

# Distribution, Plant Communities, and Ecophysiology of *Cakile edentula* (Brassicaceae), an Invasive Alien Species in Primorye Territory, Russian Federation

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**Abstract**—We studied the distribution and relationship with the indigenous supra-littoral species of the North Atlantic species *Cakile edentula* (Bigelow) Hook. along the eastern coast of Primorye Territory. The *C. edentula* annual community usually occupies sandy beaches and outer ribs of front dunes free of vegetation. This species is also associated with different plant communities of beaches and dunes: *Salsolium komarovii*, *Elymo–Caricetum kobomugi*, *Elymo–Caricetum pumilae*, *Artemisia stellerianae–Leymetum mollis*, and *Leymo mollis–Glehnietum littoralis*. Furthermore, it forms short-lived communities with *Jacobea pseudoarnica*, *Lathyrus japonicus*, and *Rosa rugosa* in some parts of the coast, and also communities with *Phragmites australis* on salt marshes in the Tumen River estuarine zone. We investigated the functional traits of *C. edentula* leaves: volume of mesophyll cell, the number of chloroplasts per mm<sup>2</sup> of leaf surface, the ratio of the total surface area cells to the unit leaf area (Ames/A), the total number of chloroplasts per cell. The high values of the integral parameters of *C. edentula* leaf mesophyll are quite comparable to those of desert halophytes and 1.5–4 times higher than the values reported for several of the Northeast Asian coastal species such as *Artemisia stelleriana*, *Chorisis repens*, *Glehnia littoralis*, *Jacobea pseudoarnica*, *Lathyrus japonicus*, et al. According to its ecological strategy, *C. edentula* can be attributed to ruderal–stress-tolerant (RS) species. This study was based on standard phytosociological and physiological methods with examination of quantitative leaf anatomy.

**Keywords:** *Cakile edentula*, plant communities, non-indigenous species, naturalization, quantitative leaf anatomy, Peter the Great Bay, Russia

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## INTRODUCTION

Marine waters, coasts, shelf islands, and estuarine zones are ecosystems that are highly exposed to biological pollution. Many countries, including the Russian Federation, organize targeted studies and monitoring of potentially dangerous non-indigenous marine and coastal species that can have negative impacts on populations and communities of native species to minimize risk of their wide distribution (Cohen and Carlton, 1996; Ruiz et al., 1997, 1999; Adrianov, 2014; Dgebuadze, 2014). Such studies were conducted in Peter the Great Bay by researchers of the Center for the Study of Marine Bioinvasions at the model object “Far Eastern Marine Biosphere State Nature Reserve.” They have registered a total of 194 alien species, including 72 higher vascular plants that naturalized on islands and the coast (Ivin et al., 2014;

Chubar, 2015). This checklist includes also *Cakile edentula* (Bigelow) Hook. (*Brassicaceae*).

*Cakile edentula* is considered as an alien and invasive species in many countries across the world. Its biological and ecological characteristics have been considered in a number of dedicated studies (Barbour and Rodman, 1970; Rodman, 1974, 1986; Boyd and Barbour, 1986; Cody, M.L. and Cody, T.W., 2004; Taira and Hiroko, 2006; Kil and Lee, 2008; Kiyosue and Asai, 2009; Cousens, R.D. and Cousens, J.M., 2011; Cousens et al., 2013; Ryu et al., 2018). This plant is characterized by high growth rate, short life cycle, and great reproductive effort, which are manifested in harsh environmental conditions (Maun and Payne, 1989; Maun et al., 1990; Zhang and Maun, 1992). It produces dimorphic fruit which can float on water for up to 10 weeks and exposed seeds thereof may germinate (Rodman, 1974). *Cakile edentula* seeds and seed-

ling vary in quality: seeds from the lower and upper segments of fruit differ significantly in seed mass, cotyledon area, chlorophyll content (Zhang, 1993) and also in phenotypic plasticity in response to soil moisture and sand burial (Zhang, 1995). All these characteristics provide a high adaptive potential of *C. edentula* to various habitat conditions. Also, such factors as unoccupied habitats (Rodman, 1986), the local climate that fits into the range of climatic conditions of original habitat (Ryu et al., 2018), the production of dimorphic fruits, distal and proximal, with the different routes of dispersal (Sauer, 1965; Payne and Maun, 1981; Maun and Payne, 1989; Maun et al., 1990) and fruit and seed polymorphism (Zhang, 1993, 1994, 1995) provide the invasion of *C. edentula* through all its world-wide range.

As is known, after invading the natural coastal vegetation in Northeast Asia, *C. edentula* then competes with indigenous species therein (Taira and Hiroko, 2006; Fukuda et al., 2013; Ryu et al., 2018). Our previous study (Chubar, 2015) showed that local populations of *C. edentula* on the coast of Peter the Great Bay can be ephemeral and shift annually along sandy beaches. A monitoring of the spread of *C. edentula* has shown that its presence is more consistent and stable within fore-dune systems. Similarly, as in other parts of its invasive range in Northeast Asia, *C. edentula* co-dominates here forming mixed communities with indigenous species into the *Salsolietum komarovii* Ohba, Miyawaki et Tx. 1967 ephemeral community, and also into the *Leymetum mollis* Ohba, Miyawaki et Tx. 1973 initial community. Its coverage and number are significantly reduced in the *Elymo–Caricetum kobomugi* Miyawaki 1967, *Elymo–Caricetum pumilae*, *Leymo mollis–Glehnietum littoralis* nom. nov. prov., and *Leymo mollis–Lathyroetum japonici* Ohba, Miyawaki et Tx. 1973 communities. Furthermore, some expansion of the *C. edentula* coenotic area is also observed. It has invaded the *Leymo mollis–Rosetum rugosae* nom. nov. prov., *Artemisia stellerianae–Leymetum mollis* Ohba, Miyawaki et Tx. 1973, and *Leymo mollis–Senecionetum pseudoarnicae* Tatewaki et Yamanaka 1939 communities, and also *Phragmitetum australis* Savich 1926 estuarine community. Such activity of *C. edentula* requires monitoring its reproduction and distribution continuously.

