



Spatial distribution and habitat preferences of the Japanese eel, *Anguilla japonica*, at the reach and channel-unit scales in four rivers of Kagoshima Prefecture, Japan

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Abstract

Catches of Japanese eels have been decreasing at an alarming rate and extinction of wild stocks is of concern. Therefore, conservation of eel habitats has become increasingly important. Here, we analyzed the habitat preferences of Japanese eels using generalized linear models from the relationships between presence/absence or population density with physical environmental factors. The models suggested the characteristics of preferred habitats that should be conserved. In the tidal reaches, the densities of small eels (< 255 mm total length) at the reach scale (generally channel width $\times 10^1$ in flow direction) were only correlated with riverbed gradient, with densities decreasing with increasing gradients. Within the low-gradient reaches, small eels appeared at shallow depths (about 15–30 cm) and slow-flow runs at the channel-unit scale (generally channel width $\times 10^0$ in flow direction) and their preferred substrate type was gravel (< 100 mm). The densities of large eels (≥ 255 mm total length) at the reach scale were only correlated with the percentage of concrete revetment along shoreline, with their densities decreasing with increasing revetment shoreline. At the channel-unit scale, the densities of large eels were correlated only by predominant substrate type, and they appeared to prefer rock (≥ 100 mm). Few small eels were found in the non-tidal reaches; therefore, their habitat preferences were not analyzed there. By contrast, large eels were frequently distributed at the lower riverbed gradient reaches. At the channel-unit scale, the densities of large eels increased with water depth and their preferred substrate type was rock. These habitat preferences suggest diversification of habitat with growth and difference in the preferred substrate type depending on body size at the channel-unit scale. These results indicated that various environments in rivers should be preserved. In addition, we suggest the necessity to restore habitats affected by revetment. Eel habitat preferences, especially in the non-tidal reaches, also will contribute to determining what kind of cross-river structures affect eel distribution in rivers.

Keywords Freshwater eel · Habitat · Environment · Conservation · GLM

Introduction

Japanese eel, *Anguilla japonica*, is a facultative catadromous fish that spawns in the area along the West Mariana Ridge (Tsukamoto and Arai 2001; Chow et al. 2008; Kurogi et al. 2011; Tsukamoto et al. 2011) and spends most of their life (5–17 years) in riverine and coastal habitats around East Asia as the “yellow eel” until maturation (Matsui 1972; Kotake et al. 2007). This anguillid species is an important food fish

for commerce in Japan and other East Asian countries, but fishery catches of eels in rivers have declined severely since the 1970s (Fisheries Agency of Japan 2018). This species was listed as endangered on the Red List revised by the Ministry of the Environment of Japan in 2013 (The Ministry of the Environment of Japan 2014) and the International Union for Conservation of Nature in 2014 (Jacoby and Gollock 2014). The reduction of eel catches may have been caused by three main factors: climate change in the ocean environments, excessive fishing, and human alterations to rivers and coasts (Tsukamoto et al. 2009; East Asia Eel Resource Consortium 2012; Itakura et al. 2015a, b). Management of the ocean environments artificially is very difficult, although the fishing catches and environments in rivers and coasts can be managed. In addition, since habitat restoration takes much

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time and leads to decrease eel mortality indirectly unlike managing the fishing catches, improving the environments in the growth habitats requires longer to contribute to eel stocks than managing the fishery. Thus, conservation of eel habitats in rivers and coasts is urgently required.

In rivers, two main problems have been reported. First, cross-river structures are obstacles to upstream travel by glass eel, elver, and early yellow eels (East Asia Eel Resource Consortium 2012). In other anguillids, the smaller eels migrate actively (Imbert et al. 2010) and weirs and sluice gates prevent their upstream migration (White and Knights 1997). Then such barriers to migration appear to be one of the factors decreasing wild stock (Feunteun 2002). In Japanese eels, inhibition of upstream migration by cross-river structures also may reduce their distribution area (Iwasaki and Yoshimura 2012; The Ministry of the Environment of Japan 2016). Second, revetment of the shoreline degrades the eel habitats. Itakura et al. (2015b) suggested that non-revetment habitats were superior to revetment habitats in for Japanese eel abundance, fatness, number of feeding individuals, weight of stomach contents, and species diversity of stomach contents.

It is important to understand the preferred habitats of target species for conservation of fish habitats in rivers. Recently, many studies have quantitatively elucidated the relationship between the population density or presence/absence (P/A) and physical environmental factors in order to reveal the habitat preferences for some endangered species in rivers (Watanabe and Ito 1999; Yamazaki et al. 2006; Ichianagi et al. 2012; Ishiyama et al. 2012; Onikura et al. 2012; Koyama et al. 2016). However, because Japanese eels usually hide in holes, crevices, and burrows, it is difficult to capture them (Aoyama et al. 2005; The Ministry of the Environment of Japan 2015, 2016). In addition, because eels are distributed widely, ranging from the estuary to the upper reaches of rivers, investigation of their whole distribution takes much time and effort. Consequently, some studies have only shown that their densities are higher in the lower reaches (Yokouchi et al. 2008; Inui et al. 2016). Recently, the Ministry of the Environment of Japan (2015, 2016) investigated the spatial distribution of eels from lower reaches to upper reaches of rivers. They focused on verifying the inhibition of upstream migration by weirs rather than specifying the environmental characteristics of habitats. Therefore, there is no knowledge quantitatively explaining eel habitat preferences, covering their whole distribution in rivers with few obstacles to migration.

