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Coralline Algae in a Changing Mediterranean Sea: How Can We Predict Their Future, if We Do Not Know Their Present?

Fabio Rindi^{1*}, Juan C. Braga², Sophie Martin³, Viviana Peña⁴, Line Le Gall⁵, Annalisa Caragnano¹ and Julio Aguirre²

¹ Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Ancona, Italy, ² Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain, ³ Équipe Écogéochimie et Fonctionnement des Écosystèmes Benthiques, Laboratoire Adaptation et Diversité en Milieu Marin, Station Biologique de Roscoff, Roscoff, France, ⁴ Grupo BioCost, Departamento de Biología, Universidad de Coruña, A Coruña, Spain, ⁵ Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, Paris, France

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Anne Chenuil,
Centre National de la Recherche
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*Correspondence:

Fabio Rindi
f.rindi@univpm.it

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In this review we assess the state of knowledge for the coralline algae of the Mediterranean Sea, a group of calcareous seaweeds imperfectly known and considered highly vulnerable to long-term climate change. Corallines have occurred in the Mediterranean area for ~140 My and are well-represented in the subsequent fossil record; for some species currently common the fossil documentation dates back to the Oligocene, with a major role in the sedimentary record of some areas. Some Mediterranean corallines are key ecosystem engineers that produce or consolidate biogenic habitats (e.g., coralligenous concretions, *Lithophyllum byssoides* rims, rims of articulated corallines, maerl/rhodolith beds). Although bioconstructions built by corallines exist virtually in every sea, in the Mediterranean they reach a particularly high spatial and bathymetric extent (coralligenous concretions alone are estimated to exceed 2,700 km² in surface). Overall, composition, dynamics and responses to human disturbances of coralline-dominated communities have been well-studied; except for a few species, however, the biology of Mediterranean corallines is poorly known. In terms of diversity, 60 species of corallines are currently reported from the Mediterranean. This number, however, is based on morphological assessments and recent studies incorporating molecular data suggest that the correct estimate is probably much higher. The responses of Mediterranean corallines to climate change have been the subject of several recent studies that documented their tolerance/sensitivity to elevated temperatures and pCO₂. These investigations have focused on a few species and should be extended to a wider taxonomic set. Phylogeography, genomics, transcriptomics, and associated microbiomes are fields in which the information for Mediterranean corallines is very limited. We suggest that future work on Mediterranean corallines should be based on a multidisciplinary perspective combining different approaches, and that it should consist of large-scale efforts by scientists based both in western and eastern Mediterranean areas.

Keywords: climate change, Corallinales, ecosystem engineers, Hapalidiales, marine bioconstructions, paleontological records, Sporolithales, taxonomy

INTRODUCTION

The Mediterranean is the largest (2,969,000 km²) and deepest (average 1,460 m, maximum 5,267 m) enclosed sea on Earth (Coll et al., 2010). Although it represents only 0.82% in surface area and 0.32% in volume of the world oceans (Bianchi and Morri, 2000), it is a well-known hotspot of marine biodiversity, with not <20,000 species recorded (Pascual et al., 2017). Such diversity originates from its complex paleoceanographic history and changes in its paleogeographic configurations (particularly through the Cenozoic) and from the current diversity of oceanographic conditions among different regions of the basin (Bianchi and Morri, 2000). The events that characterized the geological history of the Mediterranean in the last 15 My produced a high number of endemic species (which led Bianchi and Morri, 2000 to define the Mediterranean “a factory designed to produce endemics”).

The Mediterranean, however, is also highly impacted and threatened. Climatic models predict that the Mediterranean basin will be one of the regions most affected by the ongoing warming trend and by an increase in extreme events (Lejeune et al., 2010; Galli et al., 2017). These predictions are supported by climatological data: the average maximum summer seawater temperature has risen by 1°C in 20 years in some areas of the western Mediterranean (Marbà and Duarte, 2010) and a 0.4°C warming per decade since 1986 was reported for the entire Mediterranean Sea by Sakalli (2017). Seasonal and depth-related warming trends were documented by Nykjaer (2009) and Coma et al. (2009), respectively. Studies that measured and modeled pH changes since preindustrial times in the Mediterranean (Hassoun et al., 2015; Goyet et al., 2016) provided evidence of acidification related to excessive increase of atmospheric CO₂. The mean surface pH has decreased by ~0.002 units per year from 1994 to 2006 in the northwestern Mediterranean (Howes et al., 2015; Kapsenberg et al., 2017) and by 0.004 units at the Strait of Gibraltar (Flecha et al., 2015). These trends are projected to continue throughout the twenty-first century.

The impact of climate change on Mediterranean marine biota is expected to be strong, because it will interact with anthropogenic disturbances operating at local scales (e.g., chemical pollution, eutrophication, increase in sediment load, habitat degradation caused by trawling). Mediterranean coastal ecosystems have been exploited by humans for millennia, and have been therefore altered in many ways. Nowadays Mediterranean shores are heavily urbanized and support a high population density; impacts of human activities are proportionally stronger in the Mediterranean than in any other sea of the world (Coll et al., 2010). Habitat loss, degradation and pollution, overexploitation of marine resources and invasions of alien species are the main drivers of change, which in future decades will overlap and interact with climate-related changes.

Coralline algae have existed in the Mediterranean (or in the area corresponding to the present Mediterranean) for ~140 My (Chatalov et al., 2015) and are ubiquitous on modern Mediterranean rocky shores. They are key components in some of the most common Mediterranean benthic communities, such as coralligenous concretions (Figure 1A), *Lithophyllum byssoides* rims (Figure 1B), maerl/rhodolith beds (Figure 1C),

barrens formed at sites subjected to heavy grazing (Figure 1D), rims of *Ellisolandia elongata* and other articulated corallines (Figure 1E), and the epiphytic assemblage of the seagrass *Posidonia oceanica* (Figure 1F). In these communities coralline species often play a key role as ecosystem engineers: the accumulation of their calcareous thalli produces bioconstructions that modify the tridimensional structure of the substratum and profoundly influence ecosystem functioning (Bressan et al., 2009; Ingrosso et al., 2018). Mediterranean bioconstructions built by corallines are known as major repositories of biodiversity (e.g., coralligenous communities host not <1,700 animal and algal species; Ballesteros, 2006) and carbonate-producing ecosystems (Cebrián et al., 2000; El Haikali et al., 2004; Canals and Ballesteros, 2007; Bracchi and Basso, 2012). Furthermore, although bioconstructions formed by corallines exist in every sea, in the Mediterranean they reach a particularly high spatial and bathymetric extent (coralligenous concretions alone are estimated to exceed 2,700 km² in surface; Martin et al., 2014). There is evidence that some of these bioconstructions are undergoing substantial degradation and that the corallines that produce them are suffering a loss of vitality (Laborel et al., 1993; Blanfuné, 2016); in general, observations of bleaching and necroses in Mediterranean corallines have become increasingly common in recent years (Hereu and Kersting, 2016; Basso et al., 2018; Quéré et al., 2019; Figure 2).

The need of a deep understanding of the biology of Mediterranean corallines is therefore more important than ever. Mediterranean corallines have a long history of study and in the last few decades have attracted great interest from marine biologists. Despite of this, many aspects of their biology are still poorly or insufficiently known. It is also noteworthy that detailed information is available for relatively few species (mainly those shown in Figure 3). It is thus timely to summarize the state of knowledge for these seaweeds and highlight gaps on which future research should concentrate, which we aim to do in this review. This review focuses strictly on the biology of coralline species and does not deal with Mediterranean communities/habitats built or dominated by corallines, for which detailed summaries are already available (coralligenous communities: Ballesteros, 2006; rhodolith beds: Basso et al., 2017; Bracchi et al., 2019a; *Lithophyllum byssoides* rims: Laborel, 1987; Bressan et al., 2009; Verlaque, 2010; *Ellisolandia elongata* rims: Laborel, 1987; Ballesteros, 1988; Bressan et al., 2009; epiphytic community of *Posidonia oceanica*: Piazzini et al., 2015).

HISTORICAL SUMMARY

Being unusual among algae, corallines have long intrigued scientists. If detailed observations were provided in the eighteenth century, corallines were often studied together with other calcified organisms currently classified among animals. Calcareous algae in the Mediterranean were first described more than two centuries ago, and some species of the genus *Corallina* with distribution encompassing the

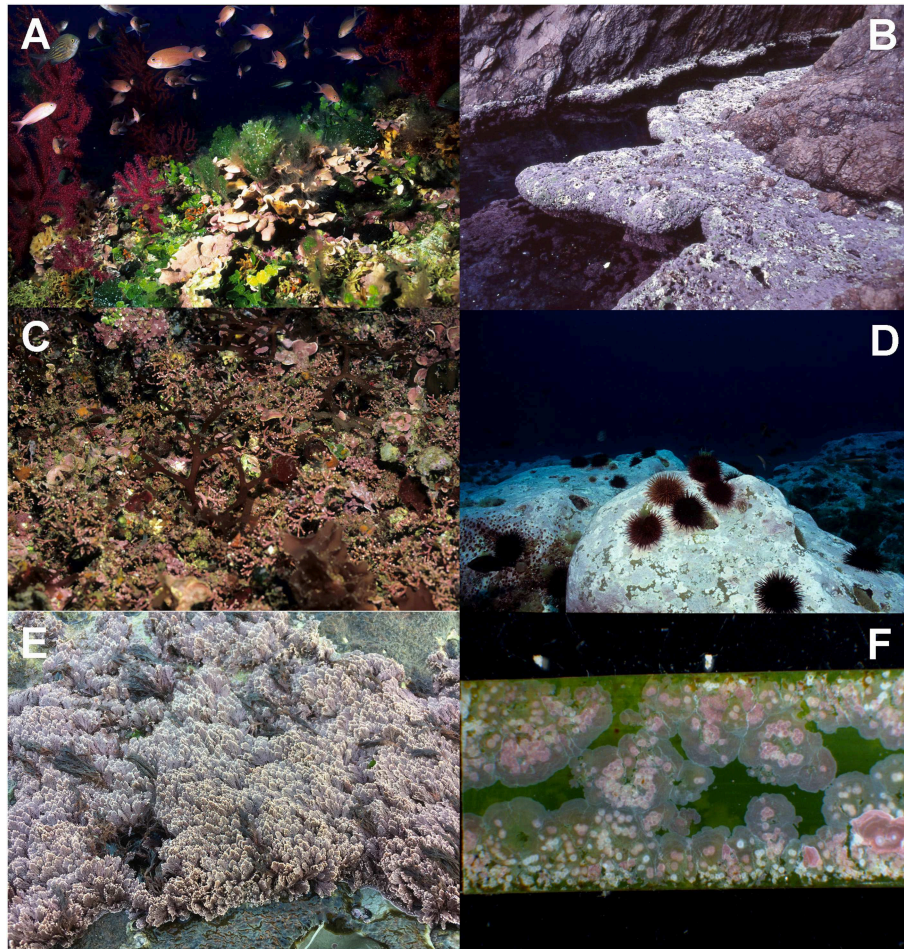


FIGURE 1 | Examples of coralline-dominated habitats in the Mediterranean. **(A)** A coralligenous community (Islas Columbretes, Spain); copyright: Enric Ballesteros (kike@ceab.csic.es). **(B)** A *Lithophyllum byssoides* rim (Cala Litzia, Scandola Nature Reserve, Corsica, France); copyright: Marc Verlaque (marc.verlaque@mio.osupytheas.fr). **(C)** Detail of a maerl bed (Islas Columbretes, Spain); copyright: Enric Ballesteros (kike@ceab.csic.es). **(D)** A barren ground dominated by encrusting corallines on a bottom heavily grazed by sea urchins (Alboran Island, Spain); copyright: Enric Ballesteros (kike@ceab.csic.es). **(E)** An intertidal rim of articulated corallines (Passetto di Ancona, Italy). **(F)** Detail of a leaf of the seagrass *Posidonia oceanica* covered by epiphytic encrusting corallines (Ischia Island, Italy); copyright: Maria Cristina Gambi (gambimc@gmail.com). All pictures were provided by the copyright owners and reproduced with their permission.

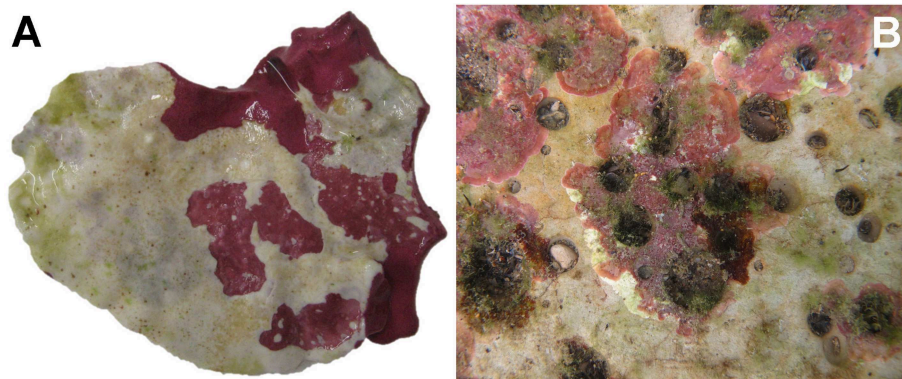


FIGURE 2 | Examples of necroses in Mediterranean corallines. **(A)** *Lithophyllum cabiochae*, close-up view of a specimen largely bleached. **(B)** Encrusting corallines showing incipient bleaching at the edges (Piscinetta del Passetto, Ancona, Italy).

