

NOVEL SPECIES RECORD OF *ULVA INTESTINALIS* (CHLOROPHYTA, ULVACEAE) FOR KAMCHATKA (NE ASIA) FROM AN ISOLATED INLAND LOCALITY

Roman E. ROMANOV * and Olga A. CHERNYAGINA **

* Komarov Botanical Institute of the Russian Academy of Sciences, 2 Professora Popova St., Saint Petersburg, Russian Federation, RU-197376, romanov_r_e@mail.ru, ORCID: 0000-0002-6137-3586.

** Kamchatka Branch of the Pacific Geographical Institute of the Far East Branch of the Russian Academy of Sciences, Petropavlovsk-Kamchatsky, Russian Federation, RU-683000, kamchatika@mail.ru, ORCID: 0000-0003-0801-8961.

DOI: 10.2478/trser-2024-0001

KEYWORDS: Esso, floristic novelty, green algae, Kamchatka, thermal springs.

ABSTRACT

A novel inland record of the green alga *Ulva intestinalis* was found in central Kamchatka, in a brackish stream originating from cooled waters of drilled thermal springs. This species was observed in May 2017, but not encountered again at the same site despite targeted search. Its occurrence in central Kamchatka was surprising given the natural environment, and was probably related to both the presence of thermal springs and human disturbance. The sporadic inland appearance of *U. intestinalis* in this region suggests it may be unable to maintain stable populations in this region, and experience repeated local extinctions and recolonizations.

RÉSUMÉ: Enregistrement d'une nouvelle espèce d'algue, *Ulva intestinalis* (Chlorophyta, Ulvaceae) dans la péninsule du Kamtchatka (Asie du Nord-Est) dans une localité isolée de l'intérieur des terres.

La nouvelle espèce d'algue verte *Ulva intestinalis* (Chlorophyta, Ulvaceae) a été trouvée dans le centre de la péninsule du Kamtchatka, dans un cours d'eau saumâtre provenant des eaux refroidies de sources thermales forées. Cette espèce a été repérée pour la première fois en mai 2017 et n'a plus été revue sur le même site malgré des recherches ciblées. Sa présence dans le centre du Kamtchatka contraste clairement avec le contexte environnemental naturel et était probablement liée à la fois, à la présence de sources thermales et à la transformation humaine de l'environnement. L'apparition sporadique d' *U. intestinalis* à l'intérieur des terres dans cette région suggère qu'elle pourrait être incapable de maintenir des populations stables dans cette région, de connaître des extinctions et des recolonisations locales répétées.

REZUMAT: Înregistrări noi ale speciilor de *Ulva intestinalis* (Chlorophyta, Ulvaceae) pentru Kamchatka (NE Asia) din localitatea izolată interioară.

O nouă înregistrare continentală a algei verzi *Ulva intestinalis*, a fost găsită în centrul Kamchatka, într-un curs de apă salmastru provenit din apele răcite ale izvoarelor termale forate. Această specie a fost observată în mai 2017, dar nu a mai fost întâlnită în același sit, în ciuda căutărilor direcționate. Apariția sa în centrul Kamchatka a fost surprinzătoare, având în vedere mediul natural și a fost probabil legată atât de prezența izvoarelor termale, cât și de perturbarea umană. Apariția sporadică a *U. intestinalis* în această regiune sugerează că ar putea fi incapabilă să mențină populații stabile în această regiune și să experimenteze extincții și recolonizări locale repetitive.

INTRODUCTION

Many green algae in the genus *Ulva* L. are economically important; useful in the case of cultivated edible species, or causing grave economic damage in green tide algal blooms (Zhang et al., 2019; Fort et al., 2020; Harsha Mohan et al., 2023). Species with tube thalli, earlier placed in the genus *Enteromorpha* Link (Hayden et al., 2003), can colonize inland waters (Bliding, 1963; Li and Bi, 1998; Messyasz, 2009; Mareš et al., 2011; Rybak, 2015, 2018, 2021; Saber et al., 2018; Škaloud et al., 2018). Inland populations are generally found in hard, brackish waters of arid and semiarid areas that have hot summers, e.g., southeastern Europe (Zhakova, 2006; Zinchenko et al., 2021; iNaturalist, 2024; Romanov, unpubl. data), western and central Asia (Muzaferov, 1965; Nahucrishvili, 1986; Maulood et al., 2013; Zhakova, 2013; Tekebaeva et al., 2014; Sametova et al., 2019; Mohebbi and Zarezadeh, 2023; Romanov, unpubl. data), southern Ural (Yatsenko-Stepanova and Ignatenko, 2018), southern Siberia (Safonova and Ermolaev, 1983; Kuklin, 2017; Efremov, 2018; Tokar, 2018; Bazarova and Kuklin, 2021; Romanov, unpubl. data), Mongolia (Tsegmid and Baigal-Amar, 2018), and China (Li and Bi, 1998). Inland populations are also known from northeastern Siberia (Skvortsov, 1917; Kopyrina et al., 2020) and even in the lowermost locality of the Earth (-455 m below sea level) near Dead Sea (Barinova et al., 2004).

Thermal springs, as well as manmade water bodies, often have temperature regimes and chemical compositions that contrast with surrounding aquatic habitats, analogous biogeographically to isolated islands or oases (Glazier, 2009). Thermal springs are widely recognized as key habitats and biodiversity hotspots (see references in Cantonati, 2022). In addition to species of algae and cyanobacteria (e.g., Elenkin, 1914; Doemel and Brock, 1971; Gromov et al., 1991; Nikitina, 2005; Cantonati et al., 2010; Beauger et al., 2022; see references in Cantonati, 2022), thermal springs can harbor populations of macroscopic algae, e.g., Characeae, far from their main distributional range dictated by climatic and other large-scale ecological factors (e.g., Langangen, 2000; Romanov and Chernyagina, 2018; Langangen et al., 2020; Romanov and Vishnyakov, 2023). The same seems to be true for some water bodies with artificial thermal effluents (Romanov et al., 2018). This paper describes a recent isolated record of *Ulva intestinalis* L. (formerly *Enteromorpha intestinalis* (L.) Link) from central Kamchatka, a humid continental area with subarctic climate, i.e., cold without distinct wet or dry seasons and having cold summers (Köppen-Geiger climate classification = Dfc, Peel et al., 2007), and mostly soft oligotrophic fresh waters (Litvinenko and Zakharikhina, 2020) that are unlike the normal inland habitats of *Ulva* (e.g., Messyasz and Rybak, 2010).

