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VEGETATION CLASSIFICATION

Floristic classification of opportunistic green macroalgae communities of the European myxomesohaline seas

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A B S T R A C T

Shallow-water communities of opportunistic green marine macroalgae in eutrophicated areas are currently gaining an advantage over communities dominated by other groups of macrophytes. Therefore, their classification, study of composition and observation of structural changes are of particular importance. One class (Ulvae intestinalis–Ulvetea linzae), one order (Ulvae intestinalis–Ulvetalia linzae), three alliances (Ulvae intestinalis–Ulvion linzae, Ulvae intestinalis–Ceramion virgati, Ulvae rigidae–Gelidion spinosi) and three new associations of macroalgal communities of meso- and polysaprobic sublittoral vegetation within the shelf of the Black, Azov and Baltic Seas are described for the first time, using the Braun-Blanquet approach. Principal components analysis revealed two main factors influencing the floristic composition of the investigated communities: salinity and nutrient enrichment with associated turbidity. The proposed classification of opportunistic communities of green algae should be used in assessing the dynamics of the state of vegetation during eutrophication of the aquatic environment.

Keywords: syntaxa, macroalgae, mesosaprobionts, polysaprobionts, eutrophication, sublittoral zone, Azov Sea, Black Sea, Baltic Sea

Р Е З Ю М Е

Афанасьев Д.Ф., Абдуллин Ш.Р. Флористическая классификация сообществ оппортунистических зеленых макроводорослей миксомезогалинных морей Европы. Сообщества оппортунистических зеленых макроводорослей эвтрофированных морских мелководий в настоящее время получают преимущество перед сообществами, в которых доминируют другие группы макрофитов. Поэтому их классификация, изучение состава и мониторинг структурных изменений приобретают особое значение. С использованием подхода Брауна-Бланке впервые описаны один класс (Ulvae intestinalis–Ulvetea linzae), один порядок (Ulvae intestinalis–Ulvetalia linzae), три союза (Ulvae intestinalis–Ulvion linzae, Ulvae intestinalis–Ceramion virgati, Ulvae rigidae–Gelidion spinosi) и три новые ассоциации сообществ макроводорослей мезо- и полисапробной сублиторальной растительности на шельфе Черного, Азовского и Балтийского морей. Анализ главных компонентов выявил два основных фактора, влияющих на флористический состав исследованных сообществ: соленость и трофность с сопутствующей мутностью. Предложенную классификацию сообществ оппортунистических зеленых макроводорослей можно использовать при оценке динамики состояния растительности при эвтрофикации водной среды.

Ключевые слова: синтаксоны, макроводоросли, мезосапробионты, полисапробионты, эвтрофикация, сублиторальная зона, Азовское море, Черное море, Балтийское море

In recent decades, alongside the comparatively well studied bloom caused by phytoplankton, a bloom of marine and fresh waters caused by littoral benthic macroalgae of three genera – *Ulva*, *Cladophora*, and *Spirogyra* – have become a global phenomenon (Ye et al. 2011, Gladyshev & Gubelit 2019). Eutrophication (the supply of nitrogen and phosphorus from agricultural lands, industrial and domestic wastewaters, and aquaculture) is the evident cause of the increase in algal biomass (Gladyshev & Gubelit 2019). To assess the dynamics of bottom vegetation in areas of increasing eutrophication, it is necessary to build a reliable classification system of plant communities. However, such systems are still preliminary (Bültmann et al. 2015, Mucina et al. 2016).

The Braun-Blanquet vegetation classification approach (syntaxonomy) was successfully used to classify vascular plant communities, macroalgae communities (MAC) and cyanobacterial-algal cenoses (CAC) in various ecosystems, ranging from terrestrial to marine environments, from the Atlantic Ocean and the Mediterranean Sea to soil algae in natural and disturbed environments (Margalef 1949, 1951, Den Hartog 1959, Giaccone 1965, Pignatti & Pignatti 1966, Petrovska & Stoyanov 1975, Giaccone et al. 1993, 1994, Bobrov et al. 2005, Dell'Uomo 2010, Bobrov & Chemeris 2012, Mirkin & Naumova 2012, Abdullin & Mirkin 2015, Afanasyev & Abdullin 2013, 2014, Abdullin 2020). Data on CAC and MAC were summarized only recently (Bültmann et al. 2015, Mucina et al. 2016). The high-ranked syntaxa of algae have been compiled for the first Europe-wide checklist that includes 13 classes, 24 orders and 53 alliances (Mucina et al. 2016). At the same time, algal blooms still weren't investigated from the point of syntaxonomy, marine communities of green algae, dominated by numerous species of the genera *Ulva* and *Cladophora*, including those that cause "green tides", is practically not systematized on a global scale (Ye et al. 2011).

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The syntaxonomic scheme for such vegetation has been developed only for the Mediterranean Sea and the European coast of the Atlantic Ocean: all green algae communities here are united in one order Ulvetalia lactucae Molinier 1960, which is included in the class Cystoseiretea Giaccone 1965. The order combines photophytic marine macroalgal communities on nutrient enriched hard substrates in the (eu-) infralittoral and circalittoral zones along the Mediterranean Sea and Atlantic Ocean shores (Mucina et al. 2016). The order contains two alliances: Ulvo lactucae–Corallinion mediterraneae Vignes ex Julve 1992 (photophytic marine macroalgal communities on nutrient enriched hard substrates exposed to wave action in the (eu-)infra- and circalittoral zones of the Mediterranean Sea) and Ulvion rigidae Berner 1931 corr. Giaccone et al. 1994 (photophytic marine macroalgal communities on nutrient enriched, sheltered hard substrates of the lower eulittoral zone of the shores of the Mediterranean Sea and the Atlantic Ocean) (Mucina et al. 2016). The existing syntaxonomy of these communities raises a number of serious questions. First, the assignment of the order to the class Cystoseiretea Giaccone 1965 is probably a tribute to an exclusively historical tradition, since communities of the order have been for the first time described in the Mediterranean Sea, where *Ulva* ssp. often grows together with species of *Cystoseira* sensu lato. However, the species of *Ulva* are distributed throughout the world, where they form communities without the participation of *Cystoseira* sensu lato. Secondly, it is still unclear which species of *Ulva* are diagnostic for the order Ulvetalia lactucae Molinier 1960, its two alliances, and some associations. In this regard, in the prodromus of the vegetation of Italy, the following wording of the vegetation of the order Ulvetalia lactucae Molinier 1960 is given: thionitrophilic vegetation consisting of communities dominated by opportunistic species of the order Ulvales (Blasi 2010). Thirdly, the existing syntaxonomy includes only thionitrophilic vegetation in euhaline waters; however, many species of the genus *Ulva* also develop in myxohaline waters. Fourthly, with all the diversity of communities, only two alliances are distinguished in the order, one of which – Ulvo lactucae–Corallinion mediterraneae Vignes ex Julve 1992 – is given only for the Mediterranean Sea, and includes only two associations. The prodromus of Europe indicates that this alliance is placed in the order provisionally (Mucina et al. 2016).

