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Predation risk and competition affect habitat use of adult perch (*Perca fluviatilis*)

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Abstract

The aim of this study was to examine how the presence of a predator and an interspecific competitor influence the habitat use of adult perch (*Perca fluviatilis*; size: 15.1 ± 0.5 cm) when given the choice between two adjacent habitats. By means of aquarium experiments, the habitat occupancy of *P. fluviatilis* was documented in presence and absence of a predator (pike *Esox lucius*; size: 25.4 ± 2.1 cm) and a potential competitor (ruffe *Gymnocephalus cernuus*; size: 14.1 ± 0.3 cm) fish species. The two *P. fluviatilis* individuals generally shared the same habitat. In the presence of a conspecific, *P. fluviatilis* favoured the structurally more complex artificial macrophyte habitat over the less structured rock and sand habitat, which in turn were used in about equal proportions. In the predator- and competitor treatments, *P. fluviatilis* seemed to adapt their habitat use to the habitat occupancy of *E. lucius* and *G. cernuus* in the *Macrophyte vs. Rock* and, in the predator treatment, also in the *Macrophyte vs. Sand* habitat combination, by increasingly occupying a habitat that was used less by the predator or competitor species, respectively. This suggests that *P. fluviatilis* tried to avoid the other fish species by choosing a, in some cases less preferred, predator- or competitor-free habitat. This study emphasizes the importance of biological interactions, illustrated by the potential of predation risk and competition to structure fish communities by influencing habitat use at small spatial scales.

Keywords: competition, fish community, habitats, *Perca fluviatilis*, predation, structural complexity

Introduction

Interspecific interactions, such as predation and competition, play a major role in structuring fish communities (De Bernardi, 1981; Boaden & Kingsford, 2015; Heck & Orth, 1980; Hixon & Jones, 2005) and are strongly influenced by the structural complexity of the environment i.e. of the habitats (e.g. Chacin & Stallings, 2016; Livernois et al., 2019; Reichstein et al., 2013; Reynolds et al., 2018). Predation and competition in relation to habitat complexity can have significant impacts on fish community structure (Heck & Orth, 1980; Kovalenko et al., 2012), for example, by restricting the habitat use of fish subjected to predation pressure (Eklöv & Diehl, 1994; Persson, 1991; Snickars et al., 2004; Werner et al., 1983).

Habitat complexity can interfere with predator-prey interactions by influencing predation rates and correspondingly prey fish mortality. Increased habitat complexity, such as enhanced macrophyte density, usually leads to a diminished predation success with positive consequences for prey fish survival, but decreased predator growth rates (e.g. Beukers & Jones, 1997; Chacin & Stallings, 2016; Crowder & Cooper, 1982; Savino & Stein, 1982; Warfe & Barmuta, 2004). In fish communities, both predator and prey fish change their behaviour in response to habitat complexity. Whereas search mode and activity, choice of prey species and diet breadth of predators vary, prey adapt different antipredator behaviours depending on the structural complexity of their environment (Anderson, 1984; Christensen & Persson, 1993; Eklöv & Hamrin, 1989; Savino & Stein, 1982). One often observed antipredator response of fish is a change in habitat use, where a different, occasionally less preferred and usually more complex (e.g. vegetated) habitat is increasingly occupied, serving as a hiding place or refuge in the presence of predators. This shift in habitat use is frequently accompanied by a diet shift leading to decreased growth rates of prey fish due to less favourable food resources in these refuge habitats (Eklöv & Persson, 1996; Persson, 1991, 1993; Snickars et al., 2004; Werner et al., 1983).

Perch *Perca fluviatilis* L. 1758 has served as a model organism to examine effects of interspecific interactions on habitat use of fish in relation to structural complexity, by means of laboratory and field experiments. In the presence of a predator, juvenile *P. fluviatilis* use structurally complex habitats, such as simulated vegetation and rock habitats, more compared to open water areas (e.g. Christensen & Persson, 1993; Diehl & Eklöv, 1995; Eklöv & Diehl, 1994; Eklöv & Persson, 1995; Snickars et al., 2004), showing that more structured habitats can act as a refuge for juveniles of this species. However, Eklöv & Persson (1996) observed that juvenile *P. fluviatilis* switched less between structurally more complex and less complex habitats in the presence of freely moving piscivorous *P. fluviatilis* and instead increased their occupancy of the habitats where the predator was not present, thus actively avoiding the predatory fish. A similar antipredator behaviour for juvenile *P. fluviatilis* has been shown by Skov et al. (2007). The implications of interspecific competition for *P. fluviatilis* have been examined in several studies with roach *Rutilus rutilus* (L. 1758) and ruffe *Gymnocephalus cernuus* (L. 1758) as the competitor species assessing their impact on diet, foraging and growth rates of *P. fluviatilis* (e.g. Dieterich et al., 2004; Persson, 1986; Persson & Greenberg, 1990; Schleuter & Eckmann, 2006). However, the influence of competition on the habitat use of *P. fluviatilis*, as it has been examined for predation, has received less attention.

Therefore, the aim of this study is to examine the effects of interspecific interactions (i.e. predation and competition), represented through the presence of a predator and a competitor fish species, on the habitat use of *P. fluviatilis* in several habitat types that offer

differing structural complexities. Studies investigating how predation pressure influences habitat use have so far predominantly focussed on juvenile *P. fluviatilis* (e.g. Diehl & Eklöv, 1995; Eklöv & Persson, 1996; Snickars et al., 2004). We instead assessed the effects of predator presence for adult *P. fluviatilis* (about 15 cm in size) in order to see whether their habitat use is affected the same way by a predator (pike *Esox lucius* L. 1758) as has been shown for juveniles. We also tested the impact of competition on habitat use of adult *P. fluviatilis*, using *G. cernuus* as the potentially competing species, as both species use the same habitats and are benthic feeders preying on macroinvertebrates during all (*G. cernuus*) or some (*P. fluviatilis*) life stages (Bergman, 1991; Fischer & Eckmann, 1997; Henseler et al., 2019; Schleuter & Eckmann, 2008). We hereby use the term “competition” in the context of studying behaviour that could be linked to direct interference regarding habitat use between different individuals, and thus do not examine other aspects of competition, such as resource competition.

