Aquatic Invasions (2016) Volume 11, Issue 1: 55–65

Research Article

Movement patterns and shelter choice of spiny-cheek crayfish (*Orconectes limosus*) in a large lake's littoral zone

Philipp E. Hirsch[1,2,3]*, Patricia Burkhardt-Holm[2], Iris Töpfer[1] and Philipp Fischer[1,4]

[1] *Limnological Insitute, University of Konstanz, Mainaustrasse 252, D-78464 Konstanz, Germany*
[2] *Program Man-Society-Environment, Vesalgasse 1, CH-4051 Basel, Switzerland*
[3] *Research Center for Sustainable Energy and Water Supply (FoNEW), University of Basel, Switzerland*
[4] *Alfred-Wegener-Institute, Helmholtz Centre for Polar- and Marine Research Bremerhaven, Biological Institute Helgoland, Kurpromenade, D-27498 Helgoland, Germany*

**Corresponding author*

E-mail: philipp.hirsch@unibas.ch

Received: 11 May 2015 / Accepted: 11 September 2015 / Published online: 12 October 2015

Handling editor: Christoph Chucholl

Abstract

The study of individual movement patterns and habitat choice is a fundamental step to assess an invasive species' range extension and to inform possible management options. The spiny-cheek crayfish is an invasive species currently spreading in Europe and also in Lake Constance. This is of concern because the greater Lake Constance area still holds refugial populations of native crayfish that might be endangered by the invader. In invasive crayfish, individual movement patterns and the availability of suitable shelters can predict an invasive population's spread. In a radio telemetry and mark-recapture study and in semi-natural outdoor experiments, we investigated movement patterns and shelter choice of spiny-cheek crayfish. In the field, radio-tagged and marked crayfish moved distances up to 1200 m within 4 and 13 days, respectively and mostly prevailed within the littoral zone at less than 3 m depth. Tracked crayfish resided close to artificial structures such as boat harbours in the study area. In the outdoor experiments spiny-cheek crayfish used litter as daytime shelter but also chose natural stones and macrophytes. We provide the first large-lake telemetry data on crayfish movement and our results suggest that spiny-cheek crayfish will expand its range within the lake moving along the shoreline. Artificial structures such as boat harbours and litter might facilitate this spread by providing suitable shelters. Our results can help to inform the implementation of countermeasures against the spread of invasive crayfish populations.

Key words: colonization, invasive species, radio telemetry, range extension, ephemeral home range

Introduction

Movement patterns of animals influence the dynamics of populations and communities and need to be investigated if any animal population should be managed for conservation or containment purposes (Baker 1978). Individual movement patterns are key for the spread of any animal population and especially for invasive species. Many species arriving in a new area will facilitate the establishment of a new population which increases invasion success of a species (Lockwood et al. 2005). Invasive species will be more like to establish if they can use the new environment's habitats requirements. Indiscriminate habitat requirements are traditionally viewed as an important factor for the success of invasive species (Lodge 1993). An invasive species that tolerates a broad range of habitat conditions is likely to find suitable habitats also outside of its native range (Lodge 1993). A comprehensive understanding of animal movement and how it is affected by habitat requirements is central for investigating the spread, and consequently the management options for invasive species (Bubb et al. 2008).

Invasive crayfish are a group of species whose spread is of particular concern to conservationists. Many invasive crayfish are superior competitors for or predators of native species and can profoundly affect native ecosystems (reviewed in Holdich et al. 2009). Furthermore, invasive crayfish can be vectors for the disease crayfish plague caused by the fungal-like pathogen *Aphanomyces astaci* (Schikora, 1903) (Holdich et al. 2009). On the one hand, dramatic losses of native crayfish populations due to contact with invasive species are reported (Gherardi et al. 2011). On the other hand, there are reports of co-existence of native and invasive species within one water body (Schrimpf et al. 2012). Discussed mechanisms behind this co-existence are the differential susceptibility of native crayfish to pathogens or the presence of refugia in large water bodies which minimize direct encounters between species and pathogens (Bubb et al. 2006; Pearl et al. 2013). Researchers and conservationists aim to conserve refugia for native crayfish by preventing the further spread of invasive crayfish that already have established in a given ecosystem. Recent studies have shown that a detailed knowledge of the movement patterns and the dispersal properties is important to predict (and possibly prevent) the spread of invasive crayfish into native crayfish refugia (Bubb et al. 2006). A key factor for the spread of crayfish is the availability of suitable shelters (Nakata and Goshima 2003). Shelters provide protection from predators and from intraspecific aggression, and the absence of suitable shelters can limit the occurrence and movement of crayfish (Nyström 2005). For such management goals however, a detailed and species specific knowledge about the usage of shelters types by an invasive crayfish species is needed. For example, if refugia are present for native crayfish within a lake, then shoreline management could be designed to create obstacles for the movement of invasive crayfish into these refugia or manual removal efforts can be instigated that halt the spread.

