THE INGESTION AND DIGESTION OF ALGAL AND OTHER FOODS BY LARVAL BLACK FLIES (DIPTERA: SIMULIIDAE) OF NEWFOUNDLAND

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ISBN 0-315-54984-X

THE INGESTION AND DIGESTION OF ALGAL AND OTHER FOODS BY LARVAL BLACK FLIES (DIPTERA:SIMULIIDAE) OF NEWFOUNDLAND

by Bruce Hunter Thompson

a thesis
presented to Memorial University of Newfoundland
(Department of Biology)
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in Biology

St. John's, Newfoundland, 1989

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ABSTRACT

Feeding selectivity in larval simuliids of several Newfoundland species was studied by comparing relative abundances of algal taxa in the guts of field-collected larvae with those in the associated seston and periphyton. With the exception of the first instar of Prosimulium mixtum Syme & Davies, larvae of P. mixtum, Stegopterna mutata Malloch, Cnephia ornithophilia Davies et al., Simulium vittatum Zetterstedt, Simulium venustum Say and S. verecundum Stone & Jamnback utilized the seston almost exclusively for provision of food. No evidence was found to suggest that algal particles were selected on a qualitative basis, nor did the data indicate striking dissimilarities among species of similar physiological age, as to selectivity based on particle size. However, differing selectivities on the basis of particle size were observed among conspecific larvae of different physiological age. C. ornithophilia appeared to be exceptional, showing selectivity for relatively large diatom particles over much smaller bacterial particles, as compared to other species of larvae tested. Selectivity for particles within a certain intermediate size range (5-15 μm) was comparatively high for this species.

Measurements of gut passage rates in the eurythermal S. vittatum indicated that feeding rates increased generally with increased temperature and particulate matter (PM)

concentration. Feeding efficiency, however, decreased with increased PM concentration and with increased current velocity. The "completeness" of digestion, studied by using diatoms as indicators, increased generally with increasing temperature in S. vittatum and the warm stenothermal S. verecundum. In P. mixtum, a cold stenothermal species, the reverse temperature relationship was shown. Algae of different taxa varied markedly in susceptibility to digestion.

Larvae of different species were capable of utilizing a wide variety of particulate foods, including algae, bacteria and detritus. In feeding trials, overall larval growth was highest when fed on diatoms, lowest when fed on leaf litter and intermediate when reared on green algae or bacteria. The nutritional importance of various classes of suspended particulate matter is a function of its availability in the seston, its susceptibility to ingestion, its inherent digestibility and its nutrient content.

Key words:

Simuliids, filter-feeding, selectivity, grazing, algae, bacteria, digestion, productivity, nutrition, feeding rates.

ACKNOWLEDGEMENTS

I am grateful to Brian Adams, Jeanne Harding, Wendy Nagles, Helen O'Brien and Jerry Porter, who willingly assumed the task of providing larvae with food during some of the laboratory trials.

My thanks are also due to those at M.U.N. Technical Services for their perfectionist work in producing various components of the rearing apparatus and other equipment.

I am grateful to Dr. G.F. Bennett, Dr. M. Colbo, Dr. J. Gow and Dr. A. Whittick, for their advice and encouragement throughout the course of the work.

The assistance of Terry Taerum, Department of Computing Sciences, University of Alberta, for his time and patience in introducing me to a number of statistical techniques is most gratefully acknowledged.

Finally, I thank my wife Judith, who provided inspiration and unwavering support throughout the course of my efforts.

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CHAPTER 1 BACKGROUND AND OBJECTIVES OF STUDY

The ecologically sound management of drainage basins requires an understanding of the complex interactions of biotic and abiotic factors operating in lotic systems. In recent years, stream ecologists have focussed increasing attention on the means by which autochthonous and allochthonous inputs of nutrients and energy to streams are processed. The concept of "spiralling" (Vannote et al. 1980) has been developed to describe the form of energy/nutrient cycling that takes into account the longitudinal displacement characteristic of all stream ecosystems. Central to the question of energy/nutrient spiralling is the role of suspended fine particulate organic matter (FPOM; <1mm) and, in particular, ultra-fine organic matter (UTOM; 0.5 - 50 μm). UTOM has been shown in a number of studies to be a major form of transported organic matter in streams (Vannote et al. 1982; Wallace et al. 1982; Minshall et al. 1983), comprising 50% or more of particulate organic matter in transport, and perhaps one quarter of total organic matter (Cummins 1987). The ultra-fine organic fraction of stream seston normally consists of a mixture of decaying vegetation and other detrital matter, algae, bacteria and microinvertebrates.

Benthic invertebrates play a major role in the processing of particulate organic matter in stream ecosystems. Cummins (1973, 1974) outlined the various

functional feeding groups of lotic ecosystems, as a means of elucidating how members of stream food webs interact to process autochthonous and allochthonous organic inputs. Scrapers (grazers) remove periphytic or other material attached to the substrate. Shredders break down plant material into successively smaller particles. Collector-gatherers or deposit-feeders feed primarily on sedimented (or surface) material, whilst collector-filterers trap and consume a wide range of particles in the seston. Predators utilize all of the foregoing groups as food.

The activities of the collector-filterers guild represent an important component in the transport and cycling of FPOM in stream ecosystems (Cummins 1973; Peterson and Cummins 1974; Short and Maslin 1977; Wallace et al. 1977). By capturing, utilizing and egesting suspended particulate material, they affect the downstream movement of seston, and provide an important source of energy for higher trophic levels, while retarding the loss of energy and nutrients downstream (Wallace et al. 1977; McCullough et al. 1979). Filter-feeding organisms increase the efficiency of a given stream segment in processing organic inputs (Vannote et al. 1980; Wallace and Merritt 1980). In effect, they shorten the spiralling length by apprehending and utilizing particulate seston in place (Wallace et al. 1977, Newbold et al. 1982). More specifically, filter feeders affect the regeneration rate of nutrients through assimilation and subsequent excretion; influence the downstream displacement

rate of particulate matter, through capture and egestion; and affect the particle-size distribution of seston, through clumping it as faecal material or reducing it by digestion, thus altering the rate of subsequent microbial breakdown (Newbold et al. 1982).

There is much yet to be learned on the ways that communities of filter-feeding invertebrates function in processing particulate organic matter in stream ecosystems. Of special interest is the means in which the particulate resource is apportioned among populations, since as a general ecological principle, increased specialization of resource utilization (resource partitioning) reduces levels of competition. Ultimately, niche segregation of this sort serves to promote co-existence of different populations within a resource-limited habitat, and tends to increase the overall efficiency with which the resource is utilized (i.e., tighter spiralling). In an extensive series of studies of filter-feeding larval Trichoptera in North American streams, for example, Wallace and co-workers (Wallace 1975; Wallace and Malas 1976; Malas and Wallace 1977; Ross and Wallace 1982) demonstrated that the various species co-occurring in stream habitats divided the seston resource into niches based on the type of food (animal, algal, vascular plant, detrital) and on its particulate size. Such niche segregation, along with temporal distribution, was thought to permit co-existence of a range of species and age groups in restricted habitats.

Larval Simuliidae (black flies) are an important component of the collector guild in streams throughout most parts of the world.[1] The pre-imaginal stages are passed in the running waters of streams or rivers of a wide range of size, where larvae of the majority of species are passive filter feeders. Labral fans remove particulate matter from the flowing water. The food of larvae consists mainly of seston in the UTOM range (e.g., Williams et al. 1961; Chance 1970). Filter feeding appears to be the major mode of ingestion, but deposit feeding, grazing (scraping) and predation have been reported in some simuliid genera (Currie and Craig 1987).

In several studies, the filter-feeding activities of Simuliidae have been shown to have a measurable impact on the seston (inter alia Maciolek and Tunzi 1968; Ladle et al. 1972). Voshell (1985) reported that the growth of invertebrates in a study stream was enhanced by approximately 11% after removal of an upstream S. jenningsi population. Hart (1986, 1987) has provided evidence that simuliid larvae may be food-limited, and compete with each other at an individual level through aggressive interactions aimed at enhancing the delivery of current-borne particulate material from upstream. In addition to this quantitative role, there is also a qualitative role, in which simuliid

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[1]For reviews of larval black fly bionomics and feeding, see Colbo and Wotton (1981), Walsh (1985) and Currie and Craig (1987).

larvae remove nutrients from ingested food to some degree, change its particulate size and possibly alter the microbial flora as well. Coprophagy (re-ingestion of faeces by another individual) may be important to downstream populations (Wotton 1980), especially to other types of organism, since material processed by one species may well be especially useful to another with different requirements (Cummins 1987).

Studies of filter feeding in larval Simuliidae have focussed largely on the ingestion of inorganic particles under controlled conditions (inter alia Chance 1970; Wotton 1976, 1977, 1978; Kurtak 1978, 1979; Schroeder 1987a, 1987b). In recent years, Craig and co-workers (Ross and Craig 1980; Craig and Chance 1982; Craig and Galloway 1987) have developed a model of filter feeding based on non-sieving filtration mechanisms (Rubenstein and Koehl 1977), which is proving to be valuable to an understanding of feeding preferences in larval Simuliidae and other filter-feeding aquatic organisms (Braimah 1987a, 1987b). Schroeder (1986a, 1986b) has examined feeding selectivity, in European simuliids, for synthetic and other naturally occurring particles in field situations, and has provided evidence for inter- and intra-specific food resource partitioning based on size of certain diatoms and preference for diatoms relative to other algae (Schroeder 1987a, 1987b, 1987c, 1988). Apart from this, relatively little is known on the ways populations of simuliid larvae exploit and

apportion the particulate seston resource in stream habitats.

Although the feeding of simuliid larvae on synthetic particles has been studied in laboratory trials, little experimental work has focussed on feeding in respect to the different types of algae that occur in the natural seston. Preliminary observations by the author indicated that a substantial share of the total volume of gut contents of simuliids collected at sites in the study area was composed of algal particles. Algal material in the mid-gut, however, often appeared superficially to be intact, raising questions as to the actual degree of utilization of algae in the diet, and hence as to the ways in which larvae exploit the available food resource. Furthermore, the fact that algae represent a diverse assortment of particle types and sizes enables their use as ideal indicators of the ingestive and digestive characteristics of the larvae that feed on them.

In keeping with the quantitative and qualitative roles outlined above, the ways that simuliid larvae utilize and apportion the food resource may be expected to be shown in the selectivity with which they ingest and digest available particulate matter. In the present study, therefore, it was hypothesized that there are two levels of selectivity, i.e., ingestive and digestive. It was further hypothesized that ingestive and digestive efficiencies, and hence the range of potential food types actually utilized, might change in

response to different environmental conditions. Expressed in ecological terms, the hypothesis predicted that there is both an ingestive and a digestive component to the larval "feeding niche", and that the niche might expand or contract according to the advent of favourable or unfavourable conditions. The objective of the present research, then, was to examine selectivity of feeding and digestion in larval simuliids of a particular study area under different environmental conditions, using algae as identifiable and quantifiable indicators; and to determine whether there were differences in the ways the various populations of the study community utilized that resource.

It was expected that the findings, by yielding information on larval nutrition in the field, might also help to explain differences in productivity of larval simuliid populations at different sites in the study area (Colbo 1979, 1982) on the basis of quality, as well as quantity, of food. Colbo and Porter (1979) have shown that fecundity, size of adults and larval developmental times are related to the quantity of food available to larvae. Other studies (e.g., Carlsson et al. 1977; Wotton 1978, 1979; Richardson 1984) have suggested that high densities of simuliid larvae near lake outlets stem from the relatively high quantity and/or quality of lacustrine food at these sites.

In addition to presenting a set of problems relevant to an understanding of the functioning of lotic food webs, haematophagous simuliids represent a severe nuisance to humans in many areas of the world, and cause mortality and growth loss in livestock in some areas (e.g., cattle in western Canada). A major, debilitating parasitic disease, onchocerciasis (river blindness), is transmitted from human to human by Simulium damnosum Theobald s.l. in West Africa, and by several other simuliid species in Central America. A knowledge of feeding selectivity in these animals, therefore, would assist the development of control techniques that depend on ingestion of particulate larvicides such as Bacillus thuringiensis.

Specifically, the experiments of the study were formulated to address the following four sets of questions:

1. Are some available algal types ingested selectively? Do different populations of the study community utilize different portions of the assortment of algae available?

2. Do the various types of algae differ inherently in nutritional value to simuliid larvae, and how do algae compare generally in this respect with other available material such as bacteria or detritus? Do the simuliid species of the study community differ regarding which foods are most nutritious?

3. In what ways and to what extent do environmental factors

representative of different local stream conditions or times of year influence the degree to which algal material is acquired and digested while passing through the larval gut?

4. Are some types of algae more resistant to digestion than others?

The present research was carried out on the northern Avalon Peninsula of insular Newfoundland in the general vicinity of St. John's. All of the common simuliid species in the study area were used.[2] These included: Prosimulium mixtum Syme and Davies, Stegopterna mutata Malloch and Cnephia ornithophilia Davies, Peterson and Wood, which occur in the larval stages throughout the winter; members of the Simulium venustum Say/ S. verecundum Stone and Jamnback complex, and S. tuberosum Lundstrom, which exist as larvae during the summer months; and the bivoltine S. vittatum Zetterstedt, whose larvae inhabit local streams both in the winter and summer months.

Questions 1 to 4 were addressed separately by performing the field and laboratory experiments described in the following four chapters. The final chapter discusses the results in a more general context.

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[2]An overview of simuliid life cycles and ecology, focussing on the species used in this research, is given in Appendix I; for further reviews of simuliid ecology, etc. see Laird (1981).

CHAPTER 2 INGESTION AND SELECTIVITY

2.1 INTRODUCTION

To determine whether members of the simuliid community[3] shared a largely similar food resource (i.e., widely overlapping niches, resource sharing) or exploited different fractions of this resource (niche segregation, resource partitioning) in the study area, a study of feeding selectivity by different larval populations was undertaken. Selectivity was assessed primarily in terms of the types of algae ingested by larvae in the field.

Feeding selectivity towards inorganic particles, focussing on particle size, has been studied in larval simuliids by Williams et al. (1961), Chance (1970), Wotton (1976, 1977, 1978), Elsen (1979), Merritt et al. (1978, 1982), Kurtak (1978 and 1979), Braimah (1987a, 1987b) and Schroeder (1987b and 1988). The findings indicate generally that simuliid larvae feed on particles of a wide range of size. Apart from some of the observations of Schroeder (e.g., Schroeder 1987a) and Wotton (1984) evidence for pronounced selectivity is lacking.

Using models for several simuliid species and other aquatic filter-feeding insects, it has been shown (Craig and

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[3]The term "community" as used here refers to the set of simuliid populations inhabiting streams of eastern Newfoundland. "Populations" are defined according to (i) species of simuliid, and (ii) physiological age.

Chance 1977; Craig and Galloway 1987) that hydrodynamic conditions and morphological adaptations are such as to permit water to pass between adjacent primary rays of typical simuliid fans, allowing filtration to occur. This is different from the case of some marine copepods, where bristled appendages serve as "paddles" rather than "rakes" (Cheer and Koehl 1987a, 1987b). The same authors (Chance 1977; Ross and Craig 1980; Craig and Chance 1982; Braimah 1987a and 1987b; Craig and Galloway 1987) have presented evidence for the operation, in larval simuliids, of filtration mechanisms other than, or in addition to, sieving[4]. Specific filtration mechanisms have been proposed for particles of different size and for various water current velocity regimes (Braimah 1987a, 1987b) on the basis of scaled-up laboratory models. The operation of a number of such filtration mechanisms incorporated in the action of a single filtering organ may help to explain the very wide range of particle sizes reported from simuliid larval guts.

Records of the algal taxa observed in larval guts appear in the simuliid literature (e.g., Rubtsov 1940; Anderson and Dicke 1960; Peterson 1965; Burton 1973; Moore 1977a, 1977b). Schroeder assessed feeding selectivity for certain algal groups in several European and Polynesian simuliids (Schroeder 1983, 1986, 1987a, 1987c). However, no quantitative assessments of selectivity with respect to all

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[4]the lodging of particles between adjacent fibers spaced less than the particle diameter

of the different taxa of naturally occurring algae have been made on any simuliid community.

In the following investigations, the proportionate abundances of cells of the various algal taxa recovered from guts of field-collected larvae were compared with that in the seston and periphyton of the habitat, providing a measure of selectivity. In addition, laboratory trials were performed to assess selectivity by simuliids of four species toward a representative alga (diatom) of relatively large particle size, as opposed to non-algal, very small particles in the form of bacteria. Diatoms and bacteria are significant constituents of seston in most local habitats.

2.2 MATERIALS AND METHODS

2.2.1. Gut-Content Analysis of Field-Collected Larvae:

Larvae of the following species of simuliid (see Appendix I) were collected from six streams at various times of year between October 1977 and February 1981: Simulium vittatum; S. venustum/ S. verecundum complex; S. tuberosum; Stegopterna mutata; Prosimulium mixtum; Cnephia ornithophilia. Larvae of early- and mid-instars were collected, when available, in addition to late-instar larvae.[5]

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[5]The term 'mid-instar' refers to the size equivalent of 4th-instar S. verecundum, for which head-capsule dimensions were known for each instar in the study area, and which was used as a standard.

2.2.1.1. Collection Methods:

Collections of larvae were timed and located so that a broad range of ecological and seasonal situations might be included in the study. Streams draining mesotrophic water bodies (Beachy Cove Bk., Healey's Pond outlet), and oligotrophic lakes and bogs (Mt. Scio Bk., Goat Cove Bk., Flat Rock Bk.) were used, and at two stations (Beachy Cove Bk., Healey's Pond outlet), collections were carried out at various times of year (see Appendix II for details).

Seston:

Immediately before each collection of larvae (i.e., within no more than 2 minutes) a sample of stream water flowing within the immediate vicinity of the larvae to be collected, was taken. This was done by quickly dipping a clean, cylindrical, 1-litre (12-cm diameter) polyethylene container below the surface in such a way that water flowed directly into the container. This was repeated until 2-3 litres had been accumulated in a larger, sealed polyethylene container. Sampling sites were always approached from downstream, to prevent re-suspension of sedimented or attached material by turbulence caused by the activities of the investigator. Because the sites chosen were places of relatively shallow, turbulent stream conditions, and because water samples were always taken within about 20 cm of the larvae to be collected, the water samples were considered to be representative of the seston to which larvae were exposed

just prior to collection. On return to the laboratory, 1000 ml of the water sample was poured, after shaking, into a 1000 ml glass graduate cylinder. Lugol's iodine/iodide solution was added, and the cylinder was sealed airtight and left for 3-4 days. After that period, formalin was added to achieve 2% formaldehyde, and the sediment was collected and preserved in a glass vial.

Larvae:

Larvae were collected at the same time and place as the corresponding seston samples by excising pieces of trailing vegetation with attached larvae and plunging them quickly into 30 ml glass vials containing ice-cold phosphate-buffered (pH 7.2) 5% formalin (2% formaldehyde). For collections from rock surfaces, larvae were removed using forceps and similarly treated. Previous laboratory tests had shown that larvae do not regurgitate gut contents when preserved in this manner. In all cases, collections were made over a very small surface area, so as to minimize the influence of spatial variation in habitat. If possible, a scraping of material attached to the substrate (i.e., periphyton) from which the larvae were collected was taken.

2.2.1.2. Dissection:

Larvae were removed from the formalin preservative and rinsed for approximately 10 min. in membrane-filtered (0.2 μm) water. Each was then mounted in filtered water on a microscope slide, and severed transversely with a scalpel blade at a point just posterior to the origin of the proleg.

The anterior portion of the body was lightly compressed so that the most anterior portion of mid-gut contents was extruded in the form of a "plug". This plug was recovered with a 20-μl micropipette and transferred to a drop of filtered water of volume 14-16 μl on another glass slide. The plug was then teased apart with dissecting pins, after which a cover slip was applied. As the underlying water slowly evaporated, the cover slip was gently pushed horizontally back and forth 30-40 times. When the plug contents had been dispersed by this action, the cover slip was sealed around the edges, and the sample was then ready for viewing under a phase contrast compound microscope, at 400X magnification.

The algal populations of the associated seston samples were studied by re-suspending the sedimented seston sample in 5 ml of the preservative solution and examining 20-μl aliquots with a phase contrast microscope at 400X magnification. For periphyton, a small sample was scraped from the appropriate substrate and examined in similar fashion.

2.2.1.3. **Enumeration**:

All cells in each sample, each one taken from one larval gut, were counted by scanning in transects across the slide. This usually resulted in a total of 500-1000 individual algal cells. In larger samples, the survey was terminated after the total count exceeded this range. This was done for solitary and colonial algal types alike. In a few cases, however, thi· was not practical either because of the vast number of tiny cells comprising a filament, or because the delineations between adjoining cells of a filament were not clear. Such was the case for all filamentous Cyanobacteria (blue-green algae) and for some filamentous Chlorophyta (green algae). In such cases the counts represent the number of separate filaments. Bacteria, fungi, detrital matter and vascular plant fragments were not counted because of inherent taxonomic and enumerative difficulties. Also not included in the counts were very small and fragile organisms such as small chlorophyte and some chrysophyte flagellates, which tended to become deformed in the larval guts. The algal taxa that were enumerated are listed in Table 1. In all, 273 larvae were examined.

To put the observations into a somewhat broader context ecologically, and to estimate the selectivity towards food types other than algae, qualitative examinations were made on simuliid larvae and seston from many collections from

Table 1 List of algae observed in seston, periphyton and larval guts[1]

Taxon	Size Class/Compartment	Taxon	Size class/Compartment
Cyanobacteria			
Chroococcus	1 s	Meridion	2
Microcystis	1 s	Asterionella	1 s
filaments	p	Diatoma	1-2 p
		Rhizoselenia	2 s
Chlorophyta		Achnanthes	3 p
Ankistrodesmus	2-3 s	Tabellaria (flocculosa)	2 p
Scenedesmus	2	Tabellaria (fenestrata)	1-2 p
Elakatothrix	1-2	Synedra (radians)	2 p
Chlorella	3	Synedra (acus)	1 s
Cosmarium	2	Cymbella	
Closterium	2	Gomphonema	2 p
Staurastrum	2	Eunotia "A"	2
Arthrodesmus	2	Eunotia "B"	1
Euastrum	2	Fragilaria	1-2 p
Tetraedron	2	Pinnularia	1-2
Netrium	2	Diatom "B1"	2
Micrasterias	2	Navicula	3 s
filaments	p	Nitzchia	1-2 p
		Centric diatoms	
Chrysophyta		Misc. pennate diatoms	1
Dinobryon	1 s	Misc. pennate diatoms	2
Chrysosomatidae	3 s		
chrysophyte "A"	3 s	Pyrrhophyta	
chrysophyte "B"	3 s	Glenodinium	1 s
chrysophyte "C"	2 s	Peridinium	1 s
Dictyosphaeria		Gymnodinium	1 s

[1]size classes: 1 - large particles (large cells or aggregates >40 um maximum diameter).
2 - small particles (15-40 um maximum diameter)
3 - very small particles (<15 um maximum diameter)
s - found exclusively in seston
p - frequently dominant in periphyton but also present in seston

other streams over a wider area than covered in generating the quantitative data (see Appendix III for sites).

2.2.1.4. Analysis of Selectivity:

proportionate abundance:

The proportionate abundance of algal type 'i' in any larval gut sample was defined as r_i, where:

$$r_i = \frac{\text{number of algal specimens of type 'i'}}{\text{total number of algal specimens}}$$

The equivalent variable for the corresponding seston sample was defined as p_i. Both r_i and p_i were transformed to arcsine square root prior to statistical analysis, as a sample of frequency distributions had shown that this transformation produced an approximately normal distribution (Sokal and Rohlf 1969).

analysis of variance/ regression analysis:

To examine for overall selectivity of feeding, r_i (dependent variable) was plotted against p_i (independent variable), running all algal types and all collection samples together. A significant regression, with slope of unity and relatively high r^2 value, would indicate non-selectivity of feeding, i.e., larval diets reflect the assortment available in the environment. Multivariate analysis of variance (MANOVA) was run with simuliid species

and physiological age (instar) added as independent effects in separate runs.

selectivity indices:

Selectivity towards specific algal types and size classes was assessed across all collections using Ivlev's (1961) index of electivity (E_i). Ivlev's index has been the most commonly used index of electivity, and therefore provides comparability with other work. Lechowicz (1982) has reviewed the properties of the various electivity indices, and concludes that they may differ in distribution and absolute value for a given set of data, but that they yield similar results if ranking-type non-parametric tests are used. They can thus be used to compare selectivity for a given 'prey' (algal) type among 'predator' (larval) populations, or to compare selectivity towards various algal types by a single larval population.

In the present study, trends observed using E_i were confirmed using Jacob's D_i (Jacobs 1974), and W_i and E_i^* (Vanderploeg & Scavia 1979a, 1979b). The latter indices were developed to avoid sensitivity to differences among samples in the shape of the offered food size spectrum and to the number of food classes.[‘] Cases in which $r_i + p_i < 0.01$ were eliminated, to avoid the introduction of highly deviant data stemming from very low counts. Details of the indices are

---

[‘]The degree to which this is true is subject to some degree of uncertainty (Lechowicz 1982).

given in Appendix VII.

dietary overlap and niche breadth:

The niche overlap measure developed by Feinsinger et al. (1981) (B_f) and used by Schroeder (1987a) was utilized to compare similarity of diets among pairs of simuliid species. The mean proportionate abundance (r_i) data were used to make all possible comparisons of dietary similarity among late-instar populations of different species taken together in the same collections. As a complement, Horn's (1966) coefficient of dietary overlap (C) was used to assess similarity in diets in the same way as was used to compare diets of other aquatic invertebrates by Fuller and McKay (1981).

Hurlbert's (1978) measure of niche breadth B_h was used to assess the fit between available and ingested algal types for early and late-instar populations. Hurlbert's index maximizes as the fit between utilization and availability of food types improves, is insensitive to the number of resource class divisions, and fits a chi-square distribution (Petraitis 1981). Schoener's index (B_s, Schoener 1974) and Schroeder's R (Schroeder 1987a, as adapted from Levitten 1978) were also used to assess niche breadth, but it is to be noted that the latter two indices suffer from certain statistical limitations (i.e., sensitivity to the means in which the resource is subdivided into classes, and failure to maximize appropriately in all situations (Petraitis

1981)). B_h tends toward unity for non-selective feeding, whilst B_s tends toward 1/n (where n is the number of food classes). For comparability, therefore, B_s was multiplied by the number of algal taxa enumerated. Niche breadths using each of the three indices were compared between age groups (all species combined) and between species, using non-parametric statistics.