Specifically, this study focusses on (1) which habitat type is preferred by *P. fluviatilis* when given the choice between two habitats, and (2) whether habitat use is influenced by the presence of a predator (*E. lucius*) or by a potentially competing fish species (*G. cernuus*). Simultaneously, we examine (3) whether two *P. fluviatilis* select habitats individually or together as a pair. The overall study aim is to assess how interspecific interactions (potential predation and competition) influence *P. fluviatilis* habitat use. Since predation and competition represent important mechanisms for structuring communities, this study gives more in-depth information on how these biological interactions are linked to the habitat use of adult fish and thus on how fish communities are organized in coastal ecosystems consisting of a mosaic of different habitats.

Methods

To examine the impact of a predator (*E. lucius*) and a potentially competing (*G. cernuus*) fish species on the habitat use of *P. fluviatilis*, aquarium experiments were conducted at Husö Biological Station on the Åland Islands, northern Baltic Sea, during July and August 2018. The tested habitat types included simulated macrophyte, rock and sand habitats, representing typical coastal habitats in the Baltic Sea (Rönnbäck et al., 2007) with differing structural complexities. The study complied with the recommendations in the Finnish Act on the Protection of Animals Used for Scientific or Educational Purposes (2013/497) and was approved by the project approval committee of the Government of Åland (project 1/2016). No attacks were observed during the treatments involving predator presence, and no injured prey fish from unsuccessful attacks were observed in the holding tanks.

Fish collection and holding

For the experiments, fish were caught using live traps and eel fykes in shallow bays around the field station between 11 June and 10 August 2018. *P. fluviatilis* (n = 45) and *E. lucius* (n = 5) were kept separately in large holding tanks (1 m length x 1 m width x 60 cm height) and *G. cernuus* (n = 4) in a smaller one (70 cm length x 30 cm width x 30 cm height). *P. fluviatilis* were held at densities of 10 to 15 individuals per tank. Holding tanks were aerated and equipped with a flow-through system providing sand-filtered water directly from the bay nearby the station. Water conditions (e.g. temperature and salinity) therefore reflected natural ambient conditions. The bottom of the tanks was covered with sand, whereas stones, flowerpots and pipes served as shelter for the fish. Tanks were subjected to ambient natural light conditions and additional artificial light during daytime (12h artificial light during the day without artificial simulation of dusk and dawn; light intensity above tanks during the day: $0.97 \pm 0.28 \mu\text{E s}^{-1} \text{m}^{-2}$). Holding tanks were thoroughly cleaned and hydrographic conditions in them measured once a week (overall mean values \pm standard deviation for holding tanks: temperature = 20.1 ± 3.3 °C; salinity = 4.9 ± 0.2 ; pH = 7.8 ± 0.4 ; oxygen content = 8.59 ± 0.59 mg/l, oxygen saturation = $95.6 \pm 2.3\%$). *P. fluviatilis* and *G. cernuus* were fed with a mix of natural invertebrate food items (e.g. amphipods and polychaetes), whereas *E. lucius* were fed juvenile *P. fluviatilis* and Cyprinids. All individuals were fed once every day during daytime. To acclimatize to aquarium conditions prior to experimental trials, *P. fluviatilis* were kept in holding tanks for at least two weeks, and *E. lucius* and *G. cernuus* for ten days. After the experiments, fish were released at the site they had been caught (on 28 August 2018).

Experiment set-up

Experiment trials were conducted from 17 July to 28 August 2018 (6 weeks), including 31 experiment days, at the same time of day between 8 am and 5 pm. For each trial, two of the three habitat types (macrophyte, rock, sand) were positioned at opposite sides in 72 l rectangular glass aquaria (60 cm length x 40 cm width x 30 cm height) resulting in the following habitat combinations: *Macrophyte vs. Rock*, *Macrophyte vs. Sand* and *Rock vs. Sand* (Figure 1). To simulate the macrophyte habitat, four artificial aquarium plants (1 x 30 cm, 3 x 20 cm height), resembling the structure of *Myriophyllum* sp. and *Potamogeton perfoliatus*, were attached to a plastic grate, which was placed on the bottom of the aquaria and covered with sand. The rock habitat consisted of seven rocks, with one of them positioned partly on top of another rock creating a small cave-like structure. The sizes of the rocks, originating from shallow bays, were between 10 and 15 cm at their widest point. In all simulated habitats, the bottom of the aquarium was covered with a 3 cm thick layer of sieved sand (0.5 mm) and each

habitat covered an area of about 40 cm x 27 cm. To make a clear division between the macrophyte and rock habitat, a sand area of about 6 cm width was arranged in between the two habitats. This “grey zone” ensured that the fish were not able to position themselves in both habitats at the same time. To avoid disturbance of the fish during experiment trials, aquaria were covered with black plastic sheets from the outside. In total, four experiment aquaria were used simultaneously. Habitat combinations as well as the positioning of the habitats within the aquaria were randomly assigned. In each experiment trial, fish were allocated to one of the following treatments: a) two *P. fluviatilis* (single-species treatment), b) two *P. fluviatilis* and one *E. lucius* (predator treatment), or c) two *P. fluviatilis* and one *G. cernuus* (competitor treatment). *P. fluviatilis* were used as pairs during the experiment, since this species naturally occurs in small groups of two to over ten individuals (Eklöv, 1997). Each treatment in the *Macrophyte vs. Rock* and *Macrophyte vs. Sand* habitat combination was replicated ten times resulting in 30 experiment trials per habitat combination (Figure 1). In the *Rock vs. Sand* combination, treatments had the following replicate numbers: a) 17 replicates, b) 11 replicates, c) 11 replicates (39 trials in total). Treatments were randomly assigned to experiment aquaria and habitat combinations on each experiment day aiming for a randomized design. However, since not all *E. lucius* and *G. cernuus* were yet acclimatized to aquarium conditions when the experiment started, proportionally more single-species trials were conducted in the beginning of the experimental period (i.e. approximately the first three weeks; 84% of all single-species trials). Predator- and competitor trials prevailed towards the end of the experiment (i.e. the following three weeks; 84%/65% of all predator/competitor trials). Fish individuals were randomly chosen from a holding tank for each trial. After the experiment, they were kept in a separate holding tank for 24 h to avoid using them on two consecutive days, before transferring them to the main holding tanks. This procedure applied to *P. fluviatilis*, *E. lucius* and *G. cernuus* individuals. Thus, individual *P. fluviatilis*, *E. lucius* and *G. cernuus* were used in multiple trials. On average, each of the 45 *P. fluviatilis* was used in four trials, each of the five *E. lucius* in six trials and each of the four *G. cernuus* individuals in eight trials. All individual *P. fluviatilis* were used in all treatments. *P. fluviatilis* and *G. cernuus* had similar sizes (mean size \pm standard deviation for *P. fluviatilis*: 15.1 \pm 0.5 cm; *G. cernuus*: 14.1 \pm 0.3 cm), whereas *E. lucius* were larger (25.4 \pm 2.1 cm).

