Research Paper

Relationship between physical environmental factors and presence of molluscan species in medium and small river estuaries

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Abstract

River estuaries are critical aquatic environments characterized by large environmental gradients in their water quality, riverbed material, and microtopography in the longitudinal and transverse directions. Molluscan fauna are sensitive to changes in water quality or bottom sediment conditions, and include species that inhabit unique environments or have a high capacity to thrive in different habitats. The interrelations between ecology and whole physical environment of molluscan fauna have rarely been studied, especially in medium and small sized river estuaries. This study was conducted to investigate the relationship between molluscan fauna and multiple hierarchical physical factors in river estuaries, and develop a prediction model for each of the molluscan species under study. The study focused on molluscan fauna in river estuaries in medium and small size rivers, where knowledge is particularly limited. Results obtained from quadrats were classified into three groups related to physical factors, including wave and river energy and habitat scale factors. Prediction models for molluscan species indicated that physical factors affected different species at varied scales. There were species influenced by watershed scale, habitat scale, or both. Because the physical factors influenced species at different scales, prediction of potential molluscan fauna on a site is also critical, in addition to the conservation or restoration of habitats.

Keywords river estuaries; molluscan fauna; physical environments; prediction model; estuarine conservation

1. Introduction

Estuaries are located at the boundary between the land and ocean and have fluctuating environments due to the mixing of freshwater and seawater, or the action of periodical tides and waves (Dyer, 1997; Schröder-Adams et al., 2014). Ecosystem services of estuaries are numerous and diverse, including nutrient circulation, climate change mitigation, habitat provision, and recreation use (Carpenter et al., 2009). Costanza et al (1997) estimated the value of estuarine ecosystem services to be 22,832 $ /ha/yr, the maximum among biomes. However, estuaries have been under increasing anthropogenic pressure because of their rich biodiversity, abundant natural resources, and fertile alluvial land (Edgar et al., 2000). In the entire world, four billion people live in an area within 60 km from the coastline. (Kennish, 2002). As a result, problems such as water degradation, habitat loss, and shortage of natural resources have become more acute (Kennish, 2002; Howarth, 2008).

Predicting the potential biota based on the understanding the relationship between estuarine ecosystems and physical environments is crucial for the conservation or restoration of estuarine environments. Multiple taxonomic groups including birds, fish, benthic invertebrates, and plankton have been previously studied as biota representing the estuarine environment. Some studies that have been conducted regarding various aspects of estuarine environments include evaluation of foraging habitats using birds (Froneman et al., 2011; Bellio and Kingsford, 2013; Bluso-Demers et al., 2016), assessment of fish habitat environment and environment alternation (Whitfield and Elliott, 2002; Villéger et al., 2010; Nicolas et al., 2010; Lechêne et al., 2018), the relationship between plankton fauna and water quality and its monitoring (Cloern, 2001; Zhou et al., 2008; Paerl et al., 2010; Dalu et al., 2018), and the evaluation of microhabitats using benthic animals (Nanami et al., 2005; Strayer and Malcom, 2007).

Monitoring changes in biota due to anthropogenic impacts is also critical for evaluating ecological integrity and facilitating the implementation of integrated conservation strategies in estuaries (Diaz et al., 2004; Henriques et al., 2008; Pérez-Domínguez et al., 2012). Based on such scientific and technological knowledge, comprehensive frameworks for estuarine conservation have been developed. In the European Union (EU), an integrative assessment including physicochemical and biological features (phytoplankton, zooplankton, benthos, algae, phanerogams, and fishes) was conducted (Rogers et al., 2007) based on the EU Water Framework Directive focusing on understanding and integrating all aspects of the water environment to promote sustainability (Teodosiu et al., 2003; Borja et al., 2008a; Voulvoulis et al., 2017). Conversely, United States Environmental Protection Agency conducted the National Coastal Assessment to evaluate ecological conditions and human use impacts using five primary indices: Water Quality Index (WQI), Sediment Quality Index (SQI), Benthic Index (BI), Coastal Habitat Index (CHI), and Fish Tissue Contaminants Index (FTCI) (Borja et al., 2008b; Hyland et al., 2003; Macauley et al., 2007).

Among the taxonomic groups used for estuarine environmental evaluation, benthic animals including molluscan fauna, are used on because of their high index performance should be defined in the present context. Molluscan species are one of the major macroinvertebrates that play major ecological roles in nutrient dynamics in the ecosystem because they form critical links within the food web as predators, herbivores, detritivores, and filter feeders (Pawar, 2012; Premcharoen et al., 2016). In addition, molluscan fauna are sensitive to changes in water quality or bottom sediments, and represent species that inhabit a unique environment or have low capacity to thrive in different habitats (Itsukushima et al., 2017). Molluscan species at specific locations directly reflect the environmental conditions of those locations (Sato, 2011). Consequently, molluscan species are ideal for evaluating environmental conditions or for determining the impact of human activities (Zenetos, 1996; Koutsoubas et al., 2000). Distribution patterns of molluscan fauna or relationships with physical environment have been studied in various geomorphic environments, such as sandy beaches (lagoon) (Pérès and Picard, 1964; Sheppard, 1984; Quintino et al., 1987), tidal marshes (Kneib, 1984; Thiet et al., 2014), tidal flats (Barnes and Barnes, 2012; Liu et al., 2014), seagrass meadows (Chemello and Milazzo, 2002), and continental shelves (Freitas et al., 2011; Martins et al., 2014). In such cases, molluscan fauna were associated with sediment composition, beach slope, wave action, salinity concentration, sea grass, species of algae, and hydrodynamic regimes. Because molluscan fauna demonstrate high sensitivity to local environments, revealing and understanding relationships between them and the physical environment could facilitate conservation or restoration of estuarine environments (Elliott and Quintino, 2007).

Most of the studies introduced above were conducted on the sea side from the river mouth, for example, on coastlines, offshore tidal flats, or continental shelves. Conversely, research results from river estuaries are limited. River estuaries located upstream of river mouths are high environmental gradient habitats. Such environments are under the great influence of fresh water and changing water quality, sediment materials, and microtopography in the longitudinal and transverse direction (Kusuda, 2008). River estuaries are unique habitats where specific organisms adapted to the brackish water live and grow in addition to organisms that inhabit both freshwater and seawater. However, molluscan fauna in river estuaries have rarely been studied, particularly in medium and small sized rivers. Furthermore, in countries belonging to the Asian monsoon region, including Japan, understanding the relationships between molluscan fauna and physical environment is challenging. This is because such countries have very complex topographies (i.e., numerous peninsulas and islands) and geographical fluctuation of waves or tides are extensive. In contrast, river estuary ecosystems are under stress from anthropogenic impacts such as riverbed excavation to improve flood flow capacity or embankment construction for the prevention of tsunami propagation along rivers.

