

Mediterranean Marine Science

Vol 24, No 3 (2023)

VOL 24, No 3 (2023)



Halimeda incrassata (Bryopsidales, Chlorophyta) in Rhodes, Greece, Eastern Mediterranean

GERASIMOS KONDYLATOS, KONSTANTINOS KALAENTZIS, EIRINI GRATSIA, DIMITRIOS MAVROULEAS, PANAGIOTIS KASAPIDIS, KONSTANTINOS TSIAMIS, DIMITRIS KLAOUDATOS

doi: [10.12681/mms.35435](https://doi.org/10.12681/mms.35435)

To cite this article:

KONDYLATOS, G., KALAENTZIS, K., GRATSIA, E., MAVROULEAS, D., KASAPIDIS, P., TSIAMIS, K., & KLAOUDATOS, D. (2023). Halimeda incrassata (Bryopsidales, Chlorophyta) in Rhodes, Greece, Eastern Mediterranean. *Mediterranean Marine Science*, 24(3), 633–638. <https://doi.org/10.12681/mms.35435>

Halimeda incrassata* (Bryopsidales, Chlorophyta) in Rhodes, Greece, Eastern Mediterranean*Gerasimos KONDYLATOS¹, Konstantinos KALAENTZIS¹, Eirini GRATZIA², Dimitrios MAVROULEAS¹, Panagiotis KASAPIDIS², Konstantinos TSIAMIS³ and Dimitris KLAOUDATOS⁴**¹Hellenic Centre for Marine Research, Hydrobiological Station of Rhodes, Cos Street, 85131 Rhodes, Greece²Hellenic Centre for Marine Research, Institute of Marine Biology, Biotechnology and Aquaculture.

P.O. Box 2214, 71003 Heraklion, Crete, Greece

³Karaiskaki 16 Voula, Athens, 16673, Greece⁴University of Thessaly (UTH), School of Agricultural Sciences, Department of Ichthyology and Aquatic Environment (DIAE), Fytokou Street, 38446, Volos, GreeceCorresponding author: Gerasimos KONDYLATOS; gkondylatos@hcmr.gr

Contributing Editor: Sotiris ORFANIDIS

Received: 19 September 2023; Accepted: 05 October 2023; Published online: 21 November 2023

Abstract

The first record of the tropical green seaweed *Halimeda incrassata* (Bryopsidales, Chlorophyta) in the Eastern Mediterranean Sea is presented, based on several thalli found in the stomach of a silver-cheeked toadfish (*Lagocephalus sceleratus*), collected off Plimmiri beach, Rhodes, Greece. Species identification was based on morphological and molecular identification using the *tufA* gene as a molecular marker. The finding comes 10 years after a report on the species in Mallorca (Western Mediterranean Sea), where *H. incrassata* has spread rapidly. The pathway of its introduction in the Eastern basin is unknown, although shipping or the aquarium trade could be involved in this new introduction. Further studies are necessary for visual documentation of the infested areas around Rhodes and assessment of its possible spread in the following years.

Keywords: Non-Indigenous Species (NIS); Chlorophyta; Levantine; DNA barcoding.**Introduction**

During the last decades, intensification of human activities in the Mediterranean Sea has resulted in accelerated phenomenon marine biological invasions (Pancucci-Papadopoulou *et al.*, 2012; Bianchi *et al.*, 2014; Zenetos *et al.*, 2022). The marine waters surrounding the island of Rhodes, especially along the southern part of the island that is constantly influenced by the Asia Minor Current (AMC; Gaines *et al.*, 2006), present subtropical environmental characteristics that are ideal for the colonization of non-indigenous species (NIS) of tropical or subtropical origin (Papaconstantinou, 2014).

Macroalgae consist of an important group of species in terms of their ecosystem services, acting as carbon sinks, storage sites, habitat-engineering and nutrient removers (Granier, 2012). In the Mediterranean Sea, macroalgae is the fourth most successful group of NIS in terms of establishment success, with 77% of the 161 species considered established (Zenetos *et al.*, 2022). NIS macroalgae in Hellenic marine waters (Aegean, Cretan, Ionian and Levantine Seas) include four species of Ochrophyta, 12 Rhodophyta and four Chlorophyta, excluding cryptogenic and questionable taxa, according to the latest published

data (Tsiamis, 2012; European Commission *et al.*, 2021). In the southern Aegean Sea, 11 species are classified as established NIS, of which five are invasive, one is casual and two are questionable as regards their establishment status (Zenetos *et al.*, 2020), whereas the potential pathway of introduction of the majority is shipping, followed by angling/fishing, unaided and intentional/unintentional release.

