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Seasonal changes of submerged macrophyte community with different depth profile in a calm bay of Lake Biwa, Japan

Akihisa HATTORI

Faculty of Liberal Arts and Education, Shiga University, 2-5-1 Hiratsu, Otsu, Shiga 520-0862, Japan

服部昭尚：琵琶湖の穏やかな湾内における水深構造の違いと沈水植物群落の季節変化
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滋賀大学教育学部　〒520-0862　大津市平津2-5-1

Abstract: The structure of a submerged macrophyte community (vegetation cover, species richness and species composition) and the seasonal changes were investigated at the littoral zone (< 6 m deep) of a calm bay in Northern Basin of Lake Biwa, Japan, where the transparency is high and no waterfowl grazers exist. To evaluate the effect of a small difference in depth profile on the community structure, the vegetation map of 35 m-belt transect (4 m wide) was made monthly at two sites (30 m apart) between March and November 1997. In total, the same 11 species were observed in the two sites, including two alien species, *Egeria densa* and *Elodea nuttallii*, and an endemic species, *Vallisneria biwaensis*. There was no significant difference in species richness in a census between the two sites. The species zonation was unclear in both sites: various mixed species patches were found throughout the study period. There were differences in the growth patterns of five species between the two sites. In a calm and clear-water littoral zone, where there is no disturbance by wave action, a small difference in depth profile can affect the growth patterns of several macrophyte species and then affect the three-dimensional structure of the macrophyte community, which can be a crucial determinant of the habitat structure of small aquatic animals.

Key words: depth profile, growth pattern, Lake Biwa, seasonal change, submerged macrophyte

Introduction

Submerged macrophyte communities play an important role in ecosystem dynamics in lakes and ponds (Hutchinson 1975; Scheffer et al. 2001; Strand & Weisner 2001; Kalff 2002), where the structure of a submerged macrophyte community (vegetation cover or abundance, species richness and species composition) usually varies in the littoral types (Bernatowicz & Zachwieja 1966; Hutchinson 1975). Especially in a large lake, the structure of a submerged macrophyte community varies within the lake depending on the local littoral type, which involves depth profile (Duarte & Kalff 1986, 1990; Kalff 2002; Riis & Hawes 2003). Several authors have suggested that wave exposure is a crucial determinant of the structure of a submerged macrophyte community: shore slope angle or depth profile, a correlate of wave action, is often a good predictor for littoral macrophyte biomass (Duarte & Kalff 1986, 1990; Duarte et al. 1986; Kalff 2002; Riis & Hawes 2003). Furthermore, shore slope angle or depth profile may affect the seasonal changes of the community structure, because individual species of submerged macrophytes usually have a preferred water depth for growing (Kalff 2002).

Lake Biwa is an ancient tectonic freshwater lake, largest

Recived 19 August 2003; Accepted 25 March 2004
e-mail: *hattori@sue.shiga-u.ac.jp*

in Japan (surface area = 674.4 km^2, maximum depth = 104 m): it consists of large and deep Northern Basin (surface area = 617.6 km^2, average depth = 45.5 m, clear-water state) and small and shallow Southern Basin (surface area = 56.8 km^2, average depth = 3.5 m, turbid-water state). The lake has a unique ecosystem with many endemic species, which partially depends on a variety of littoral type: sandy beaches, rocky reefs and calm bays with wetlands and so on (Hamabata 1991a; Research Group for Natural History of Lake Biwa 1994). The structure of a local community of submerged macrophytes is strongly influenced by wave exposure, bottom characteristics and water transparency (Hamabata 1991b; Imamoto et al. 1998). While the community structure of submerged macrophytes in relation to the littoral types has been studied in a spatially large scale (Hamabata 1991b; Imamoto et al. 1998), little information is available on the seasonal changes of the structure of a local community, especially in a calm littoral zone where wave action is weak. Although the general growth patterns of individual species in Lake Biwa are known (Ikushima 1966), the exact growth patterns of individual species in a local community have not been examined.

In Lake Biwa, for last decades, reclamation has been carried out in many parts of the littoral zone (Research Group for Natural History of Lake Biwa 1994; Kawanabe et al. 1999). Reclamation directly reduces emergent and submerged macrophytes. Furthermore, it often involves the disappearance of shallows and then changes the depth profile of littoral zone. Since individual submerged macrophyte species usually have a preferred water depth for growing, their community structure and the seasonal changes might be greatly influenced by the modification of depth profile. For example, an alien species, *Elodea nuttallii*, might predominate after the disappearance of shallows that is caused by the reclamation of shallow littoral zone. This is because *E. nuttallii* prefers deep zones to shallow zones, especially in a place of high water transparency (Hamabata 1991b, 1997). No information is available on the effect of depth profile on the growth patterns of individual species and species composition.

Macrophytes in littoral zones usually play an important role in animal community structure (Mitsch & Gosselink 2000; Strand & Weisner 2001). For instance, emergent macrophytes are important elements of shore landscapes usually providing habitats for many waterfowl and waterbirds, and the modification of a shore landscape often means the destruction of their natural habitats (Mitsch & Gosselink 2000; Hattori & Mae 2001). Submerged macrophytes also provide habitats or refuges for small aquatic animals such as fish and crustacean larvae (Strand & Weisner 2001). If the modification of depth profile changes the growth patterns of individual species of submerged macrophytes, it will involve the change of the three-dimensional structure of their community. Accordingly, the modified depth profile of the littoral zone may change the habitats of small aquatic animals. In order to conserve natural habitats of small aquatic animals, we should know the relationship between depth profile in the littoral zone and the seasonal changes of the structure of submerged macrophyte community.

To know the seasonal changes of the structure of a submerged macrophyte community in relation to depth profile, I described vegetation cover, species richness, and the growth patterns of individual species in two sites with different depth profiles in a local community in a calm and clear-water littoral zone of Northern Basin of Lake Biwa.

