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Environmental Characteristics accounting for Odonate Assemblages in Rural Reservoir Ponds in Japan

Kenji HAMASAKI[1]*, Takehiko YAMANAKA[1], Koichi TANAKA[1], Yukinobu NAKATANI[2], Nobusuke IWASAKI[3] and David S. SPRAGUE[3]

[1] Biodiversity Division, National Institute for Agro-Environmental Sciences (NIAES) (Tsukuba, Ibaraki 305–8604, Japan)
[2] Natural Resources Inventory Center, NIAES (Tsukuba, Ibaraki 305–8604, Japan)
[3] Ecosystem Informatics Division, NIAES (Tsukuba, Ibaraki 305–8604, Japan)

Abstract

To clarify the effect of environmental factors on odonate assemblages in rural reservoir ponds, we surveyed the odonate adults (Zygoptera and Anisoptera) in 70 study ponds in Ibaraki Prefecture, Japan, during three sampling periods in 2005. Cluster analysis, indicator species analysis (INSPAN), and non-metric multidimensional scaling (NMDS) were used in combination to determine the relationship between odonate assemblages and environmental variables, i.e., biotic, physicochemical, and regional variables (the types of land use surrounding the ponds). A total of 41 odonate species were recorded in the study ponds, and 24 of them, excluding rare species, were used for each analysis. The study ponds were classified into six groups, and significant indicator species were selected from four of these groups. Examination of the correlation between each environmental variable and NMDS axes 1 and 2 revealed the profound effects of the presence of forest, paddy field, or open area around the ponds on the indicator species composition of each group. It was also revealed that the aquatic vegetation and forests around the ponds provide desirable conditions for the odonates and, in contrast, concrete revetment has a detrimental effect. These results suggest that the recent decrease of forests around ponds and the reconstruction with concrete revetment will have a negative effect on the odonate assemblages in ponds.

Discipline: Agricultural environment
Additional key words: odonata, agricultural landscape, alternative habitat, freshwater ecosystem, Non-metric multidimensional scaling

Introduction

In agricultural landscapes, farm ponds represent important alternative habitats for some freshwater organisms and play an important role in maintaining regional biodiversity[6, 39]. In Japan, irrigation ponds that supply water to rice paddy fields were constructed mainly from the 17th to 19th C., and there were ca. 300,000 ponds in the 1950s. However, the number of irrigation ponds had decreased to ca. 70% of the maximum number by the end of the 1990s[35]. Consequently, the abundance of many pond-inhabiting species has been reduced, and some species are listed in the red data books[12]. The scientific basis for pond conservation is not, however, well elaborated compared to that for other freshwater habitats. To conserve and manage freshwater biodiversity, it is important to clarify the relationships between pond environments and freshwater species.

Odonate species, dragonflies and damselflies, are good indicators of freshwater habitat conditions because they depend on both aquatic and terrestrial habitats to maintain viable populations[2, 30]. Previous field studies on factors affecting odonate species have identified the importance of aquatic and riparian vegetation[7, 31], predatory fish[21, 22, 25, 27], water quality[3, 4], landscape structure[16, 20, 29, 41], and spatial autocorrelation[15]. However, these studies have investigated either a single or several environmental factors. Only a few comprehensive analyses of these factors have been undertaken[5, 14, 32, 42].

The objectives of our study were to clarify the environmental characteristics that influence pond odonate assemblages. In general, species distribution data often encounter spatial autocorrelation[18]. Ignoring spatial autocorrelation

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*Corresponding author: e-mail kenjih@affrc.go.jp
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may cause misleading associations between species composition and environmental factors[17, 18]. We have already discussed using redundancy analysis (RDA) and variation partitioning to address this problem in Hamasaki et al.[13]. On the other hand, environmental factors affecting the species composition may be obscured in such analyses if the environmental factors themselves are spatially structured [19]. In addition, RDA combined with a stepwise parameter selection may mask the importance of the factors if there are strong multi-colinearities among the environmental factors[38].

In this paper, we re-analyzed our previous field research data using a different rationale from our previous study[13]. The odonate species composition was summarized objectively by applying three indirect gradient analyses, i.e., cluster analysis, indicator species analysis (INSPAN), and non-metric multidimensional scaling (NMDS). In this analysis, spatial autocorrelation was assumed to be cancelled out by sampling as many as 70 ponds. We specifically tried to interpret the results of the indirect gradient analyses applying *ad hoc* univariate regression analyses of every environmental factor and to discuss the impact of pond environmental alterations on odonate assemblages. We will also briefly discuss the difference between the results of our previous paper and those obtained here.

