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Settlement seasonality and temporal changes in hard substrate macrozoobenthic communities of Lesina Lagoon (Apulia, Southern Adriatic Sea)

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The macrofauna settling on experimental substrates was studied at two sites of the Lesina Lagoon to test its possible role in monitoring ecological variations in a brackish-water ecosystem. The community settlement was seasonally investigated on 3-month-old wooden poles; the development was monitored from 2001 to 2005. Comparisons with benthic assemblages settled on 10-yr-old poles were also performed. The main hydrological parameters were periodically measured during the study. A total of 38 species were collected. The assemblage reached the highest development in the central lagoon, showing relevant carbonate structures which supported a rich vagile fauna. Close to the sea-water inlet species richness and abundance values were lower, with the disappearance of some brackish-water species. A remarkable salinity drop during 2004 produced some faunistic changes in the assemblages, which however maintained different structures between the study sites, thus confirming macrozoobenthos as an efficient bioindicator of different environmental conditions for transition biotopes and a useful investigation tool in monitoring programmes.

Keywords: Benthic community; Bioconstructions; Biomonitoring; Coastal lagoon; Mediterranean Sea

1. Introduction

Together with water chemistry, biological assessments can be used for the long-term monitoring of water conditions [1]. Bioassessments of water resources can be integrated with the study of water quality over time and are sensitive to multiple aspects of environmental changes. At present, water-resource monitoring using aquatic macroinvertebrates is one of the most common methods used, since such organisms are ubiquitous and almost stationary; furthermore, their large species diversity provides a spectrum of responses to environmental change [2]. Aquatic macroinvertebrates may reside in the environment from a period of months to many years and are sensitive to most hydrological parameters as well as sedimentation and

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nutrient enrichment. They are sensitive to chemical and organic pollution [3] and can provide biogeographical information [4].

Macroorganisms settling on artificial hard substrates, often referred to as fouling organisms, have been proposed by many authors as possible bioindicators in lagoon ecosystems, both when they grow on artificially placed natural substrates (e.g. the 'bricole' in the Venice Lagoon) [5, 6] and when they settle on experimental substrates [7]. At Lesina Lagoon, the abundance of artificial hard substrates supported the development of a rich and complex community, changing according to the ecological conditions of different areas of the basin [8].

The aim of the present work was to identify possible modifications of the hard substrate macrofauna from the Lesina Lagoon in relation to temporal variations of some hydrological parameters (water temperature, salinity, and dissolved oxygen). In addition, the study contributes to the knowledge of the settlement seasonality and temporal development of the macrobenthic hard-bottom community, with the final purpose of evaluating its possible role as a bioindicator in a brackish-water ecosystem.

2. Material and methods

2.1 Study area

The Lesina Lagoon (figure 1) is a coastal basin located along the northern coast of the Gargano Promontory (Apulia, SE Italy), where it stretches for 25 km East to West, with a maximum width of 2 km; its mean depth is 80 cm [9]. The basin is connected to the Southern Adriatic Sea by two artificial canals, the western (Acquarotta canal) is longer and narrower, and the eastern is often blocked. The sea-water inflow is assured by tides (70 cm maximum, according to data available from the Vieste tide-station). Freshwater inflows are scarce [10] and are assured by seasonal streams, mostly located in the eastern area of the lagoon [11]. The combination of sea water and freshwater inflows with the dominant winds blowing from the North-West produces a salinity gradient with values decreasing from West to East.

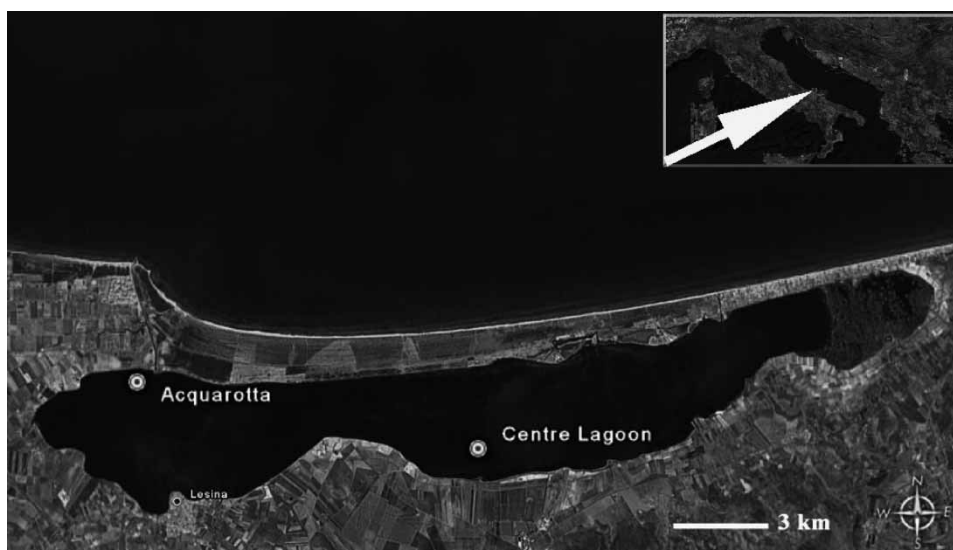


Figure 1. Location map of sampling sites.

