

# Macrophytobenthos of the Caspian Sea: Diversity, Distribution, and Productivity

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**Abstract**—In the Russian sector of the northern and middle Caspian Sea, 36 species of macroalgae have been identified. The green and red algae from the mesosaprobic group are dominant. An increase in the number of green algae species is revealed. The distribution of macroalgae is inhomogeneous. It is confined to the solid substrate and epiphyton. The biomass of seaweeds reaches 1.5 kg/m<sup>2</sup>. Climate change has little influence on the appearance of new species in the northern Caspian Sea, but new invaders can appear in the Middle and Southern Caspian. The distribution of aquatic and coastal hygrophytic vegetation shows considerable spatial dynamics due to fluctuations in the level and salinity of the Caspian Sea. The biomass of aquatic vegetation varies in a wide range from 0.5 to 10.0 kg/m<sup>2</sup>. Spatially detailed mathematical models adequately reflect the changes in key species of aquatic plants in space and time. It is shown that expansion of the zone of the seagrass *Zostera noltii* to shallow water areas is occurring at present, as well as shrinkage of the range of the dominant littoral aquatic plant *Phragmites australis*.

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## INTRODUCTION

The macrophytobenthos plays an important role in the nearshore ecosystem of the Caspian Sea. Macroalgae and seagrasses are photosynthetic organisms, which provide a constant input of organic matter for heterotrophic organisms and form a vegetative canopy: a biotope for invertebrates and phytophilic fish species. The dynamics of aquatic vegetation largely determines changes in benthic communities, their distribution, and reserves. Of special interest is the study of phytobenthos for the northern and middle Caspian Sea, where variability of the water environment and sea level is maximal [26]. In recent years, communities of seagrasses and algae have been considered indicators of long-term climatic and anthropogenic changes [39].

Studies of the Caspian Sea flora began with the expeditions of P.-S. Palass, K.M. Baer, and S.G. Gmelin and date back more than 200 years. The first integrated surveys of phytobenthos in the Caspian Sea were performed by Volkov [5] during the N.P. Knipovich's famous voyages in 1913–1917. During the large expeditions of the 1930s–1960s, the species composition of macroalgae and seagrasses was determined; major areas of aquatic vegetation were revealed, and commercial stocks were estimated; the biology and ecology of some species were studied [3, 8, 10–13, 18, 27]. These studies were conducted during the lowering of the Caspian Sea level. The subsequent sea level rise in the late 1970s and related

changes in the hydrological and hydrochemical parameters of the aquatic environment, reduction in water salinity, and intensified eutrophication resulted in significant reorganization of the northern Caspian ecosystem in the 1990s [21–23, 26]. The transformation of the Caspian ecosystem affected the phytobenthos: the spatial distribution of algae and seagrasses changed, as well as the species composition and production parameters in some water areas; resources decreased [4, 6, 7]. In the early 2000s, all Caspian countries began active development of oil and gas fields on the Caspian shelf; large-capacity shipping intensified [23]. During this period, the ctenophore *Mnemiopsis leidyi* penetrated and developed intensively, which significantly affected the life of the marine ecosystem [21–23, 26]. Despite increasing interest in Caspian Sea problems, the current state of aquatic vegetation is poorly understood.

The aim of this work was to assess the current diversity, productivity, and spatial distribution of macrophytobenthos in the Caspian Sea.

## MATERIALS AND METHODS

Materials for the study included the collections of the author and those of members of the Azov Branch of the Murmansk Marine Biological Institute, Russian Academy of Sciences, and the Southern Scientific Center, Russian Academy of Sciences, in the northern

and middle Caspian Sea during the period from 2004 to 2011 (Fig. 1), as well as available literature data [6, 7, 15, 25, 31–36].

Phytoplankton samples on loose grounds were taken from on board the R/V *Deneb* using a Van Veen grab sampler (capture area 0.13 m<sup>2</sup>); in the coastal area, small frames (0.025 m<sup>2</sup>) and a scraper were used. One to two samples were taken at each station. The total numbers of samples were 117 for quantitative analysis and 258 for qualitative analysis.

Mathematical simulation methods combined with GIS technologies were used to analyze the long-term vegetation dynamics. Two spatially detailed mathematical models were proposed for the dynamics of aquatic (*Potamogeton pectinatus* and *Zostera noltii*) and coastal (*Phragmites australis*) vegetation. The methodology of the mathematical experiments is reported in detail in [2].

The structure of the mathematical model includes the following variables: salinity, depth, biogenic elements, water temperature, and ground type. From the calculation results, a distribution map was compiled for the biomass of specific vegetation species depending on the variables used. Data on the dynamics of climatic factors during the period from 1930 to 2010 were prepared using GIS and developed software modules. The model included the following equation for the growth dynamics of the vegetation biomass:

$$\frac{dB_k}{dt} = (P_k - m_k) B_k,$$

where  $B_k$  is the biomass;  $P_k$  is the growth rate;  $m_k$  is the dying rate of the  $k$ -th species of marine flowering plants.

