

Bioconstruction and biodiversity: their mutual influence*

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SUMMARY: This paper describes the functional role of main benthic constructor organisms and reviews processes by which bioconstructions increase diversity and abundance of associated biota, and the reverse. Based on the literature, patterns of diversity of carbonate bryozoan bioconstructions, one of the most important groups performing important constructional roles, have been analysed. Diversity of bryozoan bioconstructors seems not to follow the latitudinal gradient, from tropics to increasing distance from tropics, recognised for coral bioconstructors. The only case of a “high diversity bryozoan reef” (Joulters Cays, Bahamas) represents a situation virtually unique in carbonate environments. Dimension and extension of bryozoan bioconstructions show their maximum in temperate environments, where seasonality or variability of environmental parameters could afford advantages for success to bryozoans. With only one exception (the bryozoan-serpolid build-ups from South Australia), diversity of biota associated with bryozoan bioconstructions is high, but comparison is not possible due to the fact that exhaustive faunal studies are rare, sometimes referring only to one taxon, and environments differing in depth range, salinity, hydrodynamics, trophic diversity, etc. are involved.

Key words: biodiversity, biological habitat provision, bioconstructor, physical habitat structure, associated fauna, Bryozoa.

RESUMEN: BIOCONSTRUCCIÓN Y BIODIVERSIDAD: SU INFLUENCIA MUTUA. – Se describe el papel funcional de los principales organismos bentónicos constructores y se revisan los procesos por los que las bioconstrucciones aumentan la diversidad y la abundancia de la biota asociada, y al revés. Sobre la base de la bibliografía, se han analizado los patrones de diversidad de las bioconstrucciones carbonatadas de los briozoos, uno de los grupos más importantes por su papel constructor. La diversidad de los briozoos en tanto que bioconstructores no parece seguir el gradiente latitudinal, desde los trópicos hasta distancias crecientes de éstos, que se ha reconocido para los bioconstructores que son los corales. El único caso de “arrecife de briozoos de gran diversidad” (los cayos Joulters, Bahamas), representan una situación prácticamente única en ambientes carbonatados. La dimensión y la extensión de las bioconstrucciones de briozoos presentan su máximo en ambientes templados, en los que la estacionalidad o la variabilidad de los parámetros ambientales pueden proporcionar ventajas para el éxito de los briozoos. Con una sola excepción (los edificios de briozoos y serpúlidos de Australia del Sur), la diversidad de la biota asociada con las bioconstrucciones de briozoos es elevada, pero no es posible la comparación debido al hecho de que los estudios faunísticos exhaustivos son raros, a veces se refieren únicamente a un taxón, y a que se trata de ambientes que difieren en rango batimétrico, salinidad, hidrodinamismo, diversidad trófica, etc.

Palabras clave: biodiversidad, provisión de hábitat biológico, bioconstructores, estructura física del hábitat, fauna asociada, briozoos.

INTRODUCTION

Many marine organisms, both plants and animals, build bioconstructions, i.e. durable elevated

biogenic structures, through the aggregation and accumulation of their calcareous skeleton. The resulting permanent structures grow at various depths, can be variable in shape and dimension and often enjoy a rich fossil record extending back to centuries or millennia (Laborel, 1987).

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Bioconstructions may be highly dynamic, involving skeletal growth processes and biotic interactions established among co-occurring species. Processes of physical and biological destruction can be included as well. Bioconstructions are intrinsically complex, in terms of their physical structure, associated biota and processes they generate, which can be apparent from biogeographic scales to scales of centimetres. It has been demonstrated that the creation and modification of habitats, in term of physical habitat structure, not only increase habitat diversity, but in turn directly control the distribution and abundance of species (Jones *et al.*, 1994; Rebele, 1994).

