Effects of motorboat noise on foraging behaviour in Eurasian perch and roach: a field experiment

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ABSTRACT: The negative impact of anthropogenic noise on marine animals is receiving increasing attention. In order to study the effect of motorboat noise on foraging behaviour in fish, we chose 2 species with different hearing abilities. The roach *Rutilus rutilus* has a better developed sense of hearing than the Eurasian perch *Perca fluviatilis*. The study took place in an inlet of the Bothnian Sea where boat traffic is almost absent. Groups of 6 fish were placed in field enclosures containing either one of the species or equal numbers of perch and roach. Half of each enclosure was covered with artificial vegetation. The fish were fed with pieces of saithe twice a day, both with and without the disturbance of an outboard motor. Sound pressure level and particle acceleration were measured for the motor, which was run at 2000 rpm. The trials were repeated for 5 d. Perch made fewer feeding attempts during noise exposure compared to controls in the single-species enclosures. As the experiment progressed, they gradually increased feeding and time spent in the open area, both with and without noise, indicating habituation. Habitat utilization was affected by the interaction of noise exposure and day. Roach responded to noise exposure with fewer feeding attempts, higher latency to enter the open area, and longer time spent in the vegetation compared to the controls without noise. Roach behaviour changed with time only when housed together with perch. This study, using authentic sound in a natural habitat, shows that noise exposure may affect the feeding behaviour of fish, that the response is species-specific, and that habituation and the presence of other species may modify the effects.

KEY WORDS: Anthropogenic noise · Feeding activity · Field enclosures · *Perca fluviatilis* · *Rutilus rutilus* · Sound disturbance

INTRODUCTION

For several decades, human activities have resulted in increasing noise levels in the oceans (Ross 1976, 2005). The increase in low-frequency noise in the Northeast Pacific since the 1960s can be explained by the increase in commercial shipping during the same time period (McDonald et al. 2006). Furthermore, pile driving, different types of sonars, transport ferries, fishing vessels, and recreational boats all contribute to increasing noise levels in the aquatic environment.

There is currently an increase in studies evaluating the impacts of anthropogenic noise disturbance on fish. Noise exposure has been shown to cause temporary hearing threshold shifts (Scholik & Yan 2002, Smith et al. 2004, Popper et al. 2005) and damage to the auditory systems of fish (McCauley et al. 2003, Casper et al. 2013). Short-term studies have also revealed other negative impacts, such as increased heart rates (Simpson et al. 2005, Graham & Cooke 2008), and elevated cortisol (stress hormone) levels (Santulli et al. 1999, Smith et al. 2004, Wysocki et al. 2006, Nichols et al. 2015, Johansson et al. 2016). Consequently, noise appears to be a potential stressor for a number of fish species.

Many studies have focused on the masking effects of biologically relevant sound in terms of communi-

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cation or detection of predators, food, and obstacles (Wysocki & Ladich 2005, Gutscher et al. 2011). Boat noise, for example, appears to mask intra-specific communication in a number of vocalizing fish species (Vasconcelos et al. 2007, Codarin et al. 2009, Radford et al. 2014). In addition, noise can have behavioural effects on fish. Fish shoals have been shown to change their vertical movement and their shoaling structure in the presence of passing boats (Drastik & Kubecka 2005, Sarà et al. 2007) and when exposed to artificial sound (Neo et al. 2014, 2016). Also, in-creased swimming speed and change of habitat uti-lization have been found in connection with boating activities (Jacobsen et al. 2014). There may be simi-larities between anti-predator behaviour and actions caused by human disturbance, both leading to trade-offs between energy intake and risk avoidance (Frid & Dill 2002). Escape reactions (Karlsen et al. 2004), cover seeking (McLaughlin & Kunc 2015), and habi-tat avoidance (Jacobsen et al. 2014) in response to noise may decrease time spent foraging and thus have negative impacts on fish fitness.

Presently, little is known about the effects of noise on the feeding performance of fish, although there are some studies. Reduction in feeding rates in con-nection with increased boating activity has been found in mulloway *Argyrosomus japonicus* (Payne et al. 2015) and in damselfish *Chromis chromis* (Bracciali et al. 2012). Both three-spined stickleback *Gasterosteus aculeatus* (Purser & Radford 2011) and zebrafish *Danio rerio* (Shafiei Sabet et al. 2015) showed increased food-handling errors when ex-posed to sound. These studies indicate that noise exposure can alter fish behaviour and affect feeding performance, although the reason for this response is not fully understood. Distraction could be one expla-nation (Purser & Radford 2011), and masking effects another, since many fish species use their hearing ability to localize food (Hoin-Radkovsky et al. 1984) or avoid predation (Sand et al. 2000, Wilson et al. 2011). The effects of noise on foraging efforts and food-handling errors in fish have primarily been studied in laboratory experiments using artificial or playback sounds (Purser & Radford 2011, Voellmy et al. 2014a, McLaughlin & Kunc 2015, Shafiei Sabet et al. 2015).

In this study, we performed an enclosure study in the Bothnian Bay of Sweden to evaluate the potential impact of authentic sound from a motorboat on the feeding performance and habitat use of fish. We used Eurasian perch *Perca fluviatilis* and roach *Rutilus rutilus*, 2 species with different hearing sensitivities, to investigate differences in response to noise expo-

sure. We repeated the treatment over several days to explore potential habituation to the sound. We kept the 2 species both separately and together, to de-termine whether their response to sound could be influenced by the presence of another species.

