

Seasonal dynamics of subtidal macrophyte assemblages in Sobol Bay (Peter the Great Bay, Sea of Japan) in relation to depth

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*This paper describes the species composition, vertical distribution, and the seasonal changes in the biomass of subtidal macrophytes in Sobol Bay (Peter the Great Bay, Sea of Japan). The samples were collected in the depth-range from 0.5 to 4 m. A total of 65 macrophyte species were identified, among which were 10 species of Chlorophyta, 17 of Phaeophyceae, 37 of Rhodophyta and 1 of Magnoliophyta. Multivariate analyses were performed to detect spatial and temporal variations. Maximum species richness was registered in June, with a particularly dramatic biomass increase of brown algae. Both the number of species and the biomass of macrophytes decreased with increasing depth. Depth clearly affected the patterns of seasonal fluctuations of the species composition and biomass. In the study area, the species composition of the shallow-water algal assemblages was more stable throughout the year compared to that of the algal assemblages found in deeper waters. In total, four macrophyte assemblages were identified in the bay. A *Phyllospadix iwatensis* and *Coccoloba langsdorfii* dominated assemblage occupied muddy-gravel bottoms in depths from 0.5 to 2 m throughout the year. An assemblage, co-dominated by annual brown algae *Desmarestia viridis* and *Costaria costata*, occurred at depths more than 3 m at late spring. Two other assemblages occurred on the rock and boulder bottom at 0.5–2 m depths, but they were temporally separated. An assemblage co-dominated by annual laminarian algae (*Undaria pinnatifida* and *Costaria costata*) developed at late spring and was succeeded in the autumn and winter by a *Tichocarpus crinitus*, *Ulva lactuca*, *Sargassum pallidum* and *Codium fragile* co-dominated assemblage. A comparison between the data obtained in the present study and the results of a previous study conducted in 1927 shows that the macrophytes assemblages in Sobol Bay underwent little change.*

Keywords: macrophyte, subtidal, seasonal changes, vertical distribution, assemblages, Peter the Great Bay, Sea of Japan

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INTRODUCTION

Macrophytes are key components of marine coastal ecosystems where they play a fundamental role in determining the biomass and production of organic matter and biodiversity. Marine macrophytes are sensitive to anthropogenic stress and climatic changes (Domin *et al.*, 2004; Krause-Jensen *et al.*, 2004; Serio *et al.*, 2006), therefore, they are considered as good indicators of changes in benthic communities and are widely utilized to characterize and monitor coastal ecosystems (Lirman & Biber, 2000). However, the use of macrophytes for local ecological monitoring requires detailed knowledge of the community structure and dynamics. The knowledge of macrophyte seasonality is important when developing monitoring programmes in the coastal waters near populated areas, and the lack of information on this dynamic may lead to inaccurate conclusions on the long-term changes of macrophyte communities.

Although macroalgae and seagrasses are significant components of coastal ecosystems within the Sea of Japan and intertidal and subtidal marine vegetation has been extensively

reported (e.g. Perestenko, 1980; Kafanov & Zhukov, 1993; Kashenko, 1999, 2002; Gusarova, 2003, 2008; Yoo 2003a, b; Yatsuya *et al.*, 2007; Kang *et al.*, 2008; Kozhenkova, 2008; Shin *et al.*, 2008), only limited information is available on the dynamics of macrophytes communities. Some publications have described long-term and seasonal changes in macroalgal assemblages along the Russian coast of the Sea of Japan (Kafanov & Zhukov, 1993; Gusarova, 2003, 2008; Kozhenkova, 2008; Levenets & Skriptsova, 2008a) or the eastern coast of Korea (Kim *et al.*, 1998; Kang *et al.*, 2008; Shin *et al.*, 2008), and only a few studies have analysed temporal variations of macrophytes communities in the eastern part of the Sea of Japan (Yatsuya *et al.*, 2007). Studies of seasonal variations of macrophyte assemblages based on quantitative and qualitative estimates of species occurrence showed that both the species diversity and total biomass of the algal community in Peter the Great Bay (Russian coast of the Sea of Japan) were highest from April to July (Kafanov & Zhukov, 1993; Gusarova, 2003). On the eastern coast of Korea the maximum species richness was found during summer (Shin *et al.*, 2008), while on the south coast of the Korea peninsula the highest number of seaweed species was registered in winter (Kim *et al.*, 1998). Year-round variations of species composition have undoubtedly led to seasonal change in community structure (for example see Kim *et al.*, 1998; Shin *et al.*, 2008).

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When studying temporal variations of macrophyte communities, the effect of water depth on their seasonal changes should be considered. Kim *et al.* (1998) concluded that depth is a primary factor constraining the seasonal fluctuations of the numbers and abundance of species in subtidal benthic algal communities. Studies have shown that deep-water algal assemblages are more stable throughout the year compared to shallow-water assemblages (Kim *et al.*, 1998; Piazzì *et al.*, 1999, 2002). In general the number of species as well as the percentage cover and biomass of macrophytes decreases with increasing depth independent of season (Kim *et al.*, 1998; Yoo, 2003a).

