



HAL
open science

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

Margalida Monserrat, Daniela Catania, Valentina Asnaghi, Mariachiara Chiantore, Rodolphe Lemée, Luisa Mangialajo

► To cite this version:

Margalida Monserrat, Daniela Catania, Valentina Asnaghi, Mariachiara Chiantore, Rodolphe Lemée, et al.. The role of habitat in the facilitation of *Ostreopsis* spp. blooms. *Harmful Algae*, 2022, 113, pp.102199. 10.1016/j.hal.2022.102199 . hal-03613440

HAL Id: hal-03613440

<https://hal.sorbonne-universite.fr/hal-03613440v1>

Submitted on 18 Mar 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

2 Margalida Monserrat^{a,b,c*}, Daniela Catania^a, Valentina Asnaghi^d, Mariachiara Chiantore^d,

3 Rodolphe Lemée^b and Luisa Mangialajo^{a, c}

4 ^aUniversité Côte d'Azur, CNRS, UMR 7035 ECOSEAS, Nice, France.

5 ^bSorbonne Université, CNRS, UMR 7093 Laboratoire d'Océanographie de Villefranche,

6 Villefranche-sur-mer, France.

7 ^cFederative Research Institute – Marine Resources, Université Côte d'Azur, Nice,

8 France.

9 ^dUniversità degli Studi di Genova, DiSTAV, Genova, Italy.

10 *Corresponding author. E-mail address: [11 \[cotedazur.fr\]\(mailto:margalida.monserrat-barcelo@univ-cotedazur.fr\)](mailto:margalida.monserrat-barcelo@univ-</p></div><div data-bbox=)

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; Coahu 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 Coahu 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.

441 **Acknowledgements**

442 This work is supported by a PhD grant funded by the Région Provence-Alpes-Côte
443 d'Azur (contract *Emplois Jeunes Doctorants* 2019-2022), CoReFOs and the project
444 CONVOST (UCA^{JEDI} Investments ANR-15-IDEX-01).

445 **Bibliography**

446 Abbate, M., Bordone, A., Cerrati, G., Di Festa, T., Melchiorre, N., Pastorelli, A.M.,
447 Peirano, A., Petruzzelli, M.R., Ungaro, N., 2012. A new method for sampling
448 potentially toxic benthic dinoflagellates. *Cryptogam. Algol.* 33, 165–170.
449 <https://doi.org/10.7872/crya.v33.iss2.2011.165>

450 Açağ, L., Saab, M.A.-A., Khoury-Hanna, M., Lemée, R., 2020. Bloom dynamics of the
451 newly described toxic benthic dinoflagellate *Ostreopsis fattorussoi* along the
452 Lebanese coast (Eastern Mediterranean). *Reg. Stud. Mar. Sci.* 101338.
453 <https://doi.org/10.1016/j.rsma.2020.101338>

454 Accoroni, S., Colombo, F., Pichierri, S., Romagnoli, T., Marini, M., Battocchi, C., Penna,
455 A., Totti, C., 2012. Ecology of *Ostreopsis* cf. *ovata* blooms in the northwestern
456 Adriatic Sea. *Cryptogam. Algol.* 33, 191–198.
457 <https://doi.org/10.7872/crya.v33.iss2.2011.191>

- 458 Accoroni, S., Percopo, I., Cerino, F., Romagnoli, T., Pichierri, S., Perrone, C., Totti, C.,
459 2015. Allelopathic interactions between the HAB dinoflagellate *Ostreopsis* cf.
460 *ovata* and macroalgae. *HARMFUL ALGAE* 49, 147–155.
461 <https://doi.org/10.1016/j.hal.2015.08.007>
- 462 Accoroni, S., Romagnoli, T., Colombo, F., Pennesi, C., di Camillo, C.G., Marini, M.,
463 Battocchi, C., Ciminiello, P., Dell’Aversano, C., Dello Iacovo, E., Fattorusso, E.,
464 Tartaglione, L., Penna, A., Totti, C., 2011. *Ostreopsis* cf. *ovata* bloom in the
465 northern Adriatic Sea during summer 2009: Ecology, molecular characterization
466 and toxin profile. *Mar. Pollut. Bull.* 62, 2512–2519.
467 <https://doi.org/10.1016/j.marpolbul.2011.08.003>
- 468 Accoroni, S., Romagnoli, T., Pichierri, S., Totti, C., 2016. Effects of the bloom of harmful
469 benthic dinoflagellate *Ostreopsis* cf. *ovata* on the microphytobenthos community
470 in the northern Adriatic Sea. *HARMFUL ALGAE* 55, 179–190.
471 <https://doi.org/10.1016/j.hal.2016.03.003>
- 472 Accoroni, S., Totti, C., 2016. The toxic benthic dinoflagellates of the genus *Ostreopsis* in
473 temperate areas: a review. *Adv. Oceanogr. Limnol.* 7.
474 <https://doi.org/10.4081/aiol.2016.5591>
- 475 Accoroni, S., Totti, C., Romagnoli, T., Giuliotti, S., Glibert, P.M., 2020. Distribution and
476 potential toxicity of benthic harmful dinoflagellates in waters of Florida Bay and
477 the Florida Keys. *Mar. Environ. Res.* 155.
478 <https://doi.org/10.1016/j.marenvres.2020.104891>

- 479 Aligizaki, K., Nikolaidis, G., 2008. Morphological identification of two tropical
480 dinoflagellates of the genera *Gambierdiscus* and *Sinophysis* in the
481 Mediterranean Sea. *J. Biol. Res.* 9, 75–82.
- 482 Aligizaki, K., Nikolaidis, G., 2006. The presence of the potentially toxic genera *Ostreopsis*
483 and *Coolia* (Dinophyceae) in the North Aegean Sea, Greece. *HARMFUL ALGAE*
484 5, 717–730. <https://doi.org/10.1016/j.hal.2006.02.005>
- 485 Anderson, C.R., Berdalet, E., Kudela, R.M., Cusack, C.K., Silke, J., O'Rourke, E., Dugan,
486 D., McCammon, M., Newton, J.A., Moore, S.K., Paige, K., Ruberg, S., Morrison,
487 J.R., Kirkpatrick, B., Hubbard, K., Morell, J., 2019. Scaling up from regional case
488 studies to a global harmful algal bloom observing system. *Front. Mar. Sci.* 6.
489 <https://doi.org/10.3389/fmars.2019.250>
- 490 Arbelaez, N.M., Pineda, J.E.M., Reguera, B., 2017. Epiphytic dinoflagellates of *Thalassia*
491 *testudinum* in two coastal systems of the Colombian Caribbean [Dinoflagelados
492 epífitos de *Thalassia testudinum* en dos sistemas costeros del Caribe
493 colombiano]. *Boletín Investig. Mar. Costeras* 46, 9–40.
494 <https://doi.org/10.25268/bimc.invemar.2017.46.2.725>
- 495 Asnaghi, V., Bertolotto, R., Giussani, V., Mangialajo, L., Hewitt, J., Thrush, S., Moretto,
496 P., Castellano, M., Rossi, A., Povero, P., Cattaneo-Vietti, R., Chiantore, M., 2012.
497 Interannual variability in *Ostreopsis ovata* bloom dynamic along Genoa coast
498 (North-western Mediterranean): a preliminary modeling approach. *Cryptogam.*
499 *Algol.* 33, 181–189. <https://doi.org/10.7872/crya.v33.iss2.2011.181>

- 500 Assis, J., Fragkopoulou, E., Frade, D., Neiva, J., Oliveira, A., Abecasis, D., Faugeron,
501 S., Serrão, E.A., 2020. A fine-tuned global distribution dataset of marine forests.
502 Sci. Data 7, 119. <https://doi.org/10.1038/s41597-020-0459-x>
- 503 Ballantine, D.L., Tosteson, T.R., Bardales, A.T., 1988. Population dynamics and toxicity
504 of natural populations of benthic dinoflagellates in southwestern Puerto Rico. J.
505 Exp. Mar. Biol. Ecol. 119, 201–212. [https://doi.org/10.1016/0022-](https://doi.org/10.1016/0022-0981(88)90193-1)
506 0981(88)90193-1
- 507 Battocchi, C., Totti, C., Vila, M., Maso, M., Capellacci, S., Accoroni, S., Rene, A., Scardi,
508 M., Penna, A., 2010. Monitoring of toxic microalga *Ostreopsis* (Dinoflagellate)
509 species in Mediterranean coastal waters using the PCR based-assay combined
510 with light microscopy. Biol. Mar. Mediterr. 17, 362–363.
- 511 Bellassoued, K., Hamza, A., van Pelt, J., Elfeki, A., 2013. Seasonal variation of *Sarpa*
512 *salpa* fish toxicity, as related to phytoplankton consumption, accumulation of
513 heavy metals, lipids peroxidation level in fish tissues and toxicity upon mice.
514 Environ. Monit. Assess. 185, 1137–50. [https://doi.org/10.1007/s10661-012-](https://doi.org/10.1007/s10661-012-2621-1)
515 2621-1
- 516 Ben Gharbia, H., Laabir, M., Ben Mhamed, A., Gueroun, S.K.M., Daly Yahia, M.N., Nouri,
517 H., M'Rabet, C., Shili, A., Kéfi-Daly Yahia, O., 2019. Occurrence of epibenthic
518 dinoflagellates in relation to biotic substrates and to environmental factors in
519 Southern Mediterranean (Bizerte Bay and Lagoon, Tunisia): An emphasis on the
520 harmful *Ostreopsis* spp., *Prorocentrum lima* and *Coolia monotis*. HARMFUL
521 ALGAE 90. <https://doi.org/10.1016/j.hal.2019.101704>

