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

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12

13 **Abstract**

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

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

40 **1 Introduction**

41 Over the past decades, coastal areas throughout the world experienced an accelerating
42 trend of Harmful Algal Blooms (HABs) events (Anderson et al., 2019) including the ones
43 due to benthic species (Parsons et al., 2012). A significant proportion of studies
44 concerning benthic HABs is focused on tropical benthic dinoflagellate ecology, mostly
45 because of the incidence of ciguatera fish poisoning (CFP) in tropical and subtropical
46 areas (Litaker et al., 2009) and the geographic expansion of some toxic species in
47 temperate waters (Rhodes, 2011). Among them, recurrent *Ostreopsis* spp. blooms have
48 been recorded throughout the globe: in the Mediterranean Sea (Vila et al., 2001; Penna
49 et al., 2005; Turki, 2005; Aligizaki and Nikolaidis, 2006; Mangialajo et al., 2008a; Totti et
50 al., 2010; Cohu et al., 2011; Ismael and Halim, 2012; Manca et al., 2015; Açaf et al.,
51 2020; Gémin et al., 2020), the East Atlantic Ocean (Solino et al., 2020), the West Atlantic
52 Ocean (Nascimento et al., 2012; Tibirica et al., 2019), the South-West Pacific (Chang et
53 al., 2000; Rhodes et al., 2000; Shears and Ross, 2009), the North-West Pacific
54 (Yamaguchi et al., 2012; Zou et al., 2020), the South-West Indian Ocean (Lenoir et al.,
55 2004) and the Red Sea (Gomaa et al., 2018). At least five out of the eleven identified
56 species (Fukuyo, 1981; Norris et al., 1985; Quod, 1994; Faust and Morton, 1995; Faust,
57 1999) produce palytoxin-like compounds, one of the most toxic marine compounds
58 (Usami et al., 1995; Ukena et al., 2001; Ciminiello et al., 2010; Suzuki et al., 2012; Varela
59 et al., 2021), causing respiratory disease after inhalation of marine aerosols (Tichadou
60 et al., 2010; Tubaro et al., 2011; Vila et al., 2016). The whole ecosystem is affected by
61 *Ostreopsis* spp. blooms (Turner et al., 2021), due to mass mortalities of invertebrates
62 such as bivalves, gastropods, crustaceans, and echinoderms (Shears and Ross, 2009;
63 Ramos and Vasconcelos, 2010; Guidi-Guilvard et al., 2012; Parsons et al., 2012;
64 Accoroni and Totti, 2016; Migliaccio et al., 2016; Neves et al., 2018). In order to
65 effectively manage and mitigate *Ostreopsis* spp. blooms, a thorough understanding of

66 the bloom dynamics of these species is needed. Samplings have been worldwide
67 restricted mostly to shallow waters as it has been demonstrated in both tropical and
68 temperate areas that *Ostreopsis* spp. cell abundances are negatively correlated with
69 depth_(Richlen and Lobel, 2011; Cochu and Lemee, 2012). The mechanisms that affect
70 *Ostreopsis* spp. populations are unclear, but most studies relate larger abundances of
71 *Ostreopsis* spp. to sheltered zones or in low hydrodynamic conditions (Di Turi et al.,
72 2003; Chiantore et al., 2008; Shears and Ross, 2009; Battocchi et al., 2010; Cabrini et
73 al., 2010; Richlen and Lobel, 2011; Accoroni and Totti, 2016; Mohammad-Noor et al.,
74 2016; Boisnoir et al., 2018; Hachani et al., 2018; Meroni et al., 2018), while others
75 suggest larger abundances of *Ostreopsis* spp. in higher or slightly higher levels of water
76 motion (Vila et al., 2001; Selina et al., 2014). The inshore occurrence of *Ostreopsis* spp.
77 has also raised the question concerning their association with nutrient enrichments due
78 to human activities (Faust et al., 1996), but there are mixed conclusions on how nutrient
79 concentrations influence population dynamics of *Ostreopsis* spp. (Ungaro et al., 2010;
80 Cochu et al., 2011; Accoroni et al., 2012; Asnaghi et al., 2012). A concise summary of the
81 effects of surface seawater temperature, salinity and nutrient concentrations on
82 *Ostreopsis* spp. populations in temperate areas can be found in Accoroni and Totti's
83 (2016) and Tester's et al. (2020) reviews. Results from the above-mentioned studies are
84 sometimes contradictory, likely due to the fact that *Ostreopsis* spp. blooms are a global
85 phenomenon controlled by several factors in very different contexts and, as a
86 consequence, blooms are very variable in space and time, making difficult defining
87 general trends (Mangialajo et al., 2011).

