

Editorial

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Phylogeny and ecology of the green seaweed *Ulva*

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Algae of the genus *Ulva* are of central importance in both applied and basic research, as they present a fascinating mix of biological, ecological, evolutionary, physiological, and genetic research priorities (Blomme et al. 2023; De Clerk et al. 2018; Wichard et al. 2015). Due to their crucial role in coastal ecosystems and their burgeoning commercial use for aquaculture, *Ulva* spp. have become the focus of many (applied) scientific studies (Bolton et al. 2016; Simon et al. 2022; Steinhagen et al. 2021; Wichard 2023). The cultivation of seaweed for food, feed and useful chemicals has the potential to increase significantly and sustainably. It could provide alternative protein sources, alleviate food shortages and meet increasing demand by utilizing the largely untapped aquatic environment (Barbier et al. 2020; Buck and Shpigel 2023). In any case, the reliable identification of the morphologically variable species and ecotypes of *Ulva* remains of particular interest and a prerequisite for many applications (Steinhagen et al. 2019).

Despite their paramount importance, a comprehensive understanding of the ecology, phylogeny, and key characteristics across various *Ulva* species remains elusive. Advancements in cutting-edge technologies and sophisticated molecular techniques have propelled scientific research, unlocking some of the mysteries of this ecologically and economically significant genus. The quest to unravel the complexities of *Ulva* continues. This Special Issue consolidates pertinent scientific contributions spanning species-specific ecological traits, intricate phylogenetic aspects, and insightful aquaculture case studies.

Acknowledging the considerable interest and commitment demonstrated by all contributors to this Special Issue,

we express gratitude for their valuable research. This collection delves into diverse aspects of *Ulva* and showcases the advancements in the field made by these research contributors. Notably, this Special Issue is presented in two volumes, reflecting the extensive coverage of the multifaceted topics explored and the increasing interest in *Ulva* research.

The article collection is dedicated to our friend and colleague, Prof. Dr. Klaus Lüning, who unfortunately passed away last year. With profound sorrow, we announce the passing of a stalwart in the wide field of phycology, whose invaluable contributions have left an indelible mark on the scientific community. Prof. Lüning, a distinguished biologist and marine botanist, dedicated his life to unravelling the intricacies of marine macroalgae. Throughout his illustrious career, he held a professorship at the University of Hamburg and was the head of the Department of Marine Botany at the Biologische Anstalt Helgoland (later part of the Alfred-Wegener-Institut, Bremerhaven, Germany). His research spanned diverse facets of seaweed ecology, focusing on the ecophysiology of marine macroalgae, the regulation of algal development, biogeography and macroalgal cultivation for commercial applications. As a result of his research activities, Prof. Lüning has published more than 100 scientific articles as well as the book *Seaweeds: their environment, biogeography, and ecophysiology* (Lüning 1990) and successfully implemented his scientific work by founding the company Sylter Algenfarm GmbH & Co.KG, for the biomass production of macroalgae. As we reflect on his remarkable life and legacy, let us honour Prof. Dr. Klaus Lüning's enduring contributions to phycology, and especially his contributions to the genus *Ulva*, which will continue to shape the future of marine science for years to come. Notably, Prof. Lüning's contribution intended for this Special Issue was published in advance in *Botanica Marina* (Lüning 2023).

The EU-funded Cooperation in Science and Technology (COST) Action SeaWheat (CA20106) “Tomorrow's ‘wheat of the sea’, *Ulva* a model for an innovative mariculture (sea-wheat)” has brought together macroalgal researchers to build up a new network dedicated to macroalgal research and its applications (<https://www.cost.eu/actions/CA20106/04/10/2021–03/10/2025>). The COST Action aims to integrate *Ulva* into various aspects of industry and daily life, from food production to biotechnology, focusing on sustainability and

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environmental considerations. It seeks to leverage European expertise, quality standards, and dietary habits to facilitate the adoption of *Ulva*-based products. Inspired by this newly launched network coordinated by Prof. Dr. Muki Shpigel (University of Haifa, Israel), we developed the concept for a Special Issue focused on the ecology and phylogeny of *Ulva*.