Experiment trials

Before commencing an experiment trial, hydrographic conditions were measured in the experiment aquaria (temperature, pH, salinity, oxygen concentration, light intensity above and below water), and fish were measured and weighed before introducing them into the aquaria. Fish were acclimatized to experiment aquaria for one hour, during which *P. fluviatilis* were kept in between two black plastic sheets between the habitat sides, whereas *E. lucius* and *G. cernuus* were placed in either of the habitats. The aquaria were aerated during the acclimation period, but air bubbling was removed during the actual experiment trial to ensure good visibility of the fish in the aquaria. Experiments started when the plastic sheets were removed and each trial lasted for six hours, during which the experiment aquaria were filmed by four webcams connected to a laptop using the free software XSplit Broadcaster (<https://www.xsplit.com/broadcaster>). Videos were automatically saved. After each trial, all water variables were recorded once more, experiment aquaria were cleaned and the water exchanged.

Statistical and video analysis

All analysis was carried out in the open source software R, version 3.4.2 (R Core Team, 2019). To examine whether *P. fluviatilis* sizes, water temperature measured before trials (starting temperature) and oxygen consumption during experiment trials (oxygen measured before trial minus oxygen measured after trial) differed between treatments for any of the habitat combinations, linear models were applied (lm, base R function). Mean *P. fluviatilis* size per trial, starting temperature and oxygen consumption, respectively, were included as dependent variables, and treatment as fixed factor in the models. F-tests were conducted on model outputs with the ANOVA of Type II Sum of Squares from the car package (Fox & Weisberg, 2011). Residuals were plotted versus fitted values to check that models met their assumptions. When model assumptions of data normality and homogeneous variances were not met, data was log-transformed prior to analysis. To test whether predator- or competitor treatments differed from the single-species treatment concerning the dependent variables, post-hoc tests with the Bonferroni correction were conducted after F-tests.

Videos were analysed by noting the habitat position of all fish every 10 min during the 6 h trials, commencing 10 min after the experiment start, resulting in 36 data points (counts) for each fish per experiment trial. Fish were recorded to be in the “grey zone” when they were positioned in the sand area between the macrophyte and rock habitat or when they were in very close proximity to rocks or macrophytes, but not entirely inside the habitat. Habitat use was calculated for different categories (Table 1) in each trial per habitat combination and treatment taking into account the position of all individual fish. For instance in the single-species treatment, the two *P. fluviatilis* individuals either used the habitats together or they used different habitats (split habitat use) resulting in three categories (also see Figure 2). For the predator- and competitor treatment, six categories were used taking into account the habitat use of *E. lucius* and *G. cernuus* (also see Figure 3). Data points from the “grey zone” were excluded because it was assumed that fish had not chosen a habitat when present in this area (Snickars et al., 2004).

To determine whether *P. fluviatilis* actively choose habitats (i.e. non-random habitat use), and whether this choice depends on the presence of other species, the observed habitat distribution in each habitat combination and treatment was compared to an expected (even) distribution. For the single-species treatment, the habitat use categories were compared against a 25/50/25%- distribution (see Figure 2a), whereas categories from the predator- and competitor treatments were compared against a 12.5/12.5/25/25/12.5/12.5% distribution (see Figure 3a). The expected distributions were calculated based on the hypothesis that all individual fish had an equal probability of being in either of the two compared habitats, independently of the habitat use of the other individuals present during the trials. As an example, the calculations for the single-species treatment are the following: Both *P. fluviatilis* are in habitat 1 (or habitat 2) with a probability of 25% (derived from $0.5 \cdot 0.5 = 0.25$), and the two *P. fluviatilis* use different habitats (split habitat use) with a probability of 50% (derived from $2 \cdot [0.5 \cdot 0.5] = 0.5$). For the predator- and competitor treatments, there is a 12.5% probability of both *P. fluviatilis* staying in habitat 1 or habitat 2 while the other species (predator or competitor) occupies either habitat 1 or 2. The probability of the two *P. fluviatilis* staying in different habitats (split habitat use) while the other species uses either habitat 1 or 2 is 25%. To test whether the habitat use of *P. fluviatilis* was influenced by the presence of a predator or competitor, the observed habitat distribution of *P. fluviatilis* was compared between the single-species treatment and the predator/competitor treatments, respectively.

We used a Chi square goodness of fit test on the count data for both comparisons (i.e. comparison of observed versus expected distributions for all treatments and comparison between treatments). We assessed which habitat use category contributed most to the difference between distributions by considering the contribution of each category to the total Chi square value (X^2). For the comparison of habitat use between treatments, count data from the predator- and competitor treatments only focussing on *P. fluviatilis* habitat use were compared against the “expected” distribution calculated from mean habitat use values from *P. fluviatilis* in the single-species treatment.

Results

Background biological and hydrographic properties

In this paragraph, variables are given in the form “mean value \pm standard deviation”. The sizes of *P. fluviatilis* used during the experiment ranged between 14.0 and 16.6 cm (overall mean size: 15.1 ± 0.5 cm) and did not differ between the treatments for any of the habitat combinations (Table 2). Water temperature in the experiment aquaria changed over the course of each trial with a mean difference of 0.1 ± 0.2 °C, following ambient conditions. This was consistent for all trials and was not considered to impact treatment comparison. However, starting temperature was highest in the single-species treatment (overall mean temperature: 22.8 ± 1.7 °C), compared to the predator (overall mean: 20.1 ± 2.1 °C) and competitor treatments (overall mean: 20.9 ± 2.4 °C), differing significantly between treatments for all habitat combinations (Table 2). All post-hoc tests had a p-value smaller than 0.05, except for *Macrophyte vs. Sand* where no significant difference was found for starting temperature between the single-species- and competitor treatments ($p = 0.295$). Water oxygen content decreased during the course of all trials with a mean decrease of 2.1 ± 0.9 mg/l. Oxygen consumption during trials differed significantly between treatments for all habitat combinations (Table 2). The decrease was stronger in the predator treatment (overall mean oxygen consumption: 3.2 ± 0.6 mg/l) than in the single-species (overall mean: 1.6 ± 0.5 mg/l; all post-hoc tests: $p < 0.001$) and competitor (overall mean: 1.8 ± 0.4 mg/l; post-hoc tests between single-species- and competitor treatments: $p > 0.05$) treatments. The lowest measured oxygen content after one predator treatment trial was 4.5 mg/l corresponding to an oxygen saturation of 53.5%. Due to these differences between treatments in starting temperature and oxygen consumption, the comparisons of habitat use between the predator/competitor treatments and the single-species treatment have to be considered with caution since the analyses cannot strictly separate the effects of treatment on habitat use from potential temperature or oxygen content effects.

