

# AN EXPERIMENTALIST'S VIEW OF ZOOPLANKTON MODELS

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## ABSTRACT

The experimentalist can perhaps determine an appropriate mathematical relationship between particular environmental parameters and a metabolic or behavioral response of zooplankton in the laboratory. Small scale distributions of zooplankton in nature must then be studied over time to determine the parameters which different animals actually experience. The heterogeneous and probabilistic nature of the pelagic environment is in contrast to the homogeneous, deterministic approach taken in most models.

## INTRODUCTION

My purpose here is not to exacerbate any intellectual tensions between experimentalists and theorists, but rather to indicate some general problems whose solutions would be of interest to advocates of both approaches. I am concerned primarily with those models in which the several underlying processes which regulate biomass or size of population are described mathematically, and these mathematical formulations are then combined in such a way that spatial or temporal patterns of biomass or size of population may be "predicted" from a set of relatively routine measurements of environmental parameters. The usual goal of such models is not just to predict patterns or events, but to do so from *a priori* knowledge and description of causal relationships, so that successful prediction implies some understanding.

It will be obvious that the difficulties I will illustrate are by no means peculiar to models of the zooplankton, or even to the pelagic environment. What may be peculiar is that the major problem in modeling the dynamics of zooplankton may not be so much in documenting the necessary equations as in verifying a particular model through field data. First, the zooplankton is a very heterogeneous group, defined operationally by the gear used for capture rather than by a discrete position in the food web. In this respect, the zooplankton is a much less "natural" grouping than the phytoplankton, both conceptually and analytically. Second, the zooplankton is patchy in horizontal and vertical distribution, as are the component species; this patchiness exists on several spatial scales, and is not always obviously related to physical parameters. Third, the zooplankton moves horizontally with currents and vertically through diel migrations of the older developmental stages of some species. All this means that the interpretation

of sequential samples is fraught with difficulty, and that spatial and temporal patterns can only be determined with great imprecision. Hence, verification of a particular model, or distinguishing between two models which lead to slightly different predictions, may have to rest not on the predictions concerning the dynamics of zooplankton but on predictions of other properties (e.g. dissolved nutrients) which can be measured with greater precision. (Steele and Mullin, in press).

## FORMULATIONS

Returning to models themselves, I would categorize one set of difficulties by the following question: What mathematical formulation should be used to describe the relationship between a particular environmental parameter and the zooplankton? As an illustration, consider the effect of temperature on a metabolic rate such as ingestion or growth. A general relationship of such a rate ( $R$ ) to the bodily weight ( $W$ ) of an individual animal is given by  $R = aW^b$  (or, as a weight-specific rate,  $R/W = aW^{b-1}$ ) where  $a$  and  $b$  are constants. Values of  $b$  for respiration of zooplankton are summarized by Conover (1968) and Marshall (1973). It is usually assumed that temperature affects the value of  $a$  and not that of  $b$ , although some studies (e.g. Ikeda, 1970; Champalbert and Gaudy, 1972) have suggested that the value of  $b$  for respiration also depends on environmental temperature.

In an empirical approach, Comita (1968) has used a multiple regression equation to describe the experimentally determined respiratory rates of freshwater copepods, in effect using an exponential function of temperature to replace  $a$ , and Conover (1968) found that the same equation gave reasonably good estimates of the respiratory rates of much larger, marine copepods.

In many physiological studies, the effect of temperature has been expressed as  $Q_{10} = (R_2/R_1)^{10/(t_2-t_1)}$ , where  $R_2$  and  $R_1$  are rates at temperatures  $t_2$  and  $t_1$  ( $^{\circ}\text{C}$ ), respectively. Hence, assuming that  $b$  is independent of temperature, a general expression for any metabolic rate could take the form:

$$R_{w,t} = c(Q_{10}^{(0.1t-1)})W^b \quad (1)$$

where  $c$  is a constant giving the metabolic rate of an animal of unit weight at  $10^{\circ}\text{C}$ . The chief difficulty with this formulation is that  $Q_{10}$  is not a true constant, but itself varies somewhat with

temperature (e.g. Comita, 1968) and is dependent upon the state of acclimation (i.e. the previous exposure to temperature) of animals used in an actual measurement.

McLaren (1963) reviewed several formulations for the effect of temperature on metabolic rates and strongly urged the use of Belehrádek's equation, of which the classical "normal curve" of Krogh is a special case. This equation has the form,  $R = g(t - \alpha)^h$ , where  $g$  and  $h$  are constants governing mean slope and degree of curvature of the relationship, and  $\alpha$  is a "biological zero" which in effect shifts the scale of temperature. This constant also reflects the state of acclimatization. The constant ( $g$ ) is dependent on the metabolic process being studied, and for copepod eggs at least, appears also to vary with diameter, i.e. proportional to  $W^{0.3}$  (McLaren, 1966; Corkett and McLaren, 1970; Corkett, 1972). If this proves to be generally true, a modified equation might then take the form:

$$R_{w,t} = k(t - \alpha)^h W^{b+0.3} \quad (2)$$

where  $k$  is a constant incorporating  $g$  and the metabolic rate of an animal of unit weight,  $a$ .

