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Round goby movement patterns in a non-navigable river

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ABSTRACT

Understanding non-native species dispersal is vital for their future management. The round goby (*Neogobius melanostomus*) has greatly extended its range since 1990s, with commercial shipping being the main vector. However, our knowledge regarding their secondary dispersal from points of introduction is surprisingly limited. In this study, a series of field experiments were undertaken on a mid-sized river to assess goby dispersal patterns within an established population, following a simulated release of a large number of propagules, or at a simulated invasion front. Most of the established population remained stationary and just a few individuals undertook long-distance dispersal (principally upstream). Mean distance travelled was 1.1 m.day$^{-1}$ (max. 29.6 m.day$^{-1}$). While site fidelity appeared to last for most of the year (including winter), it was surprisingly relaxed during the spawning season. Concentrated release of a large number of propagules resulted in appreciably greater movement rates than in the established population, with upstream movement again dominating. In general, smaller, mostly male fish tended to move further and appeared as first colonisers in uninvaded areas.
1 Introduction

Quantifying the extent of movement activity (dispersal) in non-native fish is one of the key factors in predicting invasion potential and speed of colonisation in a new area (Radinger and Wolter 2014). Fish introductions outside of their native range have been relatively well studied, with most cases attributable to shipping (Ricciardi and MacIsaac 2000; Wonham et al. 2000; Gozlan et al. 2010), imports of ornamental fish (Padilla and Williams 2004; Keller and Lodge 2007), escapes from aquaculture (Cook et al. 2008; Gozlan et al. 2010) or intentional introductions for sport fishing (Gozlan 2008; Rahel and Smith 2018). However, relatively little is known about non-native fish movements after the initial introduction. Yet such knowledge could yield valuable information on the species’ biology and inform management and control efforts (Skalski and Gilliam 2000; Landsman et al. 2011; Coulter et al. 2016). In other words, while we know much about how fish can be transported over long distances (e.g. via shipping), we know very little about what happens after they are released.

The round goby (*Neogobius melanostomus*), a small benthic fish originating in the Ponto-Caspian region, has greatly increased its range since the 1990s (see Roche et al. 2013 for a review). Round gobies usually become established relatively quickly in newly colonised areas due to a number of traits typical of invasive species, e.g. rapid range expansion, super-dominant population growth, rapid genomic adaptation and life history trait plasticity (Cerwenka et al. 2014; Brandner et al. 2015). Nevertheless, aspects of movement activity and the scale of movement have received relatively little scientific attention. For example, while numerous otherwise-oriented studies have taken place in the Laurentian Great Lakes region following round goby introduction in the 1990s, just 2.7% (3 of 112) of all fish movement studies dealt with aspects of round goby movement in 2010, despite the species’ potential for altering and disrupting native fish communities (Landsman 2011).
While the number of studies on round goby range expansion has increased in recent years, most such studies describe expansion along navigable rivers and canals, based on the assumption that transport via shipping has been the main vector facilitating long-range ‘leap-frog’ dispersal (e.g. see Ahnelt et al. 1998; Wiesner 2005; Gutowsky and Fox 2011; Cammaerts et al. 2012; Roche et al. 2013). ‘Natural’ expansion (i.e. continuous range expansion by swimming alone) into and along invaded non-navigable rivers has been examined much less intensively, with most studies restricted to reporting the pace of invasion front shifts (Bronnenhuber et al. 2011; Brownscombe and Fox 2012; Šlapanský et al. 2017) or describing which fish occur first in newly colonised areas (Phillips et al. 2003; Brandner et al. 2013b). Little is known about the mobility of invasive gobies at small spatial scales (Brandner et al. 2015), even though small-scale post-introduction movements are crucial to our understanding of subsequent dispersal and for predicting the extent and speed of range expansion (LaRue et al. 2011). Papers that have dealt with small-scale round goby dispersal to date have tended to do so only marginally (e.g. Wolfe and Marsden 1998; Cookingham and Reutz 2008; Brandner et al. 2015). To the best of our knowledge, only two studies have provided a more in-depth view, i.e. those of Lynch and Mensinger (2012), who quantified movement patterns of individually tagged round gobies in Lake Superior, and Christoffersen et al. (2019), who studied diel and seasonal migration of gobies along a Baltic Sea estuary using acoustic telemetry. In addition, it is hard to generalise the information gained from such studies as they are restricted by regional and ecotype coverage (most information originating exclusively from slow flowing or standing waters, with Europe largely understudied) and contrasting results.

