Contemporaneous Disequilibrium, a New Hypothesis to Explain the "Paradox of the Plankton"*

Peter Richerson, Richard Armstrong†, and Charles R. Goldman

DEPT. OF ZOOLOGY AND INSTITUTE OF ECOLOGY, UNIVERSITY OF CALIFORNIA, DAVIS, CALIF. 95616

Communicated by G. Evelyn Hutchinson, September 1, 1970

Abstract. The diversity of lake phytoplankton is unexpectedly high, since the epilimnion of a lake is continuously mixing and might be expected to have only one or at most a few niches for primary producers. However, a carefully replicated series of samples from Castle Lake, Calif., showed a high degree of patchiness for many phytoplankton species, indicating that the rate of mixing is slow enough relative to the reproductive rate of the algae for many different niches to exist simultaneously. Productivity per unit biomass ratios, measured at Lake Tahoe, California–Nevada, shows that the turnover times for carbon in even this ultraoligotrophic lake are often less than 1 day. High diversity is associated with high productivity per unit biomass and high zooplankton populations in this lake.

A contemporaneous disequilibrium model to explain the diversity of the lake phytoplankton is therefore highly plausible. At any one time, many patches of water exist in which one species is at a competitive advantage relative to the others. These water masses are stable enough to permit a considerable degree of patchiness to occur in phytoplankton, but are obliterated frequently enough to prevent the exclusive occupation of each niche by a single species.

The structure and functional relationships of lake phytoplankton exhibit many puzzling phenomena. One of the most perplexing is the unexpectedly high diversity encountered in even small samples of phytoplankton. G. E. Hutchinson[1] has dealt at length with this problem terming it "the paradox of the plankton." Briefly stated, this paradox is that the examination of a small volume of water (e.g., 10 ml) usually yields a list of some tens of species where the competitive exclusion principle[2] might lead us to expect only one or a few species. One can argue that the epilimnion of a lake is as nearly homogenous as any habitat can be expected to be due to turbulent mixing and that the competitive exclusion principle would, if its postulates were met, lead to the exclusive occupation of the habitat by a single species best adapted for living there.

The competitive exclusion principle has two postulates that may explain its apparent inapplicability to the phytoplankton. It assumes that the competing species are at equilibrium and that the axiom of inequality holds (that is, that two material systems are never exactly equivalent and therefore cannot have a competition coefficient of zero). Hutchinson believes that the main answer to the paradox of the plankton lies in the violation of the first assumption. Since conditions change quite rapidly in the plankton habitat, perhaps one, and then

another, organism is the superior competitor, but in such rapid succession that no one organism has the advantage long enough to cause the extinction of the others. No evidence seems to contradict this explanation, although decisive observational support is also lacking.

Riley[3] offers another explanation centering around the second assumption. He believes that natural selection has caused phytoplankton to approach asymptotically some upper limit of efficiency which makes differences between species so small that extinction, even in an equilibrium state, would proceed at a very slow rate. Hutchinson[4] also discusses two additional mechanisms—symbiosis and niche diversification—and believes that it is possible that some phytoplankton are meroplanktonic and are not able to reproduce in the plankton indefinitely. There is some reason to think that many phytoplankton are just opportunistic forms that happen to find the pelagic habitat suitable for growth for restricted periods.

The various hypotheses are not mutually exclusive and any one can help to explain "the paradox of the plankton." Available evidence indicates that all hypotheses are plausible; such evidence is insufficient to assign relative importance to any hypothesis, much less eliminate any entirely. Hutchinson notes that this unexpected diversity "perhaps has never been fully explained." This view is clearly not an overstatement of the difficulty encountered.

Our data[5] from Castle Lake, a mesotropic subalpine lake of 0.2 km² in Northern California, combined with the previous evidence and certain observations made by the authors at Lake Tahoe suggest a contemporaneous disequilibrium model similar to Hutchinson's. 72 replicate samples, distributed from six different epilimnetic stations, were taken. Two indices of patchiness, Fisher's k statistic and the variance to mean ratio, were calculated for these data, as shown in Table 1. Fisher's k was calculated by a maximum likelihood method[6] with a digital computer. Many of the species found in such samples were very patchily distributed. The pattern produced must be attributed to reproduction as most of the species involved were diatoms and other nonmotile or slightly motile forms. Although the subject of patchiness in phytoplankton has had much less attention than in zooplankton, some other examples of phytoplankton superdispersion are available.[7] The existence of patchiness is contrary to Hutchinson's implicit assumption about phytoplankton. He states the problem as one in which many species must be maintained in the face of a "relatively isotropic or unstructured environment all competing for the same sorts of materials." If patches based upon reproductive patterns are possible, there must be enough structural stability, relative to the reproductive rate of phytoplankton in the environment, for such patches to be established. There is some tendency for the rarer organisms to be either very patchy or random to slightly underdispersed, suggesting that such temporary niches are most important in maintaining these rarer organisms.

