

## Crayfish as geomorphic agents and ecosystem engineers: Biological behavior affects sand and gravel erosion in experimental streams

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### *Abstract*

Effects of animals on the transport of solids (e.g., sediments) can modify earth-surface processes and landforms (role as geomorphic agents) and resources for other organisms (role as ecosystem engineers). Therefore, we studied the impact of crayfish (*Orconectes limosus*) behavior on sand-gravel erosion and bottom habitat over riffle-pool sequences in experimental streams. We manipulated the availability of crayfish food and refugia. Refugia availability had clear effects on overall crayfish activity. The establishment of dominance hierarchies among the crayfish produced patterns in crayfish activity that differed between riffles and pools. Crayfish activity significantly affected sand and gravel erosion. High local sediment erosion averaged  $\approx 2.8$  (riffles) and  $\approx 1.4$  (pools) kg dry weight  $m^{-2} d^{-1}$  when crayfish hierarchies were established and refugia were available. Removing the refugia increased these rates to  $\approx 4.0$  (riffles) and  $\approx 3.2$  (pools) kg dry weight  $m^{-2} d^{-1}$ . This direct erosion caused by crayfish should be lower than that caused by floods. Crayfish distinctly (1) increased bedform roughness (riffles), (2) decreased sand dune height (pools), (3) shifted the transition between gravel (riffles) and sand (pools) downstream, (4) decreased sand in gravel interstices (riffles), (5) decreased filamentous algae growth on gravel (riffles), and (6) decreased biofilm cover on sand dunes (pools). These sediment changes due to crayfish activity at baseflow should have opposite effects on sediment erosion during subsequent floods. Crayfish impact on physical habitat at baseflow could largely affect population and community structure of the benthos, as well as egg survival of gravel-breeding fish.

The effects of animals on the transport of solids (e.g., sediments) concern geomorphology and ecology, as there is growing evidence that animals may play a role as geomorphic agents (Butler 1995) or ecosystem engineers (Jones et al. 1994). Thus, studying these effects is fundamental for a thorough understanding of earth-surface processes and landforms (Butler 1995) and of resource modifications (e.g., physical state changes) for other species (Jones et al. 1994). For streams, the obvious examples of animals as geomorphic agents or ecosystem engineers are dam-building beaver (Jones et al. 1994) or salmonids that erode stream-bed gravel

during the construction of spawning nests (Kondolf et al. 1993; Montgomery et al. 1996). The less obvious examples of stream animals having such physical effects on bottom sediments concern primarily invertebrates that may increase or decrease the transport of solids in running water systems.

Many stream invertebrates are bioturbators of fine organic and inorganic sediments: (1) freshwater shrimp may erode fine sediments deposited on the surface of coarser bottom material (Pringle and Blake 1994); (2) stream insects increase the particle export from a small stream catchment (Wallace et al. 1982, 1993); (3) stream mayflies create a flow vortex to erode surface sand, so that they can prey on small interstitial invertebrates (Soluk and Craig 1990); and (4) hungry predaceous stoneflies are so active in their pursuit of food that they reduce the fine sediment in the interstices of coarse bottom material in riffle habitats (Statzner et al. 1996; Zanetell and Peckarsky 1996). In contrast, silk-producing caddisflies prevent the erosion of stream gravel by silk bridges fixing individual gravel pieces together (Statzner et al. 1999). In addition, fecal pellet production by stream black flies may reduce the transport of fine particles (Wotton et al. 1998).

All these studies demonstrate the potential importance of stream invertebrates as geomorphic agents and/or ecosystem engineers. However, the evidence for these various function-

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al roles is not always solid. It is least solid for the role of invertebrate behavior that increases erosion of inorganic sediments from stream riffles. Statzner et al. (1996) only speculated that hungry (and thus more active) stoneflies may erode  $\approx 200\text{--}400\text{ kg sand m}^{-2}\text{ yr}^{-1}$  from such habitats, and it remained unclear if this sediment was transported from riffles toward pools or even further downstream.

In order to quantify the effect of an invertebrate on the sediment transport across riffles and pools, we designed an experiment studying invertebrate behavior and sand-gravel erosion at riffle-pool conditions. We worked with nonburrowing aquatic crayfish that can move bottom sediments in three different ways: (1) the third and fourth pair of the walking legs provide most of the propulsion during walking (Pond 1975), i.e., the friction between the tip of these legs and the bottom should be relatively high; (2) frightened crayfish escape by backward swimming achieved by tail flips; the take-off thrust produced by the uropods and the telson is  $\approx 1\text{ N}$  (Webb 1979), i.e., escaping crayfish create a considerable force above a small bottom area when taking off from it; and (3) crayfish that walk downstream in faster currents press the uropods firmly on the substrate and jab the claws periodically into the substrate to slow their movement (Maude and Williams 1983). These mechanisms of particle erosion may be particularly effective during fights, as crayfish exhibit strong interspecific and intraspecific aggressive behavior (Lodge and Hill 1994). Shelter availability (Lodge and Hill 1994), the establishment of dominance hierarchies (Guiasu and Dunham 1997), and food availability (Hazlett et al. 1975) modify this aggressive behavior, as well as crayfish mobility (Bovbjerg 1959). These results suggest that crayfish have the potential to move sand and gravel, and that their behavior could modify this potential.

We also worked with crayfish because this group is widely distributed (partly through species introductions: Laurent 1997) and often dominates the macroinvertebrate biomass in streams, lakes, or ponds (Momot et al. 1978). For example, crayfish biomass in streams may be as high as  $300\text{--}400\text{ g wet weight m}^{-2}$ , and density may reach  $33\text{ individuals m}^{-2}$  (Momot et al. 1978). Finally, we used crayfish because the species are rather flexible in habitat use. They often occur in lakes as well as running waters and use relatively different flow conditions in the latter (Maude and Williams 1983; Gore and Bryant 1990; Laurent 1997). This flexible habitat use matched our question about sediment transport across riffle-pool sequences.

We wished to test previous speculations about the role of stream invertebrate behavior as geomorphic agent or ecosystem engineer (Statzner et al. 1996) under well-controlled experimental conditions. Therefore, we replicated natural riffle-pool conditions and natural river densities of the crayfish *Orconectes limosus* (Rafinesque) in experimental flumes and compared these treatments to replicated controls. We manipulated availability of food and crayfish refugia. We quantified the erosion of sand and gravel during the experiment and bottom habitat (interstitial conditions, bedform roughness, algae growth) at the end of the experiment. We also quantified crayfish behavior at four occasions to relate sediment erosion to general patterns in crayfish behavior (omitting subtleties of the behavior of the individual groups here).