Eurasian perch (hereafter perch) and roach are among the most common fish species in Sweden and inhabit both freshwater habitats and the brackish water of the Baltic Sea. They are often found together in mixed-species shoals, sometimes in areas where they are likely to encounter various kinds of anthro-pogenic noise produced by small fishing vessels, transport ferries, and recreational boats. Perch, like most fishes, rely mainly on particle acceleration for their hearing. Still, this entity is rarely measured, despite its high relevance to disturbance (Nedelec et al. 2016). Furthermore, audiograms are usually pre-sented as sound pressure, with the particle motion component usually ignored (but see Horodysky et al. 2008, Radford et al. 2012). In this study, noise produc-tion was measured as both sound pressure levels and particle acceleration.

Roach have better hearing ability than perch (Amoser et al. 2004). This is because of the connec-tion between the swim bladder and the ear by the Weberian ossicles, found in cyprinid fish, which gives a higher sensitivity to sound pressure (Hawkins 1993, Popper & Fay 2011). Roach are sensitive to low frequencies, with the lowest sound pressure level threshold (about 60 dB re 1 µPa) between 500 and 1000 Hz, but also have good hearing abilities up to several kHz (Amoser et al. 2004). Perch lack any con-nection between ear and swim-bladder, and with their lower hearing sensitivity, rely more on acoustic particle motion (Popper & Fay 2011, Ladich & Fay 2013). An audiogram shows that perch have sound pressure threshold levels between 90 and 120 dB re 1 µPa at a frequency range between 100 and 1000 Hz, with best sensitivity at 200 to 300 Hz (Amoser et al. 2004). The upper limit was found to be 300 Hz (Wolff 1967, Sand 1974). For both roach and perch, thresh-olds of particle acceleration have been measured only as a reaction to infrasound, and found to be 27 dB re 1 µm s^{-2} (roach) and 46 dB re 1 µm s^{-2} (perch), for frequencies lower than 10 Hz (H. E. Karlsen pers. comm.).

One hypothesis for our study was that roach would show a stronger response to the boat motor sound than perch, due to higher hearing sensitivity in this species. Based on an earlier study on stress response to noise (Johansson et al. 2016), we also predicted that the response would weaken with time due to habituation. Finally, if the 2 species retrieve informa-

tion about the environment in different ways (Goodale et al. 2010), interspecific information transfer may lead to different responses to noise exposure in the mixed-species treatment compared to when species are kept separated.

MATERIALS AND METHODS

Experimental animals and location

Perch and roach were caught with a beach seine net in Lake Ängersjön located near Umeå, Sweden, and transported to Umeå Marine Science Centre. Fish were held in 1 m³ tanks supplied with running water at natural temperatures and a salinity of ca. 3 ppt. The fish were fed small pieces (ca. 0.5 cm³) of saithe *Pollachius virens* fillet for 2 to 3 wk to acclimate them to brackish water and the new food source. All fish quickly learned to use the food source and readily ate the fish pieces before the start of the experiments. The study was performed in a coastal location outside Hörnefors, Sweden (63° 37′ N, 19° 54′ E), in an inlet of the Bothnian Sea where boat traffic is almost absent. Experimental enclosures, made of white PVC mesh (mesh size 0.5 cm), with a water volume of 1.125 m³ (area 75 × 150 cm², depth 1 m), were placed on the side of a floating pontoon (Fig. 1). The water depth beneath the enclosures was 3.5 to 4.0 m. Artificial vegetation (plastic ribbons, ca. 40 strands, i.e. 70 m⁻²) covered half the area of each enclosure. Between observations, the enclosures were covered with plastic net to avoid attacks from sea birds. A recreational boat (aluminium hull), 5 m long, with a 70 hp, 4-stroke outboard motor was used as the noise source (at 2000 rpm). It was placed

with the bow facing the floating pontoon (Fig. 1). At the stern of the boat, 2 ropes were attached and anchored on land to allow stationary operation of the boat with the outboard motor at 8.0 m distance from the floating pontoon. We measured the body mass of individual fish and estimated approximate length using length–weight correlations from other fish of the same populations. The mean (±SD) size of the fish used in the single-species enclosures was 29.9 ± 11.7 g for perch (ca. 14.0 cm, n = 36) and 29.4 ± 14.6 g for roach (ca. 14.2 cm, n = 36); in the mixed-species enclosures, mean size was 19.1 ± 3.9 g for perch (ca. 12.5 cm, n = 18) and 9.7 ± 2.3 g for roach (ca. 11.3 cm, n = 18). Water temperature was measured once a day; temperature averaged around 18.0°C on all occasions.