Materials and methods

1. Study sites

The study area is located in the northeastern Kanto plain, Ibaraki Prefecture, Japan and measures 10 km × 10 km (36°08′–36°13′N, 140°08′–140°15′E). The typical land use in this area is a mixture of forest, fruit orchards, crop fields, paddy fields, and residential areas. We selected 70 ponds (20 ponds exist within golf courses) as the study sites within this region using national basic maps with a scale of 1: 2500.

2. Field research data

In this paper, our previous field research data, such as odonate adult composition and environmental variables in each study pond (Tables 1 and 2), were used for the indirect gradient analyses. Only brief explanations of the methods are given below (see Hamasaki et al. [13] for details).

(1) Surveying adult odonates

We surveyed the odonate adults in the study ponds on 18-20 May, 22-24 June and 20-22 July, 2005. We observed all odonate species flying over or perching inside and outside (within 5 m of the edge) of the ponds during a one-way walk along the pond edge. A maximum of 30 min was spent searching in each pond. The observations were conducted between 08:00 and 17:30 h on sunny or slightly clouded days by two research groups. Each of them was constructed by three or four researchers. We counted the number of each species individually from one to ten individuals and recorded the number greater than 10 as ">10". The odonate species were identified in the field, but if there was any difficulty in identifying them we captured them using insect nets. The specimens were identified using available keys for adult odonates[33] and released at the capturing point. The numbers of individuals of each species in the three surveys were summed for each study pond and classified into four abundance ranks: 0 (0), 1 (1-3), 2 (4-10), 3 (>10). The rank was designed to correspond with the log-transformation ($\frac{1}{2}\log_{10}(x+0.5)$; x = abundance), as such data reduction enhanced the statistical power of our method for the strong heteroscedastic and no upper-bounded data[40].

(2) Quantifying environmental factors

Environmental variables such as the biotic, chemical, and physical factors in each pond were recorded once in August 2005. The environmental variables are all listed in Table 1[13].

We surveyed the abundance of fish species using D-flame net and/or casting net in the littoral area during an about 20-min period. The predominant fishes were *Micropterus salmoides*, *Lepomis macrochirus*, and *Cyprinus carpio*. The abundance of each fish was classified in three categories: 0 (0), 1 (1-10), and 2 (>10). We also surveyed the abundance of benthos in the littoral area. Four samples were collected from each pond. Chironomid larvae and Oligochaeta (naidid worms) were sorted, and their wet weights were measured. The average of the four samples was calculated for each pond. We collected zooplankton samples from a single site in each pond by dipping a plastic bucket into the water. Sample volumes ranged from one to ten liters. Water was sieved through a 200-µm-mesh net. Zooplankton were sorted from the net and counted. The data were expressed as the number of individuals per liter. We recorded the coverage area of aquatic and riparian vegetation inside the pond. Vegetation was grouped into three types: tall emergent plants, short emergent plants, and floating plants. The coverage of each vegetation type was measured in the field and its area calculated. The areas of different combinations of two or three vegetation types were also calculated. We measured water pH, electrical conductivity (EC), and dissolved oxygen concentration (DO) in the surface water once in each pond. We also measured the depth of debris (dead branches and leaves) at three points in the littoral area. The average of the three values was calculated for each pond.

To extract the land use around the ponds, we created a digital land use map, which is available for geographic information systems (GIS), using Erdas Imagine 8.7 (Leica Geosystems, Georgia, USA) based on national basic maps (1:2500). Land use was grouped into five categories: forest area, open area, water area, paddy field area, and residential area. The area and perimeter of each pond were measured using this digital map. The revetment length was measured in the field, and the revetment as a percentage of the perimeter was calculated. We examined all of these land use categories at buffer levels around the pond of 10, 25, 50, 100, 200, and 300 m from the outer edge of the pond. The percentage of each land use category was calculated at every buffer level using GIS software ArcView 9.1 (ESRI, Redlands, CA, USA).