The purpose of the present study is to investigate the relationship between molluscan fauna and multiple hierarchical physical factors. Moreover, we developed a prediction model for molluscan species. Our findings could contribute to the conservation of molluscan fauna and the formulation of river estuary conservation strategies or goals for restoration projects.

2. Materials and Methods

2.1. Description of study area

We investigated 68 river estuaries in Kyushu region in Japan (Fig. 1). The watershed area in investigated rivers ranged from 1 km^2 to 60 km^2. We selected river estuaries for investigation based on environmental diversity such as the Ariake Sea and Buzen Sea (where the tide ranges are large) and rivers flowing into the Sea of Japan (where high energy waves are dominant.)

2.2. Field Surveys and data collection

We defined the research area as one reach (approximately ten times the river width) upstream from the river mouth in each estuary. Field surveys were conducted at low tide of the middle and spring tide. The survey was conducted from April 28, 2015 to November 23, 2017. In the dried out land habitats, molluscan species (*Bivalvia*, *Gastropoda*, and *Polyplacophora*) were collected and identified in surface layers and 10 cm depth within a 50 cm quadrat at each habitat. Depending on the surface area of the habitat, one to three quadrats were sampled in each habitat.

Seven types of habitats were classified including silt (D50 [median particle diameter] < 0.075 mm), sand (0.075 mm ≦ D50 < 2 mm), gravel (2 mm ≦ D50 < 75 mm), rock (D50 ≧ 75 mm), bedrock, artificial structures (revetment, foot protection rubble, mounds, or riprap), and vegetation. In the silt and sand habitats, bottom sediment was sampled and particle size distribution was determined using a laser diffraction-type particle size measuring device (SALD3100) when the particles were not larger than 3.0 mm. In case the bottom sediment contained particles larger than 3.0 mm, a sieve analysis test was conducted after drying the samples in a constant temperature drier. In the gravel habitat, the major and minor axes of 50 gravels randomly selected were measured, and particle size distribution was obtained by calculating geometric mean diameter of two axes using the following formula (Sakashita, 2005) (Equation 1):

$$d = (a + b)^{0.5} \quad \text{(Eq.1)}$$

Where d: geometric mean diameter of two axes (mm), a: major axis (mm), b: minor axis (mm).

2.3. Physical factors and calculation methods

To investigate the relationship between molluscan fauna and physical factors, two levels (habitat and watershed scale) were selected. Habitat scale factors included (1) D50, (2) distance from the river mouth (L), and (3) presence of vegetation (V). Watershed scale factors included the following: (4) tidal range (T, factors of tide energy), (5) wave exposure (W, factors of wave energy), (6) direct fetch (F, factors of wave energy), (7) slope of the investigation section (S, factors of river energy), and (8) friction velocity at the river mouth (τ, factors of river energy).

Calculation methods for physical factors T, W, and F are reported by Itsukushima et al

(2017). Calculation of S was performed by calculating the bed slope of the investigation section from the survey data. For τ, first, we calculated flow discharge of occurrence probability 1/5 of each river using rational runoff formula based on the rainfall intensity equation published by river administrator (Fukuoka prefecture, 2006; Saga prefecture, 2012; Nagasaki prefecture, 2010; Kumamoto prefecture, 2008; Oita prefecture, 1997; Miyazaki prefecture, 2017; Kagoshima prefecture, 2008). Coefficient of discharge was set at 0.8 for the three rivers (Saigo river, Tounobaru river, and Juro river) flowing down densely populated areas, and 0.7 for other rivers (Water and disaster management Bureau of Ministry of Land, Infrastructure, Transport and Tourism, Japan et al., 2013). In addition, flow time was calculated using the Kraven equation (Iguchi, 1957). Finally, friction velocity was calculated using the following formula (Equation 2):

$$u_* = g^{0.5} n^{0.3} Q^{0.3} I^{0.35} B^{-0.3} \quad \text{(Eq.2)}$$

Where g: gravitational acceleration (m/s^2), n: roughness factor, Q: flow discharge (m^3/s), I: bed slope of the section under investigation, B: width of the river mouth (m). According to Institute of Country-ology and Engineering (2003), the roughness factor was defined as 0.015 for mud dominated river, 0.020 for sand dominated river, and 0.023 for gravel dominated river.

2.4. Statistical Analysis

2.4.1. Relationship between molluscan fauna and physical factors

Non-Metric Multidimensional Scaling (NMDS) (Minchin, 1987) was conducted to identify the potential groupings of similar molluscan fauna between quadrats in river estuaries and relationships between classification results of the molluscan fauna and physical factors. The Bray–Curtis similarity index was used to summarize the composition of molluscan fauna in all the habitats studied. NMDS was conducted in 418 quadrats in 68 river estuaries where presence of molluscan species was confirmed. To ensure a normal distribution, the number of individuals was used after logarithmic conversion [log (e + 1)]. As a result of the permutation test, physical factors ($p < 0.05$) were presented as vectors. Additionally, indicator species in each group were determined using the indicator value method (IndVaL) (Dufrêne and Legendre, 1997). To investigate the statistical significance in a physical factor among groups classified by NMDS, the average values of physical factors in each group were analyzed using the Kruskal–Wallis test and Steel–Dwass test. The analyses were conducted using the statistical analysis software R.

2.4.2. Modelling method for appearance prediction model using physical factors

To investigate the relationship between number of molluscan individuals and physical factors for each of the molluscan species, three different techniques were applied to develop predictive models for the number of molluscan species: Generalized Linear Model (GLM), Generalized Additive Models (GAM), and Classification and Regression Trees (CART). We analyzed 25 molluscan species whose appearance was confirmed in more than 15 quadrats.

Generalized Linear Model (GLM)

GLM is an extended model of the linear model, which allows the incorporation of non-normal distributions of the response variables and transformations of the dependent variables linearly (McCullagh and Nelder, 1989). To model the population of each molluscan species in the quadrats, we used Poisson distribution with a log link function. We compared the Akaike Information Criteria (AIC: Burnham and Anderson, 2002) of each model obtained from the method by increasing and decreasing the variables. Finally, we adopted the lowest AIC model as the best model for each of the species. GLM was conducted with the MASS (Version 7.3-50) package.