88 Due to their benthic nature, *Ostreopsis* spp. develop in close relation with a substrate.
89 *Ostreopsis* spp. are often described as epiphytic on macroalgae and seagrasses
90 (Rhodes, 2011), but can also be found on dead corals, sediments, rocks, and in the water
91 column (Bomber et al., 1989; Vila et al., 2001; Shears and Ross, 2009, 2010; Totti et al.,
92 2010). However, the substrate preferences of *Ostreopsis* spp. are still ambiguous (Vila

93 et al., 2001; Cohu et al., 2013; Sparrow et al., 2017; Ternon et al., 2020; Tester et al.,
94 2020), although some studies reported larger abundances on some substrates
95 compared to others (Vila et al., 2001, 2012; Mohammad-Noor et al., 2007; Widiarti, 2008;
96 Cabrini et al., 2010; Totti et al., 2010; Accoroni et al., 2011, 2012; Mangialajo et al., 2011;
97 Accoroni and Totti, 2016; Yong et al., 2018; Boisnoir et al., 2019; Bravo et al., 2020; Lee
98 et al., 2020). Such comparisons are tricky because of the limits of cell quantification in
99 function of the type of substrate (i.e. surface for rocks, fresh weight for macrophytes),
100 but also because the measures depend often on some characteristics of the substrate
101 (i.e. the specific weight of sampled species). As an example, some macroalgae species
102 seem to host larger abundance of *Ostreopsis* spp. than most other species, e.g. *Corallina*
103 spp. (Simoni et al., 2004; Aligizaki and Nikolaidis, 2006; Monti et al., 2007; Chiantore et
104 al., 2008) and *Padina* spp. (Aligizaki and Nikolaidis, 2006; Cabrini et al., 2010; Hachani
105 et al., 2018 ; Gémin et al., 2020). Nonetheless, other species provide discordant patterns
106 such as: *Ulva* spp. (Aligizaki and Nikolaidis, 2006; Monti et al., 2007; Okolodkov et al.,
107 2007; Totti et al., 2010 ; Ismael and Halim, 2012), *Dictyota* spp. (Cohu et al., 2013 ;
108 Blanfune et al., 2015; González et al., 2019; Gémin et al., 2020 ; Ternon et al., 2020),
109 and *Cystoseira sensu lato* spp. (Aligizaki and Nikolaidis, 2006; Monti et al., 2007;
110 Aligizaki and Nikolaidis, 2008; Blanfune et al., 2015; Catania, 2017; Moncer et al., 2017;
111 Meroni et al., 2018). *Ostreopsis* abundances on different substrates are highly variable
112 and, despite the technical issues linked to the measurement cited above, several biotic
113 factors acting at different spatial scales can be responsible for such variability:
114 morphology and palatability of macrophytes, herbivory and allelopathic interactions due
115 to the production of secondary metabolites by living substrates, among others (Cruz-
116 Rivera and Villareal, 2006; Totti et al., 2010; Accoroni et al., 2015; 2016; Ternon et al.,
117 2020).

118 Benthic ecosystems are dynamic systems and, especially due to human impacts, can
119 experience regime shifts, resulting in profound changes in the structure and composition

120 of communities (Hughes, 1994; Benedetti-Cecchi et al., 2001; Chemello et al., 2018;
121 Filbee-Dexter and Wernberg, 2018; Johns et al., 2018; Melis et al., 2019; Pessarrodona
122 et al., 2021). In both temperate and tropical reefs, regime shifts cause a change from
123 healthy communities dominated by foundation species to communities dominated by
124 less structurally complex species (Filbee-Dexter and Scheibling, 2014; Jouffray et al.,
125 2015; Wernberg et al., 2016; O'Brien and Scheibling, 2018; Pessarrodona et al., 2021).
126 In temperate areas canopy-forming algae are lost and replaced by less complex algae-
127 dominated communities (Strain et al., 2014; Vergés et al., 2014; Bulleri et al., 2016);
128 several studies relate major densities of *Ostreopsis* spp. on algal turfs (Bravo et al., 2020)
129 and in particular on highly urbanised coasts that are usually characterized by post-regime
130 shift algal communities (Mangialajo et al., 2008a; Widiarti et al., 2008; Cohu et al., 2013),
131 compared to healthier habitats dominated by forest-forming brown algae (Meroni et al.,
132 2018). In tropical areas, ciguatera fish poisoning episodes recurrently follow
133 disturbances to coral reefs by natural and artificial events such as heat waves,
134 hurricanes, dredging, and shipwrecks, among others, where regime shifts from coral to
135 algae are observed (de Sylva, 1994; Jouffray et al., 2015; Rains and Parsons, 2015;
136 Johns et al., 2018). In this case, higher benthic dinoflagellate abundances are recorded,
137 both on turf-forming (Yong et al., 2018; Lee et al., 2020) and forest-forming species, such
138 as *Sargassum* spp., Chinain et al., 2020).

139 To our best knowledge, only few studies assessed the variability of *Ostreopsis* spp. at a
140 level higher than the substrate (Cohu et al., 2013; Meroni et al., 2018; Yong et al., 2018;
141 Bravo et al., 2020; Lee et al., 2020) with the aim of comparing different habitats to help
142 understanding *Ostreopsis* spp. variability. To ascertain how the habitat positively or
143 negatively affects *Ostreopsis* spp. blooms, a literature review was conducted in order to
144 describe trends at different spatial scales. In this review we define: 1) the microhabitat
145 (substrate, spatial scale of cm²), as the biotic or abiotic object sampled to quantify/collect
146 *Ostreopsis* spp. cells (including living or dead organisms and abiotic substrates), 2) the

147 mesohabitat, as the community or the abiotic material patch where the substrate is
148 sampled (spatial scale of few to a dozen of m², e.g. the macroalgal turf where a certain
149 macroalgal species is sampled as a substrate or the sandy bottom where a pebble is
150 sampled as a substrate; Meroni et al., 2018; Bravo et al., 2020; Lee et al., 2020), and 3)
151 the macrohabitat, as the ecosystem or the seascape (spatial scales of
152 hundreds/thousands of m²) where the mesohabitat is found (i.e. coral reefs, macroalgal-
153 dominated rocky shores; Yong et al., 2018).