In this regard, it is appropriate to recall that the vegetation of eutrophic waters with the dominance of species of *Ulva* has repeatedly been proposed to distinguish as a separate class – Enteromorphetea (Waern 1952), Ulvetea lactucae Julve 1992 (Julve 1992).

In this work, the authors classify the meso- and polysaprobiont communities of the sublittoral zone of the European mixomesohaline seas and identify the main factors influencing their distribution in monitoring purposes of the areas of increasing eutrophication.

MATERIAL AND METHODS

The study is based on 80 geobotanical relevés of *Ulva* ssp. dominated communities performed in the sublittoral zone of the North Caucasus shelf of the Black Sea, the Azov Seas (42 relevés) and Western Baltic (38 relevés) (Fig. 1) in 2012–2019.

Salinity was measured at each site using a calibrated handheld refractometer with automatic temperature compensation (Euromex, Arnhem/NL). Relevés were conducted from a depth of 0 m to the depth of 3 m. Communities were described on sites from 0.0625 to 0.25 m^2. The algae were determined mainly during the description and verification of the determinations, and the refinement of the taxonomic identity of some species was carried out in the laboratory. Identification was based on typical morphological characters using identification keys (Zinova 1967, Kornmann & Sahling 1989, Pankow 1990, Brodie et al. 2007). Some species of *Acrochaetium*, *Cladophora*, *Ceramium* and *Polysiphonia* could not be identified confidently and were marked as *Acrochaetium* sp., *Cladophora* sp., *Ceramium* sp. and *Polysiphonia* sp. Nomenclature is given according to Guiry & Guiry (2023). Saprobity of the species is given according to the unpublished data of A.A. Kalugina-Gutnik.

Classification of macroalgal communities followed the Braun-Blanquet approach (Braun-Blanquet 1964, Mirkin et al. 2001). Syntaxon names follow the International Code of Phytosociological Nomenclature (Theurillat et al. 2020). Characteristic tables include 37 relevés. To assess the abundance of species, a modified Braun-Blanquet scale was used: r – rarely occurs; + – insignificant participation of the coenopopulation of the species in the phytocenosis; 1 – projective cover up to 5 %; 2 – 6–15 %; 3 – 16–25 %; 4 – 26–50 %; 5 – more than 51 % (Neshataev 2001). The constancy scale was used in compiling the synoptic tables: r – 0.1–5 %;

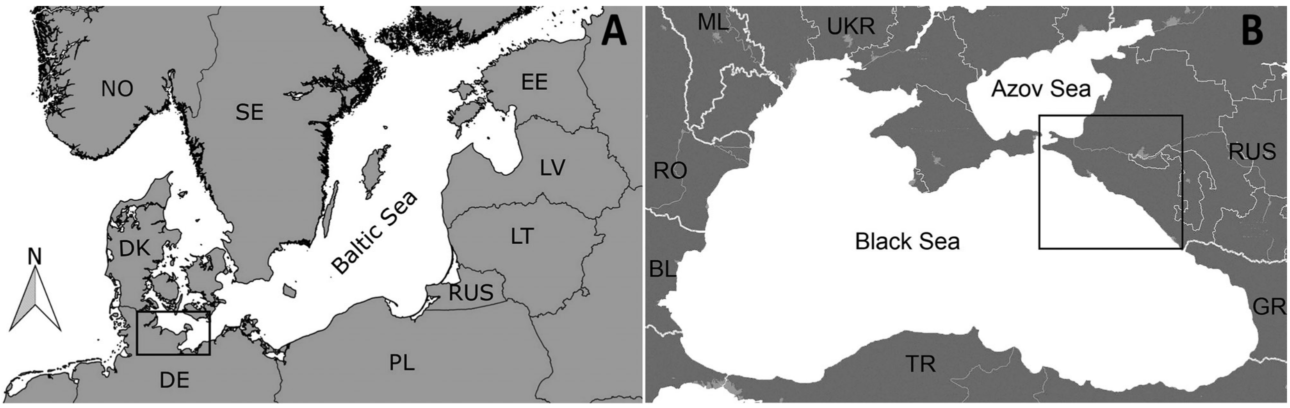

Figure 1 Research areas. (A) Baltic Sea; (B) Black and Azov Seas. Squares indicate the areas of sampling

+ – 6–10 %; I – 11–20 %; II – 21–40 %; III – 41–60 %; IV – 61–80 %; V – 81–100 %.

The Jaccard Resemblance Coefficient (JRC) was applied for the species composition similarity.

Ordination analysis was performed using Canoco 4.5/ CanoDraw 4.0 software (ter Braak & Šmilauer 2002). The structure of the dataset was tested with detrended correspondence analysis (DCA), and the gradient length of the first DCA axis (1.000 SD units) indicated an application of linear ordination techniques. Principal components analysis (PCA), considering axes 1 and 2, was performed to detect the main environmental factors affecting the species composition of the sites in question, and to visualize any differences between them. Default options included: focus scaling on intersample distances, species scores divided by standard deviation, centering by samples and without transformation of the species data applied in PCA.

RESULTS

Description of new syntaxa

In the studied area of the sublittoral zone of the Black, Azov Seas and Western Baltic, 39 species and intraspecific taxa of algae were identified, belonging to three phyla: Rhodophyta, 20 species and intraspecific taxa; Chlorophyta, 16 species; Ochrophyta, Phaeophyceae, 3 species (see Tables 1–4).

As a result of processing the collected material, we identified one previously described association and described three new associations, three alliances, one order, and one class, which combine meso- and polysaprobic vegetation of the sublittoral zone of the myxomesohaline seas of Europe.

Class: **Ulvae intestinalis–Ulvetea linzae** Afanasyev & Abdullin **cl. nov.**

Holotypus: Ulvae intestinalis–Ulvetalia linzae Afanasyev & Abdullin (described in this paper).

Diagnostic species: *Ulva intestinalis* L., *Ulva linza* L.

Description: Communities of the class grow in waters enriched with nutrients, on a solid substrate at a depth of 0 to 2–3 m. The salinity of seawater in the areas of growth of the communitiesvery wide – from typically marine to almost fresh waters. Limiting factors: absence of solid substrata, very intense hydrodynamics, dis- and oligotrophic conditions. Communities of the class are found on eutrophic shelf areas in the Black, Azov and Baltic Seas (Table 5). Diagnostic species of the class are cosmopolitans and characterized by high ecological plasticity, which allows them to occur in a wide range of salinity, temperature, and hydrodynamics. All these species are meso- and polysaprobionts. Diagnostic species of the class Ulvae intestinalis–Ulvetea linzae are also diagnostic ones of some Mediterranean and Atlantic associations from euhaline waters enriched by nutrients.

Comment: The class includes one order and three alliances, forming an ecological series in order of salinity increasing and nutrient load decreasing: Ulvae intestinalis–Ulvion linzae – Ulvae intestinalis–Ceramion virgati – Ulvae rigidae–Gelidion spinosi.

