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Application of large wood in regulated riverine habitats facilitates native fishes but not invasive alien round goby (*Neogobius melanostomus*)

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Editor’s note:
This study was first presented at the Centre for Wetland Ecology (CWE) symposium (24 June 2016, Wageningen, the Netherlands) on the role of exotic species in aquatic ecosystems ([https://www.wetland-ecology.nl/en/calendar/good-bad-or-bit-both-role-exotic-species-aquatic-ecosystems](https://www.wetland-ecology.nl/en/calendar/good-bad-or-bit-both-role-exotic-species-aquatic-ecosystems)). This symposium provided a venue to unravel how exotic plants and animals impact ecosystem functioning, find out whether they coexist or compete with native species and discover their impact on native flora and fauna.

Abstract
Regulated rivers in Western Europe have rapidly been colonized by invasive alien Pontoo-Caspian gobies. In particular, the round goby (*Neogobius melanostomus*) can reach high densities in habitats with hard substratum, such as groynes and dams made of basalt stones. High densities of Pontoo-Caspian gobies negatively impact native benthic fishes. It is hypothesized that natural complex three-dimensional structures in Western European rivers, such as (pieces of) large wood (e.g., trees that fell into the river), are a less attractive habitat for Pontoo-Caspian gobies. These bottom-dwelling fishes are strongly associated with sheltered places on the river bottom and may avoid the three-dimensional structure of large wood in the water column. The colonization of littoral zones provided with large wood (i.e., entire trees) by round goby and native fishes was studied in the River Lek (a distributary of the River Rhine) in the Netherlands during the period 2014–2016. The fish assemblage of four reference sites dominated by basalt stones was compared with that of four large wood sites. Counts of round goby in large wood habitats were significantly lower than in habitats dominated by basalt stones, while native fishes were more abundant in large wood habitats. In large wood habitats counts of native fishes were significantly higher than those of round goby, whereas the reverse was true in the reference habitat. Counts of the entire fish assemblage did not significantly differ between habitat types. These results suggest that large wood in regulated Western European rivers predominantly functions as a suitable habitat for native fishes whereas the invasive bottom-dwelling round goby only uses large wood habitats to a limited extent. Large wood may be applicable as a management tool to stimulate native fish fauna with minimal facilitation of the round goby.

Key words: habitat restoration, hard substratum, littoral zone, non-native species, Pontoo-Caspian species, River Lek, River Rhine
Introduction

Since 2002, several regulated rivers in Western Europe (e.g., Rivers Rhine, Meuse, Scheldt and Elbe) have been rapidly colonized by four species of invasive Ponto-Caspian gobies (Gobiidae) (Verreycken et al. 2011; Cammaerts et al. 2012; Van Kessel et al. 2013, 2016; Buřič et al. 2015). These bottom-dwelling gobies show a strong preference for man-made habitats with hard substratum, such as groynes and dams made of basalt stones, rip rap in the littoral zone and pebbles; habitat types that are common in the regulated rivers of Western Europe as they protect the banks from erosion and maintain the main river channel (Ray and Corkum 2001; Young et al. 2010; Van Kessel et al. 2013; Pander and Geist 2016). As a consequence, mean densities of gobies on this hard substratum can be very high, e.g., up to 145 individuals per 100 m² (Van Kessel et al. 2016). These high goby densities may negatively impact native benthic fish species, in particular Cottus species. In the Netherlands and Belgium two native Cottus species have been distinguished, viz. river bullhead Cottus perifretum and stream bullhead C. rhenanus (Stemshorn et al. 2011; Colleye et al. 2013). Differences in morphological and genetic identity of these Cottus species are under debate: the literature also refers to both species as Cottus gobio (Grabowska et al. 2016). The rapid colonization of the lower Meuse by round goby (Neogobius melanostomus) resulted in a strong decline of Cottus perifretum, a protected and endangered species (Van Kessel et al. 2016). Such negative effects of invasive alien gobies on native benthic fish species have also been found elsewhere (Jude et al. 1995; Corkum et al. 2004; Dubs and Corkum 1996; Janssen and Jude 2001; Lauer et al. 2004; Jurajda et al. 2005; Balshine et al. 2005; Von Landwüst 2006; Karlson et al. 2007; Bergstrom and Mensinger 2009; Kornis et al. 2012).

