THE ENERGETICS OF ALGAL SYMBIOSIS: IMPLICATIONS FOR EVOLUTION

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In 1981, I published a simple iterative simulation model of algal symbiosis. Host and symbiont growth were assumed to be functions of nutrient utilization efficiencies of host and symbionts. Under conditions where feeding by the host is the principal source of the growth-limiting nutrient and where solar energy is not limiting, the model indicates that the scarcer the food, the greater the energetic and growth advantage of mixotrophic nutrition over purely autotrophic or heterotrophic nutrition. In other words, when dissolved inorganic nutrients, and consequently nutrients fixed into organic matter, are very scarce in a euphotic environment, the advantage goes to symbioses that can both feed and photosynthesize. The host-symbiont system functions as a primary producer that captures scarce nutrients in packets of particulate organic carbon, the only concentrated source of nutrients under these conditions.

The implications of this model have been used to explain why algal symbiosis should be a powerful driving force for evolution in shallow-water, nutrient-poor environments. The characteristic rapid diversifications and abrupt extinctions seen in lineages of many planktic foraminifera, larger benthic foraminifera, reef-building corals, rudistid bivalves, and some other groups, illustrate some of the evolutionary consequences of algal symbiosis.

Some of the assumptions of the original model need to be reassessed and updated. The basic assumption of nutrient-limitation of growth is still correct, though recent experiments point to fixed nitrogen as the critical nutrient. A surprising prediction of the original model was that the algae could release in excess of 90% of their photosynthate to the host and still greatly benefit from the symbiosis. Recent physiological studies of coral and foraminiferal symbioses indicated that the symbionts indeed often release more than 90% of their photosynthate.

One assumption that is incorrect is that energy for respiration is also nutrient limited. In fact, the more nitrogen-limited the algae are, the higher the proportion of photosynthate that they release to the host, though that photosynthate has relatively little fixed nitrogen. Often the host cannot utilize all of the photosynthate provided and must excrete the excess as mucus. Recent experiments have shown that nutrient limitation is actually essential to maintaining healthy algal symbioses. The more dissolved inorganic nitrogen available to the symbiotic algae, the faster they grow and increase in density. Under these circumstances, the algae actually contribute less photosynthate to the host. A serious consequence of high algal-cell densities is greater respiratory demand for oxygen at night when photosynthesis ceases.

Mixotrophic nutrition is as basic a trophic mode as autotrophy and heterotrophy. Unfortunately, mixotrophic nutrition does not fit standard ecological energetic models and is often ignored. Mixotrophs essentially provide "free" links in the food chain; for each unit of biomass consumed by the host (as particulate organic matter), the host-symbiont unit is able to grow by very nearly an equivalent unit. In addition, excess photosynthate, which the host excretes as mucus, provides a substrate for bacterial production that feeds other members of the community. Finally, the relationship between symbiosis and calcification must be mentioned. Though certainly not all organisms that calcify are mixotrophic nor do all mixotrophs calcify, algal symbiosis can greatly increases the calcification potential of the host. As a result, in nutrient-deficient environments, populations of mixotrophic organisms: a) concentrate biomass, b) contribute to the biomass of associated organisms, and c) rapidly calcify, which can result in habitat for other organisms. As a consequence, evolution and extinction of mixotrophic lineages often results in evolutionary events at community and ecosystem levels. Better understanding of the ecologic and evolutionary role of mixotrophy is essential to understanding tropical marine ecosystems in the past and present, and to predicting their future under anthropogenic influence.

https://doi.org/10.1017/S247526220000160X Published online by Cambridge University Press