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A model of primary and secondary production

by

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SUMMARY

This is an interim report on the development of a 'realistic' model of primary and secondary production. It is envisaged that the model will have a possible use eventually in the study of recruitment problems. The model is termed 'realistic' in that the daily weather conditions are incorporated and in that it resembles as closely as possible the known biology of the algae and herbivores. An initial simulation of a recorded production cycle is presented and the conclusions reached are that such an approach is feasible and may be obligatory, and that further research into specific biological fields is necessary.

INTRODUCTION

The success of the primary and secondary production cycles must affect the numbers of fish larvae that survive in any year. More precisely, Cushing (1972) has suggested that it is the match or mismatch of the timing of the primary and secondary production cycles with the fairly constant time of spawning of the fish that is important. Consequently we should know how the primary and secondary production cycles are generated year by year. To achieve such insight a model of primary and secondary production has been developed at the Fisheries Laboratory, Lowestoft, but before describing it two other models should be mentioned. The first, by Parker (1973), describes the cycles produced by the interaction of two algal species and two herbivore species in Lake Kootenay, British Columbia. The algal reproduction function is similar to Steels's (1965) model and the one used in this paper, but the herbivore biomass is achieved by a balance between the algae eaten and mortality, with no description of the biology of succession. Consequently, although good results appear to have been

obtained they do lack realism. The second model, that of Steele (1974a), is more realistic and pertinent to the North Sea but, in order to elucidate more general biological features, he has had to ignore the vagaries of the weather. The model presented in the present paper attempts to include the daily weather conditions and where possible is compared directly with Steele's model. A systems chart of the model is given in Figure 1.

THE MODEL

1. Algal reproduction

The average number of algae, A , over a variable mixing depth, D , is calculated, as in Wyatt & Horwood (1973), using the relationship $A^{t+1} = A^t \cdot \exp(\alpha - \beta)$, where $\alpha = Q.P. \exp(1.0) \cdot \left[\exp\{-\exp(-D.K) \cdot I_0/I_m\} - \exp\{-I_0/I_m\} \right] / D.K$, the instantaneous reproductive rate in t^{-1} , Q is a modifying factor depending on the level of nutrients available, P is the maximum photosynthetic rate, D is the depth of mixing in m , K is the extinction coefficient in m^{-1} , I_0 is the radiation at the surface in langley/day, I_m is the radiation level at which maximum photosynthesis occurs and β is the respiration, set at $0.1.P$. P is a temperature-dependent term (Eppley 1972) and is given as $\log_{10}(24.P) = 0.0275.T - 0.07$, where T is the water temperature in degrees Celsius. The mixing depth D is a function of wind strength, such that $D = 8.4.W$ for $W \leq 6$ m/sec and $D = 4.055.W^{1.5}$ for $W > 6$ m/sec. (Sverdrup, Johnson & Fleming 1942, p. 494), but this formulation may be changed later. The extinction coefficient is chosen using as guidelines the water types given by Jerlov (1951), but to represent the effects of shading it is linearly increased as the number of algae increase exponentially such that $K = 0.5(0.7 - K_0) \log(A) + 2.K_0 - 0.7$ for $\log(A) \geq 2$ and $K = K_0$ for $\log(A) \leq 2$.

The surface radiation is calculated each hour from the altitude of the sun and the prevailing cloud cover. The equations used are those of Lumb (1964) but initially only four degrees of cloud cover have been used to represent thick, medium, light and no cloud with no surface reflection; this is adequate at this stage since the example considered is in qualitative rather than quantitative terms

but will be refined later. The radiation level at which maximum photosynthesis occurs is held constant at 90 langley/day (Steele, 1965).

The nutrient modifying factor Q is represented, as in Steele's model, by the Michaelis-Menton equation, where $Q = N/(S+N)$. S is the half saturation coefficient and N is in μmol of NO_3^-/l ; this formulation is discussed in Eppley & Thomas (1969). The number of algae are given a minimum of 50/ml. This is a somewhat arbitrary value but a background minimum can be considered, because the model does not include horizontal diffusion. It is in the algal reproduction that the main difference between this and Steele's model occurs. In Steele's model, except for the nutrient effect, $(\alpha-\beta)$ is held constant. He justifies this by suggesting that, as his model is fairly stable, then stochastic variations in the reproductive rate will not have much effect. This aspect will be discussed later.