The aim of the present study is to contribute to the knowledge of macrophyte assemblages and seasonal patterns of variation of macrophyte composition and biomass in relation to water depth in Peter the Great Bay. Peter the Great Bay is the largest bay in the Sea of Japan. It is located in the north-western part of the sea and occupies an area of about 6000 km². The study was carried out in Sobol Bay, which is a typical rocky shore within Peter the Great Bay and for the north-western part of the Sea of Japan in the whole. According to Mathieson & Nienhuis (1991) this type of habitat in general fits to the rocky subtidal ecosystem of the northern Pacific. Early descriptions of marine flora of Sobol Bay date back to the 1920s (Zaks, 1927), and at that time the macrophyte assemblages were characterized by high biodiversity. The author described three major macrophyte assemblages in this bay: (1) a *Phyllospadix iwatensis* Makino (= *Zostera* A in Zaks, 1927) dominated assemblage in the inner part of the bay in the 0.5–2 m depth-zone; (2) an assemblage co-dominated by *Sargassum* spp., *Cystoseira crassipes* (Mertens ex Turner) C. Agardh and *Coccolophora langsdorfii* (Turner) Greville on the boulders at 0–1 m depth; and (3) a *Desmarestia viridis* (O.F. Müller) J.V. Lamouroux dominated

assemblage located at a depth greater than 4 m. Since then, the quality of the coastal environment of this area has deteriorated due to coastal development and human population increase. Therefore, in the present paper we also discuss long-term changes of the macrophytes assemblages in Sobol Bay.

MATERIALS AND METHODS

Study area

Sobol Bay is an open embayment subjected to significant wave action. It is located in the central part of Peter the Great Bay (43°04'N and 131°08'E) and has a coastline of about 800 m (Figure 1). This area is protected from northerly winds by a cliff, and thus is exposed only to southerly winds. The bay is bounded by a large rock to the north-east and by the Basargina Peninsula to the south-west. The substrate along the beach is generally composed of gravel in the north-eastern and south-eastern parts of the bay and muddy-gravel in the central part of the bay with boulders of varying size. A narrow rocky platform (2–4 m in width) is situated at a distance of 20–30 m from the beach and extends from 0.5 to 1–1.5 m depth below mean lower low water level. The platform ends in a vertical incline and a sandy bottom at 3–4 m depth. The site does not experience strong tidal currents but is exposed to strong wave action when the wind blows from the south. Waves usually are limited by 1.5 m during storms; they regularly move stones weighing up to several kilograms that are located between the beach and the platform. The tidal range is not over 0.5 m; typical water clarity generally varies in a range of 6–10 m. The salinity is relatively stable at 30.5–33.3‰ throughout the year. According to our observations, the temperature in the bay varied from –1.5°C

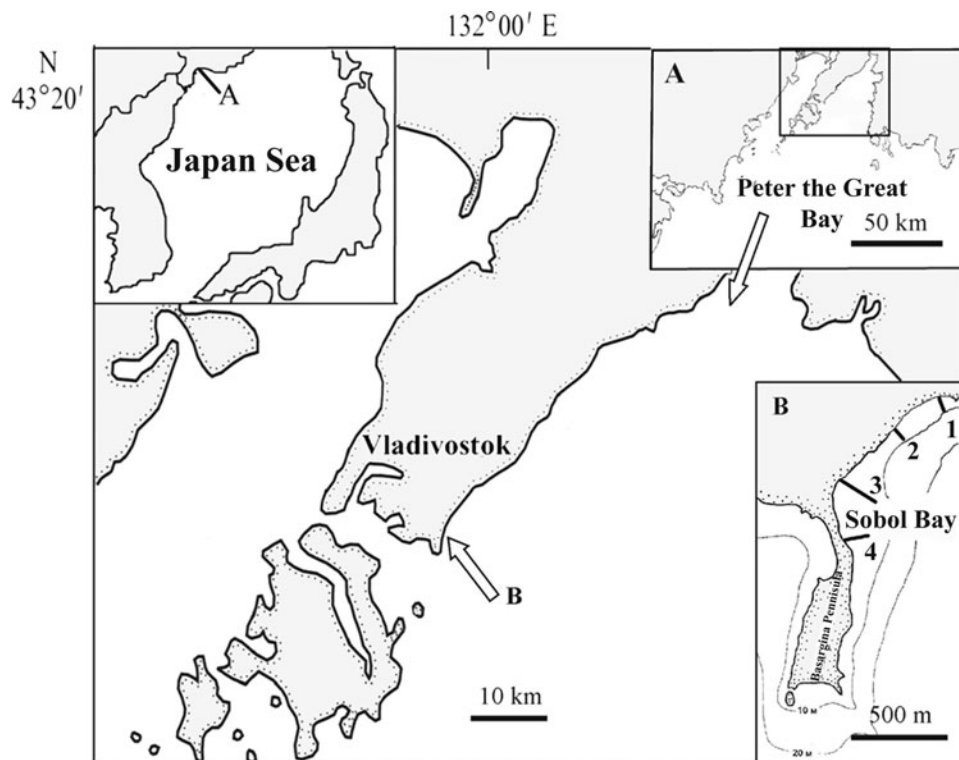


Fig. 1. Location of the study area in Peter the Great Bay. Numerals mean site numbers.

during the winter (from December to early March) to 20–22°C in August. Neither the temperature nor the salinity varied markedly within the bay. The bay is not covered with ice during the winter (Tarasov *et al.*, 2005). Macrophytes occur from the low intertidal zone to 9–12 m depth. They form a continuous bed from 0.5 to 3–4 m depth on the rocky platform and incline, and at depths below 4 m they grow in small patches on boulders of varying size, which are sparsely distributed on the sandy bottom.

Sampling

Macrophyte species composition in Sobol Bay was studied seasonally in March, June, August and December 2004. Fluctuations in biomass as well as species composition in relation to depth were examined subtidally in June and December 2005 and February 2006. Macrophyte communities were analysed at four sites within Sobol Bay (Figure 1; Table 1). Site 1 was located on a rock at the north-eastern edge of the bay. Site 2 was situated 200 m to the south-east of Site 1. Site 3 was located in the central part of the bay 300 m from Site 2. Site 4 was located in the south-eastern part of the bay 300 m from Site 4. The environmental conditions (temperature, salinity, nutrient concentrations and turbidity) did not differ significantly between the sites.