154 **2 Materials and methods**

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

162 To quantify and compare the relationship between *Ostreopsis* spp. and the micro- meso
163 and macrohabitats, only articles involving field collection of *Ostreopsis* spp. were
164 included in this review. The key information extracted from each article included, when
165 available: microhabitat (e.g. sampled substrates such as macrophytes, rocks, shells,
166 artificial substrates, others), mesohabitat (community/abiotic patch type), macrohabitat
167 (ecosystem/seascape), ocean and sea of study, country, temperate or tropical area
168 (tropical areas were defined as areas between -35° and 35°, including both tropical and
169 subtropical climate), geographic coordinates (if not available, they were obtained from
170 Google Earth, whenever possible) of the sampling location where *Ostreopsis* spp. were
171 sampled, maximum recorded abundance in the study and sampling dates. The maximum

172 abundances of *Ostreopsis* spp. recorded in the studies were classified in three
173 categories: No bloom (<200x10³ cells per gram fresh weight (FW) of macrophyte),
174 Bloom (>200x10³ cells per gram FW of macrophyte) and Major bloom (>1000x10³ cells
175 per gram FW of macrophyte) as in Mangialajo et al. (2017). Several studies (132) were
176 conducted in two or more separate regions around the globe, seas, countries, locations
177 and/or involving different substrates. In this case, a different line was inserted in the table
178 for each different score, therefore it is possible that one article was accounted more than
179 once. All the graphs have been produced using R Project version 3.6.2.

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

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

198 - Forest-forming algae: cylindrical axes, branched and tree like characterised by a
199 complex tri-dimensional structure, generating a canopy. Algae having a large size
200 compared to other algae growing in the same region. This term is generally used
201 for Laminariales, Fucales and some Tilopteridales (Sala et al., 2012; Strain et al.,
202 2014; Thiriet et al., 2014, 2016; Bertolini, 2019; Shelamoff et al., 2019; Assis et
203 al., 2020).

204 **3 Results**

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

211 The number of studies per year reveals a positive trend of ecological studies involving
212 sample collection in the field (Figure 1) in both temperate and tropical areas. The first
213 studies involving field sampling were performed in the tropics, but, since year 2000,
214 studies performed in temperate areas have exceeded in number the tropical ones. Since
215 2018 tropical studies are again more numerous than in temperate areas, but this trend
216 has to be verified in the next years. Nearly half of the 957 different locations investigated
217 between 1972 and 2019 are in temperate areas (471), the other half (486) in tropical
218 ones. The exact geographical coordinates were available for 595 (62.2%) sampling
219 locations and it was possible to position 132 (13.8%) additional ones on the basis of the
220 description of the location in the text. A distribution map of the 727 locations, out of the
221 957 sampled in the 249 relevant studies, is reported in Figure 2.

222 3.1 Spatial scales

223 3.1.1 Macrohabitat

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

231 3.1.2 Mesohabitat

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

238

239 3.1.3 Microhabitat

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

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

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

250 Artificial substrates, that allow an easier standardisation of *Ostreopsis* spp. abundances
251 (i. e. Yong et al., 2018; Jauzein et al., 2018; Fernandez-Zabala et al., 2019; Lee et al.,
252 2020); were used in 24 out of the 249 studies (3.6% in temperate areas and 6% in
253 tropical), and in 136 out of the 1644 sampled substrates (2.3% in temperate areas and
254 a 6% in tropical). Seawater is also commonly sampled and, in some countries, thresholds
255 alerts are based on cell concentrations in seawater at dozen of centimetres above the
256 sea bottom (Funari et al., 2015). Water was sampled in 100 out of the 249 studies (32.5%
257 in temperate and 7.6% in tropical areas) and represent 332 out of the 1644 sampled
258 substrates (15.7% in temperate and 4.5% in tropical areas).

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

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

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

292 Of the 249 studies, 82 (32.9%) reported abundances of *Ostreopsis* spp. cells per gram
293 FW of macrophyte. Such quantification is dependent on the specific weight and
294 morphology of the different species (Mangialajo et al., 2017) and would not, ideally, allow
295 a direct comparison of abundances on different macroalgal species. At present, the few
296 alternative methods allowing a standardised quantification (Tester et al., 2014; Jauzein
297 et al., 2016; Mangialajo et al., 2017) are only sporadically applied and large-scale
298 comparisons are performed on the measures of cells per gram FW. In order to have a
299 global vision of the *Ostreopsis* spp. abundances, the maximal abundance reported on

300 each study indicating the host macrophyte has been reported, when available, in Table
301 1 (expressed as cells/g of macroalga FW). From the data reported on Table 1, the
302 maximum cell densities of *Ostreopsis* spp. (cells g⁻¹ FW macroalgae) are grouped
303 according to the type of mesohabitat the macroalgae sampled can form and the intensity
304 of the bloom (Mangialajo et al., 2017; N= 54; Figure 8). In the case of Bloom and No
305 bloom scenarios (according to Mangialajo et al., 2017), the abundance of *Ostreopsis*
306 spp. cells seems to be higher on shrub and turf-forming species. For the Major bloom
307 scenario (see classification in Mangialajo et al., 2017), the abundance of *Ostreopsis* spp.
308 seems to be higher on shrub- forming species in temperate areas (followed by high
309 values in forest forming) and on forest-forming species in tropical areas.

