

## From isolated ramets to coral colonies: the significance of colony pattern formation in reef restoration practices

Nimrod Epstein<sup>1,2\*</sup>, Baruch Rinkevich<sup>1</sup>

<sup>1</sup>Minerva Center for Marine Invertebrate Immunology and Developmental Biology, Israel Oceanographic and Limnological Research, National Institute of Oceanography, Tel Shikmona, Haifa, Israel

<sup>2</sup>Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O.Box 94766, 1090 GT, Amsterdam, The Netherlands

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### Abstract

Fragmentation in scleractinian corals has been recognized as an important facet in the life history portrait of many species. Fragments (ramets) isolated from existing genets may establish new colonies; a phenomenon that is widely used in a variety of management measures, including restoration of denuded coral reef areas. An analysis of regenerating branches of the Indo-Pacific coral *Stylophora pistillata* reveals that the architectural complexity of isolated branches may have a significant impact on the initiation of the regeneration process towards the typical structure and complexity of an intact colony. It is suggested that the 3-D structure complexity of isolated ramets should be taken into consideration when applying reef restoration practices.

Die Fragmentierung bei skleraktinischen Korallen ist für das Lebenszyklus-Portrait vieler Arten als wichtiges Merkmal erkannt worden. Fragmente (Rameten), die von existierenden genetischen Individuen (genets) isoliert wurden, können neue Kolonien etablieren; dies ist ein Phänomen, das bei Management-Messungen vielfach genutzt wird, zum Beispiel in der Restoration erodierter Riffe. Eine Analyse der sich regenerierenden Äste der indopazifischen Koralle *Stylophora pistillata* zeigte, dass die Komplexität der Architektur isolierter Äste einen signifikanten Einfluss auf die Initiierung des Regenerationsprozesses im Hinblick auf die typische Struktur und Komplexität einer intakten Kolonie hat. Es wird vorgeschlagen, dass die 3D-Struktur-Komplexität von isolierten Rameten berücksichtigt werden sollte, wenn Riff-Restorations-Maßnahmen angewandt werden.

**Key words:** Architectural complexity – pattern formation – coral ramets – reef restoration – *Stylophora pistillata*

\*Corresponding author: N. Epstein, Minerva Center for Marine Invertebrate Immunology and Developmental Biology, Israel Oceanographic and Limnological Research, National Institute of Oceanography, Tel Shikmona, P.O. Box 8030, Haifa 31080, Israel, Phone: ++972-4-8515202, Fax: ++972-4-8511911, E-mail: [nimrod@ocean.org.il](mailto:nimrod@ocean.org.il)

Fission (Hughes & Jackson 1980), budding and physical as well as biological forces that cause breakage of scleractinian corals (Highsmith 1982) are common agents for the formation of ramets *in-situ*. Both damaged natal colonies and coral fragments as small as a single branch or a nubbin (Rinkevich & Shafir 2000), initiate after breakage a series of developmental processes aiming to regain the species-specific 3-D colony structure. Loya (1976) who examined regeneration in broken colonies of the Indo-Pacific branching coral *Stylophora pistillata* has suggested that an injured colony will allocate resources from its healthy parts to the damaged branches in order to restore its former shape. An isolated ramet, however, reconstitutes a whole colony configuration from even a minute, non-branching portion. This mode of regeneration, known as epimorphosis is characterized by growth of new, correctly patterned branches and leads to the re-formation of whole colonies via an asexual propagation pathway.

The measure of coral transplantation is probably the most common management practice used to facilitate natural recovery of damaged reef sites (Edwards & Clark 1998). The rationale that ramets will grow and replace lost colonies inspires the use of coral fragments as the best material for transplantation (Harriot & Fisk 1988, Rinkevich 1995). An improved approach to reef restoration is the measure of 'gardening' (Rinkevich 1995). The gardening concept does not leave the ramet's regeneration to the leniency of local reef conditions and adds, as an intermediate phase, coral mariculture in underwater nurseries before the transplantation of the new colonies into denuded reef sites. Like other transplantation practices, the gardening concept focuses on the criteria of ramet survivorship and growth rates as measures for success. The idea that ramet's structural complexity may significantly influence its growth and regenerative ability received little attention and, when discussed, its importance was attributed to ecological rather than to developmental concepts. One example is Highsmith (1982) who briefly remarked that a 3-D ramet shape could prevent branch burial under sediment. Here, we explore the idea that an architectural complexity threshold of the isolated ramet is required for faster regeneration to a full colony structure. We suggest that a developmental biology concept of colonial pattern formation should be considered as an additional criterion (to the well discussed criteria of survivorship and growth) in the applied discipline of coral transplantation for reef restoration. This is particularly relevant to branching forms.

A branching coral colony may be considered as an integrated three-dimensional structural entity, where physiological parameters such as reproduction and

growth patterns are synchronized between different parts (Rinkevich *in press*). Following this tenet, regeneration of isolated ramets should reflect not only superficial linear branch elongation, but also coordinated, 3-D pattern formation processes that include a unique mode of apical ramification, lateral growth and spatial organization of the newly formed axes according to a precise architectural model (Dauget 1991, Kaandorp 1999).

