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RESEARCH ARTICLE

Distribution and abundance of *Ostreopsis* spp. and associated species (Dinophyceae) in the northwestern Mediterranean: the region and the macroalgal substrate matter

Aurélie Blanfuné[1] · **Charles François Boudouresque**[1] · **Hubert Grossel**[2] · **Thierry Thibaut**[1]

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Abstract The range of *Ostreopsis* (Dinophyceae), a taxon harmful to both human health and ecosystems, has spread from a tropical and subtropical range of distribution to temperate areas, such as the Mediterranean Sea. This study has evidenced widespread summer occurrence in the northwestern Mediterranean, from French Catalonia to the French Riviera and Corsica. *Ostreopsis* spp. are usually associated with two other dinophycean taxa, *Prorocentrum lima* and *Coolia* spp. No obvious correlation (indicative of competition and/or facilitation) between the abundance of the three taxa was evidenced. In addition to local variability, we observed regional variability, with low abundance and local absence in French Catalonia and Languedoc, which contrasted with overall abundance and blooms in Provence, the French Riviera and Corsica, especially in late summer. Possible causes for this regional variability are discussed. Furthermore, the three taxa can grow on a variety of macroalgal substrates: 34 taxa belonging to the fleshy, bushy, flat and erect morpho-functional groups. Some macroalgal species were correlated with either high or low abundance of the studied dinophycean taxa and could therefore enhance or hinder their blooming.

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✉ Aurélie Blanfuné
aurelie.blanfune-thibaut@mio.osupytheas.fr

[1] Aix Marseille University, CNRS/INSU, University Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, 13288 Marseille, France

[2] Ifremer, Institut français de recherche pour l'exploitation de la mer, Centre de Méditerranée, Laboratoire Environnement/Ressources, ZP de Brégaillon, BP 330, 83507 La Seyne sur mer, France

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Introduction

For several decades, occurrences of harmful benthic 'microalgal'[1] blooms have strongly increased worldwide in frequency and intensity. This trend is likely to continue (Rhodes 2011). Among the Dinophyceae (kingdom Alveolata), these phenomena are observed in particular for the genus *Ostreopsis*. In the past, species of *Ostreopsis* were often observed in tropical and subtropical areas (Ballantine et al. 1988; Morton et al. 1992; Grzebyk et al. 1994). In 1995, the worldwide distribution of *Ostreopsis* spp. ranged between latitudes 28° N and 20° S (Faust et al. 1996). However, today, its distribution area has considerably expanded (Rhodes 2011) and extends between latitudes 45° N and 35° S. Over the last decade, massive proliferations of *Ostreopsis* spp. have become more common in temperate areas. Two species are mainly involved, *Ostreopsis siamensis* Schmidt and *Ostreopsis ovata* Fukuyo (Rhodes 2011). In the southern hemisphere, proliferation of *Ostreopsis* spp. has been reported in New Zealand (Chang et al. 2000; Rhodes et al. 2000; Shears and Ross 2009), Australia (Pearse et al. 2001; Rhodes 2011), Brazil (Granéli et al. 2002) and Hawaii (Parsons and Preskitt 2007). In the northern hemisphere, outbreaks of *Ostreopsis* spp. were reported in Japan (Taniyama et al. 2003; Rhodes 2011), Russia (Selina and Orlova 2010; Selina and Levchenko 2011) and throughout the Mediterranean Sea. Concerning the Mediterranean Sea, the authors referred to the observed material as *Ostreopsis* sp.,

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[1] Inverted commas highlight the fact that the term 'algae' does not refer to a taxon, but to a highly polyphyletic set of unrelated taxa.

Ostreopsis spp., *O. ovata*, *O.* cf. *ovata*, *O. siamensis*, and *O.* cf. *siamensis*. In the western Mediterranean, two distinct species have been reported, *O.* cf. *siamensis* from Catalonia, Andalusia and Sicily and *O. ovata* from Catalonia, the Balearic Islands, the Ligurian coast and the southern Tyrrhenian Sea (Penna et al. 2005, 2010; Battocchi et al. 2010; Bravo et al. 2010). The first observation of *Ostreopsis* sp. dates back to 1972 at Villefranche-sur-Mer (southern France) (Taylor 1979), but the first bloom event of *O.* cf. *ovata* occurred in 1998 in Tuscany (Italy) (Sansoni et al. 2003). Subsequently, *Ostreopsis* spp. outbreaks have been reported in the Balearic islands (Vila et al. 2001a, 2001b; Penna et al. 2005; Battocchi et al. 2010), the Ligurian Sea (Ciminiello et al. 2006; Mangialajo et al. 2008, 2011; Cohu et al. 2011), the Tyrrhenian Sea (Tognetto et al. 1995; Simoni et al. 2003; Penna et al. 2005; Zingone et al. 2006; Guerrini et al. 2010), the Adriatic Sea (Monti et al. 2007; Battocchi et al. 2010; Totti et al. 2010; Guerrini et al. 2010), the Aegean Sea (Aligizaki and Nikolaidis 2006; Aligizaki et al. 2008), Lebanon (Abboud-Abi Saab 1989; Abboud-Abi Saab and El-Bakht 1998) and Tunisia (Turki 2005). These massive proliferations of *Ostreopsis* spp. are usually associated with two other taxa of Dinophyceae, namely *P. lima* and *Coolia* spp. (Vila et al. 2001a; Aligizaki and Nikolaidis 2006) and occur in shallow waters close to the shoreline on macroalgal substrata. The environmental conditions required for blooming are unclear and seem to be very complex (Cohu et al. 2011). Species of the genus *Ostreopsis* produce palytoxin-like toxins and derivates (Ciminiello et al. 2008). This toxin is one of the most potent natural non-protein compounds known to date. Palytoxin-like compounds differ, depending on the *Ostreopsis* species incriminated: *O. siamensis* produces the ostreocin-d (Usami et al. 1995; Ukena et al. 2001) whereas *Ostreopsis* cf. *ovata* produces ovatoxin-a (Ciminiello et al. 2008). The impact of massive proliferations of *Ostreopsis* is harmful to both human health and ecosystems, such as causing negative effects on benthic 'invertebrates',[2] e.g. a loss of spines in the sea urchin *Evechinus chloroticus* (Valenciennes, 1846) (Simoni et al. 2003; Shears and Ross 2009; Shears and Ross 2010; Faimali et al. 2012; but see Blanfuné et al. 2012). Adverse effects on human health such as respiratory difficulties, conjunctivitis and skin irritation can occur either by direct contact with cells and by inhalation (Simoni et al. 2003; Brescianini et al. 2006; Ciminiello et al. 2006; Mangialajo et al. 2008; Tichadou et al. 2010) or by indirect contact through ingestion of seafood (Ito et al. 1996; Yasumoto 1998; Rhodes et al. 2002; Taniyama et al. 2003; Deeds and Schwartz 2010). To date, no intoxication by ingestion has been reported in the Mediterranean Sea (Aligizaki et al. 2008), and symptoms disappear at the same rate as the intensity of the blooms decreases (Durando et al. 2007). In urbanized areas, blooms of *Ostreopsis* spp. can induce beach closures or evacuation of the shoreline, resulting in economic loss for the tourism industry (Sansoni et al. 2003; Ciminiello et al. 2006; Mangialajo et al. 2008; Lemée et al. 2012). Furthermore, in the case of bloom events in mussel culture areas, the closure of fish farms can be imposed, also inducing economic loss.

