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Author(s)	Hasegawa, Koh; Maekawa, Koji
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Effect of habitat components on competitive interaction between native
white-spotted charr and introduced brown trout

Koh Hasegawa^a and Koji Maekawa

Laboratory of Conservation Biology, Field Science Center for Northern Biosphere,
Hokkaido University, Sapporo, Hokkaido 060-0809, Japan

ABSTRACT

In salmonid species, interspecific competition has been affirmed as the major mechanism of the replacement of native species by introduced species. However, competitive interactions are variable according to various habitat components. Our study on native white-spotted charr and introduced brown trout in a small creek in southwestern Hokkaido, Japan indicates that the intensity of the interspecific competition was reduced in structurally complex habitats, areas with numerous woody debris, because the native species were able to survive in those environments. Therefore, the replacement may be inhibited in structurally complex habitat.

INTRODUCTION

Salmonid species have been introduced for more than 100 years throughout the world because they are valuable fishery resources (Fausch 1988, Krueger and May 1991). As a result of salmonid introductions, replacement of native salmonids by introduced salmonids has consequently been reported in many studies (e.g., Krueger and May 1991), and competitive exclusion has been affirmed as the major mechanism of the replacement (Nakano and Taniguchi 1996). Interspecific competition during the adult stage may hold the key to the replacement, because adult density is related more strongly to population persistence than is juvenile density (Elliot and Hurley 1998, Morita and Yokota 2002). Salmonid species compete for their foraging habitats through interference competition defined as direct aggression in which subordinate individuals or species are forced to shift to a poorer habitat (Nakano 1995, Nakano et al. 1998). Thus, native salmonids are replaced when they are competitively inferior to introduced salmonids.

However, competitive interactions among species may vary with environmental factors (Dunson and Travis 1991). For stream-dwelling salmonids, habitat types, such as pool or riffle, and water temperature may effect the consequences of interspecific competition (Glova 1986, Taniguchi et al. 1998). The intensity of interference competition decreases in structurally complex habitat because visual contact between competitors decreases with the increase of habitat complexity (Imre et al. 2002). Therefore, the relationship between habitat components and interspecific competition should be examined to understand competitive exclusion.

In Hokkaido, northern Japan, the introduced salmonid, brown trout (*Salmo trutta*)

^aCorresponding author; E-mail:hasekoh@exfor.agr.hokudai.ac.jp

has spread since the 1980's and been discovered in 42 rivers at present (Takami and Aoyama 1999, Kudo 2001). Takami et al. (2002) supposed that trout have replaced the white-spotted charr (*Salvelinus leucomaenis*), widely native salmonid. Actually, trout are competitively superior to charr (Hasegawa et al. 2004). Hasegawa and Maekawa (2006) demonstrated in an artificial stream that habitat preferences of charr and trout overlap, and charr are forced to shift to poorer habitat through interference by trout. Thus, competitive exclusion of charr by trout is plausible. However, we have no information about the effect of habitat components on competition between trout and charr.

In this study, we focused on the relationship between the degree of dominance of trout and some habitat components that generally correlate with habitat selection by salmonids in order to speculate about which components affect the intensity of competition in a small stream.

METHODS AND MATERIALS

The study was conducted in the headwaters of Mamachi Creek (42°46'N, 141°33'E), a branch of the Chitose River, in southwestern Hokkaido, northern Japan. Mamachi Creek has two main branches, Ikejirimamachi Stream (IM) and Yusuinosawa Stream (YS). Both streams are spring-fed and having pebble substrate. Water temperature was around 9-11 °C during our survey. Brown trout were first found in Mamachi Creek in 1985 (T. Takami, Hokkaido Fish Hatchery, personal communication). White-spotted charr and masu salmon (*Oncorhynchus masou*) inhabit in the creek as native salmonids. However, masu salmon is seldom affected by trout because of habitat segregation (Hasegawa and Maekawa 2006).

