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PECULIARITIES OF POPULATION STRUCTURE AND BIOCENOTIC RELATIONSHIPS OF *RAPANA VENOSA* (VALENCIENNES, 1846) (GASTROPODA, MURICIDAE) IN THE DONUZLAV BAY (THE BLACK SEA)

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The Western Pacific gastropod *Rapana venosa* (Valenciennes, 1846) is classified among the hundred most dangerous invasive species of the Black and Mediterranean seas. Moreover, it is recognized as a dangerous invader in a number of coastal water areas on both sides of the Atlantic Ocean that determines the relevance of the study of population characteristics and biocenotic relationships of the rapa whelk in the areas of its invasion. The analysis of a previously unexplored *R. venosa* population in the Donuzlav Bay (the Northwestern Crimea) of the Black Sea in 2020 showed as follows: in the occurrence of an abundant and diverse food base, the rapa whelk does not form mass aggregations and, consequently, does not significantly affect benthic biocenoses. This fact is also confirmed by the ratio of biomass of the predatory mollusc and its prey. *R. venosa* mean biomass in the study area was 3.8 g·m^{-2}, and the mean biomass of its food objects (Bivalvia) was 162.8 g·m^{-2}. The features of the population structure and biocenotic relationships of the rapa whelk in the Donuzlav Bay are considered and discussed for the first time. Direct underwater observations and indirect evidence indicate that the distribution of this invader is controlled by aboriginal predators, crabs. The main species limiting *R. venosa* abundance in the study area is the crab *Carcinus aestuarii* Nardo, 1847.

Keywords: biocenoses, algae, invasive species, crabs, molluscs, predator–prey

A large predatory gastropod *Rapana venosa* (Valenciennes, 1846) entered the Black Sea from the Sea of Japan in the early 1940s and significantly affected bottom biocenoses [Bondarev, 2014; Chukhchin, 1961b, c; Pereladov, 2013; Snigirov et al., 2013] and the sea ecosystem in general [Alien Species Alert, 2004; Chukhchin, 1984; Katsanevakis et al., 2014; Zolotarev, 1996]. *R. venosa* mostly feeds on bivalves [Bondarev, 2010, 2011, 2015a, 2016, 2020; Chukhchin, 1961b, c, 1984; Kosyan, 2013; Savini et al., 2004; Zolotarev, Yevchenko, 2010] whose complex plays an important role of a biofilter in the Black Sea ecosystem [Zenkevich, 1963]. The Black Sea rapa whelk tends to completely exterminate its food objects within the habitat [Chukhchin, 1961b], and this fact was the ground for its inclusion in the top 100 of the most dangerous invasive species of the Black Sea [Feneva, Kosyan, 2018] and Mediterranean Sea [Streftaris, Zenetos, 2006]. In the USA, various methods to control the unwanted invader are being developed, including extensive public education programs and paying a bounty to remove any collected rapa whelk and its egg capsules [Alien Species Alert, 2004].

The success of the Black Sea colonization by *R. venosa* is believed to be related not only to tolerance to abiotic environmental factors, but also to occurrence of a rich food supply along with the absence of trophic competitors and predators [Alien Species Alert, 2004; Chukhchin, 1984; Katsanevakis et al., 2014; Zolotarev, 1996]. The rapa whelk has filled a free niche among second-order heterotrophs [Chukhchin, 1984], and the main factor limiting its development is food [Chukhchin, 1961b]. At the same time, in the most northwestern Black Sea, with numerous food resources (molluscs), *R. venosa* is not abundant [Zolotarev, 1996]. The Donuzlav Bay is one of the areas characterized by the occurrence of a wide range of food items, but the rapa whelk is not widely distributed there.

The first study of the Donuzlav Bay fauna was conducted in 1981, 20 years after a channel was dug, and the bay was connected with the sea. As found, since then, fauna of the formerly hypersaline lake has acquired a benthos composition characteristic of the Black Sea, and biocenoses occurring at appropriate sea depths have been formed there. As revealed, gastropods predominantly inhabit sand and coquina biotopes on algae and sediments, where the rapa whelk was also found [Chukhchin, 1992]. *R. venosa* occurrence in benthic communities of the Donuzlav Bay was established in subsequent investigations as well [Boltacheva et al., 2002; Kosyan, 2013, 2016; Pereladov, 2013]. As noted, the rapa whelk distribution was limited to an area near the strait connecting the Donuzlav Bay with the sea, and its settlement density at the detection site was less than 0.01 ind.$\cdot$m^{-2}. Importantly, the diversity and quantity of food objects did not limit *R. venosa* distribution throughout the bay [Pereladov, 2013].

Based on observations in an aquarium, one species that possibly could control *R. venosa* distribution is the blue crab *Callinectes sapidus* Rathbun, 1896 [Harding, 2003]. This rather large crab (its carapace width is up to 230 mm) from the western Atlantic is already widespread in the Mediterranean Sea. In the Black Sea, the species was first recorded in 1967 but is still rare [Makarov, 2004]. In the Donuzlav Bay, *C. sapidus* has not been revealed yet. As assumed, a limiting role in the rapa whelk distribution and abundance is played by local species of blue crabs which may consume its juveniles in shallow waters [Pereladov, 2013]. To date, biological methods of controlling *R. venosa* have been poorly investigated [Feneva, Kosyan, 2018].

The study of *R. venosa* structure and biocenotic relationships in local populations, where its development is limited by natural factors, can both contribute to understanding the processes of equilibrium interaction between this invasive species and native fauna and provide insight into possible ways of limiting the mollusc distribution. The aim of this work was to obtain such information on the example of a local population of the rapa whelk in the Donuzlav Bay. Population structure of *R. venosa* was considered: its distribution pattern and size, weight, age, and sex composition in the study area. When analyzing biocenotic relationships, the confinement of the rapa whelk to specific biocenoses was established. Attention was focused on feeding spectrum and relationships with predators.

MATERIAL AND METHODS

The Donuzlav Bay is located on the western coast of Crimea (Fig. 1) and borders the Tarkhankut Peninsula from the south. The bay length is about 30 km, and its width averages 5 km. The widest spot (8.5 km) is at the mouth which was originally separated from the Black Sea by a sandy spit.

In 1961, a channel of about 200 m wide was dug, and two sandy spits were formed. The northern part of the former spit is called the Belyaus Spit, while the southern is called the Southern Spit. The salinity of most water area of the modern bay corresponds to the Black Sea salinity (17.5–18.2‰). In summer, the water temperature rises to +24…+25 °C, and in shallows, the value is even higher. In winter, it drops to 0 °C, and the bay is partially or completely covered with ice. Water exchange between the sea and bay occurs practically throughout its entire area and involves the water column from the surface to the bottom [Zuev, Boltachev, 1999].

Fig. 1. Schematic map of the study area with indication of the sampling sites and population abundance (A) of *Rapana venosa* (ind.·m^{-2})

In most areas of the bay, depths of less than 4–5 m prevail; in the central basin, the depth reaches 28 m. Bottom sediments are chiefly represented by multigrain sands silted to varying degrees, while in shallow areas and in the deepest part of the bay, silts predominate. At various depths, along the bay perimeter, coquina occur, as well as rocky outcrops of hard calcareous sandstones in the form of slabs, individual fragments, and stone rubble.

There are eight main biocenoses within the bay: sand with *Venus*, sand with *Chara*, *Chara*, *Zostera* on sandy mud, mussel and mussel–oyster coquina, silty sand, silt with *Abra*, and deep-water mud. It is consistent with the data of the previous study [Chukhchin, 1992].

The distribution of *R. venosa*, its potential prey, and predators was examined visually *in situ* from the bay mouth to the inner area. Benthos was sampled in the summer–autumn period of 2020 (28 June – 28 September); molluscs were collected with scuba diving equipment, totally from the area of 1,000 m^2 at each station. At 7 stations within the bay, 300 specimens of the rapa whelk were sampled. At each station, *R. venosa* settlement density was estimated based on the results of sampling (Fig. 1); in the mollusc aggregations, with a 1 × 1 m frame. To determine the quantitative and taxonomic composition of food items of the rapa whelk in biotopes, macrobenthos was sampled with the 1 × 1 m frame simultaneously from the surface of solid substrate and algae and from the surface layer of loose sediments (5-cm layer). Then, it was washed through a sieve with a mash diameter of 5 mm. One frame sample was taken at each station on a characteristic spot of the water area.

The feeding spectrum of the rapa whelk and crabs was studied by prey items taken directly from feeding individuals. In total, 59 feeding *R. venosa* and 72 feeding crabs were found. During feeding, rapa whelks hold their prey with leg muscles. Crabs feed on their prey while clamping it in the claw. In 20 *R. venosa* individuals, food contents of the gastrointestinal tract were investigated under an MBS-10 stereo microscope.

When analyzing each *R. venosa* specimen, we determined the following parameters: shell height (SH) from the apex to the end of the siphonal canal; wet weight of the mollusc with its shell (total weight, TW); sex (F, female; M, male); and age. In our samples, only mature individuals were taken into account. Sex was determined by the presence/absence of penis and color of gonads, and age was established by spawning marks [Bondarev, 2015b; Chukhchin, 1961a, c]. In parallel, we sampled crabs – potential predators of the rapa whelk; their size was estimated by carapace width (CW). The length of valves (L) of bivalves taken directly from feeding *R. venosa* was measured as well. Since soft tissues of these preys were partially or completely eaten, data on their mass are not representative. The quantitative proportion of each prey species of *R. venosa* (Q_1, %) in the total amount of recorded food objects was estimated. For comparison, according to sampling data, the mean value of the quantitative contribution (Q_2, %) of bivalves on which the rapa whelk feeds was determined in Bivalvia taxocenes of the Donuzlav Bay. The mean biomass of *R. venosa* and bivalves in the study water area was estimated.

Linear sizes of mollusc shells were established, and crab carapaces were measured with a caliper with an accuracy of 0.1 mm. Wet weight of individuals was determined on electronic scale WLM-200 with an accuracy of 0.1 g.

Graphs were plotted, and mean values (M) and standard deviation (σ) were calculated using programs within MS Office Excel, v. 10.

RESULTS

Population structure of *Rapana venosa*. Shell height values of sexually mature rapa whelks in the Donuzlav Bay are characterized by a wide range (32.1–135.0 mm), the same as wet weight values of studied molluscs (4.0–365.2 g). In the sample, males predominate (57.7%), and their size and weight have higher maximum and mean values (Table 1).

Table 1. Size and weight characteristics of *Rapana venosa* in the Donuzlav Bay divided by sex: F, females; M, males; *N*, number of individuals; SH, shell height; TW, individual wet weight; min–max, minimum and maximum values; *M*, mean value; σ, standard deviation

Sex	*N* (%)	SH, mm			TW, g		
		Min–max	*M*	σ	Min–max	*M*	σ
F	127 (42.3)	32.1–126.0	82.8	18.6	4.0–335.1	107.5	76.7
M	173 (57.7)	34.4–135.0	89.7	20.1	6.1–365.2	140.8	96.9
F + M	300 (100)	32.1–135.0	86.6	19.8	4.0–365.2	126.8	90.3

Three components of population structure – size (determined by shell height), age (established by spawning marks), and weight ones – with regard to sex are provided in Fig. 2. In the size group of 30–40 mm, females predominate (90%); in the group of 41–50 mm, the abundance of males and females is equal; and in the larger-size groups, except for that of 61–70 mm (F, 65%; M, 35%), males prevail. As SH increases, the proportion of males rises. In the size group of 130 mm and more (1% of the sample), there are no females (Fig. 2A).

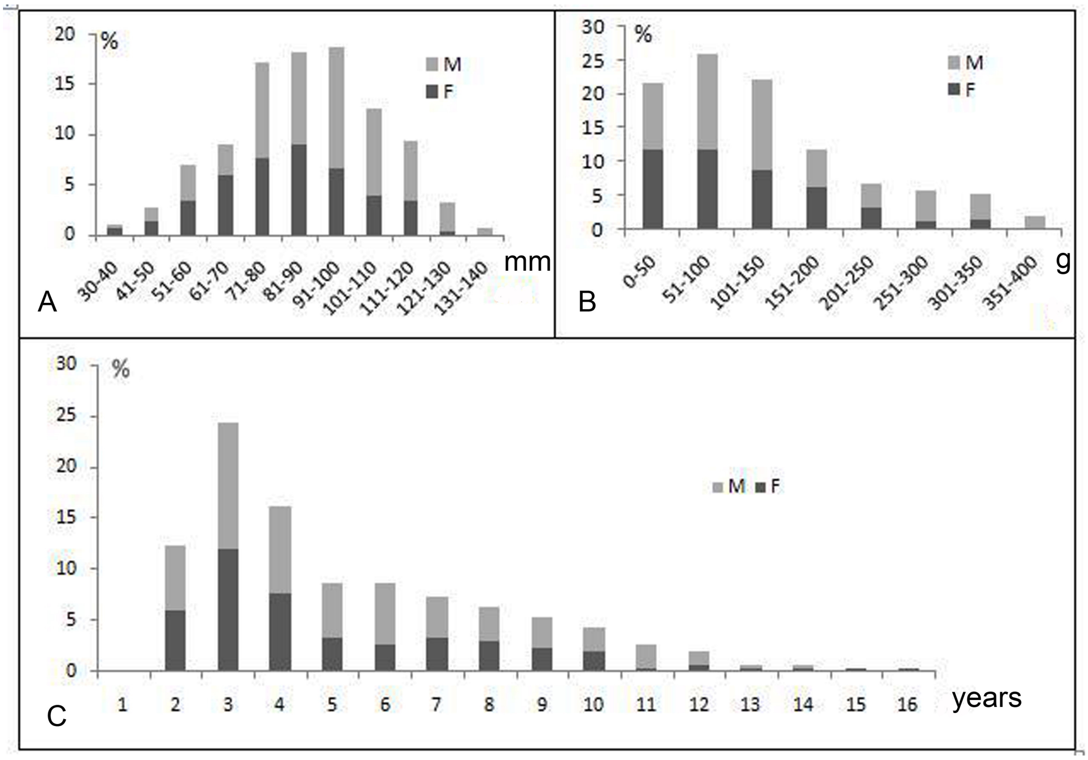

Fig. 2. Population structure of *Rapana venosa* in the Donuzlav Bay divided by sex (F, females, M, males): A, size; B, weight; C, age

In the group with individual weight up to 50 g, females predominate (54%); in all other ones, males prevail. In the group with the highest TW (> 350 g; 1.7% of the sample), there are no females (Fig. 2B), the same as in the group with the maximum SH. The mean biomass of the rapa whelk in the study area was 3.8 $g \cdot m^{-2}$.

In the age groups of 2 to 12 years, males predominate (56%); in the groups of 2 to 4 years, sex ratio is close to parity (F, 49%; M, 51%). As the age increases, the proportion of males rises. Notably, in the groups of 13 and 14 years (1.4% of the sample), the proportions of males and females are equal. Out of rapa whelks at the age of 15 and 16 years (0.35% of the sample each), only females are revealed.

Biocenotic relationships of *Rapana venosa*. In the Donuzlav Bay, the mollusc was found in a depth range of 1.0–5.0 m in biocenoses of sand with *Venus*, sand with *Chara*, coquina, *Chara*, and *Zostera*. Rapa whelks were observed copulating, forming egg capsules, feeding, and moving on the substrate.

The mollusc distribution is irregularly patchy. Its maximum concentrations in June–September are related to spawning; therefore, most *R. venosa* were sampled in areas with hard substrates (rocky outcrops or individual stones) where females attach egg capsules. Sometimes, other rapa whelks, algae, or objects of anthropogenic origin serve as a substrate for attaching egg capsules.

The rapa whelk and its egg capsules were not found in the inner area of the bay despite the abundance and diversity of potential Bivalvia food items (oysters, mussels, scallops, *Venus*, *Cardium*, and *Anadara*) and the occurrence of rocky substrate. The highest density of *R. venosa* is characteristic of the bay spots with patchy combination of different biocenoses: it provides an opportunity for the species development at all stages of ontogenesis after larvae settling on the substrate. Individuals of all sizes are found there, and the distribution density is maximum, up to 0.1 ind.$\cdot$m^{-2} (Fig. 1). When both copulating and feeding, *R. venosa* can form groups of several individuals (up to 10 ind.$\cdot$m^{-2}).

Feeding spectrum. We found 43 *R. venosa* individuals feeding on Bivalvia (14.3% of the total abundance). The food objects of the mollusc identified for the study area are listed in Table 2.

Table 2. Species list of molluscs – food objects of *Rapana venosa* in the Donuzlav Bay, their size (L), proportion as prey (Q_1), and mean value of their quantitative input to the Bivalvia taxocene (Q_2)

Taxon	L, mm	Q_1, %	L, mm	Q_2, %
Cerastoderma glaucum (Bruguière, 1789)	28.0–40.2	4.7	6.1–42.6	3.9
Chamelea gallina (Linnaeus, 1758)	11.6–27.8	34.8	5.0–27.6	20.4
Flexopecten glaber (Linnaeus, 1758)	37.7	2.3	9.1–60.2	5.1
Gastrana fragilis (Linnaeus, 1758)	26.3	2.3	12.2–26.8	0.1
Gouldia minima (Montagu, 1803)	7.2	2.3	5.5–10.6	2.0
Irus irus (Linnaeus, 1758)	14.4	2.3	10.2–15.2	0.2
Lucinella divaricata (Linnaeus, 1758)	5.2–6.7	4.7	5.0–7.9	4.0
Modiolus adriaticus Lamarck, 1819	25.2–38.0	25.5	6.5–35.2	10.2
Mytilaster lineatus (Gmelin, 1791)	15.0–23.7	4.7	5.0–24.1	22.1
Parvicardium exiguum (Gmelin, 1791)	12.0–12.5	4.7	5.0–14.1	17.7
Pitar rudis (Poli, 1795)	12.0	2.3	5.5–12.7	3.3
Polititapes aureus (Gmelin, 1791)	14.5–25.0	9.4	6.0–27.0	5.1
Other Bivalvia	–	–	5.4–84.2	5.9

The established feeding spectrum of the rapa whelk in the study area covers 12 Bivalvia species, and their sizes (L) vary from 5.2 mm (*Lucinella divaricata*) to 40.2 mm (*Cerastoderma glaucum*). Among *R. venosa* preys, *Chamelea gallina* prevailed: it was found in 34.8% of individuals feeding on Bivalvia. *Modiolus adriaticus* ranked second in frequency of capture by the rapa whelk (25.5%). It was followed by *Polititapes aureus* (9.4%). Remaining species were registered as *R. venosa* preys once (2.3%) or twice (4.7%) each (Table 2).

In the area of the rapa whelk habitat, the mean biomass of Bivalvia on which it feeds is 162.8 g$\cdot$m^{-2}.

In the Donuzlav Bay, in addition to bivalves, *R. venosa* feeds on the green alga *Chara* sp. (Fig. 3). Its fragments were recorded in esophagus and stomach of 16 molluscs, and this number exceeded the number of the rapa whelk feeding on *Ch. gallina*. Thus, the proportion of feeding *R. venosa* in the bay was about 20% of the total sample.

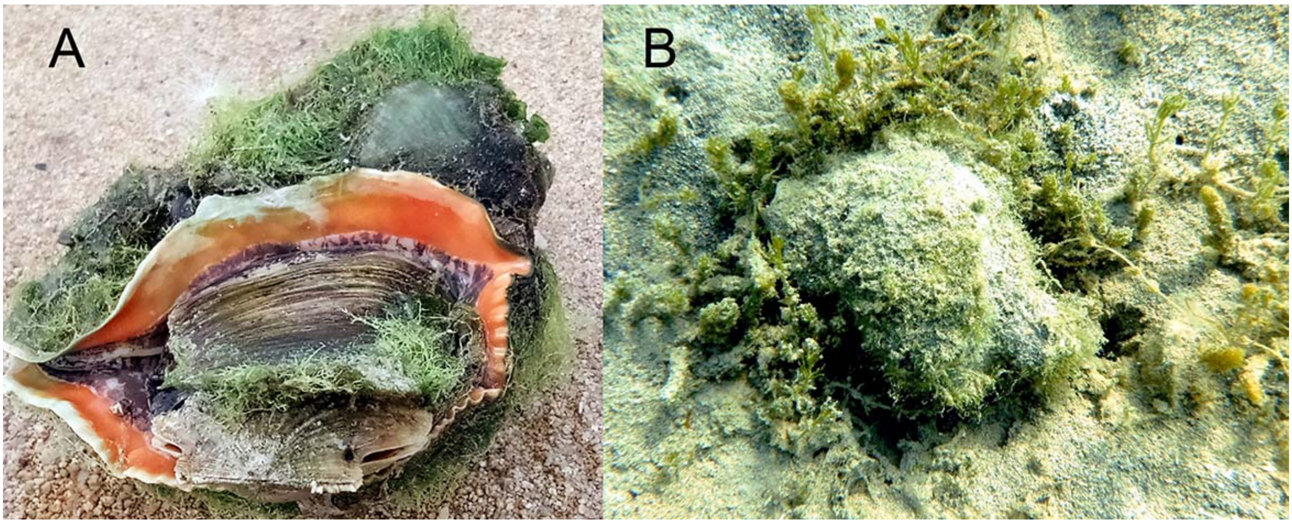

Fig. 3. *Rapana venosa* feeding on the bivalve *Flexopecten glaber* (A) and the green alga *Chara* sp. (B)

Predator–prey. According to *in situ* observations, the Mediterranean green crab *Carcinus aestuarii* Nardo, 1847 (Fig. 4A) feeds on the rapa whelk. In accordance with our data, in the Donuzlav Bay, males of this crab reach a weight of 168 g with a carapace width (CW) of 86.2 mm. The distribution density of *C. aestuarii* by visual assessment during daylight averages 0.05 ind.·m^{-2}.

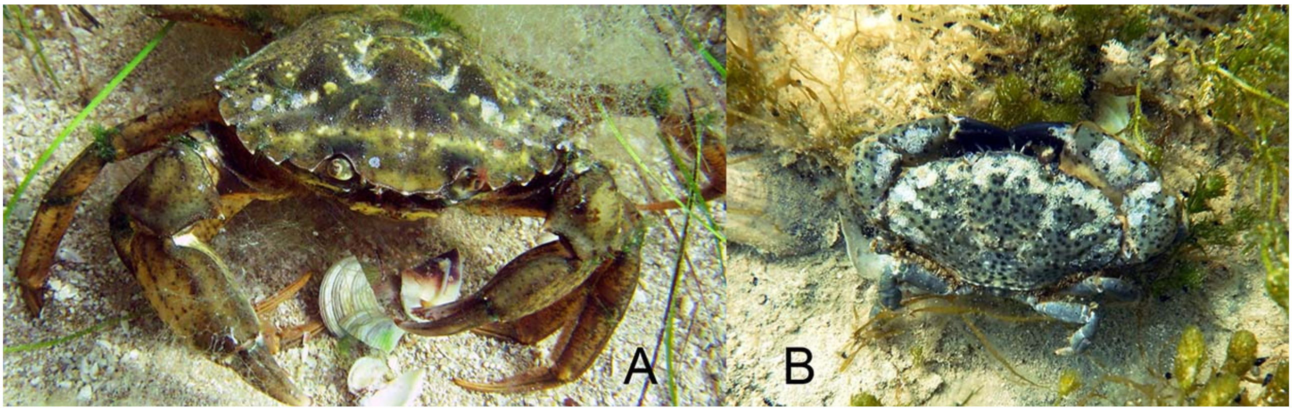

Fig. 4. Crabs – predators of the rapa whelk: A, *Carcinus aestuarii* (CW of 78.2 mm) broke *Chamelea gallina* shell and feeds on its meat, the Donuzlav Bay, depth of 2.8 m; B, *Xantho poressa* (CW of 46 mm) feeds on *Mytilaster lineatus*

In the Donuzlav Bay, the Mediterranean green crab is the object of active amateur fishing; however, it maintains high abundance due to a rich food base including bivalves and gastropods, *inter alia* the rapa whelk. *In situ* observations (5 cases) showed as follows: *C. aestuarii* feeds on *R. venosa* juveniles (SH up to 22 mm) first crushing a shell with its claws. It is not the only mollusc among the crab food items. With its strong claws, *C. aestuarii* is capable of crushing both a relatively thin-walled shell of *M. adriaticus* (3 observations) and a thicker-walled shell of *Ch. gallina* (14 observations) (Fig. 4A). These two Bivalvia species, the same as the rapa whelk, are food objects of the Mediterranean green crab.

Relatively small (SH up to 65 mm) *R. venosa* individuals were repeatedly (6 observations) attacked by *C. aestuarii*, with the crab not releasing its prey and dragging it along the bottom even in case of alarm (a close approach of a diver). Larger rapa whelks of the Donuzlav Bay often have traces of crab attacks – characteristic traces of damage to basal and palatal edges of the mouth (Fig. 5) [Bondarev, 2013]. The height of the largest damaged shell at the time of injury was 122 mm, which means that even large *R. venosa* can be attacked by crabs. More than a half (52%) of the mollusc individuals in the study area have at least one scar on the shell from damage by crab claws in different places, from its top to its last whorl.

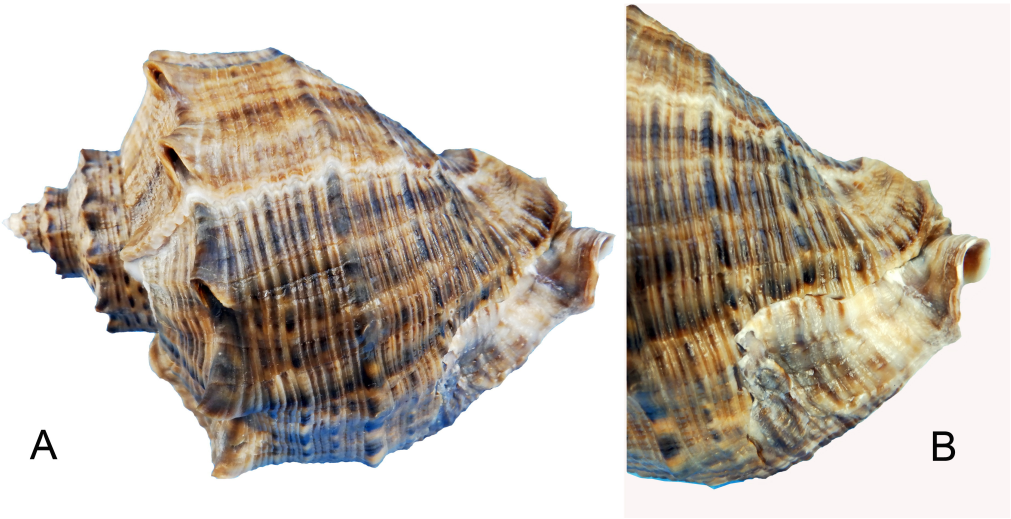

Fig. 5. A, dorsal side of *Rapana venosa* shell (SH of 90.0 mm) with a regenerated area; B, the basal part of the shell (×1.5)

In general, the feeding spectrum of *C. aestuarii* is close to that of *R. venosa*, as it includes all Bivalvia species on which the rapa whelk feeds. Also, it includes fish, algae, and *R. venosa* itself.

Apparently, a potential predator for the rapa whelk juveniles is the jaguar round crab *Xantho poressa* (Olivi, 1792) (Fig. 4B). This small crab with a carapace width (CW) up to 42.3 mm [Kobyakova, Dolgopolskaya, 1969], and possibly up to 47 mm [Makarov, 2004], has relatively large claws and is capable of crushing shells of *Mytilaster lineatus* (Gmelin, 1791) (Fig. 4B) and *R. venosa* juveniles. The largest specimen of this crab for the study area (Fig. 4B), with CW of 46 mm and weight of 24.7 g, was found on rocks among *Chara* sp. thickets. In the Donuzlav Bay, this species is often encountered among stones, on mussel beds, and among algae.

Single and copulating individuals of the grey swimming crab *Liocarcinus vernalis* (Risso, 1827) were noted in the bay water area on sandy sediments. This small (CW up to 39 mm) crab [Makarov, 2004] is inferior in abundance and size to two above-mentioned species, and there is no direct evidence that it feeds on the rapa whelk. However, considering the size of its claws, *L. vernalis* is capable of crushing shells of *R. venosa* juveniles.

DISCUSSION

In material of the first study of the Donuzlav Bay benthos carried out in 1981 [Chukhchin, 1992], the size of found rapa whelks is not specified. In 2007, the mean SH of single individuals was 86 mm; absence of *R. venosa* egg capsules, juveniles, and empty shells was reported [Pereladov, 2013]. In 2009–2012 in the Donuzlav Bay on sandy sediments, 60 *R. venosa* (SH of 30–79.9 mm; age of 3–5 years) were sampled [Kosyan, 2013, 2016]. The mean size of the rapa whelk shells in our sample (SH of 86.6 mm) is close to that of individuals recorded in 2007 by M. Pereladov [2013]. Since noticeably smaller and larger rapa whelks were not registered in a sample of 2007, it can be assumed that the above mean size does not differ significantly from the extreme values.

In the mature part of *R. venosa* population in the Donuzlav Bay, there are individuals with a wide range of SH – from 32.1 to 135.0 mm. Quite a high abundance of young, 2–3-year-old, rapa whelks (52.8%) and the occurrence of 14–16-year-old ones (1.4%) (Fig. 2) indicate the sufficiency of food resources for the species.

To date, *R. venosa* with SH of 40–90 mm is most common off the Crimean coast, but this parameter can differ significantly in various populations. Most of recent rapa whelk populations off the Crimean coast consist of "dwarf" individuals – with the size (SH) at mature and old age not exceeding 50–60 mm [Bondarev, 2010, 2011, 2016]. A decline in growth rates and a clear tendency to the mollusc size drop in the Black Sea, as compared to those at the initial stage of its introduction, were recorded already in the late 1950s, and this was associated with a decrease in food base [Chukhchin, 1961b, c]. In the Kerch region, until the early 1990s, the modal size (SH) of *R. venosa* was 90–110 mm; in 1990–1994, it was 80–100 mm; in 1997–2000, SH was 55–85 mm; and in 2001–2006, it was 50–90 mm [Evchenko, 2010]. According to data of a study of 1,581 *R. venosa* in the southeastern Black Sea off the coast of Turkey in January–August 2000, the maximum size of individuals (SH) was 90.0 mm, and the mean one was (53.82 ± 0.410) mm [Sağlam, Düzgüneş, 2014].

A wide range of size and weight indicators of *R. venosa* is maintained in the Donuzlav Bay. Feeding on the alga *Chara* sp. provides additional opportunities for the rapa whelk survival by expanding its food base. Apparently, such an addition to the mollusc feeding spectrum in the bay contributes to the formation of large shells (SH up to 135 mm) and survival of old (16 years) individuals against the backdrop of the general opposite trend observed in the Black Sea. The established occurrence of mature *R. venosa* with SH of 30–50 mm corresponds to previously reported facts of coexistence of individuals differing significantly in size within local Black Sea populations [Bondarev, 2010, 2011; Pereladov, 2013].

Sex ratio F : M = 1 : 1.36 (F, 42.3%; M, 57.7%) in the studied population also indicates rather favorable conditions of its existence. In an "ideal" population, sex ratio is 1 : 1; such a ratio was recorded for the rapa whelk in the Sevastopol Bay in the late 1950s [Chukhchin, 1961a]. In modern populations of *R. venosa* in the Black and Mediterranean seas, the proportion of males usually exceeds that of females [Bondarev, 2010, 2011, 2014, 2016; Sağlam et al., 2009; Savini et al., 2004]. On average, F : M for coastal populations of the Crimean Peninsula is 1 : 1.85 (F, 35%; M, 65%); sometimes, it is 1 : 4.5 (F, 18%; M, 82%) (in 2002 in the Kerch region) [Bondarev, 2011]. F : M = 1 : 1.6 disproportion is reported for the rapa whelk of the Turkish coast of the Black Sea [Sağlam et al., 2009]. Sex ratios similar to our data are provided for *R. venosa* of the Adriatic Sea: females account for 47% of the population on sandy sediments and 43% on rocky sediments [Savini et al., 2004].

The predominance of males in *R. venosa* populations seems to be due to the fact that females incur increased energy costs for reproduction forming a cluster of capsules filled with eggs [Chukhchin, 1970]. Compensation of such energy costs is possible only if there is a sufficient food base. Deficiency in feeding results in increased mortality among females of predominantly older age, and this leads to the observed disproportion of sex ratio in *R. venosa* populations [Bondarev, 2010, 2016]. Features of the Donuzlav Bay are the parity of sexes among 13- and 14-year-old rapa whelks and the occurrence of only females in the oldest age groups, 15 and 16 years. One of the factors contributing to the survival of older females seems to be their smaller size which means that the mollusc does not require a large amount of food to sustain life.

Biocenotic relationships of *Rapana venosa*. During the first survey of the Donuzlav Bay benthos in 1981, it was noted that the mollusc is often found in its southern area in the biocenosis of coquina and is not recorded within other biocoenoses [Chukhchin, 1992]. Our studies confirmed the occurrence of the rapa whelk aggregations on coquina which are predominantly formed around rocky sediments. *R. venosa* confinement to this biocenosis in the summer–autumn period is related to the occurrence of substrate for attaching egg capsules and abundance of potential preys which mostly inhabit sandy sediments surrounding rocky outcrops. For *R. venosa*, widely distributed in the Black Sea food objects are as follows: *Ch. gallina*, *C. glaucum*, *Gastrana fragilis*, *Gouldia minima*, *L. divaricata*, *Parvicardium exiguum*, *P. aureus*, and *Pitar rudis*. Those are typical representatives of infauna of loose sediments. *Flexopecten glaber*, *M. adriaticus*, *M. lineatus*, and *P. exiguum* occur both on loose sediments and solid substrates (coquina and rocks) and on algae. According to our data, the highest density and abundance of the rapa whelk are characteristic of the Donuzlav Bay areas with coexisting different biocenoses: their patchiness provides conditions for the development of all stages of the mollusc ontogenesis from the moment of larvae settling on the bottom. On solid substrate and algae, *R. venosa* attaches egg capsules; in algae, juveniles take shelter and find food; and on loose sediments, most of the rapa whelk finds its prey.

In the summer of 2007 in the Donuzlav Bay water area, *R. venosa* was sporadically recorded at a site about 2 km from the open sea. There, the species settlement density was less than 0.01 ind.·m^{-2}. On a spot about 4 km from the open sea, the rapa whelk was not noted at all, despite a pretty high abundance of mussel banks, live relict oysters, and scallop aggregations. In the center and in the inner area of the Donuzlav Bay, *R. venosa* was also not registered. According to local divers, it is found in significant quantities only in the water area adjacent to the channel which connects the bay with the open sea [Pereladov, 2013]. In 2009–2012, the mollusc was sampled in a sand biotope at depths of 5–8 m [Kosyan, 2013, 2016].

According to our data, in the Donuzlav Bay, the rapa whelk was encountered in a depth range of 1–5 m in biocenoses of sand with *Venus*, sand with *Chara*, coquina, *Chara*, and *Zostera*. The settlement density at most stations was < 0.01 ind.·m^{-2}. At some sites, it increased by an order of magnitude – up to 0.1 ind.·m^{-2} (Fig. 1); sometimes, the value reached 10 ind.·m^{-2}.

