Habitat selection by larvae of a fluvial lamprey, *Lethenteron reissneri*, in a small stream and an experimental aquarium

Hiroko Sugiyama* and Akira Goto✉

Laboratory of Breeding Science, Graduate School of Fisheries Sciences, Hokkaido University 3-1-1 Minatocho, Hakodate 041-8611, Japan (e-mail: akir@fish.hokudai.ac.jp)
* *Present address: Tochigi Agriculture Public corporation, 2-3-12 Ichinosawa, Utsunomiya 320-0047, Japan*

Received: November 1, 2000 / Revised: September 12, 2001 / Accepted: October 18, 2001

Ichthyological Research

Ichthyol Res (2002) 49: 62–68

Abstract Habitat selection by fluvial lamprey larvae, *Lethenteron reissneri* (Petromyzontidae), was studied in a natural stream and an experimental aquarium to clarify microhabitat requirements for future conservation of natural populations. A gross collection survey of lamprey larvae in the Monbetsu River, southeastern Hokkaido, Japan, revealed a remarkable bias toward distribution in sandy-mud beds. An analysis using Jacobs' electivity index showed that the larvae selectively utilized spaces having regard to shallow water, weak current, deep sandy-mud, and fine substrate particles. A comparison of microhabitat use between small- (≤5 cm) and large-sized larvae (>5 cm) indicated that the latter utilized the space with greater ranges in both water depth and substrate particle size than the former. Both the field survey and laboratory experiments on larval selectivity of physical habitat variables clearly demonstrated that substrate particle size was the most important variable for small-sized larvae whereas both water depth and substrate depth were more important for large larvae. These findings should be applicable in directing attempts at fluvial habitat restoration for conservation of this endangered lamprey species.

Key words Lamprey ammocoetes · Distribution pattern · Physical habitat variables · Habitat preference · Conservation

For suitable and effective maintenance of biodiversity in a local area, conservation of at least the present richness of species or populations of which the local fauna and flora are composed is important (Primack, 1995; Washitani and Yahara, 1996). Many conservation biologists have pointed out that one of the most important issues for the maintenance of species richness is conservation of suitable habitats of the respective component species in a local environment (Moyle and Williams, 1990; Primack, 1995; Bruton, 1995; Washitani and Yahara, 1996).

Freshwater fishes, being components of freshwater ecosystems, may be the vertebrate group most vulnerable to human-induced environmental perturbations such as water pollution, hydrological manipulation, overfishing, and introduction of alien fishes (Regier and Meisner, 1990; Bruton, 1995). Factors that have caused fishes to become threatened are varied and differ from one biogeographic area to another (Andrews, 1990; Pollard et al., 1990; Regier and Meisner, 1990; Maitland, 1994; Bruton, 1995).

To date, 34 species of freshwater lampreys have been recorded from the Northern Hemisphere, one now being considered extinct and 9 others threatened (Renaud, 1997; Yamazaki and Goto, 2000a). Kappus et al. (1995) pointed out that loss of suitable habitats would be one of the main reasons for the endangered *Lampetra planeri* populations in the Danube River basin. In Japan, the Far Eastern brook lamprey, *Lethenteron reissneri*, has been recently recognized as a threatened species (Red data list of threatened natural animals; Environment Agency, Japan Government, 1999).

Lethenteron reissneri has a nonparasitic, fluvial lifestyle, being distributed throughout Hokkaido, Honshu, and Shikoku Islands, and Kyushu Island excluding Kagoshima and Miyazaki Prefectures (Miyadi et al., 1976; Yamazaki and Goto, 1996). Recent studies have demonstrated that two genetically divergent forms (northern and southern forms) exist, although they have very similar morphological characteristics (Yamazaki and Goto, 1996, 1997, 1998). The northern form is distributed in Hokkaido Island and the northeastern part of Honshu Island, whereas the southern form ranges from Yamagata Prefecture to Yamaguchi Prefecture in Honshu Island, and in Shikoku and Kyushu Islands (Yamazaki and Goto, 1996). In some sympatric sites of the two forms, strict reproductive isolation has been found to occur (Yamazaki and Goto, 1996, 2000b).

The aims of the present study were to elucidate the distribution pattern within a natural stream and the physical habitat features utilized by larvae of the northern form of *L. reissneri* to establish relevent biological information necessary for conservation of the species.

