A Preliminary Observation of Rapid Changes of Gill Raker Number in Miyabe Charr (Salmonidae) over a Short Term Period

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ABSTRACT

We present a preliminary discussion of a case study that is underway to examine whether gill raker number of Miyabe charr (*Salvelinus malma miyabei*) on Hokkaido, Japan is undergoing a rapid adaptive response to changing environmental conditions. The study involves two populations, one in Shikaribetsu Lake and the other in the Torizaki River. Preliminary data based on museum specimens and recently collected material suggest a rate of increase in gill raker number in the Shikaribetsu Lake population over the past 60 years that is an order of magnitude greater than the estimated average rate of increase since the population became isolated about 10,000 years ago. Conversely, gill raker number in the Torizaki population has decreased since introduction about 30 years ago. We discuss both microevolution and phenotypic plasticity in relation to the observed changes. We emphasize the importance of natural history collections to the study of microevolution.

Keywords: Changing environment, Rapid evolution, Microevolution, Miyabe charr

INTRODUCTION

Artificial introduction of new competitors or food resources, or the introduction of a native species from an original habitat into new habitats, may induce changes in both the food habits of the native species and its morphological characters related to feeding [e.g., 1]. Grant [2] and Grant and Grant [1] indicated that the beak shape of Darwin's finch inhabiting in the Galapagos Islands changed after a drastic reduction of or increase in seed abundance. When the lizard *Anolis sagrei* was exposed to new environmental conditions or transplanted into new habitats, the length of legs changed rapidly in response to the new habitat [3]. These changes may fluctuate with changing environmental conditions over a short-term period (so-called microevolution) by natural selection, sexual selection, or sometimes genetic drift [4].

In fishes, the potential for microevolutionary changes, in response to environment, in gill raker number and length has been demonstrated by many researchers [e.g., 5]. Gill rakers act as a comb-like filter to sieve food items. A low number of gill rakers with large spaces is effective for feeding on large food items, whereas a high number of gill rakers with narrow spaces is effective for trapping small items. The number of gill rakers appears to change drastically under fluctuating environmental conditions or under competition with a closely related species, adapting to optimal selection of prey size [e.g., 6]. However, we lack a comprehensive understanding of the process of this change.

Here we review a preliminary case study that uses historical and recently collected specimens of Miyabe charr to investigate whether morphological characters of this fish have changed in response to changing environmental conditions. We demonstrate

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how specimens that have been preserved in museum and university collections for long periods can play an important role in this type of study.

OBSERVATIONS, INTERPRETATION AND DISCUSSION

Miyabe charr (*Salvelinus malma miyabei*) inhabits Shikaribetsu Lake, Hokkaido, Japan as the only native fish in the lake, where it is a plankton feeder [7]. A subspecies of Dolly Varden (*S. malma malma*), Miyabe Charr (*S. malma miyabei*) has been declared a natural monument by the Hokkaido Government. Our mitochondrial analysis indicates that this charr derived from an anadromous population of Dolly Varden and has been landlocked in the lake for probably around 10,000 years (Yamamoto et al., unpublished). Miyabe charr has a higher number of gill rakers than any other populations of Dolly Varden, which are typically piscivorous. Thus, gill raker number has apparently increased in the charr over the past 10,000 years, possibly to allow for greater plankton retention efficiency [7]. During the last 50 years, however, various fishes (salmonids and planktivorous fishes) were introduced into the lake. Artificial introduction of new competitors or food resources may induce changes in both the food habits of Miyabe charr and its morphological characters related to feeding.

To determine whether gill raker number has increased in Miyabe charr since 1940, we examined specimens from the Hokkaido University Forest Museum, Hokkaido University Fisheries Museum, and a laboratory at Kyushu University, collected between 1940 and 1986. We also collected specimens from the lake after 2000. Unfortunately, the oldest specimens, collected in the 1930s, have not been found. These were reported by Oshima (1965) as a new species, *Salvelinus miyabei* (named in memory of the late professor emeritus Kingo Miyabe, one of the most famous professors of Hokkaido University). These specimens may have been lost.

Another population of Miyabe charr exists that was introduced upstream of a natural fall in the Torizaki River, southern Hokkaido in 1974 and 1981. The fall prevents migration of any other charr and trout upriver, so that the introduced population of Miyabe charr has remained genetically isolated. The main food of the charr in the river is likely insects, which are large compared to the plankton fed upon by the source population in Shikaribetsu Lake (Kobayashi and Maekawa unpublished). Thus, this introduced population provides a good opportunity to determine whether a rapid decrease in gill raker number has occurred as an adaptive response to feeding on insects. We collected Miyabe charr in the Torizaki River in 1995 ($N = 40$) and 2001 ($N = 50$) to compare gill raker number of the introduced population to that in the source population 21–27 years previously (Shikaribetsu Lake, 1974, $N = 31$).

The gill raker number of Miyabe charr increases rapidly up to 60–70 mm in fork length and thereafter remains constant with no sexual dimorphism [7]. Therefore, we used only specimens over 100 mm in fork length, and counted all the gill rakers of the first gill arch using a microscope. (Fig. 1).

