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Porifera and Bryozoa on artificial hard bottoms in the Venice Lagoon: Spatial distribution and temporal changes in the northern basin

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Abstract

The spatial distribution and temporal changes of demosponges and bryozoans in the northern basin of the Venice Lagoon were studied from samples collected from wooden piles and artificial rocks in June and October 2001. Twenty species of demosponges and 18 species of bryozoans were recorded. Sponges were found at 10 out of 11 sampling stations, while bryozoans were found at all 11 sampling stations. The studied taxocoenoses showed a high percentage cover of the lagoon hard bottoms. Eleven out of the 20 detected species of sponges were reported in a previous study on this taxocoenosis carried out on material collected in 1954–1955. Moreover, the most abundant species were also recorded during a study in 1989. These observations suggest a remarkable degree of persistence of the sponge community. Among bryozoans, the comparison with literature data showed a wider variation in species composition, with the occurrence of five new species in the studied area. The Indo-Pacific invasive *Tricellaria inopinata* replaced the native *Bugula* spp. in the role of dominant species. Finally, a significant increase in species richness along the salinity gradient, more evident for sponges than for bryozoans, was identified.

Keywords: *Venice Lagoon, Porifera, Bryozoa, hard bottoms, ecological gradients*

Introduction

In the confined coastal environments of the Mediterranean Sea, animal benthic assemblages usually considered as characteristic of hard bottoms may be widely represented, constituting a very important component of the zoobenthic communities (Corriero 1984; Nonnis Marzano et al. 2002, 2003a, 2003b; Sconfietti et al. 2003). This is strictly dependent on the availability of artificial hard substrates (Corriero 1984; Sconfietti 1989) but also on the occurrence of biogenic concretions (Bianchi & Morri 1996; Nonnis Marzano et al. 2002). Among such benthic communities, Porifera and Bryozoa appear to be very abundant. High sponge richness and abundance is reported for the Stagnone di Marsala (Tyrrhenian Sea), the Bay of Porto Cesareo, and the Mar Piccolo di Taranto (Ionian Sea) (Corriero 1989; Mercurio et al. 2001; Longo et al., 2004) where, due to the large sea inlets and the scarcity of continental water inflow, little thermohaline oscillations occur. A few sponge species are described for brackish lagoons and coastal lakes from the Tyrrhenian and Adriatic seas (Cognetti et al. 1981; Nonnis Marzano et al. 2003a, 2003c), where, however, a single species of sponge may cover up to 75% of the available substrates (Nonnis Marzano et al. 2003a, 2003b).

Unlike sponges, bryozoans show a better tolerance to brackish waters, and exhibit a large number of species in transitional environments (Winston 1977). As regards the Italian coasts, Occhipinti-Ambrogi (1981) recorded 26 species as the most frequent and abundant, after a survey of 33 lagoons. Generally, such benthic animals are well represented in all brackish Italian environments, where they frequently coexist in the same habitats occupied by the sponges (Gherardi & Lepore 1974; Corriero

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1984; Tursi et al. 1984; Nonnis Marzano et al. 2003b; Marchini et al. 2004; Rismondo et al. 2005).

The Venice Lagoon is a shallow Mediterranean coastal area with high habitat heterogeneity, different environmental conditions, strong anthropic impact and continuous evolution of its geomorphological structure, due to land subsidence, eustacy and variations in sea level (Ravera 2000). In particular, the northern basin (Figure 1) is very heterogeneous because of (i) the input of both continental freshwater (from the Dese River) and tidal seawater (from the Lido Mouth), (ii) the presence of the nearby urban centre of Venice, and (iii) its own morphology, which favours eutrophication (Tagliapietra et al. 1998).

