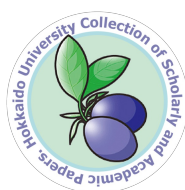




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Title: Combined effects of immigration potential and habitat quality on diadromous fishes

Authors: Akira Terui^{1,*} and Yusuke Miyazaki²

¹ Department of Forest Science, Graduate School of Agriculture, Hokkaido University, Kita 9, Nishi 9, Kita-ku, Sapporo 060-8589, Japan.

² Department of Child Education and Welfare, Shiraume Gakuen College 1-830 Ogawa-cho, Kodaira-shi, Tokyo 187-8570

* Corresponding author. Tel., Fax: +81 11 706 3842

E-mail address: hanabi0111@gmail.com (A. Terui)

ABSTRACT

In river systems, considerable debate exists as to why small-scale conservation with a primary focus on habitat quality brings little improvement to biological communities. To reveal potential causes of the enigmatic consequences, further explorations should focus on how species' response to local environments is determined within a watershed. Here, we examined how immigration potential influences habitat associations of four diadromous fishes in the Shubuto River system in Hokkaido, Japan: sculpins (*Cottus* sp. ME and *C. hangiongensis*), gobies (*Gymnogobius opperiens*) and sea lamprey larvae (*Lethenteron japonicum*). We used closeness to the sea (i.e., distance from the sea) as a proxy for immigration potential, since the source of immigrants of the diadromous fishes is the river mouth. A multilevel modeling approach revealed that immigration potential had a "bottom-up effect" on local habitat-abundance relationships (current velocity and substrate coarseness), but habitat preferences did not vary along the gradient of immigration potential. This likely reflects the limited dispersal capabilities of the study species, whereby shorter travel distances may greatly enhance colonization success. Our study raises the possibility that the effectiveness of small-scale riverine conservation can be improved by selecting areas where successful colonization would be expected. Explicitly incorporating this consideration into conservation decision-making would help achieve greater success of environmental restoration and preservation actions.

30

31 **Keywords:** amphidromous, anadromous, Bayesian framework, immigration, stream

32 conservation

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34

35 **INTRODUCTION**

36 In recent decades, human activities have severely altered natural landscapes, so that habitat

37 protection and restoration are now an integral element of conserving biodiversity (Kuussaari et

38 al. 2009). Habitat fragmentation and degradation are among the most serious threats to

39 biodiversity, and landscape-level conservation is thought to be ideal for mitigating these impacts

40 (McKenzie et al. 2013). Nevertheless, such practices are challenging because land management

41 for biodiversity conservation frequently conflicts with arguments for human benefit and safety

42 (Dudgeon et al. 2006; McKenzie et al. 2013).

43 This conflict comes to the surface in riverine systems, where human and natural

44 systems are inherently linked through water demands and natural disasters (Nakamura et al.

45 2006). Consequently, most river conservation projects today are implemented at the reach scale

46 (typically <1 km) with a primary focus on channel form and physical structures (Palmer et al.

47 2014; Roni et al. 2002). However, the resulting response of biological communities to improved

physical habitats is highly inconsistent among sites (Roni et al. 2002; Stewart et al. 2009), and considerable debate exists as to why only a few notable exceptions have achieved their conservation goals (e.g., Boulton et al. 2013; Nakamura et al. 2014). The scarcity of successful restoration is problematic because, in the United States for example, public and private organizations have spent ~\$10 billion on more than 30,000 river and wetland restoration projects since 1990 (Malakoff 2004). To reveal potential causes of the enigmatic consequences of conservation projects and to allocate conservation budgets more wisely, further explorations should focus on how species' response to physical environments is determined in a landscape.

Immigration potential is a likely variable that controls habitat associations of aquatic organisms (Gowan and Fausch 1996; Lake et al. 2007). Because organisms may select or settle into preferable habitats following chance dispersal to a given locality (i.e. a set of local habitats), immigration potential can have an “overriding” effect on habitat associations by producing initial variation in propagule size. Quantifying the impact of sequential processes would help predict potential benefits of small-scale conservation and help identify the highest priority areas within a watershed. However, despite the importance of spatial processes being widely recognized in applied contexts (Stoll et al. 2013), the combined effects of immigration potential and habitat quality have rarely been quantified in aquatic ecosystems (but see Olds et al. 2012).

Benthic fish with diadromous life histories (migration between marine and freshwater) are undergoing rapid global declines (Limburg and Waldman 2009), partly because migration of benthic fish is easily impaired by river-crossing structures (Lucas et al. 2009). Despite this obstacle, diadromous benthic fish provide a unique opportunity to uncover possible interactions between immigration potential and local environments for the following reasons. First, given their migratory life history and the linear arrangement of river networks, we can assume the river mouth is the source point of immigrants (Cote et al. 2009). Although immigration potential can be measured in a variety of ways, from the nearest-neighbor distance to more complex formulas that account for matrix resistance (Kuroe et al. 2011; Moilanen and Nieminen 2002), the directional dispersal of migrants (upstream migration from the sea) allows us to define watercourse distance from the source as a simple proxy for immigration potential (McDowall 1996, 1998; Miyazaki and Terui 2016). Second, benthic fish show clear preferences for physical conditions such as current velocity (Sugiyama and Goto 2002; Van Liefferinge et al. 2005), which makes the detection of responses to those environments easier. Therefore, studies of diadromous benthic fish may provide valuable insights that can be applied to many other organisms.

