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Optimal Feeding Position for Stream Fishes in Relation to Invertebrate Drift[1)]

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Abstract

The vertical and horizontal distributions of invertebrate drift, and the horizontal distribution of macrobenthic animals, were studied in a mountain stream to define advantageous feeding positions for visual feeding stream fishes during the summer season. The diurnal drift abundance of benthic or fallen animals were respectively linearly or exponentially correlated with the current speed. The estimated total daytime amounts of invertebrate drift passing downstream through the study pool reached about 72 g in wet weight, of which fallen drift accounted for 73 %. It is therefore suggested that the swift surface current layer is the most advantageous feeding position for visual feeding stream fishes.

Key words: Invertebrate drift, Salmonid food

Introduction

Invertebrate drift has long been recognized as an available food resource for stream resident salmonid fishes (Needham, 1928). Since Müller (1954) reported that macrobenthic drift was not an accidental phenomenon but rather a normal and positive behaviour of macrobenthic animal, it has been recognized to as part of invertebrate drift. Several workers have subsequently paid attention to the relationship between the components of invertebrate drift and the diet of stream fishes, and to the availability of drift as food (Elliott, 1967a, b, 1970, 1973; Chaston, 1968, 1969; Waters, 1969; Jenkins, *et al.*, 1970; Griffith, 1974; Furukawa-Tanaka, 1985).

Further studies have revealed that stream resident salmonid fishes exhibit a social hierarchy or territoriality, both in the aquarium (Kalleberg, 1958; Yamagishi, 1962; Fausch, 1983; Ishigaki, 1984) and in nature (Newman, 1956; Jenkins, 1969; Bachman, 1984; Furukawa-Tanaka, 1985; Tanida *et al.*, 1989). To elucidate the relationship between individual feeding habits and the choice of feeding position by the fish, the latter of which is considered to be realized mostly by social status (Jenkins, 1969; Fausch, 1983; Bachman, 1984; Furukawa-Tanaka, 1985; Tanida *et al.*, 1989), it is necessary to accurately estimate the micro-distribution and composition of both invertebrate drift in the water column and macrobenthic animals on the substratum.

The present study was designed to clarify the microdistribution and composition of macrobenthic animals in a stream, and of drift in a stream pool occupied by large, dominant salmonid fish (Jenkins, 1969; Fausch, 1983; Furukawa-Tanaka, 1985).

1) A part of doctoral thesis of Kyoto University.

Materials and Methods

The study was performed in August 1978 at Sawamata (34° 13'N, 135° 55'E, 880 m altitude) of the Jindoji-dani, a typical mountain stream of the Kumano River System, flowing from the southern slope of Mt. Sanjo-gatake (1719 m) in the centre of the Kii Peninsula (Fig. 1). This is a third order stream, 3-8 m in width and 1-2 m in maximum depth. The stream bed was formed by bedrock, large boulders and gravels. Terrestrial vegetation consisted of successional bushes after clear cutting for logging, but a little virgin forest remained near both sides of the stream. The portion upstream of Sawamata was covered with virgin forest. The water temperature at Sawamata varied within a narrow range of 15.5℃ (2:00-6:00)-16.5℃ (12:00-18:00) during 2 days of measurement (August 6 to 7).

At the Sawamata station, resident red-spot masu salmon, *Salmo (Parasalmo) masou macrostomus*, GÜNTHER, predominated, followed by resident Japanese charr, *Salvelinus leucomaenis* (PALLAS). A small number of the cyprinid, *Phoxinus oxycephalus*, SAUVAGE et DABRY, was also present. Bottom and surface iso-current speed lines based on 1 metre grid interval measurement over the study area, which was composed of a pool area (point 11-14 in Fig. 2) and a downstream C-riffle area (point 1-10, for definition of C-riffle see Furukawa-Tanaka, 1985), were drawn based on measurements made using an SPC-5 compact current speed meter (Sanko Precision Machinery; fan diametre 20 mm, Tokyo, Japan).

Macrobenthic animals were sampled at the pool area, C-riffle area, and adjacent

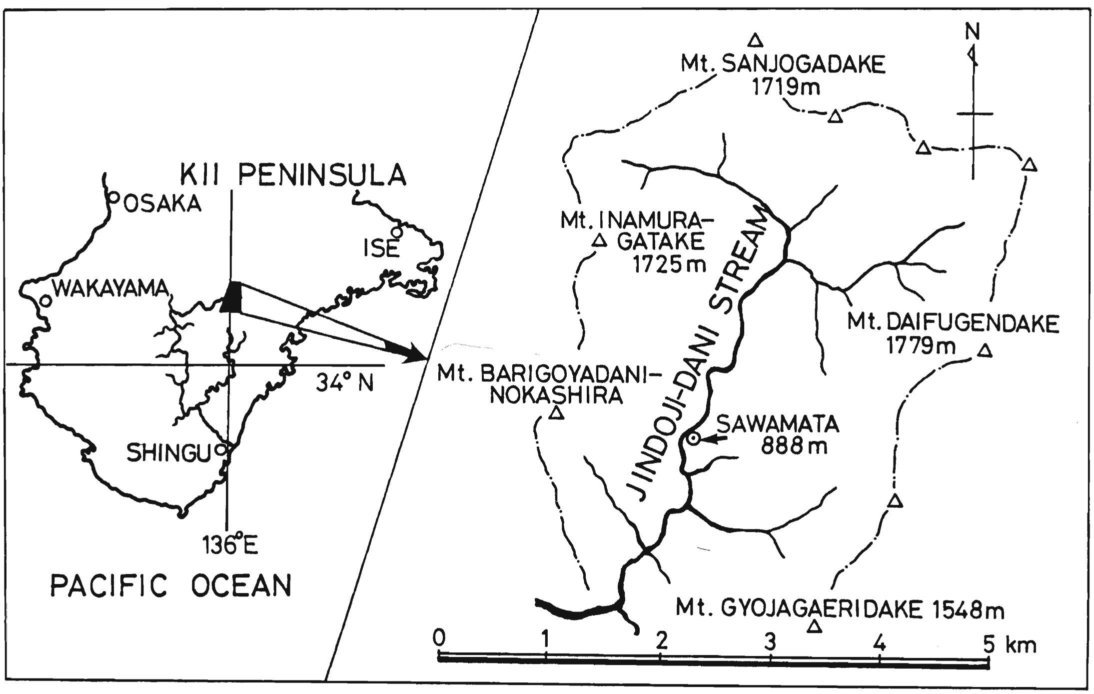

Fig. 1. Map of study area. The Kii Peninsula is located in the centre of Honshu Island.