Halimeda incrassata (J. Ellis) J.V. Lamouroux (Bryopsidales, Chlorophyta) is a calcified green macroalgal species, considered as NIS in the Mediterranean Sea, and was first reported in the basin from Mallorca in 2011 (Alos *et al.*, 2016). In Mallorca, *H. incrassata* exhibited invasive behaviour due to its rapid population growth within a few years. The species has also been reported from Madeira, north-eastern Atlantic (Wirtz & Kaufmann, 2005) and the Canary Islands (Sangil *et al.*, 2018). The species has been flagged as top-priority NIS in the EU-scale Horizon Scanning of marine NIS (Tsiamis *et al.*, 2020). Naturally, it is distributed in the tropical western Atlantic, the Indo-Pacific Ocean and the Red Sea (Guiry & Guiry, 2021; Fig. 1).

Within its natural range, the species usually inhabits shallow sandy bottoms, although it has also been found in

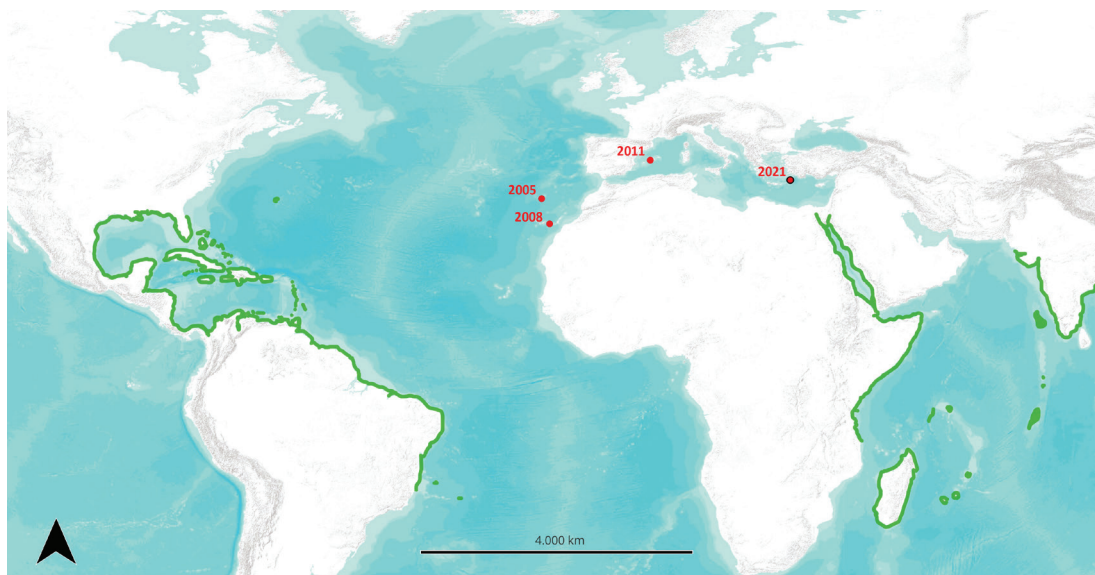


Fig. 1: Distribution of *Halimeda incrassata* in the proximity of the invaded areas. The green line indicates the approximate natural range according to Guiry and Guiry (2021); the red dots indicate the invaded areas.

deeper than 60 m waters (Littler & Littler 2000 in Sangil *et al.*, 2018). In the invaded marine waters of the Canary Islands, it was found to dominate the mid and deep-water habitats, whereas in Mallorca the species was not found below 20 m (Alos *et al.*, 2016; Sangil *et al.*, 2018).

