

Review

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What's new in marine botany of the Eastern Mediterranean?

<https://doi.org/10.1515/bot-2022-0040>

Received June 16, 2022; accepted June 21, 2022;
published online July 21, 2022

Abstract: This article provides a topical review of East Mediterranean phycology and seagrass biology, with a special focus on the outcomes of the multi-year project “Brown algal biodiversity and ecology in the Eastern Mediterranean Sea” supported by the TOTAL Foundation. Following a general overview of East Mediterranean seaweed biogeography and taxonomy, the review covers seagrasses, deep-water (circalittoral) macroalgal diversity, pathogens and algal defence, human impacts and biotic indices, alien species as well as the papers of this special issue.

Keywords: Croatia; Cyprus; Greece; seagrasses; seaweeds; Turkey.

1 Background

To track the history behind this special issue, we should go back to February–March 2009, when a group of phycologists (Christos Katsaros, Frithjof C. Küpper, Konstantinos Tsiamis, Dieter G. Müller, Hiroshi Kawai, Martina Strittmatter and Maria Karadanelli; Sotiris Orfanidis and his group were not able to participate in the Lesbos trip, but subsequently played a very active role in the consortium project) paid a visit to Lesbos Island (Aegean Sea, Greece),

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and for three weeks made field trips to different coasts, exploring the marine flora of the area. The observations during this trip and the general impression of this group convinced them that it was worthwhile preparing a proposal and organizing a consortium project to study “Brown algal biodiversity and ecology in the Eastern Mediterranean Sea”. This proposal was submitted to the TOTAL FOUNDATION (Paris, France) in November of the same year and accepted for funding shortly afterwards. The main aim of this project was to achieve a more comprehensive understanding of the region’s seaweed biodiversity as well as the effects of the climate change, pollution and invasive species on the Mediterranean marine vegetation. The project was a truly multinational effort – even though the effort was centred in Greece, it had major contributions by scientists from Croatia, Cyprus, Turkey, Israel, California, France, Japan and Scotland. It has now inspired us to edit this special issue and to provide a topical review of highlights of marine botanical research in the Eastern Mediterranean within the framework of (but not limited to) this project.

2 East Mediterranean seaweed biogeography and taxonomy

About 270 taxa of brown algae had been recorded in the Mediterranean Sea by 2012 (Cormaci et al. 2012; Ribera et al. 1992). However, when it comes to the Eastern basin, the number is far lower. It is not clear whether this is actually due to a lower algal diversity in this part of the Mediterranean Sea due to differences in geological history, rocky coastline fragmentation and to proximity to the Atlantic or Indian Oceans (Lüning 1990; Mannino et al. 2017) or whether it rather reflects fewer biodiversity studies in the Eastern than in the Western basin. Indeed, an east-west disconnection and environmental heterogeneity that was hypothesised earlier (Orfanidis and Breeman 1999) and verified recently (Konstantinidis et al. 2022), is dated back to the transition from Pleistocene to Holocene and the post-glacial era. On the other hand, the decline of the algal habitat-forming forests composed of fucalean brown

seaweeds (*Cystoseira*, *Ericaria*, and *Gongolaria*) is spatial-scale dependent and seems to affect the perennial more than the semi-perennial species (Orfanidis et al. 2021a). Therefore, the distribution of such species can remain unnoticed because numerous pristine areas in the Eastern Mediterranean Sea remain poorly surveyed, either for political reasons (e.g., the coasts of northern Cyprus) or because they occur in hard-to-reach shallow or deep reefs, which tend to be less explored.

