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Flood pulse effects on benthic invertebrate assemblages in the hypolacustric interstitial zone of Lake Constance

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Abstract – In contrast to rivers, the effects of water level fluctuations on the biota are severely understudied in lakes. Lake Constance has a naturally pulsing hydrograph with average amplitudes of 1.4 m between winter drought and summer flood seasons (annual flood pulse (AFP)). Additionally, heavy rainstorms in summer have the potential to create short-term summer flood pulses (SFP). The flood pulse concept for lakes predicts that littoral organisms should be adapted to the regularly occurring AFP, *i.e.* taking advantage of benefits such as an influx of food sources and low predator pressure, though these organisms will not possess adaptations for the SFP. To test this hypothesis, we studied the aquatic invertebrate assemblages colonizing the gravel sediments of Lake Constance, the AFP in spring and a dramatic SFP event consisting of a one meter rise of water level in 24 h. Here, we introduce the term 'hypolacustric interstitial' for lakes analog to the hyporheic zone of running water ecosystems. Our results confirm the hypothesis of contrasting effects of a regular AFP and a random SFP indicating that the AFP enhances the productivity and biodiversity of the littoral zone with benthic invertebrates displaying an array of adaptations enabling them to survive. The littoral zones of lakes deliver important ecosystem services by regulating flood effects, producing biomass and supporting biodiversity. To maintain and foster these services, the maintenance or reintroduction of natural water level fluctuations and the conservation of the habitat structures of the hypolacustric interstitial are urgently needed.

Key words: Water level fluctuations / flood pulse / benthic invertebrate / lake / hypolacustric interstitial

Introduction

All natural water bodies show fluctuations of the water level. The effects of water level fluctuations on ecological processes and biotic structures have been studied in detail for flood-pulsing rivers and tidal marine systems (see Junk and Wantzen, 2006 for review). Flood-pulse effects on lakes, however, are understudied (Wantzen *et al.*, 2008b). In Central Europe, this is mainly due to early human efforts to regulate the water level of lakes starting with efforts put forth by cities and monasteries in the Middle Ages (Wantzen *et al.*, 2008a). In a naturally fluctuating lake, the littoral zone is strongly affected by the hydrological dynamics. The change between wet and dry conditions generally results in variations in environmental conditions such as the thermal budget (Arscott *et al.*, 2001), wave impact (Scheifhacken *et al.*, 2007), trophic interactions (Wantzen *et al.*, 2002; Paetzold *et al.*, 2005) and oxic/anoxic conditions (Adis, 1997) in floodplains. The flood pulse concept (FPC) for river–floodplain-systems (Junk *et al.*, 1989; Junk and Wantzen, 2004) and its update for lakes (Wantzen *et al.*, 2008a) predict that a regularly occurring flood pulse enhances the productivity and diversity in the Aquatic-Terrestrial Transition Zone (ATTZ).

In Lake Constance, one of the few unregulated lakes in Central Europe, the water level drops from summer to winter, as precipitation is stored as snow in the alpine regions of the catchment during winter leaving large areas of the littoral zone exposed from December to about March. During this time the exposed superficial sediment layer generally freeze, while the layers below, which are oxygen-poor to anoxic, remain unfrozen. The drawdown process in the previously flooded littoral causes the development of zones of preferential flow of the surface-near the groundwater. These may also remain unfrozen, depending on the flow and temperature conditions. In spring and early summer, the melting snow and rainfall result in an increasing water level, flooding the eulittoral zone and reaching its maximum around June/July. In autumn, the water level falls again due to reduced rainfall and

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beginning of snow storage in the high altitude parts of the catchment (Fig. 2).

This study aims to determine whether the benthic fauna of Lake Constance is adapted to flood pulses, specifically if benthic invertebrates colonize the interstitial zone falling dry during winter and use this habitat in early spring and summer as it is slowly submerged by the surface-near the groundwater. According to the FPC, the regularity and predictability of the pattern of increase and subsequent decline in the water level is the prerequisite of an enhanced productivity and biodiversity in the lake littoral zone and the development of adaptations enabling species to survive in a fluctuating environment, and to profit by the "windows of opportunity" of environmental conditions provided by the change from dry to wet conditions and vice versa (Gafny *et al.*, 1992; Junk and Wantzen, 2004; Tockner *et al.*, 2010). Many species are adapted to utilize this "flood pulse advantage" (Bayley, 1995). Thus, we expected samples obtained during an annual flood pulse (AFP) in spring–early summer to contain benthic invertebrates physiologically adapted to survive water level fluctuations and able to take advantage of the benefits brought on by the flood pulse, such as an influx of food sources and low pressure of predators that are bound to open water.

On the other hand, rare and/or untimely changes between wet and dry conditions may have deleterious effects on the littoral fauna and flora, especially if early life cycle stages have a "physiological and phenological window of susceptibility" (Junk and Wantzen, 2004), such as fledglings of beach-breeding birds, or recently established vegetation. Even without these dramatic effects, the inaptitude of the fauna to use the flood pulse advantage of an untimely event can be anticipated.