Habitat use of *P. fluviatilis*, *E. lucius* and *G. cernuus*

We found distinct habitat use of *P. fluviatilis* in the different treatments and habitat combinations. In the single-species treatment, the distributions in all habitat combinations differed significantly from the expected distribution (Figure 2, Table 3). In *Macrophyte vs. Rock* and *Macrophyte vs. Sand*, the category “Both Macrophyte” contributed most to the difference (based on its contribution to the Chi square value X^2) indicating that *P. fluviatilis* used the macrophyte habitat together more than the expected 25% ($73 \pm 6\%$ for *Macrophyte vs. Rock* and $64 \pm 8\%$ for *Macrophyte vs. Sand*; mean \pm standard error used to describe habitat use). In *Rock vs. Sand*, the split habitat use “Split Rock-Sand” was mostly responsible for deviation from the expected distribution. Specifically, split habitat use of *P. fluviatilis* ($22 \pm 5\%$) was lower than expected (50%), and both *P. fluviatilis* occupied the rock and sand habitats together to equal amounts ($39 \pm 8\%$ and $39 \pm 7\%$, respectively). In all habitat combinations, split habitat use of the two *P. fluviatilis* was lower than expected ($19 \pm 4\%$ for *Macrophyte vs. Rock*, $19 \pm 6\%$ for *Macrophyte vs. Sand* and $22 \pm 5\%$ for *Rock vs. Sand*).

In the predator treatment, observed distributions in all habitat combinations deviated from the expected distribution (Figure 3b, Table 3). Moreover, *P. fluviatilis* habitat use differed between the predator- and single-species treatments (Table 4). In *Macrophyte vs. Rock*, the following categories contributed most to the difference to expected values: The proportions of both “Macrophyte/Macrophyte” ($28 \pm 7\%$) and “Rock/Macrophyte” ($22 \pm 6\%$) were larger

than the expected 12.5%, whereas the proportions of “Split Macrophyte-Rock/Macrophyte” ($11 \pm 3\%$) and “Split Macrophyte-Rock/Rock” ($12 \pm 7\%$) were smaller than expected (25%). Regarding the comparison of *P. fluviatilis* habitat use to the single-species treatment, “Both Rock” contributed most to the Chi square value, indicating that *P. fluviatilis* used the rock habitat more in the presence of *E. lucius*. In *Macrophyte vs. Sand*, “Macrophyte/Sand” was most responsible for deviation from the expected distribution having a higher proportion in the observed distribution ($44 \pm 10\%$). *P. fluviatilis* habitat use in the predator treatment differed from the one in the single-species treatment (mainly due to a higher proportion of “Split Macrophyte-Sand”), however the Chi square value of this comparison was comparatively small ($X^2 = 29$; Table 4) indicating that differences were not as strong as in other comparisons. In *Rock vs. Sand*, “Sand/Sand” had a higher proportion ($32 \pm 6\%$, highest contribution to X^2) in the observed than in the expected habitat use. The difference of *P. fluviatilis* habitat use compared to the single-species treatment was comparatively low ($X^2 = 33.2$) with “Both Rock” having a smaller proportion in the predator treatment.

In the competitor treatment, observed habitat distributions differed from the expected one in all habitat combinations (Figure 3c, Table 3), as did *P. fluviatilis* habitat use between the competitor- and single-species treatments (Table 4). In *Macrophyte vs. Rock*, “Macrophyte/Macrophyte” contributed most to differences between observed and expected distributions having a higher observed proportion ($53 \pm 9\%$). Concerning the comparison of *P. fluviatilis* habitat use to the single-species treatment, “Both Rock” contributed most, suggesting that both *P. fluviatilis* stayed in the rock habitat more in the presence of *G. cernuus*. Regarding the comparison of observed versus expected proportions in *Macrophyte vs. Sand*, “Macrophyte/Macrophyte” contributed most, having a higher observed value ($37 \pm 10\%$). The difference of *P. fluviatilis* habitat use between the competitor- and single-species treatments was less pronounced ($X^2 = 51.5$), though significant, with “Split Macrophyte-Sand” having a higher proportion in the presence of *G. cernuus*. In *Rock vs. Sand*, “Rock/Rock” contributed most to the comparison between observed and expected distributions, with a higher observed proportion ($31 \pm 9\%$). *P. fluviatilis* habitat use did not differ strongly between competitor- and single-species treatments ($X^2 = 6.6$). The category contributing most (“Split Rock-Sand”) had a slightly lower proportion in the competitor treatment. Both in the predator- and competitor treatments, split habitat use of the two *P. fluviatilis* was lower than the expected cumulative 50% in all habitat combinations, indicating that *P. fluviatilis* predominantly selected habitats together.

Discussion

To assess the impact of predation risk and competition on the habitat use of a common coastal fish species, *P. fluviatilis*, aquarium experiments were performed, using *E. lucius* as a predator and *G. cernuus* as a competitor species. When neither predator nor competitor were present, adult *P. fluviatilis* favoured the artificial macrophyte over the rock and sand habitat, not showing any preference for either of the latter habitats. In the presence of *E. lucius* or *G. cernuus*, *P. fluviatilis* expressed a certain degree of avoidance of the other fish species, seemingly adapting their habitat use to the habitat occupancy of *E. lucius* and *G. cernuus*, respectively. However, *P. fluviatilis* habitat use did not seem to be affected by either predator or competitor without the artificial macrophyte option available (in *Rock vs. Sand*), as *P. fluviatilis* occupied the same habitats as the other species, not showing any behavioural pattern of avoidance. Correspondingly, *P. fluviatilis* habitat distribution did not differ much from the single-species treatment, suggesting that this fish species does not differentiate between the rock and sand habitat. This study deepens the knowledge on how interspecific interactions can influence the habitat use of fish and thus emphasizes their role in structuring fish communities in mosaic coastal ecosystems.

