

REEF PERSPECTIVES

Sir Ronald Fisher's "runaway natural selection" for *Acropora*

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Sir Ronald Fisher, British statistician, evolutionary biologist and geneticist (1890–1962)

Consistently greater numbers of offspring should have a relatively strong control in natural selection, and energy and materials for traits that are less influential might be traded for increased reproduction. As the peahen is especially attracted to peacocks with the largest tails, runaway selection led to peacocks increasing the size and splendor of their tails in competition for reproduction, despite the ultra large tails seeming maladaptive by reducing ability to escape predation (Fisher 1930, Zahavi 1975). The *Acanthaster planci* (CoTS) complex has been around for at least one, and maybe up to three, million years (Nishida and Lucas 1988), yet *Acropora* spp. seem to have remained the favorite prey of CoTS, butterflyfishes, and many other corallivores. When observing the devastation CoTS can do to *Acropora* populations (Fig. 1), one wonders why there has been no effective selection for anti-predator traits after one to three million years. This may be what Ronald Fisher (you probably remember that Ronald Fisher developed ANOVA and the genetical theory of natural selection) envisioned as "runaway natural selection", where the selective advantage of increased reproductive output overwhelms the selection for future defense against predators and tolerance of harsh physical environments. Fast growth may be a trade-off with lower production of heat-shock proteins and other complexities of tolerances, predicting that fast-growing corals may bleach sooner than slow-growing corals (which is a testable hypothesis). Increasing fecundity with rapid growth at the cost of greater vulnerability to predation, disease, and physical environmental stresses may be the "peacock's tail" of fast-growing corals.

Natural selection acts in the present. It sometimes appears to fail in predicting the future. When the abiotic and biotic environments are favorable during many generations for a species, natural selection can sometimes reward diverting resources to prolific production rather than cautiously investing for the unknown future. As with *Acropora*, Coley et al. (1985) pointed out for vegetation that when the environment is favorable and resource availability is high, the rates of herbivory are also high, but the rapidly-growing plants have low production of defensive metabolites. There are at least 128 corallivorous species of fishes (Cole et al. 2008) and 314 species of corallivorous invertebrates (Stella et al. 2011). For fishes, the diets of the majority of corallivores have shown "only a small suite of available prey" (Cole et al. 2008) and the fast-growing *Acropora* and *Pocillopora* are the usually preferred prey for both fishes and invertebrate corallivores. The Neogene, and especially the Pleistocene, were the best times for reef-building corals in geologic history (Kleypas et al. 2001). This predicts that fast-growing corals such as *Acropora* would become especially important while investing little in defenses. Pocilloporids *Stylophora* and *Pocillopora* were predominant in the

Caribbean in the Pliocene and most of the Pleistocene (Budd 2000), but during millions of years of good times, natural selection seems to lose caution for future changes.

Lamont C. Cole (1954) explained how reproducing in abundance early is a powerful trait, determining whether a species will be predominant. Having a larger surface area for a colonial coral could mean more polyps and a greater fecundity. Growing fast means a greater potential fitness with greater fecundity earlier. Selection for the benefits of abundant gamete production may reward some corals that invest much of their resources into fast growth and reproduction at the expense of defense and tolerances of physical factors such as unusually warm or turbid waters. Runaway selection may take traits to the extreme, but not to where fitness is lost, although the cost may lead to handicaps (Zahavi 1975). The harm from runaway selection comes when environmental conditions change the rules of the game and the r-selected corals are caught especially unprepared.

In contrast, when slower-growing massive corals are under stress, they typically shift energy from reproduction to survival. Perhaps they are selected to survive during hard times and reproduce when things get less risky for recruits. One might classify slow-growing corals as K-selected. With heat stress, *Orbicella* may postpone reproduction for 4 years (Levitani et al. 2014). Kojis and Quinn (1984) suggested variation in coral fecundity could be used to monitor environmental stress on corals. But fast-growing corals like *Acropora* seem to trade investment in survival for fast growth and reproduction. We might classify fast-growing corals, such as *Acropora*, which are dominant during good times for reef-building, as r-selected.

Over the past four decades in American Samoa, the relative abundance of fast-growing branching coral genera (e.g., *Acropora* and *Pocillopora*) generally decreased significantly (though see Fig. 2), while some slower-growing massive or encrusting genera (e.g., *Porites* and *Pavona*) increased significantly. There is a pattern of shifting the predominance of fast-growing to slow-growing scleractinians when environmental conditions become more stressful that has been repeated on three scales: geological time, ecological time, and in laboratory simulation experiments.

There have been three periods in geologic history of strong reef growth by scleractinians, and in these periods, fast-growing genera were prevalent. Kleypas et al. (2001) made a good point that the biological and geological performances of coral reefs are largely independent at the ecological scale. But for now, on the geological scale, we assume that during periods in which reef-growth was strong, the environment was good for corals. The first period was in the later Triassic when the fast-growing



Figure 1. Indo-Pacific acroporids have been preyed upon by *Acanthaster* for 1 – 3 million years, yet there has been no evident selection for defense against CoTS or many other types of predators. Has Fisher's "runaway selection" for rapid and prolific reproductive output been realized by trading off defense against predation and by weakened tolerance of physical stresses?

phaceloid (the “branching form” of the Triassic) genus *Retiophyllia* prevailed, with at least 34 species and was found all around the tropical world of the time. The second period was the mid-Jurassic when the fast-growing *Thamnasteria* also prevailed around the tropical world with at least 57 species. The third period is the present Neogene, in which it appears that *Acropora* may be a representative of fast-growing, speciose genera. When these periods of strong reef growth by scleractinians came to an end, the predominant fast-growing genera seemed to become dead genera walking, but many of the slow-growing scleractinian genera became relatively more abundant. I hope that *Acropora* does not do badly while slower-growing species do better if conditions get worse for corals in modern times, but our surveys over the past four decades in American Samoa indicate that this pattern in geologic time may be repeating now in ecological time.