In order to validate our hypotheses of opposing effects of regular and random flood pulses, we sampled invertebrates of the interstitial zone of the littoral of Lake Constance. Samples were obtained throughout the annual drawdown and return of the water level (AFP), beginning in December 2004, until May of the following year. During the AFP, we expected to find (1) aquatic invertebrates in the dry littoral zone adapted to withstand desiccation, cold temperature and even freezing. We anticipated (2) taxa with migration patterns and life cycle adaptations enabling them to not only survive in this fluctuating environment but also to make use of the advantages provided by the flood pulse. We hypothesized that (3) the re-colonization would be dominated by species benefitting from low predator pressure and possessing characteristics typically employed by r-strategists, such as short generation times, large clutch size and small body size.

A strong rainstorm in August 2005 gave us the opportunity to test the effects of randomly occurring flood pulses. The water level rose by nearly one meter within 24 h, therefore we continued sampling in August and September 2005 (summer flood pulse (SFP)). We expected the randomly occurring SFP to be met with (1) a general lack of adaptations to survive flooding; (2) finding terrestrial organisms below the water level and aquatic organisms stranded on dry land after the water had begun its decline. Similar to the AFP we anticipated (3) a slow re-colonization of the area affected by the flood with r-strategists being the first to return and (4) finding only few or no predators in the littoral zone being re-exposed after the water receded.

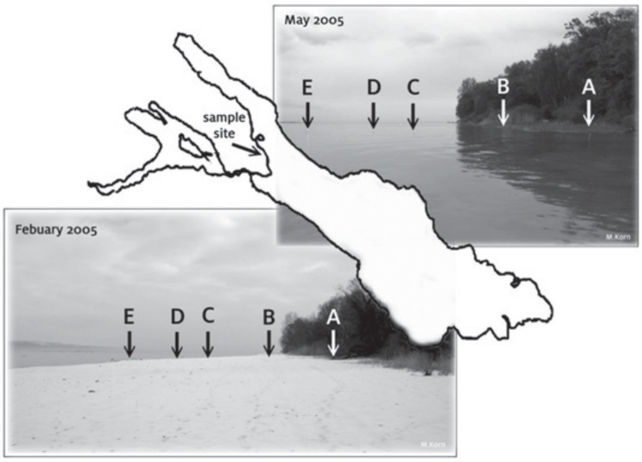

Fig. 1. Sample site at Lake Constance depicting the ATTZ: terrestrial habitat in winter (February 2005) turns into an aquatic habitat in summer (May 2005).

We introduce the term 'hypolacustric zone' and its synonym, 'hypolacustric interstitial' here, in analogy to the 'hyporheon' or 'hyporheic interstitial zone' of rivers and streams (Orghidan, 1959; Schwoerbel, 1961). The hypolacustric zone is defined as 'the wet or humid interstitial pore-space in the sediments of lakes. It is an ecotone, which is transient to the epibenthic zone at the sediment surface above it and to the groundwater zone (*stygon*) below it. Due to water-level fluctuations, variable porosity of the sediments and variable recharge/discharge situations of the groundwater, it may expand and contract along with the littoral zone of the lake and it may be transient to the hyporheic zone in in- and outflow areas of lakes.' In the case of prevailing sandy sediments, the term is synonymous to the *mesopsammon* known from freshwater (Pennak, 1940) and marine (Remane, 1952) habitats. We avoid the use of the Greek term 'limne (λίμνή)' for 'lake' here as this would have caused confusion with the existing term 'hypolimnion'.

Material and Methods

Sampling site and sampling dates

All samples were taken in the littoral zone of Lake Constance between Konstanz-Egg and the 'Littoral Garden' (Fig. 1 and see Scheifhacken *et al.* (2007) or Pabst *et al.* (2008) for a site description) The site is characterized by gravel sediments in the upper section, which are increasingly covered by fine lake sediments (organic matter mixed with calcium carbonate deposits

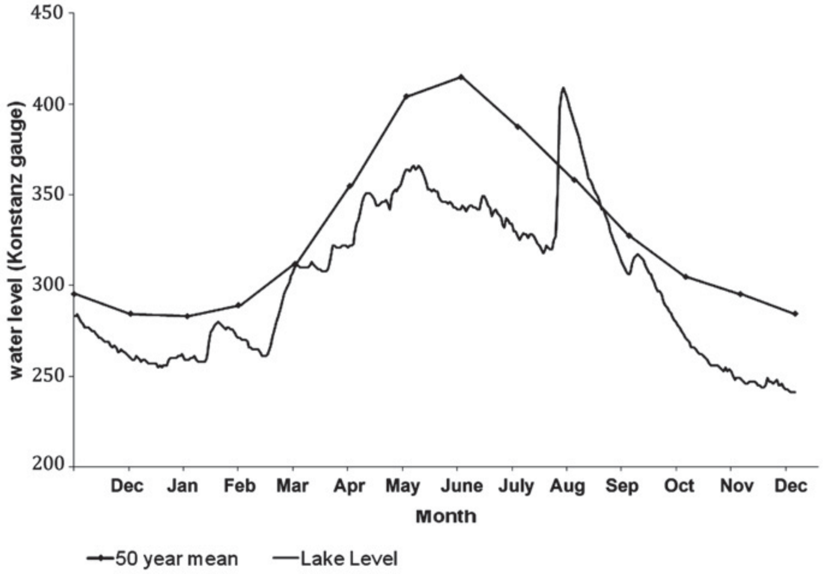

Fig. 2. Water level in Lake Constance from December 2004 to December 2005 compared to the 50-year mean.