A linear regression analysis revealed that gill raker number has changed at a rate of 0.011 gill-rakers/year over the past 60 years (randomization test, $P < 0.01$, Kobayashi and Maekawa, unpublished). This may reflect rapid evolution due to recent environment changes in the lake caused by fish introductions. It is a much higher rate than that calculated assuming a constant rate of change over the past 10,000 years or so since the Miyabe charr became isolated from sister populations of Dolly Varden. Mean gill raker number in Miyabe Charr is five more than in Dolly Varden [7]. If the ancestral population of Miyabe charr originally had the same number of gill rakers as Dolly Varden (and also assuming that the number in Dolly Varden has changed little or not at all since isolation of Miyabe charr), then the rate of increase in Miyabe charr would have been five gill rakers in 10,000 years, or 0.0005 gill-raker/year. However, another explanation for an apparent recent increase in rate of change may be that gill raker number has fluctuated over time, and that the apparent recent rate increase is part of normal fluctuation around a long-term average.

The stomach contents of Miyabe charr in the lake did not appear to markedly differ before and after the fish introductions (the main food resource was zooplankton, Kobayashi and Maekawa unpublished). The number of gill rakers continues to increase with time since the last ice age as mentioned above (Kobayashi and Maekawa unpublished). In salmonid fishes, the sockeye salmon and the kokanee (*Oncorhynchus nerka*) have the highest number of gill rakers (the number = 33~44) [6], and are adapted to feed on zooplankton. Furthermore, there are benthic and limnetic morphs in salmonids, with the former having fewer and shorter gill rakers than the latter [8]. In general, the gill raker number of fish is strongly heritable [6, 9]. Considering the gill raker number of other salmonid species, those of Miyabe charr may continue to change to stay optimal like

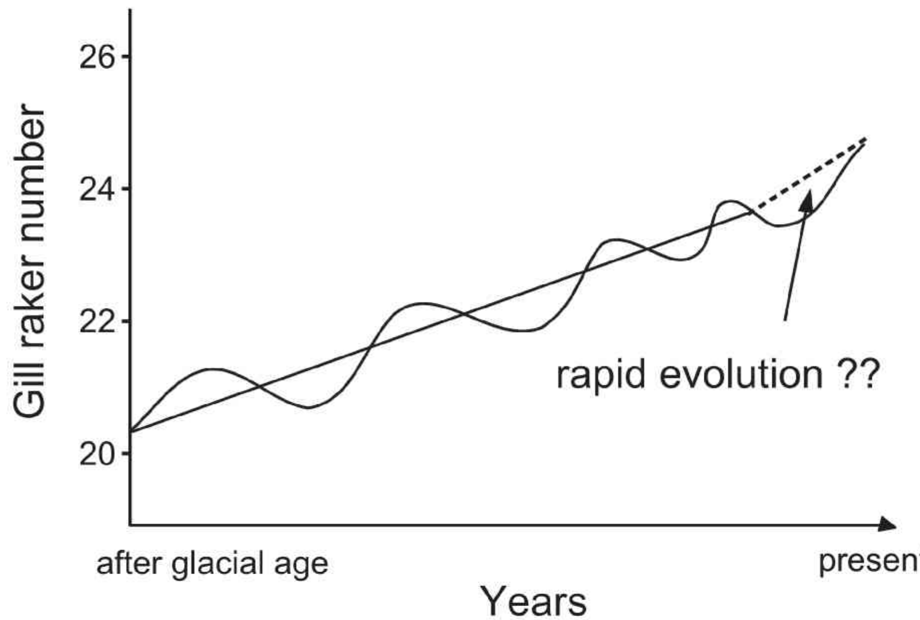

Fig. 1 Hypothetical process of change of the gill raker number after the last glacial age. The change in gill raker number may fluctuate slowly (slow evolution) or rapidly (rapid evolution) but increase on average (solid line). Dotted line represents relatively rapid rate of change compared to the long-term average.

other planktivorous salmonid fish such as sockeye salmon or kokanee [10]. Therefore, a possible consideration is that the higher the number of gill rakers, the higher the fitness by strongly depending on plankton as food, or being in competition with introduced planktivorous fishes.

The food items of Miyabe charr that were introduced into Torizaki River from Shikaribetsu Lake about 30 years ago consisted entirely of aquatic and/or terrestrial invertebrates. Surprisingly, a comparison between Torizaki River and Shikaribetsu Lake populations indicated that the number of gill rakers of the former population had decreased significantly (ANOVA, $P < 0.05$), suggesting a rapid and adaptive response to the new habitat in this population of Miyabe charr (Kobayashi and Maekawa unpublished). It may be that the lower the number of gill rakers reflects a higher fitness in the presence of only large food items. This population may continue to decrease in gill raker number to that (about 22 on average) of stream-dwelling Dolly Varden in Hokkaido.

Phenotypic plasticity can be seen as a change in a character in response to the current environmental conditions [e.g., 11]. For example, quick response in gill raker structure in roach may be an adaptation to deal with the rapid population dynamics of zooplankton [12]. The rapid change in the number of gill rakers of salmonid or other fishes may be due to phenotypic plasticity effected, for instance, by an environmental change such as change in water temperature or temporal variation in resource conditions [12, 13]. In our study, we observe phenotypic change without documenting genetic and environmental components of that change. Therefore, we cannot distinguish between genetic change and environmentally induced phenotypic change. We may conduct a common garden experiment in the future. This experiment will give us important information about not only phenotypic plasticity but also the correlation between fitness and the number and heritability of gill rakers in Miyabe charr.

Here, we would like to emphasize the importance of deposition in museums of many specimens of preserved living organisms, because these provide us good opportunities to examine evidence for microevolution. We also demonstrate the need that facilities and operation of the Hokkaido University Museum should be established as soon as possible.

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