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## Dinoflagellate resting cysts from surface sediments of the Adriatic Ports: Distribution and potential spreading patterns

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## ABSTRACT

The ability of microalgae to preserve viable in coastal sediments as resting forms provides a reservoir of biodiversity and a useful tool to determine species spreadings. This study represents the first port baseline survey on dinoflagellate cysts, investigated in nine Adriatic ports during a cross border project. 40 dinoflagellate taxa were detected. The assemblages resulted in all ports dominated by *Lingulodinium polyedra* and *Alexandrium minutum/affine/tamutum* group. General separation to the western and eastern side of the Adriatic regarding cysts assemblage composition, partially abundance, was observed. Six taxa were detected as non-indigenous species for the Adriatic. Two taxa are included in the list of harmful aquatic organisms, indicating the potential threat of ballast waters in the Adriatic. Potential spreading of taxa by general circulation and ballast waters, intra- and extra-Adriatic was investigated. The entering in to force of the ballast waters management regulations should enhance prospects to minimize future harmful impacts.

### 1. Introduction

Coastal waters host many planktonic organisms that spend most of their lifecycle in a resting phase (Boero et al., 1996). Benthic cysts play a pivotal role in the ecology of dinoflagellates (Walker, 1984; Dale, 1983), since they allow survival through adverse environmental conditions, such as nutrient depletion, grazing, competition, high turbulence and temperature decrease (Figueroa and Bravo, 2005; Nagai et al., 2002; Pospelova et al., 2008). Cyst-forming species are not equally distributed among the extant dinoflagellate orders, being much more common for the Peridiniales, Gonyaulacales and Gymnodiniales, and quite rare for the Dinophysiales and Prorocentrales (Faust, 1990, 1993; Moita and Sampayo, 1993; Head, 1996). Cells are not-motile and

are commonly produced through sexual reproduction (Walker, 1984). Cysts are surrounded by a dense, resistant wall, which cause their settling on the sea bottom (Montresor et al., 1998). Their ability to preserve viable in sediments for decades provides a reservoir of biodiversity and a suitable tool to study temporal changes in phytoplankton populations in a given area (Lundholm et al., 2011). Cysts also act as “seeds” for initiation of blooms once favourable conditions are re-established (Pfiester and Anderson, 1987). In the phylum Dinophyta, at least 200 species can produce cysts (Dale and Dale, 2002), and more than 16 species are known to be toxic and cause harmful red-tide events (Matsuoka and Fukuyo, 2000). This number is expected to increase even further since new cyst morphotypes continue to be discovered (Satta et al., 2010). Surveys of cyst assemblages in recent sediments are

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thus important to forecasting the occurrence of future bloom events and give early warnings of the presence of toxic or non-toxic species (Anderson et al., 1983, 2003; Giannakourou et al., 2005; Lundholm et al., 2011). Information on the distribution and abundance of cysts is also essential for understanding the ecology and bloom dynamic of many harmful aquatic organisms (HAOs) (Joyce, 2004; Rubino et al., 2010, 2017). The application of cyst assemblage studies to harmful algal species will extend knowledge of these microalgae; this approach increases the likelihood of detecting the occurrence of species not previously reported from particular areas (e.g., *Alexandrium* species; Montresor et al., 1998; Joyce et al., 2005; Bravo et al., 2006). Cyst distribution dynamics could be controlled by various biological and environmental factors: primary production and physico-chemical conditions such as sea-surface temperature, sea-surface salinity (Candel et al., 2012), including sediment physical characteristics (Anderson et al., 2005; Anglès et al., 2010; Horner et al., 2011). Several studies suggest that highest cyst abundances are correlated with fine sediment fractions (Triki et al., 2017).

The Adriatic is located in the northernmost part of the Mediterranean. The economic development and social existence of their countries depend on the preservation of the basin, which is an important international and local seaway subjected to intense commercial maritime traffic. For these reasons, Adriatic ports, also featured by shallow water, low hydrodynamic forcing, can represent a reservoir of biodiversity and potential hotspots of species dispersions (Dale, 1983; Belmonte et al., 1995; Garcés et al., 1999). In such areas, and especially those hosting shellfish farms, where the transfer of organisms occurs intentionally, the risk of introducing Non-Indigenous Species (NIS) can be high (Hégaret et al., 2008). Biological invasions can also happen unintentionally, with the maritime traffic.

The International Maritime Organization (IMO) has adopted in 2004 the “International Convention for the Control and Management of Ship's Ballast Water and Sediments” (BWM Convention), aimed to reduce the spread of Harmful Aquatic Organisms and Pathogens (HAOP) among ports and areas, by establishing standards and procedures for the management and control of ships' ballast waters (BW) and sediments (Cabrinì et al., 2019; this Issue). BW is seawater carried in ships' ballast tanks to improve stability, balance and trim. It is taken up or discharged when cargo is unloaded or loaded, or when a ship needs extra stability in foul weather. Ballast water discharge can introduce potential HAOP causing negative impact to aquatic ecosystems, human health and economic activities worldwide. BW studies conducted in different world's oceans, have demonstrated that ships are involved in the transfer of aquatic organisms across natural boundaries (Howarth, 1981; Carlton, 1985; Williams et al., 1988; Hallegraeff, 1993; Rigby and Hallegraeff, 1996; Macdonald and Davidson, 1997; Hay et al., 1997; Gollasch, 1998; Gollasch et al., 2000a, 2000b; Olenin et al., 2000; Ruiz et al., 2000; Wonham et al., 2001; Gollasch, 2002; Gollasch et al., 2002; Murphy et al., 2002; Coutts et al., 2003). It is estimated that BW are responsible for the transfer of approximately 7,000–10,000 different marine species globally every day (Carlton and Geller, 1993; Carlton, 1999; Gollasch, 2002). In the last decades, introductions have increased in frequency, volume, and in the degree of global biotic homogeneity (Lodge, 1993). In shipping, organisms are transferred inside ballast tanks, in the sediments and/or attached to the ship's hull. The introduction of NIS via ships' BW can influence marine ecosystems by causing major alterations in the composition and function of ecological communities' worldwide (Carlton, 1987, 1989; Lodge, 1993; Williamson, 1996). Not all the organisms survive in tanks, but some of them after the release establish populations in new locations. Some species have already harmfully impacted natural environments, human health and caused economic losses (David et al., 2007) by harming aquaculture farms by diminishing availability of healthy stocks (Graneli et al., 1998; Camacho et al., 2007; Hallegraeff, 2010). New invasions will intensify, since trades and transport routes are expanding to regions around the world (Carlton, 1985; Carlton, 1989; Chapman and

Carlton, 1991; Baldwin, 1992; Berman et al., 1992; Hutchings, 1992; Carlton and Geller, 1993; Buttermore et al., 1994). In intra-coastal voyages, with shorter resilience days in tanks, organisms have greater possibility to survive; indeed, several studies suggest that intra-coastal transport may be even more significant in the spread of organisms (Williams et al., 1988). BW are proven vector of spreading phytoplankton species, including dinoflagellate vegetative and resting stages, over the large distances across the oceans (Baldwin, 1992; Hallegraeff et al., 1990; Hamer et al., 2000). Indeed, high densities and wide diversities of dinoflagellate cysts are reported to withstand the severe conditions existent within ballast tanks, such as absence of light, reduced food availability and strong fluctuations of physico-chemical conditions (Hallegraeff and Bolch, 1991, 1992; Kelly, 1993; Chu et al., 1997; Macdonald and Davidson, 1998).

The aim of this study, conducted in the frame of the EU IPA Adriatic BALMAS project (Ballast water management system for Adriatic Sea protection), was to perform a Port Baseline Survey (PBS) in order to investigate on the species composition, abundance and distribution of dinoflagellate cyst assemblages in 9 Adriatic ports located along the Italian, Slovenian and Croatian coasts. A special effort was carried out on the detection of a baseline list of potentially HAOs and NIS, and on the tracking of the possible relationship between cyst presence and the BW transport. To date, no cross-border study evaluated both cyst diversity and abundance and the potential effect of harmful dinoflagellate cysts in the Adriatic port surface sediments.

## 2. Methods

### 2.1. Study sites (characterization of the ports)

Since major ports are often the first places where marine species are introduced, the aim of the sampling and laboratory activities, were to provide information about the presence and possible negative effects of both non-indigenous and native harmful species in ports, as hotspots of BW discharges. Therefore, an extensive field sampling performed twice a year (in spring and autumn when possible) was conducted in 9 Adriatic ports along the Italian (Trieste, Venice, Ancona, Bari), the Slovenian (Koper) and the Croatian (Pula, Rijeka, Šibenik, Split) coasts (Fig. 1, Table 1). Sampling was performed according to the BALMAS PBS procedures (Ninčević Gladan et al., 2014) based on the CRIMP protocol (Hewitt and Martin, 2001), modified in order to meet specific needs of the Adriatic Sea.

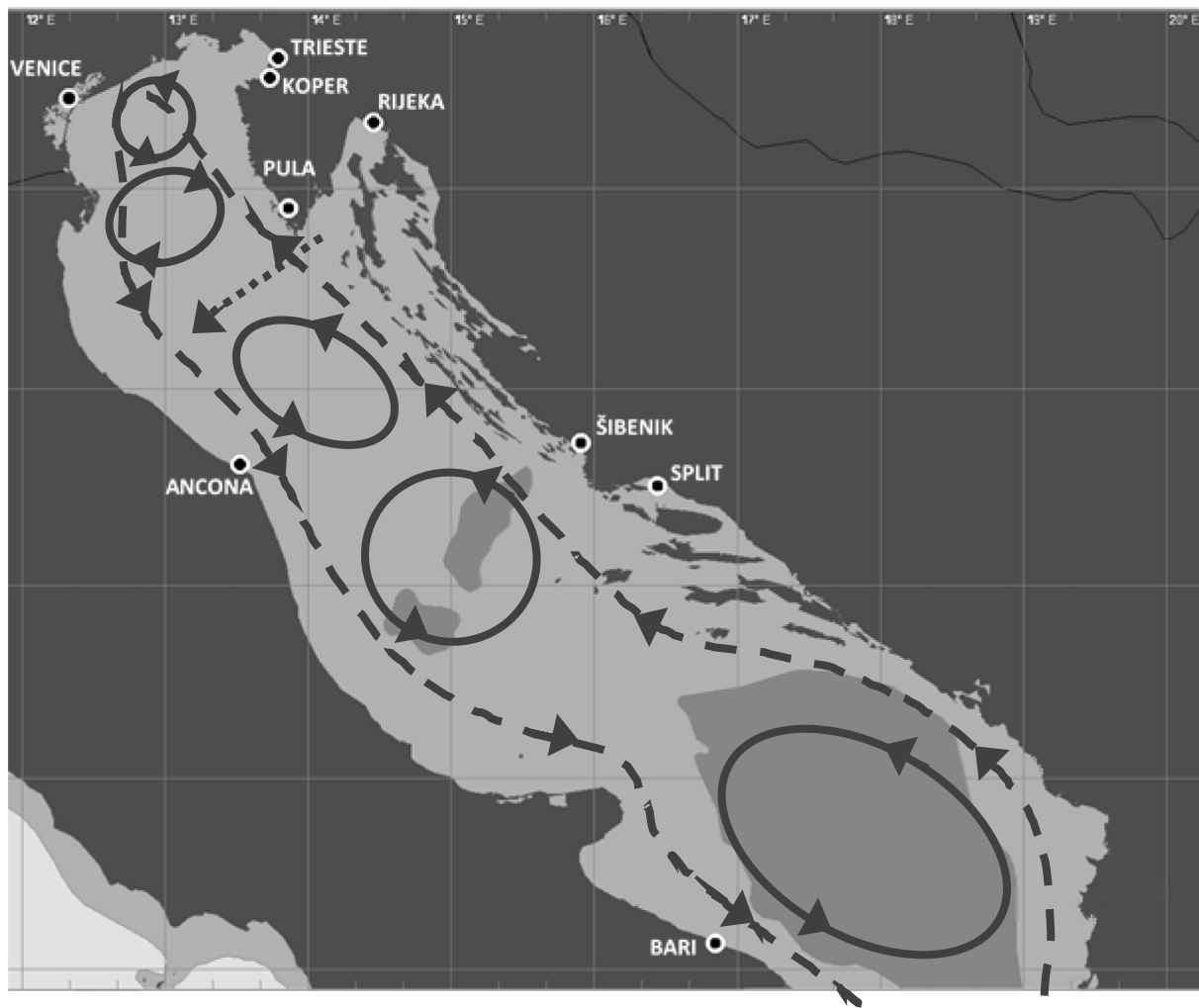
All selected ports are characterised by intense marine traffic and thus subjected to direct (ballast water-bw) or indirect (channel marker - chm) influence of BW, further in text: impacted (bw). Industrial areas, sites hosting or close to cargo, ferryboat and tanker terminals, with current/former shipping operations were selected for the purpose of this study. Adjacent sites outside ports, with presumably lower impact of BW, were contemporary sampled as control stations, including reference – ref., and anchorage – anc, further in text: control (ref). A complete list of the BALMAS PBS sampling sites with maps and coordinates are given in Kraus et al. (2019a). Short account of samples collection, applied treatments and analysis of samples is given in Table 2.

### 2.2. Phytoplankton sampling and analysis

Phytoplankton was sampled both for quantitative and qualitative analyses at each station and the frequency was designed to cover two seasons, spring/autumn. For detailed description of the sampling method and microscopic analyses of phytoplankton we refer to Mozetič et al. (this issue).

### 2.3. Sediment sampling and processing

Sampling of sediments was performed according to the BALMAS



**Fig 1.** Map of the Adriatic Sea showing the 9 ports selected for dinoflagellate cysts investigation during Port Baseline Surveys (Split, Šibenik, Rijeka, Pula, Koper, Trieste, Venice, Ancona, and Bari). Schematics of Adriatic surface circulation layer is drawn on the basis of plots given by [Supić et al. \(2003\)](#), [Krajcar \(2003\)](#) and [Kraus et al. \(2019b\)](#); general circulation pattern (dashed line), gyres (solid) and current induced by Bora episodes (dotted).

guidelines, proposed in the PBS protocol ([Kraus et al., 2019a](#)), using either scuba divers or benthic cores and grabs, when the manual collection of sediments was not applicable. All samples were pre-treated and processed as described in [Table 2](#). Cleaning and concentration of cysts from surface sediments was performed following the equivalent methodological procedures described in the PBS protocol according to [Blanco \(1986\)](#), [Bolch \(1997\)](#) or the palinological procedures as stated in [Matsuoka and Fukuyo \(2000\)](#) ([Table 2](#)). All samples were stored in the dark at 4 °C until microscopical analysis. Sub-samples were collected to obtain DW by drying the samples at 105 °C for one week.