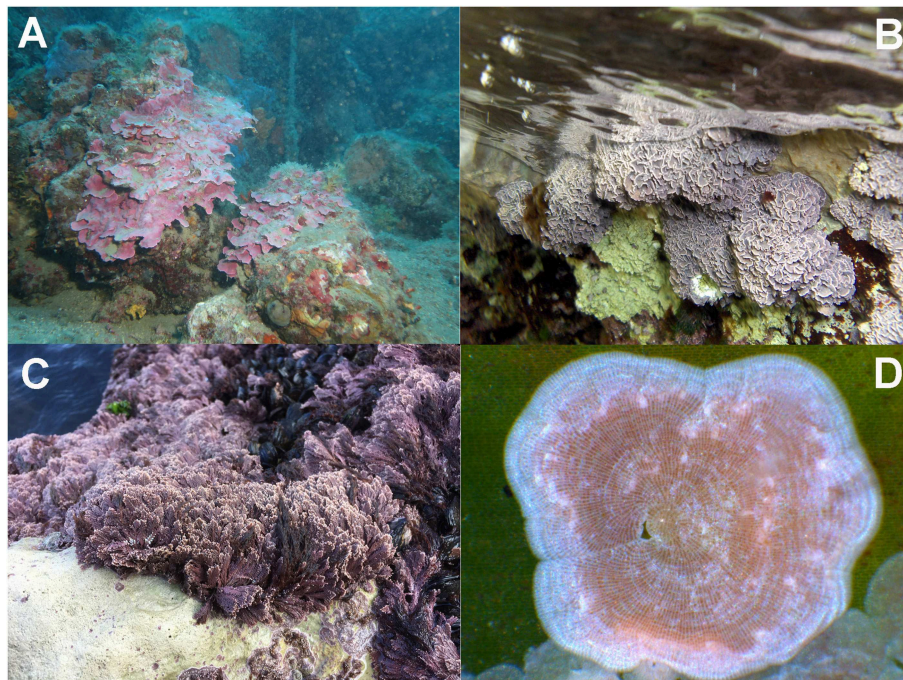


FIGURE 3 | Examples of Mediterranean corallines that have been subject of many studies. **(A)** *Lithophyllum stictiforme*, bioconstructor species of coralligenous concretions (reported in many studies as *Lithophyllum cabiochae*); copyright: Carlo Cerrano (c.cerrano@univpm.it). **(B)** *Lithophyllum byssoides* forms biogenic rims ("trottoirs") in the intertidal zone; copyright: Sara Kaleb (sara.kaleb@gmail.com). **(C)** Articulated corallines (usually identified as *Ellisolandia elongata*) are common in the Mediterranean low intertidal and shallow subtidal zones. **(D)** *Pneophyllum fragile*, a common epiphyte on the leaves of the seagrass *Posidonia oceanica*; copyright: Maria Cristina Gambi (gambimc@gmail.com). All pictures were provided by the copyright owners and reproduced with their permission.

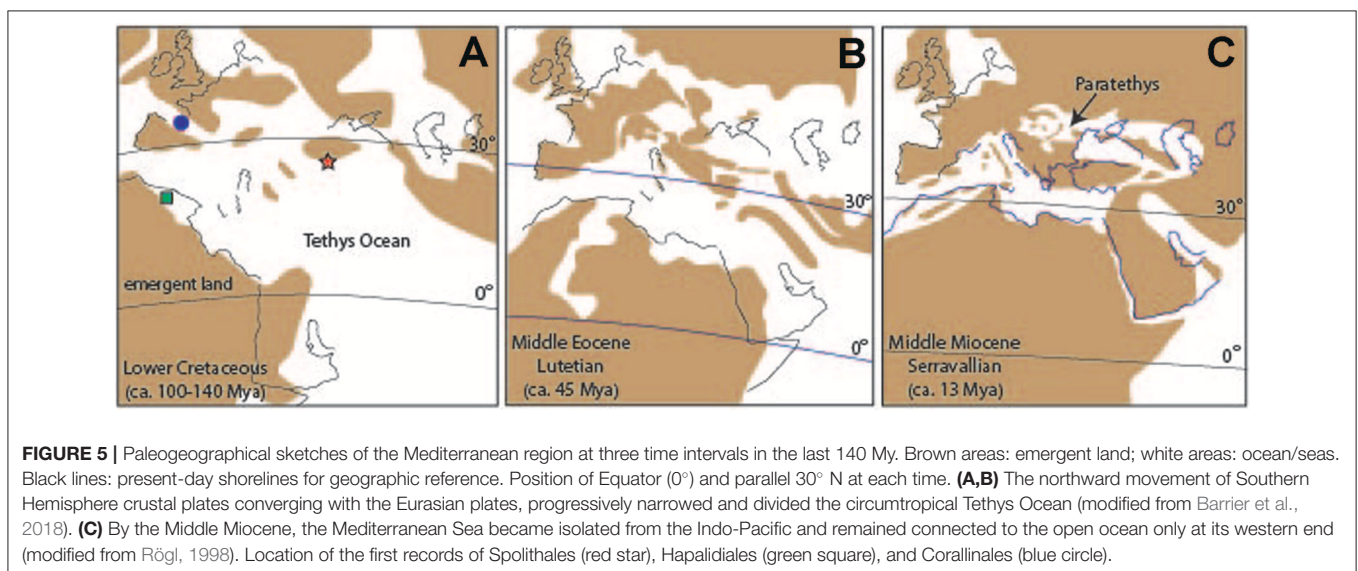
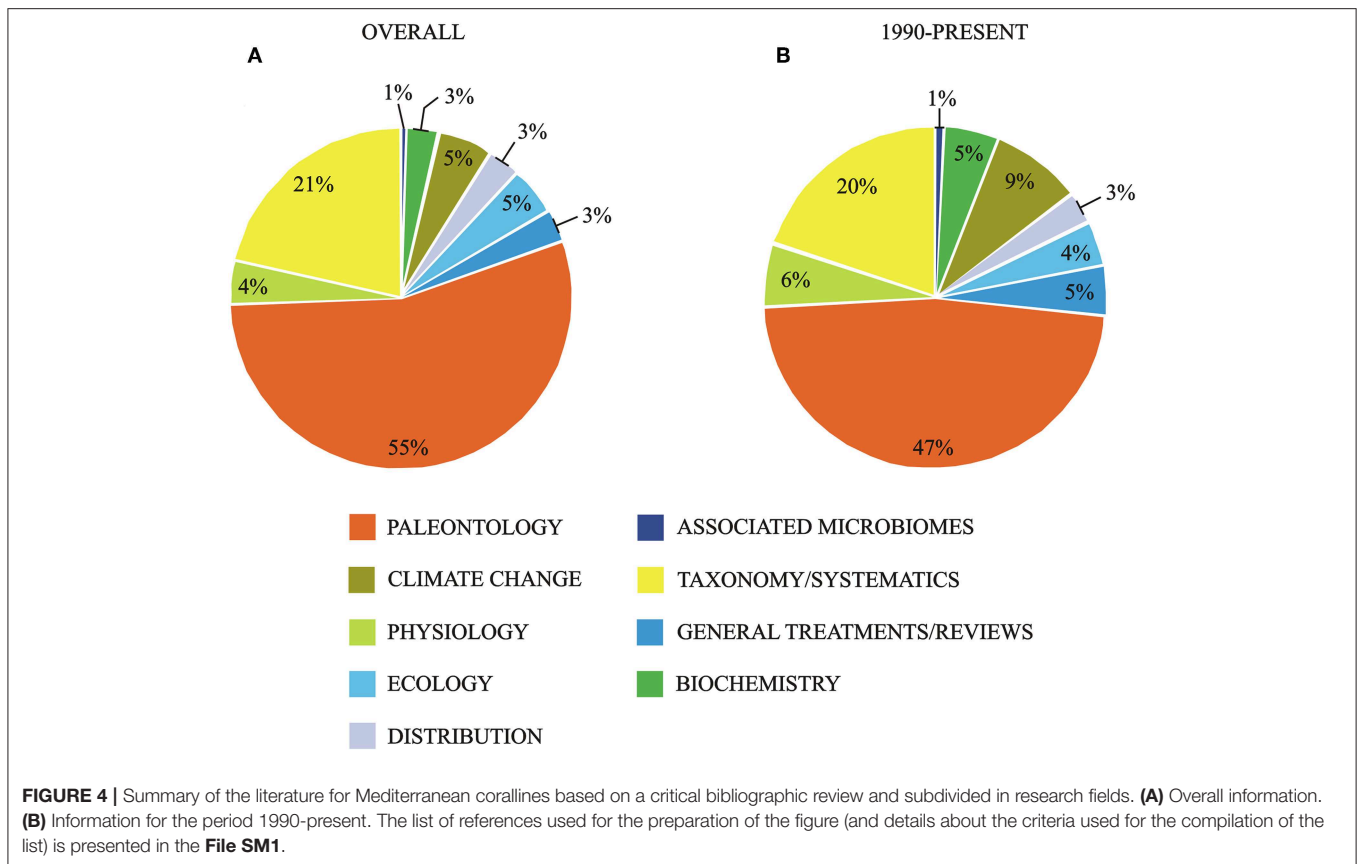
Mediterranean were among the first seaweeds described with Latin binomials in the Linnaean system (Linnaeus, 1758). Many species that are common in the Mediterranean were described in the late eighteenth and early nineteenth centuries (Ellis, 1768; Ellis and Solander, 1786; Esper, 1796; de Lamarck, 1801; Bory de Saint-Vincent, 1832). The subsequent work carried out until the 70s–80s of the twentieth century consisted mainly of paleontological studies, floristic inventories, traditional taxonomy based on morphology, and descriptive distributional and ecological studies (Bressan, 1974; Bressan and Babbini, 1995, and references therein). Most ecological studies had in fact a general perspective and concerned coralline-dominated habitats (mainly coralligenous concretions and *Lithophyllum byssoides* rims), rather than coralline biology itself.

A critical review of the literature concerning Mediterranean corallines (results summarized in **Figure 4**; the list of references used is reported in the **File SM1**) shows that in the last decades paleontological record, taxonomy and phylogenetic diversity, responses to climate change and physiology are the main aspects on which research has focused. So, in this review we discuss primarily the state of knowledge in these fields. Remarkably, phylogeography, genomics, transcriptomics, study of associated microbial communities and mineralization are fields in which the information for Mediterranean corallines is still very limited.

GEOLOGICAL HISTORY OF THE MEDITERRANEAN AND PALEONTOLOGICAL RECORD OF MEDITERRANEAN CORALLINES

The present-day configuration of the Mediterranean Sea is the result of a complex geological history. The evolutionary history of Mediterranean corallines has taken place in a changing environment with long-term but major changes in paleogeography, climate and oceanography since the early Lower Cretaceous, for about 140 My. The paleogeographic evolution of the Mediterranean is part of the progressive closing and partitioning of the Tethys, the ancient circumtropical ocean, due to the convergence of Southern Hemisphere crustal plates with the northern ones (Scotese, 2014a; **Figure 5**). The global trends of ocean temperatures during such a long period show an initial rise up to the mid-Cretaceous climate maximum (some 95 Mya) and, since then, temperature has been declining with frequent and sometimes large reversals (Zachos et al., 2001; Friedrich et al., 2012; O'Brien et al., 2017).

A critical review of hundreds of publications on fossil corallines shows that 359 species have been reported in Cretaceous to Pleistocene deposits in different regions of the Mediterranean (**File SM2**, list of references in **File SM6**). These can be attributed to the orders Sporolithales (80 species, **File SM3**), Hapalidiales (159 species, **File SM4**), and Corallinales



(120 species, **File SM5**). The oldest known fossil corallines attributable to extant orders occur in the Lower Cretaceous (Valanginian, 137 Mya) in northern Greece. They are scarce specimens of *Sporolithon* that lived on a carbonate platform surrounding an island at the northern margin of the Tethys (Chatalov et al., 2015; **Figure 5A**). For millions of years, the only

recorded corallines are rare encrusting *Sporolithon* associated to coral reefs (Conrad and Masse, 1989; Arias et al., 1995; Tomás et al., 2007; Bucur, 2008; Woelkerling et al., 2014). In the late Barremian-Aptian (126–113 Mya), the Spoilithales became more frequent and diverse with several extinct genera (*Agardhiellopsis*, *Kymalithon*, *Paraphyllum*) (Moussavian, 1993).

In this time interval, there are also poorly contrasted reports of Hapalidiales (*Lithothamnion*) at the southern margin of the Tethys (Algeria, Lemoine, 1939) and Corallinales (*Lithoporella* and Corallinoideae) in the marine passage that corresponds to the present-day Pyrenees (Poignant, 1968; Lemoine, 1970). In the Albian (113–100 Mya), the morpho-species diversity of Sporolithales increases and locally they are common components of carbonate rocks (Lemoine, 1970; Moussavian, 1993; Bucur, 1994; Rosales, 1995; Lopez-Horgue et al., 2009). Reports of Hapalidiales (as *Lithothamnion* and *Melobesia*) are scarce and inconclusive (Lemoine, 1970; Poignant, 1981). Few scattered records might correspond to geniculate Corallinoideae (Maslov, 1956; Lemoine, 1970). For most of the Upper Cretaceous (Cenomanian–Campanian, 100–72 Mya) coralline algae continue to be generally scarce components of carbonate platforms. The relatively few records scattered all over the region indicate an increase in Sporolithales (mainly of *Sporolithon*) with the appearance of a new genus in this order, *Hemiphyllum*, now extinct. Reports of Hapalidiales, both *Lithothamnion* and *Mesophyllum* (Lemoine, 1970; Poignant, 1981), are poorly illustrated and remain doubtful. Within Corallinales, the first occurrence in the region of reliable representatives of Neogoniolithoideae sensu Rösler et al. (2016) is recorded (*Spongites* as *Lithophyllum*, Bucur and Baltres, 2002). In the Maastrichtian (72–66 Mya), the last stage of the Cretaceous, the number of Hapalidiales increases (Poignant, 1978, 1981). The oldest-known Hydrolithoideae (*Karpathia*, Bassi et al., 2005 and references therein) also appear in this time interval, together with a few more Corallinales (Rösler et al., 2017).

The Tethys narrowed during the Cretaceous in its western end with the progressive convergence of African and European plates, but in the Paleocene (66–56 Mya) an uninterrupted marine connection continued to exist at low latitudes around the globe. The partial emergence of the Pyrenees and large areas of western Europe reduced the passages from the Tethys to the Atlantic. Two-thirds of the coralline species disappeared during the Cretaceous mass extinction (Aguirre et al., 2000a,b), but the number of recognized morpho-species recovered and substantially increased during the Paleocene (Aguirre et al., 2000a,b, 2007). This recovery was mainly due to the increase in Hapalidiales (*Lithothamnion*, *Mesophyllum*, and *Phymatolithon*) and Corallinales, whilst the Sporolithales started a decrease that continued throughout the Cenozoic with minor reversals. All genera of Sporolithales other than *Sporolithon* recorded in Cretaceous rocks disappeared before the Paleocene. Corallines from this epoch occur in coral-bearing carbonates, either *in situ* in shallow-water paleoenvironments (e.g., Moussavian, 1993; Aguirre et al., 2007) or re-deposited in deeper settings (Stockar, 2000).