2.2.2. Capture Efficiency of Fine Particulate Matter

Six late-instar larvae each of S. vittatum, P. mixtum, St. mutata and C. ornithophilia were introduced to each of a number of polyethylene rearing containers containing 350 ml clear water at 10.5-11.0°C and stirred with a 7.5-cm stirbar at 75 rpm. At the beginning of each trial, dispersed suspensions of Nitzchia diatoms and Pseudomonas (trial 1) or Micrococcus (trial 2) bacteria were added to each rearing container simultaneously such that the wet, packed volume of bacterial cells in the suspension was either 3, 4.5 or 6 times the packed volume of Nitzchia cells. The absolute concentration of Nitzchia cells in each bath was 5 mg/l dry weight.

After an exposure period of 1.5-3 h, larvae were removed individually and dissected immediately. The anterior 10-15% of the mid-gut contents were removed, broken and dispersed with dissecting needles in a separate drop of water and transferred, using a 20 µl capillary tube, to a glass centrifuge tube containing a 1-ml aliquot of filtered

(0.2 μm pore), distilled water.

By performing several cycles of centrifugation and removal of supernatant, the solid contents of each 1-ml sample were concentrated into 5-10 μl of fluid in a 20-μl capillary tube and plugged with agar at the lower end. Centrifugation of the contents packed the suspended material into a small "plug", of which the dimensions could be measured. The volume in the circular concavity of the agar meniscus was computed as the volume of the segment of a sphere, using integration. The volume of the plug in the cylindrical portion above the meniscus was estimated as pi x $(D/2)^2 L$, where L is the mean (four measurements) height of the plug above the edge of the agar meniscus. The total volume was obtained by adding the two portions. The total number of frustules in each of the 1-ml samples was obtained by counting the number in each of three 5-μl sub-samples taken before the concentration procedure described above, and multiplying this figure by 200. Seven such runs were performed, for four species of larvae; three samples were lost due to breakage during centrifugation.

In this way, the relative quantities of diatom frustules (number) and bacteria (volume) could be assessed in any sample. The respective quantities of each were determined for the stock suspensions to the baths, by treating 1-ml aliquots in the same manner as described above.

2.3 RESULTS

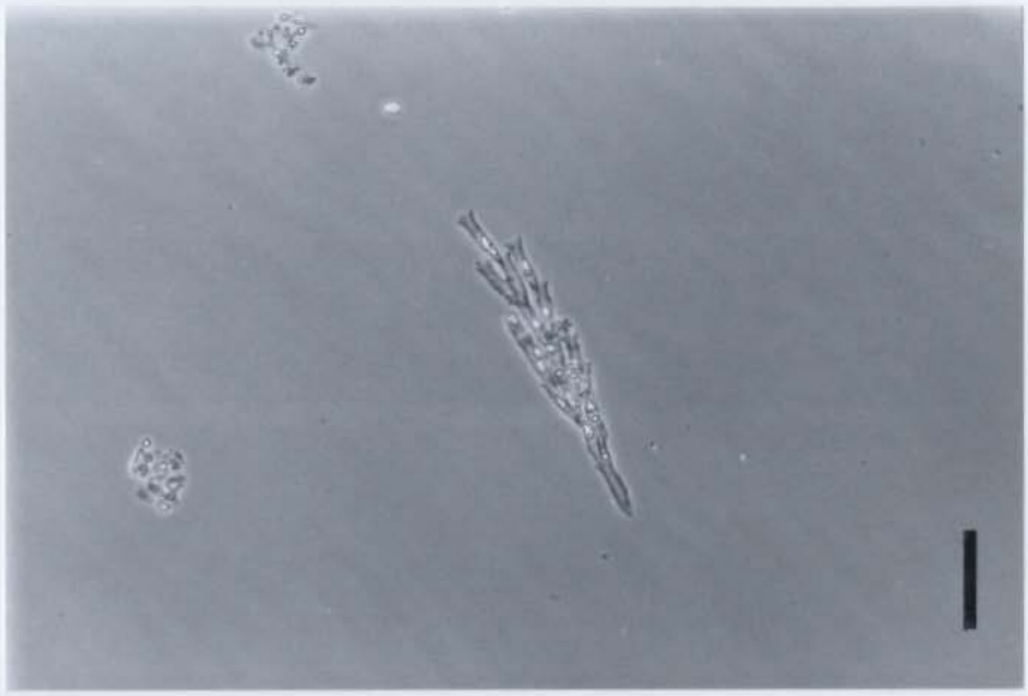
In all of the field observations, algae of a wide range of forms were encountered in the seston and in larval guts (Figs. 1-12).

The relative abundances of the various algal taxa in the seston varied considerably according to site and season of collection. Streams draining both oligotrophic and mesotrophic lakes were usually dominated by certain chrysophytes (chiefly Dinobryon spp.) and diatoms, largely of lacustrine origin. In mesotrophic situations, certain Cyanobacteria and Chlorophyta were abundant in summer/autumn collections. Desmidaceae of many taxa were relatively abundant in streams draining bogs. Periphyton collections were strongly dominated by diatoms and filamentous algae, and were quite distinct in composition fr corresponding seston samples. Miscellaneous or damaged algal cells of unknown taxonomic identity typically comprised less than 4% of all algal cells observed.

Qualitative observations made from the survey of gut contents of field-collected larvae from various sites are given in Appendix III. The composition of the ingested food (proportion that was algal as opposed to other types of particulate matter; major groups of algae present) varied considerably among sites and among various times of the year but was invariably similar to that of the seston collected at the same time and place.

Fig. 1. Dinobryon sp.: colony of about 18 cells. (Taken from water sample at Healey's Pond Brook, 80-03-17) (Scale bar = 50 μm).

Fig. 2. Tabellaria flocculosa (T); Chrysophyte "C" (X); Dinobryon sp. (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).



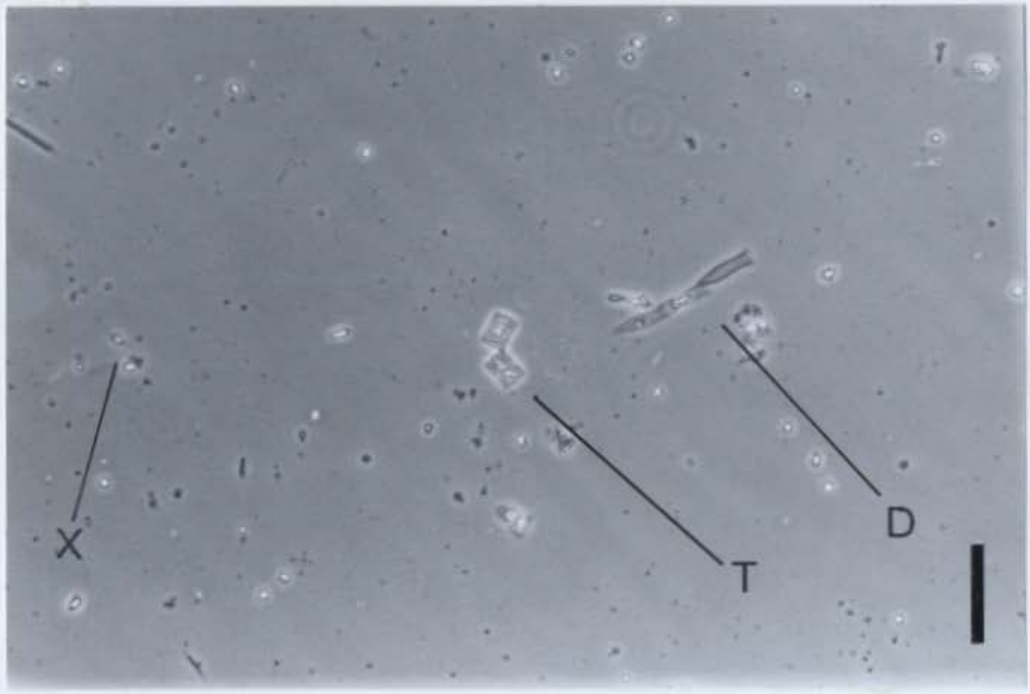
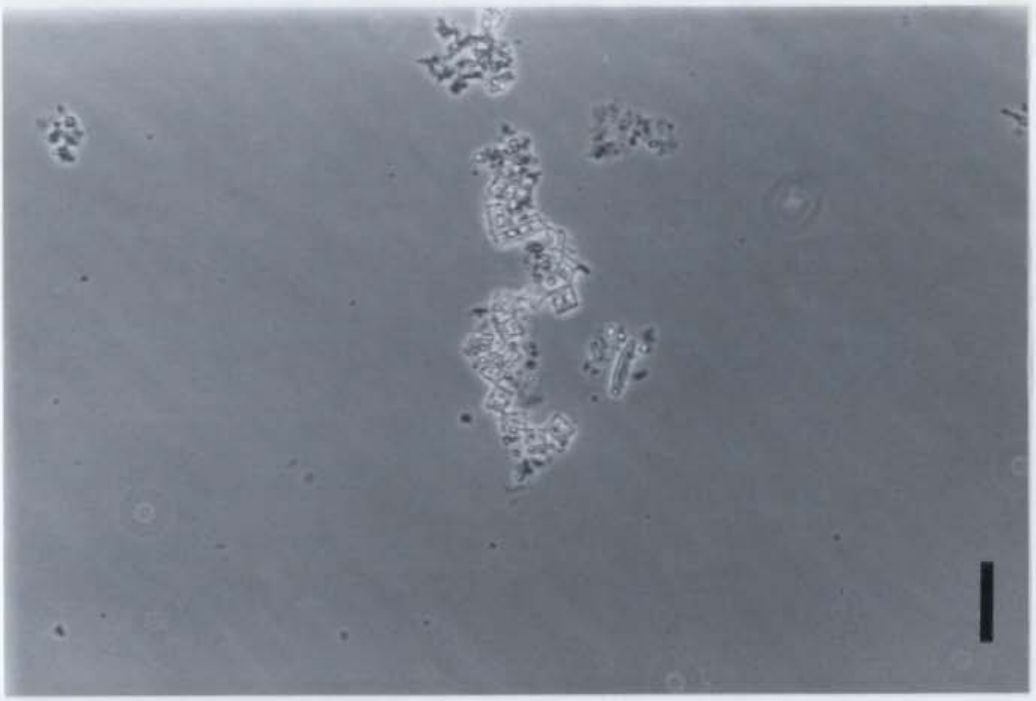

X
T
D

Fig. 3. Tabellaria flocculosa, showing chain-like structure of colony. (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).

Fig. Fig. 4. Synedra sp. (S); also showing various chrysophytes etc. (small, light-toned particles) comprising much of total algal volume in this collection (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).



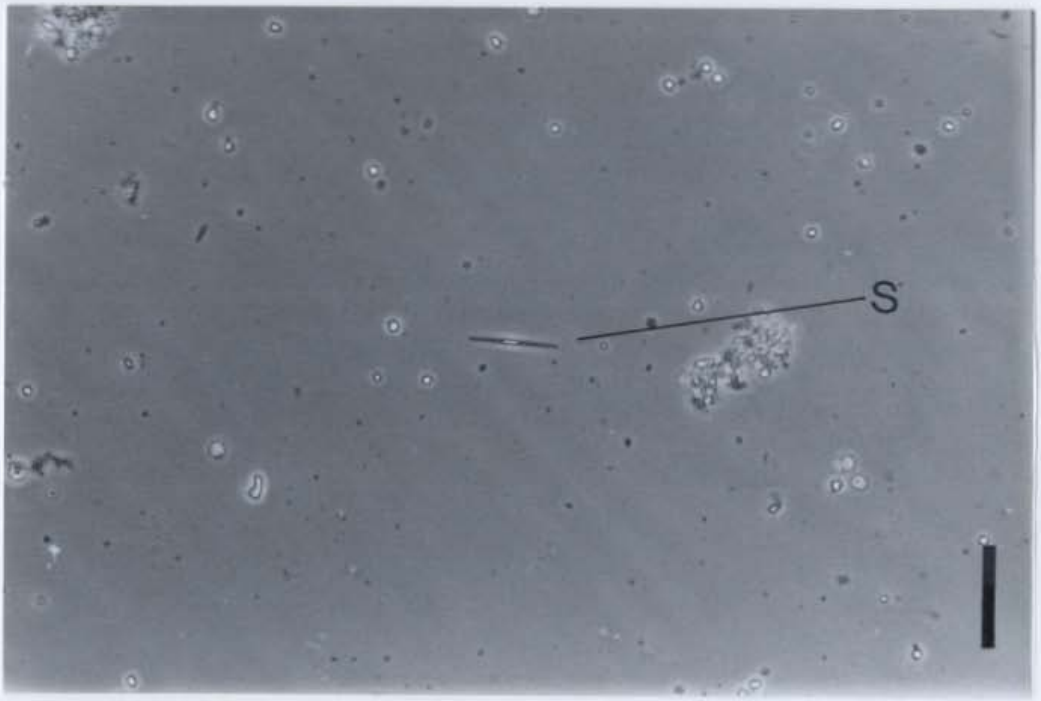
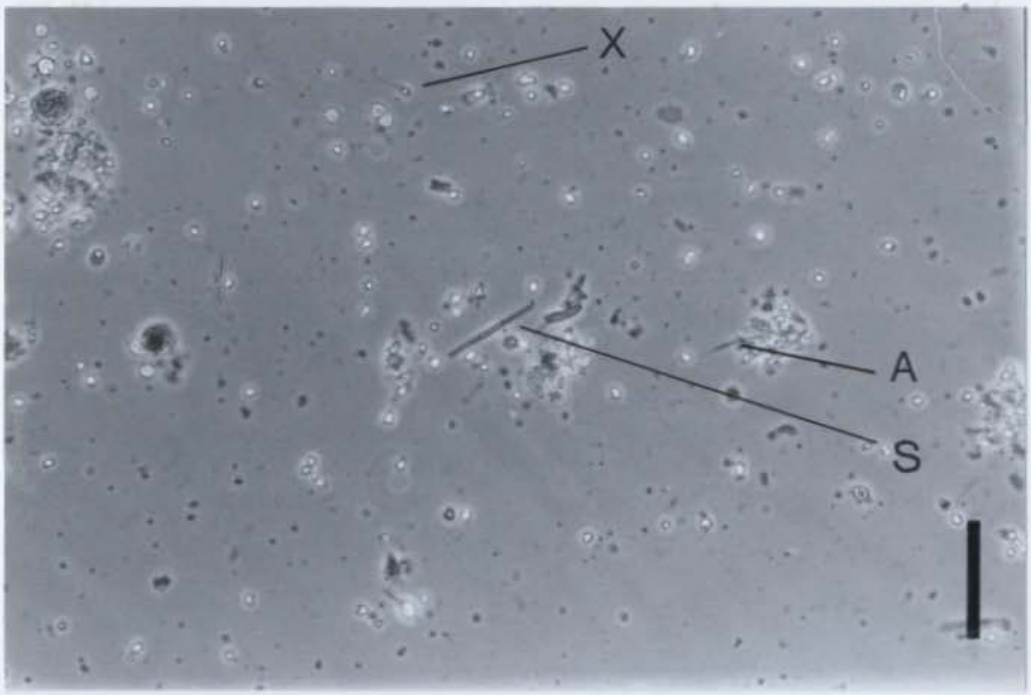

S

Fig. 5. Chrysophyte "C" (X); Synedra (S); Ankistrodesmus (A) (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).

Fig. 6. Tabellaria (T); Dinobryon (D); Ankistrodesmus (A); Chrysophyte "A" (Y). (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).


X
A
S

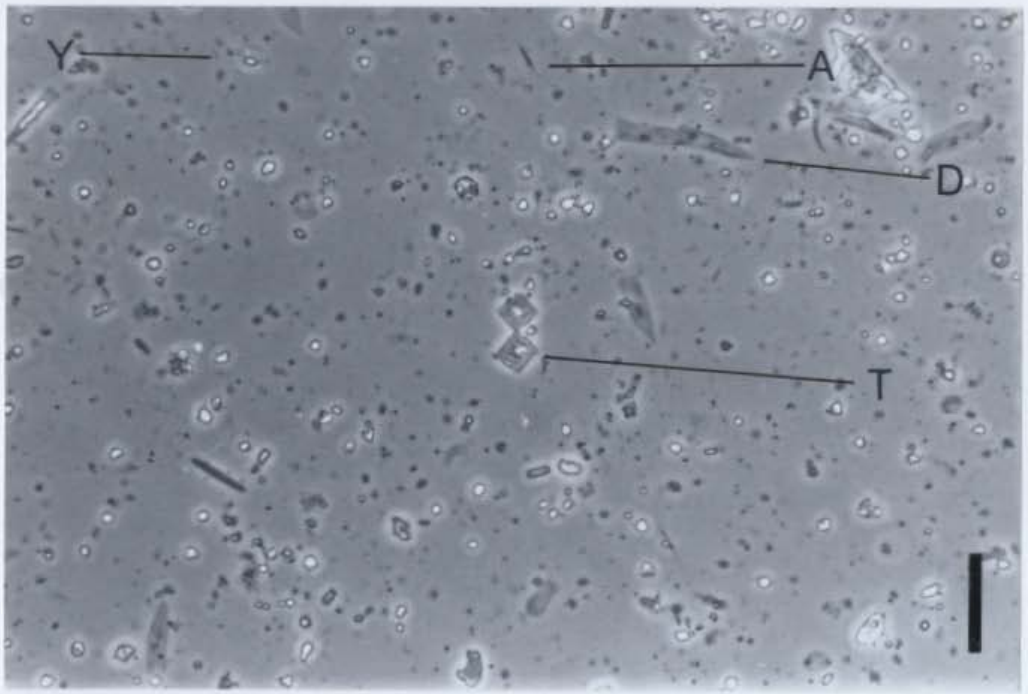
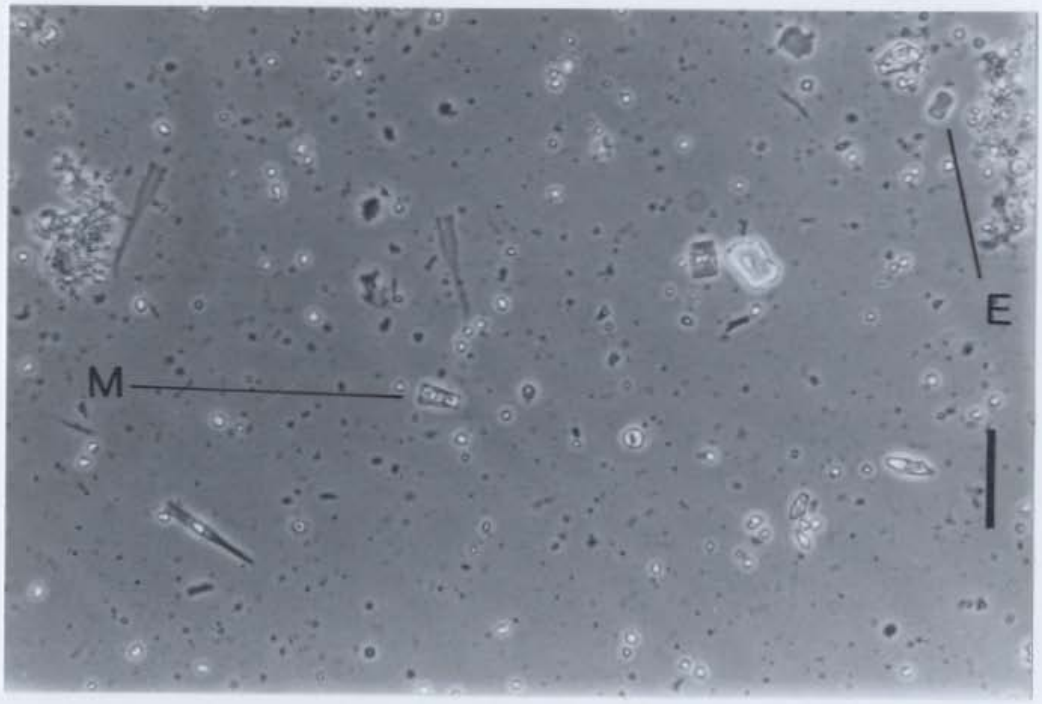

Y
A
D
T

Fig. 7. Meridion sp. (M); Eunotia sp. (E) (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).

Fig. 8. Gomphonema sp. (G) (Taken from water sample at Healey's Pond Brook, 80-03-17) (Scale bar = 50 μm).


M
E

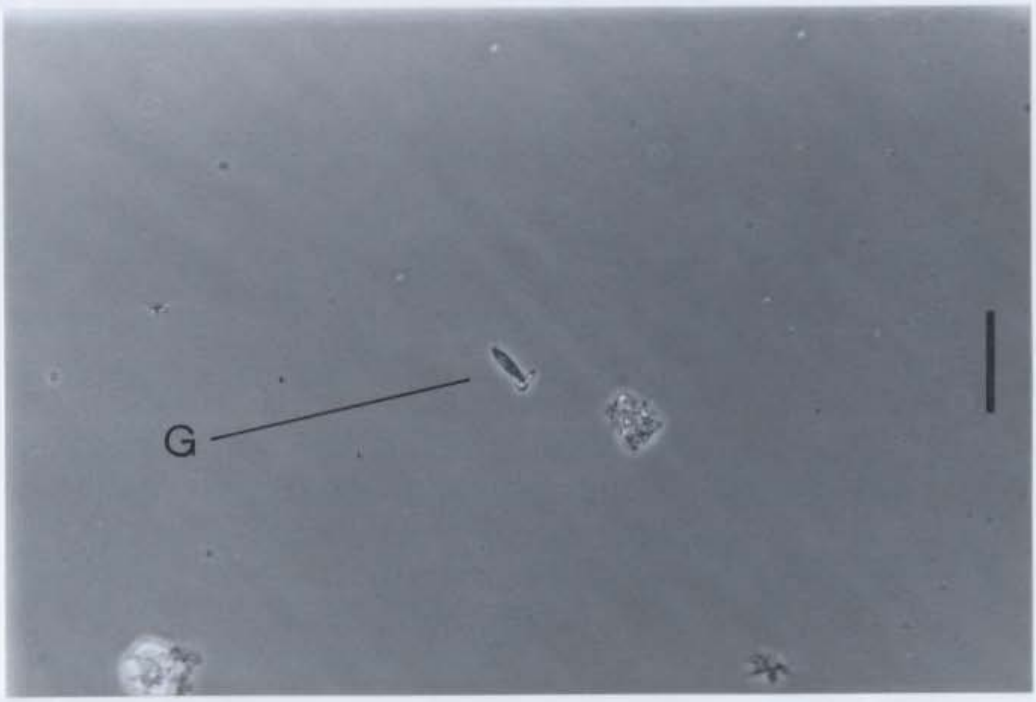
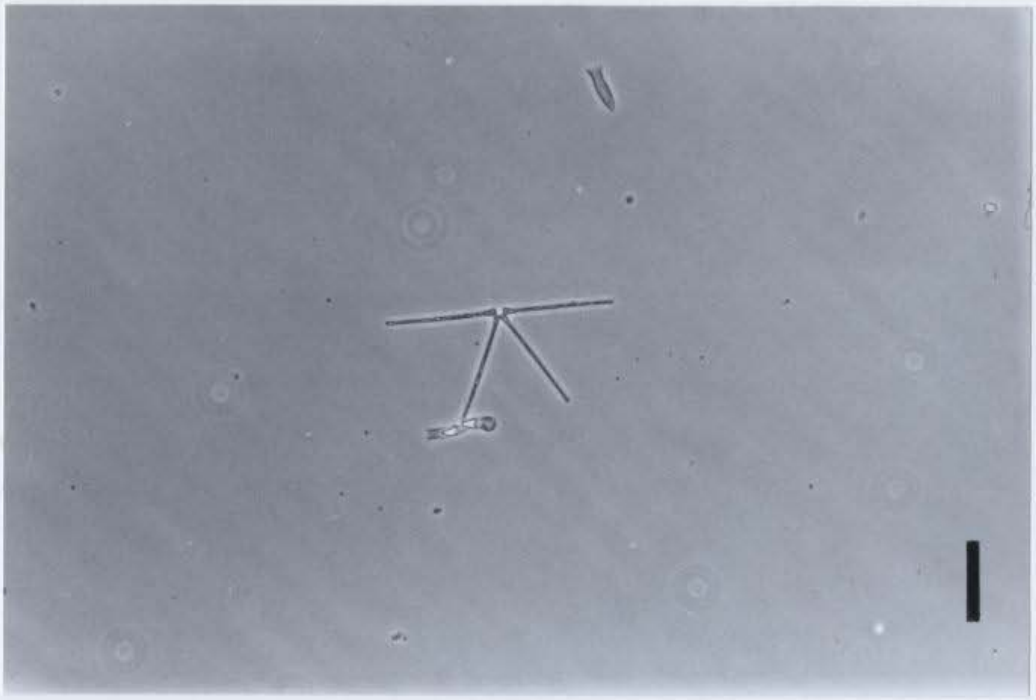

G

Fig. 9. Asterionella sp., showing radial nature of diatom colony. (Taken from water sample at Healey's Pond Brook, 80-02-11) (Scale bar = 50 μm).