310 **4 Discussion**

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

327 Benthic dinoflagellate development is affected by interacting biotic and abiotic factors
328 linked to the habitat and acting at different scales (i.e. substrate, benthic community and
329 seascape). Interestingly the present study highlighted that the sampled substrate (herein
330 the microhabitat, e.g. coral fragment, macroalgal species) and the ecosystem (herein the
331 macrohabitat, e.g. coral reefs, macroalgal-dominated rocky shores, sandy or muddy
332 bottoms) where *Ostreopsis* spp. are sampled are generally reported and described. In
333 98% and 79% of the studies the sampled substrate and the seascape are respectively
334 described or, alternatively, the text allows undoubtful extrapolation of this information.
335 Concerning the microhabitat, and in particular organic substrates, most studies detail the
336 species (56.8%), or at least the genus (20.1%) of the organisms sampled. Yet, even if
337 the coral fragment or shell is identified at the species level, it is not clearly reported if 1)
338 it is a living organism and 2) it is the direct *Ostreopsis* spp. host. Some studies (Widiarti,
339 2008; Yong et al., 2018) suggested that small filamentous macroalgae developing on
340 dead or damaged coral surfaces could foster *Ostreopsis* spp. development, showing the
341 role of macroalgae as a favourable substrate. The same considerations could be valid
342 for shells, pebbles, and stones, but there is no specific literature on these particular cases
343 to our knowledge. On the contrary, the description of the mesohabitat (e.g. macroalgal
344 turfs, macroalgal forests, coral-dominated communities, seagrasses, or sandy patches)
345 is rarely reported (35% of the considered studies). As highlighted in Pavaux et al. (2020)
346 it is undeniable that only a small part of the research on *Ostreopsis* spp. is focused on
347 ecological aspects. Interestingly, recent studies, mainly focused on tropical species
348 related to ciguatera, suggest that habitat heterogeneity and complexity affect benthic
349 dinoflagellate communities (Rains and Parsons, 2015; Meroni et al., 2018; Yong et al.,
350 2018; Boisnoir et al., 2019; Bravo et al., 2020; Lee et al., 2020). In particular Yong et al.
351 (2018) found higher *Gambierdiscus*, *Prorocentrum* and *Amphidinium* cell abundances
352 on reefs with high turf algal cover and coral rubble, while *Ostreopsis* preferred
353 mesohabitats with high coral cover. Lee et al. (2020) found that the mesohabitat
354 influence the distribution of benthic harmful algal blooms and that *Ostreopsis* and

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

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

383 spp. settlement preferences and that other factors such as other organisms of the
384 epiphytic community (bacteria, viruses, parasites, microalgae, and fauna) and the whole
385 surrounding community are likely to modulate the growth of *Ostreopsis* spp.

386 With respect to the mesohabitat, the information in the literature is scarce. The most
387 sampled macroalgae are species forming medium to low complexity communities, such
388 as shrubs formed by *Padina* spp., *Dictyota* spp., *Halopteris* spp. (Cabrini et al., 2010;
389 Widiarti and Anggraini, 2012; Cohu et al., 2013; Blanfune et al., 2015; Boisnoir et al.,
390 2019) and turfs formed by *Corallina* spp., *Jania* spp., *Laurencia* spp., *Hypnea* spp.
391 (Simoni et al., 2004; Monti et al., 2007 ; Totti et al., 2010 ; Kim et al., 2011 ; Abbate et
392 al., 2012; Ismael and Halim, 2012 ; Blanfuné et al., 2015; Yong et al., 2018). The
393 sampling is often performed on the most abundant or predominant macroalgal species
394 (e. g. Accoroni et al., 2011, 2020; Mangialajo et al., 2008a, 2011; Cohu and Lemee,
395 2012; Rhodes et al., 2017; Jauzein et al., 2018; Boisnoir et al., 2019; Chinain et al., 2020;
396 Gémin et al., 2020) and it can therefore be deduced that the representative mesohabitats
397 in the sites where scientists study *Ostreopsis* spp. blooms are potentially characterized
398 by algal shrubs and turfs. This is in agreement with the results of the few ecological
399 studies considering the mesohabitat scale, where larger *Ostreopsis* spp. densities are
400 found on low-complexity macroalgal communities (shrubs or turfs) characteristic of post-
401 regime shift scenarios in highly impacted locations (Mangialajo et al., 2008a; Meroni et
402 al., 2018; Bravo et al., 2020; Lee et al., 2020). This is particularly true in temperate areas,
403 where macroalgal communities dominate rocky reefs, and suggest that lower
404 abundances of *Ostreopsis* spp. could be found on large brown algae forests of fucoids
405 and kelps (e.g. *Cystoseira sensu lato* spp., *Sargassum* spp., etc; Mangialajo et al.,
406 2008b; Catania, 2017; Meroni et al., 2018). Nevertheless, blooms are observed on
407 *Ericaria crinita* in the Adriatic Sea (Pfannkuchen et al., 2012) and on *Carpophyllum*
408 *plumosum* populations in New Zealand (Shears and Ross, 2009). In tropical areas
409 important blooms of *Ostreopsis* spp. can be observed on forest-forming macroalgal