Study sites and methods

The field study on a local submerged macrophyte community was conducted in a calm littoral zone of Okude Bay (35°28'47"N; 136°08'05"E. Fig. 1), Northern Basin of Lake Biwa, Japan. In order to describe the structure of the community in relation to depth profile, a 35 m-transect line was set out from the shore to offshore at two sites with different depth profiles (the site A had a sigmoid profile and the site B had a gentle slope, 30 m apart, Fig. 1 & 2), and visual censuses were carried out monthly along each line. To minimize the effects of local differences in bottom sediment characteristics, water quality and waterfowl grazing on the community, I selected closely located two sites with small difference in depth profile at a place where no water discharges within 400 m (Fig. 1) and no waterfowl grazers exist.

To describe the depth profile of each site, water depth was measured by a digital depth meter (Seiko Air Diver's 200 m) every 5 m along the lines in May 1997 (Fig. 2). The maximum depth difference in a same zone of the tran-

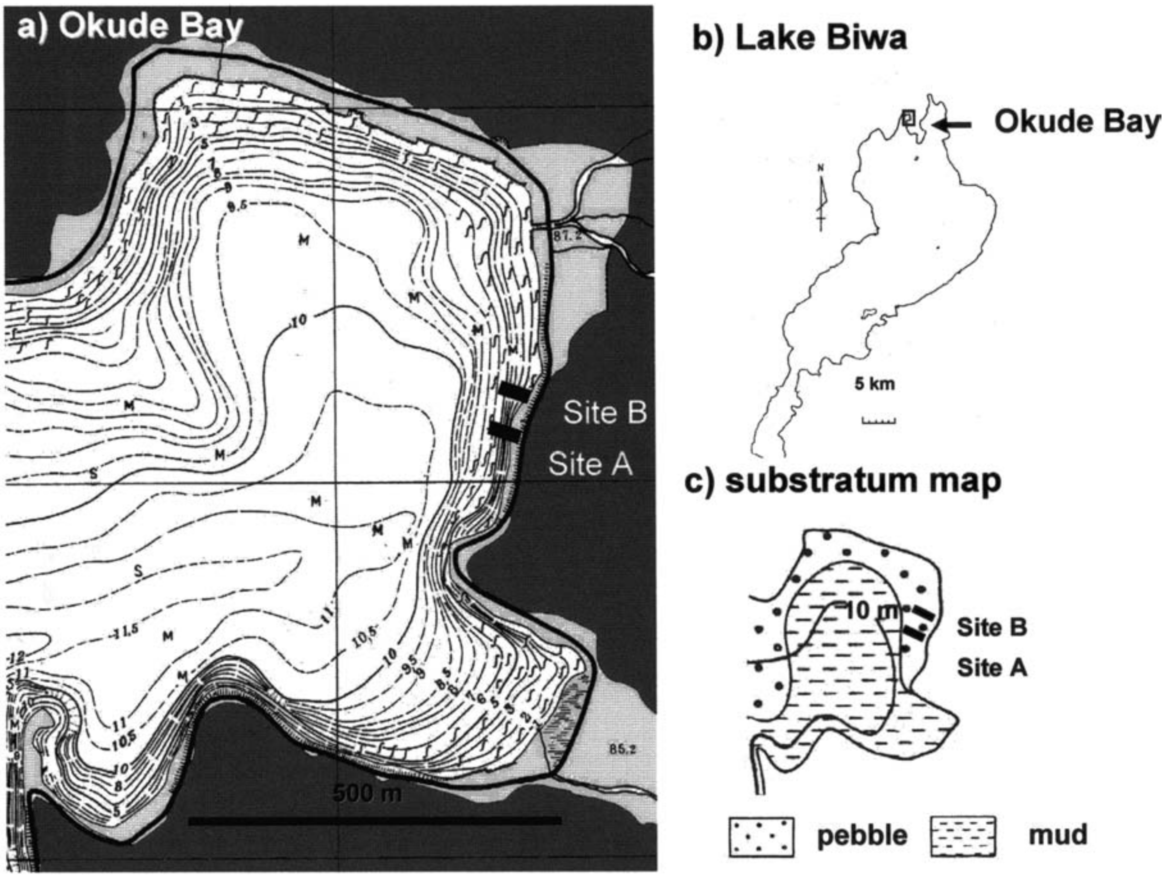


Fig. 1. Lake chart around the present study sites. (a) Locations of the study sites A and B and the modified lake chart of Okude Bay (original chart: 1/10000, Lake Chart, Biwako2-2, Shiozuwan 1, 1961-1962, Geographical Survey Institute, Ministry of Land, Infrastructure and Transport, Japan). The unshaded area, the light shaded area and the darker shaded area is the water surface, a plain and a mountain, respectively. A curved black line indicates a road. M. S and *S* means mud, sand and submerged macrophytes, respectively. Seventeen contours indicate the depth form 1 m to 12.5 m. (b) Location of Okude Bay in Lake Biwa. (c) Substratum map of Okude bay, which is in the original chart (1/10000, Lake Chart, Biwako2-2, Shiozuwan 1, 1961-1962, Geographical Survey Institute). Pebble in this chart means pebble with sediments such as sand or mud.

sect lines between the two sites was 1.3 m in 10 m offshore point, but the maximum depth difference in well-vegetated zone (> 2 m deep) was less than 0.8 m. There was no significant difference in average water depth between the two sites (the site A, 3.08 m ± 2.17 SD, max = 5.90 m; the site B, 3.00 m ± 1.67 SD, max = 5.10 m; t-test, $ts = 0.09$, $p > 0.05$). There was no large difference in the bottom sediment between the two sites (Fig. 1): pebble (> 2 mm) with sand in the shallow zone and mud (< 0.1 mm) in the deep zone. The water level of Lake Biwa has been artificially and daily regulated to be around Lake Biwa Standard Level (BSL, 84.371 m above sea level) since 1905, and it has been daily recorded by Shiga Prefecture. The water level was +0.25 m BSL at the beginning of the present study period. It decreased to −0.30 m BSL by September 1997, kept between −0.4 m and −0.2 m until October 1997, and decreased to −0.65 m in November 1997 http://www.lbri.go.jp/DataBank/w_level/display-j.htm (25 March 2004). The fluctuation in the present study period was within 0.9 m.