Order: **Ulvae intestinalis–Ulvetalia linzae** Afanasyev & Abdullin **ord. nov.**

Holotypus: Ulvae intestinalis–Ulvion linzae Afanasyev & Abdullin (described in this paper).

Diagnostic species: those of the class.

Description: those of the class.

Comment: those of the class.

Alliance: **Ulvae intestinalis–Ulvion linzae** Afanasyev & Abdullin **all. nov.**

Holotypus: Ulvetum intestinalis Feldmann 1937

Diagnostic species: those of the order.

Description: The alliance communities are formed on hard substrates, at a depth from the water's edge to 0.5(1) m in waters enriched with nutrients and not too intense hydrodynamics. The range of water salinity at which communities develop is very wide – from typically marine to almost fresh waters. The range of nutrient load under which communities are formed is just as wide – from moderately trophic to eutrophic waters.

Comment: The alliance includes two associations, a characteristic feature of which is they are species poor, probably due to the instability of habitat conditions.

Association: **Ulvetum intestinalis** Feldmann 1937

Diagnostic species: *Ulva intestinalis.*

Description: The communities of the association are monodominant, widespread in the Baltic Sea, often found in the Black Sea and in the southern part of the Sea of Azov. They occupy depths from 0.15 m above the water's edge to 0.3–0.5 m below it and found in a wide salinity gradient: from brackish waters (7–8 ‰ in the Sea of Azov) to waters with marine salinity (up to 15 ‰ in the Baltic Sea, up to 18 ‰ in the Black Sea). The communities develop on vertically and horizontally oriented hard surfaces, on stones, pebbles, concrete structures, etc. Phytocenoses of the association occur in waters with a high concentration of nutrients and with-stand low transparency. Despite the fact that communities are found both near open coasts and in closed water areas, they prefer water areas with reduced intensity of water movement. The floristic core of the association includes only a diagnostic species; other species are found with low abundance and low constancy. The average number of species at the plots is close to one; therefore, most of the phytocenoses of the association are single species (Table 1). The maximum abundance of the community is reached in spring and summer.

Comment: The association Ulvetum intestinalis Feldmann 1937 was first described in the northwestern Mediterranean on the French coast of the Commune des Alberts (côte des Albères) (Feldmann 1937, 1938). In Europe, such communities are found in the Mediterranean, Adriatic, White, Baltic, Black, Azov and Caspian Seas, where they occur in the salinity range from 0.5 to 35 ‰ (Feldmann 1937, 1938, Morozova-Vodyanitskaya 1959, Coppejans 1972, Vinogradova 1974, Kalugina-Gutnik 1975, Lovric 1978, Gromov 1998, Afanasyev et al. 2022). In the Black Sea, the association of *Ulva intestinalis* was described in terms of the dominant approach (Kalugina-Gutnik 1975). It was pointed out that monodominant polysaprobic phytocenoses of this association are confined to heavily polluted bays with low salinity at depths of 0–0.2 m. There were less than 10 species of macroalgae in the communities, and it was noted that under conditions of very strong pollution and very low salinity, only *U. intestinalis* was found in phytocenoses (Kalugina-Gutnik 1975). Single species phytocenoses of the association are identical to those described by us. Phytocenoses described by A.A. Kalugina-Gutnik (1975) with more diverse floristic composition, from our point of view, should be considered as ecotone.

Association: **Ulvetum linzae** Afanasyev & Abdullin **ass. nov.**

Holotypus: Rel. 2 of Table 2 in this paper

Diagnostic species: *Ulva linza*.

Description: Communities of the association are monodominant, oligospecies, found on solid substrates (boulders, concrete structures) at depths from 0 to 0.5 m or more in waters with salinity from 12 to 17 ‰. Phytocenoses of the association, as a rule, develop in waters with an increased concentration of nutrients, both at open and closed shores. The floristic core of the association includes only a diagnostic species; other species are found with low constancy and abundance, with the exception of species of *Cladophora*, the

Table 1. Association Ulvetum intestinalis Feldmann 1937.

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Constancy
No. of species	2	2	1	1	1	1	1	1	1	1	1	2	1	1	1	1	
Diagnostic species of the ass. Ulvetum intestinalis Feldmann 1937, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae																	
Ulva intestinalis L.	5	5	5	5	5	4	4	4	4	4	3	3	3	3	3	1	V^{1-5}
Other species																	
Vertebrata reptabunda (Suhr) Díaz-Tapia & Maggs	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I

Notes.

Sporadic species. Rel. 12: *Cladophora liniformis* Kützing +.

Sampling data. Rel. 1: Russia, cape Zhelezny Rog, Black Sea, 21.05.2014, 45°6.581'N 36°44.116' E. **Rel. 2**: Russia, cape Zhelezny Rog, Black Sea, 21.05.2014, 45°6.581'N 36°44.116'E. **Rel. 3**: Germany, Hohen Wieschendorf, Baltic Sea, 18.07.2013, 53°56.962'N 11°20.661'E. **Rel. 4**: Germany, Eckernforde, Kiekut, Baltic Sea, 17.08.2013, 54°26.89'N 9°52.322'E. **Rel. 5**: Germany, Westerberg, Fehmarn, Baltic Sea, 19.08.2013, 54°26.137'N 11°6.046'E. **Rel. 6**: Russia, Yuzhnaya Ozereyevka, Black Sea, 25.05.2015, 44°40.198'N 37°37.856'E. **Rel. 7**: Germany, Kirchdorf, Poel, Baltic Sea, 19.07.2013, 53°59.83'N 11°26.692'E. **Rel. 8**: Germany, Glucksburg, Baltic Sea, 16.08.2013, 54°50.328'N 9°31.191'E. **Rel. 9**: Germany, Weissenhauser strand, Baltic Sea, 29.08.2013, 54°18.759'N 10°47.432'E. **Rel. 10**: Germany, Neustadt, Neustadter Binnenwasser, Baltic Sea, 29.08.2013, 54°6.626'N 10°48.774'E. **Rel. 11**: Russia, Yuzhnaya Ozereyevka, Black Sea, 22.06.2012, 44°10.162'N 37°37.694'E. **Rel. 12**: Russia, Yuzhnaya Ozereyevka, Black Sea, 22.06.2012, 44°40.122'N 37°37.551'E. **Rel. 13**: Germany, Redentin, Baltic Sea, 19.07.2013, 53°55.914'N 11°28.79'E. **Rel. 14**: Germany, Poel, Baltic Sea, 19.07.2013, 53°58.247'N 11°28.333'E. **Rel. 15**: Germany, Sussau, Baltic Sea, 19.08.2013, 54°16.58'N 11°5.058'E. **Rel. 16**: Russia, Kulikovskoye girlo, Azov Sea, 01.10.2015, 45°22.84'N 37°31.789'E.

Author of relevés. Rel. 1–16: Afanasyev D.F.

Depth (m). Rel. 1, 6, 11, 12, 16: 0–0.5. **Rel. 2, 7, 10, 15**: -0.1–0. **Rel. 3, 4**: 0.1–0.2. **Rel. 5**: 0.2. **Rel. 8**: -0.1–0.1. **Rel. 9**: 0.2–0.3. **Rel. 13**: 0–0.2. **Rel. 14**: 0.15.