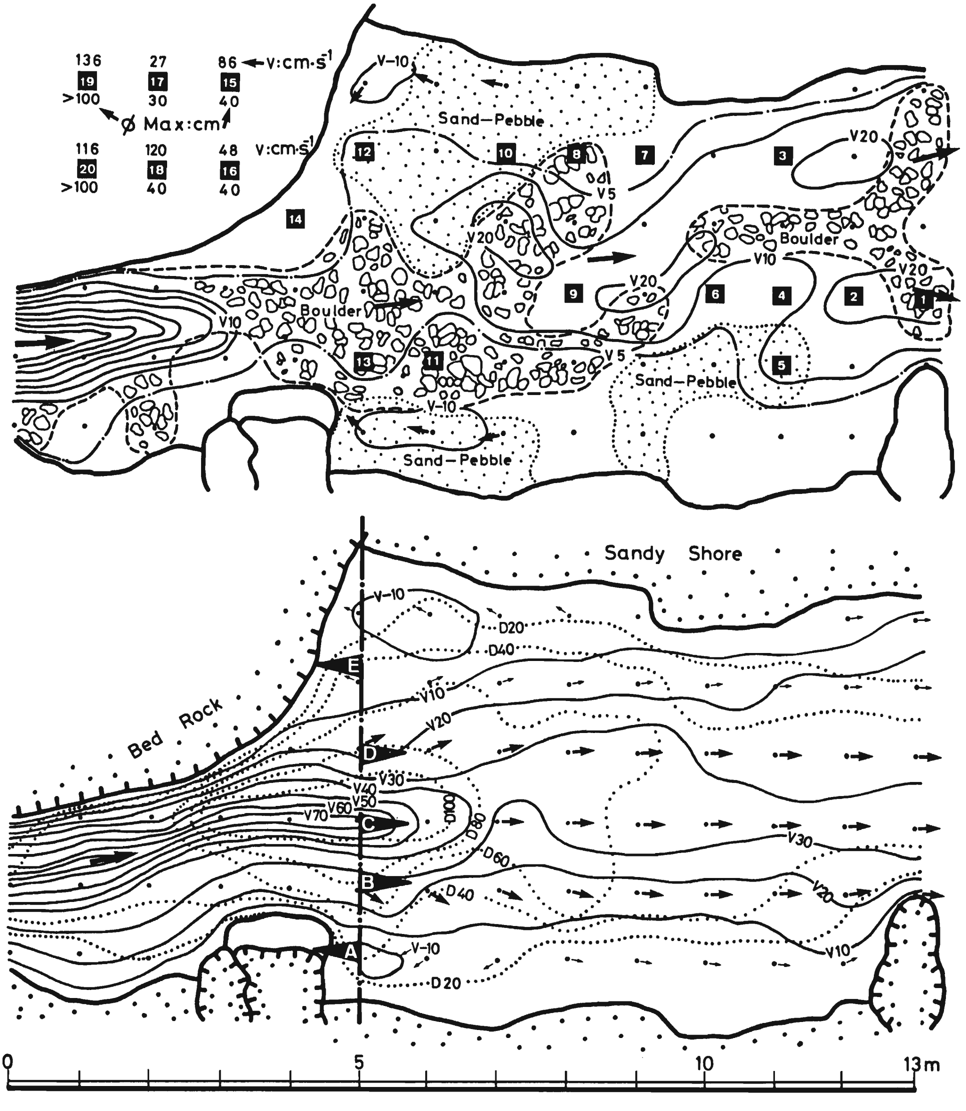

Fig. 2. The isopleths of the bottom current speed ($cm \cdot s^{-1}$) and the outline of substratum (upper), and the surface current speed and water depth (lower). The terms, sand-pebble (dotted area), pebble (blank area) and boulder (illustrated area) follow Hynes (1970). Each isopleth is drawn based on every one meter grid measurement (dotted 67 points). Solid and chain lines in the upper figure indicate bottom current speed ($cm \cdot s^{-1}$) and solid and broken lines in the lower figure indicate surface current speed and depth of the water (cm), respectively. The minus value of the current speed in the both sides of transect line of the pool indicates counter current. The macrobenthos were sampled from 1-14 in the figure and from adjacent R-riffle (15-20). The water depths of these R-riffle areas were 20-30 cm. The maximum diameter of bottom stones (ϕmax in cm) and bottom current speed is shown in the upper left corner of the figure.

upstream R-riffle area (point 15-20, for the definition of R-riffle see Furukawa-Tanaka, 1985) by a Surber net sampler (25 cm×25 cm, GG 40 with 475 μm mesh) on August 9 to 10. Drifting animals were collected by bag-like nets which were made of black-coloured polyester gauze (20 cm×20 cm in mouth, 1 m long, 100 μm mesh). Twelve nets were set vertically and horizontally on a transect running across the centre of the pool (Figs. 2 and 3) on August 6 to 7. Surface nets (A-1, B-1, C-1, D-1 and E-1) were set with half of the net-mouth above the stream surface to collect the surface drift. Current speed at each net-mouth was measured just after the first setting of drift nets at 16:00 on August 6. Normal and constant discharge seemed to persist throughout the sampling period.

Macrobenthos and drift samples were preserved immediately in 3% formalin solution and returned to the laboratory where they were sieved by a 1 mm-mesh sieve and sorted to order by naked eye. After sorting, specimens were examined under a dissecting binoculer microscope and, if possible, identified to species, following Tsuda (ed.) (1970) or Kawai (ed.) (1985).

Results

Amount and distribution of macrobenthic animals

Surface and bottom current speeds, the substratum topography, and the depth of water are shown in Fig. 2. The high current speed area was restricted to the head of the pool and eddies were present at both sides of the pool. The difference between surface and bottom current speed was largest at the

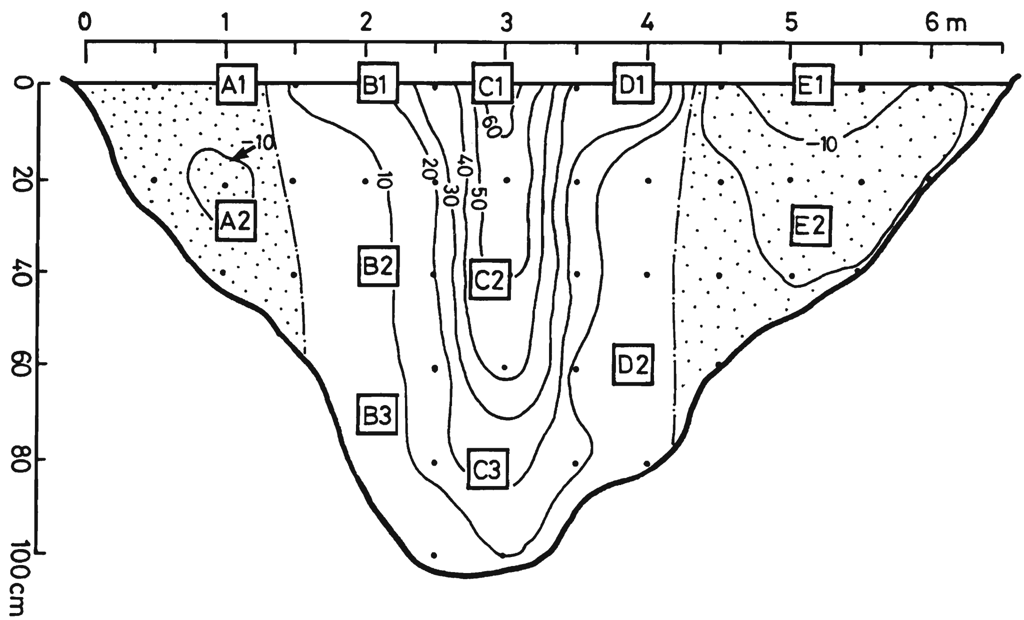

Fig. 3. The position of drift nets set in the centre of the study pool. The isopleths of current speed ($cm \cdot s^{-1}$) are drawn based on 47 point measurements (dotted points). Dotted areas in both sides of the figure represent the counter current against the main current and the chain lines indicate supposed border lines between these currents.

deepest point of the pool area, whereas it was small in the shallow area at both sides of the pool and in the shallow C-riffle area below the pool.

The substratum types in the study area was seemed to be roughly correlated with the surface current speed, but not with the bottom current speed. Substrata under the surface main current course were composed of large boulders and pebbles, while those of the shallow areas at both sides of the pool were sand and pebbles. The terms used here to describe particles follow Hynes (1970).

In the current speed range of 0 to 50 cm · s^{-1}, the density (significant at 1 % level), biomass, and number of species (significant at 0.1 % level) of macrobenthic animals at the sampling points generally showed an increase with the bottom current speed, but they tended to decrease with current speeds higher than 50 cm · s^{-1}, they were especially low at the points of large rock surface (Fig. 4). The relationship among these three variables and the substratum was unclear. Differences in the density or biomass of macrobenthos between substrata were smaller than results represented by Tsuda (1959), Mizuno *et al*. (1966) or those by Furukawa-Tanaka (1985) who studied other Japanese mountain streams.

Epeorus uenoi, MATSUMURA, *Pseudocloeon* sp. and Simuliidae were restricted to the swift current R-riffle area. *Baetis* spp. were abundant in the swift current R-riffle area, but a small number of them were found on all substrata with any current speed (Table 1). Net-spinning Trichoptera larvae of Stenopsychidae and Hydropsychidae are usually abundant and have a large biomass in other Japanese mountain streams (Tsuda, 1959), but they were scarce in this study area.

