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# Molluscs on subtidal cliffs: patterns of spatial distribution

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The distribution of molluscan assemblages across and along a vertical rocky cliff near Otranto (southern Adriatic Sea, Italy) was studied. Sampling was undertaken in May and November 2000 at three sites approximately 100 m apart. Three depths (5, 15, 25 m) were sampled at each site, by scraping off three replicate 20 × 20 cm quadrats. Samples yielded 6722 specimens, referred to as 133 species. Multivariate analyses showed that the structure of the assemblages significantly differed among depths with a clear gradient of distribution from shallow to deep stands. However, a considerable variation in the structure of the assemblage was also observed among sites at each of the three depths. The species contributing most to characterize depths and/or differentiating sites at each level of the shore were identified. Some potential causes of the observed differences are discussed.

## INTRODUCTION

The interaction between biotic and abiotic factors is responsible for the temporal and spatial variability in the species abundance in biological communities (Danielson, 1991). Such changes occur at different scales, along a hierarchy reflecting different processes determining the observed patterns. Identification of temporal and spatial scales of variation allows the understanding of the role of these processes (Underwood & Chapman, 1996). Quantifying this variability at different scales is thus a prerequisite to the proposal and test of explanatory models of observed distributional patterns (Underwood, 2000). The spatial patterns in the structure of assemblages on hard substrates have been widely documented from intertidal substrates (e.g. Benedetti-Cecchi, 2001a and references therein). In the subtidal, information is still scant and mainly limited to sessile (e.g. Boero & Fresi, 1986) and easily recognisable taxa (Ferdeghini et al., 2000; Fraschetti et al., 2001). Quantitative information on the pattern of distribution of vagile invertebrate assemblages is very poor and limited to few groups (i.e. polychaetes, Giangrande, 1988). Molluscs have been rarely considered despite their consolidate taxonomic knowledge and their wide distribution in marine communities. Quantitative information on distribution patterns of molluscan assemblages is mainly focused on soft substrates and coral reefs and derive from studies along Norwegian fjords (Buhl-Mortensen & Høisæter, 1993), Antarctic Sea (Cattaneo et al., 2000) and tropical environments (Esqueda et al., 2000; Bouchet et al., 2002). In the Mediterranean, except for pioneering and mainly qualitative studies (e.g. Ledoyer, 1966; Bombace, 1969; Conti & Rossini, 1985), quantitative studies on molluscan assemblages from hard subtidal substrates are still scant (Milazzo et al., 2000). The main objective of this study is to provide precise information about the composition of Mediterranean molluscan assemblages from hard substrates. The study is also aimed at quantifying possible differences in assemblage structure along a depth gradient and among sites at each of the considered level of the shore.

## MATERIALS AND METHODS

### *Study area*

The study site is located along the south-eastern coast of Apulia (Italy) (Figure 1). It is characterized by vertical

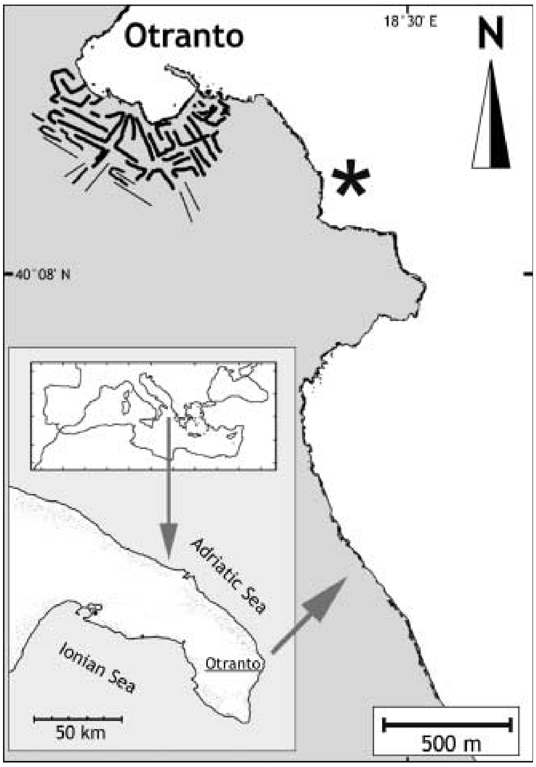

**Figure 1.** Sampling location (*) and its positioning in the Mediterranean region.

**Table 1.** *Taxonomic list of the species recorded.*

- **POLYPLACOPHORA**
  - LEPIDOPLEURIDAE
    - *Lepidopleurus (Leptochiton) scabridus* (Jeffreys, 1880)
  - ISCHNOCHITONIDAE
    - *Callochiton septemvalvis euplaeae* (Costa, O.G., 1829)
    - *Lepidochitona furtiva* (Monterosato, 1879)
    - *Lepidochitona monterosatoi* Kaas & Van Belle, 1981
  - CHITONIDAE
    - *Chiton (Rhyssoplax) olivaceus* Spengler, 1797
  - ACANTHOCHITONIDAE
    - *Acanthochitona fascicularis* (Linné, 1767)

