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Distribution pattern of epiphytic microcrustaceans in relation to different macrophyte microhabitats in a shallow wetland (Upo wetlands, South Korea)

by

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Abstract

Macrophytes determine the physical complexity of aquatic environments and provide a suitable habitat for colonization by microcrustaceans. We evaluated the effects of a seasonal growth pattern and structure of macrophyte species on epiphytic microcrustaceans collected from macrophyte surfaces (stems and leaves) in shallow wetlands from May 2011 to October 2012. In 2011, epiphytic microcrustaceans that preferred free-floating macrophytes (*Spirodela polyrhiza* and *Salvinia natans*) and submerged macrophytes (*Potamogeton crispus* and *Ceratophyllum demersum*) were affected by the seasonal growth of these species. Epiphytic microcrustaceans were abundant on the surface of *Spirodela polyrhiza* in June and August and on *Salvinia natans* in September and October. In 2012, epiphytic microcrustaceans preferred submerged macrophyte species over the free-floating ones. The results of stable isotope analysis showed that epiphytic microcrustaceans depend on epiphytic particulate organic matter (EPOM) from each macrophyte species rather than on suspended particulate organic matter. Small species (*Coronatella rectangula*, *Pleuroxus laevis*, and *Chydorus sphaericus*) used EPOM (dominated by epiphytic algae) on free-floating and submerged macrophyte species; however, relatively larger species (*Ilyocryptus spinifer* and *Macrothrix rosea*) used EPOM only from submerged macrophytes. Based on these findings, we conclude that the distribution of epiphytic microcrustaceans is determined by seasonal characteristics, morphology of macrophyte species, and abundance of food resources.

Key words: epiphytic algae, microhabitat structure, free-floating macrophyte, submerged macrophyte

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Introduction

Aquatic macrophytes can have dramatic effects on physical structures in water (O'Hare et al. 2006, Smokorowski & Pratt 2007). They support various herbivorous animal species that rely on macrophyte biomass (Otto & Svensson 1981). Furthermore, one major apparent role in aquatic ecosystems is the construction of a heterogeneous mosaic of niches at different scales through (1) provision of refuge against predators and suitable spawning and foraging substrates (Warfe & Barmuta 2004) and (2) mediation of trophic interactions among various biotas (Jeppesen et al. 1998, Pelicice & Agostinho 2006). Moreover, macrophytes often hold particles such as phytoplankton and bacteria, and have strong allelopathic effects; they enhance edible prey resources for zooplankton (van Donk and van de Bund 2002). Thus, macrophytes can support more individuals and increase species diversity of animal communities (Tolonen et al. 2005). Among diverse animals using the macrophyte habitat, freshwater microcrustaceans are well documented to exploit macrophytes as a habitat and/or refuge (Kuczyńska-Kippen & Nagengast 2006). In freshwater ecosystems, microcrustaceans are frequently a primary resource to higher trophic levels such as fish, and they require macrophyte habitats to avoid predators (Venugopal & Winfield 1993, Sagrario et al. 2009). Moreover, the surface of leaves and/or stems of macrophytes is used as a habitat for epiphytic microcrustacean species (i.e. *Chydorus*, *Coronatella*, and *Pleuroxus*; Sakuma et al. 2002, Choi et al. 2014c). Therefore, understanding the interaction between aquatic macrophytes and microcrustaceans has gradually become crucial to limnological research, especially in systems abundant in macrophytes.

Morphological characteristics of macrophytes determine the distribution of microcrustaceans. Among the various macrophytic life forms, submerged macrophytes increase the physical complexity of aquatic environments and provide a suitable habitat for colonization by microcrustaceans (Jeppesen et al. 1998, Manatunge et al. 2000). Moreover, the majority of studies that focused on the interactions between macrophytes and zooplankton have emphasized the role of submerged macrophytes (Stansfield et al. 1997, Muylaert et al. 2010). These studies argued that submerged macrophytes largely contribute to survival and growth of microcrustaceans (e.g. cladocerans) through an increase in heterogeneous space in the water. In contrast, the importance of free-floating macrophytes has been emphasized in subtropical lagoons (Meerhoff et al. 2007). Epiphytic microcrustacean species (i.e. plant-attached species) with high biomass were also often found on floating-leaved macrophytes (Moss et al. 1998). Therefore, a mixture of diverse macrophyte species in vegetated beds leads to high abundance and diversity of microcrustaceans (Choi et al. 2014a). Despite the various microcrustacean responses to macrophytes, the currently available information regarding the surface-dwelling macrophytes (i.e. free-floating and/or floating-leaved plants) focuses mainly on pelagic microcrustaceans (Brendonck et al. 2003; Meerhoff et al. 2006). The pattern of macrophyte utilization by epiphytic microcrustaceans is still unclear, and their abundance is usually underestimated. In shallow water ecosystems where macrophytes frequently dominate, epiphytic microcrustacean species are important for the determination of microcrustacean species diversity (Castilho-Noll et al. 2010, Gyllström et al. 2005, Kuczyńska-Kippen & Nagengast 2006).

The primary objective of our study was to investigate the pattern of distribution of epiphytic zooplankton associated with different morphological types of macrophytes. We expected that different plant types (emergent, free-floating, floating-leaved, and submerged) strongly influence the abundance and species composition of epiphytic microcrustaceans. Moreover, we considered that biological habitats such as macrophytes change with a seasonal change in the growth pattern of macrophytes, thereby leading to seasonality of epiphytic microcrustaceans. This study aims to advance our current understanding of the distribution of epiphytic microcrustaceans in freshwater ecosystems. Furthermore, the correlation of the distribution of epiphytic microcrustacean species with different plant preferences is discussed.