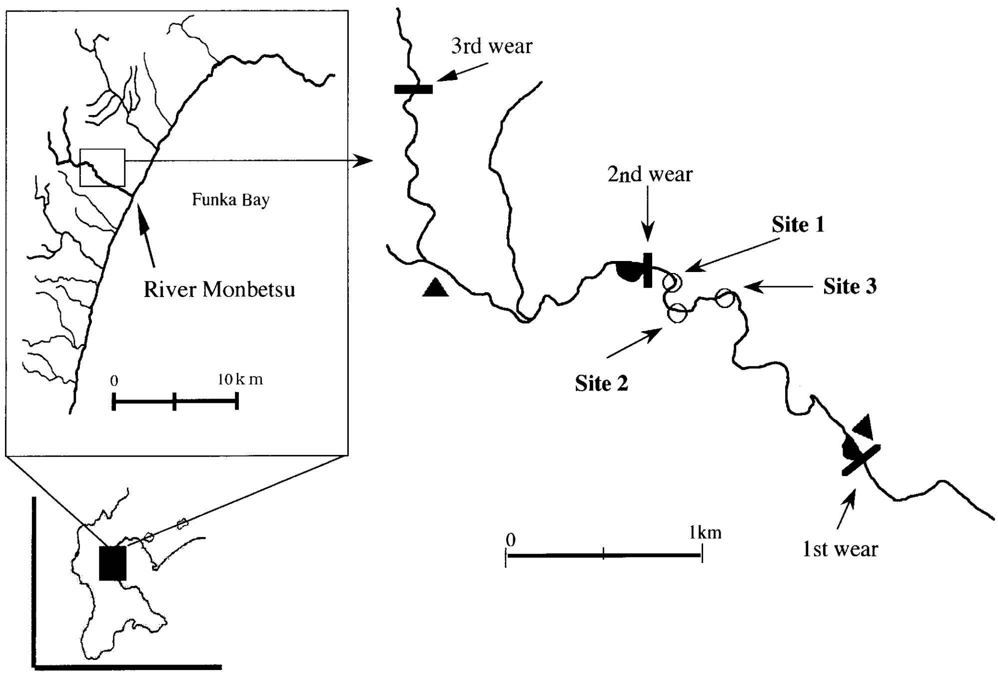

Fig. 1. Maps showing the location of the Monbetsu River and the streamcourses grossly surveyed in this study (▲–▼). *Open circles*, study sites (St. 1–St. 3)

Materials and Methods

Study sites and environmental features.—The field survey was carried out during the period from July to early October in 1998 and 1999 in the Monbetsu River, located on the southernmost part of Hokkaido Island and draining into Funka Bay (Fig. 1). This river is about 13 km long, having three large mainstream weirs that completely prevent upstream migration of fishes.

Three study sites, each 80 m long (St. 1–3), were established along the mainstream course, characterized by a Bb riverbed type (Kani, 1944), between the first and the second weirs to examine the distribution pattern and habitat utilization of larvae of the northern form of *Lethenteron reissneri* (hereafter abbreviated as *L. reissneri*). In addition to the lamprey, the study sites were inhabited by *Oncorhynchus mykiss*, *O. masou*, *Carassius auratus langsdorfi*, *Noemacheilus barbatulus toni*, and *Chaenogobius urotaenia*.

Habitat measurements and fish collection.—The field survey to determine larval habitat utilization was conducted at three study sites. Four physical environmental variables were measured at 45 equally spaced measuring points of transects at 10-m intervals along the stream, established at each study site: water depth, substrate depth (= thickness of deposited sand and silt), current velocity, and substrate type. Both water depth and substrate depth were measured using a metallic measuring stick to the nearest 1 cm. Current velocity was measured using a portable current meter (3631 modified type; Yokogawa Electric, Japan) positioned 0.6 unit below the water surface. Following Bain et al. (1985), substrate type was classified as bedrock, sand (dominant particle size <2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), or boulder (>256 mm), being determined for a 50-cm square at each measuring point. The substrate types were coded in order of coarseness as follows: 1, sand; 2, gravel; 3, pebble; 4, cobble; 5, boulder; 6, bedrock. After the habitat measurements, collection of lamprey larvae was carried out at the study sites using an electric fisher (Fish Schocker II Light Model; Frontier Electric, Japan). The larvae collected in this survey ranged 13–171 mm TL. At each point where larvae were captured, the aforementioned habitat variables were remeasured in the same manner as previously described.

A total of 39 sandy-mud beds, which were defined as the deposit of sand and silt being formed mainly on the banks of a pool, were located in the study sites. In each of 39 sandy-mud beds (#1–#39), the following five habitat variables were measured: water depth, substrate depth, current velocity, particle-size composition of substrate, and amount of fallen leaves deposited on substrate. Each of the former three variables was measured at the cross points of equally spaced transects at 0.5-m intervals on the beds, in the same manner as previously described. A substrate sample (170 cm^3) was taken at the cross points of 1-m-wide, equally spaced transects established on the beds.

The substrate samples were transported to the laboratory and dried in a vacum oven at 180°C for 8 h. The dried samples were then divided randomly into small subsamples, one being seived so as to separate the following two particle-size classes (abbreviated as PS), PS $\leq$ 0.125 mm and PS > 0.125 mm, according to the Wentworth (1922) classification of substrate. The two particle-size components of the subsample were then weighed using an electronic balance. The particle-size composition of each sandy-mud bed was represented by the percentage of the weight of dried sandy-mud of PS $\leq$ 0.125 mm to the total weight of the subsample. The amount of fallen leaves, which are reduced to detritus and thereby made available for consumption by lamprey larvae (Malmqvist et al., 1978; Moore and Mallatt, 1980), was roughly recorded as the percentage of the surface area of each bed covered by leaves to the overall area of that bed.