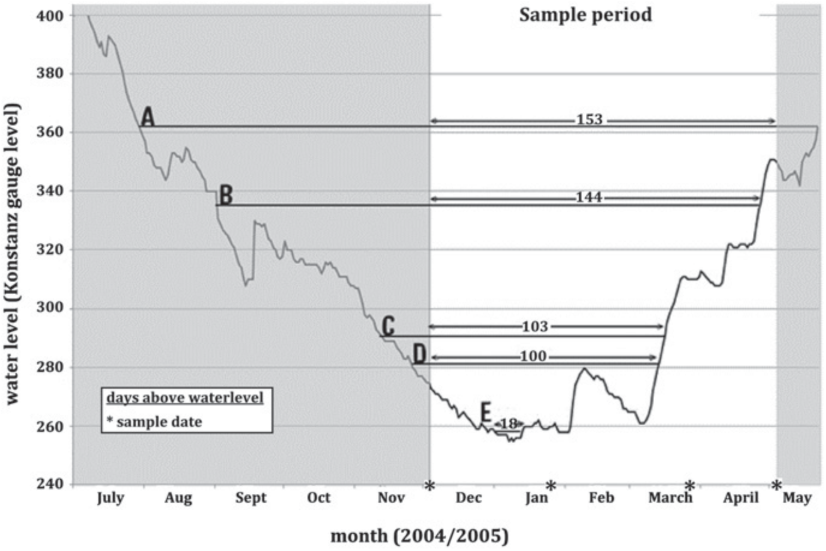

Fig. 3. Water level in Lake Constance around the AFP (July 2004–May 2005) showing the number of days the sample levels A–E were above the water level before being sampled. Sample dates are marked*.

originating from calcite precipitation and activities of characean macro algae). The sampling process during the AFP took place on December 2, 2004 and January 24, March 21 and May 5, 2005. Five samples levels (levels A–E) were selected parallel to the water level (Fig. 2). They were established with the intention of level A remaining dry and the lowest level, E, being submerged throughout the sampling period. The uppermost and the lowest levels were 32.35 m apart. On the first sampling date, level E was marked at 258 cm (Konstanz gauge level), 0.25 m below the water line. Level A (364 cm) had been dry for 116 days before the first sampling date. The levels were marked with a wooden stake and measured with a laser level (Fig. 3). Data loggers were buried at each level in order to establish the temperature in the sediment during the sampling period; the temperature was logged every 10 min. The loggers were recovered periodically and then reburied, resulting in three sample periods: December 2, 2004–January 27, 2005, February 2, 2005–March 24, 2005 and March 23, 2005–March 24, 2005. Due to vandalism, not all periods could be logged in all sample levels.

The initial flooding event of the SFP occurred on August 22, 2005. The previously established AFP sites were flooded at this time; therefore, we decided to take samples above and below the waterline, thereby following the "moving littoral". We sampled on August 26 (4 days past flooding) and again on September 2, 9 and 20, respectively 7, 14 and 25 days after the initial flood. Four days after the summer pulse the water level was located at 409 cm (all data obtained from the Konstanz gauge level). Samples were obtained 10 cm above (+ 10 cm) and 30 cm below (− 30 cm) the water level, with three samples each from the crude and more fine substrate, totaling to six samples taken above and six samples below the waterline. Seven days after the flood, with the water level at 387 cm, samples (three replicates per level from the crude and fine substrate) were obtained 10 cm above and 30, 50 and 100 cm below the waterline. Fourteen days after the initial flood with the water level at 359 cm and 25 days after the flooding (water level 333 cm) samples were obtained above and below the waterline in the same fashion as 4 days after the flooding.

Sampling process and identification

On each sample date three replicates were obtained at each level using a 25 × 25 cm aluminum frame pressed into the sediment. The top 6 cm were extracted using a trowel and placed in a bucket. When the sample site was below the water level, benthic organisms were stirred up and collected in a bucket using a landing net. Oxygen concentrations in the interstitial water were not measured; however, the dark to black color of the sediments deeper than 4–6 cm indicated low to lowest concentrations (Marmonier *et al.*, 2004). The exact sampling place was slightly shifted for each subsequent sampling. In spring, holes created through sampling quickly filled with water. The sediment was rinsed in a metal sieve (mesh size of 1 × 1 cm) and the filtrate then poured through a 200 μm sieve. Gravel and stones were removed and placed in a glass dish and searched for mussels and snails, which removed and conserved in ethanol. Samples were conserved in 70% ethanol and stained using Rose Bengal. Animals were picked out under a stereo microscope and subsequently identified at the level of order, family or genus. Because of the high content of early larval stages, identification at a higher resolution was not possible. The results were statistically analyzed by ANOVA using the computer program Statistica.