Samples were collected by SCUBA divers. At each site one permanent transect was laid out perpendicular to the shore within the subtidal zone. Macrophytes were collected within 0.25 m² quadrats randomly placed over the bottom along transects at 0.5, 1.5–2 and 3–4 m depths at each of the four sites. At each depth three samples were collected during each sampling period at each site (a total of 36 samples were collected per each sampling period). During each sampling period three new quadrats were randomly placed within the depth-zones along each transect. This procedure made it possible to avoid multiple re-sampling of the same quadrats. Within each quadrat, all visible plants were collected by hand.

The samples were sorted by species, which were identified based on the identification keys of Perestenko (1980, 1994). Plants were wet weighed with a digital balance (± 0.1 g). Microscopic species (<1–2 mm tall) were included in the analysis of seasonal changes of macrophyte assemblages; they were assumed to weigh <0.001 g.

Data analysis

The similarity in species composition and biomass among samples collected at different sites and depths was analysed

Table 1. Characteristics of collection sites where permanent transects were established.

Site	Location	Site description
1	Northern cape of the bay	Rocky bottom, below 6 m sandy bottom with boulders ranging in size from 0.5 to 1 m across
2	200 m south of the northern cape	Rocky platform at 0.5–3 m depth; boulders in sand below
3	Central part of the bay	Muddy-gravel bottom in upper subtidal zone (at depth from 0.5 to 2 m), boulders in sand below
4	Southern part of the bay	Boulders at 1–3 m depth; boulders in sand below

by calculating the Bray–Curtis similarity coefficient (Clarke & Green, 1988) with a preliminary square root transformation of the data. For graphical representation of the data set from the 2005–2006 sampling period, cluster analysis (group average method) and non-metric multidimensional scaling (MDS) ordination were carried out (Clarke & Gorley, 2001). The significance of the resulting groups was tested using the one-way analysis of similarities (ANOSIM) (Clarke & Gorley, 2001). The similarity percentage (SIMPER) method was used to determine the most important species that contributed to groups identified by the cluster and MDS analyses (Clarke & Gorley, 2001). Three replicate quadrats within each zone and sampling period were averaged prior to the analyses to reduce the number of permutations. All analyses were carried out using the software package PRIMER 5.0.

RESULTS

A total of 65 species of macrophytes were found during the study, among which were 10 species of Chlorophyta, 17 of Phaeophyceae, 37 of Rhodophyta and one of Magnoliophyta (Table 2). The species composition, particularly the species number, varied widely in the subtidal zone (Table 2).

There were conspicuous seasonal differences in the species composition in relation to depth, but not between sites. The species richness decreased with increasing water depth independently of the season (Figure 2A, B). Proportions of macrophytes of different phyla were similar at 0.5 and 2 m depths and did not differ between seasons. During the winter (December and February) and late spring (June) the proportions were as follows: Rhodophyta 59–65%, Phaeophyceae 24–32% and Chlorophyta 6–10% of the flora composition. Marked seasonal differences in species composition were found at depths of 3 m or greater. Twenty algal species were identified at this depth in the winter: Rhodophyta 65%, Phaeophyceae 30% and Chlorophyta 5% (Figure 2A). In spring (June) only 6 algal species were found at depths of 3 m or more (*Desmarestia viridis*, *Costaria costata*, *Undaria pinnatifida*, *Scytosiphon lomentaria*, *Pachyarthon compressum* and *Ceramium kondoi*), representing Rhodophyta 33% and Phaeophyceae 67% (Figure 2B).

The total biomass of macrophytes varied between seasons, sites and depths (Figure 2C–F). The average biomass of macrophytes at all sites and in the whole depth-range was low in February and reached the maximum in June. The highest biomass of macrophytes was generally observed at a 2 m depth.

The seasonal variation in the biomass of different species of macrophytes was similar at Sites 1, 2 and 4 (Figure 3); therefore, Figure 2 presents data only for Sites 2 and 3, which were different. In general, the highest biomass of seaweeds at Site 2 was observed at 2 m depth during both seasons. However, the biomass of Rhodophyta, Chlorophyta and Phaeophyceae differed depending on both season and depth. During winter, red seaweeds dominated and accounted for over 40% of the total biomass at 0.5 and 2 m depths. Brown algae (mainly *Sargassum pallidum* and *Scytosiphon lomentaria*) dominated at depths of 3 m or more (Figure 2C). In June, red algae dominated only at 0.5 m, contributing 62% of the total biomass, whereas brown algae (mainly *Desmarestia viridis* and *Costaria costata*) predominated at 3 m or more (Figure 2D). The biomass of Rhodophyta and Phaeophyceae were almost

Table 2. Species list of macrophytes recorded in the Sobol Bay.

