead gobies in May 2012 (2.5 Ind./m²). In general, asp yielded the lowest densities from all analyzed species (Wilcoxon, p<0.0001), whereas round goby had the highest densities (Wilcoxon, p<0.0001). Interspecific significant differences were also obtained for all other species (Wilcoxon, p<0.05), except for the combination of bighead and monkey goby (Wilcoxon, p=0.4650).

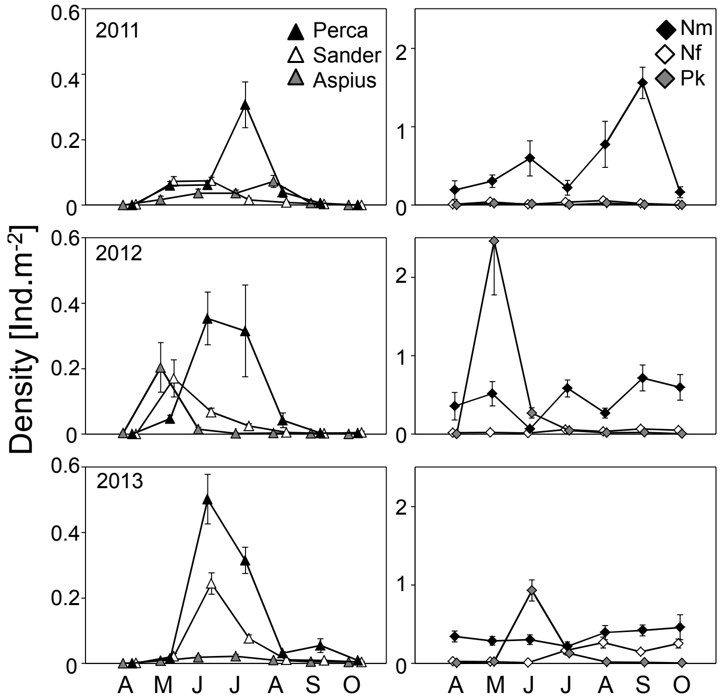

Figure 1. Densities (mean ± SE) of native (left) and invasive species (right) for the three years in course of the season. Please note the varying density scales for native and invasive species.

Table 2. Amount and percentage of empty stomachs/digestive tracts of all analyzed fishes.

Species	N empty	Empty stomach / digestive tract [%]
Aspius	1	0.24
Nf	6	0.99
Nm	3	0.19
Perca	11	0.18
Pk	2	0.32
Sander	9	2.06

Gastrointestinal analyses

From 4,243 analyzed gastrointestinal tracts only 32 (0.75 %) were found empty. Not surprisingly, pikeperch as a piscivorous species had the highest amount of empty stomachs with 2.06 % (Tab. 2). Overall, most abundant prey items were chironomid larvae and gammarids, mainly the invasive *Dikerogammarus villosus* (Fig. A3). For bighead goby, perch and pikeperch fish gained more importance in course of the season, going along with increasing total length. Pikeperch already included fish to a considerable proportion into its diet in May (37 %), whereas piscivorous diet of perch never exceeded 20 % during the whole season. Besides the main prey types, molluscs were of relevance for monkey and round goby, again mainly represented by an invasive species (*Corbicula fluminea*). Asp, as a surface predator, fed primarily on imagos of terrestric insects, while gammarids and fish made up only a small share of the diet (< 15 %), and chironomids being even more seldom found (< 4 %).

Individual consumption

Consumption rates between all species varied significantly (Wilcoxon, $p<0.05$, Fig. 2), with bighead goby showing by far the highest individual consumption rate with a mean daily intake of 0.151 ± 0.094 g per gram body mass, followed by round goby (0.097 ± 0.049 $g*g^{-1}*d^{-1}$), pikeperch (0.086 ± 0.137 $g*g^{-1}*d^{-1}$), asp (0.081 ± 0.051 $g*g^{-1}*d^{-1}$), monkey goby (0.076 ± 0.053 $g*g^{-1}*d^{-1}$), and finally perch (0.041 ± 0.042 $g*g^{-1}*d^{-1}$). For perch individual consumption rate was stable across the years (Wilcoxon, $p>0.05$), while seasonal trends were obtained with highest values generally being reached at the beginning of the season (May and June). Pikeperch also had stable consumption rates over the years (Kruskal-Wallis, $p=0.1489$). Highest rates were yielded as well in May and June, with an exceptional maximum value reached in June 2012 (0.199 ± 0.197 $g*g^{-1}*d^{-1}$), followed by a sharp decline till the end of the season (October 2012: 0.042 ± 0.048 $g*g^{-1}*d^{-1}$). For asp, 2012 had a significantly lower consumption rate than the other two years (Wilcoxon, $p<0.001$), mainly due to the extremely low food uptake in October 2012 (0.019 ± 0.009 $g*g^{-1}*d^{-1}$). In course of the season the consumption rate of asp generally declined in August (Wilcoxon, $p<0.001$), while it was stable the rest of the season (besides the mentioned extreme in October 2012). Monkey goby had stable consumption rates from 2011 to 2013 (Kruskal-Wallis, $p=0.1041$) and also over the season, except for 2013 where consumption rates were considerably higher in June and July (Wilcoxon, $p<0.005$).

Consumption rates for round goby were slightly higher in 2011 with a mean of 0.11 ± 0.046 (Wilcoxon, $p<0.001$), whereas 2012 and 2013 were comparable with 0.09 ± 0.047 and 0.092 ± 0.055 gram per body mass per day, respectively (Wilcoxon, $p>0.5$). Food uptake peaked in the middle of the season (June and July) and from then onwards declined up to October. However, patterns were not as pronounced as for the other goby species. Especially bighead goby showed strong seasonal differences with peaking consumption rates in June and July, respectively, being two to four times higher than values at the beginning or end of the season. Maximum values were gained in July 2011 (0.224 ± 0.063 $g*g^{-1}*d^{-1}$), lowest in May 2013 (0.041 ± 0.037 $g*g^{-1}*d^{-1}$). Here, a wide variance could also be observed across the years (Wilcoxon, $p<0.05$) with a clear decline from 2011 (0.184 ± 0.077 $g*g^{-1}*d^{-1}$) to 2013 (0.132 ± 0.086 $g*g^{-1}*d^{-1}$).

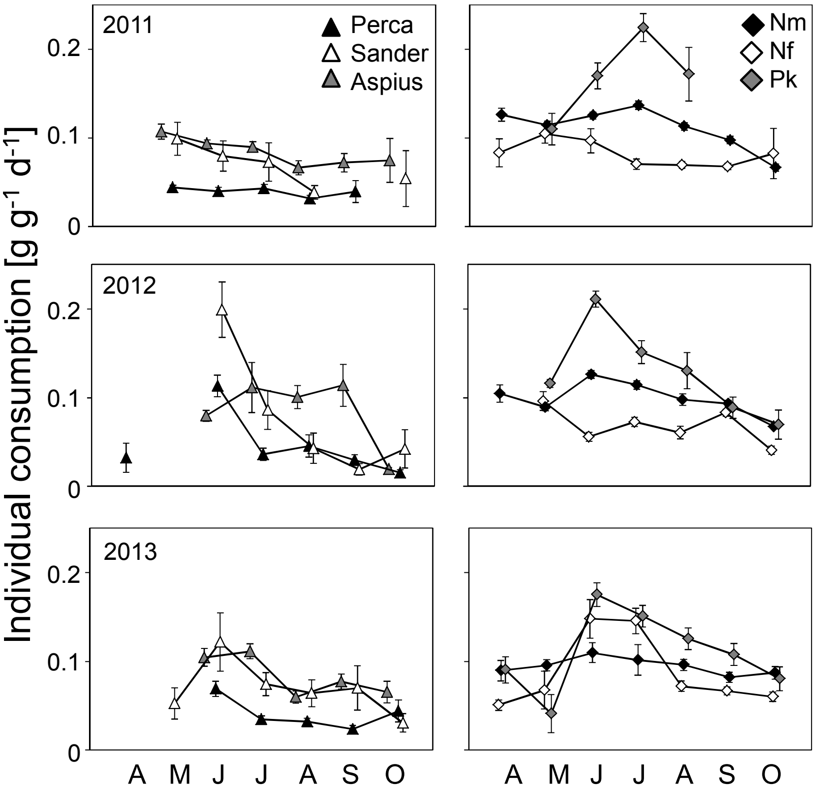

Figure 2. Individual consumption rates (mean ± SE) of native (left) and invasive species (right) for the three years in course of the season.

Weighted diet overlap O_{DW}

The weighted diet overlap not only incorporates the intra- and interspecific dietary overlap per se, it also includes the density of all species, which determines the encounter rate and possibility of competitive interactions. Overlaps were stable across the years (Kruskal-Wallis, p=0.9131), whereas the differences between the species were highly significant (Kruskal-Wallis, p<0.0001, Fig. 3). Asp showed the lowest overlap values, differing significantly from all other species except pikeperch (Wilcoxon, asp compared to: Nf &Nm p<0.0001; Perca p=0.0011; Pk p=0.02408; Sander p=0.9112). Values ranged from 0.51 to 0.68 with one exception being very high in October 2012, where an overlap of 0.8 could be detected. Generally, overlaps were slightly higher at the beginning of the season for this species and then decreasing until October. The weighted diet overlap of perch ranged from 0.61 (August 2012 and 2013) to 0.86 (May 2011), with a mean of 0.71 ± 0.07 and differing significantly from all other species except bighead goby and pikeperch (Wilcoxon, perch compared to: asp p=0.00113; Nf p=0.0002; Nm p=0.0357; Pk p=0.9112; pikeperch p=0.076). Higher overlaps were detected at the beginning and end of the season, whereas in August always the lowest values were obtained. Pikeperch had a mean weighted overlap of 0.64 ± 0.1, ranging from 0.49 (October 2012 and August 2013) to 0.87 (October 2011), differing significantly from monkey (Wilcoxon, p<0.0001) and round goby (Wilcoxon, p=0.002).

The invasive gobies showed the highest overlap values. Monkey goby had the greatest mean overlap with 0.81 ± 0.04, displayed by a small range from 0.71 – 0.87 and differing from all other species (Wilcoxon, all combinations $p<0.05$). Round goby followed with a weighted overlap of 0.77 ± 0.05. Here, values were more fluctuating ranging from 0.62 (August 2011) up to an overlap of 0.83 (October 2011, May 2012). Weighted overlap values differed significantly from all other species except bighead goby (Wilcoxon, Nm compared to: asp $p<0.0001$; Nf $p=0.0357$; perch $p=0.0357$; Pk $p=0.9112$, pikeperch $p=0.0002$). As for monkey goby, no clear seasonal trend was obvious for round goby. For bighead goby overlap values showed a higher variation across the season, with overlaps being less pronounced in the mid-season around August. Values ranged from 0.5 (August 2011) up to a very large overlap of 0.91 in May 2012, where the distinct peak of freshly hatched bighead gobies occurred. Mean weighted overlap for bighead goby yielded 0.73 ± 0.11, showing significant differences from asp (Wilcoxon, $p=0.0204$) and monkey goby (Wilcoxon, $p=0.0357$).

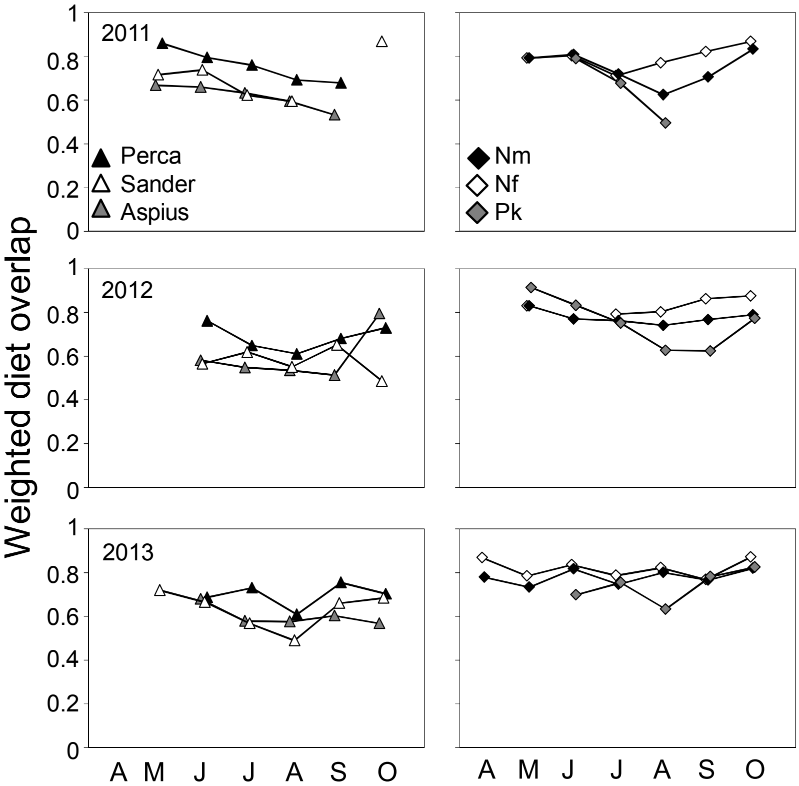

Figure 3. Weighted diet overlap O_{DW} (incorporating the density, intra- and interspecific overlaps) of native (left) and invasive species (right) for the three years in course of the season.

ISF_{MAX}

The desired food uptake, described by the ISF_{MAX}, varied greatly between the species (Fig. 4). Round goby yielded the most stable values within the years, as well as across the years. Inter-annual variability was also negligible in asp, whereas for the other species the range was greater between the years, with pikeperch showing the greatest spread (2011: 8.62 % - 2012: 14.75 %). For further analyses only the overall mean of the ISF_{MAX} per species was taken for all three years. Highest values were calculated for pikeperch (11.7 %), closely followed by bighead goby (9.89 %). Round goby (5.59 %), monkey goby (5.16 %) and asp (5.19 %) had comparable values, whereas perch showed the lowest desired intake (3.75 %).

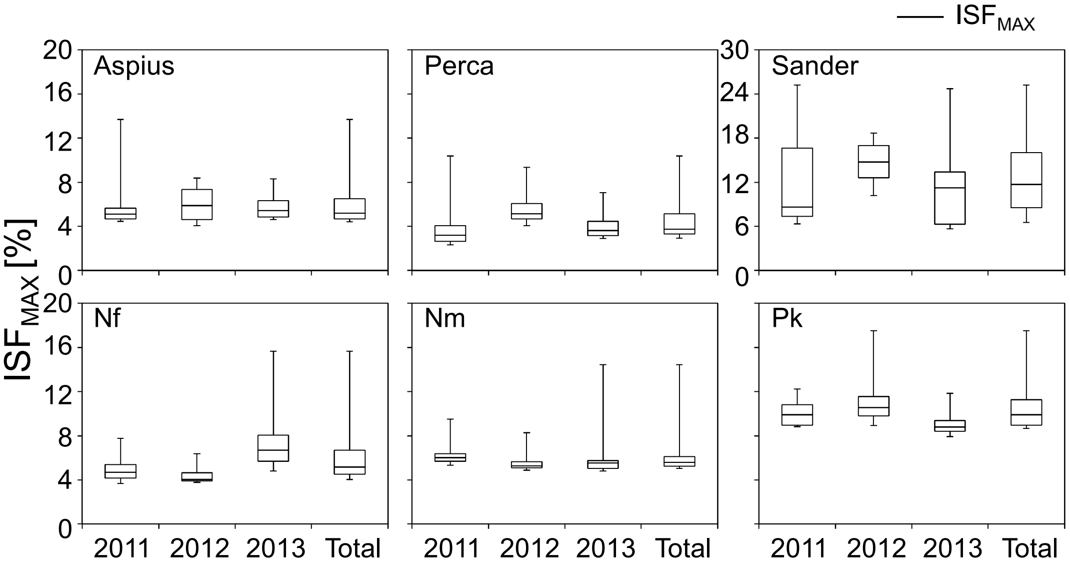

Figure 4. Boxplot (minimum, 25 % quantile, median, 75 % quantile and maximum) of the ISF_{MAX} values for the single species and years and total ISF_{MAX}, whereof the median was used for following dietary competition calculations.

