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RESEARCH PAPER

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Drift patterns of particulate matter and organisms during artificial high flows in a large experimental channel

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Abstract Using a large experimental channel, five artificial high flows with different flow regimes were launched to reveal the precise temporal sequences of drifting particulate matter and organisms during the high flows. Drifting fine particulate matter and organisms were collected by sampling bottles and a water pump, respectively. The peaks of drift abundance occurred before the peak discharges, and the abundance declined quickly within several minutes during the rising phase of high flows. The major determinant of drift abundance of particulate matter and organisms was periods of stable conditions before each high flow (tested by determination coefficients in a correlation analysis). The drift of macroscopic plant material also accelerated the drifts of epiphytic fauna and infauna, which drifted with plants and bed sediments. The magnitude (discharge and duration of peak flows) of high flows only slightly affected drift abundance. The fauna more resistant to high flows were invertebrates that fasten their cases or retreats by silk threads on the substrata. Invertebrate taxa having sucking apparatus or high swimming activity were also resistant to high flows.

Key words Benthic invertebrates · Initial drift · Stream drift · Temporal sequence

Introduction

Stream drift, defined as the drift of organisms by current (Kohler 1985), has received considerable attention from stream ecologists since the 1950s. Stream drift is one of the important processes in the population regulation, dispersal, and life cycles of river benthic invertebrates (Müller 1954; Waters 1966; Cereghino and Lavandier 1998; Maier 2001; Elliott 2002b).

At normal or base flows, most lotic invertebrates have clear diel periodicities in stream drifts, and nocturnal drift is much more abundant than daytime drift (Tanaka 1960; Waters 1972; Anholt 1995; Giller and Malmqvist 1998; Elliott 2002a). Compared to these drift studies at normal or base flows, destructive drifts caused by floods or flashes have been less well investigated (Minshall 1988; Statzner et al. 1988).

Destructive drift generates substantial losses of benthic invertebrates (Cobb et al. 1992). The drift of particulate matter and organisms at high flows is more abundant than that at normal flows (Minshall 1988; Statzner et al. 1988; Matthaei et al. 1997; Lake 2000). Temporal sequences of drifts of organisms and matter during natural floods have been investigated for fine particulate matter (Quay et al. 1992; Robinson et al. 2004b), invertebrates (Tockner and Waringer 1997; Robinson et al. 2004a), and water quality (e.g., pH, alkalinity, and electric conductivity; Ebise and Nagafuchi 2002), and strong relationships exist between their drift abundance and discharges.

However, there are few studies on precise drift sequences of particulate matter and organisms during floods or flashes (Kurashige 1993; Tockner and Waringer 1997) because the time and magnitude of floods or flashes are hard to predict in natural streams and rivers. Drifting organisms are fairly difficult to collect during natural floods, other than during some artificial floods (Robinson et al. 2004a). A large experimental channel having a similar scale to natural waterways enabled us to collect drifting fine particulate organic matter (FPOM), fine particulate inorganic matter (FPIM), macroscopic plant material (hydrophytes and filamentous algae) (MPM), and invertebrates with intervals of several minutes during artificial high flows.

The major objectives of this study are to describe the precise temporal sequences and to reveal major determinants of the magnitude of drifting particulate matter and organisms.

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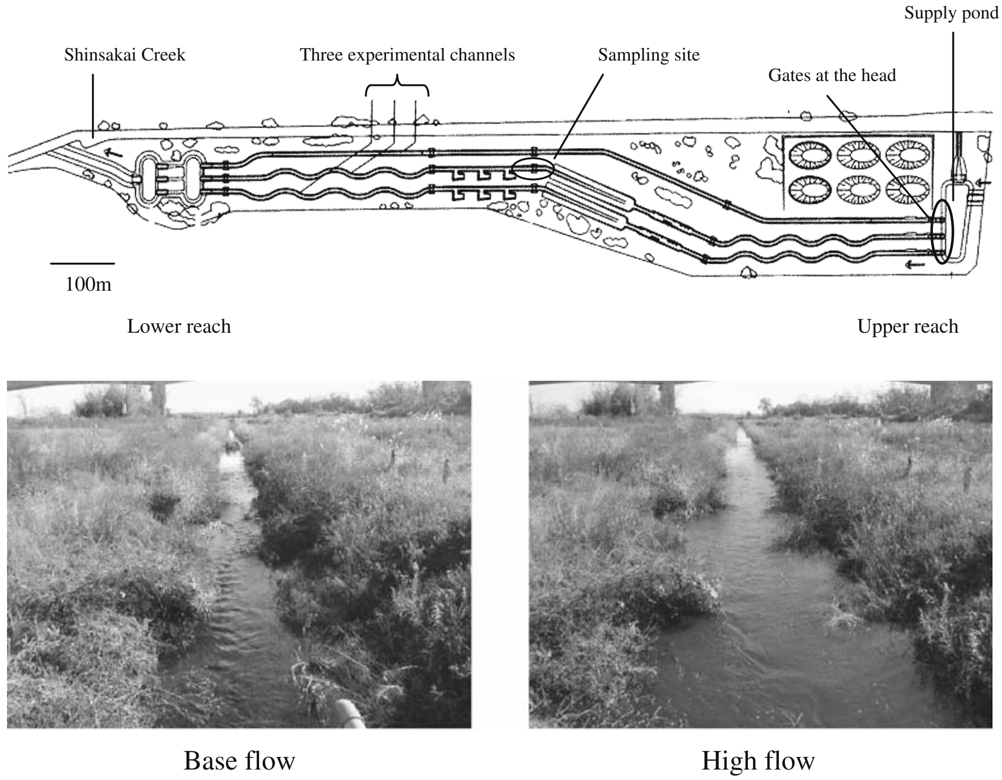

Fig. 1. Plan of experimental channels at the Aqua Restoration Research Center (ARRC), Gifu Prefecture; *arrows* indicate direction of water flow. Photographs below the diagram show the sampling site at base flow (*left*) and high flow (*right*) on December 5, 2001. Base flow, $0.3\,m^3 s^{-1}$; high flow, $1.5\,m^3 s^{-1}$

Methods

Experimental channel

The large outdoor experimental channels are constructed in the Aqua Restoration Research Center (ARRC) close to the Kiso River in Gifu Prefecture, central Japan (35°36′N, 136°46′E; Fig. 1). The center has three experimental channels, each 800 m long, from 2.5 to 6.0 m in width, and with a bed slope between 1:200 and 1:800. The experimental channels have dimensions similar to Shinsakai Creek, adjacent to the ARRC, and are intended to reveal the effects of environmental fluctuations on river biotic communities under seminatural conditions. Shinsakai Creek was constructed in 1932 on a floodplain of the Kiso River as a floodway of the Sakai Stream, a tributary of the Kiso River. The creek has a mean discharge rate of $1.7\,m^3 s^{-1}$ and a drainage area of $42.63\,km^2$ (Shimatani et al. 1998).

