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# ASSESSMENT OF CARBON STOCK IN THE *ZOSTERA MARINA* LINNAEUS, 1753 ECOSYSTEM ON SANDY SEDIMENTS OF THE SREDNYAYA BIGHT (PETER THE GREAT BAY, THE SEA OF JAPAN) BASED ON FIELD OBSERVATIONS


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Coastal seagrass ecosystems, particularly *Zostera marina* Linnaeus, 1753 ones, are capable of accumulating organic carbon by fixing carbon dioxide *via* photosynthesis. Seagrass biomass is considered as a short-term carbon storage, and underlying bottom sediments, as a long-term one. The research on organic matter accumulation by seagrass ecosystems is mostly carried out in areas with stable sedimentation. For such ecosystems, the importance of seagrass areas within the concept of blue carbon was shown. However, for the seas of temperate latitudes, coastal waters with unstable sedimentation and prevalence of sandy sediments are common, and the scale of carbon storage in seagrass ecosystems is not obvious. In this work, biomass and carbon stock in *Z. marina* leaves and roots, as well as $C_{org}$ concentration and carbon stock in the upper layers of bottom sediments (0.25 m and 1 m thick), were determined for typical habitats in the semi-open Srednyaya Bight (Peter the Great Bay, the Sea of Japan), where sandy sediments prevail. *Z. marina* roots were characterized by 3–20 times lower biomass than its leaves. This difference increased from April to July in accordance with seasonality. Carbon concentrations in the seagrass leaves and roots were similar (33.3 and 31.3% dry weight, respectively). In the habitats with a projective coverage of 50–80%, carbon stock in *Z. marina* tissues was (96.8 ± 37.4) $g\,C{\cdot}m^{-2}$; with 100% coverage, the value increased to 253 $g\,C{\cdot}m^{-2}$. $C_{org}$ concentration in bottom sediments of the Srednyaya Bight ranged within 0.04–0.46% and correlated with content of silt fractions. Under dense *Z. marina* coverage, $C_{org}$ content and the fraction of silt particles in sediments were higher than under sparse ones. The vertical distribution of $C_{org}$ concentration within the upper 15–35-cm layer did not reveal a downward trend in the cores. The main factor controlling $C_{org}$ content was the particle-size distribution of sediments, which suggests a weak expression of reduction diagenesis and the effect of wave mixing of the upper layer of sandy sediments. Data on the bulk density and $C_{org}$ concentration in sediments allowed to calculate carbon stock for the layers of 0.25 and 1 m. The quota of organic carbon in the seagrass tissues did not exceed a third of its amount in the upper layer (0.25 m) of underlying sandy sediments. When extrapolated to a 1 m thick layer, the quota of bottom sediments to $C_{org}$ pool exceeds 90%. Organic carbon enrichment of sandy sediments under the seagrass beds compared to sands of similar particle size beyond the seagrass beds indicates a significant role of *Z. marina* in carbon storage, even in the habitats with the lack of stable and intensive sedimentation. The major factor controlling carbon stock in *Z. marina* ecosystems is $C_{org}$ content in underlying bottom sediments which depends primarily on their particle-size distribution. In this case, the range of variation in carbon stock in the upper layer is an order of magnitude or more. Maps of the seagrass distribution in April and July 2021 were built. The absolute values of carbon stock were calculated, both accumulated in *Z. marina* biomass and deposited in the seagrass-covered sediments. The area of potential *Z. marina* distribution in the Srednyaya Bight was modelled using the MaxEnt 3.4.4 program. According to the results, areas with a predicted probability exceeding 0.5 for the seagrass occurrence occupy about a third of the total area of the bight; out of them, the area with a probability of *Z. marina* occurrence exceeding 0.75 accounts for 11.83 hectares. In fact, the seagrass meadows occupied > 70% of the area with a predicted probability of the species occurrence exceeding 0.5. As shown, the assessment of the contribution of seagrass ecosystems to the storage of carbon accumulating in the coastal zone requires differentiation of water areas by sedimentation regimes and types of bottom sediments. Moreover, the creation of databases with data on $C_{org}$ concentration and stock *per* unit area is needed. Information on the areas of ecosystem distribution obtained by direct mapping and remote sensing is of high significance as well.

**Keywords:** blue carbon, *Zostera marina*, carbon concentration in sandy bottom sediments, remote sensing, Sea of Japan, Peter the Great Bay

Seagrasses are a group of species inhabiting shallows and forming underwater meadows with the area from a few square meters to hundreds of square kilometers. Coastal seagrass ecosystems are capable of fixing carbon dioxide *via* photosynthesis and storing organic carbon in both plant biomass and sediments [Fourqurean et al., 2012; Röhr et al., 2018]. According to some estimates, seagrass habitats occupying 0.1% of seabed surface account for about 10% of annual ocean carbon sequestration [Duarte et al., 2005; Fourqurean et al., 2012]. Biomass of riparian vegetation which is only 0.05% of biomass of terrestrial plants accumulates comparable amounts of carbon over the year [Duarte et al., 2005; McLeod et al., 2011]. At the same time, there are data that these global values of carbon stock in seagrass ecosystems are overestimated [Prentice et al., 2020; Röhr et al., 2018]. However, protection and restoration of seagrass ecosystems are considered among the pillars of the concept of blue carbon to offset increases in atmospheric carbon dioxide [Duarte et al., 2005; McLeod et al., 2011].

Aboveground seagrass biomass serves as a short-term carbon storage due to rapid microbial oxidation under aerobic conditions and grazing by herbivores [Fourqurean et al., 2012]. In contrast, sediments of meadows formed by belowground biomass, plant detritus, and allochthonous organic matter are considered as a long-term carbon storage [Bouillon, Boschker, 2006]. Two mechanisms for increasing $C_{org}$ concentration in bottom sediments of biotopes with seagrasses can be distinguished:

1) synthesis of organic matter by plants and associated epiphytes, with the subsequent partial accumulation of this autochthonous material in sediments;
2) the effect of thickets on local hydrodynamics which leads to accelerated sedimentation of material, prevents resuspension, and is accompanied by a rise in the proportion of aleuropelites in sediments with a corresponding increase in concentration of both autochthonous and allochthonous $C_{org}$ [Lei et al., 2023].

