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Determining the relative importance of catchment- and site-scale factors in structuring fish assemblages in small coastal streams

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Abstract – Coastal streams provide important habitat for many diadromous fish species, which migrate between freshwater and the sea during their life cycle. However, coastal systems are poorly studied in comparison to large, continental river systems. Furthermore, the relative importance of catchment- and site-scale factors in structuring lotic fish communities is largely unknown. In this study, I addressed these issues by surveying the fish fauna of small coastal streams on Sado Island (northwest Japan) and determining the relative importance of catchment- and site-scale factors to the structure of freshwater fish assemblages. In total, 14 freshwater fish species were collected from the 19 streams. All but one of the fish species collected were diadromous and 9 of the species (64%) were amphidromous, primarily represented by the goby group including the genera *Rhinogobius* and *Gymnogobius*. Variance partitioning analyses showed that catchment-scale factors (namely, stream discharge) were better predictors of both fish species richness and composition than site scale and spatial factors. These results indicate that discharge, which is directly linked to habitat stability, can have a major role in structuring coastal fish assemblages, likely because small coastal streams experience extreme discharge fluctuations associated with regional weather conditions.

Keywords: coastal streams / catchment scale / diadromous fishes / assemblage structure

Résumé – Détermination de l'importance relative des facteurs à l'échelle du captage et du site dans la structuration des assemblages de poissons dans les petits cours d'eau côtiers. Les cours d'eau côtiers fournissent un habitat important à de nombreuses espèces de poissons diadromes qui migrent entre l'eau douce et la mer pendant leur cycle de vie. Cependant, les systèmes côtiers sont mal étudiés par rapport aux grands systèmes fluviaux continentaux. De plus, l'importance relative des facteurs à l'échelle du captage et du site dans la structuration des communautés de poissons lotiques est largement inconnue. Dans cette étude, ces questions sont abordées en examinant la faune halieutique des petits cours d'eau côtiers de l'île de Sado (nord-ouest du Japon) et en déterminant l'importance relative des facteurs à l'échelle du captage et du site pour la structure des assemblages de poissons d'eau douce. Au total, 14 espèces de poissons d'eau douce ont été prélevées dans les 19 cours d'eau. Toutes les espèces de poissons, à l'exception d'une seule, étaient diadromes et neuf (64 %) étaient amphidromes, principalement représentées par le groupe des gobies, y compris les genres *Rhinogobius* et *Gymnogobius*. Les analyses de partitionnement des variances ont montré que les facteurs à l'échelle du captage (à savoir le débit des cours d'eau) étaient de meilleurs prédicteurs de la richesse et de la composition des espèces de poissons que l'échelle du site et les facteurs spatiaux. Ces résultats indiquent que le débit, qui est directement lié à la stabilité de l'habitat, peut jouer un rôle important dans la structuration des assemblages de poissons côtiers, probablement parce que les petits cours d'eau côtiers connaissent des fluctuations extrêmes de débit associées aux conditions météorologiques régionales.

Mots-clés : cours d'eau côtiers / échelle du captage / poissons diadromes / structure d'assemblage

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1 Introduction

Coastal streams on islands are typically small, steep and flow directly into the sea. Although such streams have limited freshwater fauna due to their hydraulic characteristics and geographical locations, they are often important habitats for diadromous species that migrate between the sea and freshwater (Maciolek and Ford, 1987; Keith, 2003; Thuesen *et al.*, 2011). For example, diadromous fishes comprise the bulk (25 of 26 species) of the fish assemblages in coastal streams of northeastern Australia (Thuesen *et al.*, 2011) . Further, all five freshwater fish species found on the remote Hawai'ian islands are diadromous (Michael *et al.*, 2002). Also, small coastal streams can provide important nursery areas for certain salmonid species (Glova, 1987; Rosenfeld *et al.*, 2002). However, small streams flowing through coastal areas have been studied far less than larger inland rivers, especially with respect to their temperate zones. Moreover, most studies of coastal streams are focused on only one or a few basins. It is necessary to compare multiple streams that vary in characteristics to improve our understanding and management of stream ecosystems. In addition, most previous studies primarily focused only on salmonids, resulting in limited knowledge of fish species richness and the composition of fish assemblages inhabiting small coastal streams.