- **GASTROPODA**
  - FISSURELLIDAE
    - *Emarginula octaviana* Coen, 1939
    - *Emarginella huzardii* (Payraudeau, 1826)
    - *Diodora gibberula* (Lamarck, 1822)
  - SCISSURELLIDAE
    - *Scissurella costata* D'Orbigny, 1823
    - *Sinezona cingulata* (Costa, O.G., 1861)
  - HALIOTIDAE
    - *Haliotis tuberculata tuberculata* Linné, 1758
  - TURBINIDAE
    - *Homalopoma sanguineum* (Linné, 1758)
    - *Tricolia pullus pullus* (Linné, 1758)
  - TROCHIDAE
    - *Clanculus (Clanculus) corallinus* (Gmelin, 1791)
    - *Clanculus (Clanculopsis) cruciatus* (Linné, 1758)
    - *Gibbula (Colliculus) turbinoides* (Deshayes, 1835)
    - *Jujubinus exasperatus* (Pennant, 1777)
    - *Jujubinus gravinae* (Dautzenberg, 1881)
    - *Jujubinus striatus* (Linné, 1758)
    - *Calliostoma laugeri* (Payraudeau, 1826)
    - *Calliostoma zizyphinum* (Linné, 1758)
  - CINGULOPSIDAE
    - *Eatonina (Coriandria) fulgida* (Adams, J., 1797)
  - RISSOIDAE
    - *Rissoa guerinii* Récluz, 1843
    - *Alvania cancellata* (Da Costa, 1778)
    - *Alvania cimex* (Linné, 1758)
    - *Alvania discors* (Allan, 1818)
    - *Alvania hallgassi* Amati & Oliverio, 1985
    - *Alvania lineata* Risso, 1826
    - *Alvania pagodula* (Bucquoy, Dautzenberg & Dollfus, 1884)
    - *Alvania subcrenulata* (Bucquoy, Dautzenberg & Dollfus, 1884)
    - *Crisilla semistriata* (Montagu, 1808)
    - *Manzonia crassa* (Kanmacher, 1798)
    - *Pusillina inconspicua* (Alder, 1844)
    - *Pusillina philippi* (Aradas & Maggiore, 1844)
    - *Pusillina radiata* (Philippi, 1836)
    - *Rissoina bruguieri* (Payraudeau, 1826)
  - CERITHIIDAE
    - *Cerithium rupestre* Risso, 1826
    - *Cerithium vulgatum* Bruguière, 1792
    - *Bittium latreillii* (Payraudeau, 1826)
    - *Bittium reticulatum* (Da Costa, 1778)
  - VERMETIDAE
    - *Vermetus (Thylacodus) granulatus* (Gravenhorst, 1831) (juvenile)
    - *Dendropoma* sp. (juvenile)
  - CAPULIDAE
    - *Capulus ungaricus* (Linné, 1758)
  - CYPRAEIDAE
    - *Luria lurida* (Linné, 1758)
  - NATICIDAE
    - *Natica dillwynii* (Payraudeau, 1826)
  - CERITHIOPSIDAE
    - *Cerithiopsis nana* Jeffreys, 1867
    - *Cerithiopsis tubercularis* (Montagu, 1803)
    - *Dizoniopsis coppolae* (Aradas, 1870)
  - TRIPHORIDAE
    - *Marshallora adversa* (Montagu, 1803)
    - *Monophorus thiriotae* Bouchet, 1984
    - *Similiphora similior* (Bouchet & Guillemot, 1978)
    - *Metaxia metaxa* (Delle Chiaje, 1828)
  - EULIMIDAE
    - *Vitreolina philippi* (Rayneval & Ponzi, 1854)
  - MURICIDAE
    - *Hexaplex trunculus* (Linné, 1758) (juvenile)
    - *Muricopsis cristata* (Brocchi, 1814)
    - *Ocinebrina aciculata* (Lamarck, 1822)
    - *Ocinebrina edwardsii* (Payraudeau, 1826)
  - CORALLIOPHILIDAE
    - *Coralliophila meyendorffii* (Calcara, 1845)
  - BUCCINIDAE
    - *Buccinulum corneum* (Linné, 1758)
    - *Engina leucozona* (Philippi, 1843)
    - *Pollia scacchiana* (Philippi, 1844)
  - COLUMBELLIDAE
    - *Columbella rustica* (Linné, 1758)
  - NASSARIIDAE
    - *Nassarius (Hinia) incrassatus* (Stroem, 1768)
  - FASCIOLARIIDAE
    - *Fusinus (Barbarofusus) rudis* (Philippi, 1844)
    - *Colubraria reticulata* (Blainville, 1826)
  - CYSTISCIDAE
    - *Gibberula miliaria* (Linné, 1758)
  - MARGINELLIDAE
    - *Volvarina mitrella* (Risso, 1826)
  - MITRIDAE
    - *Mitra cornicula* (Linné, 1758)
  - COSTELLARIIDAE
    - *Vexillum (Pusia) ebenus* (Lamarck, 1811)
    - *Vexillum (Pusia) tricolor* (Gmelin, 1790)
  - CONIDAE
    - *Mitrolumna crenipicta* Dautzenberg, 1889
    - *Mitrolumna olivoidea* (Cantraine, 1835)
    - *Mangelia multilineolata* (Deshayes, 1835)
    - *Mangelia unifasciata* (Deshayes, 1835)
    - *Clathromangelia granum* (Philippi, 1844)
    - *Raphitoma bicolor* (Risso, 1826)
    - *Raphitoma laviae* (Philippi, 1844)
    - *Raphitoma linearis* (Montagu, 1803)
    - *Leufroyia concinna* (Scacchi, 1836)
    - *Leufroyia leufroyi* (Michaud, 1828)
  - OMALOGYRIDAE
    - *Omalogyra simplex* (Costa, O.G., 1861)
    - *Ammonicera fischeriana* (Monterosato, 1869)
  - PYRAMIDELLIDAE
    - *Clathrella clathrata* (Philippi, 1844)
    - *Odostomia striolata* Forbes & Hanley, 1850
    - *Odostomia turrita* Hanley, 1844
    - *Chrysallida intermixta* (Monterosato, 1884)
    - *Chrysallida obtusa* (Brown, T., 1827)
    - *Folinella excavata* (Philippi, 1836)
    - *Odostomella doliolum* (Philippi, 1844)
    - *Turbonilla sinuosa* (Jeffreys, 1884)
    - *Euparthenia humboldti* (Risso, 1826)
  - HAMINOEIDAE
    - *Haminoea hydatis* (Linné, 1758)
  - APLYSIIDAE
    - *Aplysia (Pruvotaplysia) parvula* Guilding in Moerch, 1863