Halimeda incrassata can reproduce both sexually and asexually by rhizoidal extension and fragmentation (van Tussenbroek & Barba Santos, 2011), having considerable growth rates (Multer, 1988; Multer & Clavijo, 2004 and references within). It is characterized as an ecological engineer with a great potential for modifying native habitats (Vivó-Pons *et al.*, 2020), with both positive and negative impacts (Tsirintanis *et al.*, 2022). The species is involved in the formation of carbonate sediments with a considerable annual production of calcium carbonate (CaCO_3), depending on the solar cycle (Freile & Hillis, 1997; van Tussenbroek & van Dijk, 2007). Furthermore, the species provides oxygen (e.g. 25.1 mg of O_2 per g of decalcified dry weight per day in Tahiti: Payri, 1988), nourishment (e.g. for the sea-urchin *Diadema antillarum* in Jamaica: Hillis-Colinvaux, 1974; for the bucktooth parrotfish *Sparisoma radians* in Virgin Islands: Lobel & Ogden, 1981 and for the pinfish *Lagodon rhomboides* in the Florida Keys: Ribble, 2019), shelter to other species (Heck & Wetstone 1977) and an ideal surface for the development of epifaunal organisms (Mateo-Ramírez *et al.*, 2022). Although *H. incrassata* is not a significant competitor of the native phanerogam *Posidonia oceanica*, it is known to compete with other macrophytes including *Dasycladus vermicularis* (Sureda *et al.*, 2017) and *Thalassia testudinum* (Davis & Fourqurean, 2001). The species could be favoured by the increasing temperature of the Mediterranean Sea, regardless of acidification, as demonstrated in aquarium experiments (Campbell *et al.*, 2016).

Herein, the presence of the species in the Eastern Mediterranean Sea is reported for the first time from Rhodian Levantine waters, identified by morphological observations and DNA barcoding. Possible pathways of introduction and future challenges are discussed.

Material and Methods

Several thalli of *Halimeda incrassata* (Fig. 2) were found in the stomach content of a silver-cheeked toadfish *Lagocephalus sceleratus* individual (TL 59.5 cm, weight 2350.2 g) caught off Plimmiri beach, SE Rhodes (35.917203°N, 27.860926°E) with bottom long lines (length 600 m, 100 hooks size No 10-12) during experimental fishing with the most commonly used fishing gear, including static nets, longlines, jigs and bottom traps, from April 2021 to March 2022. The fishing gear was deployed by a commercial 106.5 KW fishing vessel at 11-14 m depth, over a sandy-muddy substrate early in the morning of 6 October 2021 and was retrieved one hour later. Along with six more individuals of the species, caught with the same bottom longline, specimens were transported to the Hydrobiological Station of Rhodes (HSR), measured and photographed, while their stomach was removed and analysed for contents. Apart from the chlorophyte, viewing under a stereoscope revealed pieces of a freshly preyed Atlantic horse mackerel *Trachurus trachurus*, an unidentified decapod and a small unidentified pelagic crustacean in the stomach of the aforementioned specimen. Some of the thalli of *H. incrassata* were placed in absolute ethanol for DNA extraction, whereas the remaining were preserved in 70% ethanol and deposited at the HSR collection (catalogue number HSR560).

A Nikon SMZ800 stereoscope and a Nikon AW111 camera were used for morphological observations and photographs of the *H. incrassata* samples.

For the molecular identification of the specimen, the plastid gene *tufA* was used, following Cremen *et al.* (2016). Total genomic DNA was extracted from a sample of tissue (50mg) using the DNeasy Plant Pro kit (QIAGEN), according to the manufacturer's instructions. The plant tissue was homogenized using TissueLyzer II (two rounds of shaking at 25 Hz). Extracted DNA was PCR-amplified using the primers *tufAF* and *tufAR* from Fama *et al.* (2002) and *tufGF4* (5'-GGNGCNGCN-



Fig. 2: Thalli of *Halimeda incrassata* from Rhodes, Greece. (Photo credit: G. Kondylatos).

CAAATGGAYGG-3') from Saunders & Kucera (2010), in two different PCR combinations (tufAF-tufAR and tufGF4-tufAR). PCR reactions were performed in a total volume of 12.5 μ l and consisted of 1 μ l (~20ng) template DNA, 7.75 μ L of ddH₂O, 2.5 μ L of MyTaq Red Reaction Buffer (5x), 0.25 μ l of MyTaq™ Red DNA Polymerase (meridian BIOSCIENCE) and 0.5 μ L of each primer (10 μ M). PCR conditions were as in Cremen *et al.* (2016). Sanger sequencing reactions (both forward and reverse) were performed using the BigDye™ Terminator v3.1 Cycle Sequencing Kit and were electrophoresed on an ABI 3730xl DNA Analyzer (Applied Biosystems™). The produced sequence was compared to existing GenBank sequences using BLAST and was deposited in GenBank under accession number OQ871581.