It is well known that leaf anatomy structures play an important role in plant ecology (Mokronosov, 1978; Gorishina, 1989; Pyankov, 1993). The mesostructure parameters of the photosynthetic apparatus characterize the potential photosynthetic capacity of leaves and can be used as a marker of species' ecological strategy (Pyankov et al., 1998). The leaf mesostructure and functional characteristics of the invasive plant *Heracleum sosnowskyi* Manden. differ significantly from those of the indigenous plant *Heracleum sibiricum* L. Structural and functional traits of the leaves and roots provided 2-fold higher net assimilation rate and 2.5-fold larger relative growth rate in the

invasive species *H. sosnowskyi* (Veselkin et al., 2017; Betekhtina et al., 2019). No such comparative physiological studies have been conducted for the genus *Cakile* Mill. It is reported, however, that the non-indigenous European species *C. maritima* Scop. was replaced by the introduced Atlantic species *C. edentula* in south-western North America (Barbor and Rodman, 1970; Boyd, 1988), New Zealand (Cousens, R.D. and Cousens, J.M., 2011), and Australia (Cousens et al., 2013).

*Cakile edentula* has been categorized as a C<sub>3</sub>-species, with  $\delta^{13}\text{C}$ -value reaching 29‰ (Martin et al., 1982). It is a diploid,  $2n = 18$  (Kruckeberg, 1948; Mulligan, 1964; Taylor and Mulligan, 1968; Probatova et al., 2012). Its leaf is unifacial and has an average thickness of 1020  $\mu\text{m}$ . The leaf tissue layers include upper epidermis (4%), upper mesophyll (37%), vascular tissue/central parenchymal cells (18%), lower mesophyll (37%) and lower epidermis (4%) (Hancock, 2009).

Since this species can potentially pose a threat to indigenous species, we carried out a comparative analysis of leaf mesostructure in *C. edentula* and Northeast Asian maritime (=supralittoral) species such as *Glehnia littoralis* Fr. Schmidt, *Chorisis repens* DC., *Jacobea pseudoarnica* (Less.) Zuev, *Linaria japonica* Miq., *Lathyrus japonicus* Willd., *Honkenya peploides* subsp. *major* (Hook.) Hultén, *Artemisia stelleriana* Besser, *Artemisia littorcola* Kitam., *Carex pumila* Thunb., *Leymus mollis* (Trin.) Pilg., typical halophytes such as *Salicornia europaea* L. and *Suaeda salsa* (L.) Pall., and also the halotolerant species *Phragmites australis* L. in order to assess their potential competition for environmental resources.

According to various estimates, the Northeast Asian supralittoral flora includes 12–30 native species (Ohba et al., 1973; Ihm et al., 2001). An analysis revealed the presence of the main groups of halophytes on sea coasts: euhalophytes, crinohalophytes, and glycohalophytes with succulent, dorsoventral, and homogeneous types of leaf structure (Voronkova et al., 2008). Members of these groups significantly differ in parameters of leaf mesostructure, which indicates the diversity of pathways of their structural adaptation to habitat conditions on the sea coasts (Burundukova et al., 1997; Burkovskaya, 2008).

The current study aimed to investigate the distribution of *C. edentula* on the Peter the Great Bay coast. Another goal was to carry out a comparative analysis of the leaf mesostructure parameters in *C. edentula* specimens from three localities in order to identify, on their basis, the ecological strategy type of this species. Also, we carried out a comparison analysis of *C. edentula* leaf mesostructure parameters with those of leaves of indigenous coastal species of the succulent, homogeneous and dorsoventral types and assessed the competitiveness of *C. edentula* in conditions of Northeast Asia sea coast.

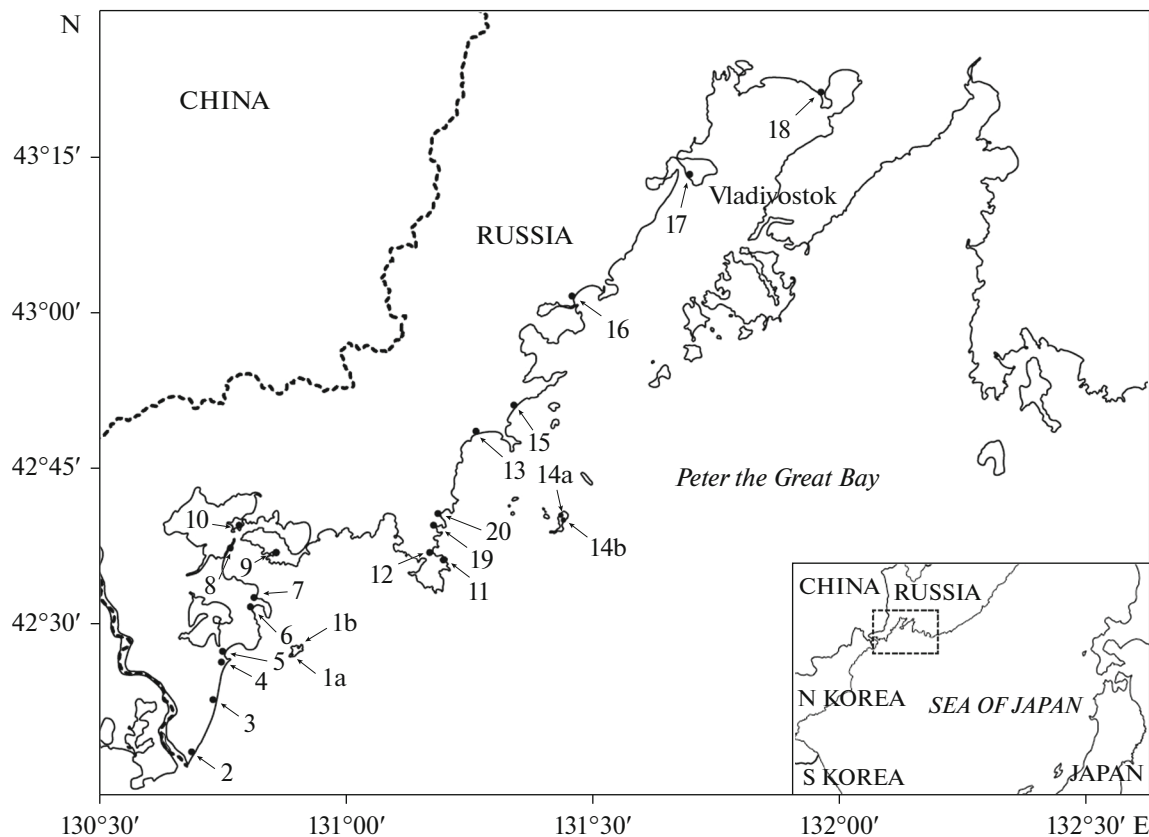


Fig. 1. Locations of *Cakile edentula* in Primorye Territory (number of location corresponds to the number of the site in Table 1).