Species	Depth	Site	Dec	Mar	Jun	Aug
Chlorophyta						
<i>Acrosiphonia saxatilis</i> (Ruprecht) K.L. Vinogradova	0.5–1	2		++		
<i>Bryopsis plumosa</i> (Hudson) C. Agardh	0.5–1.5	2	+	+	+	+
<i>Chaetomorpha moniligera</i> Kjellman	0.5	2,3,4			+	
<i>Codium fragile</i> (Suringar) Hariot	0.5–2	1,2,3,4				
<i>Kornmannia leptoderma</i> (Kjellman) Bliding	0.5	4		+e ¹		
<i>Monostroma grevillei</i> (Thuret) Wittrock	0.5	2,3		+e ¹		
<i>Acrosiphonia duriuscula</i> (Ruprecht) Yendo	0.5–1	2,4	+	++		
<i>Ulva clathrata</i> (Roth) C. Agardh	0.5	1,2		+		
<i>Ulva lactuca</i> Linnaeus	0.5–>3	1,2,3,4	+++	+++	+++	+++
<i>Ulva linza</i> Linnaeus	0.5–1	1,2,3,4			+	
Phaeophyceae						
<i>Analipus japonicus</i> (Harvey) M.J. Wynne	0.5	2			+	
<i>Chorda filum</i> (Linnaeus) Lamouroux	0.5–1	3			+	
<i>Chordaria flagelliformis</i> (O.F. Müller) C. Agardh	0.5	1,2,4	++	++	++	++
<i>Coccolophora langsdorffii</i> (Turner) Greville	0.5–2	2,3,4	++	++	++	++
<i>Coilodesme japonica</i> Yamada	0.5–1	2			+	
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Verbis et Solier	0.5–>3	2,3,4		+		
<i>Costaria costata</i> (C. Agardh) D.A. Saunders	0.5–>3	1,2,3,4	+	+++	+++	
<i>Cystoseira crassipes</i> (Mertens ex Turner) C. Agardh	0.5–2	1,2,3,4	++	++	++	++
<i>Desmarestia viridis</i> (O.F. Müller) J.V. Lamouroux	1–>3	1,2,3,4		+++	+++	
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	0.5	2,4	+		+	+
<i>Punctaria plantaginea</i> (Roth) Greville	0.5–2(>3)	1,2,3,4		++	++	
<i>Saccharina cichorioides</i> (Miyabe) C.E. Lane, C. Mayes, Druehl & G.W. Saunders	1–2	1,2,4			+	
<i>Sargassum pallidum</i> (Turner) C. Agardh	0.5–>3	2,3,4	++	++	++	+
<i>Sargassum miyabei</i> Yendo	0.5	2,3,4	+	+	+	+
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	0.5–>3	1,2,3,4		++	+	
<i>Sphacelaria rigidula</i> Kützting	0.5–2	2,3,4	+	+	+	+
<i>Undaria pinnatifida</i> (Harvey) Suringar	0.5–3	1,2,3,4	++	+++	+++	
Rhodophyta						
<i>Ahnfeltiopsis flabelliformis</i> (Harvey) Masuda	0.5–2(>3)	1,2,3,4	+	+	+	+
<i>Bossiella compressa</i> Kloczcova	0.5–>3	2,3,4	+	+	+	+
<i>Callophyllis rhynchocarpa</i> Ruprecht	1–3	2,3,4	+e ²			
<i>Campylaephora hypnaeoides</i> J. Agardh	0.5–1	2		+		
<i>Ceramium japonicum</i> Okamura	0.5–2	2,3,4			+e ¹	
<i>Ceramium kondoi</i> Yendo	0.5–>3	1,2,3,4	+	+	+	+
<i>Chondria decipiens</i> Kylin	1–1.5	1,2,3,4	+	+	+	+
<i>Chondrus armatus</i> (Harvey) Okamura	1–1.5	2,3,4	+		+	+
<i>Chondrus pinnulatus</i> (Harvey) Okamura	1–1.5	4	+	+	+	+
<i>Corallina pilulifera</i> Postels & Ruprecht	0.5–1	2,3,4	+	+	+	+
<i>Chrysmenia wrightii</i> (Harvey) Yamada	0.5–1.5	2,4			+	+
<i>Dasya sessilis</i> Yamada	1–>3	1,2,3,4	+			+
<i>Delesseria serrulata</i> Harvey	1–>3	1,2,3,4	++	++	+	
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	0.5	4			+e ⁵	
<i>Gelidium elegans</i> Kützting	1–2	2,4		+e ²		
<i>Gloiosiphonia capillaris</i> (Hudson) Carmichael	1.5–>3	1,2,3,4	+	++		
<i>Grateloupia divaricata</i> Okamura	0.5	1,2,3,4	+	+	+	+
<i>Grateloupia turuturu</i> Yamada	0.5–2	1,2,3,4				++
<i>Janczewskia morimotoi</i> Tokida	0.5	1,2,3,4	+e ³	+e ³	+e ³	+e ³
<i>Laurencia nipponica</i> Yamada	0.5–2(>3)	2,3,4	+	+	+	+
<i>Laurencia pinnata</i> Yamada	0.5	2,3,4	+	+	+	+
<i>Lithophyllum tumidulum</i> Foslie	0.5–1	3	+e ⁴	+e ⁴	+e ⁴	+e ⁴
<i>Mastocarpus pacificus</i> (Kjellman) Perestenko	0.5	4	+	+	+	+
<i>Mazzaella japonica</i> (Mikami) Hommersand	1–3	2,3,4		+		
<i>Mazzaella parksii</i> (Setchell & N.L. Gardner) J.R. Hughey, P.C. Silva & Hommersand	0.5–2	1,2,3,4	++	++	++	++
<i>Neorhodomela aculeata</i> (Perestenko) Masuda	0.5–2(>3)	1,2,3,4	+++	+++	+++	+++
<i>Neorhodomela munita</i> (Perestenko) Masuda	0.5–1	2,4				+
<i>Nienburgella angusta</i> (Zinova) Perestenko	1–2	2		+	+	+
<i>Palmaria stenogona</i> Perestenko	0.5–>3	1,2,3,4	+	+++	++	
<i>Polysiphonia morrowii</i> Harvey	0.5–>3	1,2,3,4	++	++	++	++
<i>Pterosiphonia bipinnata</i> (Postels & Ruprecht) Falkenberg	1–>3	1,2,4	+e ¹	+e ¹		
<i>Ptilota filicina</i> J. Agardh	0.5–>3	1,2,3,4	+	++		

Continued

Table 2. Continued.