It is assumed that the growth rate is a function of salinity  $f_1(S)$ , depth (lightning)  $f_2(H)$ , available nutrients  $f_3(B_k)$ , water temperature  $f_4(T)$ , and ground type  $f_5(D)$ ; thus,  $P_k = P_k^o f_1(S) f_2(H) f_3(B_k) f_4(T) f_5(D)$ , where  $P_k^o$  is the optimum growth rate for the  $k$ -th species.

The variable calculation parameters are as follows:  
 time interval for which calculation is performed;  
 calculation step,  $\tau$ ;  
 plant species characteristics;  
 growth rate function parameters;  
 dying rate parameters;  
 optimal growth rates;  
 original biomass (determined or random, normally distributed).

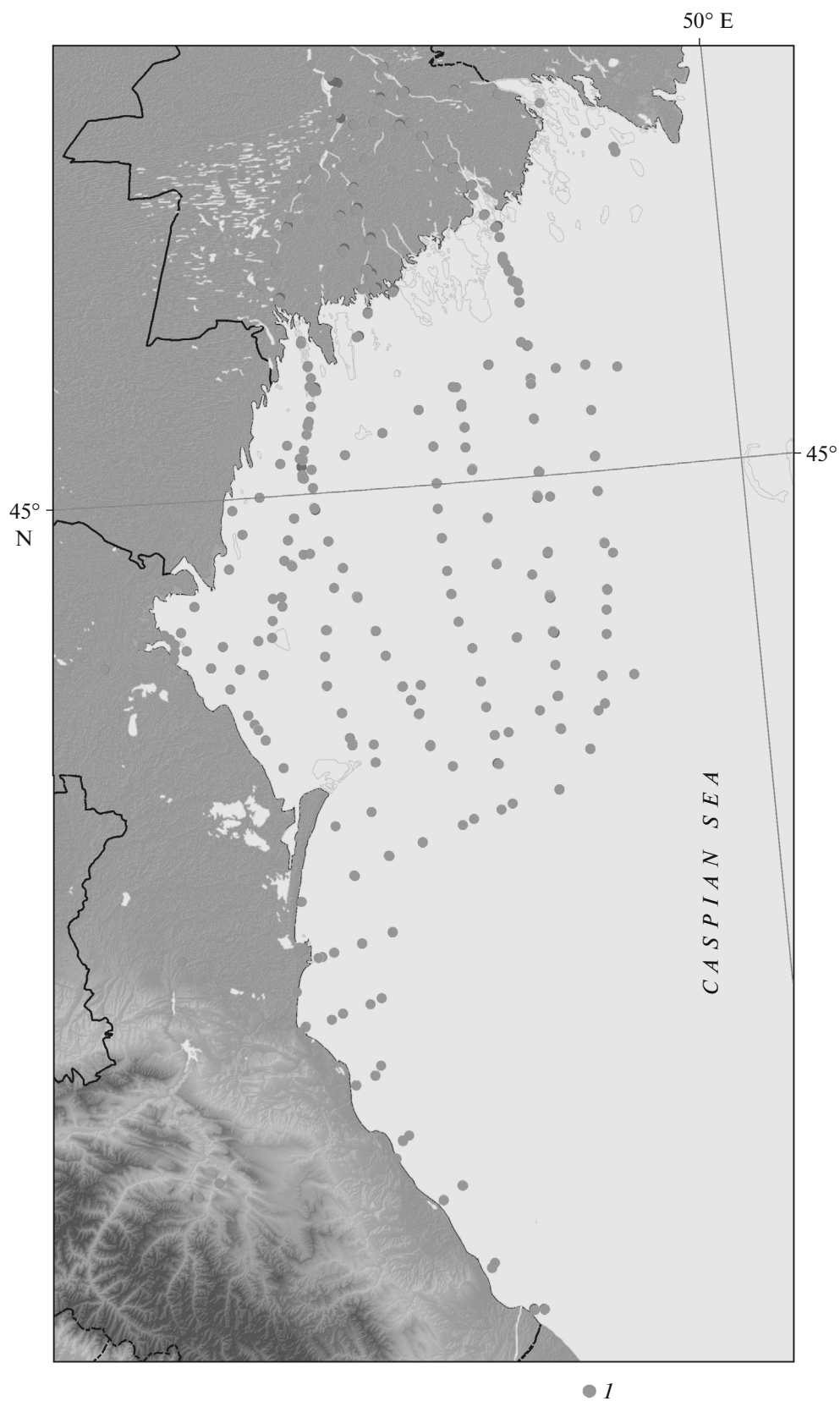
Cartographic documents were created using Arc-Map of ArcGis 9.1.

