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Abstract: Harmful benthic microalgae blooms represent an emergent phenomenon in temperate zones, causing health, ecological and economic concern. The main goal of this work is to compile records of *Ostreopsis* at large temporal and spatial scales, in order to study the relationship between cell abundances, the periodicity and intensity of the blooms and the role of sea water temperature in 14 Spanish, French, Monegasque and Italian sites located along the northern limits of the Mediterranean Sea. General trends are observed in the two considered basins: the north-western Mediterranean Sea, in which higher cell abundances are mostly recorded in mid-summer (end of July), and the northern Adriatic Sea where they occur in early fall (end of September). The sea water temperature does not seem to be a primary driver, and the maximal abundance periods were site and year specific. Such results represent an important step in the understanding of harmful benthic microalgae blooms in temperate areas, and provide a good base for managers in the attempt to monitor and forecast benthic harmful microalgae blooms.

Trends in *Ostreopsis* proliferation along the Northern Mediterranean coasts

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Abstract

Harmful benthic microalgae blooms represent an emergent phenomenon in temperate zones, causing health, ecological and economic concern. The main goal of this work is to compile records of *Ostreopsis* at large temporal and spatial scales, in order to study the relationship between cell abundances, the periodicity and intensity of the blooms and the role of sea water temperature in 14 Spanish, French, Monegasque and Italian sites located along the northern limits of the Mediterranean Sea. General trends are observed in the two considered basins: the north-western Mediterranean Sea, in which higher cell abundances are mostly recorded in mid-summer (end of July), and the northern Adriatic Sea where they occur in early fall (end of September). The sea water temperature does not seem to be a primary driver, and the maximal abundance periods were site and year specific. Such results represent an important step in the understanding of harmful benthic microalgae blooms in temperate areas, and provide a good base for managers in the attempt to monitor and forecast benthic harmful microalgae blooms.

Keywords: Harmful algae; Benthic microalgae; *Ostreopsis*; North Western Mediterranean Sea; Northern Adriatic Sea; Sea Water Temperature

1 Introduction

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4 *Ostreopsis* species are benthic dinoflagellates generally recorded in tropical and subtropical seas,
5 but the worldwide occurrence of this genus increased markedly in the last decade and this trend is
6 likely to continue (Rhodes, 2010). In particular, during the last 15 years, *Ostreopsis* cf. *ovata* and/or
7 *Ostreopsis* cf. *siamensis* were found in high concentrations during the summer in temperate regions
8 such as New-Zealand (Chang et al., 2000; Rhodes et al., 2000, Shears & Ross, 2009) and the
9 Mediterranean Sea (Vila et al., 2001; Penna et al., 2005; Mangialajo et al., 2008; Totti et al., 2010);
10 high concentrations of *Ostreopsis* were also observed in the waters of Japan, witnessed by the
11 presence of a considerable number of microalgae cells in parrotfishes (Taniyama et al., 2003), and
12 of Russia (Selina & Orlova, 2010). Those observations imply an extension of the area of
13 distribution of *Ostreopsis* in both the northern and southern hemispheres (Shears and Ross, 2009).
14 As suggested by Miraglia et al. (2009), the changing global climate could affect the distribution of
15 Harmful Algal Blooms (HABs) and the related sanitary problems. Whether this extension
16 represents a new introduction supported by climate change or represents the proliferation of species
17 that have already been present for a long time at low concentrations (Tognetto et al., 1995) is still
18 questionable. In fact *Ostreopsis* sp. (probably *O. ovata*) was already observed during the seventies
19 in the bay of Villefranche (northern Mediterranean; Taylor, 1979).
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33 In tropical zones, several species of *Ostreopsis* are commonly associated with *Prorocentrum* and
34 *Gambierdiscus* and therefore were suspected to be involved in ciguatera fish poisoning (Tosteson et
35 al., 1989; Tindall & Morton, 1998). Now it has been clarified that *Ostreopsis* species produce
36 palytoxin (PTX) and analogs (Riobó et al., 2006; Ciminiello et al., 2008) and a number of deaths
37 directly associated with the ingestion of PTX contaminated seafood, i.e. crustacean (Alcala et al.,
38 1988) or fish (Onuma et al., 1999; Taniyama et al., 2003), were reported.
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44 In temperate zones, *Ostreopsis* blooms were mainly involved in i) intoxications by inhalation
45 (Gallitelli et al., 2005; Durando et al., 2007), ii) irritations by contact and iii) mass mortalities of
46 invertebrates. Intoxications by ingestion have not been reported, even if PTX and/or analogs have
47 already been found in seafood by chemical or toxicological analysis (Taniyama et al., 2003;
48 Aligizaki et al., 2008; Amzyl, pers. comm.).
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53 The most important inhalation intoxications were observed in Italy in 2001 (Casavola et al., 2005)
54 and in 2005 (Brescianini et al., 2006) and in Spain in 2004 and 2006 (Alvarez et al., 2005; Barroso
55 Garcia et al., 2008; Vila et al., 2008), concerning more than 200 persons each time (from swimmers
56 to beach walkers or local residents). During the summer of 2009, local newspapers reported the
57 intoxication of several hundreds of persons in Algeria, related to *Ostreopsis* blooms (Illoul, pers.
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1 comm.). Respiratory intoxications are due to inhalation of seawater droplets containing *Ostreopsis*
2 cells or fragments of cells and/or aerosolized toxins.

3 Irritations due to contact (mainly skin irritations) have also been reported (Tichadou et al., in press),
4 but generally the extent of such events can be underestimated due to the non-specificity of the
5 symptoms and to the fact that medical support is generally not necessary and affections are
6 therefore not recorded.
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10 Invertebrate mass mortalities linked to *Ostreopsis* blooms have been observed by several authors in
11 the Mediterranean Sea (Sansoni, 2003; Simoni et al., 2003; Totti et al., 2010), in Brazil (Granéli et
12 al., 2002) and in New-Zealand (Shears & Ross, 2009). Even if oxygen depletion or high seawater
13 temperature (often associated to HAB blooms) could also be involved in those mortalities, the role
14 of the toxic microalgae seems to be substantial (Shears & Ross, 2009).
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18 Therefore, from the management perspective, the *Ostreopsis* bloom phenomenon is complex and
19 shows several intermingled facets, from human intoxication to potential ecosystemic modifications
20 and loss of resources. While intoxications by inhalation are mostly linked to the cell concentrations
21 in the water (planktonic cells), the irritations by contact are potentially mostly linked to the
22 abundance of benthic cells. The mass mortalities are potentially linked to both planktonic (*via* the
23 filter-feeders) and benthic (*via* herbivores) cells. The link between planktonic and benthic
24 abundances is still unclear: Mangialajo et al. (2008) and Vila et al. (2001) found a simultaneous
25 increase of abundances in both matrices, while Totti et al. (2010) mostly observed, at a small
26 temporal scale, increases of cell concentrations in the water column closely related to hydrodynamic
27 events. Unfortunately, the dynamics of benthic and planktonic *Ostreopsis* cells are still poorly
28 known, as are the ecological factors involved in the blooms. The temperature seems to be a crucial
29 parameter, as already reported following field observations (Sansoni et al., 2003; Simoni et al.,
30 2003; Mangialajo et al., 2008; Cabrini et al., 2010) and *in vitro* experiments (Granéli et al., in
31 press), but the role of such a parameter is still being debated (Vila et al., 2001; Selina & Orlova,
32 2010, Totti et al., 2010). The evaluation of the effect of seawater temperature on the development of
33 *Ostreopsis* species at their biogeographical limits is therefore of great interest, especially with
34 regard to global warming.
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38 The main goal of this work is to compile records of *Ostreopsis* abundances at large temporal and
39 spatial scales in order to study the relationship between benthic and planktonic abundances, the
40 periodicity and intensity of the blooms and the role of sea water temperature in the distribution of
41 *Ostreopsis* at its Mediterranean northern limits (Spain, France, Monaco and Italy).
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50 51 52 53 54 55 56 57 58 59 60 2 Materials and methods 61 62 63 64 65

2.1 Benthic and planktonic abundances

A total of 14 sites were considered for this study. From West to East (Fig. 1), 1 site was sampled in Spain (Sant Andreu de Llavaneres), 6 in France (Morgiret, Endoume, Méjean, Rochambeau, Marinières and Lido), 1 in Monaco (Larvotto) and 6 in Italy (Quarto, Pontetto, Portofino, Passetto, Portonovo and Santa Croce). Wave exposure, substrate type, geographic coordinates and the research group that carried out the sampling are listed in Table 1.