For the numerically dominant 5 taxa,

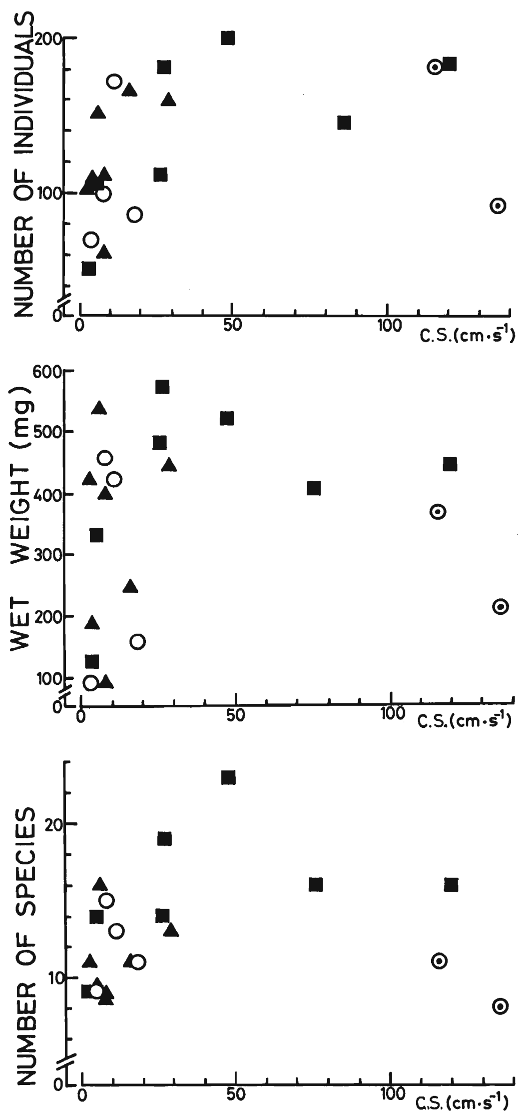

Fig. 4. Relationships of the density, biomass (wet weight in mg) and number of species of collected macrobenthic animals (625 cm^2) to bottom current speed at each sampling point. Marks in the figure indicate the maximum diameter of stones in the substratum sampled (dotted open circle: >50 cm; solid square: 50-20 cm; solid triangle: 19-5 cm; open circle: <5 cm).

Table 1. The density (in 625 cm^2) and biomass (mg wet weight per 625 cm^2 in parentheses) of macrobenthic animals in the study pool and adjacent upstream R-riffle at Swamata of the Jindoji-dani Stream in August 1978. The microlocation of each sampling point is shown in Fig. 2. Asterisks (*) indicates the available benthic food animals, which are tentatively defined as more than 1 % mean wet weight contribution in the stomach contents of either resident salmon or charr inhabiting this stream (Furukawa-Tanaka, unpublished). The current speed was measured just above the substrata sampled.

Sampling Point	19	18	20	15	16	17	2	1	9	3	5	6	7	12	4	13	8	10	11	14
Current Speed ($cm \cdot s^{-1}$)	136	120	116	86	46	27	29	26	18	16	11	8	8	8	6	5	4	4	4	4
Diameter of Bottom Stones (cm)	100	20-40	100	20-40	20-40	20-30	5-10	50	3-5	3-15	2-3	2-10	5-15	3	5-10	50	10-30	3-5	50	5-10
*Epeorus ueoi** (n)	9	1	23	8	9	1														
(w)	(65)	(2)	(106)	(54)	(59)	(2)														
Pseudocloeon sp. (n)	36	4	67	4	12	3	1							1						
(w)	(24)	(2)	(52)	(2)	(9)	(2)	(+)							(+)						
Baetis spp.* (n)	7	76	18	49	39	22	11	11	8	40	14	3	10	16	15	17	19	18	14	8
(w)	(6)	(90)	(36)	(70)	(51)	(30)	(15)	(15)	(12)	(23)	(10)	(2)	(8)	(11)	(16)	(15)	(15)	(17)	(22)	(9)
*Epeorus latifolium** (n)				4	21	15	2	2		1			3	1	2	9	1		1	1
(w)				(52)	(65)	(53)	(28)	(10)		(+)			(80)	(1)	(8)	(8)	(20)		(1)	(31)
*Ephemerella cryptomeria** (n)		23	5	34	12	16	33	17	10	12	14	8	11	9	24	8	7	1	3	10
(w)		(187)	(40)	(121)	(95)	(112)	(193)	(98)	(49)	(86)	(97)	(47)	(87)	(9)	(204)	(48)	(47)	(9)	(17)	(94)
Rhithrogena sp.* (n)		30		17	37	17	52	38	45	15	10	17	9	1	43	3	1	4	8	5
(w)		(39)		(37)	(76)	(54)	(91)	(53)	(61)	(13)	(7)	(18)	(21)	(+)	(49)	(2)	(+)	(5)	(8)	(5)
*Ecdyonurus kibunensis** (n)		9		2	5	67	25	2	4	60	41	5	58	10	18	29	58	28	8	40
(w)		(3)		(1)	(2)	(66)	(17)	(4)	(3)	(56)	(32)	(5)	(52)	(8)	(13)	(24)	(68)	(34)	(4)	(34)
*Stenopsyche marmorata** (n)				3	2	6					1									
(w)				(7)	(17)	(24)					(1)									
Rhyacophila spp. (n)	2		1		5	2		2	1					2	1		1			
(w)	(75)		(9)		(47)	(40)		(11)	(5)					(14)	(9)		(5)			
Dinarthrodes sp.* (n)							1													
(w)							(1)													
Perlidae (n)		6	1	5	8	1	2	2	1			1			2			1	1	2
(w)		(75)	(27)	(9)	(38)	(8)	(12)	(13)	(5)			(+)			(122)			(6)	(11)	(+)
Chloropelidae (n)	1	13	2	10	32	13	28	25	12	31	78	24	15	43	35	30	21	12	14	26
(w)	(4)	(10)	(1)	(6)	(22)	(7)	(19)	(15)	(11)	(28)	(69)	(16)	(14)	(29)	(28)	(27)	(15)	(8)	(13)	(19)
Simulidae (n)	32	4	59		1															
(w)	(25)	(5)	(67)		(1)															
Eriocera spp. (n)						5	2	5		2	3		3	4	3		1		1	4
(w)						(164)	(60)	(251)		(28)	(163)		(131)	(64)	(75)		(15)		(41)	(176)
Gomphidae (n)														2		3				1
(w)														(190)		(162)				(63)
Others (n)	4	17	5	8	17	13	2	7	4	4	11	2	2	9	9	7		4	3	4
(w)	(11)	(27)	(24)	(43)	(35)	(6)	(8)	(5)	(7)	(9)	(41)	(1)	(2)	(130)	(10)	(40)		(10)	(4)	(9)
TOTAL (n)	90	183	181	144	200	181	159	111	85	165	172	60	111	98	152	106	109	68	53	101
(w)	(210)	(440)	(362)	(402)	(517)	(568)	(443)	(475)	(153)	(243)	(420)	(89)	(395)	(456)	(534)	(326)	(185)	(89)	(121)	(440)
TOTAL No. of Available (n)	15	139	46	117	125	144	124	70	67	128	80	33	91	37	102	66	86	51	34	64
Animals (w)	(71)	(321)	(182)	(342)	(365)	(341)	(344)	(180)	(125)	(178)	(147)	(72)	(248)	(29)	(290)	(97)	(150)	(65)	(52)	(173)
TOTAL No. of Species	8	16	11	16	23	19	13	15	11	11	13	9	9	15	16	14	9	9	9	11

Baetis spp., *Ephemerella cryptomeria* (IMANISHI), *Rhithrogena* sp., *Ecdyonurus kibunensis* (IMANISHI) and various Chloroperid species, which were apparently evenly distributed over the pool and the adjacent C-riffle areas (sampling points, 1-14), the degree of habitat overlap between species was calculated (a matrix of Morisita's C'_δ, 1971, Table 2). The smallest degree (0.42) was found between the same crawling life-forms of Ephemeroptera nymphs, *E. kibunensis* and *Rhithrogena* sp. The former was more abundant at medium to low current area, while the latter was more abundant at high current area (Table 1). The habitat of *E. cryptomeria* shows a high degree of overlap with that of *Baetis* spp., *Rhithrogena* sp. and Chloroperlidae. These 5 taxa and *Eriocera* spp. comprised the majority of macrobenthos in number (mean, 92 %; range, 82-97 %) and in biomass (mean, 78 %; range, 27-99 %) in both the pool and C-riffle areas.