As a marked reversal of the general global cooling trend initiated in the mid-Cretaceous, during the Early and Middle Eocene epochs (56–38 Mya) global temperatures were higher than in older and younger Cenozoic times (Zachos et al., 2001, 2008; Anagnostou et al., 2016). During this warm interval, large coral reefs disappeared from low latitudes (Scheibner and Speijer, 2008; Kiessling, 2010; Perrin and Kiessling, 2010). The global sea level was several tens of meters higher than in the modern

ocean (Miller et al., 2011), favoring the development of extensive carbonate platforms dominated by larger benthic foraminifers and algae (Nebelsick et al., 2005; Scheibner and Speijer, 2008; Norris et al., 2013). The emergence of the antecedent reliefs of the Alpine mountain belts (Alps, Carpathian mountains) as many small islands caused a complex paleogeography of the northern margin of the Tethys, which extended north of the modern Black and Caspian seas (Scotese, 2014b; **Figure 5B**). Coralline algae occurred in rhodolith beds and in bioclastic facies in platform deposits or in deep-water, re-worked sediments (e.g., Aroldi and Bucur, 2002; Nebelsick et al., 2005). Numbers of reported species and relative proportions of coralline orders did not change throughout this interval (Aguirre et al., 2000a).

In the Late Eocene (38–34 Mya) global temperatures and sea level progressively decreased (Zachos et al., 2001; Miller et al., 2011). In addition to rhodolith beds (and maerl) and bioclastic facies, coralline algae of this age occurred associated with corals in shallow water carbonates (Bassi, 1998; Rasser, 2000; Nebelsick et al., 2005; Barattolo et al., 2007) at both margins of the Tethys in the Mediterranean region. The number of reported morpho-species of Hapalidiales and Corallinales slightly increased, whereas Sporolithales resumed their diversity decline after a long interval of stability.

The most dramatic global cooling of the Cenozoic era took place at the Eocene–Oligocene transition (at 34 Mya). Development of Antarctic ice sheets and onset of glaciation marked the beginning of the modern icehouse world (Zachos et al., 2001). A significant sea-level drop was coeval of these processes. The continued rising of Alpine belts led to the separation of the Paratethys, a large marine body extending to the north of the Alps, from the Rhône Basin over eastern Europe to the east of the modern Caspian Sea (Popov et al., 2004). Since the Oligocene (34–23 Mya) the Paratethys was an individual paleobiogeographic province with connections to the Tethys/Mediterranean Sea during most of its paleogeographic evolution (Harzhauser and Piller, 2007). The marine connections remained continuous from the present-day Indo-Pacific to the North Atlantic oceans (Rögl, 1998).

In the majority of localities, Oligocene corallines occur in coral reef deposits or in laterally associated sediments as rhodoliths, coralline debris, or as crusts directly growing on the soft sea floor (Fravega et al., 1987; Brandano, 2017). Occasionally, rhodoliths and algal debris have also contributed as important carbonate producers in late Oligocene homoclinal carbonate ramps in the western Tethys (Bover-Arnal et al., 2017). They also occur in deep-water, re-deposited carbonates (Rasser and Nebelsick, 2003). Most reports of Oligocene coralline algae derive from the northern margin of the Western Tethys, especially from the Piedmont and Ligurian basins, and the circumalpine area (north-eastern Italy, northern Slovenia, Austria and southern Bavaria) (Nebelsick et al., 2005). Hundreds of species of Oligocene corallines were described in these areas in the last century (Airoldi, 1932; Conti, 1950; Mastrorilli, 1968; Fravega et al., 1987; further references in Braga et al., 2010). Long species lists were also reported from the Balkan and Carpathian mountains (Lemoine, 1977; Bucur et al., 1989). Oligocene corallines were also described from Algeria at the southern margin of the

Western Tethys (Lemoine, 1939) and from ancient islands in the Tethys, such as Maltese Islands (Brandano, 2017), Salento Peninsula, southern Italy (Bosellini and Russo, 1992), and the Malaguide Complex in southern Spain (Braga and Bassi, 2011). *Titanoderma pustulatum* occurred in the early Oligocene from NW Iran (Basso et al., 2019), an area connecting the Indian Ocean and the Tethys before its final closure in the middle Miocene. This new finding places the oldest record of the *Titanoderma/Lithophyllum pustulatum* group in this area rather than in the late Oligocene from the Central Pacific as previously recorded (Bassi et al., 2009). Reported diversity of morpho-species of Corallinales and Hapalidiales continued the rise initiated in the late Eocene. By contrast, the number of species of *Sporolithon* decreased (Aguirre et al., 2000a).

Continued convergence of African and European plates and emergence of Alpine mountain belts led to significant palaeoceanographic changes during the Miocene (23–5.3 Mya). The long-lasting circum-tropical ocean was partitioned by land masses, changing the global geography and major current patterns. The connections of the Mediterranean to the Indian Ocean were interrupted in the middle Miocene (at about 14 Mya, Rögl, 1998) by the emergence of the Middle East reliefs. The Paratethys was strongly isolated during the late Miocene and its European sub-basins became continental (Rögl, 1998; Popov et al., 2004; Harzhauser and Piller, 2007). At the western end of the Mediterranean, uplift of the Betic-Rifean reliefs gradually closed the seaways to the Atlantic Ocean. The connections were temporarily interrupted during the Messinian Salinity Crisis at about 5.5 Mya (Hsü et al., 1977). The opening of the Gibraltar Straits established the present-day configuration of Mediterranean Sea as a partially isolated, evaporitic water body, which needs inflow from the Atlantic Ocean to maintain its level (Mariotti et al., 2002). A global warm phase, the Mid-Miocene Climatic Optimum (about 15 Mya), took place after a brief glaciation interval in the earliest Miocene. Since that phase, the Earth's climate has been cooling with reversals (Zachos et al., 2001). The Northern Hemisphere ice-sheets started growing in the late Miocene. During the Miocene, global sea-level fluctuations of 50–60 m on the million-year scale and superimposed oscillations controlled by orbital obliquity (41,000 year cycles) did not show a marked ascending or descending trend (Miller et al., 2011).

Rhodolith beds were widespread in Miocene platform carbonate and siliciclastic deposits in the Mediterranean and Paratethys (Halfar and Mutti, 2005; Braga, 2017). They were most common in carbonate ramps together with small coral buildups, and locally they occurred in reef-rimmed shelf deposits (Hrabovský et al., 2016; Braga, 2017). Coralline biostromes (*coralligène de plateau*) were reported in the Maltese Islands (Bosence and Pedley, 1982). Rhodoliths and coralline debris also occur as deep re-deposited sediments (Bassi et al., 2017).

The number of fossil non-geniculate coralline species reported in the literature reached its maximum in the early Miocene and then decreased with small reversals (Aguirre et al., 2000a). Some available modern accounts based on comparable diagnostic characters seem to confirm a morphospecies richness reduction throughout the Miocene. While Checconi (2006)

describes 35 species in the early Miocene (Burdigalian) of the Southern Apennines (Italy), only 21 morphospecies were found in the late Miocene (Messinian) reefs in Salento and Sorbas Basin together (Braga et al., 2009). The reduction is even more marked within some genera, such as *Spongites*, encompassing 13 species during the Burdigalian (Checconi, 2006) and only 5 during the Messinian in southern Italy (Braga et al., 2009). *Lithophyllum* (and *Lithophyllum* gr. *pustulatum* –*Titanoderma*, Bassi et al., 2009) is first recorded in the Mediterranean region in the early Miocene from SE France (Burdigalian; Coletti et al., 2018a). In the Miocene, for the first time in the evolutionary history of corallines, Mediterranean assemblages differ from their pantropical counterparts at the genus level (Braga et al., 2010). *Spongites*, *Neogoniolithon*, and *Lithophyllum* are the main components in shallow-water Miocene Mediterranean paleoenvironments, including coral reefs. *Porolithon*, *Hydrolithon* gr. *boergesenii*, and *Aethesolithon* J.H. Johnson, which occur with those genera in coral reefs in low latitudes, are absent in the Mediterranean basins. This biogeographical differentiation was probably due to the isolation of the Mediterranean from the Indian Ocean, complete by the middle Miocene (Rögl, 1998; **Figure 5C**). Although coral reefs persisted in the Mediterranean until the latest Miocene, after its eastern closure the coral diversity decreased (Bosellini and Perrin, 2008). The strong decline of species number of *Sporolithon*, a genus of tropical affinity, after the middle Miocene, might also be due to the isolation from the Indian Ocean (Braga and Bassi, 2007).

The general configuration of the modern Mediterranean was established in the Pliocene (5.3–2.6 Mya). Paleogeography within the basin, however, changed substantially due to the uplift of modern reliefs, with a progressive reduction of the areas invaded by the sea. Global temperatures continued the decrease initiated in the middle Miocene (Zachos et al., 2001) and sea level followed a falling trend modulated by oscillations with amplitude of several tens of meters (Miller et al., 2011).

Rhodolith beds are scarcer than in Miocene rocks but have been reported in southern Spain (Aguirre, 1998; Aguirre and Jiménez, 1998; Aguirre et al., 2012) and northern Italy (Vannucci et al., 1996; Checconi et al., 2007). Corallines also occur in vermetid reefs in early Pliocene deposits of northeastern Spain (Aguirre et al., 2014). Here, *Spongites fruticosus* is the main coralline, differently from modern Mediterranean vermetid reefs, in which *Neogoniolithon brassica-florida* is the dominant species (Boudouresque, 2004; Langar et al., 2011). The Pliocene coralline morphospecies in the few published accounts are similar to those of the present-day Mediterranean. More than 90% of the 19–20 species identified in early Pliocene in southern Spain (Aguirre et al., 2012) and 88% of the 8 reported in the late Pliocene of Tuscany (Italy) (Checconi et al., 2007) are living in the Mediterranean and Lusitanian provinces.

Except in areas with intense recent uplift such as Sicily, the Quaternary (last 2.6 My) shorelines of the Mediterranean at high sea levels were close to the present-day situation. The few Pleistocene and Holocene inventories suggest that Mediterranean Quaternary corallines were not different from the modern ones. They occurred in build-ups (*coralligène de plateau*) (Nalin et al.,

2006; Coletti et al., 2018b; Bracchi et al., 2019b), in rhodolith beds, and in rhodoliths and debris dispersed in siliciclastic deposits (Di Geronimo, 1998; Coletti et al., 2018b). The dramatic global climatic and sea level changes that took place repeatedly during the Pleistocene (e.g., Rohling et al., 2014) did not substantially affect coralline assemblages in the Mediterranean, although a few species might have migrated into the Mediterranean from the North Atlantic in the colder periods (Di Geronimo, 1998).

FLORISTIC DIVERSITY

Due to the long history of taxonomic studies, it is not surprising that a plethora of names (both species and intraspecific taxa) has accumulated for Mediterranean corallines. The nomenclatural history of these algae is very complicated and would be impossible to summarize in a concise form. A comprehensive summary of the names available and information about their taxonomic validity can be found in the account of Cormaci et al. (2017) and in AlgaeBase (Guiry and Guiry, 2019). Here we follow primarily the taxonomy of Cormaci et al. (2017). These authors reported for the Mediterranean 57 species; with the addition of *Lithophyllum yessoense* (recorded by Verlaque, 2001), *Pneophyllum cetinensis* (freshwater species described by Žuljević et al., 2016) and *Lithophyllum nitorum* (recorded by Peña et al., 2018), the Mediterranean coralline flora as currently known consists of 60 species (Table 1). The genus *Lithophyllum* is the species-richest (16 species), followed by *Mesophyllum* (6 species), and *Amphiroa*, *Jania*, and *Lithothamnion* (5 species each). Twenty-seven species were originally described based on Mediterranean material (see type localities in Table 1). For details of morphology and habitat for each species, see Irvine and Chamberlain (1994), Bressan and Babbini (2003), and Cormaci et al. (2017).

MOLECULAR STUDIES OF MEDITERRANEAN CORALLINES

Taxonomy, Phylogeny, and Geographical Distribution

There are well-founded reasons to believe that the current estimate of 60 species is an underestimation of the real species number. The taxonomy of Mediterranean corallines so far has been based almost entirely on morphological data. Species circumscriptions have been based on gross morphology and morpho-anatomical characters observed in light and electron microscopy (Hamel and Lemoine, 1953; Huvé, 1962; Bressan, 1974; Bressan et al., 1977; Boudouresque and Verlaque, 1978; Woelkerling, 1983, 1985; Woelkerling et al., 1985; Athanasiadis, 1989, 1995, 1997, 1999a,b; Basso, 1995; Bressan and Babbini, 1995; Basso et al., 1996, 2004, 2011; Furnari et al., 1996; Chamberlain, 1997; Cabioch and Mendoza, 1998, 2003; Bressan and Cabioch, 2004; Basso and Rodondi, 2006; Athanasiadis and Neto, 2010; Kaleb et al., 2011, 2012; Cormaci et al., 2017).

In recent decades, DNA sequence data have become a widespread tool in coralline taxonomy and have played an increasingly important role in species circumscriptions. After

the first studies published around the end of the last century (Bailey and Chapman, 1996, 1998), the last decade has seen an exponential increase of DNA-based phylogenetic and taxonomic studies. Investigations of molecular-assisted alpha taxonomy (MAAT) have now become the normality in coralline taxonomy and systematics. This approach uses molecular markers to assign collections to genetic groups followed by detailed morphological observations (Hind et al., 2014). Such new information has revolutionized our understanding of coralline diversity and evolution (Nelson et al., 2015) and has drawn a new scenario in which some points are now well-established. First, coralline algae are characterized by high levels of cryptic diversity. The genetic diversity of these organisms unraveled by DNA sequence data is much higher than indicated by morpho-anatomical data, both in geniculate and non-geniculate species. Cryptic diversity has been shown to abound in marine macroalgae (De Clerck et al., 2013; Verbruggen, 2014); although corallines have a morpho-anatomical structure that offers more characters for species discrimination compared to other red seaweeds, they are perhaps the group of rhodophytes in which this situation is most pervasive (Pezzolesi et al., 2019). Second, many morpho-anatomical features traditionally used to identify corallines are not reliable for identification purposes. Therefore, a taxonomy based entirely or mostly on these characters (as it is the case for the Mediterranean) is likely to be misleading, with substantial risk of misidentifications and underestimation of species numbers (e.g., for the genus *Lithophyllum* Hernandez-Kantun et al. (2016) estimated a species diversity likely two to four times greater than currently estimated in each geographic region). Third, special care must be used in the application of species names. When cryptic diversity is demonstrated and a morphospecies turns to represent a complex of cryptic species, it may be very difficult to decide to which cryptic species the Linnaean binomial is correctly assigned. This may create great confusion when different cryptic species have different geographical distributions. Considering this problem, in absence of molecular data the practice of identifying specimens from a certain geographical region with names of species described from widely separated regions should be abandoned (Pezzolesi et al., 2019).