#### 2.4. Microscopic analysis

Aliquots of final samples were counted in sedimentation chambers with inverted light microscopes at 200 and 400× magnifications, according to the [Utermöhl \(1958\)](#) method and [Zingone et al. \(2010\)](#) ([Table 2](#)). Counts were carried out noting the number of viable cysts of each species in half of sedimentation chamber. Dinoflagellate cysts were identified based on available morphological characteristics, such as the shape of cyst body and its ornamentation, wall structure and color, and types of aperture or archeopyle as stated in [Matsuoka and Fukuyo \(2000\)](#), [Bringue et al. \(2016\)](#), [Kokinos and Anderson \(1995\)](#), [Pitcher and Joyce \(2009\)](#), [Rochon et al. \(1999\)](#), [Wang et al. \(2007\)](#). Morphological identification was performed for cysts with distinctive

species-specific morphological features. However, many cysts could not be identified at the species level mainly as available taxonomic keys do not always exist among related species, and/or available morphological features largely vary in the same species among different environments ([Ellegaard, 2000](#); [Matsuoka et al., 2009](#)). Alternatively, the corresponding vegetative forms were used for species identification through germination of some cysts ([Gu et al., 2013](#); [Ellegaard et al., 2003](#)). Unfortunately, the germination of many cysts could not be successfully achieved in each port since some of the laboratories were not equipped for germination experiments. Empty cysts were not considered for the identification. Densities were expressed in number of cysts per gram of dry sediment ( $\text{g}^{-1}$  DW).

#### 2.5. Statistical analysis

For statistical analyses of cysts dataset PRIMER (Plymouth Routines In Multivariate Ecological Research) v6 and PERMANOVA+ add on to PRIMER software package was used ([Clarke and Warwick, 2001](#)). Routines applied were Cluster analysis, MDS, ANOSIM and SIMPER. As a transformation method, 4th root transformation was applied, to down-weight considerably the impact of the abundant taxa, allowing the rare taxa to exert some influence on the similarity calculations. For similarity measures Bray-Curtis coefficient was used. Cluster analysis was performed using group-average linking.

**Table 1**

List of the BALMAS PBS sampling sites with depths and coordinates in nine Adriatic ports where dinoflagellate cysts were investigated. The name of each sampling site is a compound of: port name (in capital letters), type of sampling site (bw = directly impacted by ballast water, chm = channel marker site, anc = anchorage site, and ref. = control site), and a suffix identifying the institution in charge of the PBS (internal reference coding, e.g. J1, K1, 4A...).

Country	PORT	Sampling station	Depth	Latitude	Longitude
Croatia	Split	STbwJ1	17.0	43°32'18.42"N	16°26'21.01"E
		STbwK1	17.0	43°32'05.71"N	16°27'48.42"E
		STbwL1	10.0	43°31'40.98"N	16°28'07.75"E
		STbwL2	15.0	43°31'44.65"N	16°27'49.25"E
		SIbw1	15.0	43°43'30.54"N	15°53'57.41"E
	Šibenik	SIbw3	33.0	43°44'37.68"N	15°52'50.77"E
		RIbwB	7.0–8.8	45°19'42.42"N	14°25'50.16"E
		RIbwS	7.3–8.2	45°19'20.40"N	14°26'19.68"E
	Pula	RIchm	56.7–57.2	45°19'30.30"N	14°23'49.38"E
		RIref	30.2–35.5	45°18'51.06"N	14°28'08.82"E
Slovenia	Koper	PUBwC	7.0–7.8	44°51'59.46"N	13°49'41.82"E
		PUBwS	5.7–6.2	44°53'30.54"N	13°48'07.74"E
		PUchm	12.1–12.5	44°52'43.20"N	13°50'24.00"E
		PUref	33.7–36.7	44°52'33.78"N	13°47'34.74"E
		KOanc4A	17.0	45°33'48.66"N	13°42'52.86"E
	Trieste	KObw1A	10.0	45°33'05.10"N	13°44'11.04"E
		KObw2A	13.1	45°33'27.36"N	13°44'12.00"E
		KObw3A	12.5	45°33'52.44"N	13°44'11.10"E
		VEancPTF	16.0	45°18'49.79"N	12°30'31.79"E
Italy	Venice	VEbwP1	12.0	45°26'13.17"N	12°18'39.98"E
		VEbwW2	7.0	45°26'54.19"N	12°15'29.87"E
		TSbw1	18.5	45°38'01.08"N	13°45'09.24"E
		TSbw2	16.0	45°37'47.22"N	13°46'10.98"E
		TSbw3	14.0	45°37'04.08"N	13°46'30.96"E
	Ancona	TSbw4	14.0	45°36'41.04"N	13°46'30.96"E
		TSrefC1	18.0	45°42'03.00"N	13°42'36.00"E
		ANancAPI	13.0–16.0	43°40'29.72"N	13°24'34.37"E
		ANbwDS	10.0–11.0	43°37'12.97"N	13°29'48.20"E
	Bari	ANbwLR	5.0–6.0	43°37'30.91"N	13°29'40.00"E

### 3. Results

#### 3.1. Taxa and cyst densities

Summarized information on abundance and total number of observed taxa is given in Table 3. Abundance ranged from minimum of 4 cysts g<sup>-1</sup> DW (in port of Venice, at impacted stations in May and October 2014) to the maximal 11,554 cysts g<sup>-1</sup> DW (in port of Split, in April 2011, due to high contribution of *L. polyedra*, contribution of 90%). The highest number of observed taxa per single sample was observed in port of Trieste, 20 taxa per sample, followed by 15 in Koper and Split, and lowest, only three taxa in Venice and Ancona (Table 3). At port level, the highest diversity (number of observed taxa) was observed in port of Trieste (30 in the entire port, 29 taxa at impacted and 18 at control stations (Table 4). During sampling in March, 27 taxa was found at impacted and 15 at control stations, while in May, taxa count was lower, 21 and 12, respectively. The lowest diversity characterised Ancona and Venice, where spring/summer and autumn count, at both impacted and control stations, ranged from 3 to 5. The lowest cysts diversity, only three observed taxa, was reported for impacted stations during May and July, in Venice and Ancona, respectively (Table 4).

#### 3.2. Cyst assemblages

Complete taxa listing of identified cysts during PBS performed in nine ports is presented in Table 4.

Taxa observation is reported per specific port, month of sampling and type of sampling station. Samplings were performed at sampling

**Table 2**

Used devices and followed methods in dinoflagellate cysts sample collection, treatment and microscopic analyses in nine Adriatic ports.

Port	Month	Observed taxa			Cysts abundance (g <sup>-1</sup> DW)		
		Ave	Min	Max	Ave	Min	Max
SPLIT	4	12	9	15	3399	252	11554
	6	7	7	7	680	680	680
	10	8	8	8	1060	1060	1060
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
ŠIBENIK	in total	10	7	15	2556	252	11554
	6	7	3	10	2745	610	4880
	11	6	5	7	350	300	400
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
RIJEKA	in total	6	3	10	1547	300	4880
	4	7	5	10	130	64	204
	12	7	4	9	109	49	149
	ref	7	7	7	89	64	113
	bw	7	4	10	130	49	204
PULA	in total	7	4	10	120	49	204
	5	8	6	10	328	80	516
	12	7	5	10	330	44	763
	ref	8	7	8	336	224	449
	bw	7	5	10	326	44	763
KOPER	in total	7	5	10	329	44	763
	6	13	10	15	588	372	805
	11	12	10	14	789	546	923
	ref	13	12	14	793	781	805
	bw	13	10	15	653	372	923
TRIESTE	in total	13	10	15	688	372	923
	3	17	14	20	42	22	60
	5	14	11	16	122	17	232
	ref	13	11	15	36	17	55
	bw	16	13	20	94	22	232
VENEZIA	in total	15	11	20	82	17	232
	5	4	3	5	6	4	9
	10	5	4	5	6	4	8
	ref	5	5	5	9	8	9
	bw	4	3	5	5	4	6
ANCONA	in total	4	3	5	6	4	9
	7	4	3	5	46	15	95
	10	5	4	5	52	21	104
	ref	4	4	4	100	95	104
	bw	5	3	5	24	15	30
BARI	in total	4	3	5	49	15	104
	5	13	13	14	113	60	164
	11	14	13	15	132	109	175
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
in total	in total	14	13	15	122	60	175

stations directly impacted by BW discharge (further in text: impacted stations), and in six ports also at control stations (referent or anchorage sites). 18 taxa were observed only at impacted, and remaining 26 taxa at both impacted and control stations. Not a single taxa was observed exclusively at control station.

From a total of 62 sediment samples collected during the Adriatic PBS in nine ports, 40 distinct dinoflagellate taxa were identified (Table 4). Besides, a group of round brown cysts and small round cysts were distinctive from other unidentified cysts. In total, 29 taxa were identified to the species level, while other cysts were determined as a “group” (i.e., *Alexandrium minutum/affine/tamutum*, and *A. tamarense/catenella*, and *Diplopsalis*), several to the genus and one to the family level (*Thoracosphaeraceae*). As many as twenty species belonged to the following three genera, *Protoperidinium*, *Scrippsiella* and *Alexandrium*, (nine, eight and three, respectively). The two most abundant taxa, *Lingulodinium polyedra* and *A. minutum/affine/tamutum* group, were also the only two taxa that were observed in all nine investigated ports.

Presence of vegetative form of each observed cyst taxa in each of investigated ports during PBS, which is presented in separate paper of this special issue (Mozetič et al., this issue), was checked and findings included in Table 4 (grey fields). Out of 40 distinct dinoflagellate taxa and three unidentified groups, 21 was observed in cyst and vegetative form, 14 at both impacted and control stations and 7 only at impacted



**Table 3**

Average, minimal and maximal number of observed taxa (including unidentified groups) and cysts abundance ( $\text{g}^{-1}$  DW) per port: (a) per month of sampling (two to three different months), (b) per type of sampling station (ballast water impacted - bw and referent stations - ref), and (c) all data included (- in total; all sampling station types and sampling months). Not available due to missing data (n.a.).

Port	Month	Observed taxa			Cysts abundance ( $\text{g}^{-1}$ DW)		
		Ave	Min	Max	Ave	Min	Max
Split	4	12	9	15	3399	252	11,554
	6	7	7	7	680	680	680
	10	8	8	8	1060	1060	1060
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Šibenik	in total	10	7	15	2556	252	11554
	6	7	3	10	2745	610	4880
	11	6	5	7	350	300	400
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Rijeka	in total	6	3	10	1547	300	4880
	4	7	5	10	130	64	204
	12	7	4	9	109	49	149
	ref	7	7	7	89	64	113
	bw	7	4	10	130	49	204
Pula	in total	7	4	10	120	49	204
	5	8	6	10	328	80	516
	12	7	5	10	330	44	763
	ref	8	7	8	336	224	449
	bw	7	5	10	326	44	763
Koper	in total	7	5	10	329	44	763
	6	13	10	15	588	372	805
	11	12	10	14	789	546	923
	ref	13	12	14	793	781	805
	bw	13	10	15	653	372	923
Trieste	in total	13	10	15	688	372	923
	3	17	14	20	42	22	60
	5	14	11	16	122	17	232
	ref	13	11	15	36	17	55
	bw	16	13	20	94	22	232
Venezia	in total	15	11	20	82	17	232
	5	4	3	5	6	4	9
	10	5	4	5	6	4	8
	ref	5	5	5	9	8	9
	bw	4	3	5	5	4	6
Ancona	in total	4	3	5	6	4	9
	7	4	3	5	46	15	95
	10	5	4	5	52	21	104
	ref	4	4	4	100	95	104
	bw	5	3	5	24	15	30
Bari	in total	4	3	5	49	15	104
	5	13	13	14	113	60	164
	11	14	13	15	132	109	175
	ref	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	bw	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	in total	14	13	15	122	60	175

ones, whereas 22 were present only in cyst form, one half being observed only at impacted and the other at both type of stations.

A review of earlier findings of each taxa identified during this PBS endeavour, in the Adriatic and further afield, although primarily in the Mediterranean, is presented in Table 5. Based on existing/available literature, we established that out of 40 observed taxa in this PBS (Table 6):

- 1) six were assumed as new introductions for the Adriatic as no previous reports of observation were available for any area in the Adriatic: *Alexandrium affine*, found in ports of Rijeka and Pula, *Alexandrium insuetum* and *Alexandrium margaleffii*, found in port of Trieste, *Polykrikos hartmanii*, found in ports of Bari, Rijeka and Pula, *Preperidinium meunieri*, found in ports of Bari, Rijeka and Split, and

*Scrippsiella cf. rotunda*, found in ports of Trieste and Koper; and

- 2) eleven were observed in the port/s endorsed in area/s where until now no observation were reported, although were reported in at least one other area of the Adriatic: *Alexandrium tamarense/catenella* group, *Biecheleria* spp., *Cochlodinium* spp., *Gonyaulax scrippsae*, *Gymnodinium impudicum*, *Protoceratium reticulatum*, *Protopteridinium compressum*, *Protopteridinium conicoides*, *Protopteridinium leonis*, *Protopteridinium pentagonum*, and *Scrippsiella precaria*.

Description of each port regarding seasonal aspect and station types, based on integral dataset (not shown), follows and is described in Fig. 2.

**Split** – Samplings in this port were performed in April 2011, October 2011 and June 2014. In this port no control location was investigated. Overall, cyst abundance was highest in this port. PBS maximum was reported in April (station STbwK1, 11,554  $\text{g}^{-1}$  DW) and third highest PBS abundance in October (STbwJ1, 1060  $\text{g}^{-1}$  DW). Cyst diversity in April (19 taxa) was considerably higher than in October (8) and June (7). However, four stations were investigated in April (in each 9, 11, 12 and 15 taxa were determined, 19 in total), and only one per other two occasions. As two stations (STbwK1 and STbwJ1) sampled in April were resampled in October and June, diversity can be more closely compared: decrease from 15 to 7 taxa, and 9 to 8, respectively. The most abundant cyst was *L. polyedra* (contribution of 85–86%) in April and October, which evidently dominated the cyst assemblage and was present in bloom abundances. In June, contribution of *L. polyedra* decreased to (26%), and co-dominated with undetermined cysts of genus *Gymnodinium* (44%) and cysts identified as group *A. minutum/affine/tamutum* (12%). During this PBS, *Protopteridinium pentagonum* was found only in port of Split, at three out of four investigated influenced locations in April.

**Šibenik** – Two PBS samplings were performed in November 2013 and June 2014. In this port no control location was investigated. At influenced locations, cyst abundance and diversity were considerably higher in June than in previous November. The second highest abundance during PBS performed in all nine ports was observed in this port, in June 2014 at sampling station SIbw1, due to especially high abundance of cysts identified as group *A. minutum/affine/tamutum* (4800  $\text{g}^{-1}$  DW). This group was dominant in November (53%), with undetermined cysts of genus *Polykrikos* (14%), *S. acuminata* (13%) and *A. tamarense/catenella* (11%), and again in extreme amount in June, contributing with high 91% in total abundance. No species were observed solely in this port.

**Rijeka** – During the two PBS samplings, in December 2014 and May 2015, cyst diversity remained similar, even at sampling location level, around averages of PBS, while abundances slightly decreased at influenced locations and increased at the control one. In December, the most abundant cysts at control were *L. polyedra* (50%), undetermined cysts of genus *Biecheleria* (32%) and *Gymnodinium* (12%). At impacted stations, the same taxa were dominant (17, nine and 41%, respectively), including also undetermined cysts of genus *Protopteridinium* (12%). Dominant taxa slightly changed during May, *L. polyedra* (57%), cysts identified as group *A. minutum/affine/tamutum* (17%) and unidentified cysts (13%) at control location, and undetermined cysts of genus *Protopteridinium* (28%) and *Biecheleria* (16%), *L. polyedra* (12%) and unidentified cysts (20%) at impacted locations. No species were observed solely in this port.