To estimate the habitat preference of *L. reissneri* larvae, Jacobs' electivity indices (Jacobs, 1974) were calculated using the following formula:

$$D_{sa} = (r_s - p_a)/(r_s + p_a - 2r_s p_a)$$

where D_{sa} is the electivity index of species s to microhabitat type a, r_s is the ratio of microhabitat type a to all the microhabitat types utilized by species s, and p_a is the ratio of microhabitat type a to all the microhabitat types in the study area.

Habitat selection experiments.—Laboratory experiments were carried out to examine habitat selection for water depth, sandy-mud depth, and substrate particle size in October 1999 at a constant temperature at 15°C, using 141 *L. reissneri* larvae that had been collected from the Monbetsu River in early July 1999. A glass aquarium (13 × 42 × 26 cm), in which three equal-sized plastic containers (12.8 × 14.8 × 12 cm) were arranged side by side, was utilized.

For water depth selection experiments, three different water depths (3.5, 7.5, and 13.5 cm) were prepared in the aquarium as follows. Two of the three containers were jacked by wood blocks to heights of 10 and 6 cm, respectively. After each container was completely filled with sandy-mud, the aquarium was filled with water to a depth of 25.5 cm.

For the sandy-mud depth selection experiments, three different sandy-mud depths (2, 6, and 12 cm) were prepared in the aquarium as in following procedure. Two containers were jacked by wood blocks to heights of 10 and 8 cm, respectively. After each container was completely filled with sandy-mud, the aquarium was filled with water to a depth of 5 cm.

For the substrate particle-size selection experiments, the three containers were completely filled with dried sandy-mud of the following particle sizes: 2 mm > PS ≥ 1 mm, 1 mm > PS ≥ 0.125 mm, and 0.125 > PS ≥ 0.006 mm, respectively. Subsequently, the aquarium was filled with water to a depth of 5 cm.

Under these conditions, five individuals of small (<5 cm) or large (10–15 cm) larvae were deposited onto the water surface in the aquarium for single test trials. Two days after such introductions, the three containers were carefully removed from the aquarium and the number of individuals in each was recorded. For each selection experiment, the test trials were repeated 9–11 times.

Data analysis.—The preference of *L. reissneri* larvae for the four habitat variables (water depth, substrate depth, current velocity, and substrate type) was estimated from Jacobs' electivity indices for each habitat variable, the plus values indicating the positive preference for a given habitat and minus values indicating negative preference. To examine differences in habitat utilization between small (≤5 cm) and large (>5 cm) larvae, a Mann–Whitney U test was done for each habitat variable.

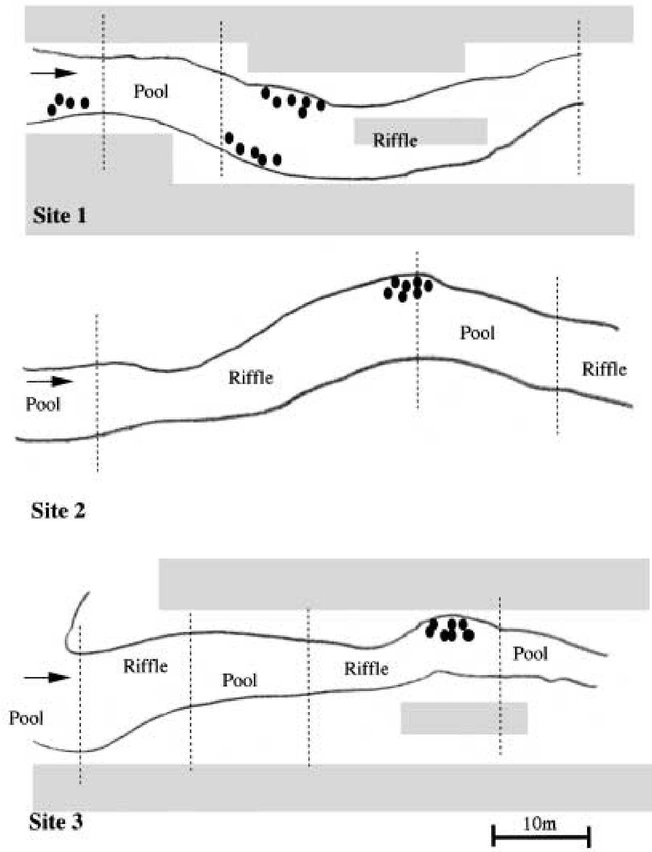

Fig. 2. Distribution pattern of *Lethenteron reissneri* larvae at three study sites in the Monbetsu River. *Hatched areas*, sandy-mud bottom; *solid circles*, position on beds inhabited by larval lampreys; *arrows* and *wd*, direction of water flow and woody debris, respectively

To clarify physical microhabitat conditions, microhabitat variables (water depth, sandy-mud depth, current velocity, particle size of sandy-mud, and amount of fallen leaves) were compared between beds inhabited and not inhabited by lamprey larvae, using the Mann–Whitney U test. For the habitat selection experiments, analyses by chi-square contingency tests indicated whether the larvae were uniformally distributed in the three containers with different habitat variables.