Habitat use of adult *P. fluviatilis*

In the single-species treatment, the two *P. fluviatilis* individuals occupied the artificial macrophyte habitat more than the rock or sand habitat, which in turn were used to an equal degree. The macrophyte habitat represented a structurally more complex habitat compared to the other two habitats, providing a complex three-dimensional structure reaching from the bottom almost to the water surface and most likely giving the impression of a safer refuge. Sand, on the other hand, possessed no structure at all, whereas the rocks covered the bottom of aquaria, but did not reach the same height and complexity as the macrophytes, confining the structure to the lower part of the aquaria. Thus, under these experimental conditions, *P. fluviatilis* seem to favour more complex habitats over less complex ones and do not appear to differentiate between rock and sand habitats, probably due to their similarity in structural complexity. This is in agreement with other studies, which have shown that *P. fluviatilis* prefer vegetation structure to non-structured open areas (Bean & Winfield, 1995; Christensen & Persson, 1993). Correspondingly, *P. fluviatilis* occupy vegetated habitats to a large extent in lakes, although especially older individuals have also been caught in open waters (Fischer & Eckmann, 1997; Persson, 1987). Our results thus highlight the importance of vegetated habitats with a higher complexity for adult specimen of this fish species. Overall, the two *P. fluviatilis* individuals mainly selected habitats together, which reflects that *P. fluviatilis* is a schooling fish species occurring in groups of two to over ten individuals in the field (Eklöv, 1997). In the following paragraphs, we focus on the habitat chosen by the two *P. fluviatilis* individuals together.

Impact of predation risk on habitat use of adult *P. fluviatilis*

Predation risk seems to have influenced the habitat use of *P. fluviatilis* to a certain degree in the habitat combinations with artificial macrophytes. In *Macrophyte vs. Rock*, *P. fluviatilis* occupied the rock habitat (with *E. lucius* present in the macrophyte habitat) more than expected. Simultaneously, they used the rock habitat more in the predator treatment compared to the single-species treatment indicating that *P. fluviatilis* adapted their habitat use to predator presence by decreasing their occupancy in their favoured macrophyte habitat and instead using a less preferred habitat. Hence, *P. fluviatilis* might have partially avoided *E.*

lucius by increasingly staying in a predator-free habitat that offered a lower predation risk. This is corroborated by the observations in *Macrophyte vs. Sand*, where *P. fluviatilis* mainly occupied the macrophyte habitat while *E. lucius* stayed in the sand area. However, predator presence does not seem to have influenced the general habitat use of *P. fluviatilis* severely in this habitat combination since the proportions of *P. fluviatilis* using the macrophyte or sand habitat together did not greatly differ between predator- and single-species treatments. This could be mainly due to *E. lucius* apparently favouring the sand habitat making it possible for *P. fluviatilis* to stay in their favoured macrophyte habitat without coming into close contact with the predator. Nevertheless, in both habitat combinations, adult *P. fluviatilis* seemed to increase the use of a predator-free habitat; a response, which has previously been shown for juvenile *P. fluviatilis* in the presence of piscivorous *P. fluviatilis* and *E. lucius* (Eklöv & Persson, 1996; Skov et al., 2007). In contrast, juvenile *P. fluviatilis* often increase their use of structurally more complex habitats in the presence of a predatory fish species (Christensen & Persson, 1993; Diehl & Eklöv, 1995; Eklöv & Diehl, 1994; Persson, 1993; Snickars et al., 2004). However, in several of these experiments, the predator was restricted to one habitat not able to enter the more complex habitat. Our results therefore emphasize the importance of freely moving predators in this kind of experiment in order to fully capture the interactions of habitat use between predator and prey (Skov et al., 2007), and to mimic natural conditions more closely. Experimental studies have shown that juvenile *P. fluviatilis* always favour the vegetated habitat even when a predator is present there as well (Christensen & Persson, 1993; Eklöv & Persson, 1996). This behaviour can be partly seen in our study with *P. fluviatilis* occupying the macrophyte habitat in *Macrophyte vs. Rock* in the presence of *E. lucius* to a rather high percentage (more than expected, see result section). This suggests only partial predator avoidance, and that *P. fluviatilis*, at least to some extent or at certain times, occupy a favoured, structurally complex habitat regardless of predator location.

Impact of competition on habitat use of adult *P. fluviatilis*

Similar to predation risk, potential competition by *G. cernuus* appeared to affect the habitat use of *P. fluviatilis*. *G. cernuus* expressed a strong preference for the macrophyte habitat, barely occupying rock or sand habitats. In *Macrophyte vs. Sand*, both *P. fluviatilis* occupied the macrophyte habitat together with *G. cernuus* more than expected. *P. fluviatilis* habitat distribution differed between competitor- and single-species treatments only based on a slightly higher split habitat use of macrophyte and sand in the presence of *G. cernuus*. Thus, *P. fluviatilis* habitat use did not seem to be affected by *G. cernuus* in this habitat combination as they maintained their occupancy of the preferred macrophyte habitat. In *Macrophyte vs. Rock*, there was a similar pattern with *P. fluviatilis* mostly staying in the macrophyte habitat in the presence of *G. cernuus*. However, *P. fluviatilis* also increased their proportional time spent in the rock habitat compared to the single-species treatment, while *G. cernuus* used the opposite macrophyte habitat. This suggests that *P. fluviatilis* tried to avoid *G. cernuus* by increasing the presence in the habitat that was occupied less by this species, resembling the results from the predator treatment. In our experiment, *P. fluviatilis* and *G. cernuus* both showed a preference for the macrophyte habitat (*P. fluviatilis* in the single-species treatment and *G. cernuus* in the competitor treatment) indicating a potential habitat overlap. Indeed, the two fish species occupy the same benthic habitats at several locations, such as the Baltic Sea, Lake Constance and Swedish lakes, with only slight differences in their distribution (Bergman, 1988, 1991; Fischer & Eckmann, 1997; Henseler et al., 2019; Mustamäki et al., 2016). In addition to overlap in habitat preference and occupancy, *P. fluviatilis* and *G. cernuus* possess similar diets, potentially causing competition. However, the diet overlap between the

two species depends on the size and the seasonal feeding behaviour of *P. fluviatilis* (Bergman, 1991; Bergman & Greenberg, 1994; Ogle et al., 1995; Schleuter & Eckmann, 2008). Moreover, *P. fluviatilis* hunt during the day, whereas *G. cernuus* feed mostly during the night (Ogle et al., 1995; Schleuter & Eckmann, 2008), which reduces their encounter rates when foraging and might therefore limit potential food competition. Studies examining competition between the two species showed that *P. fluviatilis* diet, consumption rates and growth were negatively impacted by high *G. cernuus* densities (Bergman & Greenberg, 1994; Schleuter & Eckmann, 2006). However, this interspecific competition for food seems to depend on several factors, such as food amount and substrate type (Dieterich et al., 2004) making the interactions between *P. fluviatilis* and *G. cernuus* rather complex. Hence, more studies are needed to gain a better understanding of the competitive abilities of the two species and eventually the existing competition between them in nature. In our study, we show that a potential for competition based on habitat use exists, since the presence of *G. cernuus* appeared to affect the habitat use of similar-sized adult *P. fluviatilis* to some extent. However, this interference might be context-dependent, as we only found an effect of *G. cernuus* in one of three habitat combinations (i.e. *Macrophyte vs. Rock*). Thus, *P. fluviatilis* might make a higher use of the rock habitat with a competitor present in their preferred habitat, but the same does not apply when a sand habitat is offered as alternative. In the latter case, the benefits of staying in the preferred habitat in competitor presence may outweigh the ones of avoiding the competitor but simultaneously occupying a rather exposed non-structured habitat.