Eight articles present a broad view of exciting topics (Figure 1), including studies on the main tasks of the COST Action SeaWheat project, such as the interconnected topics: (i) cultivation, (ii) ecology/biology, and (iii) evolution/biodiversity.

Several authors make use of molecular data to refine the taxonomy and nomenclature of Ulvaceae species and provide a more accurate understanding of their relationships and distribution. Hughey et al. (2024) highlight the importance of DNA sequencing for the type specimens of each species of *Ulva* to ensure the accurate application of names in repositories, which is essential for applied research. Following this approach, Maggs et al. (2024) reassign, for example, *Ulva gigantea* to *Ulva compressa* based on *rbcl*, *tufA*, and ITS sequences from the holotype. In field studies, Gabrielson et al. (2024) describe the foliose green seaweed flora of the Galápagos Archipelago, whereas Zhong et al. (2024) demonstrate the impact of dynamic environmental conditions and latitudinal gradients on phenotypic and genetic patterns of *Ulva* species in the North West Pacific.

Two studies in this issue have contributed to a better understanding of the cross-kingdom interactions between *Ulva* and its associated bacteria and fungi. The study of Noor et al. (2024) focuses on the isolation and biological evaluation of the under-investigated endophytic fungi found in *Ulva* spp. isolated from the Bay of Bengal (Bangladesh). Similarly, Hmani et al. (2024) suggest that *Ulva*-growth-promoting microbial traits can change with temperature, emphasizing the need for a comprehensive approach that combines microbiome analysis with functional examinations.

Green seaweed aquaculture is a small industry where optimal cultivation practices are being developed to scale up production. *Ulva lactuca* was identified by Gnayem et al. (2024) as a valuable source of high-value fatty acids depending on its specific harvest seasons. It underscores the significance of *Ulva* spp. as contributors to sustainable alternatives for essential fatty acids traditionally sourced from wild fish. Finally, Rautenberger (2024) explore the value and potential cost of using germanium dioxide as an antifouling agent against the bio-fouling diatoms in *Ulva*'s land-based aquaculture.

In conclusion, this Special Issue comprehensively explores diverse facets of *Ulva*, shedding light on its ecological, phylogenetic, and practical dimensions. Through collaborative and pioneering research, the collection significantly advances our comprehension of this fascinating