Since 2008, further studies have been undertaken along the French Mediterranean coast, but only a few sites were studied; every year, blooms reappear during summer time. They start in June and never persist beyond August (Mangialajo et al. 2011; Cohu et al. 2011, 2013).

The goal of the present study was (i) to assess the distribution and abundance of *Ostreopsis* spp., together with associated Dinophyceae, along the French Mediterranean Coast from the Spanish to the Italian border and around Corsica Island (3 186 km, measured on a 1/2 500 map) and (ii) to investigate the possible relationship between the abundance of the studied dinophycean taxa and the macroalgal substrates.

Materials and methods

During summer 2011, three sampling campaigns were carried out: the first in June (weeks 23–24), the second in July (weeks 27–28) and the third in August (weeks 31–32). Seventy-nine sites were studied along the French Mediterranean coast (Fig. 1): 20 sites in French Catalonia and Languedoc (LC1 through LC20), 39 in Provence and the French Riviera (PR1 through PR39) and 20 in Corsica (CO1 through CO20). Only three campaigns were carried out, as the kinetics of the bloom was beyond the scope of the present study. Locality, acronym and coordinates of each study site are given in Table 1.

Samples of 'macroalgae' were randomly collected on available hard substrates; the distance (as the crow flies) between samples was ~25–50 km, while closer samples (~5–10 km) were collected along the rocky shore of French Catalonia and in Provence and the French Riviera in order to assess the local variability. The depth was 0.3 to 0.5 m; depth was referred to the limit between the midlitoral and the infralitoral zones (according to Pérès and Picard 1964). This depth range corresponds to the maximum abundance of *Ostreopsis* spp. (Cohu et al. 2013). Macroalgae were gently placed in a plastic flask with the surrounding water in order to limit the loss of dinophycean cells. Samples were immediately fixed with 2 % acid Lugol's solution and kept at 4 °C in the dark. The epibiontic cells were separated from the macroalgae by vigorous shaking. The surrounding water was first filtered on a 250-μm meshed grid, followed by filtration on a 100-μm meshed grid. This protocol was repeated twice by adding 300 mL of filtered sea water (10 μm) each time. The final volume of the surrounding water containing epibiontic cells

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[2] Inverted commas highlight the fact that invertebrates do not refer to a taxon, but to a paraphyletic set of taxa.

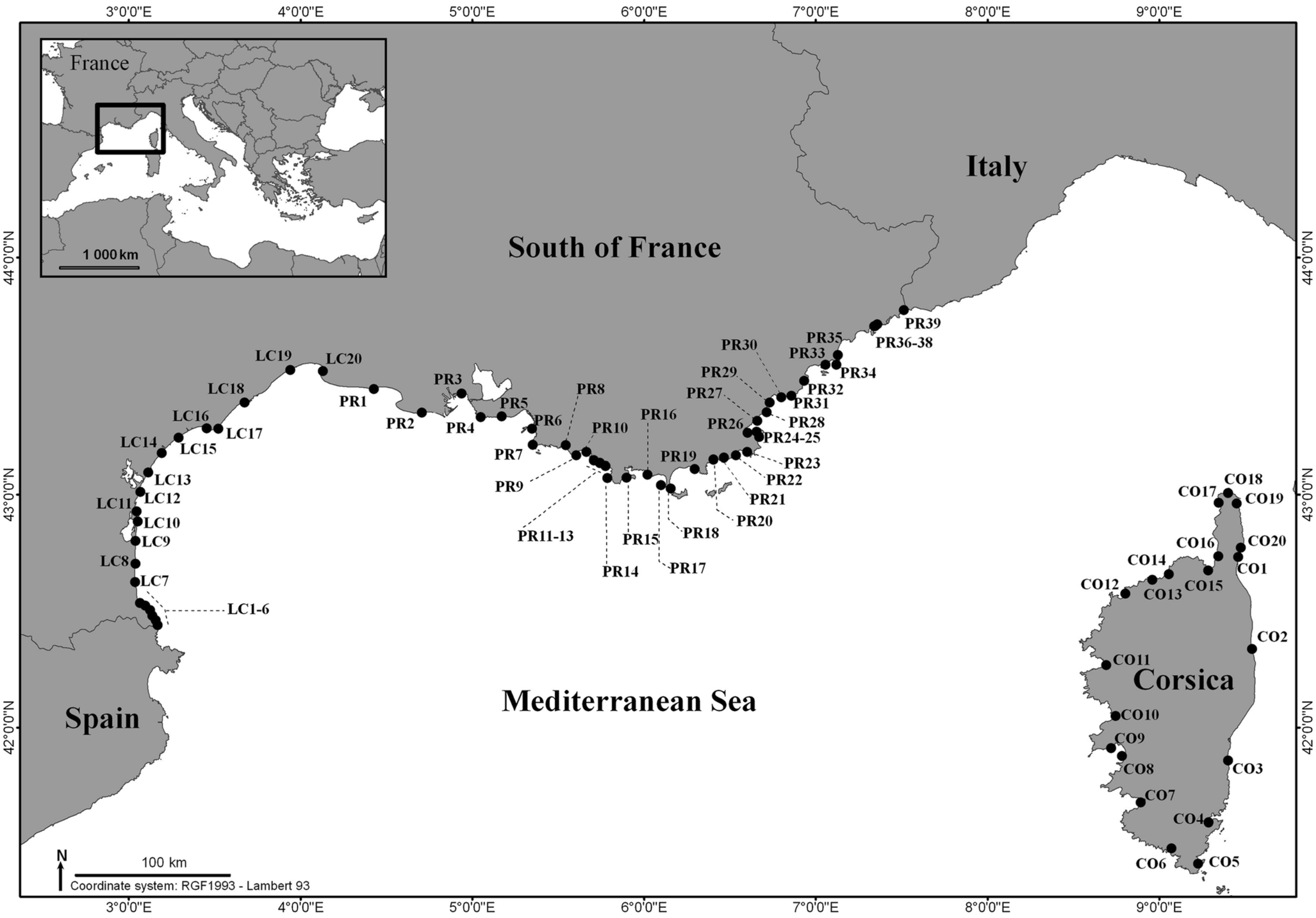

Fig. 1 The 79 sites studied along the French Mediterranean coast during summer 2011

was 1 L. Prior to being weighed (wet mass, ±0.01 g), the macroalgae were cleaned of detritus and roughly wiped with absorbent paper. Only three Dinophyceae taxa were taken into account in the assessment of cell abundance: *Ostreopsis* spp., *P. lima* (Ehrenberg) F. Steinand and *Coolia* spp. Cells were counted by means of an optical microscope using calibrated squared chambers (1 mL; Sedgwick Rafter®). Results were expressed as number of cells per gram of wet mass of macroalgae (cell g^{-1} WM).

Macroalgae that constitute the substrate of Dinophyceae belonged to Chlorophyta, Florideophyceae (kingdom Archaeplastida) and Phaeophyceae (kingdom Stramenopiles). Identification was done by one of the co-authors of this work (TT). In each sample, only taxa accounting for at least 20 % of the wet mass were taken into consideration here.