The first study presenting molecular data for Mediterranean corallines was published by Walker et al. (2009). These authors presented *cox1* and SSU rRNA sequences for 2 samples of *Corallina ferreyrae* (as *Corallina elongata*) from northern Greece in their taxonomic study of European articulated corallines. At present, there are in GenBank 1153 sequences obtained from Mediterranean corallines, which were produced in 18 different studies (among which De Jode et al., 2019 provided the largest contribution, 812 sequences; Table S1). These sequences were generated by PCR amplification and Sanger sequencing of selected markers. The plastid gene of the photosystem II protein D1 (*psbA*), the mitochondrial COI-5P fragment of the cytochrome c oxidase I gene, the mitochondrial *cox2,3* spacer, and the nuclear genes of the small subunit (SSU) and large subunit (LSU) of the ribosomal RNA have been the main markers used (Table S1). To date, the transcriptomic data presented by De Jode et al. (2019) are the

TABLE 1 | Species of coralline algae reported for the Mediterranean Sea and currently regarded as taxonomically valid.

Species	Synonyms frequently used in the mediterranean literature	Habit	Type locality	Known distribution in the mediterranean	Important references
<i>Amphiroa beauvoisii</i> J.V. Lamouroux		Geniculate	Portugal	Widespread. SP, FR, IT, MA, CR, TK, CY, SY, IL, TU, AG, MO	Cormaci et al., 2017
<i>Amphiroa cryptarthrodia</i> Zanardini		Geniculate	Trieste (Italy), Istria and Dalmatia (Croatia)	Reported as widespread, but in need of reassessment due to previous confusion with <i>A. rubra</i> . SP, FR, IT, MA, SL, CR, AL, GR, TK, CY, SY, LE, IL, LI, TU, AG, MO	Rosas-Alquicira et al., 2010; Cormaci et al., 2017
<i>Amphiroa fragilissima</i> (Linnaeus) J. V. Lamouroux		Geniculate	" <i>In Indiis</i> " (probably Jamaica)	Poorly-known species, reported only from some areas in the western and central Mediterranean. SP, FR, IT, AG	Cormaci et al., 2017
<i>Amphiroa rigida</i> J.V. Lamouroux		Geniculate	Mediterranean Sea	Widespread. SP, FR, IT, MA, CR, AL, GR, TK, CY, SY, LE, IL, EG, LI, TU, AG, MO	Cormaci et al., 2017
<i>Amphiroa rubra</i> (Philippi) Woelkerling		Geniculate	Sicily	Rarely recorded. IT, TK.	Cormaci et al., 2017
<i>Boreolithon vanheurckii</i> (Chalon) A.S. Harvey et Woelkerling	<i>Melobesia vanheurckii</i> (Heydrich) De Toni	Encrusting	St. Brelade, Jersey, Channels Islands, U.K.	Rarely recorded. SP, IT	Irvine and Chamberlain, 1994
<i>Choreonema thuretii</i> (Bornet) Schmitz		Filamentous endophytic	Pointe de Querqueville, France	Widespread, more common in the western and central Mediterranean than in the eastern. SP, FR, IT, MA, SL, CR, AL, GR, TK, CY, AG, MO	Hamel and Lemoine, 1953; Irvine and Chamberlain, 1994
<i>Corallina ferreyrae</i> E. Y. Dawson, Acleto et Foldvik	<i>Corallina caespitosa</i> Walker, Brodie et L.M. Irvine	Geniculate	Pucusana, Peru	All records as <i>C. caespitosa</i> . Rarely reported, but probably much more common than the current records suggest. SP, FR, IT, GR	Walker et al., 2009; Pardo et al., 2015; Williamson et al., 2015; Bustamante et al., 2019
<i>Corallina officinalis</i> Linnaeus		Geniculate	" <i>Hab. O. Eur.</i> " (European seas)	Widespread. SP, FR, IT, MA, SL, CR, AL, GR, TK, CY, SY, IL, EG, LI, TU, AG, MO	Brodie et al., 2013; Pardo et al., 2015; Williamson et al., 2015
<i>Ellisolandia elongata</i> (J. Ellis et Solander) K. Hind et G.W. Saunders	<i>Corallina elongata</i> J. Ellis et Solander; <i>Corallina mediterranea</i> Areschoug	Geniculate	Cornwall, U.K.	Widespread. SP, FR, IT, MA, CR, AL, GR, TK, CY, SY, LE, IL, EG, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Brodie et al., 2013; Pardo et al., 2015
<i>Harveyolithon rupestre</i> A. Rösler, Perfectti, V. Peña et J. Braga	<i>Hydrolithon rupestre</i> (Foslie) Penrose	Encrusting	Ocean Beach, Phillip Island, Victoria, Australia	In the Mediterranean known only from Vis Island, Croatia. Considered an introduction from tropical regions of the southern hemisphere	Wolf et al., 2015
<i>Hydrolithon boreale</i> (Foslie) Y.M. Chamberlain	<i>Fosliella farinosa</i> var. <i>solmsiana</i> (Falkenberg) W.R. Taylor	Encrusting	Roundstone, Co. Galway, Ireland	Reported mostly from the western and central Mediterranean, rarely from the eastern. SP, FR, IT, CR, GR, TU	Irvine and Chamberlain, 1994
<i>Hydrolithon cruciatum</i> (Bressan) Y.M. Chamberlain	<i>Fosliella cruciata</i> Bressan	Encrusting	Gulf of Trieste, Adriatic Sea	Reported mostly from the western and central Mediterranean, rarely from the eastern. SP, FR, IT, MA, SL, GR, CY	Irvine and Chamberlain, 1994; Bressan and Babbini, 2003
<i>Hydrolithon farinosum</i> (J.V. Lamouroux) Penrose et Y.M. Chamberlain	<i>Fosliella farinosa</i> (J.V. Lamouroux) M. Howe	Encrusting	Mediterranean Sea	Widespread. SP, FR, IT, MA, SL, CR, AL, GR, TK, CY, SY, LE, IL, EG, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Jania adhaerens</i> J.V. Lamouroux		Geniculate	Mediterranean Sea	Widespread. SP, FR, IT, GR, CY, IL, EG, TU, AG, MO	Cormaci et al., 2017
<i>Jania longifurca</i> Zanardini ex Zanardini		Geniculate	Harbor of Zadar, Croatia	Widespread. SP, FR, IT, MA, CR, GR, TK, CY, SY, IL, EG, LI, TU, AG, MO	Cormaci et al., 2017

(Continued)

TABLE 1 | Continued

Species	Synonyms frequently used in the mediterranean literature	Habit	Type locality	Known distribution in the mediterranean	Important references
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux		Geniculate	"In Oceano Europaeo" (European seas)	Widespread. SP, FR, IT, MA, SL, CR, AL, GR, TK, CY, SY, LE, IL, EG, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Jania squamata</i> (Linnaeus) J.H. Kim, Guiry et H.G. Choi	<i>Halptilon squamatum</i> (Linnaeus) H.W. Johansen, L.M. Irvine et A. Webster	Geniculate	"In O. Europaeo" (European seas)	Widely reported but many records in need of reassessment, due to possible confusion with <i>Corallina officinalis</i> and <i>Elisolandia elongata</i> . FR, IT, GR, TK, CY, TU	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Jania virgata</i> (Zanardini) Montagne	<i>Corallina granifera</i> J. Ellis et Solander; <i>Halptilon virgatum</i> (Zanardini) Garbary et H.W. Johansen	Geniculate	Not designated in the protologue, but the original material was collected from the Adriatic Sea	Widespread. SP, FR, IT, MA, SL, CR, AL, GR, TK, SY, LE, IL, EG, LI, TU, AG, MO	Bressan and Babbini, 2003; Cormaci et al., 2017
<i>Lithophyllum byssoides</i> (Lamarck) Foslie	<i>Lithophyllum lichenoides</i> Philippi; <i>Goniolithon byssoides</i> (Lamarck) Foslie	Encrusting.	Effectively unknown ("La Manche"; see Pezзолesi et al., 2017)	Common in the western and central Mediterranean, rare in the eastern Mediterranean. SP, FR, IT, MA, CR, AL, GR, TK, IL, EG, TU, AG, MO	Chamberlain, 1997; Verlaque, 2010; Pezзолesi et al., 2017
<i>Lithophyllum corallinae</i> (P.L. et H.M. Crouan) Heydrich	<i>Titanoderma corallinae</i> (P.L. et H.M. Crouan) Woelkerling, Y.M. Chamberlain et P.C. Silva	Encrusting.	Banc du Chateau and Baie de La Ninon, Brest, France	Widespread. SP, FR, IT, SL, CR, GR, TK, CY, LI, TU	Irvine and Chamberlain, 1994
<i>Lithophyllum cystoseirae</i> (Hauck) Heydrich	<i>Titanoderma cystoseirae</i> (Hauck) Woelkerling, Y.M. Chamberlain et P.C. Silva	Encrusting	Adriatic Sea	Widespread. SP, FR, IT, MA, SL, CR, GR, TK, CY, IL, LI, TU, AG, MO	Bressan and Babbini, 2003; Cormaci et al., 2017
<i>Lithophyllum decussatum</i> (J. Ellis et Solander) Philippi		Encrusting	Coast of Portugal	Rare, known only from the western and central Mediterranean. SP, FR, IT, LI, MO.	Cormaci et al., 2017
<i>Lithophyllum dentatum</i> (Kützting) Foslie		Encrusting, or unattached forming rhodoliths	Naples, Italy	Common in the western and central Mediterranean, rare in the eastern Mediterranean. SP, FR, IT, MA, CR, AL, GR, TU, AG, MO	Woelkerling, 1985; Bressan and Babbini, 2003
<i>Lithophyllum hibernicum</i> Foslie		Encrusting	Fahy Bay, Ballynakill Harbor, Co. Galway, Ireland	Presence in the Mediterranean demonstrated by DNA sequence data. Currently documented for SP and FR, but probably more widely distributed	Hernandez-Kantun et al., 2015a
<i>Lithophyllum incrustans</i> Philippi		Encrusting, or unattached forming rhodoliths	Sicily	Widespread, but many records should be reassessed based on DNA sequence data. SP, FR, IT, MA, SL, CR, AL, GR, TK, SY, LE, EG, LI, TU, AG, MO	Hernandez-Kantun et al., 2015a
<i>Lithophyllum nitorum</i>		Encrusting	Port Erin Harbor, Isle of Man, U.K.	Presence in the Mediterranean demonstrated by DNA sequence data. Currently documented for SP, but probably more widely distributed	Irvine and Chamberlain, 1994; Peña et al., 2018
<i>Lithophyllum orbiculatum</i> (Foslie) Foslie		Encrusting	Kristiansund, Norway	Uncommon, reported mostly from the western and central Mediterranean, rarely from the eastern. SP, FR, IT, GR, TK, AG, TU	Irvine and Chamberlain, 1994
<i>Lithophyllum papillosum</i> (Zanardini ex Hauck) Foslie	<i>Dermatolithon papillosum</i> (Zanardini ex Hauck) Foslie; <i>Goniolithon papillosum</i> (Zanardini ex Hauck) Foslie	Encrusting	West coast of Susak Island, Croatia	Reported mostly from the western and central Mediterranean, rarely from the eastern. SP, FR, IT, CR, GR, TK, AG, MO	Cormaci et al., 2017

(Continued)

TABLE 1 | Continued

Species	Synonyms frequently used in the mediterranean literature	Habit	Type locality	Known distribution in the mediterranean	Important references
<i>Lithophyllum pustulatum</i> (J.V. Lamouroux) Foslie	<i>Dermatolithon pustulatum</i> (J.V. Lamouroux) Foslie; <i>Titanoderma pustulatum</i> (J.V. Lamouroux) Nägeli	Encrusting	France	Widespread. SP, FR, IT, MA, SL, CR, GR, TK, CY, SY, LE, EG, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Lithophyllum racemus</i> (Lamarck) Foslie		Unattached, forming rhodoliths/maërl	Capri, Gulf of Naples, Italy	Reported mostly from the central Mediterranean. SP, FR, IT, MA, SL, CR, AL, GR, LI, TU, AG	Basso et al., 1996; Cormaci et al., 2017
<i>Lithophyllum stictiforme</i> (Areschoug) Hauck	<i>Pseudolithophyllum expansum</i> (Philippi) Me. Lemoine; <i>Pseudolithophyllum cabiochae</i> Boudouresque et Verlaque; <i>Lithophyllum cabiochae</i> (Boudouresque et Verlaque) Athanasiadis; <i>Lithophyllum frondosum</i> (Dufour) Furnari, Cormaci et Alongi	Encrusting	Mediterranean Sea	Widespread. SP, FR, IT, MA, SL, CR, AL, GR, TK, SY, IL, EG, LI, TU, AG, MO	Athanasiadis, 1999a
<i>Lithophyllum trochanter</i> (Bory) Huvé ex Woelkerling	<i>Titanoderma trochanter</i> (Bory) Benhissoune, Boudouresque, Perret-Boudouresque et Verlaque	Encrusting	Greece	Warmer parts of the Mediterranean. Most common in the eastern Mediterranean, probably absent in the western; records from France and Algeria probably refer to <i>L. woelkerlingii</i> . FR, IT, CR, AL, GR, CY, SY, IL, LI	Bressan and Cabioch, 2004; Cormaci et al., 2017
<i>Lithophyllum woelkerlingii</i> Alongi, Cormaci et Furnari	<i>Titanoderma ramosissimum</i> (Heydrich) Bressan et Cabioch	Encrusting	Algeria	SP, FR, AG. Distribution in need of reassessment due to the previous confusion with <i>L. trochanter</i>	Bressan and Cabioch, 2004; Cormaci et al., 2017
<i>Lithophyllum yessoense</i> Foslie		Encrusting	Yoichi, Shiribeshi Province, Hokkaido, Japan	FR. Known only from the Thau Lagoon, where it was introduced with Asian oysters and is now well-established	Verlaque, 2001
<i>Lithothamnion corallioides</i> (P.L. et H.M. Crouan) P.L. et H.M. Crouan		Unattached, forming rhodoliths/maërl	Rade de Brest, France	Widespread. SP, FR, IT, MA, CR, GR, CY, LI, TU	Irvine and Chamberlain, 1994
<i>Lithothamnion crispatum</i> Hauck		Encrusting, or unattached forming rhodoliths/maërl	Rovinj, Croatia	Widespread, in general more common in the western and central Mediterranean than in the eastern. SP, FR, IT, CR, GR, TK, LI, AG	Basso et al., 2011; Cormaci et al., 2017
<i>Lithothamnion minervae</i> Basso		Unattached, forming rhodoliths/maërl	Pontian Islands, Italy.	Central Mediterranean; FR, IT, MA. Possibly underrecorded due to the deep subtidal habitat	Basso, 1995; Basso et al., 2004; Cormaci et al., 2017
<i>Lithothamnion sonderi</i> Hauck		Encrusting	Helgoland, Germany	Not common in the Mediterranean, but reported with wide distribution. SP, FR, IT, GR, IL, TU	Irvine and Chamberlain, 1994
<i>Lithothamnion valens</i> Foslie		Unattached, forming rhodoliths/maërl	Probably Adriatic Sea, see Woelkerling et al. (2005)	Western and central Mediterranean; SP, FR, IT, CR, TU. Possibly underrecorded due to the deep subtidal habitat	Basso, 1995, Woelkerling et al., 2005
<i>Melobesia membranacea</i> (Esper) J.V. Lamouroux	<i>Epilithon membranaceum</i> (Esper) Heydrich	Encrusting	West coast of France	Widespread. SP, FR, IT, SL, CR, GR, TK, CY, SY, IL, TU, AG, MO	Chamberlain, 1985; Irvine and Chamberlain, 1994
<i>Mesophyllum expansum</i> (Philippi) Cabioch et Mendoza		Encrusting	Sicily	SP, FR, IT, GR. Records of this species for other countries require reassessment; most are probably incorrect and should be referred to <i>Lithophyllum stictiforme</i>	Athanasiadis and Neto, 2010; Peña et al., 2015a