Salinity (‰). Rel. 1, 2: 16. **Rel. 3, 7, 14**: 11. **Rel. 4, 9**: 14. **Rel. 5, 15**: 10. **Rel. 6, 11, 12**: 17. **Rel. 8**: 15. **Rel. 10, 13**: 13. **Rel. 16**: 8.

Plot size (m^2). Rel. 1, 2: 0.0625. **Rel. 3–5, 7, 8, 10, 13–15**: 0.01. **Rel. 6, 9, 11, 12**: 0.25. **Rel. 16**: 0.09.

Macroalgae cover (%). Rel. 1: 80–85. **Rel. 2**: 90–95. **Rel. 3**: 70–90. **Rel. 4**: 80. **Rel. 5**: 85. **Rel. 6, 16**: 50–60. **Rel. 7**: 55–65. **Rel. 8**: 60–70. **Rel. 9**: 60–75. **Rel. 10**: 50. **Rel. 11, 12**: 40. **Rel. 13**: 45–55. **Rel. 14**: 25–30. **Rel. 15**: 35–45.

Substrate. Rel. 1–2: lithified shell rock. **Rel. 3, 9–13, 15, 16**: boulders. **Rel. 4, 7, 8**: pebbles. **Rel. 5–6, 14**: pebbles and boulders.

Table 2. Association Ulvetum linzae Afanasyev and Abdullin ass. nov.

No. of relevé	1	2*	3	4	5	Constancy
No. of species	3	1	1	3	4	
Diagnostic species of the ass. Ulvetum linzae, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae						
Ulva linza L.	5	5	5	4	4	V^{4-5}
Other species						
complex *Cladophora vagabunda* (L.) Hoek	2	.	.	.	2	II

Notes. * – holotypus.

Sporadic species. Rel. 1: *Cladophora sericea* (Hudson) Kütz. 2. **Rel. 4**: *Callithamnion corymbosum* (Smith) Lyngb. 1. **Rel. 4**: *Sphacelaria cirrosa* (Roth) C. Ag. r. **Rel. 5**: *Ceramium tenuicorne* (Kütz.) Waern 1. **Rel. 5**: *Acrochaetium* sp. +.

Sampling data. Rel. 1: Germany, Kiel Bay, Dusternbrook, Baltic Sea, 17.07.2013, 54°19.783'N 10°8.973'E. **Rel. 2**: Germany, Gruner Brink, Fehmarn, Baltic Sea, 19.08.2013, 54°31.085'N 11°10.773'E. **Rel. 3**: Germany, Aschau, lagoon, Baltic Sea, 21.08.2013, 54°27.579'N 9°55.451'E. **Rel. 4**: Russia, cape Bol'shoy Utrish, Black Sea, 05.2012, 44°45.464'N 37°22.761'E. **Rel. 5**: Germany, Schonhagen, Baltic Sea, 21.08.2013, 54°38.001'N 10°1.975'E.

Author of relevés. Rel. 1–5: Afanasyev D.F.

Depth (m). Rel. 1: 0–0.08. **Rel. 2**: 0.15–0.3. **Rel. 3**: 0–0.15. **Rel. 4**: 0–0.5. **Rel. 5**: 0–0.3.

Salinity (‰). Rel. 1, 5: 14. **Rel. 2**: 15. **Rel. 3**: 12. **Rel. 4**: 17.

Plot size (m^2). Rel. 1–3, 5: 0.01. **Rel. 4**: 0.09.

Macroalgae cover (%). Rel. 1: 100. **Rel. 2**: 70–80. **Rel. 3**: 90. **Rel. 4**: 70. **Rel. 5**: 50–70.

Substrate. Rel. 1, 4: concrete. **Rel. 2, 5**: boulders. **Rel. 3**: pebbles and boulders.

projective cover of which in some plots can be significant. The number of species at the plots varies from 1 to 4. In total, 7 species of macroalgae in phytocenoses of the association have been identified.

Comment: In terms of the dominant approach the association *Ulva linza* + *Polysiphonia opaca* (C. Agardh) Moris & De Notaris was described for the Black Sea (original name: *Enteromorpha linza* + *Polysiphonia opaca*) by Kalugina-Gutnik (1975). According to this author, annual monodominant mesosaprobic phytocenoses of this association are confined to closed and open shores at depths of 0–5 m. During the study it was revealed 15 species of macroalgae for the association (Kalugina-Gutnik 1975). The association is quite similar to that described by us, however, it includes a number of species that we did not find at all under pollution conditions (in particular, *Polysiphonia opaca*), as well as species characteristic of other communities. Thus, only a part of the phytocenoses described by Kalugina-Gutnik (1975) can be considered as similar to those described by us, while the other part of her descriptions clearly refers to ecotone cenoses. JRC of the species composition of the associations described by us and by Kalugina-Gutnik (1975) is 33 %. In the Atlantic Ocean, off the coast of France, an association Ulvetum linzae Julve & Manneville 2006 was described from the position of floristic classification (Julve 2006). Such phytocenoses are found in a wide range of depths and are confined to eutrophic water areas. At the same time, the species composition of these phytocenoses is much richer, including at least 13 species, some of which characterized by high constancy and coverage. However, the description of the phytocenoses is invalid, since the authors did not provide the holotypus of the association. Thus, *Ulva linza*-dominated Atlantic communities should be redescribed under a different name.

Alliance: **Ulvae intestinalis–Ceramion virgati** Afanasyev & Abdullin all. nov.

Holotypus: Ulvae intestinalis–Ceramietum virgati (described in this paper).

Diagnostic species: *Ceramium virgatum* Roth

Description: Communities of the alliance are formed on solid substrates, at a depth from the water's edge to 0.5–1 m in waters with a salinity of 10–18 ‰, with a high content of nutrients and weak hydrodynamics. They are found in closed and eutrophic bays of the Black Sea.

Comment: All species, except *Callithamnion corymbosum* (Smith) Lyngbye, found in the communities of the alliance are cosmopolitan and subcosmopolitan species.

Association: **Ulvae intestinalis–Ceramietum virgati** Afanasyev & Abdullin **ass. nov.**

Holotypus: Rel. 8 in Table 3 in this paper

Table 3. Association Ulvae intestinalis–Ceramietum virgati Afanasyev and Abdullin ass. nov.

No. of relevé	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8***	**9**	**10**	**11**	**Constancy**
No. of species	3	4	3	3	5	2	3	3	2	5	5	
Diagnostic species of the ass. Ulvae intestinalis–Ceramietum virgati, the all. Ulvae intestinalis–Ceramion virgati, the ord. Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, and the cl. Sphacelarietea cirrosae Afanasyev & Abdullin 2022												
Ceramium virgatum Roth	2	1	+	1	1	2	1	3	1	2	1	V^{+-3}
Diagnostic species of the ass. Ulvetum intestinalis Feldmann 1937, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae												
Ulva intestinalis L.	3	1	1	1	1	5	5	5	3	2	1	V$^{1-5}$
Diagnostic species of the ass. Ulvetum linzae, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae												
Ulva linza L.	5	5	5	5	5	.	.	.	.	4	4	IV$^{4-5}$
Other species												
Callithamnion corymbosum (Smith) Lyngb.	.	1	.	.	.	.	1	1	.	.	+	II
Ulva flexuosa Wulfen	.	.	.	.	2	.	.	.	.	+	1	II
Ceramium siliquosum (Kütz.) Maggs & Hommersand	.	.	.	.	+	.	.	.	.	+	.	I

Notes. * – holotypus.