Species composition and abundance of fish and benthic invertebrates in the experimental channels were similar to those of Shinsakai Creek (Kayaba 2000; Shimizu 2000). Filamentous algae (*Oedogonium* sp., *Spirogyra* sp., and *Stigeolonium* sp.), hydrophytes [*Egeria densa* (Planch) and *Potamogeton oxyphyllus* (Miquel)], and emergent plants (*Typha angustifolia* L., *Typha latifolia* L., and *Phragmites japonica* Stend.) abundantly covered the channel bed in 2001, and filamentous algae and hydrophytes were abundant in drift (Minagawa 2002; Mochizuki 2002). In July and August 2002, these plants were removed to decrease the water resistance; these removals were conducted at base flow condition.

In 2001 and 2002, the central channel of the ARRC was used for artificial high flows, and a sampling site at the middle reaches was situated 450 m downstream from the head of the channel (see Fig. 1), with its bed predominantly covered by loose or embedded cobbles (diameter, 64–256 mm) with pebbles (diameter, 16–64 mm), gravel (diameter, 2–16 mm), and sand (diameter, <2 mm). The water was collected from nearby Shinsakai Creek and stored in a supply pond above the head of the channels. The annual current flow ranged from 0.03 to $0.16\,m\,s^{-1}$. The annual water temperature ranged from 0.4° to 30.5°C.

Operation of the experimental channels

Water supply to the experimental channels was started on May 10, 2001. After several flush operations, which were repeated to remove construction waste soil from May 10 to June 1, 2001, five series of artificial high flows were launched on July 13, September 28, and December 5, 2001, and on July 31 and August 21, 2002 (Table 1). An experiment on September 4, 2001 was not monitored.

The first experiment in July 2001 was conducted 42 days after the last flush operation (see Table 1). The durations of stable condition (base flow without distinct disturbances) in 2001 were 23 and 67 days before experiments in September and December, respectively. In 2002, the high flow in July was launched 55 days after the removal of filamentous

Table 1. Flow regimes of artificial high flows and other operations

Date	Peak discharge ($m^3 s^{-1}$)	Peak duration (min)	Total duration (min)[a]	Base flow ($m^3 s^{-1}$)	Duration of stable condition (days)[b]
May 10, 2001	Introduction of water into the channel:				
June 1, 2001	Last flush operation:				
July 13, 2001[c]	2.5	50	90	0.08	42
Sept. 4, 2001	2.0	180	220	0.07	52
Sept. 28, 2001[c]	2.0	180	220	0.07	23
Dec. 5, 2001[c]	1.5	10	50	0.30	67
June 3–5, 2002	Removal of filamentous algae, hydrophytes, and emergent plants from the channel bed:				
July 31, 2002[c]	2.0	60	100	0.07	55
Aug. 21, 2002[c]	1.0	120	160	0.07	20

[a] At the head of the channel, both rising and recession times were fixed at 20 min in every experiment
[b] Duration of stable condition: duration of base flow without distinct disturbances
[c] Surveyed artificial high flow

Table 2. Ratios of initial discharge (%) and initial drift ratios (%) of abundances of FPOM, FPIM, MPM, and total invertebrates in artificial high flows

Experiment	Rising time (min)	Discharge (%)	FPOM (%)	FPIM (%)	MPM (%)	Total invertebrates (%)
July 2001	30	16.6	36.3	23.6	79.0	67.1
Sept. 2001	41	17.1	18.5	26.6	59.3	64.8
Dec. 2001	22	44.3	69.9	81.3	91.9	97.1
July 2002	28	31.6	45.4	48.8	n.d.	77.6
Aug. 2002	30	17.5	33.7	22.9	n.d.	57.7

Initial discharge and drift abundances were defined as the cumulative volume or abundance during the rising limb; initial drift ratio was defined as the ratio of initial drift to total drift
FPOM, fine particulate organic matter; FPIM, fine particulate inorganic matter; MPM, plant material including filamentous algae and hydrophytes; n.d., no data because of scarce drift abundance

algae, hydrophytes, and emergent plants. The high flow in August was launched 20 days after that in July (see Table 1).

Flow regimes of artificial high flows

The flow regime of the experimental channel can be controlled by the steel flush board gates at the head of the channel. The gates were operated by a personal computer. The base flows were from 0.07 to 0.08 $m^3 s^{-1}$ in four series of experiments, but the base flow in December 2001 was 0.30 $m^3 s^{-1}$ (see Table 1). A high flow (maximum discharge, 4.0 $m^3 s^{-1}$) of about 13 to 60 times the base flows (0.07–0.30 $m^3 s^{-1}$) can be produced by feeding peak discharges and time sequences into a personal computer.

Both rising and recession times were fixed as 20 min in every high flow (see Table 1). The peak discharge and duration were modified between experiments. The water level and current flow at the head of the channel were measured every minute throughout high flows. These high flows had a similar magnitude to flashes in small natural channels in Japan, which frequently occur during rainy and typhoon seasons (Ohte et al. 2001; Onda et al. 2001).

In all experiments, the water level and current flow were measured every minute throughout high flows nearby the sampling site. The discharge at the sampling site was evaluated from these measurements. The magnitude of high flows at the sampling site was similar to those at the head of the channel. However, high flows at the sampling site occurred 7–24 min later than at the head. The rising times became 2–21 min longer at the sampling site than at the head (Table 2).

Drifting particulate matter and organisms

During the high flows, drifting particulate matter and organisms were collected considering three phases of high flows: rising limb, peak time, and recession limb (Allan 1995). Three 250-ml water samples were collected by sampling bottles just below the water surface every 4 min during the rising limb and within 2–8 min after peak time. In December 2001, however, three 250-ml water samples were collected every 4 min throughout the high flow. Three 250-ml water samples were also collected at base flow just before each high flow. These water samples were used to estimate the amount of fine particulate organic matter (FPOM) and fine particulate inorganic matter (FPIM).

