A fish-passable barrier to stop the invasion of non-indigenous crayfish

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ABSTRACT

The invasion of non-native signal crayfish into European ecosystems has resulted in a drastic reduction of native European crayfish, with adverse effects on ecosystems and fisheries. This study aimed to determine whether native crayfish can be protected by physical barriers that do not hinder fish migration, but prohibit the upstream migration of non-native crayfish. Laboratory experiments were carried out to test a barrier design consisting of a gently-inclined, smooth, prismatic, cross-channel structure. Barrier efficiency appeared to depend on barrier roughness, barrier slope and flow velocity directly above the barrier crest. The maximum barrier slope that can be climbed by crayfish decreases with increasing flow velocity in a non-linear way. This observation is in agreement with the physics of crayfish locomotion as demonstrated by applying Newton's laws of motion to crayfish. Contrary to general acceptance, signal crayfish do deliberately deploy their swimming capacities to pass barriers, proving the general belief that crayfish only swim as an escape response to be untrue. This suggests that crayfish are able to pass all barriers regardless of barrier slope or barrier roughness if the flow velocity is below the maximum velocity against which crayfish can swim. Nevertheless, physical crayfish barriers are an effective method to protect indigenous crayfish in streams with sufficiently high flow velocities. Promising barrier locations are pre-existing structures such as fish ladders alongside weirs, where flow velocities are controlled, sedimentation risks are low, maintenance is done regularly and the bed profile is suitable to connect barriers to.

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1. Introduction

The invasion of non-native signal crayfish (*Pacifastacus leniusculus*; Dana, 1852) into European ecosystems has resulted in a drastic reduction of native European crayfish (Holdich et al., 2009; IUCN, 2012), such as the gourmet crayfish *Astacus astacus* (Linnaeus, 1758). In addition, signal crayfish were observed to have a negative impact on populations of invertebrates (e.g., Usio et al., 2009), macrophytes (e.g., Usio et al., 2009), benthic fish (e.g., Guan and Wiles, 1997; Bubb et al., 2009) and pelagic fish (e.g., Griffiths et al., 2004; Peay et al., 2009). Furthermore, the invasion of signal crayfish leads to a reduced water quality (Hänfling et al., 2011) and increases sediment-related flood risks (Harvey et al., 2011). Problems started in 1959 (Abrahamsson, 1973), when signal crayfish were brought from America to Europe as a food species, but continue today (e.g. Skov et al., 2011). Signal crayfish are not only competitively superior to native crayfish (e.g., Söderbäck, 1991, 1995), they also transmit the crayfish plague *Aphanomyces astaci*, a fungal disease harmless to signal crayfish but lethal to native crayfish (Unestam, 1972; Alderman and Polglase, 1988). When signal crayfish intrude into a watershed, downstream populations of native crayfish are exposed to the plague due to transport of spores by flowing water, whereas both downstream and upstream populations are exposed due to migration of infected crayfish.

Fortunately, the upstream spread of the crayfish plague is often halted by barriers such as waterfalls, culverts and dams (Alderman and Polglase, 1988; Taugbol et al., 1993; Kerby et al., 2005). Therefore, some residual populations of native crayfish have been able to survive in river headwaters. These remaining populations now are in great danger due to the implementation of the European Water Framework Directive (EU, 2000), a legally-binding agreement that requires the restoration of the ecological continuity of water bodies by 2015. This implies that anthropogenic barriers that hinder fish migration must be removed or provided with a fish ladder. It may be clear that this is beneficial for migratory fish species (e.g. salmon) and gene flow in residential species populations, but threatening to native crayfish, because it promotes the invasion

of signal crayfish. Quite similar debates on the merits of connectivity versus isolation of freshwater bodies have been had in North America (Fausch et al., 2010).

If we want native crayfish to survive, measures must be taken urgently. In addition to the political challenge of stopping the ongoing introduction of non-native species to European ecosystems (cf. Keller et al., 2011), we also have to deal with the signal crayfish that have already passed through the first two stages of biological invasion – namely introduction and establishment on site – and are now in the final stage of impacting the ecosystem by spreading massively (Vander Zanden and Olden, 2008). The preferred solution is to eradicate these crayfish (e.g., Holdich et al., 1999; Sandodden and Johnsen, 2010), but available eradication methods are either extremely time consuming, ineffective or harmful to other organisms (Ellis, 2005). Partial eradication of crayfish populations has even proven to result in faster growth rates and improved body condition in the remaining population (Moorhouse and Macdonald, 2011). The only alternative solution is the management and confinement of native crayfish populations in isolated 'ark sites' (Peay, 2009), free from non-native crayfish and the threat of colonisation by non-native crayfish. Crayfish barriers can protect native crayfish in such ark sites in the hope that acceptable eradication methods against invaders will be developed soon.

In the past, some success has been achieved with electrical crayfish barriers (e.g., Unestam et al., 1972) but these were never applied widely, because they need an uninterruptible power supply, which makes them rather costly to implement in remote areas. A promising alternative are physical crayfish barriers (e.g., Thompson, 1990; Ellis, 2005; Dana et al., 2011), which are cheap, easy to maintain and do not require power supply. Physical crayfish barriers typically consist of a smooth, cross-channel vane with a height of 25–30 cm, often with an overhanging drop, that is placed vertically or slightly tilted on the river bed (Ellis, 2005). Some variants have stone walls that rise above the waterline and allow downstream water flow only over a small barrier spring (Dana et al., 2011).

A disadvantage of the present generation of physical crayfish barriers, however, is that they are not (e.g. Dana et al., 2011) or not fully (e.g. Ellis, 2005) passable for fish. Laboratory investigations with several barrier types (Ellis, 2005) show that even if barriers allow upstream migration of pelagic fish they hinder the migration of benthic fish.

