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Transformation processes and growth of new polymorphs in Bryozoan *Mollia rosselii* (Audouin, 1826)

(Bryozoa: Gymnolaemata: Cheilostomata: Microporidae)

Abstract

A set of living colonies of the Bryozoan *Mollia rosselii* (Audouin) was picked out at a depth of 30-40 m offshore the town of Estapona (Spain). The fluctuations of West Alboran Gyre, the seasonal water bloomings, the mixing of Mediterranean and Atlantic waters contribute to develop a discontinuous and unpredictable bottom environment that optimize the occurrence of *r*-selected organisms (*r*- is the maximal intrinsic rate of natural increase). The maintenance of a strong phenotypic plasticity associates to competitive growth alterations. The energy demand of *M. rosselii* to perform a reactive strategy is probably obtained by a phenotypic transformation of approximately oval zooids into compact clusters of flattened polygonal individuals. The newly formed polymorphs rearrange funicular strands tissue and acts as a depository of available energy. Finally it is worth to note that the flat surfaces of new formed modules attenuates the collision with moving objects under the forces of flowing waters.

Key words: Unstable environments, zooidal regenerative transformations of autozooids and kenozooids.

Riassunto

[*Processi di trasformazione e crescita di nuovi polimorfi nel Briozoo Mollia rosselii* (Audouin, 1826)]

Un gruppo di colonie viventi del Briozoo *Mollia rosselii* (Audouin) è portato alla luce da una profondità di 30-40m al largo della città di Estapona (Spagna). Le fluttuazioni del Western Alboran Gyre, le fioriture stagionali, il miscelamento delle acque Mediterranee e Atlantiche, contribuiscono alla formazione di un ambiente di fondo fortemente discontinuo e imprevedibile. La condizione fisica del biota ottimizza lo sviluppo di organismi *r*-selezionati (*r*- è il tasso intrinseco massimo di incremento naturale) e induce forti alterazioni nelle caratteristiche fenotipiche degli individui. La richiesta di energia di *M. rosselii* per attuare una strategia reattiva si associa probabilmente alla trasformazione di zooidi approssimativamente ovali in gruppi compatti di individui poligonali appiattiti. I polimorfi neoformati riordinano i fili del tessuto funicolare e agiscono come deposito di energia disponibile a tutta la colonia. Da ultimo si può notare come le superfici frontali piatte dei moduli neoformati attenuino la collisione con oggetti in movimento per le forze generate dal flusso delle acque.

Study area and collected materials

A sampling survey was carried out by SCUBA diving in Alboran Sea offshore the city of Estapona (autonomous community of Andalusia) during the 2008 summer season (Fig. 1). A set of 30 samples containing colonies of the Bryozoan *Mollia rosselii* (Audouin, 1826) (Genus *Mollia*, Family *Microporidae*, Suborder *Anasca*, Order *Cheilostomata*, Class *Gymnolaemata*, Phylum *Bryozoa* or *Ectoprocta*) was picked up from a sampling area 30–40m depth. A large part of specimens showed a firmly intact frontal membrane (Fig. 2 A-D), while in other individuals only the skeletal structure was preserved. All the specimens of *M. rosselii* were separated and prepared for scanning electron microscope (SEM) by removing intimately associated epifaunal component such as barnacles, ascidians, polychaete annelids, microalgal cover and unnamed encrusting cheilostomes. The Alboran Sea is characterized by Western Anticyclonic Gyre, an almost permanent feature that feeds the western coast as well as the phytoplankton primary productivity zone (HAUSCHILDT et al., 1999) (Fig. 1). Simultaneously coastal upwelling currents induce the rise of waters from subsurfaces toward the surface; the outcropping waters, rich in nutrient, go around the Estapona gyre, contributing to seasonal fertilization of the basin. Large masses of water with contrasting densities move on the bottom, eroding and shaping the coasts of Iberian Peninsula and Moroccan zone (ERCILLA et al., 2016). With respect to the tides, the current velocity in the semidiurnal band has a barotropic character. As a consequence the semidiurnal tide dominates transport and dispersal of pollutants (PERIÁÑEZ, 2007).