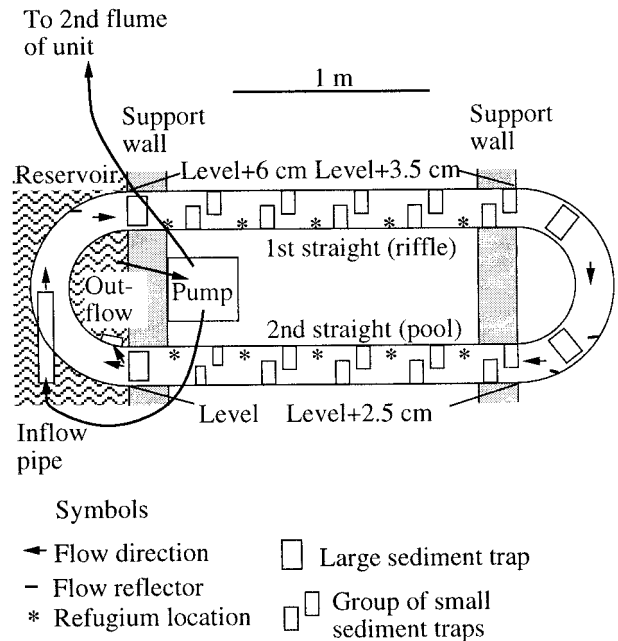


Fig. 1. Aerial view of one experimental flume. One pump discharged toward a unit of a pair of flumes, and we replicated five of these units. The most important details were that (1) the flume was tilted (1.25% slope from the beginning to the end of each the first and second straight); (2) water was pumped uphill toward the highest flume point; (3) excess water was discharged to a reservoir common for all flumes and pumps; (4) flumes were installed outdoors; and (5) the first straight represented riffle and the second one pool conditions (see Fig. 2).

## Materials and methods

*Design of the experimental flumes*—We worked with a flume type that enables a good replicability of hydraulic conditions and provides a continuous sequence of riffle-pool conditions for the crayfish to avoid the problems of migration barriers encountered in straight experimental flumes (see Borchardt and Statzner 1990). Our flume was oval (Fig. 1) and made from PVC (4 mm), so that the oval could be tilted. Thus, we could create a slope in the flume and we used the energy of the water pumped into it to bring water uphill to the highest flume point. The flume had a bottom area of  $1.25\text{ m}^2$ . We added flow reflectors to the outer radius directing the water into its first and second straight (Fig. 1). A net (mesh size: 2 mm) closed the outflow opening. A tailgate allowed adjustment of the outflow.

Flexible pipes connected the inflow pipes of a pair of flumes to one centrifugal pump (0.55 kW; 15,000 rpm; maximal discharge  $18\text{ m}^3\text{ h}^{-1}$ ). Valves controlled the discharge toward each of the flumes. We had five units of paired flumes. The five pumps got their water from one common reservoir and the 10 flumes discharged to this reservoir. The water volume in the reservoir was  $6.48\text{ m}^3$ . It received a constant groundwater discharge of  $3.6\text{ m}^3\text{ h}^{-1}$  (immersed vertical pump). About half of this discharge reached the reservoir at one end (flume 10), and the other half reached it at the middle of the reservoir (between flumes 5 and 6). A reservoir overflow (near flume 1) discharged excess water

toward a pond. We covered the reservoir with a strong plastic net to prevent material from falling into it, as these installations were outdoors (in the floodplain of the Rhône River, Parc de Miribel, upstream of the city of Lyon). We oriented the reservoir east–west, so that the flume ovals were oriented north–south. A distant eastern row of trees had slight effects on differences in shading ( $\approx 20$  min during sunrise) among the 10 flumes.

We added the following equipment to this general installation for our crayfish experiment (Fig. 1). We placed four large sediment traps and 10 groups of small sediment traps in each of the flumes. We arranged these traps in a way that the flume bottom was not totally blocked by these traps, so that crayfish could easily pass these trap barriers. Later observations showed that the groups of smaller traps sampled all and the larger traps almost all material eroded upstream of them. The sediment traps had a height of 5 cm and an overall surface area of 0.22 m<sup>2</sup>, leaving  $\approx 1$  m<sup>2</sup> flume space for sediments. We filled this space with gravel (to a height of 5 cm). We fixed this gravel with silicon downstream of the inflow pipe to avoid erosion by the high energy of the inflowing water. We evenly distributed 15 L of sand on the gravel surface of each flume before opening the pump valves. We cut hollow brick stones to produce crayfish refugia, which had a length of 13 cm, a width of 3.5 cm, and a height of 3.5 cm. Their upstream and downstream side and bottom side were open. We placed these refugia at and parallel to the inner flume wall (Fig. 1) after sand dunes stabilized in the flumes (*see below*). We covered each flume with mosquito net to prevent crayfish escape and to prevent material that could clog the net at the flume outflow from falling into the flume.

*Crayfish*—We worked with *O. limosus* because it was easily available. This North American species was introduced in France ( $\approx 1910$ ) and rapidly colonized all major rivers and many lakes (Laurent 1997). In contrast to many other crayfish, it does not dig deep burrows into the sediment (Kaestner 1967). This species reproduces at 5–6 months and reduces its activity below 10°C (Kaestner 1967). In Europe, this species reaches a maximal age of 4–5 yr, with individual wet weights achieving 40 g (males) to 59 g (females). The percentage of females ranges between 30 and 44%. *O. limosus* feeds primarily on macrophytes and lives often in zones with macrophytes (Kossakowski 1971; Orzechowski 1984). However, the species also uses other food and habitats (Kaestner 1967). High mean density or biomass (wet weight) records for this species are 39 g m<sup>-2</sup> in a pond (Momot et al. 1978) or 52–72 individuals m<sup>-2</sup>, respectively, 200–310 g m<sup>-2</sup> in macrophytes of a river reservoir (Orzechowski 1984).

We could not find published information about the hydraulic conditions used or preferred by *O. limosus*. Our species and many other North American *Orconectes* occur in many different habitats (lakes, rivers, e.g., Maude and Williams 1983; Laurent 1997). Maude and Williams (1983) showed that the differences in physical habitat limits and preferences among species from fast- and slow-flowing habitats were relatively small in *Orconectes*. Gore and Bryant (1990) showed that a different *Orconectes* species preferred intermediate velocities when younger and lower velocities

when adult (except egg-bearing females, which preferred higher velocities than the young crayfish). Overall, this species preferred water depths ( $D$ ) of  $\approx 10$ –30 cm and mean water column velocities ( $U$ ) of  $\approx 10$ –30 cm s<sup>-1</sup>. This implied that its preferred Froude number ( $Fr = U/[Dg]^{0.5}$ ) was in the range 0.06–0.3.

We obtained the crayfish from a professional fisherman on the Saône River. He trapped them using bait in box traps, which he retrieved a few hours before we released the crayfish in our experimental flumes. The Saône had a temperature of 8°C at the trapping site, and all but one of the trapped individuals were males. We stocked each of the five crayfish flumes with 10 males having approximately a similar range of carapace length. This crayfish density corresponded to high adult densities observed in the Saône River ( $\approx 8$  adults m<sup>-2</sup>, Grenouillet, pers. comm.). We stored crayfish in baskets in the reservoir to eventually replace dead or oddly behaving individuals in the experiment with individuals of identical carapace length. This happened once (one individual) in three different flumes. We retrieved all 50 crayfish in good condition at the end of the experiment.

We checked these retrieved specimens for morphological details indicating sexual activity of this species (Mancini 1989). All 50 males belonged to the sexual active form I. We measured the carapace length with a slide caliper (from the posterior orbit edge to the posterior carapace edge), the maximal width of the right and left claw (i.e., the main weapons of crayfish), and the wet weight, and we counted the number of injuries (missing parts) on claws and walking legs. Analyses of variance (ANOVAs) on these variables using flume as factor showed that the crayfish groups never differed among flumes ( $p$  values: carapace length = 0.95; right claw width = 0.62; left claw width = 0.62; wet weight = 0.94; injury number = 0.36). Therefore, we calculated mean  $\pm 1$  standard error (SE) for all 50 males to characterize our experimental material as: carapace length =  $32.4 \pm 0.3$  mm; right claw width =  $12.8 \pm 0.4$  mm; left claw width =  $13.6 \pm 0.2$  mm; wet weight =  $21.8 \pm 0.6$  g; injury number =  $0.12 \pm 0.05$ . With 10 crayfish 1.25 m<sup>-2</sup> per flume, the mean crayfish biomass (wet weight) in our experiment was thus 174.4 g m<sup>-2</sup>.