Results

Distribution pattern and habitat selection in a stream. A gross collection survey of lamprey larvae from all three study sites revealed that the distribution of larval *Lethenteron reissneri* was remarkably biased toward areas characterized by a sandy-mud bed (Fig. 2).

The habitat preference of larvae in the study sites was estimated from the Jacobs' electivity index for each physical habitat variable. The index of water depth showed positive values for 0–30 cm depth and negative values for >30 cm depth (Fig. 3). The index of substrate depth showed negative values for 0–2 cm depth and positive values for >2 cm depth

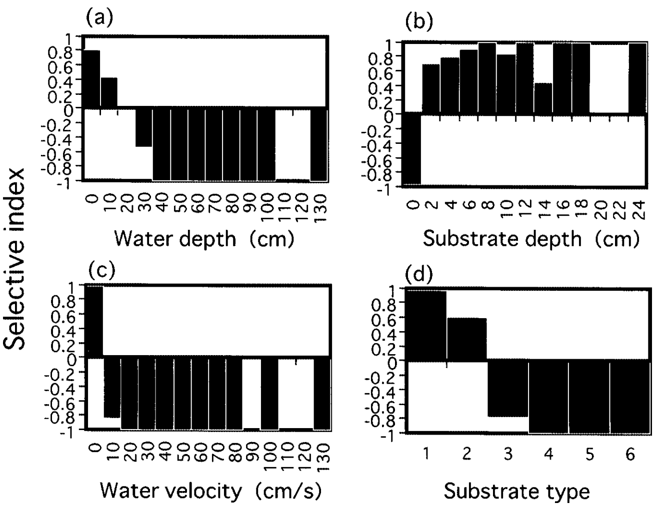

Fig. 3. Habitat selection by *L. reissneri* larvae at study sites in the Monbetsu River. Positive and negative values of Jacobs' electivity indices indicate that physical habitat variables [water depth (**a**), substrate depth (**b**), current velocity (**c**), and substrate coarseness (**d**)] were used by larvae more or less frequently, respectively, than those expected from random availability. *Numbers* in (**d**) indicate the following substrate types: *1*, sand; *2*, gravel; *3*, pebble; *4*, cobble; *5*, boulder; *6*, bedrock

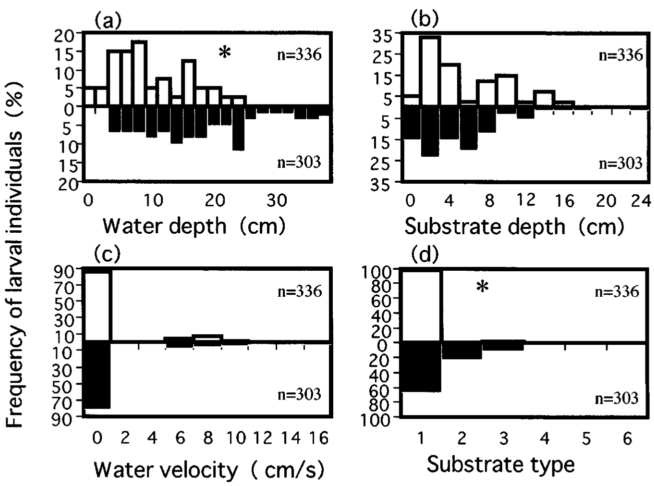

Fig. 4. Comparison of habitat use by groups of small (≤5 cm, *open bars*) and large (>5 cm, *solid bars*) *L. reissneri* larvae. *Numbers* in (**d**) indicate the following substrate types: *1*, sand; *2*, gravel; *3*, pebble; *4*, cobble; *5*, boulder; *6*, bedrock. *Asterisks* indicate a significant difference between the two size groups ($P < 0.05$; Mann–Whitney U test)

(Fig. 3). The index of water velocity indicated positive values for 0–10 cm/s and negative values for >10 cm/s (Fig. 3). The index of substrate particle size showed positive values for classes 1–2 and negative values for class 3 or larger (Fig. 3).

Comparison of habitat utilization between the small- and large-sized larvae revealed significant differences in water depth (Mann–Whitney U test, $z = -4.109$, $P < 0.001$) and substrate particle size ($z = -2.554$, $P < 0.05$). The large larvae appeared to occupy a wider depth range (0–38 cm) in the water column than the small larvae (0–24 cm) and also

