

The Ingestion and Digestion of Algae
by *Chloeon dipterum* L.
(Ephemeroptera)

by

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With 7 tables and 2 figures in text

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I. INTRODUCTION

From a comparison of the gut contents of larvae of *C. dipterum* with the flora of two ponds WISSMEYER (1926) concluded that the larvae did not ingest particular algae selectively. He suggested that when algae were relatively more abundant in the gut than in the habitat the larvae had been feeding on local concentrations of these species. IVANOVA (1958) showed that when Ephemeropteran larvae were allowed a choice between compartments containing various species of algae and vascular plant foods, they congregated in those compartments that contained the food material that was ingested most frequently under natural conditions. *C. dipterum* showed a preference for filamentous algae, *Centroptilum luteolum* MULL. and *Baetis* sp. for diatoms, and several species including *Heptagenia sulphurea* MULL. and *Ephemerella ignita* PODA for dead leaves. There was also evidence that among the filamentous algae offered *C. dipterum* selected *Spirogyra*.

The results of a long series of food analyses of the food of larvae of *C. dipterum* collected in the field showed that the larvae did not ingest all the algae available to them in the habitat (BROWN, 1960). Selection was more marked by the smaller larvae and the experiments described below were carried out in order to investigate the relationship between the size of larvae and the size of algae that they were able to ingest.

Several authors have commented on the low proportion of vegetable material that appears to be assimilated by aquatic invertebrates of the total quantity ingested (GATJEN 1926, GAESKAYA 1956, FRYER 1957b); the most detailed study of this phenomenon is by LEVANIDOV (1949). Algal cells have been observed to pass apparently unchanged through the gut of larvae of Ephemeroptera (WISSMEYER 1926, IVANOVA 1958, MOON unpublished data). These observations cast some doubt on the importance of algae as food and the results are given below of experiments with *Chloeon dipterum* which showed that many species of algae are digested with great efficiency.

II. INGESTION

1. Method.

Larvae were starved for 12 hours and those in which the gut was empty were placed in dishes containing a single species of alga after their length, from the front margin of the head capsule to the base of the cerci, had been measured. After 1 hour they were killed in 5 % formalin and the alimentary canal was examined for the presence of algae. The mean width of the filaments, or the dimensions of the cells,

of the algae provided as food were measured. Algae used in the experiments were maintained in pure cultures derived from material obtained from local habitats and from the Botany Department, Cambridge.

2. Results.

The results obtained for the ingestion of algae by *C. dipterum* are given in Table I.

With the exception of coccoid cells that occurred in all larvae, *Hydrodictyon* and *Cladophora*, a direct relationship was found between the frequency with which the algae used in the experiments were ingested and the size of the larvae (Table I.)

TABLE I

The ingestion of algae by C. dipterum.

Key to algae.

- | | |
|---|--------------------------------------|
| i. <i>Spirogyra</i> 1. | vii. <i>Oedogonium cardiacum</i> . |
| ii. <i>Spirogyra</i> 2. | viii. <i>Ulothrix subtilissima</i> . |
| iii. <i>Cladophora crispata</i> (whole). | ix. <i>Oscillatoria</i> sp. |
| iv. <i>Cladophora crispata</i> (chopped). | x. <i>Anabaena</i> sp. |
| v. <i>Hydrodictyon</i> (whole) | xi. <i>Closterium leibleinii</i> . |
| vi. <i>Hydrodictyon</i> (chopped). | xii. Coccoid cells.* |

n. – number of larvae used in experiment.

% – percentage in which alga was present.

* Included in this category were all small round green cells that it was impossible to identify; several genera of Chlorococcales are probably represented.

For those species of algae for which values of 0 and 100 % occurrence were not obtained directly these values were obtained by extrapolation of graphs (Figs. 1 & 2). The largest size of larva in which 0 % occurrence for a particular alga was recorded was referred to as the minimum larval size (MLS) for that alga. Similarly, the larval size in which occurrence was 100 % was referred to as the optimum larval size (OLS) for ingestion of that alga. These sizes are listed below (Table II) and it is evident that algae of small size were ingested at a lower MLS and eaten freely at a correspondingly lower OLS than larger species. *Ulothrix* was ingested by all the sizes of larvae used but the decrease in its frequency of occurrence in larvae of less than 2.5 mm. indicated that it was ingested with more difficulty in the smaller larvae.