Our finding of a wider *R. venosa* distribution and areas with a higher settlement density, as compared to those in previous studies, is explained by the nature of its distribution (aggregation and patchiness) and targeted search for the object. In the inner area of the Donuslav Bay, we also did not find the rapa whelk despite the occurrence of coquina and rocky sediments with live molluscs. Several bivalve species included in *R. venosa* feeding spectrum inhabit sand, *inter alia* mussel which occurs on rocks as well (up to 20 ind.·m^{-2}). On rocky sediments, the density of oysters alone reaches 5 ind.·m^{-2} on some spots [Pereladov, 2016]. Apparently, *R. venosa* distribution towards the inner area of the Donuzlav Bay is hindered by mass development of the Mediterranean green crab.

Feeding spectrum. The rapa whelk is obviously selective regarding food items (Table 2). The preference for *Ch. gallina* is especially evident; this species accounts for 20.4% of the total Bivalvia abundance in the study area and 34.8% of *R. venosa* preys. Specimens sampled in the Donuzlav Bay in 2012 on sandy sediments also predominantly fed on *Ch. gallina* [Kosyan, 2013, 2016].

The rapa whelk prefers this mollusc to other species in modern populations of loose sediments biotopes in most Black Sea areas [Bondarev, 2016, 2020; Kosyan, 2016; Zolotarev, Yevchenko, 2010]. In the northeastern Black Sea from Chauda Cape (the Crimea) to Batumi, only bivalves were recorded in *R. venosa* feeding spectrum, and out of them, *Ch. gallina* accounted for 80% [Zolotarev, Yevchenko, 2010]. Predominant feeding on this species is characteristic of the rapa whelk inhabiting sandy sediments in the bays of Sevastopol [Bondarev, 2016]. In the mollusc feeding spectrum in the Kazachya Bay (Sevastopol, the Crimea), *Ch. gallina* accounted for 80% of preys; *M. adriaticus*, 5%; *P. rudis*, 5%; *P. exiguum*, 4%; *P. aureus*, 3%; *C. glaucum*, 2%; and *G. minima*, 1% [Bondarev, 2020].

Such a group of molluscs with a similar proportion of most prey species is also characteristic of our sample from the Donuzlav Bay. The main differences are a smaller proportion of *Ch. gallina* (34.8%) and significantly higher contribution of *M. adriaticus* (25.5%) – the species accounting on average for 10.2% of the total Bivalvia abundance in the bay biocenoses (Table 2). *P. aureus* is also more frequently recorded among *R. venosa* preys (9.4% *vs.* 5.1% in biocenoses), while *M. lineatus* and *P. exiguum* are noticeably more abundant in biocenoses (22.1% and 17.7%, respectively) than among the rapa whelk preys (4.7% each). One of the factors of the revealed selectivity seems to be the size of Bivalvia individuals (Table 2). Earlier, the correspondence between the size characteristics of *R. venosa* and its preys was evaluated [Bondarev, 2016; Kosyan, 2013; Sağlam, Düzgüneş, 2014]; as shown, since the Donuzlav Bay is inhabited by quite a lot of large rapa whelks, small-sized Bivalvia species are less frequently selected as preys.

Notably, large Bivalvia representatives which were previously considered as the main food objects of *R. venosa* (*Mytilus galloprovincialis* Lamarck, 1819 and *Ostrea edulis* Linnaeus, 1758) were not registered as its preys in the study area, although both species occur in the Donuzlav Bay benthos. Moreover, feeding on the scallop *F. glaber* which forms aggregations in some bay areas with a settlement density of more than 10 ind.$\cdot$m^{-2} was recorded only once. In the immediate vicinity of numerous scallop individuals, we repeatedly registered the rapa whelk feeding on *Ch. gallina* and *M. adriaticus*.

This situation seems to be due to the fact that the largest (SH > 110 mm) *R. venosa* individuals were copulating at that time and did not feed until late September (the month to which the research season was limited). As known, during the degradation of the Gudauta Bank biocenoses and the disappearance of mussels and oysters, out of large Bivalvia, only the scallop remained. It is assumed that large bivalves were destroyed by *R. venosa*, and the scallop survived due to its ability to swim away from predators [Chukhchin, 1961b]. According to our survey, *F. glaber* reacts to the approach of a potential predator (a diver) by closing its valves without changing the position, and the rapa whelk shows no active food interest in this scallop either in natural or in laboratory conditions. In an aquarium, food reaction of *R. venosa* to *O. edulis* was weak, or there was no reaction at all [Pereladov, 2013]. Apparently, the contribution of the rapa whelk to extermination of the Black Sea oysters and scallop is overestimated. As already noted, the issue of its fatal effect on oyster settlements in the Black Sea remains debatable [Pereladov, 2013].

The mean biomass of the mollusc in the study area was 3.8 g·m^{-2}, and the mean biomass of its food objects, Bivalvia, was 162.8 g·m^{-2}. It indicates a sufficient food supply and the lack of a significant negative effect of the predator.

Fragments of the alga *Chara* sp. were found in the esophagus and stomach of large *R. venosa* (SH > 90 mm). Previously, feeding of its juveniles (SH of 12–31 mm) on periphyton formed on the walls of the aquarium was established [Pereladov, 2013]. Actually, the difference in the feeding mechanism of herbivorous gastropods is that those scrape food with their radula, while the rapa whelk uses its radula to bite off pieces of the prey meat [Chukhchin, 1970] and, as it turned out, algae fragments. Algae in *R. venosa* digestive tract are also partially grinded with this anatomical structure. Notably, the species is able to bore shells of not only juveniles but also aged molluscs with its radula [Kosyan, 2016], and this is confirmed by our data. Maybe, the rapa whelk is not an obligate predator, and this expands its adaptive potential. However, this issue requires further research.

Crabs and smaller carnivorous crustaceans (hermit crabs and shrimps) feeding on *Chara* sp. were also recorded in the study area. These algae are known to be a source of food for waterfowl which mainly feed on oospores filled with starch and fat droplets. Due to the high abundance of lime in them, *Chara* algae are applied as fertilizer for heavy soils [Gollerbakh, 1977]. Obviously, the complex of the above important components of *Chara* sp. is actively used by many carnivorous invertebrates.

Predator–prey. Damage to *R. venosa* shells by crabs was previously described for the individuals of the bays of Sevastopol [Bondarev, 2013], where, in addition to *C. aestuarii*, *Eriphia verrucosa* (Forskål, 1775) occurs – the warty crab inhabiting the Black Sea but not found in the Donuzlav Bay. This crab is the largest of the native species and has the strongest first pair of pereopods. The warty crab was repeatedly registered by the author *in situ* with adult rapa whelk in its claws. Crushing of a small *R. venosa* shell (SH of 25 mm) with a wall thickness of about 1.0 mm by the warty crab in an aquarium was recorded as well [Bondarev, 2013].

C. aestuarii is the most common and abundant crab in the Black Sea occurring down to a depth of 70 m. This species usually forms large aggregations in the littoral and sublittoral zone and in lagoons. It inhabits sandy sediments or coquina, lives among algae or, less frequently, on gravel or under rocks. In the XX century (especially before the 1970s), the Mediterranean green crab was most common in the northwestern Black Sea [Makarov, 2004], and this circumstance can explain the previously observed paradoxically low abundance of the rapa whelk in this area against the backdrop of significant amounts of bivalves [Zolotarev, 1996]. To date, as a result of habitat destruction and excessive recreational fishing on some spots, the frequency of *C. aestuarii* occurrence noticeably dropped, and the species is listed in the regional Red Data Book [Krasnaya kniga goroda Sevastopolya, 2018].

The Donuzlav Bay, with its abundant food base including *R. venosa*, is obviously a comfort zone for the development of *C. aestuarii* population; therefore, there are individuals with sizes exceeding the previously known maximum ones. In accordance with literature data, in the Black Sea, the maximum carapace width (CW) of the Mediterranean green crab is 80 mm with a length of 63 mm [Kobyakova, Dolgopolskaya, 1969]. In the Donuzlav Bay, *C. aestuarii* with CW > 80 mm is not rare, and the maximum CW, according to our data, is 86.2 mm. In the Mediterranean Sea population and in other newly formed populations (those of Japan, Australia, New Zealand, and North America), the Mediterranean green crab has significantly smaller CW – up to 65 mm [Yamada, Hauck, 2001]. The large size of *C. aestuarii* in the Black Sea and Donuzlav Bay allows it to hunt not only rather large Bivalvia and *R. venosa* juveniles, but also mature individuals. According to our data, the Mediterranean green crab has a feeding spectrum similar to that of *R. venosa*, with a predominance of bivalves. Thus, for *R. venosa*, *C. aestuarii* is both a trophic competitor and predator.

Importantly, after settling on sediments, the rapa whelk suffers the greatest losses from benthic predators during the early stages of its growth. Right after settling, its juveniles are about 1 mm in size; in two weeks, those grow to 1.5 mm; and in another 6 days, those grow to 2 mm [Chukhchin, 1970]. Therefore, even small-sized crab species can significantly affect *R. venosa* abundance. So, the effect of these crabs on the rapa whelk population should not be underestimated. Although adult large mollusc is also attacked by large-sized crabs, it is much less likely to become prey; moreover, it is capable of regenerating damaged and even lost shell fragments (Fig. 5) [Bondarev, 2013]. Apparently, crab cultivating can contribute to regulating *R. venosa* abundance and limiting its expansion.

Conclusion. There is a stable population of *Rapana venosa* in the Donuzlav Bay – with a complete structure, actively reproducing, and provided with a variety of food items.

With the occurrence of potential food objects throughout the bay, the rapa whelk distribution is limited to the central and southwestern Donuzlav Bay. There, its density ranges from < 0.01 to 0.1 ind.·m^{-2}.

R. venosa food competitors and predators are native Black Sea crabs limiting the abundance and, probably, distribution of this invasive gastropod.

Revealing of the alga *Chara* sp. in the rapa whelk stomachs indicates an expansion of its feeding spectrum and requires further study: it may evidence for the fact that this species has a greater adaptive potential than previously known.

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ОСОБЕННОСТИ ПОПУЛЯЦИОННОЙ СТРУКТУРЫ И БИОЦЕНОТИЧЕСКИХ СВЯЗЕЙ *RAPANA VENOSA* (VALENCIENNES, 1846) (GASTROPODA, MURICIDAE) В ЗАЛИВЕ ДОНУЗЛАВ ЧЁРНОГО МОРЯ

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Западно-тихоокеанский брюхоногий моллюск *Rapana venosa* (Valenciennes, 1846) отнесён к 100 наиболее опасным инвазионным видам Чёрного и Средиземного морей, а также признан опасным вселенцем в ряде районов прибрежных вод по обе стороны Атлантического океана. Это обстоятельство определяет актуальность изучения популяционных особенностей и биоценотических связей рапаны в районах вселения. Исследования ранее не проанализированной локальной популяции *R. venosa* в заливе Донузлав (Северо-Западный Крым) Чёрного моря в 2020 г. показали, что при наличии обильной и разнообразной пищевой базы рапана не формирует массовых скоплений и, следовательно, не оказывает существенного влияния на донные биоценозы. Этот вывод подтверждается и соотношением биомассы хищного моллюска и его жертв. Средняя биомасса *R. venosa* в обследованном районе составляла 3,8 $г \cdot м^{-2}$, а средняя биомасса объектов её питания (Bivalvia) — 162,8 $г \cdot м^{-2}$. Особенности популяционной структуры и биоценотические связи рапаны в заливе Донузлав рассмотрены и обсуждены впервые. Прямые и косвенные данные свидетельствуют, что распространение вида-вселенца *R. venosa* контролируется аборигенными хищниками — крабами. Основным видом, ограничивающим численность рапаны в исследованном районе, является краб *Carcinus aestuarii* Nardo, 1847.

Ключевые слова: биоценозы, водоросли, инвазионный вид, крабы, моллюски, хищник — жертва

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DISTRIBUTION AND ABUNDANCE OF WATER BIRDS AND SEABIRDS IN SOME AREAS OF THE SOUTHWESTERN KARA SEA IN THE SUMMER-AUTUMN PERIOD 2015–2020

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The southwestern Kara Sea is a scarce studied area in terms of summer-autumn migrations and feeding nomadism of water birds and seabirds. Its shelf includes promising areas for extraction of hydrocarbon raw materials and intensification of navigation along the Northern Sea Route, which makes it necessary to carry out constant monitoring of birds in the area of possible negative effect of those factors. In August–September 2015–2016 and 2018–2020 and in late September–first and second decades of October 2017, bird counts were carried out in the southwestern Kara Sea. Method of ship transect census was applied to obtain the abundance of individuals *per* 1 km^2. For this water area, 28 species of birds representing 7 families were identified (Gaviidae, Sulidae, Procellariidae, Anatidae, Laridae, Stercorariidae, and Alcidae), including 6 species of conservation status. For the group of water birds, the data obtained in August–October are most detailed for the black-throated diver, long-tailed duck, and king eider (Gaviidae and Anatidae). *Prior* to autumn migration (August), their abundance increased in the shallow area adjacent to the coast, later followed by their dispersal to deeper areas west of the Yamal Peninsula. In coastal shallow areas, the population density during the period of the most active colonization of this biotope is as follows (ind.·km^{-2}): (0.17 ± 0.036) for the black-throated diver, (4.87 ± 1.2) for the long-tailed duck, and (2.1 ± 1.25) for the king eider. Presumably, the values are significantly higher for all three species at shorter distances from the coast not examined from the vessel. Other species of the group of water birds (the red-throated diver, Steller’s eider, dark-bellied brant goose, European white-fronted goose, and bean goose) are rare in open waters and, apparently, are mainly confined to a narrower coastal zone during the entire summer-autumn period. The same indicator of abundance of migratory seabirds (Procellariidae, Laridae, Stercorariidae, and Alcidae), calculated for the entire water area of the survey site, averaged for 5 years for August–September (ind.·km^{-2}): (0.078 ± 0.026) for the fulmar, (0.067 ± 0.014) for the glaucous gull, (0.061 ± 0.016) for the black-legged kittiwake, (0.025 ± 0.015) for the Arctic tern, (0.066 ± 0.0049) for the Heuglin’s gull, (0.046 ± 0.0074) for the pomarine skua, (0.014 ± 0.0023) for the Arctic skua, (0.0039 ± 0.00095) for the long-tailed skua, (0.16 ± 0.094) for the Brünnich’s guillemot, and (0.0026 ± 0.0012) for the black guillemot. In late September and October, the abundance of the black-legged kittiwake, fulmar, and Brünnich’s guillemot slightly decreases or remains at the level of September one, while the abundance of the black guillemot increases by 7 times. The Arctic tern, Heuglin's gull, and long-tailed skua disappear from the water area. The glaucous gull, pomarine skua, and Arctic skua become much rarer or almost disappear (5-, 40-, and 30-fold drop in abundance, respectively). In general, in the long-term aspect, the fulmar, three Stercorariidae species, the glaucous gull, black-legged kittiwake, Arctic tern, and black guillemot colonize the entire survey site. Interestingly, for the fulmar, black-legged kittiwake, and glaucous gull, uneven distribution is recorded in some years, which is expressed in significant (3 to 17 times) differences in abundance between large (about 25 thousand km^2) spots of the studied water area. During their entire stay at the survey site, the Heuglin's gull and Arctic tern are mainly confined to coastal shallow areas; there, up to 80–90% of the total abundance of individuals in the studied water area is concentrated during periods of seasonal maximum. On the contrary, the Brünnich's guillemot avoids shallow areas (depth of < 50 m). Rare species are vagrant ones (the northern gannet, black-headed gull, European herring gull, and common gull), those found in the peripheral area of their common range (the great skua and grey petrel), and those considered rare at the present stage of the existence of their populations (the white-billed diver). Also, rare species are the birds with insufficiently studied main habitat (the velvet scoter, Steller's eider, dark-bellied brant goose, bean goose, and European white-fronted goose) and seasonally rare ones (the little auk).

Keywords: Kara Sea, seabirds and water birds, migrations, nomadism, annual and seasonal population dynamics

For waters of the southwestern Kara Sea, 33 species of birds are registered in the summer-autumn period; those represent the families Gaviidae, Procellariidae, Sulidae, Anatidae, Stercorariidae, Laridae, and Alcidae [Decker et al., 1998; Lunk, Joern, 2007; Popov, 2012]. With a fairly good study of the species composition of birds in this area, there are no modern data on their abundance (population density) and its dynamics over a number of years which are necessary both for gaining an insight into birds of the spot in population and biocenotic aspects and for assessing their vulnerability to probable negative effect during the exploitation of local promising oil and gas fields. This report is devoted to a description of the species composition and abundance of birds in the southwestern Kara Sea. This area is located west of the Yamal Peninsula, between N70°40′ and N73°50′ and E62°40′ and E70°00′. The data obtained are not an exhaustive description of the bird fauna of the entire southwestern sea area, for those characterize a biotopically specific site: predominantly a medium-deep open water area adjacent to the Arctic tundra zone. This site does not include such bird habitats, as littoral and supralittoral zones, estuaries, islands, lagoons, wet meadows, *etc.*

MATERIAL AND METHODS

Over five seasons, bird counts in the southwestern Kara Sea were carried out in August–September (2015–2016 and 2018–2020); once, a census was carried out later, September 28 to October 22 (2017). Survey routes ran within boundaries of the site with an area of 56 thousand km^2 (Fig. 1) [Itogovyi otchet, 2015, 2016, 2017, 2018a, b, 2019a, b, 2020a, b].

In terms of the depth regime, the area can be classified as zones of the internal shelf (down to 100 m) and, to a lesser extent, external one (100–200 m). According to 293 measurements, the depth at the survey site averages 70 m. Interestingly, the zone with depths down to 100 m occupies 75% of the area, and with a depth 100 to 150 m, 25%. At a minimum depth (6 m), the water area was surveyed at a distance of 3 km from shore (this is the shortest distance from the coast). There was no ice at the survey site in all years of observation. Ice cover in the Kara Sea was low: during investigation periods, ice occurred in small quantities only in the far north and northeast of the sea. The survey site features interaction of the Arctic water mass of the Kara Sea, waters of river runoff, and Atlantic water masses flowing through the Yugorsky and Kara straits. In summer, the vertical structure of the temperature field in the western sea is characterized by occurrence of an upper heated layer, a seasonal thermohalocline, a layer of subsurface minimum (residual cold winter layer), and a layer of Atlantic-origin waters. The vertical distribution of salinity shows its significant increase in the thermohalocline down to depths of 20–30 m and a further gradual rise to bottom horizons. The spot of the bottom slope – the transition from depths of 18–20 to 100–120 m is the location of the frontal zone of the Yamal Current [Zatsepin et al., 2010].

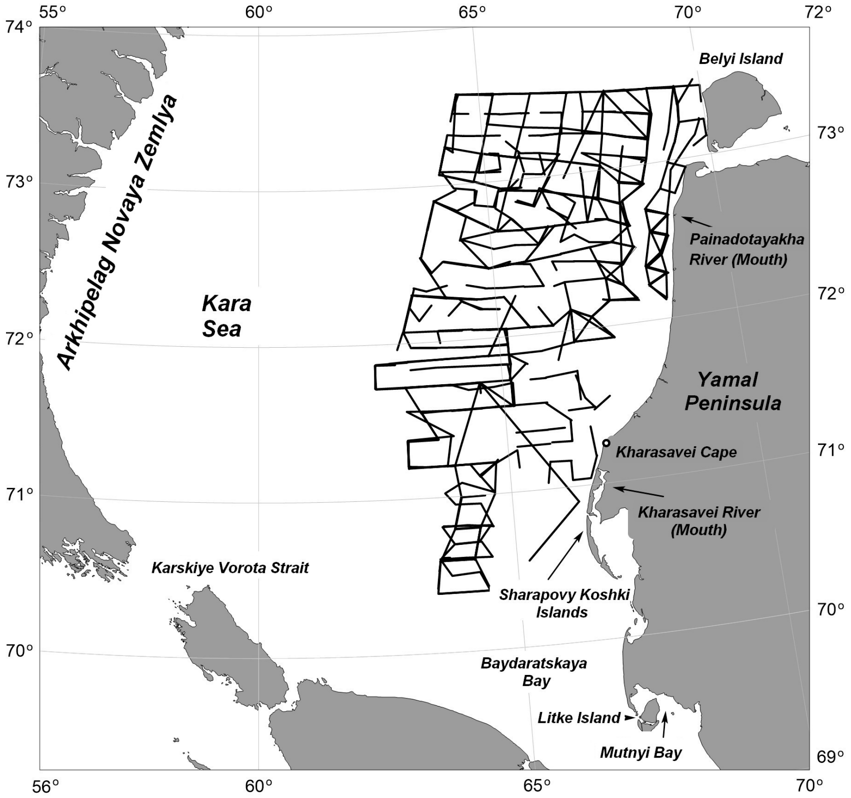

Fig. 1. Map of survey routes in the southwestern Kara Sea in August–October 2015–2020

Bird feeding in this area has not been studied. The potential forage base of piscivorous and planktivorous species (Gaviidae, Sulidae, Procellariidae, Laridae, and Alcidae representatives) may include the most abundant pelagic and bottom–pelagic fish: the polar cod *Boreogadus saida* (Lepechin, 1774), the capelin *Mallotus villosus* (Müller, 1776), and the navaga *Eleginus nawaga* (Walbaum, 1792), as well as pelagic juveniles of various species (*inter alia* benthic ones) of the families Cottidae, Agonidae, and Liparidae. Also, the forage base may cover large zooplankton, primarily of the families Euphasiidae, Hyperiidae, *etc.* Apparently, the diet of Anatidae feeding at sea chiefly includes gastropods common in shallow areas [*Lunatia pallida* (Broderip & G. B. Sowerby I, 1829), *Limneria undata* (T. Brown, 1839), *Buccinum belcheri* (Reeve, 1855), *Buccinum fragile* (Verkrüzen, 1878), and *Murex pullus* (S. Woodward, 1833)], bivalves [*Serripes groenlandicus* (Mohr, 1786) and *Ciliatocardium ciliatum* (O. Fabricius, 1780)], amphipods [*Sabinea septemcarinata* (Sabine, 1824) and *Sclerocrangon ferox* (G. O. Sars, 1877)], as well as such species, as *Stegocephalus inflatus* (Krøyer, 1842), *Lebbeus polaris* (Sabine, 1824), *Pandalus borealis borealis* (Krøyer, 1838), and *Saduria sabini* (Krøyer, 1849) [Ekosistema Karskogo morya, 2008].

We applied the technique of ship transect census [Gould, Forsell, 1989]. While the vessel was moving, a section of the water area limited by distances of 300 m forward and 300 m perpendicular to each side (0.18 km^2) was visually identified. Within a section, all birds were counted for 5–10 s (a so-called snapshot was made). After completing a 300-m distance, the next section was visually identified and inspected in the same way. The time of completing each 300-m section of the transect was determined using a "period" option of a handheld GPS Garmin GPSmap 64st. The mean distribution density of birds at the survey site was calculated by relating the sum of counted individuals to the total area of the transect. For the most common species, the standard error of the mean and the significance of the difference in means were determined (using Student's t-test); for this purpose, densities were also established for individual sections of the transect, about 20 km long (and for corresponding areas of about 12 km^2). The water area was surveyed during daylight hours, for 10 h (twilight was excluded from the time of bird counts), by a naked-eyed observer. The observation point was located at a height of 7 m above water. The speed of the vessel was approximately 15 km·h^{-1}. Data on the route length in individual years and the corresponding area of the transect are provided in Table 1.

Table 1. Timing and scope of work at the survey site in the southwestern Kara Sea in 2015–2020

Year, months	Transect length, km	Transect area, km^2
2015, August–September	2,692	1,613
2016, August–September	1,563	938
2017, September–October	1,250	750
2018, August–September	1,548	928
2019, August–September	1,694	1,016
2020, August–September	1,378	827

The interannual dynamics of abundance for the investigation period is a series of mean distribution density values calculated from all dates in August and September for each year. The seasonal dynamics in August–October was determined by similar dates for all years grouped into two-decade time periods. The intersection of individual sections of the survey site within the route differed by dates during the investigation period. Also, Gaviidae and Anatidae distribution is characterized by high seasonal and spatial unevenness there. Due to these facts, it is worth noting as follows: the mean abundance values for August–September cannot serve as an indicator of the interannual dynamics for this group of birds. For this purpose, only fluctuations within August–October were compared. The occurrence of shorebirds (waders) in the marine area is not discussed in this report. Names of birds in Latin are given according to a summary [Koblik et al., 2006].

RESULTS AND DISCUSSION

In August–October, 11 species of water birds (Gaviidae and Anatidae) and 17 species of seabirds (Procellariidae, Sulidae, Laridae, Stercorariidae, and Alcidae) were recorded in the southern Kara Sea (Table 2).

Table 2. Species composition and conservation status of seabirds and water birds recorded at the survey site in the southwestern Kara Sea in August–October 2015–2020

Taxon	Species conservation status
Order Gaviiformes	
Family Gaviidae	
Red-throated diver *Gavia stellata stellata* (Pontoppidan, 1763)	–
Black-throated diver *Gavia arctica arctica* (Linnaeus, 1758)	–
White-billed diver *Gavia adamsii* (J. E. Gray, 1859)	IUCN (NT), RF (3 VU III), NAO (3), YaNAO (4)
Order Procellariiformes	
Family Procellariidae	
Fulmar *Fulmarus glacialis glacialis* (Linnaeus, 1761)	–
Grey petrel *Puffinus griseus* (Gmelin, 1789)	–
Order Suliformes	
Family Sulidae	
Northern gannet *Morus bassanus bassanus* (Linnaeus, 1758)	–
Order Anseriformes	
Family Anatidae	
Dark-bellied brant goose *Branta bernicla bernicla* (Linnaeus, 1758)	–
European white-fronted goose *Anser albifrons albifrons* (Scopoli, 1769)	–
Bean goose *Anser fabalis* (Latham, 1787)	RF (2 EN II)
Long-tailed duck *Clangula hyemalis* (Linnaeus, 1758)	IUCN (VU)
King eider *Somateria spectabilis* (Linnaeus, 1758)	–
Steller's eider *Polysticta stelleri* (Pallas, 1769)	IUCN (VU), RF (2 VU III), YaNAO (3)
Common scoter *Melanitta nigra* (Linnaeus, 1758)	–
Velvet scoter *Melanitta fusca* (Linnaeus, 1758)	IUCN (VU), NAO (3), YaNAO (4)
Order Charadriiformes	
Family Stercorariidae	
Great skua *Stercorarius skua* (Brünnich, 1764)	–
Pomarine skua *Stercorarius pomarinus* (Temminck, 1815)	–
Arctic skua *Stercorarius parasiticus* (Linnaeus, 1758)	–
Long-tailed skua *Stercorarius longicaudus longicaudus* (Vieillot, 1819)	–
Family Laridae	
Black-headed gull *Chroicocephalus ridibundus* (Linnaeus, 1766)	–
European herring gull *Larus argentatus argentatus* (Pontoppidan, 1763)	–
Heuglin's gull *Larus heuglini antelius* (Iredale, 1913)	–
Glaucous gull *Larus hyperboreus hyperboreus* (Gunnerus, 1767)	–
Common gull *Larus canus canus* (Linnaeus, 1758)	–

Continued on the next page…

Taxon	Species conservation status
Black-legged kittiwake *Rissa tridactyla tridactyla* (Stephens, 1826)	IUCN (VU)
Arctic tern *Sterna paradisaea* (Pontoppidan, 1763)	–
Family Alcidae	
Little auk *Alle alle* (Linnaeus, 1758)	–
Brünnich's guillemot *Uria lomvia lomvia* (Linnaeus, 1758)	–
Black guillemot *Cepphus grylle* (Linnaeus, 1758)	–

Note: IUCN, The IUCN Red List of Threatened Species [2023]; RF, The Red Data Book of the Russian Federation [2021]; NAO, The Red Data Book of the Nenets Autonomous Okrug [2020]; YaNAO, The Red Data Book of the Yamalo-Nenets Autonomous Okrug [2023]. Categories according to the IUCN Red List: NT, near threatened; VU, vulnerable. Rarity status of wildlife objects: 2, declining in abundance and/or distribution; 3, rare; 4, uncertain status. Status of the threat of extinction of wildlife objects characterizing their state in natural habitat: EN, endangered; VU, vulnerable. Degree and priority of environmental measures taken and planned (environmental status): priority II, it is necessary to implement one or more special measures to preserve wildlife objects; priority III, general measures are enough, provided by regulatory legal acts of the Russian Federation in environmental protection, organization, protection, and use of specially protected natural areas, and protection and use of wildlife and the habitats, for the conservation of fauna and flora objects listed in the Red Data Book of the Russian Federation.

Water birds. During the investigation period, the most common species of this group were the black-throated diver, long-tailed duck, and king eider.

The black-throated diver. From 8 August to 7 October, it was registered everywhere (Fig. 2). In general, for the entire survey site in August–September, according to averaged data for 2015–2020, the population density varied by 1.8 times [(0.034 ± 0.15) *vs.* (0.06 ± 0.01) ind.·km^{-2}, $P > 0.05$]. During the investigation period, the distribution of birds in the water area changed significantly. In August, density of the black-throated diver was the highest in shallow areas with a mean depth of 12 m (those occupy only 11% of the survey site) at a distance up to 20 km from the Yamal shore, where their abundance accounted for (0.156 ± 0.046) ind.·km^{-2} (Fig. 3). It was the nesting season, and birds seemed not only to stay in the water area, but also to fly out to sea to search for food. At a distance exceeding 20 km from shore, abundance dropped sharply, and birds were pretty evenly distributed up to the western boundary of the survey site, with an 18-fold lower density than in above-mentioned shallow areas [(0.0086 ± 0.0027) ind.·km^{-2}, $P < 0.001$]. In September, as the black-throated diver migrated to its wintering grounds, its distribution was more uniform throughout the survey site. At distances of 0–40 and 40–100 km from the Yamal Peninsula coast, the population density differed only by 2 times [(0.17 ± 0.036) *vs.* (0.082 ± 0.019) ind.·km^{-2}, $P < 0.05$]. Then, throughout the entire survey site to its boundaries (distance from shore up to 180 km), the value was 5 times lower, changed slightly, and averaged (0.018 ± 0.0065) ind.·km^{-2} (the difference with the value at a distance of 40–100 km is significant, $P < 0.01$) (Fig. 3). Next month, a sharp drop in abundance was noted, and the black-throated diver was not counted later than on 8 October. The mean density for the survey site was 6 times lower than in September, (0.01 ± 0.0033) ind.·km^{-2}. According to literature data, in the area of the Yamal Peninsula coast in the southern Baydaratskaya Bay, formed migrating groups of the black-throated diver appear around mid-September; the largest number of groups and the highest abundance of birds in them (up to 62 ind.) is recorded in the third decade; and the last birds disappear from their nesting sites in the third decade of September [Sokolov, 2003]. Within the indicated dates, we did not see even such relatively small groups. Probably, migration of the black-throated diver over the sea is more diffuse there. According to other data [Andreev et al., 2016a], its migration in the Kara Sea ends in the last decade of September – in early October. This is consistent with our observations.

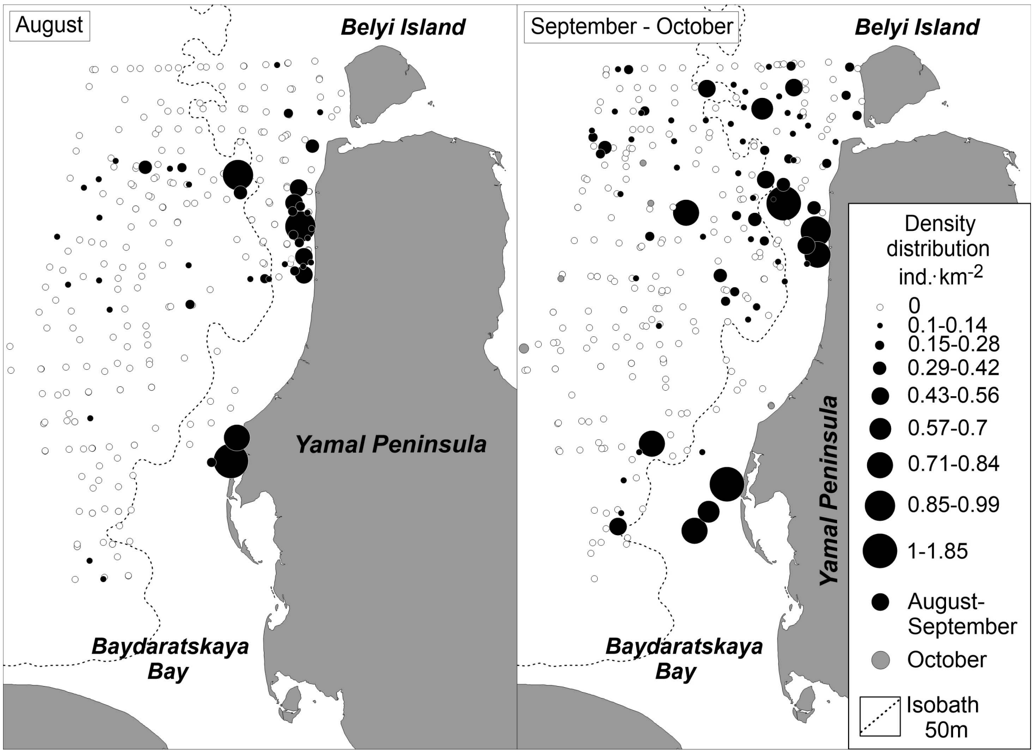

Fig. 2. Distribution of the black-throated diver in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

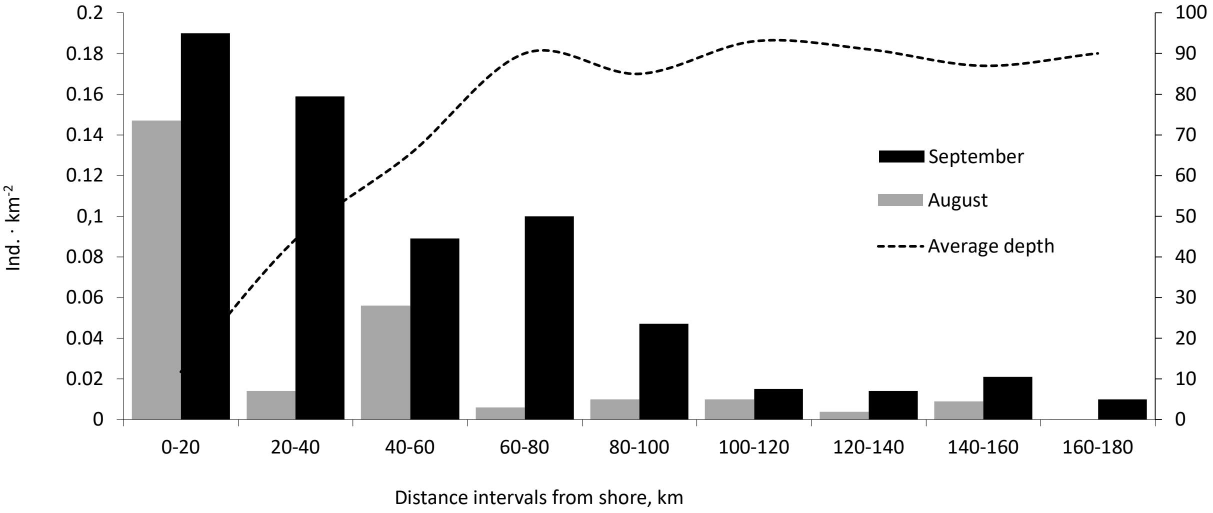

Fig. 3. Distribution of the black-throated diver in the survey site area in the southwestern Kara Sea at different distances from the Yamal Peninsula coast in August and September

The red-throated diver. Single individuals were recorded on 22 September, 2015, and 5 September, 2020, in 47 and 11 km from shore, respectively. The lack of counts on earlier dates may be due to the fact that this bird colonizes biotopes not fully investigated by us. Thus, according to some data, on the western Yamal, the red-throated diver uses the sea area during its nesting season moving away from shore mostly up to 10 km [Dmitriev et al., 2015]. Later, 28 September to 20 October (2017), we also did not see this species at the survey site, despite the fact that these dates correspond to the time of autumn migration in the studied area [Dmitriev et al., 2015; Sokolov, 2003].

