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GRAZING
OF
ZOOPLANKTON
IN THE
OCEANIC ENVIRONMENT

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INTRODUCTION

Grazing in the oceans, in general, refers to herbivores feeding on plant material. It is an important factor in determining primary production in the sea, and is difficult to estimate. Also, this energy transfer seems at least in part to be responsible for population changes which occur in the ocean.

Since it is only in the coastal waters that other plant material besides the phytoplankton is abundant (seaweed) and that other zooplankton organisms besides the copepods are abundant (meroplankton: the planktonic larval stages of Mollusca,Echinodermata and worms), attention will be primarily focused on the relation between phytoplankton organisms and copepods. (Marshall and Orr, 1966b) Most experimental work has been done with copepods,although other planktonic animals (Euphausids, Chaetognaths etc.) are abundant at certain places for part of the year.

In order to understand the problems involved in studying the quantitative aspects of grazing, a general discussion of the patterns of feeding is necessary (Chapter I).

The second chapter provides the theoretical background (mathematical models) for a discussion of the methods used and measurements obtained in chapter three.

The last chapter discusses grazing as it relates to the ecological problem of population control and evaluates the progress made in this area of research.

I. FEEDING BEHAVIOR.

The grazing activities of zooplankton appear to be diverse and complicated: experiments have shown that different groups of animals use different mechanisms in varying degrees; that there are significant changes during the life cycle of a particular species; that some species exhibit marked differences between the sexes; finally it has been shown that changes occur within one particular animal over a relatively short period of time.

Basic mechanisms:

Filter feeding has been described by Marshall and Orr (1955), using Calanus as experimental animal. Water is filtered through the stationary maxillae, while movements of other mouthparts set up a current. The setae on the maxillae are approximately 40 microns apart; this measurement determines the maximum size of food particles which can be obtained by this method (Gauld,1962). Based on experiments with other copepods, Jørgensen (1966) suggests that filter feeding generally occurs among adults when particles are more than 3 to 5 microns and less than 40 to 50 microns in diameter.

Conover (1966b) describes the feeding mechanism used by Calanus hyperboreus to capture large particles: a sweeping movement of the first and second maxillae and the maxillipeds seizes the food object and brings it to the mouth. The same method of 'active hunting' is used by Euchaeta, while Acartia and Anomalocera use their maxillae only (Gauld,1966). Acartia, being a small copepod,uses this method to catch mainly diatoms and dinoflagellates; Anomalocera, a larger animal, uses the same actions to capture animal food.

A third method, 'encounter feeding',has been proposed by Cushing (1959a). A chance encounter of large food particles with tactile appendages (antenulles) elicits a feeding response of the organism which consists of actively seizing its prey. Conover (1966a), however, shows that large particles must be encountered by a body region much smaller than that proposed by Cushing in order to be captured. Moreover, removal of the antennules does not alter feeding responses of Calanus hyperboreus (personal communication from Mullin to Cushing; in Cushing,1968). In this last paper, Cushing modifies his theory and seems to propose a mechanism of feeding which is identical to the 'sweeping movements' described above.

Variations in feeding behavior:

The following three groups of pelagic copepods have been established (Wickstead, 1962) on the basis of their feeding behavior:

(1) Herbivorous or mainly herbivorous forms (*Calanus*, *Acartia*);

  (a) selective herbivores (*Eucalanus*),

  (b) random herbivores;

(2) Mixed feeders (*Temora*, *Centropagus*);

  (a) true mixed feeders,

  (b) facultative mixed feeders (feeding on one type in the absence of the other);

(3) Carnivorous or mainly carnivorous feeders (*Euchaeta*, *Anomalocera*);

  (a) selective carnivores,

  (b) random carnivores.

Conover (1968) states that most zooplankton are, at times anyway, omnivorous and could be considered as mixed feeders. This would make Wickstead's groupings rather meaningless.

Gauld (1962) reports that four of the genera tested (*Acartia*, *Anomalocera*, *Labidocera* and *Euchaeta*) use the 'sweep-net' method only; none of these copepods obtain food through filter feeding. The other four (*Centropagus*, *Temora*, *Pseudocalanus* and perhaps *Calanus*) use both filter feeding and sweeping movements, although the extent to which they use each method is quite different. Although no particular feeding mechanism is exclusively related to one type of feeding, it is generally accepted that the filter mechanism is used by most plant feeders while carnivorous forms utilize the 'sweep-net' movement (Mullin,1966).

Differences in feeding behavior during development have been described by several investigators. Marshall and Orr (1962a) find that no feeding takes place during the first and second Nauplius stages of Calanus. From examinations of fecal pellets they conclude that small diatoms and other organisms can be ingested from the third Nauplius stage onwards,while larger diatoms could not be taken till the copepodite stages. Quantitative differences between the developmental stages of Calanus have been demonstrated by Gauld (1951) and are illustrated in Fig.1.

Mullin (1963) finds that grazing rates of male Calanus helgolandicus on Ditylum were 1/3 to 1/10 of those of the females; in one of his experiments,male Calanus did not remove Ditylum at all, although females of the population showed a high grazing rate on the same suspension. Raymont (1963) reports that the grazing rate of male Calanus finmarchicus is 1/15 to 1/40 of those of females of that population.

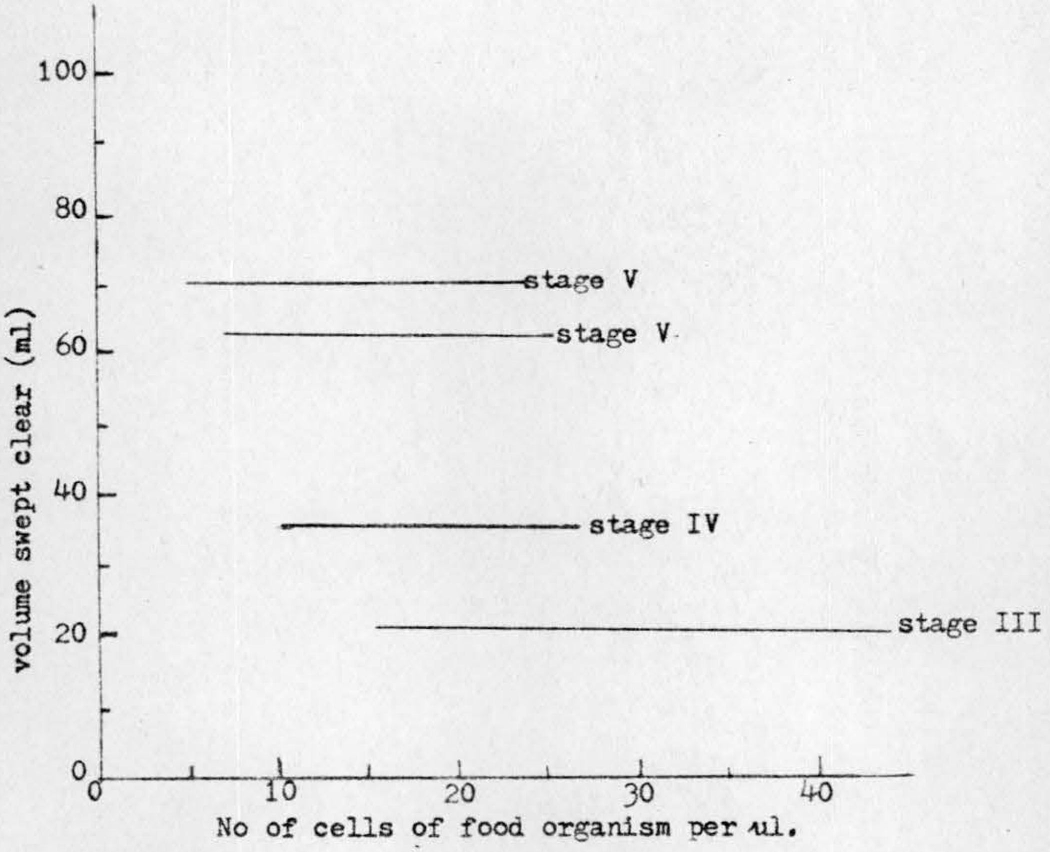

Fig.1. Calanus finmarchicus. Volume (ml) of cultures swept clear compared with the concentration of the control culture, measured as cells per µl. (After Gauld, 1951).

