Role of algae in the diet of *Chironomus plumosus* F. semireductus from the Bay of Quinte, Lake Ontario

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Abstract

The importance of algae and different algal species to the chironomid diet was investigated through examination of the guts of chironomids taken from 5 locations in Big Bay (Bay of Quinte, Lake Ontario) at 6 times during the ice-free period. A comparison of the density and condition of algal cells at the two ends of the gut provided information on the digestibility of each algal species and the algal biomass assimilated by the chironomids. Diatoms and two species of green algae were assimilated over much of the summer, but the blue green algae were digested only late in the season when their populations were aged and/or dying. In terms of energy contribution, diatoms, especially *Stephanodiscus* spp. and *Melosira* spp., were most important in May (99% of all algal biomass assimilated), August (98%), and Octobr (92%), while the blue green species, *Microcystis aeruginosa,* was predominant in September (76%). Only a few small greens were assimilated in June and July. The contribution of algae as a food source to chironomid energetics was small, and reached a maximum in August and September (15%–34%). It is postulated that bacteria are a more important food source.

Introduction

In conjunction with the study of *C. plumosus* f. *semireductus* energetics in the Bay of Quinte, Lake Ontario (Johannsson 1980), an investigation was undertaken the same summer into the importance of algae and different algal species to the diet of this chironomid.

The foods of several *Chironomus* species *(C. modestus, C. decorus, C. remplii, C. tentans, C. anthracinus,* and *C. plumosus)* have been described qualitatively as a mixture of dead and live algae (especially diatoms), detritus with its associated bacteria, and inorganic matter (Sadler 1935; Rodina 1949; Provost & Branch 1959; Hamilton 1966; Jónasson & Kristiansen 1967; Kajak & Warda 1968; Izvekova & Sorokin 1969; Margolina 1971; Monakov 1972). The actual importance of the various components of the diet, however, has not been determined. This knowledge may increase our understanding of how changes in eutrophy may affect chironomid populations.

Previous dissections of the guts of *C. p.* f. *semireductus* from the Bay of Quinte revealed large numbers of diatoms, especially *Melosira* spp. The energetics of *C. p.* f. *semireductus* was suspected, therefore, to depend on diatoms in general, but especially on *Melosira* spp. population dynamics. Results from the study of the chironomid's energetics conform well with the hypothesis of diatom and, in particular *Melosira* spp., importance to the diet (Johannsson 1980). Chironomid assimilation efficiencies were highest during the latter part of *Melosira* spp. and *Melosira* spp. – *Stephanodiscus* spp. maximum population densities. Assimilation efficiencies did not correlate with total algal biomass in the water column indicating that some types of algae, eg. Chrysophyceae and Cyanophyceae, were

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not eaten or not assimilated.

This study was designed to determine whether algae contribute significantly to chironomid energy requirements, and which species of algae are ingested, which assimilated, and which provide the most energy over the growing season. The significance of the results are considered with respect to chironomid energetics especially as affected by changes in algal community dynamics with changes in eutrophy.

Methods and materials

Study site

The Bay of Quinte is a 64 km long inlet which conducts flow from the Trent and Moira River systems into the north-eastern corner of Lake Ontario (Fig. 1). In the eutrophic upper reaches of the bay (Big Bay), the water is turbid and uniformly shallow (6 m). The bottom sediment is composed of organically rich, unconsolidated mud. Oxygen levels near the bottom in 1978 were usually above 6 mg $\cdot$ l^{-1} (S. Millard, pers. comm.) and the temperature of the mud ranged from 2–4 °C in winter to approximately 25 °C in summer. The principle benthic invertebrates were oligochaetes and chironomids, principally *C. p.* f. *semireductus.* The average standing stock of chironomids was 0.913 g ash free dry weight $\cdot$ m^{-2} and they contributed 90% of the annual benthic production of 305–314 J $\cdot$ m^{-2}

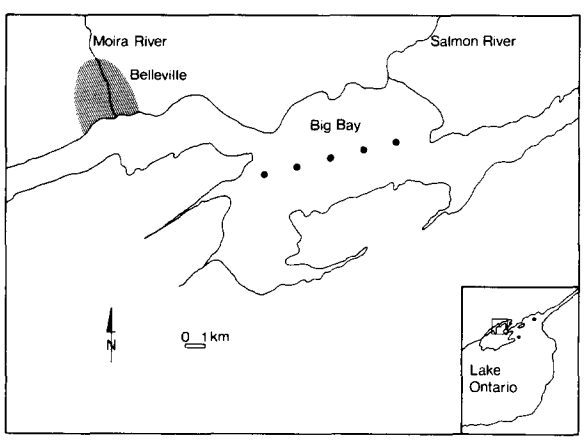

Fig. 1. Location of the Bay of Quinte on Lake Ontario showing details of Big Bay and the sampling sites (●).

