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The role of habitat in the facilitation of *Ostreopsis* spp. blooms

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Abstract

In recent decades, recurrent *Ostreopsis* spp. blooms have been recorded throughout the globe, causing public health issues and mass mortalities of invertebrates. *Ostreopsis* species are benthic and develop in shallow waters in close relation with a substrate, but possible substrate preferences are still ambiguous. Bloom develops on both living and dead substrates and several interacting biotic and abiotic factors acting at different spatial scales can potentially foster or regulate *Ostreopsis* spp. development. The objective of this review is to collect and summarize information on *Ostreopsis* spp. blooms related to the habitat at different spatial scales, in order to assess preferences and trends. References including *Ostreopsis* spp. samplings in the field were analysed in this review, as potentially including information about the micro- (substrate), meso- (community) and macrohabitat (ecosystem) related to *Ostreopsis* spp. blooms. The sampled substrate and the ecosystem where *Ostreopsis* spp. were collected were generally reported and described in the studies, while the description of the mesohabitat was rarely reported. *Ostreopsis* spp. were generally described as attached to biotic substrates and in particular, macroalgae, even in studies conducted in coral reefs, where macroalgae are generally not dominant (but they can be in case of coral reef degradation). In both temperate and tropical areas, *Ostreopsis* spp. were mostly sampled on algal species usually forming medium or low complexity communities (erect or turf-forming algae), often characteristic from post-regime shift scenarios, and rarely on canopy-forming species (such as fucoids and kelps). This literature review highlights the need of collecting more information about the mesohabitat where important *Ostreopsis* spp. blooms develop, as much as of the underlying mechanisms driving eventual differences on *Ostreopsis* spp. abundances. This knowledge would allow a better risk assessment of *Ostreopsis* spp. blooms, identifying areas at high risk on the base of the benthic habitats.

Keywords: benthic HABs*,* *Ostreopsis*, substrate, community, habitat, ecosystem, algae

1 Introduction

Over the past decades, coastal areas throughout the world experienced an accelerating trend of Harmful Algal Blooms (HABs) events (Anderson et al., 2019) including the ones due to benthic species (Parsons et al., 2012). A significant proportion of studies concerning benthic HABs is focused on tropical benthic dinoflagellate ecology, mostly because of the incidence of ciguatera fish poisoning (CFP) in tropical and subtropical areas (Litaker et al., 2009) and the geographic expansion of some toxic species in temperate waters (Rhodes, 2011). Among them, recurrent *Ostreopsis* spp. blooms have been recorded throughout the globe: in the Mediterranean Sea (Vila et al., 2001; Penna et al., 2005; Turki, 2005; Aligizaki and Nikolaidis, 2006; Mangialajo et al., 2008a; Totti et al., 2010; Cohu et al., 2011; Ismael and Halim, 2012; Manca et al., 2015; Açaf et al., 2020; Gémin et al., 2020), the East Atlantic Ocean (Solino et al., 2020), the West Atlantic Ocean (Nascimento et al., 2012; Tibirica et al., 2019), the South-West Pacific (Chang et al., 2000; Rhodes et al., 2000; Shears and Ross, 2009), the North-West Pacific (Yamaguchi et al., 2012; Zou et al., 2020), the South-West Indian Ocean (Lenoir et al., 2004) and the Red Sea (Gomaa et al., 2018). At least five out of the eleven identified species (Fukuyo, 1981; Norris et al., 1985; Quod, 1994; Faust and Morton, 1995; Faust, 1999) produce palytoxin-like compounds, one of the most toxic marine compounds (Usami et al., 1995; Ukena et al., 2001; Ciminiello et al., 2010; Suzuki et al., 2012; Varela et al., 2021), causing respiratory disease after inhalation of marine aerosols (Tichadou et al., 2010; Tubaro et al., 2011; Vila et al., 2016). The whole ecosystem is affected by *Ostreopsis* spp. blooms (Turner et al., 2021), due to mass mortalities of invertebrates such as bivalves, gastropods, crustaceans, and echinoderms (Shears and Ross, 2009; Ramos and Vasconcelos, 2010; Guidi-Guilvard et al., 2012; Parsons et al., 2012; Accoroni and Totti, 2016; Migliaccio et al., 2016; Neves et al., 2018). In order to effectively manage and mitigate *Ostreopsis* spp. blooms, a thorough understanding of the bloom dynamics of these species is needed. Samplings have been worldwide restricted mostly to shallow waters as it has been demonstrated in both tropical and temperate areas that *Ostreopsis* spp. cell abundances are negatively correlated with depth (Richlen and Lobel, 2011; Cohu and Lemee, 2012). The mechanisms that affect *Ostreopsis* spp. populations are unclear, but most studies relate larger abundances of *Ostreopsis* spp. to sheltered zones or in low hydrodynamic conditions (Di Turi et al., 2003; Chiantore et al., 2008; Shears and Ross, 2009; Battocchi et al., 2010; Cabrini et al., 2010; Richlen and Lobel, 2011; Accoroni and Totti, 2016; Mohammad-Noor et al., 2016; Boisnoir et al., 2018; Hachani et al., 2018; Meroni et al., 2018), while others suggest larger abundances of *Ostreopsis* spp. in higher or slightly higher levels of water motion (Vila et al., 2001; Selina et al., 2014). The inshore occurrence of *Ostreopsis* spp. has also raised the question concerning their association with nutrient enrichments due to human activities (Faust et al., 1996), but there are mixed conclusions on how nutrient concentrations influence population dynamics of *Ostreopsis* spp. (Ungaro et al., 2010; Cohu et al., 2011; Accoroni et al., 2012; Asnaghi et al., 2012). A concise summary of the effects of surface seawater temperature, salinity and nutrient concentrations on *Ostreopsis* spp. populations in temperate areas can be found in Accoroni and Totti's (2016) and Tester's et al. (2020) reviews. Results from the above-mentioned studies are sometimes contradictory, likely due to the fact that *Ostreopsis* spp. blooms are a global phenomenon controlled by several factors in very different contexts and, as a consequence, blooms are very variable in space and time, making difficult defining general trends (Mangialajo et al., 2011).