From these water samples, the macroscopic particulate matter was filtered using a sieve with 0.850-mm mesh, but the residues on the sieve were negligible. Fine particulate matter was precipitated by leaving the water samples standing in a refrigerator (about 4°C, NR-204T; Matsushita

Electric, Osaka, Japan) for about 12h. The deposits were desiccated in a drying oven (WFO-600ND; Eyela, Tokyo, Japan) at 60°C for about 12h. The dry weight was measured by electric balance (HR-120; AND, Tokyo, Japan) to the nearest 0.01mg. The desiccated deposits were burned in a muffle furnace (AT-E58; Isuzu, Tokyo, Japan) at 600°C for 2h, and the ignition residue was weighed by the electric balance to the nearest 0.01mg. The ignition residues and ignition loss were assigned to the abundances of FPIM and FPOM, respectively.

To test the reliability of this precipitation method, we compared it to the filtering method by glass fiber filter (GF-C; Whatman, London, UK). Ten 250-ml samples of natural flood water were collected from a stream (Ki River or Kinokawa; Hashimoto, Wakayama), of which five samples were treated by each of the two methods. There were no significant differences in the abundances of FPIM and FPOM between these two methods (Mann–Whitney test, $P > 0.05$).

For drifting plants (MPM) and invertebrates, a 100-l water sample was collected by a water pump (KL-24X; capacity, $900\,\mathrm{l\,min^{-1}}$; nozzle size, 150mm in diameter; Komatsu, Tokyo, Japan). The nozzle of the pump was set about 10mm above the channel bed.

Twenty 100-l samples of water at base flow were collected just before each high flow, and we did not detect any disturbance of channel bed by this pumping method (our observation at base flow). In each high flow, 11–21 pump samples of 100l of water were collected every 2min during the rising time, 5 water samples of 100l were collected with intervals of 3min at the initial phase of peak time, and an additional 4 water samples of 100l at 5-min intervals during the peak time. In December 2001, however, the additional samples at 5-min intervals were collected to the end of the recession limb.

The 100-l water samples were filtered through a net with 334-μm mesh, and the residue on the net was preserved in 2%–5% formalin for further laboratory observations.

The drifting MPM and invertebrates in the residues were sorted under a stereomicroscope (MZ12; Leica, Solms, Germany). The MPM was desiccated in a drying oven at 60°C for more than 12h, and the weight was measured by the electric balance to the nearest 0.01mg. MPM were not analyzed in 2002 because they became very scarce when we removed emergent and submerged plants from the channel.

The drifting invertebrates were identified to genera or species according to Wiederholm (1983), Merritt and Cummins (1996), Thorp and Covich (1991), Kawai (1985), Kathman and Brinkhurst (1998), and Kondo et al. (2001) under the stereomicroscope; some species were identified under a light microscope (DME; Leica, Solms, Hessen, Germany). However, invertebrates in the early or pupal stages were identified only to family level. Severely damaged invertebrates, which accounted for less than 1% of the number of individuals, were excluded from the present analyses. The genera of Tubellaria and Nemertinea were not identified, and they were negligible in their abundances (less than 1.6% of total). Individuals of Copepoda were numerous. Most species of freshwater Copepoda are found in standing waters such as lakes and ponds (Mizuno 1991; Williamson and Reid 1991). A few species appear in groundwater and downstream reaches of rivers, but they rarely appear in small streams (Mizuno 1991; Williamson and Reid 1991). Therefore, Copepoda in the drift might come mostly from a supply pond. Tubellaria, Nemertinea, and Copepoda were excluded from the present analysis.

A sampling by drift net with 334-μm mesh was tried at base flow ($0.07\,\mathrm{m^3\,s^{-1}}$) and a high flow ($1.5\,\mathrm{m^3\,s^{-1}}$) on May 22, 2001, before the present experiments. The sampling was not successful because of heavy clogging during a high flow. From three samples at base flow in May, the drift densities of MPM and invertebrates were $4.22 \pm 0.39\,\mathrm{mg\,m^{-3}}$ and 11.73 ± 12.33 individuals $\mathrm{m^{-3}}$, respectively, which were within the range of the drift densities at base flow collected by the pumping method (Table 3).

Benthic invertebrates

Five quantitative samples of benthic invertebrates were collected from a quadrat of $0.15 \times 0.15\,\mathrm{m^2}$ by a Surber net with 334-μm mesh. The samples were collected at riffles near the sampling site from 10 to 14 days before each high flow. The samples were preserved in 2%–5% formalin for laboratory inspection. The compositions and abundances of invertebrate communities scarcely changed within about 30 days (Mochizuki 2002). Benthic invertebrates were not collected before the experiment in August 2002 because there were overlaps with other experiments.

Benthic invertebrates were identified by the same method as drifting invertebrates.

Data analyses

Drift abundance was defined as the total abundance of particulate matter or organisms passing through a section of channel per unit time (Elliott 1967, 1970). The drift abundance (a_i) was calculated by the following formula:

$$a_i = d_i \times w_i$$

where a_i is drift abundance at time i (number or $\mathrm{mg\,s^{-1}}$), d_i is drift density in a unit volume of water at time i (number or $\mathrm{mg\,m^{-3}}$), and w_i is discharge at time i ($\mathrm{m^3\,s^{-1}}$).

Drift abundance of particulate matter and organisms increased and peaked during the rising limb but declined quickly within 2–4min. The abundances of drifting particulate matters and organisms were fairly stable during peak in every high flow, and those were stable throughout the peak and recession limb in the high flow in December 2001. Thus, we postulated that the drift abundance was maintained at a constant level throughout the peak and recession limb in all high flows. We divided each high flow into two phases, initial drift (rising limb) and subsequent drift (peak and recession limb), and estimated the cumulative abundances of initial and subsequent drifts.

Initial drift ratios were defined as the ratio of cumulative abundances of initial drift to total abundances (= initial drift + subsequence drift).