Selective feeding:

Most early investigators regard plankton grazers as 'indiscriminate' or 'automatic' feeders in the sense that they remove particulate matter from the water regardless of whether or not they are able to digest this material (Fuller, 1937; Fleming,1939).

Harvey (1937) shows conclusively that the filtration capacity of Calanus is influenced by the size of the diatoms being consumed: larger diatoms are filtered out at a higher rate. Based on the observation that the smaller Nitzschia is ingested preferentially over the larger Chaetoceros by Calanus, Gauld (1951) concludes that "selection is not merely a matter of size,and some more active mechanism may be involved, but sufficient evidence is not available for further discussion to be profitable"(page 705). A possible meachanism for the selective feeding of Calanus is found in the fact that it feeds by two different methods as explained above (Gauld, 1962).

Investigating the mouthparts and gut contents of 19 species of planktonic copepods, Mullin (1966) concludes that most species can tentatively be classified as either particle grazers or predators, although there seems to be a considerable overlap in food preferences of different species. In other words,the particle grazers on the one hand and the predators on the other "seem to be rather unselective as to diet and opportunistic in what they ingest"(page 553).

Rejection by some individuals of *Calanus hyperboreus* after the food was brought to their mouth leads Conover (1966b) to suggest that a chemical sense or 'taste' may also be involved in food selection. This might explain the findings of Corner (1961): of the 44 mg removed by *Calanus helgolandicus*, 35 mg was organic and only 9 mg was inorganic material. The initial suspension used in this experiment consisted of 55.8% organic material (dry weight). A more detailed study by Paffenhöfer and Strickland (1970) shows that *Calanus helgolandicus* feeds on living and dead particles (dead diatoms and fecal pellets), but never on 'natural' detritus (the 'structureless' material in the ocean). But since materials as unlikely as polystyrene beads (30 microns in diameter, and therefore comparable to diatoms) were ingested, and no data on digestion of the ingested material are given, this selectivity may be associated more with the physical state of a particle than its chemical composition.

The apparent selectivity can operate on different levels (inorganic - organic; living - non-living) and is, at least in part, a function of the size and shape of the food particle and the structure of the feeding appendages (Hargrave and Geen,1970).

Superfluous feeding:

When actively feeding animals stop responding to an increase in standing crop of their food by an increase in assimilation, superfluous feeding is said to take place. Whether it occurs in the ocean is still a question.

Harvey et al (1935) observed the great abundance of green fecal pellets during spring blooms, and he contributed this to excessive feeding by the zooplankton. Clarke (1939) confirmed this observation. Beklemishev (1962) formalized the theory and based it on his observation that during blooms herbivorous zooplankton species do not fully utilize their food because their gut contents and fecal pellets contain a certain percentage of undigested food. Cushing (1962b) links this phenomenon to the feeding opportunity or the distance the animal has to swim to find food (see table I). Superfluous feeding exists only when the animal does not need to swim at all. Reproduction is limited to that period almost exclusively,but even after taking this into account there would be an excess of grazing of nearly 300 %.

Conover (1966a) reasons that, if superfluous feeding

Daily ration/body weight	Reproductive capacity	Feeding opportunity
Superfluous feeding (370%)	Many eggs (18.5 per female per day)	No swimming for food (0.88 lengths per cell)
Adequate feeding (26%)	Some eggs (2.0 per female per day)	A little swimming for food (1.93 lengths per cell)
Low feeding (0.8%)	No eggs	Much swimming for food (4.5 lengths per cell)

Table I. The nature of feeding (low,adequate and superfluous) as related to feeding opportunity and egg production. (After Cushing,1962b).

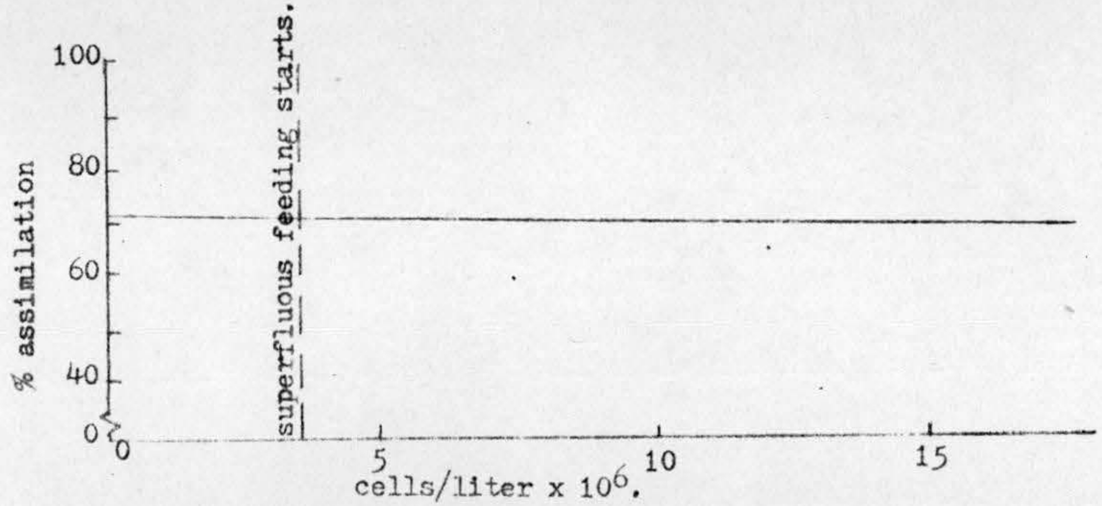

Fig.2. Relationship between food concentration and percentage of assimilation in Calanus hyperboreus feeding on Thalassiosira fluviatilis. (After Conover, 1966a).

occurs, one would expect to find a decreasing percentage of assimilation with increasing concentration of food. His laboratory experiments with Calanus hyperboreus (feeding on a monotypic culture forming chains!) fail to show any significant decrease in percentage assimilated with food levels ranging from 0.09 to 1.80 micrograms of Carbon per liter (see Fig. 2), although he admits that this does not exclude the occurance of superfluous feeding in nature. The experimental work of Marshall and Orr (1962b) suggests that, even when feeding rapidly, most of the food ingested by copepods is digested (50 to 80 %). As far as Harvey's observation of an excess of green fecal pellets during blooms, Conover suggests that during spring blooms the chlorophyll constitutes a larger proportion of the total particulate matter.