Sampling data. Rel. 1: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.292'N 37°46.686'E. **Rel. 2**: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.293'N 37°46.684'E. **Rel. 3**: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.293'N 37°46.686'E. **Rel. 4**: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.294'N 37°46.685'E. **Rel. 5**: Russia, Novorossiysk, central embankment, Black Sea, 29.05.2012, 44°43.294'N 37°46.684'E. **Rel. 6**: Russia, Novorossiysk, central embankment, Black Sea, 29.05.2012, 44°43.292'N 37°46.683'E. **Rel. 7**: Russia, Novorossiysk, central embankment, Black Sea, 29.05.2012, 44°43.29'N 37°46.682'E. **Rel. 8**: Russia, Novorossiysk, central embankment, Black Sea, 29.05.2012, 44°43.291'N 37°46.681'E. **Rel. 9**: Russia, cape Tuzla, Black Sea, 31.05.2012, 45°11.822'N 36°35.889'E. **Rel. 10**: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.292'N 37°46.687'E. **Rel. 11**: Russia, Novorossiysk, central embankment, Black Sea, 28.05.2012, 44°43.291'N 37°46.686'E.

Author of relevés. Rel. 1–11: Afanasyev D.F.

Depth (m). Rel. 1: 0–0.2. **Rel. 2–8, 11**: 0–0.3. **Rel. 9**: 0–0.5. **Rel. 10**: 0.1–0.3.

Salinity (‰). Rel. 1–8, 10, 11: 17. **Rel. 9**: 16.

Plot size (m^2). Rel. 1–8, 10, 11: 0.09. **Rel. 9**: 0.25.

Macroalgae cover (%). Rel. 1–3, 6–8, 10, 11: 90–100. **Rel. 4**: 100. **Rel. 5**: 95–100. **Rel. 9**: 70–90.

Substrate. Rel. 1–8, 10, 11: embankment concrete structures. **Rel. 9**: concrete.

Diagnostic species: those of the alliance.

Description: The communities are oligodominant, develop on solid substrates at a depth of up to 0.5–1 m. The communities contain only meso- and polysaprobiont species, which reflects the confinement of communities to water areas with a very high amount of biogenic elements. In addition, waters where association communities are found are characterized by low transparency, a high degree of silting of the substrate, and low intensity of water movement. The number of species at the plots varies from 2 to 5. In total, 6 species and then two tiers were identified in the communities. The upper tier is formed by the dominant species of *Ulva intestinalis* and *Ulva linza* and has a high projective cover – from 60–70 to 80–90 %. The second tier is represented by red algae *Ceramium virgatum* и *Callithamnion corymbosum*. The projective cover of this tier is relatively low (from 5 to 20–30 %).

Comment: In terms of the dominant approach the association *Ulva intestinalis* + *Ceramium virgatum* + *Callithamnion corymbosum* was described for the Black Sea by Kalugina-Gutnik (1975) (original name: *Enteromorpha intestinalis* + *Ceramium rubrum* + *Callithamnion corymbosum*). Earlier, similar phytocenoses were described by Morozova-Vodyanitskaya (1959) in the Black Sea. Polysaprobic phytocenoses with the dominance of the species mentioned above are confined to isolated polluted areas of bays. From 12 (Morozova-Vodyanitskaya 1959) to 28 (Kalugina-Gutnik 1975) species of macroalgae were indicated for these communities. Accordingly, JRCs of the species composition of the phytocenoses, which described in this study and previously, varies from 21 % (with the association described by Kalugina-Gutnik (1975) to 41 % (with the association described by Morozova-Vodyanitskaya (1959)). Thus, as in the case of previous communities, only a part of the previously described phytocenoses is similar to ours, while the other part, with a more diverse species composition, is clearly an ecotone.

Alliance: **Ulvae rigidae–Gelidion spinosi** Afanasyev & Abdullin **all. nov.**

Holotypus: Ulvae rigidae–Gelidietum spinosi (described in this paper).

Diagnostic species: *Ulva rigida* C. Ag., *Gelidium spinosum* (S.G. Gmelin) P.C. Silva.

Description: Communities of the alliance are formed on solid substrates, at a depth of 0 to 1–2 m in waters with a salinity of 16–18 ‰, with a high content of nutrients and quite intense water mobility. Communities are found in open and closed areas of the Black Sea coast.

Comment: Most of the species found at the communities of the alliance belong to cosmopolitan and subcosmopolitan species, and a smaller part, to species of Atlantic genesis.

Association: **Ulvae rigidae–Gelidietum spinosi** Afanasyev & Abdullin ass. nov.

Holotypus: Rel. 5 in Table 4 in this paper.

Diagnostic species: those of the alliance

Description: Oligodominant communities of the association develop at a depth of up to 1 m, on vertical and horizontal solid surfaces, in bays, in waters with a salinity of at least 16 ‰, rich in nutrients. The transparency of water in the areas where the communities grow, as a rule, is not lower than 1.5–2.0 m. The number of species at the plots is quite high and varies from 7 to 9. In total, 13 species of algae were identified in the communities, mainly belonging to the group of mesosaprobionts. It is possible to distinguish four tiers in the communities. The upper tier is formed by species of *Ulva*, primarily *U. rigida* and *U. intestinalis*, which determine the appearance of communities. The second tier is represented by bushes of *Cladophora vagabunda* (L.) Hoek, *Ceramium virgatum* and *Callithamnion corymbosum*. The projective cover of the tier varies from 15 to 30–40 %. The third tier is composed of fairly dense turfs of *Gelidium spinosum* and *Corallina officinalis* L. with a cover of up to 50 %. The fourth tier is represented by encrusting algae with a projective cover of 1–5 %.

Comment: In terms of the dominant approach the association *Ulva rigida – Ceramium virgatum* was described for the Black Sea (original name: *Ulva rigida – Ceramium rubrum*) (Kalugina-Gutnik 1975). According to Kalugina-Gutnik (1975), three-tier mesosaprobic phytocenoses of this association are confined mainly to protected, polluted areas at depths from 0.2 to 5–6 m. There were indicated 51 species of macroalgae for the association, including 21 with 100 % occurrence (Kalugina-Gutnik 1975). According to our data, the association *Ulva rigida – Ceramium rubrum* is very similar to ours, however, as in the previous cases, it includes a number

Table 4. Association Ulvae rigidae–Gelidietum spinosi Afanasyev and Abdullin ass. nov.