Materials and methods

The study site (Upo Wetlands) is located in the southeastern parts of South Korea, and it is connected to the lower part of the Nakdong River (Fig. 1). Four distinct seasons lead to dynamic succession among biological communities in this freshwater ecosystem. The wetland surface area is

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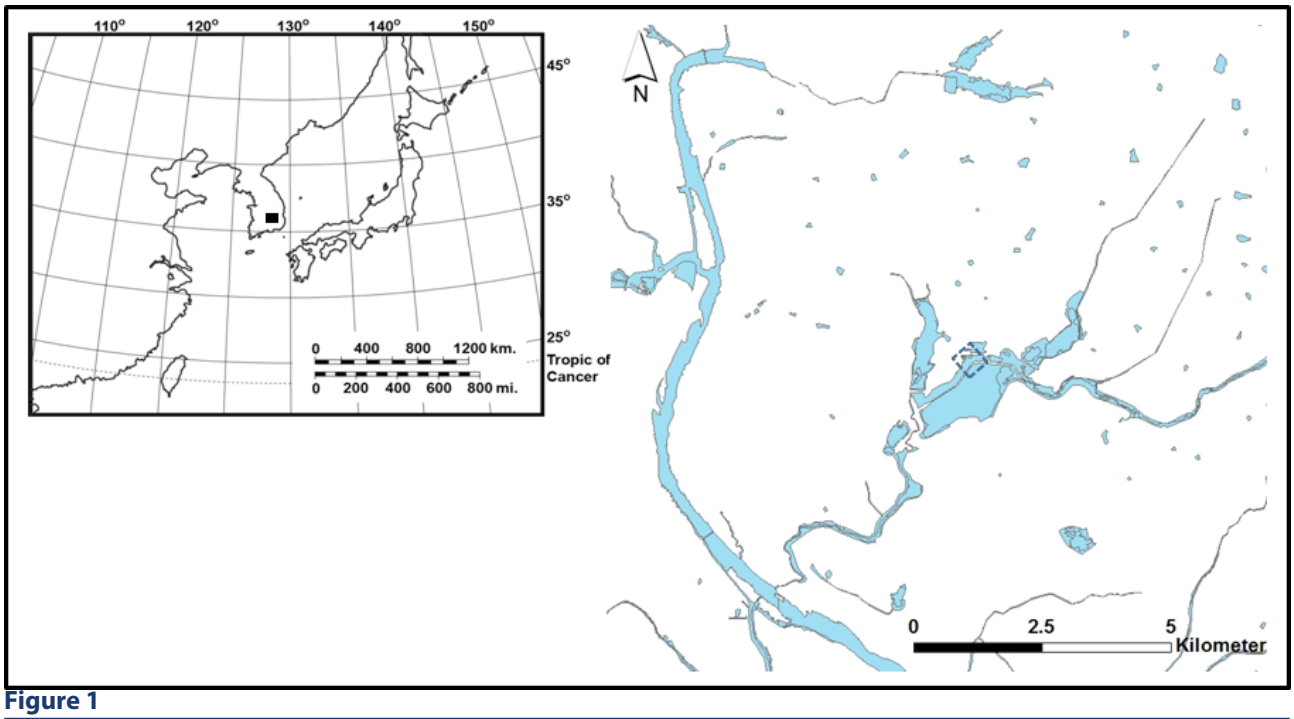


Figure 1

Map of the study sites. The study sites located in southeast South Korea are indicated by solid squares (■). (a) The map in the upper left corner shows the Korean Peninsula. (b) The map in the upper right corner shows the Upo Wetlands. The sampling point is indicated by an open circle (○).

2.7 km^2, and the annual average depth ranges from 0.8 to 1.4 m. The study site is almost completely covered with macrophytes from spring (May) to autumn (November). The dominant land cover surrounding the wetlands is of agricultural type, and non-point sources continuously influence the wetland ecosystems.

We monitored the study site at Upo Wetlands for two years (2011 and 2012), from May to October. Before the initiation of monitoring, we explored possible locations with similar macrophyte species composition and established six squares (0.5 m^2) along the littoral area of the study site. Of the six squares, three squares were used for quantification of epiphytic microcrustacean individuals, and the remaining three squares were used to collect samples for stable isotope analysis. Sample collection for stable isotope analysis was conducted only in spring (May) and autumn (October). To avoid sampling bias, previously sampled points were not resampled. We identified all macrophytes within each square to the species level and collected epiphytic microcrustaceans from each macrophyte species. Only the submerged parts of macrophytes were considered as a substrate for epiphytic microcrustaceans, because these animals inhabit underwater environments. Therefore, we removed organs emerging above the water surface (i.e. stalks and flowers) in all macrophyte species. Cautious handling of macrophytes was required to prevent accidental detachment of microcrustaceans.

