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NOTE

Spatio-temporal distribution of *Diaphanosoma brachyurum* (Cladocera: Sididae) in freshwater reservoir ecosystems: importance of maximum water depth and macrophyte beds for avoidance of fish predation

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ABSTRACT

In empirical studies, Cladocera is commonly utilized as a primary food source for predators such as fish, thus, predator avoidance are important strategies to sustain their population in freshwater ecosystems. In this study, we tested the hypothesis that water depth is an important factor in determining the spatial distribution of Diaphanosoma brachyurum *Liévin, 1848 in response to fish predation. Quarterly monitoring was implemented at three water layers (*i.e.*, water surface and middle and bottom layers) in 21 reservoirs located in the southeastern part of South Korea.* D. brachyurum *individuals were frequently observed at the study sites and exhibited different spatial patterns of distribution in accordance with the maximum depth of the reservoirs. In the reservoirs with a maximum depth of more than 6 m, high densities of* D. brachyurum *were observed in the bottom layers; however, in the shallower reservoirs (maximum depth <6 m),* D. brachyurum *were concentrated in the surface layer. Moreover, during additional surveys, we observed a trend in which* D. brachyurum *densities increased as the maximum depth or macrophyte biomass increased. Gut contents analysis revealed that predatory fishes in each reservoir frequently consumed* D. brachyurum*; however, the consumption rate abruptly decreased in reservoirs where the maximum depth was more than 11 m or in the shallow reservoirs supporting a macrophyte bed. Interestingly, the reservoirs more than 11-m depth supported high densities of* D. brachyurum *in the bottom layer and in the surface macrophyte bed. Based on these results, reservoirs with a maximum depth of more than 11 m or those with a macrophyte bed may provide a refuge for* D. brachyurum *to avoid fish predation. Compared with other cladoceran species,* D. brachyurum *readily exploits various types of refugia (in this study, the deep layer or surface macrophyte bed), which may help explain why this species is abundant in various types of reservoirs.*

Key words: Diaphanosoma brachyurum*, water depth, macrophyte, fish predation, freshwater reservoir, spatio-temporal distribution.*

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INTRODUCTION

In empirical studies, the spatial distribution of freshwater Cladocera is mainly determined by interactions with their predators. Cladoceran species are strategically distributed to minimize predation pressure, and their spatial pattern of distribution largely depends on ecosystem characteristics such as depth and habitat heterogeneity. In deep lakes, *Daphnia* avoids visual predators by migrating vertically into the colder, darker, hypolimnetic layer (diel vertical migration, DVM; Lampert, 1993; Von Elert and Loose, 1996). However, light may penetrate to the bottom layers in shallow lakes, leading to the unavailability of a hypolimnetic refuge. Thus, in shallow lakes where DVM is probably less advantageous, Cladocera may migrate into a vegetated bed. This behavioural pattern is termed diel horizontal migration (DHM; Lauridsen and Buenk, 1996; Burks *et al.*, 2002), and is assumed to be an alternative predator avoidance strategy to DVM. Predator avoidance is commonly accepted as the primary reason for DVM, and is also a favoured hypothesis for why Cladocera undergo DHM (Lauridsen *et al.*, 1996; Scheffer, 1998). However, this predator avoidance mechanism is primarily associated with daphniids, which are favoured prey items of fish. In some lentic ecosystems, cladoceran species other than daphniids often dominate the cladoceran assemblage. In such ecosystems, they are the primary prey of predatory fish, yet are insufficiently studied.

Diaphanosoma brachyurum (Cladocera: Sididae) is a common limnetic species in temperate and tropical water bodies (Sarma *et al.*, 2005; Mohammed and Agara, 2006). Compared with other cladoceran species, *D. brachyurum* readily adapts to relatively high temperatures, as a stenothermic thermophile (approximately 24.5°C; Verbitskii *et al.*, 2009), and is prevalent in temperate zones during the summer, and is a dominant species in tropical regions (Herzig, 1984). In most freshwater ecosystems in South Korea, *D. brachyurum* is the dominant zooplankton during the summer season (Choi *et al.*, 2012, 2013). Coincidentally, their predators (mainly fish) also exhibit increased foraging on zooplankton such as *D. brachyurum* during the summer season (Bohl, 1979). This period synchronization between *D. brachyurum* and predatory fish thus exposes cladoceran species to high predation pressure during summer. Nevertheless, as *D. brachyurum* is frequently observed at high densities during the summer, it is reasonable to hypothesize that they use an efficient strategy of population distribution to avoid predators. Unfortunately, although some studies reported seasonal variation in *D. brachyurum*, their spatial distribution in relation to predation avoidance has been insufficiently studied.

In this study, we investigated the relationship between *D. brachyurum* and important refuge characteristics in reservoir ecosystems, namely, maximum water depth and macrophyte distribution. We hypothesized that *D. brachyurum* may prefer deeper water layers or areas in shallow wetlands where macrophytes are available as refugia. To test this hypothesis, we investigated the following: i) the influence of maximum water depth and habitat structure (*i.e.*, macrophytes) on the spatial distribution of *D. brachyurum;* and ii) the impact of fish predation on *D. brachyurum* at different depths and according to habitat structure.

METHODS

Study sites

South Korea is located in East Asia, and has a temperate climate with four distinct seasons. Seasonal transitions lead to the dynamic succession of biological communities in the freshwater ecosystems. Our study sites were located in the southeastern part of South Korea, near the middle and lower reaches of the Nakdong River (Fig. 1). The dominant land cover surrounding the reservoir sites is agricultural, and non-point source inputs continuously influence the study sites (Korean Ministry of Environment, 2006).