## MATERIALS AND METHODS

### *Study Area and Plant Communities*

The southwestern coast of Peter the Great Bay and islands were surveyed during 2007–2020 (from April to November) to identify the pattern of distribution of *C. edentula*. Geographical coordinates of *C. edentula* individuals that invaded the coast were recorded with GPS receiver. The distribution of *C. edentula* and its approximate number at 20 sites are shown in Table 1 and Fig. 1. To examine the plant communities with *C. edentula*, we used the phytosociological methods with the emphasis on species composition (Braun-Blanquet, 1964; Westhoff and Maarel, 1973). A total of 60 phytosociological relevés were collected from 20 sites along the coastline. The size of the relevé area is equal to the minimum area; this parameter varies between different sites of the coast. Forty relevés from monitored ten sites were included in the phytosociological table. Twenty repetitive relevés of pure *C. edentula* ephemeral communities and single relevé of *Leymo mollis*–*Glehnietum littoralis* community (at unmonitored sites in Srednyaya Cove) were not included in the calculations. Plots were stratified into floristically similar groups on the basic presence-absence criteria TWINSPAN (Hill, 1979). Also, to evaluate habitats, the methods of the coastal fore-

dune zoning (Doing 1981, 1985) were used. The calculation procedures were carried using the program MS Excel. The nomenclature of syntaxa was according to the International Code of Phytosociological Nomenclature (Weber et al., 2000). New syntaxa (*Leymo mollis*–*Glehnietum littoralis*, *Leymo mollis*–*Rosetum rugosae*, *Leymo mollis*–*Caricetum pumilae*) were introduced by us provisionally, as more research on coastal vegetation in Primorye Territory was needed. The nomenclature of the species was according to Plant of the World Online.

### *Quantitative Leaf Anatomy*

The quantitative characteristics of leaf mesostructure were studied using the method of Mokronosov (1978). The cell number per leaf area and the chloroplast number per cell were estimated using the material fixed with a 3.5% glutaraldehyde solution in phosphate buffer (pH 7.0). Pieces of leaves of specified area, cut out of the middle part of five leaves, were macerated by heating briefly in 50% KOH at 80–90°C. Cells were counted in a Goryaev' chamber under a light microscope (20 replicates). The number of chloroplasts, in 30 cells, as well as the width and length of 30 cells and chloroplasts, were determined in a cell suspension made from leaf pieces cut out of the

**Table 1.** The studied localities and the occurrence of *Cakile edentula* in Primorye Territory

Number of site	Locality	Latitude N	Longitude E	Approximate number* (total count)	Fieldworks (research period)
1a	Western coast of Furugelm Island	42°27'51.2"	130°54'47"	+++	Aug. 25, 2007–June 21, 2019
1b	Northern coast of Furugelm Island	42°28'19.9"	130°55'38.6"	++++	Aug. 10, 2008–July 25, 2011; Sept. 3, 2018; June 22, 2019
2	Northern sea coast in the Tumen River estuarine zone	42°21'39.5"	130°44'42.6"	++	Aug. 30, 2009–Oct. 27, 2013; June 19, 2016
3	Sea coast in the vicinity of Mount Golubiny Utes	42°25'9.3"	130°45'45.3"	++	Aug. 28, 2009–Aug. 13, 2017
4	Cape Ostrovok Falshivy	42°27'8.1"	130°47'0.4"	+++	Aug. 20, 2009–Sept. 22, 2017
5	Sivuchya Cove	42°28'13.7"	130°46'56.1"	++++	Aug. 13, 2008–Oct. 24, 2018
6	Kalevala Cove	42°32'1.8"	130°50'12.6"	+++	Jan. 8, 2017; Oct. 10, 2019
7	Pemzovaya Cove	42°32'36.6"	130°50'33.3"	+++	Sept. 4, 2018; June 24, 2019
8	Cape Nazimov and Nazimov sea spit	42°36'42.3"	130°46'43.1"	+++	Sept. 8, 2012
9	Minonosok Cove	42°32'51"	130°52'23.3"	++	Sept. 5, 2018; Oct. 12, 2019
10	Postovaya Cove (in Posjet Bay)	42°39'0.3"	130°47'51.1"	+++	Sept. 6, 2018; June 24, 2019
11	Spaseniya Cove	42°36'24.1"	131°13'18.1"	+++	July 3, 2018–Oct. 4, 2020
12	Astafyev Cove	42°37'08.7"	131°11'91.7"	++	July 18, 2018
13	Boysman Cove	42°46'24.6"	131°15'33.2"	++	Aug. 10, 2012
14a	Western coast of Bolshoy Pelis Island	42°40'21"	131°27'39.9"	+	June 29, 2011–Aug. 6, 2012
14b	Eastern coast of Bolshoy Pelis Island	42°39'11.7"	131°27'42.1"	+	Oct. 18, 2011
15	Baklan Cove	42°49'54.8"	131°22'2.8"	+	Oct. 20, 2011
16	Narva Cove	43°0'21.3"	131°29'54.4"	+	Aug. 20, 2012
17	Peschany Peninsula	43°10'32.6"	131°45'26.5"	+	Aug. 7, 2018
18	De Vries Peninsula	43°18'28"	131°58'18.7"	+	Oct. 12, 2016
19	Srednyaya Cove	42°36'27.1"	131°12'21.5"	++	Sept. 21, 2019; July 15, 2020
20	Gorshkov Cove	42°40'11"	131°12'52.9"	+	Sept. 23, 2019

\* Sign+, means that from 1- to a few individuals were observed; ++, up to 100 individuals; +++, 1000 individuals; +++++, 10000 and more individuals.

middle part of five leaves macerated in 5% CrO<sub>3</sub> in 1 N HCl. The cell suspension mounts were examined under Zeiss Axioskop-40 light micro-scope and photographed with Zeiss AxioCam (HRs) digital camera using AxioVision ver. 4.8.3. Some of measurements (leaf thickness, cell and chloroplast length and width) were made using the microscope images. The cell volume and cell surface area were calculated using the geometric formula describing a cylinder. The chloroplast surface area was calculated using the geometric formula describing an ellipsoid. The integral characteristics were determined as follows: the number of chloroplasts per unit area of leaf was calculated as the number of chloroplasts per cell multiplied by the number of cells per unit area of leaf; the total cell surface area per unit leaf area (Ames/A) was determined by multiplying the average cell surface area by the cell number per leaf area. The total chloroplast surface area per unit leaf area (Achl/A) was determined by multiplying the average chloroplast surface area and the chloroplast number per unit leaf area.