3. Statistical analysis

To classify the study ponds into similar groups of odonate species composition, we employed cluster analysis using the flexible beta ($\beta = -0.25$) linkage method with the Bray-Curtis distance measure. The criteria for pruning the dendrogram were objectively determined using indicator species analysis (INSPAN)[10] by selecting the number of clusters that showed the lowest average *P*-value and highest number of indicator species[23]. The statistical significance of the indicator values in each cluster was tested with Monte Carlo randomization tests (999 iterations). Using this procedure, we were able to set up optimal groups of study ponds, and some groups had several indicator species. All of these analyses were performed using the software PC-ORD version 4.0[24].

To extract the gradients in odonate species composition patterns among the ponds, which are related to some environmental variables, the study ponds were ordinated by non-metric multidimensional scaling (NMDS) with the Bray-Curtis distance measure using the PC-ORD version 4.0[24]. NMDS is a computer-intensive method that searches for the most stressless configuration in the *k*-di-

Table 1. Environmental variables measured for each study pond and the range of obtained data (from Hamasaki et al.[13])

Category	Description	Range
Biotic variables	Fish (largemouth bass, bluegill and common carp) [a] (three categories: 0 (0), 1 (1-10), 2 (>10))	
	Benthos (chironomid larvae and naidid worms: wet weight) (g)	0-5.8
	Zooplankton (>200µm) (number of individuals L^{-1})	0-221.0
	Vegetation area (three types: tall emergent plant, short emergent plant and floating plant) (m^2) [b]	0-3729
Chemical variables	pH	5.7-9.8
	EC (electrical conductivity; mS m^{-1})	5.4-56.3
	DO (dissolved oxygen concentration; mg L^{-1})	2.5-13.8
Physical variables	Debris (depth of dead branches and leaves) (cm)	0-11.3
	Pond area (m^2)	85.7-24515.8
	% revetment (revetment length per perimeter of pond)	0-100
Regional variables	% forest area (broadleaf, conifer and bamboo)	0-100
(Land use [c])	% open area (cropland, wasteland and orchard)	0-100
	% water area (wetland, pond, river and ditch)	0-19.9
	% paddy field area (paddy field)	0-88.6
	% residential area (house, building and road)	0-99.9

[a] : Large mouth bass: *Micropterus salmoides*, bluegill: *Lepomis macrochirus*, common carp: *Cyprinus carpio*.

[b] : Tall emergent plants (cattails: *Typha latifolia* and *Typha domingensis*, sweet flag: *Acorus calamus*, yellow iris: *Iris pseudacorus*, reed grass: *Phragmites australis*, water-oats: *Zizania latifolia*), short emergent plants (sedges: *Cyperus microiria*, *Schoenoplectus mucronatus*, *Bolboschoenus fluviatilis*, *Scirpus wichurae* and *Carex* sp., grass weeds: *Leersia japonica* and *Isachne globosa*), floating plants (lotus: *Nelumbo nucifera*, water lilies: *Nymphoides peltata* and *Nymphaea* sp.). Each vegetation type and all combinations among them were used for each multivariate analysis.

[c] : The buffers were cut at distances of 10, 25, 50, 100, 200, and 300 m from the outer edges of the ponds, and % area of each land use category in each buffer was calculated.

Table 2. Odonate species found in the study ponds and the number of ponds where each species was found (from Hamasaki et al.[13])