Two species have been identified in the western Mediterranean Sea, *Ostreopsis* cf. *ovata* and *O.* cf. *siamensis* (Penna et al., 2005; 2010). In all the sites considered in this study, taxonomic and/or genetic analysis highlighted the single presence of *O.* cf. *ovata*. Nevertheless we cannot exclude the sporadic presence of *O.* cf. *siamensis*.

In each site, abundances of epiphytic and planktonic *Ostreopsis* cells were recorded. Seawater samples for estimating abundances of planktonic cells were collected at shallow depth (approximately 0.5 m depth) using a plastic flask (from 250 ml to 1 l, according to the research group sampling protocols) and fixed with 2 - 4% neutralized formaldehyde or a 1 - 2 % Lugol's solution (and in this case kept in the dark at 4°C before counting). Macroalgal samples for estimating abundances of benthic cells were sampled opening a plastic flask or bag on the chosen macroalgae in shallow waters (0.5 - 1 m for all the research groups except Trieste groups that performed the sampling at 2 m depth). The macroalgae were then delicately torn away and kept in the flask or bag. Different species of macroalgae (Table 2) were collected according to the site and the period; sampled macroalgae generally corresponded to the most abundant species in each site. Benthic samples were fixed with 2 - 4 % neutralized formaldehyde or a 1 - 2 % Lugol's solution (and in this case kept in the dark at 4°C before counting).

Concentrations of *Ostreopsis* in the water samples were evaluated with an inverted microscope using the Utermöhl method (settling a minimum of 50 ml of sea water). The abundance of benthic cells was evaluated after a vigorous shake of the macroalgae samples, followed by the separation of macro and micro algae. *Ostreopsis* cells were then counted following the Utermöhl method, or using a direct microscope with calibrated slides. Results were expressed as the abundance of planktonic cells per liter and of benthic cells per gram of fresh weight of macroalgae (g FW).

2.3 Sea water temperature

In order to study the role of sea water temperature (SWT) on the dynamics of blooms, we used, when available, the temperature values measured *in situ* by each group during the sampling. In order to give a general seasonal characterization of the temperature of the surface waters in the

1 study area, satellite derived Sea Surface Temperatures (SST) were also used to generate monthly or
2 seasonal average temperature maps. Satellite derived SST images are computed from the Thermal
3 Infra-Red bands of coarse resolution satellite sensors (see for example Barton (2001) for a review
4 on the data and methods). They are nowadays available globally, thanks to international
5 collaboration projects such as the Global Ocean Data Assimilation Experiment (GODAE, Donlon et
6 al. 2007). The data used in this study, kindly provided by the CERSAT (Centre of Research and
7 Satellite exploitation of IFREMER, French National Oceanography Research Institute), were
8 produced by Meteo-France for the Ocean & Sea-Ice Satellite Application Facility (Copyright 2010
9 EUMETSAT; see SAFOSI (2009) for details on the product). The sensor used in this case was
10 NOAA/AVHRR (the Advanced Very High Resolution Radiometer of the National Oceanographic
11 and Atmospheric Administration, USA), the image resolution being of approximately 1 km. With
12 several AVHRR sensors operational at the present time, several images were available each day.
13 Images of June to October for the years 2007, 2008 and 2009 were processed into monthly and
14 summer averages.
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25 26 27 3 Results

28 29 30 3.1 Benthic and planktonic *Ostreopsis* abundances

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32 A total of more than 600 samples was analyzed in order to assess abundances of both benthic and
33 planktonic *Ostreopsis* cells. Data relative to monthly maximal values of cell abundances (EMV:
34 epiphytic maximal value; PMV: planktonic maximal value) for each considered site and year are
35 reported in Table 2, together with the sampling dates and the *in situ* measured sea water temperature
36 (SWT).
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39 Although the distribution of points seems quite scattered (Figure 2), the correlation between EMV
40 and PMV in a logarithmic scale is significant ($n = 124$; $r = 0.7246$; $p < 0.01$) and the percentage of
41 variation explained is not negligible ($R^2 = 0.5251$). Benthic cell abundances are more conservative,
42 showing more regular increase and decrease during the considered period, while planktonic cell
43 abundances can show abrupt changes and a less regular trend over the summer period, as the
44 concentrations in the water may change drastically due to sea conditions. For these reasons, the
45 quantification of benthic cell abundance is a better indicator of the occurrence of blooms and we
46 focus our synthesis mostly on the dynamics of EMV, which we consider more informative in the
47 attempt to forecast *Ostreopsis* blooms that may represent a real health risk.
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3.2 Temporal and spatial variability

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2 As reported in the Materials and methods section, each research group involved in this study,
3 although using a similar method of sample collection and treatment, collected different macroalgal
4 species, in function of the most abundant species found in the benthic vegetation of the study sites.
5 The Barcelona group always collected *Corallina elongata* or *Stypocaulon scoparium*, choosing the
6 most abundant when they co-occurred; the Toulon group collected a mix of ribbon-like *Dictyota*
7 and thin articulated Corallinales (mostly *Jania rubens* and *Haliptilon virgatum*), the Nice,
8 Villefranche and Genoa groups *Stypocaulon scoparium*, the Trieste group *Dictyota dichotoma* and
9 the Ancona group a different macroalgal species for each year/site (*Hypnea musciformis*, *Dictyota*
10 *dichotoma*, *Polysiphonia* sp. and *Ulva* cf. *laetevirens*), as specified in Table 2. It is therefore very
11 difficult to compare the different sites on an absolute quantitative basis (Lobel et al., 1988);
12 nevertheless, when comparing sites sampled by the same group, or sites with the same macroalgal
13 species, some sites consistently appear to have lower EMV values (e.g. Lido compared to Larvotto,
14 Marinières and Rochambeau; Portofino compared to Pontetto and Quarto; Endoume compared to
15 Méjean and Morgiret).

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17 The periods of occurrence of relative maximal EMV values for each year (Y-EMV) were site and
18 year specific. In the NW Mediterranean, most of Y-EMVs occurred in July (15 out of 24 records)
19 and especially in the second half of the month (12 records). Y-EMVs in August are common (6
20 records), although two of them correspond to the first day of the month and can be included in the
21 end-of-July group. Maximal values were recorded only once in June, September and October, while
22 maximal values in November were never recorded. Nevertheless, it should be underlined that the
23 sampling is not balanced and especially that June, October and November data are less abundant,
24 due to the lower health risk linked to lower beach attendance. Most of the late-in-the-season Y-
25 EMVs occurred in the N Adriatic Sea, where the highest concentrations are generally recorded at
26 the end of September or at the beginning of October (4 records out of 5). In Passetto in 2009 the Y-
27 EMV was recorded at the end of August, but EMV values were still high (same order of magnitude)
28 in the first days of September. Benthic cell abundances seem to be very low in early summer,
29 increasing rapidly in late summer and autumn, as in S. Croce where the maximum abundance was
30 recorded at the end of September 2009.

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32 Most of the relative maximal PMV values for each year (Y-PMV) were also recorded in July (15
33 records out of 24), especially in the second half of the month (12 records). Nine Y-PMVs occurred
34 in August, 3 in September and 1 in June and October. It is worth noting that Y-PMVs often occur in
35 the same month as the Y-EMVs (15 records out of 24), and in most cases (11 records) in the very
36 same week.