- 522 Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoidi, L., Relini, G.,
523 Cinelli, F., 2001. Predicting the consequences of anthropogenic disturbance:
524 large-scale effects of loss of canopy algae on rocky shores. *Mar. Ecol. Prog. Ser.*
525 214, 137–150. <https://doi.org/10.3354/meps214137>
- 526 Bertolini, C., 2019. Can secondary species maintain a primary role? Consistent inter-
527 regional effects of understory algae on diversity. *Mar. Biodivers.* 49, 841–849.
528 <https://doi.org/10.1007/s12526-018-0862-0>
- 529 Bire, R., Trotureau, S., Lemee, R., Delpont, C., Chabot, B., Aumond, Y., Krys, S., 2013.
530 Occurrence of palytoxins in marine organisms from different trophic levels of the
531 French Mediterranean coast harvested in 2009. *HARMFUL ALGAE* 28, 10–22.
532 <https://doi.org/10.1016/j.hal.2013.04.007>
- 533 Bire, R., Trotureau, S., Lemee, R., Oregoni, D., Delpont, C., Krys, S., Guerin, T., 2015.
534 Hunt for Palytoxins in a Wide Variety of Marine Organisms Harvested in 2010 on
535 the French Mediterranean Coast. *Mar. DRUGS* 13, 5425–5446.
536 <https://doi.org/10.3390/md13085425>
- 537 Blanfune, A., Boudouresque, C.F., Gossel, H., Thibaut, T., 2015. Distribution and
538 abundance of *Ostreopsis* spp. and associated species (Dinophyceae) in the
539 northwestern Mediterranean: the region and the macroalgal substrate matter.
540 *Environ. Sci. Pollut. Res.* 22, 12332–12346. [https://doi.org/10.1007/s11356-015-](https://doi.org/10.1007/s11356-015-4525-4)
541 [4525-4](https://doi.org/10.1007/s11356-015-4525-4)
- 542 Blanfune, A., Cohu, S., Mangialajo, L., Lemee, R., Thibaut, T., 2012. Preliminary
543 assessments of the impact of *Ostreopsis* cf. *ovata* (Dinophyceae) development

- 544 on macroinvertebrates in the North Western Mediterranean Sea. *Cryptogam.*
545 *Algol.* 33, 129–136. <https://doi.org/10.7872/crya.v33.iss2.2011.129>
- 546 Boisnoir, A., Pascal, P.-Y., Chomerat, N., Lemee, R., 2020. Distribution of potentially toxic
547 epiphytic dinoflagellates in Saint Martin Island (Caribbean Sea, Lesser Antilles).
548 *Cryptogam. Algol.* 41, 47–54. [https://doi.org/10.5252/cryptogamie-
algologie2020v41a7](https://doi.org/10.5252/cryptogamie-
549 algologie2020v41a7)
- 550 Boisnoir, A., Pascal, P.-Y., Cordonnier, S., Lemee, R., 2019. Spatio-temporal dynamics
551 and biotic substrate preferences of benthic dinoflagellates in the Lesser Antilles,
552 Caribbean Sea. *HARMFUL ALGAE* 81, 18–29.
553 <https://doi.org/10.1016/j.hal.2018.11.012>
- 554 Boisnoir, A., Pascal, P.-Y., Cordonnier, S., Lemee, R., 2018. Depth distribution of benthic
555 dinoflagellates in the Caribbean Sea. *J. SEA Res.* 135, 74–83.
556 <https://doi.org/10.1016/j.seares.2018.02.001>
- 557 Bomber, J.W., Tindall, D.R., Miller, D.M., 1989. Genetic variability in toxin potencies
558 among seventeen clones of *Gambierdiscus toxicus* (dinophyceae). *Genet. Var.*
559 *Toxin Potencies Seventeen Clones Gamb. Toxicus Dinophyceae* 25, 617–625.
- 560 Bravo, I., Rodriguez, F., Ramilo, I., Afonso-Carrillo, J., 2020. Epibenthic Harmful Marine
561 Dinoflagellates from Fuerteventura (Canary Islands), with Special Reference to
562 the Ciguatoxin-Producing *Gambierdiscus*. *J. Mar. Sci. Eng.* 8.
563 <https://doi.org/10.3390/jmse8110909>
- 564 Brescianini, C., Grillo, C., Melchiorre, N., Bertolotto, R., Ferrari, A., Vivaldi, B., Icardi, G.,
565 Gramaccioni, L., Funari, E., Scardala, S., 2006. *Ostreopsis ovata* algal blooms

- 566 affecting human health in Genova, Italy, 2005 and 2006. *Euro Surveill. Bull. Eur.*
567 *Sur Mal. Transm. Eur. Commun. Dis. Bull.* 11, E060907.3.
- 568 Brissard, C., Herrenknecht, C., Sechet, V., Herve, F., Pisapia, F., Harcouet, J., Lemee,
569 R., Chomerat, N., Hess, P., Amzil, Z., 2014. Complex Toxin Profile of French
570 Mediterranean *Ostreopsis cf. ovata* Strains, Seafood Accumulation and
571 Ovatoxins Prepurification. *Mar. DRUGS* 12, 2851–2876.
572 <https://doi.org/10.3390/md12052851>
- 573 Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J., 2016. Facilitation and the niche:
574 implications for coexistence, range shifts and ecosystem functioning. *Funct. Ecol.*
575 30, 70–78. <https://doi.org/10.1111/1365-2435.12528>
- 576 Cabrini, M., Fornasaro, D., Lipizer, M., Guardiani, B., 2010. First report of *Ostreopsis cf.*
577 *ovata* bloom in the Gulf of Trieste. *Biol. Mar. Mediterr.* 17, 366–367.
- 578 Carella, F., Sardo, A., Mangoni, O., Di Cioccio, D., Urciuolo, G., De Vico, G., Zingone,
579 A., 2015. Quantitative histopathology of the Mediterranean mussel (*Mytilus*
580 *galloprovincialis* L.) exposed to the harmful dinoflagellate *Ostreopsis cf. ovata*. *J.*
581 *Invertebr. Pathol.* 127, 130–140. <https://doi.org/10.1016/j.jip.2015.03.001>
- 582 Carnicer, O., Guallar, C., Andree, K.B., Diogene, J., Fernandez-Tejedor, M., 2015.
583 *Ostreopsis cf. ovata* dynamics in the NW Mediterranean Sea in relation to biotic
584 and abiotic factors. *Environ. Res.* 143, 89–99.
585 <https://doi.org/10.1016/j.envres.2015.08.023>
- 586 Carnicer, O., Okolodkov, Y.B., Garcia-Altare, M., Keith, I., Andree, K.B., Diogene, J.,
587 Fernandez-Tejedor, M., 2020. *Ostreopsis cf. ovata* and *Ostreopsis lenticularis*

- 588 (Dinophyceae: Gonyaulacales) in the Galapagos Marine Reserve. *Sci. Mar.* 84,
589 199–213. <https://doi.org/10.3989/scimar.05035.08A>
- 590 Casabianca, S., Capellacci, S., Giacobbe, M.G., Dell'Aversano, C., Tartaglione, L.,
591 Varriale, F., Narizzano, R., Risso, F., Moretto, P., Dagnino, A., Bertolotto, R.,
592 Barbone, E., Ungaro, N., Penna, A., 2019. Plastic-associated harmful microalgal
593 assemblages in marine environment. *Environ. Pollut.* 244, 617–626.
594 <https://doi.org/10.1016/j.envpol.2018.09.110>
- 595 Casabianca, S., Casabianca, A., Riobo, P., Franco, J.M., Vila, M., Penna, A., 2013.
596 Quantification of the Toxic Dinoflagellate *Ostreopsis* spp. by qPCR Assay in
597 Marine Aerosol. *Environ. Sci. Technol.* 47, 3788–3795.
598 <https://doi.org/10.1021/es305018s>
- 599 Catania, D., 2017. The influence of macroalgae on the proliferation and regulation of the
600 benthic dinoflagellate *Ostreopsis* cf. *ovata* blooms (PhD thesis). Université Côte
601 d'Azur. <https://tel.archives-ouvertes.fr/tel-01682210/document>
- 602 Catania, D., Richlen, M.L., Mak, Y.L., Morton, S.L., Laban, E.H., Xu, Y., Anderson, D.M.,
603 Chan, L.L., Berumen, M.L., 2017. The prevalence of benthic dinoflagellates
604 associated with ciguatera fish poisoning in the central Red Sea. *HARMFUL*
605 *ALGAE* 68, 206–216. <https://doi.org/10.1016/j.hal.2017.08.005>
- 606 Chang, F.H., Shimizu, Y., Hay, B., Stewart, R., Mackay, G., Tasker, R., 2000. Three
607 recently recorded *Ostreopsis* spp. (Dinophyceae) in New Zealand: Temporal and
608 regional distribution in the upper North Island from 1995 to 1997. *N. Z. J. Mar.*
609 *Freshw. Res.* 34, 29–39. <https://doi.org/10.1080/00288330.2000.9516913>

- 610 Chemello, S., Vizzini, S., Mazzola, A., 2018. Regime shifts and alternative stable states
611 in intertidal rocky habitats: State of the art and new trends of research. *Estuar.
612 Coast. Shelf Sci.* 214, 57–63. <https://doi.org/10.1016/j.ecss.2018.09.013>
- 613 Chiantore, M., Mangialajo, L., Castellano, M., Privitera, D., Costa, E., Canepa, C.,
614 Cattaneo-Vietti, R., 2008. Bloom dynamics of *Ostreopsis ovata* in the Ligurian Sea.
615 *Biol. Mar. Mediterr.* 15, 18–20.
- 616 Chinain, M., Gatti, C.M. iti, Ung, A., Cruchet, P., Revel, T., Viallon, J., Sibat, M., Varney,
617 P., Laurent, V., Hess, P., Darius, H.T., 2020. Evidence for the Range Expansion
618 of *Ciguatera* in French Polynesia: A Revisit of the 2009 Mass-Poisoning Outbreak
619 in Rapa Island (Australes Archipelago). *TOXINS* 12.
620 <https://doi.org/10.3390/toxins12120759>
- 621 Ciminiello, P., Dell'Aversano, C., Dello Iacovo, E., Fattorusso, E., Forino, M., Tartaglione,
622 L., Benedettini, G., Onorari, M., Serena, F., Battocchi, C., Casabianca, S., Penna,
623 A., 2014. First Finding of *Ostreopsis cf. ovata* Toxins in Marine Aerosols. *Environ.
624 Sci. Technol.* 48, 3532–3540. <https://doi.org/10.1021/es405617d>
- 625 Ciminiello, P., Dell'Aversano, C., Iacovo, E.D., Fattorusso, E., Forino, M., Grauso, L.,
626 Tartaglione, L., Guerrini, F., Pistocchi, R., 2010. Complex palytoxin-like profile of
627 *Ostreopsis ovata*. identification of four new ovatoxins by high-resolution liquid
628 chromatography/mass spectrometry. *Rapid Commun. Mass Spectrom.* 24,
629 2735–2744. <https://doi.org/10.1002/rcm.4696>
- 630 Cochu, S., Lemee, R., 2012. Vertical distribution of the toxic epibenthic dinoflagellates
631 *Ostreopsis cf. ovata*, *Prorocentrum lima* and *Coolia monotis* in the NW
632 Mediterranean Sea. *Cah. Biol. Mar.* 53, 373–380.