410 species (*Sargassum* spp., Chinain et al., 2020), where regime shifts from coral to algae
411 (often with a dominance of large size species; Payri and Naïm, 1982; Stiger and Payri,
412 1999) and subsequent coral reef degradation, are usually associated to human impacts
413 (Stiger and Payri, 1999). But such results, based on the maximum *Ostreopsis* spp.
414 abundances occurring at a study site have to be considered with care, because of the
415 potential bias linked to the classic sampling method, that quantify cells/gram of
416 macroalga, providing an estimate that is species dependent (i.e. specific weight,
417 Mangialajo et al. 2017).

418

419 **5 Conclusions**

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

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

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

438

439 **Conflict of interest**

440 The Authors declare that there is no conflict of interest.

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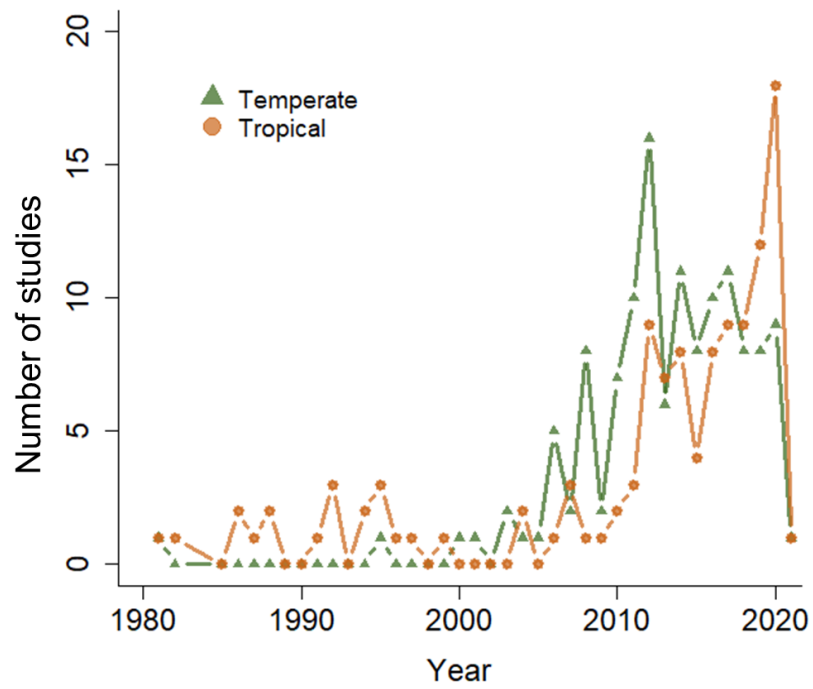
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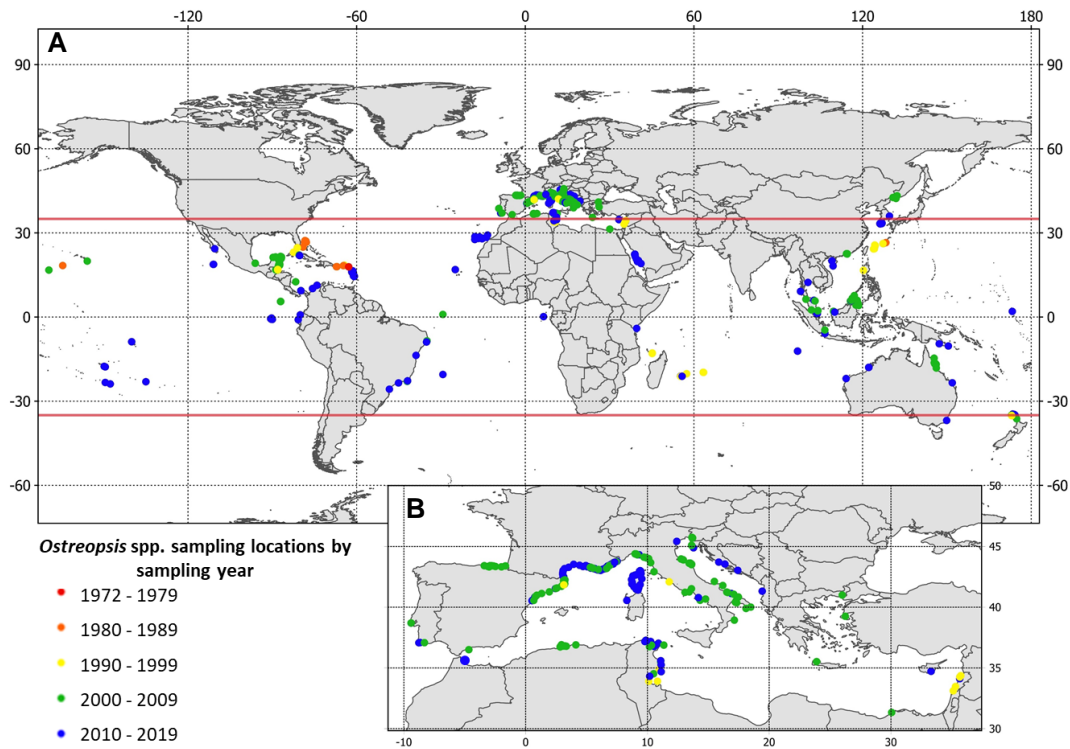
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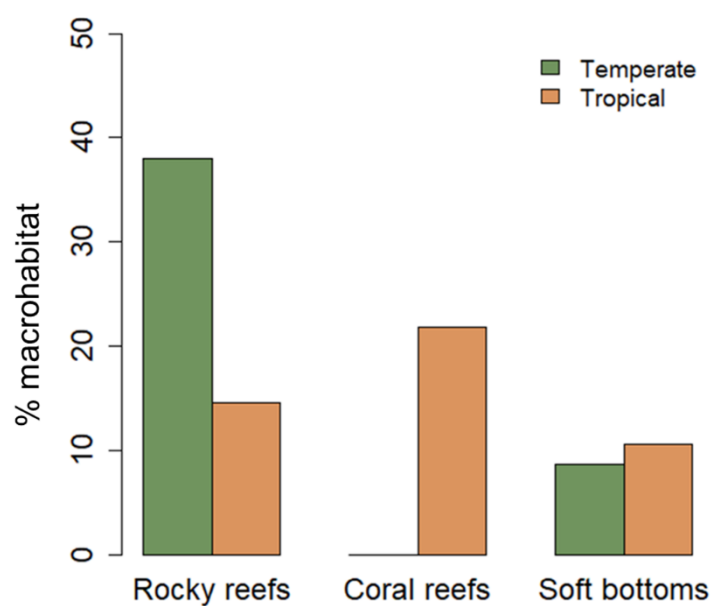
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1086 **Figure 1:** Trend of the number of peer-reviewed studies involving field sampling of1087 *Ostreopsis* spp. from 1981 to 2021.