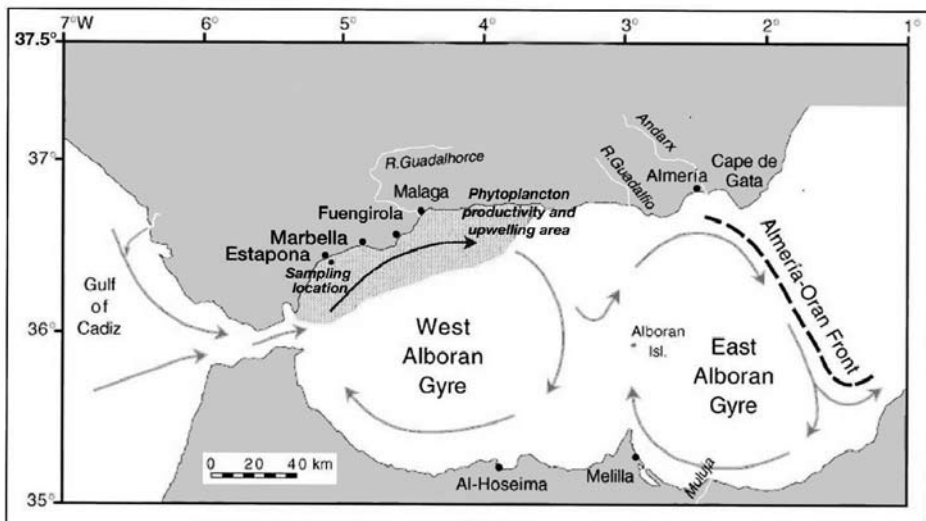


Fig. 1 - Location of the sampling area offshore the town of Estapona (Spain). Redrawn from HAUSCHILDT et al. (1999).

The seafloor of Alboran Sea identifies with Flysch Units consisting of Early Cretaceous to Early Miocene deep marine clastic deposits. The graded rock are characterized by marl, shales and muds in different states of induration, ritmically interbedded with conglomerates, coarse sandstone and graywackes (WILDI, 1983; PLATT & VISSERS, 1989).

Geographic distribution and ecology

Mollia rosselii is an Atlantic temperate boreal species ranging extensively around the south and west of British Islands and along the coasts of Shetland and Cape Verde (RYLAND & HAYWARD, 1977). In the Mediterranean basin the species occurs in Northern Adriatic sea, Gulfs of Naples, Marseilles, Alger, Gibraltar, Sète de Banyuls, Majorque and Genoa at a depth between 40 and 60 m (GAUTIER, 1962; HAYWARD & MCKINNEY, 2002). *M. rosselii* is able to colonizes a variety of hard substrata, typically coastal detrital sediments and empty shells of molluscs. In the Rhone delta, colonies of *M. rosselii* are found in areas of slow or absent deposition at a depth of 40m (LAGAAIJ & GAUTIER, 1965). The global depth range is unknown.

Morphology

Zoarium encrusting, unilaminar, multiserial. Autozooids almost oval in outline, distally arched and proximally truncated or rastremate by immediately preceding zooidal series. Vertical walls prominently raised as a crenellate ridge that surrounds the entire perimeter of the cryptocystal shelf. Kenozooids pyriform, with a broad distal window (see detailed description in the following section). They intervene where quincuncial series of zooids is disrupted. Opesium ogival with frequent irregular arcuations at the proximal edge. Gymnocyst totally absent. Cryptocyst forming a slightly convex grained or tuberculate surface, gently grading toward the inner edge of lateral walls. Basal wall weakly mammelled with apical holes from which radicles emerge to fix the colony to the substrate. Spines sporadic, randomly arranged at a lateral cryptocystal extremity (Fig. 2C). Orifice and operculum of small size, confined to the upper end of the frontal membrane and reinforced by marginal sclerites. Lophophore bell-shaped or rarely crescentic, bearing a series of 15 finely ciliated tentacles. Ovicells bagpipes-shaped, deeply embedded in the upper end of the wall, closed by the operculum. Sexually produced embryos are released by ovicell as planktotrophic larvae (cyphonautes?). They settle after liberation to metamorphose in an ancestrula. Breeding season in March and November. Fixation of the ancestrula in first fortnight of June (GAUTIER, 1962).