Generalized Additive Models (GAM)

Generalized Additive Models (GAM) using logistic regression replace the linear prediction part of GLM with the sum of the smoothing function, which make them useful in modelling non-linear responses of data into environmental parameters (Wood and Augustin, 2002). All possible combinations of the predictor variable were analyzed and the best models were selected by AIC. A Poisson distribution with a log link function was applied. We conducted GAM using R software and "mgcv" library (Wood, 2000).

Classification and Regression Trees (CART)

CARTs (Breiman et al., 1984) were developed for the prediction of the number of molluscan individuals in each quadrat and were resolved using the Gini Index. Resulting CARTs were pruned via test sample cross validation (Fielding and Bell, 1997). Across the nine tests, the smallest tree with a CV (Cross-Validation cost) cost within one standard error of the minimum CV cost was selected.

3. Results

3.1. Overview of molluscan fauna in quadrats

A total of 81 species and 18,204 individuals were collected in the 529 quadrats of 68 river estuaries. Among the targeted 529 quadrats, molluscan species were confirmed in 418 quadrats. The species with the largest number of individuals was *B. multiformis*, with 4,798 individuals in 169 quadrats, followed by *L. brevicula* with 1,036 individuals in 93 quadrats. There were 735 *C. retropictum* individuals in 93 quadrats. In addition, the characteristics of molluscan fauna in each river estuary were described (Itsukushima et al., 2018).

3.2. Assemblage composition and physical factors

418 quadrats were classified into three groups (group A, B, and C) surrounded by curves of NMDS grade level (Fig. 2). In addition, seven physical factors were selected as significant factors for classification by the permutation test ($p < 0.05$). The selected physical factors were placed in the positive direction of the first axis with L and V, which are habitat scale factors. River energy factors (τ and S) and wave energy factors (W and F) were placed in the positive direction of the second axis. D50 was placed in the negative direction of the first axis (Fig. 2, Table 1).

Group A (N = 216) was centrally located in the first quadrat, composed of habitats with small grain sizes and dominated by vegetation. Species with high IndVaL value were confirmed in group A, indicating a high diversity in molluscan fauna (Table 2). The IndVaL values for *B. multiformis*, *B. cumingii*, and *P. conulus* were particularly high. *B. multiformis* and *B. cumingii* prefer inhabiting the inland bay whereas *P. conulus* primarily inhabits shells of *B. Snails* (Table 2. Conversely, group B (N = 115) was centrally located in the second and third quadrat, composed of habitats with large grain sizes and influenced by large waves and high river energy. IndVaL values for *M. galloprovincialis*, *L. brevicula*, *L. intermedia*, *R. claviger*, and *N. japonica* were high (Table 2). The species inhabit the rocky area attached to the large gravel or bedrock. In addition, group C (N = 87) was centrally located in the fourth quadrat, composed of habitats with great distance from river mouth and influenced by low wave energy. IndVaL values for molluscan species were the highest in *C. retropictum* (Table 2). However, the value was lower than that of indicator species of other groups. *C. retropictum* is an amphidromous species that inhabits both freshwater and brackish water.

3.3. Characteristic of physical factors

A boxplot of seven quantitative physical variables is presented in Fig. 3. Average value for D50 was highest in group B (90.65 ± 23.34 cm), followed by group C (10.52 ± 13.72 cm), and group A (3.82 ± 6.89). Results of the Kruskal–Wallis test revealed significant differences among groups ($p < 0.01$). In addition, Steel–Dwass test revealed that the D50 of group B was significantly higher than that of group A ($p < 0.01$) and group C ($p < 0.01$), whereas that of group C was higher than that of group B. Group B exhibited the lowest value for distance from the river mouth (53.9 m), followed by group C (101.8 m), and group A (102.0 m). The results of the Kruskal–Wallis test indicated significant differences in distance from the river mouth among the three groups ($p < 0.01$). The Steel–Dwass multiple comparison test also showed a significant difference between group B and the other two groups ($p < 0.01$).

Wave energy factors, F and W showed similar results. The highest values for both factors were observed in group B, followed by group C, and group A. The Kruskal–Wallis test showed a significant difference among the three groups ($p < 0.01$). The Steel–Dwass multiple comparison test also showed a significant difference between group A and the other two groups ($p < 0.01$) in the wave energy factors. River energy factors, S and τ showed similar results. The highest values for both factors were observed in group C, followed by group B, and group A. The Kruskal–Wallis test revealed significant differences among the three groups ($\mathrm{p} < 0.01$). The Steel–Dwass multiple comparison test also revealed a significant difference between group A and the other two groups ($p < 0.01$).

3.4. Prediction model for molluscan species

Analysis of the relationship between the number of molluscan species and physical factors revealed that the value of R-squared was high in the order of CART, GAM, and CART for most of the targeted species. (Table 3). Degree of conformance of models varied greatly depending on the species. Relatively high prediction accuracy was confirmed in *B. multiformis*, *Assiminea* sp., and *P. alata*. Conversely, the R-squared values in *R. clavigera*, *P. pygmaea*, *N. japonica*, and *C. chinensis* were relatively low. In addition, the physical factors selected as explanatory variables for predicting number of molluscan species exhibited similar trends in GLM and GAM. However, in CART, number of physical factors selected as explanatory variables was smaller than the other two methods.

4. Discussion

4.1. Classification result of molluscan fauna and physical factors

As a result of the NMDS, physical factors related to wave energy (W and F) and river energy (τ and S) were selected as factors of watershed scale affecting the classification of molluscan fauna in each quadrat. However, tide energy was not selected as a key factor influencing molluscan fauna. Moreover, Cerithidea such as *B. multiformis* or *B. cumingii* are indicator species in group A and are known to inhabit inner bays with high tidal variation. There were significant differences in D50 between group A and B. Consequently, the classification of molluscan fauna was largely determined by differences in habitat particle size rather than tidal variation. In addition, group A was largely composed of quadrats that were far from the river mouth compared to group B. This is because rivers inhabited by *B. multiformis* generally have high tidal variation. Therefore, seawater invades the upper reaches and *B. multiformis* can inhabit the upper reaches of the river estuaries. In contrast, indicator species in group B, such as *R. clavigera*, *N. japonica*, and *M. confuse*, which inhabit sea spray area do not invade the upper reaches of river estuaries. Consequently, L is an appropriate physical factor for distinguishing groups A and B.