2.2 Sampling and analysis

The two sampling stations (figure 1), about 10 km apart, were chosen to describe the area close to the inlet of the western canal (Acquarotta station) and the central portion of the basin (Centre Lagoon station) on the basis of previous studies [8]. Three wooden poles identical to those used by local fishermen were sunk into the bottom at each study site in July 2001 and again in October 2001, January 2002, and May 2002 and marked for future identification. The settlement seasonality was investigated during the first year of study by sampling the macrofauna from the poles 3 months after their immersion. The temporal evolution of the association was studied on poles set up in July 2001, and sampling was carried out 3, 6, 10, 34, and 51 months after the immersion of the substrates.

The sampling of sessile and vagile macrofauna settled on the poles was performed underwater by scraping off the substrate (20 × 10 cm, three replicates). The volumes of the samples of bioconstructions settled on the poles were estimated by placing each sample in a graduated cylinder and recording the volume of water displaced. The associated organisms were carefully extracted from the bioconstruction under a stereomicroscope, identified to the species level, and counted where possible. As regards uncountable organisms like sponges and bryozoans, their abundance was estimated as percentage cover of the bioconstruction.

The colonization development was analysed by means of colonization curves, computed using the total number of species occurring. Colonization and defaunation rates were also computed from the number of new and lost species at each sampling date in comparison with the previous one.

Abundance data of macrofauna (number of individuals) were pooled in a matrix of temporal replicates (observations) and species (variables), which was submitted to Factorial Analysis of Correspondence (FAC) [12]; the significance of the axes was tested using the test of Frontier [13].

To test whether changes occurred in the 'mature' macrozoobenthic association, samples of macrofauna were collected in May 2004 at both the study sites from wooden poles left submerged by local fishermen for more than 10 yr ('old' poles). The resulting data were compared with those recorded by the authors in May 2001 [8].

Finally, seasonal data on the macrozoobenthos from old wooden poles recorded by the authors in the period 2000–2001 [8] were compared with data from experimental poles ('new' poles) supplied by the present study. A matrix was compiled with the species as variables and the temporal replicates of macrofauna abundance data as observations. This matrix was submitted to FAC as described above.

During the investigation period, the main hydrological parameters (temperature, salinity, and dissolved oxygen) were periodically measured at both sampling sites using a multifunctional probe (Idronaut Ocean Seven 501).

3. Results

3.1 Hydrological parameters

Figure 2 shows the values of water temperature, salinity, and dissolved oxygen measured during the study period. Water temperature and dissolved oxygen followed the typical seasonal cycles at both the sampling stations, with quite comparable values in different years. As regards salinity, there is a clear difference between values recorded in 2000–2002 and 2004. At Acquarotta, where salinity was constantly higher than at Centre Lagoon, the values ranged from 23.6 to 41.2‰ in the period 2000–2002 and from 15.1 to 22.9‰

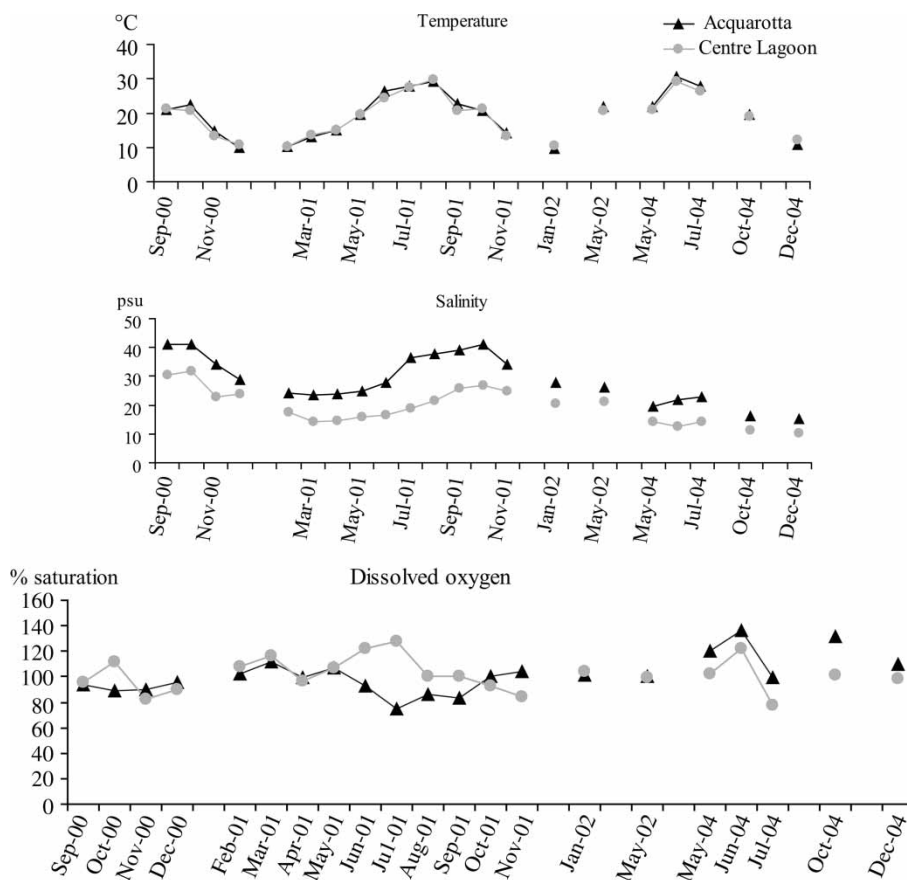


Figure 2. Hydrological parameters recorded during the study period at the sampling sites.

in 2004. At Centre Lagoon, the salinity ranges were 14.4–31.9‰ and 10.4–14.2‰, respectively.