Suborder	Family	Species [a]	Abbreviations [b]	No. of ponds
Zygoptera	Coenagrionidae	*Cercion calamorum calamorum* (Ris)	CCA	21
		Cercion sexlineatum (Selys) *		1
		Cercion sieboldii (Selys)	CSI	32
		Ceriagrion melanurum Selys*		2
		Ischnura asiatica Brauer	IAS	48
		Ischnura senegalensis (Rambur)	ISE	22
	Platycnemididae	*Copera annulata* (Selys)	CAN	15
	Lestidae	*Indolestes peregrinus* (Ris)	IPE	32
		Lestes temporalis Selys	LTE	9
		Lestes sponsa (Hansemann) *		1
	Calopterygidae	*Calopteryx atrata* Selys*		7
		Mnais pruinosa costalis Selys*		7
Anisoptera	Gomphidae	*Asiagomphus melaenops* (Selys) *		2
		Gomphus postocularis Selys *		3
		Trigomphus melampus (Selys) *		3
		Sinictinogomphus clavatus (Fabricius)	SCL	15
	Cordulegastridae	*Anotogaster sieboldii* (Selys)	ASI	31
	Aeshnidae	*Aeschnophlebia longistigma* (Selys) *		1
		Aeshna nigroflava Martin*		1
		Anax nigrofasciatus nigrofasciatus Oguma	ANI	15
		Anax parthenope julius Brauer	APA	29
		Oligoaeschna pryeri (Martin) *		2
	Corduliidae	*Epitheca marginata* (Selys) *		3
		Macromia amphigena amphigena Selys*		5
		Epophthalmia elegans elegans (Brauer)	EEL	20
		Somatochlora viridiaenea (Uhler) *		1
	Libellulidae	*Crocothemis servilia mariannae* Kiauta	CSE	23
		Deielia phaon (Selys)	DPH	13
		Libellula quadrimaculata asahinai Schmidt *		2
		Lyriothemis pachygastra (Selys)	LPA	10
		Orthetrum albistylum speciosum (Uhler)	OAL	67
		Orthetrum japonicum japonicum (Uhler)	OJA	13
		Orthetrum triangulare melania (Selys)	OTR	27
		Pantala flavescens (Fabricius)	PFL	16
		Pseudothemis zonata (Burmeister)	PZO	66
		Rhyothemis fuliginosa Selys *		3
		Sympetrum darwinianum (Selys)	SDA	36
		Sympetrum eroticum eroticum (Selys) *		1
		Sympetrum frequens (Selys)	SFR	26
		Sympetrum infuscatum (Selys)	SIN	57
		Sympetrum kunckeli (Selys)	SKU	12

[a] : Asterisks indicate the rare species (found in 10% or less of the study ponds).

[b] : Rare species were eliminated from statistical analyses.

mensions (axes) by iteratively permuting the *n*-entities (sample units). Since the scaling is based on the rank of the entity in the ordination space, it can be applied to almost any type of data, e.g., species abundance, presence/absence, and rank categories. This method is one of the most defensible techniques[26] and also much more robust for determining non-linear species response to environmental gradient than the other ordination techniques such as detrended correspondence analysis (DCA)[11, 23]. The ordination results are presented as pond scores and species scores. Species scores were calculated by weighted averaging of the pond scores. The relationship between the ordination scores and single environmental variables was tested by *ad hoc* regression analyses (Spearman's rank correlation coefficient, r_s). Regression analyses were conducted using the software JMP 5.01 (SAS Institute, Cary, NC, USA). The ordination scores were also regressed on the species richness of the ponds (i.e., the number of species observed) to interpret the ponds' condition in the ordination space.

Results

We recorded 41 odonate species (Zygoptera: 12, Anisoptera: 29) in the 70 study ponds (Table 2)[13]. The largest number of species found in a single pond was 22, and the smallest number was two. The most widespread species were *Orthetrum albistylum speciosum*, *Pseudothemis zonata*, *Sympetrum infuscatum*, and *Ischnura asiatica*, which were present in 67, 66, 57, and 48 ponds, respectively. Seventeen species were present in 10% or less of the ponds. These rare species were eliminated from the multivariate analysis because of the possibility they might have an unduly large influence on the ordination and regression analysis[23, 34].

1. Classification

The cluster dendrogram based on the odonate species rank data is shown in Fig. 1. The study ponds were classified into six groups based on the results of INSPAN. The indicator values of each species for each group are shown in Table 3. There are three statistically significant indicator species in group 1, eight species in group 2, one species in group 3, and four species in group 4. In groups 5 and 6, however, no significant indicator species were found.

2. Ordination

The NMDS ordination diagram of the study ponds is shown in Fig. 2-A. A two-dimensional solution was se-