In order to compare macroalgal assemblage composition, as a function of the various factors of dinophycean abundance, regional effect on dinophycean abundance and potential competition/facilitation effect between the three studied taxa, we performed a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) based on the S17 Bray Curtis similarity matrixes (Clarke and Warwick 1994; Clarke and Gorley 2006). *P* values were obtained by 999 permutations of residuals under a reduced model. The possible effects of the macroalgal substrate were analysed through a multivariate exploratory approach using non-metric multi-dimensional scaling (nMDS) (Clarke and Gorley 2006). Similarity measure matrixes were calculated from the initial data matrix containing, for each sample, the abundance of considered Dinophyceae after square root transformation. The chosen similarity measure was the S17 Bray Curtis similarity (Clarke and Warwick 1994; Clarke and Gorley 2006); nMDS represents samples as points in low-dimensional space such that the relative distances apart of all points are in the same rank order as the relative similarities of the samples. Finally, for each taxon, correlations of the main macroalgal substrate with the 2-D ordination plot of samples were plotted by displaying correlation vectors. Spearman correlation was used. Only samples with cell abundance higher than 1000 cell g^{-1} WM were considered for nMDS analyses.

Results

Apart from the three studied dinophycean taxa (see below), no other dinophycean taxon was ever found in significant amount

Table 1 Acronym, locality and coordinates of sampling sites. See Fig. 1 for localisation

Acronym	Locality	Coordinates (WGS 84)
LC1	Cerbère	42°26,430 N 3°10,080E
LC2	Banyuls-sur-Mer (Plage de Peyrefitte)	42°27,672 N 3°09,462E
LC3	Banyuls-sur-Mer (Laboratoire Arago)	42°28,907 N 3°08,210E
LC4	Port-Vendres (Anse de Paulilles)	42°30,272 N 3°07,430E
LC5	Collioure (Anse del Rages)	42°31,448 N 3°05,749E
LC6	Argelès-sur-Mer (Le Racou)	42°32,117 N 3°03,903E
LC7	Saint-Cyprien	42°37,496 N 3°02,272E
LC8	Canet-en-Roussillon	42°42,218 N 3°02,355E
LC9	Le Barcarès (Port)	42°48,064 N 3°02,383E
LC10	Leucate	42°53,078 N 3°03,154E
LC11	Leucate (La Franqui)	42°55,753 N 3°02,735E
LC12	Port-la-Nouvelle	43°00,786 N 3°04,078E
LC13	Gruissan (Plage)	43°05,689 N 3°06,835E
LC14	Fleury d'Aude (Saint-Pierre-sur-Mer)	43°10,619 N 3°11,552E
LC15	Valras-Plage	43°14,536 N 3°17,472E
LC16	Agde (Grau d'Agde)	43°16,863 N 3°27,265E
LC17	Agde (Rochers La Roquille)	43°16,852 N 3°31,254E
LC18	Sète (Le Lazaret)	43°23,466 N 3°40,397E
LC19	Palavas-les-Flots	43°31,768 N 3°56,432E
LC20	Grau-du-Roi (Port Camargue)	43°31,434 N 4°07,742E
PR1	Saintes-Maries-de-la-Mer	43°26,940 N 4°25,740E
PR2	Arles (between Beauduc and Grand-Rhône mouth)	43°20,893 N 4°42,531E
PR3	Fos-sur-Mer (Pointe Saint-Gervais)	43°25,728 N 4°56,367E
PR4	Martigues (Cap Couronne)	43°19,775 N 5°03,053E
PR5	Carry-le Rouet (Le Rouet)	43°19,957 N 5°10,311E
PR6	Marseille (Anse des cuivres)	43°16,814 N 5°20,990E
PR7	Marseille (Callelongue)	43°12,733 N 5°21,162E
PR8	Cassis	43°12,628 N 5°32,665E
PR9	La Ciotat	43°09,992 N 5°36,388E
PR10	La Ciotat (Les Lecques)	43°10,934 N 5°39,974E
PR11	Saint-Cyr-sur-Mer (Port d'Alon)	43°08,844 N 5°42,584E
PR12	Bandol	43°08,094 N 5°44,649E
PR13	Sanary-sur-Mer (Baie de Cousse)	43°07,374 N 5°46,590E
PR14	Six-Fours-les Plages (Petit Gaou)	43°04,420 N 5°53,978E
PR15	La Seyne-sur-Mer (Les Sablettes)	43°04,420 N 5°53,978E
PR16	Le Pradet (Oursinières)	43°05,206 N 6°01,262E
PR17	Hyères-les-Palmiers (Giens, La Madrague)	43°02,466 N 6°06,035E
PR18	Hyères-les-Palmiers (Giens, la Tour Fondue)	43°01,663 N 6°09,340E
PR19	Bormes-les-Mimosas (Plage de l'Estagnol)	43°06,572 N 6°17,718E
PR20	Le Lavandou (Plage d'Aigue Belle)	43°08,970 N 6°24,281E
PR21	Rayol-Canadel-sur-Mer (Plage du Cavidel)	43°09,437 N 6°27,934E
PR22	Cavalaire-sur-Mer	43°10,034 N 6°32,170E
PR23	La Croix-Valmer	43°10,910 N 6°36,119E
PR24	Ramatuelle (Plage Tahiti)	43°14,447 N 6°40,142E
PR25	Saint-Tropez (Moulin Blanc)	43°16,451 N 6°39,238E
PR26	Gassin (Cogolin)	43°15,454 N 6°36,131E
PR27	Sainte-Maxime (La Madrague)	43°18,843 N 6°39,617E
PR28	Roquebrune-sur-Argens (Les Issambres)	43°21,008 N 6°42,845E
PR29	Fréjus (Saint-Aygulf)	43°23,468 N 6°43,912E
PR30	Saint-Raphaël (Anse de la Peyguière)	43°24,465 N 6°47,551E

Table 1 (continued)

Acronym	Locality	Coordinates (WGS 84)
PR31	Saint-Raphaël (Anthéor)	43°25,214 N 6°51,423E
PR32	Théoule-sur-Mer (Miramar)	43°29,144 N 6°56,036E
PR33	Cannes	43°33.030 N 7°03,440E
PR34	Juan-les-Pins	43°33,086 N 7°07,188E
PR35	Antibes (Fort Carré)	43°35,555 N 7°07,680E
PR36	Beaulieu-sur-Mer (Port)	43°42,785 N 7°20,464E
PR37	Beaulieu-sur-Mer (Petite Afrique)	43°42,833 N 7°20,667E
PR38	Eze-sur-Mer	43°43,300 N 7°21,481E
PR39	Menton	43°46,842 N 7°30,728E
CO1	San-Martino-di-Lota (Grigione)	42°44,014 N 9°27,661E
CO2	Valle-di-Campoloro	42°20,310 N 9°32,518E
CO3	Sari-Solenzara	41°51,376 N 9°24,131E
CO4	Porto-Vecchio	41°35,316 N 9°17,275E
CO5	Bonifacio (Sant'Amanza)	41°24,530 N 9°13,630E
CO6	Pianotolli-Caldarello	41°28,513 N 9°04,292E
CO7	Propriano	41°40,516 N 8°53,665E
CO8	Grosseto-Prugna (Porticcio)	41°52,598 N 8°47,110E
CO9	Ajaccio	41°54,618 N 8°43,349E
CO10	Calcatoggio (Sagone)	42°03,031 N 8°44,818E
CO11	Ota (Porto)	42°16,159 N 8°41,539E
CO12	Lumio	42°34,346 N 8°48,161E
CO13	Monticello	42°38,073 N 8°57,734E
CO14	Palasca (Ostriconi, Plage Algajola)	42°39,544 N 9°03,439E
CO15	Saint-Florent	42°40,544 N 9°17,183E
CO16	Farinole	42°44,216 N 9°20,704E
CO17	Centuri	42°57,860 N 9°20,816E
CO18	Ersa (Barcaggio)	43°00.425 N 9°24,129E
CO19	Rogliano (Maccinaggio)	42°57,659 N 9°27,178E
CO20	Brando (Erbalunga)	42°46,414 N 9°28,508E

at any site. It is of interest to note that before the beginning of the blooms of *Ostreopsis* spp., a short-lasting bloom of the diatom *Coscinodiscus* sp. (Coscinodiscophyceae) was very often observed.