## RESULTS AND DISCUSSION

**Species diversity.** In the 1970s, the list of Caspian Sea macroalgae contained 63 species, including 29 green algae, 13 brown algae, and 21 red algae [14, 16]. During the study, 36 macroalgae species and 3 sea-grass species were revealed (table). The dynamics of the proportions of the main algae groups depends on changes in sea level and salinity (Fig. 2). It can be seen that the proportions of algae groups changed in the last years and the number of green algae species increased. At the same time, it should be kept in mind that our studies did not touch upon the eastern region of the Caspian Sea, which was indicated earlier as the localization zone of red algae [8]. In terms of macroalgae species diversity, the Caspian Sea occupies an intermediate position between the Sea of Azov and the Black Sea [30]. Green algae and seagrasses are predominant in the northern Caspian Sea; green and red algae prevail in the middle and southern Caspian Sea. Green algae of the genera *Ulva*, *Cladophora*, and *Ulothrix* form the nucleus of Caspian flora, which indicates the significant effect of river runoff. However, marine red algae of the genera *Polysiphonia*, *Laurencia*, and *Ceramium* dominate in the leading groups, as before [8]. The algae flora of the Caspian Sea is of Atlantic origin [14]; 79.3% of the Caspian algae are encountered in the Atlantic, and 77.8% of them are found in the Black Sea. The flora of the Caspian Sea has a latitudinal-boreal biogeographical composition, but the presence of two endemic genera and eight endemic species emphasizes the peculiarity of this water body and indicates its early isolation from the other parts of the Mediterranean basin [14].

The increase in diversity of macroalgae in the Caspian Sea was favored by the opening of the Volga–Don Canal in the early 1950s and the acclimation of invertebrates and fish. The macroalgae *Urospora penicilliformis*, *Ectocarpus siliculosus*, *Myrionema strangulans*, *Phaeostroma bertholdii*, and *Ceramium diaphanum* invaded more than 50 years ago and occupied the dominant position in the Caspian Sea [11, 17]. *Ceramium diaphanum*, a Black Sea algae of Atlantic origin, is presently the dominant species in the benthic and periphytonic communities of the northern Caspian Sea. The taxonomic report on *Ceramiales* [36] suggests that the species name of *Ceramium diaphanum* corresponds to several species in this case. It is known that *Ceramium diaphanum* is a mesosaprobiont settling in areas with increased water trophicity [16]. Note that no new macroalgae species have been found in recent decades. In the recent report by Karpinskii [18], ten invading algae species are listed for the Caspian Sea with reference to Zevina [9], but this information is out of date, revised only in the 1960s [10, 11].

There is the probability of discovering new algae species. Shipping (sea crust, ballast water) is the main



**Fig. 1.** Schematic map of marine studies of Southern Scientific Center, Russian Academy of Sciences, in 2004–2011: (1) oceanological stations and phytobenthos sampling sites.

## List of Caspian Sea macroalgae

	Species	I	II	III	IV	V	VI
CHLOROPHYCEAE							
1	<i>Ulothrix flacca</i>	meso	a	a	r	NC	[16, 10], ad
2	<i>U. pseudoflacca</i>	meso	a	a	r	NC	[16, 10],
3	<i>U. implexa</i>	meso	a	a	r	NC	[16, 4, 7], ad
4	<i>U. zonata</i>	meso	c	a	r	NC	[16, 4]
5	<i>Ulvella lens</i>	*	bt	a	r	MC, SC	[16, 4]
6	<i>Pringsheimiella scutata</i>	*	bt	a	s	MC, SC	[16]
7	<i>Entocladia viridis</i>	*	c	a	s	NC, MC, SC	[16], ad
8	<i>Acrochaete parasitica</i>	*	ub	a	*	NC, MC, SC	[4], ad
9	<i>Monostroma wittrockii</i>	*	mb	a	r	NC, MC	[16], ad
10	<i>Blidingia minima</i>	meso	bt	a	r	MC, SC	[16], ad
11	<i>B. marginata</i>	*	bt	a	r	MC, SC	[16, 4]
12	<i>Ulva prolifera</i>	poly	c	a	r	NC, MC, SC	[16, 4], ad
13	<i>U. flexuosa</i>	meso	bt	a	s	EC, MC	[16, 2, 4], ad
14	<i>U. linza</i>	meso	bt	a	d	EC, MC	[16, 2, 4], ad
15	<i>U. intestinalis</i>	poly	c	a	d	NC, EC, MC	[2], ad
16	<i>E. torta</i>	meso	mb	a	s	NC, MC, SC	[4]
17	<i>E. ahlneriana</i>	meso	mb	a	r	EC, MC	[16, 2, 4, 7]
18	<i>E. clathrata</i>	meso	c	a	s	NC, MC, SC	[16, 4, 7]
19	<i>E. kyllinii</i>	*	ub	a	r	NC, MC	[4]
20	<i>Gomontia polyrrhriza</i>	meso	mb	?	r	NC, MC, SC	[16, 4]
21	<i>Chaetomorpha aerea</i>	meso	bt	a	s	NC, MC, SC	[16, 4], ad
22	<i>C. linum</i>	meso	bt	a	s	EC, MC	[16, 2, 4], ad
23	<i>C. gracilis</i>	*	lb	a	s	EC, MC	[2]
24	<i>Rhizoclonium riparum</i>	*	c	a	r	NC, MC, SC	[16, 4], ad
25	<i>R. implexum</i>	meso	bt	a	r	EC, MC	[16, 2, 4], ad
26	<i>R. hieroglyphicum</i>	meso	c	a	r	NC, MC, SC	[16, 4], ad
27	<i>Cladophora sericea</i>	*	mb	a	r	NC, MC, SC	[16, 4], ad
28	<i>C. vagabunda</i>	meso	mb	a	d	NC, MC, SC	[16, 4], ad
29	<i>C. siwascensis</i>	*	lb	a	r	NC, MC	[16], ad
30	<i>Urospora penicilliformis</i>	poly	a	sw	s	EC, MC	[16, 5]
31	<i>Ostreobium queckettii</i>	*	c	?	r	NC, MC, SC	[16]
32	<i>Chara aspera</i>	meso?		a		EC, MC	[2], ad
33	<i>Chara crinita</i>	meso?		a		EC, MC	[2]
34	<i>Chara foetida</i>	meso?		a		EC, MC	[2], ad
35	<i>Chara hispida</i>	meso?		a		EC, MC	[2]
36	<i>Chara intermedia</i>	meso?		a		EC, MC	[2], ad
37	<i>Lamprothamnium alopecuroides</i>	meso?		a		EC, MC	[2]