Here, we explored how immigration potential influences the local habitat associations of four benthic fish species in a Japanese river: sculpins (*Cottus* sp. ME [a species complex of *C.*

pollux or *C. reinii*] and *C. hangiongensis*), gobies (*Gymnogobius opperiens*) and sea lamprey larvae (*Lethenteron japonicum*). These diadromous fish (amphidromous or anadromous) encompass a range of habitat requirements and taxonomic groups (Cottidae, Gobiidae and Petromyzontidae). For example, sculpins favor riffle habitats with coarse substrata (Goto et al. 2002), whereas gobies and sea lamprey larvae inhabit static water bodies (Nagayama et al. 2012; Stevenson 2002). Such local habitat-abundance relationships may vary depending on their immigration potential. The present study tackled this issue with a multilevel modeling approach that explicitly deals with the sequence of pre- (i.e. immigration) and post-settlement processes (i.e. local habitat selection).

METHODS

STUDY AREA AND SPECIES

We collected data in the Shubuto River system, located near Kuromatsunai, Hokkaido Prefecture, Japan (42°40'N, 140°18'E). The mean annual temperature and cumulative precipitation at the site are 7.4°C and 1461.8 mm, respectively. The water catchment area encompasses ~367 km², and the length of the main river is ~40 km.

This system presents an excellent model to test an effect of immigration potential

because the river environment is relatively intact and confounding factors (e.g. water quality) can be effectively controlled. Water quality is suitable for most freshwater organisms throughout the river system (dissolved oxygen >95% saturation, pH 7.0–8.1, biochemical oxygen demand 0.5–1.7 mg L⁻¹ and ammonia concentration 0.05–0.13 mg L⁻¹) (Terui et al. 2014). No dams or weirs prevent fish migration in the mainstem.

The peak migration seasons of the four study species vary from June to August in the Shubuto River (Miyazaki and Terui 2016). Adults of the three amphidromous species (sculpins and gobies) spawn in the river and their larvae drift down to the sea immediately after hatching (Kawanabe and Mizuno 1998). Developed juveniles return to the river in July (sculpins) or August (gobies) following a short marine life stage (a few weeks) (Kawanabe and Mizuno 1998). In contrast, adult sea lampreys migrate into the river for spawning (i.e. anadromous life history), and then hatched larvae (ammocoetes) burrow into the silt–sand substrate where they stay for 2–3 years before transforming into parasitic adults (Kawanabe and Mizuno 1998).

Rapid declines of these species have been observed across Japan, and *Cottus* sp. ME and *L. japonicum* are listed as endangered on the national Red List (categories CR and EN, respectively) (Ministry of the Environment 2013). Sea lamprey populations in the Shubuto River are believed to have declined over the past few decades (Miyazaki et al. 2012), which has received a great deal of attention because the species is an important food resource for local

people.

FISH SAMPLING

We measured fish abundance using a nested sampling design during the summer (late-June to July) of 2010 and 2011. This data set includes, but is not limited to, previously published data (Miyazaki and Terui 2016, in press; Terui and Miyazaki 2016). We surveyed 47 reach replicates, 27 of which were surveyed twice across 2 years (Fig. 1). Sampling reaches were scattered across the river network, and this sampling design helps ameliorate a spurious correlation between immigration potential of diadromous fishes (i.e., distance from the sea) and longitudinal gradients of any environmental variables (see also Discussion). The spatial extent of study reaches (20–55 m) was intended to coincide with daily movements of benthic fish (Ovidio et al. 2009; Quintella et al. 2005). The tributary sites did not have weirs under their channels except for the uppermost site at the Neppu River (the filled point in Fig. 1). Each reach comprised one to five local habitats, each of which can be grouped into either mid-channel, river margin or backwater habitats (Fig. 1). We selected local habitats to encompass a range of water depth, current velocity and substrate coarseness. The areal extent of individual local habitats (i.e. sampled area) ranged from 1 to 120 m² (mean: 39.1, SD: 22.0).

In each local habitat, we conducted one-pass electrofishing (LR-20B, Smith-Root Inc.,

Vancouver, WA, USA) from the lower to upper borders of the local habitat with three investigators using D-shaped hand nets (2-mm mesh), following the methods of Katano et al. (2006). In total, we surveyed 195 replicates of local habitats over the 2-year sampling period. Except some specimens (one or two individuals per species) for museum deposition (Miyazaki et al. 2013), all captured fish were released back into the habitats where they were caught.

In 2010, we could not confidently discern sea lamprey larvae from those of a closely related species, *Lethenteron reissneri*. Thus, we recorded these larvae as “NA” and imputed within a simulation-based Bayesian framework (see *Statistical analysis*). We excluded from counts 0+ fish that may not have settled yet into their primary habitats.

