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Size-dependent changes in habitat use of Japanese eel *Anguilla japonica* during the river life stage

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Abstract Japanese eel (*Anguilla japonica*) is a commercially important species; however, its population has declined in recent years. Appropriate conservation management, including habitat protection, is required to reverse this decline. However, their habitat use pattern during the riverine life stage is poorly understood. In this study, we investigated the longitudinal distribution and microhabitat of small-sized (<200 mm total length) and large-sized (≥200 mm total length) Japanese eels observed in 83 and 124 quadrats (1 m × 1 m), respectively, placed at seven stations in the Nikkeshi River in Fukushima Prefecture, Japan. Analysis using generalized linear models revealed that the eel density of both size classes decreased with increasing distance from the river mouth. In addition, the density of small-sized eels, but not large-sized ones, decreased as weir numbers increased. Moreover, analysis using generalized additive models showed that microhabitat uses differed between the size classes. The small-sized eels used near-shore habitats which had low current velocities. Their preferred habitats contained both complex substrates with smaller particle sizes and simple substrates with relatively large particle sizes. In contrast, the large-sized eels used both near-shore habitats with lower current velocities and the center of the river which had high current velocities. They preferred simple riverbed habitats with large particle-sized substrates and no underwater vegetation. These results suggest that there is a size-dependent change in the longitudinal distribution and microhabitat use of Japanese eels during their river life stage. These findings provide valuable information for the conservation and management of Japanese eels in rivers.

Keywords *Anguilla japonica* · Body size · Longitudinal distribution · Microhabitat · Riverine life stage

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Introduction

Japanese eels are catadromous fish that spawn in open seas and grow in continental waters (Tsukamoto et al. 2011). Although Japanese eel is one of the most commercially valuable fishery resources in East Asia, including Japan, the stock has been rapidly decreasing since the 1970s due to habitat degradation (i.e., construction of concrete riverbanks and dams) and overfishing of glass, yellow, and silver eels (Tsukamoto et al. 2009; Itakura et al. 2015; Kaifu et al. 2018; Kaifu 2019). On average, 78.6% of the effective habitats of Japanese eels have been lost in East Asian rivers (Chen et al. 2014). Consequently, this species is currently categorized as endangered in the International Union for Conservation of Nature Red List (Jacoby and Gollock 2014). Therefore, to undertake effective management and conservation measures of wild Japanese eel stocks, it is necessary to understand the ecology of their whole life cycle.

Several ecological aspects of yellow and silver eels inhabiting fresh/brackish waters have been well investigated. For example, based on otolith Sr/Ca ratios, habitats for eels from the elver to silver stages before spawning migration have been reported to extend from coastal to fresh waters (Tsukamoto and Arai 2001; Kaifu et al. 2010; Yokouchi et al. 2012), and their growth rates in coastal/brackish waters are higher than those in freshwater habitats (Yokouchi et al. 2008; Kaifu et al. 2013; Wakiya et al. 2016), as shown in other anguillids (Morrison and Secor 2003; Daverat and Tomás 2006; Walsh et al. 2006; Cairns et al. 2009). Yellow eels use various types of riverbed materials as refuges to avoid predation and strong currents (Aoyama et al. 2005; Tomie et al. 2017; Christoffersen et al. 2018), whereas young eels at the elver and young yellow stages use riverbed materials with smaller particle sizes (Kume et al. 2019). Understanding the habitat uses of target fishes throughout their life history is important to implement appropriate conservation strategies and restore their habitats. Despite extensive studies of the across-life-stage distribution of eels in rivers, including Japanese eels (e.g., Tzeng et al. 1995; White and Nights 1997; Domingos et al. 2006; Lasne and Laffaille 2008; Yokouchi et al. 2008; Kwak et al. 2019), data on the use habitat of micro- and reach-scales by eels in the glass/elver and yellow stages in natural environments are lacking (Laffaille et al. 2003; Johnson and Nack 2013; Kume et al. 2019).

In this context, the aim of the present study was to assess the impact of (i) hydrological and anthropogenic factors and (ii) longitudinal distribution on the riverine habitat use of Japanese eels in a small river, characterized by intensive agricultural use in its catchment area. Moreover, we compared these results between two size classes, small-sized and large-sized eels. In Japan, many small rivers are utilized and modified (i.e. channelized) for paddy field irrigation, leading to degradation of riverine habitats of aquatic organisms. Although such rivers may be potentially used to restore the habitats because they can be easier to apply and monitor than in large rivers, they have not been considered for the conservation efforts of aquatic organisms, including Japanese eels. Thus, knowledge of eel habitat use in these rivers will contribute to the establishment of comprehensive management and conservation strategies for wild eel stocks.

Materials and methods

Study site

We conducted field surveys in the Nikkeshi River (~11.5 km long, 3.0–25.0 m wide), Fukushima Prefecture, Japan (Fig. 1) on 23–24 April 2018. This river flows into the southern part of the Matsukawa-ura lagoon (6.46 km^2), which is connected to the open ocean via a single narrow channel (about 100 m wide) (Fig. 1B). The lower and middle course of this river run through a lowland area that mainly consists of paddy fields. To enable agricultural management, these courses were channelized with concrete, and weirs were built to prevent fine sediment deposition on the riverbeds as well as to maintain a high water level to supply the paddy fields during the agricultural season. Since we sampled at the beginning of the agricultural season, the water levels were relatively high. We randomly chosen seven stations (St. 1–7) in the river (Fig. 1C). All reaches were located entirely within freshwater areas and had concrete banks on both sides. No reared eels were released by fisheries cooperative associations in this river.