*Measuring the flume environment*—We analyzed the dry weight of grain sizes of the gravel and sand as in Statzner et al. (1999). We measured flume discharge at the outflow using a PVC tub (19.5 liters) and a stopwatch to determine the time until the tub was completely filled. We regularly brushed the net closing the outflow and adjusted the water level at the outflow using the tailgate and a meter stick. We measured water depth (meter stick), mean water column velocity (OTT-C2 mini propeller positioned at 0.4 times water depth above the gravel bottom), and shear stress (*see* Statzner et al. 1991) in the median between the flume walls. We surveyed water temperature daily with a minimum–maximum thermometer placed in each of the most distant flumes (1 and 10, at the edges of the reservoir).

We emptied the sediment traps daily using fingers and a sucking pipe (treating a group of small traps as one sampling unit). We separately determined the volume of the gravel and the sand (plus the water in the interstices) in a graduated

cylinder filled with water and distributed the material uniformly across a line immediately downstream from the trap where it was found. We put the material of the trap at the end of the second straight in front of the inflow pipe. We deviated from this procedure on four occasions. We did not measure the sediment volume and released the material from all traps in front of the inflow pipe on the first sampling occasion, and we removed the trapped material from all flumes on the two sampling occasions before we added crayfish to the five treatment flumes and on the last sampling occasion. We were careful to handle the trapped sediments as gently as possible to minimize destruction of the biofilm on the particles. For example, we measured the sediment volume in water without compacting the sediment by shaking the measuring cylinder. Therefore, we produced calibrations to transform these volume values ( $x$ , ml) to dry weight ( $y$ , g). These calibrations were  $y = 1.48 (\pm 1 \text{ SE: } 0.01)x$  for gravel and  $y = 1.57 (\pm 0.01)x$  for sand.

We drained all flumes at the end of the experiment. We took standardized (same distance and angle) photos of the sediment surface at three different locations in each flume. We used these photos later to quantify filamentous algae growth (on randomly selected gravel pieces) as well as biofilm and gravel cover of the sand dunes. We also measured the distance between the flume bottom and a ruler placed across the flume on a median line, neglecting the space occupied by sediment traps. Finally, we used a ruler to rake the sediment surface upstream of each sediment trap (group of traps) until the trap was full. We wet-sieved this material (mesh size: 2 mm) to separate sand and gravel and determined their volumes as described above.

**Observing crayfish**—The crayfish were mainly night active, so observing them required caution to avoid perturbations. We decided to observe them in the first night and later only if the measured erosion rates indicated behavioral changes (which occurred on three occasions). We used a weak red light for a quick check of each crayfish flume at hourly intervals (from 1800 to 2400 h) on each occasion. We noted the position of the visible crayfish and assigned them to the following behavioral categories: hidden (either in a brick stone refugium or below the inflow pipe), inside a sediment trap, on the gravel/sand but not moving, moving, or fighting. We also noted if they fed. We avoided further disturbance of the crayfish except the day we removed the brick stone refugia from the flumes. On that occasion, we measured the carapace length of each crayfish found in a refugium and put it immediately back on the spot we found it. The crayfish often used the sediment traps or the angle of the flow deflectors (in addition to the inflow pipe) to hide during daytime after the refugia removal. We noted the position of these specimens daily before emptying the sediment traps.

**Experimental design**—Preliminary experiments showed that  $\approx 10$  d were sufficient to stabilize sediment distribution and transport and to grow an abundant biofilm in the flumes (Fontveille, pers. comm.). Crayfish need a few hours to a few days to establish dominance hierarchies (Bovbjerg 1956), a week of starvation increases crayfish aggression

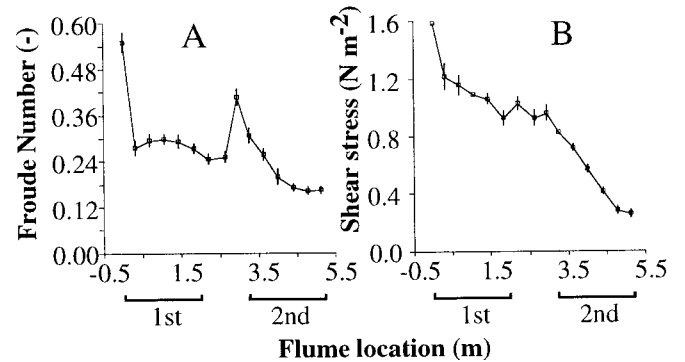


Fig. 2. Physical initial conditions (mean  $\pm 1$  standard error [SE]) measured on 9 November on a median line from the beginning of the first (marked 1st) to the end of the second (2nd) straight of the flumes. (A) Ratio of inertial to gravitational forces in the flow. (B) Shear prevailing at the flume bottom.

(Hazlett et al. 1975), and longer lasting experiments may cause complications in crayfish behavior (Hazlett et al. 1975). Therefore, we used 9–17 November 1998 for the preexperimental phase and added crayfish on 17 November. We randomly selected the five crayfish flumes (one from each of the five flume units, the other flume of each unit served as control). We split the following 12 d into blocks of 6, 3, and 3 d for experimental manipulations. We had all 10 flumes in the setup of Fig. 1 (brick stone refugia in) from 17–23 November. We added half a trout plus half a carrot (carrot is often fed to *O. limosus* in experiments) fixed to each other by a wire to each straight of all 10 flumes on the afternoon of 23 November. We fixed these food packages at the interior flume wall in the middle of each straight. Finally, we removed the brick stone refugia from all 10 flumes on the afternoon of 26 November and observed this setup over the last 3 d of the experiment.

**Flume environment**—We used gravel and sand of the narrowest size range available as building material. Our gravel had the following size distribution (mm and percentage):  $>2$ –5, 1.7;  $>5$ –6.3, 7.6;  $>6.3$ –8, 17.9;  $>8$ –10, 32.8;  $>10$ –12.5, 35.3;  $>12.5$ –20, 4.7. The sand had these values:  $>0.05$ –0.315, 1.9;  $>0.315$ –0.5, 30.8;  $>0.5$ –0.8, 53.9;  $>0.8$ –1.25, 13.3. Numerous shear stress measurements in different stream types (e.g., Lamouroux et al. 1992) showed that riffles often have  $\approx 1.5$  and pools  $\approx 0.2$  (or less)  $\text{N m}^{-2}$  at baseflow discharge. This shear stress range would represent conditions being above as well as below the critical value for the erosion of our sand but always below that value for our gravel (Petit 1994).

