

Seasonal dynamics of upper sublittoral assemblages on Mediterranean rocky shores along a eutrophication gradient



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ABSTRACT

Changes in the seasonal dynamics of Mediterranean macroalgal-dominated assemblages from the upper sublittoral zone are described along a gradient of sewage pollution. Algal coverage and composition were measured for more than one year at approximately monthly intervals. Nutrients concentrations (nitrites, nitrates, ammonia and phosphates) showed different seasonal patterns depending on the distance to the pollution focus. *Ulva*-dominated assemblages appearing close to the sewage outfall showed maximal coverage during early spring and started to decrease in May. *Corallina*-dominated assemblages – replacing ulvacean algae at intermediate levels of pollution – followed the same pattern, peaking in March and decreasing in May. In contrast, *Cystoseira*-dominated assemblages, present at sites with low or no influence of sewage, increased coverage in May and continued with high coverage until the end of summer. Neither ephemeral algae (*Ulva* spp.), nor stress-tolerant algae (*Corallina elongata*), nor canopy-forming algae (*Cystoseira* spp.) have a seasonal growth cycle governed by eutrophication. Results demonstrate also that the period from May to July is the best time of the year for Water Framework Directive (WFD) monitoring purposes as less variability is observed within the assemblages.

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1. Introduction

In several coastal areas, human activities have led to eutrophication processes implying increased nutrient availability and primary production (Kautsky et al., 1986; Rönnerberg and Bonsdorff, 2004). Wastewater discharges close to the coastline deteriorate water quality and spoil macroalgal communities thriving in rocky-shores (e.g. Bellan-Santini, 1968; Borowitzka, 1972; Munda, 1974; Littler and Murray, 1975; Arévalo et al., 2007; Pinedo et al., 2007, 2013). This deterioration consists of changes both at the population, community or, even, at the ecosystem level (Soltan et al., 2001; Lotze et al., 2001; Arévalo et al., 2007). Sensitive species are replaced both by stress-tolerant and opportunistic species when pollution levels increase (e.g. Munda, 1974; Murray and Littler, 1978; Tewari and Joshi, 1988; Díez et al., 1999; Arévalo et al., 2007) entailing a simplification of the architectural complexity of the communities (Borowitzka, 1972; Belsher, 1974, 1979; Gorostiaga and Díez, 1996; Middelboe and Sand-Jensen, 2000; Arévalo et al., 2007).

Seasonal patterns on rocky shore communities are strongly determined by physical factors, being initiated by light, temperature and desiccation (Underwood and Jernakoff, 1984; Gunnarsson and Ingólfsson, 1995) and subsequently curtailed by nutrients (Ballesteros, 1989; Gunnarsson and Ingólfsson, 1995). Low nutrient availability is one of the major environmental factors limiting macroalgal growth and determining species composition in temperate shores (Lotze et al., 2000; Worm and Lotze, 2006). Macroalgae experience periods of very low N and P concentrations in the surrounding waters (Ballesteros, 1989; Delgado et al., 1994) and some slow-growing perennials rely on nutrient storage for growing when day length and temperature increase. In contrast, growth of opportunistic macroalgae completely rely on dissolved nutrient concentrations in seawater. Thus, sites of high nutrient loading, such as near wastewater outfalls, are suitable environments for opportunistic algae to proliferate (Pedersen et al., 2010).

Although the effects of eutrophication on rocky shore assemblages are well known (Middelboe and Sand-Jensen, 2000; Eriksson et al., 2002; Díaz et al., 2002; Díez et al., 2003; Worm and Lotze, 2006; Arévalo et al., 2007; Pinedo et al., 2013) and modifications in macroalgal composition following water quality improvements have been described (Hardy et al., 1993; Bokn et al., 1996; Gorostiaga and Díez, 1996; Soltan et al., 2001; Archambault et al.,

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2001; Díez et al., 2009; Tsiamis et al., 2013; Pinedo et al., 2013), the seasonal patterns in assemblages located along a gradient of nutrient enrichment have been far less studied (López Gappa et al., 1993; Abou-Aisha et al., 1995; Rodríguez-Prieto and Polo, 1996; Archambault et al., 2001).

Here we describe the seasonal variability in the structure and coverage of upper sublittoral assemblages located along a nutrient gradient caused by the discharge of a domestic sewage outfall in order to test whether: (1) differences on species richness and total coverage among assemblages are maintained over the whole seasonal cycle; (2) the abundance of the species defining the assemblages change over the year and if nutrient uploads can modify the seasonal growth cycle of canopy-forming of the genus *Cystoseira*, even at moments that growth could be limited by nutrient availability (summer); (3) differences on the assemblages are maintained over the year, spring being the season with a highest distinctness of the assemblages, and (4) the coverage of species showing seasonality responds to nutrient concentrations in sea water.

2. Materials and methods

2.1. Study site

Tossa de Mar (Spain, Northwestern Mediterranean; Fig. 1) is a highly ranked tourist destination (Sardá et al., 2005), whose sewage is composed only of domestic waste. There is no industrial development in the area and agriculture is extremely reduced. Most of the land (>90%) is covered by extensive Mediterranean forests of cork oak and pines and thus pollution from run-off waters is very low. Domestic waters receive two treatments before they are discharged to the sea: (1) biological treatment from autumn to spring when the total population is low, and (2) primary and biologic treatment during summer when the tourist population is the highest. The sewer outfall discharged an average of 2703 m³/day during the sampling period (4023 m³/day in summer and 1485 m³/day in winter). Wastewater from the outfall usually flows to the south along the coast following the direction of dominant currents.