Field survey

We collected eels at the seven stations during daytime (Fig. 1). Sampling was performed by three people: one person operated the electrofishing unit (LR-20B, SmithRoot, Vancouver, WA, USA) while the others caught the eels using dip-nets (39 cm × 40 cm opening, 40 cm depth, 1 mm mesh size). We moved upstream, zigzagging across the river to guarantee complete coverage within each station. All stations were sampled once. All sampling procedures of this study were

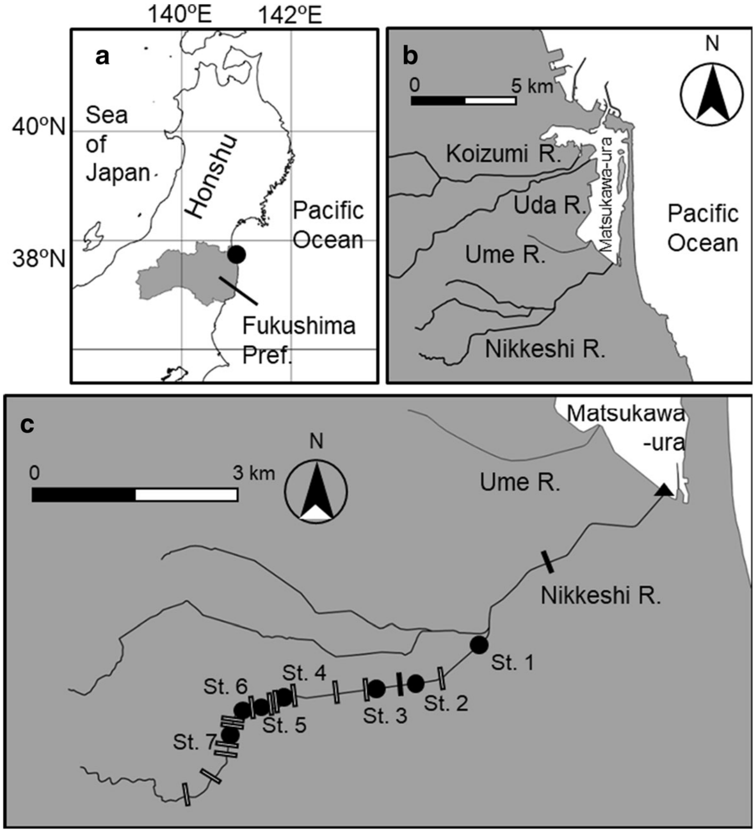

Fig. 1 Maps (a–c) of the study area. (a) Maps show northern Honshu and Fukushima Prefecture, Japan, (b) Matsukawa-ura lagoon and its tributaries, and (c) the Nikkeshi River. Circles indicate sampling stations. Triangle indicates water gate. Closed and open squares indicate inflatable rubber weir and vertical wall weir, respectively (see Table 2)

performed in accordance with the "Guidelines for the Use of Fishes in Research" published by the Ichthyological Society of Japan in 2003 (http://www.fish-isj.jp/6nglish/guidelines.html).

We targeted eels encompassing all riverine life stages. In the field, we determined the size class of eels to classify those of small size [<200 mm total length (TL), which corresponds to the elver and yellow stages (Fukuda et al. 2013)] and those of large size [≥200 mm TL, which corresponds to the yellow stage (Okamura et al. 2007)] through visual observation. No glass or silver eels were found during the sampling. The in situ catch points of the collected eels were marked on the riverbed for subsequent measurements using a numbered location marker. The captured eels were then temporarily kept in buckets to avoid repetitive catches. To check the accuracy of our visual measurements, a fraction of the captured eels (Table 1), which were randomly selected, was frozen using dry ice after anesthesia with clove oil (Walsh and Pease 2002) and transported to the laboratory. The TL of small-sized eels was then measured using a digital caliper (to the nearest 0.1 mm) and that of large-sized eels was measured using a scale (to the nearest 1 mm). The TLs of small-sized eels ranged from 52.8 to 127.0 mm (mean = 81.7 mm) and those of large-sized eels ranged from 200 to 657 mm (mean = 351.6 mm) (Fig. 2; Table 1). The remaining eels were released in the same station from where they were caught.