Dietary competition D_C

Values of dietary competition were fitted with a linear mixed model, with “species” and “month” as fixed terms and year integrated as random effect (Tab. 3, A3). Highest strength in the overall competitive ability was detected for round goby with a mean of 58 % of potential food uptake, peaking in June with 70 % and having lowest values found in October (40 %, Fig. 5). A mean of 40 % was achieved by bighead goby, however, strongly scattering with a sharp peak of 62 % in June and lowest values in October (28 %). Monkey goby yielded 48 %, and here values also varied greatly over the season ranging from 33 % (October) – 77 % (June). All gobies showed a seasonal pattern peaking in summer and from then onwards decreasing up to October, however, this was more pronounced in monkey and bighead goby, whereas round goby displayed more stable values. From the native species highest values were reached by asp with a mean of 49 %, ranging between 22 % in October to 66 % in May, showing a less distinct seasonal pattern. Perch and pikeperch displayed the same seasonal trend as the gobies, but had much lower values, revealing clearly lower strengths in their overall competitive ability. Perch achieved 32 % of desired food uptake, ranging from 20 % (October) – 52 % (June). Pikeperch in contrast, only came at meager 19 %, spanning from 10 % (October) to 30 % (June).

Table 3. ANOVA results of the linear mixed effect model concerning competitive strength with year as random factor, and month and species as fixed effects (for single t- and p-values compare Table A3).

	Numerator df	Denominator df	F	p-value
Intercept	1	4199	11704.466	<0.0001
Species	5	4199	117.055	<0.0001
Month	6	4199	89.536	<0.0001
Species:Month	30	4199	2.998	<0.0001

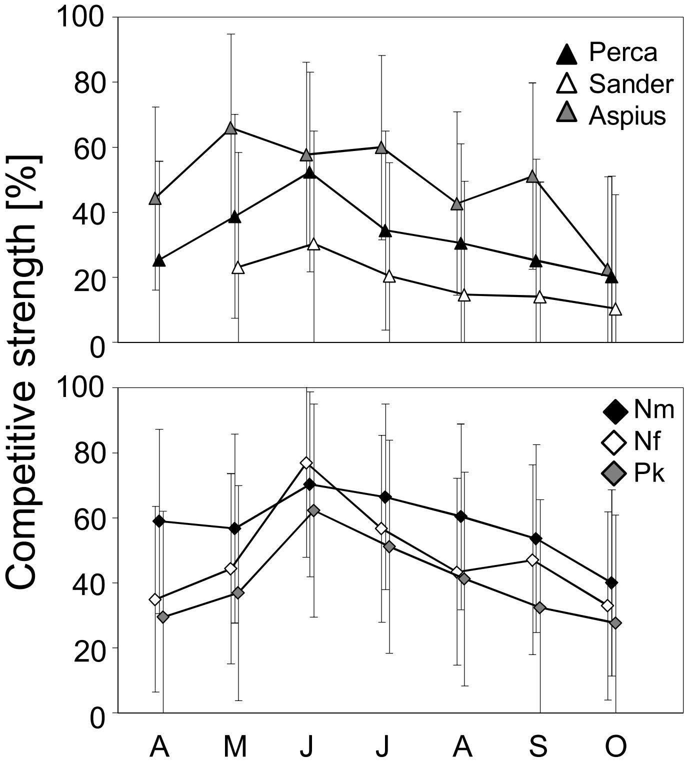

Figure 5. Competitive strength, defined as the proportion of the ISF_{MAX} (%, fitted values ± SE), indicating the dietary competitive ability, that is yielded per species in course of the season.

Dietary competition D_C versus weighted diet overlap O_{DW}

Here we refer to the fitted values of the linear mixed model. As year was integrated as random factor, only few data points (7: April to October) remain per species, making it difficult to detect significant correlations between the competitive strength and the weighted diet overlap, especially if values of the weighted diet overlap were stably high, as in case of the Gobiidae. Thus, it is not surprising, that linear regressions revealed no significant correlations with competitive strength ($p>0.05$ for all species, Fig. 6). However, for some species trends were visible (for correlations of individual consumption on weighted overlap see Fig. A4). For round goby ($p=0.432$), as for monkey goby ($p=0.242$), competitive ability decreased with increasing values of the weighted overlap. This pattern, also less pronounced, could also be seen for asp ($p=0.717$), whereas perch showed the opposed trend with an increasing competitive ability as the weighted overlap increased ($p=0.423$). Contrary, for bighead goby ($p=0.857$) and pikeperch ($p=0.709$) no trend was detectable, thus their strength in the dietary competitive ability was independent of the weighted overlap.

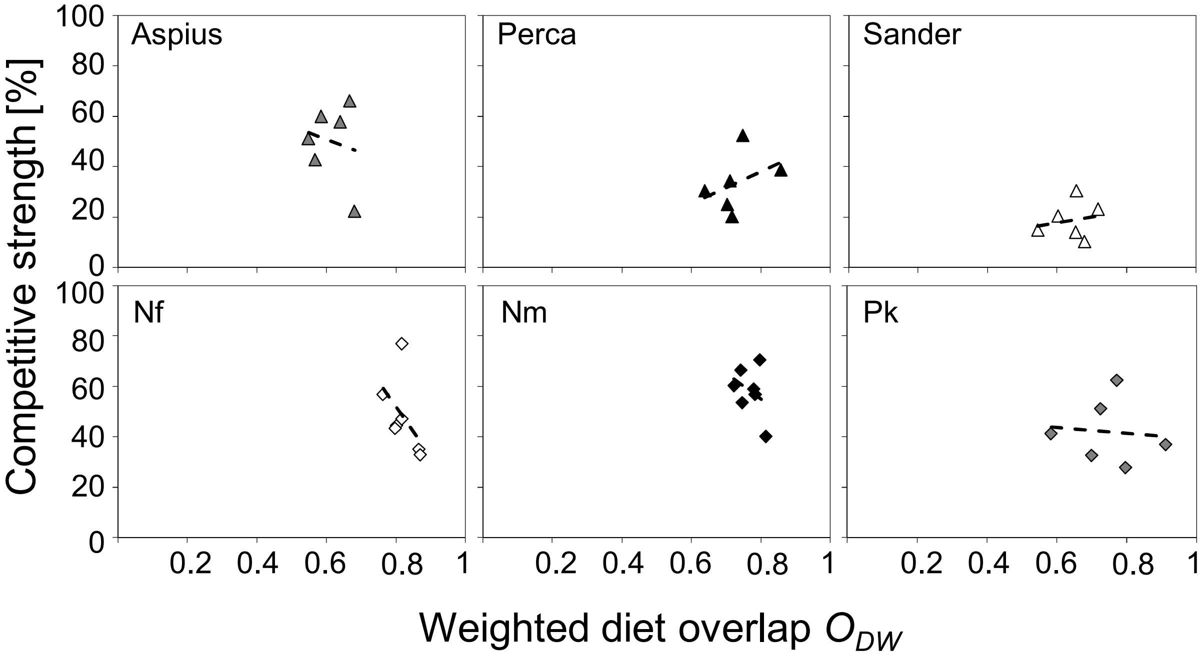

Figure 6. Correlation of the competitive strength and weighted diet overlap for the single species. Every point represents one month (Apr – Oct, fitted values).

Discussion

The first aim of our study was to establish an estimate of dietary competition, which should incorporate quantitative (ISF, consumption rates) and qualitative (diet overlaps) data, as well as the referring densities of the according species. The basis of this estimate is the calculation of the maximum ISF (ISF_{MAX}). For round gobies, this value was in good accord with the maximum consumption rate defined by a bioenergetic model (Lee and Johnson, 2005), based on *ad libitum* feeding (dreissenid mussels). Also for perch the defined maximum consumption rate fits well with data from *ad libitum* feeding experiments on food uptake of 0+ fishes (Borcherding et al., 2007). Smaller fish generally have a higher weight specific consumption rate than larger fish (Hanson et al., 1997), therefore we suggest to apply this method only on fishes of the same ontogenetic stages, or to calculate different ISF_{MAX} values for the different stages, respectively. Additionally, as we sampled at three different daytimes, we accounted for potential differences in feeding time. The estimate of competitive strength was complemented by the weighted diet overlap (O_{DW}), incorporating the diet overlaps with all species, as well as the referring densities, thereby including the impact of the invasive gobies´ high abundances and the situation of a limited system at the Lower Rhine. However, to not overestimate competitive effects and to avoid inaccuracy, it should not be applied to systems where main feeding guilds were not analyzed.

Regarding the ongoing disappearance of connected floodplain areas (Buijse et al., 2002), which normally serve as spawning and nursery areas for native species (Scharbert and Borcherding, 2013), the importance of groin fields as recruitment habitats for juvenile fishes is widely accepted. The dominance of invasive gobies in 0+ assemblages in those habitats at the Lower Rhine, reflect the same alarming pattern as earlier studies could reveal for this region (Borcherding et al., 2011; Borcherding et al., 2013). Food capacities at the Lower Rhine have strongly decreased in the past decades (Hardenbicker et al., 2014). Limited food resources, and thereby high levels of dietary competition, could also clearly be validated by this study, displayed by the proportion of desired food uptake per species (competitive strength), which never yielded values above 80 %. Here, strong differences between the single species could be detected showing the varying levels of sensitivity to competitive interactions.

The diet of invasive gobies reflected mainly an opportunistic feeding style and was consistent with those found in other regions (Adamek et al., 2007) and earlier in that study area (Borcherding et al., 2013). Round gobies had high individual consumption rates and weighted diet overlaps, but showed the best competitive ability of all species. Monkey gobies displayed low consumption rates combined with a low

ISF_{MAX}, which additionally were stable across the years, revealing the lowest energy demands of the three gobies, and showing a quite good competitive ability. Contrary, individual consumption rate was by far greatest for bighead goby, with the ISF_{MAX} also being very high, indicating elevated energy demands for this species. Yet, weighted diet overlap values were also high and competitive strength was only intermediate, weakening the impact of this species when compared with monkey and round goby.

Contradictory to other regions (Krpo-Cetkovic et al., 2010), asp showed no piscivorous behavior in its first year of life, with its main prey type being insect imagos picked from the surface. Insects could be validated as prey category for the largest asp larvae in Poland (Kujawa et al., 1998), indicating that this might be an intermediate ontogenetic step before switching to piscivory. This additional food category wasn´t used by any of the other investigated species and clearly released this species from interspecific competition. Not surprisingly, asp had the lowest weighted diet overlap values and a good competitive ability, being the only native species, which yielded as high values as the gobies. One exception could be observed in October 2012, where asp showed an increased weighted diet overlap going along with dramatically decreased consumption rates and competitive ability. As in 2012 asp had the highest densities and as it was the coldest October from all analyzed years, we assume that the preferred prey of insect imagos might have already decreased and that asp was not able to switch to and/or compete for another prey category ad-hoc. Therefore, for this species interactions of intraspecific competition seem to be of greater importance than interspecific effects. Although it is known that dietary interspecific competition may result in such diet specialization (Winemiller, 1989), of course it remains speculative, if competitive interactions have led asp to that choice of prey. Nevertheless, asp is the species, which is least affected by dietary competition exerted by the invasive gobies.

The diet of perch and pikeperch overlaped to some extent with the gobies, mainly by consumption of the amphipod *Dikerogammerus villosus*. Pikeperch included fish earlier, and to a greater extent into its diet than perch, thereby using a food source that was not used by the gobies in those stages. Early piscivory of pikeperch could be shown to result in better growth and survival (Persson and Brönmark, 2002). However, weighted diet overlap values were still high for both species, with perch being ahead of pikeperch. Perch had the lowest individual consumption rate and ISF_{MAX}, whereas pikeperch showed the highest ISF_{MAX} values due to its early piscivory. Both Percidae ranked last in competitive ability, clearly suffering by the food shortage imposed by the invasive gobies.

Besides those general differences between the single species, seasonal trends of competitive interactions could also be detected. Although less pronounced in the strong competitors round goby and asp, in general, the competitive ability of all species was subject to a seasonal pattern, peaking in mid-season and reflecting that of food abundance in the River Rhine (Van Riel et al., 2011). This supports the idea of a limited system going along with dietary competition even more. Highest values were reached in the mid-season (June – August), when macrozoobenthos densities were also highest (Van Riel et al., 2011). Contrary, weighted diet overlaps were high and, going along with that, competitive strength low at the beginning of the season, when the individuals were smallest. As smaller individuals have higher specific metabolic rates than larger individuals (Post and Parkinson, 2001), the obtained high levels of competition set on at a critical point in fish development and may thus result in reduced growth or mortality (Tonn et al., 1992).

Additionally, competitive ability of all species decreased dramatically in October at the end of the season, reflecting the scarcity of food resources before winter. Densities of amphipods and other macroinvertebrate organisms decline during winter (Borcherding and Sturm, 2002; Van Riel et al., 2011). Thus it is important, that juvenile fishes take up a lot of food at the end of the season as energy storage for winter, when dietary sources are even more sparse (Post and Parkinson, 2001). Mortality has been shown to be size-selective in juvenile fishes, favoring larger individuals which have enhanced energy stores or grew into a size refuge of predators (Persson et al., 1996; Heermann et al., 2009). Considering the high dietary competition in October and the great competitive ability of monkey and round gobies, it is likely, that small perch and pikeperch might suffer from winter starvation.

The dietary competitive ability of perch and pikeperch was clearly below that of the invasive gobies and underlay a strong seasonal pattern with lowest values in the critical phases of early development and winter storage. This strongly leads to the assumption that these species are forced into a juvenile competitive bottleneck. Early piscivory of 0+ perch can prevent juvenile competitive bottlenecks, if prey fishes matching the consumable prey size are abundant (Borcherding et al., 2010). It remains questionable why perch and pikeperch did not include fish earlier and to a greater extent in their diet. Prey fishes in all sizes were abundant the whole season, due to a continuous spawning of round and monkey goby up to September (Gertzen et al, 2016). Juvenile perch and pikeperch might have not (yet) adapted to that new kind of prey. Mechanisms that give rise to the consumption of non-native prey organisms can be learning, social transmission, ontological changes in morphology, and evolutionary adaptations (Carlsson et al., 2009). In Lake Erie all size classes of an endangered water snake adapted to the new prey source (round gobies) within just two generations, finally making up more than 92 % of its diet (King et al., 2006). Yet, a premise to become piscivorous is to reach a size advantage to potential prey fishes (Mittelbach and Persson, 1998), which requires resource availability of smaller items like zooplankton at the beginning of the season. Our data showed that competition was already very high at that point of time, possibly explaining the low share of piscivorous individuals. Dietary competition affected juvenile pikeperch even stronger than perch, showing only around 20 % of the desired food uptake. However, this species consumed fish prey earlier and to a greater extent than perch in course of the season. Thereby a prey category was used, that was not included in the diet of juvenile gobies, and which in turn may reduce levels of competition. Additionally, the consumption of fish can yield higher growth rates and lipid storage than other prey categories (Borcherding et al., 2007). Yet, as fish prey was only used by a subset of the pikeperch population, both native Percidae seem to be heavily affected by dietary competition in juvenile stages. Species, which feed on the same resources as juveniles and adults (like the gobies) are often more competitive than those feeding only in juvenile stages on that resource (Werner and Gilliam, 1984). Thereby, a juvenile competitive bottleneck is enhanced and very likely to act in this system on perch and pikeperch.

In general, weighted dietary overlaps were highest for the invasive gobies, especially for round goby, as this species occurred in extremely high densities. Although here levels of competition were highest, round goby achieved the best values of desired food uptake over the whole season, showing its great competitive ability. Additionally, together with asp, round goby displayed the most stable values of individual consumption rates, $\mathrm{ISF_{MAX}}$ and competitive ability, showing that even seasonal or annual fluctuations did not influence food uptake, and thus, being less affected by dietary competitive interactions. Competitive ability of bighead goby was only intermediate and strongly scattering in course of the season, similar to the pattern and values of perch. Additionally, bighead gobies showed decreasing consumption rates in course of the years, with strong seasonal patterns. Quantitative food consumption is determined by competition for limited resources and is regarded as the link between density and individual growth (Amundsen et al., 2007). Going along with decreasing densities over the season, as well as over the years (Borcherding et al., 2013, unpublished data), this clearly indicates a competitive disadvantage for bighead gobies. Thus, the invasive gobies not only impose a threat on native species, but also suppress other invasive species.

Impacts of invasive species are often reinforced by additional invasive species (Strayer, 2012). This could be validated by our data for round and monkey goby, both having additive detrimental effects on the native Percidae. The competitive disadvantage is due to a depletion of the anyway limited resources, which might be enhanced by interference competition displayed as aggressive contacts with the gobies hindering food uptake (Schoener, 1974). For round gobies, higher competitive ability due to a high level of aggressiveness could already been shown (Dubs and Corkum, 1996). This might further deplete energy storages of competitors, thereby increasing the negative impact (Schoener, 1974).

For monkey and round goby, the trend was detectable, that competitive ability decreased with increasing weighted overlap as one would expect it. For perch however, it was the other way around: competitive ability increased with increasing weighted diet overlap. This could on the one hand be due to the fact that the weighted overlap of monkey and round gobies was high anyway, whereas for perch it was a bit lower, sometimes only being at the edge of a significant overlap. On the other hand, the weighted diet overlap also incorporates the intraspecific diet overlap and the referring densities. Thus one could also formulate, that perch has a greater competitive ability, when occurring in high abundances and preying on the same food items. Perch in juvenile stages is a shoaling species (Eklöv, 1997) and grouping behavior has been found to be related to improvement in individual foraging success, especially if resources are scarce, by the use of public information (Clark and Mangel, 1984).