Upon the collection, epiphytic microcrustaceans were temporarily preserved in filtered wetland water. Two liters of wetland water were filtered using a plankton net (32-μm mesh size) to remove animals, including microcrustaceans from the water and the water was stored in 5 l tanks; this water was used as a temporary storage for epiphytic microcrustaceans. We allocated one tank per macrophyte species, and the number of tanks for every square was determined by the number of sampled macrophyte species. Collected macrophytes were shaken vigorously more than 50 times inside the tanks to detach all microcrustaceans (see Sakuma 2002 for the detaching process). Microcrustaceans suspended in the water were filtered using a 68 μm mesh net. Each sample used for quantification of individual microcrustaceans was immediately

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fixed in sugar formalin (final concentration, 4% in the form of aldehyde; Haney & Hall 1973), whereas microcrustacean samples for stable isotope analysis were sorted using a micropipette according to species, and the microcrustaceans were separated from other organic matter. The remaining macrophytes were dried at 60°C for 2 d and their dry weight was then measured. The densities of epiphytic microcrustaceans attached to macrophyte species (total 8 species; *Phragmites australis* (Cav.) Trin., *Spirodela polyrhiza* (L.) Sch, *Salvinia natans* (L.) All., *Trapa japonica* Flerow, *Hydrocharis asiatica* Miq., *Potamogeton crispus* L., *Ceratophyllum demersum* L. and *Najas graminea* Delile.) were expressed as a number of individuals per gram of dry weight of each macrophyte species (ind. g^{-1} dw). The sampled epiphytic microcrustaceans were identified according to Mizuno & Takahashi (1991) and counted under a microscope (Axioskop 40, 100×; Carl Zeiss Microscopy GmbH, Jena, Germany). The microcrustacean species accounted for more than 5% of the total microcrustacean abundance were included in the analysis. This was because the main goal of this study was to discover a general pattern of epiphytic microcrustacean distribution in the wetland system. During the study period, we found some microcrustacean species that occurred temporarily or with very small abundance at the study site. A total of 6 epiphytic microcrustacean species (*Coronatella rectangula* (Sars 1861), *Pleuroxus laevis* (G. O. Sars, 1861), *Chydorus sphaericus* (O. F. Mueller, 1785), *Ilyocryptus spinifer* Herrick, 1882, *Macrothrix rosea* (Liéven, 1848), and *Cyclops vicinus* (Ulyanin, 1875)) were frequently observed at the study site, and they were used in the analysis. We measured the body size of each epiphytic microcrustacean species to understand different distributions of epiphytic microcrustacean species on macrophyte species. Moreover, we examined the differences in the density of epiphytic microcrustaceans between macrophyte species with ANOVA test using SPSS version 20 (IBM Corp., Armonk, NY, USA).

For the evaluation of epiphytic microcrustaceans' food source, samples of suspended particulate organic matter (SPOM) and epiphytic particulate organic matter (EPOM) were also assessed in stable isotope analysis. SPOM samples were obtained through re-filtration using a 5 µm mesh net after organisms were filtered out with a 68 µm net. EPOM samples were obtained by scraping the surface of leaves and/or stems of each macrophyte species using a brush. To improve the understanding of microcrustacean distribution on macrophyte species, we additionally collected epiphytic algae samples from leaves and/or stem surface of each macrophyte species using a brush. Epiphytic algae samples were preserved with Lugol's solution (ca. 5%), and algal cells (identified at the class level; such as Chlorophyceae, Bacillariaceae, Cyanophyceae, Euglenophyceae, Chrysophyceae, Synurophyceae, Dinophyceae) were counted under a Zeiss IM 35 inverted microscope at ×400 magnification (Carl Zeiss Canada Ltd., Toronto, Ontario, Canada).

The collected SPOM and EPOM samples were treated with 1 N HCl to remove inorganic carbon and rinsed with distilled water to remove the acid. Microcrustacean samples were not acidified to remove inorganic carbonates, because the acidification has detrimental effects on nitrogen values (Pinnegar & Polunin 1999). All samples were freeze-dried and homogenized with a mortar and pestle, and the powdered samples were kept frozen (-70°C) until analysis. Carbon and nitrogen isotope ratios were determined using the continuous-flow isotope mass spectrometry. Dried samples (ca. 1 mg for microcrustacean samples and 1.5 mg for SPOM and EPOM) were combusted in an elemental analyzer (EuroVector SpA, Milan, Italy) and the resultant gas (CO_2 and N_2) was introduced to an isotope ratio mass spectrometer (CF-IRMS, IsoPrime) in a continuous flow using a helium carrier. Data were expressed as a relative concentration (‰) difference between a sample and conventional standards of Pee Dee Belemnite carbonate (PDB) for carbon and air N_2 for nitrogen according to the following equation:

$$\delta X(‰) = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

Where X is ^{13}C or ^{15}N and R is the ^{13}C:^{12}C or ^{15}N:^{14}N ratio. A secondary standard of known relation to the international standard was used as a reference material. Standard deviations of $\delta^{13}C$ and $\delta^{15}N$ for analyses with 20 replicates of 'Peptone' standard were ±0.1 and ±0.2 (‰), respectively.