Table 3. Mean drift densities of FPOM, FPIM, MPM, and total invertebrates, and mean benthic density of total invertebrates

	Experiment	Base flow density	Peak density	Subsequent density
FPOM ($mg\,m^{-3}$)	July 2001 b	0.20 ± 0.20 (n = 3)	46.62 ± 21.82 (n = 9)	5.42 ± 2.30 (n = 9)
	Sept. 2001 b	0.03 ± 0.06 (n = 3)	34.84 ± 16.18 (n = 9)	6.22 ± 0.34 (n = 9)
	Dec. 2001 a	1.50 ± 0.48 (n = 3) B	73.67 ± 34.85 (n = 12) A	24.93 ± 3.20 (n = 27) B
	July 2002 b	1.73 ± 0.28 (n = 3)	14.89 ± 7.80 (n = 9)	6.13 ± 2.10 (n = 9)
	Aug. 2002 b	1.53 ± 0.36 (n = 3)	8.62 ± 2.35 (n = 9)	2.89 ± 1.04 (n = 9)
FPIM ($mg\,m^{-3}$)	July 2001 b	4.00 ± 0.36 (n = 3)	236.36 ± 105.28 (n = 9)	39.51 ± 8.74 (n = 9)
	Sept. 2001 b	0.10 ± 0.17 (n = 3)	142.84 ± 61.90 (n = 9)	11.64 ± 0.34 (n = 9)
	Dec. 2001 a	0.70 ± 0.78 (n = 3) B	277.47 ± 167.63 (n = 12) A	51.53 ± 24.98 (n = 27) B
	July 2002 b	4.83 ± 0.25 (n = 3)	57.73 ± 29.92 (n = 9)	14.04 ± 2.74 (n = 9)
	Aug. 2002 b	2.03 ± 0.21 (n = 3)	46.80 ± 7.69 (n = 9)	27.33 ± 10.93 (n = 9)
MPM ($mg\,m^{-3}$)	July 2001 a	20.95 ± 10.29 (n = 20)	741.00 ± 655.92 (n = 6)	12.67 ± 4.17 (n = 3)
	Sept. 2001 b	0.70 ± 1.03 (n = 20)	33.63 ± 21.43 (n = 8)	2.00 ± 2.00 (n = 3)
	Dec. 2001 a,b	4.65 ± 1.93 (n = 20) B	353.40 ± 84.80 (n = 5) A	114.29 ± 65.79 (n = 7) B
	July 2002	n.d.	n.d.	n.d.
	Aug. 2002	n.d.	n.d.	n.d.
Total invertebrates (number m^{-3})	July 2001 b	65.00 ± 40.07 (n = 20)	4973.33 ± 2230.69 (n = 6)	286.67 ± 65.06 (n = 3)
	Sept. 2001 b	11.00 ± 12.52 (n = 20)	2416.25 ± 1139.66 (n = 8)	93.33 ± 57.74 (n = 3)
	Dec. 2001 a	10.00 ± 11.24 (n = 20) B	14930.00 ± 8654.29 (n = 5) A	208.75 ± 72.00 (n = 7) B
	July 2002 b	9.00 ± 9.12 (n = 20)	2700.00 ± 576.61 (n = 6)	306.67 ± 75.06 (n = 3)
	Aug. 2002 b	23.50 ± 12.26 (n = 20)	1418.33 ± 1075.67 (n = 6)	170.00 ± 40.00 (n = 3)
		(Benthic density)		
Total benthic invertebrates (number m^{-2})	July 2001 b	5973.33 ± 1371.89 (n = 5)		
	Sept. 2001 b	5253.33 ± 1797.23 (n = 5)		
	Dec. 2001 a	16915.56 ± 7590.48 (n = 5)		
	July 2002 a	13520.00 ± 4511.43 (n = 5)		
	Aug. 2002	n.d.		

Peak density was defined as the average from the maximum to the 75th percentile densities
A, B, significant differences in densities between base-flow, peak, and subsequent phases, $P < 0.05$ (Tukey's multiple comparison test), respectively; a, b, significant differences in densities between experiments, $P < 0.05$ (Tukey's multiple comparison test); mean ± standard error
FPOM, fine particulate organic matter; FPIM, fine particulate inorganic matter; MPM, macroscopic plant material, n.d., no data

The peak drift densities were defined as average values from the maximum to the 75th percentile. Drift densities of FPOM, FPIM, MPM, and total invertebrates were tested by a two-way analysis of variance (two-way ANOVA) with main factors being the three phases of discharge (density at base flow phase, peak density at rising phase, and density at subsequent phase corresponding to peak and recession limb) and experiments. Significant P values ($P < 0.001$) were obtained for both main effects and the interaction. The drift densities were also tested by a one-way analysis of variance (one-way ANOVA) to compare between three phases of discharge and experiments. Tukey's multiple comparison test was used to test for significant differences in drift densities among the phases of discharge, as well as significant differences in drift densities among all experiments within each drifting material (FPOM, FPIM, MPM, and total invertebrates). Benthic densities of total invertebrates were also tested between experiments by one-way ANOVA followed by a Tukey's multiple comparison test.

For FPOM, FPIM, MPM, and total invertebrates, the relationships of their peak densities with durations of base flow before high flows (= stable condition), peak discharges, and base flow densities were tested by a Spearman's rank correlation analysis. For total invertebrates, the relationship of peak densities to benthic densities was also tested by a Spearman's rank correlation analysis.

Invertebrate taxa having more than 100 individuals m^{-2} of density in at least three sampling occasions were selected as major invertebrate taxa. Peak drift ratios were calculated for the major invertebrate taxa according to Elliott (1970):

$$r_d = d_p/d_b$$

where r_d is peak drift ratio, d_p is peak density (number m^{-3}), and d_b is benthic density (number m^{-2}).

The peak drift ratios of major taxa in all experiments were compared by a multiple comparison test (Steel–Dwass test).

Results

Temporal patterns of drifting particulate matter and organisms

Peaks of drift abundance of FPOM occurred during the rising limb of 12, 12, 11, 8, and 16 min after the beginnings of high flows in July, September, and December 2001, and in July and August 2002, respectively (Fig. 2). In December 2001, the drifting FPOM was more abundant than in other experiments, and the peak value of drift abundance was about 100 $mg\,s^{-1}$ (Fig. 2). In other experiments, the peak values of drift abundances were 7–25 $mg\,s^{-1}$ (Fig. 2). The peak of drift abundance declined more quickly in December 2001 than in other experiments, in which the peaks were obscure (Fig. 2).