Taking into account all this information, we adjusted the mean discharge in the 10 flumes to  $1.29 (\pm 1 \text{ SE: } 0.01) \text{ L s}^{-1}$  and the water depth at the outflow to 11 cm. We thereby created physical initial conditions shown in Fig. 2 (note that these physical data were obtained for eight flumes only because of a failure of the current meter). The flow reflectors generated relatively high Froude numbers at the entrance to the first and second straight. Shear stress steadily decreased along the flumes. Using ANOVAs on these physical variables and the flume as a factor demonstrated no significant

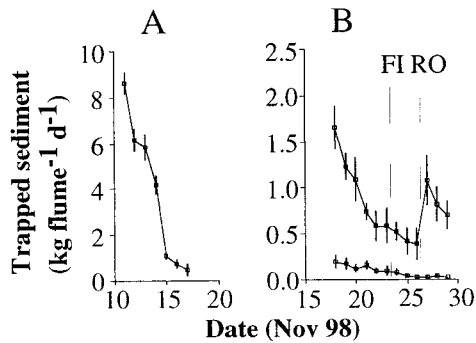


Fig. 3. Mean ( $\pm 1$  SE) daily sediment transport (as dry weight) in (A) the five control flumes (all traps per flume pooled) in the preexperimental period and (B) in the five crayfish (upper line) and the five control flumes (all traps per flume pooled) over the period of the crayfish treatment (FI, food in; RO, refugia out). Note the differently scaled y-axes.

differences among the flumes for the Froude number ( $p = 0.11$ ) and shear stress ( $p = 0.99$ ).

Thus, our initial conditions replicated physical variability along the flumes. The shear stress gradient corresponded to a riffle-pool sequence in natural streams. The Froude number range was usually in that one used by *Orconectes* (0.06–0.3, see above), particularly because the values near the flume walls must have been lower than those shown in Fig. 2 (measured in the flume median).

We found less than a dozen gravel pieces in the control traps over the entire period shown in Fig. 3. Therefore, we omitted gravel transport in the control flumes in further considerations.

The flow environment caused replicated patterns of sand erosion, as demonstrated by the five control flumes (Fig. 3). ANOVA showed that the control flumes eroded sand in a similar way ( $p = 0.98$ ) over the preexperimental and during the experimental (crayfish in treatment flumes) period. The control flumes transported plenty of sand in the preexperimental period (Fig. 3A), when sand dunes moved downstream. These sand dunes started to stabilize on 15 November, when most of the sand had left the first straight. After the removal of the trapped sand from the flumes on 16 and 17 November, the control flumes transported very little sand (Fig. 3B).

The flumes had a very stable water temperature. In the most distant flumes (i.e., at the edges of the reservoir), the mean minimum values ( $\pm 1$  SE) in  $^{\circ}\text{C}$  were  $13.7 \pm 0.2$  (flume 1) and  $14.2 \pm 0.1$  (flume 10). The maximum values were  $14.9 \pm 0.1$  (flume 1) and  $15.0 \pm 0.1$  (flume 10). The slightly higher temperature range in flume 1 was related to its position near the reservoir overflow (i.e., flume 1 received water that had passed the entire installation). The mosquito net covering the flume reduced the photosynthetic active radiation by one-third (Fontveille, pers. comm.). The groundwater pumped into the reservoir and subsequently into the flumes had mean values (in a 5-month survey in 1993) of  $495 \mu\text{S cm}^{-1}$  (conductivity),  $< 0.02 \text{ mg L}^{-1}$  ( $\text{NH}_4\text{-N}$ ),  $8.4 \text{ mg L}^{-1}$  ( $\text{NO}_3\text{-N}$ ), and  $< 0.05 \text{ mg L}^{-1}$  ( $\text{PO}_4\text{-P}$ ; Bornette and Heiler 1994).

## Results

**Crayfish behavior**—Most of the visible crayfish used the brick stone refugia during the day. Some specimens used the space below the inflow pipes as refugium during the daytime. Removing the brick stone refugia changed this daytime behavior. We observed more individuals below the inflow pipes. In addition, we often saw individuals in the sediment traps, in the angle of the flow reflectors, or between the food package and the inner flume wall. Crayfish became distinctly more active shortly after nightfall (1800 h) and remained active until midnight, when we stopped our hourly observations. They fed on the trout and carrot we added to the flumes after six nights. A single crayfish fed on one food package at all these occasions and we never saw aggressive encounters for food.

Most of the other behavioral categories were significantly correlated, so we focused on the number of individuals outside the refugia (brick stones, inflow pipe), which indicated the overall crayfish activity. We observed the crayfish at four dates of November 1998 (17—crayfish added, brick stone refugia available, no food; 21—brick stone refugia available, no food; 25—brick stone refugia and food available; 28—food available, brick stone refugia not available). On all four dates, the mean ( $\pm 1$  SE) number (per hourly check) of crayfish observed outside the refugia was similar in the second straight of the flumes ( $3.2 \pm 0.2$ ,  $2.2 \pm 0.2$ ,  $2.6 \pm 0.2$ ,  $2.4 \pm 0.2$ , respectively;  $p = 0.2$ ; one-way repeated measures ANOVA on four repeated measures per flume). In contrast, the number of crayfish observed outside the refugia in the first straight decreased from 17 to 25 November and increased after the refugia removal ( $2.7 \pm 0.2$ ,  $1.6 \pm 0.2$ ,  $0.9 \pm 0.2$ ,  $2.4 \pm 0.3$ , respectively;  $p = 0.003$ ). This change in the nocturnal use of the first straight was related to changes in the overall aggression level in the crayfish groups (the number of crayfish outside the refugia and the number of fighting crayfish was positively correlated;  $p = 0.00002$ ).

The use of the brick stone refugia during daytime differed from the nocturnal use of the straights observed on 25 November (brick stone refugia and food available). We found exactly the same mean number (3.0) of crayfish in the refugia of the first and second straight when we removed the brick stones during daytime on 26 November. However, the crayfish in the second straight were significantly ( $p = 0.003$ ; ANOVA) larger than those in the first straight. Crayfish from refugia in the second straight had a mean ( $\pm 1$  SE) carapace length of  $33.5 \pm 0.4 \text{ mm}$ , and those from the first straight of  $31.0 \pm 0.7 \text{ mm}$ . Crayfish visible during daytime after the removal of the brick stone refugia tended ( $p = 0.10$ ) to be more abundant in the first (mean  $\pm 1$  SE:  $2.9 \pm 0.4$ ) than in the second ( $2.0 \pm 0.3$ ) straight.

Thus, crayfish had about equal nocturnal activities in both straights when their overall activity and aggression levels were high (first night in flumes and after the refugia removal). They maintained a high overall activity in the second straight on 21 and 25 November, when lower nocturnal activities occurred in the first straight. Larger individuals used the refugia of the second straight compared to the first straight during daytime when overall nocturnal activity in

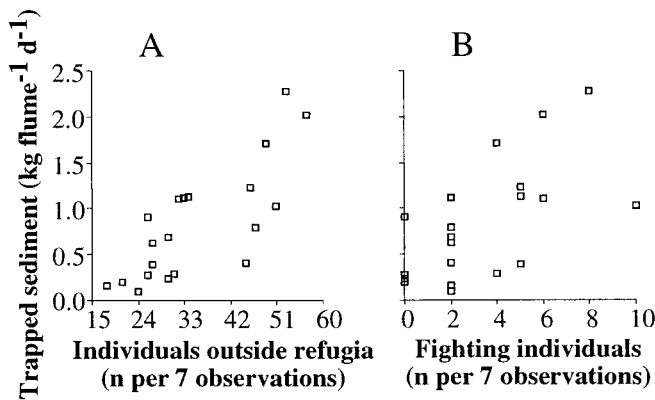


Fig. 4. Sediment transport (see Fig. 3 for details) and nocturnal crayfish behavior in the five crayfish flumes. (A) Overall activity sum of crayfish per flume. (B) Overall aggression level of crayfish per flume (note that odd numbers of fighting individuals resulted from battles among three crayfish).

the first straight was low. However, the same number of individuals used the straights during daytime when overall nocturnal activity in the first straight was either low or high.

