Global Ecology and Conservation 25 (2021) e01421

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Barriers against invasive crayfish species in natural waters and fish passes - Practical experience

Raphael Krieg, Alex King, Armin Zenker*

University of Applied Sciences and Arts Northwestern Switzerland, School of Life Sciences, Institute for Ecopreneurship, Hofackerstrasse 30, 4132, Muttenz, Switzerland

ARTICLE INFO

Article history:
Received 13 November 2020
Received in revised form 16 December 2020
Accepted 17 December 2020

Keywords:
Containment
Signal crayfish
Dam
Spread
Migration
Obstacles

ABSTRACT

The spread of non-indigenous crayfish species poses a threat to local populations of crayfish as well as to other fauna and flora across Europe and around the world. Several methods have been used in attempt to reduce their numbers and stop their further spread. Crayfish barriers are the best way to stop the non-anthropogenic spread of established invasive crayfish populations. Up to now there are very few published papers regarding crayfish barrier design and practical experience in construction. For the last seven years, we have optimised construction and functionality of crayfish barriers, tested various building materials and planned construction of many barriers across Switzerland. In this article, we highlight our experience, share the acquired knowledge and present the newest findings regarding considerations, which must be made when planning a barrier to stop the upstream movement of non-indigenous crayfish species. From our experience we conclude that crayfish barriers work in preventing the movement of invasive species if certain factors are taken into account. Barrier design and construction must be specific for each project, because the size of the watercourse, flow velocity, bank conditions, existing constructions and accessibility, all change the way a barrier should be set-up.

1. Introduction

Aquatic habitats are continuously being overtaken by invasive non-indigenous crayfish species (NICS). In Europe, the number of species of NICS now outnumber that of indigenous crayfish species (ICS) (Kouba et al., 2014). It is predicted that if nothing is done to stop the spread of NICS, they may dominate European waterways completely within the next two decades (Holdich et al., 2009). During the mid-twentieth century, invasive American signal (*Pacifastacus leniusculus* Dana, 1852), red swamp (*Procambarus clarkii* Girard, 1852), spiny-cheek (*Faxonius limosus* Rafinesque, 1817) and marbled (*Procambarus virginalis* Lyko, 2017) crayfish were introduced into Europe (Holdich et al., 2009; Faulkes 2010; Souty-Grosset et al., 2016) for culinary reasons (Holdich et al., 1995; Magalhães et al., 2005; Rosecchi, 1997), as pets (Chucholl, 2013a; Faulkes, 2018; Patoka et al., 2014) or to replace noble crayfish (*Astacus astacus* Linnaeus, 1758) populations which had been lost to the crayfish plague (Bohman et al., 2011; Westman, 1973).

NICS often have negative impacts on existing ecosystems (Nyström et al., 1996; Twardochleb et al., 2013; Vaeßen and Hollert, 2015). They can substantially reduce the abundance of water plants which consequently results in more turbid

* Corresponding author.
E-mail addresses: raphael.krieg@fhnw.ch (R. Krieg), gnikxela@hotmail.co.uk (A. King), armin.zenker@fhnw.ch (A. Zenker).

https://doi.org/10.1016/j.gecco.2020.e01421

waters (Rodríguez et al., 2003) and a reduction in density and diversity of macroinvertebrates (Moorhouse et al., 2014; Phillips et al., 2009; Ruokonen et al., 2014). A study in Germany revealed that invasive red swamp crayfish can even support other invasive species namely, the western waterweed *(Elodea nuttallii)*, by reducing indigenous water plants, including species of *Chara* and spiked water-milfoil *(Myriophyllum spicatum)* (Chucholl, 2013b). NICS can also have a negative impact on fish and other fauna through competition for food and resources (Wilson et al., 2004). NICS have an ecological advantage compared with ICS and replace them in their natural habitat. Their species specific faster growth (Hossain et al., 2019) and higher reproduction rate (Guan and Wiles, 1999) means that they put pressure on ICS by competing for food and shelter (Söderbäck, 1994). Therefore, co-existence of ICS and NICS is not possible for a long-term period (Westman et al., 2002; Westman and Savolainen, 2001). This fact emphasises the importance of preventing the spread of invasive crayfish.

North American crayfish species pose a major threat to European ICS due to their ability to carry and spread the crayfish plague (*Aphanomyces astaci* Schirkora, 1906); this can lead to collapse of local crayfish populations (Martín-Torrijos et al., 2019). The oomycete was introduced to Europe at the end of the nineteenth century (Alderman, 1996). North American crayfish species are mostly resistant to the disease. However, occasionally they lose their resistance against the plague and will also die; this usually happens when individuals have another disease or if there is a high population density (Rantamäki et al., 1992; Vey et al., 1983). *A. astaci* is one of the hundred worst invasive species in the world (Lowe et al., 2000) and is still responsible for mass mortalities of European crayfish (e. g. Kozubíková et al., 2008; Collas et al., 2016; Mojžišová et al., 2020). In contrast to earlier assumptions, some European crayfish can survive infection by certain strains of crayfish plague; afterwards they become carriers of the disease. (Kokko et al., 2012; Kušar et al., 2013; Viljamaa-Dirks et al., 2011). There are reports of plague-free populations of spiny-cheek crayfish (Schrimpf et al., 2013) and signal crayfish (Robinson et al., 2018). Therefore, in the long run, crayfish plague seems to be less dangerous to native species than the introduced carriers of the plague themselves. After no invasive crayfish can be detected, the site can be restocked with ICS or if there are some remaining which have survived the crayfish plague outbreak they can rebuild a new population.

Immediate action to stop the spread of NICS is important as they can spread extremely quickly through a waterbody; some were shown to spread several km per year (Weinländer and Füreder, 2010). Artificial and natural barriers, weirs, dams and waterfalls can hinder or slow the upstream movement of NICS (Manenti et al., 2014; Rahel, 2007; Rosewarne et al., 2013). In Europe, ICS occur mainly in tributaries, which are often isolated by artificial or natural barriers (Puky et al., 2005; M. Scalici and Gibertini, 2005; Gil-Sánchez and Alba-Tercedor 2006; Scalici et al., 2009; Chucholl and Schrimpf 2016). Therefore, the systematic promotion of insurmountable barriers is our best chance to safeguard these threatened species by creating protected ark sites for them.

There are very few scientifically published papers regarding experience in the construction, maintenance and functionality of crayfish barriers. Findings from published papers are often theoretical and not tested under field-conditions. Laboratory tests have been carried out with signal crayfish to test various surface materials, different velocities (Frings et al., 2013), and a range of barrier models to assess if the barrier is possible to overcome (Ellis, 2005). In Spain, a barrier was built with an overhanging lip and wide side walls at either bank to prevent red swamp crayfish from moving upstream (Dana et al., 2011). In South-Germany, United Kingdom and the US barriers have also been built to protect populations of ICS from invasion by signal crayfish but these results have not yet been published. The published papers often show that there was no function monitoring performed; however, it will only be known if the barrier successfully works when invaders reach it.

There are still open questions with regards to the long-term construction and maintenance of barriers and the ability for them to allow weak swimming fish to pass. From 2013 to 2016, we carried out practical field-tests and planned barrier constructions across Switzerland. This paper summarises the experience we have gained in Switzerland regarding crayfish barrier construction, including various ways to construct barriers with appropriate functional monitoring and how to adapt barrier design for artificial and natural waters. These findings will help people all around the world to build crayfish barriers to prevent upstream migration of invasive crayfish species.

2. Material & methods

2.1. Artificial flow regime sites

In industrial channels and fish ladders, there is a constant velocity of water which ensures functionality. In artificial setups, a water velocity of $\geq$0.65 m/s combined with smooth surfaces are sufficient to act as a barrier against crayfish, even if they attempt to overcome it by jack-knifing (Frings et al., 2013; Herberholz et al., 2019). It is possible to build barriers passable by fish but which prevent crayfish passing with a controlled constant water velocity, this works because most fish species are generally better swimmers than crayfish and can reach higher swimming speeds (Castro-Santos et al., 2013).

2.1.1. Fish-passable barrier in an artificial channel, St. Albanteich

A barrier was constructed under field conditions in a 5 m wide artificial channel, *St. Albanteich*, which is fed with water from a hydroelectric power plant in the River *Birs*. The aim was to build a barrier, which would be passable by fish and to evaluate the effectiveness of the barrier in preventing crayfish from passing. The banks of the channel are vertical concrete walls. A sluice generated a constant water flow and velocity in the channel. Invasive signal crayfish were already present in the River *Birs* as well as in the channel.

The mid-section of the barrier consisted of a concrete block, which was covered by stainless steel with an overhanging lip. A gap of 50 cm at either side created passages for upstream migration of fish. Aluminium plates were placed on the channel bed and on the sidewalls at a length of 40 cm. The plates aimed to prevent individuals grabbing on a rough surface to move upstream against the current. The water velocity in the side fish passages and on the overhanging lip was between 1.4 and 1.6 m/s. Unexpected construction work during the experiment decreased the water level lowering the velocity to 1 m/s.

The barrier was designed so that any crayfish which managed to swim over the overhanging lip would be directed into a lateral catch basket and removed (Fig. 1). The whole construction was built on the stony channel bed. Shortly after installation, the stones under the fish-passages at either side were washed away. Consequently, a metal mesh (mesh-size 1 cm) was incorporated into these gaps to prevent the barrier from being overcome underneath the aluminium plates.

For the function monitoring of the barrier, two-hundred signal crayfish were caught and marked with a single hole in the telson using punch pliers and released downstream of the barrier. Four traps (Bock-Ås Ltd., Finland) baited with dry dog-food or dead fish were placed 5 m upstream and another two 5 m downstream of the barrier. Five additional traps were placed 150 m downstream of two 1 m high dams in order to catch marked crayfish which were migrating downstream. The traps were monitored 45 times throughout June and September. Any caught crayfish which had been marked were released back to the original release location, downstream of the barrier and unmarked crayfish were removed.

