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RESEARCH PAPER

Composition of aquatic invertebrates associated with macrophytes in Lake Tonle Sap, Cambodia

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Abstract Faunal composition of aquatic invertebrate communities associated with submerged parts of several species of macrophytes were studied in different areas in littoral Lake Tonle Sap in Cambodia, with special reference to those in root systems (interrhizon) of a free-floating water hyacinth (*Eichhornia crassipes*). Nine phyla of invertebrates were collected, of which oligochaetes, shrimps and *Limnoperna* mussels were abundant along with meiobenthic crustaceans. The macrophyte-associated invertebrates in Lake Tonle Sap might be unique in having abundant sessile animals, such as sponges, bryozoans and *Limnoperna* mussels. The *Limnoperna* mussels attached to macrophytes were more abundant in offshore and inundated forest than in secluded vegetational stands toward the shoreline. It suggests that water movement can be an important factor determining the distribution and abundance of the sessile animals by controlling larval dispersions and might be associated with the hydrological characteristic of the lake, i.e., the lake opens to the large Mekong River with drastic seasonal changes in water level.

Keywords Lake Tonle Sap · Cambodia · Aquatic macrophytes · Invertebrates · Interrhizon · *Eichhornia crassipes*

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Introduction

It is widely recognized that macrophytes in freshwater play important roles in aquatic ecosystems. They offer many microhabitats for animals, where various kinds of invertebrates and vertebrates can live, hide, feed and oviposit, thereby creating diverse communities. Invertebrates associated with aquatic macrophytes are important natural food sources for fishes and other higher consumers.

Vast areas of wetlands are often covered with a number of aquatic macrophytes in tropical wet-and-dry climatic zone. Such areas have large water level fluctuations, as known for Amazonia (Sioli 1984), Pantanal wetland (Por 1995; Heckman 1998a) and Lake Tonle Sap basin (CNMC/NEDECO 1998a, b), with free-floating vegetation dominating there. The submerged parts of the floating vegetation construct a complicatedly intertwined root and rhizome system, making a special biotope harboring diverse aquatic organisms, sessile algae, zoo- and phytoplankton, invertebrates including many species of insect larvae, mollusks, crustaceans, and juvenile and adult fishes (Dioni 1967;

Junk 1973; Junk and Howard-Williams 1984; Heckman 1998a, b). Heckman (1994) termed such a community "interrhizon" and recognized its biological and ecological importance in tropical freshwaters, especially in wet-and-dry climatic zones. In addition to providing diverse habitats for invertebrates, the submerged rhizoid systems can supply oxygen in water around the roots (e.g., Armstrong and Armstrong 1990) and retain detritus (Poi de Neiff et al. 1994). They could serve as suitable habitats for many invertebrates in terms of better oxygen conditions, and a rich food or a safely shelter. Heckman (1994) pointed out that free-floating plants sometimes develop also in cooler temperate zones, but the interrhizon is poor and plays a minor role in the ecology of the water bodies there. Junk (1977), Gopal (1987), Heckman (1994, 1997, 1998a, b), Poi de Neiff and Carignan (1997), Uenishi et al. (2005, 2006), Ohtaka et al. (2006) and others listed many species of plants and animals as members of interrhizon communities from various parts of tropical zones.

It is expected that invertebrate communities associated with aquatic macrophytes, especially interrhizon, develop in Lake Tonle Sap, and they might be unique for the region. However, such a community has been poorly explored there. Therefore, to clarify the faunal characteristics, the composition and abundance of invertebrates were studied in submerged parts of several macrophytes, especially *Eichhornia crassipes*, as a part of comprehensive scientific research on the lake carried out in 2003–2005.

Study sites and methods

Lake Tonle Sap is the largest inland lake in Southeast Asia, and is also characterized by drastic changes in water level (annually ca. 8 m) caused by changes in the hydrological balance between the dry (November–April) and rainy (May–October) seasons. The whole waterlogged area reaches ca. 9000–14000 km^2 at the peak period of flooding, which is approximately four times as large as that in the lowest water season (CNMC/NEDECO 1998a, b). A vast area of inundated forest and floating vegetation appears in the flood plain during high-water seasons.

