

COMMUNITY VERSUS BIOCOENOSIS IN MULTIVARIATE ANALYSIS OF BENTHIC MOLLUSCAN THANATOCOENOSSES

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Riassunto. Nell'ecologia del benthos, le comunità e le biocenosi sono unità descrittive non perfettamente corrispondenti. Benché lo schema concettuale basato sulle comunità, originariamente definite con un approccio statistico quantitativo, appaia più adeguato ad inquadrare i risultati di un trattamento statistico di dati di tanatocenosi, per il benthos mediterraneo questo schema appare un'eccessiva semplificazione delle reali unità ecologiche. Al contrario, la bionomia bentonica con le biocenosi, identificate da un gruppo di specie fedeli al biotopo (indipendentemente dalla loro abbondanza) deriva da un approccio qualitativo che ha riscontrato maggior successo tra i ricercatori dell'area mediterranea. Un gruppo di dodici tanatocenosi tirreniche è stato elaborato con entrambi gli approcci per mettere in luce una strategia pratica di analisi statistica multivariata dei modelli di distribuzione in paleoecologia del benthos, che combini i vantaggi degli approcci qualitativo e quantitativo. Nel caso in cui si debba trattare statisticamente una matrice di grandi dimensioni di dati di tanatocenosi bentoniche, si raccomanda di usare un approccio qualitativo per una drastica riduzione della matrice di partenza, trattenendo solo le specie con un preciso significato bionomico, prima di procedere all'analisi multivariata quantitativa (classificazione, ordinamento, analisi della similarità e dissimilarità). La procedura appare la più adeguata all'identificazione di gruppi "naturali" di biotopi, in quanto il risultato non è confuso dalla dominanza delle specie più comuni ed ubiquiste.

Abstract. Community and biocoenosis as descriptive units for benthic ecology are not perfectly interchangeable. Although the conceptual framework based on communities, originally defined by a statistical quantitative approach, appears to be the most suitable in the statistical treatment of thanatocoenoses data, this framework appears to oversimplify the picture of the most important ecological units in the Mediterranean benthos. On the contrary, the benthic bionomy with the biocoenoses, identified by a group of characteristic species (disregarding their abundance) derives from a qualitative approach which has been more successfully adopted for the research in the Mediterranean area. A group of twelve thanatocoenoses from the Tyrrhenian Sea has been treated with both approaches with the aim to identify a practical strategy for analysing multispecies distribution patterns in benthic paleoecology, trying to combine the advantages of both quantitative and qualitative approaches. When dealing with large-sized data matrices of benthic thanatocoenoses, it is recommended to use a qualitative approach for data reduction, on the basis of their significance in benthic bionomy, prior to perform the quantitative multi-

variate analysis (classification, ordination, similarity and dissimilarity analysis). This procedure appears to be the most suitable for the identification of "natural" grouping of biotopes, since the results are not obscured by the diffuse occurrence of the most common and ubiquitous species.

Introduction

The use of more or less conservative associations among several organisms as descriptive units for a considered area is widely accepted as a major tool in benthic ecology and palaeoecology. However, different conceptual approaches produced several frameworks of classification, which are only partially compatible. Among them, those based on the concepts of *biocoenosis* and *community* have been widely applied in the biological literature.

At the end of XIX century Karl Möbius (1877) introduced the new term "biocoenosis" to include all individuals (plants or animals) living in the same area, being closely connected to the mean environmental conditions of their habitat and by reciprocal interspecific functional relations. The concept of *biocoenosis* is strictly associated to that of *biotope*, defined as the physical space (surface or volume) where the dominant conditions (biological and abiological environmental variables) are homogeneous. The biocoenoses have been widely used to describe the distribution of benthic organisms, in relation to the environmental variables, within the framework of the *benthic bionomy*, especially developed in the Mediterranean by the French scientists of the Station Marine d'Endoume (among others, Pérès & Picard 1964).

The delimitation of the biocoenoses is carried out by identifying a list of the characteristic species, classified in function of their fidelity to the biotope. For example, the *exclusive characteristic* (excl) species are those

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E119	Am15E	Bel7E	MC22	E115
<i>Abra alba</i>				1	4		22	1	9	11		26
<i>Abra nitida</i>							143		11			
<i>Abra ovata</i>	1034	542	205									
<i>Abra prismatica</i>							6	1	1	1	2	240
<i>Acanthocardia echinata</i>												3
<i>Acanthocardia paucicostata</i>							37		9	8		
<i>Acanthocardia tuberculata</i>							3		3			
<i>Aciniopsis hirta</i>											12	
<i>Aciniopsis cancellata</i>				139	131	6		39				2
<i>Aclis minor</i>												1
<i>Acmaea virginea</i>				3	2	1		17			18	
<i>Acteon tornatilis</i>								1				5
<i>Actonia testae</i>								2				
<i>Aequipecten commutatus</i>							9		6	10		
<i>Aequipecten opercularis</i>						7		10	17			207
<i>Alvania consociella</i>											21	
<i>Alvania discors</i>	3	2		117	228	10		66			342	4
<i>Alvania lineata</i>				24	30							
<i>Alvinia jeffreysi</i>												2
<i>Anadara diluvii</i>												12
<i>Anodontia fragilis</i>						4						
<i>Anomia ephippium</i>				3	2		24	5	79	15		26
<i>Apicularia similis</i>				6	22							
<i>Aporrhais pespelecani</i>						2	12	3		1		28
<i>Arca noae</i>				3	12	1		11				
<i>Arca tetragona</i>						1		20			5	18
<i>Arsenia punctura</i>											1	1
<i>Astarte fusca</i>						14		1				2
<i>Astarte sulcata</i>												2
<i>Astraea rugosa</i>				3	4	82		122			13	5
<i>Atys brocchii</i>	2	14	1									
<i>Axinulus croulinensis</i>											75	
<i>Azorinus chamasolen</i>									2			4
<i>Barbatia barbata</i>				26	14	1					3	
<i>Barfeeia rubra</i>				14	43							
<i>Bathycarca grenophia</i>												22

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E119	Am15E	Bel7E	MC22	E115
<i>Bela brachystoma</i>							2		23	6		57
<i>Bela nebula</i>							2	1				2
<i>Bela turgida</i>									4	3		
<i>Bellaspira rigida</i>												13
<i>Bellaspira septangularis</i>				2	1							
<i>Bittium gr. reticulatum</i>	1839	4954	450	1143	2190	584		4367	4		2203	356
<i>Bittium lacteum</i>				10								
<i>Bolinus brandaris</i>								1		1		
<i>Bornia sebetia</i>	96	114	42									
<i>Bulla striata</i>				16								
<i>Calliostoma conulus</i>				10	7	8						
<i>Calliostoma laugierii</i>				23	20							
<i>Calliostoma wiseri</i>							1					
<i>Calliostoma zizyphinum</i>						1		6				
<i>Callista chione</i>							1		1	1		
<i>Calyptrea chinensis</i>				9	8	8	1	7	4	2		227
<i>Cantharus dorbignyi</i>				3	11							
<i>Capulus ungaricus</i>					1			2				6
<i>Cardiomya costellata</i>												3
<i>Cardiomya striolata</i>												8
<i>Cardita calyculata</i>				14	15							
<i>Cerastoderma glaucum</i>	3801	5404	549									
<i>Cerithidium submamillatum</i>							9		5			
<i>Cerithiopsis fayalensis</i>				2								
<i>Cerithiopsis scalaris</i>												2
<i>Cerithiopsis tiara</i>												1
<i>Cerithiopsis tubercularis</i>				12								3
<i>Cerithium vulgatum</i>	2346	7780	2170	10	21			150			21	20
<i>Chama gryphoides</i>				17	19	2						
<i>Chamelea gallina</i>			8									10
<i>Chauvetia minima</i>				32	51							
<i>Chauvetia vulpecula</i>								1				
<i>Chlamys flexuosa</i>				1		2			1	2		2
<i>Chlamys glabra</i>				3	2							
<i>Chlamys multistriata</i>				4	3	1		2			1	5

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E19	Am15E	Bel7E	MC22	E15
<i>Chlamys varia</i>				4	3			3			15	19
<i>Chrysallida doliolum</i>				1		1						
<i>Chrysallida excavata</i>								1				
<i>Clanculus corallinus</i>		3		4	4			3			4	
<i>Clanculus cruciatus</i>				47	64							
<i>Clathromangelia quadrillum</i>											1	
<i>Clausinella brogniarti</i>						5		3			4	9
<i>Columbella rustica</i>				1								
<i>Columbelopsis minor</i>								7			11	2
<i>Comarmondia gracilis</i>						2		4	1	1	1	23
<i>Conus ventricosus</i>	7	2		16	44							
<i>Coralliophila lamellosa</i>								3				
<i>Corbula gibba</i>					2	19	49	223	110	50	1	881
<i>Crepidula unguiformis</i>				6	5	1						
<i>Ctena decussata</i>				26	22	9		1			6	
<i>Cultellus tenuis</i>							53		11			
<i>Cuspidaria cuspidata</i>							9		1	1		3
<i>Cuspidaria rostrata</i>									1			
<i>Cyclope neritea</i>	261	1824	57									2
<i>Cylichna alba</i>												10
<i>Cylichna crossei</i>							1					
<i>Cylichna cylindracea</i>									2		4	1
<i>Cylichnina subcylindrica</i>						1		2				
<i>Dentalium dentalis</i>						1						38
<i>Dentalium inaequicostatum</i>							7		4	4		
<i>Digitaria digitata</i>										2		
<i>Diodora gibberula</i>		1		10	5							
<i>Diodora graeca</i>				16	7						1	2
<i>Diodora italica</i>												2
<i>Diplodonta apicalis</i>				3	3							
<i>Diplodonta rotundata</i>									1		3	1
<i>Divaricella divaricata</i>					3	75	7	2	9		9	83
<i>Donax trunculus</i>									1			
<i>Donax variegatus</i>				3	10							
<i>Donax venustus</i>									2	1		2

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E19	Am15E	Bel7E	MC22	E15
<i>Dosinia exoleta</i>		8		4	13							
<i>Emarginula adriatica</i>											2	
<i>Emarginula elongata</i>	4	6						2				1
<i>Emarginula huzardii</i>				11	6			9				
<i>Emarginula punctulum</i>											9	
<i>Emarginula rosea</i>								1				5
<i>Emarginula tenera</i>											4	
<i>Ensis ensis</i>							2		1			
<i>Ensis siliqua minor</i>							1					
<i>Epilepton clarkiae</i>											4	
<i>Epitonium aculeatum</i>						1			1			
<i>Epitonium clathratulum</i>											1	
<i>Epitonium commune</i>						1						6
<i>Epitonium tiberii</i>											3	
<i>Epitonium turtoni</i>											1	
<i>Eulimella turris</i>							1		2			
<i>Fossarus ambiguus</i>				1								
<i>Fusinus giglioli</i>								4				
<i>Fusinus pulchellus</i>					2							
<i>Fusinus rostratus</i>							1					3
<i>Fusinus rudis</i>								3			20	5
<i>Fustiarina rubescens</i>						1						9
<i>Galeodina carinata</i>				2								
<i>Galeomma turtoni</i>					3							
<i>Gibberula caelata</i>								1				
<i>Gibberula miliaria</i>				40	143			2			31	
<i>Gibberula philippii</i>	12	12	3									
<i>Gibberulina clandestina</i>	5	7	2	3	13						71	
<i>Gibberulina occulta</i>						9		7			4	17
<i>Gibbula adansoni</i>				2	1							
<i>Gibbula ardens</i>				4	6							
<i>Gibbula fanulum</i>				1		1		42				1
<i>Gibbula guttadauri</i>				5	2							
<i>Gibbula magus</i>						6		13				4
<i>Gibbula rarilineata</i>	13	17	23		4							