Indeed, the idea that habitat diversity promotes species diversity was recognised since the 1940s (Williams, 1943); subsequently, it has been demonstrated that habitat complexity induced by benthic constructors promotes biological diversity (calcareous algae: Hong, 1982; Freiwald and Henrich, 1994; corals: Sorokin, 1995; vermetids: Ben-Eliahu and Safriel, 1982; Pandolfo *et al.*, 1992; mussels: D'Anna *et al.*, 1985; Dittmann, 1990; Günther, 1996; oysters: Lenihan, 1999; polychaetes: Porras *et al.*, 1996; Bianchi and Morri, 1996; barnacles: Thompson *et al.*, 1996; bryozoans: Bradstock and Gordon, 1983; Ferdeghini and Cocito, 1999).

The coral reef is the paragon of a rich marine community (Cornell and Karlson, 2000). In areas of the world, mainly in shallow, tropical seas, where coral reefs, i.e. the largest biologically constructed features, are present and represent an important source of human sustenance (commercial and subsistence food species, medical useful compounds, tourism, etc.), their great significance in generating and maintaining marine biodiversity has been highlighted. Moreover, maintenance of bioconstruction and biodiversity have been advocated as goals for ecologically sustainable development (Done, 1995).

Since factors responsible for differences in species richness is of central concern to ecologists, a general analysis of processes generated by the main constructors promoting biodiversity in marine benthic ecosystems is needed.

This paper aims 1) to describe the functional role of the principal benthic constructor organisms and 2) to review processes by which bioconstructions increase diversity and abundance of associate biota. Conspicuously lacking from the list of key processes in ecological works is the influence of diversity both of bioconstructors and associated biota on the building process. For example, reduction of diversity of bioconstructing corals along a latitudinal gra-

dient, from the tropics to higher latitudes, has been recognised (Wood, 1999). For other bioconstructors the same pattern has not yet been demonstrated. A third objective of the present work based on the literature is to analyse patterns of diversity of carbonate constructions by bryozoans, one of the most important groups performing a constructional role, especially in the past (Cuffey, 1972; 1974).

MATERIALS AND METHODS

In order to define the functional role of bioconstructors, definitions of growth form and growth habit by Fagerstrom (1988, 1991), Insalaco (1998) and Wood (1999) have been compared with references to skeletal properties (size and strength), growth direction and functional morphology.

Papers describing modification of physical structure during the framework building by different constructor organisms have been compared in order to single out common processes influencing diversity of biota associated with bioconstructions.

RESULTS AND DISCUSSION

Who is (acts as) a bioconstructor?

According to Fagerstrom (1991), assignment of an organism to a particular building group is based on its growth form and growth habit. Erect and large, well-skeletonized mound or branched organisms, belonging to the functional unit of 'constructors', provide most of the volume and rigidity to the framework if compared to encrusters, which expand and unite the components of the framework and the settling sediment, these last belonging to the functional unit of 'binders'. Other erect, non-skeletal to poorly skeletonized organisms, usually smaller than constructors, act as 'bafflers' reducing current velocity on the framework surface, enhancing sediment deposition and cavity filling within the framework. Because of their poor skeletonisation, sometime bafflers can remain within the framework in their original position after death (Cocito *et al.*, 2000). If soft-bodied, bafflers can disappear after complete overgrowth by encrusting animals with mineralised skeletons (Pouyet, 1971; Taylor, 1990).

High packing density and/or morphologic plasticity may enable various taxa to perform more than one role in the success of the building, and such taxa

consequently belong to more than one functional unit (Fagerstrom, 1991).

A 'primary framework' is recognised by many authors as the product of erect organisms, whereas a 'secondary framework' is generated by mutual interconnections of encrusting organisms (Insalaco, 1998).

A prerequisite for the formation of well-structured bioconstructions is the persistence of dense assemblages which in turn depends on continual larval settlement, rapid growth and clonal growth with fragmentation or partial mortality (Jackson, 1977). Relatively small and short-lived aclonal/solitary organisms usually produce crusts that do not project substantially above the substrate. On the contrary, they may form dense aggregations in crypts. Clonal/modular organisms, characterised by longevity and large-size, can create structures with permanent attachment to extensive substrates, considerable elevation above the substrate (decimetres or meters) with large cavities and thus high spatial heterogeneity (Wood, 1999).