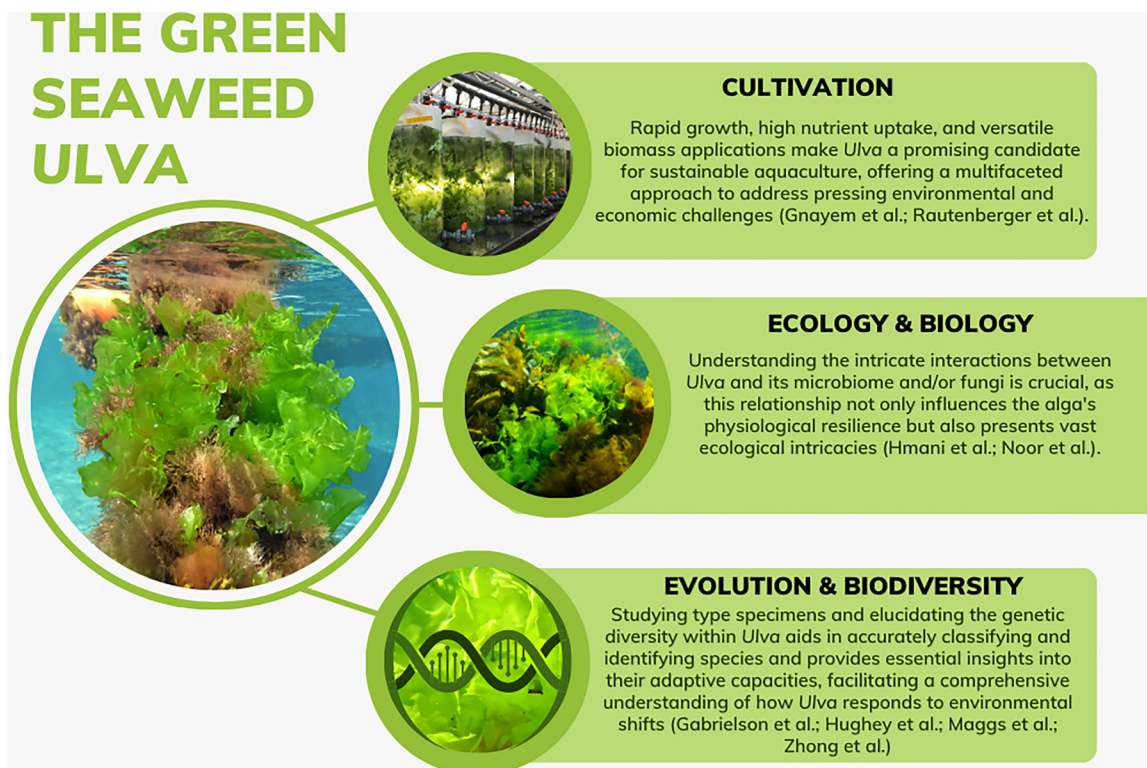


Figure 1: The highlights of *Ulva* research can be divided into three main research areas, which are reflected in this special edition.

genus, emphasizing its potential in sustainable aquaculture and ecological contexts.