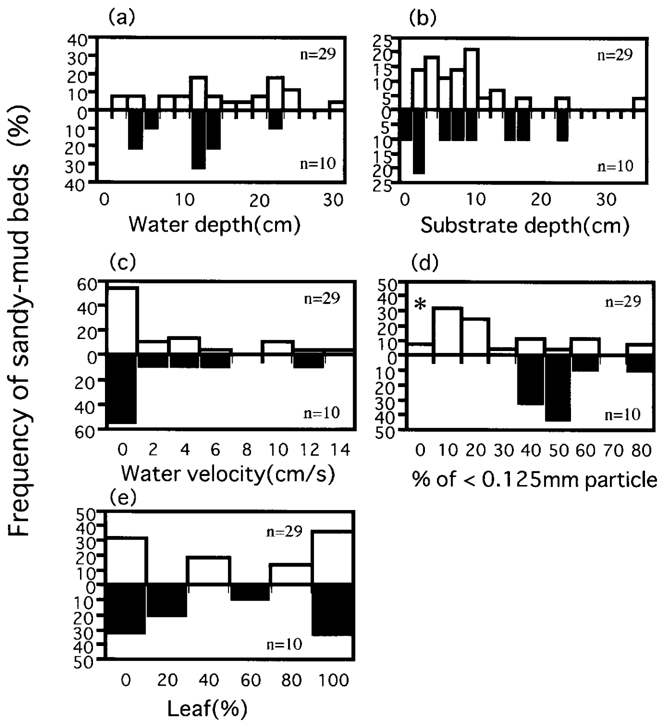

Fig. 5. Comparison of physical habitat variables [water depth (**a**), substrate depth (**b**), current velocity (**c**), substrate coarseness (**d**), and amount of fallen leaves (**e**)] in sandy-mud beds inhabited by small-sized *L. reissneri* larvae (≤5 cm) (*solid bars*) and uninhabited beds (*open bars*). *Asterisk* indicates a significant difference between beds ($P < 0.05$; Mann–Whitney U test)

to utilize a greater substrate particle size range (0–17 mm) than the latter (0–2 mm) (Fig. 4). However, no significant differences were found in substrate depth ($z = -8.16$, $P > 0.05$) and water velocity ($z = -0.190$, $P > 0.05$) (Fig. 4).

Of the 39 sandy-mud beds located in the study sites, only 10 were inhabited by small-sized larvae. On the other hand, large-sized larvae inhabited 22 beds. Comparison of five physical habitat variables (water depth, substrate depth, current velocity, substrate coarseness, and amount of fallen leaves) in the sandy-mud beds inhabited by the small larvae (≤5 cm) with those uninhabited revealed a significant difference in substrate coarseness (Mann–Whitney U test, $z = -2.702$, $P < 0.01$), an indication that the larvae selected beds composed of fine substrate particles (Fig. 5). However, no significant differences were found for water depth ($z = -0.997$, $P > 0.05$), substrate depth ($z = -0.338$, $P > 0.05$), current velocity ($z = -0.257$, $P > 0.05$), and amount of fallen leaves ($z = -0.129$, $P > 0.05$) (Fig. 5).

A similar comparison of physical habitat variables for the large-sized larvae (>5 cm) revealed significant differences in both water depth (Mann–Whitney U test, $z = 2.379$, $P < 0.05$) and substrate depth ($z = 2.393$, $P < 0.05$), an indication that the larvae selected beds in deep water with thick sandy-mud (Fig. 6). However, no significant differences were found for current velocity ($z = -0.085$, $P > 0.05$), substrate depth ($z = -0.991$, $P > 0.05$) and amount of fallen leaves ($z = -0.245$, $P > 0.05$) (Fig. 6).

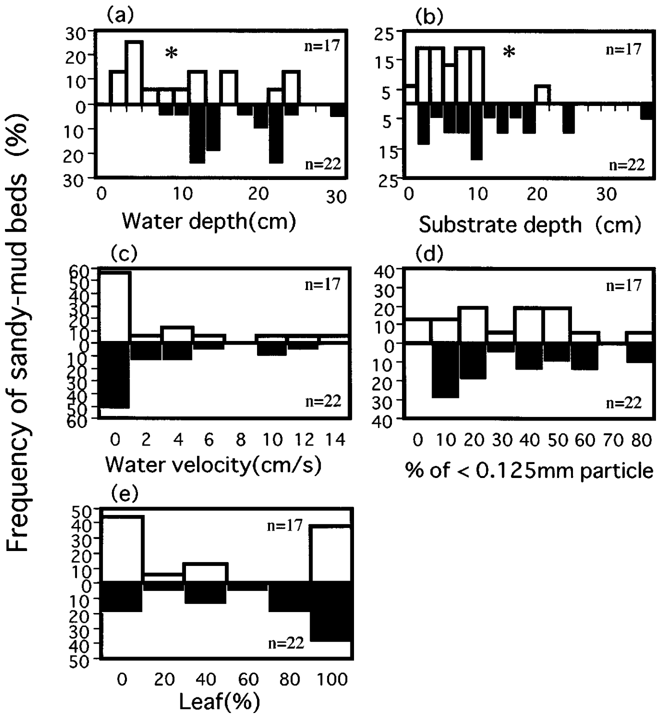

Fig. 6. Comparison of physical habitat variables in sandy-mud beds inhabited by large-sized *L. reissneri* larvae (>5 cm) (*solid bars*) and uninhabited beds (*open bars*). *Asterisks* indicate a significant difference between beds ($P < 0.05$; Mann–Whitney U test)