The potential doubling times of algae are very short. In Lake Tahoe, an ultraoligotrophic lake, average turnover rates for the whole water column (determined from the ratio of ¹⁴C productivity to carbon biomass, assuming carbon to be 13% of the total biomass) are as low as 1.4 days; individual samples are

TABLE 1

Species	Mean	Fisher's k^{10}	Variance to mean
Botryoccus braunii	34.89	7.70	5.35
Cosmarium bioculatum	0.56	*	0.84
Cosmarium circulare	46.93	36.26	2.29
Oocystis lacustris	0.17	—	1.00
Oocystis naegliī†	2.65	1.79	2.38
Quadrigula chodati†	4.51	0.29	12.04
Quadrigula sp.†	0.21	0.17	4.93
Staurastrum curvatum	0.38	—	1.00
Staurastrum brevispinum†	0.19	1.90	1.09
Dinobryon sertularia†	45.57	1.54	23.46
Achnanthes minutissima†	0.81	1.17	1.71
Achnanthes linearis	1.11	—	0.96
Asterionella formosa†	0.08	0.02	4.25
Cyclotella meneghiniana†	0.78	2.22	1.51
Cymbella gracilis	0.08	—	0.92
Cymbella turgida	0.08	—	0.92
Cymbella ventricosa†	0.15	0.56	1.21
Diatoma anceps†	0.42	3.41	1.12
Diatomella balfouriana†	0.08	0.08	1.58
Epithemia zebra†	0.17	0.79	1.17
Eunotia incisa†	0.08	0.26	1.25
Fragilaria brevistriata†	0.53	1.41	1.26
Fragilaria construens†	0.31	0.03	5.24
Fragilaria virescens†	0.08	0.02	2.92
Fragilaria pinnata†	0.53	0.97	1.58
Gomphonema ventricosum	0.25	—	0.86
Navicula capitata	0.14	—	0.86
Navicula cryptocephala	1.54	—	0.68
Navicula lanceolata	1.40	9.89	1.14
Navicula minima	0.29	—	0.90
Navicula monmouth-stodderi†	0.10	0.42	1.19
Navicula radiosa	0.50	—	1.00
Pinnularia biceps†	0.08	0.08	1.58
Surirella intermedia	0.08	—	0.91
Synedra radians b.†	0.47	4.07	1.12
Synedra radians c.†	0.50	9.00	1.06
Tabellaria flocculosa†	0.42	0.14	5.12
Nitzschia amphibia	0.69	10.59	1.07
Opephora martyi†	1.72	0.04	79.89
Ceratium hirundinella	0.61	—	0.93
Anabaena affinis†	12.11	0.39	17.25
Chroococcus limneticus distans	10.22	5.22	2.92
Gloeocapsa granosa†	1.97	1.13	3.90
Merismopedia glauca†	2.54	0.07	16.06
Polycystis aeruginosa	516.03	68.91	8.39
Euglena sp.	61.67	5.00	12.35

Means and indices of patchiness for algae in Castle Lake. Portion of slide counted is equivalent to 3 ml of lake water and the total number of samples counted was 72. Organisms with less than 6 total occurrences omitted.

* k was not calculated for species with variance to mean ratios less than 1.

† k of less than 5, indicating appreciable departure from randomness.

occasionally observed with turnover rates as low as 8 hr. Phytoplankton diversity in Tahoe appears uncorrelated with zooplankton diversity but related to grazing pressure, since it is highest during the summer–fall zooplankton bloom, especially during high populations of *Daphnia pulicaria*. Fig. 1 shows the high,
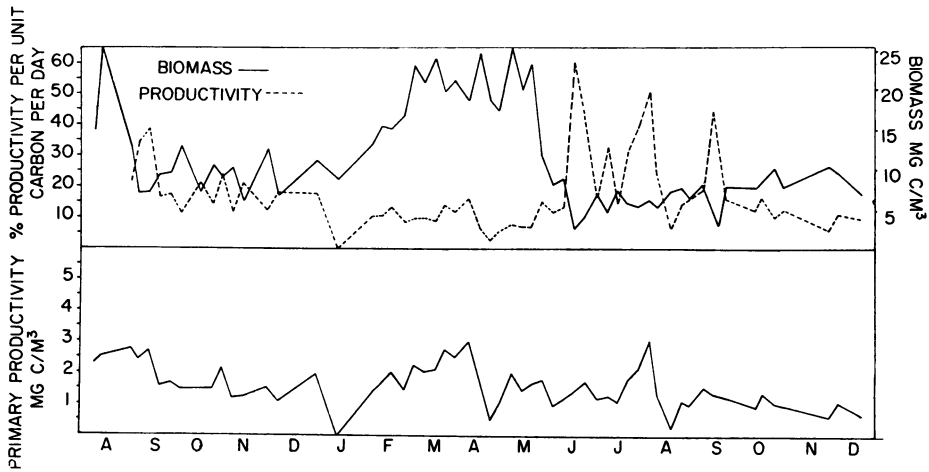
FIG. 1. Primary productivity, productivity per unit biomass, and biomass curves for phytoplankton in Lake Tahoe.

