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Broad-Scale Environmental Factors Determining Fish Species Composition of River Estuaries in the Japanese Archipelago

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Abstract

This study was conducted to clarify the relationship between fish species composition and environmental factors at various scales in river estuaries in the Japanese archipelago. The estuaries harbor diverse fish species composition due to their complex topography, varied climatic zones, and ocean currents. Non-hierarchical cluster analysis classified the fish species composition of 100 river estuaries (58 families, 152 species, and 486,356 individuals) into five groups. The highest number of species was confirmed in the group of river estuaries located in southwestern Japan and flowing into the inner bay (55.1 ± 9.6 species), characterized by an abundance of the number of Gobiidae species. In contrast, the species number was the lowest in the groups consisting of river estuaries that primarily belong to the northern Japanese archipelago (15.3 ± 3.3 species) that were characterized by an abundance of the number of cold-water fishes such as Salmonidae, Pleuronectidae, and Osmeridae. The highest fish species diversity was confirmed in the groups consisting of river estuaries flowing into the inner bays of southwestern Japan, which had a large tidal range (344 ± 132 cm), suggesting that the large tidal differences create a diverse tidal flat environment that supports fish species diversity. These results indicate that regional species diversity and geographical factors influence the classification of fish fauna. In northeastern Japan, the classification was influenced by geographic area and associated water temperature changes, whereas in southwestern Japan, tidal differences and wave effects could be more important. Understanding the factors that influence the fish species composition of a target river is fundamental to estuarine conservation, and the findings of this study provide basic knowledge for conservation.

Keywords River estuary · Fish species composition · Environmental factors · Tidal difference · Wave energy

Introduction

Estuaries provide diverse ecosystem services, including fishery nurseries, filtering of nutrients and pollutants, carbon sequestration and storage, elevation maintenance, and various recreational and cultural uses (Boorman 1999; Craft et al. 2009; Kelleway et al. 2017). Their value is extremely high, with its annual supply of services estimated at 22,832 USD/ha/year, making them the most valuable biome (Groot et al. 2012; Costanza et al. 2014). The high ecosystem services of estuarine areas have led to their use by humans since ancient times (Lesourd et al. 2001; Lotze et al. 2006). A study has estimated that 61% of the world's population lives in coastal areas (Alongi 1998). The estuary is one of the most threatened natural systems due to very high anthropogenic impacts (Lotze et al. 2006; Barbier et al. 2011). Salt marshes, tidal flats, and mangrove forests are disappearing around the world due to anthropogenic impacts such as reduced sediment supply from dam construction, coastal development involving land reclamation, and navigation channel dredging (Blum et al. 2009; Kirwan and Megonigal 2013; Murray et al. 2014; Goldberg et al. 2020; Lopes et al. 2021). Loss and degradation of estuarine biodiversity and ecosystem functions promote increased biological invasion, degraded water quality, and vulnerability of estuarine and coastal areas to flooding and storm surges (Koch et al. 2009; Temmerman et al. 2013; Lagos et al. 2017).

It is important to understand the relationship between the organisms that inhabit the estuary and environmental factors to conserve and restore the estuarine environment.

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Various taxonomic groups such as fish, benthic animals, and plankton have been used to represent the biota of estuarine environments. For example, fish fauna and benthic animals were used as the environmental indicators for evaluating habitat diversity and environmental change (Edgar and Barrett 2002; Nanami et al. 2005; Strayer and Malcom 2007; Nicolas et al. 2010; Villéger et al. 2010; Itsukushima et al. 2017a; 2019; Lechêne et al. 2018). Furthermore, plankton were used to evaluate the water quality environment and its monitoring (Zhou et al. 2008; Paerl et al. 2010; Dalu et al. 2018). Fish are particularly important as a taxon for assessing estuarine environments because they represent a variety of trophic levels, utilize both aquatic and terrestrial sources of food, are resident or migratory, and can indicate a wide range of effects rather than just stressors within a particular area (Whitfield and Elliott 2002). Furthermore, the temporary invasion of freshwater and saltwater fish has also resulted in spatiotemporally complex community structures (Blaber et al. 1989; Simier et al. 2004).

Among the estuarine environments, river estuaries have complex dynamic habitats due to the influence of waves, periodic tides, and the mixing of freshwater and saltwater (Dyer 1997; Schröder-Adams et al. 2014). The river estuarine biological community comprises marine and freshwater organisms in addition to the brackish water-dependent species such as *Periophthalmus modestus*, *Helice tridens*, and *Batillaria multiformis* (Sousa et al. 2007; Sheaves and Johnston 2008; Whitfield et al. 2012). Furthermore, the intertidal environment provides important nursery habitats for larval and juvenile fishes (Bozeman and Dean 1980; Winkler et al. 2003; Vanalderweireldt et al. 2019). It is important to elucidate the biota that inhabits the estuaries and the relationships between biota and environmental factors to conserve and restore river estuarine ecosystems. The relationship between habitat-scale non-biological factors and estuarine fish fauna has been investigated such as salinity (Martino and Able 2003; Feyrer et al. 2015), physical habitat structure (Szedlmayer and Able 1996; Hosack et al. 2006), water temperature (Harrison and Whitfield 2006; Vasconcelos et al. 2010), and precipitation (Hossain et al. 2012). However, since river estuaries are influenced by various scales of the upstream catchment factors including habitat, reach, segment, and stream system (Frissell et al. 1986), it is important to elucidate the relationship between anthropogenic influences of the upstream area and environmental change in river estuaries. The effects of reduced freshwater supply and altered sediment dynamics associated with dam construction on estuarine plankton (Domingues and Galvão, 2006; Domingues et al. 2012), changes in terrestrial and aquatic plant communities (Colonnello and Medina 2004), and changes in fish community structure (Chícharo et al. 2006) have been investigated. However, there is a lack of knowledge on broad-scale anthropogenic factors, including land use and the environmental degradation of riverine estuaries. In addition, studies on the relationship between fish fauna and environmental factors in riverine estuaries have mainly focused on local ecological region scale studies, and there are limited examples of studies on the relationship between environmental factors at various scales for a nationwide, broad-scale fish community. However, to manage the conservation and restoration of the fish fauna in river estuaries, it is necessary to elucidate the species that characterize the local fish fauna and identify community structure and influential physical environmental factors based on broad-scale data.

The Japanese archipelago, the target of this study, is one of 34 hotspots worldwide (Mittermeier et al. 2004), and a diverse range of fish species inhabit its riverine estuaries. Because the archipelago contains diverse climatic zones, tropical, subtropical, temperate, subarctic, and frigid marine species occur in river estuaries (Itsukushima 2023). The fish species that inhabit river estuaries vary greatly due to complex ocean currents (Itsukushima and Kano 2021; 2022). In addition, the hydrologic environment and sediment dynamics that form the physical basis of riverine estuaries are complex, and the large sediment production capacity and river flood discharge in the Japanese archipelago profoundly affect the river estuarine habitat and environment formation. In order to conserve the fish fauna of river estuaries, it is necessary to understand the regional characteristics of the fish fauna and to develop conservation measures based on a comprehension of the relationship between the fish fauna and environmental factors. This study aims to accumulate the fundamental knowledge necessary for the conservation of fish species composition in river estuaries by elucidating (1) the regional characteristics of riverine estuary fish species composition and (2) the relationship between riverine estuary fish species composition and environmental factors at various scales in the Japanese archipelago.

