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Visitor pressure in protected areas: Interactions between river tourists and freshwater pearl mussels in the Central European national park Šumava

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ABSTRACT

The freshwater pearl mussel *Margaritifera margaritifera* (FPM) is an endangered bivalve species occurring in oligotrophic rivers. FPMs can be found in the Upper Vltava River in the Šumava National Park (Czech Republic, Central Europe), where suitable conditions exist for both adult and juvenile mussels. Non-consumptive human leisure activities are known to negatively affect wildlife in fragile aquatic ecosystems, and in the Vltava River boating tourism in particular may be a threat to local mussel populations. This study focused on an assessment of interactions between river tourists and the FPM, using "pseudo-mussels" in both field and lab experiments. In the field, fake concrete mussels were exposed at three rest sites for river tourists, and in the lab experiment glued shells were placed at the water-sediment interface in an aquarium tested for mechanical impacts of paddles (dislodgement and crushing). Interactions of river tourists with fake mussels were most frequent at low water levels (10–20 cm), and within 2 m from the nearest river bank. Mussel visibility and the presence/absence of a guide played an important role in peoplé̌s reactions, but site-specific effects were also found. Unintentional interactions (60–69%) were mostly observed at less-attractive sites (with a limited area of shallow water where people spent most time outside the river channel), whereas visual and manipulative interactions (76%) dominated at a more-attractive site (the confluence of two rivers where people move across and inspect the river channel). Crash tests revealed that 8.03 ± 1.37 (mean±SD) and 7.88 ± 1.13 (mean±SD) hits by paddles were needed for dislodgment and crushing, respectively. Those findings indicate that the direct effects of recreational boating might be less detrimental than those of accompanying activities (such as wading, bathing, and swimming). The role of trampling (and handling) disturbances should be investigated in more detail to help conserve FPM populations in protected areas.

1. Introduction

Aquatic ecosystems are one of the most endangered ecosystems worldwide (Malmqvist and Rundle, 2002). The freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758) (FPM) is particularly affected by anthropogenic negative influences due to its complex life cycle (including host fish species) and habitat requirements (Bauer, 1988; Clements et al., 2018; Geist, 2010). FPMs require slightly acidic river waters, which are often found in catchments where granite and gneiss are predominant (Bauer, 1988; Geist, 2010; Hauer, 2015). In Central Europe, these geological preconditions are mainly present in the Bohemian Massif, which extends across the Czech Republic, Germany and Austria (Flödl and Hauer, 2019; Hauer, 2015). The greatest problems facing the FPM and its habitat include eutrophication, excessive sediment input, and the absence of fish hosts (Bauer, 1988; Denic and Geist, 2015; Flödl and Hauer, 2019; Geist, 2010; Geist and Auerswald, 2007; Hauer, 2015; Hoess and Geist, 2020). One issue that has received less research attention is recreational inland navigation and boating. Industrialized inland navigation poses a serious threat to aquatic ecosystems due to the spread of invasive species (Boltovskoy et al., 2006; Drake et al., 2007), the action of waves (Fleit et al., 2021; Gabel et al., 2017), and chemical pollution (Dafforn et al., 2011; French McCay et al., 2004). However, boating tourism has also been associated with environmental problems in water bodies and their surroundings (Graham

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and Cooke, 2008; Křenová, 2018; Polat et al., 2016).

Outdoor leisure activities are common and widespread, and participation in those activities has been growing (Knight and Gutzwiller, 1995; Miller et al., 2001). Non-consumptive types of recreation are rapidly increasing, and hiking, mountain biking and recreational boating have all become popular forms of outdoor activities (Blanc et al., 2006; Graham and Cooke, 2008; Taylor and Knight, 2003). Although such "quiet" recreation can be considered an essential element of local economies (Blanc et al., 2006) and even a benign use of natural areas (Reed and Merenlender, 2008), interference with wildlife makes such recreation a potential source of disturbance (Blanc et al., 2006).

Reserve networks around the world attempt to provide recreational use while conserving wildlife (Hardiman and Burgin, 2011; Reed and Merenlender, 2008). Most studies have focused on interactions between non-consumptive leisure activities and both aquatic and terrestrial birds or mammals (for recent review, see Dertien et al., 2021). Visitors of protected areas with high-profile sites (such as national parks, which are typically extremely popular; McGinlay et al., 2020) are unaware of the majority of species and consequently of their current status of endangerment (Behrens et al., 2009), and difficult to observe and/or unknown species may be much more threatened by visitors. Examples include the endangered rock partridge *Alectoris graeca saxatilis* in the Alpine Hohe Tauern National Park (Bednar-Friedl et al., 2012; Behrens et al., 2009), and the capercaillie *Tetrao urogallus* in Central European national parks (Šumava and Bavarian Forest National Parks; Rösner et al., 2014).

Several authors have been interested in the impacts of leisure activities on aquatic ecosystems, as assessing their components in protected areas is critical for sustaining both ecosystem health and recreation (Cao et al., 2016; Hardiman and Burgin, 2011; Sordello et al., 2020). For instance, bathers in Peñalara Lake (Natural Park of Peñalara, Spain) were found to cause resuspension of the sediment, changing (micro-)habitat conditions (Toro and Granados, 2002). Deposited eggs of fairy shrimps (*Chirocephalus marchesonii* and *C. sibyllae*) endemic to the Pilato and Palazzo Borghese Lakes (Sibillini Mountains National Park, Italy) are exposed to the pressure of trampling, pushing them deeper into the sediments (Carosi et al., 2022, 2021). Endangered benthic diatomic species have also been recorded in those high-elevation aquatic habitats (Padula et al., 2021). In comparison, running waters have been relatively neglected and only a few studies have focused on recreational activities within river environments; e.g., the effects of boating on the filtration activity of mussels (Lorenz and Pusch, 2012; Lorenz et al., 2013).

The Šumava National Park (Czech Republic, Central Europe) (ŠNP) was established in 1991 to protect a forested mountain range with various aquatic ecosystems (rivers, streams, springs, peatlands and glacial lakes) over an area of 68.500 ha (Křenová, 2018; Křenová and Kiener, 2012; Křenová and Kindlmann, 2015). The ŠNP together with the adjacent Bavarian Forest National Park (24.300 ha) in Germany form the largest wilderness area in the Central European cultural landscape (Křenová and Vrba, 2014). Public access in the core zone of the ŠNP is restricted in order to promote species conservation, mainly those sensitive to human-induced disturbance; e.g., the capercaillie *Tetrao urogallus*, the Eurasian lynx *Lynx lynx* and the FPM (Křenová, 2018; Křenová and Kiener, 2012; Křenová and Kindlmann, 2015). Although the previously numerous FPM population in the Upper Vltava River has been largely reduced due to water pollution and water reservoir construction (Simon et al., 2015), suitable conditions for adult and juvenile FPMs (e.g., water chemistry, oxygen saturation and food supply (detritus from water macrophytes)) have been found there (Bílý et al., 2021; Černá et al., 2018; Matasová et al., 2013; NCA CR, 2013).

Despite being situated within a restricted protected area, the ŠNP mussel population is exposed to recreational boating tourism (Křenová, 2018; Křenová and Kindlmann, 2015; NCA CR, 2013). Boating in the Upper Vltava River has been permitted since 1993, and it is the only way to enter into the most protected areas of the ŠNP (Nykles, 2014). The intensity of boating rapidly increased and resulted in damage to water macrophytes during low-flow conditions (Zelenková, 2008). While the risk of direct contact between humans and mussels was also likely high (Lorenz et al., 2013; NCA CR, 2013), this was not investigated. However, starting in 2004 boating became more regulated (allowed when a minimum water level is exceeded; Simon and Kladivová, 2006), and in 2009 additional rules were established; e.g., restrictions in the number of boats and registration with a user fee required (Diviš, 2009). Since 2012, almost all boats must be accompanied by a guide. The level of boating has thus gradually been reduced: whereas more than 12.000 boats were recorded in 2005 and 2006, this was down to 4.000 boats in 2009. Since then, it has ranged from 2.000 to 4.000 boats per year, mainly canoes with two passengers (Křenová, 2018). While such severe reductions in visitor numbers can lead to higher-quality tourism (Bednar-Friedl et al., 2012), there is still a lack of knowledge on the direct effects of regulated recreational boating on the FPM. Boating is assumed to be accompanied by other activities, such as wading and river bed disturbance (Cole and Landres, 1995). Studies have demonstrated the negative effects of "trampling" on mussel beds (Calcagno et al., 2012) as well as handling of individual mussels (Ohlman and Pegg, 2020), and FPM shells can be susceptible to damage from mechanical impact (Bílek, 2013). However, the responses of freshwater mussel populations to these anthropogenic disturbances have been poorly studied (Ziuganov et al., 2000).

