

The molluscan assemblage of a transitional environment: the Mediterranean *maërl* from off the Elba Island (Tuscan Archipelago, Tyrrhenian Sea)

Daniela Basso & Francesco Brusoni

Università degli Studi di Milano, Bicocca
Dipartimento Scienze Geologiche e Geotecnologie,
Piazza della Scienza 4,
20126 Milano, Italy,
Fax: 0264484273,
daniela.basso@unimib.it

Abstract

A newly discovered *maërl* bottom was sampled by grab at 45 m depth off the western coasts of Elba Island. Although the dominant, branched free-living corallines represent the *maërl* facies of the Coastal Detritic Biocoenosis (DC), the living molluscs are related to a different biocoenosis: the Coarse Sands and Fine Gravels under bottom currents (SGCF). In the molluscan shell assemblage, 2186 specimens belonging to 123 species have been analyzed on the basis of abundance, life habit, state of preservation, substrate preference and trophic behaviour. The evolution of the bottom has been traced, from terrigenous SGCF to biogenic DC in the recent past and toward SGCF again in the present. It is suggested that the *maërl* facies in the Mediterranean, at the boundary between DC and SGCF, would require a dynamic equilibrium between the two Biocoenoses and the ecological factors subtending them.

Riassunto

L'associazione a molluschi di un ambiente transizionale: il *maërl* mediterraneo dell'isola d'Elba (Arcipelago Toscano, Mar Tirreno). Viene esaminato un campione di sedimento prelevato a 45 m di profondità in prossimità della località di Pomonte (Isola d'Elba occidentale). La dominanza di talli viventi di Rhodophyceae calcaree ramificate libere fa attribuire il biotopo alla Biocenosi del Detritico Costiero (DC) nella sua facies del *maërl*, segnalata per la prima volta in questa località. La tanatocenosi a molluschi viene descritta in base alle abbondanze, alla conservazione, alle affinità per i diversi tipi di substrato e le differenti biocenosi, all'habitus e al trofismo. Questo permette di ricostruire l'evoluzione del fondale da una Biocenosi SGCF a DC nel recente passato, con una nuova tendenza verso SGCF testimoniata dalla malacofauna vivente. Si ipotizza che il mantenimento della facies di *maërl* sia condizionato dall'esistenza di un equilibrio dinamico tra le due biocenosi.

Key words

Mollusca, thanatocoenosis, benthic bionomy, Mediterranean, *maërl*, Elba Island.

Introduction

The Coastal Detritic Biocoenosis (DC) of the Mediterranean circalittoral zone can develop to several facies, identified by the local dominance of one or a little group of species, without affecting the qualitative composition of the biocoenosis (Péres & Picard, 1964; Picard, 1965). Among these, the coralline-dominated facies (calcareous Rhodophyta, Corallinales and Peyssonneliaceae) are usually related to relatively high water energy (Péres & Picard, 1964; Bourcier, 1981; Basso, 1992, 1998).

The growth and subsequent fragmentation and multiplication of branched, free-living coralline algae and the accumulation of their remains generate new biogenic hard substrates, more frequently 1 to 5 cm in diameter, on the original detritic bottom. The biogenic accumulation of mixed living and dead thalli is called *maërl* (a Breton word).

Mediterranean *maërl* is poorly known in comparison with its Atlantic counterpart and its occurrence is considered rare (Jacquotte, 1962; Bellan-Santini *et al.*, 1994).

The coralline flora of a *maërl* bottom identified for the first time and sampled in 1990 along the western coast of Elba Island (abe 120-121; Fig. 1), was studied by Mari (1999), who reported a rich and diversified coralline flora. Beside the dominant free-living corallines, the sampled sediment represented a unique opportunity to investigate the composition of the

molluscan dead assemblage of a Mediterranean *maërl* bottom, unknown so far.

The western Elba Island has a wide shelf, regularly deepening with a gradient lower than 1:40 (Fabbri & Selli, 1972). Further west of sample abe 120-121, toward the open sea, the bottom gradually deepens down to the continental slope. During the sampling cruise, a *Posidonia* meadow and shallower sandy sediments were recorded in the area between abe 120-121 and the coast.

The prevailing edaphic factor in the sampling area is a current flowing northward along the western coast of the Elba Island, both at surface and at the sampling depth (45 m) (Stocchino & Testoni, 1968). This paper is aimed to present and discuss the composition and ecological meaning of the living and dead molluscan assemblages occurring in the *maërl* bottom off the Elba Island.

The *maërl*

According to marine benthic bionomy (Péres & Picard, 1964), the substrate of the DC Biocoenosis consists of present-day and recent detritic deposits, including the biogenic gravels, issued by neighbouring infralittoral or circalittoral environments, like the *Posidonietum* complex or the Coralligenous Biocoenosis, respectively.

The *maërl* is as a facies of DC identified by the dominance of

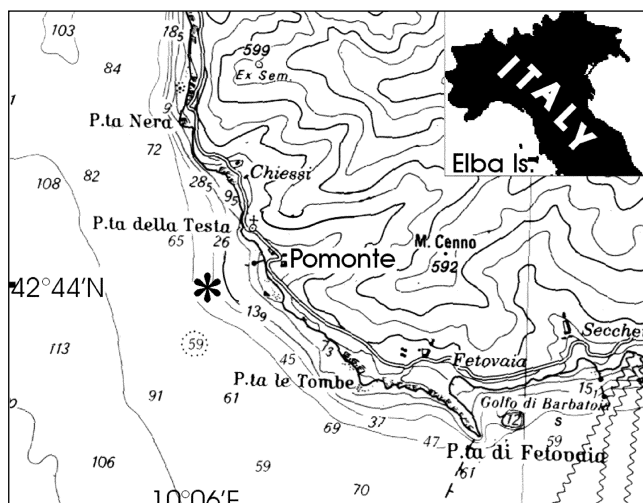


Fig. 1. Sampling area and location of sample abe 120-121 (asterisk).

Fig. 1. Area di campionamento e località del prelievo abe 120-121 (asterisco).

free-living, branched coralline algae. It is not a distinct biocoenosis, because of the absence of exclusive characteristic taxa (Jacquotte, 1961; Pérès & Picard, 1964; Falconetti, 1969). The colonization of detritic/sandy sediments by the coralline flora is controlled by suitable conditions of light, water motion and low sedimentation rate (Jacquotte 1962, Pérès & Picard, 1964; Falconetti, 1969; Basso, 1998). The formation of the *maërl* banks is not due to passive transport of thalli, but to the accumulation of living and dead thalli on the place of origin.

Following Jaquotte (1962), the major environmental constrain for the life of *maërl* is the occurrence of bottom currents typical of capes and channels between islands. The *maërl* association develops under the highest level of water energy that the DC Biocoenosis can tolerate. Under stronger water energy DC is replaced by the SGCF Biocoenosis, where corallines are still present but with a minor abundance and diversity (Basso, 1998). Other factors like temperature and slight variations in salinity seem to not affect the *maërl*.

Data about the living fauna of this algal facies in the Mediterranean were provided by Dieuzeide (1940), Jacquotte (1962), Pérès & Picard (1964), Picard (1965) and Falconetti (1969).

Jacquotte (1962) discussed the distinctiveness of the *maërl* association, remarking that DC and SGCF characteristic species are often found together. She concluded that it is not possible to identify any exclusive characteristic species of *maërl*, and since most of species are DC-related, *maërl* must therefore be considered as a facies of DC. In a study about the bionomy of the Castiglione Bay (Algeria), Falconetti (1969) showed that *maërl* can superimpose on both DC and SGCF biocoenoses, in a situation of disequilibrium ("*déséquilibre biocoenotique*"). He concluded that the *maërl* facies is independent from the pre-existing benthic biocoenosis, being controlled only by a peculiar combination of light, mud fraction and water energy.