(Continued)

TABLE 1 | Continued

Species	Synonyms frequently used in the mediterranean literature	Habit	Type locality	Known distribution in the mediterranean	Important references
<i>Mesophyllum lichenoides</i> (J. Ellis) M.me Lemoine		Encrusting, occasionally unattached	Cornwall, U.K.	Reported as widespread, but all Mediterranean records of this species need reassessment based on DNA sequence data. SP, FR, IT, CR, AL, GR, TK, CY, LE, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Peña et al., 2015a
<i>Mesophyllum macedonis</i> Athanasiadis		Encrusting	Pigeon Cave, Sithonia Peninsula, Greece	Known only from the type locality. GR	Athanasiadis, 1999b
<i>Mesophyllum macroblastum</i> (Foslie) W.H. Adey		Encrusting	Gulf of Naples, Italy	Western and central Mediterranean. SP, FR, IT	Kaleb et al., 2011; Peña et al., 2015a
<i>Mesophyllum philippii</i> (Foslie) W.H. Adey	<i>Lithothamnion philippii</i> Foslie	Encrusting, or unattached forming rhodoliths/maërl	Banyuls-sur-Mer, France	Reported mostly from the western and central Mediterranean, rarely from the eastern. SP, FR, IT, CR, GR, CY, LI, AG, MO	Cormaci et al., 2017
<i>Mesophyllum sphaericum</i> V. Peña, Bárbara, W.H. Adey, Riosmena-Rodríguez et Choi		Unattached, forming rhodoliths/maërl; occasionally encrusting	Benencia Island, Ria de Arousa, Galicia, Spain	SP, IT. Presence in the Mediterranean demonstrated using DNA sequence data; distribution probably much wider than currently known	Peña et al., 2015a
<i>Neogoniolithon brassica-florida</i> Mason	<i>Neogoniolithon mamillosum</i> (Hauck) Setchell et Mason <i>nom. illeg.</i> , is a species widely cited in the Mediterranean literature, for which the distinction from <i>N. brassica-florida</i> is unclear. Cormaci et al. (2017) consider it a species of uncertain identity, in need of taxonomic reassessment	Encrusting, or unattached forming rhodoliths/maërl	Algoa Bay, Cape Province, South Africa.	Widely recorded, but Mediterranean records of this species in need of reassessment based on DNA sequence data. SP, FR, IT, CR, AL, GR, TK, CY, SY, LE, IL, TU, AG, MO	Bressan and Babbini, 2003; Cormaci et al., 2017
<i>Phymatolithon calcareum</i> (Pallas) W.H. Adey et D.L. McKibbin ex Woelkerling et L.M. Irvine		Unattached, forming rhodoliths/maërl; occasionally encrusting	Falmouth Harbor, Cornwall, U.K.	Widespread. SP, FR, IT, MA, CR, GR, LE, IL, LI, TU, AG, MO	Irvine and Chamberlain, 1994; Wolf et al., 2016
<i>Phymatolithon lamii</i> (M.me Lemoine) Y.M. Chamberlain		Encrusting	Pointe de Cancaval, Rance, France	Reported in the Mediterranean only from the Gulf of Trieste (northern Adriatic Sea). IT	Irvine and Chamberlain, 1994; Kaleb et al., 2012
<i>Phymatolithon lenormandii</i> (Areschoug) W.H. Adey	<i>Lithothamnion lenormandii</i> (Areschoug) Foslie	Encrusting	Arromanches-le-Bains, Calvados, France	Widespread. SP, FR, IT, MA, SL, CR, GR, TK, SY, LE, EG, LI, AG, MO	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Phymatolithon lusitanicum</i> V. Peña		Unattached, forming rhodoliths/maërl	Con de Pego, Ria de Vigo, Galicia, Spain	This recently described species is known from the Alboran Sea and the Balearic Islands, but its distribution in the Mediterranean is probably wider. SP	Peña et al., 2015b
<i>Pneophyllum cetinanensis</i> Kaleb, Žuljević, et V. Peña		Encrusting	River Cetina, Croatia	Freshwater species, known only from the type locality. CR	Žuljević et al., 2016
<i>Pneophyllum confervicola</i> (Kützting) Y.M. Chamberlain		Encrusting	Trieste, Italy	Widespread. SP, FR, IT, SL, CR, GR, TK, TU	Irvine and Chamberlain, 1994
<i>Pneophyllum coronatum</i> (Rosanoff) Penrose	<i>Pneophyllum caulerpae</i> (Foslie) P.L. Jones et Woelkerling	Encrusting	Port Phillip Bay, Victoria, Australia	Western and central Mediterranean. SP, FR, IT, MA, LI, TU, AG	Irvine and Chamberlain, 1994; Cormaci et al., 2017
<i>Pneophyllum fragile</i> Kützting	<i>Fosliella lejolisii</i> (Rosanoff) M. Howe	Encrusting	Mediterranean Sea	Widespread. SP, FR, IT, MA, SL, CR, GR, TK, CY, SY, LE, TU, AG, MO	Irvine and Chamberlain, 1994; Cormaci et al., 2017

(Continued)

TABLE 1 | Continued

Species	Synonyms frequently used in the mediterranean literature	Habit	Type locality	Known distribution in the mediterranean	Important references
<i>Pneophyllum zonale</i> (P. Crouan et H. Crouan) Y.M. Chamberlain	<i>Fosliella zonalis</i> (P. Crouan et H. Crouan) J. Feldmann; <i>Melobesia zonalis</i> P. Crouan et H. Crouan) Foslie	Encrusting	Rade de Camaret, Brest, France	Species of uncertain taxonomic identity. SP, FR, IT, MAL, GR, TU	Feldmann, 1939; Cormaci et al., 2017
<i>Spongites fruticulosus</i> Kützing		Encrusting, or unattached forming rhodoliths/maërl	Mediterranean Sea	Widespread. SP, FR, IT, SL, CR, GR, TK, CY, LI, TU, AG, MO	Woelkerling, 1985; Basso and Rodondi, 2006; Rösler et al., 2016
<i>Sporolithon ptychoides</i> Heydrich		Encrusting, occasionally unattached	Sinai Peninsula, Egypt	Western and central Mediterranean. SP, FR, IT, MA	Cormaci et al., 2017; Richards et al., 2017
<i>Tenarea tortuosa</i> (Esper) M.me Lemoine	<i>Lithophyllum tortuosum</i> (Esper) Foslie	Encrusting	Mediterranean Sea	Central and eastern Mediterranean. Records of this species from the western Mediterranean are most probably misidentifications of <i>Lithophyllum byssoides</i> . IT, CR, AL, GR, TK, CY, SY, LE	Woelkerling et al., 1985; Bressan and Babbini, 2003; Cormaci et al., 2017

For details of basionyms and taxonomic synonymies see Cormaci et al. (2017) and Guiry and Guiry (2019). Codes for countries: SP, Spain; FR, France; IT, Italy; MA, Malta; SL, Slovenia; CR, Croatia; AL, Albania; GR, Greece; TK, Turkey; CY, Cyprus; SY, Syria; LE, Lebanon; IL, Israel; EG, Egypt; LI, Libya; TU, Tunisia; AG, Algeria; MO, Morocco. Distribution information based on Bressan and Babbini (2003) and Guiry and Guiry (2019, and references therein). Herein we define western Mediterranean as the part of the basin extending from the Strait of Gibraltar to the western coasts of Corsica and Sardinia; eastern Mediterranean the part extending from the line Cape Matapan (Greece)-Benghazi (Libya) to the Levant States (Syria, Lebanon, Israel); and central Mediterranean the part comprised between western and eastern Mediterranean.

only molecular data other than Sanger sequences produced from Mediterranean corallines.

Of the 18 studies, only 8 focused totally or mainly on Mediterranean taxa: Hernandez-Kantun et al. (2015a), Peña et al. (2015a), Wolf et al. (2015, 2016), Žuljević et al. (2016), Pezzolesi et al. (2017, 2019), and De Jode et al. (2019). Five of these (Peña et al., 2015a; Žuljević et al., 2016; Pezzolesi et al., 2017, 2019; De Jode et al., 2019) provided most of the DNA sequence data available (Table S1) and have particularly contributed to our current understanding of the genetic diversity of Mediterranean corallines.

The integrative study of Peña et al. (2015a) on the genus *Mesophyllum*, based on molecular (COI-5P, *psbA*) and morphological data redefined the distribution of four species in Atlantic Europe and the Mediterranean. *M. expansum*, *M. macroblastum*, and *M. sphaericum* were detected in the Mediterranean. The results suggested that *M. expansum* is a major contributor to bioconstruction of coralligenous concretions and occurs also in the Atlantic Iberian Peninsula and Macaronesia. This species was found from the intertidal to -50 m, with a positive correlation between depth and the maximum sea surface temperature, suggesting that this species may mitigate future consequences of global warming by changes in depth profile. By contrast, *M. macroblastum* appears to be restricted to the Mediterranean. Two *Mesophyllum* species reported in the Mediterranean literature (*M. lichenoides* and *M. alternans*) were not recorded and their presence in the Mediterranean requires confirmation based on molecular data. The Atlantic Iberian *M. sphaericum* was first reported in the

Mediterranean, under two different growth-forms (rhodolith and crustose).

The study of Pezzolesi et al. (2017) on the intertidal bioconstructor *Lithophyllum byssoides* was the first phylogeographic investigation of a Mediterranean coralline. Using *psbA* and *cox2,3* sequences, these authors unraveled a high haplotypic diversity and detected 7 lineages, whose geographical distribution did not follow the main biogeographical boundaries recognized in the central Mediterranean. For several lineages the distribution was restricted to one or few sites. The results also showed a clear genetic differentiation between Mediterranean and Atlantic *Lithophyllum byssoides*, suggesting a likely separation at species level (which could not be confirmed due to insufficient data from the Atlantic).

The two recent studies of Pezzolesi et al. (2019) and De Jode et al. (2019) unraveled a striking case of cryptic diversity: the *Lithophyllum stictiforme* complex. *Lithophyllum stictiforme* and *Lithophyllum cabiochiaie* have been long known as common species in the Mediterranean subtidal, where they are major contributors to the formation of coralligenous concretions (Athanasiadis, 1999a; see also Boudouresque and Verlaque, 1978; Furnari et al., 1996). Whereas some authors have separated these species, others (Cormaci et al., 2017; Guiry and Guiry, 2019) consider *L. cabiochiaie* and *L. stictiforme* conspecific. Pezzolesi et al. (2019), sequencing three markers (*cox2,3*, *psbA*, *rbcL*) in samples collected from many sites in the western and central Mediterranean, concluded that *Lithophyllum stictiforme* represents a complex of at minimum 13 cryptic species. De Jode et al. (2019), combining Sanger sequencing (COI, *psbA*, LSU) and transcriptomics, reached very similar conclusions, showing

that on the French coasts specimens with the *L. stictiforme/L. cabiochia* morphology represent a complex of 8 cryptic species. De Jode et al. (2019) demonstrated also the reproductive isolation of these species and documented differences in their depth range. Both Pezzolesi et al. (2019) and De Jode et al. (2019) noted that for several cryptic species the geographical distribution appears restricted to one particular area or site.

Pezzolesi et al. (2017, 2019) interpreted the patterns observed for *L. byssoides* and the *L. stictiforme* complex as consequences of past hydrogeological and climatic events, in combination with modern oceanographic features. The fossil documentation suggests that these algae have existed in the Mediterranean, respectively, since the Messinian (7.3–5.3 Mya, Braga and Aguirre, 2001; Braga et al., 2009) and the late Langhian (14.5 Mya, Hrabovský et al., 2016). Spatial fragmentation of populations that took place during the Messinian Salinity Crisis (5.96–5.33 Mya) may have stimulated genetic differentiation, and, in the case of the *Lithophyllum stictiforme* complex, allopatric speciation. Subsequent climatic events such as the Quaternary glaciations (2.6 Mya to present), which also altered the Mediterranean coastline and partially separated different sectors, probably further contributed to shape the current distribution of these algae.

