Habitat Characteristics Influencing Distribution of the Freshwater Mussel Pronodularia japanensis and Potential Impact on the Tokyo Bitterling, Tanakia tanago

ZOOLOGICAL SCIENCE **27**: 912–916 (2010)

Habitat Characteristics Influencing Distribution of the Freshwater Mussel *Pronodularia japanensis* and Potential Impact on the Tokyo Bitterling, *Tanakia tanago*

Yoshihiro B. Akiyama* **and Takashi Maruyama**

Department of Aquatic Bioscience, Tokyo University of Fisheries, 4-5-7, Konan, Minato-ku, Tokyo 108-8477, Japan

The physical habitat characteristics associated with spatial distribution patterns of the freshwater mussel *Pronodularia japanensis*, which is used for oviposition by the Tokyo bitterling *Tanakia tanago*, were investigated in a small stream within a Tokyo bitterling protected area. The distribution of the mussels was found to be in an under-dispersed, non-random spatial pattern. Mussel occurrence correlated negatively with sediment softness, and positively with flow velocity, while mussel abundance was associated negatively with sediment softness and positively with sediment type (particle size). Furthermore, mussels were scarce in riverbed areas with a lack of sediment. These correlations suggest that the population dynamics of mussels and Tokyo bitterling may be influenced by changes in stream sediment conditions. To conserve the symbiosis between Tokyo bitterlings and mussels, a suitable benthic environment is required.

Key words: sediment softness, sediment type, symbiosis, conservation, Unionidae

INTRODUCTION

The Tokyo bitterling *Tanakia tanago* (Tanaka), a cyprinid that lives only in the Kanto district of Japan (Nakamura, 1969; Taki et al., 1994), uses freshwater mussels of the order Unionoida, such as *Pronodularia japanensis* (Lea), for their oviposition sites (Toida, 1988; Suguro, 1998 ; Hatakeyama and Akiyama, 2007). Accordingly, Tokyo bitterlings cannot reproduce in areas without unionid mussels, leading to population declines. Tokyo bitterlings were once widely distributed in the Kanto district; however, many populations were lost in the latter half of the 20th century. The cause of these extirpations is poorly understood, as the occurrences were not investigated at the time. In other bitterling species, however, the causes for their decline is reported to be the decreased abundance of mussels for oviposition (Reichard et al., 2004). The number of mussels available for oviposition constrains the total number of eggs spawned by females. Therefore, factors affecting mussel population dynamics are thought to influence the bitterling population. It has been reproted that the distribution of freshwater mussels, which depends on landscape attributes (Vaughn and Taylor, 2000), is influenced by physical environmental factors (Negus, 1966; Way et al., 1989), and that such factors may also result in a decrease of bitterling populations. In the present study, environmental factors affecting the population of *P. japanensis* were determined.

* Corresponding author. Phone: +81-52-789-4250;
E-mail: akiyama.yoshihiro@h.mbox.nagoya-u.ac.jp
doi:10.2108/zsj.27.912

MATERIALS AND METHODS

Study area

Sampling was performed in a protected area for *T. tanago* and *P. japanensis* in Ohtawara City, Tochigi Prefecture, central Japan. The protected area consists of a 4 ha pond and a small stream (Fig. 1). The pond is surrounded by deciduous broad-leaved forest. The pond water flows into the stream, which flows through rice paddies, coniferous and broad-leaved forests, and into a marsh. The stream is 750 m long with a 0.84 m mean wetted width (range 0.3–1.6 m). Part of the upper portions of the stream banks is protected with bamboo logs.

T. tanago, and bivalves including *P. japanensis*, *Corbicula* sp. (probably *C. leana* (Prime): Komaru A. 2004, personal communication) and *Anodonta* sp. were observed in the stream on October 24th, 2001. Although annual investigations have been performed, *T. tanago* has not been found in the stream since 2002 (Kaga and Oda, 2005, 2006; Oda, 2005; Sakai and Doi, 2007; Sakai et al., 2008, 2009). Meanwhile, *P. japanensis* has been observed in later years, but the rate of juvenile mussels has gradually decreased (Kaga and Oda, 2006; Sakai and Doi, 2007). The presence of *T. tanago* and *P. japanensis* was restricted to the stream. Corbiculids are not used as an oviposition site for bitterlings in Japan (Kihira, 1977; Fukumoto et al., 2008). *Anodonta* sp. was mainly present in the pond, and rarely observed in the stream. Periodically, within the protected area, accumulated mud on the streambed is removed and weeds on the banks are cut for agricultural purposes. *P. japanensis* dug up with the mud were released into the sampling location. The removal of accumulated mud was carried out for agricultural management only in March every year.