No. of relevé	1	2	3	4	5*	Constancy
No. of species	9	7	8	8	7	
Diagnostic species of the ass. Ulvae rigidae–Gelidietum spinosi, and the all. Ulvae rigidae–Gelidion spinosi						
Ulva rigida C. Ag.	.	1	1	2	2	IV^{1-2}
Diagnostic species of the ass. Ulvae rigidae–Gelidietum spinosi, the all. Ulvae rigidae–Gelidion spinosi, the ord. Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, and the cl. Sphacelarietea cirrosae Afanasyev & Abdullin 2022						
Gelidium spinosum (S.G. Gmelin) P.C. Silva	1	2	1	1	3	V^{1-3}
Diagnostic species of the ass. Ulvetum intestinalis Feldmann 1937, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae						
Ulva intestinalis L.	4	4	4	3	3	V^{3-4}
Diagnostic species of the ass. Ulvetum linzae, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae						
Ulva linza L.	.	.	+	.	1	II
Diagnostic species of the ass. Ulvae intestinalis–Ceramietum virgati, the all. Ulvae intestinalis–Ceramion virgati, the ord. Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, and the cl. Sphacelarietea cirrosae Afanasyev & Abdullin 2022						
Ceramium virgatum Roth	+	1	+	.	2	IV^{+-2}
Other species						
Corallina officinalis L.	2	1	+	2	3	V^{+-3}
complex *Cladophora vagabunda* (L.) Hoek	+	.	1	3	2	IV^{+-3}
Ceramium deslongchampsii Chauvin ex Duby	+	.	1	+	.	III^{+-1}
Callithamnion corymbosum (Smith) Lyngb.	1	1	.	.	.	II
indet. Corallinales	+	.	.	+	.	II

Notes. * – holotypus.

Sporadic species. Rel. 1: *Ceramium siliquosum* var. *elegans* (Roth) G. Furnari +. **Rel. 2**: *Acrochaetium* sp. +. **Rel. 4**: *Ulva flexuosa* Wulfen +.

Sampling data. Rel. 1: Russia, Novorossiysk, central embankment, Black Sea, 23.05.2012, 44°42.075'N 37°47.338'E. **Rel. 2**: Russia, Novorossiysk, central embankment, Black Sea, 23.05.2012, 44°41.843'N 37°47.416'E. **Rel. 3**: Russia, Novorossiysk, central embankment, Black Sea, 23.05.2012, 44°41.738'N 37°47.459'E. **Rel. 4**: Russia, Novorossiysk, central embankment, Black Sea, 23.05.2012, 44°41.935'N 37°47.358'E. **Rel. 5**: Russia, Novorossiysk, central embankment, Black Sea, 23.05.2012, 44°41.658'N 37°47.514'E.

Author of relevés. Rel. 1–5: Afanasyev D.F.

Depth (m). Rel. 1–5: 0–0.7.

Salinity (‰). Rel. 1–5: 17.

Plot size (m^2). Rel. 1–5: 0.16.

Macroalgae cover (%). Rel. 1, 4: 70. **Rel. 2**: 70–80. **Rel. 3**: 80. **Rel. 5**: 90.

Substrate. Rel. 1–5: boulders.

of species found in other communities. This fact allows us to consider part of the cenoses attributed by Kalugina-Gutnik to this association, as an ecotone. JRC calculated for the associations we described here and those identified previously is 25 %. However, if we do not take into account the species that Kalugina-Gutnik is considered as random, then the similarity increases to 62 %.

In the Mediterranean, several associations are described with the domination of the species found in the Black Sea cenoses: Ulvetum rigidae Berner 1931, Ceramietum rubri Berner 1931, Corallinetum officinalis Berner 1931, Dictyopteretum polypodiodis Berner 1931 and Pterocladiello–Ulvetum rigidae Molinier 1958. The first four associations were described for the first time on the coast of Marseille, the latter – on Cape Corsica. Currently, they are found in the entire Mediterranean Sea, including the Adriatic (Lovric 1978, Giaccone et al. 1994, Blasi 2010).

The association Ulvetum rigidae Berner 1931 develops on solid substrates of the upper sublittoral, in sheltered bays, sometimes in littoral basins, under conditions of intense illumination, calm hydrodynamic, in waters enriched by nutrients. Phytocenoses are tolerant to significant low salinity and high temperatures in the summer. Communities are species poor, but with a high abundance of green algae (Giaccone et al. 1994). Berner (1931) named the association Ulvetum lactucae, however, according to the latest data, *Ulva lactuca* L. does not occur in the Mediterranean (Cormaci et al. 2014). Due to the fact that the most common species of the genus in the Mediterranean Sea is *Ulva rigida*, which was previously incorrectly identified as *U. lactuca* (Boudouresque & Perret 1977), it was proposed to rename the association to Ulvetum rigidae. Later, based on the assumption that *U. rigida* is a synonym of *U. laetevirens* J.E. Areschoug, some authors began to use the name Ulvetum laetevirentis for the association (Giaccone et al. 1994). However, these taxa are now separated again (Cormaci et al. 2014). Moreover, *U. laetevirens* has been recognized as a synonym of *U australis* Areschoug, a species that was accidentally introduced into the Mediterranean in the 1980s probably with oyster aquaculture (Verlaque et al. 2015), and it was also shown that this species, in contrast to *U. rigida*, occurs mainly in an environment with a low concentration of nutrients (Sfriso 2010).

The conditions in which communities of the ass. Pterocladiello–Ulvetum rigidae Molinier 1958 association develop are similar to those described for the ass. Ulvetum rigidae, with a difference in the direction of less illumination and higher intensity of hydrodynamics (Giaccone et al. 1994). The ass. Ceramietum rubri Berner 1931 develops at shallow depths in biotopes with low salinity, weak hydrodynamics, and low light intensity. The maximum intensity of development of the community of this association is reached in the spring (Giaccone et al. 1994). Phytocenoses of the ass. Corallinetum officinalis Berner 1931 are formed in biotopes with low salinity, intense hydrodynamics and under intense lighting conditions (Giaccone et al. 1994). The ass. Dictyopteretum polypodiodis Berner 1931 occurs in areas of low light intensity with weak hydrodynamics (Giaccone et al. 1994).

Despite the obvious similarity in the composition of the dominant species, the Black Sea communities differ from the Mediterranean ones in the absence of many species, including some diagnostic for the Mediterranean associations, for example: *Deltalsia parasitica* (Hudson) Díaz-Tapia & Rodríguez-Buján, *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier, *Dictyopteris polypodioides* (De Candolle) J.V. Lamouroux, *Chondracanthus acicularis* (Roth) Fredericq. These species in the Black Sea either do not occur at all, or are rare.

Of all the listed Mediterranean associations, the closest to the Black Sea phytocenoses is Ulvetum rigidae Berner 1931. The Black Sea ass. Ulvae rigidae–Gelidietum spinosi can be considered as a depleted variant of the Mediterranean Ulvetum rigidae Berner 1931.