MATERIAL AND METHODS

Study area

The survey of aquatic habitats associated with thermal springs was done around Esso Village, located within Bystrinsky Nature Park, a section of the UNESCO World Heritage “Volcanoes of Kamchatka” area belonging to the Far East monsoon area (Kondratyuk, 1974) and having continental climate with a cold winter (below to -42°C), short warm summer (up to 32°C) and small annual precipitation (390 mm). The natural thermal effluents were altered after human changed the environment. Groundwater with a temperature at drill outlet of 72-100°C is collected from diverse outlets into a pipe and is released into a pool. The *Ulva* was found in the outflow on this pool (Fig. 1). The waters are siliceous (H_2SiO_3 – 169 mg.dm⁻³), weakly alkaline to alkaline (pH 8.9-9.8), with a salinity of 1.0-1.5 g.dm⁻³. Components are sulphates (SO₄), calcium, and sodium (Ca-Na), with trace components (As, B, F, Li). The nitrogen is the main dissolved gas (Kiryukhin et al., 2010; Muradov et al., 2013).

Sampling and laboratory study

The plants were collected by hand and stored in 70% ethanol. The images were taken using a Carl Zeiss Axiolab A microscope equipped with an AxioCam MRs-5 digital camera. A voucher specimen was deposited in the collection of algae of the herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences (LE). The species was identified using key references (Bliding, 1963; Vinogradova, 1974, 1979; Moshkova and Hollerbach, 1986; Li and Bi, 1998; Ichihara et al., 2009; Mareš et al., 2011; Škaloud et al., 2018). Taxonomy follows the most recent reference for continental species (Škaloud et al., 2018). Although morphological variability of this genus complicates species identification and sometimes require genetic analyses (Bartolo et al., 2022; Steinhagen et al., 2023), the morphological traits of the studied population were clear enough for identifying our specimens as *U. intestinalis*.

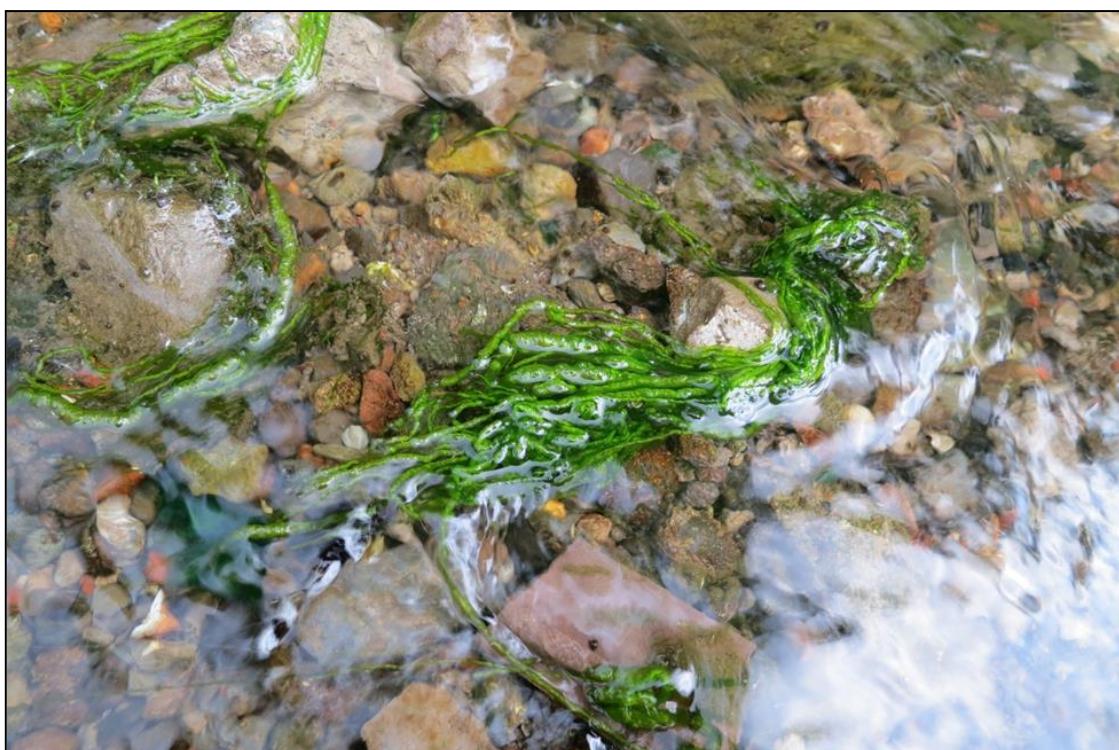


Figure 1: General appearance of *Ulva intestinalis*
in a stream flowing from the swimming basin collecting water
from the drilled thermal springs in the villages of Esso,
Kamchatka during May 2017.

RESULTS AND DISCUSSION

Studied plants, their description and habitat

Studied specimens

Kamchatka Krai, Bystrinsky District, settlement of Esso, a stream outflow from the pool receiving water from thermal effluents, 55.924135° N, 158.701082° E, 490 m a.s.l., attached to the stones, at the depth of few cm, mainly in upper water layer, at water temperature of 22-23°C, 29 May 2017, abundant, O. A. Chernyagina (LE).