More recently, an increasing concern on the rarefaction of some *maërl* species, like *Lithothamnion corallioides* and *Phymatolithon calcareum* has lead to the inclusion of *maërl* in the list of priority habitats (Annex V of the EU Habitats Directive). Impact of dredging and trawling on *maërl* beds in the Mediterranean have been recently addressed (Pinot, 1997; BIOMAERL team, 2003; Bordehore *et al.*, 2003).

Both *L. corallioides* and *P. calcareum* are presently included in the protected flora of Italy.

The *maërl* is an intertidal to sublittoral algal association along the European Atlantic coasts. Because of the commercial use of these biogenic coastal deposits (e.g. for the correction of soil acidity), the structure, composition, faunal association and response to human disturbance are much better known for the Atlantic *maërl* than the Mediterranean one (among others: Cabioch, 1968; Keegan, 1974; Bosence, 1979; Bosence & Wilson, 2003; Hall-Spencer & Moore, 2000; Hall-Spencer *et al.*, 2003; Kamenos *et al.*, 2003).

Material and methods

Material is from a single station, 45 m depth (Lat. 42°44.21'N, Long. 10°06.46'E), sampled by a modified Van Veen grab (capacity 50 dm³, sampled surface 2500 cm²) during the cruise ATAU90 of the *R/V Minerva*. Two samples (abe 120 and abe 121) from the same station have been cumulated.

A sub-sample was taken for particle size analysis by dry sieving for the fraction > 63 µm and by sedimentation column for pelite (Buchanan & Kain, 1971). All living corallines were collected for the floristic analysis of the algal association (Mari, 1999). The sample was then sieved on 1 mm mesh and the living molluscs were picked up. The residual 8800 cc of sediment was air dried and stored for the study of the dead molluscan assemblage. Seven sub-samples (500 cc each) were analyzed separately and used to calculate the volume/species curve.

The species identification under stereomicroscope and the specimens counting was limited to molluscs, whilst for the other phyla (coralline fragments and skeletal remains of echinoderms, annelids, brachiopods, crustaceans and bryozoans) we performed an estimate of their percentage abundance (volume) in the sediment. However, chitons were excluded from further consideration given the difficulty to define the number of individuals from the number of disarticulated valves. Molluscan taxonomy follows Sabelli *et al.* (1990-1992).

The criteria for retaining and counting shell remains in paleoecological analyses are given by Di Geronimo & Robba (1976). For each species we evaluated the "status" (juveniles only, adults only or population) and the degree of shell preservation and calculated abundance and percentage dominance. In order to allow the numerical treatment, we coded the status and preservation, following Basso & Corselli (in press); Brett & Baird, 1986; Kowaleski *et al.*, 1995; Davies *et al.*, 1990; Powell *et al.*, 2002. In the code "state of preservation", the preservation of soft parts (ligament, periostracum) and original colors, the occurrence of abrasion, breakage, dissolution and loss of ornaments have been collectively considered in order to assign the code. Each species is given a code of preservation according to its best preserved specimen. State of preservation ranges from 1 (very poorly preserved specimens) to 4 (very fine preservation) with code 5 only given to populations occurring both in the live and dead assemblages.

The acronyms of Biocoenoses follow Pérès & Picard (1964; Table 1).

Results

The sediment is composed of 87% sand and about 8% gravel, testifying the winnowing action of the water energy. The sieved fraction (>1 mm) is mostly biogenic (82%), mainly consisting of corallines and molluscan hard parts. The remain-

ing 18% consists of terrigenous clasts (Tab. 2). This composition falls within the definition of the RHODALGAL sedimentary facies (Carannante *et al.*, 1988).

The living molluscan association (Tab. 3) is also present in the shell assemblage, with the exception of *Ensis ensis*, and is composed of 89% infaunal species.

In the dead assemblage, 2186 specimens of molluscs belonging to 123 species, of which 73 Gastropoda, 1 Scaphopoda, 46 Bivalvia (Tab. 4) were collected. Among the chitons, some valves of *Acanthochitona fascicularis* (Linneo, 1767), *Callochiton septemvalvis euplaeae* (O.G. Costa, 1829) and a third unidentified species were recognized. The volume/species curve (Fig. 2) indicates that 3500 cc of sediment is the minimum volume to provide a representation of the whole dead assemblage.

Discussion

The living molluscan association is dominated by current-loving/SGCF species (Fig. 3). However, the surface and volume

Acronym	Meaning
AP	Photophilic algae
C	Coralligenous
DC	Coastal detritic
HP	<i>Posidonia</i> meadows (complex)
SFBC	Fine well-sorted sands
SGCF	Coarse sands and fine gravels under bottom currents
SVMC	Muddy sands in sheltered areas
VP	Bathyal muds
PE	Heterogeneous assemblage

Table 1. Explanation of the acronyms used in the text. Acronyms were formed from the original French name of Biocoenoses (Péres & Picard, 1964).

Tab. 1. Spiegazione degli acronimi utilizzati nel testo. Gli acronimi sono derivati dai nomi francesi originali delle Biocenosi (Péres & Picard, 1964).

Coralline fragments	53%
Terrigenous clasts	18%
Molluscan shell remains	14%
<i>Posidonia oceanica</i> remains	6%
Peyssonneliaceae	3%
Bryozoans	2%
Echinoderms	2%
Annelids	1%
Crustaceans, benthic foraminifers, other remains	1%

Table 2. Visual estimate of the residue after 1 mm sieving as percentage of the total volume.

Tab. 2. Composizione del residuo dopo setacciatura su maglia da 1 mm, espressa come percentuale del volume totale.

Species	abundance
<i>Acanthochitona fascicularis</i> (Linneo, 1767)	1
<i>Vexillum ebenus</i> (Lamarck, 1811)	1
<i>Striarca lactea</i> (Linneo, 1758)	1
<i>Glycymeris</i> sp.	1 juv.
<i>Astarte fusca</i> (Poli, 1795)	3
<i>Plagiocardium papillosum</i> (Poli, 1795)	1
<i>Mactra</i> sp.	1 juv.
<i>Ensis ensis</i> (Linneo, 1758)	1
<i>Clausinella brongniartii</i> (Payraudeau, 1826)	7
<i>Gouldia minima</i> (Montagu, 1803)	1
<i>Venus casina</i> Linneo, 1758	2

Table 3. Living molluscs collected in sample abe 120-121.

Tab. 3. Molluschi viventi raccolti nel campione abe 120-121.

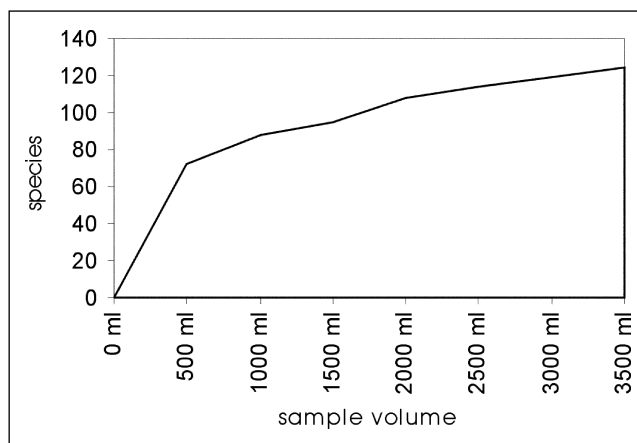


Fig. 2. Volume/species curve for sample abe 120-121, showing the number of species in the sample (Y axis), at each incremental sub-sample, 500 cc each. At the seventh sub-sample, for a total volume of 3500 cc, the increase in number of species is very small and tends to zero.