Station	ST12	ST10	ST13	BarA	BarB	EI70	Sca2E	EI19	Am15E	Bel7E	MC22	EI15
<i>Gibbula turbinoides</i>				10	15							
<i>Gibbula varia</i>				21	35	1						
<i>Glans aculeata</i>												97
<i>Glans trapezia</i>				29	40	52						
<i>Glycymeris glycymeris</i>										1		
<i>Glycymeris insubrica</i>							1		1			4
<i>Gonilia calliglypta</i>						13		2				3
<i>Goniostoma auriscalpium</i>	5			34	62							
<i>Gouldia minima</i>				17	38	70	1	60			96	87
<i>Hadriania craticuloides</i>				7	3	1		1		1		
<i>Haliotis tuberculata</i>												
<i>Haminoea cymoellum</i>		1										
<i>Haminoea hydatis</i>				4	4			1				9
<i>Hiatella rugosa</i>				6	10			3	4	1	4	43
<i>Hinia incrassata</i>				99	205					1		
<i>Hinia limata</i>												1
<i>Hinia pygmaea</i>									15			
<i>Homalopoma sanguineum</i>				22	42	20		17			9	
<i>Hyala vitrea</i>							3		4			
<i>Hyalina mitrella</i>											2	
<i>Hyalopecten similis</i>							8	3	3			108
<i>Hydrobia stagnalis</i>	66880	61952	17872									
<i>Irus irus</i>		43		3								
<i>Jujubinus exasperatus</i>				114	255	136		152			26	15
<i>Jujubinus gravinae</i>				18	25							
<i>Jujubinus miliaris</i>												11
<i>Jujubinus montagui</i>						6		33				5
<i>Jujubinus striatus</i>	4	7		2	7							
<i>Kellia suborbicularis</i>											2	
<i>Kelliella abyssicola</i>							1					
<i>Laevicardium crassum</i>						6		2				5
<i>Laevicardium oblongum</i>				1	1				1			
<i>Lepetella laterocompressa</i>				33				4	1		2	
<i>Lepton nitidum</i>											1	13
<i>Lepton solidolum</i>								1				11

Station	ST12	ST10	ST13	BarA	BarB	EI70	Sca2E	EI19	Am15E	Bel7E	MC22	EI15
<i>Lima hians</i>				1	7							
<i>Lima inflata</i>				3								
<i>Lima lima</i>				9	6							
<i>Limatula gwyni</i>							1					4
<i>Limatula subauriculata</i>											1	5
<i>Limea loscombi</i>						1				1		
<i>Lissopecten hyalinus</i>				15	7	2		1	1			
<i>Littorina neritoides</i>				64	123				1			
<i>Loripes lacteus</i>	3390	4447	524		1				1			
<i>Lucinoma boreale</i>						3						4
<i>Lunatia catena</i>												30
<i>Lunatia macilenta</i>							8		5	5		
<i>Lunatia pulchella</i>				2		24		10			7	70
<i>Lyonsia norvegica</i>							3		2			
<i>Mactra stultorum</i>				1								
<i>Mamilloretusa mamillata</i>					1							
<i>Mangelia attenuata</i>									8	2	3	14
<i>Mangelia paciniana</i>												3
<i>Mangelia rugulosa</i>				19	9	14	8	7	2	7		4
<i>Mangelia scabrada</i>								5				25
<i>Mangelia smithi</i>						8					1	13
<i>Mangelia stossiciana</i>				3	7							
<i>Mangiliella taeniata</i>				4	3				1			
<i>Melanella polita</i>								2	1		3	
<i>Metaxia metaxae</i>				7	15							
<i>Mitra cornicula</i>				1								
<i>Mitrolumna olivoidea</i>					2			11			8	
<i>Modiolula phaseolina</i>							3	1			7	
<i>Modiolus barbatus</i>				10	16			1				2
<i>Monodonta mutabilis</i>	11	10	152									
<i>Montacuta substriata</i>								3				3
<i>Muricopsis aradasi</i>								1			4	2
<i>Muricopsis cristata</i>				27	28	3						
<i>Musculus costulatus</i>					4							
<i>Musculus discors</i>								2				5

Station	ST12	ST10	ST13	BarA	BarB	EI70	Sca2E	EI19	Am15E	Bel7E	MC22	EI15	
<i>Musculus subpictus</i>						1							
<i>Myrtea spinifera</i>							5	8	5	3	3	10	1047
<i>Mysella bidentata</i>										6		3	4
<i>Mytilaster minimus</i>								1					
<i>Nassarius comiculis</i>				3									
<i>Naticarius punctatus</i>								2		1	3		
<i>Neverita josephinia</i>		13	1										
<i>Nucula nucleus</i>				10	9			52	29	16	44	2	98
<i>Nucula sulcata</i>						54		1			13		234
<i>Nuculana fragilis</i>								2					1195
<i>Nuculana pella</i>						65	4			4	2		187
<i>Ocenebrina aciculata</i>				4	7							23	
<i>Odostomia acuta</i>												2	
<i>Odostomia conoidea</i>				3	4	10	3	1	7	1			12
<i>Odostomia turrita</i>							2						
<i>Opalia hellenica</i>						2							
<i>Ostrea edulis</i>													9
<i>Ovatella myosotis</i>		124	1										
<i>Palliolium incomparabile</i>											3		4
<i>Paludinella littorina</i>				1									
<i>Pandora inaequivalvis</i>							1						
<i>Pandora obtusa</i>							26			5			
<i>Pandora pinna</i>									3	2			
<i>Parvicardium minimum</i>						2	20		26	6	48	3490	
<i>Parvicardium ovale</i>							10	1	3	1	14		
<i>Parvicardium roseum</i>						1		7					
<i>Patella caerulea</i>				62	13								249
<i>Pecten jacobaeus</i>									2				1
<i>Peplum clavatum</i>													11
<i>Petricola lajonkairii</i>				3	7								1
<i>Philine aperta</i>								1					
<i>Philine scabra</i>								1					7
<i>Phyllonotus trunculus</i>	1												
<i>Pisania striata</i>					19								
<i>Pitar rudis</i>						20	4	5	8	3			29

Station	ST12	ST10	ST13	BarA	BarB	EI70	Sca2E	EI19	Am15E	Bel7E	MC22	EI15
<i>Plagiocardium papillosum</i>				64	89	46		48	3	1		538
<i>Pododesmus patelliformis</i>												4
<i>Pododesmus squamula</i>								2	1		18	174
<i>Propilidium scabrosum</i>								1				
<i>Psammobia costulata</i>				5	5						1	56
<i>Psammobia depressa</i>				3								
<i>Psammobia fervensis</i>						3						
<i>Pseudactaeon luteofasciatum</i>									1	1		
<i>Pseudochama gryphina</i>				1								
<i>Puncturella noachina</i>								3			7	19
<i>Pyrene scripta</i>				1	1			14				
<i>Raphitoma concinna</i>											4	
<i>Raphitoma echinata</i>				3				2		1	3	5
<i>Raphitoma histrix</i>								5			2	10
<i>Raphitoma leufroyi</i>				4	5							
<i>Raphitoma linearis</i>				19	27	2		9			14	46
<i>Raphitoma philberti</i>				1	6							
<i>Raphitoma purpurea</i>				4	5			4				
<i>Retusa truncatula</i>	6	43									1	
<i>Ringicula conformis</i>												5
<i>Rissoa variabilis</i>				36	67							
<i>Rissoa ventricosa</i>	338	32	92	63	81							
<i>Rissoa violacea</i>				10	33			1			14	
<i>Rissoina bruguieri</i>				56	111	3						
<i>Scaphander gracilis</i>												1
<i>Scaphander lignarius</i>						2						
<i>Setia semistriata</i>				1								
<i>Smaragdia viridis</i>				1	5	1			8			
<i>Solecurtus scopula</i>										1		
<i>Spisula subtruncata</i>						3		5	8	1		15
<i>Striarca lactea</i>				192	225	22		122			148	97
<i>Strombiformis bilineatus</i>											1	7
<i>Strombiformis glaber</i>						1		1				
<i>Tapes decussatus</i>	2	102	6			1						
<i>Tellina balaustina</i>				2	1							3

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E119	Am15E	Bel7E	MC22	E115
<i>Tellina crassa</i>						1					4	3
<i>Tellina distorta</i>							21		33	6		
<i>Tellina donacina</i>				20	21	21		5			4	24
<i>Tellina fabula</i>							2		4			
<i>Tellina pulchella</i>									1			35
<i>Tellina serrata</i>						2	2			1		50
<i>Teretia teres</i>												3
<i>Thracia convexa</i>							1					
<i>Thracia corbuloides</i>									1			
<i>Thracia distorta</i>				1			2					
<i>Thracia papyracea</i>				1	1							
<i>Thyasira alleni</i>							11		7			
<i>Thyasira flexuosa</i>							24		17			
<i>Thyasira granulosa</i>							20					
<i>Timoclea ovata</i>		13				44	17	53	13	2	67	2353
<i>Tricolia pullus</i>				156	237	123			1	10		2
<i>Tricolia speciosa</i>				53	75							
<i>Tricolia tenuis</i>	15	12									16	
<i>Trimusculus mamillaris</i>				1								
<i>Triphora perversa</i>				47	116	1		28			23	5
<i>Trophonopsis multilamellosa</i>								2				
<i>Trophonopsis muricata</i>							1	6				25
<i>Truncatella subcylindrica</i>	2	1574		9	9							
<i>Turboella dolium</i>				3	8	6		13			42	
<i>Turboella lavalei</i>												1
<i>Turboella lineolata</i>						5						
<i>Turbona cimex</i>	21	6	2	74	123						105	
<i>Turbona cimicoides</i>						50		248			27	5
<i>Turbona geryonia</i>				36	43							
<i>Turbona reticulata</i>						101		67				8
<i>Turbonilla acuta</i>						1						
<i>Turbonilla delicata</i>							1					
<i>Turbonilla lactea</i>					3	2						
<i>Turbonilla rufa</i>						9		3	1		2	1
<i>Turbonilla scalaris</i>				2	7							

Station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E119	Am15E	Bel7E	MC22	E115
<i>Turritella communis</i>				2	2	30	346	208	1284	2383		450
<i>Turritella turbona</i>											39	
<i>Venericardia antiquata</i>				5	5	6						
<i>Venerupis aurea</i>		84	3									7
<i>Venerupis lucens</i>				15	23							
<i>Venus casina</i>								2	81		5	
<i>Venus nux</i>									5			
<i>Venus verrucosa</i>				28	28	3			1			
<i>Vexillum ebenus</i>				1								
<i>Vexillum savignyi</i>								11				
<i>Vexillum tricolor</i>				12	45	3		3			2	
<i>Weinkauffia semistriata</i>							1				1	1
<i>Weinkauffia turgidula</i>								1				

Tab. 1a - Abundance of molluscan species in thanatocoenoses at the the twelve stations considered for the statistical analysis. Stations are ordered from left to right following the increasing depth. Species are listed in alphabetic order.

location	S.Teodoro	S.Teodoro	S.Teodoro	Baratti	Baratti	Elba	Calabria	Elba	Calabria	Calabria	Montecristo	Elba
station	ST12	ST10	ST13	BarA	BarB	E170	Sca2E	E119	Am15E	Bel7E	MC22	E115
sample volume	10 l	10 l	10 l	10 l	10 l	10 l	50 l	10 l	50 l	50 l	10 l	50 l
depth (m)	0,1	0,2	0,3	10	10	37	43	48	50	50	58	71
sampling	direct	direct	direct	direct	direct	grab	grab	grab	grab	grab	grab	grab

Tab. 1b - Summary of location, sample volume, depth, sampling device and abbreviation for the 12 stations. Stations are ordered following the increasing water-depth.

strictly localised at the stations of a given biotope, regardless of their abundance or dominance, while the *preferential characteristic* (pref) species are much more abundant in a given biotope compared with other biotopes. A biocoenosis can develop a *facies* when one or more species become dominant, leaving unchanged the overall qualitative composition of the biocoenosis. In the framework of the benthic vertical zonation, the biocoenoses are named on the basis of the main characteristics of the substrate, for example, the biocoenosis of well-sorted fine sands (SFBC from the French "Sable Fins Bien Calibrés"). This allows to trace the analogues of the modern Mediterranean SFBC both in space (such as outside the Mediterranean; Pérès 1982) and time (in the fossil record; Piazza & Robba 1998).

In the benthic bionomy the emphasis is mainly on the quality of the association among all living organisms and their environment, and not on quantity. In other words, the occurrence of few individuals of an exclusive characteristic species is more significant than a hundred specimens of an ubiquitous species. In an opposite approach, the concept and the name of each community as described by Petersen (1915, for example) is based on the quantitative assessment of the few dominant species in a given area, disregarding the role of less abundant species, even if characteristic of the environment. The latter approach has been more widely applied in the Atlantic.