Experimental procedure

Experiments were performed with 1 species per enclosure or with mixed species (3 individuals of each) in July and August 2012 and July 2013. Before the experiment, 36 individuals of either perch or roach, or 18 of each species, were randomly selected from the holding stock and transported to the enclosures at the study site. Six individuals were placed in each of the 6 enclosures and left to acclimate for 2 d. The experiment started in the morning (09:00 to 11:00 h) without motorboat noise exposure (control). Each feeding session lasted 5 min, and fish were hand-fed 24 pieces of saithe during this period. The covering net was removed from the open part of the enclosure leaving the vegetated part still covered, and, as a result, all the fish sought shelter in the vegetation. The first saithe piece was dropped in the
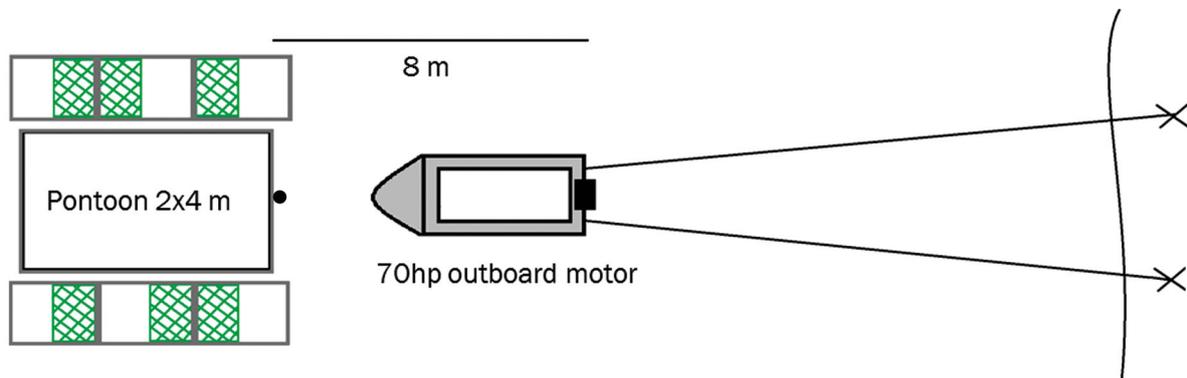

Fig. 1. Experimental setup used in this study. Six enclosures with artificial vegetation (checkered regions) covering half of the area, were mounted on a floating pontoon. A 5 m long recreational boat with a 70 hp, 4-stroke outboard motor was used to create the anthropogenic noise. It was anchored on land and operated from a stationary position, with the motor 8.0 m from the floating pontoon. Black bullet: location of the hydrophone

centre of the open area after 20 s, and food delivery continued at 10 s intervals. The fish pieces slowly sank through the water, and fish were observed attacking the food on its way down. Fish behaviour was video-recorded from above throughout the feeding experiment and was analysed afterwards (see below) using both the film and the spoken comments of observers in the video. In the afternoon (14:00 to 16:00 h), a new feeding session began, this time with noise exposure (for a total time of 30 min). The procedure was repeated for 4 more days, with the order of the 'noise' and 'silent' sessions alternated. To avoid a confounding effect between day and feeding order, the order of the enclosures was kept the same, since the data were compared within each enclosure (on the effect of noise and day of experiment).

Sound measurements

Prior to fish introduction into the enclosures, the sound was characterised in the same location as where the fish study was later conducted. The sound pressure and particle acceleration of the motorboat noise and of background (ambient) noise only (as during controls) were measured (see the Supplement at www.int-res.com/articles/suppl/m564p115_supp.pdf for more details). Particle motion can be expressed as displacement (m), velocity (m s^{-1}) or acceleration (m s^{-2}). The reason for using acceleration in this study and not velocity or displacement is that the hearing organ utilizes acceleration for detecting sound (Fay & Popper 2000, Martin et al. 2016). It could be argued a fish ear is a biomechanical organ that is similar to an accelerometer, which would favour the use of acceleration. Particle acceleration was measured with a particle motion sensor sensitive to frequencies in the range of 0.1 to 300 Hz, and pressure was measured with a hydrophone (Model LC32; Atlantic Research) sensitive to frequencies in the range of 1 to 170 kHz. The 2 sensors were deployed on the short side of the pontoon facing the boat (Fig. 1). Ambient noise level was recorded during a 5 min period. Noise levels from the outboard motor were recorded for 10 min at each of 7 different distances from the noise source (8 to 19 m), in order to establish the relationship between sound levels and distance to the noise source. Equipment used in the particle acceleration measurements was developed by the Department of Meteorology at Stockholm University and the Swedish Defence Research Agency. For detailed descriptions of the acoustic device, see Sigray & Andersson (2011) and Mueller-Blenkle et al.

(2010). All sound measurements were conducted during 1 d (17 June 2013).

Feeding attempts

Foraging behaviour was recorded as number of feeding attempts, i.e., when the delivered food item was attacked by a fish. Data were collected from the video recording of the feeding sessions, which lasted 5 min for each enclosure, combined with direct observations during the trials. Feeding attempts were registered as 0 (no attempt) or 1 (attempt) for each food item released (maximum possible number of feeding attempts = 24). In mixed-species enclosures, 2 feeding attempts could be recorded for each food item; one for each fish species. Individual fish of the same species could not be distinguished. Thus, the scores for each enclosure consist of the pooled feeding attempts, estimated separately for each of the 2 species.

Habitat utilization

Video recordings played at half speed were used for analyses of habitat utilization. The recordings lasted for 5 min and 2 parameters were measured: (1) latency to enter the open area without vegetation (measured as seconds until the first fish enters the open area) and (2) time spent in the open (number of seconds that at least 1 fish occupied the open area).

Statistical analyses

Differences in feeding attempts, latency to enter the open area, and time spent in the open area during control and noise exposure were analysed using generalized estimating equation (GEE). The GEE approach is especially suited for longitudinal or repeated-measures data, with a non-normally distributed response variable (Liang & Zeger 1986). Separate GEEs (Poisson distribution, log-linear link function) were conducted for single-species and mixed-species enclosures, with perch and roach analysed separately. The enclosure ID was added as a subject effect, and the repeats per test (5 control sessions + 5 noise sessions = 10 repeats) as a within-subject effect. The effects of exposure (factor) and day (covariate) were evaluated for 3 dependent variables (feeding attempts, latency to enter open area, and time in the open area) in separate GEEs. All sta-

tistical analyses were performed in SPSS Statistics 21 (IBM). Particle acceleration and sound pressure data were analysed in Matlab r2008b signal processing software (MathWorks).