- 633 Cohu, S., Mangialajo, L., Thibaut, T., Blanfune, A., Lemee, R., 2011. Development of the
634 benthic toxic dinoflagellate *Ostreopsis* cf. *ovata* in the NW Mediterranean Sea.
635 Eur. J. Phycol. 46, 55.
- 636 Cohu, S., Mangialajo, L., Thibaut, T., Blanfune, A., Marro, S., Lemee, R., 2013.
637 Proliferation of the toxic dinoflagellate *Ostreopsis* cf. *ovata* in relation to depth,
638 biotic substrate and environmental factors in the North West Mediterranean Sea.
639 HARMFUL ALGAE 24, 32–44. <https://doi.org/10.1016/j.hal.2013.01.002>
- 640 Connell, S., Foster, M., Airoidi, L., 2014. What are algal turfs? Towards a better
641 description of turfs. Mar. Ecol. Prog. Ser. 495, 299–307.
642 <https://doi.org/10.3354/meps10513>
- 643 Cruz-Rivera, E., Villareal, T.A., 2006. Macroalgal palatability and the flux of ciguatera
644 toxins through marine food webs. HARMFUL ALGAE 5, 497–525.
645 <https://doi.org/10.1016/j.hal.2005.09.003>
- 646 de Sylva, D.P., 1994. Distribution and Ecology of Ciguatera Fish Poisoning in Florida,
647 with Emphasis on the Florida Keys. Bull. Mar. Sci. 54, 944–954.
- 648 Di Pippo, F., Congestri, R., 2017. Culturing Toxic Benthic Blooms: The Fate of Natural
649 Biofilms in a Microcosm System. MICROORGANISMS 5.
650 <https://doi.org/10.3390/microorganisms5030046>
- 651 Di Turi, L., Lo Caputo, S., Marzano, M.C., Pastorelli, A.M., Pompei, M., Rositani, L.,
652 Ungaro, N., 2003. *Ostreopsidiaceae* (Dinophyceae) presence along the coastal
653 area of Bari. Biol. Mar. Mediterr. 10, 675–678.

- 654 Faust, M.A., 2009. Ciguatera-causing dinoflagellates in a coral-reef mangrove
655 ecosystem, Belize. Atoll Res. Bull. 1–32.
656 <https://doi.org/10.5479/si.00775630.569.1>
- 657 Faust, M.A., 1999. Three new *Ostreopsis* species (Dinophyceae): *O. marinus* sp. nov.,
658 *O. belizeanus* sp. nov., and *O. caribbeanus* sp. nov. *Phycologia* 38, 92–99.
659 <https://doi.org/10.2216/i0031-8884-38-2-92.1>
- 660 Faust, M.A., Morton, S.L., 1995. Morphology and ecology of the marine dinoflagellate
661 *Ostreopsis labens* sp. Nov. (Dinophyceae). *J. Phycol.* 31, 456–463.
662 <https://doi.org/10.1111/j.0022-3646.1995.00456.x>
- 663 Faust, M.A., Morton, S.L., Quod, J.P., 1996. Further sem study of marine dinoflagellates:
664 The genus *Ostreopsis* (Dinophyceae). *J. Phycol.* 32, 1053–1065.
665 <https://doi.org/10.1111/j.0022-3646.1996.01053.x>
- 666 Fernandez-Zabala, J., Tuya, F., Amorim, A., Soler-Onis, E., 2019. Benthic
667 dinoflagellates: Testing the reliability of the artificial substrate method in the
668 Macaronesian region. *HARMFUL ALGAE* 87.
669 <https://doi.org/10.1016/j.hal.2019.101634>
- 670 Filbee-Dexter, K., Scheibling, R.E., 2014. Sea urchin barrens as alternative stable states
671 of collapsed kelp ecosystems. *Marine Ecology Progress Series* 495, 1–25.
672 <https://doi.org/10.3354/meps10573>
- 673 Filbee-Dexter, K., Wernberg, T., 2018. Rise of Turfs: A New Battlefield for Globally
674 Declining Kelp Forests. *BioScience* 68, 64–76.
675 <https://doi.org/10.1093/biosci/bix147>

- 676 Fricke, A., Pey, A., Gianni, F., Lemee, R., Mangialajo, L., 2018. Multiple stressors and
677 benthic harmful algal blooms (BHABs): Potential effects of temperature rise and
678 nutrient enrichment. *Mar. Pollut. Bull.* 131, 552–564.
679 <https://doi.org/10.1016/j.marpolbul.2018.04.012>
- 680 Fukuyo, Y., 1981. Taxonomical Study on Benthic Dinoflagellates Collected in Coral
681 Reefs. *Nippon Suisan Gakkaishi Jpn. Ed.* 47, 967–978.
682 <https://doi.org/10.2331/suisan.47.967>
- 683 Funari, E., Manganelli, M., Testai, E., 2015. *Ostreopsis cf. ovata* blooms in coastal water:
684 Italian guidelines to assess and manage the risk associated to bathing waters
685 and recreational activities. *HARMFUL ALGAE* 50, 45–56.
686 <https://doi.org/10.1016/j.hal.2015.10.008>
- 687 Gémin, M.-P., Réveillon, D., Hervé, F., Pavaux, A.-S., Tharaud, M., Séchet, V., Bertrand,
688 S., Lemée, R., Amzil, Z., 2020. Toxin content of *Ostreopsis cf. ovata* depends on
689 bloom phases, depth and macroalgal substrate in the NW Mediterranean Sea.
690 *HARMFUL ALGAE* 92. <https://doi.org/10.1016/j.hal.2019.101727>
- 691 Giussani, V., Asnaghi, V., Pedroncini, A., Chiantore, M., 2017. Management of harmful
692 benthic dinoflagellates requires targeted sampling methods and alarm
693 thresholds. *HARMFUL ALGAE* 68, 97–104.
694 <https://doi.org/10.1016/j.hal.2017.07.010>
- 695 Gladan, Z.N., Arapov, J., Casabianca, S., Penna, A., Honsell, G., Brovedani, V., Pelin,
696 M., Tartaglione, L., Sosa, S., Dell'Aversano, C., Tubaro, A., Zuljevic, A., Grbec,
697 B., Cavar, M., Buzancic, M., Bakrac, A., Skejic, S., 2019. Massive Occurrence of

- 698 the Harmful Benthic Dinoflagellate *Ostreopsis* cf. *ovata* in the Eastern Adriatic
699 Sea. TOXINS 11. <https://doi.org/10.3390/toxins11050300>
- 700 Gomaa, M.N., Hannachi, I., Carmichael, W.W., Al-Hazmi, M.A., Abouwarda, A.M.,
701 Mostafa, E.A.H., Mohamed, H.E., Sheikho, K.M., Mulla, D.J., 2018. Low diversity
702 triggers harmful algae bloom (Hab) occurrence adjacent to desalination plants
703 along the red sea. Desalination Water Treat. 114, 1–12.
704 <https://doi.org/10.5004/dwt.2018.22323>
- 705 González, A., Broce, K., Fábrega-Duque, J., Tejedor-Flores, N., Young, K., 2019.
706 Identification and Monitoring of Microalgal Genera Potentially Capable of
707 Forming Harmful Algal Blooms in Punta Galeta, Panama. Air Soil Water Res. 12.
708 <https://doi.org/10.1177/1178622119872769>
- 709 Guidi-Guilvard, L.D., Gasparini, S., Lemee, R., 2012. The negative impact of *Ostreopsis*
710 cf. *ovata* on phytal meiofauna from the coastal NW Mediterranean. Cryptogam.
711 Algol. 33, 121–128. <https://doi.org/10.7872/crya.v33.iss2.2011.121>
- 712 Hachani, M.A., Dhib, A., Fathalli, A., Ziadi, B., Turki, S., Aleya, L., 2018. Harmful
713 epiphytic dinoflagellate assemblages on macrophytes in the Gulf of Tunis.
714 HARMFUL ALGAE 77, 29–42. <https://doi.org/10.1016/j.hal.2018.06.006>
- 715 Hughes, T.P., 1994. Catastrophes, Phase Shifts, and Large-Scale Degradation of a
716 Caribbean Coral Reef. Science 265, 1547–1551.
717 <https://doi.org/10.1126/science.265.5178.1547>
- 718 Illoul, H., Rodriguez Hernandez, F., Vila, M., Adjias, N., Younes, A.A., Bournissa, M.,
719 Koroghli, A., Marouf, N., Rabia, S., Ameer, F.L.K., 2012. The genus *Ostreopsis*