The censuses were conducted underwater with the aid of SCUBA from May to November 1997 at the two sites, where submerged macrophytes are usually abundant in the zone of 5-30 m (2-5 m deep) and no macrophytes were found in 60 m offshore (> 7 m deep) (Hattori 1997). In the present study sites, visual water transparency was

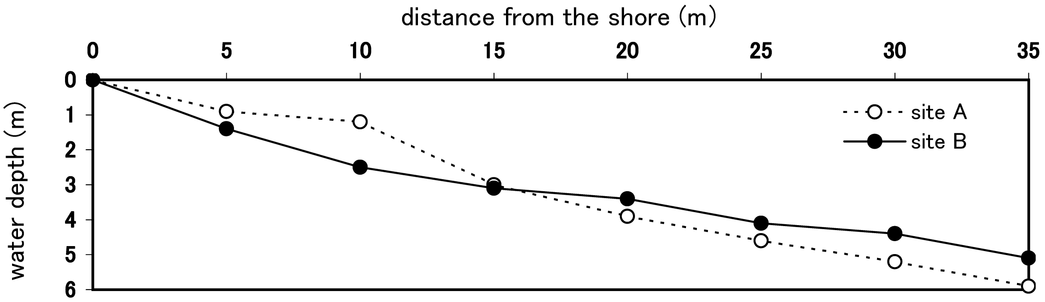


Fig. 2. Depth profiles of the study sites A and B in May 1997.

Table 1. Species name of submerged macrophytes and species richness observed in this study.

Species name	Japanese name	Abbreviations	May	Jun.	July	Aug.	Sep.	Oct.	Nov.
*Elodea nuttallii**	kokanadamo	EN	+	+	+	−	−	+	+
Potamogeton crispus	ebimo	PC	+	+	+	−	−	−	−
P. perfoliatus	hirohanoebimo	PP	+	+	+	+	+	+	−
P. maackianus	senninmo	PM	+	+	+	+	+	+	+
P. leptocephalus	hirohanosenninmo	PL	+	+	+	+	+	+	+
Myriophyllum spicatum	hozakinohusamo	MS	+	+	+	+	+	+	+
*Vallisneria biwaensis***	nejiremo	VB	−	+	+	+	+	+	+
Hydrilla verticillata	kuromo	HV	−	−	+	+	+	+	+
*Egeria densa**	ookanadamo	ED	−	−	−	+	+	+	+
Ceratophyllum demersum	matsumo	CD	−	−	−	−	+	+	+
P. anguillanus	oosasaebimo	PA	−	−	+	+	+	−	−
Species richness			6	7	9	8	9	9	8

*: alien species; **: endemic species.

always larger than 5 m. In each census, a diver moved slowly (35 m/60 min) along a transect line and drew a vegetation map on waterproof graph paper within a zone 2 m either side of the line. Configurations of homogenous patches were sketched on the map being identified the species, distinguished a patch of one species from that of mixed species, and measured the width of each patch and the height at the center by a ruler (1 m long). The share of each component in the same type of mixed species patch could not be distinguished. The height of the tallest individuals of each species in a census was used for the description of growth pattern of the species. Since the main stems of a species often complicatedly branched off, it was difficult to measure the stem density underwater. The area of each patch was measured on the vegetation map using a digitizer. In this study, open space near shore, including exposed area, is called "shallow open space", and open space in the other zone is called "deep open space". To compare the diversity of patches, including shallow and deep open spaces, between the two sites, Shannon-Wiener's diversity index (H') was calculated and the relative area of each patch was used for the calculation. Although several theoretical studies have pointed out several problems of Shannon-Wiener's diversity index (Ito & Sato 2002), it was able to use in this study because the two study sites had the same area and basically the same environmental conditions, and there was no rare species.

Results

Structure of submerged macrophyte community

The area of submerged vegetation cover was always smaller in the site A and there was a significant difference in the area between the two sites (the site A, $\bar{x} = 97.8\ \mathrm{m}^2 \pm 20.1$ SD; the site B, $\bar{x} = 126.3\ \mathrm{m}^2 \pm 19.6$ SD. Mann-Whitney U-test, $Us = 6$, $p = 0.018$, Fig. 3). Shallow open space, including exposed area, was always larger in the site A (Fig. 3, Mann-Whitney U-test, $Us = 0$, $p = 0.0017$)