Colony growing pattern

Subcircular colonies in the periancestrular zone, then geometrically irregular depending on the condition and availability of the substrate. Ancestrula bears three potentially budding loci: one distal and two distolateral. Daughters zooid identify three multiserial sectors that gemmate in radial arrangement (Fig. 2-A). Each of them has a theoretical axis that extends sideways with a continuous occupation of the substrate. At the distal margin of the colony many segments are inflected in spiral growth to melt with the contiguous zooidal series. The fusion of differently oriented sectors contributes to the compactness of the colony. All these processes correlate with the morphological plasticity of individuals, able to fold in on themselves with angles above 45°. In some portion of the zoarium the zooids appear slightly disjointed, each connected to its neighbor by means of 9-14 tubular processes, arising from the basal pore chambers (see *Mollia cristinae* Souto et al., 2010).

Clusters of polygonal heterozooids, born in advanced stages of astogenetic growth, are examined and discussed in the following paragraphs.

Kenozooids

Kenozooids are commonly defined as heterozooids without aperture, lophophore, gut, and associated musculature, collectively referred as polypides (Fig. 3B-C). Operationally they are small intercalary units budded from neighbour zooids to fill empty spaces as well as to strengthen and support the colony. Sometime kenozooids are regarded as abortive autozooids unable to obtain a minimum functional size due to crowding (TAYLOR, 1985).

In many specimens of *M. rosselii* the kenozooidal aperture exhibit all sorts of distortions ranging from vast to wholly obliterated: actually aperture is an unstructured part of frontal wall covered only by cuticle. Taking into account that polymorphism is defined as a discontinuous variation in the morphology of individuals arising at the same astogenetic stage (BOARDMAN et al., 1969, page. 303), all kenozooids are considered to be polymorphs. If a kenozooid replaces an autozooid at the growing edge of a colony, the new polymorph is potentially capable of further budding (SILEN, 1977).

The presence of kenozooids is assumed to be triggered mainly by ecophenotypic reaction to mechanical stresses and to substrate-associated biologic processes (YOSHIOKA, 1982, *inter alia*).