**Pula** – During the two PBS samplings, in December 2014 and May 2015, cyst diversity and abundances remained similar, even at sampling type level. In December, the most abundant cysts at control location were undetermined cysts of genus *Protopteridinium* (33%), *L. polyedra* (32%), *Polykrikos hartmanii* (20%) and generally undetermined cysts (15%), while at influenced locations, *L. polyedra* with 76% was predominant. In May, diversity was more uniform across the port, with *L. polyedra* (53%) and generally undetermined cysts (16%). No species were observed solely in this port.

Table 4

Check-list of taxa observed during samplings conducted in nine Adriatic ports. Species names follow biological taxonomy system. Sampling stations are divided in ballast water impacted (bw) and controls (ref). Port names are abbreviated as follows: Split (ST), Šibenik (SI), Rijeka (RI), Pula (PU), Koper (KO), Trieste (TS), Venice (VE), Ancona (AN), and Bari (BI). Finding of specific taxa at impacted stations is marked by black square (■) and at control one by white one (□). Presence of vegetative form of each observed cyst taxa in seawater during any of seasons (Y) in each investigated port is presented with grey square (after [Mozetić et al., this issue](#)). All blank fields indicate absence of specific taxa.

Taxa	Month Station	Apr STbw	Jun STbw	Oct STbw	Y	Nov SIbw	Dec RIbw	Y	May PUref	Dec PUref	Y	Jun KOanc	Nov KOanc	Y	Mar TSbw	May TSbw	Y	Oct VEanc	May VEbw	Y	Jul ANanc	Oct ANanc	Y	May BIbw	Nov BIbw	
<i>Alexandrium affine</i>																										
<i>Alexandrium insuetum</i>																										
<i>Alexandrium margaleffii</i>																										
<i>Alexandrium</i> spp.																										
<i>Alexandrium tamarense / catenella</i>																										
<i>Biecheleria</i> spp.																										
<i>Cochlodinium</i> spp.																										
<i>Diplopsalis</i> group																										
<i>Gonyaulax scrippsae</i>																										
<i>Gonyaulax spinifera</i>																										
<i>Gonyaulax</i> spp.																										
<i>Gymnodinium</i> spp.																										
<i>Gyrodinium impudicum</i>																										
<i>Lingulodinium polyedra</i>																										
<i>Pentaptharsodinium dalei</i>																										
<i>Pentaptharsodinium tyrrenicum</i>																										
<i>Polykrikos hartmannii</i>																										
<i>Polykrikos</i> spp.																										
<i>Preperidinium meunieri</i>																										
<i>Prorocentrum cordatum</i>																										
<i>Protoceratium reticulatum</i>																										
<i>Protoperidinium cf. avellana</i>																										
<i>Protoperidinium claudicans</i>																										
<i>Protoperidinium compressum</i>																										
<i>Protoperidinium conicoides</i>																										
<i>Protoperidinium conicum</i>																										
<i>Protoperidinium divaricatum</i>																										
<i>Protoperidinium leonis</i>																										
<i>Protoperidinium oblongum</i>																										
<i>Protoperidinium pentagonum</i>																										
<i>Protoperidinium</i> spp.																										
<i>Scrippsiella acuminata</i>																										
<i>Scrippsiella crystallina</i>																										
<i>Scrippsiella lachrymosa</i>																										
<i>Scrippsiella operosa</i>																										
<i>Scrippsiella precaria</i>																										
<i>Scrippsiella cf. ramonii</i>																										
<i>Scrippsiella cf. ratunda</i>																										
<i>Scrippsiella trifida</i>																										
<i>Scrippsiella</i> spp.																										
<i>Thoracosphaera</i> ceae indet.																										
round brown cysts																										
small round cysts																										
N.I. cysts																										
Total		19	7	8	21	10	7	11	8	11	7	10	14	20	12	18	15	27	10	20	5	4	5	5	17	15
Port total																									18	

**Table 5**

Check-list of the taxa observed during PBS in the nine Adriatic Sea. Taxa are named after biological taxonomy system (after global algal database of taxonomic, nomenclatural and distributional information, AlgaeBase; [www.algaebase.com](http://www.algaebase.com)) including biological and paleontological synonyms. Underlined taxa are (potentially) toxic; basic information about toxicity is included. Taxa distribution is reported for: Europe/European Seas (source: AlgaeBase), Mediterranean Sea (All) including sub-basins: Alboran (Alb), Algerian (Alg), Balear-Provencal (Bal), Ligurian (Lig), Tyrrhenian (Tyr), Ionian (Ion), Aegean (Aeg), Levantine (Lev), Marmara (Mar) and Adriatic (Adr), after Gómez (2003), and the Adriatic Sea, divided in six areas: south-eastern (SE), mid-eastern (mE) – endorsing area of ports of Split and Šibenik; north-eastern (NE) – endorsing area of ports of Rijeka, Pula, Koper and Trieste; north-western (NW) – endorsing area of port Venice; mid-western (mW) – endorsing area of port Ancona; and south-western (SW) – endorsing area of port Bari.

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><u>Alexandrium affine</u></b> (H.Inoue & Y.Fukuyo) Balech (syn. <i>Protogonyaulax affinis</i> H.Inoue & Y.Fukuyo 1985; <i>A. fukuyoi</i> Balech 1985) <b>Toxicity</b> Low toxicity/non-toxic, weak production of Neosaxitoxin, Saxitoxin and Gonyautoxin (Nguyen-Ngoc, 2004)	France, Portugal, Spain	Tyr: Fertouna-Bellakhal et al., 2014 Alb: Penna et al., 2008 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Mar: Balkis et al., 2016 (as <i>A. cf. affine</i> )	NEW introduction
<b><u>Alexandrium insuetum</u></b> Balech <b>Toxicity</b> Species of unknown toxicity, although associated with harmful algal blooms (Ignatiades and Gotsis-Skretas, 2010 and references within); potentially harmful species for PSP toxins (Shin et al., 2014; Spatharis et al., 2007)	Corsica, Mediterranean, Spain	Tyr: Gómez, 2003; Penna et al., 2008 Bal: Penna et al., 2008	NEW introduction
<b><u>Alexandrium margalefii</u></b> Balech, 1994	Balearic Islands, Denmark, Italy, Mediterranean, Netherlands, Portugal, Spain, Sweden	Bal: Satta et al., 2013; Gómez, 2003; Penna et al., 2008 Tyr: Gómez, 2003; Penna et al., 2008	NEW introduction
<b><u>Alexandrium minutum/affine/tamutum</u></b> <b><u>Alexandrium minutum</u></b> Halim 1960 (syn. <i>Pyrodinium minutum</i> (Halim) Taylor; <i>A. ibericum</i> Balech 1985; <i>A. lusitanicum</i> Balech 1985; <i>A. angustitubulatum</i> F.J.R.Taylor 1995) <b>Toxicity</b> Gonyautoxin producer species, although nontoxic strains also occur e.g., in the Mediterranean Sea (Ignatiades and Gotsis-Skretas, 2010 and references within) For <b><u>Alexandrium affine</u></b> see above <b><u>Alexandrium tamutum</u></b> M.Montresor, A.Beran & U.John	For <i>A. minutum</i> Adriatic, Balearic Islands, Baltic, Black Sea, Britain, Denmark, France, Greece, Ireland, Italy, Mediterranean, Netherlands, Portugal, Sardinia, Spain, Turkey  For <i>A. affine</i> see above  For <i>A. tamutum</i> Britain, Italy, Sardinia, Spain	For <i>A. minutum</i> Alb: Penna et al., 2008 Bal: Gómez, 2003; Penna et al., 2008; Satta et al., 2013, 2014 Tyr: Gómez, 2003; Montresor et al., 2004; Penna et al., 2008; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Gomez, 2003; Penna et al., 2008; Ferraro et al., 2017 Aeg: Gomez, 2003; Penna et al., 2008; Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Gomez, 2003; Penna et al., 2008; Rubino et al., 2017 Mar: Balkis et al., 2016 Adr: Gomez, 2003  For <i>A. minutum</i> type Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Mar: Aydin and Uzar, 2014  For <i>A. affine</i> see above  For <i>A. tamutum</i> Bal: Penna et al., 2008 Tyr: Montresor et al., 2004; Penna et al., 2008	For <i>A. minutum</i> all: Gómez, 2003; Honsell, 1993 mE: Viličić et al., 2002 NE: Viličić et al., 2002; Montresor et al., 2004; Cabrini et al., 2012; Toebe et al., 2013; Rogelja et al., 2018 NW: Penna et al., 2008; Bastianini et al., 2016 (A. cfr. <i>minutum</i> ) mW: Caroppo, 2000 SW: Rubino et al., 2002  For <i>A. affine</i> see above  For <i>A. tamutum</i> NE: Montresor et al., 2004 NW: Penna et al., 2008; Bastianini et al., 2016 (A. cfr. <i>tamutum</i> )

(continued on next page)

Table 5 (continued)

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Alexandrium tamarens/catenella</i></b> <b><i>Alexandrium tamarens</i></b> (Lebour) Balech 1995 (syn. <i>Gonyaulax tamarens</i> Lebour 1925; <i>Gessnerium tamarens</i> (Lebour) Loeblich III & L.Loeblich 1979; <i>Protogonyaulax tamarens</i> (Lebour) F.J.R.Taylor 1979; <i>Gonyaulax tamarens</i> var. <i>excavata</i> T.Braarud 1945; <i>Gonyaulax excavata</i> (Braarud) Balech 1971; <i>Protogonyaulax excavata</i> (Braarud) F.J.R.Taylor 1979; <i>A. excavatum</i> (Braarud) Balech & Tangen 1985; <i>A. tamarens</i> f. <i>excavatum</i> (T.Braarud) G.V.Konovalova 1993) <b>Toxicity</b> Gonyautoxin producer species (Ignatiades and Gotsis-Skretas, 2010 and references within) <b><i>Alexandrium catenella</i></b> (Whedon & Kofoid) Balech (syn. <i>Gonyaulax catenella</i> Whedon & Kofoid 1936; <i>Protogonyaulax catenella</i> (Whedon & Kofoid) Taylor 1979; <i>Gessnerium catenella</i> (Whedon & Kofoid) F.J.R.Taylor 1979; <i>Gonyaulax washingtonensis</i> Hsu 1967; <i>A. fundyense</i> Balech 1985) <b>Toxicity</b> Harmful algal bloom species, paralytic shellfish poisoning (PSP) toxins-producing species (Anderson et al., 2012 and references within), c1-c4 toxins, Saxitoxins and Gonyautoxins producer (Ignatiades and Gotsis-Skretas, 2010 and references within) <i>Alexandrium</i> spp. Halim, 1960	Balearic Islands, Baltic Sea, Black Sea, Britain, Faroe Islands, France, Greece, Ireland, Italy, Mediterranean, Netherlands, Norway, North sea, Portugal, Sardinia, Spain, UK (as <i>A. tamarens</i> )  Netherlands (as <i>Gonyaulax tamarens</i> )  Britain (as <i>Gonyaulax excavata</i> , <i>G. catenella</i> and <i>G. tamarens</i> )  France, Greece, Mediterranean, Sardinia, Spain (as <i>A. catenella</i> )	For <i>A. tamarens</i> Bal: Gómez, 2003; Penna et al., 2008; Satta et al., 2013, 2014 Lig: Gómez, 2003; Zonneveld et al., 2013 Tyr: Gómez, 2003; Montresor et al., 2004; Penna et al., 2008; Toebe et al., 2013; Zonneveld et al., 2013 Ion: Rubino et al., 2002; Gomez, 2003; Penna et al., 2008; Zonneveld et al., 2013; Ferraro et al., 2017 Aeg: Gomez, 2003; Penna et al., 2008; Zonneveld et al., 2013 Lev: Gomez, 2003; Zonneveld et al., 2013 Mar: Balkis et al., 2016 Adr: Gomez, 2003; Zonneveld et al., 2013  For <i>A. catenella</i> Alb: Gomez, 2003; Penna et al., 2008 Bal: Gomez, 2003; Montresor et al., 2004; Penna et al., 2008; Fertouna-Bellakhal et al., 2014; Satta et al., 2014 Tyr: Gomez, 2003; Penna et al., 2008; Fertouna-Bellakhal et al., 2014 Lev: Gomez, 2003  For <i>A. tamarens</i> / <i>catenella</i> complex Aeg: Aydin and Uzar, 2014; Aydin et al., 2015  All: Gómez, 2003; Bal: Penna et al., 2008; Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Penna et al., 2008; Fertouna-Bellakhal et al., 2014 Ion: Penna et al., 2008; Ferraro et al., 2017 Aeg: Penna et al., 2008 Lev: Penna et al., 2008; Rubino et al., 2017 Mar: Balkis et al., 2016  Bal: Satta et al., 2013, 2014 (as <i>B. cincta</i> )  Alb, Tyr, Lig, Adr, Lev: Gómez, 2003 Bal: Gómez, 2003; Satta et al., 2013 (as <i>C. polykrikoides</i> ) Ion: Gómez, 2003; Ferraro et al., 2017 (as <i>C. polykrikoides</i> ) All: Gómez, 2003 (as <i>D. lenticula</i> ); Zonneveld et al., 2013 (as <i>Brigantidium</i> sp.) Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 (as <i>D. lenticula</i> ) Ion: Rubino et al., 2002; Ferraro et al., 2017 (as <i>D. lenticula</i> ) Lev: Rubino et al., 2017 (as <i>D. lenticula</i> ) Mar: Balkis et al., 2016	For <i>A. tamarens</i> All: Zonneveld et al., 2013 NE: Rogelja et al., 2018 NW: Sangiorgi and Donders, 2004 (cf. <i>A. tamarens</i> type) For <i>A. cf. tamarens</i> NE: Nichetto et al., 1995 SW: Rubino et al., 2002  For <i>A. catenella</i> All: Gomez, 2003  For <i>A. fundyense</i> SE: Saracino and Rubino, 2006b; Rubino et al., 2009  SE: Saracino and Rubino, 2006b mE: Totti et al., 2000 NE: Cabrini et al., 2012; Rogelja et al., 2018 NW: Penna et al., 2008; Bastianini et al., 2016 mW: Caroppo, 2000; Totti et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2009 NW: Bastianini et al., 2016  SE: Saracino and Rubino, 2006b; Rubino et al., 2009 NE: Cabrini et al., 2012; Rogelja et al., 2018 (as <i>C. polykrikoides</i> ) SW: Rubino et al., 2009 All: Gómez, 2003 (as <i>D. lenticula</i> ); Zonneveld et al., 2013 (as <i>Brigantidium</i> sp.) SE: Viličić et al., 2002; Drakulović et al., 2012 (as <i>D. lenticula</i> ) mE: Viličić et al., 2002 NE: Nichetto et al., 1995; Viličić et al., 2002; Cabrini et al., 2012; Rogelja et al., 2018 (as <i>D. lenticula</i> ) mW: Caroppo, 2000 SW: Caroppo et al., 1999; Rubino et al., 2002
<i>Biecheleria</i> spp. Moestrup, Lindberg & Daugbjerg, 2009 <i>Cochlodinium</i> spp. F.Schütt, 1896			
<i>Diplopsalis</i> group R.S.Bergh, 1881			