The present study was therefore focused on the following research questions: (i) could interactions between river tourists and FPMs be related to the abiotic conditions; e.g., water depth, substrate and flow conditions; (ii) what is the typical behavior (and reasons) of tourists as a result of interactions; and (iii) how many hits by paddles are needed for a FPM to be mechanically disturbed/damaged? Our aim was to provide data that could be used to improve management related to conservation of the FPM in the ŠNP.

2. Study area

The Upper Vltava River flows through the ŠNP, and is a unique river floodplain system in Central Europe (see Fig. 1). It is a mountain meandering river with high water quality, a natural bed with dense macrophyte cover and regular floods, and is surrounded by numerous peatbogs, oxbow lakes, wet meadows and forest communities (Bílý et al., 2021; Černá et al., 2018; Křenová, 2018; NCA CR, 2013). The Upper Vltava River is a part of several protected areas: the UNESCO Biosphere Reserve "Šumava", Ramsar Convention Site "Šumava peatlands", and European Union's Natura 2000 Site "Šumava" (for the protection of endangered FPM and habitat type 3260 (Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation); Křenová, 2018; Křenová and Kindlmann, 2015). The floor of the river valley slopes gently from 760 to 720 m a. s. l. over about 15 km distance, but with a much longer meandering river channel (about 30 km), and the floodplain is relatively wide (about 1.5 km) (Černá et al., 2018; Křenová, 2018).

The oligotrophic river with high-level water chemistry, oxygen-rich river-bed substrate and presence of water macrophytes as a food source (Bílý et al., 2021; Černá et al., 2018; NCA CR, 2013) provides suitable habitats for sensitive mussel species, and FPMs have been confirmed within a 30-km long river stretch (Lenora-Nová Pec) (Černá et al., 2018; NCA CR, 2013) although the population is sparse (Matasová et al., 2013; NCA CR, 2013). The population size has been estimated at up to several hundreds of adults and several tens of subadults (captive-bred individuals that were released in 1998) (Matasová et al., 2013; NCA CR, 2013; Simon et al., 2015), along with other single individuals that have been recently observed (J. Horáčková, pers. communication).

The studied stretch of the Vltava River is situated between S. Most (48°54'27"N, 13°49'38"E; river km 389.8) and Pěkná (48°51'7"N, 13°55'14"E; river km 373.5). The width of the river channel ranges from 6 to 15 m (in river meanders up to 30 m) during mean flow conditions (Bílý et al., 2021; Simon and Kladivová, 2006). Mean annual values of water depth and flow at the gauging station "Chlum" (river km 377.6)

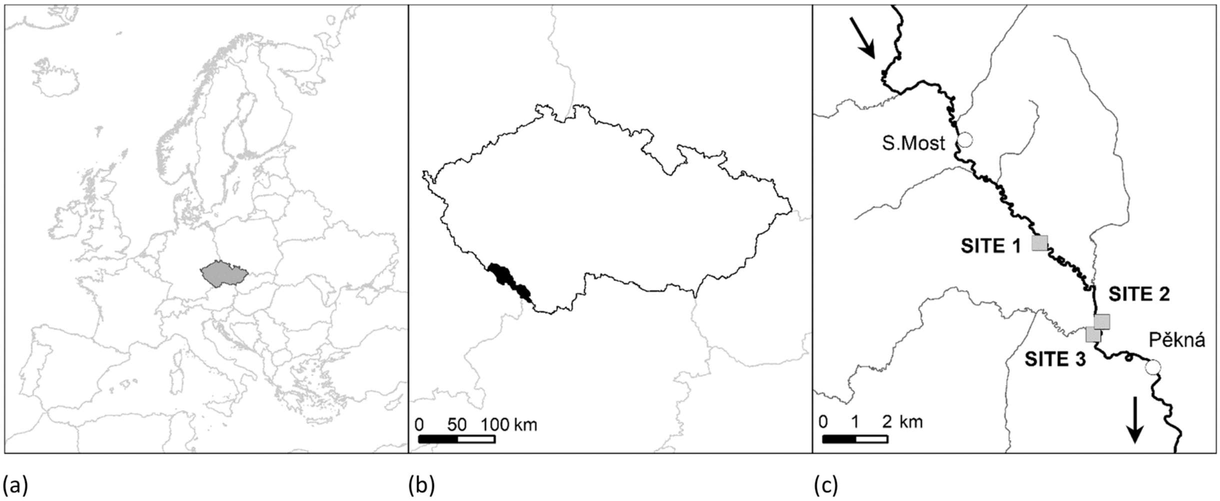

Fig. 1. Location of the study area: (a) Czech Republic; (b) Šumava National Park; (c) Upper Vltava River (the river stretch with the most strict rules for boating; entrance/exit site – white circle, rest site – grey square).

are 72 cm and 5.8 $m^3.s^{-1}$, respectively (CHMI, 2022). The river bed composition varies from sand, gravel to stones (Bílý et al., 2021). This river stretch covers the main area with the occurrence of FPMs, and therefore boating has been permitted only under very strict conditions. Rules for boating include allowed days, times and types of boats (canoes and kayaks), a minimum water level, a limited number of boats per hour, and a guide mandatory for groups. A registration charge is also required (Bílek, 2013) (500–600 CZK (20–24 EUR) per boat in 2022), with boat registrations on the river controlled by park rangers. Rafts and larger boats are no longer allowed (Křenová, 2018). According to the international scale of river difficulty in boating, the river stretch can be classified as "Easy" (Class I) to "Novice" (Class II). There are three rest sites where people are allowed to get out of their boats: "Dobrá" (Site 1, river km 383.2), "Chlum" (Site 2, river km 377.6), "Soutok" (Site 3, river km 376.7) (see Fig. 1c; Bílek, 2013).

3. Material and methods

3.1. Field study

The interactions and impacts of river tourists on FPMs were investigated at the rest sites described above. Due to the fact that the FPM is a critically endangered species in the Czech Republic (Simon et al., 2015), fake mussels had to be used for that testing. These were made from fine-grained grey concrete to mimic the actual shape of FPM shells, and placed along the river bank, mostly in five groups (with 5–6 individuals per group; see Fig. 2) to represent variable abiotic conditions (depth, river-bed substrate, distance from the river bank and local flow conditions). It was assumed that mussels occurring in colonies would be exposed to an increased susceptibility to disturbance (Blanc et al., 2006). Based on pilot testing in June 2015, several parameters were distinguished for groups of fake concrete mussels during the main experiment period (June-September 2016) (see Table 1), adjusted to site-specific conditions. Placement of the fake mussels simulated the real conditions for FPMs based on mussel requirements (cf. Degerman et al., 2009; Geist, 2010; Skinner et al., 2003) as well as local knowledge from the Upper Vltava River.

Fig. 2. A group of fake mussels during a field exposure.

Exposures of fake mussels were performed at each site from the morning to the early evening on 19 separate days (3 in 2015, 16 in 2016). Two researchers were positioned on the river bank during testing and recorded the behavior of passing people ("reactions"). No distinct effect of the researchers′ presence on tourists′ behavior was observed in 2015, thus the study conditions did not change in 2016. Three types of reactions were distinguished: (1) *unintentional* (people stepped on mussels and/or hit them by boats or paddles), (2) *intentional visual* (people observed mussels and discussed them with each other or with the guide), (3) *intentional manipulative* (people took mussels out of the water and put them back, threw them away, brought them to the researchers or even stole them). All reactions were noted for each particular group of fake mussels (see Table 1).

3.2. Lab experiment

During pilot phase of the field study, it was confirmed that people did hit the fake concrete mussels with paddles. Therefore, a supplementary lab experiment was designed to isolate the effects of this human-induced disturbance (see Ohlman and Pegg, 2020) and quantify that effect

Table 1
Basic characteristics for groups of fake mussels during a field exposure. (Depth category: A 10–20 cm, B 20–50 cm, C 50–80 cm. The visibility assessment was based on the effects of water depth, substrate, local flow conditions and sunshine.).

	Group 1	Group 2	Group 3	Group 4	Group 5
Depth	Low (A)	Low (A)	Middle (B)	Middle (B)	High (C)
Substrate	Sand	Sand	Gravel (Sand)	Gravel	Stones (Gravel)
Visibility	Very good	Good	Very good	Good	Bad
Distance from the bank (m)	0–2	0–2	2–4	2–4	4–6

("crash tests"). In August 2015, eight models were made from empty FPM shells and cotton stuffing to simulate mussel tissue. Previous studies have used similar "sham" mussels (shells filled with sand or agar and bonded together with glue or a non-toxic silicone) to examine the effects of freshwater mussels (specimens and their shells) on U.S. and Australian stream benthic and fish communities (e.g., Hopper et al., 2019; McCasker and Humphries, 2021; Spooner and Vaughn, 2006; Spooner et al., 2013). In the present study, most cracks on the shell surface were fixed with glue, and then all parts of the models joined together (with some gaps left for the entry of water into the model body to simulate live mussels) (see Fig. 3a). For the experiments, a 425-liter aquarium with a substrate layer (wet-sieved sand with gravel, grain size >0.2 mm, thickness ca 20 cm) and water column (tap water, height ca 40 cm) was used. The risk of contact between a paddle and the river-bed substrate had been observed in the field to increase with lower water columns, with the highest level of disturbance at depths of 35–45 cm (boating in shallower sites is almost impossible). Mussel models were deployed at the water-sediment interface according to photos of real mussels living within the Upper Vltava River (see Fig. 3b). The paddle motion used for crash-tests was simulated from video records of real tourists during boating along the river (in July 2015).