Another disadvantage of existing crayfish barriers is that they are only effective against crayfish walking along the river bed. Crayfish, however, also have another way of locomotion: rapid backward swimming by flipping their tail. This type of locomotion is used as a flight reflex and is typically caused by a rapid visual stimulus from the anterior direction (Wine and Krasne, 1972; Webb, 1979). Usually, it is believed that swimming events are too infrequent and too short of duration for crayfish to breach barriers by swimming, which is supported by laboratory investigations (Webb, 1979; Light, 2005; Ellis, 2005; Foster and Keller, 2011). However, signal crayfish from a population in the Iter (Germany) were regularly found to swim distances of up to one meter in a container (Vaeßen, personal observation). This suggests that these crayfish could be able to breach physical barriers by swimming.

The objective of this study was to explore whether it is possible to construct a physical crayfish barrier that does not hinder the upstream migration of fish, but prohibits the upstream migration of non-native crayfish by all types of locomotion. In this way, protection of native crayfish species can be achieved in combination with improving fish passability, thereby meeting multiple management objectives simultaneously. In contrast to previous studies, we propose a barrier with a triangular prismatic design with inclined barrier surfaces in order to minimize impact on migrating fish (Fig. 1a). Theoretical calculations of crayfish locomotion and laboratory experiments were carried out to test the efficiency of the proposed barrier design. Particular efforts were made to determine the minimum slope needed to halt walking crayfish and the minimum flow velocity needed to halt swimming crayfish. The analyses are complemented with a discussion on the passability of barriers for fish, on constructional aspects of crayfish barriers and on potential barrier locations.

2. Theory

Basic guidelines for constructing the new barrier (Fig. 1a) can be derived by considering the forces that act on a crayfish (Fig. 2) and applying Newton's laws of motion. In the case of crayfish walking a barrier, the relevant forces are: F_m, the muscular force of the crayfish (N); F_f, the Coulomb friction force due to the friction between the crayfish legs and the barrier surface (N); F_d, the drag force exerted by the fluid (N); and $F_{G//}$ the net downslope gravity force acting on the crayfish (N). A barrier is effective if the magnitude of the forces that pull the crayfish downslope (F_d and $F_{G//}$) exceeds the magnitude of the forces that pull the crayfish upslope (F_m and F_f):

$$F_d + F_{G//} > F_m + F_f \tag{1}$$

with:

$$F_d = 0.5\rho C_d A u^2 \tag{2}$$

$$F_{G//} = (G - B)\sin(\alpha) = (\rho_c - \rho)Vg\sin(\alpha) \tag{3}$$

$$F_f = \mu(G - B)\cos(\alpha) = \mu(\rho_c - \rho)Vg\cos(\alpha) \tag{4}$$

Here, G (=$\rho_c Vg$) represents the gravity force (N), B (=ρVg) the buoyancy force (N), α the barrier slope (°), ρ_c the bulk density of the crayfish' body (kg/m³), ρ the water density (998 kg/m³), V the crayfish volume (m³), g the gravitational acceleration (9.81 m/s²), C_d the drag coefficient (–), A the frontal surface area of crayfish exposed to the flow (m²), u the flow velocity parallel to the barrier surface (m/s) and μ the Coulomb friction factor (–). Combination of Eqs. (1)–(4) leads to the following expression:

$$\sin(\alpha) - \mu\cos(\alpha) > \frac{F_m - 0.5\rho C_d A u^2}{(\rho_c - \rho)Vg} \tag{5}$$

which shows that in order to be effective against walking crayfish, crayfish barriers must be steeper if the barrier has a high surface roughness than if the barrier has a low surface roughness. Equally, crayfish barriers must be steeper in situations with low flow velocities than in situations with high flow velocities. Flow velocity influences barrier efficiency in a highly non-linear way.

Eq. (5) also allows visualizing the effect of crayfish properties on barrier efficiency. A sensitivity analysis in which F_m, A and C_d were systematically varied keeping the other variables constant (Fig. 3) shows that the maximum slope that can be walked by crayfish under still-water conditions ($u = 0$ m/s) depends on the muscular strength of crayfish (F_m), but not on their body shape (represented by A and C_d). Furthermore, the maximum velocity against which crayfish can walk a barrier of a given slope increases if crayfish have a higher muscular force (F_m), a lower frontal area (A) or a more streamlined body with lower drag coefficient (C_d).

Eq. (5) cannot be used directly to determine the minimum slope and roughness needed for a crayfish barrier, because the hydrodynamic properties of signal crayfish (ρ_c, V, A, C_d), their muscle force (F_m) and the friction coefficient of the barrier surface (μ) have not been documented with sufficient detail in scientific literature. Experimental tests of the proposed barrier design therefore remain indispensable.
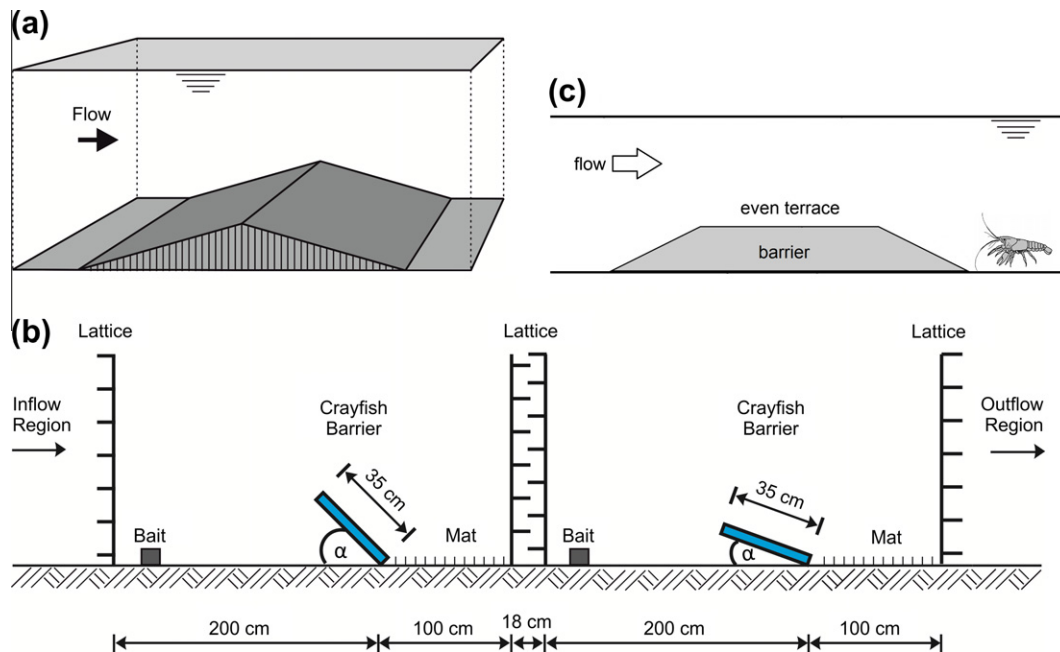
Fig. 1. Barrier and experimental design: (a) proposed barrier design, (b) design of flume experiments, (c) improvement to the barrier design by introducing a horizontal platform at the barrier crest (cross-channel view).
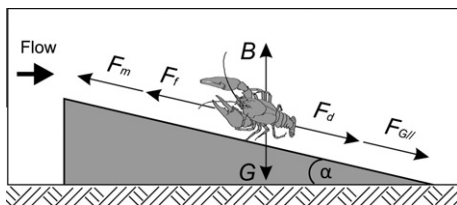

