

Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan

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The important contribution of terrestrial invertebrates to the energy budget of drift-foraging fishes has been well documented in many forested headwater streams. However, relatively little attention has been focused on the behavioral mechanisms behind such intensive exploitation. We tested for the hypothesis that active prey selection by fishes would be an important determinant of terrestrial invertebrates contribution to fish diets in a forested headwater stream in northern Japan. Rainbow trout, *Oncorhynchus mykiss*, were estimated to consume $57.12 \text{ mg m}^{-2} \text{ day}^{-1}$ (dry mass) terrestrial invertebrates, 77% of their total input ($73.89 \text{ mg m}^{-2} \text{ day}^{-1}$), there being high selectivity for the former from stream drift. Both the falling input and drift of terrestrial invertebrates peaked at around dusk, decreasing dramatically toward midnight. In contrast, both aquatic insect adults and benthic invertebrates showed pronounced nocturnal drift. Because the prey consumption rates of rainbow trout were high at dawn and dusk, decreasing around midnight, the greater contribution of terrestrial invertebrates to trout diet was regarded as being partly influenced by the difference in diel periodicity of availability among prey categories. In addition, selectivity also depended upon differences in individual prey size among aquatic insect adults, and benthic and terrestrial invertebrates, the last category being largest in both the stream drift and the trout diets. We concluded that differences in both the timing of supplies and prey size among the three prey categories were the primary factors behind the selective foraging on terrestrial invertebrates by rainbow trout.

Key words: diel periodicity; forest stream; prey size, selective foraging; stream salmonid; terrestrial invertebrates.

INTRODUCTION

There is much empirical evidence and many theoretical predictions that flexible behavior of organisms has a major impact on food web structure and dynamics (Abrams 1996; Persson *et al.* 1997). To increase fitness, predators actively choose prey that

minimize energy spent on capturing and handling while maximizing energy intake, with prey size, morphology and behavior also being factors in their selection (Stephens & Krebs 1986). Consequently, the selective foraging by many types of predators on a given type of prey may be disproportionate to the relative abundance of the latter in the environment (Hughes & Croy 1993; Hughes 1997). Thus, adaptive feeding selectivity by predators can be recognized as an important element determining food web static and dynamics, and in turn energy flow in ecosystems.

Riparian zones play a major role in regulating nutrient and energy flow in headwater stream ecosystems, in which the input of particulate

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organic matter from terrestrial ecosystems represents an important trophic basis of production (Vannote *et al.* 1980; Naiman & Décamps 1997). Most stream food web models have traditionally focused on the input of terrestrial plant matter, which is only indirectly available to top consumers such as predatory fish via invertebrate secondary production (Minshall 1967; Cummins *et al.* 1995; Wallace *et al.* 1997). Recent studies, however, have provided insights into the significance of terrestrial invertebrate input, which represents a high-quality food resource directly available to predatory fishes, thus influencing energy flow in the forest-stream ecotone (Mason & MacDonald 1982; Garman 1991; Garman & Moring 1992; Edwards & Huryn 1996; Wipfli 1997; Nakano *et al.* 1999b). To date, the important contribution of terrestrial invertebrates in the diets of drift-foraging fishes (e.g. salmonidae, cyprinidae and centrarchidae) has been well documented in many forested headwater streams, where terrestrial invertebrates occasionally comprise more than 50% of fish diets during summer and are often preferred over aquatic prey (Furukawa-Tanaka 1985; Garman 1991; Nakano & Furukawa-Tanaka 1994; Nakano *et al.* 1999a,b; see review by Hunt 1975). Such allochthonous input can provide a tremendous energy subsidy and increase the abundance of predatory fishes (Waters 1993). Analyses of production budgets for trout streams, for example, have generally shown that prey production was insufficient to support trout production while simultaneously providing a reasonable surplus of prey (Allen paradox; Allen 1951; Hynes 1970; Allan 1983; Waters 1988). Waters (1988, 1993) suggested that non-benthic, allochthonous energy sources (i.e. terrestrial invertebrates) may help explain the Allen paradox. Furthermore, Nakano *et al.* (1999b) provided experimental evidence that terrestrial invertebrate input had an indirect but prominent effect on a stream benthic community by altering the intensity of fish predation in the stream food web. Nevertheless, relatively little attention has been focused upon the behavioral mechanisms behind such intensive exploitation of terrestrial invertebrates by stream fishes.