Lake Constance is a suitable model system to address the issue of invasive crayfish potentially spreading into the range of native species. The lake and its tributaries feature populations of three European crayfish species and is currently experiencing the invasion of the spiny-cheek crayfish *Orconectes limosus* (Rafinesque, 1817). The spiny-cheek crayfish first appeared in Lake Constance in the late 1980s (Hirsch et al. 2008). Recent research suggests that spiny-cheek crayfish will continue to spread into previously pristine areas of the lake where native crayfish might still occur (Hirsch and Fischer 2008; Hirsch 2009; Berger et al. 2015). Three plague-susceptible European species might be threatened by the spread of spiny-cheek crayfish. Narrow-clawed crayfish (*Astacus leptodactylus* Escholtz, 1823), which is also a European plague-susceptible astacid crayfish but which is not native to the lake, stone-crayfish (*Austropotamobius torrentium* Schrank, 1803), and noble crayfish (*Astacus astacus* Linnaeus, 1758). The last record of stone crayfish in the lake dates back more than 10 years and noble crayfish are only very rarely reported. However, both native species do occur in localized refugia in Lake Constance's tributaries and the hinterland (Hirsch 2009). The spread of spiny-cheek crayfish within the lake and further into the localized refugia would endanger remaining native crayfish populations that could be outcompeted for food and shelter, or fall victim to the crayfish plague (Hirsch 2009). We use Lake Constance as a model system to study individual movements and shelter choice of the spiny-cheek crayfish by means of a radio telemetry, mark-recapture, and shelter choice study. Based on data on tracked crayfish from lotic systems (Gherardi and Babaresi 2000; Bubb et al. 2006; Buric et al. 2009) we hypothesized crayfish individuals to perform substantial movements of approx. hundreds of meters within a few days. We further hypothesized that crayfish moving in the lake will find a large variety of suitable shelters in the littoral zone. Because we are not able to infer shelter choice directly from our telemetry data, we use shelter-choice experiments to test that shelter requirements are indeed non-specific. Finally, we discuss the relevance of our findings for the management of invasive crayfish.

Materials and methods

Study area

The study took place at a riparian strip of ~ 2 km length on the south-western shoreline of the Upper Lake Constance that is believed to be the centre of spread for spiny-cheek crayfish within the lake (Hirsch 2009) (Figure 1, coordinates: 47.694 N, 9.197 W). The bottom substrate at the study site was dominated by sand and mud including patches of larger stones and rocks. Vegetation in the shallow littoral zone was scarce (with vegetation cover < 5 % of the total littoral area). A recreational boat harbour and two foot-bridges are situated within the study area (Figure 1).

Radio telemetry

Radio telemetry is the optimal method if one is interested in natural, fine scale movements of crayfish (Bubb et al. 2008). We conducted the telemetry study between 10th of May and 26th of June. In smaller running waters spiny-cheek crayfish have been shown to make large-scale movements in early spring and late autumn. Migration into or out of tributary areas has been