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2 Whenever a long sampling season occurred (at least 4 months), it was quite common to observe a
3 second *Ostreopsis* bloom following the first one (in 7 cases out of 14 selected sites/years). This is
4 especially obvious in the NW Mediterranean sites showing a first bloom in early summer (*e.g.* St
5 Andreu de Llavaneres 2009, Marinières 2008 and 2009, Rochambeau 2009, Quarto 2007 and
6 Portofino 2007). In Sant Andreu de Llavaneres in 2008, the October bloom was even higher than
7 the July one, while in the same site in 2007 only the July bloom was recorded, as in Morgiret and
8 Lido in 2009. This phenomenon was not observed in the N Adriatic sites, although in Passetto in
9 2007 a decrease in benthic cell abundances is observed in September. A second increase of
10 planktonic *Ostreopsis* cells was observed in 5 cases out of the 7 second benthic blooms, but, not
11 surprisingly, a second increase of planktonic cells in the absence of second benthic bloom was
12 never observed. Nevertheless the amount of data collected in this period of the year is lower than in
13 the summer, and higher benthic and planktonic cell abundances may be more frequent than
14 observed.
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27 3.3 Role of sea water temperature

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29 The correlation between EMV and PMV and the measured Sea Water Temperature (SWT) is
30 reported on Fig. 3 and 4. The abundance of benthic cells was significantly correlated to the
31 measured SWT ($n = 108$; $r = 0.2837$; $p < 0.05$), as much as the abundance of planktonic cells ($n =$
32 108 ; $r = 0.2289$; $p < 0.05$). In both cases the percentage of variation explained is negligible (EMV-
33 $R^2 = 0.0805$; PMV- $R^2 = 0.0524$): less than 10% of the variation observed for EMV and PMV is
34 explained by the sea water temperature.
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40 The monthly evolution of SST in the considered summer seasons is reported on Fig. 5. The warmest
41 month was consistently August, when the SST reached 28°C in most of the area. In June and
42 October, SST never reached 24°C in the NW Mediterranean Sea, while it was higher in the N
43 Adriatic Sea (more than 25°C). In the Gulf of Lyon the SST was consistently lower, mainly due to a
44 high number of windy days, resulting in a drop of temperature due to the upwelling of cold deep
45 seawater in several zones. Consequently, three zones can clearly be identified in the study area. The
46 first zone (A), corresponding to Western Provence and the Gulf of Lyon, which includes the
47 Morgiret, Endoume and Méjean sampling sites and is the coldest. The second zone (B),
48 corresponding to the Balearic and Ligurian seas, includes the Sant Andreu de Llavaneres,
49 Rochambeau, Marinières, Lido, Larvotto, Quarto, Pontetto and Portofino sampling sites and is
50 characterized by intermediate summer temperatures. The third zone (C), corresponding to the N
51 Adriatic Sea, includes the Passetto, Portonovo and Santa Croce sampling sites and always shows
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1 higher SST than zones A and B. The differences between the 3 zones are very clear, independently
2 from the considered month and year, especially in July and August, when the difference of SST
3 between A and C can reach 8 °C. As it can be observed on Figure 5, inter-annual SST variability
4 can be substantial, the SST values in the summers of 2007 and 2009 being higher than in 2008.
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6 Y-EMVs and Y-PMVs are shown superimposed to mean summer SST in Fig. 6. A general trend
7 can be identified at basin scale: in the NW Mediterranean Sea, the maximal abundances of
8 *Ostreopsis* were recorded in July-August, with the exception of Méjean in 2007 (Y-EMV in
9 September) and Sant Andreu de Llavaneres in 2008 (Y-EMV in October). It is worth stressing that,
10 in both cases, at the end of July cell abundances were very high, of the same order of magnitude as
11 the registered Y-EMV. Although the mean summer SST was generally higher in the sites near
12 Barcelona, Nice and Genova (Zone B) than in the sites sampled in the Gulf of Lyon (Zone A, and in
13 particular Morgiret and Endoume), no particular difference in the Y-EMV and Y-PMV was
14 observed, except in 2008 when a delay of two weeks to one month was observed. Conversely, in the
15 N Adriatic Sea (Zone C) the Y-EMVs and Y-PMVs always occurred in late summer-early fall, the
16 abundance of cells being negligible in early summer.
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30 4 Discussion

31 32 33 4.1 Benthic and planktonic *Ostreopsis* abundances

34 Harmful benthic microalgae development is an emergent phenomenon in temperate areas and the
35 interest of scientists for *Ostreopsis* has recently increased (Shears & Ross, 2009). Nevertheless, the
36 dynamics of benthic microalgae blooms are still mostly unknown. In the present study we found a
37 relatively good correlation between epiphytic and planktonic cell abundances, as already observed
38 by Mangialajo *et al.* (2008); this result, together with the relatively good correspondence between
39 the dates of Y-EMV and Y-PMV, confirms that the benthic cells can be considered as the stock of
40 available biomass. The delays observed between Y-EMV and Y-PMV can be related to the re-
41 suspension of cells by wave action (*e.g.* Totti *et al.*, 2010) and by vertical migration (*e.g.* Vila *et al.*,
42 2001). In general we can consider that hydrodynamism (waves, boat traffic) and human trampling
43 (especially in highly touristic zones) are important factors causing re-suspension of cells in shallow
44 coastal areas at the local scale. Vertical migration of cells on a daily cycle (Vila *et al.*, 2001) should
45 also be considered, possibly linked to a potential critical density threshold (as observed for the
46 migration of benthic diatoms up and down in the sediment, Guarini *et al.*, 2008). More efforts are
47 needed to disentangle the mechanism involved in the transfer of *Ostreopsis* cells from the benthos
48 to the water column and *vice versa*.
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1 High planktonic cell abundances represent a health risk for inhalation while benthic cell abundances
2 are potentially mostly involved in irritations by contact. Both planktonic and benthic cells are
3 involved in the invertebrates' mass mortalities, with consequent potential modifications at the
4 ecosystem level and loss of resources. No critical intoxication events have been recorded in the
5 studied sites in the considered years. Nevertheless, some cases of inhalation and/or contact
6 intoxication have been reported to the respective health vigilance systems in Sant Andreu de
7 Lllavaneres, Morgiret, Marinières, Larvotto, Quarto and Passetto. In August 1998, an event of
8 invertebrates' mass mortality was reported in Sant Andreu de Lllavaneres (Vila et al, 2008) and in
9 2006 in Quarto (July) and in Morgiret (august) (author's unpublished data), but no evident mass
10 mortalities were recorded during the study period in the NW Mediterranean Sea, although some
11 counts of limpets in Marinières showed a certain decrease, (author's unpublished data). In the N
12 Adriatic Sea, and in particular in Passetto, deaths of benthic invertebrates (echinoderms and
13 molluscs) have been observed in circumscribed shallow areas in all the considered years (Totti et
14 al., 2010).

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25 Considering that planktonic abundances are highly variable (probably due to hydrodynamic events
26 at local scale) and always occur concurrently to high benthic abundances, we recommend to
27 managers to primarily monitor benthic abundances, which are more conservative and represent the
28 stock of available biomass. For the monitoring of benthic *Ostreopsis* cells, it is important to deal
29 with the variability linked to the macroalgal species sampled. Several options can be considered by
30 managers: i) always sample the same macroalgal species (if the same species is common in all the
31 sites and all along the year), ii) try to estimate conversion factors between different species, in order
32 to be able to compare different sites and/or periods, iii) calculate the macroalgal biomass for a
33 surface unit of sea bottom and extrapolate the number of *Ostreopsis* cells per square meter of
34 bottom (in this case, all the conspicuous macroalgal species should be considered in order to have
35 cell abundances actually representative of the site).