One of the characteristics of the river environment is spatial hierarchy, which means that an environment at a larger spatial scale is composed of environments at smaller scales (Nagayama et al. 2015). The environmental factors characterizing the riverine organism habitats are different for each spatial scale; thus, the habitat preferences of riverine fishes

must be investigated at each scale (Watanabe et al. 2001; Yamazaki et al. 2006; Ichianagi et al. 2012). The common spatial scales from largest to smallest are the stream, the segment, the reach, the channel-unit, and the subunit. The reach and channel-unit scales often have been targeted in order to clarify the spatial distribution and habitat preferences of anguillids (Jowett and Richardson 1995; Glova et al. 1998, 2001; Domingos et al. 2006) and other river fishes (Watanabe et al. 2001; Yamazaki et al. 2006; Ichianagi et al. 2012; Onikura et al. 2014; Nagayama et al. 2015).

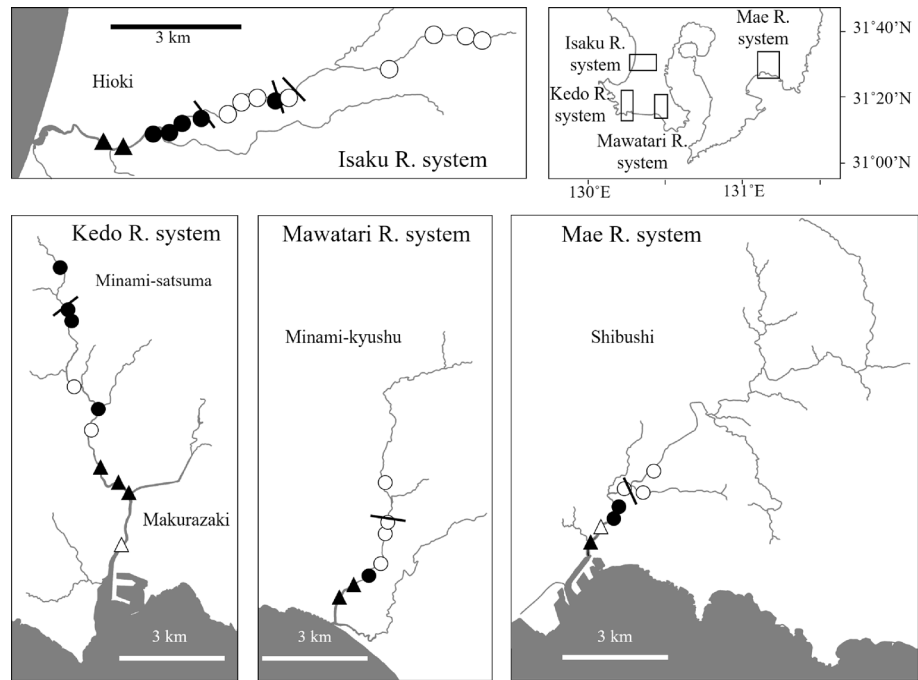
In this study, we elucidated the habitat preferences of Japanese eels at the reach and channel-unit scales. Habitat preferences at the reach scale show longitudinal distribution of eels corresponding to the gradients of environments along flow direction (Glova et al. 2001; Domingos et al. 2006). Habitat preferences at the channel-unit scales show habitat selection of eels associated with patchy environments within reaches (Jowett and Richardson 1995; Glova et al. 1998). The results at multiple scales lead to understand general knowledge about preferred habitats of eels (Glova et al. 1998, 2001), which must indicate the characteristics of the river environment to be conserved for eel conservation efforts.

Materials and methods

Study areas. Field surveys were conducted in four river systems: the Isaku River, Kedo River, Mawatari River, and Mae River systems (approximately 13.7, 12.0, 11.0, and 20.1 km in main river lengths, respectively) in the Kagoshima Prefecture, Japan (Fig. 1). The gradients of the Isaku and Kedo rivers were gentle ($\leq 1\%$) in almost all of the lower and middle reaches (to 4.7 and 5.6 km upstream from the river mouths, respectively), whereas those in the Mawatari and Mae rivers were gentle ($\leq 1\%$) only in lower reaches (to 2.5 and 3.7 km upstream from the river mouths, respectively), but thereafter rose steeply in almost all of the middle and upper reaches (about 1.0–3.5%).

Several weirs were found in the sections without fluctuation of the water level due to the tide (the non-tidal reaches) within our study areas. In the Isaku River, there was one 0.8-m-high weir and two 2.0-m-high weirs at approximately 4.7, 7.4, and 7.9 km, respectively, from the river mouth. In the Kedo River, there was one approximately 2.0-m-high weir at about 9.5 km from the river mouth. In the Mawatari and Mae rivers, there was one approximately 2.0-m-high weir at about 3.6 km from the river mouths. Most of the weirs were beyond 1.0 km upstream of main distribution areas of eels. There were no weirs or dams in the tidal reaches and the glass eels could migrate upstream easily. In almost all of the reaches, the riverbed was not protected by artificial structures and the

Fig. 1 Map of study area and sampling stations for Japanese eels. Each triangle and circle shows sampling stations in the tidal and the non-tidal reaches, respectively. Closed and open symbols show the stations that eels were captured and not captured, respectively. Each black bar shows a weir



natural shoreline was conserved especially in the non-tidal reaches. Although the Kagoshima Prefectural Fisheries Technology and Development Center has released cultured eels into the Kedo River system, no eels were released by fisheries cooperative associations. Because the cultured eels were tagged before release, they can be distinguished from wild eels.