(Johnson & Brinkhurst 1971). At a site near the west end of Big Bay primary production averaged 8.11 ± 4.92 mg C $\cdot$ l^{-1} between May 1 and September 18, 1978 (S. Millard, pers. comm.). Diatoms dominated the open water phytoplankton community (K. Nichols, pers. comm.) starting in May with successive population maxima of *Melosira* spp., *Diatoma tenue* var. *elongatum, Stephanodiscus astrea, Asterionella formosa* and *Fragilaria capucina.* For a short period at the end of June diatoms lost their dominance while small algal cells *(Dinophyceae* and *Cryptomonas)* became abundant. Biomass dropped to the seasonal low at this time (0.9 mm^3 $\cdot$ l^{-1}). During July *Melosira* became dominant again and remained abundant during August when several blue green species of *Anabaena* bloomed. Biomass peaked at 14.2 mm^3 $\cdot$ l^{-1} in early August. *Lyngbya* sp. and *Microcystis aeruginosa* were abundant at the beginning of September. *Melosira* spp. populations increased again in the latter part of September, and *Oscillatoria* spp. peaked in early October.

Sample collection and processing

Chironomid guts were sampled on six occasions during the ice-free period: dates chosen to correspond to changes in the algal community (May 23, June 20, July 19, August 2, September 8, October 18, 1978) (K. Nicholls, pers. comm.). Mud was taken with an Ekman dredge at 5 equi-distant stations along a SW-NE transect across Big Bay (Fig. 1). Small volumes of mud were immediately sieved extremely slowly and gently. The first 12 non-prepupal fourth instar larvae were removed on sight and placed in cold (oc) dilute Lugol's solution. This procedure prevented regurgitation.

Food passes directly from the esophagus into the midgut, the foregut being virtually absent in this species (Kurazhkouskaya 1966). The hindgut is also small and often devoid of material. Thus, comparisons of food at the beginning and end of the midgut should provide reasonable information on the digestibility and dietary importance of different algal species. To dissect the gut, the head and last abdominal segment were cut from the body, the body wall slit lengthwise and the gut removed to a small glass dish containing a dilute Lugol's solution. A 1 mm length (approximately 10% of total midgut length) was cut from the anterior end of the midgut and

transferred to a drop of water. The gut wall was removed and the dimensions of the food bolus recorded. The gut contents were teased apart and the food slurry and washings transferred to a vial and preserved with Lugol's. The end of the midgut was treated similarly. The gut contents of 5 (May 23, June 20) or 8 (remaining dates) chironomids were pooled per station.

The algae were counted using an inverted microscope method. At least 200, though usually many more, pieces of algae were counted and 90% (either of biomass or of numbers) of all those counted were identified to species. Cell volumes were determined by relating the algal shapes to geometric forms. The algae in the chironomid gut samples were classified further by the condition of their chloroplasts into intact, disintegrating and empty cells.

Assimilation and biomass calculations

To determine how effectively *C. p.* f. *semireductus* assimilated each algal species found in the gut, the difference in the proportions of algal cells containing 'food' between the two ends of the midgut was calculated. Calculating assimilation this way was possible as algal cell walls remained intact along the length of the gut. For each algal species, the numbers of intact, disintegrating and empty cells, and the total number of cells were summed over the five sampling stations, a total of 25 (May, June) or 40 (remaining dates) chironomids per estimate. The proportion (P) of cells containing 'food' in the front (P_F) and the end (P_E) of the midgut, and the proportion of total cells assimilated (P_A) were calculated as follows:

$$P_F = \frac{\text{No. intact cells}_F + \tfrac{1}{2}\,\text{No. disintegrating cells}_F}{\text{total number cells}_F} \quad (1)$$

Disintegrating cells were included as a source of food for, on average, they should contain half of their original cell contents.

P_E is calculated similarly using the cell counts from the end of the midgut.

$$P_A = P_F - P_E \quad (2)$$

If P_A did not vary over the season, the numbers were summed over the six sampling periods and a seasonal estimate of P_A calculated.

In the two instances (*Microcystis aeruginosa* – September, *Fragilaria* spp. – October) where cell walls were digested, assimilation was calculated by the difference in cell number between the two ends of the midgut.