The main purpose of this study was to understand the influence of maximum water depth and macrophyte presence on the spatial distribution of *D. brachyurum* in reser-

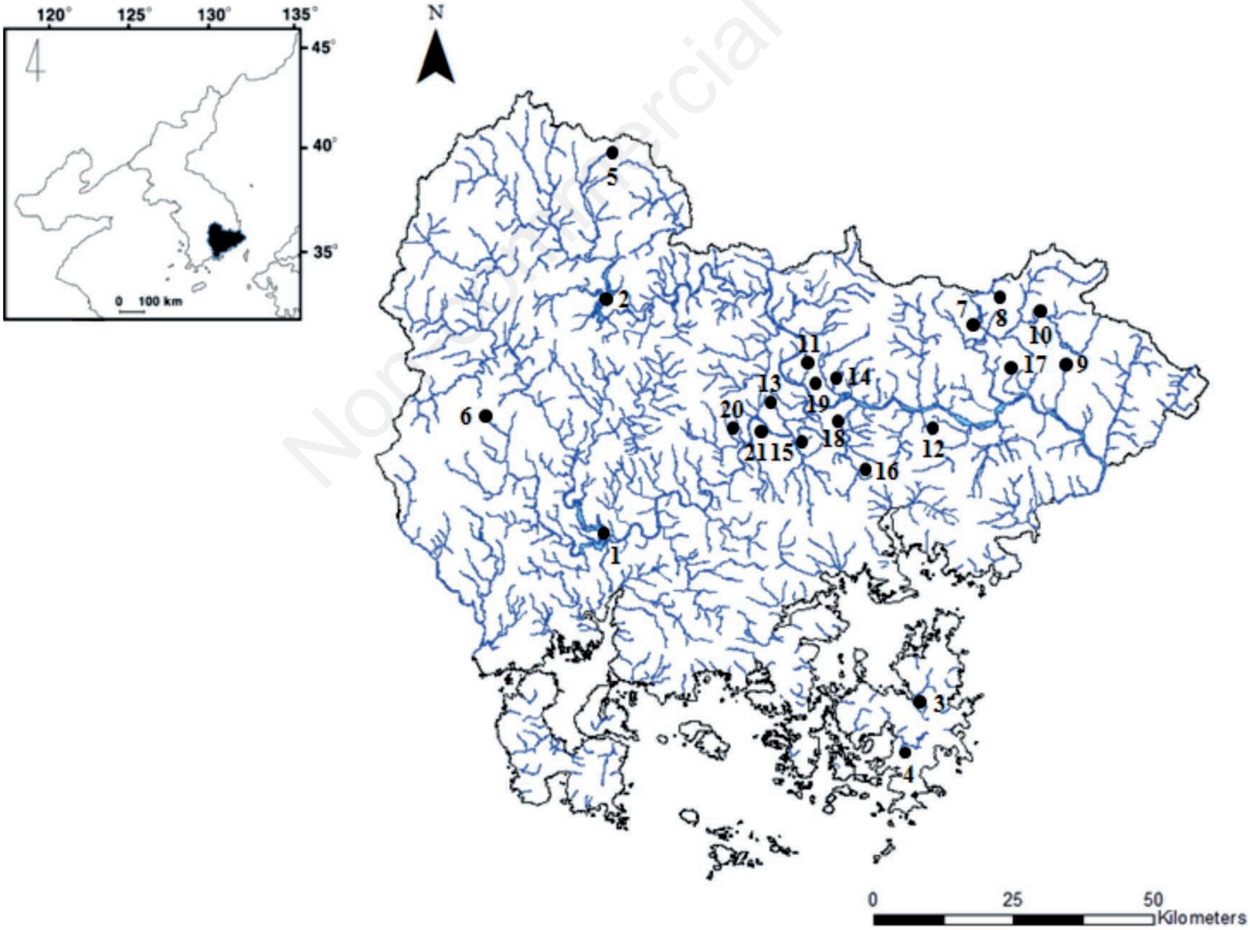

Fig. 1. Map of the study area in south-eastern South Korea. The study sites are indicated as solid circles (●). The small map in the upper left corner indicates the Korean Peninsula.

voirs where fish predation was present. We collected a database of lentic ecosystems in the river basin (Gyeongsangnam-do Province, 2012), which catalogued information regarding zooplankton and fish distribution in the reservoirs (for a total of 164 reservoirs). Using this database, we used two selection criteria to identify appropriate reservoirs for the study: i) the frequent observation of *D. brachyurum*; and ii) relatively similar physico-chemical characteristics (water temperature, dissolved oxygen, and chlorophyll-*a* concentration) and fish species. Using these criteria, we selected 21 reservoirs for study. These reservoirs have diverse maximum water depths (ranging from 2.2 to 29.6 m), and some reservoirs with maximum depth (D_{max}) <6 m were occupied by diverse macrophyte species. Through our literature survey, we identified a total of eight macrophyte species (*Phragmites australis* Trin. (Cav.)*, Paspalum distichum* L.*, Zizania latifolia* Griseb.*, Spirodela polyrhiza* L.*, Salvinia natans* L.*, Trapa japonica* Flerov.*, Ceratophyllum demersum* L.*,* and *Hydrilla verticillata* (LF) Royle) in the shallow reservoirs. Interestingly, the reservoirs were primarily occupied by surface-dwelling macrophytes (free-floating or floating-leaved macrophytes, including *Spirodela polyrhiza, Salvinia natans,* and *Trapa japonica*) compared with other macrophyte types (emergent or submerged macrophyte).

Monitoring strategy and data analysis

We investigated environmental factors and zooplankton abundance during each season (winter, February; spring, May; summer, August; autumn, October 2012) at 21 reservoirs. In each reservoir, sampling locations were established in the centre of the reservoir, where the maximum water depth was recorded. To investigate the spatial distribution of *D. brachyurum*, we collected three water samples at each of the three layers (surface, middle, and bottom layers, for a total of nine samples) using a 5 L Van Dorn water sampler. Diurnal sampling was conducted during the daytime and at night (day, 12:00 h; night, 00:00 h). The depth of middle layer was determined from the maximum depth, but sampling of this layer was not implemented in reservoirs with D_{max}<5 m.