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Table 5 (continued)

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Gonyaulax scrippsae</i></b> Kofoid (syn. <i>Spiniferites bulloideus</i> (Deflandre & Cookson) Sargeant)	Black Sea, Britain, Mediterranean, Netherlands, Portugal	Bal, Lig: Gómez, 2003 Tyr: Gómez, 2003; Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Gómez, 2003; Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Gomez, 2003; Aydin and Uzar, 2014 Mar: Aydin and Uzar, 2014	All: Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) NE: Nichetto et al., 1995; Rubino et al., 2000 (as <i>S. bulloideus</i> ); Cabrini et al., 2012 NW: Sangiorgi and Donders, 2004 (as <i>S. bulloideus</i> ); Rubino et al., 2000 (as <i>S. bulloideus</i> ) mW: Rubino et al., 2000 (as <i>S. bulloideus</i> ) SW: Rubino et al., 2002
<b><i>Gonyaulax spinifera</i></b> (Claparède & Lachmann) Diesing (syn. <i>Peridinium spiniferum</i> Claparède & Lachmann 1859; <i>Peridinium levanderi</i> Lemmermann; <i>Spiniferites ramosus</i> (Ehrenberg) Mantell; <i>G. levanderi</i> (Lemmermann) Paulsen 1907; <i>Tectatodinium pellitum</i> Wall 1967) <b>Toxicity</b> Yessotoxin and Homoyessotoxin producer (Rhodes et al., 2006; Riccardi et al., 2009)	Adriatic Sea, Baltic Sea, Black Sea, Britain, Georgia, Greece, Helgoland, Ireland, Mediterranean, Netherlands, Portugal, Romania, Sweden	All: Gómez, 2003; Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Aeg: Aydin et al., 2015 (as <i>G. spinifera</i> complex) Mar: Aydin and Uzar, 2014 (as <i>S. ramosus</i> ); Balkis et al., 2016	All: Gómez, 2003; Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) SE: Saracino and Rubino, 2006b; Rubino et al., 2009; Drakulović et al., 2012 mE: Viličić et al., 2002 NE: Viličić et al., 2002; Cabrini et al., 2012 NW: Tolomio and Bullo, 2001; Sangiorgi and Donders, 2004; Bastianini et al., 2016 (also cyst) mW: Caroppo, 2000 SW: Caroppo et al., 1999; Rubino et al., 2002, 2009 All: Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) SE: Drakulović et al., 2012 mE: Totti et al., 2000 NE: Nichetto et al., 1995; Viličić et al., 2009; Cabrini et al., 2012; Rogelja et al., 2018 NW: Sangiorgi and Donders, 2004; Bastianini et al., 2016 mW: Caroppo, 2000; Totti et al., 2000 SW: Caroppo et al., 1999 all: Gómez, 2003 NE: Rogelja et al., 2018
<b><i>Gonyaulax</i> spp.</b> Diesing, 1866 (syn. <i>Spiniferites</i> spp.)		All: Gómez, 2003; Zonneveld et al., 2013 (as <i>Spiniferites</i> sp.) Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Aydin and Uzar, 2014; Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	
<b><i>Gymnodinium impudicum</i></b> (S.Fraga & I.Bravo) Gert Hansen & Ø.Moestrup (syn. <i>Gyrodinium impudicum</i> S.Fraga & I.Bravo) <b>Toxicity</b> Non-toxic, bloom forming species (Ignatiades and Gotsis-Skretas, 2010 and references within)	Black Sea, Mediterranean  Portugal (as <i>Gyrodinium impudicum</i> )	Alb, Tyr, Adr: Gómez, 2003 Bal: Gómez, 2003; Satta et al., 2014 Ion: Gómez, 2003; Ferraro et al., 2017 Lev: Gómez, 2003; Rubino et al., 2017	
<b><i>Gymnodinium</i> spp.</b> F.Stein, 1878 <b>Toxicity</b> All species of the family Gymnodiniaceae are toxic expect <i>Gymnodinium impudicum</i> (Ignatiades and Gotsis-Skretas, 2010 and references within)		All: Gómez, 2003 Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin et al., 2015 Lev: Rubino et al., 2017 Mar: Balkis et al., 2016	All: Gómez, 2003 SE: Viličić et al., 2002; Saracino and Rubino, 2006b; Rubino et al., 2009; Cabrini et al., 2012; Drakulović et al., 2012 mE: Totti et al., 2000; Viličić et al., 2002; Cabrini et al., 2012 NE: Nichetto et al., 1995; Rubino et al., 2000; Viličić et al., 2002; Bernardi Aubry et al., 2004; Viličić et al., 2009; Cabrini et al., 2012; Rogelja et al., 2018 NW: Rubino et al., 2000; Bernardi Aubry et al., 2004; Sangiorgi and Donders, 2004; Bastianini et al., 2016 mW: Caroppo, 2000; Rubino et al., 2000; Totti et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2002, 2009

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Table 5 (continued)

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Lingulodinium polyedra</i></b> (F.Stein) J.D.Dodge (syn. <i>Gonyaulax polyedra</i> F.Stein 1883; <i>L. machaerophorum</i> (Deflandre & Cookson) Wall 1967) <b>Toxicity</b> Saxitoxin (Bates et al., 1978; Bruno et al., 1990), Yessotoxin and probably Homoyessotoxin producer (Yasumoto and Satake, 1998; Paz et al., 2004)	Adriatic Sea, Baltic Sea, Black Sea, Croatia, Mediterranean, Netherlands, Portugal, Romania, Spain, Sweden, Turkey  Britain, Ireland, Netherlands, Romania (as <i>G. polyedra</i> )	All: Gómez, 2003; Zonneveld et al., 2013 Bal: Satta et al., 2013 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Aydin and Uzar, 2014; Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	All: Gómez, 2003; Zonneveld et al., 2013 SE: Rubino et al., 2002; Viličić et al., 2002; Saracino and Rubino, 2006b; Rubino et al., 2009 mE: Totti et al., 2000; Viličić et al., 2002 NE: Nichetto et al., 1995 (as <i>G.</i> <i>polyedra</i> ); Rubino et al., 2000; Viličić et al., 2002, 2009; Cabrini et al., 2012, Rogelja et al., 2018 NW: Rubino et al., 2000; Tolomio and Bullo, 2001; Sangiorgi and Donders, 2004; Bastianini et al., 2016 mW: Caroppo, 2000; Rubino et al., 2000; Totti et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2002 All: Zonneveld et al., 2013 NE: Rogelja et al., 2018 NW: Sangiorgi and Donders, 2004 SW: Rubino et al., 2002 All: Zonneveld et al., 2013 SE: Saracino and Rubino, 2006b; Rubino et al., 2009 NE: Rogelja et al., 2018 SW: Rubino et al., 2002
<b><i>Pentaparsodinium dalei</i></b> Indelicato & Loeblich III	Baltic Sea, Black Sea, Britain, Netherlands, Sweden	All: Zonneveld et al., 2013 Bal: Satta et al., 2013, 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Lev: Rubino et al., 2017	All: Zonneveld et al., 2013 NE: Rogelja et al., 2018 NW: Sangiorgi and Donders, 2004 SW: Rubino et al., 2002 All: Zonneveld et al., 2013 SE: Saracino and Rubino, 2006b; Rubino et al., 2009 NE: Rogelja et al., 2018 SW: Rubino et al., 2002
<b><i>Pentaparsodinium tyrrhenicum</i></b> (Balech) Montresor, Zingone & Marino (syn. <i>Peridinium tyrrhenicum</i> Balech; <i>Calcicarpinum bivalvum</i> Versteegh)	Black Sea, Italy, Mediterranean	All: Zonneveld et al., 2013 Bal: Satta et al., 2013, 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Tyrrhenian: Montresor et al., 1993, 1994, 1998; Gomez, 2003; Gottschling et al., 2005 Lev: Rubino et al., 2017 Tyr: Gómez, 2003; Fertouna-Bellakhal et al., 2014 Lev: Rubino et al., 2017	SW: Rubino et al., 2002 All: Zonneveld et al., 2013 SE: Saracino and Rubino, 2006b; Rubino et al., 2009 NE: Rogelja et al., 2018 SW: Rubino et al., 2002
<b><i>Polykrikos hartmannii</i></b> W.Zimmermann (syn. <i>Pheopolykrikos hartmannii</i> (W.Zimmermann) Matsuoka & Fukuyo 1986)	Black Sea, Mediterranean, Netherlands, Portugal (as <i>Pheopolykrikos hartmannii</i> )	Tyr: Gómez, 2003; Fertouna-Bellakhal et al., 2014 Lev: Rubino et al., 2017	NEW introduction
<b><i>Polykrikos</i></b> spp. Bütschli, 1873 Possibly including: <b><i>Polykrikos schwartzii</i></b> Bütschli 1873 <b><i>Polykrikos kofoidii</i></b> Chatton 1914 (syn. <i>Polykrikos schwartzii</i> Kofoid)	Baltic Sea, Black Sea, Britain, Greece, Helgoland, Mediterranean, Netherlands, Portugal, Turkey (as <i>P. schwartzii</i> )  Adriatic Sea, Black Sea, Britain, Germany, Greece, Helgoland, Mediterranean, Netherlands, Portugal (as <i>P. kofoidii</i> )  Romania (as <i>P. schwartzii</i> )	For <i>P. schwartzii</i> : Alb, Bal, Lig: Gómez, 2003 Tyr: Montresor et al., 1998; Gómez, 2003; Zonneveld et al., 2013 Ion: Rubino et al., 2002; Zonneveld et al., 2013 Mar: Zonneveld et al., 2013; Balkis et al., 2016 Aeg: Zonneveld et al., 2013; Aydin and Uzar, 2014; Aydin et al., 2015 Adr: Zonneveld et al., 2013  For <i>P. kofoidii</i> : Bal, Ion, Lig: Gomez, 2003 Alg: Zonneveld et al., 2013 Alb, Adr: Gomez, 2003; Zonneveld et al., 2013 Tyr: Montresor et al., 1998; Gomez, 2003; Zonneveld et al., 2013; Fertouna-Bellakhal et al., 2014 Aeg: Gomez, 2003; Zonneveld et al., 2013; Aydin and Uzar, 2014; Aydin et al., 2015 Mar: Aydin and Uzar, 2014; Balkis et al., 2016  For <i>P. schwartzii</i> and <i>P. kofoidii</i> : Ion: Ferraro et al., 2017  For <i>P. schwartzii</i> / <i>kofoidii</i> : Lev: Rubino et al., 2017  For <i>Polykrikos</i> sp.: Bal: Satta et al., 2013	All: Gómez, 2003; Zonneveld et al., 2013 ( <i>P. kofoidii</i> ) All: Zonneveld et al., 2013 ( <i>P.</i> <i>schwartzii</i> ) SE: Saracino and Rubino, 2006b; Rubino et al., 2009 ( <i>P.</i> <i>schwartzii</i> ) mE: Viličić et al., 2002 ( <i>P.</i> <i>kofoidii</i> ) NE: Nichetto et al., 1995; Rubino et al., 2000; Rogelja et al., 2018 ( <i>P. schwartzii</i> ) NW: Rubino et al., 2000; Sangiorgi and Donders, 2004 ( <i>P.</i> <i>schwartzii</i> ) mW: Rubino et al., 2000; Zonneveld et al., 2013 ( <i>P.</i> <i>schwartzii</i> ) SW: Caroppo et al., 1999 ( <i>P.</i> <i>kofoidii</i> ); Rubino et al., 2002, 2009; Zonneveld et al., 2013 ( <i>P.</i> <i>schwartzii</i> )

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Table 5 (continued)

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Preperidinium meunieri</i></b> (Pavillard) Elbrächter (syn. <i>Peridinium meunieri</i> Pavillard 1912; <i>Diplopsalis lenticula</i> f. <i>minor</i> Paulsen 1907; <i>Peridinium lenticulum</i> Mangin 1911; <i>Peridinium paulsenii</i> Mangin 1911; <i>Peridinium lenticulatum</i> L.A.Mangin 1911; <i>Diplopeltopsis minor</i> Pavillard 1913; <i>Preperidinium paulseni</i> (Mangin) Mangin 1913; <i>Diplopsalis minor</i> (Paulsen) Lindemann 1927; <i>Glenodinium lenticula</i> f. <i>minor</i> Schiller 1937; <i>Zygabikodinium lenticulatum</i> Loeblich Jr. & Loeblich III 1970)	Baltic Sea, Black Sea, Helgoland, Mediterranean, Netherlands, Portugal  Spain (as <i>D. lenticula</i> f. <i>minor</i> )  Netherlands (as <i>Diplopeltopsis minor</i> )  Britain, Netherlands, Norway, Sweden (as <i>Z. lenticulatum</i> )	Lig, Lev: Gómez, 2003 Bal: Gómez, 2003; Satta et al., 2013 (as <i>P. cf. meunieri</i> ) Tyr: Montresor et al., 1998; Gómez, 2003 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Mar: Balkis et al., 2016	NEW introduction
<b><i>Protoceratium reticulatum</i></b> (Claparède & Lachmann) Bütschli  (syn. <i>Peridiniopsis reticulatum</i> (Claparède & Lachmann) Starmach; <i>Peridinium reticulatum</i> Claparède & Lachmann 1859; <i>Gonyaulax grindleyi</i> Reinecke 1967; <i>Operculodinium centrocarpum</i> (Deflandre and Cookson) Wall)	Adriatic Sea, Baltic Sea, Black Sea, Helgoland, Mediterranean, Netherlands, Romania, Sweden (as <i>P. reticulatum</i> )  Romania (as <i>Peridiniopsis reticulatum</i> )  Adriatic Sea, Black Sea, Britain, Portugal, Turkey (as <i>G. grindleyi</i> )	All: Gómez, 2003; Zonneveld et al., 2013 Bal: Satta et al., 2013 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Aydin and Uzar, 2014 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	all: Gómez, 2003; Zonneveld et al., 2013 NE: Nichetto et al., 1995 (as <i>G. grindleyi</i> ); Viličić et al., 2002 NW: Sangiorgi and Donders, 2004; Bastianini et al., 2016 (also cyst) SW: Rubino et al., 2002, 2009
<b>Toxicity</b> Yessotoxin toxin producer (MacKenzie et al., 1998; Paz et al., 2004; Samdal et al., 2004; Miles et al., 2005a, 2005b; Paz et al., 2006; Loader et al., 2007; Ignatiades and Gotsis-Skretas, 2010 and references within)			
<b><i>Protoperidinium cf. avellana</i></b> (Meunier) Balech (syn. <i>Brigantedinium cariacense</i> (Wall) Lentin and Williams)	Baltic Sea, Britain, Portugal (as <i>P. avellana</i> )	All: Zonneveld et al., 2013 Tyr: Montresor et al., 1998 (as <i>P. avellanum</i> ) Aeg: Aydin et al., 2015	All: Zonneveld et al., 2013 (as <i>Brigantedinium</i> sp.) NW: Sangiorgi and Donders, 2004 NW: Sangiorgi and Donders, 2004; Bastianini et al., 2016 NE: Nichetto et al., 1995; Rubino et al., 2000
<b><i>Protoperidinium claudicans</i></b> (Paulsen) Balech (syn. <i>Peridinium claudicans</i> Paulsen 1907; <i>Votadinium spinosum</i> Reid)	Baltic Sea, Black Sea, Britain, Helgoland, Mediterranean, Netherlands, Portugal, Turkey	Bal: Gómez, 2003; Zonneveld et al., 2013 (as <i>V. spinosum</i> ); Satta et al., 2013 Alb, Alg, Lig, Lev: Gómez, 2003 Tyr: Montresor et al., 1998; Gómez, 2003; Fertouna-Bellakhal et al., 2014 Aeg: Gomez, 2003; Aydin and Uzar, 2014; Aydin et al., 2015 Mar: Aydin and Uzar, 2014 Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Evangelopoulos and Nikolaidis, 1996 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 All: Zonneveld et al., 2013	NW: Sangiorgi and Donders, 2004; Bastianini et al., 2016 NE: Nichetto et al., 1995; Rubino et al., 2000 NW: Rubino et al., 2000 mW: Rubino et al., 2000 SW: Rubino et al., 2002, 2009
<b><i>Protoperidinium compressum</i></b> (Abé) Balech (syn. <i>Peridinium compressum</i> (Abé) Nie; <i>Stelladinium reidii</i> Bradford)	South-west Asia: Turkey	Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Evangelopoulos and Nikolaidis, 1996 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 All: Zonneveld et al., 2013	NE: Nichetto et al., 1995; Rubino et al., 2000 NW: Rubino et al., 2000 mW: Rubino et al., 2000 SW: Rubino et al., 2002, 2009
<b><i>Protoperidinium conicoides</i></b> (Paulsen) Balech (syn. <i>Peridinium conicoides</i> Paulsen; <i>Brigantedinium simplex</i> (Wall) P.C.Reid)	Baltic Sea, Black Sea, Britain, Mediterranean, Netherlands, Portugal, Sweden	Bal: Satta et al., 2013 Tyr: Fertouna-Bellakhal et al., 2014 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Gómez, 2003 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 All: Gómez, 2003; Zonneveld et al., 2013 (as <i>S. quanta</i> ) Bal: Satta et al., 2013 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	All: Zonneveld et al., 2013 (as <i>Brigantedinium</i> sp.) NW: Sangiorgi and Donders, 2004
<b><i>Protoperidinium conicum</i></b> (Gran) Balech (syn. <i>Peridinium divergens</i> var. <i>conica</i> Gran 1900; <i>Peridinium conicum</i> (Gran) Ostenfeld & Schmidt 1902; <i>Selenopemphix quanta</i> (M.R.Bradford) Matsuoka 1985)	Adriatic Sea, Baltic Sea, Black Sea, Britain, France, Greece, Helgoland, Mediterranean, Netherlands, Portugal, Sweden, Turkey	All: Gómez, 2003; Zonneveld et al., 2013 (as <i>S. quanta</i> ) Bal: Satta et al., 2013 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	all: Gómez, 2003; Zonneveld et al., 2013 (as <i>S. quanta</i> ) SE: Viličić et al., 2002; Saracino and Rubino, 2006b mE: Viličić et al., 2002 NE: Rubino et al., 2000; Viličić et al., 2002; Cabrini et al., 2012; Rogelja et al., 2018 NW: Rubino et al., 2000; Sangiorgi and Donders, 2004; Bastianini et al., 2016 mW: Rubino et al., 2000 SW: Rubino et al., 2002