A detailed study of the leaf mesostructure was carried out using the equipment of the Center for Microscopy at the Botanical Garden-Institute, FEB RAS (Vladivostok, Russia).

#### Statistical Analysis

The mesostructure parameters were determined at three sites (Furugelm Island, Cape Ostrovok Falshiviy, Sivuchya Cove). The parameters were compared using analysis of variance (ANOVA) with a post-hoc Tukey's test. Differences were considered significant at  $P < 0.05$ . The significance of differences between *C. edentula* and species with a succulent, homogenous and dorsoventral leaf structure was assessed using the nonparametric Kruskal–Wallis (ANOVA) test. The boxes indicate mean and standard error, and whiskers are standard deviation.

## RESULTS

### Distribution and Communities of *Cakile edentula*

In Peter the Great Bay *C. edentula* was first found as a few individuals on the Furugelm Island coast in 2006, which coincided in time with the finding of this species on Korea (Chubar, 2008; Kil and Lee, 2008). During the past 14 years, it has spread approximately 350 km northward along the coastline of Primorye Territory and is currently recorded from 20 localities (Fig. 1).

The number of individuals in the local populations of *C. edentula* varies significantly, exceeding 1000 individuals at some southern points (Table 1). *Cakile edentula* shows a high dominance (with a cover of 25–75%) on open sandy beaches free of vegetation and also in the *Salsolietum komarovii* Ohba, Miyawaki et Tx. 1967 ephemeral community as well as on sandy

beaches as on embryo dunes (Table 2). It forms a similar percentage of cover in the *Leymetum mollis* (= *Elymetum mollis*) Ohba, Miyawaki et Tx. 1973 initial community on the frontal part of fore-dunes (Table 2). A smaller percentage (cover 5–12%) is observed in the *Elymo–Caricetum kobomugi* Miyawaki 1967, *Artemisia stellerianae–Leymetum mollis* Ohba, Miyawaki et Tx. 1973, *Leymo mollis–Glehnionetum littoralis*, and *Leymo mollis–Caricetum pumilae* communities in the stabilized sand-dune areas. *Cakile edentula* is less common in the *Leymo mollis–Rosetum rugosae*, *Leymo mollis–Lathyroetum japonici* (= *Lathyro japonici–Elymetum mollis*) Ohba, Miyawaki et Tx. 1973, and *Leymo mollis–Senecionetum pseudoarnicae* Tatewaki et Yamanaka 1939 initial communities, where it forms a smaller percentage cover (Table 2). The latter three communities above are associated mostly with habitats on poorly stabilized substrates: elevated sandshingly storm deposits. The *Rosa rugosa* community generally tends to high coastal terraces and dunes but in some places it forms on sandy embryo dunes, and at foot of coastal cliffs. *Cakile edentula* occurs also in the *Phragmitetum australis* community on salt marshes, sand deposits, and waterlogged areas in the Tumen River estuarine zone but with the lower frequency and a cover of 0.5–1% (Table 2). Its fruits enter saline habitats with tides and storms through a system of communicating ducts; seedlings develop after habitats dries out.

Thus, the sea coasts of the Korean Peninsula, Japanese Archipelago, and Primorye Territory have similar characteristics of habitats and vegetation with the invasive species *C. edentula*. The new invaded plant communities on the Peter the Great Bay coast are *Artemisia stellerianae–Leymetum mollis*, *Leymo mollis–Rosetum rugosae*, *Leymo mollis–Senecionetum pseudoarnicae*, and *Phragmitetum australis*. *Cakile edentula* has an unstable status in the latter three communities.

### Quantitative Leaf Anatomy

Leaf of *C. edentula* is succulent with the isolateral-palisade type of mesophyll structure. The results of a comparative research showed that the structural characteristics of *C. edentula* leaves from the three studied localities have significant differences in the following parameters: leaf thickness, cell volume and the number of chloroplasts in them, and number of cells (Table 3). The greatest leaf thickness (1600 μm) corresponds to the largest number of cells per area of the leaf, but, at the same time, the minimum cell volumes and number of plastids in them were recorded from the plants found on Furugelm Island (site 1a). The maximum size of mesophyll cells and their minimum number per unit of leaf area were in plants from Cape Ostrovok Falshiviy (site 4).

The integral parameters of leaf mesostructure such as Ames/A, Achl/A, and the number of chloroplasts



Table 2. (Contd.)

Association	A			B			C			D			E			F			G			H			I			Constancy	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26			
Sequential number	(1a)*	(5)	(11)	(1b)	(4)	(5)	(12)	(1a)	(10)	(1a)	(1a)	(5)	(12)	(7)	(11)	(5)	(7)	(2)	(3)										
Site number	sb	sb	sb	sd	sd	sd	sd	sd	sd	ssht	sd	sd	sd	sht	sshb	sd	sht	m	m										
Habitats	100	20	50	100	10	25	20	100	25	5	20	100	50	100	100	25	10	100	100										
Area, m <sup>2</sup>	10	45	65	70	50	50	55	65	45	70	55	40	100	55	50	50	55	80	100										
Total cover, %	Number of species																												
Name of species	9	12	9	5	4	4	5	17	29	27	11	9	8	15	17	6	20	19	10										
<i>Polygonum fusco-ochreatum</i> Kom.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Tripolium pannonicum</i> (Jacq.) Dobroc. ( <i>Asper tripolium</i> L.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Suaeda salsa</i> (L.) Pall. ( <i>S. heteroptera</i> Kitag.)	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Isatis tinctoria</i> L. ( <i>I. japonica</i> Miq.)	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Scutellaria strigillosa</i> Hemsl.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Puccinellia nipponica</i> Ohwi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Carex scabrifolia</i> Steud.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Spergularia marina</i> (L.) Besser	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Inula japonica</i> var. <i>ramosa</i> (Kom.) C.Y. Li	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Dianthus chinensis</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Ligusticum scoticum</i> subsp. <i>hultenii</i> (Fernald) Calder & Roy L. Taylor	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Lamium album</i> subsp. <i>barbatum</i> (Siebold & Zucc.) Mennema	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Chenopodium album</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Thlaspi arvense</i> L.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Onagra biennis</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Bunias orientalis</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Oxybasis glauca</i> (L.) S. Fuentes, Uotila & Borsch ( <i>Chenopodium glaucum</i> L.)	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Galium spurium</i> subsp. <i>spurium</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Bolboschoenus yagara</i> (Ohwi) Y.C. Yang & M. Zhan	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
<i>Humulus scandens</i> (Lour.) Merr. ( <i>Humulopsis scandens</i> (Lour.) Grudz.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