Results

Thalli light-green to dark green, calcified, erect, sparsely branched, composed of segments; segments rather flat, becoming barrel-shaped towards the base; they are unlobed or trilobed, obovate–cuneate, broadest at or near their tip rather than at or near their base; segment dimensions ranged between 4.16–5.88 mm in height, 2.19–3.55 mm in width, and 0.67–1.57 mm in thickness; holdfasts were missing.

Anatomical observation revealed a cortex composed of 2–3 (rarely 4) layers of utricles; utricles not inflated, but rather cylindrical; peripheral utricles adhere to one another at their distal end; they measure 70–90 μ m in height and 40–60 μ m in width; sub-peripheral utricles measure 100–130 μ m in height and 50–70 μ m in width; peripheral utricles in surface view are polygons with slightly rounded corners, 40–55 μ m in diameter. Our specimens are in good match with previous descriptions of the species (Verbruggen *et al.*, 2006; Alos *et al.*, 2016).

The molecular analysis of the specimen produced a sequence of 813 bp in length, which presented 100% sim-

ilarity with *H. incrassata* sequences deposited in GenBank (accession numbers: FJ624534.1, AM049958.1, KT781884.1), thus confirming the morphological identification. Moreover, the resulting sequence presents less than 98% similarity with all the other deposited sequences of *Halimeda* species. More specifically, our specimen presents 98% similarity with *Halimeda simulans* M.A.Howe, 1907 (accession number: AM049963.1), 97% with *Halimeda monile* (J.Ellis & Solander) J.V.Lamouroux, 1816 (accession number: AM049962.1) and *Halimeda cylindracea* Decaisne, 1842 (accession number: KM820164.1).

Phylogenetic analysis further shows that our specimen (GenBank: OQ871581) is grouped together in a separate clade with *Halimeda incrassata* sequences from GenBank (accession numbers: FJ624534.1, AM049958.1 and KT781884.1). GenBank sequences AM049957.1 and AM049959.1 are deposited in GenBank under species name *Halimeda incrassata*. However, after revision of the paper (Verbruggen *et al.*, 2006), they are identified as *Halimeda heteromorpha* and *Halimeda kanaloana*, respectively, and are represented as such in the phylogenetic tree (Fig. 3).

Discussion

The *L. sceleratus* individual containing the thalli of *H. incrassata* was collected from shallow, 11–14m deep, coastal waters, a depth range where *H. incrassata* can proliferate (Wirtz & Kaufmann, 2005; Alós *et al.*, 2016; Sangil *et al.*, 2018). This information is rather significant because it provides an indicative depth zone where initial underwater observations can begin for the investigation of the current status of *H. incrassata* and its spread in Rhodian waters.

The presence of thalli of *H. incrassata* in the stomach content of the strictly carnivorous *L. sceleratus* is considered a collateral prey item. However, this is a very impor-