Fig. 2. Curva volume/specie per il campione abe 120-121, che mostra il numero di specie nel campione (asse delle Y), all'aggiunta di sotto-campioni di 500 cc ciascuno. Dopo il settimo sotto-campione, per un volume totale di 3500 cc, l'incremento in numero delle specie è molto piccolo e tende a zero.

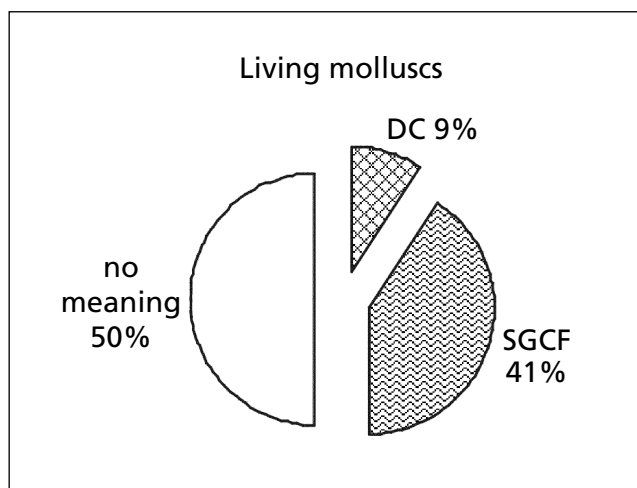


Fig. 3. The present-day biocoenosis of abe 120-121 (only living molluscs).

Fig. 3. L'attuale biocenosi di abe 120-121 (solo molluschi viventi).

dominance of branched, free-living corallines defines the *maërl* facies of DC (Mari, 1999). The life habit of the living molluscs is mainly infaunal, in agreement with Falconetti (1969; 78% infauna and 22% epifauna).

In the molluscan shell assemblage (= thanatocoenosis), the species with the maximum abundance is the byssate bivalve *Striarca lactea* (9.8%), which frequently occurs in small crevices and in the lattice of interlocked coralline branches. Among the other high-abundance species, *Bittium reticulatum* (8.9%) is an ubiquitous detritus feeder and *Gonilia calliglypta* (8.7%) is a sand-loving species, frequently occurring on current-swept bottoms. Among the molluscs accounting for more than 3% in dominance, two species are DC characteristic (*Gouldia minima* 6.3% and *Turritella turbona* 3.1%). *Timoclea ovata* (3.6%) is also commonly found in detritic bottoms. On the contrary, other two species are SGCF characteristic (*Glycymeris glycymeris* 4.4%, with a poor preservation, and *Clausinella brongniartii* 4.1%) accompanied by *Astarte fusca* (3.4%), which is common in many DC and SGCF bottoms. The

Species	Ab.	D %	Pres	St.	bioc.
<i>Striarca lactea</i> (Linneo, 1758)	215	9,800	5	A	
<i>Bittium reticulatum</i> (Da Costa, 1778)	195	8,900	4	A	
<i>Gonilia calliglypta</i> (Dall, 1903)	193	8,700	3	A	
<i>Gouldia minima</i> (Montagu, 1803)	138	6,300	5	P	DC pref
<i>Glycymeris glycymeris</i> (Linneo, 1758)	96	4,400	2	P	SGCF excl
<i>Clausinella brongiartii</i> (Payraudeau, 1826)	90	4,100	5	P	SGCF pref
<i>Timoclea ovata</i> (Pennant, 1777)	78	3,600	4	P	
<i>Astarte fusca</i> (Poli, 1795)	74	3,400	5	P	
<i>Turritella turbona</i> (Monterosato, 1877)	67	3,100	3	P	DC excl
<i>Spisula subtruncata</i> (Da Costa, 1778)	66	3,000	2	J	SFBC excl
<i>Anomia ephippium</i> (Linneo, 1758)	56	2,600	2	P	DC pref
<i>Bolma rugosa</i> (Linneo, 1767)	54	2,500	3	J	DC pref
<i>Plagiocardium papillosum</i> (Poli, 1795)	54	2,500	5	P	DC pref
<i>Chlamys varia</i> (Linneo, 1758)	50	2,300	4	P	DC pref
<i>Jujubinus exasperatus</i> (Pennant, 1777)	41	1,900	3	P	
<i>Lucinella divaricata</i> (Linneo, 1758)	36	1,650	4	P	
<i>Alvania beani</i> (Hanley in Thorpe, 1844)	34	1,600	4	A	DC excl
<i>Corbula gibba</i> (Olivi, 1792)	33	1,500	3	P	PE
<i>Alvania geryonia</i> (Nardo, 1847)	30	1,400	4	A	
<i>Jujubinus montagui</i> (Wood, 1828)	26	1,200	3	J	
<i>Calliostoma ziziphinum</i> (Linneo, 1758)	25	1,140	3	J	DC pref
<i>Parvicardium minimum</i> (Philippi, 1836)	25	1,140	2	A	
<i>Nucula sulcata</i> (Bronn, 1831)	23	1,050	2	P	
<i>Arca tetragona</i> (Poli, 1795)	23	1,050	2	P	DC pref
<i>Euspira nitida</i> (Donovan, 1804)	22	1,000	2	J	
<i>Goodallia triangularis</i> (Montagu, 1803)	19	0,870	2	A	
<i>Tellina donacina</i> (Linneo, 1758)	19	0,870	4	P	DC excl
<i>Calyptrea chinensis</i> (Linneo, 1758)	17	0,780	3	P	
<i>Gibbula guttadauri</i> (Philippi, 1836)	16	0,700	3	J	
<i>Cerithium vulgatum</i> (Bruguere, 1792)	14	0,640	3	J	SVMC pref
<i>Hiatella arctica</i> (Linneo, 1767)	13	0,590	3	P	
<i>Hyalopecten similis</i> (Laskey, 1811)	12	0,550	3	A	
<i>Psammobia costulata</i> Turton, 1822	12	0,550	3	A	SGCF excl
<i>Alvania cimex</i> (Linneo, 1758)	11	0,500	2	P	
<i>Vexillum tricolor</i> (Gmelin, 1791)	11	0,500	4	P	AP pref
<i>Murexsul aradasi</i> (Poirier, 1883 ex Monterosato ms.)	10	0,460	3	P	
<i>Mitrolumna olivoidea</i> (Cantraine, 1835)	10	0,460	4	P	
<i>Raphitoma hystrix</i> (Bellardi, 1847)	10	0,460	4	P	
<i>Limea loscombi</i> (Sowerby G.B.I, 1823)	10	0,460	2	A	DC excl
<i>Glans aculeata</i> (Poli, 1795)	10	0,460	3	J	
<i>Modiolula phaseolina</i> (Philippi, 1844)	9	0,400	4	J	DC excl
<i>Raphitoma linearis</i> (Montagu, 1803)	8	0,360	3	A	C pref
<i>Diplodonta apicalis</i> Philippi, 1836	8	0,360	4	P	SGCF excl
<i>Gibbula fanulum</i> (Gmelin, 1791)	7	0,300	2	J	DC pref
<i>Homalopoma sanguineum</i> (Linneo, 1758)	7	0,300	2	A	
<i>Alvania hispidula</i> (Monterosato, 1884)	7	0,300	2	A	
<i>Muricopsis cristata</i> (Brocchi, 1814)	7	0,300	2	P	
<i>Pododesmus patelliformis</i> (Linneo, 1761)	7	0,300	2	J	
<i>Calliostoma conulus</i> (Linneo, 1758)	6	0,270	3	J	
<i>Alvania cancellata</i> (Da Costa, 1778)	6	0,270	2	P	
<i>Fusinus rudis</i> (Philippi, 1844)	6	0,270	2	J	
<i>Granulina occulta</i> (Monterosato, 1869)	6	0,270	4	A	
<i>Alvania cimicoides</i> (Forbes, 1844)	5	0,230	3	A	VP pref
<i>Alvania testae</i> (Aradas & Maggiore, 1844)	5	0,230	2	A	
<i>Raphitoma concinna</i> (Scacchi, 1836)	5	0,230	4	P	
<i>Volvarina mitrella</i> (Risso, 1826)	5	0,230	3	A	
<i>Chlamys flexuosa</i> (Poli, 1795)	5	0,230	4	P	DC excl
<i>Neolepton sulcatulum</i> (Jeffeys, 1859)	5	0,230	2	A	
<i>Fissurellidae</i> sp.	4	0,180	3	A	
<i>Monophorus perversus</i> (Linneo, 1758)	4	0,180	3	A	
<i>Comarmondia gracilis</i> (Montagu, 1803)	4	0,180	2	A	C pref
<i>Gibberula miliaria</i> (Linneo, 1758)	4	0,180	4	A	HP pref
<i>Dentalium dentalis</i> (Linneo, 1758)	4	0,180	3	P	
<i>Palliolium incomparabile</i> (Risso, 1826)	4	0,180	4	A	DC excl

