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

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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.

1. 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 Maclsaac, 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 Maclsaac, 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

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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 about round goby, knowledge about reproductive modes of Ponto-Caspian Gobiidae, particularly in their native habitats, is scarce (see Table 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.

2. Methods

2.1. 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 × 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 m^2). 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) (Table 2, Figure S1 and Table S2 supplement).

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 total length 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).

2.2. 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 lengths of the first cohort of every sampling date with the mean total lengths of the following sampling event (Heermann and Borcherding, 2013).

$$G = (\mathrm{TL}t_2 - \mathrm{TL}t_1) * \Delta \mathrm{d}_{t_1 t_2}^{-1}$$

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 $\nabla \mathrm{d}_{t1t2}$ = 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 $G = (32.64\ \mathrm{mm} - 30.67\ \mathrm{mm})/9$ days = 0.219 mm per day. For