In early studies, it was reported that round gobies display poor natural dispersal ability, especially when travelling upstream (Bronnenhuber et al. 2011; Brownscombe and Fox 2012), due to their morphology (typical of small benthic fishes) and small home ranges (based on the studies of Wolfe and Marsden (1998) and Ray and Corkum (2001)). However, subsequent
studies have reported both larger home ranges (Cookingham and Reutz 2008; Christoffersen et al. 2019), long-distance natural dispersal (Šlapanský et al. 2017; Christoffersen et al. 2019) and a relatively fast rate of spread into non-navigable rivers (Kornis and Vander-Zanden 2010; Bronnenhuber et al. 2011; Brownscombe and Fox 2012; Brandner et al. 2013b). Furthermore, it remains unclear as to which individuals (in terms of sex and size) are most involved in the process of invasion, i.e. as first colonisers or pioneers (Gutowsky and Fox 2011; Brandner 2013b; Brownscombe and Fox 2012; Masson et al. 2016).

The main goal of this study was to evaluate both the extent of round goby movement in a European mid-sized lowland river and any sex- or size-specific or seasonal patterns. To this end, we conducted a series of field experiments designed to ensure that the dispersal observed was free of any possible human involvement. The first of these experiments describes dispersal patterns in an established round goby population, allowing us to determine common movement rates, identify the most probable migrants (pioneers) and the time of year when migration is most likely; the second describes dispersion patterns following a mass release of propagules by observing goby dispersal from a single ‘introduction’ spot; while the third describes dispersion patterns in a simulated invasion front by monitoring recolonisation of areas cleared of gobies.

2 Material and methods

2.1 Study area

The study took place on a 23 km stretch (river km 17 to river km 40) of the River Dyje (Danube basin, Czech Republic; Fig. 1). Between 1968 and 1982, the Dyje was channelised and its riverbanks stabilised with rocky rip-rap (15–25 cm diameter; though stones of 40-60 cm also occur at some locations). The river has a channel width of 30–50 m, a depth of 0.5–1.0 m. and an annual mean discharge rate over the study stretch of 41.7 m³ s⁻¹ (Czech
Hydrometeorological institute; http://portal.chmi.cz). Current velocity along the banks rarely exceeds 0.4 m.s\(^{-1}\). The bottom substrate comprises sand, gravel and pebbles with patches of silt and aquatic vegetation, woody debris, pools and riffles occur only rarely. The Dyje is non-navigable throughout the study stretch, thereby ensuring that the dispersal observed did not occur through boat transport but almost certainly through natural means alone.

The Dyje has a relatively diverse fish assemblage, originally dominated by native cyprinid species such as roach *Rutilus rutilus*, chub *Leuciscus cephalus*, common bream *Abramis brama*, barbel *Barbus barbus*, bleak *Alburnus alburnus*, European bitterling *Rhodeus amarus* and white-finned gudgeon *Romanogobio vladykovi* (Jurajda and Peňáz 1994; Valová et al. 2006). In recent years, the assemblage has come to include stable populations of non-native tubenose goby (*Proterorhinus semilunaris*), which was introduced in the 1990s, and round goby, introduced in 2008. Both gobiid species soon became established following introduction (Janáč et al. 2012; Janáč et al. 2016) and have come to dominate the Dyje fish assemblage (Valová et al. 2015; Šlapanský et al. 2017).

### 2.2 Data collection

For all three field experiments, fish were sampled by electrofishing, using a portable backpack unit (SEN, f. Bednář, Czech Republic; frequency 75-85 Hz; maximum output 225/300 V) fitted with a small elliptical stainless-steel anode (25 x 15 cm) with 4 mm mesh netting (see Janáč et al. 2016 for further details). Sampling always took place during the day between 9:00 and 17:00.

Based on our own long-term experience, electrofishing by slow wading upstream along the bank has proved to be the most effective method for catching all age-classes of fish inhabiting the littoral rip-rap. Other methods were not used due to inappropriate conditions (beach seining) or low efficiency (traps) in this part of the Dyje. Electrofishing of the nearshore
zone is a reliable and commonly used method for sampling not only round goby assemblages (Brander et al. 2013a) but also for describing riverine fish communities in general (FAME Consortium 2004). As the river is relatively shallow, we were able to sample the whole nearshore water column up to a distance of 2–4 m from the bank (depending on slope), thus covering the whole rip-rap zone in this stretch of the river. Earlier observations (using angling, traps and electrofishing) showed no presence of round gobies on the sandy bottom in the middle of the river.