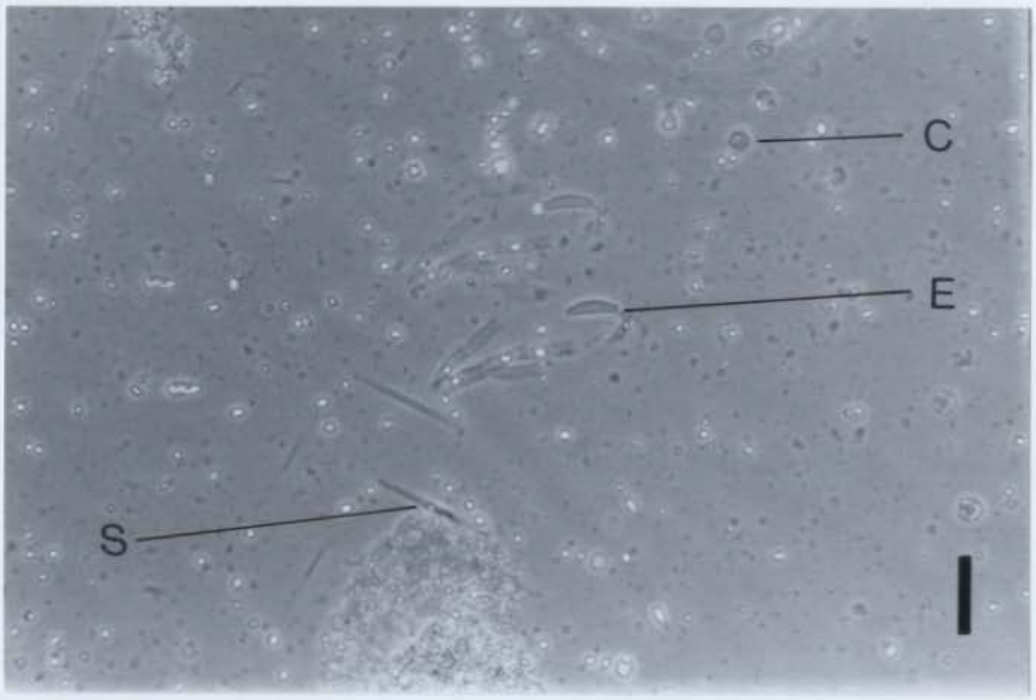
Fig. 10. Dinoflagellate lorica (DF); chrysophyte "C" (X) (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).

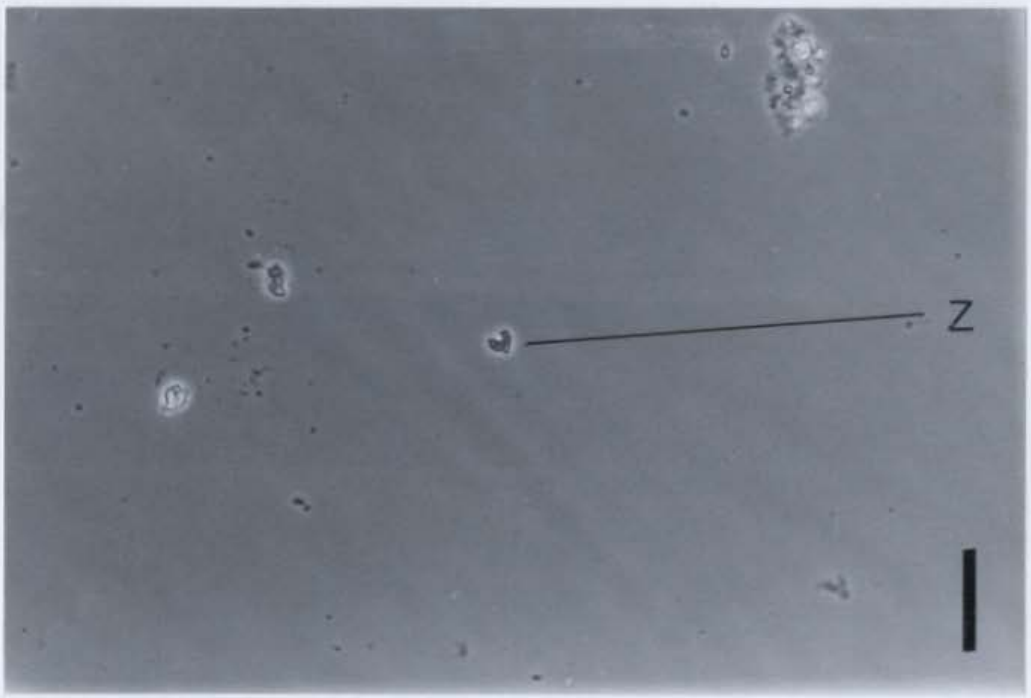



Df
X

Fig. 11. Eunotia sp. (E); Synedra sp. (S); unicellular chlorophyte, probably chlamydomonad (C). The latter were usually damaged, in larval guts, and therefore were not quantified. (Taken from water sample at Healey's Pond Brook, 80-04-30) (Scale bar = 50 μm).

Fig. 12. Chrysophyte "B", in centre (Z). (Taken from water sample at Healey's Pond Brook, 80-03-17) (Scale bar = 50 μm).


C
E
S


Z

The numbers of larvae of various simuliid populations examined for each of the 14 collections are shown in Table 2. The r_i data derived from the quantitative gut-content analyses of these larvae, together with corresponding seston values (p_i) for all of the enumerated taxa, and results of one-way analyses of variance among r_i means appear in Appendix IV (Tables A1 to A11).

2.3.1. **Overall Selectivity:**

An overall lack of selectivity in feeding on the various algal types by the different populations of simuliid larvae was shown in multivariate ANOVA of r_i plotted against p_i (Table 3), in which the relationship between r_i and p_i for all larval populations combined was highly significant ($P < 0.001$). When r_i was plotted against p_i for each sampled population (Table 4), all correlations except that for first-instar *P. mixtum* and that for periphyton, were highly significant ($P < 0.0001$). All regression slopes, except that for late-instar *C. ornithophilia*, were not significantly different from 1.0. Relatively high r^2 values indicated that abundance in the gut was strongly correlated with abundance in the seston, and hence that a high proportion of variance in r_i was attributable to different availabilities (i.e., among collections) of algal types in the seston.

Table 2 The numbers of field-collected larvae dissected

Species	B1 Beachy Up 77-10-27	B2 Beachy DN 77-10-28	H1 Healey 78-02-13	B3,4 Beachy 78-03-14	H2,3 Healey 80-03-17 Veg'n	H2,3 Healey 80-03-17 Rock	H5 Healey 81-02-11
Seston	1	1	1	upstrm: 1 dnstrm: 1	1		1
P. mixtum, 1st instar		10					
P. mixtum, 2nd instar		10					
P. mixtum, mid-instar		10	10				
P. mixtum, late-instar				5[e]	5	5	
C. ornith., mid-instar	6		10				
C. ornith., late-instar				5[d]	3	5	5[b]
St.mutata, mid-instar		4	2				
St.mutata, late-instar					5	5	
S. vittat., mid-instar			5				
S. vittat., late-instar			10		5	6	5[b]
Periphyton					1	1	1[b]
Analysis[a]							

[a] statistical analysis: columns not separated by vertical line were grouped when carrying out ANOVA.

[b] taken from macrophyte stem.

[c] taken from bottom of rock.

[d] from upstream site

[e] from downstream site

Table 2 (cont'd.)

Species	B5 Beachy 78-07-03	G1 Goat 79-06-16	B6 Beachy 1 79-06-16	B7 Beachy 2 79-06-16	M1 Mt. Scio 79-05-12	H4 Healey 80-04-30	F1 Flat Rk. 80-05-09
Seston	1	1	1	1	1	1	1
S. vittat., mid-instar							
S. vittat., late instar	10			7		5[c]	
S. venust., 2nd instar	10		5			5[c]	
S. venust., 4th instar	10		5				
S. venust., 6th instar (from leaf)	10	5	5	5			
S. venust., 6th instar (from rock)		5	5	5			
S. tuberosum		5					
P. mixtum					5	5[b]	5[g]
St. mutata					5	5[b]	5[f]
C. ornithophilia							5[f]
Analysis[a]							

[f] right at headwater

[g] downstream from headwater 10m.

Total larvae dissected: 273

Table 3 Result of multivariate ANOVA examining variation of r_i, with p_i, larval species[2] and physiological age[3] added as independent variables, and using all larval groups[1].

1. With p_i and species as independent variables:

Source of variance	F	df	F prob.
p_i	2308	1	< 0.001
species	1.41	4	NS
interaction	0.84	4	NS

2. With p_i and age as independent variables:

Source of variance	F	df	F prob.
p_i	1956	1	< 0.001
age	5.06	2	< 0.01
interaction	3.83	2	< 0.025

[1] r_i = proportionate abundance of alga "i" in larval gut samples; p_i = proportionate abundance of alga "i" in seston.
[2] compared r_i among species, using late instars only.
[3] compared r_i among age groups (i.e., 2nd-instar/mid-instar/late-instar) for all species combined.

Table 4 Regression analysis of r_i plotted against p_i for different larval populations, using all algal taxa and all collections.

Population	n of larvae	slope (X ± s.e.)	P(slope n.e. 1)[1]	r^2
P. mixtum				
1st-instar	10	N.S.	-	
2nd-instar	10	0.927 ± 0.066	N.S.	0.93
mid-instar	20	0.973 ± 0.054	N.S.	0.91
late-instar	30	1.018 ± 0.051	N.S.	0.82
St. mutata				
mid-instar	6	0.872 ± 0.083	N.S.	0.77
late-instar	25	0.958 ± 0.059	N.S.	0.78
C. ornithophilia				
mid-instar	16	0.907 ± 0.053	N.S.	0.90
late-instar	23	0.886 ± 0.046	<0.02	0.82
S. vittatum				
mid-instar	5	1.018 ± 0.086	N.S.	0.90
late-instar	48	0.965 ± 0.040	N.S.	0.83
S. verecundum				
2nd-instar	20	0.819 ± 0.097	N.S.	0.57
mid-instar	15	0.945 ± 0.073	N.S.	0.81
late-instar	40	0.973 ± 0.040	N.S.	0.89

[1] t-test determining whether slope departs significantly from unity.

This general lack of selectivity was shown also in the overall mean values for the electivity indices E_i and D_i, which were close to zero for most algae, when all larval populations were pooled (Table 5, two left columns). Ivlev's index and Jacob's index theoretically vary between -1 and +1. Values above zero indicate preference by the larvae for the algal taxon, while negative values indicate degrees of rejection. Zero represents neutrality of preference (seston and gut frequencies are equal). E_i responds very rapidly to changes from 0 to 0.10 (Lechowicz 1982), so only values greater than about 0.10 should be considered as substantive. Of the several exceptions, Glenodinium frequencies in larval diets were likely under-estimated, since cells of this fragile dinoflagellate were observed to be considerably damaged in larval guts. Ankistrodesmus, Chlorella and Achnanthes are relatively small in size; the importance of particle size is discussed below.

Comparisons of mean E_i (or D_i) values among different algae using all instars combined showed no significant differences (examples given in Table 5 at bottom), giving little evidence of strong preferences for specific food types within the simuliid community. The overall lack of selectivity for specific algal types by most larval populations is borne out also by the paucity of substantial differences between r_i and p_i means in Tables A1-11 (Appendix IV).

Table 5 Electivity (E_i (Ivlev 1961)) values for late- and mid-instar populations of all species, comparing E_i with D_i (Jacobs 1974) for all ages combined.

Alga	Size Class	All instars[1]		Late-instar	Mid-Instar	
		D_i	E_i	E_i	E_i	P^2
Chroococcus	1	- 0.01	- 0.01	- 0.01	- 0.02	NS
Dinobryon	1	+ 0.05	+ 0.01	+ 0.03	- 0.02	<0.001
Asterionella	1	+ 0.05	+ 0.05	+ 0.11	+ 0.01	NS
Tabellaria (all)	1-2	- 0.01	- 0.01	0.00	- 0.22	<0.01
Diatoma	1-2	- 0.02	- 0.03	- 0.02	- 0.10	NS
Synedra (all)	1-2	- 0.06	- 0.06	- 0.14	+ 0.01	<0.001
Gomphonema	2	0.00	0.00	- 0.10	+ 0.60	<0.001
Glenodinium	1	- 0.59	- 0.58	- 0.59	- 0.57	NS
Algal filaments		- 0.01	- 0.01	+ 0.01	- 0.15	<0.005
Diatom "B1"	2	+ 0.38	+ 0.40	+ 0.04	+ 0.69	<0.001
Ankistrodesmus	2-3	- 0.15	- 0.14	- 0.24	+ 0.22	<0.001
Chlorella	3	- 0.08	- 0.08	- 0.08	- 0.07	NS
Achnanthes	3	- 0.05	- 0.05	- 0.32	+ 0.35	<0.001
All large algae (size 1)		+ 0.03	0.00	+ 0.02	- 0.03	<0.001
All small algae (size 2-3)		- 0.06	- 0.06	- 0.16	+ 0.03	<0.001
All very small algae (size 3)		- 0.04	- 0.04	- 0.14	+ 0.17	<0.001

1 Except first and second instars

2 Probability that late-instar and mid-instar populations differ significantly (Mann-Whitney U test)

3 Examples of inter-algal comparisons (on Jacob's D, left column): Chroococcus/Dinobryon -- NS (P=0.29)
Asterionella/Ankistrodesmus -- NS (P=0.51)
All small/All large -- NS (P=0.12)
(Wilcoxon Matched-Pairs Signed-Ranks Test)

2.3.2. Inter-specific Differences:

In ANOVA (Table 3), 'species' did not significantly affect the correlation between r_i and p_i. Regression analysis (Table 4) yielded relationships between r_i and p_i that were largely similar among simuliid species. Analysis using the Feinsinger et al. (1981) (= Schroeder's theta (1987)) index of dietary similarity (B_f) yielded high similarity values for most species pairs, but revealed consistent differences between late-instar C. ornithophilia and late instars of all other species tested (Table 6). For all pairs in which C. ornithophilia was a member, the mean (±s.d.) index value was 0.738 ± 0.090, whereas for all other pairs the corresponding mean was 0.905 ± 0.066 ($P < 0.001$; Kruskal-Wallis one-way ANOVA).

Horn's index analyses, too, indicated significant overlap and similarity among diets of the species examined.

Niche breadth estimates using Hurlbert's B_h gave further evidence of differences between C. ornithophilia and other species inhabiting winter habitats (Table 7). Differences between C. ornithophilia and the three other 'winter species' combined were also significant using Schoener's B_s and Schroeder's R ($P < 0.001$; Mann-Whitney U-test). These differences were removed when algal types of size class 3 (Table 1) were omitted from the counts.

Table 6 Dietary overlap estimates for 8 species pairs, using measure of Feinsinger et al. (1981). Late-instar larvae compared within collections in which they co-occurred. Collection number in parentheses.

	St. mutata	P. mixtum	C. ornithophilia	S. vittatum
S. vittatum	0.96 (H2)	0.96 (H2)	0.80 (H2)	
	0.88 (H3)	0.86 (H3)	0.76 (H3)	
	0.97 (H4)	0.94 (H4)	0.80 (H5)	
C. ornithophilia	0.79 (H2)	0.80 (H2)		
	0.74 (H3)	0.74 (H3)		
	0.69 (F1)	0.52 (F1)		
P. mixtum	0.94 (H2)			
	0.95 (H3)			
	0.92 (H4)			
	0.92 (M1)			
	0.76 (F1)			
S. verecundum				0.96 (B5)
				0.80 (B7)
Periphyton	0.14 (H2)	0.14 (H2)	0.16 (H2)	0.13 (H2)
	0.12 (H3)	0.11 (H3)	0.10 (H3)	0.13 (H3)
			0.07 (H5)	0.08 (H5)

Mean (± s.d.) where C. ornithophilia is one of paired species: 0.738 ± 0.090 (n=9)
Mean (± s.d.) for all other pairs: 0.905 ± 0.066 (n=14)
Means differ significantly ($P < 0.001$; Mann-Whitney U-test).
S. verecundum diet was largely similar to that of S. tuberosum ($B_f = 0.85$ (G1)).

Table 7 Niche breadth means B_h of Hurlbert (1978), B_s of Schoener (1974) and R of Schroeder (1987a) for simuliid populations co-existing in winter habitats.

A. Hurlbert Index (B_h)

	late-instar	mid-instar
P. mixtum	0.633	0.288
St. mutata	0.677	0.350
S. vittatum	0.656	0.200
C. ornithophilia	0.441	0.376

B. Schoener Index (B_s)

	late-instar	mid-instar
P. mixtum	0.788	0.060
St. mutata	0.800	0.107
S. vittatum	0.588	0.047
C. ornithophilia	0.143	0.044

C. Schroeder Index (R)

	late-instar	mid-instar
P. mixtum	0.762	1.134
St. mutata	0.718	1.259
S. vittatum	0.711	1.138
C. ornithophilia	0.909	1.021

For B_h, B_s and R, late-instar values differ from mid-instar, all species combined ($P < 0.05$, $P < 0.001$, $P < 0.001$; Mann-Whitney U-test)
For B_h, B_s and R, late-instar C. ornithophilia differs from late instars of other 3 species ($P < 0.001$, $P < 0.001$, $P < 0.01$)

The niche-breadth data indicate that the fit between available and ingested food spectra was different for C. ornithophilia as compared to the three other species co-habiting winter niches. There was evidence that late-instar C. ornithophilia showed preference for algae of particle size 5 - 15 μm diameter (size class 3 in Table 1). Mean r_i values for C. ornithophilia feeding on these taxa were frequently statistically different from those of other species taken from the same collections (Table 8). When a new algal class was created by summing counts for all taxa of this size range, selectivity index (E_i and D_i) values were significantly greater for late-instar C. ornithophilia than for late instars of all other winter species. Mean D_i (and 95% C.L.) for C. ornithophilia was +0.030 (0.024 to 0.036), while for the others D_i was -0.165 (-0.25 to -0.09) ($P < 0.0001$; Mann-Whitney U-test).

The dietary overlap and r_i data suggest that the 'summer species' S. venustum/ verecundum and S. tuberosum had virtually similar diets.

2.3.3. Differences among Age Classes:

In MANOVA (Table 3), larval age was a highly significant factor affecting r_i ($P < 0.01$). The significance of the interaction effect (age x p_i) reflected differential feeding by age groups upon a certain fraction of the available algal spectrum.

Table 8 r_i (x100%) values for five selected algal taxa of small particulate size[1] for simuliid larvae of four species

Collection	Taxon	S. vittatum	P. mixtum	St. mutata	C. ornithophilia	F prob.[2]
B3,4	chrysophyte A	-	0	-	0	-
	chrysophyte B	-	0.62	-	2.02	-
	chrysophyte C	-	0	-	0	-
	chrysosomatid	-	0.04	-	0.56 *	<0.02
	Chlorella	-	0.27	-	1.18	-
H2	chrysophyte A	0.08	0.10	0	11.89 *	<0.01
	chrysophyte B	0	0	0	0	-
	chrysophyte C	0.25	0.10	0.10	0.12	-
	chrysosomatid	0.03	0	0	0.35	-
	Chlorella	0.79	0.49	1.45	2.45	-
H3	chrysophyte A	0.14	0.07	0.21	5.30 *	<0.01
	chrysophyte B	0.09	0	0	0.08	-
	chrysophyte C	0.29	0.07	0.07	0.21	-
	chrysosomatid	0.14	0.06	0.03	0.53	-
	Chlorella	1.91	0.75	2.45	15.76 *	<0.01
H5	chrysophyte A	0	-	-	0.05	-
	chrysophyte B	0.52	-	-	19.84 *	<0.01
	chrysophyte C	0.27	-	-	0.06	-
	chrysosomatid	0.04	-	-	0.88	-
	Chlorella	0.21	-	-	0.13	-

[1] cells of these taxa were 5-15 um maximum diameter, except for chrysophyte C, which was similar in appearance to chrysophyte A and chrysophyte B but had long projections about 30 um in length.

[2] F probability for 1-way ANOVA comparing r_i values for indicated algal taxon among simuliid populations; asterisk follows means significantly different from others in same row.

The selectivity patterns are given in more detail in Table 9, showing E_i values for the various populations ingesting four representative types of algae, as well as 'small' and 'large' size classes (see Table 1 for classes). E_i values for large or colonial algae (e.g., Dinobryon, Asterionella) were greater among late-instar larvae than among younger conspecifics. The reverse was true for smaller algae (e.g., Achnanthes, Gomphonema). In this analysis, too, larval age, but not species, was a significant factor determining selectivity (Table 9). Fig. 13 shows the mean E_i values for three size groups of algae, for each of three age groups of larvae (all species combined).

Analysis of niche breadth offered further evidence for different food preferences among age groups (Table 7). Hurlbert index values indicated that early instars of P. mixtum, St. mutata and S. vittatum exploited a narrower spectrum of available food than did late-instar conspecifics ($P < 0.05$; Mann-Whitney U test). Schoener index analysis gave similar results ($P < 0.001$; Mann-Whitney test), while significant differences were also noted in Schroeder's index of overlap ($P < 0.001$).

The frequency distribution of the various algae in guts of first-instar P. mixtum was radically different from those observed in guts of other conspecific age groups, and from the seston sample collected at the same site and time. Substantial differences for specific algal types existed

Table 9 Mean values of E_i (Ivlev 1961) for six algal taxa or groups, all collections.

	Dinobryon	Asterionella	Achnanthes	Gomphonema	all small algae	all large algae
P. mixtum						
1st-instar	-.99	-1.00	+.97	0.99	+.97	-.98
2nd-instar	+.02	-.70	+.64	-	+.45	-.01
mid-instar	-.06	+.24	+.70	+.62	+.01	-.04
late-instar	+.01	+.74	-.88	-.89	-.22	+.03
	**	**	**	**	**	**
St. mutata						
mid-instar	-.29	-.01	+.62	+.95	+.38	-.18
late-instar	+.07	1.00	-.60	-.73	-.26	+.10
	**		**	**	**	**
C. ornithophilia						
mid-instar	-.01	+.01	+.67	+.47	+.05	-.07
late-instar	+.04	+.10	-.40	-.39	-.17	+.01
			**	**	**	**
S. vittatum						
mid-instar	-.03	-	+.73	+.77	-.21	-.03
late-instar	+.06	+.05	-.10	-.01	-.17	+.01
	*		**	**		
S. verecundum						
2nd-instar	-.21	-.57	+.01	+.61	+.04	-.17
mid-instar	+.01	-.04	-.04	+.35	0	+.01
late-instar	+.01	+.03	-.17	+ 03	-.14	0
		*		**	**	*
Mean, all groups[1]					-0.055	0.000
X^2 prob. among age groups[2]					<0.0001	<0.0001
X^2 prob. among species[3]					0.4378	0.0685

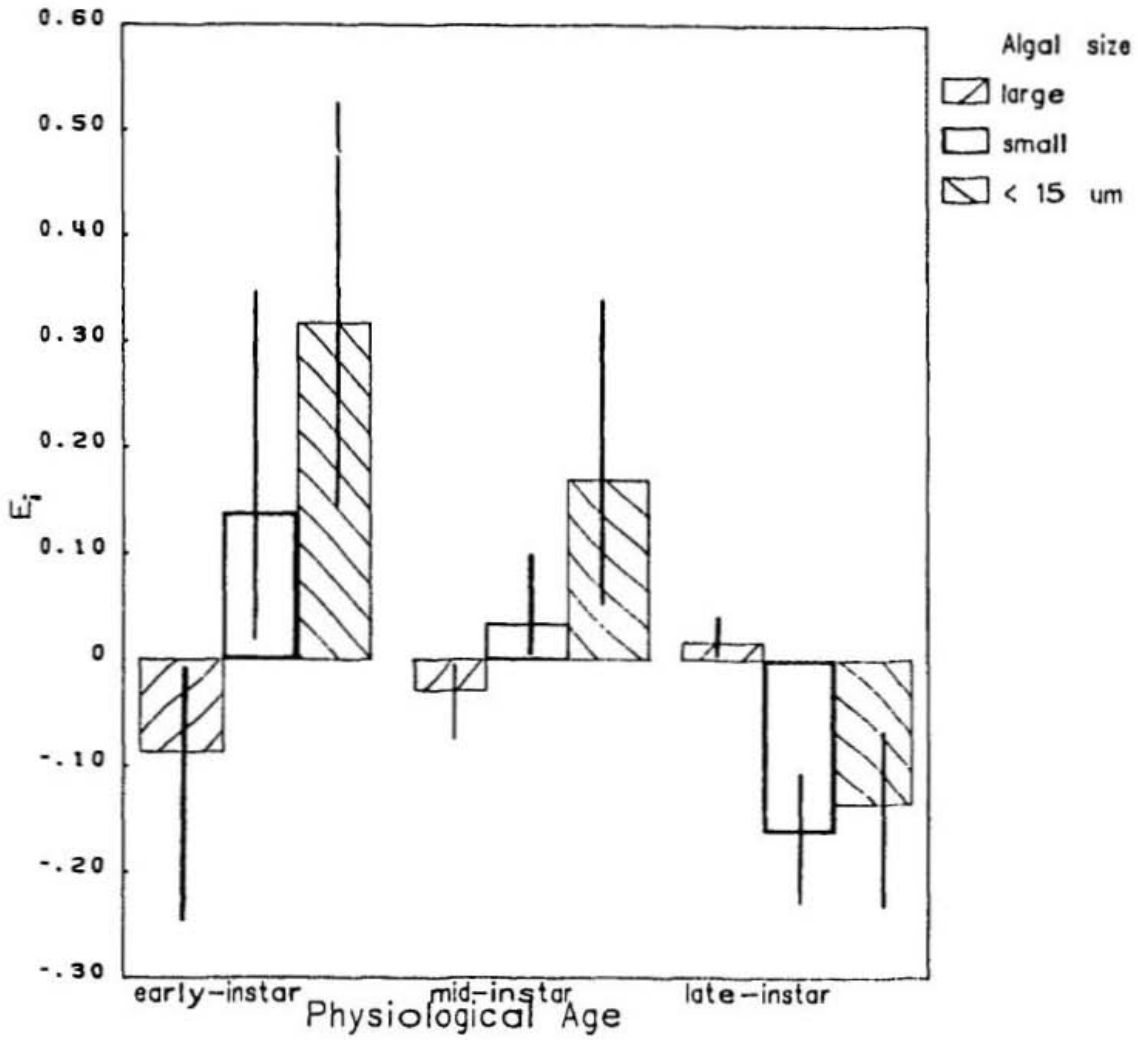
[1] 1st-instar P. mixtum omitted

[2] comparing 2nd/mid/late-instar groups (all species combined); Kruskal-Wallis 1-way ANOVA.

[3] comparing late-instar samples among the different species (Kruskal-Wallis 1-way ANOVA).
* above (i.e., within cell) means differ significantly (* $P < 0.05$; ** $P < 0.01$).

[4] all analyses were re-run using electivity indices Di, Wi and E*i. Although absolute values differed for the various indices, trends and relationships were similar to the above.

Fig. 13. Mean electivity (E_i (Ivlev (1961)) values for three size classes of algae for each of three age groups of larvae (all simuliid species combined; bars indicate 95% C.L.). Early- and mid- and late-instar equivalent to 2nd, 4th and 6th-instar S. verecundum, respectively.