The intensive exploitation of terrestrial invertebrates by stream fishes may be a simple consequence of their random foraging on stream drift. Greater terrestrial invertebrate inputs to streams

during summer, when benthic invertebrate biomass is generally at its lowest (Hynes 1970), could skew considerably the prey composition in the stream drift (e.g. Furukawa-Tanaka 1992) and consequently in fish diets. However, if stream fishes selectively consume terrestrial invertebrates from stream drift because of some preferred prey characteristics, the contribution of the latter to fish diets should be greater than to drift. Many studies have attempted to determine the mechanisms of prey selection by stream salmonids, typical water-column drift foragers, by comparing the composition of diets with available drift prey (Bisson 1978; Ringler 1979; Forrester *et al.* 1994; Nakano *et al.* 1999a). These studies have demonstrated selection for different prey taxa (Forrester *et al.* 1994) and also for larger prey (Irvine & Northcote 1983; Grant & Noakes 1986). In addition, diel changes in foraging efficiency are another important aspect of the foraging behaviour of stream salmonids (Allan 1981; Forrester *et al.* 1994). Salmonid foraging should differ between day and night because the fishes are visual foragers. In fact, the majority of studies have suggested that most feeding occurs during daylight in summer (Bisson 1978; Angradi & Griffith 1990). Therefore, when terrestrial invertebrates differ in size and/or diel periodicity in availability from benthic invertebrates, this should strongly influence the prey selection of stream salmonids.

Here we present the results of a field study on the prey selection of rainbow trout, *Oncorhynchus mykiss*, which are typical drift foragers, in a headwater stream running through second-growth deciduous forest in northern Japan. In the study, we examined the diel periodicity and size of terrestrial invertebrates in falling input, stream drift and trout diet, compared with benthic invertebrates and emerged aquatic insect adults, to test the above hypotheses.

METHOD

Study area

We carried out a field study in the Horonai Stream, a second-order stream running through the Tomakomai Experimental Forest of Hokkaido University (TOEF; 42°43'N, 141°36'E) in

Hokkaido, the northernmost island of the Japanese archipelago in summer (July–August) 1995. We established a study reach of 150 m in length in this small, cold spring-fed stream (14 km long, 2–5 m width, gradient < 1%), of which the riparian zone was covered with secondary-growth deciduous forest dominated by oak (*Quercus crispula*), ash (*Fraxinus mandshurica*) and maple (*Acer mono*). Approximately 95% of the entire width of the stream was covered by forest canopy. The stream discharge usually remained stable ($0.25\text{--}0.29\text{ m}^3\text{ s}^{-1}$) throughout the year, with major disturbances rarely occurring. Water temperature was relatively stable ($8\text{--}10^\circ\text{C}$) and almost within the preferred range for stream salmonids (Bjornn & Reiser 1991) during summer.

The study reach of the Horonai Stream was dominated by rainbow trout and freshwater sculpin (*Cottus nozawae*), with small numbers of white-spotted charr (*Salvelinus leucomaenis*), Dolly Varden (*Salvelinus malma*) and masu salmon (*Oncorhynchus masou*) also being captured (Urabe & Nakano 1998). The density and standing crop of rainbow trout in the study reach during the study period were estimated as 0.2 m^{-2} and $2.1\text{ g dry mass m}^{-2}$, respectively, by the three-pass removal method using a back-pack electrofishing unit (Model 12, Smith-Root Inc., Vancouver, USA; S. Nakano, unpubl. data, 1996). The species was accidentally introduced into the stream approximately 30 years ago from a local fish hatchery and has established a self-sustainable population (Kitano *et al.* 1993). The mean biomass of benthic invertebrates, measured from early July 1995 to late July 1996, varied considerably among seasons, peaking in early summer (May–June) and decreasing toward autumn (September–October; S. Nakano, unpubl. data, 1997). In the study reach, the biomass estimated from samples collected with a 225- μm mesh Surber net sampler (25 cm \times 25 cm quadrat, 100 cm long) from 24 randomly chosen locations was 1.8 ± 0.2 (SE) g dry mass m^{-2} in the study period. Terrestrial invertebrate input to the stream measured in the same periods as above, also fluctuated among seasons, peaking during summer (June to August; S. Nakano, unpubl. data, 1997). The study period was chosen because both terrestrial and benthic invertebrates were relatively more equally available compared to other seasons.