In addition to corals, a wide range of organisms acts as bioconstructors (Table 1): calcareous algae, barnacles, sabellariid and serpulid polychaetes, vermetids, oysters, mussels, bryozoans, sponges, and other non-calcified organisms, especially microbial biofilms, where rapid precipitation of carbonate is enhanced. They build differently sized topographic structures, from the largest bioconstructed features (the Great Barrier Reef) which extends for thousand of kilometres off Australia to the 'micro-reefs' (Scholz and Hillmer, 1995), generated by calcifying bryozoans and measurable in terms of mm to cm, and to the thin layered 'stromatolite reefs', reaching up to 2.5 m high (Littler and Littler, 2001), made by cyanobacteria and diatom communities. These bioconstructions can be found in a wide range of environmental settings. Information on their global dis-

tribution, modified from Wood (1999), is reported in Table 1.

How bioconstruction influences biodiversity

By building a framework, bioconstructors generate physical structures thus modifying the habitat and its structural complexity. This implies direct provision of living space by the physical structure and quantitative changes in the amount of living space as the framework grows. Habitat structure has long been considered an important determinant of the number, identity and abundance of species present in biological communities (Menge and Sutherland, 1976; Commito and Rusignuolo, 2000) through the so called 'biological habitat provision' (Thomspon *et al.*, 1996). Creation of new habitat not only increases habitat diversity, but causes an increase in species diversity (Rebele, 1994).

Moreover, the increase in size of bioconstructions induces modifications in the composition of biota participating in their formation and in the shape and growth rate of these structures.

Relationship also exists between size, degree of three-dimensionality or spatial heterogeneity and the availability of cryptic refuges. Offering protection from predation, wave scour and high light irradiance, crypts represent a better habitat to many organisms, which are far more abundant in crypts than on open surfaces (Buss and Jackson, 1979).

Physical habitat structure can directly influence local species through physical-biological coupling, that is by altering physical variables which have subsequent biological effects (Lenihan, 1999). For example, effects caused by structural changes in the benthic habitat during bioconstruction of living mussel beds have been compared with those caused by biological activities (Günther, 1996; Crooks and

TABLE 1. – Main framework builders, their functional role in the bioconstruction process and their global distribution.

Main framework builders	Functional role	Distribution
Calcareous algae	baffle, binder	tropical to polar
Photosymbiotic corals	constructor, baffle, binder	tropical to temperate
Non-photosymbiotic corals	constructor, baffle	tropical to polar
Vermetids	constructor	subtropical to temperate
Sabellariids	constructor	subtropical to temperate
Serpulids	constructor	tropical to polar
Oysters	constructor	subtropical to temperate
Mussels	constructor	tropical to subpolar
Barnacles	constructor	tropical to polar
Bryozoans	constructor, binder	tropical to polar
Sponges	baffle, binder	tropical to polar
Cyanobacteria and diatom biofilms	binder	tropical to temperate

Khim, 1999; Lawrie and McQuaid, 2001). Physical structure of multi-layered mussel beds alters hydrodynamic, sedimentary and microtopographic features on the tidal flat. They have complicated effects on the local water flow, which could influence, for example, the recruitment of macrofauna. Enhancement of settlement and subsequent recruitment of certain planktonic larvae by providing a greater number of suitable sites has been demonstrated. Harris *et al.* (1998) found a highly significant correlation between recruitment intensity and adult density of mussels.

Increasing the variety of suitable feeding sources is another process which influences biodiversity of associated biota. Differentiation of feeding habits of the associated biota has been analysed in *Mytilus edulis* beds (Tsuchiya and Nishihira, 1986): many gastropods, bivalves and errant polychaetes, generally deposit feeders, filter feeders or carnivores-scavengers, inhabit the lower layer or deeper portion of cavities where sediment, shell fragments and dead organisms settle and accumulate. Mussel beds trap and incorporate shells, sediment, algae, thus increasing the supply of materials, for example, for tube-builders and provide a stable matrix in which tubes can be built. The structure surface serves as substrate for bacteria, microalgae and small invertebrates. Attached algal thalli support various animals as well, such as herbivores, grazers and filter-feeders.