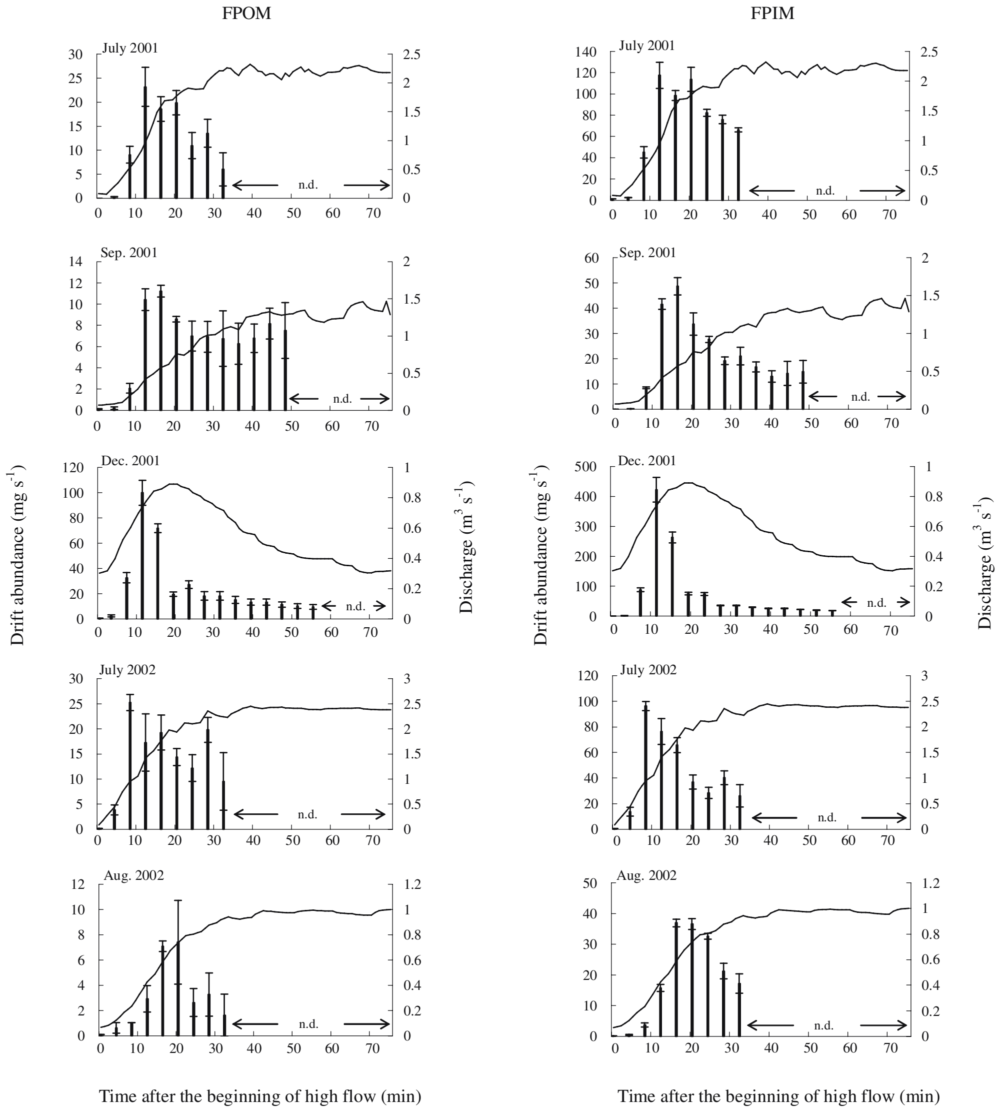

Fig. 2. Temporal sequences of drifting fine particulate organic matter (*FPOM, left*) and fine particulate inorganic matter (*FPIM, right*) (mean ± standard error, $n = 3$). *Graphed lines* indicate the discharge measured close to the sampling site ($m^3 s^{-1}$); *vertical bars* are the mean drift abundance ($mg s^{-1}$) of FPOM and FPIM; *x*-axes indicate time after the beginning of high flow; *n.d.*, no data

Peaks of drift abundance of FPIM also occurred during the rising limb of 12, 12, 11, 8, and 16 min after the beginning of high flows in July, September, and December 2001, and in July and August 2002, respectively (see Fig. 2). In December 2001, the drifting FPIM was the most abundant, and the peak value of drift abundance was about 422 $mg s^{-1}$ (Fig. 2). In other experiments, the peak values of drift abundance were 36–117 $mg s^{-1}$ (Fig. 2). The peak of drift abundance declined more quickly in December 2001 than in other experiments, in which the peaks were obscure (Fig. 2). FPIM were heavier than FPOM in every experiment (see Fig. 2).

Peaks of drift abundance of macroscopic plant material (MPM) occurred during the rising limb of 7, 20, and 12 min after the beginnings of high flows in July, September, and December 2001, respectively (Fig. 3). The peak values of drift abundances were higher in July (711 $mg s^{-1}$) and December 2001 (340 $mg s^{-1}$) than in September 2001 (14 $mg s^{-1}$) (Fig. 3). The peaks of drift abundances declined 2–4 min after the peaks in July and December 2001 (Fig. 3). In September 2001, overall drift abundance of MPM was less and the peak was obscure (Fig. 3).

Peaks of drift abundance of total invertebrates occurred during the rising limb of 9, 10, 6, 14, and 10 min after the beginning of high flows in July, September, and December 2001, and in July and August 2002, respectively (Fig. 4). In July and August 2002, the drift abundances declined 2 min after the peaks (Fig. 4). In July, September, and December 2001, the second peaks of drift abundance occurred 4–6 min after the first ones, and the abundance declined 2 min after the second peaks (Fig. 4). The peak value of drift abundance was the highest in December 2001 (14296–14513 individuals s^{-1}) (Fig. 4). In December 2001, overall drift abundance was also distinctly more abundant but declined more quickly than in other experiments (Fig. 4).

