Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars

SHIGERU NAKANO1 AND TETSUO FURUKAWA-TANAKA2

1Nakagawa Experimental Forest, Faculty of Agriculture, Hokkaido University, Otoneppu, Nakagawa, Hokkaido, 098-25 and 2Division of Ecology, Museum of Nature and Human Activities, Sanda, Hyogo, 669-13 Japan

Aggressive interactions, foraging behavior, habitat use and diet were studied in sympatric populations of white-spotted char, Salvelinus leucomaenis, and Dolly Varden, Salvelinus malma, in a Japanese mountain stream. Underwater observations on individuals of both species revealed two distinct behavioral regimes: aggressive drift foragers and non-aggressive benthos foragers. Aggressive drift foragers defended partial territories around focal points from which they made forays to capture invertebrates drifting in the water column. Non-aggressive benthos foragers cruised around and beneath cobble in large foraging ranges that overlapped each other. Intra- and interspecific, size-dependent dominance hierarchies were recognized among aggressive drift foragers, whereas non-aggressive benthos foragers showed no such relationships. Terrestrial invertebrates were the most abundant prey in the diets of drift foragers, whereas a very small proportion of the diet of benthos foragers was made up of these taxa. Benthos foragers showed more complex diet composition than drift foragers. These results suggest that non-aggressive benthos foragers may avoid not only interference but also exploitative competition by using alternative foraging tactics. The proportion of drift foragers to benthos foragers among white-spotted char was more than 35 times that among Dolly Varden. The significant difference in the proportion of each species using the two types of foraging strategy results in interspecific food segregation in sympatric populations.

Key words: dominance hierarchy; food segregation; foraging tactics; interspecific competition; salmonidae.

INTRODUCTION

During past decades, many theoretical papers have dealt with the role of interspecific competition as a determinant of animal community structure (e.g. MacArthur 1972; Schoener 1983; Abrams et al. 1986; den Boer 1986). However, most studies of interspecific competition have concentrated on the outcome of competition without ascertaining the actual mechanisms of competition. For example, although it has been suggested that interference competition results in resource partitioning (Shoener 1983), direct observations of behavioral interactions among individuals of competing species as they simultaneously attempt to exploit the same resources or partition alternative resources have been carried out rarely. In many competitive systems, the influence of interference on resource use was merely presumed from observations of asymmetric, aggressive interactions and niche shifts by one species, both of which were usually studied at the population level (Larson 1980; Hixon 1981; Pacala & Roughgarden 1982; Edington & Edington 1983).

Numerous studies have explored the competitive relationships between various sympatric salmonid species. These studies demonstrated that habitat use and/or diet of one species shifted in the presence of more than one competing species (e.g. Nilsson 1965, 1967; Fausch & White 1981, 1986; Ishigaki 1984; Hindar et al. 1988; Langeland et al. 1991). Furthermore, especially for stream-dwelling salmonids, intraspecific dominance hierarchies within local groups are important determinants of patterns of

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microhabitat and food resource use by individuals (Kalleberg 1958; Jenkins 1969; Fausch 1984). Such dominance hierarchies are also formed among heterospecific individuals in sympatric zones (Newman 1956; Kalleberg 1958; Jenkins 1969; Fausch & White 1986). As pointed out by Morse (1974), such mixed, interspecific social interactions may change the resource use of individuals in a local group and, eventually, a whole population. Interspecific dominance hierarchies, however, have received less attention and their role as determinants of resource use patterns still remains unclear (Fisler 1977). Although they have been reported in a wide range of animals, most studies have simply demonstrated that one species always dominates the other (Wilson 1975). The dominant–subordinate relationship among species, in fact, may be more dynamic, if examined at the individual level.

Two native congeneric species of chars, white-spotted char, *Salvelinus leucomaenis* and Dolly Varden, *Salvelinus malma*, occur sympatrically in streams of Hokkaido, the northern island of Japan (Kawanabe 1989). It has been suggested that they are strong competitors, based on comparisons of diets in allopatry and sympatry, preliminary observations on aggressive interactions in an aquarium and removal experiments in a natural habitat (Ishigaki 1984; Furukawa-Tanaka 1989).

In this paper, the results of studies on interactions, and patterns of microhabitat and prey use, for sympatric populations of white-spotted char and Dolly Varden in a natural habitat are presented. The approach was to focus primarily on delineation of detailed competitive mechanisms at the individual level, rather than simply showing the existence of competition in a whole population.

**STUDY AREA**

The study was performed from 1 to 14 August 1989 in the Poroshiri Stream and a tributary, the Migisawa Stream (42°41'N, 142°41'E), both of which are headwater tributaries of the Niikappu River located in the Hidaka Mountains (Fig. 1). The river discharges into the Pacific Ocean on the

![Fig. 1. Location of the study area and the observed pools (A and B) in the headwater reaches of the Niikappu River, Contours (dotted) show 200 m elevations.](image-url)