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Results

We found a total of eight species of macrophytes at sampled locations during the study period (Table 1): *P. australis*, *S. polyrhiza*, *S. natans*, *T. japonica*, *H. asiatica*, *P. crispus*, *C. demersum*, and *N. graminea*. Among macrophyte species, *P. australis* showed the largest dry weight (mainly during September), and the dry weight of other macrophyte species varied with the season. In 2011, the dry weight of free-floating macrophytes (*S. polyrhiza* and *S. natans*) was higher than the dry weight of other macrophyte species (excluding the emergent macrophyte species), whereas in 2012, the macrophytes were dominated by submerged species (*P. crispus*, *C. demersum*, and *N. graminea*). In contrast, floating-leaved macrophytes (*T. japonica* and *H. asiatica*) did not show any clear seasonality.

polyrhiza in June and August (average 62 ind. g^{-1} dw) and on *S. natans* in September and October (average 67 ind. g^{-1} dw). Seasonal distribution of microcrustaceans was also observed on submerged macrophyte species (*P. crispus* and *C. demersum*). Epiphytic microcrustaceans preferred the surface of *P. crispus* in May and August but shifted to *C. demersum* thereafter. In contrast, seasonality was not observed in microcrustaceans from both free-floating and submerged macrophyte species in 2012; epiphytic microcrustaceans were mainly supported by submerged macrophytes (*P. crispus* and *C. demersum*), followed by free-floating macrophytes. The abundance of microcrustacean epiphytes on the remaining macrophyte species did not show seasonality or inter-annual variability.

The results of stable isotope analysis indicated seasonality of the $\delta^{13}C$ and $\delta^{15}N$ values for epiphytic

Table 1

Monthly macrophytes dry weight during the study period (May to October; n = 3 for each month and site). PA, *Phragmites australis* (Cav.) Trin.; SP, *Spirodela polyrhiza* (L.) Sch.; SN, *Salvinia natans* (L.) All.; TJ, *Trapa japonica* Flerow; HA, *Hydrocharis asiatica*; PC, *Potamogeton crispus* L.; CD, *Ceratophyllum demersum* L., NG, *Najas graminea* Delile

Years	Months	Emergent	Free-floating		Floating-leaved		Submerged		
		PA	SP	SN	TJ	HA	PC	CD	NG
2011	May	24.5	5.4	-	17.8	-	5.6	-	-
	Jun.	28.7	28.2	-	19.7	-	12.4	-	-
	Jul.	33.2	34.6	5.4	33.8	-	16.7	9.4	-
	Aug.	40.4	22.9	24.9	34.1	19.7	4.0	16.4	10.3
	Sep.	46.7	4.2	37.4	28.4	20.9	-	18.7	14.3
	Oct.	32.5	-	28.9	10.8	21.6	-	19.8	16.5
2012	May	22.4	8.8	3.1	2.4	-	12.4	6.1	-
	Jun.	26.6	10.4	11.1	14.7	-	28.8	21.0	-
	Jul.	31.2	16.2	14.2	21.4	12.6	35.2	26.3	-
	Aug.	38.2	21.6	16.6	23.8	15.7	38.4	30.8	-
	Sep.	47.1	19.7	18.4	26.5	16.4	32.2	24.9	18.4
	Oct.	37.8	17.1	9.3	15.8	10.2	30.8	-	21.4

The distribution pattern of epiphytic microcrustaceans was related to morphological structure and seasonal abundance of macrophyte species (Fig. 2 and 3). In 2011, the epiphytic microcrustaceans were more abundant on the surface of free-floating (*S. polyrhiza* and *S. natans*) and submerged macrophyte species (*P. crispus* and *C. demersum*). A high density of epiphytic microcrustaceans was found on the surface of *S.*

microcrustaceans and potential food sources (SPOM and EPOM) (Fig. 4). The $\delta^{13}C$ values of SPOM were significantly different between the spring and autumn (t-test, t = -3.1, p = 0.032), and they were higher in the autumn compared to the spring. The $\delta^{13}C$ values of EPOM for each macrophyte species were higher than the values of SPOM during all seasons and higher in the autumn than in the spring. The $\delta^{13}C$ values of EPOM for each macrophyte

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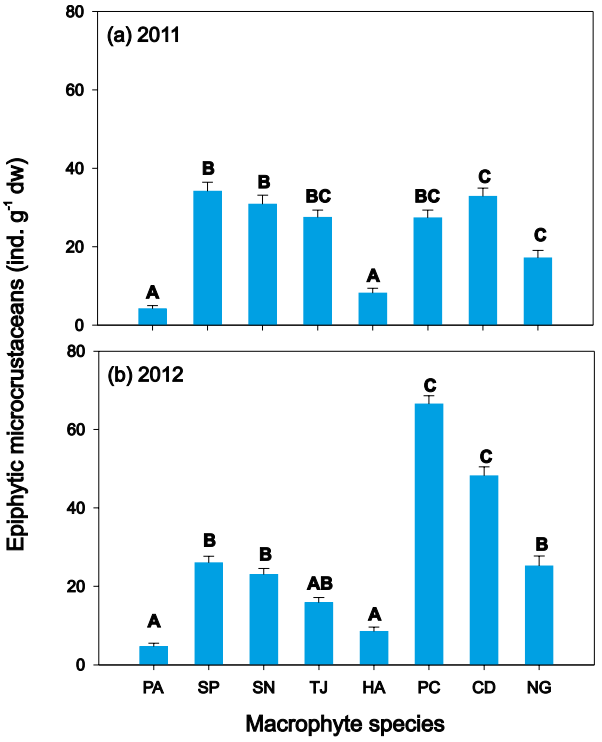


Figure 2

Density of epiphytic microcrustaceans (ind. g^{-1} dw) from each macrophyte species at Upo wetland