Understanding factors and processes influencing biotic communities is fundamental issue in ecology and ecosystem management. Many studies on the lotic fauna have focused on site-level factors such as substrate condition, water depth and current velocity. Water depth was the most important factor for determining fish species diversity in a central New York creek (Sheldon, 1968). By studying small streams in eastern Tennessee, Harvey and Stewart (1991) found a strong positive relationship between pool depth and the size of the largest fish within a pool. Such site-specific knowledge has played an important role in conservation of fish diversity and restoration of stream environments. Conversely, there has been an increasing focus on the impact of larger scale factors on stream ecosystems via macroecology, landscape ecology and community ecology. Some studies have revealed that agricultural land use and deforestation within catchment area influence on fish assemblages by changing habitat structure in streams (Eikaas *et al.*, 2005; Dala-Corte *et al.*, 2016; Molina *et al.*, 2017). Thus, although fluvial fish assemblages are influenced by factors across scales, there is no consensus on the relative importance of site- and catchment-scale variables.

To address this knowledge gap, I assessed the fish assemblages inhabiting 19 small coastal streams on an Island in the Japan Sea, northwest Japan. My specific objectives were to: (i) describe the structure of fish assemblages in small coastal streams located in temperate zone and (ii) to determine the relative importance of the catchment- and site-scale factors on structuring freshwater fish assemblages.

2 Materials and methods

2.1 Study streams

I conducted field surveys in streams on Sado Island (northwest Japan) to address the structure of fish assemblages in temperate coastal streams and the relative importance of the catchment- versus site-scale factors. Sado Island is located about 35 km west from Honsyu and is assumed to have never been connected to other islands or continents. The mean annual precipitation is approximately 1700 mm and the mean annual temperature is about 13.4 °C.

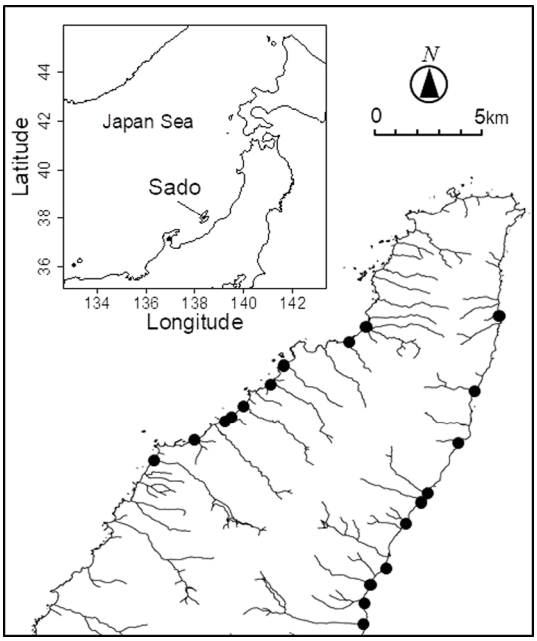

Fig. 1. The geographical location of Sado Island and the study streams.

Nineteen small coastal streams that flow independently into the sea were selected (Fig. 1). The catchment area and the summer water temperature I recorded at each stream and ranged from 0.52 to 14.9 km^2 and from 17.5 to 31.1 °C, respectively. Land use of the watersheds is dominated by natural and secondary forest. There are no barriers to fish migration at the mouth of any of the streams surveyed. I did not observe any streamflow droughts during the study period.

2.2 Sampling methods

To record the fish species and measure environmental factors, I sampled the steams twice in 2015 (mid-summer and late-autumn). Sampling was focused within the lowest 50 m reach of each stream. Fish populations were collected using a dip net (1 mm mesh) and a cast net (9.5 mm mesh) in each steam. Species lists were recorded in situ and the collected fish were then released. Sampling time was set depending on stream width. I measured following variables as site scale factors at the time fish were sampled: (1) wetted width, (2) water depth, (3) current velocity, (4) substrate, (5) pH, (6) dissolved oxygen (DO, mg l^{-1}) and (7) electrical conductivity (EC, $\mu S\ cm^{-1}$). Wetted width was measured every 10 m. Also water depth, current velocity and substrate were recorded every 10 m in the middle of flow. Substrate was categorized as bedrock, large boulder (>300 mm), small boulder (150–300 mm), cobble (50–149 mm), gravel (3–49 mm) or sand

Table 1. Occurrence of the fish species in the small coastal streams, northwest Japan.