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Table 5 (continued)

Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Protoperidinium divaricatum</i></b> (Meunier) Balech (syn. <i>Peridinium divaricatum</i> Meunier 1919; <i>Peridinium gainii</i> P.-A.Dangeard 1920; <i>Protoperidinium gainii</i> (P.-A.Dangeard) Balech 1974; <i>Xandarodinium xanthum</i> Reid)	Asia: East China Sea, Yellow Sea	Tyr: Montresor et al., 1998 Ion: Ferraro et al., 2017 Aeg: Zonneveld et al., 2013 (as <i>X. xanthum</i> ) Aydin and Uzar, 2014; Aydin et al., 2015 Adr: Zonneveld et al., 2013 (as <i>X. xanthum</i> ) Mar: Aydin and Uzar, 2014	All: Zonneveld et al., 2013 (as <i>X. xanthum</i> ) NW: Rubino et al., 2000; Sangiorgi and Donders, 2004 NE: Rubino et al., 2000 mW: Rubino et al., 2000
<b><i>Protoperidinium leonis</i></b> (Pavillard) Balech (syn. <i>Peridinium leonis</i> Pavillard 1916; <i>Peridinium saltans</i> Pavillard 1915; <i>Quinquecusps concreta</i> (Reid) Head)	Adriatic Sea, Baltic Sea, Black, Britain, France, Greece, Helgoland, Mediterranean, Netherlands, Portugal, Sweden, Turkey	Alb, Alg, Adr: Gómez, 2003; Zonneveld et al., 2013 Bal: Gómez, 2003; Zonneveld et al., 2013; Satta et al., 2014 Tyr: Montresor et al., 1998 (as <i>P. leone</i> ); Gomez, 2003; Zonneveld et al., 2013; Fertouna-Bellakhal et al., 2014 Lig: Gomez, 2003 Ion: Zonneveld et al., 2013; Ferraro et al., 2017 Aeg: Gomez, 2003; Zonneveld et al., 2013; Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Gomez, 2003; Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 Alb, Lig: Gómez, 2003 Bal: Gómez, 2003; Zonneveld et al., 2013 (as <i>V. calvum</i> ); Satta et al., 2013 Tyr: Montresor et al., 1998; Gómez, 2003; Zonneveld et al., 2013 (as <i>V. calvum</i> ); Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Zonneveld et al., 2013 (as <i>V. calvum</i> ); Ferraro et al., 2017 Aeg: Zonneveld et al., 2013 (as <i>V. calvum</i> ); Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Gomez, 2003; Aydin and Uzar, 2014; Rubino et al., 2017 Mar: Balkis et al., 2016 Adr: Gomez, 2003; Zonneveld et al., 2013 (as <i>V. calvum</i> )	all: Gómez, 2003; Zonneveld et al., 2013 SE: Viličić et al., 2002 NE: Viličić et al., 2002; Cabrini et al., 2012 NW: Rubino et al., 2000; Sangiorgi and Donders, 2004 mW: Rubino et al., 2000
<b><i>Protoperidinium oblongum</i></b> (Aurivillius) Parke & Dodge (syn. <i>Peridinium divergens</i> var. <i>oblongum</i> Aurivillius 1898; <i>Peridinium oblongum</i> (Aurivillius) Cleve 1900; <i>Peridinium oceanicum</i> var. <i>oblongum</i> (Aurivillius) Paulsen 1908; <i>Peridinium oceanicum</i> f. <i>oblongum</i> (Aurivillius) Broch 1910; <i>Votadinium calvum</i> Reid 1977)	Baltic Sea, Black Sea, Britain, Helgoland, Ireland, Mediterranean, Netherlands, Portugal, Sweden	Alb, Alg, Bal, Adr: Gómez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ) Ion: Rubino et al., 2002; Gomez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ); Ferraro et al., 2017 (as <i>T. applanatum</i> ) Aeg: Gomez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ); Aydin et al., 2015 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 Lev: Gomez, 2003 All: Gómez, 2003 Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	all: Gómez, 2003; Zonneveld et al., 2013 SE: Saracino and Rubino, 2006b NE: Nichetto et al., 1995; Cabrini et al., 2012 NW: Rubino et al., 2000; Sangiorgi and Donders, 2004 mW: Rubino et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2002
<b><i>Protoperidinium pentagonum</i></b> (Gran) Balech (syn. <i>Peridinium pentagonum</i> Gran 1902; <i>Peridinium sinuosum</i> Lemmermann 1905; <i>Protoperidinium parapentagonum</i> Wang 1936; <i>Trinovantedinium applanatum</i> (Bradford) Bujak and Davies)	Baltic Sea, Black Sea, Britain, Helgoland, Mediterranean, Netherlands, Portugal, Romania, Turkey	Alb, Alg, Bal, Adr: Gómez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ) Ion: Rubino et al., 2002; Gomez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ); Ferraro et al., 2017 (as <i>T. applanatum</i> ) Aeg: Gomez, 2003; Zonneveld et al., 2013 (as <i>T. applanatum</i> ); Aydin et al., 2015 Mar: Aydin and Uzar, 2014; Balkis et al., 2016 Lev: Gomez, 2003 All: Gómez, 2003 Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1998; Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002; Ferraro et al., 2017 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Lev: Rubino et al., 2017 Mar: Aydin and Uzar, 2014; Balkis et al., 2016	all: Gómez, 2003 SE: Viličić et al., 2002; Rubino et al., 2009; Drakulović et al., 2012 mE: Viličić et al., 2002 NE: Nichetto et al., 1995; Rubino et al., 2000; Viličić et al., 2002; Cabrini et al., 2012; Rogelja et al., 2018 NW: Rubino et al., 2000; Bastianini et al., 2016 mW: Caroppo, 2000; Rubino et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2002, 2009
<b><i>Protoperidinium</i> spp.</b> R.S.Bergh, 1881 (syn. <i>Brigantedinium</i> )			

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Table 5 (continued)

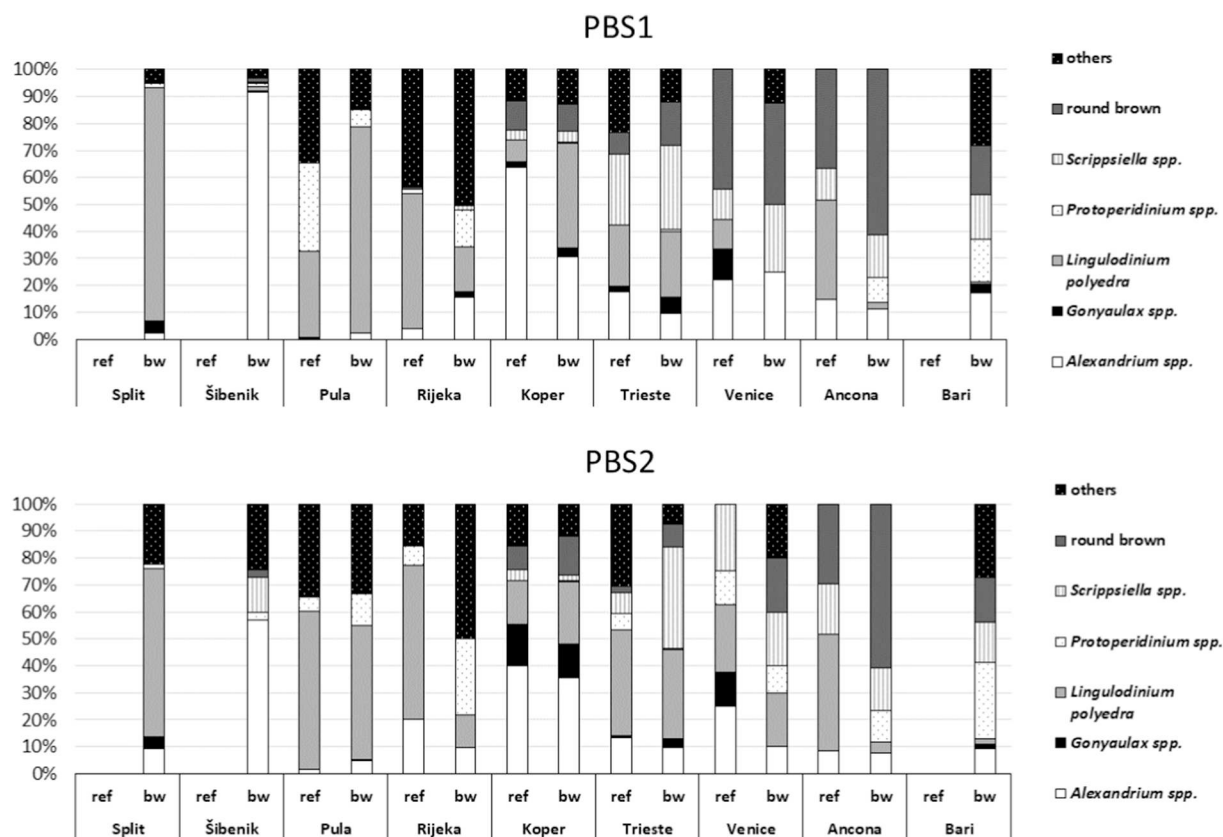
Taxa with synonyms and references to toxicity	Distribution		
	Europe or closest (source: AlgaeBase)	Mediterranean sub-basins (after Gómez, 2003)	Adriatic Sea
<b><i>Scrippsiella acuminata</i></b> (Ehrenberg) Kretschmann, Elbrächter, Zinssmeister, S. Soehner, Kirsch, Kusber & Gottschling (syn. <i>S. trochoidea</i> (Stein) Loeblich III)  <b>Toxicity</b> Bloom forming species of unknown toxicity (Ignatiades and Gotsis-Skretas, 2010 and references within)	Adriatic Sea, Baltic Sea, Black Sea, Britain, France, Germany, Greece, Helgoland, Italy, Mediterranean, Netherlands, Norway, Portugal, Romania, Spain, Sweden, Turkey (as <i>S. trochoidea</i> )	(as <i>S. acuminata</i> ) Tyr: Gottschling et al., 2005 Ion: Ferraro et al., 2017 Lev: Rubino et al., 2017 (as <i>S. trochoidea</i> ) All: Gómez, 2003 Alb, Bal: Meier and Willems, 2003 Tyr: Montresor and Zingone, 1988; Montresor et al., 1994, 1998, 2003; Meier and Willems, 2003 Ion: Rubino et al., 2002; Meier and Willems, 2003 Lev: Meier and Willems, 2003 Mar: Balkis et al., 2016 (as <i>S. trochoidea</i> complex) Bal: Satta et al., 2013, 2014 Tyr: Fertouna-Bellakhal et al., 2014 Tyr: Montresor et al., 1998 Ion: Ferraro et al., 2017 Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1994, 1998; Gómez, 2003 Ion: Rubino et al., 2002; Ferraro et al., 2017	All: Gómez, 2003 SE: Saracino and Rubino, 2006b; Rubino et al., 2009 mE: Viličić et al., 2002 NE: Nichetto et al., 1995; Rubino et al., 2000; Viličić et al., 2002; Cabrini et al., 2012; Rogelja et al., 2018 NW: Rubino et al., 2000; Tolomio and Bullo, 2001 mW: Caroppo, 2000; Rubino et al., 2000 SW: Caroppo et al., 1999; Rubino et al., 2002, 2009
<b><i>Scrippsiella crystallina</i></b> J.Lewis	Britain	Tyr: Montresor et al., 1998 Ion: Ferraro et al., 2017	NE: Nichetto et al., 1995
<b><i>Scrippsiella lachrymosa</i></b> J.Lewis	Britain, Helgoland, Mediterranean, Norway, Portugal	Bal: Satta et al., 2013, 2014 Tyr: Montresor et al., 1994, 1998; Gómez, 2003 Ion: Rubino et al., 2002; Ferraro et al., 2017	NE: Rubino et al., 2000; Rogelja et al., 2018 NW: Rubino et al., 2000 mW: Rubino et al., 2000 SW: Rubino et al., 2002 NE: Rubino et al., 2000; Rogelja et al., 2018 mW: Rubino et al., 2000 SW: Rubino et al., 2002
<b><i>Scrippsiella operosa</i></b> (Deflandre) Montresor (syn. <i>Calciadinellum operosum</i> Deflandre)	Italy, Mediterranean	Alb, Bal: Meier and Willems, 2003 Tyr: Gómez, 2003; Montresor et al., 1994, 1997, 1998; Gottschling et al., 2005 Ion: Rubino et al., 2002; Ferraro et al., 2017 (as <i>C. operosum</i> ) Lev: Meier and Willems, 2003; Rubino et al., 2017 Bal: Satta et al., 2013, 2014 Tyr: Gómez, 2003; Montresor and Zingone, 1988; Montresor et al., 1994, 1998; Fertouna- Bellakhal et al., 2014 Ion: Rubino et al., 2002 (as <i>S. cf. precaria</i> ); Ferraro et al., 2017 Mar: Balkis et al., 2016 Bal: Satta et al., 2013 (as <i>S. ramonii</i> ) Tyr: Montresor et al., 1998, 2003 (as <i>S.</i> <i>ramonii</i> ); Gómez, 2003; Gottschling et al., 2005 (as <i>S. ramonii</i> ) Ion: Rubino et al., 2002; Ferraro et al., 2017 Lev: Rubino et al., 2017 Bal: Satta et al., 2014 (as <i>S. rotunda</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Gottschling et al., 2005 (as <i>S. rotunda</i> ) Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Mar: Balkis et al., 2016	SE: Saracino and Rubino, 2006b; Rubino et al., 2009 SW: Rubino et al., 2002 (as <i>S. cf.</i> <i>precaria</i> )
<b><i>Scrippsiella precaria</i></b> M.Montresor & A.Zingone	Italy, Mediterranean	Bal: Satta et al., 2013, 2014 Tyr: Gómez, 2003; Montresor and Zingone, 1988; Montresor et al., 1994, 1998; Fertouna- Bellakhal et al., 2014 Ion: Rubino et al., 2002 (as <i>S. cf. precaria</i> ); Ferraro et al., 2017 Mar: Balkis et al., 2016 Bal: Satta et al., 2013 (as <i>S. ramonii</i> ) Tyr: Montresor et al., 1998, 2003 (as <i>S.</i> <i>ramonii</i> ); Gómez, 2003; Gottschling et al., 2005 (as <i>S. ramonii</i> ) Ion: Rubino et al., 2002; Ferraro et al., 2017 Lev: Rubino et al., 2017 Bal: Satta et al., 2014 (as <i>S. rotunda</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Gottschling et al., 2005 (as <i>S. rotunda</i> ) Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Mar: Balkis et al., 2016	SE: Saracino and Rubino, 2006b; Rubino et al., 2009 SW: Rubino et al., 2002 (as <i>S. cf.</i> <i>precaria</i> )
<b><i>Scrippsiella cf. ramonii</i></b> M.Montresor	Italy, Mediterranean	Bal: Satta et al., 2013 (as <i>S. ramonii</i> ) Tyr: Montresor et al., 1998, 2003 (as <i>S.</i> <i>ramonii</i> ); Gómez, 2003; Gottschling et al., 2005 (as <i>S. ramonii</i> ) Ion: Rubino et al., 2002; Ferraro et al., 2017 Lev: Rubino et al., 2017 Bal: Satta et al., 2014 (as <i>S. rotunda</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Gottschling et al., 2005 (as <i>S. rotunda</i> ) Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Mar: Balkis et al., 2016	NE: Rubino et al., 2000; Rogelja et al., 2018 NW: Rubino et al., 2000 mW: Rubino et al., 2000 SW: Rubino et al., 2002
<b><i>Scrippsiella cf. rotunda</i></b> J.Lewis	Britain, Italy, Mediterranean, Norway	Bal: Satta et al., 2014 (as <i>S. rotunda</i> ) Tyr: Montresor et al., 1998; Gómez, 2003; Gottschling et al., 2005 (as <i>S. rotunda</i> ) Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Mar: Balkis et al., 2016	NEW introduction
<b><i>Scrippsiella trifida</i></b> J.Lewis	Britain, Spain	Tyr: Fertouna-Bellakhal et al., 2014 Ion: Rubino et al., 2002 Mar: Balkis et al., 2016	NE: Rubino et al., 2000; Rogelja et al., 2018 NW: Rubino et al., 2000 mW: Rubino et al., 2000 SW: Rubino et al., 2002 SE: Viličić et al., 2002; Saracino and Rubino, 2006b; Rubino et al., 2009; Drakulović et al., 2012; mE: Totti et al., 2000 NE: Nichetto et al., 1995; Rubino et al., 2000; Viličić et al., 2002, 2009, Cabrini et al., 2012; Rogelja et al., 2018 NW: Rubino et al., 2000; Bastianini et al., 2016 (also cyst) mW: Rubino et al., 2000 SW: Rubino et al., 2002, 2009 NE: Rogelja et al., 2018
<b><i>Scrippsiella</i></b> spp. Balech ex A.R.Loeblich III		Bal: Satta et al., 2013, 2014 Aeg: Aydin and Uzar, 2014; Aydin et al., 2015 Ion: Rubino et al., 2002; Ferraro et al., 2017 Tyr: Gottschling et al., 2005; Fertouna- Bellakhal et al., 2014 Lev: Rubino et al., 2017	
<b><i>Thoracosphaeraceae</i></b> indet. Schiller, 1930 (syn. <i>Calciadinellaceae</i> )		Ion: Ferraro et al., 2017 Arg, Bal, Tyr, Ion, Aeg, Lev: Gómez, 2003	



