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THE FILTER-FEEDING OF *ARTEMIA*

I. IN PURE CULTURES OF PLANT CELLS

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INTRODUCTION

Although Cannon (1928) would distinguish between 'true' filtering and straining, a filter-feeding animal is generally considered to be one equipped with means of removing particles in suspension from its surrounding environment, in which manner it obtains most or all of its food. The rate at which water passes through its food-catching apparatus has been called the 'filtration rate' (Gauld, 1951), and the rate of consumption of particles thus caught is called the 'ingestion rate'.

Until the work of Ryther (1954) on *Daphnia magna* it had long been assumed that the filter-feeding of zooplankton organisms was quite automatic, in the sense that a given animal would clear all the food particles from a definite volume of water per unit of time irrespective of the concentration of food particles in the water. Statements to this effect are to be found in Lucas (1936), Fuller (1937), Fleming (1939), Harvey (1942) and Riley (1946). Gauld (1951) in extensive experiments found this principle to hold in the copepods *Calanus*, *Centropages* and *Temora* feeding on concentrations of *Chlamydamonas* ranging from 5 to 100 cells/mm.^{3}. Ryther (1954), however, found that with increasing concentrations of *Chlorella* there was a marked reduction in filtration rate, as also did Marshall & Orr (1955) using *Calanus* feeding on various food cells at three different concentrations. Conover (1956) using *Acartia* feeding on *Skeletonema*, and Bourne (1959) using *Daphnia magna*, reported a decrease at the highest concentrations used. Richman (1958) using *Daphnia pulex* feeding on *Chlorella* at concentrations of up to 100/mm.^{3} found no variations in the filtration rate; but using *Daphnia magna* feeding on yeast cells Rigler (1961) observed this species to have a maximum rate of cell ingestion.

The feeding mechanism of *Artemia* itself has not been extensively studied except in larval forms (Gauld, 1959), though a close relative, *Chirocephalus diaphanus* has been the subject of much detailed work by Cannon (1928, 1933) and Lowndes (1933). The mouthparts of *Artemia* have been figured by Cannon & Leak (1933).

MATERIALS AND METHODS

In all the experiments to be described filtered and sterilized Plymouth 'Outside' sea water was used. Dried eggs of *Artemia salina* (L.) were obtained through the General Biological Supply House of Chicago, from the Great Salt Lake, Utah. Three food cells, *Phaeodactylum tricornutum* Bohlin, *Dunaliella tertiolecta* Butcher and *Chlorella stigmatophora* Butcher, were obtained through the kindness of Dr Mary Parke of Plymouth Marine Laboratory.

A stock culture of *Artemia* was reared on *Phaeodactylum* at 16 ± 2° C. in an aquarium room. All the experiments were performed at 20 ± 1° C. in a dark cupboard in the laboratory. Filtration and ingestion rates, as ml. of medium swept clear, and number of food cells ingested per animal per hour were calculated from the equation of Gauld (1951) by counting the number of cells in the medium before and after experiments. Counting was performed by taking the mean of 10 fields of a Sedgewick Rafter chamber, and had an accuracy of ± 10–15% at 95% confidence level (see Reeve (1962) for details of computation of limits). Control experiments in which no animals were present were carried out to make certain that the concentration of food cells remained constant, being neither increased by reproduction nor decreased by settling on the bottom of the vessel.

The experimental work fell into two sections. The first consisted of a series of 6 experiments (A–F), feeding *Phaeodactylum* in different concentrations to *Artemia* of varying ages (0·5, 1·0, 2·0, 5·0, 7·5 and 10·0 mm. approximate lengths).

In feeding experiments, in which the concentration of food cells varied over two or more orders of magnitude, it was found that a ratio of the volume of medium (V) to the number of animals (N), with which a measurable decrease in cell concentration could be detected at the lowest concentrations, did not show detectable decrease at the highest concentrations. The ratio V/N had to be much lower in the latter case. To this end N was kept constant and V was progressively decreased with higher concentrations. Even so, cell concentrations higher than 2000 cells/mm.^{3} could not be used without reducing V so drastically that this factor of itself would affect the experiment by depressing feeding activity (Marshall & Orr, 1955).