Most Western European rivers are interconnected via multiple canal systems (Leuven et al. 2009). This makes it impossible to prevent the spread and settlement of Ponto-Caspian gobies. Before the major river regulations in the 19th and 20th centuries, stony habitats were not commonly present in lowland reaches and distributaries of large Western European rivers. The only natural complex three-dimensional structures in such water bodies were formed by woody material, i.e., entire trees or branches and trunks that fell into the river (here called “large wood”), and aquatic macrophytes. These structures formed an important habitat for macro-invertebrates and fishes (Dollof and Warren 2003; Pander and Geist 2016). Over the last century almost all dead large wood in and along Western European rivers has been removed in order to improve water discharge and reduce risk of collision with ships and weirs. Recently, managers have tried to restore these original complex large wood habitats by installing large trees under water in the littoral zones (Van Kessel et al. 2008; Pettit et al. 2013; Dossi et al. 2015; Pander and Geist 2016). In contrast to the large surface of stone habitats on the river bottom for which gobies have a strong preference, the complex structure of large wood habitats fills the whole water column with tree branches and roots, with only a small part of the structure resting on the bottom. To assess the ecological effects of habitat restoration, the National Water Authority of the Netherlands started a pilot project in which large wood structures were artificially submerged and anchored in the littoral zones of the River Lek, a distributary of the River Rhine (Schoor et al. 2015) characterized by high densities of round goby (Van Kessel et al. 2013, 2014a).

The aim of our study was to investigate whether the application of large wood in regulated rivers could be a management tool that facilitates native fish species in favour of invasive alien round goby. Native species are expected to profit from natural habitat complexity in littoral zones. While artificial basalt stone habitats are supposed to be preferred habitats for round goby (Van Kessel et al. 2016), large wood may be less suitable because it contains fewer shelters. We therefore hypothesized that the introduction of large wood (i.e., the introduction of entire trees including branches, trunks and roots) in the littoral zone of regulated rivers would favour native fish species (especially non-benthic species) over round goby.

Methods

Study sites

The study was carried out at eight sites in the River Lek near Everdingen in the centre of the Netherlands (51.969607°N; 5.162606°E). Five sites were situated in the littoral zone of this river and the three other sites in a floodplain lake that was hydrologically connected with the main channel (Figure 1). The sites in the floodplain lake were not directly affected by river dynamics and currents, in contrast to the river bank sites. The Dutch river authority, Rijkswaterstaat, limited the number of sites for this pilot study due to potential risks of large wood floating and subsequently damaging infrastructure and ships. Moreover, the costs of this kind of pilots and measurements are very high. Based on budgets, logistics and potential risks it was not possible to increase the number of sites.
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Figure 1. Map of the study area in the River Lek (a Rhine distributary; arrow in the upper right panel indicates the location in the Rhine-Meuse delta in the Netherlands) showing reference sites (n = 4) and large wood sites (n = 4). Study sites were situated in the littoral zones of the main channel and a hydrologically connected floodplain lake. Letters refer to Table 1.

Table 1. Geo-reference and dimensions of surveyed transects at each study site (Letters correspond to sites in Figure 1).