Occurrence and abundance of *Ostreopsis* spp.

On the basis of visual examination, the collected material seems to correspond to *O. ovata* (small size) rather than to *O. siamensis*. However, in the absence of more accurate taxonomical characterization (electronic microscopy, genetic analysis), which would be beyond the scope of the present study, we hereafter refer the sampled material to *Ostreopsis* spp.

At 9 out of the 20 sites sampled in French Catalonia and Languedoc, *Ostreopsis* spp. were never observed during the 3 months of the study period (LC1, LC2, LC3, LC7, LC11, LC13, LC15, LC18 and LC20). Where present, it was very uncommon, with a maximum density of 56 cells g^{-1} WM (Table 2).

In Provence and the French Riviera, *Ostreopsis* spp. were was observed at all the study sites, with the exception of PR2. Its abundance generally conspicuously increased from June to August and was higher in the eastern part (PR31 through PR39), with density up to ~195,000 cells g^{-1} WM than in the western part, with density generally lower or very much lower than 10,000 cells g^{-1} WM (Table 3).

In Corsica, *Ostreopsis* spp. were recorded at all the study sites. As in Provence and the French Riviera, a distinct seasonal pattern was observed, generally peaking in August. The density was higher along the west coast (CO7 through CO13: up to ~207,000 cells g^{-1} WM) than in other areas (always less than 5000 cells g^{-1} WM) (Table 4).

Occurrence and abundance of *P. lima* and *Coolia* spp.

P. lima and *Coolia* spp. were relatively abundant in the south-western part of French Catalonia and Languedoc (LC1 through LC6) and even conspicuously more abundant than

Table 2 Abundance of the studied dinoflagellates (cells g^{-1} WM macroalgae) along the Languedoc and French Catalonia coast and dominant macroalgae (at least 20 % of the wet mass). For macroalgal abbreviations, see text

	Month	LC 1	LC 2	LC 3	LC 4	LC 5	LC 6	LC 7	LC 8	LC 9	LC 10
Ostreopsis spp.	June	0 - TA	0 - L, TA	0 - DDI, L	7 - HS	9 - C, HS, UL	8 - C, DF	0 - C	9 - P	12 - C, UL, WS	4 - C
	July	0 - L	md	0 - HS	17 - HS	16 - C	21 - HS	md	0 - C	29 - CE	0 - C
	August	0 - L	0 - L	0 - HS	28 - HS	0 - HS	0 - HS	md	0 - C	md	md
Prorocentrum lima	June	8 - TA	115 - L, TA	61 - DDI, L	98 - HS	497 - C, HS, UL	110 - C, DF	7 - C	13 - P	8 - C, UL, WS	8 - C
	July	451 - L	md	3 333 - HS	2 220 - HS	263- C	6 241 - HS	md	24 - C	57 - CE	65 - C
	August	467 - L	26 - L	1 679 - HS	917 - HS	4 870 - HS	2 842 - HS	md	0 - C	md	md
Coolia spp.	June	8 - TA	6 - L, TA	71 - DDI, L	29 - HS	1 012 - C, HS, UL	445 - C, DF	7 - C	4 - P	4 - C, UL, WS	0 - C
	July	133 - L	md	748 - HS	1 556 - HS	82- C	536 - HS	md	0 - C	0 - CE	65 - C
	August	200 - L	0 - L	71 - HS	56 - HS	348 - HS	237- HS	md	0 - C	md	md
	Month	LC 11	LC 12	LC 13	LC 14	LC 15	LC 16	LC 17	LC 18	LC 19	LC 20
Ostreopsis spp.	June	0 - TA	9 - C	0 - C	5 - JR	0 - C, UL, WS	8 - C, PC	3 - C	0 - DF	0 - C, UL	0 - CE, GN
	July	0 - DI	37 - L	0 - C	26 - C	0 - UL	0 - C	56 - C, EC	md	40 - C	0 - P
	August	0 - DDI, TA	md	md	0 - C	md	0 - HS	0 - C	md	0 - C	md
Prorocentrum lima	June	16 - TA	3 - C	0 - C	5 - JR	0 - C, UL, WS	23 - C, PC	0 - C	54 - DF	9 - C, UL	0 - CE, GN
	July	26 - DI	37 - L	29 - C	0 - C	0 - UL	36 - C	111 - C, EC	md	120 - C	0 - P
	August	1 129 - DDI, TA	md	md	0 - C	md	0 - HS	0 - C	md	79 - C	md
Coolia spp.	June	5 - TA	0 - C	0 - C	0 - JR	0 - C, UL, WS	31 - C, PC	10 - C	444 - DF	19 - C, UL	0 - CE, GN
	July	1 105 - DI	1 296 - L	0 - C	26 - C	0 - UL	0 - C	0 - C, EC	md	40 - C	0 - P
	August	1 129 - DDI, TA	md	md	0 - C	md	0 - HS	0 - C	md	79 - C	md

md missing data

Table 3 Abundance of the studied dinoflagellates (cells g^{-1} WM macroalgae) along the Provence and French Riviera coast and dominant macroalgae (at least 20 % of the wet mass). For macroalgal abbreviations, see text