The white-billed diver. It was recorded only once during the investigation period. On 15 August, 2015, a bird flew southwest–west at a point with coordinates 71°71′N, 62°39′E.

The long-tailed duck. On all observation dates, its habitat was limited almost exclusively to a spot in the northern part of the survey site with an area of 16,700 km^2 (almost 30% of the total area). Therefore, all indicators were calculated only for this spot (Fig. 4).

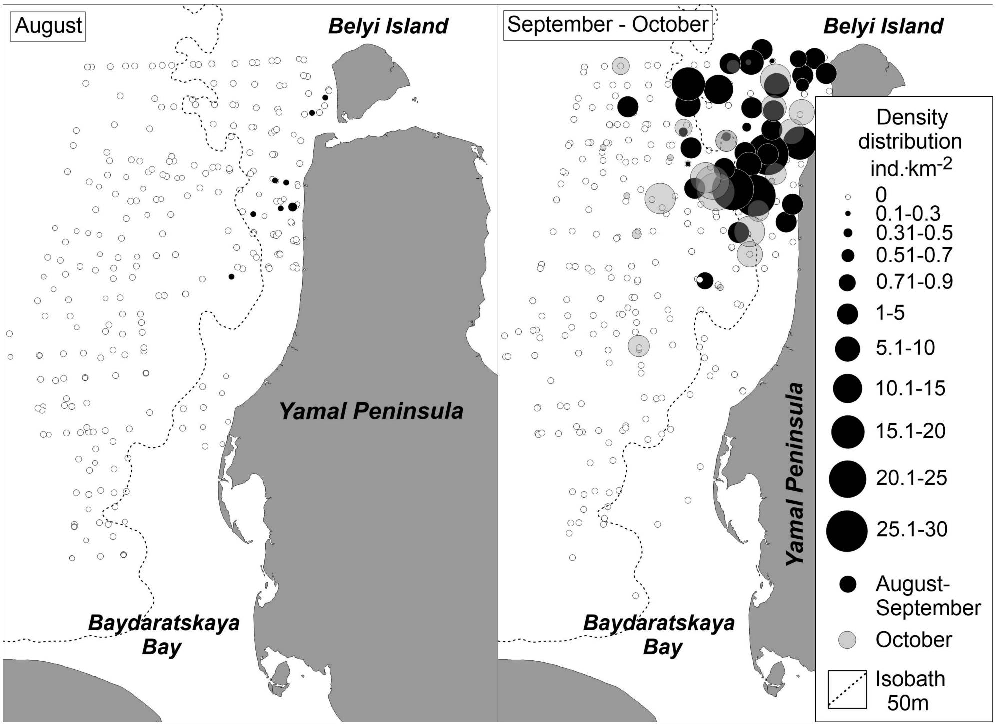

Fig. 4. Distribution of the long-tailed duck in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The first long-tailed ducks were noted in the last decade of August. On these dates, birds were concentrated in a strip of the water area 0–60 km from the Yamal Peninsula. Their abundance decreased with distance from shore, and it differed by 5 times for distances of 0–20 and 20–60 km [(0.1 ± 0.059) *vs.* (0.02 ± 0.013) ind.·km^{-2}, $P < 0.05$]. As known, this bird uses shallow areas adjacent to the Yamal Peninsula from the west not only during pre-migration, but also during molting [Ryabitsev, 1986]. For example, thousands of ducks of an unknown species (assumably, including the long-tailed duck) were recorded on 31 August in the vicinity of the Painadotoyakha River mouth (72°66′N). Taking into account this assumption, the population density of birds during pre-migration may reach its maximum in a narrow coastal strip already in late August. The species was not observed further from shore, in the sea. During September, the area of bird encounters expanded westward to a distance of 120 km from shore.

Within 0–60 and 60–120 km, the distribution density averaged (2.58 ± 0.72) and (0.99 ± 0.51) ind.·km^{-2}, respectively; interestingly, with a visible difference in its values, statistically significant differences were not revealed. Abundance continued to increase in October and exceeded values of August by 88 times [(4.87 ± 1.2) *vs.* (0.055 ± 0.026) ind.·km^{-2}]. Apparently, the water area to the south of the survey site is used by the long-tailed duck in August–October much less frequently. Thus, on 1–24 September in different years, observations were carried out along 3,000 km of the route there, but the long-tailed duck was not registered even off the coast. A census in the southern part of the survey site on 6–22 October, 2017, showed that bird occur in low abundance, while in the northern part, even on 28 September – 5 October, the long-tailed duck was common and most abundant. Thus, in the first five days of October, autumn migration of this species seems to be directed to the southwest: from shallow areas adjacent to the Malygin Strait and Bely Island to the Kara Strait. This is consistent with dates of migration in the Onega Bay of the White Sea, where the long-tailed duck migrates en masse on 2–9 October, with a pronounced peak on 6–7 October [Kondratyev et al., 2016]. During the investigation period, among individuals whose plumage could be clearly seen, only females were noted (and, possibly, similarly colored immature birds).

The king eider. This species was recorded from 19 August until the latest observation date, 22 October; probably, it occurred in the studied water area later as well. The distribution in August was clearly confined to shallow areas off the western coast of the Yamal Peninsula (Fig. 5). Specifically, on 19–31 August, with the mean value for the survey site of (0.0091 ± 0.0053) ind.·km^{-2}, the population density in shallow areas, at a distance of 0–20 km, was 89 times higher than in water areas with other depths [(0.046 ± 0.043) *vs.* (0.00052 ± 0.00051) ind.·km^{-2}]. In September, abundance in the survey site area increased by 26 times, to (0.24 ± 0.1) ind.·km^{-2}.

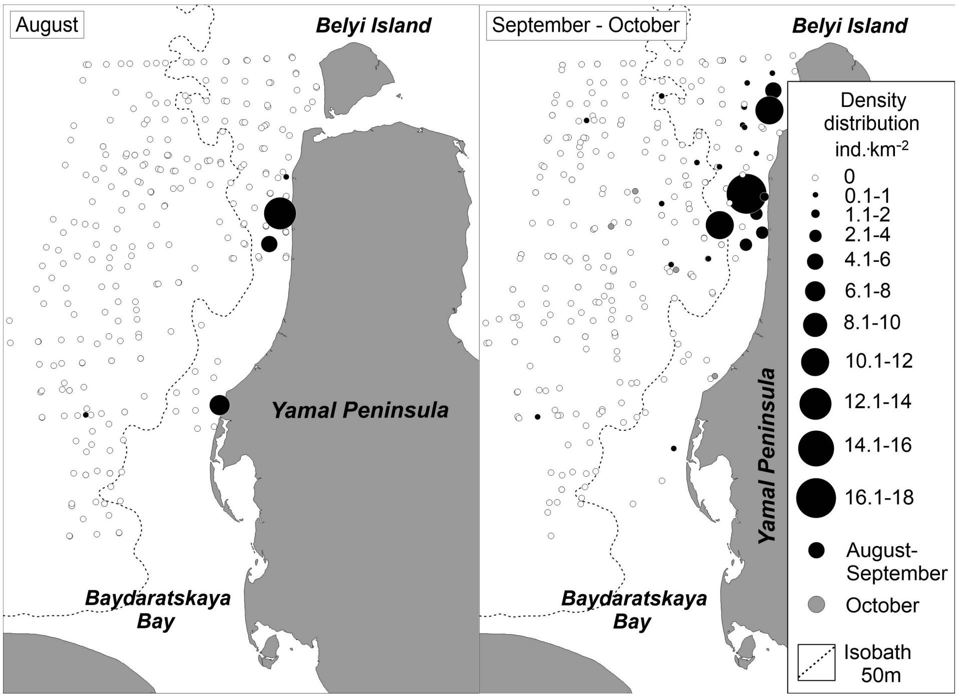

Fig. 5. Distribution of the king eider in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The same as in August, the overwhelming majority of birds (87%) stayed in shallow areas, 0–20 km from shore [(2.1 ± 1.25) ind.·km^{-2}]. As moving further from shore, the distribution density dropped sharply and averaged (0.067 ± 0.055) ind.·km^{-2} for the remaining part of the survey site, *i. e.*, it was more than 30 times lower than in shallow areas. Observations on 28 September – 22 October, 2017, showed that abundance of the species was low everywhere (only 26 ind. *per* 1,250 km of the route, or about 0.02 ind.·km^{-2}, with a fairly uniform distribution throughout the studied water area). Changes in population density of the king eider recorded west of the Yamal Peninsula in August–September seem to be governed by the fact that birds use this water area during molting and pre-migration. King eiders (both immature and adult) are believed to molt near the nesting sites, and the studied Kara Sea area may be one of such sites for the Yamal group of this species. Mass aggregations of molting king eiders were reported for the middle part of the Yamal Peninsula western coast, between Cape Kharasavey and Mutnyi Bay [Brude et al., 1998; Vidy – biologicheskie indikatory, 2020]. As already mentioned, we observed thousands of large ducks of an unknown species (assumably, including the king eider) on 31 August much further north, in the vicinity of the Painadotoyakha River mouth. Birds preferred shallow areas (depth of 10–15 m) 1 km from shore or closer; however, because of the large distance from the vessel (about 5 km), we were unable to identify them down to the species level.

The mass migration of this species to its wintering grounds occurs, probably, in the first half of October. This is supported by the fact that the authors observed flocks of hundreds of king eiders flying through the Kara Strait into the Barents Sea during the indicated period. In another case, a similar migration was seen earlier, in early October, by Yu. Krasnov [Krasnov et al., 2002]. At the survey site, no such migrations were recorded in October, and this evidences for the fact that birds flew mostly near the Yamal shore and over the Baydaratskaya Bay mouth, *i. e.*, in areas almost not investigated by us on these dates. Importantly, in addition to precisely identified individuals of the of king eider, there were many eiders that observers reported as “unidentified down to the species level” and did not use later when determining abundance. Assumably, those were mostly king eiders; however, there were several common eiders whose occurrence is likely in this area, according to reports of rare cases of their nesting on the Yamal [Danilov et al., 1984]. Taking into account this assumption, the distribution density of the species may be approximately 30% higher than determined by us. During the investigation period (2015–2020), only birds colored as females were registered (females themselves and, probably, young individuals similar to them).

The dark-bellied brant goose. We recorded this species only three times in five years – on 8 September, 2018, 28 August, 2019, and 4 September, 2020 (30, 47, and 55 ind., respectively) – at a distance of 35–60 km from shore. According to O. Brude *et al.* [1998], mass aggregations of the dark-bellied brant goose, up to 1,000 ind., during the non-breeding period were observed off the Yamal Peninsula coast, *e. g.*, in lagoons between Cape Kharasavey and Litke Island, as well as off the Bely Island. The period of our most active survey (between mid-August and the first decade of September) coincided with the autumn migration of this species [Andreev et al., 2016b]. Its abundance was insignificant in our observations before and during migration, and this seems to result from the fact that birds inhabit a narrow coastal strip of the water area or tundra mostly inaccessible for the research from the vessel. The geographical location of the area might be important as well: on 20 August, 2020, during work outside the survey site, in shallow areas of the Baydaratskaya Bay (120 km south of the studied water area, 15 km from shore), we noted 31 dark-bellied brant geese during 10 h of our work at the station (6, 5, and 20 ind.).

The European white-fronted goose. This species was seen only once, on 4 September, 2020, 10 km west of the Bely Island. It was a flock of 6 ind.

The bean goose. Birds were recorded on 12 August – 8 September, chiefly in the southern part of the survey site, at a distance of 7–130 km from the Yamal shore. In total, there were 5 registrations of the bean goose (1 to 150 ind.). Encounters of this bird over the sea may evidence for its migration (probably, for its very beginning and in rarely used areas). Specifically, according to V. Sokolov [2003], in southwestern Yamal, the mass migration of geese (the European white-fronted and bean ones) occurs mostly along seashore and is noted on 21–25 September (up to 800 birds *per* day); after 28 September, no geese were registered. On 28–30 September and the first two decades of October, we encountered the bean goose only once (near the southern boundary of the survey site).

The Steller's eider. This bird was seen twice, on 30 August, 2018 (1 female), and 20 August, 2019 (4 males and 11 females), in 5 and 30 km from shore, respectively, in the northern part of the survey site. Males were partially molted and distinguished from females by their white wing coverts. Also, on 30 August, 2015, 10 ind. were noted not during the transect census, but while drifting at the station. The species nests in tundra of the Yamal Peninsula adjacent to the survey site [Dmitriev et al., 2015]. During the non-breeding period, the Steller's eider prefers the marine area, but at the survey site, as well as in other parts of its range, the bird seems to inhabit the shallowest littoral zone [del Hoyo et al., 1992] not examined by us.

The common scoter. One individual was recorded on 8 September, 2018, near the southern boundary of the survey site (70°66′N, 64°20′E), 80 km from the Yamal Peninsula coast.

The velvet scoter. One bird was registered on 6 September, 2020, 8 km from Cape Kharasavey (71°25′N, 66°70′E).

A small number of observations of *Melanitta* scoters may result from the fact that the surveyed water area is rarely used by those species or is used beyond the dates of our census. A high abundance of velvet and common scoters is likely in July, when there is the mass migration of mixed flocks of males of these species through the southern Kara Sea to the Baltic Sea for molting [Krasnov et al., 2002]. However, there are no data on whether the migration passes through the survey site or is oriented further south (the northern border of the nesting range of both species is located in the Yamal Peninsula area at approximately 70°N, 100 km south of the survey site). According to some our observations outside the studied water area, spots of concentration of scoters are situated, for example, to the west and south of Litke Island, in Mutnyi Bay (120 km south of the described water area): there, we registered 572 scoters along 55 km of the route on 6 September, 2020. Moreover, 200 km north of this spot, we also observed a large aggregation of ducks (approximately, up to 10 thousand individuals) on 28 August, 2019, from one of marine ship stations. It was noticeable even at a distance of 10 km. Birds were taking off into the air and landing again on water at the Kharasaveyakha River mouth which is separated from the sea by the Sharapovy Koshki Islands. Because of the great distance, it was impossible to identify the species; perhaps, those were also scoters.

Seabirds. The seasonal distribution of several studied species within the survey site area (the fulmar, black-legged kittiwake, glaucous gull, Heuglin's gull, and Brünnich's guillemot) is shown in Figs 6–10. The interannual and seasonal population dynamics of the most common seabirds are shown in Figs 11–13. Distribution and abundance of other species are not illustrated, but are discussed in the text.

The fulmar. Its mean long-term population density during the investigation period was (0.078 ± 0.008) ind.·km^{-2}; lim (range of values) was 0.028–0.18. Abundance differed significantly between 2016–2018 ($P < 0.01$) and between 2018–2020 ($P < 0.05$). In 2015–2020, the species colonized the entire survey site, but in some years, its distribution over the area was noticeably uneven. Thus, in 2016, abundance was significantly higher in the northern part of the survey site (north of the conventional boundary along 72°N) differing from the value in the southern part by 4.2 times [(0.08 ± 0.011) *vs.* (0.02 ± 0.014) ind.·km^{-2}, $P < 0.05$]. In 2019, on the contrary, 3 times more birds were concentrated in the southern half [(0.035 ± 0.011) *vs.* (0.1 ± 0.026) ind.·km^{-2}, $P < 0.05$]. In the year of the highest abundance (2018), the distribution density in the northern and southern parts of the survey site was almost the same accounting for (0.17 ± 0.058) and (0.19 ± 0.03) ind.·km^{-2}, respectively. We did not record mass feeding aggregations of the fulmar which are characteristic, for example, of the Barents Sea. The number of individuals simultaneously observed in a section of 300 × 600 m (0.18 km^2, see “Material and Methods” section) was no more than 1–2 in 90% of cases and 3–5 in 9% of cases. Flocks of 10–40 ind. were encountered only twice – in the extreme western part of the survey site (less than 0.5% of cases). August to September, on average for several years, no trend in abundance was revealed for the species (differences were non-significant between the means for the groups of dates 1–20 August, 21 August – 9 September, 10–29 September, and 30 September – October 22). In October, the population density of the fulmar might remain relatively high, although data for this month are based on observations from one year (2017) and may not be consistent with those for several years.

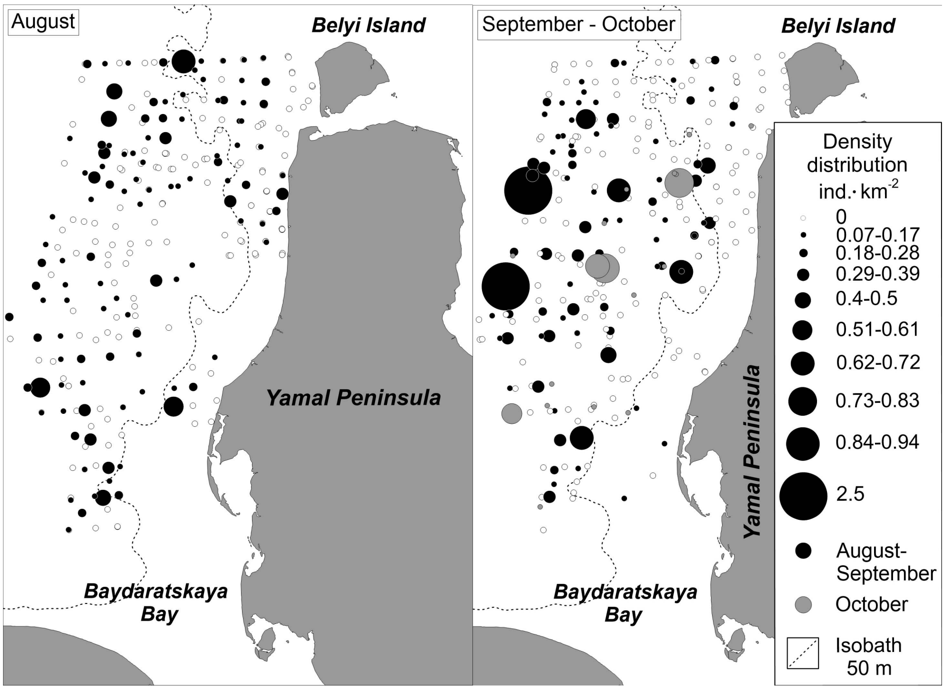

Fig. 6. Distribution of the fulmar in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The grey petrel. Apparently, this species expands its range of summer nomadism eastward in recent decades [Goryaev et al., 2021]. At the survey site, single birds were recorded twice: on 20 September, 2016 (73°53′N, 63°38′E), and 2 September, 2018 (72°68′N, 65°73′E). Outside the studied area, the grey petrel was also registered: off the eastern coast of the Yugorsky Peninsula (69°71′N, 63°75′E).

The black-legged kittiwake. During the investigation period, the mean long-term abundance of this species was (0.061 ± 0.007) ind.·km^{-2}; lim was 0.005–0.096. According to the results of observations of 2015–2020, the bird was recorded throughout the survey site. Importantly, it was noticeably more common in its northern half, where the population density over five years was on average approximately twice as high as in the southern half [(0.073 ± 0.01) *vs.* (0.037 ± 0.0079), $P < 0.05$]. In some years, such unevenness was characterized by a difference from 6.8 times [(0.016 ± 0.0057) *vs.* (0.11 ± 0.024) ind.·km^{-2} in 2015] to 14 times [(0.0037 ± 0.0037) *vs.* (0.051 ± 0.0099) ind.·km^{-2} in 2016]. On average for the investigation period, the black-legged kittiwake was the most abundant in the extreme northwestern part of the survey site, where its density was (0.15 ± 0.038) ind.·km^{-2}. We did not note mass aggregations: in 77% of cases, the number of birds simultaneously observed in a section of 0.18 km^2 was 1–2, and in other ones, 3–10. The share of encounters of more abundant groups (*e. g.*, 45 ind. on 25 August) did not exceed 1.5%. In a seasonal aspect, on average for several years, abundance increased August to September. Thus, according to our census in October 2017, distribution within the survey site was uniform, and population density was relatively high, close to the maximum for August–September 2015–2020: the value was (0.11 ± 0.023) ind.·km^{-2} (for two-decade time periods we identified, means are significantly different, $P < 0.01$). Dynamics registered in August–October is generally consistent with phenology and nature of post-breeding nomadism of the black-legged kittiwake during which birds are widely distributed throughout the water area; under favorable conditions in terms of food supply, they can stay in these spots until late autumn [Krasnov, Nikolaeva, 2016]. A high abundance persisting in October can be partly determined by migration of birds from waters adjacent to the Kara Sea (on the islands of the Severnaya Zemlya archipelago and on other islands, colonies consist of about 20 thousand pairs) which they leave in late September and in October, sometimes even in late October [Brude et al., 1998; Vidy – biologicheskie indikatory, 2020]. The black-legged kittiwake is also known to nest on the western shore of the Novaya Zemlya archipelago and to migrate through the Kara Sea to the Pacific Ocean [Ezhov et al., 2021].

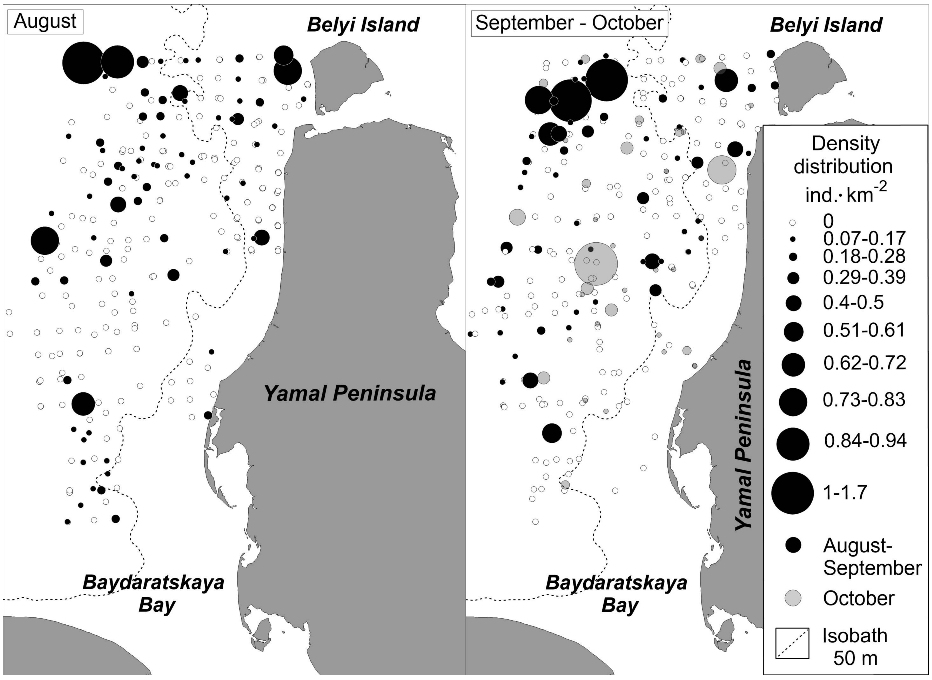

Fig. 7. Distribution of the black-legged kittiwake in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The glaucous gull. Its mean long-term abundance during the investigation period was (0.067 ± 0.014) ind.·km^{-2}; lim was 0.031–0.1. With the exception of a pair of 2018 and 2019, differences between years are significant (P from < 0.01 to < 0.05). The glaucous gull was recorded throughout the survey site. However, in some years, we revealed a definite confinement to shallow areas (< 50 m) adjacent to the Yamal Peninsula coast. For example, in August–September 2019 and 2020, more than 82% of birds were counted within the boundaries of the specified area (0.12 and 0.025 ind.·km^{-2} for shallow areas and other depths, respectively, $P < 0.001$). No latitudinal interannual differences were established in distribution throughout the survey site (see paragraphs on the fulmar and black-legged kittiwake). There was practically no flocking: in 95% of cases, the number of glaucous gulls simultaneously observed in a section of 0.18 km^2 was 1–2, and the highest number registered did not exceed 10 (less than 1% of encounters). In August–September, population density was stable or slightly decreased in the second half of September (the differences for three identified two-decade time periods are non-significant). In October, the value was 5 times lower (difference with abundance in the second and third decades of September is significant, $P < 0.01$).

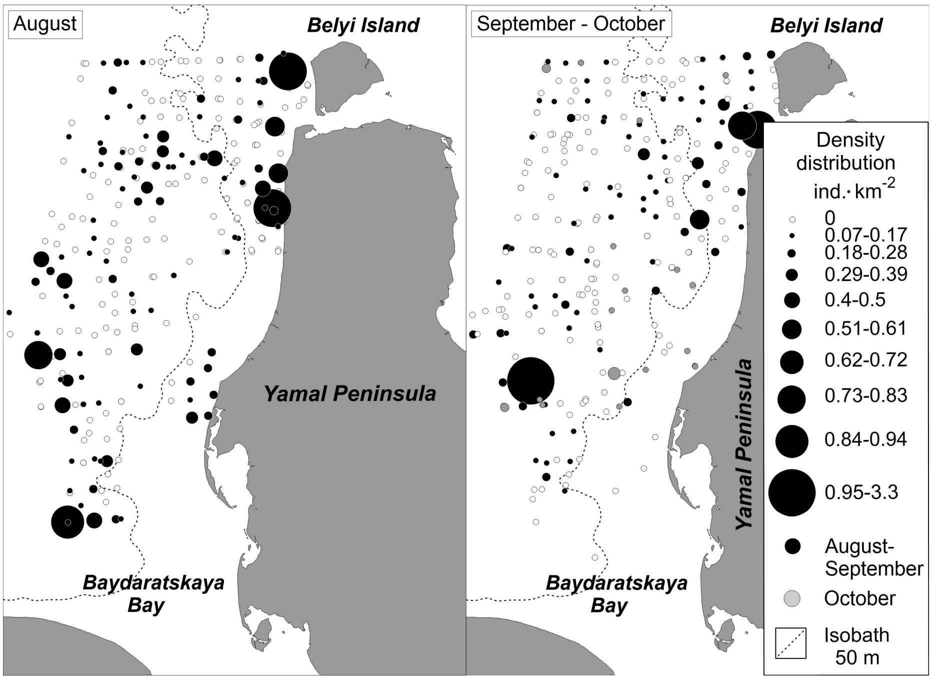

Fig. 8. Distribution of the glaucous gull in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The Heuglin's gull. Interannual fluctuations in its abundance are the least pronounced among those for Laridae representatives. Specifically, with the mean long-term population density of (0.066 ± 0.0049) ind.·km^{-2}, the minimum and maximum in 2015–2020 were related as 1 : 1.6 accounting for 0.05 and 0.08 ind.·km^{-2}, respectively (differences in annual values are non-significant). Assumably, this is driven by the facts that the species is not prone to long migrations and inhabits tundra and coastal zone for most of summer: there, food resources are more stable, and their occurrence is more predictable [Yudin, Firsova, 2002]. This assumption is consistent with the recorded change in the seasonal distribution of the Heuglin's gull, as it preferred coasts and shallow areas in August and September. Within 1–20 August on average for 2015–2020, this species stayed in coastal shallow areas: at a distance of 0–20 km from shore, birds were encountered 4.7 times more often than in other spots [(0.043 ± 0.025) *vs.* (0.009 ± 0.0036) ind.·km^{-2}, $P < 0.005$]. Within 21 August – 9 September, with a 5-fold rise in the total distribution density throughout the survey site (0.016 to 0.08 ind.·km^{-2}, $P < 0.01$), the difference in values was 3.4 times [(0.2 ± 0.049) *vs.* (0.058 ± 0.091) ind.·km^{-2}]. For 10–30 September, we have no data for the immediate coastal area (0–20 km). A comparison of the population density in a zone of 20–40 km and in other water areas even shows a slight relative increase in abundance with distance from shore [(0.025 ± 0.01) *vs.* (0.032 ± 0.01) ind.·km^{-2}] (the difference for these two areas is non-significant) against the backdrop of a decrease in abundance in the survey site area compared to that for previous time period by 2.6 times (0.08 to 0.03 ind.·km^{-2}, $P < 0.001$). Birds were seen until 24 September. Taking into account the complete absence of encounters in the first two decades of October (2017), we can presume that the latest dates of the Heuglin's gull leaving the site are the last five days of September.

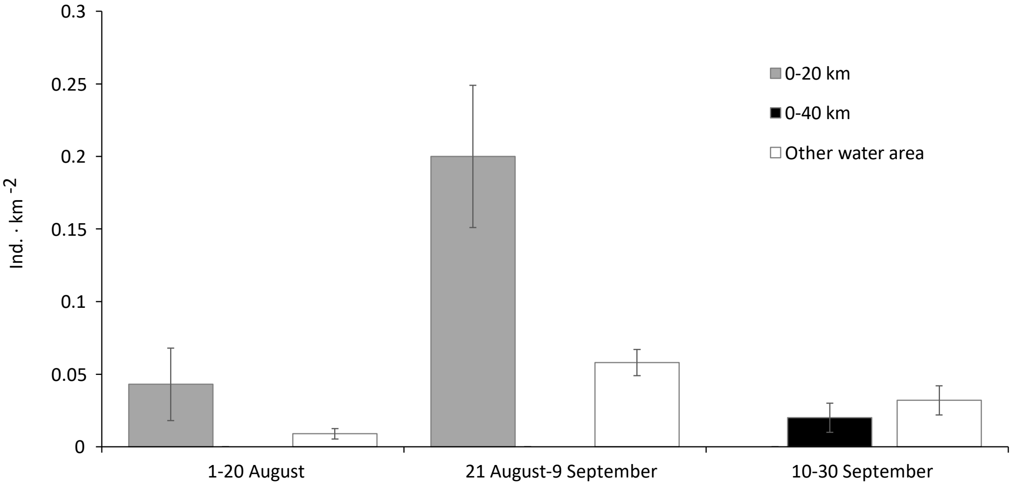

Fig. 9. Seasonal changes in the distribution density of the Heuglin's gull at different distances from the coast in the southwestern Kara Sea

The Arctic tern. Apparently, the given graph of the interannual dynamics of the species abundance does not reflect the real picture. The peak in the population density in 2019 is a consequence of the coincidence of observation dates within many sections in the coastal zone with the dates of the seasonal concentration of birds in this biotope. So, the mean annual abundance of the Arctic tern at the survey site was lower than that determined for five years [(0.025 ± 0.015) ind.·km^{-2}]. Moreover, annual fluctuations occurred within a range of values for other years (lim was 0.0026–0.014). In August, the mean abundance for the entire area was (0.036 ± 0.014) ind.·km^{-2}. Birds were noted everywhere, but way more often (by 9 times), they were encountered at a distance up to 20 km from the Yamal Peninsula coast [(0.13 ± 0.06) *vs.* (0.014 ± 0.0061) ind.·km^{-2}, $P < 0.01$]. In September, the Arctic tern was no longer recorded in the coastal zone; throughout the survey site, the distribution density averaged (0.0014 ± 0.00087) ind.·km^{-2} having decreased by 25 times compared to that for August ($P < 0.01$). In the studied water area, the same as in many other spots of the range, the coastal zone is the main place for searching for food during the nesting season [Dmitriev et al., 2015]. According to our data, the confinement of migrating broods of the Arctic tern to coastal shallow areas may be due to a persistent preference of this zone as the main feeding biotope at the beginning of autumn migration.

A 20 km wide strip of the water area named coastal is arbitrary, as it shows the difference between two identified zones quite schematically. Probably, closer to shore, the population density can be much higher than 0.13 ind.·km^{-2}.

The pomarine, Arctic, and long-tailed skuas. The mean abundance for these three species for 2015–2020 was (0.046 ± 0.0074), (0.014 ± 0.0023), and (0.0039 ± 0.00095) ind.·km^{-2}, respectively (72, 22, and 6%). Taking into account individual significantly different pairs of years (2015 and 2020 for the pomarine skua, $P < 0.01$; 2019 and 2016 for the Arctic and long-tailed skuas, $P < 0.05$), lim values for three species were close to 0.025–0.1, 0.0047–0.29, and 0.002–0.01 ind.·km^{-2}, respectively, *i. e.*, ratios were fairly similar (1 : 4, 1 : 6, and 1 : 5). Fluctuations in the population density of the long-tailed skua are likely to be greater: its abundance is extremely low, and in some years, no birds of this species were observed in sections. In 92% of cases, the pomarine skua was noted in a section of 0.18 km^2 alone or in pairs; in 7% of cases, 3–6 ind. were recorded. The most abundant group consisted of 17 birds (< 1% of cases). For the Arctic skua, the results of division into similar groups show encounters of 1–2 ind. in 100% of cases; for the long-tailed skua, those show encounters of single birds in 100% of cases. The quantitative prevalence of the pomarine skua is consistent both with its greater propensity for sea nomadism, especially in years of poor breeding [Yudin, Firsova, 2002], and with a higher abundance in nesting sites. Thus, observations in a permanent stationary spot of 25 km^2 on the Yamal Peninsula (data averaged for 1988–1993) allowed revealing a ratio of breeding pairs (%) close to 84 : 8 : 8 [Ryabitsev, 1995]. In our study, all three species were represented almost exclusively by adult and immature individuals older than one year which were found everywhere. During the investigation period, we saw a yearling (a skua unidentified down to the species level) only once, and this suggests either very low breeding success in all years of observation, or minor use of the marine area by young skuas during our bird counts. The last single pomarine and Arctic skuas were noted on 9 and 20 October, respectively.

The great skua. The survey site is located near the modern periphery of the species range; apparently, this factor, along with other ones, determines the rarity of this bird in the studied water area [The IUCN Red List, 2023]. A total of 6 great skuas were encountered over five summer seasons (26 August to 12 September): from 1 ind. *per* season (2015, 2018, and 2020) to 2 ind. *per* season (2019). This bird was not noted in 2016.