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude (°N)</th>
<th>Longitude (°E)</th>
<th>Transect length (m)</th>
<th>Transect width (m)</th>
<th>Surface area (m²)</th>
<th>Depth range (m)</th>
<th>Habitat type</th>
<th>Type of structure</th>
<th>Location</th>
<th>Number of trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>51.969205</td>
<td>5.151040</td>
<td>15</td>
<td>3.0</td>
<td>45</td>
<td>1.5–2.5</td>
<td>large wood</td>
<td>a, c</td>
<td>lake</td>
<td>1</td>
</tr>
<tr>
<td>B</td>
<td>51.972936</td>
<td>5.146682</td>
<td>30</td>
<td>3.0</td>
<td>90</td>
<td>0.5–2.5</td>
<td>large wood</td>
<td>a, c</td>
<td>lake</td>
<td>2</td>
</tr>
<tr>
<td>C</td>
<td>51.973403</td>
<td>5.147257</td>
<td>139</td>
<td>1.5</td>
<td>209</td>
<td>0.5–1.5</td>
<td>reference</td>
<td>b, c</td>
<td>lake</td>
<td>–</td>
</tr>
<tr>
<td>D</td>
<td>51.969074</td>
<td>5.179999</td>
<td>234</td>
<td>1.5</td>
<td>351</td>
<td>0.5–2.5</td>
<td>reference</td>
<td>b, c, d</td>
<td>river</td>
<td>–</td>
</tr>
<tr>
<td>E</td>
<td>51.968644</td>
<td>5.171697</td>
<td>35</td>
<td>3.0</td>
<td>105</td>
<td>0.5–1.5</td>
<td>large wood</td>
<td>a, c</td>
<td>river</td>
<td>2</td>
</tr>
<tr>
<td>F</td>
<td>51.968457</td>
<td>5.173850</td>
<td>260</td>
<td>1.5</td>
<td>390</td>
<td>0.5–2.0</td>
<td>reference</td>
<td>b, c, d</td>
<td>river</td>
<td>–</td>
</tr>
<tr>
<td>G</td>
<td>51.967840</td>
<td>5.176670</td>
<td>170</td>
<td>1.5</td>
<td>255</td>
<td>0.5–2.5</td>
<td>reference</td>
<td>b, c, d</td>
<td>river</td>
<td>–</td>
</tr>
<tr>
<td>H</td>
<td>51.967336</td>
<td>5.177640</td>
<td>15</td>
<td>3.0</td>
<td>45</td>
<td>0.5–2.0</td>
<td>large wood</td>
<td>a, c</td>
<td>river</td>
<td>1</td>
</tr>
</tbody>
</table>

a: entire dead tree, b: basalt stones, c: clay-sand bottom, d: vertical wooden piles, -: not applicable.

Large wood, consisting of oak (*Quercus robur*), was introduced in March 2014 to four sites (two in the littoral zone of the river and two in the floodplain lake, Table 1). At each site, complete trees approximately 15 m long (including roots, stem and main branches) were positioned horizontally on the sandy river bottom close to basalt stones (varying in distance from 11–57 m). Each tree was firmly anchored with steel chains to poles in the river bottom, preventing emergence and drift into the main channel. The steel chains and poles do not have a complex three-dimensional structure, so the contribution of these artificial structures to the complexity of the large wood habitat is negligible. At two sites, two trees were placed adjacent to each other, while single trees were placed at the two remaining sites. Maximum water depth at all four sites varied from 1.5–2.5 m, and in all cases the branches of each tree reached the water surface. The three-dimensional structure of the trees thus occupied the entire water column from river bottom to water surface.

In addition to the four large wood sites, four nearby sites with other representative river habitat types that have a relatively high degree of structural complexity (basalt stones) were selected as reference sites (Table 1). The distance between reference and large wood sites varied from 10–612 m. The reference sites were covered with continuous areas of stone. The size and volume of stones varied between 4–30 cm and 0.2–21 L. Stones were present in groynes as well as zones of vertical wooden poles that were installed to break shipping induced waves and to prevent bank erosion. Three reference sites were positioned close to the large wood sites in the main channel and one reference site was located in the floodplain lake in an open connection to the river. In all sites, the
substratum consisted of a clay-sand mixture underlining the stones or wood. Aquatic macrophytes were absent.

The large wood sites did not contain basalt blocks and were originally free of complex structures. Fish data before the introduction of trees to these sites was lacking. Therefore, data from nearby sites with clay-sand substratum were used in place of a before-after comparison.