The value for V was never reduced below 50 or raised above 1000 ml., and in order to produce a significant fall in cell concentration during experiments N had to be as high as 200 in series A, falling to 6 in series F. The lower range of concentration was set mainly by the difficulty of rapid precise estimation of low-density cultures and was about 10 cells/mm.^{3}. A set of 8 concentrations was used for each series of experiments, namely 10, 20, 50, 100, 200, 500, 1000 and 2000 cells/mm.^{3}. Each set of 8 experiments for a given age of animal lasted about 24 hr. and was repeated the following day using the same animals. Further repetition would not have increased the accuracy, because feeding rates were also increasing rapidly, especially at the ages when the animals were growing rapidly.

After the age at which sexual differences became apparent, males and females were maintained in equal numbers. The animals were allowed several hours to adjust to the experimental temperature. All food-cell cultures were used only in their exponential growth phase, but to avoid possible effects of substances which might be present in the water in which the plant cells were cultured, all cultures were centrifuged and re-suspended in fresh sea water before use.

The second experimental section was similar in design and made use of *Dunaliella* and *Chlorella* but was conducted at only one age, which corresponded to series F of the first section. The range of cell concentration was changed because preliminary tests had shown the need for lower concentrations of the larger and more easily counted *Dunaliella* (2-500 cells/mm.^{3}) and for higher concentrations of the smaller *Chlorella* (15–3000 cells/mm.^{3}).

Supplementing this work, the mouthparts, food-groove and thoracic appendages

were observed with a microscope, the animal being fixed ventral side uppermost in a dish of water by trapping the tip of its abdomen underneath a wide rubber band stretched around a flat disk of plasticine. The animal quickly regained its metachronal limb motions as if moving freely and would maintain them for many hours. The methods used by Cannon (1928) and Lowndes (1933) for restraining *Chirocephalus*, the former by embedding the abdomen in plasticine and the latter by using rubber solution to affix a fine wire to the head, proved of little aid in securing the considerably smaller *Artemia*.

RESULTS

Graphs of the variation of filtration and ingestion rates with cell concentration have been plotted (Figs. 1 A–F) for each series, the plotted points being the average of the duplicates. Figures 2 A and B represent the variation with cell concentration of filtration and ingestion rates respectively of *Artemia* feeding on *Chlorella* and *Dunaliella*. Results for *Phaeodactylum* series F have been superimposed on these figures for comparison. From Figs. 1 A–F certain points emerge:

(1) Filtration rate is dependent on cell concentration. A maximum filtration rate is maintained in the lowest concentrations and then begins to fall rapidly as the concentration increases.

(2) Ingestion rate is not directly proportional to cell concentration over the whole range. A maximum ingestion rate is attained in the higher concentrations.

An attempt has been made to define quantitatively the cell concentrations at which filtration rate begins to fall (P) and at which ingestion rate levels off (Q). For simplicity it has been arbitrarily assumed that each curve may be reduced to two straight lines, a horizontal one of maximum filtration or ingestion rate, and a sloping line of decreasing filtration rate or increasing ingestion rate. These lines have been drawn in by eye and their respective intersections taken as points P and Q. Though in some cases these lines fit the data very well, a more accurate representation would be afforded by drawing a single line through the points, which though straight at the higher and lower cell concentrations would be curved in the regions of P and Q. However, by the former method, definite values of concentration could be assigned to P and Q, and these are tabulated in Table 1 for series A–F.

Table 1. *Approximate concentration of cells (per mm.*^{3}*) at which filtration rate begins to fall from maximum* (P) *and at which ingestion rate levels off* (Q) *for series A–F*

Series	P	Q
A	160	220
B	90	180
C	100	210
D	55	120
E	70	145
F	15	160

These figures suggest, though not conclusively, that as the animal becomes older the range of cell concentrations over which the maximum filtration rate is maintained, and before maximum ingestion rate is reached, becomes progressively reduced. They were subjected to a linear regression analysis achieved by regressing points P and Q on age (as a logarithm of length), from which it was possible to say that the trend of P