Several misidentifications and unconfirmed records as well as recent findings of new species suggest that there are still significant gaps in the knowledge of seaweed diversity of the Eastern Mediterranean basin (Tsiamis and Panayotidis 2016). Indeed, a recent increase in phycological expeditions and overall research effort in the Eastern basin have revealed numerous new macroalgal records, in particular for Greece such as *Discosporangium mesarthrocarpum* (Tsirika and Haritonidis 2005), *Cystoseira schiffneri* (as *Cystoseira foeniculacea* f. *schiffneri*), *Sebdenia dichotoma* (Tsiamis et al. 2013) and *Cystoseira funkii* (Tsiamis et al. 2016), Cyprus (Tsiamis et al. 2014) and Turkey (Taşkın 2008, 2013b, Taşkın and Öztürk 2007, 2008). The TOTAL Foundation-funded consortium project has revealed numerous new records for the Eastern Mediterranean (see below for representative examples), and also two new species, *Padina ditristomatica* and *Padina pavonicoides* (Ni Ni et al. 2011). Material from expeditions of consortium members around the Mediterranean enabled revision of the genus *Cutleria* (Kawai et al. 2012). The project also enabled compilation of the first checklist of the seaweeds of Cyprus (Tsiamis et al. 2014) in an unprecedented collaboration and co-authoring of contributors from the two communities in Cyprus plus Greece, Turkey and the UK (constituting one of the first, if not the first, scientific publications with co-authors from both Cypriot communities since 1974). Moreover, Tsiamis and his collaborators conducted a series of studies on the seaweeds of the Greek coasts (Tsiamis et al. 2013, 2014) as well as on native and alien macroalgal diversity of the Eastern Mediterranean (Tsiamis and Verlaque 2011; Tsiamis et al. 2013, Tsiamis et al. 2016). Also, the combined use of algal culturing and molecular techniques (in particular, the Germling Emergence Technique) has unravelled additional new records and hitherto-undescribed taxa from the Eastern Mediterranean (Peters et al. 2015) – including the first East Mediterranean record of *Schizocladia ischiensis*, which belongs to a monospecific sister group of the brown algae (Rizouli et al. 2020), the first report of the North Atlantic myrionematoid brown alga *Ulonema rhizophorum* (Phaeophyceae, Chordariaceae) in the Mediterranean Sea (Taşkın 2013a) and numerous new records from the Maltese

islands (Bartolo et al. 2021b). Within the framework of the consortium project, two countries stand out with a wealth of new information: Croatia and Turkey. In Croatia and the surrounding Adriatic region, outcomes included species inventories of brown (Antolic et al. 2010) and red seaweeds (Antolic et al. 2011a), the application of a European Union Water Framework Directive-compliant monitoring method used in the Western Mediterranean Sea (cartography of littoral rocky-shore communities, CARLIT) as a tool for ecological quality assessment of coastal waters in the Eastern Adriatic Sea (Nikolic et al. 2013) and surveys of marine benthic macroflora from Rijeka Bay (Antolić et al. 2011b) as well as of *Cystoseira* species in Montenegro (Macic et al. 2010). Croatian scientists also contributed molecular identification of *Cystoseira* spp. from the Adriatic Sea (Rozic et al. 2012). In Turkey, apart from the first record of *Ulonema rhizophorum* (Taşkın 2013a), new records of three Dictyotalean (Taşkın 2013b) and other marine algae (Taşkın 2013; Taşkın and Öztürk 2007, 2008, 2013) as well as a list of the Phaeophyceae of the country (Taşkın and Öztürk 2013) have been published. A revised and updated checklist of the seaweeds and seagrasses of the Egyptian Mediterranean coast, based on literature records, was also recently provided (Shabaka 2018). Furthermore, the benthic macrophyte communities of different substratum types (soft, hard) also were studied as bioindicators of 11 differently impacted sites belonging in two different water typologies (transitional waters: Lesina Lagoon, Varna Lake; coastal waters: Varna Bay) and two ecoregions (Mediterranean Sea and Black Sea; Orfanidis et al. 2014).

However, further overall progress in Mediterranean seaweed taxonomy and biogeography is hampered by limited coverage of Mediterranean taxa by DNA barcode sequences (Bartolo et al. 2020).

3 Seagrasses

Seagrasses are ecosystem engineers in seabed communities in many tropical to temperate seas of the world (Waycott et al. 2006). They play major roles as shelters, nurseries (Ermgassen et al. 2016) and for benthic carbon sequestration (Trevathan-Tackett et al. 2015). Seagrasses are polyphyletic members of the Alismatales, whose evolutionary ancestors have returned to the sea (Waycott et al. 2006). In the Mediterranean, four seagrass species are native: *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina* and *Z. noltei* (Tsioli et al. 2022). A fifth estuarine/marine perennial or annual angiosperm that is sometimes called a seagrass is the euryhaline angiosperm, widgeon-

