APPLIED ISSUE

Effects of ship-induced waves on littoral benthic invertebrates

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SUMMARY

1. Ship-induced waves can affect the physical characteristics of lake and river shorelines, and laboratory studies have shown effects on littoral invertebrates. Here, we explored whether these effects could be observed under field conditions along a natural lake shore affected by wave sequences (trains) produced by boats.

2. Individuals of five invertebrate species (Bithynia tentaculata, Calopteryx splendens, Dikerogammarus villosus, Gammarus roeselii, Laccophilus hyalinus) were exposed to waves with increasing shear stress in five habitats differing in structural complexity.

3. Detachment of invertebrates increased with increasing shear stress and was best modelled using sigmoid response curves. Habitat structural complexity mitigated the effects of shear stress, and detachment rate was influenced more by habitat type than by species. A threshold (90% of the individual invertebrates unaffected) stress level of 0.64 N m⁻² was found for a structurally complex reed habitat, compared to 0.37 N m⁻² for a simple sand habitat.

4. Shear stress associated with wave trains created by recreational boating at a distance of 35 m from the shore and at a speed of 11 km h⁻¹ resulted in 45% detachment of littoral invertebrates. Decreasing the boat-to-shore distance to 20 m increased wave shear stress by 30% and invertebrate detachments up to 75%.

5. Disturbance of littoral habitats and invertebrate assemblages are widespread in inland waters used for recreational and/or commercial navigation. Our findings show that the integrity of littoral zones of navigable surface waters could be much improved by implementing management measures such as physically protecting complex habitats with dense reed belts and tree roots, and reducing boat speeds and increasing their minimum shoreline distance.

Keywords: field experiment, inland navigation, invertebrate detachment, shear stress, structural habitat complexity

Introduction

Littoral zones of lakes and rivers are amongst the most productive, but most threatened aquatic habitats in the world (Vadeboncoeur, Lodge & Carpenter, 2001; Jenkins, 2003; Strayer & Findlay, 2010). Characterised by a complex spatial structure and variable environmental conditions, littoral zones provide habitats for numerous species of water fowl, fish and invertebrates (Strayer & Findlay, 2010). However, littoral zones are often heavily modified, as they are preferred for human settlement and intensively used for recreation (Gonzalez-Abraham et al., 2007). Activities affecting littoral areas include angling and swimming as well as boating and inland navigation (see reviews of Liddle & Scorgie, 1980; Burgin & Hardiman, 2011). Water pollution and mechanical impacts from
ship-induced waves are the main pressures affecting littoral habitats (Mosisch & Arthington, 1998). The intensity of ship-induced waves depends on vessel characteristics such as travelling speed, draught and distance to shoreline. Characteristics of the water body and shoreline that can influence the impacts on littoral zones include water depth, slope and width of the water body. Ship-induced waves increase shoreline erosion, sediment suspension and turbidity (Hilton & Phillips, 1982; Garrad & Hey, 1987; deWit & Kranenburg, 1997; Anthony & Downing, 2003) and may even uproot and negatively affect growth of aquatic macrophytes (e.g. Liddle & Scorgie, 1980; Murphy & Eaton, 1983; Asplund & Cook, 1997). Intense wave action may also displace juvenile fish (e.g. Morgan et al., 1976; Holland, 1986; Arlinghaus et al., 2002; Wolter & Arlinghaus, 2003; Wolter et al., 2004; Kucera-Hirzinger et al., 2008), affect fish feeding behaviour (Stoll & Fischer, 2011) and alter predator–prey relationships between fish and invertebrates (Gabel et al., 2011a).

Recent studies have suggested that ship-induced waves will also affect aquatic invertebrates colonising littoral zones, thus impacting a key element of the food web. Bishop (2008) found that waves generated by a small vessel may detach invertebrates from flapping seagrass blades in a coastal Australian lagoon, reducing abundance and species richness for at least one hour after the disturbance. Similarly, laboratory flume studies using substrata mimicking typical littoral habitats showed that the number of detached invertebrates increased with wave-induced shear stress (Gabel et al., 2008), following a sigmoid-shaped response pattern. The detachment rate was significantly lower in structurally complex habitats, such as reed and submerged tree roots, where the kinetic energy of waves was more efficiently dissipated and where invertebrates found more shelter. Conversely, habitats with low structural complexity, such as sand, provide little fixing possibilities for invertebrates and are less effective at dissipating wave kinetic energy (e.g. Knutson, Seeling & Inskeep, 1982; Gabel et al., 2008).