Results

Water level development compared to 50-year mean

In January, the water level was approximately 65 cm below the 50-year mean at 260 cm (Konstanz gauge level) and then began to steadily increase during the AFP, rising to about 360 cm in June, but remaining below the 50-year mean which usually continues to increase until mid July (~ 410 cm) before declining again and reaching its minimum around December (Fig. 2). Level A was dry for 120 days before the sampling period began and remained dry throughout May 15 (153 days), while level B had been dry for 92 days before the sampling period started and remained dry for 144 days. Levels C and D were above the water level when the sampling process started and remained dry for 103 and 100 days, respectively, before the water flooded these levels. The lowest sample level E was flooded when the sampling began and ended but fell dry for 18 days during January (Fig. 3).

The summer of 2005 was a dry summer with the water level of Lake Constance remaining approximately 90 cm below the usual level at this time of year. On August 15, the water level was at 327 cm Constance gauge level dropping to 318 cm by August 15 and then increasing to 327 cm again by August 22. A strong rainfall on August 22 caused the water level to increase by 52 cm breaking the previous 24-h record and affecting the entire pre-alpine region. On August 23, the waterline was at 353 cm further increasing to 409 cm by August 26 before beginning its decline. On September 22 with the water level at 329 cm, the lake had almost reached its previous level again. With only little rain in the following autumn the water level continued dropping until the end of the year (241 cm). December saw a record low waterline, dropping 5 cm below the previous lowest December level of 1948.

Temperature

Unfortunately, due to vandalism and other difficulties in recovering and reinstalling the temperature loggers at various levels we do not have continuous data for each level. We are able to determine however, to which extent invertebrates surviving on dry ground would need to be able to survive temperatures below and around freezing.

At level A, the temperature ranged between 0 and 1 °C for 31 days during December and January and dropped below freezing only on 1 day. At level B, the temperature dropped below 0 °C on 49 days during December and January; for 38 days the temperature ranged between 0 and 1 °C. The data logger from level C provided information only during two sample periods (February 12, 2004–January 27, 2005; March 24–May 18, 2005); the temperature was just above freezing (0–1 °C) on 29 days, mainly in January, while dropping below 0 °C on 10 days. At level D, the temperature sank beneath the freezing point on only 13 days during the end of February/beginning of March, from January to March the temperature ranged between 0 and 1 °C on 31 days. Finally, the temperature in the sediment of level E was sampled only during the last two sample periods. During this time, the temperature did not drop below 0 °C and ranged between 0 and 1 °C on 3 days.

At level B, the temperature dropped below 0 °C on 49 days during December and January; for 38 days the temperature ranged between 0 and 1 °C. The data logger from level C provided information only during two sample periods (February 12, 2004–January 27, 2005; March 24—May 18, 2005); the temperature was just above freezing (0–1 °C) on 29 days, mainly in January, while dropping below 0 °C on 10 days. At level D, the temperature sank beneath the freezing point on only 13 days during the end of February/beginning of March, from

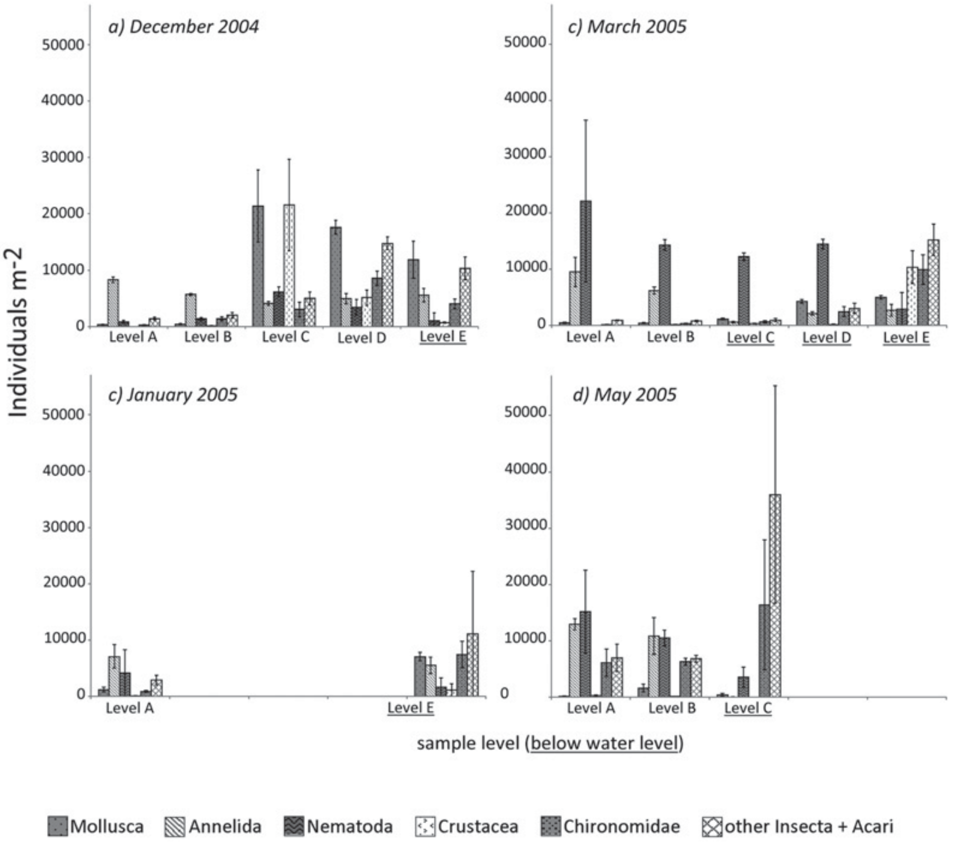

Fig. 4. Temporal and spatial distribution of main taxa found during the AFP at the different sampling dates: (a) December, (b) January (c) March and (d) May. Underlines indicate level was flooded at the time of sampling. In January, only levels A and E were sampled, in May only levels A–C. Error bars depict standard error.