Temporal patterns of drifting particulate matter and organisms during the high flows indicate that the peaks occur at the initial time of the rising limb and that their drift abundance declines within 2–4 min after the peaks. Tempo-

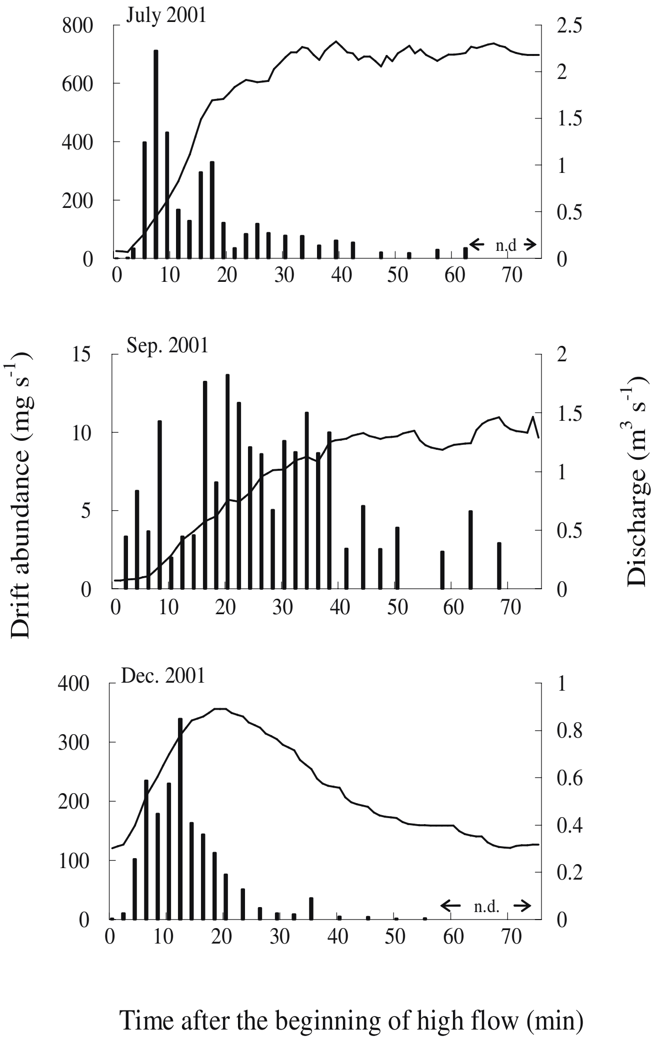

Fig. 3. Temporal sequences of drifting macroscopic plant material (MPM; hydrophytes and filamentous algae). *Graphed lines* indicate the discharge measured close to the sampling site ($m^3 s^{-1}$); *vertical bars* are the drift abundance ($mg s^{-1}$) of MPM; *x*-axes indicate time after the beginning of high flow; *n.d.*, no data

ral patterns of drift density were similar to those of drift abundance.

The initial drift ratios of FPOM, FPIM, MPM, and total invertebrates were higher than the ratios of initial discharges in every experiment (see Table 2). The initial drift ratios of MPM and total invertebrates were distinctly higher than the ratios of FPOM and FPIM in every experiment (Table 2). During the rising limb of high flows, about 60% of the drift of MPM and total invertebrates occurred (see Table 2).

Drift magnitude of particulate matter and organisms

There were significant differences in drift densities of particulate matter and organisms between the three phases of discharge (base flow, rising, and subsequent) (one-way ANOVA, $F = 6.7–39.9$, $P < 0.01$). The peak densities during

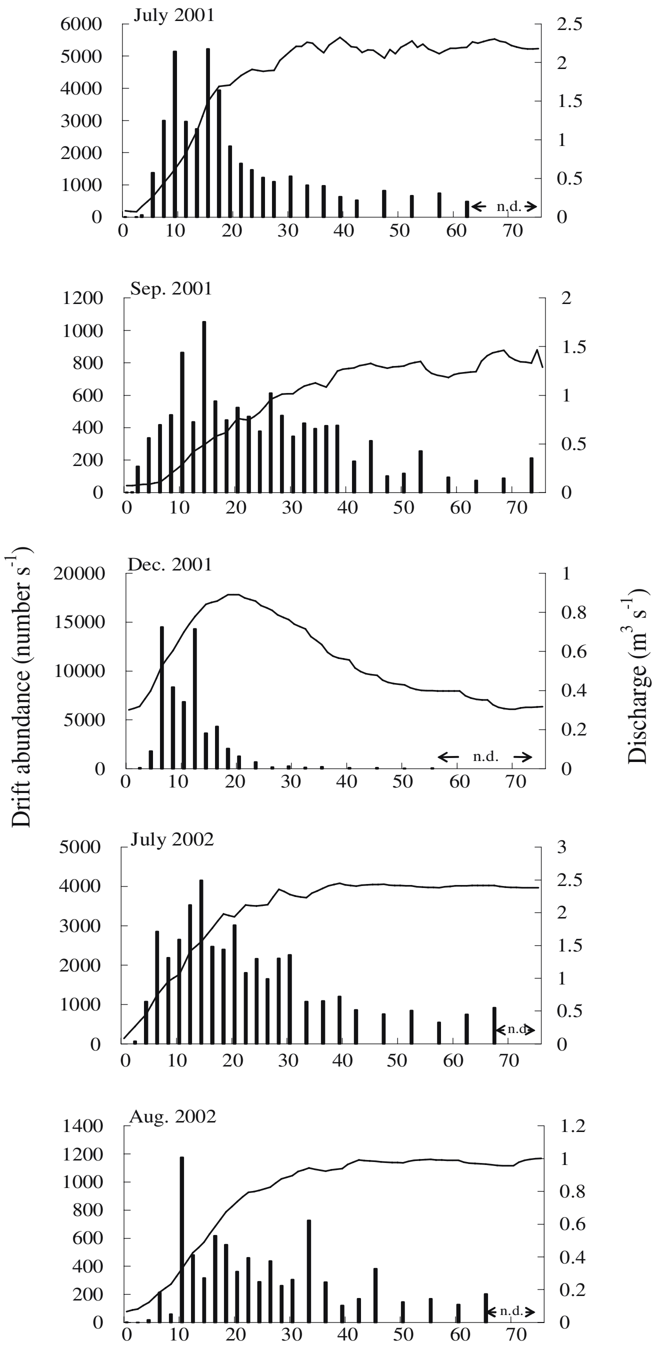

Fig. 4. Temporal sequences of drift abundance in total invertebrates. *Graphed lines* indicate the discharge measured close to the sampling site ($m^3 s^{-1}$); *vertical bars* are the total abundance ($number\ s^{-1}$) of drifting invertebrates; *x*-axes indicate time after the beginning of high flow; *n.d.*, no data

rising phases were significantly higher than drift densities at base flows and subsequent phases in all experiments (Tukey's multiple comparison test, $P < 0.01$; Table 3). Although subsequent densities were higher than base flow densities, there were no significant differences between them for FPOM, FPIM, MPM, and total invertebrates (Tukey's multiple comparison test, $P > 0.05$; see Table 3).