Isotope studies of the genesis of organic matter in sediments based on $\delta^{13}C$ and $\delta^{15}N$ characteristics indicate as follows: the proportion of allochthonous organic matter is usually significantly higher than that of seagrass-synthesized organic matter [Kennedy et al., 2010; Prentice et al., 2020; Röhr et al., 2018]. However, even if in terms of the isotopic composition, most of organic matter in bottom sediments of biotopes with seagrasses is associated with sedimentary material, its accumulation in these biotopes is precisely due to the occurrence of seagrass thickets. Anyway, for correct assessments of the role sea meadows play in $C_{org}$ accumulation in coastal marine ecosystems, it is necessary to differentiate the effect of the production characteristics of the seagrass and sedimentation conditions on $C_{org}$ fluctuations in bottom sediments. Most obviously, sedimentation conditions are reflected in the particle-size distribution of bottom sediments, and this, in turn, affects $C_{org}$ content because of organic matter concentration in silt fractions [Romankevich, 1977]. Therefore, when estimating the difference between $C_{org}$ concentration in bottom sediments of ecosystems with seagrass and without it, it is important to take into account variations in particle-size distribution as clearly as possible, but this task is a challenging one [Miyajima et al., 2017; Prentice et al., 2020].

From the perspective of the concept of blue carbon, the main factor is not so much the supply of organic carbon in plants and the upper layer of bottom sediments, but the rate of its accumulation and removal from the cycle which is controlled primarily by the rate of sedimentation [Gullström et al., 2018; Mazarrasa et al., 2017; Samper-Villarreal et al., 2016]. The most common way to assess the dynamics of sediment accumulation over 50–150 years is the analysis of the vertical distribution of $^{210}Pb$ and $^{137}Cs$ radioisotopes in bottom sediment cores [Marbà et al., 2015]. A similar approach is successfully implemented in water areas with fairly stable accumulation of silty sediment [Lafratta et al., 2020; Tishchenko et al., 2022]. Precisely this set of sedimentary conditions receives the most attention in studies of seagrass ecosystems due to the obvious key role production processes and accumulation of organic carbon in bottom sediments of coastal waters play in carbon sequestration [Lafratta et al., 2020]. Notably, in water areas of temperate latitudes, in particular in the Sea of Japan, thickets of higher vegetation are quite common on predominantly sandy soils [Paimeyeva, 1973, 1979]; there, the upper layer is subject to wave mixing, and the rate of sedimentation is significantly lower [Röhr et al., 2018]. It can be assumed that carbon stock and dynamics of carbon accumulation in such ecosystems will differ from those in ecosystems with silty sediments, but the actual data on sandy biotopes with unstable sedimentation are insufficient.

This work is aimed at determining carbon concentration and stock in the benthic ecosystem of the seagrass *Zostera marina* Linnaeus, 1753, mapping its thickets to take into account the spatial heterogeneity of the ecosystem when estimating carbon stock at the local scale of the study area, and using the results of modeling the potential distribution area of the seagrass when interpreting the data obtained.

## MATERIAL AND METHODS

The study site is the Srednyaya Bight situated in the Far East Marine Reserve (area of 100.57 ha). In terms of the combination of morpholithogenic, hydroclimatic, and biotic characteristics, this bight is typical of the southwestern coast of Peter the Great Bay (the Sea of Japan) (Fig. 1A).

The bight was formed from the lower parts of three smaller drainage basins. The entrance capes are steep, with characteristic cliffs and benches. At the bayhead, ancient ledges with a low sea terrace reach out to the sea [Korotky, Khudyakov, 1990]. The underwater slopes of abrasion zones at the entrance and intra-bay capes are formed by outcrops of bedrock and coarse clastic material. Benches composed of rocky and coarse clastic material are often covered with mosaic thickets of macrophytes. On the flat accumulative surfaces in the northern and southern Srednyaya Bight at depths of 0.5–8 m, seagrasses are widespread, with *Z. marina* prevailing. Accumulative plains occupying most of the water area are covered with sand mixed with shells, shell detritus, and silt. At the bight outer part, at depths of 9–15 m, mixed-grained sand with varying degree of siltation predominates.

Water transparency is pretty high for coastal waters of temperate latitudes. Throughout the year, it varies depending on the dynamics of coastal runoff and periods of plankton blooms. The highest water transparency (down to 10–15 m) is recorded January to March and July to October.

The idea of the landscape-facies structure of the bight was formed based on expert interpretation of the RGB-synthesized image of IKONOS-2 [Zharikov et al., 2017] and information on the distribution of seagrass thickets obtained using radiometric correction methods for Landsat-8 data [Zharikov et al., 2018].