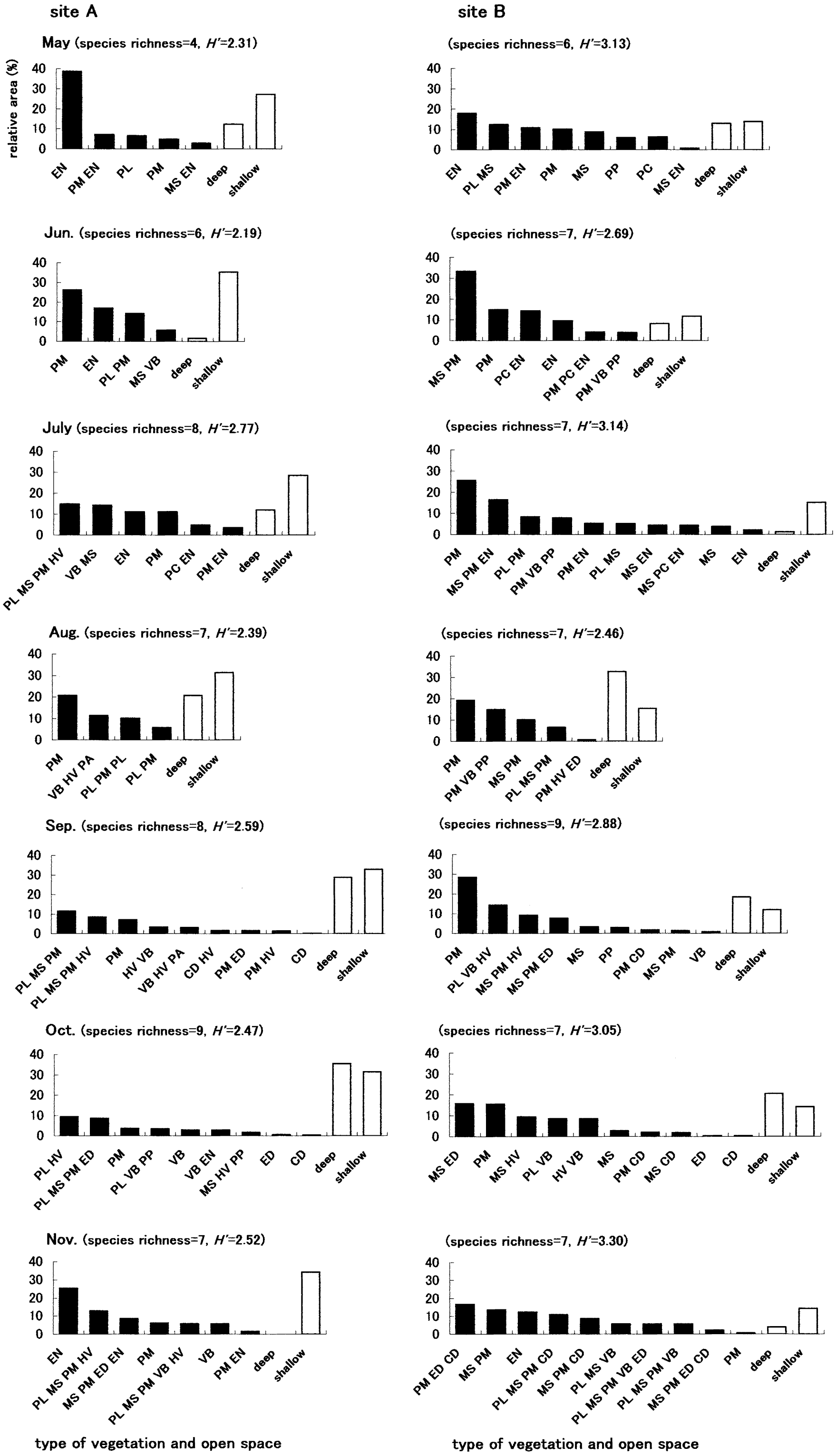


Fig. 3. Changes of vegetation types in each study site (A and B) from May to November 1997. Relative area (%) of each vegetation type and each open space type is shown. ■; vegetation type. □; open space type without vegetation. See Table 1 for abbreviations of species names.

Table 2. Species composition of mixed species patches and one species patches observed in the study sites. See Table 1 for abbreviations of species name. The number of census that a patch was observed is in parenthesis.

	five-species patch	four-species patch	three-species patch	two-species patch	one-species patch
Site A	PL MS PM VB HV (1)	PL MS PM HV (3)	VB HV PA (2)	PM EN (3)	PM (7)
		PL MS PM ED (1)	PL MS PM (1)	PL PM (2)	EN (4)
		MS PM ED EN (1)	PL PM ED (1)	MS VB (2)	CD (2)
			PL VB PP (1)	MS EN (1)	VB (2)
			MS HV PP (1)	VB HV (1)	PL (1)
				PC EN (1)	ED (1)
				PL HV (1)	
				PM HV (1)	
				PM ED (1)	
				VB EN (1)	
				CD HV (1)	
Site B	PL MS PM VB ED (1)	PL MS PM VB (1)	PM VB PP (2)	MS PM (4)	PM (7)
		PL MS PM CD (1)	PL MS PM (1)	PM EN (2)	EN (4)
		MS PM ED CD (1)	PL MS VB (1)	MS EN (2)	MS (4)
			PL VB HV (1)	PL MS (2)	CD (1)
			MS PM HV (1)	PM CD (2)	VB (1)
			MS PM ED (1)	PL PM (1)	PL (1)
			MSPM EN (1)	VB HV (1)	ED (1)
			MS PM CD (1)	PC EN (1)	PA (1)
			MS PC EN (1)	PL VB (1)	PC (1)
			PM HV ED (1)	MS HV (1)	PP (1)
			PM ED CD (1)	VB HV (1)	
			PM PC EN (1)	MS ED (1)	
				MS CD (1)	
				PM PP (1)	

because of the shelf-like topography in the 0-10 m shore zone. There was no significant difference in the area of deep open space between the two sites (Mann-Whitney U-test, $Us = 23$, $p > 0.05$).