**Fish sampling**

The fish assemblage of each site was sampled seven times, in May, June, July and September 2014, July 2015, and August and October 2016. The fish surveys were conducted in permanent transects using a small powered boat with electro fishing equipment (DEKA 7000 N, Mühlenbein, DEKA Gerätebau, Marsberg, Germany). This method is suited to sample fish assemblages in structurally complex habitats such as wood, branches and basalt stones (Van Kessel et al. 2016), and was applied similarly to all sites. At all large wood sites, the survey transects encircled the entire tree(s), i.e., the entire surface of the large wood habitat was sampled. This resulted in transect lengths varying from 15–53 m, depending on the exact length and number of trees added to each site. Transect lengths of reference sites (139–260 m) were longer than those of large wood sites as all microhabitats types, such as variation in basalt stone structure and water depth, were encompassed in the surveys. The width of transects at reference sites was 1.5 m and at large tree sites 3.0 m, determined by the effective range of the electro fishing equipment. Transect lengths were measured with a hand-held GPS. The bottom varied in depth from 0.5–2.5 m for both reference and large wood sites, and was thus accessible to the electrofishing apparatus. Captured fishes were immediately identified and released again into the river.

In addition to the fish data collected in the present study, a 3-year fish survey had been conducted by the Dutch water authority in the period 2013–2016 in the River Lek, approximately 16 km upstream from the sites in the present study (starting at the coordinates 51.964°N latitude and 5.344°E longitude). Twelve fixed transects in the main channel (mean surface of 2845 m²) were sampled using a 3 m wide bottom trawl. Four transects in the shallow littoral zone (mean surface of 598 m²) were sampled using electro fishing. Details of this survey are provided in Van Kessel et al. (2014b). The data on mean fish density were used to characterize the occurrence of round goby and native fish species in the year prior to the introduction of large wood (i.e., 2013).

**Data analysis**

For each date and each sampling site, fish counts and sampled surface area were available. The effects of habitat type and survey date on the fish assemblage were assessed by fitting generalized linear mixed models with a log-link function based on Poisson distributions.

First, models were constructed to compare counts of round goby and native fishes within a single habitat type (either reference habitat or large wood). Fish counts were the dependent variable, while species (round goby versus native fish species), date of survey, and their interaction were fixed factors. Sampled surface area was included as an offset to account for differences between sites. The spatial effect of site (main channel or floodplain lake) was included as a random factor.

Second, models were constructed to compare counts of round goby and native fish species and the total fish assemblage in which counts of all seven surveys were pooled together. Subsequently, models were developed where habitat type was set as a fixed factor and either counts of round goby, native fish species, or the total fish assemblage were set as the dependent variable. Other species (round goby versus native fish) were set as a fixed factor and sampled surface area was used as an offset to account for differences in sampled surface area between sites. The spatial effect of sites and the temporal effect of date of survey were included as random factors.

Models were fitted with the glmer function in the lme4 package (Bates et al. 2017). Additive overdispersion was modelled by adding an extra count random factor according to Nakagawa and Schielzeth (2010), i.e., over-dispersion is absorbed by this added count term. To test the significance of all model factors and interactions, we performed deviance tests (likelihood ratio tests) comparing the maximum likelihood estimated from models including the fixed variable of interest and models without them (Crawley 2007; Zuur et al. 2009). All statistical analyses were performed in R version 3.3.1 (R Development Core Team).

Since surveyed habitats differed in sampled surface area (i.e., reference sites had a larger sampled surface area than large wood sites, Table 1), fish densities (i.e., fish counts corrected for the sampled surface area) were used in graphs to allow direct comparisons.

**Results**

In total, 17 fish species were observed during the seven surveys (Table 2). The number of observed species was higher in the large wood habitat (15 species) than
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### Table 2. Mean density (individuals 100 m−2 ± SE) of fish species observed during the study period (based on mean densities per site of seven sampling dates in the period 2014–2016). For both the reference and large wood habitat type, four replicate sites were available.