Table. (Contd.)

	Species	I	II	III	IV	V	VI
PHAEOPHYCEAE							
38	<i>Pylaiella littoralis</i>	meso	a	sw	r	EC, MC	[4, 10, 16], ad
39	<i>Ectocarpus siliculosus</i>	meso	c	sw	s	EC, MC	[12, 16], ad
40	<i>E. caspicus</i>	*	e	sw	s	NC, MC, SC	[10], ad
41	<i>E. humilis</i>	*	lb	sw	s	NC, MC, SC	[10]
42	<i>Entonema oligosporum</i>	*	mb	sw	r	NC, MC, SC	[16, 10]
43	<i>E. effusum</i>	*	mb	sw	r	NC, MC, SC	[16]
44	<i>Phaeostroma bertholdii</i>	*	lb	?	r	NC, MC, SC	[16, 12]
45	<i>Myrionema strangulans</i>	*	mb	sw	r	EC, MC	[16, 12]
46	<i>Ascoecyclus orbicularis</i>	*	lb	ss	r	NC, MC, SC	[16, 10]
47	<i>Microspongium gelatinosum</i>	*	ub	?	r	NC, MC, SC	[16, 10]
48	<i>Monosiphon caspicus</i>	*	e	a	r	EC, MC	[4, 10]
RHODOPHYCEAE							
49	<i>Asterocystis ramosa</i>	*	bt	ss	r	EC, MC	[16, 4, 10]
50	<i>Bangia fuscopurpurea</i>	poly	mb	sw	d	NC, MC	[16, 10]
51	<i>B. atropurpurea</i>	*	mb	sw	r		[16, 10]
52	<i>Kylinia parvula</i>	meso	a	a	r	EC, MC	[16, 4]
53	<i>K. hallandica</i>	meso	a	a	r	EC, MC	[16, 4, 10]
54	<i>K. virgatula</i>	meso	mb	a	d		[16]
55	<i>Acrochaetium daviesii</i>	*	mb	a	r		[16]
56	<i>Acrochaetium thuretii</i>	*	mb	ss	s	EC, MC	[4, 10], ad
57	<i>Hildenbrandtia prototypes</i>	meso	bt	p	r	MC, SC	[16, 10], ad
58	<i>Lithoporella lapidea</i>	*	e		r	MC, SC	[4]
59	<i>Ceramium tenuissimum</i>	meso	bt	a	r	NC, MC, SC	[16, 10], ad
60	<i>C. diaphanum</i>	meso	bt	a	d	NC, EC, MC	[16, 2, 4, 7]
61	<i>C. elegans</i>	oligo	st	ss	r	EC, MC	[16, 4, 10], ad
62	<i>Callithamnion kirillianum</i>	oligo	e	ss	r	WC, SC	[10, 11], ad
63	<i>Polysiphonia violacea</i>	*	mb	a	r	NC, MC, SC	[16, 10], ad
64	<i>P. sanguinea</i>	*	lb	a	r	NC, MC, SC	[16, 10], ad
65	<i>P. denudata</i>	meso	bt	a	d	NC, MC, SC	[16, 10], ad
66	<i>P. caspica</i>	*	e	a	r	EC, MC	[4, 10], ad
67	<i>Lophosiphonia obscura</i>	meso	lb	a	s	WC, EC, NC, MC, SC	[16, 10], ad
68	<i>Laurencia caspica</i>	*	e	ss	d	WC, EC, NC, MC, SC	[4, 11, 10], ad
69	<i>Laurencicolax polyspora</i>	*			r	WC, MC, SC	[13]
70	<i>Dermatolithon caspicum</i>	*	e		r	WC, EC, MC, SC	[11]

I. Saprobity: (poly) polysaprobic species; (meso) mesosaprobic species; (oligo) oligosaprobic species. II. Phylogeographical characteristic: (a) arctic; (ub) upper boreal; (mb) middle boreal; (lb) lower boreal; (bt) boreal-tropical; (st) subtropical; (c) cosmopolite; (e) endemic. III Vegetation duration: (p) perennial; (a) annual; (ss) seasonal summer; (sw) seasonal winter. IV. Species occurrence: (d) dominant; (s) secondary; (r) rare. V. Distribution area: (NC) northern Caspian; (MC) middle Caspian; (SC) southern Caspian; (WC) western coast; (EC) eastern coast. VI. Source (see References): (ad) author's data. (\*) No data.