- PLEUROBRANCHIDAE
  - *Pleurobranchus membranaceus* (Montagu, 1815)
  - *Berthella aurantiaca* (Risso, 1818)
- ONCHIDORIDIDAE
  - *Onchidoris neapolitana* (Delle Chiaje, 1841)
- DISCODORIDIDAE
  - *Discodoris atromaculata* (Bergh, 1881)
- PHYLLIDIIDAE
  - *Phyllidia flava* Aradas, 1847
- SIPHONARIIDAE
  - *Williamia gussoni* (Costa, O.G., 1829)

**BIVALVIA**

- NUCULIDAE
  - *Nucula nitidosa* Winckworth, 1931
- ARCIDAE
  - *Arca noae* (Linné, 1758)
  - *Barbatia barbata* (Linné, 1758)
- NOETIDAE
  - *Striarca lactea* (Linné, 1758)
- MYTILIDAE
  - *Mytilus galloprovincialis* Lamarck, 1819
  - *Modiolus barbatus* (Linné, 1758)
  - *Modiolula phaseolina* (Philippi, 1844)
  - *Crenella pellucida* (Jeffreys, 1859)
  - *Modiolarca subpicta* (Cantraine, 1835)
  - *Musculus costulatus* (Risso, 1826)
  - *Lithophaga lithophaga* (Linné, 1758)
  - *Rhomboidella prideauxi* (Leach, 1815)
- LIMIDAE
  - *Lima lima* (Linné, 1758)
  - *Lima (Limaria) hians* (Gmelin, 1791)
- PECTINIDAE
  - *Chlamys multistriata* (Poli, 1795)
- LUCINIDAE
  - *Ctena decussata* (Costa, O.G., 1829)
- GALEOMMATIDAE
  - *Galeomma turtoni* Turton, 1825
- KELLIIDAE
  - *Kellia suborbicularis* (Montagu, 1803)
- LASAEIDAE
  - *Lasaea rubra* (Montagu, 1803)
- MONTACUTIDAE
  - *Mysella bidentata* (Montagu, 1803)
- CARDITIDAE
  - *Cardita calyculata* (Linné, 1758)
  - *Glans trapezia* (Linné, 1758)
- CHAMIDAE
  - *Chama gryphoides* (Linné, 1758)
  - *Pseudochama gryphina* (Lamarck, 1819)
- CARDIIDAE
  - *Plagiocardium (Papillocardium) papillosum* (Poli, 1795)
- MACTRIDAE
  - *Spisula subtruncatula* (Da Costa, 1778)
- TRAPEZIIDAE
  - *Coralliophaga lithopagella* (Lamarck, 1819)
- VENERIDAE
  - *Gouldia minima* (Montagu, 1803)
  - *Irus irus* (Linné, 1758)
  - *Venerupis* sp.
- GASTROCHAENIDAE
  - *Gastrochaena dubia* (Pennant, 1777)
- HIATELLIDAE
  - *Hiatella rugosa* (Linné, 1767)
- THRACIIDAE
  - *Thracia (Ixartia) distorta* (Montagu, 1803)

**Table 2.** *Results of the two-way crossed ANOSIM testing for differences among sites (averaged across depths) and among depths (averaged across sites) in both times of sampling.*

| | May | | November | |
|---|---|---|---|---|
| | R value | *P* | R value | *P* |
| Global differences | | | | |
| Among sites | 0.64 | ** | 0.35 | ** |
| Among depths | 0.86 | ** | 0.67 | ** |
| Pairwise tests | | | | |
| 5 vs 15 | 0.97 | ** | 0.71 | * |
| 5 vs 25 | 0.99 | * | 0.93 | * |
| 15 vs 25 | 0.69 | ** | 0.42 | * |

*, $P<0.05$; **, $P<0.01$.