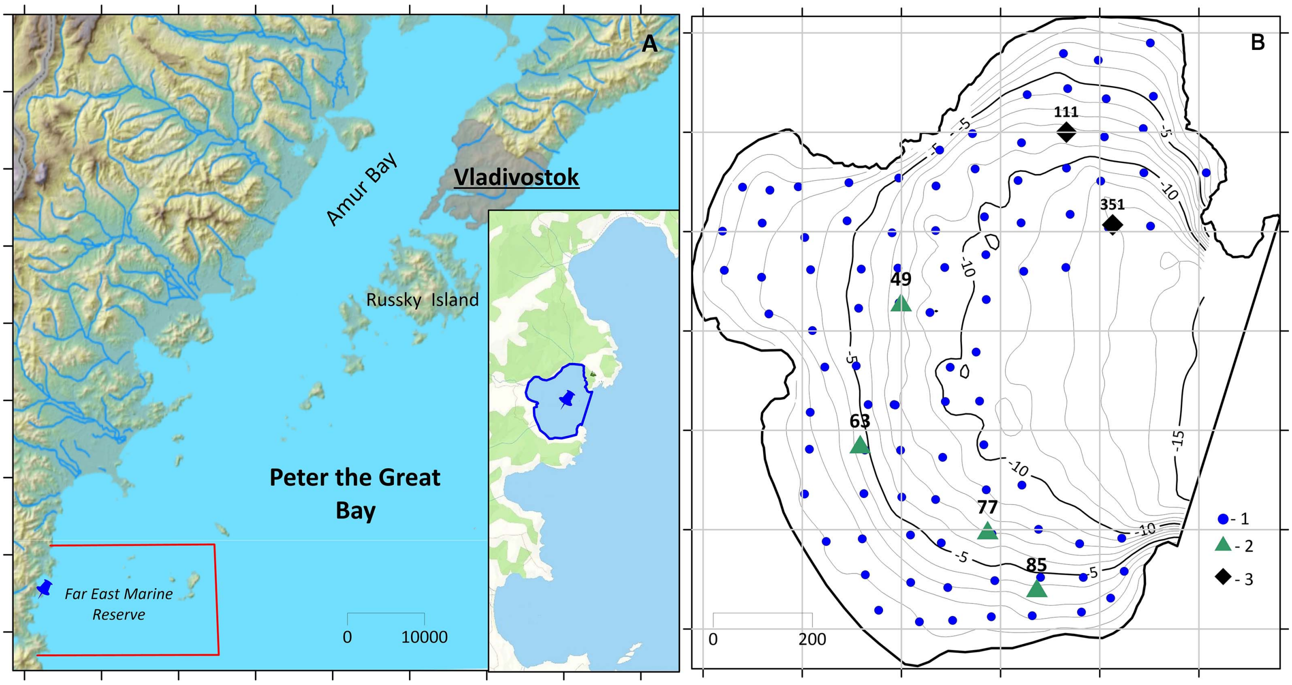


**Fig. 1.** A, location of the study area within Peter the Great Bay, the Sea of Japan, with mainland coast of the Far East Marine Reserve on the inset; B, mapping points (1), sampling points in the seagrass-covered areas (2), and sampling points on bare sands (3) (depth distribution is shown by isobaths based on a digital elevation model)

Field survey was carried out in 2021, in April (*prior* to the beginning of intensive growth of the seagrass) and July (during the peak of growing season). Material was sampled with scuba diving equipment. When mapping thickets, a BestWill CR110-7A cable video camera (China) was used. *Z. marina* occurrence and coverage (%) were determined from a monitor image synchronized with GPS recordings. The reliability of video assessments was controlled by scuba diving. Seagrass thickets with a projective coverage of bottom of less than 50% were considered sparse, and more than 50%, dense. A Garmin echoMAP 50dv navigator (the USA) mounted on an inflatable boat was used to position points and carry out echo sounding measurements. The location of mapping points and sampling stations is shown in Fig. 1B.

Sediments and the seagrass were sampled in April 2021 from four typical sites with different *Z. marina* coverage (stations 63, 85, 77, and 49) and two sandy habitats with no seagrass (sta. 111 and 351). From the same four stations, samples were taken in July 2021, during the peak of *Z. marina* production (Fig. 1B). The density of thickets was determined in a 0.25-$m^2$ frame. The aboveground (leaf blades) and belowground (shoots and roots) parts of the seagrass were separated, washed from sedimentary material, and rinsed with freshwater. Then, leaves and roots were cleaned with a scalpel from epiphytes, detritus, and hydrobionts. All plant material was dried for 48 h at +60 °C to constant weight.

Sediment cores for determination of particle-size distribution and carbon content were sampled manually by a scuba diver using PVC tubes 50 cm long and 5 cm in diameter. The density of sandy sediments allowed to sample cores 15–35 cm long. On the coast, sediment cores were divided into 3-cm intervals and hermetically sealed for subsequent sampling to analyze particle-size distribution and to assess the bulk density and $C_{org}$ content.

In a laboratory, from samples of bottom sediments of natural moisture, 5-$cm^3$ fragments were taken with a 20-mL polyethylene syringe with the front part cut off. Those were weighed before and after drying at +105 °C to determine the bulk density (d, $g \cdot cm^{-3}$). Part of a dried sample of bottom sediments and samples of the seagrass leaves and roots were homogenized in an agate mortar. Ground samples (0.3–0.6 g) were investigated for carbon content by catalytic oxidation with a Shimadzu TOC-V cpn analyzer (Japan) with an accuracy of 0.05%. According to preliminary determination of inorganic carbon (carbonates), more than 99% of total organic carbon was represented by $C_{org}$.

Another part of a dried sample was sieved through a 1-mm sieve to determine the proportion of coarse fraction; it did not exceed 2.5% and averaged 0.5% by mass. Then, the fraction of < 1 mm was used to analyze the particle-size distribution by laser diffraction on Fritsch Analysette 22 Nano (Germany). This technique provides obtaining data on distribution of particles with a size of 0.08–2,000 μm with a standard error of ±2.3% based on the results of five parallel determinations. Particle-size and chemical analysis of samples was carried out at the center of shared use at the Pacific Geographical Institute FEB RAS.

Carbon stock in individual layers of bottom sediment cores ($S_{Corg}$, $g\,C \cdot m^{-2}$) was estimated assuming its uniform distribution in the core within the layer by the formula:

$$S_{C_{org}} = C_{org} \times d \times L \times 10^4 ,$$

where $C_{org}$ is carbon concentration, weight %;

d is bulk density of sediments, $g \cdot cm^{-3}$;

L is thickness of the layer of bottom sediments, cm;

$10^4$ is conversion factor between $g \cdot cm^{-2}$ and $g \cdot m^{-2}$.

Carbon stock in the entire core was determined by summing stock in individual layers. Most publications on the assessment of the role of seagrass ecosystems in the carbon storage use data on carbon stock in the upper 1-m layer of sediments, including those obtained by extrapolation [Fourqurean et al., 2012]. We carried out a similar extrapolation to a 1-m layer of sediments applying data on $C_{org}$ concentration and bulk density obtained for lower layers of the cores.

The difference between $C_{org}$ concentration and $C_{org}$ stock in sediment samples was assessed by the nonparametric Mann–Whitney *U* test and *t*-test in PAST3 software package [Hammer et al., 2001].

Based on field mapping, applying Surfer 23.1.162 software package (Golden Software LLC), maps of the distribution of *Z. marina* thickets and bottom substrates were constructed with a resolution of 10 m; a digital elevation model of the Srednyaya Bight bottom was created. Regular data grids were calculated by kriging using a linear variogram model with scale and anisotropy parameters equal to 1. Smoothing was carried out with a standard Gaussian filter (3 × 3 in size; 5 passes). To estimate the error in mapping the seagrass meadows, we used the magnitude of the discrepancy between the calculated grid and original data. The discrepancy was characterized by the ratio of the root of the mean square of the remainder between these values (an indicator calculated by cross-validation) to the mean value of projective coverage area in the tabular data [Sukhanov, 2005].