Environmental variables (water depth, water temperature, % saturation of dissolved oxygen, turbidity, and chlorophyll-*a*) and zooplankton community composition, including *D. brachyurum,* were determined from the collected water samples. The EK-500 echo sounder was used to measure maximum water depth. A YSI Model 58 oxygen meter (YSI Inc., Yellow Springs, OH, USA) was used to measure water temperature and % saturation of dissolved oxygen. Turbidity levels and chlorophyll-*a* concentrations in the water samples were measured in the laboratory. Turbidity was measured using a turbidimeter (HF Scientific Inc.; Model 100B). For the determination of chlorophyll-*a* concentrations, water samples were filtered through a Mixed Cellulose Ester (MCE) membrane filter (Advantech, Taipei, Taiwan; Model No. A045A047A; pore size 0.45 μm), and the filtrates analysed as described by Wetzel and Likens (2000). For zooplankton enumeration, water samples were filtered through a plankton net (32-μm mesh size), and the filtrates were preserved in sugar formalin (for a final concentration of 4% formaldehyde; Haney and Hall, 1973). Zooplankton identification and enumeration at the species level was performed using a Zeiss Axioskop 40 (Zeiss, Göttingen, Germany) at 200× magnification, based on the classification key prepared by Mizuno and Takahashi (1999).

To investigate the influence of fish on *D. brachyurum*, we collected fish using a gill net (6 mm×6 mm), cast net (7 mm×7 mm), and scoop net (5 mm×5 mm). At the sampling location in each reservoir, the gill net was set for 3 h after placement, while the cast net and the scoop net were used for 30 min and 20 min, respectively. The gill net was primarily used in reservoirs with D_{max}>6 m (sites 1 to 10), and the cast net and scoop net were utilized for relatively shallow reservoirs (D_{max}<6 m; sites 11 to 21). All of the collected fish individuals were preserved in methanol-formaldehyde solution immediately after identification to the species level according to Kim and Park (2002) and the classification system of Nelson (1994), and stored for further analysis of their gut contents.

All of fish samples were utilized in gut content analysis. Because there was almost no information about the consumption of *D. brachyurum* by freshwater fish, we utilized all of fish guts from the samples and investigated the prey items in the guts. The only fish samples contained *D. brachyurum* was used in further analysis. We identified and counted all of the zooplankton species in the gut samples, and the proportional abundance of *D. brachyurum* in every fish gut was calculated. To do the analysis, one eviscerated gut sample was placed on a Sedgewick-Rafter chamber, and we carefully incised the gut to extract gut contents. 1 mL of distilled water was slowly trickled on the gut contents within the gut, in order to wash the gut contents. The flown-out gut contents were then investigated by a microscope (Zeiss Axioskop 40; Zeiss) at 200× magnification. Among the gut contents, some samples were broken or not complete, which were not included in the counting of gut contents in order to keep consistency.

To understand the distribution of *D. brachyurum* with respect to maximum depth and habitat structure (*i.e.*, macrophytes) more clearly, we conducted additional collections of *D. brachyurum* at four different reservoirs. First, the two deepest reservoirs (site number 1 and 2) out of 21 reservoirs were identified, and we randomly selected 20 sampling locations in each reservoir. Maximum depth at each sampling location was measured with the EK-500 echo sounder, and *D. brachyurum* was collected from the bottom water layer at each location. Using this dataset, we compared *D. brachyurum* densities among locations to determine the influence of maximum depth on the density gradient of *D. brachyurum*. The other two reservoirs (site number 11 and 13) were used to identify the quantitative influence of macrophyte beds; therefore, we selected reservoirs that supported the highest biomass of macrophytes among the 21 study sites. We again randomly selected 20 sampling locations in each of these reservoirs, and collected *D. brachyurum* from each location. In addition, we collected all macrophytes within a quadrat (size 1 m×1 m) placed at each sampling site, and the collected macrophytes were transferred to the laboratory and dried at 60°C for two days. The measured dry weight of the macrophytes was then compared with *D. brachyurum* densities collected at the macrophyte sampling location.

Data analysis

Biological diversity (H') and evenness (J) was calculated to identify the changing pattern of zooplankton community structure with respect to time and sites (Shannon and Wiener, 1949; Pielou, 1966). We used regression analysis to analyse the influence of maximum depth and macrophyte biomass on the density of *D. brachyurum* in the study sites. Also, we applied cluster analysis to the data of zooplankton species composition so as to examine similarity between the study sites. All statistical analyses were accomplished using a statistical package SPSS for Windows (ver. 14).

RESULTS

Environmental variables

The environmental variables from the reservoirs reflected the characteristics of temperate lakes (Supplementary Tabs. 1 to 4). A vertical gradient in these parameters was apparent in reservoirs with D_{max} >6 m (sites 1 to 10), while little difference was observed between the surface and bottom layers in the relatively shallow reservoirs (D_{max} <6 m; sites 11 to 21). In reservoirs with D_{max} >6 m, differences in water temperature between the surface and bottom layers were relatively large in summer, but shallow reservoirs showed small difference between layers. Interestingly, presence of macrophyte caused larger difference between layers during autumn (sites 11, 13, 14, 18, 19, and 21). This pattern was also observed for dissolved oxygen. In reservoirs with D_{max} >11 m, dissolved oxygen in the bottom layers was lower than that in surface layers (ca. 5 to 14%). In contrast, shallow reservoirs where macrophytes were present generally exhibited lower levels of dissolved oxygen at both layers during summer and autumn (ca. 23 to 44%), and the diurnal difference was negligible.

However, turbidity and chlorophyll-*a* exhibited different patterns in accordance with seasons, water layers, and the study sites. The highest turbidity value was observed in the summer, particularly in reservoirs with D_{max} <6 m. In summer, turbidity levels of the water layers were similar in reservoirs with D_{max} <6 m, but reservoirs with D_{max} >6 m showed similar turbidity level between only surface and bottom layers. In other seasons, however, turbidity levels were highest in the surface layer. In contrast, chlorophyll-*a* concentrations were higher in autumn in most of the reservoirs, followed by spring. During spring and autumn, the highest concentration of chlorophyll-*a* was found in water surface, but the chlorophyll-*a* increased in middle- and/or bottom layers in summer. Also, we observed higher chlorophyll-*a* concentrations in shallow reservoirs compared with reservoirs with D_{max} >6 m.