grass, *Ruppia maritima*. It is a temperate aquatic plant species complex that also inhabits the coastal lagoons and brackish habitats of the Mediterranean Sea (Tsioli et al. 2019). Among these, the two most important structuring species of seagrass communities are *P. oceanica* and *C. nodosa*, which also host a range of epiphytic algae (Balata et al. 2008; Tsioli et al. 2021). *Cymodocea nodosa* is considered a pioneering species and is thought to be more tolerant to environmental fluctuations than *P. oceanica* (Den Hartog 1970; Pergent et al. 2014). It has been shown that a succession of *C. nodosa* communities often precedes *P. oceanica* climax communities (Cancemi et al. 2002). Two studies explored the population genetics of *C. nodosa* in Greek waters (Gkafas et al. 2016; Konstantinidis et al. 2022), with the more recent highlighting that the most parsimonious historical scenario is that the drop in sea level during the Pleistocene epoch has left a genetic signature in populations of this seagrass. This scenario supports the isolation of the north-western, north, and north-eastern areas of the Mediterranean, and the subsequent recolonization after the post-glaciation sea level rise may explain the north-western differentiation as well as the present-day dispersion of *C. nodosa*. In the south-eastern Mediterranean, the tropical species *Halophila stipulacea* is a recent arrival through the Suez Canal (Sghaier et al. 2011). Using DNA barcoding, García-Escudero et al. (2022) showed that *H. stipulacea* is the only non-indigenous seagrass in the Mediterranean, and that findings reported by Gerakaris et al. (2020) actually correspond to *H. stipulacea* and not to *Halophila decipiens*. Mediterranean seagrasses have also been used for assessing benthic marine environmental quality (Orfanidis et al. 2001, 2010; Papathanasiou and Orfanidis 2018). Seagrass meadows, mainly of *P. oceanica* and *C. nodosa*, generally occupy a small proportion of the Mediterranean seafloor compared to the entire surface of this inland sea, from the sea surface to 40–45 m depth. However, they constitute the most valuable habitats in coastal waters, providing a range of ecosystem functions and services for human well-being (Campagne et al. 2015). In Greece, the first attempt to map meadows of the endemic Mediterranean seagrass *P. oceanica* took place in 2001 (Panayotidis et al. 2002), within the framework of the EU Habitat Directive (92/43/EEC). An updated map of large-scale *P. oceanica* distribution across the coastal waters of the Hellenic territory is published in the present Special Issue (Panayotidis et al. 2022).

Temperature and salinity are considered key stressors for seagrasses, since they are relevant both in an indirect context such as global climate change (Küpper and Kamenos 2018), and also more directly, such as for saline brine discharges from desalination plants and industry.

Seagrasses often experience salinity and temperature stresses simultaneously, affecting multiple levels of biological hierarchy, from molecular to sub-cellular and physiological, which decrease their growth and fitness (Pandey et al. 2017). For example, at the transcriptomic level, the expression of genes encoding photosynthetic proteins (including PS II reaction centre proteins) of *C. nodosa* was significantly downregulated in the first 24 h of heat stress (Malandrakis et al. 2017). A more recent study explored the responses of *C. nodosa* to high salinity and high temperature, alone and in combination (Tsioli et al. 2022). Both affected ion equilibrium in the plant cells. Non-synonymous mutations marked the transcriptomic response to salinity and temperature stress at loci related to osmotic stress. Cell structure, especially the nucleus, chloroplasts, mitochondria and organization of the microtubule cytoskeleton, was also altered. Both temperature and salinity stress negatively affected photosynthetic activity as evidenced by $\Delta F/F_m'$, following an antagonistic interaction type. Overall, this study showed that all biological levels investigated were strongly affected by temperature and salinity stress, but with the latter having more severe effects. Macro-nutrients, toxic metal contamination, and turbidity (low irradiance) are also affecting *C. nodosa* shoots, especially those collected from highly stressed meadows, studied by laboratory experiments (Papathanasiou et al. 2015) or field monitoring (Papathanasiou and Orfanidis 2018; Papathanasiou et al. 2016) approaches. In addition, the effects of other contaminants such as titanium dioxide nanoparticles (TiO₂ NPs; Mylona et al. 2020) or bisphenol A (Malea et al. 2022) on physiology and cell structure of *C. nodosa* have been studied.