Field data collection

Our research was carried out from 4 to 21 October 2001, seven months after the removal of accumulated mud from the streambed. The short-term effects of removal of accumulated mud on mussel distribution and mussel habitats were not considered major, given the length of time between mud removal and our research. Seventy-five sampling stations (total area 3 m^2) were established in the stream at 10 m intervals except for the location 370 m downstream from the uppermost research station, indicated by the arrow in the right-hand map in Fig. 1, which is a narrow closed conduit. A small iron frame (0.2 m × 0.2 m × 0.3 m) was placed on the stream substrate at a randomly selected point from the right, center, and left side of each station.

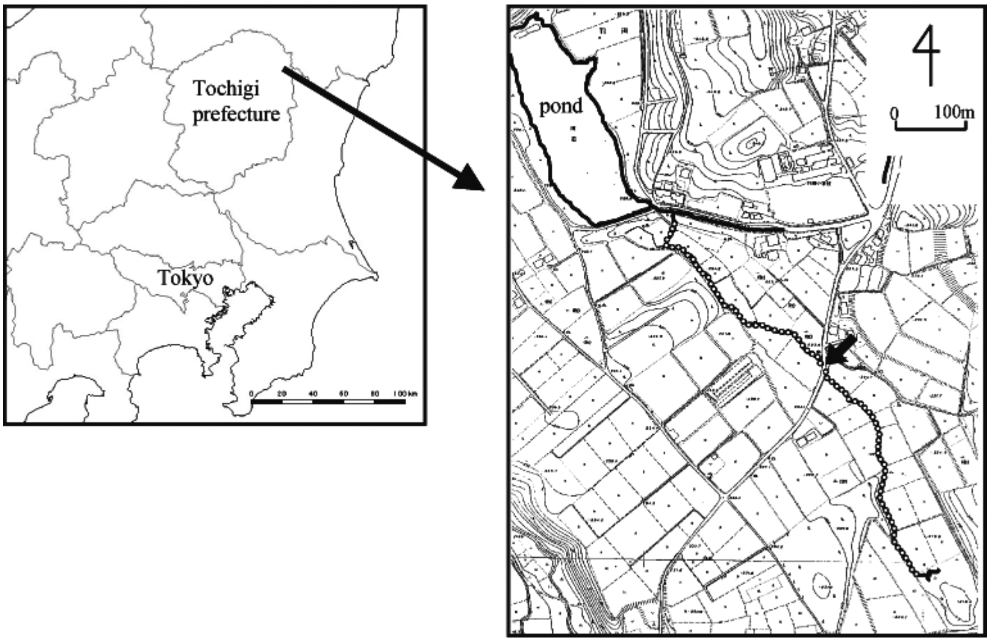

Fig. 1. Study site in the northern region of Tochigi Prefecture in central Japan. Seventy-five open circles and an arrow in the right figure indicate sampling stations, and the location of a narrow closed conduit, respectively.