46 47 4.2 Temporal and spatial variability

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50 From a temporal point of view, in the NW Mediterranean Sea, the period when blooms can more
51 likely occur is the end of July, while in the N Adriatic Sea blooms occur later in the season. We
52 suggest to managers to increase the monitoring intensity in these periods. A second bloom, often of
53 the same order of magnitude as the first one, can occur in late summer-fall, especially in the NW
54 Mediterranean basin. Although this second bloom is less alarming in terms of beach attendance (the
55 bathing season generally ends in September), managers should not neglect these blooms that may
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1 represent a danger by potential contamination of seashells (Aligizaki et al., 2008) and cause benthic
2 invertebrate mortalities.

3 From a spatial point of view, our results allowed to highlight that some sites seem to be more prone
4 to *Ostreopsis* development than others. In Endoume, Lido and Portofino, benthic cell abundances
5 were consistently lower than in neighboring sites, although the general characteristics of the sites
6 (e.g. rock type, conformation of the coast, macroalgal communities, wave exposure, see M&M
7 section) can be considered comparable. In these sites, planktonic abundances also are always low,
8 never reaching 10 000 cells/l. As most episodes with health concern were associated with cell
9 concentrations above 30 000 cells/l (Mangialajo et al., 2008; author's unpublished data), we can
10 consider that in some areas the risk is higher and managers should therefore focus their attention on
11 monitoring sites where substantial blooms were observed in the past and are consequently more
12 likely to occur.
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24 4.3 Role of temperature

25 The potential role of sea water temperature (SWT) in regulating *Ostreopsis* blooms in temperate
26 areas has been highlighted by previous studies (Mangialajo et al., 2008; Shears & Ross, 2009),
27 although similar studies did not identify any direct correlation between cell abundances and SWT
28 (Vila et al., 2001; Totti et al., 2010; Selina & Orlova, 2010). Granéli et al. (in press) found a strong
29 relationship between temperature and *Ostreopsis* growth rate in culture and suggested that sea water
30 temperature increase resulting from global warming could play a crucial role in inducing the
31 geographical expansion and biomass accumulation by blooms of *Ostreopsis ovata*.
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39 If sea water temperature is one of the major factors affecting *Ostreopsis* blooms, the Y-PMV and/or
40 Y-EMV observed in this study should (1) occur in relation with thermal cycle of each defined zone
41 (A, B and C) and (2) vary according to the interannual variability recorded during the study period.
42 Our results highlighted a very low correlation between both EMV and PMV with SWT measured *in*
43 *situ* and the shifts in periods of higher abundance of *Ostreopsis* between the 3 zones are not in
44 agreement with the differences in SST. The delay observed between the two basins is the opposite
45 of what one would have expected following the temperature differences (an early bloom in the N
46 Adriatic Sea, where summer SST is higher, and a later bloom in the NW Mediterranean sites where
47 summer SST is lower).
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55 We cannot exclude that such differences may be explained with the occurrence of different strains
56 having different temperature affinities. The Adriatic and Tyrrhenian strains investigated by Guerrini
57 et al. (2010), presented significant differences in cell volumes (the Adriatic strain being nearly twice
58 the size of the Tyrrhenian one), although in a recent biogeographical analysis, all the
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1 Atlantic/Mediterranean *Ostreopsis* samples have been assessed to belong to a single clade (Penna et
2 al., 2010).

3 In the NW Mediterranean Sea, obvious SST differences are noticed between zone A (Gulf of Lyon)
4 and B (Balearic and Ligurian Sea), but no corresponding delay in *Ostreopsis* blooms is observed,
5 except for the summer of 2008, where the blooms in the Gulf of Lyon were actually delayed by 2 to
6 4 weeks (especially in the Endoume and Morgiret sites). Although the sea water temperature may
7 play a major role in a specific site, such a relationship is not visible any more when increasing the
8 study scale to the basin level. It is likely that a minimum threshold temperature is needed for
9 *Ostreopsis* proliferation: in a previous work, Mangialajo et al. (2008) hypothesized that *Ostreopsis*
10 proliferation may be facilitated by a SWT above 26°C. Nevertheless, in this paper we report high
11 benthic cell abundances at lower SWT levels (23°C in the NW Mediterranean and less than 20°C in
12 the N Adriatic Sea). Unfortunately the data collected do not allow us to directly compare the
13 intensity of blooms in the three considered zones.

14 The role of temperature requires further investigation and the impacts of other drivers have to be
15 elucidated to better explain the bloom dynamics. Such drivers may be inorganic nutrients
16 concentration and/or their ratio, substrate characteristics (*e.g.* composition of macroalgal
17 communities), competitive and trophic interactions, or regulation of dinoflagellates by parasites
18 (Chambouvet et al., 2008). Hydrodynamism due to waves and/or currents should also play an
19 important role in regulating benthic dinoflagellate abundances, but the effect of this abiotic factor is
20 very difficult to evaluate. Finally, human-induced drivers, such as eutrophication, which is known
21 to facilitate microalgal blooms (Heisler et al., 2008), should also be taken into account. Human-
22 induced impacts can act in a direct way (*e.g.* increased nutrients availability), but also indirectly,
23 interacting with other factors (*e.g.* herbivory, Buskey, 2008; Smayda, 2008). In a changing world, in
24 which human impacts are cumulated (Halpern et al., 2008) and interact in different ways (Crain et
25 al., 2008), the mechanisms of facilitation of new phenomena should consider the interaction of
26 human-driven and natural factors. This is particularly true in the investigated area (NW
27 Mediterranean and N Adriatic Seas), where human pressure is high and historically rooted.

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Figure captions:

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3 Fig. 1: Location of sampling sites along the North-Western Mediterranean and Northern Adriatic
4 coasts.
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7 Fig. 2: Correlation between Epiphytic Maximal Value (EMV) and Planktonic Maximal Value
8 (PMV) for all the study sites, on a logarithmic scale.
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11 Fig. 3: Correlation between Epiphytic Maximal Value (EMV) and measured Sea Water
12 Temperature (SWT) for all the study sites; EMV is expressed in logarithmic scale.
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16 Fig. 4: Correlation between Planktonic Maximal Value (EMV) and measured Sea Water
17 Temperature (SWT) for all the study sites; PMV is expressed in logarithmic scale.
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21 Fig. 5: Monthly average satellite derived Sea Surface Temperature maps for summer and early fall
22 for 2007, 2008 and 2009. Zone A: Western Provence and the Gulf of Lyon; Zone B: Balearic and
23 Ligurian seas; Zone C: Adriatic Sea.
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27 Fig. 6: Maps of summer average of satellite derived Sea Surface Temperature together with dates
28 (day/month) of the yearly Epiphytic Maximal Value (Y-EMV) and yearly Planktonic Maximal
29 Value (Y-PMV).
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Figure 1
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Figure 2
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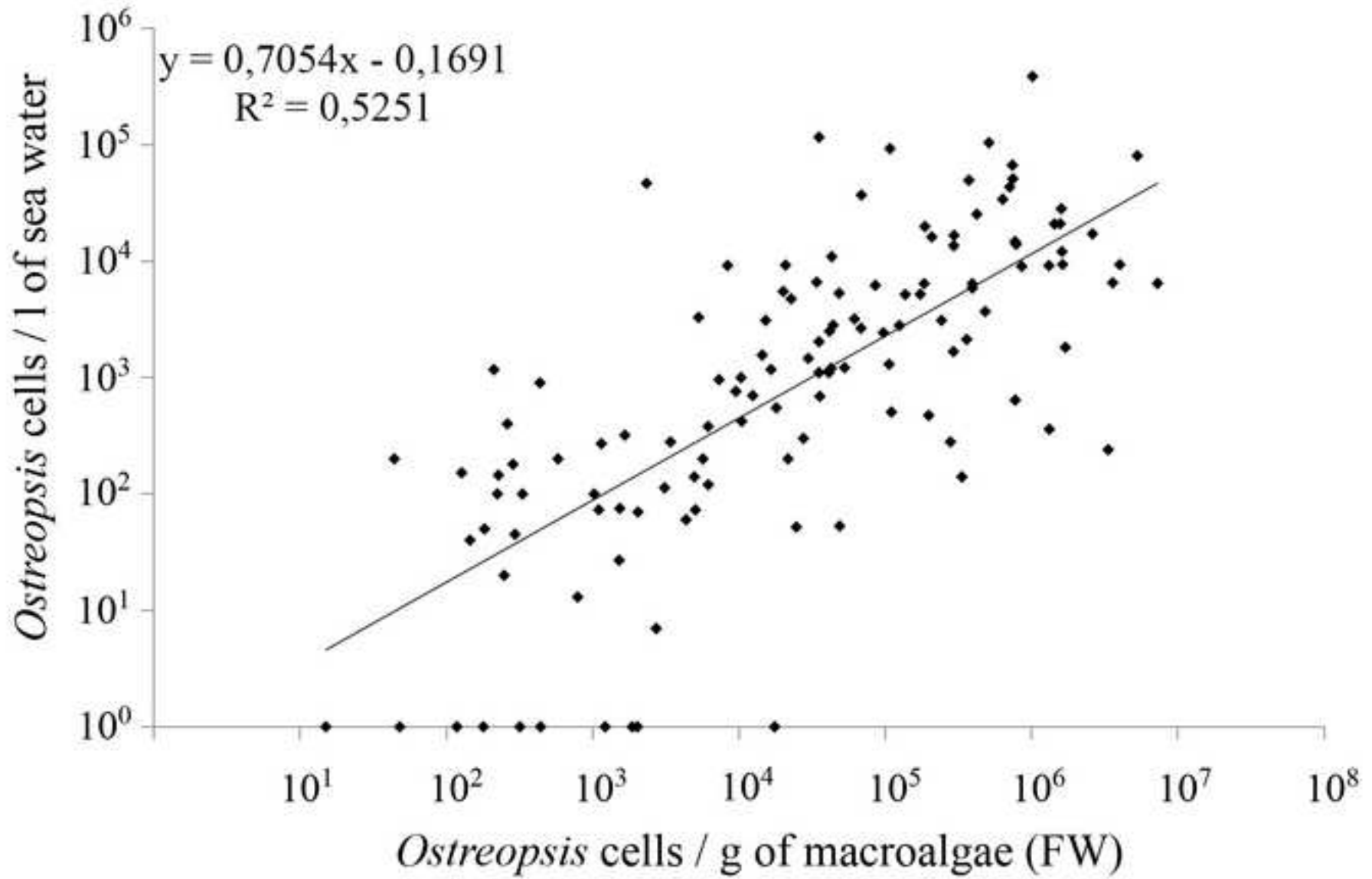


Figure 3
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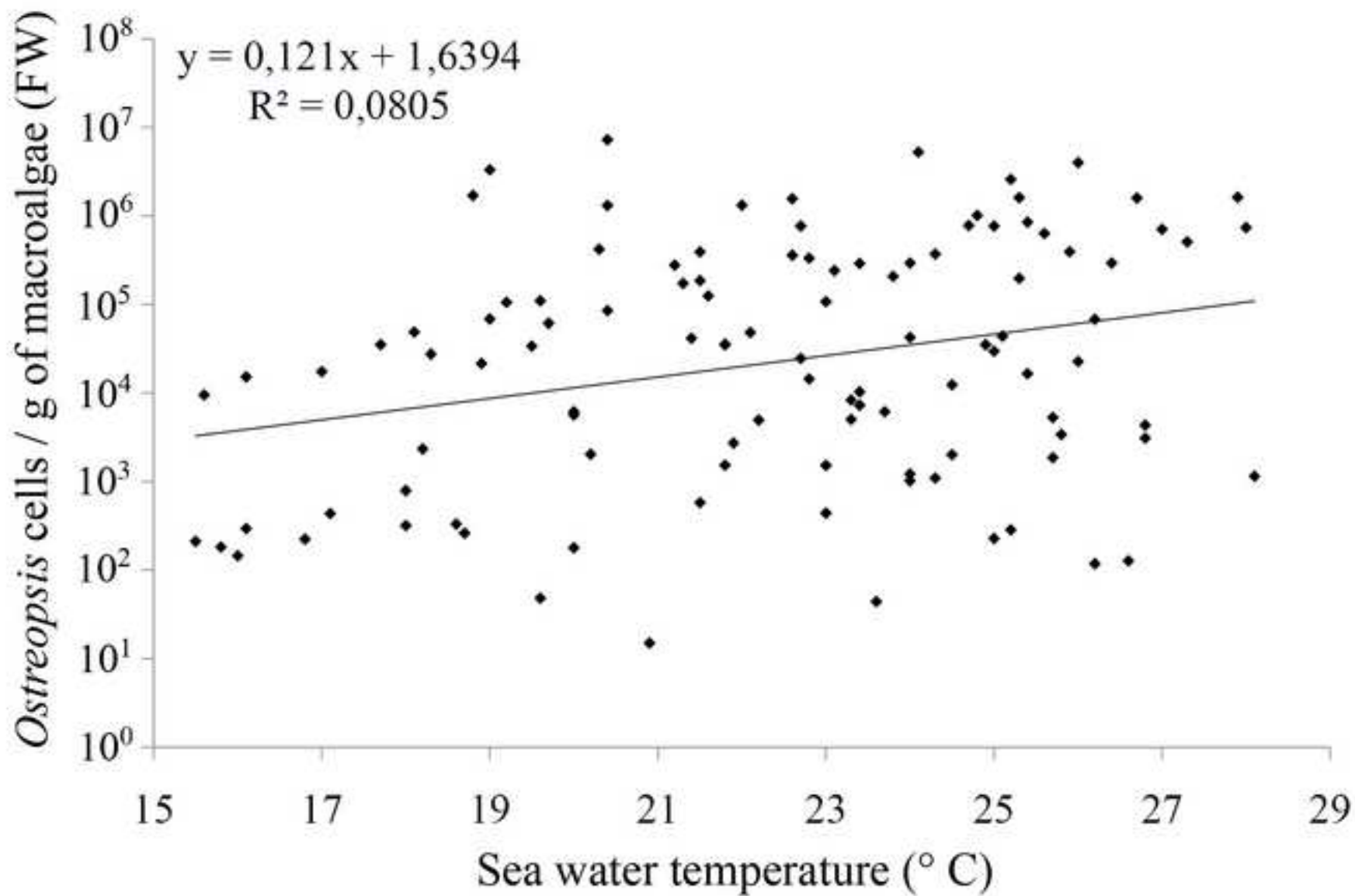