Species	Ab.	D %	Pres	St.	bioc.
<i>Glans trapezia</i> (Linneo, 1767)	4	0,180	2	A	
<i>Laevicardium crassum</i> (Gmelin, 1791)	4	0,180	2	A	SGCF pref
<i>Venus casina</i> (Linneo, 1758)	4	0,180	5	P	SGCF excl
<i>Pitar rudis</i> (Poli, 1795)	4	0,180	2	P	DC pref
<i>Emarginula rosea</i> (T. Bell, 1824)	3	0,140	4	A	
<i>Pusillina marginata</i> (Michaud, 1832)	3	0,140	3	A	
<i>Rissoina bruguieri</i> (Payraudeau, 1826)	3	0,140	3	A	
<i>Cerithidium submamillatum</i> (De Rayneval & Ponzi, 1845)	3	0,140	2	A	
<i>Cerithiopsis tubercularis</i> (Montagu, 1803)	3	0,140	3	A	
<i>Mitrella</i> sp cfr <i>scripta</i> (Linneo, 1758)	3	0,140	2	J	
<i>Mangelia unifasciata</i> (Deshayes, 1835)	3	0,140	4	P	
<i>Turridae</i> sp. 1	3	0,140	2	A	
<i>Ringicula conformis</i> (Monterosato, 1877)	3	0,140	3	A	
<i>Ctena decussata</i> (Costa O.G., 1829)	3	0,140	2	P	
<i>Dipladonta brocchi</i> (Deshayes, 1852)	3	0,140	4	J	
<i>Paphia aurea</i> (Gmelin, 1791)	3	0,140	2	J	SVMC pref
<i>Thracia pubescens</i> (Pulteney, 1799)	3	0,140	2	J	
<i>Emarginula tenera</i> (Monterosato in Locard, 1892)	2	0,090	2	A	
<i>Tricolia pullus pullus</i> (Linneo, 1758)	2	0,090	1	J	
<i>Alvania consociella</i> (Monterosato, 1884)	2	0,090	2	A	
<i>Alvania lineata</i> (Risso, 1826)	2	0,090	2	A	
<i>Bittium jadertinum</i> (Brusina, 1865)	2	0,090	3	A	
<i>Metaxia metaxa</i> (Delle Chiaje, 1828)	2	0,090	4	A	
<i>Aporrhais serresianus</i> (Michaud, 1828)	2	0,090	2	J	
<i>Dermomurex scalaroides</i> (Blainville, 1829)	2	0,090	2	A	
<i>Chauvetia brunnea</i> (Donovan, 1804)	2	0,090	1	A	
<i>Mitrella minor</i> (Scacchi, 1836)	2	0,090	4	P	
<i>Vexillum ebenus</i> (Lamarck, 1811)	2	0,090	5	P	
<i>Raphitoma laviae</i> (Philippi, 1844)	2	0,090	3	A	
<i>Mangelia costulata</i> (Blainville, 1829)	2	0,090	2	A	
<i>Haminoea hydatis</i> (Linneo, 1758)	2	0,090	3	A	
<i>Odostomia conoidea</i> (Brocchi, 1814)	2	0,090	2	A	
<i>Nuculana pella</i> (Linneo, 1767)	2	0,090	2	A	PE
<i>Tellina crassa</i> Pennant, 1777	2	0,090	3	P	SGCF excl
<i>Paphia lucens</i> (Locard, 1886)	2	0,090	4	J	
<i>Patella</i> sp.	1	0,046	1	J	
<i>Diodora graeca</i> (Linneo, 1758)	1	0,046	1	J	
<i>Gibbula magus</i> (Linneo, 1758)	1	0,046	2	A	DC pref
<i>Manzonina crassa</i> (Kanmacher, 1798)	1	0,046	2	A	
<i>Rissoa auriscalpium</i> (Linneo, 1758)	1	0,046	1	A	
<i>Triphora</i> sp.	1	0,046	2	A	
<i>Epitonium algerianum</i> (Weinkauff, 1866)	1	0,046	4	A	
<i>Capulus ungaricus</i> (Linneo, 1758)	1	0,046	4	J	
<i>Crepidula unguiformis</i> (Lamarck, 1822)	1	0,046	1	J	
<i>Cyclope neritea</i> (Linneo, 1758)	1	0,046	1	J	
<i>Philbertia pseudohystrix</i> (Sykes, 1906)	1	0,046	1	A	
<i>Mangelia smithii</i> (Forbes, 1840)	1	0,046	1	A	
<i>Turridae</i> sp. 2	1	0,046	2	A	
<i>Bulla striata</i> (Bruguere, 1789)	1	0,046	1	J	
<i>Bathyarca grenophia</i> (Risso, 1826)	1	0,046	2	A	
<i>Limatula gwyni</i> (Sykes, 1903)	1	0,046	3	J	DC excl
<i>Loripes lacteus</i> (Linneo, 1758)	1	0,046	2	J	SVMC excl
<i>Kellia suborbicularis</i> (Montagu, 1803)	1	0,046	2	A	DC pref
<i>Donax semistriatus</i> (Poli, 1795)	1	0,046	2	A	SFS excl
<i>Dosinia exoleta</i> (Linneo, 1758)	1	0,046	3	A	SGCF excl

Table 4. The molluscan shell assemblage (thanatocoenosis) from sample abe 120-121. Ab = Abundance; D = Dominance; Pres = Preservation: 5 for species occurring both in living and dead assemblage; 4, 3 = well preserved; 2, 1 = poorly preserved; St = Status: A = adults; P = population; J = juvenile (Basso & Corselli, in press). Bioc. = exclusive or preferential characteristic of Biocoenosis (Pérès & Picard, 1964).

Tab. 4. Elenco dei molluschi (tanatocenosi) del campione abe 120-121. Ab = Abbondanza; D = Dominanza; Pres = Grado di conservazione: 5 per le specie presenti sia nell'elenco dei molluschi viventi sia in tanatocenosi; 4, 3 = ben conservati; 2, 1 = mal conservati. St = Status: A = adulti; P = popolazione; J = stadio giovanile (Basso & Corselli, in stampa); Bioc. = caratteristica esclusiva o preferenziale della Biocenosi (Pérès & Picard, 1964).

bivalve *Spisula subtruncata* (3%), characteristic of infralittoral sandy bottoms (SFBC), occurs as juvenile, poorly preserved specimens. *S. subtruncata* is therefore ecologically inconsistent with the *maërl* biotope and its occurrence is possibly due to one or several past episodes of accidental colonization by juveniles that could not attain the adult stage (Fraschetti *et al.*, 1997; Staff & Powell, 1988).

The molluscan dead assemblage is characterized by exclusive and preferential characteristic species of the DC Biocoenosis (Fig. 4).