0.60
0.50
0.40
0.30
0.20
0.10
0
-.10
-.20
-.30
E_i
early-instar
mid-instar
late-instar
Physiological Age
Algal size
large
small
< 15 um

even between that population and second instars of P. mixtum, as shown by selectivity index data (Table 9) and by r_i values (Table 10). The occurrences of algae abundant in the periphyton (Achnanthes, Tabellaria, Synedra radians, Gomphonema) were substantially greater in first-instar P. mixtum, while for algae that are found primarily in the seston (e.g., Chroococcus, Dinobryon), they were much lower than for the other populations. The data suggest that P. mixtum first instars acquired much of their algal food from the periphyton rather than the seston.

For later instars of all species, the relatively low values for dietary overlap (Table 6) with the array of food types available in the periphyton was indicative of reliance on the seston, rather than the attached flora, as primary source of food.

2.3.4. Habitat:

In collections where larvae of the same species and of similar age were taken from trailing vegetation or from rock surfaces, the respective r_i data failed to show any substantial or uniform differences in diet of populations taken from these two different substrates. This is illustrated by the data from two sites situated approximately 2 km apart, on Beachy Cove Brook, at each of which larvae were collected from both substrates. Type of substrate proved to be unimportant in influencing diet of S. verecundum (two-factor ANOVA; Table 11), but between-site

Table 10 Proportionate abundances[1] of selected algal taxa in larval guts and seston, expressed as percentages (Collection B2). Groups I and II represent algal types found predominantly in seston and periphyton, respectively.

Alga	Seston	P. mixtum 1st-instar (n=10)	P. mixtum 2nd-instar (n=10)	P. mixtum mid-instar (n=10)	St. mutata mid-instar (n=4)
Group I					
Chroococcus	29.8	0.3 a	19.8 b	30.8 b	37.1 b
Dinobryon	63.4	0.1 a	65.1 b	55.9 b	49.2 b
Synedra acus	0.17	0 a	0.43 a,b	1.52 c	1.11 b,c
Group II					
Achnanthes	0.3	10.9 a	0.5 a,b	0.1 b	0.2 b
Tabellaria	0.4	15.0	0.2	1.0	0.4
Synedra radians	0.5	13.0 a	0.1 b	0.4 b	1.4 a,b
Gomphonema	0	4.0	0	0.1	0.1

[1] r_i x 100% (larval gut samples) or p_i x 100% (seston samples); lower-case letters indicate inclusion in SNK ranges in 1-way ANOVA ($P < 0.05$) within rows.

Table 11 The effect, on larval diet, of two levels of habitat choice: mean r_i (x100%) for S. verecundum collected from two types of substrate and from two widely separated sites on Beachy Cove Brook. Corresponding seston values (p_i) also shown.

	Site A (upstream)			Site B (downstream)			F prob. for effects[1]		
Algae	seston	vegetation	rock	seston	vegetation	rock	site	substrate	interaction
Dinobryon	21.49	21.62	19.41	0	0.09	0	<0.001	0.288	0.880
Diatoma	4.81	2.55	6.75	38.38	59.17	63.24	<0.001	0.126	0.599
Achnanthes	2.86	0.89	0.51	7.39	2.67	2.29	<0.001	0.221	0.742
Synedra acus	13.00	15.38	24.04	1.06	1.15	0.35	0.002	0.764	0.092
Gomphonema	0.41	0.84	1.05	13.03	9.92	9.80	<0.001	0.860	0.687
Fragilaria	0.82	0	0.29	8.27	6.10	6.81	<0.001	0.557	0.798
Nitzchia	2.25	0.56	1.09	19.01	7.24	5.94	<0.001	0.855	0.159

[1] results of 2-way ANOVA testing effects of site (site A versus site B) and substrate (vegetation versus rock) on variation in r_i; n=5 for each substrate x site group

differences in r_i were highly significant ($P < 0.001$). These differences were reflected by between-site differences in p_i values for seston samples, suggesting that dietary differences between sites stemmed from different levels of availability in the seston. Algae predominantly in the periphyton (Diatoma, Achnanthes, Gomphonema, Fragilaria, Nitzchia) were more heavily represented in downstream seston samples, while members of the lacustrine flora (Dinobryon, Synedra acus) were more abundant at the upstream site.

2.3.5. Capture Efficiency of Fine Particulate Matter:

The Nitzchia frustule is elongate, measuring approximately 30 μm x 5 μm. Pseudomonas aeruginosa, a rod-like bacterium, is about 0.5 μm in length, and Micrococcus luteus is a small, spherical bacterium, about 0.2 μm in diameter. Examinations of sample gut contents showed that very little particulate matter other than the diatoms and the bacteria were present in the test baths. The relative abundance of ingested frustules to bacteria was therefore expressed as number of frustules per unit volume of gut contents and was derived as:

V = frustules per sample/ solids volume per sample

If selectivity of Nitzchia over bacteria were absolute, then the expected value of V (V_e) would be equal to the observed value of V for a pure suspension of Nitzchia (Vn). If, however, selectivity for bacteria over Nitzchia were

absolute, V_e would be zero. If no selectivity were to operate, then $V_e = (Vn)/(a+1)$ where "a" is the volumetric proportion of bacteria to Nitzchia offered as food. Let us assume that selection is thus neutral. Since "a" is known for each sample, V_e can be computed and compared with the observed V (V_o). The ratio V_o/V_e is a measure of selectivity. A value of 1 indicates no selectivity. Values more than 1 indicate selectivity for the diatoms.

The mean V_o/V_e ratios for S. vittatum, P. mixtum, and St. mutata ranged from 1.40 to 1.72 but the mean ratio for C. ornithophilia (4.19; Table 12) was significantly higher ($P < 0.005$; Kruskal-Wallis one-way ANOVA). This suggests that selectivity for Nitzchia relative to the bacteria was significantly greater in C. ornithophilia than in the other three species. Preference for the diatoms was shown relative to both Pseudomonas and Micrococcus but was more pronounced when Pseudomonas was used.

2.3.6. Labral fan morphology:

The microtrichia of C. ornithophilia (Figs. 14, 15, 16) are long (30 μm), set approximately 5 μm apart, and appear to form a more or less continuous mesh over the cross-sectional area of the labral fan. Those of S. vittatum and the other species are short (4 - 8 μm) and arranged at intervals of only about 0.5 μm (Figs. 17-21).

Table 12 Results of seven laboratory trials comparing selectivity by four species of simuliids for two particulate foods of different size: a diatom (*Nitzchia*) and bacteria (*Pseudomonas*, *Micrococcus*). Data in cells is selectivity expressed as the ratio V_o/V_e[1]

Trial:	1	2	3	4	5	6	7	Mean ± s.d.[3]
S. vittatum	1.89	0.63	1.58	0.38	1.79	1.44	3.11	1.55 ± 0.90
P. mixtum	0.54	0.87	-	3.17	2.13	2.01	1.61	1.72 ± 0.95
St. mutata	1.17	1.51	1.63	0.13	1.55	-	2.43	1.40 ± 0.75
C. ornithophilia	3.45	-	5.55	4.66	3.72	3.19	4.59	4.19 ± 0.89
offered solution[2]	3:1	4.5:1	6:1	5.5:1	5.1:1	5.1:1	5.1:1	

[1] V_o = observed mean number of *Nitzchia* particles per packed volume gut contents; V_e = expected value of V. V for pure *Nitzchia* culture (packed cells) = 11.97 for trials 1-3, and 9.09 for trials 4-7. Trials 1-4 used *Pseudomonas* as bacterial representative; trials 5-7 used *Micrococcus*.

[2] relative volumes of packed cells in solution offered to larvae, bacteria:diatoms.

[3] means significantly different (X^2 = 13.56; $P < 0.005$; Kruskal-Wallis 1-way ANOVA).

Fig. 14. Head capsule of C. ornithophilia Davies, Peterson and Wood, showing semi-extended labral fans (SEM; Scale bar = 200 μm).

Fig. 15. Primary ray of labral fan, C. ornithophilia, showing long, slender microtrichia (SEM; Scale bar = 20 μm). The microtrichia appear to be sufficiently long to form a continuous mesh between adjacent primary rays. The mesh size would thus be approximately 5 μm.

Fig. 16. More highly magnified view of microtrichia on primary ray of labral fan, C. ornithophilia (SEM; Scale bar = 5 μm).

Fig. 17. S. vittatum Zetterstedt: section of primary ray (SEM; Scale bar = 5 μm). The microtrichial arrangement differs markedly from that of C. ornithophilia, the microtrichia being about 5 μm in length and arranged at intervals of about 0.5 μm.

Fig. 18. P. mixtum Syme and Davies: section of primary ray (SEM; Scale bar = 5 μm). The microtrichial arrangement is somewhat similar to that of S. vittatum but with relatively long microtrichia spaced at 20-μm intervals among the more numerous shorter ones.

Fig. 19. St. mutata Malloch: primary rays (SEM; Scale bar = 20 μm).

Fig. 20. St. mutata: primary rays (SEM; Scale bar = 5 μm).

Fig. 21. S. venustum/verecundum: section of primary ray (SEM; Scale bar = 5 μm).

2.4 DISCUSSION

2.4.1. General Findings:

There was wide variation, among samples of larval gut contents taken at different sites or times of the year, with respect to relative amounts of algal matter, detritus or other classes of material (Appendix III). Within the algal component, there was wide variation in relative abundances of the various algal groups (Appendix IV, Tables A1 to A11). This broad variation was related to site/seasonal differences, rather than any other factor such as species differences or physiological age. The prevalence of algae in the diet was directly related to what was available in the immediate environment. The amount and types of algae ingested might therefore be expected to vary according to site and to season, as the relative abundances of the various algal populations rise and decline.

The apparent linkage between simuliid larval diet and the selection of algae available in the immediate habitat helps to explain the wide range of simuliid gut contents reported in the literature, drawing from various geographic, seasonal and ecological situations. Koslucher and Minshall (1973), for example, observed that S. argus Williston consumed both detritus and diatoms indiscriminately. Muttkowski and Smith (1929) and Coffman et al. (1971)

reported simuliid larvae consuming more algae than detritus. However, Chapman and Demory (1963) observed that most of the food of the simuliids they studied was detritus but that diatoms were taken on occasion; and Smock and Roeding (1986) found S. taxodium Snoddy & Beshear to consume more detritus than algae. Minshall (1967) reported that guts of Simulium always contained the full spectrum of available plant materials but that detritus always constituted most of the volume. Cummins (1973) observed that algae may form the bulk of gut contents of simuliid larvae in eutrophic situations. Kurtak (1979) reported that proportional constituents of larval gut contents of several simuliid species agreed generally with their proportions in the seston, and the thrust of Schroeder's findings on European simuliids is similar (Schroeder 1983a, 1983b, 1986a, 1986b, 1987a, 1987b, 1987c, 1988).

The present study examined selectivity at the level of specific algal types (genera). The data indicate that larvae of all observed species exploited the seston, rather than the periphyton, for virtually all of the total food acquisition. In exploitation of the food of the seston, little selectivity existed by the larvae for specific types of algae. Exceptions to this general finding, relating to larval physiological age, utilization of periphyton, habitat and to relative use of particulate matter of certain size ranges, are discussed below.

2.4.2. Larval size/Physiological age:

Apart from availability in the seston, particle size was the only other factor significantly affecting diet. The size spectrum ingested by younger larvae appeared to be truncated at the upper end, as evidenced by the relatively small proportionate abundances of large or colonial algae for early-instar populations. Schroeder (1980b, 1981a, 1981b) made similar observations in laboratory trials using S. ornatum Meigen (cited as Odagmia ornata) feeding on two types of algae, and in field studies with diatoms (Schroeder 1983). Later work by that author (Schroeder 1983b, 1986a, 1987a, 1987c) revealed that intra-specific differences were generally greater than inter-specific differences. Decrease in ingestion of small diatoms with increasing larval size was noted, while medium (10-50 μm) and large (>50 μm) diatoms increased with larval size. Elsen (1979) observed differences in the particle size range taken by different instars of S. damnosum s.l., but no clear trends among instars in this respect were noted by Merritt et al. (1982). Wotton (1984) concluded that larvae of S. noelleri Friederichs filtered the full range of particles available in the seston. Ability to capture particles larger than 52 μm diameter increased with larval size, while ability to capture particles less than 13 μm (i.e., the particle sizes used in the trials) declined.

Craig and Chance (1982) have observed that larvae of S. vittatum perform some sorting of captured material, using the mouthparts to reject large particles and to guide others to the mouth for ingestion. This mechanism may be used by the younger larvae in order to reject particles too large to be ingested readily. Alternatively, some large particles may escape capture in the labral fans due to their relatively great mass and associated inertial force. Among older larvae, the upper ingestible size limit is extended, but the ability to capture and ingest small particles is apparently retained, as evidenced by the ready uptake of bacterial-sized particles. With increase in larval instar, however, the proportionate representation of the smaller algae is reduced. This could be accounted for by a greater efficiency at capturing larger particles or by reduced efficiency at capturing the smaller. Probably both factors operate. First, for a sieving model of filtration, the "mesh" size (i.e., the distance between adjacent primary fan rays) increases with larval instar, increasing the lower limit below which particles escape by passing between the rays. Second, for the predominant non-sieving filtration mechanisms (Rubenstein and Koehl 1977), the efficiency of capture is proportionate to the ratio of particle diameter to "fiber" diameter. As ray thickness increases with larval instar, the size of particle captured with maximal efficiency will thus increase accordingly, and smaller particles will be captured with less efficiency.

2.4.3. Ingestion of Periphyton:

The first instar of P. mixtum was unique in that ingested algae were heavily represented by those types normally associated with the periphyton. These were most likely taken through grazing, but possibly through deposit feeding as well (Currie and Craig 1987). With the advent of the second instar, gut contents were comprised mainly of algae more typical of the seston, indicating dominance of the filter-feeding mode seen in later instars. It is noteworthy that first-instar P. mixtum have very much reduced labral fans, whereas in the second and subsequent instars the fans are well developed.

Among larvae of all other groups, there was no indication, from gut-content analysis, of reliance upon sessile algae for nutrition; the grazing mode seemed to be responsible for no more than a very small proportion of total food intake. The somewhat higher frequencies of total filamentous algae occasionally encountered in larval guts compared to those in the seston may reflect a certain level of grazing behaviour aimed not primarily at nutrition but rather at maintaining a relatively clear substrate immediately around the larvae so that the functioning of the feeding apparatus and the pattern of flow of water (as outlined by Craig and Chance 1982) might not be impaired. According to Barr (1982), the production of attachment pads in S. vittatum occurs two or three times over the course of

a day. It may be that this 'house-cleaning' type of grazing is aimed at maintaining a cleared area around the larva in preparation for construction of the next attachment pad.

2.4.4. Habitat:

Habitat choice played a role in determining diet of larval simuliids. Water leaving a lake outlet normally contains a typically lacustrine planktonic flora and fauna. As it passes downstream it progressively loses particulate matter through various processes including sedimentation, diversion, entrapment and capture by filter-feeding organisms. At the same time, members of the periphyton - a community quite different in species composition from the lacustrine community - are constantly being washed from the substrate by the stream current. Hence, with further distance downstream from the lake outlet, the "riverine" flora changes progressively from one dominated by lacustrine phytoplankton (mainly green, blue-green algae and chrysophytes, e.g., Dinobryon, Ankistrodesmus, Synedra acus, Chroococcus, Microcystis, Chrysosomatidae, chlamydomonads) to one dominated by stream periphyton (mainly filamentous algae and diatoms, such as Gomphonema, Diatoma, Achnanthes, Meridion, Nitzchia and Synedra radians).

A form of resource partitioning may thus exist as a secondary effect of habitat choice with respect to longitudinal location within a river. Larvae of two species may exploit the local seston food resource in exactly the

same manner, but if one species inhabits the lake outlet whilst the other inhabits the lower stretches, the former species will ingest a much higher proportion of planktonic or tychoplanktonic algae. Larvae of the species inhabiting the downstream stretch will inevitably exploit a higher proportion of periphytic diatoms, algal and fungal filaments etc. that are part of the more strictly riparian, rather than lacustrine, flora. Thus, the diets of C. ornithophilia, (which inhabits lake outlets) may differ markedly from that of P. mixtum inhabiting downstream stretches of the same stream. Similarly, populations of S. venustum/verecundum inhabiting upstream and downstream stretches may exhibit qualitatively different intakes of food. Whether the ultimate reason, in the evolutionary sense, for choice of in-stream habitat is based on trophic or on other factors, is speculation at this point.

2.4.5. Resource Partitioning:

Although no strong evidence was given for selectivity or partitioning based on the nature of algal particle (i.e., diatoms versus desmids versus green algae, etc.), the selectivity and niche-breadth/overlap data provide some evidence for resource partitioning based on the size of algal particle. Evidence for intra-specific selectivity and partitioning, based on particle size, was stronger than that for inter-specific.

At this point, it is useful to explore the interpretation of the data generated using the various niche-breadth measures, and the ways in which they related to other data. Of the indices used, B_s responds most sensitively to differences between r_i and p_i, and this is particularly so with food classes that are rare in the environment (seston), thus tending to bias the results; B_s also suffers from the disadvantages that it is sensitive to the number of food classes used in enumeration, and that it fails to maximize properly in all situations. Schroeder's index (R) essentially compares evenness of the frequency distributions of food classes between diet (gut samples) and environment; r_i and p_i are not coupled for any food class, and hence the relative abundances of foods in diet and environment could be quite distinct and yet not be detected by this index. Hurlbert's B_h, while not as sensitive as B_s, suffers from none of the above disadvantages, and is perhaps the best measure, overall, tending toward 1 when there is no selectivity.

The behaviour of the three indices in respect to different diets is illustrated in Appendix VII (Table D1) using simulated data for environment and diets of two foraging species. When counts of rare food classes are inflated somewhat (species 'B'), B_s drops sharply, responding to differences between r_i and p_i. B_h declines moderately, while Schroeder's index increases, due to the increase in evenness of the diet as compared to the

environment. The indices thus respond in quite different ways to the same data, and caution must be used in their interpretation. In the present study, both intra-specific (between age classes) and inter-specific (between C. ornithophilia and others) differences were observed using each of the indices. The above illustrates that such differences could be explained by higher counts among the relatively rare food (algal) types, but the other selectivity parameters must be examined to elucidate this.

There are several lines of evidence suggesting that the above niche-breadth differences stemmed from selectivity toward algae of relatively small particulate size. The fact that differences in B_s and B_h between C. ornithophilia and others were removed when algae of the smallest size class (most of which were rare) were left out of the analysis, suggests that such is in fact the case. That selectivity indices E_i and D_i highlighted substantial differences between C. ornithophilia and the others in respect to selectivity towards algae of that size class supplies further evidence.

The selectivity data also suggest differences between age classes in respect to preference for the smallest algae. The data suggest that early instars of S. vittatum, P. mixtum and St. mutata exploited slightly different, but broadly overlapping feeding niches from that of late instars. Larger, relatively abundant taxa were less

represented in diets of early instars, leading to poorer fit between seston and diet.

On general grounds, the most intense competition for food -- and hence the development of resource partitioning mechanisms to reduce interference -- might be expected to occur between larval simuliid species most closely associated in time and in space. Larvae of S. vittatum, P. mixtum, St. mutata and C. ornithophilia all inhabit the headwaters of streams during the winter and early spring. S. venustum/ verecundum and S. tuberosum larvae develop throughout the summer. Little evidence of inter-specific food partitioning was shown, however, among S. vittatum, P. mixtum and St. mutata, or between S. verecundum and S. tuberosum, suggesting either that food is not limiting in such situations, or that other resource partitioning mechanisms operate. C. ornithophilia displayed somewhat different selectivity from that shown by the other three winter species. This is discussed in more detail in Chapter 6.

2.4.6. Sources of Variance:

Within-group variance was higher than might be expected if samples were simply drawn at random from the seston. A number of factors could explain this. Craig and Galloway (1987) have suggested that relatively dense material rolling downstream along the substrate surface may be entrained by vortices created by the larvae themselves, and swept up into

the labral fans. Since this material would likely contain a high proportion of periphytic algae, hydrodynamic factors varying over a small spatial scale might influence the relative abundance of this faction of algae in the diet of individuals. As mentioned previously, periodic grazing by larvae could also enhance the representation in larval diets, of periphytic algal types. The ingestion of faecal pellets from upstream organisms of specialist feeding habits could potentially influence the findings by accentuating the representation of the specific algal types preferred by them. Cytotypic differences within the larval populations defined in the study did not likely affect the data, since S. vittatum, C. ornithophilia, P. mixtum and St. mutata are believed to consist of single entities in Newfoundland. Members of the S. venustum / verecundum complex, if collected in early Spring at lake outlet habitats would likely be cytotype EFG (Rothfels et al. 1978), while those collected later and at more downstream habitats would be any of six cytotypes (M. Colbo and J. McCreadie, pers. comm. 1989). Further work is necessary to determine whether there are feeding differences among cytotypes of S. venustum /verecundum. Substantial differences would seem to be unlikely, however, as no evidence of distinct divisions within or among sampled populations on the basis of diet (e.g., marked preference for grazing) is apparent in the data.

CHAPTER 3 NUTRITIVE VALUE OF SELECTED ALGAL AND OTHER PARTICULATE MATERIALS

3.1 INTRODUCTION

Chapter 2 addressed the question of whether simuliids in their natural habitat selected certain types of particulate matter for ingestion as potential food. The conclusion was that, apart from particle-size effects, little selection occurred. Because there was initial, visual evidence that algae, at least, were incompletely digested, the question was raised as to whether larvae were selective in utilizing ingested materials as food. The potential value of any material as 'food' is a function both of the nutritional content of the material and the degree to which these nutrients are released from it during the period that it passes through the gut. Food quality may be defined as the growth-producing nutritive content per unit mass, as opposed to food quantity, i.e., the density per unit of environment (Cummins 1974; Ward and Cummins 1979). A direct way of assessing the potential food value of a given material is to offer experimental subjects pure diets of it, and measure larval growth over time.

Growth and survival rates (Fredeen 1964; Ladle and Hansford 1981) and assimilation efficiencies (McCullough 1975; Wotton 1978; Schroeder 1979) have been measured in larvae of other species of simuliids (S. posticatum Meigen (as S. austeni), Wilhelmia Enderlein sp.) reared on diets of

certain algae and bacteria, but no studies have been carried out on Newfoundland species. In the following laboratory trials, larvae of four species of the study area were reared on standardized suspensions of unialgal cultures, bacteria or detrital matter. Mean larval growth was used as a variable to compare the nutritional values of 12 potential foods representative of seston components commonly available in local habitats.

3.2 MATERIALS AND METHODS

3.2.1. Larval Rearing:

Cohorts of larvae were reared simultaneously and under similar conditions except for the type of food offered. Such experiments require a reliable and efficient means of rearing larval cohorts simultaneously for relatively long periods with little mortality. During the early stages of work, a significant amount of time was spent developing such a procedure for larval simuliids. The method that was used is described by Colbo and Thompson (1978).

In most cases the food was a unialgal culture or a suspension of a particular bacterial species. Pulverized leaves of speckled alder (Alnus rugosa) - a common local riverside shrub and probably a major source of detrital particulate matter through shed leaves - were also used as a test diet. In each experiment, the amount of food given to each larval cohort was carefully standardized in terms of

dry weight of culture so that regardless of the type of food offered, each cohort was supplied with the same daily dry mass of food. After the exposure period, which varied among experiments from 9 to 20 days, surviving larvae were collected and preserved in ice-cold phosphate-buffered 5% formalin.

3.2.2. Measurement of Larval Growth

Cohorts of early-instar larvae for each species were formed by selecting from a large batch of larvae those that were of a given instar based on a narrow range of head-capsule widths. Just before the exposure period, one cohort was randomly selected; larvae in this sample were preserved in formalin immediately as a pre-treatment sample. The others were exposed to the various treatments for the remainder of the experiment. A second control group received no food.

At the end of the trial, larvae were removed from the formalin preservative and immersed in 5% formalin in a chamber fixed by a narrow ring of modelling clay fastened around the perimeter of a microscope slide. A second microscope slide was placed on top of the ring and carefully pressed onto it. This chamber was mounted on the stage of a projector positioned so that an image of the contents of the chamber was focussed on the measuring tablet of a Zeiss MOP-3 Digital Analyzer. The image of each larva, in lateral view, was traced with the sensing device, and the area of

the magnified image (in mm^2) was thus computed by the instrument. The labral fans, proleg and anal gills were not included in the trace.

The projected area provides a relative measure of larval size, which, when corrected for mean pre-trial size, yields a relative measure of larval growth. Because it may be expected to vary as the two-thirds power of larval volume (which is related to mass), the above measure is used herein for comparative purposes only. Merritt et al. (1982) determined, through direct measurements, that there was a firm ($r^2 > .90$) correlation between larval dry mass and larval length in *D. mixtum* and *St. mutata*, suggesting that areal size (proportionate to the second power of length) correlates with mass. The data were transformed to $\log(x + 1)$, as this procedure produced an approximately normal frequency distribution (Sokal and Rohlf 1969).

3.2.3. Production of Diet Cultures:

Algal cultures were grown in defined salt media (Bold's Basal and Chu #10), and were grown under continuous light at 20°C. The inocula for the cultures were obtained either from the Memorial University culture collection or from commercial suppliers. Some were isolated, by the author, from local collections of stream water or periphyton, by culture on agar plates (*Scenedesmus*, *Nitzchia*, palmelloid *Chlamydomonas*).

Bacterial cultures were scraped from agar plates and dispersed in water, to be used as stock mixture.

Fallen alder leaves were collected from the ground near the banks of a local stream, desiccated and then processed with water in a tissue grinder until a very fine suspension was formed.

The diets used in the experiments are listed below:

group	species	source[7]
(a) green algae	Chlamydomonas rheinhardii	M.U.N.
	Scenedesmus sp.	B.H.T.
	Ankistrodesmus sp.	Ward's
	Chlorella pyrenoidosa	M.U.N.
	Chlamydomonas sp. (forms only palmella in Chu #10 medium)	B.H.T.
(b) diatoms	Navicula sp.	M.U.N.
	Nitzchia sp.	B.H.T.
(c) bacteria	Bacillus subtilis	M.U.N.
	Pseudomonas aeruginosa	M.U.N.
(d) Cyanobacteria	Oscillatoria sp.	B.H.T.
(e) alder leaves		

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[7]
B.H.T. = isolated locally by author
M.U.N. = from culture collection, Memorial University Department of Biology
Ward's = from Ward's Natural Science, U.S.A.