To account for environmental factors affecting mussel distribution, the type of terrestrial landscape surrounding mussel habitat needs to be considered, as the landscape exerts a large influence on stream structure and function, and thus the distribution of stream organisms (Allan, 1995) including freshwater mussels (Vaughn and Taylor, 2000) as well. The longitudinal characters of the stream were divided into upper, middle, and lower reaches based on riverbank landscape. The range of the upper reach was between 0 to 210 m from the uppermost station, located along the edge of the forest. The middle reach ranges between 220 and 570 m from the uppermost station. This section is surrounded by paddy fields. The lower reach is located between 580 and 750 m, along the edge of the forest as in the upper reach, but in this section sluggish flow is dominant. These reach types were qualitatively coded, i.e. upper reach (1), middle reach (2) and lower reach (3), and were used for statistical analyses described below. The average water depth from four measurements at four corners of a quadrate, flow velocity just above the riverbed, sediment softness, and sediment type were measured at the center of each quadrate. Flow velocity was measured five times with a current meter (Kosumo-Rikken, Osaka, Japan) and averaged. Sediment softness was determined by immersing an aluminum bar (φ 8.5 mm) into the sediment with a downward pressure of 1 kg at the top of the bar. This method is very similar to the method in Kakino and Mizutani (2008) for evaluating the benthic habitats of the unionid mussel, *Inversiunio jokohamensis* (Kobelt). Although the diameter of the bar in our method is different from that of Kakino and Mizutani (2008) using a bar (φ 7.4 mm), our method is effective for measuring the benthic habitat for mussels. Riverbed surface sediment type was visually observed and qualitatively coded into three categories, i.e. mud (1), sand (2), and pebble (3). To collect mussels, the iron frame was inserted into sediment and all substrates to a 10 cm depth inside the frame were collected and sieved with a 1 cm mesh size strainer, as *P. japanensis* can be found in depths of up to 5 cm of sediment (Onitsuka T, 2000, unpublished data). The number of mussels in the sample was counted, and shell lengths were measured with a vernier caliper. Sampling was performed from downstream to upstream stations, consecutively. Water temperature varied from 14.6 to 17.6°C during the research period, and no marked environmental changes within the protective area were observed.

Statistical analyses

Morisita's index of dispersion (I_δ) was used to determine the spatial pattern of mussel distribution (Morisita, 1959). If individuals are randomly distributed within the plot, $I_\delta = 1$; however, if individuals are distributed in clumps or patches (under-dispersed), $I_\delta > 1$, while if individuals are uniformly distributed (hyper-dispersed), $I_\delta < 1$. The significance of bias from distribution randomness was tested by *F*-test (Morisita, 1959), with $p < 0.05$ considered to be statistically significant. Generalized linear mixed models (GLMMs, McCullagh and Nelder, 1989) were used to assess environmental variables affecting mussel distribution. GLMMs are an extension to generalized linear models (GLMs) in which the linear predictor accounts for random effect in addition to the usual fixed effects. The code of longitudinal reach type was used as random effect parameter in GLMMs. To analyse the relationship between mussel occurrence and environmental variables, GLMMs with binomial error distribution assumption and a logit-link function were used, whereas for the relationship between mussel abundance and environmental variables, GLMMs with a Poisson error assumption and a log-link function were used. Variance inflation factors (VIFs) were determined to check the presence of multicollinearity. High VIF values (> 10) indicate multicollinearity between variables (Quinn and Keough, 2002), and these were removed from the list of explanatory variables. A dispersion parameter, which was available residual deviance divided by the residual degrees of freedom, was used for detecting the presence of overdispersion (Crawley, 2007). Values of the dispersion parameters for GLMMs were 1.050 for the binomial error model, and 2.378 for the Poisson error model. Although the former was nearly 1, the latter was much greater than 1, which shows overdispersion of residual deviance. Accordingly, we chose variables based on Akaike's information criterion (AIC, Akaike, 1974) for GLMMs with binomial error and the quasi-Akaike's information criterion (QAIC; Lebreton et al., 1992), which is a modification of AIC for model selection when residual deviance is over-dispersed (Burnham and Anderson, 2002; Richards, 2008), was used for GLMMs with Poisson error. The model with the lowest AIC or QAIC score is most likely to best represent the data. AIC or QAIC of models were calculated and models with ΔAIC or ΔQAIC < 2 were selected. We used the R.2.5.1 (R Development Core Team, 2007) and glmmML package for R (Brostrom, 2006) for the analyses.

RESULTS

P. japanensis was observed at 27 of the 75 stations, and 79 individuals were collected. Mussels were mainly distributed in upstream and downstream portions of the stream. The mean density was 26.3 individuals m^{-2} (0–525). Morisita's index was 6.96; the mussels were therefore considered to be distributed in patches ($F = 7.28$, $p < 0.01$). The mussels were principally clumped the transitional area between riffle and pool. The shell length of the collected mussels ranged from 10 to 74 mm (Fig. 2).