To clarify the structure of macrophyte-associated communities, aquatic invertebrates were collected from several species of macrophytes on 5–11 November 2003, when the vegetational assemblage in the lake was characterized by free-floating plants and floating-emergent plants (Hirabuki et al. 2009). (1) Two submerged plants, *Hydrilla verticillata* (Hydrocharitaceae) and *Utricularia aurea* (Lentibulariaceae), (2) underwater roots of two free-floating plants, *Eichhornia crassipes* (Pontederiaceae) and *Salvinia cucullata* (Salviniaceae), and (3) underwater stems and roots of floating forms in two primarily emergent plants,

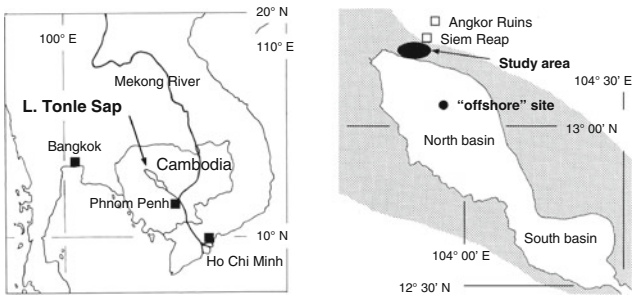

Fig. 1 Location of Lake Tonle Sap on the Indo-Chinese peninsula (*left*), and a map of the lake showing the location of study site and area (*right*). "Study area" in the right map covers all the vegetational stands studied except for the "offshore" site. *The shoreline* of the lake indicates those in the low-water level season, and *the shaded area* indicates floodplain in the high-water season

Monochoria hastata (Pontederiaceae) and *Polygonum tomentosum* (Polygonaceae), were studied as invertebrate habitats. Among them, the *Eichhornia* was studied offshore in the north basin of the lake (13°03′34.5″N, 103°55′19.8″E, 7.0 m deep; Fig. 2, top), inundated forest (13°14′N, 103°48–49′E, 2.7–5.1 m deep) and flooded areas in Chong Khnies and Phnom Krom off Siem Reap (13°13–16′N, 103°43–49′E, 0.5–3.6 m deep) (Fig. 1). Other macrophytes were studied at the inundated forest and the flooded area mentioned above, respectively. Collecting of invertebrates was made in the daytime. Submerged parts of the aquatic plants mentioned above were removed in water and washed with lake water in a bucket on the boat. Then released invertebrates were recovered by sieving with a dip net with a mesh of 0.1 mm. The invertebrates collected were fixed immediately in 5–10% formalin solutions, identified mostly into phylum to family levels and counted under a stereomicroscope in laboratory. Extension areas of roots studied were measured for *Eichhornia*, *Monochoria* and *Salvinia*, and total shoot lengths studied were measured for *Hydrilla*, *Polygonum* and *Utricularia*. Sponges, bryozoans and other sessile animals often attached onto the macrophytes, but they were not studied quantitatively in the present survey except for a mussel, *Limnoperna* sp. Shell length of the *Limnoperna* sp. attached to *Eichhornia* in the inundated forest was randomly measured for 51 specimens.

To clarify the differences in plant structure and composition and standing crop of interrhizon macroinvertebrates between locations in the lake, two *Eichhornia* stands, both in northeastern Lake Tonle Sap off Siem Reap, were studied in the daytime on 5–6 December 2005 when the water level was still high. One of the *Eichhornia* stands was located at the canal in Chong Khnies ("Canal", 13°14′39.1″N, 103°49′19.4″E, 2.5 m deep), and another stand was located near the offshore-side margin of inundated forest off Chong Khnies ("Inundated forest,"

Fig. 2 Study site scenes in Lake Tonle Sap for *Eichhornia* survey. *Top* offshore lake in November 2003, showing drifting individuals; *bottom left* vegetation in the "Canal" stand; *bottom right* those in the "Inundated forest" stand

13°14′59.6″N, 103°45′17.0″E, 3.5 m deep) (Fig. 1). The "Canal" stand was mostly composed of *Eichhornia* alone, while in the "Inundated forest" stand, the *Eichhornia* was intermingled with *Polygonum* (Fig. 2, bottom).