All fish captured were identified to species and measured to the nearest millimetre (standard length, SL) on the bankside. Non-gobiid species were then released to the water after noting the numbers caught and all gobies retained and handled for each experiment as described below. Goby sex was determined through examination of the urogenital papillae. Fish with a SL < 40 mm, or those with a SL of 40-55 mm whose sex could not otherwise be determined, were recorded as juveniles.

2.3 Field experiments

Three field experiments were conducted in order to: (i) reveal common movement rates of gobies in an established population and seasonal aspects of any movement patterns (herein Movement); (ii) reveal how far gobies spread following simulated colonisation events from single release points (herein Release); and (iii) reveal which gobies first colonise a stretch where gobies have previously been eradicated (herein Colonisation).

2.3.1 Movement experiment

In this experiment, we divided an approximately 2 km long river stretch into 10 m sections, the GPS coordinates at the start and end of each stretch being recorded to ensure localisation during recapture events. We continuously surveyed sections in the middle of the stretch (approx. 300-
500 m from each end) by electrofishing. Each round goby caught was measured and sexed and, with the exception of fish in poor condition and small fish (SL < 50 mm), tagged with an VI Alpha tag (Visible Implant Alpha Tag; Northwest Marine Technology Inc.) inserted subcutaneously to the ventral part of body with a VI Alpha injector needle (Standard 1.2 mm x 2.7 mm needle V; Northwest Marine Technology Inc.). Each tag carried a unique alphanumerical code allowing identification of each individual. After tagging, the fish were placed into buckets containing clean river water and allowed to recover fully for 15 minutes. Each tagged fish was then released in the same 10 m section from which it was captured.

Three short-term capture-mark-recapture campaigns were undertaken to assess movement during the pre-spawning (691 fish tagged, capture 22.4.15, recapture 18.5.15, 26 days with discharge between 23-38 m$^3$.s$^{-1}$), spawning (635 fish tagged, capture 13.5.14, recapture 17.6.14, 35 days with discharge between 12-29 m$^3$.s$^{-1}$) and post-spawning (390 fish tagged, capture 14.8.13, recapture 16.9.13, 33 days with discharge between 13-27 m$^3$.s$^{-1}$) periods. Seventeen tagged fish were recaptured after more than 200 days (i.e. outside of the planned recapture date), all fish being recaptured after winter. These fish were not included into the analysis but are reported in the text as overwintering individuals. Recapture surveys started at the same site where the fish were tagged and extended 300–600 m upstream and downstream. When an individual was captured at the edge of the defined area, electrofishing was extended by a minimum of 200 m upstream or downstream. Several control sites were also sampled at greater distances in order to ensure capture of potential remote migrants. During the recapture campaigns, all round gobies caught were measured, sexed, checked for tags and the section in which they were captured recorded. Each tagged fish was humanely dispatched with an overdose of clove oil and frozen for later laboratory analysis. Round goby movement was quantified by recording the displacement distance between capture and recapture.

2.3.2 Release experiment
In this experiment, we simulated the release of a large number of individuals (propagules) at a single release point in order to monitor movement activity of fish originating from a single strong introduction event (e.g. by release of large numbers of fish from ship ballast water). First, we partially depleted both banks (right bank = 900 m, left bank = 600 m) of a selected river stretch by electrofishing over 16-17 July 2013. All fish captured in each section were measured and sexed and then tagged with VIE tags (Visible Implant Elastomer, Northwest Marine Technology, Inc.) using a 1 mm single-use syringe (0.30 mm diameter needle). Each tag was inserted subcutaneously to the ventral part of the body along the anal fin on the right or left side at the place of capture (left or right bank). In total, 1912 round gobies were tagged; 984 on the right bank and 928 on the left bank. After tagging, all fish were held in a large wire cage in the river for one hour to recover. After convalescence, the gobies were released at a single release point located in the middle of the respective stretch.

After 30 days (discharge between 14-32 m$^3$.s$^{-1}$), we sampled 1400 m of the right bank and 1200 m of the left bank immediately adjacent to the release points. In addition, several 200 m control stretches were sampled at greater distances from the central release point in order to check for possible strays with exceedingly high levels of movement activity. The control stretches comprised sections of rip-rap (chosen as the most appropriate habitats for round gobies) located 1.6 and 16.1 km upstream and 6.3 km downstream from the release point (Fig. 1). Within the main control stretch, the length sampled was determined by the distance to which tagged fish were observed, the minimum being 200 m from the last point where a tagged goby was captured. For the recapture campaigns, the river stretch divided into 10 m sections and movement was quantified by recording the distance between the release point and the 10 m recapture section (i.e. based on a 10 m scale).