Spatial zonation patterns of associated biota have been discussed also for bryozoan constructions, distinguishing 'nanno-habitats' provided to bacteria, diatoms and fungi, and 'micro-habitats' to algae, hydrozoans, bryozoans and other invertebrates (Scholz and Hillmer, 1995).

Thigmotactic responses to physical structures is shown by some motile benthic species which actively choose sites (Olyslager and Williams, 1993). Among co-occurring species, these organisms have to be added to the 'dwelling' ones, which are neither actively building nor destroying (boring or rasping) the framework. Taxonomic diversity of dwellers is usually higher than any other functional groups described in the previous paragraph.

How biodiversity influences bioconstruction

Framework building, at least for the most studied ancient and modern structures (i.e. the reefs), is guaranteed by the combined processes of construction, baffling, trapping, binding and cementation. Each of these processes in turn is strongly dependent

on the participation of all functional groups of building organisms.

Composition of biota, both in qualitative and quantitative terms, participating in the bioconstruction process is variable. Different organisms may alternate more or less regularly or occur at different stages in the construction, giving birth to increased-size masses (Moissette and Pouyet, 1991). In large, spatially heterogeneous constructions rich aggregations of sciaphilic calcareous algae, bryozoans and madreporarians living in crypts or cavities add their calcareous skeleton to the framework, thus increasing its thickness and robustness.

Not only diversity of associated biota can influence outcome of bioconstruction process but also bioconstructors' diversity itself. Coral reefs, the largest bioconstructed features known, widespread in the tropics, are formed by a large number of species (high diversity reefs), whereas a few species or, in some cases, only one species, participate in biogenic constructions (low diversity reefs), for example, in temperate areas. For corals, reduction of bioconstructors' diversity along a latitudinal gradient, from tropics to higher latitudes, has been recognised. For other organisms the same pattern is not clear. Similarly, dimension and extension of coral bioconstructions show the same distributional pattern. But correlation between dimension and extension of bioconstructions and bioconstructors' diversity is still an hypothesis.

Diversity patterns of bioconstructions: an example from bryozoans

Bryozoans are known to form the structural basis of biohermal mounds, and some erect species comprise the principal frame-builder of assemblages that attract epibionts and entrap sediments (Battershill *et al.*, 1998).

Records of modern frame-building activities of bryozoans are not numerous even if comparable in some cases to those of corals. The most important, in terms of extension and dimension, come from New Zealand (Bradstock and Gordon, 1983), Netherlands (Bijma and Boekschoeten, 1985), South Australia (Bone and Wass, 1990) and the Bahamas (Cuffey *et al.* 1977). Number and identity of the bryozoan species building those frameworks are known, but exhaustive faunal studies have not always been done either within or around those structures (Table 2). The Bahamian 'tidal channel bryozoan reefs' rise up to 3 m above the bottom.

TABLE 2. – Some examples of bryozoan constructions from different geographic areas: bioconstructors' diversity, main frame-builders, location and associated biota from literature review (1: Cuffey *et al.*, 1977; 2: Bradstock and Gordon, 1983; 3: Bone and Wass, 1990; 4: Bijma and Boekschoten, 1985; 5: Battershill *et al.*, 1998; 6: McKinney and Jaklin, 2000; 7 and 9: Ferdeghini and Cocito, 1999; 8: Maluquer, 1985).