Diel change and composition of benthic and fallen drift

In this study, three time periods, daytime (4:40-5:10, 6:00-6:30, 8:00-8:30, 10:00-10:30, 12:00-12:30, 16:00-16:30, 18:00-18:30), nightfall (20:00-20:30) and nighttime (22:00-22:30, 0:00-0:30, 2:00-2:30) were adopted in the following analyses.

The numerically dominant components of benthic drift (consisted of macrobenthos) was *Baetis* spp., *Pseudocloeon* sp., *Ecdyonurus kibunensis* , *Rhithrogena* sp., *Epeorus latifolium* (UENO), *Ephemerella cryptomeria*, Chloroperlidae, Chironomidae and Simuliidae (Table 3). Among these components, *Baetis* spp. predominated throughout the day, followed by *Pseudocloeon* sp. These nine components occuppied 85 % of the total daytime catch, 92 % of the total nightfall catch, and 93 % of the total nighttime catch of benthic drift in number.

The similarity index of the faunal composition (C_λ of Morisita, 1959) between the total daytime and night (including the night fall) catches, based on these major 9 taxa mentioned was 0.97. The similarity indices between the faunal composition of the total catches of 12 nets collection based on these major 9 benthic taxa were close to 1 (Table 4). As a whole, the composition of benthic drift was quite similar, not only between the day and night, but also between the nets.

A marked difference was evident in several taxa between the total number of fallen drift (consisting of fallen terrestrial and fallen emerged aquatic animals) collected in the three time periods (Table 3). Imagines or subimagines of Ephemeroptera, adult Diptera, Hymenoptera (including Formicidae) and Odonata were abun-

Table 2. Degree of spatial overlap among 5 taxa of macrobenthos, which were collected together in the same sample from many sampling points (see Table 1), by the indices of Morisita's C'_δ (1971).

Species or taxon	*Ecdyonurus kibunensis*	*Rithrogena* sp.	*Baetis* spp.	Chloroperlidae
Rithrogena sp.	0.42			
Baetis spp.	0.54	0.65		
Chloroperlidae	0.69	0.66	0.61	
Ephemerella cryptomeria	0.55	0.85	0.79	0.74

Table 3. The total catches of benthic and fallen drifts sampled by 12 nets. (daytime; 4:40-5:10, 6:00-6:30, 8:00-8:30, 10:00-10:30, 12:00-12:30, 16:00-16:30, 18:00-18:30; nightfall; 20:00-20:30; nighttime; 22:00-22:30, 0:00-0:30, 2:00-2:30; n: number of individuals caught, w: wet weight in mg)

	Daytime				Nightfall				Nighttime			
	n	%	w	%	n	%	w	%	n	%	w	%
BENTHIC DRIFT												
EPHEMEROPTERA [total]	[88]	[28]	[135]	[7]	[343]	[79]	[534]	[44]	[679]	[80]	[1099]	[64]
Baetis spp.	48	15	68	3	228	52	339	28	434	51	659	38
Pseudocloeon sp.	11	3	13	1	26	6	23	2	66	8	71	4
Epeorus uenoi	1	+			1	+	2	+	7	1	19	1
Epeorus latifolium	4	1	9	+	12	3	44	4	20	2	32	2
Ecdyonurus kibunensis	9	1	7	+	31	7	31	3	60	7	59	3
Rhithrogena sp.	4	1	9	+	27	6	46	4	56	7	72	4
Ephemerella cryptomeria	6	1	27	1	11	3	40	3	15	2	67	4
Ephemerella setigera	5	1	2	+	5	1	8	1	9	1	3	+
others					2	1	1	+	12	1	117	7
TRICHOPTERA [total]	[3]	[1]	[12]	[1]	[7]	[2]	[10]	[1]	[11]	[1]	[21]	[1]
PLECOPTERA [total]	[4]	[1]	[4]	[+]	[20]	[5]	[28]	[2]	[29]	[3]	[20]	[1]
Chloroperidae	2	1	+	+	8	2	6	1	19	2	12	1
others	2	1	4	+	12	3	23	2	10	1	8	1
DIPTERA [total]	[12]	[4]	[22]	[1]	[16]	[4]	[13]	[1]	[47]	[6]	[38]	[2]
Chironomidae	4	1	5	+	10	2	7	1	23	3	17	1
Simulidae	4	1	9	+	6	1	5	+	19	2	20	1
others	4	1	8	+					5	1	2	+
OTHERS [total]	[1]	[+]	[3]	[+]	[4]	[1]	[10]	[1]	[1]	[+]	[4]	[+]
BENTHIC ANIMALS [total]	(108)	(33)	(176)	(8)	(390)	(89)	(595)	(49)	(767)	(91)	(1182)	(69)
FALLEN DRIFT												
EPHEMEROPTERA	17	5	87	4								
TRICHOPTERA	3	1	8	+	11	3	428	35	2	+	52	3
PLECOPTERA	1	+	2	+								
DIPTERA	128	39	151	7	16	4	12	1	51	6	54	3
HYMENOPTERA	7	2	329	15	1	+	+	+				
Formicidae	41	12	87	4	11	3	34	3	8	1	23	1
COLEOPTERA	6	2	27	1	4	1	143	12	6	1	148	9
HOMOPTERA	6	2	50	2					1	+	+	+
HETEROPTERA									1	+	39	2
LEPIDOPTERA	1	+	108	5								
ODONATA	3	1	1042	48					1	+	220	13
ARANEAE	3	1	61	3					4	1	4	+
OTHERS	5	2	24	1	3	1	3	+	5	1	4	+
FALLEN ANIMALS [total]	(221)	(67)	(1976)	(92)	(46)	(11)	(620)	(51)	(79)	(9)	(544)	(32)

Table 4. A matrix of similarity of faunal composition represented by C_{λ} (Morisita, 1959) among 12 nets set vertically and horizontally. As daytime and nighttime faunal composition were quite similar (see text), 11 time samples of each net were combined. Calculation was based on 9 major benthic taxa, *Baetis* spp., *Pseudocloeon* sp., *Epeorus latifolium*, *Ecdyonurus kibunensis*, *Rhithrogena* sp., *Ephemerella cryptomeria*, Chloroperlidae, Chironomidae and Simuliidae, in the drift collection.

Net	A-2	B-1	B-2	B-3	C-1	C-2	C-3	D-1	D-2	E-1	E-2
A-1	1.02	1.04	1.03	0.94	1.05	1.04	1.03	0.94	1.06	1.06	1.00
A-2		1.00	0.98	0.98	0.97	0.98	0.98	0.84	1.01	0.99	0.88
B-1			1.00	0.96	0.99	0.99	0.98	0.88	1.02	1.00	0.90
B-2				0.89	1.03	1.03	1.04	1.03	1.06	1.07	1.05
B-3					0.89	0.90	0.89	0.75	0.95	0.89	0.74
C-1						1.00	0.99	0.94	1.01	1.04	0.97
C-2							1.00	0.93	1.02	1.04	0.96
C-3								0.93	1.01	1.03	0.96
D-1									0.92	1.03	1.00
D-2										1.04	0.95
E-1											1.05

dant in the daytime, whereas Coleoptera were abundant at night. In the nightfall, adults of Trichoptera and Coleoptera predominated in the fallen drift, especially in terms of weight.