Although these laboratory studies have shown significant effects of waves on invertebrate detachment rates, to our knowledge, field assessments of detachment rates are lacking. Indeed, field studies are important as waves created under laboratory conditions in a wave tank consist of solitary waves (solitons), whilst water craft generate wave trains, that is, a series of several waves striking an area in rapid succession.

We conducted experiments in the near-natural littoral zone of a lake to quantify the effects of ship-induced waves. The goal of this study was to evaluate the relationship between wave-induced shear stress created by different boat velocities, passing distances and habitat complexity on the number of detached individuals. Five species, previously studied in laboratory studies, on patches of varying habitat type [coarse woody debris (CWD), reed, sand, stones and tree roots] were exposed to ship-induced waves with shear stresses ranging from 0.3 to 1.5 N m\(^{-2}\) (0.4–2.2 N m\(^{-2}\) under laboratory conditions).

**Methods**

**Experimental set-up**

Experiments were conducted along the shoreline of Lake Kalksee located south-east of Berlin (52°27′30″N, 13°6′9″E) in September 2007. The lake has a surface area of 84 ha (length 2 km and width at maximum 650 m) and a maximum depth of 10 m. Lake Kalksee is connected to the River Spree and used as a navigational waterway for barges and recreational boats, although traffic is relatively low. The study site was located on an open, gently sloping sandy beach on the eastern shore. During the experiment, the surface water was characterised by a temperature of 13 °C, pH of 8.5, conductivity of 1300 μS cm\(^{-1}\) and a dissolved oxygen concentration (daily average) of 8 mg L\(^{-1}\). Water depth at the study sites was 25–30 cm. The sites were situated far enough off shore to ensure that wave reflections did not affect invertebrate detachment.

The study design consisted of three replicate cages (140 × 60 × 50 cm; L × W × H), open at the top, bottom and front, and with the sides and back covered by 1-mm nylon mesh (Fig. 1). The cages may have reduced the effects of wave action, but this effect was assumed to be

![Fig. 1 Experimental set-up on the lake shore: (1) removable Perspex cage in which invertebrates were exposed in different habitats (here stones); (2) fixed cages surrounding the Perspex cage; (3) Vectrinos; (4) pressure sensors used to measure wave characteristics; and (5) underwater video cameras used to record invertebrate detachment.](image-url)
negligible, underestimating invertebrate drift. In each cage, smaller, solid-wall Perspex cages (60 × 34 × 40 cm) were used to prevent the loss of invertebrates between the experimental runs (i.e. when no waves were created). The smaller Perspex cages were removed before a wave hit the study area, whereas the larger net cages were left in place to prevent invertebrates from being displaced too far. In the Perspex cages, the five habitats were installed successively.

Wave velocity was measured with a Vectrino (recording at 25 Hz; Nortek AS, Rud, Norway) centrally placed 25 cm in front of each habitat measuring 5 cm above the bottom. Wave heights were recorded by a pressure sensor (CAU-T precision pressure transmitters second generation, 10 Hz; Aktiv Sensor, Stahndorf, Germany) placed in front of each study area and partly buried in the sand (beneath the Vectrino), with c. 0.5 cm of the pressure transducer visible. Each study area was surveyed by an underwater camera (Selvac OC-1; Selvac, Leer, Germany) placed next to the habitats in order to determine the number of detached individuals (i.e. displaced in the water column).

Waves were generated with a 6.5-m-long, V-hulled vessel with a width of 2.3 m, a displacement of 1 m³ and a motor capacity of 36.8 kW. The vessel passed the study site at varying speeds and distances from shore. Vessel velocity was determined by GPS (nüvi 550 Garmin, Olathe, KS, U.S.A.), and distance to shore was measured with a Laser Golf Rangefinder (Nikon, Düsseldorf, Germany).

Habitats

Five habitat types [CWD, reed, sand, stones and tree roots], each covering an area of 0.23 m², were placed in the Perspex cages. The habitats had contrasting structural complexity and were spatially arranged as in previous laboratory experiments (Gabel et al., 2008). The CWD habitat was comprised of four flat pieces of ridged bark. Reed habitat consisted of 42 reed (Phragmites australis (Cav.) ex. Trin. Steud.) stems randomly distributed in the habitat, whereas the larger net cages were left in place to prevent invertebrates from being displaced too far. In the Perspex cages, the five habitats were installed successively.