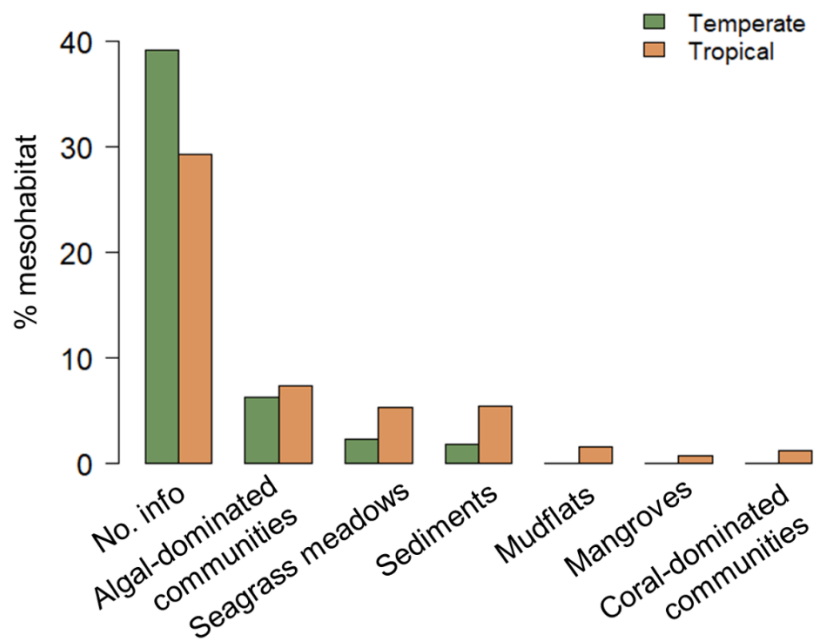
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1089 **Figure 2:** Map of the sampling locations. The colour corresponds to the year it was first
 1090 sampled. The two red lines (35°N and 35°S) separate the tropical/subtropical from the
 1091 temperate areas; a) global distribution; b) detailed map for the Mediterranean Sea.