**Erosion of sand and gravel**—Sediment transport in the control flumes decreased steadily until 26 November, when it almost ceased (Fig. 3B). Flumes with crayfish had distinctly more sediments in the traps (all pooled) than the controls (Fig. 3B). Crayfish flumes had a decreasing mean sediment transport until 22 November, when transport leveled off (Fig. 3B). Adding food to the flumes had little effect, but removing the brick stone refugia caused an immediate increase of the mean sediment transport in the crayfish flumes. A repeated measures ANOVA on the 12 repeated measures per flume and the grouping factor crayfish presence/absence showed significant effects of crayfish ( $p = 0.0004$ ), date ( $p < 10^{-7}$ ), and their interaction ( $p = 0.00003$ ), i.e., the ANOVA indicated a different amount and temporal pattern of trapped sediment in the crayfish and the control flumes. We could relate four of the transport values to the respective activity sum observed in the four nights in each crayfish flume. The sediment transport in the crayfish flumes was very significantly ( $p = 0.00005$ ) related to the overall crayfish activity (Fig. 4A) and significantly ( $p = 0.003$ ) related to the crayfish aggression level (Fig. 4B).

We used the data from the groups of small sediment traps to relate erosion to an area. We focused on date and flume straights, as erosion was not significantly different in the control flumes and as crayfish behavior was significantly related to date and straight. Mean sand erosion similarly decreased with time in the first and second straight of the control flumes (Fig. 5A) and was distinctly lower than sand erosion in the crayfish flumes (Fig. 5B). In the latter, the temporal pattern of sand erosion in the second straight (Fig. 5B, 2nd) resembled the overall sediment transport pattern in all crayfish flumes (Fig. 3B). The sand erosion in the first straight (Fig. 5B, 1st) distinctly deviated from this pattern, as sand erosion increased for 3 d, decreased the next 3 d, and stayed relatively stable in the remaining days. These differences in temporal patterns in the crayfish flumes made

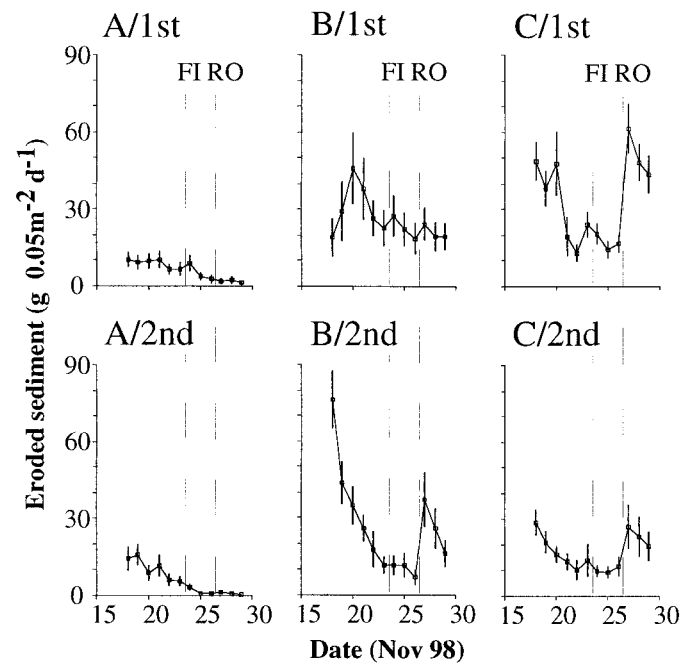


Fig. 5. (A), (B) Eroded sand or (C) gravel in the first (1st) or second (2nd) straight of the (A) five control and (B) (C) the five crayfish flumes (note that the controls had no gravel erosion). We indicated the mean ( $\pm 1$  SE) of the 25 groups of small sediment traps for each date and grouping. FI, food in; RO, refugia out.

sand erosion distinctly different between the straights on some dates (e.g., 18 November, the first date), but it was similar on other dates (e.g., 20 November, the third date). Gravel erosion in both straights of the crayfish flumes (Fig. 5C) had also a pattern similar to that of the overall sediment transport (Fig. 3B). However, gravel erosion changed more distinctly in the first than in the second straight. Therefore, gravel erosion differed much between the straights on the first and last three dates, but it was similar between the two straights on the remaining dates.

Adding food to the crayfish and control flumes had no effects on the erosion rates in all six groupings of Fig. 5. Removing the brick stone refugia had no effects on sand erosion in the control flumes and the first straight of the crayfish flumes. However, refugia removal distinctly affected sand erosion in the second straight and gravel erosion in both straights of the crayfish flumes (Fig. 5). High mean erosion rates for a given date were  $\approx 60$  g (gravel) or  $\approx 75$  g (sand)  $0.05 \text{ m}^{-2} \text{ d}^{-1}$  in the crayfish flumes. Low erosion rates for both gravel or sand were  $\approx 10$  g  $0.05 \text{ m}^{-2} \text{ d}^{-1}$  in these flumes.

**Habitat changes**—The flume bottom stayed even in the first straight of the control flumes (Fig. 6A) where the elevation remained near the height (5 cm) of the initial gravel fill. It became slightly more uneven and excavated in the first radius of the controls. Sand dunes of subsequently increasing height occurred in the second straight of the controls. In contrast, the gravel bottom became much more uneven in the first straight and the first radius of the crayfish flumes and slightly increased in mean bed elevation (as the surface gravel formed loosely packed heaps). In addition, the

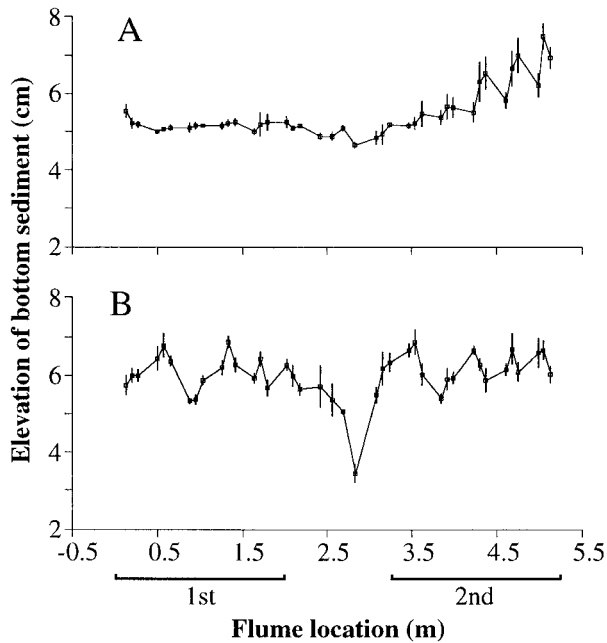


Fig. 6. Mean ( $\pm 1$  SE) height of the bottom sediment at the end of the experiment from the beginning of the first (marked 1st) to the end of the second (2nd) straight in (A) the five control and (B) the five crayfish flumes.

sand dunes did not subsequently increase in height in the second straight of the crayfish flumes (Fig. 6B). The mean difference in elevation between neighboring low and high points on the bed were  $\approx 0.3$  cm in the first straight and  $\approx 0.5$  cm between the end of the first radius and the beginning of the second straight in the controls, although they were  $\approx 1.5$  cm and  $\approx 3.5$  cm in the crayfish flumes. In contrast, the mean difference in sand dune elevation at the end of the second straight was  $\approx 1.5$  cm in the controls and  $\approx 0.8$  cm in the crayfish flumes.