Pérès (1982) tried to summarise and integrate the results achieved by the two opposite approaches (biocoenoses and communities) into a comprehensive publication where the term *assemblage* is used to include both, in a world-wide perspective.

Especially during the last 50 years, an increasing amount of data have been collected, aimed at a better understanding of the benthic ecology. However, the increasing diffusion and application of computer-based multivariate statistics has incremented the use of quantitative approaches on these data, discouraging any preliminary, time-consuming assumption or qualitative elaboration on the species lists.

In a quantitative statistical approach, abundant and ubiquitous species result to be much more important in defining similarities between sites than characteristic, rare species do. Even if double square-root transformation of raw abundance data is often used to reduce the contribution of abundant, ubiquitous species (Field et al. 1982; Clarke et Green 1988; Warwick & al. 1990; Basso & Spezzaferri 2000), they remain on top scores in the analysis of similarity matrices, often leading to sites clustering and ordination based on poorly significant taxa. Databases are often very large and require data reduction, for several reasons: a) in any survey, there is a redundancy in the full species matrix; b) computer elaboration become excessively time-consuming and most statistical packages can deal with a limited number of

rows/columns in the matrix; c) since species abundance arrays are usually very sparse (the predominant entry being zero), it is suggested to attain multivariate normality of distribution by a transformation coupled with a substantial reduction in species considered, to the most abundant ones (Clarke & Green 1988).

Paleoecologists use fossil assemblages to reconstruct paleoenvironments. For a given time-slice, the comparison of fossil assemblages (or shell assemblages) from different sites through a multivariate statistical analysis can give a picture of the distribution of past benthic biotopes. For the Mediterranean Pleistocene/Holocene, the possibility to compare the fossil assemblage with the modern biocoenoses described by the benthic bionomy allows a very detailed reconstruction of the marine environment. However, the use of quantitative statistical methods, which highlight the contribution of abundant species, appears inappropriate and misleading within a qualitative conceptual framework like the benthic bionomy.

This paper is aimed to explore a practical strategy for analysing multispecies distribution patterns in benthic paleoecology, trying to combine the advantages of both quantitative and qualitative approaches.

Material and Methods

In order to allow their comparison, twelve stations (Tab. 1a-b) have been selected with the following criteria: a) located in the same geographic area (Tyrrhenian Sea); b) located on the continental shelf; c) samples having defined and comparable volumes and collected at a precise point (no dredging; Tab. 1); d) molluscan shells picked up from samples sieved on the same mesh-size (1 mm); e) available attribution of the biota to a specific benthic biocoenosis.

A raw matrix of abundance data of molluscan thanatocoenoses have been created from literature (Corcelli 1981, 1987; Giacobbe & Mondello 1994; Sculco 1992; Basso 1995; Fallini 1994). Molluscan nomenclature follows Bruschi et al. (1985).

Acronyms used in the text follows Pérès & Picard (1964) and are shown in Table 2.

Some univariate measures of diversity have been calculated (total number of species, total number of individuals, species richness (Margalef's d), Shannon diversity (H') and evenness (Pielou's J), using logarithms to the base e in the calculations throughout. The k -dominance curves (Platt et al. 1984) for species abundance have been calculated combining the stations with the highest similarity (>55% of Bray-Curtis similarity).

In the framework of a quantitative approach, a first hierarchical agglomerative clustering and non-metric MDS ordination have been performed on the full matrix (12 columns/stations and 329 rows/species) of double

Acronym	Meaning	
AP	Algues photophiles	Photophilic algae
C	Coralligène	Coralligenous
DC	Detritique Cotier	Coastal detritic
DE	Detritique Envasé	Muddy coastal detritic
HP	Herbier de Posidonia	Posidonia meadows (complex)
LEE	Lagunes eurythermes et euryhalines	Eurythermal and euryhaline lagoons
PE	Peuplement hétérogène	Heterogeneous assemblage
SFBC	Sables fins bien calibrés	Fine well-sorted sands
SGCF	Sables grossiers et fins graviers sous l'influence des courants de fond	Coarse sands and fine gravels under bottom currents
SVMC	Sables vaseux en mode calme	Muddy sands in sheltered areas
VTC	Vase terrigène cotière	Coastal muddy (terrigenous) bottom

Tab. 2 - Acronyms and corresponding full name of the biocoenoses described by Pérès & Picard (1964) and cited in the text. An English translation is given.

square root transformed abundance data. The non-metric multi-dimensional scaling ordination (MDS; Kruskal 1977) is a non-parametric method which uses the rank order of similarities between samples rather than their absolute values. The method has been tested to be statistically very robust and sensitive in community studies (Field & al. 1982; Warwick & Clarke 1991). Double square root transformation reduce the weighting of abundant species and when coupled with the Bray-Curtis similarity (B-C sim.) index, the obtained similarity coefficient is invariant to a scale change (e.g. the dimension of the sample; Field et al. 1982). Then the same statistical treatment has been performed after a series of data reductions of increasing severity: a) selecting only the 154 more important species on the basis of their

Pérès & Picard 1964; Picard 1965). After this first reduction (elaboration named "b154"), the matrix contained 12 stations x 154 species. For a further, more severe data reduction, only the species exclusive or preferential characteristic of biocoenoses have been retained (elaboration named "b80"; 80 species retained). After this series of reductions, classification and MDS ordination based on Bray-Curtis similarities have been performed as specified above.

The similarity analyses have been performed for the reduced data matrices, both in the quantitative and qualitative approach, in order to know the contribution of each species to the total similarity within a given group (indicator species, Field et al. 1982). For selected elaborations, also the breakdown of dissimilarity between different clusters have been considered, in order to identify the discriminant species. The package used for computer statistics is PRIMER v.4 (Plymouth Marine Laboratory).

Biocoenoses and thanatocoenoses at the considered stations

Columns St12, St10 and St13 in the data base (Tab. 1a) list the thanatocoenoses recognized at stations S12, S10 and S13a respectively, sampled in the S. Teodoro lagoon (Northeastern Sardinia), and more precisely in the Pescaia area, which is connected to the open sea (Tab. 1b). The molluscan thanatocoenosis was characterized by a mixture of paralic (biocoenosis LEE) and marine (biocoenosis SVMC) species (Corselli 1987).

The BarA and BarB columns correspond to stations A and B sampled in a current-swept channel close to a *Posidonia* meadow, in the Gulf of Baratti (Tuscany). They represent two mixed (only partially autochthonous) shell assemblages, since the living molluscan assemblage is characterised by current-related species (SGCF biocoenosis), while the shell assemblages show a mixture of autochthonous SGCF and DC species mixed with a majority of allochthonous species transported from by the neighbouring *Posidonia* meadow (AP, HP) and other soft bottom biocoenoses (SVMC, SFBC etc.; Corselli 1981).

Station	Species	Individuals	Richness	Shannon	Evenness
ST12	25	80098	2,13	0,738	0,229
ST10	32	89153	2,72	1,18	0,342
ST13	20	22163	1,9	0,805	0,269
BarA	123	3464	15	3,28	0,681
BarB	111	5644	12,7	2,99	0,634
EI70	84	1879	11	2,99	0,674
Sca2E	61	1024	8,66	2,74	0,667
EI19	102	6413	11,5	1,68	0,364
Am15E	76	1931	9,91	1,75	0,404
Bel7E	46	2624	5,72	0,579	0,151
MC22	87	3764	10,4	2,05	0,458
EI15	129	13575	13,5	2,82	0,58

Tab. 3 - Summary of total number of species, total number of individuals, species richness (Margalef's d), Shannon diversity (H') and evenness (Pielou's J) for the twelve stations listed in Table 1.

abundance and co-occurrence (this elaboration has been named "n154"); b) selecting only the species with at least 1% dominance at each station (elaboration named "p>1%"); c) selecting only the species with at least 3% dominance at each station (elaboration named "p>3%").

For the qualitative approach, the original list of 329 species has been reduced eliminating all species with a wide ecological distribution or without a specific significance in benthic bionomy (Ire. and sspr. respectively,

Biocoenosis	Species	QUANTITATIVE			QUALITATIVE	
		n154	p>1	p>3	b154	b80
	GASTROPODA					
AP excl	<i>Haliotis tuberculata</i> LAMARCK				Haliotube	Haliotube
Ire	<i>Emarginula adriatica</i> COSTA					
meso-infra	<i>Emarginula elongata</i> COSTA					
	<i>Emarginula huzardii</i> PAYRAUDEAU					
infra-circa	<i>Emarginula punctulum</i> MONTEROSATO in PIANI	Emarg huza				
DC C	<i>Emarginula rosea</i> (BELL)	Emarg punc			Emarg rose	
DC C	<i>Emarginula tenera</i> MONTEROSATO in LOCARD				Emarg tene	
infra-circa	<i>Puncturella noachina</i> (L.)					
pss	<i>Diodora gibberula</i> (LAMARCK)	Diodo gibb				
	<i>Diodora graeca</i> (L.)	Diodo grae			Diodo grae	
meso-infra	<i>Diodora italica</i> (DEFRANCE)					
AP DC C	<i>Acmaea virginea</i> (MULLER)	Acmae virg				
	<i>Patella caerulea</i> L.	Patel caer	Patel caer			
	<i>Propilidium scabrosum</i> JEFFREYS					
circa-bat	<i>Lepetella laterocompressa</i> (DE RAYNEVAL & PONZI)	Lepet late				
HP acc	<i>Jujubinus exasperatus</i> (PENNANT)	<i>Jujub exas</i>	<i>Jujub exas</i>	<i>Jujub exas</i>	<i>Jujub exas</i>	
	<i>Jujubinus gravinae</i> (MONTEROSATO)	<i>Jujub grav</i>				
pss	<i>Jujubinus miliaris</i> (BROCCHI)				Jujub mili	
	<i>Jujubinus montagui</i> (WOOD)	<i>Jujub mont</i>				
sspr	<i>Jujubinus striatus</i> (L.)					
	<i>Monodonta mutabilis</i> (PHILIPPI)	Monod muta				
	<i>Gibbula adansonii</i> (PAYRAUDEAU)					
AP HP	<i>Gibbula ardens</i> (VON SALIS)				Gibbu arde	
HP DC	<i>Gibbula fanulum</i> (GMELIN)	Gibbu fanu			Gibbu fanu	
sspr	<i>Gibbula guttadauri</i> (PHILIPPI)					
DC pref	<i>Gibbula magus</i> (L.)	Gibbu magu			Gibbu magu	<i>Gibbu magu</i>
	<i>Gibbula rarilineata</i> (MICHAUD)					
	<i>Gibbula turbinoides</i> (DESHAYES)	Gibbu turb				
	<i>Gibbula varia</i> (L.)	Gibbu vari				
sspr	<i>Calliostoma conulum</i> (L.)	Calma conu				
AP HP	<i>Calliostoma laugierii</i> (PAYRAUDEAU)	Calma laug			Calma laug	
	<i>Calliostoma wiseri</i> (CALCARA)					
DC	<i>Calliostoma zizyphinum</i> (L.)				Calma zizy	
HP C	<i>Clanculus corallinus</i> (GMELIN in L.)				Clanc cora	
	<i>Clanculus cruciatus</i> (L.)	Clanc cruc	Clanc cruc			
C DC	<i>Astraea rugosa</i> (L.)	Astra rugo	<i>Astra rugo</i>	<i>Astra rugo</i>	Astra rugo	
HP C	<i>Homalopoma sanguineum</i> (L.)	Homal sang	Homal sang		Homal sang	
infra	<i>Tricola pullus</i> (L.)	<i>Trico pull</i>	<i>Trico pull</i>	<i>Trico pull</i>		
Ire	<i>Tricola speciosa</i> (VON MUHLFELDT)	<i>Trico spec</i>	<i>Trico spec</i>			
AP HP	<i>Tricola tenuis</i> (MICHAUD)	<i>Trico tenu</i>			Trico tenu	
AP HP	<i>Smaragdia viridis</i> (L.)	Smara viri			Smara viri	
	<i>Littorina neritoides</i> (L.)	Litto neri				
LEE excl	<i>Hydrobia stagnalis</i> (BASTER)	<i>Hydro stag</i>	<i>Hydro stag</i>	<i>Hydro stag</i>	<i>Hydro stag</i>	<i>Hydro stag</i>
LEE	<i>Paludinella littorina</i> (DELLE CHIAJE)				Palud litt	
LEE	<i>Truncatella subcylindrica</i> (L.)	Trunc subc	Trunc subc		Trunc subc	
	<i>Barleeia rubra</i> (ADAMS)	Barle rubr				
	<i>Hyalia vitrea</i> (MONTAGU)	Hyalia vitr				
	<i>Setia semistriata</i> (MONTAGU)					
	<i>Apicularia similis</i> (SCACCHI)	Apicu simi				
	<i>Goniosoma auriscalpium</i> (L.)	Gonio auri	Gonio auri			
	<i>Rissoa variabilis</i> (VON MUHLFELDT)	Risso vari	Risso vari			
	<i>Rissoa ventricosa</i> DESMAREST	Risso vent	Risso vent			
AP HP	<i>Rissoa violacea</i> DESMAREST	Risso viol			Risso viol	
HP acc	<i>Turboella dolium</i> (NYST)	Turbo doli	Turbo doli		Turbo doli	
	<i>Turboella lavalei</i> (SEGUENZA)					
HP acc	<i>Turboella lineolata</i> (MICHAUD)	Turbo line			Turbo line	
	<i>Acinopsis hirta</i> (MONTEROSATO)	Acino hirt				
	<i>Acinopsis cancellata</i> (DA COSTA)	<i>Acino canc</i>	<i>Acino canc</i>	<i>Acino canc</i>		
HP VP	<i>Actonia testae</i> (ARADAS & MAGGIORE)					
sspr	<i>Alvania consociella</i> MONTEROSATO	Alvan cons				
AP HP	<i>Alvania discors</i> (ALLAN)	<i>Alvan disc</i>	<i>Alvan disc</i>	<i>Alvan disc</i>	<i>Alvan disc</i>	
infra	<i>Alvania lineata</i> RISSO	Alvan line			Alvan line	
	<i>Alvinia jeffreysi</i> (WALLER)					
infra-circa	<i>Arsenia punctura</i> (MONTAGU)					
	<i>Galeodina carinata</i> (DA COSTA)					
HP acc	<i>Turbona cimex</i> (L.)	Turbn cime	Turbn cime		<i>Turbn cime</i>	
pss VP	<i>Turbona cimicoides</i> (FORBES)	Turbn cimi	<i>Turbn cimi</i>	Turbn cimi	Turbn cimi	
	<i>Turbona geryonia</i> (CHIEREGHIN in NARDO)	Turbn gery	Turbn gery			
DC excl	<i>Turbona reticulata</i> (MONTAGU)	Turbn reti	Turbn reti	Turbn reti	Turbn reti	<i>Turbn reti</i>
AP HP	<i>Rissoina bruguierei</i> (PAYRAUDEAU)	Rissn brug			Rissn brug	
VTC pref	<i>Turritella communis</i> RISSO	<i>Turri comm</i>	<i>Turri comm</i>	<i>Turri comm</i>	<i>Turri comm</i>	<i>Turri comm</i>
DC excl	<i>Turritella turbona</i> MONTEROSATO	Turri turb	Turri turb		Turri turb	Turri turb
AP HP Ire	<i>Bittium reticulatum</i> (DA COSTA)	<i>Bitti reti</i>	<i>Bitti reti</i>	<i>Bitti reti</i>	<i>Bitti reti</i>	
	<i>Bittium lacteum</i> (PHILIPPI)	Bitti lact				
circa	<i>Cerithidium submamillatum</i> (DE RAYNEVAL & PONZI)	Ceritd sub				
SVMC HP	<i>Cerithium vulgatum</i> (BRUGUIERE)	<i>Cerit vulg</i>	<i>Cerit vulg</i>	<i>Cerit vulg</i>	<i>Cerit vulg</i>	
	<i>Cerithiopsis fayalensis</i> WATSON					
	<i>Cerithiopsis scalaris</i> (MONTEROSATO)					
	<i>Cerithiopsis tiara</i> WATSON in MONTEROSATO					
C	<i>Cerithiopsis tubercularis</i> (MONTAGU)	Certps tub			Certps tub	
sspr	<i>Metaxia metaxiae</i> (DELLE CHIAJE)	Metax meta				
C	<i>Triphora perversa</i> (L.)	Triph perv	Triph perv		<i>Triph perv</i>	
infra	<i>Epitonium aculeatum</i> (ALLAN)					