4 Deep-water (circalittoral) macroalgal diversity

Populations of other species endemic to the Mediterranean Sea, such as the deep-water kelp *Laminaria rodriguezii* Bornet, are found in the western Mediterranean and the Adriatic Sea (Guiry and Guiry 2021). The species has also been reported in the Eastern basin (Turkey; Aysel et al. 2008; Taşkın and Öztürk 2013) but this needs to be confirmed by new collections. When it comes to the Adriatic Sea, extensive surveys have demonstrated a significant decline in the range of the species due to bottom trawling (Žuljević et al. 2016). A computer model was developed which is capable of predicting deep-water kelp habitats in warm-temperate and tropical seas (Graham et al. 2007). At the onset of this study, it appeared to be an attractive tool to

select target areas for ship-based surveys. Based upon prediction maps from this model, extensive ROV surveys were conducted in both the northern Aegean and Ionian Seas but these did not produce any evidence for the occurrence of deep-water kelp in Greek waters, even though the prediction maps had suggested a high likelihood (Küpper et al. 2019). Instead, the survey enabled the rare deep-water red alga *Sebdenia monnardiana* to be collected, a new record for the Eastern Mediterranean, and also enabled its molecular study (Küpper et al. 2019). Also, the recent records of *Cystoseira funkii* (Tsiamis et al. 2016) from circalittoral sites in Ikaria and Paxoi, Greece, highlight the value of deep-water algal surveys.

5 Pathogens and algal defence

The Mediterranean region is poorly covered by studies investigating pathogens of seaweeds. In this regard, this consortium project has enabled several new biogeographic records, but also new insights into the cell biology of seaweed pathogens: Strittmatter et al. (2013), working in Lesbos Island, reported the first records of *Anisolpidium ectocarpii* and *Anisolpidium sphacellarum* for the Mediterranean, together with LSU sequences of the basal oomycete *Eurychasma dicksonii*, also detected there, while another study (Fletcher et al. 2015) detected *Olpidiopsis feldmanni* in the red alga *Asparagopsis* sp. from Croatia. Tsirigoti and co-workers (Tsirigoti et al. 2013, 2014) conducted the first studies of the ultrastructure of brown algal cells infected by *E. dicksonii*, while another study discovered that prostaglandin A₂ is a very potent inducer of defence reactions in brown algae (Zambounis et al. 2012).

6 Human impacts and biotic indices

Being a part of the world with a long history of human civilization, i.e. having been surrounded by population centres for millennia, the Mediterranean has a correspondingly long history of human impacts such as sewage discharge resulting in eutrophication, overfishing, alterations of coastal topography due to construction works, and litter pollution. By mining decades of survey data obtained for the Greek national water board (ΕΥΔΑΠ), Panyotidis et al. (2004) and Tsiamis et al. (2013) were able to trace the major changes in macroalgal community composition on the shores of Saronikos Gulf following the

commissioning of the Psittalia sewage treatment plant in 1998. Before this, up to one million tons of raw, untreated sewage had entered this large bay on the south shore of Athens every day. This effort has been realized within the European Water Framework Directive (WFD-2000/60/EC), which demands assessments of the ecological status of coastal and transitional waters by using biotic indices. Among others, the Ecological Evaluation Index (EEI-c; Orfanidis et al. 2010) for the rocky upper sublittoral communities and CymoSkew (Orfanidis et al. 2020) for the *C. nodosa* meadows have been used to implement the WFD and the European Marine Strategy Framework Directive (MSFD-2008/56/EC) or simply to assess the anthropogenic impact in the Eastern Mediterranean Sea, such as the coasts of Greece (Simboura et al. 2014), Cyprus (Kletou et al. 2018), and Turkey (Taşkın et al. 2020).