In group C, prominent indicator species were few, and the IndVaL values for *C. retropictum* and *Assiminea* sp. were slightly higher than in the other species. Group C was mainly composed of quadrats that had a long distance from the river mouth and low wave energy. Because C. retropictum inhabits regions from the upper reach of brackish water to freshwater areas, it is an appropriate indicator species in group C.

Studies on estuary classification using geography, physical environment, and biota have been conducted for a relatively long period. From a perspective of topography and physical environment, classification magnitude of tidal variability (Davies, 1964), geomorphological history and processes (Fairbridge, 1980; Boyd et al., 1992; Heap et al., 2001) were used to classify the estuarine types. Whereas, classification in the present study was done using molluscan fauna, and wave and river energy were selected as controlling factors. Tide energy, which is a key factor for topographic classification (Fairbridge, 1980; Boyd et al., 1992) was not selected. This is because there was no significant difference in the tide levels in the river estuary area investigated in this study, and it was not significant enough to affect the structure of the molluscan community. However, for prediction models for each of the molluscan species, tidal range was selected as a key variable influencing the number of individuals in *B. multiformis*, *L. brevicula*, or *R. philippinarum* (Table 3). In the present study, we investigated the relationship between watershed scale factors and molluscan fauna. Conversely, because the habitat structures in the river estuaries have a strong relationship with watershed scale factors, it is necessary to evaluate the biota as well as to understand the relationship between habitat structure and the watershed index.

4.2. Relationship between physical factors and molluscan species

The application of different techniques generally results in models differing in their responses. Some explanatory factors were identified by the three methods for each of the species. The most prominent example was D50, which was identified as an explanatory factor in 13 species, including *L. brevicula* or *C. retropictum*, by all three models. Among the watershed scale factors, T was identified in the all three models for five species, including *B. multiformis* and *Assiminea* sp. In addition, τ was identified in the all three models for six species, including *B. cumingii* and *C. rhizophorarum*. Conversely, among the habitat scale factors, few species had vegetation as an explanatory variable. Nevertheless, vegetation was identified as a key factor in all three models for *Assiminea* sp. and *C. rhizophorarum*. Among the physical factors, D50 was selected for many species, suggesting that the number of molluscan species was highly dependent on particle size. Although vegetation was a factor in few species, in *Assiminea* sp, the R-squared value was high, suggesting the importance of vegetation or some habitat scale factors for specific species.

Three major types of physical factors were commonly identified in all models for *B. multiformis*, *L. brevicula*, *N. radula*, and *C. nigrolineata*. Conversely, no physical factors were commonly identified by all three models for *N. nigrans*, *C. sinensis*, and *P. alata*. In addition, watershed scale factors were selected for predicting *B. multiformis*, *B. cumingii*, and *R. philippinarum*, whereas habitat scale factors were selected for predicting *M. confusa*, *L. japonica*, and *B. virescens*. However, both watershed scale and habitat scale factors were chosen for predicting *L. brevicula*, *N. radula*, and *C. nigrolineata*.

4.3. Past knowledge of molluscan habitat and prediction model of molluscan species

According to the results, *B. multiformis* favors gravel, sandy gravel, and sand sediments (Maki et al., 2002), which is contrary to the research results that report that it prefers the sand mud of inner bays (Abe, 1934; Adachi and Wada 1998). The reason for the difference in sedimentary preference could be specificity of location or interspecific relationships. In the CART model for *B. multiformis*, habitat scale factors were not selected as physical factors influencing the number of individuals, whereas watershed scale factors, including tide, wave, and river energy were selected. Matsuo et al (2011) observed that *B. multiformis* inhabited various bottom sediments from the low tide zone to high tide zone in the Sea of Ariake. Therefore, *B. multiformis* habitats were influenced by the watershed scale factors, for example inner bays with high tidal variation rather than habitat scale factors such as bottom sediment.

For *C. rhizophorarum*, vegetation was the factor influencing the number of individuals in all three models (Table 3). Climbing vegetation was observed in the *C. rhizophorarum* habitat (Wakamatsu and Tomiyama, 2000). The number of *P. australis* in the *C. rhizophorarum* habitat was significantly higher than in the habitats of other species (*P.cingulate* and *P. alata*) (Otani et al., 2011). In addition, *C. rhizophorarum* is only found in the reed bed located in the upper part of the intertidal area following tsunami activity (Kanaya et al., 2012). Because the presence of *C. rhizophorarum* depends on the vegetation in the reed field, a strong relationship between the presence or absence of vegetation and number of *C. rhizophorarum* individuals was confirmed in the present study. In addition, L was identified as a key factor influencing the number of *C. rhizophorarum* individuals in GLM and GAM procedures (Table 3). *C. rhizophorarum* is found in the upper part of the intertidal zone with little influence from seawater (Wells 1983) and have higher freshwater and desiccation tolerance compared to other *Pirenella* species (Yamamoto and Wada 1999; Wakamatsu and Tomiyama 2000). These research findings introduced above support the results of this study.

In addition, D50 and L were identified as key factors influencing the number of *P. pygmaea*, *N. radula* and *C. nigrolineata* individuals, belonging to Gasteropoda, and *L.*

japonica belonging to Polyplacophora. W was selected for *N. radula*, and S was selected for *C. nigrolineata*. The two species inhabit the reef or boulder stone area, attaching to bedrock or pebbles (Iwasaki, 1994; Sogame et al., 2009). The number of *C. nigrolineata* individuals was positively correlated with the volumes of boulder stones (Inadome and Yamamoto, 2005). In addition, *C. nigrolineata* prefer saltwater splash and tend to inhabit areas around the river mouth rather than the upper reaches of the river estuary (Ortega, 1987). Our modelling results also revealed a strong relationship between the number of individuals and L. In the pebble shore area, which is a major habitat for the species, the number of species and individuals increased with increase in size of bottom sediments (McGuinness, 1987a; b), and the diversity of biological communities increases with increase in geomorphological complexity (Raffaelli and Hawkins, 1996). The results of the present study indicated that the molluscan species inhabits attaching to gravels are indicator species of river estuaries where river and wave energy are dominant. Consequently, knowledge of habitat conditions and how they influence molluscan species in river estuaries is also critical for river estuary conservation activities.