HABITAT ATTRIBUTES

Local-level variables

We measured physical attributes commonly assessed in river restoration projects (water depth, current velocity, substrate coarseness) concurrently with the fish abundance surveys. We placed one to twelve 0.25-m² quadrats in each local habitat so that quadrat density exceeded 1 quadrat/10 m². We measured water depth with a meter stick and current velocity at 60% depth with a flow meter (VE20, VET-200-10PII; KENEK, Tokyo, Japan). We measured substrate coarseness following a modified method of Bain et al. (1985). The proportion of each of the

following categories was visually estimated in each quadrat: particles <0.063 mm = silt, 0.063–2 mm = sand, 2–64 mm = pebble, 64–256 mm = cobble. These categories were then coded by midpoint values of each size class: silt = 0.0315, sand = 1.032, pebble = 33 and cobble = 160. The substrate coarseness of the quadrat was calculated by the following equation: $\text{substrate coarseness} = \sum (\text{material code} \times \text{proportion of the category})$. We averaged duplicate measurements for each local habitat and used the averaged values for further analysis.

Reach-level variables

We used closeness to the sea (i.e. watercourse distance from the sea to the site) as the simplest measure of immigration potential. Previous studies, including ours, suggested that migrants of diadromous fish (e.g. recruiting juveniles) decrease with distance from the sea (McDowall 1998; Miyazaki and Terui 2016). We measured immigration potential as the shortest distance from the river mouth to the reach along connecting waterways. We acknowledge that the “true” sources of sea lamprey larvae (i.e. spawning grounds) may be located somewhere upstream of the sampling reaches. However, we roughly defined immigration potential for the sea lamprey in the same manner, as the number of sea lamprey larvae should reflect, to a lesser extent, immigration of spawning adults from the sea.

Catchment area and elevation were also calculated at each sampling reach, as those

might be related to fish abundance through influences on gross primary production and/or water temperature (Altermatt et al. 2013; Finlay 2011). We preferred the use of the proxy because temporal integration of productivity and temperature measures across the watershed was impractical. We estimated watercourse distance, catchment area, and elevation using ArcGIS 10.1 with 1:25,000 topographic and digitized elevation maps.

STATISTICAL ANALYSIS

We used a multilevel Bayesian model (Amano et al. 2011; Gelman and Hill 2007) to assess interacting effects across spatial levels (reach and local levels). Multilevel models, also known as hierarchical linear models, use nested regression equations to investigate associations between variables at multiple hierarchies or scales. This approach enabled us to simultaneously evaluate the impact of reach-level factors (e.g. immigration potential) on both fish abundance and local habitat quality (current velocity, substrate coarseness and water depth).

In the model, observed fish abundance $Y_{i,k(j)}$ (fish species i in local habitat j nested within reach k) was assumed to follow a Poisson distribution, $Y_{i,k(j)} \sim \text{Poisson}(\lambda_{i,k(j)})$ and was related to linear predictors via a log-link function as

$$\log(\lambda_{i,k(j)}) = \beta_{0,i,k} + \beta_{1,i,k} \cdot \text{Depth}_j + \beta_{2,i,k} \cdot \text{Velocity}_j + \beta_{3,i,k} \cdot \text{Substrate}_j + \beta_{4,i} \cdot \text{Year}_j + \log(\text{Area}_j) + \varepsilon_i,$$

where $\beta_{0,i,k}$ and $\beta_{1,i,k}$ – $\beta_{3,i,k}$ are reach-specific intercept and regression coefficients, respectively.

$\beta_{4,i}$ is the effect of sampling year (incorporated as a dummy variable, in which “2010” and “2011” equal 0 and 1, respectively). The areal extent of local habitat j (Area_j) was included as an offset term. Another parameter (ε_i) is a random effect that mitigates overdispersion (Kéry 2010) and is normally distributed as $\varepsilon_i \sim \text{Normal}(0, \sigma^2_\varepsilon)$.

The reach-specific intercept and coefficients $\beta_{m,i,k}$ ($m = 0$, intercept; $0 < m \leq 3$, coefficients) were modeled as random effects and were assumed to follow normal distributions with means determined by a global intercept (or global coefficients) and reach-level covariates as follows:

$$\beta_{m,i,k} = \beta 0_{m,i} + \beta 1_{m,i} \cdot \text{Distance}_k + \beta 2_{m,i} \cdot \text{Elevation}_k + \beta 3_{m,i} \cdot \text{Catchment area}_k + \omega_{m,i},$$

Species-specific means and variances for $\beta 0_{m,i}$ – $\beta 3_{m,i}$ were drawn from normal distributions with hyper-means $\mu_{\beta m}$ and hyper-variances $\sigma^2_{\beta m}$. It is important to note that the use of hyper-parameters ($\mu_{\beta m}$ and $\sigma^2_{\beta m}$) improves parameter estimates for species with limited information (i.e. the sea lamprey *L. japonicum*, for which one-year data were available). Since all of the explanatory variables were standardized prior to analysis, global coefficients $\beta 0_{m,i}$ ($m = 1$ – 3) represent the average effect of each local habitat quality variable. The coefficients of distance, elevation and catchment area ($\beta 1$ – $\beta 3_{m,i}$) can be interpreted as interactive effects across spatial levels (Gelman and Hill 2007). The error term $\omega_{m,i}$ was normally distributed as $\omega_m \sim \text{Normal}(0, \sigma^2_{\omega m})$. Note that catchment area and elevation were included to control potential

effects of local productivity and water temperature.