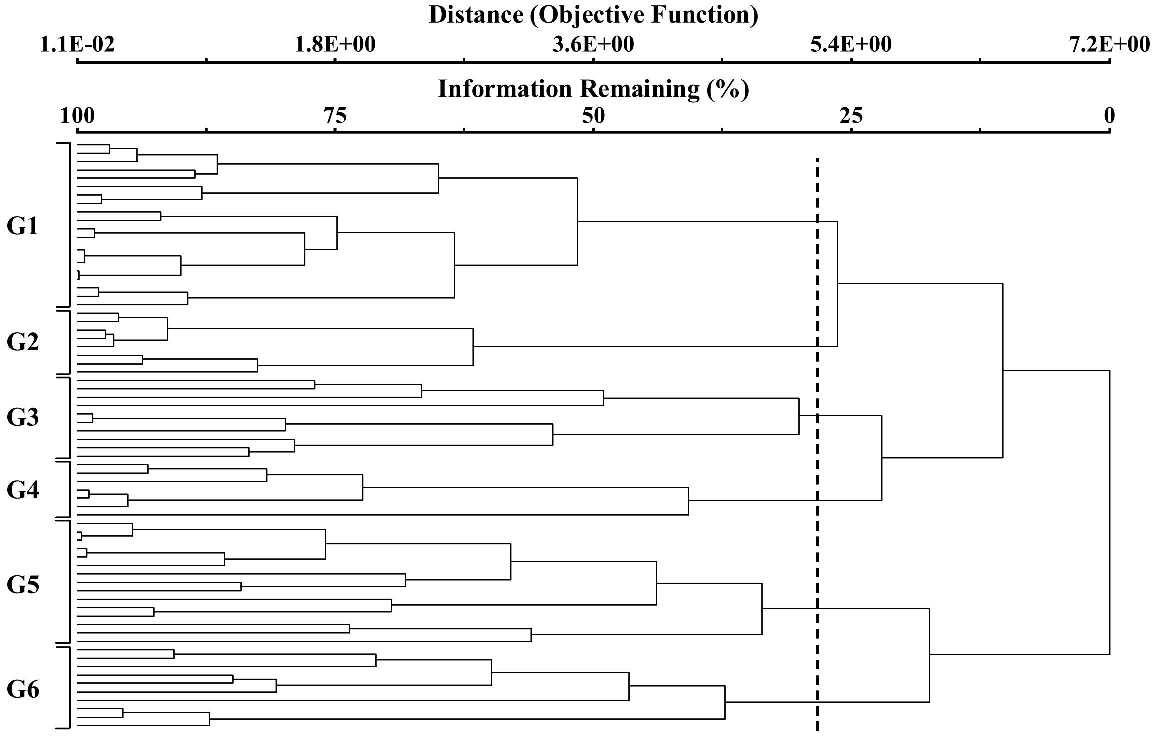

Fig. 1. Dendrogram of 70 ponds based on the dragonfly species rank data using the flexible beta (β = 0.25) linkage method with the Bray-Curtis distance measure

The dashed line indicates the cutoff levels for each cluster group decided by INSPAN.

lected as the most stressless configuration in this analysis. Although the score of the stress is rather high (0.236), the results appear to be ecologically interpretable. In the NMDS diagram of the study ponds, ponds categorized in groups 1, 2, and 4 are located on the left side of the ordination space, while those in groups 5 and 6 are located on the right side. Groups 2 and 6 on the one hand and groups 3 and 4 on the other are distributed separately from each other along axis 2. Groups 1 and 5 are located at the middle of axis 2. These results are concordant with the classification by cluster analysis; groups 1, 2, and 4 as generated by cluster analysis are also segregated in the ordination space, although group 3 overlaps broadly with the other groups. Groups 5 and 6 are located on the right side apart from the other groups, although they overlap each other.

The NMDS ordination diagram of the odonate species is shown in Fig. 2-B. The statistically significant indicator species in group 2 are located on the upper left side of the ordination space, while those in groups 3 and 4 are located on the lower left side. In contrast, the indicators of group 1 excluding *S. infuscatum* are located in the middle of the ordination space. These results are consistent with the distribution of each pond group (Fig. 2-A).

Spearman's rank correlation coefficients between each environmental variable and NMDS axes 1 and 2 are shown in Table 4. The variables that were significantly correlated with axis 1 and/or axis 2 (P<0.05) are listed in the table. Axis 1 is correlated positively with % revetment length, pH, DO, and % open area (50-200 m), and negatively with debris, benthos, % forest area (10-50 m), % paddy field area (100-200 m), and each combination of the vegetation coverage excluding floating plants. Axis 1 is also correlated negatively with the odonate species richness. Axis 2 is correlated positively with pond area,