It is interesting that the relatively fast-growing, competitively superior, species in species complexes may also be more likely to go extinct than the slower-growing species in the group. In the Caribbean *Orbicella annularis* complex, the organ-pipe *Orbicella* grew in tall thin columns and seemed to displace the other *Orbicella* into deeper waters. When it went extinct, the other slower-growing *Orbicella* species replaced it in shallower water (Pandolfi et al. 2002).

It is predicted by IPCC and many studies that if tropical sea surface temperatures warm by 1.5 °C to 2 °C above those in the early 1800s, coral-reef systems will collapse, greatly reducing diversity, and with net calcification changing to net dissolution. However, a recent set of simulation experiments of what will happen under future climate change (Jury et al. 2024) found that: 1) net calcification rates often declined with decrease in the abundance of corals, but nearly always remained positive. Figure 2 in Kiessling (2009) shows that between periods of strong growth of reefs in the Mesozoic and Paleogene, there were still traces of positive net growth by scleractinians as well as by bivalves, CCA, and cyanobacteria. 2) Corals showed reduced abundance, but were never extirpated. Despite prehistoric mass mortalities, a number of important genera of scleractinians are still here. 3) When corals show reduced abundance, the community composition shifts by reducing prevalence of fast-growing corals. In the experiments, fast-growing pocilloporids showed investment into large numbers of recruits, but had relatively poor survival, as might be expected of r-selected genera.

Competition for space has a major influence on coral community structure and we automatically include competition as a default trait acted upon by natural selection. *Acropora* is often categorized as a fast-growing, r-selected, “competitive” coral because of its predominance. It is true that some relatively slow-growing corals (K-selected) are adapted to competition (Lang 1973), but Fisher’s runaway natural selection may favor rapid growth in three dimensions for increased fecundity to the extent that *Acropora* may become a superior competitor as a byproduct. With Occam’s razor, we might consider that r-selected *Acropora* is a superior competitor because it grows fast, rather than it grows fast as an adaptation to be a superior competitor. Winning in competition has indirect benefits for fecundity, but we should compare the total fecundity provided by fast growth of living cover with the fecundity made possible by winning living cover in competition.

There are a number of genera of slow-growing corals that have been called “Lazarus corals” because they reoccur after mass mortalities (Rosen 2000). Fast-growing corals are sometimes called “Faustian corals” because runaway selection gives them lives of glory and dominance by increased investing in growth by divesting many defenses and tolerances; but when conditions change for the worse, they become victims of their glorious dominance in the past.

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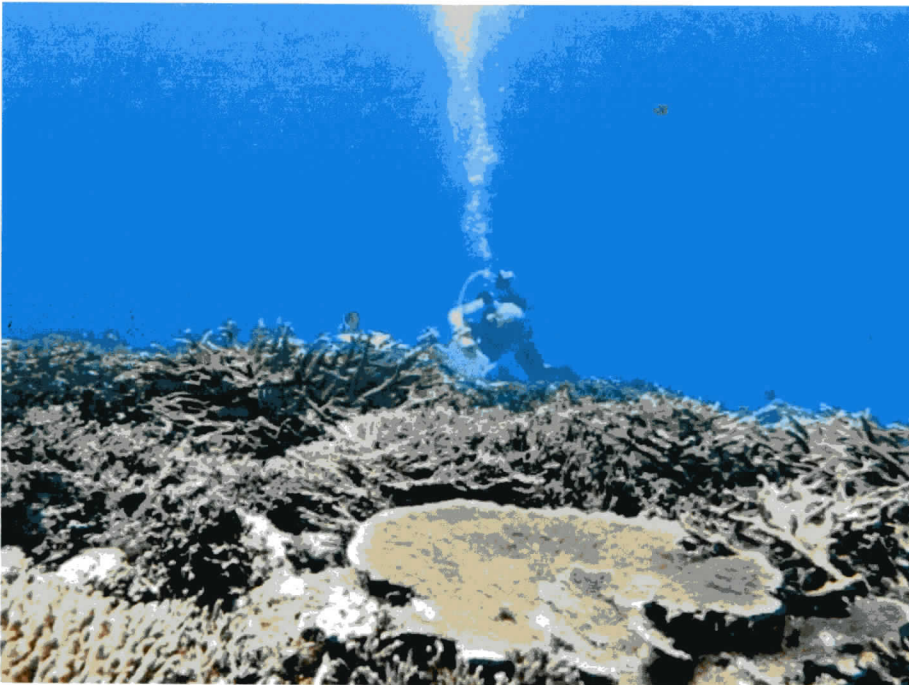


Figure 2. Fagatele Bay National Marine Sanctuary has been a conspicuous exception to this generalization. *Acropora* has significantly increased in this small (0.25 mi²) bay over the past four decades. Photo by Alice Lawrence.