Five species, differing in body shape and attachment strategy, were used as model organisms: Bithynia tentaculata L. [Gastropoda] (mean body length ± SE, 9.5 ± 0.07 mm), Calopteryx splendens Harris [Odonata] (15.9 ± 0.4 mm), Dikerogammarus villosus Sowinsky [Crustacea] (15.2 ± 0.2 mm), Gammarus roselii Gervais [Crustacea] (14.0 ± 0.2 mm) and Laccophilus hyalinus DeGeer [Coleoptera] (4.8 ± 0.04 mm). The organisms had body sizes similar to those used in earlier laboratory experiments (Gabel et al., 2008). Specimens pool consisted of 300 individuals of each species. Individuals were collected from the River Spree and Lake Müggelsee (for further details see Gabel et al., 2008), which are part of the same river system as Lake Kalksee, where studies were conducted. Prior to the experiment, individuals were kept in aquaria with aerated water from Lake Kalksee. New individuals were used in each habitat–species combination and in each replicate in order to avoid individual adaptation to disturbance or decreasing fitness of individuals.

Individuals were marked with bright colours to facilitate visual distinction of detached individuals from drifting organic or inorganic particles. Marking methods differed amongst species. C. splendens and B. tentaculata were marked with white nail lacquer containing a small amount of bright orange stamping ink. L. hyalinus individuals received a small dot of the white lacquer on their dorsal surfaces. To mark amphipods, a small piece of pink foil was applied to their dorsal surface with superglue. All marking methods were tested several weeks before the start of the experiments and resulted in no changes in behaviour or survival rate.

Experimental design

Experiments followed a cross-design between the five habitats and the five invertebrate species. Twenty individuals were exposed to waves of increasing shear stress for each replicated habitat–species combination. Waves of six different levels of shear stress were generated at random, with an inter-wave time interval of 15 min. This
time period allowed detached individuals to recover from disturbance by reattachment or evasion. Moreover, this time interval reflects conditions in navigable waterways (e.g. on the nearby Havel River the interval of ship passage was determined to be 10.3 ± 2.4 min, F. Gabel, unpubl. data). The Perspex cages were removed shortly before each wave was produced and replaced immediately after. For each wave produced, wave velocity and amplitude were recorded, and one person visually counted the number of detached individuals. Additionally, video records were analysed as a quality control check of the visual counts. Each experiment was replicated three times.

Shear stress calculation and wave characteristics

Maximum shear stress ($\tau$, N m$^{-2}$) of the wave trains generated by the vessel in front of the habitats was calculated as:

$$\tau = 0.5 \rho f_w U_b^2 \ast 10$$

where $\rho$ is the density of water (1000 kg m$^{-3}$), $f_w$ is the wave friction factor, and $U_b$ (m s$^{-1}$) is the orbital wave velocity. Wave friction factor was calculated following Dyer (1986) as:

$$f_w = 2\sqrt{\frac{v}{\nu A_b}}$$

where $v$ is the kinematic viscosity of water (c. $10^{-6}$ m$^2$ s$^{-1}$) and $A_b$ (m) is the maximum bottom wave amplitude, since shear stress was mainly produced by main flow, as flow was not turbulent. Reynolds numbers were approximately $10^4$, which is one order of magnitude lower than the critical value for turbulent flow (Jensen, 1989).

The vessel passed the study area at five different speeds (9–18 km h$^{-1}$) and two distances from the shoreline (20 and 35 m), creating reproducible waves of six different levels shear stress ranging from 0.3 to 1.5 N m$^{-2}$ (Table 1). Wave trains consisted of several wave crests hitting the study area for 20–60 s. For each level of shear stress, no difference in shear stresses was found amongst the three replicates (ANOVA, $n = 25$ per test, $P > 0.05$ for all tests).