During the decade 1990–2000, this lagoon underwent the following profound changes: a consistent decrease in the nutrient load (Sfriso et al. 2005); a change in the direction of waste discharges from the Marghera refinery complex from the central basin to the southern basin (Sorokin et al. 2002); an increase in the natural sediment erosion and water turbidity due to intense trawl fishing for clams (Sfriso et al. 2003); the massive arrival of invasive species (Mizzan 1999; Occhipinti-Ambrogi 2000a), which represents a serious ecological and economic threat, leading to loss of biodiversity and unbalancing of the ecosystem (Occhipinti-Ambrogi & Savini 2003). These alterations of the lagoon environment must be added to the rising sea level (Day et al. 1999; Carbognin & Tosi 2002), with higher frequency and intensity of 'high water' events (Ravera 2000). The increased internal hydrodynamics, which in turn triggered the lagoon floor erosion (Carbognin & Tosi 2002), the disappearance of marshes and the reduction of river inputs (Day et al. 1999) also led to a general marinization of the lagoon.

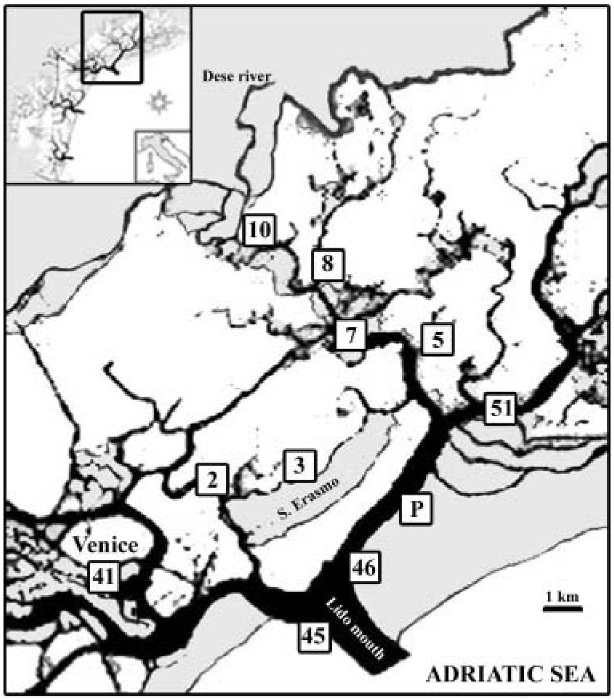

Figure 1. Venice Lagoon: location of the sampling stations in the northern basin.

Several recent studies on specific taxocoenoses revealed important and rapid variations of the biological communities in response to such environmental modifications (Tagliapietra et al. 1998; Sfriso et al. 2003; Curiel et al. 2004). As regards the hard-bottom zoobenthos, a trend of homogenization of the community structure, with loss of peculiar species associations, was reported for the whole macrobenthic community (Sconfietti et al. 2003).

Sponges from the Lagoon of Venice were previously described by Sarà (1960) who, studying samples collected in 1954–1955, reported 15 species with rich assemblages, mostly localized near the sea mouth. Further data on the most common species of demosponges were reported by Sconfietti & Marino (1989). No more recent and exhaustive data are available on the sponges from the Venice Lagoon.

Literature data on the bryozoans of the Venice Lagoon (Gautier 1958; Occhipinti-Ambrogi 1980, 1985, 1991, 2000b) highlight their richness and the high faunal variability in response to the profound changes that have affected the lagoon during the last decades.

The present paper reports the results of a survey on demosponges and bryozoans on artificial hard bottoms from the northern basin of the Venice Lagoon. The aim of the research was to investigate these two taxocoenoses in order to compare the present species composition with literature data. In addition, the distributional pattern was analysed with particular attention to the salinity gradient, one of the most important ecological parameters affecting benthic distribution in brackish waters (Sacchi & Occhipinti Ambrogi 1992).

Materials and methods

Natural hard substrates are not present in this lagoon, although some artificial ones were considered for sampling, namely wooden piles (*bricole*), that have been 'naturalized' by their being permanently immersed in the lagoon waters over a long time and colonized by a complex benthic community (Occhipinti-Ambrogi et al. 1988; Sconfietti et al. 2003).