The main direct effects of human disturbances on aquatic organisms in heavily visited areas include the dislodgement and crushing of individuals (Brosnan and Crumrine, 1994). Therefore, the first part of experiment was focused on knocking a FPM model out of the substrate. Each FPM model was tested alone in the aquarium (with four replicate series of paddling attempts). After that, actual crash tests with the same models were performed. After each hit, it was necessary to return the FPM model to the initial position (paddle hits were repeatedly aimed at the upper part of the "emerged mussel", but its orientation in the soft substrate changed during the experiment). The experiment was ended when at least one shell of each model was partially broken.

3.3. Statistical analysis

Numbers of interactions between people and fake concrete mussels (yes-no) among categories of abiotic conditions (depth, substrate and visibility) were compared using Pearson's chi-squared test after checking the test requirements (i.e., expected frequencies higher than five). The same test was used for comparisons of numbers of unintentional and intentional reactions among sites (with visual and manipulative types joined together to meet the aforementioned requirements). Mean numbers of hits by paddles for dislodgement and crushing of each mussel model (crash-tests) were compared using a paired t-test after checking the test requirements (i.e., normality of data (by Shapiro-Wilk test)). All analyses were performed in R version 3.6.0 (R Core Team, 2020).

4. Results

4.1. Field study

During 19 observation days, 1079 people getting out of boats and 165 reactions to exposed fake concrete mussels were recorded at three rest sites between S. Most and Pěkná in the Upper Vltava River. Most people stopped at Site 1 (the first rest site in the studied river stretch), but almost 60% of all reactions were found at Site 3 (a more-attractive site at the confluence of the Studená and Teplá Vltava Rivers; see Table 2).

4.1.1. Abiotic conditions

Interactions of tourists with fake mussels were most frequent for those mussels exposed at the shallowest depth (A; 11.6% of potential interactions). For groups installed at the intermediate depth, the interaction rate decreased (B: 6.5%), and was lowest for groups at the highest depth (C: 0.6 %; see Fig. 4a). Differences in interactions among depth categories were found to be significant ($p < 0.001$).

Based on the prevalent river-bed grain size at experimental sites (according to the local investigation), tourists had the highest level of interaction with fake mussels placed in sandy and stony bottoms (both 6.1 % of potential interactions). When mussels were placed in gravel, the interaction rate dropped by half (3.3 %; see Fig. 4b). However, differences in interactions among substrate types were non-significant ($p > 0.05$).

According to the visibility of fake mussels, interactions of tourists were most numerous when mussel visibility was very good (13.7 % of potential interactions). Frequencies of interactions when visibility was poorer decreased, but was similar for both "good" and "bad" visibility (6.2 % and 5.8 %, respectively; see Fig. 4c). Differences in interactions among categories of visibility were found to be significant ($p < 0.001$).

4.1.2. Site-specific reaction types

The most frequent tourist reactions to fake mussels were unintentional (60 %) at Site 1, where people mostly stepped into mussel groups. Intentional visual reactions were less numerous (33 %; people mostly observed mussels and discussed them with each other). Manipulative reactions were the least frequent (7 %; see Fig. 5a); however, two

Table 2
Number of observation days, people getting out of boats and their reactions to fake mussels at three rest sites in the Upper Vltava River (river stretch S. Most-Pěkná).

	Site 1	Site 2	Site 3	SUM
Days	8 (42.1 %)	5 (26.3 %)	6 (31.6 %)	19
People	481 (44.6 %)	161 (14.9 %)	437 (40.5 %)	1079
Reactions	57 (34.5 %)	13 (7.9 %)	95 (57.6 %)	165

Fig. 3. (a) Mussel model (close-up), and (b) deployment in the aquarium for the lab experiment.

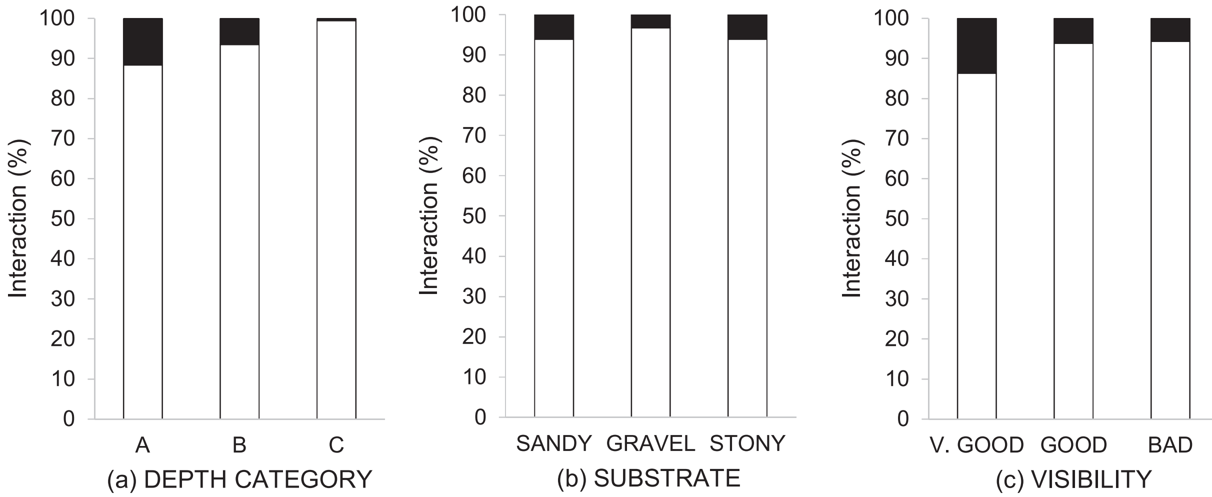

Fig. 4. Interactions of river tourists and FPMs (yes – black, no – white): (a) Effect of water depth ("A": N = 862, "B": N = 949, "C": N = 530), (b) river-bed substrate (sandy: N = 587, gravel: N = 544, stony: N = 621), and (c) visibility (very good: N = 445, good: N = 801, bad: N = 928) during the field study with fake mussels.

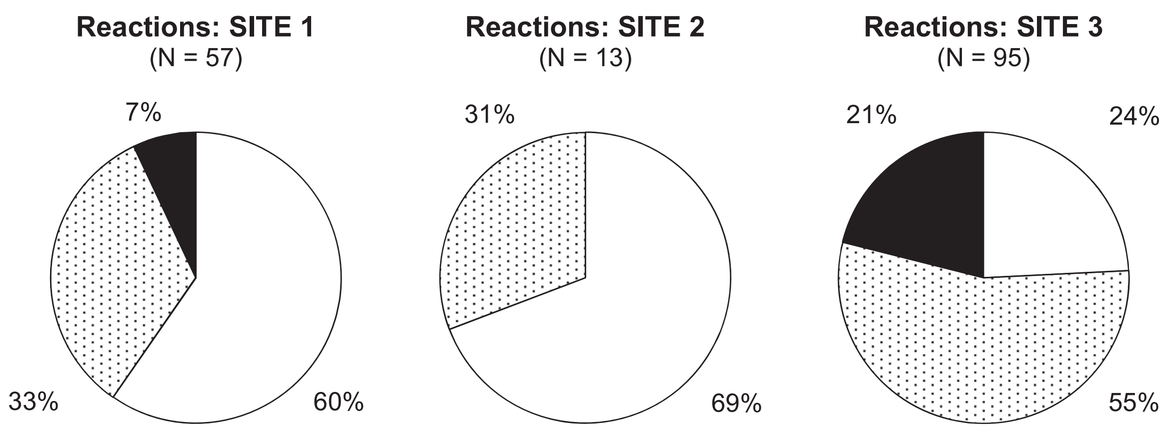

Fig. 5. Site-specific types of reactions (*unintentional* – white, *intentional visual* – dotted, *intentional manipulative* – black) during the field study with fake mussels.

tourists stole a few fake mussels despite a guide being present. Although not many reactions were observed at Site 2, their distribution was similar to at Site 1, being dominantly unintentional (almost 70 %; people impacted fake mussels by trampling or with paddles) and visual reactions (people only observed mussels) reaching 30 % frequency (see Fig. 5b). No manipulative interactions were recorded. The most frequent tourist reactions were observed at Site 3. Visual reactions represent the most common type (55 %), and people mostly spoke about their findings with each other or with a guide. Unintentional reactions were less frequent (24 %, with the same characteristics as at Site 2). As for manipulative reactions (21 %; see Fig. 5c), people usually took mussels out of the water and then put them back. But one unique event was recorded in July 2016 when a large guided group of tourists found the fake concrete mussels. Assuming that the mussels were alive, people brought them to the researchers and wanted to open them for pearls! Differences in reactions among the experimental sites were found to be significant ($p < 0.001$).