(1a)\*, Number of the site in Table 1; 1\*\*, J. Braun-Blanquet (1964) scale (r–5), A, *Salsoletum komarovii* community; B, *Leymetum mollis* community; C, *Elymo–Caricetum pumilae* community; D, *Leymo mollis–Rosetum rugosae* community; E, *Elymo–Caricetum kobomugi* community; F, *Leymo mollis–Senecionetum pseudoarcticae* community; G, *Leymo mollis–Artemisietum stellerianae* community; H, *Leymo mollis–Lathyroetum japonici* community; I, *Piragmitetum australis* community; sb, sandy beaches; sd, sandy dunes; sht, shingly beaches; sshb, shingly/sandy beaches; sst, shingly terraces, m, salt marshes. Non-diagnostic species included in one or two relevés are as follows: *Angelica gmelinii* (DC.) Pimenov7; +; *Ambrosia artemisiifolia* L. 10; r; *Artemisia scoparia* 10; +; *Iris oxypetala* Bunge 10; r; *Lactuca indica* L. 7; +; *Solanum nigrum* L. 7; +.

**Table 3.** Leaf mesostructure characteristics of *Cakile edentula*

Parameters	Location		
	Cape Ostrovok Falshivy	Furugelm Island	Sivuchya Cove
Leaf thickness, $\mu\text{m}$	1000 $\pm$ 150a	1600 $\pm$ 240b	1100 $\pm$ 187a
Number of chloroplasts in cell, sample	205 $\pm$ 19a	83 $\pm$ 12b	120 $\pm$ 15c
Cell volume of mesophyll, $\times 10^3 \mu\text{m}^3$	138 $\pm$ 16a	50.5 $\pm$ 6.3b	70.5 $\pm$ 8.4b
Number of mesophyll cells per $\text{mm}^2$ of leaf surface, $\times 10^1$	203 $\pm$ 10a	479 $\pm$ 24b	318 $\pm$ 17c
Number of chloroplasts per $\text{mm}^2$ of leaf surface, $\times 10^4$	41.6 $\pm$ 6.2a	39.8 $\pm$ 7.8a	38.4 $\pm$ 6.8a
Total mesophyll cell surface area per unit leaf area (Ames/A), $\text{mm}^2/\text{mm}^2$	29.9 $\pm$ 4.5a	29.2 $\pm$ 4.1a	25.4 $\pm$ 3.8a
Total chloroplast surface area per leaf unit area (Achl/A), $\text{mm}^2/\text{mm}^2$	15.1 $\pm$ 2.3a	14.3 $\pm$ 2.1a	13 $\pm$ 1.9a

The letters indicate the significance of differences by post-hoc Tukey' test at  $P < 0.05$ : different letters indicate significant differences between the species in this parameter; the same letters indicate no differences.

per unit of leaf area had similar values for all three sites examined.