Fig. 2. Force balance of crayfish on a sloping bed (F_m = muscle force, F_f = friction force, F_d = drag force, $F_{G//}$ = downslope gravity force, G = gravity force, B = buoyancy force, α = angle of slope).

3. Methods

3.1. Flume experiments

The new crayfish barrier design (Fig. 1a) was tested in one of the flumes of the Institute of Hydraulic Engineering and Water Resources Management (RWTH Aachen University, Germany). The flume, which has a width of 1 m, a height of 1 m and a length of 30 m, was divided into four sections using lattices with 2.25×2.25 cm openings (Fig. 1b). In each of the two central sections, a crayfish barrier was installed. In order to facilitate adjustment of the barrier slope, we decided not to install the full barrier, but only the downstream part of the barrier, which is the part that has to hold back the crayfish. The simplified barriers consisted of PVC plates with a thickness of 1.5 cm and a length of 35 cm, which were attached to the flume bottom with hinges in order to allow quick adjustment of the barrier slope. The flume bottom downstream of the barriers was covered with erosion control mats (BECO-Bermüller BEMAT) in order to create a rough surface as in the crayfish's natural habitat.

A total of 32 experiments were conducted (Table 1), differing with respect to flow velocity (0.04–0.77 m/s), barrier slope (0–48°) and barrier roughness (0–0.16 mm). Variation in flow velocity was accomplished by changing the flume discharge, variation in barrier slope by adjusting the barrier position, and variation in roughness by covering the barrier surface with emery

paper (FEFA P100 grit) (Table 1). Because the barriers must be passable for fish, the water depth above the barrier was at least 10 cm throughout the experiments.

Before each experiment, the water depth and flow velocity above the barrier crests were measured. The velocity measurements were carried out with propeller current meters (Ott) and represent the average value of the downstream velocity component in the first 5 cm above the barrier crest.

At the beginning of an experiment, eight adult crayfish were placed downstream of the barrier, whereas bait (dog food) was placed upstream. The crayfish were obtained from a population in the Iter, a small stream near Aachen (Germany). Between capture and experiments, the crayfish were kept in a 1.1 m long and 0.9 m wide, oxygenated container, where they were fed once a day. Crayfish length varied between 9 and 14 cm, whereas crayfish mass (M) varied between 26 and 114 g, with an average of 57 g. Other relevant hydrodynamic crayfish properties (Eq. (5)) were an average density (ρ_c) of 1105 kg/m³, an average volume ($V = M/\rho_c$) of 0.000052 m³ and an frontal surface area (A) for a crayfish of average mass of 0.0016 m². ρ_c was determined by weighing 14 randomly-selected adult signal crayfish, putting them into a water-filled measuring glass and dividing the mass by the volume of water replaced. A was determined by taking photographs of six signal crayfish from a front view, counting the number of pixels occupied by the crayfish using image-analysis software, and multiplying the outcome with the surface area of a pixel.

During the experiments, crayfish behavior was recorded with infrared cameras (Lupusnight LE137, LE171N). Two additional infrared light sources (B&S Technology, SAL 10) were placed above each of the barriers to provide clear vision of crayfish activity during the night. The experiments were run until one of the crayfish breached the barrier. The recorded videos were inspected to determine whether the barrier had been breached by walking or swimming. If the barrier was not breached within 48 h by any crayfish, the experiment was terminated and the barrier considered effective.

Water temperatures during the experiments averaged 22.5 °C and once rose to 29 °C. These temperatures are optimal for growth of signal crayfish (Firkins and Holdich, 1993), which have been
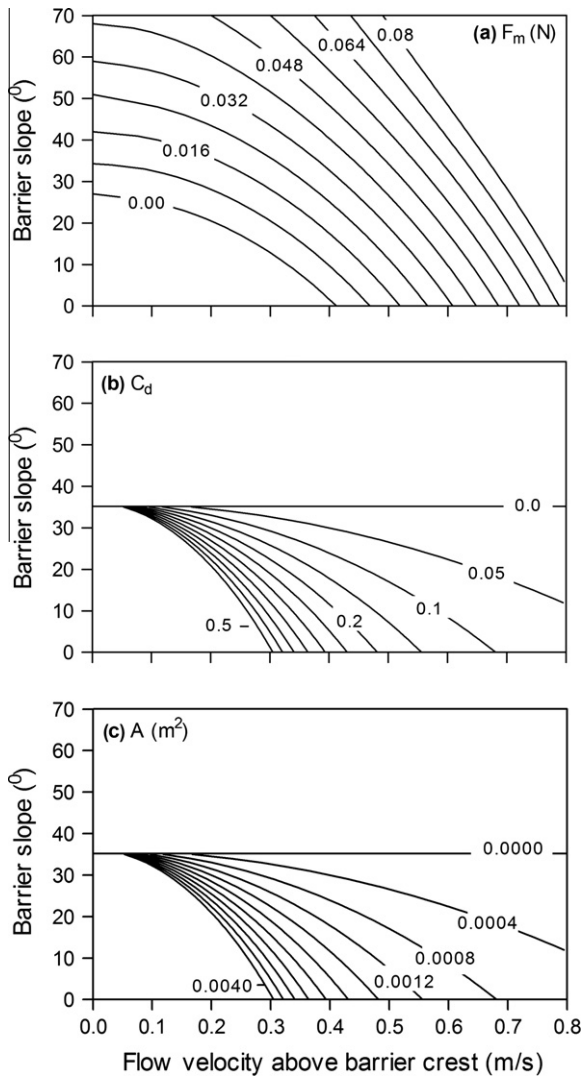
Fig. 3. The influence of muscle force (a), drag coefficient (b) and frontal surface area (c) on barrier efficiency, as determined from a theoretical force balance (ρ_c = 1105 kg/m^3, V = 0.000052 m^3, μ = 0.5, A = 0.0016 m^2, C_d = 0.2 and F_m = 0.01 N unless indicated otherwise in the panels). Shown is the maximum slope that can be climbed by signal crayfish at a given flow velocity.