Dry-weight concentrations of algal, bacterial and leaf suspensions were determined by passing an aliquot of suspension through a pre-weighed membrane filter (0.4 μm), which was subsequently dried at 60°C for at least 4 h and re-weighed.

3.2.4. Schedule of Experiments:

Nine rearing trials were carried out using S. verecundum, S. vittatum, P. mixtum or C. ornithophilia. Table 13 gives for each experiment the diets used as treatments and information on the conditions under which the larvae were reared. The appropriate daily food mass and temperature regimes were selected according to the species, the stage of development at the outset of the trial, and the intended duration.

3.3 RESULTS

The mean relative sizes of larvae (i.e., area of projected image) in cohorts reared on the various foods are shown for each of the nine trials in Table 14. The specific data collected during the trials are given in Tables B1-B9 (Appendix V). All diets provided at least some increase in mean larval size, as compared to the pre-trial or control (no food) means, but some diets yielded larger increases than others.

TABLE 13 Schedule of laboratory rearing trials using different foods as treatments, for larvae of four species

Trial No.	species	duration	temp.	food per day[a]	Chlamydomonas	Scenedesmus	Ankistrodesmus	Chlorella	Chlamy. palmellae	Navicula	Nitzchia	Gm + bacteria	Gm - bacteria	Oscillatoria	leaves
1	S.verecundum	10 days	21°	2 mg	1	1		1		1		1	1		1
2	"	9 "	21°	2 mg	1	1		1		1		1	1		1
3	"		18-20°	0.05 mg	1	1		1		1		1	1		1
4	C.ornithophilia		12°	"	1	1		1		1		1	1		1
5	P.mixtum		5°	"	1	1		1		1		b.	1		1
6	S.vittatum	20 "	18.5-20°	0.05 to 1 mg	1	1	1	1	1		1	1	1		1
7	S.verecundum	19 "	18.5-20°	0.05 to 1 mg	1	1	1	1	1		1	1	1		1
8	S.vittatum	17 "	16.5-19.5°	2 mg	1	1	1	1	1		1	1	1	1	1
9	C.ornithophilia	17 "	11-12°	2 mg	1	1	1	1	1		1	1	1	1	1

a. where a range is specified, it indicates progressive increases in food offered at points in the trial, for all treatments at once. All cohorts in each of the trials were given equal amounts (mg dry weight) on any given day.

b. apparatus failed

Table 14 Mean relative sizes of larvae in cohorts reared on different foods[1]

	S. verecundum				*S. vittatum*		*C. ornithophilia*		*P. mixtum*
Trial no.:	1	2	3	7	6	8	4	9	5
Amount (mg./day)	2	2	0.05	0.05-1	0.05-1	2	0.05	2	0.05
Duration (days)	10	9	15	19	20	17	20	17	20
Larvae per cohort	25	25	30	28	25	30	20	20	20
Rations:									
Diatoms	1212 a	1983 a	1959 a	442	1243 a	1190 a	3420 a	1080 ab	1203 a
Chlamydomonas	1366 a	1661 a	-	0	699 bc	813 ab	-	1375 a	-
Chlorella	690 b	1189 a	1400 b	0	0	293 cd	2163 ab	1218 ab	851 b
Scenedesmus	491	1195 a	910 b	0	447	234 cd	1113 bc	722 c	648 bc
Ankistrodesmus	-	-	-	212	776 b	386 c	-	946	-
Bacteria gm+	807 b	1087 a	1372 b	0	604 bc	296 cd	2513 ab	1259 ab	633 bc
Bacteria gm-	571	853 ab	1046 b	97	603 bc	231 cd	2480 ab	736 bc	726 b
Leaves	612 bc	501 b	611 c	0	0	0	1832 b	832 bc	665 b
No food	196	426 b	535 c	-	-	174 d	1021 c	873 bc	553 bc
Pre-treatment	480 c	364 b	106 d	65	521 c	108	240 d	121	489 c

[1]Relative size = area of projected larval image, in mm^2; a zero indicates no surviving larvae: dash indicates this diet not used, or all larvae died early in trial from unexplained causes.
Lower-case letters indicate inclusion in SNK ranges ($P < 0.05$) in within-trial 1-way ANOVA (i.e., comparing means within columns).

Diatom diets generally produced larger larvae than did other diets. Larvae reared on Chlamydomonas flagellates were also relatively large in most trials.

Bacterial diets generally produced smaller larvae than did diatoms or Chlamydomonas diets. Gram-positive bacterial diet often produced larger larvae than did Gram-negative bacteria, but these differences were not statistically significant. Leaf litter produced, overall, the smallest larvae. Surprisingly, larvae that were offered no food in most cases increased in size, though not to as great a degree as those offered the various diets. The reason for this is not clear. Examination of the rearing water revealed no significant source of contamination, although colloidal material may have been formed from flocculation of dissolved organic matter in the water.

To further examine differences among the types of food offered, the foods were grouped as follows: diatoms (Navicula, Nitzchia); thin-walled Chlorophyta (Chlamydomonas flagellates); firm-walled Chlorophyta (Ankistrodesmus, Chlorella, Scenedesmus); bacteria (Bacillus, Pseudomonas); and leaf material. Growth of individual larvae in test cohorts was expressed as the projected image size minus the mean larval image size in the corresponding pre-trial sample; this is referred to hereafter as the corrected size. Table 15 shows the mean corrected sizes for each simuliid species, and results of Kruskal-Wallis one-way analysis of

Table 15 Relative corrected size (mean ± s.e.) of larvae in cohorts provided five different diets[1]

Food class	S. verecundum	S. vittatum	C. ornithophilia	P. mixtum
Diatoms	1401 ± 94	903 ± 77	1946 ± 247	714 ± 68
Chlamydomonas	1018 ± 98	450 ± 55	1254 ± 109	-
Ankistrodesmus/ Scenedesmus/ Chlorella	894 ± 53	203 ± 35	1032 ± 76	242 ± 50
Bacteria	775 ± 53	110 ± 26	1626 ± 125	204 ± 42
Leaf material	339 ± 42	0	1052 ± 115	176 ± 28
Total n of larvae	309	153	178	68
X^2 (prob.)	73.2 (P<0.001)	77.6 (P<0.001)	24.0 (P<0.001)	25.8 (P<0.001)

[1]mean corrected size of projected larval image; X^2 values from Kruskal-Wallis 1-way ANOVA among diet groups, within larval species.
For all species combined, diatoms > all other groups ($P < 0.001$); Ankistrodesmus/Scenedesmus/ Chlorella > bacteria ($P < 0.05$); bacteria > leaf material ($P < 0.005$)(Mann-Whitney U-test).

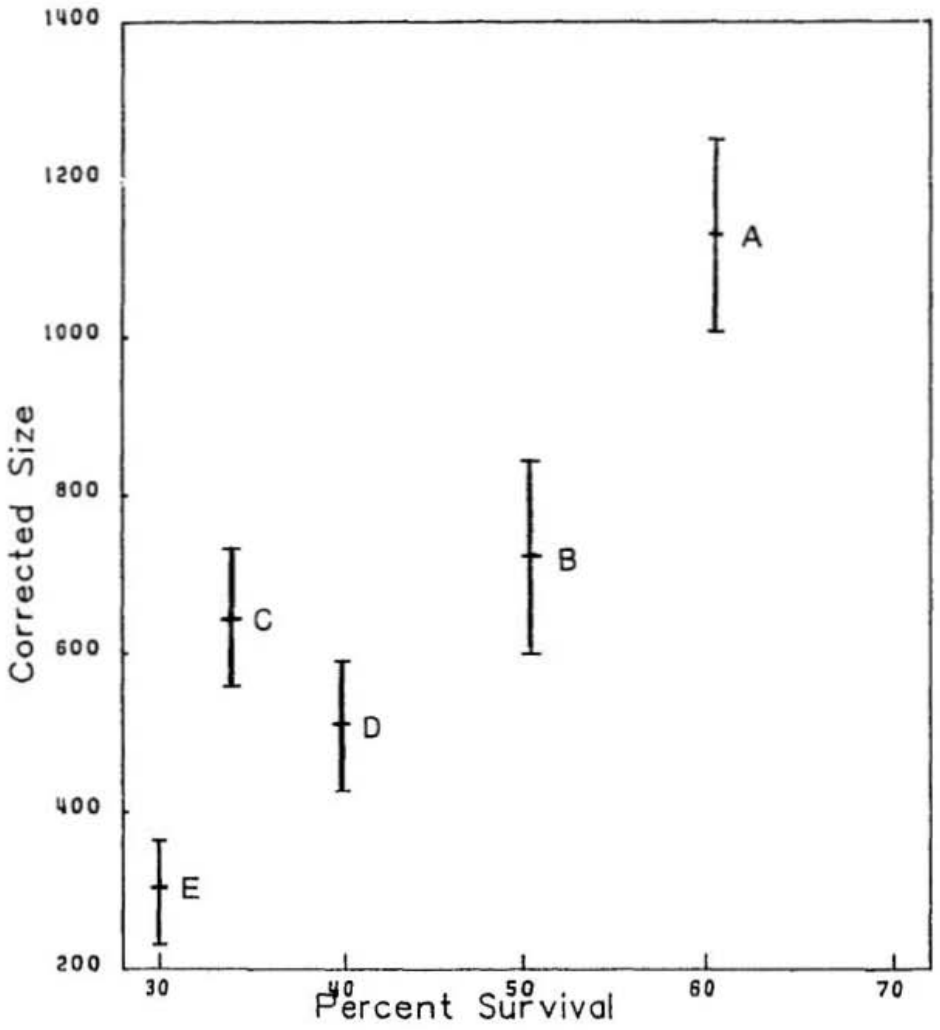
variance, for these five groups of foods. For each of the four simuliid species, the growth means of larvae differed significantly ($P < 0.001$) among diet groups.

The ranking of the diets in respect to larval growth was as listed in the above paragraph, with diatoms providing the greatest growth, and leaf material providing the least. The ranking was similar for each of the four simuliid species, except that for C. ornithophilia, growth on the bacterial diet ranked second to that on diatoms.

For all species combined, growth of larvae reared on diatoms was significantly greater ($P < 0.001$; Mann-Whitney U-test) than that for larvae provided with any other diet, while leaf material yielded the lowest growth. Growth on bacterial diet was significantly less than that for the thick-walled Chlorophyta ($P < 0.05$; Mann-Whitney U-test), but significantly greater than for leaf material ($P < 0.005$).

Fig. 22 shows, for S. verecundum, S. vittatum and P. mixtum combined, the mean corrected larval size plotted against the overall survival rate, assessed at the end of each trial. Diatoms and Chlamydomonas diets not only provided relatively high rates of growth, but led to higher rates of survival than other foods. The opposite was true for the leaf diet.

Fig. 22. Growth (mean bounded by 95% C.L.) and survival of simuliid larvae reared on different classes of food, in 9 laboratory trials (A, diatoms; B, Chlamydomonas; C, Ankistrodesmus/ Scenedesmus/ Chlorella; D, bacteria; E, leaf litter).


1400
1200
1000
800
600
400
200
Corrected Size
A
B
C
D
E
30
40
50
60
70
Percent Survival

When the data was re-expressed in terms of corrected size per degree-day of rearing treatment, the findings were similar, except that growth on bacteria and leaf diets were virtually equal. This sheds some doubt on the previous finding that bacteria represented a superior food to leaf material. The above relationships among food values of diatoms, green algae and bacteria/leaf material, however, remained unequivocal ($P < 0.0001$).

3.4 DISCUSSION

Although no other study has compared growth of larval simuliids reared on the range of diets represented in the present study, the results are generally consistent with the findings of other workers studying simuliid feeding and nutrition on specific foods. High assimilation efficiencies for simuliids fed on diatoms have been reported by McCullough (1975) and by Schroeder (1979). Ladle and Hansford (1981) observed that diatoms (Stephanodiscus hantzchii) yielded high growth and survival rates in S. posticatum; Pseudomonas and riverine detritus yielded poor growth and survival rates. Fuller and Mackay (1981) reported substantially greater larval weight increases of the caddis larva Hydropsyche when fed on a diet of diatoms than when fed on a diet of leaf detritus or faecal material from 'shredder' invertebrates. Wotton (1978) reported assimilation efficiencies of less than 2% in simuliid larvae given natural detritus as food. Ward and Cummins (1979)

observed that growth rates of the chironomid larva Paratendipes albimanus Meigen reared on bacterial foods were generally poor relative to those on algal foods. These authors also found that "natured" (i.e., colonized by saprophytic micro-organisms) dead leaves were more valuable as food than unnatured dead leaves, suggesting that it was bacterial matter associated with the leaf material and containing digestible nutrients derived from it, that was actually utilized by the larvae. Lawson et al. (1984) made similar observations for the cranefly larva Tipula abdominalis. Webster and Benfield (1986), however, suggest that the attribution of invertebrate growth solely to microbial biomass is contradicted by evidence that microbial biomass is insufficient to support invertebrate growth. Although the leaf material in the present trials was collected from the ground adjacent to streambanks, it was not intentionally subjected to any process of naturing before use, and the suspension remained in the rearing baths for only one day before being replaced with fresh suspension. The leaf material used, therefore, was probably not colonized to a great degree by micro-organisms.

In Chapter 2, it was shown that the range of particles ingested in field populations of larval simuliids largely reflected the selection of particles available in the habitat. The information in the present Chapter suggests that there were differences in the degree to which the various ingested items were utilized in larval nutrition. As

in Chapter 2, however, major differences were not observed among simuliid species in this respect.

CHAPTER 4 FACTORS INFLUENCING RATES OF INGESTION AND DIGESTION

4.1 INTRODUCTION

In Chapter 2, it was determined that a wide variety of algal and other materials were ingested, largely indiscriminately, by larvae of the simuliid species of the study area. The findings of Chapter 3 indicated that not all materials were equally nutritious, as reflected in larval growth. However, the degree of digestion of any food, and hence its realized nutritional value, may change with the various physical factors of the ambient environment. The aim of the following experiments was to examine the degree to which the ingested food was utilized under the variety of physical conditions that may occur seasonally in local simuliid habitats.

A number of studies have examined relationships between ingestion rates and ambient physical factors (temperature, PM concentration, current velocity) in certain simuliid species (e.g., Ladle et al. 1972; Webster 1973; Mulla and Lacey 1976; Elouard and Elsen 1977; Moore 1977a and 1977b; Kurtak 1978; Lacey and Mulla 1979; Schroeder 1980a, 1980b, 1981a and 1981b; Hart and Latta 1986). The influence of larval physiological age and species differences on ingestion rates have also been examined (Ladle et al. 1972;

Mulla and Lacey 1976; Elsen 1978; Wotton 1978). Assimilation efficiencies reported in the literature range from about 2% (detritus; Wotton 1978) to 68-79% for green algae (Schroeder 1979), and 7.6-99% for diatoms (McCullough 1975; Ladle and Hansford 1981). As to the influence of environmental factors on the degree to which ingested materials are digested, however, little is known apart from the work of Schroeder (1981a) on assimilation efficiencies for green algae at different temperatures in S. ornatum.

In designing the trials, it was hypothesized that the rate at which food is ingested might influence the degree of digestion, by determining residence time in the gut and hence the duration of exposure to digestive influences (i.e., enzymes, pH). Hence, the first set of experiments examined ingestion of algal particles under various ambient conditions, including temperature, particulate matter concentration, and current velocity. The remaining experiments examined degrees of digestion of algal food, under different conditions of the same factors. Four local species with various seasonal distributions were used to compare relationships for cold stenothermal (P. mixtum, C. ornithophilia), warm stenothermal (S. verecundum) and eurythermal (S. vittatum) entities.

4.2 MATERIALS AND METHODS

Larvae of S. verecundum, S. vittatum, C. ornithophilia and P. mixtum were introduced to 1000-ml glass beakers, each equipped with a stirring bar as referenced in chapter 3, and allowed to equilibrate to the various temperature and other conditions for 1-2 days. At the beginning of each trial, the rearing water was replaced and a sufficient volume of a previously calibrated stock solution of mixed algal cultures was pipetted into each rearing bath. The period of exposure was 1.2 - 4 h, according to expected passage rates at the various temperatures.

Larvae were offered dilutions (50, 10, 2, 0.4 mg/l) of suspensions containing the following algal or other components:

Navicula (diatom)
Nitzchia (diatom)
Scenedesmus (green alga)
Ankistrodesmus (green alga)
Chlamydomonas, palmelloid form
alder leaves (to make up bulk)

Apart from different concentrations of suspension in the baths, treatment conditions included different temperatures (0.5-1°, 11° or 22°)* and relative current velocities (300, 150, 75 or 48 rpm rotation of the stirring

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*See tables for exact temperatures in each trial

bar). Final or penultimate instars were used in the trials but the observations included a number of younger larvae (equivalent to fourth-instar S. verecundum, as well.

At a specific time before the end of the trial, finely pulverized charcoal (<100 μm particle size) was added to each bath at concentration equivalent to 5% of total suspended solids, to serve as a marker in the plug of gut contents. The progression of the marker posteriorly expressed as a proportion of total mid-gut length, was used as a measure of passage rate of food in the gut.

At the end of the experimental period, larvae were removed from each container and placed in ice-cold phosphate-buffered 5% formalin. On dissection, the position of the marker was recorded and expressed as a percentage of the total length of the mid-gut. Past studies of feeding rates in simuliid larvae have equated rate of ingestion (i.e., amount of particulate matter ingested per unit time) with the rate of passage of ingested materials along the mid-gut (inter alia Mulla and Lacey 1976; Chance 1977; Wotton 1978; Lacey and Mulla 1979; McCullough et al. 1979; Hart and Latta 1986). This has been based on the grounds that the simuliid mid-gut is a cylindrical tube of reasonably constant diameter throughout its length, the particles are packed tightly and homogeneously throughout, and there is no evidence of peristalsis or other forces affecting the longitudinal movement of ingested material

once it has entered the mid-gut. The particulate materials selected for the present feeding trials represented types that had been observed not to be lost or reduced in volume substantially in passing through the mid-gut. Accordingly, the 'passage rate' of indigestible marker particles along the mid-gut was taken as a relative measure of the rate at which particulate matter was ingested, hereafter referred to as 'ingestion rate' (in units equal to the mid-gut length, per hour).

The gut was then opened and the most posterior 1/8 of the mid-gut contents were removed, placed in a drop of water on a second microscope slide, dispersed and examined, as described in Chapter 2. For all diatoms, an arbitrary criterion for digestion was chosen: if less than 40% of the cytoplasm remained in any frustule, the particular cell was considered to have been digested.

Current velocity in the rearing vessels was determined by direct measurement with a Nixon Streamflo (model 422) turbine-type velocity meter, at a range of stirbar rotation speeds. The instrument integrated current velocities over a 0.785-cm^2 area 3-13 mm from the bottom surface and 2-12 mm from the side. From the resulting curve, the current velocities at 48, 75, 150 and 300 rpm, respectively, were 7, 9, 15 and 28.5 cm/sec.

Continuity of filtration:

The time during which the labral fans of S. verecundum were extended into the normal feeding position (fully abducted) or adducted was recorded on individual larvae in glass rearing containers, with different treatments of temperature, PM concentration and current velocity. In each observation, a larva was observed continuously for 10 min. The beginning and end of each period of adduction of more than 1 second (thus excluding the routine "flicking" movements carried out to remove captured material from the fans) were recorded. In this way, 178 such 10-min observations were made. Observations were also made of S. vittatum larvae in treatment baths of the trials described above.

4.3 RESULTS

4.3.1. Ingestion Rates:

For S. vittatum, C. ornithophilia and P. mixtum, ingestion (passage) rates generally increased with increasing temperature and with increasing PM concentration (Tables 16, 17 and 18). Ingestion rate data for some trials were not available because the delimitation of the marker proved not to be clearly distinct in the gut contents.

S. vittatum fed significantly at a greater range of temperatures than did C. ornithophilia or P. mixtum. In C. ornithophilia, very low ingestion rates were demonstrated at

Table 16 Mean (± s.d.) passage rates (in midgut-lengths/h) of ingested material in larval S. vittatum guts under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature		
	22° C	11° C	1° C
50 mg/l	1.67 ± 0.61	0.65 ± 0.21	0.27 ± 0.12
10 mg/l	1.13 ± 0.59	0.77 ± 0.16	0.24 ± 0.05
2 mg/l	1.28 ± 0.63	0.71 ± 0.52	0.21 ± 0.05
0.4 mg/l	0.42 ± 0.15	0.19 ± 0.08	-

Results of two-way ANOVA testing concentration and temperature effects, at 2-50 mg/l PM concentration:

Source of variance	Sum of squares	df	F	F prob.
Concentration	0.163	2	0.48	0.625
Temperature	7.743	2	22.60	0.000
Conc. x Temp.	0.540	4	0.79	0.541
Explained	8.411	8	6.138	0.000
Residual	5.310	31		
Total	13.721	39		

Means among temperatures at 2-50 mg/l differed significantly between 1° and 11° treatments ($P < 0.0001$) and between 11° and 22° treatments ($P < 0.01$; Mann-Whitney U-test); temperature treatments at 0.4 mg/l differed significantly from each other ($P < 0.05$; 1-way ANOVA).

Means among concentration treatments differed significantly between 0.4 mg/l and all other treatments combined ($P < 0.001$; Mann-Whitney U-test).

Table 17 Mean (± s.d.) passage rates (in midgut-lengths/h) of ingested material in larval C. ornithophilia guts under different conditions of temperature and PM concentration (9 cm/s current).

Concentration	Temperature		
	22° C	11° C	1° C
50 mg/l	0 ± 0	0.57 ± 0.36	0.40 ± 0.19
10 mg/l	sporadic feeding	0.74 ± 0.51	0.54 ± 0.29
2 mg/l	0 ± 0	0.54 ± 0.24	0.14 ± 0.04
0.4 mg/l	0.05 ± 0.03	0.27 ± 0.08	-

Results of two-way ANOVA testing concentration and temperature effects, at 2-50 mg/l PM concentration:

Source of variance	Sum of squares	df	F	F prob.
Concentration	0.553	2	2.986	0.071
Temperature	1.315	2	7.103	0.004
Conc. x Temp.	0.100	4	0.271	0.893
Explained	1.815	8	2.451	0.046
Residual	2.036	22		
Total	3.851	30		

Table 18 Mean (± s.d.) passage rates (in midgut-lengths/h) of ingested material in larval P. mixtum guts under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature		
	22° C	11° C	1° C
10 mg/l	-	0.74 ± 0.43	0.56 ± 0.12
2 mg/l	-	0.65 ± 0.25	0.39 ± 0.17

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	0.066	1	0.905	0.360
Temperature	0.191	1	2.612	0.132
Conc. x Temp.	0.0051	1	0.072	0.793
Explained	0.263	3	1.196	0.353
Residual	0.879	12		
Total	1.142	15		

the highest temperature (22° C): rather, the "optimum" was at 11° C. C. ornithophilia larvae were almost certainly under some degree of thermal stress at 22° C. Apart from this, the data trends for treatments typical of the range of field conditions for C. ornithophilia (0.4-10 mg/l; 0.5-11°) were consistent with those for S. vittatum. It was known from other laboratory work that a temperature of 22° causes considerable thermal stress in P. mixtum and this treatment was not included in the trial for that species.

The influence of PM concentration for S. vittatum and C. ornithophilia was shown mainly at the lower end of the concentration range, suggesting a 'saturation' effect at levels above about 2 mg/l.

Current velocity (rpm) did not appear to be important in influencing passage rate ($P > 0.50$ for S. vittatum, C. ornithophilia; Table 19).

4.3.2. Residence time and feeding efficiency:

Two important variables can be derived from measurements of ingestion (passage) rate. The first is gut residence time (hereafter 'T_r', where T_r = 1/passage rate; units = hours), which is a measure of the period over which ingested food is exposed to the digestive conditions of the larval gut lumen. The computed gut residence times under the various experimental conditions are shown graphically in

Table 19 Mean (± s.d.) passage rates, residence times and relative feeding efficiencies for late-instar S. vittatum and C. ornithophilia larvae, as related to current velocity, at 11° and 10 mg/l PM concentration.

A. Passage Rate:

	S. vittatum	C. ornithophilia
7 cm/s	0.72 ± 0.20	0.61 ± 0.58
9 cm/s	0.77 ± 0.16	0.74 ± 0.51
15 cm/s	0.68 ± 0.09	0.83 ± 0.14
F Prob.	NS	NS

B. Residence Time (h)

	S. vittatum	C. ornithophilia
7 cm/s	1.39 ± 0.39	1.64 ± 1.56
9 cm/s	1.30 ± 0.27	1.35 ± 0.93
15 cm/s	1.47 ± 0.19	1.20 ± 0.20
F prob.	NS	NS

C. Relative Feeding Efficiency

	S. vittatum	C. ornithophilia
7 cm/s	1.02 ± 0.29	0.87 ± 0.82
9 cm/s	0.86 ± 0.18	0.82 ± 0.56
15 cm/s	0.46 ± 0.06	0.55 ± 0.09
F Prob.	$P < 0.05$	

Figs. 23, 24 and 25. In S. vittatum, C. ornithophilia and P. mixtum, shorter residence times were generally observed at the higher temperatures. For S. vittatum, differences in T_r at 2-50 mg/l were significant between 1°C and 11°C conditions ($P < 0.0001$), and between 11°C and 22°C conditions ($P < 0.01$; Mann-Whitney U-test); the former margin was greater than the latter (Fig. 23).

A general trend of shorter T_r with increasing PM concentration was evident for all three species (although there was some trend reversal at the highest concentration, due, perhaps, to saturation). In S. vittatum, T_r at 0.4 mg/l was significantly greater than at all other concentration levels combined ($P < 0.001$; Mann-Whitney U-test) but levelled out at PM concentrations of greater than 2 mg/l. Mean residence times in S. vittatum and C. ornithophilia at 7, 9 and 15 cm/s current velocities did not differ significantly from each other (Table 19).

The mean residence time among mid-instar S. vittatum (0.99 h) was not significantly different ($P > 0.40$) from that of late instars (1.3 h); but high variance among the mid-instar group (C.V. = 55%) may have obscured significant differences.

The second measure to be derived from passage rate is feeding efficiency. To measure efficiency of filtration (or ingestion) in an absolute sense, it is necessary to determine the ratio of the number of particles captured by

Fig. 23. Relationship between gut residence time and PM concentration at three temperatures, for *S. vittatum* larvae (mean ± 1 s.e.). Current velocity ≈ 9 cm/s.