The mean proportion of sand in the upper sediment layer upstream of the beginning of the second straight varied more in the control than in the crayfish flumes (Fig. 7). It was  $\approx 20\%$  in the controls and  $\approx 10\%$  in the crayfish flumes at most of the flume locations. This sand proportion increased considerably into the downstream direction of the second straight in the control flumes. In the crayfish flumes, it increased most distinctly toward the end of the second straight but remained relatively similar there (Fig. 7).

The photos made on identical spots in all 10 flumes showed that the controls had distinctly more growth of filamentous algae and biofilm than the crayfish flumes (Table 1). In contrast, the latter had distinctly more gravel pieces on the sand dune surface than the former (Table 1).

## Discussion

*Realism of the observed patterns*—Experiments such as ours require a careful discussion of the realism of the observed patterns. The potential biotic impact on sediment erosion depends at least on the realized experimental niche space and the related performance of a test organism (e.g.,

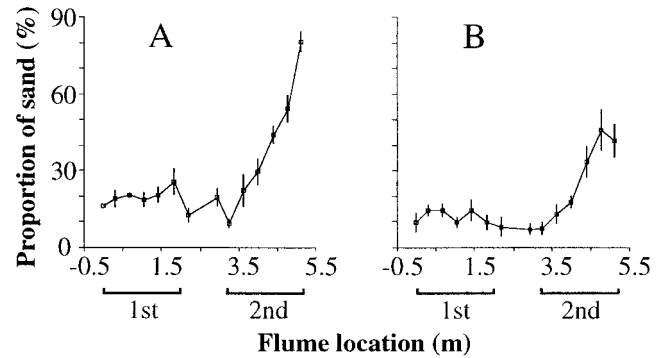


Fig. 7. Mean ( $\pm 1$  SE) proportion of sand in the surface sediment at the end of the experiment from the beginning of the first (marked 1st) to the end of the second (2nd) straight in (A) the five control and (B) the five crayfish flumes.

Statzner 1997), the prevailing erosive forces critical for a given sediment size (e.g., Petit 1994), and the abundance of a given sediment size (e.g., Moog and Whiting 1998).

Facing these many degrees of freedom, we designed our experiment in such a way that it replicated real conditions. We replicated high adult densities occurring in the Saône River in our flumes, but our density ( $8 \text{ males m}^{-2}$ ) was much lower than that often observed in streams (e.g., four of the six permanent stream entries about crayfish densities in table 2 of Momot et al. 1978 had more than the double of our densities). Concerning the biomass, the  $174.4 \text{ g m}^{-2}$  in our flumes were less than half of the maximum value reported for streams (Momot et al. 1978). We expected artifacts in crayfish behavior at the beginning of the experiment, as crayfish were transported and grouped together in a habitat unknown to them. However, such regrouping of individuals in new habitats should be a normal event in natural streams, as *Orconectes* extensively migrates upstream (Momot 1966). Finally, we replicated physical habitat conditions typically used by crayfish in nature. We offered a range of habitat conditions (a riffle-pool sequence) that corresponded to the range used by a different North American *Orconectes* species (Gore and Bryant 1990), and the temperature in our flumes ranged between 14 and  $15^\circ\text{C}$ , i.e., it was above the  $10^\circ\text{C}$  at which *O. limosus* reduces its activity (Kaestner 1967).

We potentially biased for increased aggressive interactions (and thus increased sediment transport) by using form I

Table 1. Mean ( $\pm 1$  SE) sediment surface characteristics obtained by quantitative analysis of standardized color photos of the five crayfish and control flumes.

Surface characteristics	Crayfish	Control
Gravel pieces with filamentous algae ( $n$ )*	$3.6 \pm 1.6$	$42.4 \pm 7.2$
Sand dune cover by brownish biofilm (%)†	$3.6 \pm 1.7$	$89.4 \pm 5.9$
Sand dune cover by gravel pieces ( $n$ )†	$65.2 \pm 10.7$	$0.4 \pm 0.4$

\* From 50 pieces each in the beginning of the first straight and in the first radius.

† At the end of the second straight.

males of approximately equal size, as it is assumed that form I males of equal size need more time to establish dominance hierarchies (Guiasu and Dunham 1997). However, the overall crayfish mobility may be the same for males of form I, form II, and females (Mobberly and Owens 1966). On the other hand, our sediment traps biased the reported transport or erosion rates toward minimum values. All material fallen into the traps could not be eroded until we emptied the traps and put the material back on the gravel surface. This bias was less important in control flumes because transport in these was very low.

*Crayfish behavior*—Our results on crayfish behavior clearly confirmed the known facts that crayfish are aggressive (e.g., Lodge and Hill 1994), establish dominance hierarchies that reduce aggressive interactions (e.g., Guiasu and Dunham 1997), need at maximum a few days to establish these dominance hierarchies (Bovbjerg 1956), and that refugia modify aggressive encounters among them (e.g., Lodge and Hill 1994). They also confirmed that adult decapods can starve for considerable time (e.g., Kaestner 1967), since adding food after 6 d barely affected crayfish behavior (in contrast to the observations of Hazlett et al. 1975).

When active and most aggressive, crayfish used both straights about equally during the night. However, when overall activity and aggression were lowest, they preferred the second straight (pool conditions) over the first straight (riffle conditions) during night. This pattern suggested that the establishment of dominance hierarchies displaced losers toward less preferred habitat conditions. Correspondingly, larger individuals (i.e., more successful aggressors being the first to mark preferred refugia by their odors: Lodge and Hill 1994; Quinn and Graves 1998) used the refugia during daytime in the second straight. We observed a carapace length difference of 2.5 mm between the two straights, which is largely sufficient to establish clear dominance hierarchies in crayfish (Penn and Fitzpatrick 1963).

Thus, although the general patterns of our crayfish behavior were clear and corresponded to known patterns in this group, the environmental flume conditions modified these behavioral responses. The modifications of these behavioral responses affected the sediment transport (*see below*) because the latter was significantly related to crayfish activity (Fig. 4).