Methods

Study Area and Fish Species Composition Data

The ocean currents around the Japanese archipelago are complex, with the Kuroshio Current (warm current) and the Kurile Current (cold current) on the Pacific Ocean side and the Tsushima Current (warm current) and the Liman Current (cold current) on the Sea of Japan side, as well as various other currents of different sizes. In addition, the coastal area is approximately 35,000 km long, giving rise to a complex topography. This diversity of currents and landforms has given rise to a variety of river estuarine biota. The Fossa Magna corresponds to the boundary between the North

American Plate and the Eurasian Plate and is one of the major rift zones in Japan, and in geology, it is the border zone between northeast and southwest Japan (Naumann 1885; Yanai et al. 2010) (Fig. 1).

To investigate the relationship between the fish species composition of riverine estuaries and environmental factors, fish species composition data from 100 rivers in the Japanese archipelago, where surveys of the fish species composition of riverine estuaries are regularly conducted by the National Census on River Environment (1992–2019) conducted by the Ministry of Land, Infrastructure, Transport, and Tourism, Japan (http://www.nilim.go.jp/lab/fbg/ksnkankyo/), were included in the analysis. Rivers with estuarine lakes in their estuaries were excluded from the analysis because of their unique environments. In addition, the Nansei Islands are an important habitat for endemic saltwater and brackish water fish (Yoshigou 2014; Sekiguchi 2015); however, they were excluded from the analysis because there are no long-term data on the fish fauna of river estuaries and no large rivers are directly managed by the central government on these islands.

Surveys of the National Census on River Environment are conducted at approximately 5-year intervals for each water system, with each river surveyed between three and five times. For each river, cast nets and hand nets were used to collect fish at all survey sites. The estimated amount of sampling effort was of approximately five cast nets for each habitat appearing at the target site and approximately one person × 1 h/survey site for hand nets sampling. In addition, depending on the environmental characteristics of the study area, additional capture by set nets, gill nets, scoop nets, longline, fish pots, seine nets, fish cage, minnow trap, dive surveys, and digging back was conducted. The surveyed area was 1127 ± 1027 m, although it varied according to the size of the river. In order to obtain an unbiased understanding of the fish species inhabiting the various environments in each investigation site, sampling was conducted in rapids, pools, backwater, abandoned channel, springs, and others (e.g., run, glides, tidal flats, and other habitats). Data from sites in the most downstream tidal zone of each water system were used. If the species was present at least once during these surveys, it was considered to inhabit the site. The total number of individuals that appeared in all surveys of the target river estuaries during the period covered by the National Census on River Environment was used as quantitative data (Table S1). In addition, only species identified at the species level were included. In order to verify the validity of using quantitative data, the same analysis was conducted using presence/absence data of the analyzed species, and the results showed that 93% of the rivers were classified in agreement (Table S2); thus, the use of quantitative data was deemed appropriate.

Settings for Environmental Factors

To characterize the environment of each watershed, variables that describe the characteristics of the watershed

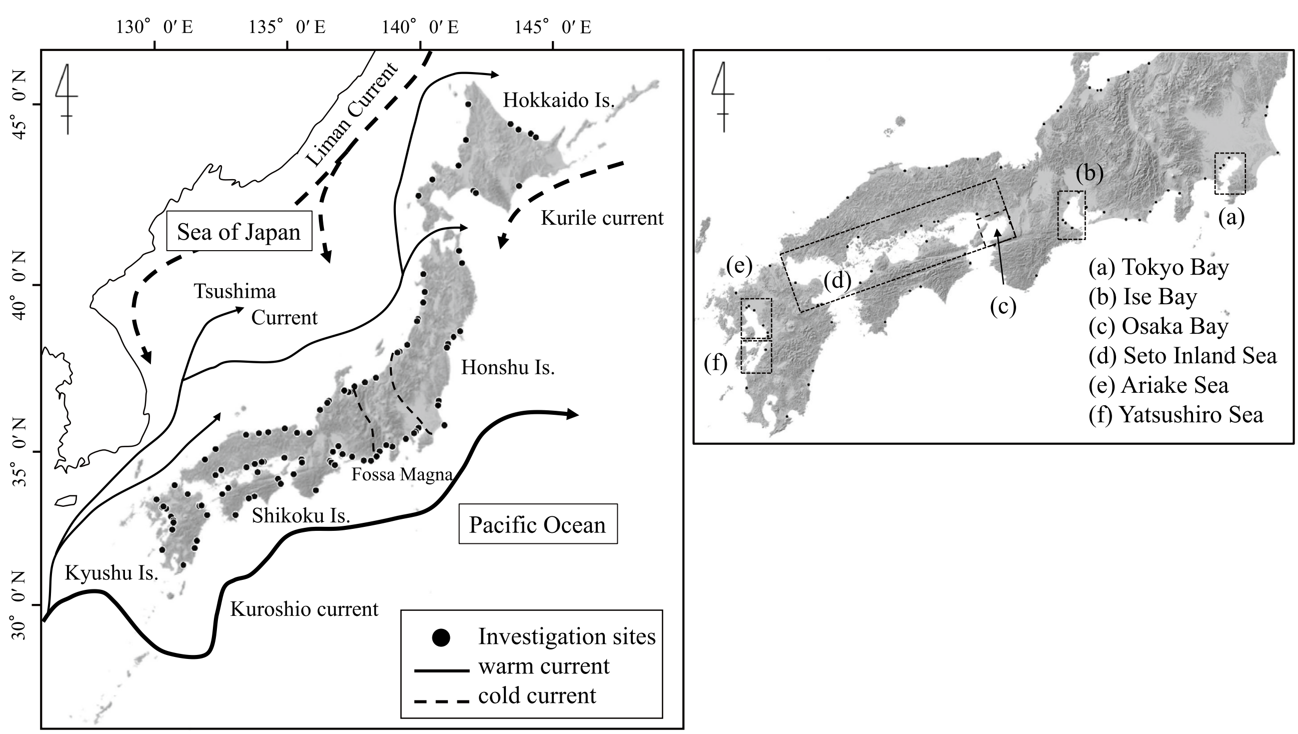


Fig. 1 Location of the study site

(hereafter referred to as “environmental factors”) were calculated through geographic information systems (ESRI ArcGIS Version 10.3) and literature. A total of 35 environmental factors were used, including physical environmental (five indicators), topographic (6 indicators), hydrologic (7 indicators), anthropogenic (5 indicators), geological (3 indicators), and water quality (9 indicators) factors of river estuaries (Table 1).

