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Letter to the Editor

How similar are branching networks in nature? A view from the ocean: Caribbean gorgonian corals

Tree-like branching networks are omnipresent in nature (e.g. Turcotte et al., 1998). Despite the ubiquity of this pattern across both species and levels of organization, in most cases we do not know how branching patterns evolve or even how they form. Comparisons between river and leaf networks have been used to suggest that branching systems, both biotic and abiotic, exhibit similar statistical properties (Pelletier and Turcotte, 2000). River networks tend to follow the same statistical patterns (Montgomery and Dietrich, 1992) but there has been a degree of variation at fine level studies (Dodds and Rothman, 2001). Statistical similarity has also been found between geological and geophysical branching patterns (Turcotte et al., 1998; Turcotte and Newman, 1996). To further examine the generality of these observations, we compared the tree-like structures of colonial marine invertebrates (Caribbean gorgonian corals: Cnidaria) with river and leaf branching patterns. Gorgonian corals are colonial sessile marine animals, which exhibit diverse tree-like structures. Some aspects of gorgonian form have been analysed using the Horton–Strahler approach (Brazeau and Lasker, 1988; Mitchell et al., 1993) whereas other species are not amenable to that approach due to excessive side branching (Lasker and Sanchez, 2002). We examined four species of gorgonian corals, including side-branched species. Since rivers and leaves had shown compelling statistical similarity (Pelletier and Turcotte, 2000) we expected some similarity with modular animal tree-like networks such as the gorgonian corals.

A common feature of the networks of both rivers and leaves is the nearly perfect linearity in the number of branches (N) per order (i) when using semi-log scale (Pelletier and Turcotte, 2000). Both systems fit

$$N \propto R^i, \tag{1}$$

where the bifurcation ratio $R_b \approx 4.68$. Those analyses also report mean branch length (L) in terms of order in rivers and leaves is also a linear function using semi-log scale, $L \propto R^i$, where $R_b \approx 2.2$. We replicated those analyses on Caribbean coral networks using the Tokunaga ordering system, which allowed us to include branching patterns that contain many side branches (Tokunaga, 1978, see also Turcotte et al., 1998). This scheme gives a side branch a double index ($N_{i,j}$) based on order and the source branch it is attached from. For instance, the number of source branches of order 2 that connect with another source branch at a bifurcation is denoted as $N_{2,2}$ and their side branches will be $N_{1,2}$ and so forth. Fig. 1 shows the plots $N(i)$, for four species of gorgonian corals, where i is branch order. The best fit function obtained from these data, for the sea candelabra *Eunicea* spp. (Fig. 1 A–B), resembled the function for rivers and leaves ($N \propto R^i$, *Eunicea calyculata*, $r^2 = 0.99$, $P < 0.04$, $R_b \approx 2.88$; *E. tourneforti*, $r^2 = 0.99$, $P < 0.04$, $R_b \approx 2.69$). The bifurcation ratios of these coral species suggests that they produce "simple" networks close to that of a colony with $R_b = 2$ which generates a perfectly dichotomous tree. Branching among sea feathers, i.e. *Pseudopterogorgia* spp., on the other hand, was best described by the power function $N \propto i^{\gamma'}$ (Range of *Pseudopterogorgia bipinnata* colonies: $0.98 < r^2 < 0.99$, $P < 0.01$, $\gamma' = 1.71$; *P. elisabethae*, $0.97 < r^2 < 0.99$, $P < 0.01$, $\gamma' = 1.49$). This nonlinear relationship differed from that observed for rivers, and leaves, as well as for other gorgonians such as the *Eunicea* spp. Pinnate feathers like *Pseudopterogorgia* spp. can be characterized as "complex" networks with multiple side branches. The power function from sea feathers seems to be dependent on the number of branches of orders 1 and 2. Although deviation from (1) is expected for the 2 and 3 orders (Dodds and Rothman, 1999), such deviation among first order branches is not a trivial point for sea feathers *Pseudopterogorgia* where 90% of the branches are order 1 and orders 1 and 2 combined make up >98% of the branches. The two functions identified in our analysis of gorgonian branching and their respective parameters provide a method to distinguish the quantitative organization $N(i)$ of different coral branching networks (e.g. simple vs complex).