Spatial and temporal distribution of *D. brachyurum*

A total of 66 zooplankton species were identified from 21 reservoirs: 44 rotifer species, 15 cladoceran species, and 7 copepod species. Zooplankton density was different in accordance with season and study site (Fig. 2). The density of zooplankton was greater in shallow reservoirs (D_{max} <6 m) than in reservoirs with D_{max} >6 m. The highest density of zooplankton was found in summer, followed by autumn. A high density of zooplankton was recorded at site 1, 11 and 13 (>3000 ind. L^{-1}). The zooplankton species diversity and evenness also were higher in summer and autumn compared with other seasons (Supplementary Tab. 5), and this pattern was clearer in shallow reservoirs (D_{max} <6 m). However, some reservoirs where *D. brachyurum* prevailed showed relatively lower diversity and evenness in summer because of dominance of *D. brachyurum*. *Keratella cochlearis* Gosse, 1851, *Polyarthra vulgaris* Carlin, 1943, and *Bosmina longispina* O.F. Müller, 1785 were frequently found in the reservoirs with D_{max} >6 m, while the shallow reservoirs were primarily occupied by *Lecane hamata* Stokes, 1897*, Mytilina ventralis* Ehrenberg, 1832*,* and *Chydorus sphaericus* O.F. Müller, 1785. *D. brachyurum* was commonly observed at overall the study sites during the study period, but generally did not dominate the zooplankton assemblage.

According to the cluster analysis results, the study sites were largely classified into two groups (Fig. 3). The first group was comprised of reservoirs with D_{max} >6 m (site 11, 13, 14, and 18) in which macrophyte domaniated and relatively large zooplankton diversity was maintained. The other group collected the sites with comparatively lower diversity of zooplankton.

Consumption pattern of *D. brachyurum* by predatory fish

D. brachyurum was observed in all seasons except winter, and the summer season supported the highest densities (Tab. 1). During the summer, highest densities of *D.*

brachyurum were observed at sites 1 and 11, and persisted until autumn. In contrast, *D. brachyurum* was not observed at site 15, and this species appeared only in spring at site 20. *D. brachyurum* also exhibited a striking spatial distribution pattern in accordance with the maximum depth of the reservoirs. In reservoirs with D_{max} >6 m, highest abundance of this species was found in the bottom layers, except for several reservoirs (*i.e*., sites 7, 8, 9, and 10 ranged between 6 and 11 m) which supported relatively low densities of *D. brachyurum* in the bottom layer. Nevertheless, in the majority of reservoirs studied, *D. brachyurum* were concentrated in the deeper layers. In reservoirs with D_{max} <6 m, however, *D. brachyurum* was not concentrated in the bottom layer, but was primarily found in surface waters. Specifically, this species tended to be present at high densities in surface waters at locations where macrophytes were present (sites 11, 13, 14, 18, 19, and 21). Furthermore, our surveys showed that *D. brachyurum* densities increased according to maximum depth and macrophyte biomass (Fig. 4). We observed little difference in *D. brachyurum* densities between samples collected during the daytime *versus* night. In reservoirs with D_{max} >6 m, *D. brachyurum* densities were slightly decreased in the bottom layer at night, and showed a small increase in the middle and surface layer. However, they were still present at high densities in the bottom layer during the night.

During the study period, we collected a total of seven fish species: *Micropterus salmoides* Lacepéde, 1802*, Lepomis macrochirus* Rafinesque, 1819*, Pseudorasbora parva* Temminck and Schlegel, 1846*, Opsariichthys uncirostris amurensis* Berg, 1940*, Carassius auratus* Linnaeus, 1758*, Pseudobagrus fulvidraco* Richardson, 1846*,* and *Misgurnus anguillicaudatus* Cantor, 1842. Of these, *M. salmoides* (156 ind.) and *L. macrochirus* (214 ind.) accounted for ca. 70% of the total fish collected (total 628 ind.). Total length of fish samples ranged between 60-337 mm, and relatively larger fish were caught from reservoirs with D_{max} >6 m (124-337 mm; 60-168 mm from shallow reservoirs). Fish smaller than total length 131 mm consumed *D. brachyurum*, and mostly they were juvenile fish. The following prey consumption analysis was adapted to those small fish samples.

The consumption pattern of prey zooplankton species by fish was different between each reservoir (Fig. 5; Supplementary Tabs. 6 to 8). Fish tended to consume zoo-