reported to tolerate temperatures up to 31.1 °C (Nakata et al., 2002). The oxygen content of the water stayed near saturation (above 96%) at all times, creating appropriate conditions for the animals. They showed normal behavior and many of them even molted during the experiments.

3.2. Still-water experiments

Swimming experiments were conducted under still-water conditions to determine the maximum swimming velocity of signal crayfish. A fish tank with a 60 × 40 cm base and clear bottom pane was placed upon a sheet of grid paper. Water was filled in up to a height of 4.5 cm so that the grid lines remained clearly visible from above. Over the tank, a video camera (Panasonic NV-GS27) was positioned on a tripod, looking down in a 90° angle to record swimming behavior.

Ten swimming experiments were conducted (Table 2). At the beginning of each experiment, a signal crayfish of random size and sex (varying between 6 and 11 cm in total body length) was placed in the tank and stimulated to show flight reflex (tail flip escape response) by putting the edge of an aluminum ruler on

the root of the abdomen and pushing the animal down slightly. After holding it to the ground for a few moments, pressure was removed, resulting in the crayfish swimming backwards. The videos recorded during the experiments were used to determine the swimming velocity: jumping from frame to frame, the distance covered by the swimming crayfish was measured using the underlying grid paper and divided by the time lag between successive frames (0.04 s).

4. Results

During the flume experiments, crayfish continuously tried to breach the barrier, showing positive rheotaxis immediately after insertion into the flume. No difference in crayfish activity was observed between daily and nightly hours. The high surface roughness of the erosion control mats enabled all crayfish to reach the barrier. Here, crayfish kept moving in upstream direction, usually solely, but in some cases also by accumulating on the barrier. The 90°-angle between the barrier and the flume walls seemed to be a preferred place for crayfish to put the tips of their legs when walking up the barrier. If the barrier was neither too steep, nor too smooth, crayfish were able to reach the barrier crest. Here, crayfish were fully exposed to the water flow. If the drag force exerted by the flow was too strong, the animals were simply washed downstream. Otherwise, crayfish pulled themselves over the barrier crest, dropped themselves onto the bed and continued walking in upstream direction until they arrived at the bait.

Crayfish were able to breach the barrier by means of walking in 14 out of 32 experiments (Table 1 and Fig. 4). Whether or not crayfish were able to breach the barrier depended on barrier roughness, barrier slope and flow velocity directly above the barrier crest. The maximum barrier slope that could be breached by walking crayfish decreased with increasing flow velocity in a non-linear way (Fig. 4a). During the experiments with smooth barriers, for instance, crayfish were able to climb slopes of at least 24° at flow velocities of about 0 m/s, but appeared unable to pass slopes of 0° at flow velocities of about 0.5 m/s. During the experiments with a higher barrier roughness, crayfish had a better grip on the barrier surface and were able to climb steeper slopes at higher flow velocities. Again, however, the maximum passable slope decreased with increasing flow velocity (Fig. 4b).

During the flume experiments some crayfish deliberately tried to pass the barrier by using swimming as a way of locomotion (Table 1). This behavior was only observed if efforts to pass the barrier by walking remained unsuccessful for some time, varying between 1 h (experiment 17) and 33 h (experiment 20). First, crayfish turned their tail towards the flow and then set off without external stimulation, swimming in backward and upward direction towards the water surface by flipping their tails. Once there, they continued swimming in upstream direction closely below the water surface, either directly to the other side of the barrier, or to the barrier crest. In the latter case, the crayfish clung to the crest, took a short rest, and then tried to pass the barrier as described above.

Only in 5 out of 32 experiments, crayfish succeeded in passing the barrier by means of swimming. The experimental set-up did not allow accurate determination of the swimming velocity of crayfish, but since during the swimming events distances of at least 35 cm (the barrier length) were covered in about two seconds, the swimming velocity of a crayfish relative to the flume walls must have been at least 0.175 m/s. The swimming velocity relative to water flow was much higher, as during the swimming events the water itself had a velocity towards the opposite direction of 0.06–0.44 m/s (Table 1). At higher flow velocities all trials to pass the barrier by swimming were unsuccessful. Whereas the swimming velocity of crayfish during the flume experiments must

Table 1
Flume experiments.