2. Herbivore biology

In the northern and central North Sea Calanus is perhaps the major herbivore and it is the biology of Calanus that has been built into the model.

Eggs are laid over a period of seven days (Marshall & Orr, 1972) and the numbers appear to be related to the availability of food. The numbers of eggs laid/female/day, E , is given by

$$E = E_m \left\{ 1 - 0.82 \cdot \exp(-C \cdot AV) \right\}, \text{ where}$$

E_m is the maximum number of eggs laid per female per day, given unlimited food, AV is the average number of algae/ml over the previous two weeks, and C is a constant depending on the quality or size of the food.

Like Steele, I have assumed a fixed final weight for the adult copepods (given by Kamishlov 1951) but, whereas Steele's development with time depends primarily on the food eaten, the development time in this model is given by $D = \left\{ 27.7 / (T + 4.57)^{1.1} \right\} \cdot B$. This is the development time of eggs (Corkett 1972) multiplied by B , the ratio of the total time from egg to adult to egg development time. The duration time of one stage relative to another is independent of temperature (Horwood, 1973); thus the duration time of any stage is calculated by multiplying the relative stage duration time by D in the equation for which T is the average temperature the copepod

has experienced in that stage. However, if the copepod has not eaten enough to enable it to make the weight increment of the next stage it is held back until it has eaten enough. Corner et al (1972) have shown that for Calanus feeding on Biddulphia 34.1% of the captured food is absorbed, and if we assume a 70% efficiency this gives 24.1% for growth and 10% excreted. The other 65.9% gives the faecal pellets.

The adults live for a period of time, which is put into the model as a variable, and then they lay eggs on each of the next seven days, after which they are killed off. Although the females do not die after their initial brood, and perhaps lay again after another 14 days, by that time their numbers are sufficiently reduced that they may be neglected.

The copepod mortality is prescribed in a density-dependent form such that $N^{t+1} = N^t (1 - M1 - M2.N^t)$, where M1 and M2 are the density-independent and density-dependent coefficients respectively. This describes a mortality in which the reduction in numbers is greatest in the egg and naupliar stages, as observed by Marshall et al. (1934, p. 795).

3. Grazing

The main interaction between the algae and herbivores is through grazing and this is essentially described by the 'volume swept clear' concept given by Cushing (1968). The numbers eaten/ml/day, G , are given by, $G = \sum_i X_i \cdot T_1 \cdot A \cdot V_i / (1 + A \cdot T_2 \cdot V_i)$ where

X_i is the number of copepods in stage i in numbers/ml,

T_1 is the number of seconds over which grazing operates/day,

T_2 is the handling time in seconds,

A is the number of algae/ml, and

V_i is the volume swept clear in ml/sec. This can be expressed as

$V_i = (\pi r_i^2) \cdot s \cdot l_i$ where

$s \cdot l_i$ is the swimming speed in lengths/sec, with l_i the length (in cm) of the stage i copepod, and s is a constant.

r_i is the 'radius of perception' and this can be expressed as a constant proportion of the body length, thus $r_i = c \cdot l_i$, and so V_i can be given as $V_i = \pi a \cdot l_i^3$, where $a = s \cdot c^2$, a constant of dimension sec^{-1} . The lengths of the naupliar and copepodite stages are taken from Ogilvie (1953) and Gunther (1934).

As will be appreciated, at low algal values the grazing function gives a linear relationship between the algae eaten and the algae present. This differs significantly from Steele's threshold response, where at low algal numbers grazing is suppressed. The presence of the threshold greatly enhances the stability of these models but its biological existence is still uncertain, as can be seen from the work of Frost (1972), and Gaudy (1974) has suggested that even greater grazing rates occur at lower algal values. However, Poulet (1974) gives data which might suggest switching if a choice of foods is available.