Implications of habitat shifts for *P. fluviatilis*

The observed habitat shifts of *P. fluviatilis* triggered by predation risk and competition in *Macrophyte vs. Rock* in our study can provide insights into the structure and organization of *P. fluviatilis* populations in nature. Positive consequences connected to avoidance of the habitat occupied by the predator and competitor fish species comprise increased survival of *P. fluviatilis* due to reduced predation risk (e.g. Diehl & Eklöv, 1995) and decreased competition pressure, e.g. for food resources, due to the absence of competing fish. However, the habitat shift documented for *P. fluviatilis* in the presence of *E. lucius* and *G. cernuus* with an increased use of the less preferred rock habitat in *Macrophyte vs. Rock* could have negative effects on *P. fluviatilis* populations. This active avoidance and habitat changing behaviour of *P. fluviatilis* could lead to a reduction of other activities, such as foraging, causing decreased growth rates, as shown for coral reef fish (Hall & Kingsford, 2016). Predation-induced habitat shifts result in lower growth rates for several fish species (e.g. *P. fluviatilis*; *R. rutilus*, bluegill sunfish *Lepomis macrochirus* Rafinesque 1819) since foraging conditions are occasionally less favourable in the newly occupied habitat, so that prey fish must adapt their diet to alternative food resources (Diehl & Eklöv, 1995; Persson, 1993; Persson & Eklöv, 1995; Werner et al., 1983). This could also apply to *P. fluviatilis*. Their favoured macrophyte habitat provides important macroinvertebrate food resources for benthivorous *P. fluviatilis* (Eklöv, 1997; Persson, 1993) and thus a shift to rock habitats could negatively change feeding conditions for them, as different habitats possess a rather distinct macroinvertebrate community (Henseler et al., 2019), and higher prey biomass is associated with an increased structural complexity of the environment (Diehl, 1993). Yet, foraging efficiency of *P. fluviatilis* is lower in complex vegetation compared to open water areas (Diehl, 1988). Experiments have therefore shown that juvenile *P. fluviatilis* increasing the usage of vegetated areas as a response to predatory *E. lucius* occupying alternative open habitats, expressed lower growth rates (Diehl & Eklöv, 1995). In contrast, 2-year-old *P. fluviatilis* were able to maintain constant growth in vegetation over time (Diehl, 1993). Furthermore, despite their lower feeding efficiency in vegetation, *P.*

fluviatilis were more abundant in vegetated lake areas, and are regardless more efficient in capturing prey in vegetated areas compared to other freshwater fish species such as bream *Abramis brama* (L. 1758) and *R. rutilus* (Diehl, 1988), seemingly competitively superior in vegetated habitats. Hence, there appears to be a trade-off between a higher prey availability, but potentially lower feeding efficiencies in vegetation for *P. fluviatilis* making the consequences of a habitat shift out of macrophyte habitats difficult to predict. Nevertheless, predation risk and competition might have several complex implications for fish communities by causing habitat shifts.

Experiment restrictions

The comparison of *P. fluviatilis* habitat use between treatments has to be evaluated with some caution due to differences in temperature and oxygen content among experiment treatments. Water temperature in experiment aquaria was on average about 2 °C higher in the single-species treatment than in the other two treatments. This is because ambient temperatures peaked in the beginning of the experiment period with accordingly higher water temperatures (water temperature during the first three experiment weeks: 24.1 ± 0.9 °C = mean \pm standard deviation) when relatively more single-species trials were conducted. Contrary, when the majority of predator- and competitor trials was run, water temperatures had decreased (water temperature during the last three experiment weeks = 19.4 ± 1.9 °C). Since temperature can have an impact on the activity of fish (Hokanson, 1977), the higher temperatures may have altered the behaviour of *P. fluviatilis* and thus affected their habitat use in the single-species treatment. For instance, higher swimming activity has been recorded with increasing temperatures for this fish species (Bergman, 1987). However, since temperatures were the same in holding tanks and experiment aquaria, *P. fluviatilis* should have been adapted to the higher or lower temperatures, respectively. Moreover, a temperature difference of 2 °C might not be severe enough to affect *P. fluviatilis* behaviour to the extent that it would override the effect of treatment on habitat use, especially since temperatures in all treatments lay well within the reported preferred temperature range of this species (18 - 27.3°C; Hokanson, 1977). Water oxygen content in the experiment aquaria decreased most strongly during the course of trials in the predator treatment, the cause very likely being the presence of *E. lucius*, which due to their larger size and body mass consumed more oxygen compared to *P. fluviatilis* and *G. cernuus*. Reduced oxygen content can influence fish activity including vertical and horizontal changes in habitat use and decreased predation rates (Breitburg et al., 1994; Kramer, 1987). Thus, the lower oxygen content in the predator treatment might have altered the behaviour of both *P. fluviatilis* and *E. lucius*. Yet, the lowest measured oxygen value at the end of one predator treatment trial (4.5 mg/l) was still very close to the oxygen limit that fish can tolerate (e.g. oxygen requirement for white perch *Morone americana* (Gmelin 1789) = 5 mg/l; Murray et al., 2009). Only concentrations of less than 3.5 mg/l at temperatures of 15 to 26 °C have been reported to be harmful/lethal for fish (Moore, 1942). Furthermore, oxygen content in the predator treatment must have decreased gradually, reaching lower values only towards the end of the experiment, limiting the period during which fish behaviour could have been affected by low oxygen.