2.2. Sampling design and analytical procedures

Sampling was conducted from August 2002 to September 2003 along a 1.5 km length of coast near to Tossa de Mar, in the influence area of sewage effluent from the treatment plant. The discharge outfall is located at the coastline in a highly exposed sea-cliff (Fig. 1). Five sampling sites were situated at increasing distances of the outfall (2, 8, 84, 163 and 1350 m), the most distant being used as control site (Fig. 1). Sites were selected to be as similar as possible with respect to orientation, coastal slope and wave exposure in order to decrease assemblage variability due to environmental factors other than nutrient concentrations in the water column.

Sampling was conducted in the upper sublittoral zone (0.1–0.3 m depth). Three samples were taken at each sampling site each 40 days by scraping off all organisms from a 225 cm² surface. This surface area is sufficiently large to permit a quantitative description of the upper sublittoral macroalgal assemblages in the Northwestern Mediterranean (Coppejans, 1980; Verlaque, 1987; Ballesteros, 1992). Samples were preserved in formalin: sea-water at 4% and sorted in the laboratory. Algae and invertebrates were identified to species level and quantified in terms of coverage. Species coverage was measured as horizontal surface area (cm²) covered by spreading specimens over a laboratory tray to form a thin layer (Ballesteros, 1986; Sales et al., 2012).

Three water samples were collected at each sampling site every 20 days with clean plastic bottles and kept frozen until chemical analyses were done. Water samples were analyzed for dissolved nutrients (phosphates, nitrates, nitrites and ammonia) on a Bran-Luebbe® TRAACS 2000 Autoanalyzer.

2.3. Data analysis

Seasonal differences at each site for assemblage data, species coverage, and nutrients analysis were determined by non-parametric tests (Kruskall-Wallis), as normality was never met after different data transformation using Systat (version 9). Spearman correlations between seasonal nutrient concentration and algal

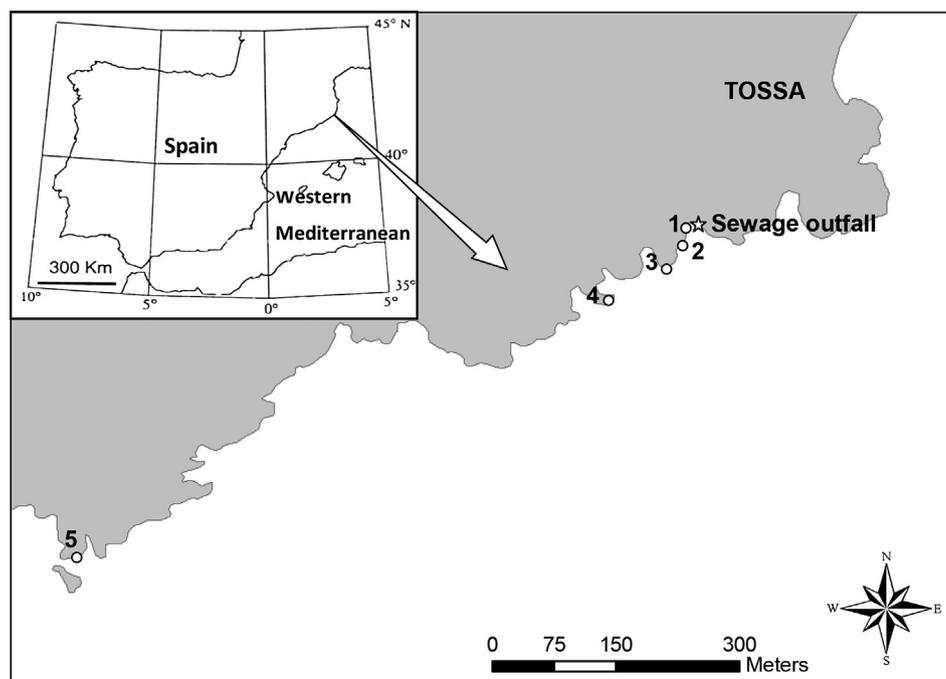


Fig. 1. Location of study area and sampling sites. Sewage effluent indicated with *.

coverage (main species) were performed to test the response of species to nutrient pollution. No data transformation was done. A correspondence analysis (CA) was performed on species coverage data at each seasonal period in order to determine the affinity between samples using CANOCO software (ter Braak, 1988). The mean of each three replicates was used to characterize the assemblage at each sampling date. Species occurring in less than 2% of samples were excluded from the analysis. SIMPER analysis (PRIMER v.6, Clarke and Gorley, 2006) was carried out in order to identify the species that contributed the most to differences between samples at each seasonal period.