Bars represent an average of replicates (±SE). Letters above the bars indicate statistically different mean values. PA - *Phragmites australis* (Cav.) Trin.; SP - *Spirodela polyrhiza* (L.) Sch.; SN - *Salvinia natans* (L.) All.; TJ - *Trapa japonica* Flerow; HA - *Hydrocharis asiatica*; PC - *Potamogeton crispus* L.; CD - *Ceratophyllum demersum* L., NG - *Najas graminea* Delile

species widely ranged from -31.69‰ to -22.69‰, and were significantly different between macrophyte species (one-way ANOVA, $p < 0.05$). The $\delta^{13}C$ values of EPOM for the surface of free-floating (*S. polyrhiza* and *S. natans*) and submerged macrophyte species (*P. crispus* and *C. demersum*) were always higher than the values for other macrophyte species. Moreover, the $\delta^{13}C$ values of EPOM between the free-floating and submerged macrophyte species varied with seasons. In the spring, the $\delta^{13}C$ values of EPOM for submerged macrophyte species (*P. crispus* and *C. demersum*) were higher than the values for free-floating macrophyte species (*S. polyrhiza* and *S. natans*), but they were lower than the $\delta^{13}C$ values of EPOM for free-floating macrophyte species in the autumn. The $\delta^{13}C$ values of the epiphytic microcrustaceans differed between species; in most of the species, they were higher in the autumn than in spring. Among the epiphytic microcrustacean species, the $\delta^{13}C$ values for *C. vicinus* were always lower than the values for the epiphytic cladoceran species (i.e. *C. rectangula*, *P. laevis*, *C. sphaericus*, *I. spinifer*, and *M. rosea*) throughout the sampling period. In contrast, the $\delta^{15}N$ values for all samples did not differ significantly between the seasons.

The $\delta^{13}C$ values of the epiphytic microcrustaceans indicated a shift in the composition of their food sources (SPOM and EPOM) and reflected seasonal changes in the $\delta^{13}C$ values of SPOM and EPOM (Fig. 4). During the study period, epiphytic microcrustaceans were more related to the EPOM from each plant species than the SPOM. Among the epiphytic microcrustaceans, epiphytic cladoceran species used mainly EPOM from the free-floating (*Spirodela polyrhiza* and *Salvinia natans*) and submerged macrophyte species (*Potamogeton crispus* and *Ceratophyllum demersum*). In particular, *C. rectangula*, *Pleuroxus laevis*, and *Chydorus sphaericus* relied on the abundance of EPOM, mainly from the free-floating and submerged macrophyte species, whereas *I. spinifer* and *M. rosea* used only EPOM attached to the submerged macrophyte species. In contrast, *C. vicinus* partly relied on SPOM and EPOM on *T. japonica*.

The body size of epiphytic microcrustacean collected from macrophyte varied by microcrustacean species (Table 2). Among epiphytic cladoceran species, *C. rectangular, P. laevis,* and *C. sphaericus* were relatively smaller than *I. spinifer* and *M. rosea* during the study period. Compared with epiphytic cladoceran, the body size of *C. vicinus* was two times larger. However, no significant difference was found in the body size related to seasons.

In order to understand the pattern of microcrustaceans' high dependency on EPOM, we investigated the composition of epiphytic algae on the surface of macrophyte species. The seasonal abundance of epiphytic algae on each macrophyte species was similar to the seasonal distribution of epiphytic microcrustaceans (Table 3). In 2011, epiphytic algae were more abundant on free-floating macrophyte species, but in 2012, they were abundant on submerged macrophyte species. However, the overall composition of epiphytic algae was similar between macrophyte species during the two years. Bacillariaceae were dominant among the epiphytic algae, followed by Chlorophyceae.

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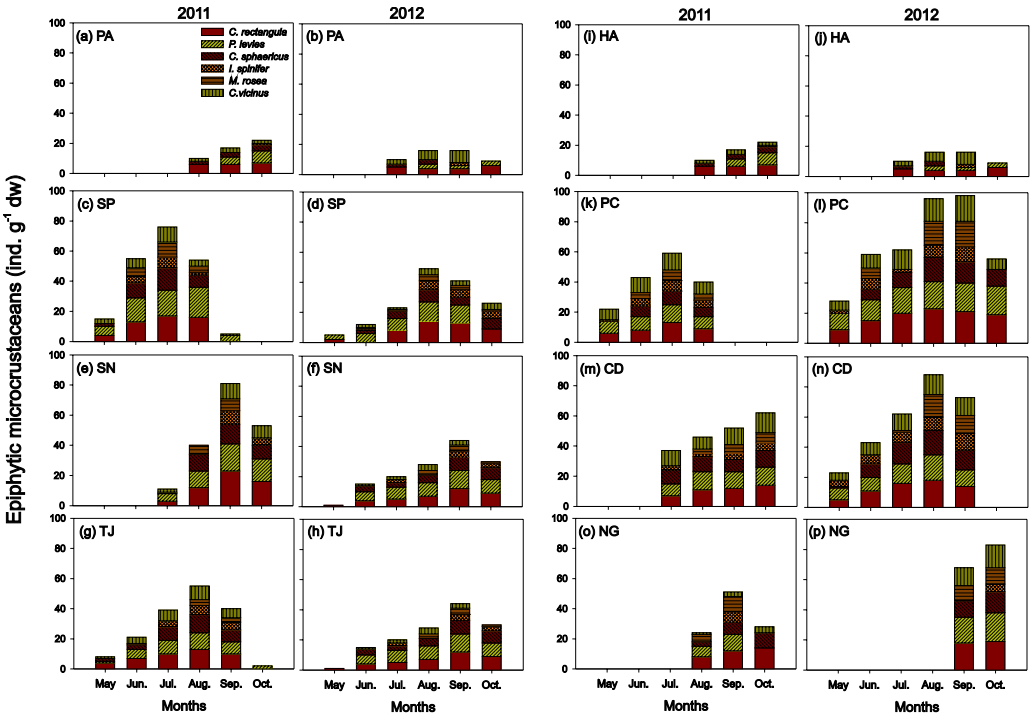