4. Nutrients

The nutrients provide a second means of interaction between the algae and the herbivores, with the nutrient level affecting the algal reproductive rate through the Michaelis-Menton equation and the nutrient level being altered by the algal reproduction and the herbivore excretion. The nutrient is measured in $\mu\text{mol. NO}_3/\text{l}$, and is taken into the algal cells at reproduction, but 10% of the algae eaten by the herbivores are excreted and so some nitrate is returned to the system. This obviously reduces the nitrate throughout the year (as in Steele, 1974a, Fig. 5.3) and slows down the algal production. Bacteria regeneration and diffusion across the thermocline occur in Steele's model but not in this model, and the faeces and growth material are lost to the system; however an extra source of nitrate would come from the excretion of the herbivore predators, and although this is not in the present model it will be included later.

THE SIMULATION

The model, in its present form, has only recently been developed, but an initial series of runs have been carried out to see if this attempt at 'realism' is feasible. Some of the best data on primary and secondary production cycles are those recorded by Marshall, Nicholls & Orr (1934) for Loch Striven. As the rainwater catchment area for this Loch is small (Marshall and Orr, 1927) no fjord-type circulation exists and so it was decided to try and model this system.

1. Physical Parameters

The wind strength and cloud cover were taken from the daily weather reports for Renfrew, twenty miles away, but as Renfrew is exposed and the loch is very sheltered the wind speeds were, somewhat arbitrarily, divided by three. The cloud cover is recorded as low, medium, high and in tenths covered, and this was reduced to the none, little, medium or thick categories of the model. As the number of copepods is uncertain, because of net avoidance and unknown predation, an accurate model of the numbers has not been attempted at this stage. The stress has been laid upon obtaining the correct number of cycles and the correct order of magnitude of the numbers; consequently the coarse approximations of the wind, and radiation will be balanced by grazing coefficients and copepod numbers to give a reasonable, qualitative picture.

The water temperature was recorded at the surface and at 30m, but as differences did occur an average of the two values was taken for each day. The water in Loch Striven was regarded as clear coastal water and a value of $K_0 = 0.22 \text{ m}^{-1}$ was used as the initial extinction coefficient.

2. Biological Parameters

The coefficients in the algal biology were chosen to represent the biology of the diatom Skeletonema, and thus a low half saturation coefficient of $S = 2$ was chosen; this is much lower than that used in Steele's model. The handling time of the cells, by the copepods, was set at 0.25 sec and has been deduced from feeding rates given by Corner *et al.* (1972). As laboratory work has not yet been completed on the duration times of Calanus the parameter B was chosen such that the model copepods developed at about the rates observed in the loch. The density-independent (M1) and density-dependent (M2) coefficients were 0.001 and 0.015 respectively, acting on numbers of copepods/l, and the maximum number of eggs/female/day (E_m) was 40.

Figure 2 shows the succession of developmental stages through each breeding period, taken from Marshall, Nicholls & Orr (1934), along with the percentages recorded in the model. Figure 3 gives the observed and calculated algal numbers.

DISCUSSION

As can be seen from Figure 2 the copepod succession is reasonably represented, but this would be expected because information from the observed sequence has been used in the model. However, no such information was used about the algal succession, and the calculated results on Figure 3 do not disagree with the observed values except in that the first algal bloom at the surface provides an anomaly.

At this stage I do not wish to make any detailed comments on the results, except to say that they appear encouraging and suggest that we are at a stage when 'realistic' models can be contemplated. However I would like to make three general points.

Firstly, this model has assumed an implicit diffusion in giving a lower algal limit, and obviously the heterogenic structure should be modelled, but this is still at a very theoretical stage; encouragement should be given to such works as those of Platt (1974), Denman and Platt (1974) and Steele (1974b) in which spatial structures are investigated.

Secondly, Steele has justified his constant algal reproduction formulation by suggesting that small day-to-day variations will have no appreciable effect. However, this is not obvious because a depression will last for about five days and the algal reproduction will be depressed over all this period. If this period coincides with the younger to middle copepodites they may reduce the algae to such low numbers that there might not be enough standing crop left to respond to the more favourable conditions at the end of the depression, and to provide enough food for the copepodites to grow to adults. Consequently, variations in the weather, at critical times, may alter appreciably the whole series of cycles after it, and hence a 'realistic' approach to these models may be obligatory.