RESULTS

Sound measurements

Analysis of the measured acoustic data showed that energy levels were low in the frequency range of 50 to 100 Hz and increased for frequencies higher than 100 Hz (Fig. 2a). Maximum spectral energy was found in the interval 150 to 600 Hz (Fig. 2b); at frequencies higher than 600 Hz, spectral energy levels decreased (Fig. 2b). The maximum spectral level calculated in 1 Hz bands was 126 dB re 1 µPa (rms). The broadband sound pressure level for frequencies higher than 100 Hz was 152 dB re 1 µPa (rms) at 8.2 m. Notable is that the low-frequency part of the spectra, spanning from 0 to 300 Hz, was similar for particle acceleration and sound pressure (Fig. 2a,c). Ambient noise was dominated by sound generated by the pontoon and the sea. Background levels were comparable for frequencies lower than 100 Hz and considerably lower than the levels obtained with the motor turned on (Fig. 2a–c) for frequencies higher than 100 Hz. Weather conditions were stable throughout the whole study, thus the measured ambient levels can be regarded as representative of the ambient noise experienced by the fish. The difference in distance to the motor between the closest and farthest cage was 3 m. Using the obtained relationship, the differences in sound levels were estimated to be 3 dB re 1 µm s^{-2} and 2 dB re 1 µPa (Fig. 2d). The same relationship was used to estimate the gradient inside the enclosures. The difference was 1.1 dB re 1 µm s^{-2} and 0.8 dB re 1 µPa. Thus, during noise exposure, the sound pres-

sure and particle acceleration levels at the centre of the closest cage was 152 and at the farthest 150 dB re 1 µPa (rms), and 75 and 72 dB re 1 µm s^{-2} (rms), respectively. For more details see the Supplement at www.int-res.com/articles/suppl/m564p115_supp.pdf.

Feeding behaviour

Perch

In the single-species enclosures, feeding performance of perch was negatively affected by motorboat noise, with more feeding attempts made during control periods compared to periods with noise exposure (Table 1, Fig. 3). A significant effect of day was found for this species, with more feeding attempts made at
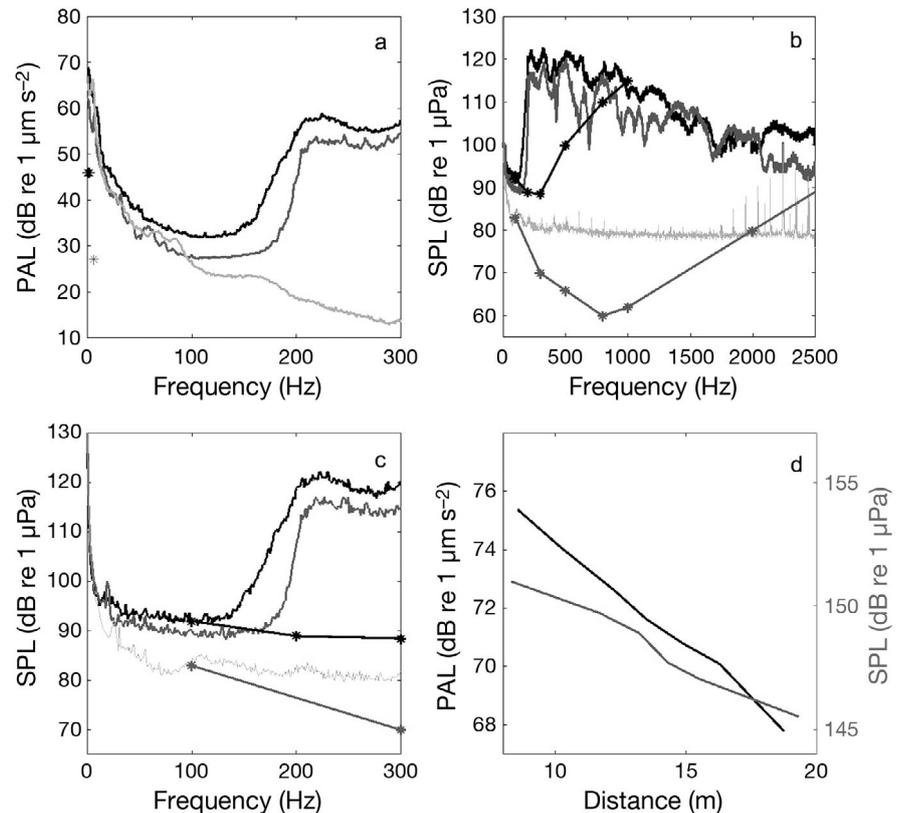

Fig. 2. (a) Particle acceleration level (PAL) measured at a distance of 8.2 m (black line) and 14.1 m (grey line) from the outboard motor. The background noise level with the motor off is marked with a light grey line. Black star: hearing threshold for perch *Perca fluviatilis*; grey star: threshold for roach *Rutilus rutilus* (H. K. Karlsen pers. comm.). (b) Sound pressure level (SPL) measured at 8.2 m (black line) and 14.1 m (grey line) from the motor. Light grey line: background noise levels when the motor was turned off; light grey line with stars: hearing threshold for roach; black line with stars: hearing threshold for perch (from Amoser et al. 2004). (c) The same data as in panel (b) but for the frequency interval 0 to 300 Hz for comparison with PAL. (d) The attenuation of PAL (black line) and SPL (grey line) with distance from the outboard motor