We considered 11 stations in the northern basin of the lagoon (Figure 1), whose circulation is mainly driven by sea flow from the Lido Mouth (Solidoro et al. 2004). This basin can be further divided into two parts: the far northern sub-basin, influenced by the Dese River input, and the northern central sub-basin, which includes the island of Venice and all its polluted urban canals; consequently, our stations are representative of different salinity and trophic regimes. Two sampling campaigns were performed in 2001 (July and October), chosen as moments of great development of the sessile benthos; the survey was carried out in the intertidal and subtidal zones by scuba divers at a depth ranging between 0 and 150 cm in high-tide sea conditions. Since direct enumeration of individuals of modular organisms like sponges and bryozoans is difficult, abundance has been expressed as cover percentage (Boudouresque 1971; Warwick 1993). Percentage cover values (x=<25%; xx=25% to <50%; xxx=50% to <75%; xxxx=>75%) were recorded at each sampling station for the most common species before collection, over a 1 m^2 unit area, corresponding to about the mean submerged surface of each pile at the considered depth interval. This sampling methodology, which requires taxonomist divers, was necessary due to the marked patchiness of the studied assemblages, characterized by large specimens and/or colonies, which may cover a surface of several square centimetres. In addition, large portions of substrate within the studied surface were collected in order to detect cryptobiotic or boring species. The volume of the largest sponge species collected was measured in a graduated beaker filled with seawater.

Biological samples were fixed with 4% formaldehyde in seawater, and preserved in 70% alcohol. Sponges were sorted in the laboratory, and slides of dissociated spicules and transversal sections of paraffin embedded sponges were prepared to study the spicular arrangement and skeletal structure. Bryozoans were sorted under a stereomicroscope in order to confirm species identification and to detect inconspicuous colonies.

Presence/absence data of sponges and bryozoans together were analysed by cluster analysis on a Bray–Curtis similarity matrix using the average linkage clustering technique according to the PRIMER software (Clarke & Warwick 1994).

Water salinity was measured during the first survey (July 2001) by a hand-held refractometer (Aquafauna, Biomarine) and, in addition, the mean salinity values, measured each month from July to October 2001, were obtained for five stations (Rismondo, personal communication).

Results

A total of 20 demosponge and 18 bryozoan species was found (Table I). The highest number of species, of which sponges represented the main component, was observed at the stations located near the lagoon mouth (45 and 46), whereas the stations mostly influenced by river input (8 and 10) hosted only two species of bryozoans (Figure 2). Demosponges were found at 10 out of the 11 sampling stations while bryozoans were found at all of them. Generally, the benthic assemblage appeared as a multilayered covering, with bryozoans epibiontic over the sponge surface, but sometimes sponges settled over a biogenic basal layer consisting of bivalve shells. Among sponges, *Halichondria bowerbanki*, *Hymeniacidon perlevis* (=*H. sanguinea*), *Tedania anhelans* and *Haliclona palmata* showed the highest frequency values, occurring in more than 70% of the examined stations. *H. perlevis*, *Mycale contarenii* and *T. anhelans* reached the highest cover values, up to about 75% (Table I). In particular, *T. anhelans* and *M. contarenii* showed unusually large size (more than 500 ml in volume) and uncommon external morphology: the former being bushy and the latter branching, with branches more than 15 cm long. Even though *H. perlevis* did not attain large dimensions, it was present with a high number of specimens, frequently occurring on the upper portion of the wooden piles, subject to tidal emersion.

With regard to temporal comparisons, a high percentage (about 80%) of the demosponge species reported by Sarà (1960), referring to material collected in the Venice Lagoon during 1954–1955, was also collected during this research (Table II). Among the 11 species common to the two lists it is possible to recognize all the species that show the highest covering values in this research (Table I). In addition, the occurrence of such high-cover species was also reported by Sconfietti & Marino (1989) in a paper on the whole hard-substrate benthic community. Three demosponges among those reported by Sarà (1960) were not found in the present research (*Stelletta grubii*, *S. stellata*, and *Haliclona angulatus*), while nine of the species reported here are new records (Table I).