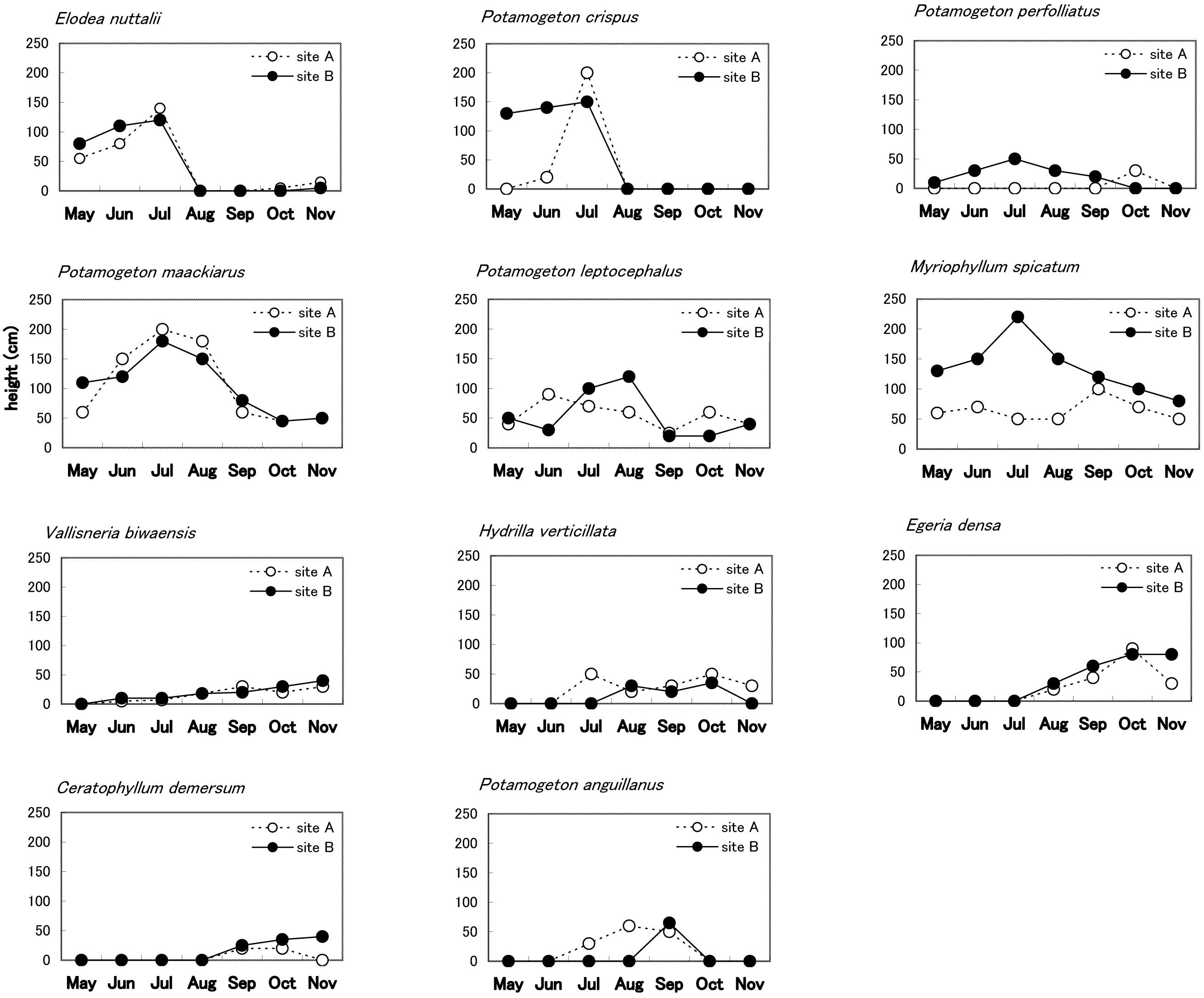
In total, the same 11 species were found in the two sites: the species included two alien species, *Egeria densa* and *Elodea nuttallii*, and one endemic species, *Vallisneria biwaensis* (Table 1). Species richness in a census fluctuated between 4 and 9 in the site A and between 6 and 9 in the site B (Fig. 3): there was no significant difference in species richness in a census between the two sites (Mann-Whitney U-test, $Us = 21.5$, $p > 0.05$, n = 7). Species richness was highest in October in the site A and in September in the site B. In both sites, in May, species richness was lowest, and the same four species, *Potamogeton maackianus, P. leptocephalus, Elodea nuttallii* and *Myriophyllum spicatum*, were found. All species but one, *Hydrilla verticillata*, often formed one-species patches (Table 2). Out of 90 one-species patches, 54 (60%) were formed by *Potamogeton maackianus* and 17 (18.9%) were formed by *Elodea nuttallii*.

In the two sites, species did not show clear zonation. There existed 44 combinations of mixed species patches (Table 2), and eight of them comprised of four ($n = 6$) or five species ($n = 2$). The two types of five-species patches and four types of four-species patches included *Potamogeton leptocephalus, P. maackianus* and *Myriophyllum spicatum*. Those species except *P. maackianus* never formed dense vegetations, unlike *Elodea nuttallii*. Out of the 44 combinations, 36 (81.2%) included *Potamogeton leptocephalus, P. maackianus* or *Myriophyllum spicatum*. Those three species were always found in both sites throughout this study. The combination of *Potamogeton crispus* and *Egeria densa*, and that of *Elodea nuttallii* and *Hydrilla verticillata* were never found in any mixed species patches. The number of types of observed patch was lowest in August in both sites, and it was also lowest in June in the site A (Fig. 3). The number of types of observed patch was always larger in the site B except September but there was no significant difference in the number between the two sites (Fig. 3, Mann-Whitney *U*-test, $Us = 11$, $p > 0.05$). Shannon-Wiener's diversity index (H') was always larger in the site B and there was a significant difference in the index between the two sites (Fig. 3, Mann-Whitney *U*-test, $Us = 5$, $p = 0.015$).

Withered *Potamogeton maackianus* or withered *Elodea nuttallii* often formed dense mats covering potential open space. Withered *Potamogeton maackianus* was abundant in both sites in May and October, when live *P. maackianus* was short (Fig. 4). Withered *Elodea nuttallii* was abundant in both sites in August and September, just after live *E. nuttallii* grew tallest in July. Withered macrophyte beds were sometimes abundant in one of the two sites (Table 3).