The relevance of past climatic events in the diversification of Mediterranean corallines is highlighted by a discovery of particular interest made in recent years, i.e., the first known freshwater coralline alga: *Pneophyllum cetinaensis*, endemic to the Cetina River, Croatia (Žuljević et al., 2016). This species, which is fully adapted to freshwater conditions, descends from an ancestor that was preadapted to changes in water salinity produced in landlocking events such as the last glaciation (120,000–20,000 years ago). In addition, molecular data obtained in this study exclude a close phylogenetic relationship between the freshwater *P. cetinaensis* and other Mediterranean and Atlantic *Pneophyllum* species.

Among other studies, Hernandez-Kantun et al. (2015a) reassessed the taxonomic identity of the generytype species *Lithophyllum incrustans* using a partial *rbcL* sequence obtained from the lectotype specimen (epizoic on a sea snail shell, collected in Sicily). The results re-defined the distribution of *L. incrustans* and highlighted that this is mainly a subtidal species. The presence in the Mediterranean of *Lithophyllum hibernicum* was also demonstrated. Additional data were provided by Bittner et al. (2011), who sequenced 9 unidentified samples of Mediterranean corallines in their phylogenetic assessment of the order Corallinales (*psbA* and, in part, COI-5P). Rösler et al. (2016) published 21 new sequences for Mediterranean collections, including one for a specimen therein designated as epitype of *Spongites fruticulosus*. Additional data produced new records for the Mediterranean flora: *Harveyolithon rupestre* (as *Hydrolithon rupestre*, Wolf et al., 2015); *Phymatolithon lusitanicum* (Peña et al., 2015b); the attached encrusting form of the maerl-forming *Phymatolithon calcareum* (Wolf et al., 2016); and *Lithophyllum nitorum* (Peña et al., 2018). Finally, some sequences of Mediterranean fossil corallines were published by Hughey et al. (2008).

Molecular Data and Application of Taxonomic Names in Mediterranean Corallines

In situations where cryptic diversity is discovered, the only definitive solution for a correct application of Linnaean names is to obtain sequences from the type specimen, the only one to which a species name is unambiguously attached. In this way, the type specimen can be linked to one of the lineages recovered in molecular phylogenies, and the species name will therefore be attached to that lineage. Fortunately, in the case of coralline algae this approach has generally worked. In air-dried coralline specimens, DNA is preserved in a form that is often adequate to obtain partial sequences for one or more markers (either by high-throughput sequencing methods or by nested PCR performed with adequate equipment). Sequences of sufficient quality have been produced from many type specimens, allowing an accurate assessment of many species (e.g., Adey et al., 2015; Hernandez-Kantun et al., 2015a, 2016; Hind et al., 2016; Richards et al., 2017, 2018; Gabrielson et al., 2018; Peña et al., 2018). Conversely, for some species to obtain sequences from type specimens is impossible (either because the type material is in very limited amount, or because it is formol-preserved). In these cases, a different specimen should be sequenced and used as molecular reference for the species. Such specimen should be collected at the type locality, and the details of its morphology and habitat should be in agreement with the protologue of the original description. If the nature of the original type is ambiguous, this specimen can be designated as epitype following the article 9.9 of the ICN (Turland et al., 2018).

For corallines occurring in the Mediterranean, an assessment based on sequences generated from type specimens has been made for 11 species. Sequences were obtained from holotypes, lectotypes, or isotypes for *Corallina ferreyrae* (Bustamante et al., 2019; previously reported in the Mediterranean as *Corallina caespitosa*, Walker et al., 2009), *Lithophyllum incrustans* (Hernandez-Kantun et al., 2015a), *Lithophyllum nitorum* (Peña et al., 2018), *Lithophyllum stictiforme* (Pezzolesi et al., 2019), *Mesophyllum sphaericum* (Peña et al., 2011), *Phymatolithon lusitanicum* (Peña et al., 2015b), and *Pneophyllum cetinanensis* (Žuljević et al., 2016). For *Spongites fruticulosus*, Rösler et al. (2016) generated SSU, LSU, COI, and 23S sequences from the epitype specimen. For *Corallina officinalis* and *Ellisolandia elongata*, Brodie et al. (2013) designated epitype specimens, from which they obtained *cox1* and *rbcL* sequences. Finally, Hernandez-Kantun et al. (2015b) produced SSU and *psbA* sequences from the neotype of *Phymatolithon calcareum* (designated by Woelkerling and Irvine, 1986).

PRESENT-DAY DISTRIBUTION AND BIOGEOGRAPHY

Our knowledge of the distribution of Mediterranean corallines is largely based on records derived from morpho-anatomical identifications (see Bressan and Babbini-Benussi, 1996, for a synthesis of the information available until the late 90s of the last century). Six species were recorded in recent

years based on molecular data: *Corallina ferreyrae*, reported as the heterotypic synonym *C. caespitosa* (Walker et al., 2009), *Harveyolithon rupestre* (Wolf et al., 2015), *Lithophyllum hibernicum* (Hernandez-Kantun et al., 2015a), *Lithophyllum nitorum* (Peña et al., 2018), *Mesophyllum sphaericum* (Peña et al., 2015a), and *Phymatolithon lusitanicum* (Peña et al., 2015b).

Based on the present knowledge, 7 species are Mediterranean endemics (*Amphiroa rubra*, *Lithophyllum trochanter*, *L. woelkerlingii*, *Lithothamnion minervae*, *L. valens*, *Mesophyllum macedonis*, *Pneophyllum cetinaensis*) (Table 1). In terms of distribution, it is possible to recognize three main groups. Some species are clearly widespread throughout the Mediterranean, having been recorded in all regions of the basin. This group includes 27–28 species, which usually also occur on Atlantic European coasts and in Macaronesia; examples are *Ellisolandia elongata*, *Hydrolithon farinosum*, *Jania rubens*, *Lithophyllum incrustans*, and *Pneophyllum fragile*. A smaller number of species (16–17) occurs only in the western and central Mediterranean, or is much more common there than in the eastern Mediterranean. Examples are *Choreonema thuretii*, *Mesophyllum macroblastum*, *Lithophyllum byssoides*, *L. dentatum*, and *Lithothamnion valens*. Finally, two species (*Lithophyllum trochanter* and *Tenarea tortuosa*) are clearly associated with the warmer parts of the basin and reliable records refer mostly to the eastern Mediterranean. At present, two species are considered introduced. *Lithophyllum yessoense* was recorded by Verlaque (2001) from the Lagune de Thau (Hérault, France), a well-known hotspot of introduction of alien species; the species was probably introduced from the North Pacific by transfer of Asian oysters. *Harveyolithon rupestre* was recorded by Wolf et al. (2015) from Vis Island (Croatia) (as *Hydrolithon rupestre*). These authors believed that the species was probably introduced in the area by shellfish aquaculture activities.

It can be expected, however, that future studies incorporating molecular data will lead to geographical reassessments for many species. The main change that we expect is an increase in the number of endemic species. This expectation is based on theoretical grounds (the hydrogeological history of the Mediterranean in the last 15 My and the high number of endemics in many animal groups) and on the results of some recent studies. For the *Lithophyllum stictiforme* complex, De Jode et al. (2019) and Pezzolesi et al. (2019) discovered numerous cryptic species for which the present known distribution is restricted to the Mediterranean. Although some of these species surely will be shown to occur in neighboring Atlantic regions, we feel that almost certainly several others will turn to be real Mediterranean endemics. *Lithophyllum byssoides* is another candidate for Mediterranean endemism: Pezzolesi et al. (2017) showed that Mediterranean samples of this species are genetically distinct from Atlantic samples to an extent that may justify separation at species level. If future studies incorporating additional extra-Mediterranean samples confirm this separation, the Mediterranean population will have to be considered an endemic species. The same situation applies to *Mesophyllum macroblastum*: Peña et al. (2015a) noted that extra-European specimens identified with this name were resolved in molecular analyses as different species from Mediterranean

specimens (which can be considered the real *M. macroblastum*: the type locality is the Gulf of Naples, Italy); thus, the occurrence of this species out of the Mediterranean has to be definitively demonstrated yet. Pardo et al. (2015), in a taxonomic investigation focusing on *Corallina* and *Ellisolandia* of the Atlantic Iberian Peninsula, discovered a species of *Corallina* with distribution encompassing Atlantic and Mediterranean shores (for which they did not provide a formal description and named it *Corallina* sp.2). Pardo et al. (2015) remarked that Atlantic and Mediterranean forms of this species showed clear morphological differences and had different COI-5P haplotypes. It cannot be discounted that future studies will lead to separation at species level between the two forms; in that case, the Mediterranean form would probably be an endemic Mediterranean. Based on these examples we suggest that, for all species originally described from the Mediterranean, the distribution should be reassessed using DNA sequence data produced from the whole geographic range.

REPRODUCTIVE BIOLOGY

The life histories of Mediterranean corallines have not been investigated in detail using culture studies. Evidence based on observation of field-collected material suggests that these algae have the triphasic life history typical of later-divergent florideophytes, with one haploid generation reproducing sexually (the gametophyte) and two diploid generations reproducing asexually by spores (the carposporophyte and the tetrasporophyte) (Graham et al., 2018).

Nearly all information available on the reproductive biology of Mediterranean coralline is based on observation of reproductive specimens in the field and in the laboratory. The only information based on molecular evidence has been provided by De Jode et al. (2019). Analyzing their multilocus genotypes for clonality, these authors documented sexual reproduction in the *Lithophyllum stictiforme/cabiochiai* complex and demonstrated sexual isolation among the 8 cryptic species occurring on French shores. This is to date the only study providing robust support for the biological species concept in a taxon of Mediterranean corallines.

In general, observations of reproductive specimens/structures in Mediterranean corallines are not infrequent. Bressan and Babbini (2003) provided general information about the reproductive periods for many species (i.e., reported the months in which a species is reproductive); however, they did not specify the source of this information and if they referred to sexual or asexual phases. Most observations of reproduction available in the literature have been published as records of reproductive specimens in field investigations, reporting the reproductive structures observed (spermatangia, carposporangia, tetrasporangia, bisporangia; or sexual vs. asexual conceptacles) (Feldmann, 1939; Cecere et al., 1996; Cormaci et al., 1997, 2000; Catra et al., 2006; Falace et al., 2011).

Most records are based on observations made in a limited timespan. Investigations over extended periods are more useful to define temporal patterns and understand the environmental factors influencing reproduction, but unfortunately are less

frequent. Vatova (1948) summarized the reports of fertility available for the seaweeds of the area of Rovinj (Croatia). Gómez-Garreta et al. (1982) studied for 2 years the phenology of the most common seaweeds, including several coralline species, in four benthic communities in the Balearic Islands. Soto and Conde (1989) made similar observations over a 5 years period at several sites in southeastern Spain. Overall, inconsistent patterns were found in these studies, i.e., different reproductive periods were reported for the same species in the different areas considered. A common aspect, however, is that reproductive specimens were more frequently recorded in articulated species (*Amphiroa* spp., *Jania* spp., *Ellisolandia elongata*) than in encrusting species (possibly because observation of conceptacles in encrusting forms is generally more difficult, especially in the field). Another common feature (remarked by Soto and Conde, 1989) is that asexual structures were much more frequent than sexual (i.e., sporangial conceptacles were more frequently observed than gametangial conceptacles). This has been reported in many field studies of red seaweeds, even Mediterranean (Rindi and Cinelli, 2000) and is considered related to the presumed low rate of fertilization due to absence of flagellate gametes in red algae.

Additional information on reproductive phenology has been reported separately for few species (usually ecologically important). For *Lithophyllum byssoides*, the reproduction of tetrasporophytes has been reported in March–July at Marseilles and in February–December in the Balearic Islands; the reproduction of gametophytes only in autumn (October) (Verlaque, 2010, based on Huvé, 1956a,b; Gómez-Garreta, 1981; Chamberlain, 1997). The main period of recruitment for this species appears to be the autumn (Verlaque, 2010, according to Huvé, 1954, 1970).

The most detailed studies of reproduction in Mediterranean corallines focused on forms of coralligenous habitats (Garrabou and Ballesteros, 2000; Rodriguez-Prieto, 2016). Garrabou and Ballesteros (2000) studied populations of *Lithophyllum* and *Mesophyllum* (identified as *L. frondosum* and *M. alternans*, respectively) in a coralligenous community in Catalonia for 2 years. By photographic sampling, they estimated the percentage of reproductive specimens throughout the study period (by observation of mature conceptacles in their images). They found no seasonal trends in *Mesophyllum*, for which ~25% of the specimens had mature conceptacles in each sampling date. Conversely, in *Lithophyllum* the percentage of thalli with mature conceptacles was significantly higher in early autumn in both years. Based on these differences and differences in growth patterns, Garrabou and Ballesteros (2000) remarked the ecological differences between the two species, concluding that *Mesophyllum* has a more opportunistic life strategy, whereas *Lithophyllum* has a more conservative strategy. Rodriguez-Prieto (2016) carried out experiments in controlled conditions (temperature, daylength and photon irradiance) on *Lithophyllum stictiforme* from Catalonia. She concluded that an irradiance of 20 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ combined with 10–12°C and a 8:16 h light:dark regime was the most favorable condition for the species. In culture, the conceptacles matured in conditions simulating late summer–early autumn, in agreement with the behavior of field specimens. Rodriguez-Prieto (2016) noted that,

in culture, maturation and release of reproductive cells are rare events, since no development of new conceptacles was observed after the release of reproductive cells.

Information on reproduction by vegetative propagules or thallus fragmentation in Mediterranean corallines is very limited. Coppejans (1978) documented multicellular vegetative propagules in *Hydrolithon farinosum* (as *Fosliella farinosa*) from Corsica, describing their development and release (previously reported only by Solms-Laubach, 1881). Additional records of these structures in the same species were provided by Cormaci and Furnari (1988). Thallus fragmentation is frequent in maerl/rhodolith-forming species, especially branched species with thin branches such as *Lithothamnion corallioides* and *Phymatolithon calcareum* (Bosence, 1976; Peña et al., 2014). It can be expected that this type of reproduction plays an important role in Mediterranean rhodolith beds, but there are no experimental studies or genetic data that allow generalizations about its relative contribution compared to reproduction by spores.