Biocoenosis	Species	QUANTITATIVE			QUALITATIVE	
		n154	p>1	p>3	b154	b80
circa	<i>Epitonium clathratulum</i> (ADAMS)					
sspr	<i>Epitonium commune</i> (LAMARCK)					
circa-bat	<i>Epitonium tiberii</i> (BOURY)					
SFBC excl	<i>Epitonium turtoni</i> (TURTON)				Epito turt	Epito turt
pss	<i>Opalia hellenica</i> (FORBES)				Opali hell	
	<i>Acilis minor</i> (BROWN)					
DC excl	<i>Melanella polita</i> (L.)				Melan poli	Melan poli
circa	<i>Strombiformis bilineatus</i> (ALDER)					
	<i>Strombiformis glaber</i> (DA COSTA)					
	<i>Fossarus ambiguus</i> (L.)					
pss	<i>Capulus ungaricus</i> (L.)				Capul unga	
pss	<i>Calyptraea chinensis</i> (L.)	Calyp chin	Calyp chin		Calyp chin	
sspr	<i>Crepidula unguiformis</i> LAMARCK					
misto	<i>Aporrhais pespelecani</i> (L.)	Aporr pesp	Aporr pesp		Aporr pesp	
sspr	<i>Lunatia catena</i> (DA COSTA)	Lunat cate				
	<i>Lunatia macilenta</i> (PHILIPPI)	Lunat maci				
lre	<i>Lunatia pulchella</i> (RISSO)	Lunat pulc	Lunat pulc			
SFBC excl	<i>Neverita josephina</i> RISSO				Never jose	Never jose
sspr	<i>Naticarius punctatus</i> (CHEMNITZ in KARSTEN)					
sspr	<i>Bolinus brandaris</i> (L.)					
sspr	<i>Phyllonotus trunculus</i> (L.)					
lre	<i>Muricopsis aradasi</i> MONTEROSATO in POIRIER					
C pref	<i>Muricopsis cristata</i> (BROCCHI)	Muric cris			Muric cris	<i>Muric cris</i>
VP	<i>Trophonopsis multilamellosa</i> (PHILIPPI)				Troph mult	
sspr	<i>Trophonopsis muricata</i> (MONTAGU)					
sspr	<i>Hadriana craticuloides</i> (VOKES)					
infra	<i>Ocenebrina aciculata</i> (LAMARCK)	Ocine acic				
sspr	<i>Coralliophila lamellosa</i> (DE CRISTOFORIS & JAN)					
infra-circa	<i>Cantharus dorbignyi</i> (PAYRAUDEAU)					
	<i>Chauvetia minima</i> (MONTAGU)	Chauv mini				
	<i>Chauvetia vulpecula</i> (MONTEROSATO)					
	<i>Pisania striata</i> (GMELIN in L.)	Pisan stri				
sspr	<i>Columbellopsis minor</i> (SCACCHI)	Colbsis mn				
	<i>Pyrene scripta</i> (L.)	Pyren scri				
AP excl	<i>Columbella rustica</i> (L.)				Colum rust	Colum rust
LEE acc	<i>Cyclope neritea</i> (L.)	Cyclo neri	Cyclo neri		Cyclo neri	
	<i>Hinia incrassata</i> (STROM)	<i>Hinia incr</i>	<i>Hinia incr</i>	Hinia incr		
pss	<i>Hinia limata</i> (DESHAYES in LAMARCK)				Hinia lima	
SFBC pref	<i>Hinia pygmaea</i> (LAMARCK)	Hinia pygm			Hinia pygm	Hinia pygm
	<i>Nassarius corniculatus</i> (OLIVI)					
	<i>Fusinus giglioli</i> (MONTEROSATO)					
pss	<i>Fusinus pulchellus</i> (PHILIPPI)				Fusin pulc	
misto	<i>Fusinus rostratus</i> (OLIVI)				Fusin rost	
HP acc	<i>Fusinus rudis</i> (PHILIPPI)	Fusin rudi			Fusin rudi	
infra	<i>Mitra cornicula</i> (L.)					
	<i>Vexillum ebenus</i> (LAMARCK)					
	<i>Vexillum savignyi</i> (PAYRAUDEAU)					
sspr	<i>Vexillum tricolor</i> (GMELIN in L.)	Vex tricol				
AP excl	<i>Conus ventricosus</i> GMELIN in L.	Conus vent			Conus vent	<i>Conus vent</i>
infra-circa	<i>Mitrolumna olivoides</i> (CANTRAINE)	Mitro oliv				
	<i>Bellaspira rigida</i> (FORBES in REEVE)					
	<i>Bellaspira septangularis</i> (MONTAGU)					
	<i>Bela brachystoma</i> (PHILIPPI)	Bela brac	Bela brac			
SFBC excl	<i>Bela nebula</i> (MONTAGU)				Bela nebu	Bela nebul
	<i>Bela turgida</i> (FORBES in REEVE)					
sspr	<i>Clathromangelia quadrillum</i> (DUJARDIN)					
SFBC excl	<i>Mangelia attenuata</i> (MONTAGU)	Mange atte			Mange atte	Mange atte
	<i>Mangelia paciniana</i> (CALCARA)					
	<i>Mangelia rugulosa</i> (PHILIPPI)	Mange rugu				
	<i>Mangelia scabrata</i> (MONTEROSATO)					
infra-circa	<i>Mangelia smithi</i> (FORBES)	Mange smit				
	<i>Mangelia stossiciana</i> (BRUSINA)					
infra-circa	<i>Mangiliella taeniata</i> (DESHAYES)					
sspr	<i>Comarmondia gracilis</i> (MONTAGU)					
sspr	<i>Raphitoma concinna</i> (SCACCHI)					
sspr	<i>Raphitoma echinata</i> (BROCCHI)					
sspr	<i>Raphitoma histrix</i> (DE CRISTOFORIS & JAN)				Raphi hist	
sspr	<i>Raphitoma leufroyi</i> (MICHAUD)					
C pref	<i>Raphitoma linearis</i> (MONTAGU)	Raphi line			Raphi line	Raphi line
	<i>Raphitoma philberti</i> (MICHAUD)					
	<i>Raphitoma purpurea</i> (MONTAGU)					
DC pref	<i>Teretia teres</i> (FORBES in REEVE)				Teret tere	Teret tere
	<i>Gibberula caelata</i> (MONTEROSATO)					
HP excl	<i>Gibberula miliaria</i> (L.)	Gibbe mili	Gibbe mili		<i>Gibbe mili</i>	<i>Gibbe mili</i>
	<i>Gibberula philippii</i> (MONTEROSATO)					
HP acc	<i>Gibberulina clandestina</i> (BROCCHI)	Gibber cla	Gibber cla		Gibber cla	
pss	<i>Gibberulina occulta</i> (MONTEROSATO)	Gibber occ			Gibber occ	
	<i>Hyalina mitrella</i> (RISSO)					
SFBC excl	<i>Acteon tornatilis</i> (L.)					Acteo torn
	<i>Pseudacteon luteofasciatum</i> (MUHLFELT)					
	<i>Cylichnina subcylindrica</i> (BROWN)					
pelo	<i>Mamilloretusa mamillata</i> (PHILIPPI)				Mamil mami	
misto	<i>Retusa truncatula</i> (BRUGUIERE)				Retus trun	
sspr	<i>Ringicula conformis</i> MONTEROSATO					