Due to their benthic nature, *Ostreopsis* spp. develop in close relation with a substrate. *Ostreopsis* spp. are often described as epiphytic on macroalgae and seagrasses (Rhodes, 2011), but can also be found on dead corals, sediments, rocks, and in the water column (Bomber et al., 1989; Vila et al., 2001; Shears and Ross, 2009, 2010; Totti et al., 2010). However, the substrate preferences of *Ostreopsis* spp. are still ambiguous (Vila et al., 2001; Cohu et al., 2013; Sparrow et al., 2017; Ternon et al., 2020; Tester et al., 2020), although some studies reported larger abundances on some substrates compared to others (Vila et al., 2001, 2012; Mohammad-Noor et al., 2007; Widiarti, 2008; Cabrini et al., 2010; Totti et al., 2010; Accoroni et al., 2011, 2012; Mangialajo et al., 2011; Accoroni and Totti, 2016; Yong et al., 2018; Boisnoir et al., 2019; Bravo et al., 2020; Lee et al., 2020). Such comparisons are tricky because of the limits of cell quantification in function of the type of substrate (i.e. surface for rocks, fresh weight for macrophytes), but also because the measures depend often on some characteristics of the substrate (i.e. the specific weight of sampled species). As an example, some macroalgae species seem to host larger abundance of *Ostreopsis* spp. than most other species, e.g. *Corallina* spp. (Simoni et al., 2004; Aligizaki and Nikolaidis, 2006; Monti et al., 2007; Chiantore et al., 2008) and *Padina* spp. (Aligizaki and Nikolaidis, 2006; Cabrini et al., 2010; Hachani et al., 2018 ; Gémin et al., 2020). Nonetheless, other species provide discordant patterns such as: *Ulva* spp. (Aligizaki and Nikolaidis, 2006; Monti et al., 2007; Okolodkov et al., 2007; Totti et al., 2010 ; Ismael and Halim, 2012), *Dictyota* spp. (Cohu et al., 2013 ; Blanfune et al., 2015; González et al., 2019; Gémin et al., 2020 ; Ternon et al., 2020), and *Cystoseira sensu lato spp.* (Aligizaki and Nikolaidis, 2006; Monti et al., 2007; Aligizaki and Nikolaidis, 2008; Blanfune et al., 2015; Catania, 2017; Moncer et al., 2017; Meroni et al., 2018). *Ostreopsis* abundances on different substrates are highly variable and, despite the technical issues linked to the measurement cited above, several biotic factors acting at different spatial scales can be responsible for such variability: morphology and palatability of macrophytes, herbivory and allelopathic interactions due to the production of secondary metabolites by living substrates, among others (Cruz-Rivera and Villareal, 2006; Totti et al., 2010; Accoroni et al., 2015; 2016; Ternon et al., 2020).

Benthic ecosystems are dynamic systems and, especially due to human impacts, can experience regime shifts, resulting in profound changes in the structure and composition of communities (Hughes, 1994; Benedetti-Cecchi et al., 2001; Chemello et al., 2018; Filbee-Dexter and Wernberg, 2018; Johns et al., 2018; Melis et al., 2019; Pessarrodona et al., 2021). In both temperate and tropical reefs, regime shifts cause a change from healthy communities dominated by foundation species to communities dominated by less structurally complex species (Filbee-Dexter and Scheibling, 2014; Jouffray et al., 2015; Wernberg et al., 2016; O'Brien and Scheibling, 2018; Pessarrodona et al., 2021). In temperate areas canopy-forming algae are lost and replaced by less complex algae-dominated communities (Strain et al., 2014; Vergés et al., 2014; Bulleri et al., 2016); several studies relate major densities of *Ostreopsis* spp. on algal turfs (Bravo et al., 2020) and in particular on highly urbanised coasts that are usually characterized by post-regime shift algal communities (Mangialajo et al., 2008a; Widiarti et al., 2008; Cohu et al., 2013), compared to healthier habitats dominated by forest-forming brown algae (Meroni et al., 2018). In tropical areas, ciguatera fish poisoning episodes recurrently follow disturbances to coral reefs by natural and artificial events such as heat waves, hurricanes, dredging, and shipwrecks, among others, where regime shifts from coral to algae are observed (de Sylva, 1994; Jouffray et al., 2015; Rains and Parsons, 2015; Johns et al., 2018). In this case, higher benthic dinoflagellate abundances are recorded, both on turf-forming (Yong et al., 2018; Lee et al., 2020) and forest-forming species, such as *Sargassum* spp., Chinain et al., 2020).

To our best knowledge, only few studies assessed the variability of *Ostreopsis* spp. at a level higher than the substrate (Cohu et al., 2013; Meroni et al., 2018; Yong et al., 2018; Bravo et al., 2020; Lee et al., 2020) with the aim of comparing different habitats to help understanding *Ostreopsis* spp. variability. To ascertain how the habitat positively or negatively affects *Ostreospis* spp. blooms, a literature review was conducted in order to describe trends at different spatial scales. In this review we define: 1) the microhabitat (substrate, spatial scale of cm^2), as the biotic or abiotic object sampled to quantify/collect *Ostreopsis* spp. cells (including living or dead organisms and abiotic substrates), 2) the mesohabitat, as the community or the abiotic material patch where the substrate is sampled (spatial scale of few to a dozen of m^2, e.g. the macroalgal turf where a certain macroalgal species is sampled as a substrate or the sandy bottom where a pebble is sampled as a substrate; Meroni et al., 2018; Bravo et al., 2020; Lee et al., 2020), and 3) the macrohabitat, as the ecosystem or the seascape (spatial scales of hundreds/thousands of m^2) where the mesohabitat is found (i.e. coral reefs, macroalgal-dominated rocky shores; Yong et al., 2018).

2 Materials and methods

A bibliographic review assessment was performed using three databases: Aquatic Science and Fisheries Abstracts (ASFA), Web of Science (WoS) and SCOPUS (last update at 1st February 2021). Search parameters were kept as wide as possible to ensure that all the relevant publications on the topic were found in the database search. The keyword used for the search was "*Ostreopsis*" and the parameters of the search were to find the word "*Ostreopsis*" 'everywhere' in the body or text of the publications, between anytime and February 1st, 2021.

To quantify and compare the relationship between *Ostreopsis* spp*.* and the micro- meso and macrohabitats*,* only articles involving field collection of *Ostreopsis* spp. were included in this review. The key information extracted from each article included, when available: microhabitat (e.g. sampled substrates such as macrophytes, rocks, shells, artificial substrates, others), mesohabitat (community/abiotic patch type), macrohabitat (ecosystem/seascape), ocean and sea of study, country, temperate or tropical area (tropical areas were defined as areas between -35° and 35°, including both tropical and subtropical climate), geographic coordinates (if not available, they were obtained from Google Earth, whenever possible) of the sampling location where *Ostreopsis* spp. were sampled, maximum recorded abundance in the study and sampling dates. The maximum abundances of *Ostreopsis* spp. recorded in the studies were classified in three categories: No bloom (<200x103 cells per gram fresh weight (FW) of macrophyte), Bloom (>200x103 cells per gram FW of macrophyte) and Major bloom (>1000x103 cells per gram FW of macrophyte) as in Mangialajo et al. (2017). Several studies (132) were conducted in two or more separate regions around the globe, seas, countries, locations and/or involving different substrates. In this case, a different line was inserted in the table for each different score, therefore it is possible that one article was accounted more than once. All the graphs have been produced using R Project version 3.6.2.