Statistical analysis

To obtain overall detachment thresholds, we calculated the average shear stress for each habitat species combination when 10, 25 and 50% of individuals were detached. Sigmoid regression analysis ($\ln y = b_0 + b_1/t$) was used to describe the relationships between the number of detached individuals and bottom shear stress, since a sudden exponential increase in the number of detached individuals was observed above a certain threshold, levelling off at high shear stress levels. Detachment values of 0 were replaced by the value 0.00001 to calculate the regression models. Average detachments for the five species studied (average across replicates ± SE, $n = 3$ for the sum of all detached individuals of generated waves divided by the number of generated waves) were analysed by ANOVA with an associated post hoc test (Scheffe procedure). To determine whether the number of detached individuals amongst habitats was influenced by species identity, the proportion of variance explained by species and habitats, respectively, was calculated separately using a multiple classification analysis (MCA, Andrews et al., 1973; see Gabel et al., 2008 for detailed explanations).

Relationships between the structural complexity of the habitats (expressed as their FD) and detachment of invertebrates were explored using Spearman rank correlations. Detachment rates from previous laboratory (flume studies) and our field studies were compared using nonparametric tests for paired samples (Wilcoxon tests).

Deviation of the data from normality and homogeneity of variances was tested using Shapiro–Wilk’s and Levene’s tests before statistical analyses. All statistical tests and regressions were performed using PASW Statistics (v. 17; SPSS, Chicago, IL, U.S.A.).

Results

Field experiments

The number of detached individuals generally increased with increasing shear stress (Fig. 2). On average, 10% of the individuals were detached at a shear stress of 0.4 N m$^{-2}$, 25% were detached at a shear stress of 0.6 N m$^{-2}$, and 50% were detached at a shear stress of 1.2 N m$^{-2}$ (average for all species and for all habitats). For all species in CWD, reed, sand and stone habitats, sigmoid relationships between wave-induced shear stress and number of detached individuals were significant and explained 72% (mean) of the variance. Response curves revealed typical phases: an initial low-effect phase, followed by a steep increase in the detachment effect and finally a saturation phase (e.g. Fig. 2, B. tentaculata in sand habitat). In contrast, a sigmoid model was not significant for four of five of the investigated species in the root habitat (Table 2).
**Table 1** Characteristics of vessel passages ($n = 25$) and resulting wave parameters (mean ± SD) at the study site

<table>
<thead>
<tr>
<th>Vessel speed (km h$^{-1}$)</th>
<th>Distance to shore (m)</th>
<th>Max. wave velocity (cm s$^{-1}$)</th>
<th>Max. wave height (cm)</th>
<th>Max. shear stress (N m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>35</td>
<td>10.51 ± 2.26</td>
<td>3.69 ± 0.94</td>
<td>0.26 ± 0.08</td>
</tr>
<tr>
<td>11</td>
<td>35</td>
<td>16.15 ± 3.31</td>
<td>4.84 ± 0.71</td>
<td>0.44 ± 0.09</td>
</tr>
<tr>
<td>11</td>
<td>20</td>
<td>21.19 ± 3.58</td>
<td>5.35 ± 0.80</td>
<td>0.63 ± 0.10</td>
</tr>
<tr>
<td>12</td>
<td>20</td>
<td>34.67 ± 4.17</td>
<td>9.52 ± 2.01</td>
<td>0.95 ± 0.10</td>
</tr>
<tr>
<td>14</td>
<td>20</td>
<td>44.95 ± 5.95</td>
<td>12.96 ± 1.37</td>
<td>1.21 ± 0.13</td>
</tr>
<tr>
<td>18</td>
<td>20</td>
<td>55.31 ± 8.78</td>
<td>14.93 ± 1.81</td>
<td>1.51 ± 0.12</td>
</tr>
</tbody>
</table>

Fig. 2 Number of detached individuals (max. 20 ind.) for five habitats, five species and shear stress caused by ship-induced waves. Plotted values represent the mean number of detached individuals (±SE) for three replicates. Results for each habitat are connected by lines. CWD, coarse woody debris.

The number of detached individuals (averaged for the five species at the highest level of shear stress) varied amongst habitats. Significantly more individuals were detached from sand habitat (mean ± SE, 19.9 ± 0.1; P < 0.003; ANOVA, Scheffé post hoc test, n = 75) than from CWD (12.3 ± 1.4), stones (11.5 ± 1.9), reed (10.9 ± 1.6) (no significant differences were noted amongst these three habitat types) or tree root (1.1 ± 0.5; P < 0.004; ANOVA, Scheffé post hoc test) habitats. Furthermore, fewer individuals (P < 0.001) were detached from tree root habitats compared to the other habitat types. For sand habitat, 10% of individuals were detached at an average shear stress of 0.37 N m⁻², whereas for reed habitat, 10% detachment of organisms did not occur until a shear stress of 0.64 N m⁻² (average for all species). For three species in tree root habitats, detachment levels remained below 10% even at the highest levels of shear stress.