To identify the potential distribution area of the seagrass-dominated community, the maximum entropy method was used implemented in MaxEnt 3.4.4 [Phillips et al., 2006]. This program models habitat suitability based on data on the species occurrence [Elith et al., 2011]; the result is the probability distribution of its detection in each raster cell. Given the constraints, the best probability representation of the distribution has the maximum entropy, *i. e.*, it reproduces the data with the highest accuracy. To date, MaxEnt is one of the most popular programs for studying the distribution of marine macrophytes [Bertelli et al., 2022].

When modeling, we used information on the species occurrence obtained during field survey in 2013–2016 and 2021 (in total, 102 points). The entire sample was divided into test (25%) and training sets. Data on environmental parameters included continuum layers (a digital elevation model and distribution of bottom sediments) and a categorical raster (landscape-facies structure of the bight).

## RESULTS

**Carbon concentration and stock in the seagrass and bottom sediments of the Srednyaya Bight.** Biomass of *Z. marina* and carbon stock in its leaves and roots for typical habitats of the Srednyaya Bight are provided in Table 1. The biomass of the seagrass roots was 3–20 times lower than that of its leaves. Interestingly, the difference increased from April to July in accordance with the seasonality of the species vegetation, and it was most pronounced in biotopes with the projective coverage of 50% or less. Carbon concentrations in *Z. marina* leaves and roots were quite close – 33.3 and 31.3% of dry weight, respectively. It is safe to say that the fluctuation in carbon stock in the vegetative components of seagrass ecosystems is controlled by the variability in their biomass. In biotopes with the projective coverage of 50–80%, carbon stock in *Z. marina* tissues was (96.8 ± 37.4) $g\,C\cdot m^{-2}$. However, in biotopes with 100% seagrass coverage, carbon stock increased to 253 $g\,C\cdot m^{-2}$, and the thickness of a root layer, turf, reached 10 cm.

**Table 1.** Biomass and carbon stock in *Zostera marina* roots and leaves in typical biotopes of the Srednyaya Bight with different projective seagrass coverage

| Station no. | Month | Projective coverage, % | *Zostera marina* biomass, g dry weight·$m^{-2}$ | | | Carbon stock in *Zostera marina*, g C·$m^{-2}$ | | |
|---|---|---|---|---|---|---|---|---|
| | | | Leaves | Roots | Gross | Leaves | Roots | Gross |
| 85 | July | 100 | 517.3 | 258.2 | 775.5 | 172.3 | 80.8 | 253.1 |
| 77 | July | 80 | 236.7 | 77.5 | 314.2 | 24.3 | 2.4 | 26.7 |
| 77 | April | 80 | 159.1 | 96.6 | 255.7 | 53.0 | 30.2 | 83.2 |
| 63 | July | 50 | 356.6 | 41.0 | 397.6 | 118.8 | 12.8 | 131.6 |
| 63 | April | 15 | 120.2 | 6.8 | 127.0 | 40.0 | 2.1 | 42.1 |
| 49 | July | 15 | 87.0 | 30.0 | 117.0 | 29.0 | 9.4 | 38.4 |
| 49 | April | 50 | 108.3 | 10.7 | 119.0 | 36.1 | 3.4 | 39.5 |

In bottom sediments of the Srednyaya Bight, carbon concentration varied from 0.04 to 0.46% (Table 2), while in sandy sediments under dense seagrass thickets, its content was significantly (according to the Mann–Whitney *U* test) higher than under *Z. marina* thickets with the projective coverage of < 50%. Sediments in the cores with similar seagrass densities did not differ noticeably by $C_{org}$ concentration (Table 2).

**Table 2.** $C_{org}$ concentration (%) in the cores from the seagrass-covered areas and bare sands of the Srednyaya Bight

| | Seagrass > 50 % | | Seagrass < 50 % | | Bare sands | |
|---|---|---|---|---|---|---|
| No. | 85 | 77 | 63 | 49 | 111 | 351 |
| *n* | 9 | 10 | 10 | 5 | 5 | 5 |
| *X* | 0.29 | 0.24 | 0.07 | 0.10 | 0.17 | 0.32 |
| *SE* | 0.035 | 0.021 | 0.0068 | 0 | 0.0143 | 0.0136 |

**Note:** No., station number; *n*, number of samples; *X*, the mean value; *SE*, the standard error.

$C_{org}$ content in bare sands varied within 0.15–0.35% depending on the particle-size distribution and was proportional to the share of silt fractions. However, the angle of the line of $C_{org}$ dependence on content of particles < 0.05 mm in size was noticeably smaller than in seagrass-covered sands (Fig. 2). This means a higher rate of organic matter accumulation during siltation against the backdrop of the seagrass occurrence.

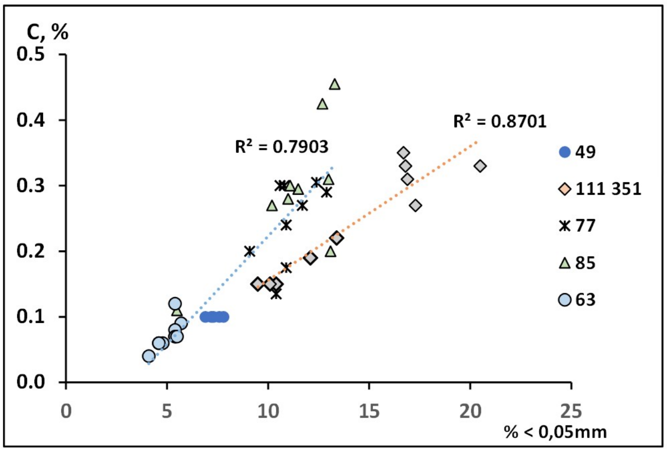


**Fig. 2.** Dependence of $C_{org}$ concentration on the fraction of silt particles (< 0.05 mm) in bottom sediments of the Srednyaya Bight from the seagrass habitats (sta. 49, 63, 77, and 85) and bare sands (sta. 111 and 351)

Analysis of the vertical distribution of $C_{org}$ concentration within the upper 15–35-cm layer of sandy sediments in the Srednyaya Bight does not allow us to unambiguously state the downward trend in the cores. $C_{org}$ content was the most variable in the cores sampled at stations with a high percentage of *Z. marina* coverage (Fig. 3).