3. Results

3.1. Nutrients

Nutrients showed a clear and significant seasonal trend ($p < 0.001$) at the five sampling sites (Fig. 2), with dissolved nutrients concentrations decreasing from sites 1 to 5. Highest values were registered at sites 1 and 2 during spring (April) and summer (July–August) for phosphates, nitrites, nitrates and ammonia. Lowest values were observed between October and February at both sites. Phosphates were never higher than $36 \mu\text{mol/l}$ (August) at site 1 and higher than $30 \mu\text{mol/l}$ (May) at site 2. Nitrites peaked up to $29 \mu\text{mol/l}$ at site 1 but did not exceed $21 \mu\text{mol/l}$ at site 2, both in August. Nitrates reached $35 \mu\text{mol/l}$ at site 1 in August, but $34 \mu\text{mol/l}$ in late April at site 2. For ammonia the maximum value was registered in August at site 1 ($260 \mu\text{mol/l}$), while $50 \mu\text{mol/l}$ were reached in April and August at site 2. A high variability in the ammonia seasonal pattern was observed at site 1.

The seasonal patterns of nutrients observed at sites 3 and 4 were very similar (Fig. 2) with the exception of phosphates. Maximum values were registered in August for nitrites (less than $1.3 \mu\text{mol/l}$), silicates (around $5 \mu\text{mol/l}$), and ammonia ($33 \mu\text{mol/l}$ at site 3 and $25 \mu\text{mol/l}$ at site 4); while nitrates reached the maximum in winter (9 and $5 \mu\text{mol/l}$ at sites 3 and 4, respectively). The variability observed for phosphates showed maximum values in August at site 3 ($1.1 \mu\text{mol/l}$), and in April at site 4 ($2.2 \mu\text{mol/l}$), although a second peak was also registered in August at the last site. Seasonal patterns of nutrient concentrations observed at site 5 were slightly different (Fig. 2). Registered values were very low compared with the rest of sampling sites. Maximum values were observed mainly in winter, between November and March: in February for nitrates ($3.8 \mu\text{mol/l}$), nitrites ($0.4 \mu\text{mol/l}$), and phosphates (less than $0.1 \mu\text{mol/l}$) and in November for ammonia ($2.2 \mu\text{mol/l}$).

3.2. Species

The canopy-forming alga *Cystoseira mediterranea* showed high coverage values at the sites situated further away from the outfall (3, 4, and 5), while *Ulva* spp. dominated at site 1 and *Corallina elongata* was dominant at site 2. Filter feeders such as *Mytilus galloprovincialis*, *Mytilaster minimus*, *Modiolus barbatus*, and *Perforatus perforatus* were common at sites 3, 4, and 5, attached to the rock under the canopy of *C. mediterranea*. Other macroinvertebrates such as the small sea cucumber *Ocnus planci* and the grazer *Patella* sp. were present at site 2. No grazers were observed at site 1.

Temporal changes in species richness varied between sites (Fig. 3). Species richness was the highest in September at site 5 (28 species) and the lowest at site 1 (2 species almost all over the year). The highest value at site 1 was observed between February and April with only 3 species. The number of species ranged between 9 and 15 at site 2, between 13 and 25 at site 3, between 15 and 26 at site 4, and finally, between 15 and 28 at site 5. Nevertheless,

significant seasonal differences were only observed at sites 3 ($p < 0.01$) and 4 ($p < 0.05$), with the highest values in autumn–winter.

Total species coverage (Fig. 4) showed significant differences at all the studied sites with maximum values in March (sites 1 and 2, $p < 0.01$) and May (site 3, $p < 0.01$; site 4, $p < 0.05$; and site 5, $p < 0.05$) and it followed the changes in the abundance of the main species observed at each site. Significant temporal variations (Fig. 5) were observed for *Ulva* spp. ($p < 0.05$) at site 1; *C. elongata* ($p < 0.001$) at site 2; *Ceramium virgatum* ($p < 0.05$), *C. mediterranea* ($p < 0.01$), and *M. galloprovincialis* ($p < 0.05$) at site 3; *C. mediterranea* ($p < 0.05$) at site 4; and again *C. mediterranea* ($p < 0.01$) at site 5. *Ulva* spp. peaked in March at site 1 when *C. elongata* showed the maximum values at site 2. *C. virgatum* started to increase in May reaching the highest value in August at site 3, while *M. galloprovincialis* was very variable showing a peak in February and another in June. *C. mediterranea* variability pattern was similar at sites 3, 4, and 5, increasing coverage in February, showing the highest values in May, and maintaining high coverage until August, when it started to decrease.

Temporal variations of mean coverage data of the species for the five sampling sites at each season are presented in Fig. 6. The first and second axes explained 62.5%, 64.2%, 63.5%, and 73.8% of the total variance in summer, autumn, winter and spring, respectively. Hence, spring was the seasonal period with less variability within sites while summer showed the highest. The second axis was a quadratic function of the first (Guttman effect), indicating that samples were arranged along a strong environmental gradient (Hill, 1973). Three different groups of samples were highlighted by the analysis. The grouping of sites was similar for summer, winter and spring where the first set was composed by all samples from site 1, dominated by *Ulva* spp.; the second group was defined by samples corresponding to site 2, dominated by *C. elongata*; and the third group was composed by samples corresponding to sites 3, 4, and 5, dominated by *C. mediterranea*. The differences between the three seasonal periods were related to the composition of the assemblages related with *C. elongata* abundance. During summer and winter *C. mediterranea* dominated assemblages at sites 3, 4, and 5 but *C. elongata* was also present, being more relevant in summer at site 3 and in winter both at sites 3 and 4. The relative abundance of this species at site 5 was never very important. Site 5 showed the maximal differences between samples during autumn when sampling sites were grouped in a different way. The proximity of sites 2, 3 and 4 in the ordination was again related to the relative abundance of *C. elongata* that was not present or was almost absent at site 5 in terms of relative coverage, while it reached coverage values equal or higher than *C. mediterranea* at sites 3 and 4 during this season. Site 1 remained always separated from the rest of sites and showed the highest variation between samples during summer. Site 2 showed the lowest variation during the four seasons, while site 3 showed the highest. Sites 3, 4, and 5 showed different positions along the studied period except during spring.