In September, an additional 100 signal crayfish were marked with a line across on their carapace using a white lacquer pen. Following the release of the crayfish downstream of the barrier, two night inspections were carried out to search for pen-marked crayfish 250 m up- and downstream of the barrier.

The barrier cost CHF 6′500 to build including machines, workers and materials.

2.1.2. Fish-passable barrier in the hydroelectric power plant, Neue Welt

In a fish ladder, aluminium was used to coat the sidewalls and the bottom of the passage between the two pools of a vertical-slot fish-pass to create smooth surface which aimed to prevent upstream movement of signal crayfish (Fig. 2). The velocity in barrier passage was slowed from 1.7 to 0.6–0.7 m/s by damming the downstream pool of the fish-pass using a formwork panel.

Forty signal crayfish were marked with holes in their telson using punch pliers and placed in the pool directly downstream of the barrier. Four baited traps were placed in the pools up- and downstream of the fish-pass to observe the movement of marked crayfish. Caught, marked crayfish were released again in the pool downstream of the barrier. Caught, unmarked signal crayfish were removed from the river. Crayfish were in the experimental set-up for 57 days and traps were emptied a total of 33 times. After removing the formwork panel at the end of the crayfish experiment, the fish trap at the upstream exit of the fish-pass was monitored for two weeks to see if the barrier hindered fish migration with a water velocity of 1.7 m/s.

The barrier cost CHF 300 to build including machines, workers and materials.

2.1.3. Fish-passable barrier in the hydroelectric power plant, Schaffhausen

The barrier was built-in the fish ladder of a hydroelectric power plant in the River Rhine at Schaffhausen. No invasive or native species of crayfish occurred in this section of the River Rhine.

To ensure a constant flow rate of water, the barrier was built at the upstream exit of the fish-pass. A 50 cm long aluminium plate was used to cover the width of the section and another was placed on the sidewalls up to a height of 60 cm. A small passage, 20–30 cm, was created using formwork panels to ensure a constant velocity of $\geq$0.65 m/s (Fig. 3).

Eighteen male and two female noble crayfish with carapace-lengths 6.1–8.1 cm where placed downstream of the barrier. A metal mesh frame was installed to hinder crayfish migration down the fish-passes. In order to try and keep crayfish downstream of the barrier, tubes with a diameter of 6 cm were placed downstream of the barrier to create artificial refuges.

A GoProHero3+ (California, USA) was installed to record when crayfish tried to overcome the barrier. The camera took pictures every 2 s over fourteen nights. An additional 22 h of footage were recorded with an underwater camera, to document when fish passed-by. This was necessary because the quality of the photo produced by the GoProHero 3+ was not clear enough to determine the species of fish. A 150 W halogen floodlight was placed above the barrier to improve light conditions for recording.

The barrier cost CHF 2′500 to build including machines, workers and materials.

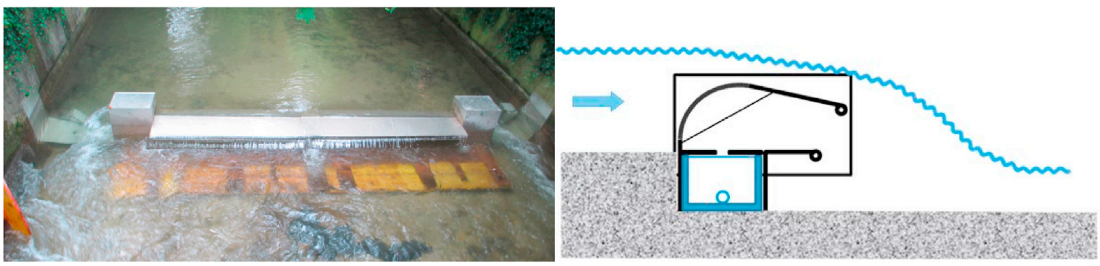

Fig. 1. A fish-passable barrier with side fish passages (left image). Overhanging lip with catch basket behind it (right image).

Fig. 2. Vertical-slot fish-pass with aluminium coating on the sections between the two pools.

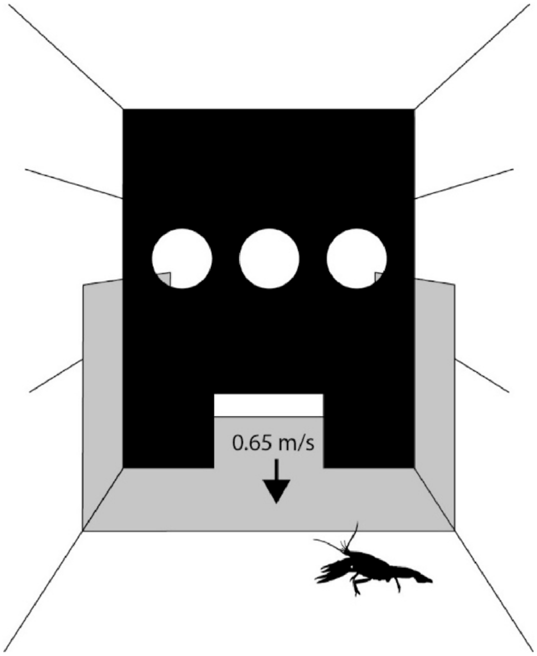

Fig. 3. The aluminium plate (grey) and formwork panel (black) in the upper entrance of the fish-pass.

2.1.4. Fish-passable barrier in the hydroelectric power plant, Wettingen

The barrier at *Wettingen* was installed in the connecting sections between two vertical-slot fish-passes of a hydroelectric power plant; this created a more laminar flow at the barrier here compared to at *Neue Welt* (see chapter 2.1.2). The necessary current of ≥0.65 m/s was achieved by narrowing this section with a u-shaped glass-fibre reinforced plastic (GRP) frame over a stretch of 20 cm (Fig. 4). The GRP-barrier was attached to two concrete-blocks which were fixed onto the sidewalls. The u-shaped frame created a 10 cm vertical obstacle making it difficult for crayfish to overcome the barrier while still allowing bullheads and other fish to migrate upstream. Only vertical obstacles over 15 cm in height are not passable by bullheads (Weibel and Peter 2013).

A PIT-Tag antenna system was installed to record up- and downstream migration of crayfish as well as when they rested directly in front of the barrier. Antennas were placed directly in the GRP barrier construction, 4 m upstream and 3 m downstream of the barrier. 68 signal crayfish with carapace lengths of 3.1–6.1 cm were caught from the same river and PIT-Tags were glued onto the upper side of their carapace. Afterwards they were released downstream of the barrier. The experiment lasted for 57 days from the end of June until mid-August. Again, a GoProHero3+ was placed downstream of the barrier and used to record fish which passed it.

The barrier cost CHF 12′000 to build including machines, workers and materials.

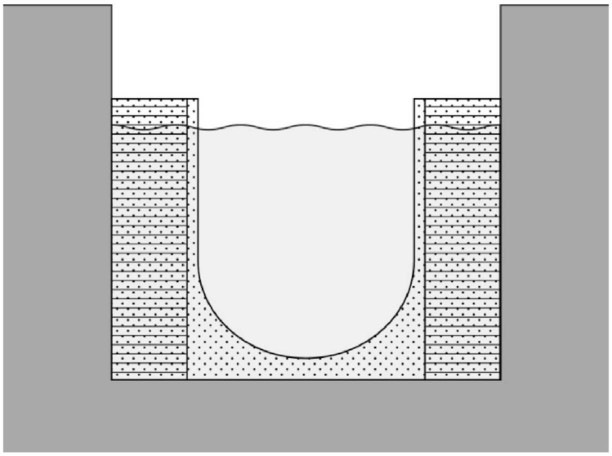

Fig. 4. GRP crayfish barrier (dotted) attached to concrete blocks (horizontal lines) in a fish-pass (dark grey).

2.1.5. Fish-passable barrier in a hydroelectric power plant, Mühleberg (planned but not completed)

Mühleberg is a hydroelectric power plant that dams the River *Aare* over a stretch of 12 km and creates *Lake Wohlen*. The *Aare* flows into *Lake Biel* where signal crayfish can be found. Upstream of the power plant, several tributaries to the *Aare* are inhabited by native noble and white-clawed crayfish. Again, the construction of a fish lift is designed to ensure that fish are still able to freely pass. At the same time, signal crayfish occurring downstream will not be able to move upstream. On the far left and right side of the power plant, two vertical slot fish-pass are planned which will lead to the fish lift. During flood events, these vertical-slot fish-passes will be entirely flooded creating low current around the barrier. It is planned that five crayfish barriers are constructed at *Mühleberg* but these are not yet built. All barriers include a narrow section with smooth surfaces to generate flow velocities of over $\geq$0.65 m/s and to prevent crayfish from crossing the barrier by climbing the wall.

It is planned that the first two crayfish barriers are built by the entrances into the fish passes on either bank. The barriers will consist of stainless-steel frames placed 40 cm above the river bed.

Additional two barriers are planned on both sides of the horizontal adjoining channel, which will connect the two vertical-slot fish-passes and lead to the fish lift. The passageway of these barriers is 30 cm above the ground and has a rounded 20 cm overhang tilted downstream. The fifth construction is planned before the fish lift entrance. The proposed modular barrier means that the parts can be easily removed and replaced.

2.2. Natural flow regime sites

In natural waterways, there are large differences in the amount of water flowing throughout the year. Therefore, the construction of crayfish barriers in natural waters poses several difficulties. Unlike in artificial flow regime sites, in natural waters it is not possible to stop the migration of NICS with a constantly high water velocity (chapter 2.1). Furthermore, boulders and driftwood can affect barrier functionality. It is also more difficult to prevent the barrier from being overcome overland on a natural bank compared to in an artificial setting.