$C_{org}$ deposition in bottom sediments of the Srednyaya Bight is significantly affected by their particle-size distribution; it is reflected in a noticeable correlation with aleuropelite content throughout the sample (Fig. 2). The effect of the seagrass is expressed in the fact as follows: with similar particle-size distribution, bottom sediments under dense thickets contain more $C_{org}$ (see sta. 77 and 85 in Fig. 2). This fact indicates that *Z. marina* both serves as a source of carbon in bottom sediments and contributes to the accumulation of fine-grained material. The absence of a significant downward trend in the cores (Fig. 3) distinguishes sandy sediments from silty ones: there, an elevated $C_{org}$ concentration in the upper 5–10-cm layer results in a noticeable drop in underlying layers due to aerobic oxidation within the upper layer and reductive diagenesis in underlying sediments [Tishchenko et al., 2022].

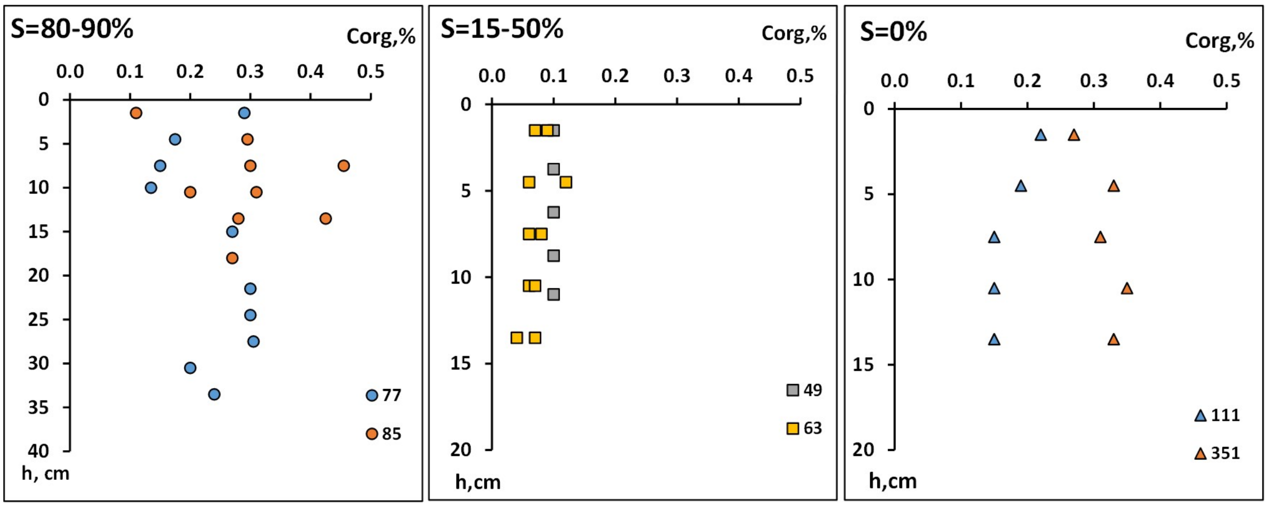


**Fig. 3.** Changes in $C_{org}$ concentration in the bottom sediment cores of the Srednyaya Bight with different projective seagrass coverage (S)

In contrast to carbon concentration, the bulk density of sandy sediments in the Srednyaya Bight fluctuated within a fairly narrow range, 1.17–1.35 $g \cdot cm^{-3}$. The obtained data on $C_{org}$ content and the bulk density in sediments allow calculating carbon stock in a layer of bottom sediments of a certain thickness. The results of carbon stock assessment will be proportional to the thickness of the layer analyzed. We carried out calculations according to two patterns: the first one, for a 0.25-m layer [Prentice et al., 2020]; the second one, extrapolated for a 1-m layer of sediments, since a 1-m layer is mainly used in assessments in relation to the concept of blue carbon [Fourqurean et al., 2012]. However, in the latest global summary, a 20-cm layer was used for calculations [Kennedy et al., 2022], and this made it possible to significantly expand the database applied: many researchers sampled 15–35 cm long cores, the same as we did.

**Table 3.** $C_{org}$ stock ($g\,C \cdot m^{-2}$) in the upper 0.25-m layer and 1-m sediment layer of the seagrass-covered areas and bare sands in the Srednyaya Bight

| | Seagrass > 50 % | | Seagrass < 50 % | Bare sands | |
|---|---|---|---|---|---|
| Station No. | 85 | 77 | 63 and 49 | 111 | 351 |
| Number of samples | 9 | 10 | 15 | 5 | 5 |
| $C_{org}$ stock in the 0.25-m layer, *X* | 817 | 708 | 231 | 506 | 986 |
| $C_{org}$ stock in the 0.25-m layer, *SE* | 75 | 62 | 18 | 48 | 42 |
| $C_{org}$ stock in the 1-m layer, *X* | 3,644 | 2,933 | 958 | 1,901 | 4,070 |
| $C_{org}$ stock in the 1-m layer, *SE* | 431 | 260 | 71 | 177 | 168 |

**Note:** *X*, the mean value; *SE*, the standard error.

**Spatial distribution of *Zostera marina* in the Srednyaya Bight according to field observations and MaxEnt 3.4.4 modeling.** To take into account the spatial heterogeneity of the seagrass ecosystem when estimating carbon stock at the bight scale, maps of the distribution of *Z. marina* meadows in April and July 2021 were constructed according to field survey data (Fig. 4A and B). Based on the results of modeling by the maximum entropy method, the potential distribution range of *Z. marina* in the study area was revealed (Fig. 4C).