The Brünnich's guillemot. Its mean long-term abundance was (0.16 ± 0.094) ind.·km^{-2}; lim was 0.001–0.44. The southern Kara Sea is the area of post-breeding migrations of this species, presumably, from the nearest colonies of the Southern Island of the Novaya Zemlya [Belopolsky, 1957; Vidy – biologicheskie indikatory, 2020]. In its vicinity and to the west, a high abundance of the Brünnich's guillemot (up to 5.2 ind.·km^{-2}) is revealed since the first five days of August, and values can remain at this level up to the third decade of October [Krasnov et al., 2002]. Population density of birds migrating to the survey site fluctuates sharply from year to year; probably, it depends on the state of food supply both in the southeastern Barents Sea and southern Kara Sea. Dynamics of the species abundance in the studied water area is not similar to dynamics of abundance of the above-mentioned black-legged kittiwake and fulmar which also migrate there from the Barents Sea. Accordingly, abundance of the Brünnich's guillemot may vary depending on availability of other food items localized in the depth range inaccessible to the fulmar and kittiwake. The results of hydrobiological studies in the Kara Sea evidence for the formation of a high density of macroplankton in August–September in the southern sea (in the area exposed to the effect of Atlantic water masses). Macroplankton belongs to key food items of the Brünnich's guillemot in some parts of its range [Bakken, 1990; Barrett et al., 1997]. Moreover, distribution of macroplankton [*Themisto libellula* (Lichtenstein in Mandt, 1822) (Hyperiidae) and *Thysanoessa inermis* (Krøyer, 1846) (Euphausiidae)] may be related to the occurrence of the guillemot in the studied water area [Ekosistema Karskogo morya, 2008]. In September, aggregations of the polar cod 8–25 cm long are noted there as well [Dolgov et al., 2011; Ekosistema Karskogo morya, 2008]. The fact that the Brünnich's guillemot searches for food at relatively great depths can be indirectly confirmed by frequent observations of its diving for 2–3 min. Its low abundance in the shallow coastal zone with a depth down to 50 m (in a shelf area with a moderate distribution density of food zooplankton) can also indicate the specificity of its feeding [Orlov et al., 2020]. Thus, for 2,502 km of the route within the boundaries of indicated shallow areas in 2015–2020 (31% of the total length of the route), 27 Brünnich's guillemots were encountered (2.5% of the total). Outside shallow areas, these birds were recorded everywhere, without a noticeable drop in population density with increasing depth and even *vice versa*. Thus, the species was more often registered in the deepest parts of the survey site: in isobath intervals of 50–100 and 100–150 m, with similar census, we encountered 264 and 646 ind., respectively. Apparently, the seasonal dynamics of the Brünnich's guillemot is not correct for 10–29 September: within these dates, the vessel was located in the northern part of survey site, where the population density of this species was relatively low in all years of observation. Analyzing data for October 2017, it can be assumed as follows: abundance of the Brünnich's guillemot was also high in August–September of the year when there were no bird counts. Because of molting of flight feathers in August and September and the loss of the ability to fly, 86% of birds were observed on water during these months (in October, only in 29% of cases). Birds formed small groups, and population density was similar in August and September 2019 and 2020 and in October 2017: (3.57 ± 0.3), (3.43 ± 0.27), and (3 ± 0.37) ind. *per* encounter, respectively.

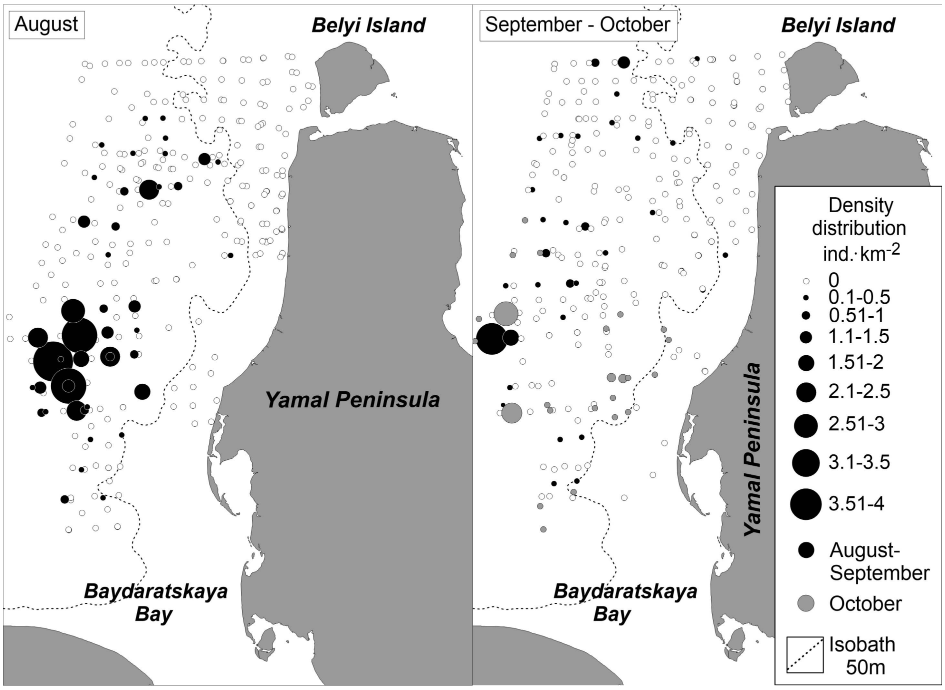

Fig. 10. Distribution of the Brünnich's guillemot in the survey site area in the southwestern Kara Sea in August–September 2015–2020 and October 2017

The black guillemot. This Alcidae species is also characterized by sharp fluctuations in the population density over the years. With the mean value for five years close to (0.0026 ± 0.0012) ind.·km^{-2} and lim of 0.0006–0.007, against the backdrop of significant differences in data for adjacent years (2018, 2019, and 2020, $P < 0.01$), abundance values between individual years could be related as 1 : 13. In a seasonal aspect, there is a gain in the number of the black guillemot encounters, especially clear September to October: the population density rises (0.004 ± 0.002) to (0.03 ± 0.014) ind.·km^{-2} ($P < 0.05$). In the European North, juvenile migrations of the black guillemot occur in August–September and are followed by mass post-molting migrations in October [Gaginskaya, 2016]. This may have caused an increase in abundance we observed in October. The black guillemot winters in polynyas of the southwestern Kara Sea (Ob–Yenisei and Yamal polynyas) [unpublished data of Yu. Goryaev]. A noticeable rise in its population density by autumn may also be associated with the beginning of concentration in spots of upcoming wintering. We registered the first birds in winter plumage already on 24 August, and such encounters amounted to more than half of all observations in September.

The little auk. This rare species was seen in the survey site area during its migration. It was noted only once, on 3 October, 2017. There were no observations on earlier dates, and this may evidence for the fact that the little auk does not appear at the site until October.

Possible reasons for fluctuations in abundance of some seabirds at the survey site. Groups of seabirds of various species in the studied water area may include different individuals: for some of them, summer-autumn nomadism may be limited to the Kara Sea, while for others, it may also cover the Barents Sea. The similarity of these water areas as a habitat for birds during the investigation period is confirmed, for example, for the black-legged kittiwake, fulmar, and Brünnich's guillemot [Seabird Tracking Database, 2023; Seapop, 2023]. For other species of seabirds, migration to the Kara Sea from neighboring seas (or its absence) has not been proven, and it remains unclear within the boundaries of which areas certain factors determine dynamics of the population density. For some species migrating to the Kara Sea from the Barents Sea, abundance in the studied area may be driven, among other factors, by the trophic situation outside the Kara Sea. Thus, as established earlier, the summer-autumn distribution of the black-legged kittiwake and fulmar in the Barents Sea is largely governed by abundance and localization of mass species of schooling fish, in particular, the polar cod and capelin in the eastern sea [Borkin et al., 2006]. When comparing the dynamics of the total stock of these fish in the Barents Sea [Barentsportal, 2023] with the interannual dynamics of density for the black-legged kittiwake and fulmar, a certain negative correlation ($r = -0.83$) can be traced, for example, for the black-legged kittiwake. This may evidence for its more active penetration into the Kara Sea during years of the low stock of the polar cod in the eastern Barents Sea due to the lack of concentration of this food items and wider dispersal of birds during feeding nomadism. A less close correlation is seen (in 2016–2020) for the fulmar which is also concentrated in the Barents Sea on aggregations of the polar cod and capelin (Fig. 11). According to the literature source cited, the size of stock of the capelin and polar cod is given with an indication of possible over- or underestimations of the results of ichthyological surveys. Our data on abundance are also characterized by pretty high representativeness errors. Anyway, for the black-legged kittiwake and fulmar, values of the maximum and minimum abundance coincide with values of the minimum and maximum stock of the capelin and polar cod in the Barents Sea, respectively.

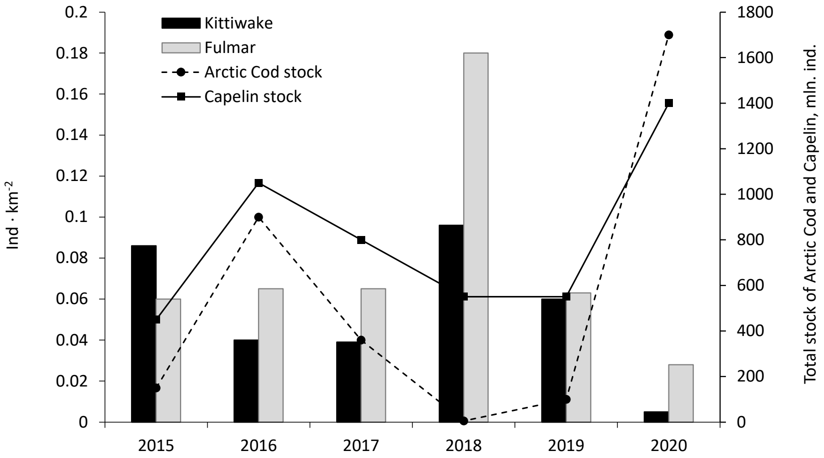

Fig. 11. Population dynamics of the black-legged kittiwake and fulmar at the survey site in the southwestern Kara Sea and stock of the polar cod and capelin in the Barents Sea (stock is given according to [Barentsportal, 2023])

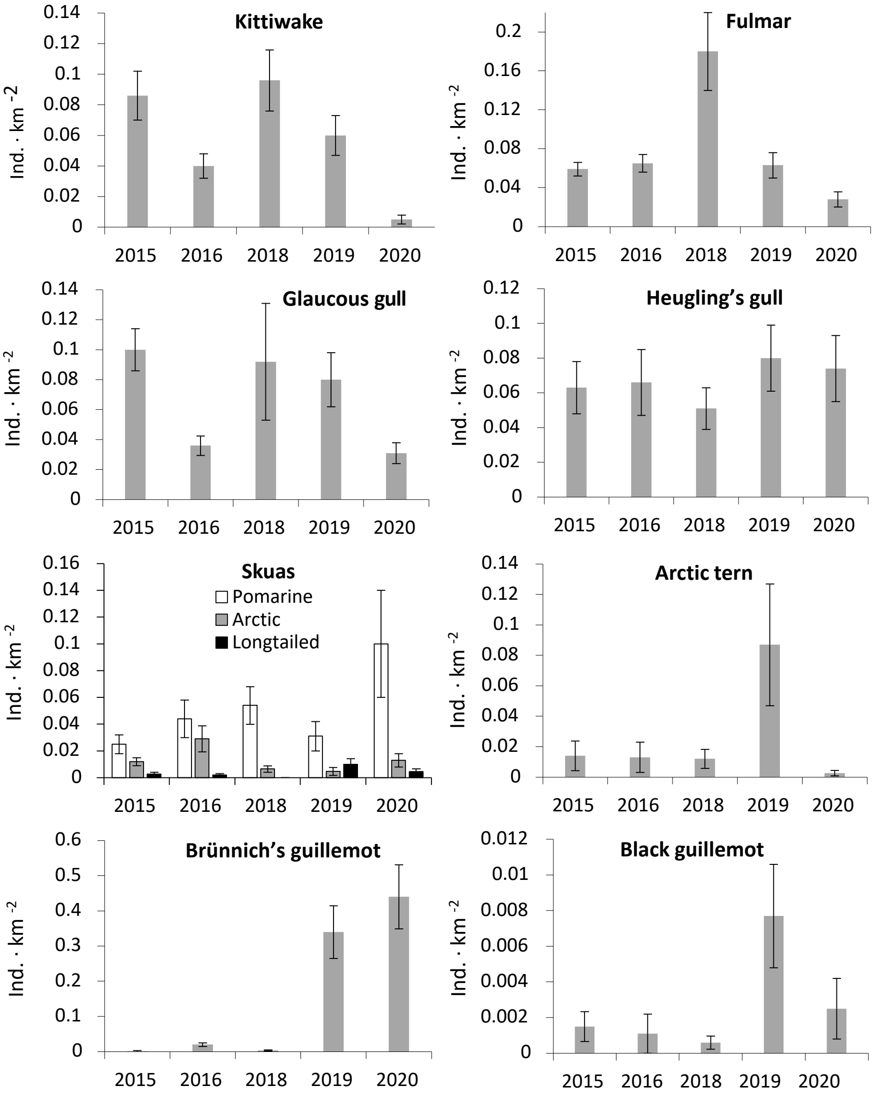

Fig. 12. Interannual dynamics of Procellariidae, Laridae, Stercorariidae, and Alcidae birds at the survey site in the southwestern Kara Sea in August–September 2015, 2016, and 2018–2020

Vagrant species. The group of species recorded outside the range includes the northern gannet, common gull, black-headed gull, and European herring gull observed 1 to 2 times over six years. When reporting vagrant species at the survey site or in its vicinity, other researchers also listed the lesser black-backed gull *Larus fuscus* (Linnaeus, 1758), great black-backed gull *Larus marinus* (Linnaeus, 1758), and the little gull *Larus minutus* (Pallas, 1776) not encountered by us [Dmitriev et al., 2006; Lunk, Joern, 2007].

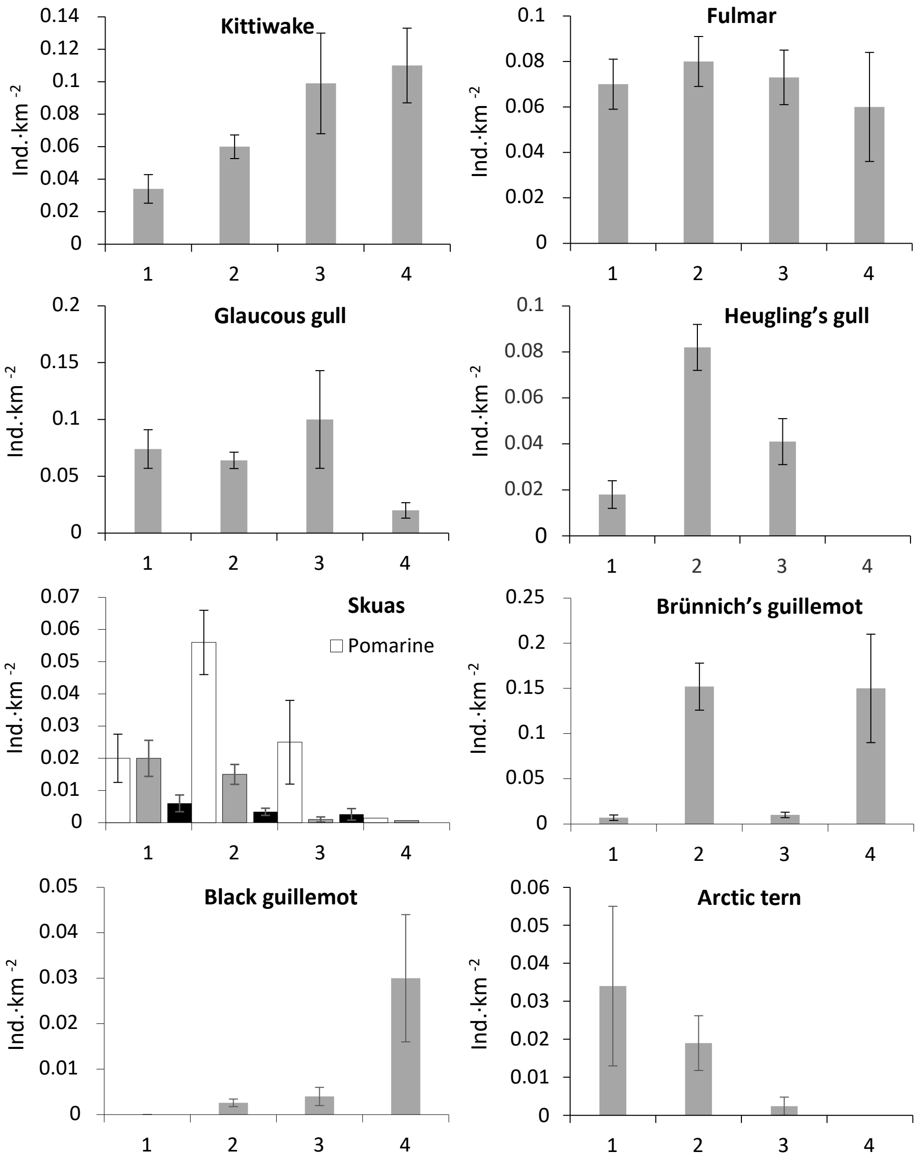

Fig. 13. Seasonal dynamics of Procellariidae, Laridae, Stercorariidae, and Alcidae birds at the survey site in the southwestern Kara Sea in August–October 2015–2020 (1, 1–20 August; 2, 21 August – 9 September; 3, 10–29 September; 4, 30 September – 19 October)

Conclusion. In the studied area of the southwestern Kara Sea, 28 species of water birds and seabirds of 7 families were recorded in the summer-autumn period which use these waters during autumn migration and feeding nomadism.

Among water birds, the most abundant ones are the long-tailed duck, king eider, and black-throated diver (about 62, 14, and 10% of all birds in this group, respectively). Within the summer-autumn season, these species are concentrated in shallow coastal areas of the survey site which may be preceded by their molting in these waters. There is a simultaneous redistribution of the long-tailed duck and divers (it is not yet related to the mass migration) to more seaward areas, up to 200 km from shore. Other Gaviidae and Anatidae species characterized by the low occurrence within the survey site seem to be concentrated or migrate to the south of the studied area or in close proximity to shore.

On average for several years, the group of seabirds is dominated by the Brünnich's guillemot (31%), fulmar (15%), glaucous gull (13%), Heuglin's gull (13%), black-legged kittiwake (11%), and pomarine skua (10%). Less abundant species are the Arctic tern (5%), Arctic skua (2.5%), long-tailed skua (0.7%), and black guillemot (0.5%).

Values of population density we determined are based on a relatively small number of years; those are characterized by high statistical errors and, apparently, do not fully reflect real variability over years and months. Data obtained require further clarification, with the identification and more thorough investigation of individual areas of open water (coastal shallow areas, littoral zone, *etc.*) and analysis of habitat conditions (food supply, breeding conditions, and so on) both within the survey site and in a wider zone of the summer-autumn stay. Taking this into account, the results of the work can have both general scientific significance (study of population dynamics) and environmental one. These data can serve as the basis for the development of a package of measures to protect birds from possible negative effects during the intended exploitation of hydrocarbon deposits on the shelf and the intensification of shipping along the Northern Sea Route.

Field observations were carried out within the environmental monitoring in the licensed areas of the Kara Sea in 2015–2016 and 2018–2020 (Krasnoyarskgazprom Neftegazproekt) and within the industrial environmental monitoring during construction of wells in the licensed areas on the Kara Sea shelf in 2018–2020 (Institute of Environmental Survey, Planning & Assessment). The material was sampled within environmental studies in the Kara Sea waters by order of Gazprom Nedra for Gazprom.

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РАСПРЕДЕЛЕНИЕ И ЧИСЛЕННОСТЬ ВОДНЫХ И МОРСКИХ ПТИЦ В НЕКОТОРЫХ РАЙОНАХ ЮГО-ЗАПАДНОЙ ЧАСТИ КАРСКОГО МОРЯ В ЛЕТНЕ-ОСЕННИЙ ПЕРИОД 2015–2020 ГГ.

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Юго-западная часть Карского моря — малоизученная область летне-осенних нагульных кочёвок и сезонных миграций водных и морских птиц. Её шельф включает районы, перспективные для добычи углеводородного сырья и интенсификации судоходства по Северному морскому пути, что делает необходимым постоянный мониторинг птиц в зоне воздействия этих факторов. На протяжении августа и сентября 2015–2016 и 2018–2020 гг., а также в конце сентября — первой и второй декадах октября 2017 г. проведены учёты птиц на участке акватории в южной части Карского моря. Использована методика судового трансектного учёта для получения показателя численности особей на 1 км^2. На этой акватории определено 28 видов птиц из 7 семейств (гагаровые, олушевые, буревестниковые, утиные, чайковые, поморниковые и чистиковые), в том числе 6 видов, имеющих охранный статус. Из группы водных птиц полученные данные исследований в августе — октябре наиболее обстоятельны для чернозобой гагары, морянки и гаги-гребенушки (гагаровые и утиные). Численность этих видов накануне осеннего отлёта птиц (август) нарастала в мелководной части акватории, прилегающей к побережью; позднее следовало их рассеяние в более глубоководные районы к западу от полуострова Ямал. Плотность популяций на прибрежных мелководьях в период наиболее активного освоения этого биотопа составляет (ос.·км$^{-2}$): чернозобой гагары — (0,17 ± 0,036), морянки — (4,87 ± 1,2), гаги-гребенушки — (2,1 ± 1,25). Предположительно, показатель плотности значительно больше для всех трёх видов птиц на меньших дистанциях от берега, не осмотренных с борта судна. Прочие виды группы водных птиц (краснозобая гагара, сибирская гага, чёрная казарка, белолобый гусь и гусь-гуменник) на открытой акватории редки и, по-видимому, на протяжении всего летне-осеннего периода в основном приурочены к более узкой прибрежной зоне. Этот же показатель численности кочующих особей морских птиц (буревестниковые, чайковые, поморниковые и чистиковые), рассчитанный для всей акватории полигона, в среднем за 5 лет для августа и сентября составляет (ос.·км$^{-2}$): для глупыша — (0,078 ± 0,026), бургомистра — (0,067 ± 0,014), моевки — (0,061 ± 0,016), полярной крачки — (0,025 ± 0,015), западносибирской чайки — (0,066 ± 0,0049), среднего, короткохвостого и длиннохвостого поморников — (0,046 ± 0,0074), (0,014 ± 0,0023) и (0,0039 ± 0,00095) соответственно, толстоклювой кайры — (0,16 ± 0,094), атлантического чистика — (0,0026 ± 0,0012). В конце сентября — октябре численность моевки, глупыша и толстоклювой кайры незначительно снижается или остаётся на уровне сентябрьской, а численность атлантического чистика увеличивается в 7 раз. Полярная крачка, западносибирская чайка и длиннохвостый поморник исчезают с акватории, а бургомистр и средний и короткохвостый поморники встречаются значительно реже или почти исчезают (5-, 40- и 30-кратное снижение численности соответственно). В целом, в многолетнем аспекте, глупыш, три вида поморников, бургомистр, моевка, полярная крачка и атлантический чистик осваивают всю акваторию полигона. При этом для глупыша, моевки и бургомистра в отдельные годы наблюдений отмечена неравномерность распределения, выражающаяся в существенных (от 3 до 17 раз) различиях численности на крупных (порядка 25 тыс. км^2) участках исследованной акватории. Западносибирская чайка и полярная крачка в продолжение всего пребывания на акватории приурочены в основном к прибрежным мелководьям, где в периоды сезонного максимума сосредоточено до 80–90 % общего количества особей на полигоне. Напротив, толстоклювая кайра избегает зоны мелководий (глуби́ны до 50 м). Редки на обследованной акватории залётные виды (северная олуша, сизая, озёрная и серебристая чайки), виды, встреченные в периферийной части их общего ареала (большой поморник и серый буревестник), виды, редкие на современном этапе существования их популяций (белоклювая гагара), а также те птицы, основной биотоп обитания которых был недостаточно изучен (турпан, сибирская гага, чёрная казарка, гусь-гуменник и белолобый гусь), и сезонно редкие (люрик).

Keywords: Kara Sea, seabirds and water birds, migrations, nomadism, annual and seasonal population dynamics

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COMPOSITION, STRUCTURE, AND DYNAMICS OF COMMUNITIES OF FISH AND DECAPODS OFF THE SOUTHERN COAST OF THE CRIMEA (THE BLACK SEA)

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Under climatic and anthropogenic factors, the Black Sea ecosystem is being transformed and replenished with new species of fish and Decapoda. Therefore, regular monitoring studies become relevant which allow identifying the effect of these processes on biocenoses of the Crimean Peninsula coastal waters. The aim of this work was to investigate taxonomic, structural, and quantitative characteristics of decapods and ichthyofauna of the Black Sea in the area of the Cape Martyan nature reserve. To make the results more complete, both adult individuals and planktonic and larval stages were sampled and analyzed. Fish and decapods were sampled with fixed nets, bottom traps, and hand nets. Ichthyoplankton and Decapoda larvae were sampled with an ichthyoplankton cone-shaped net IKS-80. For decapods, a high level of species diversity was revealed: those were represented by 17 species from 14 families. Two species, *Alpheus dentipes* Guérin, 1832 and *Lysmata seticaudata* (Risso, 1816), were recorded in the study area for the first time. The taxonomic composition of ichthyofauna was formed by about 30 species, mostly benthic and demersal fish. The structure of fish communities was quite stable; there was a trend towards an increase in diversity, a decrease in the prevalence of certain species, and an overall improvement in their state. A rise in abundance of some Atlantic–Mediterranean species, such as *Serranus scriba* (Linnaeus, 1758) and *Chromis chromis* (Linnaeus, 1758), can serve as an indicator of variations in hydrological and hydrochemical parameters of the environment related to general climate and ecological changes. The values of the quantitative parameters of fish eggs and larvae, (76.3 ± 11.4) and (18.8 ± 4.6) ind.$\cdot$m^{-2}, respectively, were sufficiently high for the Black Sea coastal waters. However, the proportion of living, normally developing fish eggs in the water area was low, 28.6% of the total. The data obtained can be used for comparative analysis during long-term monitoring in the Black Sea water area.

Keywords: Black Sea, ichthyofauna, ichthyoplankton, Decapoda, Cape Martyan nature reserve

One of the unique features of the Black Sea is a significant variety of its ecological conditions. This is driven by its internal location affecting its climate conditions and by the presence of a number of large and small rivers, with many of them being concentrated in a relatively small area. In this regard, the fauna of various spots of the coastal zone, even very close to each other, often has peculiarities related to both species composition and characteristics of hydrobionts: quantitative, ecological, and biological ones. According to the zoning carried out by V. Vodyanitsky [1949] for the shores of the Crimean Peninsula, the area of its southern coast stands out due to its natural-historical and zoogeographic features. Specifically, the coastal zone from Cape Aya to Feodosiya Bay is characterized by the maximum development of two main types of biotopes and related communities: rocky-stony and pebbly-boulder ones [Boltachev, Karpova, 2017]. Such a combination of biotopes is not reported for other areas of the Crimea, and it determines characteristic features of the composition of local fish communities. At the same time, up to 65% of the coastline is concreted, and only the vicinity of capes remains almost intact [Goryachkin, 2015]. Thus, the level of anthropogenic transformation of the coastal zone is very significant and continues to increase.

To date, typical underwater biocenoses in a relatively intact state can be found only in some sites of the coastal zone. One of them is the Cape Martyan protected water area. The Cape Martyan nature reserve was organized according to the Decree of the Council of Ministers of the Ukrainian SSR No. 84 dated 20.02.1973 with the aim of protecting typical terrestrial and aquatic natural complexes of the southern coast of the Crimea. The reserve water area borders two capes, Nikitin and Martyan. It has an area of 120 hectares, a width of 300–500 m, and a length of about 2,200 m along the shore [Marine Protected Areas of the Crimea, 2015].

The fact that these waters belong to protected areas ensured no fishing activities with coastal fixed fishing gear and a relatively low level of anthropogenic load.

Cape Martyan is a limestone massif consisting of marble-like limestones and cemented breccias that come ashore and are subject to intense wave abrasion [Yena et al., 2013]. The coastal zone is formed by alternating limestone entrances with steep cliffs up to 20 m high and narrow pebble beaches. Bottom underwater landscapes consist of block and boulder-block heaps and pebble-boulder sections of the surf zone near the shores. From a depth of 8 m and deeper, those are replaced by loose sandy deposits with admixtures of silt and shells. Water salinity is stable, 17–18‰. This area can serve as a testing ground for studying features of regional communities of marine fauna and long-term changes occurring there under natural and anthropogenic factors.

The first data on ichthyofauna of this water area provided information on the registration of 71 fish species [Boltachev et al., 2014]. Decapoda fauna, according to [Grintsov et al., 2008], was represented by only 5 species. However, researchers have never focused on the cenotic role of species, their distribution, abundance, structural characteristics of communities, and trends in their variations. To date, salinization and changes in the mean annual temperature are recorded in the Black Sea [Kazmin et al., 2010; Shaltout, Omstedt, 2014]. Over 10 years, the salinity growth averaged 0.0038‰ [Belokopytov, 2017]. The mean annual water temperature, according to observations of 1982–2015, increases every decade by an average of 0.64 °C [Sakalli, Basusta, 2018]. Variations in hydrological and hydrochemical parameters result from global climate changes, water influx from the Sea of Marmara, and a decrease in freshwater runoff from the mainland. These processes contribute to the natural dispersal of the fauna inhabiting the Mediterranean Basin and Indian Ocean [Boltachev et al., 2009; Oven, Salekhova, 1969; Pusanow, 1967; Puzanov, 1965; Vinogradov et al., 2017]. Taxonomic and structural characteristics of the coastal zone communities are undergoing certain changes. Since the regional features of these changes are closely related to the ecosystem characteristics of the sea coastal areas, local biocenosis is studied in detail. At the same time, transformations in species composition are often not indicative. With sufficiently long-term investigations, as well as the use of various methods of material sampling to level the selectivity of fishing gear, most species of the sea fauna come to the attention of researchers. Characteristic features and changes occurring in communities can be more reliably revealed based on the analysis of their structure and quantitative parameters.

The aim of this work is to assess the current state of coastal communities of fish and decapods, to analyze the cenotic role of species in the Cape Martyan vicinity, and to determine their abundance in order to reveal changes in communities and processes of fish reproduction occurring in this area under various environmental factors.

MATERIAL AND METHODS

The work is based on material sampled in expeditions during the warm period of several years (May–July 2010, 2011, and 2013; July–September 2019) in the Cape Martyan vicinity and in the Cape Martyan protected water area (Fig. 1).

Fig. 1. The study area, Cape Martyan protected water area (the points indicate sampling locations)

Fish and decapods were sampled with fixed single-walled nets, bottom traps, and hand nets. We used nets with a length of 30 m, a canvas height of 1.8 m, and a mesh of 15, 20, 25, 35, and 45 mm. Sampling was carried out at various depths, both perpendicular and parallel to the shore. The depth of net setting varied within 1–8 m; nets were set up overnight, 20:00 to 07:00. Bottom traps, with a mesh of 6–8 mm, were set up at depths of 1–2 m. Sampling was followed by the analysis of catches: the species were identified; the abundance and weight of individuals of each species of hydrobionts were determined.

Ichthyoplankton and Decapoda larvae were sampled in July 2019 at 10 stations in the nature reserve and adjacent water area (Fig. 1, Table 1). Coastal stations were located at a distance of 130–160 m from the water edge; offshore stations, at a distance of 300–500 m. Depths ranged within 5–16 m. At each station, vertical sampling from the bottom to the surface was carried out with an ichthyoplankton cone-shaped net IKS-80, with mesh of 400 µm and the inlet area of 0.5 m^2. The temperature of the surface water horizon was measured; during our work, it was +23.0…+25.0 °C. The coordinates of the boat position were recorded.

To determine the actual depth of the net immersion, the angle of deviation from the vertical of the cable was measured at the lower position of the net. In the calculation, the following formula was used:

$$b = c \times cosa \,,$$

where b is the depth of the actual immersion of the net;

c is the length of the etched cable;

a is the angle of deviation of the cable from the vertical.

Table 1. Plankton sampling in the nature reserve waters and in the adjacent water area, 17.07.2019

Station number	Coordinates	Depth, m	Station number	Coordinates	Depth, m
1	44°30′14.5″N, 34°14′18.4″E	8	6	44°30′11.6″N, 34°15′7.2″E	16
2	44°30′3.5″N, 34°14′26.3″E	14	7	44°30′24.6″N, 34°15′28.8″E	16
3	44°30′3.2″N, 34°14′43.6″E	15	8	44°30′30.5″N, 34°15′19.8″E	6
4	44°30′15.0″N, 34°14′43.8″E	10	9	44°30′40.6″N, 34°15′49.3″E	14
5	44°30′17.8″N, 34°14′58.9″E	6	10	44°30′42.1″N, 34°15′42.1″E	5

The identification of species of hydrobionts and the order of taxa arrangement are given according to modern concepts [Catalog of Fishes, 2021; Vasil’eva, 2007].

Ichthyoplankton species were determined in accordance with T. Dekhnik [1973] and E. Kalinina [1976].

Diversity indices for communities of fish and decapods were calculated according to Yu. Odum [1986]:

- Shannon species diversity index, $H = -\Sigma P_i \times \log_2 P_i$;
- Margalef species richness index, $D = (S - 1) / \lg N$;
- Simpson dominance index, $c = \Sigma(n_i / N)^2$;
- Pielou evenness index, $e = H / \log S$.

RESULTS

Ichthyofauna. Sixteen fish species belonging to 9 orders and 14 families were identified in net catches in the coastal water area. Out of them, Labridae was the most diverse family (three species). Other families were represented by one species each (Table 2).

Table 2. Species composition and proportion of fish in net catches

Family	Species	Mean abundance of fish in catches, %	
		2010–2013	2019
Dasyatidae	*Dasyatis pastinaca* (Linnaeus, 1758)	0	0.5
Lotidae	*Gaidropsarus mediterraneus* (Linnaeus, 1758)	1.2	1.1
Mugilidae	*Chelon auratus* (Risso, 1810)	3.6	0
Scorpaenidae	*Scorpaena porcus* Linnaeus, 1758	42.0	27.4
Serranidae	*Serranus scriba* (Linnaeus, 1758)	0	8.1
Carangidae	*Trachurus mediterraneus* (Steindachner, 1868)	1.2	19.4
Sparidae	*Diplodus annularis* (Linnaeus, 1758)	1.8	2.7
Sciaenidae	*Sciaena umbra* Linnaeus, 1758	2.4	0.5
Mullidae	*Mullus barbatus ponticus* Essipov, 1927	1.8	6.5
Pomacentridae	*Chromis chromis* (Linnaeus, 1758)	0	10.8
Labridae	*Symphodus ocellatus* (Linnaeus, 1758)	1.8	1.6
	Symphodus roissali (Risso, 1810)	13.0	11.8
	Symphodus tinca (Linnaeus, 1758)	23.7	7.5
Uranoscopidae	*Uranoscopus scaber* Linnaeus, 1758	1.2	1.1
Blenniidae	*Parablennius sanguinolentus* (Pallas, 1814)	5.3	1.1
Gobiidae	*Ponticola eurycephalus* (Kessler, 1874)	1.2	0

In the study area, the basis of fish communities during the summer period were sedentary species (the ones that do not perform significant migrations). It was mainly *Scorpaena porcus*, but there were several Labridae representatives as well: *Symphodus tinca* and *S. roissali*. Such a combination is quite common for rocky and stony biotopes of the Black Sea coastal zone. Abundance of mass migratory species is subject to significant interannual variability. In 2010, 2011, and 2013, *Trachurus mediterraneus* accounted for slightly more than 1% in catches, while in 2019, the proportion of this species reached 19.4%. The proportion of *Mullus barbatus ponticus* varied within 1.6–6.8% in different years.

Unusual trends were revealed for *Serranus scriba* and *Chromis chromis*. Previously, these species were rare, especially the first one. At present, according to our data, their abundance noticeably increased. In 2019, their proportions in catches amounted to 8.1 and 10.8%, respectively. Such a high abundance of these species is more characteristic of the Mediterranean Sea than of the Black Sea.

All registered species are typical allochthonous representatives of marine fauna, except for *Ponticola eurycephalus* belonging to the autochthonous Ponto-Caspian group.

The quantitative indicators of catches (catch *per* unit effort) are provided in Table 3.