Biocoenosis	Species	QUANTITATIVE			QUALITATIVE	
		n154	p>1	p>3	b154	b80
sspr	<i>Bulla striata</i> BRUGUIERE	Bulla stri				
sspr	<i>Alys brocchii</i> (MICHELOTTI)					
sspr	<i>Haminoea cymoelium</i> MONTEROSATO					
sspr	<i>Haminoea hydatis</i> (L.)					
infra-circa	<i>Weinkauffia semistriata</i> (REQUIEN)					
psammo	<i>Weinkauffia turgidula</i> (FORBES)					
psammo	<i>Philine aperta</i> (L.)					Phili aper
psammo	<i>Philine scabra</i> (MULLER)					
psammo	<i>Cylichna alba</i> (BROWN)					
psammo	<i>Cylichna crossei</i> (B.D.D.)					
sspr	<i>Cylichna cylindracea</i> (PENNANT)					
sspr	<i>Scaphander gracilis</i> WATSON					
sspr	<i>Scaphander lignarius</i> (L.)					
infra-circa	<i>Chrysallida dollolum</i> (PHILIPPI)					
infra-circa	<i>Chrysallida excavata</i> (PHILIPPI)					
infra-circa	<i>Eulimella turris</i> (FORBES)					
infra-circa	<i>Odostomia acuta</i> JEFFREYS					
infra-circa	<i>Odostomia conoidea</i> (BROCCHI)					
infra-circa	<i>Odostomia turrata</i> HANLEY					
infra-circa	<i>Turbonilla acuta</i> (DONOVAN)					
infra-circa	<i>Turbonilla delicata</i> (MONTEROSATO in KOBELT)					
psammo	<i>Turbonilla lactea</i> (L.)					Turbl lact
PE	<i>Turbonilla rufa</i> (PHILIPPI)					Turbl rufa
PE	<i>Turbonilla scalaris</i> (PHILIPPI)					
PE	<i>Ovatella myosotis</i> (DRAPARNAUD)					
PE	<i>Trimusculus mammillaris</i> (L.)					
SCAPHOPODA						
infra-circa	<i>Dentalium dentalis</i> L.					
misto	<i>Dentalium inaequicostatum</i> DAUTZENBERG					
misto	<i>Fustiaria rubescens</i> (DESHAYES)					
misto	BIVALVIA					
misto	<i>Nucula nucleus</i> (L.)					
VP	<i>Nucula sulcata</i> BRONN					
misto	<i>Nuculana fragilis</i> (CHEMNITZ)					
PE excl	<i>Nuculana pella</i> (L.)					
AP pref	<i>Arca noae</i> L.					
misto	<i>Arca tetragona</i> POLI					
lre	<i>Barbatia barbata</i> (L.)					
misto	<i>Anadara diluvii</i> (LAMARCK)					
pss	<i>Bathyarca grenophia</i> (RISSO)					
pss	<i>Striarca lactea</i> (L.)					
SGCF excl	<i>Glycymeris glycymeris</i> (L.)					
SFBC excl	<i>Glycymeris insubrica</i> (BROCCHI)					
SFBC excl	<i>Mytilaster minimus</i> (POLI)					
SFBC excl	<i>Musculus costulatus</i> (RISSO)					
SFBC excl	<i>Musculus discors</i> (L.)					
infra-circa	<i>Musculus subpictus</i> (CANTRAINED)					
DC excl	<i>Modiolula phaseolina</i> (PHILIPPI)					
DC excl	<i>Modiolus barbatus</i> (L.)					
DC pref	<i>Chlamys flexuosa</i> (POLI)					
sspr	<i>Chlamys glabra</i> (L.)					
sspr	<i>Chlamys multistriata</i> (POLI)					
pss	<i>Chlamys varia</i> (L.)					
DC excl	<i>Pecten jacobaeus</i> (L.)					
pss	<i>Hyalopecten similis</i> (LASKEY)					
HP excl	<i>Lissopecten hyalinus</i> (POLI)					
C excl	<i>Palliolium incomparabile</i> (RISSO)					
C excl	<i>Aequipecten commutatus</i> (MONTEROSATO)					
sspr	<i>Aequipecten opercularis</i> (L.)					
sspr	<i>Peplum clavatum</i> (POLI)					
pss	<i>Anomia ephippium</i> L.					
lre	<i>Pododesmus patelliformis</i> (L.)					
lre	<i>Pododesmus squamula</i> (L.)					
HP excl	<i>Lima hians</i> (GMELIN in L.)					
HP excl	<i>Lima inflata</i> (LINK)					
lre	<i>Lima lima</i> (L.)					
DC excl	<i>Limatula gwyni</i> (SYKES)					
VP excl	<i>Limatula subauriculata</i> (MONTAGU)					
DC excl	<i>Limea loscombi</i> MAC GILLIVRAY					
DC excl	<i>Ostrea edulis</i> L.					
SVMC excl	<i>Ctena decussata</i> (O.G. COSTA)					
SVMC excl	<i>Loripes lacteus</i> (L.)					
sspr	<i>Divaricella divaricata</i> (L.)					
sspr	<i>Anodontia fragilis</i> (PHILIPPI)					
PE excl	<i>Lucinoma boreale</i> (L.)					
lre	<i>Myrtea spinifera</i> (MONTAGU)					
VTC excl	<i>Axinulus croulinensis</i> (JEFFREYS)					
VTC excl	<i>Thyasira alleni</i> CARROZZA					
pelo	<i>Thyasira flexuosa</i> (MONTAGU)					
VP excl	<i>Thyasira granulosa</i> (JEFFREYS in MONTEROSATO)					
SGCF excl	<i>Diplodonta apicalis</i> (PHILIPPI)					
pelo	<i>Diplodonta rotundata</i> (MONTAGU)					
AP HP	<i>Chama gryphoides</i> L.					
AP HP	<i>Pseudochama gryphina</i> (LAMARCK)					

Biocoenosis	Species	QUANTITATIVE			QUALITATIVE	
		n154	p>1	p>3	b154	b80
circa	<i>Lepton nitidum</i> TURTON <i>Lepton solidulum</i> MONTEROSATO <i>Galeomma turtoni</i> (G.B. SOWERBY) <i>Bornia sebetia</i> (O.G.COSTA)					
DC pref	<i>Kellia suborbicularis</i> (MONTAGU)				Kelli subo	Kelli subo
sspr	<i>Montacuta substriata</i> (MONTAGU)					
VTC excl	<i>Mysella bidentata</i> (MONTAGU)	Mysel bide			Mysel bide	Mysel bide
sspr	<i>Epilepton clarkiae</i> (W. CLARK)					
misto	<i>Cardita calyculata</i> (L.)	Cardi caly				
HP excl	<i>Glans aculeata</i> (POLI)	Glans acul			Glans acul	
HP pref	<i>Glans trapezia</i> (L.)	Glans trap	Glans trap			<i>Glans trap</i>
SGCF acc	<i>Venericardia antiquata</i> (L.)	Veneri ant			Veneri ant	Veneri ant
DL excl	<i>Astarte fusca</i> (POLI)	Astar fusc			Astar fusc	
	<i>Astarte sulcata</i> (DA COSTA)					Astar sulc
	<i>Digitaria digitaria</i> (L.)					
	<i>Gonilia calliglypta</i> (DALL)	Gonil call				
psammo	<i>Acanthocardia echinata</i> (L.)				Acant echi	
pelo	<i>Acanthocardia paucicostata</i> (SOWERBY)	Acant pauc	Acant pauc	<i>Acant pauc</i>	Acant pauc	
SFBC excl	<i>Acanthocardia tuberculata</i> (L.)	Acant tube			Acant tube	Acant tube
misto	<i>Parvicardium minimum</i> (PHILIPPI)	Parvi mini	Parvi mini	<i>Parvi mini</i>	Parvi mini	
sspr	<i>Parvicardium ovale</i> (SOWERBY)	Parvi oval				
	<i>Parvicardium roseum</i> (LAMARCK)					
DC pref	<i>Plagiocardium papillosum</i> (POLI)	<i>Plagi papi</i>	Plagi papi	<i>Plagi papi</i>	<i>Plagi papi</i>	<i>Plagi papi</i>
LEE excl	<i>Cerastoderma glaucum</i> (POIRET)	<i>Ceras glau</i>	<i>Ceras glau</i>	<i>Ceras glau</i>	<i>Ceras glau</i>	<i>Ceras glau</i>
SGCF pref	<i>Laevicardium crassum</i> (GMELIN in L.)	Laevi cras			Laevi cras	Laevi cras
DC excl	<i>Laevicardium oblongum</i> (GMELIN in L.)				Laevi oblo	Laevi oblo
SFBC excl	<i>Maetra stultorum</i> (L.)	Maetr stul			Maetr stul	Maetr stul
SFBC excl	<i>Spisula subtruncata</i> (DA COSTA)	Spisu subt			Spisu subt	Spisu subt
pelo	<i>Cultellus tenuis</i> PHILIPPI	Culte tenu	Culte tenu	Culte tenu	Culte tenu	
SFBC acc	<i>Ensis ensis</i> (L.)	Ensis ensi			Ensis ensi	
SFBC excl	<i>Ensis siliqua minor</i> (CHENU)	Ensis mino			Ensis mino	Ensis mino
misto	<i>Tellina balaustina</i> L.	Telli bala			Telli bala	
SGCF excl	<i>Tellina crassa</i> PENNANT	Telli cras			Telli cras	
PE	<i>Tellina distorta</i> POLI	<i>Telli dist</i>	<i>Telli dist</i>		<i>Telli dist</i>	
DC excl.	<i>Tellina donacina</i> (L.)	Telli dona	Telli dona		Telli dona	<i>Telli dona</i>
SFBC excl	<i>Tellina fabula</i> GRONOVIOUS	Telli fabu			Telli fabu	Telli fabu
SFBC excl	<i>Tellina pulchella</i> LAMARCK	Telli pulc			Telli pulc	Telli pulc
DE excl	<i>Tellina serrata</i> RENIER in BROCCCHI	Telli serr			Telli serr	Telli serr
SFHN excl	<i>Donax trunculus</i> L.	Donax trun			Donax trun	Donax trun
SGCF excl	<i>Donax variegatus</i> GMELIN in L.	Donax vari			Donax vari	Donax vari
SFBC excl	<i>Donax venustus</i> POLI	Donax venu			Donax venu	Donax venu
SGCF excl	<i>Psammobia costulata</i> (TURTON)	Psamm cost			Psamm cost	Psamm cost
HP excl	<i>Psammobia depressa</i> (PENNANT)	Psamm depr			Psamm depr	Psamm depr
DC excl	<i>Psammobia fervensis</i> (GMELIN in L.)	Psamm ferv			Psamm ferv	Psamm ferv
pelo	<i>Abra alba</i> (WOOD)	<i>Abra alba</i>	<i>Abra alba</i>		<i>Abra alba</i>	
VTC excl	<i>Abra nitida</i> (MULLER)	Abra niti	Abra niti	Abra niti	Abra niti	<i>Abra nitid</i>
LEE excl	<i>Abra ovata</i> (PHILIPPI)	Abra ovat	Abra ovat		Abra ovat	Abra ovat
DC excl	<i>Abra prismatica</i> (MONTAGU)	Abra pris	Abra pris		Abra pris	<i>Abra pris</i>
	<i>Azorinus chamasolen</i> (DA COSTA)					
	<i>Solecurtus scopula</i> (TURTON)					
ire	<i>Kelliella abyssicola</i> (FORBES)					
SGCF excl	<i>Venus casina</i> L.	Venus casi	Venus casi	Venus casi	Venus casi	Venus casi
	<i>Venus nux</i> GMELIN in L.	Venus nux				
HP excl	<i>Venus verrucosa</i> L.	Venus verr			Venus verr	Venus verr
SFBC pref	<i>Chamelea gallina</i> (L.)	Chame gall			Chame gall	Chame gall
SGCF pref	<i>Clausinella brogniarti</i> (PAYRAUDEAU)	Claus brog			Claus brog	Claus brog
misto	<i>Timoclea ovata</i> (PENNANT)	<i>Timoc ovat</i>	<i>Timoc ovat</i>	<i>Timoc ovat</i>	<i>Timoc ovat</i>	<i>Timoc ovat</i>
DC acc	<i>Gouldia minima</i> (MONTAGU)	<i>Gould mini</i>	<i>Gould mini</i>	<i>Gould mini</i>	<i>Gould mini</i>	<i>Gould mini</i>
SGCF excl	<i>Dosinia exoleta</i> (L.)	Dosin exol			Dosin exol	Dosin exol
psammo	<i>Callista chione</i> (L.)	Calli chio			Calli chio	
DC pref	<i>Pitar rudis</i> (POLI)	Pitar rudi	Pitar rudi		Pitar rudi	<i>Pitar rudi</i>
	<i>Irus irus</i> (L.)					
SVMC excl	<i>Tapes decussatus</i> (L.)	Tapes decu			Tapes decu	Tapes decu
SVMC excl	<i>Venerupis aurea</i> (GMELIN in L.)	Veneru aur			Veneru aur	Veneru aure
SGCF excl	<i>Venerupis lucens</i> (LOCARD)	Veneru luc			Veneru luc	<i>Veneru luc</i>
	<i>Petricola lajonkairii</i> (PAYRAUDEAU)					
PE pref	<i>Corbula gibba</i> (OLIVI)	<i>Corbu gibb</i>	<i>Corbu gibb</i>	<i>Corbu gibb</i>	<i>Corbu gibb</i>	<i>Corbu gibb</i>
pss	<i>Hiatella rugosa</i> (PENNANT)	Hiate rugo			Hiate rugo	
VTC excl	<i>Thracia convexa</i> (W. WOOD)	Thrac conv			Thrac conv	Thrac conv
HP excl	<i>Thracia corbuloides</i> DESHAYES	Thrac corb			Thrac corb	Thrac corb
sspr	<i>Thracia distorta</i> (MONTAGU)					
SFBC excl	<i>Thracia papyracea</i> (POLI)	Thrac papy			Thrac papy	Thrac papy
misto	<i>Lyonsia norvegica</i> (CHEMNITZ)	Lyons norv			Lyons norv	
	<i>Pandora inaequalis</i> (L.)					
DC excl	<i>Pandora obtusa</i> LAMARCK	Pando obtu	Pando obtu		Pando obtu	Pando obtu
	<i>Pandora pinna</i> (MONTAGU)					
DC excl	<i>Cardiomya costellata</i> (DESHAYES)	Carmy cost			Carmy cost	Carmy cost
	<i>Cardiomya striolata</i> (LOCARD)					
sspr	<i>Cuspidaria cuspidata</i> (OLIVI)	Cuspi cusp				
misto	<i>Cuspidaria rostrata</i> (SPENGLER)				Cuspi rost	