Median and ranges of water depth and velocity, as well as sediment softness within the stream for all stations and for stations in which *P. japanensis* was found are presented in Table 1. Mud, sand, and pebble substrata were observed at 15, 42, and 18 stations, respectively. The range of sediment softness in which *P. japanensis* were observed was more restricted than that in all sites (Table 1). Suitable hard sediment for mussels (≤ 12.4 cm) was more dominant in the upper stream and accounted for 100%, 72%, and 65% in upper, middle and lower reaches. The VIFs of all measured variables were < 10, i.e. water velocity, 1.290; water depth, 1.138; sediment softness, 1.238; sediment type, 1.159, and thus all these variables were included as explanatory variables in model selection. Four models for the occurrence of mussels and three models for their abundance of were selected (Tables 2, 3). Sediment softness was the best predictor in the variables applied to GLMMs for the occurrence of the mussels because it was selected only in all models (Table 2). Flow velocity, which remained in three of four fitting models, represented the second best predictor. Sediment softness negatively correlated with the occurrence of the mussels. In contrast, flow velocity positively correlated with mussel occurrence. In other words, the probability of the mussel occurrence was low in areas with slower water flow and thickly accumulated sediments on the bottom of the stream. In fact, the mussels were not observed in areas where the thickness of accumulated sediments on the bottom of the stream was > 13 cm (Fig. 3A). However, mussels were scarce in areas where accumulated sediment layer on the streambed was very thin or absent (Fig. 3A). In terms of flow velocity, a positive relationship to mussel occurrence could be found, but was weak (Fig. 3B). Meanwhile, sediment type and sediment softness were the best and the second-best predictors in the fitting models for the abundance of the mussels, as the former was selected in all fitting models and the latter was selected in two of three (Table 3). Sediment type correlated positively with the abundance of the mussels, while sediment softness correlated negatively. Mussels were scarce in areas with small particle size sediments, or thickly accumulated sediments on the stream bottom (Fig. 3A, C).

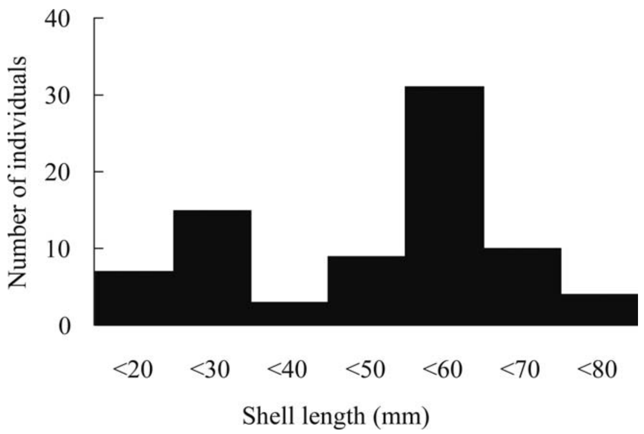

Fig. 2. Size frequency of *Pronodularia japanensis* in the study area.

Table 1. Observed ranges of physical environmental variables.

	All sites			Sites with *P. japanensis*		
	Median	95% CI	Range	Median	95% CI	Range
Water depth (cm)	11	5–22	5–28	12	6–18	5–19
Velocity (cm/s)	16	7–28	4–36	17	8–31	6–36
Sediment softness (cm)	7.6	1.1–30.8	0–40.9	4.9	1.3–11.6	0–12.4

Table 2. Regression coefficients ± SE for the fitted models with ΔAIC < 2 predicting the occurrence of *Pronodularia japanensis* based on flow velocity, water depth, sediment softness, and sediment type (particle size of sediment) using GLMMs with a binomial error and logit link.

ΔAIC	Velocity	Water depth	Sediment softness	Sediment type	Intercept
0	0.085 ± 0.054		–0.131 ± 0.065		–1.082 ± 1.268
0.667			–0.159 ± 0.063		0.578 ± 0.618
1.429	0.100 ± 0.059	0.062 ± 0.083	–0.127 ± 0.064		–2.117 ± 1.893
1.986	0.086 ± 0.056		–0.134 ± 0.067	–0.061 ± 0.512	–0.968 ± 1.583

Table 3. Regression coefficients ± SE for the fitted models with ΔQAIC < 2 predicting the abundance of *Pronodularia japanensis* based on flow velocity, water depth, sediment softness, and sediment type (particle size of sediment) using GLMMs with a Poisson error and log link.