We studied habitat preferences of Japanese eels at the reach and channel-unit scales. The reach scale survey was conducted at 39 stations (10 stations in the tidal reaches and 29 stations in the non-tidal reaches), 300 m in length in each river (Fig. 1). The channel-unit scale survey was conducted at 138 transects (generally 30 m in flow, 1–5 m in width) within 39 stations. In each station, various environments were found at the channel-unit scale. We set the transects to cover all of such environments in terms of shoreline structure, water depth, water flow velocity, and substrate as much as possible. The number of transects in each station was 1–6, commonly four. The distance between the upper limits of each transect within each station was 0–212 m and mean of that was 54 m. When the field surveys were conducted, the water temperature was 13.8–29.1 degrees and salinity was 0.0–20.3 at each transect by portable instrument (EC300, YSI Inc.). It was reported that other anguillid eels seasonally migrate for overwintering (Thibault et al. 2007), and burrow mud-sediment in winter (Tomie et al. 2017). For Japanese eels, Itakura et al. (2018) reported that reduction in activity of yellow eels was conspicuous below about thirteen degrees of water temperature and eels might overwinter in burrows. However, temperatures measured in our surveys always exceeded thirteen degrees; thus, there would be little

seasonal changes in eel behavior when our field surveys were conducted.

Eel collection. Eels were collected from June to November 2016 and May to November 2017 by handmade electrofisher (1200 V and 469 Hz in air). Electrofishing was conducted by wading in the water throughout each transect in upstream directions twice (double-pass fishing). Our fishing team was composed of one person with the electrodes and one to three persons catching eels in scoop nets (3 mm mesh). Generally, eels were caught by a scoop net attached to the electrode. Although we tried to capture all eels on the transects, several eels escaped by swimming rapidly and were not caught. In this case, the approximate total length (TL) was estimated visually and recorded. When escaped eels were observed, eel collection at other transect within the same station was generally not conducted on the same day to avoid repeated counting of escaped eels at multiple transects. However, in one station of Kedo River, we continued collecting at another transect on the same day after escaped eels were observed, but captured eels were remarkably different from escaped eels in terms of body size. Eels were collected only at low tide in the tidal reaches.

The captured eels were immediately anesthetized (FA100, DS Pharma Animal Health Co., Ltd.). The TL of all anesthetized eels was measured to the nearest 1 mm. The developmental stages (glass eel, elver, yellow eel, and silver eel) were determined in accordance with Fukuda et al. (2013) and Okamura et al. (2007). Then the eels were tagged for individual identification providing recaptured eel data for future study. One Passive Integrated Transponder tag (HPT8™, BIOMARK) was inserted into the abdominal

cavity of each eel ≥ 240 mm TL. Visible Implant Elastomer tags (Northwest Marine Technology Inc.) were hypodermically injected into one to three locations in the abdomen of each eel < 240 mm TL. After awaking from anesthesia, the eels were immediately released near where they were collected. In our collection, seven eels released by the Kagoshima Prefectural Fisheries Technology and Development Center were captured; however, in order to elucidate habitat preferences of wild eels, the data of those cultivated eels were not used in this study. Those cultivated eels were distributed locally, and four of seven eels were captured at specific one station of Kedo River. However, because wild eels were also distributed with relatively high density at the station (0.067 eels m^{-2}), cultivated eels appeared to have less influence on habitat selection of wild eels.

Survey of environmental information. At the same time as eel collection, the channel-unit scale survey was conducted to measure four physical environmental factors: the percentage of revetment (RV), water depth (DE), water flow velocity (FV), and substrate type. In this study, RV was defined as the percentage of concrete revetment along both right and left shorelines. Because habitat selections of Japanese eels appear to be not affected by artificial riverbank structures with many gaps (Itakura et al. 2015b), stone walls and cages filled with rocks were not regarded as concrete revetment. When the width of the channel with water was much smaller than the channel width, there was often dry riverbed between the concrete revetment and the shoreline. In this case, the shoreline was not considered to have concrete revetment. In our survey area, most of the concrete revetment was made with “Kenchi blocks”, which are rectangular concrete blocks. The revetment walls consisted of stacked blocks fixed by backfilled concrete (Fig. 2). At each transect, DE and FV were decided at the center of transect width of three locations: the upstream point, midstream point, and lower stream point of the transects. The arithmetic means of those factors for each transect were used for the channel-unit scale analyses. DE was measured to the nearest 10 cm using an aluminum ruler. When DE was less than 10 cm, it was measured to the nearest 1 cm. FV was measured to the nearest 0.1 cm/s at the surface layer using a current meter (VR-301, KENEK Corporation). FV was calculated as the mean flow rate during 30 seconds. At each transect, substrates were classified visually as one of the following types: silt and sand (< 2 mm), gravel (< 100 mm), rock (≥ 100 mm), and bedrock. The substrate type characterizing the largest area on each transect was chosen for the channel-unit scale analyses as predominant substrate type.

Following the channel-unit scale survey, the reach scale survey measured six physical environmental factors: the average riverbed gradient (GR), the distance from the upstream limit of the tidal influence (DI), RV, DE, FV, and substrate type. GR and DI were measured using the



Fig. 2 Concrete revetment along shoreline in the tidal reaches of Kedo River on August 13, 2018

topographic map (Geospatial Information Authority of Japan). In this study, the upstream limits of the tidal influence were defined as upstream ends of the stations located furthest upstream in the tidal reaches of each main river. RV, DE, and FV at the reach scale were defined as the weighted means of values at all the transects in each station. The weighted means were calculated by multiplying the value at the channel-unit scale by the area of each transect (calculated by length \times width of transects). The areas of transects in each station were summed for each substrate type and one substrate type with the largest area was used for the reach scale analyses as predominant substrate type.