Sampling

The daily input of falling terrestrial invertebrates was estimated from samples collected by five pan traps (100 cm \times 100 cm area, 15 cm depth) in the study reach every day from 24 July to 26 August 1995. The traps were filled with water and two-three drops of surfactant, and set across the entire length of the study reach. Pan contents were sieved (with 225- μm mesh) after daily deployment. In addition, diel changes in terrestrial invertebrate input were surveyed intensively for 4 days on every other day between 28 July and 7 August (see Fig. 1), pan contents being sieved every 4 h (20.00, 24.00, 04.00, 08.00, 12.00, and 16.00 h) over each 24-h period. Total area of pan traps contributed to only 1% of the surface area of the study reach. All pan trap samples were preserved in 5% formalin solution until analyzed.

Stream drift was censused at four locations > 30 m apart with drift-nets (20 cm \times 20 cm opening, 100 cm long, 185- μm mesh) on the same days as the above survey on diel changes in terrestrial invertebrate input. Concurrently at each sampling site, a drift-net was placed in the stream for 20 min every 4 h (22.00, 02.00, 06.00, 10.00, 14.00, and 18.00 h) over each of the 24-h periods, their openings extending above the water surface so as to capture floating terrestrial invertebrates. Water volume sieved was estimated from the current velocity measured at the center of each net opening using a portable current meter (Model CR-7, Cosmo-Riken Inc., Kashihara, Japan; Tanida *et al.* 1985). All drift net samples were preserved in 5% formalin solution until analyzed.

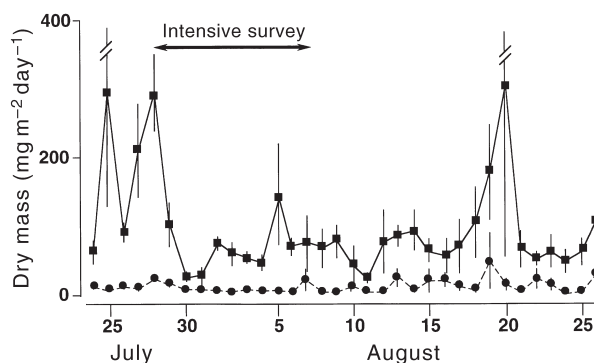


Fig. 1. Daily changes in the inputs (mean \pm 1 SE) of terrestrial invertebrates (\blacksquare) and aquatic insect adults (\bullet) to a study reach in the Horonai Stream.

To analyze diel periodicity of fish foraging and dietary composition, rainbow trout were haphazardly collected with a back-pack electrofishing unit every 4 h (20.00, 24.00, 04.00, 08.00, 12.00, and 16.00 h) on the same days of and just after each stream drift sampling procedure. Electrofishing proceeded upstream until six specimens were captured, within a period between 40 and 50 min irrespective of the time periods of the day. Captured fish were anesthetized (with 2-amino-4-phenylthiazole hydrobromide), measured (fork length) to the nearest 0.1 cm and weighed to the nearest 0.1 g wet mass. Captured fish were 13.8 ± 0.2 (SE) cm in fork length and 36.7 ± 2.1 (SE) g in wet mass ($n=144$), both of which were nearly equal to those captured during the population estimation in the study reach (S. Nakano, Y. Kawaguchi, H. Miyasaka, unpubl. data, 1996). The stomach contents were collected by stomach pumping with a 2-mL pipette to flush prey items from the entire stomach region (Giles 1980). The fish were marked by cutting the upper lobe of the caudal fin and then released at their original capture locations. Each individual was captured only once over the study. Stomach content samples were preserved in 5% formalin solution until analyzed.