Macroalgal species are characterised by different sizes and shapes, and the communities dominated by different species can be more or less structurally complex, comparable to continental forests, shrubs and turfs, terms often used in the scientific literature (see below). Because abundances of *Ostreopsis* spp. on macroalgae are subjected to differences in the structure, surface, and fresh weight, the different algal species sampled as a substrate in the reviewed studies were grouped in the following three categories according to their structural morphology:

- Turf-forming algae: algae with tightly packed fronds and filamentous thin cylindrical axes, with a horizontal coverage several times higher than their height forming a dense and compact mat (Stewart, 1983; Tittley and Neto, 1995; Sales and Ballesteros, 2010; Sala et al., 2012; Connell et al., 2014; Thiriet et al., 2016; Mauffrey et al., 2020).
- Shrub-forming algae: foliose laminar, ribbon-like, massive or fan-like thallus and erect arborescent tufts. Algae usually having a smaller size and forming less complex communities than forest forming species. At the same time, in their region, they generally have a bigger size and form communities characterised by higher complexity than turf forming algae (Sala et al., 2012; Thiriet et al., 2016; Bertolini, 2019).

- Forest-forming algae: cylindrical axes, branched and tree like characterised by a complex tri-dimensional structure, generating a canopy. Algae having a large size compared to other algae growing in the same region. This term is generally used for Laminariales, Fucales and some Tilopteridales (Sala et al., 2012; Strain et al., 2014; Thiriet et al., 2014, 2016; Bertolini, 2019; Shelamoff et al., 2019; Assis et al., 2020).

3 Results

The bibliometric search resulted in 1157 publications including the word "*Ostreopsis"* in the text from 1973 to 2021. Only 249 studies, published from 1981 to 2021, were based on field sampling of *Ostreopsis* spp. cells and were therefore considered as relevant for the review. The 249 considered studies comprise 957 sampling locations, involving a total of 1644 different substrates sampled between 1972 and 2019. 90% of the papers from this review (224) focused on *Ostreopsis cf. ovata*.

The number of studies per year reveals a positive trend of ecological studies involving sample collection in the field (Figure 1) in both temperate and tropical areas. The first studies involving field sampling were performed in the tropics, but, since year 2000, studies performed in temperate areas have exceeded in number the tropical ones. Since 2018 tropical studies are again more numerous than in temperate areas, but this trend has to be verified in the next years. Nearly half of the 957 different locations investigated between 1972 and 2019 are in temperate areas (471), the other half (486) in tropical ones. The exact geographical coordinates were available for 595 (62.2%) sampling locations and it was possible to position 132 (13.8%) additional ones on the basis of the description of the location in the text. A distribution map of the 727 locations, out of the 957 sampled in the 249 relevant studies, is reported in Figure 2.

3.1 Spatial scales

3.1.1 Macrohabitat

The macrohabitat was detailed in a total of 197 out of the 249 papers (79.1%). In 12 of them (6.1% studies) at least two different ecosystems/seascapes were sampled. From the 957 sampled locations, 897 (93.7%) included or allowed extrapolation of the information at the large scale (ecosystem/seascape; Figure 3). In temperate areas, *Ostreopsis* spp. is mostly sampled in rocky reefs (usually dominated by macroalgal communities), while in tropical areas *Ostreopsis* spp. is generally sampled in coral reefs. Soft bottoms are also regularly sampled, especially in tropical areas.

3.1.2 Mesohabitat

The mesohabitat was detailed in a total of 87 out of the 249 papers (34.9%). In 30 of them (12% studies) at least two different mesohabitats were sampled. From the 957 sampled locations, 301 (31.4%) included or allowed extrapolation of the information at the intermediate scale (Figure 4). In temperate and in tropical areas, *Ostreopsis* spp. is mostly sampled in algal communities (6.2% and 7.3% respectively). Seagrass meadows are also regularly sampled, especially in tropical areas (5.2%).

3.1.3 Microhabitat

The microhabitat was detailed in a total of 243 out of the 249 (97.6%) studies considered. In almost half of the studies (113 studies, 45.4%) at least two different substrates were sampled. From the 957 sampled locations, 950 (99.3%) included information about the sampled substrate. On 527 (55.1%) sampled locations out of the 957, two or more substrates were sampled, resulting in a total of 1644 different sampled substrates. The frequency of the total sampled substrates is reported in Figure 5.

Three additional substrates were sampled and are not accounted for in the present study: a Bryozoan (Di Pippo and Congestri, 2017), the gut contents of the herbivorous fish

Sarpa salpa (Bellassoued et al., 2013) and floating plastic debris (Masó et al., 2003; Casabianca et al., 2019; Tibirica et al., 2019).

Artificial substrates, that allow an easier standardisation of *Ostreopsis* spp. abundances (i. e. Yong et al., 2018; Jauzein et al., 2018; Fernandez-Zabala et al., 2019; Lee et al., 2020); were used in 24 out of the 249 studies (3.6% in temperate areas and 6% in tropical), and in 136 out of the 1644 sampled substrates (2.3% in temperate areas and a 6% in tropical). Seawater is also commonly sampled and, in some countries, thresholds alerts are based on cell concentrations in seawater at dozen of centimetres above the sea bottom (Funari et al., 2015). Water was sampled in 100 out of the 249 studies (32.5% in temperate and 7.6% in tropical areas) and represent 332 out of the 1644 sampled substrates (15.7% in temperate and 4.5% in tropical areas).

Without considering seawater, macroalgae are by far the preferred substrate for sampling *Ostreopsis* spp. Out of the 249 studies, 179 (71.9 %) included at least a macroalgal sample. A total of 792 macroalgae specimens were sampled in tropical and temperate areas. Macroalgae are commonly sampled both in temperate (where they dominate rocky reefs habitats) and in tropical areas (where, on the contrary, habitats are usually dominated by corals). The second preferred substrate is represented by seagrasses, followed by sand and sediments, coral fragments, pebbles/rocks and dead mollusc shells. Most studies (56.8%) sampling macrophytes identified the sample at the species level, while 20.1% out of them identified the macrophyte at genus level. Some studies (2.9%) identified the species sampled only at a level higher than genus or using non taxonomic classification (i.e. turf). The remaining fraction (20.2%) did not provide any taxonomic information. It is worth noting that quantification of *Ostreopsis* spp. cell abundances on invertebrates (corals or molluscs) is generally performed on dead coral fragments or shells (Faust et al., 1996; Faust, 1999; Mohammad-Noor et al., 2007; Okolodkov et al., 2007; Xu et al., 2014).

Macroalgae samples, that involved the collection of 792 different specimens, represent nearly half of the sampled substrates (47.7%) and are a polyphyletic and extremely diversified group of organisms. The different macroalgal phyla, Rhodophyta, Ochrophyta and Chlorophyta (Ruggiero et al., 2015) were sampled in different proportions, in particular in temperate areas where Rhodophyta (49.2%) seem to be sampled preferentially, followed by Ochrophyta (36.7%) and Chlorophyta (14%). In tropical areas, the sampling frequency of each phylum is similar (39.4%, 36.7% and 23.8%, respectively; Figure 6).