There has been no research carried out looking at the behaviour of signal crayfish when they reach a barrier. It is well known that crayfish can walk overland (Herrmann et al., 2018), however, less is known about how often this happens and if there is a way to construct a barrier to prevent crayfish from overcoming a barrier overland. The studies below show our experience in constructing crayfish barriers and the difficulties we encountered when building them.

2.2.1. Barrier in a small forest brook, Winterthur

The barrier was constructed in a 1.5 m wide, steep banked forest brook, which was inhabited by signal crayfish. During the first of two trials, the barrier design included a 30 cm high vertical iron plate which was extended on both banks for an additional metre. 1.5 m long sheets of wood were placed downstream of the barrier parallel with each bank to guide crayfish back into the water (later referred to as “land barrier”) (Fig. 5). Plastic buckets were buried in the ground at the downstream end of both land barriers to catch crayfish walking overland. A small dam was constructed 3.5 m downstream of the barrier to create a slow flowing 30 cm pool of water to prevent marked crayfish moving directly downstream. Artificial refuges were placed in the pool to minimize the urge to migrate downstream. Wooden stakes (later referred to as “driftwood retention structure”) were put into the waterbed 5 m upstream of the barrier to stop branches being caught in the barrier, which would aid crayfish movement over the barrier.

During the first trial, 50 signal crayfish of both sexes (1:1 ratio) with carapace lengths 2.8–6 cm were numbered with white paint and released downstream of the barrier during the night. Over 37 days, 18 night searches were carried out, 50 m upstream and 250 m downstream of the barrier, in order to search for crayfish in the brook, in buckets and on the banks.

Fig. 5. Barrier with driftwood retention structure upstream and small dam further downstream.

Crayfish which had fallen into a bucket were released again downstream directly in front of the barrier. After 21 days, the land barrier was lengthened 4.5 m up the bank, using plastic foil which is used for frog fences, to determine how far signal crayfish migrate on land (Fig. 6). Again, a bucket was buried on each bank to catch crayfish moving along the extended land barrier.

In order to further prevent overland movement of crayfish the barrier was modified by installing a 40 cm high, 1.5 m long aluminium plate in the waterbody directly downstream of the barrier on either bank (Fig. 7). A GoProHero3+ camera was installed which took a picture every 5 s to document the behaviour of crayfish downstream of the barrier. Glow sticks of different colours and sizes were glued in various combinations on the carapace of 60 signal crayfish for identification. Marked crayfish were released at night and behaviours including land movement and passing of barrier were observed for 3 h. After 1.5 h, crayfish which were found 30 m downstream of the barrier were collected and released again in the pool directly in front of the barrier.

The barrier cost CHF 2′000 to build including machines, workers and materials.

2.2.2. Crayfish barrier in a fish-pass, Gretzenbach (planned but not completed)

This project aimed to clarify whether a crayfish barrier can be installed into a fish-pass to prevent the upstream movement of signal crayfish from the main river system into a small tributary inhabited by native white-clawed crayfish. The fish-pass had an adjoining walkway to allow overland movement of small mammals, amphibians and reptiles; this overland movement had to be guaranteed even after the installation of the barrier. During floods, the adjoining walkway will act as a bypass channel for the water.

A stainless-steel barrier with a free fall of 30 cm is planned to stop the movement of crayfish upstream while still allowing brown trout (*Salmo trutta fario* Linnaeus, 1758) to jump over the barrier. Additionally, stainless steel plates on both banks

Fig. 6. Barrier including an extended land barrier on both banks.

Fig. 7. Modified barrier with aluminium plates on both banks.

aimed to prevent crayfish from passing the barrier overland. Construction of a pool downstream of the barrier is planned to help fish namely, brown trout, to jump up the barrier.

2.2.3. Crayfish barrier, Etzgerbach

The *Etzgerbach* flows into the River Rhine and has an average flow rate of 0.3 m^3/s. The catchment is inhabited by several populations of native, endangered stone crayfish. In the River Rhine there are invasive spiny-cheek and signal crayfish. This barrier provided a great opportunity to evaluate the functionality of the crayfish barrier in protecting a whole catchment area against invasion of NICS as well as indicating its ability to allow trout to pass.

The barrier was installed at a pre-existing vertical dam to reduce costs (Fig. 8). At the site there was a hydrological monitoring station which is frequently visited, this ensured a regular functionality monitoring of the barrier could be easily carried out. The barrier was made of a steal beam which was placed across the width of the stream and created a free fall with a 30 cm overhanging lip. Steel plates were attached on the wall on each bank to prevent crayfish from successfully climbing up them to overcome the barrier.

A PIT-Tag antenna system was used to record the up- and downstream movement of crayfish and brown trout. The pass-over-antennas were placed 9 m upstream and 60 m downstream of the barrier to detect when the barrier was passed as well as any downstream movement. In September, after barrier construction, 112 brown trout and 102 bullheads were placed 80 m downstream of the barrier and 107 crayfish were put in the pool directly downstream the barrier.

NICS did not inhabit the *Etzgerbach*; therefore, to test functionality of the barrier native noble crayfish with carapace lengths of 4.3–7.8 cm were used in the study. No population of noble crayfish inhabited this catchment either so only male individuals were used, to prevent establishment of a genetically foreign population.

Fig. 8. Crayfish barrier with overhanging lip in the *Etzgerbach*.

Throughout the duration of one year, the antennas recorded when crayfish and fish passed over them. The site was visited once a week during the experimental period to download data, check antenna functionality and ensure barrier maintenance.

The barrier cost CHF 10′000 to build including machines, workers and materials.

2.2.4. Crayfish barrier, Lützel

In the past, the River *Lützel* was home to the largest population of white-clawed crayfish in the whole of Switzerland. In 2014, a crayfish plague outbreak led to their mass mortality (Collas et al., 2016). Given that no signal crayfish were detected five years after the outbreak, and the fact that this river is very natural and hardly polluted by agriculture and villages, it has been considered as a restocking site for white-clawed crayfish.

To prevent signal crayfish from migrating from the main river into the *Lützel* a crayfish barrier was constructed. It consisted of an aluminium plate with a 30 cm overhanging lip which was screwed to a steel H-beam to create a free fall. (Fig. 9). The aluminium plate had a slight downstream facing angle to make it easier for trout to jump upstream. The H-beam was set on large blocks of natural stone which acted as a foundation. The barrier was placed directly upstream of the bridge so that the pillars of the bridge could be used as pre-existing barriers to prevent overland movement. On both bridge pillars, aluminium plates were screwed on to prevent crayfish from overcoming the barrier by climbing up rough surfaces.

The barrier cost CHF 30′000 to build including machines, workers and materials.

2.2.5. Crayfish barrier, Pfaffnern

The Pfaffnern has an average flow rate of 0.69 m^3/s and connects to the River Aare, which is inhabited by signal crayfish. A crayfish barrier, which is passable by fish, was built by the local fishery department to prevent the invasive crayfish from moving upstream into the catchment of the Pfaffnern.

In contrast to the previous examples of barrier models in natural waters which were not passable by weak-swimming fish, this barrier was built directly on the river bed and without a free fall so as to allow weak-swimming fish to pass (Fig. 10). The barrier was placed on the upstream section of a long passage. The barrier consisted of a 30 cm high concrete bar which stood on the bottom of the brook. A stainless-steel plate created a 20 cm overhanging lip angled downstream. On each side of the river there was a concrete path which allowed mammals, amphibians and reptiles to walk alongside the water. As this was a possible pathway for crayfish, an additional steel plate was laterally attached to prevent crayfish from climbing onto it and walking around the barrier. The barrier creates a slow-moving pool upstream which leads into the two concrete paths as well as being released at high velocity through a gap at the centre of the barrier. The high velocity at the centre is to stop crayfish but allow fish to pass. A Bluetooth camera in front of the barrier allowed real-time monitoring of the site via smartphone to detect whether the barrier had been made passable by driftwood or stones.

The barrier cost CHF 42′000 to build including machines, workers and materials.

2.2.6. Crayfish barrier, Roulave (planned and construction will be completed soon)

The *Roulave* is inhabited by white-clawed crayfish, which are threatened by signal crayfish spreading from the main river. To prevent future upstream movement of signal crayfish into the *Roulave* the local fishery department has planned to build a crayfish barrier which is also passable by brown trout. A bridge with a 5 m wide passage was selected in which to construct the barrier.

The barrier consisting of a vertical wall with a free fall of 40 cm was planned directly at the upstream end of a bridge. Due to the low flow rate in the river, the barrier was designed with a bend in the middle to gather the water and guarantee a high enough volume to allow fish to move upstream over the barrier. Downstream of the barrier a pool will allow trout space to

Fig. 9. Crayfish barrier in the *Lützel* with aluminium plates attached on to the pillars of the bridge.

Fig. 10. Crayfish barrier in the *Pfaffnern* with a high-flow mid-section which is passable by fish.

gain speed to jump over the barrier. The bridge pillars will again be used as a barrier to prevent overland movement and will be covered with 4 m long and 1 m high stainless-steel plates. The overhanging lip of the barrier will consist of stainless steel screwed to a steel H-beam which will make it easier to replace the overhanging lip if it is damaged. It is planned that the overhang would be around 30 cm long with a downward facing angle of 20°. The barrier will be built on a foundation of three big, square stones.

The cost is budgeted at CHF 20′000 including machines, workers and materials.