In order to clarify the structure of our shell assemblage and to discriminate among different molluscan associations that did not live contemporaneously and are now possibly mixed together (*time-averaging*; Walker & Bambach, 1971; Fürsich & Aberhan, 1990) we considered separately the life-habit of the well preserved specimens (preservation code from 3 to 5; Basso & Corselli, in press) versus the poorly preserved specimens (preservation code 1 and 2). Poorly preserved specimens mainly belong to infauna (61%), whereas among the well preserved

molluscan shells the epifaunal species are slightly prevailing (50% epifaunal vs. 45% infaunal). This result is puzzling when considering that the living molluscan association is largely dominated by infaunal species and the major underwater taphonomic processes (transport, abrasion, dissolution etc.) affect more heavily the epifauna than the infauna, in particular in coarse sediments (Powell, 1992; Best & Kidwell, 2000). As a result, we expected the infaunal fraction of our shell assemblage to be better preserved than the epifaunal one. In our sample the opposite is observed.

The positive correlation between the occurrence of coarse grains/small hard substrata and the sessile epifauna is well known in literature (Craig & Jones, 1966; Clausade, 1969; Feder *et al.*, 1994), however it is necessary to make a distinction between the coarse-grained fraction of DC sediments and the coarse-grained fraction of SGCF sediments as a possible substrate for mollusc settlement. Strong water energy, like it occurs in SGCF biotopes, removes reactive organic matter and presumably contributes to significant reductions in total faunal biomass (Pères & Picard, 1964; Nacorda & Yap, 1996; Aller, 1997; Maslowski, 2003). At extremely strong water flows at the bottom, organism sizes and biomass are reduced and epifauna can be completely eliminated by the exceeding disturbance and instability (Aller, 1997). On the contrary, the *maërl* facies of DC requires a water flow close to the bottom and some turbidity or a mud fraction in the sediment. Algal nodules and interlocking branches of *maërl* provide a three-dimensional structure promoting the settlement of small epifaunal molluscs (Bosence, 1979) and hampering the molluscan infauna (Falconetti, 1969).

The relationship between substrate preference and state of preservation shows that in the well preserved fraction of the shell assemblage the sand-loving species have a lower dominance than in the poorly preserved fraction, whereas the species adapted to hard-substrates and mixed sediments are about four times more abundant in the well preserved fraction (Fig. 5 a-b).

As long as the feeding strategy is concerned, the suspension feeders largely dominate the thanatocoenosis (66%; Fig. 6), disregarding of the state of preservation.

The molluscan shell assemblage shows a recent (centuries?)

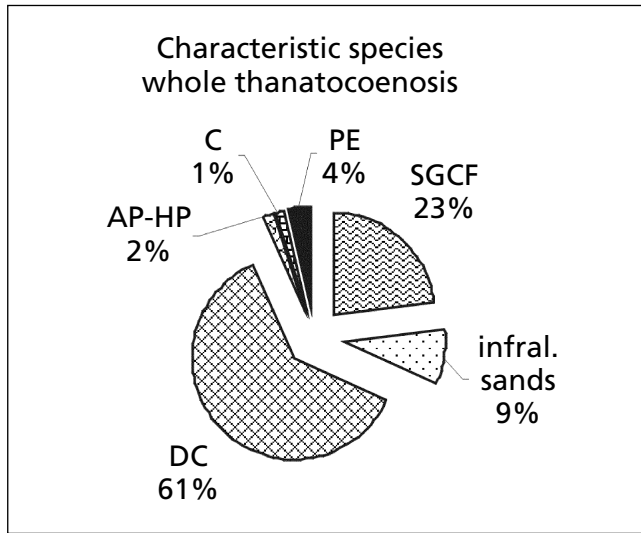


Fig. 4. The biocoenoses represented in the dead molluscan assemblage of abe 120-121. Only the exclusive and preferential characteristic species are retained.

Fig. 4. Le biocenosi rappresentate nella tanatocenosi di abe 120-121. Sono riportate solo le specie caratteristiche esclusive o preferenziali.

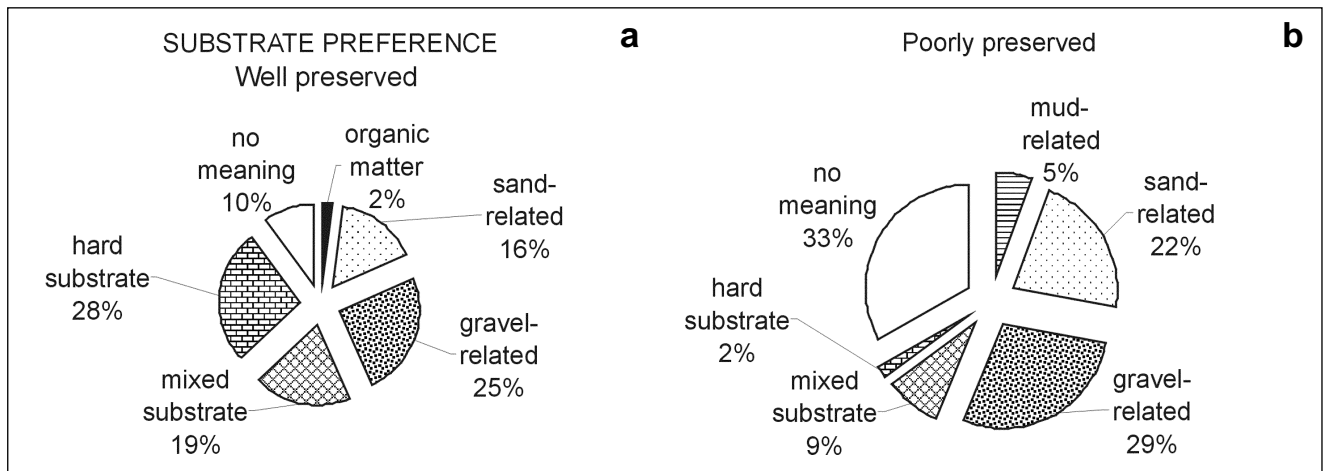


Fig. 5. Sample abe 120-121. **a.** Substrate preference of the well preserved molluscan shell assemblage (preservation code 3-5). **b.** Substrate preference of the poorly preserved molluscan shell assemblage (preservation code 1-2).

Fig. 5. Campione abe 120-121. **a.** Affinità edafica della frazione ben conservata della tanatocenosi a molluschi (conservazione 3-5). **b.** Affinità edafica della frazione mal conservata (conservazione 1-2).

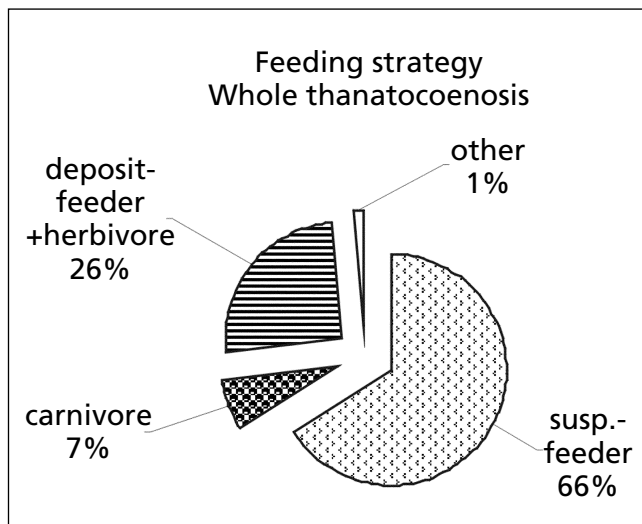


Fig. 6. Sample abe 120-121. Feeding strategy, whole thanatocoenosis.

Fig. 6. Campione abe 120-121. Trofismo, intera tanatocenosi.