	Month	PR1	PR2	PR3	PR4	PR5	PR6	PR7	PR8	PR9	PR10
Ostreopsis spp.	June	0 - C	0 - UL	0 - DDD	67 - DF	70 - AA	0 - CE, GC, UL	23 - C	243 - HV	33 - DDI, L	0 - DF
	July	0 - UI	0 - HS	1 125 - DDI	0 - DF	md	143 - L	750 - DI	9 304 - HS	38 - HS	350 - L
	August	27 - UL	0 - HF	5 111 - DDD	321- DDI	md	2 560 - CL, UL	4 348 - DI	18 222 - L	1 240 - JR	200 - L
Prorocentrum lima	June	0 - C	0 - UL	0 - DDD	233 - DF	224 - AA	83 - CE, GC, UL	68 - C	568 - HV	3 267 - DDI, L	63 - DF
	July	0 - UI	32 - HS	63 - DDI	286 - DF	md	918 - L	0 - DI	1 870 - HS	1 712 - HS	900 - L
	August	0 - UL	0 - HF	56 - DDD	929 - DDI	md	1 800 - CL, UL	0 - DI	1 524 - L	10 160 - JR	100 - L
Coolia spp.	June	0 - C	0 - UL	525 - DDD	1 317 - DF	3 496 - AA	50 - CE, GC, UL	45 - C	297 - HV	433 - DDI, L	0 - DF
	July	0 - UI	0 - HS	1 000 - DDI	286 - DF	md	531 - L	0 - DI	826 - HS	269 - HS	150 - L
	August	0 - UL	0 - HF	0 – DDD	107 - DDI	md	40 - CL, UL	0 - DI	63 - L	80 - JR	300 - L
	Month	PR11	PR12	PR13	PR14	PR15	PR16	PR17	PR18	PR19	PR20
Ostreopsis spp.	June	0 - HS	40 - HS	0 - DI	0 - CA	0 - CA	160 - HS	13 - HS	0 - DF, DI, HF	5 - UI	23 - HS
	July	519 - DF, HS	3 587 - HS	4 692 - PA	1 795 - HS	2 267 - CCO, L	1 273 - HS	540 - HS	113 - HS, JR	333 - HS	459 - HS, JR
	August	1 000 - L	11 108 - L	1 674 - HS	2 641 - CBB, CC, PP	1 350 - LV, PP	879 - HS, JR	204 - HS	1 087 - HI	66 - CR	605 - HS
Prorocentrum lima	June	3 529 - HS	8 600 - HS	1 615 - DI	163 - CA	0 - CA	3 431 - HS	443 - HS	188 - DF, DI, HF	64 - UI	2 331 - HS
	July	1 241 - DF, HS	7 778 - HS	2 282 - PA	45 182 - HS	3 833 - CCO, L	14 667 - HS	6 400 - HS	3 825 - HS, JR	681 - HS	2 000 - HS, JR
	August	1 128 - L	1 846 - L	2 087 – HS	4 391- CBB, CC, PP	1 800 - LV, PP	2 925 - HS, JR	920 - HS	1 748 - HI	246 - CR	3 263 - HS
Coolia spp.	June	1 500 - HS	560 - HS	821 - DI	14 - CA	0 - CA	195 - HS	135 - HS	254 - DF, DI, HF	0 - UI	423 - HS
	July	37 - DF, HS	683 - HS	2 051 - PA	1 409 - HS	517 - CCO, L	1 515 - HS	300 - HS	413 - HS, JR	83 - HS	279 - HS, JR
	August	128 - L	585 - L	739 - HS	297 - CBB, CC, PP	125 - LV, PP	56 - HS, JR	35 - HS	78 - HI	0 - CR	553 - HS
	Month	PR21	PR22	PR23	PR24	PR25	PR26	PR27	PR28	PR29	PR30
Ostreopsis spp.	June	md	0 - DI, TA	0 - UI	0 - HS	0 - CV	0 - CV, HS	24 - DI	0 - DF	10 - C	136 - HF, HV
	July	0 - JR	48 - L	69 - HS, JR	52 - HS, JR	68 - HS	15 - HS	333 - HS	md	220 - HS	582 - HI, HS
	August	303 - JR	667 - JR	578 - HS, JR	1 093 - JR	470 - HS	468 - HS	519 - HS	210 - HS	1 043 - HS	3 521- HI, HS
Prorocentrum lima	June	md	553 - DI, TA	5 - UI	531 - HS	1 432 - CV	285 - CV, HS	3 168 - DI	345 - DF	51- C	2 526 - HF, HV
	July	1 000 - JR	3 024 - L	379 - HS, JR	3 794 - HS, JR	6 822 - HS	1 279 - HS	2 500 - HS	md	260 - HS	1 031 - HI, HS
	August	136 - JR	6 519 - JR	289 - HS, JR	2 813 - JR	1 545 - HS	3 000 - HS	1 012 - HS	827 - HS	429 - HS	2 438 - HI, HS
Coolia spp.	June	md	142 - DI, TA	0 - UI	47 - HS	256 - CV	37 - CV, HS	1 217 - DI	2 151 - DF	24 958 - C	446 - HF, HV
	July	87 - JR	167 - L	425 - HS, JR	82 - HS, JR	384 - HS	103 - HS	214 - HS	md	60 - HS	51 - HI, HS
	August	45 - JR	241 - JR	108 - HS, JR	393 - JR	197 - HS	85 - HS	235 - HS	0 - HS	57 - HS	313 - HI, HS
	Month	PR31	PR32	PR33	PR34	PR35	PR36	PR37	PR38	PR39	
Ostreopsis spp.	June	15 - DDD	0 - C	6 - CCO	12 - DF, TA	md	20 - HS, JR	0 - TA	20 - TA	35 - C	
	July	20 - HS, JR	1 885 - C, HS	56 - DP	2 043 - HS	8 - C	571 - HS, JR, PP	md	50 385 - JR	37 538 - C, CE	
	August	49 474 - HS	195 152 - HS	23 927 - HS, JR	153 548 - HS, JR	300 - HS	183 768 - HS, JR	md	144 000 - HS	md	
Prorocentrum lima	June	1 015 - DDD	110 - C	0 - CCO	1 460 - DF, TA	md	401 - HS, JR	511 - TA	632 - TA	88 - C	
	July	717 - HS, JR	754 - C, HS	3 417 - DP	1 213 - HS	26 - C	29 - HS, JR, PP	md	2 115 - JR	821 - C, CE	
	August	11 579 - HS	5 455- HS	3 273 - HS, JR	34 839 - HS, JR	100 - HS	0 - HS, JR	md	6 222 - HS	md	

Table 3 (continued)

Coolia spp.	June	134 - DDD	16 - C	31 - CCO	377 - DF, TA	md	281 - HS, JR	511 - TA	3 103 - TA	18 - C	
	July	10 - HS, JR	98 - C, HS	431 - DP	43 - HS	0 - C	29 - HS, JR, PP	md	5 192 - JR	0 - C, CE	
		August	3 789 - HS	606- HS	291 - HS, JR	1 290 - HS, JR	0 - HS	1 159 - HS, JR	md	2 222 - HS	md

md missing data

Ostreopsis spp. In contrast, in the other study areas, they were generally less abundant than *Ostreopsis* spp. Massive proliferations were recorded at, e.g. PR29 (*Coolia* spp. ~25,000 in June) and PR14 (*P. lima* ~45,000 in July). No abundance higher than 100,000 cells g^{-1} WM was recorded (Tables 2, 3 and 4).

Regional effect on abundances of the three dinophycean taxa

Abundances of the three dinophycean taxa, *Ostreopsis* spp., *P. lima* and *Coolia* spp., were significantly dependent on the region (Table 5a). When focusing on Provence and the French Riviera, where abundances were high, the regional effect was no longer significant (Table 5b).

Correlation between *Ostreopsis* spp., *P. lima* and *Coolia* spp. abundance

The abundance of *Ostreopsis* spp. was not correlated (positively or negatively) with the presence and abundance of the two other dinophycean taxa, *P. lima* and *Coolia* spp. (Table 6). That means there is neither competition between these taxa, for example access to a resource, nor inhibition through, e.g. toxic compounds produced by one of the dinophycean taxa, nor facilitation.

Effect of the macroalgal substrate

The macroalgal species composition of each sample was highly variable and the three dinophycean taxa were associated with 34 macroalgal taxa: 4 Chlorophyta (CR=*Caulerpa cylindracea* Sonder (=*Caulerpa racemosa var. cylindracea*); CL=*Cladophora laetevirens* (Dillwyn) Kützing, UI=*Ulva intestinalis* Linnaeus and UL=*Ulva lactuca* Linnaeus), 14 Florideophyceae (Rhodophyta) (AA=*Asparagopsis armata* Harvey, CE=*Ceramium* spp., C=*Corallina elongata* (J. Ellis & Solander) K.R. Hind & G.W. Saunders, GN=*Gelidiella nigrescens* (Feldmann) Feldmann & Hamel, GC=*Gelidium crinale* (Hare ex Turner) Gaillon, HV=*Haliptylon virgatum* (Zanardini) Garbary & H.W. Johansen, HI=*Halopitys incurvus* Hudson, JR=*Jania rubens* (Linnaeus) J.V. Lamouroux, L=*Laurencia* spp., LV=*Liagora viscida* (Forsskål) C. Agardh, PA=*Parviphycus pannosus* (Feldmann) G. Furnari, PC=*Plocamium cartilagineum* (Linnaeus) P.S. Dixon, P=*Polysiphonia* spp., WS=*Womersleyella setacea* (Hollenberg) R.E. Norris) and 16 Phaeophyceae (CV=*Cladostephus verticillatus* (Lightfoot) Lyngbye, CA=*Cystoseira amentacea* (C. Agardh) Bory de Saint-Vincent, CB=*Cystoseira barbata* (Stackhouse) C. Agardh, CBB=*Cystoseira brachycarpa* var. *balearica* (Sauvageau) Giaccone, CCO=*Cystoseira compressa* (Esper) Gerloff & Nizamuddin, CC=*Cystoseira crinita* Duby, DP=