A diel periodical pattern of benthic drift was especially evident in samples from the nets in the swift current areas (C-1, C-2, C-3 and B-1), but the periodicity was unclear at the other 8 nets (Fig. 5). In the fallen drift collections, no such periodical pattern was evident at any nets.

In the surface net collections, the fallen drift component was more abundant than benthic drift in the daytime, whereas at night (including nightfall), the benthic drift component was more abundant in all net collections. The benthic drift component in the total nighttime catch exceeded the fallen drift both numerically (10 times) and in biomass (2 times), whereas the fallen drift component in the total daytime catch was twice as numerous and 11 times larger in wet weight than that of the benthic component (Table 3). During the nightfall, the benthic drift and fallen drift fractions were equal in weight.

Microdistribution of drift abundance and drift density

Drift abundance was proposed firstly by Wankowski and Thorpe (1979) to measure a value for feeding position of a salmonid fish. Here the term drift abundance is used to refer to "the amount of organisms passing a vertical unit area (a square metre) at right angle to the current direction per unit time (a second)", which is the slightly modified unit from that of Dill *et al.* (1981). Fig. 6 shows the vertical and horizontal distribution of the mean daytime drift abundance and of the mean daytime drift density (Elliott, 1967a) in number and in wet weight.

It is clear that the drift abundance of the fallen and benthic drift both in number and

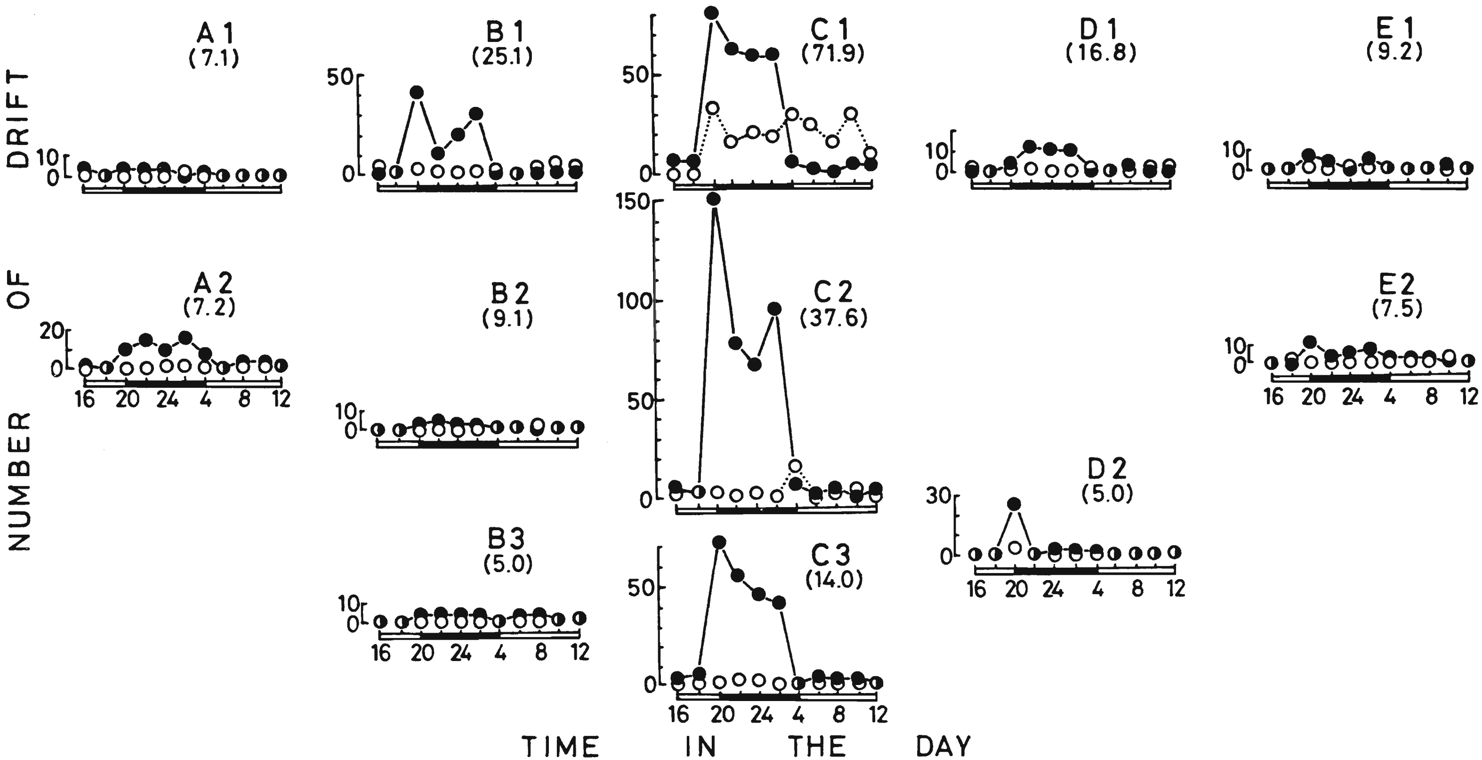

Fig. 5. Diel change of invertebrate drift sampled by the 12 nets (see Fig. 2). Number of drift animals is represented by total catches for 30 minutes of every 2 hours on August 6 to 7, 1978 at Sawamata. The solid and open circles are benthic and fallen drifts, respectively. Figures in parentheses show the mean current speed of five measurements. The surface nets (A-1, B-1, C-1, D-1 and E-1) were immersed into a half depth of the net mouth (area, 20 cm × 10 cm) and the other nets were immersed entirely (area, 20 cm×20 cm).

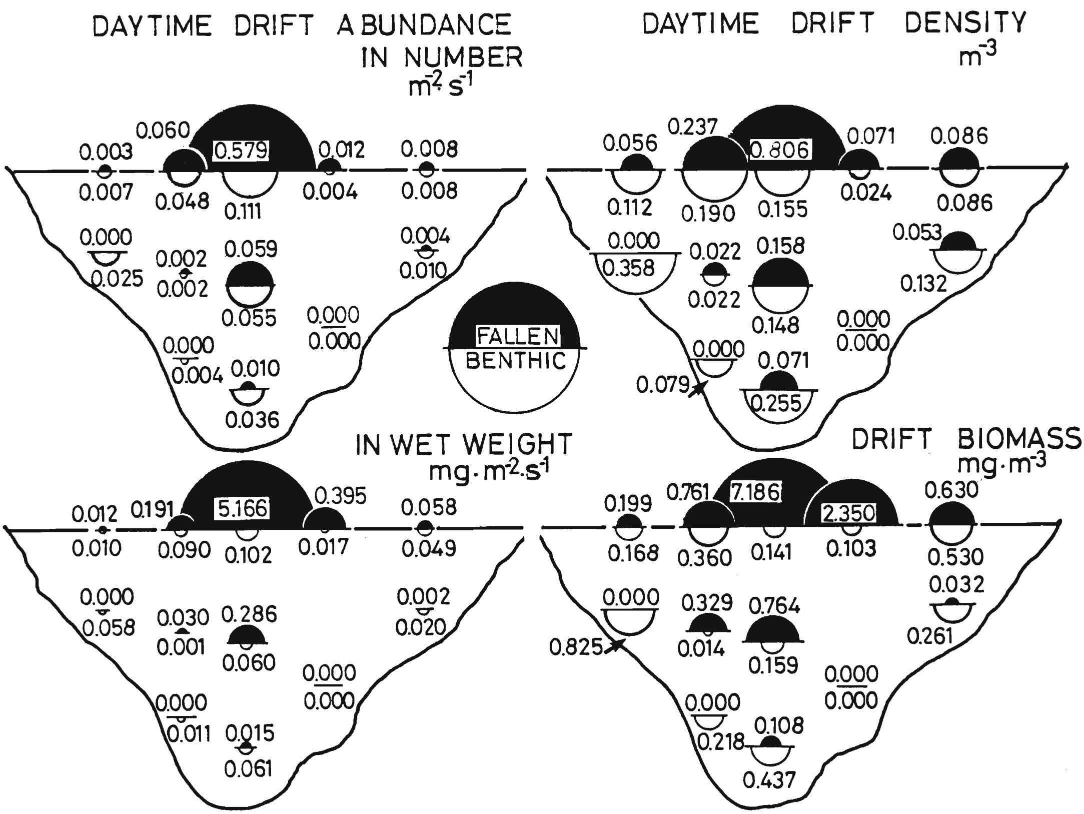

Fig. 6. Vertical and horizontal distribution of the mean daytime drift abundance in number ($m^{-2} \cdot s^{-1}$) and in wet weight ($mg \cdot m^{-2} \cdot s^{-1}$), and of the mean daytime drift density (m^{-3}) and of the mean daytime drift biomass ($mg \cdot m^{-3}$). Solid upper half circles and open lower half circles indicate the fallen animals and the benthic animals, respectively. The current speed is shown in Fig. 3.

in weight was extremely large in the surface layer of the main current course, and decreased vertically and horizontally with distance. In net C-1, the drift abundance of fallen animals was 5 and 52 times as large as that of benthic animals in number and weight, respectively.