With its hot climate and little, erratic rainfall, the Eastern Mediterranean region is one of the most water-stressed regions in the world. To counter supply shortages, seawater desalination has emerged as a major source of freshwater, especially in Cyprus, Israel, the smaller, southern Greek islands and Malta. Seawater desalination requires significant amounts of energy and produces a hypersaline brine, which is usually discharged into coastal waters where it may impact benthic communities due to its high density compared to seawater. While there are numerous studies from Spain in the Western Mediterranean (Fernández-Torquemada and Sánchez-Lizaso 2005; Fernández-Torquemada et al. 2005, 2013, 2019; Garrote-Moreno et al. 2014; Sánchez-Lizaso et al. 2008), there has been a critical shortage of comparable studies from the East. In this respect, the recent study by Xevgenos et al. from Cyprus (Xevgenos et al. 2021) addresses this gap and showed that density of shoots and leaf surface area in *Posidonia oceanica* was strongly reduced in brine-impacted seabed areas.

7 Alien species

Non-native species are a particular form of human impact. For the past two centuries, biodiversity in the Mediterranean Sea has been changing at an alarmingly high rate due to an interplay of “chance and necessity”. Most tropical species did not return to the sub-tropical Eastern Mediterranean after its desiccation (Messinian crisis), leaving space for speciation and invasion. Furthermore, during contemporary times the diversity of the Mediterranean Sea has been affected by human-mediated stressors, such as habitat modification, pollution, coastal urbanization, etc.,

facilitating species replacements (Orfanidis et al. 2021b). Today, the Mediterranean Sea is a hotspot of marine non-invasive species (NIS) invasions on Earth (Rilov and Galil 2009), and it is by far the major site for NIS among European seas including macrophytes, invertebrates and fishes (Katsanevakis et al. 2013, 2016; Streftaris et al. 2005). The primary route of Mediterranean immigration is *via* the Suez Canal, the so-called Lessepsian immigration (after Ferdinand de Lesseps, French diplomat and director of the construction of the Suez Canal), a unique situation, which has *de facto* removed a major, continental biogeographic boundary. The rate of this immigration has increased in recent decades with important ecological, social and economic impacts (Zenetos and Galanidi 2020; Zenetos et al. 2012). The Eastern Mediterranean basin is more susceptible to introductions of subtropical and tropical NIS *via* the Suez Canal than the Western Basin because of physical and biological characteristics which offer conditions more appropriate to the invasive fauna and flora coming from the Indian Ocean – in addition to the obvious geographical proximity to the Suez Canal. It possesses more subtropical physical conditions (i.e. a generally warmer climate and an overall more arid nature of the surrounding terrestrial environment) and maintains a relatively low number of species (i.e. leaving empty niches) compared to the Western Mediterranean. The construction of major infrastructures, such as the Aswan Dam in 1966 in the River Nile, had major impacts on the physico-chemical conditions of the Eastern Mediterranean by reducing the input of freshwater and nutrients and increasing salinity along the Egyptian coasts. Two main terms have been added in invasion biology studies of the Mediterranean Sea: *Tropicalization* and *Meridionalization*. The “tropicalization” of the Mediterranean Sea refers to the increasing appearance of thermophilous species throughout the Mediterranean Sea and is described as a combined effect of four different phenomena: introduction of NIS of tropical Atlantic origin, Lessepsian immigration, man-made introductions and sea-water warming (Bianchi and Morri 2003). “Meridionalization” describes the homogenization of fauna and flora, in particular the northward extension of thermophilous species and the recession of boreal ones (Massuti et al. 2010).

A recent study recorded about 300 macroalgae on the Israeli Mediterranean shores, with 86 species having Indo-Pacific (68%), Atlantic (20%), or uncertain (12%) origin, being alien to the Levantine basin (Israel and Einav 2017). Recent findings also include numerous new records of alien species (Tsiamis et al. 2010, 2013), with *Caulerpa taxifolia* var. *distichophylla* being recorded for the first time