	Barrier characteristics			Flow characteristics			Crayfish characteristics				Test result	
ID	S (°)	e (m)	k_s (mm)	Q (m³/s)	h (m)	$\bar{u}$ (m/s)	u (m/s)	n (–)	M (g)	L (m)	Class	t (min)
1	8	0.07	<0.01	0.035	0.28	0.12	0.12	4/4	29–93	0.090–0.120	Wa	1
2	1	0.03	<0.01	0.035	0.34	0.10	0.10	4/4	29–93	0.090–0.120	Wa	1
3	25	0.17	<0.01	0.035	0.19	0.18	0.18	4/4	30–93	0.090–0.125	Wa	27
4	17	0.12	<0.01	0.035	0.24	0.15	0.15	3/5	26–57	0.090–0.120	Wa	1
5	48	0.27	<0.01	0.035	0.10	0.35	0.38	4/4	30–93	0.090–0.125	O	
6	8	0.07	<0.01	0.150	0.32	0.48	0.44	5/3	37–94	0.100–0.125	O	
7	1	0.03	<0.01	0.150	0.33	0.45	0.48	2/6	28–55	0.095–0.115	Wa	104
8	8	0.07	<0.01	0.091	0.31	0.29	0.30	4/4	32–45	0.095–0.115	Wa	6
9	0	0.02	<0.01	0.091	0.36	0.26	0.27	2/6	29–61	0.095–0.115	Wa	3
10	32	0.20	<0.01	0.091	0.20	0.46	0.50	4/4	32–45	0.095–0.115	O	
11	24	0.16	<0.01	0.091	0.22	0.42	0.44	2/6	29–61	0.095–0.115	Sw	1468
12	48	0.27	<0.01	0.010	0.17	0.06	0.07	8/0	44–89	0.105–0.125	Sw	1557
13	12	0.09	<0.01	0.171	0.30	0.57	0.57	6/2	39–113	0.100–0.130	O	
14	0	0.02	<0.01	0.171	0.33	0.51	0.53	7/1	36–84	0.100–0.125	O	
15	24	0.16	<0.01	0.010	0.27	0.04	0.04	8/0	43–94	0.105–0.130	Wa	15
16	40	0.24	<0.01	0.010	0.20	0.05	0.06	8/0	43–94	0.105–0.130	Sw	136
17	48	0.27	<0.01	0.010	0.16	0.06	0.07	8/0	43–94	0.105–0.130	Sw	62
18	16	0.11	<0.01	0.091	0.26	0.35	0.35	8/0	43–94	0.105–0.130	Wa	6
19	40	0.24	<0.01	0.035	0.13	0.27	0.31	6/2	36–111	0.110–0.130	O	
20	32	0.20	<0.01	0.035	0.16	0.22	0.26	8/0	43–94	0.105–0.130	Sw	1986
21	10	0.08	<0.01	0.118	0.28	0.42	0.46	3/5	31–45	0.100–0.115	O	
22	6	0.06	<0.01	0.118	0.28	0.43	0.50	5/3	31–89	0.100–0.120	O	
23	0	0.02	0.16	0.142	0.29	0.49	0.51	8/0	41–114	0.105–0.140	Wa	4
24	0	0.02	0.16	0.142	0.23	0.63	0.60	7/1	38–93	0.095–0.130	Wa	8
25	16	0.11	0.16	0.170	0.23	0.72	0.72	8/0	41–114	0.105–0.140	O	
26	0	0.02	0.16	0.170	0.25	0.67	0.71	7/1	38–93	0.095–0.130	Wa	12
27	4	0.04	0.16	0.170	0.17	0.98	0.77	7/1	38–93	0.095–0.130	O	
28	24	0.16	0.16	0.060	0.13	0.47	0.53	8/0	54–113	0.105–0.130	Wa	?
29	22	0.15	0.16	0.060	0.13	0.47	0.56	6/2	43–93	0.100–0.125	O	
30	30	0.19	0.16	0.060	0.11	0.55	0.62	7/1	40–108	0.100–0.140	O	
31	37	0.23	0.16	0.060	0.13	0.46	0.53	4/4	28–66	0.095–0.115	O	
32	32	0.20	0.16	0.060	0.14	0.43	0.47	7/1	38–93	0.100–0.120	Wa	?

e = Barrier height; h = Water depth above barrier crest; k_s = Barrier roughness; L = Corpus length of crayfish (min–max); M = Mass of crayfish (min–max); n = Number of crayfish (males/females); O = Barrier not breached; Q = Flow discharge; S = Barrier slope; Sw = Barrier breached by swimming; t = time to breach; u = Flow velocity in 5 cm zone above barrier crest; $\bar{u}$ = Average flow velocity above barrier (=Q/hW); Wa = Barrier breached by walking.

Table 2
Still-water experiments.

ID	G (–)	L (m)	v (m/s)	Remarks
s01	M	0.080	0.25	
s02	M	0.085	0.25	
s03	M	0.100	0.14	
s04	M	0.100	0.33	One-clawed crayfish
s05	F	0.085	0.27	Egg-bearing crayfish
s06	M	0.110	0.19	
s07	M	0.060	0.31	Crayfish with injured abdomen
s08	F	0.100	0.29	Egg-bearing crayfish
s09	F	0.105	0.13	Egg-bearing crayfish
s10	F	0.085	0.38	One-clawed crayfish

G = Gender; L = Corpus length; v = Maximum swimming velocity

have been at least (0.175 + 0.44=) 0.62 m/s, the maximum swimming velocity during still-water experiments was markedly lower: 0.38 m/s (Table 2).

5. Discussion

5.1. Barrier efficiency

The flume experiments confirm the theoretical guidelines (Section 2) that in order to be effective against walking crayfish, crayfish barriers must be steeper in situations with low flow velocities than in situations with high flow velocities (Fig. 4). Equally, crayfish barriers must be steeper if the barrier has a high surface roughness than if the barrier has a low surface roughness (Fig. 4).

The experimental results can be reproduced theoretically with Eq. (5) by a proper choice of the coefficients. A good fit of the experimental results is obtained if ρ_c, V, and A are set to 1105 kg/m³, 0.000052 m³ and 0.0016 m² respectively (see Section 3.1) and if C_d, μ and F_m are set to 0.2, 0.5 and 0.01N respectively for the smooth barrier, or to 0.2, 1.3 and 0.01N for the rough barrier (Fig. 4). Other combinations of C_d, μ and F_m (e.g. 0.25/0.25/0.025N for the smooth barrier) however also provide acceptable fits.

In order to be effective against swimming crayfish, the flow velocity needs to be above the critical velocity against which crayfish can swim. If the flow velocity is lower, crayfish are able to pass all barriers, either in walking mode or in swimming mode. In low-velocity streams, an increase of the slope of crayfish barriers therefore is an ineffective measure to protect indigenous crayfish species. Barrier slope only becomes important if the flow velocity exceeds the maximum current velocity against which crayfish can swim. If the barrier slope is too low in this case, crayfish will be able to overcome the barrier in walking mode. A sufficiently high slope is needed to make a barrier efficient here.