To collect the interrhizon macroinvertebrates, three individuals of the *Eichhornia* were scooped at each stand by means of a screen with 0.5 mm mesh. The *Eichhornia* collected was carefully washed in the bucket, and the invertebrates released were recovered by sieving with the screen mentioned above. *Limnoperna* sp. attached to the *Eichhornia* roots were carefully removed and included in the animal sample. Meiobentic invertebrates, for example, copepods and cladocerans, and colonial sessile animals, bryozoans and sponges were not studied quantitatively in this survey. The macroinvertebrate samples were identified into higher taxonomic levels and counted under a stereomicroscope in the laboratory. Oligochaetes collected were examined specifically for wholly mounted specimens on slides in Canada balsam after being dehydrated in a graded series of ethanol and water solutions, and then cleared in methyl salicylate. In this article, the naidine genus *Pristinella* Brinkhurst is merged into the genus *Pristina* Ehrenberg, according to Collado and Schmelz (2000), and *Dero* and *Aulophorus* are regarded as independent genera. After removing the interrhizon animals, the root system of each *Eichhornia* individual collected was measured for the extension and weighed for the fresh weight using a spring balance. In addition, to clarify the plant body structure, 8 (Canal) and 21 (Inundated forest) individuals of *Eichhornia* were collected at each stand, and their lengths and fresh weights were measured for the aerial and submerged parts. Temperature (TOA CP14P) and pH (Narika α-Pack Test) were measured for surface water at each study site. The significance of differences in environmental and faunal parameters was tested by ANOVA.

Detailed faunal compositions of the invertebrate specimens collected in the present study have been studied by many specialists in different taxonomic groups, and a part of the results have been published independently for sponges (Masuda 2004), turbellarians (Kawakatsu and Ohtaka 2007), clam shrimps (Martin et al. 2003), cladocerans (Tanaka and Ohtaka 2010), copepods (Ishida and Tomikawa 2007), isopods (Nunomura 2006), trichopterans (Malicky 2006; Ito and Kuhara 2007) and bryozoans (Hirose and Mawatari 2007). A part of the identified specimens have been deposited at the Division of Biological Science, Graduate School of Science, Hokkaido University (ZIHU).

Results

Aquatic invertebrate communities in different vegetational stands in the 2003 survey

Temperature and pH of the surface water in the study sites in the 2003 survey ranged from 30.7 to 31.8°C and from 7.1 to 8.5, respectively.

Twenty-four taxonomic groups belonging to eight phyla of invertebrates were collected in the samples (Table 1). Although composition and abundance of the invertebrates were different between macrophyte species and localities, cladocerans, copepods, ostracods, nematodes and oligochaetes occurred in all macrophyte samples examined in large numbers. Acari, chironomids and hemipterans were the next most common, found from all but one each of the macrophyte stands examined. On the other hand, hydrids, gastropods, conchostracans and natantians were collected in restricted samples, though they are often represented by rather large numbers of specimens. In the inshore zone of littoral Lake Tonle Sap, *Utricularia* tended to harbor larger numbers of invertebrates than other macrophyte species.

Eichhornia crassipes was the most common macrophyte species in the area studied, being distributed not only in the littoral zone but also offshore as drifting individuals. *Eichhornia* harbored more shrimps than other macrophyte species. Interestingly, abundance and composition of invertebrates differed between localities in *Eichhornia*-associated communities. In macrofauna, offshore *Eichhornia* harbored more decapods but fewer oligochaetes than those in inundated forest and inshore zones (Fig. 3). A few to several individuals of crabs were found in every drifting *Eichhornia* individual offshore. A mussel, *Limnoperna* sp. (Mytilidae), was also more common offshore and in inundated forest than in the inshore zone. The *Limnoperna* mussels on the *Eichhornia* roots were variable in size; the shell length ranged from 1.9 to 12.7 mm with an

Table 1 Densities of meio- and macroinvertebrates associated with aquatic macrophytes in Tonle Sap in November 2003