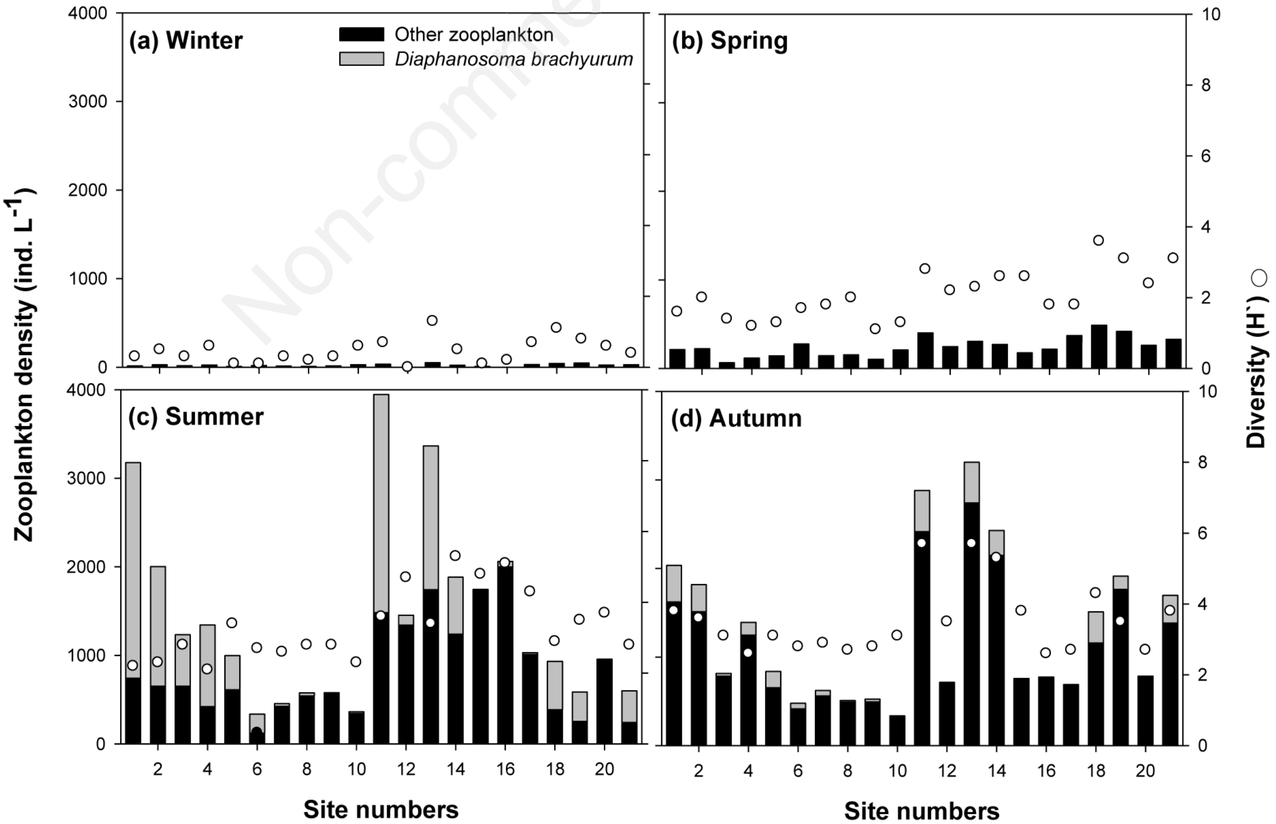

Fig. 2. Seasonal density (ind. L^{-1}) of *Diaphanosoma brachyurum* and other zooplankton during the study period.

plankton more in reservoirs with D_{max} <6 m than reservoirs with D_{max} >6 m. In reservoirs with D_{max} >11 m, consumption of *D. brachyurum* by fish was relatively low. Similarly, in reservoirs with macrophytes, fish predation on *D. brachyurum* was also relatively weak, and large densities of *D. brachyurum* in the surface layer were observed. In contrast, in some reservoirs in which the maximum depth ranged between 6 and 11 m, we observed high consumption rates of *D. brachyurum* by fish (*i.e*., sites 7 and 8). These consumption patterns found in reservoirs with macrophytes were absent (*i.e*., sites 12, 16, 17, and 20).

DISCUSSION

In these results, we found different spatial distribution of *D. brachyurum* in accordance with the maximum depth of the reservoirs. The different distribution patterns can be defined as the beneficial effects of a species' evolutionary reaction that has the purpose of solving problems caused by environmental constraints. Some studies reported that the hypolimnion was utilized by cladoceran (*e.g*., *Daphnia*) as a daytime refuge to avoid fish predation, and that at nighttime, prey individuals moved towards surface waters where their food source was abundant (diel vertical migration, DVM; Lampert, 1993; von Elert and Loose, 1996). This is the typical behavioural pattern of cladoceran species, which overcome food shortages at the bottom layers by moving towards water surface with food-sufficient areas (*e.g*., area with phytoplankton abundance). However, we did not observe this migration pattern in this study, and most *D. brachyurum* individuals remained in the bottom layer during the night in reservoirs with D_{max}>6 m. Adamczuk (2009) also reported that *D. brachyurum* did not perform migrations pattern. They seem less susceptible to fish predation as indicated by the low alteration of their vertical distribution (Thys and Hoffmann, 2005). Therefore, *D.*

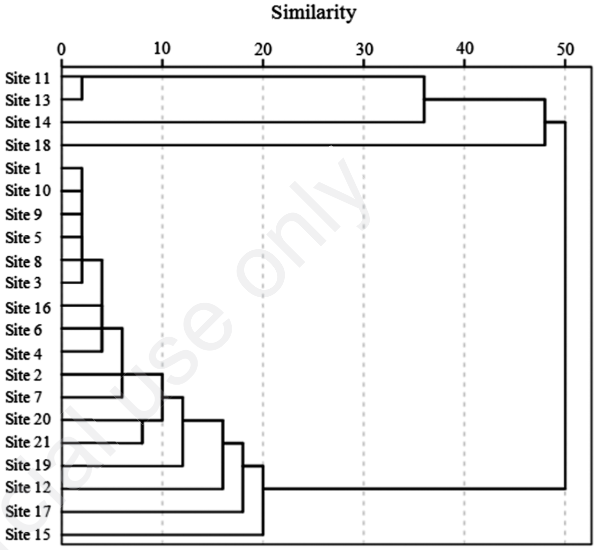

Fig. 3. Result of cluster analysis on zooplankton species composition among 21 reservoirs.