Elevation was positively correlated with distance from the sea (Pearson's $r = 0.92$, $p < 0.001$). Therefore, we used residuals of a linear relationship fitted between elevation and distance from the sea to avoid multicollinearity. The residuals provide a relative measure of the elevation, independent of the distance, in which positive values reflect a greater elevation than expected for a given distance, whereas negative values reflect a lower elevation than expected. Correlation coefficients for the other combinations of explanatory variables were < 0.65 .

Vague priors were assigned for the parameters: i.e. normal distributions (mean = 0, variance = 50) for $\mu_{\beta m}$, and truncated normal distributions (mean = 0, variance = 50, range: 0–50) for variance parameters (σ^2_{ϵ} , $\sigma^2_{\beta m}$ and $\sigma^2_{\omega m}$). The model was fitted to the data with JAGS ver. 4.1.0 and the package “rjags” in R 3.2.3 (Plummer 2014). Three Markov Chain Monte Carlo chains were run with 30 000 iterations (10 000 burn-in) and 1000 samples per chain were used to calculate posterior probabilities. Convergence was assessed by examining whether the R-hat indicator of each parameter approached 1 (Gelman and Hill 2007). We also checked the model performance with a Bayesian p -value (Kéry 2010). The Bayesian p -value, which was based on a sums-of-square discrepancy, approaches 0.5 if the model completely reproduces the data.

227

228 **Results**

229 *Fish abundance and environmental conditions*

230 Fish abundance varied among sampling reaches as well as local habitats within a reach. The
231 most abundant fish was *G. opperiens* (0.25 ± 0.41 SD individuals/m²), followed by *L. japonicum*
232 (0.20 ± 0.98), *C. hangiongensis* (0.05 ± 0.13) and *Cottus* sp. ME (0.02 ± 0.04). Hypothesized
233 influential variables spanned a wide range of values and are summarized in Table 1.

234

235 *Effects of immigration potential on local habitat–abundance relations*

236 The Bayesian *p*-value of the multilevel model was 0.50, indicating that the model performance
237 was reasonably good. Indeed, the model precisely predicted the observed abundance of each
238 species (Fig. S1). Moreover, the estimated variance parameters for the random effects were
239 relatively small ($\sigma^2_\epsilon = 0.47\text{--}1.73$, $\sigma^2_\omega = 0.22\text{--}1.43$), suggesting that the influence of unmodeled
240 variables was not substantial.

241 Distance from the putative source (i.e. the sea) had significant effects on the
242 reach-specific intercept for all of the species (βI_0 ; Fig. 2a), reflecting sharp declines in fish
243 abundance with increasing distance at the reach scale (Fig. 3). The multilevel model predicted
244 that more than half of individuals were distributed within 10 km of the river mouth (Fig. 3).

The global coefficient for current velocity had a strong effect on all of the species (Fig. 4), although it was insignificant for *Cottus* sp. ME and *G. operiens* (β_{02} ; Fig. 2c). The sculpins preferred local habitats with faster current velocity, whereas gobies and sea lamprey larvae tended to prefer slow currents. Closeness to the sea had a “bottom-up effect” on the local current–abundance relationship (especially for *C. hangiongensis*; Fig. 4), primarily due to the greater fish abundance at reaches close to the sea (Fig. 3). However, no significant effects of the interaction terms (β_{12}) were detected for any of the species (Fig. 2c), indicating that their habitat associations did not vary along the gradient of immigration potential.

Similarly, the local substrate-abundance relationship shifted upward with increasing immigration potential for sculpins and gobies (i.e. the effect of distance on the reach-specific intercepts; Fig. 5), although interaction terms were not statistically significant for all the species (Fig. 2d). Sea lamprey larvae showed an unclear response to the environment, irrespective of distance from the sea (Fig. 5).

Water depth had little effect on fish abundance (Fig. 2). The estimated coefficient was highly variable and its 95% credible intervals (CIs) included zero (Fig. 2).

Elevation negatively influenced local densities of *C. hangiongensis* and *G. operiens* (β_{20} ; Fig. 2a). Catchment area had a positive influence on sea lamprey larvae (β_{30} ; Fig. 2a).

None of the local variables significantly interacted with distance, elevation or catchment area to

influence fish abundance (β_{1-3} , β_{2-3} and β_{3-3} ; Fig. 2b-d). The year effect β_4 was positive for the goby (0.54, 95%CI: 0.07–1.05) but negative for the other species (*Cottus* sp. ME [Median: -0.83, 95%CI: -1.52– -0.20], *C. hangiongensis* [Median: -0.79, 95%CI: -1.56– -0.16]). We could not estimate the year effect for the sea lamprey, because the data set in 2010 is lacking.

