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Thermal changes in the gastric evacuation rate of the freshwater sculpin *Cottus nozawae* Snyder

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Abstract We experimentally measured thermal changes in the gastric evacuation rate (GER) of the freshwater sculpin *Cottus nozawae* Snyder under three water temperature regimes (2°, 7°, and 12°C). Laboratory experiments showed that the GER was accelerated with increasing water temperature. This result suggests that the daily food rations of fish are more likely to be underestimated at higher water temperatures if estimation is simply based on the stomach content weight alone. By comparing the GER for various fish species from subfrigid to temperate streams, we found a general pattern that the GER increases with water temperature, regardless of taxonomic group or foraging mode. However, the reaction norms of the GER against water temperature showed considerable interspecific variation. This means that stomach content weight is not comparable as a simple measure for determining the daily rations

among fish species when water temperature regimes are different. To consider the temperature-dependent pattern of such a physiological phenomenon is important in understanding the feeding ecology of fishes and their roles in material cycles through food webs in aquatic ecosystems.

Key words *Cottus nozawae* · Feeding physiology · Gastric evacuation rate · Reaction norm · Water temperature

Introduction

Fishes have the potential to influence material cycles through food webs in aquatic ecosystems (e.g., Carpenter and Kitchell 1993). In streams, fishes primarily exhibit two forms of foraging, swimming and benthic foraging. Swimming foragers feed primarily upon drifting terrestrial and aquatic invertebrates (Nakano et al. 1999; Nakano and Murakami 2001), whereas benthic foragers feed upon benthic invertebrates on the bottom (Yamamoto et al. 1988). Thus, the relative abundance of each forager characterizes the food web structure in stream ecosystems. In subfrigid to temperate streams, salmonids are ecologically and commercially significant species that have been intensively studied and to which the basic concepts of fisheries science have been applied (e.g., Elliott 1972). In contrast, little is known about the feeding ecology of benthic foragers, such as cottid and gobiid fishes, which are often common in subfrigid to temperate streams (but see Specziár 2002).

For fish species, daily food rations have traditionally been estimated based on stomach content weight. However, such an estimation of daily rations is influenced by the rate at which the stomach contents are evacuated (Wootton 1998); one factor determining this rate is the physiological performance of assimilation, which is strongly affected by water temperature (Brett 1956; Suzuki 1993; Gerking 1994). Therefore, to understand the feeding ecology of fishes and their roles in material cycling within aquatic ecosystems, there is a need to accumulate information on reaction

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Table 1. Collection site information and sampling design for *Cottus nozawae* collected from the Horonai Stream, Hokkaido, Japan

	Sampling dates		
	April 30, 1995	August 5, 1995	February 24, 1996
Site information			
Water temperature	7.3 ± 0.1	11.8 ± 0.2	1.8 ± 0.2
Population density of <i>C. nozawae</i> (fish·m ⁻²)	–	1.13 ± 0.13 ^a	2.80 ± 0.86
Sampling design			
Sample size	34	30	42
Total length (cm)	9.2 ± 0.1	9.3 ± 0.2	11.3 ± 0.2
Wet body mass (g)	13.9 ± 1.0	14.9 ± 1.1	28.5 ± 1.6

Values are mean ± SE

^aData from Miyasaka and Nakano (1999)

norms of the gastric evacuation rate (GER) against fluctuating water temperature for a variety of fish taxa. In this study, we measured thermal changes in the GER of the benthic foraging freshwater sculpin *Cottus nozawae* Snyder under laboratory conditions.

Materials and methods

Study area

We conducted the study in the Horonai Stream running through the Tomakomai Experimental Forest (TOEF; 42°43' N, 141°36' E), southwestern Hokkaido, Japan, from April 1995 to March 1996. This small, spring-fed stream (14 km long, 2–5 m wide, <1% gradient) discharges directly into the Pacific Ocean. The discharge was relatively constant throughout the year, ranging between 0.18 and 0.30 m³·s⁻¹. We sampled sculpins 1.5–2.5 km downstream from the headwater spring to measure their GER in our laboratory. The water temperature was monitored automatically every hour at a hydrologic observatory located within the sampling area.