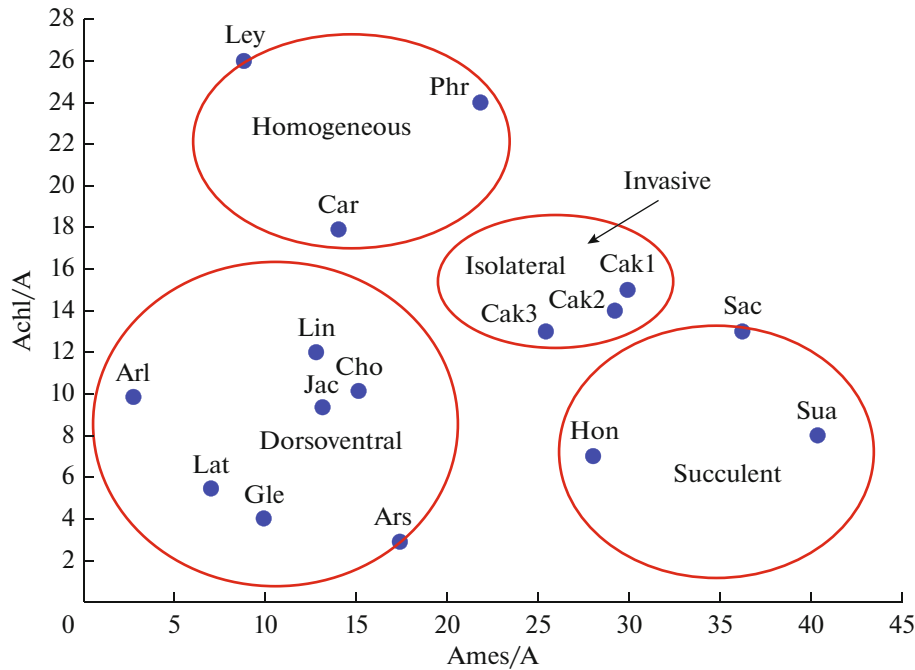
## DISCUSSION

Most plant communities invaded by *C. edentula* on the coastline of Peter the Great Bay belong to the Holarctic class *Honkenyo–Elymetea* Tx. 1966, the order *Honkenyo majoris–Elymetalia mollis* Ohba, Miyawaki et Tx. 1973, the alliance *Senecioni pseudoarnicae–Leymion mollis* Ohba, Miyawaki et Tx. ex Peinado et al. 2011. This vegetation is widely represented on the Pacific coasts of North America and East Asia (Ohba et al., 1973; Ihm et al., 2001; Peinado et al., 2011) including Primorye Territory (Dudov, 2018). The *Rosa rugosa* shrub community typical belongs to the East Asia class *Rosetea multiflorae* Ohba, Miyawaki et Tx. 1973, the order *Rosetalia rugosae* Ohba, Miyawaki et Tx. 1973, and the alliance *Rosion rugosae* Ohba, Miyawaki et Tx. 1973 (Ohba et al., 1973). Plant mixed communities, with co-dominant diagnostic species of the alliances *Senecioni pseudoarnicae–Leymion mollis* and *Rosion rugosae*, are often found on the coast of Peter the Great Bay. The coenotic activity characteristics of *C. edentula* (abundance, frequency, and constancy of its plants) and its impact on the indigenous plant communities are comparable to those in its native range in the mid-Atlantic, where it is dominant species on beaches and a subdominant on adjacent stabilized fore-dunes (Tyndall, 1985). The soil moisture deficit is a possible explanation for the significant decrease in its relative occurrence and projective coverage in stabilized dunes conditions (Tyndall et al., 1986; Cole, 2015). The low values of coverage and occurrence of *C. edentula* in the *Leymo mollis–Senecionetum pseudoarnicae* and *Leymo mollis–Rosetum rugosae* communities in habitats on well-drained sub-

strates are an indirect confirmation of this hypothesis. In contrast to the type of vegetation above, the high competition for resources with dominant and subdominant species can be a cause of the lower frequency and cover of *C. edentula* in the *Phragmitetum australis* community on salt-marsh habitats with substrates of silted-up sands. Plant communities dominated by reeds occupy large areas in the lower Tumen River Valley, particularly in the Pra-Tumen River Late Holocen lagoon-estuary system and wetlands in the recent river delta, and frequently on flat sand terraces formed by severe storms (Chubar, 2000). This vegetation is specific, with communities associated with halophytes *Suaeda salsa* (L.) Pall. (= *S. heteroptera* Kitag.), *Puccinellia nipponica* Ohwi, *Carex scabrifolia* Steud., and psammophytes, including some coastal sea species, such as *Carex pumila* Thunb., *Chorisia repens* DC., and *Leymus mollis* (Trin.) Pilg. All the associations dominated by *Phragmites australis* L. are typically included in the alliance *Phragmitiom communis* W. Koch 1926, the order *Phragmitetalia* W. Koch 1926, and the class *Phragmito–Magno–Caricetea* Klika in Klika et Novák 1941 (Sinelnikova and Taran, 2006; Chytrý, 2007–2013; Onyshchenko and Andrienko, 2012; Golub et al., 2015). A natural salt-marsh, salt swamp vegetation with *Phragmites australis* has been described in a few general reviews and dedicated works (Maarel et al., 1985; Rodwell, 1995; Ihm et al., 2007; Cho et al., 2017; Lee et al., 2018). No dedicated studies on this vegetation in Primorye Territory have been conducted to date.

A comparative analysis of the integral parameters of leaf mesostructure in *C. edentula* and those in Northeast Asian coast plant species has shown as follows. *Cakile edentula* occupies a central position in the scatter plot diagram inferred from the Ames/A (total



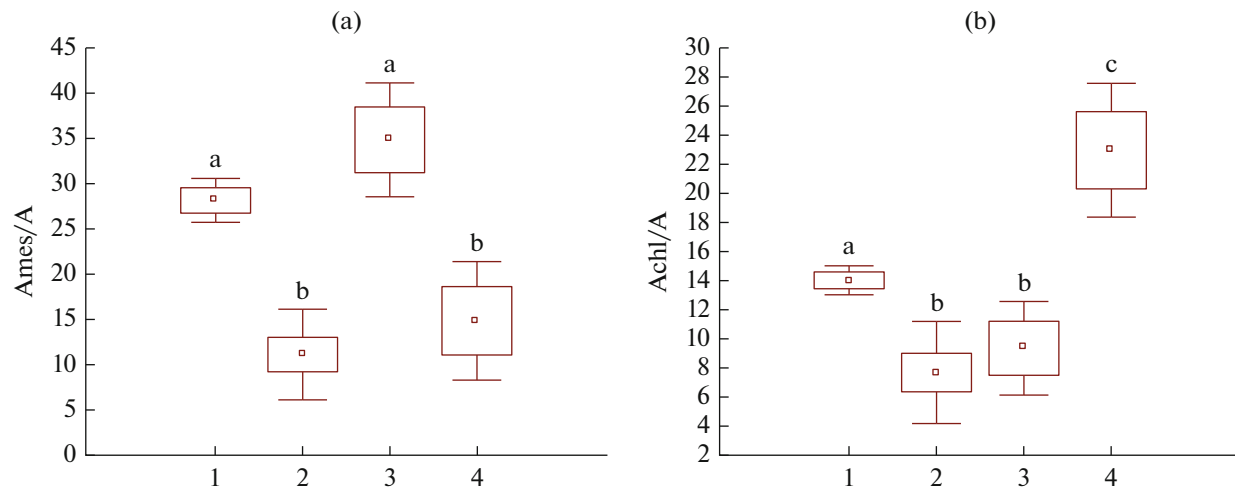


**Fig. 2.** Positions of *C. edentula* and Northeast Asia coastal dicot  $C_3$  species with succulent, dorsoventral, homogeneous mesophyll types in scatter plot diagram of integral characteristics of leaf mesostructure. The letter designations of the species are as follows: Cak1–Cak3, invasive *Cakile edentula* with isolateral–palisade mesophyll type. Species with dorsoventral mesophyll type: Lin, *Linaria japonica*; Gle, *Glehnia littoralis*; Cho, *Chorisia repens*; Lat, *Lathyrus japonicus*; Arl, *Artemisia littoricola*; Ars, *Artemisia stelleriana*; Jac, *Jacobsaea pseudoarnica*. Species with succulent mesophyll type: Sac, *Salicornia europaea*; Sua, *Suaeda salsa*; Hon, *Honkenya peploides* subsp. *major*. Species with homogeneous mesophyll type: Ley, *Leymus mollis*; Car, *Carex pumila*; Phr, *Phragmites australis*. (The values of parameters of supralittoral plants are according to Burundukova et al., 1997; Voronkova et al., 2008; Burkovskaya, 2008.)