Invasive goby success has been related to the selection of superior food resources (Polacik et al., 2009), to a high aggressiveness towards conspecifics (Dubs and Corkum, 1996) and to higher competitive abilities concerning food uptake (Karlson et al., 2007). Our data clearly support these findings. Dietary competition is very high among 0+ assemblages at the Lower Rhine and there is evidence for a temporal variability in competitive effects up to recruitment. The resulting high level of competitive interactions is clearly on behalf of the invasive gobies, mainly round and monkey goby, whereas juvenile perch and pikeperch suffer by being forced into a competitive bottleneck, as could also be observed for juvenile flounders and yellow perch in other areas (Karlson et al., 2007; Houghton, 2015). Native predators are supposed to be the key in controlling invasive prey species in long-term (Carlsson et al., 2009), thus it is important that recruitment is not hampered by that exotic prey. Perch and pikeperch are known to prey on gobies in adult stages (Chapter V), if this can diminish the effects of decreased recruitment rates needs to be revealed in future studies. Invasive bighead goby too, is competitively inferior to the other two goby species, therefore being regarded as less menacing for native species. For this species we assume, that densities will further decrease in the next years. Contrary, asp was not affected by dietary competition imposed by the Ponto-Caspian invaders, yet it might be influenced by intraspecific competition when densities of the dominant prey category are low. This study not only detected the strength of dietary competition with data originating directly from the field, but also evaluated the varying impacts on the different species with regard to the changing densities in course of the season.

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References

Adamek, Z., Andreji, J., Gallardo, J. M., 2007. Food habits of four bottom-dwelling Gobiid species at the confluence of the Danube and Hron Rivers (South Slovakia). Internat. Rev. Hydrobiol. 92, 554-563.

Amundsen, P. A., Knudsen, R., Klemetsen, A., 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. J. Anim. Ecol. 76, 149-158.

Biró, Zs., Lanszki, J., Szemethy, L., Heltai, M., Randi, E., 2005. Feeding habits of feral domestic cats (*Felis catus*), wild cats (*Felis silvestris*) and their hybrids: trophic niche overlap among cat groups in Hungary. J. Zool. 266, 187-196.

Bohn, T., Amundsen, P. A., 2001. The competitive edge of an invading specialist. Ecology 82, 2150-2163.

Borcherding, J., Beeck, P., DeAngelis, D. L., Scharf, W. R., 2010. Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. J. Anim. Ecol. 79, 1101-1112.

Borcherding, J., Hermasch, B., Murawski, P., 2007. Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. Ecol. Freshwat. Fish 16, 198-209.

Borcherding, J., Staas, S., Kruger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Borcherding, J., Sturm, W., 2002. The seasonal succession of macroinvertebrates, in particular the zebra mussel (*Dreissena polymorpha*), in the River Rhine and two neighbouring gravel-pit lakes monitored using artificial substrates. Internat. Rev. Hydrobiol. 87, 165-181.

Borcherding, J., Dolina, M., Heermann, L., Knutzen, P., Krüger, S., Matern, S., van Treeck, R., Gertzen, S., 2013. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. Limnologica - Ecology and Management of Inland Waters 43, 49-58.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., Van Geest, G. J., Grift, R. E., Ibelings, B. W., Oosterberg, W., Roozen, F. C. J. M., 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwat. Biol. 47, 889-907.

Carlsson, N. O., Sarnelle, O., Strayer, D. L., 2009. Native predators and exotic prey-an acquired taste? Front. Ecol. Environ. 7, 525-532.

Charlebois, P. M., Corkum, L. D., Jude, D. J., Knight, C., 2001. The round goby (*Neogobius melanostomus*) invasion: Current research and future needs. J. Great Lakes Res. 27, 263-266.

Clark, C. W., Mangel, M., 1984. Foraging and flocking strategies: information in an uncertain environment. Am. Nat., 626-641.

Colwell, R. K., Futuyma, D. J., 1971. On the measurement of niche breadth and overlap. Ecology, 567-576.

Connell, J. H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat., 661-696.

Copp, G. H., 2008. Putting multi-dimensionality back into niche: diel vs. day-only niche breadth separation in stream fishes. Fund. Appl. Limnol. 170, 273-280.

Dubs, D. O. L., Corkum, L. D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. 22, 838-844.

Eklöv, P., 1997. Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can. J. Fish. Aquat. Sci. 54, 1520-1531.

Gorchov, D. L., Cornejo, F., Ascorra, C. F., Jaramillo, M., 1995. Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. Oikos, 235-250.

Gurevitch, J., Morrow, L. L., Alison, W., Walsh, J. S., 1992. A Meta-Analysis of Competition in Field Experiments. Am. Nat. 140, 539-572.

Hanson, P. C., Johnson, T. B., Schindler, D. E., Kitchell, J. F., 1997. Fish Bioenergetics 3.0 for Windows. University of Wisconsin, Sea Grant Institute, Madison, Wisconsin, USA.

Hardenbicker, P., Rolinski, S., Weitere, M., Fischer, H., 2014. Contrasting long-term trends and shifts in phytoplankton dynamics in two large rivers. Int. Rev. Hydrobiol. 99, 287-299.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Heermann, L., Eriksson, L. O., Magnhagen, C., Borcherding, J., 2009. Size-dependent energy storage and winter mortality of perch. Ecol. Freshwat. Fish 18, 560-571.

Houde, E. D., 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. J. Fish Biol. 51, 52-83.

Houghton, C. J., 2015. Round goby-induced changes in young-of-year yellow perch diet and habitat selection.PhD thesis. University of Wisconsin Milwaukee, 81 pp.

Hyslop, E. J., 1980. Stomach content analysis - a review of methods and their application. J. Fish Biol. 17, 411-429.

James, C. D., 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (Ctenotus: Scincidae) in central Australia. Oecologia 85, 553-561.

Jaroszewska, M., Dabrowski, K., Wilczynska, B., Kakarekok, T., 2008. Structure of the gut of the racer goby *Neogobius gymnotrachelus* (Kessler, 1857). J. Fish Biol. 72, 1773-1786.

Jurajda, P., Cerny, J., Polacik, M., Valova, Z., Janac, M., Blazek, R., Ondrackova, M., 2005. The recent distribution and abundance of non-native Neogobius fishes in the Slovak section of the River Danube. J. Appl. Ichthyol. 21, 319-323.

Karlson, A. M. L., Almqvist, G., Skora, K. E., Appelberg, M., 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64, 479-486.

King, R. B., Ray, J. M., Stanford, K. M., 2006. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. Can. J. Zool. 84, 108-115.

Koblickaya, A. P., 1981. Key for identifying young freshwater fishes (in Russian). Light and Food Industrial House, Moskau.

Kottelat, M., Freyhof, J., 2007. Handbook of European freshwater fishes. Publications Kottelat, Cornol, Switzerland.

Krpo-Cetkovic, J., Hegedis, A., Lenhardt, M., 2010. Diet and growth of asp, *Aspius aspius* (Linnaeus, 1758), in the Danube River near the confluence with the Sava River (Serbia). J. Appl. Ichthyol. 26, 513-521.

Kujawa, R., Mamcarz, A., Skrzypczak, A., Kucharczyk, D., 1998. Feeding habits of asp *Aspius aspius* larvae (Cyprinidae) in Lake Maroz, Poland. Ital. J. Zool. 65, Suppl., 235-236.

Lee, V. A., Johnson, T. B., 2005. Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). J. Great Lakes Res. 31, 125-134.

MacArthur, R. H., Pianka, E. R., 1966. On optimal use of a patchy environment. Am. Nat., 603-609.

Mittelbach, G. G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences [Review]. Can. J. Fish. Aquat. Sci. 55, 1454-1465.

Mooij, W. M., 1989. A key to the identification of larval bream, *Abramis brama*, white bream, *Blicca bjoerkna*, and roach, *Rutilus rutilus*. J. Fish Biol. 34, 111-118.

Nakayama, S., Fuiman, L. A., 2010. Body size and vigilance mediate asymmetric interference competition for food in fish larvae. Behav. Ecol. 21, 708-713.

Neill, W. E., 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. Ecology, 809-826.

Osenberg, C. W., Mittelbach, G. G., Wainwright, P. C., 1992. Two-stage life histories in fish: the interaction between juvenile competition and adult performance. Ecology, 255-267.

Perry, G., Pianka, E. R., 1997. Animal foraging: past, present and future. Trends Ecol. Evol. 12, 360-364.

Persson, A., Brönmark, C., 2002. Foraging capacity and resource synchronisation in an ontogenetic diet switcher, pikeperch (*Stizostedion lucioperca*). Ecology 83, 3014-3022.

Persson, L., 1988. Asymmetries in competitive and predatory interactions in fish populations. In: Eds: B. Ebenman, L. Persson, Size-Structured Populations. Springer-Verlag, Berlin, Heidelberg, pp. 203-218.

Persson, L., Andersson, J., Wahlström, E., Eklöv, P., 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology 77, 900-911.

Persson, L., Greenberg, L. A., 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. Ecology 71, 44-56.

Pilger, T. J., Gido, K. B., Propst, D. L., 2010. Diet and trophic niche overlap of native and nonnative fishes in the Gila River, USA: implications for native fish conservation. Ecol. Fresh. Fish 19, 300-321.

Pinder, A. C., 2001. Keys to larval and juvenile stages of coarse fishes from freshwaters in the British Isles. Freshwater Biological Association, Ambleside.

Polacik, M., Janac, M., Jurajda, P., Adamek, Z., Ondrackova, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecol. Fresh. Fish 18, 640-649.

Popova, O. A., Sytina, L. A., 1977. Food and feeding relations of Eurasian perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*) in various waters of the USSR. J. Fish Res. Board Can. 34, 1559-1570.

Post, J. R., Parkinson, E. A., 2001. Energy allocation strategy in young fish: Allometry and survival. Ecology 82, 1040-1051.

Ross, S. T., 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia, 352-388.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N., Weller, S. G., 2001. The population biology of invasive species. Ann. Rev. Ecol. System. 32, 305-332.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348-360.

Schoener, T. W., 1974. Resource Partitioning in Ecological Communities. Science 185, 27-39.

Schoener, T. W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51, 408-418.

Schoener, T. W., 1983. Field experiments on interspecific competition. Am. Nat., 240-285.

Staas, S., 1996. Anleitung zur Bestimmung von 0+ - Jungfischen aus dem Rhein.Report Ecological Field Station Rees-Grietherbusch. University of Cologne, 14 pp.

Strayer, D. L., 2012. Eight questions about invasions and ecosystem functioning. Ecol. Lett. 15, 1199-1210.

Tilman, D., 1987. The importance of the mechanisms of interspecific competition. Am. Nat., 769-774.

Tonn, W. M., Paszkowski, C. A., Holopainen, I. J., 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. Ecology, 951-958.

Urho, L., 1996. Identification of perch (*Perca fluviatilis*), pikeperch (*Stizostedion lucioperca*) and ruffe (*Gymnocephalus cernuus*) larvae. Ann. Zool. Fennici 33, 659-667.

Van Riel, M. C., Van der Velde, G., Bij de Vaate, A., 2011. Dispersal of invasive species by drifting. Curr. Zool. 57, 818-827.

Vohmann, A., Borcherding, J., Kureck, A., Bij de Vaate, A., Arndt, H., Weitere, M., 2010. Strong body mass decrease of the invasive clam *Corbicula fluminea* during summer. Biol. Invasions 12, 53-65.

Wallace, R. K., 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110, 72-76.

Warren Jr, M. L., Burr, B. M., Tomelleri, J. R., 2014. Freshwater Fishes of North America: Volume 1: Petromyzontidae to Catostomidae, 1 ed. JHU Press.

Werner, E. E., Gilliam, J. F., 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. System. 15, 393-425.

Wiesner, C., 2005. New records of non-indigenous gobies (*Neogobius* spp.) in the Austrian Danube. J. Appl. Ichthyol. 21, 324-327.

Winemiller, K. O., 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environ. Biol. Fish. 26, 177-199.

Wu, Z., Li, Y., Wang, Y., Adams, M. J., 2005. Diet of introduced bullfrogs (*Rana catesbeiana*): predation on and diet overlap with native frogs on Daishan Island, China. Journal of Herpetology 39, 668-674.

Appendix Chapter IV

Table A1. Number of performed beach seinings per light regime and year.

Seinings (N)	Light Regime	2011	2012	2013
April	Day	7	6	12
	Night	0	3	6
May	Day	4	18	25
	Night	3	8	15
June	Day	19	17	18
	Night	9	10	9
July	Day	18	25	24
	Night	9	15	14
August	Day	6	25	18
	Night	3	11	9
September	Day	18	18	18
	Night	10	9	9
October	Day	4	6	18
	Night	0	3	9
Total	Day	76	115	133
	Night	34	59	71
Total		110	174	204

Table A2. Weighted diet overlaps O_{DW} per year, month and species. Bold numbers indicate significant weighted diet overlaps.

Year	Month	Aspius	Nf	Nm	Perca	Pk	Sander
2011	April						
	May	**0.67**	**0.79**	**0.79**	**0.86**		**0.72**
	June	**0.66**	**0.80**	**0.81**	**0.80**	**0.79**	**0.74**
	July	**0.63**	**0.71**	**0.72**	**0.76**	**0.68**	**0.62**
	August	**0.60**	**0.77**	**0.62**	**0.69**	0.50	0.59
	September	0.53	**0.82**	**0.71**	**0.68**		
	October		**0.87**	**0.83**			**0.87**
2012	April						
	May		**0.83**	**0.83**		**0.91**	
	June	0.58	**0.79**	**0.77**	**0.76**	**0.83**	0.56
	July	0.55	**0.80**	**0.76**	**0.65**	**0.75**	**0.62**
	August	0.54	**0.86**	**0.74**	**0.61**	**0.63**	0.55
	September	0.51		**0.77**	**0.68**	**0.62**	**0.65**
	October	**0.80**	**0.88**	**0.79**	**0.73**	**0.77**	0.49
2013	April		**0.87**	**0.78**			
	May		**0.78**	**0.73**			**0.72**
	June	**0.68**	**0.84**	**0.82**	**0.69**	**0.70**	**0.66**
	July	0.58	**0.79**	**0.75**	**0.73**	**0.75**	0.57
	August	0.58	**0.82**	**0.80**	**0.61**	**0.63**	0.49
	September	**0.60**	**0.77**	**0.76**	**0.75**	**0.78**	**0.66**
	October	0.57	**0.87**	**0.82**	**0.70**	**0.82**	**0.68**
	Mean	**0.60**	**0.81**	**0.77**	**0.71**	**0.73**	**0.64**
	SD	0.07	0.04	0.05	0.07	0.11	0.10

Table A3. Results of the linear mixed effect model incorporating year as random effect and month and species as fixed effects.