Tab. 4 - List of the species in the original data matrix (systematically ordered) with their bionomical/ecological significance. The list of the species retained at each step of data reduction, both in the quantitative and qualitative approaches are also shown. Names of indicator species which best explain the average similarity within the clusters are in *Italic*. Species significant at all steps of data reduction are in **bold**. Abbreviations are: meso = mesolittoral; infra = infralittoral; circa = circalittoral; bat = bathyal; pss = small solid substrates; misto = related to mixed sediments; pelo = mud-related; psammo = sand-related.

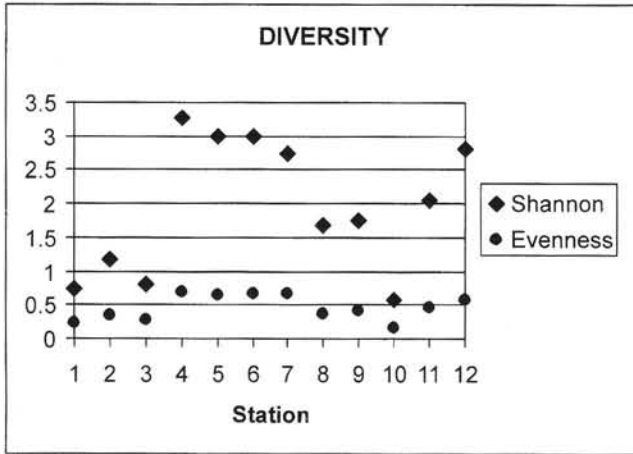


Fig. 1 - Comparison of Shannon diversity and Evenness for the twelve stations in Tab. 1.

Four samples (columns El70, El19, El15 and MC22) were collected off the coasts of the Elba and Montecristo Islands (Tuscan Archipelago), during the TSM Project (Basso et al. 1990; Tab.1b). Station min90abe70 (=El70) has a sediment made of biogenic coarse sand. The living association is composed of a dominant group of DC species (50%) accompanied by a conspicuous SGCF stock (33,3%) (Corselli & al. in prep.). The corresponding thanatocoenosis is dominated

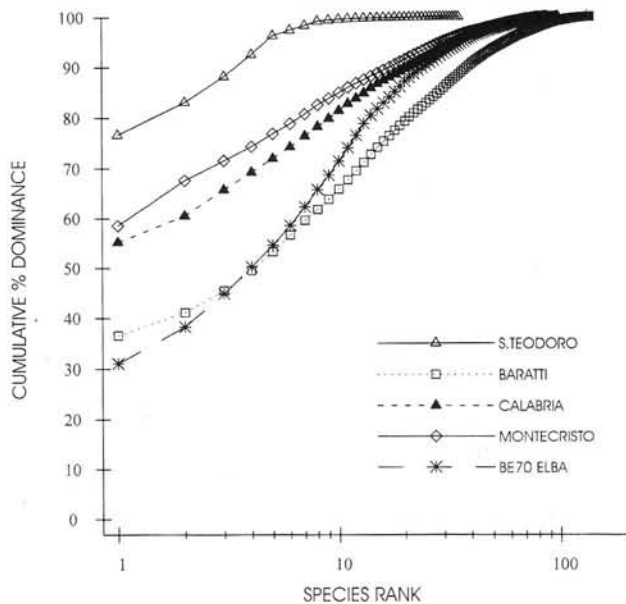


Fig. 2 - K-dominance curves for species abundance for the molluscan shell assemblages identified at S. Teodoro (three stations combined), Baratti (two stations combined), be70 Elba and Calabrian coasts (stations 2E and 15E combined). Stations have been joined when exceeding 55% of Bray-Curtis similarity in the full-matrix dendrogram (Fig.3a). On the X-axis the species are plotted on a logarithmic scale of rank abundance. The corresponding dominance of each species is cumulated on the Y-axis.

Quantitative approach "n154"			
Species	Av. abund.	% S	% S cum.
Cluster A - S. Teodoro			
Av. Similarity 77.05			
<i>Hydrobia stagnalis</i>	48901.33	24.62	24.62
<i>Cerithium vulgatum</i>	4098.67	13.23	37.85
<i>Cerastoderma glaucum</i>	3251.33	11	48.85
<i>Loripes lacteus</i>	2787	10.8	59.65
<i>Bittium reticulatum</i>	2414.33	9.95	69.6
<i>Abra ovata</i>	593.67	7.87	77.47
Cluster B - Calabria			
Av. Similarity 64.04			
<i>Turritella communis</i>	1337.67	10.9	10.9
<i>Corbula gibba</i>	69.67	5.93	16.82
<i>Nucula nucleus</i>	37.33	4.96	21.79
<i>Anomia ephippium</i>	39.33	4.56	26.35
<i>Timoclea ovata</i>	13.33	4.05	30.4
<i>Abra alba</i>	14	3.95	34.35
<i>Tellina distorta</i>	20	3.87	38.22
Cluster C - Baratti			
Av. Similarity 88.43			
<i>Striarca lactea</i>	208,5	-	-
<i>Bittium reticulatum</i>	1666,5	-	-
<i>Tricolia pullus</i>	196,5	-	-
<i>Jujubinus exasperatus</i>	184,5	-	-
<i>Alvania discors</i>	172,5	-	-
<i>Hinia incrassata</i>	152	-	-
<i>Acinopsis cancellata</i>	135	-	-
Cluster D - Elba + Montecristo			
Av. Similarity 51.23			
<i>Bittium reticulatum</i>	1877.5	7.51	7.51
<i>Gouldia minima</i>	78.25	4.29	11.8
<i>Striarca lactea</i>	97.25	3.99	15.79
<i>Timoclea ovata</i>	629.25	3.98	19.77
<i>Jujubinus exasperatus</i>	82.25	3.5	23.27
<i>Turbona cimicoides</i>	82.5	2.99	26.26
<i>Astraea rugosa</i>	55.5	2.87	29.14

Tab. 5 - Breakdown of average similarity within each cluster identified in dendrogram of Fig. 3c. Species are listed in order of contribution, up to 80% of similarity. Asterisks indicate the species not retained in the qualitative approach (see also Table 4).

by DC species (55,9%), followed by a significant stock of PE species (20%) and a 5,5% of SGCF-characteristic species (Fallini 1994).

Station min90abe19 (=El19) was characterised by large concretions of calcareous red algae mixed with mud. The molluscan living association corresponds to a transition between a DC and C bottom. As expected, the thanatocoenosis is dominated by hard bottom species occurring in the AP, HP and C biocoenosis (75%), followed by the DC related molluscs (9,6%), the mud-related species (VTC + VP = 6,9%) and the PE related species (3,4%) (Basso 1995).

Column El15 (=station min90abe15) represents a coastal muddy detritic bottom (DE), whose thanatocoenosis is dominated by a group of DC species (56,7%), mixed with a minor group of PE (7,8%) and VTC species (3,3%). Only 1,2% of the thanatocoenosis is composed of molluscs related to the DE biocoenosis (Basso 1995).

Column MC22 corresponds to station

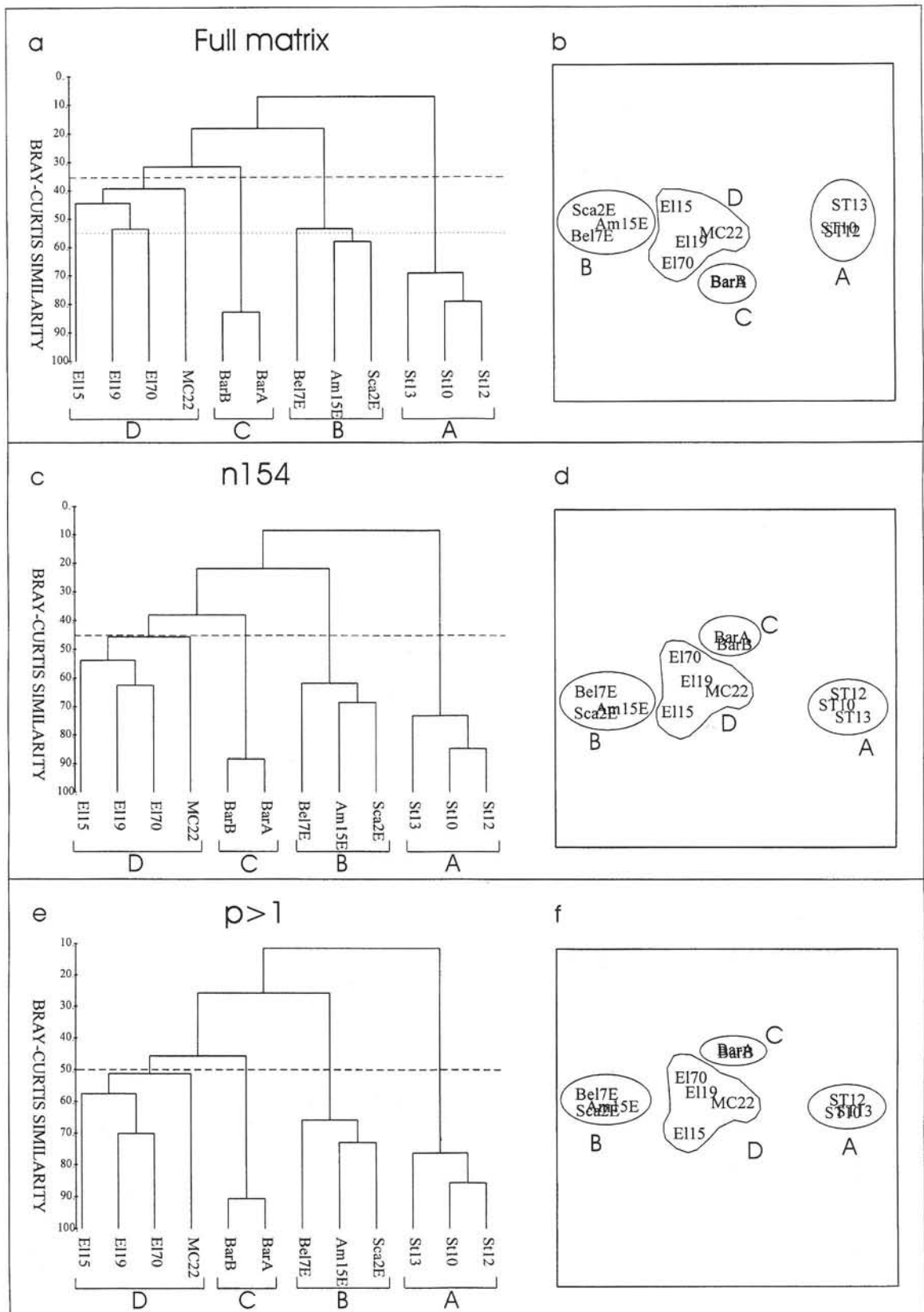


Fig. 3 - Dendrogram (a,c,e) resulting by hierarchical agglomerative clustering of 12 stations, based on B-C sim., double square-root transformation and correspondent MDS (b,d,f). a, b - Complete data set. The dashed line at the 35% of B-C sim. in the dendrogram separates four clusters (A-D) which have been indicated in the MDS (Stress 2-D = 0.02). The dotted line at the 55% of B-C sim. separates the groups of stations joined in the K-dominance curves of Fig. 2. c, d - Retaining the 154 most important species. The dashed line at the 45% of B-C sim. in the dendrogram separates four clusters (A-D) which have been indicated in the MDS (Stress 2-D = 0.02). e, f - Retaining only the species reaching at least 1% dominance ($p > 1\%$) at each station. At the 50% of B-C sim. (dashed line in the dendrogram) the same clusters are identified than those in Figs. 3a and 3c. They have been indicated in the MDS (Stress 2-D = 0.03).