- 720 along the Algerian coastal waters (SW Mediterranean Sea) associated with a
721 human respiratory intoxication episode. *Cryptogam. Algal.* 33, 209–216.
722 <https://doi.org/10.7872/crya.v33.iss2.2011.209>
- 723 Irola-Sansores, E., Delgado-Pech, B., Garcia-Mendoza, E., Nunez-Vazquez, E.J.,
724 Olivos-Ortiz, A., Almazan-Becerril, A., 2018. Population Dynamics of Benthic-
725 Epiphytic Dinoflagellates on Two Macroalgae From Coral Reef Systems of the
726 Northern Mexican Caribbean. *Front. Mar. Sci.* 5.
727 <https://doi.org/10.3389/fmars.2018.00487>
- 728 Ismael, A., Halim, Y., 2012. Potentially harmful *Ostreopsis* spp. in the coastal waters of
729 Alexandria - Egypt. *Mediterr. Mar. Sci.* 13, 208–212.
730 <https://doi.org/10.12681/mms.300>
- 731 Jauzein, C., Acaf, L., Accoroni, S., Asnaghi, V., Fricke, A., Hachani, M.A., Saab, M.A.-
732 A., Chiantore, M., Mangialajo, L., Totti, C., Zaghmouri, I., Lemee, R., 2018.
733 Optimization of sampling, cell collection and counting for the monitoring of benthic
734 harmful algal blooms: Application to *Ostreopsis* spp. blooms in the Mediterranean
735 Sea. *Ecol. Indic.* 91, 116–127. <https://doi.org/10.1016/j.ecolind.2018.03.089>
- 736 Johns, K.A., Emslie, M.J., Hoey, A.S., Osborne, K., Jonker, M.J., Cheal, A.J., 2018.
737 Macroalgal feedbacks and substrate properties maintain a coral reef regime shift.
738 *Ecosphere* 9, e02349. <https://doi.org/10.1002/ecs2.2349>
- 739 Jouffray, J.-B., Nyström, M., Norström, A.V., Williams, I.D., Wedding, L.M., Kittinger,
740 J.N., Williams, G.J., 2015. Identifying multiple coral reef regimes and their drivers
741 across the Hawaiian archipelago. *Philosophical Transactions of the Royal*

- 742 Society B: Biological Sciences 370, 20130268.
743 <https://doi.org/10.1098/rstb.2013.0268>
- 744 Kim, H.S., Yih, W., Kim, J.H., Myung, G., Jeong, H.J., 2011. Abundance of epiphytic
745 dinoflagellates from coastal waters off Jeju Island, Korea During Autumn 2009.
746 *Ocean Sci. J.* 46, 205–209. <https://doi.org/10.1007/s12601-011-0016-9>
- 747 Kohler, S.T., Kohler, C.C., 1992. Dead bleached coral provides new surfaces for
748 dinoflagellates implicated in ciguatera fish poisonings. *Environ. Biol. Fishes* 35,
749 413–416. <https://doi.org/10.1007/BF00004993>
- 750 Lee, L.K., Lim, Z.F., Gu, H., Chan, L.L., Litaker, R.W., Tester, P.A., Leaw, C.P., Lim,
751 P.T., 2020. Effects of substratum and depth on benthic harmful dinoflagellate
752 assemblages. *Sci. Rep.* 10. <https://doi.org/10.1038/s41598-020-68136-6>
- 753 Lemee, R., Chiantore, M., Mangialajo, L., 2012. Proceedings of the International
754 Congress on *Ostreopsis* Development (ICOD, April 2011, France). *Cryptogam.*
755 *Algol.* 33, 79–80. <https://doi.org/10.7872/crya.v33.iss2.2011.079>
- 756 Lenoir, S., Ten-Hage, L., Turquet, J., Quod, J.-P., Bernard, C., Hennion, M.-C., 2004.
757 First evidence of palytoxin analogues from an *Ostreopsis mascarenensis*
758 (*Dinophyceae*) benthic bloom in southwestern Indian Ocean. *J. Phycol.* 40,
759 1042–1051. <https://doi.org/10.1111/j.1529-8817.2004.04016.x>
- 760 Litaker, R.W., Vandersea, M.W., Faust, M.A., Kibler, S.R., Chinain, M., Holmes, M.J.,
761 Holland, W.C., Tester, P.A., 2009. Taxonomy of *Gambierdiscus* including four
762 new species, *Gambierdiscus caribaeus*, *Gambierdiscus carolinianus*,

- 763 Gambierdiscus carpenteri and Gambierdiscus ruetzleri (Gonyaulacales,
764 Dinophyceae). Phycologia 48, 344–390.
- 765 Manca, V., Mocci, G.A., Nigra, C., Russu, C., 2015. *Ostreopsis* cf. *ovata* in three areas
766 of the North Sardinia. Biol. Mar. Mediterr. 22, 208–209.
- 767 Mangialajo, L., Bertolotto, R., Cattaneo-Vietti, R., Chiantore, M., Grillo, C., Lemee, R.,
768 Melchiorre, N., Moretto, P., Povero, P., Ruggieri, N., 2008a. The toxic benthic
769 dinoflagellate *Ostreopsis ovata*: Quantification of proliferation along the coastline
770 of Genoa, Italy. Mar. Pollut. Bull. 56, 1209–1214.
771 <https://doi.org/10.1016/j.marpolbul.2008.02.028>
- 772 Mangialajo, L., Chiantore, M., Cattaneo-Vietti, R., 2008b. Loss of furoid algae along a
773 gradient of urbanisation, and structure of benthic assemblages. Mar. Ecol. Prog.
774 Ser. 358, 63–74. <https://doi.org/10.3354/meps07400>
- 775 Mangialajo, L., Fricke, A., Perez-Gutierrez, G., Catania, D., Jauzein, C., Lemee, R.,
776 2017. Benthic Dinoflagellate Integrator (BEDI): A new method for the
777 quantification of Benthic Harmful Algal Blooms. HARMFUL ALGAE 64, 1–10.
778 <https://doi.org/10.1016/j.hal.2017.03.002>
- 779 Mangialajo, L., Ganzin, N., Accoroni, S., Asnaghi, V., Blanfuné, A., Cabrini, M., Cattaneo-
780 Vietti, R., Chavanon, F., Chiantore, M., Cohu, S., Costa, E., Fornasaro, D.,
781 Gossel, H., Marco-Miralles, F., Masó, M., Reñé, A., Rossi, A.M., Sala, M.M.,
782 Thibaut, T., Totti, C., Vila, M., Lemée, R., 2011. Trends in *Ostreopsis* proliferation
783 along the Northern Mediterranean coasts. Toxicon 57, 408–420.
784 <https://doi.org/10.1016/j.toxicon.2010.11.019>

- 785 Masó, M., Garcés, E., Pagès, F., Camp, J., 2003. Drifting plastic debris as a potential
786 vector for dispersing Harmful Algal Bloom (HAB) species [Los plásticos flotantes
787 son potenciales vectores de dispersión de especies formadoras de
788 proliferaciones algales nocivas]. *Sci. Mar.* 67, 107–111.
789 <https://doi.org/10.3989/scimar.2003.67n1107>
- 790 Mauffrey, A.R.L., Cappelatti, L., Griffin, J.N., 2020. Seaweed functional diversity
791 revisited: Confronting traditional groups with quantitative traits. *Journal of*
792 *Ecology* 108, 2390–2405. <https://doi.org/10.1111/1365-2745.13460>
- 793 Melis, R., Ceccherelli, G., Piazzini, L., Rustici, M., 2019. Macroalgal forests and sea urchin
794 barrens: Structural complexity loss, fisheries exploitation and catastrophic regime
795 shifts. *Ecol. Complex.* 37, 32–37. <https://doi.org/10.1016/j.ecocom.2018.12.005>
- 796 Meroni, L., Chiantore, M., Petrillo, M., Asnaghi, V., 2018. Habitat effects on *Ostreopsis*
797 *cf. ovata* bloom dynamics. *HARMFUL ALGAE* 80, 64–71.
798 <https://doi.org/10.1016/j.hal.2018.09.006>
- 799 Migliaccio, O., Castellano, I., Di Cioccio, D., Tedeschi, G., Negri, A., Cirino, P., Romano,
800 G., Zingone, A., Palumbo, A., 2016. Subtle reproductive impairment through nitric
801 oxide-mediated mechanisms in sea urchins from an area affected by harmful
802 algal blooms. *Sci. Rep.* 6. <https://doi.org/10.1038/srep26086>
- 803 Mohammad-Noor, N., Al-Has, A., Saad, S., Aung, T., 2016. Comparison on the Cell
804 Abundance of Benthic Dinoflagellates in Macrophytes and Water Column
805 Collected from Open Coastal Waters and Semi-Enclosed Lagoon. *SAINS*
806 *Malays.* 45, 595–599.

- 807 Mohammad-Noor, N., Daugbjerg, N., Moestrup, Ø., Anton, A., 2007. Marine epibenthic
808 dinoflagellates from Malaysia - A study of live cultures and preserved samples
809 based on light and scanning electron microscopy. Nord. J. Bot. 24, 629–690.
810 <https://doi.org/10.1111/j.1756-1051.2004.tb01938.x>
- 811 Moncer, M., Hamza, A., Feki-Sahnoun, W., Mabrouk, L., Hassen, M.B., 2017. Variability
812 patterns of epibenthic microalgae in eastern Tunisian coasts. Sci. Mar. 81, 487–
813 498. <https://doi.org/10.3989/scimar.04651.17A>
- 814 Monti, M., Minocci, M., Beran, A., Iveša, L., 2007. First record of *Ostreopsis* cfr. *ovata* on
815 macroalgae in the Northern Adriatic Sea. Mar. Pollut. Bull. 54, 598–601.
816 <https://doi.org/10.1016/j.marpolbul.2007.01.013>
- 817 Moreira, A., Rodriguez, F., Riobo, P., Franco, J.M., Martinez, N., Chamero, D., Alonso,
818 C., 2012. Notes on *Ostreopsis* sp from southern-central coast of Cuba.
819 Cryptogam. Algol. 33, 217–224. <https://doi.org/10.7872/crya.v33.iss2.2011.217>
- 820 Morton, S.L., Faust, M.A., 1997. Survey of toxic epiphytic dinoflagellates from the
821 belizean barrier reef ecosystem. Bull. Mar. Sci. 61, 899–906.
- 822 Nascimento, S.M., França, J.V., Gonçalves, J.E.A., Ferreira, C.E.L., 2012. *Ostreopsis*
823 cf. *ovata* (Dinophyta) bloom in an equatorial island of the Atlantic Ocean. Mar.
824 Pollut. Bull. 64, 1074–1078. <https://doi.org/10.1016/j.marpolbul.2012.03.015>
- 825 Neves, R.A.F., Contins, M., Nascimento, S.M., 2018. Effects of the toxic benthic
826 dinoflagellate *Ostreopsis* cf. *ovata* on fertilization and early development of the
827 sea urchin *Lytechinus variegatus*. Mar. Environ. Res. 135, 11–17.
828 <https://doi.org/10.1016/j.marenvres.2018.01.014>