Analyses

Pan trap, drift and stomach content samples were sieved once with 225- μ m mesh, to equalize the minimum size of invertebrates, and sorted under a binocular microscope. Terrestrial invertebrates and aquatic insect adults were identified to order and benthic invertebrates to family. Larvae and adults of terrestrial insects were treated separately. The biomass of each of the 48 taxa obtained was measured as wet mass to the nearest 0.01 mg after blotting for approximately 10 s. The error incurred for repeated measurements of damp mass was within $\pm 6\%$ (S. Nakano, unpubl. data, 1995). Dry mass (after dried at 60°C for 24 h) of random subsamples was measured to the nearest 0.01 mg for each category, and damp mass converted to dry mass according to regressions through the origin (range of slopes = 0.085–0.337, $n=7$ –30, $r^2=0.71$ –0.99, $P<0.001$ for all 48 categories). Invertebrates here were categorized as either terrestrial, benthic or aquatic insect adults. The mean dry mass of

invertebrate individuals found in stream drift and stomach contents was estimated by dividing the total mass by the total number in each taxa, and subsequently averaged for the above three categories. For analyses of fish diets, the dry mass of individual prey for each of the three prey categories was determined for individual fish, and averaged when combining the 4-day data.

To demonstrate the diel periodicity of prey consumption rates, we estimated the dry mass of prey consumed by trout during each of the six 4-h sampling periods over a 24-h period following Elliott & Persson (1978):

$$C_t = \frac{S_t - S_0 e^{-Rt}}{1 - e^{-Rt}}$$

where C is the dry mass (mg) of prey consumed per 100 mg dry mass of fish in a sampling interval of t hours, S_0 and S_t are the mean dry mass of prey in the stomach of 100 mg dry mass of fish at the beginning and end of the interval, respectively, e is the exponent of natural logarithms and R is the rate of gastric evacuation. The dry mass of captured fish was estimated from the wet mass measured according to a simple linear regression (Y. Kawaguchi and S. Nakano, unpubl. data, 1995). The mean dry mass of the captured fish was estimated as $10\,496 \pm 598$ (SE) mg ($n=144$). The gastric evacuation rates were estimated as 0.042 in rainbow trout at 9°C following Elliott's (1972) equation (Y. Kawaguchi and S. Nakano, unpubl. data, 1996). We assumed the gastric evacuation rates were constant among prey categories and during the study period. Finally, the daily prey consumption rate was calculated for each prey category, the values being converted into an area-based unit ($\text{mg m}^{-2} \text{day}^{-1}$), thus taking fish standing crop into consideration.

Overall prey selectivity was calculated for individual fish and data from the four days of sampling averaged (\pm SE). Manly's Index (Chesson 1978) was used as a measure of prey selectivity:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, \quad i = 1, \dots, m$$

where r_i and n_i are the proportions in biomass of prey category i (of m categories) occurring in stomach contents and stream drift, respectively. The index, which removes bias caused by differing

availability of prey categories, lies between 0 (prey never eaten) and 1 (only one prey category eaten).

All statistical tests were two-tailed unless otherwise stated. $\log_{10}(X+1)$ transformations for exact values and arcsine-square-root transformations for percentages were conducted in order to standardize variances and improve normality to satisfy the assumption of ANOVA. When the normality was violated, even after the data transformations, non-parametric tests (Mann–Whitney or Kruskal–Wallis test) were used. For any ANOVA models, multiple comparisons using Scheffé tests were conducted after one-way ANOVA when necessary. Dunnett tests were used for multiple comparisons, if necessary, after Kruskal–Wallis tests.

RESULTS

Input and drift of prey invertebrates

In the Horonai Stream, the mean input (dry mass) of falling terrestrial invertebrates was 94.39 ± 12.86 (SE) $\text{mg m}^{-2} \text{day}^{-1}$ and that of aquatic insect adults 9.83 ± 1.76 $\text{mg m}^{-2} \text{day}^{-1}$ during the overall 34-day study period (Fig. 1). Two-way ANOVA (factors=prey category, day) revealed that the input of terrestrial invertebrates was significantly greater than that of aquatic insect adults ($F_{1, 272} = 425.66$, $P < 0.001$), with significant daily fluctuations also being evident ($F_{33, 272} = 2.56$, $P < 0.001$). The interaction effect was not significant however ($F_{33, 272} = 1.01$, $P = 0.458$).