Random effects	Stand. Dev.
Intercept	0.004839294
Residual	28.17978

Fixed effects	Estimate	SE	DF	t-value	p-value
Intercept	44.28762	28.17978	4199	1.5716098	0.1161
Nf	-9.38462	28.57951	4199	-0.3283686	0.7426
Nm	14.64637	28.34127	4199	0.5167859	0.6053
Perca	-18.99894	30.43764	4199	-0.6241922	0.5325
Pk	-14.80266	32.53921	4199	-0.4549178	0.6492
Sander	-43.07748	34.51304	4199	-1.2481508	0.212
August	-1.60127	28.30311	4199	-0.0565758	0.9549
July	15.65779	28.30419	4199	0.5531967	0.5802
June	13.5031	28.33944	4199	0.4764774	0.6338
May	21.73363	28.78587	4199	0.7550106	0.4503
October	-21.82973	28.47799	4199	-0.7665476	0.4434
September	6.9211	28.64559	4199	0.2416112	0.8091
Nf:August	10.08824	28.83012	4199	0.3499201	0.7264
Nm:August	2.99369	28.54831	4199	0.1048639	0.9165
Perca:August	6.7646	30.68026	4199	0.2204872	0.8255
Pk:August	13.2834	32.84815	4199	0.404388	0.6859
Sander:August	15.10682	34.78718	4199	0.4342641	0.6641
Nf:July	6.05218	28.82436	4199	0.2099677	0.8337
Nm:July	-8.12739	28.53294	4199	-0.2848423	0.7758
Perca:July	-6.55275	30.62458	4199	-0.2139702	0.8306
Pk:July	5.94948	32.76264	4199	0.1815933	0.8559
Sander:July	3.58584	34.74192	4199	0.1032135	0.9178
Nf:June	28.49144	29.02337	4199	0.9816724	0.3263
Nm:June	-2.1275	28.55615	4199	-0.0745024	0.9406
Perca:June	13.54135	30.68371	4199	0.4413207	0.659
Pk:June	19.31808	32.73326	4199	0.5901665	0.5551
Sander:June	15.60003	34.71599	4199	0.4493615	0.6532
Nf:May	-12.29181	29.35124	4199	-0.4187832	0.6754
Nm:May	-23.99576	29.00382	4199	-0.8273311	0.4081
Perca:May	-8.22807	31.38534	4199	-0.2621629	0.7932
Pk:May	-14.39799	33.14819	4199	-0.4343521	0.6641
Sander:May	0.14303	35.18642	4199	0.0040649	0.9968
Nf:October	19.83591	29.02431	4199	0.6834239	0.4944
Nm:October	2.88437	28.67218	4199	0.1005982	0.9199
Perca:October	16.8245	30.9524	4199	0.5435604	0.5868
Pk:October	19.95889	33,26016	4199	0.600084	0.5485
Sander:October	30.85169	35,22972	4199	0.8757289	0.3812
Nf:September	5.2512	29,14077	4199	0.1802012	0.857
Nm:September	-12.24504	28,85605	4199	-0.424349	0.6713
Perca:September	-7.03854	31,09824	4199	-0.2263325	0.821
Pk:September	-3.98377	33,1437	4199	-0.120197	0.9043
Sander:September	5.95627	35,23753	4199	0.1690321	0.8658

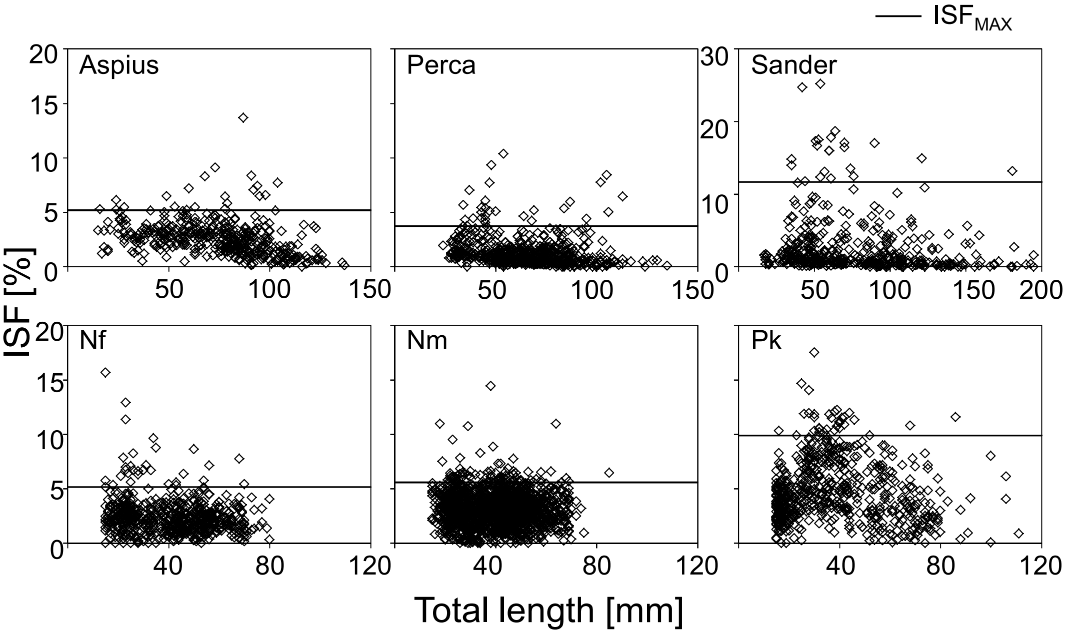

Figure A1. ISF values of the single species in relation to total length of all analyzed individuals. The line represents the ISF_{MAX} (median of the highest 10 % of all ISF values).

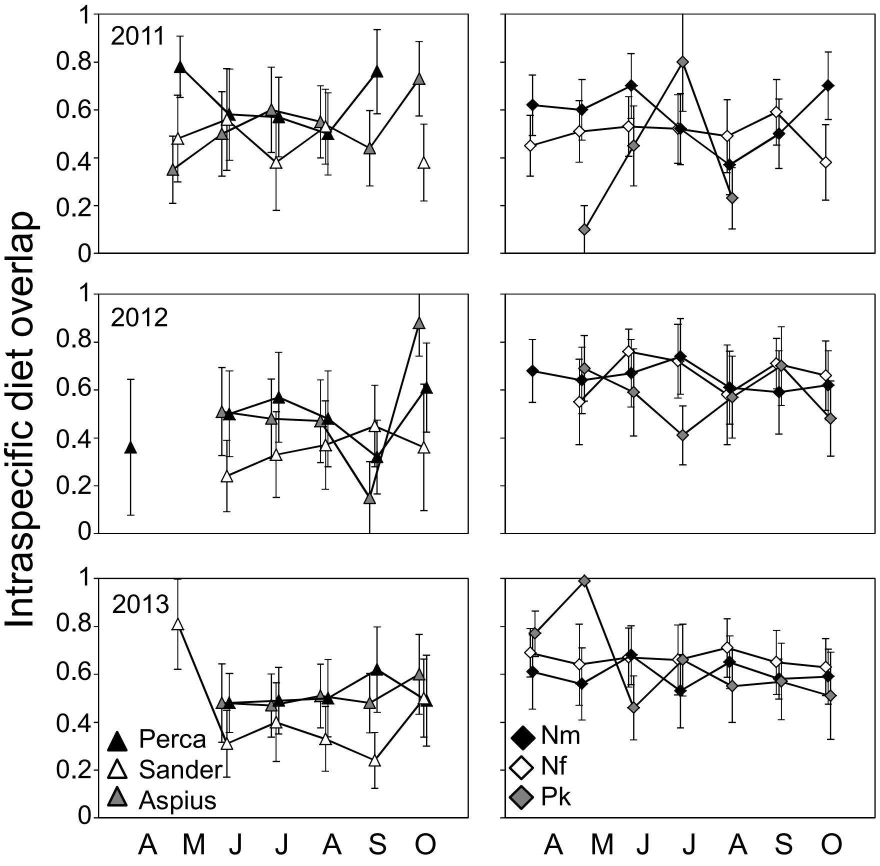

Figure A2. Intraspecific diet overlap for native (left) and invasive species (right) in course of the season for the three investigated years. In case that more than 50 individuals were analyzed per month, 50 individuals were randomly chosen to calculate the intraspecific diet overlap.

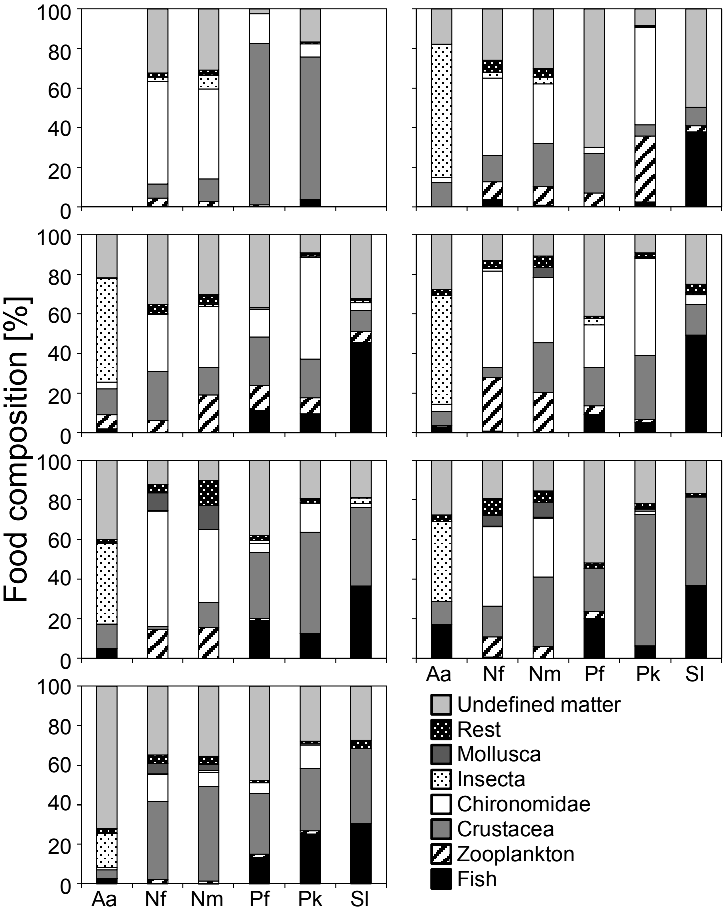

Figure A3. Monthly diet composition of the six species in course of the season (April upper left – October bottom left). Shown are the relative proportions of the most common food categories fish, zooplankton, Crustacea, Chironomidae, Insecta, Mollusca, the rest (=all other categories) and the amount of undefined matter.

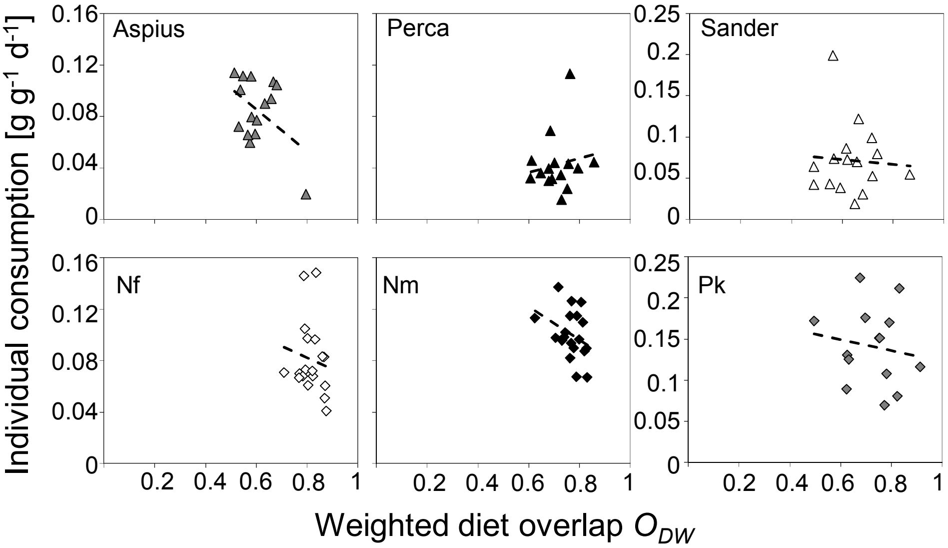

Figure A4. Relationship between individual consumption and weighted diet overlap for the single species. Every point represents one month (Apr – Oct) of one of the three years.

CHAPTER V

Are invasive gobies a beneficial prey? – Two native predators adapting to novel prey fshes in varying extent and pace

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Abstract

Detrimental effects of invasive gobies on juveniles of native Percidae could be shown at the Lower Rhine, by forcing those into a juvenile competitive bottleneck. As predation might be one key for long-term regulation of invasive species, the extent of gobies in the diet of two Percidae, Eurasian perch, *Perca fluviatilis,* and pikeperch, *Sander lucioperca*, was analyzed for individuals of all length classes five to eight years after introduction. Besides differences in the onset and extent of piscivory between both Percidae in general, strikingly diverse patterns of adaptation were observed. Piscivory was low for small perch individuals, yet gobies were already included in the diet. Further, perch switched earlier to an exclusively piscivorous diet than observed elsewhere by feeding almost exclusively on round gobies *Neogobius melanostomus*. Pikeperch in contrast included fish to a great extent already in the smallest size class, but favored native prey during early ontogeny. Later on, pikeperch preyed to equal amounts on gobies (all three species) and several native species, showing no selectivity at all. A strong increase in predation on gobies was observed for the last year (2014), going along with significantly increasing condition of perch and pikeperch. Although first signs of adaptation are obvious, this process has apparently just started and might yet not diminish the negative competitive effects of invasive gobies on juvenile Percidae. If youngest 0+ individuals of perch and pikeperch would also adapt to this novel prey and adult specimens would keep on preying to a great extent on gobies, this could counteract the hyper-abundance of invasive Gobiidae and reduce levels of competition effectively.

Keywords: *Perca fluviatilis* * *Sander lucioperca* * Gobiidae * invasion process * condition

Introduction

Due to increasing globalization the quantity and pace of invasion processes has increased dramatically and become one of biodiversity's greatest threats (Ricciardi and MacIsaac, 2000; Novacek and Cleland, 2001; Clavero and Garcia-Berthou, 2005; Meyerson and Mooney, 2007). Not only environmental, but also economic and even human health detriments can be the consequences of successful invasions (Pejchar and Mooney, 2009). Such negative effects of non-native species in their new environment have been studied quite well across a broad range of taxa (Lowe et al., 2000; Clavero et al., 2009). Especially direct species interactions as competition with, or predation on endemic species are well documented (e.g., Human and Gordon, 1996; Brown et al., 2002; Beisner et al., 2003). As both, competition and predation, are strong structuring forces for communities (Sih et al., 1985), this can finally result in the displacement of the native species (e.g., Mooney and Cleland, 2001). Further, as non-natives often occur in heavily raised abundances, a disruption of the whole food web is possible (Vander Zanden et al., 1999; Roemer et al., 2002). Thus, not only the impact on prey specimens or resources can be enormous and result in exploitation, also other species might be directly or indirectly concerned, affecting several trophic levels.

Such comprehensive effects of invasions are especially severe in isolated ecosystems like islands. A prominent example is the accidental introduction of the brown treesnake *Boiga irregularis* in Guam (Rodda and Fritts, 1992), which led to several extirpations of birds, bats and reptiles (Rodda et al., 1997). In combination with other factors increasing the vulnerability of Guam, the consequences were really dramatic, mainly due to a missing coevolution between predator and native prey specimens, that even fostered the further establishment and population growth of more aliens (Fritts and Rodda, 1998).

Besides those negative effects, impact of invasive species can also facilitate natives under certain circumstances (Rodriguez, 2006). Mostly, facilitation occurs indirectly as for the invasive Asian hornsnail *Battilaria attramentaria*, which obliquely promotes densities of native mudflat species by grazing effects and bioturbation (Wonham et al., 2005). But facilitation can also act directly, e.g., when the invasive species represents a limiting resource (Rodriguez, 2006). Urban butterflies in California for example breed almost exclusively on alien plants (Shapiro, 2002), and invasive gypsy moths seem to improve native cuckoo populations as hyper abundant prey during outbreak years (Barber et al., 2008).

Predation mortality in fishes is often underestimated (Tyrrell et al., 2011), but predator-prey interactions play an important role in keeping the ecosystem at a stable state and can result in trophic cascades if major changes, like the introduction of a new prey species, occur (Barrientos et al., 2014). In cases where the prey was the introduced species, predation might have been the reason of colonization failure, or, when colonization already proceeded, predation may be the factor allowing for co-existence of competitors by limiting invasive species densities (Lodge, 1993). Additionally, predation is assumed to potentially hinder the further spread of non-natives (deRivera et al., 2005).

However, it can take some time for native predators to increase their own population and to adapt to prey efficiently on a novel prey species (Carlsson et al., 2009; Carlsson et al., 2011). Thus, before adaptation, predation might even facilitate non-natives in the first place by reducing potential native competitors and rejecting the novel prey (Simoncini and Miller, 2007). Adaptation on prey species can act on several levels, like phenotypic plasticity, learning, social transmission and evolutionary mechanisms (Agrawal, 2001; Carlsson et al., 2009), thus operating on a small time scale up to several generations. Whereas some native predators could directly feed on introduced prey items, as they fit into their natural feeding capabilities and habits (e.g., Kelleher et al., 1998), other predator-prey interactions take generations to be effective (e.g., Lopez et al., 2010). For instance, the Australian black snake (*Pseudechis porphyriacus*) had first to evolve a resistance to the toxin of the introduced cane toad *Bufo marinus* before it could prey on it (Phillips and Shine, 2006). As predation of invasive species is primarily beneficial for the native predator (Carlsson et al., 2009), predation on invasive species might secondarily also led to negative effects for other native species, if the predator population increases and native prey items are increasingly included into the predator´s diet (Noonburg and Byers, 2005).

All these examples provide evidence that it is necessary to analyze the biotic interactions of an invasive species in a new habitat to accurately assess the ramifications. At the Lower Rhine four invasive Gobiidae from the Ponto-Caspian area have established self-sustaining populations, of which three occur in high densities (Borcherding et al., 2011; Borcherding et al., 2013). Detrimental effects of gobies, especially round goby *Neogobius melanostomus*, have been well documented, including changes in the food web, like decreasing macroinvertebrate diversity (Kipp et al., 2012), as well as competition for food and spawning sites with native species (Chotkowski and Marsden, 1999; Janssen and Jude, 2001). Further, exploitative competition between gobies and native species could be shown to result in juvenile competitive bottlenecks (Karlson et al., 2007). In fact, this mechanism seems to act on the native predators in the Lower Rhine as well (Chapter IV). By forcing the juveniles into this devastating situation, it gets even more important to assess levels of predation of those concerned species to evaluate if predatory interactions could potentially outweigh the competitive losses during early ontogeny.