**Table 6**

Check-list of the taxa observed during PBS in the nine Adriatic Sea endorsed in five regions of the Adriatic (mE = mideastern with ports of Split and Šibenik, NE = northeastern with ports of Rijeka, Pula, Koper and Trieste; NW = northwestern with port of Venice, mW = Midwestern with port of Ancona; and SW = southwestern with port of Bari), including references to literature findings generally in the Adriatic (ADRIATIC) and per region (including SE = southeastern, mE, NE, NW, mW and SW) based on information given in [Tables 4 and 5](#). First reports in bold, for entire Adriatic on grey.

	ADRIATIC		NW	NE		MW	ME	SW	SE			
	Lit.	Lit.	Ports	Lit.	Ports	Lit.	Ports	Lit.	Ports	Lit.		
Alexandrium affine					PU RI							
Alexandrium insuetum					TS							
Alexandrium margaleffii					TS							
Alexandrium minutum/affine/tamutum	x	x	VE	x	TS RI PU KO	x	AN	x	ST SI	x	BI	
Alexandrium spp.		x		x	TS PO RI	x		x	ST	x		x
Alexandrium tamarense / catenella	x	x		x	TS RI KO PU				ST SI	x	BI	x
Biecheleria spp.		x			RI PU KO							
Cochlodinium spp.				x					ST SI	x		x
Diplopsalis group	x			x	TS	x		x	ST SI	x	BI	x
Gonyaulax scrippsae	x	x		x	TS KO RI	x			ST SI	x		
Gonyaulax spinifera	x	x	VE	x	TS KO	x		x	ST SI	x	BI	x
Gonyaulax spp.	x	x		x	TS KO PU RI	x		x		x		x
Gymnodinium impudicum	x			x	TS KO				ST			
Gymnodinium spp.	x	x	VE	x	PU RI	x		x	ST	x		x
Lingulodinium polyedra	x	x	VE	x	TS KO PU RI	x	AN	x	ST SI	x	BI	x
Pentapharsodinium dalei	x	x		x	TS KO					x		
Pentapharsodinium tyrrhenicum	x			x	TS KO					x		x
Polykrikos hartmanii					PU RI						BI	
Polykrikos spp.	x	x		x	TS KO	x		x		x		x
Preperidinium meunieri					RI				ST		BI	
Protoceratium reticulatum	x	x		x	TS KO				ST	x		
Protoperidinium cf. avellana	x	x			TS						BI	
Protoperidinium claudicans		x		x	RI						BI	
Protoperidinium compressum		x		x	PU RI	x			ST	x	BI	
Protoperidinium conicoides	x	x							ST		BI	
Protoperidinium conicum	x	x		x	TS KO PU RI	x		x	ST	x		x
Protoperidinium divaricatum	x	x		x	KO	x						
Protoperidinium leonis	x	x		x		x			ST		BI	x
Protoperidinium oblungum	x	x		x	TS PU	x				x		x
Protoperidinium pentagonum	x	x				x			ST	x		x
Protoperidinium spp.	x	x	VE	x	PU RI	x	AN	x	ST SI	x	BI	x
Scrippsiella acuminata	x	x		x	TS KO	x		x	ST SI	x	BI	x
Scrippsiella crystallina				x	TS KO							
Scrippsiella lachrymosa		x		x	TS KO	x				x	BI	
Scrippsiella operosa				x	TS KO	x				x		
Scrippsiella precaria					TS KO					x		x
Scrippsiella cf. ramonii		x		x	TS	x				x		
Scrippsiella cf. rotunda					TS KO							
Scrippsiella trifida		x		x	TS	x				x		
Scrippsiella spp.		x	VE	x	TS KO RI	x	AN	x		x	BI	x
Thoracosphaeraceae indet.				x	TS							
round brown cysts			VE		TS KO RI		AN		SI		BI	
small round cysts									ST SI			
N.I. cysts					TS KO PU RI				ST		BI	



**Fig. 2.** Contribution in each port of the dinoflagellates cysts groups at sampling sites impacted by ballast water (bw) and controls (ref) in the first and second Port Baseline Survey (PBS1 and PBS2). All the samples of PBS1 go from April to July, except for Rijeka and Pula (December 2014) and Šibenik (November 2013); samples of PBS2 go from October to December except for Pula and Rijeka (April 2015) and Trieste (March 2015).

**Koper** – On average, a slight increase of cysts abundance and decrease of cyst diversity was observed between the first PBS sampling in June 2014 and the second one in November 2014. Control location values were above the averages of cysts abundance and diversity in the port. June control location was characterised by undetermined *Alexandrium* cysts (50%), *A. minutum/affine/tamutum* group (13%) and undetermined cysts (20%), while at influenced locations, lower contribution of undetermined *Alexandrium* cysts (24%), *L. polyedra* (39%) and same contribution of undetermined cysts were observed. In November, in entire port there was a dominance of undetermined *Alexandrium* cysts (31%), *L. polyedra* (21%), and generally undetermined cysts (23%) and specifically of the genus *Gonyaulax* (13%). During this PBS, *Protoperidinium divaricatum* was found only in port of Koper, at influenced locations on both sampling dates.

**Trieste** – When two spring PBS samplings are compared (May 2014 and March 2015), a noticeable decrease of cysts abundance and diversity increase can note between the two. At the control location in May 2014, cysts abundance and diversity were considerably lower than at impacted ones, while in March 2015, values at all investigated locations were rather similar. At one influenced station, TSBw1 in March 2015, 20 taxa were observed, which is maximum of the entire PBS, while this port was generally characterised by highest diversity. Control location in May 2014 was dominated by *L. polyedra* (40%) and undetermined cysts (30%), while at impacted locations, besides *L. polyedra* (33%) and undetermined cysts (15%), undetermined cysts of *Scripsiella* (24%) and *Alexandrium* genus (8%) were reported. In March 2015, cysts assemblage was dominated by *Alexandrium* and *Scripsiella* genuses, while the most abundant species were *L. polyedra* (24%), *Scripsiella acuminata* (7%), undetermined cysts of *Scripsiella* genus (17%), and other undetermined cysts (25%). During this PBS, several species were found only in port of Trieste: *Alexandrium insuetum*,

*Alexandrium margaleffii* and *Protoperidinium cf. avellana* (only in March), *Scripsiella ramonii* and *Scripsiella trifida* (in May and March), only at impacted locations. Interestingly, undetermined cysts from *Thoracosphaeraceae* were reported at impacted location in May 2014 and at control location in March 2015.

**Venice** – During the two PBS samplings, in May and October 2014, the lowest abundances of entire PBS were reported for this port (average of  $6 \text{ g}^{-1} \text{ DW}$ ). Cyst diversity was among lowest observed, in total 7 taxa over both samplings. Higher contribution in May was reported for undetermined cysts of genus *Scripsiella* (18%), cysts identified as group *A. minutum/affine/tamutum* (24%) and unidentified cysts (41%), and in October, first two remained with contributions of 22 and 17%, respectively, with *L. polyedra* (22%). No species were observed solely in this port.

**Ancona** – During the two PBS samplings, in July and October 2014, cysts abundance was close to minimal values of entire PBS and diversity was PBS lowest, in total 5 taxa over both samplings. Interestingly, during both samplings, the most dominant was *L. polyedra* (40%), with unidentified cysts (33%) at control location, while at impacted ones, contribution of *L. polyedra* was negligible (3%), whereas unidentified cysts remained present in noticeably elevated contribution (61%). No species were observed solely in this port.

**Bari** – The two samplings, performed in May and November 2014, revealed that in comparison with other ports, rather low cyst abundance and high cyst diversity, characterise this one. In this port no control location was investigated. At influenced locations in May dominated *A. minutum/affine/tamutum* group (11%) and *S. acuminata* (10%), with large amount of undetermined and round brown cysts (42%). In November, undetermined cysts were observed in decreased amount (28%), with dominant cysts of genus *Protoperidinium* (20%) and *Preperidinium meunieri* (10%). No species were observed solely in this port.

**Table 7**

PRIMER SIMPER procedure calculations of average similarity (SIM.) and average dissimilarity (DISS.) (both expressed as %) based on original abundance dataset modified to include original referent values and averaged values from all impacted sampling stations based on  $\sqrt{v}$ -transformed values and Bray-Curtis similarities. Seasons 1 and 2 stand generally for samplings performed in two various months (for details on sampling months see Table 2).

	ST	SI	RI	PU	KO	TS	VE	AN	BI	MIN	MAX	AVE
SIM. all stations	48.76	57.50	58.09	72.67	74.82	61.58	65.35	79.47	84.16	48.76	84.16	66.42
SIM. referent stations	n.a.	n.a.	60.08	71.91	77.59	56.83	75.00	95.98	n.a.	56.83	95.98	72.90
SIM. impacted stations	48.76 <sup>b</sup>	57.50 <sup>b</sup>	60.14	79.76	82.27	72.68	76.47	96.53	84.16 <sup>b</sup>	48.76	96.53	73.14
DISS. referent-impacted	n.a.	n.a.	42.92	28.91	27.73	40.01	39.85	28.92	n.a.	27.73	42.92	34.72
SIM. season 1	n.a.	n.a.	53.53	71.38	69.73	62.19	65.05	70.86	n.a.	53.53	71.38	65.46
SIM. season 2	n.a.	n.a.	63.62	67.42	75.53	55.60	65.46	71.30	n.a.	55.60	75.53	66.49
DISS. season 1–2	51.24 <sup>a</sup>	42.50	42.15	25.69	24.08	37.08	34.61	16.33	15.84	15.84	51.24	32.17

<sup>a</sup> In port Split, data was collected over three different months and only an average is given here.

<sup>b</sup> In ports Bari, Sibenik and Split no samplings were performed at referent locations, therefore similarities based on data at all stations equal similarities from impacted ones.