It is interesting to note the way in which both the proponents and opponents use ecological arguments to make their views acceptable. According to Beklemishev (1962), superfluous feeding is the "evidence of an imperfect community"(page 111), and although it probably is not of any use to the community where it takes place (although the regulation of population densities is mentioned), it clearly adds to the improvement of feeding conditions of the underlying communities. Conover (1966a), on the other hand, fails to see what selective advantage the mechanism of superfluous feeding could have, and how it could persist for long in the ecosystem since the process is energy-consuming and without any benefit for the zooplankton engaging in this mechanism.

II. MATHEMATICAL MODELS.

In estimating primary production in the ocean, the algal mortality due to grazing is considered to be an important factor: this process seems to be primarily responsible for the difference between productivity and standing crop (Raymont, 1963), while turnover rates will vary depending on local conditions. To measure the productivity certain assumptions are made and a model is set up to facilitate calculations. Most investigators admit that this will only give an approximation of actual values, since many variables operate within this system, a few of which have been discussed in the previous chapter. When measuring grazing activities, 'filtering rates' or 'volumes swept clear' are estimated either by direct measurement (Fuller, 1937; Fleming, 1939; Riley et al, 1949) or through theoretical approximation (Cushing, 1959a & 1968).

A different approach has been proposed by ecologists studying the dynamics of trophic levels in the sea. Both Margalef (1967) and Conover (1968) find that measurements of energy input and output are much more useful in determining the activities of grazers and their influence on the community as a whole. A major advantage is that estimates of both ingestion and digestion can be obtained in this way. The practical application of this tentative model to actual situations is still very much in the beginning stage, and will not be discussed further.

Productivity models:

First, two models will be described, which incorporate a direct measurement of grazing into a complete system of productivity.

Fleming (1939) assumes that (1) grazers feed indiscriminately, (2)diatoms divide at a constant rate, (3) the rate of division of diatoms is independent of grazing, (4) the daily fraction removed by grazing increases and (5) the change in the diatom population only depends on grazing. These oversimplifications enable him to set up a simple equation expressing the time rate of change of the diatom population: $\frac{dP}{dt} = P\left[a - (b+ct)\right]$, where P is the diatom population, 'a' is the rate of diatom division, 'b' is the initial grazing rate and 'c' is the rate at which grazing increases; a, b and c are considered constants. If the population is at a maximum, i.e. $\frac{dP}{dt} = 0$, then $a = b + cT$, where T is the time between the initial and maximum population. At time T, the rate of increase of the diatoms is just balanced by the grazing. Two concepts, specifically related to grazing, are developed by Fleming: the grazing factor (the difference between the multiplication factor and the increase factor): $g_T = e^a - 1$; and the grazing fraction (the fraction of the diatom population which is removed): $F_T = 1 - \frac{1}{e^a}$.

In terms of filtration capacity, $\frac{dP}{dt} = P(N_t v)$, where N is the number of grazers per volume, and 'v' is the volume filtered per animal per day. Fleming assumes here that all diatoms are removed from the water when grazed (i.e. grazing is 100 % efficient), and apparently has omitted the 'a'-constant from this equation (since he says: $N_t v = b + ct$). He goes on to say that "At the population maximum, $a = b + cT$, therefore, $N_T = a$. That is, the total filtration volume necessary to balance production depends only upon the rate of division and is equal to 'a'."(page 221). But since the assumptions made are not all correct this conclusion does not seem to be warranted at all. Also, the theoretical 'maximum P' on which most of his working formula's are based seems very unrealistic.

Riley et al (1949) stresses the importance of knowing the effects of various environmental factors on the physiology of the plankton. Secondly, these physico-chemical changes are expressed as smooth curves based on the means of field observations. The basic equation for the rate of change of a phytoplankton population is $\frac{dP}{dt} = P(P_h - R_p - G)$, where P is the total phytoplankton population and P_h, R_p and G are coefficients of photosynthesis, respiration and grazing, resp..

Grazing is measured by the formula $G = W H$, in which H is the total herbivore population and W is the grazing constant. W is defined as the ratio of the volume of water filtered per unit time per unit zooplankton (W'), to the volume of water containing the phytoplankton crop, (L). This ratio, $\frac{W'}{L}$, is called the filtering rate. An additional ratio, $\frac{P_L}{P}$, is added to account for sinking, where P_L is the quantity of phytoplankton in the euphotic zone. The grazing constant, then, is $W = \frac{W'}{L} \frac{P_L}{P}$. The errors of oversimplification are such that the value of W for a given W' will generally be too large. As Riley continues, "The fundamental assumption will not be that the method is correct, but rather that in comparing one region with another the errors are systematic" (page 112). A line which has been overlooked by the many, who have used Riley's figures as absolute.

Finally, based on the assumption that the grazing coefficient ('w', in cm^3 filtered) is a simple filtration factor,independent of the concentration but proportional to the respiratory coefficient ('r_h', in grams of C consumed; varies with temperature), Riley develops a simple equation $W = 23.5 \times 10^6 r_h$. In other words, it is assumed here that there is a direct relation between grazing and respiration, overlooking the growth processes and reproductive factor. It also assumes that all feeding is filter-feeding and that no superfluous feeding takes place. But then again, the results might be useful for comparative studies rather than as absolute measurements.

Simple feeding rates:

Many investigators, interested mainly in feeding rates, have developed formula's to estimate filtering rates.

Fuller (1937) determines the amount of water swept clear of diatoms by each copepod in 'x' hours (W_x) by means of the following equation: $W_x = V \ln \frac{C_1}{C_2}$, where 'V' is the volume per copepod, and C_1 and C_2 the concentrations of diatoms at the beginning and at the end of 'x' hours.

Gauld (1951), assuming that a copepod is a filter feeder, finds that in an experimental vessel where the phyical and chemical conditions are kept constant, the concentration of food particles in the presence of a steadily grazing copepod will decline exponentially according to the equation $C_t = C_0 e^{-kt}$, where

C_t is the concentration of food particles after time 't', and C_0 is the initial concentration. Further, if 'v' is the volume of water per animal, then 'vk' is the volume of water swept clear by one animal per unit time, so that the filtration rate (F) is given by $F = vk$. Substituting for 'k', the equation becomes

$$F = v \frac{\ln C_0 - \ln C_t}{t} .$$

Adams and Steele (1966) obtain the <u>filtering rate</u> (F) from the equation $F = \frac{1}{nt} \ln \frac{C_o}{C_t}$, where n is the number of grazers per liter, 't' is the duration of the experiment in days, C_o is the concentration of chlorophyll a (or counts per minute) of the control and C_t of the grazed water.

Although all three formula's are rather similar, it is difficult to see how they could measure exactly the same quantity, and how comparable results could be obtained. It seems that the formula's used are adapted to the data which are obtained through a particular method. Comparing Fuller's and Adams & Steele's formula's it is evident from them that $V = \frac{1}{nt}$ if both would measure the same quantity. There certainly is a relationship between these two quantities, but this relation is much more complicated than is indicated here.