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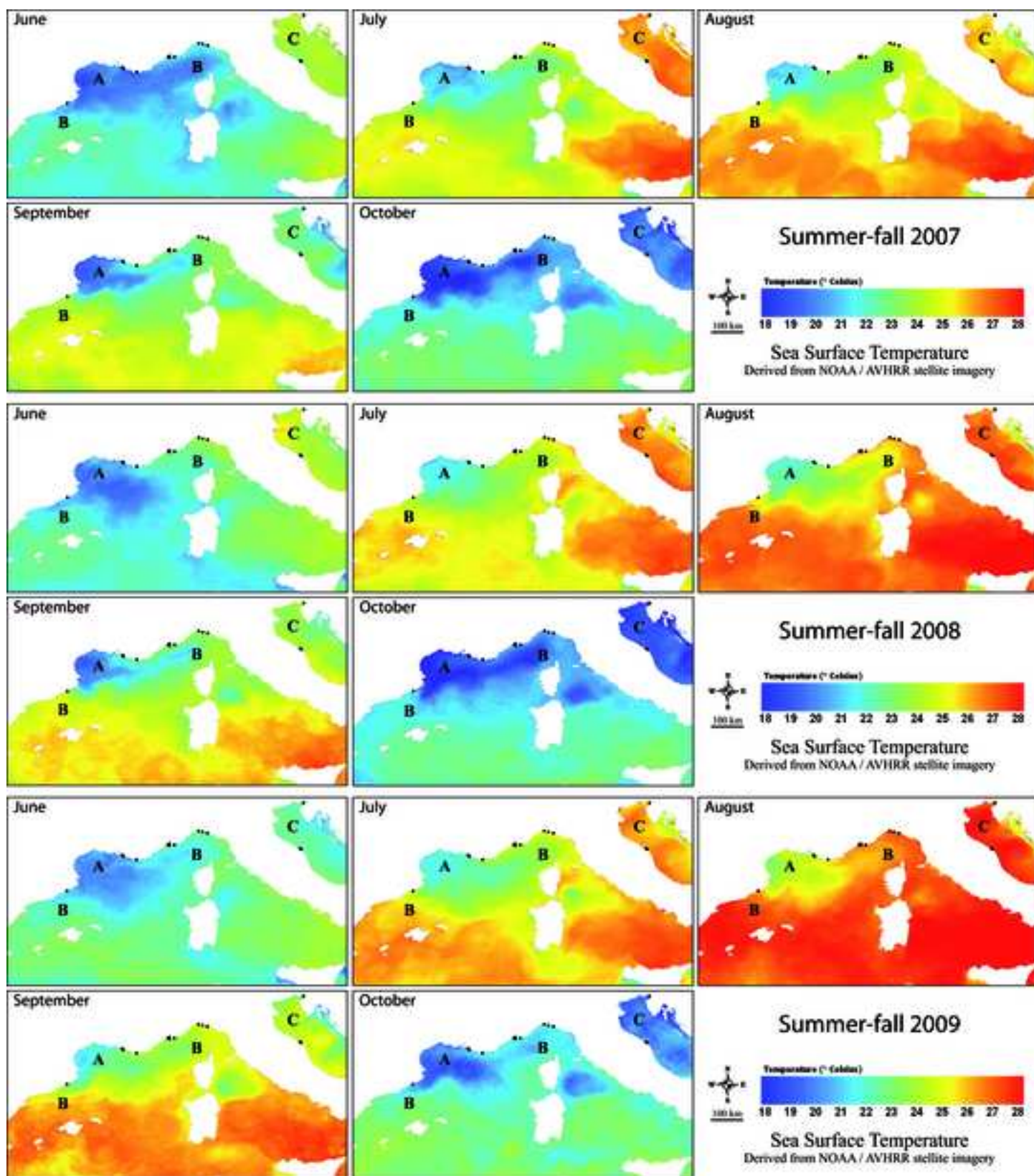


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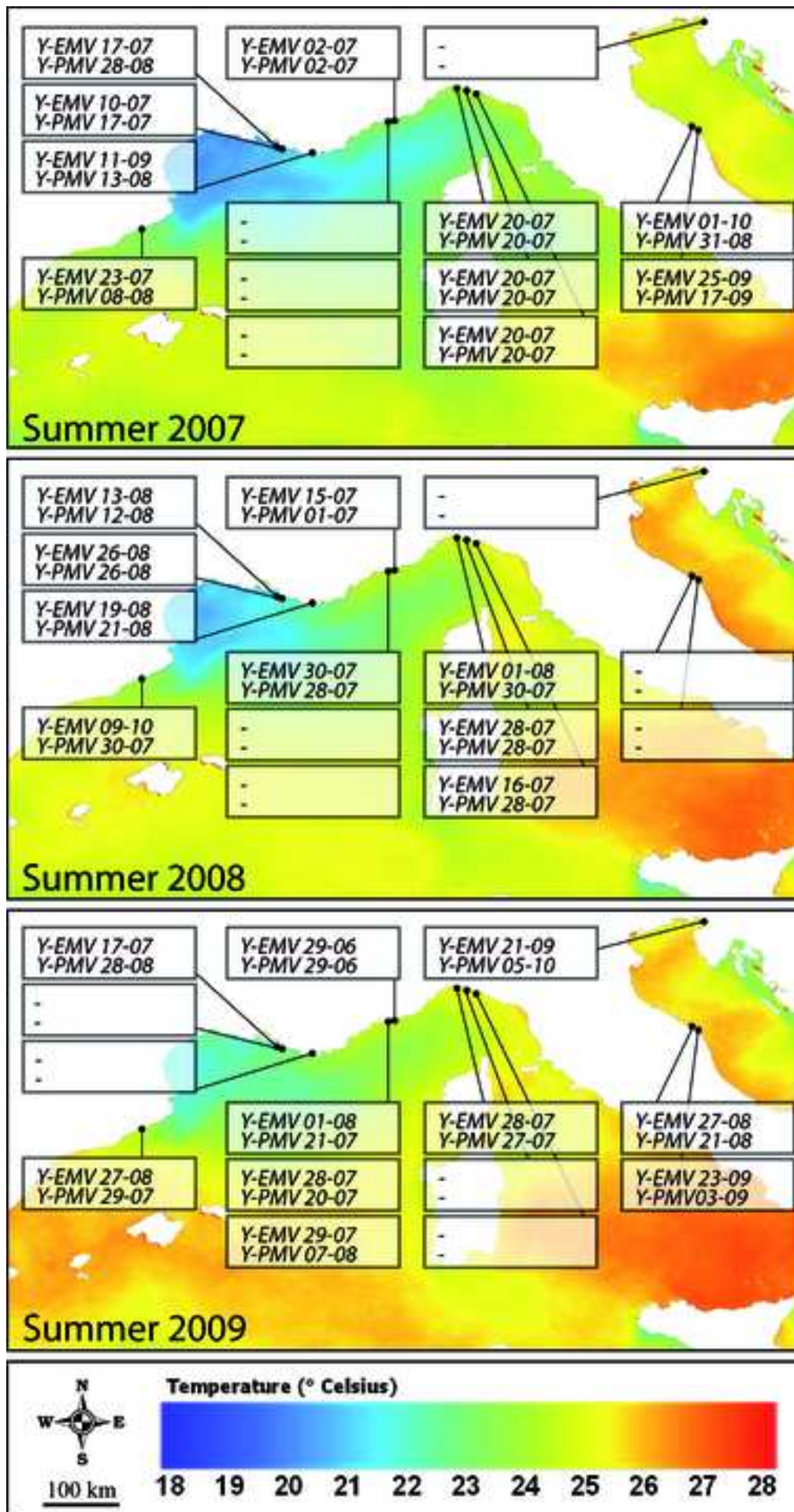


Table 1. Sampling sites, research group that performed the sampling and the sample treatment, characteristics of the site and geographical coordinates.

Site	Research group	Wave exposure	Substrate	Coordinates
St Andreu de Llavanes	Barcelona	Exposed	Natural rock	41° 33' 07.8" N / 02° 29' 32.4" E
Morgiret	Toulon	Exposed	Natural rock	43° 16' 55.7" N / 05° 18' 20.2" E
Endoume	Toulon	Semi-enclosed bay	Natural rock	43° 16' 48.7" N / 05° 20' 60.0" E
Méjean	Toulon	Semi-enclosed bay	Natural rock	43° 06' 25.9" N / 05° 58' 23.1" E
Marinières	Nice-Villefranche	Semi-enclosed bay	Artificial rock	43° 42' 09.2" N / 07° 18' 12.1" E
Rochambeau	Nice-Villefranche	Semi-enclosed bay	Artificial and natural rock	43° 41' 34.7" N / 07° 18' 32.1" E
Lido	Nice-Villefranche	Semi-enclosed bay	Natural rock	43° 41' 30.3" N / 07° 19' 15.5" E
Larvotto	Nice-Villefranche	Exposed	Artificial rock	43° 44' 44.3" N / 07° 26' 04.1" E
Quarto	Genoa	Exposed	Natural rock	44° 23' 17.5" N / 08° 59' 37.3" E
Pontetto	Genoa	Exposed	Natural rock	44° 22' 33.6" N / 09° 04' 32.0" E
Portofino	Genoa	Exposed	Natural rock	44° 19' 03.6" N / 09° 09' 51.6" E
Santa Croce	Trieste	Semi-enclosed bay	Natural rock	45° 44' 26.7" N / 13° 40' 08.5" E
Passetto	Ancona	Semi-enclosed bay	Natural rock	43° 36' 38.1" N / 13° 32' 20.6" E
Portonovo	Ancona	Exposed	Natural rock	43° 33' 50.9" N / 13° 35' 28.2" E

Table 2

Table 2: Synthesis of available data collected in the study sites in summer 2007, 2008 and 2009.