Figure 3

Seasonal density (ind. g^{-1} dw) of epiphytic microcrustaceans on macrophyte species during the study period (May to October) PA - *Phragmites australis* (Cav.) Trin.; SP - *Spirodela polyrhiza* (L.) Sch.; SN - *Salvinia natans* (L.) All.; TJ - *Trapa japonica* Flerow; HA - *Hydrocharis asiatica*; PC - *Potamogeton crispus* L.; CD - *Ceratophyllum demersum* L., NG - *Najas graminea* Delile

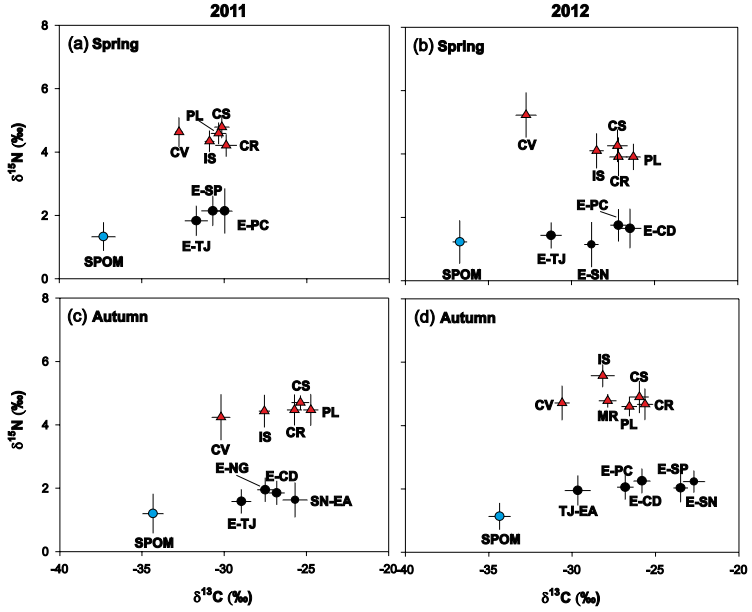


Figure 4

Carbon and nitrogen isotope plots of samples (n = 3) in spring (May) and autumn (September) SPOM, suspended particulate organic matter; E-SP - epiphytic particulate organic matter (EPOM) on *Spirodela polyrhiza*; E-SN - EPOM on *Salvinia natans* (L.) All.; E-TJ - EPOM on *Trapa japonica* Flerow; E-PC - EPOM on *Potamogeton crispus* L.; E-CD - EPOM on *Ceratophyllum demersum* L.; E-NG - EPOM on *Najas graminea* Delile; CR - *Coronatella rectangula*; PL - *Pleuroxus laevis*; CS - *Chydorus sphaericus*; IS - *Ilyocryptus spinifer*; MR - *Macrothrix rosea*; CV - *Cyclops vicinus*

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Table 2

Seasonal body size (μm) of epiphytic microcrustacean on macrophyte species at study site

Microcrustacean species	2011		2012	
	Spring	Autumn	Spring	Autumn
Coronatella rectangula	427.1±23.1	435.2±38.3	432.6±34.2	438.1±34.7
Pleuroxus laevis	436.7±26.9	441.5±31.4	445.2±36.3	448.4±43.8
Chydorus sphaericus	413.9±32.6	428.4±26.7	421.8±35.8	432.7±32.5
Ilyocryptus spinifer	594.4±36.3	621.2±34.8	602.7±38.9	638.4±42.6
Macrothrix rosea	587.5±42.5	643.7±38.6	598.3±32.2	624.8±43.4
Cyclops vicinus	1756.2±94.5	1784.5±118.7	1808.0±105.3	1817.7±114.5

Table 3

Seasonal mean abundance of major epiphytic algal groups collected from each macrophyte species (cells g^{-1} dw) at study site

Season (year)	Taxonomical groups	Emergent	Free-floating		Floating-leaved		Submerged		
		PA	SP	SN	TJ	HA	PC	CD	NG
Spring, (2011)	Chlorophyceae	32	144	-	47	-	90	-	-
	Bacillariaceae	66	243	-	63	-	309	-	-
	Cyanophyceae	18	122	-	33	-	31	-	-
	Euglenophyceae	-	86	-	19	-	18	-	-
	Chrysophyceae	19	56	-	5	-	19	-	-
	Synurophyceae	-	25	-	-	-	16	-	-
	Dinophyceae	19	38	-	19	-	47	-	-
	Total	143	714	-	187	-	528	-	-
Autumn (2011)	Chlorophyceae	59	348	379	138	74	-	156	106
	Bacillariaceae	67	472	724	178	113	-	199	274
	Cyanophyceae	26	106	102	214	53	-	49	27
	Euglenophyceae	29	48	56	50	47	-	79	21
	Chrysophyceae	29	45	47	36	36	-	52	10
	Synurophyceae	19	29	38	-	24	-	45	15
	Dinophyceae	33	31	39	-	31	-	33	83
	Total	263	1079	1263	617	378	-	614	535
Spring (2012)	Chlorophyceae	37	118	132	38	-	245	353	-
	Bacillariaceae	68	165	189	78	-	378	434	-
	Cyanophyceae	46	68	94	30	-	149	132	-
	Euglenophyceae	28	34	38	21	-	80	85	-
	Chrysophyceae	29	38	42	23	-	51	55	-
	Synurophyceae	27	59	68	27	-	45	43	-
	Dinophyceae	27	81	78	18	-	58	55	-
	Total	261	563	640	234	-	1006	1157	-
Autumn (2012)	Chlorophyceae	157	148	214	80	77	314	563	135
	Bacillariaceae	90	317	414	93	101	538	505	186
	Cyanophyceae	39	109	81	57	92	225	215	52
	Euglenophyceae	52	58	65	58	79	241	275	76
	Chrysophyceae	85	35	32	21	70	239	136	32
	Synurophyceae	43	46	50	46	48	178	152	38
	Dinophyceae	27	34	45	20	35	41	50	28
	Total	492	747	901	374	502	1776	1896	547