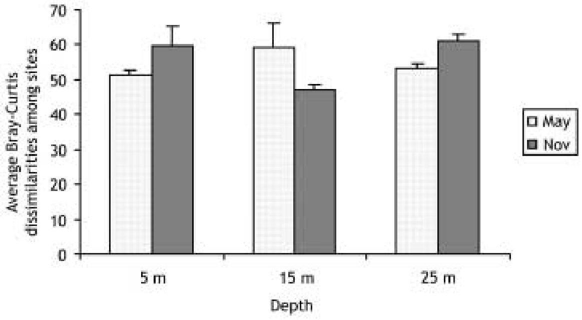

**Figure 2.** Average Bray–Curtis dissimilarity among sites at each of the three depths in both periods of sampling (±SE, N=3).

rocky substrates from the surface to about 30 metres. Below, the slope decreases and rocks alternate with sand patches. From the surface to 5–7 m, patches of hydroids (*Aglaophenia* sp., *Eudendrium* sp.) and photophilic algae (*Dictyota* sp., *Laurencia* sp., *Acetabularia* sp. and *Corallina* sp.) alternate with less colonized patches of encrusting calcified red algae (*Peyssonnelia* sp., *Lithophyllum* sp., *Mesophyllum* sp.), encrusting (e.g. *Crambe crambe*) and globose (e.g. *Chondrilla nucula*) sponges (Fraschetti et al., 2001). Between 12–15 and 20 m, erect algae (*Flabellia petiolata*, *Padina pavonica*, *Peyssonnelia squamaria*) encrusting calcified red algae and sponges (*Agelas oroides*, *Phorbas* spp. *Ircinia* spp. and *Sarcotragus* spp.) characterize the assemblage. Below 20 m, the so-called 'coralligenous formations', a term broadly defining the bioconstructions by concretioning organisms (i.e. encrusting calcified red algae, Bryozoans, Serpulids and the complex biota inhabiting them; Sarà, 1969), make up the substrate. Among sessile invertebrates, the most characteristic species are large sponges (*Axinella* spp.), Anthozoa (*Leptosammia pruvoti*, *Parazoanthus axinellae*), Bryozoans (*Calpensia nobilis*, *Myriapora truncata*, *Pentapora fasciata*) and Ascidians (*Microcosmus* sp. and *Halocynthia papillosa*) (Ferdeghini et al., 2000).

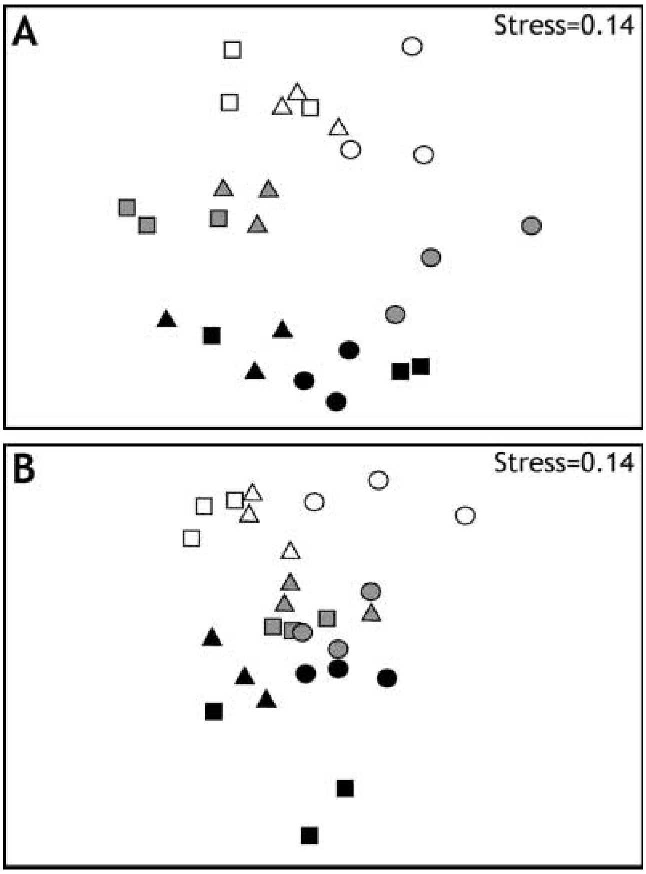

**Figure 3.** Two-factor nMDS plot showing differences among sites and among depths in both periods of sampling, (A) May; and (B) November. Each point represents the assemblages from the three replicates (see Materials and Methods). (White, 5 m; Grey, 15 m; Black, 25 m). (○; □; △=Sites 1, 2 and 3, respectively).