Following eel sampling, river width at three lines within each station and length of each station were measured and used to calculate the area of each station. Three physical environmental variables, including distance from the nearest riverbank (DR: cm), current velocity (CV: cm/s), and substrate composition (%), were measured and used for subsequent analyses. We set 48 eel-present and 35 eel-absent quadrats (1 m × 1 m) of small-sized eels, and 23 eel-present and 101 eel-absent quadrats (1 m × 1 m) of large-sized eels for the abiotic measurements. The absent quadrats were set in three and five reaches for comparisons of small-sized (St. 2–4) and large-sized eels (St. 2–6) at random. DR was measured from the center of each quadrat to the nearest shore using an aluminum ruler (accurate to the

Table 1 Density and total length (TL; mean ± standard deviation) of captured eels used in the general linear model analyses

	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Small-sized eel							
Density (eel/m^2)	0.433	0.091	0.091	0.010	0	0	0
Number of eel captured	39	11	11	1	0	0	0
TL (mm)	68.3 ± 20.3	100.7 ± 11.5	99.8 ± 11.5	111.8	–	–	–
	(*n* = 33)	(*n* = 9)	(*n* = 11)	(*n* = 1)	–	–	–
Large-sized eel							
Density (eel/m^2)	0.100	0.050	0.007	0.010	0.035	0.021	0
Number of eel captured	9	6	1	1	4	2	0
TL (mm)	354 ± 88.3	300 ± 68.8	657	482	329 ± 70.9	302	–
	(*n* = 7)	(*n* = 6)	(*n* = 1)	(*n* = 1)	(*n* = 4)	(*n* = 1)	–

n indicates sample size

nearest 1 cm). Because this river was shallow (mean ± standard deviation = 18.9 ± 10.2 cm depth), the CV at a 60% depth from the water surface was measured three times at the center of the quadrat using an electromagnetic current meter (VE20/VET-200-10PII, KENEK Co., Ltd., Tokyo, Japan); the mean value of the three readings was used for analyses. Substrate composition (%) in each quadrat was recorded by visual observation using four categories: sand/gravel (<4 mm), pebble (4–64 mm), cobble (64–256 mm), and boulder (≥256 mm). We used Simpson's *D* (Hunter and Gaston 1988) as an index of substrate complexity (ISC) based on substrate composition in each quadrat. This index ranges from 0 (only one category in substrate composition) and 1 (highly complex substrate composition). We used the dominant substrate (DS) and ISC for quantitative analyses. In addition, the presence/absence (1/0) of underwater vegetation (UWV) in each quadrat was recorded by visual observation.

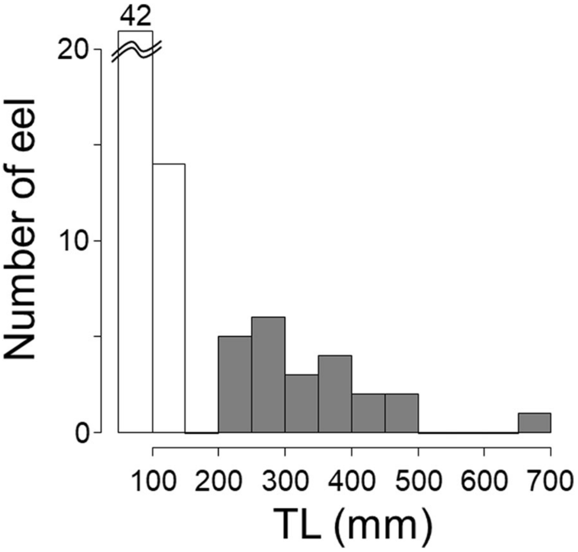

Fig. 2 Total length (TL) distribution of small-sized (white bars) and large-sized (shaded bars) eels observed in our study site

We also recorded geographical data for each station. Distance from the river mouth (m) of the station was registered using QGIS ver. 2.18.3 software (QGIS development team 2016). Moreover, we counted the number of weirs from the river mouth and measured the heights of weirs using a laser distance meter (DISTOTM D510, Leica Geosystems, Switzerland), as these structures could function as potential barriers against the upstream migration of eels (White and Knights 1997; Ministry of the Environment, Japan 2016; Kume et al. 2019; Kwak et al. 2019). We used the number of weirs and their maximum height above the water surface from the river mouth for analyses. Of the total 15 weirs, 13 were made of concrete and presented a vertical wall, whereas the other two were inflatable rubber weirs that were inflated from April to September for irrigating the paddy fields (Table 2). In Japan, both types of weirs are commonly used in small rivers that flow through paddy areas. The two inflatable rubber weirs have an integrated fish pass so that eels can move upstream. The heights above the water surface of the other weirs ranged from 19 to 154 cm (average 68.3 cm; Table 1). The sediment of upstream of all weirs consisted of natural substrates, while that of downstream was either natural substrates or a concrete floor. Weir surfaces were crusted with periphyton mats (~1 mm thickness).

Table 2 Summary of weir characteristics in Nikkeshi River

Order from the river mouth	Weir height (cm)	Weir width (m)	Distance from the river mouth (km)	Weir type	Fish pass present (P)/absent (A)
1st	80	25.0	2.20	Inflatable rubber	P
2nd	83	9.9	4.78	Vertical wall	A
3rd	154	13.3	5.37	Inflatable rubber	P
4th	71	5.0	5.90	Vertical wall	A
5th	135	5.3	6.24	Vertical wall	A
6th	85	6.3	7.09	Vertical wall	A
7th	37	6.1	7.16	Vertical wall	A
8th	45	6.5	7.43	Vertical wall	A
9th	35	8.0	7.68	Vertical wall	A
10th	86	7.0	7.88	Vertical wall	A
11th	19	6.9	8.00	Vertical wall	A
12th	36	7.8	8.26	Vertical wall	A
13th	52	5.2	8.41	Vertical wall	A
14th	44	6.2	9.02	Vertical wall	A
15th	63	6.9	9.30	Vertical wall	A

Statistical analyses

All statistical tests were carried out using R software ver. 3.3.2 (R Core Team 2017).