Discussion

The present study found that immigration potential plays a pivotal role in determining habitat–abundance relationships of aquatic organisms. Although the habitat preferences of the four species did not vary along the gradient of immigration potential, it did raise the baselines of the habitat-abundance relationships (i.e. reach-specific intercepts). This pattern was consistent across species with differential dispersal abilities and habitat requirements. Thus, selection of sites in a watershed can have dramatic consequences on the outcome of small-scale conservation efforts, emphasizing the critical importance of spatial planning. Our findings, together with recent notable research (Stoll et al. 2013; Sundermann et al. 2011), may offer a possible explanation for the scarcity of successful restoration projects (e.g., Stranko et al. 2012).

Despite the fact that the species can access nearly the entire river network, the reaches within 10 km of the sea appear to be core areas for settlement and spawning (Fig. 3), which

281 suggests high mortality or limited motility of migrants (Lucas et al. 2009; McDowall 1998).
282 Shorter travel distances may effectively enhance the probability of colonization success and
283 thereby raise the occupancy of available microhabitats. Moreover, lamprey larvae are known to
284 attract spawning adults using pheromones (Li et al. 1995), further strengthening the relationship
285 between immigration potential and fish abundance. These factors likely contribute to the strong
286 impact of immigration potential on local fish abundance.

287 The observed local habitat associations were understandable when considering food
288 availability and/or microhabitats. The positive (sculpins) and negative (lampreys) effects of
289 current velocity may be related to their food availability. Benthic macroinvertebrates, a primary
290 prey item for Japanese sculpins (Natsumeda et al. 2012), may be continuously supplied in
291 fast-current habitats (Inoue et al. 2005), whereas abundant detritus would be available for
292 detritivorous lamprey larvae (Sutton and Bowen 1994) in depositional areas with slow currents.
293 In contrast, the substrate–abundance relationships were consistently positive across sculpins and
294 gobies. This is probably because coarser substrata provided a common microhabitat (interspaces
295 among cobbles) for sculpins and gobies (Natsumeda 2001; Stevenson 2002). Collectively, these
296 patterns may reflect the fact that individuals settled in favorable local habitats following chance
297 dispersal to each locality.

298 The effects of water depth were unclear in this study. Although water depth is widely
299 known to affect the distribution of aquatic organisms by limiting primary productivity (Doi
300 2009; Terui et al. 2011), the spatial extent of our study (i.e. within-reach scale) may be too small
301 to make such a difference for benthic fishes. Previous studies have also found water depth
302 uninformative in predicting benthic fish abundance at comparable spatial scales (Donaldson et
303 al. 2013).

304 One potential criticism is that we used a proxy variable to infer the impact of
305 immigration potential on local processes (i.e. distance from the sea), because a variety of
306 environments could associate with the distance. For example, primary and macroinvertebrate
307 productions are generally higher in downstream reaches (Finlay 2011) and these might lead to
308 increased fish abundance at sites close to the sea. However, such a spurious correlation is less
309 likely to fully explain the observed patterns, given that our sampling sites included “headwater”
310 tributaries flowing into downstream segments of the mainstem (thus, close to the sea; see Fig. 1).
311 Despite that such small streams are typically low in *in situ* productivity, the tributaries were
312 frequently utilized by the study species, probably owing to the high accessibility from the sea.
313 The use of the proxy limits our ability to infer causality, but this fact suggests that distance from
314 the sea may, at least in part, reflect immigration potential of diadromous fishes.

315 Although watershed-scale management is ideal for the maintenance of regional
316 biodiversity (Palmer et al. 2014), this ultimate form of conservation is often impractical in the
317 short term (Boulton et al. 2013). For this reason, small-scale conservation remains crucial.
318 However, in Japanese river systems, immigration potential has not been fully considered when
319 choosing conservation sites. Broadly speaking, our study raises the possibility that the
320 effectiveness of small-scale riverine conservation can be improved by selecting areas where
321 successful colonization would be expected. Specifically, in the Shubuto River system, we
322 suggest that reaches within 10 km of the putative source should be prioritized for conservation
323 and/or restoration of diadromous benthic fish habitats. This must be validated in the context of
324 ongoing restoration or degradation, yet explicitly incorporating this consideration into
325 conservation decision-making would help achieve greater success of environmental restoration
326 and preservation actions.

327

Ethics

Field surveys on animals were conducted with the permission of Hokkaido prefecture

Authorship's contributions

AT and YM conducted the sampling and participated in conception, discussion of the results, and manuscript preparation.

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Supporting Information

Figure S1 Comparison between predicted and observed fish abundance.

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475 **Table 1** Environmental conditions among sampling sites.

Scale	Variable	Mean (SD)	Range
Reach	Distance from the sea (km)	15.7 (9.0)	2.4–40.0
	Elevation (m)	34.2 (35.7)	3–192
	Catchment area (km ²)	107.3 (116.7)	3.1–357.6
Local	Water depth (cm)	37.0 (21.9)	2.3–96.8
	Current velocity (cm s ⁻¹)	24.3 (22.8)	0–131.5
	Substrate coarseness ^a (mm)	74.2 (44.2)	0.03–155.2

476 ^a Substrate coarseness was evaluated by a modified method of Bain et al. (1985).