<table>
<thead>
<tr>
<th>Alien species</th>
<th>Scientific name</th>
<th>Reference habitat mean ± SE</th>
<th>Large wood habitat mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Round goby</td>
<td>Neogobius melanostomus</td>
<td>47.63 ± 5.06</td>
<td>5.83 ± 1.35</td>
</tr>
<tr>
<td>Bighead goby</td>
<td>Ponticola kessleri</td>
<td>1.97 ± 0.32</td>
<td>0.19 ± 0.10</td>
</tr>
<tr>
<td>Asp</td>
<td>Aspius aspius</td>
<td>0.20 ± 0.18</td>
<td>0.34 ± 0.18</td>
</tr>
<tr>
<td>Monkey goby</td>
<td>Neogobius fluviatilis</td>
<td>0.02 ± 0.02</td>
<td>0.02 ± 0.02</td>
</tr>
<tr>
<td>Whitefin gudgeon</td>
<td>Romanogobio belingi</td>
<td>– –</td>
<td>0.02 ± 0.02</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Native species</th>
<th>Scientific name</th>
<th>Reference habitat mean ± SE</th>
<th>Large wood habitat mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roach</td>
<td>Rutilus rutilus</td>
<td>10.86 ± 3.80</td>
<td>62.31 ± 19.63</td>
</tr>
<tr>
<td>Eurasian perch</td>
<td>Perca fluviatilis</td>
<td>1.14 ± 0.29</td>
<td>6.54 ± 2.20</td>
</tr>
<tr>
<td>European eel</td>
<td>Anguilla anguilla</td>
<td>2.91 ± 0.68</td>
<td>0.03 ± 0.03</td>
</tr>
<tr>
<td>Bleak</td>
<td>Alburnus alburnus</td>
<td>– –</td>
<td>1.85 ± 0.85</td>
</tr>
<tr>
<td>Ide</td>
<td>Leuciscus idus</td>
<td>0.84 ± 0.41</td>
<td>0.39 ± 0.20</td>
</tr>
<tr>
<td>Pike-perch1</td>
<td>Sander lucioperca</td>
<td>0.02 ± 0.02</td>
<td>0.97 ± 0.38</td>
</tr>
<tr>
<td>Common bream</td>
<td>Abramis brama</td>
<td>– –</td>
<td>0.08 ± 0.08</td>
</tr>
<tr>
<td>Rudd</td>
<td>Scardinius erythrophthalmus</td>
<td>– –</td>
<td>0.07 ± 0.05</td>
</tr>
<tr>
<td>Silver bream</td>
<td>Blicca bjoerkna</td>
<td>– –</td>
<td>0.05 ± 0.05</td>
</tr>
<tr>
<td>Three-spined stickleback</td>
<td>Gasterosteus aculeatus</td>
<td>0.05 ± 0.05</td>
<td>– –</td>
</tr>
<tr>
<td>Common nase</td>
<td>Chondrostoma nasus</td>
<td>– –</td>
<td>0.03 ± 0.03</td>
</tr>
<tr>
<td>Bitterling2</td>
<td>Rhodeus amarus</td>
<td>0.02 ± 0.02</td>
<td>– –</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Totals</th>
<th></th>
<th>Reference habitat mean ± SE</th>
<th>Large wood habitat mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alien fish – total</td>
<td>49.83 ± 5.26</td>
<td>6.41 ± 1.47</td>
<td></td>
</tr>
<tr>
<td>Native fish – total</td>
<td>15.89 ± 4.21</td>
<td>72.45 ± 19.89</td>
<td></td>
</tr>
<tr>
<td>All fish – total</td>
<td>65.72 ± 7.26</td>
<td>78.86 ± 19.86</td>
<td></td>
</tr>
<tr>
<td>Number of alien species</td>
<td>4</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Number of native species</td>
<td>8</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Number of all fish species</td>
<td>12</td>
<td>15</td>
<td></td>
</tr>
</tbody>
</table>

–: species not observed.