3.2 Community development on newly submerged substrates

Values of species richness, abundance, diversity, and evenness of 3-month-old faunal assemblages from poles set up in different seasons are shown in figure 3. The Acquarotta station was characterized by peaks of species richness and abundance on summer poles and a higher diversity index and evenness on spring poles (figure 3). In total, 11 pioneer species were collected from this station. As regards the sessile fauna recorded (three species), in addition to the constantly present bryozoan *Conopeum seurati*, the barnacle *Balanus eburneus* was found on poles placed during spring–summer (being especially abundant on those set up in July), and the sponge *Halichondria panicea* on poles set up in May. Among vagile species, the isopods *Sphaeroma serratum* and *Limnoria lignorum* were the most abundant in July/October and in January, respectively.

At Centre Lagoon, the four parameters showed the highest and the lowest values on poles set up in July and October, respectively, with remarkable differences in the species richness, abundance and diversity index. A total of 18 species were recorded here, seven of which were

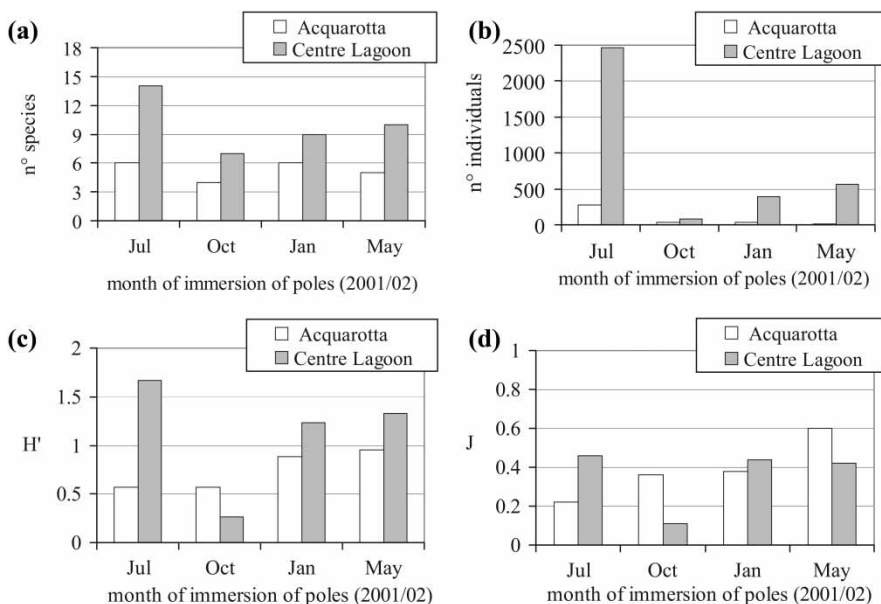


Figure 3. Settlement monitoring on 3-month-old poles set up in different seasons: species richness (a), abundance (b), diversity (c), and evenness (d) referring to the sampling sites.

sessile. All the sessile species were present on poles placed in July, where *B. eburneus* and the polychaetes *Ficopomatus enigmaticus* and *Hydroides dianthus* were particularly abundant. Among the five sessile species recorded from spring poles, the most abundant were *B. eburneus*, the bivalve *Mytilaster marioni*, and *C. seurati*. Poles placed in October and January were both colonized by three sessile species, with an abundant covering of *H. panicea* and the constant presence of *C. seurati*. As regards vagile fauna, the isopod *S. serratum* with its commensal *Jaera hopeana*, and the amphipod *Corophium insidiosum* dominated the pioneer assemblage from summer poles; the isopod *Idotea baltica* and the amphipods *Echinogammarus stocki* and *C. insidiosum* were dominant on poles placed in January. On poles placed in October and May, *C. insidiosum* and *Lekanesphaera hookeri* were the most abundant species, respectively.

A total of 29 zoobenthic species, nine sessile (about 31%) and 20 vagile, were collected in the period October 2001–October 2005 from experimental poles placed in July 2001 (table 1). Most of the species found were brackish-water halolimnobic, such as *H. panicea*, *Mytilaster lineatus*, *F. enigmaticus*, *H. dianthus*, *B. eburneus*, *C. seurati*, and the vagile species *Hediste diversicolor* and *C. insidiosum*. Some free-living species are typically euryhaline, common in coastal shallow Mediterranean waters (*I. baltica*, *Lekanesphaera monodi*, *Corophium acherusicum*, *Echinogammarus olivii*, *E. stocki*). Other species are common in marine shallow waters and in environments with freshwater influence such as *Genetyllis rubiginosa*, *Gammarus aequicauda*, *Gammarus insensibilis*, *Melita palmata*, *S. serratum*, and *J. hopeana*. The polychaetes *Nereis succinea*, *Perinereis cultrifera*, and *Platynereis dumerilii* are typically marine species.