Statistical analyses. The tidal reaches differ from the non-tidal reaches in terms of the fluctuation period of the water flow velocity and water level. Thus, it is difficult to directly compare the environmental characteristics of the tidal and the non-tidal reaches and our analyses separated the tidal and the non-tidal reaches. Furthermore, the habitat preferences of Japanese eels may differ depending on their body size (Yokouchi et al. 2008; Kaifu et al. 2010; Asakura et al. 2011). Therefore, we analyzed three groups separately: small eels in the tidal reaches (group A), large eels in the tidal reaches (group B), and large eels in the non-tidal reaches (group C). In this study, based on the median TL of all the captured eels, eels were defined as small when less than 255 mm TL and large when over 255 mm TL. Because there were few small eels in the non-tidal reaches, their habitat preferences were not analyzed. R software version 3.3.2 was used for all statistical analyses (R Core Team 2016).

We examined the relationships between environmental factors (explanatory variables) and P/A or population density of eels (response variables) at the reach and channel-unit scales by Generalized Linear Models (GLM) using “glm” or “glm.nb” functions in “MASS” package. In each scale analysis for each group, GLM with the lowest Akaike’s

information criterion was selected as the best model by stepwise procedures using “stepAIC” function in “MASS” package. The best models indicated the physical environmental characteristics of the preferred habitats at the reach and channel-unit scales.

In the reach scale analyses, the six explanatory variables examined were DI, GR, RV, DE, FV, and substrate type (Table 1). Substrate type was described using three dummy variables (S1, S2, and S3). If the substrate type was silt and sand, only S1 was 1 and the others were 0. If the substrate type was gravel, only S2 was 1 and the others were 0. If the substrate type was rock, only S3 was 1 and the others were 0. If the substrate type was bedrock, all dummy variables were 0. For groups A and B, the response variable was the number of eels and the total area of all transects in each station (TA) was used as the offset term. A negative binomial error structure and a log link function were used in building the GLMs. For group C, the response variable was the P/A of eels and TA was added into the explanatory variables examined, because eel densities in each station of

the non-tidal reaches were too low to use the number of eels as the response variable. A binomial error structure and a logistic link function were used in building the GLMs. A Receiver Operating Characteristic (ROC) analysis was conducted using “prediction” and “performance” functions in “ROCR” package in order to verify the probability of occurrence estimated by the best model for group C. This analysis evaluates the strength of the relationship between a continuous and a binary variable (Akobeng 2007). The cut-off point, which is used as reference when the value of a binary variable is predicted based on the value of a continuous variable, was also calculated by ROC analysis.

In the channel-unit scale analyses, the six explanatory variables examined were RV, DE, (DE)², FV, (FV)², and substrate type (Table 1). By building the GLM using (DE)² and (FV)², it is possible to express that eels prefer intermediate depth and flow velocity (Onikura et al. 2014). Three dummy variables (S1, S2, and S3) indicating substrate types were used using the same method as the reach scale analyses. For all three groups, the response variable was the number of

Table 1 Environmental factors used in statistical analysis of Japanese eels at two spatial scales (reach and channel-unit) in four river systems

Environmental factors	Mean (Range)		
	Groups A & B (tidal reaches)		Group C (non-tidal reaches)
Reach	(n = 10)		(n = 29)
DI (km)	1.0 (0.3–3.2)		0.4 (0.2–10.0)
GR (%)	0.3 (-0.1–1.0)		1.0 (0.0–3.7)
RV (%)	49.7 (5.7–100.0)		31.7 (0.0–75.4)
DE (cm)	29.1 (14.3–51.1)		36.4 (19.1–58.3)
FV (cm/s)	29.7 (7.5–58.7)		32.6 (12.6–71.9)
Substrate type			
S1 (dummy)	0.2 (0–1)		0.1 (0–1)
S2 (dummy)	0.4 (0–1)		0.5 (0–1)
S3 (dummy)	0.4 (0–1)		0.2 (0–1)
TA (m ²)	231.2 (75.0–347.5)		215.7 (37.5–330.0)
	Group A	Group B	Group C
Channel-unit	(n = 18)	(n = 26)	(n = 53)
RV (%)	32.8 (0.0–100.0)	28.9 (0.0–100)	31.9 (0.0–100.0)
DE (cm)	27.7 (3.7–56.7)	30.7 (3.7–66.0)	34.2 (9.7–66.7)
(DE) ²	976.5 (13.4–3211.0)	1211.0 (13.4–4356.0)	1337.0 (93.4–4444.0)
FV (cm/s)	18.8 (0.6–48.4)	20.2 (0.6–48.4)	36.2 (7.1–90.8)
(FV) ²	518.0 (0.4–2341.0)	590.6 (0.4–2341.0)	1605.0 (50.9–8245.0)
Substrate type			
S1 (dummy)	0.5 (0–1)	0.4 (0–1)	0.1 (0–1)
S2 (dummy)	0.3 (0–1)	0.3 (0–1)	0.5 (0–1)
S3 (dummy)	0.2 (0–1)	0.4 (0–1)	0.2 (0–1)
Area of each line	47.6 (10.0–97.5)	55.1 (10.0–135.0)	68.4 (13.0–135.0)

Groups A, B, and C are small eels in the tidal reaches, large eels in the tidal reaches, and large eels in the non-tidal reaches, respectively

DI: the distance from river mouth, GR: riverbed gradient, RV: the percentage of revetment along shorelines, DE: water depth, FV: water flow velocity, TA: the total area of all lines within each station

eels and the area of each transect was used as the offset term. For groups A and B, a negative binomial error structure and a log link function were used in building the GLMs. For group C, a Poisson error structure and a log link function were used. In order to determine habitat preferences at the channel-unit scale within preferred habitats at the reach scale, the transects within low-population-density stations were not used in the channel-unit scale analyses. In the analyses for groups A and B, low-population-density stations were defined as those where population density predicted by the best model at the reach scale was less than the reference density (calculated by dividing one eel by the median of TA). In the analyses for group C, low-population-density stations were defined as those where the absence of eels was predicted by the best model and the cut-off point.