ΔQAIC	Velocity	Water depth	Sediment softness	Sediment type	Intercept
0			–0.055 ± 0.027	0.821 ± 0.212	–1.514 ± 0.680
1.365		0.051 ± 0.037	–0.054 ± 0.027	0.822 ± 0.213	–2.126 ± 0.852
1.816				0.970 ± 0.203	–2.238 ± 0.613

DISCUSSION

Various sizes of mussels, including small juveniles, were collected in the study area. This suggests that the mussels had reproduced in previous years and that mussels of various ages survived, indicating that the stream is a suitable habitat for the mussels. *P. japanensis* were found in clumped or under-dispersed distributions. In a previous study, mussels were also reported to be unevenly distributed (Kitamura, 2007). One of the causes of the patchy distribution of mussels is the condition of the streambed sediment. The distribution of freshwater mussels has been reported to be influenced by sediment condition, flow velocity, water depth, wetted riverbed width, and canopy (Neves and Widlak, 1987; Hastie et al., 2000; Johnson and Brown, 2000; Stone et al., 2004). In our study, canopy was not

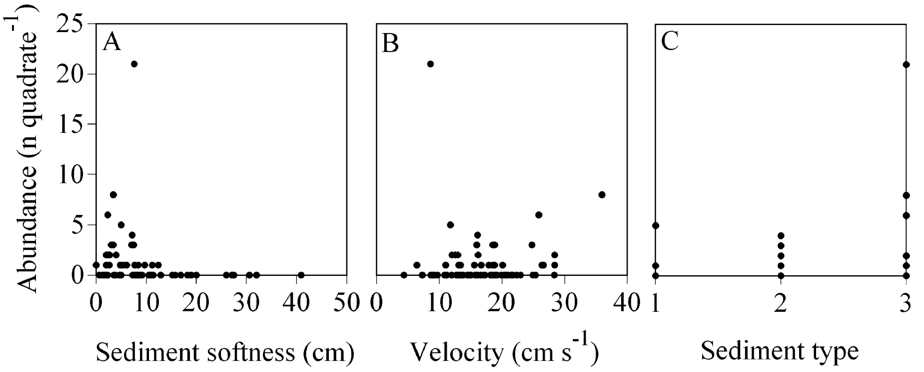

Fig. 3. Scatter-plots of abundance of *Pronodularia japanensis* against sediment softness **(A)**, flow velocity **(B)** and surface sediment type **(C)** in the study area. The codes of sediment type indicate mud (1), sand (2), and pebble (3) for each quadrate.