Fallen drift density or biomass was also high in the surface nets, especially in net C-1 and then B-1 or D-1. Such a clear trend was not observed in the benthic drift density or biomass, which seemed to show an even vertical distribution within the water column.

Linear correlations were observed in the relationship between benthic drift abundance and current speed, and exponential correlations were observed between fallen drift abundance and current speed (Fig. 7).

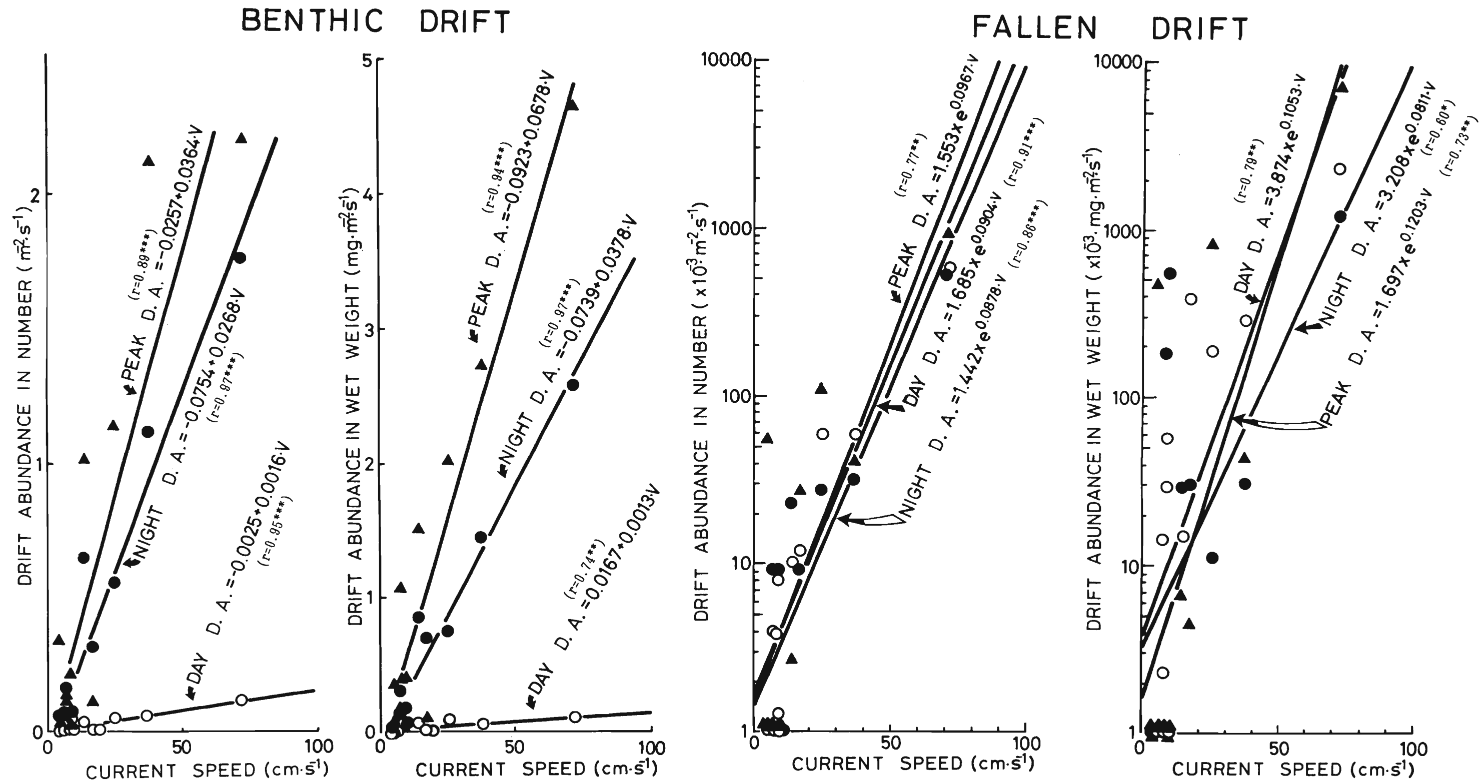

Fig. 7. Relationships between the drift abundance (D.A.) and the current speed. The drift abundance of the benthic component and that of the fallen component were fitted separately to the liner and exponential curve regression, respectively. Solid circles, open circles and solid triangles indicate the drift abundance at night, in the daytime, and the nightfall peak.
(asterisk means significant level: *** 0.1 %, ** 1 %, * 5 %)

Discussion

Importance of daytime fallen drift as a food resource of fishes

Furukawa-Tanaka (1985) showed that Japanese charr are unable to feed at night and noted that other salmonid fishes also seem to be daytime visual feeders. So it is considered that the salmonid fishes inhabiting this stream are unable to feed on the bulk of drift at night. The total weight of the fallen drift collection exceeded that of the benthic drift by 11 times in the daytime (Table 3). Fallen animals are usually much more abundant in stomach contents of lotic salmonids (Hunt, 1975; Nagoshi and Sakai, 1980; Smith, 1980; Mason and Macdonald, 1982; Furukawa-Tanaka, 1985; Tanida *et al.*, 1989). It is concluded, therefore, that fallen drift is the most important food resource for daytime visual drift feeding fishes, at least in the summer season. And, this important food resource was not evenly distributed in the water column, but was much more abundant in the main current course near the surface (Fig. 6).

To estimate the total amount of drift passing downstream through the study pool, the following three assumptions were used: (1) the drift abundance changed with current speed in accordance with the regression formulae given in Fig. 7, (2) the area of each current speed range was calculated based on the iso-current-speed figure of Fig. 3, (3) the median of each current speed range was tentatively used.

Table 5 shows the estimated amounts of drift in each current range passing through the study pool during the three time periods. The total amounts of drift during the daytime, the nightfall, and the nighttime were 71.8, 20.4 and 173.1g, respectively. The estimated total amount of daytime fallen drift was about three times that of benthic drift.

Since there is no report concerning daily

Table 5. The amounts of drift passed downstream through a transect plane of the study pool during the daytime, nightfall and nighttime in August 6 to 7, 1978. The detail calculation procedures are given in the text. The nighttime period excludes the nightfall.
(B: benthic drift, F: fallen drift, +: less than 0.1 mg.)

Current Speed	Area (Vertical section)	Daytime Drift 5:00-19:00		Nightfall Drift 20:00-20:30		Nighttime Drift 20:30-5:00	
		B	F	B	F	B	F
$cm \cdot s^{-1}$	m^2	g	g	g	g	g	g
65	0.06	0.3	11.0	0.5	0.5	4.4	1.1
55	0.27	1.2	17.3	1.8	0.6	16.6	2.3
45	0.51	1.9	11.4	2.7	0.3	25.4	1.9
35	0.72	2.3	5.6	3.0	0.3	27.5	1.2
25	1.27	3.1	3.4	3.7	0.1	33.9	0.9
15	2.68	4.9	2.5	4.5	+	40.4	0.9
5	4.55	5.3	1.5	2.0	+	16.0	0.7
Total	10.06	19.1	52.7	18.7	1.7	164.1	9.0

food requirements of resident red-spot masu salmon or Japanese charr in natural conditions, the daily ration of the brown trout, *Salmo trutta*, which comprises 10 % of body wet weight of a 10-50 g fish (Elliott, 1975) was adopted to enable a rough estimation of the food level for the salmon and charr inhabiting this pool. Since the salmon and charr are considered not to utilize nocturnal drift, including that during the night fall period, the amount of daytime drift can theoretically sustain a total of 700 g of these fishes. This figure corresponds well with the total wet weight (400-500g) of fishes inhabiting this pool (Furukawa-Tanaka, unpublished data).