### 3.3. Cyst assemblage comparison

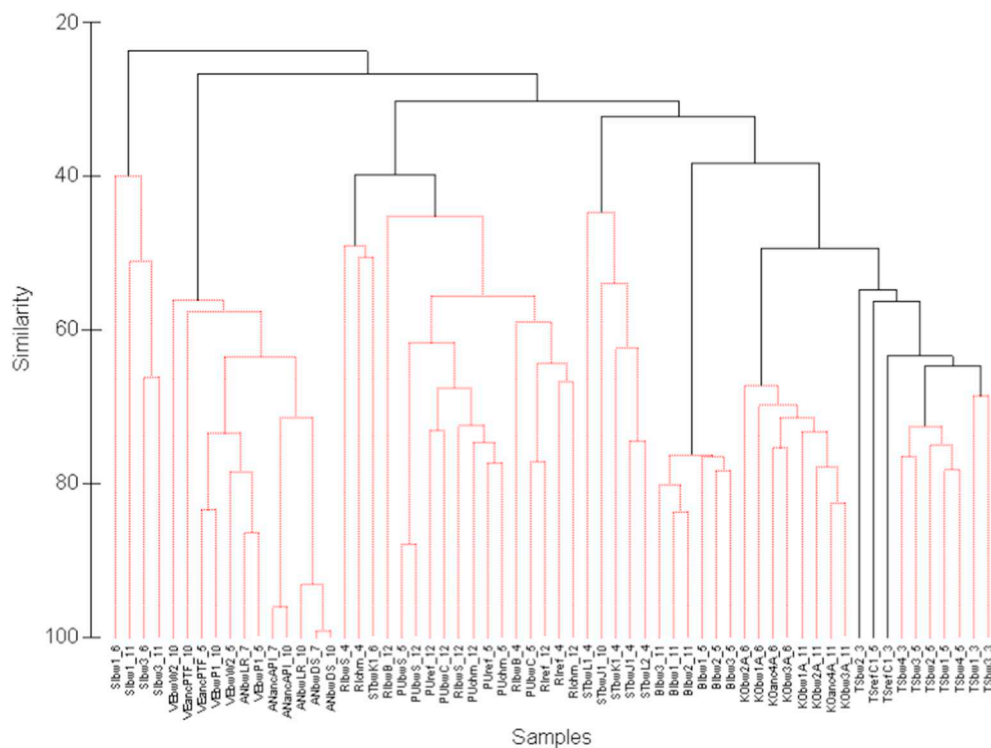
Our similarity analysis based on specific port dataset, including all data, and between control-impacted stations, as well as seasonal data (Table 7) revealed that overall cyst assemblage in port of Bari is most consistent (highest similarity per port, 84.16%) and between two

seasons (lowest dissimilarity, 15.84%). In port of Ancona assemblage is most consistent at impacted and referent stations (highest similarity, around 96%). Cyst assemblage of the highest variability was found in port of Split (lowest similarity, 48.76%), due to high seasonal variability (highest dissimilarity, 51.24%). The most prominent difference between cyst communities between impacted and control stations was

**Table 8**

Taxa contribution (%) delivered by PRIMER SIMPER procedure on original abundance dataset modified to include original referent values and averaged values from all impacted sampling stations based on  $\sqrt{v}$ -transformed values and Bray-Curtis similarities. Cut off for low contributions at 90%. Minimal and maximal value calculated on basis  $\geq 2$  ports, and median  $\geq 3$  ports.

Taxa PORT	ST	SI	RI	PU	KO	TS	VE	AN	BI	MIN	MAX	AVE	MED
<i>Alexandrium affine</i>										–	–	–	–
<i>Alexandrium insuetum</i>										–	–	–	–
<i>Alexandrium margalefii</i>										–	–	–	–
<i>Alexandrium minutum/affine/tamutum</i>	18.15	27.11	17.47		9.98	8.34	28.20	21.18	7.89	7.89	28.20	17.29	17.81
<i>Alexandrium tamarense/catenella</i>						5.67			6.91	5.67	6.91	6.29	–
<i>Alexandrium</i> spp.					14.80	9.46				9.46	14.80	12.13	–
<i>Biecheleria</i> spp.			18.97	8.57	6.68					6.68	18.97	11.41	8.57
<i>Cochlodinium</i> spp.										–	–	–	–
<i>Diplopsalis</i> group	5.43	13.55								5.43	13.55	9.49	–
<i>Gonyaulax scrippsae</i>	17.72									–	–	17.72	–
<i>Gonyaulax spinifera</i>						4.93	4.57		5.54	4.57	5.54	5.01	–
<i>Gonyaulax</i> spp.					8.48	3.34				3.34	8.48	5.91	–
<i>Gymnodinium impudicum</i>	12.47									–	–	12.47	–
<i>Gymnodinium</i> spp.			14.10	6.06						6.06	14.10	10.08	–
<i>Lingulodinium polyedra</i>	32.11		25.24	25.46	12.83	14.37	13.62	18.48	4.83	4.83	32.11	18.37	16.43
<i>Pentapharsodinium dalei</i>					2.89	2.34				2.34	2.89	2.62	–
<i>Pentapharsodinium tyrrhenicum</i>										–	–	–	–
<i>Polykrikos hartmannii</i>				17.32						–	–	17.32	–
<i>Polykrikos</i> spp.						2.80				–	–	2.80	–
<i>Preperidinium meunieri</i>									6.50	–	–	6.50	–
<i>Protoceratium reticulatum</i>	4.55									–	–	4.55	–
<i>Protoperidinium cf. avellana</i>										–	–	–	–
<i>Protoperidinium claudicans</i>									5.47	–	–	5.47	–
<i>Protoperidinium compressum</i>									5.13	–	–	5.13	–
<i>Protoperidinium conicoides</i>										–	–	–	–
<i>Protoperidinium conicum</i>						2.51				–	–	2.51	–
<i>Protoperidinium divaricatum</i>										–	–	–	–
<i>Protoperidinium leonis</i>									6.21	–	–	6.21	–
<i>Protoperidinium oblongum</i>										–	–	–	–
<i>Protoperidinium pentagonum</i>										–	–	–	–
<i>Protoperidinium</i> spp.		13.55	15.17	15.41					8.44	8.44	15.41	13.14	14.36
<i>Scrippsiella acuminata</i>		16.12			2.82	4.25			7.89	2.82	16.12	7.77	6.07
<i>Scrippsiella crystallina</i>										–	–	–	–
<i>Scrippsiella lachrymosa</i>									7.54	–	–	7.54	–
<i>Scrippsiella operosa</i>					2.90					–	–	2.90	–
<i>Scrippsiella precaria</i>										–	–	–	–
<i>Scrippsiella cf. ramonii</i>										–	–	–	–
<i>Scrippsiella cf. rotunda</i>										–	–	–	–
<i>Scrippsiella trifida</i>										–	–	–	–
<i>Scrippsiella</i> spp.					6.29	11.23	29.62	23.77		6.29	29.62	17.73	17.50
<i>Thoracosphaeraeaceae</i> indet.										–	–	–	–
Round brown		13.55			11.49	9.23	15.73	32.86	10.02	9.23	32.86	15.48	12.52
Small round cysts		16.12								–	–	16.12	–
N.I. cysts				18.50	11.44	12.5			9.41	9.41	18.50	12.96	12.96



**Fig. 3.** Dendrogram for hierarchical clustering of complete dataset obtained during PBS in all nine ports, using group-average linking of Bray-Curtis similarities calculated on  $\sqrt{v}$ -transformed abundance data. Dotted branches indicate significant relationships resulting from SIMPROF test.

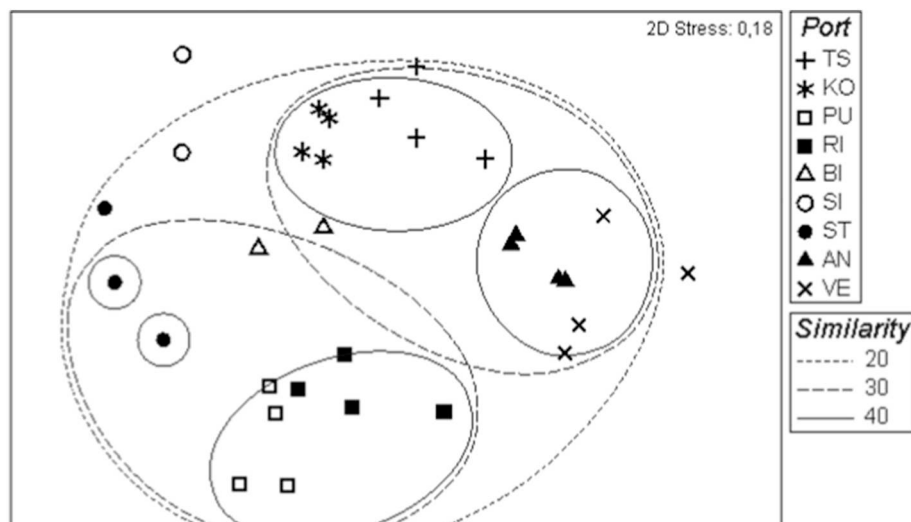
detected in port of Rijeka (dissimilarity 42.92%).

In general, the dissimilarity between control and impacted stations, as well as between seasonal data, is very low (32–35%, indicating communities to be rather uniform inside one particular port, regardless of observed taxa number in respective port (as low as in port of Ancona, or as high as in port of Trieste).

Taxa composition among the ports did not exhibit significant differences, indeed the most abundant species appear to be largely shared by all the ports (Table 8). Three most dominant taxa, based on highest taxa contribution in each port ( $> 18\%$ ) and observation frequency ( $\geq 4$  ports), were *L. polyedra* (in 8 ports, with average contribution of 18%), *A. minutum/affine/tamutum* (in 8 ports, with 17%) and unidentified *Scripsiella* species (in 4 ports, with 18%). Interestingly, the subsequent three taxa which followed by high contribution (16–17%), were of scarce frequency, one port only, *Gonyaulax scrippsae* in Split, *Polykrikos*

*hartmannii* in Pula and small round cysts in Šibenik. In contrast, taxa composition changed significantly among ports as confirmed by AN-OSIM, Global  $R = 0.909$ , significance level  $< 0.001$ . The differences among ports are mainly due to: 1) marked dissimilarities in biomass and frequency of a pool of taxa common to all ports, and 2) the presence of specific taxa that were associated, albeit to different degrees, with individual port.

Port coherency investigation performed by Cluster (Fig. 3) and MDS ordination (Fig. 4) with the integral cysts dataset delivered outcome of spatial aggregation among the ports: Trieste - Koper, than with Bari and Split at lower similarity, followed by Rijeka - Pula, than Venice - Ancona, whereas Šibenik showed least similarity with the rest of the ports. The MDS ordination showed, above all, a significant difference between samples collected in different ports. Further similarity investigation by SIMPER procedure (Table 9) indicated lowest dissimilarity between



**Fig. 4.** Two-dimensional MDS configuration of original abundance dataset modified to include original referent values and averaged values from all impacted sampling stations based on  $\sqrt{v}$ -transformed values and Bray-Curtis similarities with superimposed clusters performed at complete dataset as presented at Fig. 3 (similarity levels 20, 30 and 40).

**Table 9**

PRIMER SIMPER procedure calculations of average dissimilarity (%) between the ports, based on original abundance dataset modified to include original referent values and averaged values from all impacted sampling stations based on  $\sqrt{\sqrt{}}$ -transformed values and Bray-Curtis similarities. Dissimilarities above and under range of first standard deviation ( $66.6 \pm 10.0\%$ ) were marked in bold, and highest/lowest are within square.

	ST	SI	RI	PU	KO	TS	VE	AN	BI
ST									
SI	61,8								
RI	65,2	72,8							
PU	66,4	<b>79,6</b>	<b>42,2</b>						
KO	64,0	68,2	63,9	64,8					
TS	73,3	72,7	68,8	73,8	<b>48,5</b>				
VE	<b>84,1</b>	<b>78,6</b>	67,3	<b>81,2</b>	<b>78,8</b>	66,2			
AN	<b>78,1</b>	67,7	62,4	76,0	65,9	60,5	<b>38,4</b>		
BI	68,7	<b>56,7</b>	62,4	61,4	61,5	57,4	<b>72,8</b>	65,5	

**Table 10**

Main taxa accountable for dissimilarity between the ports (highest contribution) obtained by PRIMER SIMPER procedure calculations based on original abundance dataset modified to include original referent values and averaged values from all impacted sampling stations based on  $\sqrt{\sqrt{}}$ -transformed values and Bray-Curtis similarities. *Alexandrium minutum/affine/tamutum* (Amat). *Alexandrium* spp. (Alex). *Biecheleria* spp. (Biec). *Gonyaulax scrippsae* (Gscr). *Lingulodinium polyedra* (Lpol). *Polykrikos hartmannii* (Phar). *Protoperidinium* spp. (Prot). N.I. cysts (N.I.) and round brown (R.B.).

	ST	SI	RI	PU	KO	TS	VE	AN	BI
ST									
SI	Lpol								
RI	Lpol	Amat							
PU	Gscr	Amat	Phar						
KO	Alex	Amat	Alex	Alex					
TS	Lpol	Amat	Biec	Phar	Alex				
VE	Lpol	Amat	Biec	Lpol	Alex	N.I.			
AN	Lpol	Amat	R.B.	N.I.	Alex	N.I.	R.B.		
BI	Lpol	Amat	R.B.	Lpol	Alex	Prot	N.I.	N.I.	

Ancona and Venice (38.4%), low between Pula and Rijeka, Trieste and Koper, while the high dissimilarity was among pairs, Venice-Koper, Venice-Pula, Venice-Šibenik, Ancona-Split, Pula-Šibenik, and the highest between Venice and Split (84.1%). In 27 out of 36 pairs that nine investigated ports form, there were only four taxa attributed as a major foundation of dissimilarity in the pair as delivered by SIMPER (Table 10); *Alexandrium* cysts determined only to genus level (8 pairs), *L. polyedra* (8 pairs), *A. minutum/affine/tamutum* group (6 pairs) and generally unidentified cysts (5 pairs).

#### 4. Discussion

In addition to regular production of dinoflagellate cysts during sexual reproduction phase, encystment can be triggered in response to unfavourable environmental conditions (Taylor, 1987; Garcés et al., 2002). Accordingly, in addition to being introduced in ship tanks during ballast intake, cysts formation may be triggered by unfavourable conditions for vegetative stages during voyages (Casas-Monroy et al., 2013). During an 18 months investigation of phytoplankton contained in ballast tanks of 19 cargo vessels calling in Taranto port, a total of 48 phytoplanktonic species in the water and 51 different morphotypes of resting stages in the sediments were recorded, representing 17 dinoflagellate genera (Saracino and Rubino, 2006a). Due to difficulties encountered in collecting, the results were reported to be, almost certainly, underestimated. Another study focused on variability between tanks proved that species diversity and their relative abundance showed

significant variability, when a total of 21 dinoflagellate species were identified from 31 distinctive cyst morphotypes in four ballast water tanks of a single ship (Hamer et al., 2000). Reports show that the resting stages produced by potentially toxic dinoflagellate species of the genus *Alexandrium* were present in 40% of the sediment samples from the Taranto port (Saracino and Rubino, 2006a), and occurrence of potentially toxic species, *Alexandrium tamarense* and other unidentified *Alexandrium* cyst morphotypes detected in three of the four investigated tanks in another study (Hamer et al., 2000), confirm and substantiate the concern of the inadvertent transport of the potentially toxic dinoflagellate species (Hallegraeff and Bolch, 1991, 1992).