Positive impacts could be shown for native fish predators consuming round gobies in the Great Lakes, showing a better body condition and increased growth rates after the invasion (Steinhart et al., 2004; Crane et al., 2015). Further, a threatened water snake in the USA displayed higher growth rates and larger sizes after preying on round gobies and this occurred just within one or two snake generations (King et al., 2006). Thus, adaption on this novel prey is assumed also likely to occur at the Lower Rhine five to eight years after invasion.

While many studies focus on one predator species interacting with one prey species, this study includes two piscivorous predators, Eurasian perch, *Perca fluviatilis,* and pikeperch, *Sander lucioperca*, as well as three invasive goby species (bighead goby *Ponticola kessleri*, monkey goby *Neogobius fluviatilis* and round goby *N. melanostomus*), all co-occurring at the Lower Rhine. In this stage-structured predator-prey system, levels of competition could already be shown to be extraordinarily high in juvenile stages and to counteract the development of young of the year Percidae by forcing those into a juvenile competitive bottleneck (Chapter IV). The present study now focusses on the extent and impact of predation on gobies in this system, to round out the picture of competitive/predatory interactions in fish communities at the Lower Rhine. Therefore, the main aim of this study was to define the proportion of gobies in the diet of two native predators during their ontogeny and to search for patterns of adaptation to this novel prey in the course of the years. As a proxy for changes within the group of predators, condition of Percidae was analyzed for each length class, as the results should finally help to predict the outcome of the interactions between the invasive gobies and native predators: displacing competitors or beneficial prey?

Material and Methods

Fish origin

All fishes were caught at the Lower Rhine (Germany) close to the city of Rees (Rhine-km 831-845). A combination of different fishing methods was used to get access to the different species and length classes. While juveniles of both species were mainly caught with beach seining in sandy groin fields of the River Rhine, adults were fished via angling or electro-fishing. Beach seining in the sandy groin fields, which served as nursery habitat for native species as well as for invasive gobies, was regularly conducted from 2011 to 2013 several times per month (April – October) and at different daytimes (morning 9 am, afternoon 3 pm and at night 8-11 pm, cf. Gertzen et al., 2016). In 2014 beach seining frequency was lowered, but still included samplings from different months and daytimes. To ensure the capture of different size classes, two nets with varying lengths and mesh sizes were used (10 m x 1.5 m, mesh size 1 mm; 15 m x 1.5 m, mesh size 4 mm), which were hand-dragged against the current. Electro-fishing was performed in the riprap areas surrounding those groin fields with a portable backpack gear (maximum output 225-300 V, frequency 55–75 Hz, dip net anode 40 x 20 cm, mesh size 4 mm, SEN f.Bednar, Czech Republic) at least twice a year and also including different daytimes. To catch large, adult predators not accessible via seining or electro-fishing, angling was executed at several sites in irregular intervals across the four years. Here, various baits mainly for spin fishing were used. All individuals up to 50 mm total length (TL) were preserved in ethanol right on site, whereas larger individuals up to 200 mm were placed on ice and rapidly frozen at -18°C. Specimens exceeding 200 mm in TL were expertly killed directly after catching, before their innards including the stomach were removed and transferred into ethanol.

Table 1. Number of analyzed fish per species and length class (TL, mm).

Species	<50 mm	<100 mm	<150 mm	<200 mm	<250 mm	>250 mm	Total
Perca fluviatilis	142	410	99	24	11	18	704
Sander lucioperca	132	212	99	43	15	59	560

Gastrointestinal analyses

In total, 1,264 specimens (704 perch, 560 pikeperch), with a size range from 24 to 520 mm TL for perch and 17 to 720 mm TL for pikeperch, respectively, were dissected and their stomach content analyzed (Tab. 1). For every individual, total length was measured to the nearest 1 mm and wet weight was noted before the stomach was removed from the body cavity, freed from other organs and weighted (nearest 0.0001 g, stomach full S_f). Then the contents were carefully removed or flushed out and the empty stomachs were reweighted (stomach empty S_e). All items were classified to the lowest taxonomic unit possible. Especially fish prey was thoroughly examined and, in case the digestive process allowed for it, prey total length was also noted, before the proportion of all items to the whole content was visually estimated (Polacik et al., 2009). For quantitative objectives the wet weight of the contents (S_c) [1], the index of stomach fullness (ISF, Hyslop, 1980) [2], as well as the adjusted condition factor *K* (Borcherding et al., 2013) [3] were determined as follows:

[1] $S_c = S_f - S_e$

with S_c = wet weight of stomach content [g], S_f = wet weight of full stomach [g], and S_e = wet weight of empty stomach [g].

[2] ISF [%] = $\frac{Sc}{W-Sc} * 100$

with W = wet weight of the fish [g].

[3] $K = 10^5 \times \frac{W-Sc}{TL^{\wedge}-3}$

with TL = total length of the fish [mm].

Data proceedings and statistics

All analyzed fishes were divided into six length classes, representing their total length in 50 mm steps. This classification was justified as between those length classes differences in all forms of diet choice (including ontogenetic diet shifts) were most obvious. The last length class included all individuals being larger than 250 mm TL, as no further shift or the like could be obtained, and of course catching rate strongly decreased with increasing total length. For diet composition analyzes specimens with an empty stomach were excluded. 3.5 % of all 704 perches had an empty stomach (25 individuals, Tab. 2.), while for pikeperch the share was slightly higher with 30 out of 560 analyzed stomachs being empty (5.4 %). For all remaining individuals the mean percentage of all food categories was calculated per length class and species.

Table 2. Number and percentage of analyzed fish per species, amount of empty tracts and piscivorous specimens segmented into prey categories (undefined fish, native or invasive fishes). Percentages refer to the total amount of analyzed individuals, except * = percentage of fish prey, ** = percentage of identifiable fish prey.

	Perca		Sander	
	N	%	N	%
Total	704		560	
Empty tracts	25	3.5	30	5.4
Fish prey	198	28.1	303	54.1
Fish undefined*	108	48	177	52
Native fishes**	11	11.5	66	48.2
Gobiidae**	83	88.5	71	51.8

Prey predator ratio (PPR) data, condition values and data on the yearly proportion of gobies in the diet of perch and pikeperch were neither normal distributed, nor revealed homogenous variances, thus non-parametric Kruskal-Wallis tests were applied to search for significant differences. In case of significance, Wilcoxon-tests between the single groups (species, length classes, years, prey categories) were performed to specify differences.

Results

Diet composition

Most important food items for the smallest length class of perch (up to 50 mm TL) were insect larvae (22.2 %, mainly Chironomidae), Crustacea (16.6 %, mainly the invasive amphipod *Dikerogammarus villosus*), and zooplankton (15.9 %), whereas fish was only consumed to a low amount (7 %, thereof 1.4 % Gobiidae, Fig. 1). In contrast, for pikeperch fish was already the main prey category in the smallest length class (38.7 %), followed by Crustacea (12.2 %) and Insecta (8 %). An increase in piscivory for perch was observed at sizes larger than 100 mm (61.9 %), where additionally only Crustacea was of importance as prey category (18.1 %). Finally, at a size greater than 150 mm TL, fish became the only relevant prey category of perch (> 90 %). For pikeperch Crustacea remained an important prey category up to length class four (200 mm TL, 35 %). The proportion of fish as prey category did not vary from 100 mm TL up to 200 mm TL (46 – 50 %), but a considerable increase could be observed for the next length classes (> 200 mm), where fish always contributed more than 83 % of the pikeperch's diet.

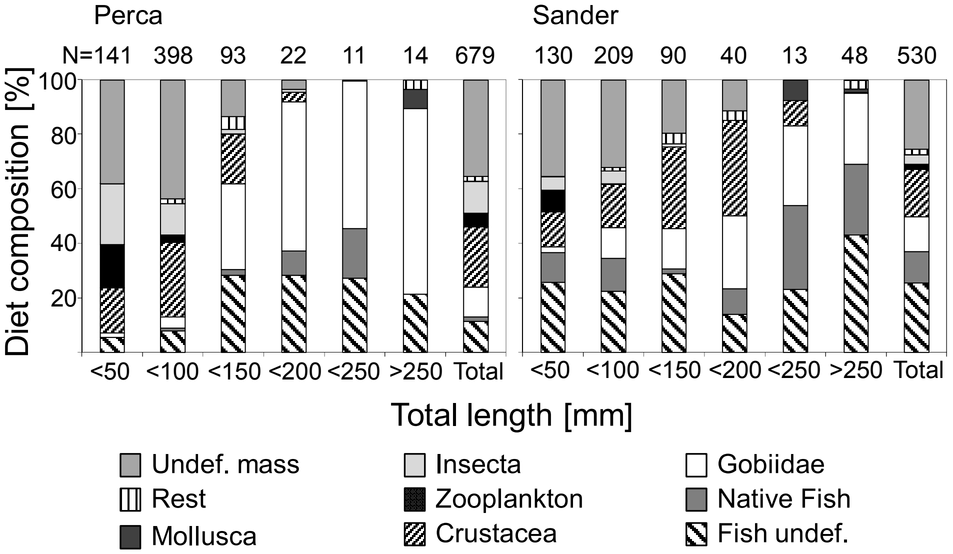

Figure 1. Diet composition of perch (Perca, left) and pikeperch (Sander, right) for the different length classes and for all individuals analyzed (total), excluding individuals with empty stomachs. Number of analyzed specimens per length class is shown above bars.

198 out of 704 analyzed perches preyed on fish, half of those prey items were still identifiable and could either be classified as Gobiidae or native species, with Gobiidae clearly being the dominant prey type (gobies: 88.5 %, natives: 11.5 %, Tab. 2). Contrary, of 303 pikeperches with fish as prey, and whereof also half of the items were identifiable, this species picked native fishes as often as gobies (52 % Gobiidae, 48 % native fishes). For length class 1 of perch all fish items that could

clearly be identified were invasive gobies, and from then on, gobies always contributed to a much greater share than natives regardless of length class. For pikeperch, fish already was a main category for length class 1, but only 2 % was made up by gobies compared to 10.9 % of native prey. For length classes 3 and 4 (individuals from 100-200 mm TL) gobies even prevailed in the diet of pikeperch, but natives were also still included in the diet. For the other length classes, gobies and natives were preyed upon equally.

Differences between the two predators could not only be obtained in the choice of endemic or invasive species, but also within the group of invasive gobies. Perch preyed almost exclusively on the most abundant round goby (27 out of 28), as only one goby could be identified as monkey goby. Pikeperch by contrast preyed upon both, round (52 %) and monkey goby (39 %), and also included the third gobiid species bighead goby (10 %). Additionally, the native fishes taken by pikeperch were represented by several taxa involving different Cyprinidae (deep-bodied and shallow-bodied species), Percidae (also cannibalistic acts) and three-spined stickleback *Gasterosteus aculeatus*. Thus, the perch population at the Lower Rhine clearly included round goby into its diet and fed almost exclusively on this species when reaching piscivorous stages (see also Costello plots, Fig. A1). Pikeperch on the other hand preyed less on gobies by ingesting native species equally (Fig. A2), and further showed no preference for single species.

Prey spectrum and PPR

Earliest piscivory of perch was observed for an individual of 37 mm TL, for pikeperch smallest piscivorous size was 30 mm TL. Fish prey size spectrum ranged from 6 mm up to 114 mm TL for perch and between 5 mm and 160 mm TL for pikeperch. Native fishes that were consumed by perch had significantly larger prey predator ratios than gobiid prey taken by perch (Wilcoxon p=0.018, Fig. 2), whereas for pikeperch no difference could be detected, neither between natives and Gobiidae (Wilcoxon p=0.150), nor between the single goby species (Wilcoxon Nm-Nf p=0.307, Nm-Pk p=0.105, Nf-Pk p=0.278).

Overall PPR of pikeperch (0.262 ± 0.11) was slightly greater than for perch (0.231 ± 0.09), but interestingly prey predator ratios increased during ontogeny for perch (Wilcoxon LC 2 - 5 p=0.007, Fig. 3), while for pikeperch it was the other way around (Wilcoxon LC 2 - 5 p=0.044). PPR for perch and pikeperch differed the greatest for length class two, with pikeperch having a PPR almost twice the ratio of perch (pikeperch: 0.362 ± 0.11; perch: 0.199 ± 0.09; Wilcoxon p=0.0002), whereas for the greater length classes ratios approximated each other. Solely the last length class of perch showed no further increase, yet, this isn´t surprising, as this group includes all individuals being larger than 250 mm TL up to very huge specimens (520 mm TL).

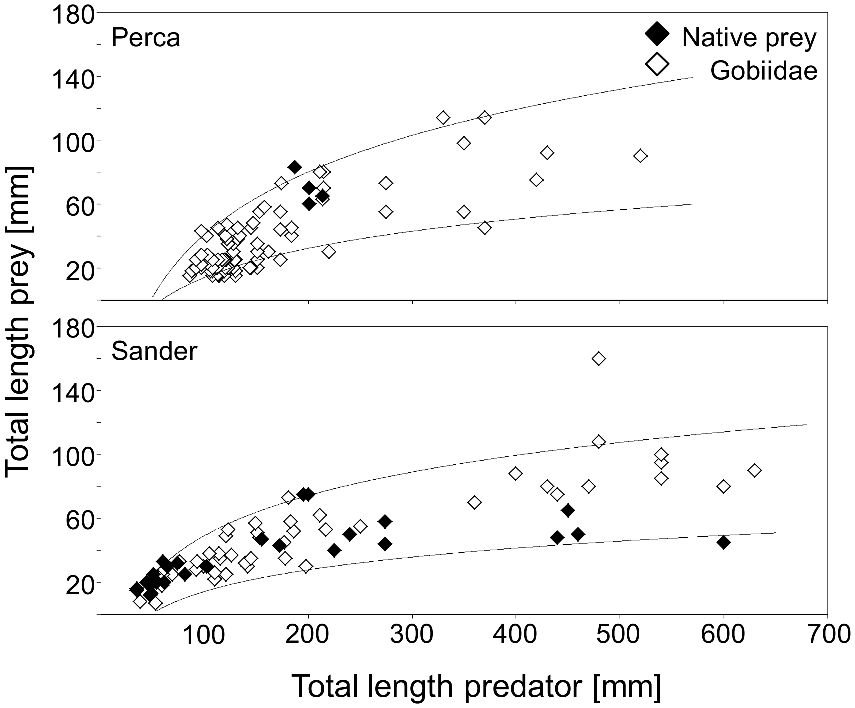

Figure 2. Prey predator ratio for all consumed fishes that could be defined as either Gobiidae (white rhombuses) or native species (black rhombuses) for perch (above) and pikeperch (bottom). Upper and lower boundaries were fitted by eye.

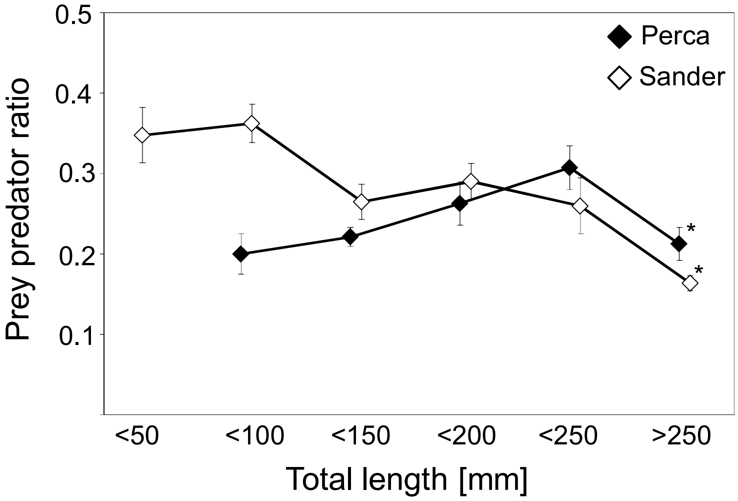

Figure 3. Mean prey predator ratio (± SE) for the different length classes of perch (black) and pikeperch (white). *= Note that the last length class has no defined end, and thus includes also very large individuals.