2.3. A test of how easily various materials with biofilm growth are overcome by crayfish

The aim of this experiment was to discover whether crayfish use biofilm to overcome smooth surfaces even with flow velocities of ≥0.65 m/s, which are recommended to prevent upstream movement of crayfish in fish-passable barriers. In addition, tests were carried out to determine biofilm growth on various materials. This information could consequently be used for future barrier construction.

Eight different materials were tested: stainless steel, copper, glass fibre reinforced plastic (GRP) in black and white, steel, brass, PVC and aluminium. For two months during summer, plates from the test materials were placed in two settling tanks at a water treatment plant; one which was exposed to the sun and another which was covered preventing any light from entering.

Afterwards an experiment was set up to test the ability of crayfish to pass these plates. A modified experimental aquarium was divided lengthwise into two parts using a PVC plate. Water was pumped from one side of the tank to the other to create a constant velocity of ≥0.65 m/s in the experimental half of the tank (Fig. 11). Crayfish were grouped for testing by sex and by three size classes: 3–6 cm, 6–9 cm and 9–13 cm (group 1 to 3, respectively). No bait was used during the experiment to tempt individuals to cross the material. For each trial, five signal crayfish from the same size-ranked group were placed in the starting area which was covered with sand paper. This plate was used as a control to indicate how well crayfish would pass over a rough surface. The various plates with biofilm growth were placed in the experiment tank for 1 min and the behaviour of the crayfish was recorded to indicate whether individuals were successful in standing for at least 5 s in the current on the experimental material plate or whether it could be overcome.

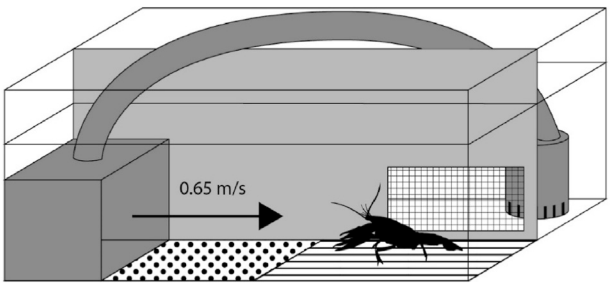

Fig. 11. Experiment set-up which tests how easily various materials with biofilm growth are overcome by crayfish. Experiment material (dotted); start area with sand paper (lines).

3. Results

3.1. Migration of crayfish

With the exception of the barriers at *St. Albanteich* and *Winterthur,* there was no recorded upstream movement of crayfish. At *St. Albanteich* no crayfish were caught in the lateral catch baskets of the barrier. Only one hole-punched female signal crayfish with a carapace-length of 6 cm was trapped upstream of the barrier at *St. Albanteich*. This happened one day after water levels were dropped for construction work, which caused a decrease in water velocity. Here, no crayfish were caught in the traps which were 150 m downstream of the barrier. During the two nocturnal searches, the marked crayfish which was found furthest from the original site was 130 m downstream of the barrier after the two large dams. Marked crayfish were seen actively walking against the current.

In the hydroelectric power plant at *Schaffhausen,* noble crayfish were documented attempting to pass the barrier a total of 1015 times. Several attempts were almost successful as crayfish could hold onto the edge of the formwork panel. Crayfish were also observed climbing up at the corners of the barrier. One crayfish tried to pass the barrier nine times in a row. Attempts to move upstream were recorded during the day as well as at night.

In *Winterthur,* 1 h after release of the white-marked crayfish the first individual was observed climbing up the bank downstream of the barrier. A total of 98 crayfish were caught by hand of which 29 were captured on land close to the barrier or in the buckets. The carapace lengths of crayfish caught on land were between 3 and 5.4 cm. Thirteen of the 29 caught crayfish were marked individuals. Distances walked over land varied from 3.6 to 4.5 m before they were captured by hand or in a buried bucket. Overland movement of crayfish was only observed in the area 2 m downstream the barrier. There was no movement of crayfish on land after the barrier had been modified with metal plates on both banks. The barriers on the banks meant that all crayfish were led back downstream when reaching the obstacle.

During the material experiment, all crayfish began to walk against the current immediately after they were placed on the starting area. The sand paper control was quickly overcome by crayfish of both sex and all size classes (Table 1). None of the crayfish were able to pass any of the test materials. One crayfish could stand for 5 s on stainless steel, four individuals on brass and white GRP, five on PVC and nine on aluminium. However, no crayfish were able to stand on plates of copper, black GRP or steel. In 23 of 54 (~42%) of the experimental group runs, crayfish were observed helping each other by climbing over each other or by building a chain (leg up behaviour). Small crayfish were observed holding on to algae filaments to stand in the current. Crayfish from group 1 had fewer problems staying in the current on the tested materials compared to group 2 and 3. All crayfish tried to hold on to edges of the tank. Crayfish pushed their claws to the ground when in the water current in order to avoid being washed-away by the water flow.

3.2. Material of crayfish barrier

Plates placed in the covered settling tank which was not exposed to sunlight had no algae growth. In the sunlight-exposed settling tank the least algae growth was recorded on brass and copper plates. All other materials showed high algae growth with a maximum of around 1 cm. Steel additionally showed strong oxidation, which led to a rougher surface area and lower algae growth because of erosion.

3.3. Fish passability

Fish passable barriers which use a combination of water velocity and a smooth surface were passed by one 16.5 cm long grayling (*Thymallus thymallus* Linnaeus, 1758), western vairone (*Telestes souffia* Risso, 1827), 9.5–13 cm long, brown trout, 11.5–13 cm long *(Neue Welt),* barbell (*Barbus barbus* Linnaeus, 1758), 5–40 cm long *(Schaffhausen and Wettingen)* as well as

Table 1
Total number of crayfish able to stand for 5 s on various algae covered plates. * = *leg up behaviour*.

Material	Total crayfish length						Standings for 5 s in current per material
	3–6 cm (group 1)		6–9 cm (group 2)		9–13 cm (group 3)		
	male	female	male	female	male	female	
Sand paper (control)	5	5	5	5	5	5	30
Stainless steel	0	1	0*	0*	0*	0*	1
Copper	0	0	0*	0	0*	0*	0
GRP black	0	0	0	0	0	0	0
GRP white	1*	2*	1*	0	0*	0*	4
Steel	0	0*	0*	0	0	0*	0
Brass	1	1*	1	0	0*	1*	4
PVC	3	2	0	0	0*	0*	5
Aluminium	3	3	1	1*	0*	1*	9
Total per size class without control	17		4		2		

smaller unidentified fish with body lengths around 7 cm *(Wettingen)*. The barrier with an overhanging lip and free fall of 30 cm at *Etzgerbach* was passed by 79 of the 112 marked brown trout, all with fork lengths ranging from 11.5 to 49 cm.

3.4. External factors influencing barrier function

In several of the experiments, *St-Albanteich*, *Lützel* and *Winterthur*, branches were caught in the barrier and at *Winterthur* debris gathered by the built-in driftwood retention structure. Throughout the study, the barrier in the *Etzgerbach* showed no damage and the pool downstream of the barrier was not filled up with boulders or bed-load. Three years after construction of the barriers at *Winterthur* and in the *Lützel,* a 3 mm layer of biofilm growth as well as lime scale deposits were seen on the side plates. During the experiment at *Schaffhausen*, zebra mussels *(Dreissena polymorpha,* Pallas, 1771) began to colonize the edges of the aluminium plate.

4. Discussion

4.1. Barrier design

A barrier should be constructed directly upstream of existing artificial obstacles such as walls, bridges, dams, channels and culverts. These pre-existing structures lead crayfish back downstream and prevented them from migrating overland as well as reduce costs and increase functionality, this was shown by the barriers constructed in the *Etzgerbach*, *Lützel*, *Pfaffnern*, *Roulave* and *Winterthur.* A barrier should be constructed directly upstream of a bridge or a culvert using pre-existing structures, bridge pillars or walls to lead crayfish back downstream and prevent overland migration. This behaviour of crayfish was observed in the *Winterthur* study. Barriers should be placed on both banks to prevent crayfish from overcoming the obstacle by walking overland. Further, it is recommended to build at least two barriers in a row to reduce the risk of further spread of ICS in order to protect a catchment area. This ensures that crayfish which pass the first barrier can be removed from the intermediate area before overcoming the second.

The barrier built at *St. Albanteich* was only a temporary installation and as such was not as robust or securely attached to the ground as the other permanent barriers; therefore, the substrate under the barrier and the areas by the side fish-passages were washed away. This could explain why one crayfish was able to move upstream of the barrier at *St. Albanteich*. Barrier parts must be fixed firmly to a ground or on a foundation which cannot be washed away. The simplest design is to build the barrier out of concrete directly on the bed of the river. Alternatively, stone blocks and an stainless steel H-beam can be used. Metal mesh can be used to close the gaps on the ground. A modular construction with an overhanging plate screwed onto the foundation or the steel H-beam allows easy replacement of parts when needed. There were no crayfish caught in the lateral catch basket at *St. Albanteich*. The most likely reason for this is that it is difficult for crayfish to overcome an overhang in a waterbody (Ellis, 2005).

At *Neue Welt,* the aluminium barrier between the two pools of the vertical-slot fish-pass was easy to install and the material costs were very low. The barrier here can easily be adapted for construction in other fish ladders because fish ladders are often built with similar designs. When installing a barrier into an existing fish-ladder the ground must be level and any gravel or stones removed before installation to stabilise the floor so that no crayfish are able to pass beneath the barrier. At *Schaffhausen*, mussels attached themselves to the barrier making it easier for crayfish to climb on it. Therefore, the barrier at *Wettingen* was improved by including rounded corners to allow for easy maintenance and to prevent mussels from settling on it.

