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An Atlantic origin for the introduced species *Halimeda incrassata* (Bryopsidales, Chlorophyta)

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The tropical calcified green alga *Halimeda incrassata* (J.Ellis) J.V.Lamouroux has been found as an introduced species in the Mediterranean Sea with the first observations in Mallorca dating back to 2011 (Alós *et al.*, 2016). The species spread rapidly at this location, but had not been reported from outside this region until recently. A report published in *Mediterranean Marine Science* provides additional records of this species from Rhodes (Kondylatos *et al.*, 2023). Even though the only observations from that location are from the gut content of silver-cheeked toadfish, *Lagocephalus sceleratus* (Gmelin, 1789), the evidence is very convincing, including a combination of morphological and DNA evidence.

In addition to the possibility of an accidental release from a private aquarium, two alternative colonisation pathways for the arrival of *Halimeda incrassata* in the Eastern Mediterranean Sea based on shipping were described by Kondylatos *et al.* (2023). The first pathway is from the western Mediterranean or the Atlantic via the Strait of Gibraltar; the second from the Red Sea or Indian Ocean via the Suez Canal. While we cannot exclude the possibility of an accidental release, in this paper we argue that of the two shipping scenarios, only the first is realistic. Our argument centres on (1) accurate interpretations of global *Halimeda incrassata* records based on current taxonomic knowledge, (2) historical biogeographic interpretations of *Halimeda* phylogenies, (3) the common nature of west-to-east migration of introduced species in the Mediterranean.

The name *H. incrassata* has been applied across all tropical regions, including the Caribbean region, the Indian Ocean and the Pacific. However, molecular data has shown that Indo-Pacific records are not in fact *H. incrassata* but two look-alike species, the Pacific deep-water species *Halimeda kanaloana* Vroom and the widespread Indo-Pacific species *Halimeda heteromorpha* N'Yeurt (Verbruggen *et al.*, 2006). Other Indo-Pacific species that could possibly be mistaken for *H. incrassata* in terms of overall morphology are *H. borneensis* W.R.Taylor, *H. cylindracea* Decaisne and *H. stuposa* W.R.Taylor, although these species can be distinguished with anatomical characters or DNA-based methods. In Figure 1, we compile published distribution records of these *Halimeda* species, which were either verified with molecular data or based on morphological identification by expert taxonomists with knowledge of the latest molecular taxonomic insights (Verbruggen *et al.*, 2009; Dijoux *et al.*, 2012; Marcelino, 2012; Pongparadon *et al.*, 2015; Alós *et al.*, 2016; Ximenes *et al.*, 2017; Kondylatos *et al.*, 2023). These results clearly show that *H. incrassata* is limited to the Atlantic Ocean plus the recent records in the Mediterranean Sea. All records from the Red Sea and the Indo-West Pacific are of other species.

Historical biogeographical insights have shown a strong divide of the main *Halimeda* lineages (the taxonomic sections of the genus; Verbruggen & Kooistra, 2004) into Atlantic and Indo-Pacific subclades (Kooistra *et al.*, 2002; Verbruggen *et al.*, 2005a; Verbruggen *et al.*, 2009). The sequences of the introduced Mediterranean species clearly correspond to *H. incrassata*, which is closely related to *H. simulans* M.Howe and *H. monile* (J.Ellis & Solander) J.V.Lamouroux, two species that are also restricted to the Atlantic Ocean based on molecular evidence. It is important to note here that these species too, have misidentified records in the Indo-Pacific in public databases, but molecular data shows such records should be placed under *H. borneensis* for *H. simulans* records or under either *H. cylindracea* or *H. stuposa* for *H. monile* records (Verbruggen *et al.*, 2005b). The fact that the species *H. incrassata* is nested in a lineage of Atlantic endemics reinforces the notion that this region represents the origin of the introduced species found in the Mediterranean Sea.

We acknowledge that a large number of the introduced species in Rhodes, and the eastern Mediterranean more broadly, are Lessepsian migrants originating from the Red Sea and Indian Ocean, and the dispersion of these species in the Mediterranean always proceeds east to west and south to north (it cannot be otherwise). However, there are many examples of species that were introduced or first colonized the western part of the Mediterranean and made their way to the east. These include several fish species, like the bastard grunt *Pomadasys incisus* Bowdich, 1825 (Bodilis *et al*., 2013) and the Ma-