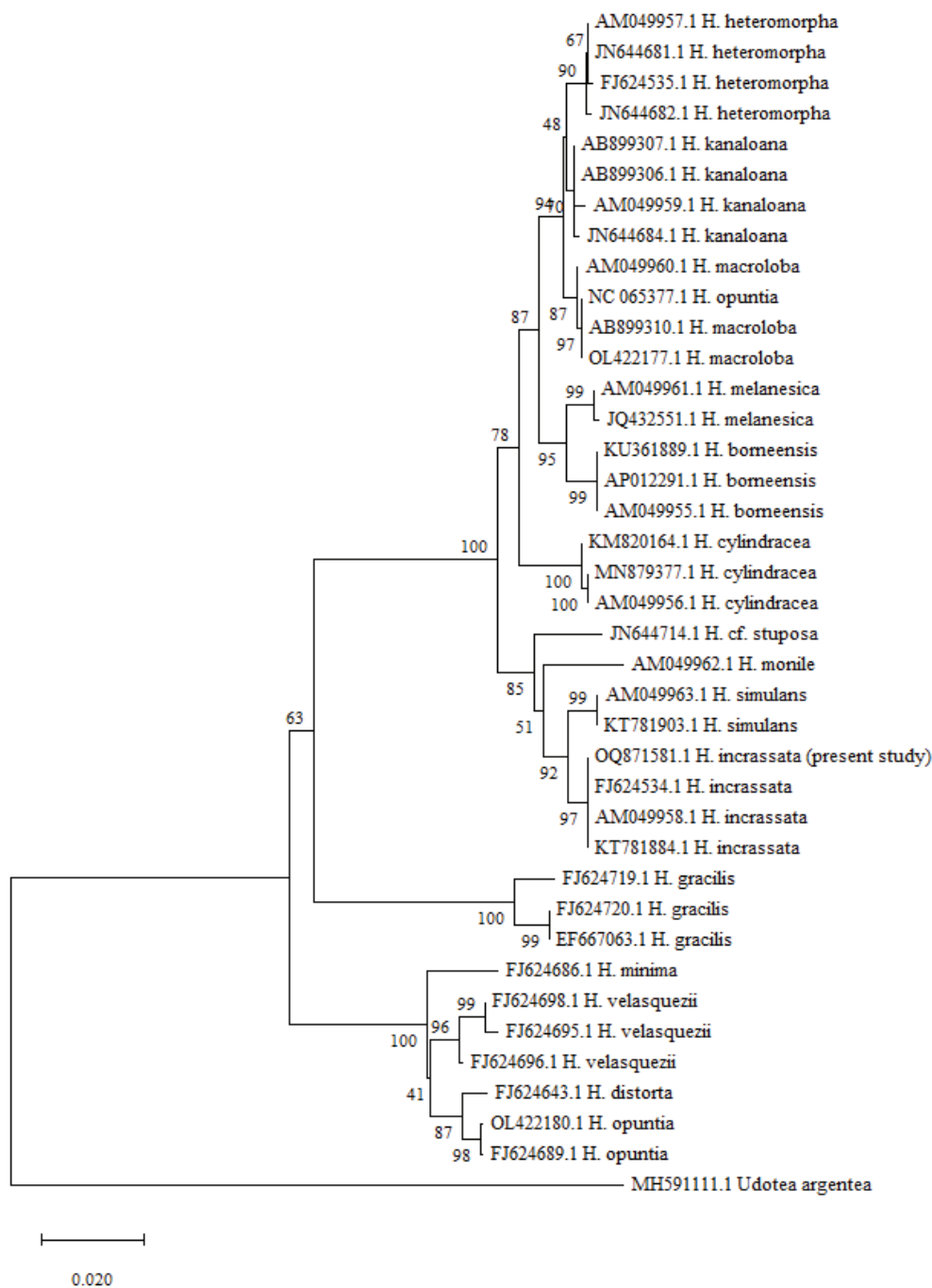


Fig. 3: The phylogenetic position of the *Halimeda incrassata* specimen in relation to other *Halimeda* species with available *tufA* sequences in GenBank (Neighbour-joining tree using Kimura-2P distances and 1000 bootstrap replicates).

tant finding not only because this is the first record of *H. incrassata* in the Eastern Mediterranean Sea, but also because it reveals another possible pathway for the spread of the species. When the undigested thalli are expelled through the faeces in an area far from the praying site, it is likely that *H. incrassata* will have the opportunity to germinate and start developing a new population.

It is worth mentioning that during the study period (April 2021 – March 2022), a total of 724 individuals of *L. sceleratus* were collected, mainly with longlines and jigs. Analysis of their stomach contents revealed the presence of six specimens of another macrophyte NIS, *Halophila stipulacea* (Forsskål) Ascherson. The species is considered as an established NIS in the south Aegean Sea

(Zenetos *et al.*, 2020). The finding of *H. incrassata* in the stomach contents of only one out of the 724 examined *L. sceleratus* individuals, suggests the possibility of an early stage of the colonization process of the species.