Fish tagging appeared to have no negative effect on specific groups of fish as the sex and size of recaptured fish did not differ from a random subsample of tagged fish from the Release
experiment and the three mark-recapture campaigns in the *Movement* experiment (Supplementary information, Table S1, Figs. S1-S4).

2.3.3 Colonisation experiment

This experiment took place in September 2012 over a 1 km rip-rap stretch of the Dyje, within ten 20 m sections randomly chosen for sampling. Each section was then electrofished (three pass depletion) and all fish caught (894 round gobies, 952 other fish species) were removed from the section. The round gobies were then overdosed with clove oil and frozen for later dietary analysis in the laboratory and all other fish were released back to the river. Four days after depletion, a resampling campaign took place in the same 20 sections, again using three pass electrofishing. For each round goby captured colonising the emptied section, we measured the distance from the edge of the section (0.1 m precision) and recorded the sex and size. Discharge was stable at 17.5 m$^3$.s$^{-1}$ throughout the experiment.

2.4 Data analysis

2.4.1 Movement experiment

The distances recorded in the *Movement* experiment included a large proportion of zeros (see Results); hence, we analysed movement patterns using three independent tests. First, using generalised linear models (GLM) we assessed which factors affected whether a fish had moved or not from the original 10 m capture section (response variable Bernoulli distributed; binomial part of the zero-altered model, according to Zuur et al. 2009), with sex, size, season and their interaction used as predictors. Second, using GLM, we assessed which factors affected the distance reached by those fish that had moved from the capture (release) section (response
variable negative binomial distributed; count part of the zero-altered model), with sex, size and season used as predictors (interactions excluded due to small dataset size).

Finally, we assessed whether the fish that had moved had gone upstream or downstream, by testing the significance of the intercept in GLM predicting direction (0 = downstream, 1 = upstream; Bernoulli distributed).

2.4.2 Release experiment

For each fish, the distance reached from the release point was expressed as the number of 10 m sections travelled (independent of whether movement was upstream or downstream). The effect of dispersal direction (upstream, downstream), sex, size and their interaction on distance reached was tested using GLM (response variable negative binomial distributed). In order to test whether recaptured fish moved preferentially upstream or downstream from the release point, we tested the significance of the intercept in GLM predicting direction (0 = downstream, 1 = upstream; Bernoulli distributed).

2.4.3 Colonisation experiment

In order to show which fish were the most ‘active’ colonisers, we tested for the possible effect of size, direction of colonisation (upstream, downstream) and their interaction on distance from the 20m section border using generalised linear mixed models (GLMM; response variable distance binomially distributed [ranging from 0 to 100 dm sections of the 100 possible]), with section as the random factor. The analysis was repeated on a reduced dataset containing only adult fish in order to reveal any effect of sex, colonisation direction and their interaction. As
overdispersion was detected in both original GLMMs, individual-level random effects (Elston et al 2001) were included into the binomial GLMMs.

2.4.4 Model selection and validation

In all analyses, non-significant terms were removed from the model based on a comparison of Akaike information criteria (AIC) for models with and without the particular term (choosing models with a lower number of parameters with ΔAICc < 2). This rule was relaxed for the GLMM, which provides only rough AIC estimates. In this case, the degree of (non)significance in the removed term was used as a supporting criterion for removing a term from the model. Where the removal of a term was uncertain (ΔAICc was close to 2 after removing the term), we present both possible final models. The models were validated through visual inspection of residual patterns, with an alpha level of 0.05 set for all analyses. All data were analysed using R statistical software v 3.5.0 (R Core Team 2018), using the base (R Core Team 2018), MASS (Venables and Ripley 2002), VGAM (Yee 2015), lme4 (Bates et al. 2015), MuMIn (Bartoń 2018) and pscl packages (Zeileis et al. 2008).

3 Results

3.1 Movement experiment

Fish in the established population were predominantly stationary, with more than half (56 of 95, 58.9%) being recaptured within the same 10 m section in which they were released approximately one month before. While sex and size did not affect whether fish moved from the release section (all interactions containing these terms, as well as the terms themselves, were removed from the model; Table S2), there was a significant difference between seasons (GLM, df = 2, 92, P = 0.002). Sampling in both the pre-spawning and post-spawning periods produced
a higher proportion of 'no-moves' (i.e. fish recaptured in the same section in which they were released) than in the spawning period (pre-spawn: 30 of 41 fish, 73.2%; spawn: 12 of 34, 35.3%; post-spawn: 14 of 20, 70%; GLM, df = 1,73, P < 0.001, df = 1,52, P = 0.012, both significant after Bonferroni correction for multiple testing).