Significant diel changes were found in the falling input of both terrestrial invertebrates ($H = 29.24$, $P < 0.001$ by Kruskal–Wallis tests) and aquatic insect adults ($H = 13.71$, $P = 0.013$), although the input of the former was significantly greater than that of the latter ($U = 1548$, $P < 0.001$ by Mann–Whitney U -test; Fig. 2). The input of falling terrestrial invertebrates peaked around dusk (16.00–20.00 h), decreased dramatically toward midnight (20.00–24.00 h), increased again toward dawn (24.00–04.00 h), and was relatively stable in the remaining time periods (04.00–16.00 h). In contrast, the input of aquatic insect adults showed a peak just before midnight (20.00–24.00 h) and was constant at a low level during the remaining time periods (24.00–

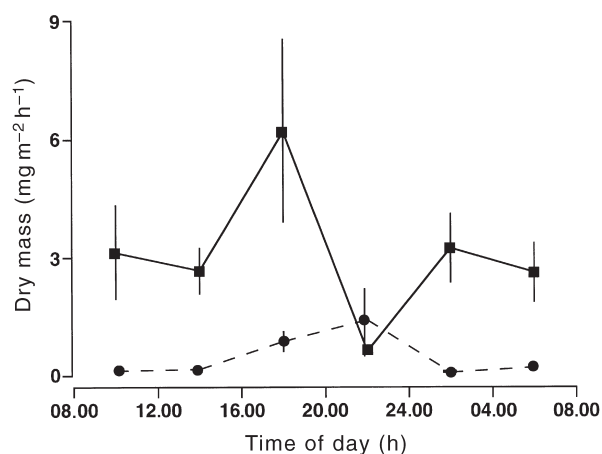


Fig. 2. Diel changes in the inputs (mean \pm 1 SE) of terrestrial invertebrates (—■—) and aquatic insect adults (---●---) to a study reach in the Horonai Stream.

20.00 h). The mean daily input during this intensive survey was approximately 20% smaller for terrestrial invertebrates (73.89 ± 12.96 (SE) $\text{mg m}^{-2} \text{day}^{-1}$), but approximately 14% greater for aquatic insect adults (11.20 ± 3.86 $\text{mg m}^{-2} \text{day}^{-1}$), than the averages over the entire 34-day study period, respectively.

Significant diel changes were also observed in the drift of terrestrial ($H = 11.66$, $P = 0.04$ by Kruskal–Wallis tests) and benthic invertebrates ($H = 69.93$, $P < 0.001$), and aquatic insect adults ($H = 11.17$, $P = 0.048$), with drift biomass differing significantly among the three prey categories ($H = 151.55$, $P < 0.001$; Fig. 3). The drift biomass of benthic invertebrates was significantly greater than that of terrestrial invertebrates and aquatic insect adults ($P < 0.01$ for both categories by Dunnett test), the latter in turn showing a significantly smaller biomass than terrestrial invertebrates ($P < 0.01$). The drift biomass of terrestrial invertebrates during both dusk (16.00–20.00 h) and dawn (04.00–08.00 h) tended to be greater than in the remaining time periods, being smallest in the period leading up to midnight (20.00–24.00 h). For aquatic insect adults, the drift biomass peaked just before midnight (20.00–24.00 h) and dramatically decreased thereafter. Benthic invertebrates showed a clear nocturnal peak in drift biomass, which increased between 20.00 h and 04.00 h, but remaining relatively low during the other time periods.

