Is the impact of ship-induced waves on benthic invertebrates mitigated by littoral habitats with high structural complexity?

Xavier-François Garcia[1], Friederike Gabel[1], Henrike Hochmuth[1], Mario Brauns[1], Alexander Sukhodolov[1], Martin T. Pusch[1].
[1]*Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB)*
Müggelseedamm 301, D-12587 Berlin, Germany. garcia@igb-berlin.de

Introduction

Ship-induced waves constitute a major hydraulic disturbance for animals living in the littoral zones of lakes and rivers, because of their strong amplitude, their high frequency of occurrence and the short-term increase of flow velocity they cause. Yet, the impact of ship-induced waves on littoral species assemblages has rarely been documented. Bishop & Chapman (2004) shown that abundances of estuarine benthic invertebrates colonising the blades of sea grass were lower in boat-wash zones by comparison to non boat-wash zones. Similarly, Holland (1986) observed an eggs mortality of 20 to 50% in fish communities due to tows passing by on the Mississippi River. However, focusing on single individuals little is known about the response of invertebrates to ship-induced wave disturbance along gradients of wave strength and habitat structural complexity.
Hence, we investigated the resistance of invertebrate species to increasing wave disturbance for habitats of different degrees of structural complexity, in order to assess how physical characteristics of littoral habitats mitigate the adverse effect of ship-induced waves on benthic invertebrates.

Method

In an experimental wave tank (L: 3 m, W: 0.80 m and H: 0.60 m), the invertebrate species *Bithynia tentaculata, Calopteryx splendens*, *Dikerogammarus villosus, Gammarus roeseli* and *Laccophilus hyalinus* were exposed to single waves of increasing strengths (shear stress range: 4.3-21.9 dyn/cm^2). Two series of experiments were conducted. In the first series, the five species were exposed in five different natural habitat types: sand, coarse woody debris (CWD), stones, reed and tree roots. In the second series of experiments, the same five species were exposed in reed habitats of four different stem densities (45, 127, 175 and 250 stems/m²). In both series, the habitats depict a comparable gradient of structural complexity, as quantified by their fractal dimensions (FD). This experimental design allowed us to mutually consider the diversity and the density of the habitat structures, two complementary components of the habitat structural complexity.
Flow motion in the wave tank was approximately unidirectional. The zero vertical and lateral velocity components supported the conditions for a laminar flow. Consequently, wave strength was expressed by the bottom shear stress τ (dyn/cm^2) caused by the wave at the location of the habitat (1). Shear stress was calculated with the wave friction factor (f) formula from Dyer (1986) for laminar flow (2):

$$\tau = 0.5 f \rho U_b^2 \qquad (1)$$

$$f = 2\sqrt{\frac{\nu}{U_b A_b}} \qquad (2)$$

f: wave friction factor
ρ: density of water (1 g/cm^3)
U_b: maximum wave orbital velocity (cm/s)
(measured by an acoustic Doppler velocimeter, 50 Hz)
A_b: maximum bottom wave amplitude (cm)
(measured by an acoustic wave sensor, 20 Hz)
ν: water viscosity (~0.01 cm²/s)

Prior to the experiments, we tested the stability and reproducibility of the hydraulic conditions in the wave tank. Hence, the 10 different shear stress levels possibly produced were significantly different from each other (ANOVA, Post-Hoc test, Scheffé procedure, N=10, p=0.023 at the lowest) and reproducible over time (coefficient of variation: 0.36-2.17 %, N=10 per shear stress level). Waves were also vertically and laterally uniform (ANOVA on shear stress values, Post-Hoc test, Scheffé procedure, N=10 per test, p>0.05 for all tests).
The five habitat types and species selected are common for the littoral zones of Northeast German lakes. Besides, species were also chosen to depict contrasted body shapes and behaviours, which should influence their fixing and hiding capabilities. The design of the habitats (two trays of 0.115 m² area each) in the wave tank followed spatial arrangements and densities commonly observed in natural conditions. The habitat structural complexity increased in the following sequence: sand (FD=1), CWD (1.30), stones (1.34), reed (1.39) and roots (1.80) for habitat-types and reed$_{45}$ (FD=1.02), reed$_{127}$ (1.29), reed$_{175}$ (1.39) and reed$_{250}$ (1.45) for habitat densities (FD calculated with