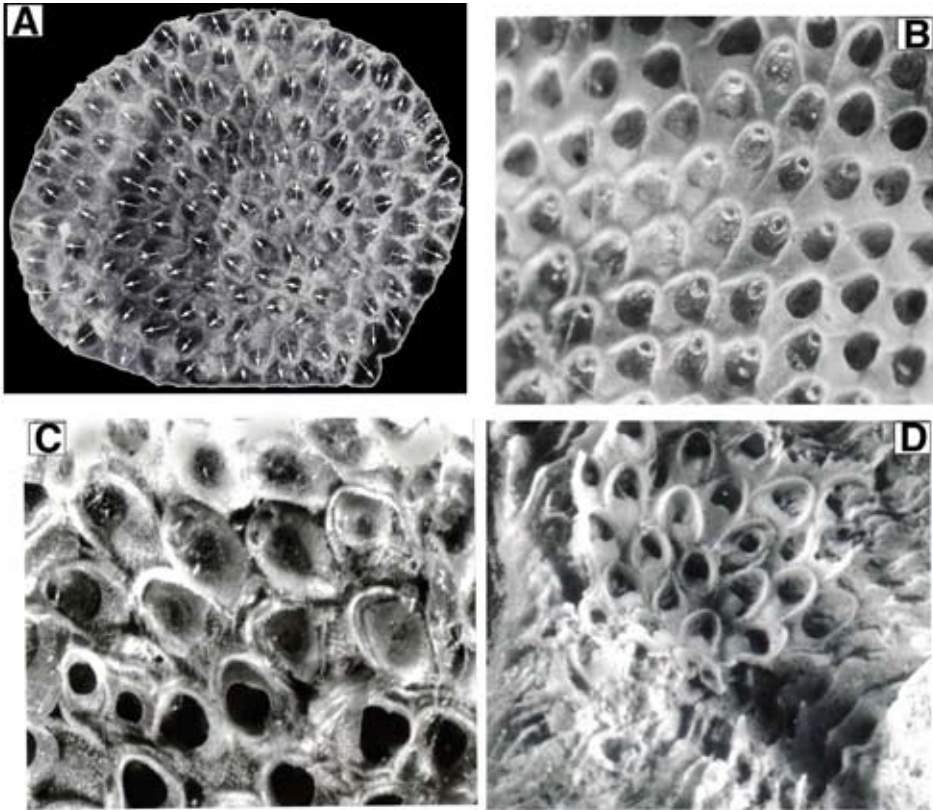


Fig. 2-A - *Mollia rosselii*: encrusting unilamellar colony with subcircular growth around the ancestrular area. Multiserial branch of the colony wrapped in a radial arrangement.

Fig. 2-B - Proximal zone of the colony with cryptocyst covered by cuticle; distal peripheral sectors with denuded zoecia.

Fig. 2-C - Zooids with abraded or removed frontal surface. Thin sporadic spines at the bases of lateral walls.

Fig. 2-D - Small group of zooids and kenozooids grown on a shell fragment.

Morphological changes of pre-existing clonal modules and origin of new polymorphs

As previously reported, *M. rosselii* is a sheet-like bryozoan (BUSS, 1979), a competitively superior form capable to monopolize the entire substrate and to minimize the chance of overgrowth by adjacent space competitors. Calcified part of the zoarium are double-layered: an outermost cuticular layer that is sustained by an interior skeletal apparatus (see LIDGARD & JACKSON, 1989). The distinctive

calcium carbonate skeleton of *M. rosselii* is secreted in the form of Calcite (97%), Aragonite (3%) and 9 Mols % MgCO₃ in Calcite (POLUZZI & SARTORI, 1973). Beyond the primary zone of repetition (BOARDMAN et al., 1969), zoarium of *M. rosselii* exhibits isolated clusters of auto- and eterozoids in which a progressive skeletal resizing leads to a new polymorph where nothing remain of the parental zooids; changes in individuals ontogeny occur along a gradient of partial dissolution, which extends from marginal walls to the center of the autozoid (Fig. 3C-D). The survey on *M. rosselii* aggregates highlight: (a) a progressive ontogenetic transformations of some individuals under bio-mineralogical forces; (b) the definitive development of completely new polymorphs as product from replacement of pre-existing zooids.

The main sequence of morphofunctional changes is as follows:

- i) (*k*-kenozooidal polymorphs). Intercalary polymorphs (Fig. 3A-B-C) clearly derived from original kenozooids: their vertical walls tend to be absorbed and blended with frontal surface. These individuals are regarded as transient precursors of frontal reworking process. If a polymorph substitutes a marginal autozoid, the former is capable of a further budding (MCKINNEY et al., 2003): funicular system remains active to ensure physiological integration of all the zooids; connectedness between clonal modules is predicted to increase with both the size of the colony and the level of specialization (polymorphism) (BONE & KEOUGH, 2010);
- ii) (*p*-increasing polymorphs). Partially changed polymorphs (Fig. 3B-C): a cluster of not entirely modified individuals occurs inside the complex of phenotypically uniform autozooids. In many cases the window of some modules appear distorted while the frontal surface exhibit perforations of predatory origin (Fig. 2C);
- iii) (*u*-ultimate transformed polymorphs). Large polymorphs polygonal in outline (Fig. 3D): the last product of skeletal transformations. They form clusters of about ten individuals strictly spaced but not clearly separated by decalcified lateral walls. Frontal surface slightly concave, striated by descending granulated grooves. At the orifice of the *k-p-u*-polymorphs, a small circular area of terminal membrane remains uncalcified. This apical aperture is slightly depressed and may be partially or wholly obliterated by a cuticular membrane (see SILEN, 1977, page. 190).