Growth pattern of individual species and preferred water depth

The growth patterns of *Elodea nuttallii*, one of the dominant species in Lake Biwa, were very similar in the two sites and quite different from those of other species observed in this study (Fig. 4, Table 1). It had already grown in more than 50 cm in May, grew tallest in July, withered or disappeared in August and began growing in September. *Potamogeton crispus* showed different growth


Elodea nuttalii

Potamogeton crispus

Potamogeton perfolliatus

Potamogeton maackiarus

Potamogeton leptocephalus

Myriophyllum spicatum

Vallisneria biwaensis

Hydrilla verticillata

Egeria densa

Ceratophyllum demersum

Potamogeton anguillanus

Fig. 4. Growth patterns of individual species in the two study sites (A and B) between May and November 1997.

Table 3. Withered macrophyte beds observed in each census at each site.

Species	Site A							Site B						
	May	Jun	July	Aug.	Sep.	Oct.	Nov.	May	Jun	July	Aug.	Sep.	Oct.	Nov.
Egeria densa	−	−	−	−	−	−	−	+	−	−	−	−	−	−
Elodea nuttallii	−	−	−	+	+	+	−	−	−	−	+	+	−	−
Potamogeton leptocephalus	−	+	−	−	−	−	−	−	−	−	−	−	+	−
P. maackianus	+	+	−	−	−	+	−	+	−	+	−	+	+	−

patterns in the two sites. It grew tallest in July and disappeared by August in the two sites, but it did not exist in May in the site B. *Potamogeton perfoliatus* also showed different growth patterns in the two sites. It did not exist between May and September in the site A, while it existed in the site B, and it disappeared by November in both sites. The growth patterns of *Potamogeton maackianus*, another dominant species in Lake Biwa, were very similar in the two sites. It was abundant between June and August, grew tallest in July and became shortest in October in both sites. *Potamogeton leptocephalus* and *Myriophyllum spicatum* had difference growth peaks in the two sites. *Myriophyllum spicatum* always grew taller in the site B. *Vallisneria biwaensis* showed similar growth patterns in the two sites: it gradually grew tallest by November. *Hydrilla verticillata* had different growth peaks in the two sites and it was almost always abundant in the site A, but it did not exist until July in both sites. *Egeria densa* and *Ceratophyllum demersum* showed similar growth patterns in the two sites. Those two species were rare in the first half of the study period and grew in the last half. *Potamogeton anguillanus* showed different growth patterns in the two sites but it did not exist in the beginning and the end of the study period. It was almost always abundant in the site A.

Potamogeton maackianus always grew tallest in 25-35 m offshore zone (deepest zone, 4-6 m deep) except in November in the site B (Fig. 5). *Elodea nuttallii* usually grew tallest in the deepest zone but in October in the site A and in June in the site B it grew tallest in other zones. *Potamogeton crispus, Egeria densa, Ceratophyllum demersum* and *Myriophyllum spicatum* often changed the zones of their highest growth. *Potamogeton anguillanus, P. perfoliatus* and *Vallisneria biwaensis* always grew tallest in 5-15 m offshore zone (shallowest zone, 1-3 m deep). *Potamogeton leptocephalus* and *Hydrilla verticillata* always grew tallest in 5-20 m offshore (1-4 m deep). In the site B. *Potamogeton anguillanus, P. perfoliatus, P. leptocephalus* and *Vallisneria biwaensis* often grew tallest near the shore (5-10 m offshore zone). In the site B, in addition, fewer species grew tallest in same zones in a month, though there was no significant difference in the number of species that grew tallest in same zones between two sites (Mann-Whitney *U*-test, $Us = 14$, $p > 0.05$).

Discussion

Submerged macrophytes are often expected to show a clear zonation in a littoral zone because individual species of submerged macrophytes usually have a preferred depth for growing (Bernatowicz & Zachwieja 1966; Mitsch & Gosselink 2000; Kalff 2002). In Lake Biwa, exactly, individual species have a preferred depth (Hamabata 1991b, 1997; Imamoto et al. 1998), and their distribution patterns are well explained by the degree of wave exposure, bottom sediment characteristics and light conditions at the bottom, which are correlates of water depth (Imamoto et al. 1998). In a littoral zone, *Elodea nuttallii* dominates in the deepest zone, *Vallisneria biwaensis* does in the shallowest zone and *Potamogeton maackianus* in the intermediate zone (Hamabata 1991b, 1997). In the present study sites, however, species did not show such a clear zonation except in site B in May (Fig. 5), though individual species seemed to have a preferred depth for growing. In addition, *Elodea nuttallii* often preferred a shallower zone than *Potamogeton maackianus* (Fig. 5). In the present study sites, as the water transparency was high and there was no disturbance by wave action, superior competitors, such as *E. nuttallii* and *P. maackianus*, might not be able to exclude other species in their best growth zones. In both sites, many types of mixed species patch were observed throughout the study period (Fig. 3). Since there were no large differences in the degree of wave exposure (almost no wave action) and in