Area:	OTS	OTS	ITS	ITS	ITS	LTS	LTS	LTS	LTS	LTS	LTS	ITS	LTS
Substrate:	EC	EC	EC	EC	EC	EC	MH	SC	UA	UA	UA	PT	HV
Unit of substrate:	100 cm^2	100 cm^2	100 cm^2	100 cm^2	100 cm^2	100 cm^2	100 cm^2	100 cm^2	100 cm	100 cm	100 cm	100 cm	100 cm
Hydridae	13	8	67	3	49	4	0	0	0	0	0	1	1
Turbellaria	4	1	0	0	11	5	2	1	1	0	1	0	0
Nematoda	9	2	8	39	5	18	26	22	53	6	4	3	18
Limnoperna sp.	1	1	3	0	1	0	0	0	0	0	0	0	0
Gastropoda	9	7	18	0	0	5	18	2	0	0	0	0	2
Oligochaeta	4	3	30	276	22	101	70	69	293	212	49	35	17
Hirudinea	0	1	0	0	0	3	1	0	0	0	2	0	0
Acarina	1	5	50	109	26	76	29	15	95	15	0	1	2
Cladocera	9	9	53	385	86	182	62	45	425	1090	428	20	76
Conchostraca	0	0	0	12	2	40	0	0	24	0	2	0	0
Copepoda	18	13	75	176	103	143	189	144	177	221	107	11	309
Ostracoda	27	29	67	644	49	47	107	4	51	15	74	26	33
Natantia	12	41	20	5	23	3	0	0	1	0	0	0	0
Brachyura	1	1	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	2	8	0	7	0	26	0	0	3	2	0	0	1
Odonata	0	1	1	1	1	1	0	0	0	0	0	0	1
Hemiptera	0	8	2	4	1	6	9	1	17	9	4	3	5
Trichoptera	0	0	0	0	0	0	0	0	0	0	0	1	0
Coleoptera	2	13	2	6	0	1	14	2	1	0	0	0	1
Chironomidae	10	7	5	47	5	74	6	9	51	10	0	7	15
Culicidae	0	0	0	0	0	0	0	1	0	0	0	0	0
Ceratopogonidae	0	0	0	0	0	0	0	1	0	0	0	0	0
Total	122	159	400	1715	382	734	533	316	1194	1580	671	108	479

Sponges and bryozoans also occurred, but they were excluded from the list

Area: OTS, offshore in Lake Tonle Sap; ITS, inundated forest in littoral Lake Tonle Sap; LTS, inshore zone of littoral Lake Tonle Sap, excluding inundated forest

Substrate: HV, *Hydrilla verticillata*; UA, *Utricularia aurea*; EC, *Eichhornia crassipes*; SC, *Salvinia cucullata*; MH, *Monochoria hastata*; PT, *Polygonum tomentosum*

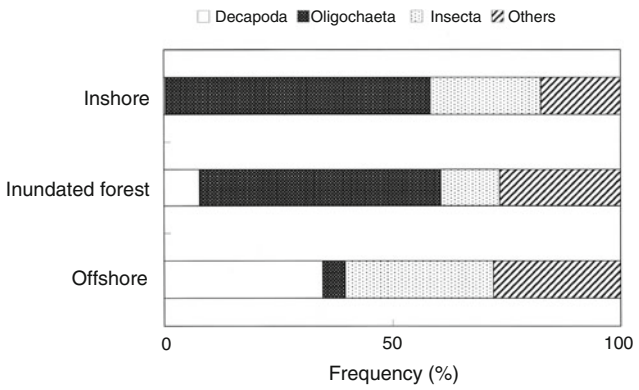

Fig. 3 Relative abundance of macroinvertebrates associated with *Eichhornia crassipes* roots in three different zones of northeastern Lake Tonle Sap in November 2003. Mean values are shown for each zone

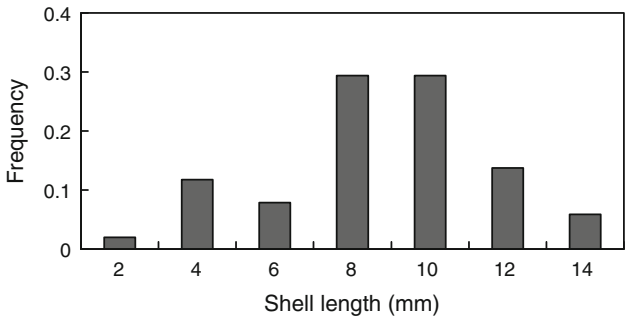

Fig. 4 Frequency distribution in shell length of a mussel, *Limnoperna* sp., on *Eichhornia* roots in Lake Tonle Sap in November 2003. Fifty-one specimens from inundated forest were pooled

average of 7.9 mm (Fig. 4). As for meiofauna, cladocerans, copepods, ostracods and acari were less abundant in offshore *Eichhornia* than in inundated and inshore areas.