As regards spatial differences within the basin, at Acquarotta a total of 23 species were collected, with *B. eburneus*, *S. serratum*, *C. acherusicum*, and *C. insidiosum* being the first to colonize the poles and the dominant species. At Centre Lagoon, where the total number of species found was 24, *F. enigmaticus*, *B. eburneus*, *S. serratum*, *C. insidiosum*, and *E. stocki* were the first species to colonize the substrate and the most abundant in the assemblage (table 1). The long-term monitoring carried out on poles submerged in July 2001 showed

Table 1. Long-term monitoring on poles submerged in July 2001: species from the study sites.

	Oct 2001	Jan 2002	May 2002	May 2004	Oct 2005
Acquarotta					
<i>Conopeum seurati</i> (Canu) (BRY)	30%	30%	30%	90%	90%
<i>Balanus eburneus</i> Gould (CRU)	119.3	263.7	163.7	102	62
<i>Sphaeroma serratum</i> Fabricius (CRU)	10	31	48	1104	219
<i>Corophium insidiosum</i> Crawford (CRU)	4.7	327.3	174	74.7	245
<i>Perinereis cultrifera</i> (Grube) (POL)	1.3	0.7	5.3	6	
<i>Corophium acherusicum</i> A. Costa (CRU)	2	158.3	180		
<i>Echinogammarus stocki</i> G. Karaman (CRU)		4	2		44
<i>Limnoria lignorum</i> (Rathke) (CRU)		1.3	0.7		
<i>Jaera hopeana</i> A. Costa (CRU)			6.3	60	17
<i>Ophiodromus pallidus</i> (Claparède) (POL)			1	10.3	
<i>Melita palmata</i> (Montagu) (CRU)			17.7		14
<i>Idotea baltica</i> (Pallas) (CRU)			4.3		24
Nemertea			4.7		
<i>Platynereis dumerilii</i> (Audouin and Milne-Edwards) (POL)			0.3		
<i>Halichondria panicea</i> Pallas (POR)				70%	
Actiniaria (CNI)				2	
<i>Hydroides dianthus</i> (Verrill) (POL)				10.7	
<i>Mytilaster lineatus</i> (Gmelin) (MOL)				2	
<i>Ficopomatus enigmaticus</i> (Fauvel) (POL)					39
<i>Hediste diversicolor</i> (O.F. Müller) (POL)					11
<i>Balanus improvisus</i> Darwin (CRU)					27
<i>Echinogammarus olivii</i> (Milne-Edwards) (CRU)					3
<i>Gammarus insensibilis</i> Stock (CRU)					4
Centre Lagoon					
<i>Conopeum seurati</i> (Canu) (BRY)	30%	30%	30%	90%	90%
<i>Ficopomatus enigmaticus</i> (Fauvel) (POL)	187.3	151.7	89.3	814	804.3
<i>Mytilaster lineatus</i> (Gmelin) (MOL)	3	26	7	398	17.7
<i>Balanus eburneus</i> Gould (CRU)	409.7	600.3	129	23.3	5.3
<i>Echinogammarus stocki</i> G. Karaman (CRU)	22.3	218.7	380.7	31.3	37.7
<i>Jaera hopeana</i> A. Costa (CRU)	38	26.7	56.7	30	5.3
<i>Sphaeroma serratum</i> Fabricius (CRU)	276.7	243	279.7	485.7	710
<i>Mytilaster marioni</i> (Locard) (MOL)	3	9	2.7	113	21.7
<i>Corophium insidiosum</i> Crawford (CRU)	153.3	2408	343	7.3	
<i>Halichondria panicea</i> Pallas (POR)	30%	45%	65%		
<i>Hydroides dianthus</i> (Verrill) (POL)	25.7	25	6.3		
<i>Idotea baltica</i> (Pallas) (CRU)	9.3	5.3	19.7		
<i>Lekanesphaera monodi</i> (Arcangeli) (CRU)	23.7	27.7	2		
<i>Corophium acherusicum</i> A. Costa (CRU)	2.3				
Nemertea		20.3	5.7		
<i>Platynereis dumerilii</i> (Audouin and Milne-Edwards) (POL)		0.7	1		
<i>Genetyllis rubiginosa</i> (Saint-Joseph) (POL)		1			
<i>Gammarus aequicauda</i> (Martynov) (CRU)			4.7	2	5.3
<i>Nereis succinea</i> (Freyand Leuchart) (POL)			0.3		
<i>Perinereis cultrifera</i> (Grube) (POL)			0.3		
<i>Melita palmata</i> (Montagu) (CRU)			1.7		
<i>Echinogammarus olivii</i> (Milne-Edwards) (CRU)				35.7	194.7
<i>Lekanesphaera hookeri</i> (Leach) (CRU)				34	
<i>Hediste diversicolor</i> (O.F. Müller) (POL)					23

Note: Abundance is expressed as number of individuals or percentage cover (mean of three replicates).

higher values of species richness, abundance, and diversity at Centre Lagoon, with a reversal recorded 51 months after the beginning of the study (figure 4a). An initial progressive increase in number of species was registered at both stations, with the highest values observed after 10 months. A sharp decrease was recorded on 34-month-old poles, with eight and 10 species lost