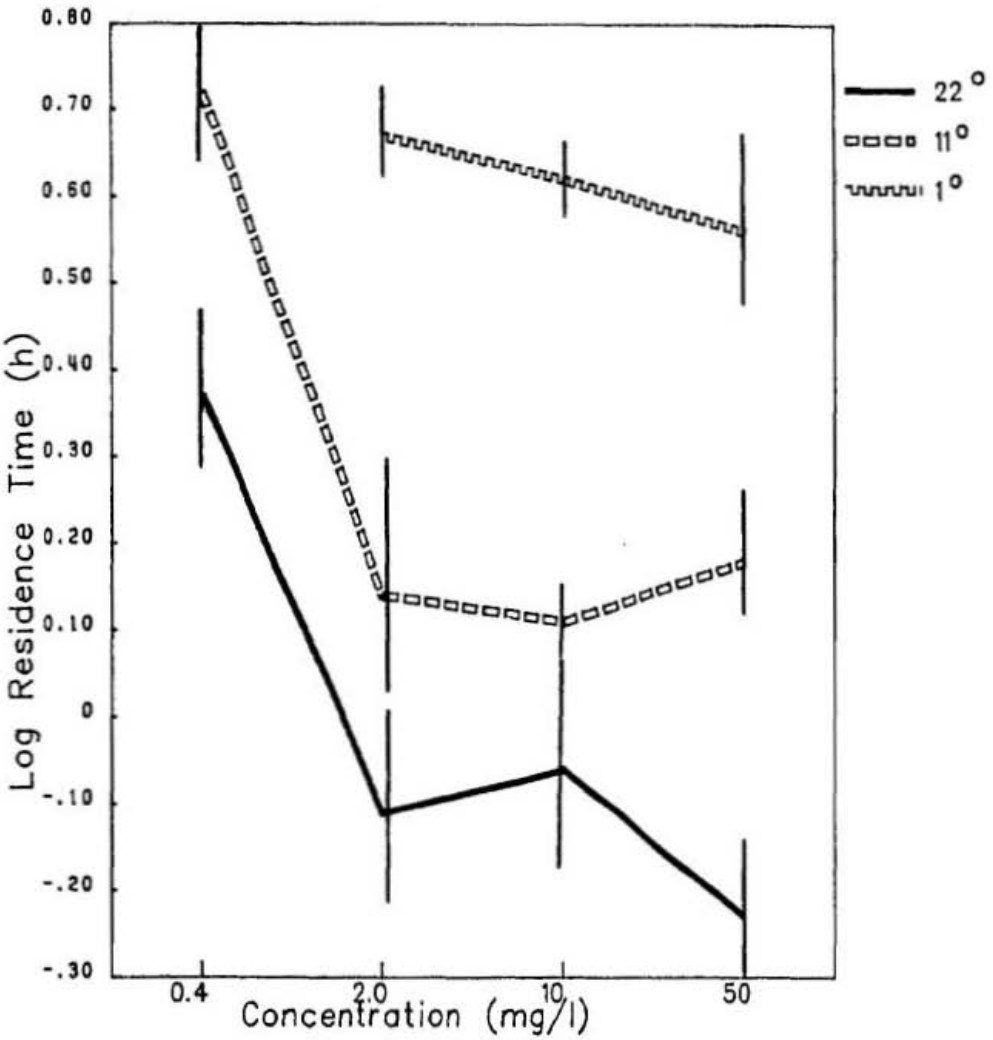

0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0
-.10
-.20
-.30
Log Residence Time (h)
0.4
2.0
10
50
Concentration (mg/l)
22°
11°
1°

Fig. 24. Relationship between gut residence time and PM concentration at two temperatures, for *P. mixtum* larvae (mean ± 1 s.e.). Current velocity = 9 cm/s.

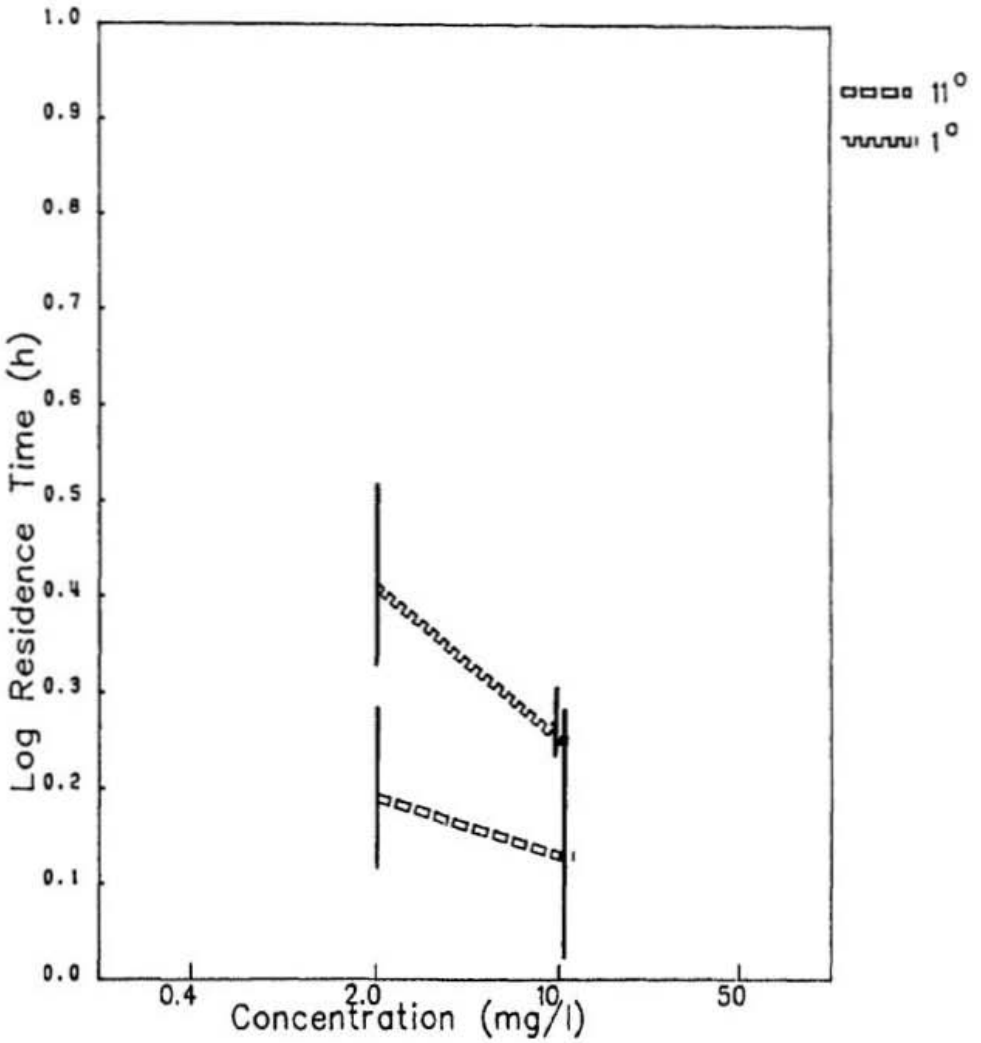
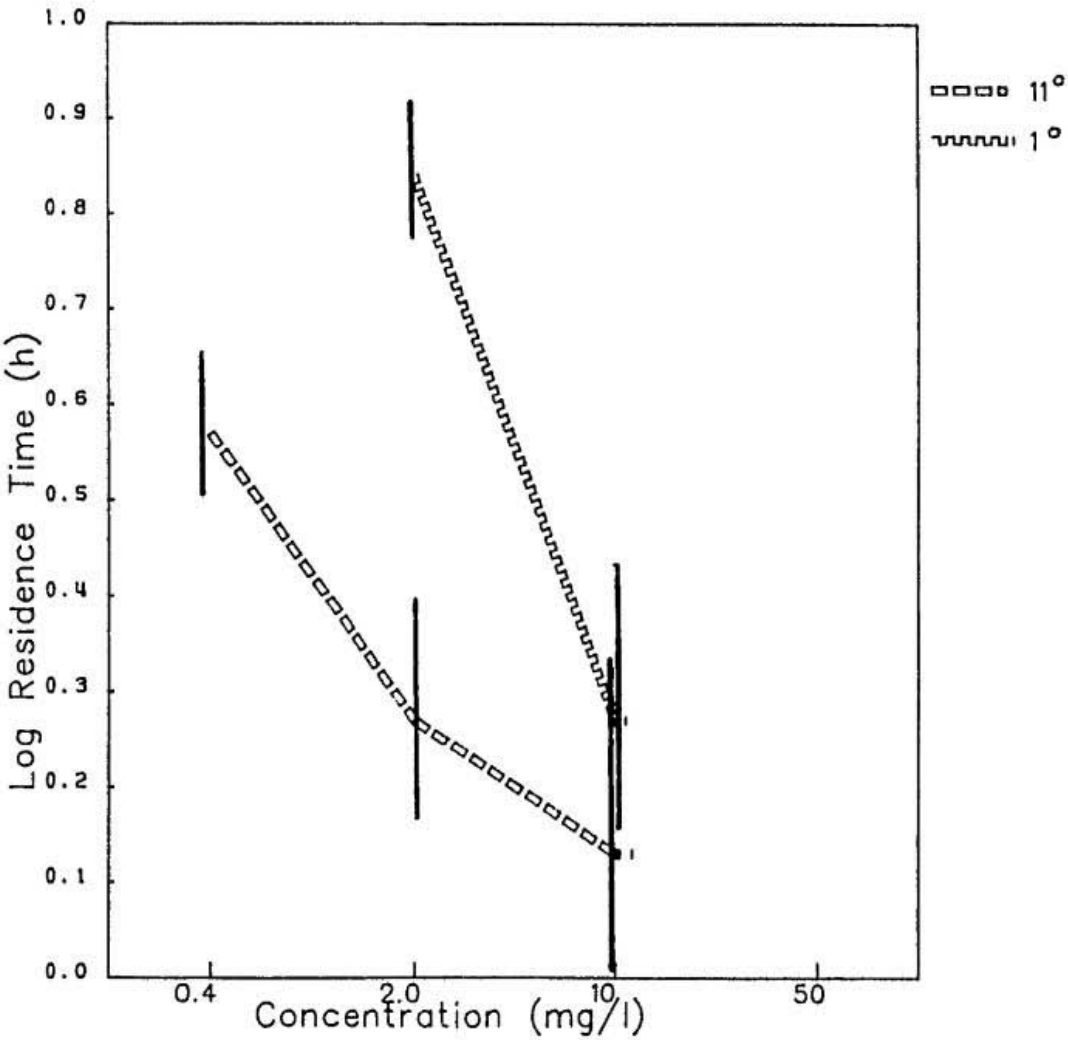

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Log Residence Time (h)
0.4
2.0
10
50
Concentration (mg/l)
11°
1°

Fig. 25. Relationship between gut residence time and PM concentration at two temperatures, for C. ornithophilia larvae (mean ± 1 s.e.). Current velocity = 9 cm/s.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Log Residence Time (h)
0.4
2.0
10
50
Concentration (mg/l)
11°
1°

the labral fans (or ingested) to the number passing through the fan over a similar period of time. Determination of the integrated flow through the labral fans is complex and subject to certain limiting assumptions. However, a relative measure of ingestion efficiency can be attained by taking the gut passage rate as ingestion rate, and by taking the product of PM concentration and velocity as the availability of 'food':

$$\text{efficiency} \propto \text{passage rate}/(\text{concentration} \times \text{velocity})$$

For S. vittatum, P. mixtum and C. ornithophilia, relative feeding efficiency was greater at higher temperatures and at lower PM concentrations (Figs. 26, 27, 28 and Table C5 in Appendix VI). Efficiency was also greater at lower current velocities ($P < 0.05$; Table 19).

Feeding behaviour itself was influenced by PM concentration and temperature, in S. verecundum larvae. At low concentration levels, larvae filtered nearly all of the time over which they were observed (Fig. 29). At higher PM concentrations, however, the proportion of time spent filter feeding dropped substantially. The relationship between temperature and proportion of time spent feeding was direct, although this was most marked at relatively high concentrations. The mean proportion of time feeding was nearly equal at substantially different stirring speeds

Fig. 26. Relationship of relative feeding efficiency and PM concentration at three temperatures, for *S. vittatum* larvae (mean ± 1 s.e.), at 9 cm/s current. Efficiency in the present sense is a relative measure, and as the units have no absolute significance, the values are not shown on the ordinate scale. However, the efficiencies can be attributed absolute values if the following assumptions are made:

mean mid-gut dimensions: length = 2.27 mm; diameter = 0.286 mm (from measurements of larvae used in trial)

specific gravity of gut contents = 1.1 (with dry weight 20% of gross)

frontal area of both labral fans = 0.96 mm² (Chance 1970)

current velocity = 9 cm/s (actual)

Then Efficiency = (P * 0.1029)/C

where P = passage rate (mid-gut lengths/h)

and C = PM Concentration (mg.dw/l)

Efficiencies on graph range from 0.06% to 10.8%, corresponding to range reported in literature (0.01-12%)(Kurtak 1978).

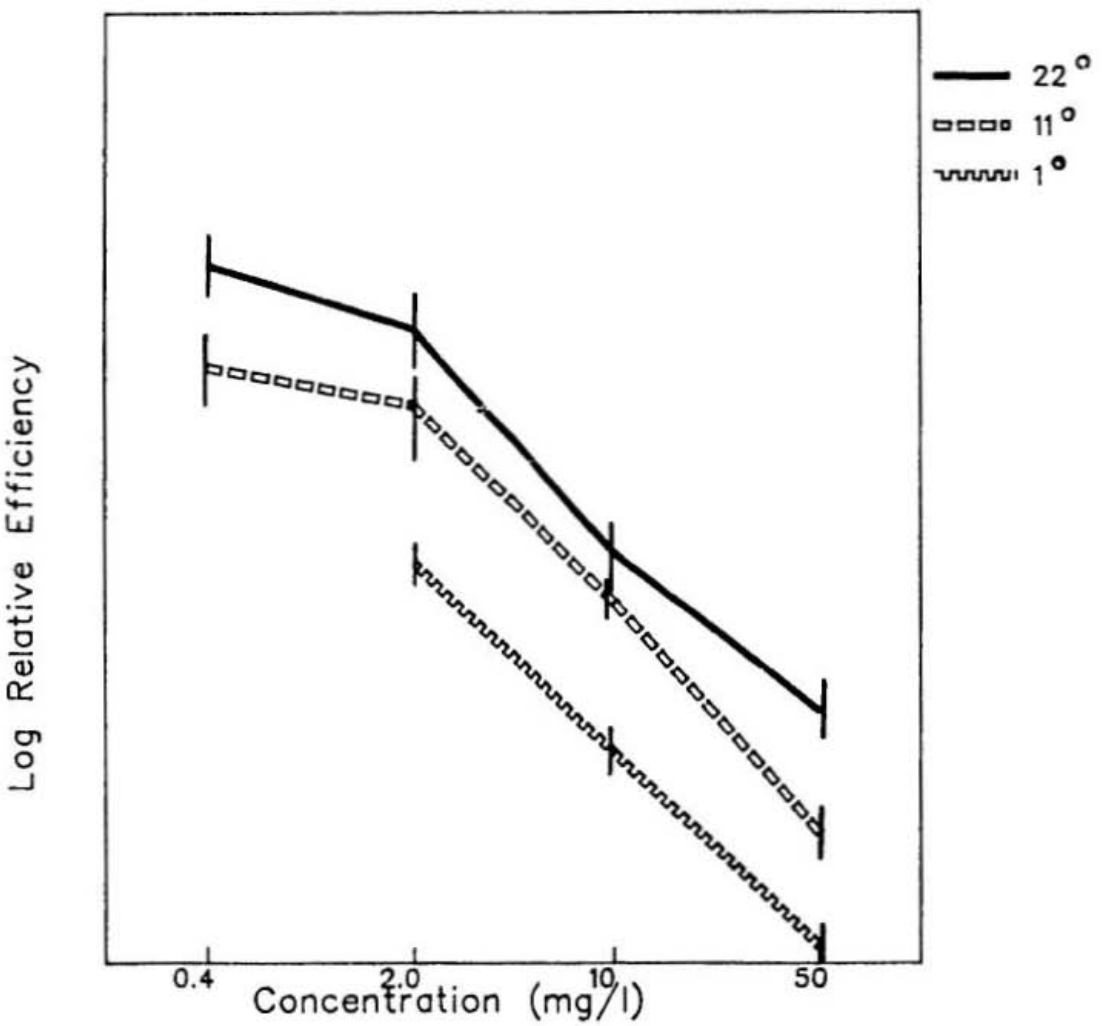

22°
11°
1°
Log Relative Efficiency
0.4
2.0
10
50
Concentration (mg/l)

Fig. 27. Relationship of relative feeding efficiency and PM concentration at two temperatures, for *P. mixtum* larvae (mean ± 1 s.e.), at 9 cm/s current velocity.

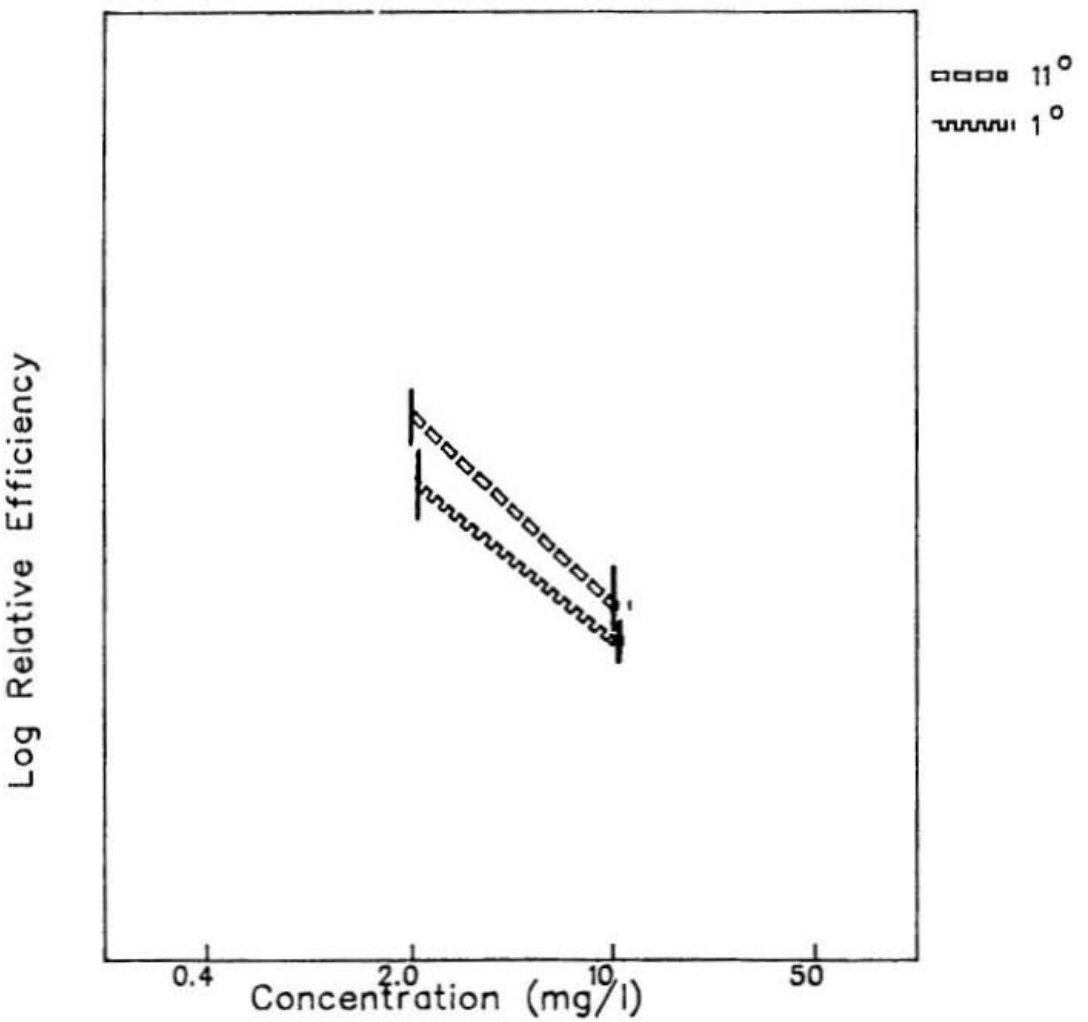

11°
1°
Log Relative Efficiency
0.4
2.0
10
50
Concentration (mg/l)

Fig. 28. Relationship of relative feeding efficiency and PM concentration at two temperatures, for C. ornithophilia larvae (mean ± 1 s.e.), at 9 cm/s current velocity.

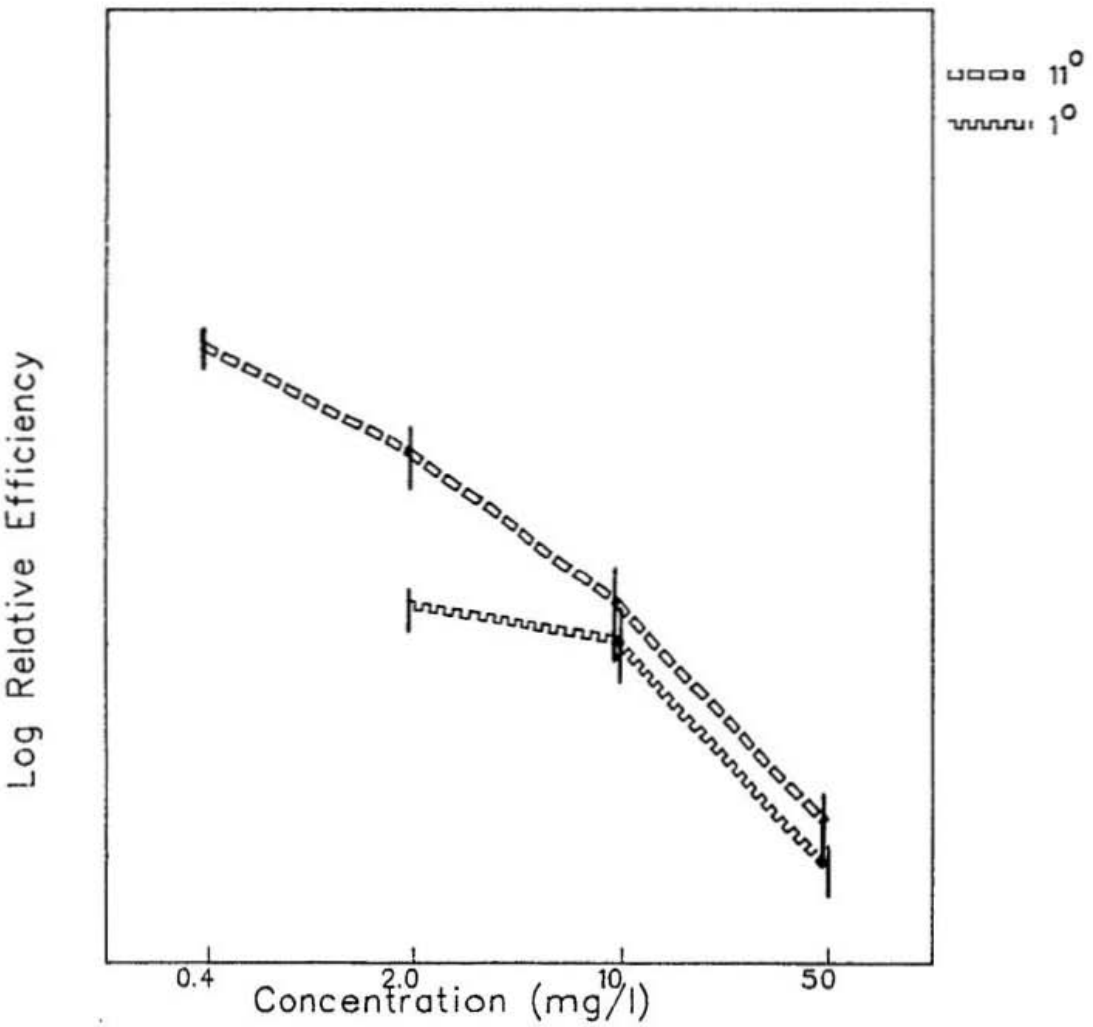
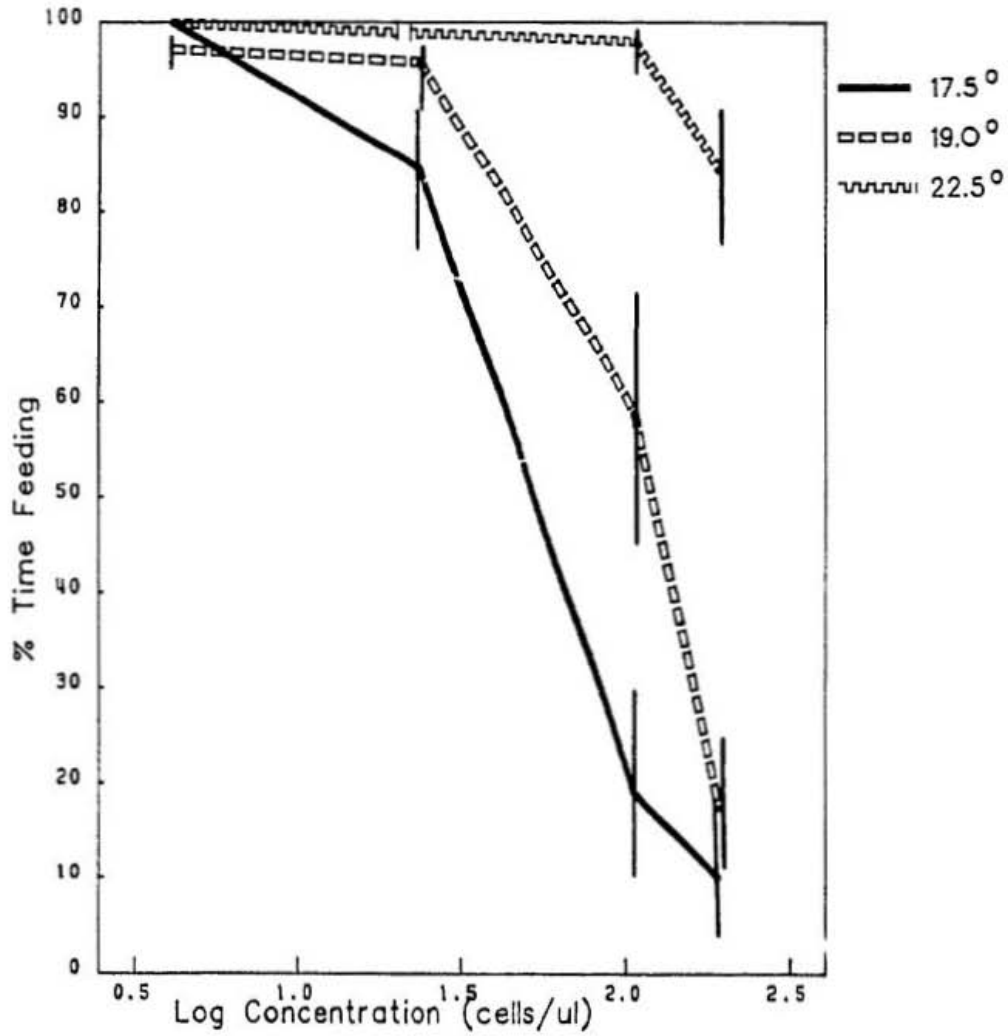

11°
1°
Log Relative Efficiency
0.4
2.0
10
50
Concentration (mg/l)

Fig. 29. Proportion of time spent filter-feeding, by *S. verecundum*, at different conditions of PM concentration and temperature (mean ± 1 s.e.).