4.4. River estuarine conservation

Results of the prediction models for appearance of molluscan species revealed that factors associated with the physical environment that influenced molluscan species were spatially varied across species. Restoration of river estuaries requires the prediction of appearance species after restoration. Our findings suggested that some species that strongly were influenced by watershed scale physical factors could not appear even following an increase in habitat diversity in cases where watershed scale factors were not suitable for colonization by the species. Consequently, restoration of river estuaries requires before-after analyses based on the prediction of species after restoration and consideration of the conditions of watershed scale physical variables. Furthermore, the research results may also be applied in the conservation of river estuaries. For example, when conducting river improvement work that degraded a molluscan habitat, for instance, a riverbed excavation, the results of the present study can inform stakeholders on how to preserve habitat structure and maintain the integrity of molluscan fauna.

5. Conclusion

This study was conducted to investigate the relationship between molluscan fauna and multiple hierarchical physical factors in the river estuaries, and help develop prediction models for each of the molluscan species observed. The study focused on molluscan fauna in estuaries of medium and small size rivers, where knowledge on the relationship between molluscan fauna and physical factors is limited. The major conclusions and recommendations of the present study are as follows:

- Prediction models for molluscan species indicated that physical factors influenced different species at different scales. Some species were mainly influenced by watershed scale factors, other by habitat scale factors, whereas others were influenced by both watershed and habitat scale factors.
- Because the physical factors influenced species at different scales, the ability to predict potential appearance species in a site is critical, in addition to the conservation or restoration of habitats.

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References

Abe, N., 1934. Ecological observations on Batillaria multiformis (Lischke). Sci. Rep. Tohoku Imp. Univ., Ser, 4, 8, 383-398.

Adachi, N., Wada, K., 1998. Distribution of two intertidal Gastropods, Batillaria multiformis and B. cumingi (Batillariidae) at a Co-occurring Area. Venus: journal of the Malacological Society of Japan 57, 115-120.

Barnes, R.S.K., Barnes, M.K.S., 2012. Shore height and differentials between macrobenthic assemblages in vegetated and unvegetated areas of an intertidal sandflat. Estuar. Coast. Shelf. S. 106, 112-120.

Bellio, M., Kingsford, R.T., 2013. Alteration of wetland hydrology in coastal lagoons: Implications for shorebird conservation and wetland restoration at a Ramsar site in Sri Lanka. Biol. Conserv. 167, 57-68.

Bluso-Demers, J.D., Ackerman, J.T., Takekawa, J.Y., Peterson, S.H., 2016. Habitat Selection by Forster's Terns (Sterna forsteri) at Multiple Spatial Scales in an Urbanized Estuary: The Importance of Salt Ponds. Waterbirds 39, 375-387.

Borja, Á., Tueros, I., Belzunce, Ma. J., Galparsoro, I., Garmendia, J.M., Revilla, M., Solaun, O., Valencia, V., 2008a. Investigative monitoring within the European Water Framework Directive: A coastal blast furnace slag disposal, as an example. J. Environ. Monitor. 10, 453-462.

Borja, A., Bricker, S.B., Dauer, D.M., Demetriades, N.T., Ferreira, J.G., Forbes, A.T., Hutchings, P., Jia, X., Kenchington, R., Marques, J.C., Zhu, C., 2008b. Overview of integrative tools and methods in assessing ecological integrity in estuarine and coastal systems worldwide. Mar. Pollut. Bull. 56, 1519-1537.

Boyd, R., Dalrymple, R., Zaitlin, B.A., 1992. Classification of clastic coastal depositional environments. Sediment. Geol. 80, 139-150.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees, Chapman and Hall/CRC, New York.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-model Inference, second ed., vol. XXVI. Springer, p. 488.

Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., Defries, R.S., Diaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J., Whyte, A., 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. P. Natl. Acad. Sci. Usa. 106. 1305-1312.

Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: Some evidence from phytal molluscs. Mar. Biol. 140, 981-990.

Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser., 210, 223-253.

Costanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van Den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Dalu, T., Magoro, M.L., Tonkin, J., Human, L.R.D., Perissinotto, R., Deyzel, S.H.P., Adams, J.B., Whitfield, A.K., 2018. Assessing phytoplankton composition and structure within micro-estuaries and micro-outlets: a community analysis approach. Hydrobiologia 818, 177-191.

Dias, M.P., Granadeiro, J.P., Lecoq, M., Santos, C.D., Palmeirim, J.M., 2006. Distance to high-tide roosts constrains the use of foraging areas by dunlins: Implications for the management of estuarine wetlands. Biol. Conserv. 131, 446-452.

Dias, M.P., Lecoq, M., Moniz, F., Rabaça, J.E., 2014. Can human-made saltpans represent an alternative habitat for shorebirds? Implications for a predictable loss of estuarine sediment flats. Environ. Manage. 53, 163-171.

Diaz, R.J., Solan, M., Valente, R.M., 2004. A review of approaches for classifying benthic habitats and evaluating habitat quality. J. Environ. Manage. 73, 165-181.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345-366.

Dyer, K. R., 1997. Estuaries, A Physical Introduction, 2nd Edition. John Wiley & Sons, Chichester.

Edgar, G.J., Barrett, N.S., Graddon, D.J., Last, P.R., 2000. The conservation significance of estuaries: A classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. Biol. Conserv. 92, 383-397.

Elliott, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Mar. Pollut. Bull. 54, 640-645.

Fairbridge, R.W., 1980. The estuary: Its definition and geodynamic cycle. In Chemistry and Biogeochemistry of Estuaries; Wiley: New York, NY, USA, 1–35.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38-49.

Freitas, R., Ricardo, F., Pereira, F., Sampaio, L., Carvalho, S., Gaspar, M., Quintino, V., Rodrigues, A. M., 2011. Benthic habitat mapping: Concerns using a combined approach (acoustic, sediment and biological data). Estuar. Coast. Shelf. S. 92, 598-606.

Froneman, P.W., Blake, J.D., Hulley, P., 2011. Aspects of population dynamics and feeding by piscivorous birds in the intermittently open Riet River estuary, eastern cape, South Africa. Afr. J. Aquat. Sci. 36, 101-107.

Fukuoka prefecture, 2006. Probable rainfall intensity equation of Fukuoka prefecture. Available from: http://www.pref.fukuoka.lg.jp/contents/kouukyodo.html, Accessed date: 1 August 2018.

Grant, J., 1984. Sediment microtopography and shorebird foraging. Mar. Ecol. Prog. Ser. 19, 293-296.