Native or alien status of pike-perch1 and bitterling2 is debated. In the present study both species are considered as naturalized since they were introduced in the Netherlands before the 20th century and have been widely distributed over the country for more than 100 years.

in the reference habitat (12 species). Five alien fish species were observed during the study, with the round goby completely dominating the fish assemblage (Table 2). Of the native fish species, roach, perch, eel and bleak were observed in the highest densities (mean density in either reference or large wood habitat > 1 individual 100 m−2, Table 2).

Round goby showed significantly higher counts than the native fish species in the reference habitats (Figure 2a, AICf = 447; AICwv = 469; χ² = 26.15 df = 2; P < 0.001), while at the sites with large wood, counts of native fish species were significantly higher than counts of round goby (Figure 2b, AICf = 419; AICwv = 447; χ² = 32.61 df = 2; P < 0.001). Neither date of survey (reference site: AICf = 447; AICwv = 444; χ² = 1.15 df = 2; P = 0.563; large wood: AICf = 419; AICwv = 416; χ² = 1.53 df = 2; P = 0.465) nor the interaction between date of survey and species (reference site: AICf = 447; AICwv = 445; χ² = 1.52 df = 2; P = 0.218) had a significant effect in either habitat.

When data from all surveys were pooled, there was a strong difference in densities of round goby between reference habitats and large wood habitats (Figure 3b). Reference habitats had a significantly higher density of round goby than large wood habitats (AICf = 376; AICwv = 425; χ² = 50.83 df = 1; P < 0.001) and higher counts of round goby than native fish species (AICf = 444; AICwv = 468; χ² = 25.94 df = 1; P < 0.001). Large wood habitats showed the opposite effects with significantly higher counts of native fish species (AICf = 444; AICwv = 468; χ² = 10.56 df = 1; P = 0.001) than the reference habitats and native fish species showing significant higher counts than round goby (AICf = 416; AICwv = 445; χ² = 31.11 df = 1; P < 0.001). However, counts of the total fish assemblage (Figure 3a) were not significantly different between reference and large wood habitats (AICf = 544; AICwv = 544; χ² = 1.75 df = 1; P = 0.186).

Fish surveys that were conducted in the period 2013–2014 in a nearby part of the River Lek showed that the round goby was already present in this reach in 2013, the year prior to introduction of large wood.
Figure 2. Mean density of invasive round goby (Neogobius melanostomus) and total native fish species (all native fishes pooled) in (a) reference habitats and (b) large wood habitats during seven fish surveys in the period 2014 - 2016. Asterisks indicate significantly different fish counts between round goby and native fish species during the surveys based on generalized linear mixed models (***: \( P < 0.001 \)). To allow direct comparisons of habitats with different sampled surface areas, fish assemblages in the figure panels are expressed as densities rather than counts.

Figure 3. Mean density for (a) the total fish assemblage and (b) invasive round goby (Neogobius melanostomus) and the native fish species in reference and large wood habitat. Asterisks and letters show results of generalized linear mixed model comparisons of fish counts between reference versus large wood habitats for round goby, native fish species and for the total fish assemblage, or between native fish species versus round goby within a single habitat. To allow direct comparisons of habitats with different sampled surface areas, fish assemblages in the figure panels are expressed in densities rather than counts. Similar asterisks or letters indicate significant differences between species or habitats respectively: round goby in reference vs. large wood: ***: \( P < 0.001 \); native fishes in reference vs. large wood habitat: **: \( P = 0.001 \); round goby vs. native fish in reference habitat: A: \( P < 0.001 \); round goby vs. native fishes in large wood habitat: B: \( P < 0.001 \); total assemblage between reference and wood habitat: NS: not significant, \( P = 0.186 \).
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Figure 4. Mean density of invasive round goby (Neogobius melanostomus) and native fish species (all species pooled) for the main channel and shallow bank near the study sites (Data from: Van Kessel et al. 2014b).

(Figure 4). Mean densities of round goby in the main channel remained relatively constant (Figure 4a), whereas densities on the shallow bank showed a peak in 2014 (Figure 4b). Densities of native fish species were relatively stable during the period 2013–2015.