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References

- Barbier, M., Araújo, R., Rebours, C., Jacquemin, B., Holdt, S.L., and Charrier, B. (2020). Development and objectives of the PHYCOMORPH European Guidelines for the sustainable aquaculture of seaweeds (PEGASUS). *Bot. Mar.* 63: 5–16.
- Blomme, J., Wichard, T., Jacobs, T.B., and De Clerck, O. (2023). *Ulva*: an emerging green seaweed model for systems biology. *J. Phycol.* 59: 433–440.
- Bolton, J.J., Cyrus, M.D., Brand, M.J., Joubert, M., and Macey, B.M. (2016). Why grow *Ulva*? Its potential role in the future of aquaculture. *Perspect. Phycol.* 3: 113–120.
- Buck, B.H. and Shpigel, M. (2023). *Ulva*: tomorrow’s “wheat of the sea”, a model for an innovative mariculture. *J. Appl. Phycol.* 35: 1967–1970.
- De Clerck, O., Kao, S.-M., Bogaert, K.A., Blomme, J., Foflonker, F., Kwantes, M., Vancaester, E., Vanderstraeten, L., Aydogdu, E., Boesger, J., et al. (2018). Insights into the evolution of multicellularity from the sea lettuce genome. *Curr. Biol.* 28: 2921–2933.
- Gabrielson, P.W., Smith, A.C., Bruno, J.F., Vision, T.J., and Brandt, M. (2024). Taxonomic assessment of blade-forming *Ulva* species (Ulvales, Chlorophyta) in the Galápagos Archipelago, Ecuador using DNA sequencing. *Bot. Mar.* 67: 153–164.
- Gnayem, N., Unis, R., Gnaim, R., Chemodanov, A., Israel, Á., Gnaim, J., and Golberg, A. (2024). Seasonal and culture period variations in the lipid and fatty acid content of *Ulva lactuca* cultivated in Mikhmoret onshore (Israel). *Bot. Mar.* 67: 101–114.
- Hmani, I., Ghaderiardakani, F., Ktari, L., El Bour, M., and Wichard, T. (2024). High-temperature stress induces bacteria-specific adverse and reversible effects on *Ulva* (Chlorophyta) growth and its chemosphere in a reductionist model system. *Bot. Mar.* 67: 131–138.
- Hughey, J.R., Miller, K.A., and Gabrielson, P.W. (2024). Genetic analysis of *Ulva* (Ulvaceae, Chlorophyta) type specimens resolves northeast Pacific blade-forming species. *Bot. Mar.* 67: 165–179.
- Lüning, K. (1990). Seaweeds: their environment, biogeography and ecophysiology. John Wiley & Sons., New York - Chichester-Toronto-Brisbane-Singapore.
- Lüning, K. (2023). Long-term unialgal seaweed cultivation in artificial seawater without water change. I. Laboratory investigations of *Ulva*. *Bot. Mar.* 66: 559–565.
- Maggs, C.A., Bunker, A.R., Bunker, F.S.P.D., Harries, D., Kelly, J., Mineur, F., Blomster, J., Diaz-Tapia, P., Gabrielson, P.W., Hughey, J.R., et al. (2024). Updating the Ulvaceae in the green seaweeds of Britain and Ireland. *Bot. Mar.* 67: 181–203.
- Noor, S., Begum, M.N., Rony, S.R., Uddin, M.Z., Sohrab, M.H., and Mazid, M.A. (2024). Bioactivity and chemical screening of endophytic fungi associated with the seaweed *Ulva* sp. of the Bay of Bengal, Bangladesh. *Bot. Mar.* 67: 115–129.
- Rautenberger, R. (2024). Germanium dioxide as agent to control the biofouling diatom *Fragilariopsis oceanica* for the cultivation of *Ulva fenestrata* (Chlorophyta). *Bot. Mar.* 67: 93–100.
- Simon, C., McHale, M., and Sulpice, R. (2022). Applications of *Ulva* biomass and strategies to improve its yield and composition: a perspective for *Ulva* aquaculture. *Biology* 11: 1593.
- Steinhagen, S., Karez, R., and Weinberger, F. (2019). Cryptic, alien and lost species: molecular diversity of *Ulva sensu lato* along the German coasts of the North and Baltic Seas. *Eur. J. Phycol.* 54: 466–483.
- Steinhagen, S., Enge, S., Larsson, K., Olsson, J., Nylund, G.M., Albers, E., Pavia, H., Undeland, I., and Toth, G.B. (2021). Sustainable large-scale aquaculture of the northern hemisphere sea lettuce, *Ulva fenestrata*, in an off-shore seafarm. *J. Mar. Sci. Eng.* 9: 615.
- Wichard, T. (2023). From model organism to application: bacteria-induced growth and development of the green seaweed *Ulva* and the potential of microbe leveraging in algal aquaculture. *Semin. Cell Dev. Biol.* 134: 69–78.
- Wichard, T., Charrier, B., Mineur, F., Bothwell, J.H., De Clerck, O., and Coates, J.C. (2015). The green seaweed *Ulva*: a model system to study morphogenesis. *Front. Plant Sci.* 6: 72.
- Zhong, K.-L., Hiraoka, M., Gao, X., Russell, B., Hu, Z.-M., Chen, W., Kim, J.-H., Yotsukura, N., Endo, H., Oka, N., et al. (2024). Environmental gradients influence geographic differentiation and low genetic diversity of morphologically similar *Ulva* species in the Northwest Pacific. *Bot. Mar.* 67: 139–151.

Bionotes



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Thomas Wichard is a research group leader and lecturer in Analytical Chemistry at the Institute for Inorganic and Analytical Chemistry of the Friedrich Schiller University Jena (Germany). After being awarded a PhD in Biochemistry (Max Planck Institute for Chemical Ecology), he investigated the metal recruitment of nitrogen fixers at the Princeton Environmental Institute (USA). His team applies various analytical chemistry, chemical ecology, and molecular biology methodologies to understand the basis of eco-physiological processes in bacteria-macroalgae interactions (cross-kingdom interactions).

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