Heap, A. Bryce, S. Ryan, D. Redke, L. Smith, R., 2001. Australian Estuaries and Coastal Waterways: A Geoscience Perspective for Improved and Integrated Resource Management; Record 2001/07, Australian Geological Survey Organization, Canberra, Australia.

Henriques, S., Pais, M.P., Costa, M.J., Cabral, H., 2008. Efficacy of adapted estuarine fish-based multimetric indices as tools for evaluating ecological status of the marine environment. Mar. Pollut. Bull. 56, 1696-1713.

Howarth, R.W., 2008. Coastal nitrogen pollution: A review of sources and trends globally and regionally. Harmful Algae 8, 14-20.

Hyland, J.L., Balthis, W.L., Engle, V.D., Long, E.R., Paul, J.F., Summers, J.K., Van Dolah, R.F., 2003. Incidence of stress in benthic communities along the U.S. Atlantic and Gulf of Mexico coasts within different ranges of sediment contamination from chemical mixtures. Environ. Monit. Assess. 81, 1-3, 149-161.

Iguchi, S., 1957. Origin of the Rziha equation and Kraven table pertinent to flood concentration time. JSCE Magazine, “Civil Engineering” 42, 25-27.

Inadome, T., Yamamoto T., 2005. Relationship between the molluscan community and characteristics of boulders on lava shores of Sakurajima Island. Venus: journal of the Malacological Society of Japan 64, 177-190.

Itsukushima, R., Yoshikawa, H., Morita, K., 2018. A dataset of molluscan fauna sampled in river estuaries of medium and small size river in Kyushu island, Japan. Biodiversity Data Journal 6, e26101.

Itsukushima, R., Morita, K., Shimatani, Y., 2017. The use of molluscan fauna as model taxon for the ecological classification of river estuaries. Water 9, 356.

Iwasaki, K., 1994. Intra- and interspecific variation in activity patterns of intertidal limpets. Venus: journal of the Malacological Society of Japan 53, 85-104.

Japan Institute of Country-ology and Engineering, 2003. Guideline of examination for river channel planning. Sankaid, Tokyo.

Kagoshima prefecture, 2008. Probable rainfall intensity curve and equation. Available from: file:///E:/data/11618_20130417105133-1.pdf, Accessed date: 1 August 2018.

Kanaya, G., Suzuki, T., Maki, H., Nakamura, Y., Miyajima, Y., Kikuchi, E., 2012. Effect of the 2011 tsunami on the topography, vegetation, and microbenthic fauna in Gamo Lagoon, Japan. Japanese Journal of Benthology 67, 20-32.

Kennish, M.J., 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. 29, 78-107.

Kneib, R.T., 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: Causes and questions. Estuaries 7, 392-412.

Koutsoubas, D., Arvanitidis, C., Dounas, C., Drummond, L., 2000. Community structure and dynamics of the Molluscan Fauna in a Mediterranean lagoon (Gialova lagoon, SW Greece). Belg. J. Zool. 130, 131-138.

Kumamoto prefecture, 2008. Calculation for the probable rainfall intensity in Kumamoto prefecture. Available from: http://www.pref.kumamoto.jp/kiji_9022.html, Accessed date: 1 August 2018.

Kusuda, T., Yamamoto, K., 2008. River Brackish Area; Gihodo Shuppan: Tokyo, Japan.

Lechêne, A., Boët, P., Laffaille, P., Lobry, J., 2018. Nekton communities of tidally restored marshes: A whole-estuary approach. Estuar. Coast. Shelf. S. 207, 368-382.

Liu, W., Tanimura, A., Imai, T., Kanaya, G., Niiyama, T., Maegawa, S., Kohzu, A., Kimura, T., Toyohara, H., 2014. Distribution of gastropods in a tidal flat in association with digestive enzyme activities. Plankton and Benthos Research 9, 156-167.

Macauley, J.M., Harwell, L.C., Alafita, H.V., 2007. The ecological condition of Veracruz, Mexico Estuaries. Environ. Monit. Assess. 133, 177-185.

Maki, E., Ohtaki, H., Tomiyama, K., 2002. Distribution and Substrate Preference among Four Batillarid and Patamidid Species, with Observations on Seasonal Changes in the Distribution of Cerithideopsilla djadjariens（K.Martin, 1889) (Gastropoda: Potamididae). Venus: journal of the Malacological Society of Japan 61, 61-76.

Martins, R., Sampaio, L., Quintino, V., Rodrigues, A.M., 2014. Diversity, distribution and ecology of benthic molluscan communities on the Portuguese continental shelf. J. Sea. Res. 93, 75-89.Matsuo, K., Masuda, T., Misonou, T., Igarashi, M., Morimoto, K., Takikawa, K., 2011. Study on indicator species of tidal flat in Ariake Bay. Journal of Japan Society of Civil Engineers, Series B2 67, I _481- I _486.

McCullagh, P., Nelder, J., 1989. Generalized Linear Models (second ed.), Chapman and Hall/CRC, Boca Raton.

McGuinness, K.A., 1987a. Disturbance and organisms on boulders - I. Patterns in the environment and the community. Oecologia 71, 409-419.

McGuinness, K.A., 1987b. Disturbance and organisms on boulders - II. Causes of patterns in diversity and abundance. Oecologia 71, 420-430.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89-107.

Miyazaki prefecture, 2017. Probable rainfall intensity curve of Miyazaki prefecture Available from: https://www.pref.miyazaki.lg.jp/kasen/shakaikiban/kasen/20180605130554.html, Accessed date: 1 August 2018.

Mouritsen, K.N., Jensen, K.T., 1992. Choice of microhabitat in tactile foraging dunlins Calidris alpina: the importance of sediment penetrability. Mar. Ecol. Prog. Ser. 85, 1-8.

Nagasaki prefecture, 2010. Guidelines for development permission system. Available from: https://www.doboku.pref.nagasaki.jp/~kenchiku/kaihatu/kouukyoudo201003.pdf, Accessed date: 1 August 2018.

Nanami, A., Saito, H., Akita, T., Motomatsu, K.-I., & Kuwahara, H. (2005). Spatial distribution and assemblage structure of macrobenthic invertebrates in a brackish lake in relation to environmental variables. Estuar. Coast. Shelf. S. 63, 167-176.