Table 4 Abundance of the studied dinoflagellates (cells g^{-1} WM macroalgae) along the Corsica coast and dominant macroalgae (at least 20 % of the wet mass). For macroalgal abbreviations, see text

	Month	CO1	CO2	CO3	CO4	CO5	CO6	CO7	CO8	CO9	CO10
Ostreopsis spp.	June	49 - C, TA	74 - HS, TA	85 - HS	62 - HF	234 - HS	111 - HF	50 - HS	98 - CC	23 - HS	0 - CA
	July	57 - HS, JR	837 - HS	594 - HS	49 - CBB, DI, HS, PP	10 - DI, DP, HS	75 - CB, HS	12 198 - HS, JR	64 - HS	29 - HS	0 - HS, JR
	August	147 - HS, JR	921 - HS	205 - HS	117 - C, HS	4 403 - HS	89 - HS	206 977 - JR	184 - JR	107 839 - JR	3 276 - HI, JR
Prorocentrum lima	June	1 307 - C, TA	345 - HS, TA	13 618 - HS	154 - HF	18 070 - HS	1 111 - HF	594 - HS	4 439 - CC	3 147 - HS	503 - CA
	July	340 - HS, JR	6 250 - HS	4 970 - HS	8 155 - CBB, DI, HS, PP	5 400 - DI, DP, HS	336 - CB, HS	793- HS, JR	1 664 - HS	1 755 - HS	1 309 - HS, JR
	August	2 517 - HS, JR	1 842 - HS	3 402 - HS	268 - C, HS	2 013 - HS	133 - HS	45 736 - JR	3 701 - JR	33 270 - JR	1 952 - HI, JR
Coolia spp.	June	425 - C, TA	591 - HS, TA	2 423 - HS	92 - HF	10 643 - HS	74 - HF	1 089 - HS	1 634 - CC	1 096 - HS	632 - CA
	July	132 - HS, JR	87 - HS	257 - HS	641 - CBB, DI, HS, PP	590 - DI, DP, HS	28 - CB, HS	264- HS, JR	773 - HS	765 - HS	245 - HS, JR
	August	589 - HS, JR	164 - HS	114 - HS	0 - C, HS	354 - HS	0 - HS	35 659 - JR	266 - JR	20 650 - JR	1 197 - HI, JR
	Month	CO11	CO12	CO13	CO14	CO15	CO16	CO17	CO18	CO19	CO20
Ostreopsis spp.	June	25 - C	49 - CC, HS	0 - CC	17 - JR	83 - HS	0 - CC, JR	75 - CB, L, PP	0 - CC, JR	0 - DF	211 - HS, JR
	July	38 - HS, JR	0 - CC, HS	38 - HS	0 - CC, HS	295 - HS	400 - HS	164 - C	0 - CC, DDI, JR, PP	51 - HS, JR	179 - JR
	August	48 889 - C, P	32 941 - JR	14 528 - CC	1 279 - CV, JR	283 - CV, HS, JR	2 131 - CC, JR	1 196 - JR	4 731 - JR	1 893 - CV	572 - HS, JR
Prorocentrum lima	June	25 - C	6 677 - CC, HS	575 - CC	417 - JR	6 898 - HS	607 - CC, JR	2 400 - CB, L, PP	6 713 - CC, JR	2 981 - DF	7 107 - HS, JR
	July	1 179 - HS, JR	873 - CC, HS	1 150 - HS	635 - CC, HS	267 - HS	371 - HS	137 - C	743 - CC, DDI, JR, PP	153 - HS, JR	103 - JR
	August	5 641 - C, P	6 542 - JR	3 984 - CC	1 586 - CV, JR	3 284 - CV, HS, JR	852 - CC, JR	3 677 - JR	4 360 - JR	1 514 - CV	10 268 - HS, JR
Coolia spp.	June	0 - C	810 - CC, HS	281 - CC	583 - JR	1 773 - HS	658 - CC, JR	1 100 - CB, L, PP	1 121 - CC, JR	1 966 - DF	898 - HS, JR
	July	132 - HS, JR	254 - CC, HS	225 - HS	63 - CC, HS	38 - HS	10 - HS	27 - C	0- CC, DDI, JR, PP	0 - HS, JR	0 - JR
	August	0 - C, P	6 083 - JR	1 289 - CC	563 - CV, JR	148- CV, HS, JR	654 - CC, JR	299 - JR	482 - JR	535 - CV	376 - HS, JR

Table 5 Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of the abundance of the three studied dinophycean taxa (*Ostreopsis* spp., *Prorocentrum lima* and *Coolia* spp.), as a function of the region (regional effect)

Source	df	SS	MS	Pseudo-F	P(perm)	perms
(a) All regions (French Catalonia, Languedoc, Provence, French Riviera and Corsica)						
Regional effect	4	40,752	10,188	6.5307	0.001[a]	997
Residual	151	2.3556E5	1560			
Total	155	2.7632E5				
(b) Only 2 regions (Provence and French Riviera) using S17 Bray Curtis similarities						
Regional effect	1	487.95	487.95	0.27045	0.818	999
Residual	84	1.5155 E5	1804.2			
Total	85	1.5204 E5				

[a] Highly significant

Dictyopteris polypodioides (A.P. De Candolle) J.V. Lamouroux, DDD=*Dictyota dichotoma* (Hudson) J.V. Lamouroux var. *dichotoma*, DDI=*Dictyota dichotoma* var. *intricata* (C. Agardh) Greville*,* DF=*Dictyota fasciola* (Roth) J.V. Lamouroux, DI=*Dictyota implexa* (Desfontaines) J.V. Lamouroux, EC=unidentified Ectocarpales, HF=*Halopteris filicina* (Grateloup) Kützing, HS=*Halopteris scoparia* (Linnaeus) Sauvageau, PP=*Padina pavonica* (Linnaeus) Thivy, TA=*Taonia atomaria* (Woodward) J. Agardh).

Table 7 shows that the abundance of the three taxa of Dinophyceae significantly differed according to the species composition of the macroalgal substrate. Samples composed of *J. rubens* and *H. scoparia* exhibited the highest abundance of *Ostreopsis* spp. (>100,000 cell g^{-1} WM) in contrast to samples composed of *U. lactuca*, *C. elongata*, *Laurencia* spp., *D. fasciola* and *T. atomaria* which presented lower abundances (1000 to 10,000 cell g^{-1} WM). *Coolia* spp. followed the same trend, unlike *P. lima* that showed the opposite trend (Fig. 2).

When the regional effect was removed, i.e. when the nMDS ordination was focused upon Provence and the French Riviera (excluding therefore the other regions), a larger number of macroalgae were associated with dinophycean abundance. In addition to the former species, *U. intestinalis*, *C. amentacea*, *D. dichotoma* var. *intricata* and *D. dichotoma* var. *dichotoma* emerged (Fig. 3). The two varieties of *Dictyota* and *C. amentacea* were associated with high densities of *Ostreopsis* spp. and *Coolia* spp. and low densities of *P. lima*, while the opposite was the case with *U. lactuca*, *C. elongata*, *D. fasciola* and *T. atomaria*. In addition, the status of three macroalgae was slightly changed (*J. rubens*, *Laurencia* spp. and *H. scoparia*).