In this stream, freshwater sculpin (*Cottus nozawae*) and rainbow trout (*Oncorhynchus mykiss*) were the numerically dominant taxa in the fish community. The former is a bottom-dwelling fish widely distributed in the streams of Hokkaido, Japan (Goto 1980), and is also native to the study stream. The latter is a nonnative salmonid which immigrated from a nearby fish hatchery approximately 30 years ago.

Sampling and experimental designs

We sampled sculpins from riffles using a backpack electrofishing unit (Model 12, Smith-Root, Vancouver, Washington, USA). Our sampling design and sampling site information are shown in Table 1. The population density of *C. nozawae* was estimated by a three-pass removal sampling method (Li and Li 1996). Because *C. nozawae* exhibits noc-

turnal foraging activity (Miyasaka and Nakano 1999), we sampled sculpins early in the morning (0400–0600 h). Once collected, we transferred fish to our laboratory within 30 min, and stocked them in an aerated tank (3.5 m long, 0.7 m wide, and 0.3 m deep; see Miyasaka and Nakano 2001 for details). The tank was filled with groundwater and the temperature was controlled by a thermostat. Water temperature was set at 2°, 7°, and 12°C to simulate the ambient water temperature of their natural habitat (see Table 1). Stocked sculpins were kept in a dark regime with a low-flow condition (5–25 cm·s⁻¹) using an airlift pump. We did not provide any food for the stocked sculpins during the experimental period.

For a base measurement for GER (i.e., time 0 h), the stomach contents of some fish were weighed immediately after the transfer to the stock tank. Thereafter five to six individuals were randomly selected from the stock tank every 2 h for stomach content analysis. After anesthetizing the fish with 2-phenoxyethanol, we measured their total length to the nearest 0.1 cm and wet body mass to the nearest 0.1 g before the stomach content analysis. We collected the stomach contents by pumping stomachs with a 2-ml pipette to flush prey items from the stomachs (Giles 1980). The stomach pumping was repeated until no prey items emerged from the stomach. We excluded stone cases of caddis fly and sand particles from the stomach contents. The flushing efficiency (i.e., the weight proportion of prey items collected by the stomach pumping to the total contents including residuals in the stomach) was 98.8% ($n = 20$). We weighed the stomach contents to the nearest 0.01 mg after drying at 60°C for 24 h. Body sizes varied between fish collected at different sampling dates (Table 1). To quantify and standardize stomach fullness for all fish, we used the proportional weight of the stomach contents to the body mass. We defined the stomach fullness index (SFI) as follows:

$$\text{SFI} = \ln \left[\frac{1000 \times (\text{dry mass of stomach contents})}{(\text{dry mass of fish body})} + 1 \right]$$

The dry body mass (y mg) was converted from the wet body mass (x g), based on a simple linear regression equation ($y = 185x$, $r^2 = 0.99$, $P < 0.001$, $n = 106$).

Estimation of gastric evacuation rate

To estimate the gastric evacuation rate (GER), we first plotted the SFI against time (T h) for the three water temperature regimes (Fig. 1). Following Elliott (1972), the relationship between SFI and T was:

$$\text{SFI} = A - RT \quad (1)$$

where R is the slope and A is the intercept of the regression line. This R value was taken as the GER.