477

Figure captions

Fig. 1 (a) Map of the Shubuto River system. Points indicate sampling reaches. The filled point is the sampling reach located above a small weir (the Neppu River). (b) Schematic diagram of a nested sampling design. Each reach replicate comprises one to five local habitats with different water body types (gray shaded area).

Fig. 2 The estimated parameters for the multilevel model fitted to abundance data of four benthic fish species (*Cottus* sp. ME, *Cottus hangiongensis*, *Gymnogobius opperiens* and *Lethenteron japonicum*). Points represent the median estimates and bars denote their 95% credible intervals (CIs). Parameters for which 95% CIs did not include zero were shown as filled points.

Fig. 3 The cumulative proportion of fish abundance increased clearly with increasing distance from the sea. Lines are based on fish abundance predicted by the multilevel model. All the other explanatory variables were fixed at mean values for the prediction.

Fig. 4 Impact of immigration potential on local current–abundance relationships. Predicted abundance of the four benthic fish species is shown along a gradient of current velocity. Solid

lines with gray backgrounds show median predictions and associated 95% CIs. All the other explanatory variables were fixed at mean values for the prediction. Broken and broken-dot lines represent predictions for the explanatory variable of interest at reaches with high (broken lines: 20 percentile of distance from the sea) and low immigration potential (broken-dot lines: 80 percentile of distance from the sea).

Fig. 5 Impact of immigration potential on local substrate–abundance relationships. Predicted abundance of the four benthic fish species is shown along a gradient of substrate coarseness. Lines and backgrounds are as defined in Fig. 4.