- 829 Norris, Bomber, J.W., Balech, E., 1985. Benthic dinoflagellates associated with ciguatera
830 from the Florida Keys. 1. *Ostreopsis heptagona* sp. nov. Toxic dinoflagellates, 39
- 831 O'Brien, J.M., Scheibling, R.E., 2018. Turf wars: competition between foundation and
832 turf-forming species on temperate and tropical reefs and its role in regime shifts.
833 Mar. Ecol. Prog. Ser. 590, 1–17. <https://doi.org/10.3354/meps12530>
- 834 Okolodkov, Y.B., Campos-Bautista, G., Gárate-Lizárraga, I., González-González,
835 J.A.G., Hoppenrath, M., Arenas, V., 2007. Seasonal changes of benthic and
836 epiphytic dinoflagellates in the Veracruz reef zone, Gulf of Mexico. Aquat. Microb.
837 Ecol. 47, 223–237. <https://doi.org/10.3354/ame047223>
- 838 Park, J., Hwang, J., Hyung, J.-H., Yoon, E.Y., 2020. Temporal and Spatial Distribution
839 of the Toxic Epiphytic Dinoflagellate *Ostreopsis cf. ovata* in the Coastal Waters off
840 Jeju Island, Korea. SUSTAINABILITY 12. <https://doi.org/10.3390/su12145864>
- 841 Parsons, M.L., Aligizaki, K., Bottein, M.-Y.D., Fraga, S., Morton, S.L., Penna, A., Rhodes,
842 L., 2012. *Gambierdiscus* and *Ostreopsis*: Reassessment of the state of
843 knowledge of their taxonomy, geography, ecophysiology, and toxicology.
844 HARMFUL ALGAE 14, 107–129. <https://doi.org/10.1016/j.hal.2011.10.017>
- 845 Parsons, M.L., Preskitt, L.B., 2007. A survey of epiphytic dinoflagellates from the coastal
846 waters of the island of Hawai'i. HARMFUL ALGAE 6, 658–669.
847 <https://doi.org/10.1016/j.hal.2007.01.001>
- 848 Pavaux, A.-S., Berdalet, E., Lemee, R., 2020. Chemical Ecology of the Benthic
849 Dinoflagellate Genus *Ostreopsis*: Review of Progress and Future Directions.
850 Front. Mar. Sci. 7. <https://doi.org/10.3389/fmars.2020.00498>

- 851 Payri, C., Naïm, O., 1982. Variations entre 1971 et 1980 de la biomasse et de la
852 composition des populations de macroalgues sur le récif corallien de Tiahura (Île
853 de Moorea, Polynésie française). CRYPTOLOGIE. ALGOLOGIE 3, 229–240.
- 854 Penna, A., Vila, M., Fraga, S., Giacobbe, M.G., Francesco, A., Riobó, P., Vernesi, C.,
855 2005. Characterization of *Ostreopsis* and *Coolia* (Dinophyceae) isolates in the
856 western Mediterranean Sea based on morphology, toxicity and internal
857 transcribed spacer 5.8s rDNA sequences. J. Phycol. 41, 212–225.
858 <https://doi.org/10.1111/J.1529-8817.2005.04011.x>
- 859 Perini, F., Casabianca, A., Battocchi, C., Accoroni, S., Totti, C., Penna, A., 2011. New
860 approach using the real-time PCR method for estimation of the toxic marine
861 dinoflagellate *Ostreopsis* cf. *ovata* in marine environment. PLoS ONE 6.
862 <https://doi.org/10.1371/journal.pone.0017699>
- 863 Pessarrodona, A., Filbee-Dexter, K., Alcoverro, T., Boada, J., Feehan, C.J., Fredriksen,
864 S., Grace, S.P., Nakamura, Y., Narvaez, C.A., Norderhaug, K.M., Wernberg, T.,
865 n.d. Homogenization and miniaturization of habitat structure in temperate marine
866 forests. Global Change Biology n/a. <https://doi.org/10.1111/gcb.15759>
- 867 Pfannkuchen, M., Godrijan, J., Pfannkuchen, D.M., Ivesa, L., Kruzic, P., Ciminiello, P.,
868 Dell'Aversano, C., Dello Iacovo, E., Fattorusso, E., Forino, M., Tartaglione, L.,
869 Godrijan, M., 2012. Toxin-Producing *Ostreopsis* cf. *ovata* are Likely to Bloom
870 Undetected along Coastal Areas. Environ. Sci. Technol. 46, 5574–5582.
871 <https://doi.org/10.1021/es300189h>

- 872 Pocsidio, G.N., Dimaano, L.M., 2004. The population densities of potentially toxic
873 epiphytic dinoflagellates in Lingsat Reef, La Union Province, Philippines. Philipp.
874 Agric. Sci. 87, 148–159.
- 875 Quod, J.P., 1994. *Ostreopsis mascarenensis* sp. nov. (Dinophyceae), a new toxic
876 dinoflagellate from coral reefs in the South West Indian Ocean. Cryptogam. Algol.
877 Paris 15, 243–251.
- 878 Rains, L.K., Parsons, M.L., 2015. Gambierdiscus species exhibit different epiphytic
879 behaviors toward a variety of macroalgal hosts. HARMFUL ALGAE 49, 29–39.
880 <https://doi.org/10.1016/j.hal.2015.08.005>
- 881 Ramos, V., Vasconcelos, V., 2010. Palytoxin and analogs: Biological and ecological
882 effects. Mar. Drugs 8, 2021–2037. <https://doi.org/10.3390/md8072021>
- 883 Rhodes, L., 2011. World-wide occurrence of the toxic dinoflagellate genus *Ostreopsis*
884 Schmidt. Toxicon 57, 400–407. <https://doi.org/10.1016/j.toxicon.2010.05.010>
- 885 Rhodes, L., Adamson, J., Suzuki, T., Briggs, L., Garthwaite, I., 2000. Toxic marine
886 epiphytic dinoflagellates, *Ostreopsis siamensis* and *Coolia monotis*
887 (Dinophyceae), in New Zealand. N. Z. J. Mar. Freshw. Res. 34, 371–383.
888 <https://doi.org/10.1080/00288330.2000.9516939>
- 889 Rhodes, L.L., Smith, K.F., Verma, A., Murray, S., Harwood, D.T., Trnski, T., 2017. The
890 dinoflagellate genera *Gambierdiscus* and *Ostreopsis* from subtropical Raoul
891 Island and North Meyer Island, Kermadec Islands. N. Z. J. Mar. Freshw. Res. 51,
892 490–504. <https://doi.org/10.1080/00288330.2016.1270337>

- 893 Richlen, M.L., Lobel, P.S., 2011. Effects of depth, habitat, and water motion on the
894 abundance and distribution of ciguatera dinoflagellates at Johnston Atoll, Pacific
895 Ocean. *Mar. Ecol. Prog. Ser.* 421, 51–66. <https://doi.org/10.3354/meps08854>
- 896 Ruggiero, M.A., Gordon, D.P., Orrell, T.M., Bailly, N., Bourgoin, T., Brusca, R.C.,
897 Cavalier-Smith, T., Guiry, M.D., Kirk, P.M., 2015. A Higher Level Classification of
898 All Living Organisms. *PLOS ONE* 10, e0119248.
899 <https://doi.org/10.1371/journal.pone.0119248>
- 900 Sala, E., Ballesteros, E., Dendrinou, P., Di Franco, A., Ferretti, F., Foley, D., Fraschetti,
901 S., Friedlander, A., Garrabou, J., Güçlüsoy, H., Guidetti, P., Halpern, B.S., Hereu,
902 B., Karamanlidis, A.A., Kizilkaya, Z., Macpherson, E., Mangialajo, L., Mariani, S.,
903 Micheli, F., Pais, A., Riser, K., Rosenberg, A.A., Sales, M., Selkoe, K.A., Starr,
904 R., Tomas, F., Zabala, M., 2012. The Structure of Mediterranean Rocky Reef
905 Ecosystems across Environmental and Human Gradients, and Conservation
906 Implications. *PLoS ONE* 7. <https://doi.org/10.1371/journal.pone.0032742>
- 907 Sales, M., Ballesteros, E., 2010. Long-term comparison of algal assemblages dominated
908 by *Cystoseira crinita* (Fucales, Heterokontophyta) from Cap Corse (Corsica,
909 North Western Mediterranean). *Eur. J. Phycol.* 45, 404–412.
910 <https://doi.org/10.1080/09670262.2010.498585>
- 911 Selina, M.S., Morozova, T.V., Vyshkvartsev, D.I., Orlova, T.Yu., 2014. Seasonal
912 dynamics and spatial distribution of epiphytic dinoflagellates in Peter the Great
913 Bay (Sea of Japan) with special emphasis on *Ostreopsis* species. *HARMFUL*
914 *ALGAE* 32, 1–10. <https://doi.org/10.1016/j.hal.2013.11.005>

- 915 Shah, Md.M.R., An, S.-J., Lee, J.-B., 2013. Seasonal abundance of epiphytic
916 dinoflagellates around coastal waters of Jeju Island, Korea. *J. Mar. Sci. Technol.-*
917 *TAIWAN* 21, 156–165. <https://doi.org/10.6119/JMST-013-1220-5>
- 918 Shears, N.T., Ross, P.M., 2010. Toxic cascades: Multiple anthropogenic stressors have
919 complex and unanticipated interactive effects on temperate reefs. *Ecol. Lett.* 13,
920 1149–1159. <https://doi.org/10.1111/j.1461-0248.2010.01512.x>
- 921 Shears, N.T., Ross, P.M., 2009. Blooms of benthic dinoflagellates of the genus
922 *Ostreopsis*; an increasing and ecologically important phenomenon on temperate
923 reefs in New Zealand and worldwide. *HARMFUL ALGAE* 8, 916–925.
924 <https://doi.org/10.1016/j.hal.2009.05.003>
- 925 Shelamoff, V., Layton, C., Tatsumi, M., Cameron, M.J., Wright, J.T., Johnson, C.R.,
926 2019. Ecosystem engineering by a canopy-forming kelp facilitates the
927 recruitment of native oysters. *Restor. Ecol.* 27, 1442–1451.
928 <https://doi.org/10.1111/rec.13019>
- 929 Simoni, F., Di Paolo, C., Nuti, S., Lepri, L., Melley, A., Gaddi, A., 2004. Harmful epiphytic
930 dinoflagellates on the reefs of North Tyrrhenian Sea. *Biol. Mar. Mediterr.* 11, 530–
931 533.
- 932 Skinner, M.P., Lewis, R.J., Morton, S., 2011. The abundance of potentially toxic epiphytic
933 dinoflagellates and nutrients from Bali and Gili Trawangan, Indonesia. *Mar. Res.*
934 *Indones.* 36, 11–23.