Discussion

The introduction of large wood in the river system resulted in the rapid colonization of the provided habitat by fishes, i.e., high fish densities were observed around the large wood in the year of introduction. The total number of observed species in the large wood habitat was higher than in adjacent reference habitats (15 species versus 12 species). The fish assemblage of large wood predominantly consisted of native fish species, whereas the reference habitats were dominated by the invasive alien round goby. This pattern was more or less consistent over the whole study period, indicating that round goby hardly colonizes large wood habitats in contrast to basalt stone habitats. However, there were a few native species that also had lower densities in the large wood habitat than in the reference habitat, most notably the European eel (Anguilla anguilla) and Ide (Leuciscus idus).

The fish survey in the nearby part of the River Lek showed that round goby had already colonized this river in 2013 and maintained relatively stable densities in the main channel in the period 2013–2015, although densities on the shallow bank were more variable. Native fish species also showed relatively stable densities in this part of the river, both in the main channel and shallow bank. This suggests that at the sites in the present study, established populations of both round goby as well as native fish species were present, representative of the fish population in the River Lek.

The driving mechanisms that explain the differences in densities of round goby between the investigated habitats may be part of the ecological strategy of the species. First, this species has a strong bottom associated lifestyle. Round goby does not have a swim bladder (Belanger and Higgs 2005). Therefore, the species is strongly associated with the bottom and cannot easily colonize structures in water compartments with high dynamics (e.g., shipping induced water displacements and flow changes) and lack of shelter. Second, the round goby uses small holes and crevices for shelter (Balshine et al. 2005; Van Kessel et al. 2011, 2016). Despite the complex three-dimensional structure of large wood, visual observations during the fish surveys revealed that shelter space for benthic fish species was only present at the root-bottom interface. As a result, the largest part of the wood structure is not a suitable habitat for round goby. Round goby is a strong competitor for shelter and without shelter it is highly sensitive to predation by native predatory fish species (such as pike-perch Sander lucioperca), waterbirds (such as cormorants) and water snakes (Somers et al. 2003; King et al. 2006; Hempel et al. 2016).

In contrast to the bottom-dwelling round goby, all observed native fish species have a swim bladder and are relatively good swimmers that can easily move throughout the water column. Since the water velocity in the River Lek is very low because of the presence of weirs, these native fish species can easily reach the structure provided by large wood. It is also likely that the large wood habitat provides a large amount of food for zoobenthivorous and zooplanktivorous fish species, resulting in an attractive
feeding habitat (Dollos and Warren 2003; Nagayama et al. 2008; Petit et al. 2013; Dossi et al. 2015; Pander and Geist 2016). Since fish density is relatively high around the large wood structures, piscivorous fish species also use large wood as a feeding and/or shelter habitat type, as illustrated by the higher density of pike-perch at the large wood compared to reference habitats (Table 1).

Although the densities of round goby are significantly lower at the large wood habitat in comparison with nearby reference habitats, the present study shows that the species is able to use the large wood habitat to some extent. Where wood structures come in contact with the bottom, they may provide some shelter for round goby. In the Gulf of Gdansk in the south Baltic Sea, round goby use sandy bottoms that are devoid of cover around large wood structures (Sapota and Skóra 2005). Therefore, it is likely that large wood will always harbour small numbers of round goby, although much less than in river habitats with numerous shelter places such as stony banks. The difference between large wood versus the basalt stones as a causative factor explaining densities of round gobies and native fish species is important. The effects of large wood on fish assemblages in areas with basalt stones are still unknown. Therefore, we recommend further research regarding the role of large wood in shaping fish assemblages in various types of littoral zones of rivers.

In conclusion, in rivers dominated by structures made of basalt stones, large wood predominantly functions as an attractive habitat type for different feeding guilds of native fishes whereas the invasive bottom-dwelling round goby only uses the large wood habitat to a small extent. Large wood may be applicable as a management tool favouring return of native fish species without greatly facilitating round goby.

Acknowledgements


Large wood in rivers facilitates native fish but not round goby


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