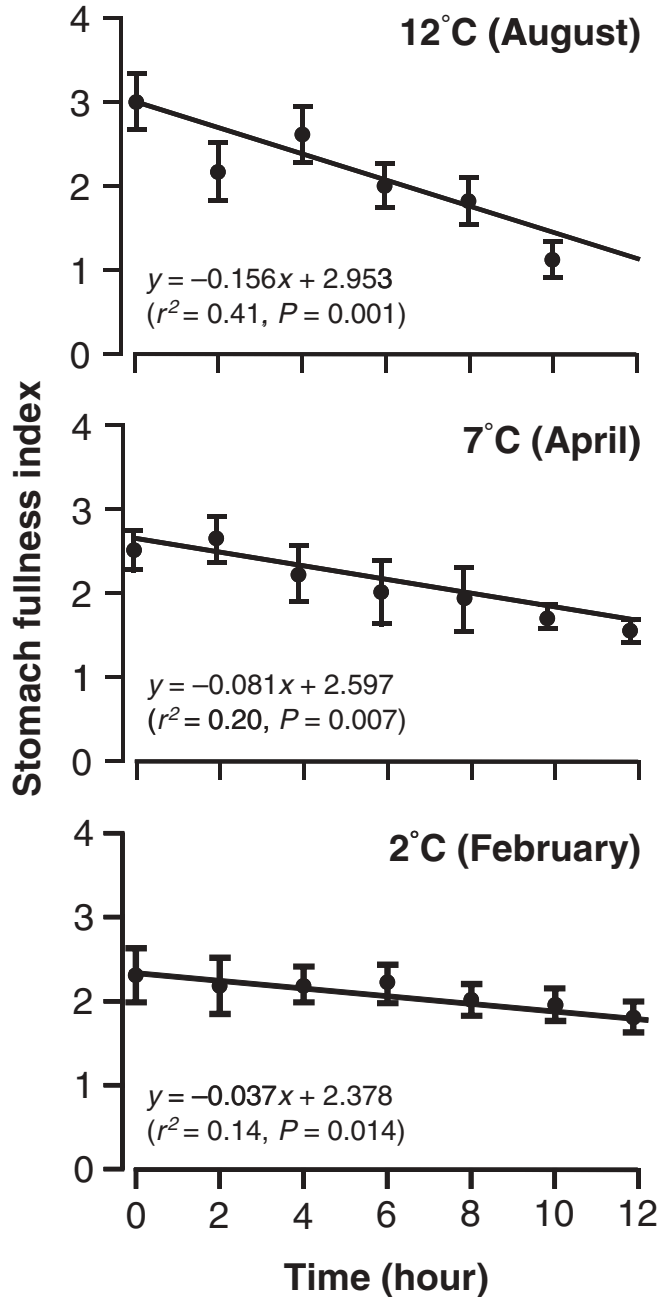


Fig. 1. Temporal changes in the stomach fullness index (SFI) under different water temperature regimes (2°, 7°, and 12°C). Lines were fitted by a simple linear regression

The regression slope R values were compared among the three water temperature regimes. If there was a significant difference among them, the Bonferoni method was used as a multiple comparison test. The adjusted α value was set at 0.016 ($=0.05/3$) for statistical significance. Data were log-transformed to standardize variance and were fitted to the normal distribution. Although the log-transformation of the Y axis affected distribution of residuals in one treatment (Hartley's text for homogeneity; 2°C: $F_{\max} = 3.012$, $P = 0.250$, 7°C: $F_{\max} = 36.409$, $P = 0.027$, 12°C: $F_{\max} = 3.613$, $P = 0.241$), we calculated the R s according to Elliot (1972) because our main purpose was to compare them with those of other species examined elsewhere in the same way. These statistical results are therefore explained with cautiousness.