Flessa & Kowalewski, 1994) transition from a SGCF to a DC Biocoenosis (Fig. 7 a-b). Time averaging decreases the temporal resolution but also filters out short-term variations, such as seasonal changes or aperiodical events (Kidwell & Flessa, 1995). The oldest SGCF bottom is recorded by the terrigenous gravels (about 18%) and the poorly preserved thanatocoenosis, made of mainly infaunal and sand-loving/SGCF-related species (Figs 5b, 7b). The coralline facies gradually superimposed, modifying the original sandy-gravelly substrate into a mixed, coarse, biodetritic accumulation of unattached coralline branches and associated remains. The occurrence of species belonging to shallower biocoenoses (AP, Fig. 7a) can be explained with the present-day transport by currents and wave action. This transport is testified in our sample by the *Posidonia oceanica* remains and the occurrence of an extended *Posidonetum* reaching down to 38 m depth.

Since no data are available on the dead molluscan assemblage of other Mediterranean *maërl* facies, we compared abe 120-121 with the molluscan assemblage of another sample, abe 06, collected at 43 m depth off Capo d'Enfola (North Elba Island) (Fallini, 1994). The sediment of sample abe 06 is made of

coralline algal gravel (dead *maërl*) mixed with sand and mud, but no living *maërl* occurs. The living molluscan association is SGCF related (Bianchi, 1993). In the thanatocoenosis, the DC exclusive and preferential characteristic species prevail, associated with about 20% of mud-related molluscs with a circalittoral/bathyal distribution (Fig. 8a). The well preserved fraction of the shell assemblage is mainly infaunal (72%).

On the contrary, the poorly preserved molluscan assemblage (characteristic species only) is dominated by infralittoral, epifaunal species, mostly related to the *Posidonetum* and/or soft algae biotopes and other hard substrates like corallines (Fig. 8b). Parts of the latter are likely to be transported from the neighbouring macrophyte-dominated biotopes (Fallini, 1994). Deposit feeders dominate the whole thanatocoenosis (71%). The past occurrence of the coralline facies did not significantly affect the composition of the molluscan shell assemblage, probably because its permanence did not last enough.

The good preservation of the mud-related molluscs (Fig. 8c) is evidence of a recent mud increase which was probably responsible of the drowning of corallines. This mud increase was apparently episodic, testified by the group of species indicative of bottom sediment instability (*Nuculana pella*) or opportunistic (*Corbula gibba*) included in the so-called "peuplements éterogènes" (13%). The phase of increased mud and organic matter input was followed by the settlement of the present-day SGCF biocoenosis.

Conclusions

Composition and bionomic structure of the molluscan dead assemblage confirm the conclusions of previous authors concerning *maërl* as a DC facies under relatively strong water energy.

The interpretation of the molluscan dead assemblage based on its bionomic structure, state of preservation and life habit allows to follow the recent evolution of two coastal environments of the northern Elba, belonging to the same present-day biocoenosis (SGCF) but with different histories.

In the molluscan dead assemblage of sample abe 120-121, with living *maërl*, we recognized a group of poorly preserved, mainly infaunal and SGCF-related shells and another group of well-preserved, mainly epifaunal and DC-related shells.

In sample abe 06, collected in the same area and at a similar

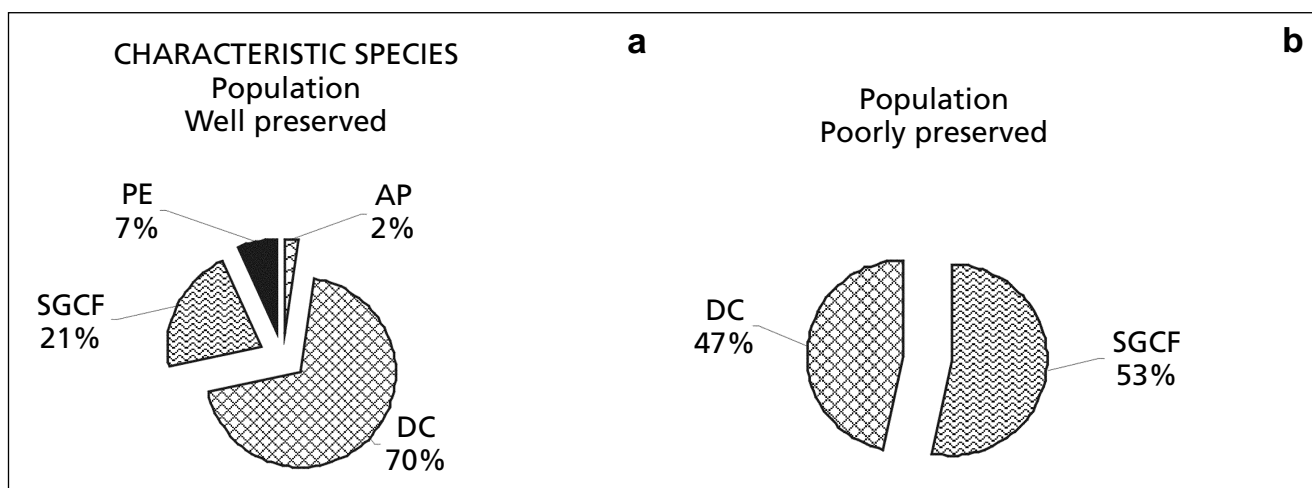


Fig. 7. Sample abe 120-121. Only the exclusive and preferential characteristic species occurring as population are retained. **a.** Biocoenoses represented in the well preserved molluscan shell assemblage. **b.** Biocoenoses represented in the poorly preserved molluscan shell assemblage.

Fig. 7. Campione abe 120-121. Dati relativi solo alle specie caratteristiche esclusive o preferenziali presenti come popolazioni. **a.** Biocenosi rappresentate nella frazione ben conservata della malacofauna. **b.** Biocenosi rappresentate nella frazione mal conservata della tanatocenosi.

depth, living *maërl* is not present, but abundant coralline branches are included in the sediment. The molluscan dead assemblage is composed of a group of poorly preserved infralittoral and epifaunal shells, probably transported by the neighbouring *Posidonietum* and a group of mainly epifaunal and DC-related shells. Another group of well preserved mud-related molluscan shells together with evidence of bottom instability testify a temporary increase of pelite in the sediment, which was probably responsible of the coralline facies decline. The comparison between the two samples, on the basis of the occurrence of mud-related species and of the relative dominance of SGCF species points to a stronger, but not constant, current influence in abe 120-121 than in abe 06 (Fig. 7a, 8c).