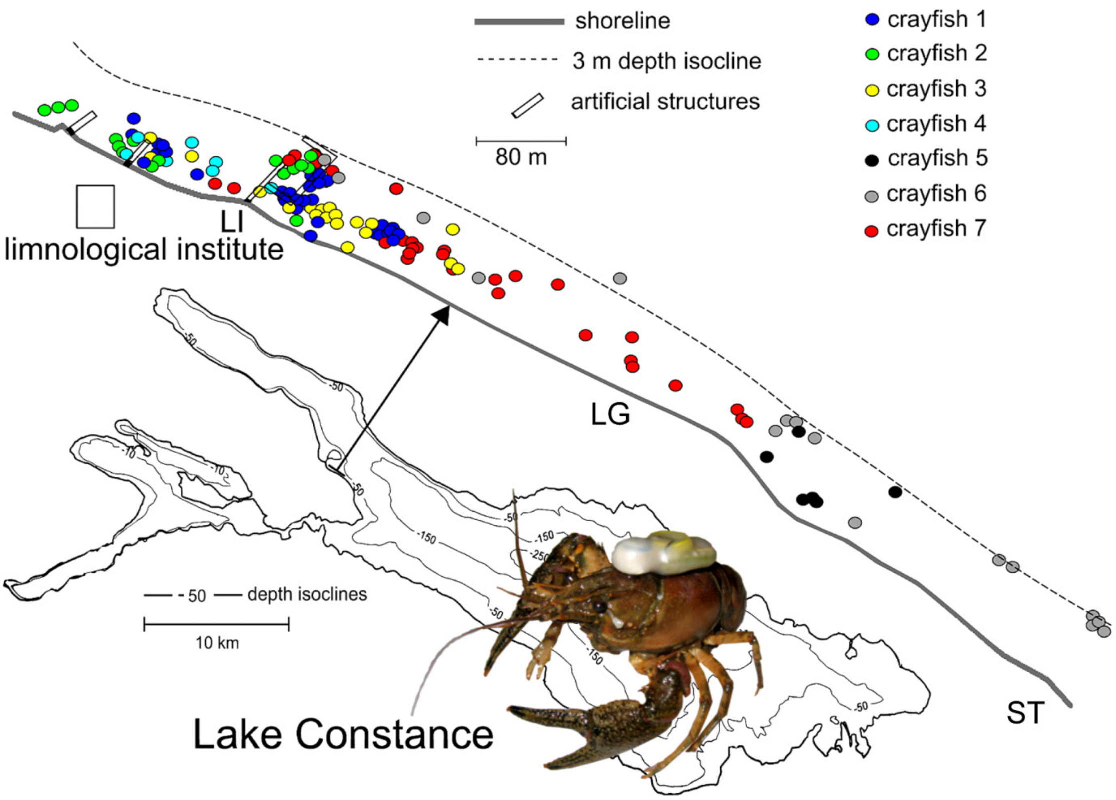

Figure 1. Study area and crayfish positions. Map of Lake Constance with 50-meter depth isoclines and zoom in of the study area with a 3m isocline. The summary figure of the study area shows the radio-telemetry-tracked positions of seven crayfish coded with a different colour each. The solid line represents the shoreline, the dashed line marks the 3 m depth isocline. Artificial structures (footbridges, boat harbour) are also indicated. For more detailed information on e.g. start and end-position of tracked crayfish please refer to the individual-specific data and figures in the appendix (Appendix 2, Figures S1-S7).

suggested to be related to temperature changes and reproductive behaviour (Buric et al. 2009 a, b). Environmental factors (e.g., temperature) in a large lake's littoral zone are more stable than in smaller running waters and the period of radio tracking falls outside of the typical spring or autumn periods of reproductive activity in spiny-cheek crayfish. We therefore assume our study period to represent a season of non-migratory summer movements (*cf.* Buric et al. 2009 a, b). The mean monthly temperatures in the lake during that period ranged between 12°C in May and 18 °C in June. We caught seven spiny-cheek crayfish using fyke nets (similar to eel-traps) or by snorkelling and handpicking in the study area. We were also interested in the movement patterns of female crayfish and therefore tracked two 'berried' females which carried eggs under their pleon. All other crayfish were males. For all crayfish the carapace length (CL) from the tip of the rostrum to the posterior median edge of the cephalothorax was measured to the nearest 0.1 mm using a vernier scale. See Appendix 1 for further information on crayfish. All individuals were tagged with radio transmitters manufactured at the technical facilities of the University of Constance. For fixation of the tags, the rostrum of each crayfish was cleaned using a sheet of blotting paper, then a tag was fixed in the depression between the eyes in the caudal part of the rostrum using standard retail two-component adhesive. Tags measured 2.7 cm × 1.2 cm × 0.8 cm, were potted in paraffin wax, customized to 7 different frequencies between 119.999 and 150.0 MHz, had a predicted battery lifespan of approx. 6 weeks in air, and weighed 3 g (+/- 0.1g SD) in air (approx. 15% of body weight of crayfish, Appendix 1). No animal showed signs of injury or annoyance in response to tagging, e.g. no tailflapping or defense reactions or attempts to

Table 1. Distances moved and recording intervals. Data on overall distances moved (m), duration of the observation (days), distance moved per day (m), and number of night- and daytime- recordings of all seven crayfish. For all data the mean and standard deviation (SD) are provided in the last row.

crayfish No.	overall distance covered (m)	duration of tracking (days)	distance moved (m day $^{-1}$)	nightime recordings	daytime recordings
1	850	30	28	43	18
2	893	6	149	17	6
3	742	9	82	17	5
4	320	2	160	10	15
5	1433	31	46	13	9
6	253	14	18	13	14
7	1282	4	320	20	19
mean (± SD)	825 (±409)	14 (±11)	115 (±99)	19 (±10)	12 (±5)

remove the tag with its chelae. After tagging we observed animals to move like before tagging. The tag-to-animal size and weight ratio was slightly higher than in previous studies conducted in rivers and brooks (around 30% of body length and around 10% of body weight, *cf.* Gherardi and Babaresi 2000; Bubb et al. 2006 and 2008). However, we deem this acceptable because, unlike other studies in rivers, our transmitters had an internal rather than external antenna. An internal antenna would certainly be less likely to hamper movement of a crayfish than an internal one but it also increases the tag's dimensions and weight. Furthermore, as opposed to most small running waters, which are rather shallow, we had to use transmitters with higher performance that allowed for detection down to larger water depths. High transmitter performance inevitably increases the weight and dimensions of the tag due to utilisation of larger batteries. The depth range of the transmitters was tested by measuring the signal strength at different depths and we extrapolated that the signal would be undetectable (i.e. approaching 0 m range) at approx. 15 m depth. Tracking was conducted using a small boat, a Wide Range Receiver AR8200 (AOR (UK) ltd.) and a Diamond Antenna (May 1000, 120–500 MHz, Yagi-Type). For post-tagging accommodation, all tagged crayfish were held individually in an outdoor mesocosms of 1 × 1m base dimensions (20 cm water depth) supplied by lake water. The crayfish had stones as shelters and were held for at least 24h in the mesocosm to ensure that the transmitter held and was fully functional. We also observed whether the animals were healthy, used shelters and showed the same type and frequency of movements as un-tagged crayfish. Then, the individuals were released for tracking at the location they were originally caught. To monitor nocturnal movements, crayfish were located an average of 19 times (range: 10 to 43 times, Table 1) every night between 8 p.m. and 6 a.m. During daytime we located crayfish on average 12 times every day (range: 5 to 19 times, Table 1). The total number of observations and the intervals were determined by the technical restrictions such as need to refuel the boat and manpower that limited the amount of time the boat could be used for tracking. If a crayfish could be not located for five consecutive days, it was classified as lost. Positions of the crayfish were recorded by a handheld GPS (Garmin®, GPS II plus). Water depth was also recorded using a sounding weight tied to a scaled line. The accuracy of the position recordings was tested by determining a fixed transmitter's position in repeated test trials. Based on this procedure, a radius of 8.5 m around the recorded GPS-position was defined to comprise the true position of the transmitter in more than 95 % of all cases. To further exclude any inter-observer bias in the recordings of positions, all positions were recorded by the same observer. As distance measure we applied the minimum moved distance between two tracking points.