One of the major limitations and controversies for studying macrophyte preferences is the difficulty of standardising cell densities. In order to compare and assess the role of each macroalgae species in structuring the community, we classified the macroalgae sampled as a substrate in three different groups according to their physical structure. The algae sampled in the considered studies were classified, based to our knowledge about their mean size and their appearance in "forest-forming", "shrub-forming" and "turf-forming", as defined in the "Materials and methods" section. Following this classification, most of the macroalgae sampled in both temperate and tropical areas correspond to the category shrub-forming (55.9%), followed by the turf-forming (31.7%) and the forest-forming (12.3%; Figure 7).

Of the 249 studies, 82 (32.9%) reported abundances of *Ostreopsis* spp. cells per gram FW of macrophyte. Such quantification is dependent on the specific weight and morphology of the different species (Mangialajo et al., 2017) and would not, ideally, allow a direct comparison of abundances on different macroalgal species. At present, the few alternative methods allowing a standardised quantification (Tester et al., 2014; Jauzein et al., 2016; Mangialajo et al., 2017) are only sporadically applied and large-scale comparisons are performed on the measures of cells per gram FW. In order to have a global vision of the *Ostreopsis* spp. abundances, the maximal abundance reported on each study indicating the host macrophyte has been reported, when available, in Table 1 (expressed as cells/g of macroalga FW). From the data reported on Table 1, the maximum cell densities of *Ostreopsis* spp. (cells g^{-1} FW macroalgae) are grouped according to the type of mesohabitat the macroalgae sampled can form and the intensity of the bloom (Mangialajo et al., 2017; N= 54; Figure 8). In the case of Bloom and No bloom scenarios (according to Mangialajo et al., 2017), the abundance of *Ostreopsis* spp. cells seems to be higher on shrub and turf-forming species. For the Major bloom scenario (see classification in Mangialajo et al., 2017), the abundance of *Ostreopsis* spp. seems to be higher on shrub- forming species in temperate areas (followed by high values in forest forming) and on forest-forming species in tropical areas.

4 Discussion

The first indexed papers involving *Ostreopsis* spp. sampling have been published in tropical areas. The bibliometric study shows a rise in scientific publications presumably linked to the increasing HABs incidences in recent decades (Anderson et al., 2019), and in particular since *Ostreopsis* spp. blooms have spread in temperate areas (Shears and Ross, 2009). The search performed in this study did not take into account non-indexed papers or grey literature likely providing a low estimation of old papers, in particular in developing countries. Since the 90s *Ostreopsis* spp. are reported in temperate areas; a rapid increase in publications in temperate areas after 2006 is likely due to the first recognised mass intoxication in Genoa (Italy) in 2005 (Brescianini et al., 2006) that encouraged several European research groups to focus on this emergent phenomenon. An increase in publications in tropical areas is registered after 2010, often in synergy with research performed in temperate areas. It is worth noting that the peak of *Ostreopsis* spp. publications in temperate areas registered in 2012 is due to the publication of 18 articles in a special issue (*Cryptogamie Algologie*) resulting from the proceedings of the International Congress on *Ostreopsis* Development (ICOD conference, 2011; Lemee, et al., 2012).

Benthic dinoflagellate development is affected by interacting biotic and abiotic factors linked to the habitat and acting at different scales (i.e. substrate, benthic community and seascape). Interestingly the present study highlighted that the sampled substrate (herein the microhabitat, e.g. coral fragment, macroalgal species) and the ecosystem (herein the macrohabitat, e.g. coral reefs, macroalgal-dominated rocky shores, sandy or muddy bottoms) where *Ostreopsis* spp. are sampled are generally reported and described. In 98% and 79% of the studies the sampled substrate and the seascape are respectively described or, alternatively, the text allows undoubtful extrapolation of this information. Concerning the microhabitat, and in particular organic substrates, most studies detail the species (56.8%), or at least the genus (20.1%) of the organisms sampled. Yet, even if the coral fragment or shell is identified at the species level, it is not clearly reported if 1) it is a living organism and 2) it is the direct *Ostreopsis* spp. host. Some studies (Widiarti, 2008; Yong et al., 2018) suggested that small filamentous macroalgae developing on dead or damaged coral surfaces could foster *Ostreopsis* spp. development, showing the role of macroalgae as a favourable substrate. The same considerations could be valid for shells, pebbles, and stones, but there is no specific literature on these particular cases to our knowledge. On the contrary, the description of the mesohabitat (e.g. macroalgal turfs, macroalagal forests, coral-dominated communities, seagrasses, or sandy patches) is rarely reported (35% of the considered studies). As highlighted in Pavaux et al. (2020) it is undeniable that only a small part of the research on *Ostreopsis* spp. is focused on ecological aspects. Interestingly, recent studies, mainly focused on tropical species related to ciguatera, suggest that habitat heterogeneity and complexity affect benthic dinoflagellate communities (Rains and Parsons, 2015; Meroni et al., 2018; Yong et al., 2018; Boisnoir et al., 2019; Bravo et al., 2020; Lee et al., 2020). In particular Yong et al. (2018) found higher *Gambierdiscus*, *Prorocentrum* and *Amphidinium* cell abundances on reefs with high turf algal cover and coral rubble, while *Ostreopsis* preferred mesohabitats with high coral cover. Lee et al. (2020) found that the mesohabitat influence the distribution of benthic harmful algal blooms and that *Ostreopsis* and

Gambierdiscus are both associated with turf algal communities and hard coral. Bravo et al. (2020) observed an influence of the macrophyte's thallus architecture on dinoflagellates abundances and also reported higher abundances of *Ostreopsis* on turf Rhodophyta, while *Gambierdiscus* and *Sinophysis* seem to be more abundant on Rhodophyta and Ochrophyta. More information at the global scale on how habitat affects benthic dinoflagellate blooms would allow to better disentangle the different factors playing a role in *Ostreopsis* spp. blooms.

Results from this literature review highlight that most data available on benthic substrates are from studies focusing on *Ostreopsis* spp. attached to biotic substrates and in particular, macroalgae. Interestingly, independently of the macrohabitat sampled, most of the studies in both temperate and tropical areas chose macroalgae (mainly visually obvious macroalgae species) as substrate. Even in studies conducted in coral reefs (where macroalgae are usually not dominant), macroalgae, rather than living corals or dead coral fragments, are selected as sampled substrate, meaning that i) macroalgae could be very abundant in this particular site and/or ii) scientists believe there are larger abundances of *Ostreopsis* spp. on macroalgae rather than on other substrates. However, choosing macroalgae over corals as substrate to be sampled could be for ethical reasons (coral species may be protected under international or national environmental law) or other practicalities of the sampling. Concerning the different species, Park et al. (2020) report higher *Ostreopsis* spp. abundances on red (*Spyridia filamentosa* and *Laurencia* complex) and brown macroalgae (i.e. *Dictyota spp., Halopteris scoparia, Dictyopteris polypodioides and Carpophyllum plumosum*) that are also the most sampled macroalgal groups while lower densities are reported in Chlorophyta, and in particular *Ulva* spp. Conversely, some of these results contrast with the results from studies on the effect of metabolites from macroalgae on the growth and settlement of *Ostreopsis cf. ovata* (Accoroni et al., 2015; Ternon et al., 2020) that suggest a strong negative effect of some Dictyotales on *O.* cf. *ovata*. However, Pavaux et al. (2020) and Ternon et al. (2020) suggest that macroalgae surface chemistry may be not enough to explain *Ostreopsis* spp. settlement preferences and that other factors such as other organisms of the epiphytic community (bacteria, viruses, parasites, microalgae, and fauna) and the whole surrounding community are likely to modulate the growth of *Ostreopsis* spp.