Table 1. Generalized estimating equation (GEE) and the effect test (Wald χ^2 test) for perch *Perca fluviatilis* and roach *Rutilus rutilus* in single-species enclosures. The effects of exposure (factor) and day (covariate) were evaluated for 3 dependent variables: feeding attempts, latency to enter the open area, and time spent in the open area. Significant values are in **bold**; *0.05 < p < 0.1

Single-species	Perch		Roach	
Variable	Wald χ^2	p	Wald χ^2	p
Feeding attempt				
Exposure	**8.704**	**0.003**	**16.671**	**<0.001**
Day	**52.086**	**<0.001**	0.434	0.510
Exposure × day	1.241	0.265	0.749	0.387
Latency to enter the open area				
Exposure	0.086	0.770	3.624	0.057*
Day	**9.101**	**0.003**	0.001	0.972
Exposure × day	0.560	0.454	0.648	0.421
Time in the open area				
Exposure	0.559	0.455	3.482	0.062*
Day	**14.556**	**<0.001**	1.059	0.303
Exposure × day	0.105	0.746	0.375	0.540

the end of the experiment compared to the start, both during noise exposure and control treatments. No feeding attempts were seen during the first day of the experiments. In the mixed-species enclosures, no effect of noise disturbance was observed in perch, but also here a day effect was found, with very few or no feeding attempts during the first 2 d (Table 2, Fig. 3).

Roach

In single-species enclosures with roach, there were significantly fewer feeding attempts made during noise exposure treatments compared with the controls, and no effect of day was found (Table 1, Fig. 3). In the mixed-species enclosures, number of feeding attempts increased significantly with day, resulting in a significant interaction between noise treatment and day (Table 2, Fig. 3). During noise exposure, no feeding attempts were observed for the first 2 d, although a few were made during the control treatment during that time (Fig. 3).

Habitat utilization

Perch

In the single-species enclosures, only day had a significant effect of the latency of perch to enter the open area and the time spent in the open, but there was no effect of noise exposure (Table 1, Fig. 4). No fish entered the open area the first day of the experiment, but latency to leave the vegetation for the open area decreased with time; that is, it took less time for the first fish to enter the open area at the end of the experiment compared to the start (Fig. 4). Noise did not have any effect on the latency of perch to enter open areas in mixed-species enclosures, but time spent in the open differed between noise exposure and control (Table 2, Fig. 4). There was, however, a significant interaction between noise exposure and day, and the effect of the noise showed different directions during different days (Fig. 4).
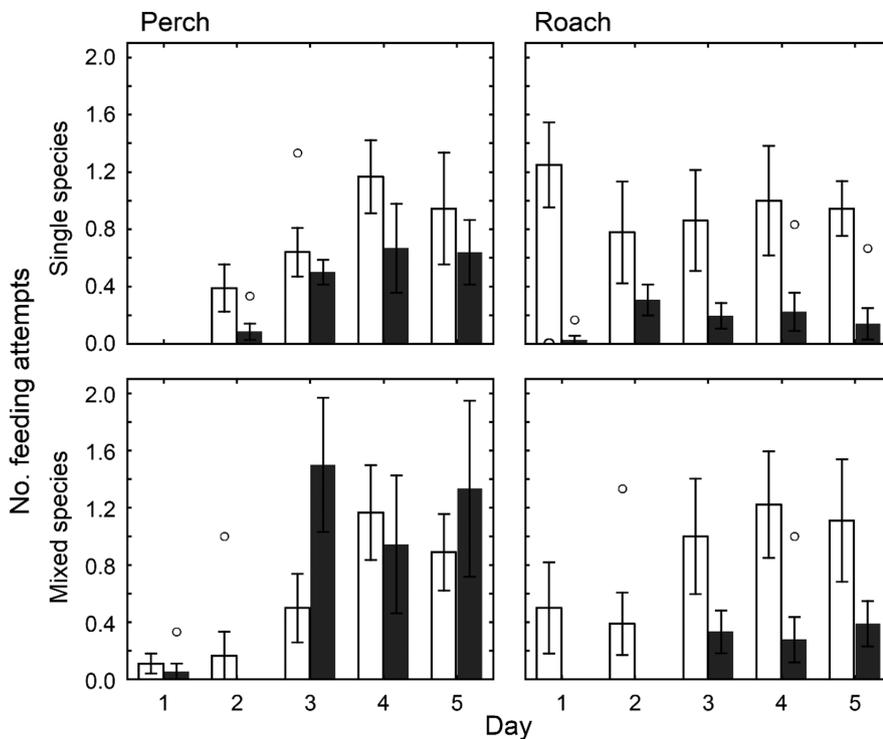

Fig. 3. Mean (±SE) number of feeding attempts of perch *Perca fluviatilis* and roach *Rutilus rutilus* in single- and mixed-species enclosures when subjected to either silent (control) conditions (open bars) or noise exposure (filled bars). Scores show the average number of feeding attempts for 6 individuals in the single-species enclosure and 3 individuals in the mixed-species enclosure. Circles denote outliers