Mark-recapture study

To additionally assess the movement of crayfish by a more hands-off approach we conducted a mark-recapture study. A mark-recapture study is likely to have less impact on the natural crayfish behaviour: the handling time is shorter than in the case of the tagging, the crayfish is not maintained in a mesocosm prior to its release, and the individual's movement is not influence by the tag weight that the individual has to carry.

To catch crayfish for the mark-recapture study we used three sets of fyke nets at three different locations (Figure 1): Limnological Institute (LI) 47.6959 N, 9.1931 W, littoral garden (LG) 47.6916 N, 9.2025 W and village of Staad (ST) 47.6879 N, 9.2074 W. LI was situated 1200 m westerly of ST while LG was situated in the middle between LI and ST (Figure 1). Each fyke net set consisted of four connected fyke nets. One double fyke net (length 14 m) exposed riparian-parallel and two single fyke nets (length 8.5 m, bar mesh size 22 mm) exposed riparian normal. Each fyke net set was exposed in 0.5 to 1.5 m depth in a cross-like orientation with the single fyke nets as the cross' bars and the double fyke net as the cross' stand. For the first catch campaign fyke nets were set the 2nd of August and emptied on the 8th of August and all caught animals were measured for CL and marked. Each crayfish was marked with a different code by punching holes into the uropodes using a belt punch, a method well established for crayfish mark-recapture studies. After handling (which took approx. 2 hours) the crayfish were set free again at the place they were caught. Fyke nets were again emptied on the 20th of August. Hence, there were 13 days between marking and recapturing.

Shelter-choice experiments

Comparison of the movements found in both tagged and marked crayfish can inform about the distances crayfish move with or without carrying a transmitter. In shallow running waters the observers can record the shelter choice of a tracked individual directly. Radio-telemetry in lakes does not allow for such *in situ* records of shelter choice. Therefore, we complemented our telemetry approach with a study on the shelter choice of crayfish under semi-natural conditions in large outdoor mesocosms. Shelter-choice experiments were conducted between the 23rd of June and 20th of July in a large (5 × 10 × 2 m) outdoor overflow mesocosms supplied by lake water. The inlet and outlet of water were on opposite ends of the shorter sides of the rectangular mesocosm. The inflow was set at 8 litres minute^{-1} which ensured a complete water exchange of the total mesocosm volume within 24 hours. This water exchange rate decreased temperature differences across shelters and possibly also reduced the accumulation of chemical cues from e.g. faeces. Four types of shelter were provided in opposite corners of the sand-covered mesocosm bottom.

- **Stones:** round to elliptic natural stones obtained from a local quarry, average diameter 14.1 cm (SD ± 3.0 cm), area 70 × 80 cm, were arranged as a double layer with each stone of the second layer positioned between at least three stones of the first layer.
- **Macrophytes:** *Potamogeton perfoliatus* (Linnaeus, 1758) stems 10 to 60 cm long, collected from the lake by snorkelling were evenly fixed on a 25 × 62 cm metal grid, resulting in a stem count of 1300 stems m^{-2}.
- **Shadow:** A dark pvc plate (48 × 75 cm) was fixed in the mesocosm corner, 20 cm above but without contact to the bottom.
- **Litter:** different types of emptied hollow-ware, covering an area of 70 × 70 cm were placed in one mesocosm corner including, two 100 ml plastic-cups (diameter 7.0–7.5 cm), six metal tins (diameter of 6.6–8.5 cm) and four halves of 1 L beverage cartons (19.5 × 9.0 × 5.8 cm dimensions) all evenly spread across the bottom. Each piece of hollow-ware was thoroughly rinsed with detergent and tap water and dried before use to exclude the presence of olfactory cues.

All four shelter types are variously present in the littoral zone of the lake. Stones are likely the most common shelter type for benthic fish and crayfish in the wild (Hirsch and Fischer 2008), *P. perfoliatus* forms monospecific patches and is a dominant macrophyte species in the lake. Shadow was introduced as a test to assess whether protection from light would be sufficient as a shelter and be chosen by crayfish. Litter might also serve as a shelter because it is frequently found around footbridges in the littoral zone as a result of human activities (personal observations).