The biomasses (B) assimilated by *C. p.* f. *semireductus* were calculated for each date for each algal species:

$B = P_A$	· Cell density	· Cell volume	· Cell Ash-free dry density
$\mu g \cdot mm^{-3}$ gut contents	No. $\cdot$ mm^{-3} gut contents	μl	$\mu g \cdot \mu l^{-1}$

Table 1. Seasonal variation in the abundance of assimilated algal species in the gut of *C. p.* f. *semireductus*. Mean ± 1 S.E. (N = 10, except *M. aeruginosa* Sept., N = 5).

	May 23	June 20	July 19	Aug. 2	Sept. 8	Oct. 18
Bacillariophyceae						
Stephanodiscus spp.	628 ± 90	648 ± 127	636 ± 107	398 ± 77	519 ± 139	252 ± 63
S. astraea	231 ± 48	312 ± 66	259 ± 45	190 ± 58	364 ± 109	157 ± 37
Melosira spp.	12 716 ± 2 995	8 247 ± 1 816	16 067 ± 2 940	16 706 ± 2 320	8 323 ± 1 241	1 855 ± 435
Fragilaria spp.	2 130 ± 437	6 078 ± 2 765	882 ± 252	716 ± 178	322 ± 159	8 043 ± 1 136
Diatoma tenue var. *elongatum*	6 170 ± 1 648	187 ± 74	85 ± 48	16 ± 11	26 ± 14	0 ±
Chlorophyceae						
Scenedesmus spp.	950 ± 182	1 112 ± 377	2 818 ± 605	829 ± 180	1 660 ± 353	844 ± 256
Oocystis sp.	35 ± 35	224 ± 106	135 ± 89	308 ± 133	757 ± 261	349 ± 109
Cyanophyceae						
Microcystis aeruginosa	0	1 338 ± 1 195	12 846 ± 4 373	10 231 ± 3 414	141 629 ± 42 677	17 823 ± 8 583
Aphanothece clathatra	13 326 ± 9 595	28 755 ± 16 605	279 852 ± 86 074	121 937 ± 30 786	299 703 ± 70 328	87 102 ± 35 052
Coelosphaerium spp.	99 ± 87	3 848 ± 3 053	563 ± 258	5 101 ± 3 379	17 507 ± 7 098	18 429 ± 2 253
Oscillatoria (amoena?)	0	105 ± 74	94 ± 33	287 ± 70	212 ± 72	3 158 ± 400

Cell density. The average number of cells · mm^{-3} of gut contents was calculated from the numbers of cells · mm^{-3} at both ends of the gut from all five sampling stations (Table 1). Standard errors ranged from 13%–100% with those of diatoms averaging 27.8%, greens, 40.0% and blue greens, 45.1%.

Cell volume. The mean cell volumes were averaged over the season as inspection of cell sizes of the 20 most common algae revealed no seasonal trends. However, for a few species , whose cell size varied by more than 50%, the average volumes were calculated directly from the cells counted over the year: *Oscillatoria* (amoena?) *M. aeruginosa, Dictyosphaerium pulchellum, Pediastrum Boryanum, P. simplex, P. duplex, Scenedesmus opoliensis, S. quadricauda, S. acuminatus, Melosira ambigua, M. varians, Stephanodiscus* sp.

Ash-free dry density. Values were calculated from information provided by Nalewajko (1966, Table 1). If data for a particular species were not given, the value of a similar species was assigned (Appendix 1).

The total biomass contributed by algae to chironomid energetics was summed for each sampling date and compared with chironomid energy intake determined by Johannsson (1980). Chironomid assimilation per volume gut contents was calculated as $\mu g \cdot mm^{-3}$ using Johannsson's Table 1 as follows:

assimilation/day / chironomid	= daily assimilation	· chironomid weight	· 10^3
($\mu g \cdot day^{-1}$)	($\mu g \cdot day^{-1} \cdot mg^{-1}$)	(mg)	

weight of food passed/day	= weight of gut contents	· 24 ÷	gut filling time	
($\mu g \cdot day^{-1}$)	(μg)		($h \cdot day^{-1}$)	(h)

Dry weight of gut contents per volume of gut = 91 ± 9 $\mu g \cdot mm^{-3}$ (S.E.) (N = 19)

volume passed/day	= dry weight of food passed/day	÷ 91	
($mm^3 \cdot day^{-1}$)	($\mu g \cdot day^{-1}$)		($\mu g \cdot mm^{-3}$)

assimilation/volume gut contents	= assimilation/day · chironomid	÷	volume gut contents passed/day
($\mu g \cdot mm^{-3}$)	($\mu g \cdot day^{-1}$)		($mm^3 \cdot day^{-1}$)

Results

Patterns of algal ingestion and assimilation

Table 2 summarizes the information on the algae found in the gut contents of *C. p.* f. *semireductus*

Table 2. Summary of the algal genera found in the guts of *C. p.* f. *semireductus* from Big Bay and the digestibility of the more common algal species: May 23–October 18, 1978.