evaluated as most trees were defoliating during the research period, and we could not discriminate between the presence and absence of canopy. In these factors, sediment condition has been reported to significantly influence the distribution of many mussel species (Harman, 1972; Box and Mossa, 1999; Hastie et al., 2000). In our study area, the range of the habitat occupied by *P. japanensis* was limited by sediment softness rather than flow velocity. Accordingly, the abundance of the mussels decreased with the increasing softness of the riverbed substrate, and with the accumulation of fine or sediment, or the lack of sedimentation. These results suggest that sediment condition is one of the significant factors for the habitat of the mussels and that the preferable sediment condition for the mussels, i.e., hard pebbly sediment, could be often found in the area with narrow stream width and rapid flow over hard sediment. This concurs with other studies reporting that sediment type affects the abundance of mussels. Kondo (1998) showed that the density of *P. japanensis* decreased with a reduction of sediment particle size similar to the results of the present study, but that study does not clarify the relationship between thickness of accumulated fine sediment and mussel abundance. Fine substrate sediments have been reported to increase the mortality rate in some freshwater mussel species (Ellis, 1936). The mortality rates of four freshwater mussel species, *Lampsilis teres* (Rafinesque), *Obliquaria reflexa* (Rafinesque), *Quadrula quadrula* (Rafinesque) and *Q. metanevra* (Rafinesque), are reported to be very low for those that live in areas with little silt, but their mortality rate is ≥ 90% when a silt layer permanently covers the sand or gravel (Ellis, 1936). The result of this experiment demonstrates that mortality is influenced by not only sediment particle size but also sediment softness, as substrate covered with silt could be assumed to be softer than substrate with little silt. Moreover, sediment condition may also influence the population dynamics of *T. tanago*, as the rate of bitterling reproductive success depends on the number of mussels. The total number of eggs spawned by female bitterlings has shown to be constrained by the number of mussels available for oviposition (Reichard et al., 2004). Furthermore, fine sediments can clog the gills of mussels (Ellis, 1936) and interfere with filter feeding (Kat, 1982; Aldridge et al., 1987), thereby decreasing the flow rate of water through the mussels and affecting the embryonic development of bitterlings due to a lack of oxygen (Kamler, 1992; Aldridge, 1999). For the preservation of symbiosis between bitterlings and mussels, a suitable benthic environment as well as adequate water quality and food resources for both animals, and the presence of host fish for mussels, are all required. However, the method by which sediment condition influences *P. japanensis* was not clear in the present study. Hence, a laboratory experiment regarding the effects of sediment on mussels, i.e. an experiment on the relationship between sediment size and abundance and the physiological responses of mussels is required to assist in the conservation and restoration of *T. tanago*.

ACKNOWLEDGMENTS

We thank N. Oda, M. Hoshino, and N. Koizumi for their cooperation in the field, T. Itoh, D. Uenoyama, and Y. Yoshida for research assistance, Dr A. Komaru for identification of *Corbicula* sp., T. Ikeda for the correction of English grammar, and Dr T. Iwakuma for helpful comments on the manuscript. The study complies with the current laws of Japan.

REFERENCES

Akaike H (1974) A new look at the statistical model identification. IEEE Automat Contr 19: 716–723

Aldridge DC (1999) Development of European bitterling in the gills of freshwater mussels. J Fish Biol 54: 138–151

Aldridge DW, Payne BS, Miller AC (1987) The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. Environ Pollut 45: 17–28

Allan JD (1995) Stream ecology: Structure and function of running waters. Chapman and Hall, London

Box JB, Mossa J (1999) Sediment, land use, and freshwater mussels: prospects and problems. J N Am Benthol Soc 18: 99–117

Brostrom G (2006) glmmML: Generalized linear models with clustering. R package version 0.65–5

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York

Crawley MJ (2007) The R book. John Wiley & Sons Ltd, Chichester, England

Ellis MM (1936) Erosion silt as a factor in aquatic environments. Ecology 17: 29–42

Fukumoto K, Suguro N, Maruyama T (2008) An experimental study of the roles of *Pronodularia japanensis* and *Corbicula* spp. as hosts of *Tanakia tanago* in the Handa Miyakotanago (*Tanakia tanago*) protection area. Jap J Conserv Ecol 13: 47–53 (in Japanese)

Harman WN (1972) Benthic substrates: Their effect on fresh-water mollusca. Ecology 53: 271–277

Hastie LC, Boon PJ, Young MR (2000) Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L.). Hydrobiol 429: 59–71

Hatakeyama R, Akiyama N (2007) Annual reproductive cycle of a bitterling, *Tanakia tanago*, reared in an outdoor tank. Zool Sci 24: 614–622

Johnson PD, Brown KM (2000) The importance of microhabitat factors and habitat stability to the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad). Can J Zool 78: 271–277

Kaga T, Oda N (2005) Establishment of the technology to conserve and propagate rare fishes: investigation of Tokyo bitterling abundance. Bull Tochigi Pref Fish Exp Sta 48: 29–36 (in Japanese)

Kaga T, Oda N (2006) Establishment of the technology to conserve and propagate rare fishes: investigation of Tokyo bitterling abundance. Bull Tochigi Pref Fish Exp Sta 49: 32–39 (in Japanese)

Kakino W, Mizutani M (2008) Influence of habitat environment on the distribution of the freshwater unionid mussel *Inversiunio jokohamensis* in hill-bottom valley ditches. Trans JSIDRE 255: 83–86 (in Japanese with English abstract)