Table 3. Indicator values by indicator species analysis

Species	No. of ponds	Pond groups					
		1	2	3	4	5	6
Sympetrum infuscatum	57	**25**	13	23	24	6	1
Orthetrum albistylum speciosum	67	**22**	21	5	18	17	15
Pseudothemis zonata	66	**22**	20	12	13	15	13
Lestes temporalis	9	13	2	0	0	5	0
Cercion calamorum calamorum	21	3	**68**	0	1	1	3
Deielia phaon	13	2	**61**	1	1	0	1
Sinictinogomphus clavatus	15	6	**49**	1	0	1	0
Ischnura senegalensis	22	1	**47**	5	2	2	1
Crocothemis servilia mariannae	23	14	**43**	0	0	1	3
Cercion sieboldii	32	10	**37**	0	17	0	10
Ischnura asiatica	48	24	**35**	6	0	4	14
Epophthalmia elegans elegans	20	10	**28**	0	1	0	8
Sympetrum frequens	26	5	25	9	3	5	0
Anax parthenope julius	29	21	22	0	12	2	1
Orthetrum japonicum japonicum	13	3	14	0	12	1	1
Sympetrum kunckeli	12	9	14	4	2	0	0
Lyriothemis pachygastra	10	4	5	**23**	0	0	0
Copera annulata	15	4	1	2	**58**	0	0
Anax nigrofasciatus nigrofasciatus	15	3	1	3	**47**	1	0
Orthetrum triangulare melania	27	6	19	1	**40**	1	0
Sympetrum darwinianum	36	11	23	14	**26**	1	0
Anotogaster sieboldii	31	10	14	13	18	2	0
Indolestes peregrinus	32	8	6	4	14	23	0
Pantala flavescens	16	1	10	1	0	12	12

Bold letters indicate significant indicator values (P<0.05)

% revetment length, pH, DO, and % open area (10-300 m), and negatively with debris, benthos, and % forest area (10-100 m).

Discussion

1. Odonate species composition

According to the results of the NMDS ordination, the environmental characteristics of groups 1 to 4 can be summarized as follows. The ponds of group 2 are relatively large in area and surrounded by both open and forested areas. The ponds of groups 3 and 4 are relatively small in area and surrounded by forests, and the pond bottoms are thus covered with debris. Group 1 has environmental characteristics that are intermediate between those of groups 2 and 4. The indicator species for group 2 (i.e., *C. calamorum calamorum*, *D. phaon*, *S. clavatus*, and *E. elegans elegans*) are known to appear in large and open ponds, and those for group 4 (i.e., *C. annulata*, *A. nigrofasciatus nigrofasciatus*, and *O. triangulare melania*) are reported to inhabit shady and small ponds[33]. Their habitat preference is consistent with the environmental characteristics of groups 2 and 4. However, the environmental characteristics of group 3 are different from the habitat preference of its indicator species, *L. pachygastra*, which inhabits wetlands and non-cropping paddy fields[33]. We postulated that our study area contained only a few preferable habitats of *L. pachygastra* since we only surveyed ponds, causing this spurious correspondence. The indicator species for group 1 were observed in many of the study ponds and may not be associated with particular environmental variables. From these results, we conclude that the indicator species of these groups can be categorized as open-specific (group 2), forest-specific (group 4), and unspecific (eurytopic) species (group 1). This classification agreed with the ecological characteristics of each indicator species and previous research[14, 42].

The NMDS ordination shows that the surroundings of the ponds in groups 5 and 6 were characterized by small vegetation coverage, open areas, and long revetment lengths. These groups are characterized as having lower species richness than groups 1, 2, and 4 because the species richness is negatively correlated with axis 1 (Table 4). The aquatic and riparian vegetation plays an important role in various activities of the odonates by providing oviposition and perching sites for the adults and a refuge from predators for the larvae[9]. The forests around