Description of specimens

The light fresh green wrinkled tubular thalli were harboring air bubbles inside, attached to the stones in clusters, up to 10 cm in length, less than 0.5 cm in width, had more or less uniform width throughout most of the plant, gradually narrowed to the base, unbranched at general appearance, very rarely shortly branched (Figs. 1 and 2). The branches were not filiform. They were always short in comparison with main tube width. No branches of second order and proliferations were found. Cells were placed without any order throughout thallus, and only short irregular lines of cells could be spotted at short branches and in basal parts of plants. Cells were more or less isodiametric to somewhat elongated, up to 2 times longer of width, 9.0-10.7 x (4.8)5.4-8.4 μ m. Almost exclusively one pyrenoid per cell was traceable.

The studied specimens were in good agreement to descriptions of this species (see list of references in “Materials and methods”), but did differ with smaller cell size. They were overlapping in this trait expression, but were not identical in all characters with *Enteromorpha intestinalis* f. *saprobica* Vinogr. reported from the Sea of Japan and the Black Sea (Vinogradova, 1974; Moshkova and Hollerbach, 1986).

Habitat and frequency of occurrence

The ice-free stream (Fig. 1) from the large water-cooling swimming pool collecting cooled waters from drilled natural thermal springs called Esso springs after their use for house heating. The plants were found in May 2017 only, and not found at the same site in August 2017, nor during subsequent visual surveys conducted 2-3 times per year in 2018-2024 by O. A. Chernyagina.

Ecology and distribution of *U. intestinalis* in neighboring regions

The closest known inland localities of *U. intestinalis* are from thermokarst lakes in the basin of the Lena River in NE Siberia (Skvortsov, 1917; Kopyrina et al., 2020) similar climate, i.e., cold, without dry season and with very cold winter (Köppen-Geiger classification = Dfd, Peel et al., 2007), and in urban stream in Primorye Territory (Kukharenko, 1989) from cold, with dry winter and warm summer (Dwb; Peel et al., 2007). In southern Siberia, this species was found in hardwater, circumneutral to alkaline, slightly to properly brackish, mesotrophic and eutrophic lakes, ponds, endorheic rivers in steppe and forest-steppe (Tripolitowa, 1928; Pirozhnikov, 1929; Yakubova, 1953; Andreev et al., 1963; Khalfina, 1964; Ermolaeva, 1967; Safonova and Ermolaev, 1983; Safonova and Shishkina, 1986; Sviridenko, 2000; Kipriyanova and Romanov, 2010; Efremov and Sviridenko, 2016; Sviridenko et al., 2016; Tokar, 2018; Romanov, unpubl. data), as well as in rivers with elevated sulphates, brackish endorheic lakes, and in drainage waterbodies of the ash yard of big thermal power in steppe landscapes (Kuklin and Zamana, 2011; Kuklin, 2017; Bazarova and Kuklin, 2021). These sites are sited in areas with two types of climate: mostly cold, without dry season, with warm summer and mostly cold, with dry winter, with cold summer (Dfb and Dwc; Peel et al., 2007). The continental sites of this species are broadly spread across Eurasia, but seem to be concentrated in arid and subarid regions with brackish water bodies (see all references cited above).