Crayfish for the shelter-choice experiment where caught near the Limnological Institute with fyke nets (mean carapace length CL 3.9 cm ± 0.23 SD, Appendix 1). Tagging and determination of daytime shelter preferences in the mesocosm experiment was conducted with the same gear as described above for the telemetry study. Shelter choice was determined by walking along the mesocosms' sides and pointing the antenna directly towards the shelter. This allowed for a very accurate position recording. The experiments commenced with releasing four crayfish into the middle of the mesocosm around noon. The shelter choice of each four crayfish was then recorded every day in the afternoon for six consecutive days. After the seventh day the first four crayfish were retrieved, and four new crayfish were tagged and introduced into the mesocosm. This

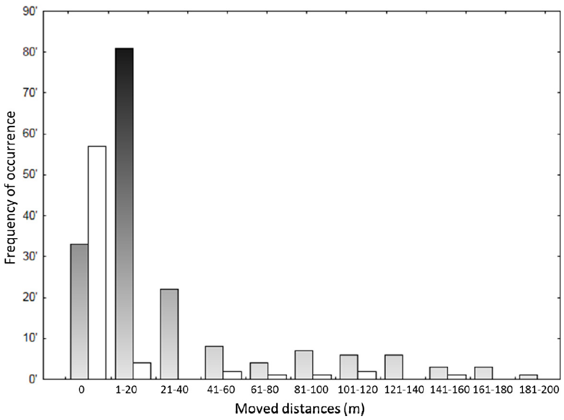

Figure 2. Frequency distribution of movements suggests Lévy processes in crayfish. The histogram of recorded movements in male (black bars) and female (blank bars) crayfish is suggestive of 'ephemeral home ranges'. This concept posits that crayfish reside longer periods in a restricted area (showing a high frequency of short-distance movements) and occasionally show short periods of long-distance movements (low frequency of long-distance movements).

procedure was repeated four times resulting in four replicates with four crayfish each. At three occasions during the experiment we tracked crayfish for four hours at night to ensure that all shelters were inspected by the crayfish. To reduce possible bias due to different solar exposition or accumulation of faeces or other cues in any corner, we exchanged shelters between opposite corners after 14 days. We acknowledge, however, that conditions across shelters could not be entirely standardized because we prioritized conditions close to nature and transferable to field condition over full control of all environmental factors. Food was provided *ad libitum* in the centre of the mesocosm in form of approximately 20 g of frozen chironomid larvae every second day. In the field spiny-cheek crayfish occur in densities of up to 16 individuals m^{-2} (Hirsch 2009). Given this natural density, we are confident that each of the shelter types (spread out over more than $1m^2$) provided sufficient shelter to accommodate all test crayfish. We therefore assume shelter choice to be unaffected by shelter competition. Temperature was measured daily and ranged from 10–20°C (mean=16.9) and variance in temperature was higher within than among shelters (ANOVA: $F_{3,76}=0.262$, $p>0.05$). Because shelter choices of crayfish were not fully independent from one another we tested for differences using the Cochran's *Q* test which is designed to detect differences in proportion-type data (shelter choice in %) of inter-dependent samples (four night-time shelter choices of a single crayfish recorded subsequently (Hill and Lewicki 2006). This means that the dependence of observations among crayfish and among days (65 observations = 16 crayfish tagged × 4 days of daily shelter choice recordings) is mathematically reduced to three degrees of freedom. As a pairwise post-hoc test following the Cochran's *Q* test we computed the McNemar test. The McNemar is an alternative to the *t*-test for dependent samples (several shelter choices by the same crayfish) and when the variable of interest is dichotomous (shelter chosen or not chosen) (Hill and Lewicki 2006).

Results

Radio-telemetry study

Crayfish used a depth range of 0.2 down to a maximum of 5 m (Figure 1, Appendix 2 with Figures S1–S7). Only three crayfish (crayfish 3, 5, and 7) resided for shorter periods (one to three days) deeper than 3 m and crayfish 7 moved down to a depth of 5 m (Figure S3, S5, S7). All other crayfish remained within less than 3 m depth. The two female crayfish moved into depths of approx. 1.8 and 1.2 m respectively after release but sought refuge in shallower water areas of 0.2 to 0.4 m depth after one or two days and stayed there for 29 to 30 days until the transmitters batteries faded (Figure 1, S4, S6). Crayfish showed considerable variation in distances moved. Distances moved within a day varied from 0 to 195 m (Table 1). For example, crayfish 7 showed very long movements along the shoreline, not residing in an area for longer than one day (Figure 1, S7). For crayfish 1, 2, and 3 an average of 17.5% (standard deviation = SD ± 2) of records was within 20 m or less distance from artificial structures as e.g. the recreational boat harbour (Figure 1, S1, S2, S3, S4). Overall, there were more recordings of short-distance movements (<20m) than of long-distance movements (>20m) (Figure 2). Crayfish appeared to reside longer periods of time in a rather restricted area (high frequency of short-distance movements) with interspersed short periods of long-distance movements (corresponding to 'ephemeral homeranges' *in sensu* Gherardi et al. 1998; Robinson et al. 2000; Loughman et al. 2013).