Two thirds of fish that moved beyond the area of release moved upstream (26 fish upstream, 13 downstream, the difference being significant: GLM, df=37, P = 0.041). On average, fish moving beyond the release section travelled 79 m, compared to an average of 33.3 m for all recaptures. This figure was significantly affected by three long-distance migrants that travelled 420, 560 and 770 m (Fig. 2). Distance travelled was unaffected by movement direction, season, size or sex (all terms removed from the model; Table S2). Note, however, that both size and sex were close to significance (Table S2; GLM, both df = 1, 37, P = 0.072 for size and 0.051 for sex) and, if kept in the final model, this would suggest that smaller fish and males travelled longer distances (Fig. 2).

Distances reached by overwintering fish (i.e. fish from long-term recaptures that stayed over winter) were similar to those of short-term recaptures. Of the 17 fish caught, eleven were recaptured within 40 m of the release section (64.7%, six males, five females; Fig. 3), seven (41.3%) within 10 m and four (23.5%, two males, two females) within the same section where they were released. Five fish were recaptured downstream of the original section and eight upstream (Fig. 3).

3.2 Release experiment

Of the 107 gobies (68 females, 39 males) recaptured 30 days after release, six (5.6%); three males, three females) moved less than 10m, 20 (18.7%); nine females, eleven males) moved downstream and 81 (75.7%); 56 females, 25 males) upstream (Figs. 4 and 5), the difference
between upstream and downstream movement being significant (GLM, df = 100, P < 0.001).

Recaptured fish accounted for 5.7% of the 1867 tagged fish released.

Two final models were chosen when predicting distance reached, the first including the term direction only (lowest AICc; Table S3) and the second including the terms direction, sex, size and sex:size interaction (ΔAICc after removing interaction term = 1.8; Table S3). The first model indicated that fish moved a significantly longer distance upstream (mean upstream distance reached = 199.17 m, mean downstream distance = 65.65 m; Fig. 5). In the second model, only the terms direction and sex:size interaction were significant (all df = 1,105, P < 0.001 for direction, P = 0.603 for sex, P = 0.605 for size and P = 0.045 for sex:size). Partial tests showed that, while distance was independent of size in females (GLM, df= 1,66, P = 0.193), smaller males moved significantly more than larger males (GLM, df=1, 37, P = 0.038; Fig. 6). Eight fish were also recorded crossing to the other riverbank (7.5% of recaptured fish) where they moved 200 to 670 upstream, thereby exceeding the overall mean distance reached.

3.3 Colonisation experiment

While distance reached from the section border was independent of sex and colonisation direction (the terms sex, direction, sex:direction and size:direction removed from the final model; Table S4), it decreased significantly with fish size (GLMM, df =1,361, P =0.009; Fig. 7).

4 Discussion

Movement of the established round goby population (Movement experiment) corresponded well with a leptokurtic dispersal kernel (Fraser et al. 2001; Radinger and Wolter 2014), i.e. a large number of no- or small movements with few individuals exhibiting large-
scale movement activity. The majority of fish, therefore, exhibited high site fidelity, with almost
60% being recaptured within the same 10 m section they were released in. This is in sharp
contrast to findings of Christoffersen et al. (2019), who reported site fidelity as low as 2% in
gobies moving along the Baltic Sea coast. In this case, environmental conditions (estuarine with
tidal currents and mixing salinities as compared to relatively stable freshwater conditions) may
have played a role in limiting goby dispersal. In other freshwater systems, studies tend to report
high site fidelity (Wolfe and Marsden 1998; Ray and Corkum 2001; Lynch and Mensinger
2012), as in our study, with some reports exceeding our values with up to 90% or more fidelity.
One possible reason for the relatively low fidelity recorded in our study (compared with the
freshwater studies mentioned above) may be our use of unbaited sampling. Previous studies
used either baited traps or rod and line fishing, thereby introducing possible bias (over-
estimating site fidelity) by including fish that are attracted to the bait from elsewhere.
Furthermore, we studied relatively small-scale fish movements (over 10m sections) and/or used
relatively long recapture times (approx. 30 days). Nevertheless, our rate of fidelity was still
high and provides strong evidence that the majority of the established goby population consisted
of highly stationary individuals. A similar pattern has also been reported for other small benthic
fishes, including darters (Hicks and Servos 2017), balitorids (Mitsuo et al. 2013) and,
especially, cottids (Hudy and Shiflet 2009).