Species	Family	Migration Type	Occurrence
Gymnogobius petschiliensis	Gobiidae	Amphidromous	18
Rhinogobius nagoyae	Gobiidae	Amphidromous	15
Luciogobius guttatus	Gobiidae	Amphidromous	14
Plecoglossus altivelis	Osmeridae	Amphidromous	13
Gymnogobius opperiens	Gobiidae	Amphidromous	11
Rhinogobius sp. CO	Gobiidae	Amphidromous	7
Rhinogobius sp.	Gobiidae	Amphidromous	6
Cottus kazika	Cottidae	Catadromous	5
Cottus hangiongensis	Cottidae	Amphidromous	5
Rhinogobius brunneus	Gobiidae	Amphidromous	4
Oncorhynchus masou	Salmonidae	Anadromous	3
Salvelinus leucomaenis	Salmonidae	Anadromous	3
Oncorhynchus keta	Salmonidae	Anadromous	1
Misgurnus anguillicaudatus	Cobitidae	–	1

(<3 mm), and I recorded the most dominant category in a 50 × 50 cm quadrat placed in the middle of flow. Water chemistries were measured in the surface water using portable field devices (pH: Horiba B-212, DO: Lutron DO-5509, EC: Horiba B-173). In addition, I measured catchment area, average slope and unforested area as catchment scale variables for each stream using 1:25 000 maps and satellite images. The following analysis were carried out using the average values (across the two samplings) for the local variables in each reach.

3 Analysis

To evaluate the relative importance of catchment- and site-scale factors on fish assemblages, I used variation partitioning techniques. Variance partitioning can be used to quantify the pure and joint contributions of predictor variables to the observed variance. The central model for species richness was a partial multiple linear regression and for species composition was a partial redundancy analysis. To assess the relative impact of catchment- and site-scale factors, I included spatial predictors in my analyses to account for the spatial configuration of habitats. Spatial factors were constructed using principle coordinate analysis of the neighbor matrix using watercourse distance (*i.e.*, distance along a coast line) (Borcard and Legendre, 2002), and then the positive eigenvectors were extracted. A permutational forward selection procedure was used to identify the variables that significantly predicted species richness and species composition for each data set. Then, to relate the species data to the main environmental factors selected by above procedure, a simple linear regression (for richness) and a redundancy analysis (for composition) were carried out.

All environmental factors were log-transformed and species compositions were Hellinger-transformed before the analyses. Forward selection was run using the packfor package and variation partitioning and redundancy analyses were run using the vegan package in the R (version 2.0–9; Oksanen *et al.*, 2013).

4 Results

Fourteen species of freshwater fish (965 individuals) were collected through all sampling in the 19 coastal streams. The most frequently sampled species was *Gymnogobius petschiliensis* (Tab. 1). The goby group (*Gymnogobius* and *Rhinogobius* fishes) accounted for about 64% of the collected species (Tab. 1). Conversely, *Misgurnus anguillicaudatus* was observed in only one stream and *Oncorhynchus masou* and *Salvelinus leucomaenis* were found in three streams (Tab. 1). The average number of species observed per stream was 5.5 (SD = 2.1). The most species-rich stream harbored nine taxa while there was only one species (*Luciogobius guttatus*) in the least taxonomically diverse stream. Of the 14 species sampled, 13 were diadromous and 9 were amphidromous. The only pure freshwater fish collected, *M. anguillicaudatus*, was likely non-indigenous, having been widely introduced throughout Sado Island as a food source for the highly endangered Crested Ibis (*Nipponia nippon*).

The forward selection procedure identified one catchment-scale factor (discharge $R^2_{adj} = 0.444$, $P = 0.004$) and two site-scale factors (water depth $R^2_{adj} = 0.622$, $P = 0.001$; current velocity $R^2_{adj} = 0.130$, $P = 0.030$) as significantly related to species richness. Similarly, two catchment-scale factors (discharge $R^2_{adj} = 0.113$, $P = 0.003$; unforested area $R^2_{adj} = 0.101$, $P = 0.007$) and two site-scale factors (water depth $R^2_{adj} = 0.076$, $P = 0.022$; DO $R^2_{adj} = 0.083$, $P = 0.009$) were determined to significantly influence species composition. The variance partitioning analyses showed that the best descriptors of fish assemblages in the small coastal streams were catchment scale factors (Fig. 2). The interactive effect of catchment- and site-scale factors explained a larger portion of the variance in the fish species data. The linear regression indicated that species richness was strongly and positively related to discharge. The redundancy analysis showed that ayu *Plecoglossus altivelis* tended to dominante numerically in streams having greater discharge (Fig. 3). The amount of unforested area in the catchment was associated with *Rhinogobius nagoyae* and *Gymnogobius petschiliensis* and streams with more unforested catchments harbored similar fish assemblages (characterized by *R. nagoyae*) (Fig. 3).