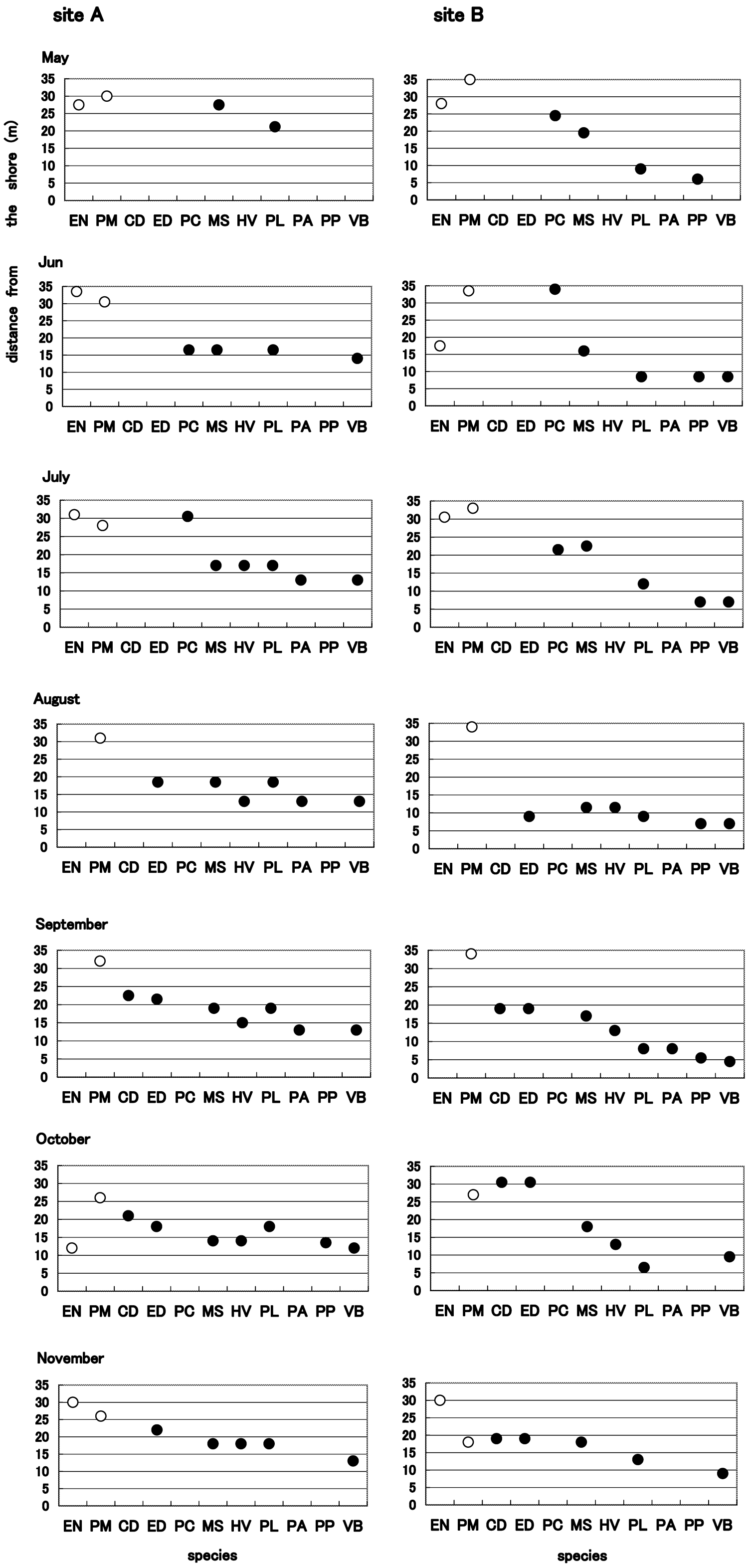


Fig. 5. The highest growth points of individual species in each study site (A and B) from May to November 1997. Those points are indicated as the distance from the shore. ○; two dominant species in Lake Biwa, *Elodea nuttallii* (EN) and *Potamogeton maackianus* (PM). ●; other species. See Table 1 for abbreviations of species names.

the bottom sediment characteristics between the two sites, intensive interspecific competition among submerged macrophytes might have caused unclear zonation in both sites. In calm and clear-water littoral zones, unclear zonation of submerged macrophytes may be common.

In Lake Biwa, except windy zones, littoral zone less than 3 m deep with a gentler slope is known to have a larger cover of submerged macrophytes (Hamabata 1991b, 1997; Imamoto et al. 1998). In this study, the site A had shelf-like shallows in the 0-10 m zone and a steep slope in the 10-35 m zone, while the site B had a gentle slope over the 0-35 m zone. The area of submerged vegetation cover was significantly smaller in the site A because the shelf-like shallows (< 1 m deep) had dried when water level was low (a range between −0.30 m and −0.65 m BSL, between September and November, 1997). While shallow open space, including exposed area, was always larger in the site A, there was no significant difference in the area of deep open space between the two sites. These results suggest that depth profile especially in shallows less than 1 m deep greatly affects the area of submerged vegetation cover, though it did not affect the species richness. The area of submerged vegetation cover is subjected to changes in such shelf-like shallows when water level changes.

In this study, there was no significant difference in species richness, and the same 11 species were found in the two sites. The species richness of submerged macrophytes usually increases with lake size or the area of littoral zone (Kalff 2002). The two sites had the same area with no large difference in environmental conditions, and the maximum depth difference in the same zone was 1.3 m at the 10 m offshore points. These results indicate that such a small difference in depth profile do not affect the species richness and the species composition of submerged macrophyte community. However, there existed differences in the growth patterns of five species between the two sites (Fig. 4), and four species grew tallest nearby the shore in the site B (Fig. 5). These suggest that a small difference in depth profile do affect the growth patterns of submerged macrophytes. Furthermore, Shannon-Wiener's diversity index (H') was always larger in the site B and there was a significant difference in the index between the two sites. This implies that a small difference in depth profile affect the diversity of underwater landscape.