Fig. 2 presents the graphs of branch length $L(i)$ for the four species. Qualitatively, we again observed different outcomes for *Eunicea* spp. and *Pseudopterogorgia* spp. For the "simple" species (*Eunicea*) we observed no apparent change among orders in the semi-logarithmic plot, which suggests that all orders have approximately

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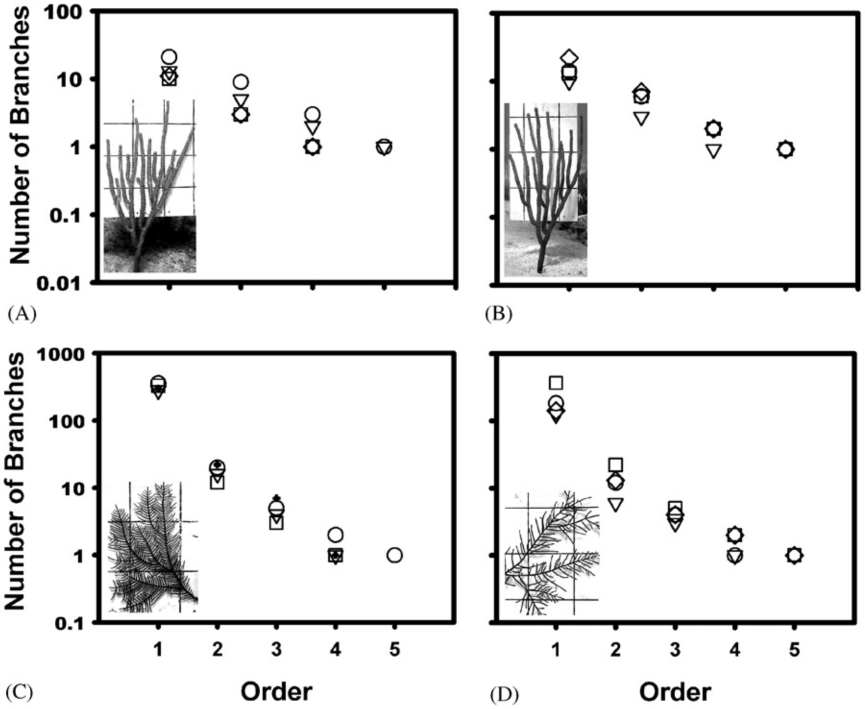

Fig. 1. Plot of the number of branches (logarithmic scale) as a function of order. (A) *E. calyculata*, (B) *E. tourneforti*, (C) *P. bipinnata* and (D) *P. elisabethae* (symbols on plot indicate different colonies) and photographs of the same species (inset: Grid 10 × 10 cm.). Data from Caribbean gorgonian corals were taken using SCUBA at the fore-reef terrace on reefs in the Exuma Cays and San Salvador, Bahamas (12–20 m in water depth). Images were taken with a digital underwater camera and were fixed for distortion according to a 10 × 10 cm background grid using Adobe Photoshop (v. 4.0; free transform and skew commands, scaled to 25 pixels per cm). We examined four different adult colonies for each species (16 colonies, 1759 branches). For each colony we counted, measured, and classified the order of every branch using the image analysis program ImageJ (Java version of NIH-image, National Institutes of Health, USA).

the same growth behavior. On the other hand, *Pseudopterogorgia* spp. exhibited a great deal of within- and among-order variation that could be due to the differential growth rates observed between main and side branches (i.e. Lasker et al., submitted). $L(i)$ for these corals is very different from that of rivers and leaves, and the data for these gorgonians did not fit any continuous function. Therefore, we can conclude that the behavior of mean branch length per order is not universally similar in the branching patterns analysed here. Consequently, there was not a significant correlation between the logs of the bifurcation ratio over the branch length ratio of gorgonian corals as happens in leaves and rivers (Pelletier and Turcotte, 2000).