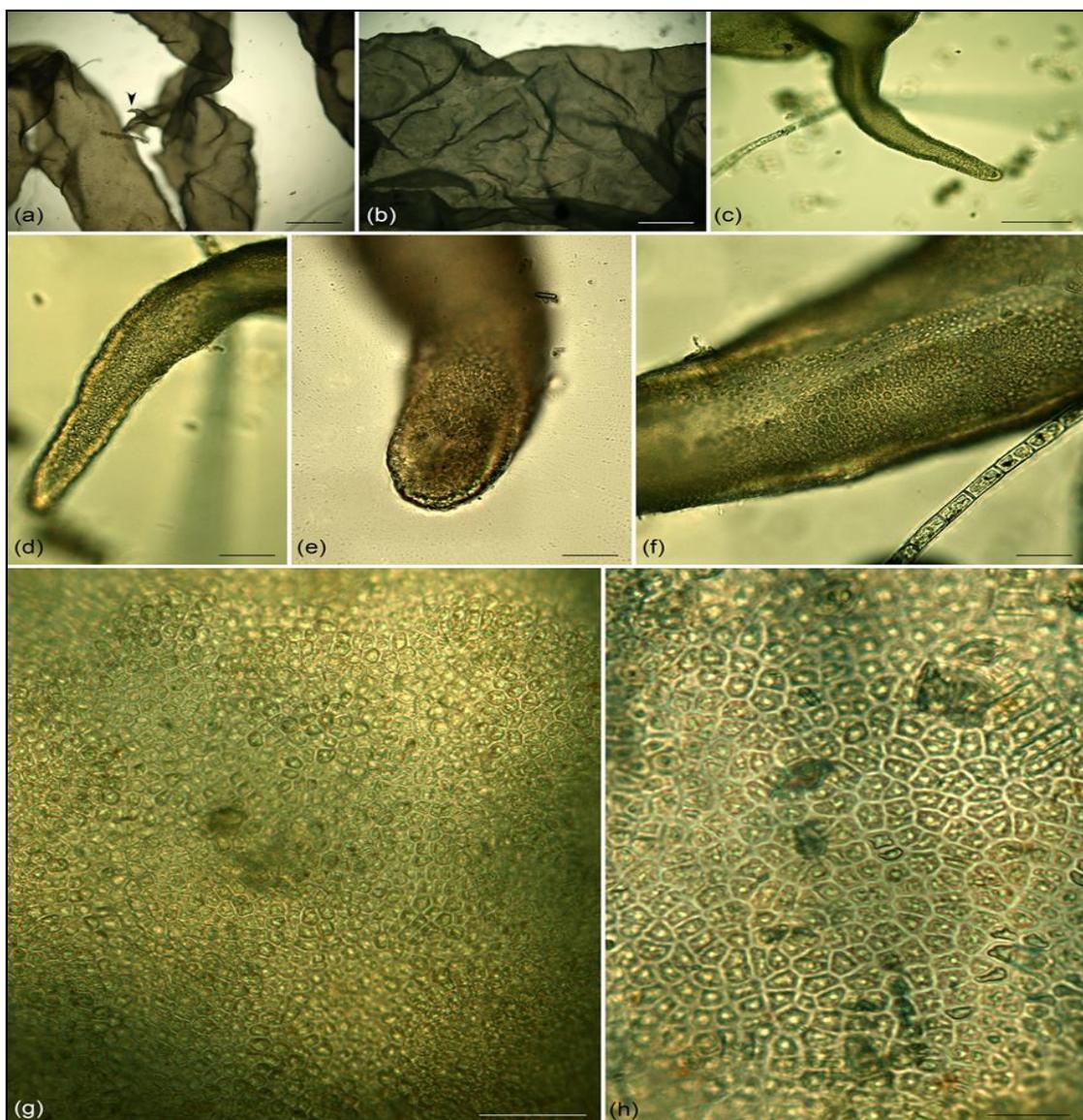


Figure 2: Key morphological traits of *Ulva intestinalis* from a stream flowing from the basin collecting water from the drilled thermal springs in Esso village, Kamchatka in May 2017 (LE): a, b – wrinkled tubular thalli with short robust primary branches (arrowhead), c – short robust primary branch, d – cells at primary branch illustrated at c, e – view of tangential irregular cross section at basal part of plant, f – lateral view of basal part of plant with narrow strip of cells having different general appearance, i.e., more narrow, elongated and with degraded chloroplasts, a filament of *Tribonema viride* Pascher (Ochrophyta, Xanthophyceae, Tribonemataceae) is visible at low right corner, g, h – irregular placement of cells with solitary pyrenoids in wide parts of plant, view from above. Scale bars: a, b – 400 µm, c – 200 µm, d-g – 40 µm, h – 20 µm.

It is unclear if *U. intestinalis* can sustain reproduction in study locality. This species could be occasionally colonize the site, in agreement with the *r*-strategy of opportunistic *Ulva* species (Burkholder and Glibert, 2013; Fort et al., 2020). Such species are widely known benefit from excessive anthropogenic nitrogen (Fort et al., 2020), making them useful ecological indicators of eutrophic waters (e.g., Areco et al., 2021; Rybak, 2021). Considering rare and unstable occurrence of *U. intestinalis* in inland Kamchatka, it could be there as a rare aquatic weed unable to maintain a stable population. Aquatic birds, known to transport and disperse a wide spectrum of plants, may be their main dispersal vectors (Lovas-Kiss et al., 2018).

Whereas seacoasts and estuaries are typical habitats for *Ulva* species worldwide (see references in Rybak, 2018; Bartolo et al., 2022), species with tubular thalli (former genus *Enteromorpha*) are also known from inland localities (Blidig, 1963; Moshkova and Hollerbach, 1986; Li and Bi, 1998; Ichihara et al., 2009; Messyasz, 2009; Mareš et al., 2011; iNaturalist, 2024). *Ulva intestinalis* has not been reported from new sites in marine habitats of Kamchatka and neighboring areas after its first records by Ruprecht and Woronichin from southern coasts of this peninsula (Ruprecht, 1850; Woronichin, 1914; Vinogradova, 1974, 1979; Klochkova and Berezovskaya, 1997, 2001; Klochkova et al., 2009a, b; Selivanova and Zhigadlova, 1997a, b, 2009a, b). According to Vinogradova (1979), *U. intestinalis* is not typical for Far East seas. The same can be suggested for continental water bodies of Primorye Territory (Kukharenko, 1989; Medvedeva and Nikulina, 2014). Close marine localities are known from the Okhotsk Sea and the Sea of Japan in Sakhalin Region, Khabarovsk Territory and Primorye Territory (Ruprecht, 1850; Sinova, 1928; Nagai, 1940; as *E. intestinalis* f. *saprobia*; Vinogradova, 1974; Kudrjaschov et al., 1976; Levenets, 2011; Kozhenkova, 2020).

CONCLUSIONS

A population of *Ulva intestinalis* living more than 200 km from the ocean in central Kamchatka, a region with a largely unsuitable climate and water chemistry, seems to be possible in only waters originating from thermal springs and experiencing eutrophication. Sporadic records of this species from Kamchatka suggest it may be unable to maintain stable populations in this region, and experience repeated local extinctions and recolonizations.

ACKNOWLEDGEMENTS

The authors are grateful to James K. Wetterer for English improvement of our manuscript. The research of R. E. Romanov was supported by of the state assignments of the Komarov Botanical Institute of the Russian Academy of Sciences, the project “Flora and taxonomy of algae, lichens and bryophytes in Russia and phytogeographically important regions of the world” (no. 121021600184-6), the research by O. A. Chernyagina was supported by the state assignment of the Kamchatka Pacific Institute of Geography of the Far East Branch of the Russian Academy of Sciences, the project “Terrestrial and marine ecosystems of Kamchatka and north-eastern part of Pacific region: study of biodiversity, development of methodological framework for sustainable use of natural resources” (no. of the state registration 122011400140-4). The research was done using equipment of the core facilities center “Cell and molecular technologies in plant science” at the Komarov Botanical Institute RAS (St. Petersburg, Russia).

