

Do multi-branched colonial organisms exceed normal growth after partial mortality?

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One of the advantages of modular colonial growth is the capability to recover after partial mortality. Tolerance to partial mortality is a known property of some resistant species of plants that respond to mortality with vigorous regrowth or overcompensation. It is not clear whether modular marine invertebrates such as octocorals overcompensate. This study provides evidence that following injury to colonies (by breaking apical dominance), new growth exceeds normal rates of branching, as observed in some plants, in a degree correlated to the original multi-branched network setting (e.g. the number of original branches connected to main stem), in colonies of the Caribbean gorgonian octocoral *Pseudopterogorgia bipinnata*. This can be explained by the network of communicating vessels and canals inside octocoral colonies, which provide the structure for effective allocation of resources to regenerating parts.

Keywords: gorgonian coral; Octocorallia; branching; growth; regeneration; overcompensation

1. INTRODUCTION

Modular organisms such as octocorals have a great capability to regenerate following colony damage (Wahle 1983; Meszaros & Bigger 1999). Regeneration has a special priority in the functioning of modular colonial organisms (Rinkevich 1996), which has been considered as an adaptive capability (Meesters *et al.* 1997). In the case of gorgonian octocorals, adult colonies of *Plexaura kuma* shed large fragments of the colony as a stable clonal propagation strategy, suggesting the existence of tolerant mechanisms as a response to grazing and disturbance effects (Lasker 1990). Another Caribbean octocoral, *Pseudopterogorgia elisabethae*, has been harvested for the extraction of active chemicals (Mayer *et al.* 1998) and areas that have been harvested recovered sufficiently to allow harvesting after 2–3 years. These colonies exhibit high recovery rates, independent of the number of branches left on the colony (Castanaro & Lasker 2003).

Tolerance to partial mortality is a known property of some resistant species of plants. In plants, this

phenomenon is characterized by overcompensation: a growth response to damage that exceeds the normal performance and is most common in species with apical dominance. These species exhibit few fast-growing mother branches that branch daughter branches just below the tip or apex. Breaking apical dominance by means of grazing or clipping is the proximate explanation for overcompensation (Huhta *et al.* 2000). Overcompensation has been attributed to traits facilitating regrowth, such as storage organs, dormant buds and meristems, an ability to relocate energetic resources to injured areas, and also the capacity to capture resources from newly recovered tissues (see review in Belsky *et al.* 1993). Marine colonial organisms such as gorgonian octocorals do not have storage organs but have a number of analogous characteristics that could provide the basis for overcompensation. For instance, the polyps are interconnected by a network of stem canals (Bayer 1973). The connections among polyps continue along the branch axis and form a branching tree-like structure of higher complexity, which has numerous canals in the main stem and progressively fewer as the branches decrease in size (J. A. Sánchez, in preparation). Branching in Caribbean gorgonian octocorals also shows apical dominance (Sánchez *et al.* 2004). The aim of this study is to compare the regenerative capability of different colony parts after breaking apical dominance, and to examine the relationship between regrowth, branching and colony organization in a Caribbean octocoral.

2. METHODS

To determine whether there was a differential response to partial mortality in relationship to apical dominance and previous colony organization, a regeneration experiment was carried out at San Salvador, Bahamas (figure 1). Using young colonies of *Pseudopterogorgia bipinnata* that still had a single apical mother branch, colonies were cut in half (e.g. the growing apex and the basal portion: figure 1a,b,e,f) and attached to concrete trays. Additionally, as experimental controls, two colonies of similar size to the half colonies were positioned in the same cement flats. One of the colonies was cut down to the uppermost daughter branch to control for the effect of clipping (figure 1d,h). The other colony was left intact as an overall control for the procedure (figure 1c,g). The experiment was replicated four times at a depth of 17 m. After six months, the experimental colonies were photographed. Since we are expecting a variable outcome in the regrowth response that depends on the original colony network, we initiated a second experiment using adult colonies of *P. bipinnata* at Carrie Bow Cay, Belize (3–4 m depth). Thirty adult colonies with multiple apical mother branches of a range of sizes were photographed and clipped down to a single main trunk with approximately 40 daughter branches during November 2001. The experimental colonies were placed on five cement flats as described above. In July 2002, the regenerating colonies were collected (only 16 survived), the number of new branches counted and the diameter at the base measured with a caliper. In addition, all of the colonies were photographed (November 2001 and July 2002) and the length of the clipped mother branch as well as the fast-growing daughter branch of each experimental colony were measured to compare their growth rates (see methods in Sánchez *et al.* 2003).