When evaluating aspects for coral reef restoration (Rinkevich 2000, *unpubl.*) we have found that the original architectural complexity of isolated ramets may influence their ability to swiftly commence these specific 3-D growth patterns. An example is illustrated in Figure 1 (a-d) where 4 fragments taken from a single *Stylophora pistillata* colony (labeled by alizarin Red S), were cultured *in-situ* side by side on concrete plates at 6 m' depth (Rinkevich 2000). These ramets, a small fragment of 2 cm long (Fig. 1a), a branch fragment of 4 cm long (Fig. 1b), a fragment of a bifurcated tip (about 3.5 cm long, Fig. 1c) and a ramet of about 5 cm long with two major branches (Fig. 1d) were cultured for 8 months after isolation. Subsequently, the branches were brought to the lab, their tissue was removed and skeletal growth patterns above and below the alizarin mark were examined. It is evident that the type of fragment influenced growth rate as well as architectural complexity. While in simple, linear coral fragments (Fig. 1a, b) only apical growth was recorded, within the same time course, fragments like the ramet in Figure 1c displayed additional morphometric growth patterns, such as side branching (seen at its left fork) and a fission that formed a new double tip at its right fork. In a more complex morphology, (Fig. 1d), many new side-growing knobs appeared below the area of apical growth, along the main ramet axis. These protrusions will develop into side-growing branches, indicating an advanced 3-D pattern formation process (Fig. 1d; arrows beneath the alizarin line). In comparison to fragments 'a', 'b' and also 'c', ramet 'd' (Fig. 1) will most likely be able to regain the typical spherical colony shape (Loya 1976) in the shortest period of time. Fragment 'd' probably possessed the minimal complexity required to initiate not only apical extension but also 3-D growth patterns. Growth rate alone is, therefore, not the sole parameter for consideration when the regeneration of isolated branch fragments is analyzed.

During the above experiment, we followed the regeneration of additional 37 branches (20 single tip and 17 ramified ramets). Of the single tip group, 17 branches (85%) displayed only a linear, apical extension while 3 cases developed, each, an additional new tip through fission. Conversely, from the ramified

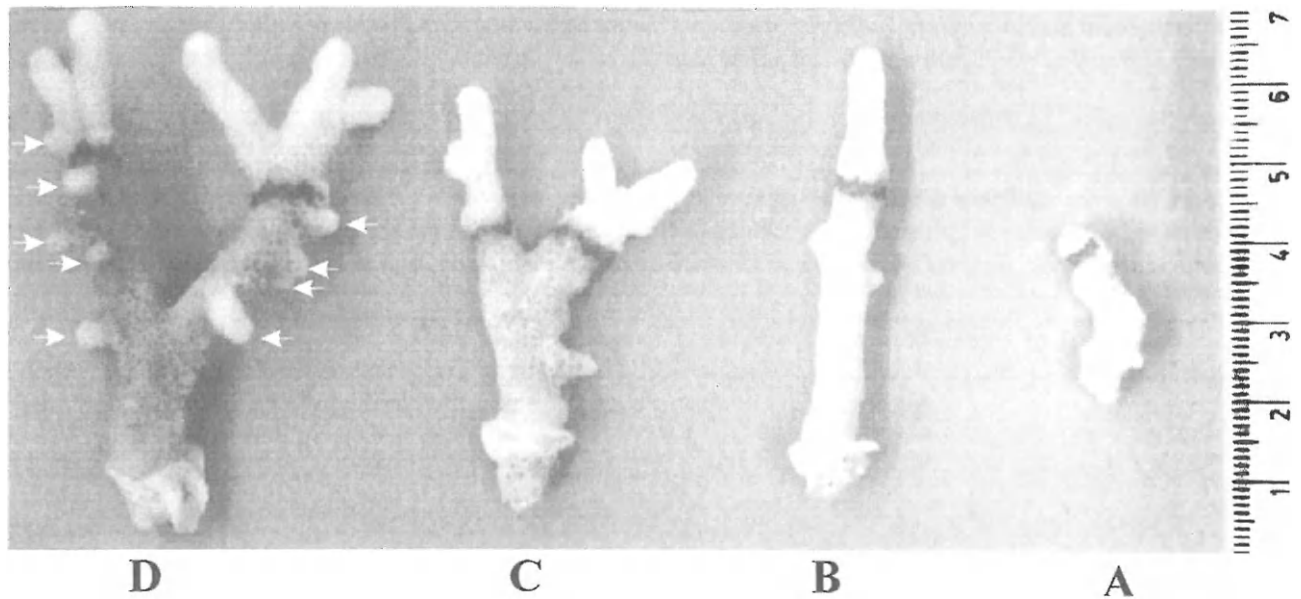


Fig. 1(a-d). Four fragments (a-d) with different architectural complexities taken from a single *S. pistillata* genet (from Rinkevich 2000). Black lines refer to alizarin marks. Photographs were taken at the end of the experiment. Alizarin marks reveal sizes at the beginning of the experiment. Scale on right in cm.

ramets group, only 2 (11.8%) displayed just linear extension while 15 ramets (88.2%) developed new tips and branches on at least one of the forks, in addition to lateral protrusions on the main axis ( $P < 0.0001$ ; Fisher exact tests). The fragments shown in Figure 1 represent, therefore, the typical growth of many similar size fragments and illustrate early stages at a multi-dimensional regenerative process which leads to the typical structure of *S. pistillata* colony (Rinkevich in press).

Three-dimensional growth patterns in regenerating *S. pistillata* ramets are probably 'canalized' (Waddington 1942) in accordance with the species' 'developmental rules' that denote the recreation of its iterated branching system and the typical colony shape. This architectural design may be the expression of the coral structural blueprint (such as homeobox genes) that encodes for specific biochemical processes (Gellon & McGinnis 1998), or can be the outcome of secreted waterborne bioactive chemical signals (isomonones) that regulate and control branch growth rates and positions within the internal volume of the colony (Rinkevich & Loya 1985). For the applied technique of coral mariculture, isolation of ramified branches may therefore significantly accelerate regeneration and shorten mariculture duration. Therefore, the constraint of minimal structural complexity, imposed on ramets as a critical factor for fast 3-D regeneration, should be considered along with the growth rates and the survivorship criteria in reef restoration activities.

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