Nicolas, D., Lobry, J., Lepage, M., Sautour, B., Le Pape, O., Cabral, H., Uriarte, A., Boët, P., 2010. Fish under influence: A macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. Estuar. Coast. Shelf. S. 86, 137-147.

Oita prefecture, 1997. Probable rainfall intensity curve of Oita prefecture.

Ortega, S., 1987. Habitat segregation and temporal variation in some tropical intertidal populations. J. Exp. Mar. Biol. Ecol. 113, 247-265.

Otani, S., Kozuki, Y., Yamanaka, R., 2011. Distribution characteristics and population dynamics of Cerithidea cingulate in tidal flat of river mouth. Journal of Japan Society of Civil Engineers, Series B2 67, Ⅰ_487- Ⅰ_492.

Paerl, H.W., Rossignol, K.L., Hall, S.N., Peierls, B.L., Wetz, M.S., 2010. Phytoplankton community indicators of short- and long-term ecological change in the anthropogenically and climatically impacted neuse river estuary, North Carolina, USA. Estuar. Coast. 33, 485-497.

Pawar, R., 2012. Molluscan diversity in mangrove ecosystem of Uran (Raigad), Navi Mumbai, Maharashtra, west coast of India. Bulletin of Environment, Pharmacology and Life Science 1, 55-59.

Pérès, J.M., Picard, J., 1964. Nouveau Manuel de Bionomie Benthique de la Mer Méditerranée; Station Marine d'Endoume: Marseille, France.

Pérez-Domínguez, R., MacI, S., Courrat, A., Lepage, M., Borja, A., Uriarte, A., Neto, J. M., Cabral, H., St.raykov, V., Franco, A., Alvarez, M.C., Elliott, M., 2012. Current developments on fish-based indices to assess ecological-quality status of estuaries and lagoons. Ecol. Indic. 23, 34-45.

Premcharoen, S., Witirawat, S., Tharapoom, P., 2016. Molluscan fauna in bang taboon mangrove estuary, inner gulf of Thailand: Implications for conservation and sustainable use of coastal resources. Matec. Web. Conf. 60, 02003.

Quintino, V., Rodrigues, A.M., Gentil, F., Peneda, M.C., 1987. Macrozoobenthic community structure in the Lagoon of Albufeira, western coast of Portugal. J. Exp. Mar. Biol. Ecol. 106, 229-241.

Raffaelli, D. Hawkins, S., 1996. Intertidal ecology. Chapman & Hall, London.

Rogers, S.I., Tasker, M.L., Earll, R., Gubbay, S., 2007. Ecosystem objectives to support the UK vision for the marine environment. Mar. Pollut. Bull. 54, 128-144.

Saga prefecture, 2012. Probable rainfall intensity equation in Saga district. Available from: http://www.pref.saga.lg.jp/kiji00312117/3_12117_1_201236205440.pdf, Accessed date: 1 August 2018.

Sato, S., 2011. Report on Four Academic Societies Joint Symposium of Biodiversity Conservation of Ariake Bay. Japanese Journal of Benthology 66, 102-116.

Sakashita, S., 2005. Fundamental powder technology for engineer related to colour material field: Chap. 1 physical property of particle and powder. J. Jpn. Soc. Colour. Mater. 78, 168-184.

Schröder-Adams, C.J., Boyd, R.L. Tran, T., 2014. Estuarine foraminiferal biofacies pattern compared to the brackish ichnofacies model: Port Stephens, southeast Australia. Estuar. Coast. Shelf. S. 139, 78-87.

Sheppard, A.L.S., 1984. The molluscan fauna of Chagos (Indian Ocean) and an analysis of its broad distribution patterns. Coral Reefs 3, 43-50.

Sogame, T., Owada, M., Kanazawa, K., 2009. Comparison of defensive behaviors in limpets inhabiting an intertidal zone. Science Journal of Kanagawa University 20, 89-92.

Strayer, D.L., Malcom, H.M., 2007. Submersed vegetation as habitat for invertebrates in the Hudson River estuary. Estuar. Coast. 30, 253-264.Wetzel, M.A., Von Der Ohe, P.C., Manz, W., Koop, J.H.E., Wahrendorf, D.-S., 2012. The ecological quality status of the Elbe estuary. A comparative approach on different benthic biotic indices applied to a highly modified estuary. Ecol. Indic. 19, 118-129.

Teodosiu, C., Barjoveanu, G., Teleman, D., 2003. Sustainable water resources management 1. River basin management and the EC water framework directive. Environ. Eng. Manage. J. 2, 377-394.

Thiet, R.K., Kidd, E., Wennemer, J.M., Smith, S.M., 2014. Molluscan community recovery in a New England back-barrier salt marsh lagoon 10 years after partial restoration. Restor. Ecol. 22, 447-455.

Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010 Contrasting changes in taxonomie vs. functional diversity of tropical fish communities after habitat degradation. Ecol. Appl. 20, 1512-1522.

Voulvoulis, N., Arpon, K.D., Giakoumis, T., 2017. The EU Water Framework Directive: From great expectations to problems with implementation. Sci. Total. Environ. 575, 358-366.

Wakamatsu, A., Tomiyama K., 2000. Seasonal changes in the distribution of Batillarid snails on a tidal flat near the most northern mangrove forest in Atago river estuary, Kyushu, Japan. Venus: journal of the Malacological Society of Japan 59, 225-243.

Water and disaster management Bureau of Ministry of Land, Infrastructure, Transport and Tourism, Japan., National institute for land and infrastructure management of Ministry of Land, Infrastructure, Transport and Tourism, Japan., Incorporated administrative agency of public works research institute, Japan. 2013. Technical standards for River Works: Practical Guidelines for Methods of Investigation, and its reference materials". Technical note of NLIM, No.712. We added the references as follow.

Wells, F.E., 1983. The Potamididae (Mollusca : Gastropoda) of Hong Kong, with an examination of habitat segregation in a small mangrove system. Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong 139-154.

Whitfield, A.K., Elliott, M., 2002. Fishes as indicators of environmental and ecological changes within estuaries: A review of progress and some suggestions for the future. J. Fish. Biol. 61, 229-250.

Wood, S.N., 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. Journal of the Royal Statistical Society. Series B: Statistical Methodology 62, 413-428.

Wood, S.N., Augustin, N.H., 2002. GAMs with integrated model selection using penalized regression splines and applications to environmental modelling. Ecol. Model. 157, 157-177.

Yamamoto, Y., Wada, K., 1999. Distribution of four batillarid snails on tidal flat, in relation to environmental conditions. Nankiseibutsu, the Nanki Biological Society 41, 15-22.