A total of 35 environmental factors were used for the analysis (Table 1). The physical environmental factors in the river estuary were wave exposure (WE), direct fetch (DF), tidal difference (TD), friction velocity at the river mouth

Table 1 Environmental factors calculated for statistical analysis

Environmental factors	Explanation	Average ± standard deviation	Correlation factors (|r|> 0.4)
River estuarine environmental factors			
WE	Wave exposure	11.56 ± 6.00	DF +, BM +, AH +
DF (km)	Direct fetch	614.72 ± 519.64	WE +
TD (cm)	Tidal difference	172.81 ± 128.74	WT +, PH +
FV (m^2/s^2)	Friction velocity	111.25 ± 110.55	BM +
BM	River bed material	1.35 ± 0.48	FV +
Topographic factor			
WA (km^2)	Watershed area	2200.88 ± 2894.37	SL +, ND +
SL (km)	Stream length	820.61 ± 1060.73	WA +, ND +
AH (m)	Altitude of the riverhead	1417.37 ± 650.92	WE +, TG +
TG	Terrain gradient	0.0162 ± 0.0096	AH +
FR	Form ratio	0.17 ± 0.09	
DD (km^{-1})	Drainage density	0.40 ± 0.15	WT +
Flow regime			
SDmax ($m^3/s/km^2$)	Maximum specific discharge	179.65 ± 127.67	WT +, CR +
SD75 ($m^3/s/km^2$)	75-day specific discharge	5.16 ± 2.62	SDo +, SD275 +, SD355 +, SDmin +
SDo ($m^3/s/km^2$)	Ordinary specific water discharge	3.12 ± 1.71	SD75 +, SD275 +, SD355 +, SDmin +
SD275 ($m^3/s/km^2$)	275-day specific discharge	2.09 ± 1.24	SD75 +, SDo +, SD355 +, SDmin +
SD355 ($m^3/s/km^2$)	355-day specific discharge	1.26 ± 0.92	SD75 +, SDo +, SD275 +, SDmin +
SDmin ($m^3/s/km^2$)	Minimum specific discharge	0.85 ± 0.73	SD75 +, SDo +, SD275 +, SD355 +
CR	Coefficient of river regime	477.24 ± 823.69	SDmax +
Anthropogenic factor			
ND	Number of dams	13.77 ± 17.06	WA +, SL +
PD (people per km^2)	Human population density	397.13 ± 1049.17	COD +, TN +, TP + UR +
MO (%)	Percentage of mountain area	76.17 ± 17.59	TN −, AG −, UR −
AG (%)	Percentage of agricultural area	16.10 ± 10.73	TN +, MO −
UR (%)	Percentage of urban area	6.79 ± 10.23	COD +, TN +, TP +, PD +, MO −
Geology			
SR (%)	Percentage of sedimentary rock	66.03 ± 25.21	IR −
IR (%)	Percentage of igneous rock	28.72 ± 23.26	SR −
MR (%)	Percentage of metamorphic rock	5.25 ± 11.11	
Water quality			
WT (°C)	Average water temperature	15.32 ± 3.26	TD +, PH, DO −, DD +, SDmax +
PH	Potential of hydrogen	7.58 ± 0.33	TD +, WT +
BOD (mg/L)	Biochemical oxygen demand	1.15 ± 0.65	COD +, TN +, TP +, CGL +
COD (mg/L)	Chemical oxygen demand	2.97 ± 1.34	BOD +, TN +, TP +, CGL +
SS (mg/L)	Suspended solids	10.19 ± 11.21	
DO (mg/L)	Dissolved oxygen	9.90 ± 1.15	WT −
TN (mg/L)	Total nitrogen	1.16 ± 1.02	BOD +, COD +, TP +, CGL +, PD +, MO −, AG +, UR +
TP (mg/L)	Total phosphorus	0.070 ± 0.075	BOD +, COD +, TN +, CGL +, PD +, UR +
CGL (pieces/mL)	Number of colitis germ legions	11,426.00 ± 13,465.88	BOD +, COD +, TN +, TP +

in flow discharge of occurrence probability 1/5 (FV), and river bed material (BM). Itsukushima et al. (2017b; 2019) described the calculation methods for these indicators. Watershed area (WA), stream length (SL), altitude of the riverhead (AH), terrain gradient (TG), form ratio (FR), and drainage density (DD) were used as topographic factors. Specific focus was afforded to the flow regime, and various specific discharge values were used as hydrological indicators, including the maximum specific discharge (SDmax), 75-day specific discharge (SD75), ordinary specific discharge (SDo), 275-day specific discharge (SD275), 355-day specific discharge (SD355), and minimum specific discharge (SDm). In addition, the coefficient of river regime (CR) was used as an indicator of disturbance, calculated by dividing SDmax by SDmin. Anthropogenic factors included the number of dams (ND), obtained from the Japanese Dam Foundation (2019), human population density (PD) in the watershed, and land use (percentage of mountain area (MO), percentage of mountain agriculture area (AG), percentage of urban area (UR)). Based on the generation process, geology is roughly classified into sedimentary rock (SR), igneous rock (IR), and metamorphic rock (MR). The water quality indicators were average water temperature (WT), potential of hydrogen (PH), biochemical oxygen demand (BOD), chemical oxygen demand (COD), suspended solids (SS), dissolved oxygen (DO), total nitrogen (TN), total phosphorus (TP), and number of colitis germ legions (CGL). The calculation methods for these indicators are described in the supplementary method and Itsukushima (2021).

The above 35 environmental factors showed great variation and various correlations among the target watersheds (Table 1). The relationship between water temperature (WT) and maximum specific discharge (SDmax) was observed, reflecting the climatic characteristics of the Japanese archipelago. Human population density (PD), which indicates anthropogenic influence, was correlated with the percentage of the urban area (UR), total nitrogen (TN), and total phosphorus (TP). In the statistical analysis, the correlation coefficients between variables were considered in the variable selection.

Statistical Analysis

The analysis included 486,356 individuals of 152 species in 15 orders and 58 families that occurred in at least 5 of the 100 rivers to eliminate the influence of infrequently occurring species. The number of individual fish species was used after logarithmic conversion [$\log_e (x + 0.5)$] (x: number of individuals) to approach a normal distribution (Yamamura 1999). A non-hierarchical cluster analysis using the k-mean method was conducted to classify the fish species composition. The optimal number of divisions was the one that maximized the Calinski-Harabasz index (Caliński and Harabasz 1974). The Calinski-Harabasz Index is an evaluation index based on the degree of dispersion between clusters and clusters (Wang and Xu 2019). In addition, non-metric multidimensional scaling analysis (NMDS) was conducted to summarize the composition of fish community structure using the Bray–Curtis similarity index. Furthermore, to eliminate the occurrence of multicollinearity of environmental factors, I narrowed the number of variables from 35 environmental factors to 17 so that the variance inflation factor (VIF) would be less than 10 (Kennedy 1992). In addition, environmental factors with a significant effect ($p < 0.001$) on the NMDS axis were selected by the Monte Carlo permutation test and illustrated (Becker et al. 2017). Additionally, indicator species of each group were obtained using the indicator value method (IndVal) (Dufrêne and Legendre 1997).