4.2. *Lab experiment*

The lab experiment using FPM models revealed that mussels were knocked out of the sediment after 8.03 ± 1.37 (mean±SD) paddle hits. Actual crash tests showed that mussel shell damage (see Fig. 6a, b) was caused by 7.88 ± 1.13 (mean±SD) hits (see Fig. 6c). Differences in hit frequencies for mussel disturbance among both tests were found to be non-significant ($p > 0.05$).

5. Discussion

Within the ŠNP area in the Czech Republic, navigating the Upper Vltava River in a small boat (canoe and kayak) is an important and popular tourist attraction. However, recreational boating can have negative impacts on the aquatic ecosystem. This study focused on a field assessment of interactions between river tourists and fake FPMs under variable abiotic and site-specific conditions. Moreover, the effects of mechanical impacts on FPMs were investigated in a lab experiment using mussel shells.

5.1. *Visitor pressure and the role of abiotic conditions*

The effects of recreational boating on FPMs in the ŠNP area were characterized by the placement of fake mussels in both shallow and deep sites along the river banks. River tourists mostly affected fake mussels in very shallow locations with depths of 10–20 cm. Several authors have stated that the FPM shows a habitat preference for "shallow" running waters (e.g., Degerman et al., 2009; Moorkens and Killeen, 2014; Outeiro et al., 2008); however, the term *shallow* is not precisely defined. An average depth of 15–18 cm was found in an Irish river with sustainable FPM recruitment (Moorkens and Killeen, 2014). River tourists in the Upper Vltava River were observed to move across shallow locations (<0.5 m) at rest sites to get out of their boats and spend a short period of time (a few minutes) in the river channel. Thus, both adult and younger specimens may be threatened by recreational boating and

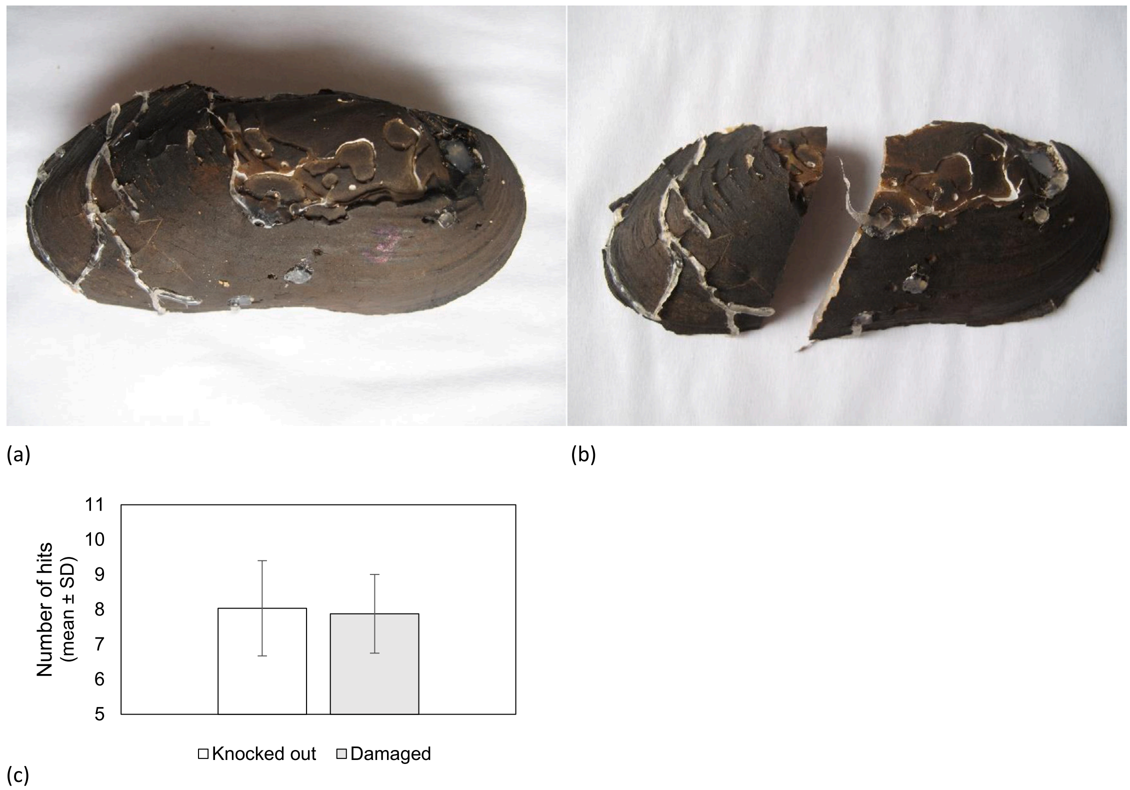

Fig. 6. A mussel model (a) before and (b) after a crash test; (c) number of paddle hits needed for a mechanical effect to be seen on mussel models (knocked out of the sediment/shell damaged).

accompanying activities. Nevertheless, FPMs have also been found in deeper locations across Europe (e.g., Hastie et al., 2000; Ostrovsky and Popov, 2011; Varandas et al., 2013), and Degerman et al. (2009) stated that Scandinavian mussel populations occurred at various depths up to 5–6 m. Visitors often use only areas for bathing where the depth does not exceed 2 m (Escarpinati et al., 2011), but wading is more widespread in the ŠNP area. In the present study, the interaction rate between river tourists and FPMs decreased with increasing water level, therefore mussels occurring at deeper sites (>0.5 m) should be less likely to be disturbed.

At the rest sites along the Upper Vltava River investigated here, the water depth increased with distance from the river banks. The most affected fake mussels were located in the 2-m wide strip close to the edge of the river where people stopped and their boats accumulated. Thus, locations with the most numerous interactions between river tourists and FPMs could be described not only by shallow water but also by closeness to the riparian zone. FPMs are generally found within 4 m of the nearest bank, as confirmed by several mussel surveys (e.g., Hastie et al., 2000; Outeiro et al., 2008; Sousa et al., 2015), which makes mussels vulnerable to visitor disturbance. Few FPMs were observed in the middle of the river channels in Portugal (Sousa et al., 2015, 2013), although those in large populations can spread out across the river bed and colonize open areas (Varandas et al., 2013). Interactions of wading tourists with mussels in small rivers and streams with narrow channels could be much more frequent; however, it can be assumed that such watercourses are not generally used for boating. Nevertheless, habitat quality for the FPM depends strongly on river bottom characteristics (Geist and Auerswald, 2007).

Results from the field study indicate that river tourists mostly affected fake mussels located in both sandy and stony substrates. The FPM requires a stable river-bed substrate, usually made from sand, gravel and small stones (Degerman et al., 2009; Moorkens and Killeen, 2014; Ostrovsky and Popov, 2011; Outeiro et al., 2008) where adults and juveniles can burrow. Mussels were found to be lacking in large areas of sandy sediments in the Waldaist River (Austria) (Jung et al., 2013), but large FPM populations in Russia can inhabit those habitats due to the slow current velocity and specific river morphology reducing flood forces (Ostrovsky and Popov, 2011). In the ŠNP area, sand was the preferred type of river-bed substrate for people to get out of their boats, explaining why most interactions of visitors with fake mussels were recorded at such sites. Surprisingly, FPMs located among larger stones were also exposed to visitor disturbances, but mussel visibility and visitors ́reactions played important roles in this case (see Section 5.2). Larger sized material can improve the stability of sand and gravel in suitable FPM locations (Geist and Auerswald, 2007; Hastie et al., 2000; Hauer, 2015; Jung et al., 2013). Sandy (or gravel) patches among stones were also recorded at the rest sites in the Upper Vltava River. On the contrary, unstable silted substrates are a poor habitat for the FPM (Boon et al., 2019). Rare silty locations in the Upper Vltava River were found to be not suitable for placing fake mussels, and were excluded from the field study.