Of the blue-green algae, *Oscillatoria* occurred in a high percentage of larvae in the 0.5–2.5 mm size groups, while *Anabaena* was present in only 2 out of a total of 41 that were fed upon it. The width

of the filaments of these algae did not differ greatly and the marked difference in the extent to which they were ingested appeared to be due to some factor other than size.

TABLE II

The minimum (MLS) and optimum (OLS) sizes of larvae of C. dipterum for the ingestion of various species of algae

Species of algae	MLS.	OLS.	Dimensions of algae
<i>Ulothrix subtilissima</i>	less than 0.5 mm.	2.5—3.0 mm.	13 μ .
<i>Spirogyra</i> 1.	0.0—0.5	2.0—2.5	26 – 35
<i>Oedogonium cardiacum</i>	0.5—1.0	1.5—2.0	26 – 116
<i>Closterium leibleinii</i> (dead)	1.5—2.0	4.0—4.5	116 × 33— 206 × 33
<i>Hydrodictyon</i> (chopped)	2.0—2.5	4.0—4.5	39 – 133
<i>Cladophora crispata</i> (whole)	2.0—2.5	5.0—5.5	100 – 115
<i>Closterium leibleinii</i> (fresh)	3.5—4.0	5.5—6.0	116 × 33— 206 × 33
<i>Spirogyra</i> 2.	2.5—3.0	> 6.0	93

The shorter dimension measured in *Closterium* was the perpendicular distance between two imaginary parallel lines passing between the apices of the cell and touching the convex wall of the cell.

The frequency of ingestion of *Hydrodictyon* and *Cladophora* varied greatly and never exceeded 66 %. When the algae were chopped up finely both species were ingested far more readily, the OLS for *Hydrodictyon* being about 4.5 mm, and for *Cladophora* 2.5 mm. The % occurrence of these algae remained low when they were whole even in the largest larvae examined, ie. 6.0—6.5 mm in the case of *Cladophora*, and appeared to vary independently of the size of the larvae (*Hydrodictyon*) or to increase only slightly with larval size (*Cladophora*). In addition to the width of the filament there may be another property of these algae that limits the extent to which they are ingested the effect of which is reduced or destroyed by chopping the algae up.

Cultures of *Closterium leibleinii* contained large numbers of empty cells often in a folded or twisted condition, which it seemed would be ingested more easily than the living cells. Because of this an accurate picture of the extent to which living *Closterium* was ingested could not be obtained by recording the frequency of empty cell walls in the food. The results of feeding experiments in which the numbers

