

COMMENT

Comments on the analysis of grazing in Lake Erken¹

Nauwerck's (1963) data on the relationship between zooplankton and phytoplankton in Lake Erken have been partly reanalyzed and reinterpreted by Cushing (1976). Cushing's work is motivated by Nauwerck's unsettling conclusion that the zooplankton of Lake Erken cannot be nourished exclusively by the phytoplankton, nor can the zooplankton constitute the principal source of mortality for the phytoplankton. Cushing's analysis, although quite ingenious, is entirely founded on the fallacious assumption that the major phytoplankton taxa have identical (average) growth rates at any given time (p. 349). Although we must grant some license to anyone who attempts this kind of analysis, the key assumption is in this case highly questionable and thus seems to invalidate the work.

The net growth rates of phytoplankton species change seasonally as do the growth rates of division or class-level groupings of species, which are typically controlled by one or at most a few dominants. This variation results in succession. The net growth rates are of course a function of both biomass accretion and biomass loss. Differential biomass loss by sinking (Hutchinson 1967; Smayda 1970) and by grazing (Burns 1968, 1969; Wilson 1973; Porter 1973) has been documented in nature and experimentally. Differential biomass accretion, while more difficult to quantify, has also been demonstrated (Watt 1971; Stull et al. 1971). While these points seem widely accepted, Cushing seems to have simplified reality by the assumption that differential biomass accretion is not significant. The probable inaccuracy of this assumption is well illustrated by the data of Stull et al., which show variations in biomass renewal rate of three orders of

magnitude between important phytoplankton species in Castle Lake. It is also clear from their data that division or class-level species groupings would differ substantially.

The improbability of Cushing's assumption can also be demonstrated directly from the Erken data. The seasonal pattern of dinoflagellate abundance is given in Nauwerck's fig. 15. There is a dramatic rise in abundance over a 7-day period in the second week of August during which the standing crop changes from 275×10^6 to $4,900 \times 10^6 \mu^3$ liter⁻¹. The value of R at this time from Cushing's fig. 1 is 0.25 d^{-1} . Using Cushing's formula with these data produces a value of Z (instantaneous algal mortality) equal to -0.161 . Since negative mortality rates are impossible, and since this is a rather substantial negative rate, something must be seriously wrong with the data or with Cushing's assumptions. It seems most likely that the anomalous behavior of Z is produced by R , which is based on the community average turnover and not on dinoflagellate turnover specifically. Similar but less obvious distortions of Z must be produced throughout the analysis by the erroneous assumption.

If Z is not a reliable measure of mortality rate, then the correlation of Z values with other variables cannot be interpreted readily. This is particularly true of the intercept values of regressions involving Z . Intercept values of parametric regressions using nonnormal data, as these clearly are, must be considered unreliable under any circumstances, and this merely compounds the unreliability of Z itself. The significant correlations discovered by Cushing probably do have some biological meaning, perhaps even that which he attributes to them, but they cannot be interpreted with any certainty under these circumstances.

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William M. Lewis, Jr.

Department of Environmental, Population
and Organismic Biology
University of Colorado
Boulder 80309

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Analyzing the significance of grazing in Lake Erken

Cushing (1976) has presented an analysis of Nauwerck's (1963) data seeking to show that direct zooplankton grazing controls the phytoplankton populations in Lake Erken and provides sufficient energy flow to support the observed zooplankton growth. The analysis consisted of correlating phytoplankton mortality with biomass estimates for various components of the zooplankton community. Significant relationships were interpreted as evidence that the phytoplankton were being eaten directly by the zooplankters involved. The approach is an imaginative combination of the technique of food value analysis used by Edmondson (1965) and that of estimating algal growth rate based on carbon fixation and standing stock (Nauwerck 1963; Jassby and Goldman 1974; Kalff et al. 1975). Unfortunately, several mathematical errors were made which invalidate the analysis as it was presented. While there are questions in my mind as to the procedure's ability to prove the particular points made by the author, I do believe it has the potential to help elucidate phytoplankton-zooplankton interactions and I thus offer these comments to aid its future application.

In the first equation the algal reproductive rate (R), estimated as the carbon produced per day divided by the carbon standing stock, was compared to values based on observed population changes (P_0 becoming P_1 over time interval t) in order to estimate a mortality rate (Z) as

$$Z = R - [(1/t)\ln(P_1/P_0)]. \quad (1a)$$

The problem here is that these values of R are actually division rates, whereas the equation requires that they instead be instantaneous growth rates. Equation 1a can be restated in more conventional notation as

$$d = b - [(1/t)\ln(N_t/N_0)], \quad (1b)$$

where b and d are the instantaneous growth (birth) and mortality (death) rates, with N_t and N_0 the population size at time t and time zero. The growth rate should be calculated as

$$b = (1/t)\ln[(C_{\text{produced}} + C_{\text{stock}})/C_{\text{stock}}], \quad (2)$$

where C_{stock} is the standing stock of carbon at the beginning of time interval t . The division rates calculated by Cushing are always equal to or larger than the instantaneous growth rates required in Eq. 1b and