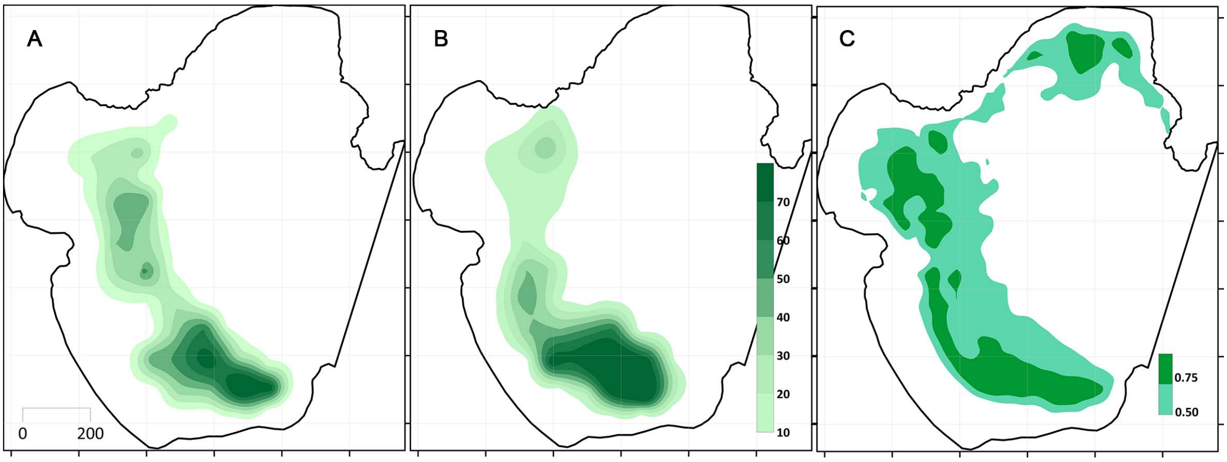


**Fig. 4.** Distribution of the seagrass meadows in the Srednyaya Bight according to field underwater mapping data in April (A) and July (B) (the color scale indicates projective coverage area) and according to the results of modeling the potential area of *Zostera marina* occurrence (C) (the color scale indicates calculated probability of the species occurrence)

Data on the areas of sparse and dense thickets calculated from the constructed maps are included in Table 4.

**Table 4.** Areas of the seagrass meadows in the Srednyaya Bight evaluated by underwater mapping data and remote sensing data with radiometric correction [Zharikov et al., 2018]

| Period | Thicket area, hectares, with the projective coverage | | |
|---|---|---|---|
| | 10–50 % | > 50 % | Total |
| 28.04.2021–29.04.2021 | 19.53 ± 4.88 | 3.54 ± 0.85 | 23.08 ± 5.95 |
| 27.07.2021–28.07.2021 | 17.91 ± 4.48 | 5.67 ± 1.41 | 23.58 ± 5.89 |
| 12.10.2001 | 9.54 ± 3.18 | 2.70 ± 0.22 | 12.24 ± 2.74 |
| 05.10.2013 | 15.57 ± 5.24 | 4.50 ± 0.29 | 20.07 ± 4.29 |
| 08.10.2014 | 18.40 ± 6.14 | 7.40 ± 2.47 | 25.80 ± 5.52 |

Sparse meadows with the projective coverage 10 to 50% which border washed sorted sands are localized in the central and southwestern Srednyaya Bight. Dense thickets with the projective coverage of > 50% are confined to silty sandy soils and concentrated in the south (see Fig. 4A and B).

The relative contribution of variables to the model was as follows: digital elevation model, 44.6%; distribution of bottom sediments, 30.7%; and landscape-facies structure of the bight, 24.6%. Potential areas with a predicted probability of the species occurrence of > 0.5 (Fig. 4C) are of 32.47 ha – about ⅓ of the total area of the bight. Out of 32.47 ha, the area with a probability of the species occurrence of > 0.75 is 11.83 ha.

The results of field mapping for April and July (Fig. 4A and B) show that *Z. marina* thickets occupy ⅔ of the area with a predicted probability of the species occurrence of > 0.5 and are located chiefly in sites protected from direct storm effect.

During the research period, the seagrass meadows accounted for about ¼ of the bight area (23.2%). Considering that sparse and dense thickets covered 80.2 and 19.8% of the total area under higher vegetation, respectively, the absolute values of carbon stock were calculated both in *Z. marina* biomass and deposited in 1-m sediments covered with meadows (347.17 tons). About 95% of this amount of carbon is localized in bottom sediments under thickets.

## DISCUSSION

The proportion of organic carbon in the seagrass tissues, even with 100% projective coverage, does not exceed ⅓ of carbon in the 25-cm layer of underlying sandy sediments. When considering a 1 m thick layer, it is obvious that the contribution of sediments to the total pool of organic carbon in seagrass ecosystems becomes overwhelming (> 90%) (see Tables 1 and 3). Probably, in ecosystems with seagrasses on silty soils containing 1–3% of $C_{org}$, the role of bottom sediments in organic carbon storage will be even more significant. Thus, despite the fact that the functioning of seagrass ecosystems is driven precisely by the vital activity of seagrasses, most of organic carbon is accumulated and stored in material of bottom sediments. Accordingly, from the perspective of the concept of blue carbon, the role of seagrass ecosystems in carbon fixation is determined by $C_{org}$ amount in underlying sediments.

A noticeable enrichment in organic carbon of sandy sediments of the Srednyaya Bight under *Z. marina* thickets, in comparison with bare sands of a similar particle-size distribution (Fig. 2), confirms a significant role of the seagrass ecosystems in carbon accumulation even in open water areas like this bight, with the lack of stable and intensive sedimentation, where $C_{org}$ concentration in sandy sediments does not exceed 0.5%. In the upper layer of sediments of semi-enclosed inlets of Peter the Great Bay (in Voevoda and Novgorodskaya bays), in areas not covered with *Z. marina*, $C_{org}$ content was of 2–3% [Tishchenko et al., 2022]. The lack of data on the particle-size distribution of these sediments does not allow to compare directly their material with our results. However, the dependence of $C_{org}$ concentration on the degree of siltation of bottom sediments has been repeatedly recorded [Kennedy et al., 2022; Prentice et al., 2020]. Analyzing the above, we can assume a fairly high siltation of sediments in semi-enclosed and enclosed inlets of Peter the Great Bay. Interestingly, coastal waters of the northwestern Sea of Japan mostly have sandy bottom sediments similar to those in the Srednyaya Bight, and the seagrass-dominated ecosystems are very widespread there [Arzamastsev, Preobrazhensky, 1990; Kolpakov, 2013; Manuilov, 1987; Paimeyeva, 1973, 1979].

When comparing data on carbon stock in the upper 25-cm layer of bottom sediments in the Srednyaya Bight with similar data obtained for the seagrass ecosystems on the northwestern coast of the USA and Canada [Prentice et al., 2020], it becomes obvious that our results for the bight fit very well into the general trend (Fig. 5) characterizing the dependence of $C_{org}$ stock on its content in bottom sediments. Data in [Tishchenko et al., 2022] on more silted sediments, recalculated for a 25-cm layer, also adequately coincide with the general trend line but in the area of a fairly high $C_{org}$ concentration in bottom sediments (Fig. 5).