Table 2. Generalized estimating equation (GEE) and the effect test (Wald χ^2 test) for perch *Perca fluviatilis* and roach *Rutilus rutilus* in mixed-species enclosures. The effects of exposure (factor) and day (covariate) were evaluated for 3 dependent variables: feeding attempts, latency to enter the open area, and time spent in the open area. Significant values are in **bold**

Mixed-species	Perch		Roach	
Variable	Wald χ^2	p	Wald χ^2	p
Feeding attempt				
Exposure	1.021	0.312	**19.529**	**<0.001**
Day	**24.065**	**<0.001**	**17.943**	**<0.001**
Exposure × day	0.019	0.922	**12.324**	**<0.001**
Latency to enter the open area				
Exposure	0.629	0.428	**5.202**	**0.023**
Day	**5.371**	**0.020**	**4.123**	**0.042**
Exposure × day	0.219	0.640	0.164	0.685
Time in the open area				
Exposure	**5.104**	**0.024**	**34.624**	**<0.001**
Day	**29.105**	**<0.001**	**129.961**	**<0.001**
Exposure × day	**6.812**	**0.009**	**99.114**	**<0.001**

DISCUSSION

Our results show that motorboat noise has the potential to affect the foraging behaviour of both perch and roach. Roach, in both single- and mixed-species enclosures, made fewer feeding attempts during treatments with motorboat noise compared to the silent control condition. In perch, the same pattern was found in the single-, but not in the mixed-species enclosures. Lower feeding frequencies and changes in diet composition have previously been observed in both the Mediterranean damselfish *Chromis chromis* and the mulloway *Argyrosomus japonicus* during periods of increased boating activity (Bracciali et al. 2012, Payne et al. 2015). The altered mulloway behaviour was suggested to be caused by stress, which is a common consequence of noise disturbance (Kight & Swaddle 2011). Ship noise has also been shown to be a stressor for 3 freshwater fish species (common carp *Cyprinus carpio*, gudgeon *Gobio gobio*, and perch), inducing higher cortisol release (Wysocki et al. 2006). Similarly, motorboat noise caused an increase in cortisol levels in both perch and roach (Johansson et al. 2016), indicating

Roach

Roach from the single-species enclosure appeared to have a shorter latency to enter, and spent more time in the open area during control conditions compared to periods with noise disturbance (Fig. 4), but the observed differences were only close to significant (Table 1). A significant difference between sound treatments was, however, observed for both latency and time spent in the open area in the mixed-species enclosure (Table 2, Figs. 4 & 5). A significant day effect was also found for roach in the mixed-species enclosure for both these measures (Table 2, Figs. 4 & 5). However, a significant interaction between noise treatment and day and time spent in the open was explained by the data from the last day, during which the fish decreased time spent in the open from the previous day in the control, but increased in the noise treatment (Fig. 5).
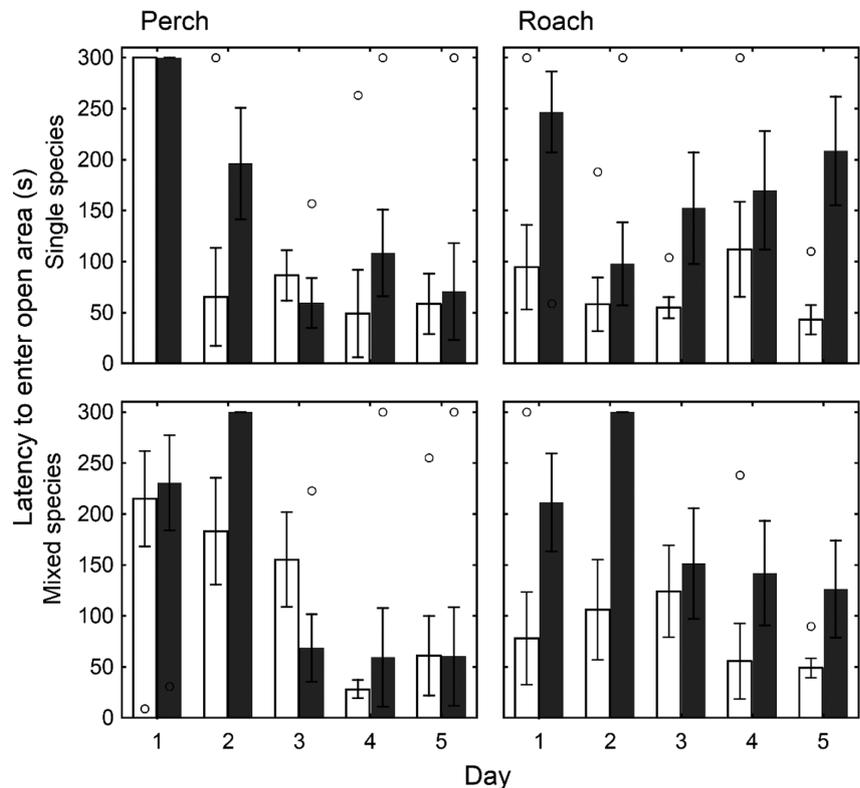