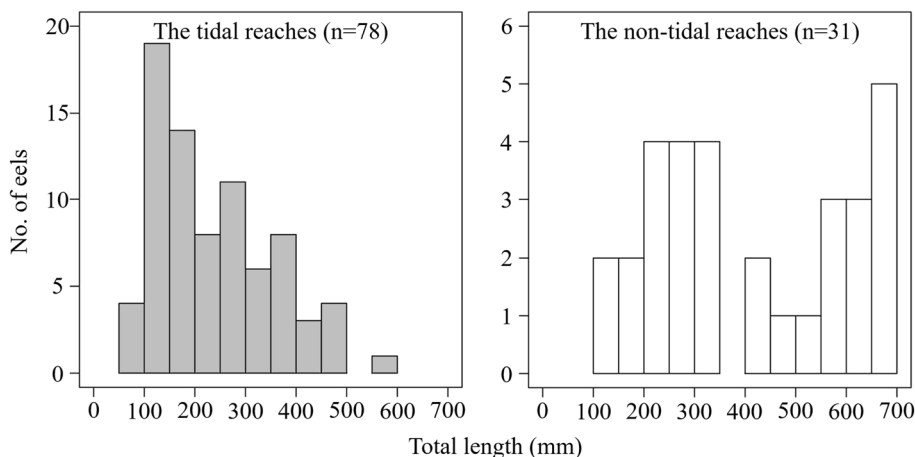
In order to eliminate multicollinearity, one of the pairs of explanatory variables that had strong correlation (Pearson’s correlation coefficient > 0.65) was not used for building the GLMs. Pearson’s correlation coefficient between explanatory variables was calculated using “hetcor” function in “polycor” package. In the reach scale analyses for groups A and B, three pairs (DI-S1, FV-S2, and S2-S3) indicated strong correlations; therefore, S1 and S2 were eliminated from the explanatory variables examined. To verify the accuracy of the six best models (three groups × two scales), the areas under the ROC curves (AUC) and the Spearman’s rank correlation coefficients (rs) were calculated using “prediction” and “performance” functions in “ROCR” package and “cor.test” function in “stats” package. Accuracy was classified by three levels: low (rs < 0.4 or AUC < 0.7), moderate (0.4 ≤ rs < 0.7 or 0.7 ≤ AUC < 0.9), and high (rs ≥ 0.7 or AUC ≥ 0.9). Since models with ΔAIC < 2 should be referred as reasonable alternative models of the best model (Burnham and Anderson 2002), we calculated all models with ΔAIC < 2 using “dredge” function in “MuMIn” package and counted the number of each variable selected in models with ΔAIC < 2.

Results

A total of 109 eels was collected at 20 stations (Fig. 3). Their distribution ranged from the lower to upper reaches (to 7.1 km and 10.8 km upstream from the river mouths) in the gentle gradient river systems (Isaku and Kedo river systems, respectively), while they were restricted to the lower reaches (to 1.8 km and 2.6 km upstream from the river mouths) in the steep gradient river systems (Mawatari and Mae river systems, respectively; Fig. 1). We used 145 eels in the statistical analyses, including 36 uncaptured eels that were classified visually as small (< 255 mm TL) or large (≥ 255 mm TL) eels. Eels were distributed mainly in the lower reaches, with greater densities in the tidal reaches (0.050 eels m⁻²) than in the non-tidal reaches (0.003 eels m⁻²). In particular, the majority of small eels were distributed in the tidal reaches (Fig. 3). In contrast, eels > 600 mm TL occurred only in the non-tidal reaches. Overall, mean TL of captured eels was significantly smaller in the tidal reaches (mean ± standard deviation: 240 ± 115 mm) than in the non-tidal reaches (408 ± 186 mm; Mann-Whitney U test, p = 1.325 × 10⁻⁵). The most of eels were “yellow eel” and only three eels were early “silver eel” stages as defined by Okamura et al. (2007). It suggests that seasonal occurrences of glass and silver eels scarcely affected our data; thus, there would be little influences by long-term sampling across seasons on the distribution and body size of captured eels. Three silver eels, which did not indicate different distribution than individuals of similar body size, might be immediately after beginning to mature for spawning migration.

The six best models (three groups × two scales) were obtained (Table 2). Accuracy of two best models for groups A and B at the reach scale was high (rs ≥ 0.7 or AUC ≥ 0.9) (Table 2). The four best models for group C at the reach scale and groups A to C at the channel-unit scale