As the ballast water tanks are usually cleaned only when the ship is in dry dock, within each separate ballast tank of an individual ship, a mixture of sediments from several different ports typically accumulates, with high potential for development of different assemblages of dinoflagellate resting stages originated from several years of vessel operations (Hamer et al., 2000). Their extreme resilience enables cysts to endure ship transport for several years (Rigby and Hallegraeff, 1994). Although sediments accumulate at the bottom of ballast tanks, their resuspension during de-ballasting enables any amount of its content to be discharged (Villac et al., 2001). Ports represent a logical place to initiate biological surveys as the most likely area for new marine introduction by BW (Awad et al., 2014). Furthermore, confined areas in coastal areas, such as ports, were reported to host high densities and diversities of cysts assemblages (Rubino et al., 2002).

The PBS conducted as one of research activities of the BALMAS project, included investigation of dinoflagellate resting stages in nine ports along the Adriatic, including 26 sampling stations impacted by BW and 6 control locations. Our comparison of dinoflagellate cysts assemblages based on sampling location types, i.e., between the ones that are potentially under direct impact of BW and those without any or under indirect impacts (control), pointed out that essentially there are no observable differences. The highest dissimilarity between cyst assemblage at impacted and control station was obtained in port of Rijeka. However, the rationale behind this result is hardly a straightforward one. The topography of the port itself seems to have low impact on potential cysts spread, based on all dissimilarities calculations between impacted and control sites of the investigated ports. Locations of control sites, which were outside ports in coastal area of the “open” type ports, like Trieste, Koper and Pula, or outside ports in open coastal zone of the “closed” type ports, like Venice (naturally enclosed inside a lagoon), Ancona and Rijeka (artificially enclosed ports), did not reflect in any diversities of the cysts assemblages respective to sampling site type. Although choice of control and impacted sampling sites was based on current understanding of the circulation pattern of the respective port, we are inclined to conclude that choice of control sites have to be further afield, in an area of high settling rate, and limited connection to the port by circulation pattern. As detailed investigations of the ports seem to be rare (e.g., Mali et al., 2017), this issue might remain challenging in the close future.

Irrespective of sampling location type, our investigation of cysts assemblages among the ports revealed seasonal variability to be most pronounced in port of Split, high in Rijeka and Šibenik, low in Ancona, Koper and Pula, and least evident in Bari. However, differences seem to be restricted to quantitative aspect, as qualitatively, cyst assemblage remained rather constant inside each specific port. Evidently lower cyst abundance, respective to other ports, was observed in ports of Ancona and Venice, which is in contrast to the general observations that in secluded areas (e.g., ports), limited hydrodynamics favours accumulation of sinking cysts within the sediments (e.g., Satta et al., 2010, 2013) but we have to consider that Venice (Umgiesser et al., 2004) and Ancona (Fabi et al., 2016) present peculiar higher hydrodinamism. This finding highlights the complexity of factors inducing encystment and their settlement and accumulation. Actually, hydrographic and sedimentary processes, such as currents and cysts sinking rates, appear to be also species selective, complicating further understanding of cysts settlement process (Matsuoka et al., 2003).



Dinoflagellate cyst assemblages were predominated by heterotrophic organic Peridiniales at the western side of the Adriatic, comprising ports of Bari, Ancona and Venice, and autotrophic/mixotrophic Gonyaulacales at the eastern. Other autotrophs, namely calcareous Peridiniales, were codominant in all western ports, and one eastern, port of Trieste. However, often referred to as a widely distributed and present in high relative abundances, *Scrippsiella acuminata* (e.g., Persson et al., 2000; Satta et al., 2013; Wang et al., 2007) was restricted to five ports, Trieste, Koper, Split, Šibenik and Bari, while only in last two it was observed in high relative abundances (~10–13%). Interestingly, Gymnodiniales occasionally contributed with considerable abundances to the cyst assemblage. Specifically, with *Polykrikos hartmannii* in port of Pula (in May and December), with unidentified *Gymnodinium* species in ports of Rijeka (especially in April), Split (in June) and Venice (especially in October), and in Šibenik, *Polykrikos* (in November).

General separation to the western and eastern side of the Adriatic, regarding cysts assemblage composition, and partially abundance, potentially might be related to events triggered by bora, pronounced at the eastern coast (e.g., Alpers et al., 2009). Bora is dry strong north to north-eastern wind blowing along the eastern Adriatic coast usually during cold part of the year; episodes last on average for 40 h, being strongest for about 12 (Orlić et al., 1994; Cushman-Roisin et al., 2001). Bora episodes can induce strong evaporation and consequently impact the circulation pattern of the Adriatic (e.g., Lyons et al., 2007; Supić et al., 2012); inducing mixing of the water column, usually in the eastern (Wang et al., 2007), and during severely intense episodes, also in the western Adriatic (Boldrin et al., 2009). Efficient mixing of the water column at the eastern coast during bora might potentially favour intense cysts settlement at the eastern side of the Adriatic, resulting in distinct abundance gradient. Role of surface heat losses in phytoplankton dynamics and introducing species from sediment into water column was already discussed by Kraus and Supić (2015), whereas here we suggest the opposite, the settlement of phytoplankton cysts from the water column into the sediment. High contribution of heterotrophic taxa might also be related to observed eutrophic conditions in coastal waters (Thorsen and Dale, 1997; Dale et al., 1999; Matsuoka, 1999; Dale, 2001, 2009), and to the heavy impact of the prevailing sewage and industrial pollution (Matsuoka, 1999). Additionally, trophicity of the taxa might be accountable, as distribution of heterotrophic dinoflagellates is partially controlled by prey availability (diatoms and small flagellates) (Matsuoka, 1999), while those of phototrophic depends on light and dissolved nutrients availability (Dale, 2001). There is also a possibility that ports at the western side are more impacted by BW, in which heterotrophic taxa were found predominant over autotrophic, consequential to light deprivation within ballast water tanks, facilitating higher resilience and survival rate of the heterotrophs (Casas-Monroy et al., 2013).

One species of large distribution over the Adriatic coast, which was observed in all investigated ports, was autotrophic *Lingulodinium polyedra* (Gonyaulacales). Indeed, this ubiquitous species is widely distributed, from temperate zones in Northern to subtropical in Southern hemisphere, over rather wide temperature range (above 10 °C in summer and 0 °C in winter) and in a broad salinity range (Zonneveld et al., 2013), with noted preference for lower salinity, and relatively high nutrient concentration (e.g., Zonneveld et al., 2010). However, the relative contribution and abundances of *L. polyedra* in our ports ranged considerably. Hence, it was the quantitative aspect of *L. polyedra* which was accountable as one of four main sources of dissimilarity identified among studied ports. We believe the explanation is probably port specific as distribution range of *L. polyedra* cysts potentially can be inflicted by a variety of external factors inducing *L. polyedra* encystment, such as turbulence (Figueroa and Bravo, 2005). Some of the highest relative abundances were reported in the vicinity of the active upwelling cells and near river mouths, and seasonal production upon development of stratified upper waters following turbulence (Zonneveld et al., 2013). Furthermore, high *L. polyedra* abundances are considered to be related to eutrophication (Dale and Fjellså, 1994; Dale et al., 1999), relatively

warmer sea surface temperatures (Thorsen and Dale, 1997), lower salinity (Morzadec-Kerfourn, 1977), or even almost entirely limited to estuarine systems (Wall et al., 1977), whereas one survey suggests association to estuarine areas subjected to eutrophication or land-runoff (Persson et al., 2000). Other taxa accountable for dissimilarity identified among studied ports were *Alexandrium minutum/affine/tamutum* group, undetermined taxa of the genus *Alexandrium*, and generally undetermined dinoflagellate morphotypes.

Despite shortcomings of a relatively low sample counts to substantiate reliable conclusions regarding BW impacts in different ports, general insight regarding cysts distribution is rather attainable. Our results are consistent with observations of a study conducted in the Gulf of Trieste (Nichetto et al., 1995) where taxa detected in port and coastal area have only a fair number of taxa shared among both areas (9), with several restricted to port (6), and a higher number exclusively to the coastal area (18). Namely, during this study numerous taxa were not detected in port/s which are endorsed in previously reported region of observation (Tables 5 and 6). For example, *Scrippsiella lachrymosa* was reported for several regions of the Adriatic, NW and mW (Rubino et al., 2000), SW (Rubino et al., 2002) and NE (Rubino et al., 2000; Rogelja et al., 2018). However, during this study it was observed only in ports of Trieste and Koper (NW region) and Bari (SW region), thus confirming that spreading taxa over entire region, including port areas, is not necessarily a process which is certain to occur. This is also documented by rather high dissimilarity of cyst communities between ports of Venice and Trieste or Koper, all endorsed in the Northern Adriatic, a part of the Adriatic often characterised by a closed circulatory pattern separating this one from the other parts of the Adriatic. On the other hand, spreading between the two ports in close proximity seems to have occurred, as observed for Trieste-Koper, Pula-Rijeka or even for Venice-Ancona, although this was not observed in the case of ports of Šibenik and Split, which are also two rather proximate ports. For example, *Biecheleria* spp. was reported in NW region (Bastianini et al., 2016), but was undetected in port of Venice during this study, whereas *Protoperidinium conicum* was reported in mE region (Viličić et al., 2002), but was observed only in port of Split during this study (and not in port of Šibenik).

Spreading of dinoflagellates over coastal areas, and across the Adriatic by natural pattern, by general circulatory system and/or large gyres connecting western and eastern part of Adriatic, seems to be rather limited. Nevertheless, three taxa were observed in a new region during this study, whereto the spreading might have occurred by general anticyclonic currents system: *Scrippsiella precaria* spread from SE (Saracino and Rubino, 2006; Rubino et al., 2009) up the eastern coast to NE (observed in port/s of Trieste and Koper), and *Protoperidinium claudicans* down the western coast, from NW (Sangiorgi and Donders, 2004; Bastianini et al., 2016) down to SW (observed in port of Bari). *Protoperidinium compressum*, observed in port of Split might have spread by large gyres eastwards from mW (Rubino et al., 2000) and/or SW (Rubino et al., 2002, 2009) and then up the eastern coast by general anticyclonic system. We want to point out that their spread might have occurred also by BW, from intra-Adriatic marine traffic, or from BW originating from outside the Adriatic. For more detailed insight into Adriatic circulatory pattern related to potential spreading of species as opposed to BW transfer refer to Kraus and co-authors (2019b).

In this study we confirmed the presence of taxa already described in literature for some Adriatic regions (Tables 5 and 6). However, these taxa were reported also as generally present in the Adriatic, without specifying any particular region (Gómez, 2003; Zonneveld et al., 2013). Now, we point out their observation in a region/s unreported until now: *A. tamarense/catenella* group, *Gonyaulax scrippsae*, *Protoceratium reticulatum*, and *Protoperidinium pentagonum* were observed in mE during this study, and *Protoperidinium conicoides* and *Protoperidinium leonis* in mE and SW.

Finally, for the remaining six taxa no previous reports of observation were attainable, thus are assumed as NIS in the Adriatic. Specifically, these taxa were observed in six ports, as follows: in port of Bari *Polykrikos hartmannii* and *Preperidinium meunieri*, in port of Koper *Scrippsiella* cf.

*rotunda*, in port of Rijeka *Alexandrium affine*, *Polykrikos hartmanii*, and *Preperidinium meunieri*, in port of Pula *Alexandrium affine* and *Polykrikos hartmanii*, in port of Trieste *Alexandrium insuetum*, *Alexandrium margaleffii*, and *Scrippsiella cf. rotunda*, and in port of Split *Preperidinium meunieri*.

As already stated, our investigation indicated that considerable diversity exists among the regions along the Adriatic coast. We observed two taxa which are included in the provisional list of harmful aquatic organisms in the Adriatic, representing a constituent part of the Early Warning System for Non Indigenous Species for the Adriatic (Magaletti et al., 2018), so granting any intra-Adriatic exemptions from BW management should be taken carefully taking into account also this aspect. For example, *A. tamarense/catenella* group is not yet introduced to ports of Venice or Ancona, and *P. reticulatum* to ports of Pula, Rijeka and Šibenik considering also taxa distribution findings of vegetative forms in seawater column reported by Mozetič et al. (this issue). As concluded in the Baltic Sea case study, in order to ensure data reliability, in addition to PBS, regular monitoring programs should be undertaken during the exemption period as findings of new species influence the results of risk assessment for exemptions from BW management (David et al., 2013). As presented results of this study indicate, introduction of NIS and toxic taxa have occurred over the last years, and the potential threat of BW to Adriatic represents an issue yet to be addressed. International Maritime Organization (IMO) Ballast Water Management (BWM) Convention for the Control and Management of Ship's Ballast Water and Sediments (IMO, 2004) has entered into force on 8 September 2017. BWM Convention sets requirements to prevent organism transfers, thus enhancing prospects of improved protection of marine environment from any harmful impacts of shipping in the near future. One of the aims this study is helping scenario-specific risk assessments that help reducing risk of invasion in susceptible areas. Other approaches should be followed: BW treatment (physical, chemical or simply by introducing mid-way ballast exchange) is one of the main efforts to be gradually introduced by the new convention (David et al., 2015).

Observation of nine toxic dinoflagellate taxa (of variable toxicity, ranging from unknown/low to toxin producers), might impose an issue in extra-Adriatic traffic by meeting the criteria of issuing a warning to ships related to the risk assessment criteria of the Guidelines for Risk Assessment under Regulation A-4 of the BWM Convention (G7) (MEPC, 2007), i.e., the warning aimed at minimizing the uptake of BW which could be harmful for the recipient port or area (David et al., 2013, 2015). It has long ago been suggested that risk assessment systems might support identification of vessels likely to contain NIS or particularly undesirable species (Hayes, 1998). However, a need for accurate and readily available ships ballast log records in combination with information of the spatial and temporal distribution of target species in port areas around the world was already claimed in the past (Hamer et al., 2000).

However, some promising technical developments might enable improvements in addressing the issue of potential threats by BW. Namely, the accurate determination of dinoflagellate vegetative forms and resting stages based on microscopic examination requiring extensive taxonomic expertise, with intrinsic limitations of the method, lead to development of molecular identification techniques (Bolch, 2001; Godhe et al., 2002; Erdner et al., 2010; Penna et al., 2007). Although crosscheck between the microscopic and molecular methods is indispensable before independent application of the latter, one of the most beneficial and obvious advantages is ultimately faster identification on a high resolution of species-level (John et al., 2014). Following development of single cyst/cell-based method successfully applied at autotrophs (Bolch, 2001), especially belonging to genera of *Alexandrium* and *Gymnodinium* (Penna et al., 2008; Bolch, 2001; Godhe et al., 2002; Lin et al., 2006), recently new dinoflagellate-specific primers have been designed to increase the PCR efficiency for heterotrophs (Gao et al., 2017). The use of these faster molecular methods was tested also on limited number of ports during BALMAS PBS (Perini et al., this issue) with promising results to facilitate more efficient monitoring efforts in

the future. Importance of this issue is highlighted even more as considerable amount of cyst remained unidentified during processing samples in this study, providing additional source of potential NIS, or even harmful and toxic taxa.

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