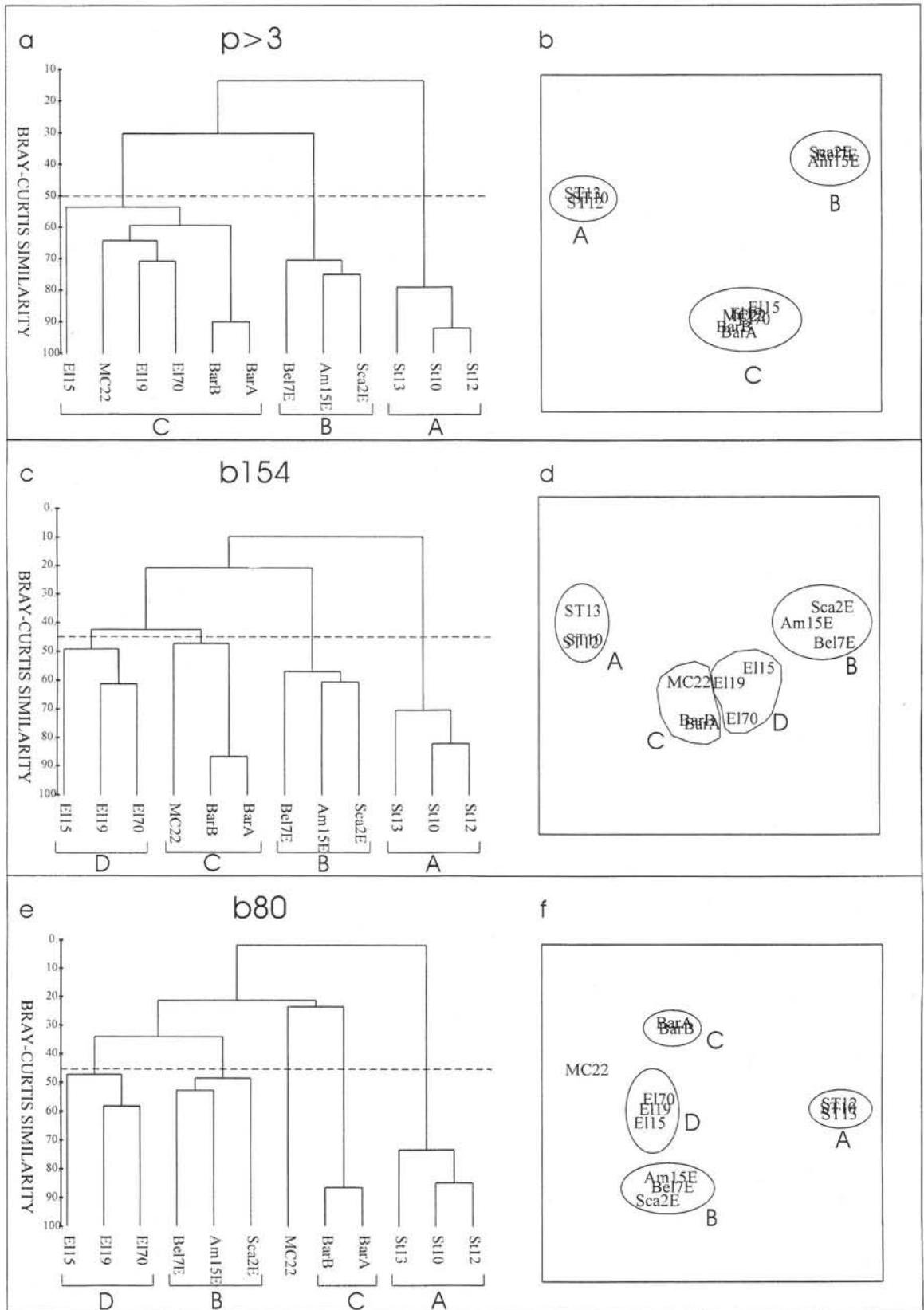


Fig. 4 - Dendrogram (a,c,e) resulting by hierarchical agglomerative clustering of 12 stations, based on B-C sim., double square-root transformation and correspondent MDS (b,d,f). a,b - Retaining only the species with $p > 3\%$. The 50% of B-C sim. (dashed line in the dendrogram) have been selected for discussion in the text and identified in the MDS (Stress 2-D = 0.01). c,d - Retaining only the species with a significance in benthic bioturbation (Table 4). In the dendrogram, the dashed line at the 45% of B-C sim. separates four clusters (A-D) which have been indicated in the MDS (Stress 2-D = 0.03). e,f - Retaining only the exclusive and preferential characteristic species (Table 4). The dashed line at the 45% of B-C sim. in the dendrogram separates four clusters (A-D) which have been indicated in the MDS (Stress 2-D = 0.03). Note the Montecristo station is excluded by the considered clustering.

min88ebe22, located off the western coast of Montecristo Island (Tuscan Archipelago). The biocoenosis is characterised by species related to the DC biocoenosis (28,5%) and sand-related species. The same stocks also occur in the shell thanatocoenosis (9,46% DC) which is dominated by hard bottom species occurring in the AP and HP biocoenoses (about 70%).

Three stations were sampled along the Calabrian coasts, where the VTC biocoenosis was recognized: Sca2E close to Cape Scalea, Am15E close to Amantea and Bel7E in front of the Belvedere Mount. A remarkable abundance of *Turritella communis* characterises the thanatofacies, which corresponds to a past high sedimentation phase (Giacobbe & Mondello 1994).

Results

Univariate statistics (Tab. 3, Fig. 1, 2) shows a low Shannon diversity (below 1.5) at stations St10, St12 and St13 of the S. Teodoro lagoon and at station Bel7E. The lowest values of Evenness (below 0.35) are also found at the same stations.

The two Baratti stations show the highest scores in the combination of species richness, diversity and evenness. Also station El70, the shallowest among those collected in the Tuscan Archipelago, shows a high diversity and evenness.

A comparison between the k-dominance curves obtained by combining the stations with more than 55% of B-C sim. (Fig. 3a) shows the lowest diversity (flat curve starting from a high percentage of cumulative dominance) for the S. Teodoro stations, the highest for the El70 and Baratti stations, with a significant crossing of the two latter lines at about 45% of cumulative abundance (Fig. 2).

The full-matrix clustering (Fig. 3a) at the 35% of B-C sim. is well reflected in the MDS ordination (Stress 0.02; Fig. 3b), producing four groups of stations: group A, with the three S. Teodoro stations, group B, with the three Calabrian stations, group C, with the Baratti stations and group D with the three Elba stations and the Montecristo station.

The quantitative approach

At the first step of data reduction, the most important 154 species, (Tab. 4) have been considered for the multivariate and similarity analyses (Figs. 3c; 3d). At the 45% of B-C sim., the same A to D clusters separate as those identified with the full-matrix clustering. Cluster A groups the S. Teodoro stations, with an average similarity of 77.05% (Tab. 5). The indicator species, e.g. those responsible for the observed similarity within cluster A, are, in order of contribution, *Hydrobia stagnalis*, *Cerithium vulgatum*, *Cerastoderma glaucum*, *Loripes lacteus*, *Bittium reticulatum* and *Abra ovata*. The

average similarity within cluster B (the Calabrian stations) is 64.04%. Following their order of contribution, the first seven indicator species are: *Turritella communis*, *Corbula gibba*, *Nucula nucleus*, *Anomia ephippium*, *Timoctea ovata*, *Abra alba* and *Tellina distorta* (Tab. 5). Cluster C (the two Baratti stations) has an average similarity of 88.43%. The first seven indicator species (Tab. 5) are: *Striarca lactea*, *Bittium reticulatum*, *Tricolia pullus*, *Jujubinus exasperatus*, *Alvania discors*, *Hinia incrassata* and *Acinopsis cancellata*. Cluster D encompasses the Elba and Montecristo stations, with an average similarity of 51.23%, mostly explained by the following species: *Bittium reticulatum*, *Gouldia minima*, *Striarca lactea*, *Timoctea ovata*, *Jujubinus exasperatus*, *Turbona cimicoides* and *Astraea rugosa*.

A further reduction of the data matrix has considered only the species with $p > 1\%$ at each station, for a total of 67 species (Fig. 3e, f; Tab. 4). The 50% B-C sim. separates again the same clusters (Fig. 3e), than those originally identified. Also the indicator species are the same as in the previous "n154" data reduction.

The MDS ordinations (Figs. 3b, 3d, 3f) shows that clusters A and B lie at the opposite ends of the environmental gradient, with clusters C and D in between. Among stations belonging to cluster D, El70 lies very close to the Baratti cluster C, whilst El15 is the furthest.

The data matrix has been reduced further, considering only the 30 species with $p > 3\%$ (= " $p > 3\%$ "; Tab. 4). In the dendrogram (Fig. 4a), at the 50% level of B-C sim. only three clusters separate, of which cluster A (S. Teodoro) and B (Calabria) are the same than those identified in the previous elaborations. The third cluster encompasses all the remaining stations from the Baratti, Elba and Montecristo areas, with an average similarity of 61.01% within the cluster. The seven most important species responsible for the observed similarity within cluster C are: *Bittium reticulatum*, *Striarca lactea*, *Jujubinus exasperatus*, *Gouldia minima*, *Alvania discors*, *Plagiocardium papillosum* and *Astraea rugosa*. The MDS ordination (Fig. 4b, stress = 0.01) shows the three clusters clearly split apart.

The qualitative approach

The classification of the 154 species with some ecological significance in benthic bionomy (= "b154"; Tab. 4) results in the dendrogram of Fig. 4c. At the 45% of B-C sim. clusters A to D separate. Cluster A groups the S. Teodoro stations, with an average similarity of 74.17% and the same indicator species as those listed for the "n154" quantitative approach. Cluster B encompasses the Calabrian stations with an average similarity of 58.12%. The first seven indicator species are also the same as those listed in the quantitative approach. Cluster C groups the Baratti and Montecristo stations, with an average similarity of 60.31% and the following indicator species: *B. reticulatum*, *S. lactea*, *A. discors*, *Tur-*

Qualitative approach "b154"			
Species	Av. abund.	% S	% S cum.
Cluster A - S. Teodoro Av. Similarity 74.17			
<i>Hydrobia stagnalis</i>	48901.33	25.58	25.58
<i>Cerithium vulgatum</i>	4098.67	13.76	39.35
<i>Cerastoderma glaucum</i>	3251.33	11.42	50.77
<i>Loripes lacteus</i>	2787	11.21	61.98
<i>Bittium reticulatum</i>	2414.33	10.34	72.32
Cluster B - Calabria Av. Similarity 58.12			
<i>Turritella communis</i>	1337.67	13.95	13.95
<i>Corbula gibba</i>	69.67	7.59	21.53
<i>Nucula nucleus</i>	37.33	6.35	27.88
<i>Anomia ephippium</i>	39.33	5.84	33.72
<i>Timoclea ovata</i>	13.33	5.19	38.91
<i>Abra alba</i>	14	5.05	43.96
<i>Tellina distorta</i>	20	4.95	48.92
Cluster C - Baratti + Montecristo Av. Similarity 60.31			
<i>Bittium reticulatum</i>	1845.33	9.66	9.66
<i>Striarca lactea</i>	188.33	5.59	15.24
<i>Alvania discors</i>	229	5.47	20.71
<i>Turbona cimex</i>	100.67	4.74	25.46
<i>Jujubinus exasperatus</i>	131.67	4.05	29.51
<i>Gibberula miliaria</i>	71.33	3.78	33.29
<i>Triphora perversa</i>	62	3.65	36.94
Cluster D - Elba Av. Similarity 53.15			
<i>Bittium reticulatum</i>	1769	7.1	7.1
<i>Gouldia minima</i>	72.33	4.37	11.47
<i>Turritella communis</i>	229.33	4.3	15.77
<i>Plagiocardium papillosum</i>	210.67	4.06	19.83
<i>Timoclea ovata</i>	816.67	4.06	23.89
<i>Corbula gibba</i>	374.33	4.05	27.94
<i>Jujubinus exasperatus</i>	101	3.95	31.89

Tab. 6 - Breakdown of average similarity within each cluster identified in dendrogram of Fig. 4c. Species are listed in order of contribution, up to 80% of similarity.

bona cimex, *J. exasperatus*, *Gibberula miliaria* and *Triphora perversa*. Cluster D encompasses the three Elba stations, with an average similarity of 53.15% and indicator species: *B. reticulatum*, *G. minima*, *T. communis*, *P. papillosum*, *T. ovata*, *C. gibba* and *J. exasperatus* (Tab. 6). The MDS plot (Fig. 4d) shows that the actual environmental gradient subtending the ordination opposes groups A and B, through the transition of C and D.