Crayfish moved significantly larger distances during the night than during the day (Mann-Whitney U-Test; $m=24$; $n=11$; $U=133$; $p<0.05$).

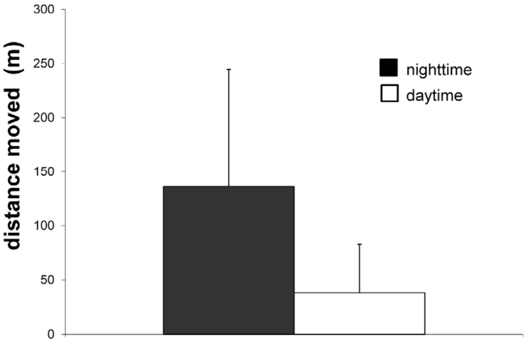

Figure 3. Diurnal movements. Mean of minimum moved distances between two recordings during the night and during the day of all tracked crayfish. Error bars denote standard deviation.

The minimum movement distance during the night was 136 m (SD ± 109) and 38 m (SD ± 45) during the day (Figure 3). On average the minimum moved distance between two tracking points for males was 141 m (SD ± 109) during the night and 104 m (SD ± 135) during the day. Females moved 149 m (SD ± 119) during the night and 60 m (SD ± 62) during the day.

Mark-recapture study

The first fyke-net withdrawal on the 8th of August revealed 65 crayfish (47 crayfish at LG, 11 crayfish at LI and 14 crayfish at ST). The second fyke-net emptying on the 20th of August revealed 37 crayfish (14 crayfish at LG, 13 crayfish at LI and 10 crayfish at ST). Four of the recaptured crayfish were previously marked. One crayfish, marked at LG was caught at LI (~800 m away). One crayfish marked at LG was recaptured at ST (~ 600 m away). Both of the other recaptures were marked at ST. One was recaptured at LG (~ 600 m away) and one at LI (~1200 m away). No crayfish was recaptured at the same site in which it was marked. Mean CL of all fyke net-caught crayfish was 3.7 cm (± 0.3 SD) and thus similar to the telemetry study and shelter-choice experiment.

Shelter-choice experiment

Shelter-choice of crayfish was significantly dependent on shelter type (Cochran's Q = 17.83, df = 3, p < 0.001). Artificial shelters were most frequently chosen (39.1 % of cases), macrophytes and stones were almost equally preferred (29.4 % and 31.5 %), and the shadow shelter was never chosen (0%, Figure 4). There were also differences within mesocosm shelter fidelity. The McNemar Chi-square post-hoc test revealed that shelter preference for stones was significant (Chi=10.8, p<0.01) but that differences in shelter choice between the other shelter types were not (Chi=0, p>0.1). In total 70% (n=64 daytime observations) of shelter choices were equal between two nights. This means that the majority of crayfish chose the same shelter again after having used it once. Some crayfish showed shelter-fidelity throughout the whole four day study period, six individuals changed their daytime-shelter three or four times. Three crayfish changed shelters once or twice during the study period.

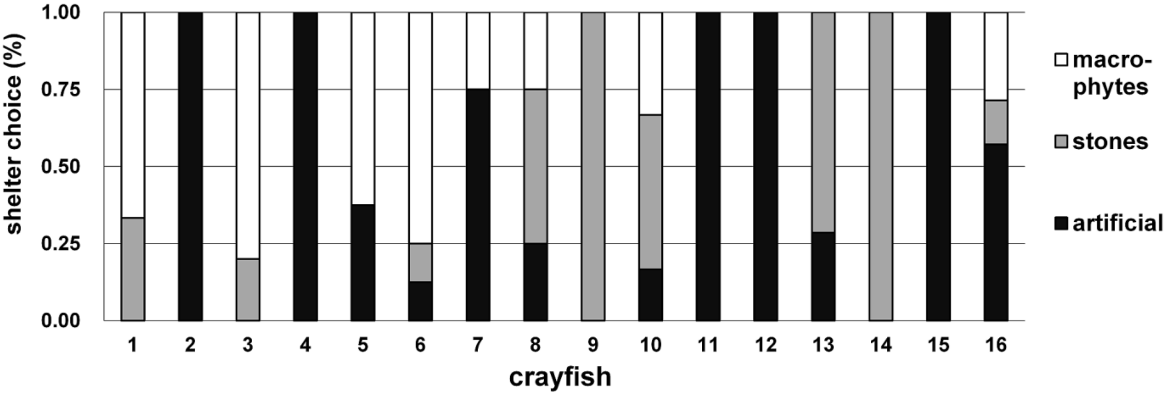

Figure 4. Shelter choice. Chosen type of daytime shelter (%) for each of 16 tracked crayfish (numbers below bars each denote an individual crayfish). The fourth shelter type (shadow) is not shown because it was never chosen as a shelter by any crayfish.