REFERENCES

1. Andreev G. P., Goryacheva G. I., Skabitchevsky A. P., Chernyavskaya M. A. and Chistyakov L. D., 1963 – The algae of Irtysh River and its drainage basin, in *The nature of Ob River floodplain and its development*, Tomsk, Tomsk State University Press, 69-103. (in Russian)
2. Areco M. M., Salomone V. N. and Afonso M. S., 2021 – *Ulva lactuca*: A bioindicator for anthropogenic contamination and its environmental remediation capacity, *Marine Environmental Research*, 171, 105468, DOI: <https://doi.org/10.1016/j.marenvres.2021.105468>.
3. Barinova, S.S., Tsarenko, P.M., Nevo, E., 2004. Algae of experimental pools on the Dead Sea coast, Israel. *Israel Journal of Plant Science*, 52, 3, 265-275. DOI 10.1560/V889-764E-MCDY-NPDP
4. Bartolo A. G., Zammit G. and Küpper F. C., 2022 – *Ulva* L. biodiversity in the central Mediterranean Sea: cryptic species and new records, *Cryptogamie, Algologie*, 43, 14, 215-225, DOI: <https://doi.org/10.5252/cryptogamie-algologie2022v43a14>.
5. Bazarova B. B. and Kuklin A. P., 2021 – Dynamics of the vegetation cover of soda lakes in the southeast of Transbaikalia, in *Diversity of soils and biota of Northern and central Asia*. IV All-Russian conference with international participation, 15-18 June 2021, Ulan-Ude, Buryatia Scientific Center of the Siberian Branch of RAS Press, 46-48. (in Russian)
6. Beauger A., Wetzel C., Volodire O., Allain E., Breton V., Miallier D. and Ector L., 2022 – *Fontina* gen. nov. (Bacillariophyta): a new diatom genus from a thermo-mineral spring of the French Massif Central, *Diatom Research*, 37, 1, 51-61, DOI: <https://doi.org/ff10.1080/0269249X.2022.2033327>.
7. Bliding C., 1963 – A critical survey of European taxa in Ulvales. Part I. Capsosiphon, Percursaria, Blidingia, Enteromorpha, *Opera Botanica*, 8, 3, 1-160.
8. Tseggid B. and Baigal-Amar T., 2018 – The conspectus of algae in Mongolia, Ulaanbaatar, Bembi, 314.
9. Burkholder J. M. and Glibert P. M., 2013 – Eutrophication and oligotrophication, in Levin S. A. (ed.), *Encyclopedia of Biodiversity*, 2nd Edition, Amsterdam, Academic Press, 347-371, DOI: <https://doi.org/10.1016/b978-0-12-384719-5.00047-2>.
10. Cantonati M., 2022 – Springs – groundwater-borne ecotones – a typology, with an overview on the diversity of photoautotrophs in springs, in Mehner T., Tockner K. (eds.), *Encyclopedia of Inland Waters*, 2nd edition, vol. 3, Amsterdam, Elsevier, 488-509, DOI: <https://doi.org/10.1016/B978-0-12-819166-8.00178-X>.
11. Cantonati M., Lange-Bertalot H., Scalfi A. and Angeli N., 2010 – *Cymbella tridentina* sp. nov. (Bacillariophyta), a crenophilous diatom from carbonate springs of the Alps, *Journal of the North American Benthological Society*, 29, 775-788, DOI: <https://doi.org/10.1899/09-077.1>.
12. Doemel W. and Brock T. D., 1971 – The physiological ecology of *Cyanidium caldarium*, *Journal of General Microbiology*, 67, 1, 17-32, DOI: <https://doi.org/10.1099/00221287-67-1-17>.
13. Efremov A. N., 2018 – Records of little-known cattails (*Typha* L., Typhaceae) in Siberia, *Bulletin of Moscow Society of Naturalists. Biological Series*, 123, 6, 69-70. (in Russian)
14. Efremov A. N. and Sviridenko B. F., 2016 – On distribution of rare hydrophytes in Omsk Region, *Botanicheskii Zhurnal*, 101, 8, 923-927, DOI: <https://doi.org/10.1134/S0006813616080044>. (in Russian)
15. Elenkin A. A., 1914 – Die Süswasseralgen Kamtschatka's, in *Expedition à Kamtchatka, organisée par Th. P. Riabouchinsky avec le concours de la Société Impériale Russe de Géographie. Section de Botanique. II. Plantes cryptogames de Kamtchatka: 1) Algues, 2) Champignons*, Moscou, Maison d'édition Ryabushinsky, 2-402, 579-591. (in Russian)
16. Ermolaeva L. M., 1967 – The phytobenthos of ponds of Bolsherechensky District, *Proceedings of the Kuybyshev Omsk State Medical Institute*, 77, 42-46. (in Russian)