At *Schaffhausen*, the smooth aluminium plate along with a water velocity of $\geq$0.65 m/s was enough to prevent crayfish from clinging to the ground or walking upstream in the fish passage. Crayfish could hold on to the narrow formwork panel due to its rough edges. Therefore, the barrier passage must be completely covered for a long distance with smooth surfaces to prevent crayfish from clinging onto it and overcoming the barrier (Frings et al., 2013). From our study at *Schaffhausen* and in the biofilm material experiment, it was found that fish-passages should contain smooth surfaced plates at least 50 cm long to stop individual crayfish aiding others over a fish-passage.

Leg up behaviour of crayfish can be used to overcome a barrier suggesting that free-fall barriers are necessary. They also require less maintenance compared to barriers without an overhanging lip or ones which are directly in the waterbody since pools downstream of a free-fall barrier need more time before they are filled with debris sufficient to allow crayfish to pass.

An overhanging lip in combination with smooth surfaces on the walls should be used in barrier design to prevent crayfish from overcoming the barrier. An overhanging lip on the plates at either bank is also always recommended to direct crayfish downstream and prevent their overland movement (*Pfaffnern* and *Winterthur)*.

4.2. Barrier material and biofilm

Small crayfish were able to use biofilm growth as grip to be able to stand in the current. It can therefore be assumed from this that, when a barrier is not cleaned regularly, crayfish may be successful in passing it. Aluminium was heavily oxidised with 1 mm deep corroded spots; this created increased friction and explains the reason why crayfish were able to hold onto aluminium for so long.

It was predicted that the less algae which was on the material the less time a crayfish could stand still in the current. In our experiment, the least algae growth was seen on brass and copper. However, our experiment showed that four crayfish could stay on brass for 5 s, but no crayfish were able to stand on copper. On brass there could be some kind of corrosion creating more grip which is not visible to the naked eye. It is recommended to use materials which inhibit algae growth when building a crayfish barrier. Brass and copper are expensive; therefore, it is possible that they could be stolen; this was experienced in Switzerland and is part of an unpublished crayfish barrier experiment. Building the barrier from stainless steel or GRP is preferable as they are cheaper and easy to use. The barrier at *Wettingen* is made from GRP which is lightweight making it easy to install and allowing corners to be rounded.

In contrast to stainless steel, the steel barrier in the *Etzgerbach* began to rust very quickly, which meant construction parts were rougher consequently making it easier to grip to overcome the barrier. It can be assumed that if the surface of the walls are sufficiently rough, crayfish would also overcome the obstacle by climbing these. This could not be observed in any of these studies.

Anti-fouling coatings on the barrier material could help to reduce cleaning efforts by slowing the build-up of biofilm. Biological non-toxic anti-fouling paints only perform properly if used in high current water flow, this works by slowly wearing-away layer by layer of paint thereby preventing adhesion of biofilm. This means that one must re-apply the anti-fouling coating on a regular basis so its use is not a long-term solution (Chambers et al., 2006). Additionally, they can have a toxic effect on the environment which in turn harms the marine and freshwater species living within it (Amara et al., 2018; Gallo and Tosti, 2014).

Crayfish can use mussels, which have settled at the edges of the smooth surfaces of a barrier to grip onto to overcome a barrier; this behaviour was observed at the barrier in *Schaffhausen*. As the mussels only settled in the corners, rounded corners can prevent biofouling.

Long-term experiments should now be carried out under field conditions to support our results which show that different materials are more suitable than others for constructing crayfish barriers. Long-term maintenance trials are also vital as they can be used to create future barrier design as well as maintenance plans.

4.3. Crayfish behaviour

Our observations in Winterthur show that overland movement of signal crayfish is very common when they reach a vertical obstacle in the waterbody. Terrestrial walking behaviour of signal crayfish was also observed in a laboratory experiment by Thomas et al. (2019). At Winterthur, signal crayfish moved up to 4.5 m away from the waterbody with no other nearby waterway in the direction of movement. Crayfish do not move in the direction of higher humidity when on land (Marques et al., 2015), which leads us to assume that crayfish do not move overland to intentionally bypass an obstacle. Instead motivation to leave the water could be related to finding a new habitat (Thomas et al., 2019). Further studies must be carried out to determine whether or not crayfish bypass an obstacle in a waterbody because of motivation to access a limited resource. Not only marked crayfish were found migrating overland, so this reaction was not due to homing behaviour or stress because of marking or translocation. All crayfish used for the experiment originated downstream of the barrier; therefore, movement over the barrier to return to original location can be excluded.

After the barrier at Winterthur was extended along the banks and directly connected to the water, no further overland movement by crayfish could be observed. As predicted, the extension of the barrier led crayfish downwards into the water and not onto land. For this reason, a barrier should be placed directly on the water line to prevent overland movement and with it stop crayfish from overcoming the obstacle.

In the study at *Wettingen* and during the material experiment, signal crayfish were observed helping each other to pass the smooth material section by leg up behaviour as observed previously by Frings et al. (2013). If a barrier is built where high densities of invasive crayfish are present this behaviour must be taken into account by lengthening the smooth surface parts of a barrier to avoid the leg up behaviour and ultimately preventing crayfish from passing the barrier. Additionally, the number of crayfish in front of the barrier should be kept low by trapping and removing or with the release of predatory fish.

4.4. Fish passability

During our trials, several species of fish were able to pass barriers with smooth surfaces where the velocity was $\geq$0.65 m/s (chapter 3.3). Brown trout can swim up to 25 times their own body length per second (Castro-Santos et al., 2013); therefore, passing of the barrier by this species was predicted. In the *Etzgerbach*, marked brown trout of different sizes were able to pass the barrier. When plunge pools are at least 40 cm deep, brown trout with a body length of $\geq$10 cm are able to overcome vertical drops of 60 cm by jumping (Kondratieff and Myrick, 2006). This could also be confirmed with the barrier at *Etzgerbach*. It indicates that in side waters which are protected from NICS, trout migration is not negatively affected by vertical drop crayfish barriers. Other fish species such as eels *(Anguilla anguilla* Linnaeus, 1758) (Knights and White, 1998) or bullheads (Utzinger et al., 1998) cannot jump over free-falls and will be stopped by the barrier.

Adult bullheads are able to swim against velocities of up to 3 m/s for a short time in vertical-slot fish-passes (Bousmar et al., 2018); therefore, they should be able to bypass grounded crayfish barriers where the water velocity is $\geq$ 0.65 m/s. At the study in the *Etzgerbach*, we marked bullheads of different sizes to observe their behaviour in front of a barrier. We did not observe any bullhead passing the barrier. We assume that the main reason for this was the height of the obstacle and not the fact that the velocity was too high. It is known that bullheads use rough river beds as friction to help bypass high flow sections of rivers (Weibel and Peter, 2013); however, it is uncertain whether bullheads are able to overcome barriers with longer sections of smooth surfaces.

It is advised that barriers are not constructed with river bed connection in natural waters so that weak swimming fish are still able to pass. During summer, in periods of increasingly extreme drought, the velocity in the passage can decrease to under 0.65 m/s and allow signal crayfish to move upstream by jack-knifing. We recommend fish-passable barriers are not built in natural waters with fluctuating flow because changes in water volume can make the barrier passable.

4.5. Maintenance

Biofilm growth was observed on several of the barriers and this can help crayfish to overcome it within the waterbody as well as over the sidewalls. Biofilm should be removed when any appears.

Crayfish are skilled climbers and can escape out of poorly covered aquaria by climbing up aeration tubes (Sienra et al., 2003; Dickey and Mccarthy, 2007). Therefore, trapped branches at *St. Albanteich* and *Winterthur* could have been the reason why crayfish were able to overcome these barriers. This issue is less relevant to barriers in fish ladders and in places outside of forests. If a crayfish barrier is built at a remote place extra maintenance costs should also be considered. The installation of a wood retention mechanism upstream of the barrier can reduce the probability of drift wood making the barrier passable by crayfish. Nevertheless, crayfish barriers should be checked regularly, especially after heavy rain events and any debris which is blocking the barrier should be removed as soon as possible so the barrier can continue to function. Frequency of maintenance visits depends on location and season; a camera can be used to monitor when maintenance actions are necessary.

4.6. Function monitoring

Function monitoring is an important means of confirming that a crayfish barrier works in preventing the upstream migration of crayfish. Every crayfish barrier is unique and should be specific for the environment where it is constructed. A function monitoring is recommended to prove barrier functionality. Indigenous noble crayfish are used for this as they are non-invasive and it can be assumed that they also are not carriers of the crayfish plague. In contrast to stone crayfish or white-clawed crayfish which are also non-invasive species, noble crayfish show similar behavioural traits to signal crayfish. A function monitoring reveals if there are any weak points in the construction design and indicates necessary adjustments which should be made before NICS have the chance to overcome the barrier. Migration and behaviour of crayfish changes with seasons (Stucki, 2002) which means that a functional monitoring should last for a minimum of one year to be able to fully gauge if the crayfish barrier is successful.

Based on our practical experience, pen markings, the use of a camera or a PIT-tag antenna system are the best ways to carry out a function monitoring, rather than using baited traps or marking crayfish with a hole in the telson. When observing up- and downstream movement of crayfish at *St. Albanteich*, more marked animals were caught with less effort using the pen-mark method compared to those caught in baited traps. This is because they can easily move in and out of standard traps (Harlioğlu, 1999; Mangan et al., 2009; Ulikowski et al., 2017). Emptying the traps several times during the night can increase catch-possibility (Harlioğlu, 1999) and more reliably confirm the number of crayfish moving upstream. Another constraint of using traps is that it is not possible to use them in waterways with low water depths; this was the case for the experiment at *Winterthur* where crayfish were caught by hand. In some instances, infection was caused when marking the telson of a crayfish with a hole; this led to marked individuals being undistinguishable from unmarked individuals with telson injuries. Further, it is known that after several molts the hole-markings will be less remarkable. This happens faster in young crayfish due to their increased frequency of molting (Guan, 1997). For this reason, it is not recommended to use this marking technique in a long-term study.