Table 4. Determination coefficients of linear regressions of peak densities of FPOM, FPIM, MPM, and total invertebrates with several factors of artificial high flows and benthic densities of total invertebrates

Peak density	Duration of stable condition (days)	Peak discharge ($m^3 s^{-1}$)	Base flow density (mg or number m^{-3})	Benthic density (number m^{-2})
FPOM ($mg\,m^{-3}$)	0.557*	0.323 n.s.	0.281 n.s.	–
FPIM ($mg\,m^{-3}$)	0.476 n.s.	0.329 n.s.	–0.046 n.s.	–
MPM ($mg\,m^{-3}$)	0.794**	0.128 n.s.	0.479 n.s.	–
Total invertebrates (number m^{-3})	0.686**	0.287 n.s.	0.231 n.s.	0.571**

Benthic density was calculated from the samples just before each high flow
FPOM, fine particulate organic matter; FPIM, fine particulate inorganic matter; MPM, macroscopic plant material
** Significant at $P < 0.01$, * significant at $P < 0.05$; n.s., not significant at $P > 0.05$

Table 5. Peak drift ratios (mean ± standard deviation) of major invertebrate taxa, which were defined as the ratios of peak densities to benthic densities

Taxa (group)	Peak drift ratio in each experiment				Average of peak drift ratios
	2001			2002	
	July ($n = 6$)	September ($n = 8$)	December ($n = 5$)	July ($n = 6$)	
Laevapex nipponica (Gastropoda; Basommatophora)	0.084 ± 0.062	9.914 ± 5.128	0.364 ± 0.139	0.053 ± 0.047	3.278 ± 5.411 ($n = 25$) a
Corbiculidae gen. sp. (Bivalvia; Venevoida)	1.446 ± 0.808	0.091 ± 0.065	2.545 ± 1.135	1.131 ± 0.271	1.157 ± 1.081 ($n = 25$) a,b
Erpobdellidae gen. sp. (Hirudinea; Erpobdellidae)	0.084 ± 0.036	0.011 ± 0.020	0.113 ± 0.103	0.057 ± 0.015	0.060 ± 0.061 ($n = 25$) c
Baetis sp. H (Insecta; Ephemeroptera)	0.118 ± 0.050	0.009 ± 0.027	0.189 ± 0.297	0.060 ± 0.060	0.083 ± 0.144 ($n = 25$) c
Baetis sp. (Insecta; Ephemeroptera)	0.381 ± 0.581	0.176 ± 0.258	0.029 ± 0.064	0.000 ± 0.000	0.153 ± 0.335 ($n = 25$) c
Cheumatopsyche brevilineata (Insecta; Trichoptera)	0.040 ± 0.036	0.017 ± 0.013	0.008 ± 0.008	0.003 ± 0.001	0.018 ± 0.023 ($n = 25$) c
Hydroptila sp. (Insecta; Trichoptera)	n.b.	0.270 ± 0.117	0.042 ± 0.041	0.048 ± 0.026	0.140 ± 0.137 ($n = 19$) c
Cricotopus sp. (Diptera; Chironomidae)	0.738 ± 0.576	0.739 ± 0.373	0.056 ± 0.074	0.001 ± 0.003	0.425 ± 0.491 ($n = 25$) a,b,c
Polypedilum sp. (Diptera; Chironomidae)	1.991 ± 1.272	0.370 ± 0.213	0.785 ± 0.481	0.077 ± 0.061	0.772 ± 0.967 ($n = 25$) a,b,c
Rheotanytarsus sp. (Diptera; Chironomidae)	2.000 ± 0.810	1.018 ± 0.625	1.703 ± 1.601	0.931 ± 0.333	1.370 ± 0.820 ($n = 25$) a,b,c

a, b, c, significant differences in the ratios among taxa, $P < 0.05$ (Steel–Dwass test); n.b., no benthic density (= 0)

There were significant differences in drift densities of particulate matter and organisms between experiments (one-way ANOVA, $F = 4.6$–60.5, $P < 0.01$). The drift densities of FPIM, FPOM, and total invertebrates in December 2001 were the highest among all experiments (Tukey's multiple comparison test, $P < 0.05$; see Table 3). The drift densities of MPM were significantly higher in July 2001 than in September 2001 (Tukey's multiple comparison test, $P < 0.05$; Table 3). There were no significant differences between the drift densities of MPM in July and December 2001 (Tukey's multiple comparison test, $P > 0.05$; Table 3). The benthic densities of total invertebrates were significantly higher in December 2001 and July 2002 than in July and September 2001 (Tukey's multiple comparison test, $P < 0.05$; see Table 3).

The duration of stable conditions had a significant correlation with the peak densities of FPOM ($r = 0.557$, $P < 0.05$), MPM ($r = 0.794$, $P < 0.01$), and total invertebrates ($r = 0.686$, $P < 0.01$), but not of FPIM ($r = 0.476$, $P > 0.05$) (Table 4). The benthic density of total invertebrates had a significant correlation with the peak density ($r = 0.571$, $P < 0.01$; Table 4). Peak discharges and base flow densities had no correlation with the peak densities of FPOM, FPIM, MPM, and total invertebrates ($r = -0.046$–0.479, $P > 0.05$; Table 4).

For major invertebrate taxa, the peak drift ratios were higher in 2001 than in 2002, especially in *Leavapex nipponica*, *Baetis* sp., *Cricotopus* sp., *Polypedilum* sp., and *Rheptanytarsus* sp. (Table 5). The major difference between 2001 and 2002 was in the drift abundance of MPM, which was abundant in 2001.