Differences in coverage of major macroalgal species and invertebrates found in the five studied sites during the four seasonal periods are presented in Appendix A. According to the SIMPER analysis, species composition and coverage at site 1 differed from the rest of sites with more than 81% during summer, autumn, and winter, arriving to 97% during spring. Site 2 showed a wide range of percentage of dissimilarity depending on the seasonal period: 81–89% in summer, 36–90% in autumn, 69–79% in winter, and 85–87% in spring. The lowest values observed in autumn are related to the proliferation of *C. elongata* and the decrease in the coverage of *C. mediterranea* at site 3. The dissimilarity observed between sites 3, 4, and 5 was lower than for the rest of sites as the

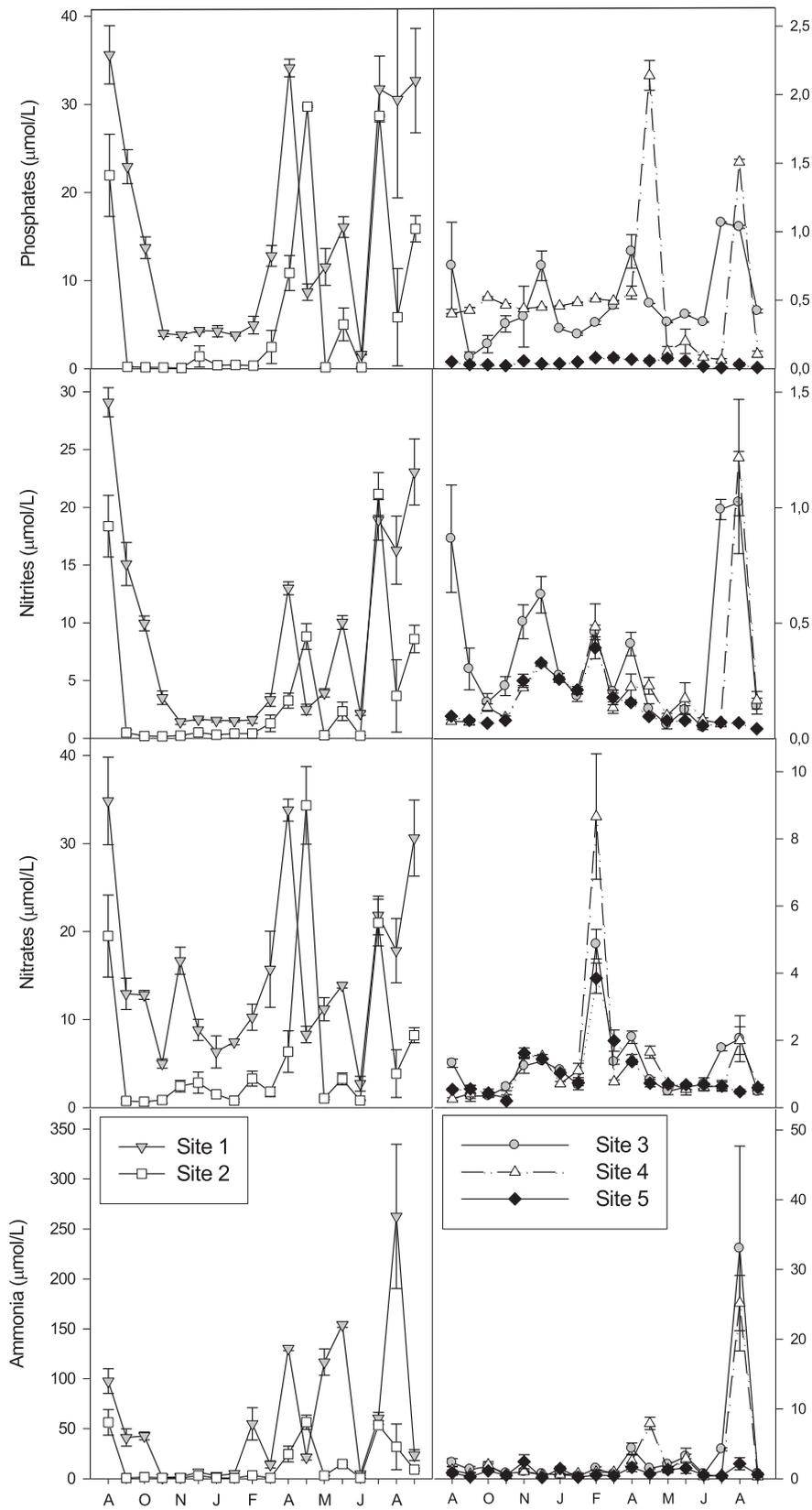


Fig. 2. Mean values (three replicates) of nutrients concentrations (phosphates, nitrates, nitrites and ammonia) for each site; vertical bars: standard error.