Halimeda incrassata is native to the western Atlantic, the Indo-West Pacific and Red Sea waters (Guiry & Guiry, 2021). Two scenarios regarding the pathways of introduction of the species to the Rhodian marine waters are considered as most probable. The first possible scenario is that *H. incrassata* reached the island through shipping, when fragments mixed with soft bottom material were caught on anchors and transported to Rhodes either from the western Mediterranean or the Atlantic via the Strait of Gibraltar or the Red Sea via the Suez Ca-

nal. Shipping is a very common vector of introduction of NIS macroalgae in the Mediterranean Sea (Zenetos *et al.*, 2018, 2020) and Rhodes is a favourite destination for cruise ships sailing around the Mediterranean and adjacent Atlantic. During the tourism seasons of 2020 and 2021, more than 200 cruise ships docked at the tourist harbour (36.445572°N, 28.233499°E) of the island (ELIME, 2023). Since our finding comes from coastal water, the anchors of western Mediterranean trawlers fishing in international waters, six nautical miles from the coasts of Rhodes, are unlikely to have been involved. Additionally, ballast waters might also have been involved in the transportation of the species because *H. incrassata* does not have planktonic spores, while its gametes and zygotes are short-lived. The second scenario involves an accidental/intentional release from home/private aquaria, which is a known pathway of NIS introduction (Zenetos *et al.*, 2018), since this macroalga is used for aquarium decoration.

In any case, visual inspection of the soft-bottoms near the ports of the town of Rhodes and along the coastal waters of southern Rhodes is necessary for drawing safer conclusions. Furthermore, relevant underwater observations in the major tourist ports of the Eastern Mediterranean, will further assist in revealing the degree of implication of shipping, mainly cruising, in the dispersion of *H. incrassata* within the basin.

Despite the uncertainty surrounding the pathway of introduction, the colonization of *H. incrassata* in the Western Mediterranean Sea has profound and documented effects on the invaded ecosystem (Tsirintanis *et al.*, 2022). These include the modification of the synthesis of the substrate and of fish communities (Nadal Nebot, 2017) and can be either positive, neutral or negative (Vivó-Pons *et al.*, 2020). For herbivorous organisms, such as herbivorous fish and sea urchins, the presence of *H. incrassata* entails the availability of a new food source. However, *Halimeda* species possess physical and chemical defences in order to avoid predation (Multer & Clavijo, 2004 and references within; Mateo Ramirez *et al.*, 2022 and references within). In that sense, the incorporation of *H. incrassata* in the diet of indigenous and NIS Mediterranean fauna needs further investigation.

Halimeda incrassata is a habitat-engineer (Granier, 2012) and the colonization of the vast sandy and muddy bottoms of the coastal waters of Rhodes could work in two ways. On the one hand, the formation of fields of calcareous algae could significantly contribute to the reduction of the niches of many fish species and other organisms that have been using the substrate for preying, burial and camouflage as pointed out by Vivó-Pons *et al.* (2020), but on the other hand this substitution could create a new niche and favour other species.

Although *H. incrassata* is known to bear epiphytes (Nadal Nebot, 2017), no epiphytes were found on the examined thali of this work, either because of the early colonization phase or the digestion process. Furthermore, the possibility of introduction of exotic epiphytes and alteration of the diversity of epifaunal organisms (Naim, 1988) should be further investigated.

Acknowledgements

The present work was undertaken within the framework of the project EXPLIAS (“Design and piloting methods of commercial exploitation of invasive alien species with a view to contributing to their population control”; <https://explias.gr/>, accessed on 24 July 2023), which was coordinated by the National Technical University of Athens (NTUA) with the collaboration of the Hellenic Centre for Marine Research (HCMR) and the University of the Aegean (UoA) and funded by the Fisheries and Maritime Operational Program 2014–2020 of the Greek Ministry of Agricultural Development and Food, and the European Maritime and Fisheries Fund (MIS No: 5049912) and also by the project “DRESSAGE” (MIS 5045792), funded by the Operational Programme “Competitiveness, Entrepreneurship and Innovation” (NSRF 2014-2020), coordinated by the HSR and co-financed by Greek and the European Union. The authors would like to thank the fisherman Mr. Osman Karaosman for his cooperation throughout the project and the two reviewers for their valuable contribution to the revision of the manuscript.