Zenetos, A., 1996. Classification and interpretation of the established Mediterranean biocoenoses based solely on bivalve molluscs. Journal of the Marine Biological Association of the United Kingdom 76 403-416.

Zhou, M.-J., Shen, Z.-L., Yu, R.-C., 2008. Responses of a coastal phytoplankton community to increased nutrient input from the Changjiang (Yangtze) River. Cont. Shelf. Res. 28, 1483-1489.

Table 1 Results of the permutation test for physical factors

Physical factors	R^2	*p* value
V	0.0526	0.001
D50	0.6004	0.001
L	0.094	0.001
T	0.0015	0.739
F	0.224	0.001
W	0.3256	0.001
τ	0.0389	0.001
S	0.0304	0.002

Table 2 IndVaL indices of molluscan species in each group

	IndVAL		
Species	A	B	C
B. multiformis	78	3	2
L. brevicula	2	26	4
M. galloprovincialis	3	31	1
C. retropictum	1	7	15
L. intermedia	0	26	2
B. cumingii	54	3	0
M. confusa	1	20	2
Assiminea sp.	4	0	12
C. rhizophorarum	14	0	4
R. clavigera	0	23	0
P. conulus	31	1	0
N. japonica	1	21	0
N. radula	1	10	0
N. nigrans	13	4	0
B. virescens	0	13	0
P. cingulata	18	0	1
L. japonica	0	12	0
B. mutabilis	0	13	0
C. nigrolineata	0	14	0
C. sinensis	12	0	0
P. alata	16	0	0
L. gracilis	10	0	0

Table 3 Selected variables (X) for generalized linear models (GLM), generalized additive models (GAM) and classification and regression trees (CART). D50 = median particle diameter, L = distance from the river mouth, V = presence of vegetation, T = tidal range, W = wave exposure, F = direct fetch, S = slope of the investigation section, τ = friction velocity at the river mouth.

Species	*B. multiformis*			*L. brevicula*			*M. galloprovincialis*			*C. retropictum*		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.22	0.38	0.46	0.14	0.32	0.11	0.14	0.25	0.12	0.10	0.30	0.32
Deviance Explained	11.5	21.5	22.4	7.4	17.4	20.7	7.2	13.1	6.0	5.2	16.1	17.6
Variables												
Habitat scale												
D50	X	X		X	X	X	X	X	X		X	X
L		X		X						X	X	X
V							X	X				
Watershed scale												
T	X	X	X	X	X	X	X	X		X	X	X
F	X	X	X		X		X			X	X	
W	X	X		X	X	X	X	X		X		
τ	X	X	X	X						X		
S			X	X			X	X		X	X	

Species	*L. intermedia*			*B. cumingii*			*M. confusa*			*Assiminea* sp.		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.18	0.24	0.41	0.12	0.27	0.32	0.09	0.18	0.23	0.40	0.47	0.52
Deviance Explained	9.3	12.6	23.2	6.4	14.8	17.6	5.1	9.7	12.0	22.3	27.4	31.0
Variables												
Habitat scale												
D50	X	X	X				X	X	X			X
L	X				X		X	X	X		X	
V				X						X	X	X
Watershed scale												
T			X		X		X	X		X	X	X
F	X	X		X	X	X	X	X			X	
W	X	X		X	X		X				X	
τ				X	X	X		X				
S							X					

Species	*C. rhizophorarum*			*R. clavig*			*P. conulus*			*P. pygmaea*		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.18	0.29	0.36	0.12	0.16	0.11	0.09	0.17	0.29	0.05	0.09	0.08
Deviance Explained	9.6	16.0	19.9	6.0	11.6	5.5	4.8	8.8	15.9	2.4	4.8	4.2
Variables												
Habitat scale												
D50				X	X	X				X	X	
L		X	X	X	X		X			X	X	X
V	X	X	X									
Watershed scale												
T		X						X				
F				X					X	X		
W	X	X		X	X		X	X		X	X	
τ	X	X	X		X		X	X	X	X		
S			X	X	X					X		

Species	*N. japonica*			*N. radula*			*N. nigrans*			*C. chinensis*		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.09	0.22	0.09	0.06	0.11	0.28	0.02	0.14	0.24	0.04	0.05	0.15
Deviance Explained	3.5	11.5	4.8	2.8	5.9	15.3	1.0	7.4	12.9	2.1	2.7	7.7
Variables												
Habitat scale												
D50	X	X	X	X	X	X		X		X		
L	X			X	X	X				X		X
V							X					
Watershed scale												
T	X	X						X		X		
F		X		X		X		X	X	X		
W		X		X	X	X	X		X			
τ									X	X	X	X
S												

Species	*B. virescens*			*L. correensis*			*R. philippinarum*			*P. cingulata*		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.06	0.07	0.06	0.04	0.08	0.33	0.04	0.06	0.28	0.05	0.18	0.29
Deviance Explained	3.3	3.7	3.3	2.0	3.9	17.9	2.0	2.8	15.0	2.7	9.2	15.6
Variables												
Habitat scale												
D50	X	X	X	X	X	X	X			X	X	X
L					X	X				X	X	
V							X			X	X	
Watershed scale												
T				X			X	X	X		X	
F					X	X	X					X
W		X		X						X	X	
τ							X	X	X	X	X	
S												

Species	*L. japonica*			*B. mutabilis*			*C. nigrolineata*			*C. sinensis*		
Modelling technique	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART	GLM	GAM	CART
R^2	0.07	0.11	0.29	0.10	0.16	0.41	0.11	0.11	0.46	0.04	0.11	0.28
Deviance Explained	3.4	6.0	15.6	5.4	8.5	23.1	5.8	10.4	26.5	1.9	5.9	15.4
Variables												
Habitat scale												
D50	X	X	X	X	X	X	X	X	X	X	X	
L	X	X	X	X	X		X	X	X		X	
V												
Watershed scale												
T	X							X			X	
F	X		X	X	X	X						X
W				X				X		X	X	
τ		X			X		X			X		
S		X					X	X	X			

Species	*P. alata*		
Modelling technique	GLM	GAM	CART
R^2	0.07	0.23	0.50
Deviance Explained	3.5	12.4	29.5
Variables			
Habitat scale			
D50		X	
L	X	X	
V			
Watershed scale			
T		X	
F			X
W	X	X	
τ		X	
S			