Finally, a decision tree model (classification and regression tree (CART)) was used to identify the environmental factors that contributed to the classification of the river estuarine fish species composition. The 17 environmental factors were used as explanatory variables, and the classification result of fish species composition was used as the objective variable. The Gini index was adopted as the judging criteria, and the optimal ramification number by cross-validation was calculated (De'Ath and Fabricius 2000). In addition, a multiple comparison test was used to compare the differences in environmental factors among groups.

All analyses were conducted using the statistical software "R" and package "rpart," "vegan," and "labdsv" (Therneau and Atkinson 1997; Roberts 2007; Oksanen et al. 2018).

Results

Non-hierarchical cluster analysis results showed that the fish species composition of the river estuaries of the Japanese archipelago could be classified into five groups (Fig. 2). Group A consisted mainly of rivers in Hokkaido, while group B consisted mainly of rivers on the Sea of Japan and Pacific Ocean sides of northern Japan. Group C was composed of rivers in southwestern Japan that all flow into inner bays. The inner bays into which the rivers in group C enter are Tokyo Bay (three rivers), Ise Bay (one river), Seto Inland Sea (seven rivers), Ariake Sea (six rivers), and Yatsushiro Sea (one river). Group D consisted mainly of rivers flowing into the Pacific and Sea of Japan sides of southwestern Japan. Rivers belonging to group E are widely distributed on the Sea of Japan and Pacific Ocean sides; however, five of the 10 rivers classified were rivers flowing through the Fossa Magna zone.

The total number of species occurring in the rivers belonging to each group, as well as the mean values for frigid/subarctic (Fr), temperate (Te), and tropical/

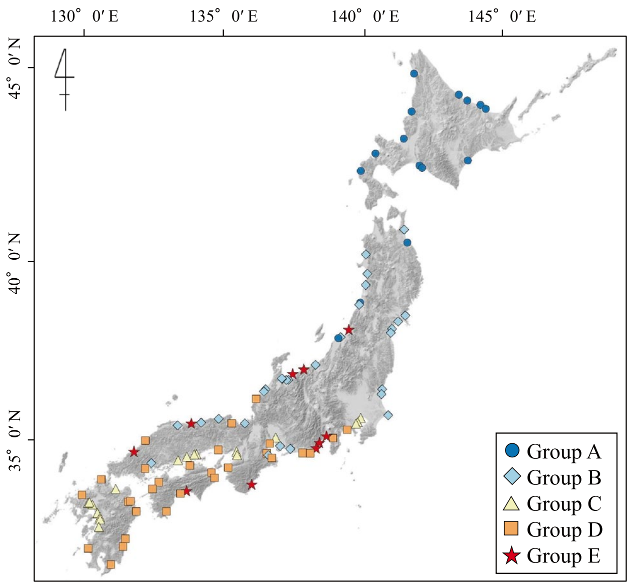


Fig. 2 Classification results of non-hierarchical cluster analysis for 1000 river estuaries in the Japanese archipelago using fish species composition

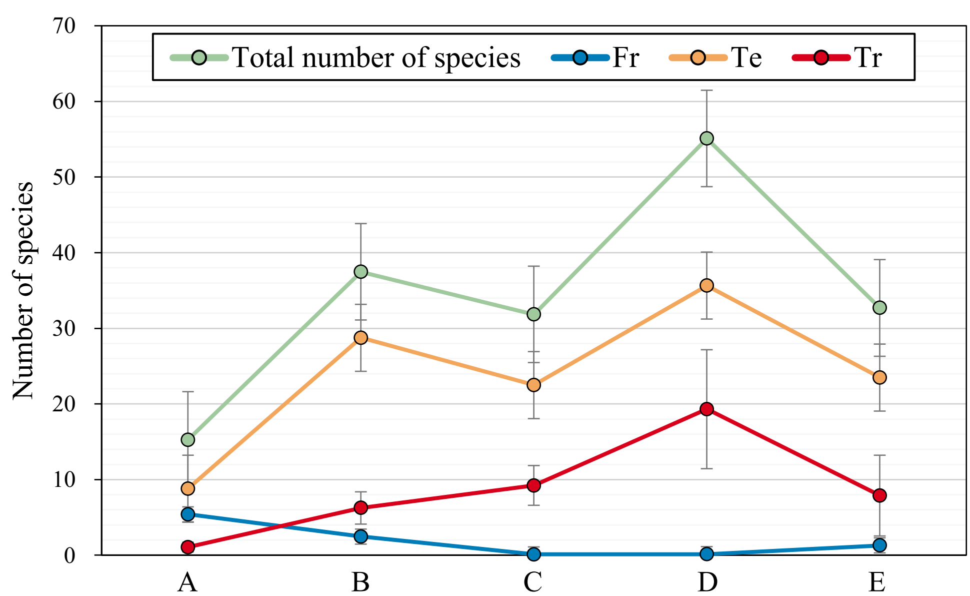
subtropical (Tr) species, is shown in Fig. 3. The total number of species was the lowest in group A and the highest in group D in southwestern Japan. The climatic zone of the component species tended to be dominated by temperate species (Te), with tropical and subtropical species (Tr) also abundant in group D. On the other hand, in group A, which consisted of riverine estuaries in Hokkaido, the species composition consisted of frigid/subarctic species (Fr) and temperate species (Te). The number of individuals that appeared in the river estuaries belonging to each group was organized by family, with fishes belonging to the Gobiidae accounting for the highest percentage in all groups (Fig. 4). In group A, the combined proportion of fish species in the families Cyprinidae, Lateolabracidae, and Osmeridae was larger than that of the Gobiidae species. In group B, the trend was similar to group A; however, the proportion of fish species in the family Engraulidae was relatively large.

In group C, fishes belonging to Gobiidae accounted for about 70% of the number of individuals, with other fish species accounting for a smaller percentage. This trend was also confirmed in group D. In contrast, the river estuaries in group E tended to have a larger proportion of Plecoglossidae than the other groups.

The results of the indicator species analysis showed high values for cold-water fish species in group A, such as *Salvelinus leucomaenis leucomaenis* and *Platichthys stellatus* (Table 2). In group B, fishes such as *Kareius bicoloratus*, *Trachurus japonicus*, and *Pseudaspius brandtii* were selected; however, these values were relatively low at around 0.3. In group C, which consisted of the inner bay inflow rivers of southwestern Japan, fishes belonging to Gobiidae, such as the *Tridentiger bifasciatus* and *Periophthalmus modestus*, showed high values. Group D tended to have higher IndVal values for subtropical and tropical fish species such as *Gerres equulus*, *Acanthopagrus latus*, and *Hippichthys penicillus*. In contrast, group E had higher indicator values for migratory fish that invade the freshwater area, such as *Rhinogobius nagoyae*, *Rhinogobius fluviatilis*, and *Plecoglossus altivelis altivelis*.