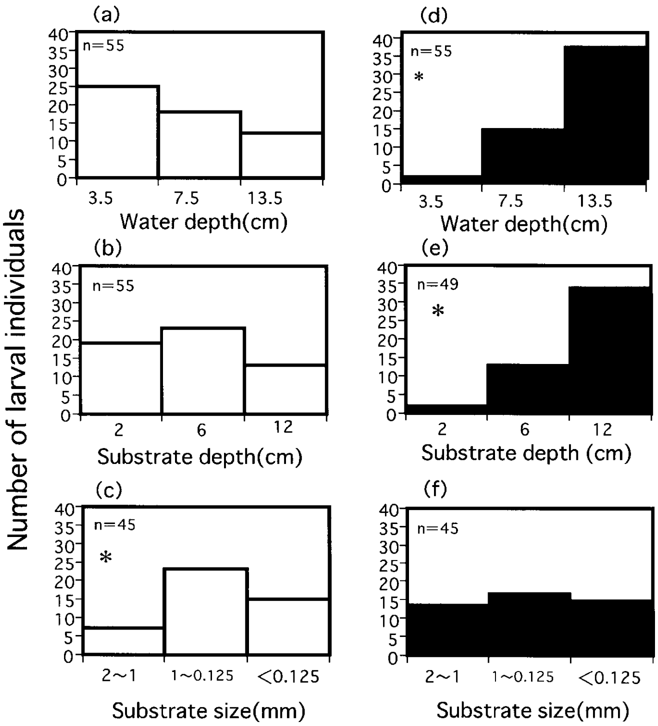

Fig. 7. Habitat selection by *L. reissneri* larvae for physical environmental factors [water depth (**a**), substrate depth (**b**), and substrate coarseness (**e**)] in an experimental aquarium. **a–c** Small-sized larvae (≤5 cm); **d–f** large-sized larvae (>5 cm). *Asterisks* indicate a significant difference among the three grades for each factor ($P < 0.05$; test for goodness-of-fit)

Habitat selectivity test in an experimental aquarium. Habitat selectivity tests were conducted for the following three physical environmental variables in an experimental aquarium: water depth, substrate depth, and substrate particle size. Small-sized larvae showed nonuniform distribution for different substrate particle sizes (chi-square test: $\chi^2 = 8.553$, $df = 2$, $P < 0.05$), although they showed a uniform distribution for both water ($\chi^2 = 4.618$, $df = 2$, $P > 0.05$) and substrate depth ($\chi^2 = 2.763$, $df = 2$, $P > 0.05$) (Fig. 7). They occupied the substrate comprising 1–0.125 mm particles more frequently than those with other particle sizes. On the other hand, the large-sized larvae showed nonuniform distributions for both water ($\chi^2 = 36.254$, $df = 2$, $P < 0.05$) and substrate depth ($\chi^2 = 32.367$, $df = 2$, $P < 0.05$), although they showed a uniform distribution for substrate particle size ($\chi^2 = 0.304$, $df = 2$, $P > 0.05$) (Fig. 7). They occupied a water depth of 13.5 mm and substrate depth of 12 cm more frequently than other water and substrate depths.

Discussion

The collection survey of lamprey larvae at study sites in the Monbetsu River of southeastern Hokkaido clearly revealed that ammocoetes of *Lethenteron reissneri* (northern form) were concentrated in sandy-mud beds, indicating that suitable habitats for *L. reissneri* larvae were restricted to sandy-mud bottoms as found for many other lamprey species (generally called ammocoetes beds) (Hardisty and Potter, 1971; Malmqvist, 1980; Young and Kelso, 1990; Beamish and Jebbink, 1994; Beamish and Lowartz, 1996).

The analysis based on Jacobs's electivity index showed that the lamprey larvae selectively utilized spaces in shallow water with weak currents, deep sandy-mud, and fine substrate particles. The comparison of habitat utilization between the small-sized and large-sized larval classes revealed that the latter utilized spaces with greater ranges of both water depth and substrate particle size than the former. This result suggests that *L. reissneri* larvae may change habitats between age 1 year and 2 years, the small-sized larvae (≤5 cm) corresponding closely to the size at age 1 and the large-sized larvae (>5 cm) to the size at age 2 years or older (Yamazaki, 1997). Similar size segregation for habitats has been found in *Geotria australis* ammocoetes in New Zealand streams (Kelso and Todd, 1993).

The results obtained from both the field survey and laboratory experiments on larval selectivity of physical environmental factors suggested that the particle-size composition of the substrate is one of the most important habitat variables for the small-sized larvae of *L. reissneri*, whereas both water depth and substrate depth are more important for large-sized larvae.

In fluvial fishes, body size is generally correlative with habitat depth, larger individuals inhabiting deeper-water areas, probably because of the greater ease of escape from predation by terrestrial animals such as carnivorous mammals and birds of prey (Power, 1987; Harvey and Stewart, 1991). Lamprey larvae remain hidden in burrows in sandy-mud bottoms in the daytime whereas at night they emerge from the burrow and move by swimming to search for more suitable habitats (Kelso, 1993). Such movements may involve a greater predation risk for larger individuals because these are more likely to be found by predators.