It should also be taken into account that individual fish were used multiple times during the experiment, rendering the statistical analysis not strictly independent. Different individual fish can repeatedly express certain characteristic behaviour. Additionally, specimens could behave differently depending on whether they are naïve (i.e. being used the first time in an experimental trial) or already experienced (i.e. being used at least for the second time) with

the experimental conditions, thus introducing a certain bias to the results. However, since we tested multiple individuals of each species (e.g. 45 *P. fluviatilis*) and these fish were, most likely, not always paired with the same other individual fish in the different treatments, the general pattern of our findings should still hold. This conclusion can be based on the presumption that individual behaviour should be flexible and partly depend on the behaviour expressed by other fish individuals during the trials. In addition, the spatial scale, at which this study was conducted, was relatively small, based on the size of aquaria, especially in comparison to natural conditions. Therefore, our findings regarding fish behaviour come from a rather restricted environment that cannot be directly translated into field conditions, but have to be considered in the light of the experimental conditions. Here, it should be noted that fish were not actively feeding during the trials, but likely resting or potentially exhibiting exploratory behaviour, which may also influence habitat choice. Yet, coastal habitats in nature do not necessarily form extensive homogeneous areas, but can be rather patchily distributed (e.g. Boström et al., 2006, 2010). This makes testing habitat-related behaviour at a smaller spatial scale appropriate, but simultaneously opens up to examine similar study questions at other scales, i.e. using large outdoor tanks.

Conclusion

In summary, the two *P. fluviatilis* individuals predominantly selected habitats together and showed a preference for the structurally more complex macrophyte habitat in the presence of only a conspecific. Our study suggests that habitat use of adult *P. fluviatilis* is influenced by predator presence, as has been shown for juveniles of the same species. We highlight that, not only predation risk, but also the presence of a potentially competing fish species affect the habitat use of *P. fluviatilis*. In both cases, *P. fluviatilis* individuals seemed to avoid the other fish species by increasingly occupying a habitat that is used less by the predator or competitor. However, the effect of interspecific interactions on *P. fluviatilis* habitat use seems context dependent, i.e. was most pronounced for certain habitat combinations. Whether an influence of predation or competition exists might depend on the structural complexity of the habitats, as no change of habitat use was recorded when the alternatives comprised structurally less complex rock and sand habitats. Overall, our findings show that presence of both predator and interspecific competitor can influence habitat use of adult fish at small spatial scales. This indicates that predation and competition might play a role in habitat selection of fish, representing highly relevant biological interactions for the structuring of adult fish communities.

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Author Contributions

- designed the aquarium experiment: CH, MCN, AT, MS, EB
- performed the experiment and video analysis: CH
- conducted the statistical analysis of the data: CH, MCN
- wrote the manuscript: CH, MCN, AT, MS, EB

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Table 1: Description of habitat use categories utilized in Figure 2 and 3. Categories are given separately for the single-species- and predator/competitor treatments. “Other species” refers to either *Esox lucius* or *Gymnocephalus cernuus* depending on treatment.

Habitat use category	Explanation
<i>Single-Species Treatment</i>	
Both Macrophyte	both <i>P. fluviatilis</i> in the macrophyte habitat
Both Rock	both <i>P. fluviatilis</i> in the rock habitat
Both Sand	both <i>P. fluviatilis</i> in the sand habitat
Split Macrophyte-Rock	one <i>P. fluviatilis</i> in macrophyte and one <i>P. fluviatilis</i> in rock
Split Macrophyte-Sand	one <i>P. fluviatilis</i> in macrophyte and one <i>P. fluviatilis</i> in sand
Split Rock-Sand	one <i>P. fluviatilis</i> in rock and one <i>P. fluviatilis</i> in sand
<i>Predator/Competitor Treatment</i>	
Macrophyte/Macrophyte	both <i>P. fluviatilis</i> in macrophyte/other species in macrophyte
Macrophyte/Rock	both <i>P. fluviatilis</i> in macrophyte /other species in rock
Macrophyte/Sand	both <i>P. fluviatilis</i> in macrophyte/other species in sand
Rock/Macrophyte	both <i>P. fluviatilis</i> in rock/other species in macrophyte
Rock/Rock	both <i>P. fluviatilis</i> in rock/other species in rock
Rock/Sand	both <i>P. fluviatilis</i> in rock/other species in sand
Sand/Macrophyte	both <i>P. fluviatilis</i> in sand/other species in macrophyte
Sand/Rock	both <i>P. fluviatilis</i> in sand/other species in rock
Sand/Sand	both <i>P. fluviatilis</i> in sand/other species in sand
Split Habitat 1-Habitat 2/Habitat 1	one <i>P. fluviatilis</i> in habitat 1 and one <i>P. fluviatilis</i> in habitat 2/other species in habitat 1
Split Habitat 1-Habitat 2/Habitat 2	one <i>P. fluviatilis</i> in habitat 1 and one <i>P. fluviatilis</i> in habitat 2/other species in habitat 2

Table 2: Comparison of mean *Perca fluviatilis* size, starting temperature and oxygen consumption between the single-species, predator and competitor treatments for each habitat combination by means of linear models and F-tests. The stars (*) indicate significant differences between treatments (significance level = 0.05).

Variable tested	Habitat combination								
	<i>Macrophyte vs. Rock</i>			<i>Macrophyte vs. Sand</i>			<i>Rock vs. Sand</i>		
	df	F	p	df	F	p	df	F	p
Mean <i>P. fluviatilis</i> size [cm]	2, 27	1.10	0.346	2, 27	0.13	0.880	2, 36	0.68	0.512
Starting temperature [°C]	2, 27	5.16	0.013*	2, 27	4.01	0.030*	2, 36	5.86	0.006*
Oxygen consumption [mg/l]	2, 27	29.7	< 0.001*	2, 27	25.4	< 0.001*	2, 36	34.1	< 0.001*

Table 3: Comparison of observed versus expected habitat distributions for all habitat combinations and treatments via Chi square goodness of fit tests. The stars (*) indicate that the observed habitat distribution differs significantly from the expected one (significance level = 0.05).

Habitat combination	Treatment								
	Single-species			Predator			Competitor		
	df	X ²	p	df	X ²	p	df	X ²	p
<i>Macrophyte vs. Rock</i>	2	434.8	< 0.001*	5	142.8	< 0.001*	5	620.9	< 0.001*
<i>Macrophyte vs. Sand</i>	2	302.8	< 0.001*	5	330.2	< 0.001*	5	216.3	< 0.001*
<i>Rock vs. Sand</i>	2	197.2	< 0.001*	5	175.4	< 0.001*	5	245.6	< 0.001*

Table 4: Comparison of observed habitat distributions of *Perca fluviatilis* in the predator- and competitor treatments versus the single-species treatment for all habitat combinations via Chi square goodness of fit tests. The stars (*) indicate that the habitat distribution differs significantly from the single-species treatment (significance level = 0.05).