Amongst bryozoans, cheilostomata were the dominant order, with 13 species, while ctenostomata were represented by 4 species and cyclostomata by 1 one species. The anascan cheilostome *Tricellaria inopinata* was the most frequent species. It occurred in all the stations except the two most influenced by the Dese River, where *Victorella* sp. became dominant. In some stations (5, 51) *T. inopinata* was the sole bryozoan observed. Other frequent species were

Table I. Venice Lagoon: distribution of sponges and bryozoan species found during the research. xxxx, >75% percentage cover; xxx, >50% to 75% percentage cover; xx, >25% to 50% percentage cover; x, <25% percentage cover; *, new record.

			Stations										
Species			45	46	P	5	51	2	3	41	7	8	10
Porifera	1	*Erylus discophorus* (Schmidt)*	x										
	2	*Geodia cydonium* (Jameson)*	x										
	3	*Cliona celata* Grant*	x										
	4	*Cliona viridis* Schmidt*	x	x									
	5	*Pione vastifica* (Hancock)*	x										
	6	*Suberites carnosus* (Johnston)	x	x		x			x				
	7	*Tethya citrina* Sarà & Melone*	x	x									
	8	*Clathria (Microciona) atrasanguinea* (Bowerbank)*								x			
	9	*Phorbas plumosus* (Montagu)			x				x				
	10	*Myxilla (Myxilla) rosacea* (Lieberkühn)		x					x				
	11	*Tedania (Tedania) anhelans* (Lieberkühn)	xxx	xxx	xxx	xx	xxx	xxx	xxx	xxx	x		
	12	*Mycale (Aegogropila) contarenii* (Martens)			x	x	xxx	x	xxx	x	x		
	13	*Halichondria bowerbanki* Burton	x	x	x	xx	x	x		x	xx	x	
	14	*Hymeniacidon perlevis* (Montagu)		xx	xx	xxx	xxx	xxx	xx	xx	xxx		
	15	*Haliclona (Reniera) stirpescens* Topsent				x	x		x	x			
	16	*Haliclona (Reniera) palmata* (Ellis & Solander)	x		x	xx	xx	xx	x	xx	x		
	17	*Ircinia variabilis* (Schmidt)*	x										
	18	*Sarcotragus spinosulus* Schmidt*	x	x									
	19	*Dysidea avara* (Schmidt)	x										
	20	*Dysidea tupha* (Martens)	x	xx									
Bryozoa	1	*Victorella* sp.										xxx	xxxx
	2	*Amathia lendigera* (Linnaeus)			xx			xxx					
	3	*Bowerbankia gracillima* (Hincks)		xx					x				
	4	*Buskia socialis* Hincks							xx	xxx			
	5	*Aetea truncata* (Landsborough)*						x					
	6	*Scruparia ambigua* (D'Orbigny)		x									
	7	*Conopeum seurati* (Canu)							x		xx	xx	x
	8	*Electra monostachys* (Busk)							x				
	9	*Electra* sp.*		x									
	10	*Scrupocellaria bertholletii* (Audouin & Savigny)			xxx			xx					
	11	*Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi	xxx	x	x	xxx	xx	xx	x	xx	xxxx		
	12	*Bugula flabellata* (Thompson in Gray)*						x					
	13	*Bugula plumosa* (Pallas)	x						xxx				
	14	*Cryptosula pallasiana* (Moll)		xxx	xxx			xxx	x				
	15	*Schizoporella errata* (Waters)	xxx	xxxx	xxx			xxxx	x				
	16	*Schizoporella unicornis* (Johnston in Wood)								xxx			
	17	*Microporella* sp.*						x					
	18	*Crisia fistulosa* Heller*			x								
		Porifera	14	9	6	7	6	5	8	7	5	1	0
		Bryozoa	3	6	6	1	1	8	8	3	2	2	2

encrusting bryozoans: the anascan *Conopeum seurati* as well as the ascophorans *Cryptosula pallasiana* and *Schizoporella errata*, the latter two being the dominant species in some stations near the Lido Mouth.