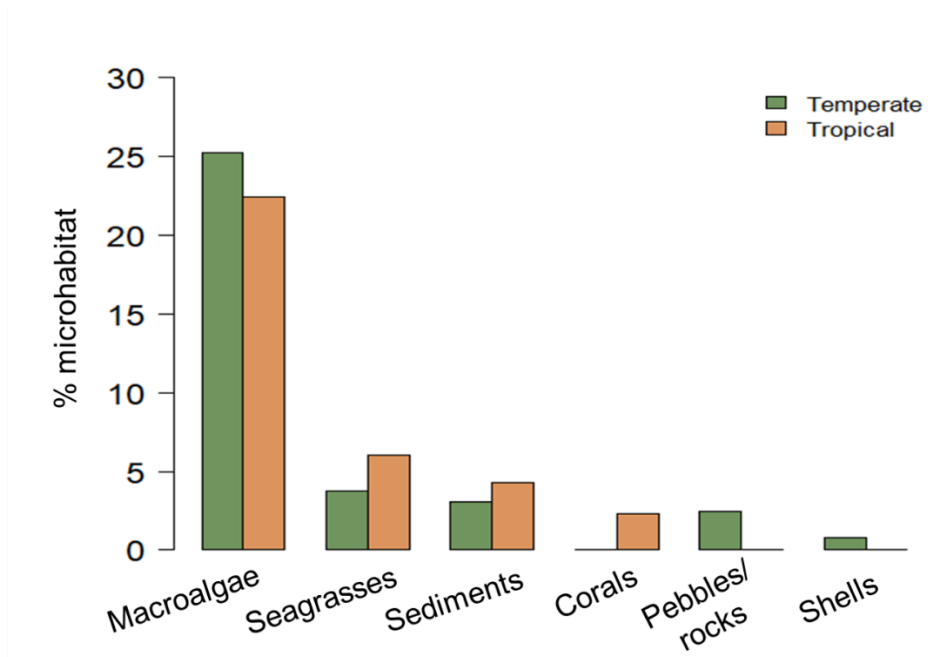
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1093 **Figure 3:** Macrohabitats where *Ostreopsis* spp. have been sampled in temperate and
1094 tropical areas.



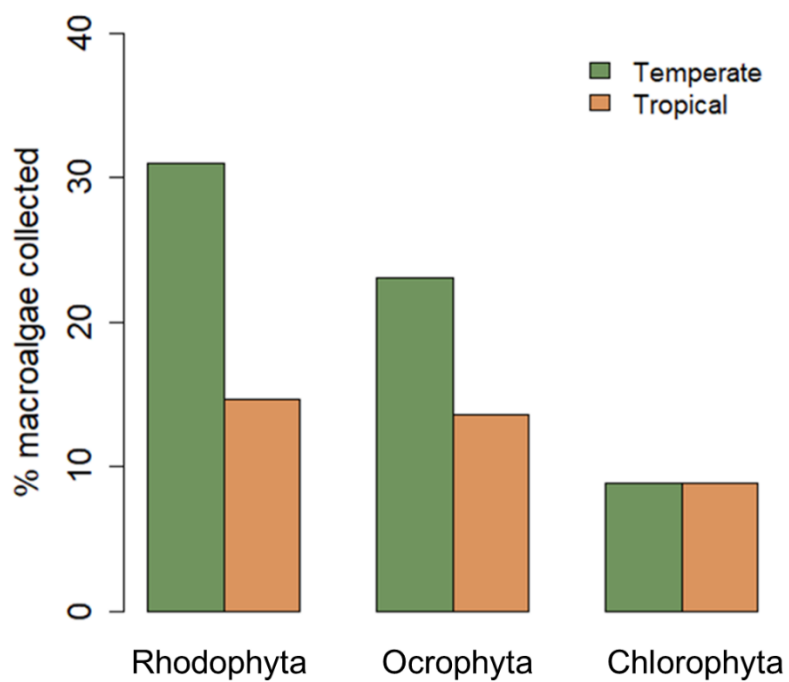
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1096 **Figure 4:** Mesohabitats where *Ostreopsis* spp. have been sampled in tropical and
1097 temperate areas.



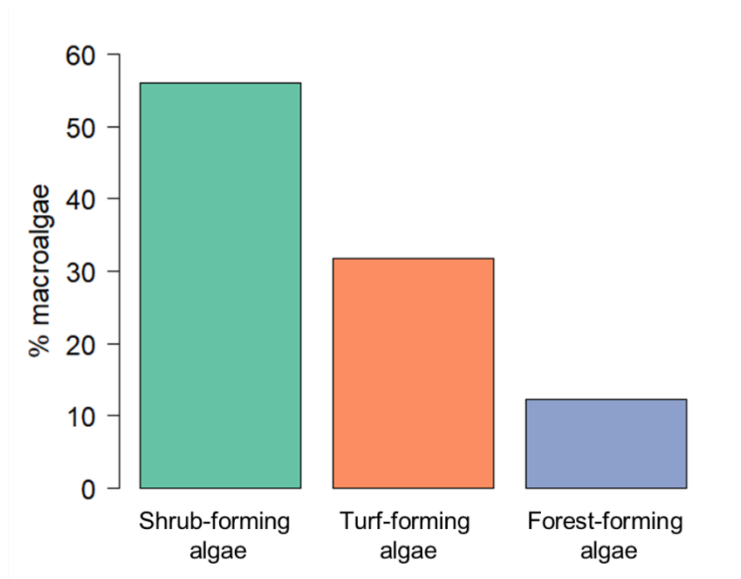
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1099 **Figure 5:** Microhabitats (substrates) where *Ostreopsis* spp. have been sampled in
 1100 temperate and tropical areas.