5.2. Visitor pressure and the behavior of people

Despite being regulated, boating in the ŠNP area can still potentially have negative impacts on the aquatic environment including mussels, fish, and their habitats (Křenová and Kindlmann, 2015; Simon and Kladivová, 2006). The consequences of underwater noise pollution have already been documented for freshwater fish (e.g., changes in behavior and physiology) (Butler and Maruska, 2020; Graham and Cooke, 2008; Wysocki et al., 2006), but other animal groups have received far less attention (Sordello et al., 2020). No studies exist on the effects of paddle noise on mussels, but it may be expected that both acoustic and mechanical visitor-induced disturbances affect aquatic biota (see below and Section 5.3) in the Upper Vltava River. However, assessing the response of endangered species is difficult because in situ disturbance should be avoided, and the capture of individuals for ex situ testing is often restricted (Thiel et al., 2008). Thus, instead of directly investigating the responses of the FPM to visitor pressure, the reactions of people to endangered mussel species were assessed using fake FPMs. Interactions between river tourists and FPMs in the Upper Vltava River were found to be dependent on the visibility of fake mussel groups. Very good visibility, related with a shallow water depth and light-colored substrate (contrasting with dark mussels), induced higher numbers of visitor reactions. However, the type of reaction played an important role. Whereas visual and related manipulative reactions (i.e., handling) were more frequent for well-visible mussels, the numbers of unintentional reactions (mainly trampling within mussel groups) increased with worsening visibility.

Traditional pearl hunting including the process of handling was a major problem for the FPM populations. Although currently the mussels are protected and pearl hunting prohibited (Degerman et al., 2009; NCA CR, 2013; Skinner et al., 2003), and manipulating FPMs during any phase of their life cycle is prohibited by law (Simon et al., 2015), illegal pearl hunters still examine mussels and specimens can be killed using destructive methods (Bauer, 1988). In the present study, some of the river tourists, who were apparently not able to differentiate the fake animals from real FPMs, acted like illegal pearl hunters when attempted to open mussel "shells".

Visitors of shallow river areas generally come into contact with the river bed: trampling can cause the death of some organisms (Escarpinati et al., 2014, 2011), and should be minimized in rivers and streams carrying FPM populations (Skinner et al., 2003). Visitor movement across the river channel is forbidden in the core zone of the ŠNP, but wading, bathing, and swimming tourists were observed at the rest sites, despite a guide being present. Such activities may lead to a prolonged time spent in the river channel, and consequently an increased risk of contact (both trampling and handling) between humans and FPMs. Juvenile mussels, which have more fragile shells, may be more protected because they live within the river bed, but some individuals move up to the water-sediment interface as a result of adverse oxygen conditions (Bílý et al., 2021). In such cases, young mussels would be potentially exposed to trampling by tourists. Trampling can also have an indirect negative consequences for FPM populations; e.g., through river-bed compaction resulting in low exchange between the water column and the bottom substrate (Boon et al., 2019; Geist and Auerswald, 2007), or the resuspension of fine material with adverse effects on mussel filter-feeding and oxygenation (Moorkens and Killeen, 2014).

Site-specific investigation in the Upper Vltava River divided the rest sites into "less-attractive" (Site 1 and Site 2) and "more-attractive" groups (Site 3). At less-attractive sites, people stop and get out of their boats within a limited area of shallow water, resulting in disturbance of the river-bed environment. They also spend most time outside the river channel, so mostly unintentional reactions with fake FPMs were recorded at those sites. On the contrary, at the more-attractive site at the confluence of the Studená and Teplá Vltava Rivers, visitors have larger areas for getting out of boats, and the water depths are very low. People often move across and inspect the river channel, so visual reactions were more frequent at that site. Overall, the typical interactions of visitors with mussels observed in this study can be characterized as non-manipulative.

5.3. Visitor pressure and mechanical impacts

River tourists can also affect mussels while boating along the river, mainly by the action of their paddles. The lab experiments performed here to quantify human mechanical impacts showed that mussel models were knocked out of the sediment after mean number of eight paddle hits. It must be stated that the relatively unstable substrate used during lab testing may have contributed to a higher risk of dislodgement. Behavioral responses of four freshwater mussel species to their removal from the substrate were investigated by Waller et al. (1999), who described three locomotor behaviors: righting (realignment to a vertical position), horizontal movement, and burrowing into the substrate. While FPMs can also re-bury themselves after dislodgement (Skinner et al., 2003), this process can induce stress, especially if there are repeated hits by paddles and changes in mussel positions.

In addition to the dislodgment, mussels can be also damaged by the paddles of river tourists. The mean number of paddle hits needed to damage FPM models was 7.88 (similar to mussels being knocked out of the substrate). In the lab experiment, the models were replaced to the vertical position after each hit. The movement of real FPMs after such a disturbance has not been documented in greater detail, though in the experiment mentioned above Waller et al. (1999) found that many mussels did not right themselves during 168 h. Ziuganov et al. (2000) investigated mutilations including shell damage (a cracked right shell) and their effects on individual FPM survival using experimental animals placed in the River Varzuga (Russia) and checked each third day. Half of 30 mussels died during the first 9 days, and the remaining specimens were dead between "day 9″ and "day 15″. Thus, having only a cracked shell and posterior adductor damage led to 100 % mortality, though handling and aerial exposure during check days may have contributed to this mortality. The same authors evaluated FPM regeneration experiments in the Thorma River (Russia) and found that three adults with shells previously damaged had completely repaired shells after two years. The FPM population in the Upper Vltava River is characterized by a decrease in longevity and increase in growth compared to northern populations (NCA CR, 2013), and may suffer from insufficient shell regeneration (Ziuganov et al., 2000). Moreover, the mechanical impacts caused by river tourists and their paddles may be repeated and also intensified by trampling during wading (and bathing).

The effects of recreational boating on river environments can also be more detrimental due to the altered flow conditions that have become more extreme as a result of climate change (Degerman et al., 2009; Santos et al., 2015; Sousa et al., 2012). Negative interactions between river tourists and FPMs might be higher when mussels are exposed to low flow and decreased water depth, as noticed for other bivalves by Lorenz et al. (2013). Animals would be more vulnerable to hits by paddles, trampling and (potential) handling. However, in the Upper Vltava River low-flow periods could also have positive effects on the FPM population, as the minimum water level used by the ŠNP Administration for permitting boating could help protect local mussel population from visitor-induced disturbances during low flows. Nevertheless, water levels are only checked at the entrance site of the study river stretch, and even under conditions permitting boating many very shallow areas were observed along the river. Moreover, prolonged low-flow conditions may lead to illegal boating without any check on touristś behavior. On the contrary, high-flow periods can also lower visitor impacts on the FPM population, as no interactions of river tourists with fake mussels were recorded during highly increased water levels. Extreme floods may greatly affect mussel populations, as FPMs can be damaged/crushed by moving substrates and/or large sediment deposits, or washed out onto riverbanks where they desiccate and die (Álvarez-Claudio et al., 2000; Hastie et al., 2001; Sousa et al., 2012). However, the Upper Vltava River has a relatively wide floodplain that can mitigate the negative impacts of high-flow conditions on mussel populations by reducing flow velocities (also see Hauer et al., 2022, this issue).

5.4. Implications for management

River tourism and regulation can be complicated due to the competing interests of nature conservation authorities, the tourism industry, and the general public. This was also the case in the ŠNP area, with discussions of a ban on recreational boating in the Upper Vltava River contrasting with an "open river" policy without any restrictions (Křenová and Kindlmann, 2015). Long-term negotiations by the ŠNP Administration led to compromise rules acceptable for the Czech Canoe Union, the major boating industry representatives, fishermen, scientists, NGO groups and local authorities. Interactions of river tourists with mussels were not studied during this process, though assessing and monitoring visitor behavior is a great challenge for managers of protected areas (McGinlay et al., 2020).

Based on the results of the present study, the effects of recreational boating along the river might be less detrimental than those of accompanying activities, such as wading, bathing, and swimming. Tourists in protected areas should be educated on how their activities affect wildlife and how they can modify their behavior to mitigate pressure on endangered species (Miller et al., 2001). The ŠNP Administration has used a set of tools for visitor education (i.e., guide presentations, an information point at the entrance site, a virtual natural trail (http://vltava.perlorodkaricni.cz/), an official boating webpage (https://splouvani.npsumava.cz/en/) and leaflets). However, our discussions with river tourists revealed them to be in doubt regarding the rules for regulated boating and FPM protection in the Upper Vltava River, especially if they had never had contact with FPMs before.

Simple and harmless method of using fake mussels can provide insights into the interactions of people and endangered mussel species and improve the level of knowledge on visitor behavior. Surprisingly, in the present study in the ŠNP area the reactions of river tourists to fake mussels were less frequent for non-guided groups. However, mostly visual reactions were recorded when guides were present, whereas non-guided visitors more often manipulated mussels. Two rest sites are located close to each other in the Upper Vltava River, and tourists with no guide were observed to stop at Site 2 (a less-attractive site), whereas guided visitors generally stopped downstream at Site 3 (a more-attractive site). This finding could be useful for the management of protected areas, and the establishment of a "buffer site" upstream of the most visited sites would mitigate visitor impacts. Nevertheless, the movement of visitors within the river channel should be strictly checked, as demonstrated by the presence of recently dead adult FPM with broken shells found in the Upper Vltava River in 2015 (Zelenková et al., 2015). If a guide is not present, information and training before recreational activities would likely help to minimize negative impacts (Escarpinati et al., 2014).