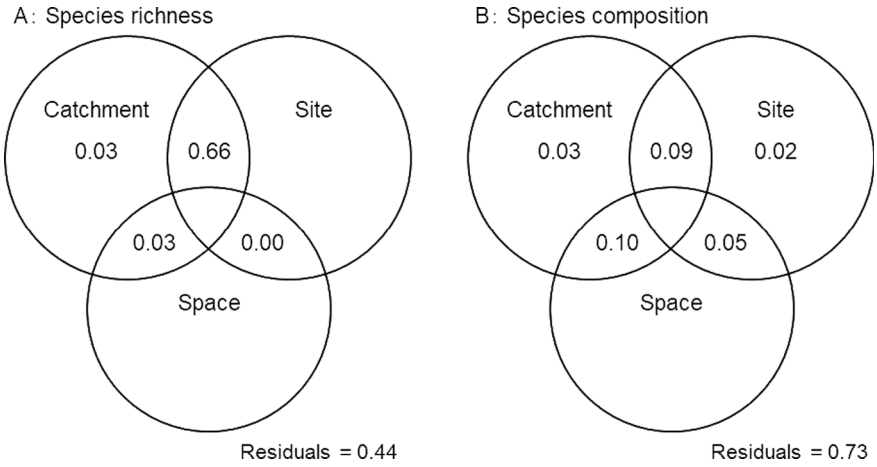

Fig. 2. The Venn diagrams based on variation partition for (A) species richness and (B) species composition. Values < 0 are omitted.

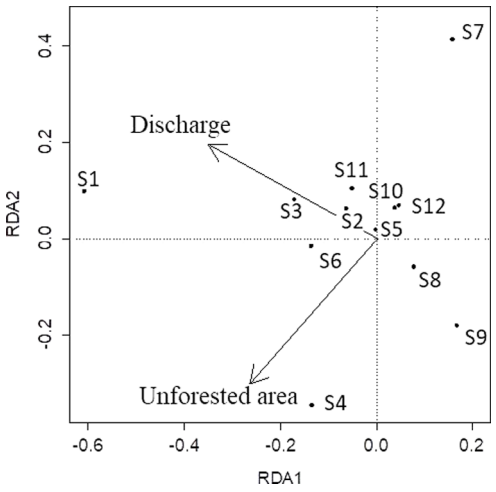

Fig. 3. Two-dimensional ordination plot of fish species resulting from RDA. Arrows indicate significant factors and the strength and direction of correlations between factors and species compositions (species in the streams: S1 *Plecoglossus altivelis*, S2 *Oncorhynchus masou*, S3 *Rhinogobius* sp. CO, S4 *Rhinogobius nagoyae*, S5 *Rhinogobius brunneus*, S6 *Rhinogobius* sp., S7 *Gymnogobius petschiliensis*, S8 *Gymnogobius opperiens*, S9 *Luciogobius guttatus*, S10 *Cottus hangiongensis*, S11 *Cottus kazika*, S12 *Salvelinus leucomaenis*).

5 Discussion

5.1 Fish fauna of small coastal streams

Although diadromous species constitute less than 1% of known freshwater fishes (McDowall, 1988), almost all fish species I sampled in the study were diadromous. Freshwater fishes with a diadromous life history pattern have been frequently observed in streams on oceanic islands such as Hawaii, and are recognized as the main group of fish fauna in Island streams (McDowall, 2004). Despite Sado Island's proximity (30 km) to the main Japanese Island of Honshu, there is no clear evidence of a previous land-bridge connection between the islands. Moreover, approximately 70% of the freshwater species known to inhabit Japanese streams are thought to be diadromous (Katsutoshi and Hiroshi, 2010). Thus, in terms of species pool, Sado Island may be similar to remote oceanic islands. Similar to my findings here, the assemblage of species on Oki Island (which has a similar topography to Sado Island) was dominated by goby including *Gymnogobius* and *Rhinogobius* fishes (Hiroyuki *et al.*, 1985).

Three salmonid species were observed in Sado Island streams. Salmonids are distributed in relatively cold waters (Coutant, 1977), and do not occur on tropical islands like Hawaii and Tahiti, where faunas are largely dominated by gobies (Radtke *et al.*, 1987; Watson, 1992). In small streams at Basse Terre, the Lesser Antilles, no salmonids occurred, while two of six species were gobies (Fiévet *et al.*, 2001). Conversely, the freshwater fish fauna of streams on several Mediterranean islands comprise mainly salmonids, while gobies are sparse (Bianco *et al.*, 1996). Thus, freshwater fish faunas can differ in their composition, depending on region, even for streams of similar scale with similar hydrographic characteristics. The fish assemblage of Sado Island is characterized by the occurrence of both salmonids and dominance of gobies.