The comparison of the 2001 samples with former data (Occhipinti-Ambrogi 1985, 1991, 2000b) showed important variations in the bryozoan community composition (Table III): the Indo-Pacific invasive *T. inopinata* replaced the native *Bugula neritina*, *Bugula stolonifera* and *Scrupocellaria bertholletii* in the role of dominant species (Occhipinti-Ambrogi 2000a). Moreover, 5 out of the 18 bryozoan species (*Aetea truncata*, *Bugula flabellata*, *Crisia fistulosa*, *Electra* sp., *Microporella* sp.) had not been reported since 1978 in the northern basin and in the whole Venice Lagoon: they are marine organisms that can occasionally be found in lagoon environments (Winston 1977).

The cluster analysis recognized three main groups of stations (Figure 3): (i) stations 8 and 10, close to the Dese River inlet, where sponges and bryozoans were represented by a few typically mesohaline and oligohaline species (*H. perlevis, H. bowerbanki, C. seurati* and *Victorella* sp.); (ii) stations 7, 5, 51, 41, P, 2, and 3, located in inner sectors of the lagoon with good seawater influx, which were mainly inhabited by species tolerant of moderate desalination (*T. anhelans, M. contarenii, H. palmata, Buskia socialis*); (iii) stations 45 and 46, located near the Lido Mouth, characterized by a strong marine influence (Figure 4) and by marine species, which are commonly found in lagoon environments with high sea-water exchange (*Geodia cydonium, Tethya citrina, C. pallasiana, S. errata*), together with some euryecious species (*Ircinia variabilis*, *Sarcotragus spinosulus*, *T. inopinata*).

Discussion

Our observations confirmed sponges and bryozoans as two of the most representative phyla with respect to number of species and percentage cover on the hard bottoms of the Venice Lagoon together with cnidarians, serpulid polychaetes and ascidians (Morri 1981; Sconfietti & Marino 1989). They constituted large and thick multilayered assemblages, very unusual for the Mediterranean basin.

Among sponges, the assemblage was characterized by species widely known in the Mediterranean area, already reported for confined environments. The highest cover values were due to the large size of some species (*T. anhelans* and *M. contarenii*), or the great number of small specimens of *H. perlevis*. Gigantism was unknown in *T. anhelans* and *M. contarenii*, which are very common in confined Mediterranean environments, but always in the form of small sized encrusting or cushion shaped specimens (Corriero 1990). The ability to survive long periods of emersion observed for *H. perlevis* in the Venice Lagoon, already reported by Sarà (1960), has been observed in other Mediterranean confined environments, where this species lives partially sunk in the sandy bottom at the tidal level, and in submerged caves (Corriero 1990; Corriero, personal observations). The ability to survive long periods of emersion, well known for extra-Mediterranean sponges subjected to high tidal excursions (Amano 1988; Steindler et al. 2002; Tanaka 2002), is unusual in the western Mediterranean where *H. perlevis* is probably the only demosponge possessing this capacity. In the Venice Lagoon, this capacity is possibly linked to the high tidal range, and it allows the sponge to colonize environments where there is no competition with other species of Porifera, so explaining its high cover.

T. anhelans and *H. perlevis*, together with *H. palmata* and *H. bowerbanki*, also showed the widest distribution throughout the northern basin of the Venice Lagoon. All occurring in the mesohaline zone of the lagoon, *T. anhelans* and *H. palmata* approached the lagoon mouth, while *H. perlevis* and *H. bowerbanki* extended to the river inlet.