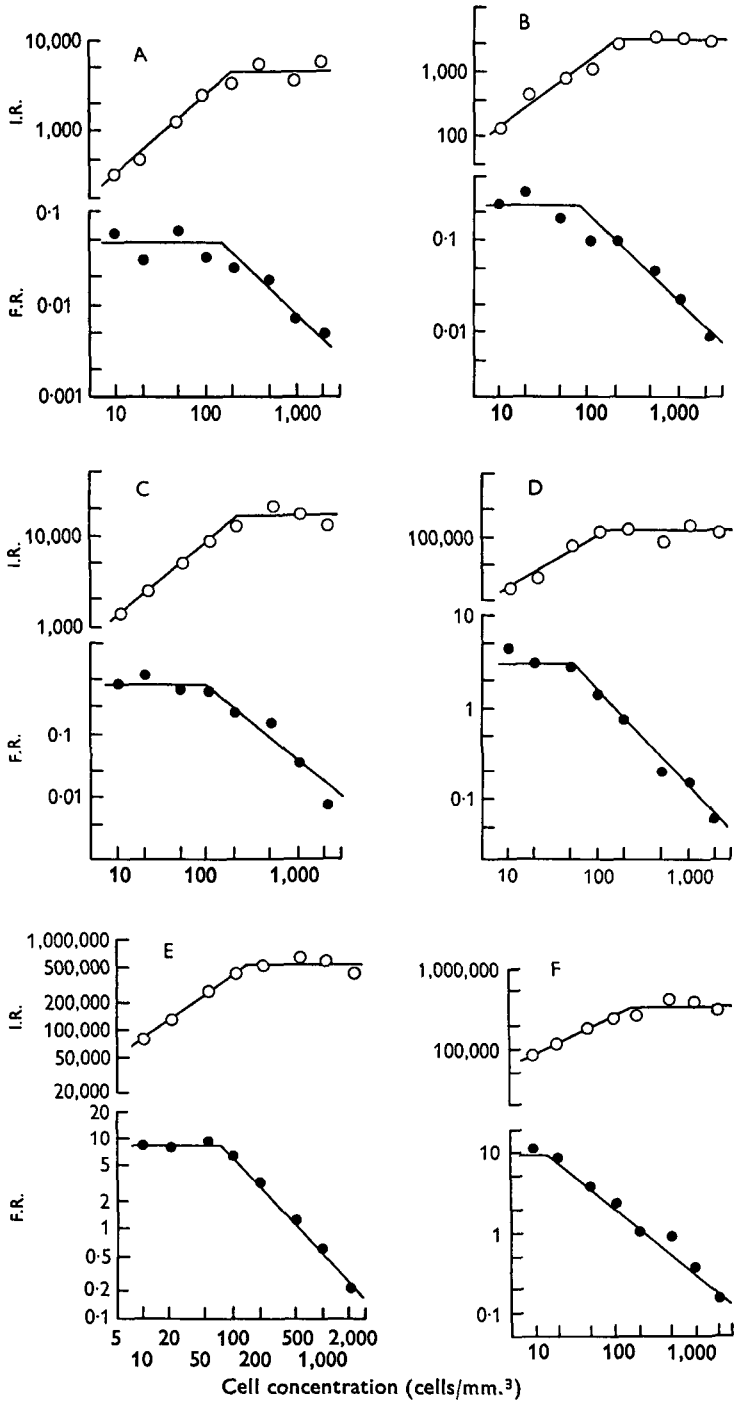

Fig. 1. Filtration and ingestion rates (F.R. and I.R. respectively) with increasing cell concentration, for *Artemia* at six different ages (increasing from A–F) feeding on *Phaeodactylum* both axes logarithmic.

and Q to decrease with age was real, though in the case of Q just fell short of 95% confidence.

Further support for the concepts of maximum filtration and ingestion rates is to be found by comparing the effects of three different food cells on animals of the same age (Figs. 2A, B), and additional information may also be extracted:

(1) The maximum filtration rate is a function of the size of the animal, and independent of the food cell.

(2) The maximum ingestion rate is dependent on the food cell for a given size of animal.