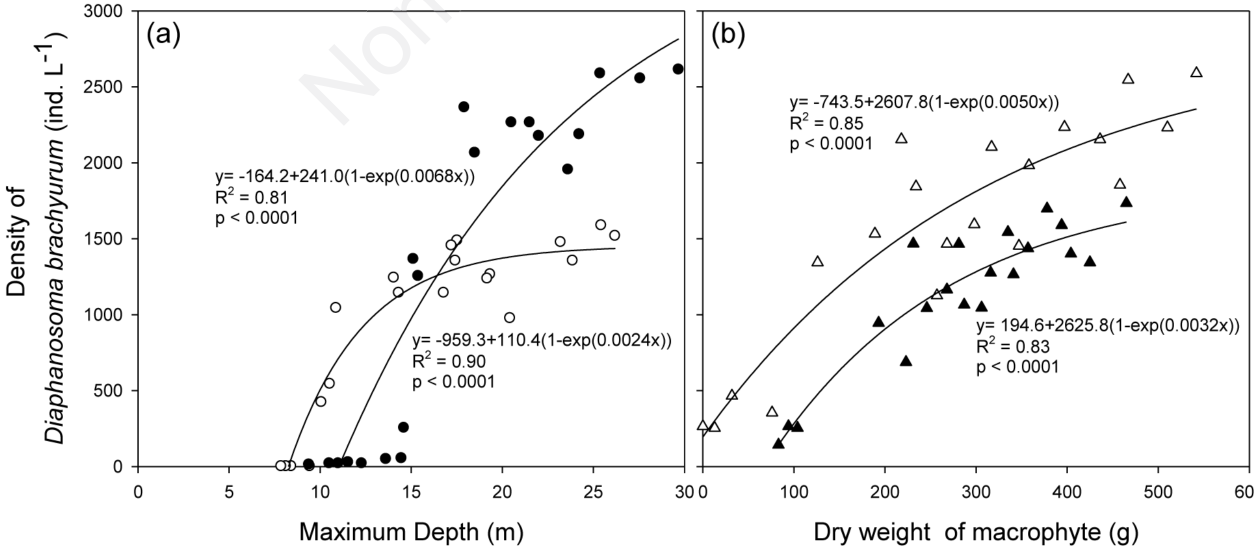

Fig. 4. Regression analysis between *Diaphanosoma brachyurum* and water body characteristics. White circles in the panel (a) indicate the data from the site 1, and the black circles are for the data of the site 2. White triangles of the panel (b) indicate site 11, and the black triangles were for the site 13.

Tab. 1. Spatial and temporal distribution pattern (mean±SD) of *Diaphanosoma brachyurum* at each study site.

Site number	Layer	Depth (m)	Winter (Feb.)		Spring (May)		Summer (Aug.)		Autumn (Nov.)	
			Day	Night	Day	Night	Day	Night	Day	Night
1	S	0.5	-	-	-	-	-	28±34.3	-	-
	M	13.3	-	-	-	-	32±16.5	216±43.6	8±1.4	23±12.3
	B	29.6	-	-	52±22.3	46±13.4	2602±154.3	2347±254.6	424±17.6	388±25.1
2	S	0.5	-	-	-		-	54±5.6	-	-
	M	13.1	-	-	-	17±5.32	154±25.6	267±128.4	12±5.3	7±0.51
	B	26.2	-	-	84±15.6	77±35.2	1518±58.4	1248±351.2	294±84.6	315±41.6
3	S	0.5	-	-	-	-	-	17±5.6	-	-
	M	12.4	-		-	-	98±21.4	124±29.4	12±2.5	8±1.2
	B	24.8	-	-	-	-	664±112.6	513±105.4	34±6.2	27±8.6
4	S	0.5	-	-	-	-	-	-	-	-
	M	10.4	-	-	-	-	102±23.5	243±57.6	34±35.2	22±1.6
	B	20.8	-	-	34±5.4	23±12.5	964±114.8	845±186.4	154±54.8	118±26.4
5	S	0.5	-	-	-	-	-	27±12.3	-	45±15.6
	M	9	-	-	-	8±1.21	112±36.4	94±21.4	142±54.6	215±68.4
	B	18	-	-	46±14.6	55±8.6	436±164.5	327±52.1	206±68.4	143±54.6
6	S	0.5	-	-	-	-	-	13±2.5	-	-
	M	8.1	-	-	-	-	42±11.6	83±19.5	18±2.51	12±3.2
	B	16.3	-	-	70±14.6	76±15.8	252±59.4	197±31.5	68±14.2	54±8.9
7	S	0.5	-	-	-	-	-	-	-	-
	M	5.4	-	-	10±2.6	13±2.1	-	16±21.6	-	21±3.5
	B	10.9	-	-	36±13.5	44±16.8	24±5.6	37±13.5	65±24.6	51±24.6
8	S	0.5	-	-	-	-	-	-	-	-
	M	3.5	-	-	12±3.5	21±5.6	16±2.4	31±12.5	-	-
	B	7	-	-	26±6.8	23±1.5	47±14.5	22±6.4	16±2.8	16±4.5
9	S	0.5	-	-	-	-	-	-	-	-
	M	3.3	-	-	-	-	-	-	-	-
	B	6.7	-	-	36±4.2	32±5.3	12±4.6	16±3.5	33±5.9	27±8.4
10	S	0.5	-	-	-	-	-	-	-	-
	M	3.3	-	-	-	21±5.1	-	15±2.5	-	-
	B	6.6	-	-	89±14.2	83±14.2	21±3.4	17±4.5	-	-
11*	S	0.5	-	-	34±3.2	54±4.2	2588±215.4	2353±231.2	504±56.8	313±84.5
	B	5	-	-	-	-	128±54.3	147±21.5	-	-
12	S	0.5	-	-	-	-	123	98	-	-
	B	4.8	-	-	-	-	-	-	-	-
13*	S	0.5	-	-	98±21.5	57±15.2	1734±165.2	1598±312.4	490±114	-
	B	4.3	-	-	-	-	154±54.2	124±34.2	84±23.4	-
14*	S	0.5	-	-	28±1.6	12±1.8	630±114.2	657±121.5	294±56.4	-
	B	4.1	-	-	-	-	210±56.4	243±35.1	154±31.4	-
15	S	0.5	-	-	-	-	-	-	-	-
	B	3.8	-	-	-	-	-	-	-	-
16	S	0.5	-	-	-	-	76±12.5	43±6.2	-	-
	B	3.4	-	-	-	-	-	-	-	-
17	S	0.5	-	-	79±24.1	68±24.6	13±2.35	20±2.2	-	-
	B	3.3	-	-	-	-	-	-	-	-
18*	S	0.5	-	-	182±53.2	154±25	588±134.5	521±56.2	364±84.2	-
	B	3.1	-	-	-	-	84±21.5	57±16.2	98±24.3	-
19*	S	0.5	-	-	132±23.4	116±24	336±142.5	327±51.2	168±35.1	-
	B	2.8	-	-	-	-	56±24.2	67±25.3	-	-
20	S	0.5	-	-	75±24.1	54±21.6	-	-	-	-
	B	2.6	-	-	-	-	-	-	-	-
21*	S	0.5	-	-	56±21.5	42±14.2	378±84.2	342±154.2	322±104	-
	B	2.2	-	-	-	-	112±54.6	97±34.2	168±51.6	-