No direct information is available about the dispersal of Mediterranean corallines. Some indirect information can be inferred from the genomic data of De Jode et al. (2019) for the most common cryptic species of the *Lithophyllum stictiforme/cabiochiai* complex of the French shores. These authors detected genetic differences at population level that suggested limited gene flow (and, indirectly, limited dispersal) even at distances of a few km. Conversely, no significant genetic differentiation was found between populations occurring in two different depth ranges (24–31 m and 37–46 m), suggesting that depth is not a barrier to dispersal. These conclusions are consistent with theoretical prediction of a generally limited dispersal in coralline algae. As for all other rhodophytes, the principal mean of dispersal is represented by non-flagellate spores (bisporos, carpospores, and tetraspores). These are small-sized cells with very limited active movement, which are able to settle only on hard substrata and remain viable for relatively short periods (Guiry, 1990; Pickett-Heaps et al., 2001). Although the magnitude of water flow greatly influences their dispersal (Norton, 1992), it is generally believed that they do not disperse over long distances. It is likely that long-distance dispersal may take place in small-sized species (*Hydrolithon* spp., *Pneophyllum* spp., *Melobesia membranacea*) that grow as epiphytes on drifting leaves of *Posidonia oceanica* or larger seaweeds. This theoretical prediction, however, needs to be corroborated by population genetic data.

MICROBIOMES OF MEDITERRANEAN CORALLINES

Marine macroalgae host a wide range of microbial organisms, among which bacteria are typically the dominant group. Bacterial communities associated with seaweeds establish strict biochemical interactions with their algal hosts and differ significantly from those found in the surrounding seawater (Brodie et al., 2016). Epiphytic bacterial communities have been reported as essential for normal morphological development of the algal host, and bacteria with antifouling properties are

thought to protect chemically undefended macroalgae from detrimental, secondary colonization by other epibionts (Egan et al., 2012). In the case of some tropical corallines associated with coral reefs, the microbiome also facilitates the larval settlement of multiple species of corals (Sneed et al., 2015).

Studies concerning the microbiomes of corallines highlighted a great diversity of these assemblages (Cavalcanti et al., 2014; Sneed et al., 2015; Brodie et al., 2016) and suggested that the associated bacterial communities contribute to biomineralization and host fitness (Cavalcanti et al., 2014). Microbiomes are therefore likely to play an important role in the responses of corallines to long-term climatic changes. Studies focusing on microbial communities, however, have mostly concerned encrusting tropical species associated with coral reefs (*Porolithon* spp., *Hydrolithon* spp., *Neogoniolithon* spp.). Limited information is available for temperate species and, to date, only the studies of Ismail-Ben Ali et al. (2012) and Quéré et al. (2019) considered the microbiomes of Mediterranean corallines. Ismail-Ben Ali et al. (2012), in a study with pharmacological focus, isolated 19 bacterial strains from the surface of *Jania rubens*. Their results revealed that the main bacterial groups were Alphaproteobacteria, Gammaproteobacteria, Bacteroidetes and Firmicutes, and that 36% of the isolates produced antibiotics effective against Gram + and Gram - bacteria and the yeast *Candida albicans*. Quéré et al. (2019), compared the microbiome of *Neogoniolithon brassica-florida* affected by white-band syndrome with that of healthy specimens; they could not identify a potential causative agent of the disease, but characterized several opportunistic bacteria colonizing diseased tissues.

BIOCHEMISTRY AND PHYSIOLOGY

Research on Mediterranean corallines in these fields is relatively recent. Excluding work focusing on responses to climate change and ocean acidification, biochemical and physiological research has considered very few species, mainly articulate. For easiness of sampling due to its intertidal/shallow subtidal habitat, *Ellisolandia elongata* has been a favored target for this type of investigations.

Early work on this species examined photosynthetic performances (Häder et al., 1996, 1997), synthesis of chlorophylls and phycobiliproteins in response to light composition (López-Figueroa et al., 1989; López-Figueroa and Niell, 1990) and effects of red and blue light on the N-metabolism (Figueroa, 1993). Estimates of productivity and calcification rates were provided by El Haikali et al. (2004) for French populations. Overall, these studies depicted *Ellisolandia elongata* as a versatile species, capable to regulate its pigment content and metabolism based on quantity and quality of the light irradiation available. It should be noted, however, that these studies were performed before the description of *Corallina caespitosa* (Walker et al., 2009), a species morphologically similar to *Ellisolandia elongata* (now considered a synonym of *C. ferreyrae*, Bustamante et al., 2019). So, the taxonomic identity of the material used in these studies should be reassessed (especially for Häder et al., 1997: these authors

distinguished two morphotypes, sun- and shade-adapted, which might represent different species).

More recent studies investigated populations of *Ellisolandia elongata* from the Alboran Sea, highlighting several metabolic features that make this alga well-adapted to withstand the environmental stresses typical of its intertidal habitat (Celis-Plá et al., 2014; Figueroa et al., 2014a; Korbee et al., 2014; Parages et al., 2014; Stengel et al., 2014). This alga is able to improve its photoprotective capacity by regulating its content in mycosporine-like aminoacids (MAAs, compounds well-known for their photoprotective role in numerous algae) in response to environmental conditions (Celis-Plá et al., 2014; Korbee et al., 2014). Stengel et al. (2014) demonstrated a reduction in the effective photosystem II quantum efficiency in the central hours of the day, and showed that the highest phycocyanin content occurred in the evening; Parages et al. (2014) performed proteomic studies on the same samples and concluded that mitogen-activated protein kinase (MAPK)-like proteins are involved in the response of this species to environmental stress. Figueroa et al. (2014b) argued that the species is resistant to UVB-radiation thanks to the high reflectance of its calcareous thallus.

Jania rubens has been another common subject for biochemical work. Biochemical data for samples identified with this name were provided in several studies performed mainly by northern African investigators. These examined the content of chemical contaminants in environmental monitoring (Al-Masri et al., 2003; Abdallah and Abdallah, 2008; Olgunoglu and Polat, 2008; Hernández et al., 2011; Laib and Legouchi, 2012), biological activities of algal extracts (Abd-Elnaby, 2010; Khairy and El-Sheikh, 2015) and biochemical composition in relation to nutritional value (Polat and Ozogul, 2009, 2013) or for biodiesel production (El Maghraby and Fakhry, 2015; Soliman et al., 2018).

RESPONSES OF MEDITERRANEAN CORALLINES TO CLIMATE CHANGE AND OCEAN ACIDIFICATION

Approaches Used in the Study of the Responses of Coralline Algae to Climate Change and Acidification

Coralline algae are sensitive to changes in temperature and CO₂ conditions and identified as being among the most vulnerable organisms to ocean acidification, because of the solubility of their high-magnesium (high-Mg) calcite skeleton (McCoy and Kamenos, 2015; Martin and Hall-Spencer, 2017). The responses of Mediterranean corallines to climate change and ocean acidification have been the subject of several studies that documented their tolerance or sensitivity to elevated temperatures and CO₂. The effects of elevated CO₂ on Mediterranean coralline algae were studied on single species (Martin and Gattuso, 2009; Martin et al., 2013a,b), in association with a small group of taxa (Asnaghi et al., 2013) and at the community scale (Porzio et al., 2011; Kroeker et al., 2012; Cox et al., 2015, 2017a,b; Marchini et al., 2019). These investigations have focused on a few species, mainly restricted to the group

of (non-geniculate) crustose coralline algae (CCA), including epiphytic (on seagrass leaves) and engineering (coralligenous bio-constructors) species. Their response to ocean acidification and/or warming was studied through a variety of different approaches, including laboratory and field experiments, *in situ* observations in natural volcanic CO₂ vent sites, and *in situ* manipulations using a Free Ocean Carbon dioxide Enrichment (FOCE) system. This variety of approaches provides critical insights in the effects of climate-related stressors on corallines isolated from their surrounding environment and in more complex ecosystems or naturally variable environments.

Impacts of Current Warming on the Health and Survival of Mediterranean Coralline Algae

Although some corallines can adapt to their local environment and acclimatize to a novel thermal regime, as recently suggested for some tropical species able to cope with thermal stress (Siboni et al., 2015), Mediterranean corallines appear particularly sensitive to warming. Several observations have been reported in different localities of the northwestern Mediterranean after summer seasons characterized by positive thermal anomalies. CCA mortality was reported at down to 30 m depth in late summer 1999, when seawater temperature was higher than normal by 2–4°C (Cerrano et al., 2000). In the laboratory, long exposure to elevated temperature (25°C) during summer was the cause of increased frequency of tissue necroses and mortality in *Lithophyllum stictiforme* (as *L. cabiochae*, Martin and Gattuso, 2009). Diseases of corallines described as white band syndrome or white patch disease (Figure 2) have recently been reported associated with high seawater temperature in the northwestern Mediterranean (Hereu and Kersting, 2016). These diseases affected the encrusting *Lithophyllum incrustans*, *Mesophyllum alternans*, and *Neogoniolithon* sp., and the geniculate *Ellisolandia elongata*, *Jania rubens* and *Amphiroa rigida* at shallow depths. The emergence of these thermo-dependent diseases is one of the most serious threats to Mediterranean coralline-dominated communities in the context of climate change.

Physiological Response of Mediterranean Coralline Algae to Climate Change and Ocean Acidification

Temperature directly affects enzymatic processes and is a dominant factor in determining physiological rates in corallines (Lüning, 1990). Rising temperature, within the range of temperature experienced in natural habitats, is beneficial for coralline algae with an increase in photosynthetic and calcification rates (Martin et al., 2006, 2013a), but increased temperature above these levels is detrimental. For example, a +3°C increase in seawater temperature was beneficial to calcification in *Lithophyllum stictiforme* (as *L. cabiochae*) in winter, when temperature is lowest, but a +3°C above maximum summer temperature caused increased frequency of necroses and mortality, and subsequent net calcification drop and further dissolution (Martin and Gattuso, 2009).

Effects of thermal stress were studied by Nannini et al. (2015) in populations of *Ellisolandia elongata* from western Italy and by Guy-Haim et al. (2016) in populations from Israel. Nannini et al. (2015) compared growth and calcification in field specimens with specimens cultured at different temperatures. They reported that thallus extension was higher in culture than in the field; the carbonate mass in the field was higher than in cultured material after 2 and 4 months, but decreased after 6 months. Guy-Haim et al. (2016) measured primary production, respiration and calcification of *Ellisolandia elongata* in the temperature range 15–35°C. In the population examined, the alga consists of the typical frondose form at temperatures <23°C; above this temperature, it switches to a reduced crustose form with short erect axes, but photosynthesis and calcification occur optimally in the interval 15–31°C. Above 31°C there is a metabolic breakdown, with bleaching and tissue necrosis. The authors argued that in the eastern Mediterranean, with continued warming, the species will experience a westward range contraction with phenological shifts, performance, and reproduction declines, population decreases and possible local extinctions.

Decreasing pH in the sea surface will cause major shifts in seawater chemistry over the course of this century, with changes in the relative proportion of the three forms of dissolved inorganic carbon (DIC) species (HCO₃⁻, CO₃²⁻, and CO₂). These changes are likely to affect photosynthesis and calcification, since these physiological processes use DIC as substrate. Increase in CO₂ may be beneficial for photosynthesis in some primary producers but the decrease in pH and CO₃²⁻ may be detrimental for the precipitation of CaCO₃ in calcifiers (Koch et al., 2013). Most of the studies on coralline algae showed that calcification is negatively affected under elevated pCO₂ (Martin and Hall-Spencer, 2017) and that this effect is exacerbated by warming (Anthony et al., 2008). However, some work shows a significant pCO₂ effect on calcification only when this is combined with an increase in temperature (Martin and Gattuso, 2009). The physiological response of coralline algae to increased pCO₂ is variable among species (Martin and Hall-Spencer, 2017) and very few studies have focused on Mediterranean species. For *Lithophyllum stictiforme* (as *L. cabiochae*) Martin and Gattuso (2009) and Martin et al. (2013a) provided evidence of the ability to maintain or even enhance rate of calcification at near future levels of pCO₂ (700 ppm). Such response may be related to the ability of this species to maintain an elevated pH at the site of calcification, despite reduced external pH that would favor CaCO₃ precipitation (Cornwall et al., 2017).

The combination of ocean warming and acidification may cause a much greater effect on corallines. In healthy specimens of *L. stictiforme*, sensitivity of photosynthesis and calcification to high temperature increased in summer when combined with elevated pCO₂ (Martin et al., 2013a). In the geniculate *Ellisolandia elongata*, such combined changes in pH and temperature can impair algal growth (Marchini et al., 2019). The combined effects of ocean warming and acidification can also make corallines more sensitive to other environmental stressors as shown by Fine et al. (2017), who studied thermal tolerance and resilience to low pH, high

light intensity and desiccation in *Neogoniolithon brassica-florida*, an encrusting species acting as consolidator of vermetid reefs. This species resulted sensitive to increased light intensity, particularly in conditions of elevated temperature and low pH, with substantial decrease in photosynthetic performances; calcification was significantly impaired at lower pH. The authors concluded that this species is likely to lose its role of reef consolidator in future, mutated climatic conditions.

Effects of Climate Change and Ocean Acidification on the Mineralogy of Mediterranean Coralline Algae

Different forms of biogenic CaCO_3 have different solubilities in seawater (aragonite > calcite). In calcite, the replacement of some Ca^{2+} by Mg^{2+} increases solubility. High-Mg calcite (>8–12 mol% MgCO_3) is the most soluble CaCO_3 form (Morse et al., 2007) and coralline algae skeletons composed of 8–29 mol% MgCO_3 (Kamenos et al., 2013) are considered highly susceptible to dissolution in the context of ocean acidification. However, potential resilience of coralline algae may occur through changes in skeletal mineralogy, either by producing calcite with lower Mg content (Agegian, 1985; Egilsdottir et al., 2013) or by favoring accumulation of carbonate forms with lower solubility such as dolomite (Diaz-Pulido et al., 2014). However, recent studies on Mg incorporation in the skeleton of Mediterranean coralline algae found no $p\text{CO}_2$ effect. Acidification did not drive any significant change in the Mg content of *Lithophyllum stictiforme* grown experimentally at 700 ppm (Nash et al., 2016). Similarly, no $p\text{CO}_2$ effect was found on the Mg carbonate composition of *Posidonia oceanica* coralline epiphytes exposed to a decrease of 0.3 pH unit by using a FOCE system (Cox et al., 2017b). Kamenos et al. (2016) also found that CCA recruited on tiles had similar Mg content in ambient and low pH (7.8) sites in CO_2 vents off Ischia Island (Italy). This lack of a $p\text{CO}_2$ effect is consistent with findings suggesting that skeletal mineralogy may be under biological control (Nash et al., 2015). The high total alkalinity of Mediterranean waters (Palmiéri et al., 2015) may also have a potential role in buffering the effect of ocean acidification.