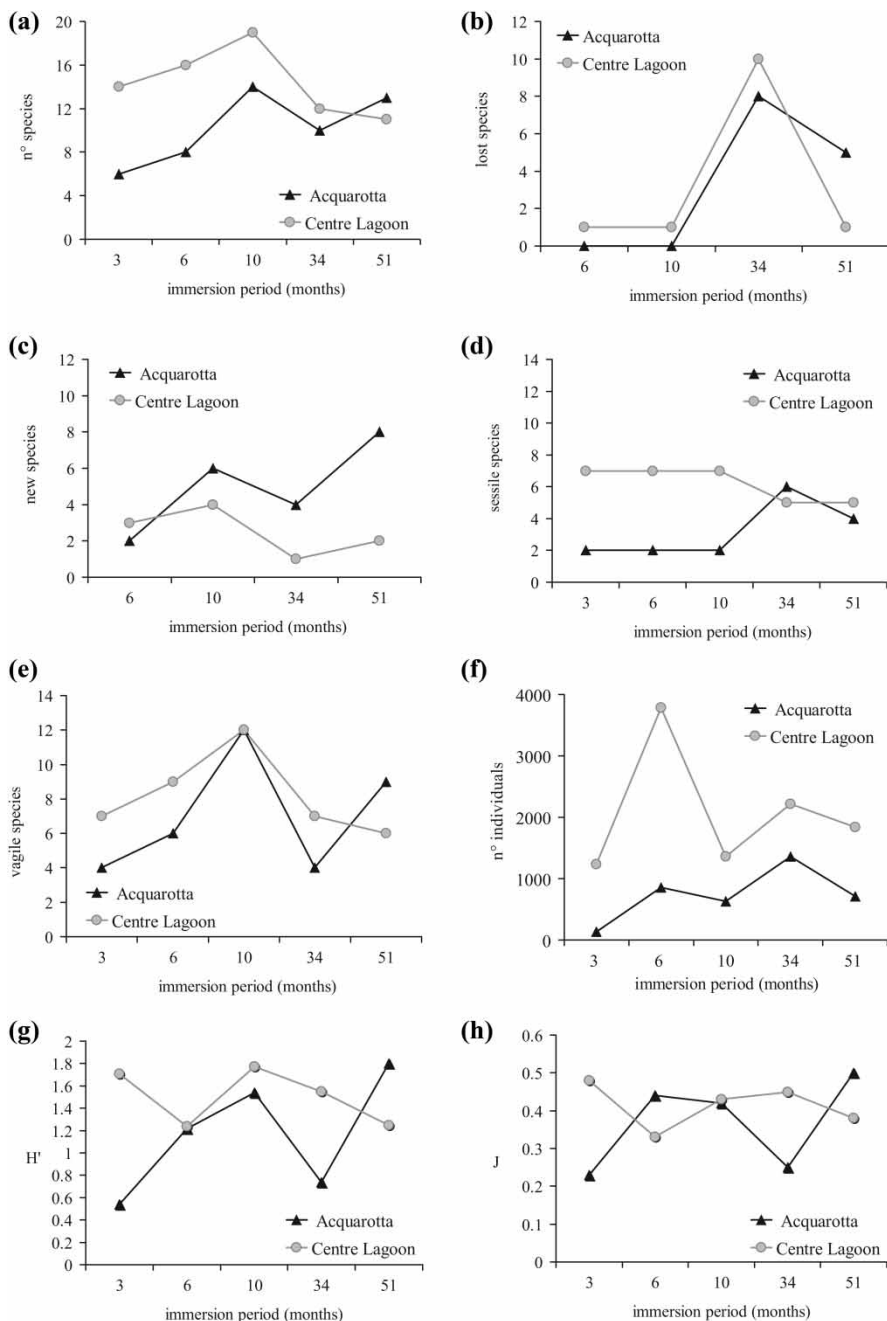


Figure 4. Long-term monitoring on poles submerged in July 2001: temporal trend of species richness (a), lost species (b), newly found species (c), sessile species (d), vagile species (e), abundance (f), diversity (g) and evenness (h), referring to the sampling sites.

at Acquarotta and Centre Lagoon, respectively (figure 4b). Some species common in sheltered coastal waters disappeared, such as *C. acherusicum* at Acquarotta and *H. panicea*, *H. dianthus*, *I. baltica*, and *L. monodi* at Centre Lagoon. In October 2005, eight new species were found at Acquarotta (figure 4c), including the sessile *F. enigmaticus* and *B. improvisus* and the vagile *H. diversicolor* and *E. olivii*.