Furthermore, the body size of lamprey larvae is known to be correlative with burrow depth, as has been reported for the sea lamprey *Petromyzon marinus* (Applegate, 1950: Hardisty and Potter, 1971; Manion and McLean, 1971). Burrow depth for the latter lamprey is less than 13 mm for larvae of 2 cm total length, less than 25 mm for 3–4 cm larvae, between 50 and 80 mm for 5–9 cm larvae, and about 120 mm for 10–16 cm larvae (Applegate, 1950). Large-sized *L reissneri* larvae prefer deeper sandy-mud substrate than the small-sized ones. Such a preferential difference in habitat depth may be attributable to the difference in body size because larger individuals require deeper burrows for hiding their entire body.

The present field survey found no significant difference in the amount of fallen leaves on beds inhabited or uninhabited by lamprey larvae. Moore and Mallatt (1980) concluded for the European brook lamprey *Lampetra planeri* in North America that suitable larval habitats were little influenced by the amount of detritus available as food. This finding does not mean that detritus is not a prerequisite for a larval habitat but suggests that either only a small amount of detritus is sufficient as a food source or that sufficient detritus for larval food is usually deposited on every sandy-mud bed. In the case of *L. reissneri*, the larval diet consists mostly of detritus with a small amount of algae, which are located on or near the substrate surface (Miyadi et al., 1976). The amount of detritus consumed by the larvae is apparently low relative to the amount usually present on sandy-mud beds in meandering stream courses (Malmqvist et al., 1978). Therefore, it is unlikely that the amount of fallen leaves is a significant factor in habitat selection of *L. reissneri* larvae.

In Japan, *L. reissneri* is included as an endangered fish species for extinction on the list of threatened natural animals (Red List) published in 1999 (Environment Agency, Japan Government, 1999), owing to its remarkable population decrease and habitat loss in recent years. This status may be attributable, at least in part, to recent artificial changes to natural streams, including the shortening of meandering streamcourses and construction of dams and weirs (Tamai, 1993; Goto, 1997; Mori, 1998). A recent ecological study of the physical structure in a small stream revealed remarkable differences in complexity and diversity beween a natural meandering stream section and an artificially altered stream section (following straightening of the streamcourse by the placement of concrete blocks on both banks), there being significantly less variability in the latter section (Inoue and Nakano, 1994). In such simplified environments of gently sloping, artificially altered streamcourses, there may be very few if any suitable habitats for *L. reissneri* larvae because of the great loss of sandy-mud beds. Similar habitat losses for lamprey larvae may also have been induced by the construction of dams and weirs, which severely restrict the supply of sand and mud to downstream reaches (Maruyama, 1997). Therefore, the present identification of habitat characteristics suitable for *L. reissneri* larvae, indicating the importance of abundant sandy-mud beds with suitable substrate particle size and depth in natural streams, may be applicable in directing attempts at fluvial habitat restoration for conservation of this endangered lamprey species.

Further ecological studies are necessary for clarification of the significant physical environmental factors by which the abundance of *L. reissneri* larvae is determined and important spawning resources for adults.

Acknowledgments We thank Y. Yamazaki, Toyama University, for his invaluable advice and suggestions. Special thanks are due to R. Wada, Hokkaido University, for his advice on the design of the field survey and assistance with fieldwork. T. Sonoda, K. Koga, T. Nagai, and M. Oda, Hokkaido University, are thanked for helpful advice and assistance with fieldwork, and G. Hardy is specially thanked for invaluable comments to our manuscript and correcting English.

Literature Cited

Andrews C (1990) The ornamental fish trade and fish conservation. J Fish Biol 37A:53–59

Applegate VC (1950) Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. Spec Sci Rep US Fish Wildl Serv 55:1–237

Bain MB, Finn JT, Bookel HE (1985) Quantifying stream substrate for habitat analysis studies. N Am J Fish Manag 5:499–506

Beamish FWH, Jebbink JA (1994) Abundance of lamprey larvae and physical habitat. Environ Biol Fish 39:209–214

Beamish FWH, Lowartz S (1996) Larval habitat of American brook lamprey. Can J Fish Aquat Sci 53:693–700

Bruton M (1995) Have fishes had their chips? The dilemma of threatened fishes. Environ Biol Fish 43:1–27

Environment Agency, Japan Government (1999) The red list of brackish water and freshwater fishes in Japan. http://www.eic.or.jp/eanet/redlistS/red4.html

Goto A (1997) Natural environments in Japanese rivers with reference to the conservation of diversity in freshwater fishes (in Japanese). Wild Forum 2:127–133

Hardisty MW, Potter IC (1971) The behaviour, ecology and growth of larval lampreys. In: Hardisty MW, Potter IC (eds) The biology of lampreys, vol 1. Academic Press, London, pp 85–125

Harvey BC, Stewart AJ (1991) Fish size and habitat depth relationships in headwater streams. Oecologia (Berl) 87:336–342

