

Patterns of bioconstruction in the cheilostome bryozoan *Schizoporella errata*: the influence of hydrodynamics and associated biota

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ABSTRACT: In the region of La Spezia (Ligurian Sea, Italy), the bryozoan *Schizoporella errata* forms sizeable buildups, termed 'giant colonies' or 'compound colonies' by previous investigators. Buildups were encrusting (up to 40 cm wide) with flat or bumpy surfaces in an exposed site, and erect (more than 20 cm high) branching anastomosed structures in a semi-exposed and in a sheltered site. The buildup architecture was significantly different in the 3 sites, with higher vertical development and number of branches per dm² in the sheltered site. The internal structure of the buildups was also different: densely packed, extensive laminated sheets developed in the sheltered site; loosely packed, concentric sheets alternating with small cavities filled with sediment and shells of associated organisms were found in the semi-exposed and exposed sites. Functional groups could be recognised among the biota associated with *S. errata* buildups. The constructional pattern was interpreted as resulting from both interactions with other organisms and hydrodynamic conditions. While in the exposed site *S. errata* showed no vertical growth, in the sheltered site soft-bodied erect organisms formed the frame around which *S. errata* deposited a multilayered structure, which eventually caused the death and disappearance of the immured organisms. Breakage of branch tips by episodic disturbance and repeated binding through a complex array of budding patterns by *S. errata* resulted in tall buildups which preserved no trace of the soft-bodied organisms. Because of the role they played, these may therefore be defined as 'ghost frame-builders'.

KEY WORDS: Bryozoa · Bioconstruction · Growth forms · Hydrodynamics · Associated biota · Mediterranean Sea

INTRODUCTION

Present-day biotic reefs are built mostly by corals and calcareous algae, but in ancient times several other phyla were also important (Fagerström 1987). The involvement of Bryozoa in forming reefs has varied considerably through geological time; they were principal frame-builders in some Palaeozoic reefs. However in present-day coral reefs, bryozoans frequently play different accessory roles related to their growth form, but normally do not function as the principal frame-building organisms (Cuffey 1972, 1974, 1977).

Nevertheless, some living bryozoans are able to build large masses and be significant rock-formers (Kosich & Cuffey 1978, Bijma & Boeschoten 1985, Scholz & Hillmer 1995, Taylor & Allison 1998). Species of the genus *Schizoporella*, whose bioherms are known from both the past and the Recent, are among the most important builders (Pouyet 1971, Cuffey & Fonda 1976, Beatty et al. 1998). In the Gulf of La Spezia (Italy), Ferdeghini et al. (2000) found sizeable living masses of *S. errata* (Waters 1878). This species is widely distributed in warm-temperate to tropical waters, but Hayward & Ryland (1979) explained its occurrence around the British Isles as owing to passive introduction amongst fouling communities on ships. The same explanation possibly holds for its occurrence in the Mediterranean Sea, as most records of its pres-

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ence are from harbours (Gautier 1962, Maluquer 1985). There, the species mostly thrives in shallow, calm water with high organic matter content, but may also inhabit areas with some hydrodynamics (Gusso Chimenz & Rivoecchi Taramelli 1972). Studies with artificial panels recorded diameter growth rates of up to 16 cm in 1 yr and showed highest reproduction and settlement during warmer months (Geraci 1974, Montanaro & Tursi 1983).

In their preliminary work, Ferdeghini et al. (2000) provided a first description of the structure of *Schizoporella errata* buildups at La Spezia. In the present paper we interpret the morphological variability of the same buildups as being plastic developmental responses to changes in environmental factors. We hypothesise that transition from multiserial encrustations to erect, branched buildups is related to the presence, in sheltered situations, of soft-bodied, erect organisms. Changes in constructional patterns of *S. errata* are interpreted as the results of the interaction with both these organisms and hydrodynamic conditions.

MATERIALS AND METHODS

Study area. The study was carried out in the region of La Spezia, an area under intense human pressure located in the Eastern Ligurian Sea (Fig. 1). The movement of water masses in the region is consistent with the Ligurian current, flowing towards the north-west (Astraldi & Gasparini 1992). In the channel between Palmaria and Tino Islands, the water flows mostly westward reaching a velocity of 80 cm s^{-1} (Cocito et al. 1998). Nutrient concentrations are significantly higher inside the Gulf of La Spezia (Cattini et al. 1992) than in the oligotrophic waters off the islands (Boniforti et al. 1993).