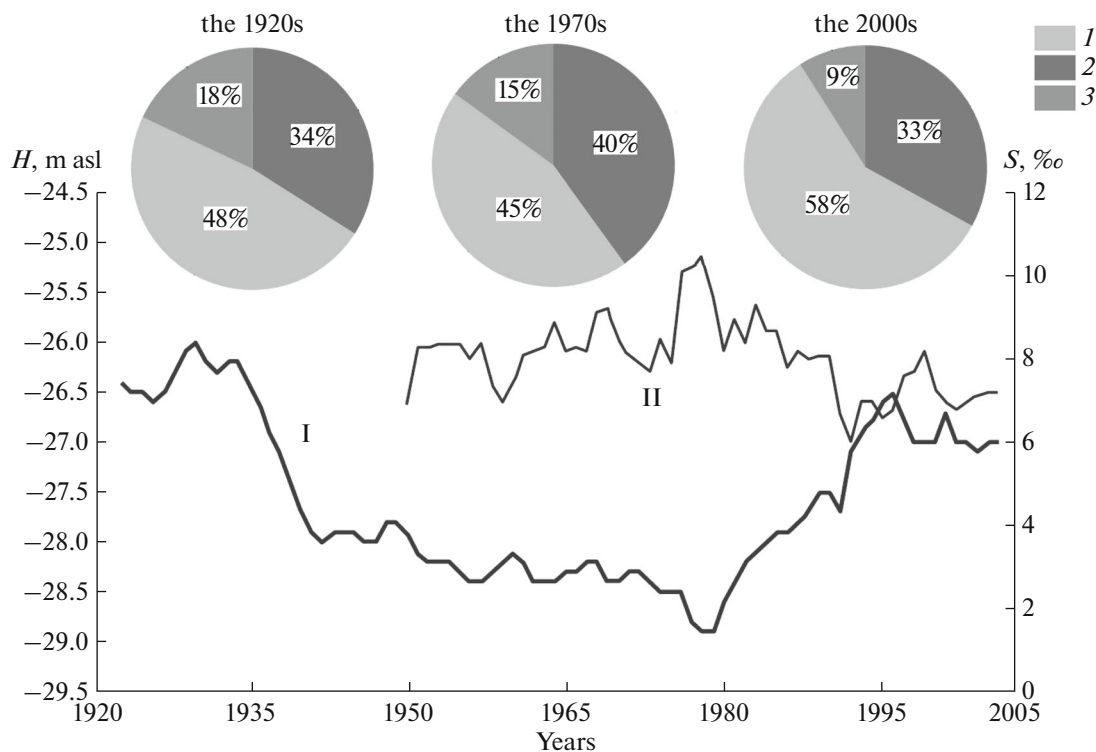


Fig. 2. Long-term dynamics of (I) Caspian Sea level, (II) northern Caspian Sea salinity, and main macroalgae groups: (1) green, (2) red, (3) brown. Sea level and salinity are shown according to [22].

source of invasions [30]. New algae species will apparently be discovered in the southern Caspian Sea.

Low salinity, relatively shallow water, good warming, and the prevalence of clay grounds are factors of increased natural trophicity of the Caspian Sea [1]. Almost all algae enter meso- and polysaprobic groups (table) and include annual or seasonal species of small size (to 5–10 cm in height) with a large specific surface area of the thallome; these are r-strategists [28]. Caspian Sea algae are characterized by rapid growth, production of abundant spores, low biomass, and relatively high productivity. Macroalgae in the middle Caspian Sea occur as a narrow zone along the shore to a depth of 20 m; they form no large growths in the majority of the northern Caspian Sea due to the absence of suitable substrates to attach to and they consist of epiphytic grasses and charophytes. Algae are components of periphytonic communities on anthropogenic substrates (buoys, vessel bottoms, and submerged parts of rig derricks and pipelines). Some species of green (*Cladophora*) and red (*Polysiphonia*, *Laurencia*) algae consist of floating forms capable of forming large agglomerations in bottom lows. Some authors [34, 36] noted intense development of green and red algae from the genera *Ulva*, *Cladophora*, and *Ceramium* in the northern Caspian Sea and along the western coast of the middle Caspian, which can indicate an increase in the trophicity of sea water, including due to

the ingress of hydrocarbons. Oil in the Caspian Sea has been actively produced for more than 100 years, but actual changes in benthic phytocommunities, which could be explained by the negative effect of oil, have been noted only in water areas chronically contaminated with oil. These areas are localized in the Bay of Baku of the Absheron Peninsula. In our opinion, the increase in euribiontic algae is related to the decrease in salinity in both the entire Caspian Sea and its northern region in recent years [22, 26]. Changes in the temperature conditions of northern Caspian waters [26] will apparently cause no increase in the warm-water algae complex, because hard winters are becoming more frequent [32].