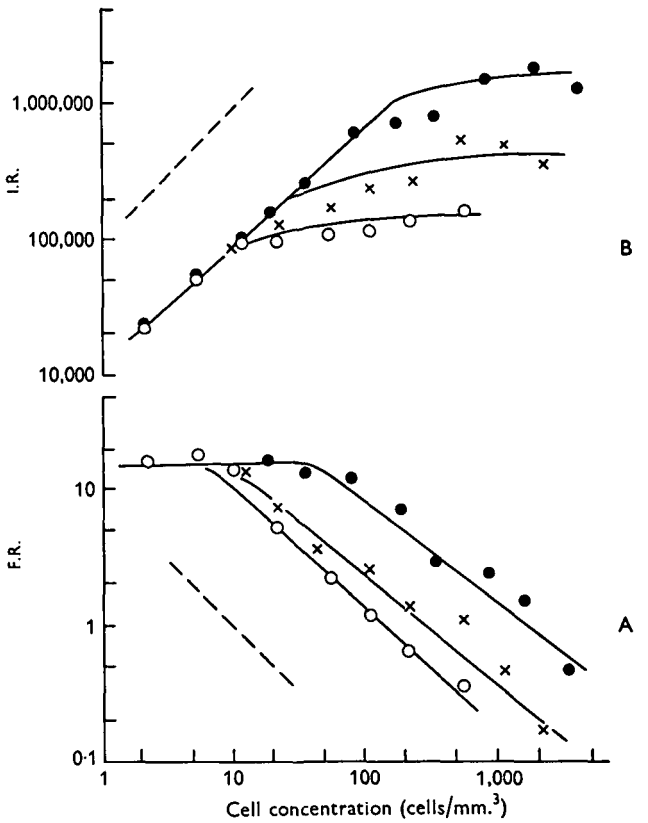

Fig. 2. Filtration and ingestion rates (F.R. and I.R. in Figs. 2A and B respectively) with increasing cell concentration, both axes logarithmic. Broken line represents the theoretical relationship. ○, *Dunaliella*; × *Phaeodactylum*; ●, *Chlorella*.

If the shape of the filtration and ingestion rate curves may be explained solely by two limiting factors, (*a*) a maximum rate at which food can be gathered and (*b*) a maximum rate at which food can be consumed, then when the cell concentration is such that (*a*) is reached the filtration rate should decrease by the same factor by which the cell concentration increases. Similarly up to the cell concentration at which (*b*) is reached the number of cells ingested should increase by the same factor as that by which the cell concentration increases. These theoretical slopes have been included (broken lines) in Figs. 2A and B, and can be seen to correspond closely with the observed slopes.

The maximum ingestion rate estimated roughly from Fig. 2B has been related to the volume of the individual food cells in Table 2. These volumes were derived by measuring the cell diameters of *Dunaliella* and *Chlorella*, and the width of disc and length of spines of *Phaeodactylum*. The means of thirty observations were 8·7, 3·9, 4·0 and 8·0 μ respectively. The assumptions that *Dunaliella* and *Chlorella* were spheres, and that *Phaeodactylum* was composed of three cones were approximate and resulted in volume estimations of unknown reliability. However, the close agreement between the maximum total volumes of each type of food cell ingested by an animal of a given size suggests that this factor must be important in the phenomena of feeding.

Table 2. *Volume of food ingested per hour by* Artemia *feeding on three different food organisms, calculated from maximum ingestion rate and cell volume*

Food cell	Maximum ingestion rate	Volume of cell (μ^3)	Volume ingested ($\mu^3 \times 10^5$)
Chlorella	1,500,000	31	465
Phaeodactylum	400,000	113	452
Dunaliella	150,000	345	518

Visual observations on the feeding mechanism using carmine particles confirmed Cannon's (1928) concept of the feeding stream in *Chirocephalus*. The long setae of the basal endites of the trunk limbs trapped particles which were then forwardly directed along the food groove towards the mouth. They first reached the tip of the labrum which is large and flexible and normally re-curved backwards almost to the level of the first trunk limb. Here they disappeared from view to enter what is in effect a tunnel leading to the mouth. The sides of this tunnel are formed by the paired lateral paragnaths which are larger posteriorly, and by the mandibles anteriorly, and the roof is formed by the labrum. By gently moving the latter the function of the paired maxillules in pushing the food forward through the tunnel and that of the mandibles of packing it into the mouth could be made out.