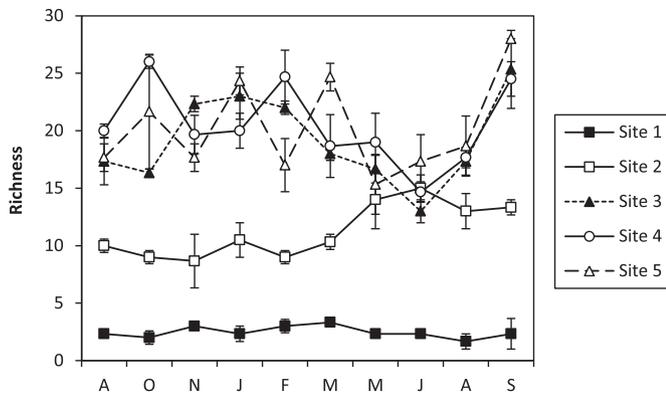


Fig. 3. Species richness (mean data of three replicates) at each site during sampling period; vertical bars: standard error.

three sites were dominated by *C. mediterranea* overtime. Anyway, it was highest in autumn (40–69 %) when *C. mediterranea* coverage decreased but other algal species proliferated, and lower in spring (23–37 %). In general, less dissimilarity was observed between sites during spring with the exception of site 2 that showed lowest values in autumn.

3.3. Species and nutrients

The relationships between nutrients concentrations and the coverage of species that showed seasonality are presented in Table 1. Negative responses with all nutrients concentrations were observed for *C. virgatum*, *C. mediterranea* and *M. galloprovincialis*. Total species richness also showed the same negative responses while coverage showed also a weak negative relationship with nitrites, nitrates and ammonia. *C. elongata* did not respond to the variations in nutrients concentrations. However, when considering different nutrients ranges, *C. elongata* responded positively when nitrites values were below 0.5 $\mu\text{mol/l}$ ($\rho = 0.403$) and negatively if values were above 0.5 $\mu\text{mol/l}$ ($\rho = -0.196$). *Ulva* spp. was the only species with a positive and significant response to increasing nutrients concentrations.

4. Discussion

All dissolved nutrients concentrations of the surface seawater were always higher at the site situated closer to the wastewater outfall and decreased at increasing distances. Summer nutrients peaks corresponded to the period of highest tourist population; the

secondary peaks observed during April at sites 1 and 2 could be related to Easter vacations when the village reaches the same levels of population as in summer. The peak observed during February for nitrate concentration at sites 3, 4, and 5 must be related to raining periods or winter seawater upwelling. For sites 1 and 2, natural inputs are masked by the high outfall-related values. The observed pattern at site 5 is similar to that reported by Ballesteros (1992) in oligotrophic zones of the same area and indicates that no human effect is observed in the seasonal cycle of nutrients.

Nutrients are critical in determining the assemblages that develop at a certain site as showed by Arévalo et al. (2007) and the present study, but they do not seem to be driving species seasonal patterns. The seasonal cycles of the dominant species at sites 1 and 2 do not respond to changes in nutrient concentrations along the year suggesting that nutrients are not a limiting factor for growth. *C. mediterranea*, the dominant species at sites 3, 4 and 5, is not able to store nutrients and its growth mainly relies on dissolved nutrients in seawater (Delgado et al., 1994). *C. mediterranea* displays its highest growth in spring (Ballesteros, 1988; Delgado et al., 1994) and the relatively high levels of dissolved N (as nitrates) and P during this period could enhance its productivity. However, it does not seem to enhance the productivity in other periods of the year when it has plenty of nutrients available at sites 3 and 4. Thus we can conclude that the nutrient enhancement observed at sites 3 and 4 do not modify the coverage values of *C. mediterranea*, and although the nutrients inputs affect the assemblage composition close to the outfall, no effects are observed into the seasonal cycle of species.

Species richness is critically affected by the outfall, with an increase from the site situated closest to the outfall to the site situated farther away. There is almost no seasonal variability in species richness at site 1 but a high variability is observed at the other sites. The highest species richness for *C. mediterranea* assemblages was observed in winter when the low coverage by the dominant species enhanced the growth of turf algae and other opportunistic species (Ballesteros, 1988, 1992; Rodríguez-Prieto and Polo, 1996). In contrast, the dominance of *C. mediterranea* at sites 3, 4, and 5 during the spring-summer period seemed to expel biodiversity by out-competing other species that are frequent during the rest of the year. Spring and summer had the highest species richness in the assemblage dominated by *C. elongata* (site 2). The turf architecture of *C. elongata* did not seem to inhibit the growth of other species at any season of the year.

Total coverage varied along the year at the studied area, reaching maximal values of 2500 cm^2 in March for assemblages dominated by *Ulva* spp. (site 1), and near to 2500 cm^2 in May for *C. mediterranea* assemblages (sites 3 and 5). Abou-Aisha et al. (1995) observed that localized phosphate pollution in the Red Sea coast of Egypt was accompanied by significant decreases in abundance compared to that recorded in the control site. This decrease in algal abundance, a possible response to pollution, contradicts our results and those found in other studies (Fishelson, 1973; Walker and Ormond, 1982), where phosphate pollution resulted in enhanced algal growth. Ephemeral species are reported to show the greatest seasonality in temperate reefs while perennial species such as furoids maintain canopy dominance all over the year although showing seasonal growth patterns (Ballesteros, 1992; Gunnarsson and Ingólfsson, 1995).