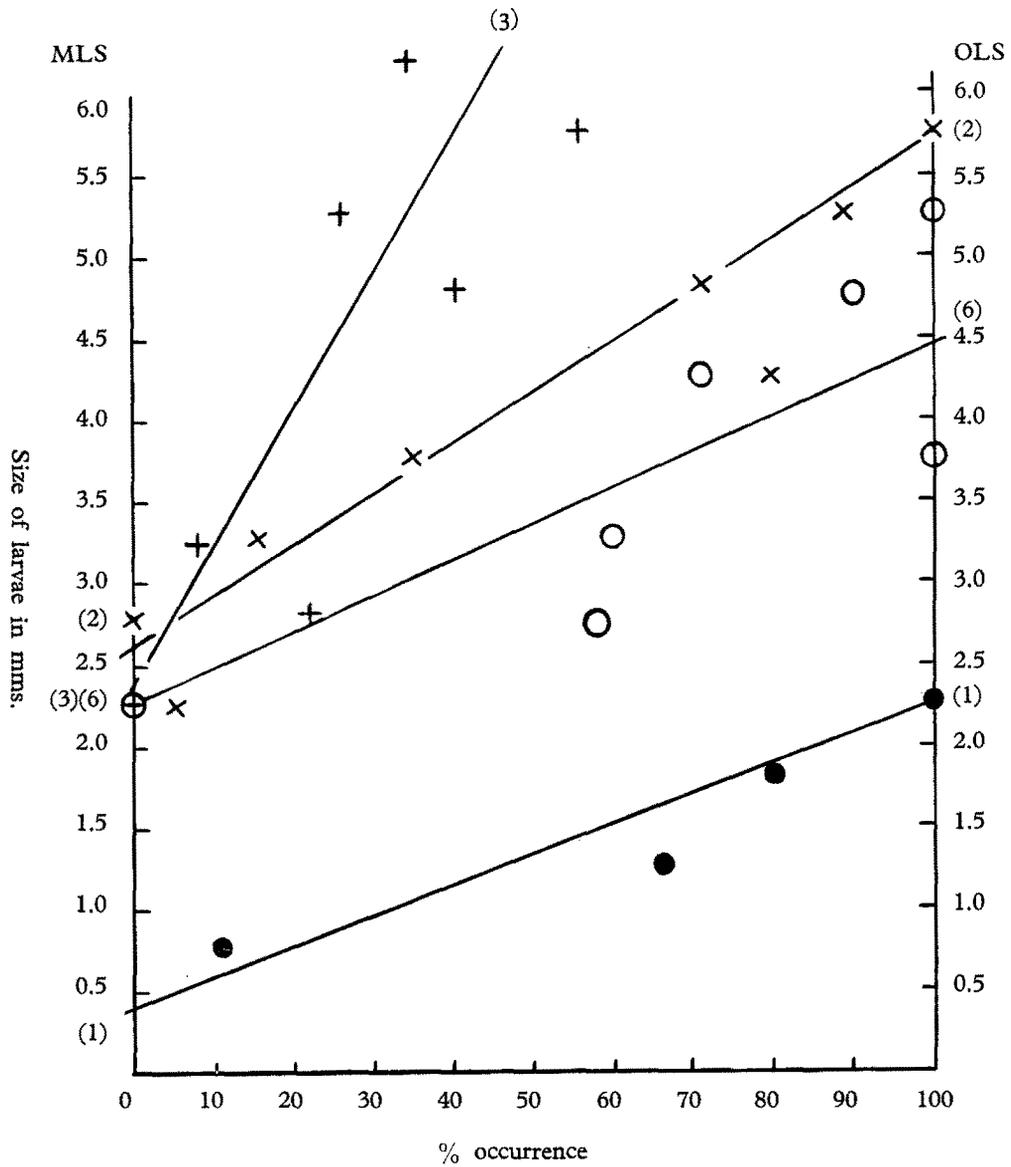


Figure 1. The frequency of ingestion of the algae *Spirogyra* 1. (1), *Spirogyra* 2. (2), *Cladophora crispata* (3), and chopped *Hydrodictyon* (6), by larvae of *C. dipterum* of various sizes. The levels at which the lines intersect the left and righthand ordinates represent the minimum and optimum larval sizes (MLS and OLS, see text) for the ingestion of these algae.