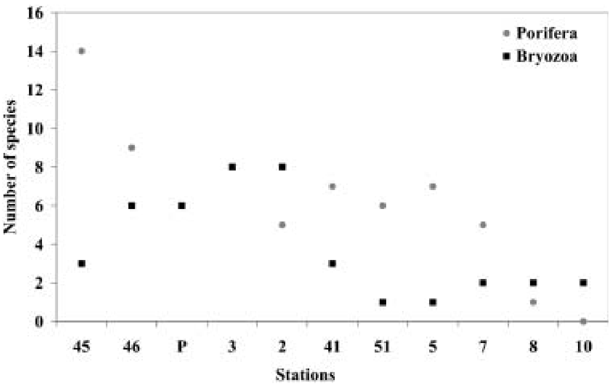

Figure 2. Venice Lagoon: number of species recorded in each sampling station.

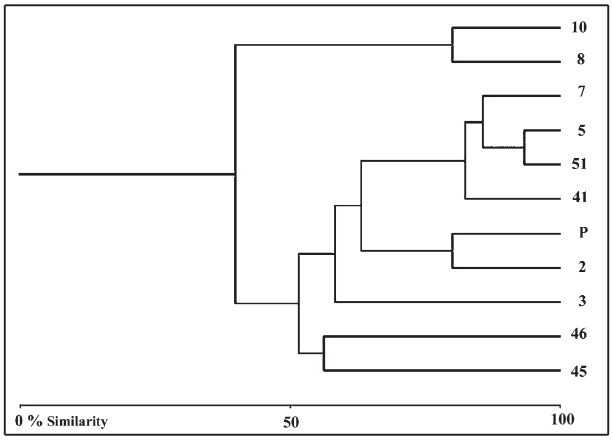

Figure 3. Venice Lagoon: Bray–Curtis Cluster Analysis (single linkage) between the sampling stations. Numbers refer to sampling stations as in Figure 1.

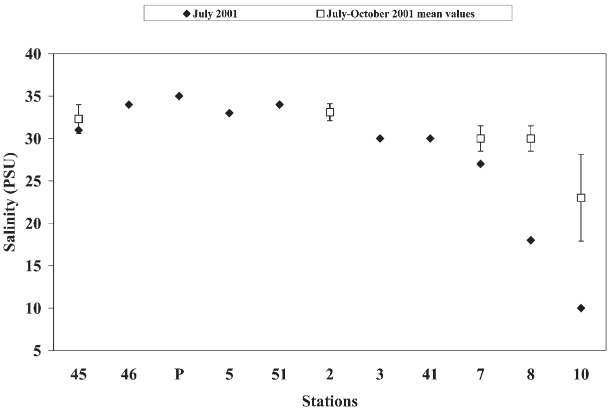

Figure 4. Venice Lagoon: salinity values measured in the sampling stations during the present study (July 2001) and mean values (±SD) for the four months July–October 2001 (Rismondo, personal communication). Stations are ordered according to the salinity gradient.

Table II. Venice Lagoon: species of demosponges recorded from 1955 to 2001 (1955, Sarà 1960; 1985, Sconfietti & Marino 1989; 2001, present study).