Ulva spp. and *C. elongata* started increasing their cover in February, reached the maximum values in March and maintained the coverage in May when they began to decline. In contrast, when *C. elongata* was present in *C. mediterranea* assemblages and it was not a dominant species (site 3), it modified its seasonal cycle and showed its highest values in October when *C. mediterranea* coverage was the lowest. The same pattern was observed by Rodríguez-Prieto and Polo (1996). This different seasonal response

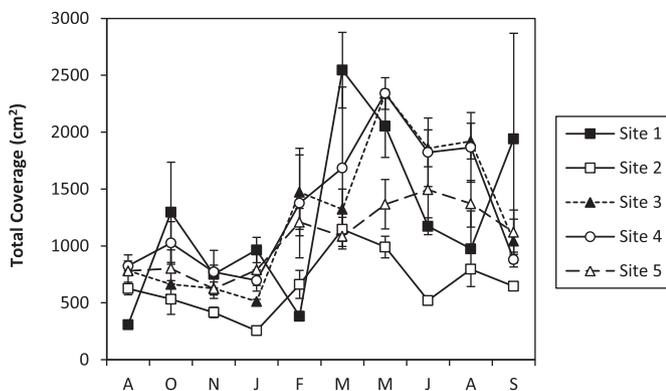


Fig. 4. Seasonal changes on total coverage of assemblages at each site during sampling period. Each point represents the mean of three replicates; vertical bars: standard error.

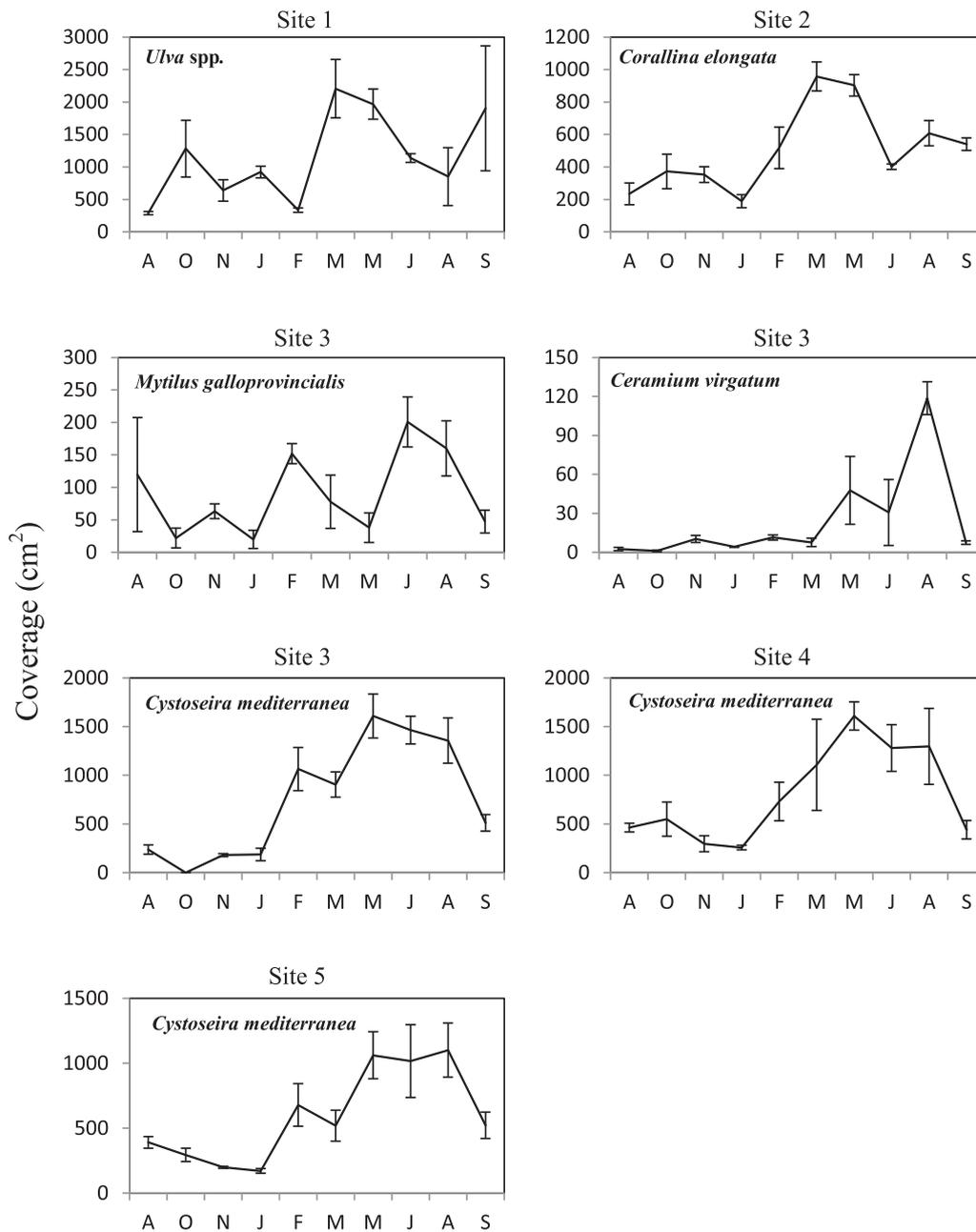


Fig. 5. Seasonal changes on coverage for the main species during sampling period. Each point represents the mean of three replicates; vertical bars: standard error.