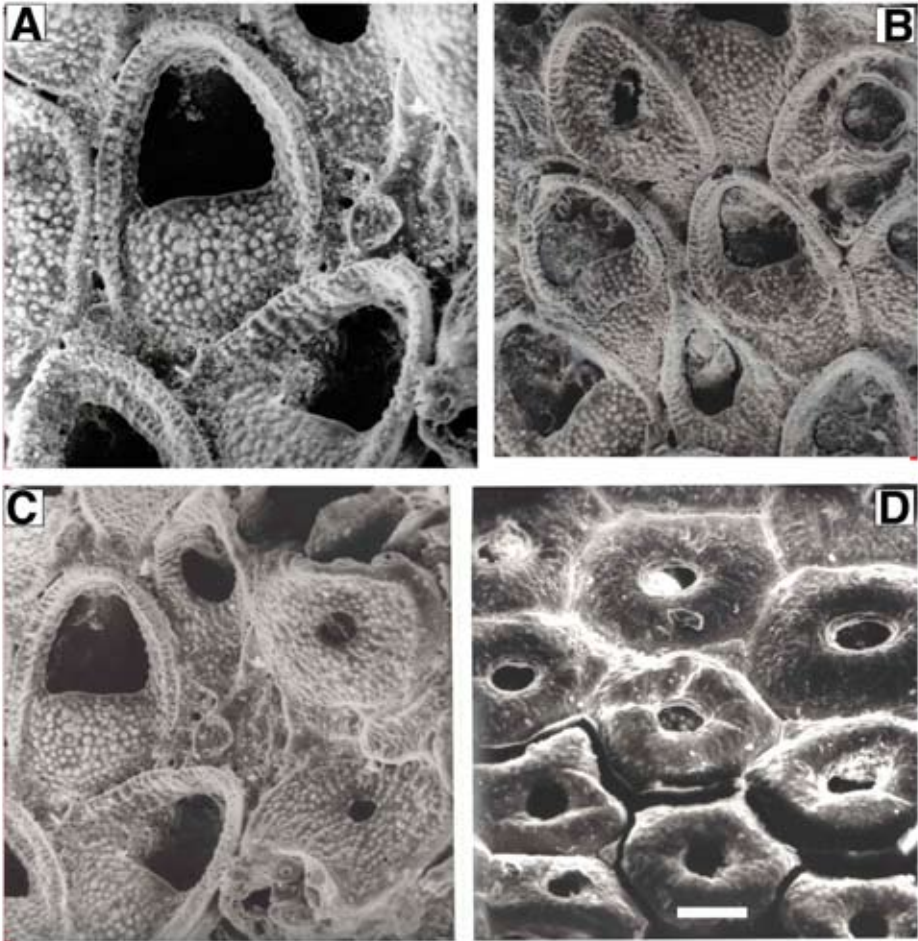


Fig. 3-A - Two zooids with thickened lateral walls. The cryptocyst exhibits a coarsely granulate surface.

Fig. 3-B - Kenozooids about to be transformed into polymorphic individuals with a central small hollow.

Fig. 3-C - Two perfectly transformed old kenozooid into new polymorphic individuals .

Fig. 3-D - A cluster of transformed tetra-esa-polygonal individuals, not clearly separated by inconspicuous shallow grooves. (Scale bar 100 micron)

Observations

The most common growth pattern for bidimensional encrusting colony was presented by BUSS (1979) and JACKSON (1979). It describes a non-linear continuum between two morphologic end points, called sheet and runner colony habit. The former escapes from opponents, exploiting their ability to bud in all directions and to move into areas free of competitors (fugitive strategy); the latter defend themselves from invaders by monopolizing the substrate with a continuous expanses of zooids (confrontational strategy) (BISHOP, 1989). The model is still in use even if it does not adequately account for some crucial variables such as the existence of spatially predictable refuges from mortality. A new revised classificatory model, consisting of two continua, "sheet-ribbon-runner" and "sheet-patch-spot" was proposed by BISHOP (1989).

In terms of the range of colonial morphology (as presented here), *M. rosselii* may be referred to the group "sheet-patch-spot", taking into account that juvenile stages of the colony are subcircular laminae of few mm in size, generated by anastomoses of pluriserial radial rows (Fig. 2A). Budding pattern is implemented at left side of the colony major axes. Sexual maturity (*i.e.* ovicells production) is delayed and occurs when the colony is as broad as long or when colony is unevenly expanded by substrate disconformity.