the Frontier's grid method, 1987). Energy lost by the wave when passing through the habitat was quantified as the shear stress difference in front and behind the habitat for incoming waves of 13.7, 16.4 and 21.9 dyn/cm^2.

For each habitat-species combination, 20 individuals of similar body size were exposed to three replicated waves per shear stress level, with a time interval of 15 minutes. Shear stress was increased until all exposed individuals were detached, or until the maximum applicable shear stress was reached. For each wave produced, wave velocity, wave amplitude and the number of individuals detached from the habitat (counted from video records) were recorded.

Results

For the five species exposed to waves, a similar response pattern of increasing number of detached individuals with increasing shear stress was observed in sand, CWD, stones and reed (Fig.1A), and in the four reed habitats differing in stem density (Fig.1B). Conversely, such pattern was not observed in root habitat from which only few individuals of each species were detached by the strongest waves (Fig.1A). The strength of this relationship, which could be well described by a sigmoid regression model, varied however according to the combination species-habitat considered.

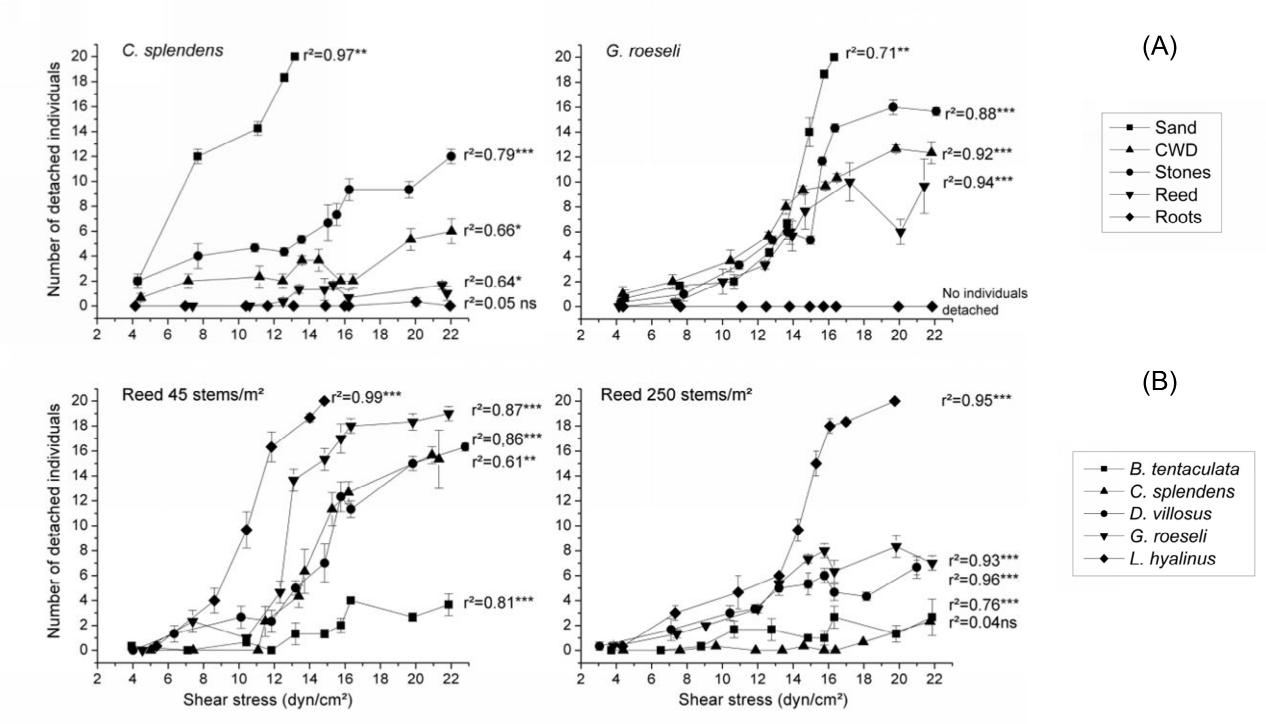

Fig.1. Number of detached individuals as a function of the shear stress produced by experimental waves (A) in five habitats for the dragonfly *Calopteryx splendens* and the amphipod *Gammarus roeseli*, and (B) for five species in reed habitat with density of 45 and 250 stems/m^2. Plotted values represent mean number of detached individuals (± SE) for three replicated waves. Regression coefficients (r^2) and significance levels (*** $p<0.001$, ** $p<0.01$, * $p<0.05$, n.s. non significant) refer to sigmoid regression models.