References

- Alós, J., Tomas, F., Terrados, J., Verbruggen, H., Ballesteros, E., 2016. Fast-spreading green beds of recently introduced *Halimeda incrassata* invade Mallorca Island (NW Mediterranean Sea). *Marine Ecology Progress Series*, 558, 153-158.
- Bianchi, C.N., Corsini-Foka, M., Morri, C., Zenetos, A., 2014. Thirty years after - dramatic change in the coastal marine habitats of Kos Island (Hellas), 1981-2013. *Mediterranean Marine Science*, 15 (3), 482-497.
- Campbell, J.E., Fisch, J., Langdon, C., Paul, V.J., 2016. Increased temperature mitigates the effects of ocean acidification in calcified green algae (*Halimeda* spp.). *Coral Reefs*, 35, 357-68.
- Cremen, M.C.M., Huisman, J.M., Marcelino, V.R., Verbruggen, H., 2016. Taxonomic revision of *Halimeda* (Bryopsidales, Chlorophyta) in south-western Australia. *Australian Systematic Botany*, 29 (1), 41-54.
- Davis, B.C., Fourqurean, J.W., 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. *Aquatic Botany*, 71, 217-232.
- ELIME, 2023. *Hellenic Ports Association*. <https://www.elime.gr> (Accessed 30 January 2023).
- European Commission, Joint Research Centre, Tsiamis, K., Paliolaxi, A., Connor, D. *et al.*, 2021. *Marine Strategy Framework Directive Descriptor 2, Non-Indigenous Species, delivering solid recommendations for setting threshold values for non-indigenous species pressure on European seas*. Publications Office of the European Union, 36+x pp.
- Fama, P., Wysor, B., Kooistra, W.H., Zuccarello, G.C., 2002. Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast *tufA* gene 1. *Journal of Phycology*, 38 (5), 1040-1050.
- Freile, D., Hillis, L., 1997. Carbonate productivity by *Halimeda incrassata* in a land proximal lagoon, Pico Feo, San