- 935 Solino, L., Garcia-Altare, M., Godinho, L., Silva, A., Costa, P.R., 2020. Toxin Profile of
936 *Ostreopsis* cf. *ovata* from Continental Portuguese Coast and Selvagens Islands
937 (Madeira, Portugal). *Mar. Drugs* 18.
- 938 Sparrow, L., Momigliano, P., Russ, G.R., Heimann, K., 2017. Effects of temperature,
939 salinity and composition of the dinoflagellate assemblage on the growth of
940 *Gambierdiscus carpenteri* isolated from the Great Barrier Reef. *HARMFUL*
941 *ALGAE* 65, 52–60. <https://doi.org/10.1016/j.hal.2017.04.006>
- 942 Stewart, J.G., 1983. Fluctuations in the quantity of sediments trapped among algal thalli
943 on intertidal rock platforms in southern California. *J. Exp. Mar. Biol. Ecol.* 73, 205–
944 211. [https://doi.org/10.1016/0022-0981\(83\)90047-3](https://doi.org/10.1016/0022-0981(83)90047-3)
- 945 Stiger, V., Payri, C.E., 1999. Spatial and Seasonal Variations in the Biological
946 Characteristics of Two Invasive Brown Algae, *Turbinaria ornata* (Turner) J.
947 Agardh and *Sargassum mangarevense* (Grunow) Setchell (Sargassaceae,
948 Fucales) Spreading on the Reefs of Tahiti (French Polynesia). *Botanica Marina*
949 42. <https://doi.org/10.1515/BOT.1999.033>
- 950 Strain, E.M.A., Thomson, R.J., Micheli, F., Mancuso, F.P., Airoldi, L., 2014. Identifying
951 the interacting roles of stressors in driving the global loss of canopy-forming to
952 mat-forming algae in marine ecosystems. *Glob. Change Biol.* 20, 3300–3312.
953 <https://doi.org/10.1111/gcb.12619>
- 954 Suzuki, T., Watanabe, R., Uchida, H., Matsushima, R., Nagai, H., Yasumoto, T.,
955 Yoshimatsu, T., Sato, S., Adachi, M., 2012. LC-MS/MS analysis of novel ovatoxin
956 isomers in several *Ostreopsis* strains collected in Japan. *HARMFUL ALGAE* 20,
957 81–91. <https://doi.org/10.1016/j.hal.2012.08.002>

- 958 Ternon, E., Paix, B., Thomas, O.P., Briand, J.-F., Culioli, G., 2020. Exploring the Role of
959 Macroalgal Surface Metabolites on the Settlement of the Benthic Dinoflagellate
960 *Ostreopsis cf. ovata*. *Front. Mar. Sci.* 7.
961 <https://doi.org/10.3389/fmars.2020.00683>
- 962 Tester, P.A., Kibler, S.R., Holland, W.C., Usup, G., Vandersea, M.W., Leaw, C.P.,
963 Teen, L.P., Larsen, J., Mohammad-Noor, N., Faust, M.A., Litaker, R.W.,
964 2014. Sampling harmful benthic dinoflagellates: Comparison of artificial
965 and natural substrate methods. *HARMFUL ALGAE* 39, 825.
966 <https://doi.org/10.1016/j.hal.2014.06.009>.
- 967 Tester, P.A., Litaker, R.W., Berdalet, E., 2020. Climate change and harmful benthic
968 microalgae. *Harmful Algae, Climate change and harmful algal blooms* 91,
969 101655. <https://doi.org/10.1016/j.hal.2019.101655>
- 970 Thiriet, P., Cheminée, A., Mangialajo, L., Francour, P., 2014. How 3D Complexity of
971 Macrophyte-Formed Habitats Affect the Processes Structuring Fish
972 Assemblages Within Coastal Temperate Seascapes?, in: Musard, O., Le Dû-
973 Blayo, L., Francour, P., Beurier, J.-P., Feunteun, E., Talassinou, L. (Eds.),
974 *Underwater Seascapes: From Geographical to Ecological Perspectives*. Springer
975 International Publishing, Cham, pp. 185–199. [https://doi.org/10.1007/978-3-319-](https://doi.org/10.1007/978-3-319-03440-9_12)
976 [03440-9_12](https://doi.org/10.1007/978-3-319-03440-9_12)
- 977 Thiriet, P.D., Franco, A.D., Cheminée, A., Guidetti, P., Bianchimani, O., Basthard-
978 Bogain, S., Cottalorda, J.-M., Arceo, H., Moranta, J., Lejeune, P., Francour, P.,
979 Mangialajo, L., 2016. Abundance and Diversity of Crypto- and Necto-Benthic
980 Coastal Fish Are Higher in Marine Forests than in Structurally Less Complex

- 981 Macroalgal Assemblages. PLOS ONE 11, e0164121.
982 <https://doi.org/10.1371/journal.pone.0164121>
- 983 Tibirica, C.E.J.A., Leite, I.P., Batista, T.V.V., Fernandes, L.F., Chomerat, N., Herve, F.,
984 Hess, P., Mafra, L.L., Jr., 2019. *Ostreopsis* cf. *ovata* Bloom in Currais, Brazil:
985 Phylogeny, Toxin Profile and Contamination of Mussels and Marine Plastic Litter.
986 TOXINS 11. <https://doi.org/10.3390/toxins11080446>
- 987 Tichadou, L., Glaizal, M., Armengaud, A., Grosseil, H., Lemée, R., Kantin, R., Lasalle, J.-
988 L., Drouet, G., Rambaud, L., Malfait, P., De Haro, L., 2010. Health impact of
989 unicellular algae of the *Ostreopsis* genus blooms in the Mediterranean Sea:
990 Experience of the French Mediterranean coast surveillance network from 2006
991 to 2009. Clin. Toxicol. 48, 839–844.
992 <https://doi.org/10.3109/15563650.2010.513687>
- 993 Tittley, I., Neto, A.I., 1995. The marine algal flora of the Azores and its biogeographical
994 affinities. Boletim do Museu Municipal do Funchal, 747-766.
995 <http://hdl.handle.net/10400.3/2015>
- 996 Totti, C., Accoroni, S., Cerino, F., Cucchiari, E., Romagnoli, T., 2010. *Ostreopsis ovata*
997 bloom along the Conero Riviera (northern Adriatic Sea): Relationships with
998 environmental conditions and substrata. HARMFUL ALGAE 9, 233–239.
999 <https://doi.org/10.1016/j.hal.2009.10.006>
- 1000 Tubaro, A., Durando, P., Del Favero, G., Ansaldi, F., Icardi, G., Deeds, J.R., Sosa, S.,
1001 2011. Case definitions for human poisonings postulated to palytoxins exposure.
1002 Toxicol. 57, 478–495. <https://doi.org/10.1016/j.toxicol.2011.01.005>

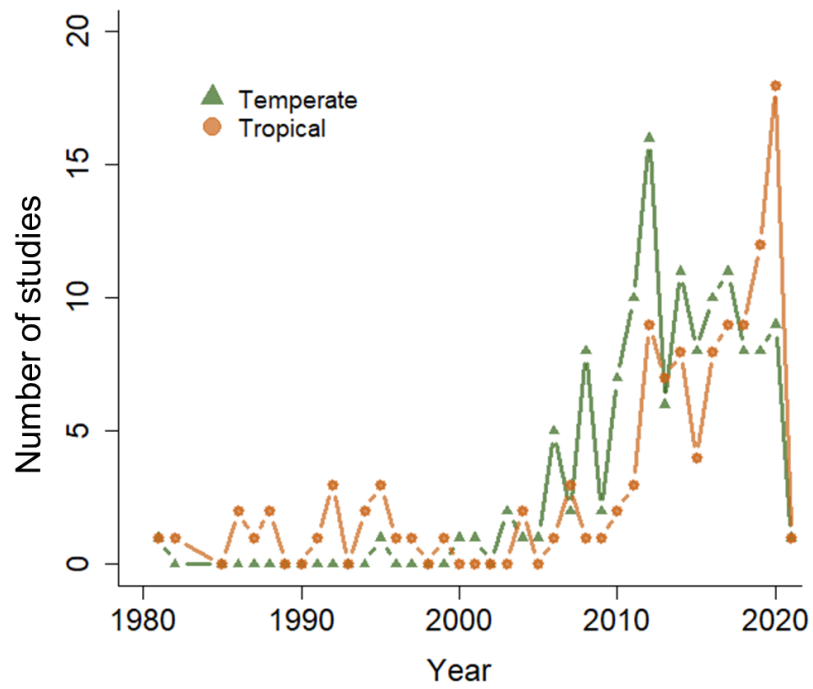
- 1003 Turki, S., 2005. Distribution of toxic dinoflagellates along the leaves of seagrass
1004 *Posidonia oceanica* and *Cymodocea nodosa* from the Gulf of Tunis. *Cah. Biol.*
1005 *Mar.* 46, 29–34.
- 1006 Turner, A.D., Lewis, A.M., Bradley, K., Maskrey, B.H., 2021. Marine invertebrate
1007 interactions with Harmful Algal Blooms - implications for One Health. *J. Invertebr.*
1008 *Pathol.* 107555. <https://doi.org/10.1016/j.jip.2021.107555>
- 1009 Ukena, T., Satake, M., Usami, M., Oshima, Y., Naoki, H., Fujita, T., Kan, Y., Yasumoto,
1010 T., 2001. Structure elucidation of ostreocin D, a palytoxin analog isolated from
1011 the dinoflagellate *Ostreopsis siamensis*. *Biosci. Biotechnol. Biochem.* 65, 2585–
1012 2588. <https://doi.org/10.1271/bbb.65.2585>
- 1013 Ungaro, N., Assennato, G., Blonda, M., Cudillo, B., Petruzzelli, M.R., Mariani, M.,
1014 Pastorelli, A.M., Aliquò, M.R., D'Angela, A., Aiello, C., Ranieri, S., 2010.
1015 Occurrence of the potentially toxic dinoflagellate *ostreopsis ovata* along the
1016 apulian coastal areas (Southern Italy) and relationship with anthropogenic
1017 pollution. *Fresenius Environ. Bull.* 19, 1813–1821.
- 1018 Usami, M., Satake, M., Ishida, S., Yasumoto, T., Oue, A., Kan, Y., 1995. Palytoxin
1019 Analogs from the Dinoflagellate *Ostreopsis siamensis*. *J. Am. Chem. Soc.* 117,
1020 5389–5390. <https://doi.org/10.1021/ja00124a034>
- 1021 Varela, A.T., Neves, R.A.F., Nascimento, S.M., Oliveira, P.J., Pardal, M.A., Rodrigues,
1022 E.T., Moreno, A.J., 2021. Exposure to marine benthic dinoflagellate toxins may
1023 lead to mitochondrial dysfunction. *Comp. Biochem. Physiol. Part C Toxicol.*
1024 *Pharmacol.* 240, 108937. <https://doi.org/10.1016/j.cbpc.2020.108937>