Feeding position to be defended

Stream resident salmonid fishes frequently show intra- and inter-specific aggressive behaviour between inhabitants, both in nature and under experimental conditions (*Thymallus*: Krat and Smith, 1979; *Salvelinus*: Newman, 1956; Noakes, 1980; *Salmo*: Kalleberg, 1958; Yamagishi, 1962; Jenkins, 1969; *Oncorhynchus*: Chapman, 1962; Stein *et al.*, 1972). Fausch and White (1981) speculated that the main function of such aggressive behaviour of brook trout, *Salvelinus fontinalis* (MITCHILL), is to defend the shelter. Other authors believe that the dominance relationship of these salmonid fishes, which is established as a result of aggressive encounters, plays an important role in defending a more advantageous feeding position, but they have given no data for distribution of available food.

As shown in this paper, the fallen drift is diurnally more abundant than benthic drift, and this important food source is extremely abundant and dense at the surface of the main current course. In addition, the mean weight of fallen animals is higher than that of benthic animals, (Furukawa-Tanaka, 1985), indicating the fallen drift is the more favourable food for stream fishes.

Therefore, the optimal foraging position for daytime visual drift feeding fishes should not be the layer close to the substratum where the benthic drift originates, but the upper surface layer of swift current, where abundant, dense and choice food occurs.

Everest and Chapman (1972) stated that fishes consistently face toward a moderate current velocity which is adjacent to an area of swift current with abundant food to maximize their net energy gain, because to maintain position in a swift current requires a large energy expenditure. But this speculation was based on few benthic drift data and they were not conscious of the importance of the fallen drift. To minimize a large swimming energy expenditure, the marked vertical and horizontal changes of current velocity in the pool area constitute a very important structural character of the lotic habitat for fishes.

On the other hand, the shallow R-riffle and C-riffle areas showed only a small change of current velocity within a short distance and in addition, the R-riffle area is usually partitioned into small spaces by boulders, cobbles and turbulent water, whereas pool areas usually have a large space without visual obstacles. Therefore, the feeding range within a pool area may be larger than that in an R-riffle area.

As it may be considered that the R-riffle area is not so effective feeding place for sal monid fishes, the drifting animals in the R-riffle are presumably under low predation pressure from these fishes. The water from the R-riffle area which contain more drifting animals flows into the head of the following pool, where the fishes can keep their position in a moderate current speed near bottom.

Furukawa-Tanaka (1985) showed that a large Japanese charr with a full stomach maintained its position at the head of the pool, while a smaller fish with low stomach content maintained its position just below the large one. This obviously shows that the opportunities for drift feeding for a fish can be severely affected by the presence of other fish occupying an upstream position. Therefore the most advantageous position for a drift feeder is at the head of a pool area.

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Appendix

Drift density and drift biomass

Vertical and horizontal change of the drift density are calculated for the benthic and fallen drifts of the C net group (Appendix table 1) and for the surface nets (Appendix table 2). The drift densities of major four taxa, *Baetis* spp., *Ecdyonurus kibunensis, Rhithrogena* sp. and *Pseudocloeon* sp. which comprised 80 % of the benthic drift, and of others were represented by small values by day, increased considerably at night.

The drift densities of *Baetis* spp. and *E. kibunensis* were highest in C-3 net both in the nighttime and at nightfall, but showed no definite vertical change in the daytime. In contrast with these three taxa, *Pseudocloeon* sp. did not show any vertical trend even in the nighttime density and seemed to be evenly distributed throughout the day. The drift density of fallen adult Diptera was highest in net C-1 and showed no noticeable diel change. In the daytime, the density of adult Diptera in net C-1 was 9 times greater than that of *Baetis* spp. of the benthic component.

In the horizontal axis, the maximum densities of *Baetis* spp. and fallen adult Diptera in the daytime were observed in net C-1, with an exceptionally high density of the former taxon in net A-1. This exception was the result of few individuals and very low current speed.

Relations of the drift densities and the drift biomass to the current speed in the three time periods (same as Tables 3 and 5, and Fig. 5) are calculated based on all collections by the 12 nets (a large Odonata caught in B-1 net is omitted because of few collections). No correlations were obtained either for the density or the biomass of the benthic drift, but those for fallen drift were as follows.

Daytime: F.D.D.$=-0.0653+0.0109V$ ($r=0.95$)
F.D.B.$=-0.6500+0.0937V$ ($r=0.89$)
Nightfall: F.D.D.$=0.0344+0.0141V$ ($r=0.58$)
F.D.B.$=0.2032+0.1002V$ ($r=0.51$)
Nighttime: F.D.D.$=-0.0479+0.0090V$ ($r=0.89$)
F.D.B.$=0.8346+0.0030V$ ($r=0.03$)

where F.D.D.: Fallen Drift Density ($n \cdot m^{-3}$)
F.D.B.: Fallen Drift Biomass($mg \cdot m^{-3}$)
V : Mean Current Speed($cm \cdot s^{-1}$)

Drift density in relation to distributional pattern of macrobenthos

The drift density of *Baetis* spp. was high in the near-bottom layer of slow current and low in the upper surface layer of swift current in the pool area (Appendix table 1). *E. kibunensis* and *Rhithrogena* sp. also showed the same tendency.

In the macrobenthos distribution (see Table 1), the highest density of *Baetis* spp. was observed in the adjacent upstream R-riffle of the study pool, though a considerable number of *Baetis* spp. were also sampled from all other substrata of the study area. *Rhithrogena* sp. and *E. kibunensis* showed high densities in the macrobenthos in the medium current speed (Table 1), and these taxa also showed wide distributions over the study pool and C-riffle areas. In contrast, *Pseudocloeon* sp., for which the drift density was evenly distributed vertically and horizontally (Appendix tables 1 & 2), show a restricted habitat of large rock surfaces with high current velocity. It seems that the animals which were distributed over a wider range of habitat, showed high drift density in the near-bottom layer of slow current under the main current course in the pool.

Appendix table 1. Vertical change of the mean drift density and the mean drift biomass (wet weight in mg) with standard deviation of C net group. The day and the night values are means of 7 and 3 sampling times as in Table 3, respectively. The mean current speed and its standard deviation of C-1, C-2 and C-3 net were 71.9±2.9, 37.5±1.7 and 14.0±1.6 cm·s^{-1}, respectively.