With respect to the mesohabitat, the information in the literature is scarce. The most sampled macroalgae are species forming medium to low complexity communities, such as shrubs formed by *Padina spp., Dictyota* spp*., Halopteris* spp*.* (Cabrini et al., 2010; Widiarti and Anggraini, 2012; Cohu et al., 2013; Blanfune et al., 2015; Boisnoir et al., 2019) and turfs formed by *Corallina* spp*., Jania* spp*., Laurencia* spp*., Hypnea* spp*.* (Simoni et al., 2004; Monti et al., 2007 ; Totti et al., 2010 ; Kim et al., 2011 ; Abbate et al., 2012; Ismael and Halim, 2012 ; Blanfuné et al., 2015; Yong et al., 2018). The sampling is often performed on the most abundant or predominant macroalgal species (e. g. Accoroni et al., 2011, 2020; Mangialajo et al., 2008a, 2011; Cohu and Lemee, 2012; Rhodes et al., 2017; Jauzein et al., 2018; Boisnoir et al., 2019; Chinain et al., 2020; Gémin et al., 2020) and it can therefore be deduced that the representative mesohabitats in the sites where scientists study *Ostreopsis* spp. blooms are potentially characterized by algal shrubs and turfs. This is in agreement with the results of the few ecological studies considering the mesohabitat scale, where larger *Ostreopsis* spp. densities are found on low-complexity macroalgal communities (shrubs or turfs) characteristic of post-regime shift scenarios in highly impacted locations (Mangialajo et al., 2008a; Meroni et al., 2018; Bravo et al., 2020; Lee et al., 2020). This is particularly true in temperate areas, where macroalgal communities dominate rocky reefs, and suggest that lower abundances of *Ostreopsis* spp. could be found on large brown algae forests of fucoids and kelps (e.g*. Cystoseira sensu lato* spp., *Sargassum* spp., etc; Mangialajo et al., 2008b; Catania, 2017; Meroni et al., 2018). Nevertheless, blooms are observed on *Ericaria crinita* in the Adriatic Sea (Pfannkuchen et al., 2012) and on *Carpophyllum plumosum* populations in New Zealand (Shears and Ross, 2009). In tropical areas important blooms of *Ostreopsis* spp. can be observed on forest-forming macroalgal species (*Sargassum* spp., Chinain et al., 2020), where regime shifts from coral to algae (often with a dominance of large size species; Payri and Naïm, 1982; Stiger and Payri, 1999) and subsequent coral reef degradation, are usually associated to human impacts (Stiger and Payri, 1999). But such results, based on the maximum *Ostreopsis* spp. abundances occurring at a study site have to be considered with care, because of the potential bias linked to the classic sampling method, that quantify cells/gram of macroalga, providing an estimate that is species dependent (i.e. specific weight, Mangialajo et al. 2017).

5 Conclusions

The present review reveals that most studies do not provide detailed descriptions of the mesohabitats (or benthic communities) where the studied blooms occur and how the mesohabitat could play a role on *Ostreopsis* spp. bloom dynamics. Benthic dinoflagellate preferences at different habitat scales (substrate, community, and ecosystem) and biotic interactions present untapped fields of research with great potential which still need to be addressed in the future.

Our results seem to predict a larger risk exposure to toxic effects for humans in post-regime shifts communities such as urban or degraded areas, where marine forests of large brown algae and/or reef building corals are often lost and replaced by less complex species that could host large densities of *Ostreopsis* spp. (Hughes, 1994 ; Benedetti-Cecchi et al., 2001; Mangialajo et al., 2008a ; Catania, 2017; Filbee-Dexter and Wernberg, 2018; Johns et al., 2018; Meroni et al., 2018). Understanding the underlying mechanisms on how the habitat can affect *Ostreopsis* spp. blooms, would allow a better risk assessment of the phenomenon, identifying areas at risk simply on the base of the benthic habitats.

These findings underline the need of a better understanding of *Ostreopsis* spp. ecology to prevent socio-economic damage, reduce human health risks in coastal regions, and reduce ecological impacts to marine coastal ecosystems.

Conflict of interest

The Authors declare that there is no conflict of interest.

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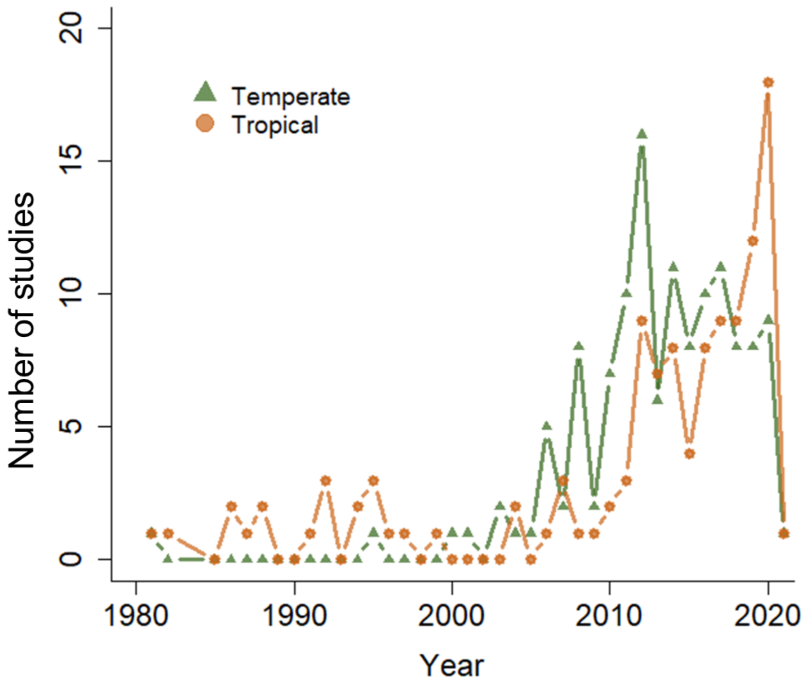

Figure 1: Trend of the number of peer-reviewed studies involving field sampling of *Ostreopsis* spp. from 1981 to 2021.