- 1025 Vassalli, M., Penna, A., Sbrana, F., Casabianca, S., Gjerci, N., Capellacci, S., Asnaghi,
1026 V., Ottaviani, E., Giussani, V., Pugliese, L., Jauzein, C., Lemee, R., Hachani,
1027 M.A., Turki, S., Acaf, L., Saab, M.A.-A., Fricke, A., Mangialajo, L., Bertolotto, R.,
1028 Totti, C., Accoroni, S., Berdalet, E., Vila, M., Chiantore, M., 2018. Intercalibration
1029 of counting methods for *Ostreopsis* spp. blooms in the Mediterranean Sea. *Ecol.*
1030 *Indic.* 85, 1092–1100. <https://doi.org/10.1016/j.ecolind.2017.07.063>
- 1031 Vergés, A., Steinberg, P.D., Hay, M.E., Poore, A.G.B., Campbell, A.H., Ballesteros, E.,
1032 Heck, K.L., Booth, D.J., Coleman, M.A., Feary, D.A., Figueira, W., Langlois, T.,
1033 Marzinelli, E.M., Mizerek, T., Mumby, P.J., Nakamura, Y., Roughan, M., van
1034 Seville, E., Gupta, A.S., Smale, D.A., Tomas, F., Wernberg, T., Wilson, S.K.,
1035 2014. The tropicalization of temperate marine ecosystems: climate-mediated
1036 changes in herbivory and community phase shifts. *Proc. R. Soc. B Biol. Sci.* 281,
1037 20140846. <https://doi.org/10.1098/rspb.2014.0846>
- 1038 Vila, M., Abos-Herrandiz, R., Isern-Fontanet, J., Alvarez, J., Berdalet, E., 2016.
1039 Establishing the link between *Ostreopsis* cf. *ovata* blooms and human health
1040 impacts using ecology and epidemiology. *Sci. Mar.* 80, 107–115.
1041 <https://doi.org/10.3989/scimar.04395.08A>
- 1042 Vila, M., Arin, L., Battocchi, C., Bravo, I., Fraga, S., Penna, A., Rene, A., Riobo, P.,
1043 Rodriguez, F., Montserrat Sala, M., Camp, J., de Torres, M., Franco, J.M., 2012.
1044 Management of *Ostreopsis* blooms in recreational waters along the Catalan coast
1045 (NW Mediterranean Sea): cooperation between a research project and a
1046 monitoring program. *Cryptogam. Algal.* 33, 143–152.
1047 <https://doi.org/10.7872/crya.v33.iss2.2011.143>

- 1048 Vila, M., Garcés, E., Masó, M., 2001. Potentially toxic epiphytic dinoflagellate
1049 assemblages on macroalgae in the NW Mediterranean. *Aquat. Microb. Ecol.* 26,
1050 51–60. <https://doi.org/10.3354/ame026051>
- 1051 Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M.,
1052 Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H.,
1053 Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A.,
1054 Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A., Wilson, S., 2016.
1055 Climate-driven regime shift of a temperate marine ecosystem. *Science* 353, 169–
1056 172. <https://doi.org/10.1126/science.aad8745>
- 1057 Widiarti, R., 2008. The potentially toxic benthic dinoflagellates on macroalgae at the reef
1058 flat of Seribu Island, north Jakarta-Indonesia. *Mar. Res. Indones.* 33, 91–94.
- 1059 Widiarti, R., Anggraini, F., 2012. The distribution of toxic dinoflagellates on sea grass
1060 *Enhalus acoroides* at Pari Island, Seribu Islands. *J. Ilmu Dan Teknol. Kelaut.*
1061 *Trop.* 4, 247–258.
- 1062 Widiarti, R., Murtiningsih, -, Suwanti, -, Mutaqin, A., Kurnia, G.E., 2008. The potentially
1063 toxic benthic dinoflagellates on macroalgae at the reef flat of Seribu Island, north
1064 Jakarta-Indonesia. *Mar. Res. Indones.* 33, 91–94.
1065 <https://doi.org/10.14203/mri.v33i1.462>
- 1066 Xu, Y., Richlen, M.L., Morton, S.L., Mak, Y.L., Chan, L.L., Tekiau, A., Anderson, D.M.,
1067 2014. Distribution, abundance and diversity of *Gambierdiscus* spp. from a
1068 ciguatera-endemic area in Marakei, Republic of Kiribati. *HARMFUL ALGAE* 34,
1069 56–68. <https://doi.org/10.1016/j.hal.2014.02.007>

- 1070 Yamaguchi, H., Tanimoto, Y., Yoshimatsu, T., Sato, S., Nishimura, T., Uehara, K.,
1071 Adachi, M., 2012. Culture method and growth characteristics of marine benthic
1072 dinoflagellate *Ostreopsis* spp. isolated from Japanese coastal waters. *Fish. Sci.*
1073 78, 993–1000. <https://doi.org/10.1007/s12562-012-0530-4>
- 1074 Yong, H.L., Mustapa, N.I., Lee, L.K., Lim, Z.F., Tan, T.H., Usup, G., Gu, H., Litaker, R.W.,
1075 Tester, P.A., Lim, P.T., Leaw, C.P., 2018. Habitat complexity affects benthic
1076 harmful dinoflagellate assemblages in the fringing reef of Rawa Island, Malaysia.
1077 *HARMFUL ALGAE* 78, 56–68. <https://doi.org/10.1016/j.hal.2018.07.009>
- 1078 Zou, J., Li, Q., Lu, S., Dong, Y., Chen, H., Zheng, C., Cui, L., 2020. The first benthic
1079 harmful dinoflagellate bloom in China: Morphology and toxicology of
1080 *Prorocentrum concavum*. *Mar. Pollut. Bull.* 158, 111313.
1081 <https://doi.org/10.1016/j.marpolbul.2020.111313>
1082