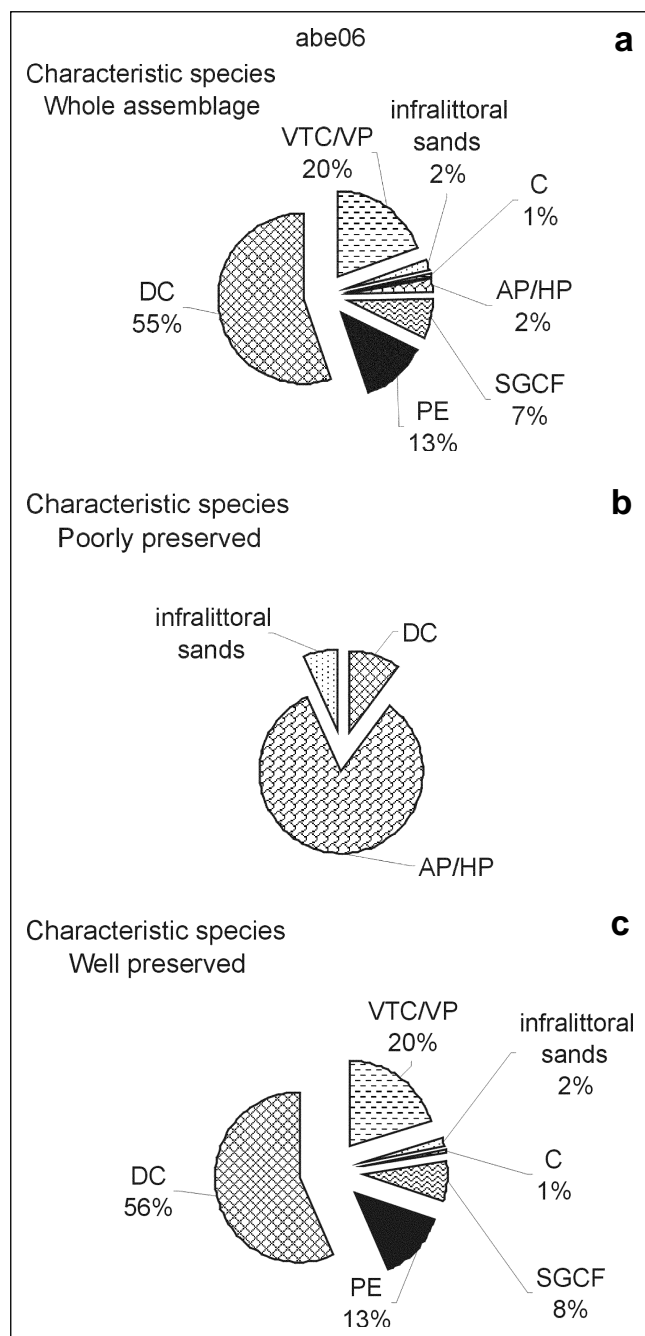


Fig. 8. Sample abe 06. Biocoenoses represented in the molluscan shell assemblage. Only the exclusive and preferential characteristic species are retained. **a.** Whole assemblage; **b.** Poorly preserved shell assemblage; **c.** Well preserved shell assemblage.

Fig. 8. Campione abe 06. Biocenosi rappresentate nella tanatocenosi. Dati relativi alle sole specie caratteristiche esclusive o preferenziali. **a.** Intera tanatocenosi; **b.** Frazione mal conservata; **c.** Frazione ben conservata.

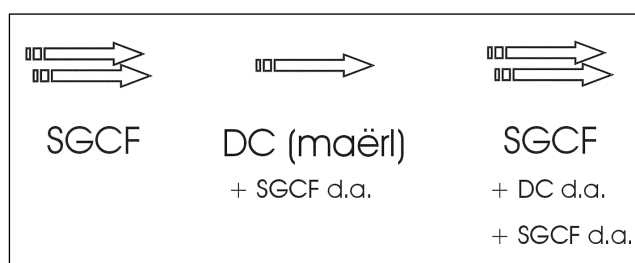


Fig. 9. Sketch of the recent evolution of the Elba *maërl* environment, based on the taphonomy and bionomy of the molluscan dead assemblage (d.a.). Arrows represent water energy. A) the oldest SGCF environment (fig. 7b); B) the intermediate (decades to centuries) DC environment with the coralline facies (fig. 7a); C) the present-day evolutionary trend (fig. 4).

Fig. 9. Schema dell'evoluzione recente dell'ambiente a *maërl* dell'Elba, basato sulla tafonomia e bionomia della tanatocenosi a molluschi (d.a.). Le frecce rappresentano l'energia dell'acqua. A) il vecchio ambiente SGCF (fig. 7b); B) l'ambiente DC con la facies a Corallinales intermedio (da decenni a secoli) (fig. 7a); C) il trend evolutivo attuale (fig. 4).

At both sites (abe 06 and abe 120-121) the molluscan associations underwent time-averaging to some extent. The analysis of shell sub-assemblages, identified on the basis of different status of preservation and described according to life-habit and biocenotic meaning, allows to recognize in both samples the occurrence of an oscillation between DC and SGCF biocoenoses (Fig. 9). A more precise timing of the observed change needs further study, however, according to site depth and sampling depth below the sea floor, it is possible to hypothesize a decadal to centennial scale.

In the Mediterranean, *maërl* is placed at the boundary between DC and SGCF (Jacquotte, 1962; Pérès & Picard, 1964; Basso, 1998) or in transitional environments of "*déséquilibre biocoenotique*" (Falconetti, 1969). Unlike other organisms that can develop with high dominance originating a facies, coralline unattached branches require decades to develop and centuries to create a biogenic deposit, because of their very slow growth. Therefore it is likely that the persistence of a transitional state could be a basic environmental requirement. This constraint would help to explain the apparent rarity and low resilience after anthropogenic disturbance of the Mediterranean *maërl* beds (Bordehore *et al.*, 2000; BIOMAERL team, 2003).

Acknowledgements

We thank Cesare Corselli for the use of the data bank "GAIA", resulting from the TSM project (Taphonomy and Sedimentology on the Mediterranean shelf). Thanks are due to Elio Robba and Alberto Cecalupo for the useful discussions during our work, and to three anonymous referees for their suggestions that improved the first draft of our manuscript.

References

ALLER J.Y., 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. *Deep-Sea Research* (Part I, Oceanographic Research Papers), **44** (1): 39-69.
 BASSO D., 1992. Phytobenthic communities in the circalittoral soft bottoms of the Tyrrhenian Sea (Mediterranean). *Atti 10° AIOL Congress*, Allassio 4-6 November 1992: 563-573.
 BASSO D., 1998. Deep rhodolith distribution in the Pontian Islands, Italy: a model for the paleoecology of a temperate sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **137**: 173-187.
 BASSO D. & CORSELLI C. (in press). Molluscan paleoecology in the reconstruction of coastal changes. In Yanko V. (Ed.), *Climate change and coastline migration*.