Species	Depth	Site	Dec	Mar	Jun	Aug
<i>Sparlingia pertusa</i> (Postels & Ruprecht) G.W. Saunders, I.M. Strachan & Kraft	1–3	1,2,3,4		++		
<i>Stylonema alsidii</i> (Zanardini) K.M. Drew	0.5–2	1,2,3,4	+e ⁵	+e ⁵		+e ⁵
<i>Symphyclocladia latiuscula</i> (Harvey) Yamada	0.5–1.5	2,3,4	++		++	++
<i>Symphyclocladia marchantioides</i> (Harvey) Falkenberg	0.5–1	2,3,4			+	
<i>Tichocarpus crinitus</i> (S.G. Gmelin) Ruprecht	0.5–3	2,3,4	+++	+++	+++	+++
Magnoliophyta						
<i>Phyllospadix iwatensis</i> Makino	0.5–1	4	+++	+++	+++	+++

Dec, December; Mar, March; Jun, June; Aug, August; e, epiphyte; +++ , common species, found in 60–100% of samples; ++ , frequently occurring algae, found in 10–59% of samples; +, rare species, found in < 10% of samples; (>3), species was rarely found on this depth; ¹, species was found as epiphyte on *P. iwatensis*, *C. langsdorfii*, *N. aculeata*, *Sargassum* spp., *Tichocarpus crinitus* as well as free-living on hard substratum; ², species was found as epiphyte on rhizoids of laminarian algae; ³, species was found as epiphyte on *Laurencia* spp. and *T. crinitus*; ⁴, species was found as epiphyte on *P. iwatensis*, *C. langsdorfii* and *N. aculeata*; ⁵, species was found as epiphyte on red algae.

equal at a 2 m depth. At Site 3 the total biomass of macrophytes decreased with increasing water depth in the winter. *Phyllospadix iwatensis* dominated in the 0.5–2 m depth-zone (Figure 2E). The total biomass of Chlorophyta increased with increasing depth. Green algae were dominant at depths of 3 m or more (representing 92% of total biomass). In June, brown algae dominated over the whole depth-range (Figure 2F). *Phyllospadix iwatensis* was abundant at 0.5 m only (contributing 40% of the total biomass).

The cluster analyses performed on the biomass data obtained in 2005–2006 clearly divided all spatial and seasonal samples into two groups (Figure 3A). Group 1 combines all the samples collected in June at depths of 3 m or more. Group 2 includes all the samples collected during the year at depths from 0.5 to 2 m at different sites. Group 2 can be divided into three sub-groups. Group 2A consists of the samples collected in different months at Site 3 in the 0.5–2 m depth-zone on the muddy-gravel bottom. Group 2B combines the samples collected in June at depths ranging from 0.5 to 2 m at Sites 1, 2 and 4 on the rock and boulders. Group 2C combines the samples collected during the winter at Sites 1, 2 and 4. The clustering of all groups was as near as identical using the MDS ordination analysis (Figure 3B) and was supported by the one-way ANOSIM test (Global R = 0.717, number of permutations: 999, number of permuted R statistics greater than or equal to Global R: 0).

The SIMPER test shows that *Desmarestia viridis* and *Costaria costata* are the most important species in Group 1. Together, these two species are responsible for over 92.8% of the total mean biomass. *Phyllospadix iwatensis* and *Coccolophora langsdorfii* dominate in Group 2A, making up nearly 50.6% of the total mean biomass. Two algal species (*Costaria costata* and *Undaria pinnatifida*) dominated in June in the 0.5–2.5 m depth-zone on the rock and on boulders (Group 2B), accounting for 54.6% of the total mean biomass. *Ulva lactuca*, *Tichocarpus crinitus*, *Codium fragile*, *Palmaria stenogona*, *Cystoseira crassipes* and *Sargassum pallidum* were the most important species determining the polydominant winter algal assemblage (Group 2C), contributing 57.9% of the total mean biomass.

Desmarestia viridis distinguished Group 1 from the others. *Undaria pinnatifida* and *Costaria costata* were the most important species to distinguish Group 2B. *Phyllospadix iwatensis* was mostly responsible for differences between Group 2A and the others (Table 3).

Seasonal variations in the biomass of dominant species were apparent, indicating that the algal assemblages in the subtidal zone fluctuated. The apparent changes were observed in the 0.5–2 m depth-range at Sites 1, 2 and 4. In this ecotope, laminarian algae (*Undaria pinnatifida* and *Costaria costata*) became dominant in terms of biomass in June (Figure 4A). The maximal biomass of both species occurred at late spring (in June). *Tichocarpus crinitus*, *Sargassum pallidum*, *Cystoseira crassipes*, *Codium fragile* and *Ulva lactuca* were present during all sampling periods, but they became conspicuous after the disappearance of laminarian algae (Figure 4A). The most apparent seasonal changes of macrophytes occurred at depths over 3 m at all sites. During the winter, *Ulva lactuca* and *Palmaria stenogona* with accompanying species *Scytosiphon lomentaria* and *Sargassum pallidum* were dominant in this depth-zone. After February, *Desmarestia viridis* and *Costaria costata* dominated at depths greater than 3 m (Figure 4B). The beds of surfgrass (*Phyllospadix iwatensis*), located on the muddy-gravel bottom at 0.5–2 m depth, were the most invariable assemblages throughout the year (Figure 4C).

DISCUSSION

The present study provides qualitative and quantitative information on the seasonal variations of species composition, vertical distribution and biomass of macrophytes in Sobol Bay. A total of 65 species of macrophytes were found in Sobol Bay, which accounts for about 30% of the total number of species recorded from Peter the Great Bay (Perestenko, 1980). Most of the species identified in the study are widely distributed in the north-western part of the Sea of Japan (Guiry & Guiry, 2009). Similar to the other studies carried out in the shallow rocky subtidal zones of the temperate region, the Rhodophyta had the highest species richness, while the Heterokontophyta (class Phaeophyceae) ranked second and Chlorophyta last (Kim *et al.*, 1998; Yoo, 2003a; Shin *et al.*, 2008). According to our previous study (Levenets & Skriptsova, 2008b) the Sobol Bay flora is characterized in its biogeographical aspect by a high incidence (49% of total species number) of Asian elements, followed by Pacific elements (29%). Zonal analysis confirms the low-boreal character of the flora due to the predominance of temperate water affinity species (58%) and warm water affinity species (21.5%).