A minimum number of interactions between river tourists and mussels was found in locations deeper than 0.5 m, so the negative impacts of visitor behavior might be lower if mussels were moved to deeper sites. However, artificial relocation of adult FPMs has not yet been shown to be effective (Cosgrove and Hastie, 2001; Hastie et al., 2003). Álvarez-Claudio et al. (2000) marked and relocated 124 specimens to conserve a FPM population in the River Narcea (Spain), but none could be found in the next year during re-sampling. Mussel watchers, photographs and scientists using manipulative monitoring methods might also harm some small mussel populations, but the level of such effects remains unknown and needs to be investigated in more extended studies. In any case, manipulating FPMs should be limited to severe threat situations (Skinner et al., 2003), such as moving mussels subject to desiccation (Sousa et al., 2018). No FPMs were found at or close to the present rest sites in the Upper Vltava River, so it is currently not necessary to relocate animals to adjacent deeper river areas. If FPM monitoring in the future would confirm the presence of the species near rest sites, the conflict between river tourism and nature conservation could be resolved by e.g., changes in the locations of rest sites. Protecting adult mussels and the maintenance of juvenile habitat should be key conservation measures for the FPM (Cosgrove and Hastie, 2001), and the non-invasive methods used here could be applied to assess visitor-induced pressure in other protected (and non-protected) areas.

6. Conclusion

The present study clearly showed that fake FPM specimens were mostly affected by river tourists in shallow running waters near the edge of the river, with both fine and coarse river-bed substrates. Based on previous surveys and studies, such habitat could be generally described as "ideal" for the FPM. Therefore, this sensitive bivalve species could be threatened by river tourism. Fake mussels that were well visible were also frequently disturbed, but the type of reaction (unintentional, visual, and manipulative) varied under site-specific conditions. Lab experiment indicated that several repeated hits by paddles are needed to both dislodge mussels and to damage their shells. Thus, the effects of recreational boating might be less detrimental than those of accompanying activities, such as wading, bathing, and swimming. Human-induced FPM disturbances related with trampling and handling should be investigated in greater detail to support mussel conservation. Relocation actions have not been very effective, so conservation measurements should be focused on the protection and maintenance of mussels and their habitats. Although effective regulation of the daily numbers of river tourists was implemented in the ŠNP area to minimalize disturbances to the FPM population, understanding visitor behavior is critical for keeping the core zone of the national park open to tourist use.

CRediT authorship contribution statement

***Vojtěch Barák*:** Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Project Administration (lead), Validation (lead), Visualization (lead), Writing – original draft preparation (equal), Writing – review & editing (equal). ***Christoph Hauer*:** Conceptualization (equal), Resources (supporting), Supervision (equal), Writing – review & editing (equal). ***Ondřej Simon*:** Funding acquisition (lead), Investigation (supporting), Methodology (equal), Resources (lead), Supervision (equal), Writing – review & editing (supporting). ***Peter Flödl*:** Conceptualization (equal), Writing – original draft preparation (equal), Writing – review & editing (supporting).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Authors' contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by VB and OS (analysis by VB). The first draft of the manuscript was written by VB and PF. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References

Álvarez-Claudio, C., García-Rovés, P., Ocharan, R., Cabal, J.A., Ocharan, F.J., Álvarez, M. A., 2000. A new record of the freshwater pearl mussel *Margaritifera margaritifera* L. (Bivalvia, Unionoida) from the River Narcea (Asturias, north-western Spain). Aquat. Conserv.: Mar. Freshw. Ecosyst. 10, 93–102. https://doi.org/10.1002/(SICI)1099-0755(200003/04)10:2%3C93::AID-AQC392%3E3.0.CO;2-4.

Bauer, G., 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in Central Europe. Biol. Conserv. 45, 239–253. https://doi.org/10.1016/0006-3207(88)90056-0.

Bednar-Friedl, B., Behrens, D.A., Getzner, M., 2012. Optimal dynamic control of visitors and endangered species in a national park. Environ. Resour. Econ. 52, 1–22. https://doi.org/10.1007/s10640-011-9515-5.

Behrens, D.A., Bednar-Friedl, B., Getzner, M., 2009. Sustainable management of an alpine national park: Handling the two-edged effect of tourism. Cent. Eur. J. Oper. Res. 17, 233–253. https://doi.org/10.1007/s10100-009-0087-1.

CHMI (Czech Hydrometeorological Institute Prague), 2022. Flood Forecasting Service: Gauging Station Chlum. https://hydro.chmi.cz/hpps/evlist.php?seq=307234. Accessed 8 June 2022.

Bílek, O., 2013. Canoeing in the Teplá Vltava River between Soumarský Most and Pěkná from year 2013. GeoVision, Pilsen (in Czech).

Bílý, M., Simon, O., Barák, V., Jahelková, V., 2021. Occurrence depth of juvenile freshwater pearl mussels (*Margaritifera margaritifera*) in a river bed tested by experimental mesh tubes. Hydrobiologia 848, 3127–3139. https://doi.org/10.1007/s10750-020-04298-8.

Blanc, R., Guillemain, M., Mouronval, J.P., Desmonts, D., Fritz, H., 2006. Effects of non-consumptive leisure disturbance to wildlife. Rev. Écol. 61, 117–133.

Boltovskoy, D., Correa, N., Cataldo, D., Sylvester, F., 2006. Dispersion and ecological impact of the invasive freshwater bivalve *Limnoperna fortunei* in the Río de la Plata watershed and beyond. Biol. Invasions 8, 947–963. https://doi.org/10.1007/s10530-005-5107-z.

Boon, P.J., Cooksley, S.L., Geist, J., Killeen, I.J., Moorkens, E.A., Sime, I., 2019. Developing a standard approach for monitoring freshwater pearl mussel (*Margaritifera margaritifera*) populations in European rivers. Aquat. Conserv.: Mar. Freshw. Ecosyst. 29, 1365–1379. https://doi.org/10.1002/aqc.3016.

Brosnan, D.M., Crumrine, L.L., 1994. Effects of human trampling on marine rocky shore communities. J. Exp. Mar. Biol. Ecol. 177, 79–97. https://doi.org/10.1016/0022-0981(94)90145-7.

Butler, J.M., Maruska, K.P., 2020. Underwater noise impairs social communication during aggressive and reproductive encounters. Anim. Behav. 164, 9–23. https://doi.org/10.1016/j.anbehav.2020.03.013.

Calcagno, J.A., Curelovich, J.N., Fernandez, V.M., Thatje, S., Lovrich, G.A., 2012. Effects of physical disturbance on a sub-Antarctic middle intertidal bivalve assemblage. Mar. Biol. Res. 8, 937–953. https://doi.org/10.1080/17451000.2012.702911.

Cao, Y., Wang, B., Zhang, J., Wang, L., Pan, Y., Wang, Q., Jian, D., Deng, G., 2016. Lake macroinvertebrate assemblages and relationship with natural environment and tourism stress in Jiuzhaigou Natural Reserve. China Ecol. Indic. 62, 182–190. https://doi.org/10.1016/j.ecolind.2015.11.023.

Carosi, A., Barelli, M.G., Ambrosi, A., Rossetti, A., Padula, R., Bifulco, C., Morandi, F., Lorenzoni, M., 2021. Conservation status of *Chirocephalus marchesonii* Ruffo & Vesentini, 1957 in the Pilato Lake (Sibillini Mountains National Park, Central Italy). Fundam. Appl. Limnol. 194, 171–185. https://doi.org/10.1127/fal/2020/1292.

Carosi, A., Barelli, M.G., Ambrosi, A., Rossetti, A., Morandi, F., Lorenzoni, F., Tagliaferri, G., Lorenzoni, M., 2022. Population status and ecology of the steno-endemic fairy shrimp *Chirocephalus sibyllae* Cottarelli and Mura, 1975 inhabiting a mountain temporary pond (Central Italy). Water 14, 1750. https://doi.org/10.3390/w14111750.

Černá, M., Simon, O.P., Bílý, M., Douda, K., Dort, B., Galová, M., Volfová, M., 2018. Within-river variation in growth and survival of juvenile freshwater pearl mussels assessed by in situ exposure methods. Hydrobiologia 810, 393–414. https://doi.org/10.1007/s10750-017-3236-x.

Clements, E.A., Thomas, R., Adams, C.E., 2018. An investigation of salmonid host utilization by the endangered freshwater pearl mussel (*Margaritifera margaritifera*) in north-west Scotland. Aquat. Conserv.: Mar. Freshw. Ecosyst. 28, 764–768. https://doi.org/10.1002/aqc.2900.