3. RESULTS

Partial mortality including a significant portion of the dominant apical branch in colonies of *P. bipinnata* generated a clear growth response (figure 1a). After six months, the basal section of the truncated colony exhibited multiple branching at several previously dormant daughter branches (figure 1e). The daughter branches close to the site of the injury were consistently the ones developing into new mother branches (figure 1a,e). The apical portion of the colony had no or very low growth (figure 1b,f). The two controls, small colonies of the same size, one

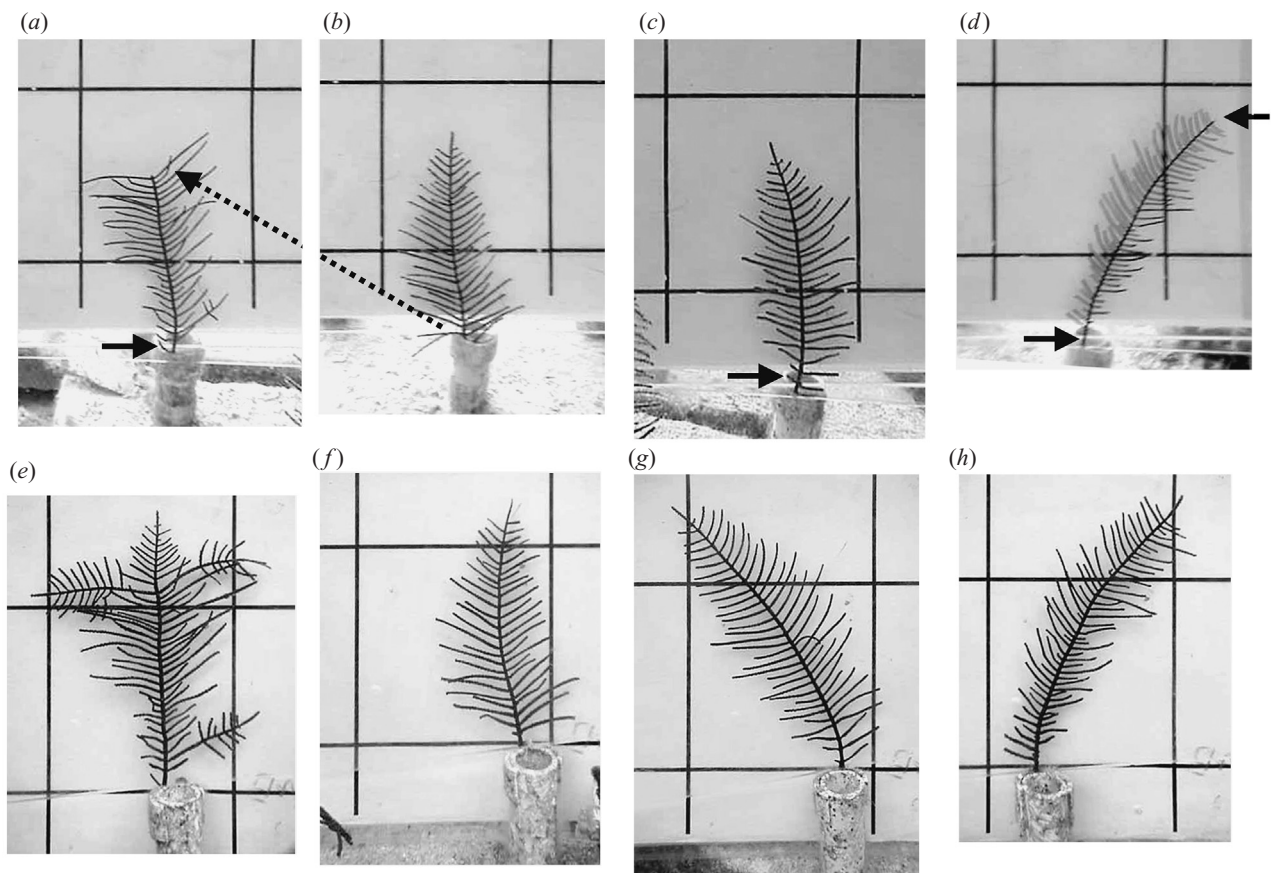


Figure 1. Sequential digital images of three colonies (*a,e* and *b,f* are the two halves of one colony; *c,g* and *d,h* are procedure controls for the setting and clipping, respectively) of *Pseudopterogorgia bipinnata* (Bahamas), on the same experimental tray (concrete blocks and four PVC tubes and rings) (grid 10 cm × 10 cm), between (*a-d*) December 1999 and (*e-f*) July 2000. The arrows show the places where cuts were made on colonies.

intact and the other slightly injured in the tip, had a similar response to the apical portion (figure 1*c,d,g,h*). The two experimental regenerating colonies (truncated trunk and slightly injured) exhibited regrowth of the dominant apical mother branch but only the truncated branch generated numerous daughter branches (figure 1*e,h*). The results were consistent in three more replicates. The regrowth after partial mortality of adult colonies of *P. bipinnata* exhibited a continuum correlated with the original multi-branched network. Despite ca. 40% mortality among the experimental colonies, a large portion of the variance in the number of new daughter branches of surviving colonies could be explained by both the diameter at the base ($r^2 = 0.39$, $p < 0.01$: figure 2*a*) and the original number of branches in the colony ($r^2 = 0.40$, $p < 0.05$: figure 2*b*). The dormant daughter branches close to the injured apical regions were also the most likely to become mother branches, with apical branching (figure 