In July 2004, we estimated the densities of charr and trout in the two headwater streams of Mamachi Creek. Five 150 m study sections, separated from one another by at least 300 m, were established in each stream. To estimate the density of charr and trout in each section, we calculated the population of both species by three-pass removal sampling using an electrofisher (Smith-Root Inc., Vancouver, Washington, USA). We blocked the upstream and downstream margins with nets to prevent fish escaping from the section. All captured charr and trout were anesthetized using phenoxyethanol, and their fork lengths were measured to the nearest 1 mm. In July, we could easily distinguish 0+ year-old fish and adult fish by the difference of fork length (Fig. 1).

We selected five habitat characteristics that correlate with habitat selection by salmonids (Neumann and Wildman 2002; Table 1). Flow (mean of the upstream and downstream margins of each section) was measured as an index of river scale. Pools, the main habitats of salmonids, were counted and their mean area calculated for each section.

The length of undercut banks wide enough to conceal fishes (wider than 0.2 m) and number of woody debris (at least 10 cm in diameter and more than 1 m long) were recorded as cover habitat following Horan et al. (2000). No significant correlation between each component was found, but the mean areas of pools became larger with flow (i.e., river scale) increment (Pearson's test; $R = 0.676$, $p = 0.032$).

We calculated density of charr and trout in each study section. Then, we estimated the degree of dominance of brown trout by determining the ratio of trout to trout plus charr (Ricciardi and Whoriskey 2004). Relationships between the trout ratio and habitat components were analyzed by Kendall's correlation test. The alpha level was set at $p = 0.05$.

RESULTS AND DISCUSSION

Although fish densities differed among sections, trout density was higher than charr density in the headwaters of Mamachi Creek (Fig. 2, Table 1). Densities of both charr and trout did not correlate with each habitat component (Pearson's test). However, the trout ratio was negatively correlated with the number of woody debris (Kendall's test, $R = -0.674$, $p = 0.033$). No other habitat components correlated with the trout ratio (Fig. 3). Although brown trout have widely invaded in Mamachi Creek, the trout ratio decreased (i.e., the white-spotted charr ratio increased) as woody debris became more abundant. Thus, we suggest that white-spotted charr might be able to persist in areas with abundant woody debris as the presence of woody debris led to a reduction in the level of competitive exclusion on charr.

Woody debris makes the habitat structure more complex in stream habitats (cf. Horan et al. 2000). Structurally complex habitats have plenty of shelters that reduce the intensity of interference competition by decreasing the visual contact between competitors (Imre et al. 2002). Subordinate competitors are not prevented from foraging by dominant competitors because subordinates can catch prey as they hide in shelters (Höjesjö et al. 2005). Thus, competitively subordinate species may be more excluded by dominant species in low complexity habitats, but they may coexist more easily with dominant species in structurally more complex habitats (Almany 2004). Therefore, charr may be able to coexist with trout in areas with abundant woody debris even though charr are competitively inferior to trout (Hasegawa et al. 2004).

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FIGURE LEGENDS

Figure 1. Frequency distributions of fork length of 0+ year-old fish and adult fish. (A) white-spotted charr and (B) brown trout.

Figure 2. Densities of charr and trout in each stream section.

Figure 3. Relations between the trout ratio and (A) flow, (B) number of pools, (C) mean area of pools, (D) total length of undercut banks and (E) number of woody debris.