Ordination analysis

Ordination analysis confirmed the reliability of our classification and showed a clear separation of all defined communities from each other. PCA analysis revealed two main factors influencing the floristic composition of communities (Fig. 2; eigenvalues: axis 1 – 0.503, axis 2 – 0.139). The first axis is interpreted as salinity. The extreme position on the right on the first axis is occupied by group D (ass. Ulvae rigidae–Gelidietum spinosi), whose salinity is not less than 16 ‰, whereas the extreme position on the left is occupied by groups A (ass. Ulvetum intestinalis Feldmann 1937) and B (ass. Ulvetum linzae), whose salinity varies from 8 to 15 ‰. The second axis, most likely, can be interpreted as nutrient enrichment with associated turbidity. The lower position on the second axis is occupied by groups A and C. The communities of these groups were revealed in the most eutrophicated areas with low transparency; whereas the MACs of other groups (B and D) were found mainly in habitats with mesotrophic conditions with higher transparency.

DISCUSSION

According to our results, in the studied areas of the Black, Azov and Baltic Seas, all meso- and polysaprobiont vegetation of solid sublittoral substrates belongs to one class Ulvae intestinalis–Ulvetea linzae, one order Ulvae intestinalis–Ulvetalia linzae, and three alliances: Ulvae intestinalis–Ulvion linzae, Ulvae intestinalis–Ceramion virgati, and Ulvae rigidae–Gelidion spinosi. In the Black Sea, under conditions of a wider salinity gradient, there are communities of all three alliances, while in the Azov and Baltic Seas – only communities belonging to the alliance Ulvae intestinalis–Ulvion linzae noted.

Of the alliances we have identified, Ulvae intestinalis–Ulvion linzae has a central position in the order Ulvae intestinalis–Ulvetalia linzae and in the class Ulvae intestinalis–Ulvetea linzae. Associations of the alliance are species poor and occur in a wide range of salinity (from fresh waters to waters with oceanic salinity), trophicity (from moderate to significant). Considering the floristic composition of communities, along with *Ulva* species, only *Cladophora* species are quite often and abundantly found. The species that make up these communities are predominantly annuals, with a maximum of development in the spring and summer. The nature of communities is opportunistic. Both of the diagnostic species of the alliance – *Ulva intestinalis* and *U. linza* – are relatively cosmopolitan species known to form blooms in a diverse range of habitats around the world, especially in eutrophic conditions (Cummins et al. 2004, Kang et al. 2016). *Ulva intestinalis* exhibits rapid nutrient uptake, growth, and osmoregulation,

Table 5. The synoptic table of MAC of the Black, Azov and Baltic Seas in meso- and polysaprobic sublittoral zones

Association	1*	2	3	4
Alliances	**UU**	**UU**	**UC**	**UG**
Number of species	3	7	6	13
Number of relevés	16	5	11	5
Diagnostic species of the ass. Ulvetum intestinalis Feldmann 1937, the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae				
Ulva intestinalis L.	V^{1-5}	.	V^{1-5}	V^{3-4}
Diagnostic species of the Ulvetum linzae (Julve & Manneville 2006), the all. Ulvae intestinalis–Ulvion linzae, the ord. Ulvae intestinalis–Ulvetalia linzae, and the cl. Ulvae intestinalis–Ulvetea linzae				
Ulva linza L.	.	V^{4-5}	IV^{4-5}	II
Diagnostic species of the ass. Ulvae intestinalis–Ceramietum virgati, the all. Ulvae intestinalis–Ceramion virgati, the ord. Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, and the cl. Sphacelarietea cirrosae Afanasyev & Abdullin 2022				
Ceramium virgatum Roth	.	.	V^{+-3}	IV^{+-2}
Diagnostic species of the ass. Ulvae rigidae–Gelidietum spinosi, and the all. Ulvae rigidae–Gelidion spinosi				
Ulva rigida C. Ag.	.	.	.	IV^{1-2}
Diagnostic species of the ass. Ulvae rigidae–Gelidietum spinosi, the all. Ulvae rigidae–Gelidion spinosi, the ord. Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, and the cl. Sphacelarietea cirrosae Afanasyev & Abdullin 2022				
Gelidium spinosum (S.G.Gmelin) P.C.Silva	.	.	.	V^{1-3}
Other species				
complex *Cladophora vagabunda* (L.) Hoek	.	II	.	IV^{+-3}
Callithamnion corymbosum (Smith) Lyngb.	.	.	II	II
Corallina officinalis L.	.	.	.	V^{+-3}
Ceramium deslongchampsii Chauvin ex Duby	.	.	.	III^{+-1}
Ulva flexuosa Wulfen	.	.	II	.
indet. Corallinales	.	.	.	II
Vertebrata reptabunda (Suhr) Díaz-Tapia & Maggs	I	.	.	.
Ceramium siliquosum (Kütz.) Maggs & Hommersand	.	.	I	.

* Notes: 1 – ass. Ulvetum intestinalis Feldmann 1937; 2 – ass. Ulvetum linzae ass. nov.; 3 – ass. Ulvae intestinalis–Ceramietum virgati ass. nov.; 4 – ass. Ulvae rigidae–Gelidietum spinosi ass. nov. alliances: **UU** – Ulvae intestinalis–Ulvion linzae all. nov.; **UC** – Ulvae intestinalis–Ceramion virgati all. nov.; **UG** – Ulvae rigidae–Gelidion spinosi all. nov.

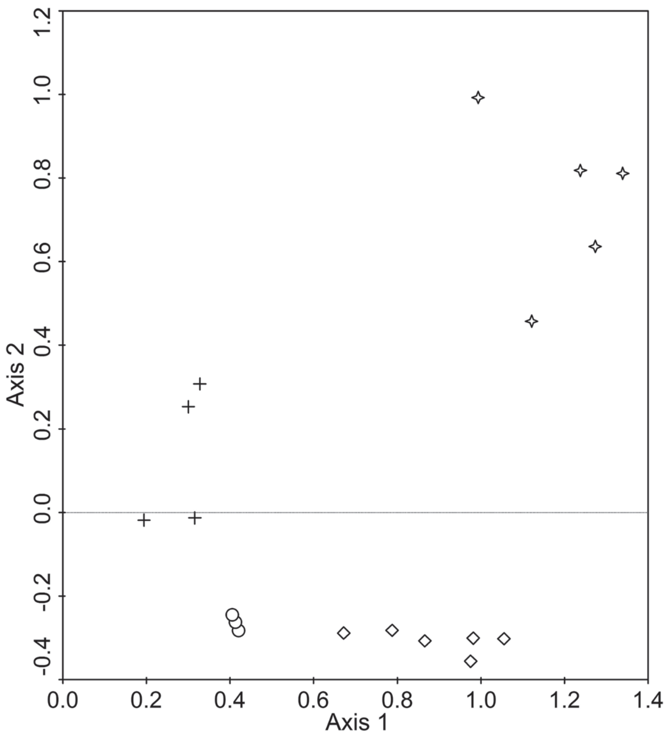

Figure 2 PCA of meso- and polysaprobiont macroalgae communities of the Black, Azov and Baltic Seas sublittoral, with axis 1 and 2 represented. A (circles): Ulvetum intestinalis Feldmann 1937, B (crosses): Ulvetum linzae, C (diamonds): Ulvae intestinalis–Ceramietum virgati, D (stars): Ulvae rigidae–Gelidietum spinosi