Comparison of detachment rates amongst species showed species-specific responses to wave-induced hydraulic disturbance according to habitat (Table 3). For CWD habitat, most individuals of *L. hyalinus* were detached, followed by *C. splendens*, *B. tentaculata*, *G. roeselii* and *D. villosus*. For reed habitat, *L. hyalinus* detachment was highest. For stones habitat, most individuals of *L. hyalinus* were detached; 10 times more individuals of *G. roeselii* were detached than that of *D. villosus*, whilst intermediate detachment rates were observed for *B. tentaculata* and *C. splendens*. For sand and tree root habitats, which exhibited the minimum and maximum detachment rates, respectively, detachment rate variability amongst species was lower than in the other habitats (Table 3).

Habitat type was the most important factor explaining the number of detached individuals, with 77.0% of the variance explained (value corrected for the influence of the species factor), whereas only 46.5% of the variance was explained by species (value corrected from the influence of the habitat factor – full model: r² = 0.82, P < 0.001, n = 75; multiple classification analysis). The number of detached individuals decreased with increasing structural complexity of the habitat, parameterised by its FD (Fig. 3). Detachments, averaged for the five species, were negatively correlated with the FD of the habitats (Spearman’s ρ = −0.71, P < 0.001, n = 5), as well as for all species separately. Correlations ranged from −0.69 (P = 0.005) for *D. villosus* to −0.97 for *B. tentaculata* (P < 0.001), with intermediate correlations found for *C. splendens* (−0.94, P < 0.001), *L. hyalinus* (−0.82, P < 0.001) and *G. roeselii* (−0.70, P = 0.004).

**Effect on navigable surface waters**

Shear stresses at which 10, 25 and 50% of all individuals were detached were exceeded by the passage of the 6.5-m vessel used in our experiments at a velocity of 11 km h⁻¹ at distances of 35 and 20 m as well as at a velocity of 14 km h⁻¹ at a distance of 20 m, respectively, from the shore. At a boat speed of 11 km h⁻¹, shear stress decreased by 30%, and the detachment of macroinvertebrates

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**Table 2** Sigmoid regression analysis (ln y = b_o + b_1/t) of number of detached individuals and shear stress

<table>
<thead>
<tr>
<th>Species</th>
<th>CWD</th>
<th>Reed</th>
<th>Sand</th>
<th>Stones</th>
<th>Tree roots</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bithynia tentaculata</em></td>
<td>0.70***</td>
<td>0.70***</td>
<td>0.70***</td>
<td>0.74***</td>
<td>0.29*</td>
</tr>
<tr>
<td><em>Calopteryx splendens</em></td>
<td>0.70***</td>
<td>0.69***</td>
<td>0.85***</td>
<td>0.57***</td>
<td>0.04 n.s.</td>
</tr>
<tr>
<td><em>Dikerogammarus villosus</em></td>
<td>0.56***</td>
<td>0.96***</td>
<td>0.71***</td>
<td>0.62***</td>
<td>0.04 n.s.</td>
</tr>
<tr>
<td><em>Gammarus roeselii</em></td>
<td>0.45**</td>
<td>0.79***</td>
<td>0.98***</td>
<td>0.39**</td>
<td>No individuals detached</td>
</tr>
<tr>
<td><em>Laccophilus hyalinus</em></td>
<td>0.70***</td>
<td>0.90***</td>
<td>0.93***</td>
<td>0.80***</td>
<td>0.26 n.s.</td>
</tr>
</tbody>
</table>

For each test, the R² value (adjusted for degrees of freedom), the corresponding significance levels (**P < 0.001, *P < 0.05, n.s., not significant**) and the curve coefficients (b_o/b_1) are given. Replicates were treated individually.