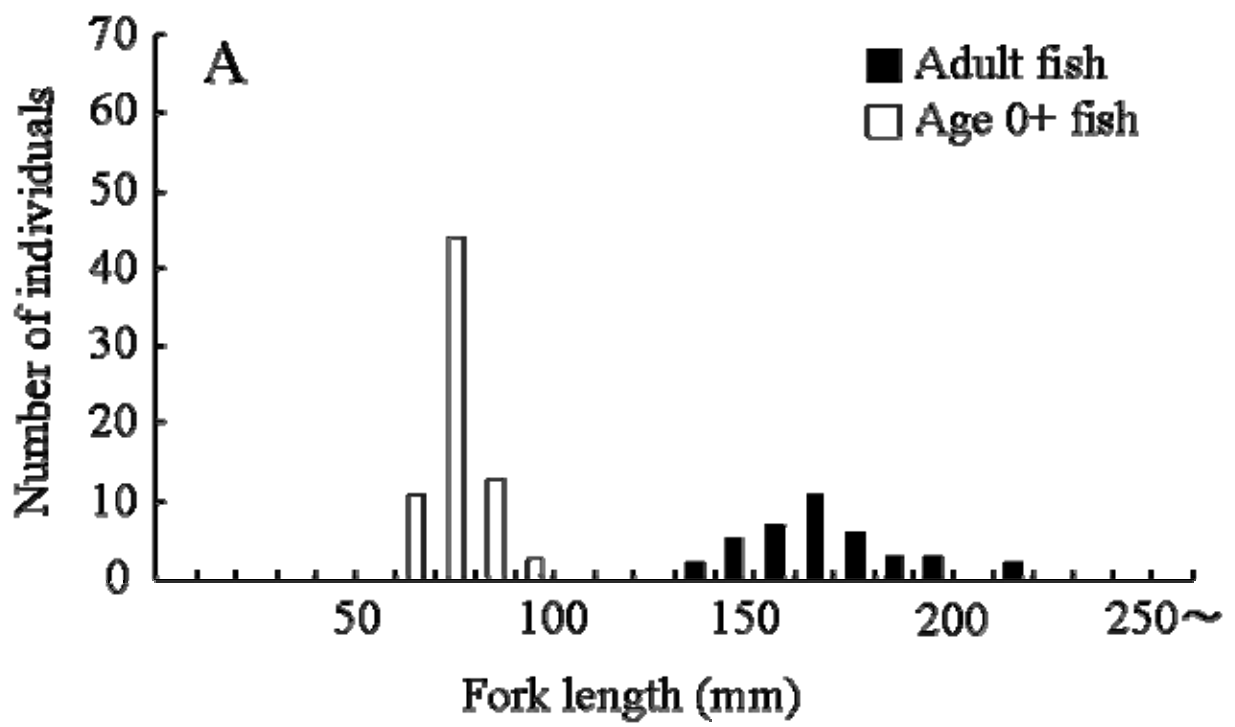


Fig 1A

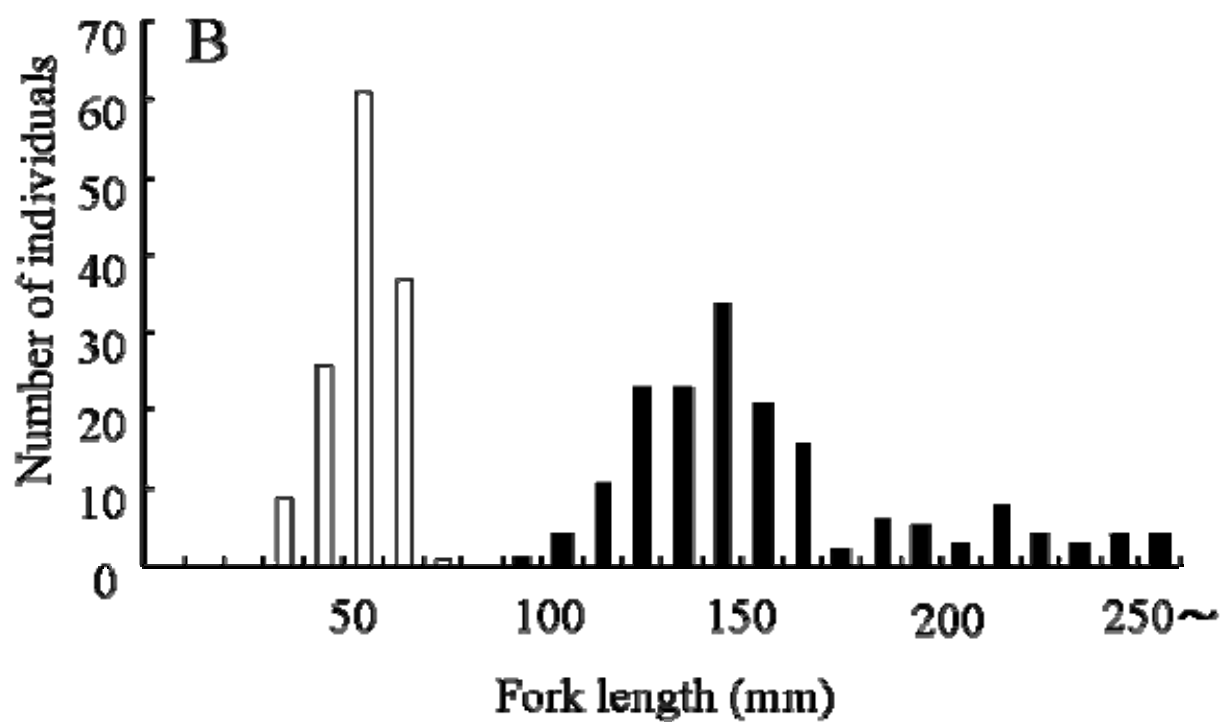


Fig 1B

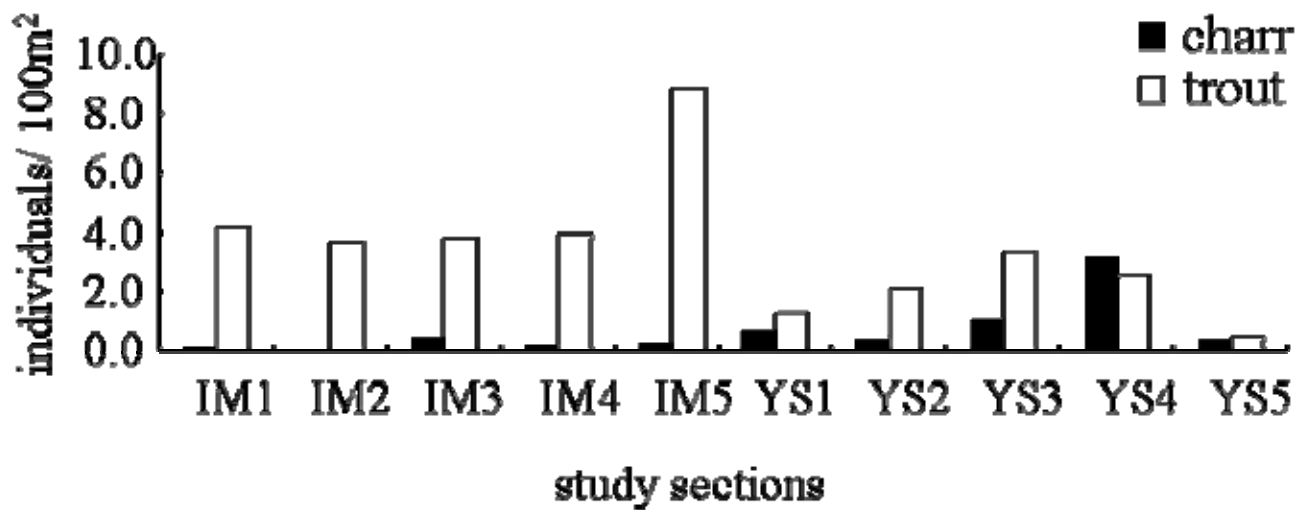


Fig 2

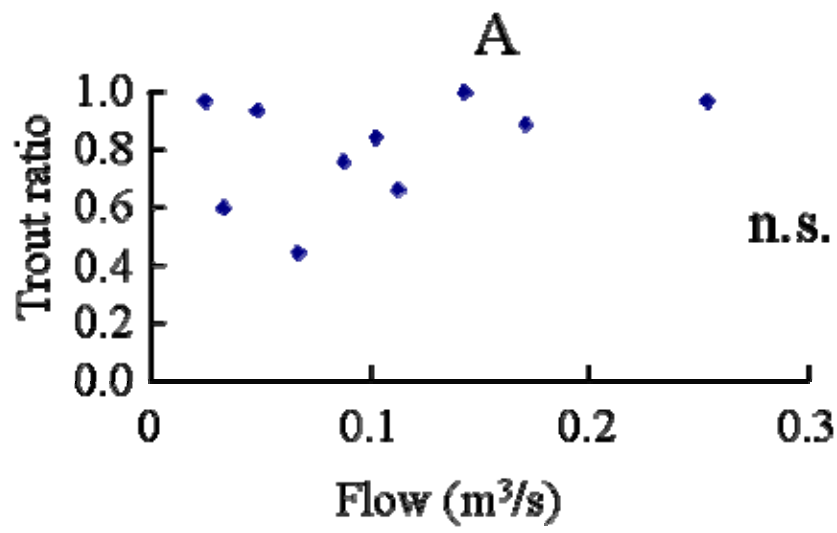


Fig 3A

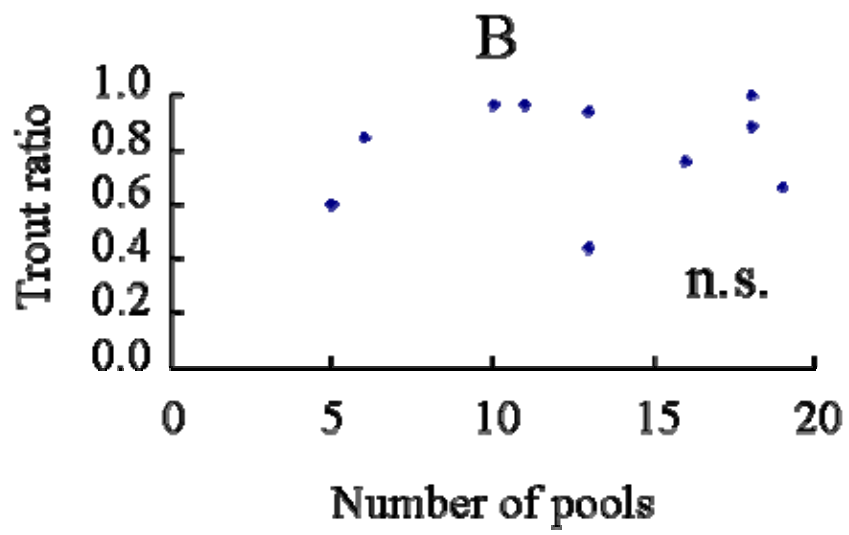