Inoue M, Nakano S (1994) Physical environment structure of a small stream with special reference to fish microhabitat (in Japanese with English summary). Jpn J Ecol 44:151–160

Jacobs J (1974) Quantitative measurement of food selection: a modification of the forage ratio and Ivlevs electivity index. Oecologia (Berl) 14:413–417

Kani T (1944) Ecology of the aquatic insects inhabiting a mountain stream (in Japanese). In: Furukawa H (ed) Insects I. Kenkyu-sha, Tokyo, pp 171–317

Kappus B, Jansen W, Fok P, Rahmann H (1995) Threatened lamprey (*Lampetra planeri*) populations of the Danube basin within Baden-Wurttemberg, Germany. Misc Zool Hung 10:85–98

Kelso JRM (1993) Substrate selection by *Geotria australis* ammocoetes in the laboratory. Ecol Freshw Fish 2:116–120

Kelso JRM, Todd PR (1993) Instream size segregation and density of *Geotria australis* ammocoetes in two New Zealand streams. Ecol Freshw Fish 2:108–115

Maitland PS (1994) Conservation of freshwater fish in Europe. Nature and environment, vol 66. Council of Europe Press, Strasbourg, pp 1–50

Malmqvist B (1980) Habitat selection of larval brook lamprey (*Lampetra planeri*, Bloch) in a South Sweden stream. Oecologia (Berl) 45:35–38

Malmqvist B, Nillson LM, Svensson BS (1978) Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal communities. Oikos 31:3–16

Manion PJ, McLean AL (1971) Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Garlic River, Michigan. 1960–1965 Great Lakes fishes. Comm Tech Rep 16:1–35

Maruyama T (1997) River engineering for the coexistence with fish (in Japanese). In: Nagata Y, Hosoya K (eds) Circumstances in endangered Japanese freshwater fishes and their protection. Midorishobou, Tokyo, pp 167–180

Miyadi D, Kawanabe H, Mizuno N (1976) Color illustrations of the freshwater fishes of Japan, 3rd edn (in Japanese). Hoikusha, Osaka

Moore JW, Mallatt JM (1980) Feeding of larval lampreys. Can J Fish Aquat Sci 37:1658–1664

Mori S (1998) The present status for concerning the nature of rivers and the perspectives (in Japanese). In: Mori S (ed) Aquatic environments viewed from fishes: toward restoration ecology—River version. Shinzan-sha Scitech, Tokyo, pp 3–11

Moyle PB, Williams JE (1990) Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conserv Biol 4:275–284

Pollard DA, Ingram BA, Harris JH, Reynolds LF (1990) Threatened fishes in Australia—an overview. J Fish Biol 37A:67–78

Power ME (1987) Predator avoidance by grazing fishes in temparate and tropical streams: importance of stream depth and prey size. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 333–351

Primack PB (1995) A primer of conservation biology (Japanese translation by Kobori H, 1997). Bun-ichi sougoushuppan, Tokyo

Regier HA, Meisner JD (1990) Anticipated effects of climate change on freshwater fishes and their habitat. Fisheries (Bethesda) 15:10–15

Renaud CB (1997) Conservation status of Northern Hemisphere lampreys (Petromyzontidae). J Appl Ichthyol 13:143–148

Tamai N (1993) Rivers and their environments (in Japanese). In: Tamai N, Mizuno N, Nakamura S (eds) Environmental river enginering. Tokyo University Press, Tokyo, pp 1–7

Washitani I, Yahara T (1996) An introduction to conservation biology: from gene to landscape (in Japanese). Bun-ichi sougoushuppan, Tokyo

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377–392

Yamazaki Y (1997) Genetic differentiation and morphological, life-history and reproductive characteristics of *Lethenteron* taxa from the Far East. Doctoral dissertation, Hokkaido University, Sapporo

Yamazaki Y, Goto A (1996) Genetic differentiation of *Lethenteron reissneri* populations, with reference to the existence of discrete taxonomic entities. Ichthyol Res 43:283–299

Yamazaki Y, Goto A (1997) Morphometric and meristic characteristics of two groups of *Lethenteron reissneri*. Ichthyol Res 44:15–25

Yamazaki Y, Goto A (1998) Genetic structure and differentiation of four *Lethenteron* taxa from the Far East, deduced from allozyme analysis. Environ Biol Fish 52:149–161

Yamazaki Y, Goto A (2000a) Present status and perspectives on the phylogenetic systematics and speciation of lampreys (in Japanese with English abstract). Jpn J Ichthyol 47:1–28

Yamazaki Y, Goto A (2000b) Breeding season and nesting assemblages in two forms of *Lethenteron reissneri*, with reference to reproductive isolating mechanisms. Ichthyol Res 47:271–276

Young RJ, Kelso JRM (1990) Occurrence, relative abundance, and size of landlocked sea lamprey (*Petromyzon marinus*) ammocoetes in relation to stream characteristics in the Great Lakes. Can J Fish Aquat Sci 47:1773–1778