2*c-e*). In addition to corroborating the findings of apical dominance in colony branching, this experiment showed a relationship between regenerative response and colony organization (e.g. number of original branches connected to the main stem and/or stem thickness). Mother branches regrew their apical portion at a similar rate to the daughter branches that became mother branches after clipping (paired *t*-test, $n = 12$, d.f. = 11, $t = 0.99$, $p > 0.05$), but branching was significantly higher in the daughter branches of each colony (paired *t*-test, $n = 12$, d.f. = 11, $t = -3.63$, $p < 0.005$).

4. DISCUSSION

Octocorals such as *P. bipinnata* exceed normal growth or overcompensate after partial mortality and/or breaking the apical dominance. The overcompensation was related to the original branching network, suggesting a connection between colony organization and regeneration. The colony organization and regenerative response observed in octocorals also suggested a substantial analogy between plant and animal branching systems.

Animal branching systems, such as corals and octocorals, exhibit the three main categories of regenerative response found in plant systems. The Red Sea coral *Stylopora pistillata*, for instance, regenerates exact parts of its colonies showing equal compensation (Loya 1976; Rinkevich & Loya 1985). Reparative regeneration in other cnidarians has also been observed in pioneering studies on regeneration (e.g. Morgan 1901). Some other species under stresses and/or bleaching, however, struggle to recover from inflicted injuries, showing signs of undercompensation (Mascarelli & Bunkley-Williams 1999). A threshold exists in the injury size relation to colony size, which determines the capability for regeneration in stony corals (Oren *et al.* 2001). Gorgonian octocorals, as observed here, showed overcompensation following partial mortality and the disruption of apical dominance. In addition, these organisms have been observed to be highly resistant to coral diseases, which involve fast regeneration mechanisms (Dube *et al.* 2002).