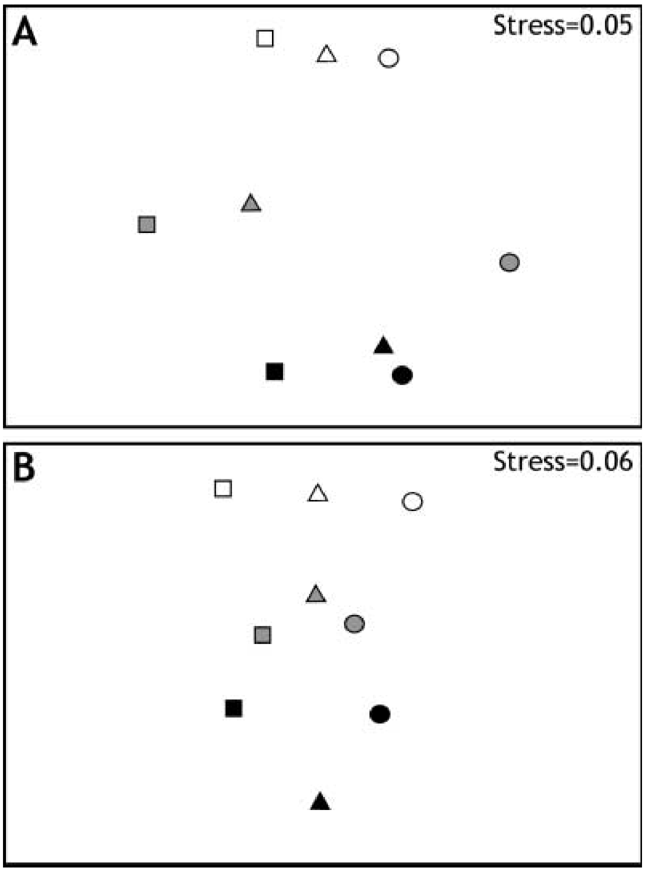

**Figure 4.** Two-factor nMDS plot showing differences among sites and among depths in both periods of sampling, (A) May; and (B) November. Each point represents the centroid of assemblages from the three replicates (see Materials and Methods). Symbols are coded as in Figure 3.

### *Sampling design and analysis of data*

Samplings were carried out in May and November 2000. Three sites (about 100 m apart) were randomly chosen along an homogeneous stretch of coast. At each site, sampling was performed by SCUBA divers at 5, 10, 25 m by three replicate samples, each involving total scraping of the rocky substrate on surfaces of 20 × 20 cm. Overall, 54 samples were obtained. After collection, samples were fixed in 4% formalin solution, molluscs were then sorted under magnification, preserved in 70% alcohol and identified to species level. Nomenclature follows Bedulli et al. (1995a) (Polyplacophora), Bodon et al. (1995) and Bedulli et al. (1995b) (Gastropoda), and Bedulli et al. (1995c) (Bivalvia).

Data were organized in a species/sample matrix and analysed by multivariate techniques. In some cases (i.e. the gastropods of the genus *Bittium*), juvenile forms and adults were counted separately and values of abundance for the same species were considered as two separate variables.

Two-way crossed Analyses of Similarity (ANOSIM, Clarke, 1993) were used to compare, in each period of sampling, the assemblage structure both among depths and among sites. Comparisons were based on Bray–Curtis similarity values ($S_{BC}$) calculated on all species within each quadrat (PRIMER, Plymouth Marine Laboratory) (Clarke, 1993). Prior to analysis, data were square root transformed. This transformation comprised all species in the same range of abundance, preventing few abundant species (or those characterized by a massive number of settlers) from dominating the analyses. Differences among depths as well as among sites at each depth were represented by non-metric multidimensional scaling ordinations (nMDS), considering all replicates and the centroids of assemblages from the three replicates collected at the three depths at each of the three sites. Similarity percentages (SIMPER, Clarke, 1993) was used to identify, for each period of sampling, the percentage contribution that each species made to the measure of similarity within each depth and, at each depth, to the dissimilarity (calculated as $1-S_{BC}$) among sites. The analysis allowed identification, at both sampling times, of the species most responsible for characterizing depths and/or for differentiating sites at each depth. Species were considered important if they exceeded an arbitrary chosen threshold value of 5% of similarity within depth and/or 2% of dissimilarity among sites at each depth.