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Benthos during the spring–early summer floodpulse (AFP)

The invertebrates contained in the benthos samples obtained during the AFP of Lake Constance showed an overall high dynamic and abundance of species belonging to the Epibenthos (Fig. 4). The samples obtained from December 2004 through May 2005 contained 24 different taxa. Despite the high variance between the sample replicates a general temporal and spatial distribution of the benthic invertebrates found in the littoral of Lake Constance from December to May was identified. The samples from the exposed interstitial of the littoral zone had higher abundances of oligochaetes and nematodes compared to those parts of the littoral which remained flooded. ANOVA (time × site) showed significant differences for total abundance ($P < 0.001$), Nematoda ($P < 0.001$), Oligochaeta ($P = 0.002$), Bithynia ($P < 0.001$) and Chironomidae ($P < 0.001$). Densities generally decreased over winter. The sites in the littoral zone which remained flooded had higher abundances of Chironomidae, *Pisidium, Radix* and *Bithynia*, as well as the crustacean taxa Ostracoda, Collembola and Harpacticoida. Additionally, Acari and the insect orders of Ephemeroptera and Trichoptera had higher abundances in the flooded zones when compared to the exposed littoral. *Dreissena. polymorpha* and Hirudinea were found exclusively in the flooded sediment. Taxa such as Nematoda and Annelida were found more frequently at higher, drier levels. The nematode abundances increased over winter, while oligochaetes, which were frequently found encapsulated, decreased. Interestingly, the mussel genus *Pisidium* occurred with an average density of 830 ind.m^{-2} over the flood gradient during winter. Densities for aquatic and semi-aquatic Diptera were also relatively high (*Bezzia* 50, Ceratopogonidae 200 and Dolichopodidae 60 ind.m^{-2}). Crustaceans showed a strong connection to the waterline and were found more frequently below at submerged levels. They were able to survive desiccation. Early larval stages of the ephemeropteran species *Ecdyonurus dispar* were exclusive found at sites above the water level of the lake. There is anecdotal evidence of *E. dispar* utilizing small pools which are filled with water before the returning water level for

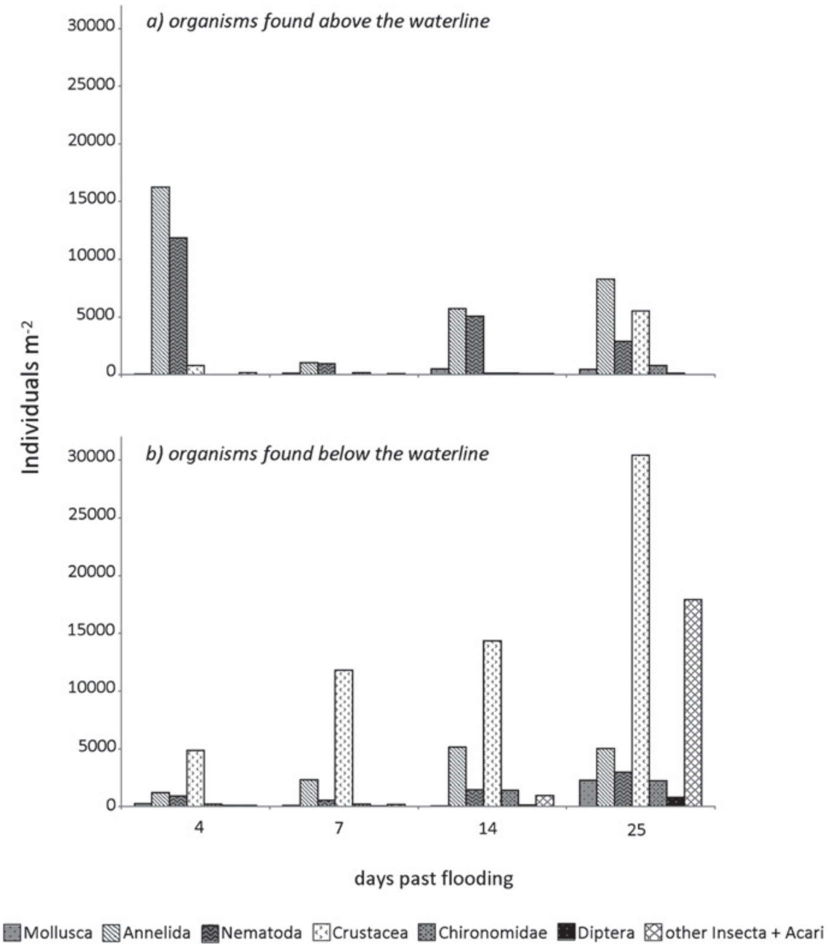

Fig. 5. Temporal and spatial distribution of invertebrates found during the SFP. (a) Depicts the main taxonomical groups found above the waterline; (b) those below the waterline.

hatching and early development (Korn, 2001). Our sampling data confirm this; when sampling holes and other crevices filled with (ground)water in spring, the species was found in high quantities (120–500 ind.m^{-2}) in these small pools.