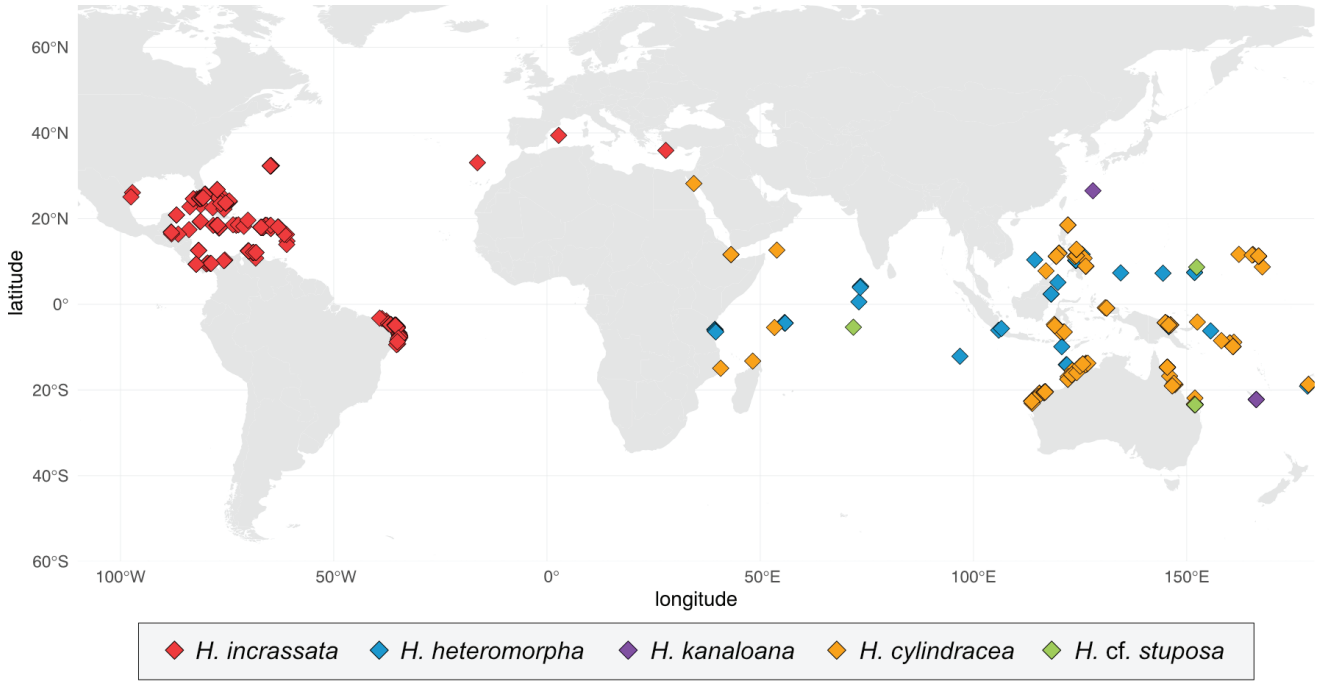

Fig. 1: Distribution of *Halimeda incrassata* and several Indo-Pacific species that it may be confused with morphologically. The species introduced in the Mediterranean Sea is the Atlantic species and the only realistic migration pathway would have been from the Atlantic Sea through the Strait of Gibraltar.

deira scorpionfish *Scorpaena maderensis* Valenciennes, 1833 (Astruch *et al.*, 2021). Two examples amongst the tunicates are those of *Microcosmus squamiger* Michaelsen, 1927 (Turon *et al*., 2007; Önen, 2020) and *Didemnum vexillum* Kott, 2002 (Çinar & Özgul, 2023). Amongst the seaweeds we can highlight the well-known invasives *Womersleyella setacea* (Hollenberg) R.E.Norris, *Phyllymenia gibbesii* (Harvey) S.M.Lin, Rodríguez-Prieto, De Clerck, Guiry (Rodríguez-Prieto *et al.*, 2021) and *Codium fragile* (Suringar) Hariot, species that were first reported in the western Mediterranean (Verlaque *et al*., 2015) and progressed to the east to reach the Levantine and Aegean Seas, respectively (Taskin *et al*., 2013; Tsiamis *et al*., 2010). Particularly fast was the expansion of the Atlantic sea urchin crab, *Percnon gibbesi*, that in only 12 years spread from the southwestern Mediterranean to the Aegean and Levantine Seas (Katsanevakis *et al*., 2011).

Although a release from a private aquarium cannot be ruled out as the introduction pathway of *Halimeda incrassata* in Greece, and *Halimeda* can be easily obtained from online shops, we also consider shipping to be a plausible source of the expansion of *H. incrassata* in the Mediterranean Sea, either directly from the western Atlantic or from the much closer populations in the Balearic Islands. The Caribbean Sea, the Balearic Islands and the Aegean are hot spots for recreational shipping and a lot of boats overwintering in the Caribbean come to the Mediterranean in summer (Gui & Russo, 2011; Rodrigue & Notteboom, 2012) and even more move from the Balearic to the Greek Islands. Ballast water or fouling do not appear likely for *H. incrassata*, but the species can probably survive for several days in the humid conditions inside anchor lockers, as has been suggested for *Caulerpa taxifolia* (Sant *et al.*, 1996), and we argue that a similar mechanism could account for the spreading of *H. incrassata* in the Mediterranean. The species occurs on sandy bottoms where recreational vessels commonly anchor. Re-attachment and growth of thallus fragments is a common mechanism of asexual propagation in *Halimeda* (Walters *et al.* 2002) and is thought to occur extensively in *H. incrassata*, specifically (Littler *et al.*, 2007). In summary, we argue that eastwards recreational shipping is a plausible explanation for the presence of *H. incrassata* in Rhodes.

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