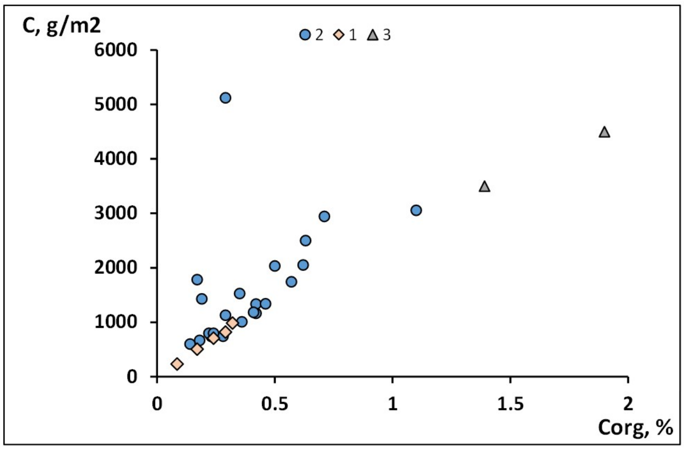


**Fig. 5.** Dependence of $C_{org}$ stock in the upper 25-cm layer of coastal sediments of the Srednyaya Bight (1), northwestern coast of North America [Prentice et al., 2020] (2), and semi-enclosed inlets of Peter the Great Bay [Tischenko et al., 2022] (3)

Thus, according to the results obtained, the key factor controlling carbon stock in the seagrass ecosystems *per* unit area is $C_{org}$ content in underlying bottom sediments which, in turn, is determined mainly by the particle-size distribution. Variations in carbon stock in the upper layer depending on the nature of bottom sediments are of the order of magnitude or more (Fig. 5).

Depth, bottom slope, slope exposure, and the nature of hydrodynamics are factors directly and indirectly affecting sedimentation regime and particle-size distribution of sediments [Dahl et al., 2016]. The distribution of seagrasses is largely governed by the geomorphological structure of submarine slopes, configuration of the coastline, and type of substrate [O'Brien et al., 2022]. The contribution of different variables to the pattern of the seagrass distribution is consistent with these ideas.

A comparison of areas covered with higher aquatic vegetation in the survey site provides insight into changes in the distribution of seagrasses (see Table 4). The differences between the areas occupied by *Z. marina* community in 2013, 2014, and 2021 are within the margin of error due to the accuracy of the mapping methods used. However, the localization of thickets changed in 2021: the seagrass meadow outlined on thematic maps in the northern Srednyaya Bight completely disappeared [Zharikov et al., 2017, 2018]. The coast of the survey site is open to eastern and southeastern winds. During the passage of the typhoon Maysak (3–4 September, 2020), wind and waves of precisely these directions had the highest intensity [Lazaryuk et al., 2021]. Because of the typhoon, a storm surge and abnormally high waves were observed in the Srednyaya Bight for three days. In the northern bight, several constructions of the security cordon in the marine reserve, which had stood on the coast for more than ten years, were completely destroyed.

Importantly, significant fluctuations in the projective coverage of bottom by seagrasses were recorded in the marine reserve area earlier. Thus, a decrease in *Z. marina* areas was noted there in the early 1990s when carrying out ichthyological observations on permanent transects [Markevich, 2002].

High interannual spatial variability was registered for seagrass communities in other areas as well. For example, long-term monitoring of *Z. marina* meadows in the Ems estuary (Wadden Sea, North Sea) showed as follows: on average, 12.9% of vegetation-covered areas annually completely lose their thickets, while about 12.7% of bare bottom areas are colonized by the seagrass [Valle et al., 2013]. Changes in area and location of *Z. marina* meadows, local disappearance of thickets, and recolonization of certain spots are considered as part of the population strategy of the species [van Katwijk et al., 2009]: it allows to restore thickets after periodic exposure to destructive factors [Trémolières, 2004].

Studies of the characteristics of the coverage area of *Z. marina* meadows and indicators of their seasonal and interannual variability are especially important when assessing carbon stock in ecosystems of large water areas. Since long-term monitoring of seagrasses is laborious and expensive, alternative approaches are needed. The required data can be obtained by remote sensing and species distribution modeling.

For long-term monitoring of seagrass meadows, remote sensing is already used – a technique ensuring research efficiency and wide coverage of distribution areas [Bramante et al., 2018; Pham et al., 2019; Poursanidis et al., 2021]. Synoptic monitoring of coastal ecosystems based on remote sensing provides important data on spatial patterns and differences in sedimentation of seagrass ecosystems [McKenzie et al., 2022; Randazzo et al., 2021]. Potential habitat range modeling characterizes ecological patterns of seagrass distribution and serves as a source of spatial data to support estimates of carbon sequestration and storage in certain habitats [Kuwae et al., 2022; O'Brien et al., 2022].

In areas with increased wind and wave load (open coasts and bights), storms can noticeably reduce the area of *Z. marina* meadows. Moreover, spatial variations in the rate of accumulation and carbon stock in sediments correlate with the intensity of hydrodynamic effect. Our results suggest as follows: in open and semi-open bights with the seagrass thickets, the values are significantly lower than in enclosed inlets.

Subregional and regional assessments of the contribution of seagrass ecosystems to coastal carbon storage are based on estimating areas covered by such ecosystems. The spatial heterogeneity of thickets determines the need for differentiation of water areas by sedimentation regimes and types of bottom sediments. To a first approximation, such differentiation leads to identification of two categories: water areas with a prevalence of sediment accumulation and possibility of carbon accumulation and water areas with a prevalence of erosion processes where carbon practically does not accumulate. As our results show, the Srednyaya Bight belongs to the second category.

So, the accumulation of data on direct measurements and calculated values of carbon concentration and stock in the coastal zone should be accompanied by assessments of the spatial distribution of biotopes using field mapping, remote sensing, and modeling. This ensures that the spatial heterogeneity of seagrass ecosystems is taken into account in integrated estimates of blue carbon.