The flume experiments in combination with the theoretical considerations show that four situations can be distinguished in relation to barrier efficiency (Fig. 4): (I) the barrier can be passed by swimming crayfish, (II) the barrier can be passed both by swimming crayfish and by walking crayfish, (III) the barrier can only be passed by walking crayfish, and (IV) the barrier cannot be passed at all. Only in the latter case, the barrier is effective. The maximum current velocity against which crayfish can swim constitutes the boundary between zones I/II and III/IV, whereas the balance of forces acting on crayfish on a sloping barrier (i.e. Eq. (5)) constitutes the boundary between zones II/III and I/IV.
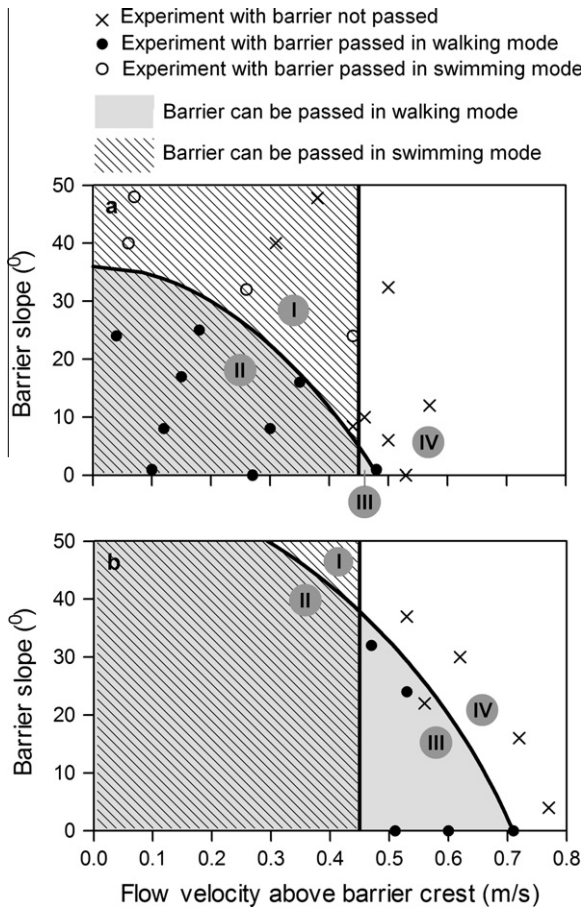
Fig. 4. Barrier efficiency as a function of barrier steepness and flow velocity, determined in flume experiments with (a) smooth barriers and (b) rough barriers: I barrier passable by swimming crayfish, II barrier passable by swimming and walking crayfish, III barrier passable by walking crayfish, IV barrier not passable. Curved class boundaries were estimated using the theoretical relation for barrier efficiency (Eq. (5)) with the following settings: $\rho_c = 1105$ kg/m^3, $V = 0.000052$ m^3, $\mu = 0.5$ (a) or 1.3 (b), $A = 0.0016$ m^2, $C_d = 0.2$ and $F_m = 0.01$ N. Straight class boundaries represent the maximum current velocity against which crayfish could swim during the experiments.

It should be clear that the boundaries representing the critical slope, roughness and flow velocity for crayfish barriers drawn in Fig. 4 only apply to the experimental conditions of this study. Experiments, can never identify the true upper threshold at which crayfish cannot pass barriers, due to the limited duration and limited number of test animals. Crayfish in an actual river have an endless amount of time to attempt barrier passage and an endless amount of time for a particularly skilled crayfish to arrive. Logistic regression allows for a statistical estimation of the uncertainty related to the barrier efficiency. We carried out two logistic regression analyses on the results of the smooth-barrier experiments, the first one with flow velocity (u) and barrier slope (α) as explaining variables, the second one with u^2 and $\sin(\alpha)$–$0.5\cos(\alpha)$ as explaining variables. The mathematical transformation of the explaining variables was deemed necessary because barrier efficiency is not a linear function of α and u according to theory (Section 2) and the flume experiments (Fig. 4). The eight crayfish in each flume experiment cannot be treated as replicates, and each flume experiment therefore was treated as a single case in the regression analyses. Both regression analyses were statistically significant and show flow velocity to be the key variable determining barrier efficiency (Fig. 5). According to the regression analysis, a flow velocity of about 0.65 m/s is enough to ensure that no signal crayfish can pass the barrier. The probability that one particularly skilled
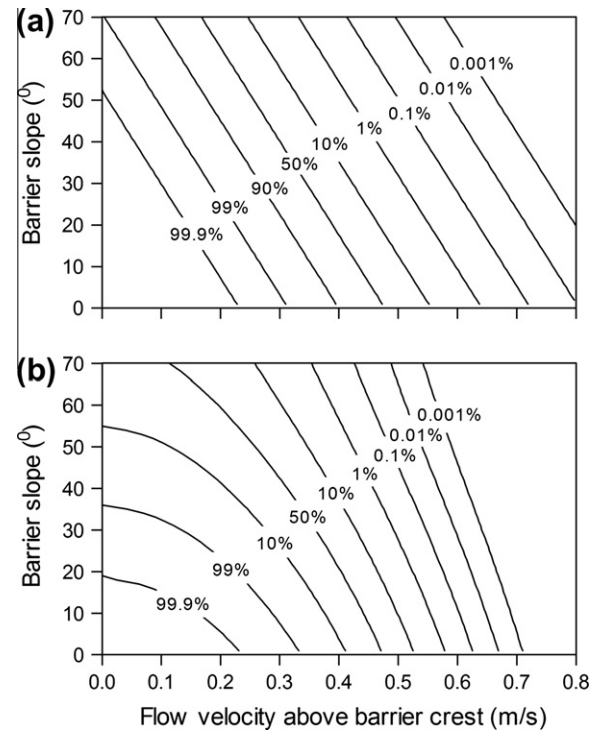

Fig. 5. Probability of crayfish passing a barrier of a given slope at the given flow velocity, based on a logistic regression with: (a) velocity (u) and slope (α) as explaining variables, (b) u^2 and $\sin(\alpha)$–$0.5\cos(\alpha)$ as explaining variables.

crayfish breaches a barrier with a slope of 25° at a flow velocity of 0.65 m/s is only 1:100,000 (Fig. 5b). Note that these results only apply to adult crayfish from the Iter population from which the test animals were drawn. The statistical analyses show that it is necessary to apply a safety margin when developing barriers, by choosing flow velocities and barrier slopes somewhat above the critical conditions for barriers suggested by the experiments.