To assess the difference in each body size class among the sampling stations, we conducted a Kruskal-Wallis test with a *post-hoc* Steel-Dwass test using the *pSDCFlig* function in the *NSM3* package (Schneider et al. 2018). To explore factors determining the longitudinal distribution of eels in each size class within a river, we used general linear models (GLMs) with a Poisson distribution and a log-link function or a Gaussian distribution and an identity-link function using the *glm* function. In these models, the number of eels captured was the dependent variable (Table 2), distance from the river mouth, number of weirs, and the maximum height of weirs (except for inflatable rubber weirs with a fish pass) from the river mouth were the predictor variables (Table 3), and the area of each reach was an offset variable (Table 3). Distance from the river mouth had the highest variance inflation factor (VIF), which indicates the existence of remarkably high multicollinearity between this variable and the others (VIF = 50.9 for distance from the river mouth, VIF = 23.6 and 11.4 for

Table 3 Summary of geographical factors in each station used in the general linear model analyses

	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	VIF
Geographical factor								
Distance from the river mouth (km)	3.91	4.79	5.78	7.12	7.63	7.86	8.19	50.9
Number of weirs from the river mouth	1	2	3	6	8	9	11	23.6
Maximum height of weirs above the water surface from the river mouth (cm) †	0	83	83	135	135	135	135	11.4
Area sampled (m^2)	90	121	135	105	115	95	240	

† excluding inflatable rubber weirs that contained fish passes

Abbreviations: VIF: variance inflation factor the number and maximum height of weirs, respectively; Table 3). However, previous studies revealed that the density of eels decreased with increasing distance from the river mouth (Tzeng et al. 1995; White and Nights 1997; Laffaille et al. 2003; Lasne and Laffaille 2008). For these reasons, we established GLMs with a two-step process.

We firstly tested the effect of distances from the river mouth on eel densities. In these analyses, the number of eels captured was the dependent variable and distance from the river mouth was the predictor variable. Following the establishment of these models, we tested the weir effects (number and maximum height) on eel density. Due to the removal of the distance effect from these models, we used the residuals of the previous GLMs (eel density versus distance from the river mouth) as the dependent variable, and the number of weirs and the maximum height of weirs as the predictor variables. There was no multicollinearity between the number and maximum height of weirs (VIF = 3.3). These VIF values were calculated using the *vif* function in the *car* package (Fox and Weisberg 2018).

To examine the microhabitat use of eels in each size class in the river, we used general additive models (GAMs) with a binominal distribution and a logit link function, using the *gam* function in the *mgcv* package (Wood 2018). We used the presence/absence of eel data (1/0) as the binary response variable, and the physical environmental data (DR, CV, DS, ISC, and presence/absence of UWV; Table 4) as predictor variables. Three predictor variables (DR, CV, and ISC) were fitted by smoothing splines. Efficiency of the smoothing parameters was estimated by minimizing the unbiased risk estimator.

For model selection of the GLMs and GAMs, we used the *dredge* function in the *MuMIn* package (Bartoń 2017). The best model was selected using Akaike's information criterion (AIC), which stipulates that the best model for any candidate set applied to a given data set is that with the lowest AIC value. Following Burnham and Anderson (2002), models with ΔAIC <2 were assumed to be reasonable alternatives to the best model, and thus were retained.

Results

We collected 48 small-sized (mean = 81.7 mm TL; range = 52.8–127.0 mm TL) and 23 large-sized eels (mean = 351.6 mm TL; range = 200–657 mm TL; Fig. 2; Table 1). The body sizes of small-sized eels in St. 1 were significantly smaller than those in St. 2 and St. 3 (Steel-Dwass test, $w = 4.877$, $p = 0.003$ for St. 1 vs. St. 2; $w = 5.554$, $p = 0.001$ for St. 1 vs. St. 3; $w = 0.402$–2.090, $p = 0.451$–0.992 for other pairs). In contrast, the TLs of large-sized eels were not significantly different among the stations (Kruskal-Wallis test, $\chi^2 = 6.016$, $p = 0.305$).