Condition

For both species condition increased with total length, as expected for fish species, which grew positive allometrically (exponent b of length-weight regression >3). Additionally the pattern was more distinct in perch, as here the exponent had a greater difference from 3 (Perca: b= 3.33, Sander: b= 3.16, Fig A3). However, for perch, condition also increased for the length classes (individuals up to 200 mm TL) in the course of the years (Fig. 4). Greatest improvement was seen for length class 1 of perch, which increased significantly from 0.7 ± 0.09 (2011) to 0.93 ± 0.06 (2014, Wilcoxon $p<0.0001$). The enhancement of length class 2 was also significant between 2011 and 2014 (Wilcoxon $p<0.0001$). For specimens between 100 and 150 mm TL at least the trend was detectable of an increasing condition from 2011 to 2014 (Wilcoxon $p=0.067$). For the fourth length class of perch no significant improvement could be detected, as here the number of caught individuals for 2011-2013 was too low to receive trustable results. The same pattern, although less pronounced, could be observed for pikeperch. Here, greatest changes were detectable for individuals between 50 and 100 mm TL from 0.52 ± 0.06 (2011) to 0.65 ± 0.12 (Wilcoxon, $p=0.0006$), followed by the smallest specimens (< 50 mm TL) from 0.53 ± 0.05 (2011) to 0.64 ± 0.05 (2014, Wilcoxon $p=0.0012$). The third length class showed stable condition values for 2011 to 2013 followed by a significant increase from 2013 to 2014 (Wilcoxon $p=0.003$). For the fourth length class of pikeperch condition even showed a decreasing trend from 2011 to 2013, but then increased significantly from 2013 to 2014 (Wilcoxon $p=0.0011$).

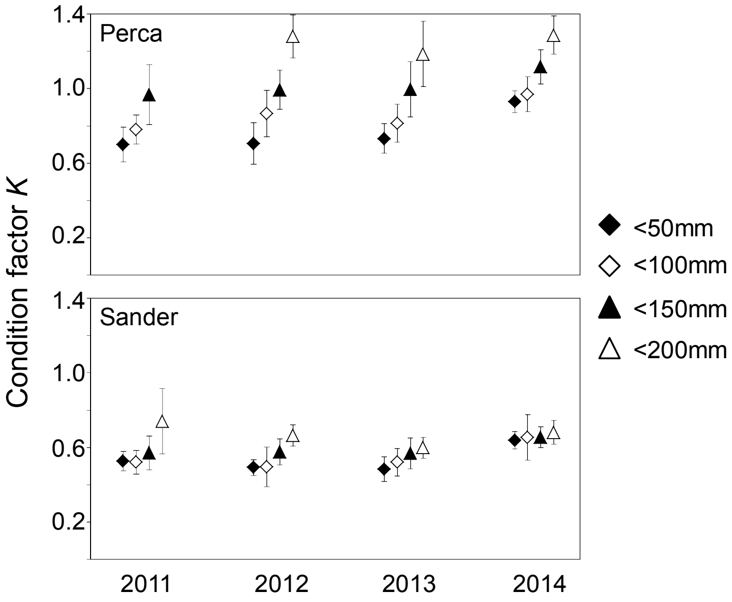

Figure 4. Adjusted condition factor K (mean ± SD) of the first four length classes of perch (above) and pikeperch (bottom) for the four analyzed years 2011 – 2014.

Annual predation on gobies

The proportion of gobies in the diet of perch and pikeperch changed dramatically in course of the years (Fig. 5). For the smallest individuals of perch (< 50 mm TL) predation on gobies was almost non-existent, with proportions ranging from 0 % (2012-2014) to 3 % (2011). Proportion of gobies in the diet of perch from length class 2 to 4 was also relatively low for the first three years, 2011 to 2013 (< 11 %). However, in 2014 a sharp increase for specimens from 100 to 200 mm TL could be observed, with gobies making up more than 48 % in the diet of those length classes. Greatest rises occurred for length class 2 from 5.2 % in 2013 up to 47.5 % in 2014 and for length class 3 from 10.7 % in 2012 up to 50.4 % in 2014. Significant differences could thereby be obtained for length classes 2 and 3 with 2014 differing from all the other years (Wilcoxon, LC2: 2011-2014 $p<0.0001$, 2012-2014 $p<0.0001$, 2013-2014 $p<0.0001$; LC3: 2011-2014 $p=0.047$, 2012-2014: $p=0.0003$, 2013-2014 $p=0.0084$). For pikeperch goby predation was already more pronounced in the preceding years. Especially in 2012 the proportion of gobies was higher than for perch, with length class 2 reaching values of 19 % and for length class 4 proportion of gobies in the diet even reached 43 %. Further, share of gobies in the diet of the smallest individuals peaked in 2012 with 5 %, thus being slightly higher than values obtained for perch, however, also being low in general. Nevertheless, a strong increase of goby prey in 2014 could be seen for length classes 3 and 4 reaching values of 54 % (LC4, Wilcoxon 2013-2014 $p=0.019$) and tremendous 77 % (LC3), differing significantly from the preceding years (Wilcoxon LC3: 2011-2014 $p=0.0002$, 2012-2014 $p<0.0001$, 2013-2014 $p<0.0001$).

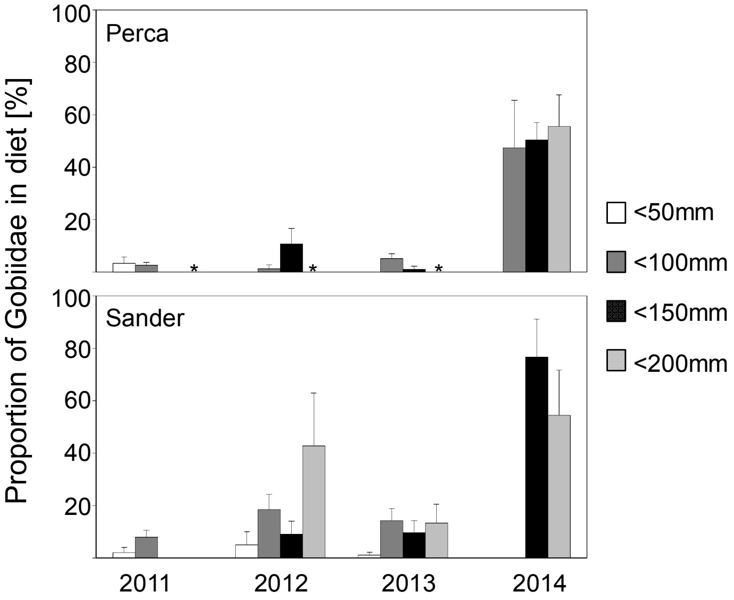

Figure 5. Proportion of Gobiidae in the diet of the first four length classes of perch (above) and pikeperch (bottom). *= Less than four individuals of this size class, thus data are not shown.

Discussion

The present study showed how two predators of the same family adapt to a novel and abundant prey in varying extent and pace. Further, the addition of those invasive species in the diet spectrum seemed to be advantageous, as an improvement in condition went along with increasing predation on Gobiidae.

Earliest onset of piscivory was for both species comparable to other areas (Van Densen, 1985; Mehner et al., 1996), but the extent of piscivory varied considerably. Fish was already the main prey category for the smallest length class of pikeperch, but then no obvious increase was observed for the following length classes. The ontogenetic switch to a piscivorous diet in pikeperch is related to zooplankton densities, which promote the growth of 0+ pikeperch to a size advantage over their possible prey fishes and further to the continuous availability of prey sizes (Persson and Brönmark, 2002). Usually, the diet of pikeperch larger than 100 mm TL is described as exclusively piscivorous (Van Densen, 1985; Buijse and Houthuijzen, 1992), while in the present study, fish only made up 45 % of all consumed prey for pikeperch between 100 and 150 mm TL. Not until sizes exceeding 200 mm the proportion of fish increased to 84 %. For perch in contrast, diet was already exclusively piscivorous at a size of 150 to 200 mm TL. For this species, piscivory also strongly depends on the availability of suitable prey fishes (Borcherding et al., 2010), but is seldom absolute, as this generalist feeder can also prey on macrozoobenthos or even switch back to zooplanktivory if here densities are increased (Van Densen et al., 1996). As an example, 71 % of fish biomass as prey was observed for 91-115 mm 0+ perch when 0+ bream was a highly abundant prey (Beeck et al., 2002), whereas onset of piscivory can also be delayed up to the second or even third summer depending on the moment when high densities of prey fishes occur (Van Densen et al., 1996). Overall, switch to an exclusively piscivory for perch was earlier than for pikeperch at a size of > 150 mm TL, whereas predation on fish for the smaller length classes was negligible. In contrast, for pikeperch piscivory already occurred for the smallest individuals, but the switch to an exclusively piscivorous diet was somewhat delayed.

The onset of piscivory strongly favors growth and survival of 0+ Percidae (Buijse and Houthuijzen, 1992; Beeck et al., 2002). Further, early onset of piscivory reduces intra- and interspecific competition by intraguild predation (Polis et al., 1989; Polis and Holt, 1992; Borcherding et al., 2010), which is considered to possibly result in stable states in case of invasion processes with booming abundances of non-native species (Bampfylde and Lewis, 2007). The smallest length class of perch preyed already on gobies, but the extent was pretty low. Pikeperch in contrast, showed higher piscivorous rates for the smallest individuals, but clearly picked native species over gobies at this size. Thus, intraguild predation acts on gobies with juvenile Percidae as predators at the Lower Rhine, yet, predation of small individuals on gobies, or fish in general was still modest.

Once both predators have started to prey on fish, they also strongly differed in the choice of prey. Perch fed almost exclusively on round gobies, the goby species with the highest densities (Borcherding et al., 2013), revealing a strong selectivity for this species (compare Costello plots, Fig. A1), which might be a potential adaptation to the hyper abundance of this species (Carlsson et al., 2009). In contrast, pikeperch showed no selectivity at all; neither between gobies or natives, nor for a single species or habitus. In other studies, active prey choice of pikeperch could be shown for single species (Van Densen, 1985; Greenberg et al., 1995), as well as for size, selecting for smaller individuals (Turesson et al., 2002).

Selective predation is a common feature of most predators and can depend on various factors, like prey density, habitat complexity, prey size, prey morphology, prey and/or predator behavior or morphological constraints of the predator itself (Wankowski, 1979; Eklöv and Hamrin, 1989; Greenberg et al., 1995; Heynen et al., 2014). Further, specific morphological prey characteristics can be preferred or rejected, like the preference of shallow-bodied over deep-bodied prey fish or the avoidance of prey fishes with spines or spiny fin rays (Hoogland et al., 1956; Fuiman and Magurran, 1994; Nilsson and Brönmark, 2000). Contrary to other regions, this seems not to act on pikeperch at the Lower Rhine, as it consumed prey from several families and body morphologies including cannibalism.

With increasing total length, prey predator ratios of pikeperch decreased as could be shown in other studies (Dörner et al., 2007), thereby displaying a familiar range of PPRs (Turesson et al., 2002), while for perch an increase was detectable up to a size of 250 mm TL. Persson et al. (2004) assumed a PPR of 0.16 as optimum for perch, a value that comes close to the PPR for perch between 50 and 100 mm TL, but is much lower as the PPR observed here for larger perch. Nevertheless, all obtained PPRs are beneath the upper limit quoted for perch piscivory (Persson et al., 2004). Due to the reversed trends of PPRs during ontogeny, small pikeperch (up to 100 mm TL) preyed upon much larger prey items than perch of the same size, with prey-predator ratios being almost twice as great. This is contrary to other studies, where prey sizes of different piscivores were pretty similar at the same total length (Mittelbach and Persson, 1998) or even increased differentially in relation to increasing size (Scharbert, 2009). However, this might be an explanation why early predation (LC 1 and 2) occurred to a greater extent in pikeperch, as this species was able to ingest a much larger prey size spectrum. Additionally, all identified prey items of small perch were invasive gobies of very small sizes, being smaller than the native species that were preyed upon by pikeperch.

Native species ingested by perch were larger than gobies. It is a common phenomenon that piscivores feed on prey smaller than the maximum ingestible size (e.g., Nilsson and Brönmark, 2000; Turesson et al., 2002), as capture success and energetic constraints of feeding and digestion are often higher for smaller prey individuals when occurring in higher densities (Lundvall et al., 1999). Additionally, satiation might restrict predators to passively choose smaller prey, especially if encounter rate is high (Turesson et al., 2006). Gobies represent an abundant prey at the Lower Rhine and occur in all size classes across the whole season, as at least round and monkey goby reproduce from mid-March up to the mid-September (Gertzen et al., 2016). In contrast, most native fishes spawn at the beginning of the season only, and the majority of them even in the backwaters that may not always be connected, especially in summer, thus, diminishing the availability of these potential prey species (Molls, 1999; Grift et al., 2003; Borcherding and Staas, 2008; Scharbert and Borcherding, 2013). This eventuates on the one hand in one size-cohort which is continuously growing in the course of the season and thus might exceed the predation window (e.g., as shown for roach in contrast to bream, cf. Heermann and Borcherding, 2013), and further results in a decreased availability of freshly hatched prey fishes at the beginning of the season. Additionally, small sized species are quite rare at the Lower Rhine, as they also prefer the backwaters (Borcherding and Staas, 2008; Scharbert and Borcherding, 2013). Thus, selection of smaller gobies than native prey in perch might rather be the result of an increased availability of small prey fishes in general and not a positive selectivity for gobies. Nevertheless, this might be the onset for an adaptation on this novel prey, as the same phenomenon could also be obtained for the endangered water snake in the US by picking gobies being much smaller than the native prey consumed (gobies: 65 g versus native: 200 g, King et al., 2006). Similar, 0+ bluefish fed on smaller shrimps than maximum edible shrimp sizes or fish prey, as handling time was higher for shrimps compared to fish, but could be compensated by ingesting the more abundant smaller shrimps (Juanes et al., 2001). Thus, it might be that handling time for the novel goby prey was also higher than for native species, but went along with an increased encounter rate. Indeed, it is a common incidence for predators that capture success is lower when exposed to a novel prey, but strongly increases with experience (e.g., Werner et al., 1981; Wainwright, 1986). However, it remains speculative and clearly needs further investigations, if it is an active prey choice in perch or a passive selection determined by prey size dependent encounter rate and capture success.

The increase in condition for both predatory species seems to correlate with the extent of predation on invasive gobies. Thus, improvement was greater for perch, which preyed almost exclusively on gobies. Indeed, an increase in growth rates going along with attainment of larger body sizes was also obtained for an endangered colubrid snake after preying intensively on round gobies (King et al., 2006). In addition it was suggested that round gobies might have facilitated the step to piscivory for juvenile smallmouth bass (*Micropterus dolomieu*) in Lake Erie due to their high densities (Steinhart et al., 2004). This might also occur for perch, as this generalist switched relatively early and stable to an exclusively piscivorous diet. Additionally, first piscivorous items were gobies, which were considerably smaller than native species at the same time (Gertzen, unpublished results). Before the sharp increase of goby prey in 2014, crustaceans were the dominant prey of perch of length classes 1 to 3, giving another hint that native prey fishes of suitable sizes were not as abundant that perch switched to early piscivory (cf. Borcherding et al., 2010 with 0+ bream as prey). Onset of piscivory was earlier in pikeperch but the switch to an entire piscivorous diet was thereafter delayed compared to other regions (Van Densen et al., 1996).

The condition of the smallest perch and pikeperch increased as well, without ingesting obvious amounts of gobies. This might have several reasons; first, fish prey might have been higher than observed, as empty stomachs, which could also be considered as possible fish feeders (cf. Scharbert, 2009) and non-identifiable fish prey items, which made up a great share, were not included in analyses. Second, competition might have already been decreased by larger Percidae preying on gobies, thus reducing the competitors of their smaller siblings (Heermann, 2008). Thirdly, an increased fitness in large predators might also result in fitter offspring, as larger, viable eggs can be the consequence of an increase in body condition (Scott et al., 2006 and references therein).

The unselective diet of pikeperch regarding fish species or habitus allowed earlier predation on gobies for at least some individuals in the course of the years compared to perch. Yet, while perch forages co-operatively and seems to profit from group foraging (Eklöv, 1992; Nilsson et al., 2006), at least in smaller sizes, for pikeperch no interactions with conspecifics are known to occur during hunting, and capture success seems to be unaffected by group size (Nilsson et al., 2006). Social learning can lead to a faster adaptation on the novel prey (Brown and Laland, 2003). Thus, social enhancement of foraging in perch might be the reason why such a large proportion of adult perch “suddenly” fed on gobies, but only a specialized fraction of the pikeperch population (compare Costello plots, Fig. A2). Indeed, the social environment and personality both could be shown to affect learning to feed on a novel prey type in perch (Magnhagen and Staffan, 2003).

