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Seasonal change in the gastric evacuation rate of rainbow trout feeding on natural prey

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Seasonal changes in the gastric evacuation rate (R) and gut contents of a wild population of rainbow trout *Oncorhynchus mykiss* feeding on natural prey at four water temperatures (2, 7, 9 and 12° C) were measured. The R and mass of the gut contents increased with water temperature, and prey items changed seasonally. These results suggest that the R of fish feeding on natural food depends primarily on water temperature, with their consumed prey being a secondary factor.

Key words: gut contents; natural prey item; *Oncorhynchus mykiss*; thermal physiology; water temperature.

Water temperature and daily ration are among the environmental factors that strongly determine the growth of fishes (Brett, 1956). Gastric evacuation rate (R) of salmonids such as rainbow trout *Oncorhynchus mykiss* (Walbaum) and brown trout *Salmo trutta* L. have been well studied because of their commercial and recreational importance (Elliott, 1972). Most of the previous studies on R, however, were conducted under artificial conditions, in which fishes were provided a specific prey item, *e.g.* chironomid larvae or commercial pellets (From & Rasmussen, 1984; Hayward & Weiland, 1998). Although some studies used a mixed diet of natural prey under artificial (Sweka *et al.*, 2004) and natural conditions (Forrester *et al.*, 1994), the latter study examined R in only one season and effects of prey types (gut contents) were not analysed. In nature, however, prey items generally vary with season (Kawaguchi & Nakano, 2001). There is

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no report in the literature on the seasonal change in the *R* of salmonids feeding on natural prey items. For problems such as the evaluation of predation impacts of fishes on invertebrate communities in natural streams, there is a need for a study that estimates the natural *R* of salmonids. In this study, the seasonal changes in the *R* and gut contents of a wild population of rainbow trout in a stream in northern Japan were measured.

Experimental fish were collected from the Horonai Stream running through the Tomakomai Experimental Forest (TOEF; 42°43′ N; 141°36′ E), south-western Hokkaido, Japan, from May 1995 to March 1996. The study area is described in Miyasaka *et al.* (2005). Rainbow trout were sampled 1·5–3·0 km downstream from the headwater spring and their *R* and gut contents were analysed in the laboratory. The study reach of the Horonai Stream was dominated by rainbow trout and freshwater sculpin *Cottus nozawae* (Snyder), with small numbers of white-spotted charr *Salvelinus leucomaenis* (Pallas), Dolly Varden *Salvelinus malma* (Walbaum) and masu salmon *Oncorhynchus masou* (Brevoort) (Urabe & Nakano, 1998). The rainbow trout is a non-native salmonid that originated from a nearby fish hatchery *c.* 30 years ago.

The water temperature was monitored every hour at a hydrologic observatory located within the sampling area. To determine the water temperature for measurement of *R* in different seasons, reference was made to the monthly data on the mean, maximum and minimum water temperatures (Fig. 1). Water temperatures for the laboratory experiments were selected: 9° C in spring (May), 12° C in summer (August), 7° C in autumn (November) and 2° C in winter (March) and controlled ±0·2° C using thermostat (Fig. 1).

The methods of Miyasaka *et al.* (2005) were used for fish sampling and collection of stomach contents. Rainbow trout were caught by electrofishing using a pulsed DC backpack apparatus (Model 12; Smith-Root, Vancouver, WA, U.S.A.) and sampling was performed between 0400 and 0500 hours when peak prey consumption was observed for rainbow trout (Nakano *et al.*, 1999). The sampling stations were in close proximity to the laboratory, generally within

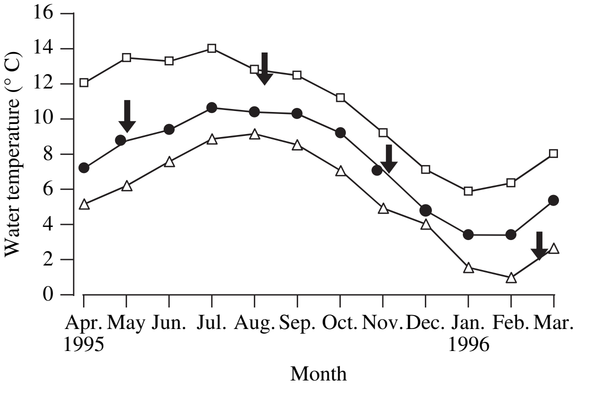

FIG. 1. Monthly water temperature between April 1995 and March 1996 in the Horonai Stream, with the mean (●), maximum (□) and minimum (△) water temperatures. ➡ (slightly offset for clarity), the water temperatures at which the gastric evacuation rates were experimentally measured.