Another classical equation not common in the literature on zooplankton but recently used to describe the maximal rate of growth of phytoplankton (Goldman and Carpenter, 1974) is  $R = ue^{-v/T}$ , where  $u$  is a rate constant and  $-v$  is the slope of an Arrhenius plot of the natural logarithm of the rate ( $R$ ) against the reciprocal of the absolute temperature ( $1/T$ ). It is doubtful that this formulation represents any improvement over those given above, since it contains no term for acclimation.

In using these formulations, one could assume that temperature affects all metabolic processes to the same degree so that the ratio of two metabolic rates for a given zooplankter is equal to the ratio of the respective constants  $c$ ,  $k$ , or  $u$ . In fact, if temperature has a differential effect on metabolic rates, then ratios such as the gross efficiency of growth (= growth/ingestion) may vary with temperature (compare Mullin and Brooks, 1970; Reeve, 1963; and Reeve, 1970 for contradictory results concerning the dependence of this efficiency on temperature for zooplankton).

The same type of difficulty is encountered when one attempts to formulate the rate of ingestion by a zooplankter as a function of the concentration of food it experiences, even in the most simple case in which only one type of food is present. Possible equations are:

$$\begin{aligned} I &= I_m(P - P_o) / (S - P_o) & \text{for } P_o \leq P \leq S \\ &= I_m & \text{for } P > S \end{aligned} \quad (3)$$

$$I = I_m(1 - e^{-(P - P_o)/\delta}) \quad (4)$$

$$I = I_m(P - P_o) / (K + P - P_o) \quad (5)$$

which are derived from slightly different

mechanistic descriptions of the feeding process. In each, the rate of ingestion ( $I$ ) is described in terms of a maximal rate ( $I_m$ ) and the biomass of phytoplankton ( $P$ ). In all cases, there is the possibility that a threshold biomass ( $P_o$ ) is necessary to stimulate feeding, i.e.  $I = 0$  for  $P \leq P_o$ . In the rectilinear equation (3), the rate of ingestion increases linearly with increasing biomass of food to some saturating value,  $S$ , and is constant thereafter. In the Ivlev equation (4), the constant  $\delta$  determines the initial slope of the curvilinear relationship, and  $K$  has the same function in the Michaelis-Menten equation (5).

Equation 3, 4, or 5 may be combined with equation 1 or 2 in the simplest way by setting  $I_m = R_{w,t}$ . However, Frost (1972) and McAllister (1970) demonstrated that  $I_m$  determined over a short experimental period is a function of whether the zooplankters were well fed or starved at the beginning of the experiment. Further, data given by Frost (1974) and Ambler and Frost (1974) suggest that  $S$ ,  $\delta$ , and  $K$  are inverse functions of the relative sizes of the particles being eaten and the zooplankter.

In an attempt to determine the best formulation for ingestion, Mullin, Stewart and Fuglister (1975) fit equations 3, 4 and 5 to data of Frost (1972), the most extensive in the literature. Equation 3 fit the data slightly better than did the other two equations, but it could not be proven statistically to remove more of the variance. That is, one could not distinguish with statistical confidence between the formulations, in spite of the large amount of data. More important for modeling was the finding that the choice of equation 3 would lead to the conclusion that there was no threshold for feeding, i.e.  $P_o = 0$ , while use of equation 4 or 5 would result in  $P_o > 0$ . The concept of a threshold is teleologically attractive because it provides the phytoplankton with a "refuge in low density" so that the plants cannot be grazed to extinction (e.g. Steele, 1974), and because the zooplankters seem to cease expending energy in the pursuit of food when it becomes unprofitable to do so.

These examples may prove to be trivial; perhaps any exponential function relating metabolism to temperature and any quasi-hyperbolic function relating ingestion to availability of food will be sufficient to model the dynamics of zooplankton. In nature, however, the zooplankters confront an array of particles of potential food differing in size, shape, degree of defensive armament, and nutritive value, and it is far from certain that ingestion can then be described using only equation 3, 4, or 5 determined for single types of food independently.

#### PATCHINESS

Having belabored the point that a variety of formulations for the relationships between

parameters are possible, and perhaps cannot be distinguished, I turn to a second, more fundamental question: Assuming that one can decide upon deterministic formulations to describe the impingement of environmental parameters on a zooplankter or the zooplankton generally, what values of the parameters do the animals actually experience? This is a question of small scale distributions which change with time. Clearly the metabolic rates of a zooplankter which migrates through a thermocline twice a day may be profoundly affected by temperature (cf. McLaren, 1974), and this behavior requires that at least a weighted mean temperature be used in equation 1 or 2, and perhaps even this is an unjustified simplification.