Table 3. Catch *per* unit effort for nets with various mesh size by abundance (ind.·h^{-1}) and biomass (kg·h^{-1}) of fish species recorded in the water area of the Cape Martyan nature reserve

Species	Net mesh size, mm				
	15	22	24	35	45
Dasyatis pastinaca (Linnaeus, 1758)					0.09 0.018
Chromis chromis (Linnaeus, 1758)	2.69 0.033				
Sciaena umbra Linnaeus, 1758				0.09 0.016	
Diplodus annularis (Linnaeus, 1758)		0.09 0.006		0.36 0.051	
Serranus scriba (Linnaeus, 1758)	0.41 0.010	0.09 0.006	0.18 0.020	0.09 0.019	0.18 0.033
Mullus barbatus ponticus Essipov, 1927	0.05 0.019	0.09 0.005			
Trachurus mediterraneus (Steindachner, 1868)	1.41 0.034	0.18 0.013	0.27 0.023		
Scorpaena porcus Linnaeus, 1758	0.95 0.216	1.18 0.153	0.45 0.035	0.91 0.173	0.18 0.015
Symphodus tinca (Linnaeus, 1758)	0.27 0.028	0.09 0.008	0.55 0.041	0.09 0.014	
Symphodus ocellatus (Linnaeus, 1758)	0.14 0.001			0.18 0.001	
Symphodus roissali (Risso, 1810)	1.32 0.020	0.36 0.015			
Uranoscopus scaber Linnaeus, 1758				0.18 0.034	
Gaidropsarus mediterraneus (Linnaeus, 1758)	0.09 0.003				
Parablennius sanguinolentus (Pallas, 1814)	0.9 0.002	0.09 0.003			

Note: above the line, abundance; below the line, biomass.

In plankton samples of the Cape Martyan water area, eggs and larvae of 14 fish species were registered (Table 4). All species were previously noted in ichthyofauna of this nature reserve [Boltachev et al., 2014]. They all spawn in summer, and their eggs and larvae are characteristic of coastal waters of the Crimea at the peak of the warm season [Dekhnik, 1973].

Table 4. Ichthyoplankton species composition for all the stations

Species	Abundance, ind.		Proportion, %	
	Eggs	Larvae	Eggs	Larvae
Engraulis encrasicolus (Linnaeus, 1758)	286	63	64.0	56.3
Chelon auratus (Risso, 1810)	1	0	0.2	0.0
Serranus scriba (Linnaeus, 1758)	1	0	0.2	0.0
Pomatomus saltatrix (Linnaeus, 1766)	1	0	0.2	0.0
Trachurus mediterraneus (Steindachner, 1868)	106	11	23.7	9.8
Diplodus annularis (Linnaeus, 1758)	18	6	4.0	5.4
Sparidae gen. sp.	1	0	0.2	0.0
Sciaena umbra Linnaeus, 1758	1	0	0.2	0.0
Mullus barbatus ponticus Essipov, 1927	25	3	5.6	2.7
Symphodus cinereus (Bonnaterre, 1788)	0	1	0.0	0.9
Trachinus draco Linnaeus, 1758	2	0	0.4	0.0
Uranoscopus scaber Linnaeus, 1758	2	0	0.4	0.0
Pomatoschistus minutus (Pallas, 1770)	–	1	–	0.9
Gobius niger Linnaeus, 1758	–	2	–	1.8
Gobiidae gen. sp.	–	1	–	–
Arnoglossus kessleri Schmidt, 1915	2	0	0.4	0.0
Damaged or unidentifiable	1	24	0.2	21.4
In total	**447**	**112**	**100.0**	**100.0**

Out of the species recorded, *Engraulis encrasicolus* was the most abundant one, but proportions of its eggs and larvae were less significant than those indicated in literature for the Black Sea coastal area off the Crimea at the peak of summer spawning. Specifically, on the Crimean shelf in July 2010, the European anchovy eggs and larvae accounted for 83.0 and 60.0% of the total, respectively [Klimova et al., 2014]. In July–August 2019, the proportion of anchovy eggs in samples was 85.0%, while the proportion of larvae was 77.0% [Klimova et al., 2020].

During the period of sampling, out of 286 anchovy eggs, 285 specimens (99.6%) were at the early stages of development: up to the stage III inclusive, according to T. Dekhnik [1973]. One living egg was at the late stage of development, the stage V. The proportion of dead anchovy eggs was 83.2%, while that of living, normally developing eggs was 16.8%.

The European anchovy prelarvae and larvae had a total length range of 1.7–5.2 mm (on fixed material). The total length of 60 specimens constituting the vast majority (95.2%) was of ≤ 3.5 mm.

Eggs of other fish species accounted for 36.0% of the total; larvae accounted for 43.7%. The most frequently found species, as expected during the summer spawning season, were the horse mackerel (23.7% of eggs and 9.8% of larvae of the total; the proportion of living eggs was 51.9%), the red mullet (5.6 and 2.7%, respectively; 36.0% of living eggs), and the annular seabream (4.0 and 5.4%, respectively; 50.0% of living eggs).

Unexpectedly large, 21.4% of the total abundance of larvae and prelarvae, was the proportion of specimens inaccessible for species identification. Those were small and the smallest larvae and prelarvae, with the total length of 1.05–1.75 mm. Many of them retained their embryonic form and had no features characteristic of postembryonic development which are necessary to identify the species. In our opinion, their occurrence in sampled material did not result from damage and destruction of eggs at the final stages of development during sampling and fixation. In this case, the proportion of eggs with mechanical damage would be noticeable, and there would be membranes of destroyed eggs in samples. In fact, we noted one destroyed egg of unidentifiable species, while empty membranes were not found at all.

Decapoda. In the summer 2019, we investigated decapod fauna in coastal waters of the Cape Martyan nature reserve. Larvae and adult specimens of 11 Decapoda species representing 9 families were identified.

Larvae of 10 decapod species were recorded in the study area. Their mean abundance was 55.2 ind.·m^{-2} (Table 5). In plankton samples, larvae of *Pilumnus hirtellus* (23.6%), *Clibanarius erythropus* (20.7%), *Hippolyte leptocerus* (20.3%), *Athanas nitescens* (18.5%), and *Pachygrapsus marmoratus* (5.1%) prevailed. Larvae of other decapods were found singly. In addition to larvae of the species previously known for the water area [Khajlenko, 2019], we registered larvae of shrimps rare for the Crimean waters: *Alpheus dentipes* and *Lysmata seticaudata*.

Table 5. Species composition and abundance of Decapoda planktonic larvae in the water area of the Cape Martyan nature reserve

Species	Abundance, ind.·m^{-2}
Athanas nitescens (Leach, 1814 [in Leach, 1813–1815])	10.2
Alpheus dentipes Guérin, 1832	1.4
Lysmata seticaudata (Risso, 1816)	0.4
Hippolyte leptocerus (Heller, 1863)	11.2
Palaemon elegans Rathke, 1836	1.4
Clibanarius erythropus (Latreille, 1818)	11.4
Pisidia longimana (Risso, 1816)	1.8
Pachygrapsus marmoratus (J. C. Fabricius, 1787)	2.8
Xantho poressa (Olivi, 1792)	1.6
Pilumnus hirtellus (Linnaeus, 1761)	13.0
In total	**55.2**

In the study area, adult decapods were represented by 9 species. Out of them, *Eriphia verrucosa* (Forskål, 1775), *P. marmoratus*, *Xantho poressa*, and *Palaemon elegans* are common. *A. nitescens*, *Pisidia longimana*, and *C. erythropus* were found in significant numbers. Out of rare species, *H. leptocerus* and *P. hirtellus* were recorded. All Decapoda representatives registered in the nature reserve waters were distributed in communities of hard bottom sediments from the surface down to a depth of 5–10 m.

DISCUSSION

The taxonomic composition of ichthyofauna in the study area was formed by about 30 species, mainly benthic fish (*S. porcus*, *P. eurycephalus*, and Blenniidae representatives) and demersal ones (Labridae, Sparidae, *etc.*). In different years, their indicators of relative abundance were characterized by significant variability. However, throughout the investigated period, diversity parameters of communities in general remained quite stable (Table 6).

Table 6. Diversity indices for communities of fish and Decapoda in the water area of the Cape Martyan nature reserve

Index	Fish					Decapoda
	2010	2011	2013	2019		2019
				Fish	Ichthyoplankton	
Shannon species diversity index, *H*	2.45	2.08	2.12	2.40	1.56	2.73
Margalef species richness index, *D*	7.25	7.65	7.40	5.73	5.50	4.74
Simpson dominance index, *c*	0.25	0.36	0.27	0.14	0.48	0.18
Pielou evenness index, *e*	0.64	0.55	0.56	0.63	0.39	0.82

Data for quantitative studies of decapod communities were obtained for the first time. Accordingly, there is no material to compare with. Based on data of plankton surveys, the main indicators of species diversity were calculated (see Table 6). The established values of the Shannon species diversity index and distribution of the relative abundance expressed by the Pielou evenness index characterize the water area as the one with a relatively low species richness of Decapoda representatives. The low value of the Simpson dominance index indicates the absence of obvious dominants more precisely than values of other indices reflecting the presence of prevailing species.

Based on the analysis of the dominance–diversity curve for fish communities (Fig. 2), it can be concluded that there is a trend towards an increase in diversity, a decrease in the prevalence of certain species, and a general complication of community structure. Apparently, a rise in *S. scriba* abundance in net catches (the species previously extremely rare for the Black Sea fauna) can serve as an indicator of variations in hydrological and hydrochemical parameters of the environment resulting from general climate and environmental changes. An increase in *S. scriba* abundance is confirmed by visual underwater observations as well.

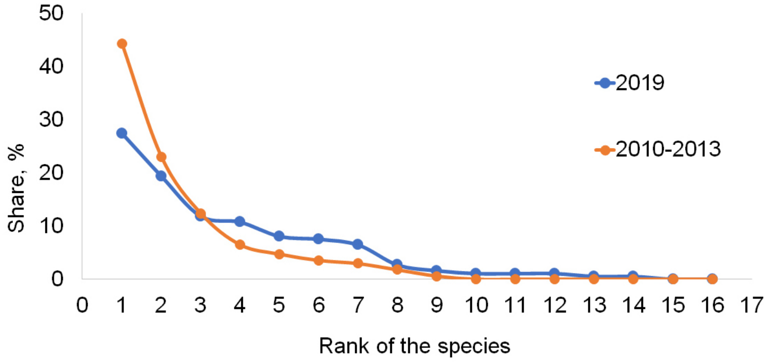

Fig. 2. Ranking of the fish species of the study water area by abundance: along the abscissa axis, the serial number of the species (species are arranged in descending order of their abundance); along the ordinate axis, the proportion of this species in the catch by abundance

The proportion of living, normally developing fish eggs in the water area, 28.6% of the total, is to be analyzed further. For example, in summer, under similar conditions (in the open sea, at coastal stations opposite Sevastopol, 250–500 m off the coast, above a depth of 10–19 m, and against the backdrop of the sea surface temperature of +20.0…+25.3 °C), the proportion of dead eggs was 55.2%, while that of living, normally developing eggs was 44.8%.

In 2002–2008, according to literature data, the proportion of dead eggs in the coastal sea area from the Sevastopol Bay to the 2-mile zone averaged 63.1% [Klimova, 2010]. The proportion of living eggs amounted to 36.9%. Importantly, this analysis refers to both summer- and winter-spawning fish species and is based on the study of samples both from the coastal area of the open sea and the innermost spot of the Sevastopol Bay, where the proportion of dead eggs was the highest [Klimova, 2010].

In ichthyoplankton of the study water area, the European anchovy was the prevailing species at the time of sampling, but proportions of its eggs and larvae were lower than those provided in literature for the Black Sea coastal water area off the Crimea in midsummer. Specifically, on the Crimean shelf in July 2010, anchovy eggs and larvae accounted for 83 and 60% of the total, respectively [Klimova et al., 2014]. In July 2017, the proportion of anchovy eggs off the Crimean coast was 77% [Klimova et al., 2021]. In July–August 2019, on the shelf off the coast of the Crimea and Russian Caucasus, the proportion of anchovy eggs in samples was 85%, and the proportion of larvae was 77% [Klimova et al., 2020].

The occurrence of anchovy eggs in samples taken at the peak of spawning in the first half of the day at the early (prevailing) and final (with much lower abundance) stages of development against the backdrop of the actual absence of eggs at the intermediate stage is described in literature [Dekhnik, 1973]. It is the norm, and it is due to features of the daily anchovy reproduction rhythm. However, our data show not only a lower proportion of eggs at the later stages of development, but their virtually complete absence, which does not correspond to the norm. The recorded proportion of dead anchovy eggs, 83.2%, significantly exceeded that noted for the Crimean shelf in July 2010, 74.0% [Klimova et al., 2014]. Living eggs are easily distinguished from dead ones; the death of eggs occurs in the sea and is not related to sampling and fixation. Thus, based on information on the proportion of living eggs in a sample, one can conclude on the degree of survival of embryos at a given stage of the development under certain conditions [Dementjeva, 1958]. Knowing the timing of the development of embryos and larvae at a given temperature, it is possible to monitor the development of each generation by abundance of survived embryos and corresponding groups of larvae, depending on their size and growth and based on the numerical prevalence of a particular group of larvae by stages of development.

In our material, the ratio of the abundance of the European anchovy prelarvae and larvae (in total, 63 ind.) to the total abundance of eggs of this species was significant, 22.0%. For the Crimean shelf in July 2010, the value was only 16.1% [Klimova et al., 2014]. Almost all of them, 95.2%, were the ones at the prelarvae stage or larvae at the earliest stage of development, on yolk feeding [Klimova et al., 2020], and were no more than a day old [Dekhnik, 1973]. Anchovy prelarvae, due to their small size (primarily body height), mostly drop out of catches, and their abundance may be underestimated by us. But even high abundance of prelarvae and a high value of the ratio of their abundance to the abundance of eggs cannot serve as an unambiguous indicator of effective spawning. According to [Productivity of the Black Sea, 1979], the mortality of anchovy is relatively low at the late stages of embryogenesis, sharply increases during the transition from embryonic to postembryonic development, and remains high throughout the entire stage of yolk feeding (a group of larvae 2.0–3.4-mm long which includes almost all anchovy larvae caught by us). With transition to mixed feeding (anchovy larvae 3.5–6.0-mm long), mortality sharply decreases again. However, only 4.8% of larvae we recorded survived and fell into this group. We did not reveal any older larvae.

Attention is to be drawn to the proportion of abnormally small and minute fish larvae and prelarvae that cannot be identified down to the species level, 21.4% of the total abundance of those in our material. The relationship between the size and general development of hatching fish larvae and water temperature is known. Specifically, for the European anchovy, it is shown that embryos hatch more developed and bigger in size at a lower temperature [Dekhnik, 1973]. By itself, the surface water temperature of the study area was not extremely high for the season; in our opinion, the reason for the observed phenomenon was not the absolute value of the temperature of the environment, but its dynamics. The negative effect of fluctuations in temperature and its deviation from optimal range at the late stages of development of eggs and early stages of postembryonic development of fish was described in detail in relation to cultivated and artificially reproduced freshwater species [Portnaya et al., 2015]. In this case, routine procedures are monitoring of the state of the environment and analysis of the dynamics of embryonic and postembryonic fish development. With an abrupt increase in the temperature of the environment during the course of embryogenesis, researchers observed early hatching, developmental anomalies, and the death of fish prelarvae and larvae even against the backdrop of optimal values of other significant factors [Portnaya et al., 2015].

According to the environmental data available at http://weatherarchive.ru [2020], in June 2019, the mean surface water temperature off the coast of Yalta (the spot of constant observation closest to the study area) was the highest for 2010–2020 and amounted to +23.2 °C. The mean temperature in July 2019, on the contrary, was the minimum over the same long period and amounted to +23.8 °C. Analysis of the satellite data archive on temperature and state of the Black Sea surface water [Arkhiv dannykh, 2022] confirms this fact. So, in July 2019, on the day of our work and on some previous days, off the southern coast of the Crimea, in particular in the study area, there were spots with the surface water temperature 1–3 °C lower than the values for adjacent open waters. For the study water area on the day of sampling, the same source showed the presence of a current directed to the coast, with a flow rate of 0.10–0.15 $m \cdot s^{-1}$. The surface temperature was of +23.0…+25.0 °C. Such a range is unusual for a small water area and may indicate the process of mixing of heated surface waters with underlying cold ones near the coast. Apparently, water mixing and variations in its temperature were a stress factor, affected the development of eggs and their survival, and caused early hatching of incompletely formed prelarvae.

The observed abundance of fish eggs and larvae, (76.3 ± 11.4) and (18.8 ± 4.6) $ind. \cdot m^{-2}$, respectively, can be considered significantly high for the Black Sea coastal area off the Crimea in July. In general, the values correspond to expected ones. For example, on the shelf off the Crimean coast from Cape Karadag to Cape Tarkhankut in July 2010, the mean abundance of eggs was 46.2 $ind. \cdot m^{-2}$, and of fish larvae, 10.1 $ind. \cdot m^{-2}$ [Klimova et al., 2014]. For the shelf opposite Yalta, the same literature source provides significantly lower estimates of ichthyoplankton abundance, 21.0 $ind. \cdot m^{-2}$ for eggs and 1.9 $ind. \cdot m^{-2}$ for fish larvae. In July 2017, on the shelf off the Crimea, the mean abundance of eggs was 25.0 $ind. \cdot m^{-2}$, and of fish larvae, 3.2 $ind. \cdot m^{-2}$ [Klimova et al., 2021].

According to literature data, 15 Decapoda species were recorded in the nature reserve waters and in the adjacent water area [Grintsov et al., 2008; Khajlenko, 2019].

The first information on Decapoda fauna in the Cape Martyan area dates back to 1976. Then, the most complete inventory of the fauna of hydrobionts for the coastal zone of the nature reserve and adjacent waters down to depths of 10–15 m was carried out. According to it, 13 species of decapods were noted: *A. nitescens*; *Palaemon adspersus* Rathke, 1836; *Upogebia pusilla* (Petagna, 1792); *P. longimana*; *Diogenes pugilator* (P. Roux, 1829); *C. erythropus*; *E. verrucosa*; *Carcinus aestuarii* Nardo, 1847; *Liocarcinus depurator* (Linnaeus, 1758); *P. marmoratus*; *X. poressa*; *P. hirtellus*; and *Macropodia czernjawskii* (Brandt, 1880) [Khajlenko, 2019].

The next stage of comprehensive studies on the species diversity of benthic invertebrates and meroplankton of the upper sublittoral zone in the nature reserve was performed in the summer season of 2004–2006. According to its results, five representatives of the order were recorded; out of them, one species, *H. leptocerus*, was reported for the fauna of the nature reserve for the first time [Grintsov et al., 2008]. Moreover, the cited paper provides data on the registration of single larvae of *A. nitescens* in plankton.

In 2017, preliminary data were obtained on the assessment of the current state of decapod fauna in the coastal zone of the nature reserve at depths of 0–2 m [Khajlenko, 2019]. According to it, in the study water area, Decapoda was represented by four species. *P. elegans* was not previously recorded in the coastal aquatic complex.

Summarizing the lists of species published for this area and our data, we can conclude as follows: Decapoda fauna in the coastal water area of the Cape Martyan nature reserve includes at least 17 species representing 14 families. Interestingly, nine species are common, six species (*P. adspersus*, *U. pusilla*, *D. pugilator*, *C. aestuarii*, *L. depurator*, and *M. czernjawskii)* are known only from literature sources, and two species (*A. dentipes* and *L. seticaudata*) are new for the protected water area [own data].

Differences in species composition are primarily due to the confinement of species to different biotopes. Specifically, *D. pugilator*, *C. aestuarii*, and *Liocarcinus vernalis* (Risso, 1827), not registered by us, are found in open spots of soft soils (silt, sand, and shell). *U. pusilla* burrows in dense, soft ground. *P. adspersus*, *D. pugilator*, *C. aestuarii*, and *M. czernjawskii* are recorded in thickets of *Zostera* and other macrophytes growing on soft soils. In the water area of the nature reserve, this type of substrates is either absent or represented by local spots; this allows us to assume that the occurrence of some species of hydrobionts is related to characteristic bottom biotopes of waters adjacent to the protected water area.

Two shrimps, *A. dentipes* and *L. seticaudata*, whose larvae were recorded in our plankton samples, are very rare due to their extremely secretive lifestyle. These are cryptobenthic species, and their life cycle is confined to biotopes formed by various species of bivalves or to pretty similar spots of the bottom (caves, grottoes, *etc.*).

Thus, for the first time for a typical water area of the southern coast of the Crimean Peninsula, the current state of communities of fish and Decapoda was analyzed, alpha-diversity indicators were described, and characteristics of the abundance of cenosis-forming species were obtained. All these data can be used as a starting point for monitoring changes in the biocenosis of the water area.

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СОСТАВ, СТРУКТУРА И ДИНАМИКА СООБЩЕСТВ РЫБ И ДЕСЯТИНОГИХ РАКООБРАЗНЫХ У ЮЖНОГО ПОБЕРЕЖЬЯ КРЫМА (ЧЁРНОЕ МОРЕ)

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Под влиянием климатических и антропогенных факторов экосистема Чёрного моря трансформируется и пополняется новыми видами рыб и десятиногих ракообразных, что обуславливает актуальность регулярных мониторинговых исследований, позволяющих выявить воздействие вышеназванных процессов на биоценозы прибрежных вод Крымского полуострова. Целью настоящей работы стало изучение таксономических, структурных и количественных характеристик сообществ декапод и ихтиофауны Чёрного моря в районе заповедника «Мыс Мартьян». Помимо зрелых организмов, в ходе работ были отобраны и проанализированы их планктонные личиночные стадии, что дополнило полученные результаты. Сбор рыб и десятиногих ракообразных осуществляли ставными сетями, донными ловушками и ручными сачками. Ихтиопланктон и личинок декапод облавливали планктонной сетью ИКС-80. Выявлен высокий уровень видового разнообразия десятиногих ракообразных, представленных 17 видами из 14 семейств. Два вида, *Alpheus dentipes* Guérin, 1832 и *Lysmata seticaudata* (Risso, 1816), отмечены для региона впервые. Таксономический состав ихтиофауны формируют около 30 видов, преимущественно донные и придонные рыбы. Структура сообществ рыб достаточно стабильна, отмечена тенденция к увеличению разнообразия, снижению доминирования отдельных видов и общему улучшению состояния. Рост численности некоторых атлантико-средиземноморских видов, таких как *Serranus scriba* (Linnaeus, 1758) и *Chromis chromis* (Linnaeus, 1758), может служить индикатором изменений гидрологических и гидрохимических параметров среды, связанных с глобальными климатическими и экологическими изменениями. Количественные характеристики икры и личинок рыб, (76,3 ± 11,4) и (18,8 ± 4,6) экз.$\cdot$м$^{-2}$ соответственно, были достаточно высокими для прибрежных вод Чёрного моря, а доля живой, нормально развивающейся икры рыб в акватории — низкой, 28,6 % от общего количества. Полученные данные могут быть использованы для сравнительного анализа при многолетних мониторинговых работах в акватории Чёрного моря.

Ключевые слова: Чёрное море, ихтиофауна, ихтиопланктон, Decapoda, заповедник «Мыс Мартьян»

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THE INFESTATION STATUS OF SYMBIOTIC CRUSTACEANS ON THE SWIMMING CRAB *CHARYBDIS TRUNCATA* (FABRICIUS, 1798) FROM NHA TRANG BAY, VIETNAM (THE EAST SEA)

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Symbioses are common relationships between organisms in marine ecosystems. Out of crabs belonging to the family Portunidae, an economically important one, *Charybdis truncata* (Fabricius, 1798) is a widely distributed species. However, the studies on its symbiotic assemblages are still limited. A total of 408 *C. truncata* were sampled in Nha Trang Bay (Khanh Hoa province, Vietnam, the East Sea) in January–August 2022. Symbionts were classified based on morphological characters. Statistical analysis was applied to compare the infestation status of symbionts. Six symbiotic species were detected, including four epibiotic barnacles [*Octolasmis angulata* (Aurivillius, 1894), *Octolasmis alata* (Aurivillius, 1894), *Octolasmis warwicki* Gray, 1825, and *Dianajonesia tridens* (Aurivillius, 1894)] and two obligate unidentified parasites [*Cancrion* sp. and *Sacculina* sp.]. Out of them, *O. alata* and *Cancrion* sp. were recorded on *C. truncata* for the first time. The overall prevalence of symbionts on the swimming crab hosts was 13%, and the number of infecting symbiont species on hosts ranged within 1–4. *O. angulata* was the dominant species, with the prevalence of 6.9%. The prevalence of this symbiotic species was significantly higher in ovigerous female crabs compared to non-ovigerous ones. Moreover, there was a noticeable rise in *O. angulata* prevalence rates as crab size increased. No significant differences were revealed in the mean intensity of symbionts by sex, reproductive status of females, and size of the crab hosts. The initial morphological modifications caused by infecting parasites, *Cancrion* sp. and *Sacculina* sp., were recorded and described. These findings provide data on the status of natural infection of symbiotic species on *C. truncata* as a basis for the management of commercial species and aquaculture development.

Keywords: *Charybdis truncata*, symbionts, epibionts, obligate parasites, Nha Trang Bay, Vietnam

Symbioses are common relationships between organisms in ecosystems which represent different associations, including mutualism, commensalism, and parasitism [Leung, Poulin, 2008]. Association between symbionts and their hosts is considered as one of the driving forces of evolution. In several cases, the finding of parasitic fauna on free-living organisms can provide new information for better understanding of host–symbiont interactions and clarify biodiversity data in the study region [Martinson, 2020].

In marine environments, crustaceans are the most diverse invertebrate organisms [Brusca, Brusca, 2003]. They are well-known to have symbiotic relationships [Ross, 1983]. Out of marine crustaceans, swimming crabs (Decapoda: Portunidae, an economically important family) are common hosts of symbiotic crustaceans. These symbionts of portunids include pedunculate barnacles (*Octolasmis* and *Dianajonesia* in the family Poecilasmatidae), acorn barnacles (*Chelonibia* in Chelonibiidae and *Semibalanus* in Balanidae), rhizocephalan barnacles (Sacculinidae and Thompsoniidae), isopods (Entoniscidae and Bopyridae), and copepods (Nicothoidae) [Jeffries et al., 1982; McDermott et al., 2019; Shields, 1992; Shields et al., 2015; Waiho et al., 2021].

Pedunculate and acorn barnacles are filter-feeding organisms attaching to the outer integument of crabs [Campos et al., 2022; Hosseini et al., 2023; Jeffries et al., 1982]. The host's respiratory currents supply them with food and oxygen [Jeffries et al., 1982]. In most cases, they are harmless to the host. However, when occurring at high intensity, they hamper the energetic condition, movement, and respiration of crabs. More seriously, the heavy infestation with epibiotic barnacles can lead to cumulative infection with rhizocephalan parasites causing serious effects on growth and development, even the death of their hosts [Campos et al., 2022; Gannon, Wheatly, 1992; Hudson, Lester, 1994].

Rhizocephalan barnacles are specialized parasites. Their body has two parts: a root-like system (interna) developing around the host's visceral organs for nutrient absorption and a female reproductive organ (externa) arising outside the host [Glenner, Hebsgaard, 2006; Walker, 2001]. The common resulting effects of rhizocephalan infection are alterations in morphological characters, physiology, and behavior of the crabs [Waiho et al., 2021]. Infected male crabs are usually found feminized – with an enlarged and more segmented abdomen, like in females. Meanwhile, the effects observed in female crabs are often unclear [Kristensen et al., 2012].

Isopods (Entoniscidae and Bopyridae) are obligate parasites within visceral cavities of crabs. Their life cycle goes through three larval stages. The eggs develop into epicardium larvae which then metamorphose into microniscus and finally into cryptoniscus larvae before becoming juveniles [Williams, Boyko, 2012]. These adult parasites are characterized by high sexual dimorphism: males are many times smaller in size than females [McDermott et al., 2019; Shiino, 1942]. Certain species could cause the castration of the host [Shiino, 1942].

Some egg-feeding copepod parasites of the family Nicothoidae were found on egg clutch and in branchial chambers of swimming crabs from India [Gnanamuthu, 1954], Australia [Shields, 1992], and Vietnam [Dang et al., 2022; Oanh et al., 2018]. Mostly, due to very low prevalence, the harmful effects of these parasites did not arouse much interest [Shields et al., 2015].

So far, eight pedunculate barnacles, two acorn barnacles, five rhizocephalans, three isopods, and one copepod species have been detected on ten species of swimming crabs on the coast of Vietnam. Out of them, both species composition and infection status of symbiotic crustaceans were studied in four commercial crabs: *Portunus pelagicus* (Linnaeus, 1758), *Portunus sanguinolentus* (Herbst, 1783), *Monomia haanii* (Stimpson, 1858), and *Charybdis feriata* (Linnaeus, 1758) [Dang et al., 2022; Oanh et al., 2018, 2022a; Vo et al., 2013]. In some cases, investigations were focused only on parasitic species. H. Boschma [1954] discovered four rhizocephalan species on six swimming crabs and described a new species, *Sacculina serenei* Boschma, 1954, on *C. feriata*. As for parasitic isopods, two new species, *Cancrion khanhensis* Oanh & Boyko, 2020 and *Stellatoniscus tentaculus* Oanh & Boyko, 2020, infesting *M. haanii* were recently described [Oanh, Boyko, 2020].

A portunid crab *Charybdis truncata* (Fabricius, 1798) is a widely distributed and commonly exploited species in the Indian Ocean (India) and the West Pacific region (Japan, China, Indonesia, Philippines, Malaysia, Singapore, and Australia) [Ng, 1998]. In Vietnam, it occurs in the Gulf of Tonkin, on central and southern coasts, in muddy or muddy-sandy seabed, at a depth of 5–60 m [Nguyen, 2002]. Several species of symbiotic crustaceans were revealed on *C. truncata*. Three epibionts, *Octolasmis angulata* (Aurivillius, 1894), *Octolasmis warwicki* Gray, 1825, and *Dianajonesia tridens* (Aurivillius, 1894), were found on crabs from Hong Kong [Leung, Jones, 2000]. A parasitic rhizocephalan *Loxothylacus nierstraszi* Boschma, 1938 was recorded in Japan [Boschma, 1938], while *Sacculina scabra* Boschma, 1931 was registered in Indonesia [Chan, 2004]. Up to now, no known investigations have been carried out on symbiotic crustaceans on *C. truncata* in Vietnam.

This study aims at determining the species composition and infestation status of symbiotic crustaceans on *C. truncata* in Nha Trang Bay, Vietnam, and carrying out initial observations on the effect of obligate parasites on the crab hosts. This preliminary research contributes to filling knowledge gaps for this crab species in Vietnam and provides information for fisheries resource management programs.

MATERIAL AND METHODS

Crab sampling and symbiont examination. Crabs were sampled in Nha Trang Bay (Khanh Hoa province, Vietnam, the East Sea) in January–August 2022 (Fig. 1). *C. truncata* specimens (*n* = 408) were randomly sampled from fishing boats, transported alive to the laboratory, and temporarily kept in a fridge at the temperature of +4 °C. The fresh crabs were examined externally; size (carapace width, hereinafter CW), sex, and reproductive status of females (ovigerous or non-ovigerous) were recorded. Following Li and co-authors [2014], crabs were divided into 3 size groups: small (< 20 mm), medium (20–35 mm), and large (> 35 mm). Also, the host morphological modifications (if any) were carefully investigated and noted.

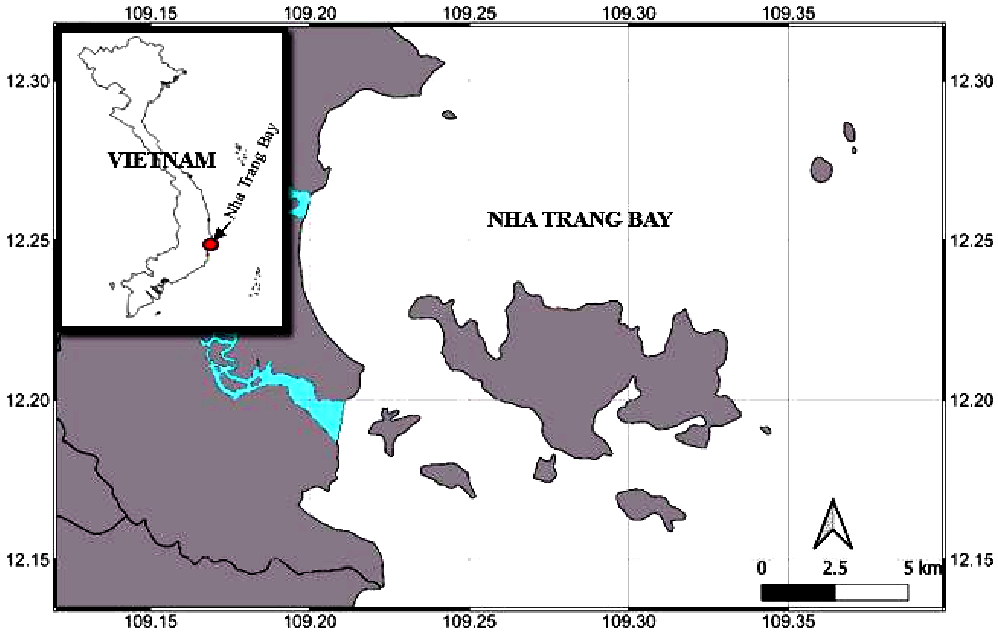

Fig. 1. Map of Nha Trang Bay (the East Sea), operation region of fishing boats from which crabs were sampled

Symbionts were examined by the naked eye, under a stereo microscope Olympus SZ61 (Japan, magnification ×10 to ×40), and under a biological microscope Olympus CX41 (Japan, magnification ×40 to ×100). The entire integument of a crab (carapace, legs, ventral surface, and abdomen) was observed.

Then, the carapace was detached to inspect gill chambers (ceiling, gills, and maxillipeds) and body cavity. The found symbiotic crustaceans were removed from the host by tweezers and placed in dishes with seawater (for external symbionts) or saline solution of 9‰ (for endosymbionts). The abundance of individuals and infesting positions of symbionts were recorded. Fresh symbionts, after being examined and described, were stored in 70% alcohol.

Symbiont identification and state of infestation. Symbiotic crustaceans were identified following the diagnostic characteristics for each sampled group. Pedunculate barnacles were determined based on the body size and characters of calcareous plates on capitular [Aurivillius, 1894; Jeffries et al., 2005; Zevina, 1982] (see Fig. 2A). Size of mantle opening, as well as shape and position of male receptacles in the externa, are taxonomic features used to identify Rhizocephala [Boschma, 1938; Chan, 2004]. Both adults and larvae are often found for entoniscid species. Therefore, for species identification, we used the following characters: oostegite structure, number, and position of ovarian processes for a female; number of pereopod segments for a male; and structure of the 6th pereopods for epicardium larvae [Shields, Earley, 1993; Shiino, 1942].

The state of infestation by symbionts was characterized *via* prevalence and mean intensity. The prevalence of infestation of a particular symbiotic species is the number of hosts infested with that symbiont divided by the number of examined crabs. Intensity represents the number of individuals of a symbiotic species in a single infested crab. The mean intensity is the total number of symbionts found in examined hosts divided by the number of crabs infested with that symbiont [Bush et al., 1997]. The state of infestation by parasitic isopod was determined based on the occurrence of female individuals [Shields, Earley, 1993]. The chi-square test was applied to analyze the prevalence differences between the host groups (sex, reproductive status of females, and size group). The independent sample *t*-test was used to reveal the differences in mean intensity between the host sex and reproductive status of a female crab. To compare mean intensities between three host size groups, the one-way analysis of variance (ANOVA) was applied. All the analysis was carried out using Statistical Product and Service Solutions (SPSS) 24.0 (https://www.ibm.com/support/pages/spss-statistics-240-fix-pack-1) [Li et al., 2014]. Crabs were sampled not in all months of the year, and the number of samples in each month was uneven; accordingly, infestation status by symbionts was not assessed.