Thirdly, although I have chosen reasonably typical values for the simulation, many reasonable combinations could produce similar patterns and consequently more biological work is needed to reduce the number of degrees of freedom in the model. At present my colleague Mrs B Thompson is investigating the duration time of Calanus with respect to food and temperature, but more precise information is needed on the

nature of egg laying and growth of Calanus and other species that are important herbivores. The algal reproduction appears to be fairly well represented (Becacos-Kontos & Svansson, 1969), but more guidance on the nature of the half saturation coefficient in the Michaelis-Menton equation would be welcome.

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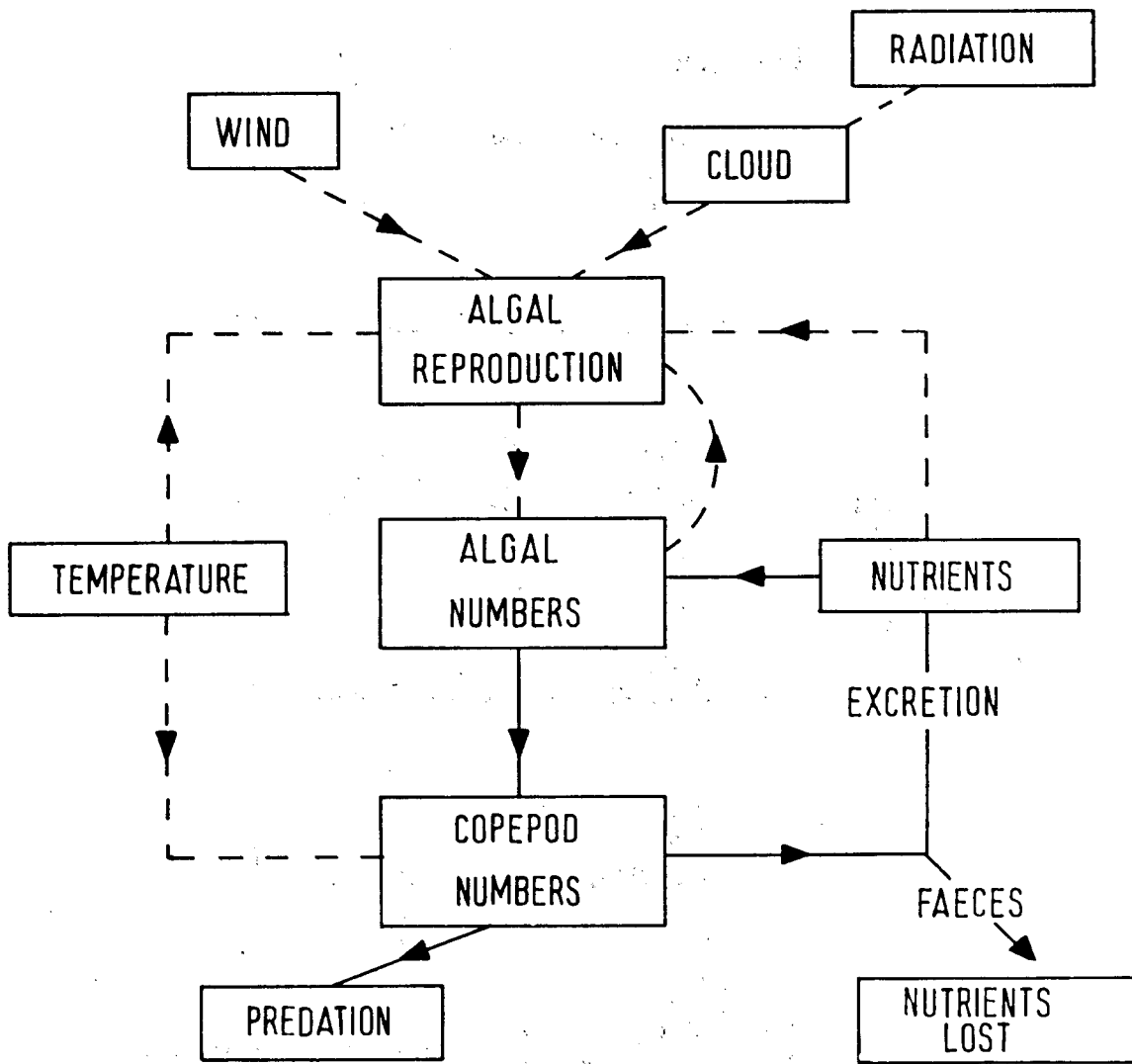


Figure 1 - Systems outline of the model.