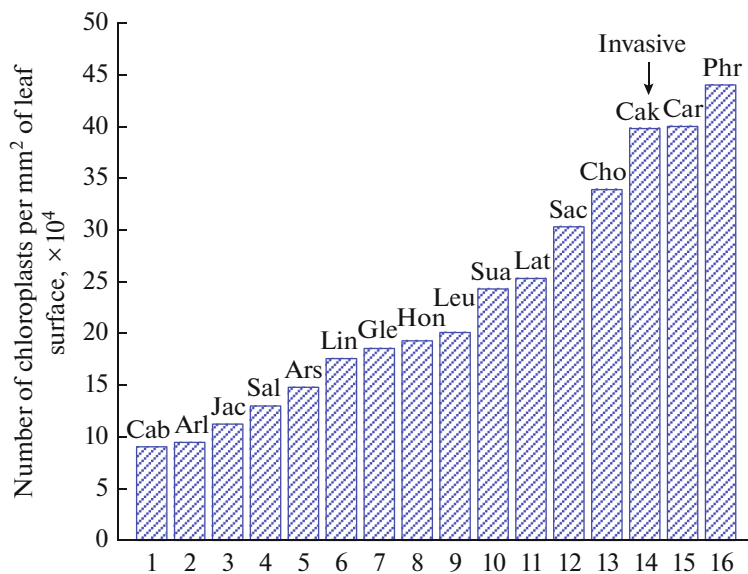
cell surface area per unit leaf area), and Achl/A (total chloroplast surface area per unit leaf area) values between species with dorsoventral, homogenous and succulent types of leaf mesostructure (Fig. 2). The diagram clearly shows that *C. edentula* is superior to species with dorsoventral mesophyll structure in both parameters, but, at the same time, it is inferior in Ames/A values to euhalophytes with the succulent mesophyll type. *Cakile edentula* has the Ames/A values, higher than those in all the studied species with dorsoventral leaf type in a range from 1.6 times (*Artemisia stelleriana*) to 9 times (*Artemisia littoricola*), with an average of 2.3 times for the group (Figs. 2–3a). It also has significantly lower Achl/A values than those in grasses with a homogenous mesophyll structure (Fig. 3b). The box plots show significant differences between *C. edentula* and the structural groups of coastal marine halophytes compared (Fig. 3). Succulents have Ames/A values similar to those of *C. edentula* as is observed in *Honkenya peploides* subsp. *major*, but in *Salicornia europaea* and *Suaeda salsa* the values are 1.3–1.4 times higher ( $p < 0.05$ ) (Fig. 3a). The values of total chloroplast surface area per unit leaf area (Achl/A) in *C. edentula* are 1.6–2 times higher, on average for the groups, than in all the studied coastal species with succulent and dorsoventral leaf structure ( $p < 0.05$ ) (Fig. 3b). The ranking of species by number of chloroplasts per unit area of leaf surface has revealed

that *C. edentula* is superior to most coastal species in this parameter, but not to *Phragmites australis* (Fig. 4). The cell volume in most coastal marine species varies within  $2.1–31.8 \times 10^3 \mu\text{m}^3$ ; the largest mesophyll cells are characteristic of euhalophytes, such as *Honkenya peploides* subsp. *major* ( $234 \times 10^3 \mu\text{m}^3$ ) and *Suaeda salsa* ( $177.1 \times 10^3 \mu\text{m}^3$ ) (Voronkova et al., 2008; Burkovskaya, 2008). *Cakile edentula*, with its value of  $50.3–138 \times 10^3 \mu\text{m}^3$ , occupies an intermediate position in these groups. Thus, the values of such parameters as cell volume, Ames/A, Achl/A, and number of chloroplasts per unit area of leaf surface in *C. edentula* are higher than those in many sea coastal species. Therefore, it manifests a higher potential photosynthetic capacity. However, *C. edentula* is probable much less resistant to saline soil than typical sea-beach and sea-marsh halophytes.

As is known, potential photosynthetic capacity is determined by the activity of each chloroplast, by the number of plastids per unit area of leaf surface, and, to a greater extent, by the number of plastids (Mokronosov, 1978). The low density of cells and chloroplasts in leaves of many sea coastal species explain the low values of intra-leaf assimilation surface expressed as Ames/A (membrane index of the cells) and Achl/A (membrane index of the chloroplasts). It has been shown that Ames/A, and Achl/A correlate



**Fig. 3.** Integral characteristics of leaf mesostructure: the total mesophyll cell surface area per unit leaf area (Ames/A) and the total chloroplast surface area per unit leaf area (Achl/A) of *Cakile edentula* (1),  $n = 3$  (three localities) and Northeast Asia coastal dicot  $C_3$  halophyte species with dorsoventral (2),  $n = 7$ , *Linaria japonica*, *Glehnia littoralis*, *Chorisis repens*, *Lathyrus japonicus*, *Artemisia littoralis*, *Artemisia stelleriana*, and *Jacobea pseudoarnica*, succulent (3),  $n = 3$ , *Salicornia europaea*, *Suaeda salsa*, and *Honkenya peplodes* subsp. *major*, homogeneous (4),  $n = 3$ , *Leymus mollis*, *Carex pumila*, and *Phragmites australis* leaf mesophyll type (the values of parameters of supralittoral plants are according to Burundukova et al., 1997; Voronkova et al., 2008; Burkovskaya, 2008). Box in mean and standard error of the mean; whiskers are standard deviation. Different letters indicate significant differences by Kruskal–Wallis ANOVA test at  $P \leq 0.05$ .