Fig. 4. Mean (±SE) time until the first fish entered the open area for perch *Perca fluviatilis* and roach *Rutilus rutilus* in single- and mixed-species enclosures, when subjected to either silent (control) conditions (open bars) or noise exposure (filled bars). Circles denote outliers
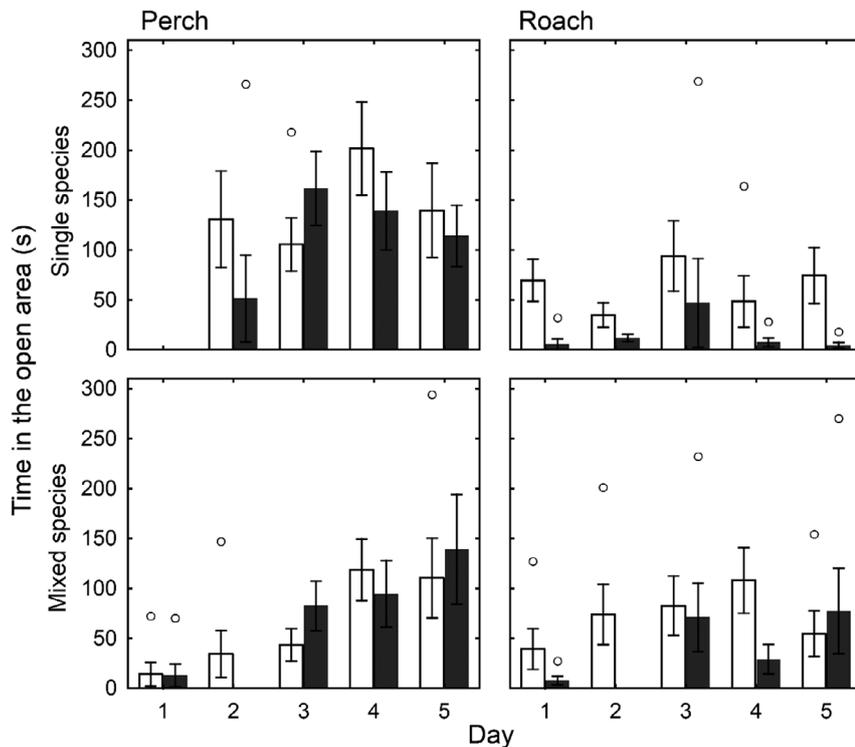
Fig. 5. Mean (±SE) time when at least 1 individual was observed in the open area for perch *Perca fluviatilis* and roach *Rutilus rutilus* in single- and mixed-species enclosures, when subjected to either silent (control) conditions (open bars) or noise exposure (filled bars). Circles denote outliers

600 Hz; measurements of sound pressure and particle acceleration follow each other quite closely. Information on particle acceleration thresholds are not available for perch and roach at these frequencies; however, studies on other fish species have shown that thresholds are lowest at low frequencies (<200 Hz) (Horodysky et al. 2008, Radford et al. 2012). The high frequencies produced by the motor would, to a high degree, be below the hearing threshold of perch, at least regarding sound pressure. Thus, a masking effect is unlikely to be the reason that perch in the single-species enclosures made fewer feeding attempts during noise exposure than during controls. Still, the perch seemed to perceive the noise in some way, possibly by particle acceleration, and their reaction may be a result of distraction or stress. Roach are more sensitive to sound pressure at the frequencies measured in the present study. The effect of noise exposure on their feeding could be explained by stress, distraction, or masking, but we cannot identify the accurate mechanisms behind their response to the disturbance.

The perch did not perform any feeding attempts on the first day in the single-species enclosures, which suggest that they had not fully adapted to the new environment. After that, although the perch consistently made fewer feeding attempts during noise exposure, the number of attempts increased with day during both treatments, indicating habituation. This is supported by the fact that latency to enter the open area also decreased with day in perch. In contrast, roach did not show any trend in the number of feeding attempts made during noise exposure, and no decrease in latency to enter the open area was found over the 5 d of the study. This implies that the roach were more disturbed by the noise than the perch, and did not habituate. The same pattern was found by Jacobsen et al. (2014), with perch (but not roach) seemingly habituating to boat noise. Habituation to noise exposure was also found in a study on stress response in perch and roach (Johansson et al. 2016). In that study, perch showed elevated cortisol levels after being subjected only once to motorboat sound, but after 11 d of exposure (2×30 min d^{-1}), cortisol

that stress response could be a possible explanation for the results in the current study.

However, there could be several reasons for reduced feeding performance during noise exposure, potentially diverging between perch and roach. Boat noise can cause a narrowing or shift in attention, distracting feeding animals and causing them to miss or ignore prey items. Chan et al. (2010) found support for this hypothesis in a playback experiment with the Caribbean hermit crab *Coenobita clypeatus*. The reduced foraging performance in three-spined sticklebacks during noise exposure was also explained by attention shift (Purser & Radford 2011). Furthermore, boat noise may mask sound produced by prey (in this study, sound produced by falling food items) (Amoser et al. 2004). Noise impacts on prey detection in fish have yet to be described — although this is relevant, since some fish species rely on their hearing abilities to find food (Hoin-Radkovsky et al. 1984). The 2 species in our study differ in their hearing sensitivities (Amoser et al. 2004). Perch are considered to rely mainly on particle acceleration for hearing, and are most sensitive to low-frequency sounds. In our study, the boat motor emitted high-frequency sounds, with maximum spectral energy in the interval of 150 to

levels did not differ between noise treatments and controls (Johansson et al. 2016). In roach, cortisol levels were higher in the short-term compared to the long-term study, but with overall higher levels in groups exposed to noise compared to control groups (Johansson et al. 2016). Similarly, red drum *Scianenops ocellatus* and spotted sea trout *Cynoscion nebulosus* showed elevated cortisol levels after short-term but not long-term exposure to playback recordings of boat noise (Spiga et al. 2012). The present study was a short-term study (duration 5 d). For that reason, we cannot say if the effects of noise exposure would persist over a longer time period. Both zebrafish (Shafiei Sabet et al. 2015) and European seabass *Dicentrarchus labrax* (Neo et al. 2014) showed stronger negative effects when sound was emitted intermittently compared to continuously, in terms of activity, foraging performance, and behavioural recovery. Thus, both the duration and the temporal pattern of noise exposure may be important for long-term effects on fish behaviour and fitness.