Colonization curves compiled by plotting the number of sessile and vagile species against time showed different trends at the study sites (figure 4d and e). Indeed, during the first year of study, *B. eburneus* and *C. seurati* were the only sessile species at Acquarotta, while in May 2004 four new species attached to the poles. At Centre Lagoon, the number of sessile species reached the maximum (seven) just 3 months after the poles were set up and remained constant, though in May 2004 (34 months after setting up) it showed a slight decrease (five species) (figure 4d). At both stations, the number of vagile species progressively increased until May 2002 (10-month-old poles), when the maximum (12 species) was recorded, then there was a decrease following the same trend as the total species curves (figure 4e). As regards abundance, a comparable trend characterized the study sites, with constantly higher values at Centre Lagoon (figure 4f). Similarly, the diversity was generally higher at Centre Lagoon, with a reversal in October 2005 (figure 4g). The temporal trend of evenness appeared quite uniform at Centre Lagoon, while it was more variable at Acquarotta (figure 4h). The graph in figure 5 shows the configuration of points in the projection plane from Correspondence Analysis applied to data from the experimental pole community for the period 2001–2005. The plane was formed by the first two significant axes, which together explain 47.6% of the total variance. Station-points were separately plotted along the first axis with points referring to Centre Lagoon located at the positive pole and those referred to Acquarotta at the negative pole. The species *E. olivii*, *F. enigmaticus*, *M. marioni*, *M. lineatus*, and *L. hookeri* were strongly associated with Centre Lagoon, whereas the negative pole was characterized by *C. acherusicum*, *L. lignorum*, and *P. cultrifera*. Species such as *S. serratum*, *J. hopeana*, *B. eburneus*, and *C. insidiosum*, abundant at both the sampling stations, were placed near the intersection of the axes, together with *P. dumerili*, *I. baltica*, and *H. dianthus*, which showed comparable abundance values at the study sites. Along the second axis, *B. improvisus*, *H. diversicolor*, and *G. insensibilis*, all collected only in October 2005, characterized the positive pole with most of the remaining species around the negative pole.

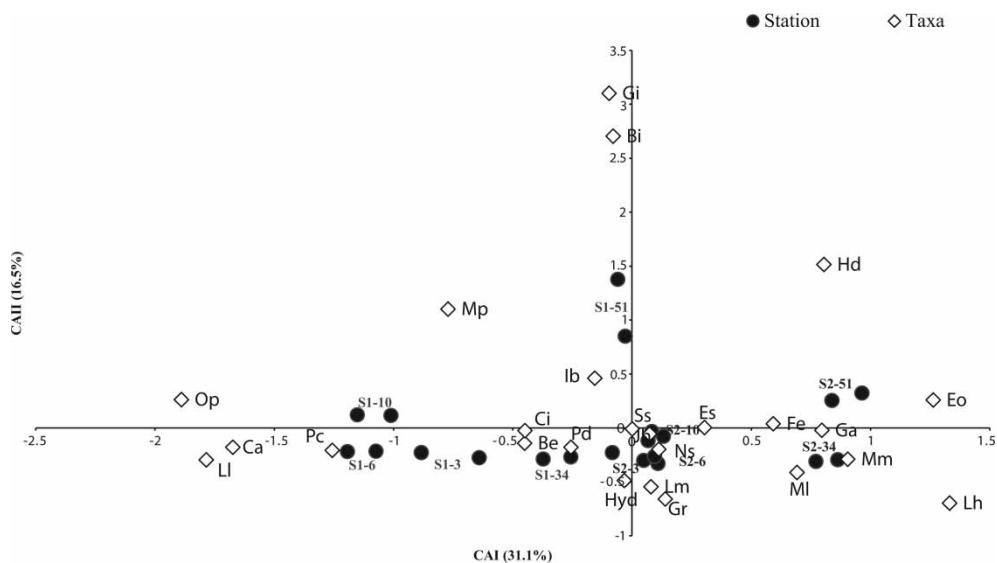


Figure 5. Long-term monitoring on poles submerged in July 2001: ordination model of station-points and species-points in the plane of the first two axes extracted by FAC. 1: Acquarotta station; 2: Centre Lagoon station. Numbers beside stations indicate the months of immersion of poles.

3.3 Mature community structure: comparison between 2001 and 2004

The macrofauna collected in May 2001 at the study sites from 'old' substrates consisted of 24 species, most represented by crustaceans and annelids (11 and 9 species, respectively) (table 2). In particular, at Acquarotta, the sessile fauna consisted of 5 species, among which the serpulids *H. dianthus* and *F. enigmaticus* were the most abundant. At Centre Lagoon, there were 7 sessile species, with *F. enigmaticus* and *M. lineatus* being dominant, together with the sponge *H. panicea* that showed a high coverage. As regards the vagile fauna, the

Table 2. Mature community structure: list of the species found in May 2001 and May 2004 at the study sites.