As a result of NMDS and the permutation test, WT, DD, PH, TD, UR, BOD, AG (first quadrant positive), SS (second quadrant positive), DF, WE, FV, BM (third

Fig. 3 The total number of species occurring in the rivers belonging to each group, as well as the mean values for frigid/subarctic (Fr), temperate (Te), and tropical/subtropical (Tr) species



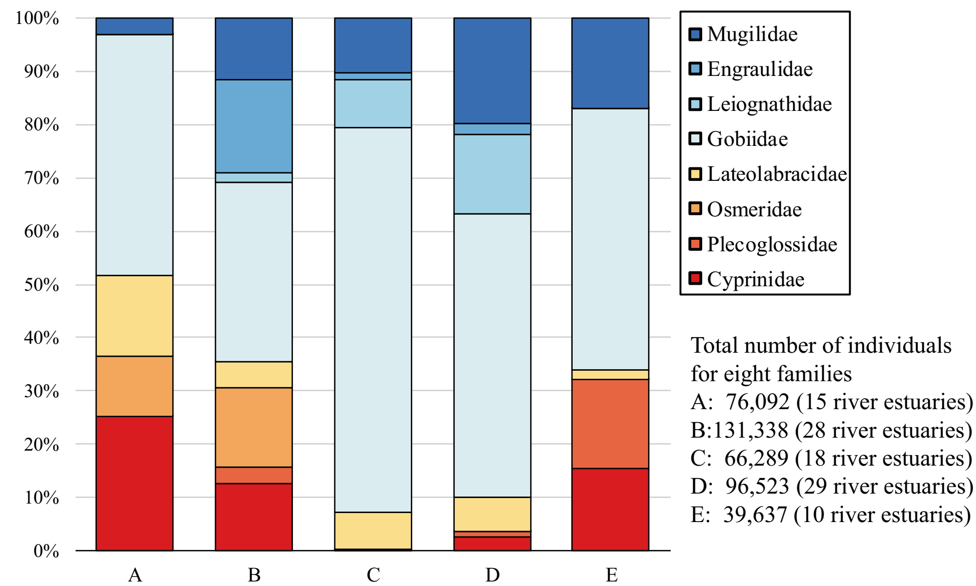


Fig. 4 Composition of the number of individuals of each group. The total number of individuals that appeared in the river estuaries belonging to each group is summed and shown as a percentage for the top five families in each group (total of eight families)

quadrant positive), and SDmax (fourth quadrant positive) were selected as the environmental factors strongly related to the ordination of fish species composition ($p < 0.001$) (Fig. 5 and Table 3).

The CART using the non-hierarchical cluster analysis classification results of the river estuarine fish species composition as the objective variable and environmental factors as explanatory variables resulted in an optimal number of branches of 7 and an overall misclassification rate of 38.6% (Fig. 6). If the average water temperature was less than 16.09 ℃ in branch 1, it was predicted to be a river group centered in northern Japan and the Fossa Magna area (groups A, B, and E). Furthermore, if the water temperature was less than 9.85 °C in branch 2, the rivers were predicted to be group A, mainly in Hokkaido. Water temperatures 9.85 °C or above and BOD 0.81 mg/L or above were predicted to be in group B, and those below 0.81 mg/L were predicted to be in group E. On the other hand, if the water temperature was greater than or equal to 16.09 °C in branch 1, it was predicted to be a group of rivers in southwestern Japan (groups C and D). In branch 7, rivers with SS greater than or equal to 7.67 mg/L were predicted to be in group C, and rivers with SS less than 7.67 mg/L were predicted to be in group D.

Discussion

Geographic and Topographic Factors on the Classification Results of Fish Species Composition

The results of the non-hierarchical cluster analysis showed that rivers in northeastern Japan were divided into Hokkaido (group A) and the rest of the northern part of Honshu Island (group B). WT was selected by CART as the factor dividing the two groups, indicating that they were classified by water temperature changes associated with regional differences. Rivers in southwestern Japan were not classified by geographic region but by whether they flowed into inner bays or the open sea (Fig. 2). One reason for the difference between being classified or not by geographic region may be the difference in the diversity of fish fauna in northeast and southwest Japan. Fish diversity in southwestern Japan is supported by temperate, subtropical, and tropical species. A comparison of the fish species composition of classified groups shows that the average number of species is the highest in group D, with temperate, subtropical, and tropical species making up the majority (Fig. 3). This is because the Kuroshio Current contributes to the dispersal of many subtropical and tropical species (Tashiro et al. 2017; Motomura and Matsunuma 2022).

Southwestern Japan has a higher number of river estuaries species, especially those belonging to Gobiidae (Koyama et al. 2019). In addition, tidal flat environments predominate in inner bay rivers with large tidal differences (Wells 1995). Rivers located in the inner bays and with abundant tidal flat environments are expected to harbor fish fauna that differ significantly from those of rivers flowing into the open ocean. *Periophthalmus modestus* and the *Tridentiger bifasciatus*, which showed high IndVal values in group C, are species that particularly prefer tidal flat environments, and it is presumed that the presence of these species led to classification by habitat rather than geographic location.

Another reason why river estuarine ichthyofauna in southwestern Japanese rivers is not classified according to geographic location seems to be the size of the river.

Table 2 High IndVal species of each group (species with $p < 0.05$ and IndVal > 0.2 are indicated; only group D is greater than 0.4) and the climatic zones where each species is distributed are also listed