Cole, D.N., Landres, P.B., 1995. Indirect effects of recreation on wildlife. In: Knight, R.L., Gutzwiller, K.J. (Eds.), Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington DC, pp. 183–202.

R. Core Team, 2020. R: A language and environment for statistical computing (version 3.6.0). R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Cosgrove, P.J., Hastie, L.C., 2001. Conservation of threatened freshwater pearl mussel populations: River management, mussel translocation and conflict resolution. Biol. Conserv. 99, 183–190. https://doi.org/10.1016/S0006-3207(00)00174-9.

Dafforn, K.A., Lewis, J.A., Johnston, E.L., 2011. Antifouling strategies: history and regulation, ecological impacts and mitigation. Mar. Pollut. Bull. 62, 453–465. https://doi.org/10.1016/j.marpolbul.2011.01.012.

Degerman, E., Alexanderson, S., Bergengren, J., Henrikson, L., Johansson, B.E., Larsen, B.M., Söderberg, H., 2009. Restoration of freshwater pearl mussel streams. WWF Sweden, Solna.

Denic, M., Geist, J., 2015. Linking stream sediment deposition and aquatic habitat quality in pearl mussel streams: Implications for conservation. River Res. Appl. 31, 943–952. https://doi.org/10.1002/rra.2794.

Dertien, J.S., Larson, C.L., Reed, S.E., 2021. Recreation effects on wildlife: a review of potential quantitative thresholds. Nat. Conserv. 44, 51–68. https://doi.org/10.3897/natureconservation.44.63270.

Diviš, A., 2009. Boating in the Teplá Vltava River in year 2009. Šumava (The Šumava Journal) 14, 26–27.

Drake, L.A., Doblin, M.A., Dobbs, F.C., 2007. Potential microbial bioinvasions via ships' ballast water, sediment, and biofilm. Mar. Pollut. Bull. 55, 333–341. https://doi.org/10.1016/j.marpolbul.2006.11.007.

Escarpinati, S.C., Roque, F.O., Medina-Jr, P.B., Raizer, J., 2011. Macroinvertebrate community in recreational areas in a karst river (Bonito, Brazil): Implications for biomonitoring of tourist activities. Tour. Karst Areas 4, 121–130.

Escarpinati, S.C., Siqueira, T., Medina-Jr, P.B., Roque, F.O., 2014. Short-term effects of visitor trampling on macroinvertebrates in karst streams in an ecotourism region. Environ. Monit. Assess. 186, 1655–1663. https://doi.org/10.1007/s10661-013-3483-x.

Fleit, G., Hauer, C., Baranya, S., 2021. A numerical modeling-based predictive methodology for the assessment of the impacts of ship waves on YOY fish. River Res. Appl. 37, 373–386. https://doi.org/10.1002/rra.3764.

Flödl, P., Hauer, C., 2019. Studies on morphological regime conditions of bi-modal grain size rivers: Challenges and new insights for freshwater pearl mussel habitats. Limnologica 79, 125729. https://doi.org/10.1016/j.limno.2019.125729.

French McCay, D., Rowe, J.J., Whittier, N., Sankaranarayanan, S., Schmidt Etkin, D., 2004. Estimation of potential impacts and natural resource damages of oil. J. Hazard. Mater. 107, 11–25. https://doi.org/10.1016/j.jhazmat.2003.11.013.

Gabel, F., Lorenz, S., Stoll, S., 2017. Effects of ship-induced waves on aquatic ecosystems. Sci. Total Environ. 601–602, 926–939. https://doi.org/10.1016/j.scitotenv.2017.05.206.

Geist, J., 2010. Strategies for the conservation of endangered freshwater pearl mussels (*Margaritifera margaritifera* L.): A synthesis of conservation genetics and ecology. Hydrobiologia 644, 69–88. https://doi.org/10.1007/s10750-010-0190-2.

Geist, J., Auerswald, K., 2007. Physicochemical stream bed characteristics and recruitment of the freshwater pearl mussel (*Margaritifera margaritifera*). Freshw. Biol. 52, 2299–2316. https://doi.org/10.1111/j.1365-2427.2007.01812.x.

Graham, A.L., Cooke, S.J., 2008. The effects of noise disturbance from various recreational boating activities common to inland waters on the cardiac physiology of a freshwater fish, the largemouth bass (*Micropterus salmoides*). Aquat. Conserv.: Mar. Freshw. Ecosyst. 18, 1315–1324. https://doi.org/10.1002/aqc.941.

Hardiman, N., Burgin, S., 2011. Effects of trampling on in-stream macroinvertebrate communities from canyoning activity in the Greater Blue Mountains World Heritage Area. Wetl. Ecol. Manag. 19, 61–71. https://doi.org/10.1007/s11273-010-9200-4.

Hastie, L.C., Boon, P.J., Young, M.R., 2000. Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L.). Hydrobiologia 429, 59–71. https://doi.org/10.1023/A:1004068412666.

Hastie, L.C., Boon, P.J., Young, M.R., Way, S., 2001. The effects of a major flood on an endangered freshwater mussel population. Biol. Conserv. 98, 107–115. https://doi.org/10.1016/S0006-3207(00)00152-X.

Hastie, L.C., Cosgrove, P.J., Ellis, N., Gaywood, M.J., 2003. The threat of climate change to freshwater pearl mussel populations. Ambio 32, 40–46. https://doi.org/10.1579/0044-7447-32.1.40.

Hauer, C., 2015. Review of hydro-morphological management criteria on a river basin scale for preservation and restoration of freshwater pearl mussel habitats. Limnologica 50, 40–53. https://doi.org/10.1016/j.limno.2014.11.002.

Hauer, C., Flödl, P., Stelzer, S., Mayer, T., Höfler, S., Ottner, F., 2022. The Wullowitz-Lakes theory: periglacial impacts on river morphology and habitat suitability for the endangered freshwater pearl mussel. Limnologica. https://doi.org/10.1016/j.limno.2022.126007. In press.

Hoess, R., Geist, J., 2020. Spatiotemporal variation of streambed quality and fine sediment deposition in five freshwater pearl mussel streams, in relation to extreme drought, strong rain and snow melt. Limnologica 85, 125833. https://doi.org/10.1016/j.limno.2020.125833.

Hopper, G.W., DuBose, T.P., Gido, K.B., Vaughn, C.C., 2019. Freshwater mussels alter fish distributions through habitat modifications at fine spatial scales. Freshw. Sci. 38, 702–712. https://doi.org/10.1086/705666.

Jung, M., Scheder, C., Gumpinger, C., Waringer, J., 2013. Habitat traits, population structure and host specificity of the freshwater pearl mussel *Margaritifera margaritifera* in the Waldaist River (Upper Austria). Biologia 68, 922–931. https://doi.org/10.2478/s11756-013-0244-9.

Knight, R.L., Gutzwiller, K.J., 1995. Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington DC.

Křenová, Z., 2018. Canoeing with pearl mussels. Int. J. Wilderness 24, 86–93. ⟨https://ijw.org/canoeing-with-pearl-mussels/⟩.

Křenová, Z., Kiener, H., 2012. Europe's Wild Heart – still beating? Experiences from a new transboundary wilderness area in the middle of the Old Continent. Eur. J. Environ. Sci. 2, 115–124. https://doi.org/10.14712/23361964.2015.32.

Křenová, Z., Kindlmann, P., 2015. Natura 2000 – solution for Eastern Europe or just a good start? The Šumava National Park as a test case. Biol. Conserv. 186, 268–275. https://doi.org/10.1016/j.biocon.2015.03.028.

Křenová, Z., Vrba, J., 2014. Just how many obstacles are there to creating a national park? A case study from the Šumava National Park. Eur. J. Environ. Sci. 4, 30–36. https://doi.org/10.14712/23361964.2015.2.

Lorenz, S., Pusch, M.T., 2012. Estimating the recreational carrying capacity of a lowland river section. Water Sci. Technol. 66, 2033–2039. https://doi.org/10.2166/wst.2012.418.

Lorenz, S., Gabel, F., Dobra, N., Pusch, M.T., 2013. Modelling the effects of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river. Freshw. Sci. 32, 82–93. https://doi.org/10.1899/12-054.1.

Malmqvist, B., Rundle, S., 2002. Threats to the running water ecosystems of the world. Environ. Conserv. 29, 134–153. https://doi.org/10.1017/S0376892902000097.

Matasová, K., Simon, O.P., Dort, B., Douda, K., Bílý, M., 2013. Recent distribution of freshwater pearl mussel (*Margaritifera margaritifera*) at historical localities in the upper part of the Vltava River basin (Czech Republic). Silva Gabreta 19, 139–148.

McCasker, N., Humphries, P., 2021. Hyriid mussels (Unionoida) enhance benthic organic matter and meiofauna densities in a temperate Australian river. Freshw. Biol. 66, 936–948. https://doi.org/10.1111/fwb.13688.