Bioconstructors diversity	Main frame-builders	Location	Associated biota diversity
Multispecific	<i>Celleporaria albirostris</i> <i>Parasmittina munita</i> <i>Rhynchozoon rostratum</i> <i>Rhynchozoon tuberculatum</i> <i>Schizoporella cornuta</i> <i>Smittipora americana</i> <i>Steginoporella magnilabris</i> <i>Stylopoma spongites</i>	(1) Bahamas Lat. 23° N	Other bryozoans, corals, serpulids, calcareous algae, sponges, bivalves, foraminiferans
Oligospecific	<i>Celleporaria agglutinans</i> <i>Hippomenella vellicata</i>	(2) New Zealand Lat. 41° S	92 bryozoans, plus serpulids, bivalves, foraminiferans, gastropods, ophiuroids, polychaetes, sponges, ascidians, holoturians, fishes
Oligospecific	<i>Membranipora aciculata</i> Unidentified serpulids	(3) South Australia Lat. 36° S	Other bryozoans; no evidence of other organisms
Oligospecific	<i>Electra crustulenta</i> Cyanophyte stromatolites	(4) Netherlands Lat. 51° N	Other bryozoans, plus hydroids, gastropods, isopods, polychaetes, eels, plants, algae
Monospecific	<i>Cintipora elegans</i>	(5) New Zealand Lat. 47° S	Other bryozoans, worm tubes, bivalves, sponges, cnidarians, ascidians, mussels, oysters
Monospecific	<i>Cellaria salicornioides</i>	(6) Croatia (NW Mediterranean) Lat. 45° N	58 species (2 algae, 7 sponges, 3 cnidarians, 4 annelids, 30 bryozoans, 2 molluscs, 7 ascidians, 3 others)
Monospecific	<i>Pentapora fascialis</i>	(7) Italy (NW Mediterranean) Lat. 44° N	84 species (27 bryozoans, 19 molluscs, 11 cnidarians, 8 annelids, 5 algae, 1 foraminifer, 2 sponges, 4 crustaceans, 2 echinoderms, 1 ascidian, 4 fishes)
Monospecific	<i>Schizoporella errata</i>	(8) Spain (NW Mediterranean) Lat. 40° N	28 species (5 bryozoans, 2 molluscs, 5 cnidarians, 2 annelids, 8 crustaceans, 2 echinoderms, 1 ascidian, 3 fishes)
		(9) Italy (NW Mediterranean) Lat. 44° N	36 species (4 algae, 2 sponges, 3 hydroids, 7 polychaetes, 7 molluscs, 4 bryozoans, 5 crustaceans, 3 ascidians, 1 fish)

These are composed of numerous bryozoan species, and, apparently, are the only example of 'high diversity reefs' built by bryozoans. In reefs the bryozoans act as frame-builders in association with other organisms, and also as hidden encrusters, cavity-dwellers and cavity-fillers (Cuffey *et al.*, 1977).

In the tropics, bryozoans have a low biovolume compared to corals and are generally excluded from reef-constructing roles. Except by Ryland and Hayward (1992), their taxonomic and morphologic diversity has not yet been sufficiently described and analysed.

Bryozoans occur in modern tropical carbonate settings but seldom in sufficient relative abundance for their remains to form a significant fraction of the carbonate sediment (Pachut *et al.*, 1995). Only outside the tropics the calcareous skeletons of modern bryozoans are major contributors to sediments and

they dominate many temperate limestones (Taylor and Allison, 1998).

In temperate waters, living bryozoans can substitute for corals in abundance and structure (Battershill *et al.*, 1998). In New Zealand, Tasman Bay bryozoan beds, up to 272 km² in extent, are made by two species ('low diversity reef'): the cheilostome *Celleporaria agglutinans*, which occurs at depths of 10-35 m forming clumps up to 0.5 m high and attaining up to 50 % cover, and *Hippomenella vellicata*, which forms coarse foliaceous colonies up to 0.2 m high and 0.3 m across. These beds provide attachment surface for other calcareous frame-building components and dwelling organisms (Table 2). Linear reefs supporting a huge range of marine life are present in south New Zealand: the cyclostome *Cintipora elegans* forms erect branching colonies of cylindrical stems more than 30 cm high, with aggre-

gate mounds displaying a total elevation of 1 m high and forming structures more than 10 km long and 0.5 km wide (Bradstock and Gordon, 1983).