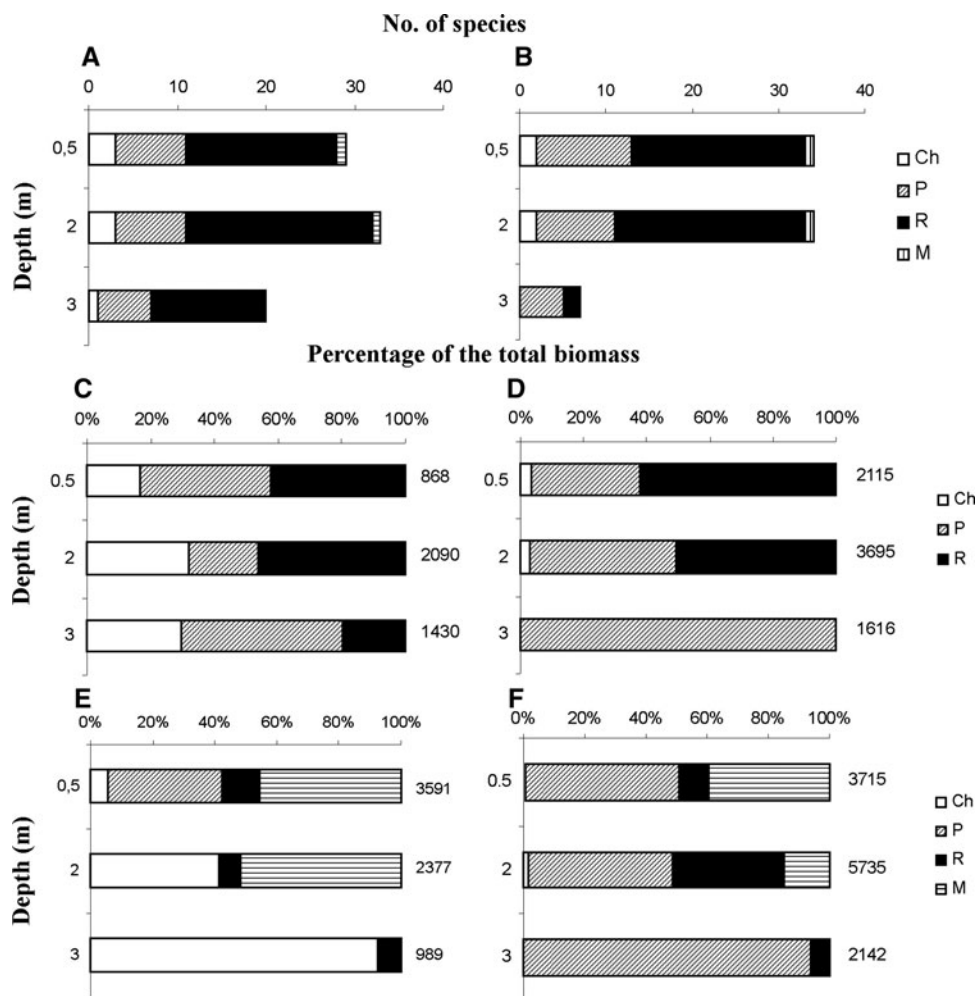


Fig. 2. Vertical profiles of the number of species (A, B) and biomass (C–F) of the different taxa of macrophytes. (A) Number of species for all sites, winter (December and February); (B) number of species for all sites, late spring June; (C) biomass distribution (Site 2), winter (December and February); (D) biomass distribution (Site 2), late spring (June); (E) biomass distribution (Site 3), winter; (F) biomass distribution (Site 3), late spring. Numerals on the Figure. (C–F) indicated average biomass of macrophytes (g m^{-2}) in the different depth-zones. Ch, Chlorophyta; P, Phaeophyceae; R, Rhodophyta; M, Magnoliophyta.

Comparison between the flora of Sobol Bay and the whole flora of Peter the Great Bay in its biogeographical aspect (Perestenko, 1980) shows their similarity (Levenets & Skriptsova, 2008b).

The highest species richness was observed from March to June. This was related to the appearance of annual cold water affinity species (e.g. *Desmarestia viridis*, *Ptilota filicina*, *Delesseria serrulata*, *Gloiosiphonia capillaris*, *Sparlingia pertusa* and *Mazzaella japonica*) and ephemeral green algae (*Monostroma grevillei*, *Kornmannia leptoderma*, *Acrosiphonia duriuscula* and *Acrosiphonia saxatilis*). The most pronounced seasonal change in species composition was the reduction in species number during the period of high temperature at the end of summer (from 45 species in June to 31 in August). During this period, some annual brown algae (*Undaria pinnatifida*, *Costaria costata*, *Desmarestia viridis* and *Punctaria plantaginea*) and most green algae disappeared, while several species of warm water affinity appeared (e.g. *Chrysmenia wrightii*, *Dasya sessilis* and *Grateloupia turuturu*). Our preliminary study also showed increased proportions of species of warm water affinity in the summer flora of Sobol Bay compared to the

winter (21.5% versus 30%) (Levenets & Skriptsova, 2008b). A decline in water temperature during the autumn coincided with the appearance of recruits of large annual brown algae, therefore, in December the species richness slightly increased compared to August. In December, perennial and summer species coexisted with recruits of some cold water affinity species, which first appeared in mid-autumn.