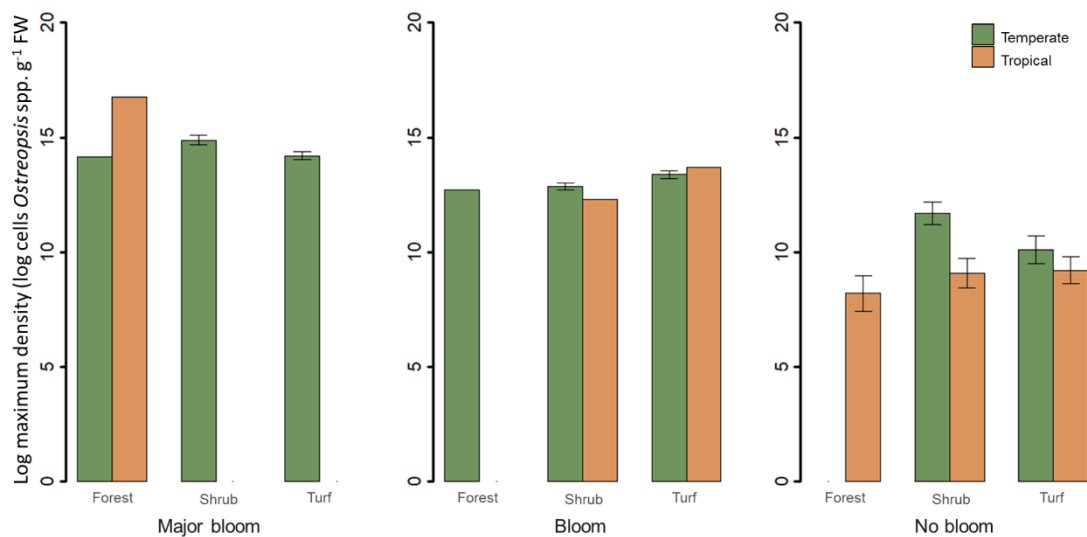
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1102 **Figure 6:** Macroalgae sampled in function of the phylum.



1103

1104 **Figure 7:** Macroalgae sampled in function of the type of community they can form.



1105

1106 **Figure 8:** Maximum cell densities of *Ostreopsis* spp. (cells g⁻¹ FW macroalgae) for

1107 each study grouped according to the morphological structure of the macroalgae

1108 sampled and the intensity of the bloom.

1109 **Table 1:** Maximum cell densities of *Ostreopsis* spp. (cells g⁻¹ FW macrophyte) for each
 1110 study on different microhabitats.

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

<i>Laurencia sp.</i>	99000	Turf	Brazil	Tropical	Nascimento et al. (2012)
<i>Pteroclatiella capillacea</i>	18194	Turf	Hawaii Island (USA)	Tropical	Parsons and Preskitt (2007)
<i>Pteroclatiella capillacea</i>	545000	Turf	Italy	Temperate	Ciminiello et al. (2014)
<i>Spyridia filamentosa</i>	2640000	Turf	Croatia	Temperate	Gladan et al. (2019)

Ochrophyta

<i>Carpophyllum maschalocarpum</i>	1095	Forest	New Zealand	Tropical	Chang et al. (2000)
<i>Carpophyllum plumosum</i>	1406000	Forest	New Zealand	Temperate	Shears and Ross (2009)
<i>Dictyopteris polypodioides</i>	1300000	Shrub	Italy	Temperate	Accoroni et al. (2012)
<i>Dictyopteris sp.</i>	33405	Shrub	Galapagos (Ecuador)	Tropical	Carnicer et al. (2020)
<i>Dictyota dichotoma</i>	330000	Shrub	Italy	Temperate	Cabrini et al. (2010)
<i>Dictyota sp</i>	79000	Shrub	Cuba	Tropical	Moreira et al. (2012)
<i>Dictyota sp.</i>	57000	Shrub	Virgin Islands	Tropical	Kohler and Kohler (1992)
<i>Dictyota sp.</i>	53231	Shrub	Mexico	Tropical	Irola-Sansores et al. (2018)
<i>Dictyota sp.</i>	44000	Shrub	Puerto Rico	Tropical	Ballantine, Tosteson and Bardales (1988)
<i>Dictyota sp.</i>	220079	Shrub	Cape Verde	Tropical	Fernandez-Zabala et al. (2019)
<i>Dictyota spp.</i>	8540000	Shrub	France	Temperate	Cohu, Mangialajo, Thibaut, Blanfune et al. (2013)
<i>Dictyota spp.</i>	24939	Shrub	Guadeloupe (France)	Tropical	Boisnoir et al. (2019)

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

Chlorophyta

<i>Cladophora sp.</i>	16000	Turf	Italy	Temperate	Battocchi, Totti, Vila, Maso, et al. (2010)
<i>Cladophora wrightiana</i>	102	Turf	Korea	Tropical	Shah, An and Lee (2013)
<i>Derbesia sp.</i>	8660	Turf	Korea	Tropical	Kim et al. (2011)
<i>Halimeda sp.</i>	596	Shrub	Kiribati	Tropical	Xu et al. (2014)
<i>Ulva rigida</i>	74000	Shrub	Italy	Temperate	Perini et al. (2011)

Seagrasses

<i>Cymodocea nodosa</i>	1940		Tunisia	Tropical	Ben Gharbia et al. (2019)
<i>Halophila stipulacea</i>	1669		Guadeloupe (France)	Tropical	Boisnoir et al. (2018)
<i>Posidonia oceanica</i>	360000		Tunisia	Tropical	Turki (2005)
<i>Posidonia oceanica</i>	2000		Tunisia	Tropical	Moncer et al. (2017)
<i>Thalassia testudinum</i>	3318		Colombia	Tropical	Arbelaez, Pineda and Reguera (2017)