Algal class	Genera observed	Species assimilated	Species not assimilated
Chlorophyceae	35	*Oocystis* sp. *Scenedesmus* spp. *S. quadricauda* *S. opoliensis*	*Coelastrum* spp. *Dictyosphaerium* spp. *Gloeocystis* spp. *Pediastrum* spp. *Planctonema lauterbornii*
Bacillariophyceae	24	*Diatoma tenue* var. *elongatum* *Fragilaria capucina* *F. crotonensis* *Melosira* spp. *Stephanodiscus* spp.	*Asterionella formosa*
Cyanophyceae	10	*Microcystis aeruginosa* *Aphanothece clathatra* *Coelosphaerium* spp. *Oscillatoria* (amoena?)	*Aphanocapsa* spp. *Chroococcus* sp. *Lyngbya limnetica* *Merismopedia tenuissima*
Chrysophyceae	10		
Cryptophyceae	3		
Dinophyceae	3		

Table 3. Seasonal variations in the proportion of assimilated cells (P_A), the proportion of cells containing 'food' in the front of the gut (P_F) and the biomass assimilated by the chironomids (B) for algal species digested by *C. p.* f. *semireductus*.

		May 23	June 20	July 19	Aug. 2	Sept. 8	Oct. 18
Bacillariophyceae							
Stephanodiscus spp.	P_A	0.21	0	0	0.07	0.07	0.07
	P_F	0.21	0.02	0.05	0.09	0.10	0.17
	B*	0.31	0	0	0.09	0.17	0.07
Melosira spp.	P_A	0.03	0	0	0.10	0.04	0
	P_F	0.60	0.28	0.36	0.52	0.21	0.19
	B	0.06	0	0	0.33	0.05	0
							cap crot**
Fragilaria spp.	P_A	0.09	0	0	0	0	0.27 0.11
	P_F	0.35	0.23	0.08	0.01	0.08	0.45 0.61
	B	0.04	0	0	0	0	0.10
Diatoma tenue	P_A	0.28	0	–	–	–	–
var. *elongatum*	P_F	0.43	0	–	–	–	–
	B	0.18	0	–	–	–	–
Chlorophyceae							
Scenedesmus spp.	P_A	0.05–0.13	0.05–0.13	0.05–0.13	0.05–0.13	0.05–0.13	0.05–0.13
	P_F	1.00	0.64	0.83	0.74	0.60	1.00
	B	<0.01	0.01	0.01	0.01	0.01	<0.01
Oocystis sp.	P_A	–	0	0	0.09	0.09	0.09
	P_F	–	1.00	1.00	1.00	0.95	1.00
	B	–	0	0	<0.01	<0.01	<0.01
Cyanophyceae							
Microcystis aeruginosa	P_A	–	0	0	0	0.98	0
	P_F	–	1.00	1.00	1.00	1.00	1.00
	B	–	0	0	0	0.75	0
Aphanothece clathatra	P_A	0	0	0	0	0	0.04
	P_F	1.00	1.00	1.00	1.00	1.00	1.00
	B	0	0	0	0	0	<0.01
Coelosphaerium spp.	P_A	–	0	0	0	0	0.10
	P_F	–	0.92	1.00	1.00	0.99	0.98
	B	–	0	0	0	0	0.01
Oscillatoria (amoena?)	P_A	–	0	0	0	0	0.02
	P_F	–	1.00	1.00	1.00	0.90	1.00
	B	–	0	0	0	0	0.01
Σ Biomass ($\mu g \cdot mm^{-3}$)		0.59	0.01	0.01	0.42	0.99	0.19

* B in $\mu g \cdot mm^{-3}$

** cap = *F. capucina*
crot = *F. crotonesis*

over the summer of 1978. Table 3 reports seasonal cell densities, P_A's, P_F's, and B's for all digested algal species, and Fig. 2, seasonal changes in the volumes of these algal species in the chironomid guts.