Table 2 Body structures of *Eichhornia crassipes* at the Inundated forest and Canal stands in December 2005

	Inundated forest ($N = 21$)	Canal ($N = 8$)
Length (cm)		
Aerial part	46.9 ± 14.5 (18–68)	85.8 ± 8.4 (68–95)
Submerged part	36.1 ± 10.3 (16–55)	68.8 ± 9.7 (53–86)
Fresh weight (g)		
Aerial part	170.2 ± 89.7 (30–375)	424.4 ± 152.5 (220–710)
Submerged part	186.7 ± 99.2 (20–410)	300.6 ± 100.7 (150–480)
Total	356.9 ± 180.3 (50–758)	725.0 ± 250.4 (370–1190)
A/S ratio	0.97 ± 0.34 (0.39–1.61)	1.41 ± 0.17 (1.25–1.76)

Mean ± SD and (range) is shown

In the other five macrophyte species, oligochaetes always dominated among macrofauna, along with many cladocerans and copepods for meiofauna. The oligochaete assemblages consisted of multiple species, being mostly represented by naidines.

"Interrhizon" invertebrates in *Eichhornia crassipes* in the 2005 survey

In the 2005 survey, the surface water temperature in the *Eichhornia*-dominant vegetations at the "Canal" and the "Inundated forest" were 28.4 and 29.3–30.5°C, and surface pHs were 6.6 and 6.9–7.3, respectively. Individual plants of the *Eichhornia* were more developed in the "Canal" than in the "Inundated forest," and the aerial and submerged parts and whole plant body were significantly longer and heavier in the "Canal" stand than in the "Inundated forest" one ($P < 0.001$; except for weight of the submerged part, $0.01 < P < 0.05$) (Table 2). The weight ratio of the aerial/submerged part of the plant was 0.97 in the "Inundated forest" stand, being significantly lower than in the "Canal" stand in which the ratio was 1.41 ($0.01 < P < 0.001$). Detrital particles or attached algae retained on the *Eichhornia* roots were less conspicuous in both vegetational stands, while many small mussels and sponge colonies were attached to the root systems (Fig. 5).

Fifteen taxonomic groups belonging to seven phyla of interrhizon macroinvertebrates were found in the *Eichhornia* roots studied (Table 3). Among them, nemerteans, hirudineans, acari and coleopterans were not collected in the "Inundated forest" stand, while trichopterans were not found in the "Canal" stand. Oligochaetes were the most dominant invertebrates in the "Canal" stand, followed by shrimps in density, while bivalves, which was composed of *Limnoperna* mussels alone, dominated in the "Inundated forest" stand. Average values of the total density and total fresh weight of macroinvertebrates per 1000 g *Eichhornia* roots were 534.4 and 2.87 g in the "Canal" stand, and 467.9 and 7.13 g in the "Inundated forest" stand, respectively, and no significant difference was detected between two stands both in density and standing crop. On the other hand, density of the *Limnoperna* mussels was significantly higher in the "Inundated forest" stand than in the "Canal" one ($P < 0.05$). In addition, although statistical differences were not detected, the average density of oligochaetes was more than twice higher in the "Canal" stand, while the average density was more than twice higher, and average fresh weight was about ten times higher in the "Inundated forest" stand for shrimps.

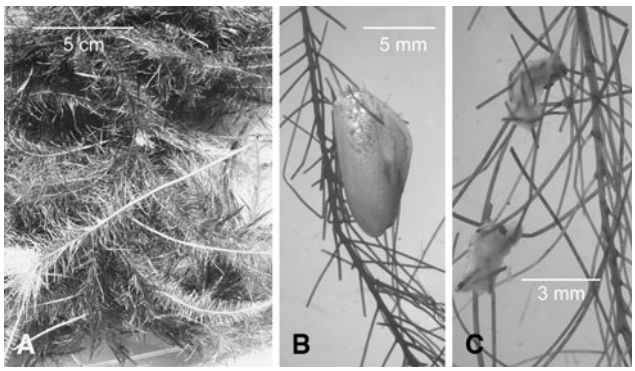

Fig. 5 *Eichhornia crassipes* roots (**a**) and the attached mussel, *Limnoperna* sp. (**b**) and sponge colonies (**c**) from the "Inundated forest" stand of Lake Tonle Sap in December 2005

More than eight genera all belonging to the family Naididae were found in the interrhizon oligochaetes. The oligochaete composition was not very different between the two stands. In both stands, *Stylaria fossularis* dominated in number, accounting for more than half of the oligochaetes in both stands (Fig. 6).