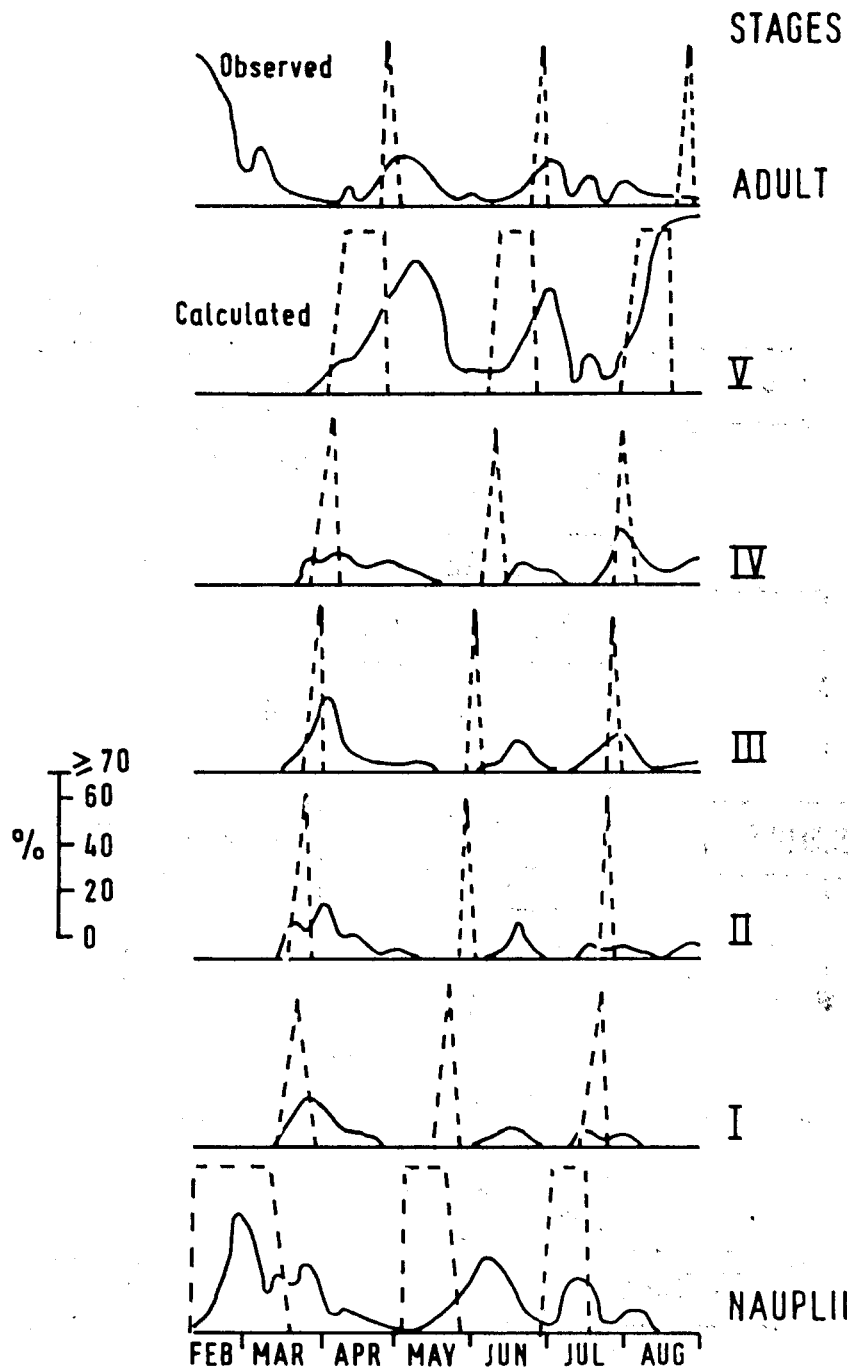


Figure 2 Observed and calculated copepod stages as percentages. Eggs are included in percentages but not in figure; their high numbers account for the apparent discrepancy in the early part of the second cycle. Observed values from Marshall, Nicholls and Orr (1934).