Habitat combination	Treatment					
	Predator			Competitor		
	df	X ²	p	df	X ²	p
<i>Macrophyte vs. Rock</i>	2	371.0	< 0.001*	2	102.1	< 0.001*
<i>Macrophyte vs. Sand</i>	2	28.8	< 0.001*	2	51.5	< 0.001*
<i>Rock vs. Sand</i>	2	33.2	< 0.001*	2	6.6	0.037*

Figure 1: Schematic illustration of the experiment set-up, showing the three habitat combinations: *Macrophyte vs. Rock*, *Macrophyte vs. Sand*, *Rock vs. Sand*, and the three treatments: a) single-species, b) predator, c) competitor treatment. Treatments were replicated ten times in *Macrophyte vs. Rock* and *Macrophyte vs. Sand*, and 17/11/11 times in *Rock vs. Sand*.

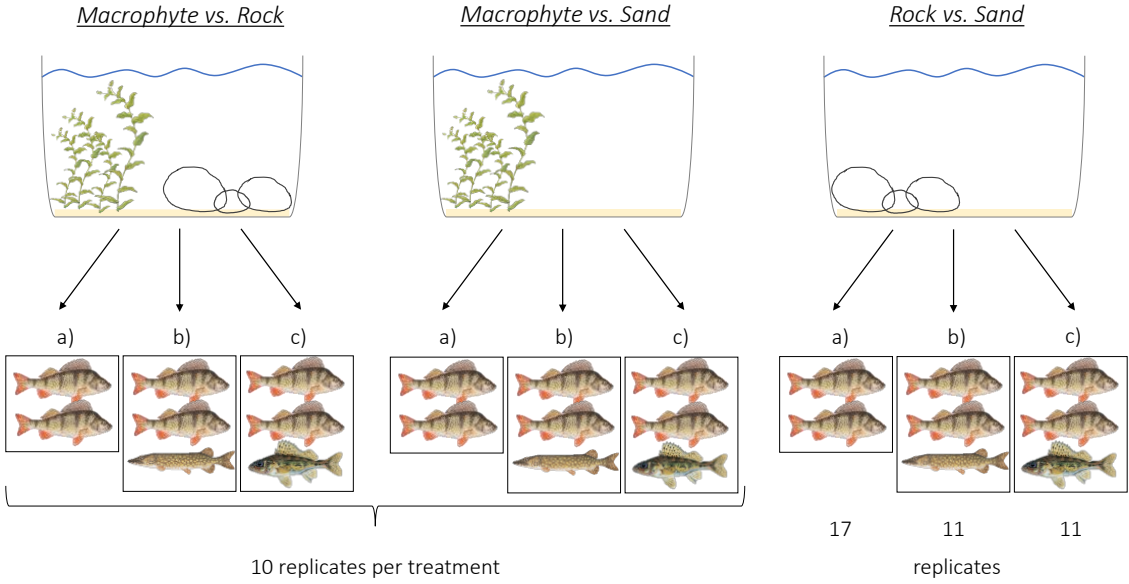


Figure 2: Mean habitat use [%] of *Perca fluviatilis* in the single-species treatment. The left panel (a) shows the expected habitat distribution based on the hypothesis that each individual fish has an equal probability of occupying either of the two habitats. The right panel (b) shows the observed habitat distribution in the three habitat combinations: *Macrophyte vs. Rock* (*M vs. R*), *Macrophyte vs. Sand* (*M vs. S*) and *Rock vs. Sand* (*R vs. S*), not taking into account *P. fluviatilis* occurrence in the grey zone and scaled to 100%. For habitat use category descriptions, see Table 1. The dashed lines mark the theoretical even distribution between the habitats at 25% and 75%.

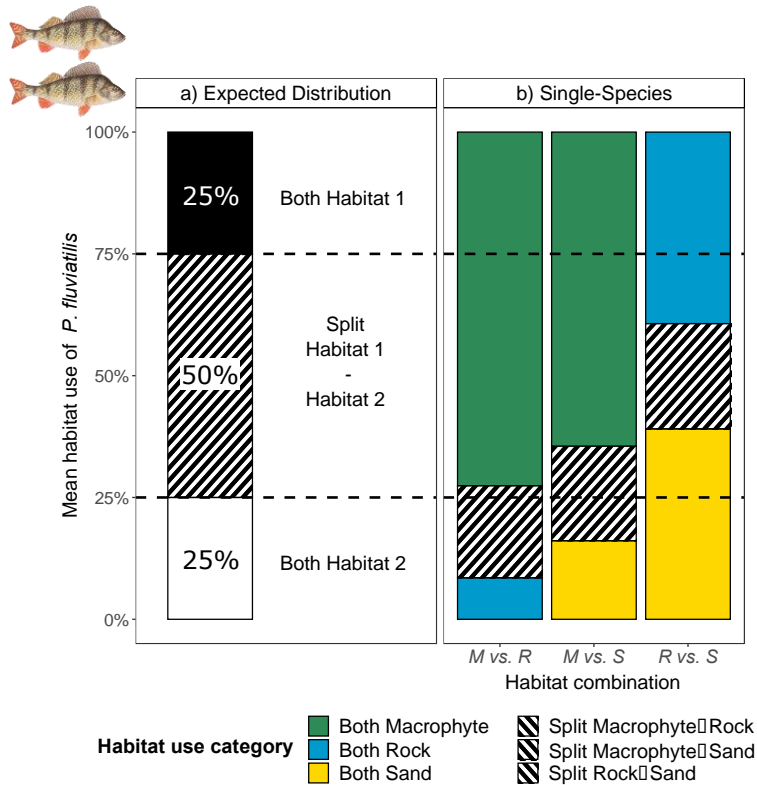


Figure 3: Mean habitat use [%] of *Perca fluviatilis*, *Esox lucius* and *Gymnocephalus cernuus*. The left panel (a) shows the expected habitat distribution based on the hypothesis that each individual fish has an equal probability of occupying either of the two habitats. The middle and right panel show the observed habitat distribution in the (b) predator- and (c) competitor treatment in the three habitat combinations: *Macrophyte vs. Rock (M vs. R)*, *Macrophyte vs. Sand (M vs. S)* and *Rock vs. Sand (R vs. S)*, not taking into account fish occurrence in the grey zone and scaled to 100%. For habitat use category descriptions, see Table 1.