Three sites were selected according to their relative degree of exposure. The first, most exposed site, was located at Tino Island, at the western border of the Gulf; the second in a semi-exposed area in the harbour of La Spezia, on the breakwater delimiting the port-complex offshore; and the third in the inner part of the sheltered, small harbour of Lerici, where *Schizoporella errata* grew close to a sewer drain. The terms 'exposed' and 'sheltered' are used here in a relative sense. According to the fetch-energy index of Hummon (1989), which assigns an energy value of 100% to a wave reaching the coast perpendicularly from an infinite fetch distance, Tino is subject to a relative wave energy of 42, La Spezia of 9 and Lerici of 3%. At Tino, waves come mostly from the south-west and can reach a height of 6.5 m (Cocito & Sgorbini 2000). The La Spezia breakwater is rarely hit by southern waves higher than 1 m (Bassano et al. 2000), whereas waves are virtually absent in the harbour of Lerici.

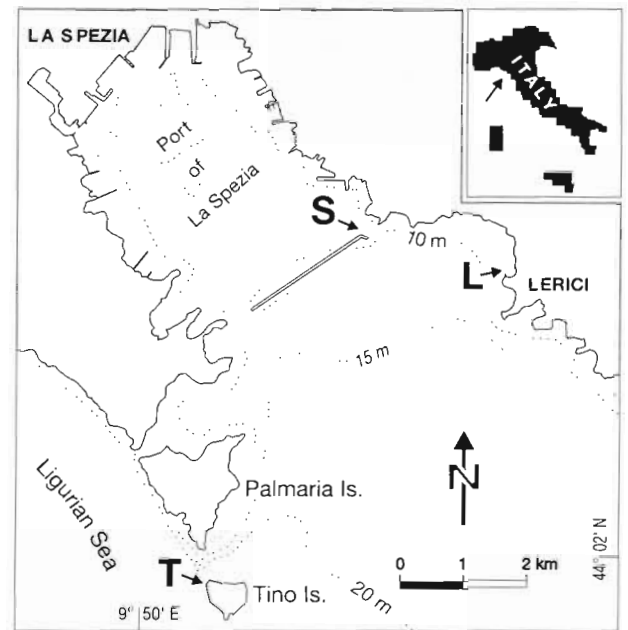


Fig. 1 Study area and location of sampling sites. T: Tino Island, exposed site; S: La Spezia harbour, semi-exposed site; and L: Lerici harbour, sheltered site

Sampling and laboratory methods. A total of 96 individual buildups (or large fragments) of *Schizoporella errata* was collected at 0.3 to 8 m depths—through snorkelling and SCUBA diving in June and July 1997—by scraping the substrate with a hammer and chisel. 32 samples were taken from Tino Island, 33 from La Spezia breakwater and 31 from Lerici harbour. After collection, each sample was bagged in polyethylene and preserved by freezing.

In the laboratory, the volume of the buildups was calculated by placing each sample in a cylinder filled with water and measuring the water displacement. Height, length and width were measured to the nearest mm. The number of branches per equivalent surface unit (dm^2) was computed by dividing the total number of branches by $V^{2/3}$ (where V = volume in dm^3). The order of branching was estimated by counting the number of bifurcations along each branch axis.

Buildups were photographed to keep a record of their external morphology, then sawn to examine their internal structure. Their basal thickness was measured at as many points as possible with a vernier calliper. Living zooid layers were recognised visually and counted under a dissecting microscope along cross sections.

Growth form was described by the height index (h) of Pichon (1987):

$$h = 2H/(D + d)$$

where H = maximum height of the buildup; D = maximum length; d = maximum width.

Differences in h , relative branch number, highest branching order and basal thickness among sites were tested with the Kruskal-Wallis 1-way ANOVA, whereas the Mann-Whitney U -test was used for pairwise site comparison (Sokal & Rohlf 1981).

The biota associated with the buildups was collected and identified to species whenever possible, taking into account only the organisms larger than 5 mm. Functional groups within this associated biota were defined according to their motility, position in the buildups and potential role in the constructional process.