**Conclusion:**

1. Based on the results of the survey, for typical habitats of the Srednyaya Bight, biomass and carbon stock in *Zostera marina* leaves and roots were determined, concentration of organic carbon in sediment cores was estimated, and carbon stock in layers of bottom sediments (0.25 m and 1 m thick) was established. Applying MaxEnt 3.4.4 program, a potential area of distribution of the seagrass-dominated community was identified. Maps of the distribution of *Z. marina* thickets in April and July 2021 were constructed.
2. In the seagrass community, the biomass of its roots was 3–20 times lower than that of its leaves. In accordance with the seasonality of the species vegetation, this difference increased from April to July. In biotopes with a projective coverage of 50–80%, carbon stock in *Z. marina* tissues was (96.8 ± 37.4) $g\,C\cdot m^{-2}$; in biotopes with 100% coverage, the value rose to 253 $g\,C\cdot m^{-2}$.
3. Carbon content in bottom sediments of the Srednyaya Bight ranged within 0.04–0.46% and was proportional to the share of silt fractions. Under dense seagrass thickets, $C_{org}$ concentration and proportion of silt particles in sediments were higher than under sparse ones. Analysis of the vertical distribution of $C_{org}$ content within the upper 15–35-cm layer of sandy sediments did not reveal a downward trend in the cores. The key factor affecting $C_{org}$ accumulation was the particle-size distribution of sediments.
4. The proportion of organic carbon in the seagrass tissues does not exceed ⅓ of the amount in the 25-cm layer of underlying sandy sediments. In a 1 m thick layer, the contribution of bottom sediments to $C_{org}$ pool exceeds 90%. Accordingly, the role of *Z. marina* meadows in fixing carbon in the Srednyaya Bight is determined by its concentration and amount in bottom sediments. The range of variation in carbon stock in the upper layer depends on the nature of bottom sediments and is of the order of magnitude or more.
5. Subregional and regional estimates of the contribution of seagrasses to coastal carbon storage require differentiation of coastal waters by sedimentation regimes and types of bottom sediments. This approach helps in improving the accuracy of estimating carbon stock in seagrass ecosystems.

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# УГЛЕРОД В ЭКОСИСТЕМЕ *ZOSTERA MARINA* LINNAEUS, 1753 НА ПЕСЧАНЫХ ГРУНТАХ БУХТЫ СРЕДНЯЯ (ЗАЛИВ ПЕТРА ВЕЛИКОГО, ЯПОНСКОЕ МОРЕ) ПО ДАННЫМ ПОЛЕВЫХ НАБЛЮДЕНИЙ

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Прибрежные экосистемы морских трав, в частности *Zostera marina* Linnaeus, 1753, способны накапливать органический углерод, фиксируя углекислый газ при фотосинтезе. При этом надземная биомасса морских трав считается краткосрочным хранилищем углерода, а донные отложения рассматриваются как его долговременное депо. Бо́льшая часть исследований накопления органического вещества экосистемами морских трав проведена в районах с устойчивым осадконакоплением. Именно для таких акваторий показана важная роль этих экосистем в рамках концепции «голубого углерода». Однако в морях умеренных широт распространены прибрежные акватории с неустойчивым осадконакоплением и с преобладанием песчанистых отложений, для которых масштаб накопления углерода в экосистемах морских трав не очевиден. В данной работе определены биомасса и запас углерода в травостое и корнях зостеры, а также концентрация $C_{орг}$ и запас углерода в верхних слоях донных осадков (толщиной 0,25 и 1 м) для типичных местообитаний вида в полуоткрытой бухте Средняя (залив Петра Великого, Японское море), где доминируют песчанистые отложения. На корни зостеры приходилось в 3–20 раз меньше биомассы, чем на травостой, причём разница возрастала от апреля к июлю в соответствии с сезонностью вегетации. Концентрации углерода в листьях и корнях *Z. marina* были близки (33,3 и 31,3 % сухого веса соответственно). В биотопах с проективным покрытием 50–80 % запас углерода в тканях зостеры составлял (96,8 ± 37,4) г C·м$^{-2}$, в биотопах со 100%-ным покрытием он повышался до 253 г C·м$^{-2}$. Концентрация углерода в донных отложениях бухты Средняя колебалась от 0,04 до 0,46 % и была пропорциональна доле алевритовых фракций. Под плотными зарослями *Z. marina* концентрация $C_{орг}$ и доля алевритовых частиц в осадках были выше, чем под разреженными. Анализ вертикального распределения концентрации $C_{орг}$ в пределах верхнего 15–35-см слоя песчаных осадков не выявил тренда изменения вниз по колонкам. Основным фактором, контролирующим концентрацию $C_{орг}$, был гранулометрический состав осадков, что предполагает слабую выраженность восстановительного диагенеза и влияние волнового перемешивания верхнего слоя песчаных отложений. По данным измерений объёмной плотности и концентрации $C_{орг}$ в отложениях был рассчитан запас углерода для слоёв 0,25 и 1 м. Доля органического углерода в тканях морской травы не превышала трети от его количества в верхнем слое (0,25 м) подстилающих песчаных отложений. При пересчёте на слой толщиной 1 м вклад донных отложений в пул $C_{орг}$ превышает 90 %. Обогащение органическим углеродом песчаных отложений под зарослями зостеры, по сравнению с песками близкого гранулометрического состава за пределами зарослей, предполагает существенную роль морских трав в накоплении углерода в акваториях с отсутствием устойчивого и интенсивного осадконакопления. Наиболее важным фактором, контролирующим запас углерода в экосистемах с *Z. marina*, является концентрация $C_{орг}$ в подстилающих донных отложениях, зависящая прежде всего от их гранулометрического состава; при этом размах вариации запасов углерода в верхнем слое составляет порядок и более. Построены карты распределения зарослей зостеры в апреле и июле 2021 г. Рассчитаны абсолютные значения запаса углерода — как накопленного в биомассе *Z. marina*, так и депонированного в осадках, которые покрыты лугами. С использованием программы MaxEnt 3.4.4 выявлена потенциальная область распространения сообщества с доминированием зостеры. Результаты моделирования показали, что области с прогнозной вероятностью присутствия *Z. marina* более 0,5 занимают около трети общей площади бухты, из них на площади с вероятностью присутствия зостеры более 0,75 приходится 11,83 га. В период исследований поля *Z. marina* занимали > 70 % области с прогнозной вероятностью присутствия вида более 0,5. Показано, что при оценках вклада экосистем с морскими травами в баланс углерода, который аккумулируется в прибрежной зоне, необходимы дифференциация акваторий по режимам осадконакопления и типам донных отложений, создание баз данных, включающих сведения по концентрации и запасам углерода на единицу площади, а также информация о площадях распространения экосистем водной растительности.

**Ключевые слова:** «голубой углерод», *Zostera marina*, концентрация углерода в песчаных отложениях, дистанционное зондирование, Японское море, залив Петра Великого