In a suspension of *Phaeodactylum* gradually increased to 2000 cells/mm.^{3}, the rate of beating of the thoracic appendages did not alter. On increasing the cell concentration beyond this, small yellowish blobs began to appear, especially in the region of the basal endites, and congested the food groove. The limbs were clearly becoming impeded in their action and also heavier, so that their rate of beating fell and became less regular.

When the cell concentration was raised to about 50–100 cells/mm.^{3} an accumulation of cells immediately behind the labrum was evident. This began as a speck and grew. Sooner or later, though at no clearly defined size, this ball of cells became caught in the setae of the first trunk limbs as the latter moved forward to begin their power stroke, the setae tearing the cells apart and scattering them into the surrounding medium on the backward stroke.

If the animal was fed cells at a concentration high enough to produce this effect, after being in water entirely free from particulate matter, it was found that the time required before the accumulation of cells became evident varied directly with the cell concentration.

DISCUSSION

On the basis of an experiment in which the yeast *Saccharomyces cerevisiae* was fed to *Daphnia magna*, where he found a maximum ingestion rate above a certain cell concentration, Rigler (1961) concluded that in cell concentrations below this the amount of food ingested by the animals was limited by their filtering ability, and above this by 'some other factor'.

That some mechanism is possessed by the animal for regulating the volume of its food intake is quite a reasonable assumption when it is considered that if all the cells were removed from a given volume of suspension in a given time, when the animal is feeding in concentrations of 5 then 5000 cells/mm.^{3}, it would consume 1000 times as many cells in the latter concentration. The food would travel through the gut 1000 times faster and the animal could possibly starve, having no time to digest it.

That older animals are able to satisfy their needs in suspensions of lower concentration might be correlated with the decrease in relative oxygen consumption (O_2 consumed/mg. dry wt.) throughout life (Eliassen, 1952), and with the increase in filtering apparatus, which consists of 2 appendages (antennae) in the nauplius and 22 thoracic limbs in the adult.

The failure to observe similar effects in copepods may be due to their well known habit of discontinuous feeding (Gauld, 1951). They may filter at a constant rate until their guts are filled, then cease feeding activity altogether until digestion and egestion have emptied their guts to some extent, though Marshall & Orr (1955) reported lower feeding rates in high cell concentrations. However, independent experiments carried out on copepods by Anraku (1962) and by Mullin (1962) at Wood's Hole Oceanographic Institution have both shown an inverse relationship between filtration rate and cell concentration. The former found that the concentration at which the filtration rate fell from its maximum was about 1 cell/mm.^{3}, suggesting that previous experiments may not have been conducted over a wide enough range of concentrations. In the work of the latter there appeared to be an optimum rather than a maximum ingestion rate. According to Ryther (1954) starved *Daphnia* on being fed with *Chlorella* did not show a reduction of filtration rate at concentrations below 200 cells/mm.^{3}, suggesting that the experiments of Richman (1958), who found no such reduction and never exceeded 100 cells/mm.^{3}, were all conducted in this region of maximum filtration rate.

It seems highly probable that the suggestion above, indicating some mechanism for controlling intake of food, is substantially correct since the animal ingested different maximum amounts of the three food cells in such a way that the volume intake was about 0·05 mm.^{3} per hour for an animal of given size at 20° C. irrespective of the food cell (see Table 2). The maximum filtration rate for a given size of animal was effectively the same, lending support to the assertion that this rate is the maximum rate at which the animal is capable of filtering sea water, otherwise it would presumably have stepped up the rate to catch an equal volume of the smaller cells if it had been able to do so. Thus that rate is probably its true automatic filtration rate and a constant figure under defined conditions of animal species, age and surrounding medium.

Similar effects of cell concentration on feeding rates have been reported by Ryther (1954) for *Daphnia* ingesting *Chlorella*, *Navicula* and *Scenedesmus*. His interpretation

of the results was based on his belief that the food cells were liberating substances harmful to the animals, as suggested by the 'Animal Exclusion' theory of Hardy (1936) and the work of Lucas (1938, 1947, 1949) in which the latter developed the theme of non-predatory relationships between groups of organisms, one of which produces external metabolites or ectocrines to affect the other.