## RESULTS

A total of 6722 specimens was collected, and characterized as 133 species of: Gastropoda (5178 individuals, 94 species), Bivalvia (1514 individuals, 33 species), and Polyplacophora (30 individuals, 6 species) (Table 1). Among Gastropods, the family of Rissoidae accounted

**Table 3.** *Characterization of depths: species most contributing to the Bray–Curtis similarity within each depth range (averaged across sites). Differentiation among sites: species most contributing to dissimilarity among sites at each depth. Values of similarity* $\geqslant 5\%$ *(in the first case) and of dissimilarity* $\geqslant 2\%$ *(in the second case) are given in bold.*

| | | Characterization of depths | | | | | | Differentiation among sites | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 5 m | | 15 m | | 25 m | | 5 m | | 15 m | | 25 m | |
| | Species | May | Nov | May | Nov | May | Nov | May | Nov | May | Nov | May | Nov |
| GASTROPODA | *Alvania cimex* | **7.2** | **10.2** | **7.7** | **9.6** | **5.8** | **5.6** | **2.6** | **3.8** | **3.1** | **2.3** | **2.3** | **4.7** |
| | *Alvania lineata* | 0.6 | 0.0 | 3.6 | **6.7** | **7.5** | **9.3** | 2.0 | 0.7 | **2.7** | **3.1** | **3.5** | **3.1** |
| | *Bittium latreillii* | **11.5** | **20.9** | **10.0** | **9.4** | **11.8** | **7.4** | **5.6** | **8.7** | **6.7** | **4.7** | **2.5** | **2.7** |
| | *Bittium latreillii* juvenile | **11.9** | **27.0** | **15.8** | **26.0** | **11.0** | **12.7** | **11.1** | **25.0** | **10.3** | **8.8** | **4.8** | **8.8** |
| | *Bittium reticulatum* | 3.1 | 0.3 | 2.1 | 0.0 | 1.8 | 1.7 | **3.1** | 2.0 | **4.1** | 0.9 | **3.1** | 1.7 |
| | *Bittium reticulatum* juvenile | 2.8 | 1.1 | **6.6** | 3.6 | 2.6 | 4.5 | **4.6** | **3.5** | **5.7** | **5.2** | **4.9** | **4.5** |
| | *Clanculus cruciatus* | 0.0 | 2.0 | 0.1 | 0.0 | 0.0 | 0.0 | 1.1 | **2.2** | 0.7 | 0.0 | 0.6 | 0.0 |
| | *Columbella rustica* | 1.8 | **6.7** | 0.1 | 0.0 | 0.0 | 0.0 | 1.1 | **4.3** | 1.1 | 0.0 | 0.0 | 0.0 |
| | *Crisilla semistriata* | 0.0 | 0.0 | 4.2 | 3.6 | **16.5** | **15.9** | 1.7 | 1.7 | **3.8** | **5.3** | **5.9** | **2.8** |
| | *Gibbula turbinoides* | 3.9 | 1.5 | 1.6 | 0.0 | 0.0 | 0.0 | **4.9** | **2.1** | 1.8 | 1.0 | 0.5 | 0.0 |
| | *Nassarius incrassatus* | 3.6 | 1.1 | 1.8 | 1.0 | 1.9 | 1.7 | 1.4 | **3.5** | 1.6 | **3.0** | 1.9 | 1.8 |
| | *Pusillina radiata* | 0.8 | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 | **2.2** | **4.7** | 0.4 | 0.0 | 0.0 | 0.7 |
| | *Ocinebrina edwardsii* | 0.7 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | **2.7** | 0.0 | 0.0 | 0.8 | 0.0 |
| BIVALVIA | *Gastrochaena dubia* | **5.2** | 3.7 | 3.4 | 1.0 | 2.6 | 0.6 | **2.4** | **5.2** | 1.4 | **2.4** | 1.4 | 1.3 |
| | *Hiatella rugosa* | **6.4** | **13.0** | **9.6** | **11.5** | **5.9** | 1.4 | 1.6 | 1.4 | 1.1 | 1.3 | **3.0** | **2.6** |
| | *Lithophaga lithophaga* juvenile | 0.0 | 1.4 | 2.3 | **6.9** | **6.4** | **11.2** | 1.0 | **2.6** | **2.4** | **3.2** | **3.3** | 1.7 |
| | *Modiolula phaseolina* | 3.9 | 0.0 | 0.1 | 0.0 | 0.9 | 0.5 | **3.2** | 0.0 | 0.7 | 0.0 | 1.4 | 1.2 |
| | *Mytilus galloprovincialis* juvenile | **23.7** | 0.0 | **10.4** | 0.0 | 1.7 | 0.0 | **10.3** | 1.2 | 0.9 | 0.0 | **2.6** | 0.0 |
| | *Nucula nucleus* | 0.0 | 0.0 | 0.7 | 0.0 | 3.4 | 0.7 | 0.0 | 0.0 | 1.5 | 0.0 | **3.2** | 2.0 |
| | *Plagiocardium papillosum* | 0.0 | 0.0 | 0.0 | 2.5 | 0.0 | 2.3 | 0.0 | 0.7 | 0.0 | **2.1** | 0.0 | **2.6** |
| | *Striarca lactea* | 2.0 | 3.4 | **7.3** | **11.2** | 2.5 | 4.94 | **2.9** | **4.1** | **4.9** | **4.2** | **3.7** | **2.7** |

for the largest number of species (14), followed by Conidae (10), Pyramidellidae (9) and Trochidae (8). Among Bivalves, the Mytilidae, with eight species, was the most speciose family. Samples were numerically dominated by gastropods of the families Cerithidae (3627 individuals), Rissoidae (849) and Trochidae (218), and by bivalves of the families Mytilidae (816), Noetidae (225), Hiatellidae (194) and Gastrochaenidae (100).