Table 6 Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of abundance of *Ostreopsis* spp. in each sample, according to the abundance of the two other dinophycean taxa, *Prorocentrum lima* and *Coolia* spp. using S17 Bray Curtis similarities. Only Provence and French Riviera were considered, in order to avoid a possible bias due to the regional effect

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Prorocentrum lima	2	5536.2	2768.1	1.7067	0.154	999
Coolia spp.	2	8205.4	4102.7	2.5296	0.056	998
P. lima×*Coolia* spp.	1	894	894	0.55121	0.621	999
Residual	80	1.2975E5	1621.9			
Total	85	1.5204E5				

Discussion and conclusion

Our study clearly showed the extensive distribution of *Ostreopsis* spp. along most of the French Mediterranean coast. In French Catalonia and Languedoc, abundance was conspicuously low, more than two orders of magnitude less than in Provence, French Riviera and Corsica; this cannot be due to the extension of beaches in Languedoc, as density was also low along the neighbouring rocky shores of French Catalonia. In addition, density was relatively high on the eastern shore of Corsica, with a similarly long extension of sandy beaches (Tables 2, 3 and 4). The reason is therefore a geographical parameter, such as temperature, salinity or the invasional process. The temperature, which is considered to enhance *Ostreopsis* blooms (Vila et al. 2001a, 2001b; Granéli et al. 2011; Mangialajo et al. 2011; David et al. 2012; Cohu et al. 2013), is lower in the Gulf of Lions than in Provence, French

Table 7 Permutation multivariate analysis of variance (PERMANOVA) on square root transformation of the abundance of the dinophycean taxa (*Ostreopsis* spp., *Prorocentrum lima* and *Coolia* spp.), as a function of the macroalgal composition of each sample (all regions and dates), using S17 Bray Curtis similarities

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Macroalgal substrate	44	1.3097E5	2976.6	1.9384	0.001[a]	998
Residual	159	2.4416E5	1535.6			
Total	203	3.7513E5				

[a] Highly significant

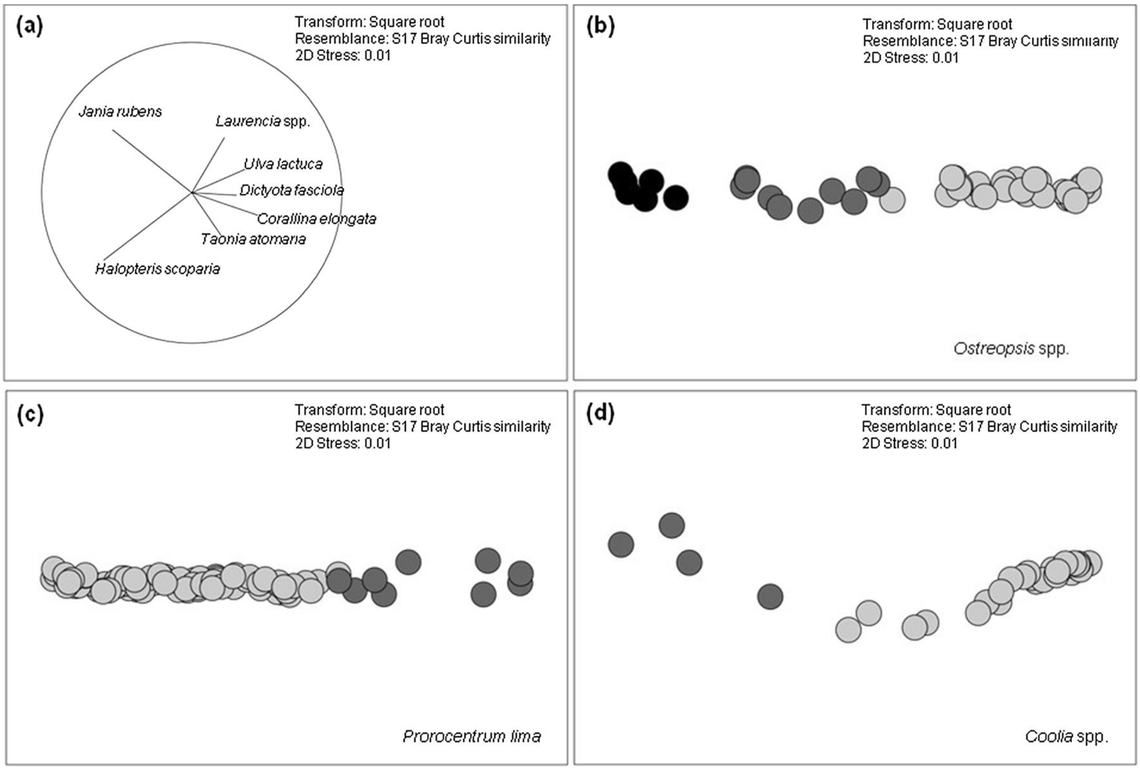

Fig. 2 Two-dimensional nMDS. **a** Correlation vectors of taxa of macroalgae vs. Dinophyceae abundance; correlation >0.3 (Spearman). All samples considered. **b** Two-dimensional nMDS ordination plot on abundance of *Ostreopsis* spp. in each sample. **c** Two-dimensional nMDS ordination plot on abundance of *Prorocentrum lima* in each sample. **d** Two-dimensional nMDS ordination plot on abundance of *Coolia* spp. in each sample. Each *circle* represents a sample. Abundance of Dinophyceae: *light grey circles*=1000 to 10,000 cell g^{-1} WM; *dark grey circles*=10,000 to 100,000 cell g^{-1} WM; *black circles*=>100,000 cell g^{-1} WM. 2D stress: 0.01

Riviera and Corsica (Nykjaer 2009; Schaeffer et al. 2011; Shaltout and Omstedt 2014). Low salinity possibly hinders *Ostreopsis* spp. (Pistocchi et al. 2011; Pezzolesi et al. 2014; Grossel et al. 2013); it is slightly lower in the Gulf of Lions than in other study regions due to the Rhone River plume (Diaz et al. 2008; Brasseur et al. 1996). Finally, the progression of *Ostreopsis* spp. could be a time-dependent process (the *Ostreopsis* invasion has not yet reached this area), rather than a habitat-linked one. Such contrasting abundances, at small scale (i.e. regional scale), were not highlighted by previous authors, who did not study such an extensive area at regional scale.

In addition to regional variability, there is also local spatial variability. Abundance was highly contrasted over short

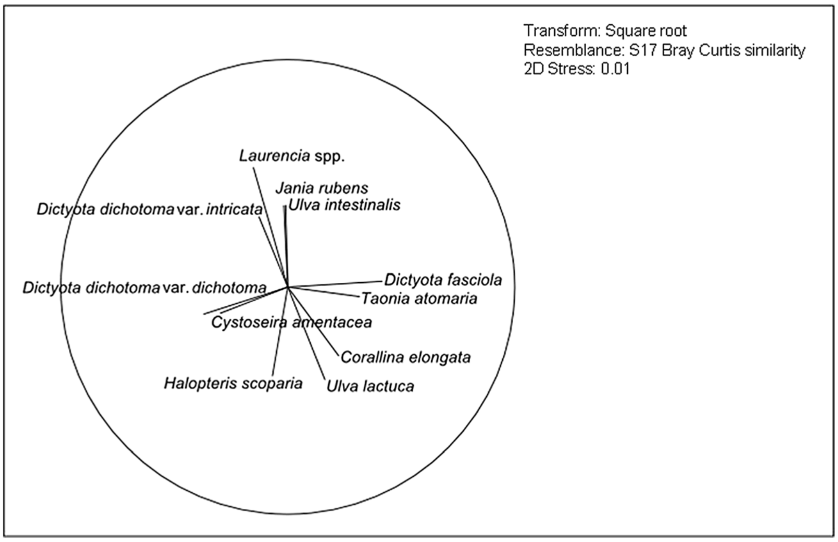

Fig. 3 Two-dimensional nMDS. Correlation vectors of taxa of macroalgae vs. Dinophyceae abundance (see Fig. 2b–d); correlation >0.3 (Spearman). Only samples from Provence and the French Riviera. 2D stress: 0.01

distances (a few kilometres), as already noted by previous authors (Aligizaki and Nikolaidis 2006; Cohu et al. 2011, 2013; Mangialajo et al. 2011).