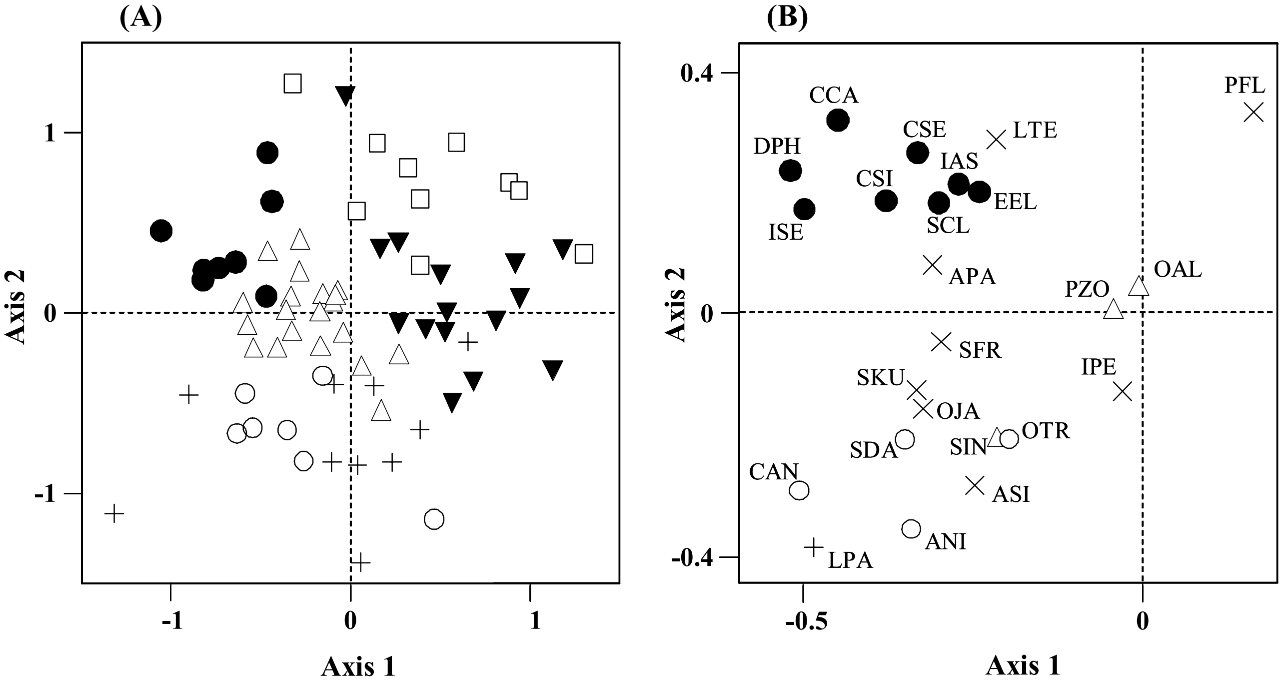

Fig. 2. NMDS ordination diagrams of axes 1 and 2 for ponds (A) and odonate species (obtained by weighted averaging of site scores) (B)

G1 to **G6** indicate groups 1 to 6 of the ponds, respectively, classified by cluster analysis and INSPAN. Symbols of the species indicate the significant indicators for each pond group and **ns** means non-significant indicator species (see Table 3). The abbreviations of the species names are listed in Table 2.

△ : **G1**, ● : **G2**, + : **G3**, ○ : **G4**, ▼ : **G5**, □ : **G6**, × : **ns.**

ponds are also important sites for odonate adults, as they provide feeding and roosting sites during the immature stage[36, 37]. These results suggest that aquatic vegetation and forests around ponds provide profitable conditions for the odonates and, in contrast, concrete revetment has a detrimental effect. Concrete revetment of the pond edge destroys the physical environments of the riparian and shore areas, resulting in a loss of the physical complexity of the habitat and of the richness of the aquatic plants and invertebrates (potential prey). These physical and biological alterations may have negative effects on the odonate assemblages and richness.

The paddy field is one of the most important habitats for those odonates that grow primarily in paddy fields during their larval stage[33]. We observed immature adults of *S. darwinianum*, *S. infuscatum*, and *S. frequens* in and around the study ponds. Upon maturation, these species disperse from their emergence sites and immigrate into ponds and the forests surrounding the ponds.

Although pH and DO have significant association with odonate species composition (Table 4), we cannot explain their effects on the odonate assemblage structure because we surveyed only odonate adults, not larvae. The adults may disperse from their emergence sites and immigrate into other ponds, which may obscure the effects of some factors such as fish predation, prey density, and water quality on larval survival. In fact, although we found no significant correlation between the odonate assemblage and the predatory fishes, some researchers have shown the effect of fish predation on odonate species abundance and composition when they surveyed odonates in larval stages or their exuviae[21, 22, 25]. Future research must include surveys of the larval stages.