Diadromous species are separated into three groups based on migration pattern (Myers, 1949). In the study streams, 9 of 13 diadromous fishes, including such as gobies and ayu, were categorized as amphidromous species. Amphidromous species primarily breed in freshwater, fry swim outmigrate to the sea, and after staying in the sea for a certain period of time, small juveniles migrate back in to freshwater. This life history is considered a benefit in colonizing fluctuating and deciduous environments, such as small coastal streams, that are susceptible to regional climate variation. Sado Island coastal streams have small catchments (average = 5.5 km^2, SD = 4.2) in which the dominance of amphidromous species likely reflects characteristics of individual catchment areas.

5.2 Relative importance of the catchment and site scale factors

Habitat size is one of the most widely recognized factors influencing the structure of stream fish assemblages. For example, Taylor (1997) demonstrated a significant relationship between fish species richness and habitat size in a small steam

in Oklahoma, and Angermeier and Schlosser (1989) found habitat size generally correlated with species richness for pools and riffles of small streams in Minnesota, Illinois, and Panamathe latter likely a consequence of increasing habitat heterogeneity and habitat volume (McGarvey and Hughesm, 2008).

Previous studies exploring the assemblages of stream fishes have focused on small-scale factors such as habitat depth and substrate. Paller (1994) found that there was strong correlation between fish assemblages and depth in coastal streams of the southeastern USA. Willis *et al.* (2005) reported that fish species density was correlated with habitat structural complexity, which was in turn associated with current velocity. Previous studies exploring the assemblages of stream fishes have focused on small-scale factors such as habitat depth and substrate. Paller (1994) found that there was strong correlation between fish assemblages and depth in coastal streams of the southeastern USA. Willis *et al.* (2005) reported that fish species density was correlated with habitat structural complexity, which was in turn associated with current velocity. For small coastal streams on Sado Island, my analysis indicated that catchment-scale factors account for a larger proportion of variation in fish assemblages than site-scale factors. The discharge rate of streams seemed to be an especially good predictor of fish assemblages, as it was a significant predictor for both richness and composition. Similar to the present study, some reports showed an association between discharge and fish species. For example, the number of fish species in African rivers was more closely related to discharge than other factors (Livingstone *et al.*, 1982). One possible explanation for this association is that streams with higher discharge rates will be less vulnerable to environmental fluctuations. Small streams have high vulnerability to periodic droughts because they are directly influenced by the regional climate fluctuations. Thus, it is believed that discharge structures fish assemblages by influencing habitat perenniality in small coastal streams.

The result from compositional analyses indicate that ayu tends to dominate numerically with increasing discharge. Ayu (Osmeriformes: Plecoglossidae) individuals prefer riffles for feeding and breeding sites. Indeed, increases in riffle habitat associated with increases in discharge lead to increases in density of ayu (Isao and Nobuhiko, 2012). These observations suggest that discharge could impact fish assemblages via changing site-scale environments, corresponding to the hierarchy hypothesis of stream ecosystems (O'Neill *et al.*, 1989). Additionally, the large joint effect observed in my variation partitioning analysis might also reflect the hierarchical impact of catchment- and site- scale factors.

Previous studies assessing the impact of catchment-scale factors on stream fish assemblages revealed that agriculture and deforestation influence the structure of fish habitat by providing sediments to streams (Russell *et al.*, 1998; Huryn *et al.*, 2002; Quinn and Stroud, 2002). In the present study, the amount of unforested area in a catchment was shown to influence fish species composition. In particular, *R. nagoyae* and *G. petschiliensis*, the two most frequently observed species in the study, showed strong associations with unforested area. Although there exists little life-history knowledge of these two species, they are of the Gobiidae family and have a benthic life style. The condition of the substrate is crucially important for benthic species because rock and gravel provide foraging, nesting and evacuation sites. Jones *et al.* (1999) revealed that riparian forest removal leads to a decrease in benthic-dependent fish species (such as *Cottus bairdii* and *Rhinichthys cataractae*) due to sedimentation on the substrate. Thus, the relationship I observed between unforested area and fish species suggests that alteration of the stream substrate through land use changes may play an important role in determining habitat suitability in small coastal streams.

The results of my study indicate that catchment-scale factors (*e.g.* land use) have greater impacts than site-scale factors on fish assemblage for small coastal streams. However, the specific mechanism underlying the relationship is still unclear. Further studies will be required to determine how catchment-scale factors structure fish assemblages in island coastal streams.

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