CWD, coarse woody debris

**Table 3** Mean number of detached individuals (average across replicates ± SE, n = 3 for the sum of all detached individuals of generated waves divided by the number of generated waves) for the cross combinations of species and habitats studied

<table>
<thead>
<tr>
<th>Species</th>
<th>CWD</th>
<th>Reed</th>
<th>Sand</th>
<th>Stones</th>
<th>Tree roots</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bithynia tentaculata</em></td>
<td>5.7 ± 1.8</td>
<td>2.1 ± 0.8</td>
<td>12.6 ± 3.3</td>
<td>2.1 ± 0.9</td>
<td>0.8 ± 0.5</td>
</tr>
<tr>
<td><em>Calopteryx splendens</em></td>
<td>8.1 ± 2.3</td>
<td>2.4 ± 0.8</td>
<td>14.9 ± 3.1</td>
<td>7.1 ± 1.6</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td><em>Dikerogammarus villosus</em></td>
<td>2.2 ± 0.7</td>
<td>8.2 ± 2.0</td>
<td>11.3 ± 3.4</td>
<td>0.9 ± 0.4</td>
<td>0.1 ± 0.1</td>
</tr>
<tr>
<td><em>Gammarus roeselii</em></td>
<td>4.3 ± 1.8</td>
<td>6.4 ± 1.9</td>
<td>12.0 ± 3.4</td>
<td>9.4 ± 3.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td><em>Laccophilus hyalinus</em></td>
<td>12.7 ± 3.7</td>
<td>12.5 ± 3.6</td>
<td>14.5 ± 3.3</td>
<td>13.2 ± 3.5</td>
<td>2.6 ± 0.7</td>
</tr>
</tbody>
</table>

CWD, coarse woody debris

decreased by 50% (up to 75% for *L. hyalinus* in reed habitat) when the distance of the passing vessel increased from 20 to 35 m.

**Comparison of field and laboratory experiments**

Comparison between field and laboratory flume experiments was carried out using three levels of shear stress (Table 4). The number of detached individuals did not differ between laboratory and field experiments for all levels of shear stress or for habitats type (Wilcoxon tests, *P* > 0.05), although the number of detached individuals was higher under field conditions.

**Table 4** Comparison of number of detached individuals in laboratory flume and field experiments (mean ± SD) and results of paired Wilcoxon tests for sand, coarse woody debris (CWD), stones and reed and tree root habitats at three levels of shear stress. Levels of shear stress used in the comparisons were low [0.44 N m$^{-2}$ (field) and 0.43 N m$^{-2}$ (laboratory)], medium [1.21 N m$^{-2}$ (field) and 1.25 N m$^{-2}$ (laboratory)] and high [1.51 N m$^{-2}$ (field) and 1.48 N m$^{-2}$ (laboratory)]. *N* = 15 for all tests

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Shear stress level</th>
<th>Detached ind. in laboratory</th>
<th>Detached ind. in field</th>
<th><em>P</em>-value</th>
<th>Diff. Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>CWD</td>
<td>Low</td>
<td>0.33 ± 0.47</td>
<td>2.27 ± 1.36</td>
<td>0.131</td>
<td>-1.511</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>5.07 ± 2.92</td>
<td>10.53 ± 6.39</td>
<td>0.138</td>
<td>-1.483</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>8.53 ± 5.60</td>
<td>12.33 ± 5.77</td>
<td>0.053</td>
<td>-1.923</td>
</tr>
<tr>
<td>Reed</td>
<td>Low</td>
<td>0.27 ± 0.43</td>
<td>2.87 ± 1.76</td>
<td>0.102</td>
<td>-1.633</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>3.27 ± 3.09</td>
<td>8.13 ± 6.77</td>
<td>0.063</td>
<td>-1.823</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>5.93 ± 6.44</td>
<td>10.87 ± 6.46</td>
<td>0.052</td>
<td>-1.932</td>
</tr>
<tr>
<td>Sand</td>
<td>Low</td>
<td>1.80 ± 0.77</td>
<td>5.13 ± 2.64</td>
<td>0.052</td>
<td>-1.932</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>11.4 ± 6.61</td>
<td>18.67 ± 0.33</td>
<td>0.053</td>
<td>-1.923</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>16.67 ± 3.72</td>
<td>19.87 ± 0.30</td>
<td>0.109</td>
<td>-1.604</td>
</tr>
<tr>
<td>Stones</td>
<td>Low</td>
<td>0.67 ± 0.78</td>
<td>2.50 ± 1.87</td>
<td>0.593</td>
<td>-0.535</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>5.07 ± 3.05</td>
<td>10.10 ± 7.59</td>
<td>0.053</td>
<td>-1.923</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>7.13 ± 6.51</td>
<td>11.47 ± 7.87</td>
<td>0.068</td>
<td>-1.826</td>
</tr>
<tr>
<td>Tree roots</td>
<td>Low</td>
<td>0.20 ± 0.45</td>
<td>0.33 ± 0.75</td>
<td>0.999</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>Medium</td>
<td>0.27 ± 0.43</td>
<td>1.27 ± 1.66</td>
<td>0.109</td>
<td>-1.304</td>
</tr>
<tr>
<td></td>
<td>High</td>
<td>0.40 ± 0.54</td>
<td>1.13 ± 1.83</td>
<td>0.180</td>
<td>-1.342</td>
</tr>
</tbody>
</table>