The different diets of perch and pikeperch might not only depend on their foraging modes and size dependencies, but also on competitive effects and/or habitat utilization. For instance, piscivorous perch shifted habitat use to littoral zones in response to competition with piscivorous pikeperch (Schulze et al., 2006). At the Lower Rhine it could be observed, that large pikeperch use shallow beach areas at night for hunting, whereas large perch were only caught close or even within the stony embankments (personal observations). Interestingly, this habitat occupation perfectly reflects the occurrence of the selected prey items (Borcherding et al., 2011; Gertzen et al., 2016), suggesting additional habitat-dependent feeding patterns.

The present results show that adaptation on the novel prey Gobiidae is still in progress and already took several years since the introduction until significant amounts of gobies were a part of the diet. In contrast, dietary adaptations of fish larvae can occur pretty fast; within a few days significant increases in capture success and efficiency were evident when exposed to a novel prey (Meyer, 1986). Foraging efficiency increased by fourfold due to experience after six to eight trials performed with bluegill sunfish (Werner et al., 1981). Further, for perch as a generalist feeder, adaptations in morphology can arise quickly during ontogeny depending on the available resources (Hjelm et al., 2000; Hjelm et al., 2001; Heermann et al., 2007). Consequently, it is unclear, why gobies were not included earlier (or to a greater extent) in the diet of perch and pikeperch, especially as it seems to be an advantageous prey item for both. In the brackish waters of northern Germany (Kiel Canal), round goby made up the most important fish prey for pikeperch and increased growth rates, biomass and condition of the predator within the same time after introduction as analyzed in this study, yet, contrary to our area, diet overlap was negligible between the juveniles of both species (Hempel et al., 2016).

As the share of gobies increased in the diet of Percidae, further impacts on the food web are expected to arise. A discontinuous availability of suitable prey sizes can counteract the switch to piscivory within the first year of Percidae (Persson and Brönmark, 2002). With the invasion of the gobies a steady access to small prey sizes is created, which could strongly favor perch and pikeperch, especially the 0+ age cohorts. Indeed, gobies as prey seem to favor an early exclusively piscivorous diet in juvenile perch by being available in high densities in all size classes (cf. Borcherding et al., 2010). This would be an important step, as increased levels of early predation on gobies could counteract the still prevailing competitive bottleneck (Gertzen and Borcherding, submitted). In a gravel pit lake 0+ perch were able to hinder 0+

cyprinids to recruitment by heavy predation, and thus, alter the adult fish community towards a perch dominated system (Beeck et al., 2002). This competitive release could be further supported by the increased predation of adults on gobies. It was stated, that native predators could be the key for long-term regulation of invading species (Carlsson et al., 2009), resulting in stable states of co-existence (Lodge, 1993). This process has probably just started at the Lower Rhine, as now gobies as prey are increasing in the diet of the two Percidae. However, the outcome is still unclear and it remains speculative, if predation can outweigh the effects of the competitive bottleneck in future.

To conclude, pikeperch and perch showed increasing predation on invasive gobies, with perch feeding almost exclusively on one goby species, whereas pikeperch preys on all three goby species and remained to prey on native species in equal shares. Although this needs to be confirmed by further studies, prey choice of perch seems to be passively by size-dependent encounter rate which is further defined by its habitat use, whereas for pikeperch size is of minor importance but diet seems to be influenced by habitat usage as well. Going along with increasing goby prey, condition strongly improved for perch as well as for pikeperch. In this sense, youngest gobies may represent the important prey item to start with piscivory, especially for perch, as the size advantage is needed early at the beginning of the season to switch to piscivory (Mittelbach and Persson, 1998; Beeck et al., 2002; Borcherding et al., 2010). The presence of freshly hatched gobies all over the season (Gertzen et al., 2016) will enable a continuously piscivorous diet for perch and pikeperch. Future studies on the development of competitive and predatory interactions between gobies and native predators will reveal if early juveniles of both Percidae will also include Gobiidae to a greater extent in their diet, and thus possibly reduce levels of competition effectively. A first increase in condition levels of several size classes gives a cautiously optimistic perspective for native predator populations. Right now invasive gobies are both: strong competitors for 0+ perch and pikeperch (Gertzen and Borcherding, submitted), and additionally beneficial prey for adults only. However, when increasingly preyed upon also by both juvenile percids, invasive gobies are expected to be forced into the bust phase that hopefully follows their actually critical boom phase in the Lower Rhine (Simberloff and Gibbons, 2004).

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References

Agrawal, A. A., 2001. Ecology - Phenotypic plasticity in the interactions and evolution of species. Science 294, 321-326.

Bampfylde, C. J., Lewis, M. A., 2007. Biological control through intraguild predation: Case studies in pest control, invasive species and range expansion. Bull. Math. Biol. 69, 1031-1066.

Barber, N. A., Marquis, R. J., Tori, W. P., 2008. Invasive prey impacts the abundance and distribution of native predators. Ecology 89, 2678-2683.

Barrientos, R., Merino-Aguirre, R., Fletcher, D. H., Almeida, D., 2014. Eurasian otters modify their trophic niche after the introduction of non-native prey in Mediterranean fresh waters. Biol. Invasions 16, 1573-1579.

Beeck, P., Tauber, S., Kiel, S., Borcherding, J., 2002. 0+ perch predation on 0+ bream: a case study on a eutrophic gravel pit lake. Freshwat. Biol. 47, 2359-2369.

Beisner, B. E., Ives, A. R., Carpenter, S. R., 2003. The effects of an exotic fish invasion on the prey communities of two lakes. J. Anim. Ecol. 72, 331-342.

Borcherding, J., Beeck, P., DeAngelis, D. L., Scharf, W. R., 2010. Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. J. Anim. Ecol. 79, 1101-1112.

Borcherding, J., Staas, S., 2008. Local riverine fish communities as promoters for habitat restoration in the floodplain area of the lower Rhine. Am. Fish. Soc. Symp. 49, 835-843.

Borcherding, J., Staas, S., Kruger, S., Ondrackova, M., Slapansky, L., Jurajda, P., 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. J. Appl. Ichthyol. 27, 153-155.

Borcherding, J., Dolina, M., Heermann, L., Knutzen, P., Krüger, S., Matern, S., van Treeck, R., Gertzen, S., 2013. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. Limnologica - Ecology and Management of Inland Waters 43, 49-58.

Brown, B. J., Mitchell, R. J., Graham, S. A., 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83, 2328-2336.

Brown, C., Laland, K. N., 2003. Social learning in fishes: a review. Fish Fish. 4, 280-288.

Buijse, A. D., Houthuijzen, R. P., 1992. Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Can. J. Fish. Aquat. Sci. 49, 894-902.

Carlsson, N. O., Bustamante, H., Strayer, D. L., Pace, M. L., 2011. Biotic resistance on the increase: native predators structure invasive zebra mussel populations. Freshw. Biol. 56, 1630-1637.

Carlsson, N. O., Sarnelle, O., Strayer, D. L., 2009. Native predators and exotic prey-an acquired taste? Front. Ecol. Environ. 7, 525-532.

Chotkowski, M. A., Marsden, J. E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. J. Great Lakes Res. 25, 26-35.

Clavero, M., Brotons, L. s., Pons, P., Sol, D., 2009. Prominent role of invasive species in avian biodiversity loss. Biol. Cons. 142, 2043-2049.

Clavero, M., Garcia-Berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20, 110.

Crane, D. P., Farrell, J. M., Einhouse, D. W., Lantry, J. R., Markham, J. L., 2015. Trends in body condition of native piscivores following invasion of Lakes Erie and Ontario by the round goby. Freshw. Biol. 60, 111-124.

deRivera, C. E., Ruiz, G. M., Hines, A. H., Jivoff, P., 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. Ecology 86, 3364-3376.

Dörner, H., Hülsmann, S., Hölker, F., Skov, C., Wagner, A., 2007. Size-dependent predator-prey relationships between pikeperch and their prey fish. Ecol. Freshwat. Fish 16, 307-314.

Eklöv, P., Hamrin, S. F., 1989. Predatory efficiency and prey selection - Interactions between pike *Esox lucius*, perch *Perca fluviatilis* and rudd *Scardinus erythrophthalmus*. Oikos 56, 149-156.

Eklöv, P., 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. Anim. Behav. 44, 313-326.

Fritts, T. H., Rodda, G. H., 1998. The role of introduced species in the degradation of island ecosystems: A case history of Guam. Ann. Rev. Ecol. System. 29, 113-140.

Fuiman, L. A., Magurran, A. E., 1994. Development of predator defences in fishes. Rev. Fish Biol. Fish. 4, 145-183.

Gertzen, S., Fidler, A., Kreische, F., Kwabek, L., Schwamborn, V., Borcherding, J., 2016. Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany). Limnologica - Ecology and Management of Inland Waters 56, 39-48.

Greenberg, L. A., Paszkowski, C. A., Tonn, W. M., 1995. Effects of prey species composition and habitat structure on foraging by two functionally distinct piscivores. Oikos, 522-532.

Grift, R. E., Buijse, A. D., Van Densen, W. L. T., Machiels, M. A. M., Kranenbarg, J., Breteler, J. P. K., Backx, J. J. G. M., 2003. Suitable habitats for 0-group fish in rehabilitated floodplains along the lower River Rhine. River Res. Applic. 19, 353-374.

Heermann, L., 2008. Who makes the best of it? Alternative feeding strategies of European perch (*Perca fluviatilis*) and their consequences. PhD-Thesis, University of Cologne,

Heermann, L., Beeck, P., Borcherding, J., 2007. Two size classes of 0+ perch: is phenotypic plasticity based on food resources? J. Fish Biol. 70, 1365-1377.

Heermann, L., Borcherding, J., 2013. Competition, predation, cannibalism: the development of young of the year perch populations in ponds with bream or roach. J. Appl. Ichthyol. 29, 549-554.

Hempel, M., Neukamm, R., Thiel, R., 2016. Effects of introduced round goby (*Neogobius melanostomus*) on diet composition, growth and biomass of zander (*Sander lucioperca*), a main predator in Northern European brackish waters. Aquat. Invasions (accepted).

Heynen, M., Rentrop, I., Borcherding, J., 2014. Age matters – Experienced predation risk affects behavior and morphology of juvenile 0+ and 1+ perch. Limnologica-Ecology and Management of Inland Waters 44, 32-39.

Hjelm, J., Persson, L., Christensen, B., 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122, 190-199.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L., Wahlström, E., 2001. Diet-dependent body morphology and ontogenetic reaction norms in Eurasian perch. Oikos, 311-323.

Hoogland, R., Morris, D., Tinbergen, N., 1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). Behaviour 10, 205-236.

Human, K. G., Gordon, D. M., 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105, 405-412.

Hyslop, E. J., 1980. Stomach content analysis - a review of methods and their application. J. Fish Biol. 17, 411-429.

Janssen, J., Jude, D. J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27, 319-328.

Juanes, F., Buckel, J. A., Scharf, F. S., 2001. Predatory behaviour and selectivity of a primary piscivore: comparison of fish and non-fish prey. Mar. Ecol. Prog. Ser. 217, 157-165.

Karlson, A. M. L., Almqvist, G., Skora, K. E., Appelberg, M., 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES J. Mar. Sci. 64, 479-486.

Kelleher, B., Bergers, P. J. M., Van den Brink, F. W. B., Giller, P. S., Van der Velde, G., Bij de Vaate, A., 1998. Effects of exotic amphipod invasions on fish diet in the Lower Rhine. Arch. Hydrobiol. 143, 363-382.

King, R. B., Ray, J. M., Stanford, K. M., 2006. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. Can. J. Zool. 84, 108-115.

Kipp, R., Ricciardi, A., Ramcharan, C. W., 2012. Impacts of the Eurasian round goby (*Neogobius melanostomus*) on benthic communities in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. 69, 469-486.

Lodge, D. M., 1993. Biological invasions: Lessons for ecology. Trends Ecol. Evol. 8, 133-137.

Lopez, M. S., Coutinho, R., Ferreira, C. E., Rilov, G., 2010. Predator-prey interactions in a bioinvasion scenario: differential predation by native predators on two exotic rocky intertidal bivalves. Mar. Ecol. Prog. Ser 403, 101-112.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group Auckland,, New Zealand.

Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can. J. Fish. Aquat. Sci. 56, 1285-1292.

Magnhagen, C., Staffan, F., 2003. Social learning in young-of-the-year perch encountering a novel food type. J. Fish Biol. 63, 824-829.

Mehner, T., Schultz, H., Bauer, D., Herbst, R., Voigt, H., Benndorf, J., 1996. Intraguild predation and cannibalism in age 0 perch (*Perca fluviatilis*) and age 0 zander (*Stizostedion lucioperca*): interactions with zooplankton succession, prey fish availability and temperature. Ann. Zool. Fennici 33, 353-361.

Meyer, A., 1986. Changes in behavior with increasing experience with a novel prey in fry of the Central American cichlid, *Cichlasoma managuense* (Teleostei: Cichlidae). Behaviour 98, 145-167.

Meyerson, L. A., Mooney, H. A., 2007. Invasive alien species in an era of globalization. Front. Ecol. Environ. 5, 199-208.

Mittelbach, G. G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences [Review]. Can. J. Fish. Aquat. Sci. 55, 1454-1465.

Molls, F., 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. J. Fish Biol. 55, 1187-1200.

Mooney, H. A., Cleland, E. E., 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the United States of America 98, 5446-5451.

Nilsson, P. A., Brönmark, C., 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos 88, 539-546.

Nilsson, P. A., Turesson, H., Brönmark, C., 2006. Friends and foes in foraging: intraspecific interactions act on foraging-cycle stages. Behaviour 143, 733-745.

Noonburg, E. G., Byers, J. E., 2005. More harm than good: when invader vulnerability to predators enhances impact on native species. Ecology 86, 2555-2560.

Novacek, M. J., Cleland, E. E., 2001. The current biodiversity extinction event: scenarios for mitigation and recovery. Proc. Natl. Acad. Sci. U. S. A. 98, 5466-5470.

Pejchar, L., Mooney, H. A., 2009. Invasive species, ecosystem services and human well-being. Trends Ecol. Evol. 24, 497-504.

Persson, A., Brönmark, C., 2002. Foraging capacity and resource synchronisation in an ontogenetic diet switcher, pikeperch (*Stizostedion lucioperca*). Ecology 83, 3014-3022.

Persson, L., Claessen, D., De Roos, A. M., Byström, P., Sjörgren, S., Svanbäck, R., Wahlström, E., Westman, E., 2004. Cannibalism in a size-structured population: Energy extraction and control. Ecol. Monogr. 74, 135-157.

Phillips, B. L., Shine, R., 2006. An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia. Proc. R. Soc. Lond. B. Biol. Sci. 273, 1545-1550.

Polacik, M., Janac, M., Jurajda, P., Adamek, Z., Ondrackova, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecol. Fresh. Fish 18, 640-649.

Polis, G. A., Holt, R. D., 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol. Evol. 7, 151-155.

Polis, G. A., Myers, C. A., Holt, R. D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev. Ecol. System., 297-330.

Ricciardi, A., MacIsaac, H. J., 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol. Evol. 15, 62-65.

Rodda, G. H., Fritts, T. H., 1992. The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam lizards. J. Herpetol. 26, 166-174.

Rodda, G. H., Fritts, T. H., Chiszar, D., 1997. The disappearance of Guam's wildlife - New insights for herpetology, evolutionary ecology, and conservation. BioScience 47, 565-574.

Rodriguez, L. F., 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol. Invasions 8, 927-939.

Roemer, G. W., Donlan, C. J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Natl. Acad. Sci. U. S. A. 99, 791-796.

Scharbert, A., 2009. Community patterns and recruitment of fish in a large temperate river floodplain - The significance of seasonally varying hydrological conditions and habitat availability. PhD-Thesis, University of Cologne, 157 pp.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348-360.

Schulze, T., Baade, U., Dörner, H., Eckmann, R., Haertel-Borer, S. S., Hölker, F., Mehner, T., 2006. Response of the residential piscivorous fish community to introduction of a new predator type in a mesotrophic lake. Can. J. Fish. Aquat. Sci. 63, 2202-2212.

Scott, B. E., Marteinsdottir, G., Begg, G. A., Wright, P. J., Kjesbu, O. S., 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). Ecol. Model. 191, 383-415.

Shapiro, A. M., 2002. The Californian urban butterfly fauna is dependent on alien plants. Divers. Distrib. 8, 31-40.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. Ann. Rev. Ecol. System., 269-311.

Simberloff, D., Gibbons, L., 2004. Now you see them, now you don't! - Population crashes of established introduced species. Biol. Invasions 6, 161-172.

Simoncini, M., Miller, R. J., 2007. Feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for a dominant native ascidian, *Aplidium glabrum*, relative to the invasive ascidian *Botrylloides violaceus*. J. exp. mar. Biol. Ecol. 342, 93-98.

Steinhart, G. B., Stein, R. A., Marschall, E. A., 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? J. Great Lakes Res. 30, 381-389.