		1955	1985	2001
1	*Stelletta grubii* Schmidt	x		
2	*Stelletta stellata* Topsent	x		
3	*Erylus discophorus* (Schmidt)			x
4	*Geodia cydonium* (Jameson)			x
5	*Cliona celata* Grant			x
6	*Cliona viridis* (Schmidt)			x
7	*Pione vastifica* (Hancock)			x
8	*Suberites carnosus* (Johnston)	x	x	x
9	*Tethya citrina* Sarà & Melone			x
10	*Clathria (Microciona) atrasanguinea* (Bowerbank)			x
11	*Phorbas plumosus* (Montagu)	x		x
12	*Myxilla (Myxilla) rosacea* (Lieberkühn)	x		x
13	*Tedania (Tedania) anhelans* (Lieberkühn)	x	x	x
14	*Mycale (Aegogropila) contarenii* (Martens)	x		x
15	*Halichondria bowerbanki* Burton	x	x	x
16	*Hymeniacidon perlevis* (Montagu)	x	x	x
17	*Haliclona (Gellius) angulatus* (Bowerbank)	x		
18	*Haliclona (Reniera) palmata* (Ellis & Solander)	x		x
19	*Haliclona (Reniera) stirpescens* (Topsent)	x		x
20	*Ircinia variabilis* (Schmidt)			x
21	*Sarcotragus spinosulus* Schmidt			x
22	*Dysidea avara* (Schmidt)	x		x
23	*Dysidea fragilis* (Montagu)	x		x
		14	4	20

According to salinity measurements (Figure 4), the mean salinity values close to 17 PSU could constitute the lowest distributional limit for such demosponges, though they seem to tolerate periodic greater reductions in this parameter. An annual mean salinity value lower than 15 PSU has also been observed to limit the distribution of *Halichondria panicea* (Pallas 1766) in Lesina Lake (Apulian coast, southern Adriatic Sea) (Nonnis Marzano et al. 2003a).

The distribution of bryozoans is also known to depend on the salinity gradient, with cyclostomes and ascophoran cheilostomes being least tolerant, and anascan cheilostomes and ctenostomes most tolerant of reduced salinity (Winston 1977). Cyclostomes and ascophorans cannot perform any osmotic regulation, due to their rigidly calcified zooid walls: they were in fact very scarce in our samples, except for *Schizoporella errata*, *Schizoporella unicornis*, and *Cryptosula pallasiana*, that covered vast portions of the sampled piles in stations with marine-like salinity values. This can be explained by the presence of *pseudopores* in their calcified *ascum* (Ryland 1970), that allow small volume changes and therefore lead to colonisation of lagoon environments. A more efficient osmotic regulation due to the variation of the tissue volume is possible for some anascans such as *T. inopinata* and *C. seurati* and especially for ctenostomes such as *Victorella* sp., whose zooid walls are uncalcified. *T. inopinata* showed the widest distribution in the northern Venice Lagoon, whereas *C. seurati* and *Victorella* sp. were the only species able to colonize the stations with lowest salinity, 8 and 10.

The species richness of the considered taxocoenoses increased where salinity approached marine values (Figure 4), in agreement with what has been observed for the whole macrobenthos from other brackish-water systems (Gonzáles-Oreja & Saiz-Salinas 1998; Ysebaert & Herman 2002).

In general, a large number of the demosponge species, encompassing those that showed the highest covering values in this study, has been nearly constant over the last five decades. Most of the differences with respect to the 1955 list reported by Sarà (1960) are due to the occurrence, in the present study, of several not previously recorded species. Most of them (*Suberites carnosus*, *G. cydonium*, *T. citrina*, *S. spinosulus*, and *I. variabilis*) were localized near the mouth of the lagoon or strictly linked to the presence of carbonatic primary substrates (i.e. boring species), and their occurrence therefore reflected the different distribution of the sampling stations together with the more accurate sampling methodologies utilized here. However, the hypothesis of ingression of new species due to marinization phenomena involving the Venice Lagoon cannot be excluded.

Table III. Venice Lagoon: species of Bryozoa recorded from 1978 to 2001 (1978/83, Occhipinti-Ambrogi 1985; 1988/89, Occhipinti-Ambrogi 1991; 1993/94 and 1996/97, Occhipinti-Ambrogi 2000b; 2001, present study).