of the same species depending on its role on the assemblages shows the high ability of species to adapt to competitive conditions. *C. mediterranea* increased its cover in February, peaked in May, maintained high values during summer and declined at the end of August. Moreover, at all sites its growth occurs in the same period regardless of the nutrients concentrations. Ballesteros (1988) and Delgado et al. (1994) also found a production period extending from winter to late spring on *C. mediterranea* populations subjected to low nutrient availability, which points to a inability of these plants to use excessive nutrients in summer and autumn. The same seasonal pattern for the species but different pattern for nutrients strongly supports that *C. mediterranea* cycle is independent from the nutrients inputs, and reflects the fact that no influence of enrichment on seasonal responses of the species is observed from site 3 to site 5. Moreover, studies based on the recovery of assemblages after the reduction of nutrient loads indicate the recovery by

fucoids (Soltan et al., 2001; Sales et al., 2011) or at least, a decrease in the abundance of green algae (Pinedo et al., 2013). These may be interpreted as an encouraging sign that proper management actions could improve the ecological quality of the algal assemblages and even substitute ulvacean algae by other species, whether stress-resistant or competitive-dominant.

Macroalgal assemblages situated close to outfalls are usually dominated by early-stage colonizing species (Archambault et al., 2001), which often show high nutrients assimilation rates at high external concentrations in order to fulfill the demands that support its fast-growing strategy (Martínez et al., 2012). Thus, their ecological strategy is well adapted to situations of high nutrient availability, whether they are seasonal or anthropogenic (Morand Briand, 1996; Worm and Lotze, 2006). This study observed this pattern at site 1, with high coverage values of *Ulva* spp. also in winter because of the continuous nutrient loading. Pedersen and

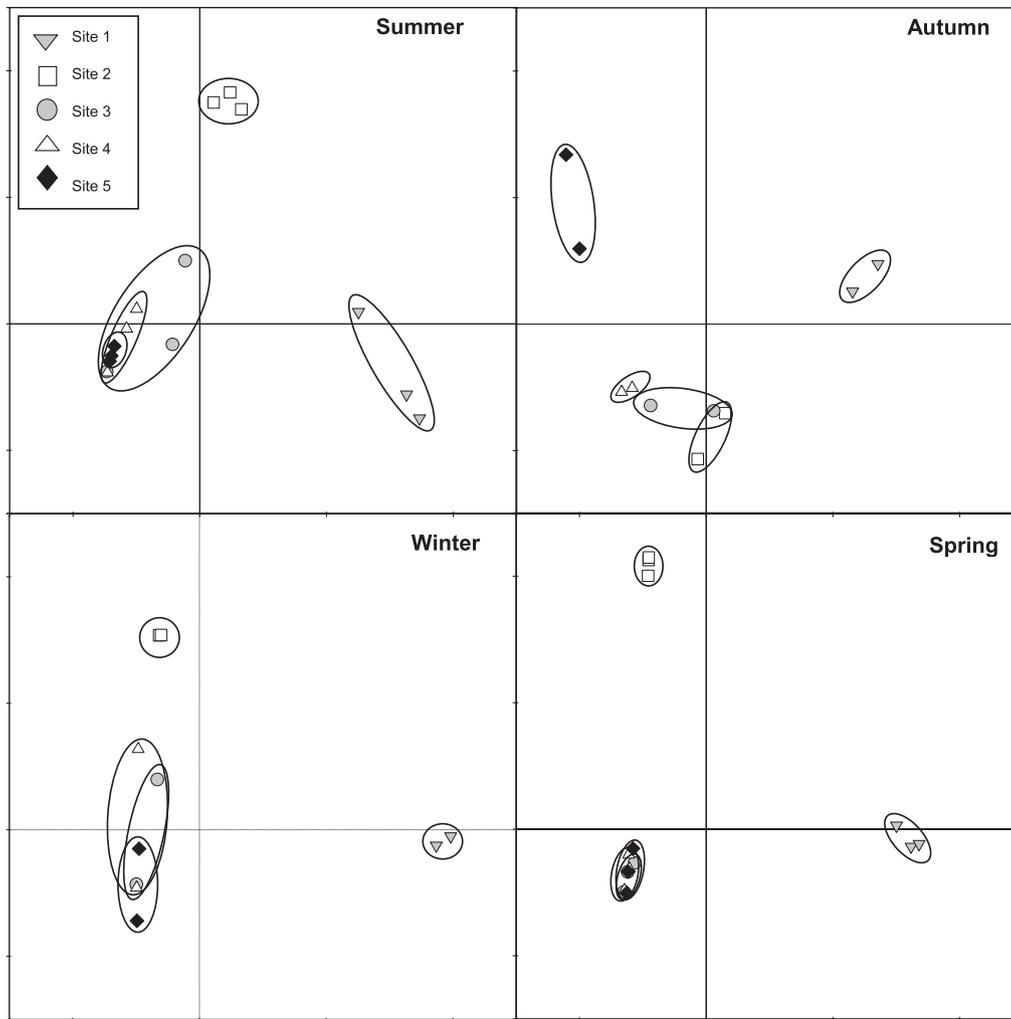


Fig. 6. Correspondence analysis (CA) ordination plot showing the distribution of samples using mean coverage data of the species (three replicates) at the five sampling sites.