16. Fort A., Mannion C., Fariñas-Franco J. M. and Sulpice R., 2020 – Green tides select for fast expanding *Ulva* strains, *Science of the Total Environment*, 698, 1, 134337, DOI: <https://doi.org/10.1016/j.scitotenv.2019.134337>.
17. Glazier D. S., 2009 – Springs, in Likens G. E. (ed.), *Encyclopedia of Inland Waters*, vol. 1, Oxford, Elsevier, 734-755, DOI: <https://doi.org/10.1016/B978-012370626-3.00259-3>.
18. Gromov B. V., Nikitina V. N. and Mamkayeva K. A., 1991 – *Ochromonas vulcania* sp. nov. (Chrysophyceae) from the acidic spring on the Kunashir Island (Kurile Islands), *Algologia*, 1, 2, 76-79. (in Russian)
19. Harsha Mohan E., Madhusudan S. and Baskaran R., 2023 – The sea lettuce *Ulva* sensu lato: Future food with health-promoting bioactives, *Algal Research*, 71, 103069, DOI: <https://doi.org/10.1016/j.algal.2023.103069>.
20. Hayden H. S., Blomster J., Maggs C. A., Silva P. C., Stanhope M. J. and Waaland J. R., 2003 – Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera, *European Journal of Phycology*, 38, 3, 277-294, DOI: <https://doi.org/10.1080/1364253031000136321>.
21. Ichihara K., Arai S., Uchimura M., Fay E. J., Ebata H., Hiraoka M. and Shimada S., 2009 – New species of freshwater *Ulva*, *Ulva limnetica* (Ulvales, Ulvophyceae) from the Ryukyu Islands, Japan, *Phycological Research*, 57, 2, 94-103, DOI: <https://doi.org/10.1111/j.1440-1835.2009.00525.x>.
22. iNaturalist, 2024. – *iNaturalist.org*, available online: <http://www.inaturalist.org>, accessed on 20 January 2024.
23. Khalfina N. A., 1964 – Towards hydrobiology of forest-steppe water bodies of West Siberia, *Izvesitya SO AN SSSR, Seriya Biologo-meditsinskikh Nauk*, 4, 1, 41-48. (in Russian)
24. Kipriyanova L. M. and Romanov R. E., 2010 – Communities of macroalgae, in Ravkin Yu. S. (ed.-in-chief), *The biodiversity of Karasuk-Burla area (West Siberia)*, Novosibirsk, SB RAS Press, 81-84. (in Russian)
25. Kiryukhin A. V., Kiryukhin V. A. and Manukhin Yu. F., 2010 – The hydrogeology of volcanogens, Saint Petersburg, Nauka, 395. (in Russian)
26. Klochkova N. G. and Berezovskaya V. A., 1997 – The algae of Kamchatka shelf. Distribution, biology, chemical composition. Vladivostok, Petropavlovsk-Kamchatskiy, Dalnauka, 155. (in Russian)
27. Klochkova N. G. and Berezovskaya V. A., 2001 – The macrophytobenthos of the Avacha Bay and its anthropogenic destruction, Vladivostok, Dalnauka, 208. (in Russian)
28. Klochkova N. G., Korolyova T. N. and Kusidi A. E., 2009a – Marine algae of Kamchatka and surrounding areas, vol. 1, Petropavlovsk-Kamchatskiy, KamchatNIRO, 217. (in Russian)
29. Klochkova N. G., Koroleva T. A. and Kusidi A. E., 2009b – Species composition and peculiarities of vegetation on the algae-macrophytes at the coasts of Starichkov Island, in *Biota of Starichkov Island and adjacent waters of Avacha Gulf / Proceedings of the Kamchatka Branch of the Pacific Institute of Geography, Far Eastern Division, Russian Academy of Sciences*, 8, 67-198. (in Russian)
30. Kondratyuk V. I., 1974 – The climate of Kamchatka, Moscow, Gidrometeoizdat, 204. (in Russian)
31. Kopyrina L., Pshennikova E. and Barinova S., 2020 – Diversity and ecological characteristic of algae and cyanobacteria of thermokarst lakes in Yakutia (northeastern Russia), *Oceanological and Hydrobiological Studies*, 49, 2, 99-122, DOI: <https://doi.org/10.1515/ohs-2020-0010>.
32. Kozhenkova S. I., 2020 – Checklist of marine benthic algae from the Russian continental coast of the Sea of Japan, *Phytotaxa*, 437, 4, 177-205, DOI: <https://doi.org/10.11646/phytotaxa.437.4.1>.
33. Kudrjaschov V. A., Tarakanova T. F. and Ivanova M. B., 1976 – On the fauna and the flora of the intertidal zone of the Shantar Islands. Coastal communities of the Far Eastern seas, *Transactions of the Institute of Marine Biology of the Far East Science Center of the Academy of Sciences of the USSR*, 6, 22-63. (in Russian)

34. Kukharenko L. A., 1989 – The algae of freshwater water bodies of Primorye Territory, Vladivostok, FEB AS USSR, 152. (in Russian)
35. Kuklin A. P., 2017 – Geochemical conditions of the landscape as a factor of formation of the species of macroscopic algae in small rivers of the Baikal and Amur basins, *Issues of modern algology*, 1, 13, 1-9. (in Russian)
36. Kuklin A. P. and Zamana L. V., 2011 – Macroalgae – indicators of river drainage of urban territories (by the example of a district of Chita), in *Evolution of biogeochemical systems (factors, processes, patterns) and problems of ecosystems exploitation. Geo-ecological, economic and social problems of ecosystem exploitation*, Chita, ZabSHPU, 106-108. (in Russian)
37. Langangen A., 2000 – Charophytes from the warm springs of Svalbard, *Polar Research*, 19, 2, 143-153, DOI: <https://doi.org/10.3402/polar.v19i2.6541>.
38. Langangen A., Ballot A., Nowak P. and Schneider S. C., 2020 – Charophytes in warm springs on Svalbard (Spitsbergen): DNA barcoding identifies Chara aspera and Chara canescens with unusual morphological traits, *Botany Letters*, 167, 2, 179-186, DOI: <https://doi.org/10.1080/23818107.2019.1672104>.
39. Levenets I. R., 2011 – Macroalgae of fouling communities in shallow waters of southern Primorye, Vladivostok, Dalnauka, 188. (in Russian)
40. Li S. and Bi L. (eds.), 1998 – Flora algarum sinicarum aquae dulcis. Vol. 5. Ulothricales, Ulvales, Chaetophorales, Trentepohliales, Sphaeropleales, Beijing, Science Press, 136. (in Chinese)
41. Litvinenko Y. S. and Zakharikhina L. V., 2020 – Hydrochemical zoning of the river network of Kamchatka, *Water Resources*, 47, 2, 269-281, DOI: <https://doi.org/10.1134/S0097807820020098>.
42. Lovas-Kiss A., Sánchez M. I., Wilkinson D. M., Coughlan N. E., Alves J. A. and Green A. J., 2018 – Shorebirds as important vectors for plant dispersal in Europe, *Ecography*, 42, 5, 956-967, DOI: <https://doi.org/10.1111/ecog.04065>.
43. Mareš J., Leskinen E., Sitkowska M., Skácelová O. and Blomster J., 2011 – True identity of the European freshwater Ulva (Chlorophyta, Ulvophyceae) revealed by a combined molecular and morphological approach, *Journal of Phycology*, 47, 1177-1192, DOI: <https://doi.org/10.1111/j.1529-8817.2011.01048.x>.
44. Maulood B. K., Hassan F. M., Al-Lami A. A., Toma J. J. and Ismail A. M., 2013 – Checklist of algal flora in Iraq, Baghdad, Ministry of Environment, 94.
45. Medvedeva L. A. and Nikulina T. V., 2014 – Catalogue of freshwater algae of the southern part of the Russian Far East, Vladivostok, Dalnauka, 271. (in Russian).
46. Messyasz B., 2009 – Enteromorpha (Chlorophyta) populations in the Nielba River and Lake Laskownickie, *Oceanological and Hydrobiological Studies*, 38, suppl., 1-9.
47. Messyasz B. and Rybak A., 2010 – Abiotic factors affecting the development of Ulva sp. (Ulvophyceae; Chlorophyta) in freshwater ecosystems, *Aquatic Ecology*, 45, 75-87, DOI: <https://doi.org/10.1007/s10452-010-9333-9>.
48. Mohebbi F. and Zarezadeh S., 2023 – A review of Ulva intestinalis, the only macroscopic alga of Urmia Lake, *Iranian Journal of Botany*, 29, 1, 83-88, DOI: <https://doi.org/10.22092/IJB.2023.361068>.
49. Moshkova N. A. and Hollerbach M. M., 1986 – The identification manual of freshwater algae of the USSR. Iss. 10. Chlorophyta: Ulotrichophyceae, Ulotrichales, Leningrad, Nauka, 360. (in Russian)
50. Muradov S. V., Kirichenko S. V. and Rogatykh S. V., 2013 – The thermomineral springs and therapeutic muds of Kamchatka Territory, Petropavlovsk-Kamchatskiy, RIOiP KKT, 238. (in Russian)
51. Muzafarov A. M., 1965 – The flora of algae of water bodies of Middle Asia, Tashkent, Nauka, 568. (in Russian)