Discussion

The results of our study complied with our expectations: crayfish are able to occasionally moved large distances of up to 1200 m within a few (i.e. four) days. Shelter choice was indeed non-specific and the provision of shadow alone seemed not to be sufficient as a shelter for crayfish. Taken together these results provide insight into the basic movement ecology of the species. Below we also discuss how these may be relevant for management options for invasive crayfish spreading in lakes.

Mechanisms behind crayfish movement

Compared to data on benthic fish species, there are relatively few studies addressing the movement behaviour of crayfish. Laboratory experiments showed that activity patterns differ across species and also vary largely among individuals (Lozan 2000). Based on field-data from a river, Webb and Richardson (2004) put forward some generally valid explanations for movement patterns in crayfish: reproduction, moulting, foraging, responding to abiotic environmental conditions and predation. The effect of predation is assumed to be less relevant for nocturnal movements (Webb and Richardson 2004). Our data, however, indicate that predator avoidance might play an important role for the movement, especially in the case of female crayfish. We suspect that the movement patterns of the female crayfish, or rather the lack thereof, may be explained by an avoidance reaction since in our study female crayfish ceased movements once they had found a suitable shelter. According to Gherardi and Barbaresi (2000) such behaviour is to be expected from egg-bearing freshwater crayfish. Females thereby decrease the chances of encountering predators or aggressive conspecifics, hence increasing survival chances of the eggs. Choosing shallow areas as a habitat makes sense for protecting the offspring. Egg-bearing females of the congeneric northern clearwater crayfish (*Orconectes propinquus* Girard, 1852) stay buried in coarse gravel during egg incubation (Stein and Magnuson 1976). The most shallow littoral zone in Lake Constance features such coarse gravel, higher temperatures, higher oxygen saturation, and lower abundance of fish predators (Stoll 2010). All these factors contribute to safe development of the eggs and hence might explain why females moved into the shallow littoral zone and stayed there. However, further telemetry studies with more egg-bearing females within lakes are needed to support these assumptions. From the perspective of an invasive species' range expansion it is important to note that an egg-bearing female will possibly introduce many new propagules into a newly colonized area. For example, high female fecundity at the invasion front has recently been implicated in accelerating the range expansion of spiny-cheek crayfish in the Danube (Pârvulescu et al. 2015).

Ephemeral home-ranges and Lévy processes in crayfish

For the other non-egg-bearing crayfish, we assume that foraging activity is likely to be the fundamental trigger for movement patterns in our study. We assume this on the basis of three reasons. Firstly, the spiny-cheek crayfish mating season in Central Europe typically starts in September; our telemetry study was conducted from May through June when there was certainly no reproductive activity or consequent movements. Secondly, there were no major changes in environmental conditions in the lake throughout the study period (no storms, high waters or other factors) therefore movement patterns are unlikely to result from responses to a change in abiotic condition. Thirdly, the individuals are unlikely to moult during the study period because moulting of adult individuals typically starts later in the season, approximately in late August in preparation for the mating (Holdich and Black 2007). Females bearing eggs do not moult at all and if crayfish had moulted in the experiments we would have noted this because we were able to directly observe the individuals.

Movement activity during foraging depends on availability of food and food detection limits. Food items of crayfish, especially larger invertebrates (preferred food items of spiny-cheek crayfish (Anwand and Valentin 1996)), are likely to be patchily distributed within the study-area (Weatherhead and James 2001). Freshwater crayfish rely mainly on chemosensors with limited food-detection range to detect their food (Breithaupt 2001). Foraging movements have been used to explain general patterns of movement in crayfish in lotic systems which are termed the "ephemeral home range" (Gherardi et al. 1998; Robinson et al. 2000; Aquiloni et al. 2005; Loughman et al. 2013). Based on the theory of ephemeral home ranges the movement behaviour of crayfish in our study can be explained as follows: after finding a suitable feeding ground associated with a suitable shelter, individuals can optimize energy uptake by decreasing their moving distances and staying and foraging within a restricted area for a longer period of time (e.g. several days). The fact that most crayfish in the experiment used the same shelter for more than one night indicates that spiny-cheek crayfish indeed show some shelter-fidelity. Thereafter, when resources within the restricted area become less available, a longer movement would bring the crayfish again into unexploited feeding grounds (Gherardi et al. 1998; Robinson et al. 2000). The idea of ephemeral home ranges is related to a cornerstone in animal behaviour research: the so-called Lévy processes (or Lévy jumps, walks, and flights (Viswanathan et al. 1999)). The concept posits that most, if not all, animals show a movement pattern where extended periods of short movements are interspersed by larger movement bouts. Because this behaviour maximizes search efficiency for patchily distributed prey, natural selection should have favoured the fixation of such a conserved behaviour across taxa. Recently, however there have been several studies advocating a more careful approach to the confirmation or rejection of the presence of Lévy processes (see for example Edwards et al. 2012 and references therein). Clearly, our study was not designed to serve as a fundamental test of such a process. Our results however, strongly suggest that Lévy processes might play a role in crayfish movements and we argue that more crayfish telemetry data can contribute to the advancement of our understanding of Lévy processes. Importantly, in smaller brooks increased movements in early spring and late autumn were suggested to result from reproductive activity (e.g. the search for mating partners) (Buric et al. 2009 a, b). This indicates that not only the maximization of foraging efficiency influences crayfish behaviour.