The comparison of the maximum numbers of detached individuals averaged for the five species showed that significantly more individuals were detached in sand than in CWD, stones, reed or roots (ANOVA with Post-Hoc test, Scheffé procedure, N=15 each, $p<0.01$ at the lowest - Fig.2A). Maximum number of detached individuals was also significantly different between roots and all other habitat types ($p<0.05$ at the lowest). No significant differences of the maximum number of detached individuals were observed between CWD, stones and reed ($p>0.05$ for the three tests). Obviously, sand habitat did not offer appropriate hiding or fixing spots for any of the five species, while the dense network of tiny and flexible branches constituting the root bunch allowed every species to enter the bunch and fix itself efficiently. In the experiments with differing reed stem densities, less individuals were detached at higher reed stem densities (Fig.2B). Significant differences in the maximum numbers of detached individuals were recorded between reed densities of 45-127 stems/m² on one side and reed densities of 175-250 stems/m² on the other side ($p<0.05$ at the lowest). Thus, the detachment of invertebrates by wave-induced hydraulic disturbance was significantly reduced in complex habitats, as more complex habitats provide more refuges and anchorage points that enable individuals to resist drag forces imposed by peaks in flow velocity.

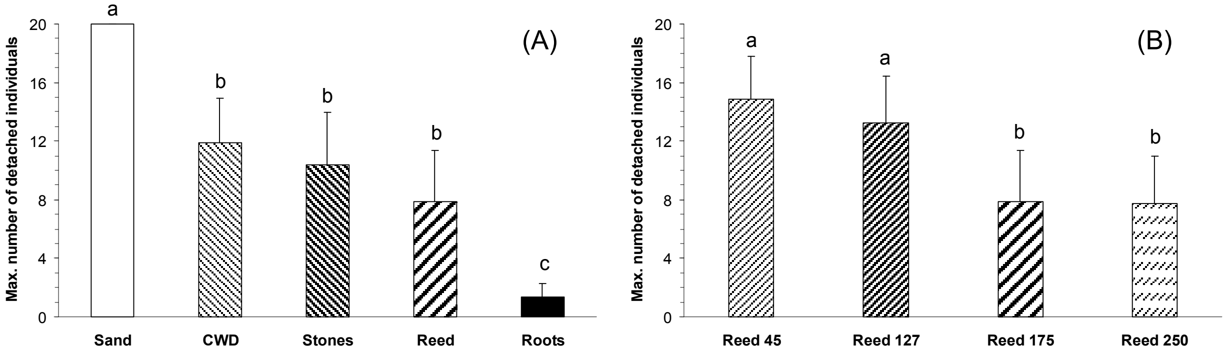

Fig.2. Maximum number (mean ± SE for the five species) of detached individuals for (A) the five habitat types used, and (B) for the four stem densities of reed used (see explanation in the text). Bars with different letters indicate significant differences (ANOVA with Post-Hoc test, Scheffé procedure, N=15 each).