Cushing's encounter theory:

A general mathematical expression of production is given by $\frac{dP}{dt} = P(R - M - G)$, where 'P' is the number of algae, 'R' is the reproductive rate of the algae, 'M' is the 'natural' mortality rate (negligible) and 'G' is the mortality due to grazing. Experimental observations on grazing depend on the following formulations: $G = R - \frac{1}{t} \ln \frac{P_1}{P_0}$ and $F = G\ V\ t$, where 'V' is the volume per animal (in mls) and 'F' is the volume swept clear (in mls). Through measurements of P_o, P_1 and R, an estimate of the volume swept clear is found, which is much higher than previous laboratory experiments indicate. Cushing's (1958) first explanation is that herbivores graze in excess. A year later (Cushing, 1959a), he postulates an 'encounter theory' of grazing to explain these high grazing rates calculated from field data. Since there is no way of distinguishing filtration from capture in formulations or experimental arrangments, a direct measurement of 'G' is preferable. This can be formulated as $S_a = \frac{S_m}{1 + a.t_h(S_m/\text{sec})}$, where '$S_a$' is the volume swept clear in mls/day at a given algal density of 'a' cells/ml, 'S_m' is the maximum volume swept clear (as if in empty water), 'a' is the algal density in numbers per ml, and 't_h' is the time (in seconds) to handle one cell. Then $G = S_a.H$ (H is the number of herbivores per liter). An estimate of 'S_m' is obtained through the equation $S_m = \pi r^2 vt$, where 'r' is the perceptive range of the herbivore (in cm) and 'v' is the speed of the animal (in cm/sec). At first, Cushing (1959a) bases his calculations on the assumptions that 'r' depends on the length of the antennules. After discovering that grazing occurs equally well without antennules, the term 'perceptive range' has to be expressed in a more general way. It is suggested (Cushing, 1968) that perceptive range might well be a function of length of the animal: $r = b(l - \alpha)$, where 'b' and 'α' are constants and 'l' is the length of the animal. Ultimately, then, "it might be possible to estimate the algal mortality due to grazing merely from the length distributions of algae and herbivores" (pages 76-77), see fig. 3.

As has been discussed in this chapter, two roads are open to estimate grazing and/or filtering rates:

(1) estimate productivity by determining standing crop and mortality directly;

(2) determine the difference between productivity and standing crop, which gives an estimate of mortality.

Sometimes it is sufficient to consider grazing mortality only (Cushing, 1959a), while at other times 'natural' mortality

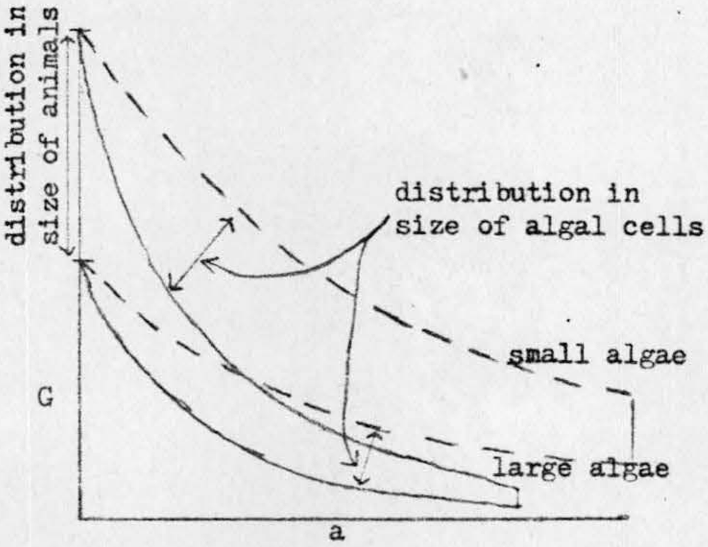

Fig. 3. Possible relation between the grazing mortality (G) and algal density (a), taken into account the size distributions of algae and grazers.
(After Cushing, 1959a).

('sinking') should be included (Riley et al, 1949). Some investigators consider grazing rates to be identical to filtering rates (Mullin, 1963), which assumes that (1) the filtration is 100 % efficient and (2) that all grazing is done through filtration (which is contrary to the findings in the first chapter). The rate of food intake is not considered in any of the models discussed.

The main points of controversy and possible causes of gross error related to these mathematical models can be summarized as follows:

(1) In order to be able to treat production as a single dynamic process which can be made to conform to an idealized mathematical model, the quantitative approach has to be supplemented by more precise qualitative data on energy dynamics and food relationships (Conover,1960).

(2) The possible effects of nutrient concentrations have been underestimated. It is assumed that grazing rates and reproductive rates are the only factors which determine phytoplankton densities. But, as Cushing (1959a) concludes, "there is no evidence that either factor is dominant, but in this paper I have taken the view that grazing is the dominant factor for the purpose of exploring theoretical possibilities" (page 36).

(3) The possibility of substantial disagreements between laboratory work and natural phenomena can not be overlooked. As will be illustrated in the next chapter, all experimental work tries to approximate the natural situation as it exists in the oceans. It is still a big question as to how close we are getting.

III. METHODS AND MEASUREMENTS.

Using a variety of methods and experimental animals, filtering rates ranging from less than 1 ml/animal/day to more than 1,000 ml/animal/day have been calculated; for results on Calanus, see table II. Some of these measurements can be disregarded because of obvious experimental error, as will be discussed. Still, there is no single most accurate estimate to measure grazing rates in the oceans. Problems related to what to measure, how to measure and when to measure have not been solved completely.

Measurements:

The measurements most commonly taken are filtering rates (or grazing rates) and feeding rates (or food taken in), according to Mullin (1963). The first is a volumetric measurement, and cannot be obtained directly (Conover, 1968); the second is an estimate of the biomass taken in. Assuming that all feeding is automatic filter feeding, these two measurements will be identical,

FEEDER	FOOD	RATE(ml/day/animal)	METHOD	REFERENCE
C.finmarchicus V + VI	Ditylum	170 - 240	Cell count	Harvey, '37
,,	Lauderia	50 - 100	,,	,,
,,	Chaetoceros	0	,,	,,
C.finmarchicus V	Nitzschia	Av. 1.09	Cell count	Fuller, '37
C.finmarchicus III	Chlamydomonas	29	Cell count	Gauld, '51
C.finmarchicus IV	,,	50	,,	,,
C.finmarchicus V	,,	100	,,	,,
C.finmarchicus fem.	<10 µ flagell.	Max. 4	32-P	Marshall et al, '55
C.finmarchicus I	>10 µ algae	Max. 2.8	32-P	Marshall et al, '56
C.finmarchicus II	,,	Max. 6.4	,,	,,
C.finmarchicus III	,,	Max. 9.2	,,	,,
C.finmarchicus V	Natural pop.	Min. 60; Max. 1,000	field obs.	Cushing, '58
C.finmarchicus + helgolandicus fem.	>10 µ flagell.	Max. 84	32-P	Marshall et al, '61
,,	>10 µ diatoms	Max. 43	,,	,,
C.helgolandicus fem.	Natural pop.	10 - 36	chem.analysis	Corner, '61
C.helgolandicus		Av. 30(winter)	amino acids	Cowey et al '63
,,		Av. 50(summer)	,,	,,
C.finmarchicus V		Av. 2,850	field est.	Cushing et al '63
C.finmarchicus V fem.	Ditylum	25 - 118	Cell count	Mullin '63
C.helgolandicus V fem.	,,	123	,,	,,
C.hyperboreus V fem.	,,	61 - 197	,,	,,
C.finmarchicus V, VI fem	Natural pop.	Av. 27	14-C, chlor.a	Adams et al '66
C.finmarchicus adults	Skeletonema	17.6	N-requir.	Corner et al '67
C.helgolandicus fem.	Chaetoceros	60	loss of C	Paffenhöfer et al '70
,,	Ditylum, detr.	31	,,	,,
,,	Skeletonema, detr.	54	,,	,,
,,	Natural detritus	0	,,	,,
,,	Fecal material	10	,,	,,

Table II. Filtering rates for different species of *Calanus*.

and can be expressed as the 'volume swept clear'. But since it is a fact that small sized organisms are filtered, while larger particles are actively seized (Gauld, 1951), the volume swept clear by a scooping animal may not be the same as that swept clear by a filtering animal. In that case, we would have to measure two feeding rates. Technically speaking, then, the grazing rate (called grazing mortality by Cushing, 1968) only tells us something about the amount of water (containing food) filtered through, while the feeding rate estimates the amount of food actually grazed.