PA - *Phragmites australis* (Cav.) Trin.; SP - *Spirodela polyrhiza* (L.) Sch.; SN - *Salvinia natans* (L.) All.; TJ - *Trapa japonica* Flerow; HA - *Hydrocharis asiatica*; PC - *Potamogeton crispus* L.; CD - *Ceratophyllum demersum* L., NG - *Najas graminea* Delile

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Discussion

Distribution of epiphytic microcrustaceans

The present study indicates that the distribution of epiphytic microcrustaceans differs among macrophyte species. The seasonality in the growth of macrophyte species creates the seasonality in epiphytic microcrustaceans as a result of different preferences of epiphytic microcrustacean species for different morphological structures of each macrophyte species. Some studies reported that the interaction between macrophytes and microcrustacean assemblages are strongly associated with physical structures as part of the 'complexity' (Krecker 1939, Rosine 1955, Heck & Westone 1977). In general, morphology of macrophytes varies, thus microhabitat structure depends on species composition of macrophytes. Moreover, seasonal succession of macrophyte species largely contributes to the physical structure of the microhabitat of microcrustaceans in the water (Theel et al. 2008). Several research also reported that microcrustaceans showed high population growth during a period with extensive growth of macrophyte biomass (Kairesalo 1984, Downing & Cyr 1985, Stayer et al. 2003). In particular, the surface of leaves and stems of macrophytes determines the distribution pattern of epiphytic species. Choi et al. (2014c) suggested that the species composition and abundance of epiphytic microcrustaceans was clearly related to the macrophyte type (emergent, free-floating, floating-leaved, and submerged). Moreover, the composition of macrophyte species in a vegetated bed is important for the determination of the diversity of epiphytic microcrustaceans (Choi et al. 2014b). Such different distribution patterns of epiphytic microcrustaceans on macrophyte species were also confirmed in the present study. Epiphytic microcrustaceans were the most abundant on the surface of free-floating and submerged macrophytes, but they depended on seasonal abundance of the free-floating and submerged macrophytes. Interestingly, submerged macrophytes were less abundant than the free-floating macrophytes in 2011, but epiphytic microcrustaceans were abundant on the surface of both free-floating and submerged macrophytes. Some studies reported that submerged macrophytes enhance the physical complexity of an aquatic environment and provide habitat for colonization by aquatic animals (Lodge 1991, Newman 1991). Therefore, we conclude that submerged macrophytes can support high species diversity and abundance of microcrustacean communities (see Douglas & Lake 1994, Cooper et al. 1997, Cheruvelil et al. 2002).

The present study also demonstrated that the abundance of epiphytic microcrustaceans is higher on complex macrophyte species (e.g. free-floating and submerged) than on simple-structured macrophytes (e.g. emergent). This indicates that the increased abundance on complex macrophytes is not simply attributable to a 'sampling effect' (Dean & Connell 1987); it should be noted that such a sampling effect must also have occurred in the present study, as a larger number of microcrustacean individuals occurred on macrophytes with more complex structures. However, if the sampling effect was present, no difference in the number of individuals per plant species would have been expected between simple and complex habitats. Therefore, the present results further contribute to the argument that complex habitats contain higher structural heterogeneity (¼ qualitative differences) that could be exploited by different microcrustacean species. Thus, we expect that the diversity or heterogeneity of habitat space (i.e. qualitative character) is more important to epiphytic microcrustacean assemblages than the size of microhabitat space (i.e. quantitative character).

Influence of potential food sources on epiphytic microcrustaceans

Microhabitat structure provided by aquatic macrophytes has a direct impact on the food supply through detritus trapping (Rooke 1984) and the growth of epiphytic algae (Dudley 1988), consequently leading, in some cases, to distinct microcrustacean communities on different types and/or species of macrophytes (Minshall 1984, Rooke 1986). The surfaces of stems and leaves of macrophytes are known to provide suitable habitats for epiphytic algae (Cattaneo & Kalff 1979, Cattaneo et al. 1998), and the heterogeneity of the substrate surface is clearly different between macrophyte species. In the present study, we found a high density of epiphytic microcrustaceans on macrophyte species supporting high abundance of epiphytic

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algae. Although epiphytic microcrustaceans do not consume only epiphytic algae, this partly explains the effect of food quantity on epiphytic microcrustaceans as a factor of differential distribution of epiphytic microcrustaceans on macrophyte species. Algae are a food source for primary consumers such as zooplankton in aquatic ecosystems (Vollenweider et al. 1974, Brett & Goldman 1997), and they are important components in the freshwater food web. In general, freshwater ecosystems with abundant macrophytes provide better conditions for the development and the growth of epiphytic algae because of a larger habitat (i.e. substrate surface). These results, however, were not indicative of correlation between the species composition pattern of epiphytic algae and the macrophyte species. The only observed correlation was between the macrophyte species and the abundance of epiphytic algae; the latter were more abundant on the surface of free-floating macrophyte species (*Spirodela polyrhiza* and *Salvinia natans*) in 2011 and on submerged macrophyte species (*Potamogeton crispus*, *Ceratophyllum demersum*, and *N. graminea*) in 2012. This distribution pattern of epiphytic algae may have partly contributed to differential distribution of epiphytic microcrustacean on macrophyte species.