The macrophytes studied exhibited clear seasonal variations of biomass, which generally followed the succession of the dominant species. In June the biomass of the macrophytes was higher compared to that registered during winter, independent of depth and site location. Spring and early summer are generally considered as a peak growth period for many types of seaweed in Peter the Great Bay (Perestenko, 1980). High biomass of macroalgae in June in our study was associated with a significant biomass increase of the annual brown algae *Undaria pinnatifida*, *Costaria costata* and *Desmarestia viridis*, which gained dominance over red and green algae.

In the present study, water depth clearly affected seasonal fluctuation of the species composition and biomass. It was shown previously that depth is a primary factor in

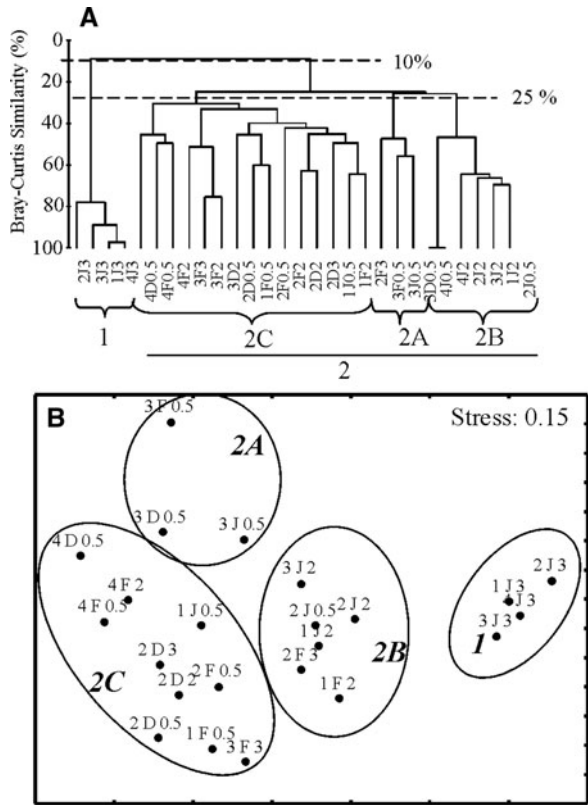


Fig. 3. Cluster (A) and non-metric multidimensional scaling ordination analyses (B) of averaged quadrat biomass data for all sites (number before letter) and depth (number after letter) from June (J) and December (D) 2005 and February (F) 2006.

constraining the seasonal fluctuations of species composition and abundance in subtidal communities (Kim *et al.*, 1998; Piazzi *et al.*, 1999; Shin *et al.*, 2008). In these studies, deep-water algal assemblages were more stable throughout the year compared to those inhabiting shallow waters. The seasonal stability of algal assemblages in deep-water habitats is attributed to low numbers of annual species. Differences in seasonal variations of community structure are detected even over a relatively narrow depth-range (from 0.5 to 5 m) (Kim *et al.*, 1998; Shin *et al.*, 2008). In contrast, our study found that the ratios of species number and biomass of green, red and brown seaweeds in the algal assemblage

Table 3. Results of the similarity percentage test on percentage contributions of species to determine significant differences among groups. ‘Groups’ is the same as in Figure 4.

Species	Groups					
	1-2A	1-2B	1-2C	2A-2B	2A-2C	2B-2C
<i>Coccophora langsdorfii</i>	12.84	2.41		8.55	10.65	2.37
<i>Costaria costata</i>	7.56	8.33	8.55	10.39	3.98	12.02
<i>Desmarestia viridis</i>	19.54	18.78	21.55	2.74		3.07
<i>Palmaria stenogona</i>		3.92	11.08	2.36	8.65	7.11
<i>Phyllospadix iwatensis</i>	17.24			12.49	13.45	3.74
<i>Ulva lactuca</i>	3.80	5.46	15.97	3.48	9.88	8.63
<i>Undaria pinnatifida</i>	2.01	14.79	4.01	12.50	2.43	11.13
Average dissimilarity	94.25	75.32	94.69	74.20	76.29	73.29

Significant values are printed in bold.

found in the 0.5–2 m depth-zone were less variable than those at depths greater than 3 m. This could be attributed to a greater percentage of perennial species and species with overlapping generations in shallow-water algal assemblages (*Tichocarpus crinitus*, *Neorhodomela larix*, *Ulva lactuca*, species of family Sargassaceae, etc.). The most pronounced seasonal changes of species composition as well as the biomass of macrophytes were observed at depths over 3 m. In this depth-zone, major seasonal changes involved a decrease in the total species number in late spring due to the disappearance of ephemeral green and red algae, while the numbers of brown algae species remained constant. Seasonal growth of *Desmarestia viridis* and *Costaria costata*