RESULTS

Occurrence

At Tino Island, the most exposed site, *Schizoporella errata* colonised the rocky bottom down to 8 m depth, developing large (up to 40 cm) encrustations with flat

or bumpy surfaces. Their substratum cover never exceeded 5% in a community dominated by algae. In the semi-exposed site on La Spezia breakwater, the species inhabited rocky blocks as well as concrete surfaces down to 5 m, together with barnacles and mussels. *S. errata* colonies were numerous but relatively small (<30 cm wide), covering in total about 20% of the substratum. The landing-wharf structures of Lerici harbour were totally colonised (100% of substratum cover) by large and erect compound colonies more than 20 cm high.

Buildup morphology

Buildups from the 3 sites showed different gross morphologies (Fig. 2). At Tino, they had an encrusting growth form with only a few squat branches. Lerici buildups were predominantly erect, with long and slender branches that formed complex and anastomosed structures with open or closed tips. La Spezia showed intermediate features.

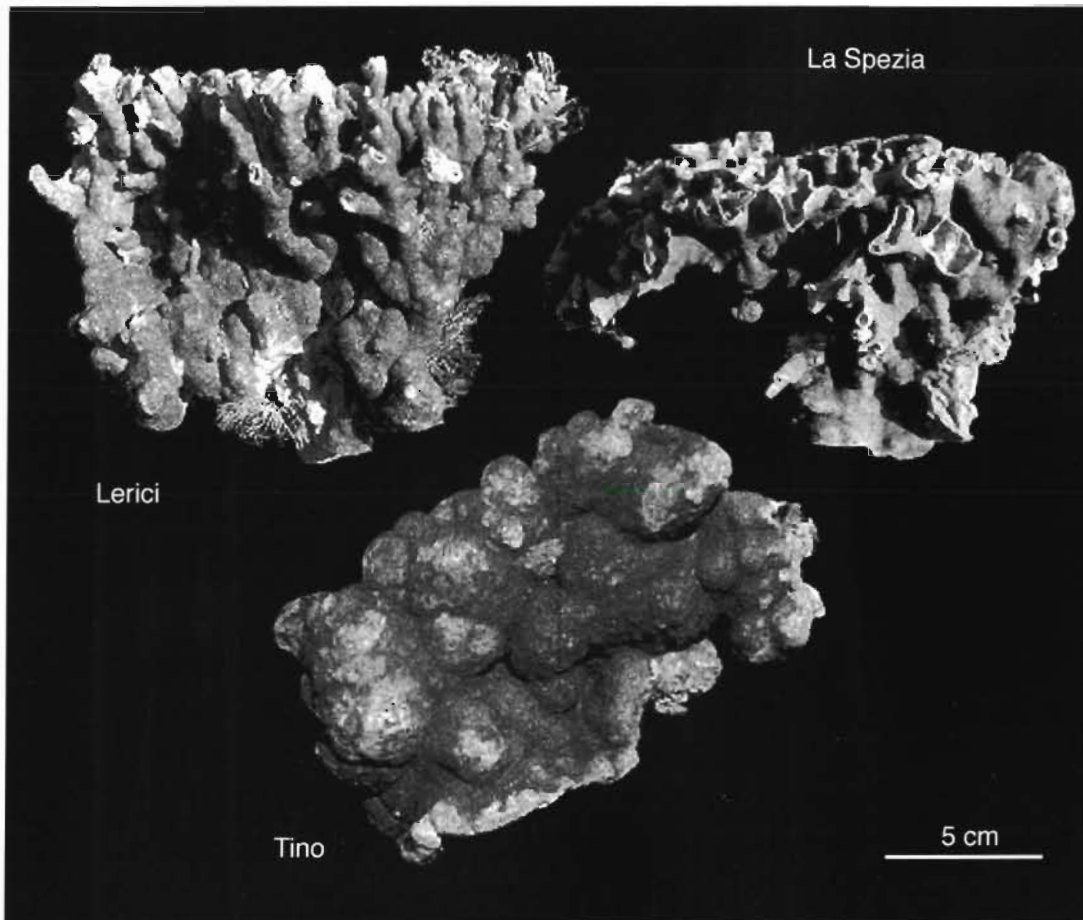


Fig. 2. Typical morphologies of *Schizoporella errata* buildups from the 3 sites

Pichon's height indices for *Schizoporella errata* buildups from the 3 sites (Table 1) were significantly different (Kruskal-Wallis 1-way ANOVA, $p < 0.0001$). All sites differed from each other (Mann-Whitney *U*-test, $p < 0.0001$ for all the 3 pairwise comparisons). At Tino, all buildups had *h* values below 0.8, indicating stout forms, as were most of those from La Spezia. Lerici buildups exhibited the widest range of *h* values, but many exceeded 1.0 (Fig. 3).