The stable isotope analysis indicated that EPOM contributed more to most of the epiphytic microcrustaceans species than SPOM. In particular, small epiphytic cladocerans (*C. rectangula*, *P. laevis*, and *C. sphaericus*) depended mainly on the EPOM attached to the free-floating and submerged macrophyte species during the study period. However, the contribution of EPOM to the epiphytic cladoceran community was determined by the abundance of free-floating and submerged macrophyte species. From the results of epiphytic algae abundance, we found higher algal abundance from free-floating and submerged macrophyte species than other plant species. Considering that epiphytic cladocerans are likely to use epiphytic algae as their food resources (Campeau et al. 1994, Sakuma et al. 2004) and higher dependence of epiphytic cladocerans on EPOM from the current study, it is expected that more abundant EPOM (possibly represented by epiphytic algae) might contribute to an increase in microcrustacean abundance on free-floating and submerged macrophytes. Similarly, Sakuma et al. (2004) also suggested that small cladocerans (i.e. *Coronatella*) select a food-rich plant surface and migrate with the seasonal change in the abundance of macrophyte species. Although we observed different seasonal distributions of epiphytic microcrustaceans between free-floating and submerged macrophyte species (in 2011), we did not record any migration of epiphytic microcrustaceans between macrophyte species. We assume that small epiphytic microcrustaceans preferred macrophyte species with a complex structure that provided abundant food sources. However, the relatively large epiphytic cladoceran species (*I. spinifer* and *M. rosea*) were associated only with EPOM from submerged macrophyte species during the study period. Moreover, larger cladoceran species are easily used by predators such as fish and, at the same time, they require larger amounts of food resources compared with small cladocerans, thereby they seem to require habitats with a complex structure such as those provided by submerged macrophytes (Hann & Turner 1999). In contrast to the epiphytic cladocerans, copepods (i.e. *C. vicinus*) do not depend solely on the epiphytic algae, and partly feed on epiphytic algae and on pelagic algae. The feeding pattern of *C. vicinus* shows "opportunistic life strategy", meaning that this species is using contemporarily available food for a population increase; dense algae blooms in spring used by nauplii to survive and complete larval development, and subsequently copepodites and adults are using zooplankton prey to reach the maturity and to produce eggs (Plaβmann et al. 1997, Brandl 1998). *C. vicinus* is a pelagic species, much less abundant in the littoral vegetation, and preys on zooplankton (selectively on rotifers; Yang et al. 1998).

Different from our expectation, composition of epiphytic algae group was similar between macrophyte species. Also, seasonality of epiphytic algae occurrence was not observed. The only difference was the abundance of epiphytic algae groups between macrophyte species. It appears from the results that the epiphytic microcrustacean distribution was more affected by the quantity than quality of epiphytic algae.

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Influence of non-point source pollution on macrophytes, algae, and microcrustaceans

In empirical studies, it is known that the massive growth of macrophytes in a wetland located in an agricultural area is determined by nutrient input coming from agricultural area (Comin et al. 1997, Kröger et al. 2007). The nutrients often enter the surface waters from diffuse or non-point sources associated with the surface runoff and from point sources typically associated with intense farming activities such as the production of livestock (Knight et al. 2000).

The Upo Wetlands are surrounded by agricultural landscape, and non-point source pollution from the land type continuously provide sources for development of aquatic macrophytes. Specifically, the abrupt nutrient loading takes place in the summer season (mainly late June to August), which results in an increased nutrient level in a water body (Park 1998). The maximum growth of aquatic macrophytes in the Upo Wetlands is typically observed in autumn (September to October; Kang et al. 2009, Choi et al. 2014a). Considering that the development of macrophytes contributes to the diversity and abundance increase of microcrustaceans in the wetland system, nutrient loading from the surrounding land cover would be one facilitating factor for both microhabitat and microcrustacean species. In his regard, we considered that the nutrient input is recognized as an important factor to support large abundance of algae and high diversity of epiphytic microcrustacean species in a wetland located in an agricultural area.

Conclusions

We suggested that the distribution of epiphytic microcrustaceans on macrophytes is determined not only by morphological structure of macrophyte species but also by the abundance of algae on macrophytes. The contemporaneous presence of different macrophyte species in freshwater wetlands could sustain the local diversity and density of epiphytic microcrustaceans. In particular, the free-floating and submerged macrophytes largely contribute to high density and a large number of species of epiphytic microcrustaceans. Furthermore, the consumption of epiphytic algae by epiphytic microcrustacean plays an important role in the freshwater food web. Materials from epiphytic algae are transported across food webs to epiphytic microcrustaceans (Schindler & Scheuerell 2002, Takai et al. 2002), and the trophic interactions can be interpreted as another route in freshwater food webs of wetlands with developed macrophytes. The presence of various interactions can contribute to the increased biodiversity in wetlands but also to a sustainable, ecologically healthy food web.

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