We evaluated the distribution of Japanese eels within the river using GLMs. In this study system, the densities of both size classes decreased with increasing distance from the river mouth (Table 5). In contrast, weir effects

Table 4 Summary of physical environment data (mean ± standard deviation) in presence/absence quadrats of small-sized and large-sized eels used in general additive model analyses

Variables	Small size		Large size	
	Presence ($n = 48$)	Absence ($n = 35$)	Presence ($n = 23$)	Absence ($n = 101$)
Current velocity (cm/s)	10.9 ± 10.1	28.8 ± 24.2	12.4 ± 18.8	16.1 ± 17.7
Distance from the nearest riverbank (cm)	42.7 ± 25.5	74.1 ± 30.4	61.3 ± 27.5	60.0 ± 31.3
Dominant substrate				
Sand/gravel	12	6	4	25
Pebble	6	4	1	25
Cobble	2	2	2	12
Boulder	28	24	17	39
Index of substrate complexity†	0.29 ± 0.22	0.31 ± 0.24	0.24 ± 0.21	0.30 ± 0.22
Presence of underwater vegetation (%)	31.3	25.7	36.9	37.6

† Simpson's *D* was calculated based on substrate composition

Table 5 Summary of results from general linear models used to assess the relationship between distance from the river mouth and eel density (small and large size classes)

Model	Variable		Weight	df	AIC
	(Intercept)	distance			
Small-sized eel					
Full	6.95***	−0.93***	1	2	119.82
Null	1.87***		0.00	1	457.63
Large-sized eel					
Full	3.61***	−0.43***	1	2	125.79
Null	1.07***		0	1	167.03

β coefficients of predictor variables are shown

Abbreviations: distance, distance from the river mouth; AIC, Akaike's information criterion

***$p < 0.001$ in a Ward test

on eel distribution differed between size classes (Table 6). The density of small-sized eels decreased as the number of weirs increased, while the density of large-size eels remained unchanged in relation to weir number.

We used GAMs to examine the microhabitat uses of eels within the river, three models with ΔAIC <2 were selected in both small-sized and large-sized eels (Table 7). In this study system, different physical environmental factors affected eel density depending on their body size (Table 7). For small-sized eels, two physical factors (DR and CV) were significantly important (Table 7). Small-sized eels preferentially used near-shore habitats (<60 cm DR; Fig. 3e) with low CV (<20 cm/s; Fig. 3c). There were no relationships between other physical factors (ISC and UWV) and eel density. There were two GAM model peaks relating to the complex substrate: one peak had an ISC of approximately 0.1 with a larger particle size (high abundance of cobble stones), and the other had an ISC of approximately 0.6 with a smaller particle size (high abundance of pebble stones) (Fig. 3a and d). The peak's occurrence probabilities were slightly lower in habitats with UWV compared with those with no vegetation (Fig. 3b).

In contrast, the density of large-sized eels was significantly related to four physical factors (DR, CV, DS, and UWV). Moreover, there were weak effects of ISC on large-sized eel occurrence. There were two peaks of DR and CV in the GAM models (Fig. 4e) indicating a positive relationship between large-sized eel density and the following: near-shore habitats (20–40 cm DR) with a low CV (<15 cm/s) and the centers of the river (70–110 cm DR) with a relatively high CV (approximately 55 cm/s). The riverbeds of theses habitats were mainly composed of large substrates (cobble stones and boulders, Fig. 4a), in a relatively simple structure (<0.3 ISC, Fig. 4d). The density of large-sized eels was not dependent on the presence of UWV in their habitats (Fig. 4b).

Table 6 Summary of general linear models with ΔAIC < 2^a to assess the effects of weir on eel density of each size class

Model	Variable			Weight	df	AIC	ΔAIC
	(Intercept)	Nweir	Hweir				
Small-sized eel							
1	1.78	−0.40		0.44	3	35.31	0
2 (Null)	−0.80			0.22	2	36.68	1.37
3 (Full)	0.97	−0.57	0.02	0.19	4	36.97	1.66
Large-sized eel							
1 (Null)	−0.86			0.50	2	37.17	0
2	0.08	−0.15		0.22	3	38.83	1.66
3	−0.18		−0.01	0.19	3	39.09	1.92
Full	−0.56	−0.28	0.01	0.09	4	40.70	3.54

[a] Based on comparisons between null and full models in general linear model results

β coefficients of predictor variables, which are not significant in a Ward test

Abbreviations: Nweir, number of weirs from the river mouth; Hweir, maximum height of weirs (excluding inflatable rubber weirs with a fish pass) above the water surface from the river mouth (cm); AIC, Akaike's information criterion

Table 7 Summary of models with ΔAIC < 2[a] to assess the effects of physical factors on the probability of eel occurrence of each size class

Model	Variable					edf			Weight	df	AIC	ΔAIC	UBRE
	(Intercept)	Peb	Cob	Boul	UWV	s(CV)	s(ISC)	s(DR)					
Small-sized eel													
1	0.28					1.00**	5.15	1.00*	0.29	8	94.05	0	0.133
2	0.31					1.00**		1.00*	0.25	3	94.28	0.23	0.136
3	0.27				0.05	1.00**	5.20	1.00*	0.10	9	96.01	1.96	0.157
Null	0.32								0.00	1	115.02	20.97	0.386
Full	0.13	0.13	1.07	1.37	−0.08	1.00**	5.15	1.00*	0.02	12	99.77	5.72	0.202
Large-sized eel													
1	−3.80*	−2.21	1.13	1.24	−1.73	4.41		7.91	0.47	17	96.16	0	−0.225
2 (Full)	−3.77*	−2.26	1.10	1.25	−1.85	4.43	1.00	7.8	0.22	18	97.71	1.55	−0.212
3	−4.46*	−2.11	0.76	1.59		2.68		8.32	0.14	14	98.58	2.42	−0.205
Null	−1.48***								0	0	120.94	24.78	−0.025