Concerning the average of peak drift ratios, *L. nipponica* was the highest among all major invertebrate taxa (Table 5). Those of Corbiculidae, *Cricotopus* sp., *Polypedilum* sp., and *Rheptanytarsus* sp. were not significantly different from that of *L. nipponica* (Steel–Dwass test, $P > 0.05$; Table 5). In contrast, those of Erpobdellidae, *Baetis* sp. H, *Baetis* sp., *Cheumatopsyche brevilineata*, and *Hydroptila* sp. were significantly lower than those of *L. nipponica* and Corbiculidae (Steel–Dwass test, $P < 0.05$; see Table 5).

Discussion

Temporal patterns of drifting particulate matter and organisms during high flows Peaks of abundances or densities of drifting FPOM, FPIM, MPM, and total invertebrates appeared distinctly earlier than the peak discharges. The peaks disappeared within several minutes, even when discharges were increasing.

In a natural headwater stream, Kurashige (1993) collected drifting particulate matter every hour during a high flow (base flow, $0.02\,m^3 s^{-1}$; peak, $0.10\,m^3 s^{-1}$; duration, about 18h). He revealed that the peak abundance of particulate matter, mostly inorganic matter, appeared before the peak discharge. In our study, drifting FPOM and FPIM showed similar temporal patterns, and their peak abundances also appeared before the peak discharge. Robinson et al. (2004b) investigated the temporal sequences of drifting invertebrates (i.e., mainly Chironomidae, Gammaridae, and Simuliidae), periphyton, and seston in four series of experimental floods in a natural river (peak discharge, about 10–30 times the base flow, 10 and $43\,m^3 s^{-1}$). Although the peak durations of floods were from 7 to 7.5h, the peaks of drifting invertebrates, periphyton, and seston appeared about 2h after the beginning of the floods. Their abundance decreased to base flow levels within 1–2h from the peaks of abundance (3–4h after the beginning of floods). In our study, the drift abundance of particulate matter and organisms also decreased within several minutes at the initial times of high flows.

Imbert and Perry (2000) investigated the temporal sequences of drifting invertebrates (i.e., mainly Chironomidae, Amphipoda, Ostracoda, and Heridae) during the high flows (base flow, $0.013\,m^3 s^{-1}$; peak, $0.032\,m^3 s^{-1}$) in an experimental channel. They applied two types of flow increment, a stepwise increment in which flow was increased by approximately $0.003\,m^3 s^{-1}$ every 30min and an abrupt increment in which flow was increased abruptly within several minutes from 0.010 to $0.032\,m^3 s^{-1}$. In a stepwise increment, the peak of drift abundance of invertebrates occurred before the peak discharge, and the abundance declined even at the rising limb. In this study, the flows increased from base flows to peak flows (5–30 times the base flow) within 20min, which corresponded to an abrupt increment of flow (Imbert and Perry 2000). Because we adopted dense samplings with short time intervals (2–5min), we could reveal more precise temporal sequences of drifting particulate matter and organisms during abrupt flow increments. Even in abrupt flow increments, the peaks of drift abundance of particulate matter and organisms occurred before the peak of discharges, and their abundance declined very quickly.

The drift abundance of particulate matter and organisms declined quickly after the peaks of the abundance itself. The experimental channel was 800m long, with a supply pond at the head. Drifting particulate matter and organisms from upstream might be limited by this structure. However, sediment and organisms at the channel bed were not exhausted by high flows in this study (Mochizuki, in manuscript). Some other studies in natural channels (Kurashige 1993; Robinson et al. 2004b) also observed that the drift abundance declined quickly after the peaks even when flow discharge was rising. Smaller sediment particles and organisms might be trapped by the complex configuration of channel bed, e.g., interstices of bed material, and pools and shores with slower current.

Major determinant of drift magnitude

The duration of stable conditions before each high flow was the most important determinant of drift abundance of particulate matter and organisms. With the longer periods, the drift abundance of particulate matter and organisms became greater. The benthic density of invertebrates was another major determinant of drift abundance of invertebrates. In August 2002, the recovery process to high flows was investigated in the experimental channel, and the benthic densities of total invertebrates quickly recovered by the reproduction of invertebrate taxa having short life cycles (Mochizuki, in manuscript). Within 10 days of base flow from June to July 2003, deposition of particulate matter and algal production accumulated about $0.10\,kg\,m^{-2}$ of inorganic matter and $0.02\,kg\,m^{-2}$ of organic matter on the channel bed (Minagawa 2003). The quick recovery of benthic particulate matter and organisms might increase their drift abundance.

The magnitude and duration of discharge of floods have been considered as important factors affecting the abundance of drifting matter and organisms (Elliott 1970; Minshall 1988; Boulton and Lake 1992). Tockner and Waringer (1997) investigated the drift densities of invertebrates and particulate organic matter (>200μm) from peak ($22.6\,m^3 s^{-1}$) to base flow ($1.6\,m^3 s^{-1}$) during an 8-day flood event in a mountain brook. They obtained five samples during 6 days of the recession limb and confirmed that there existed high correlation between the discharges and drift densities.

In this study, however, there were no clear correlations between discharges of high flows and drift densities of particulate matter and organisms. Although high flows having different peak discharges and durations were launched, they did not affect the drift abundances of particulate matter or organisms.

Peak abundances of major invertebrate taxa were higher when the drifting MPM was abundant. In the experimental channel, epiphytic fauna such as *Leavapex nipponica*, *Baetis* sp., and *Rheptanytarsus* sp. used filamentous algae and submerged parts of hydrophytes as habitat (Mochizuki 2001). Thus, the uprooting of plants enhanced the drift of epiphytic fauna. The uprooting of plants also dredged bed sediments and infauna living in a shallow stream bed, such as *Cricotopus* sp. and *Polypedilum* sp. (Wiederholm 1983; Kathman and Brinkhurst 1998).

Comparing the invertebrate taxa living on plants (epiphytic fauna) with those living in shallow bottom sediment (infauna), Erobdellidae, *Baetis* sp. H, *Baetis* sp., *Cheumatopsyche brevilineata*, and *Hydroptila* sp. had lower drift ratios even at their peaks of abundance. Erpobdellidae have sucking apparatus (Davies and Govedich 1991), and *C. brevilineata* and *Hydroptila* sp. have retreats or cases fastened to the substrate by a silk thread (Wiggins 1995). These taxa were highly resistant to high flows in this study. Invertebrate taxa having higher swimming activity, such as *Baetis* sp. H and *Baetis* sp., might seek refugia during the high flows (Imbert and Perry 2000).

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