Fig. 3 Total length distribution of captured Japanese eels



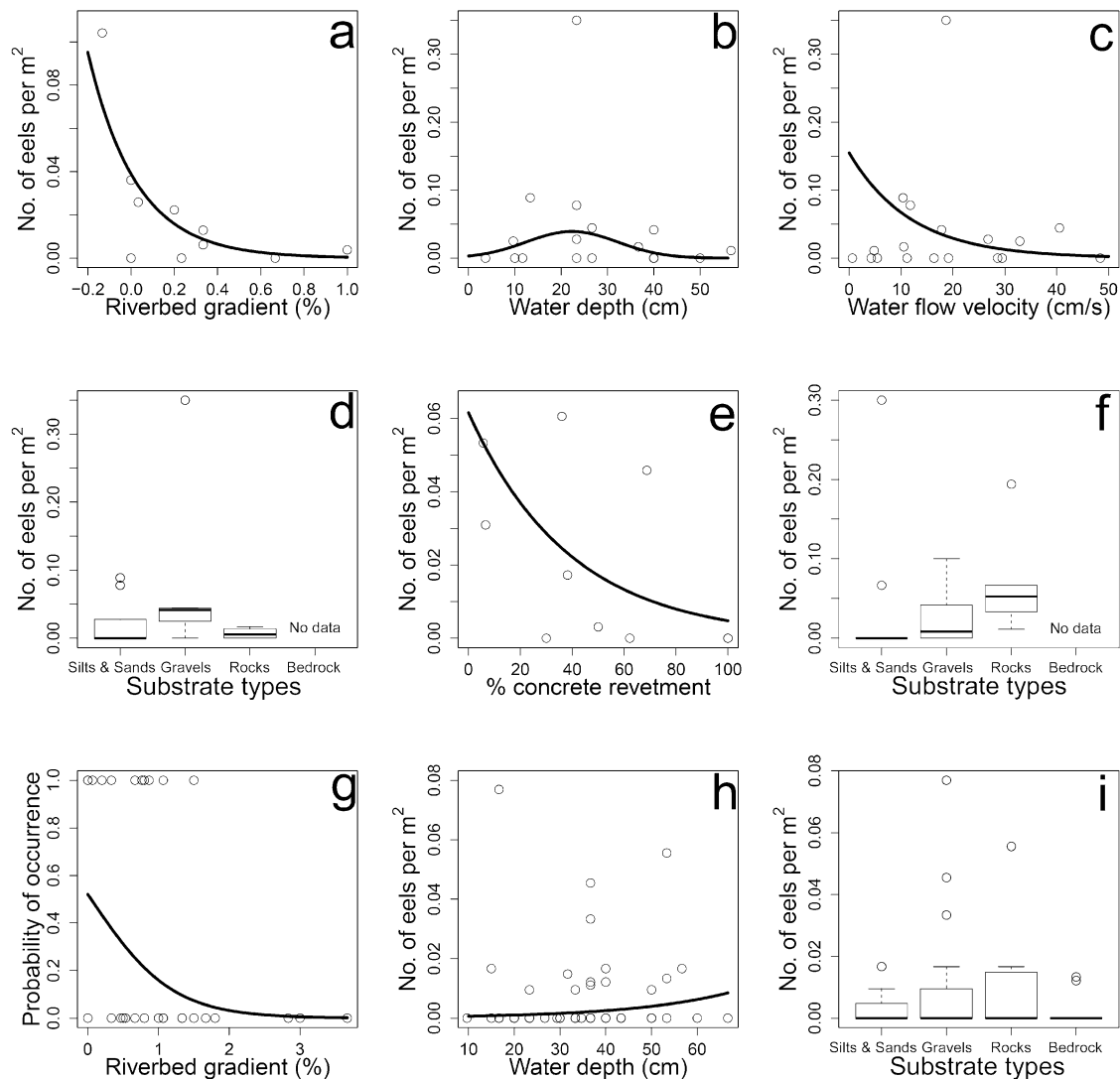


Fig. 4 The relationships between Japanese eel density or probability of occurrence and each environmental factor included in the best models. Line graphs show predicted values calculated by the best models and scatterplots and boxplots show observed values (a: the result of the reach scale analysis for group A, b–d: the results of the

channel-unit scale analysis for group A, e: the result of the reach scale analysis for group B, f: the result of the channel-unit scale analysis for group B, g: the result of the reach scale analysis for group C, and h and i: the results of the channel-unit scale analysis for group C)

to revise the difference of surveyed area between each station. The best model at the channel-unit scale included DE, S2, and S3 as explanatory variables (Table 2). The Wald 95% CI of DE did not include 0 and DE was positively correlated with their population densities (Fig. 4h). The Wald 95% CI of S2 included 0, but that of S3 did not. Both S2 and S3 were positively correlated with population densities and the coefficient of S3 was larger than that of S2 (Table 2), suggesting that large eels in the non-tidal reaches prefer rocks more than gravels as substrate.

Discussion

This study is the first to elucidate habitat preferences of Japanese eels at the reach and channel-unit scales in rivers, indicating the environmental characteristics of habitats that should be preserved for eel conservation efforts. Previous studies have reported the general tendency of eel abundance to decrease and their TL to increase with distance from river mouths (Yokouchi et al. 2008; Inui et al. 2016). Our field survey data also supported those

general tendencies by showing that eel density was greater and eel mean total length was smaller in the tidal reaches than in the non-tidal reaches. This seems to be because eels initially accumulate in the lower reaches in river and then disperse in both upstream and downstream directions following their growth (Kaifu et al. 2010). On the other hand, Yokouchi et al. (2008) argued that distance from the river mouth is insufficient to describe the spatial distribution of eels and that other meso- and micro-habitat characteristics also could affect the abundance and length of eels. In fact, other anguillids have habitat preferences at the meso- and micro-habitat, which affect their longitudinal distribution (Jowett and Richardson 1995; Glova et al. 1998, 2001; Domingos et al. 2006). Here we showed environmental characteristics of the preferred habitats of small (< 255 mm TL) and large (\geq 255 mm TL) eels at two spatial scales corresponding to the meso-habitat scale and calculated high and moderate accuracy best models (Table 2). The environmental factors included in the best models were selected more frequently in the models with Δ AIC < 2 than other environmental factors (Table 3). Our results clarified that riverbed gradient, the amount of revetment along the shoreline, water depth, water flow velocity, and substrate type are environmental factors that mainly characterize preferred eel habitats, although weak relation between habitat preferences and other environmental factors could not be denied. Our research quantitatively described multiple factors characterizing habitats at smaller spatial scales than in previous studies and supplements previous conclusions on eel spatial distribution only based on the distance from river mouth. Habitat preferences at the reach scale indicate longitudinal distribution of eels corresponding to the gradients of environments along flow direction (Glova et al. 2001; Domingos et al. 2006). Habitat preferences at the channel-unit scales indicate habitat selection of eels associated with patchy environments within reaches (Jowett and Richardson 1995; Glova et al. 1998). We discuss why eels prefer such habitats and show the management implication in terms of habitat preferences at the reach and channel-unit scales.