McGinlay, J., Gkoumas, V., Holtvoeth, J., Armas Fuertes, R.F., Bazhenova, E., Benzoni, A., Botsch, K., Cabrera Martel, C., Carrillo Sánchez, C., Cervera, I., Chaminade, G., Doerstel, J., Fagundo García, C.J., Jones, A., Lammertz, M., Lotman, K., Odar, M., Pastor, T., Ritchie, C., Santi, S., Smolej, M., Soriano Rico, F., Waterman, H., Zwijacz-Kozica, T., Kontoleon, A., Dimitrakopoulos, P.G., Jones, N., 2020. The impact of COVID-19 on the management of European protected areas and policy implications. Forests 11, 1214. https://doi.org/10.3390/f11111214.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildl. Soc. Bull. 29, 124–132.

Moorkens, E.A., Killeen, I.J., 2014. Assessing near-bed velocity in a recruiting population of the endangered freshwater pearl mussel (*Margaritifera margaritifera*) in Ireland. Aquat. Conserv.: Mar. Freshw. Ecosyst. 24, 853–862. https://doi.org/10.1002/aqc.2530.

Nykles, F., 2014. The history of boating in rivers within the Šumava National Park. Šumava (The Šumava Journal) 19, 10–11.

Ohlman, L.M., Pegg, M.A., 2020. Handling effects on survival and growth of plain pocketbook *Lampsilis cardium* (Rafinesque, 1820) freshwater mussels. Hydrobiologia 847, 457–467. https://doi.org/10.1007/s10750-019-04106-y.

Ostrovsky, A.N., Popov, I.Y., 2011. Rediscovery of the largest population of the freshwater pearl mussel (*Margaritifera margaritifera*) in the Leningrad oblast (north-west Russia). Aquat. Conserv.: Mar. Freshw. Ecosyst. 21, 113–121. https://doi.org/10.1002/aqc.1164.

Outeiro, A., Ondina, P., Fernández, C., Amaro, R., San Miguel, E., 2008. Population density and age structure of the freshwater pearl mussel, *Margaritifera margaritifera*, in two Iberian rivers. Freshw. Biol. 53, 485–496. https://doi.org/10.1111/j.1365-2427.2007.01913.x.

Padula, R., Carosi, A., Rossetti, A., Lorenzoni, M., 2021. The diatomic diversity of two Mediterranean high-elevation lakes in the Sibillini Mountains National Park (Central Italy). Environments 8, 79. https://doi.org/10.3390/environments8080079.

Polat, E., Keles, E., Uzun, F., Gul, A., 2016. Sustainable rafting tourism planning and management: An example of Antalya-Koprucay Rafting Area. J. Environ. Prot. 17, 789–795.

Reed, S.E., Merenlender, A.M., 2008. Quiet, non-consumptive recreation reduces protected area effectiveness. Conserv. Lett. 1, 146–154. https://doi.org/10.1111/j.1755-263X.2008.00019.x.

Rösner, S., Mussard-Forster, E., Lorenc, T., Müller, J., 2014. Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. Landsc. Ecol. 29, 55–66. https://doi.org/10.1007/s10980-013-9964-z.

Santos, R.M.B., Sanches Fernandes, L.F., Varandas, S.G.P., Pereira, M.G., Sousa, R., Teixeira, A., Lopes-Lima, M., Cortes, R.M.V., Pacheco, F.A.L., 2015. Impacts of climate change and land-use scenarios on *Margaritifera margaritifera*, an environmental indicator and endangered species. Sci. Total Environ. 511, 477–488. https://doi.org/10.1016/j.scitotenv.2014.12.090.

Simon, O., Kladivová, V., 2006. Study of the effects of canoeing on ecosystems of the river bottom in the Teplá Vltava River. Water Research Institute, Prague. (in Czech).

Simon, O.P., Vaníčková, I., Bílý, M., Douda, K., Patzenhauerová, H., Hruška, J., Peltánová, A., 2015. The status of freshwater pearl mussel in the Czech Republic: several successfully rejuvenated populations but the absence of natural reproduction. Limnologica 50, 11–20. https://doi.org/10.1016/j.limno.2014.11.004.

Skinner, A., Young, M., Hastie, L., 2003. Ecology of the freshwater pearl mussel. English Nature, Peterborough.

Sordello, R., Ratel, O., De Lachapelle, F.F., Leger, C., Dambry, A., Vanpeene, S., 2020. Evidence of the impact of noise pollution on biodiversity: a systematic map. Environ. Evid. 9, 20. https://doi.org/10.1186/s13750-020-00202-y.

Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J., Guilhermino, L., 2012. Massive die-offs of freshwater bivalves as resource pulses. Ann. Limnol. - Int. J. Limnol. 48, 105–112. https://doi.org/10.1051/limn/2012003.

Sousa, R., Amorim, A., Sobral, C., Froufe, E., Varandas, S., Teixeira, A., Lopes-Lima, M., 2013. Ecological status of a *Margaritifera margaritifera* (Linnaeus, 1758) population at the southern edge of its distribution (River Paiva, Portugal). Environ. Manag. 52, 1230–1238. https://doi.org/10.1007/s00267-013-0117-6.

Sousa, R., Amorim, A., Froufe, E., Varandas, S., Teixeira, A., Lopes-Lima, M., 2015. Conservation status of the freshwater pearl mussel *Margaritifera margaritifera* in Portugal. Limnologica 50, 4–10. https://doi.org/10.1016/j.limno.2014.07.004.

Sousa, R., Ferreira, A., Carvalho, F., Lopes-Lima, M., Varandas, S., Teixeira, A., 2018. Die-offs of the endangered pearl mussel *Margaritifera margaritifera* during an extreme drought. Aquat. Conserv.: Mar. Freshw. Ecosyst. 28, 1244–1248. https://doi.org/10.1002/aqc.2945.

Spooner, D.E., Vaughn, C.C., 2006. Context-dependent effects of freshwater mussels on stream benthic communities. Freshw. Biol. 51, 1016–1024. https://doi.org/10.1111/j.1365-2427.2006.01547.x.

Spooner, D.E., Frost, P.C., Hillebrand, H., Arts, M.T., Puckrin, O., Xenopoulos, M.A., 2013. Nutrient loading associated with agriculture land use dampens the importance of consumer-mediated niche construction. Ecol. Lett. 16, 1115–1125. https://doi.org/10.1111/ele.12146.

Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. Ecol. Appl. 13, 951–963. https://doi.org/10.1890/1051-0761(2003)13[951:WRTRAA]2.0.CO;2.

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R., Jenni, L., 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*. J. Appl. Ecol. 45, 845–853. https://doi.org/10.1111/j.1365-2664.2008.01465.x.

Toro, M., Granados, I., 2002. Restoration of a small high mountain lake after recent tourist impact: the importance of limnological monitoring and palaeolimnology. Water Air Soil Pollut.: Focus 2, 295–310. https://doi.org/10.1023/A:1020127313830.

Varandas, S., Lopes-Lima, M., Teixeira, A., Hinzmann, M., Reis, J., Cortes, R., Machado, J., Sousa, R., 2013. Ecology of southern European pearl mussels (*Margaritifera margaritifera*): first record of two new populations on the rivers Terva and Beca (Portugal). Aquat. Conserv.: Mar. Freshw. Ecosyst. 23, 374–389. https://doi.org/10.1002/aqc.2321.

Waller, D.L., Gutreuter, S., Rach, J.J., 1999. Behavioral responses to disturbance in freshwater mussels with implications for conservation and management. J. North Am. Benthol. Soc. 18, 381–390. https://doi.org/10.2307/1468451.

Wysocki, L.E., Dittami, J.P., Ladich, F., 2006. Ship noise and cortisol secretion in European freshwater fishes. Biol. Conserv. 128, 501–508. https://doi.org/10.1016/j.biocon.2005.10.020.

Zelenková, E., Slavík, O., Douda, K., Hladík, M., Horký, P., Simon, O., Dort, B., Tušer, M., Muška, M., 2015. Coexistence between humans and freshwater pearl mussels in the Vltavský luh area. Šumava (The Šumava Journal) 20, 8–11.

NCA CR (National Conservation Agency of the Czech Republic), 2013. Action plan for the endangered freshwater pearl mussel in the Czech Republic. NCA CR, Prague. (in Czech).

Zelenková, E., 2008. Status of river tourists in rivers within the Šumava National Park. Ochrana přírody (The Nature Conservation Journal) 3, 24–25. (in Czech).

Ziuganov, V., San Miguel, E., Neves, R.J., Longa, A., Fernández, C., Amaro, R., Beletsky, V., Popkovitch, E., Kaliuzhin, S., Johnson, T., 2000. Life span variation of the freshwater pearl shell: a model species for testing longevity mechanisms in animals. Ambio 29, 102–105. https://doi.org/10.1579/0044-7447-29.2.102.