Considering each species separately, strong disparities were observed in the maximum number of detached individuals between habitats, revealing a species-specific response to wave-induced hydraulic disturbance according to habitats (Tab.1). The detachment rate of the species studied depended on species-specific fixing or hiding capabilities, and how these capabilities matched specific physical habitat characteristics. For example, the rough ridges of CWD provided good anchorage points for species fixing themselves with big claws like *C. splendens* and *D. villosus*, but not for the snail *B. tentaculata* which needs smoother surfaces as reed stems to suck efficiently, nor for *G. roeseli* and *L. hyalinus* which possess smaller claws (Tab.1, see also Fig.1).

Tab.1: Maximum number (mean ± SE, N=3) of detached individuals for the five species in each habitats studied.

	Sand	**CWD**	**Stones**	**Roots**	**Reed$_{45}$**	**Reed$_{127}$**	**Reed$_{175}$**	**Reed$_{250}$**
B. tentaculata	20.0 ± 0.0	17.0 ± 0.6	2.3 ± 0.3	2.0 ± 0.0	3.7 ± 0.9	2.3 ± 0.3	1.3 ± 0.7	2.6 ± 1.4
C. splendens	20.0 ± 0.0	6.0 ± 1.0	12 ± 0.6	0 ± 0.0	15.3 ± 2.3	10.3 ± 0.3	1.0 ± 0.6	2.3 ± 0.9
D. villosus	20.0 ± 0.0	4.0 ± 0.6	2.0 ± 0.0	0 ± 0.0	16.3 ± 0.3	16 ± 0.6	7.3 ± 0.7	6.7 ± 0.9
G. roeseli	20.0 ± 0.0	12.3 ± 0.8	15.7 ± 0.3	0 ± 0.0	19 ± 0.6	17.7 ± 0.3	9.7 ± 2.2	7 ± 0.6
L. hyalinus	20.0 ± 0.0	20.0 ± 0.0	20.0 ± 0.0	4.7 ± 0.3	20 ± 0.0	20 ± 0.0	20.0 ± 0.0	20 ± 0.0

To account for this heterogeneity in species response, we compare the respective influences of habitat features and species characteristics on the overall detachment rates between habitats, using a multiple classification analysis (MCA, Andrews et al. 1973). MCA examines the interrelationship between several predictor variables and one dependant variable and estimates the proportion of explained variance by each predictor, both before and after taking into account the effects of all other predictors. MCA revealed that 56% of the variance in maximum number of detached individuals was explained by differences in habitat types (value corrected from the influence of the species factor) and 21% by differences between species (value corrected from the influence of the habitat factor - r^2_{model} = 0.77, p<0.001, N=75). Similarly, reed density explained 77% of the variance in maximum number of detached individuals versus 18% explained by differences in species (r^2_{model} = 0.94, p<0.001, N=45). In the latter analysis, *B. tentaculata* and *L. hyalinus* were removed as these two species did not contribute to any variance between the four stem densities. Hence differences in habitat features and densities were the main factor explaining the differences observed in invertebrate detachment rates. Consequently, the detachment rate was found to significantly decrease along the overall gradient of structural complexity depicted by the different habitats (Spearman´s r = -0.99, p<0.001, N=8 - Fig.3A). For all habitats, shear stress recorded behind the habitat was significantly lower than in front of the habitat (paired t-test, N=10 per test, p<0.001 at the lowest). The shear stress reduction increased in the following habitat sequence: sand, CWD, stones, reed, roots and with increasing reed stem densities. Consequently, shear stress reduction was found to be significantly correlated with the fractal dimension of the habitat (Spearman´s r = 0.97, p<0.001, N=8 - Fig. 3B). From the perspective of flow mechanics, the structure of the habitat provides obtrusions to the unidirectional flow that generates cross flow motions referred as turbulences. In turbulent flows, the kinetic energy of the flow is extracted by the larger vortices from the mean flow, transferred by the cascade of turbulences towards the smaller scales, where it finally dissipates into heat due to molecular viscosity (Tennekes & Lumley, 1972). Hence, the higher is the structural complexity, the more obstacles it provides, the larger portion of kinetic energy is dissipated.