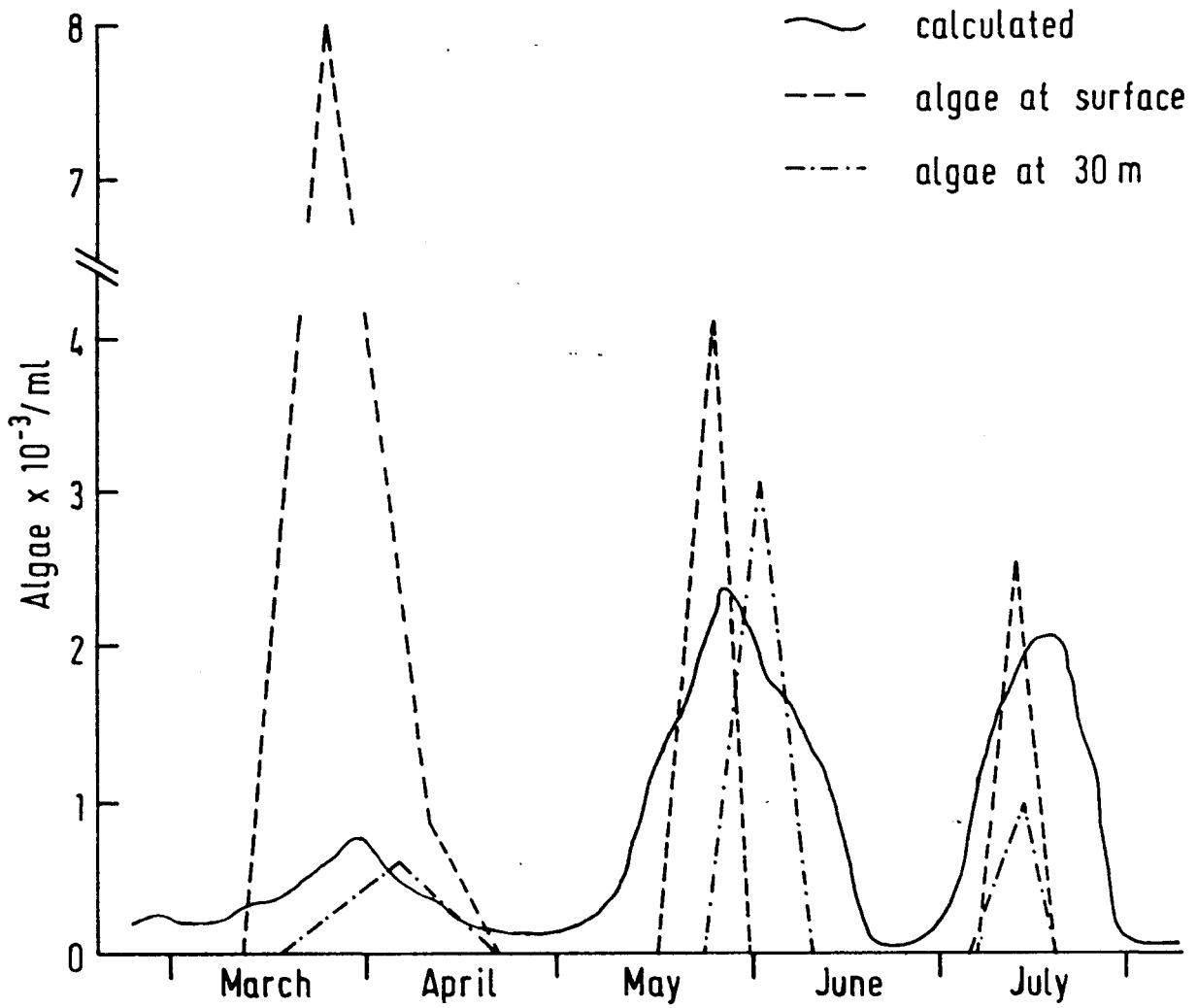


Figure 3 Observed and calculated algal numbers.