particularly in conditions of reduced salinity and light. Many populations of *U. intestinalis* can survive and grow in freshwater conditions, and the negative effects of low salinity can be offset by increased nutrient concentrations. Most *U. intestinalis* ecotypes, however, exhibit very broad salinity tolerance with optimal salinity for growth around 15–24 ‰ (Edwards et al. 1988, Martins et al. 1999, Kamer & Fong 2000, 2001, Cohen & Fong 2004, McAvoy & Klug 2005). It is known, that in the brackish environment (10 ‰) enriched by nutrients the adult thalli of *U. linza* showed two- and three-times higher growth rates than in the inshore (30 ‰, enriched by nutrients) and offshore (30 ‰, depleted by nutrients) environments, respectively (Kang et al. 2016). It was suggested that brackish areas facilitate the initiation of blooms of *U. linza* with subsequent movement of floating thalli from estuaries to the inshore and then the offshore environments (Kang et al. 2016).

An increase of water salinity and stabilization of marine conditions leads to an increase of the floristic richness of communities. Phytocenoses of the alliance Ulvae intestinalis–Ceramion virgati are able to tolerate low salinity up to 10 ‰ and are found in meso- and polysaprobic conditions. Communities of the alliance Ulvae rigidae–Gelidion spinosi occur at a salinity of at least 16‰ in mesosaprobic waters.

It should be noted that the diagnostic species of the alliances Ulvae intestinalis–Ceramion virgati and Ulvae rigidae–Gelidion spinosi – *Ceramium virgatum* and *Gelidium spinosum*, respectively, are also diagnostic species of the class of myxomesohaline oligosaprobiotic vegetation Sphacelarietea cirrosae Afanasyev & Abdullin 2022 and of the order Sphacelarietalia cirrosae Afanasyev & Abdullin 2022 (Afanasyev & Abdullin 2022). This allows us to consider these two alliances as ecotone communities between the alliance Ulvae intestinalis–Ulvion linzae, which develops in trophic waters with low salinity, and the class Sphacelarietea cirrosae – the Black Sea vegetation of clear waters.

Communities of the class Ulvae intestinalis–Ulvetea linzae under condition of a decrease in water trophicity and/or an increase of depth, often form mixed ecotone communities with representatives of other syntaxa. For example, communities, noted for moderately polluted areas of the Black Sea, with the dominance of *Cystoseira* sensu lato species (which are usual for the oligosaprobiotic alliance Gongolarion barbatae Afanasyev & Abdullin 2022, the order Sphacelarietalia cirrosae Afanasyev & Abdullin 2022, the class Sphacelarietea cirrosae Afanasyev & Abdullin 2022) also include *Ulva* species (Kalugina-Gutnik 1975, Gromov 1998). In the Baltic Sea an ecotone cenoses form between *Fucus vesiculosus*-dominated communities assigned to the alliance Ascophyllion nodosi Julve in Bültmann et al. 2015, and communities of the alliance Ulvae intestinalis–Ulvion linzae. We have identified four such mixed communities depending on depth, salinity and water mobility (Afanasyev et al. 2022).

In the Mediterranean, all meso- and polysaprobiont vegetation of solid sublittoral substrates is currently assigned to one class (Cystoseiretea Giaccone 1965), one order (Ulvetalia lactucae Molinier 1960), and two alliances (Ulvion rigidae Berner 1931 corr. Giaccone et al. 1994 and Ulvo lactucae-Corallinion mediterraneae Vignes ex Julve 1992) (Mucina et al. 2016). However, the Mediterranean order Ulvetalia lactucae Molinier 1960 with its two alliances can be included in the class of meso- and polysaprobiont vegetation with the dominance of green algae of the genus *Ulva*, proposed here. On the one hand, it will be a continuation of the ecological series of meso- and polysaprobiotic phytocenoses along the gradient of salinity increasing and, on the other hand, it will be an ecotone with the Mediterranean–Atlantic class of oligosaprobiotic vegetation Cystoseiretea Giaccone 1965. This issue still requires further investigation.

In general, according to our studies, photophilic meso- and polysaprobic myxomesohaline vegetation of the north-eastern part of the Black Sea, the southern part of the Sea of Azov and the western part of the Baltic Sea is represented by four associations from three alliances, while the similar vegetation of the upper infralittoral of the Mediterranean includes 8 associations from two alliances. Thus, the small number of species in the myxomesohaline and geologically young seas also determines the smaller number of communities. At the same time, if the Mediterranean associations occupy different ecological niches according to the gradients of illumination and hydrodynamics, then the same most eurybiont cenoses predominate in the myxomesohaline seas along the entire length of these gradients.

No analogues of some association's characteristic of the extreme variants of ecological niches were found in the myxomesohaline seas. There are no analogues of the ass. Dictyopteretum polypodiodis Berner 1931, which occurs in the Mediterranean under conditions of high nutrients load combined with low illumination and weak water mobility. We have previously shown that a very limited number of species penetrate into the Black Sea from the Mediterranean oligosaprobiont communities from horizons with low illumination (Afanasyev & Abdullin 2022). Thus, a similar pattern discovered for meso- and polysaprobiont vegetation of the Black Sea.

CONCLUSIONS

The results obtained allow us to identify a new class of vegetation – meso- and polysaprobic sublittoral vegetation of solid substrates of the myxomesohaline seas. The communities of the class are composed mainly of eurybiont, cosmopolitan species, growing in a very wide range of salinity. In general, the communities of the class Ulvae intestinalis–Ulvetea linzae, especially the phytocenoses of its central alliance Ulvae intestinalis–Ulvion linzae, are species poor. An increase of water salinity is accompanied by the appearance of local marine flora in communities, which makes it possible to consider such communities as an ecotone. Thus, our work lays the foundation for the development of a classification system for opportunistic marine benthic vegetation, which can be used to assess vegetation dynamics in areas of increasing eutrophication all over the world.

The syntaxonomic synopsis of meso- and polysaprobic vegetation of the sublittoral zone of the myxomesohaline seas of Europe

Class
Order
Alliance
Association

Ulvae intestinalis–Ulvetea linzae Afanasyev & Abdullin **cl. nov.**

Ulvae intestinalis–Ulvetalia linzae Afanasyev & Abdullin **ord. nov.**

Ulvae intestinalis–Ulvion linzae Afanasyev & Abdullin **all. nov.**

Ulvetum intestinalis Feldmann 1937

Ulvetum linzae Afanasyev & Abdullin **ass. nov.**

Ulvae intestinalis–Ceramion virgati Afanasyev & Abdullin **all. nov.**

Ulvae intestinalis–Ceramietum virgati Afanasyev & Abdullin **ass. nov.**

Ulvae rigidae–Gelidion spinosi Afanasyev & Abdullin **all. nov.**

Ulvae rigidae–Gelidietum spinosi Afanasyev & Abdullin ass. nov.

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