Benthos during the SFP

Over the total sampling period after the SFP a total of 26 taxa were identified. The composition of the taxa found above the waterline proved to be highly dynamic, changing from sample date to sample date as the water receded and increasing in diversity as time progressed (Figs. 5 and 6). There was a general decrease in total abundance, with a severe cave-in 7 days after the initial flooding event. The total abundance subsequently increased again over the next sampling dates, yet did not return to the original levels of abundance samples directly after the SFP. In general, the samples retrieved from above the water line were less diverse and had a lower abundance of benthic invertebrates than the samples obtained below the water line. With the exception of the first sampling date, when the samples obtained from above the water line were from an area unaffected by the flood pulse, there was an increase in abundance and diversity of the invertebrates found below the water line as the water levels returned to pre-flood levels.

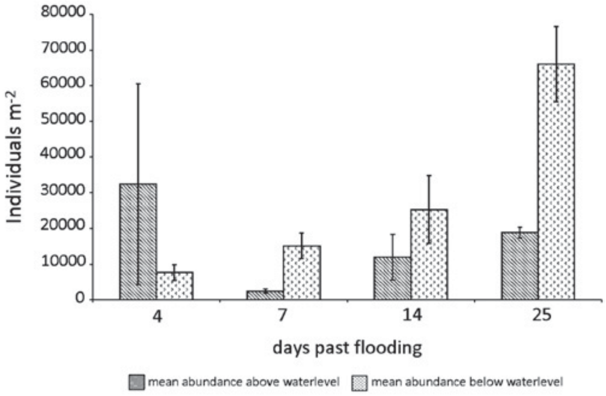

Fig. 6. Mean abundance of benthic invertebrates found above and below the water level 4, 7, 14 and 25 days past flooding. Error bars depict standard error.

Table 1. Floodpulse adaptations of Benthic invertebrates to the fluctuating environment of the littoral zone.

Floodpulse adaptations	Examples
Migration and re-colonization	
With the water level	Aquatic organisms, *e.g. Dreissena*, mites[1,2]
To higher (drier) ground	Terrestrial organisms, *e.g.* mites, Chironomidae[3–6]
Burrowing	*e.g.* Oligochaeta, decapods and beetles[2,7]
r-strategies	*e.g.* Chironomidae and mites[8]
Physiological and behavioral adaptations	
Inundation	Terrestrial organisms, nematodes[3]
Desiccation	Aquatic organisms, *e.g.* rotifers, bivalves, leeches and ostracods[9,10]
Freezing	*e.g.* gastropods, Oligochaeta, nematodes and Chironomidae[11–14]
Anoxic conditions	*e.g.* Ephemeroptera[15]
Use of flood borne resources	*e.g.* army ants feeding on other terrestrial invertebrates driven out of floodplain by the floodpulse, grasshoppers feeding on stranded algae, fish feeding on buoying terrestrial invertebrates, riparian arthropods feeding on aquatic fauna[16–20]
Life history adaptations	
Oviposition ("egg banks")/resistant eggs	*e.g.* Diptera, Plecoptera, Ephemeroptera, anostracans, notostracans, copepods and ostracods[2,21–24]
Resistant stages/diapause	Algae, flagellated protozoans, flatworms, tardigrades and chironomides[2]
Aquatic and terrestrial stages	Insect taxa and nematodes[2]

[1]Balogh *et al.* (2008), [2]Williams (2000), [3]Adis and Junk (2002), [4]Wantzen *et al.* (2008a), [5]Hunt and Jones (1972), [6]Steinhart (1999), [7]White and Miller (2008), [8]Weigman and Wohlgemut von Reiche (1999), [9]Nolte, (1988), [10]Pennak, (1940), [11]Gérard (2001), [12]Olsson (1981, 1984), [13]Timm (1996), [14]Lencioni (2004), [15]Nagell and Fagerstrom (1978), [16]Adis *et al.* (2001), [17] Bastow *et al.* (2002), [18]Wantzen *et al.* (2002), [19]Sabo *et al.* (1999), [20]Paetzold *et al.* (2005), [21]Steinhart (1999), [22]Humpesch (1980), [23]Marten (1990), [24]Furey *et al.* (2006).