but extremely variable, productivity/biomass ratio (turnover rate) during the periods of high zooplankton populations throughout the water column from May until December.   Fig. 2 is a typical productivity/unit biomass curve for Lake Tahoe showing irregular layers of high turnover.   Other studies[8] show a high degree of variability in the vertical structure of water masses, corresponding to observations of divers who report striking layering effects of the plankton. Thus, there is at least as much evidence to support the hypothesis that the major diversifying factor is contemporaneous heterogeneity, random or chaotic perhaps, but with enough persistence to allow many species to exploit the whole habitat simultaneously.   The observed relation of phytoplankton diversity to zooplankton biomass (grazing pressure) and turnover rate is especially interesting because it suggests that decreasing the doubling time of the algal biomass enables particular species to exploit smaller, or less persistent, uniquely favorable water masses through more rapid reproduction. This relationship is also interesting since it is the opposite of the one predicted by Margalef,[9] who finds that exploitation generally reduces diversity.   The concepts of within- and between-habitat diversity[10] are useful in this case.   Grazing may indeed make the diversity in one small unit of water less according to Margalef's theory, thus reducing within-habitat diversity, but it may increase
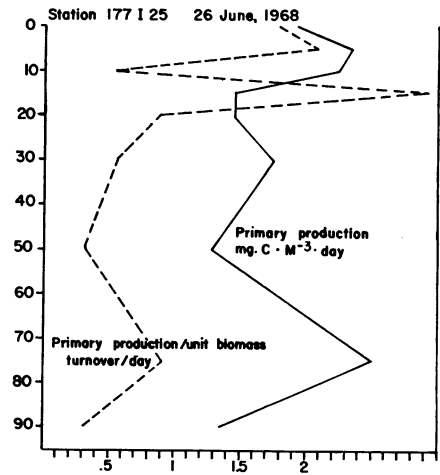

FIG. 2.   Productivity, and productivity per unit biomass, curves for Lake Tahoe. Depth is in meters.

measured diversity by reducing the size of habitats, thus increasing between-habitat diversity. Since within-habitat diversity is probably small in the plankton, the result is increased diversity. The universally observed patchiness of zooplankton must also be one of the many factors imparting uniqueness to these water masses.

This hypothesis differs from Hutchinson's by stressing the contemporaneous, rather than temporal, heterogeneity of the plankton habitat. The epilimnion of a lake is probably not completely homogenous on a time scale of a few hours, but rather provides a number of unique niches. Such a habitat is, however, quite unstable, obliterating these niches and reconstituting them at frequent, random, intervals.

It must be stressed that the two nonequilibrium hypotheses are not contradictory, but rather reinforce one another. The patch of water in which a particular species blooms and approaches a monospecific equilibrium has both spatial and temporal dimensions. It must be large enough in both its spatial and temporal dimensions relative to the reproductive rate of the species concerned and the rate of turbulent transport for one, or a very few, species to reproduce disproportionately with respect to the others present.

[1] Hutchinson, G. E., *Amer. Natur.*, **95**, 137 (1951).

[2] Hardin, G., *Science*, **131**, 1292 (1960).

[3] Riley, G. A., "Marine Biology I." *Proceeding of the First International Interdisciplinary Conference*, ed. G. A. Riley, (American Institute Biological Sciences, 1963).

[4] Hutchinson, G. E., *A Treatise on Limnology* (New York, John Wiley & Sons, 1967), vol. 2.

[5] Armstrong, R., Ph.D. dissertation, University of California, Davis (1969).

[6] Bliss, C. I., and R. A. Fisher, *Biometrics*, **9**, 177 (1953).

[7] Lund, J. W. G., C. Kipling, and E. D. LeCren, *Hydrobiologia*, **11**, 147 (1958); Margalef, R., *Perspectives in Marine Biology*, ed. A. A. Buzzati-Traverso (University of California Press, 1960), pp. 323–349.

[8] Lovett, J. R., *Limnol. Oceanogr.*, **13**, 127 (1968); Baker, A. L., *Limnol. Oceanogr.*, **15**, 159 (1970).

[9] Margalef, R., *Perspectives in Ecological Theory* (Chicago: University of Chicago Press, 1968).

[10] MacArthur, R. H., *Biol. Rev.*, **40**, 510 (1965).