The number of branches per surface unit and the branching order (Table 1) were also different among the 3 sites (Kruskal-Wallis 1-way ANOVA, $p < 0.0001$). However, while the numbers of branches in the 3 sites were different (Mann-Whitney *U*-test: Tino vs La Spezia, $p = 0.001$; La Spezia vs Lerici, $p = 0.014$; Tino vs Lerici, $p < 0.0001$), branching order was lower at Tino than at La Spezia and Lerici (Mann-Whitney *U*-test, $p < 0.0001$) but not significantly different between La Spezia and Lerici (Mann-Whitney *U*-test, $p = 0.143$). Although fusion between closed branch tips complicated counting, branching order reached the 4th degree at La Spezia and the 5th degree at Lerici (Table 1).

Internal structure

Dissection of specimens from the 3 sites showed differences in the skeletal packing patterns of the basal

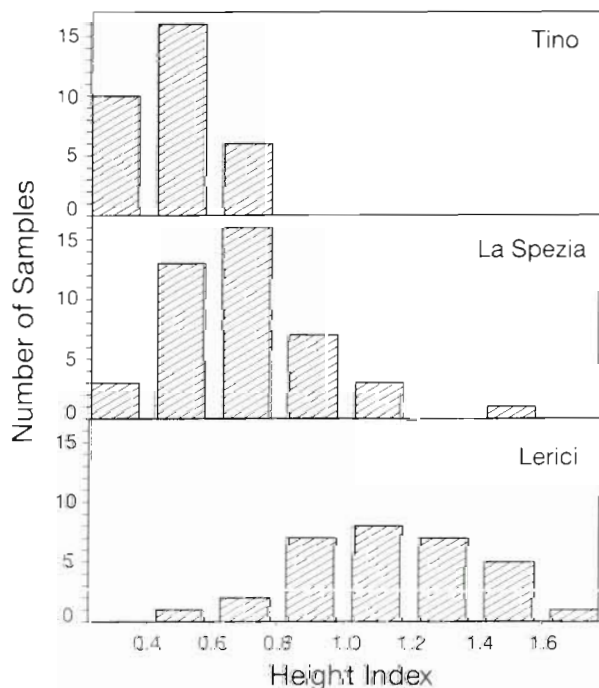


Fig. 3. Frequency distribution of height index in *Schizoporella errata* from the 3 sites. Height index was calculated according to the formula of Pichon (1978)

Table 1 Summary of measurements on *Schizoporella errata* buildups from the 3 sites

	Tino	La Spezia	Lerici
Height index			
Mean	0.48	0.69	1.13
SD	0.12	0.21	0.43
No. of samples	32	33	31
Min.	0.30	0.35	0.08
Max.	0.74	1.18	2.73
Branch number \times dm²			
Mean	0.02	0.17	0.44
SD	0.04	0.29	0.54
No. of samples	32	33	31
Min.	0	0	0
Max.	0.15	1.16	2.36
Branching order			
Mean	0.2	1.6	2.2
SD	0.5	1.6	1.6
No. of samples	32	33	31
Min.	0	0	0
Max.	2	4	5
Basal thickness (mm)			
Mean	21.3	23.2	44.9
SD	10.5	21.3	28.6
No. of measurements	53	35	27
Min.	3	5	13
Max.	42	104	104

portions. Samples from the exposed site were composed of a repetitive sequence of extensive, laminated, tightly packed sheets (Fig. 4a)

A more open framework was evident in the masses from the semi-exposed and, especially, the sheltered site (Fig. 4b). There, masses were nodular, formed of densely packed (sometimes concentric) sheets alternating with small cavities. Individuals of sessile epibionts, such as algae, hydroids, serpulids and barnacles, were found encased (and dead) between layers of *Schizoporella errata* (Fig. 5)

Basal thickness was greater at Lerici and La Spezia than at Tino (Table 1). Kruskal-Wallis 1-way ANOVA showed significant differences among the 3 sites ($p < 0.0001$). Mann-Whitney *U*-tests showed that differences were significant between Lerici and La Spezia ($p < 0.0001$) and Tino and Lerici ($p < 0.0001$), but not between La Spezia and Tino ($p = 0.423$).