EMV: Epibenthic maximal value; PMV: Planktonic maximal value. In bold the maximal values for each year and site (Y-EMV; Y-PMV).

Site (macroalgal species)	Year	Month	Sampling dates (day of the month)	EMV	EMV date (Temp°C)	PMV	PMV date (Temp°C)	
St Andreu de Llavaneres ^a (<i>Corallina elongata</i> or <i>Stypocaulon scoparium</i>)	2007	June	8, 15, 22, 25, 26, 28	124749	25 (21.6)	2800	25 (21.6)	
		July	2, 5, 9, 12, 23, 26	2600239	23 (25.2)	17127	9 (23.1)	
		August	8, 11, 13, 16, 17, 20, 24, 28, 31	634764	8 (25.6)	33908	8 (25.6)	
		September	4, 7, 11, 14, 21	294681	4 (24.0)	16608	4 (24.0)	
		October	1, 5, 11, 17, 19, 23, 31	173279	17 (21.3)	5190	17 (21.3)	
		November	5, 13, 16, 25, 29	9513	16 (15.6)	760	16 (15.6)	
	2008	June	6, 13, 19, 27	179	19 (20.0)	0	-	
		July	7, 14, 18, 21, 24, 30	5270853	24 (24.1)	80272	30 (-)	
		August	5, 11, 17, 24, 29	744955	11 (-)	50862	5 (-)	
		September	5, 12, 19, 29	771706	29 (22.7)	640	29 (22.7)	
		October	9, 24, 27	7248635	9 (20.4)	6440	27 (-)	
		November	5, 11, 18, 25	3579520	11 (-)	6520	18 (-)	
	2009	June	23	0	23 (23.0)-	0	23 (23.0)-	
		July	1, 2, 3, 7, 15, 22, 27, 29	1013139	27 (24.8)	385601	29 (24.7)	
		August	12, 27	4008204	27 (26)	9342	12 (23)	
		September	8, 15, 30	1320210	30 (22)	360	30 (22)	
		October	27	3332001	27 (19)	240	27 (19)	
		November	10	184077	10 (-)	6400	10 (-)	
Morgiret (mix of ribbon-like <i>Dictyota</i> and thin Articulated Corallinales - <i>Haliphtilon</i> , <i>virgatum</i> <i>Jania</i> spp.)	2007	June	20	12390	20 (24.5)	700	20 (24.5)	
		July	3, 10, 17, 25	105923	17 (19.2)	1300	10 (17.8)	
		August	1, 8, 16, 21, 28	48288	16 (22.1)	5300	28 (23.5)	
		September	5, 11	21609	5 (18.9)	200	5 (18.9)	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
	2008	June	18, 25	44	25 (23.6)	200	25 (23.6)	
		July	2, 9, 16, 23, 30	2018	30 (24.5)	0	-	
		August	6, 8, 12, 13, 18, 20, 26, 28	186480	13 (21.5)	19800	12 (21.0)	
		September	1, 8, 15	42581	1 (24)	1200	8 (-)	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
	2009	June	24, 29	48	24 (19.6)	0	-	
		July	7, 15, 21, 28	392756	28 (21.5)	6400	21 (19.4)	
		August	4, 11, 18, 25	41618	4 (21.4)	2500	4 (21.4)	
		September	1, 8, 15, 29	35246	8 (17.7)	116200	1 (21.2)	
		October	14, 27	27560	14 (18.3)	300	14 (18.3)	
		November	17	17487	17 (17.0)	0	-	
Endoume (mix of ribbon-like <i>Dictyota</i> and thin Articulated Corallinales - <i>Haliphtilon</i> , <i>virgatum</i> <i>Jania</i> spp.)	2007	June	20	10316	20 (23.4)	1000	20 (23.4)	
		July	3, 10, 17, 25	15209	10 (16.1)	3100	17 (18.4)	
		August	1, 8, 14, 21, 28	261	21 (18.7)	400	8 (21.6)	
		September	5, 11	436	5 (17.1)	900	11 (20.0)	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
	2008	June	18, 25	331	18 (18.6)	100	18 (18.6)	
		July	2, 9, 16, 23, 30	1022	30 (24)	100	30 (24)	
		August	6, 12, 18, 26, 27	33917	26 (19.5)	6600	26 (19.5)	
		September	1, 8, 15	5672	8 (20)	200	8 (20)	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
	Méjean (mix of ribbon-like <i>Dictyota</i> and	2007	June	26	223	26 (16.8)	100	26 (16.8)
			July	2, 9, 16, 25, 30	35138	25 (21.8)	1100	9 (20.5)
			August	6, 13, 20, 27	2331	20 (18.2)	46600	13 (19.9)
			September	5, 11	85412	11 (20.4)	6200	5 (20.4)

thin Articulated	October	-	-	-	-	-	
	November	-	-	-	-	-	
Corallinales - <i>Haliptilon</i> , <i>virgatum</i> <i>Jania</i> spp.)	2008	June	17, 23, 30	1860	30 (25.7)	0	-
		July	7, 15, 21, 28	1215	28 (24.0)	0	-
		August	4, 11, 19, 21, 25	68616	19	36900	21 (21.0)
		September	2, 9, 18	578	9 (21.5)	200	18 (19.7)
		October	-	-	-	-	-
		November	-	-	-	-	-
Marinières ^b (<i>Stypocaulon</i> <i>scoparium</i>)	2008	June	2	15	2 (20.9)	0	-
		July	1, 7, 15, 17, 21, 23, 25, 28, 30	510185	30 (27.3)	104000	28 (-)
		August	1, 4, 6, 8, 11, 13, 18, 21, 22	5294	27 (25.7)	3280	11 (-)
		September	24	1658	24 (-)	320	24 (-)
		October	22	41126	22 (-)	1100	22 (-)
		November	-	-	-	-	-
	2009	June	4, 10, 19, 24	1517	24 (23.0)	27	24 (23.0)
		July	1, 6, 9, 13, 16, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31	783387	28 (24.7)	13907	21 (24.7)
		August	1, 2, 3, 4, 5, 6, 7, 10, 12, 14, 18, 21, 24, 27	854711	1 (25.4)	9020	4 (23.8)
		September	3, 8, 17	3095	3 (26.8)	113	8 (24.3)
	October	1, 8, 15	291490	1 (23.4)	1673	15 (22)	
	November	18	789	18 (18.0)	13	18 (18.0)	
Rochambeau (<i>Stypocaulon</i> <i>scoparium</i>)	2009	June	4, 10, 19, 24	2716	4 (21.9)	7	4 (21.9)
		July	1, 6, 9, 13, 16, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30	1610462	28 (25.3)	12067	20 (23.1)
		August	1, 2, 3, 4, 5, 6, 7, 10, 12, 14, 18, 21, 24, 27	394142	1 (25.9)	5867	2 (25.8)
		September	3, 8, 17	4346	3 (26.8)	60	8 (24.4)
		October	1, 8, 15	241853	8 (23.1)	3095	8 (23.1)
		November	18	48788	18 (18.1)	53	18 (18.1)
Lido (<i>Stypocaulon</i> <i>scoparium</i>)	2009	June	4, 10, 19, 24	440	24 (23.0)	0	-
		July	1, 6, 9, 13, 16, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30	29725	29 (25.0)	1460	21 (23.2)
		August	1, 2, 3, 4, 5, 6, 7, 10, 12, 14, 18, 21, 24, 27	22695	2 (26.0)	4740	7 (24.9)
		September	3, 8, 17	1099	8 (24.3)	73	3 (26.7)
		October	1, 8, 15	5038	1 (23.3)	73	1 (23.3)
		November	18	318	18 (18.0)	0	-
Larvotto (<i>Stypocaulon</i> <i>scoparium</i>)	2007	June	-	-	-	-	-
		July	2, 9, 16, 23, 30	1565514	2 (22.6)	20936	2 (22.6)
		August	6, 13, 20, 27	16530	6 (25.4)	1172	6 (25.4)
		September	3	6152	3 (23.7)	120	3 (23.7)
		October	-	-	-	-	-
		November	-	-	-	-	-
	2008	June	16, 23	24609	23 (22.7)	52	16 (19.7)
		July	1, 7, 15, 21, 28	359865	15 (22.6)	2124	1 (24.1)
		August	4, 11, 18, 25	197467	25 (25.3)	472	4 (25.8)
		September	-	-	-	-	-
		October	-	-	-	-	-
		November	-	-	-	-	-
	2009	June	22, 29	481637	29 (-)	3688	29 (-)
	July	6, 12, 20, 27	96800	6 (-)	2424	12 (-)	
	August	3, 10, 17, 24, 31	17984	31 (-)	548	31 (-)	
	September	-	-	-	-	-	
	October	-	-	-	-	-	
	November	-	-	-	-	-	
Quarto ^c (<i>Stypocaulon</i> <i>scoparium</i>)	2007	June	7, 14, 21	136870	21 (-)	5159	21 (-)
		July	9, 16, 17, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30	708203	20 (27.0)	43278	20 (27.0)
		August	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 26, 27, 28, 29, 31	293576	7 (26.4)	13520	6 (-)
		September	1, 2, 5, 7, 8, 9, 10, 13, 16, 17, 18	8358	7 (23.3)	9160	5 (-)
		October	2, 23	110087	23 (19.6)	505	2 (23.1)