10 min maximum from the time of capturing the last fish to the arrival at the laboratory for each sample. No food was provided to the stocked rainbow trout during the experimental period. Before the stomach contents analysis, the fish were anaesthetized with 2-phenoxyethanol, and then their fork length (L_F) to the nearest 1 mm and wet body mass (M_W) to the nearest 0·1 g were measured.

For the base measurement of R, *i.e.* time zero, the stomach contents were obtained from three to seven individuals and weighed immediately after the fish were transferred to the holding tank. Thereafter, in spring, summer and autumn, three to seven individuals were randomly selected from the holding tank every 2 h and the experiments ran for 10–12 h (Table I). During winter (2° C), because of the low R, 14–15 individuals were randomly selected from the tank every 6 h and the tests ran for 48 h. To quantify and standardize stomach fullness for all fish, the proportional mass of the stomach contents (M_{SC}) to the dry body mass (M_D) was used. The stomach fullness index (I_{SF}) was defined as follows (Miyasaka *et al.*, 2005): $I_{SF} = \ln(1000 M_{SC} M_D^{-1} + 1)$.

The M_D (g) was converted from M_W (g) by using a simple linear regression equation, passing through the origin (Kawaguchi, 2000): $M_D = 0{\cdot}285 M_W$. To estimate the R of rainbow trout at four different water temperatures, I_{SF} was regressed against the time interval (t, h) using the following equation: $I_{SF} = a - tb$, where b is the slope and a is the intercept of the regression line. The b value was taken as the R (Table I). Another regression analysis was conducted to compare R determined in this study with those of other studies using the same species under experimental conditions. The mean dry mass (s, mg) of digestible organic matter in the stomach per gram dry mass of fish against the time interval (t, h) was plotted. Following Elliott (1972), the relationship between s and t was: $\ln s = \ln a - bt$, where $\ln a$ is the intercept and b is the slope of the regression line.

TABLE I. Experimental conditions and gastric evacuation rate (R) of *Oncorhynchus mykiss* collected from the Horonai Stream, Hokkaido, Japan. Values are means ± S.E.

	Season			
	Spring	Summer	Autumn	Winter
Gastric evacuation rate				
Water temperature (° C)	9	12	7	2
Duration of experiments (h)	10	10	12	48
Total number of fish tested	28	35	25	127
L_F (mm)	137 ± 6	115 ± 1	172 ± 6	146 ± 4
Wet body mass (g)	33·8 ± 5·1	34·5 ± 3·4	71·0 ± 8·4	43·3 ± 3·4
R	0·042	0·051	0·023	0·006
P-value	<0·001	<0·001	<0·05	<0·001
Gut contents				
Number of fish	20	20	20	20
L_F (mm)	141 ± 7	149 ± 5	170 ± 8	139 ± 6
Wet body mass (g)	416 ± 59	429 ± 46	692 ± 95	343 ± 54

L_F, fork length.

To analyse the gut contents of rainbow trout during four seasons, rainbow trout were collected by electrofishing in early morning (0400–0500 hours) at each water temperature (Table I). Electrofishing proceeded upstream until 20 individuals had been captured. Captured fish were immediately transported to the laboratory, anaesthetized and measured in the same way as for *R*. The stomach contents were collected by stomach pumping (Miyasaka *et al.*, 2005) and then sorted, under a binocular microscope, into terrestrial and aquatic invertebrates and adult aquatic insects. Terrestrial invertebrates and adult aquatic insects were identified to order and aquatic invertebrates to family levels. Larvae and adults of terrestrial invertebrates were treated separately. Each invertebrate category was weighed (wet mass) to the nearest 0·01 mg after blotting for *c*. 10 s; the error incurred for repeated measurements of wet mass was within $\pm$ 6% (unpubl. data). Dry mass (after drying at 60° C for 24 h) of random sub-samples was measured to the nearest 0·01 mg for each category, and wet mass was converted to dry mass by using regressions through the origin (Kawaguchi & Nakano, 2001).