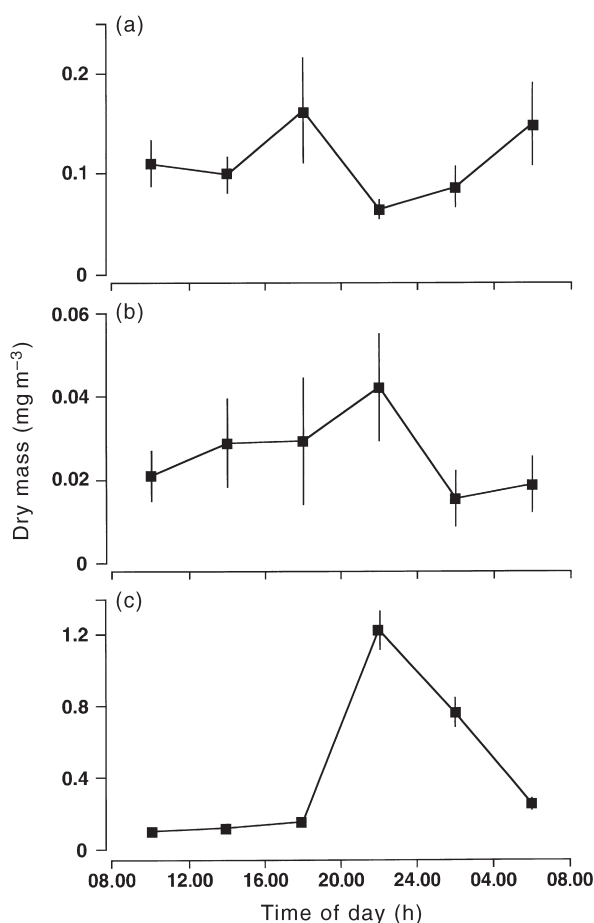


Fig. 3. Diel changes in the drift biomass (mean \pm 1 SE) of (a) terrestrial invertebrates, (b) aquatic insect adults and (c) benthic invertebrates in a study reach in the Horonai Stream.

Prey consumption by trout

Rainbow trout consumed a greater quantity of terrestrial invertebrates than aquatic insect adults and benthic invertebrates, showing clear diel periodicity in foraging activity (Fig. 4). The mean daily consumption rate by rainbow trout was 2.72 ± 1.40 (SE) $\text{mg } 100 \text{ mg}^{-1} \text{ day}^{-1}$ (72.3% of the total diet) for terrestrial invertebrates, 0.29 ± 0.22 (7.7%) for aquatic insect adults and 0.75 ± 0.29 (19.9%) for benthic invertebrates, totaling 3.76 ± 1.91 ($n=4$ for all the categories). Area-based prey consumption rates were estimated as $57.12 \pm 29.40 \text{ mg m}^{-2} \text{ day}^{-1}$ for terrestrial invertebrates, 6.09 ± 4.62 for aquatic insect adults and 15.75 ± 6.09 for benthic invertebrates, totaling $78.75 \pm 40.11 \text{ mg m}^{-2} \text{ day}^{-1}$. Kruskal–Wallis tests revealed that the prey consumption rate of trout differed

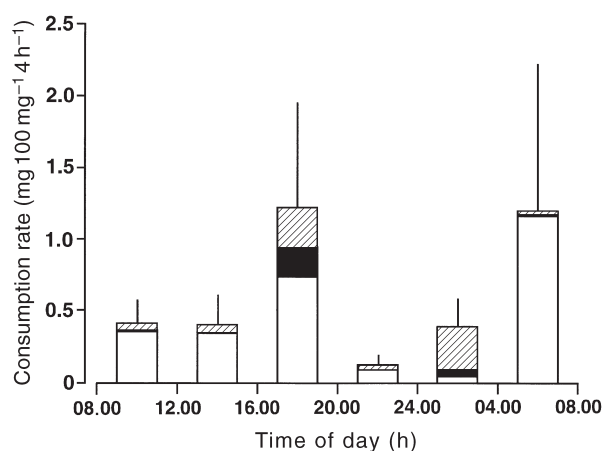


Fig. 4. Diel changes in rate of consumption (mean \pm 1 SE) of terrestrial invertebrates (\square), aquatic insect adults (hatched) and benthic invertebrates (\blacksquare) by rainbow trout in a study reach in the Horonai Stream. Standard errors are presented for total consumption rates only.

significantly among both prey categories ($H=12.66$, $P=0.014$) and time periods ($H=11.94$, $P=0.029$). The prey consumption rate decreased dramatically toward midnight (20.00–24.00 h), but peaked around both dusk (16.00–20.00 h) and dawn (04.00–08.00 h).

Terrestrial invertebrates were selectively consumed from stream drift (Table 1). The selectivity indices differed significantly among the prey categories when all the time periods were combined ($F_{2,9}=64.15$, $P<0.001$ by one-way ANOVA). The index for terrestrial invertebrates was significantly greater than those for both aquatic insect adults and benthic invertebrates ($P<0.001$ for both by Scheffé test), whereas a non-significant difference was evident between aquatic insect adults and benthic invertebrates ($P=0.161$). When the data obtained between 20.00 h and 24.00 h, during which time rainbow trout consumed only small amounts of prey, was omitted from the analysis, similar selectivity results were obtained for the prey categories ($F_{2,9}=23.82$, $P<0.001$ by one-way ANOVA). The selectivity index for terrestrial invertebrates was significantly greater than both aquatic insect adults ($P=0.002$ by Scheffé test) and benthic invertebrates ($P<0.001$), there being no significant difference between aquatic insect adults and benthic invertebrates ($P=0.356$).