The transverse sections of branches showed different filling or encrustation patterns. Some branches were tip-closed, filled by concentric, densely packed layers, except for a small cylindrical hole remaining at the centre. Organic debris or sediment occurred inside the hole. Other branches appeared as hollow, thin tubes constructed by a few layers surrounding erect sessile organisms, such as algae, hydroids, mussels and barnacles (Fig. 5).

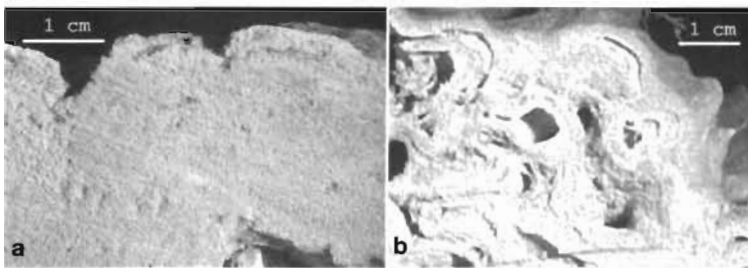


Fig. 4. Sections of the basal portions of *Schizoporella errata* buildups, showing different skeletal packing pattern at 2 sites: (a) Tino and (b) Lerici

Associated biota

Species composition of the biota associated to *Schizoporella errata* buildups showed important differences among the 3 sites, and especially between Tino and the remaining two. However, different species apparently played the same role in *S. errata* buildups from the 3 sites (Table 2).

Buildups from Tino Island had few associated fauna when compared with the other 2 sites. Barnacles were found embedded within bumps at the outer surface. Similarly, some algal bushes were found within squat branches. All other organisms were found mostly in the basal part.

At La Spezia, algae, hydroids, mussels and sabellid polychaetes were found protruding from the slender branches with open tips. Algal turf and the bushy bryozoan *Scrupocellaria reptans* (the most abundant species found here) covered extensive portions of the buildups.

Scrupocellaria reptans and *Bugula neritina* occurred in dense clumps of many colonies on the external surface of the buildups from Lerici. As at La Spezia, hydroids and algae were found inside slender branches, mussels in flared branches, and sponges and bivalves within cavities. Serpulids and ascidians were more abundant than at the other 2 sites.

Other sedentary and motile organisms were numerous at the 3 sites. The former settled on the dead portions or filled in cavities; the latter found shelter within branches or dwelt within the sediment accumulated in the interstices.

DISCUSSION

Although large dimensions and significant substratum cover were reached in all

3 sites studied, the tallest buildups of *Schizoporella errata* formed mainly in Lerici harbour, where erect growth may be favoured by crowding. Lerici was the most sheltered site. Other bryozoan bioconstructions are reported to occur in lagoons (Poluzzi 1980, Bijma & Boeschoten 1985, Sprigg & Bone 1993) and in submarine caves (Harmelin 1985, Scholz & Hillmer 1995). Thus bryozoans apparently conform to other non-anthozoan builders, such as serpulids, which form reefs mostly in quiet environments (Bianchi et al.

1995). This might be indicative of their constructions having insufficient skeletal strength to withstand wave impact (Vogel 1988).

The growth form of colonial organisms is strongly affected by water movement (Riedl 1971, Hughes 1989). Examples concerning bryozoans are provided by Stach (1936), McKinney & Jackson (1989), Okamura (1992), and Cocito & Ferdeghini (1999). Gautier (1962) observed that *Schizoporella errata* colonies develop an erect, bilaminar zoarium made up of anastomosed tubes in sheltered sites, and a unilaminar sheet-like zoarium in exposed sites.

The form of *Schizoporella errata* buildups in La Spezia region showed high correlation with exposure (Fig. 6). Erect growth in exposed conditions was apparently inhibited, whereas in sheltered situations signifi-