		1978/83	1988/89	1993/94	1996/97	2001
1	*Aetea anguina* (Linnaeus)		x		x	
2	*Aetea truncata* (Landsborough)					x
3	*Amathia lendigera* (Linnaeus)	x				x
4	*Barentsia gracilis* (M. Sars)			x	x	
5	*Bowerbankia gracilis* (Leidy)	x	x	x	x	
6	*Bowerbankia gracillima* (Hincks)			x	x	x
7	*Bowerbankia imbricata* (Adams)	x	x			
8	*Bugula flabellata* (Thompson in Gray)					x
9	*Bugula fulva* Ryland	x				
10	*Bugula neritina* (Linnaeus)	x	x	x	x	
11	*Bugula plumosa* (Pallas)	x	x			x
12	*Bugula simplex* Hincks	x	x			
13	*Bugula stolonifera* Ryland	x	x	x	x	
14	*Buskia socialis* Hincks	x	x	x	x	x
15	*Celleporella carolinensis* Ryland			x	x	
16	*Conopeum seurati* (Canu)	x	x	x	x	x
17	*Crisia fistulosa* Heller					x
18	*Cryptosula pallasiana* (Moll)	x	x	x	x	x
19	*Electra monostachys* (Busk)	x	x			x
20	*Electra* sp.					x
21	*Hippopodinella kirchenpaueri* (Heller)	x				
22	*Microporella* sp.					x
23	*Nolella gigantea* (Busk)	x	x	x	x	
24	*Notoplites* sp.	x				
25	*Pedicellina nutans* Dalyell				x	
26	*Schizoporella errata* (Waters)			x	x	x
27	*Schizoporella unicornis* (Johnston in Wood)	x		x	x	x
28	*Scruparia ambigua* (D'Orbigny)		x	x		x
29	*Scruparia chelata* (Linnaeus)		x		x	
30	*Scrupocellaria bertholletii* (Audouin & Savigny)	x	x			x
31	*Scrupocellaria reptans* (Linnaeus)	x	x			
32	*Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi	x	x	x	x	x
33	*Victorella* sp.					x
34	*Victorella pavida* Saville Kent		x	x	x	
35	*Zoobotryon verticillatum* Delle Chjaie			x	x	
		19	18	16	18	18

The present distribution of bryozoans in the northern basin, if compared to that observed in the past (Occhipinti-Ambrogi 1980), showed a less marked zonation of the species along the salinity gradient. The differences between the community directly influenced by the sea (dominated by *C. pallasiana*) and the more confined one (dominated by *C. seurati*) were made less evident because of the nearly constant presence of *T. inopinata*. In particular, *C. pallasiana* still dominated in the stations near the Lido mouth, but *C. seurati* had significantly reduced its importance in characterizing the central and inner part of the gradient.

In conclusion, the species composition of Porifera seems to have remained substantially stable with the passing of time, whereas the bryozoan taxocoenosis has undergone important changes. Such differences may be explained by the larger movement ability of bryozoans in comparison with sponges: adult bryozoans can be transported as fouling on ships' hulls (De Blauwe & Faasse 2001; Lewis et al. 2005), marine debris (Barnes 2002) and inside sea chests (Coutts et al. 2003). Some anascans with shelled, planktonic larvae (cyphonautes), able to feed and grow during several weeks or months (Ryland & Hayward 1977), can be transported also at juvenile stage. On the contrary, sponges hardly ever colonize floating objects and their dispersal ability is low due to the shortness of their larval life (Maldonado 2006).

Bryozoan taxocoenosis in the last decades has been subject to invasion by allochthonous species that have altered the community equilibrium (Occhipinti-Ambrogi 2000a) and also to the appearance of new marine species. Despite only being represented by relatively small colonies, their presence can be interpreted as one of the results of an ongoing marinization process of the Venice Lagoon, also suggested by other authors (Day et al. 1999; Carbognin & Tosi 2002; Sconfietti et al. 2003). The invasion process, in addition to the increased marine characteristics of the Venice ecosystem, might have caused unfavourable conditions for some native species, typical of lagoon environments, that have been progressively replaced by opportunistic marine species.

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