for Cyprus (Çicek et al. 2013) and Greece, where it has been documented to occur over an exceptionally wide depth range from the surface to at least 100 m (Aplikioti et al. 2016). This work also resulted in the first records of *Dictyota cyanoloma* in the Eastern Mediterranean (Taşkın 2013b) and Greece (Küpper et al. 2019). Tsioli and Orfanidis have recently published new records of alien species from the North Aegean Sea (e.g. *Acanthophora nayadiformis*, *Asparagopsis taxiformis*, *Caulerpa cylindracea* and *Codium fragile* subsp. *fragile*), one of the less alien impacted sub-regions of the Eastern Mediterranean (Katsanevakis et al. 2020). *Colaconema codicola* was recorded as an epiphyte of *Codium fragile* subsp. *fragile* during the monitoring within the Marine Strategy Framework Directive projects (Orfanidis et al. 2021a). Numerical modelling (Cumulative IMPacts of Invasive Alien, CIMPAL) has enabled the prediction of the impacts of alien species in Malta (Bartolo et al. 2021a). Croatian studies explored the effects of the invasive alga *Caulerpa racemosa* var. *cylindracea* on the biogeochemical characteristics of sediments under its canopy (organic carbon, total nitrogen and total phosphorus contents were elevated in the surface sediment at invaded sites; Matijević et al. 2013), its lack of sexual reproduction (Žuljević et al. 2012) and its impacts on a native sponge (Žuljević et al. 2011), as well the distribution of the invasive red alga *Womersleyella setacea* in the Adriatic Sea (Nikolić et al. 2010). Chemical ecology seems to play a key role in a number of cases of successful invasions – for example, the survival of the alien aplysioid anaspidean *Syphonota geographica* seems to be related to the presence of the alien seagrass *Halophila stipulacea* (Mollo et al. 2008).

8 This special issue

The present special issue comprises seven (7) papers, five (5) on seaweeds and two (2) on seagrasses. A suite of different scientific approaches has been used, from monitoring to experimental, and at all levels of biological organization from subcellular to ecosystem, to contribute the Marine Botany of the Eastern Mediterranean Sea.

Taşkın and Cakir (2022) have updated the existing checklist of marine algae from the coasts of the Aegean Sea and Levantine Sea of Turkey to a total of 573 marine algal taxa at specific and infraspecific levels. Among them, 32 are regarded as endangered or threatened macroalgae, while 36 taxa are recorded as aliens, and one is reported for the first time from the Eastern Mediterranean Sea for Turkey. Bartolo et al. (2022) used a multiphasic approach to study seaweed biodiversity, combining substratum samples,

macrophytic fragment cultivation and DNA barcoding. They succeeded in identifying two new records for the Maltese islands, one of which had been reported previously from New Zealand. Germlings of both species were observed to grow as epiphytes on benthic macrophytes.

Fucal species have been studied in three papers in the Special Issue. Ivesa et al. (2022) mapped and studied the biomass variation of two forms of *Gongolaria barbata*, attached and free-living, inhabiting the Šćuza lagoon on the southern Istrian coast, Croatia. Papadimitriou et al. (2022) studied the effects of photoperiod and temperature on photosynthesis, growth, and reproduction of *Ericaria barbatula* from Kavala Gulf, Greece. They confirmed the induction of reproductive organs under SD conditions to secure the release of zygotes and the germling's growth in the field under non-stressful Mediterranean Sea temperatures. Lardi et al. (2022) studied the reproductive phenology, embryology, and growth of *Gongolaria montagnei*, one of the commonest canopy-forming algal species of the Greek coasts. Divisions, early developmental stages, and growth are described and possible implications for future restoration efforts are discussed.

Two common seagrasses have been studied. Panayotidis et al. (2022) combined the use of optical (satellite imagery) and acoustic (sidescan sonar) remote sensing techniques, as well as *in situ* methodologies (visual census) to map the spatial distribution of seagrass habitats in the coastal waters of the Greek territory. The results of this study will support the effective management and conservation of valuable marine ecosystems. Finally, Nadzari et al. (2022) studied the effects of flooding on *Cymodocea nodosa* from two differently impacted habitats, one nearly pristine and another highly stressed, in the Kavala coasts of Greece. They found that only the photosynthetic performance of shoots from the pristine habitat was higher under flooding conditions.

Acknowledgements: Special thanks go to Laure Fournier (TOTAL Foundation) for her support through inspiring discussions, mentoring and networking.

Author contributions: All the authors have accepted responsibility for the entire content of this submitted manuscript and approved submission.

Research funding: We would like to acknowledge many years of funding support from the TOTAL Foundation (Paris) within the framework of the project “Brown algal biodiversity and ecology in the Eastern Mediterranean Sea” which has enabled and inspired much of the work covered in this article and this special issue.

Conflict of interest statement: The authors declare no conflicts of interest regarding this article.

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