The ANOSIM showed that the structure of the assemblages differed significantly among depths ($P<0.01$). Differences were sharper (as indicated by the higher value of R) in May than in November. Post-hoc comparisons showed that, in both periods, the highest differences were between 5 m vs 25 m, the lowest between 15 vs 25 m. Intermediate values of R were obtained between 5 vs 15 m (Table 2).

The ANOSIM also detected, in both periods, significant differences among sites. Overall (averaged across depths) differences among sites were higher in May than November (Table 2). The average values of dissimilarity among sites calculated at each depth in both periods are plotted in Figure 2, to illustrate how the assemblages differed among sites at each depth.

The differences in assemblage structure along the depth gradient at both periods are evident in the nMDS plot either plotting samples from all replicates (Figure 3) and the centroids of each site from the three replicate quadrats (Figure 4). Plotting the centroids also allows observation, even less clearly than observed among depths, of differences among sites at each level of the shore (Figure 4).

The SIMPER identified 19 species (11 gastropods, 8 bivalves) as most contributing to characterize depths and/or differentiating sites. Results are summarized in Table 3.

The gastropods *Alvania cimex* and *Bittium latreillii* (both juveniles and adults) characterized all depths both in May and November. The bivalve *Hiatella rugosa* was also important in characterizing all depths except 25 m in November. Juvenile forms of *Bittium reticulatum* were always present and strongly characterized 15 m in May. *Columbella rustica* was absent in the deepest stands and contributed to characterize 5 m in November. *Crisilla semistriata* was typical of 25 m in both sampling periods. Juveniles of *Mytilus galloprovincialis* were found only in May, strongly characterizing 15 m and, above all, 5 m. Juveniles of date-mussel, *Lithophaga lithophaga*, were particularly important in characterizing, in both periods, 25 m. *Striarca lactea* contributed to the characterization of 15 m assemblages both in May and November.

A set of species most contributed to differentiate sites at each depth: *Alvania cimex*, *B. latreillii* (juveniles and adults), juveniles of *Bittium reticulatum* and *S. lactea* at all depths both in May and November; *B. reticulatum* at all sites in May. *Gibbula turbinoides* (in both periods), *Clanculus cruciatus*, *C. rustica* (November) and *Modiolula phaseolina* (May) at 5 m; *Crisilla semistriata* (in both periods) and *Plagiocardium papillosum* (November) at 15 and 25 m; *H. rugosa*, in both periods, at 25 m.

## DISCUSSION

Characterizing the assemblage at a fine level of taxonomic resolution (the identification at species level) has some important implications. For instance, it means improving the information on some of rare (or considered rare) species. Some of the species recorded in this study, due to their very low abundance, did not contribute greatly to characterization of the assemblage. Their finding, however, is worthy of discussion.

*Lepidopleurus scabridus* and *Pollia scacchiana*, for instance, have both been reported for the southern Adriatic Sea. However they are considered extremely rare in the Mediterranean (Dell'Angelo & Laghi, 1980; Sabelli & Spada, 1986).

As for other congeneric species, *Colubraria reticulata* is known to be a parasite of the parrotfish *Sparisoma cretense* (Johnson et al., 1995). Therefore, its distribution reflects that of its host, which is typical of temperate warm waters of the South Mediterranean. It is worth noting, from this point of view, the recent colonization of *S. cretense* in the same locality investigated by us (Guidetti & Boero, 2001).

Amati & Oliverio (1985) gave a first description of *Alvania hallgassi* providing a *locus typicus* by Otranto. However, they based their description of the species on dead specimens from detritus material. Our finding is the first record of living *A. hallgassi* specimens.

In the Mediterranean, *Aplysia parvula* is reported from Malta and Sicily by Bebbington (1970). It is considered a lessepsian species (Cattaneo-Vietti & Chemello, 1987). Our finding of *A. parvula* represents the first record of the species along the continental coast of Italy.

A first feature of the analysis was that the molluscan assemblage differed among depths, with a clear pattern of zonation from the shallower to the deepest stations. In the Mediterranean, the only data available for studies about the distribution of hard substrate invertebrate vagile fauna along a depth gradient concerns polychaetes. Abbiati et al. (1987) and Giangrande (1988) reported a clear zonation pattern of polychaete assemblages, in relation to an expression of the biological conditioning of the substratum by algae rather than by the direct influence of physical factors.

In our study, however, considerable differences in the structure of the assemblages were also observed among sites at each depth range. Such differences were consistent at both times of sampling.