Anthropogenic noise exposure may have negative effects on predator detection, for example, in terms of increased reaction times as shown in shore crabs *Carcinus maenas* and juvenile European eels *Anguilla anguilla* (Wale et al. 2013, Simpson et al. 2015). In contrast, three-spined sticklebacks responded faster to a visual predator stimulus during noise (playback) exposure than during control conditions (Voellmy et al. 2014b). The heightened cautiousness during sound exposure could be caused by stress (Charmandari et al. 2005), but it could also be a compensatory response to auditory masking (Rabin et al. 2006). Latency to enter a novel area is often analysed as a proxy for reduced risk-taking behaviour and boldness (Brown et al. 2005, Magnhagen 2007). In our study, the latency to enter the open area was longer for roach in mixed-species enclosures during noise disturbance compared to control treatments, with a similar trend in the single-species enclosures. In general, roach spent less time in the open during noise exposure than during control conditions, but in the mixed-species enclosures this was mainly found during the first 2 d. Noise exposure can trigger anti-predator behaviour (Frid & Dill 2002), such as seeking shelter in vegetation. Both perch and roach may seek shelter under predation risk (Persson 1991). Potentially, this could explain the treatment effect on habitat utilization in roach. Noise exposure had no effects in perch regarding latency to enter the open area, and time spent in the open area varied with day with either more time during silence or during noise exposure. Thus, perch did not seem to perceive the noise as a threat.

In our study both, roach and perch responded to the boat motor noise, but the results differed between species. In another study, roach tagged with acoustic transmitters aggregated and moved away from a running outboard motor, while tagged perch only showed a short-term reaction to the motor noise and did not change habitat (Jacobsen et al. 2014). Sympatric minnows *Phoxinus phoxinus* and three-spined sticklebacks both exhibited a reduction in foraging success when exposed to the playback of ship noise, although different mechanisms may explain this effect (Voellmy et al. 2014a). Another study, comparing the response to noise in 2 species with different hearing abilities (zebrafish and Lake Victoria cichlid *Haplochromis piceatus*), found both similar and species-specific responses and concluded that responses are not necessarily related to differences in hearing (Shafiei Sabet et al. 2016).

Since roach and perch often co-occur in their natural habitat, we kept the 2 species separate and together, to determine whether their behaviour was influenced by inter-specific interactions. For perch, the number of feeding attempts per individual was higher during noise exposure in the mixed-species compared to the single-species enclosures. However, it is likely that the reduced foraging in roach affected the feeding behaviour of perch by decreasing competition for the food that was delivered. In roach, both number of feeding attempts and utilization of the open area changed with time in the mixed-species, but not in the single-species enclosures. In the single-species treatment, the roach were larger than in the mixed-species treatments, but the response to noise exposure was still similar. The significant interaction between noise exposure and time, only found in the mixed-species treatment, could possibly be affected by the smaller size of the fish in this treatment. However, it is more likely that the change in behaviour with time was due to an influence of the perch, which exhibited less of a reaction to the noise exposure, and seemed to become habituated in all treatments. This result is in line with other findings that animals select habitats using heterospecific information (Goodale et al. 2010).

Foraging efforts and food handling errors in fish during noise disturbance have primarily been studied in laboratory experiments (Purser & Radford 2011, Voellmy et al. 2014a, McLaughlin & Kunc 2015, Shafiei Sabet et al. 2015). Experiments on the effects of noise disturbance on foraging are rarely conducted outdoors (but see Bracciali et al. 2012, Payne et al. 2015). Thus, our study is among the first to study noise effects in fish under natural environmental conditions.

Another advantage of our study was that a real motorboat with an outboard motor was used to produce authentic noise. In general, most studies on noise effects on aquatic organisms use artificial sound or playback recordings. It is important to remember that the recordings used in most tank-based experiments can be very different from those produced by actual sound sources (Akamatsu et al. 2002). However, to fully understand natural conditions, future studies will have to include free-swimming (wild) individuals (e.g. Jacobsen et al. 2014). In order to understand the acoustic conditions for different fish species, both particle acceleration and sound pressure should be measured, as was done here, since fish with different hearing abilities use different components of sound for their hearing (Nedelec et al. 2016).

In conclusion, using authentic sound in a natural habitat, this study has shown that noise exposure may affect the feeding behaviour of fish, that the response is species-specific, and that habituation and the presence of other species may modify the effects. The knowledge obtained here is crucial in order to predict species-specific long-term effects of noise. For example, noise can affect species like roach and perch and lower their feeding efficiency — which can have important implications for fitness, animal welfare, and conservation (Voellmy et al. 2016). Our study also suggests that the effect of anthropogenic noise should be considered in the management of fish communities and should be included in future analyses of species interactions, growth, and reproductive success.

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