A third measurement, the rate of assimilation, gives an estimate of the amount of food digested (60 to 95 % according to Conover, 1968).

Food material:

Very few experiments have used natural sea water as food source (Adams and Steele, 1966); and whenever it is used, this is taken during spring blooms (Hargrave and Geen, 1970) so that very little is known about conditions where food is scarcer. Mostly, a monotypic or polytypic phytoplankton culture is introduced into sterile sea water, even though examinations of gut contents of Calanus by Marshall and Orr (1962a) show that the food is extremely varied, consisting of both phyto- and zooplankton.

A variety of methods have been used to determine the amount of food taken in by the grazer (for reviews, see Marshall and Orr, 1962a & 1962b; Raymont,1963; Jørgensen,1966):
(a) Counting the cells before and after the experiment will measure the ingestion directly by providing an estimate of the volume removed. This method is very time consuming, and estimates of the quantity of organic food is too high, since it is assumed that all the volume is composed of organic food material (Cushing, 1958). This overestimate, however, is likely to be constant with time.

The use of the Coulter Counter (which measures the size and the quantity of material eaten) has made this method easier (Parsons et al, 1967).

(b) The chlorophyll a method assumes that all the chlorophyll that is measured is from living material (Riley et al, 1949; Adams and Steele,1966). This is probably not so, especially during and immediately after a spring outburst. It appears, therefore, that the overestimate obtained through this method varies with the seasons.

(c) Food labelled with 32-P or 14-C (Marshall and Orr, 1955; Adams and Steele, 1966) gives us a measure of both ingestion and digestion. Results of filtering rates obtained through this method are always lower than the other methods, since up to 30 % of the 32-P may be excreted after the first 24 hours, according to Marshall and Orr (1962a).

(d) Weighing and subsequent chemical analysis of food contained in natural sea water controls, and comparing these with food contained in natural sea water after it passes through a vessel containing _Calanus_ is used by Corner (1961) to estimate the amount of food used.

Experimental animal:

Most of the experimental work has been done using _Calanus_ (Fuller, 1937; Marshall and Orr, 1955; Corner,1961; Mullin,1963; Adams and Steele, 1966; see also Table II). Few investigators have used different species: Gauld (1951) uses _Calanus_, _Pseudocalanus_, _Temora_ and _Centropagus_; Hargrave and Geen (1970) use _Pseudocalanus_, _Temora_, _Oithona_ and _Acartia_. From these, it is clear that smaller animals (_Acartia_) have much lower filtering rates than larger animals (_Calanus_), according to Jørgensen (1966).

In surveying the literature, one finds so many experimental and species-dependent variables, that it becomes difficult to make any other generalizations.

Firstly, there are the are the questions related to the feeding habits of the animals (see chapter one): the different feeding mechanisms used are not all measurable by filtering rates; the fact that some animals might use dead particles invalidates experiments using cultures; Marshall and Orr (1962a) report that some Calanus do not feed at all during an experiment, and they therefore regard the maximum value obtained as significant.

Secondly, the laboratory situation introduces many new variables: the concentrations of animals is much higher than those in nature, and extrapolating those results is questionable; contamination of cultures by other grazers is unavoidable, and can only partially be balanced by the use of controls (Adams and Steele, 1966); the size of the vessels used has a marked influence on the grazing rate (Cushing, 1958).

Thirdly, results from one particular place and time are unique due to differential geographic characteristics and seasonal changes.

Feeding and daily food requirements:

The Pütter hypothesis, formulated more than half a century ago, states that there is not enough particulate food in the sea to supply the needs of the zooplankton. Although his estimates are now shown to be in error, the same discrepancy between the food needed and the food available has been restated recently by Marshall and Orr (1955) and Jørgensen (1962).

As has been discussed before, the estimates of daily food intake are not absolute. The same holds true for daily food requirements, since the conversion of respiration data (μl O_2/mg dry weight/day) to daily amounts of food needed is questionable "due to insufficient knowledge regarding the nature of the food oxidized" (Conover, 1960, page 414).

It is interesting to see, how various investigators try to find an answer to this problem. Jørgensen (1962) assumes that, because of this discrepancy, either filter feeders clear water of phytoplankton at far greater rates than has ever been observed experimentally, or that they do not feed directly on the phytoplankton, but on detritus. The first assumption is identical to Cushing's observation (1958): during the peak spring bloom, a filtering rate of 60 mls/day is sufficient for <u>Calanus</u> to survive; during other seasons it is much higher (more than 1,000 mls/day). The second assumption has been discussed before. It has also been suggested, that our sampling techniques might overlook the μ-flagellates, which could make up the difference if they were extremely abundant (Cushing, 1958; Mullin, 1963).

Corner (1961) reports that female Calanus helgolandicus can readily meet their daily food requirements by grazing at relatively low rates (10 - 36 ml/day/copepod, computed from removal of weight of organic matter) on natural suspensions of phytoplankton during the summer months. He concludes that "the question of whether Calanus makes considerable use of dissolved organic substances in winter remains undecided" (page 14). Parsons et al (1967) agree, that in most coastal waters enough food can be obtained. But they continue on page 16 that "a very different situation must exist in the open ocean where concentrations of plant material are at least an order of magnitude lower than in coastal waters. While oceanic species may be capable of obtaining food from lower concentrations of prey, other mechanisms also may play a more important role in feeding in the oceanic environment. The aggregation of particulate material along a convergence may provide the necessary concentrations of material or alternatively some species may obtain sufficient food from a larger prey at a lower concentration (i.e. by changing from herbivorous to carnivorous feeding)."

Food concentration and feeding:

Most early investigators (Fleming, 1939; Riley et al, 1949) assume, and Gauld (1951) proves that filtering rate is independent of the concentration of the food organism (see Fig.1). In other words, they find that a certain volume of water is cleared of organisms by filtering, regardless of how many organisms to feed on are present, up to a point where the filter-mechanism becomes clogged.

Recently, however, it has been observed that food concentration has an influence on feeding.