Fig 1 Terui and Miyazaki

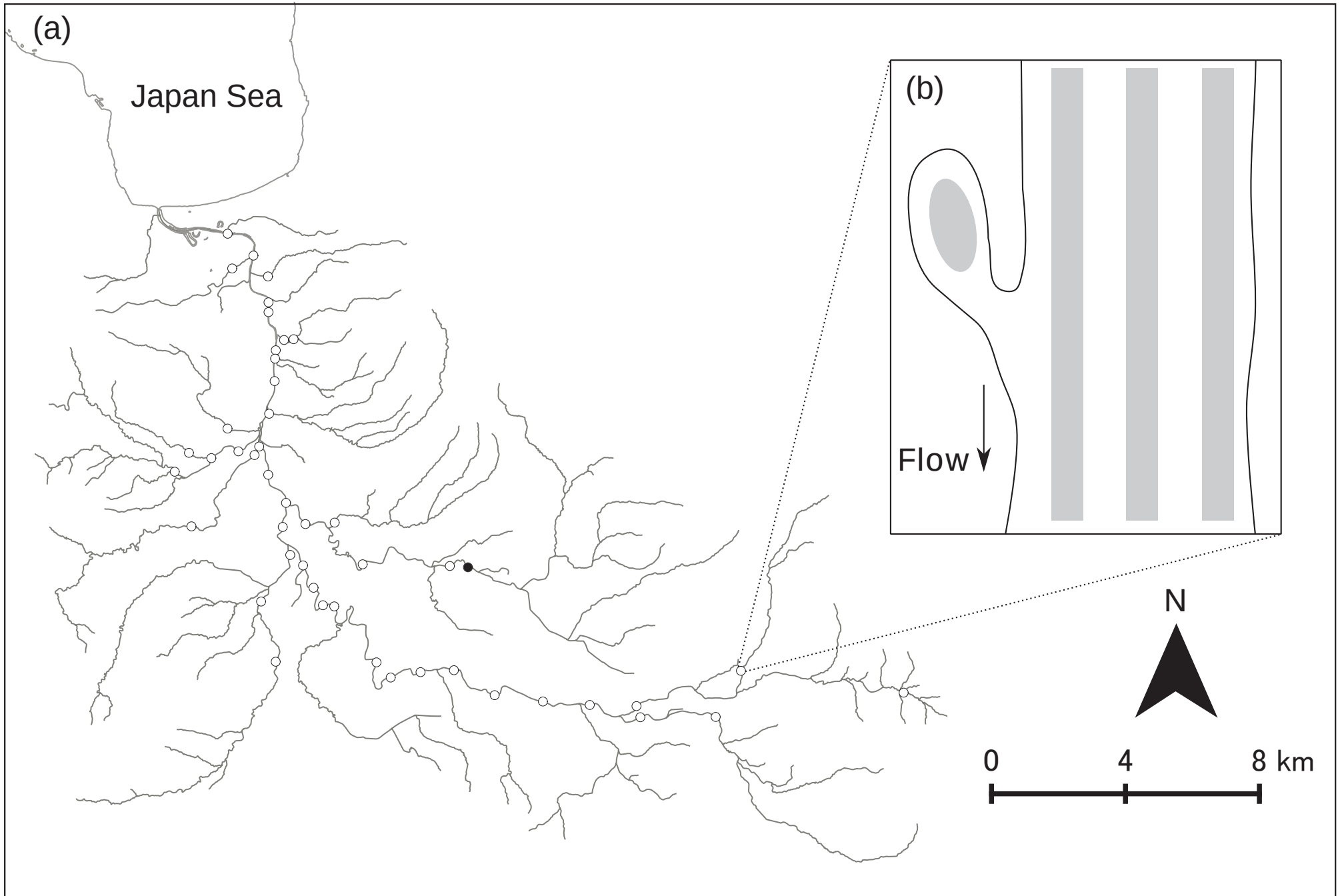


Fig.2 Terui and Miyazaki

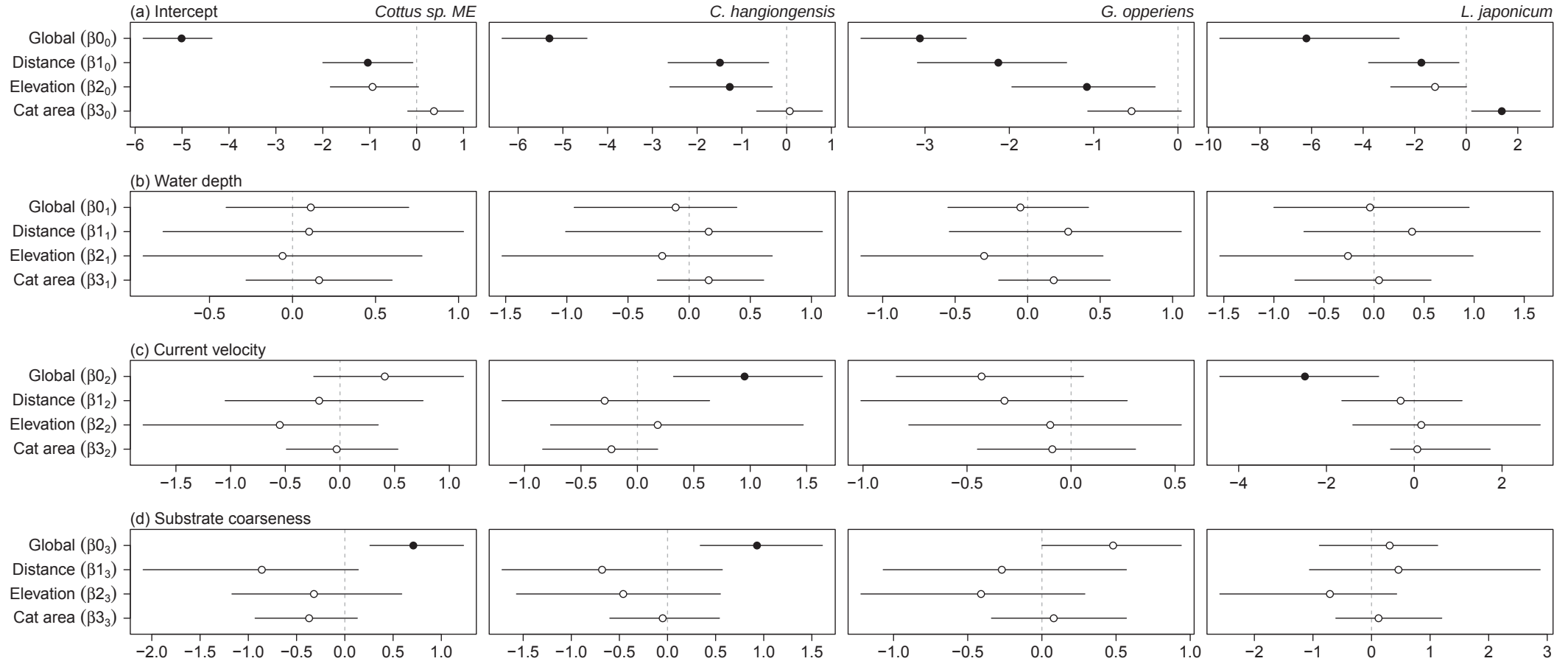