Scientific name	IndVal	*p* value	Climatic zone
Group A			
Salvelinus leucomaenis leucomaenis	0.60	0.001	Fr
Platichthys stellatus	0.59	0.001	Fr
Hypomesus nipponensis	0.55	0.001	Fr
Gymnogobius castaneus comp	0.54	0.001	Fr
Oncorhynchus keta	0.47	0.001	Fr
Gymnogobius urotaenia	0.42	0.001	Te
Gymnogobius opperiens	0.41	0.001	Fr
Osmerus dentex	0.33	0.001	Fr
Pseudaspius hakonensis	0.31	0.001	Te
Acanthogobius lactipes	0.30	0.002	Te
Oncorhynchus masou masou	0.28	0.006	Fr
Group B			
Kareius bicoloratus	0.30	0.011	Te
Trachurus japonicus	0.30	0.004	Te
Pseudaspius brandtii maruta	0.28	0.012	Fr
Chelon haematocheilus	0.27	0.020	Te
Group C			
Tridentiger bifasciatus	0.57	0.001	Te
Periophthalmus modestus	0.49	0.001	Te
Takifugu xanthopterus	0.44	0.001	Te
Nuchequula nuchalis	0.40	0.001	Te
Sardinella zunasi	0.37	0.003	Te
Konosirus punctatus	0.34	0.001	Tr
Acanthogobius hasta	0.33	0.001	Te
Nibea albiflora	0.30	0.002	Te
Acentrogobius virgatulus	0.25	0.012	Te
Acentrogobius sp. A	0.22	0.028	Tr
Group D			
Gerres equulus	0.62	0.001	Te
Sillago japonica	0.50	0.001	Tr
Acanthopagrus latus	0.49	0.001	Tr
Hippichthys penicillus	0.48	0.001	Tr
Plotosus japonicus	0.46	0.001	Tr
Dasyatis akajei	0.43	0.001	Te
Omobranchus punctatus	0.43	0.001	Tr
Chelon macrolepis	0.43	0.001	Tr
Favonigobius gymnauchen	0.42	0.001	Te
Redigobius bikolanus	0.41	0.001	Tr
Group E			
Rhinogobius nagoyae	0.72	0.001	Te
Gymnogobius petschiliensis	0.67	0.001	Te
Rhinogobius fluviatilis	0.57	0.001	Te
Plecoglossus altivelis altivelis	0.48	0.001	Te
Luciogobius guttatus	0.43	0.001	Te
Sicyopterus japonicus	0.43	0.001	Tr
Rhinogobius kurodai	0.37	0.002	Te
Rhinogobius similis	0.35	0.001	Tr
Tridentiger brevispinis	0.31	0.001	Te

The distribution area information used to determine climatic zones was based on Kawano et al. (2011) and Nakabo (2013)

Tr tropical and subtropical species, *Te* temperate species, *Fr* frigid and subarctic species

Northeastern Japan generally has many large rivers and large distances between estuaries. In contrast, southwestern Japan has fewer large rivers (Yoshimura et al. 2005). Furthermore, closer distances between estuaries make it easier for brackish and migratory fish to move through the marine area. In river groups in southwestern Japan, because of the short distance between river mouths, species with low mobility frequently may invade adjacent riverine estuaries, which is thought to increase diversity and form a complex ichthyofauna as a result of repeated migration and dispersal of more species. The complexity of riverine biota in southwestern Japan due to cross-basin migration has also been observed in pure freshwater fish and other taxa (Itsukushima 2019; 2021). The complexity of the fish fauna in river estuaries is likely to be more pronounced because fish species that inhabit riverine estuaries are mobile throughout the region and can move across watersheds more easily than freshwater fish.

In group E, the fish species composition is characterized not by brackish or saltwater fish but by migratory fish such as *Rhinogobius* and *Plecoglossus altivelis altivelis* (Table 2). The rivers belonging to group E, which includes five rivers flowing through the Fossa Magna zone, are characterized by a large topographic gradient (Fig. S1(9)), suggesting that it has a different fish species composition from the northwestern and southwestern Japanese groups. The large topographic gradient of the group E river estuaries likely resulted in the fish species composition being different from that in other rivers because of the large grain size of the bed material and the low salinity, even in brackish water, resulting in abundant habitat structure and spawning habitat favored by the species comprising the fauna. Rivers in the Fossa Magna zone have extremely high sediment production (Udo et al. 2016) and relatively high flows, resulting in a unique ichthyofauna that is different from other regions, and brackish and saltwater fish are scarce. The Fossa Magna belt is also the boundary between the freshwater ichthyofauna of southwestern and northeastern Japan (Itsukushima 2019), and its unique geologic history is also thought to influence the ichthyofauna of river estuaries.

Relationship Between the Classification of Fish Species Composition and Environmental Factors

The statistical analysis showed that group A was the river group with the lowest water temperature (WT) and drainage density (DD) among the target groups (Figs. 5 and 6). In addition, Salmonidae, such as *Salvelinus leucomaenis leucomaenis* and *Oncorhynchus keta*, and cold-water fish, such as *Platichthys stellatus*, showed high IndVal values as indicator species. Results of studies on freshwater fishes also reveal the peculiarities of rivers belonging to Hokkaido, which contains cold-water fishes (Itsukushima 2019). It has been noted that even during the lowest sea-level glacial periods, there was

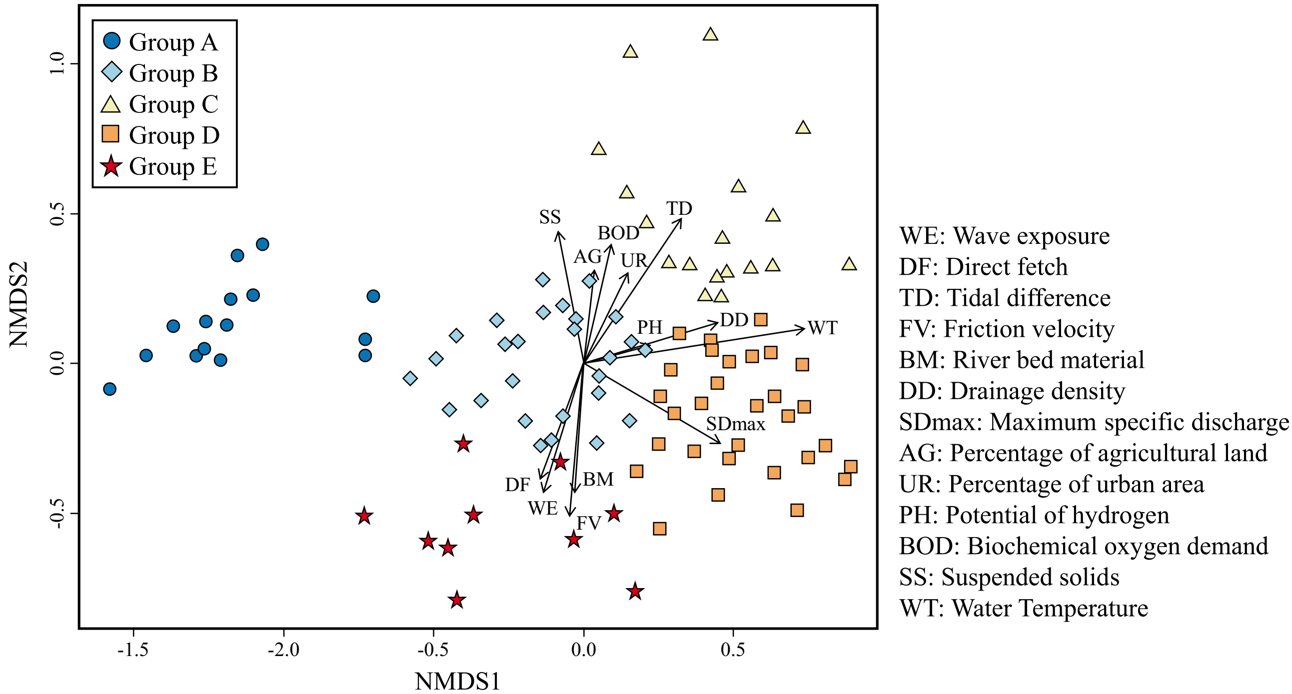


Fig. 5 Result of the non-metric multidimensional scaling analysis (NMDS) for river estuarine fish species composition. Environmental factors that were found to be significantly related ($p < 0.001$) to the NMDS axis as a result of the permutation test are shown as vectors

no terrestrial connection with the Honshu Island for freshwater fish, and the absence of species migration from other areas via the terrestrial zone resulted in a unique fish fauna (Tanaka 1931). On the other hand, brackish and saltwater fish can move the sea area, and thus, the non-connection of land cannot be a barrier to migration. However, the significantly lower water temperatures compared to other areas may have resulted in fewer warm-water species and a fish species composition that differs from other areas.