During the spawning period, site fidelity in the established population appears to have
relaxed, with 35.3% of fish remaining stationary compared with 73.2% during pre-spawning
and 70% post-spawning. Such a difference was not expected, however, as fish are likely to be
more active in the pre-spawning season as they return from their overwintering refuges, increase
feeding and seek spawning sites. Our finding of increased movement during the spawning
season was somewhat surprising as it is presumed that large territorial males remain stationary
at this time while they guard egg clutches (Corkum et al. 1998; Meunier et al. 2009; but see
Všetičková et al. 2015). A possible explanation could be that while larger territorial males remain stationary, the activity of both smaller males (supposed sneakers; Bleeker et al. 2017) and females increases as they search for suitable nests. Interestingly, while a similar seasonal activity pattern (increased activity in the spawning season) is occasionally documented in cottids (Knaepkens et al. 2004) and other, non-benthic fishes (Freeman 1995; Ovidio et al. 2002), it is not a general pattern among fish (Lucas and Baras 2008).

Site fidelity appears to be typical for gobies as long-term fidelity was also apparent in overwintering fish, most of which were recaptured within 40 m of the original capture site after more than 200 days. Though surprising, such long-term fidelity has been reported in previous studies. Lynch and Mensinger (2012), for example, noted similar fidelity in overwintering round gobies from Lake Superior, while Breen et al. (2009) and Huddy and Shiflet (2009) have reported long-term site affinity in cottids. One interpretation for our own observations is that round gobies overwinter at the same site where they stay the remainder of the year (with the exception of spawning). However, this would contradict previous studies that interpret decreases in winter round goby abundance as evidence of winter migrations to deeper areas (Sapota and Skóra 2005; Pennuto et al. 2010). While a similar decrease in winter nearshore abundance has been documented from our study site (Jurajda, unpublished data), the fidelity of overwintering fish suggests that the decrease may be attributable to reduced catchability, e.g. through temperature-related activity suppression. On the other hand, our data do not disprove the occurrence of winter migrations as our results could also be showing that gobies migrated to an (unknown) winter refuge, from where they were able to return to the same spot they left. Though there have been previous suggestions of such behaviour in round goby (e.g. see Marentette et al. 2011; Lynch and Mensinger 2012), it has yet to be confirmed; hence, this question remains open and calls for further research.
Round gobies in the established population moved 1.97 m per day on average and a maximum of 16 m per day upstream, distances similar to those reported from Lake Superior by Lynch and Mensinger (2012), i.e. 0.79 m per day on average and a maximum of 7-15 m per day during long-term dispersal (more than two weeks; see, however, Christoffersen et al. 2019 for much higher rates in the Baltic estuary). While recording upstream movement of the round goby invasion front on the River Dyje, Šlapanský et al. (2017) recorded movements of 3.2 km per year, equivalent to 8.77 m per day. A more conservative estimate by Bergstrom et al. (2008) suggested natural invasion front movements of 1 km per year, i.e. 2.74 m per day, in Lake Superior. On the other hand Cerwenka et al. (2018) documented mean dispersal rates of round gobies about 10 km per year along the upper Danube and Azour et al. (2015) even observed a range expansion on average 30 km per year along the Baltic Sea coast. The average movement rates of fish in established populations clearly do not match the speeds achieved in invasive front shifts. However, such a speed could theoretically be achieved if one considers the maximum distances recorded in established populations, which can be even higher for short-term observations, with individuals even achieving 40 to 50 m per day (Lynch and Mensinger 2012; Brandner et al. 2015). Potentially, high rates of invasion front shift thus could be maintained by a series of short-term intensive jumps. Thus far, however, it is uncertain whether long-distance dispersers can maintain such high movement rates over long periods (i.e. longer than a month), with the evidence generally suggesting otherwise (Lynch and Mensinger et al. 2012). On the other hand, fish in the invasion front encounter significantly lower intraspecific density than those in the established population (Azour et al. 2015; Šlapanský et al. 2017). Further, a number of studies have documented increased boldness and greater phenotypic plasticity in fish at the invasive front (Brandner et al. 2013b; Myles-Gonzales et al. 2015; Thorlacius et al. 2015; Brandner et al. 2018), which may even result in the ‘Olympic village effect’ (Phillips et al. 2008). Such factors can result in fish at the invasion front moving at
greater rates than those in the established population (Phillips et al. 2008; Chuang and Peterson 2016).