The most severe data reduction in the qualitative approach retains only the exclusive and preferential characteristic species from the data matrix. After this operation only 80 species are retained (= "b80"; Tab. 4). In the dendrogram (Fig. 4e), at the 45% of B-C sim. four clusters separate, of which cluster A (the three S. Teodoro stations; average similarity = 78.12%) is characterised by *H. stagnalis*, *C. glaucum* and *L. lacteus*. Cluster C (the Baratti stations, average similarity = 86.6%) is well represented by *G. miliaria*, *G. trapezia*, *C. ventricosus*, and *M. cristata*. Cluster B (the Calabrian stations) and D (the three Elba stations) have an average similarity of 50.02% and 50.97% respectively. The first two indicator species in both cluster B and D are the same: *T. communis* and *C. gibba*, but their contribution to the

total average similarity within the clusters is much higher in cluster B (48.17%) than in cluster D (21.6%). Cluster B is also characterised by *P. rudis*, *N. pella*, *A. prismatica*, *A. nitida* and *T. granulata*, whilst in cluster D are *P. papillosum*, *T. reticulata*, and *T. donacina*. The MDS ordination (Fig. 4f) shows the excluded Montecristo station at the opposite of cluster A, with clusters B, D, C laying in between, along a perpendicular gradient.

Discussion

The low diversity index and low evenness obtained for the S. Teodoro stations reflect a higher number of individuals for fewer species than in the other stations. In the case of the S. Teodoro lagoon, the species *Hydrobia stagnalis* alone composes the 70-80 % of the total number of individuals, with other few species (*Cerithium vulgatum*, *Cerastoderma glaucum*, *Loripes lacteus*) to compose most of the remaining 20-30%. Similarly, at the Calabrian station Bel7E (Belvedere) the species *T. communis* represents 90.8% of the total number of individuals.

On the contrary, the very high diversity shown by the Baratti and El70 stations is likely to be due to their shallow location and the mixed nature of the thanatocoenosis (transport from neighbouring biotopes, Corselli 1981).

The k-dominance curves of the averaged Baratti stations crossing the El70 curve means on one side that their diversity is similar (Platt & al. 1984), on the other side that the Baratti stations have less highly dominant species and more rare species than El70 (Magurran 1988).

Clusters A and B (the S. Teodoro and Calabrian stations respectively) remain clearly defined from the full-matrix preliminary analysis throughout all steps of both quantitative and qualitative approaches. In particular, cluster A joins the other clusters at the lowest level of similarity in all dendrograms, testifying the peculiarity of the paralic environment. Also the indicator species remain almost unchanged in the different approaches. The reason is that both cluster A and B are dominated by few very abundant species which have also a particular significance in benthic bionomy, namely *H. stagnalis* and *C. glaucum* for the paralic environment, *T. communis* and *C. gibba* for the *Turritella* facies of VTC (Tab. 4).

In the "quantitative" multivariate analysis, the full matrix, "n154" and "p>1%" classifications and MDS ordinations result in the same clustering of stations at increasing level of B-C similarity (Figs. 3a-3f).

Only for the most severe data reduction at $p > 3\%$, clusters C and D are reworked, with El15 splitting from the other two Elba stations and substituted by the Montecristo station (Fig. 4a). The Baratti stations (BarA+BarB) join the latter group (El70+El19+MC22)

Quantitative approach "n154"				
Species	Elba + Montecristo	Baratti	Average dissimilarity 61.97	
	Av. abund.	Av. abund.	δ%	δ % cum.
<i>Timoclea ovata</i>	629	-	1.96	1.96
<i>Hinia incassata</i> *	-	152	1.86	3.82
<i>Littorina neritoides</i> *	-	93.5	1.65	5.47
<i>Rissoa ventricosa</i> *	-	72	1.56	7.03
<i>Tricolia speciosa</i> *	-	64	1.52	8.55
<i>Cianculus cruciatus</i> *	-	55.5	1.46	10.01
<i>Parvicardium minimum</i>	885	-	1.44	11.46
<i>Rissoa variabilis</i> *	-	51.5	1.43	12.88
<i>Rissoina bruguierei</i>	.75	83.5	1.42	14.3
<i>Turbona cimicoides</i>	82.5	-	1.42	15.72
<i>Goniostoma</i>	-	48	1.4	17.12
<i>auriscalpium</i> *	-	-	-	-
<i>Tricolia pullus</i> *	31.25	196.5	1.39	18.51
<i>Chauvetia minima</i> *	-	41.5	1.36	19.87
<i>Torbona geryonia</i> *	-	39.5	1.35	21.21
<i>Myrtea spinifera</i> *	266.75	-	1.34	22.55
<i>Corbula gibba</i>	281	1	1.31	23.86
Qualitative approach "b154"				
Species	Baratti + Montecristo	Elba	Average dissimilarity 57.63	
	Av. abund.	Av. abund.	δ%	δ % cum.
<i>Turbona cimex</i>	100.67	-	2.43	2.43
<i>Timoclea ovata</i>	22.33	816.67	2.28	4.71
<i>Corbula gibba</i>	1	374.33	2.24	6.95
<i>Turritella communis</i>	1.33	229.33	2.08	9.03
<i>Parvicardium minimum</i>	16	1164	2.05	11.09
<i>Turbona reticulata</i>	-	58.67	2.05	13.13
<i>Nucula sulcata</i>	-	96.33	1.88	15.02
<i>Gibberula miliaria</i>	71.33	.67	1.81	16.83
<i>Turbona cimicoides</i>	9	101	1.67	18.49
<i>Nuculana pella</i>	-	84	1.6	20.1
<i>Corbula gibba</i>	281	1	1.31	23.86

Tab. 7 - Dissimilarity term analysis between Clusters C and D identified in Figs. 3c,d ("n154") and Figs. 4c,d ("b154"). Species are listed in order of contribution to the total dissimilarity between clusters, up to 25% of total dissimilarity. Asterisks indicate the species not retained in the qualitative approach (see also Table 4).

at about 60% of B-C sim. (Fig. 4a), while El15 joins the rest of the cluster at only 54% of B-C sim. Retaining only the species with $p > 3\%$ causes the disappearance of many species which were significant in "n154" and " $p > 1\%$ " elaborations, increases the weight of very abundant and ubiquitous species such as *B. reticulatum*, *S. lactea* and *J. exasperatus* and finally neutralises the effort to correctly estimate the latter through the double square root transformation of raw abundance data. Therefore, the data reduction at $p > 3\%$, though still effective in separating clusters at a very coarse level (a different environmental domain), appears unable to define detailed clustering within similar environments, such as the detritic bottoms and their transitions to specific facies or neighbouring biotopes.

In the "qualitative" multivariate analysis, both data reductions ("b154" and "b80") join MC22 to the Baratti stations, although at different level of similarity. The three Elba stations remain always in a clearly separate cluster and the same is true, as already observed, for the S. Teodoro and Calabrian stations. However, it is important to note that in the "b80" elaboration the Calabrian stations appear more similar to the Elba cluster (linkage at about 33% of B-C sim., than the Baratti + Monte-

cristo cluster (linkage at about 21% of B-C sim.), unlike the results of all previous elaborations (Fig. 4e-f). Considering that El15 is a muddy detritic with a VTC component, this similarity was expected. The "b80" MDS ordination (Fig. 4f) highlights the separation between the paralic and marine domains (cluster A versus the others along the horizontal gradient in Fig. 4f). It also confirms the separation of station MC22 from the Baratti cluster, clarifying the gradient of decreasing mud input and increasing current influence along the transition from cluster C to D and B.

In order to better understand the effect of the quantitative and qualitative approaches over the same data matrix, it seems useful to compare the "n154" and the "b154" data reductions, which both operate on 154 retained species (Tab. 4, Figs. 3c, 3d, 4c, 4d). The paralic environment represented by the S. Teodoro stations, and the *Turritella* facies of VTC are clearly defined in both elaborations, linking to the remaining stations at low levels of similarity (about 10% of B-C sim. for the S. Teodoro stations, about 20% for the Calabrian stations). When dealing with detritic bottoms a significantly different clustering is produced. In particular, the Montecristo station is joined to the shallow and current swept (SGCF) Baratti stations by the qualitative approach, whilst is grouped with the coastal detritic Elba bottoms by the quantitative approach. The comparison of the similarity breakdown for the "n154" and "b154" elaborations (Tables 5-6) shows that in cluster C of both tables the indicator species are known to inhabit relatively shallow habitats, often among algae or seagrasses. On the contrary, cluster D of both elaboration lists also some mud-related species such as *T. communis* or *T. cimicoides*, together with species more typical of mixed sediments and detritic biotopes, such as *G. minima*, *T. ovata* or *P. papillosum*. The thanatocoenosis of Montecristo station is actually made of coastal detritic species (much like the Elba group stations) mixed with hard-bottom and infralittoral species and sand-related species (like the mixed thanatocoenosis of the Baratti stations). Both clustering are therefore acceptable from the point of view of the possible ecological interpretation. However, a greater effort must be considered in the aim to understand the meaning of clustering where most of the indicator species have a poor ecological significance, like that resulting from the "n154" elaboration.

Looking at the dissimilarity analysis between clusters D and C in the two approaches (Tab. 7), most of the species accounting for the observed dissimilarity in the quantitative "n154" elaboration are not retained in the qualitative "b154". Only *T. ovata*, *C. gibba* and *T. cimicoides* are shared by the two dissimilarity analysis. They result to be useful discriminant species between the two clusters since they are significant for the benthic bionomy and abundant enough to have some weight in computation.

Conclusions

The stations selected for this paper represent different levels in the hierarchy of division of the benthic environment (domain>biocoenosis>facies).

The highest level of difference, that is the paralic versus open marine benthos, is easily identified by both the quantitative and qualitative approaches, at all levels of data reduction. Also the comparison of different biocoenoses leads easily to their identification. In particular, a facies of a biocoenosis (the *Turritella* facies of VTC) is easily circumscribed in respect of other biocoenoses since is not only compositionally different, but also numerically signed by the strong dominance of the species defining the facies, which justifies the similar result obtained in the two approaches. The quantitative approach is a "no assumption" method that require a considerable effort of interpretation of the obtained clustering when many poorly known or scarcely ecologically defined species are involved. It is of course the only method allowed when assumption cannot be done for lacking of basic information (fossils, unknown

species, etc.).

The most severe data reductions in the quantitative approach, in particular "p>3%" has the effect to enhance the weight of the most abundant and sometimes poorly significant species of the matrix, leading to a very coarse separation of the different biotopes.

When dealing with large-sized data matrices of Mediterranean benthic thanatocoenoses, it is recommended to use a qualitative approach for data reduction, prior to perform the quantitative multivariate analysis (classification, ordination, similarity and dissimilarity analysis). This procedure seems the most suitable for the identification of "natural" grouping of biotopes, since the results are not obscured by the diffuse occurrence of the most common and ubiquitous species.

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