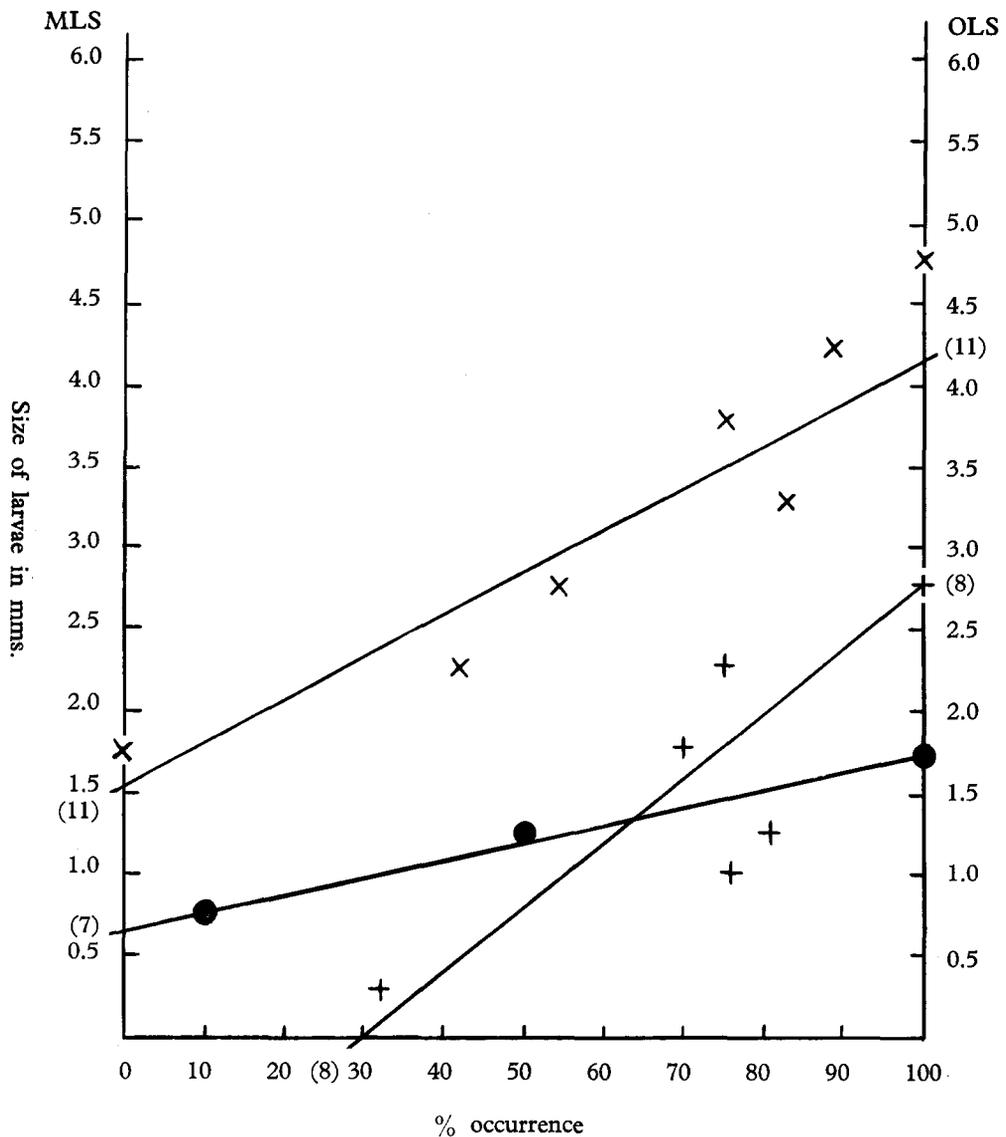


Figure 2. The frequency of ingestion of the algae *Oedogonium cardiacum*(7), *Ulothrix subtilissima* (8), *Closterium leibleinii* (11) by larvae of *C. dipterum* of various sizes. The levels at which the lines intersect the left and righthand ordinates represent the minimum and optimum larval sizes (MLS and OLS, see text) for the ingestion of these algae.

of cells in a fresh condition in the food, ie., containing at least a trace of green chloroplast, were recorded are given below (Table III). Larvae were fed for periods of 10—20 minutes only because experiments on digestion showed that this alga was fed upon discontinuously and rapidly digested. The results show that the MLS for the ingestion of live *C. leibleinii* was 3.5—4.0 mm in comparison with 1.5—2.0 mm for empty cells (Table II).

TABLE III

<i>Size of larvae.</i>	<i>No. examined.</i>	<i>Fresh cells present</i>
1.5—2.0	5	0
2.0—2.5	5	0
2.5—3.0	4	0
3.0—3.5	4	0
3.5—4.0	6	0
4.0—4.5	6	2
4.5—5.0	1	1
5.0—5.5	3	2
5.5—6.0	3	3
6.0—6.5	—	—
6.5—7.0	2	2

Coccoid cells were present in all the larvae examined. The size of the cells in the food culture was found to vary widely and a direct relationship existed between the size of the larvae and the maximum size of the cells that they ingested (Table IV). The gut contents of each of a number of measured larvae that had been starved and fed upon the alga were suspended in water on a slide, and a rapid estimation of the range of size of the cells present was made. The

TABLE IV

The mean diameter of coccoid cells in the food of small C. dipterum.

<i>Size of larva</i>	<i>dm</i>	<i>n</i>
food culture	30 μ	—
0.5—1.0	13	10
1.0—1.5	17	10
1.5—2.0	16	10
2.0—2.5	17	5

n — number of larvae examined
dm — mean diameter of largest cells

diameter of 10 of the largest cells was then measured at a magnification of X 400 with an eyepiece scale. The mean diameter (dm) of the largest cells in the food culture was found in the same manner. In larvae from 1.0—2.5 mm dm was relatively constant, but considerably smaller than dm in the culture, and larger than in larvae of less than 1.0 mm. It is probable that the food culture, which was derived from material obtained from a pond, was composed of several species of Chlorococcales and that the different values of dm obtained for the culture, larvae from 1.0—2.5 mm, and larvae from 0.5—1.0 mm represent cells of different species.

3. Summary of results.

Chloeon dipterum ingested 12 species of algae of which *Anabaena* was fed upon with least frequency.