Ryther found that animals pre-fed on *Chlorella* showed consistently lower filtration rates in 1 hr. experiments than did starved animals. This he attributed to the inhibiting effect of *Chlorella* on the pre-fed animals, though it might be expected that the starved animals would fill their guts rapidly before reaching a steady rate of ingestion, which had already been attained in the pre-fed animals. Only experiments of much longer duration in which the effect of the initial filling of the gut would be minimized could decide this. He suggested, as an explanation of decreased filtration with increasing cell concentration, that the more cells ingested the greater would be their inhibitory effect on the animal. Recording progressively lowered filtration rates with *Navicula* and *Scenedesmus*, he believed they contained increasing amounts of inhibiting substances per cell. Though the reduction in number of cells filtered was directly proportional to cell size, he discounted this factor in itself because animals allowed to pre-feed on bacteria and detritus behaved as starved animals rather than as *Chlorella*-fed animals; hence the nature and not the amount of food was the controlling factor. In *Artemia* feeding on cell concentrations of 10 and 2000/mm.^{3} the animals appear to have full guts and produce the same number of faecal pellets which do not vary in colour at both concentrations, so that it is impossible to discern by visual observation whether an animal has a full gut. Possibly Ryther's animals, feeding only on what bacteria and detritus they could obtain, had guts which were almost empty. He reports, however (personal communication), that such animals grew very well.

Although Pratt, Oneto & Pratt (1945) have shown *Chlorella vulgaris* to produce a substance which inhibits the growth of bacteria, this has not been demonstrated to the author's knowledge for either of the two other cells; and, as pointed out by Bourne (1959), in none of Ryther's experiments has the ingestion rate for a given cell in increasing concentrations of healthy plant cultures actually decreased. It is not suggested that no plant cells affect animals in this way, though Bainbridge (1953) found such exclusion the exception rather than the rule, and Marshall & Orr (1955) observed only *Gymnodinium* out of 30 food organisms tested to have any effects on *Calanus*.

It has been shown that *Artemia* is not an automatic filter feeder. However, except in food concentrations higher than any experimental levels, when the thoracic limbs become clogged with food, the rate of beating of these appendages remained constant, i.e. the appendages did not simply slow down their food-collecting effort. This suggests that they filtered a constant amount of water, though alternatively they might (*a*) increase the distance between the filtering setae (cf. Conover (1956) on the action of the second maxillae of *Acartia*), or (*b*) alter the axis of movement of the limbs in such a way as to decrease filtering (cf. Lowndes (1933) on the method of reducing velocity in *Chirocephalus*). However, that the limbs actually filter at a constant rate and collect progressively more cells as cell concentration increases is clear from the observation that the time for a mucus-entrapped ball of cells to accumulate at the front of the food groove decreased as cell concentration increased. Filtration rate defined as volume swept clear is a constant value and the filtration process itself is truly automatic.

It is the apparent volume swept clear which is being measured by recording the difference in particle concentration before and after a feeding experiment, or the volume permanently swept clear of particles (which are subsequently ingested). The real rate at which an animal can clear the surrounding medium is only measured when all the cells filtered off are consumed and none are returned to the medium, i.e. the maximum filtration rate. When a ball of cells accumulates at the tip of the labrum it is because the cells cannot enter the mouth as fast as they are being collected. This ball becomes periodically dispersed by the action of the first thoracic limbs and thus excess filtered material is disposed of. Such a mechanism has been reported in *Calanus* by Esterly (1916).

Recently Beklemishev (1961) has developed the concept of superfluous feeding in the zooplankton in which he believes that at the time of phytoplankton 'blooms', it 'destroys its food without use for itself'. He based this argument on work (Beklemishev, 1954) showing that the rate of passage of food through the gut increases progressively as the food available increases, whereas increase in growth rate (Raymont & Gross, 1942), and egg production (Marshall & Orr, 1952) does so only up to 15–40 cells/mm.^{3}; thus above this level food must be wasted. He fails to mention that these latter authors found a corresponding levelling-off of the rate of faecal pellet production (Marshall & Orr, 1955). In *Artemia* the ingestion rate undoubtedly does cease to increase above a certain level. From growth-rate experiments reported elsewhere (Reeve, 1962) it appears that in this animal the maximum ingestion rate corresponds to the maximum rate of growth and has been evolved in the animal as a resultant of two opposing forces. These are (i) that the more food digested per unit time the faster will be the growth rate, but (ii) as the food passes through the gut faster the less opportunity is there for thorough digestion. Thus though the animal may be working at a lower digestion efficiency it is not feeding superfluously if it is producing more of its own tissue per unit time. At that point where further increase in food no longer results in faster growth the animal has apparently been able to stabilize its maximum ingestion capacity. The connexion between maximum ingestion and growth rates may be the 'other factor' of Rigler (1961).