100
90
80
70
60
50
40
30
20
10
0
% Time Feeding
0.5
1.0
1.5
2.0
2.5
Log Concentration (cells/ul)
17.5°
19.0°
22.5°

(e.g., 96.8 ± 10.4% and 98.5 ± 5.7% at 7 and 28.5 cm/s, respectively; more details given in Appendix VI, Tables C1, C2). During the course of the other laboratory trials, it was observed that S. vittatum larvae spent less time actively filter feeding at the lowest temperatures than at the highest, but these observations were not quantified.

4.3.3. Degree of Digestion of Ingested Food:

4.3.3.1. Factors influencing degree of digestion:

In preliminary examinations, the silicaceous frustules of Nitzchia and Navicula showed no signs of degradation after gut passage. The mean proportion of diatoms retaining more than 40% of protoplasmic contents was significantly higher for samples taken 25-30% along the mid gut length (26.6 ± 1.5%) than for those taken from the posterior 25% (1.4 ± 0.96%; $P < 0.01$, paired t-test), giving visible and quantifiable evidence of digestion. Linear regression analysis of the proportion of frustules with less than 40% of the cell contents remaining for Navicula against the corresponding proportion for Nitzchia diatoms yielded a reasonably good fit ($r^2 = 0.7494$, $P < 0.001$, slope = 0.80), suggesting that these two food items responded similarly to digestive processes under the various environmental regimes. The variable 'D' (D = proportion of diatom frustules retaining less than 40% contents) was thus used as a measure of degree of digestion in larval guts. D was corrected for the percentage of 'digested' frustules in the stock

solution, and was transformed to arcsine square-root before statistical analysis.

For S. verecundum, both temperature and PM concentration were important factors influencing D ($P < 0.001$ for both factors; 2-way ANOVA). Mean D (i.e., the proportion of cells "digested") for both Navicula and Nitzchia diatoms was generally greater at the higher temperature and at lower levels of PM concentration (Fig. 30, Table 20 and Table C3 (Appendix VI)). Analysis using only mid-instar (IV) larvae showed similar trends to that for final-instar (VI) larvae (Table 21 and C4). Comparisons between the two age groups were carried out by performing two-way ANOVA using temperature and age as independent variables at each concentration. Although temperature was a highly significant factor determining D, age was never significant in this respect ($P > 0.20$).

For S. vittatum (Fig. 31), trends in D with temperature were consistent with those for S. verecundum, though not as pronounced (Table C6, Appendix VI). The temperature relationship is shown in Fig. 32, for S. vittatum larvae in six sets of treatments (2 trials), with D at the coldest temperature standardized to zero for each level of PM concentration in each case. Differences in D values between 11° and 22° treatments were significant ($P < 0.01$; ANOVA), while no significant difference existed between values for 1° and 11° conditions. Neither larval age ($P = 0.11$) nor

Fig. 30. Degree of digestion (D) of Nitzchia diatoms at different conditions of PM concentration and temperature, in S. verecundum larvae (mean ± 1 s.e.). Current velocity = 9 cm/s.

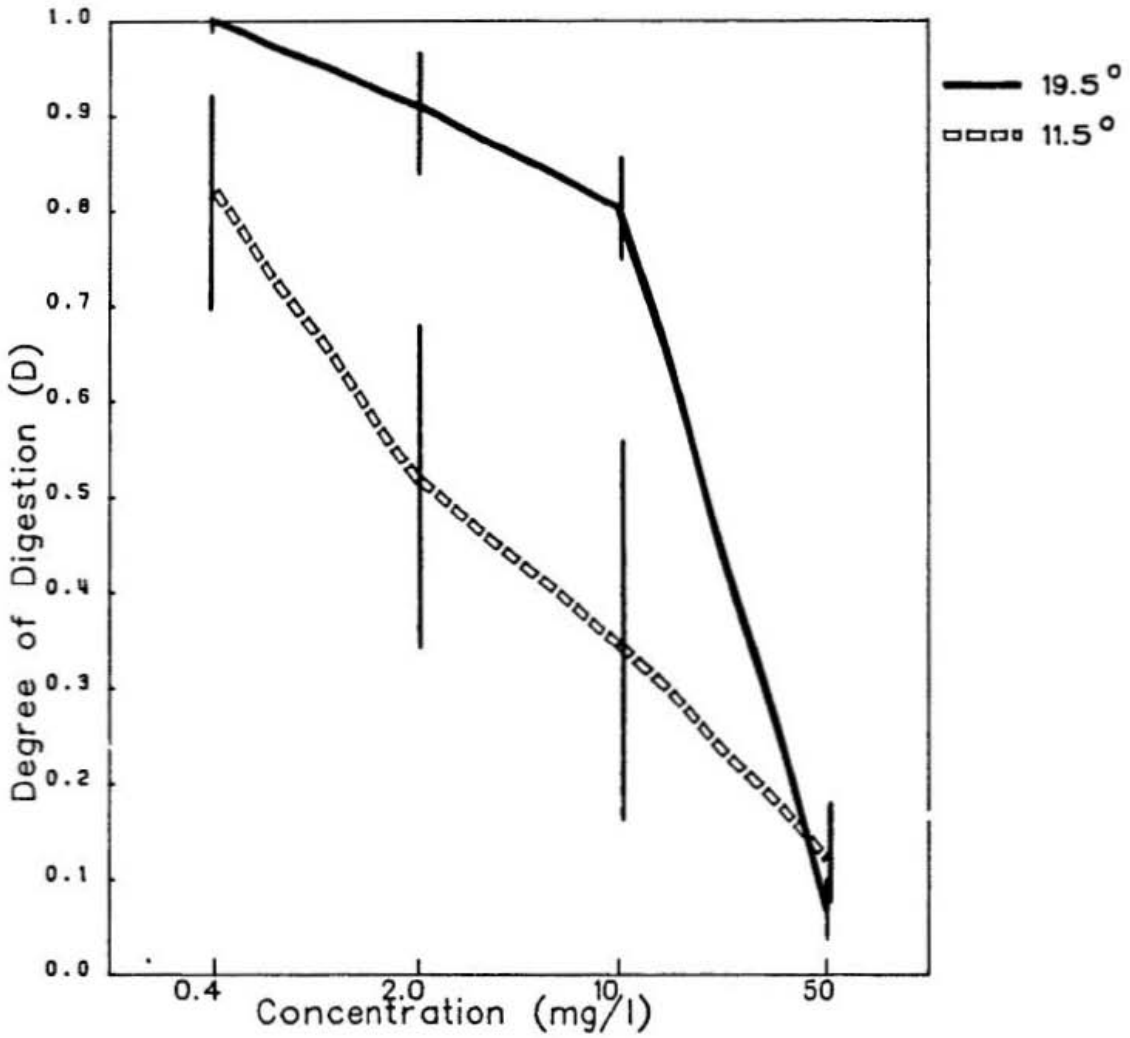

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Degree of Digestion (D)
0.4
2.0
10
50
Concentration (mg/l)
19.5°
11.5°

Table 20 Degrees of digestion (D)[1] of ingested Nitzchia diatoms in guts of late-instar S. verecundum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature	
	19.5° C	11.5° C
50 mg/l	0.069 (15.3 ± 7.2)	0.122 (20.4 ± 9.5)
10 mg/l	0.804 (63.7 ± 7.5)	0.346 (36.0 ± 24.5)
2 mg/l	0.910 (72.5 ± 13.0)	0.518 (46.0 ± 20.0)
0.4 mg/l	1.000 (90.0 ± 0)	0.821 (65.0 ± 17.0)

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	17588	4	20.93	0.000
Temperature	2654	1	12.63	0.001
Conc. x Temp.	1696	4	2.02	0.117
Explained	21939	9	11.60	0.000
Residual	6303	30		
Total	28241	39		

[1] D - proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

Table 21 Degrees of digestion (D)[1] of ingested Nitzchia diatoms in guts of early-instar S. verecundum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature	
	19.5° C	11.5° C
50 mg/l	0.200 (26.7 ± 5.5)	0.163 (23.8 ± 19.5)
10 mg/l	0.777 (61.8 ± 12.8)	0.433 (41.1 ± 1.9)
2 mg/l	0.831 (65.7 ± 22.8)	0.459 (42.6 ± 11.1)
0.4 mg/l	0.987 (83.3 ± 13.3)	-

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	7152	3	11.94	0.000
Temperature	1477	1	7.25	0.014
Conc. x Temp.	490	2	1.23	0.313
Explained	11435	6	9.54	0.000
Residual	4194	21		
Total	15629	27		

[1]D - proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

Fig. 31. Degree of digestion (D) of Nitzchia diatoms at different conditions of PM concentration and temperature, in S. vittatum larvae (mean ± 1 s.e.). Current velocity = 9 cm/s.

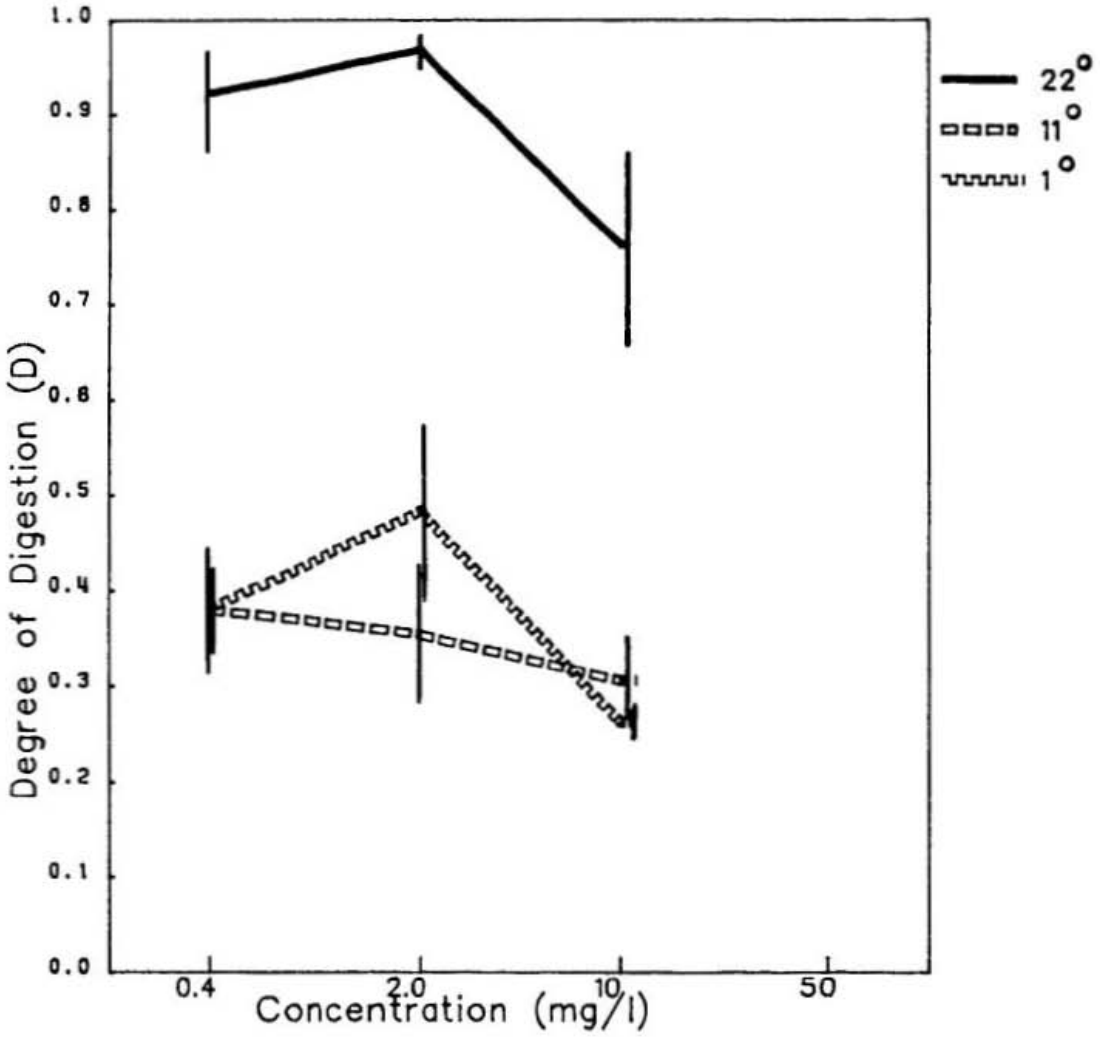
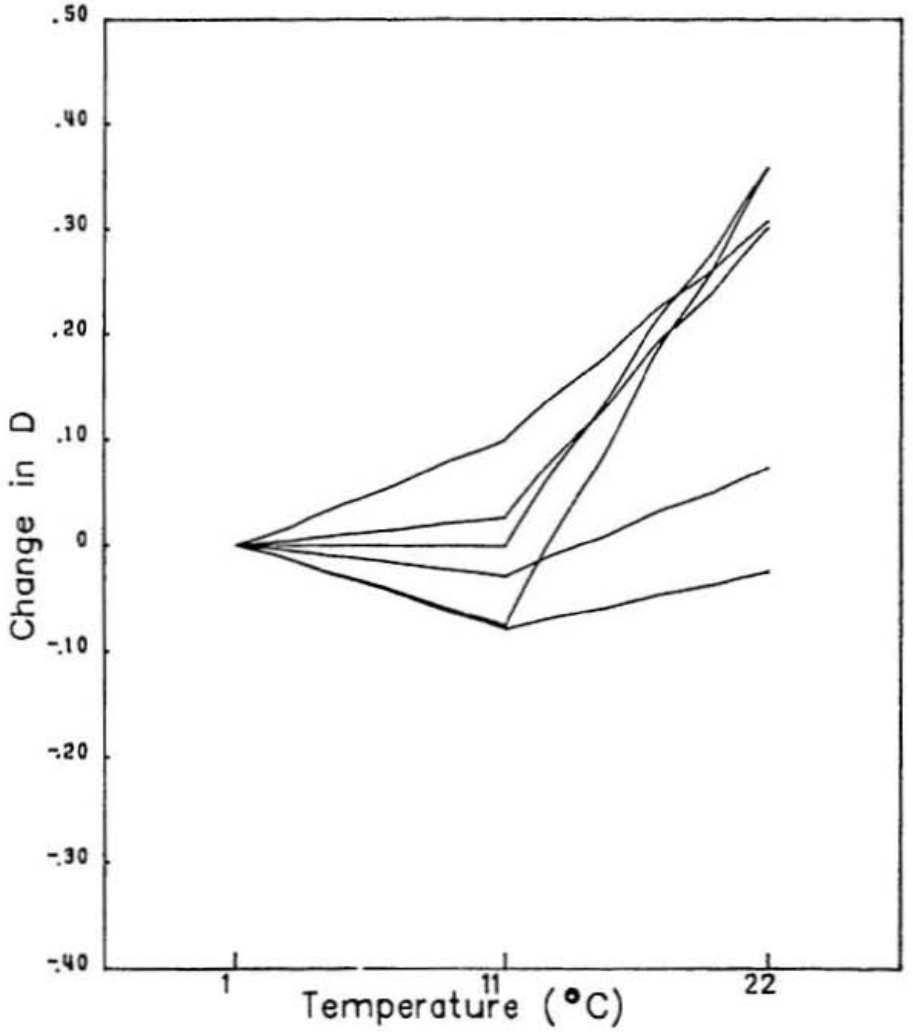

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Degree of Digestion (D)
0.4
2.0
10
50
Concentration (mg/l)
22°
11°
1°

Fig. 32. Change in degree of digestion (D) with change in temperature, S. vittatum. D was standardized by setting mean value at lowest temperature to 0. Each line represents one set of treatments at one concentration level.


.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
Change in D
1
11
22
Temperature (°C)

current velocity (P = 0.69) significantly influenced D (1-way ANOVA; Table 22).

Three-way ANOVA (with unique SS) was performed in order to incorporate the data of two similar trials investigating D in S. vittatum, examining temperature, PM concentration and trial as independent variables'. PM concentration did not significantly affect D (P = 0.21), but both temperature and trial differences were significant (P < 0.001). Two- and three-way interactions were not significant. Differences between 11° and 22° were significant but those between 11° and 1° were not. The difference in D means between the two trials may have stemmed from a difference in nutritional status between the two larval groups used (those of the first trial were kept for approximately one day without food immediately before the trial, whilst those of the second were given ample food throughout the entire pre-trial period). Hart and Latta (1986) showed that previous food deprivation influences feeding in P. mixtum/fuscum.

The relationship of D with temperature in the cold stenothermal P. mixtum was highly significant (P < 0.001). However, this relationship was the reverse of that shown for S. verecundum or S. vittatum, with greater digestion occurring at the lower temperature (Fig. 33 and Table C7 of

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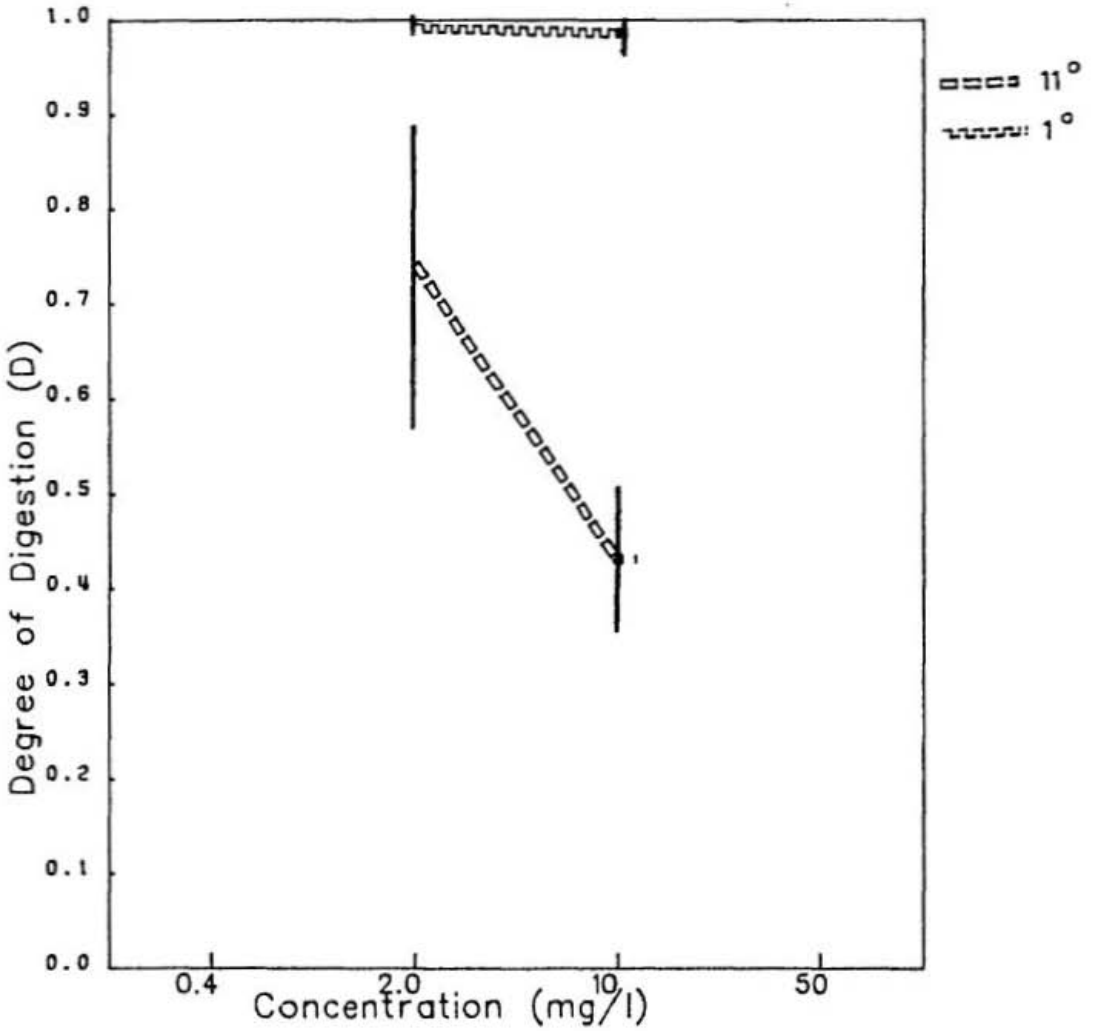
'Analysis was carried out for 1°, 11° and 22° treatments, but for 2 and 10 mg/l PM concentrations only, as there was a missing cell in one trial at 0.4 mg/l, making ANOVA inadmissable.

Table 22 Degree of digestion (D)[1] of ingested Nitzchia diatoms in late-instar S. vittatum larvae, as related to current velocity, at 10 mg/l PM concentration and 11°C.

	S. vittatum	C. ornithophilia
7 cm/s	0.396 (39.0 ± 13.9)	0.818 (64.8 ± 23.5)
9 cm/s	0.306 (33.6 ± 17.5)	0.581 (49.7 ± 15.5)
15 cm/s	0.309 (33.8 ± 8.1)	0.612 (51.5 ± 18.1)
F Prob.	NS	NS

[1]D - proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

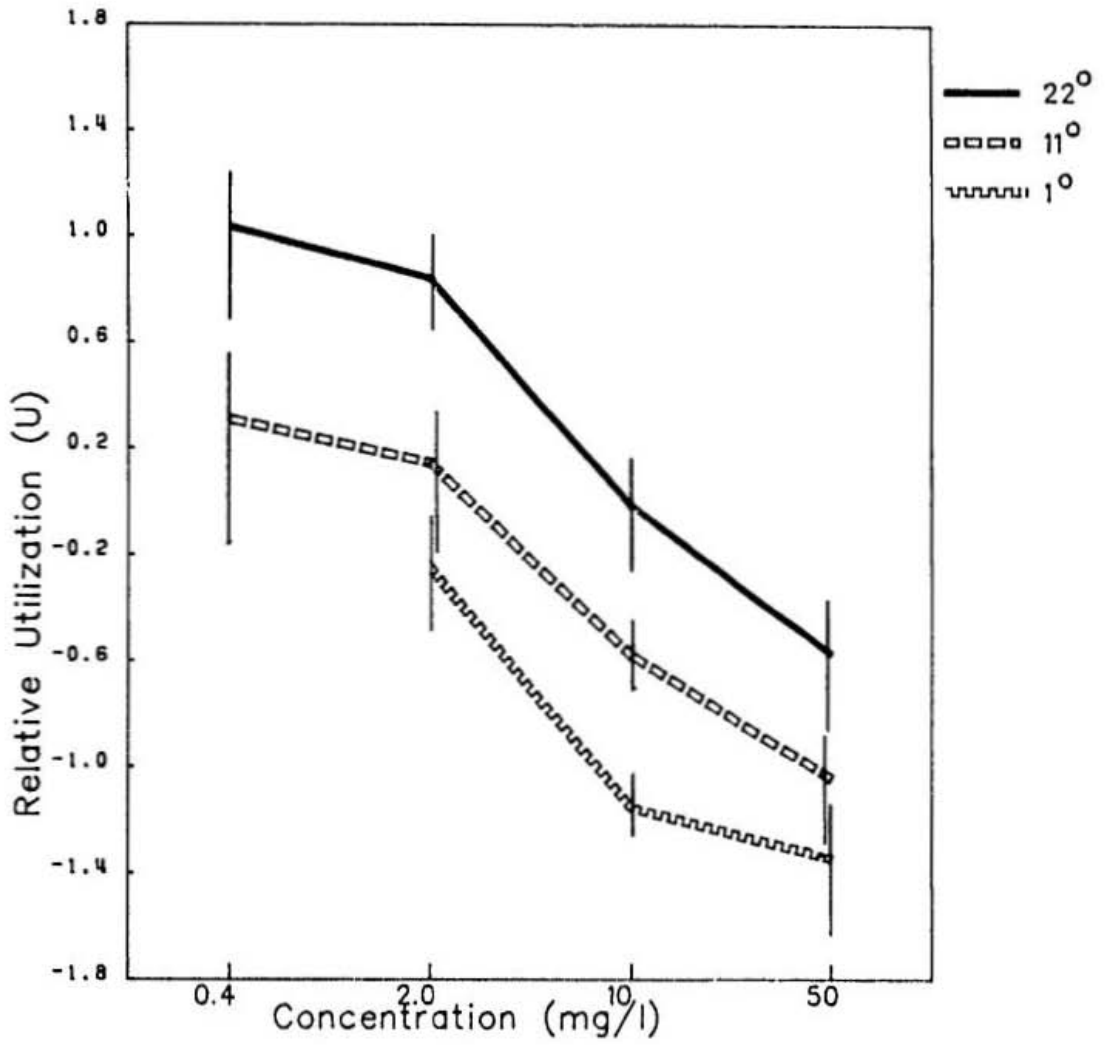
Fig. 33. Degree of digestion (D) of Nitzchia diatoms at different conditions of PM concentration and temperature, in P. mixtum larvae (mean ± 1 s.e.), at 9 cm/s current velocity.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Degree of Digestion (D)
0.4
2.0
10
50
Concentration (mg/l)
11°
1°

Appendix VI). At 1°C, D was nearly 1.00, much higher than the corresponding figure for S. vittatum, and yet the residence time for P. mixtum at 1°C was shorter than for S. vittatum under similar conditions.