Discussion

AFP versus SFP effects

The results of the AFP demonstrate that the hypolacustric interstitial of Lake Constance is settled with life throughout winter, despite the unfavorable conditions in the dry littoral zone. Aquatic, semi-aquatic and terrestrial invertebrates are able to survive in the exposed littoral zone surviving low temperature, freezing, desiccation, low oxygen and fluctuating temperatures and water levels. The composition of the benthic invertebrates found in the samples during the AFP confirms our hypotheses of a high benthic diversity and the existence of flood pulse adaptations enabling organisms to survive in this harsh environment. The samples show a high dynamic in both the spatial and temporal patterns. The flood pulse adaptations utilized by the organisms can be grouped into three categories: migration, physiological and behavioral adaptations, and life history adaptations (Table 1). Aquatic taxa showed strong connection to the water level and were found at higher abundances at sampling levels just below or just above the water line, though several species were shown to have the ability to survive on dry land before the water returned in spring. Mollusks showed both migratory behavior (*Radix*, *Bithynia:* above or along the 'moving littoral', *Dreissena:* just below it) and the physiological capability of withstanding cold temperatures and desiccation when remaining in the dry-fallen upper zone (*Pisidium*). Crustacean taxa were found more frequently at submerged levels. The establishment of egg banks by several species of aquatic insects is an example for life history adaptations (Steinhart, 1999;Williams, 2000; Table 1). The larvae then hatch and develop in small pools, tightly tying the life history of these species to the pattern of water level fluctuations found at Lake Constance. With the return of the water in spring, Chironomidae, which are classic r-strategists, are among the first organisms to re-colonize the ATTZ. The most prominent example of our study was the mayfly *E. dispar* (Curtis, 1834). This species apparently profits by the warm temperatures and the absence of predators in the small water bodies above the water line to develop fast. When these become connected to the lake water, larval stages may be large enough to escape from predators. Only larger instars were found in benthos samples in Lake Constance (Scheifhacken *et al.*, 2007; Baumgaertner *et al.*, 2008) supporting our view that the exposed hypolacustric zone provides an important habitat for larval development of this and other taxa, such as the stonefly genus *Leuctra*, whose larvae were also found in the same habitat in an earlier study (Korn, 2001). In Britain, Humpesch (1980) found an egg diapause in running water populations of *E. dispar* but not in lake populations; however, these lakes may have other hydrological conditions as Lake Constance. Here, we observed a synchronized emergence in late July/early August, when water levels generally drop. The long lag time between adult emergence/oviposition and occurrence of the larvae points toward an egg or early larval diapause as an adaptation to the flood pulse. The same may be true for Tipulidae, which we observed to oviposit in the moist organic debris above the water line in summer.

When interpreting the results of the SFP, it is important to keep in mind that as the water receded the sampling levels moved, too. The initial samples were taken

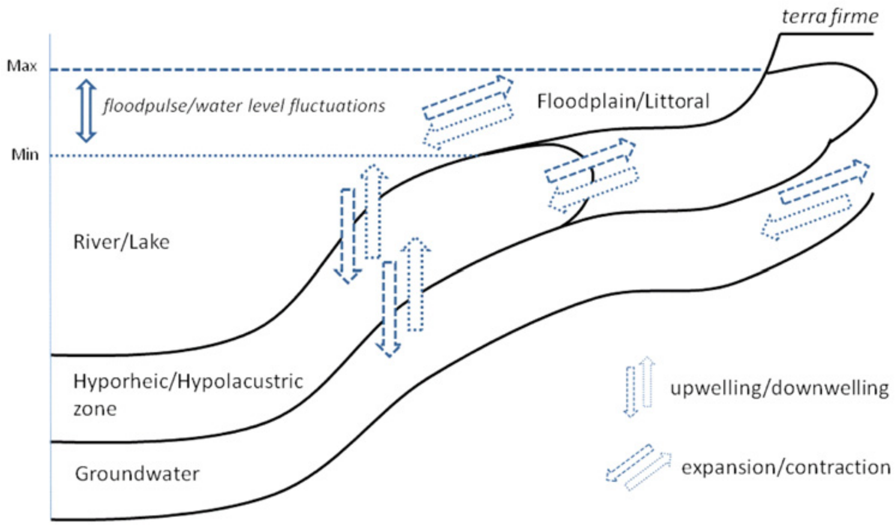

Fig. 7. Analogies between hyporheic and hypolacustric zones, transition between flood plains and interstitial zones. Max = maximum water level, Min = minimum water level (Graph: Karl M. Wantzen).

right after the flood pulse show aquatic organisms being found above the water line after they have been washed up and terrestrial organisms contained in the submerged samples that were swept up by the water. The samples obtained 7 days after flooding showed a very low abundance indicating that the flood pulse had wiped out large parts of the populations. On subsequent sample dates, there is a pattern of increasing diversity and abundance of benthic invertebrates found above the water line as the water recedes. Chironomidae were among the first to re-colonize the ATTZ, as were nematodes. Both taxa contain pioneer species with life cycles and behavioral adaptations that allow them to quickly establish themselves after such a sudden event.

The samples obtained from below the water line display a similar pattern of increasing diversity and abundance as time progressed and normal conditions returned after the disturbance of a flash flood. As the water recedes, the sample levels move back to areas that were already submerged before the flood pulse and are undisturbed by the flood pulse. On day 7 after the flood pulse samples were taken at three levels below the water line (data not shown) and the results show a clear pattern of increasing abundance and diversity with depth indicating that the randomly occurring SFP severely disrupted the benthic invertebrates inhabiting the ATTZ.

When comparing the differences between the two flood pulses it is important to keep in mind the low taxonomical resolution, which makes it difficult to compare details. We have supplied a list of organisms found during the AFP and SFP in the Appendix (Table 2, available online at the address: www. limnology-journal. org), which further emphasizes the difference in diversity. In addition, one must consider the differences in sampling. For the AFP, we had predetermined sample levels but as the SFP came unexpectedly, we could not create sampling levels but were forced to use a different approach that of sample levels which moved over time as we were always sampling above and below the waterline as it receded.