Fish in the *Release* experiment (simulating the release of large numbers at a single spot) moved approximately three times further than those in the established population, reaching up to 670 m over 30 days (average 199.17 m), or 22.33 m per day (av. 6.64 m). This relatively high movement rate most likely reflects increased intraspecific competition due to high propagule pressure, though several other factors may also have contributed. The optimal rip-rap habitat is limited to a narrow strip along the Dyje; hence, limited access to usable shelters could also increase intraspecific competition, and thus movement activity. Those gobies ‘forced’ out of the narrow rip-rap zone may be forced to enter the faster-flowing gravel section in the middle of the stream, which could further facilitate dispersal by increasing the intensity of movement to avoid unfavourable conditions (Ray and Corkum 2001; Brandner et al. 2015).

It is likely that the sub-optimal conditions in the middle of the stream contributed to the low proportion of fish crossing to the other bank (eight individuals, 7.5 %). Support for this is provided by Brandner et al. (2015), who noted that gobies in the Danube never crossed the river and that spreading took place solely along near-bank rip-rap structures. The fact that some gobies did cross the Dyje may be explained by two factors. First, the Dyje is much narrower than the Danube, making the crossing easier; second, high competition pressure generated at the release point forced large numbers of gobies to move out of the rip-rap, thereby generating short-term competitive pressure outside of the rip-rap zone itself. This may have resulted in some individuals breaking away from the population and moving to the other bank, a hypothesis supported by the above-average distances reached by the river-crossers (200–670 m). In fact, high propagule pressure at the release site (as has been suggested by genetic studies; Janáč et al. 2017) may be one cause of round gobies colonising both banks of large rivers, without the
need for independent introductions to both banks and despite a general unwillingness to cross under normal conditions (Brandner et al. 2015).

Both the Movement and Release experiments provided evidence of directional movement, with a clear preference for moving upstream. This corresponds with previous observations of relatively rapid upstream spread of round goby populations (Phillips et al. 2003; Poos et al. 2010; Šlapanský et al. 2017), with less intense downstream dispersal (Brownscombe and Fox 2012), though the latter has received relatively little study. On the other hand, passive downstream dispersal of gobiid early life stages could serve as a counterbalance for the predominant upstream movement of adults (Janáč et al. 2013a, 2013b), i.e. different age groups are responsible for the invasion process, with upstream dispersal predominantly undertaken by adults while early life stages contribute to rapid downstream dispersal (Janáč et al. 2012; Roche et al. 2015).

In each of the three experiments, there were signs of size-related movement patterns, though with some differences in each case. In the Movement experiment, for example, smaller fish tended to travel greater distances, though the effect of size was only close to significance, suggesting smaller fish in established populations travel further. In the Release experiment, smaller males moved further from the common release point than larger males, but not females. Finally, in the Colonisation experiment, smaller fish were found further from the edges of the re-colonised sections, again suggesting that smaller fish are the first colonisers of ‘goby-free’ stretches.

Greater movement by smaller fish could be explained by interspecific competition (especially in the Release experiment), with smaller fish presumably having inferior competitive ability. Ray and Corkum (2001), for example, suggested that larger gobies outcompete smaller gobies, forcing them out of the preferred rip-rap areas and onto beaches (see also Johnson et al. 2005; Bergstrom et al. 2008; Brownscombe and Fox 2012). Likewise,
Groen et al. (2012) showed that, if an opponent was only slightly larger, then the smaller round goby did not interact aggressively but rather moved to another site. This would suggest that, as the population density in the core area grows and the number of larger individuals increases, then smaller individuals are pushed to the edge of the core area and there create the invasion front (Ray and Corkum 2001, Thorlacius et al. 2015).