Rainbow trout selectively foraged on larger prey items in the stream drift (Table 1). Two-way

Table 1 Mean dry mass (± 1 SE) of individual items and mean selectivity (± 1 SE) expressed as Manly's Index for three prey categories

| Prey category | Prey mass (mg) | | Selectivity (α) | |
|---------------------------|-----------------|-----------------|--------------------------|-----------------|
| | Drift | Diet | Overall | Active time* |
| Terrestrial invertebrates | 0.25 ± 0.05 | 9.93 ± 0.65 | 0.80 ± 0.06 | 0.77 ± 0.09 |
| Aquatic insect adults | 0.08 ± 0.04 | 1.33 ± 0.47 | 0.15 ± 0.05 | 0.19 ± 0.09 |
| Benthic invertebrates | 0.08 ± 0.01 | 2.49 ± 0.17 | 0.04 ± 0.01 | 0.05 ± 0.02 |

*The time period between 20.00 h and 24.00 h was removed from the analyses.

ANOVA (factors = drift/diet, prey category) revealed that prey invertebrates included in stomach contents were significantly larger than those in stream drift ($F_{1,18} = 283.69$, $P < 0.001$) and prey size differed significantly among the three prey categories ($F_{2,18} = 43.24$, $P < 0.001$), in addition to significant interaction effect ($F_{2,18} = 29.22$, $P < 0.001$). Scheffé tests, after significant mean differences were found by one-way ANOVA ($F_{2,9} = 37.86$, $P < 0.001$), revealed that, in trout diets, terrestrial invertebrates were significantly larger than both aquatic insect adults ($P < 0.001$) and benthic invertebrates ($P < 0.001$), there being no significant difference between the latter two categories ($P = 0.096$). Similarly, terrestrial invertebrates in the stream drift were significantly larger than both aquatic insect adults ($P = 0.033$) and benthic invertebrates ($P = 0.026$), again with no significant difference being observed between the latter two categories ($P = 0.988$) based on Scheffé tests after one-way ANOVA ($F_{2,9} = 7.18$, $P = 0.014$).

DISCUSSION

In the Horonai Stream, a typical headwater forested stream, the daily input of terrestrial invertebrates from the riparian forest to the stream channel was approximately $94 \text{ mg m}^{-2} \text{ day}^{-1}$ (dry mass) during the 34-day study period in mid-summer. The inputs of terrestrial invertebrates are generally greater in headwater reaches where the stream reaches are more heavily covered by riparian canopies than downstream reaches (Cloe & Garman 1996). In addition, differing types of riparian vegetation are also known to have important influences on the input of terrestrial inverte-

brates (Edwards & Huryn 1996; Nagasaka *et al.* 1996; Wipfli 1997). Deciduous trees, for example, generally have greater associated invertebrate biomass than conifers (Southwood 1961), and, in fact, the input of terrestrial invertebrates has been found to be considerably higher in stream reaches under deciduous riparian forests (Mason & MacDonald 1982). The observed input value for the Horonai Stream was comparable to that reported in several previous studies of headwater (i.e. low order) streams in temperate deciduous forests, when converted to equivalent units (Mason & MacDonald 1982; Cloe & Garman 1996; Nagasaka *et al.* 1996; Wipfli 1997; Nakano *et al.* 1999b). For example, mean seasonal input of terrestrial invertebrates (dry mass) was estimated as approximately $120 \text{ mg m}^{-2} \text{ day}^{-1}$ in an English stream (Mason & MacDonald 1982), approximately $80 \text{ mg m}^{-2} \text{ day}^{-1}$ in a Virginia stream (Cloe & Garman 1996) and approximately $150 \text{ mg m}^{-2} \text{ day}^{-1}$ in another Hokkaido stream (Nagasaka *et al.* 1996), during spring–autumn.