Kamler E (1992) Early life history of fish: an energetics approach. Chapman & Hall, London

Kat PW (1982) Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia: Unionidae). Malacol Rev 15: 119–127

Kihira H (1977) Bitterlings and freshwater mussels. Freshwater Fish 3: 94–99 (in Japanese)

Kitamura J (2007) Reproductive ecology and host utilization of four sympatric bitterling (Acheilognathinae, Cyprinidae) in a lowland reach of the Harai River in Mie, Japan. Env Biol Fishes 78: 37–55

Kondo T (1998) Freshwater mussel community in an irrigation channel. In “The Conservation of Waterfront Environment” Ed by Y Ezaki, T Tanaka, Asakura-Shoten, Tokyo pp 80–92 (in Japanese)

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62: 67–118

McCullagh P, Nelder JA (1989) Generalized Linear Models, 2nd ed. Chapman & Hall, New York

Morisita M (1959) Measuring of dispersion of individuals and analysis of the distributional patterns. Mem Facul Sci Kyushu Univ Ser E 2: 215–235

Nakamura M (1969) Cyprinid Fishes of Japan. Research Institute of National Resource, Tokyo (in Japanese)

Negus CL (1966) A quantitative study of growth and production of unionid mussels in the River Thames at reading. J Anim Ecol 35: 513–532

Neves RJ, Widlak JC (1987) Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. Am Malacol Bull 5: 1–7

Oda N (2005) Tokyo bitterling: The beautiful fish called “Osharakubuna”. In “Present and future of rare fishes: Scenario of reactive conservation” Ed by O Katano, S Mori, Shinzansha, Tokyo, pp 168–176 (in Japanese)

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. The Press Syndicate of the University of Cambridge, Cambridge, UK

R Development Core Team (2007) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reichard M, Jurajda P, Smith C (2004) Male-male interference competition decreases spawning rate in the European bitterling (*Rhodeus sericeus*). Behav Ecol Sociobiol 56: 34–41

Richards SA (2008) Dealing with overdispersed count data in applied ecology. J Appl Ecol 45: 218–227

Sakai T, Doi T (2007) Establishment of the technology to conserve and propagate rare fishes: investigation of Tokyo bitterling abundance. Bull Tochigi Pref Fish Exp Sta 50: 54–56 (in Japanese)

Sakai T, Kubota H, Yoshida Y (2008) Investigation of aquatic organisms including rare fishes: investigation of Tokyo bitterling abundance. Bull Tochigi Pref Fish Exp Sta 51: 25–27 (in Japanese)

Sakai T, Kubota H, Yoshida Y (2009) Investigation of aquatic organisms including rare fishes: investigation of Tokyo bitterling abundance. Bull Tochigi Pref Fish Exp Sta 52: 34–35 (in Japanese)

Stone J, Barndt S, Gangloff M (2004) Spatial distribution and habitat use of the western pearlshell mussel (*Margaritifera falcata*) in a Western Washington Stream. J Freshwater Ecol 19: 341–352

Suguro N (1998) Metropolitan bitterling breeding net preserve trial in the outdoor ponds. Bull Kanagawa Pref Fish Res Inst 3: 93–101 (in Japanese)

Taki Y, Michizuki K, Akiyama N, Nakamura T, Suguro N, Nagano M, Tanaka S, Kohno H (1994) Tokyo bitterling. In “Basic Data of Rare Wild Aquatic Organisms in Japan” Ed by Fisheries Agency of Japan, Japan Fisheries Resource Conservation Association, Tokyo, pp 364–371 (in Japanese)

Toida S (1988) The examination for the conservation of *Tanakia tanago*. Bull Kanagawa Pref Freshwater Fish Breed 24: 21–22 (in Japanese)

Vaughn CC, Taylor CM (2000) Macroecology of a host-parasite relationship. Ecography 23: 11–20

Way CM, Miller AC, Payne BS (1989) The influence of physical factors on the distribution and abundance of freshwater mussels (Bivalvia: Unionidae) in the lower Tennessee River. Nautilus 103: 96–98

(Received December 4, 2009 / Accepted June 15, 2010)