Noble crayfish are similar in size to signal crayfish and have shown a similar tendency to move upstream. Noble crayfish mostly migrate upstream in rivers (Daněk et al., 2018); this could explain the behaviour seen at the barrier in *Schaffhausen*. For a function monitoring it is strongly recommended to use a non-invasive species if an invasive species is not already present locally.

At *Wettingen,* the PIT-tags which were attached to the outer carapace of crayfish worked well in tracking their movement but should only be used for short-term experiments as they will be lost in subsequent moults. It is recommended to use internal PIT-tags for future long-term observational studies. Internal PIT-tagging of bullheads and other fish should be carried out to gather more accurate results of fish movement in various barrier designs.

Glow sticks glued to the carapace of crayfish worked well in recording their activity in shallow water, during the night and over a short time period. Behaviour of crayfish was not affected by glow sticks; this was indicated by unmarked crayfish acting in a similar manner in previous experiments.

4.7. Crayfish barriers without a function monitoring

Some barriers presented in this paper are future designs and construction has not yet been finished *(Mühleberg, Roulave)* or building planning has not yet been agreed *(Gretzenbach)*. They serve as examples and show the repertoire of possibilities in which crayfish barriers can be implemented in different situations. There were several reasons why building a barrier and performing a function monitoring were not always possible namely, controversial ideas from cantonal authorities or local people or due to funding limitations.

4.8. Arguments for the installation of crayfish barriers

Many authorities try to eliminate barriers in water systems to guarantee that migration is possible for all species of fish (Acreman and Ferguson, 2010; Florea, 2017); this is a controversial topic (Tummers and Lucas, 2019). Weighing up of interests to decide whether it is beneficial to build a crayfish barrier depends on the conservation status of the affected species as well as on the effect of invasive crayfish on the whole ecosystem. At *Gretzenbach*, it was not possible to construct a barrier passable by weak swimming fish without stopping migration of land animals over the walkway. For this reason, the fish pass was built without a crayfish barrier. In this case, the importance of fish being able to pass the barrier was deemed more important than the protection of native white-claw crayfish. In America, barriers are already being used to stop the spread of invasive sea lamprey (*Petromyzon marinus* Linnaeus, 1758) (Zielinski et al., 2019) and European minnow (*Phoxinus phoxinus* Linnaeus, 1758) (Holthe et al., 2005), to the detriment of migrating fish.

In Europe, the passability of barriers by bullheads has been perceived as important; the installation of crayfish barriers is often prevented if migration of bullheads is not guaranteed. According to the IUCN Red List of Threatened Species, the conservation status of bullheads is least concern (July 2020) which is lower than that of all European ICS (which range from vulnerable to endangered). With this considered ICS should have higher priority in terms of conservation action planning. Bullheads are widely distributed in many river systems across Europe, and should not be treated as a priority when weighing up the interests against endangered ICS. Additionally, it is known that bullheads do not migrate long distances (Downhower et al., 1990; Knaepkens et al., 2005). The maximum observed distance travelled by bullheads during their spawning season was 260 m (Knaepkens et al., 2004), this can be taken into consideration so that barriers will not obstruct their normal migratory distances. Also, even natural barriers such as waterfalls, just like artificial barriers, can hinder upstream migration of bullheads (Junker et al., 2012). Further, bullheads are significantly negatively affected by the presence of signal crayfish; therefore, they will also benefit from barriers (Bubb et al., 2009; Peay et al., 2009). In Switzerland, the common nose (*Chondrostoma nasus* Linnaeus, 1758) and brook lamprey (*Lampetra planeri* Bloch, 1784) are critically endangered and endangered, respectively; therefore, a compromise or modification to the design of a crayfish barrier in rivers inhabited by these species should be considered. However, it should also be noted that NICS can also have negative effects on endangered fish species and their habitats (M. Scalici and Gibertini, 2005), meaning they could also benefit more from the construction of crayfish barriers. This indicates the need for each specific site to be considered individually when planning the construction of a crayfish barrier.

5. Conclusion

This paper provides an overview of how crayfish barriers in natural and artificial lotic waters can stop the spread of invasive crayfish. Sometimes existing obstacles can be modified slightly to create a crayfish barrier. Existing structures can reduce costs and improve functionality. Overland movement around a barrier by crayfish must also always be considered. Unlike the use of biocide, crayfish barriers can be installed anywhere without negative effects on other invertebrates. However, migration is made more difficult for fish that are weak swimmers. This indicates that a case-by-case assessment is needed to determine whether a vulnerable crayfish population should be protected from invasive crayfish replacement or whether the main focus should be on the continuity of the waterway for weak-swimming migratory fish. Due to the individuality of crayfish barrier design, function monitoring should always be carried out and, if necessary, appropriate adjustments should be made. Our findings from building crayfish barriers compliment previous theoretical experiments and will aid future barrier construction worldwide, which in turn will help to protect native crayfish, their habitat and other species living it.

Funding

This study was funded by the Swiss Federal Office for the Environment (FOEN).

Declaration of competing interest

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

Acknowledgements

The authors would like to thank Peter Jean-Richard for carrying out the crayfish experiment at *Neue Welt*; Daniel Zopfi (Fisheries inspector of Basle-Countryside) for execution of the function monitoring at *Neue Welt*; Bernhard von Felten and his team (SH Power, Schaffhausen) and Daniel Probst and his team (EWZ, Kraftwerk Wettingen) for their technical support and for giving us the permission to install the barriers in the fish-passes of the hydroelectric plants; George Hasler and Marco Testa (University of applied sciences in Muttenz) for technical support in barrier construction, Hans-Peter Jermann (Fisheries inspector of Basle city) for providing signal crayfish and Patrick Wasem (Fisheries inspector of Schaffhausen) for providing noble crayfish for use in function monitorings.

This project was funded by the Federal Office for the Environment (FOEN); naturemade star funds KW Ruppoldingen of Alpiq Hydro Aare AG (canton Solothurn), naturemade star funds of ewz (city of Zurich), Industrielle Werke Basel - IWB, cantons of Aargau, Basle-Countryside, Basle city, Geneva, Jura, Schaffhausen, St. Gallen, Tessin, Thurgau, Vaud and Zurich.

References

Acreman, M.C., Ferguson, A.J.D., 2010. Environmental flows and the European water framework directive. Freshw. Biol. 55, 32–48. https://doi.org/10.1111/j.1365-2427.2009.02181.x.

Alderman, D.J., 1996. Geographical spread of bacterial and fungal diseases of crustaceans. OIE Rev. Sci. Tech. 15, 603–632. https://doi.org/10.20506/rst.15.2.943.

Amara, I., Miled, W., Slama, R. Ben, Ladhari, N., 2018. Antifouling processes and toxicity effects of antifouling paints on marine environment. A review. Environ. Toxicol. Pharmacol. 57, 115–130. https://doi.org/10.1016/j.etap.2017.12.001.

Bohman, P., Degerman, E., Edsman, L., Sers, B., 2011. Exponential increase of signal crayfish in running waters in Sweden – due to illegal introductions? Knowl. Manag. Aquat. Ecosyst. 23, 8. https://doi.org/10.1051/kmae/2011040.

Bousmar, D., Courtois, E., Van Audenhaege, L., Rollin, X., 2018. Performance of a fish pass for multiple species: scale model investigation. E3S Web Conf. 40, 1–8. https://doi.org/10.1051/e3sconf/20184003010.

Bubb, D.H., O'Malley, O.J., Gooderham, A.C., Lucas, M.C., 2009. Relative impacts of native and non-native crayfish on shelter use by an indigenous benthic fish. Aquat. Conserv. Mar. Freshw. Ecosyst. 19, 448–455. https://doi.org/10.1002/aqc.1001.

Castro-Santos, T., Sanz-Ronda, F.J., Ruiz-Legazpi, J., 2013. Breaking the speed limit – comparative sprinting performance of brook trout *(Salvelinus fontinalis)* and brown trout *(Salmo trutta)*. Can. J. Fish. Aquat. Sci. 70, 280–293. https://doi.org/10.1139/cjfas-2012-0186.

Chambers, L.D., Stokes, K.R., Walsh, F.C., Wood, R.J.K., 2006. Modern approaches to marine antifouling coatings. Surf. Coating. Technol. 201, 3642–3652. https://doi.org/10.1016/j.surfcoat.2006.08.129.

Chucholl, C., 2013a. Invaders for sale: trade and determinants of introduction of ornamental freshwater crayfish. Biol. Invasions 15, 125–141. https://doi.org/10.1007/s10530-012-0273-2.

Chucholl, C., 2013b. Feeding ecology and ecological impact of an alien "warm-water" omnivore in cold lakes. Limnologica 43, 219–229. https://doi.org/10.1016/j.limno.2012.10.001.

Chucholl, C., Schrimpf, A., 2016. The decline of endangered stone crayfish *(Austropotamobius torrentium)* in southern Germany is related to the spread of invasive alien species and land-use change. Aquat. Conserv. Mar. Freshw. Ecosyst. 26, 44–56. https://doi.org/10.1002/aqc.2568.

Collas, M., Becking, T., Delpy, M., Pflieger, M., Bohn, P., Reynolds, J., Grandjean, F., 2016. Monitoring of white-clawed crayfish *(Austropotamobius pallipes)* population during a crayfish plague outbreak followed by rescue. Knowl. Manag. Aquat. Ecosyst. 1–8. https://doi.org/10.1051/kmae/2015037.