52. Nagai M., 1940 – Marine algae of the Kurile Islands, I, *Journal of the Faculty of Agriculture, Hokkaido Imperial University*, 46, 1-137.
53. Nahucrishvili I. G. (ed.), 1986 – Flora of Cryptogamous Plants of Georgia: Conspectus, Tbilisi, Meznierba, 885. (in Russian)
54. Nikitina V. N., 2005 – The blue-green algae (cyanobacteria) of natural thermal biotopes, Saint Petersburg, Saint Petersburg University Press, 110. (in Russian)
55. Peel M. C., Finlayson B. L. and McMahon T. A., 2007 – Updated world map of the Köppen-Geiger climate classification, *Hydrology and Earth System Sciences*, 11, 5, 1633-1644, DOI: <https://doi.org/10.5194/hess-11-1633-2007>.
56. Pirozhnikov P. L., 1929 – Towards knowledge of Lake Sartlan in limnological, hydrobiological and fishery sides, *Proceedings of the Siberian Scientific Fishery Station*, 4, 2, 3-116. (In Russ.).
57. Romanov R. E. and Chernyagina O. A., 2018 – Chara braunii, in *Red Data Book of Kamchatka Territory. Vol. 2. Plants*, Petropavlovsk-Kamchatsky, Kamchatpress, 274. (in Russian)
58. Romanov R. E., Patova E. N., Teteryuk B. Yu. and Chemeris E. V., 2018 – Charophytes (Charales, Charophyceae) on the north-eastern edge of Europe: is it something different across Northern Europe in their diversity and biogeography, *Nova Hedwigia, Beihefte*, 147, 161-181, DOI: <https://doi.org/10.1127/nova-suppl/2018/016>
59. Romanov R. E. and Vishnyakov V. S., 2023 – Chara globata Mig., in *Red Data Book of Republic of Buryatia: Plants and fungi. 4th edition, updated*, Belgorod, Konstanta, 91. (in Russian)
60. Ruprecht F. J., 1850. – Algae ochotenses. Die ersten sicheren Nachrichten über die Tange des Ochotskischen Meeres, St. Petersburg, Buchdruckerei der Kaiserlichen Akademie der Wissenschaften, 243. (in German)
61. Rybak A. S., 2015 – Revision of herbarium specimens of freshwater Enteromorpha-like *Ulva* (Ulvaceae, Chlorophyta) collected from Central Europe during the years 1849–1959, *Phytotaxa*, 218, 1, 1-29, DOI: <https://doi.org/10.11646/phytotaxa.218.1.1>.
62. Rybak A. S., 2018 – Species of *Ulva* (Ulvophyceae, Chlorophyta) as indicators of salinity, *Ecological Indicators*, 85, 253-261, DOI: <https://doi.org/10.1016/j.ecolind.2017.10.061>.
63. Rybak A. S., 2021 – Freshwater macroalga, *Ulva pilifera* (Ulvaceae, Chlorophyta) as an indicator of the trophic state of waters for small water bodies, *Ecological Indicators*, 121, 106951, DOI: <https://doi.org/10.1016/j.ecolind.2020.106951>.
64. Saber A. A., Mareš J., Guella G., Anesi A., Štenclová L. and Cantonati M., 2018 – Polyphasic approach to a characteristic *Ulva* population from a limno-rheocrenic, mineral (chloride, sodium, sulphate) spring in the Siwa Oasis (Western Desert of Egypt), *Fottea*, 18, 227-242, DOI: <https://doi.org/10.5507/FOT.2018.008>.
65. Safonova T. A. and Ermolaev V. I., 1983 – The algae of water bodies of Lake Chany complex, Novosibirsk, 153. (In Russ.).
66. Safonova T. A. and Shishkina L. N., 1986 – The algae of rivers Kargat and Chulym, in *New about flora of Siberia*, Novosibirsk, 31-41. (in Russian)
67. Sametova E. S., Nurashov S. B. and Jiyenbekov A. K., 2019 – Algoflora of the rivers of desert low mountains of the southeast of Kazakhstan, *Problems of botany of South Siberia and Mongolia*, 18, 1, 390-392, DOI: <https://doi.org/10.14258/pbssm.2019079>. (in Russian)
68. Selivanova O. N. and Zhigadlova G. G., 1997a – Macrophytes of the Commander Islands, in *Benthic flora and fauna of the shelf zone of the Commander Islands*, Vladivostok, Dalnauka, 11-58. (in Russian)
69. Selivanova O. N. and Zhigadlova G. G., 1997b – Marine algae of the Commander Islands, preliminary remarks on the revision of the flora. I. Chlorophyta, *Botanica Marina*, 40, 1-8, DOI: <https://doi.org/10.1515/botm.1997.40.1-6.1>.