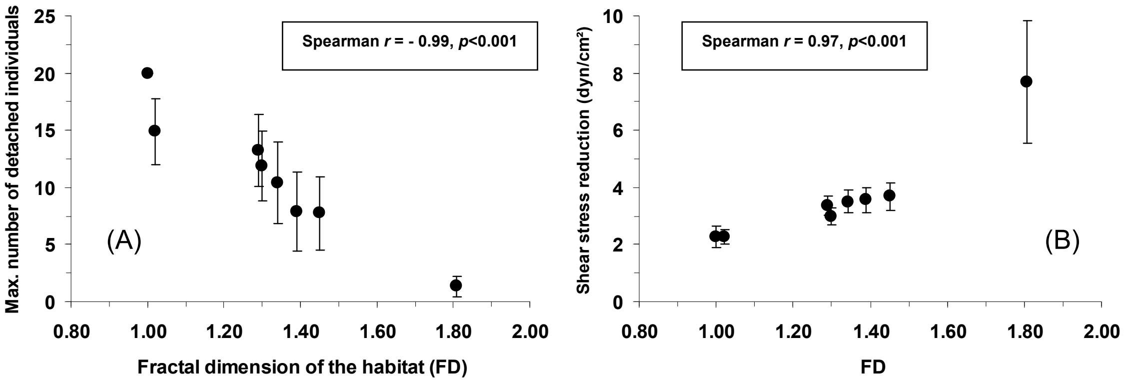

Fig.3. Relationships of the fractal dimension of the habitats (five habitat types and four stem densities for reed habitat, see equivalence in the text) with (A) the maximum number (mean ± SE for the five species) of detached individuals, and (B) the shear stress reduction (mean ± SE for three shear stress levels: 13.7, 16.4 and 21.9 dyn/cm²) caused by the habitats.

Conclusion

In this study, experimental evidence on the ecological effect of artificial wave disturbance was collected by systematically varying wave energy, habitat complexity and species-specific characteristics, under standardized conditions. The complex interactions between species and their habitat preferences were taken into account by using a set of natural habitats as well as species differing in body shapes and fixing capabilities. Also, the diversity and the density of habitat structures both contributing to the overall habitat structural complexity were mutually considered.

High structural complexity of habitats proved to be related with good sheltering conditions for invertebrates against hydraulic disturbance. This relationship could be causally explained, as high structural complexity provided more refuges or anchorage points for the invertebrates, and as it reduced substantially wave kinetic energy.

The conclusions drawn from this indoor experimental study most probably also apply in natural conditions. Waves produced in the wave tank reached maximum flow velocities up to 51 cm/s. However, 50% of the individuals were already detached at shear stress values of 6-15 dyn/cm², which correspond to flow velocities of 19-42 cm/s. By comparison, flow velocities measured in the field on Lake Langer See and on the River Spree (Berlin, Germany) ranged from a minimum of 21-44 cm/s for small private boats to a maximum of 324 cm/s for freight barges and sight-seeing passenger ships. Hence, the comparison of laboratory and field hydrodynamic conditions indicates that the detachment of organisms may be even stronger in natural conditions than demonstrated by our experiments, and probably the most important factor acting on the invertebrate assemblages exposed to ship-induced waves, even for wave of low energy.

As a consequence, the negative effects of boat traffic on littoral invertebrate assemblages is drastically increased as soon as complex littoral habitats like tree-roots or dense reed belts are degraded and disappear by frequent exposition to wave action or other human impacts.

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