More species of Chlorophyceae (greens) were observed in the guts than algae of any other class. Chlorophyceae were rarely abundant, however, and only two genera were assimilated. Bacillariophyceae (diatoms) were also common and of the five most abundant genera, four were assimilated; the data for the fifth genus was inconclusive. Fewer genera of Cyanophyceae (blue greens) were found. Assimilation was detected in half of the abundant genera, but this was observed only toward the latter part of population blooms. Few Chrysophyceae, Cryptophyceae or Dinophyceae were observed and none were assimilated.

Total algal biomass and the importance of different algal classes in the diet of *C. p.* f. *semireductus* varied throughout the year. Greens, notably *Scenedesmus* spp., were assimilated all summer, but were important only in June and July. Other digestible algae were either not available *(Stephanodiscus*

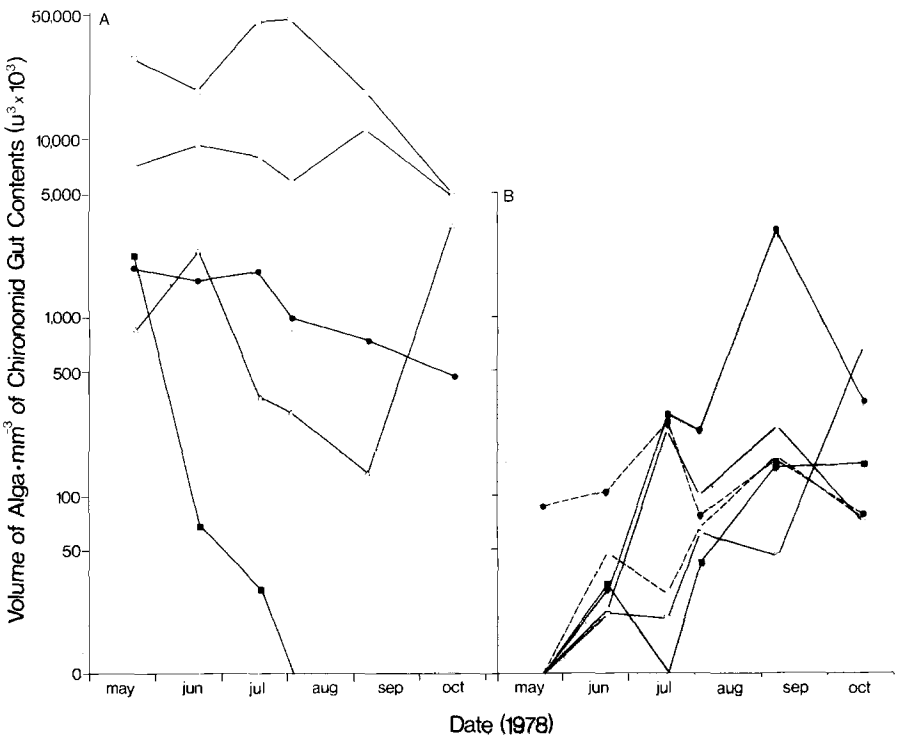

Fig. 2. Seasonal changes in the total cell volumes in the anterior tenth of the midgut for each of the ten algal genera assimilated by *C. p.* f. *semireductus.*

(A) Bacillariophyceae: *Stephanodiscus astrea* O—O, remaining *Stephanodiscus* ●—●, Melosira □—□, *Fragilaria* △—△, *Diatoma* ■—■.

(B) Chlorophyceae: *Scenedesmus* ●---●, Oocystis O---O, Cyanophyceae: *Microcystis* ●—●, *Aphanothece* O—O, Coelosphaerium ■—■, Oscillatoria □—□.

spp., *Diatoma tenue* var. *elongatum)* or were not digested (*Melosira* spp., *Fragilaria* spp., *Oocystis* sp., all blue greens) at this time. Since the P_A's of greens were very low (0.052–0.131) algal contribution to chironomid energetics was minimal in late spring and early summer. Diatoms provided the majority of assimilated algal biomass in May (99%), August (98%) and October (92%). The May and August values were amongst the largest: 20 to 60 times greater than the minimal values in June and July. All four genera were assimilated in May, but the majority of the biomass was obtained from *Stephanodiscus* spp. and *D. t.* var. *elongatum. Melosira* spp. contributed significantly in August followed by *Stephanodiscus* spp; while *Fragilaria* spp. and *Stephanodiscus* spp. were important in October. Although diatoms did not contribute the majority of the biomass in September, *Stephanodiscus* spp. and *Melosira* spp. were assimilated in reasonable quantities at this time. Blue greens were present in the guts throughout the year but were assimilated only after the species had peaked in the water column, perhaps when the cells were aging or dying. Accordingly, in September, *M. aeruginosa* was nearly totally assimilated and contributed 76% of the assimilated algal biomass. *Aphanothece clathatra, Coelosphaerium* spp. and *Oscillatoria* (amoena?) were digested to a small extent in October. Thus, most of the algal biomass assimilated by chironomids was obtained in May, August and September, the maximum being in September. The genera which contributed the most were *Stephanodiscus, Melosira, Diatoma, Fragilaria* and *Microcystis.*