[a] Based on comparisons of null and full models in the general additive models; estimated degrees of freedom (edf) of predictor variables fitted by smoothing splines and β coefficients of predictor variables are shown

Peb, pebble; Cob, cobble; Boul, boulder; ISC, index of substrate complexity; UWV, underwater vegetation; DS, dominant substrate; CV, current velocity; DR, distance from the nearest riverbank; UBRE, unbiased risk estimator; s() indicates a smoothing cubic spline

*$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$ in a Ward test

Discussion

The present study provides important data on the longitudinal distribution and microhabitat use of Japanese eels of two different size classes during their riverine life stages. As shown in previous studies, we found that the density of both small-sized and large-sized eels decreased with increasing distance from the river mouth (Tzeng et al. 1995; White and Nights 1997; Laffaille et al. 2003; Lasne and Laffaille 2008; Yokouchi et al. 2008). We also found a negative relationship between weirs and the density of small-sized eels but not large-sized eels. It is well known that weirs can prevent the upstream migration of anguillid eels, contributing to the loss of longitudinal connectivity within a watershed (White and Knights 1997; Feunteun 2002; Ministry of the Environment, Japan 2016; Kume et al. 2019; Kwak et al. 2019). Our results support those of our previous study which found that the density of small-sized eels decreased as the number of weirs increased (Kume et al. 2019). However, no relationship was found between small-sized eels and maximum weir heights (Kume et al. 2019). Weirs higher than 40 cm have been reported to hinder the upstream migration of Japanese eel elvers (Ministry of the Environment, Japan 2016). It is likely that the occurrence of periphyton mats on the weir surface, which was observed in this study, may help young eels (especially glass eels and elvers) to climb the weirs in our study system (Solomon and Beach 2004). In contrast, we found that the density of large-sized eels was not significantly related to either the number or the maximum height of weirs. Kwak et al. (2019) reported that dams shorter than 3.0 m in height did not prevent the upstream migration of yellow American eels (*A. rostrata*). In addition, yellow eels tend to show a small home range in a river (Laffaille et al. 2005; Itakura et al. 2018). Therefore, we suggest that eels can spread their distribution within a river when they are at the glass and elver stages and then they will stay there until the onset of maturation (i.e. the silver eel stage) when they move out to sea. Alternatively, large-sized eels may repeatedly move within a river until the onset of maturation. However, further research is needed to elucidate eel movement in rivers in relationship to eel growth stage and size. In addition, the climbing abilities of the two size classes we studied remain unclear. Thus, there is a need for further studies on the relationship between eel body size and weirs, particularly studies that can exclude any effects from proximity to the river mouth.

Moreover, analysis of the microhabitat uses of small-sized and large-sized eels suggested that different physical factors affected eel occurrence depending on body size. The relationship between distance from the nearest