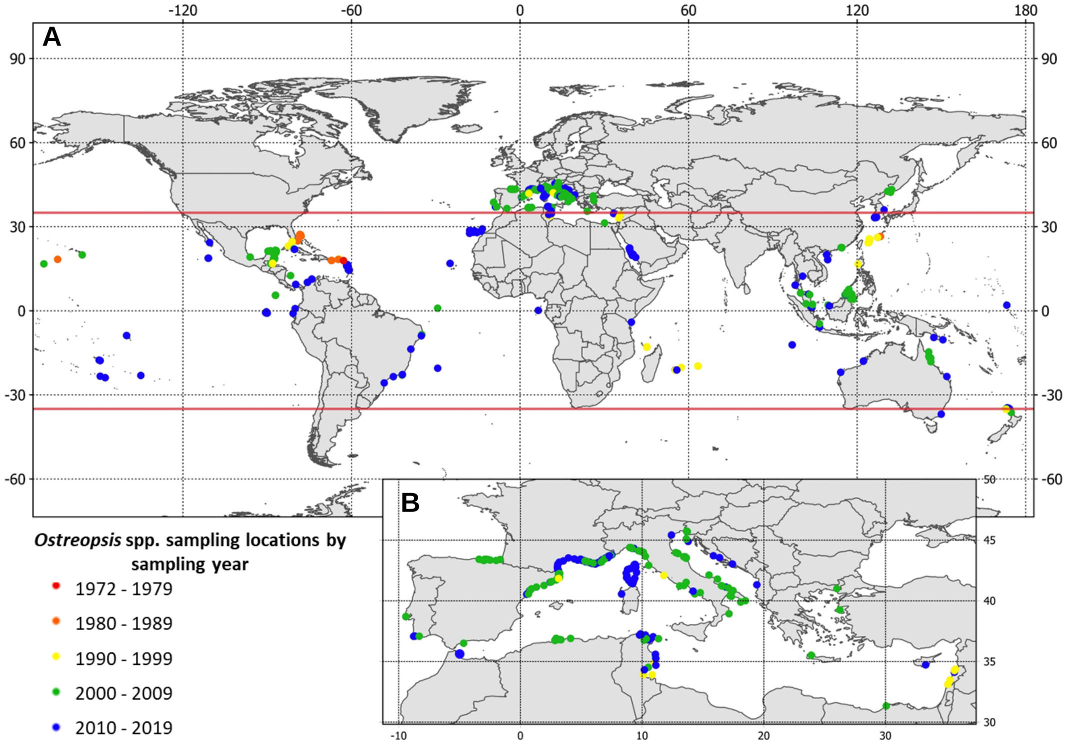

Figure 2: Map of the sampling locations. The colour corresponds to the year it was first sampled. The two red lines (35°N and 35°S) separate the tropical/subtropical from the temperate areas; a) global distribution; b) detailed map for the Mediterranean Sea.

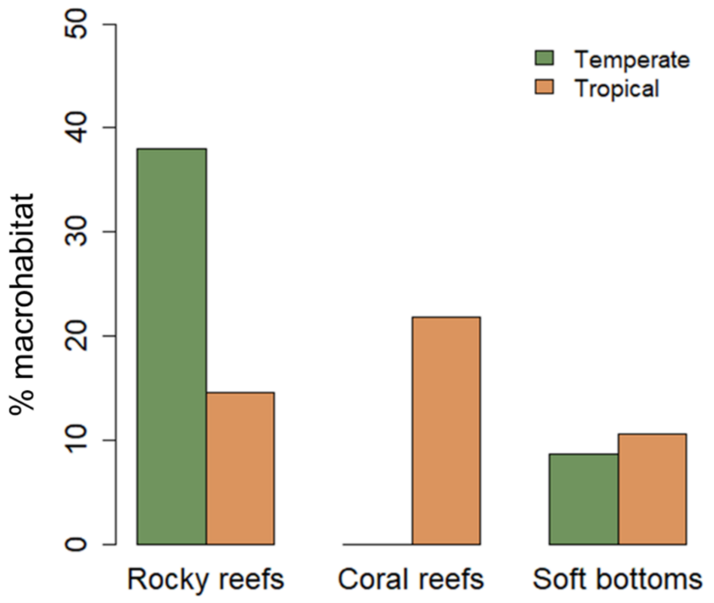

Figure 3: Macrohabitats where *Ostreopsis* spp. have been sampled in temperate and tropical areas.

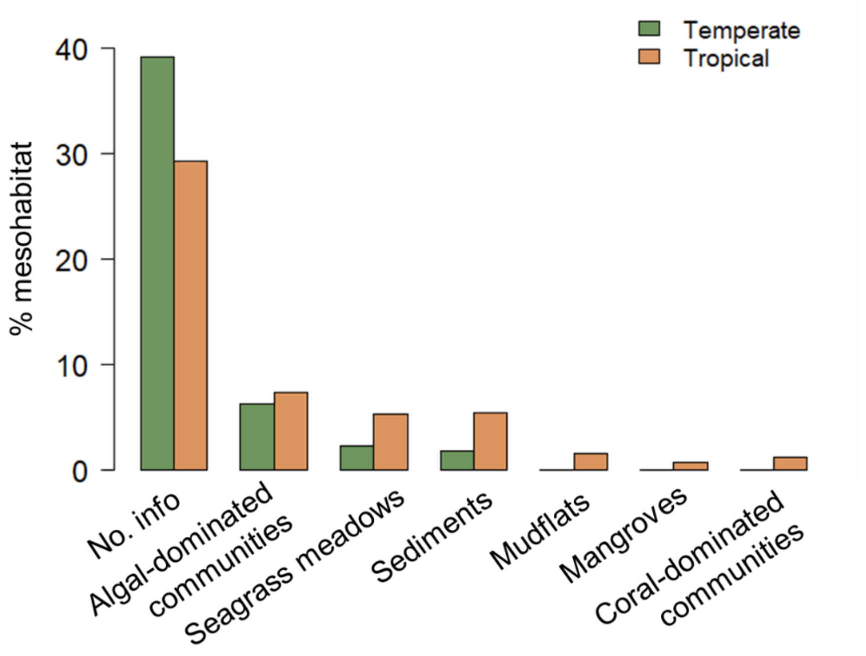

Figure 4: Mesohabitats where *Ostreopsis* spp. have been sampled in tropical and temperate areas.