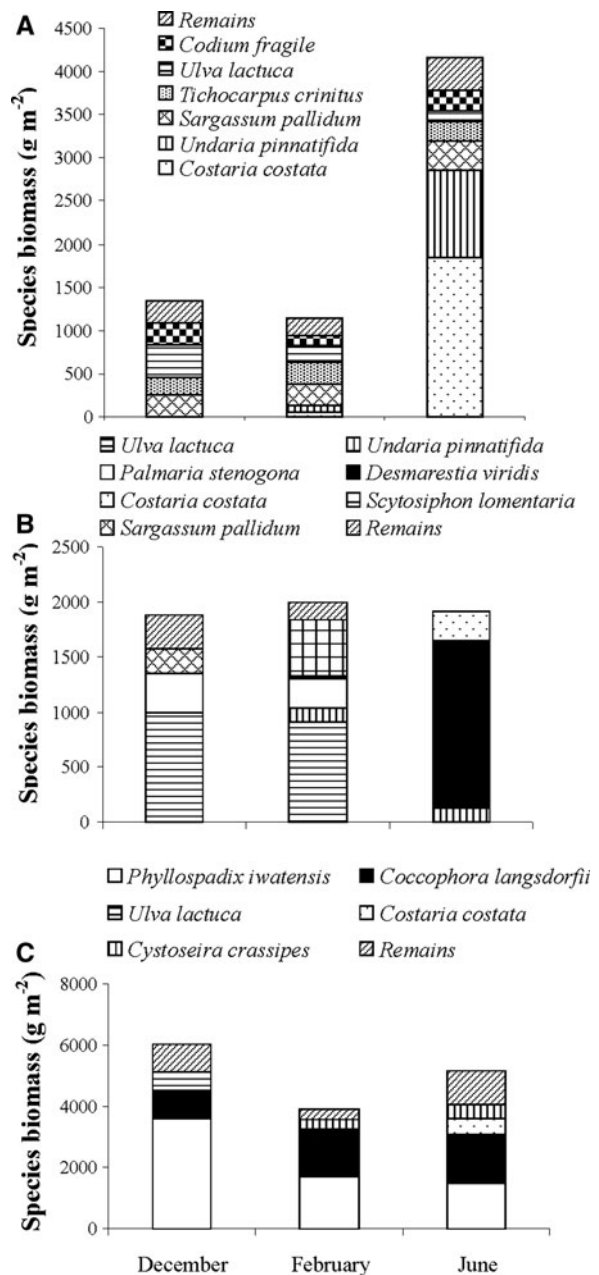


Fig. 4. Seasonal change of biomass for the most abundant species in different ecotopes (see Figure 3): (A) Group 2C, rocky-boulder bottom (Sites 1, 2 and 4), 0.5–2 m depth-zone; (B) Group 1, depth of 3 m or more; (C) Group 2A, muddy-gravel bottom (Site 3), 0.5–1.5 m depth. Remains mean biomass of all other macrophytes species.

resulted in the apparent increase of the brown alga contribution to the total biomass in June.

Significant differences in substratum types in Sobol Bay were reflected in the diversity of macrophyte assemblages. A *Phyllospadix iwatensis* bed with numerous accompanying seaweeds dominated on muddy-gravel bottoms, while rock, rocky platform and boulders were colonized by macroalgae only. Thus, the macrophyte composition in Sobol Bay showed marked differences in relation to depth and substratum type. A total of four macrophyte assemblages were identified in the bay. The first assemblage was co-dominated by *Phyllospadix iwatensis* and *Coccophora langsdorfii*. This year-round assemblage existed on muddy-gravel bottoms in the depths ranging from 0.5 to 2 m. The second assemblage, co-dominated by annual brown seaweeds *Desmarestia viridis* and *Costaria costata*, occurred at depths greater than 3 m at late spring (in June). Two other assemblages occurred on the rocky-boulder bottoms at 0.5–2 m depths, but they were temporally separated. The assemblage co-dominated by annual laminarian algae (*Undaria pinnatifida* and *Costaria costata*) developed at late spring. During autumn and winter, this assemblage was succeeded by the *Tichocarpus crinitus*, *Ulva lactuca*, *Codium fragile* and *Sargassum pallidum* co-dominated assemblage.

There are several differences between this study and former reports on Peter the Great Bay (Perestenko, 1980). First of all, according to our observations, in Sobol Bay polydominant assemblages formed by eight macrophyte species (the seagrass *Phyllospadix iwatensis*; brown algae *Costaria costata*, *Desmarestia viridis*, *Sargassum pallidum*, *Undaria pinnatifida* and *Coccophora langsdorfii*; red alga *Tichocarpus crinitus*; green algae *Ulva lactuca* and *Codium fragile*) are represented. According to Perestenko (1980), in Peter the Great Bay, the monodominant assemblages with a high number of accompanying species prevailed. Polydominant assemblages are more characteristic of the southern parts of the Sea of Japan (Kim *et al.*, 1998; Yoo 2003a, b; Chavanich *et al.*, 2006) and shallow bays of Peter the Great Bay (Kozhenkova, 2008). Secondly, among dominant species, algae of warm water affinity (*Undaria pinnatifida*, *Codium fragile*, *Ulva lactuca* and *Coccophora langsdorfii*) are represented. These species dominate along the Korean coast of the Sea of Japan (Kim *et al.*, 1998; Yoo, 2003a, b; Chavanich *et al.*, 2006). In contrast, the majority of subtidal assemblages in Peter the Great Bay are dominated by species of cold water affinity (Perestenko, 1980).

The lack of quantitative data in the previous studies of Sobol Bay macrophyte assemblages (Zaks, 1927) does not allow an adequate comparison of the results of the two works and a conclusion on the long-term changes of macrophyte assemblages. However, floristic description shows that some species of cold-water affinity, such as fuclean *Silvetia babingtonii* (Harvey) E.A. Serrão, T.O. Cho, S.M. Boo & Brawley and *Fucus* sp., reported by Zaks (1927), were not found in the present study. The disappearance of fucoids was earlier reported for other parts of Peter the Great Bay (Kozhenkova, 2008) and interpreted as being linked to both climatic changes and anthropogenic pressure. In the previous study on the species composition and biomass of subtidal macrophytes in Sobol Bay by Zaks (1927), three typical assemblages were reported in the spring–summer period: a *Phyllospadix iwatensis* assemblage; a *Sargassum* spp., *Coccophora langsdorfii* and *Cystoseira crassipes* dominated assemblage with numerous accompanying species; and an

assemblage of *Desmarestia viridis*. The main difference observed between the present study and the previous descriptions is a replacement of the assemblage of sargassaceous algae with the assemblage of laminarian algae (*Undaria pinnatifida* and *Costaria costata*). However, this phenomenon may represent normal stochastic variations of macrophyte assemblages.

We found that the macrophyte assemblages in Sobol Bay have not dramatically changed during the past 80 years. In order to understand inter-annual variations of macrophyte communities as well as the long-term changes due to human impacts or climatic change, a programme should be established to routinely monitor the macrophyte assemblages classified here using quantitative data.

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