Nevertheless, our results do indicate contrasting effects of a regularly occurring AFP and the randomly occurring SFP on the benthic invertebrates inhabiting the littoral zone of Lake Constance. During the AFP, the littoral zone is settled throughout winter, the fauna dominated by nematodes, oligochaetes and chironomids. As discussed earlier, many of the invertebrates have flood pulse adaptations making them uniquely able to survive desiccation and/or cold temperatures. Aquatic insects that establish egg banks demonstrate several species have incorporated their habitat into their life cycle and are even dependent on the AFP in order to fully develop. The results of the SFP depict the disturbance caused by such an event. Dead mollusks and crustaceans were found washed up in terrestrial areas and terrestrial organisms were found drowned. In both cases, r-strategists such as Chironomidae are among the first to re-colonize the ATTZ. There is a range of scavenging and predatory invertebrates known from pulsing tropical lake (Adis *et al*., 2001) and stream (Wantzen and Junk, 2000) habitats and from temperate streams (Paetzold *et al*., 2005); however, to our knowledge, the adaptations of terrestrial invertebrates of the littoral zone of lakes to profit by the carcasses of this kind of event have not yet been studied.

Analogies between hyporheic, hypolacustric interstitial and floodplains

In his seminal paper, Ward (1989) pointed to the fact that the hyporheic zone of streams varies in its extension due to water level fluctuations. Following the definition of the hypolacustric zone, we consider the same to be true for the lake littoral. There are important analogies between both these zones and floodplains considering this expansion and contraction cycle (Fig. 7). The flooding of the surface water bodies is accompanied by an increasing hydrostatic pressure of the water column on the interstitial zone, leading to a recharging situation, i.e. the penetration of surface water into the interstitial and groundwater zones. This water is generally oxygenated and carries suspended organic matter including living planktonic organisms and debris particles into the pore space of the interstitial zones, where they become attached to biofilms and metabolized by microbes or metazoans. The enrichment effects of floods described in the FPC (Junk *et al.*, 1989; Junk and Wantzen, 2004) can thus be analogized to that of the recharging situation. *Vice versa*, the drawdown in the littoral zones of rivers and lakes results in an outflow of groundwater, which is often charged with reduced elements (e.g. iron), which become oxidized at the surface and may form biogeochemical and biotic hot spots, as can be often observed in the floodplains of tropical rivers (Wantzen and Junk, 2006).

During drought, the interstitial zones represent an important refuge for aquatic organisms, especially invertebrates, which profit by the moisture trapped in the pore space and the difficult access for predators. As our study has shown, several species oviposit on the dry-falling littoral to protect their eggs during winter. When water levels increase, the pore space and small ponds fill with water that heats up much faster than the main water body, and provide food and shelter for the hatching offspring.

These analogies between the interstitial zones and the floodplains of lakes and rivers show that it is important to consider the sub-surface patterns and processes when studying floodplains and planning their management and conservation. For both flowing and standing waters, the hydrological dynamics and the available sediment structures are a key factor of the physical conditions of the habitats. Many wind-protected lake habitats and depositional zones of rivers tend to have very small pore spaces (which, however, can be widened by ecological engineers such as worms, crustaceans and insects) that limit its lateral and vertical extension, whereas erosional, wind-exposed lake sites and fast-flowing rivers certainly have larger interstitial zones with wider pore space and more frequent turnover of the sediments, which acts as a "rejuvenation" process for the filtering capacity of the pore space.

Perspectives

Our results show very basic patterns and first indications of the effects of an AFP in contrast to random events (e.g. SFP). Further research, in particular more detailed studies, is needed to better understand the mechanisms and patterns caused by flood pulses in the lake littoral and its interstitial zone. This understanding could prove valuable as the current change in climate conditions will affect the occurrences of both the AFP and SFP in lakes such as Lake Constance. Current climate models predict that random SFPs will become more common while the AFP will become less pronounced. The increase in temperature is resulting in less snow in the catchment and an earlier snowmelt. Thus, the mean water level is increasing and its fluctuations are becoming smaller. A smaller AFP could affect the diversity and abundance of the benthic fauna by reducing the extension of this important habitat.

Understanding the effects of naturally fluctuating water levels in lakes could also have important implications for the regulation of water reserves. Studies have already shown that different fluctuation levels affect the diversity (Aroviita and Hämäläinen, 2008). Being able to determine an optimum fluctuation level could become vital to upholding the productivity of littoral zones of lakes and water reserves.

In summary, our results show that the littoral zone of Lake Constance provides a refuge during winter though survival requires special adaptations, such as physiological tolerance of desiccation and cold temperatures, life history strategies and migration patterns. The regular pattern of the AFP is the key factor toward increasing the diversity and productivity of the littoral zone. Extreme events occurring out of order such as the SFP exceeds the physiological capabilities of parts of the benthic fauna, effectively wiping out large parts of the population. In both cases, the flood pulse has a sort of "system re-set function" and pioneer species are among the first to re-colonize the ATTZ.

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