Fig 3B

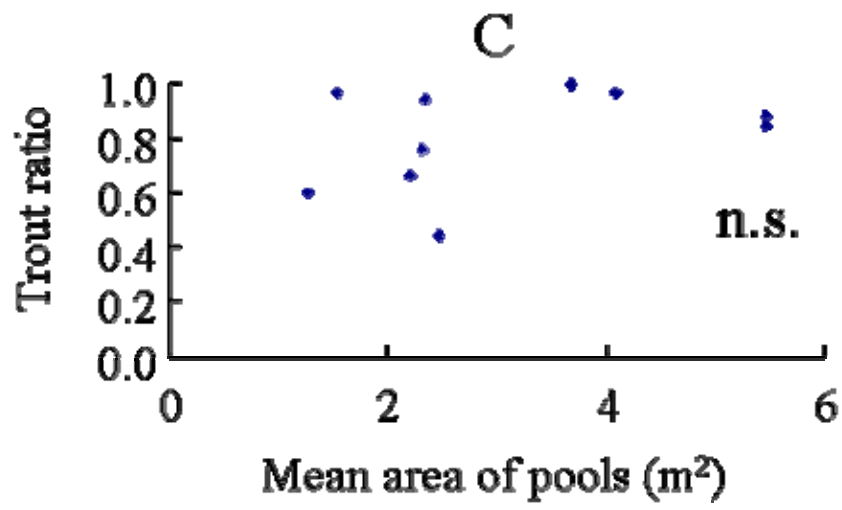


Fig 3C

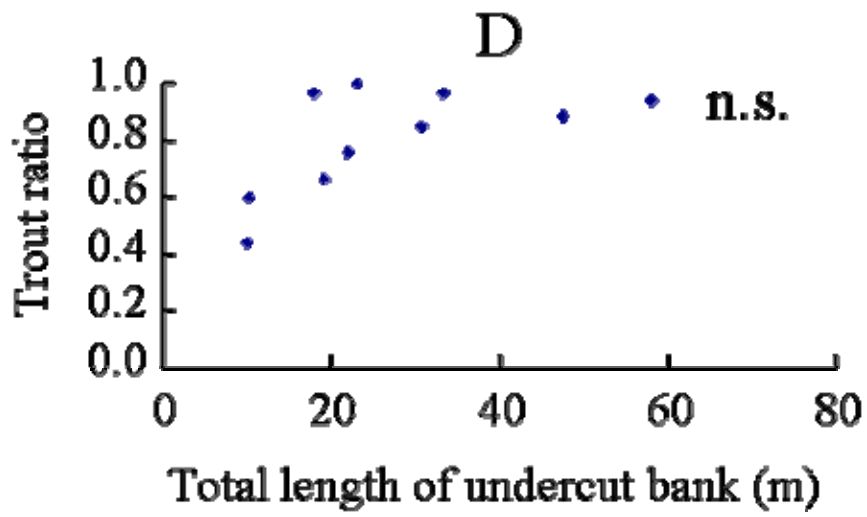


Fig 3D

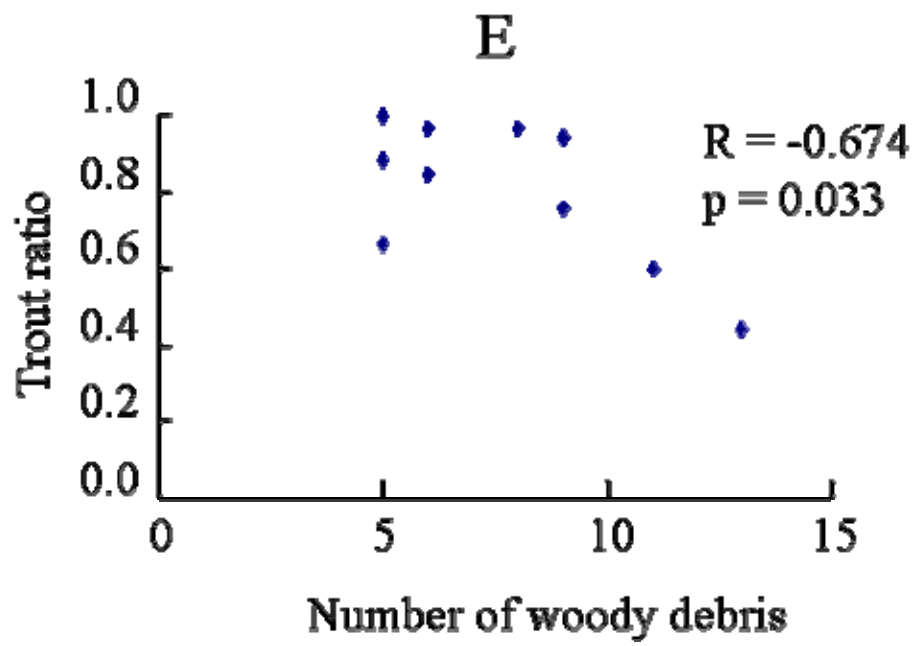


Fig 3E

Table 1. Habitat characteristics and trout ratio [(trout density)/(trout density + charr density)] of the ten study sections

Section	Flow (m ³)	No. of pools	Mean area of pools (m ²)	Undercut bank (m)	No. of woody debris	Trout ratio
IM1	0.253	11	4.09	33.3	8	0.97
IM2	0.142	18	3.67	23.0	5	1.00
IM3	0.170	18	5.46	47.5	5	0.89
IM4	0.048	13	2.35	57.9	9	0.94
IM5	0.025	10	1.54	17.9	6	0.97
YS1	0.112	19	2.20	19.1	5	0.67
YS2	0.102	6	5.47	30.7	6	0.85
YS3	0.088	16	2.32	21.8	9	0.76
YS4	0.068	13	2.47	9.9	13	0.44
YS5	0.033	5	1.26	10.0	11	0.60