Mullin (1963), using a monotypic feeding culture, finds that with increasing concentrations of cells, the intake of food by Calanus increases to a maximum value and then decreases (see Fig. 4). Similar results are reported by Conover (1966a) and Parsons et al (1967). Adams and Steele (1966), using natural food, find that the concentrations at which a decline of feeding rates takes place according to Mullin and Conover are rarely encountered in nature: over a considerable range (from 2.5 to 18 µg chlorophyll a per liter) the filtering rate fluctuates around 27 ml/animal/day

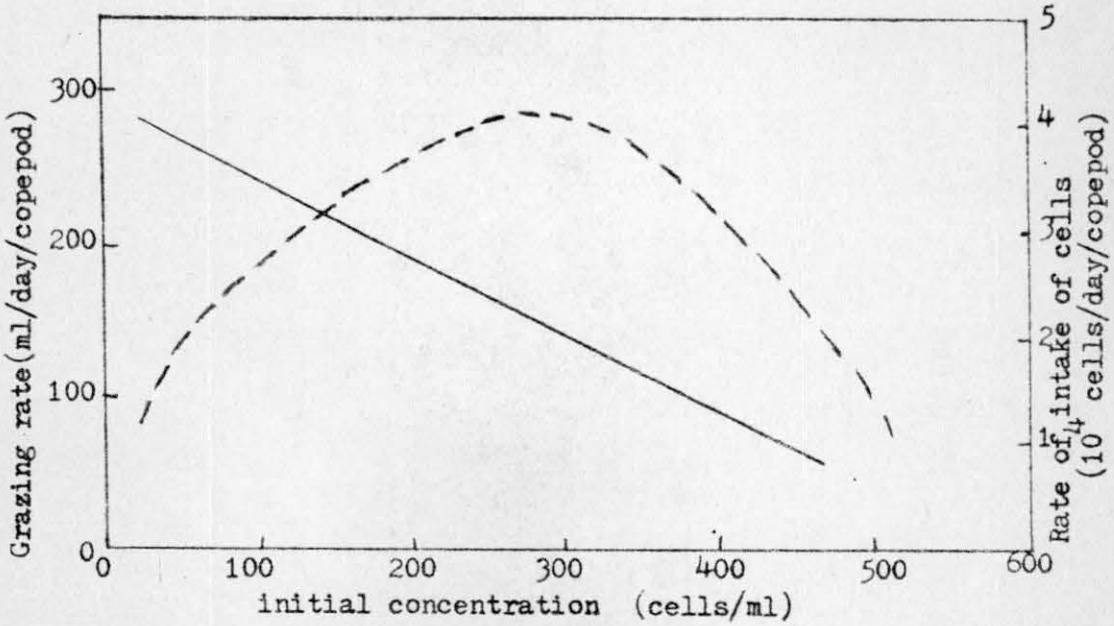

Fig.4. Grazing by female Calanus hyperboreus on various concentrations of Ditylum brightwellii. Both filtering rates (left ordinate, solid line) and feeding rates (right ordinate, broken line) are given. (After Mullin, 1963).

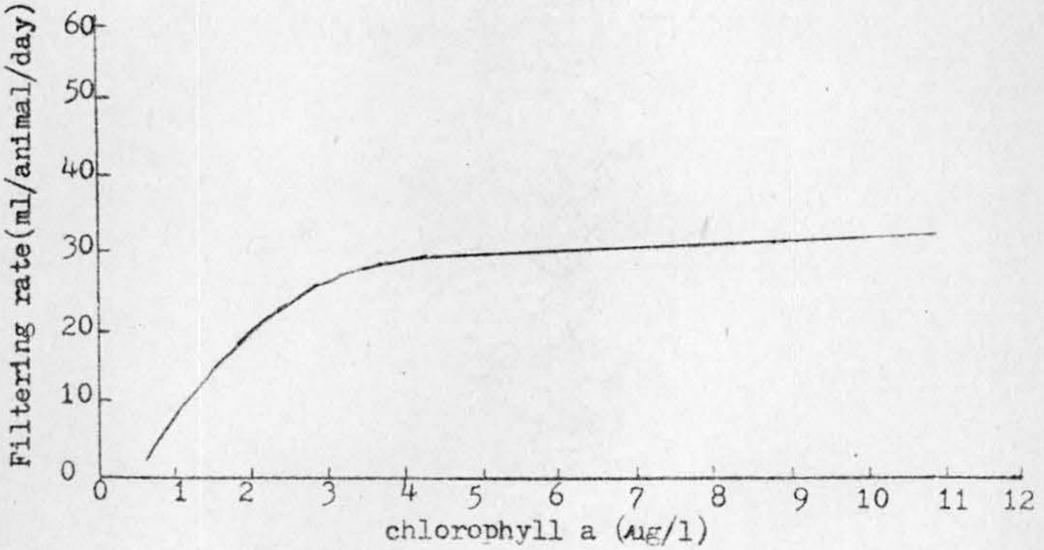

Fig. 5. Filtering rate of late stage Calanus, in ml/animal/day, plotted against chlorophyll a concentration of the water in the control bottles, in ug/l. (After Adams and Steele, 1966).

(see Fig. 5). They continue, that "the most unexpected feature of the present results is that below chlorophyll a concentrations of 2.5 µg/liter the filtering rate decreases"(page 27). This agrees with the observation of Parsons et al (1967), who conclude that grazing occurs down to some low prey level, and then ceases.

All of the above experiments are performed by inoculating different vessels with different initial concentrations of food materials and comparing them. The grazing rate of <u>Calanus</u> on monotypic cultures also decreases with time (up to 24 hours), according to Mullin (1963). Hargrave and Geen (1970) find that filtering rates of <u>Acartia tonsa</u> on natural food remain roughly constant up to 24 hours (at 7.0 ± 1 ml/copepod/day),while there is a decline in feeding rate which might be as high as 90 % over 24 hours. The concentrations of food, the different species used in these experiments (both food organisms and feeders) and the difference in size of the animals (<u>Acartia</u> is small,while <u>Calanus</u> is large) might account for these contradictory results.

Whatever the exact relationship, there is a clear 'concentration effect' (Ankaru, 1964), where, in general, feeding rates decrease with a decrease in cell concentration, but filtering rates become higher with fewer cells. And since the concentrations of food organisms do exert an influence, densities similar to those in the natural environment should be approximated in laboratory tests.

IV. DISCUSSION & CONCLUSIONS

Although certain investigators (Beklemishev, 1957) define grazing as a process occuring at different levels of the food chain (both phytoplankton and zooplankton are 'grazed down'), in this paper grazing refers only to herbivorous feeding. This causes immediate practical problems, since it has been shown that probably no type of organism is a 'pure' herbivore at all times. The entangling of the first steps of the food chain is very important, however, since the producers supply the other organisms with food through the herbivores. In a fishery-study, for instance, the available food materials ultimately depend on the production by phytoplankton and the extent of grazing. In his review, Fraser (1961) lists the possible effects of plankton on fisheries (inhibitory and promoting growth factors; direct food supplies; parasites; food for larval fish, etc.). More directly related to humans: it has been proposed (Gibor, 1956) to harvest phytoplankton for human consumption through grazing methods.

In order to assess the importance of grazing in the oceanic environment, the relationships between phytoplankton and zooplankton have been investigated. A fair amount of detailed information is available about different aspects of this relation. It is known that herbivorous zooplanktonic organisms feed in different ways and in different rates, depending on the morphology of the organisms involved and on their environment.