		November	26	294	26 (16.1)	45	26 (16.1)	
	2008	June	11, 24, 26, 28, 30	20060	26 (-)	5490	30 (28.0)	
		July	1, 2, 3, 4, 7, 8, 9, 10, 11, 14, 15, 16, 17, 18, 21, 22, 23, 24, 25, 28, 29, 30, 31	738451	30 (28.0)	66679	30 (28.0)	
		August	1, 4, 5, 6, 7, 8, 11, 12, 13, 14, 19, 21, 27	1433470	1 (-)	20863	1 (-)	
		September	-	-	-	-	-	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
	2009	June	4, 9, 15, 18, 23	52577	23 (-)	1215	18 (-)	
		July	2, 6, 7, 10, 13, 14, 15, 16, 20, 21, 22, 23, 24, 27, 28, 29, 30, 31	207685	28 (23.8)	16100	27 (24.6)	
		August	3, 4, 5, 10, 11, 12, 13, 17, 19, 20, 21, 27, 28, 31	35176	11 (24.9)	2030	3 (25.7)	
		September	-	-	-	-	-	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
Pontetto ^d (<i>Stypocaulon scoparium</i>)	2007	June	7, 14, 21	20823	21 (-)	9240	21 (-)	
		July	9, 17, 20, 26	1592511	20 (26.7)	28194	20 (26.7)	
		August	1, 7, 13, 24, 29	68138	7 (26.2)	2650	7 (26.2)	
		September	7	7292	7 (23.4)	960	7 (23.4)	
		October	2, 23	6146	23 (20.0)	380	23 (20.0)	
		November	26	182	26 (15.8)	50	26 (15.8)	
	2008	June	24, 30	1145	30 (28.1)	270	30 (28.1)	
		July	2, 4, 7, 10, 16, 22, 24, 28	372133	28 (24.3)	49480	24 (25.6)	
		August	7, 19, 27	43002	7 (-)	10925	7 (-)	
		September	-	-	-	-	-	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
Portofino ^e (<i>Stypocaulon scoparium</i>)	2007	June	7, 14, 21	1530	14 (21.8)	75	7 (20.6)	
		July	17, 20, 26	43896	17 (25.10)	2820	20 (25.4)	
		August	1, 7, 13, 24, 29	285	7 (25.2)	180	29 (23.0)	
		September	7	4947	7 (22.2)	140	7 (22.2)	
		October	2, 23	2036	23 (20.2)	70	2 (21.5)	
		November	26	145	26 (16.0)	40	26 (16.0)	
	2008	June	11, 24	248	24 (-)	20	24 (-)	
		July	16, 28	10431	16 (-)	420	28 (25.4)	
		August	19, 27	3405	27 (25.8)	280	27 (25.8)	
		September	-	-	-	-	-	
		October	-	-	-	-	-	
		November	-	-	-	-	-	
Passetto (<i>Hypnea musciformis</i>)	2007	June	20	0	-	-	-	
		July	27	0	-	-	-	
		August	8, 20, 27, 31	770238	27 (25)	14677	31 (26)	
		September	10, 17, 25	14404	10 (22.8)	1558	25 (20.4)	
		October	1, 9, 15, 29	1701614	1 (18.8)	1815	9 (17.9)	
		November	-	-	-	-	-	
	(Dictyota dichotoma)	2009	June	3, 15	0	-	0	-
			July	1, 15, 29	118	29 (26.2)	0	-
			August	4, 11, 21, 27	1626621	27 (27.9)	9355	21 (27.8)
			September	3, 9, 15, 18, 22, 29	1313309	9 (20.4)	9145	9 (20.4)
			October	6, 21, 28	211	21 (15.5)	1169	6 (21.6)
	Portonovo (<i>Polysiphonia</i> sp.)	2007	June	-	-	-	-	-
		July	-	-	-	-	-	
		August	8, 20, 27, 31	227	20 (25)	145	27 (25)	
		September	10, 16, 17, 25	422109	25 (20.3)	25279	17 (21.6)	
		October	1, 9, 15, 29	61483	1 (19.7)	3188	9 (18.4)	
		November	-	-	-	-	-	
(Ulva cf. laetevirens)		2009	June	3, 15	0	-	0	-
			July	3, 17, 31	0	-	0	-
			August	6, 11, 21, 27	127	27 (26.6)	152	27 (26.6)
			September	3, 9, 15, 23, 29	107495	23 (23)	92483	3 (26.4)
			October	6, 21, 28	35683	6 (21.8)	688	6 (21.8)

		November	-	-	-	-	-
Santa Croce (<i>Dictyota</i> <i>dichotoma</i>)	2009	June	8, 24	0	-	-	-
		July	6, 20	0	-	-	-
		August	3, 25	0	-	-	-
		September	7, 21	333793	21 (22.8)	140	21 (22.1)
		October	5, 21	278710	5 (21.2)	280	5 (21.2)
		November	-	-	-	-	-

^a Sea water samples of dates 26/07/07, 11/08/07, 16/08/07, 07/09/07, 11/09/07, 19/06/0 are missing. Macroalgal samples of dates 11/10/07, 19/10/07, 29/11/07, 06/06/08, 29/07/09 are missing.

^b Sea water samples of dates : 01/07/07, 07/07/07, 15/07/07 are missing. Macroalgal samples of date : 30/07/08 is missing

^c In 2007 macroalgal samples were collected in Quarto on fewer dates than seawater samples: 21- June; 9, 17, 20, 26- July; 1, 7, 13, 24, 29 August; 7 September; 23 October; 26 November. Seawater sample of date 23/10/2007 is missing.

^d Sea water samples of dates : 10/07/08 are missing

^e Macroalgal samples of dates: 20/07/07, 11/06/08, 28/07/08 are missing