Two important examples of oligospecific build-ups grow in the brackish inland waters of SW Netherlands and in the lagoon system of South Australia. The first, called 'growing stones', are bryozoan/stromatolite formations up to 1 m high and tens of meters across covering various substrates (Bijma and Boekschoeten, 1985). The second are laterally extensive build-ups made by mounds up to 40 cm in diameter and 30 cm in height, extending for many hundreds of meters (Bone and Wass, 1990).

In the NW Mediterranean, several bryozoan species form monospecific structures of which the associated biota has been analysed: '*Pentapora fascialis* reef' (Cocito *et al.*, 1998; Ferdeghini and Cocito, 1999), '*Cellaria salicornioides* meadow' (McKinney and Jaklin, 2000), '*Schizoporella errata* build-ups' (Cocito *et al.*, 2000). Many other cases of constructions made by bryozoans interacting with other organisms have been described but information on faunal composition is not always available.

Diversity of bryozoan bioconstructors seems not to follow the latitudinal gradient, from tropics to increasing distance from tropics, recognised for coral bioconstructors. The only case of a 'high diversity bryozoan reef' (Joulter Cays, Bahamas) represents a situation virtually unique in carbonate environments, also because in the nearby coral reefs area (Andros and Eleutra Islands, Bahamas) all of the same bryozoan reef-building species are present (Cuffey and Fonda, 1977). Obviously, these species possess constructional potential, which apparently is suppressed by coral-algal competition and released only where marginal environmental conditions eliminate that competition.

Dimension and extent of bryozoan bioconstructions show their maximum in temperate environments, where seasonality or variability of environmental parameters could afford advantages for success to bryozoans. The latitudinal pattern of bryozoans as bioconstructors is consistent with the pattern of maximum abundance of bryozoans in non-tropical latitudes. Indeed, these patterns are closely related to the high abundance of bryozoan skeletons in modern carbonate sedimentary deposits in cool temperate marine waters (Taylor and Allison, 1998).

With only one exception (the bryozoan-serpulid build-ups from South Australia), diversity of biota

associated with bryozoan bioconstructions is high, but comparison is not possible due to the fact that exhaustive faunal studies are rare, sometimes refer only to one taxon, and that environments differing in depth range, salinity, hydrodynamics, trophic diversity, etc. are involved.

CONCLUDING REMARKS

In many respects, the study of the mutual influence between bioconstruction and biodiversity represents an investigation of the basic habitat requirement of species and of the interactions among co-occurring species.

In addition to the often claimed need to promote systematics and taxonomy (Clarke, 1992), two main aspects should be studied with more detail: the positive interactions among species and the scale of complexity of secondary substrata, i.e. bioconstructions.

Structural complexity of primary substrata is known to have strong influence on the diversity and abundance of colonising species (Beck, 1998). Differently, relationship between secondary substrata and associated biota, which are determined mainly by trophic, dynamic, chemical interactions occurring within them, are still less known. Marine ecologists have devoted most of their efforts to understanding the role of negative interactions, such as competition and predation, in regulating populations and in structuring communities, but experimental work on positive interactions is spotty and detailed only for few species. For example, a better understanding of the mechanisms of coexistence between species should require attention to life histories traits that enhance reciprocal tolerance of species and to how available resources are used or shared.

Quantification of interrelationship between scales of complexity of secondary substrata and associated biota is a key requirement to understanding spatial distribution of marine benthic communities. Consequently, it will be essential to interpret the measurement and effects of complexity of secondary substrata between different bioconstructors and habitats, in order to differentiate the vast scale across which they can be observed. Embedded within the framework generated by a bioconstructor, numerous smaller-scale species interactions could be found. Thus, multi-scale investigations are needed to understand how scales influence community diversity and abundance in benthic communities.

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