It was not an explicit goal of this study to determine how crayfish gender, crayfish size and the presence of physical injuries affect barrier efficiency, but during our experiments these factors did not seem to affect the crayfish's abilities to breach the barrier seriously. Since only signal crayfish were investigated in this study, it was neither possible to determine barrier efficiency against other invasive crayfish species. Nevertheless, it is not unlikely that crayfish barriers that are effective against signal crayfish are also effective against other invasive crayfish species presently causing problems, such as Procambarus clarkii (Girard, 1852), Orconectes virilis (Hagen, 1870), Procambarus fallax forma virginalis (Martin et al., 2010) and Orconectes neglectus (Faxon, 1858) (see Jones et al., 2009; Larson and Magoulick, 2009; Filipova et al., 2010 and Aquiloni et al., 2011 for a description of the problems caused by these crayfish).

It is to be noted that although it is possible to stop the invasion of non-indigenous crayfish by barriers, they do not offer a full protection against the crayfish plague, which can be spread by fish, water birds, boats and anglers as well (e.g. Alderman and Polglase, 1988). However, as long as the habitat of European crayfish remains free of rivaling species, a resettlement of the population remains possible, which is not the case if non-indigenous species have invaded into the habitat of indigenous species.

5.2. Swimming behavior

An unexpected outcome of our experiments was the strong effect of the crayfish' swimming behavior on barrier efficiency. Wine

and Krasne (1972), Webb (1979), Holdich and Reeve (1988, op.cit. Ellis, 2005), and Light (2002) observed crayfish to use swimming as a way of locomotion only as a flight reflex in reaction to external stimuli, with swimming events being infrequent and too short of duration for crayfish to pass barriers by swimming. This has been supported by the laboratory experiments of Ellis (2005), whose attempts of motivating crayfish to pass barriers by swimming were unsuccessful.

This strongly contrasts with our experiments, in which crayfish deployed swimming behavior without external stimuli, over relatively long durations (over two seconds) and as a direct strategy to pass the barrier. In all experiments in which swimming was responsible for breaching barriers, an external stimulus, and thus the flight reflex could be excluded: humans were never in the vicinity during the swimming events and the video recordings showed that crayfish were not even in contact with other individuals immediately before the swimming event. Recently also Foster and Keller (2011) observed the crayfish species Orconectes rusticus to use swimming behavior as a direct strategy to pass physical barriers, but in contrast to our study, swimming attempts were very rare and always unsuccessful.

It is possible that the differences in crayfish behavior between previous experiments and our experiments were caused by differences in experimental conditions. Ellis (2005), for instance, conducted her experiments in a still-water pool, whereas we conducted our experiments in a flume with flow velocities of up to 0.77 m/s (Table 1). On the other hand, Ellis' experiments had a much shorter duration than ours (45–60 min versus 48 h), whereas the water temperatures were probably lower during her experiments (cf. Section 3.1). Maybe crayfish only deliberately deploy swimming as a way of locomotion (1) in running water, (2) after attempts to pass a barrier by walking have proven unsuccessful for many hours, or (3) at high temperatures (note that crayfish are poikilothermal animals). Since crayfish tend to feed and move less with declining temperatures (Nyström and Strand, 1996; Bubb et al., 2002), it is possible that they do not to deploy swimming as a way of barrier breaching at low temperatures. Further research on the influence of temperature on barrier-related crayfish behavior is recommended.

The fact that crayfish use swimming behavior to overcome barriers suggests that crayfish will be able to pass all barriers, regardless of barrier slope or barrier roughness, if the flow velocity is below the critical velocity against which crayfish can swim. Our logistic regression analysis suggest that crayfish are unlikely to swim against currents with flow velocities over 0.65 m/s (Fig. 5), but it appeared extremely difficult to investigate the swimming behavior of crayfish systematically.

Motivating crayfish to show their swimming behavior as a flight reflex was not a sinecure. The introduction of an anterior visual stimulus, as described by Wine and Krasne (1972), Webb (1979), Holdich and Reeve (1988) and Holdich (2002), proved to be inadequate. The animals responded neither to an attack with a fishing net, nor to an attack with a stick. A fake fish attached to a stick did not induce a reaction of the crayfish, either. The only way to induce the flight reflex was to touch the crayfish from behind, pressing the abdomen to the pool bottom. After releasing the pressure, the crayfish showed the flight reflex. However, distances covered and velocities attained during swimming events were always much lower than during the flume experiments. In the future, further experiments are needed to obtain accurate data on the swimming performance of crayfish. These experiments should not only focus on the maximum swimming velocity of crayfish, but also on the distance that crayfish can cover swimming. Webb (1979), for instance, demonstrated that although northern crayfish (O. virilis) attain velocities of up to 0.8 m/s, they only cover a distance of 2 cm at this velocity

5.3. Fish passability

Utzinger et al. (1998) reported that a vertical barrier of 18–20 cm in height stopped the upstream movement of European Bullheads (Cottus gobio; Linnaeus, 1758), which matches Ellis' (2005) findings that sculpins only cross a vertical barrier when chased with a net, but never unsolicited. Because the barrier design investigated in our study does not contain any vertical elements, its adverse effects on the migration of benthic fish will be limited or even absent, especially if the barrier is kept as low and gently inclined as possible. According to our experiments, even slopes as small as 25° can be sufficient to hold back crayfish (Section 5.1, Fig. 4). This is a serious advantage of the new barrier over existing barriers. Whether or not benthic fish will be able to cope with the high flow velocities that are needed to halt swimming crayfish is unknown and must be subject to further research. Pelagic fish however will easily be able to cross a barrier even under high flow conditions, since they are better swimmers than crayfish. Brown trouts and Atlantic salmon, for example, are able to reach a swimming speed of at least 4.3 m/s (Parker, 2000; Colavecchia et al., 1998).