Vertical zonation is the most obvious distribution pattern of hard substrate communities (Witman & Dayton, 2001). In the Mediterranean, the classical schemes proposed by Pérès (1982) and Riedl (1971) explained vertical zonation in subtidal communities in relation to environmental factors such as light and water movement, respectively. Vertical zonation, almost a paradigm in Mediterranean subtidal habitats, has forced some studies (mostly based on few and scarcely replicated quantitative sampling) to explain differences in the structure of assemblages in relation to an environmental gradient of light and water movement only. The limit of this approach is that it can force the interpretation of the analysis toward the most obvious gradients. However, vertical zonation alone cannot explain all the variability in patterns of spatial distribution (Benedetti-Cecchi, 2001a). There are other sources of variability, including differences among sites within any particular level of the shore and temporal changes in pattern of distribution that should require proper quantification before any conclusion about the vertical distribution of hard substrate communities can be drawn (Underwood, 2000).

It is obviously not possible to explain the differences observed in terms of specific ecological mechanisms leading to different structures in assemblages because these data are all descriptive. There are, however, some clues.

Two, more ecological, aspects of the assemblages could explain some of the differences observed. The first has already been discussed and concerns the along- and across depth spatial variability of epibenthic sessile assemblage, whose complexity could influence the structure of associated mollusc fauna (Olabarria & Chapman, 2001; Chemello & Milazzo, 2002).

The second concerns the supply of recruits. There were differences in the number of juvenile forms for some of conspicuous species (e.g. the gastropods *Bittium latreillii* and *B. reticulatum* and the bivalves *Mytilus galloprovincialis*). Juveniles of *B. latreillii* were found at all depths and in both periods of sampling. Our results are consistent with that reported by Russo et al. (2002) who described, for this species, a life cycle of 18 months, semelparous reproduction and three settlement period in October, February and June. However, the whole assemblage was also characterized by adults of this species. The same did not occur for the congeneric *B. reticulatum* whose importance in characterizing the assemblages was identified only in May, when the population notably increased in abundance due to large numbers of juveniles. The number of adults of *B. reticulatum*, however, was consistently low and scarcely contributed to characterization of the assemblage, indicating low recruitment success of the species. Similar indications about failure in recruitment derived from the bivalve *M. galloprovincialis* whose juveniles contributed greatly to characterize, in May, the assemblage at both 5 and 15 m. However, the adults of the species are completely lacking from the whole area, even above 5 m. The reason that causes failure in recruitment of these species is currently unknown and should require extensive experimentation in order to distinguish between the numerous possible explanatory models (Satuito et al., 1997).

Linked to the recruit–supply aspect is the settlement behaviour of juvenile forms of the date-mussel *Lithophaga lithophaga*. This widespread Mediterranean rock-boring bivalve usually settles on calcareous rocks that are then burrowed by glandular secretions. Fraschetti et al. (2001) reported on the environmental problems posed to the coastal zone by the destructive fisheries of this species. Adult specimens present in the area live some centimetres inside the substrate and were not collected with the sampling method adopted in the present study. In the analysis, juveniles of *L. lithophaga* were identified (due to higher abundances) as important in characterizing the 25 m. The observed pattern of distribution of *L. lithophaga* juveniles could be explained by different hypotheses. One is that coralligenous formations present at 25 m could provide a substrate easier to burrow, facilitating settlement in comparison with the shallower rocky substrates. However, at 25 m the coralligenous substrate is also friable and samples collect entire pieces of substrate increasing the probability to collect organisms living inside the substrate itself. This may have contributed to some apparent differences in abundances of juvenile of *L. lithophaga* (and therefore dissimilarities of assemblages among depth) because of an artefact of the sampling method. Whether such an artefact exists and is large enough to influence the analysis of patterns of assemblages will be examined elsewhere as part of specific hypotheses about the influence of substrate on the recruitment of *L. lithophaga*.

Understanding the processes causing or maintaining diversity in marine systems include adequate description of patterns in the structure of assemblages. As stressed in the Introduction, most studies on subtidal rocky substrate assemblages have been conducted by sampling sessile taxa (species or groups), easily recognizable by visual census and/or photographic techniques (Roberts, 1996; Fraschetti et al., 2001). This more rapid approach permits adoption of a complex experimental design able to explore the pattern of variability at a wide hierarchy of spatial scales. It has also important applicative consequences. The natural pattern of variability of sessile assemblages, in fact, can be modified by anthropogenic disturbance (Connell & Glasby, 1999; Terlizzi et al., 2002). Thus, quantifying natural variability of hard-substrate sessile assemblages and separating it from variability-induced by humans, has featured prominently in programmes to detect the biological effects of marine pollution (Benedetti-Cecchi, 2001b).

Working with vagile fauna (molluscs, in this case) is more time-consuming in terms of sorting operations and species identification. Moreover such studies require a taxonomic expertise that is becoming rarer and rarer in marine biological studies (Boero, 2001). This can partially explain the lack of quantitative studies examining the spatial distribution pattern of vagile fauna living on subtidal hard substrates (Fraschetti et al., 2002). Therefore, the proposal that molluscs from hard substrates can be a tool for determining changes induced by anthropogenic disturbance is probably premature unless more evidences can be provided about the taxonomic sufficiency (Warwick, 1988) required to well describing environmental changes minimising time, costs and error of taxonomic identification (Mistri & Rossi, 2000).

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