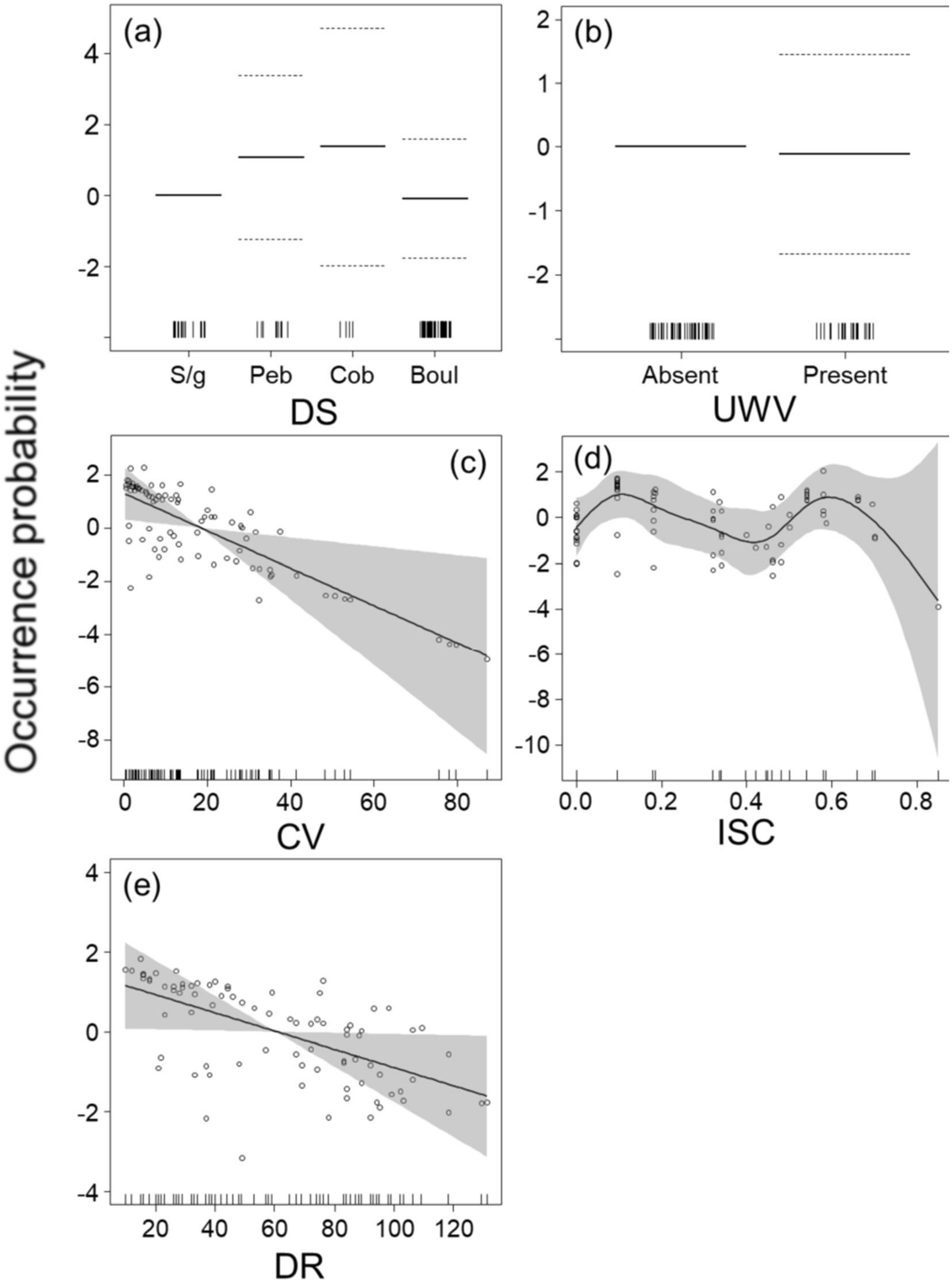

Fig. 3 Results of general additive models (full model) on the probability of small-sized eels (<200 mm in total length) occurrence in different microhabitats, including (a) dominant substrate (DS), (b) underwater vegetation (UWV), (c) current velocity (CV), (d) index of substrate complexity (ISC), and (e) distance from the nearest riverbank (DR). Circles indicate all quadrats. Lines with shaded areas (or upper and lower brackets) indicate estimated curves (or lines) with 95% confidence bands. Tick marks on x-axes show the location of observations along the range of continuous explanatory variables