To measure this feeding, several methods have been used to estimate the extent of grazing; none of these have been applied to a complete natural setting, which raises many doubts about their validity. The traditional filtering rate, as the most often used measure, supplies only secondary information about feeding (the amount of water passed through a filter). Our primary goal has to be to measure the amount of food taken in, which can be obtained either indirectly by using filtering rates (with an additional introduction of possible error) or directly through the use of feeding rates.

Mathematical models, trying to incorporate all factors operating within the process of oceanic productivity, have been set up without enough experimental data to fully substantiate the theories that are proposed. In relation to grazing, we find that assumptions are made which make most models inaccurate. It also should be noticed, that these models apply only to specific regions, whereas a generalized model has not been put forward because different geographic areas operate under various abiotic and biotic factors.

In general, it can be said that a lot of information is available, but that missing links are present everywhere. Only after these are found will it be possible to set up realistic models. In Beklemishev's words (1957): the interrelationships of zoo- and phytoplankton are so complex that their causes do not yet lend themselves to complete analysis.

The single most important aspect is probably that of control of populations. In general, phytoplankton densities are controlled by the extent of grazing. Grazers, in turn, are controlled by the amounts and kinds of phytoplankton available. Or, as Margalef (1967) puts it, phytoplankton and grazers are linked in a feedback circuit that checks mutually the population densities. It should not be overlooked, however, that these are only two components of a complicated food web, and that other factors (nutrients, carnivorous feeders) might play important roles.

There are two extreme types of productive cycles: the steady state and the unbalanced one. Both will be used as illustrations of how certain control mechanisms might operate.

The steady state is found more towards the tropics, where seasons become less evident. According to Steemann Nielsen (1958), static conditions seem to prevail in most parts of the open oceans. Margalef (1967) finds that more complicated food webs are found in steady state regions, which means a trend towards 'macrophagy' (= selecting and hunting prey). The algal reproductive rate is always more or less balanced by the grazing rates of the herbivores, so that the standing stock does not change appreciably with time. Expressed in mathematical terms, it means that $\frac{dP}{dt} = 0$, since both R, the reproductive rate, and G, the grazing rate, are zero. It has also been proposed that the low concentration of nutrient reserve in tropical waters prevents any growth in excess of that necessary to replace grazing (Hulburt,1970). This does not necessarily mean that the distribution is even. This patchy nature of the phytoplankton and the grazers can be explained by combining Bainbridge's theory (1953) and Beklemishev's observations (1957): while phytoplankton is primarily subject to surface currents, many planktonic grazers migrate down and are for part of the day carried away by deeper currents in a direction differing from that of the surface waters. Patches of phytoplankton are grazed down in this manner, while fresh growths of phytoplankton will have occurred in neighboring areas with lesser concentrations of planktonic animals.

The unbalanced state is found in more northern regions (or regions of upwelling and coastal regions), where production proceeds with a lag. Cushing (1959b) distinguishes two lag periods between phytoplankton production and grazing activity: firstly, production of herbivores (and hence grazing) cannot start until eggs are produced at the threshold level of algal numbers (at 10^6/liter); secondly, it takes approximately three weeks for the development up till the copepodite stage. The consequences of this delay are the algal outburst, the superfluous feeding and, as a consequence, the decline of nutrients (see Fig. 6). The single most important physical factor is the lack of sufficient sunlight away from the equator. It has been more or less assumed for a long time that nutrients do not limit phytoplankton densities. Theoretical calculations of the maximum size of nutrient-depleted zones about the phytoplankton cells by Hulburt (1970) show that overlapping of these zones cannot occur at cell densities less than 3×10^8/liter. And since densities in the open and coastal ocean waters rarely exceed 10^6 cells/liter, the nutrient supply is not a determinant factor in the control of phytoplankton

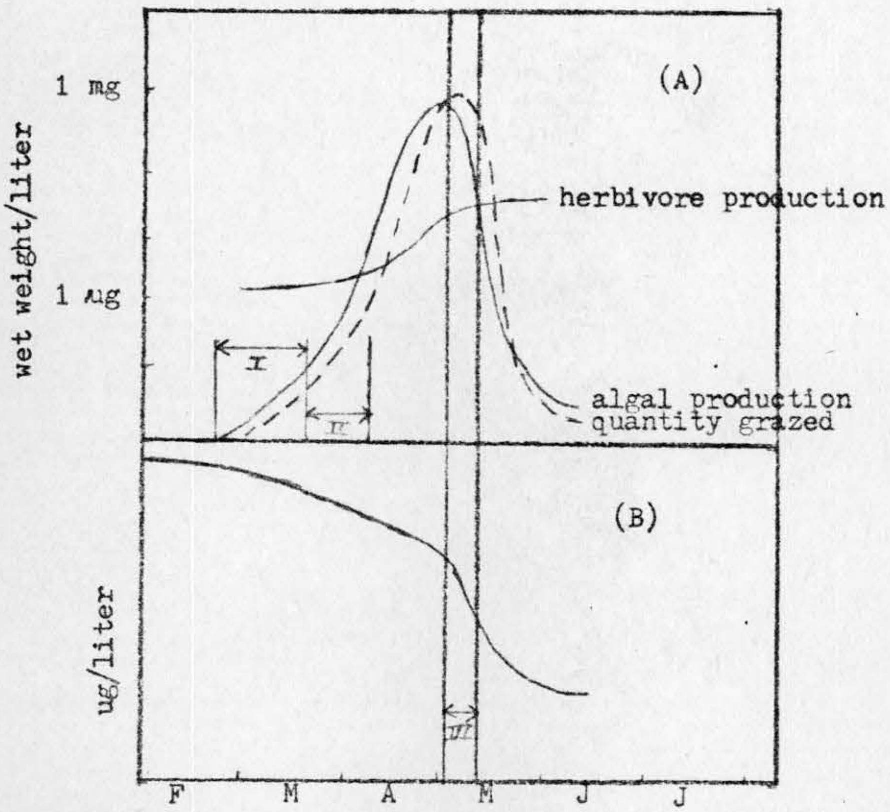

Fig.6. Algal production and nutrient loss.
(A) Weight of algae produced, algae eaten and herbivores produced from Febr. to June.
(B) The reduction in the quantity of nutrients from Febr. to June.

(I: first delay period
II: second delay period
III: period of greatest nutrient loss.)

(After Cushing, 1959b).

densities in these regions.

The illustration given above provides us with a general outline of what might happen in the oceans. More detailed information, especially about the physical and nutritive peculiarities of the organisms present and their relationships is needed.

To close with Wood (1967, page 174): "Estimates of oceanic production can only have any pretense of usefulness or accuracy when the biologists can assess the value of each component of the system in the food web. This is a saddening thought for the 'productivity' measurers, but a very reassuring one for the biologist, especially the ecologist."

REFERENCES:

Adams, J.A. and J.H.Steele, 1966. Shipboard experiments on the feeding of Calanus finmarchicus (Gunnerus).
in: Some contemporary Studies in Marine Science, pages 19 - 36. H.Barnes, Ed. George Allen and Unwin Ltd., London.

Ankaru, M., 1964. Some technical problems encountered in Quantitative Studies of Grazing and Predation by Marine Planktonic Copepods.
J.Ocean.Soc.Japan 20, 221 - 231.

Bainbridge, R., 1953. Studies on the interrelationships of zooplankton and phytoplankton.
J.Mar.biol.Assoc.U.K. 32, 385 - 447.