Table 3 Relationship between environmental factors and NMDS axis

	NMDS1	NMDS2	R2	Pr	
WE	−0.29124	−0.95665	0.2818	0.0002	***
DF	−0.33996	−0.94044	0.2346	0.0002	***
TD	0.56289	0.82653	0.4701	0.0002	***
FV	−0.09007	−0.99594	0.3608	0.0002	***
BM	−0.06354	−0.99798	0.2566	0.0002	***
TP	0.98789	0.15515	0.7680	0.0002	***
PH	0.96682	0.25544	0.1480	0.0002	***
BOD	0.22665	0.97398	0.2311	0.0002	***
SS	−0.18932	0.98191	0.2796	0.0002	***
AH	−0.31152	−0.95024	0.1084	0.0042	**
DD	0.95628	0.29246	0.3097	0.0002	***
SDmax	0.86381	−0.50382	0.3898	0.0002	***
SDo	0.06094	−0.99814	0.0705	0.0258	*
CR	0.96697	0.25488	0.0790	0.0158	*
AG	0.12350	0.99234	0.1390	0.0008	***
UR	0.44157	0.89723	0.1580	0.0008	***
MR	0.96815	−0.25037	0.0663	0.0318	*

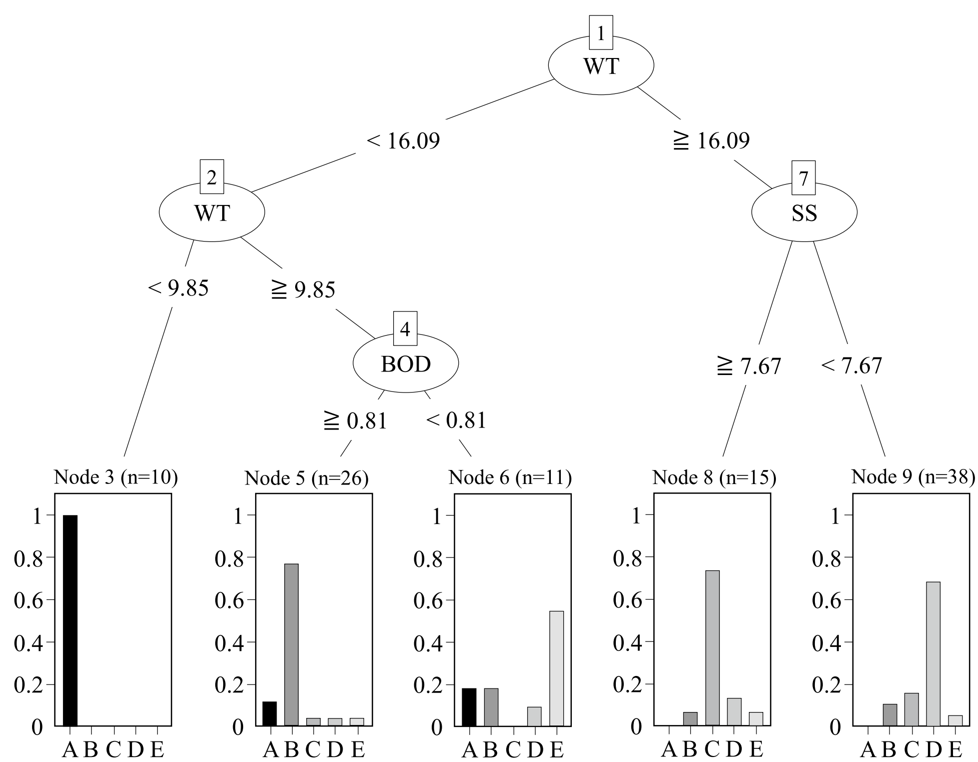
0.01 "*", 0.001, "**", 0 "***"

Group B is plotted near the origin due to ordination by NMDS and is widely distributed on the Pacific and Sea of Japan sides of northeastern Japan (Figs. 2 and 5). Although the classification results using freshwater fish fauna indicate the difference between the fish fauna of the Sea of Japan and Pacific sides of northeastern Japan (Itsukushima 2019), the differences in river estuarine fish species composition were not confirmed in this analysis. This could be the result of similar fish species composition on the Pacific and Sea of Japan sides due to the brackish and saltwater fish moving through the marine area.

The river estuaries belonging to group D are located in the fourth quadrant, where water temperature and river discharge have a large effect (Fig. 5). These rivers are widely distributed on the Pacific and Sea of Japan sides of southwestern Japan. Fundamentally, saltwater fishes differed between the Japan Sea and Pacific Ocean sides, and the Sea of Japan has been shown to have a poorer fish fauna than the surrounding waters because of the shallow depth of the Tsushima Strait and the inability of mesopelagic fishes from the Pacific to invade (Kawano et al. 2014). The analysis in this study also found several rivers classified as group B or E with low numbers of species in parts of the Sea of Japan side. However, some rivers located on the Sea of Japan side have fish species composition similar to that of the Pacific side and are classified as group D. One reason for the similarity of the fish species composition of some river estuaries on the Sea of Japan side to that of the river estuaries on the Pacific side is that the rising seawater temperatures associated with climate change have caused species that were not originally found in the Sea of Japan to expand their distribution from the Pacific side. Among the rivers on the Sea of Japan side, the warm-water fish *Acanthopagrus latus*, which had not been previously identified, was first observed during a survey in the 2010s in the Gono River, classified as group D. Other species such as *Lutjanus russellii*, *Hypoatherina valenciennei*, and *Terapon jarbua* have also been reported to have expanded their distribution area to the Sea of Japan side for the first time since the 2010s (Itsukushima 2023). In addition, a rapid increase in tropical and subtropical species including molluscan and echinoderm species has been reported since the late 1990s in the southernmost part of the Japan Sea (Kobayashi et al. 2006). Changes in the distribution area of saltwater fish species due to rising seawater temperatures associated with climate change are known to have a northward trend along the Pacific coast for tropical and subtropical species such as *Scatophagus argus*, *Lutjanus argentimaculatus*, *Redigobius bikolanus*, and *Hippichthys penicillus* (Kimura et al. 1997; Kudo 2011; Tashiro et al. 2017; Yamakawa et al. 2018, 2020). In addition, it is known that the Kuroshio Current is a source of tropical and subtropical species that invade coastal areas in areas influenced by warm currents near Japan (Tashiro et al. 2017). As a result, the distribution area of these species is expanded as seawater temperature increases, and the fish species in the riverine estuaries of the Japan Sea side and northeast Japan composition can be expected to change. Due to climate change, some rivers on the Sea of Japan side may become more similar to the fish species composition of rivers on the Pacific side, and further monitoring is needed.