Discussion

Nine phyla of invertebrates belonging to Porifera, Cnidaria, Platyhelminthes, Nemertea, Nematoda, Mollusca, Annelida, Bryozoa and Arthropoda were found in this study. According to Ohtaka et al. (2006), structures of aquatic invertebrate fauna associated with aquatic macrophytes were different between Central Kalimantan and West Java. Compared at higher taxonomic groups in their study, the faunal composition in the present macrophyte-associated

Table 3 Density and standing crop of interrhizon macroinvertebrates in the *Eichhornia crassipes* root system in two littoral sites of northwestern Lake Tonle Sap in December 2005

Taxon	Canal ($N = 3$)		Inundated forest ($N = 3$)	
	Density	Standing crop (g fresh wt.)	Density	Standing crop (g fresh wt.)
Porifera	+	ND	+	ND
Turbellaria	1.4 ± 2.4	tr	1.8 ± 1.6	tr
Nemertea	4.7 ± 3.2	0.003 ± 0.005	0	0
Gastropoda	18.7 ± 9.1	0.006 ± 0.002	15.2 ± 11.7	0.005 ± 0.005
Bivalvia	5.2 ± 6.5	0.024 ± 0.034	207.3 ± 98.9	1.926 ± 1.947
Oligochaeta	415.8 ± 183.2	0.008 ± 0.004	127.3 ± 80.8	0.001 ± 0.001
Hirudinea	5.6 ± 9.6	0.013 ± 0.022	0	0
Bryozoa	+	ND	+	ND
Acarina	9.3 ± 0.9	0	0	0
Brachyura	0.8 ± 1.5	2.016 ± 3.492	0.6 ± 1.5	0.645 ± 1.117
Natantia	42.3 ± 19.9	0.449 ± 0.193	93.6 ± 64.3	4.447 ± 2.930
Odonata	5.8 ± 3.8	0.334 ± 0.431	3.5 ± 2.4	0.095 ± 0.073
Coleoptera	2.5 ± 4.4	0.008 ± 0.013	0	0
Trichoptera	0	0	1.7 ± 2.1	0.004 ± 0.007
Diptera	22.3 ± 8.7	0.009 ± 0.012	16.7 ± 14.1	0.003 ± 0.002
Total	534.4 ± 192.7	2.870 ± 4.079	467.9 ± 258	7.127 ± 2.062

Average ± SD per 1000 g fresh weight of substrate *Eichhornia* roots is shown

ND no data

macroinvertebrate assemblages in Lake Tonle Sap resembles those in West Java more than those in Central Kalimantan, in that shrimps, ostracods and conchostracans constituted larger proportions, while chironomids occurred in low proportions. The pH of the lake waters in the present study sites of Tonle Sap (6.6–8.5) was not so acidic as those in Central Kalimantan (2.9–4.5), but as high as or a little higher than those in West Java (6.5–7.2), and this fact suggests that water acidity can have an effect on invertebrate composition.

Oligochaetes are common members of the macrophyte-associated communities. It has been recognized that many naidine species show wide distributions, probably due to their opportunistic strategy of asexual reproduction as the normal case (Erséus and Grimm 1998), although several genera, for example, *Dero*, *Aulophorus* and *Branchiodrilus*, have an equatorial bias to their distribution (Pinder and Ohtaka 2004). It is suggested that generic or species composition in tropical freshwater naidines could depend not largely on geographical difference, but rather on environments in their habitats. It has been shown that *Dero* and/or *Aulophorus* was the most common among macrophyte-associated oligochaete communities in tropical India (Naidu et al. 1981) and Paraguay (Poi de Neiff and Carignan 1997). They were common in the present study, too; however, in Lake Tonle Sap another naidine species, *Stylaria fossularis*, surpassed others among oligochaete communities. The predominant occurrence of *Stylaria*