Annual energy contributed by such allochthonous inputs to stream ecosystems may be equivalent to the potentially available energy represented by benthic invertebrate production and thus an important trophic basis for fish production, especially in fully canopied temperate headwater streams, as pointed out by Cloe and Garman (1996). Greater terrestrial invertebrate inputs during summer may be an especially important seasonal subsidy for stream fishes, because benthic invertebrate biomass is generally at its lowest at that time (see Hynes 1970) and fish require the largest energy budget in summer (Garman 1991). In the Horonai Stream, terrestrial invertebrates were the primary prey of rainbow trout, comprising 72.5% of their daily ration in summer. More-

over, rainbow trout were estimated to consume $57.12 \text{ mg m}^{-2} \text{ day}^{-1}$ of terrestrial invertebrates, comprising 77% of the total input ($73.89 \text{ mg m}^{-2} \text{ day}^{-1}$), which was nearly equal to the area-based total prey consumption rate of trout. Thus, the input of terrestrial invertebrates, if fully available, represents sufficient energy to support a rainbow trout population in the Horonai Stream.

Rainbow trout, in reality, demonstrated a highly selective utilization of terrestrial invertebrates from stream drift in the Horonai Stream. A clear diel periodicity in foraging activity of rainbow trout was evident, with prey consumption rates being high at dawn and dusk, decreasing around both noon and midnight (see also Miyasaka & Nakano 1999). Most stream salmonids are visual foragers, preying primarily upon drifting invertebrates while maintaining focal points in the water column (Angradi & Griffith 1990; Nakano 1995). In such drift foragers, the foraging efficiency generally decreases with lower light intensity (Bisson 1978; Robinson & Tash 1979; Angradi & Griffith 1990). The falling input of terrestrial invertebrates peaked around dusk, decreased dramatically toward midnight and increased thereafter, a similar diel periodicity being evident in the drift of terrestrial invertebrates. In contrast, both the input and drift of aquatic insect adults showed a peak around midnight, but remained relatively low at the other times. These diel input patterns of both terrestrial and aquatic insect adults can mirror their activity patterns (Harper *et al.* 1983; Furukawa-Tanaka 1992). Benthic invertebrates show pronounced nocturnal drift which has been interpreted as resulting from their avoidance of predation by visual drift foragers, such as rainbow trout, during the day (Waters 1972; Allan 1995; Miyasaka & Nakano 1999). In fact, the nocturnal drift biomass of benthic invertebrates was much greater than the diurnal rate in the present study. However, there was no corresponding increase in food consumption of rainbow trout at night. In addition, although the daily drift biomass of benthic invertebrates was much greater than that of terrestrial invertebrates, the latter contributed a much greater portion to the trout diet. Therefore, the greater contribution of terrestrial invertebrates to trout diet should be influenced partly by diel differences in availability.

Rainbow trout, however, showed highly selective foraging on terrestrial invertebrates even when the inactive time period (20.00–24.00 h) was omitted from the analysis. Such selectivity can be influenced by differences in individual prey size among aquatic insect adults, and benthic and terrestrial invertebrates, the last category being larger than the former two in both stream drift and trout diet. In all of the three prey categories, rainbow trout were regarded as selecting larger prey from the drift, as reported for other stream salmonids (Allan 1978, 1981; Sagar & Glova 1988; Forrester *et al.* 1994; Nakano 1995). From these analyses, we can conclude that differences in both the timing of supplies and prey size among the three prey categories are the primary factors behind selective foraging on terrestrial invertebrates by rainbow trout.

The use of terrestrial invertebrates as the energy source of predatory fishes has been reported for many forested headwater streams, the observed input values often being comparable across several temperate regions (Mason & MacDonald 1982; Cloe & Garman 1996; Nagasaka *et al.* 1996; Wipfli 1997; Nakano *et al.* 1999b). However, in reality, the contribution of such allochthonous inputs to fish energy budgets varies considerably among streams and target fish species, even in similarly sized headwater streams (see Garman 1991; Cloe & Garman 1996; Edwards & Huryn 1996; Wipfli 1997). A better understanding of the contribution of terrestrial invertebrates to stream ecosystems would be furthered by examination of detailed mechanisms of selective foraging on this allochthonous resource by fishes in various stream habitats.

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