Table 4. Spearman's rank correlation coefficients between each environmental variable and NMDS axes 1 and 2

Variables	Axis 1	Axis 2
Species richness (number of species)	–0.7975***	0.0499
Pond area	–0.1689	0.2831 *
% revetment length	0.4550 ***	0.3428 **
pH	0.3345 **	0.2943 *
DO	0.3418 **	0.5465 ***
Debris	–0.5112 ***	–0.4116 ***
Benthos	–0.2987 *	–0.2880 *
% forest area (10 m)	–0.3338 **	–0.4248 ***
(25 m)	–0.3413 **	–0.3910 ***
(50 m)	–0.2887 *	–0.3602 **
(100 m)	–0.2075	–0.2567 *
% open area (10 m)	0.1750	0.4693 ***
(25 m)	0.2108	0.5013 ***
(50 m)	0.2414 *	0.4817 ***
(100 m)	0.2717 *	0.450 ***
(200 m)	0.2378 *	0.3407 **
(300 m)	0.1470	0.2565 *
% paddy field area (100 m)	–0.2685 *	–0.2194
(200 m)	–0.2463 *	–0.1791
Vegetation coverage (total)	–0.5663 ***	–0.1685
(tall and short emergent plants)	–0.5315 ***	–0.2032
(short emergent plants and floating plants)	–0.3634 **	–0.0643
(short emergent plants)	–0.3341 **	–0.1317
(tall emergent plants and floating plants)	–0.5312 ***	–0.1710
(tall emergent plants)	–0.5049 ***	–0.2218

*** : $P<0.001$, ** : $P<0.01$, * : $P<0.05$.
The variables that are significantly correlated with axis 1 and/or axis 2 ($P<0.05$) are shown.

2. Comparison to the results of our previous study of RDA

The previous results of RDA for land use and within-habitat environment are basically the same as our current results, although we did not consider spatial autocorrelation in our current study. Major factors such as debris, DO, and forest area were also predicted to have large effects on the odonate species composition. In addition, the pond classification by cluster analysis in our current study tended to be concordant with the results of RDA. We thus concluded that there was only a slight conglomerate effect of spatial structured environmental factors considering there were only slight overlapping effects between the spatial autocorrelation and the other environment factors[13].

However, in our previous analyses, revetment length and vegetation covers were not predicted to have large effects. Though we could not rule out any other artifacts of the methodologies, such as the difference between the indirect and direct ordination technique[23] or, so to speak, the horse-shoe effects in the RDA[23] of our previous analyses, we suspect that the multi-coliniarities among the factors affected the results of our previous study during the parameter selection procedure. In fact, revetment length and vegetation covers had strong negative (-0.44) and positive (0.48) correlations to the debris, respectively. Such multi-coliniarities may mask the effect of the revetment length or vegetation covers when the debris that had larger correspondence to the species composition had been selected earlier than the others in the parameter selection procedure. Though the direct causability of the factors will remain unknown until further experiments are conducted specifically for this purpose, we postulate that they synergically affect the species composition. It is natural to assume that revetment reduces the vegetation covers and less vegetation creates less debris accumulation.

3. Conservation considerations

In this study, the 70 study ponds are classified into six groups that are characterized as having different species compositions. Our study revealed that the indicator species in different groups exhibit different habitat preferences. These results indicate that the regional odonate species richness should be conserved by maintaining the environments in the different types of ponds, particularly the ponds in groups 2 and 4. In Japan, recent intensive urbanization and agricultural development have led to an increase in the reconstruction of ponds with concrete revetments, a decrease in aquatic plant richness, and a reduction of the forest area around ponds (Sprague et al. unpublished data). These environmental alterations have an adverse effect on odonate assemblages, especially forest-specific species. To conserve the regional populations of odonate species, it is especially important to conserve ponds that contain aquatic plants and those located in forests.

The number of ponds has decreased due to their being artificially or naturally filled[35]. The decrease of ponds has also negatively influenced the regional odonate populations and assemblages. Habitat loss often results in the fragmentation of the remaining habitat. The colonization of odonates in isolated habitat patches is limited by the dispersal capability and behavior of each species[1, 8, 15]. It is also limited by the differences in landscape structure among the habitats[16, 28, 41]. The effect of the differences in connectivity and landscape structure among ponds on regional odonate populations is an important area of future research.

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