- Blas, Panama. *Proceedings of the 8th International Coral Reef Symposium*, 1, 767-772.
- Gaines, A.F., Copeland, G.J.M., Coban-Yildiz, Y., Ozsoy, E., Davie, A.M. *et al.*, 2006. The contrasting oceanography of the Rhodes Gyre and the Central Black Sea. *Turkish Journal of Engineering and Environmental Sciences*, 30, 69-81.
- Granier, B., 2012. The contribution of calcareous green algae to the production of limestones: a review. *Geodiversitas*, 34 (1), 35-60.
- Guiry, M.D., Guiry, G.M., 2021. *AlgaeBase*. <https://www.algaebase.org> (Accessed 18 January 2023).
- Heck, K.L., Wetstone, G.S., 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography*, 4, 135-142.
- Hillis-Colinvaux, L., 1974. Productivity of the coral reef alga *Halimeda* (Siphonales). *Proceedings of the 2nd International Coral Reef Symposium*, 1, 35-42.
- Littler, D.S., Littler, M.M., 2000. *Caribbean reef plants. An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico*. Offshore Graphics, Washington, USA, 542 pp.
- Lobel, P.S., Ogden, J.C., 1981. Foraging by the herbivorous parrotfish *Sparisoma radians*. *Marine Biology*, 64, 173-183.
- Mateo-Ramírez, Á., Máñez-Crespo, J., Royo, L., Tuya, F., Castejón-Silvo, I. *et al.*, 2022. A tropical macroalga (*Halimeda incrassata*) enhances diversity and abundance of epifaunal assemblages in Mediterranean seagrass meadows. *Frontiers in Marine Science*, 9, 886009.
- Multer, H.G., 1988. Growth rate, ultrastructure and sediment contribution of *Halimeda incrassata* and *Halimeda monile*, Nonsuch and Falmouth Bays, Antigua, *Coral Reefs*, 6, 179-186.
- Multer, H.G., Clavijo, I., 2004. *Halimeda* investigations: progress and problems. *NOAA/RSMAS*, 116-127.
- Nadal Nebot, M.V., 2017. *L'alga verda Halimeda incrassata com a possible vector d'introducció d'epibionts exòtics en la Badia de Palma*. Thesis, University of the Balearic Islands, Spain, 30 pp.
- Naim, O., 1988. Distributional patterns of mobile fauna associated with *Halimeda* on the Tiahura coral-reef complex (Moorea, French Polynesia). *Coral Reefs*, 6, 237-250.
- Pancucci-Papadopoulou, M.A., Raitzos, D.E., Corsini-Foka, M., 2012. Biological invasions and climatic warming: implications for South Eastern Aegean ecosystem functioning. *Journal of the Marine Biological Association of the United Kingdom*, 92 (4), 777-789.
- Papaconstantinou, C., 2014. *Fauna Graeciae. An updated checklist of the fish in the Greek Seas*. Monographs on Marine Sciences, 7, H.C.M.R., Athens, 340 pp.
- Payri, C.E., 1988. *Halimeda* contribution to organic and inorganic production in a Tahitian reef system. *Coral Reefs*, 6, 251-262.
- Ribble, K.A., 2019. *Grazing dynamics of the pinfish (Lagodon rhomboides) on Thalassia testudinum and Halimeda incrassata across a temperature gradient in the Florida Keys and implications for Ciguatera Fish Poisoning*. MSc thesis. Florida Gulf Coast University, USA, 84 pp.
- Sangil, C., Martín-García, L., Afonso-Carrillo, J., Barquín, J., Sansón, M., 2018. *Halimeda incrassata* (Bryopsidales, Chlorophyta) reaches the Canary Islands: mid- and deep-water meadows in the eastern subtropical Atlantic Ocean. *Botanica Marina*, 61 (2), 103-110.
- Saunders, G.W., Kucera, H., 2010. An evaluation of rbcL, tufA, UPA, LSU and ITS as DNA barcode markers for the marine green macroalgae. *Cryptogamie. Algologie*, 31 (4), 487-528.
- Sureda, A., Tejada, S., Capó, X., Melià, C., Ferriol, P. *et al.*, 2017. Oxidative stress response in the seagrass *Posidonia oceanica* and the seaweed *Dasycladus vermicularis* associated to the invasive tropical green seaweed *Halimeda incrassata*. *Science of The Total Environment*, 601, 918-925.
- Tsiamis, K., 2012. *Alien macroalgae of the sublittoral zone of the Greek coasts*. PhD thesis. University of Athens, Greece, 336 pp.
- Tsiamis, K., Azzurro, E., Bariche, M., Çinar, M.E., Crocetta, F. *et al.*, 2020. Prioritizing marine invasive alien species in the European Union through horizon scanning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30 (4), 794-845.
- Tsirintanis, K., Azzurro, E., Crocetta, F., Dimiza, M., Frogli, C. *et al.*, 2022. Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea. *Aquatic Invasions*, 17 (3), 308-352.
- van Tussenbroek, B.I., Barba Santos, M.G., 2011. Demography of *Halimeda incrassata* (Bryopsidales, Chlorophyta) in a Caribbean reef lagoon. *Marine Biology*, 158, 1461-1471.
- van Tussenbroek, B.I., van Dijk, J.K., 2007. Spatial and temporal variability in biomass and production of psammophytic *Halimeda incrassata* (Bryopsidales, Chlorophyta) in a Caribbean reef lagoon. *Journal of Phycology*, 43 (1), 69-77.
- Verbruggen, H., De Clerck, O., N'Yeurt, A.D.R., Spalding, H., Vroom, P., 2006. Phylogeny and taxonomy of *Halimeda incrassata*, including descriptions of *H. kanaloana* and *H. heteromorpha* spp. nov. (Bryopsidales, Chlorophyta). *European Journal of Phycology*, 41 (3), 337-362.
- Vivó-Pons, A., Alós, J., Tomas, F., 2020. Invasion by an ecosystem engineer shifts the abundance and distribution of fish but does not decrease diversity. *Marine Pollution Bulletin*, 160, 111586.
- Wirtz, P., Kaufmann, M., 2005. Pfennigalgen: Neu Für Madeira Und Den Ostatlantik: *Halimeda incrassata*. *Das Aquarium*, 431, 48-50.
- Zenetos, A., Corsini-Foka, M., Crocetta, F., Gerovasileiou, V., Karachle, P.K. *et al.*, 2018. Deep cleaning of alien and cryptogenic species records in the Greek Seas. *Management of Biological Invasions*, 9 (3), 209-226.
- Zenetos, A., Karachle, P.K., Corsini-Foka, M., Gerovasileiou, V., Simboura, N. *et al.*, 2020. Is the trend in new introductions of marine non-indigenous species a reliable criterion for assessing good environmental status? The case study of Hellas. *Mediterranean Marine Science*, 21 (3), 775-793.
- Zenetos, A., Albano, P.G., López Garcia, E., Stern, N., Tsiamis, K. *et al.*, 2022. Established non-indigenous species increased by 40% in 11 years in the Mediterranean Sea. *Mediterranean Marine Science*, 23 (1), 196-212.