How similar are octocoral branching patterns with other systems in nature? This first attempt showed that at least not all corals are statistically similar to both rivers and leaves. This also suggested to us a different direction. Pelletier and Turcotte (2000) suggested that diffusion-limited aggregation (DLA) systems also share statistical and fractal properties with rivers and leaves. DLA systems grow as the irreversible aggregation of small particles to form clusters from a seed at an origin of a lattice (Witten and Sander, 1983). The process leading to the growth of leaf veins may be a DLA system. In the case of river networks a number of different mechanisms have been proposed (see review in Rodriguez-Iturbe and Rinaldo, 1997) but the understanding of river landscape evolution is an unfinished matter. Similarly, it is still unclear what drives the growth and shape of gorgonian corals but since the statistical characteristics differ from fractal-like DLA systems it is reasonable to think that they develop through a different process. Though there are some suggestions of fractal properties of gorgonian corals in relation to their growth forms (Burlando et al., 1991; Mistri and Ceccherelli, 1993), no clear connections with a mechanism leading to growth/form has been found as in the case of leaf veins and DLA systems (Franks and Britton, 2000).

After comparing some of the statistical properties of gorgonian corals with those of rivers and leaves we conclude that the tree-like networks of gorgonian corals are not statistically similar to those of other natural systems such as leaves and river basins. Thus the proposed universality of the patterns observed in rivers (Pelletier and Turcotte, 2000) is likely incorrect and will require additional data to determine if the relationship extends to many other branching systems. Gorgonian corals branch in a subapical process that can be depicted as mother–daughter relationships among branches, but these patterns do not develop through bifurcations.

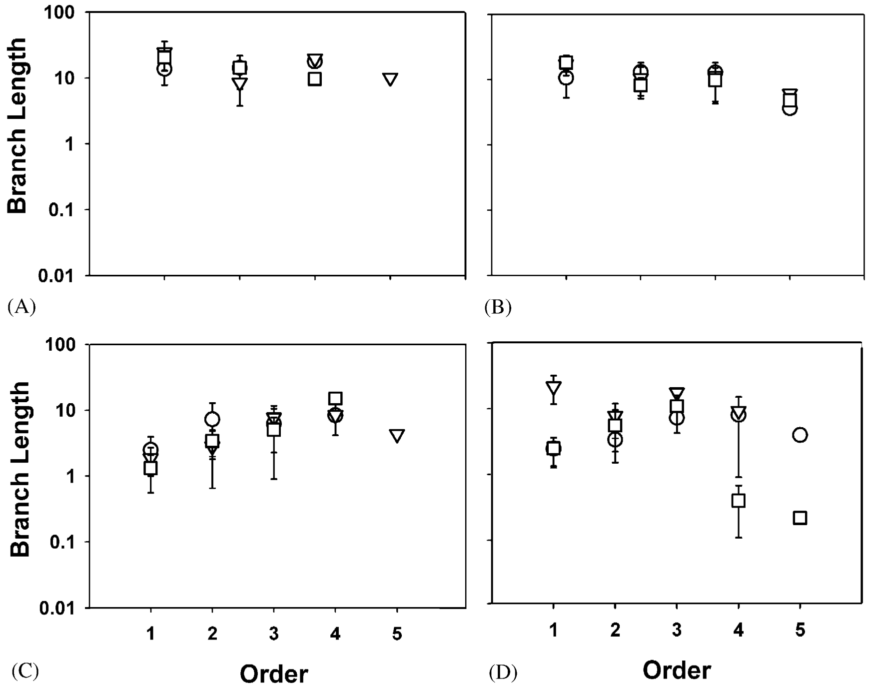

Fig. 2. Plot of the mean branch length (logarithmic scale) as a function of order. Bars are ± SD, note distortion due to log scale. (A) *E. calyculata,* (B) *E. tourneforti*, (C) *P. bipinnata* and (D) *P. elisabethae* (symbols on plot indicate different colonies per species).

Branching in gorgonians always starts with a single generation of modules, i.e. a mother branch, which then gives rise to tributary (daughter) branches (Lasker and Sánchez, 2002, and Sánchez et al., submitted). Dynamic observations and models of this process in gorgonian corals suggest that descriptions of growth based on order and bifurcation ratio probably do not work for many species. Gorgonian networks seem to be the product of a complex interaction between an intrinsic self-organized process and environmental effects that could vary from the physical properties of the habitat to the changing environment of the colony itself (Sanchez et al., submitted).

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