Borum (1996) demonstrated that fast-growing algae are stimulated by increased nutrient availability while slow-growing algae remain unaffected or are hampered due to shading.

Grazers are often pivotal to explain the seasonal changes in the abundance of sublittoral algae in the Mediterranean Sea (Tomás et al., 2005a, 2005b; Hereu, 2006; Hereu et al., 2008) and other areas (Underwood and Jernakoff, 1984; Worm et al., 2002). In contrast, Gunnarson and Ingólfsson (1995) pointed out that grazing is unlikely to be important in controlling the seasonal changes in algal cover. Even if *Cystoseira* is heavily grazed by the fish *Sarpa salpa* (Verges et al., 2009), and fish grazing is probably one of the factors explaining the *Cystoseira* decrease after August, the other Mediterranean big herbivore, the sea urchin *Paracentrotus lividus* (Ruitton et al., 2000; Hereu et al., 2004, 2012) was absent in our samples. Both limpets (*Patella* spp.) and the sea cucumber *O. planci*, which even if it is a deposit feeder it can also behave as an herbivore, are present at site 2 and could act as important grazers in this site. *Ulva* spp. is also a preferred item by *S. salpa* (Verlaque, 1990) and fish grazing could also control its biomass. Moreover, according to some authors (Lotze et al., 2001; Worm et al., 2002; Morgan et al., 2003; Lapointe et al., 2004) herbivores may be unable to control algal densities at high nutrient levels, leading to a decrease in species richness. The continuous nutrients loads and the low density of large grazers could drive the stability of *Ulva* spp.

assemblages at site 1 (Worm et al., 1999). Some small herbivores such as amphipods, isopods or herbivorous snails could control algal blooms feeding on their early life-history stages (Lotze et al., 2000) and may be responsible for the decrease in *Ulva* spp. at site 1. Anyway, although Worm and Lotze (2006) showed that grazers were important controllers of algal blooms, they cannot override the effects of increasing eutrophication on rocky shore assemblage structure and biodiversity. While grazers and predators control perennial algae under normal conditions, increased nutrient supply can change the interaction from predominant consumer control to predominant resource control. This process enhances the replacement of perennial algae to opportunistic algal assemblages and leads to marked declines in assemblage diversity.

Another factor that can drive the differences between assemblages is salinity. However we do not think that seasonal cycles are modified by salinity differences but it could contribute, together with nutrients, to the spatial gradient of assemblages. *C. mediterranea*, only present at stations 3, 4 and 5, follows a seasonal cycle very similar to that described by Ballesteros (1988a; 1992) in a natural location without freshwater inputs. The same is true for *C. elongata* (Ballesteros, 1988b, 1992). Regarding *Ulva*, salinity is not driving the seasonal differences as species of this genus are known to be unaffected by salinity fluctuations (Kumar et al., 2014).

Table 1
Spearman correlations between coverage and nutrient concentrations.

	Nitrites	Nitrates	Ammonia	Phosphates
<i>Ceramium virgatum</i>	−0.669	−0.611	−0.521	−0.489
<i>Corallina elongata</i>	0.007	−0.047	−0.158	0.03
<i>Cystoseira mediterranea</i>	−0.704	−0.573	−0.504	−0.491
<i>Mytilus galloprovincialis</i>	−0.531	−0.55	−0.457	−0.383
<i>Ulva</i> spp.	0.589	0.443	0.460	0.648
Total coverage	−0.202	−0.064	−0.044	0.035
Number of species	−0.63	−0.618	−0.667	−0.583

There are two main points in this study that are relevant for the functioning of Mediterranean algal-dominated rocky shore assemblages:

- (1) Rocky shore assemblages dominated by ephemeral or stress-resistant algae can be maintained by continuous high levels of nutrient uploads.
- (2) Canopy-forming algae of the genus *Cystoseira* have a seasonal growth cycle that cannot be unbalanced by punctual nutrient additions, even at moments that growth could be limited by nutrient availability (summer). However, at the assemblage level these nutrient additions can lead to seasonal changes in species composition, with an increase of opportunistic, fast-growing algae. Thus, assemblages dominated by *Cystoseira* can be maintained over time even when subjected to seasonal nutrient uploads that if lasting over the whole year at high levels must lead to the disappearance of these assemblages.

These could not be true in other systems where the usual nutrient concentration in seawater is much higher than in the Mediterranean. In these systems, fucoids seem to be able to remain dominant at much higher nutrient levels, preventing the blooming of ephemeral algae (Bokn et al., 2003). *C. mediterranea* seems to be adapted to the extremely low dissolved N (nitrates) in seawater, being unable to resist the effects of heavy N loading at levels (20 $\mu\text{mol/l}$ nitrates) that are normal in non-polluted temperate areas, where fucoids dominate rocky shores assemblages (Bokn et al., 2003), enabling opportunistic algae to dominate in Mediterranean nutrient enriched sites.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2015.05.004>

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