Shelter-choice is non-specific

The acceptance of litter and other shelter types suggests a rather non-specific shelter preference in spiny-cheek crayfish. The observation that shadow alone was never chosen as a shelter supports the notion that crayfish require thigmotactic cues in combination with darkness as a shelter. This behaviour was found also in other crayfish species (Antonelli et al. 1999). Because we determined shelter choice by using telemetry as a non-invasive tracking method, we conclude that disturbance of the animals during recording of the shelter was much less than using other methods which require the animal to be caught for recording of the shelter. Providing shelters in excess probably precluded the competition for shelters, which can be fierce in crayfish and might influence shelter-choice (Chucholl et al. 2008). The non-specific shelter requirements of spiny-cheek crayfish in lakes could facilitate their spread and the displacement of native crayfish as for example Stucki and Romer (2001) suggested for the narrow-clawed crayfish. The observed acceptance of shelters consisting of hollow-ware litter that we found in this study may facilitate spiny-cheek crayfish range expansion. It might allow individuals to move across a littoral area where natural shelters are absent but where litter might provide artificial shelter.

How can we improve our knowledge on crayfish movement ecology?

Samples sizes in telemetry studies are notoriously small (Lindberg and Walker 2007). In our study, the number of individuals and recordings was restricted by the time and man-power needed to trace individual crayfish in one of the largest lakes in Europe. Taken together the crayfish moved along a littoral zone longer than 4 km and more than 300 m far into the lake. This means we tracked the underwater movements of a less than 10 cm large creature in an area as large as 5 km^2. Clearly, this limits our power to test, statistically, for theoretical predictions of animal movements, such as the presence of ephemeral home ranges. We can however, for the first time, describe the range of movements made by crayfish in a large lake, with the high resolution that only telemetry data provide. Ecological theory predicts that even if long-distance movements are only displayed by a few individuals, they are of great importance for the colonisation of new habitats, and can be used to estimate whole population dispersal rates (Kot et al. 1996). The results of distances covered by marked and recaptured crayfish further confirms the ability of spiny-cheek crayfish to move substantial distances within a few days. Interestingly, as previously found in experimental studies (Lozan 2000), spiny-cheek crayfish also showed diurnal movements to some extent. This is in contrast to native crayfish which are more strictly nocturnal and might have implications for the colonization ability of invasive crayfish because they move also during day not only during night (Bohl 1999; Lozan 2000; Barbaresi and Gherardi 2001). This observation, in concert with the phenomenon of ephemeral home ranges, warrants further study and holds promise to improve our knowledge on crayfish movement ecology.

Relevance for conservation and management

Knowledge on where and how fast an invasive species spreads is an essential basis to inform management and prevention measures. For example, several areas of Lake Constance are natural reserves of exceptional conservational value. Such high-value sites can be better protected by invasion of crayfish if managers are able to predict where and how fast they might be invaded. Recent research found that removal efforts of signal crayfish (*Pacifastacus leniusculus* Dana, 1852) are more efficient in halting the invasion into new areas when they are focused on the colonization front (Moorhouse and Mcdonald 2015). If the colonization front is reduced in density the rate of spread might decrease (Moorhouse and Mcdonald 2011). Our study provides some first data on how such a colonization front could advance and how it can be tracked. Recent research suggest that trait variability in invasive crayfish from invasion fronts might influence both the velocity of range expansion and the ecological impact during the invasion (Pârvulescu et al. 2015; Rebrina et al. 2015). Such research, in combination with data on movement and shelter-choice, could further help to predict impact and design targeted removals of invasive crayfish species. For example, by allowing for a more targeted exposure of the traps in areas where more crayfish are present and traps are more likely to be used, catch per unit effort could be increased. Previous telemetry studies with crayfish have, to our knowledge, only been conducted in running waters of smaller size or else information on movements was indirectly gleaned from catches in traps and not combined with active tracking methods. Our study provides the first high-resolution data on the spatial ecology of invasive crayfish in large lakes. This novel insight can help to inform existing or emerging management plans for preventing and mitigating the ever-increasing threat of invasive crayfish species.

Acknowledgements

We would like to thank all people that helped us with work in the field especially M. Hirning, R. Heiden, C. Osseforth and N. Womann. H. Richter's help for building the transmitters and S. Schillinger's GIS work is also greatly acknowledged. H. Hofmann is kindly acknowledged for providing temperature data. Comments by three anonymous reviewers and the editor helped to improve this manuscript. This work was supported by the DFG Special Collaborative Project SFB 454 'Littoral of Lake Constance'.

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The following supplementary material is available for this article:

Appendix 1. Individual specifications of studied crayfish.

Appendix 2. Crayfish tracking data maps.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2016/Supplements/AI_2016_Hirsch_etal_Supplement.xls