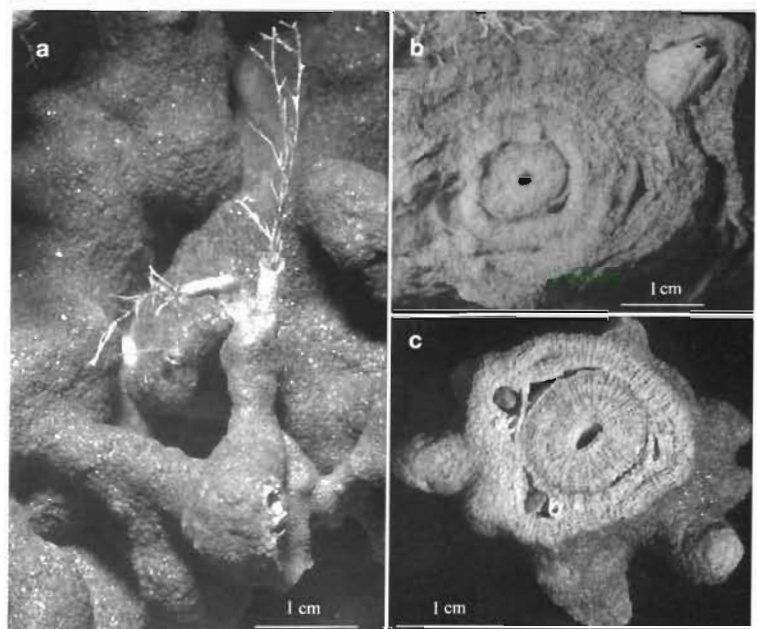


Fig. 5. Branch morphology of *Schizoporella errata* colonies from Lerici. (a) branch development around a hydroid stem. Transverse sections of well-developed branches, showing concentric layering and encased shells of dead organism, such as (b) barnacles, and (c) serpulids and small mussels

Table 2. Differences in species composition of the associated biota in the 3 sites, based on organism habit and growth form

	Tino	La Spezia	Lerici
Sessile			
Erect	Brown algae (<i>Cystoseira</i> sp.)	Articulate (<i>Corallina elongata</i>) and filamentous red algae; hydroids (<i>Eudendrium</i> sp.), sabellid polychaetes (<i>Branchiomma luctuosum</i>), bryozoans (<i>Margaretta cereoides</i> , <i>Scrupocellaria reptans</i>)	Green (<i>Ulva</i> sp.) and articulate red algae (<i>Corallina elongata</i>), hydroids (<i>Eudendrium</i> sp.), bryozoans (<i>Bugula neritina</i> , <i>Scrupocellaria reptans</i>)
Turf	Filamentous green algae, hydroid mat	Filamentous red and green algae	Filamentous green algae
Massive	Sponges (<i>Ircinia</i> sp.), barnacles (<i>Balanus perforatus</i>), ascidians (<i>Microcosmus</i> sp.)	Sponges (<i>Haliclona</i> sp.), mussels (<i>Mytilus galloprovincialis</i>), barnacles (<i>Balanus perforatus</i>), ascidians (<i>Polycarpa pomaria</i>)	Mussels (<i>Mytilus galloprovincialis</i>), barnacles (<i>Balanus perforatus</i> , <i>B. amphitrite</i>), ascidians (<i>Phallusia fumigata</i> , <i>Polycarpa pomaria</i> , <i>Styela plicata</i>)
Encrusters	Serpulids, bryozoans (<i>Watersipora subovoidea</i>)	Sponges (<i>Hymeniacion sanguinea</i>), hydroids (<i>Sertularella ellisii</i>), serpulids, spirorbids, bryozoans (<i>Watersipora subovoidea</i>)	Sponges (<i>Hymeniacion sanguinea</i>), bivalves (<i>Anomia ephippium</i>), serpulids, spirorbids
Sedentary			
Cavity fillers	Sponges, bivalves (<i>Arca noae</i> , <i>Striarca lactea</i>)	Sponges, bivalves (<i>Petricola lithophaga</i>)	Sponges, bivalves (<i>Petricola lithophaga</i>)
Motile			
Dwellers	Errant polychaetes, shrimps (<i>Alpheus</i> sp.), echinoderms (<i>Ophiotrix fragilis</i> , <i>Coscinasterias tenuispina</i>), fishes (<i>Lepadogaster lepadogaster</i> , <i>Parablennius rouxi</i>)	Gastropods (<i>Calliostoma</i> sp.), errant polychaetes, echinoderms (<i>Ophiotrix fragilis</i>)	Gastropods (<i>Gibbula varia</i> , <i>Nassarius incrassatus</i>), errant polychaetes (<i>Harmotoe areolata</i> , <i>Lepidonotus clava</i> , <i>Nereis</i> sp.), amphipods, crabs (<i>Eriphia verrucosa</i> , <i>Pilumnus hirtellus</i> , <i>Porcellana platycheles</i>)

cant vertical development was achieved by both a thicker basal portion and the production of erect branches.