More perplexing may be the value of P to use in equation 3, 4, or 5. One must first decide what portion of the spectrum of particles present in the sea really constitutes "food" in terms of the responses of the zooplankter. This portion could range from the biomass of a particular species of phytoplankton to the total particulate organic carbon, to take the extremes.

Furthermore, phytoplankton often occurs in patches or layers (e.g. Strickland, 1968). (I will here use the term "patch" to mean a volume of water containing an anomalously high biomass, but do not mean to imply that patches have discrete boundaries.) If patches of abundant phytoplankton and zooplankton occur together, the average biomass of phytoplankton in the euphotic zone (as determined by integrating a profile of chlorophyll sampled at discrete depths, for example) may seriously underestimate the value of P which is relevant for the zooplankton.

Mullin and Brooks (1972) determined the small scale distributions of phytoplankton biomass and juvenile copepods in relatively homogeneous coastal waters at six stations off Southern California. The important elements of this study were: 1) That the abundances of both plants and animals were integrated simultaneously in the same volume of water, and this volume (150 l) was "reasonable" with respect to the likely scale of short-term wanderings of a juvenile copepod; 2) Any tendency towards aggregation of the juvenile copepods in layers or patches of abundant phytoplankton could be distinguished from aggregation at a particular depth in response to some physical parameter. The juvenile copepods were more abundant, both horizontally and vertically, where the biomass of phytoplankton was higher. In this particular case, 66% of the population of juvenile copepods was found in those samples containing greater than average concentrations of phytoplankton, and these samples were 33% of the total volume of water sampled. Stated another way, the "average" zooplankter was experiencing a concentration of

food (assuming phytoplankton biomass represents food) which was higher than average, and could find this condition in only a third of the potential living space. The half of the samples in which the concentrations of phytoplankton were higher than the median concentration also contained 89% of all the juvenile copepods.

Although high concentrations of juvenile copepods and phytoplankton tended to occur together in this one study, we still have not determined the temporal coherence of this co-occurrence. That is, how long does a patch of phytoplankton persist before it is eroded by turbulence and/or grazing, and how long does the same group of zooplankters remain within such a patch (i.e. how important are immigration and emigration from a patch, either due to swimming or to physical processes)? If there is considerable active movement of animals into and out of persistent patches of phytoplankton, or if the phytoplankton patches are ephemeral, then all the individual zooplankters of a given species and age are equivalent and have a similar probability, over time, of finding food. If active movement is trivial and the patches persistent, however, then there are subpopulations of zooplankton, the "ins" and the "outs", which may have different dynamics. In particular, the "outs" will probably have a slower rate of growth and a higher mortality than the "ins", either because of outright starvation (if the "non-patch" biomass of phytoplankton is very low) or because, growing more slowly, they will remain longer in the early juvenile stages which are most vulnerable to predation. In the extreme case, a model might be most successful if it was focused upon the dynamics of the "ins" and ignored the "outs", except as food for predators (which, being thus well nourished, might then attack the "ins" in a second order interaction).

One of the curious aspects of the co-occurrence of patches is that the animals' grazing tends to reduce drastically the high biomass of phytoplankton. Hence, there is undoubtedly some probability distribution of four types of areas in the euphotic zone: 1) Areas where both phytoplankton and zooplankton are rare, and perhaps a bloom of phytoplankton may start; 2) Areas where the phytoplankton has become abundant and may have temporarily exhausted nutrients but is not heavily grazed; 3) Areas where both phytoplankton and zooplankton are abundant and rates of mortality of phytoplankton and ingestion and growth by zooplankton are high; and 4) Areas where only the zooplankton is abundant, perhaps having grazed down the phytoplankton and now being semistarved. What I am suggesting is a spatial mosaic of the elements of the classical temporal pattern of a spring bloom. A realistic model would have to take a probability distribution of this sort into account, but

in many present models it is assumed that the processes occur deterministically at approximately the same rates over a fairly large horizontal area at any one time.

### COMMENT

I hope it is clear that I do not intend to denigrate modeling as an intellectual or utilitarian pursuit by discussing these problems. Through the necessary simplification of natural processes, and particularly through sensitivity analysis, models aid in indicating the important questions for future research, quite aside from their potential value as predictive tools for management of the marine environment. Ideally, a model leads to conclusions which are not intuitively obvious, and we then learn from the reconciliation of the model and our collective intuition. Indeed, models provide the best possible excuse for those of us who enjoy working with living, aesthetically pleasing animals, or who come to appreciate the comradeship of going to sea.

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