Fig.3 Terui and Miyazaki

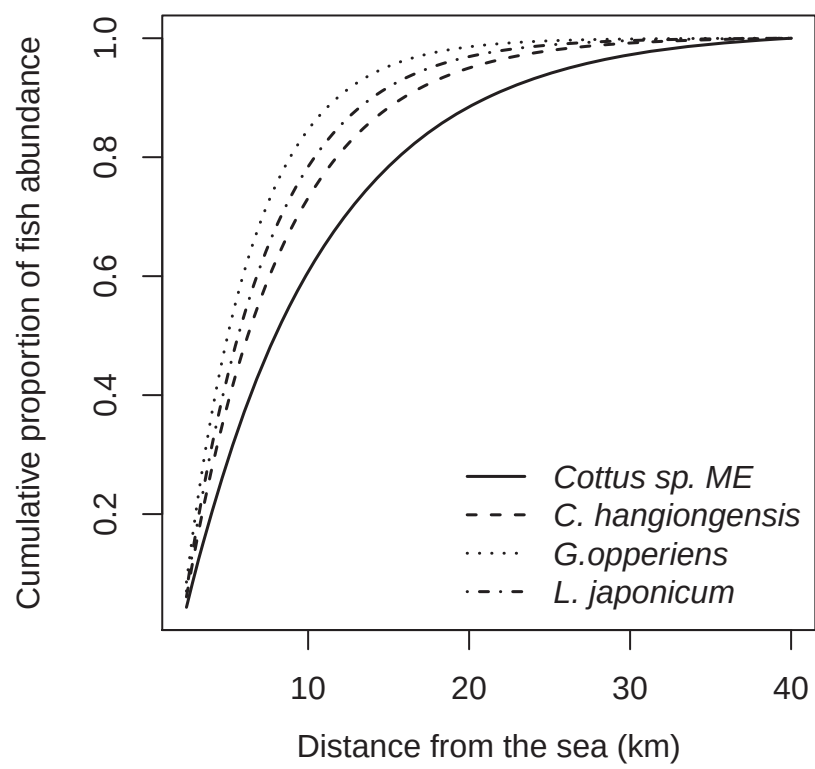


Fig.4 Terui and Miyazaki

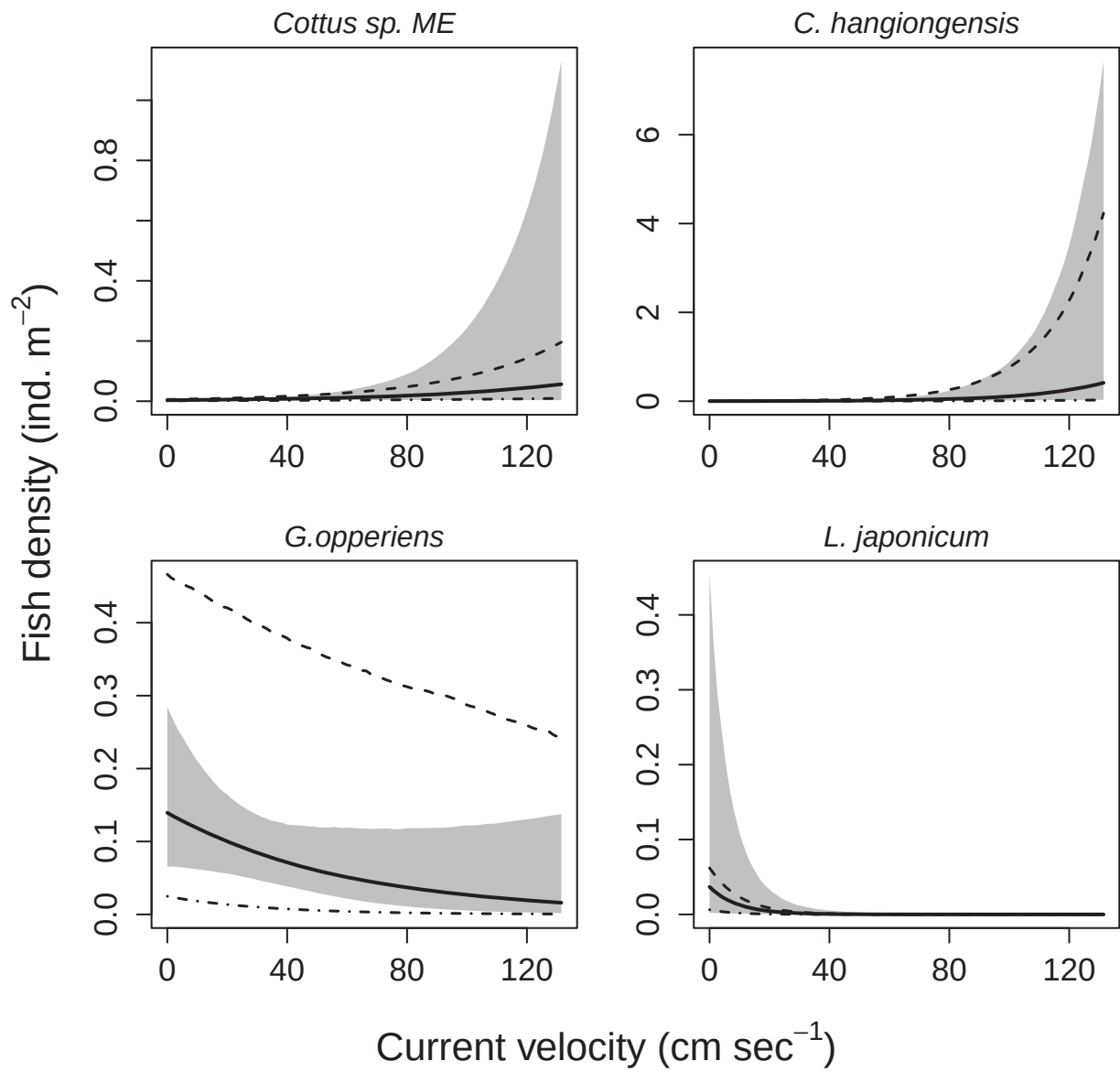


Fig.5 Terui and Miyazaki