RESULTS

Species composition and infesting position. In total, six symbiotic crustacean species were reported from 408 *C. truncata* crabs examined. Four epibiotic barnacles (Scalpellomorpha: Poecilasmatidae) were found: *Octolasmis alata* (Aurivillius, 1894), *O. angulata*, *O. warwicki*, and *D. tridens* (Fig. 2). Two obligate endoparasites, *Sacculina* sp. (Rhizocephala: Sacculinidae) (Fig. 3) and *Cancrion* sp. (Isopoda: Entoniscidae) (Fig. 4), were revealed. *O. alata* and *Cancrion* sp. were the new records both on *C. truncata* and in Vietnam.

Epibiotic barnacles. Epibiotic pedunculate barnacles are common species found on swimming crabs. Sampled *Octolasmis* and *Dianajonesia* specimens were distinguished based on number, size, and shape of calcareous plates (Fig. 2B–E). Details of taxonomic characters of epibiotic species are provided in Table 1.

In terms of infesting positions, symbiotic species occurred on their hosts at different sites. Specifically, *O. warwicki* attaches to the carapace surface, while *O. angulata*, to the ceiling of gill chambers. *O. alata* was found on the proximal surface of gills, and *D. tridens*, on gills and maxillipeds (Fig. 2F–I).

Taxonomy records. *O. angulata* was distinguished from other epibionts by the lack of two terga calcareous plates on the capitular. All three remaining species had five calcareous plates (one carina, two terga, and two scuta). Out of them, *O. warwicki* possessed a fissure in the base of the carina, and its terga were ax-shaped; *O. alata* terga were maple leaf–shaped; and *D. tridens* terga were trapezoidal (Table 1).

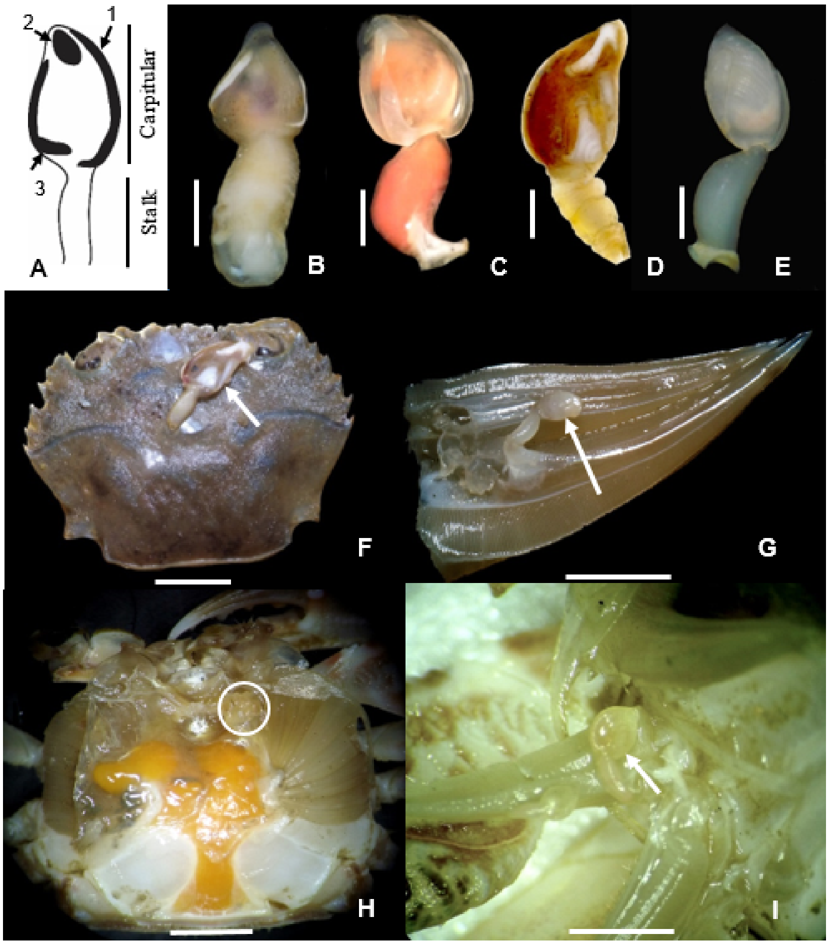

Fig. 2. Epibiotic crustacean species and their infesting positions on the swimming crab *Charybdis truncata* in Nha Trang Bay (Vietnam, the East Sea): A, illustration of calcareous plate position of pedunculate barnacles of the family Poecilasmatidae (1, carina; 2, tergum; 3, scutum); B, *Octolasmis angulata*; C, *Octolasmis alata*; D, *Octolasmis warwicki*; E, *Dianajonesia tridens*; F, *O. warwicki* (an arrow) on the host's carapace; G, *D. tridens* (an arrow) on gills; H, *O. angulata* (a circle) on the ceiling of the gill chamber; I, *O. alata* (an arrow) on gills. Scale bar: B–E, 1 mm; F–I, 5 mm

Table 1. Taxonomic characteristics of epibiotic species on *Charybdis truncata*

Epibiotic species	Number of analyzed individuals	Body size, mm	Number of calcareous plates	Number and shape of carina	Number and shape of scutum	Number and shape of tergum
Octolasmis angulata	10	3.3 ± 0.57	3	1, thin, bar-shaped	2, bar-shaped	absent
Octolasmis alata	3	3.3 ± 0.82	5	1, robust, crescent-shaped	2, robust, two-part, with the first part bar-shaped and the second part L-shaped	2, maple leaf–shaped

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Epibiotic species	Number of analyzed individuals	Body size, mm	Number of calcareous plates	Number and shape of carina	Number and shape of scutum	Number and shape of tergum
Octolasmis warwicki	5	4.6 ± 1.48	5	1, robust, crescent-shaped with a fissure in the base	2, robust, two-part, with the first part bar-shaped and the second part fan-shaped	2, ax-shaped
Dianajonesia tridens	10	3.9 ± 0.90	5	1, robust, crescent-shaped	2, robust, two-part, with the first part bar-shaped and the second part trapezoid	2, wrench-shaped

***Sacculina* sp. Main morphological characters.** The externa (reproductive organ) ellipse-shaped, (5 ± 0.82) mm in length ($n = 2$), with short stalk (see 2 in Fig. 3A); milk-white in color. Mantle opening wide, (0.7 ± 0.08) mm, located on the top of the externa (see 1 in Fig. 3A). The externa of *Sacculina* sp. was observed arising from the gut on the host abdomen (Fig. 3B, C).

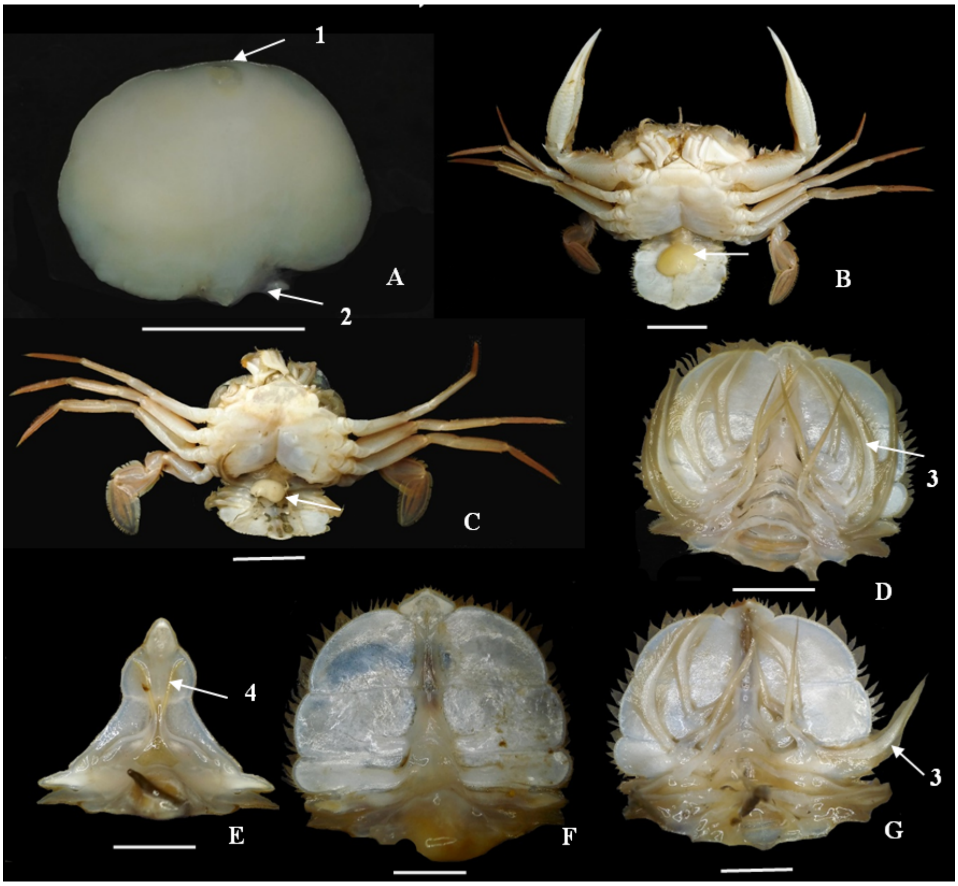

Fig. 3. Parasitic rhizocephalan *Sacculina* sp. infesting *Charybdis truncata* in Khanh Hoa, Vietnam: A, *Sacculina* sp. external view (1, mantle opening; 2, stalk); B, the externa of *Sacculina* sp. (an arrow) on a male crab's abdomen; C, the externa of *Sacculina* sp. (an arrow) on a female crab's abdomen; D, normal female abdomen (3, female pleopod); E, normal male abdomen (4, male pleopod); F, infested male abdomen without pleopods; G, infested female abdomen. Scale bar: A, 3 mm; B, C, 10 mm; D–G, 5 mm

Remark. Parasitic Rhizocephala were found on two individuals only, a 26-mm male and 22.5-mm female. The above characteristics allow determining that this parasite belongs to *Sacculina*. Due to highly reduced morphological characters, microanatomical examination and molecular analysis need to be conducted for precise species identification.

***Cancrion* sp. Main morphological characters.** Total length of a female (cephalon, thorax, and abdomen) was (18.5 ± 1.34) mm (*n* = 4). Body recurved dorsally; first oostegite consists of three parts: ascendant, transverse, and recurrent; the lamellae of pleural segments well developed; the 1st and 2nd pleopods folded, while all the remaining simple; ovaries cream to orange; dorsal and dorsolateral ovarian processes present, while ventral processes absent (Fig. 4C). A male was found on pleopod of a female with five-segmented pereopod (Fig. 4C, D). The epicaridium larvae fully filled in the marsupium of a female (Fig. 4C); the 4th pereopod without spine on merus segment; the 6th pereopod elongated with highly modified dactyl process, and no spine on merus segment (Fig. 4E). *Cancrion* sp. was found to occupy the host hemocoel (Fig. 4A).

Remark. Entoniscidae is a family of parasitic crustaceans with high sexual dimorphism. There are combination characters of females, males, and epicaridium larvae representative for the genus *Cancrion*. To date, eight *Cancrion* species have been described. *Cancrion* sp. shared almost the same taxonomic characters with *Cancrion australiensis* [Shields, Earley, 1993], except for the shape of the first oostegite of a female (complex *vs.* simple), number of segments of male pereopods (5 *vs.* 3), and spine on merus segment of the 4th pereopod of epicaridium larvae (absent *vs.* occurring). These recorded differences suggest that *Cancrion* sp. discovered on the coast of Vietnam may be a new species for science and needs to be described.

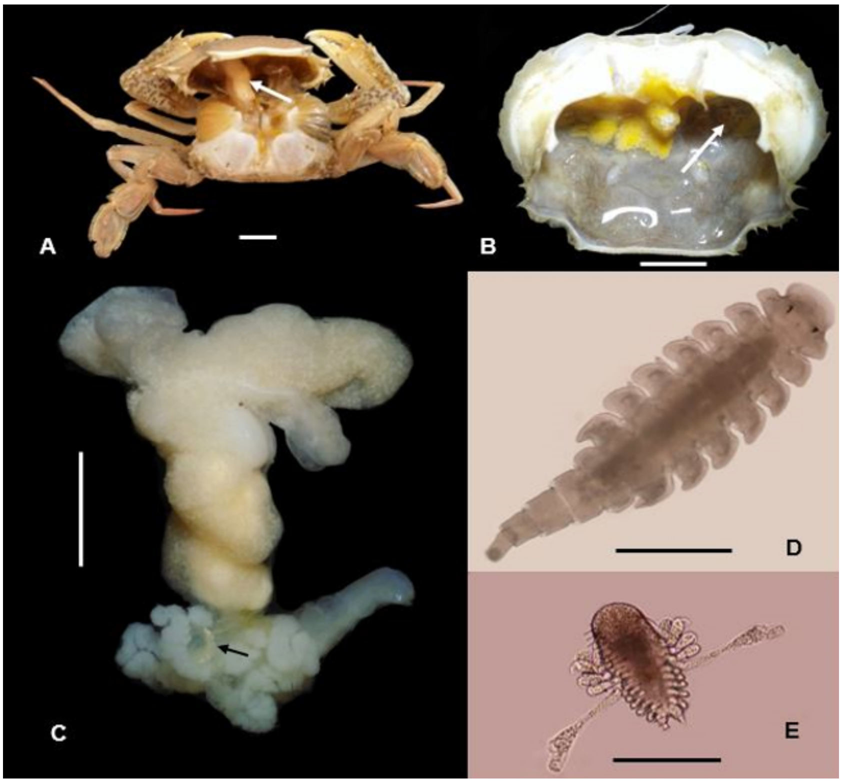

Fig. 4. Parasitic isopod *Cancrion* sp. infesting *Charybdis truncata* in Vietnam (the East Sea): A, *Cancrion* sp. on the host hemocoel (an arrow); B, a gap (an arrow) in the body cavity after *Cancrion* sp. removal; C, female *Cancrion* sp. with a male (an arrow) and a lot of epicaridium larvae in female's marsupium; D, male *Cancrion* sp.; E, epicaridium larva of *Cancrion* sp. Scale bar: A–C, 5 mm; D, 1 mm; E, 50 μm

Infestation status. The overall prevalence of symbionts on the crab hosts was 13% (54 / 408 ind.). The number of infecting symbiont species on hosts ranged one to four. The percentage of hosts infected with one and two species was 10.5% (43 / 408) and 2.2% (5 / 408), respectively, while infection with three and four species occurred in one individual only accounting for 0.2%. At the species level, *O. angulata* and *D. tridens* were found to be infected with the prevalence of 6.9 and 6.6%, respectively; the values were higher than those for other symbionts, 0.5–1.2% (Table 2).

Table 2. Prevalence and mean intensity (± standard deviation) of symbionts found on *Charybdis truncata* in Nha Trang Bay, Vietnam. Values marked with different letters represent significant differences in prevalence between ovigerous and non-ovigerous crabs (a and b) and crabs of various size groups (x, y, and z)

Symbiotic species	Crabs in total ($n = 408$)	Sex of crabs		Reproductive status of female crabs		Size of crabs		
		Male ($n = 205$)	Female ($n = 203$)	Ovigerous ($n = 92$)	Non-ovigerous ($n = 111$)	< 20 mm ($n = 54$)	20–35 mm ($n = 302$)	> 35mm ($n = 52$)
	Prevalence (%) Intensity (ind. *per* host)							
Octolasmis angulata	6.9 1.2 ± 0.54	6.8 1.4 ± 0.72	6.9 1	12^{b} 1	2.7^{a} 1	1.9^{x} 1	5.6^{y} 1.1 ± 0.47	19.2^{z} 1.3 ± 0.64
Octolasmis alata	0.5 1.5 ± 0.50	1.0 1.5 ± 0.5	–	–	–	–	–	3.8 1.5 ± 0.50
Octolasmis warwicki	1.2 1.6 ± 0.80	2.0 1.8 ± 0.83	0.5 1	–	0.9 1	1.9 1	0.7 1	3.8 2.5 ± 0.50
Dianajonesia tridens	6.6 1.6 ± 0.96	5.9 1.4 ± 0.64	7.4 1.7 ± 1.10	10.9 1.6 ± 1.2	4.5 1.8 ± 0.98	–	5.6^{x} 1.6 ± 1.08	19.2^{y} 1.3 ± 0.66
Sacculina sp.	0.5 1	0.5 1	0.5 1	–	0.9 1	–	0.7 1	–
Cancrion sp.	1.1 1	1.5 1	0.5 1	1.1 1	–	–	0.7 1	3.8 1

In terms of the host sex, no significant difference was observed in symbiont prevalence (chi-square test, $P > 0.05$). *O. alata* was found to occur only on a male crab, with low prevalence (1%). As for sampled female crabs (92 ovigerous and 111 non-ovigerous individuals), *O. warwicki* and *Sacculina* sp. were not recorded on ovigerous crabs, while *Cancrion* sp. was not registered on non-ovigerous ones. The significant difference in the prevalence of infestation was noted for *O. angulata* alone (chi-square test, 6.71, $df = 1$, $P = 0.01$) (Table 2).

Data on the state of infestation by symbiotic crustaceans in terms of crab size are provided in Table 2 and Fig. 5. The smallest *C. truncata* bearing symbiotic crustacean was a 19-mm male, and the largest was a 48-mm male. Small crabs (CW < 20 mm) were infested by two epibiotic species, *O. angulata* and *O. warwicki*. *O. alata* was recorded on large crabs (> 35 mm), while *Sacculina* sp. was noted on medium-sized specimens (20–35 mm). Significant differences in the prevalence were revealed for *O. angulata* (chi-square test, 15.28, $df = 1$, $P < 0.01$) and *D. tridens* (chi-square test, 11.60, $df = 1$, $P < 0.01$).

The maximum intensity of infestation by a symbiont species was 5 ind. *per* host (Fig. 5). The mean intensity of epibiotic species was low: the value varied within 1.2–1.6 ind. *per* host, with the highest for *D. tridens* and the lowest for *O. angulata*. Both parasitic species, *Sacculina* sp. and *Cancrion* sp., infected the swimming crab with the intensity of 1 ind. *per* host (Table 2). No significant differences were recorded between all compared host groups (sex, reproductive status of females, and size group).

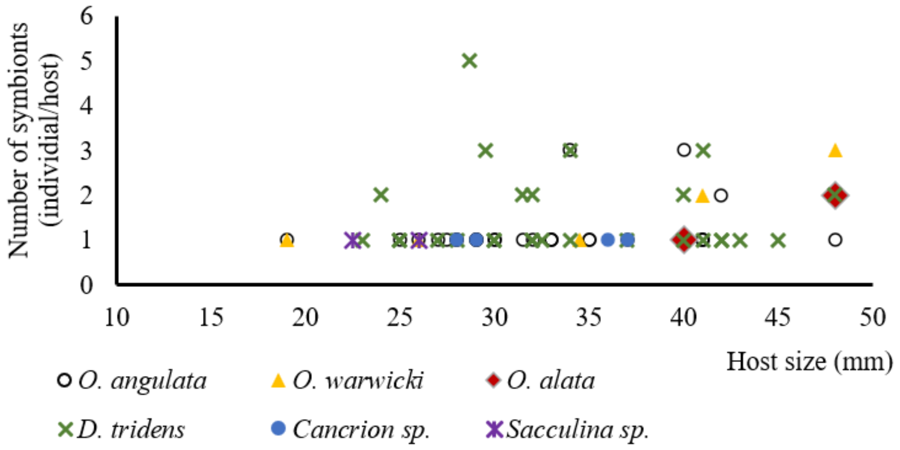

Fig. 5. Intensity of invasion by symbiotic crustaceans in the swimming crab *Charybdis truncata* of different size groups

Morphological modification of infested crabs. In the present study, epibiotic species occurred at low prevalence and intensity. No changes in the host morphology were observed.

As noticed above, *Sacculina* sp. was found on two crab individuals (a male with CW of 26 mm and a female with CW of 22.5 mm). Due to appearance of the externa on a male crab, the abdomen broadened resembling that of an adult female. The abdominal segments the 3rd to 5th distinguished, and the pleopods completely disappeared (Fig. 3F). Compared to those of a normal crab, the abdominal segments the 3rd to 5th fused, and two pleopods were present (Fig. 3E). Unlike the male host, the female one infected with *Sacculina* sp. had no obvious morphological changes (Fig. 3D, G).

Cancrion sp. infected three males of sexually mature size (CW of 28, 36, and 37 mm) and one ovigerous female (CW of 29 mm). All infected specimens performed the swelling on the dorsal surface carapace corresponding to the position of which *Cancrion* sp. occupied the body cavity (Fig. 4B).

DISCUSSION

The swimming crab *C. truncata* is a commonly exploited species in Khanh Hoa province, the south center of Vietnam. However, this species has not attracted much research interest. The present study is the initial survey on the fauna of symbiotic crustaceans of this swimming crab.

Species composition. On 408 *C. truncata* individuals randomly sampled from fishing boats operating in Nha Trang Bay, six symbiotic species were found, *inter alia* four epibiotic and two obligate parasite species. Three out of four registered pedunculate barnacles, *O. angulata*, *O. warwicki*, and *D. tridens*, are common epibionts recorded on *C. truncata* in Hong Kong [Leung, Jones, 2000] and several other crab species in Singapore, Thailand, and Pakistan [Jeffries et al., 1982, 2005; Kumaravel et al., 2009]. In Vietnam, these common barnacles were reported from four different swimming crab species: *P. pelagicus*, *P. sanguinolentus*, *M. haanii*, and *C. feriata* [Dang et al., 2022; Oanh et al., 2018, 2022a, b]. On the contrary, *O. alata* was only noted from gills of an ashore lobster *Palinurus* sp. in the Java Sea, Indonesia [Aurivillius, 1894; Zevina, 1982]. The present study recorded a new host and new geographical area of this rarely occurring barnacle. Moreover, acorn barnacles, *Chelonibia testudinaria* (Linnaeus, 1758) and *Semibalanus* sp., are epibionts occupying swimming crabs [Dang et al., 2022; Hosseini et al., 2023]. These species infestation on *C. truncata* have not recently been noted.

Rhizocephalan barnacles are specialized parasites infecting portunid crabs. Hitherto, there have been more than 50 swimming crab species infected by Rhizocephala, including six species recorded in Vietnam: *P. sanguinolentus*, *C. feriata*, *Charybdis anisodon* (De Haan, 1850), *Thalamita crenata* Rüppell, 1830, *Thalamita prymna* (Herbst, 1803), and *Podophthalmus vigil* (Fabricius, 1798) [Boschma, 1954;

Lützen, ThiDu, 1999; Oanh et al., 2018, 2022a]. As already mentioned, on *C. truncata*, two parasitic barnacle species were reported, *L. nierstraszi* in Japan [Boschma, 1938] and *S. scabra* in Hong Kong [Chan, 2004]. In the present study, Rhizocephala representatives were noted from one male and one female *C. truncata*. The initial morphological analysis suggested that those belong to the genus *Sacculina*. For proper species identification, complex analysis is required.

Isopods of the family Entoniscidae, like Rhizocephala ones, are obligate parasites on anomurans, brachyuran crabs, and caridean shrimps [McDermott et al., 2019; Shiino, 1942]. Forty-one species of this family have been described. Five species, namely *Portunion moniezii* (Giard, 1878), *Priapion fraissei* (Giard & Bonnier, 1888), *Cancrion australiensis* (Shields & Earley, 1993), *Micippion asymmetricus* (Shiino, 1942), and *C. khanhensis*, were reported on swimming crabs *Portunus puber* (Linnaeus, 1767), *Portunus holsatus* (Fabricius, 1798), *Thalamita sima* (H. Milne Edwards, 1834), *C. feriata*, and *M. haanii*, respectively [Giard, 1878; Giard, Bonnier, 1888; Mushtaq et al., 2016; Oanh, Boyko, 2020; Shields, Earley, 1993]. *Cancrion* sp. was possibly a new species to science. It may be the sixth entoniscid species that infected swimming crabs globally and the second one found in Vietnam.

Infestation and modification. Previous studies showed as follows: the number of epibiotic crustacean species *per* host ranges within 1–5; the prevalence and mean intensity by each pedunculate barnacle species varied within 22–100% and 2.5–75.6 ind. *per* host, respectively [Dang et al., 2022; Jeffries et al., 1982, 2005; Kumaravel et al., 2009; Oanh et al., 2018, 2022a, b]. Four epibiotic species infested *C. truncata* with low prevalence, 0.5–6.9%, and mean intensity of 1.2–1.6 ind. *per* host. The host's integument provides protective shelter, and respiratory currents supply epibionts with oxygen and nutrition [Jeffries et al., 1982]. *C. truncata* was smaller than other swimming crab hosts when comparing the body size; it means the space of gill chambers might be smaller, and respiratory currents might be weaker [Arudpragasam, Naylor, 1964]. These could limit the infestation by epibionts on this crab species.

O. angulata was the dominant symbiont on *C. truncata*, with the highest infestation percentage (6.9%). This value is consistent with data of studies on other swimming crab hosts [Oanh et al., 2018, 2022a, b]. The statistical analysis showed that *O. angulata* prevalence on ovigerous crabs (12%) was higher than on non-ovigerous ones (2.7%) and positively correlated with size of hosts. Epibiotic barnacle larvae reach inter-molt crabs, attach to them, and develop until being removed in the next molt of the host [Jeffries et al., 2005]. Generally, the bigger the crab, the longer the period between molts [Josileen, Menon, 2005]. Therefore, the prevalence of infestation by epibiont was usually higher in larger crabs.

The prevalence of infestation by *Sacculina* sp. (0.5%) was remarkably lower than by *Diplothylacus sinensis* (Keppen, 1877) on *P. sanguinolentus* (15%) [Lützen, ThiDu, 1999] and *S. serenei* on *C. feriata* (9.7%) [Oanh et al., 2022a] in the same region. Infection with rhizocephalan species often causes morphological changes in the crab host. Its organs may be affected by developing Rhizocephala: degradation of pleopods and appendages may occur. On the contrary, abdomen and marginal setae which help to protect parasites from external effect can grow more than usual [Waiho et al., 2021]. Morphological modifications were clearly observed in both male and female hosts, as in the case of *Sacculina beauforti* Boschma, 1949 infection on the mud crab *Scylla olivacea* (Herbst, 1796) [Waiho et al., 2017]. On the other hand, *Carcinus maenas* (Linnaeus, 1758) infected by *Sacculina carcini* Thompson, 1836 showed the changes in male crabs, while minor differences occurred in female ones [Kristensen et al., 2012]. In the present study, one infected male crab possessed a broadened abdomen, and pleopods degraded; this could lead to its castration. Despite the low infected rate (2 infected crabs out of > 400 randomly sampled ones), morphological alteration was also observed. Further studies are urgently required to determine the natural prevalence of infection, as well as possible effects on the host populations.

Parasitic isopods of the family Entoniscidae were reported to cause the vertical swelling of the crab carapace. The more profound effect may be the castration of a male and/or female in some cases [Shiino, 1942]. *Cancrion* sp. prevalence (1.1%) on Vietnamese *C. truncata* was low, compared to *C. australiensis* infection on *T. sima* (13.9%) [Shields, Earley, 1993] and *C. khanhensis* infection on *M. haanii* (10.1%) [Oanh, Boyko, 2020]. The morphological modifications which may cause the castration of infected *C. truncata* were not recorded herein. With only four infected crabs examined, it is impossible to fully assess the effects of parasitic isopods on the crab hosts. Further sampling is essential for species identification and examination of morphological and physiological changes/alterations.

Conclusion:

1. Six symbiotic crustacean species, including four epibiotic and two parasitic ones, were detected on the swimming crab *Charybdis truncata* sampled in Nha Trang Bay, Khanh Hoa province, Vietnam, the East Sea.
2. *C. truncata* is a new host record for the pedunculate barnacle *Octolasmis alata* and parasitic isopod *Cancrion* sp.
3. The intensity of symbionts did not depend on the host sex, size, and reproductive status of female crabs.
4. The infection with a rhizocephalan *Sacculina* sp. caused morphological modifications in male swimming crabs that could result in a loss of reproduction capacity of male hosts.

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СТАТУС ЗАРАЖЁННОСТИ СИМБИОТИЧЕСКИМИ РАКООБРАЗНЫМИ КРАБА-ПЛАВУНЦА *CHARYBDIS TRUNCATA* (FABRICIUS, 1798) ИЗ ЗАЛИВА НЯЧАНГ, ВЬЕТНАМ (ВОСТОЧНОЕ МОРЕ)

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Симбиоз — это довольно часто встречающиеся отношения между организмами в морских экосистемах. Среди крабов важного с экономической точки зрения семейства Portunidae широко распространён *Charybdis truncata* (Fabricius, 1798), однако его симбиотические комплексы всё ещё исследованы недостаточно. В январе — августе 2022 г. в заливе Нячанг (провинция Кханьхоа, Вьетнам, Восточное море) собрано 408 особей *C. truncata*. Симбионты классифицированы на основе морфологических характеристик. Для сравнения статуса заражённости симбионтами применён статистический анализ. Обнаружено шесть симбиотических видов, в том числе четыре вида ракообразных-эпибионтов [*Octolasmis angulata* (Aurivillius, 1894), *Octolasmis alata* (Aurivillius, 1894), *Octolasmis warwicki* Gray, 1825 и *Dianajonesia tridens* (Aurivillius, 1894)] и два облигатных паразита, не идентифицированных до вида [*Cancrion* sp. и *Sacculina* sp.]. Из них *O. alata* и *Cancrion* sp. отмечены на *C. truncata* впервые. Общая встречаемость симбионтов на крабах-хозяевах составила 13 %, а количество видов симбионтов, заселяющих хозяев, варьировало от одного до четырёх. *O. angulata* был доминантом, его встречаемость составила 6,9 %. Встречаемость *O. angulata* была значительно выше у самок крабов с кладкой икры, чем у самок без неё. Кроме того, зарегистрирован существенный рост встречаемости *O. angulata* по мере увеличения размеров крабов. Достоверных различий в средней интенсивности симбионтов по полу, репродуктивному статусу самок и размерам крабов-хозяев не выявлено. Зафиксированы и описаны первоначальные морфологические изменения, вызванные заражением краба паразитами *Cancrion* sp. и *Sacculina* sp. Эти результаты предоставляют информацию о состоянии естественного заражения *C. truncata* симбиотическими видами, важную для менеджмента рыболовства и для развития аквакультуры.

Ключевые слова: *Charybdis truncata*, симбионты, эпибионты, облигатные паразиты, залив Нячанг, Вьетнам

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ABOUT THE FINDING OF *LEPIDOCHITONA CINEREA* (LINNAEUS, 1767) IN THE TSEMES BAY (THE BLACK SEA)

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Chitons inhabiting natural hard substrates in the Tsemes Bay pseudolittoral from the central beach of Novorossiysk to the Cape Khako were investigated in summer and winter periods of 2022–2023. For the first time in the Tsemes Bay, a local population of *Lepidochitona cinerea* (Linnaeus, 1767) (Polyplacophora, Tonicellidae) was recorded on substrates of sedimentary origin. It is a rare species, and over the past 70 years, it was found in waters of the North Caucasus only three times. We registered 34 *L. cinerea* specimens with a maximum shell length of 8 mm. The age of the largest individuals (three years) was determined by the annual rings of the apex of the first shell shield. The species is distributed in the upper horizon of the Cape of Love pseudolittoral and is confined to supralittoral baths. A similar biotope, where the chiton was found as well, was discovered in 50 km from the Tsemes Bay. As assumed, the occurrence of the mollusc in the water area is precisely due to the presence of this bionomic type of habitat – supralittoral baths which are not expressed in other study sites of the bay. The aim of the research is to describe *L. cinerea* populations in a previously unspecified biotope for this species and to identify the features of this biotope and its possible effect on the chiton occurrence. Information on the geographic distribution and biotopic confinement of the species was updated. The effect of ecological, hydrochemical, and geomorphological features of the biotope on *L. cinerea* occurrence was considered.

Keywords: *Lepidochitona cinerea*, pseudolittoral, supralittoral baths, Tsemes Bay, Black Sea

Lepidochitona cinerea (Linnaeus, 1767) (Polyplacophora, Tonicellidae) is a chiton with a body length of up to 15 mm. This amphiboreal species is known for the northern Atlantic Ocean from the coast of Norway to the Mediterranean and Marmara seas; in the Pacific Ocean, it was recorded only off the coast of North America [Yakovleva, 1952]. Off the Black Sea shores, *L. cinerea* inhabits rocky and pebble soils, shell rocks, and upper horizons of the sublittoral at depths of down to 30 m [Anistratenko V., Anistratenko O., 2001]. Also, it is registered in sandy biotopes [Sinegub, 2004] and in fouling of breakwaters [Grintsov et al., 2004; Scherbina, 2010]. This species is closely related to organisms of benthic communities: it is a consort of *Rapana venosa* (Valenciennes, 1846) [Bondarev, Revkov, 2017]. Like most chitons, it is a phytophage and feeds mainly on phytoperiphyton [Currie, 1984]. In the Black Sea, the species is distributed off the coast of Crimea and Caucasus (up to Batumi) [Yakovleva, 1952]. However, in the North Caucasus coastal waters, findings of *L. cinerea* are single [Makarov, 2018; Scherbina, 2010]. Mostly, those occur in water areas of the Crimean Peninsula [Bondarev, Revkov, 2017; Khajlenko, 2019; Kovaleva, 2012, 2020; Kovalyova et al., 2016; Losovskaya, 1984;

Makarov, 2018, 2020; Sinegub, 2001; Viter, 2013] and the Kerch Strait [Biryukova et al., 2016; Terentyev, 2008, 2017]. Off the coast of the North Caucasus, this chiton was recorded only three times over the past 70 years; therefore, its finding in the supralittoral biotope is of certain interest.

Despite the wide distribution of *L. cinerea* in various spots of the Black Sea, the species was registered in the biotope of supralittoral baths for the first time. Chitons are well adapted to unfavorable conditions of the littoral zone [Yakovleva, 1952] and are important for many littoral biocenoses regulating periphyton productivity [Aguilera et al., 2013].

In inland seas, such as the Black Sea, due to the absence of tidal phenomena, the littoral is replaced by the pseudolittoral which exists due to sea-level fluctuations [Agarkova-Lyakh, Lyakh, 2022]. According to the classification of O. Kusakin [1961], littoral and supralittoral baths are distinguished as a separate bionomic type of the littoral zone; importantly, their features are the constant presence of water there, weakened effect of the surf, and sharp shifts in salinity and temperature [Butov, 2016]. In accordance with I. Butov [2016], baths are reservoirs formed in the littoral zone and can be completely or partially isolated from the sea. These include potholes, puddles, depressions on rocks, and depressions between blocks and boulders.

The aim of this work is to describe *Lepidochitona cinerea* population in a previously unspecified biotope for this species and to identify features of this biotope and its possible effect on the occurrence of the chiton.

MATERIAL AND METHODS

The study was carried out in the summer and winter of 2022–2023 off the coast of the Tsemes Bay (the Black Sea) (Fig. 1).

Fig. 1. The map of study areas off the Tsemes Bay (the Black Sea): black marks denote water sampling sites; orange mark denotes *Lepidochitona cinerea* finding site

The search for the mollusc was carried out by the route method from the central beach of Novorossiysk to the Cape Khako. Investigated depths varied from 0.3 to 2.0 m. *L. cinerea* was sampled by examining natural hard substrates – inspecting boulders and lifting rocky placers out of water. The age of individuals was estimated analyzing annual layers on the apex of the first shell shield according to the method of A. Yakovleva [1952]. Shell length was measured using the millimeter scale of a YAXUN YX-AK36 binocular (China). Salinity was determined with an RHS-10ATC refractometer for seawater (China) with an accuracy of 1‰. Acidity and alkalinity were established using an EcoDigital digital pH meter (China) with an accuracy of 0.1.