There was a direct relationship between the size of *C. dipterum* and the frequency with which 7 of the species of algae were ingested. Coccoid cells were found in all larvae and a direct relationship was found between the size of the cells ingested and the sizes of the smallest larvae. *Ulothrix* was also ingested by the whole of the size range of larvae used but was ingested less frequently by the smaller larvae. For the other species there existed a minimum size of larva below which a particular alga was not ingested, and an optimum larval size above which an alga was ingested freely. These sizes were directly related to the dimensions of the algae.

Hydrodictyon and *Cladophora* were ingested relatively infrequently and independently of the size of the larvae. This suggested the presence of a repellent factor or barrier that exerted its influence independently of the size of the larvae. Its effect was apparently destroyed by chopping the algae up finely when they were both ingested freely.

The importance of distinguishing between the ingestion of dead and living algae was demonstrated in the case of *Closterium leibleinii*. The minimum size of *C. dipterum* capable of ingesting live cells was found to be considerably higher than that at which empty husks were ingested.

III. DIGESTION. EXAMINATION OF GUT CONTENTS

In the experiments described above in which larvae were fed with green algae for 1 hour or more, algal cells in an apparently undigested condition were found in the food only when it consisted of *Ulothrix* or coccoid cells. In the case of other species the cell walls were often torn and the contents of every cell were either reduced to a greenish fluid containing starch grains or the chloroplasts were much

altered from the fresh condition. In order to investigate the speed with which this change took place, larvae were fed upon algae and the contents of the gut examined after various intervals of time.

1. *Methods.*

The gut contents of large larvae fed upon *Spirogyra* 1. and *C. leibleinii* were examined for the presence of fresh or relatively unaltered algal cells at intervals of 5 to 60 minutes after the commencement of feeding. In *C. dipterum* fed upon *Spirogyra* counts were made in 22 large larvae of the numbers of 'full' and 'empty' cells in the fore-, mid-, and hind-guts. Cells that retained any trace of contents were counted as full. Measurements were made in each region of the gut of the mean length of 30 pieces of filament in 25 larvae fed upon *Spirogyra*. These pieces were selected at random by scanning a suspension of the gut contents under a microscope until 30 pieces had been found.

2. *Results. a. Spirogyra.*

In all the larvae examined the chloroplasts were greatly altered from the fresh condition. Least alteration had taken place in those larvae killed after they had been feeding for 5 minutes. There was no difference in the appearance of the food in the anterior and posterior parts of the gut. This impression was confirmed by the lack of a significant difference between the proportion of empty and full cells in the three regions of the gut. The mean length of pieces of filament in the hind gut was significantly smaller than the mean lengths in the fore and mid-guts which were approximately the same (Table V).

TABLE V

The mean length of pieces of Spirogyra in the food of C. dipterum

		Numbers of larvae	
		+	—
F.	compared with M.	12	11
M.	H.	10	4
F.	H.	13	2

+ — mean length of 30 pieces of filament larger
 — — mean length of 30 pieces of filament smaller
 F. — fore-gut
 M. — mid-gut
 H. — hind-gut

Digestion of *Spirogyra* by *C. dipterum* was rapid and efficient. The cells were greatly altered from the fresh condition in less than 5 minutes after ingestion, a process that took place in the fore-gut there being no evidence of progressive alteration of the food posteriorly in the gut apart from a decrease in the mean length of pieces of filament between the mid and the hind-gut. That no chloroplasts in a relatively fresh condition were found in the gut after 5 minutes indicated that under the conditions of the experiments feeding was discontinuous, algae being ingested immediately at the beginning of the feeding period and then retained in the gut for periods of at least 90 minutes during which time no more were ingested.

b. *Closterium leibleinii*.

Large larvae of *C. dipterum* of over 5 mm in length that were known to be capable of ingesting living *C. leibleinii* were used in the experiments. Similar results were obtained as for *Spirogyra*. In the larvae that had been feeding for more than 20 minutes the cell contents were greatly altered from the fresh condition. Least alteration had occurred in those larvae that had been fed for 10 minutes. Feeding followed a similar discontinuous pattern, relatively fresh cells being absent from the gut from 20 to 90 minutes after the commencement of feeding.

IV. DIGESTION. THE VIABILITY OF ALGAE AFTER PASSAGE THROUGH THE GUT.

With few exceptions all the algae used in the experiments described above appeared to be thoroughly digested. To find out if this was in fact so the hind-gut contents of larvae that had been fed upon various algae in the laboratory were cultured on suitable media in order to reveal the presence of viable cells. Gut contents of larvae collected in the field were also cultured in order to find out if cells remained viable in the food ingested under natural conditions.