- tion as factors in human adaptation to the circum-pontic region: from past to forecast. NATO Science Series, Kluwer Academic Publishers.
- BEST M.M.R. & KIDWELL S.M., 2000. Bivalve taphonomy in tropical mixed siliclastic-carbonate settings. II. Effect of bivalve life habits and shell types. *Paleobiology*, **26** (1): 103-115.
- BIANCHI S., 1993. Contributo alla conoscenza delle Biocenosi del Piano Circalitorale a Nord dell'Isola d'Elba. Thesis, Dip.to Sc. Terra, Univ. Milano, unpublished.
- BIOMAERL TEAM, 2003. Conservation and management of northeast Atlantic and Mediterranean maerl beds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13** (1): S65-S76.
- BORDEHORE C., BORG J.A., LANFRANCO E., RAMOS-ESPLÁ A., RIZZO M. & SCHEMBRI P.J., 2000. Trawling as a major threat to Mediterranean maerl beds. *First Mediterranean Symposium on Marine Vegetation. Regional Activity Centre for Specially Protected Areas*, Ajaccio, Corsica, France 2-3 October 2000; Poster and extended abstract, 4pp.
- BORDEHORE C., RAMOS-ESPLÁ A.A. & RIOSMENA-RODRIGUEZ R., 2003. Comparative study of two maerl beds with different trawling history, southeast Iberian Peninsula. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **13**: S43-S54.
- BOSENCE D.W.J., 1979. Live and dead faunas from coralline algal gravels, Co. Galway. *Palaeontology*, **22** (2): 449-478.
- BOSENCE D.W.J. & WILSON J., 2003. Maerl growth, carbonate production rates and accumulation rates in the northeast Atlantic. *Aquatic Conservation: Marine and freshwater ecosystems*, **13**: S21-S31.
- BOURCIER M., 1981. Nouvelles localisations de quelques facies des fonds Detritiques Côtiers dans le Parc National de Port-Cros (France, Méditerranée) *Rapports de la Commission internationale pour la Mer Méditerranée*, **27** (2): 121-122.
- BRETT C.E. & BAIRD G.C., 1986. Comparative taphonomy: a key for paleoenvironmental reconstruction. *Palaïos*, **1**: 207-227.
- BUCHANAN J.B. & KAIN J.M., 1971. Measurement of the physical and chemical environment. In HOLME N.A. & MCINTYRE A.D. (Eds), *Methods for the study of marine benthos*. Oxford and Edinburgh, 1-334.
- CABIOCH L., 1968. Contribution à la connaissance des peuplements benthique de la Manche occidentale. *Cahiers de Biologie Marine*, **9**: 493-720.
- CARANNAnte G., ESTEBAN M., MILLIMAN J.D. & SIMONE L., 1988. Carbonate lithofacies as paleolatitude indicators. *Sedimentary Geology*, **60**: 333-346.
- CLAUSADE M., 1969. Peuplement animal sessile des petits substrats solides récoltés dans trois biocoenoses des fonds detritiques des parages de Marseille. *Tethys*, **1** (3): 719-750.
- CRAIG G.Y. & JONES N.S., 1966. Marine benthos, substrate and palaeoecology. *Palaeontology*, **9** (1): 30-36.
- DAVIES D.J., STAFF G.M., CALLENDER W.R. & POWELL E.N., 1990. Description of a quantitative approach to taphonomy and taphofacies analysis: all dead things are not created equal. In MILLER W. (Ed.), *Paleocommunity temporal dynamics: the long-term development of multispecies assemblages*. Special Publications Paleontological Society, **5**: 328-350.
- DIEUZEIDE R., 1940. Etude d'un fond de pêche d'Algérie: "la gravelle" de Castiglione. *Bulletin de la Station d'Aquaculture et Pêche de Castiglione*, n.s. **1**: 33-57.
- DI GERONIMO I. & ROBBA E., 1976. *Metodologie qualitative e quantitativa per lo studio delle biocenosi e paleocomunità marine bentoniche* - Rapporto n. 1 del "Gruppo informale di ricerca Paleobenthos", 35 pp.
- FABBRI A. & SELLI R., 1972. The structure and stratigraphy of the Tyrrhenian Sea. In STANLEY D. (Ed.), *The Mediterranean Sea: a natural sedimentation laboratory*. Stroudsburg, Pennsylvania, Dowden, Hutchinson & Ross, Inc.: 75-81.
- FALCONETTI C., 1969 (1970). Etude faunistique d'un faciès: "la Gravelette" ou maërl de Castiglione (Algérie). *Tethys*, **1** (4): 1057-1096.
- FALLINI L., 1994. Studio delle tanatocenosi circalitorali del tratto di costa tra Capo Vita e Capo d'Enfola (Isola d'Elba). Thesis, Dip.to Sc. Terra, Univ. Milano, unpublished, 103 pp.
- FEDER H.M., FOSTER N.R., JEWETT S.C., WEINGARTNER T.J. & BAXTEER R., 1994. Mollusks in the northeastern Chukchi Sea. *Arctic*, **47** (2): 145-163.
- FLESSA K.W. & KOWALEWSKI M., 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia*, **27**: 153-165.
- FRASCHETTI S., COVAZZI A., CHIANTORE M. & ALBERTELLI G., 1997. Life-history traits of the bivalve *Spisula subtruncata* (da Costa) in the Ligurian Sea (North-Western Mediterranean): the contribution of newly settled juveniles. *Scientia Marina*, **61** (Suppl. 2): 25-32.
- FÜRSICH F.T. & ABERHAN M., 1990. Significance of time-averaging for paleocommunity analysis. *Lethaia*, **23**: 143-152.
- HALL-SPENCER J.M., GRALL J., MOORE P.G. & ATKINSON R.J.A., 2003. Bivalve fishing and maerl-bed conservation in France and in the UK - retrospect and prospect. *Aquatic conservation: marine and freshwater ecosystems*, **13**: S33-S41.
- HALL-SPENCER J.M. & MOORE P.G., 2000. Scallop dredging has profound, long-term impacts on maerl habitats. *ICES Journal of Marine Science*, **57** (5): 1407-1415.
- JAQUOTTE R., 1961. Affinités du peuplement des fonds de maërl de Méditerranée. *Rapports et Procès Verbaux des Reunions CIESMM*, **16** (2): 439.
- JAQUOTTE R., 1962. Etude des fonds de maërl de Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **26** (41): 141-235.
- KAMENOS N.A., MOORE P.G. & HALL-SPENCER J.M., 2003. Substratum heterogeneity of dredged vs un-dredged maerl grounds. *Journal of the Marine Biological Association UK*, **83** (2): 411-413.
- KEEGAN B.F., 1974. The macrofauna of maërl substrates on the west coast of Ireland. *Cahiers de Biologie Marine*, **15**: 513-530.
- KIDWELL S.M. & FLESSA K.W., 1995. The quality of the fossil record: Populations, species and communities. *Annual Review of Ecology and Systematics*, **26**: 269-299.
- KOWALEWSKI M., FLESSA K.W. & HALLMAN D.P., 1995. Ternary taphograms: triangular diagrams applied to taphonomic analysis. *Palaïos*, **10**: 478-483.
- MARI M., 1999. Studio sistematico e fitosociologico di un campione di maërl dell'Isola d'Elba. Thesis, Univ. Milano, unpublished.
- MASLOWSKI J., 2003. Effects of trophic conditions on benthic macrofauna in the vicinity of the River Swina mouth (Pomeranian Bay; southern Baltic Sea). *Oceanologia*, **45** (1): 41-52.
- NACORDA H.M.E. & YAP H.T., 1996. Macroinfaunal biomass and energy flow in a shallow reef flat of the northwestern Philippines. *Hydrobiologia*, **341** (1): 37-49.
- PÉRÉS J.M. & PICARD J., 1964. Nouveau manuel de bionomie benthique de la Mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, **31**: 1-137.
- PICARD J., 1965. Recherches qualitatives sur les biocoenoses des substrats meubles dragables de la région marseillaise. *Recueil des Travaux de la Station Marine d'Endoume*, **52** (36): 3-160.
- PINOT J.-P., 1997. Une biocénose menacée par la surexploitation: le maërl, cas de la baie de Concarneau. In DAUVIN J.-C. (Ed.), *Les biocénoses marines et littorales, Atlantique, Manche et mer du Nord, synthèse, menace et perspectives*. Muséum National d'Histoire Naturelle, Paris: 149-158.
- POWELL E.N., 1992. A model for death assemblage formation. Can sediment shelliness be explained? *Journal of Marine Research*, **50**: 229-265.
- POWELL E.N., PARSONS-HUBBARD K.M., CALLENDER W.R., STAFF G.M., ROWE G.T., BRETT C.E., WALKER S.E., RAYMOND A., CARLSON D.C., WHITE S. & HEISE E.A., 2002. Taphonomy on the continental shelf and slope: two-year trends - Gulf of Mexico and Bahamas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **184**: 1-35.
- SABELLI B., GIANNUZZI-SAVELLI R. & BEDULLI D., 1990-1992. *Catalogo annotato dei molluschi marini del Mediterraneo (Annotated check-list of Mediterranean marine mollusks)*. Libreria Naturalistica, Bologna, vols 1-3, pp. 781.
- STAFF G.M. & POWELL E.N., 1988. The paleoecological significance of diversity: the effect of time averaging and differential preservation on macroinvertebrate species richness in death assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **63**: 73-89.
- STOCCHINO C. & TESTONI A., 1968. Le correnti nel Canale di Corsica e nell'Arcipelago Toscano. *Istituto Idrografico della Marina*, Genova.
- WALKER K.R. & BAMBACH R.K., 1971. The significance of fossil assemblages from fine-grained sediments: time-averaged communities. *Geological Society of America, Abstracts*, **3**: 783-784.