Dana, E.D., García-de-Lomas, J., González, R., Ortega, F., 2011. Effectiveness of dam construction to contain the invasive crayfish *Procambarus clarkii* in a Mediterranean mountain stream. Ecol. Eng. 37, 1607–1613. https://doi.org/10.1016/j.ecoleng.2011.06.014.

Daněk, T., Musil, J., Vlašánek, P., Svobodová, J., Johnsen, S.I., Barteková, T., Štrunc, D., Barankiewicz, M., Bouše, E., Andersen, O., 2018. Telemetry of co-occurring noble crayfish *(Astacus astacus)* and stone crayfish *(Austropotamobius torrentium):* diel changes in movement and local activity. Fundam. Appl. Limnol. 191, 339–352. https://doi.org/10.1127/fal/2018/1134.

Dickey, B.F., Mccarthy, T.M., 2007. Predator-prey interactions between crayfish *(Orconectes juvenilis)* and snails *(Physa gyrina)* are affected by spatial scale and chemical cues. Invertebr. Biol. 126, 57–66. https://doi.org/10.1111/j.1744-7410.2007.00076.x.

Downhower, J.F., Lejeune, P., Gaudin, P., Brown, L., 1990. Movements of the chabot *(Cottus gobio)* in a small stream. Pol. Arch. Hydrobiol. 37, 119–126.

Ellis, M.J., 2005. Crayfish barrier flume study - final report. Spring Rivers Ecol. Sci. 48.

Faulkes, Z., 2018. Prohibiting pet crayfish does not consistently reduce their availability online. Nauplius 26, 1–11. https://doi.org/10.1590/2358-2936e2018023.

Faulkes, Z., 2010. The spread of the parthenogenetic marbled crayfish, Marmorkrebs *(Procambarus sp.),* in the North American pet trade. Aquat. Invasions 5, 447–450. https://doi.org/10.3391/ai.2010.5.4.16.

Florea, L., 2017. Restoration of lateral conectivity of the Romanian Danube river, strategies and local actions. J. Wetl. Biodivers. 7, 29–44.

Frings, R.M., Vaeßen, S.C.K., Groß, H., Roger, S., Schüttrumpf, H., Hollert, H., 2013. A fish-passable barrier to stop the invasion of non-indigenous crayfish. Biol. Conserv. 159, 521–529. https://doi.org/10.1016/j.biocon.2012.12.014.

Gallo, A., Tosti, E., 2014. Antifouling compounds endangering marine invertebrates reproduction. J. Mar. Sci. Res. Dev. 5 https://doi.org/10.4172/2155-9910.1000e133.

Gil-Sánchez, J.M., Alba-Tercedor, J., 2006. The decline of the endangered populations of the native freshwater crayfish *(Austropotamobius pallipes)* in southern Spain: it is possible to avoid extinction? Hydrobiologia 559, 113–122. https://doi.org/10.1007/s10750-005-1024-5.

Guan, R.Z., 1997. An improved method for marking crayfish. Crustaceana 70, 641–652. https://doi.org/10.1163/156854097x00104.

Guan, R.Z., Wiles, P.R., 1999. Growth and reproduction of the introduced crayfish *Pacifastacus leniusculus* in a British lowland river. Fish. Res. 42, 245–259. https://doi.org/10.1016/S0165-7836(99)00044-2.

Harlioğlu, M.M., 1999. The efficiency of the Swedish trappy in catching freshwater crayfish *Pacifastacus leniusculus* and *Astacus leptodactylus*. Turk. J. Zool. 23, 93–98.

Herberholz, J., Swierzbinski, M.E., Widjaja, A., Kohn, A., 2019. Not so fast: giant interneurons control precise movements of antennal scales during escape behavior of crayfish. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 205, 687–698. https://doi.org/10.1007/s00359-019-01356-y.

Herrmann, A., Schnabler, A., Martens, A., 2018. Phenology of overland dispersal in the invasive crayfish *Faxonius immunis* (Hagen) at the Upper Rhine River area. Knowl. Manag. Aquat. Ecosyst. 30 https://doi.org/10.1051/kmae/2018018.

Holdich, D.M., Reeve, I.D., Rogers, W.D., 1995. Introduction and spread of alien crayfish in british waters – implications for native crayfish populations. Freshw. Crayfish 8, 99–112.

Holdich, D.M., Reynolds, J.D., Souty-Grosset, C., Sibley, P.J., 2009. A review of the ever increasing threat to European crayfish from non-indigenous crayfish species. Knowl. Manag. Aquat. Ecosyst. 394–395. https://doi.org/10.1051/kmae/2009025, 2009.

Holthe, E., Lund, E., Finstad, B., Thorstad, E.B., McKinley, R.S., 2005. A fish selective obstacle to prevent dispersion of an unwanted fish species, based on leaping capabilities. Fish. Manag. Ecol. 12, 143–147. https://doi.org/10.1111/j.1365-2400.2004.00436.x.

Hossain, M.S., Kouba, A., Buřič, M., 2019. Morphometry, size at maturity, and fecundity of marbled crayfish *(Procambarus virginalis)*. Zool. Anz. 281, 68–75. https://doi.org/10.1016/j.jcz.2019.06.005.

Junker, J., Peter, A., Wagner, C.E., Mwaiko, S., Germann, B., Seehausen, O., Keller, I., 2012. River fragmentation increases localized population genetic structure and enhances asymmetry of dispersal in bullhead *(Cottus gobio)*. Conserv. Genet. 13, 545–556. https://doi.org/10.1007/s10592-011-0306-x.

Knaepkens, G., Baekelandt, K., Eens, M., 2005. Assessment of the movement behaviour of the bullhead *(Cottus gobio)*, an endangered European freshwater fish. Anim. Biol. 55, 219–226. https://doi.org/10.1163/1570756054472845.

Knaepkens, G., Bruyndoncx, L., Eens, M., 2004. Assessment of residency and movement of the endangered bullhead *(Cottus gobio)* in two Flemish rivers. Ecol. Freshw. Fish 13, 317–322. https://doi.org/10.1111/j.1600-0633.2004.00065.x.

Knights, B., White, E.M., 1998. Enhancing immigration and recruitment of eels: the use of passes and associated trapping systems. Fish. Manag. Ecol. 5, 459–471. https://doi.org/10.1046/j.1365-2400.1998.560459.x.

Kokko, H., Koistinen, L., Harlioğlu, M.M., Makkonen, J., Aydın, H., Jussila, J., 2012. Recovering Turkish narrow clawed crayfish *(Astacus leptodactylus)* populations carry *Aphanomyces astaci*. Knowl. Manag. Aquat. Ecosyst. 12 https://doi.org/10.1051/kmae/2012006.

Kondratieff, M.C., Myrick, C.A., 2006. How high can brook trout jump? A laboratory evaluation of brook trout jumping performance. Trans. Am. Fish. Soc. 135, 361–370. https://doi.org/10.1577/t04-210.1.

Kouba, A., Petrusek, A., Kozák, P., 2014. Continental-wide distribution of crayfish species in Europe: update and maps. Knowl. Manag. Aquat. Ecosyst. https://doi.org/10.1051/kmae/2014007.

Kozubíková, E., Petrusek, A., Ďuriš, Z., Martín, M.P., Diéguez-Uribeondo, J., Oidtmann, B., 2008. The old menace is back: recent crayfish plague outbreaks in the Czech Republic. Aquaculture 274, 208–217. https://doi.org/10.1016/j.aquaculture.2007.11.015.

Kušar, D., Vrezec, A., Ocepek, M., Jenčič, V., 2013. *Aphanomyces astaci* in wild crayfish populations in Slovenia: first report of persistent infection in a stone crayfish *Austropotamobius torrentium* population. Dis. Aquat. Org. 103, 157–169. https://doi.org/10.3354/dao02567.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species a Selection from the Global Invasive Species Database. Published by the Invasive Species Specialist Group (ISSG) a Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), p. 12.

Magalhães, C., Bueno, S.L.S., Bond-Buckup, G., Valenti, W.C., Melo Da Silva, H.L., Kiyohara, F., Mossolin, E.C., Rocha, S.S., 2005. Exotic species of freshwater decapod crustaceans in the state of São Paulo, Brazil: records and possible causes of their introduction. Biodivers. Conserv. 14, 1929–1945. https://doi.org/10.1007/s10531-004-2123-8.

Manenti, R., Bonelli, M., Scaccini, D., Binda, A., Zugnoni, A., 2014. *Austropotamobius pallipes* reduction vs. *Procambarus clarkii* spreading: management implications. J. Nat. Conserv. 22, 586–591. https://doi.org/10.1016/j.jnc.2014.09.001.

Mangan, B.P., Savitski, J.J., Fisher, N.T., 2009. Comparison of two traps used for capturing wild crayfish. J. Freshw. Ecol. 24, 445–450. https://doi.org/10.1080/02705060.2009.9664317.

Marques, M., Banha, F., Águas, M., Anastácio, P., 2015. Environmental cues during overland dispersal by three freshwater invaders: *Eriocheir sinensis*, *Pacifastacus leniusculus*, and *Procambarus clarkii* (Crustacea , Decapoda). Hydrobiologia 742, 81–93. https://doi.org/10.1007/s10750-014-1968-4.

Martín-Torrijos, L., Kokko, H., Makkonen, J., Jussila, J., Diéguez-Uribeondo, J., 2019. Mapping 15 years of crayfish plague in the Iberian Peninsula: the impact of two invasive species on the endangered native crayfish. PloS One 14, 1–14. https://doi.org/10.1371/journal.pone.0219223.

Mojžišová, M., Mrugała, A., Kozubíková-Balcarová, E., Vlach, P., Svobodová, J., Kouba, A., Petrusek, A., 2020. Crayfish plague in Czechia: outbreaks from novel sources and testing for chronic infections. J. Invertebr. Pathol. 173, 107390. https://doi.org/10.1016/j.jip.2020.107390.