		May 2001		May 2004	
		Acquarotta	Centre Lagoon	Acquarotta	Centre Lagoon
Porifera	<i>Halichondria panicea</i> Pallas		60%	60%	
Cnidaria	<i>Aiptasia diaphana</i> (Rapp)	a	a		
Mollusca	<i>Mytilaster lineatus</i> (Gmelin)	17	32.3	2.3	38
	<i>Mytilus galloprovincialis</i> Lamarck			4	
Annelida	<i>Cirratulus cirratus</i> (Müller)	25.3	0.7	32	
	<i>Ficopomatus enigmaticus</i> (Fauvel)	42	80	60.3	98
	<i>Harmothoe lunulata</i> (Delle Chiaje)	1.7	0.3		1
	<i>Hydroides dianthus</i> (Verrill)	50	4.7	51	5
	<i>Naineris laevigata</i> (Grube)	1.7		2.7	
	<i>Nereis succinea</i> (Freyand Leuchart)				0.3
	<i>Ophiodromus pallidus</i> (Claparède)			0.3	
	<i>Perinereis cultrifera</i> (Grube)	18.3	0.7	16	0.3
	<i>Genetyllis rubiginosa</i> (Saint-Joseph)	0.3		0.7	
	<i>Platynereis dumerilii</i> (Audouin and Milne-Edwards)			4	1
	<i>Polydora ciliata</i> (Johnston)	2	6.3	2.3	8
Cirripedia	<i>Syllis gracilis</i> Grube	24.3		8.7	
	<i>Balanus eburneus</i> Gould		0.3	124	1
Isopoda	<i>Balanus improvisus</i> Darwin				4
	<i>Idotea baltica</i> (Pallas)		0.3	16.3	18
Amphipoda	<i>Jaera hopeana</i> A. Costa	52.3	31.3	76	44
	<i>Lekanesphaera monodi</i> (Arcangeli)		1		2
	<i>Limmoria lignorum</i> (Rathke)			1	
	<i>Sphaeroma serratum</i> Fabricius	317.3	48	408	220
	<i>Corophium acherusicum</i> A. Costa			212	
	<i>Corophium insidiosum</i> Crawford	2.7	75.7		18
	<i>Cyathura carinata</i> (Kroyer)	2.7	3.3	5	6
	<i>Dexamine spinosa</i> (Montagu)	0.3	1.3		7
	<i>Echinogammarus olivii</i> (Milne-Edwards)	0.7	83.3	0.7	37
	<i>Echinogammarus stocki</i> G. Karaman	0.7	15.7		19
Bryozoa	<i>Melita palmata</i> (Montagu)	15	21	11.7	4
	<i>Conopeum seurati</i> (Canu)	40%	40%	70%	40%
n. species		20	21	23	21

Note: Abundance is expressed as number of individuals or percentage cover (mean of three replicates).

^aSpecies present but values not available due to fixation problems.

isopod *S. serratum* was particularly abundant at Acquarotta, while the amphipods *E. olivii* and *C. insidiosum* were dominant at Centre Lagoon (table 2).

Thirty species were collected in May 2004, most of which belonged to crustaceans and polychaetes (14 and 12 species, respectively). In particular, at Acquarotta, the sessile fauna consisted of seven species, among which *B. eburneus* was the most abundant, together with the only sponge and bryozoan largely encrusting the poles (table 2). At Centre Lagoon, there were six sessile species, with *F. enigmaticus* and *M. lineatus* being the most abundant. Among vagile fauna, *S. serratum* and *J. hopeana* were dominant at both the sampling stations, together with *C. acherusicum* at Acquarotta and *E. olivii* at Centre Lagoon (table 2).

The comparison between macrozoobenthic assemblages sampled in 2001 and 2004 pointed out the recent disappearance of the cnidarian *Aiptasia diaphana* from the study sites and the concurrent appearance of seven species (one bivalve, three annelids, three crustaceans), among which *C. acherusicum* was the most abundant (table 2). As regards the sampling stations, in 2004 the assemblage from Acquarotta counted eight new records, with five of the seven species newly found in the lagoon, while five species disappeared. Moreover, *B. eburneus* previously only present at Centre Lagoon with a few individuals, in 2004 was also found at Acquarotta with high abundance values (table 2). At Centre Lagoon, the assemblage showed three of the seven new records found, while three species disappeared. In particular, the sponge *H. panicea*, which was very abundant at Centre Lagoon in 2001, completely disappeared in 2004 and moved to Acquarotta [14], where it largely encrusted the poles (table 2).

The comparison between assemblages from old and new substrates at the two study sites was analysed by means of the Analysis of Correspondence, which produced the graph showed in figure 6. Given the disposition of observation points on the plane formed by axes I and II, four groups of stations could be recognized, referring to old and new substrates from Acquarotta and Centre Lagoon. Old poles from Acquarotta, together with the points referring to some marine species (*S. gracilis*, *A. squamata*, *P. cultrifera*, *C. carinata*, and *N. laevigata*), characterized the positive pole of axis I; station-points of old and new substrates from Centre Lagoon and points referring to some brackish-water species (*L. hookeri*, *H. diversicolor*, *G. aequicauda*,