Branching formed a spatially complex structure, providing habitat for other sessile and motile organisms, as already described by Bradstock & Gordon (1983), Maluquer (1985) and Ferdeghini & Cocito (1999). Habitat provision by biologically generated complexity has been demonstrated as playing an important role in maintaining and enhancing marine biodiversity (Thompson et al. 1996). Building a rigid and erect framework, colonies of *Schizoporella errata* modify habitat characteristics and may thus be qualified as 'ecosystem engineers' (Jones et al. 1994).

Conversely, the associated organisms may themselves contribute to the consolidation of the buildup, not only adding their skeletal structures (Reguant & Zamarrero 1987, Moissette & Pouyet 1991), but also playing many of the functional roles described by Fagerström

(1991). Our observations suggest that competition for the substratum between *Schizoporella errata* and the other sessile species played a major and previously undescribed role, especially at La Spezia and Lerici. *S. errata* is a strong interference competitor, able to overgrow other organisms (Osman 1977, Sutherland 1978). Erect organisms may resist overgrowth (Buss

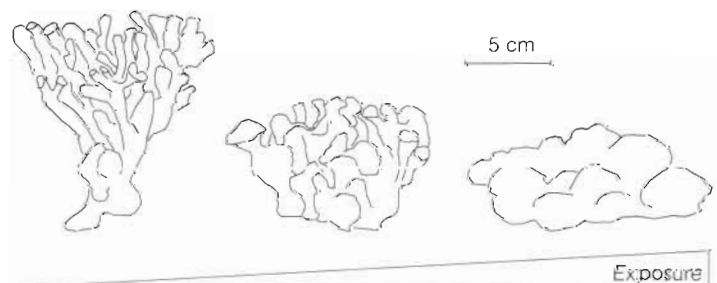


Fig. 6. Change in growth form of *Schizoporella errata* buildups according to exposure gradient in La Spezia region

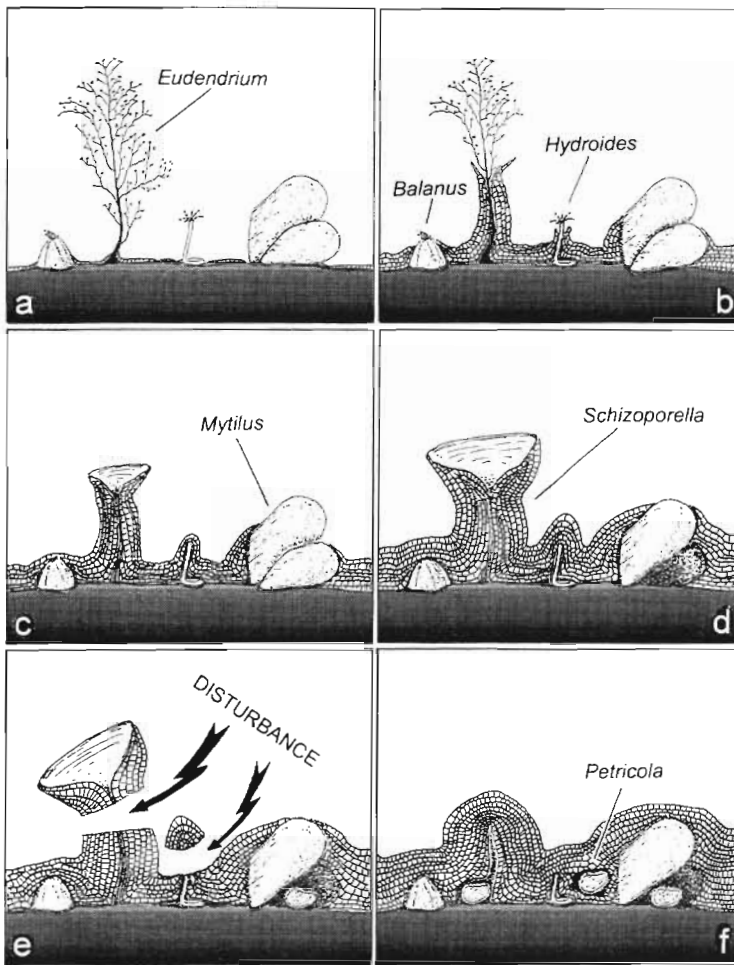


Fig. 7. Hypothetical pattern of framework construction in *Schizoporella errata* buildups: (a) *S. errata* colonises bare substratum among other sessile organisms; (b) to (d) *S. errata* overgrows the other species which eventually die, leaving branches with closed or open and flared tips; (e) episodic disturbance may break away the fragile apical portions of the erect branches; (f) final structure of the multilayered buildup of *S. errata*, the original morphology being little or no longer recognizable (see 'Discussion')