Assimilation efficiencies

From the data in Table 3, it is possible to make

rough estimates of assimilation efficiencies for the different species of algae. The proportion of cells assimilated is compared with the proportion of cells containing 'food' in the front of the midgut. The closer these values are, the greater the assimilation efficiency. The two genera of greens have fairly low assimilation efficiencies; *Oocystis* sp. (when it is digested 0.09/1.00 = 9%) and *Scenedesmus* spp. (7%–18%). Diatoms, on the other hand, present a great range of digestibility from undetectable to nearly 100%: *Stephanodiscus* spp. (May 98%, August–October 70%), *Melosira* spp. (May 5%, August 19%, September 16%). *Fragilaria* spp. (May 25%, October *F. crotonensis* 19%, *F. capucina* 59%), *D. t.* var. *elongatum* (May 64%). In blue greens levels of assimilation, when it occurred, were low (2%–13%), except for *M. aeruginosa* in September (98%).

Importance of algal biomass to chironomid energetics

When the energy obtained from algae is compared with that required by the chironomids, it is obvious that algae provide only a small, and at times insignificant, portion of the energy requirements (Table 4). Algal contribution ranged from 15%–34% in August and September, to 8% in July, 4% in May, 2% in October and 1% in June. It must be remembered that there is a large error factor in these estimates due to the large variability in species density within the samples (Table 1) and to the crude manner of calculating assimilation efficiency. It is their consistently low level that is important.

Discussion

Evaluation of methods

This technique allows the assessment of details of feeding of *in situ* animals under normal conditions. In this methodology it is assumed that on average disintegrating cells contain 50% of the edible cell contents of an intact cell and that digestion did not occur in the areas of the midgut which were sampled ($^1/_{10}$th of the extreme anterior and posterior ends of the gut). This first assumption is reasonable, the second may underestimate digestion slightly. The major source of error in this method is

Table 4. The seasonal algal biomasses assimilated by *C. p.* f. *semireductus* are compared with the total biomass requirements of the chironomids as determined by Johannsson (1980). The concentrations of bacteria required to make up the differences in biomasses are reported. The data from the two studies were not collected on the same days (although during the same summer). Therefore, calculations were made using data from adjacent sampling dates as indicated by arrows.

		Chironomid biomass requirement (μg dry wt. mm^{-3} GC*)	Algal biomass assimilated (μg dry wt. mm^{-3} GC)	Algal contribution to biomass requirement (%)	Biomass missing (μg dry wt. mm^{-3} GC)	No. bacteria · mm^{-3} required to provide missing biomass** (10^6)
May	10	13.06	↑	4.3	12.50	13.40
	23		0.555 ↑			
June	20		0.009			
July	13	2.10	↑	0.6	2.09	2.25
	19		0.012 ↓			
	26	3.44	↑	6.4	3.22	3.47
Aug.	2		0.427 ↕			
	9	5.42	↓	7.9	4.99	5.36
	23	2.72	↓	15.6	2.29	2.46
Sept.	5		↓			
	8		0.988 ↓			
	20	2.90	↓	34.1	1.91	2.05
Oct.	2	5.37	↑	2.0	5.26	5.66
	18	5.77	0.105 ↓	1.8	5.66	6.09

* GC = Gut contents

** Numbers calculated assuming 10^9 bacteria · mg dry weight^{-1} and a 93% assimilation efficiency.

the natural variability present in the data. This variability is due to the small volumes of gut analyzed, the large number of different algal species present in the samples and the natural hetergeneity of the food source. In the analysis this variability was greatly reduced by pooling the data from all the chironomids on each sampling date.

Relative importance of different algal classes

Diatoms are the most important group of algae in the diet of *C. p.* f. *semireductus.* They are abundant in the guts much of the year and, as observed in many other invertebrates, better assimilated than algae from other classes (Kajak & Warda 1968; Hargrave 1970; Fenchell 1972; Moore 1977a, b, c). Their energy contribution varies seasonally depending on abundance, proportion of cells containing 'food', species composition and assimilation efficiencies. In terms of total energy contributed to the chironomid diet, the combination of these factors means that (1) chironomids obtain most of their energy from diatoms in May and August, (2) *Melosira* is not the great food source expected by inspection of the gut contents because it is not assimilated well especially in May, although it is abundant in the gut throughout the season, and (3) *Stephanodiscus,* by virtue of its presence throughout the year, its high assimilation efficiency, and large size, is the most important algal species in chironomid energetics.