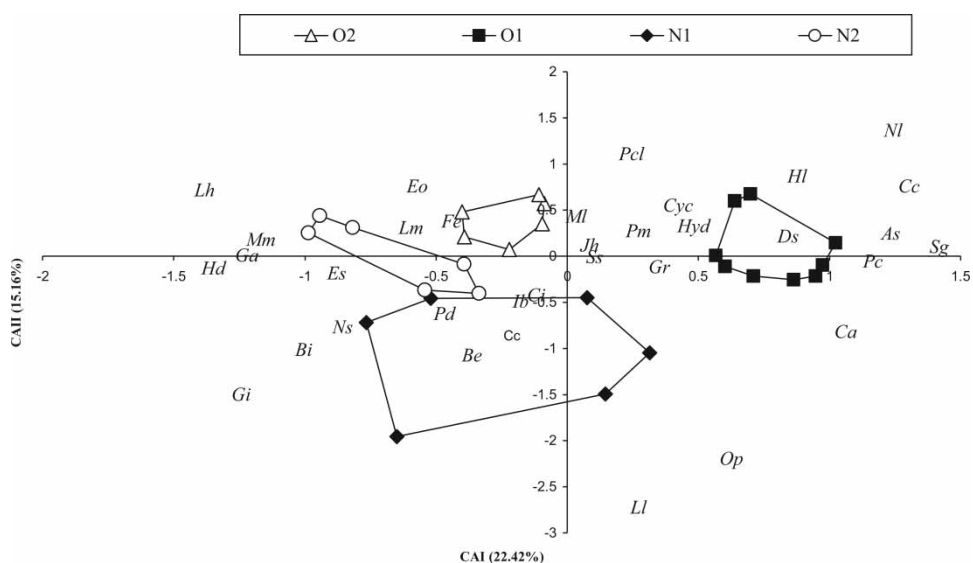


Figure 6. Comparison of macrozoobenthic communities from new (N) and old (O) poles at the sampling sites (1 = Acquarotta station; 2 = Centre Lagoon station): ordination model of station-points and species-points in the plane of the first two axes extracted by FAC.

M. marioni, and *B. improvisus*) are close to the negative pole of axis I. Station-points referring to new substrates from Acquarotta are in an intermediate position.

4. Discussion

According to Nonnis Marzano *et al.* [8, 14], the zoobenthic assemblage from the hard substrates of Lesina Lagoon shows spatial differences in species composition and abundance depending on the different ecological conditions in the lagoon. Such a distributional model has been confirmed in this research, which pointed out the occurrence of spatial differences from the first phases of the colonization (3 months) to the older assemblages (more than 10 yr). The zoobenthic assemblage showed the highest development in terms of species richness and abundance values at Centre Lagoon, where relevant carbonate structures were built on the experimental and old hard substrates by the reef-building polychaete *Ficopomatus enigmaticus*, together with *Hydroides dianthus*, the mussels *Mytilaster lineatus* and *M. marioni* and the cyrriped *Balanus eburneus*. These bioconstructions were stabilized by wide patches of *Conopeum seurati* and *Halichondria panicea*, both settling on the other sessile species. At Acquarotta, the sea-water inflow inhibited the settlement and development of brackish-water species. In particular, *F. enigmaticus* showed much lower biomass values than at Centre Lagoon, thus preventing the development of a structured and diversified assemblage, as already observed by Schwindt *et al.* in a south-western Atlantic coastal lagoon [15].

As regards the vagile fauna, at Centre Lagoon it exhibits a higher species richness and diversity for most of the study period. Such a difference is explained by the role of the *Ficopomatus* reef in increasing habitat heterogeneity thanks to its interstices filled up with sediment where a large number of motile and soft-bottom species can live. Similar reefs are common in brackish-water ecosystems throughout the world, where *F. enigmaticus* is one of the main bioconstructors [15–20], which is able to build circular calcareous reefs up to 7 m in diameter [21].

In many Mediterranean brackish biotopes, the vagile fauna associated with the *Ficopomatus* reefs is dominated by amphipods, with abundant species such as *Leptocheirus pilosus* [22], the polychaete *Polydora ciliata*, and chironomid larvae [23]. At Centre Lagoon, the vagile fauna associated with the bioconstruction mainly consisted of the isopod *S. serratum*, a typical marine species occasionally living in brackish biotopes [24], and the amphipods *Echinogammarus stocki*, *E. olivii*, and *Corophium insidiosum*.

Combined with the occurrence of different secondary substrates, recruitment seems to play a key role in determining the distribution of benthic species. Recruitment from marine populations was evident in the area close to the sea inlet, where motile marine species such as *Syllis gracilis*, *Perinereis cultrifera*, *Cirratulus cirratus*, and *Naineris laevigata* were collected. Their recruitment was probably sustained by the adjoining marine communities, according to supply-side ecology [25], while in the central area of the lagoon, larval supply was mainly assured by the neighbouring brackish populations. The study of settlement seasonality showed that the period of maximum recruitment was summer at Centre Lagoon, while Acquarotta lacked a peak in recruitment. This difference could also be explained by differences in reproductive behaviour of some benthic species in the different areas of the lagoon, as reported by Relini *et al.* [26] for the benthic communities of the Po River delta.

Temporal changes in the benthic community of Lesina Lagoon were stressed by the year-on-year decrease in salinity, which was probably responsible for some important faunistic changes recorded during 2004. In this period, the cyrriped *B. eburneus* decreased in abundance at Centre Lagoon and was partially replaced by the occurrence of the more euryhaline *B. improvisus*, while the sponge *H. panicea* disappeared from Centre Lagoon and rapidly colonized hard

substrates near the sea inlet [14]. According to Nonnis Marzano *et al.* [14], the rapid growth, continuous sexual reproduction, and ability to colonize the thalli of free living algae allowed this sponge to massively shift along the lagoon in a short time.

Despite these changes in species composition, hard-bottom assemblages from Lesina Lagoon maintained a different structure in the two areas of the basin, thus confirming that macrozoobenthos is an efficient biological indicator of environmental change in transition biotopes and can be a relevant investigation tool in monitoring programmes.

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