Although this work has been mainly concerned with the effect of food supply on feeding rates for different ages and for different food cells, it does provide some data on the rate of increase of feeding with age. The information must not be regarded as a detailed study in this respect since the experiments were not designed to demonstrate it. Feeding rates have been measured daily on a population of animals at a constant food-cell concentration (Reeve, 1962) and it emerged that there was a considerable day-to-day variation superimposed on the progressive increase consequent upon increase in size. In adults this variation was shown to be intimately connected with the breeding cycle. Using animals of different ages, as in the present work, it was not always easy to maintain comparable conditions of number of animals and vessel volume in each experiment, under which the animals were neither using up the food too fast nor yet removing insufficient for a difference in cell count to be significant. The average animal of series A, for example, though smaller and filtering less water than that of series B, ingested slightly more cells because the conditions were such that the cell concentrations were not reduced so fast.

Because these experiments show how cell concentration can affect feeding rates,

they imply that the method of measuring them which depends on a difference between initial and final concentrations is not entirely satisfactory where an absolute measure of feeding rate at a given cell concentration is required. The use of concentration difference as an indication of how much food a copepod can ingest in the sea (Fuller & Clarke, 1936) is a case in point; for unless the animal was already filtering at its maximum rate, as it progressively reduced the cell concentration in the experimental vessel it would filter faster. This difficulty might be avoided by using food cultures labelled with radio-active carbon or phosphorus and measuring the accumulation of these in the animal.

SUMMARY

1. The rates of filtration and of ingestion have been studied in *Artemia* of different ages feeding on pure cultures of plant cells of three different species, the concentrations of cells being varied over two orders of magnitude.

2. The animal is capable of regulating its rate of feeding in such a way that, as the cell concentration increases, the filtration rate maintains a constant maximum value while the ingestion rate increases. When the concentration reaches a value at which a constant maximum ingestion rate is attained, the filtration rate falls off.

3. In older animals the maximum ingestion rate is reached at a lower cell concentration than in younger animals.

4. The maximum filtration rate is independent of cell size. The maximum ingestion rate is inversely related to cell size, the total volume of cells ingested being the same for three species of plant cells.

5. The means whereby the animal maintains a maximum rate of total volume of cells ingested per unit time, irrespective of their size, has been investigated and is discussed.

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REFERENCES

ANRAKU, M. (1962). Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzard's Bay and Cape Cod Bay, Massachusetts. Unpublished manuscript, Wood's Hole Oceanographic Institution.

BAINBRIDGE, R. (1953). Studies on the interrelationships of zooplankton phytoplankton. *J. Mar. Biol. Ass. U.K.* **32**, 385–447.

BEKLEMISHEV, C. W. (1954). The feeding of some common plankton copepods in Far-Eastern seas. *Zool. J.* **33**, 1210–29.

BEKLEMISHEV, C. W. (1961). Superfluous feeding of marine herbivorous zooplankton. *Zooplankton Production, Symposium, Cons. int. Explor. Mer.* Unpublished paper no. 6.

BOURNE, N. (1959). The determination of carbon transfer from *Chlorella vulgaris* Beyerink to *Daphnia magna* Straus, using radio-active carbon as a tracer. Ph.D. Thesis, University of Toronto.

CANNON, H. G. (1928). On the feeding mechanism of the fairy shrimp *Chirocephalus diaphanus* Prévost. *Trans. Roy. Soc. Edinb.* **55**, 807–22.

CANNON, H. G. (1933). On the feeding mechanism of the *Branchiopoda*. *Phil. Trans.* B, **222**, 267–339.

CANNON, H. G. & LEAK, F. M. C. (1933). On the mouthparts of the *Branchiopoda*. *Phil. Trans.* B, **222**, 340–52.