The northern region of the Caspian Sea is characterized by the mass development of flowering aquatic plants and charophytes. They play a major role in the formation of benthic phytocenoses on loose grounds in Caspian bays. The flora of flowering marine plants includes five species: *Potamogeton pectinatus*, *Ruppia maritima*, *Zanichellia palustris*, *Zostera noltii*, and *Najas marina*. All these plants can inhabit a wide range of environmental factors. However, the optimum conditions for their vegetation are as follows: salinity, 8–15‰; water temperature, 15–25°C; depth, 0.5–5 m [38]. It was shown that *Potamogeton pectinatus* and charophytes can exist in an aquatic environment with excess phosphorus. Eutrophication does not inhibit



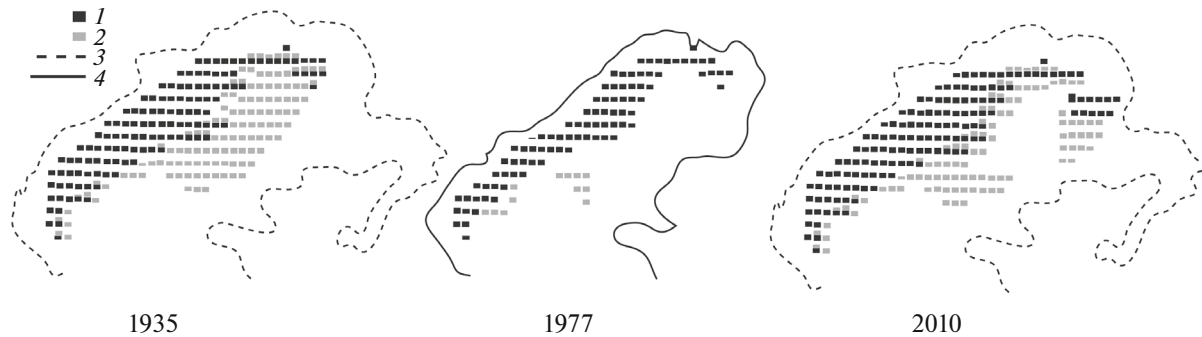


Fig. 3. Visualization of model calculation for spatial dynamics of biomass ( $1 \text{ kg/m}^2$ ) (1) *Potamogeton pectinatus* and (2) *Zostera noltii* in northern Caspian Sea; (3, 4) sea boundaries.

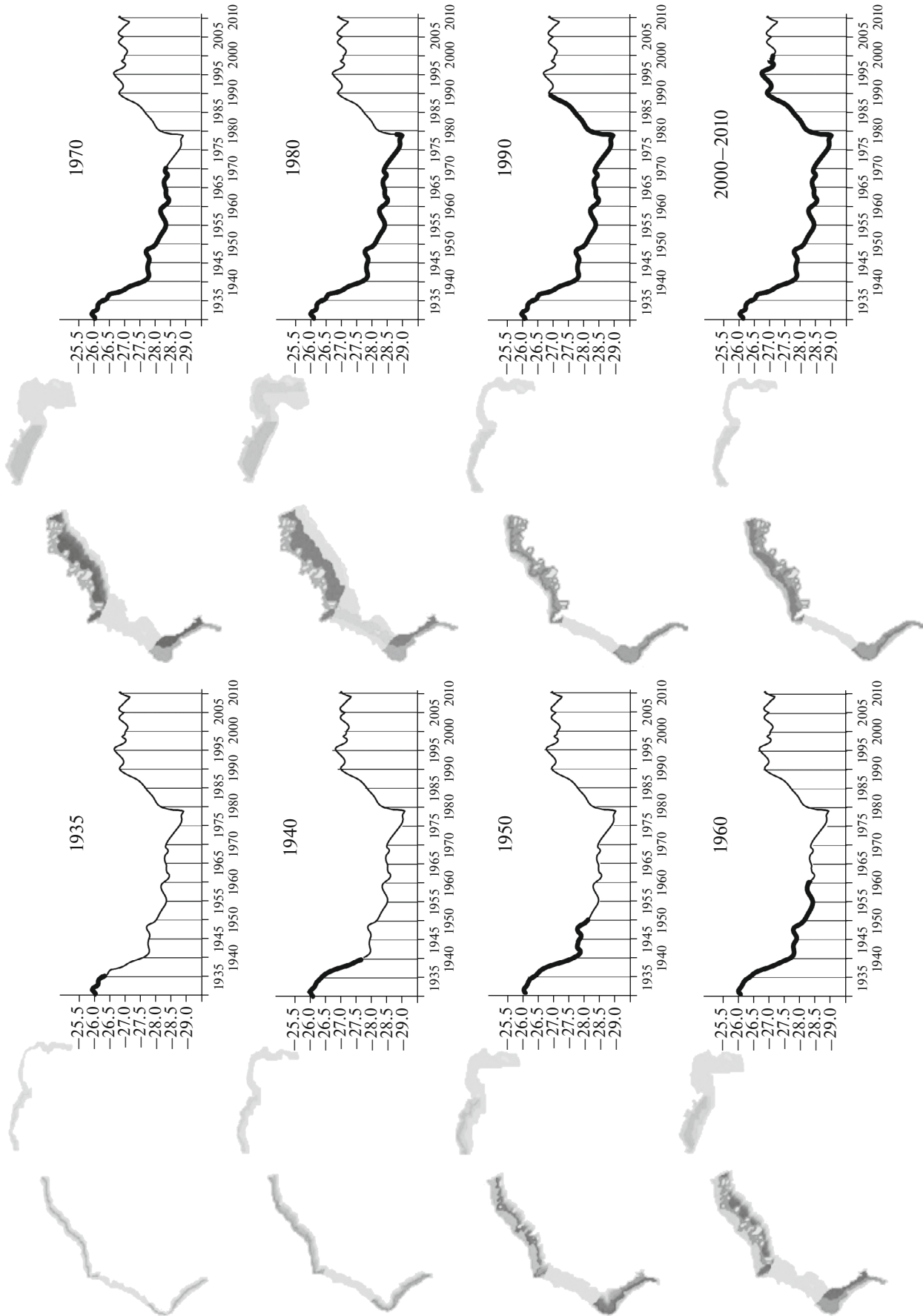
the growth of macrophytes; on the contrary, it favors the invasion of waters by these plants [38]. The growth of *Zostera marina* in the northern Caspian Sea was erroneously noted by some authors [15, 34–36]. The generalizing reports [3, 6, 7, 24] do not mention the occurrence of *Z. marina* in Caspian waters; our studies did not find this species either. Astrakhan researchers could have mistaken large specimens of *Z. noltii* for *Z. marina*. According to our observations, *Z. noltii*, in contrast to *Z. marina*, can exist in a wide range of conditions, including salinity and pollution. *Z. noltii* frequently inhabit clayey grounds contaminated with oil hydrocarbons in water areas where the salinity reaches 5‰ and *Z. marina* cannot develop normally [29].