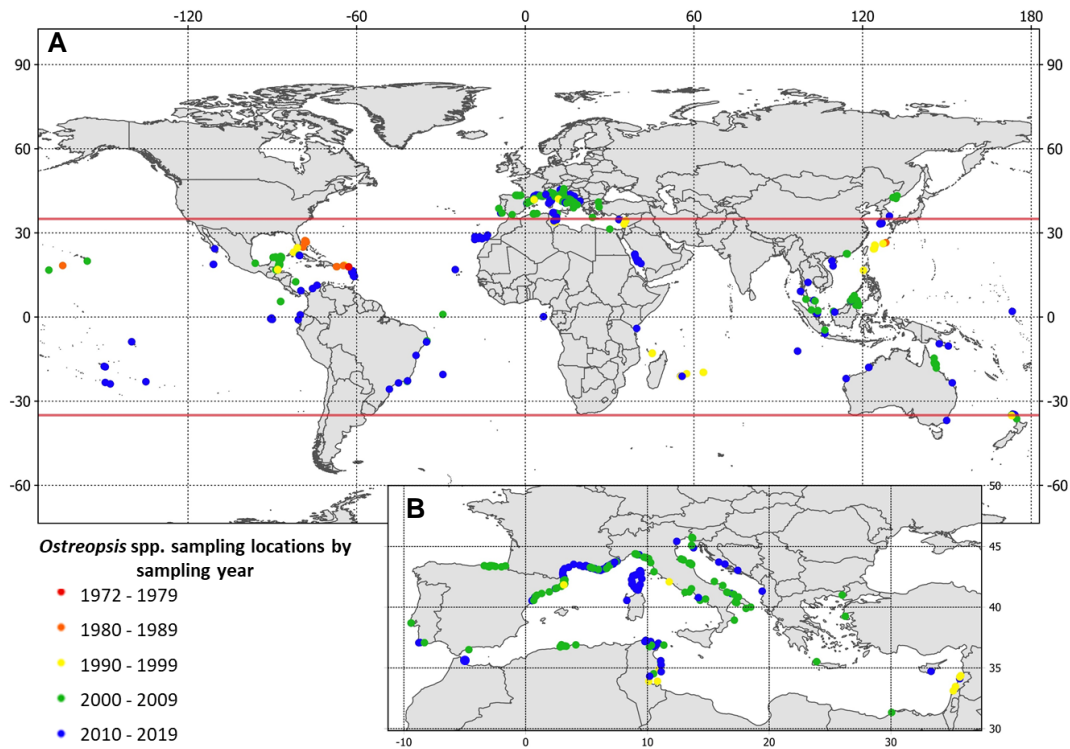
1083



1084

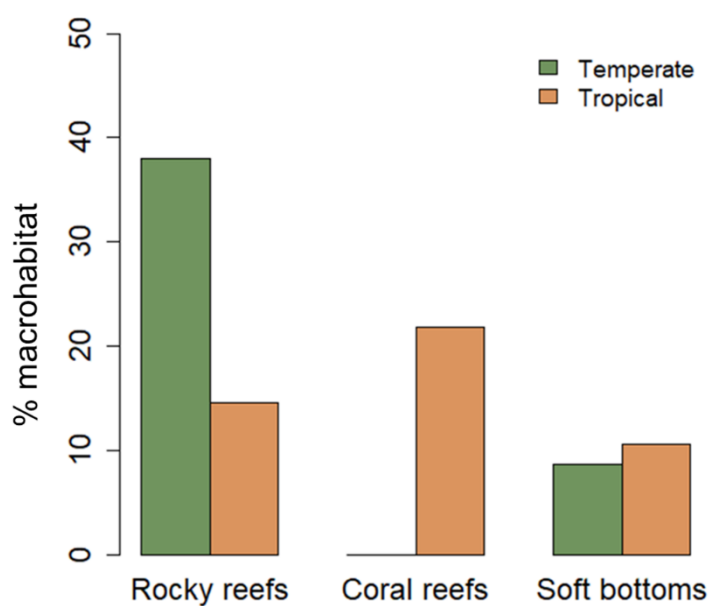
1085

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



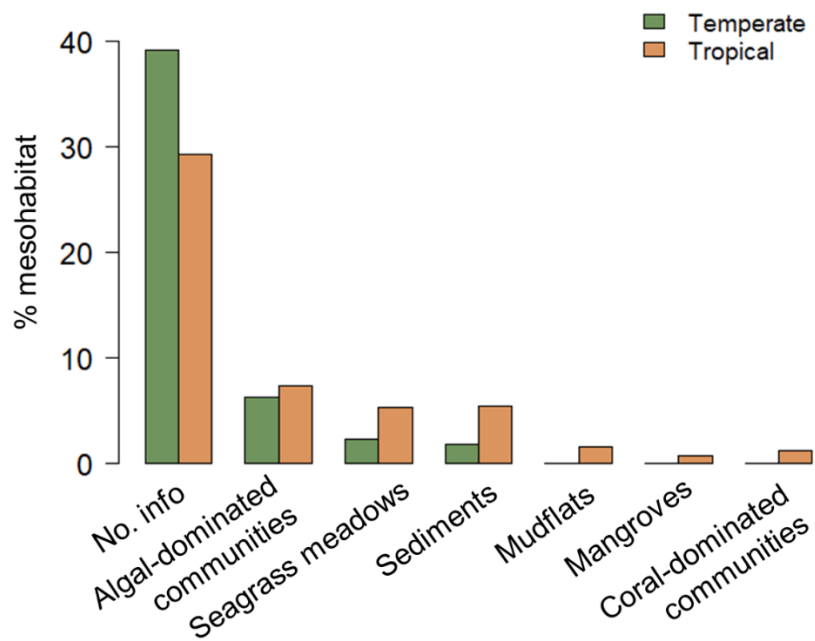
1088

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.



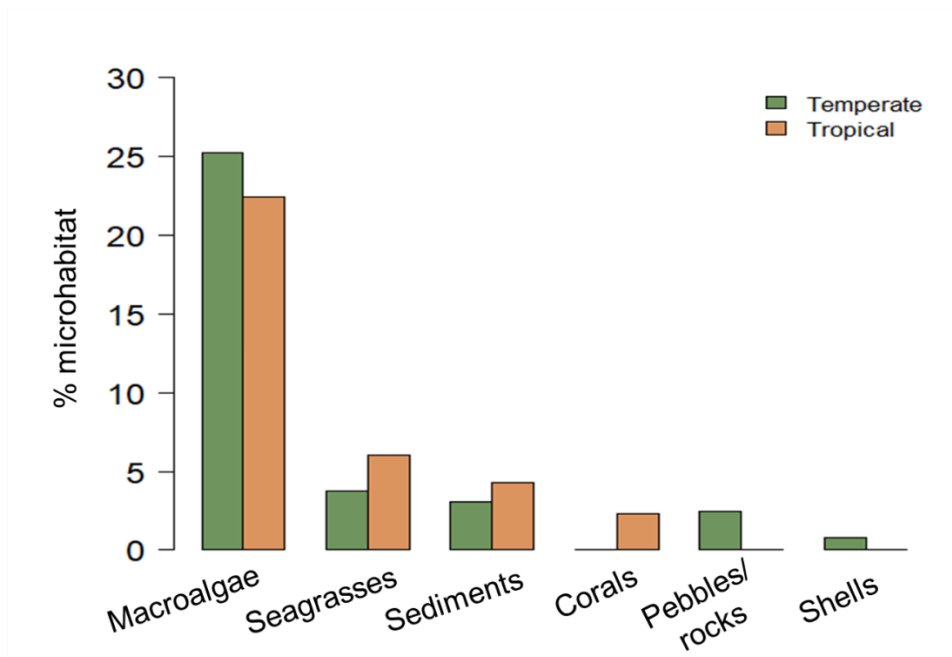
1092

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



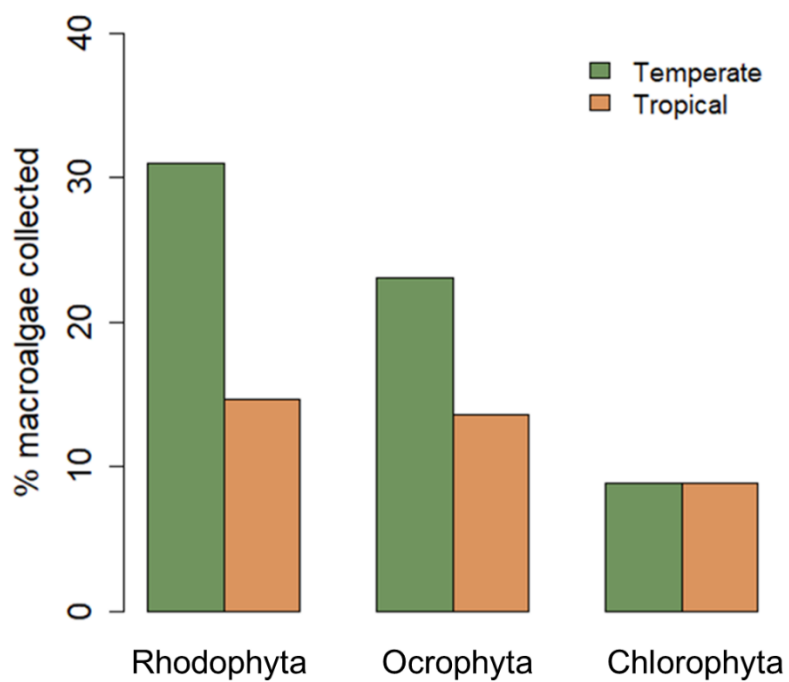
1095

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



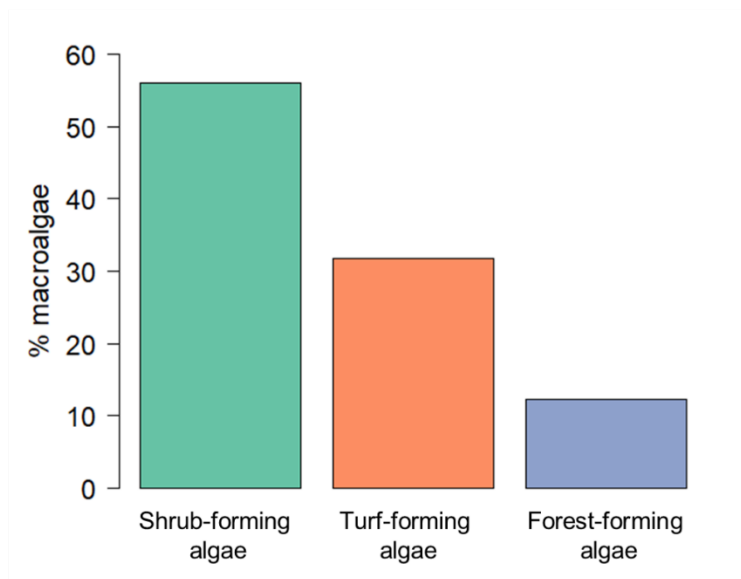
1098

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



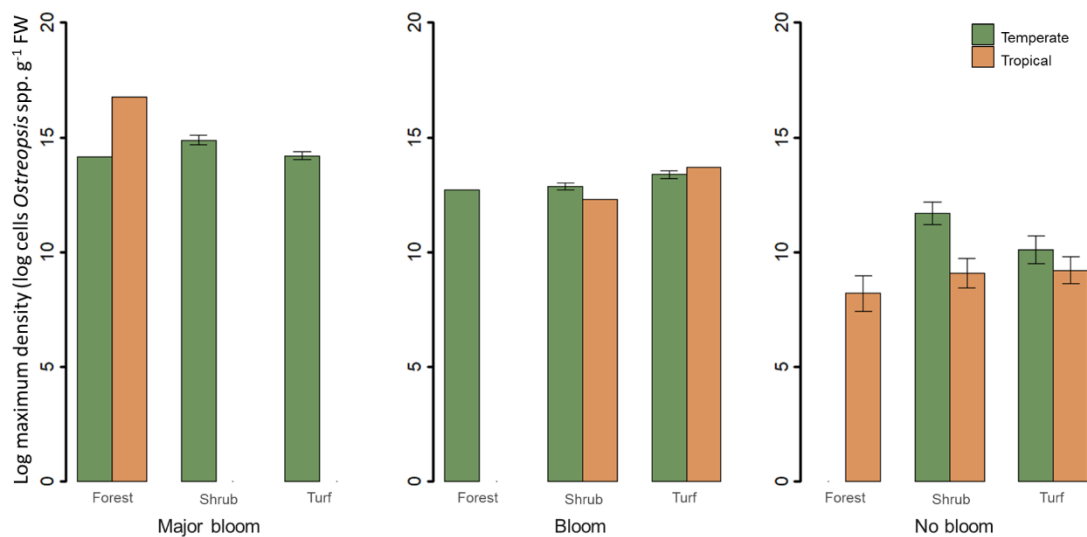
1101

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)