Habitat preferences of small eels in the tidal reaches.

The densities of small eels at the reach scale in the tidal reaches were correlated only with riverbed gradient and their density decreased with increasing riverbed gradient (Fig. 4a). This may be because yellow eels initially accumulate in brackish water and then disperse as they grow (Kaifu et al. 2010). Negative correlation between the densities and riverbed gradient shown by the best model appears to suggest that many small eels inhabit the lower reaches before dispersing. Such low-gradient reaches consisted of shallow and non-turbulent runs and deep pools (Bisson et al. 2017).

The channel-unit scale analysis suggested that small eels appear to prefer shallow (about 15–30 cm depth) and

slow-flow areas within the low-gradient reaches (Fig. 4b, c). This is consistent with previous reports indicating that relatively small eels (< 240 mm TL) had high densities at shallow runs in the lower reaches (The Ministry of the Environment of Japan 2015, 2016, 2017). Smaller eels of other anguillid species also prefer relatively shallow and slow-flow habitats such as inshore run compared to larger eels (Nishi and Imai 1969; Tesch 2003; Domingos et al. 2006). This seems to be because smaller eels are less capable of moving upstream at high flow velocity compared to larger eels (Solomon and Beach 2004). Thus, habitat preferences of small Japanese eels at the channel-unit scale may be related to their avoidance of strong water flow. The channel-unit scale analysis also showed that the preferred substrate type for small eels is gravel (Fig. 4d). Japanese eels are principally nocturnal in freshwater and estuarine habitats and hide during the daytime (Aoyama et al. 2002; Itakura et al. 2018). Because most small eels were captured from gaps between gravels in our field survey, gravels might be preferred as refuges for small eels during the daytime. Eels generally use rocks, debris, and vegetation as refuges (Tesch 2003; The Ministry of the Environment of Japan 2015, 2016) and they also can burrow into soft mud sediments (Aoyama et al. 2005; Tomie et al. 2017). However, it was known that other anguillids exhibit ontogenetic change of refuge type (Nishi and Imai 1969; Glova et al. 1998; Glova 2001). Asakura et al. (2011) reported that Japanese eels < 20 mm in body depth (< approximately 500 mm TL) frequently hid in pipes twice of their body depth in laboratory experiments and never chose pipes larger than 3 times of body depth. Therefore, gravels may provide the preferred small refuges for small individuals of Japanese eels during the daytime. This seems to be why many small eels were distributed in the channel-units with gravel substrate.

Habitat preferences of large eels in the tidal reaches.

The best model showed that large eels in the tidal reaches preferred areas with less concrete revetment along shoreline (Fig. 4e). In our field survey, many large eels hid in shoreline structures: vegetation, stone walls, and cages filled with rocks. Cavities by rocks and vegetation are common refuges for anguillid eels (Tesch 2003; The Ministry of the Environment of Japan 2015, 2016) and presence of riparian cover and collapsed banks affect the distribution of particularly large eels (Glova et al. 1998). Therefore, shoreline structures of our study area seemed to be important refuges for large eels. Disappearance of such refuges by revetment might cause low eel density at the reaches with more concrete revetment along shoreline. In addition, Itakura et al. (2015b) showed that revetment may reduce the amount and diversity of prey for Japanese eels in the lower Tone River, Japan, and suggested that higher abundances of eels in the non-revetment sites were because of different food availability. We could not survey the amount and diversity of

prey species, but food availability might be associated with negative correlation between eel densities and the percentage of concrete revetment along shoreline.

At the channel-unit scale, densities of large eels were correlated only with substrate type and large eels appeared to prefer rocks (Fig. 4f). Because small eels occurred in gravel more than rocks, Japanese eels may change their preferred substrate type with growth. This seems to be because of ontogenetic change of refuge type, which may be common feature across genus *Anguilla* (Nishi and Imai 1969; Glova et al. 1998; Glova 2001). The channel-unit scale analysis also showed that the densities of large eels did not significantly correlate with water depth or water flow velocity, in contrast to the densities of small eels (Table 3). This result suggests that eels disperse to various depths and flow channel-units as they grow. In other anguillids, small eels seem to inhabit relative shallow and slow-flow water because of lack of the ability to swim upstream against strong flow (Nishi and Imai 1969; Solomon and Beach 2004; Domingos et al. 2006), whereas large eels inhabit deeper water (Tesch 2003). Thus, the distribution of Japanese eels at the channel-unit scale may become influenced only by substrate type rather than water depth and water flow velocity, as eels grow and their swimming ability improves.

RV and S3 were included in the best models and were selected with significance most frequently by the models with $\Delta AIC < 2$ (Table 3). These results showed that population densities were correlated with the percentage of concrete revetment along the shoreline and substrate type. However, further studies may be needed to clarify habitat preferences of large eels in the tidal reaches, because the Wald 95% CI of these two variables included 0 in the best models.