70. Selivanova O. N. and Zhigadlova G. G., 2009a – Marine algae-macrophytes of the coastal waters of Starichkov Island, in *Biota of Starichkov Island and adjacent waters of Avacha Gulf: proceedings of Kamchatka Branch of Pacific Institute of Geography, Far Eastern Division, Russian Academy of Sciences*, 8, 25-57. (in Russian)
71. Selivanova O. N. and Zhigadlova G. G., 2009b – Marine benthic algae of the South Kamchatka state wildlife sanctuary (Kamchatka, Russia), *Botanica Marina*, 52, 4, 317-329, DOI: <https://doi.org/10.1515/BOT.2009.003>.
72. Sinova E. S., 1928 – Algae maris japonensis. Chlorophyceae, *Bulletins of Pacific Ocean Scientific Fishery Research Station*, 2, 2, 1-62. (in Russian)
73. Skvortsov B., 1917 – Contributions à la flore des algues de la Russie d'Asie, *Journal de la Société Botanique de Russie*, 2, 10-20. (in Russian)
74. Škaloud P., Rindi F., Boedeker C. and Leliaert F., 2018 – Freshwater flora of Central Europe, Vol 13: Chlorophyta: Ulvophyceae (Süßwasserflora von Mitteleuropa, Bd. 13: Chlorophyta: Ulvophyceae), Berlin, Springer Spektrum, 288, DOI: <https://doi.org/10.1007/978-3-662-55495-1>
75. Steinhagen S., Hoffmann S., Pavia H. and Toth G. B., 2023 – Molecular identification of the ubiquitous green algae *Ulva* reveals high biodiversity, crypticity, and invasive species in the Atlantic-Baltic Sea region, *Algal Research*, 73, 103132, DOI: <https://doi.org/10.1016/j.algal.2023.103132>.
76. Sviridenko B. F., 2000 – Flora and vegetation of water bodies of Northern Kazakhstan, Omsk, Omsk State Pedagogical University, 196. (in Russian)
77. Sviridenko B. F., Murashko Yu. A., Sviridenko T. V. and Efremov A. N., 2016 – Tolerance of hydromacrophytes to active reaction, mineralization and water hardness in natural and man-made water bodies of the West Siberian Plain, *Bulletin of Nizhnevartovsk State University*, 2, 8-17. (in Russian)
78. Tekebaeva Zh. B., Kanaev D. B. and Zhamangara A., 2014 – Towards study of species composition and ecology of phytoplankton of Shchuchinsk-Borovoe zone, in *Proceedings of the IX International Scientific Conference for students and young scholars «Science and education – 2014»*, Astana, 350-358. (in Russian)
79. Tokar O. E., 2018 – Hydromacrophytes composition in water reservoirs of the north-eastern part of the Kurgan Region, *Samara Journal of Science*, 7, 2, 120-125. (in Russian)
80. Tripolitowa T. K., 1928 – Beiträge zur Flora der Sporen-Pflanzen des Altais und des Guvernementes Tomsk. II. Algen, *Transactions of Tomsk State University*, 79, 4, 271-325. (in German)
81. Vinogradova K. L., 1974 – Ulvacean algae (Chlorophyta) of seas of the USSR, Leningrad, Nauka, 166. (in Russian)
82. Vinogradova K. L., 1979 – The identification manual for algae of Far East seas of the USSR. Green algae, Leningrad, Nauka, 147. (in Russian)
83. Woronichin N. N., 1914 – Die Meeresalgen Kamtschatka's, in *Expedition à Kamtchatka, organisée par Th. P. Riabouchinsky avec le concours de la Société Impériale Russe de Géographie. Section de Botanique. II. Plantes cryptogames de Kamtchatka: 1) Algues, 2) Champignons*, Moscou, Maison d'édition Ryabushinsky, 475-524, 592-593. (in Russian)
84. Yakubova A. I., 1953 – The vegetation of the Lake Sartlan and its changes in connection with water level oscillations, *Trudy Tomskogo Gosudarstvennogo Universiteta*, 125, Seriya biologicheskaya, 223-248. (in Russian)
85. Yatsenko-Stepanova T. N. and Ignatenko M. E., 2018 – About some results of the research of the algal flora of the specially protected area “Tuzlukkolsky Muds” (Orenburg Region, Belyaevsky District), *Bulletin of the Orenburg Scientific Center, Ural branch, Russian Academy of Sciences*, 4, 1-17, DOI: <https://doi.org/10.24411/2304-9081-2019-14003>. (in Russian)

86. Zhakova L. V., 2006 – Check-list for Caspian Sea macroalgae, in *Caspian Biodiversity Project under umbrella of Caspian Sea Environment Program*, https://www.zin.ru/projects/caspdiv/caspian_macroalgae.html
87. Zhakova L. V., 2013 – Effect of long-term changes of the salinity on the water flora composition and distribution of macrophytes in the Aral, *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, 317, suppl. 3, 113-119. (in Russian)
88. Zhang Y., He P., Li H., Li G., Liu J., Jiao F., Zhang J., Huo Y., Shi X., Su R., Ye N., Liu D., Yu R., Wang Z., Zhou M. and Jiao N., 2019 – Ulva prolifera green-tide outbreaks and their environmental impact in the Yellow Sea, China, *National Science Review*, 6, 4, 825-838, DOI: <https://doi.org/10.1093/nsr/nwz026>.
89. Zinchenko T. D., Golovatyuk L. V., Gorokhova O. G., Abrosimova E. V., Umanskaya M. V., Popchenko T. V., Shitikov V. K., Gusakov V. I., Bolotov S. E., Lazareva V. I., Selivanova E. A., Balkin A. S. and Plotnikov A. O. 2021 – Functional features of the structural organization of plankton and bottom communities in highly mineralized rivers of the hyperhaline Lake Elton Basin (Russia), *Ecosystems: Ecology and Dynamics*, 5, 1, 5-72, DOI: <https://doi.org/10.24411/2542-2006-2021-10077>. (in Russian)