*Crayfish as geomorphic agents*—Erosion rates per area (Fig. 5) were of primary interest to evaluate the role of crayfish as geomorphic agents (we expressed these rates in  $\text{kg m}^{-2} \text{d}^{-1}$  in the subsequent text, since geomorphologists are more familiar with these units). The erosion rates of sand were more complicated than those of gravel, since sand availability and transport capacity differed considerably between the first and second straight. Little sand was available in the first straight where the erosive forces were above the critical value for most of the sand. Consequently, sand erosion peaked at the third day after crayfish addition, after crayfish had moved sand out of the second straight and of the flume radius with the inflow pipe (Fig. 5B). After the peak on the third day, sand erosion dropped quickly back to a base level regardless of changes in crayfish behavior. Thus,

crayfish eroded  $\approx 0.4 \text{ kg m}^{-2} \text{d}^{-1}$  of sand at riffle conditions (first straight with little sand available and shear stress critical for most sand fractions), and crayfish behavior barely changed this erosion potential. Sand erosion patterns were more complicated in the second straight, i.e., the preferred pool habitat of the crayfish. Sand erosion dropped from  $\approx 1.5 \text{ kg m}^{-2} \text{d}^{-1}$  to stabilize  $\approx 0.2 \text{ kg m}^{-2} \text{d}^{-1}$ . Removing the refugia increased the sand erosion rates to  $\approx 0.7 \text{ kg m}^{-2} \text{d}^{-1}$ . In addition to changing crayfish behavior, this pattern was caused by habitat changes made by the crayfish. The sand dune height (Fig. 6) decreased in the second straight over the experiment, i.e., the cross section of the flow as well as the shear stress acting on the sediment surface changed (Dingman 1984). In addition, the sand availability at the sediment surface (Fig. 7) changed in the second straight, where shear stress represented a gradient of critical erosive forces for different size fractions of our sand. Thus, changes in crayfish behavior, changes of sand availability through crayfish erosion, and crayfish-induced changes of the flow forces created a wide range of sand erosion ( $\approx 0.2\text{--}1.5 \text{ kg m}^{-2} \text{d}^{-1}$ ) in the second straight of our flumes. Overall, these erosive rates for fine sediments were above those reported for other stream invertebrates (Pringle and Blake 1994; Statzner et al. 1996; Zanetell and Peckarsky 1996) but in the range observed for an infaunal, estuarine bivalve (Willows et al. 1998). Sand erosion in the controls was clearly lower than in the crayfish flumes in both straights ( $\approx 0.2 \text{ kg m}^{-2} \text{d}^{-1}$  during the first half and  $\approx 0.05 \text{ kg m}^{-2} \text{d}^{-1}$  during the second half of the crayfish experiment).

We could not find published reports on the increase of gravel erosion by benthic stream invertebrates, i.e., we perhaps demonstrated such effects for the first time. Gravel eroded at about equal rates in the first straight in the first ( $\approx 0.9 \text{ kg m}^{-2} \text{d}^{-1}$ ) and last ( $\approx 1.1 \text{ kg m}^{-2} \text{d}^{-1}$ ) 3 d of the experiments, i.e., when nocturnal crayfish activity was high in the first straight. Gravel erosion was only  $\approx 0.4 \text{ kg m}^{-2} \text{d}^{-1}$  in the remaining days, when distinctly fewer crayfish used the first straight during night. Finally, gravel erosion was lower in the second straight, being  $\approx 0.5 \text{ kg m}^{-2} \text{d}^{-1}$  at the start of the experiment and after refugia removal and reaching a minimum of  $\approx 0.2 \text{ kg m}^{-2} \text{d}^{-1}$  between these two dates. These patterns in gravel erosion were again the result of changing crayfish behavior, habitat modifications by crayfish, and prevailing erosive forces. The temporal pattern of gravel erosion and flume straight use by crayfish changed more distinctly in the first straight compared to the second straight. Sand subsequently disappeared from the gravel so that the gravel could be eroded in the second straight (Fig. 7). In addition, gravel heaps formed along the entire first straight toward the beginning of the second straight (Figs. 6 and 7). Finally, the overall higher shear stress in the first straight (Fig. 2) facilitated gravel erosion by crayfish because they had to add less momentum to a gravel particle to erode it compared to the second straight.

Thus, erosion rates were the result of complex interactions between physical habitat and crayfish behavior, overall transport capacity of the flow, and dynamic changes of this transport capacity of the habitat through the crayfish. In addition, behavioral events that could cause massive erosion (e.g., fights) were locally restricted to small flume areas. Conse-

Table 2. High erosion of sand plus gravel ( $\text{g } 0.05 \text{ m}^{-2} \text{ d}^{-1}$ ) and mean ( $\pm 1$  SE) bedload transport ( $\text{g d}^{-1}$ ) in all five crayfish flumes.

Date	High erosion*		Bedload transport	
	First straight	Second straight	First straight	Second straight
18–20	247 $\pm$ 31	185 $\pm$ 12	80 $\pm$ 10	80 $\pm$ 7
21–23	179 $\pm$ 16	98 $\pm$ 12	50 $\pm$ 7	33 $\pm$ 4
24–26	141 $\pm$ 12	68 $\pm$ 8	43 $\pm$ 6	22 $\pm$ 3
27–29	192 $\pm$ 13	160 $\pm$ 14	78 $\pm$ 8	53 $\pm$ 6

\* Indicated as the mean ( $\pm 1$  SE) of the 10 highest observed values for the groups of small sediment traps in the first and second straight. See Fig. 5

quently, the average erosion rates of 25 groups of small sediment traps per night and flume straight could not demonstrate how high the erosion potential of crayfish could be on a smaller spatial and temporal scale. Therefore, we calculated for each of the subsequent 3-d periods the mean of the 10 maximum erosion rates observed per flume straight (Table 2). When stressed by transport and a new flume environment containing refugia (date 18–20), locally high erosion rates averaged to  $\approx 5 \text{ kg m}^{-2} \text{ d}^{-1}$  in the riffle habitat (first straight) and to  $\approx 3.7 \text{ kg m}^{-2} \text{ d}^{-1}$  in the pool habitat (second straight). These erosion rates could correspond to those induced by natural or human-made perturbations that redistribute crayfish among habitats or destroy established dominance hierarchies in crayfish populations. High erosion rates averaged to  $\approx 2.8 \text{ kg m}^{-2} \text{ d}^{-1}$  in riffle and to  $\approx 1.4 \text{ kg m}^{-2} \text{ d}^{-1}$  in pool habitats when hierarchies were established, refugia used, and food available (24–26). Disturbing these peaceful crayfish by taking away their refugia increased the high average erosion rates to  $\approx 4.0$  (riffle) or  $\approx 3.2$  (pool)  $\text{kg m}^{-2} \text{ d}^{-1}$ . One liter of gravel corresponded to  $\approx 1.5 \text{ kg}$ , so peaceful crayfish having food and refugia could reduce the bottom elevation in riffles at mean high erosion rates by  $\approx 0.2 \text{ cm d}^{-1}$ . This value was far above the gross erosion rates observed in stream catchments (Morisawa 1985). All of the above high mean values applied to 10 of 75 measurements of each 3-d period, i.e., they were not very rare events.