*S, surface; M, middle; B, bottom. *Sampling point characterized by the presence of macrophytes. The unit of zooplankton density is ind. L^{-1}.*

brachyurum individuals must have profited from fish predation pressure reducing the density of competitive cladoceran populations. Although relatively low chlorophyll-*a* concentrations were found in the bottom layer, the food source available to *D. brachyurum* at bottom layer may be sufficient to sustain the high densities that we observed. Empirical data suggested that zooplankton, especially cldadoceran species, may maintain nutrient homeostasis by incorporating a greater proportion in limiting food supply (Gulati and Demott, 1997). Therefore, the need for conserving nutrients in insufficient supply increases with the increase in growth rates. Moreover, we frequently observed neonates in the layers where *D. brachyurum* was abundant at each of the reservoirs (*data not shown*). This implies that *D. brachyurum* reproduced in those layers.

No migration pattern was observed in shallow reservoirs as well (D_{max} <6 m), where *D. brachyurum* individuals were concentrated in the surface layers. In empirical studies, macrophytes can have dramatic effects on freshwater habitat structures (O'Hare *et al*., 2006; Smokorowski and Pratt, 2007), and provide a heterogeneous mosaic at different scales. Therefore, macrophytes are capable of providing habitat suitable for colonization by zooplankton, including *D. brachyurum*. Based on these observations, we propose that the deeper bottom layer may play similar role as macrophytes.

The consumption pattern of *D. brachyurum* by fish was different in accordance with the water depth of the reservoirs. In reservoirs with D_{max} >11 m, consumption of *D. brachyurum* by fish was low. This result implies that the bottom layer of the reservoirs serves as an effective refuge from fish predation. In contrast, in some reservoirs in which the maximum depth ranged between 6 and 11 m, we observed high consumption rates of *D. brachyurum* by fish (*i.e*., sites 7 and 8). Therefore, the bottom layer in these reservoirs might not be appropriate as refuge of *D. brachyurum*. Although light penetration at depth depends on turbidity and other factors, light

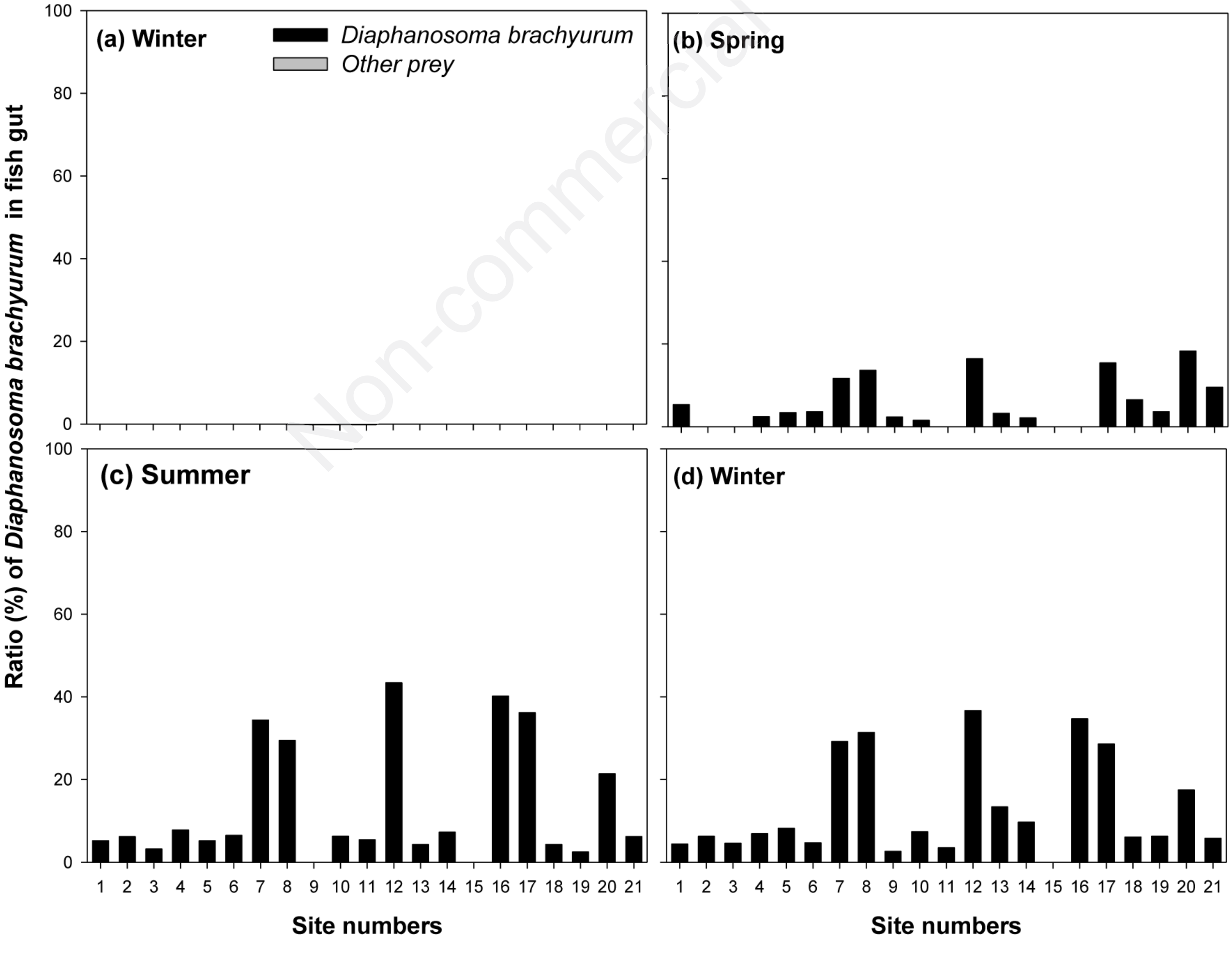

Fig. 5. Average ratio (%) of *Diaphanosoma brachyurum* on total diet composition in gut of fish at each study site.