		Daytime		Nighttime		Nightfall	
	net	density m^{-3}	biomass $mg \cdot m^{-3}$	density m^{-3}	biomass $mg \cdot m^{-3}$	density m^{-3}	biomass $mg \cdot m^{-3}$
	C-1	0.05± 0.05	0.03± 0.02	1.46± 0.02	2.32± 0.27	1.78	2.18
Baetis spp.	C-2	0.06± 0.06	0.06± 0.09	1.70± 0.23	2.25± 0.40	1.77	2.56
	C-3	0.09± 0.07	0.10± 0.10	2.61± 0.35	3.68± 0.64	4.17	6.85
Ecdyonurus	C-1	0.02± 0.03	0.01± 0.02	0.22± 0.02	0.23± 0.12	0.12	0.09
kibunensis	C-2	0.02± 0.02	0.01± 0.02	0.23± 0.15	0.21± 0.06	0.48	0.48
	C-3	0.01± 0.04	0.01± 0.03	0.53± 0.41	0.49± 0.44	0.89	1.05
	C-1	0.01± 0.02	0.01± 0.02	0.08± 0.07	0.16± 0.18	0.23	0.28
Rhithrogena sp.	C-2	0.01± 0.02	0.01± 0.02	0.27± 0.06	0.31± 0.15	0.37	0.84
	C-3	0.01± 0.04	0.08± 0.21	0.43± 0.06	0.50± 0.08	0.30	0.43
	C-1	0.02± 0.03	0.02± 0.03	0.27± 0.13	0.28± 0.21	0.27	0.34
Pseudocloeon sp.	C-2	0.02± 0.03	0.02± 0.03	0.23± 0.08	0.24± 0.16	0.37	0.31
	C-3	0.00	0.00	0.23± 0.06	0.18± 0.15	0.30	0.15
Other Benthic	C-1	0.06± 0.04	0.07± 0.08	0.43± 0.13	0.12± 0.37	0.66	3.57
Animals	C-2	0.04± 0.02	0.06± 0.04	0.53± 0.19	0.87± 0.83	1.18	1.54
	C-3	0.14± 0.16	0.25± 0.47	0.83± 0.17	1.30± 0.26	1.59	2.35
Total Benthic	C-1	0.16± 0.10	0.14± 0.12	2.45± 0.29	3.57± 0.96	3.05	6.45
Animals	C-2	0.15± 0.08	0.16± 0.13	2.97± 0.52	3.88± 0.47	5.62	7.21
	C-3	0.26± 0.16	0.44± 0.61	4.63± 0.62	6.14± 0.82	7.24	10.82
Diptera	C-1	0.52± 0.35	0.55± 0.40	0.48± 0.14	0.57± 0.08	0.43	0.37
(Adult)	C-2	0.06± 0.14	0.17± 0.37	0.07± 0.00	0.05± 0.02	0.04	0.02
	C-3	0.04± 0.05	0.04± 0.06	0.10± 0.10	0.08± 0.09	0.20	0.05
Other Fallen	C-1	0.28± 0.24	6.64± 7.28	0.23± 0.08	1.11± 0.81	0.89	9.50
Animals	C-2	0.10± 0.09	0.60± 1.16	0.01± 0.02	0.03± 0.05	0.07	0.10
	C-3	0.03± 0.04	0.14± 0.22	0.07± 0.12	0.12± 0.22	0.00	0.00
Total Fallen	C-1	0.81± 0.37	7.19± 7.21	0.71± 0.06	1.68± 0.73	1.31	9.88
Animals	C-2	0.16± 0.22	0.76± 1.53	0.09± 0.02	0.08± 0.07	0.11	0.12
	C-3	0.07± 0.06	0.12± 0.15	0.17± 0.15	0.21± 0.30	0.20	0.05

Appendix table 2. Horizontal change of the mean drift density and the mean drift biomass with standard deviation of surface nets. Each net is arranged in order of current speed, and the mean current speed and its standard deviation of C-1, B-1, D-1, E-1 and A-1 were 71.9±2.9, 25.2±3.3, 16.8±0.8, 9.2±0.7 and 6.1±0.5 (cm・s^{-1}), respectively.

		Daytime		Nighttime		Nightfall	
	net	density m^{-3}	biomass $mg\cdot m^{-3}$	density m^{-3}	biomass $mg\cdot m^{-3}$	density m^{-3}	biomass $mg\cdot m^{-3}$
Baetis spp.	C-1	0.06±0.05	0.03±0.02	1.46±0.02	2.32±0.27	1.78	2.18
	B-1	0.05±0.06	0.06±0.12	1.44±0.91	2.08±1.23	3.21	5.99
	D-1	0.00	0.00	0.72±0.25	1.06±0.54	0.33	0.23
	E-1	0.00	0.00	0.40±0.70	0.42±0.73	1.51	1.99
	A-1	0.11±0.30	0.17±0.44	0.52±0.60	1.82±1.64	0.39	0.31
Ecdyonurus kibunensis	C-1	0.01±0.03	0.01±0.02	0.22±0.02	0.23±0.12	0.12	0.09
	B-1	0.00	0.00	0.07±0.06	0.09±0.10	0.22	0.15
	D-1	0.00	0.00	0.00	0.00	0.00	0.00
	E-1	0.00	0.00	0.00	0.00	0.00	0.00
	A-1	0.00	0.00	0.00	0.00	0.00	0.00
Rhithrogena sp.	C-1	0.01±0.02	0.01±0.02	0.08±0.02	0.16±0.18	0.23	0.28
	B-1	0.00	0.00	0.15±0.06	0.24±0.30	0.33	1.02
	D-1	0.00	0.00	0.22±0.19	0.29±0.37	0.00	0.00
	E-1	0.00	0.00	0.10±0.17	0.28±0.48	0.00	0.00
	A-1	0.00	0.00	0.00	0.00	0.00	0.00
Pseudocloeon sp.	C-1	0.02±0.03	0.02±0.03	0.27±0.13	0.28±0.21	0.27	0.34
	B-1	0.02±0.04	0.26±0.13	0.27±0.13	0.27±0.17	0.22	0.09
	D-1	0.02±0.06	0.10±0.42	0.11±0.09	0.29±0.25	0.17	0.20
	E-1	0.00	0.00	0.10±0.17	0.06±0.10	0.00	0.00
	A-1	0.00	0.00	0.26±0.45	0.40±0.68	0.00	0.00
Other Benthic Animals	C-1	0.05±0.04	0.07±0.08	0.43±0.13	0.58±0.37	0.66	3.57
	B-1	0.13±0.10	0.28±0.30	0.30±0.34	0.15±0.62	0.55	0.78
	D-1	0.00	0.00	0.83±0.29	2.63±3.23	0.17	0.23
	E-1	0.09±0.15	0.53±1.20	0.20±0.35	0.10±0.17	0.91	2.51
	A-1	0.00	0.00	0.13±0.23	0.06±0.10	0.39	14.6
Total Benthic Animals	C-1	0.16±0.10	0.14±0.12	2.45±0.29	3.57±0.96	3.05	6.45
	B-1	0.19±0.14	0.36±0.35	2.21±1.10	3.03±1.62	4.54	8.03
	D-1	0.02±0.06	0.10±0.42	1.87±0.10	4.26±2.85	0.66	0.65
	E-1	0.09±0.15	0.53±1.20	0.81±0.76	0.85±0.75	2.42	4.50
	A-1	0.11±0.30	0.17±0.44	0.91±0.45	2.27±1.83	0.78	14.99
Diptera (adult)	C-1	0.52±0.35	0.55±0.40	0.48±0.14	0.57±0.08	0.43	0.37
	B-1	0.06±0.06	0.06±0.08	0.11±0.00	0.05±0.03	0.22	0.13
	D-1	0.12±0.25	0.11±0.20	0.00	0.00	0.00	0.00
	E-1	0.04±0.16	0.47±0.18	0.00	0.00	0.00	0.00
	A-1	0.00	0.00	0.00	0.00	0.00	0.00
Other Fallen Animals	C-1	0.28±0.24	6.64±7.28	0.23±0.08	1.11±0.08	0.89	9.50
	B-1	0.17±0.11	0.70±0.69	0.00	0.00	0.22	3.07
	D-1	0.10±0.13	10.36±24.20	0.06±0.10	0.18±0.31	0.17	0.56
	E-1	0.04±0.16	0.16±0.06	0.10±0.17	5.94±10.28	0.00	0.00
	A-1	0.06±0.15	0.20±0.53	0.00	0.00	0.00	0.00
Total Fallen Animals	C-1	0.81±0.37	7.19±7.21	0.71±0.06	1.68±0.73	1.31	9.88
	B-1	0.24±0.13	0.76±0.66	0.11±0.00	0.05±0.03	0.44	3.20
	D-1	0.22±0.10	10.47±24.20	0.06±0.10	0.18±0.31	0.17	0.56
	E-1	0.09±0.15	0.63±1.25	0.10±0.17	5.94±10.28	0.00	0.00
	A-1	0.06±0.15	0.20±0.53	0.00	0.00	0.00	0.00