Kajak and Warda (1968) found that *Melosira* spp. was assimilated by *C. plumosus* in Poland, whereas we found the species in the Bay of Quinte *(M. ambigua, M. granulata, M. varians, M. islandica* and *Melosira* sp.) to be poorly digested by *C. p.* f. *semireductus. Melosira* is a widely dispersed genus and species may differ from one part of the world to another. Moore (1977c) discussed the necessity of working at the species level when investigating feeding, and used information on *Navicula* (another diatom) to illustrate the diversity of species within a genus. *Navicula* displayed a wide range of shapes, sizes, silicon content, ornamentation and habitat preference. Perhaps something as simple as differences in silicon content affects digestibility. It may also be that the two chironomids, although very closely related, do not have the same feeding abilities. Infante (1973) found that *Daphnia pulex* and *D. longispina* could not assimilate the same alga equally well. Whatever the reason, *Melosira* is not well digested in this study and only contributes significantly to assimilated biomass in August when it is very abundant and its P_F is high.

Greens are poorly assimilated. Other animals also have trouble digesting greens, presumably because of their tough cellulose wall (Brown 1960; Kajak & Warda 1968; Monakov 1972; Infante 1973; Moore 1977c).

Blue greens are commonly another poor food source (Kajak & Warda 1968; Hargrave 1970; Arnold 1971; Fenchel 1972). They were only utilized by *C. p.* f. *semireductus* in the autumn after the populations had peaked and when many cells were presumably old or dying. Therefore, unlike diatoms which are abundant and available as food over long periods of time in the Bay of Quinte, blue greens may be suitable for food only for short periods depending on their rate of decay. Because of the long intervals between sampling dates, the energy contributed by blue greens is not well delineated by this study. Blue greens generally reach high population levels in late summer; and consequently, their energy input to the chironomid diet should occur principally in the autumn.

Chironomid energy requirements

Chironomids require much more energy than that provided by algae at all times of the year (Table 4). The alternate food sources are bacteria, some protozoans and free organic molecules. Bacteria seem the more likely source. A diet of bacteria is sufficient for the growth and emergence of *C. plumosus* in the laboratory (Rodina 1949), and bacteria have been shown to influence the site selection of *Chironomus lugubris* in Blaxter Lough (McLachlan & Dickinson 1977). Furthermore, Rodina (1963) noted that bacteria often surround living algae, and Smyley & Collins (1975) showed that another animal, *Ceriodaphnia quadrangula* can consume large amounts of living algae but lives on the bacteria associated with them, not on the algae *per se.*

To assess the potential of bacteria alone to provide the remaining energy, the number of bacteria required $\cdot$ mm^{-3} gut contents was calculated for each sampling date using the conversion, 10^9 bacteria $\bullet$ mg^{-1} bacterial dry weight, and a chironomid assimilation efficiency of bacteria of 93% (Table 4).

The assimilation efficiency was estimated by Johannsson and Rao (unpublished data) from plate counts taken at the two ends of the midgut: the foregut is virtually absent and the hindgut is contaminated by bacteria from the Malphigian tubules. A total of five chironomids from Big Bay were examined. The efficiency is similar to values quoted for other detritivores (Hargrave 1970; Fenchel 1972).

The calculations indicate that between 2.2 and 13.4×10^6 bacteria · mm^{-3} of food must be ingested. These values are not unreasonable. Plate counts from the front of the midgut of *C. plumosus* and *C. p.* f. *semireductus* from Big Bay had a density of $1.74 \pm 0.58 \times 10^4$ bacteria · mm^3 ($\bar{x} \pm$ ISE (N = 10)) on August 24, 1977 (Johannsson & Rao, unpubl. data). Plate counts, especially those of surface sediments, which are very similar to gut contents, greatly underestimate bacterial numbers. Rao & Burnison (1976) found that densities determined by plate counts were between 1 and 50% (Rao, unpubl. data) of densities done by direct counts. Overbeck (1974) found the efficiency of plate counts to be even less if compared with scanning electron microscope counts. Correction of plate counts from chironomid guts by 10^2 would increase the denisty to $\cong 1.74 \times 10^6$. However, this is still an underestimate. As in the algal dissections, the first tenth of the gut was taken to establish initial conditions. Assimilation of bacteria is very rapid, however, and the density of bacteria dropped 78% between the first and second tenth of the gut. Clearly approximately 40% of bacteria must have assimilated in the first tenth before initial conditions were established. Correcting for this error, the concentration of bacteria ingested Aug. 24, 1977 must have been closer to 2.9×10^6 · mm^{-3}. This density is close to the estimated 2.46×10^6 bacteria · mm^3 required to fulfill chironomid energy requirements on Aug. 23, 1978. The role of bacteria is further endorsed by *C. p.* f. *semireductus* feeding habits. It processes food at rates (4.6–4.8 ● body weight · day^{-1} at 22.0–24.5 °C (Johannsson 1980)) similar to those of freshwater deposit feeding invertebrates (cf. Hargrave 1972, Table 2). Thus, bacteria may well be an important and perhaps the principal food source of *C. p.* f. *semireductus* from the Bay of Quinte.