1. *Method.*

Material from the hind-gut was placed upon an agar plate containing Chu 10 solution with added soil extract. After 7 days the plate was examined for algal growth. Choice of the culture medium was based on preliminary experiments which showed that a greater abundance and variety of algal growth was obtained on an agar medium than in a fluid one. Agar plates also had the advantage of being easily examined. Larvae were brought to the laboratory as quickly as possible and those from which the gut contents were not required immediately for culturing were placed in clean water and

starved. Before each larva was killed it was passed through several changes of water and was examined under a binocular microscope to make sure that it was free from detritus and attached algae. It was then decapitated in such a way that the oesophagus was left intact and by its contraction prevented the food from spurting from the gut. The hind-gut was dissected out and transferred to the culture medium where the wall was broken and the contents spread over the surface of the agar. Inoculations from each of 6 larvae were made on each agar plate.

2. Results.

The results of culturing the hind-gut contents of *C. dipterum* fed upon algae for 45 minutes and starved for 15 minutes are given in Table VI.

TABLE VI

The appearance of algae in cultures of the hind-gut contents of C. dipterum fed in the laboratory

	Culture of hind-gut contents		Direct culture of alga	
	n	+	n	+
Ulothrix	6	6	9	9
Oedogonium	6	1	8	7
Vaucheria	6	0	10	10
Spirogyra	6	0	9	5
coccolid cells	6	6	10	10

n — number of inoculations

+ — number in which growth occurred

The results of a series of direct inoculations with samples of the algae used as food are included in Table VI. The medium proved to be very satisfactory with the exception of *Spirogyra*. However, as described above, this alga appeared to be efficiently digested and even if it had been possible to provide a wholly suitable medium it is most unlikely that growth would have occurred.

A very heavy algal growth was frequently obtained in cultures of the hind-gut contents of larvae collected in the field. Inoculations were made as soon as possible after collection and at various intervals after this during which the larvae were starved. The results are given in Table VII, and show that viable algae were present in the hind-gut after the food had been retained there for at least 20 hours. There was no difference in the proportion of successful cultures of *Ulothrix* obtained after 1 and 20 hours after collection. A decrease in the proportion of positive cultures was generally obtained in the cases of the other algae as the interval after collection was increased.

3. Summary of results.

All algae provided as food in the laboratory appeared to be completely digested within a short time with the exceptions of *Ulothrix*, *Oscillatoria*, and coccoid cells. *Ulothrix* and coccoid cells grew in cultures of the hind-gut contents of larvae fed upon algae in the laboratory.

Viable cells were present in the hind-gut contents of larvae collected in the field. *Ulothrix* was present in most of the cultures and the frequency of occurrence was not reduced after the food had been retained in the gut for at least 20 hours. Diatoms and coccoid species showed decreased viability when the food had been retained in the gut for 9 hours.

TABLE VII

Cultures from the hindgut of C. dipterum, collected in the field

n. = No. of inoculations.

+ = No. in which growth occurred.

T. = Time interval after collection.

T.	<i>Ulothrix</i> .		<i>Cocoids</i> .		<i>Diatoms</i> *.		<i>Spirogyra</i> .		<i>Colonial coccoid</i> .	
	n.	+	n.	+	n.	+	n.	+	n.	+
¼— 1 hr.	24	21	24	24	24	10	24	1	24	5
4 hrs.	24	23	24	23	24	7	24	0	24	4
9	10	10	10	10	10	2	10	0	10	2
12	10	7	10	6	10	0	10	0	10	0
20	8	7	8	6	8	1	8	0	8	0

* small species of *Navicula*, *Nitzschia* & *Gomphonema*.

The crop was an important site of digestion. There appeared to be no progressive change in the algae in the gut apart from a decrease in the mean length of the pieces of filamentous algae in the hind-gut.