**Fig. 4.** Positions of *C. edentula* and Northeast Asian coastal dicot  $C_3$  species with succulent, dorsoventral, homogeneous mesophyll types in scatter plot diagram of integral characteristics of leaf mesostructure (the values of parameters of supralittoral plants are according to Burundukova et al., 1997; Voronkova et al., 2008; Burkovskaya, 2008). The letter designations of the species are as follows: Cak, invasive *Cakile edentula* with isolarteral-palisade mesophyll type. Species with dorsoventral mesophyll type: Lin, *Linaria japonica*; Gle, *Glehnia littoralis*; Cho, *Chorisis repens*; Lat, *Lathyrus japonicus*; Arl, *Artemisia littoralis*; Ars, *Artemisia stelleriana*; Jac, *Jacobea pseudoarnica*. Species with succulent mesophyll type: Sac, *Salicornia europaea*; Sua, *Suaeda salsa*; Hon, *Honkenya peplodes* subsp. *major*. Species with homogeneous mesophyll type: Leu, *Leymus mollis*; Cab, *Carex kobomugi*; Car, *Carex pumila*; Phr, *Phragmites australis*.

positively with the  $CO_2$  conductance of mesophyll (Laisk et al., 1970; Nobel, 1991). The maximum values of plastid number, Achl/A, and potential photosynthesis were recorded from desert sclero-xerophytes

(Mokronosov, 1978; Vakhrusheva, 1989). Plants of the temperate climate zone generally differ from subtropical plants by lower values of plastids number per unit area of leaf surface and, Ames/A (Pyankov, 1993).

However, the mesostructure of the photosynthetic apparatus in the boreal Atlantic  $C_3$  species *C. edentula* has the characteristics of the photosynthesis system with a high potential capacity similar to the characteristics of desert xero-halophytes. This provides it with certain advantages over the Northeast Asian coastal  $C_3$  species *Artemisia littoricola*, *A. stelleriana*, *Chorisis repens*, *Glehnia littoralis*, *Lathyrus japonicus*, *Linaria japonica*, and *Jacobeia pseudoarnica*.

Thus, the high photosynthetic capacity of leaves in *C. edentula* is an important factor that increases its competitiveness to indigenous coastal Northeast Asian species.

Identification of plant strategies makes it possible to estimate its competitive potential and the ability to adapt to transitory stresses and irreversible environmental changes (Grime, 1979). The type of ecological strategy of a species is genetically determined and can be experimentally identified based on its morphological and functional characteristics (Grime, 1979; Pyankov et al., 1998). According to the *C. edentula* leaf mesostructure parameters, there is a mixed type of ecological strategy—ruderal-stress-tolerant (RS-type). The features of *C. edentula* ecological strategy, as compared to that of typical representatives of the concurrent (C), ruderal (R), and stress-tolerant (S) strategy (Pyankov et al., 1998; Burundukova et al., 2018), are a combination of traits of different strategies. It has high values of Ames/A and chloroplast number per unit of leaf surface; however, its cell number is similar to that in ruderal species, but lower than in concurrent ones; its value of cell mesophyll volume is significantly higher than in ruderal and concurrent species. In values of these parameters, it is similar to stress-tolerant species from the Middle Ural and the Russian Far East (Pyankov et al., 1998; Burundukova et al., 2018).

The mixed RS-type of strategy, identified on the basis of the data of the leaf mesostructure, explains the behavior of the *C. edentula* observed and makes it possible to predict the further situation. As a RS-strategy species, *C. edentula* does not compete with typical representatives of the C-strategy such as *Phragmites australis*. It cannot co-dominate in stable communities and only slightly penetrates into closed communities. It also cannot stand high levels of stress such as drought or high salinity. Therefore, its presence in most stable Northeast Asian coastal plant communities is limited. *Cakile edentula* actively competes with *Salsola komarovii* Iljin. *Salsola komarovii* has a similar RS-type of strategy, but differs from *C. edentula* in the photosynthesis type and leaf structure. It is characterized by  $C_4$  photosynthesis and the salsoloid type of mesophyll structure, but, at the same time, very close Ames/A values ( $24 \pm 5 \text{ mm}^2/\text{mm}^2$ ), while having, nevertheless, a lower number of chloroplasts per unit of leaf surface ( $13 \pm 2 \times 10^4 \text{ mm}^2$ ) (Burundukova et al., 2017).

Our results are consistent with the previously obtained data on the functional properties of the invasive species *Heracleum sosnowskyi* in comparison with those of the indigenous species *Heracleum sibiricum*. The most significant feature of the invasive species, as compared to the native ones, is an increase in the integral mesophyll parameters: the number of cells and chloroplasts per unit of leaf area, the total surface area of cells and chloroplasts per unit of leaf area, and the rate of  $\text{CO}_2$  assimilation (Veselkin et al., 2017). The rate of  $\text{CO}_2$  uptake per unit of leaf area was the greatest in the invasive species *Epilobium adenocaulon* Hausskn., and *E. pseudorubescens* A.K. Skvortsov vs. compared to indigenous species *E. palustre* L. (Ronzhina, 2020). As a rule, the high rate of photosynthesis in invasive species correlates with a high growth rate and productivity, which determines their higher competitiveness vs. indigenous species (Veselkin et al., 2017; Betekhtina et al., 2019; Ronzhina, 2020).

Since, marine coastal plant communities are currently exposed to a high anthropogenic pressure, their structure, as a rule, is disturbed. *Cakile edentula*, as a RS-strategist due to its high assimilation potential, manifests a greater competitive ability in comparison with most Northeast Asian coastal species, and can significantly change the type of indigenous community.

## CONCLUSIONS

On the sea coast of Peter the Great Bay (Sea of Japan, Russian Far East) *C. edentula* has invaded the vegetation of beaches, dunes, strand terraces, and salt marshes. It is now found in the *Leymetum mollis*, *Elymo–Caricetum kobomugi*, *Elymo–Caricetum pumilae*, *Leymo mollis–Artemisietum stellerianae*, *Leymo mollis–Glehnetum littoralis*, and *Salsoletum komarovii* communities, it exerts significant impact. This impact is low in the *Leymo mollis–Rosetum rugosae*, *Leymo mollis–Lathyroetum japonici*, *Leymo mollis–Senecioetum pseudoarnicae* communities, and is almost undetectable in the *Phragmitetum australis* community. The species tends to expand its coenotic range.

*Cakile edentula* compete with many typical Northeast Asian coastal species, being superior to them in potential photosynthetic capacity of the photosynthetic apparatus. *Cakile edentula* turned out to hold an intermediate position between sandy-shingly xero-halophytes and sea-marsh halophytes in terms of characteristics of their photosynthetic apparatus. By its ecological strategy, it is categorized as an RS-type species, as evidenced by values of the leaf mesostructure parameters. These specific features significantly increase the invasiveness of *C. edentula*.

## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interest.* The authors declare that they have no conflicts of interest.

*Statement on the welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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