Turesson, H., Brönmark, C., Wolf, A., 2006. Satiation effects in piscivore prey size selection. Ecol. Freshwat. Fish 15, 78-85.

Turesson, H., Persson, A., Brönmark, C., 2002. Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. Ecol. Freshwat. Fish 11, 223-233.

Tyrrell, M. C., Link, J. S., Moustahfid, H., 2011. The importance of including predation in fish population models: implications for biological reference points. Fish. Res. 108, 1-8.

Van Densen, W. L. T., 1985. Piscivory and the development of bimodality in the size distribution of 0+ pikeperch (*Stizostedion lucioperca* L.). J. Appl. Ichthyol. 3, 119-131.

Van Densen, W. L. T., Ligtvoet, W., Roozen, R. W. M., 1996. Intra-cohort variation in the individual size of juvenile pikeperch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Ann. Zool. Fennici 33, 495-506.

Vander Zanden, M. J., Casselman, J. M., Rasmussen, J. B., 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401, 464-467.

Wainwright, P. C., 1986. Motor correlates of learning behaviour: feeding on novel prey by pumpkinseed sunfish (*Lepomis gibbosus*). J. Exp. Biol. 126, 237-247.

Wankowski, J. W. J., 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. J. Fish Biol. 14, 89-100.

Werner, E. E., Mittelbach, G. G., Hall, D. J., 1981. The role of foraging profitability and experience in habitat use by the Bluegill Sunfish. Ecology 62, 116-125.

Wonham, M. J., O'Connor, M., Harley, C. D., 2005. Positive effects of a dominant invader on introduced and native mudflat species. Marine Ecology Progress Series 289, 109-116.

Appendix Chapter V

Table A1. Number of specimens per year and length class.

N	Length Class	2011	2012	2013	2014
Perca	1	58	26	50	7
	2	201	72	117	8
	3	4	28	9	52
	4		2	2	18
	5		1	1	9
	6	1	1	1	11
Sander	1	49	20	56	5
	2	109	46	46	8
	3	13	32	36	9
	4	3	7	21	9
	5	4	2	1	6
	6	18	2	5	23

Table A2. Number of analyzed fish per species and fishing method.

Species (N)	Angling	Beach Seining	Electro-fishing	Total
Perca fluviatilis	18	579	107	704
Sander lucioperca	43	512	5	560

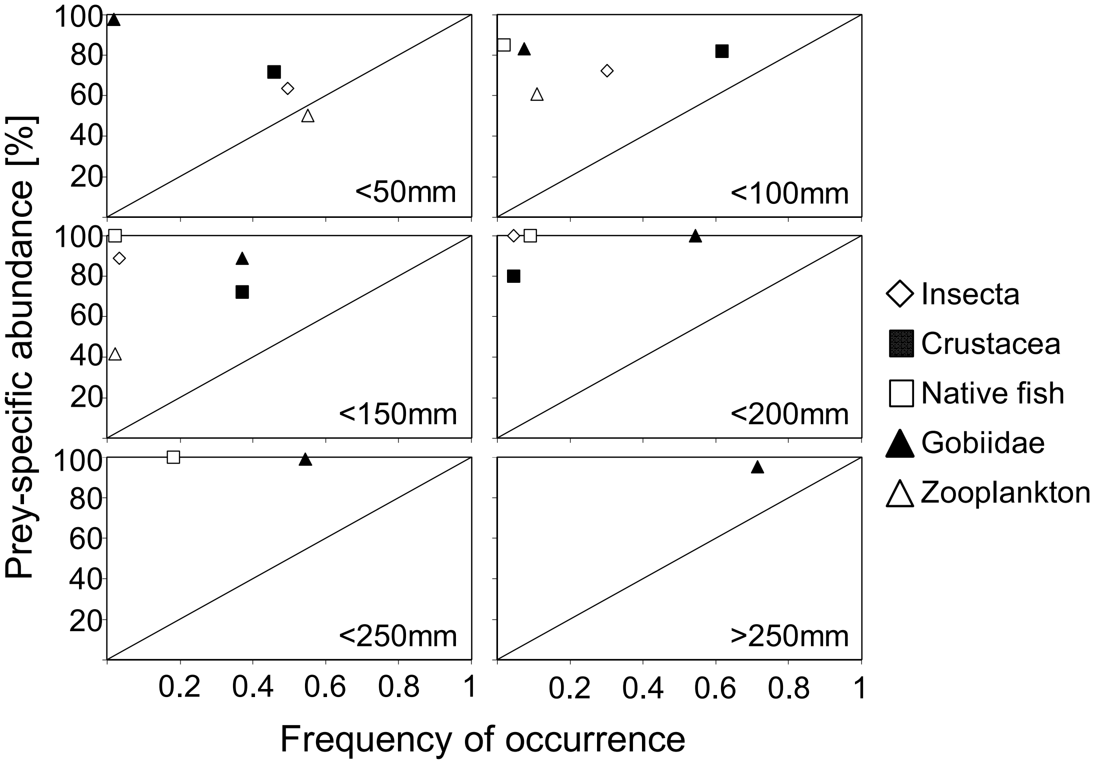

Figure A1. Costello plots for the sixth length classes of *Perca fluviatilis* for the main prey categories.

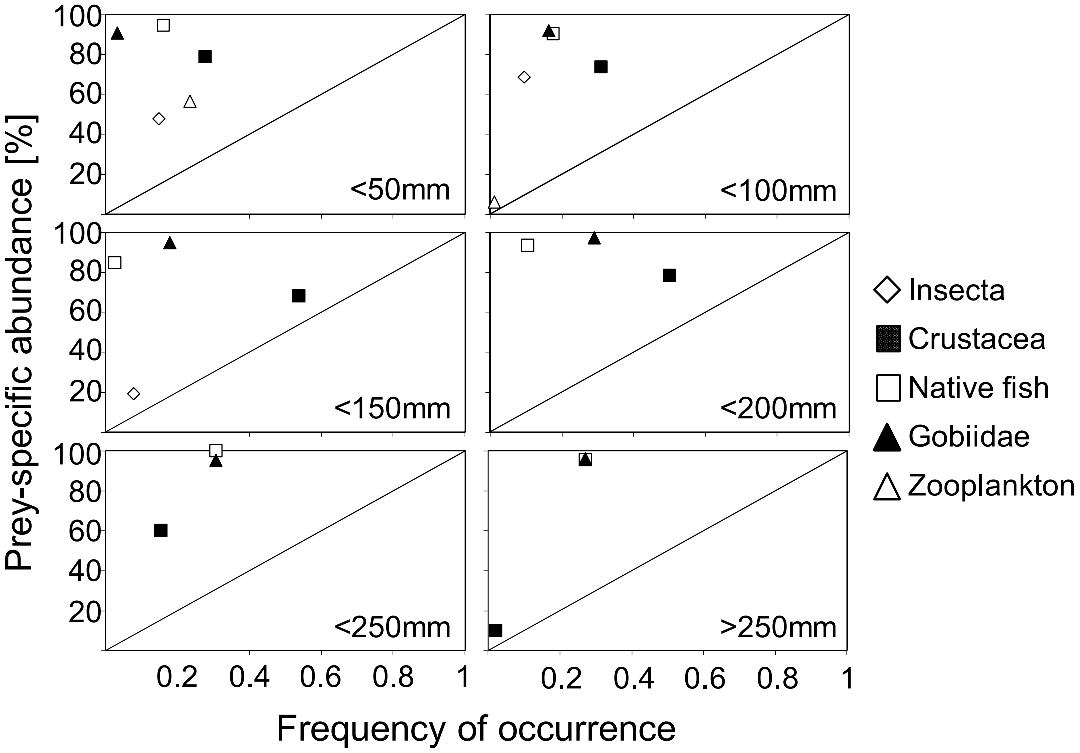

Figure A2. Costello plots for the sixth length classes of *Sander lucioperca* for the main prey categories.

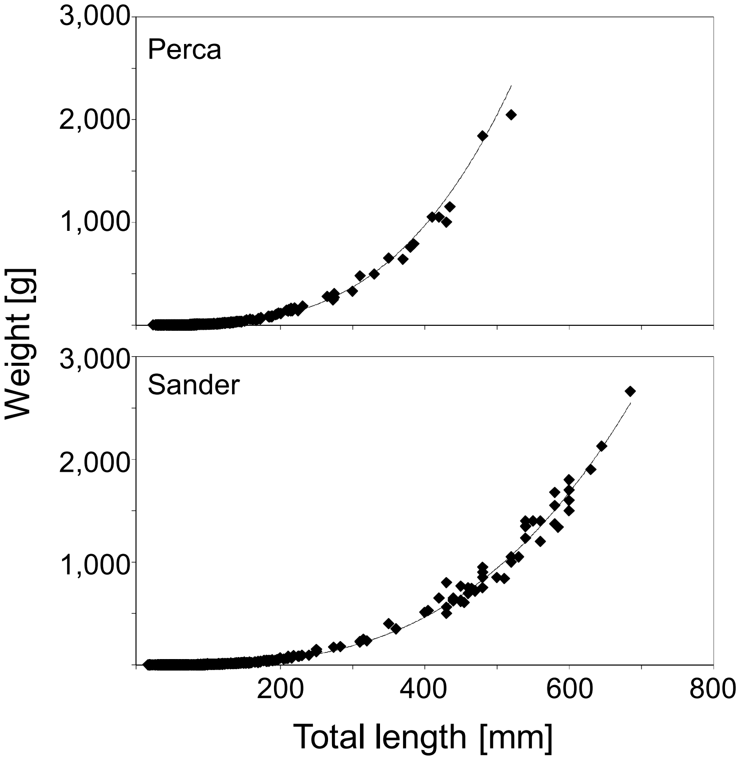

Figure A3. Length-weight regressions of perch (above) and pikeperch (bottom), equations: weight [g] = 0.0000021 TL $^{3.3341}$ (Perca) and weight [g] = 0.0000028 TL $^{3.161}$ (Sander).

KURZZUSAMMENFASSUNG

Biologische Invasionen sind ein faszinierendes Phänomen, das in den letzten Jahren immer häufiger zu beobachten ist. Aufgrund zunehmender Globalisierung und der Eröffnung neuer Transportwege gelangen immer mehr Arten in Regionen, die weit entfernt von ihrem ursprünglichen Verbreitungsgebiet liegen. Einige dieser eingebrachten Arten werden dabei zu einer regelrechten Plage und zeigen dabei nicht nur ökologische Auswirkungen, sondern können auch ökonomische und gesundheitliche Folgen mit sich bringen. Durch die Eröffnung des Rhein-Main-Donau-Kanals wurde auch der Niederrhein von einer Vielzahl nicht nativer Arten bevölkert. Unter ihnen befinden sich drei Fischarten der Familie Gobiidae aus dem Pontokaspis, die seit 2006, bzw. 2008, selbsterhaltende Populationen in diesem System entwickelt haben. Da diese eng miteinander verwandten Fische in äußerst hohen Abundanzen auftreten, wurden zum einen Nischenseparierungen zur Konkurrenzverminderung zwischen den einzelnen Grundelarten vermutet, zum anderen negative Interaktionen mit den einheimischen Fischarten erwartet. Die drei häufigsten Differenzierungen der ökologischen Nische in Fischen werden anhand der Nahrung (57 %), der Habitatnutzung (32 %), sowie entlang der temporalen Achse (11 %) beschrieben. In einer ersten Studie wurde daher die Nahrungszusammensetzung der drei invasiven Arten im Laufe ihrer Ontogenie untersucht. Alle drei Grundeln ernährten sich opportunistisch, zeigten aber distinkte Unterschiede im Laufe ihrer Entwicklung. Während der Nahrungsüberlappungsindex bei juvenilen Grundeln noch signifikante Überschneidungen zeigte, differenzierten sich adulte Grundeln auf Fisch (Kessler- und Flussgrundel) oder Muscheln (Schwarzmaulgrundel). Zusätzlich fanden Separierungen durch die Habitatnutzung statt, wobei die Kesslergrundel einen ontogentischen Habitatswechsel von den sandigen Buhnenfeldern in die Steinschüttung vollzog. Die Flussgrundel hingegen verblieb in den Buhnenfeldern, während die Schwarzmaulgrundel ubiquitär vertreten war. Weitere Unterschiede zwischen den drei Arten konnten in deren Reproduktionsmodi entdeckt werden. Während die Schwarzmaul- und Flussgrundel die gesamte Saison über Laichverhalten anzeigten, wies die Kesslergrundel nur ein einmaliges Ablaichereignis zu Beginn der Saison auf. Schwarzmaul- und Flussgrundel separierten sich dabei weiter auf der temporalen Achse, indem sie unterschiedliche Intensitäten der Laichaktivität im Laufe der Saison aufwiesen. Eine weitere Studie beschäftigte sich mit dem Driftverhalten frisch geschlüpfter Grundeln. Auch hier konnten Unterschiede im Zeitpunkt der Drift und Größe der driftenden Tiere beobachtet werden. Neben diesen zahlreichen, fein aufeinander abgestimmten Einnischungen der invasiven Grundelarten wurden auch die Interaktionen mit nativen Fischarten untersucht. Hierbei wurde in einer ersten Studie belegt, dass der Rhein stark Futterressourcen limitiert ist und folglich ein hohes Maß an Nahrungskonkurrenz, insbesondere für 0+

Individuen existierte. Dabei konnten die invasiven Grundeln, allen voran die Schwarzmaulgrundel, als konkurrenzstärkste Arten identifiziert werden. Von den untersuchten einheimischen Fischen konnte lediglich der Rapfen durch Nutzung einer anderen Nahrungskategorie mithalten. Deutlich betroffen von der Konkurrenz waren dagegen die juvenilen Perciden Barsch und Zander, die in einen sogenannten juvenilen kompetitiven Flaschenhals („juvenile competitive bottleneck“) gedrückt wurden. Demnach befasste sich die letzte Studie mit der Frage, ob Prädation auf invasive Grundeln, durch eben diese beiden Arten, die negativen Effekte der Konkurrenz in Juvenilstadien aufheben kann. Obwohl beide Arten Grundeln in ihre Nahrung inkludierten und mit der Zunahme des Verzehres von Grundeln auch ein signifikanter Anstieg der Kondition ersichtlich war, waren die Prädationsraten noch zu gering um effektiv wirken zu können.

ERKLÄRUNG

Rhede, den 10.02.2016

Ich versichere, dass ich die von mir vorgelegte Dissertation selbstständig angefertigt, die benutzten Quellen und Hilfsmittel vollständig angegeben und die Stellen der Arbeit - einschließlich Tabellen, Karten und Abbildungen -, die anderen Werken im Wortlaut, oder dem Sinn nach entnommen sind, in jedem Einzelfall als Entlehnung kenntlich gemacht habe; dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie – abgesehen von oben angegebenen Teilpublikationen – noch nicht veröffentlicht worden ist sowie, dass ich eine solche Veröffentlichung vor Abschluss des Promotionsverfahrens nicht vornehmen werde. Die Bestimmungen der Promotionsordnung sind mir bekannt. Die von mir vorgelegte Dissertation ist von PD Dr. habil. Jost Borcherding betreut worden.

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Lehre und Betreuung

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Publikationen

Borcherding, J., Gertzen, S., Staas, S., 2011. First record of Pontian racer goby, *Babka gymnotrachelus* (Gobiidae: Teleostei), in the River Rhine, Germany. Journal of Applied Ichthyology 27, 1399-1400.

Borcherding, J., Dolina, M., Heermann, L., Knutzen, P., Krüger, S., Matern, S., van Treeck, R., Gertzen, S., 2013. Feeding and niche differentiation in three invasive gobies in the Lower Rhine, Germany. Limnologica - Ecology and Management of Inland Waters 43, 49-58.

Lindner, K., Cerwenka, A. F., Brandner, J., Gertzen, S., Borcherding, J., Geist, J., Schliewen, U. K., 2013. First evidence for interspecific hybridization between invasive goby species Neogobius fluviatilis and Neogobius melanostomus (Teleostei: Gobiidae: Benthophilinae). Journal of Fish Biology 82, 2128-2134.

Gertzen, S., Fidler, A., Kreische, F., Kwabek, L., Schwamborn V., Borcherding, J., 2016. Reproductive strategies of three invasive Gobiidae co-occurring in the Lower Rhine (Germany). Limnologica - Ecology and Management of Inland Waters 56, 39-48.

Kalchhauser, I., Hirsch, P. E. , N'Guyen, A., Watzlawczyk, S., Gertzen, S., Borcherding, J., Burkhardt-Holm, P. (in press). The invasive bighead goby *Ponticola kessleri* displays small scale genetic differentiation and large scale genetic homogeneity in relation with shipping patterns. Molecular Ecology.

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