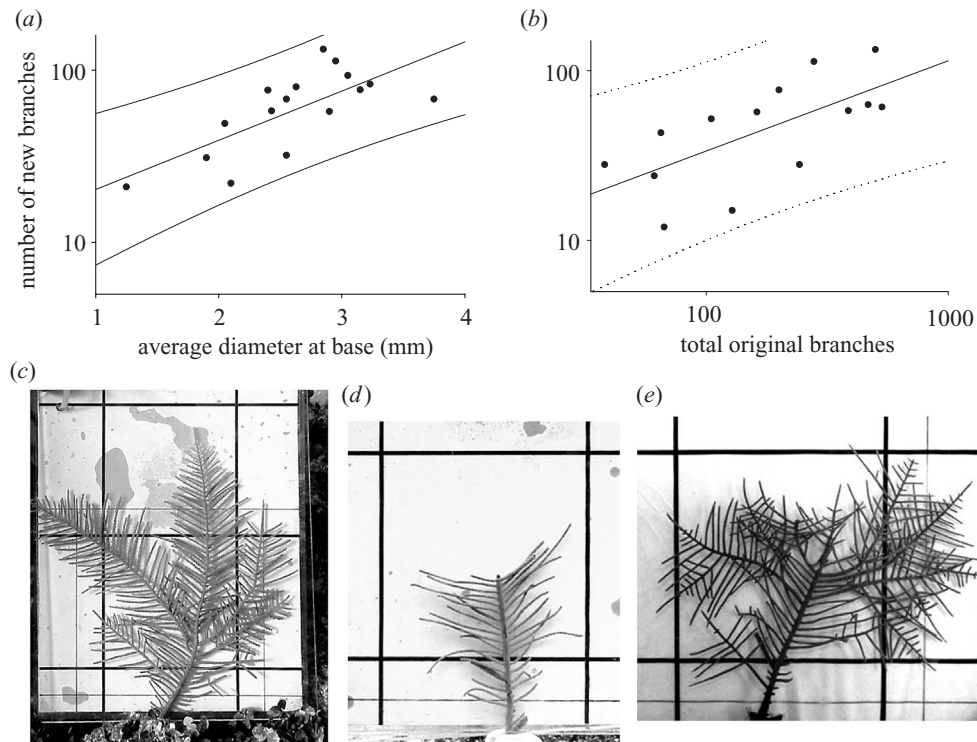


Figure 2. (a,b) Plots and results from least-squares linear regressions ((a) $r^2 = 0.40$, $p = 0.01$; (b) $r^2 = 0.04$, $p = 0.008$) (dotted lines are 95% predicted intervals). (c) Original colony before clipping (Carrie Bow Cay, Belize). (d) Clipped experimental colony in November 2001. (e) Same experimental colony in June 2003 (grid 10 cm \times 10 cm).

Since corals do not have storage organs or other means of saving resources for regeneration, the regenerative response could be related to the presence of dormant branches. They can potentially start new apical fronts as well as the structures for allocating resources to injured parts and newly growing branches. Dormant daughter branches located close to the injury had a high chance of becoming new apical mother branches. These branches branched at a higher rate than the regenerating apical mother branch, which is not the normal branching of uninjured colonies (Sánchez *et al.* 2004). It could be suggested that a surplus in resources directed toward the injured part could be opportunistically used by the dormant branches. In any case, the overcompensation in octocorals could be related to the presence of structures (i.e. stem canals) for intra-colonial allocation in both healing and growing. The basal portions of the regenerating experimental colonies always had higher growth than colonies with similar numbers of dormant branches but from younger colonies or fragments. The number of internal canals of the truncated trunk harboured more canals that, most probably, could rapidly allocate more resources to injured parts. The number of branches and polyps in a basal branch does not correspond to the number of stem canals, which ultimately provide a better structure for regeneration. Intra-colonial allocation of resources among distant parts in cnidarians such as hydroids and corals is a well-known process (e.g. Taylor 1977; Dudgeon & Buss 1996). Allocation of resources from distant parts of coral colonies to regenerating areas has been clearly demonstrated through the translocation of ^{14}C -labelled carbonates (Oren *et al.* 1997). The energy allocation for regeneration has been related to the degree of colony inte-

gration and the injury size (Oren *et al.* 2001). Active allocation of zooxanthellae has been detected in soft octocorals (e.g. Gateño *et al.* 1998; Meszaros & Bigger 1999). However, studies on the proximate mechanisms involving nutrient allocation for regeneration are necessary to test this hypothesis.

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- Bayer, F. M. 1973 Colonial organization in octocorals. In *Animal colonies, development and function through time* (ed. R. S. Boardman, A. H. Cheetham & W. A. Oliver), pp. 69–93. Stroudsburg: Dowden, Hutchinson & Ross.
- Belsky, J., Carson, W. P., Jensen, C. L. & Fox, G. A. 1993 Overcompensation by plants: herbivore optimization or red herring? *Evol. Ecol.* **7**, 109–121.
- Castanaro, J. & Lasker, H. R. 2003 Effects of clipping on growth of colonies of the Caribbean gorgonian *Pseudopterogorgia elisabethae*. *Invert. Biol.* **122**, 299–307.
- Dube, D., Kim, K., Alker, A. P. & Harvell, C. D. 2002 Size structure and geographic variation in chemical resistance of sea fan corals *Gorgonia ventalina* to a fungal pathogen. *Mar. Ecol. Prog. Ser.* **231**, 139–150.
- Dudgeon, S. R. & Buss, L. W. 1996 Growing with the flow: on the maintenance and malleability of colony form in the hydroid *Hydractinia*. *Am. Nat.* **147**, 668–691.