The nomenclature of the species is given in accordance with the current taxonomy (https://www.marinespecies.org/).

Water samples from the Tsemes Bay were studied for the content of heavy metals. Water was sampled in August 2022 from three bay sites, the Cape of Love, Cape Khako, and Sudzhuk Spit, from a 1-m depth (Table 1). In January 2023, water was sampled again from the Cape of Love where *L. cinerea* was found.

Samples were analyzed on a HACH DREL 2800 spectrophotometer (the USA). Each water sample was investigated in three analytical replicates. Content of water-soluble forms of heavy metals (copper, cadmium, cobalt, lead, manganese, and zinc) was determined. The obtained values were compared with the maximum permissible concentrations (hereinafter MPC) for fishery reservoirs [Ob utverzhdenii normativov, 2016].

Table 1. Dates, coordinates, and depth of water sampling sites in the Tsemes Bay (the Black Sea)

Bay site	Date	Coordinates		Depth, m
		N	E	
Cape of Love	21.01.2023	44°42′32.61″	37°47′20.96″	1
Cape of Love	13.08.2022	44°42′32.34″	37°47′20.93″	1
Sudzhuk Spit	13.08.2022	44°41′4.92″	37°48′12.80″	1
Cape Khako	13.08.2022	44°39′1.31″	37°44′18.34″	1

RESULTS AND DISCUSSION

Geomorphological characteristics of the studied biotopes. The Cape of Love is a continuation of the beach of the same name, along which the central embankment of Novorossiysk runs. The beach is about 100 m long and 4–5 m wide. The coast is composed of sedimentary rocks: sandstone, siltstone, quartzite [Modina, Kuznetsov, 2021], and limestone [Dembitskiy et al., 2014]. The geomorphological type of the Cape of Love coast, as well as the entire Tsemes Bay, is abrasion-bay [Dobrovolsky, Zalogin, 1982]. The cape cliff is concreted. The beach turns into a flooded abrasion-accumulative terrace (a bench), 10–12 m wide. There are similar marine terraces on many abrasion coasts, in particular, in areas adjacent to capes [Leontev, 1955]

The bench surface is almost completely surrounded by a ridge of boulders extending along the cape base. As a result of surge sea-level fluctuations, water is retained between the boulders and forms the pseudolittoral with baths of a total area of 618 m^2. There, biogenic residues actively accumulate causing siltation of the substrate. The nature of the soil is mixed; it is composed of two fractions: coarse limestone crushed stone (> 10 cm) and sharp-angled boulders (> 100 cm). In the area of the edge and below the water edge, the bottom sediments of baths are represented by rocky placers with an admixture of silt (Fig. 2).

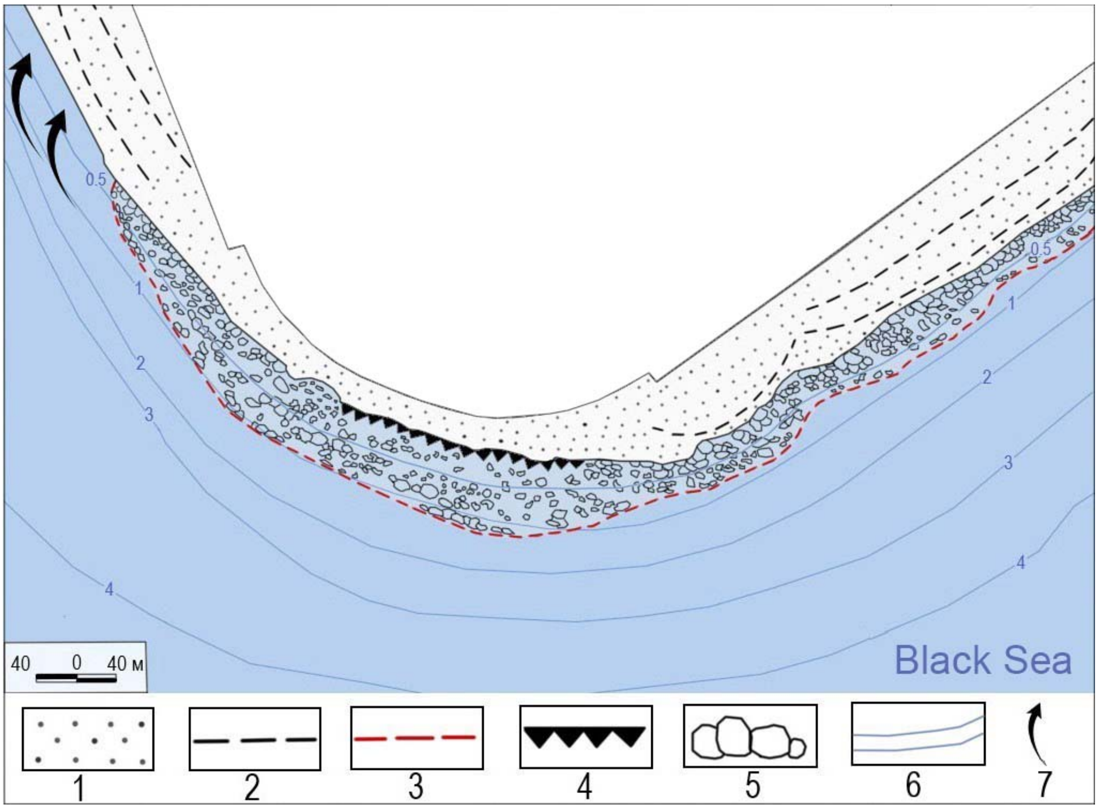

Fig. 2. Geomorphological map of the Cape Love: 1, accumulative form; 2, beach ridges; 3, conditional boundary of supralittoral baths; 4, ancient bench; 5, boulders; 6, isobaths; 7, direction of sediment

A biotope of a similar type is located in the Dzhankhot area. This is the closest site to the Cape of Love, where *L. cinerea* was registered (coordinates according to [GBIF, 2023] are 44°27′28.9″N, 38°9′27.7″E), with an abrasion cliff along the coastline. As a result of ongoing abrasion and denudation, blocky and boulder-blocky piles were formed on a pebble beach [Nikiforov, Shevchenko, 2015] similar to supralittoral baths of the Cape of Love.

In the study sites where the mollusc was not recorded, the mineral composition of the rocky soil did not differ much from that at the Cape of Love [Dembitskiy et al., 2014]. From the central beach of Novorossiysk to the Cape Khako, a noticeable difference in the size and roundness of the soil was observed. Specifically, the Cape Khako and Sudzhuk Spit coasts are represented mainly by large pebbles, while the Cape of Love coast is composed of coarse rubble and boulders.

At the Cape Khako, a dead cliff with exposed bench ridges and an adjacent accumulative terrace are clearly visible. Coastal ridges are composed of coarse pebbles, and there are depressions between them.

The Sudzhuk Spit is composed of sediments. This coastal bar is 10–15 m wide.

General characteristics of the habitat of benthic mollusc communities. The boulders are dominated by the phytocenoses of *Cladophora laetevirens* (Dillwyn) Kützing, 1843 and *Ulva rigida* C. Agardh, 1823 + *Ulva intestinalis* Linnaeus, 1753, where the species diversity of invertebrate communities is chiefly formed by crustaceans and gastropods. The lower layers of phytocenoses are represented by crusts of coralline algae. Earlier, the macrophytobenthos of the Cape of Love was fully studied at the phytocenotic level by V. Teyubova [2010]. According to her observations, the pseudolittoral is formed by five monodominant phytocenoses: *C. laetevirens*, *U. intestinalis*, *Porphyra leucosticta* Thuret, 1863, *Scytosiphon simplicissimus* (Clemente) Cremades 1990, and *Urospora peniciliformis* (Roth) Areschoug, 1866. The mollusc was not found outside surf baths, at a depth of 1.5–2.0 m. There, the bench turns into an underwater slope, and the phytocenoses of *Cystoseira barbata* (Stackhouse) C. Agardh, 1820 + *Cystoseira crinita* Duby, 1830 dominate rounded sedimentary debris.

In the Dzhankhot area, the bottom vegetation of the pseudolittoral is represented by three phytocenoses: *Dilophus fasciola* (Roth) M. A. Howe, 1914 + *Padina pavonica* (Linnaeus) Thivy, 1960, *C. barbata*, and *C. laetevirens*. These algocenoses are characteristic of the pseudolittoral of the Cape Khako and differ from the communities of the supralittoral baths of the Cape of Love.

Hydrological features of the studied biotopes. At the time of sampling, the water temperature reached +28 °C (August) and +9 °C (January). In baths having a constant connection with the sea, the salinity is about 17‰. In supralittoral baths, the value decreases to 16‰. These fluctuations fit into the range of variability of salinity in the Tsemes Bay (16.15–18.57‰) [Kachestvo morskih vod, 2020].

In the pseudolittoral, a slightly alkaline reaction of the environment is registered. The pH value is almost constant and amounts to 7.5–7.6.

Baths as a bionomic type of the littoral (pseudolittoral) are characterized by the lack of surf or its weakening while maintaining most of its aerating effect [Butov, 2016]. Chitons are sensitive to low levels of oxygen dissolved in water [Yakovleva, 1952]. The boulders are located in the constant surf zone and serve as breakwaters protecting baths from wind and wave action. At the same time, the level of water aeration increases which is necessary for chitons.

Characteristics of *Lepidochitona cinerea* population. The mollusc was recorded on sedimentary rocks at a depth of 0.3–1 m. A total of 34 ind. were found (Fig. 3). The average shell length is 6.2 mm, the maximum one is 8.0 mm. The age of *L. cinerea* individuals with a shell length of 6–8 mm is three years. Most often, the chiton was registered on solid substrates covered with microperiphyton and in synusia of crustose coralline algae, which, according to D. Currie [1984], are directly included in the species diet. Two epibionts were noted on *L. cinerea* shells: the polychaete tubeworm *Spirorbis* sp. was recorded on plates of nine chitons and *C. laetevirens* was registered on three individuals.

Fig. 3. *Lepidochitona cinerea* on hard substrates in the Cape of Love pseudolittoral (the Black Sea)

Level of water pollution with heavy metal ions. The results of the study are provided in Table 2. To compare the data obtained with MPC for fishery purposes, we used averaged values for the Cape of Love (for summer and winter periods).

Table 2. Heavy metal content ($mg \cdot L^{-1}$) in waters of the study sites off the Tsemes Bay (the Black Sea)

Heavy metal	Bay site				MPC_f
	Cape of Love		Sudzhuk Spit	Cape Khako	
	August	January			
Cd	0.0049 ± 0.0001*	0.0043 ± 0.0001*	0.0039 ± 0.0001*	0.0046 ± 0.0001*	0.01
Pb	0.011 ± 0.0001*	0.01 ± 0.0001*	0.01 ± 0.0001*	0.011 ± 0.0001*	0.01
Co	0.07 ± 0.0001*	0.07 ± 0.0001*	0.06 ± 0.0001*	0.08 ± 0.0001*	0.005
Mn	0.429 ± 0.061	0.419 ± 0.007	0.402 ± 0.017	0.407 ± 0.021	0.05
Cu	0.069 ± 0.001	0.062 ± 0.005	0.056 ± 0.003	0.063 ± 0.003	0.005
Zn	0.07 ± 0.006	0.06 ± 0.005	0.06 ± 0.005	0.07 ± 0.005	0.05

Note: MPC_f denotes maximum permissible concentration for fishery reservoirs; * indicates instrument error.

Concentration of heavy metal compounds in the study sites of the bay was characterized by little variability. Cadmium content in all water samples did not exceed the standard one, but was close to its upper limit. Copper, manganese, and cobalt occurred in water in fairly high concentrations: the values exceeded MPC by 13.1, 9.0, and 14.0 times, respectively. Concentrations of lead and zinc slightly exceeded MPC, by 1.1 and 1.3 times, respectively.

At the Cape of Love, water was sampled for the second time – to analyze hydrochemical indicators and reveal the correlation between them and occurrence of the mollusc. The values for summer and winter samples differed slightly. During winter sampling, five adult *L. cinerea* specimens were found.

To date, the Cape of Love is the only *L. cinerea* habitat recorded in the Tsemes Bay. Compared to the Cape Khako and Sudzhuk Spit biotopes, where the species was not registered, the Cape of Love biotope is subject to greater pollution.

The obtained increased values of the content of heavy metal ions can be associated with the fact that the Cape of Love is a drainage area for urban wastewater and stormwater [Teyubova, 2010]. Novorossiysk is among key transport centers of the Krasnodar Krai. There, one of the largest ports in the country operates, and it poses an environmental hazard to the bay area [Tekhnogennoe zagryaznenie, 1996]. In 2000 alone, 46 cases of emergency oil spills were recorded in the port [Fashchuk, 2019]. Other sources of pollution are oil platforms, specifically Sheskharis oil terminal [Dinamicheskie processy, 2003], and cement plants (*e. g.*, Novoroscement), machine-building enterprises (Krasny Dvigatel and Molot), and other factories [Mamas et al., 2012].

However, exceeding MPC for copper, manganese, and cobalt in water, apparently, was not a limiting factor for *L. cinerea* development in the Tsemes Bay.

Conclusion:

1. During the study carried out in 2022–2023 in the coastal zone of the Tsemes Bay (in supralittoral baths of the pseudolittoral and among rocky placers and boulders of the Cape of Love), a local population of *Lepidochitona cinerea* (34 ind.) was registered for the first time.
2. Apparently, the complex of biotopic conditions of supralittoral baths provides the formation of optimal trophic and edaphic factors for the development of this chiton.
3. Increased concentrations of several heavy metal ions (copper, manganese, lead, cobalt, and zinc) in the Cape of Love waters seem to have little effect on *L. cinerea*.
4. It is necessary to monitor the state of the environment of the chiton habitat, to search for similar biotopes in other areas of the shore, and to study coastal communities of the Cape of Love.

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О НАХОДКЕ *LEPIDOCHITONA CINEREA* (LINNAEUS, 1767) В ЦЕМЕССКОЙ БУХТЕ (ЧЁРНОЕ МОРЕ)

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Проведены исследования панцирных моллюсков, обитающих на естественных твёрдых субстратах в псевдолиторальной зоне Цемесской бухты от центрального пляжа города Новороссийска до мыса Хако, в летний и зимний периоды 2022–2023 гг. На субстратах осадочного происхождения впервые в Цемесской бухте обнаружена локальная популяция *Lepidochitona cinerea* (Linnaeus, 1767) (Polyplacophora, Tonicellidae). Это редкий вид, и за последние 70 лет он был встречен в водах Северного Кавказа лишь трижды. Найдено 34 экз. *L. cinerea* с максимальной длиной раковины 8 мм. Возраст наиболее крупных особей (три года) определён по годовым кольцам апекса первого щитка раковины. Вид распространён в верхнем горизонте псевдолиторали мыса Любви и приурочен к супралиторальным ваннам. Схожий биотоп, в котором также встречен панцирный моллюск, был обнаружен в 50 км от Цемесской бухты. Предположено, что присутствие *L. cinerea* в акватории обусловлено именно наличием данного биономического типа местообитаний — супралиторальных ванн, которые не выражены на других изученных участках бухты. Цель исследования — описать популяции *L. cinerea* в ранее не указанном для этого вида биотопе, а также выявить особенности данного биотопа и его возможного влияния на присутствие панцирного моллюска. Пополнены сведения о географическом распространении и биотопической приуроченности вида. Рассмотрено влияние экологических, гидрохимических и геоморфологических особенностей биотопа на присутствие *L. cinerea*.

Ключевые слова: *Lepidochitona cinerea*, псевдолитораль, супралиторальные ванны, Цемесская бухта, Чёрное море

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SPATIAL VARIABILITY OF THERMOHALINE PARAMETERS AND PHYTOPLANKTON COMPOSITION OF WEST ANTARCTICA IN SUMMER SEASON

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Spatial variability of thermohaline characteristics (temperature, salinity, and dissolved oxygen) and phytoplankton structure (composition, abundance, and biomass) of the Southern Ocean during austral summer were investigated. New data were obtained for a little-studied area of Antarctica: on transects along the eastern border of the Ross Sea along W156° (T1, length of 35 km, 6 stations), near the Russkaya station (T2, 87 km, 13 stations), at the single station (Roosevelt Island area, Bay of Whales, Ross Sea), and in the Bransfield Strait (T3, 118 km, 11 stations). The relevance of the analysis of this area is due to its location on the border of the shelf and continental slope with different parameters of temperature and water structure. Low salinity and different temperature characteristics were revealed in surface waters of T1 and T2: lower values for T2 (−1.5 °C) and higher for T1 (0 °C). For the Bransfield Strait waters (T3), typical data on salinity and oxygen content were obtained against the backdrop of slightly increased temperature (up to +2 °C). For the single station, relatively fresh, cold, and oxygenated water of the upper 100-meter layer was recorded, and low temperature values of the bottom area, with high mineralization, were registered. In the phytoplankton composition of the study area, 48 taxa of microalgae from 5 divisions were identified (Bacillariophyta, 38; Dinophyta, Cyanoprokaryota, and Chrysophyta, 3 taxa each; and Haptophyta, 1) and 1 macrophyte taxon (Rhodophyta). The maximum similarity in the species composition of phytoplankton (on average, 43%) was typical for shelf stations in different areas. The total abundance of phytoplankton in the study area of the Southern Ocean ranged within 4.3–264.0 thousand cells·L^{-1}, and biomass, 0.07–1.18 mg·L^{-1}. The main contributors to quantitative characteristics of phytoplankton throughout the study water area were diatoms, mainly representatives of the genus *Fragilariopsis* Hustedt, confined to the shelf and coastal areas. At a distance and in the open sea of transects T1 and T2 deeper than 50 m and in surface waters of transect T3, *Phaeocystis antarctica* Karsten (Haptophyta) developed in mass. For T2, the dependence of phytoplankton abundance on water temperature and salinity was revealed.

Keywords: West Antarctica, Bransfield Strait, shelf, spatial variability, thermohaline parameters, phytoplankton

The Southern Ocean (hereinafter SO) is one of the most highly productive in the world and plays a key role in global cycling of matter [Iida, Odate, 2014; Petrou et al., 2016; Varela et al., 2002]. In this area, temperatures have increased by more than 1 °C in recent decades [Mangoni et al., 2017]. In waters off the Antarctic Peninsula, this temperature trend is most pronounced, and it contributes to the destruction of ice shelves, receding of the ice barrier, exposure of new coastal habitats, alterations in physicochemical properties of the water column, and transformation of marine food webs [Mendes et al., 2012; Rozema et al., 2017].

Approximately 60% of the SO surface is free from ice throughout the year. In these waters, the factors limiting primary production are irradiance and availability of iron and phosphorus. The productivity of water masses of the remaining 40% of the SO surface (~ 19 million km^2) is highly dependent on seasonal ice cover and regulated by the timing of its receding, providing 5–30% of annual primary production [Biggs et al., 2019; Moreau et al., 2020; Petrou et al., 2016]. In its turn, the zonal latitudinal distribution of ice affects habitats of phytoplankton and zooplankton [Iida, Odate, 2014]. In nutrient-rich coastal waters of Antarctica, 350 algal species have been identified in phytoplankton, and cell density during blooms reaches 10^8 *per* 1 L [Deppeler, Davidson, 2017].

A significant amount of data has been accumulated on phytoplankton spatial structure, seasonal distribution, and biodiversity in the SO waters to the west of the Antarctic Peninsula (the South Shetland Islands, Bransfield Strait, and Bellingshausen Sea). The fairly complete investigation of the western Ross Sea and episodic one of the Amundsen Sea are due to the occurrence of stable polynyas in summer and nearby location of year-round Antarctic research stations. Phytoplankton of the water area from Cape Colbeck (Edward VII Peninsula, W158°) to Cape Dart (western Amundsen Sea, W126°) between the Ross and Amundsen seas, in the Russkaya station area, remains poorly studied. There, our research on transects T1 and T2 was carried out. This site is of certain interest from an oceanographic point of view: it is located in the area delimiting parts of Antarctica which differ in temperature and water structure (on the shelf and continental slope). Also, it is affected by oceanic and atmospheric circulations [Antipov et al., 2020].

The work is devoted to studying the spatial variability of thermohaline parameters, composition, and distribution of West Antarctica phytoplankton during the summer season in the Pacific sector of the Southern Ocean from Bay of Whales (Roosevelt Island area) to Cape Burks (Russkaya station area) and in the Bransfield Strait.

MATERIAL AND METHODS

Oceanographic and algological observations were carried out during the 65th Russian Antarctic Expedition on the RV "Akademik Tryoshnikov" on 06.02.2020–10.03.2020. Along the RV route, we investigated little-studied waters of West Antarctica:

- station 3 in the southeastern Ross Sea (Bay of Whales), 12 km north of Roosevelt Island (78°41.13′S, 163°42.58′W, 06.02.2020);
- transect 1 (T1), 35 km long, covering 6 stations, along the eastern border of the Ross Sea at Cape Colbeck of Edward VII Peninsula (along W156°, 07.02.2020);
- transect 2 (T2), 87 km long, covering 13 stations, 450 km to the east of T1 (Russkaya station area), 36 km from the front of the Hull Glacier shelf, crossing almost the entire shelf which is relatively narrow there (24.02.2020).

In the Bransfield Strait (area of the Antarctic Bellingshausen station, 09.03.2020–10.03.2020), transect 3 (T3), 118 km long, covering 11 stations, was analyzed. A scheme of the study area is shown in Fig. 1.

Deep-sea oceanographic observations were carried out at 34 stations with a SBE 19plus profiler (Sea-Bird Scientific) equipped with a frame for installing bathometers. It allows obtaining continuous data on temperature, salinity, and pressure profiles down to a depth of 6,000 m. Based on fluctuations in temperature and salinity, for all stations (from 5–8 horizons), right after bathometer raising, dissolved oxygen was determined iodometrically, by the Winkler titration [Shishkina, 1974].

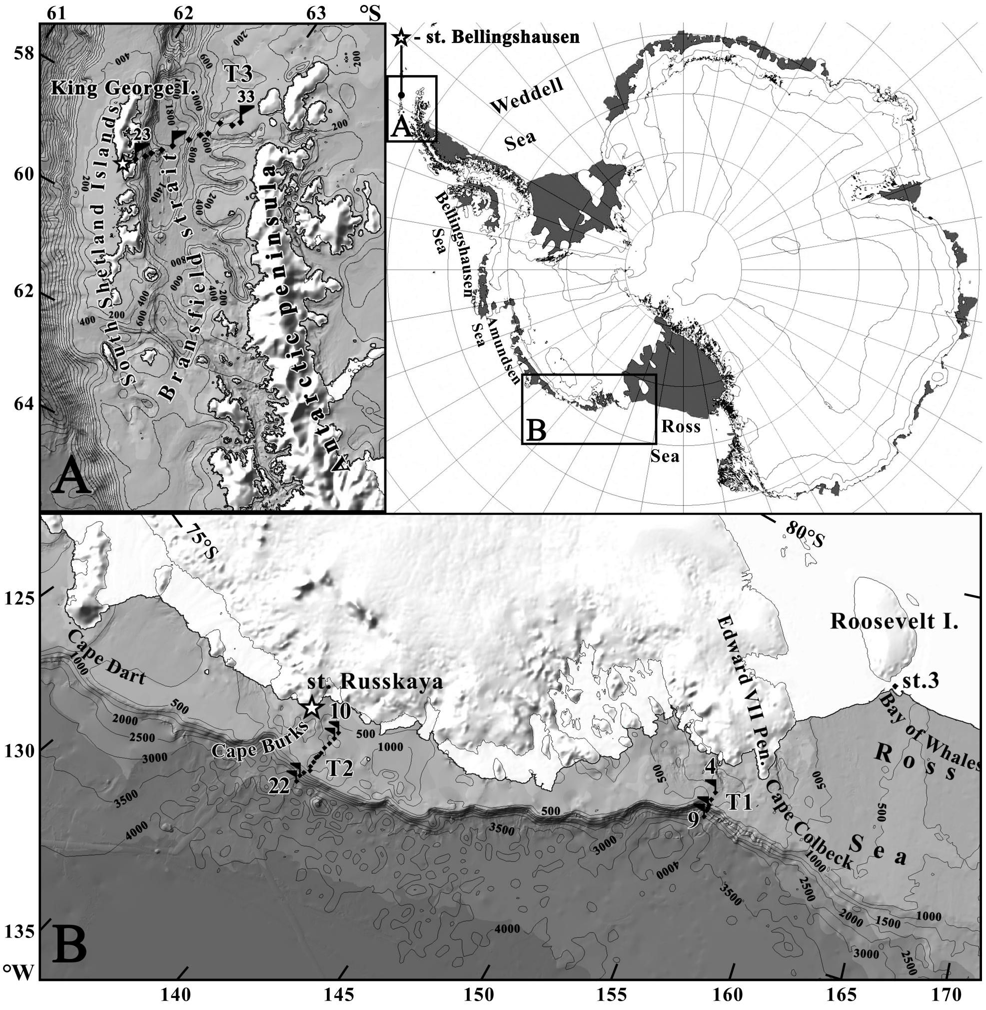

Fig. 1. Map of the study area in the Southern Ocean. A, transect 3; B, transects 1 and 2 and station 3

Water samples of 1–1.5 L in volume were concentrated using a reverse filtration funnel with Vladipor membrane filters (pore diameter of 3.0 μm) and fixed with formaldehyde to a final concentration of 1–2%. At each station, phytoplankton was sampled by the bathometric method (subsurface layer, 10 m, 50 m, and 100 m; for sta. 10, 11, and 22, 200 m as well). Data on phytoplankton from depths exceeding 100 m were not considered in the work due to their fragmentation and insignificant occurrence of algal cells. Samples were processed in a 0.01-mL Nageotte chamber. Biomass was determined by the counting–volumetric method. Permanent preparations of diatoms were made by cold combustion with a mixture of sulfuric acid and potassium chromate, followed by filling with Naphrax – highly refractive resin [Metodika izucheniya biogeotsenozov, 1975]. Samples were analyzed under an Axiostar Plus light microscope (Carl Zeiss, Germany) at a magnification of ×400 and ×1,000 (oil immersion). Species with the abundance of ≥ 10% were considered dominant ones. The taxonomic affiliation of algae of various groups was established using keys and papers on the SO planktonic flora [Carmelo, 1997; Cefarelli et al., 2010; Gerasimiuk, 2008; Gogorev, 2010, 2013; Gogorev, Samsonov, 2016; Hoppenrath et al., 2009]. The similarity in the species composition of phytoplankton was assessed by the Sørensen–Czekanowski coefficient [Magurran, 1992]. The obtained data were processed in the programs SBE Data Processing [Sea-Bird Scientific, 2023] and Surfer 11 [2023]. The statistical package R for MS Office Excel was applied as well [Novakovskiy, 2016].

RESULTS

Hydrological features. At the single station 3, the layer down to a depth of 100 m was characterized by occurrence of the warmest (−1.19 °C), least saline (32.8 PSU), and most oxygen-saturated (7.7 mL·L^{-1}) water masses. In deeper horizons, salinity rose (up to 34.24 PSU), while temperature and oxygen content dropped (to −1.93 °C and 6.39 mL·L^{-1}, respectively) (Fig. 2).

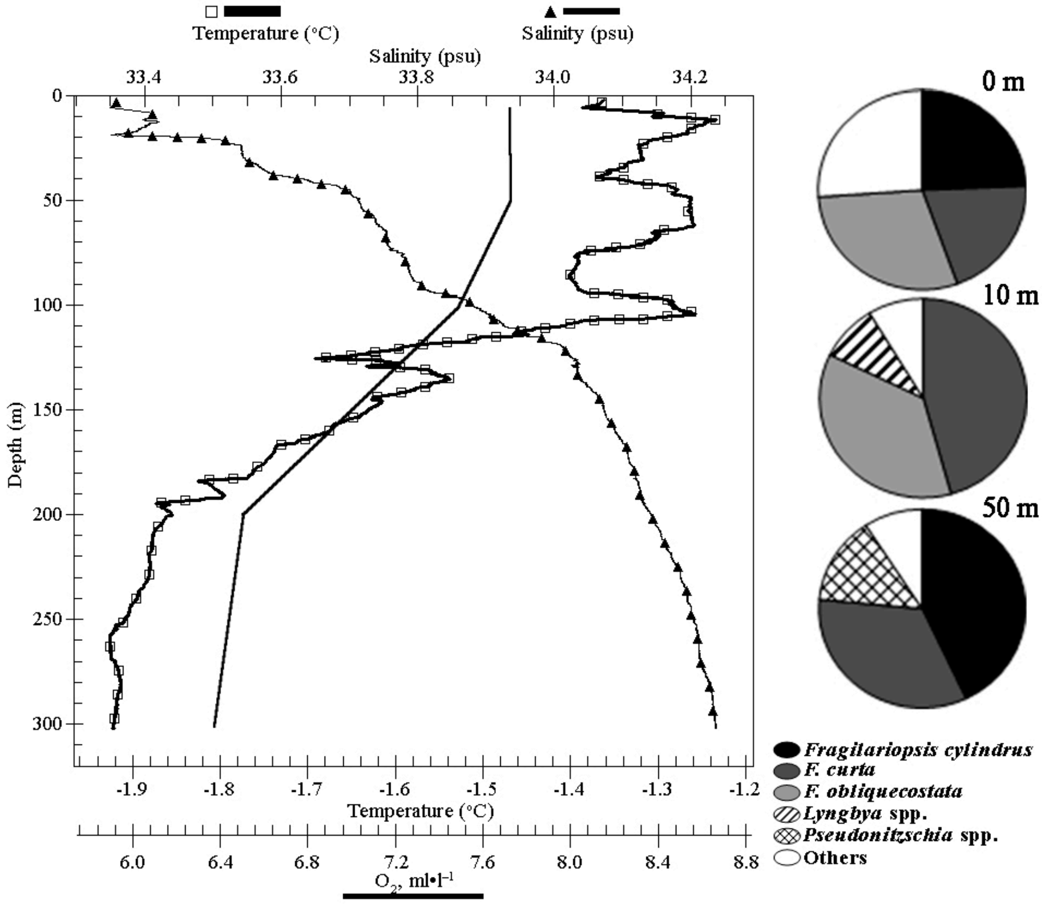

Fig. 2. Vertical profile of temperature, salinity, and oxygen concentration at station 3 and phytoplankton taxonomic composition (in the upper 50-m layer), Roosevelt Island area

Water masses of the upper 500-m layer on transect T1 had the minimum temperature down to −1.8 °C and salinity of 34 PSU and lower. At the same time, this layer was more oxygenated (> 6 mL·L^{-1}) than the layer of Circumpolar Deep Water (4 mL·L^{-1}). At a depth of down to 50 m, water temperature was about 0 °C, and oxygen content was high, 7.4–7.7 mL·L^{-1}. Significant depth of mixing and, at the same time, low salinity of the upper horizon allow explaining the greater thickness of the layer by the effect of continuous strong winds characteristic of the area (Fig. 3).

On transect T2, bottom topography was more complex than on transect T1 (see Fig. 3). There, both local depressions (with a depth of > 1,000 m) at the beginning of the transect and relatively shallow spots (a depth of < 400 m) at mid-transect were recorded. This area, from Cape Colbeck at the eastern edge of the Ross Sea to Cape Burks, has a relatively narrow shelf and the steepest continental slope in the western sector of Antarctica [Antipov et al., 2020].

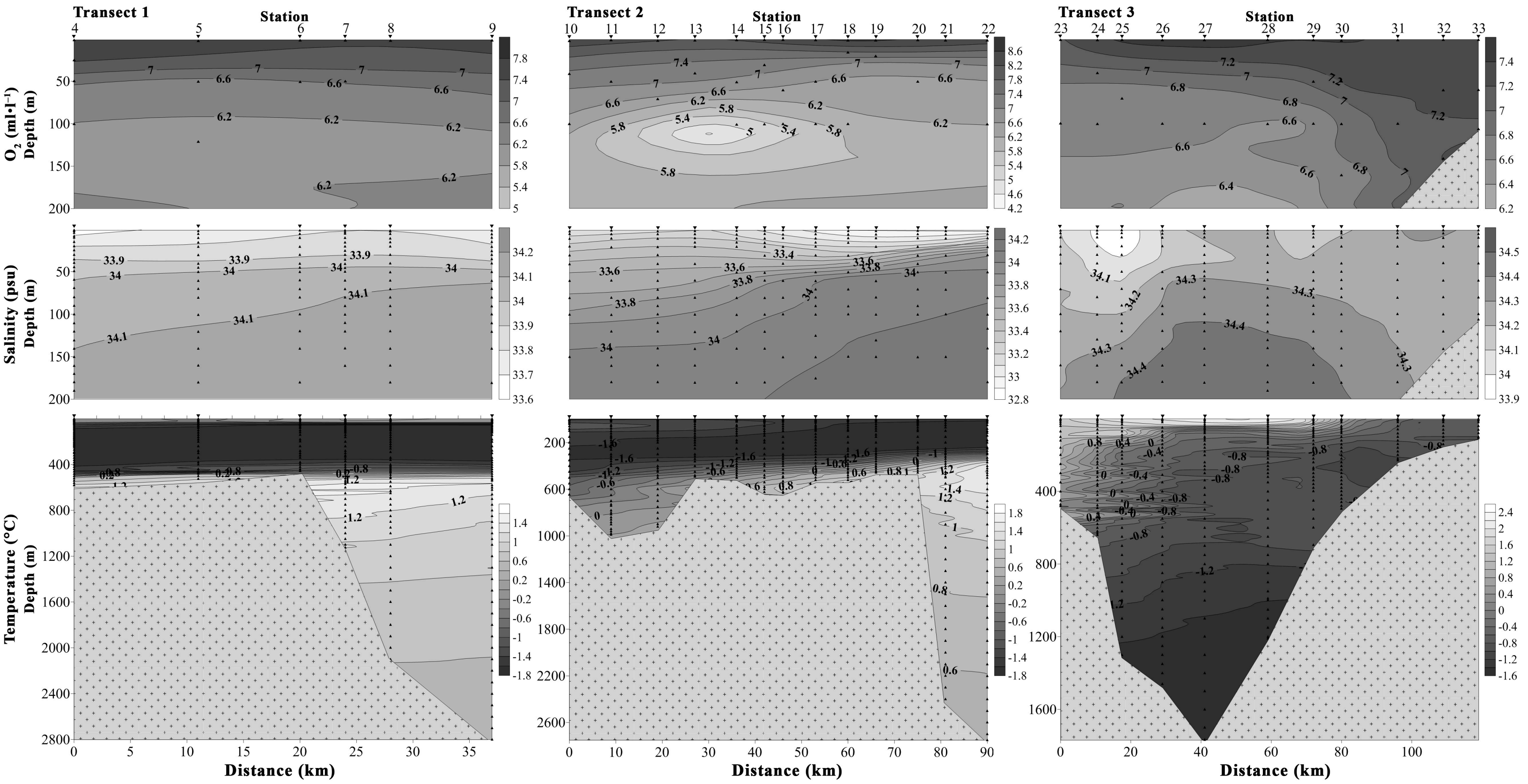

Fig. 3. Salinity (PSU), temperature (°C), and oxygen content (mL·L^{-1}) along transects 1, 2, and 3. Oxygen content and salinity are given down to depth of 200 m

On transect T2, a cold (down to −1.79 °C) layer with oxygen content of 5–7 mL·L^{-1} reached a depth of 400–500 m. The layer of water mass down to 50 m was warmer, especially in the transect gate, with high content of dissolved oxygen (8.0–8.7 mL·L^{-1}) and the lowest mineralization (32.8 PSU). The maximum temperature (+1.56 °C) and salinity (34.7 PSU) on the transect were observed at a distance of about 20 km from the shelf edge, at a depth of 450 m, and against the backdrop of a relatively low oxygen content, about 4.4 mL·L^{-1}.