Habitat preferences of large eels in the non-tidal reaches. Large eels in the non-tidal reaches were frequently found in low-gradient riverbeds (Fig. 4g). The maximum riverbed gradient was 1.5% where large eels occurred and no eels resided at the high-gradient reaches, i.e. cascade and step-and-pool reaches (Bisson et al. 2017). This may be because of the differences of the environment between high- and low-gradient reaches. One of the characteristics of high-gradient reaches is relatively small pool spacing and frequent presence of riffle and cascade, whereas pool spacing is relatively large in low-gradient reaches and fast flow channel-units rarely exist (Bisson et al. 2017). Japanese eels and other anguillids appear to have inshore home ranges in rivers (Jellyman and Sykes 2003; Itakura et al. 2018), because eels avoid strong water flow near the center of channel width (Itakura et al. 2018). Therefore, large individuals of Japanese eels in the non-tidal reaches were frequently distributed at low-gradient reaches where pool spacing is relatively large and riffle and cascade rarely exist, because eels might not prefer frequent presence of fast flow channel-units within

their home ranges. This is supported by previous studies that qualitatively described the environments which were not preferred by Japanese eels even near the river mouths in Taiwanese rivers (Shiao et al. 2003). In addition, our study indicated that eel habitat preferences cannot be described only by distance from the river mouth. The eel distribution was widespread in Isaku and Kedo river systems with gentle lower and middle reaches, whereas eels were distributed only in the lower reaches in Mawatari and Mae river systems that had relatively steep gradients (about 1.5–3.5%) in the middle to upper reaches. Our results suggest that eels prefer reaches with low riverbed gradients rather than habitats near the river mouth in the non-tidal reaches.

The channel-unit scale analysis showed that large eel densities increased with water depth and their preferred substrate type was rock (Fig. 4h, i). This may be because of their cryptic habit during the daytime. For benthic fishes, such as *Cottus nozawae* and *Pseudobagrus ichikawai*, holes and crevices are used as shelter from strong flow and predators (Watanabe and Ito 1999; Watanabe et al. 2001; Ichiyana et al. 2012). For large eels, rocks may provide such shelters in the daytime. Generally, water flow is weaker in the bottom layer than the surface layer and is weakest within the substrates. This tendency of vertical distribution became conspicuous with water depth (Suzuki 1998). Therefore, deep channel-units with rocks might be the preferred habitats for large eels particularly to avoid strong water flow.

Management implications. Our results suggest the environmental characteristics of those habitats to be preserved for eel conservation efforts and, furthermore, offer the following suggestions for conservation and restoration of eel habitats. First, various river environments should be preserved. Eel habitat preferences at the channel-unit scale in the tidal reaches suggested that they disperse to various water depths and flow speeds as they grow. In addition, the preferred substrate type appeared to be different for small and large eels at the channel-unit scale because their refuge size preferences change (Asakura et al. 2011). Hence, ideally, various environments especially in the tidal reaches should be preserved where eels of a range of body sizes live.

Recently, Ishi-kura nets, underwater piles of rocks about 15–30 cm in diameter enclosed by net (Harada et al. 2018), have been installed in rivers all over Japan and are expected to provide refuges for eels (Kaifu et al. 2018). It is known that riverine fish habitats are affected by changes of substrate, such as bedrock outcrop and riverbed armoring caused by recent upstream dam construction (Ishiyama et al. 2009; Tashiro et al. 2014); thus, Ishi-kura nets will contribute to restoration of eel habitats at the channel-unit scale by providing rocks as preferred refuges for large eels if efforts on the maintenances are sufficient to avoid troubles such as clogging by sediments. Our study also suggests that Ishi-kura nets, however, cannot provide suitable

refuges for small eels because they preferred a smaller substrate type. This hypothesis is supported by Harada et al. (2018), which showed that most eels hiding in Ishi-kura nets were ≥ 200 mm TL in two rivers, Oita Prefecture, Japan. Perhaps, it is necessary to develop another method to restore habitats for small eels as well as improvement of Ishi-kura net in terms of maintenance costs.

Second, future studies should elucidate what construction methods contribute to eel habitat improvements in rivers. Our study showed eel habitat degradation by riverbank modification as is consistent with previous studies (Itakura et al. 2015a, b). We could not clarify, however, possible effects of different revetment types on abundances of eels. Because many eels appear to have home ranges near riverbanks to avoid strong water flow (Itakura et al. 2018), construction methods that do not degrade habitats should be evaluated.

Third, characteristics of cross-river structures that affect the spatial distribution of eels (Iwasaki and Yoshimura 2012; The Ministry of the Environment of Japan 2015, 2016) should be reexamined excluding the effects of eel habitat preferences, as shown in our study. The Ministry of the Environment of Japan (2016) concluded that weirs (≥ 40 cm in waterfall height) are obstacles to upstream migration by small eels (< 240 mm TL) based on the spatial distributions of eels in five Japanese river systems; however, their analysis did not consider the habitat preferences of eels. Our study suggested that eel density and the probability of occurrence differed depending on environmental factors at the reach and channel-unit scales. Therefore, characteristics of weirs and dams that affect eel spatial distribution should be re-investigated separating the effects of eel habitat preferences.

We elucidated habitat preferences of yellow and early silver stage Japanese eels and suggested habitats that should be preserved preferentially and some management implications based on habitat preferences that change with growth. Our study, however, could not consider habitat preferences of younger stages (“glass eels” and “elvers”) or biological interactions with aquatic community. Future studies are necessary to learn the influences on eels of all developmental stages in rivers by physical and biological environmental factors, which will provide guidance on preservation of eel habitats in rivers.

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