Moorhouse, T.P., Poole, A.E., Evans, L.C., Bradley, D.C., Macdonald, D.W., 2014. Intensive removal of signal crayfish *(Pacifastacus leniusculus)* from rivers increases numbers and taxon richness of macroinvertebrate species. Ecol. Evol. 4, 494–504. https://doi.org/10.1002/ece3.903.

Nyström, P., Brönmark, C., Granéli, W., 1996. Patterns in benthic food webs: a role for omnivorous crayfish? Freshw. Biol. 36, 631–646. https://doi.org/10.1046/j.1365-2427.1996.d01-528.x.

Patoka, J., Kalous, L., Kopecký, O., 2014. Risk assessment of the crayfish pet trade based on data from the Czech Republic. Biol. Invasions 16, 2489–2494. https://doi.org/10.1007/s10530-014-0682-5.

Peay, S., Guthrie, N., Spees, J., Nilsson, E., Bradley, P., 2009. The impact of signal crayfish *(Pacifastacus leniusculus)* on the recruitment of salmonid fish in a headwater stream in Yorkshire, England. Knowl. Manag. Aquat. Ecosyst. 12 https://doi.org/10.1051/kmae/2010003.

Phillips, I.D., Vinebrooke, R.D., Turner, M.A., 2009. Experimental reintroduction of the crayfish species *Orconectes virilis* into formerly acidified Lake 302S (Experimental Lakes Area, Canada). Can. J. Fish. Aquat. Sci. 66, 1892–1902. https://doi.org/10.1139/F09-118.

Puky, M., Reynolds, J.D., Schád, P., 2005. Native and alien Decapoda species in Hungary: distribution, status, conservation importance. Bull. Français la Pêche la Piscic. 553–568. https://doi.org/10.1051/kmae:2005015.

Rahel, F.J., 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshw. Biol. 52, 696–710. https://doi.org/10.1111/j.1365-2427.2006.01708.x.

Rantamäki, J., Cerenius, L., Söderhäll, K., 1992. Prevention of transmission of the crayfish plague fungus *(Aphanomyces astaci)* to the freshwater crayfish *Astacus astacus* by treatment with MgCl2. Aquaculture 104, 11–18. https://doi.org/10.1016/0044-8486(92)90133-6.

Robinson, C.V., Uren Webster, T.M., Cable, J., James, J., Consuegra, S., 2018. Simultaneous detection of invasive signal crayfish, endangered white-clawed crayfish and the crayfish plague pathogen using environmental DNA. Biol. Conserv. 222, 241–252. https://doi.org/10.1016/j.biocon.2018.04.009.

Rodríguez, C.F., Bécares, E., Fernández-Aláez, M., 2003. Shift from clear to turbid phase in Lake Chozas (NW Spain) due to the introduction of American red swamp crayfish *(Procambarus clarkii)*. Hydrobiologia 506–509, 421–426. https://doi.org/10.1023/B:HYDR.0000008626.07042.87.

Rosecchi, E., 1997. The introduction of freshwater fish and crayfish species in the Camargue (France): history, origins and changes in assemblages. Bull. Français la Pêche la Piscic. 60, 221–232. https://doi.org/10.1051/kmae:1997024.

Rosewarne, P.J., Piper, A.T., Wright, R.M., Dunn, A.M., 2013. Do low-head riverine structures hinder the spread of invasive crayfish? Case study of signal crayfish *(Pacifastacus leniusculus)* movements at a flow gauging weir. Manag. Biol. Invasions 4, 273–282. https://doi.org/10.3391/mbi.2013.4.4.02.

Ruokonen, T.J., Karjalainen, J., Hämäläinen, H., 2014. Effects of an invasive crayfish on the littoral macroinvertebrates of large boreal lakes are habitat specific. Freshw. Biol. 59, 12–25. https://doi.org/10.1111/fwb.12242.

Scalici, M., Gibertini, G., 2005. Can *Austropotamobius italicus meridionalis* be used as a monitoring instrument in Central Italy? Preliminary observations. Bull. Fr. la Pech. la Prot. des Milieux Aquat. 613–625. https://doi.org/10.1051/kmae:2005019.

Scalici, M., Pitzalis, M., Gibertini, G., 2009. Crayfish distribution updating in central Italy. Knowl. Manag. Aquat. Ecosyst. 394–395. https://doi.org/10.1051/kmae/2009017.

Schrimpf, A., Maiwald, T., Vrålstad, T., Schulz, H.K., Śmietana, P., Schulz, R., 2013. Absence of the crayfish plague pathogen *(Aphanomyces astaci)* facilitates coexistence of European and American crayfish in central Europe. Freshw. Biol. 58, 1116–1125. https://doi.org/10.1111/fwb.12112.

Sienra, E. De, Armienta, M.A., Gonsebatt, M.E., 2003. *Potassium dichromate* increases the micronucleus frequency in the crayfish *Procambarus clarkii*. Environ. Pollut. 126, 367–370. https://doi.org/10.1016/S0269-7491(03)00249-5.

Söderbäck, B., 1994. Interactions among juveniles of two freshwater crayfish species and a predatory fish. Oecologia 100, 229–235.

Souty-Grosset, C., Anastácio, P.M., Aquiloni, L., Banha, F., Choquer, J., Chucholl, C., Tricarico, E., 2016. The red swamp crayfish *Procambarus clark*ii in Europe: impacts on aquatic ecosystems and human well-being. Limnologica 58, 78–93. https://doi.org/10.1016/j.limno.2016.03.003.

Stucki, T., 2002. Differences in life history of native and introduced crayfish species in Switzerland. Freshw. Crayfish 13, 463–476.

Thomas, J.R., Masefield, S., Hunt, R., Wood, M.J., Hart, A.G., Hallam, J., Griffiths, S.W., Cable, J., 2019. Terrestrial emigration behaviour of two invasive crayfish species. Behav. Process. 167, 10–13. https://doi.org/10.1016/j.beproc.2019.103917.

Tummers, J.S., Lucas, M.C., 2019. Role of barriers in managing aquatic invasive species. https://amber.international/wp-content/uploads/2020/07/AMBER-T4.2.2.-Role-of-barriers-in-managing-AIS-1.pdf. (Accessed 28 August 2020).

Twardochleb, L.A., Olden, J.D., Larson, E.R., 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. Freshw. Sci. 32, 1367–1382. https://doi.org/10.1899/12-203.1.

Ulikowski, D., Chybowski, Ł., Traczuk, P., Ulikowska, E., 2017. A new design of crayfish traps reduces escaping and improves opportunities for long-term catching. Turk. J. Fish. Aquat. Sci. 17, 363–369. https://doi.org/10.4194/1303-2712-v17_2_15.

Utzinger, J., Roth, C., Peter, A., 1998. Effects of environmental parameters on the distribution of bullhead *Cottus gobio* with particular consideration of the effects of obstructions. J. Appl. Ecol. 35, 882–892. https://doi.org/10.1111/j.1365-2664.1998.tb00006.x.
Vaeßen, S., Hollert, H., 2015. Impacts of the North American signal crayfish *(Pacifastacus leniusculus)* on European ecosystems. Environ. Sci. Eur. 27, 1–6. https://doi.org/10.1186/s12302-015-0065-2.
Vey, A., Söderhäll, K., Ajaxon, R., 1983. Susceptibility of *Orconectes limosus* Raff. to the crayfish plague *Aphanomyces astaci* Schikora. Freshw. Crayfish 5, 284–291.
Viljamaa-Dirks, S., Heinikainen, S., Nieminen, M., Vennerström, P., Pelkonen, S., 2011. Persistent infection by crayfish plague *Aphanomyces astac*i in a noble crayfish population - a case report. Bull. Eur. Assoc. Fish Pathol. 31, 182–188.
Weibel, D., Peter, A., 2013. Effectiveness of different types of block ramps for fish upstream movement. Aquat. Sci. 75, 251–260. https://doi.org/10.1007/s00027-012-0270-7.
Weinländer, M., Füreder, L., 2010. The continuing spread of *Pacifastacus leniusculus* in Carinthia (Austria). Knowl. Manag. Aquat. Ecosyst. 17, 10. https://doi.org/10.1051/kmae/20010011.
Westman, K., 1973. The population of the crayfish *Astacus astacus* in Finland and the introduction of the American *Pacifastacus leniusculus* Dana. Freshw. Crayfish 1, 41–55.
Westman, K., Savolainen, R., 2001. Long term study of competition between two co-occurring crayfish species, the native *Astacus astacus* L. and the introduced *Pacifastacus leniusculus* Dana, in a Finnish lake. Bull. Français la Pêche la Piscic. 613–627. https://doi.org/10.1051/kmae:2001008.
Westman, K., Savolainen, R., Julkunen, M., 2002. Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a small, enclosed Finnish lake: a 30-year study. Ecography (Cop.). 25, 53–73. https://doi.org/10.1034/j.1600-0587.2002.250107.x.
Wilson, K.A., Magnuson, J.J., Lodge, D.M., Hill, A.M., Kratz, T.K., Perry, W.L., Willis, T.V., 2004. A long-term rusty crayfish *(Orconectes rusticus)* invasion: dispersal patterns and community change in a north temperate lake. Can. J. Fish. Aquat. Sci. 61, 2255–2266. https://doi.org/10.1139/F04-170.
Zielinski, D.P., McLaughlin, R., Castro-Santos, T., Paudel, B., Hrodey, P., Muir, A., 2019. Alternative Sea Lamprey Barrier Technologies: History as a Control Tool. Rev. Fish. Sci. Aquacult. 27, 438–457. https://doi.org/10.1080/23308249.2019.1625300.