The ecology of *Ostreopsis* spp. blooms, in relation with environmental parameters, has been investigated by several authors (Vila et al. 2001a, 2001b; Penna et al. 2005; Mangialajo et al. 2008; Totti et al. 2010; Accoroni et al. 2011, 2012; Cohu et al. 2011). However, the bloom determinism seems to be complex and is still far from being fully understood. In Provence, the French Riviera and Corsica, the abundance of *Ostreopsis* spp. increased from June to August. Previous authors have already emphasized this trend (Mangialajo et al. 2008, 2011; Cohu et al. 2011, 2013). These blooms are of the same magnitude as those previously recorded in summer in Provence, French Riviera and the Ligurian Sea (Mangialajo et al. 2008, 2011; Cohu et al. 2011, 2013). Our results confirm that high densities and blooms are linked with high sea surface temperature (SST); their frequency in the French Riviera may be related to the low frequency of wind events, which induce rapid cooling episodes of the sea surface water (Schaeffer et al. 2011).

In the Mediterranean Sea, *Ostreopsis* spp. have been recorded in the water column (Taylor 1979) and on a variety of substrates, such as seagrasses, macroalgae, dead biotic material, reefs and sand (Faust et al. 1996; Turki 2005; Aligizaki and Nikolaidis 2006; Mangialajo et al. 2008; Battocchi et al. 2010; Totti et al. 2010; Cohu et al. 2013; Mabrouk et al. 2014). As far as macroalgae are concerned, previous authors did not distinguish the species of macroalgae (Mangialajo et al. 2008, 2011; Cohu et al. 2011) or only considered a very few species (Cohu et al. 2013), with the exception of Battocchi et al. 2010. Cohu et al. (2013) noted the ability of *Dictyota* spp. to support very high abundance of *O.* cf. *ovata* during blooms, but were unsuccessful in establishing significant preferences. Here, 34 taxa of dominant macroalgae hosting the species were identified. They belong to three higher taxa (Chlorophyta, Florideophyceae and Phaeophyceae) and to a variety of morphological types (articulate, fleshy, bushy, flat and erect). We have recorded blooms mainly on two varieties of *D. dichotoma*, *C. amentacea* and *H. scoparia* bearing, as epibionts, a large amount of the articulated coralline *J. rubens*. In contrast, abundance was significantly lower on *U. lactuca*, *D. fasciola*, *T. atomaria* and *C. elongata*. It is worth noting that our results explain the failure of previous authors (Cohu et al. 2013) to establish a correlation between dinophycean abundance and the presence of *Dictyota* spp.: In fact, this taxon encompasses species and varieties that present opposite trends (Fig. 3).

What could be the reasons for the correlations (positive or negative) between the abundance of dinophycean cells and the dominant macroalgae within the sample? Several features may account for these differences. (i) The morphology of macroalgae can provide a wide span of available surface area for epibiontic cells, depending upon, e.g. the high density of branches (as in *H. scoparia* and *C. amentacea*) vs. flat and sparsely branched blades (as in *Ulva* spp., *Dictyota* spp. and *T. atomaria*). The fact that *D. dichotoma* var. *dichotoma* and *D. dichotoma* var. *intricata*, on one hand, and *D. fasciola* and *T. atomaria*, on the other hand, exhibited opposite trends (Fig. 3) suggests that morphology is not the sole parameter involved in the observed correlations. (ii) Many macroalgae produce a variety of biologically active compounds (e.g. Fenical 1983; Baker 1984; Paul and Fenical 1986; Hay 2009; Michalak and Chojnacka in press). Because of their properties (antimicrobial, antiviral, antifungal and antiherbivore toxins), these compounds can hinder the settlement of epibiontic organisms, both multicellular and unicellular. *T. atomaria*, which was associated with low densities of *Ostreopsis* spp. and *Coolia* spp., exhibits high antimicrobial and antiviral activities (Caccamese et al. 1980; but see Salvador et al. 2007). *D. fasciola* contains several sesquiterpenes (Amico et al. 1979), in addition to antiviral activities (Caccamese et al. 1980); sesquiterpenes are known to exert antiherbivory properties (Boudouresque et al. 1996; Estell et al. 2008). Solid extracts of *C. elongata,* when lyophilized, exert in summer antimicrobial and antifungal activities (Salvador et al. 2007). As far as macroalgae associated with high abundances of Dinophyceae are concerned, *D. dichotoma* var. *intricata* and *H. scoparia* lack in summer antimicrobial and antifungal activities (Salvador et al. 2007). This is consistent with the behaviour of the herbivorous sea urchin *Paracentrotus lividus* (Lamarck, 1816), which strongly to moderately prefers these species when browsing, behaviour usually indicative of the scarcity of defence compounds (Boudouresque and Verlaque 2013). However, the production of active compounds cannot account for all of our results (Fig. 3). *C. amentacea* and *D. dichotoma* var. *dichotoma* exhibit antimicrobial activities (Salvador et al. 2007; Alghazeer et al. 2013), while being highly associated with Dinophyceae; in addition, the former species is strongly preferred and the latter moderately to strongly preferred by sea urchins (Boudouresque and Verlaque 2013). (iii) *Ostreopsis* spp. and associated dinophyceans can be co-consumed by herbivores, together with the macroalgal substrate (Bire et al. 2013). If small multicellular metazoans (invertebrates) and/or unicellular eukaryotic grazers actively feed on these dinophyceans, they would control their abundance in the regions or on the macroalgae where they dwell. Unfortunately, nothing is known about the direct consumption of the studied dinophyceans.

Finally, *Ostreopsis* spp. are frequently associated with two other Dinophyceae, *P. lima* and *Coolia* spp., as already highlighted by the authors (Penna et al. 2005; Turki 2005; Zenetos et al. 2005; Aligizaki and Nikolaidis 2006; Streftaris and Zenetos 2006; Zingone et al. 2006; Aligizaki et al. 2009; Ingarao et al. 2009; Ignatiades and Gotsis-Skretas 2010). Our results confirmed this frequent association of the three dinophycean taxa; they did not show any obvious competition or facilitation between them.

Our study clearly questions the dispersal of *Ostreopsis* spp. Obviously, the dispersal seems to be effective but its mechanisms remains unclear; further studies are need to disentangle the role of currents, drifting debris (Masó et al. 2003) or aerosols (Ciminiello et al. 2014) in the dispersal of the species and to determine at which stage of development (cell, dormant cysts or non-dormant cysts) it occurs. The understanding of these mechanisms would contribute to explaining the scarcity of the species in French Catalonia and Languedoc.

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