The *R* varied with water temperature (Table I) and was greatest in summer, when it was nearly nine times greater than in winter. Similarly, the gut content mass varied considerably between seasons, being highest in summer and lowest in winter (Fig. 2). In spring, the rainbow trout foraged on benthic invertebrates, *e.g.* Diptera and Trichoptera larvae, with small amounts of terrestrial invertebrates, *e.g.* earthworms. In summer, the rainbow trout fed on aquatic (Amphipoda and Diptera larvae) and terrestrial (Lepidoptera larvae and earthworms) invertebrates and adult insects (Trichoptera). In autumn, both aquatic (Amphipoda and Trichoptera larvae) and terrestrial invertebrates (earthworms) were consumed in nearly equal proportions. In winter, only aquatic invertebrates, including Amphipoda, Plecoptera larvae and Ephemeroptera nymphs, were consumed.

The regression equation line for *R* and water temperature obtained from the present study lay between two previously reported regression lines, which were

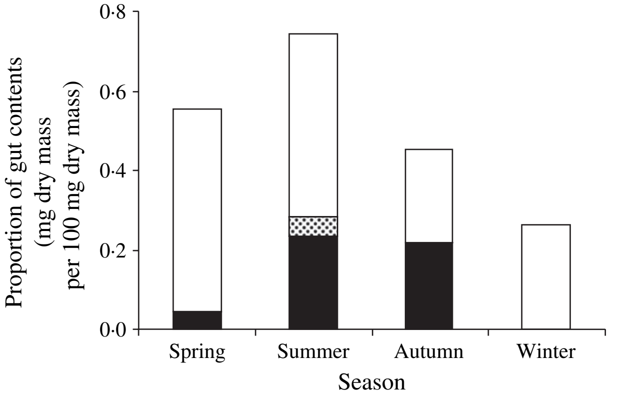

FIG. 2. Seasonal dry mass of gut contents per 100 g dry mass of fish for aquatic invertebrates (□), adult aquatic insects (⚄) and terrestrial invertebrates (■) consumed by rainbow trout in the Horonai Stream.

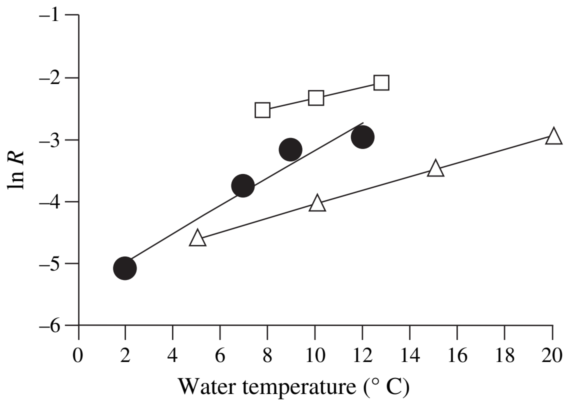

FIG. 3. Regression lines for the gastric evacuation rate (*R*, ln transformed) and water temperature for rainbow trout feeding on natural prey items, in the present study (●; $y = -5{\cdot}439 + 0{\cdot}224x$), Hayward & Weiland (1998) feeding on chironomid larvae (□; $y = -3{\cdot}207 + 0{\cdot}088x$) and From & Rasmussen (1984) feeding on artificial pellets (△; $y = -5{\cdot}167 + 0{\cdot}112x$).

based on rainbow trout fed on chironomid larvae (Hayward & Weiland, 1998) and pellets (From & Rasmussen, 1984; Fig. 3). Chironomid (dipteran) larvae were soft-bodied prey and assumed to be more rapidly digested (Sweka *et al.*, 2004) than the pellets and thus the data representing an intermediate level between these lines seems plausible because of greater variation of seasonal prey characterized by both fast and slow digestion. On the other hand, the slope of the equation obtained in the present study is steeper than the slopes from the previous studies. The extremely low *R* was probably due to the low test temperature in winter (2° C) as well as their consumption of more aquatic invertebrates with their bodies covered by indigestible exoskeleton; in fact, amphipods occupied nearly half of the gut contents. In contrast, accelerated *R* during warmer spring–summer periods resulted from both positive temperature effects and greater consumption of more soft-bodied aquatic invertebrates such as dipteran and trichopteran larvae and also the terrestrial invertebrates including Lepidoptera larvae covered by thin exoskeleton. The results imply that the *R* of fish in natural streams depends on the prey items consumed, as well as on the water temperatures.

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