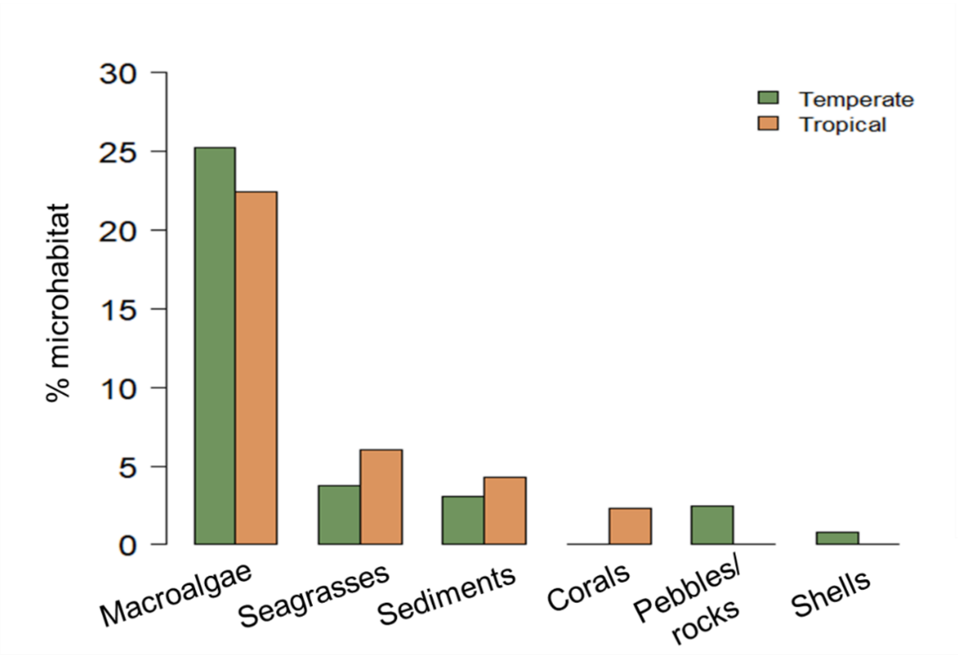

Figure 5: Microhabitats (substrates) where *Ostreopsis* spp. have been sampled in temperate and tropical areas.

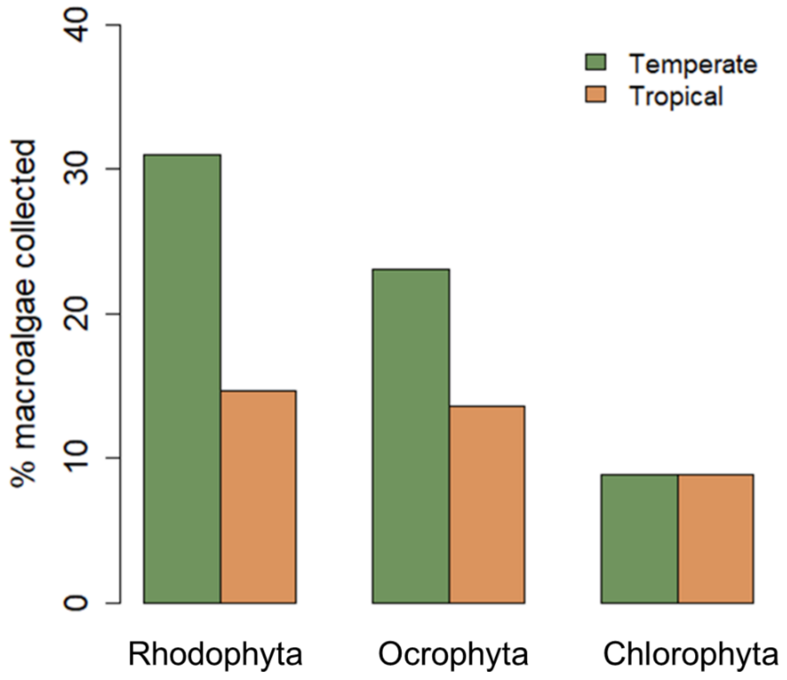

Figure 6: Macroalgae sampled in function of the phylum.

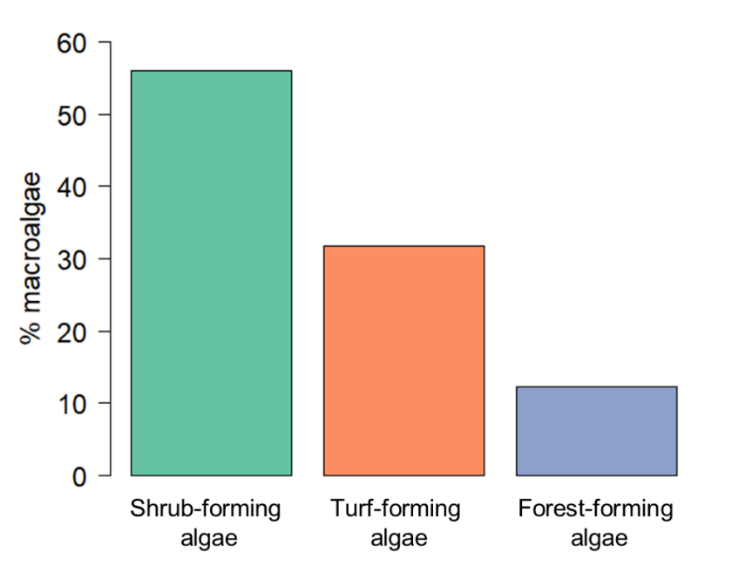

Figure 7: Macroalgae sampled in function of the type of community they can form.

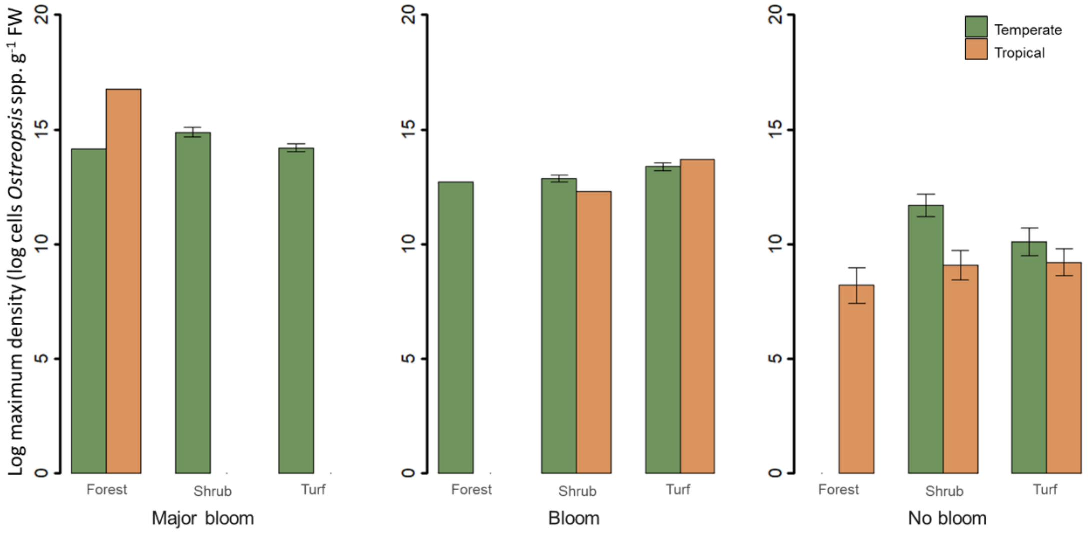

Figure 8: Maximum cell densities of *Ostreopsis* spp. (cells g^{-1} FW macroalgae) for each study grouped according to the morphological structure of the macroalgae sampled and the intensity of the bloom.