may penetrate to the bottom layer in reservoirs with D_{max} <11 m, thus enabling active visual foraging by predatory fish. Conversely, *D. brachyurum* was able to maintain high densities in the bottom layer in reservoirs with D_{max} >11 m. Some studies have suggested that turbidity is an important determinant of visual foraging by fish (Zamor and Grossman, 2007; Hazelton and Grossman, 2009), but we did not observe a large difference in turbidity between reservoirs in which D_{max} ranged from 6 to 11 m. Similarly, in reservoirs with macrophytes, fish predation on *D. brachyurum* was relatively weak, and large densities of *D. brachyurum* in the surface layer were observed. Some studies reported that excessive dominance of macrophyte in water surface may reduce light penetration in the water (shading effect; Sand-Jensen and Søndergaard, 1981), inducing decrease of fish foraging (Tatrái and Herzig, 1995), and enabling the survival of prey individuals (mainly cladocerans) that utilized these macrophytes (Manatunge *et al.,* 2000). We therefore propose that the macrophytes in these reservoirs provide refuge for *D. brachyurum*. Although most studies of macrophyte habitat reported that submerged macrophytes provided fundamental habitat for zooplankton (Jeppesen *et al.*, 1998), we observed low biomass or the complete absence of submerged macrophytes. Therefore, *D. brachyurum* appears to utilize surface-dwelling macrophytes rather than the submerged as refuge. Consequently, these areas (*i.e.*, bottom layer and surface-dwelling macrophyte bed) may function as habitat for *D. brachyurum,* as well as serving as a refuge from fish predation.

Previous studies generally have discriminated the functions of the hypolimnetic layer and macrophyte beds: the former only has a refuge role due to food scarcity and low dissolved oxygen, while the latter provides sufficient refuge space as well as food items (*e.g*., organic matters or algae; van Donk and van de Bund, 2002). The macrophyte bed structure is determined by macrophyte growth forms, density, or species composition (Lauridsen and Buenk, 1996; Stansfield *et al.,* 1997; Burks *et al.,* 2001; Choi *et al*., 2014a), and complex macrophyte structure may serve as a highly effective refuge. Therefore, complex macrophyte structure can support more aquatic animals. This usage pattern has been well documented, primarily from cladoceran groups (Walseng *et al.,* 2006). Specifically, some cladoceran species (epiphytic species: *Chydorus*, *Picripleuroxus,* and *Sida*) utilize surfaces of stems and leaves of macrophytes as habitat (Whiteside, 1974; Fairchild, 1981; Nurminen *et al.,* 2001; Choi *et al.,* 2014b). Compared with other Cladocera, *D. brachyurum* has a number of appendages, thus the morphology of *Diaphanosoma* is appropriate for attachment to macrophyte surfaces. We therefore suggest that the presence of macrophytes is an important factor for sustaining *D. brachyurum* populations in shallow reservoirs. In contrast, we observed low densities of *D. brachyurum* in the surface layer of shallow reservoirs (sites 12, 15, 16, 17, and 20) where macrophytes exhibited low biomass or were almost absent. Moreover, increased consumption of *D. brachyurum* by fish was observed in those reservoirs.

However, we also found the evidence that the bottom layer serves as habitat for *D. brachyurum.* In general, food resources in the bottom layer are insufficient to support the growth and development of aquatic animals such as *D. brachyurum,* and the space is only used as daytime refuge to avoid predation. However, we observed large densities of *D. brachyurum* in the bottom layer in reservoirs with D_{max} >6 m, moreover, they exhibited seasonal population growth. We therefore suggest that the bottom layer provides suitable habitat for the growth and development of *D. brachyurum*. In other words, the bottom layer provides refuge as well as habitat for *D. brachyurum*. Therefore, the bottom layer plays a similar role as that of the macrophyte bed. However, further investigation is needed to better understand the importance of this bottom layer for sustaining *D. brachyurum* populations.

CONCLUSIONS

D. brachyurum was frequently observed in the study sites, and the bottom layer (*i.e*., maximum depth >11 m) and surface macrophyte bed were utilized as refuge for this species. Moreover, densities of *D. brachyurum* gradually increased according to maximum depth and habitat complexity. Although predatory fishes frequently consumed *D. brachyurum* at the reservoirs, the presence of a bottom layer (*i.e*., D_{max} >11 m) or macrophyte bed greatly reduced the influence of fish predation. Consequently, reservoirs with these refugia supported large densities of *D. brachyurum*. Some empirical studies reported that macrophytes provide both refuge and food for zooplankton, but that the hypolimnetic layer is utilized only as refuge. However, we found that the bottom layer in reservoirs with D_{max} >11 m play a similar role to macrophyte beds. Consequently, both the bottom layer >11 m and complex macrophyte structure sustain *D. brachyurum* densities at the reservoirs. The presence of either the deeper layer or complex macrophyte structure appeared to correspond to high densities of *D. brachyurum,* which were the dominant cladoceran species in the studied reservoirs. Therefore, *D. brachyurum* seems to have the ability to exploit various types of refugia (in this study, the deep layer or macrophyte bed) compared with other cladoceran species, which may contribute to this species' predominance in various types of freshwater ecosystems. Unfortunately, in the current study, the simultaneous presence of both refugia was not observed. The coexistence of deeper layer and limnetic macrophyte bed is expected to further enhance *D. brachyurum* densities.

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