5.4. Barrier construction

Barriers must be connected to the bed and sides of the channel in a way that will allow them to resist floods. For bed-rock channels, a steel connection may prove useful, whereas for alluvial channels heavy concrete structures are needed to keep the barrier in place. Furthermore, as crayfish are masters of escape, it is essential to provide a tight connection between the barrier and the side walls of the installation site, with absolutely no fissures, surface wrinkling or similar possible footing. During some test runs we carried out before the experiments reported in Table 1, a small fissure (less than 0.5 mm wide) existed between the barrier and the banks. Analysis of the video footage showed that crayfish were able to breach almost all barriers regardless of their steepness by using this small fissure as a foothold. Ellis (2005) reported similar difficulties in her pool experiments, where crayfish were able to breach a vertical 12 in. aluminum barrier by using the seams at the edges of the barrier, where it had been attached to the pool walls.

In natural conditions, a barrier plate will roughen over time by corrosion, algae and other types of biofilms, thereby reducing barrier efficiency. Our experiments in which the barrier surface was covered with emery paper showed that a slightly rough surface can already lead to inefficiency of the barrier (Section 4, Fig. 4). This problem calls for a barrier material that is as resistant to corrosion and fouling as possible. Ellis (1999) suggested smooth concrete, clean metal, plastic and glass surfaces as appropriate to halt walking crayfish. In her 2005 study, more materials were evaluated. Here, stainless steel and polyurethane used as a coat on a concrete wall were considered the best solutions, the latter showing not quite as corrosion-resistant as steel (Ellis, 2005). Even with a corrosion resistant material, regular maintenance and cleaning of crayfish barriers is necessary. Algae and biofilms may otherwise roughen the barrier with time.

5.5. Optimization of barrier design

The analyses in the previous sections have clearly shown that the proposed barrier design is only effective in areas with a relatively high flow velocity of above 0.65 m/s. If such locations are not available, a modification of the barrier may help. A possibility would be the horizontal extension of the barrier in form of an even terrace (Fig. 1c) in order to increase the distance that crayfish have to swim to breach the barrier. Even if the current velocity is low enough for crayfish to swim against it to the barrier crest, the

barrier then will prove effective, because crayfish will become tired before they reach the other end of the barrier and fall down to the barrier terrace from which they will be washed back. The creation of a terrace is also likely to lead to the minimization of eddies, such as were examined in our study, creating converse currents that were even pushing crayfish towards the barrier crest. Another recommendation is to round the side angles between the barrier and the banks, which seemed to be a preferred place for crayfish to put the tips of their legs when walking up the barrier, especially during the experiments. The rounding will minimize contact surface on that behalf. The proposed improvements to the design will have to be tested under experimental conditions to evaluate their effectiveness.

5.6. Potential barrier locations

The fact that crayfish barriers are only effective at locations characterized by sufficiently high flow velocities reduces the number of potential barrier locations. Artificial preexisting structures such as dams with fish ladders, however, provide promising barrier locations. The flow velocity in a fish ladder is already controlled and if the flow velocity in the ladder would be too low, it might prove easy to increase it by reducing the cross-section width. Additionally, most fish ladders are provided with structures to reduce sedimentation, which is advantageous because sedimentation of mud, sand, gravel, wood debris and detritus can affect barrier roughness and barrier slope, thereby increasing the probability of crayfish breaching the barrier by walking. Maintenance of crayfish barriers in fish ladders is also relatively easy, because access is guaranteed and fish ladders themselves are also maintained regularly. Other advantages of fish ladders are their concrete bed and steep walls, which facilitate the connection of the barrier to the river bed and prevent crayfish from escaping by the banks. Overland dispersal is a common phenomenon in crayfish (Cooper and Braswell, 1995; Claussen et al., 2000; Cruz and Rebelo, 2007), which will render any barrier useless that leaves an open access towards the bank – something that would be hard to prevent in places with natural banks. In addition to dams with fish ladders, other artificial structures might come into consideration as possible barrier locations as well. Even abandoned structures such as old dams might qualify for this purpose.

6. Conclusions

This study showed that native crayfish can be protected by physical barriers that do not hinder fish migration, but prohibit the upstream migration of non-native crayfish.

The efficiency of the proposed barrier depends on barrier roughness, barrier slope and flow velocity directly above the barrier crest. In order to be effective, crayfish barriers must be steeper in situations with low flow velocities than in situations with high flow velocities. A roughened barrier surface provides a better grip for crayfish and therefore requires a higher slope to be effective. These observations are in agreement with the physics of crayfish locomotion.

In contrast to general acceptance and our presumptions, signal crayfish use swimming behavior to breach barriers that are not breachable for them by walking. If the flow velocity stays below a certain critical value, crayfish are able to pass all barriers regardless of barrier slope or barrier roughness. Above the critical velocity, very lightly inclined, smooth barrier plates are sufficient to stop crayfish migration. The adverse effects of low-slope crayfish barriers on the migration of benthic fish are limited, which constitutes a serious advantage over pre-existing barriers. Barrier modifications, specifically the construction of an even terrace at the barrier crest,

may lead to effective solutions with a relatively flat barrier at even lower flow velocities.

Because crayfish are masters of escape, it is essential to provide a tight connection between the barrier and the side walls of the installation site, with absolutely no fissures, surface wrinkling or similar possible footing. Furthermore, crayfish barriers must be connected to the channel bed and sides of the channel firmly in a way that allows them to resist floods. Barrier materials must be resistant to corrosion and fouling, whereas the barrier itself must be regularly cleaned and maintained. Promising barrier locations are pre-existing structures such as fish ladders alongside weirs, where flow velocities are controlled, sedimentation risks are low, maintenance is done regularly, the bed profile is suitable to connect barriers to and crayfish escape on the banks is impossible.

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