Results and discussion

The body sizes of *Cottus nozawae* differed significantly among sampling months ($F_{2,103} = 51.229$, $P < 0.001$; Table 1). The population density of this fish was nearly one-order of magnitude higher than that of the second dominant species, rainbow trout *Oncorhynchus mykiss* Walbaum (0.3 fish·m⁻², Kawaguchi and Nakano 2001). The sculpins fed mainly on Ephemeropteran nymphs (70%–90%) and Dipteran larvae (5%–20%) during all months. Elliott (1972) reported that the GER did not depend on food items in a carnivorous fish; therefore, we assumed that the effect of food items on the GER was negligible for *C. nozawae*. The SFI at 0h did not differ among water temperature regimes (one-way ANOVA: $F_{2,15} = 2.573$, $P = 1.094$). The SFI declined significantly over time under all water temperature regimes (Fig. 1). We examined the reaction norms of the GER against water temperature (Fig. 2). In *C. nozawae*, the GER was accelerated significantly with the increasing water temperature. The GER showed a significant difference among the three water temperature regimes ($F_{2,14} = 10.496$, $P = 0.002$). The difference was significant between the two extremes of these treatments (2°C versus 12°C: $t_{68} = 3.157$, $P = 0.002$). In relation to comparisons between the intermediate and extreme temperatures (7°C versus 12°C: $t_{60} = 1.673$, $P = 0.099$; 2°C versus 7°C: $t_{72} = 1.406$, $P = 0.164$), we could not draw a statistical conclusion because of the heterogeneity of variance in the 7°C treatment. Based on the GERs (i.e., the slope of SFI against time) shown in Fig. 1, the reduction time to 50% of stomach contents ($T_{50\%}$) was estimated to be 4.4h at 12°C, 8.6h at 7°C, and 18.7h at 2°C.

Our experiment could not completely exclude density-dependent effects (e.g., stress in a crowded captive condition) on the GER of stocked sculpins, as the sculpin density in the tank covaried over time. However, although the subject fish under each water temperature regime experienced a similar captive condition in relation to crowdedness, the GER showed significantly different reaction norms against water temperature. This result indicates that the physiological performance of *C. nozawae* clearly depends on water temperature. The reaction norms of the GER against water temperature are also shown for a variety of fish species from

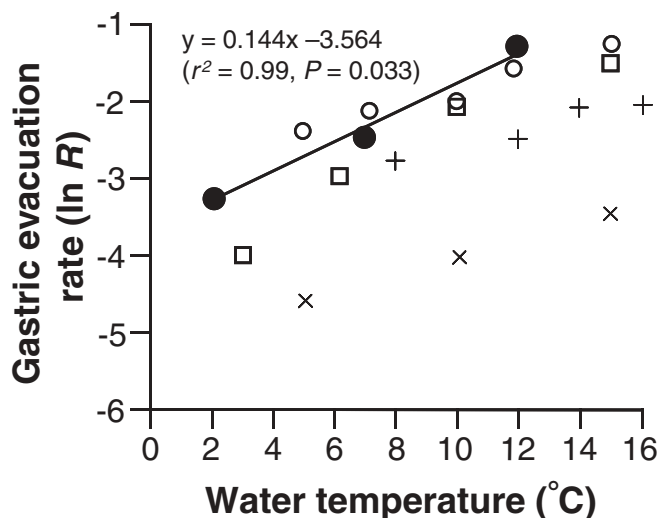


Fig. 2. The reaction norm of the gastric evacuation rate (GER) is shown against water temperature for freshwater sculpin *Cottus nozawae* (●). Other plots are data for brown trout, *Salmo trutta*, (Elliott 1972) (○); sockeye salmon, *Oncorhynchus nerka*, (Brett and Higgs 1970) (□); gibel, *Carassius auratus gibelio*, (Specziár 2002) (+); and rainbow trout, *Oncorhynchus mykiss*, (From and Rasmussen 1984) (×). The sculpin and gibel are benthic foragers, and sockeye salmon and rainbow trout are swimming foragers

subfrigid to temperate streams (Fig. 2). Interestingly, there is a general pattern of increasing GER with water temperature, although the reaction norms showed considerable interspecific variation, independent of their foraging mode and taxonomic group. It is notable that the rainbow trout, which is a nonnative species in the Horonai Stream, has a low GER in a population from Denmark (From and Rasmussen 1984), compared to that of *C. nozawae*. Even if cohabitant species have adapted to the same environment, their reaction norms of the GER may be very different. To study food resource usage in the fish community and resultant matter flow in aquatic food webs, aquatic ecologists have conventionally measured the stomach content weight as an index of daily food rations. However, such an index may never be comparable among fish species from different temperature regimes. We therefore stress the importance of considering the reaction norms of feeding physiology against water temperature in fishes to better understand food webs in aquatic ecosystems.

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