SS was selected as a factor that contributed to the classification of group C, which consists mainly of river estuaries flowing to inner bays, and group D, which consists mainly of river estuaries facing the open ocean (Fig. 6). This is thought to be because the rivers flowing to inner bays include many rivers that flow through Japan's three major metropolitan areas, i.e., Osaka Bay, Tokyo Bay, and Ise Bay, and SS concentrations in these rivers are high due to anthropogenic effects from urbanization. Since BOD and COD are also high in group C (Fig. S1), it is clear that anthropogenic influences in these areas are affecting the concentration of SS. In group C, fish species that inhabit the tidal flat environment, such as *Periophthalmus modestus* and *Tridentiger bifasciatus*, were selected as indicator species, suggesting that factors related to external forces that determine habitat structure, rather than high SS due to urbanization and other effects, are responsible for the differences in the fish species composition between the two groups. In the Seto Inland Sea, rivers in the inner part of the bay were classified as group C, while there are also several rivers classified as group D. However, the environmental factors of the

Fig. 6 Result of decision tree model using classification results of fish species composition in river estuaries by non-hierarchical cluster analysis as the objective variable and environmental factors as the explanatory variables



two groups differ in WE, DF, TD, and BM (Fig. S1). WE, DF, and TD are important environmental factors that play a role in forming the geomorphology of a river estuarine area (Yoshikawa et al. 2018; Itsukushima 2019), and the differences in these factors suggest the difference of physical environments of groups C and D. In fact, BM is significantly greater in group D, suggesting that habitat structure differs between the two, which may be the reason for the different fish species composition.

Group E, which includes five rivers flowing through the Fossa Magna zone, was plotted near the third quadrant (Fig. 5). This area has large DF and FV, strong disturbance from waves and river energy, and bigger river bed material. The Fossa Magna is an area where the active orogenic movement still produces large amounts of sediment and gravel, and even the estuary consists of a relatively large-grained river bed. *Luciogobius guttatus*, which showed high IndVal values in the indicator species analysis, is a species that uses stone and gravel for spawning (Dotsu 1957), reflecting the river estuarine environment in group E, where there is bigger river bed material. In addition, these rivers tend to have large gradients and short brackish water areas, and the IndVal values for brackish and saltwater fish tend to be small (Table 2). Thus, the results of low numbers of saltwater fish and high populations of migratory fish in the river estuaries in group E suggest that marine and terrestrial influences have important effects on the formation of the fish species composition of river estuaries.

The NMDS results showed that DD and SDmax tended to be larger in southwestern Japan, such as in groups C and D, and smaller in northeastern Japan. This indicates a difference in climatic zones, with rivers in southwestern Japan, most of which belong to a humid subtropical climate (Köppen 1936), receiving more rainfall and having higher flow discharge, and erosion tends to be more pronounced and DD, an indicator of the degree of dissection, tends to be larger. These climatic and geomorphic developmental history factors are known to influence the distribution of freshwater fishes (Itsukushima 2019) and may also have some influence on the distribution of river estuarine fishes.

Application to Environmental Management of River Estuaries

Many studies, including local ones, have investigated the relationship between estuarine fish fauna and environmental factors and shown that the entrance width of the estuary, physical environmental structure, water temperature, precipitation, and the presence or absence of mangroves are significant parameters (Thiel et al. 1995; Manson et al. 2005; Nicolas et al. 2010; Hossain et al. 2012). Although there are few examples of broad-scale studies, the findings of a New Zealand case study that investigated the diversity of fish fauna and its influencing factors at a nationwide scale suggest that at the estuary scale, air temperature, estuary and intertidal area, tidal range, and freshwater and seawater influx are predictors of fish species, and at site scale, water temperature and salinity are explainable factors of fish species (Francis et al. 2011). In this study, I used a large dataset of river estuaries in a diverse climatic zone with complex currents to determine the relationship between broad-scale fish species composition and environmental factors. The results revealed that environmental factors influencing classification results differ hierarchically, with water temperature being the first and second most dominant factor, followed by wave and tidal influences. In addition, factors influencing species diversity were also considered to differ among regions, suggesting that habitat structure is an important factor in rivers in southwestern Japan, where species diversity is high, and that indicators related to waves and tides, which are factors responsible for geomorphologies, are also important factors.

The results of this study indicate that the classification trends differ significantly between northeastern and southwestern Japan, with northeastern Japan being classified according to geographic location and water temperature. On the other hand, in southwestern Japan, river estuaries are divided between those flowing to inner bays with large tidal differences and river estuaries facing the open ocean with large wave effects, suggesting that the fish species composition may be classified according to habitat structure resulting from tide and wave energy. In fact, the distribution of tidal flats and salt marshes in Japan is concentrated in southwestern Japan and less in northeastern Japan (Fig. S2). The results that different regions have specific factors that cause differences in fish species composition can be an essential finding for environmental conservation. Since the water temperature is possibly the main factor affecting the formation of fish species composition in northeast Japan, monitoring of water temperature, especially changes in water temperature due to climate change, will be important to predict and monitor the change of fish fauna in the future. In particular, the fish species composition of group A, composed of arctic and subarctic fish species, may change drastically with changes in seawater temperature associated with climate change.

Although this study focused on large-scale environmental factors, it is also necessary to accumulate knowledge of the relationship between fish species composition and environmental factors at the habitat scale. In this study, the misclassification rate by CART was 38.6%. Although this is based on watershed-scale environmental factors explaining the classification results of fish species composition, I believe this can be improved by introducing habitat-scale environmental factors. In addition, the river estuaries of the Japanese archipelago have been used by people since ancient times, and many of the sites are degraded by the natural environment and biota. It is necessary to clarify the relationship between anthropogenic impact, external forces, habitat structure, and biota and elucidate each river estuary's potential biota and physical environment as a target for conservation and restoration. Furthermore, conservation measures based on the life history of fish species are also important. Recently, the need for ecosystem management and habitat based on the guilds approach of the species that occur in the estuary has been discussed (Potter et al. 2010, 2015). There is a need to understand at which life history stage each fish species uses the estuary to achieve more integrated river estuarine conservation.

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Data Availability Statement The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of Interest The author declare that I have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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