The coastal vegetation in the lower delta of the Volga River and the northern Caspian Sea includes 162 species from 18 families [33]. The dominant species belong to the families *Typhaceae*, *Sparganiaceae*, *Potamogetonaceae*, *Ruppiceae*, *Zannichelliaceae*, *Alismataceae*, *Cyperaceae*, *Lemnaceae*, and *Gramineae*. Common reed (*Phragmites australis*) plays a significant role in the formation of the entire complex of coastal phytocenoses. Reed stands form the vegetative edge of the Volga delta, significantly penetrate into freshened shallow waters of the northern Caspian Sea, and serve as a sort of buffer between terrestrial and aquatic vegetation. The spatial and temporal dynamics of *Phragmites australis* communities largely determines the species composition, distribution, and dynamics of aquatic plants and macrophytobenthos.

**Biomass.** In the northern Caspian Sea, aquatic plants form communities with high biomass values reaching  $10\text{--}12 \text{ kg/m}^2$ . The reserves of *Zostera noltii* were 700000 tons in the early 1940s [19]. Later, the biomass of *Z. noltii* was not estimated; however, according to the data of Gromov [6, 7], they can be assumed at approximately 200000 tons for the Northern and Caspian Sea and the western region of the middle Caspian Sea. Studies performed in the mid-2000s [31] showed an increase in the biomass of *Z. noltii* compared to the 1980s [6, 7] by 1.5–2 times,

especially in the region of Tyuleniy Island near the Kazakh coast. The spatial distribution of the macrophytobenthos changed due to fluctuations in the Caspian Sea level. At present, the northern Caspian Sea occupies about  $100000 \text{ km}^2$ , but during the regression period, the area of the northern Caspian Sea region decreased by 30–40% [20]. The northern coast of the Caspian Sea and the Volga delta are characterized by low offshore and coastal slopes. A foreshore zone is formed by surges in the northern Caspian. Low offshore slopes in the eastern part of the northern Caspian result in the drying of large areas during a decrease in sea level and their flooding during a rise in sea level [26]. In the scheme of the northern Caspian ecosystem [1], three zones are distinguished: coastal, estuarine, and marine. Each zone is characterized by a specific range of aquatic environment parameters; the boundaries between the zones are dynamic. The major reserves of aquatic plants are concentrated in the coastal and estuarine zones. At present, 80% of the macrophytobenthos, which consists of saltwater and marine grasses, is limited to the 5-m isobaths. In the majority of the area of the northern Caspian Sea, the mean biomass of flowering aquatic plants does not exceed  $0.5\text{--}3 \text{ kg/m}^2$  and coincides with depths of 1–2 m; its maximum values do not exceed  $10 \text{ kg/m}^2$ . Groups of thinned green and red algae are observed on sandy-clay bottom deeper than 5 m. Although the northern Caspian bottom is relatively flat, plant residues accumulate in bottom lows and their biomass reaches  $5\text{--}6 \text{ kg/m}^2$ . The red algae *Polysiphonia* and *Laurencia* form vast fields with a biomass more than  $1 \text{ kg/m}^2$  at depths down to 10–15 m, but these fields are small in number and localized at the boundary with the middle Caspian and along its western coast.