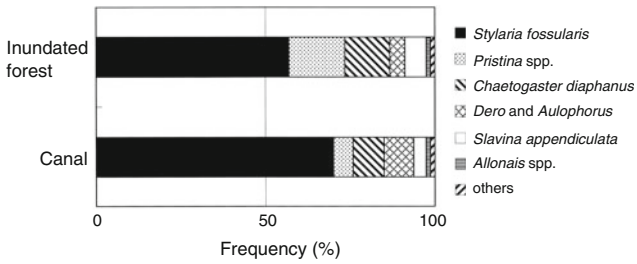

Fig. 6 Relative abundances of interrhizon oligochaetes in *Eichhornia crassipes* roots at the "Inundated forest" and "Canal" stands of northeastern Lake Tonle Sap in December 2005

fossularis was also encountered in neutral waters in Java (Ohtaka et al. 2006) and might be a unique feature of tropical southeast Asia. In the acidic peat swamp area of Central Kalimantan, *Pristina* became diverse and the most dominant of the oligochaete representatives in macrophyte-associated communities (Ohtaka et al. 2006).

It is worth noting that in Lake Tonle Sap, three groups of sessile animals (sponges, bryozoans and mussels) were common and abundant as members of invertebrates associated with macrophytes. All of them have never been recorded as macrophyte-associated forms from Java or Central Kalimantan (Ohtaka et al. 2006; Uenishi et al. 2005, 2006), and they were also not referred to in the series of studies conducted in South America cited above. The present study also showed that the *Limnoperna* mussels attached onto macrophytes were more abundant in offshore

and inundated forest than in secluded vegetational stands toward the shoreline. In addition, the *Limnoperna* shells attached to the *Eichhornia* roots were small and variable in size. These facts suggest that water movement might be an important factor determining the distribution and abundance of the sessile animals by affecting larval dispersions. The abundant occurrences of sessile animals with planktonic larvae in Lake Tonle Sap could also be attributable to the hydrological characteristic of the lake, i.e., the lake opens to the large Mekong River.

Eichhornia crassipes and *Salvinia molesta* are considered the most troublesome aquatic weeds in the world (Holm et al. 1977). In tropical Southeast Asia, the weeds form dense vegetation at the surface of various wetlands (Gopal 1987; Pieterse and Murphy 1989). Due to their rapid growth and large biomasses covering water surfaces, many harmful effects including excess evaporation, restricting water flow, physical interference for navigation, mechanical damage to hydro-electric installations and ecological changes of the water body, etc., have been pointed out (Widjaja and Wardianto 2004). On the other hand, from the view of a "cradle" for variable kinds of interrhizon biota, the floating meadows can be important for biodiversity. The complex rhizoid systems of macrophytes must serve as a shelter against many predators for juvenile fish (Junk 1984; Araujo-Lima et al. 1986; Petry et al. 2003) and small *Macrobrachium* prawns (Collart and Moreira 1993). The present study showed that decapods, including shrimps, prawns and crabs, occurred more abundantly in offshore *Eichhornia* than those in littoral areas. It suggests that the drifting plants offer rare but suitable habitats or shelters for the nektonic animals offshore of the lake, just like drifting seaweeds in marine environments, and they are important from the fisheries standpoint.

Although it is believed that the submerged rhizoid systems can provide food, oxygen and concealment for many animals inhabiting there, the environmental characteristics have not been fully understood yet. Poi de Neiff et al. (1994) reported that *Eichhornia* retained a large amount of organic and inorganic matter on the root system, which can supply food items for interrhizon animals and nutrients for *Eichhornia* themselves. In addition, floating macrophytes can supply oxygen in water around the roots and change the habitats more preferable for animals, because some macrophytes can transport atmospheric oxygen or oxygen produced by photosynthesis to the roots through the aerenchyme tissues (Armstrong and Armstrong 1990; Colmer 2003; Hirota and Tsuchiya 2003). Jedick et al. (1989) experimentally demonstrated that *Eichhornia crassipes* and *Pistia stratiotes* supplied O_2 to water beneath their stands, and Moorhead and Reddy (1988) suggested the possibility to release oxygen into water from macrophytes under experimental conditions for *Eichhornia crassipes*. In the present study, we did not measure environmental parameters except for water temperature and pH, and the environmental characteristics in Lake Tonle Sap remain unclear. Further studies regarding prey-predator relationships among organisms as well as physical and chemical characteristics in submerged systems of aquatic macrophytes are needed to clarify the comprehensive view of the distinct and important system. On the other hand, aquatic vegetation changes drastically in Lake Tonle Sap in accordance with the remarkable seasonal fluctuation of water level. Thus, it is also interesting how the diverse invertebrate communities develop in the flooded season and how they change toward disappearance of macrophytes in dry season.

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