The Mg content in coralline algae is also known to vary as function of seawater temperature (Kamenos et al., 2008; Ragazzola et al., 2019). This has been confirmed in Mediterranean *Lithophyllum stictiforme*, for which the mineralogy is primarily controlled by temperature as shown experimentally with an increase of Mg incorporation of 1 mol% MgCO_3 for an increase of 3°C (Nash et al., 2016). The high vulnerability of Mediterranean CCA skeleton to dissolution was already shown by Martin et al. (2008) and Cox et al. (2015) near and below pH_T 7.7. Under experimental conditions of elevated temperature ($+3^\circ\text{C}$) and elevated $p\text{CO}_2$ (700 ppm), the percentage of death for Mediterranean *Lithophyllum stictiforme* was 2- to 3-fold higher and was accompanied by a rate of dissolution of dead algal thalli 2- to 4- times higher (Martin and Gattuso, 2009), suggesting that net dissolution is likely to exceed net calcification in *L. stictiforme* by the end of this century.

Effects of Climate Change and Ocean Acidification on Early Life Stages of Mediterranean Coralline Algae

Early life stages of corallines are particularly vulnerable to ocean acidification. The first studies were conducted on tropical species and showed that recruitment was drastically reduced under elevated $p\text{CO}_2$ (Agegian, 1985; Kuffner et al., 2008).

In the Mediterranean, several studies were performed in CO_2 vents of Ischia (Italy), where pH decreases naturally along a gradient from ambient (pH_T 8.1) to very low pH (<7), in a range greater than expected under future climate scenarios. At these sites, the decrease in coralline cover with decreasing pH may be due to changes in physiological and competitive ability of these algae, but also to lowered reproduction (Porzio et al., 2011) or lowered recruitment (Kroeker et al., 2012). Decreased reproductive capacity has been reported for some coralline species. Cumani et al. (2010) showed in an artificial culture that CCA spore production and growth are inhibited by ocean acidification with an increase in the mortality of germination disks. Reduction in reproductive structures was also observed in the geniculate *Jania rubens* at pH 7.8 in CO_2 vents of Ischia (Porzio et al., 2011). Since these vents are open systems, the negative effects due to the lower capacity of reproduction may be masked in these sites due to the import of spores and zygotes from external or control nearby sites. In the CO_2 vents of Ischia, the recruitment of CCA appears to be inhibited at low pH. Changes in the succession of algae with a replacement of corallines by fleshy seaweeds were observed on settlement tiles at low pH (Porzio et al., 2011, 2013; Kroeker et al., 2012). The lowest pH ($\text{pH}_T < 7.2$) caused failure in coralline algal recruitment but the genera *Hydrolithon* and *Corallina* were still recruited under medium pH (pH_T 7.8; Porzio et al., 2013), suggesting that some species of corallines may be able to persist at pH levels expected for the end of this century. However, the high pH variability observed in the medium pH sites means that pH rises to/close to current pH levels regularly and may lead to an underestimation of the impact of acidification, as these sites are not remaining constantly under low pH conditions (Porzio et al., 2013). In the same area, Kamenos et al. (2016) observed that the largest individuals of CCA recruited on tiles maintained growth and were of similar size in low (7.8) and ambient (8.0–8.1) pH zones. The ability of some thalli to continue growing in lower pH suggests acclimation/adaptation to low pH conditions and ability to provide recruits for populations adapted to survive in lower pH environment in the future. Through *in situ* pH manipulation using a FOCE system in a *Posidonia oceanica* meadow, Cox et al. (2017a) also found that early stages of CCA are sensitive to decreased pH, with lower coverage of CCA on recruitment tiles placed in a pH-manipulated enclosure (-0.3 pH unit offset) compared to an un-manipulated enclosure (ambient pH). Although previous studies suggested post-settlement competition between fleshy and calcareous algae (Porzio et al., 2011; Kroeker et al., 2012; Kamenos et al., 2016), Cox et al. (2017a) suggested that losses of CCA were driven by taxa sensitivity, because the other taxa were also reduced by the lower pH conditions and there was still bare space available for colonization.

Field Assessment of the Impacts of Ocean Acidification on Mediterranean Coralline Algae

The responses of coralline algae to acidification can be altered by biotic (e.g., competition for space and resource or herbivory) and abiotic (e.g., irradiance or nutrient supply) interactions. Although most investigations on corallines were conducted in the laboratory with single taxa or relatively small groups of taxa isolated from the surroundings, some studies in the Mediterranean used whole ecosystem approaches (CO₂ vents or FOCE system) that allow to consider these interactions. These studies focused mostly on the epiphytic CCA in seagrass meadows. *In situ* observations near CO₂ vents reported clear reductions or losses of corallines where the pH is naturally lower (Hall-Spencer et al., 2008; Martin et al., 2008; Porzio et al., 2011; Kroeker et al., 2012; Baggini et al., 2014; Donnarumma et al., 2014). In the CO₂ vents of Ischia, Martin et al. (2008) showed a complete disappearance of epiphytic CCA on *Posidonia oceanica* at an average pH_T of 7.7, consistent with pH expected for the end of this century, but with large temporal pH variations from <7 to >8.1. Vent systems are not perfect predictors of future ocean ecology, due to the high pH variability in space and time that makes difficult to identify threshold or tipping points (Hall-Spencer et al., 2008; Kerrison et al., 2011). Recently, some studies reached conclusions in contrast with previous findings on ocean acidification projections. Cox et al. (2017b) found no pH effect on epiphytic CCA on *Posidonia oceanica* exposed to a decrease of -0.3 pH unit in a pH-manipulated enclosure using a FOCE system. Additional insights into community-level effects of warming and ocean acidification are beginning to emerge from longer-term multispecies laboratory experiments (Hale et al., 2011; Legrand et al., 2017). Similarly, Asnaghi et al. (2013) demonstrated that grazing activity exacerbated the effects of pCO₂ on corallines with higher weight loss in the geniculate *Ellisolandia elongata* under elevated pCO₂ in the presence of urchins. It is clear that the impact of global changes on corallines will depend on the combined influence of direct environmental effects on individual species and indirect effects mediated by changes in interspecific interactions (Harley et al., 2012). Long-term multispecies experiments combining warming and ocean acidification appear essential to improve our future understanding of Mediterranean coralline algae.

CONCLUSIONS AND DIRECTIONS FOR FUTURE WORK

The present summary shows that there are still substantial gaps in our knowledge of Mediterranean corallines, despite of the large amount of information available for some coralline-dominated habitats (particularly coralligenous). Giving the ecological importance of these algae and their sensitivity to climate change, the body of information available should be now substantially expanded.

As general recommendation, we suggest that future work on Mediterranean corallines should be based on a multidisciplinary perspective combining different approaches. So far, work on

these algae has consisted mostly of separate efforts/projects, carried out by researchers working in different fields and interested in different aspects. The integration of different approaches will be essential, in particular, to address major large-scale and long-term issues, such as the responses of individual species and populations to future, mutated climatic scenarios. We also note that most of the information currently available for Mediterranean corallines has been produced by scientists based in a relatively small number of countries (mainly France, Italy and Spain). As consequence, the body of information available for the western Mediterranean is currently much larger than for the eastern Mediterranean. This represents a major limit for the interpretation of general patterns, especially for coralline species with distribution extending to the whole Mediterranean. Within a same species, populations from the western Mediterranean (especially northwestern) and from the eastern Mediterranean are presumably characterized by different ecophysiological traits and therefore are likely to respond differently to future climatic changes. Therefore, we suggest that future research on basic aspects of the biology of Mediterranean corallines should involve many scientists with different backgrounds, based in several countries, both in the western and eastern Mediterranean.

More specifically, there are some tasks that we identify as priority for each of the main fields of investigation:

- 1) Further paleontological investigations, focusing on identification of morpho-anatomical species groups with paleoecological and/or paleobiogeographical meanings, study of the evolution of Mediterranean coralline assemblages in the context of important paleogeographic changes, and how global environmental parameters such as sea-level, ocean acidification, and global temperature affected in the past the evolution of Mediterranean species.
- 2) An accurate taxonomic reassessment of the Mediterranean coralline flora based on a modern combination of molecular, morphoanatomical and ecological data. This is also a critical requirement for an accurate biogeographic reassessment. Taxa surrounded by taxonomic uncertainty or for which molecular data are lacking should receive priority; among these, we suggest:
 - *Neogoniolithon*, a genus for which the only species *N. brassica-florida* is currently recognized in the Mediterranean, but in which species circumscription is unclear (Kato et al., 2013).
 - Members of Sporolithales, for which there are no molecular data from Mediterranean collections.
 - Maerl/rhodolith-forming species for which no sequences are available (*Lithothamnion minervae*, *L. valens*), or for which conspecificity with Atlantic counterparts should be verified (*Lithothamnion corallioides*).
 - *Lithophyllum* of intertidal and shallow subtidal zones; these algae in the Mediterranean have been usually identified as *L. incrustans*, but the data of Hernandez-Kantun et al. (2015a) highlighted that this is mainly a subtidal species, suggesting that the identity of intertidal specimens requires reassessment.

- *Lithophyllum trochanter* and *L. woelkerlingii*, two species separated by Bressan and Cabioch (2004) based on subtle characters.
- 3) Studies of reproductive biology combining observations in the field and experiments in the laboratory with molecular and biochemical studies aiming to elucidate the mechanisms triggering fertility and release of reproductive cells.
- 4) Transcriptomic studies and characterization of associated microbiomes, starting from species important as bioconstructors or habitat-formers (*Lithophyllum stictiforme*, *L. byssoides*, *Ellisolandia elongata*). Investigations of this type are necessary for a deep understanding of the molecular and biochemical processes determining responses to environmental disturbances, and for early detection of stress in populations of ecologically important species.
- 5) Extending studies on the effects of climate change and acidification to a wider set of species, and expanding them to long-term experimental investigations. We suggest that *Mesophyllum* species contributing to coralligenous concretions, maerl/rhodolith-forming species (*Lithophyllum racemus*, *Lithothamnion corallioides*, *L. minervae*, *L. valens*, *Phymatolithon calcareum*) and bioconstructor species of the intertidal/shallow subtidal zone (*Lithophyllum byssoides*, *L. trochanter*) are natural candidates for such studies. New studies focusing on the main aspects (physiology, mineralogy, vitality of early life stages) in which Mediterranean corallines may be affected by climate change and ocean acidification will represent valuable contributions.
- 6) Basic studies on mineralization. The complete lack of information for Mediterranean species is striking, considering the importance of this aspect for growth, carbonate formation, and bioconstruction activity of these algae.
- 7) Accurate phylogeographic studies based on high-resolution genetic methods, such as microsatellites, Single Nucleotide Polymorphisms (SNPs) or sequencing of Restriction Site Associated DNA markers (RAD), starting from ecologically significant species (*Lithophyllum stictiforme*, *L. byssoides*, *Mesophyllum expansum*, *Ellisolandia elongata*, *Lithothamnion corallioides*). Data of this type are essential to draw effective conservation measures for marine species. It is striking that in general studies of this type are in great shortage for Mediterranean seaweeds (ironically, from this point of view some introduced taxa have been so far the best-studied seaweeds in the Mediterranean). This is even more surprising considering that, in contrast, the amount of similar studies concerning Mediterranean fishes and invertebrates is ponderous (see Patarnello et al., 2007; Pascual et al., 2017).

We remark that these tasks can be best tackled by integrating the work in each specific field with other types of data/approaches. The integration of basic ecological, physiological and biochemical work with genomics, taxonomy and molecular phylogeny will be especially important to predict both changes in distribution and abundance of individual coralline species, and shifts in the structure of Mediterranean ecosystems built or dominated by corallines. This will be mandatory when the corallines studied turn to be complexes of cryptic species that differ in ecological and physiological traits, as recently stressed

by De Jode et al. (2019). In general, cryptic diversity in corallines is an aspect that in the future will require much more attention from Mediterranean marine biologists. Neglecting it might lead to erroneous interpretations of the results of studies in many different fields. At ecosystem level, changes in diversity of coralline assemblages, if undetected due to the cryptic nature of the species involved, may lead to shifts in ecosystem structure and functioning (Hind et al., 2019).

Even for this reason, we recommend that all future studies on Mediterranean corallines (of any type, not just taxonomic) should base their identifications on DNA sequence data and take care to deposit voucher specimens in herbaria or other permanent collections. This will give the possibility to verify the correctness of the identifications, which will be a critically important requirement for comparison of the results of different studies.

AUTHOR CONTRIBUTIONS

FR led the conceptual design of the paper, contributed to the writing of the sections Introduction, Historical Summary, Floristic Diversity, Molecular Studies of Mediterranean Corallines, Present-Day Distribution and Biogeography, Reproductive Biology, Microbiomes of Mediterranean Corallines, Biochemistry and Physiology, and Conclusions and Directions for Future Work, assembled the first version of the manuscript, and prepared the **Table 1**, the **Figures 1, 2, and 3**, and the **File SM1**. JA and JB wrote the section Geological History of the Mediterranean and Paleontological Record of Mediterranean Corallines, and prepared the **Figure 5** and the **Files SM2 – SM6**. SM wrote the section Responses of Mediterranean Corallines to Climate Change and Ocean Acidification. VP, LG, and AC contributed to the writing of the sections Introduction, Historical Summary, Floristic Diversity, Molecular Studies of Mediterranean Corallines, Present-Day Distribution and Biogeography, and Conclusions and Directions for Future Work. AC prepared the **Figure 4**. VP prepared the **Table S1**.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00723/full#supplementary-material>

Table S1 | Detail of DNA sequence data obtained from Mediterranean corallines.

File SM1 | List of references used for the compilation of the bibliographic summary of Mediterranean corallines.

File SM2 | List of fossil corallines reported from the Mediterranean area.

File SM3 | Records of fossil Sporolithales reported for the Mediterranean area.

File SM4 | Records of fossil Hapalidiales reported for the Mediterranean area.

File SM5 | Records of fossil Corallinales reported for the Mediterranean area.

File SM6 | List of references for supplementary files SM2, SM3, SM4, and SM5.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer AC declared a past co-authorship with one of the authors LG to the handling editor.

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