**Discussion**

Freshwater ecosystems are subjected to multiple anthropogenic pressures (Dynesius & Nilsson, 1994; Giller, 2005; Tockner et al., 2010). Using *in situ* experiments, we showed that ship-induced waves constitute a severe pressure to invertebrates colonising the littoral zones of inland waterways, with the magnitude of the effects dependent on wave intensity. The extent of these pressures, indicated in previous laboratory studies (Gabel et al., 2008), were verified in the present study using an *in situ* experimental design that allowed manipulation of wave disturbance whilst holding all other variables constant. Evidence from *in situ* investigations is generally considered more definitive in ecological studies (Hinkelmann & Kempthorne, 2008), as the results produced under field conditions are more reflective of real-world conditions (Hairston, 1994).

Rules for navigable surface waters in north-eastern Germany allow boat speeds of 12 km h$^{-1}$ inside a 100-m buffer zone along the shorelines of lakes that exceed 250 m in width (WSV unpubl. data). Our study shows that at 12 km h$^{-1}$, a boat may generate a wave-induced shear stress of up to 1 N m$^{-2}$, leading to the detachment of up to 45% of individual invertebrates (averaged over all species and habitats). In a littoral zone regularly exposed to strong ship-induced waves, structurally complex habitats will be reduced or destroyed, as has been shown for reed-dominant systems (Ostendorp, 1989). If only sand and stone habitats remain, the percentage of detachment at a wave-induced shear stress of 1 N m$^{-2}$ would increase to 66.5% (average over all species on sand and stone habitat).
Therefore, a speed limit of 12 km h\(^{-1}\) may be insufficient to prevent strong invertebrate detachments when boats are passing close to the shoreline. Other lakes that are popular for recreational and/or commercial boating have implemented more restrictive speed limits. For Lake Tahoe (California, U.S.A.), a speed limit of 8 km h\(^{-1}\) (5 mph) has been set for watercraft at 180 m from the shore. For Lake Windermere (U.K.), a speed limit of 9.7 km h\(^{-1}\) (6 mph) is used close to shore or in no wave zones. These speed limits, however, are restricted only to certain areas, whilst higher speed limits are often applicable elsewhere in the same lakes and in other lakes. The general speed limit for waterbodies in the Lake District of England (U.K) is 18.5 km h\(^{-1}\) (10 nautical miles per hour), and on most lakes in the state of Oregon (U.S.A.), a speed limit of 16 km h\(^{-1}\) [10 mph] is stipulated. According to our study, these speeds are high enough to induce substantial invertebrate disturbance, as well as result in resuspension of sediments that may increase the detachment of invertebrates (Ciborowski, Pointing & Corkum, 1977).