- Gateño, D., Israel, A., Barki, Y. & Rinkevich, B. 1998 Gastrovascular circulation in an octocoral: evidence of significant transport of coral and symbiont cells. *Biol. Bull.* **194**, 178–186.
- Huhta, A.-P., Hellström, K., Rautio, P. & Tuomi, J. 2000 A test of the compensatory continuum: fertilization increases and below-ground competition decreases the grazing tolerance of tall wormseed mustard (*Erysimum strictum*). *Evol. Ecol.* **14**, 353–372.
- Lasker, H. R. 1990 Clonal propagation and population dynamics of a gorgonian coral. *Ecology* **71**, 1578–1589.
- Loya, Y. 1976 Skeletal regeneration in a Red Sea scleratinian coral population. *Nature* **261**, 490–491.
- Mascarelli, P. E. & Bunkley-Williams, L. 1999 An experimental field evaluation of healing undamaged, unbleached and artificially bleached in the star coral, *Montastraea annularis*. *Bull. Mar. Sci.* **65**, 577–586.
- Mayer, A. M. S., Jacobson, P. B., Fenical, W., Jacobs, R. S. & Glaser, K. B. 1998 Pharmacological characterization of the pseudopterosins: novel anti-inflammatory natural products isolated from the Caribbean soft coral, *Pseudopterogorgia elisabethae*. *Life Sci.* **62**, PL401–PL407.
- Meesters, E. H., Pauchli, W. & Bak, R. P. M. 1997 Predicting regeneration of physical damage on a reef-building coral by regeneration capacity and lesion. *Mar. Ecol. Prog. Ser.* **146**, 91–99.
- Meszaros, A. & Bigger, C. 1999 Qualitative and quantitative study of wound healing process in the colenterate, *Plexaurella fusifera*: spatial, temporal, and environmental (light attenuation) influences. *J. Invertebr. Pathol.* **73**, 321–331.
- Morgan, T. H. 1901 Regeneration. In *Columbia University Biological Series VII*. New York: Macmillan.
- Oren, U., Rinkevich, B. & Loya, Y. 1997 Oriented intra-colonial transport of ¹⁴C labeled materials during coral regeneration. *Mar. Ecol. Prog. Ser.* **161**, 117–122.
- Oren, U., Benayahu, Y., Lubinevsky, H. & Loya, Y. 2001 Colony integration during regeneration in the stony coral *Favia fava*. *Ecology* **82**, 802–813.
- Rinkevich, B. 1996 Do reproduction and regeneration in damaged corals compete for energy allocation? *Mar. Ecol. Prog. Ser.* **143**, 297–302.
- Rinkevich, B. & Loya, Y. 1985 Coral isomone: a proposed chemical signal controlling intracolony growth patterns in a branching gorgonian. *Bull. Mar. Sci.* **36**, 319–324.
- Sánchez, J. A., Zeng, W., Coluci, V. R., Simpson, C. & Lasker, H. R. 2003 How similar are branching networks in nature? A view from the ocean: Caribbean gorgonian corals. *J. Theor. Biol.* **222**, 135–138. (DOI: 10.1016/S0022-5193(03)00017-1)
- Sánchez, J. A., Lasker, H. R., Nepomuceno, E. G., Sánchez, J. D. & Woldenberg, M. J. 2004 Branching and self-organization in marine modular colonial organisms: a model. *Am. Nat.* (In the press.)
- Taylor, D. L. 1977 Intra-colonial transport of organic compounds and calcium in some Atlantic reef corals. In *Proc. 3rd Int. Coral Reef Symp.* **1**, 431–436.
- Wahle, C. M. 1983 Regeneration of injuries among Jamaican gorgonians—the roles of colony physiology and environment. *Biol. Bull.* **165**, 778–790.