CONOVER, R. J. (1956). Oceanography of Long Island Sound 1952–54. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham Oceanogr. Coll.* **15**, 156–233.

ELIASSEN, E. (1952). The energy metabolism of *Artemia salina* in relation to body size, seasonal rhythms, and different salinities. *Univ. Bergen Årb. naturv. R.* **11**, 1–18.

ESTERLY, C. O. (1916). On the feeding habits and food of pelagic copepods and the question of nutrition by organic substances in solution in the water. *Univ. Calif. Publ. Zool.* **16**, 171–84.

FLEMING, R. H. (1939). The control of diatom populations by grazing. *J. Cons. int. Explor. Mer.* **14**, 1–20.

FULLER, J. L. (1937). Feeding rate of *Calanus finmarchicus* in relation to environmental conditions. *Biol. Bull., Wood's Hole*, **72**, 233–46.

FULLER, J. L. & CLARKE, G. L. (1936). Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull., Wood's Hole*, **70**, 308–20.

GAULD, D. T. (1951). The grazing rate of planktonic copepods. *J. Mar. Biol. Ass. U.K.* **29**, 695–706.

GAULD, D. T. (1959). Swimming and feeding in crustacean larvae: the nauplius larva. *Proc. Zool. Soc. Lond.* **132**, 31–50.

HARDY, A. C. (1936). The ecological relations between the herring and the plankton, investigated with the plankton indicator. *J. Mar. Biol. Ass. U.K.* **21**, 111–31.

HARVEY, H. W. (1942). Production of life in the sea. *Biol. Rev.* **17**, 221–46.

LOWNDES, A. G. (1933). The feeding mechanism of *Chirocephalus diaphanus* Prévost, the fairy shrimp. *Proc. Zool. Soc. Lond.* B, 1093–118.

LUCAS, C. E. (1936). On certain inter-relations between phytoplankton and zooplankton under experimental conditions. *J. Cons. int. Explor. Mer.* **11**, 343–62.

LUCAS, C. E. (1938). Some aspects of integration in plankton communities. *J. Cons. int. Explor. Mer.* **13**, 309–22.

LUCAS, C. E. (1947). The ecological effects of external metabolites. *Biol. Rev.* **22**, 270–95.

LUCAS, C. E. (1949). External metabolites and ecological adaptation. *Symp. Soc. Exp. Biol.* **3**, 336–56.

MARSHALL, S. M. & ORR, A. P. (1952). On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *J. Mar. Biol. Ass. U.K.* **30**, 527–48.

MARSHALL, S. M. & ORR, A. P. (1955). On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation, and excretion in adult and stage V *Calanus*. *J. Mar. Biol. Ass. U.K.* **34**, 495–529.

MULLIN, M. M. (1962). Some factors affecting the feeding of marine copepods of the genus *Calanus*. Unpublished manuscript, Wood's Hole Oceanographic Institution.

PRATT, R., ONETO, J. F. & PRATT, J. (1945). Studies on *Chlorella vulgaris*. X. Influence of the age of the culture on the accumulation of chlorellin. *Amer. J. Bot.* **32**, 405–8.

RAYMONT, J. E. G. & GROSS, F. (1942). On the feeding and breeding of *Calanus finmarchicus* under laboratory conditions. *Proc. Roy. Soc. Edinb.* B, **61**, 267–87.

REEVE, M. R. (1962). Quantitative aspects of feeding and food conversion in *Artemia salina* (L). Ph.D. Thesis, University of Southampton.

RICHMAN, S. (1958). The transformation of energy by *Daphnia pulex*. *Ecol. Mongr.* **28**, 273–91.

RIGLER, F. H. (1961). The relation between concentration of food and feeding rate of *Daphnia magna* Straus, *Canad. J. Zool.* **39**, 857–68.

RILEY, G. A. (1946). Factors controlling phytoplankton populations on George's Bank. *J. Mar. Res.* **6**, 54–73.

RYTHER, J. H. (1954). Inhibitory effects of phytoplankton upon the feeding of *Daphnia magna* with reference to growth, reproduction and survival. *Ecology*, **35**, 522–33.