**Spatial distribution of aquatic and littoral vegetation.** Numerical experiments were performed to assess the effect of sea level changes and related factors on the spatial distribution of two dominant seagrass species: *Zostera noltii* and *Potamogeton pectinatus*. These species



**Fig. 4.** Visualization of model calculation for long-term dynamics of littoral aquatic vegetation (*Phragmites australis*) in northern Caspian Sea; (dark background) high density; (light background) low density.



were selected, because their habitats can overlap under some conditions, which results in competition for substrate, light, and nutrients. The results are presented in the form of spatially distributed data on the standard northern Caspian grid in GIS (Fig. 3).

The simulation results revealed potential contact zones between two species with possible competitive interactions. The spatially detailed model shows that the lowering of the Caspian Sea level results in the disappearance of *Zostera noltii* at low depths and its localization in the central part of the sea at depths greater than 10 m. The distribution limit of pondweed is shifted toward lower depths; the coverage area is reduced more than twofold. An analogous succession was described by Karaeva and Zaberzhinskaya [17] for limans of the coast of Azerbaijan: in the 1950s–1960s, *Zostera noltii* dominated in benthic communities; during the rise in the sea level in the early 1980s, it was completely degraded and displaced by *Potamogeton pectinatus* in the benthic communities; in the 2000s, *Zostera noltii* appeared but did not recover its former area.

The results show that natural factors, primarily sea level and salinity, determine the distribution of aquatic plants in the northern Caspian Sea. At present, there is a possibility for an expansion of the distribution area and an increase in seagrass reserves in the northern and middle Caspian Sea. Further field studies will show whether *Z. noltii* can again occupy its lost water areas.

With a varying Caspian Sea level, changes in the area occupied by aquatic littoral vegetation (ALV) play an important role in the aquatic vegetation dynamics. Dense reed stands limit the distribution of aquatic plants, primarily pondweeds and charophytes, in shallow Caspian waters.

Common reed (*Phragmites australis*) forms the basis of ALV in the estuarine regions of the Volga, Ural, and Terek rivers. The ALV occupied a narrow (0.5–3 km) band along the marine edge of the delta until the 1930s; over the next 20 years, this area expanded as far as the sea level decreased. The quantitative estimates of the overgrowth dynamics of insular and marine areas in the Volga delta are based on aerial observation data during a period of relatively stable sea level (1963–1966) and its abrupt decrease until 1978 [2]. In the early 1960s, ALV occupied only a relatively small shallow water area at the marine edge of the delta (10–20%). The lowering of the sea level to the mark of –29 m, the abrupt decrease of depths, and the reduction of water dynamic activity resulted in the rapid development of vegetation in the delta front. To the end of the studied period, the water area occupied by vegetation exceeded 90% of the total area in some regions, and the width of the vegetation cover reached 50 km [2].

During the period of Caspian Sea regression, the dried areas of the former sea bottom in the eastern part of the northern Caspian Sea were almost completely transformed to solonchaks, where only salt-tolerant

dwarf plants well developed. Analogous processes occurred in the Agrakhan Bay (the western part of the northern Caspian Sea), the southern part of which represented a shallow saline boggy lake to 1970. The rise of the sea level after 1978 resulted in an increase of depth in the Volga delta front from 0.5–1 to 2–3 m. This negatively affected the development of ALV and resulted in its almost complete disappearance. The areas occupied by ALV shifted toward the insular zone and displaced the widely distributed hay and pasture meadows [2].

The increase in the volume of sea and river runoff since the mid-1990s resulted in the restoration of small river deltas on the western and eastern coasts of the Caspian Sea. The wetted coastal areas are actively overgrown by littoral aquatic plants. Meanwhile, the saline coastal soils still limit the development of vegetation, especially in the eastern region of the northern Caspian Sea.

From the observation data, the area of ALV exceeded 70% in almost all regions of the insular zone and the Volga delta front to 1976 [2]. Meanwhile, the model overgrowth dynamics of the insular zone and the marine delta area is generally adequate to the observation data during the lowering of the Caspian Sea level. Therefore, the obtained estimates were extrapolated to both the years when no regular natural studies were performed and the entire Volga estuary. From the calculation results (Fig. 4), the ALV in the Volga delta should be displaced by meadow plants in the early 1970s. After 1980, the ALV again developed with rising sea level, and it should be expected that it will occupy 50% of the Volga delta area. According to the calculation results for the insular zone, the ALV area remained stable (35–45%) until about 1980, increased to 75% during an abrupt rise in sea level, then decreased to 30%; it presently occupies 45–50% of the territory (Fig. 4). Thus, the insular zone should lose its importance as a biotope for water fowl, mammals, and invertebrates because of overgrowth to 1980. A further rise in sea level resulted in regression of reed beds and their localization in the insular zone. The ALV area in the Volga delta front should decrease almost to zero.

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