Beklemishev, K.V., 1957. The spatial interrelationships of marine zoo- and phytoplankton.
Trans.Inst.Okeanol. 20, 206 - 226.
Engl.Translation: Marine Biology, 1959, B.N.Nikitin, Ed.

----------------, 1962. Superfluous feeding of marine herbivorous zooplankton.
Rapp.Cons.Perm.int.Explor.Mer. 153, 108 - 113.

Clarke, G.L., 1939. The relation between diatoms and copepods as a factor in the productivity of the sea.
Quart.Rew.Biol. 14, 60 - 64.

Conover, R.J., 1960. The feeding behaviour and respiration of some marine planktonic Crustacea.
Biol.Bull. 119, 399 - 415.

------------, 1966a. Factors affecting the assimilation of organic matter by zooplankton and the question of superfluous feeding.
Limnol.Oceanogr. 11, 346 - 354.

------------, 1966b. Feeding on large particles by Calanus hyperboreus (Kröyer).
in: Some contemporary Studies in Marine Science, pages 187 - 194. H.Barnes,Ed. George Allen and Unwin Ltd.,London.

------------, 1968. Zooplankton - Life in a Nutritionally Dilute Environment.
Am.Zoologist 8, 107 - 118.

Corner,E.D.S., 1961. On the Nutrition and Metabolism of zooplankton. I. Preliminary observations on the feeding of the marine copepod, Calanus helgolandicus (Claus).
J.Mar.Biol.Assoc.U.K. 41, 5 - 16.

Corner,E.D.S., C.B.Cowey and S.M.Marshall, 1967. On the Nutrition and Metabolism of zooplankton. V. Feeding efficiency of Calanus finmarchicus.
J.Mar.Biol.Assoc.U.K. 47, 259 - 270.

Cowey,C.B. and E.D.S.Corner, 1963. On the Nutrtion and Metabolism of zooplankton. II. The relationship between the marine copepod Calanus helgolandicus and particulate material in Plymouth sea water, in terms of amino acid composition.
J.Mar.Bio.Assoc.U.K. 43, 495 - 451.

Cushing,D.H., 1958. The effect of Grazing in reducing primary production: a review.
Rapp.Cons.Perm.int.Explor.Mer. 144, 149 - 154.

-----------, 1959a. On the Nature of Production in the sea.
Fish.Invest.,London (Ser.2) 22(6), 1 - 40.

-----------, 1959b. The seasonal variation in oceanic production as a problem in population dynamics.
J.Conseil 24, 455 - 464.

-----------, 1962. The work of Grazing in the sea.
in: Grazing in Terrestrial and Marine environments, pages 207 - 225. D.J.Crisp,Ed. Oxford.

------------, 1968. Grazing by herbivorous copepods in the sea. J.Conseil 32, 70 - 82.

Cushing,D.H. and T.Vucetic, 1963. Studies on a Calanus patch. III. The quantity of food eaten by Calanus finmarchicus. J.Mar.Biol.Assoc.U.K. 43, 349 - 371.

Fleming,R.H., 1939. The control of diatom populations by grazing. J.Conseil 14, 210 - 227.

Fraser,J.H., 1961. The Oceanic and Bathypelagic Plankton of the North-East Atlantic and its possible significance to Fisheries. Marine Research (Dept. of Agr. & Fish. for Scotland) 1961, No 4, 1 - 30.

Fuller,J.L., 1937. Feeding rate of Calanus finmarchicus in relation to environmental conditions. Biol.Bull. 72, 233 - 246.

Gauld,D.T., 1951. The grazing rate of planktonic copepods. J.Mar.Biol.Assoc.U.K. 29, 695 - 706.

----------, 1962. Feeding in planktonic copepods. in: Grazing in Terrestrial and Marine environments, pages 239 - 245. D.J.Crisp,Ed. Oxford.

----------, 1966. The swimming and feeding of planktonic copepods. in: Some contemporary Studies in Marine Science. pages 313 - 334. H.Barnes,Ed. George Allen and Unwin Ltd.,London.

Gibor,A.,1956. Some ecological relationships between phyto- and zooplankton. Biol.Bull. 111, 230 - 234.

Hargrave,B.T. and G.H.Geen, 1970. Effects of Copepod Grazing on Two Natural Phytoplankton Populations. J.Fish.Res.Bd.,Canada. 27, 1395 - 1403.

Harris,J.G.K., 1968. A mathematical model describing the possible behaviour of a copepod feeding continuously in a

relatively dense randomly distributed population of algal cells.
J.Conseil 32, 83 - 92.

Harvey,H.W., L.H.N.Cooper, M.V.Lebour and F.S.Russell, 1935. Plankton production and its control.
J.Mar.Biol.Assoc.U.K. 20, 407 - 442.

Harvey,H.W., 1937. Note on selective feeding by Calanus.
J.Mar.Biol.Assoc.U.K. 22, 97 - 100.

Hulburt,E.M.,1970. Competition for nutrients by marine phytoplankton in oceanic, coastal and estuarine regions.
Ecology 51, 475 - 484.

Jørgensen,C.B., 1962. The food of Filter Feeding Organisms.
Rapp.Cons.Perm.int.Explor.Mer. 153, 99 - 106.

--------------, 1966. Biology of suspension feeding.
Pergamon, Oxford, 338 pages.

Margalef,R., 1967. The food web in the pelagic environment.
Helgoländer wiss.Meereunter. 15, 548 - 559.

Marshall,S.M. and A.P.Orr, 1955. The biology of a marine copepod. Calanus finmarchicus (Gunnerus).
Oliver and Boyd, 188 pages.

-------------------------, 1962a. Food and Feeding in copepods.
Rapp.Cons.Perm.int.Explor.Mer. 153, 92 - 98.

-------------------------, 1962b. Grazing by copepods in the sea.
in: Grazing in Terrestrial and Marine environments, pages 227 - 238. D.J.Crisp,Ed. Oxford.

Mullin,M.M., 1963. Some factors affecting the feeding of marine copepods of the genus Calanus.
Limnol.Oceanog. 8, 239 - 250.

-----------, 1966, Selective feeding by calanoid copepods from the Indian Ocean.
in: Some contemporary Studies in Marine Science, pages 545 - 554. H.Barnes,Ed. George Allen and Unwin Ltd., London.

Paffenhöfer,G.A. and J.D.H.Strickland, 1970. A note on the feeding of Calanus helgolandicus on detritus. Marine Biology 5, 97 - 99.

Parsons,T.R., R.J.LeBrasseur and J.D.Fulton, 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J.Ocean.Soc Japan 23, 10 - 17.

Raymont,J.E.G.,1963. Plankton and Productivity in the Oceans. MacMillan, New York, 660 pages.

Riley,G.A., H.Stommel and D.F.Bumpus, 1949. Quantitative ecology of the plankton of the western North Atlantic. Bull.Bingham Ocean.Collection 12(3), 169 pages.

Steemann Nielsen,E., 1958. The balance between phytoplankton and zooplankton in the sea. J.Conseil 23, 178 - 198.

Wickstead,J.H., 1962. Food and feeding in pelagic copepods. Proc.zool.Soc.Lond. 139, 545 - 555.

Wood,E.J.F., 1967. Microbiology of Oceans and Estuaries. Elsevier Publ.Co.,Amsterdam, 319 pages.