Our results for size-biased movement in the Colonisation experiment may provide the most significant contribution in the ongoing debate as to whether smaller or larger gobies are the ‘pioneers’ leading the invasion front into unsettled areas (Šlapanský et al. 2017). While the experiment was not an ideal model of an invasion front (as goby density in adjacent stretches was still high, corresponding to an established population), it demonstrated that smaller gobies were the first to move into ‘goby-free’ stretches. However, previous studies show wide variation in invasion front size composition, with fish ‘pioneers’ ranging from small (Johnson et al. 2005; Bergstrom et al. 2008; Brownscombe and Fox 2012), through medium (Azour et al. 2015) and large (Gutowsky and Fox 2011; Brandner et al. 2013), and even with differences occurring in the same river (Šlapanský et al. 2017). There are several possible explanations for this variation. First, pioneers may represent a combination of outcompeted smaller fish and larger bolder individuals that are predisposed to move further and explore areas outside the core population (e.g. see Brownscombe and Fox 2012). Indeed, many invasion front and edge populations have been shown to contain a large proportion of bolder individuals (Groen et al. 2012; Myles-Gonzales et al. 2015; Hirsch et al. 2017), though it has yet to be proved whether these fish are bold because they live in an area of low goby density or because their boldness caused them to move away from the core population. Secondly, it may take a relatively long time for gobies to disperse to the invasion edge from the core population. Hence, while the pioneer fish starts small, it may increase in weight and length relatively rapidly in new habitats with an abundant (competition free) food source. The size of fish
caught at the invasion front, therefore, would depend on any temporal lag (detection lag
phase) and regional conditions (Sakai et al. 2001).

To conclude, round goby movement activity within an established population displayed
a typical leptokurtic movement pattern, with the vast majority of the population remaining
stationary and just a few small long-range dispersers. These results also suggest that smaller
individuals most likely contribute to ‘natural’ range expansion, with intraspecific competition
the likely driver. These patterns appear to be accentuated in the lower Dyje, where optimal
habitat is limited to a narrow strip of bankside rip-rap and upstream expansion is the only option
for competitively weak smaller individuals, and especially males. Local conditions, whether
biotic or abiotic, also play a substantial role in round goby movement patterns.

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Figure captions:

Fig. 1. Map of the area studied. (a) Section of the Dyje River that was searched for tagged round gobies (*Neogobius melanostomus*). Empty circles indicate control points (200 m long) checked for the presence of potential long-distance dispersers. (b) Enlargement showing ‘core’ study section, where all fish were initially tagged and released. Black points indicate release points for *Release* experiment, grey points indicate upper and lower borders of the shoreline searched in recapture campaign. Tagging section (TS) for the *Movement* experiment is indicated by the dark grey area. Light grey area shows upstream and downstream buffer zones (BZ), at least 200 meters long, which were searched to capture fish that potentially moved out of the TS. The *Colonisation* experiment sites were randomly situated within the TS. (c) Localisation of the site (empty square) within the European continent. The Danube River and the Czech Republic are highlighted.

Fig. 2. Distance reached over one month between capture and recapture by round goby males (points) and females (triangles) during the pre-spawning (green), spawning (red) and post-spawning (blue) seasons (*Movement* experiment). Positive values show upstream movement, negative downstream. Only fish that moved beyond the original 10-m stretch (non-null movement) are shown. Fish size values in the figure were slightly adjusted by adding a random small number in order to prevent overlap of two or more points. Please note that x-axis scale interruptions were needed to show long-distance movements.

Fig. 3. Distance reached by round goby males (points) and females (triangles) between capture and recapture over periods > 200 days (239-369 days; includes winter months; *Movement* experiment). Positive values show upstream movement, negative downstream.

Fig. 4. Distance reached from release point by round goby males (full points) and females (empty squares) within 30 days and its relationship to fish size (*Release* experiment). Positive values show upstream movement, negative downstream.

Fig. 5. Cumulative proportion of round gobies dispersing up-(red area) and downstream (blue area) of the release point (0) within 30 days (*Release* experiment). Dashed and dotted white lines determine how far 50% and 75% of fish dispersed, respectively (calculated separately for up- and downstream dispersers). Points determine the mean distance reached.
Fig. 6. Distance reached from the introduction point as a function of fish size in male (upper panel) and female (lower panel) round gobies (Release experiment). Full points = upstream dispersal, empty squares = downstream dispersal. In males, the curve predicted by GLM is shown as a solid line and 95% confidence intervals as dashed lines. No such curve is shown for females as the relationship was not significant.

Fig. 7. Distance from the 20m section border in relation to fish size (Colonisation experiment). The curve predicted by GLMM is depicted by a solid line and 95% confidence intervals as dashed lines.
Movement experiment

![Graph showing movement experiment data]

Fig. 2
Fig. 3

Movement experiment

Fish size (mm)

Distance reached (m)

https://mc06.manuscriptcentral.com/cjfas-pubs
Release experiment

Fish size (SL, in mm)

Distance reached (m)

downstream  upstream

Fig. 4
Fig. 5

Release experiment

Cumulative proportion

Distance reached (m)
Release experiment

Distance reached (m) vs Fish size (mm) for males and females.

Fig. 6