V. DISCUSSION

The marked variation in the amount of algae present, the ingestion of empty cells, and the passage of viable cells through the gut, raise the question of whether algal cells are utilised as food to any great extent by Ephemeropteran larvae. RYTHER (1954) found that algal cells were undigested by *Daphnia*, whose growth was inhibited by senescent cultures. Further experimental work may reveal that the larvae of Ephemeroptera and of other orders of aquatic insects are capable of completing their growth in the absence of algal food,

although the results obtained in the present work show that *C. dipterum* at least can rapidly and efficiently digest several species of algae. The species that were only partly digested and cells of which remained viable for at least 20 hours were the narrow filamentous forms *Ulothrix* and *Oscillatoria*, small diatoms, and solitary and colonial Chlorococcales. Assuming that the larvae of Ephemeroptera lack a cellulase, the cell contents of algae, other than diatoms which possess pores in the wall of the frustule, will only be exposed to the digestive enzymes in the gut when the wall is broken. They will then be digested if suitable enzymes are present, unless a further barrier exists in the form of a protective layer on the chloroplast itself (FRYER, 1957a). Rupture of the cell wall can only take place while the algae are collected and passed between the mouthparts as no region of the alimentary canal is equipped with hard processes to act as a gizzard. There is a constriction of the gut at the junction between the mid and hind regions that may serve to break the pieces of filament of large algae, but which would be unlikely to damage a narrow filament or small cell. The structures most suited to tearing the cell walls are the sharp processes on the anterior edge of the right molar surface. Small species would be those most likely to pass between the molar surfaces without damage and it is these which were obtained in the cultures of the hind-gut contents. This conclusion agrees with the conclusions of LEBOUR (1922) that small species of diatoms passed uncrushed through the feeding apparatus and gut of calanoid copepods, and FRYER (1957b) that almost any small algal cell that was swallowed whole was likely to emerge undamaged from the anus of cycloid copepods. FRYER also considered that the possession of an external gelatinous sheath protected an algal cell from damage by the mouthparts and penetration by enzymes in the gut. Progressive dissolution of such a substance would account for the loss of viability by diatoms and colonial *Chlorococcus* after they had been retained in the gut for several hours (Table VII). Diatoms move by secreting a mucous-like substance through the pores in the frustule so that the pores are probably blocked to a varying extent when the cells are ingested, and until the mucous is dissolved the cell contents are protected from the action of the digestive enzymes. The gelatinous sheath surrounding colonial *Chlorococcus* cells must be secreted through the cell wall and it is probable that when this is dissolved away the digestive enzymes may enter through the same pores. The degree to which these algae are utilised as food thus depends on the length of time for which food is retained in the gut which in turn depends on the rate of feeding.

Blue-green algae have been reported to be refused as food and to possess toxic properties in the cases of several animals (KOLENKINA

1951, BORODITCH 1956). On the other hand JONES (1951) found that *Glossosoma boltoni* (Trichoptera) fed on large quantities of a blue-green alga and grew rapidly at this time. The natural food of *C. dipterum* did not contain blue-green algae although these were sometimes fairly abundant in the habitats. In the laboratory large numbers of *C. dipterum* of all sizes ingested *Oscillatoria*. It is thus impossible to generalise on the importance of blue-green algae in the diet of aquatic larvae.

While several species of algae have been found to be efficiently digested by *C. dipterum*, algae formed an unimportant part of the food of larvae collected in the field (BROWN, 1960). ODUM (1957) classified *Callibaetis floridanus*, a species very similar to *C. dipterum*, as "herbivorous, trophic level uncertain" and it is probable that many species of Ephemeropteran larvae utilise several trophic levels. However under certain conditions the diet may be composed almost entirely of algae (BROOK 1954, 1955 a & b) and the larvae may exert an important controlling influence on the growth of populations of algae. Under such conditions competition between different sizes of larva will be reduced by the relationship between larval size and the sizes of algae ingested. This effect will be particularly important in the case of the smallest larvae, large numbers of which appear in the habitat over a short time, but which grow rapidly with a correspondingly rapid change in the maximum size of algal cell that they can ingest.

SUMMARY

The ability of larvae of *Chloeon dipterum* L. to ingest various species of algae was investigated in the laboratory. There was a direct relationship between the size of an alga and the frequency with which it was ingested by different sizes of larva. The frequency of ingestion of *Anabaena*, *Cladophora*, and *Hydrodictyon* appeared to be governed by factors in addition to their size.

Several species of algae were thoroughly and rapidly digested by *C. dipterum* in the laboratory.

Cultures of the hind-gut contents of larvae collected in the field, and of those fed upon algae in the laboratory, showed that cells of several species of algae remained viable in the gut for periods of at least 20 hours. These were narrow filamentous forms or small cells with or without a gelatinous sheath. It is suggested that such species pass between the mouthparts without being damaged so that in the absence of a cellulase the digestive enzymes of the gut are unable to penetrate the cell walls.

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