Table 1: Maximum cell densities of *Ostreopsis* spp. (cells g^{-1} FW macrophyte) for each study on different microhabitats.

Macrophyte	**Maximum density** (cells *Ostreopsis* spp. g^{-1} FW)	**Turf, shrub or forest-forming**	**Country**	**Tropical/temperate**	**Reference**
Rhodophyta					
Acanthophora spicifera	1500	Turf	Belize	Tropical	Faust (2009)
Acanthophora spicifera	1500	Turf	Belize	Tropical	Morton and Faust (1997)
Asparagopsis taxiformis	230000	Shrub	Italy	Temperate	Carella et al. (2015)
Asparagopsis taxiformis	236276	Shrub	France	Temperate	Bire (2015)
Corallina sp.	79000	Turf	Algeria	Temperate	Illoul et al. (2012)
Hypnea musciformis	1700000	Turf	Italy	Temperate	Totti et al. (2010)
Ellisolandia elongata	760000	Turf	Spain	Temperate	Casabianca et al. (2013)
Ellisolandia elongata	28000	Turf	Lebanon	Tropical	Accoroni et al. (2016)
Ellisolandia elongata or Jania rubens	1000000	Turf	Spain	Temperate	Vila et al. (2016)
Ellisolandia elongata or Jania rubens	1480000	Turf	Spain	Temperate	Carnicer et al. (2015)
Ellisolandia elongata	880694	Turf	Lebanon	Tropical	Açaf et al. (2020)
Galaxaura elongata	186	Shrub	Philippines	Tropical	Pocsidio and Dimaano (2004)
Galaxaura sp.	10000	Shrub	Mascarene Islands	Tropical	Quod (1994)
Jania rubens	11000	Turf	France	Temperate	Cohu and Lemee (2012)
Laurencia complex	1040000	Turf	Monaco	Temperate	Fricke et al. (2018)

Laurencia sp.	99000	Turf	Brazil	Tropical	Nascimento et al. (2012)
Pterocladiella capillacea	18194	Turf	Hawaii Island (USA)	Tropical	Parsons and Preskitt (2007)
Pterocladiella capillacea	545000	Turf	Italy	Temperate	Ciminiello et al. (2014)
Spyridia filamentosa	2640000	Turf	Croatia	Temperate	Gladan et al. (2019)
Ochrophyta					
Carpophyllum maschalocarpum	1095	Forest	New Zealand	Tropical	Chang et al. (2000)
Carpophyllum plumosum	1406000	Forest	New Zealand	Temperate	Shears and Ross (2009)
Dictyopteris polypodioides	1300000	Shrub	Italy	Temperate	Accoroni et al. (2012)
Dictyopteris sp.	33405	Shrub	Galapagos (Ecuador)	Tropical	Carnicer et al. (2020)
Dictyota dichotoma	330000	Shrub	Italy	Temperate	Cabrini et al. (2010)
Dictyota sp	79000	Shrub	Cuba	Tropical	Moreira et al. (2012)
Dictyota sp.	57000	Shrub	Virgin Islands	Tropical	Kohler and Kohler (1992)
Dictyota sp.	53231	Shrub	Mexico	Tropical	Irola-Sansores et al. (2018)
Dictyota sp.	44000	Shrub	Puerto Rico	Tropical	Ballantine, Tosteson and Bardales (1988)
Dictyota sp.	220079	Shrub	Cape Verde	Tropical	Fernandez-Zabala et al. (2019)
Dictyota spp.	8540000	Shrub	France	Temperate	Cohu, Mangialajo, Thibaut, Blanfune et al. (2013)
Dictyota spp.	24939	Shrub	Guadeloupe (France)	Tropical	Boisnoir et al. (2019)

Dictyota spp.	830000	Shrub	France	Temperate	Gémin et al. (2020)
Ericaria crinita	334306	Forest	Croatia	Temperate	Pfannkuchen et al. (2012)
Halopteris scoparia	658448	Shrub	Italy	Temperate	Guidi-Guilvard et al., (2012)
Halopteris scoparia	311552	Shrub	France	Temperate	Blanfune et al. (2012)
Halopteris scoparia	330000	Shrub	France	Temperate	Bire et al. (2013)
Halopteris scoparia	2289000	Shrub	Italy	Temperate	Jauzein et al. (2018)
Halopteris scoparia	2890528	Shrub	Italy	Temperate	Meroni et al. (2018)
Halopteris scoparia	2289100	Shrub	Italy	Temperate	Giussani et al. (2017)
Halopteris scoparia	195152	Shrub	France	Temperate	Blanfune et al. (2015)
Halopteris scoparia	2900000	Shrub	Italy	Temperate	Vassalli et al. (2018)
Halopteris scoparia	3700000	Shrub	France	Temperate	Brissard et al. (2014)
Halopteris scoparia	596000	Shrub	Spain	Temperate	Vila et al., (2001)
Halopteris sp.	359900	Shrub	France	Temperate	Mangialajo et al. (2017)
Padina pavonica	1900	Shrub	Egypt	Tropical	Ismael and Halim (2012)
Sargassum sp.	2860	Forest	Indonesia	Tropical	Skinner et al. (2011)
Sargassum sp.	15000	Forest	Saint Martin Island, Lesser Antilles	Tropical	Boisnoir et al. (2020)
Sargassum sp.	19000000	Forest	French Polynesia	Tropical	Chinain et al. (2020)
Turbinaria decurrens	143	Shrub	Saudi Arabia	Tropical	Catania et al. (2017)
Chlorophyta					

Cladophora sp.	16000	Turf	Italy	Temperate	Battocchi, Totti, Vila, Maso, et al. (2010)
Cladophora wrightiana	102	Turf	Korea	Tropical	Shah, An and Lee (2013)
Derbesia sp.	8660	Turf	Korea	Tropical	Kim et al. (2011)
Halimeda sp.	596	Shrub	Kiribati	Tropical	Xu et al. (2014)
Ulva rigida	74000	Shrub	Italy	Temperate	Perini et al. (2011)
Seagrasses					
Cymodocea nodosa	1940		Tunisia	Tropical	Ben Gharbia et al. (2019)
Halophila stipulacea	1669		Guadeloupe (France)	Tropical	Boisnoir et al. (2018)
Posidonia oceanica	360000		Tunisia	Tropical	Turki (2005)
Posidonia oceanica	2000		Tunisia	Tropical	Moncer et al. (2017)
Thalassia testudinum	3318		Colombia	Tropical	Arbelaez, Pineda and Reguera (2017)