Recent studies have revealed that structural submerged macrophyte community provides small aquatic animals with temporal refuges (Lauridsen et al. 1996; Scheffer et al. 2001; Strand & Weisner 2001; Kalff 2002). In this study, the number of types of observed patch was almost always higher in the site B with a gentler slope. Furthermore, the diversity of patches, including shallow and deep open spaces, was always higher in the site B. Since the species composition in the two sites was the same, different growth patterns of several species might have caused different types of mixed patches in the two sites. Withered macrophyte beds, which also had structured space, were sometimes abundant in one of the two sites. Those withered macrophyte beds could be used by small aquatic animals such as crustacean larvae and protozoa. Further work is required to clarify the effects of a difference in depth profile on the three-dimensional structure of submerged macrophyte community, which can be a crucial determinant of the habitat structure of small aquatic animals.

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摘　要

穏やかで透明度が高く，水鳥がほとんど生息しない琵琶湖の奥出湾(西浅井町大浦)において，沈水植物群落の構造とその季節変化をSCUBA潜水により調査した．水深構造の違いが沈水植物群落へ及ぼす影響を把握できるように，岸から35 mのベルトトランゼクト(幅4 m)を水深構造が異なり30 m離れた2地点に設置し，1997年5月から11月まで毎月1回，水中植生図を作成した．両地点とも，外来種2種(オオカナダモとコカナダモ)と固有種1種(ネジレモ)を含む11種が観察され，毎月の出現種数に地点間で有意差はみられなかった．両地点とも帯状

分布が不明瞭で，混合群落がモザイク状に分布していた．少なくとも５種類（ホザキノフサモ，オオササエビモ，エビモ，ヒロハノセンニンモ，ヒロハノエビモ）には，２地点間で成長パターンに違いが見られた．本調査場所では，沈水植物の種組成を決める主要因の一つとされる波浪の影響（波浪による撹乱）が少なかったため，明瞭な帯状分布が成立しなかったと考えられる．本研究は，水深構造のわずかな違いが，種組成や種数ではなく，いくつかの種の生長パターンに影響を及ぼすことを明らかにした．また，種毎の生長パターンの違いは，水生動物の生息地に重要な沈水植物群落の立体構造に変化をもたらす可能性がある．

References

Bernatowicz S. & Zachwieja J.（1966）Types of littoral found in the lakes of the Masurian and Suwalki Lakelands. Ekologia Polska Seria A **14**: 519-545.

Duarte C. M. & Kalff J.（1986）Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnology and Oceanography **31**: 1072-1080.

Duarte C. M. & Kalff J.（1990）Patterns in the submerged macrophyte biomass of Lakes and the importance of the scale of analysis in the interpretation. Canadian Journal of Fisheries and Aquatic Sciences **47**: 357-363.

Duarte C. M., Kalff J. & Peters R. H.（1986）Patterns in biomass and cover of aquatic macrophytes in Lakes. Canadian Journal of Fisheries and Aquatic Sciences **43**: 1900-1908.

Hamabata E.（1991a）Biwa-ko no chinsui-syokubutu no bunpu to chiiki-kubun. In: Biwa-ko kogan no keikan-seitaigaku teki kubun（ed. Lake Biwa Research Institute）pp. 35-46. Lake Biwa Research Institute, Otsu（in Japanese）.

Hamabata E.（1991b）Studies of submerged macrophyte communities in Lake Biwa species composition and distribution: results of a diving survey. Japanese Journal of Ecology **41**: 125-139.（in Japanese with English summary）.

Hamabata E.（1997）Distribution, stand structure and yearly biomass fluctuation of *Elodea nuttallii*, an alien species in Lake Biwa: studies of submerged macrophyte communities in Lake Biwa（3）. Japanese Journal of Limnology **58**: 173-190.

Hattori A.（1997）Habitat structure and behavior of the bluegill sunfish, *Lepomis macrochirus*, in Lake Biwa, Japan. Bulletin of Kansai Organization for Nature Conservation **19**: 11-23.（in Japanese）.

Hattori A. & Mae S.（2001）Habitat use and diversity of waterbirds in a coastal lagoon around Lake Biwa, Japan. Ecological Research **16**: 543-553.

Hutchinson G. E.（1975）A treatise on limnology vol. III: limnological botany. John Wiley & Sons, New York.

Ikushima I.（1966）Biwa-ko no suisei koutou-syokubutu. In: Biwa-ko seibutu shigen cyousa-dan cyuukan houkoku. pp. 313-341. Ministry of Construction, Kinki District.（in Japanese）.

Imamoto H., Kato M., Horiya K. & Hara T.（1998）Studies on the coastal environment in Lake Biwa（1）: species composition and distribution of submerged macrophytes. Ecology and Civil Engineering **1**: 7-20.（in Japanese with English summary）.

Ito Y. & Sato K.（2002）Problems around the indices of species diversity for comparison of different communities. Biological Science（Tokyo）**53**: 204-220.（in Japanese）.

Kalff J.（2002）Limnology: inland water ecosystems. Prentice-Hall, New Jersey.

Kawanabe H., Coulter G. W. & Roosevelt A. C（eds.）（1999）Ancient lakes: their cultural and biological diversity. Kenobi productions, Ghent, Belgium.

Lauridsen T. L., Pedersen L. J., Jeppesen E. & Sondergaard M.（1996）The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. Journal of Plankton Research **18**: 2283-2294.

Mitsch W. J. & Gosselink J. G.（2000）Wetlands. Wiley & Sons, New York.

Research Group for Natural History of Lake Biwa（1994）The natural history of Lake Biwa. Yasaka Shobo, Tokyo.（in Japanese）.

Riis T. & Hawes I.（2003）Effect of wave exposure on vegetation abundance, richness and depth distribution of shallow water plants in a New Zealand lake. Freshwater Biology **48**: 75-87.

Scheffer M., Carpenter S., Forey J. A., Folkes C. & Walker B.（2001）Catastrophic shifts in ecosystems. Nature **413**: 591-596.

Strand J. A. & Weisner S. E. B.（2001）Dynamics of submerged macrophyte populations in response to biomanipulation. Freshwater Biology **46**: 1397-1408.