Another process of interest as a geomorphic agent is bedload transport through the cross section of a stream per unit time. This transport is often described as a power function of discharge for discharges less than or equal to bankfull discharge (Moog and Whiting 1998). Data scatter considerably around this function, but a smaller alluvial gravel stream may have a bedload transport (obtained by regression) of  $\approx 1,000 \text{ kg d}^{-1}$  at bankfull discharge of  $2.6 \text{ m}^3 \text{ s}^{-1}$  (Moog and Whiting 1998) for a stream width of  $\approx 6 \text{ m}$  (Hey and Thorne 1986). Bankfull discharge has a mean recurrence period of 1.5 yr in many streams and is considered as an important event affecting channel morphology (Leopold et al. 1964). Thus, the maximum bedload transport of this stream recurring about every 1.5 yr should be  $\approx 170 \text{ kg d}^{-1} \text{ m}^{-1}$  of stream width. Our crayfish created a bedload transport of  $\approx 40$  (first straight), respectively, 20 (second straight)  $\text{g d}^{-1}$  when peaceful and provided with food and refugia (date 24–26, Table 2). We obtained these values for a flume width of  $\approx 0.2 \text{ m}$  (exactly 0.192 m). An unconservative as-

sumption would be that peaceful crayfish having food and refugia could transport the same amount of bedload throughout the entire year in a real stream. In that case, bedload transport mediated by crayfish over a 1.5-yr period of baseflow conditions (corresponding to our experimental conditions) would be  $\approx 110 \text{ kg m}^{-1}$  “stream” width in riffle (first straight) conditions and  $\approx 55 \text{ kg m}^{-1}$  in pool (second straight) conditions. These values would be about the double for stressed crayfish (compare date 24–26 with 18–20 and 27–29, Table 2), although we would not imagine that crayfish could be stressed every day over 1.5 yr. Thus, crayfish alone would barely contribute to the overall bedload transport in streams caused by floods, as the more frequent flood levels below bankfull discharge also produce considerable bedload transport (Moog and Whiting 1998). Crayfish could be the major cause for bedload transport only in periods between major floods in natural streams. Then, they could erode gravel from riffles that should be generally trapped in the subsequent pool (see Figs. 6 and 7, which show that gravel heaps had formed at the beginning of the “pool” in the second straight of the crayfish flumes, and Table 1, which shows that gravel pieces covered the sand dunes in the pools of these flumes). In contrast, the sand eroded by them could subsequently travel across riffle-pool sequences, as they transported sand easier than gravel out of the second straight.

A last effect of crayfish to be included into geomorphic considerations was their impact on the sediment surface in terms of bottom elevation (Fig. 6), proportion of sand (Fig. 7), and biofilm on the sand dunes (Table 1). Bedload transport of a given grain size and its critical shear stress is physically complicated by bed roughness or topography, as well as by particle shape, mixture, orientation, and packing (Billi et al. 1992). In addition, postdepositional physical bed consolidation increases the critical shear stress for a given particle size (Reid in Andrews and Smith 1992). Finally, benthic microalgae stabilize sand  $< 2 \text{ mm}$  so that the critical shear stress for sand increases (Heinzelmann 1992). These conditions at the sediment surface differed between the crayfish and the control flumes, which should have changed the critical shear stress needed to erode the bottom material (e.g., during a subsequent flood event).

For example, the differences in the percentage of sand found in the upper sediment layer of the first straight between control and crayfish flumes should have stabilized the gravel in the latter because the critical gravel shear stress increases abruptly if the proportion of sand decreases beyond 20% (Wilcock 1998). In contrast, the increased overall bedform roughness in the first straight of the crayfish flumes should have decreased the critical gravel shear stress (Dingman 1984). Thus, the baseflow activities of the crayfish produced sediment changes in the first straight that would have opposite effects on the incipient gravel motion during a subsequent flood. Similarly, the reduced height differences between the sand dunes at the end of the second straight in the crayfish flumes would require higher shear stress for incipient sand motion (Dingman 1984), whereas the reduction of the biofilm cover of the sand dunes through the crayfish would decrease the shear stress for incipient sand motion (Heinzelmann 1992).

Thus, the direct effects of crayfish on sediment erosion

and bedload transport in natural streams should be significant at baseflow but relatively unimportant compared to the effects of floods. In addition, the effects of their baseflow activities on the sediment conditions should generate opposite effects on incipient particle motion in natural streams during subsequent floods. The relative importance of these opposite effects remains to be evaluated in future studies.

*Crayfish as ecosystem engineers*—The effects of crayfish on the resources of other organisms, i.e., their ecosystem engineering (Jones et al. 1994), should vary in importance. Changing the percentage of sand in the interstices of the gravel from  $\approx 20\%$  (controls) to  $\approx 10\%$  (crayfish flumes) in a riffle section (first straight and first radius) should have marginal effects on macroinvertebrate abundance (Rosenberg and Wiens 1978; Williams and Mundie 1978). Similarly, reducing the sand dune heights but not clearing the gravel from the sand in a pool section (second straight) should have only marginal effects, as the macroinvertebrate fauna would remain characteristic of sandy bottoms (Minshall 1984). However, crayfish cleared the flume bottom from sand at the beginning of the second flume straight. Thus, the transition zone between a gravel and sand section could be the only area where sand removal by crayfish could significantly affect benthic macroinvertebrate abundance and community structure in natural streams (see Minshall 1984). The effects of the filamentous algae and biofilm reduction by crayfish on the abundance of benthic invertebrate grazers should be important but complicated in real streams (Creed 1994).

Other sediment changes caused by crayfish should be more important for other benthic organisms than the previously considered effects. For example, the bedform changes create complicated and varying near-bottom flow patterns that have major effects on benthic macroinvertebrates, algae, and macrophytes (Statzner et al. 1988). The sand reduction among the gravel caused by the crayfish should also have major effects on the egg survival of salmonids that bury their eggs in the gravel. For example, brown trout egg survival to alevin emergence is  $\approx 90\%$  in gravel containing 10% sand compared to  $\approx 30\%$  survival in gravel containing 20% sand (Olsson and Persson 1988). Thus, crayfish could play an important role as ecosystem engineers in real streams as their activities may affect population and community structure of the benthos or the egg survival of gravel-breeding fish.

## Conclusions

Our results confirmed previous speculations (Statzner et al. 1996) that the behavior of lotic invertebrates may affect the transport of sand across riffle-pool sequences. In addition, we showed that invertebrates may also directly increase the transport of gravel, particularly at riffle conditions. These direct effects on erosion seemed to be marginal for sediment budgets in real streams, as floods transport much more sediment. However, these direct effects could be important for sediment budgets in streams that have a stable discharge and an abundant crayfish population (e.g., Augusta Creek; Creed 1994). In addition, we investigated just one species, and one should consider the sum of biotic activities of all species in a community to evaluate the role of organisms as geomor-

phic agents (Butler 1995). Finally, the baseflow activities of our crayfish changed the sediment conditions in only 12 d in a way that would have increased as well as decreased the critical shear stress for the gravel and the sand dunes during a subsequent flood. These opposite effects of crayfish on incipient sediment motion should be quantified in future studies to improve the evaluation of the role of crayfish as geomorphic agents in real streams. Crayfish could considerably change the physical habitat conditions at baseflow in natural streams, so we consider them as potentially effective ecosystem engineers.

However, many variables should affect these impacts of crayfish in natural streams: (1) the state of the crayfish (e.g., aggression levels as related to the availability of refugia, time after the destabilization of crayfish hierarchies); (2) the state of the physical system (e.g., shear stress conditions, available sediment of a given size, availability of crayfish refugia); (3) the impact of the physical habitat on crayfish density and behavior; and (4) the discharge variability and related changes of the shear stress caused by channel morphology. The introduction of crayfish into new geographical areas increases this complexity further. These introductions may change the dominance of crayfish species on continental (Laurent 1997) or regional (Lodge and Hill 1994) scales. Thus, understanding and predicting the potentially important role of crayfish and other animals as geomorphic agents and ecosystem engineers in stream systems requires interdisciplinary research that simultaneously addresses such biological and physical processes.

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