1981, McKinney & Jackson 1989) when bushy and grouped in dense clumps of colonies, as shown by *Scrupocellaria reptans* and *Bugula neritina*. When erect organisms grow isolated, *S. errata* easily expands above their stems and forms encrusting layers around them, thus creating cylindrical branches; this happened, for instance, with the hydroid *Eudendrium racemosum*. In this way the erect organisms may serve as a template for building an erect framework.

The possible process of buildup growth may be summarised as follows (Fig. 7). As a first step, *Schizoporella errata* colonies grow side-by-side with barnacles, mussels, algae and hydroids colonising the substratum with single-layered encrusting sheets (Fig. 7a). As free

substratum becomes exhausted, *S. errata* morphology changes from unilamellar to multilamellar, owing to an array of budding patterns (Lidgard 1985, Ristedt 1996), including self-overgrowth (McKinney & Jackson 1989). This leads to broad encrustations that expand above and unite the framework created by other organisms into the overall structure (Fig. 7b). Although partially covered by the bryozoan layers, these organisms survive for some time. When growing around tall, arborescent organisms such as hydroids, *S. errata* forms cylindrical branches which flare at their distal end because of the swinging apical parts of the arborescent organism. On wave-swept rocks in the exposed site, this swinging movement must be so continuous and intense that such branches do not develop at all. Eventually, all the organisms overgrown and surrounded by *S. errata* die (Fig. 7c). Soft-bodied organisms leave no skeletal remnants and in this case the cylindrical branches of *S. errata* appear hollow (Fig. 7d). When an episodic physical or other disturbance breaks away the fragile apical portions of those branches (Fig. 7e), the bryozoan repairs breakage through frontal and lateral budding processes, giving the branch tip a completely different shape. At this stage, *S. errata* appears to be the only organism responsible for the construction of an erect frame, whereas the contribution of shelled organisms to the thickness and solidity of the basal crust is clearly recognisable (Fig. 7f).

Studying the zoarial morphology of *Schizoporella violacea* (a junior synonym of *S. errata*, according to Hayward & Ryland 1979), Pouyet (1971) also observed hollow branches and, finding no organism remnants inside the cavities, concluded that the erect branching growth was independent of the associated biota. Our observations do not agree with Pouyet's interpretation, and lead to the hypothesis that erect growth was achieved in sheltered sites through the contribution of associated organisms, rather than by *S. errata* itself. According to our interpretation, reduced hydrodynamics is a necessary but not sufficient condition for the formation of tall buildups of *S. errata*. This formation requires the presence of erect, associated organisms that act as a support for repeated binding by the bryozoan. If soft-bodied, these organisms disappear after complete overgrowth by *S. errata*. We call these organ-

isms 'ghost frame-builders' and consider the process of 'ghost frame-building' a peculiar form of bioimmuration, i.e. the organic overgrowth of sessile organisms by encrusting animals with mineralised skeletons (Taylor 1990). Contrary to what routinely happens with bioimmuration which usually produces a precise mould, in this case, such as in the case of bryozoan building tubes around hermit crab symbionts (Taylor 1994), the exact shape of the soft-bodied organism is not preserved in the final structure, especially when morphology is altered by breakage and the repairing capacity of *S. errata*. Ghost frame-building permits the vertical growth of sheet-like encrusting organisms and represents a further example of the complexity of the interactions among epibiosis, competition and physical disturbance in the encrusting sequences and growth patterns (Wahl 1989, McKinney 1995, Spjeldnaes & Moissette 1997, Kidwell & Gyllenhaal 1998). It may be a process of more general occurrence with significant ecological and palaeontological implications (Smith 1995, Nebelsick et al. 1997). Clearly, further investigation is needed to test our hypothesis and to see whether it can be extended to other habitats and/or organisms.

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