Outside of buffer zones and on rivers in north-eastern Germany, boat speeds of up to 25 km h\(^{-1}\) are often allowed. During the field experiments, the highest shear stress generated by the small vessel reached 1.5 N m\(^{-2}\). However, littoral zones of navigable inland waters are often subjected to higher wave-induced shear stress. On the Havel River (a slow flowing, regulated lowland river in north-eastern Germany), shear stress caused by ship-induced waves can be as high as 4.2 N m\(^{-2}\) (mean shear stress ± SE, 0.83 ± 0.20 N m\(^{-2}\); \(n = 27\)) for recreational vessels and up to 2.7 N m\(^{-2}\) (0.5 ± 0.31 N m\(^{-2}\); \(n = 8\)) for commercial barges (unpubl. data). Shear stress values exceeding 1.0 N m\(^{-2}\) were measured on average six times a day (from 12:00 to 18:00) during September 2008. On the Havel River, the interval between ship passages ranged from 8.5 min in July to 13 min in September (unpubl. data). Results showed that at a shear stress of 1.0 and 1.5 N m\(^{-2}\), 45% and 50–100% (on average), respectively, of the macroinvertebrates are detached. Hence, hydraulic stress from passing vessels probably results in high detachment rates several times a day. On the basis of these assumptions, more than 15% of \(B.\ tentaculata\) individuals, a species typically occurring on stones (Schäfer, 1953), would have been detached from stones six times a day during September. For \(L.\ hyalinus\), occurring mainly on macrophytes and stones (Hendrich, 2003), more than 98% of the individuals would have been detached six times a day. By contrast,
only 5% of D. villosus individuals would have been dislodged from stones, and none from tree roots; a species typically found on stones (Hesselschwerdt, Necker & Wantzen, 2008) and roots (Devin et al., 2003), especially in the littoral zones of waterways.

Our findings of relationships between shear stress, habitat complexity and number of detached individuals are likely applicable to most commercial waterways or lentic recreational surface waters, and lend support to earlier work. For example, Verney et al. (2007) found shear stresses as high as 2 N m\(^{-2}\) for barges passing along the River Seine. Similarly, for the Göta River in Sweden, shear stresses of up to 3.9 N m\(^{-2}\) were associated with ship-induced waves (J. Althage, unpubl. data). The detachment of invertebrates from habitat surfaces because of ship-induced waves, therefore, appears to be widespread. When invertebrates become detached from a habitat, they may not be able to immediately relocate resulting in an increased risk from predation (Gabel et al., 2011a). Additionally, growth rates may be depressed by repeated wave disturbance, which has been observed for native gastropods and amphipods (Scheifhacken, 2006; Gabel et al., 2011b). Consequently, dislodgement of invertebrates can result in shifts in invertebrate community composition (Bishop, 2004; Bishop & Chapman, 2004), ultimately affecting ecosystem function and health.

Because of immediate and potentially long-term adverse impacts on shoreline communities, a primary goal of waterway management should be to mitigate the strong ecological pressure generated by intensive commercial and/or recreational navigation. Our results clearly show the effects of boat velocity and travel distance as well as habitat complexity on the disturbance of benthic invertebrates. Management strategies may focus on reducing wave generation, effective mitigation of the effects on macroinvertebrates or both. Complex shoreline habitats, such as dense reed belts or submerged tree roots, can effectively mitigate the adverse effects of ship-induced waves. However, the ability of habitat structures to withstand repeated heavy wave assaults will also diminish over time, leading to degradation and fragmentation of reeds and tree roots (Ostendorp, 1989 and references therein), and subsequently low structural complexity. Loss of habitat structural complexity will eventually compromise the habitat’s ability to intercept and dissipate wave energy, resulting in reduced fixing possibilities for invertebrates and increased invertebrate disturbance (Fig. 4).

Shoreline protection, such as off-bank revetments or shallow, submerged areas within the water body, reduces wave intensity by breaking up the waves and/or increasing dissipation (Wolter et al., 2004; Söhngen et al., 2008; Wolter, 2010), thus reducing wave-induced shear stress. In addition, adjusting navigation rules concerning maximum allowable speed and minimum passing distance should result in reduced adverse effects on macroinvertebrates. We showed that increasing the vessel to shoreline distance from 20 to 35 m decreased the wave-induced shear stress by more than 30% and macroinvertebrate detachment by up to 75% (L. hyalinus in reed habitats). Moreover, lower vessel speeds strongly reduce wave strength (Maynord, 2005) and consequently macroinvertebrate disturbance. Improvements in ship design, such as vessel hulls that create less wave action, may contribute to reduced wave disturbance (Sorensen, 1973; Day & Doctors, 2001; Söhngen et al., 2008).

Our results contribute to the development of evidence-based strategies for the management of lotic and lentic shorelines, combining the requirements of navigation and conservation. Along natural waterbodies used for inland navigation, no-wash zones should be developed and protected to serve as ecological sanctuaries in order to prevent hydraulic impacts on aquatic biodiversity at ecosystem level.

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