Bacterial population densities at the mud water interface, however, may be related to events in the algal community, for Johannsson (1980) found chironomid assimilation efficiency to be highest during the latter part of *Melosira* and *Melosira* – *Stephanodiscus* population maxima. Clearly an accumulation of dying algae on the sediment should produce increased bacterial populations in this region. As early as 1944, Weeks noted that surface sediment aerobes showed population increases following periods of phytoplankton maxima in Western Lake Erie.

Effects of changing eutrophy

Decreased phosphorus loadings to the Bay of Quinte may allow some de-eutrophication of the system. Less eutrophied systems are characterized by lower total algal biomasses, larger Crysophyceaen populations in late June–early July and the replacement of bloom-forming blue greens with non-bloom forming species in August and September (cf. Dillon *et al.* 1978). Johannsson (1980) assessed the effect of these changes in the algal community on the chironomid population, assuming that algae were the principal food source. In light of the present study, the interpretation must be changed. Firstly, increase in the Crysophyceaen populations was believed to be beneficial to the newly hatched planktonic larvae. Crysophyceaens were not abundant in the guts of the mud-dwelling 4th instar larvae and some intact cells were found at both ends of the gut. Therefore, their importance as a food source for young larvae can not be readily assumed: detrital particles in the water column might be important. Secondly, a longer summer diatom bloom was thought to be beneficial for chironomid growth while a decrease in total algal biomass (principally diatoms), non-beneficial. Although this is still true, these algae contributed only 6%–15% of the biomass assimilated by *C. p.* f. *semireductus,* and therefore these changes are less important. Thirdly, the effect of the change in dominance amongst the blue green algal species is not known, because *C. p.* f. *semireductus* digested both bloom-forming and non-bloom forming species.

Consequently changes in the algal community, per se, with changes in eutrophy may be of minor importance to chironomid energetics. The effect of changing eutrophy on bacterial production, as observed at the mud-water interface, is probably of more consequence. However, to the extent that bacterial production is linked to algal community

dynamics the latter regains its importance. The relationship is presumably expressed through the decay characteristics of the dominant algal species and the total biomass and seasonal distribution of decaying algae.

Summary

1. Members of 85 genera of algae were ingested, only 10 genera were definitely assimilated, and 10 definitely not assimilated. The other algae were present only occasionally or in very low numbers.
2. Four genera each of Bacillariophyceae and Cyanophyceae and two genera of Chlorophyceae were assimilated.
3. Bacillariophyceae, particularly, *Stephanodiscus* spp and *Melosira* spp, contributed the majority of algal biomass assimilated by the chironomids in May (99%), August (98%) and October (92%), while the cyanophyceaen *Microcystis* spp contributed (76%) in September.
4. At their peak, algae contributed only 15%–34% of chironomid energy requirements. It is suggested that bacteria may supply the remainder.

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Appendix 1. Ash-free dry weight values of algae used in biomass calculations. Values for some alga were derived from information published by Nalewajko (1966). Remaining values were assigned by similarity of algal species.

Species	Ash-free dry weight ($\mu g \cdot \mu l^{-1}$)	
	Derived	Assigned
Chlorophyceae		
Scenedesmus quadricauda	464.6	
S. spp.		464.6
Oocystis sp.		236.0 (average of 17 greens)
Cyanophyceae		
Oscillatoria sp.	248.7	
Aphanothece clathatra		248.7
Coelosphaerium spp.		248.7
Microcystis aeruginosa		248.7
Bacillariophyceae		
Stephanodiscus spp.	200.0	
Melosira spp.	107.1	
Fragilaria capucina	295.8	
F. crotonensis		295.8
Diatoma tenue var. *elongatum*		224.1 (average of 11 diatoms)

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