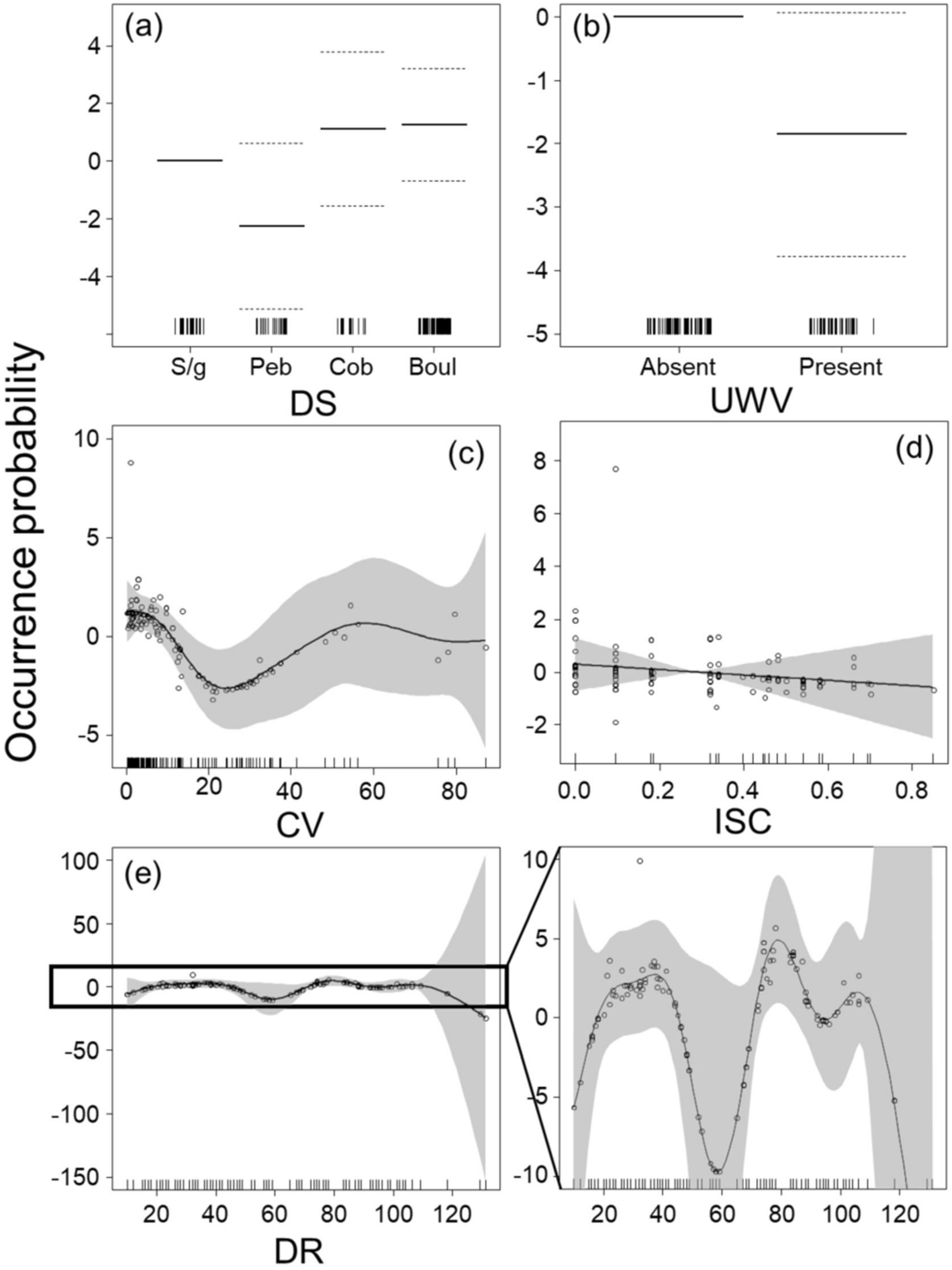

Fig. 4 Results of general additive models (full model) on the probability of large-sized eel (≥200 mm in total length) occurrence in different microhabitats. Figures show the results of (a) dominant substrate (DS), (b) underwater vegetation (UWV), (c) current velocity (CV), (d) index of substrate complexity (ISC), (e) distance from the nearest riverbank (DR) with a left panel inset in focus view. Circles indicate all quadrats. Lines with shaded areas (or upper and lower brackets) indicate estimated curves (or lines) with 95% confidence bands. Tick marks on x-axes show the location of observations along the range of continuous explanatory variables

riverbank and eel density was strong for small-sized eels but weak for large-sized eels. Our findings suggest that small-sized eels use the near-shore habitat preferentially, while large-sized eels inhabit a much wider area from the near-shore to the center of a river. These results coincide with those of a previous study on European eel (*A. anguilla*) (Laffaille et al. 2003). Our results also revealed the strong influence of CV on the habitat uses of both small-sized and large-sized eels. The density of small-sized eels increased in habitats with a CV of <20 cm/s. Previous studies demonstrated that small-sized eels preferred habitats with a slower water flow (Barbin and Krueger 1994; Linton et al. 2007). For example, American eels with a small body size (mean 56 mmTL) could not maintain their positions in water columns with a CV exceeding 35–40 cm/s (Barbin and Krueger 1994). In our study, however, large-sized eel density peaked twice, when the CV was approximately 15 and 55 cm/s. Previous studies showed that yellow European eels (mean 444 mmTL), corresponding to the large size class in our study, could swim at 30–55 cm/s under experimental conditions (Quintella et al. 2010). Therefore, the CV is likely to affect how well anguillid eels maintain their positions in the river based on the limitation of their swimming ability.

The riverbed structure is also an important factor for eel habitats because eels settle and hide in various types of riverbed materials during different riverine life stages (Dou and Tsukamoto 2003; Aoyama et al. 2005; Tomie et al. 2013, 2017; Christoffersen et al. 2018). In our study site, the small-sized eels were observed in very complex substrates, composed of small riverbed materials (i.e. pebbles) which created spatially heterogenous habitats (Kume et al. 2019). They were also observed in relatively simple substrates, containing large particle sizes (i.e. cobble). Small gaps can be found between these large particles which may provide opportunities for small-sized eels to hide. By contrast, the large-sized eels used a relatively simple riverbed with large particle sizes (i.e., boulder). Such riverbed materials create larger gaps in which large-sized eels can hide. Therefore, small-sized eels can settle and hide in a wider range of substrate types, while large-sized eels are likely to require larger gaps between larger particles in which to settle and hide.

Previous studies revealed that glass eels and elvers preferred to use habitats with UWV (Laffaille et al. 2003; Johnson and Nack 2013). However, small-sized eels, including the elver and yellow eel stages, showed no tendency to use habitats with the presence of UWV in the present study. Combining our results with those from previous studies suggests that UWV requirement differs between glass eels, elvers, and yellow eels. Thus, further studies on the UWV requirements of small-sized eels at each riverine life stage are needed. However, we also found that large-sized eels avoid habitats with UWV. Previous studies found that large-sized eels hid in UWV in relatively large rivers (Laffaille et al. 2003; Johnson and Nack 2013). Thus, both size classes of eels are likely to use UWV as their habitats.

Overall, the present study revealed size-dependent changes in the distribution and microhabitat use of Japanese eels during riverine life stages. Firstly, weirs acted as barriers to prevent eel upstream migration, and the density of small-sized eels decreased as the number of the weirs increased. The small-sized eels used near-shore habitats with low current velocities as well as relatively complex substrates with smaller particle sizes. The large-sized eels, however, used open habitats, ranging from the near-shore to the center of the river, with low current velocities and simple substrates composed of large particles. These findings provide useful information for the conservation and management of Japanese eels in rivers flowing through paddy fields, which have not yet been used as habitats for the conservation of aquatic organisms, including Japanese eels. Since Japanese eels may require a variety of habitat types depending on river sizes and riverine life stage, the generality and applicability of the obtained results should be validated in several rivers in the future to promote the comprehensive management and conservation of wild eel stocks as well as to implement effective river restoration.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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