An accurate sorting of collected materials reveals the presence small groups of encrusting zooids (Fig. 2D) growing on sand or gravel sized particles. Such a material, that recalls spot colonies, is almost completely devoid of brood chambers. Bottom circulation of water masses in West Alboran sea and submarine migration of abrasive sand-waves (Fig. 1) makes possible various form of fragmentation of the colony and the displacement of small portions far from the ancestrala settling point. Since the cheilostomes in their life-cycle shift from sexual to clonal reproduction, colony tends to proliferate indefinitely with a concomitant increase in fecundity; therefore slivers detached from the mother colony may survive indefinitely as a number of separate colony fragments. WINSTON (1983) documented that *Cellarinellidae* has maximized the ability to reproduce asexually via fragmentation.

Both the above models are based on the accomplishment of a survival design (*i. e.* unlimited propagating clonal aggregations) (JACKSON, 1977) and on the recall of a series of coupled settlement/growth strategies (*ibid.*, p. 214).

Discussion

The species with which this paper is concerned, *Mollia rosselii*, has a sheet-like growth pattern accreted in an unstable, heterogeneous, unpredictable environment. Supplies of inorganic nutrients and phytoplankton (chlorophyll *a*) are critically influenced by seasonal conditions of the basin. Nonetheless these

prohibitive conditions, Gymnolaemata of benthic epifaunal communities display a biological potential capable to react to the microenvironmental stimuli with a number of developmental trajectories (see CHEETHAM & THOMSEN, 1981). Any attack on the colony integrity enhances its potential to prevent the detrimental action by environmental stressors. Phenotypic plasticity and zooidal modifications frequently testifies a tactical reaction to lethal or sublethal aggressions to the colony (KASELOWSKY et al., 2001).

By examining two emblematic species from literature, it is possible to recognize somatic changes followed to episodes of aggression:

(1) The amphiatlantic, encrusting *Membranipora membranacea* (L) forms extensive patches of rectangular zooids with chitinous tubercles at the distal corner of the modules. The large zooidal opesia lined only by outermost cuticular layers, makes the colony subject to perforation and sucking out of internal organs (see BERNING, 2008). Predation of nudibranches trigger a rapid induction of polymorphic spines all along a lateral walls. Costs of such a defensive strategy include lower growth and a falling of reproductive rate (HARWELL CD, 1984; YOSHIOKA, 1982).

(2) The ubiquitous, encrusting *Jellyella tuberculata* (Bosc) exhibit degenerative processes in some groups of peripheral zooids induced by factorial effects of high CO₂ pressure and cold water temperature. The overall efficiency of the colony is not altered because a compensatory exchange of metabolic substances is carried out by the healthy districts of the colony, redirecting the energy to the growth and maintenance of new zoods (SWEZEY, 2017).

Consideration of these adaptations in a r- to K- selection continuum (r- refers to the maximal intrinsic rate of species natural increase; K- refers to the carrying capacity with respect to environmental resources (ROSS, 1979). MAC ARTHUR & WILSON (1967) suggest to place *M. rosselii* on an extreme r-endpoint. Under this critical situation the survival strategy of *M. rosselii* is: 1) to channel all available energy into reproduction and maintenance of a large number of individuals at each new offspring; 2) yield as many total progeny as soon as possible (PIANKA, 1970, page. 592). Actually *M. rosselii* colonies proliferate by modifying their life histories and environmental adaptation (The surplus of required energy is probably provided by clusters of the transformed polymorphic heterozoid (Fig. 3A-D): mesenchymatous fibers of the funicular network conveys renewed energy through the colony toward zorial sectors where sexual and clonal reproduction takes place.

The funicular strands bridge the coelum of two consecutive individuals, exceeds the inner wall of a pore chamber and extends to the lacking zooids. Actually the colony efficiency relies mainly on energy distribution among somatic, sexual and maintenance tissues.

Finally it could be observed that the mosaic of regenerated polymorphs, consisting of polygonal-flattened individuals, offers less resistance to the currents that sweep the horizontal surface of the colony (Fig. 3D)

The relationship between transformed polymorphs and funicular frame is a purely heuristic approach and is presented as a conclusive working hypothesis. Further research can be useful for correlations between zooidal growth and pathway of energy flows all along the funicular strands (see PALUMBI & JACKSON, 1983)

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