The SO waters at the northern tip of the Antarctic Peninsula (T3, Bransfield Strait) were characterized by an uneven distribution of thermohaline parameters. Importantly, this area has a large number of islands and complex bottom topography (Figs 1, 3).

At a depth of down to 100 m, water masses with temperature above 0 °C were distributed almost up to the southern coast of the strait. On the northern transect, warm (0…+2 °C), less saline, and less oxygen-saturated waters prevailed; these waters originated from the southwest – from the Bellingshausen Sea. Above-zero temperatures persisted in the water column down to 500 m over a distance of 15 km from the transect gate. Within the range of 300–500 m, oxygen saturation was of 4.8–5.5 mL·L^{-1}, and salinity was of 34.6 PSU. Cold waters of the Weddell Sea dominated the area adjacent to the Antarctic Peninsula. In general, salinity in the surface layer was of 34.0–34.5 PSU, and oxygen content was of 7.2–7.5 mL·L^{-1}; interestingly, this layer extended to a greater depth in the southern Bransfield Strait (Fig. 3). The maximum depth on the transect reached 1,770 m; waters were saline (34.55 PSU) and relatively oxygenated (6.5–6.7 mL·L^{-1}); and the temperature was of −1.5 °C.

Spatial distribution of phytoplankton. Phytoplankton of the study SO areas covered 49 algal species and intraspecific taxa. Bacillariophyta division included 38 representatives; out of them, the most diverse genus was *Fragilariopsis* Hustedt: *Fragilariopsis curta* (Van Heurck) Hustedt, *F. cylindrus* (Grunow ex Cleve) Helmcke et Krieger, *F. ritscheri* Hustedt, *F. obliquecostata* (Van Heurck) Heiden, *F. rhombica* (O'Meara) Hustedt, *F. pseudonana* (Hasle) Hasle, *F. separanda* Hustedt, and *F. kerguelensis* (O'Meara) Hustedt. Plankton included Dinophyta, Cyanoprokaryota, and Chrysophyta – 3 representatives each, as well as Haptophyta and, presumably, Rhodophyta – 1 taxon each. At stations of transects T1 and T2 and at the single station 3, the structure was generally typical for coastal areas of Antarctica: we recorded species of the genera *Fragilariopsis*, *Pseudo-nitzschia* H. Peragallo, *Azpeitia* M. Peragallo, *Actinocyclus* Ehrenberg, *Thalassiosira* Cleve, *Chaetoceros* Ehrenberg, *Corethron* Castracane, *Porosira* Jørgensen, and *Eucampia* Ehrenberg. The maximum species richness was typical for surface horizons against the backdrop of the predominance of diatoms (Table 1). On T1, the diversity of phytoplankton communities decreased from the shelf (sta. 4) to the edge (sta. 7) and the deep-sea area (sta. 9). On T2, species richness increased from a southern station in 35 km from the front of the Hull Glacier shelf (sta. 10) to a deep-sea one (sta. 22). There, the most even phytoplankton composition was recorded (similarity of 58% according to the Sørensen–Czekanowski coefficient). On T3, 17 algal taxa were identified; out of them, 12 were diatoms. The minimum diversity of diatoms (3 species each) was observed at sta. 23 and 27. At all stations of this transect, fragments of macrophyte thalli were noted in the water column, presumably of the genus *Helminthora* J. Agardh (Rhodophyta). Similarity of phytoplankton across transect stations was very low, 17%.

For similar stations in terms of location relative to the shelf, on different transects, similarity in the species composition of phytoplankton was maximum on the shelf, (43 ± 7) %, with a range of 23–64%. Between stations of the edge area, similarity was lower, (33 ± 5) %, with a range of 30–50%. At deep-sea stations, it was minimum, (20 ± 1) %, with a range of 19–22 % (Fig. 4). A comparison of phytoplankton composition within transects showed its similarity at deep-sea stations and in the edge area at the level of 30%; at shelf and deep-sea stations, 31% (up to 56%); and at shelf stations and in the edge area, 38% (up to 72%).

Table 1. Phytoplankton composition at different stations of transects 1–3 and at the single station

Area	Station number	Species number				
		Bacillariophyta	Haptophyta	Rhodophyta	Other	In total
Transect 1	4	18	1	–	2	21
	7	7	1	–	3	11
	9	6	–	–	3	9
	4–9	29	1	–	5	35
Transect 2	10	16	–	–	–	16
	11	14	–	–	1	15
	21	20	–	–	2	22
	22	19	1	–	–	20
	10–22	30	1	–	3	34
Transect 3	23	3	1	1	3	8
	27	3	1	1	–	5
	33	7	–	1	2	10
	23–33	12	1	1	3	17
Single station	3	11	–	–	1	12
Total		38	1	1	9	49

Phytoplankton abundance in the study SO areas ranged within 4.3–264.0 thousand cells·L^{-1}, and biomass varied within 0.07–1.18 mg·L^{-1}. The main contributors were diatoms. Particularly high abundance and biomass values were revealed at sta. 21 (T2) in less saline surface layers (Fig. 5). An increase in cell abundance at a depth of 50 m was registered at sta. 7 (T1) at the edge of layers with different temperatures and at sta. 11 (T2).

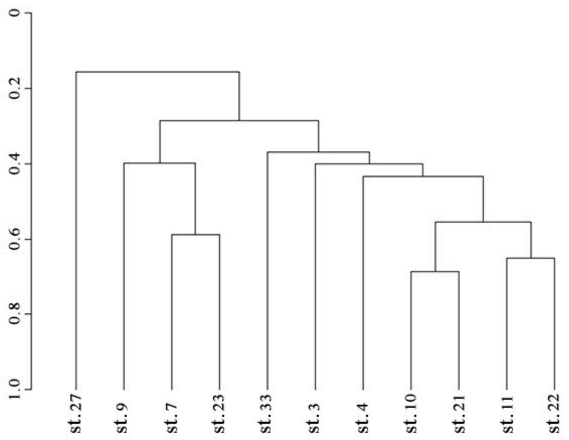

Fig. 4. Similarity tree of algal species composition at the stations of the study area

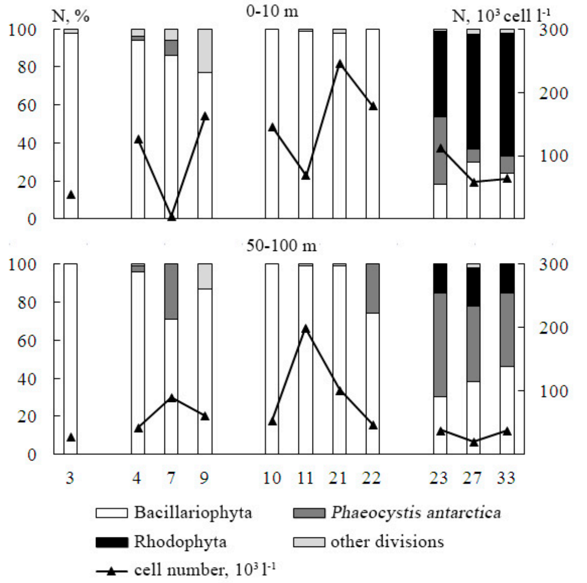

Fig. 5. Bacillariophyta, Rhodophyta, and Haptophyta contribution (in %) in total abundance of phytoplankton at the stations of the study area in 0–10-m and 50–100-m layers

At sta. 3, the main contributors to phytoplankton abundance (39 thousand cells·L^{-1}) and biomass (0.10 mg·L^{-1}) were diatoms of the genus *Fragilariopsis* (74% of the total abundance). In the surface layer, the maximum values were noted; to the horizon of 50 m, those decreased by 1.5 times.

On T1, mean values of phytoplankton abundance were of (107.4 ± 27.7) thousand cells·L^{-1}, and biomass was of (0.55 ± 0.26) mg·L^{-1}. In addition to *Fragilariopsis* representatives, abundant development was characteristic of *Corethron pennatum* (Grunow) Ostenfeld, *Thalassiosira lentiginosa* (Janisch) Fryxell, and *Thalassiosira antarctica* Comber. In the surface water layer, the distribution of the phytoplankton community formed by diatoms and *Phaeocystis antarctica* Karsten (Haptophyta) had a sharp drop in the total abundance of algae at mid-transect above the slope at sta. 7 and an increase at sta. 9. At mid-transect (sta. 7), at 50-m depth, there was a peak in the development of microalgae (Fig. 5). There, 29% of the abundance were formed by *Ph. antarctica*.

In T2 water area, phytoplankton abundance varied 100 to 250 thousand cells·L^{-1}, and biomass varied 0.44 to 1.18 mg·L^{-1}. The maximum values were recorded above the slope (sta. 21), in the surface layer. The entire transect was characterized by the massive development of *Fragilariopsis* and *Thalassiosira* representatives, *Pseudo-nitzschia seriata* (Cleve) H. Peragallo, and *Thalassionema synedriforme* (Greville) Hasle. *Ph. antarctica* was registered only at the final station of the transect (sta. 22) at a depth of > 50 m; it formed 25% of phytoplankton abundance there.

On T3, the mean phytoplankton abundance was (73.1 ± 16.4) thousand cells·L^{-1}, and biomass was (0.09 ± 0.01) mg·L^{-1}. The highest values of quantitative development of microalgae were noted on the shelf on the northern transect (sta. 23), where the main contributors for the surface layer were Rhodophyta representatives (45%) and *Ph. antarctica* (36%). At a depth of 50 m, the latter one formed 55% of the abundance, while diatoms (*Fragilariopsis*, *Thalassiosira*, and *Azpeitia* representatives) formed about 30%. Interestingly, the proportion of red algae at this depth rapidly dropped (see Fig. 5).

Analysis of the relationship between the degree of phytoplankton development and hydrological and hydrochemical parameters of the SO water masses made it possible to identify negative correlations of algae cell density on water temperature and salinity (Table 2). The correlation coefficients are significant for the relationship between phytoplankton abundance and water temperature on T2 for surface horizons and on T1 and T3 for the water column down to 50 m.

Table 2. Correlation coefficients of thermohaline characteristics and phytoplankton abundance in the study area

Phytoplankton abundance	Temperature, °C	O_2, mg·dm^{-3}	Salinity, mg·dm^{-3}
Transect 1, surface	−0.34	0.12	−0.98*
Transect 1, mean over horizons	−0.97*	0.37	−0.92*
Transect 2, surface	−0.90*	0.25	−0.89*
Transect 2, mean over horizons	−0.43	0.81	−0.71*
Transect 3, surface	0.42	−0.65	−0.91*
Transect 3, mean over horizons	−0.89*	0.41	−0.87*

Note: * denotes results significant at $p \leq 0.05$.

For all transects, both for the surface layer and the entire water column, a noticeable correlation of phytoplankton abundance and salinity was revealed, with the coefficient for different stations varying from −0.63 to −0.98. Correlation coefficients between algae abundance and concentration of dissolved oxygen were not significant. Also, correlation analysis showed a natural rise in species richness at stations of T2 with lower salinity (0.79; $p \leq 0.05$).

DISCUSSION

In recent years, there is a noticeable increase in volume of data on hydrological parameters and phytoplankton structure in the Amundsen Sea [Bett et al., 2020; Jenkins et al., 2018; Mattson et al., 2012; Schofield et al., 2015; The Amundsen Sea Expedition, 2018] and in the Ross Sea, especially in its western area [Andreoli et al., 1995; Fonda et al., 2005; Guo et al., 2021; Kaufman et al., 2017; Mangoni et al., 2017; Mosby, 2013; Porter et al., 2019; Shields, 2007].

Desalinated water with a lower temperature and higher oxygen content, compared to those according to literature data (in summer, salinity usually varies between 34.0 and 34.8 PSU, and temperature varies between −1 and +1 °C), was recorded at sta. 3, in the immediate vicinity to the ice shelf [Mattson et al., 2012; Porter et al., 2019; Shields, 2007]. For the bottom area of the Ross Sea shelf (sta. 3), remote both from trenches and inflows of Circumpolar Deep Water, low temperatures are quite typical, in contrast to low mineralization [Porter et al., 2019].

The formation of supercooled dense Antarctic shelf water between the Ross and Amundsen seas (T1 and T2) was not registered according to the data of the 59th (2014) and 65th Russian Antarctic Expeditions [Antipov et al., 2020]. In T1 area, the shelf receives salty but relatively warm Circumpolar Deep Water carried out by the Antarctic Circumpolar Current. The low salinity of T1 and T2 areas recorded during the 65th expedition most likely indicates long-term wind mixing and seems to be associated with intense ice melting under the effect of modified Circumpolar Deep Water [Antipov et al., 2020; Schofield et al., 2015]. Also, the supply of these water masses can serve as an additional source of nutrients and contribute to massive bloom observed in polynyas of the Amundsen Sea [Schofield et al., 2015]. We identified the highest values of abundance and biomass for phytoplankton precisely on transects T1 and T2.

For T1 and T2, a distinctive feature is the temperature of the 50-m layer – a relatively high one on T1 (up to 0 °C) and lower one on T2 (about −1.5 °C). Notably, T2 is located closer to the Amundsen Sea, and works were carried out much later on this transect. Apparently, the above-mentioned differences in thermohaline indicators for T1 and T2 are driven by the cyclicity of hydrological parameters, as shown in a number of works on the western sector of Antarctica [Guo et al., 2021; Jenkins et al., 2018; The Amundsen Sea Expedition, 2018].

The obtained values of hydrological parameters for the most studied spot in the vicinity of the Antarctic Peninsula and the South Shetland Islands (T3) are consistent with the data of other researchers [Cefarelli et al., 2011; Dotto et al., 2021; García et al., 2002; Garibotti et al., 2003; Hofmann et al., 1996; Mendes et al., 2012; Rozema et al., 2017; Varela et al., 2002]. The effect of the Antarctic Circumpolar Current and influx of the Bellingshausen Sea water ensured above-zero temperatures down to a 400-m depth over a distance of 30 km from the transect gate. A layer up to 200 m thick, with the temperature of 0…+2 °C, covered almost the entire Bransfield Strait. Data analysis for a wide area from Elephant Island to Palmer Archipelago, with the Bransfield Strait included, also showed that the warmest waters are traditionally concentrated off the South Shetland Islands. The most saline water masses are located both along the South Shetland Islands and off the Antarctic Peninsula, probably, depending on seasonal changes [García et al., 2002; Garibotti et al., 2003]. On T3, the temperature maximum was observed at a depth of down to 200 m; this fact was described earlier as well [Hofmann et al., 1996]. The Weddell Sea coastal waters (east of the Antarctic Peninsula) are saltier and denser than warmer waters around the South Shetland Islands. In the southern area of T3, we registered maximum oxygen content near the northern Antarctic Peninsula and Gerlache Strait, and it was determined by the effect of the Weddell Sea water masses [Dotto et al., 2021].

In high latitudes, the phytoplankton community was formed chiefly by Bacillariophyta and Haptophyta representatives which is typical for the SO [Gogorev, 2010, 2013; Gogorev, Samsonov, 2016; Kuzmenko, 2004; Nissen, Vogt, 2021]. Shifts in phytoplankton species composition and quantitative characteristics we recorded can be associated with different sampling time (summer for T1 and T2; early autumn for T3) and features of transect location, as well as with the penetration of waters of various origin into the study areas, *e. g.*, Circumpolar Deep Water or glacier meltwater.

The values of phytoplankton abundance and biomass in the study SO areas do not exceed those provided in literature, 1×10^3 to 1×10^6 cells·L^{-1} [Andreoli et al., 1995; Cefarelli et al., 2011; Fonda et al., 2005; Kang, Fryxell, 1993]. However, the summer research season is characterized by a narrower range of values, with phytoplankton abundance usually higher in the southern summer, 1×10^6 to 1×10^8 cells·L^{-1} [Cefarelli et al., 2011; Deppeler, Davidson, 2017]. Diatoms had the highest abundance in phytoplankton throughout the study SO areas. *Fragilariopsis* representatives are generally typical for the SO waters [Carmelo, 1997; Cefarelli et al., 2010; Kennedy et al., 2019] and develop in mass both in the water column and in ice, near the ice edge or off the coast. Their widespread distribution and development were noted in our survey as well. At some stations of transects at a depth of > 50 m, high abundance of *Ph. antarctica* was recorded (15–39% of the total). According to previous investigations, the intensive vegetation of this species results from its development in mixed and iron-poor open waters of the SO [Mendes et al., 2012; Petrou et al., 2016; Varela et al., 2002], with high irradiance and low salinity mostly in surface layers [Goffart et al., 2000; Schofield et al., 2015]. Information on development of diatoms and haptophytes, both spatial and temporal, is widely presented in literature [Kang, Fryxell, 1993; Kaufman et al., 2017; Mangoni et al., 2017; Mosby, 2013; Nissen, Vogt, 2021]. In particular, there are extensive data on the central Ross Sea [Andreoli et al., 1995; Goffart et al., 2000; Mosby, 2013].

To date, the limited information on the algal flora on transects T1 and T2 does not allow us to identify the key factors affecting phytoplankton species composition and quantitative characteristics. Apparently, the most significant ones are seasonal successions associated with the availability of sunlight, ice melting, and nutrient balance. A relationship was revealed between the abundance of algae and water temperature on T2 in the surface layer (0–10 m) and with the salinity which may be a consequence of alterations in ice conditions and insolation.

The unevenness of hydrological parameters of the water column on T3 results from the water influx from the Bellingshausen and Weddell seas, effect of the Antarctic Circumpolar Current and Circumpolar Deep Water, and occurrence of seasonal changes. Obviously, this unevenness determines the minimum similarity in phytoplankton composition between stations. Specifically, with distance from islands and relatively warm water masses with high salinity, phytoplankton abundance decreased on T3 by more than 2 times. Similar changes in phytoplankton development on this transect and its low species richness were noted in other works [Garibotti et al., 2003; Kuzmenko, 2004; Mendes et al., 2012; Varela et al., 2002]. Our results differ from those available in literature: we registered fragments of red algae thalli occurring in mass in the surface layer on T3. This fact requires further study.

Conclusion. Oceanographic data, including results of hydrophysical research and analysis of the structure of phytoplankton communities, were obtained during the 65th Russian Antarctic Expedition on the RV "Akademik Tryoshnikov" in the Pacific sector of Southern Ocean. These data supplemented the material of the program of regular observations of the little-studied region from Cape Colbeck to Russkaya station and in the Bransfield Strait.

At the single station in the southeastern Ross Sea, relatively fresh, cold, and oxygenated waters were recorded in the upper 100-m layer. Low temperature values, along with higher salinity, were registered in the bottom area.

In surface waters of transects T1 and T2, low salinity and different temperature characteristics were revealed: lower values on T2 (−1.5 °C) and higher on T1 (0 °C). For the Bransfield Strait water (transect T3), typical data on salinity and oxygen content were obtained, against the backdrop of slightly increased temperature values (up to +2 °C).

In the phytoplankton community of the study areas, 48 taxa of microalgae from 5 divisions were identified (Bacillariophyta, 38; Dinophyta, Cyanoprokaryota, and Chrysophyta, 3 taxa each; and Haptophyta, 1), as well as 1 macrophyte taxon, Rhodophyta. The spatial distribution of phytoplankton was characterized by significant patchiness; the Southern Ocean areas differed in species composition and contribution of certain species and groups to the total abundance and biomass of plankton. The similarity of phytoplankton species composition was maximum for shelf stations, on average 43%. The main contributors to the quantitative characteristics of phytoplankton throughout the study water area were diatoms, chiefly *Fragilariopsis* representatives confined to the shelf and coastal areas. At a distance or in the open sea, the proportion of diatoms decreased, and the species *Phaeocystis antarctica* developed in mass. A correlation was revealed between the abundance of algae, water temperature on transect T2, and salinity in the 0–50-m layer of water masses.

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ПРОСТРАНСТВЕННАЯ ИЗМЕНЧИВОСТЬ ТЕРМОХАЛИННЫХ ПАРАМЕТРОВ И СОСТАВА ФИТОПЛАНКТОНА ЗАПАДНОЙ АНТАРКТИКИ В ЛЕТНИЙ ПЕРИОД

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В результате исследования пространственной изменчивости термохалинных характеристик (температура, солёность и растворённый кислород) и структуры фитопланктона (состав, численность и биомасса) Южного океана в летний период получены новые данные для малоизученного региона Антарктики — разрезов вдоль восточной границы моря Росса по меридиану 156° з. д. (P1, протяжённость 35 км, 6 станций) и вблизи станции Русская (P2, 87 км, 13 станций), а также одиночной станции (район острова Рузвельт) и пролива Брансфилд (P3, 118 км, 11 станций). Актуальность анализа этого региона обусловлена его расположением на границе шельфа и материкового склона с разными параметрами температуры и структуры вод. В поверхностных водах P1 и P2 выявлены низкая солёность и различные температурные характеристики — более низкие значения на P2 (−1,5 °C) и более высокие на P1 (0 °C). Для вод пролива Брансфилд (P3) получены типичные данные по солёности и содержанию кислорода, но несколько повышенные значения температуры (до +2 °C). На одиночной станции зарегистрирована относительно пресная, холодная и насыщенная кислородом вода верхнего 100-метрового слоя и отмечены низкие значения температуры придонной части, а также высокая минерализация. В составе фитопланктона исследованных районов определены 48 таксонов микроводорослей из 5 отделов (Bacillariophyta — 38, Dinophyta, Cyanoprokaryota и Chrysophyta — по 3, Haptophyta — 1) и 1 таксон макрофитов (Rhodophyta). Максимальное сходство видового состава фитопланктона (в среднем 43 %) характерно для шельфовых станций разных районов. Общая численность фитопланктона изученной акватории Южного океана колебалась в пределах 4,3–264,0 тыс. кл.·л$^{-1}$, биомасса — 0,07–1,18 мг·л$^{-1}$. Основной вклад в количественные характеристики фитопланктона во всей исследованной акватории вносили диатомовые водоросли, преимущественно представители рода *Fragilariopsis* Hustedt, приуроченные к шельфу и прибрежным районам. При удалении от берега и в открытом море на разрезах P1 и P2 глубже 50 м и в поверхностных водах на разрезе P3 отмечено массовое развитие вида *Phaeocystis antarctica* Karsten (Haptophyta). Для P2 выявлена зависимость численности фитопланктона от температуры и солёности воды.

Ключевые слова: Западная Антарктика, пролив Брансфилд, шельф, пространственная изменчивость, термохалинные параметры, фитопланктон

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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].

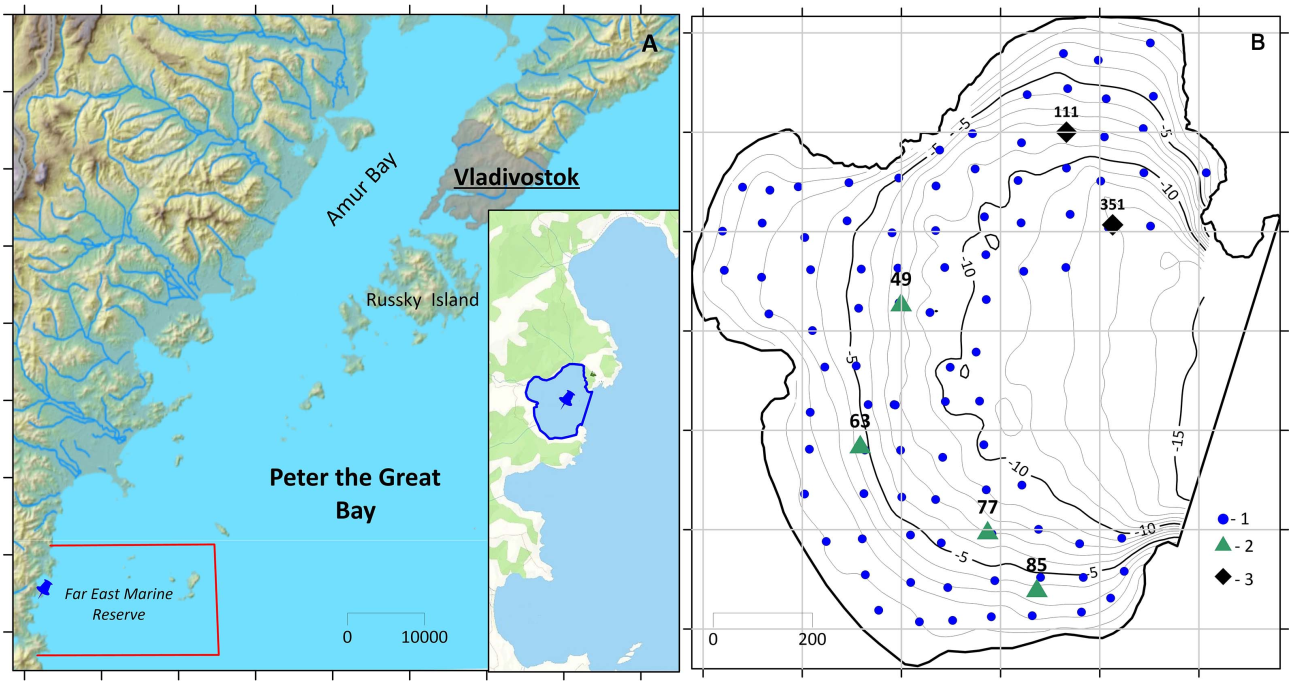

Fig. 1. A, location of the study area within Peter the Great Bay, the Sea of Japan, with mainland coast of the Far East Marine Reserve on the inset; B, mapping points (1), sampling points in the seagrass-covered areas (2), and sampling points on bare sands (3) (depth distribution is shown by isobaths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

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

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) $\mathrm{g\,C \cdot m^{-2}}$. However, in biotopes with 100% seagrass coverage, carbon stock increased to 253 $\mathrm{g\,C \cdot m^{-2}}$, 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.

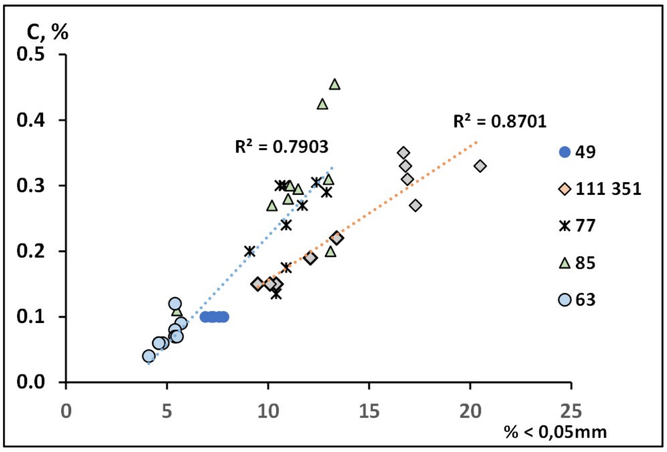

Fig. 2. Dependence of C_{org} concentration on the fraction of silt particles (< 0.05 mm) in bottom sediments of the Srednyaya Bight from the seagrass habitats (sta. 49, 63, 77, and 85) and bare sands (sta. 111 and 351)

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].

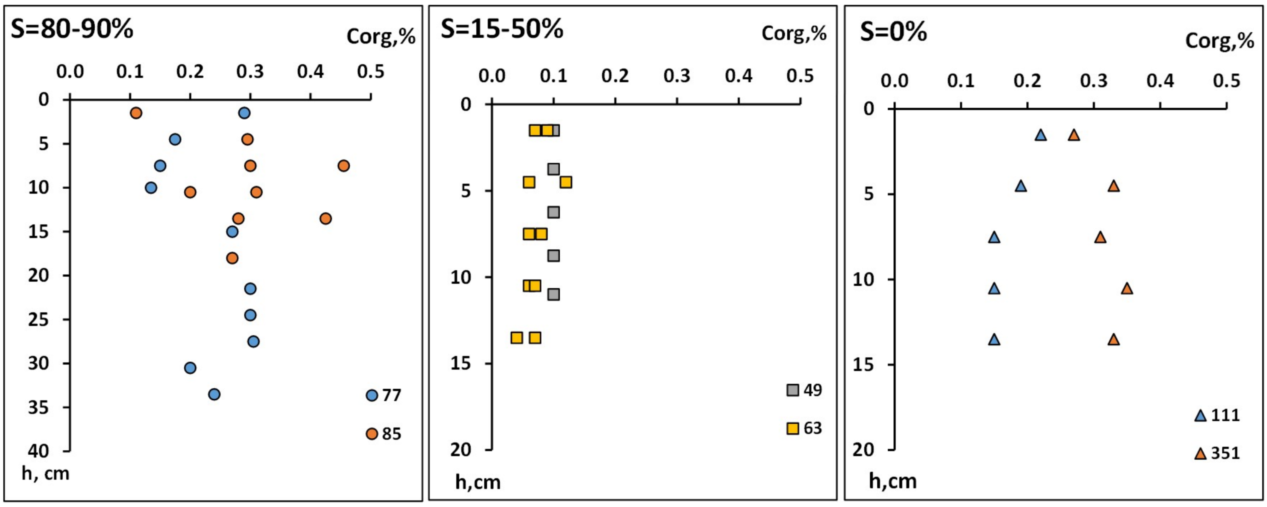

Fig. 3. Changes in C_{org} concentration in the bottom sediment cores of the Srednyaya Bight with different projective seagrass coverage (S)

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).

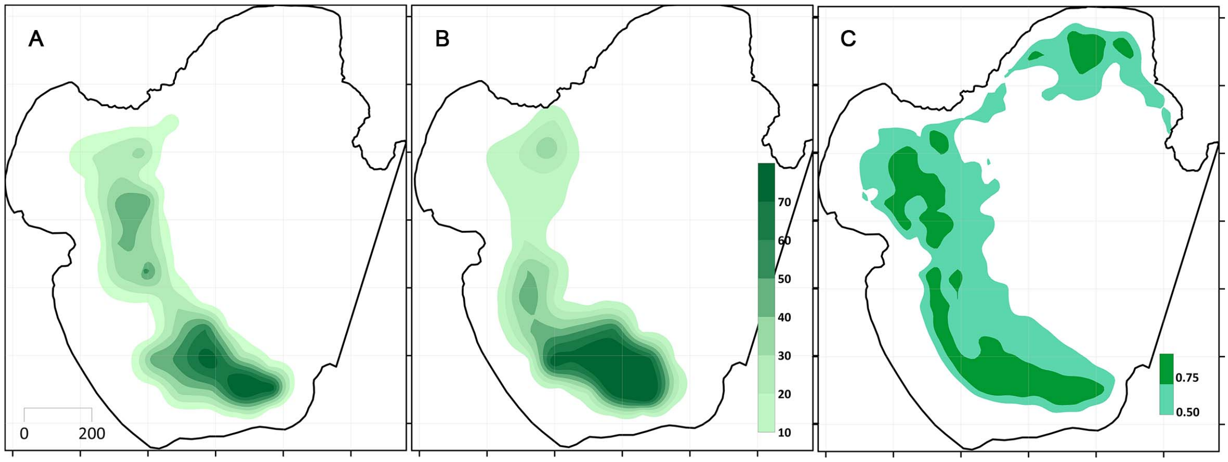

Fig. 4. Distribution of the seagrass meadows in the Srednyaya Bight according to field underwater mapping data in April (A) and July (B) (the color scale indicates projective coverage area) and according to the results of modeling the potential area of *Zostera marina* occurrence (C) (the color scale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

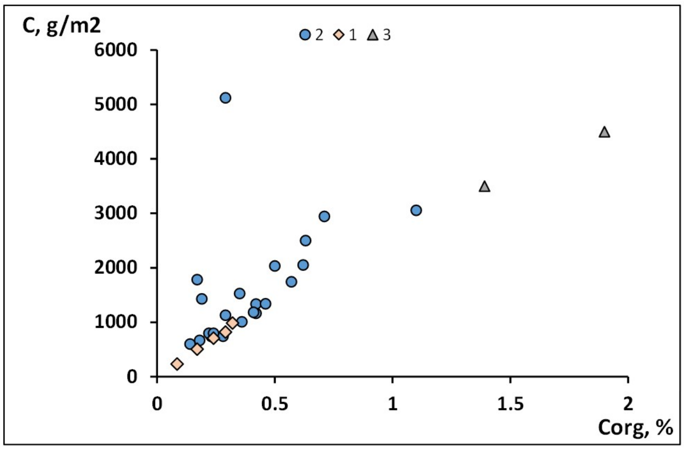

Fig. 5. Dependence of C_{org} stock in the upper 25-cm layer of coastal sediments of the Srednyaya Bight (1), northwestern coast of North America [Prentice et al., 2020] (2), and semi-enclosed inlets of Peter the Great Bay [Tischenko et al., 2022] (3)

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) $\mathrm{g\,C{\cdot}m^{-2}}$; in biotopes with 100% coverage, the value rose to 253 $\mathrm{g\,C{\cdot}m^{-2}}$.
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. Бóльшая 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) $г\,C{\cdot}м^{-2}$, в биотопах со 100%-ным покрытием он повышался до 253 $г\,C{\cdot}м^{-2}$. 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

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CHRONICLE AND INFORMATION

IN MEMORIAM: VLADISLAV KHLEBOVICH, THE OUTSTANDING RUSSIAN HYDROBIOLOGIST

Three days before his 92nd birthday, on 23 February, 2024, Vladislav Khlebovich passed away. He was an outstanding Russian hydrobiologist, zoologist, physiologist, and evolutionist. He was experimenter and theorist, thoughtful citizen, teacher, colleague, friend, interesting companion, and amazingly talented man.

The combination of logic and intuition, exhaustive clarity of formulations, and deepest knowledge and erudition allowed him to create verbal models equal in their rigor to mathematical ones. These were the concepts of critical salinity (as a key factor affecting biological processes, as a marker of the transition from the potassium era to the sodium one, and as an aspect of acclimation) and the role of hereditary triads in speciation.

In our memory, V. Khlebovich remains as a talented organizer – a director of the White Sea Biological Station of the Zoological Institute of the Academy of Sciences of the Soviet Union and a head of expeditions to the Arctic, Far East, and Chernobyl.

Without seeming to make any special efforts, Vladislav Khlebovich trained a galaxy of hydrobiologists studying brackish waters. His students and followers, now scattered throughout research centers of our country and abroad, constitute a real scientific school, albeit unofficial.

His contribution to scientific education is invaluable (and has not yet been clearly appreciated) – namely to *education*, since the modern term *popular science* is completely inapplicable to him. To understand this, you only need to read his fascinating works: “Not yet domestic” (1987), “Agrozoology” (1991), “Individual as a quantum of life” (2015), “Animals and us” (2015), and “On the origin and fate of civilizations” (2019). Being purely scientific publications, nevertheless, those are quite understandable to a wide range of readers.

Essays have been written about him, but he spoke best about himself in the book “Pictures from the life of a zoologist. Memories.” We are all incredibly lucky that we met him and had the opportunity to communicate with him! The memory of Vladislav Khlebovich will always be with us, as well as a feeling of great gratitude.

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ПАМЯТИ ВЫДАЮЩЕГОСЯ РОССИЙСКОГО ГИДРОБИОЛОГА ВЛАДИСЛАВА ВИЛЬГЕЛЬМОВИЧА ХЛЕБОВИЧА

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