Feeding efficiency and degree of digestion can be used to formulate a third variable, the degree of utilization (U), where U = Feeding efficiency x Degree of digestion. Since feeding efficiency is a relative measure only, and D is based on an arbitrary criterion, values of U have relative, rather than absolute significance. However, U is an expression of the superimposed effects of feeding efficiency and digestive efficiency, and as such it can be used in a relative sense to elucidate differences in the net use of food based on the rate at which it is made available. U for S. vittatum was computed from the mean feeding efficiency values of Table C5 and from the mean D values of Table C6, and plotted on a logarithmic scale versus PM concentration, for different temperatures (Fig. 34). Variances were computed using the 95% confidence intervals for the constituent variables. The relative degree of utilization was higher at the lower PM concentrations used, and increased with increasing temperature. When similar plots were constructed for C. ornithophilia and P. mixtum, no differences in U were noted between different temperatures, nor among the three species.

Fig. 34. Index of relative utilization of diatoms (as logarithm of mean U (±s.d.)) by S. vittatum larvae, plotted against PM concentration, at 9 cm/s current velocity. Values have relative, rather than absolute significance. U = Feeding efficiency x Degree of digestion. U can be interpreted as being relative to the probability that a diatom immediately upstream from the labral fan of a larva will be captured and digested to the extent that


1.8
1.4
1.0
0.6
0.2
-0.2
-0.6
-1.0
-1.4
-1.8
Relative Utilization (U)
0.4
2.0
10
50
Concentration (mg/l)
22°
11°
1°

4.3.3.2. Sources of Variance:

Variance within treatment groups might have originated from a number of sources. While current velocities were kept relatively low, in order to minimize turbulence and consequent variation in current velocity, there was a range of ±13% over measurements taken at different points on the surface of the rearing containers. Crowding of larvae in the jars (and consequent interference through competitive interactions or altered hydrodynamics) and depletion of the concentration of PM through larval feeding were minimized by using only a small number of larvae in each rearing container. Although all larvae were treated similarly before the trial, nutritional status might somehow have differed among individuals, possibly affecting feeding rate/digestion rates. Intermittency of filter feeding would also affect feeding rate, and thus possibly degree of digestion. Cytotypic differences did not likely affect the data, since S. vittatum, C. ornithophilia, P. mixtum and St. mutata are believed to consist of single entities in Newfoundland. Larvae of the S. verecundum complex, which were collected from egg masses, could have been of either the ACD or AA types, or both (Rothfels et al. 1978). Finally, the stage of development within the larval stadium (i.e., the onset of ecdysis) may influence feeding behaviour, and larvae of the experimental cohorts likely varied in that respect. Larvae that had reached the stage of pharate pupa were not used in the analysis; final instar larvae were observed to feed

readily, and the fact that differences in ingestion rates and degree of digestion were not observed between early-instar and final-instar larvae indicates that the use of late- or final-instar larvae in the trials did not compromise the results. Each of the conclusions made in the study was based on a statistically significant result using an appropriate statistical test, and they are thus not made inadmissable by the observed variance.

4.3.3.3. Appearance of Algal Cells in Gut:

Algal cells of various types recovered from larval guts in the laboratory trials are shown in Figs. 35 and 36.

The cytoplasm of Nitzchia and Navicula diatoms was removed to a variable extent, as has been discussed above. Semi-digested cytoplasm was pale-green, contrasting with the normal yellow-brown colour.'[10]

The cell wall of Scenedesmus apparently remained intact in the larval gut. The cytoplasm was removed quite slowly and then only under conditions where cytoplasm of diatoms had been completely digested. Chlamydomonas flagellates were digested easily, and reduced to small irregularly shaped fragments. There was no evidence of digestion of Chlamydomonas palmellae.

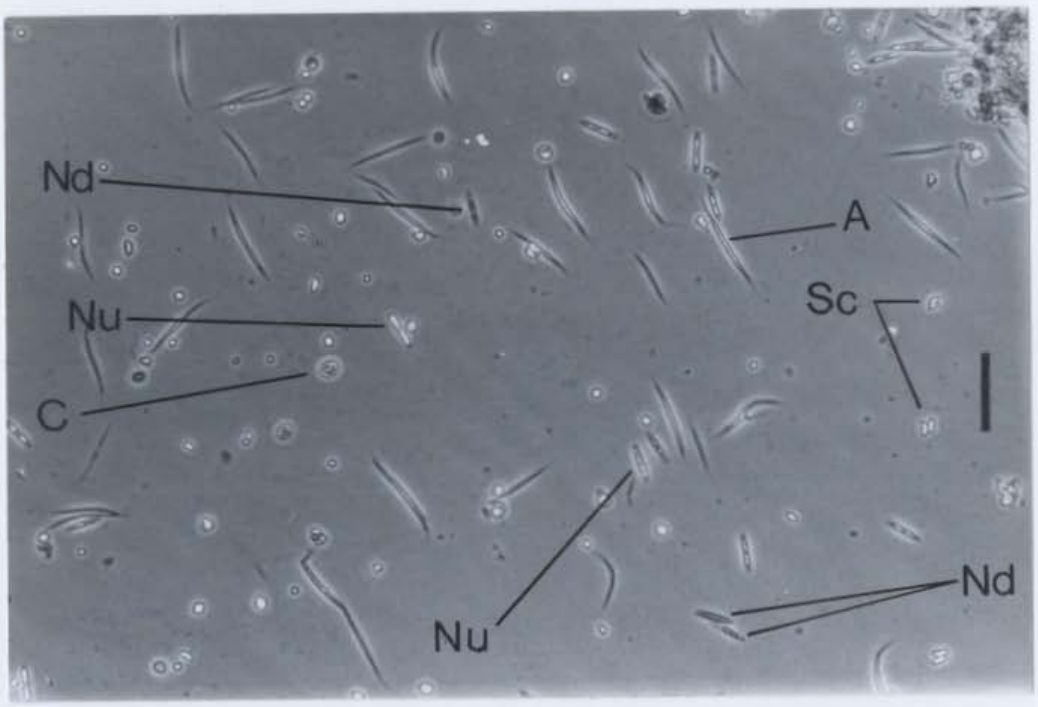
'[10]The major light-harvesting pigment of diatoms is the carotenoid fucoxanthin. Its removal would 'un-mask' the underlying chlorophylls *a* and *c*, resulting in a shift in colour.

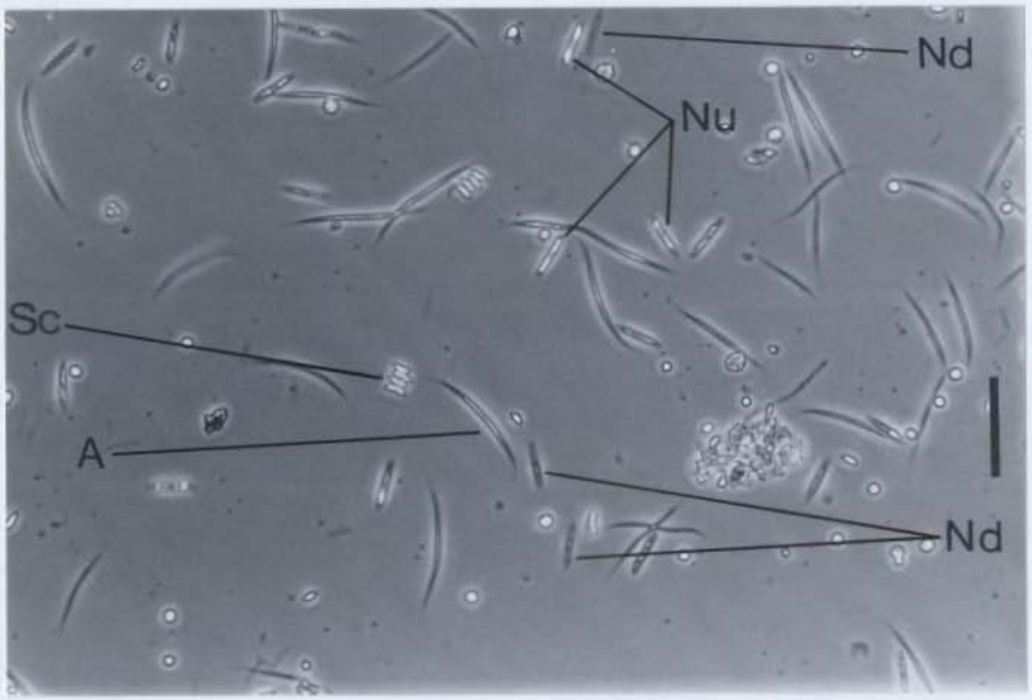
Fig. 35. Sample of gut contents from S. vittatum, showing Nitzchia diatoms in various stages of digestion.
Nd = digested; Nu = undigested, according to criterion.
A = Ankistrodesmus; C = Chlamydomonas.

(Scale bar = 60 μm)

Fig. 36. Sample of gut contents from S. vittatum, showing Nitzchia diatoms in various stages of digestion.
Nd = digested; Nu = undigested, according to criterion.
A = Ankistrodesmus; Sc = Scenedesmus

(Scale bar = 60 μm)


Nd
A
Sc
Nu
C
Nu
Nd


Nd
Nu
Sc
A
Nd

Ankistrodesmus seemed to be intermediate in susceptibility to digestion. Digested cells were colourless and 'withered', compared to the normal sickle shape.

4.4 DISCUSSION

The direct relationship of ingestion rate with temperature is in agreement with the results of Lacey and Mulla (1979), and Mulla and Lacey (1976), which showed ingestion rates in S. vittatum larvae to rise with increasing ambient temperature over a given range. Webster (1973) reported an optimum ingestion rate for that species, of 20° C, in a range of 2-25° C. Schroeder (1980a) observed that ingestion rates rose with increased temperature (5-15°C) in S. ornatum. The present data also correspond with work on S. vittatum by Lacey and Mulla (1979) and on P. mixtum/fuscum Syme and Davies by Hart and Latta (1986) in which ingestion rates rose with PM concentration.

Residence times of food in the mid-gut reported for simuliids have generally ranged from 0.5-2 h (Fredeen 1964; Chance 1970; Ladle et al. 1972; McCullough et al. 1979; Ladle and Hansford 1981). McCullough et al. (1979) observed greater residence times at lower temperatures (15.4°) than at higher temperatures (19°). Shorter residence times have been observed for younger larvae than older (McCullough 1975; Mulla and Lacey 1976; Wotton 1978), but both Schroeder (1979) and Ladle and Hansford (1981) found no differences in that respect.

The present findings in terms of feeding efficiency are also generally in agreement with those of other investigators. The observed direct relationship between feeding efficiency and temperature is consistent with data of Lacey and Mulla (1979) and Mulla and Lacey (1976) using S. vittatum. That efficiency varied inversely with concentration of particulate matter, is consistent with observations made by Kurtak (1978) for S. pictipes Hagen. The efficiency of feeding in S. vittatum inferred from Lacey and Mulla's (1979) data declined steadily with increasing concentration, over the entire range used. In the Hart and Latta (1986) study of feeding in P. mixtum/fuscum, feeding rate (as measured by "flick" rates of labral fans) rose with increasing PM concentration, but feeding efficiency was observed to decline. Kurtak's finding (1978) that efficiency in S. pictipes decreased with increased temperature from 15° to 23° C may be related to the choice of experimental subject species. In the same study, Kurtak (1978) reported decreased feeding efficiencies with increased current velocity for a number of species. Calculation of efficiency rates (in the present sense) from Lacey and Mulla's (1979) data showed that for S. vittatum, feeding efficiency declined with increasing current velocity over the range 26-53 cm/s.

There are two functional components to the feeding action of larval simuliids. The filtration of particulate matter from water, by the labral fans, is largely a passive

action powered by the motion of the current. The removal of the trapped material from the fans by the mandibular brushes and other mouthparts (Chance 1970) is an active mechanism. Each mechanism is associated with an efficiency (termed here "capture" and "removal" efficiencies respectively), with the "ingestion efficiency" incorporating both processes. Although "capture efficiency" is of interest from the viewpoint of filtration mechanics, ingestion efficiency is of greater interest to the present study, representing the nutritional input in the context of the available food supply. The ingestion efficiency appeared to be influenced by ambient temperature, by particulate matter concentration and by current velocity. There are several ways through which this might occur. These are detailed below.

The filtering apparatus may operate less efficiently at higher PM concentrations because of relatively rapid saturation of available adhesion or entrapment sites (i.e., 'clogging'), and consequently a lesser proportion of time spent with fans in the feeding position. The active component may also operate less efficiently under such conditions, where greater loading of the removal mechanism might result in proportionately more loss between capture and ingestion. However, some evidence for regulation of the maximum degree of loading of the fans with trapped material has been presented by Hart and Latta (1986), who found that the labral fans of P. mixtum/fuscum Syme and Davies retracted after a fixed number of particles had accumulated,

rather than after a given period of time. But if it has to flick more often, then the proportion of time with fans abducted is less. The effect of higher current velocity may be to reduce the proportion of particles that are arrested by the filtering apparatus due to increased particle momentum or to altered hydrodynamic patterns (Craig and Chance 1982). Chance and Craig (1986) have shown that the angle assumed by the larva, with respect to the current flow direction, changes with current velocity; since this would change the area presented to the current by the labral fans, efficiency of filtration would be affected by velocity. Temperature may control the rate at which the mandibular brushes operate to clean the fans, and thus influence the rate of ingestion.

Both temperature and concentration affected the proportion of time S. verecundum larvae devoted to filter feeding. This factor may influence the overall rate of ingestion and hence the efficiency. Craig and Chance (1982) measured the proportion of time that both fans of laboratory S. vittatum were held open actively feeding (70%). They suggested that the frequency of fan adduction for species that are more efficient at ingestion of suspended particulates is lower than that for the less efficient (e.g., S. vittatum), and that the greater proportion of time actually spent filtering may lead, along with morphological characters of the fan, to the heightened efficiency. Mokry (1975) Chance (1977), Craig (1977) and Schroeder (1980a)

have observed that simuliid larvae of certain species spend a considerable proportion of time (roughly 30%) browsing, cleaning mouthparts or simply remaining inactive with both labral fans closed.

The ingestion-rate responses to temperature are consistent with the seasonal distributions of the three species. C. ornithophilia, which occurs in the larval stages during the winter months, failed to feed to an appreciable extent at the warmest temperature regime (22°). Similarly, it was known from preliminary trials by the author and colleagues that P. mixtum, whose larvae inhabit local streams throughout the winter, fails to thrive in the laboratory at temperatures approaching 20°C. By contrast, the bivoltine S. vittatum, whose larvae occur year-round in local streams, fed at all three temperatures, with the highest ingestion rates being at the warmest temperature.

It was hypothesized that the degree to which food is digested is a function of mid-gut residence time (Tr) and the temperature in the gut lumen. In the present study, regression analysis using D as dependent variable, and residence time and temperature as independent variables was not appropriate, because of the discontinuously distributed data across temperature treatment levels and the proportionate nature of the digestion data. Nonetheless, the data for the eurythermal S. vittatum are suggestive of some functional correlation among temperature, residence time and

degree of digestion, as outlined below.

The activities of the digestive enzymes in insect guts normally follow a bell-shaped distribution; the temperatures within the organism's normal range generally fall within the "left side" of the curve and the activity increases with temperature according to the Arrhenius relation, with insect Q_{10} values generally lying between 2 and 3 (Wigglesworth 1972, p. 687)[11]. Since 1° - 22°C is representative of the normal range encountered by S. vittatum year-round, the theoretical relative digestive activity[12] would likely follow a relationship with temperature similar to that shown in Fig. 37 (dashed lines), for Q_{10} values of 2, 2.5 and 3. If gut residence time were constant under all conditions, then at lower temperatures, ingested food would experience fewer degree-minutes of exposure to digestive influences during passage through the mid-gut, resulting in some refractory types of food being egested virtually unutilized.

Figure 37 also shows the observed relationship of residence time with temperature for S. vittatum (solid line), using pooled data for the various PM concentration levels. The residence-time and digestive-activity relationships are mutually opposed, so that as temperature is lowered and relative digestive activity decreases,

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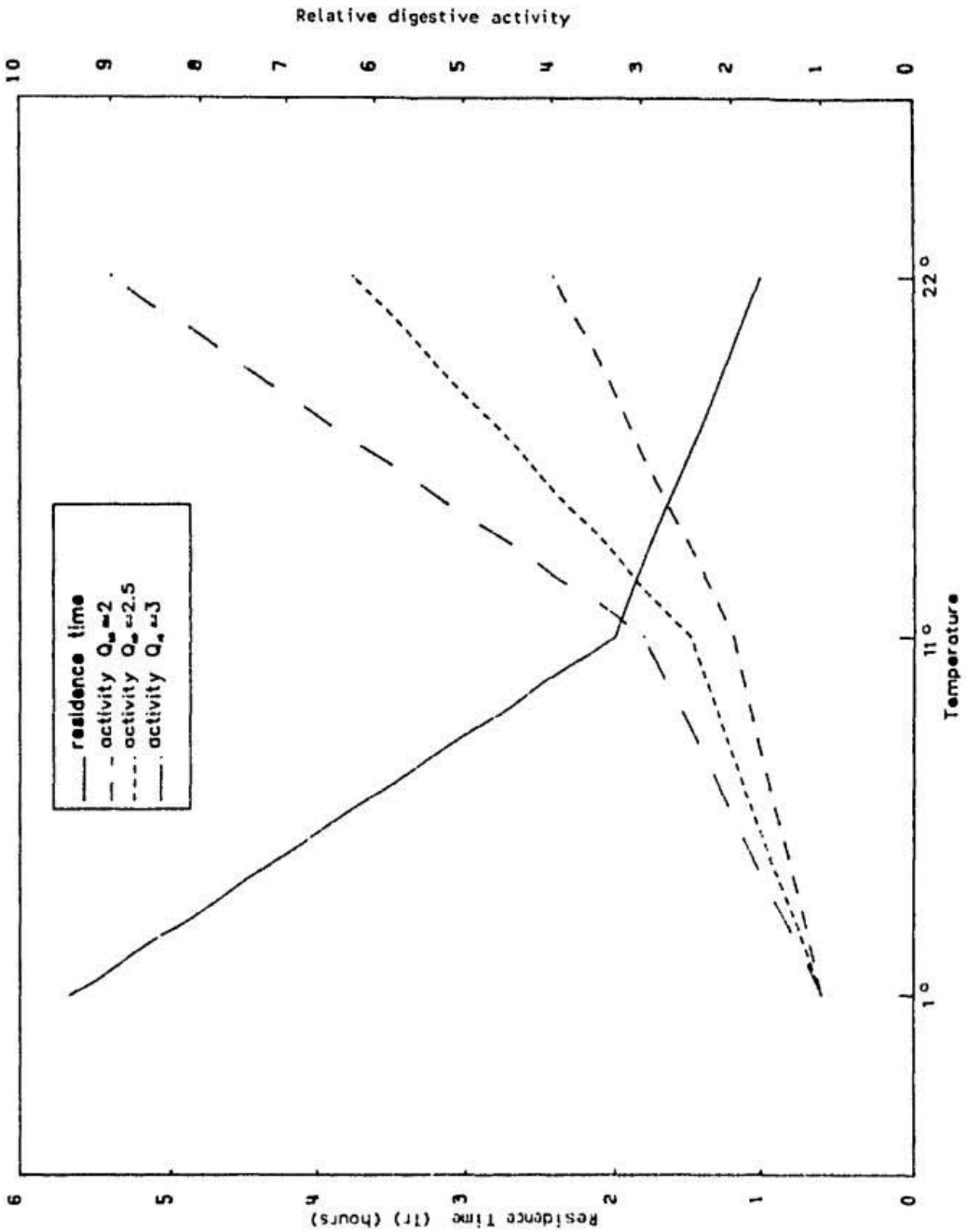
[11]Colbo and Porter (1981) observed Q_{10} values ranging from 2.14 to 2.83 for S. vittatum growth in laboratory rearing trials, over the temperature range 15-25°.

[12]i.e., the rate at which chemical digestive processes proceed

Fig. 37. Theoretical relative digestive activity (dashed lines) for three values of Q_{10} and observed residence times (solid line) for ingested food in S. vittatum at three experimental temperatures.


Relative digestive activity
0
1
2
3
4
5
6
7
8
9
10
Residence time (Tr) (hours)
0
1
2
3
4
5
6
1°
11°
22°
Temperature
residence time
activity Q_{10}=2
activity Q_{10}=2.5
activity Q_{10}=3

residence time is increased. In this way, the effect of lower ambient temperature in increasing digestion activity, would be counter-acted by the increased residence time. The increased residence time at lower temperatures stems from the temperature-efficiency interaction outlined previously. In this regard, it is noteworthy that the margin in residence time between 1° and 11° treatments is greater than that between 11° and 22° (Fig. 23). The margin in D between 1° and 11° conditions, on the other hand, is negligible compared to that between 11° and 22° (Fig. 31). This is consistent with a greater compensating effect of residence time between 1° and 11°, and lends some credence to the operation of such a mechanism.

A similar sort of compensating effect may operate in response to changes in PM concentration. If feeding efficiency were constant under all conditions, ingestion rate would vary directly with the rate at which particulate matter is supplied by the current, and residence time would thus be inversely proportional to PM concentration. In itself, this would potentially result in very low degrees of digestion at high concentrations. However, the curves for observed residence-time values at the various temperatures, above PM concentrations of 0.4 mg/l at least, are far flatter than would be expected if such were the case. The inverse relationship between feeding efficiency and PM concentration may serve to maintain residence time, and hence degree of digestion, within certain bounds with wide

changes in PM concentration.

The above mechanisms are illustrated for S. vittatum, in the relationship of the variable U (index of relative utilization) with temperature, PM concentration and current velocity. Larvae ingested only a portion of available suspended food, and digested only a portion of that amount, in effect 'skimming the surface' of the supply made available by the current. As the delivery rate of food (a function of PM concentration and current velocity) decreased, or as temperature rose, their proportionate utilization of the available supply increased.

CHAPTER 5 RESISTANCE OF ALGAE TO DIGESTION

5.1 INTRODUCTION

The findings of Chapter 4 indicated that digestion of algae in larval guts was incomplete under most sets of conditions, and thus that larvae utilized only a portion of ingested food. Qualitative visual observations suggested that differences in digestibility exist among algal types in their susceptibility to digestion by larval simuliids. The objective of the present laboratory trials was to establish that algae passed through the gut undigested, using another measure of susceptibility to digestion: the loss of algal viability on passage. In addition, the trials were designed to compare representative forms of algae in the degree to which they resisted digestion, thus yielding information on the digestive component of the feeding niche referred to in Chapter 1.

Scattered references to the degree of apparent digestion of ingested algae exist in the literature (e.g., Moore 1977b) but these are mainly casual observations, unsupported by relevant data. Schroeder (1981a) has recorded differences in assimilation efficiencies with different algal diets in S. ornatum. Apart from this, little is known regarding the susceptibility of specific algae to digestion in simuliid larval guts.

5.2 MATERIALS AND METHODS

Fifteen to twenty late-instar S. vittatum were introduced to each of 3 polyethylene jars on the rearing apparatus referenced previously. The bath temperature in jar 1 was 19°C and in jars 2 and 3 it was 10°C. The stirring speed in all jars was 75 rpm. At the beginning of the trial, the water in each bath was replaced. Aliquots of a stock feeding mixture containing known densities of Ankistrodesmus falcatus, Scenedesmus obliquus, Chlamydomonas rheinhardii and Nitzchia sp. and pulverized alder leaves (for bulk) were added to the jars so that the final dry-weight concentration in jars 1 and 2 was 5 mg/l and, in jar 3, 1 mg/l.

After 40 min. (jar 1), 2.5 h (jar 2) or 3.5 h (jar 3) (timed to allow for varying passage rates due to temperature and concentration effects), the larvae were removed and rinsed thoroughly in three baths of ice-cold 0.2-μm filtered water. The hind-gut was removed from the rest of the specimen and the contents were pressed out, captured with a 20 μl micropipette and transferred to a 0.5 ml aliquot of ice-cold distilled water in a glass centrifuge tube. If possible, the larva was induced to defaecate, and the faecal pellet was similarly treated. Six larvae were thus used to 'inoculate' each of a total of ten samples (total 60 larvae). To test for the effect of surface contamination from other than the intended hind-gut sample, two control samples were made by drawing water from around each of 6

intact hind-guts per control sample in the same way as described above, except that the hind-gut contents were not included. Dilutions of 0.1 and 0.01X were made in separate test tubes for each sample and for the stock mix. A 40-μl aliquot of the dispersed suspension was spread over the surfaces of three agar plates composed of Chu #10 agar.

The plates were left for 10 days at 10°C with continuous light. The algal colonies were then counted. The plates were examined under low magnification with a dissecting microscope. Even when extremely small, colonies of the four different species could be differentiated. Chlamydomonas colonies were circular and pale-green, and the palmelloid cells, separated from each other by gelatinous material, were distinct. Ankistrodesmus colonies had a characteristic crescent shape, making them clearly distinct from all others. Scenedesmus formed circular, raised, compact colonies that were dark-green in colour. Nitzchia was easily distinguishable by the brown colour of its colony. In this way, the mean number (n=3) of viable cells per 40 μl volume was determined for each of the samples. The concentration of Nitzchia frustules (frustules/μl) was estimated by direct count in ten 1-μl drops for each of the 0.5 ml samples, controls and stock mix.

To evaluate selectivity of ingestion from the available array of algal species in the rearing bath, 12 of the larvae used in the above trial were further dissected and the

anterior-most portion (approximately 5% of length) of the contents of the mid-gut were removed, tranferred and dispersed in a 2-ml aliquot of filtered (0.2-μm pore) water. The relative abundances of the four algal species in that sample and in the stock mix were then determined by direct count..

Viability Estimates:

To make estimates of viability (i.e., "survival") rates of the four species of algae, Nitzchia frustules, which are silicaceous and cannot be digested during their passage through the larval gut, were used as a reference point in the following manner.

If the mean concentration of frustules/μl in the stock mix is Ds, each of the plates inoculated with the 40 μl of stock mix received 40xDs frustules. If the viability rate were 100%, then 40xDs colonies would appear on the plate. If the actual number of colonies is D_1, then the true viability rate is (D_1/40Ds) x 100%. Thus, in the stock mix (i.e., the presented food) there are D_1/40Ds viable Nitzchia for each frustule. Similarly, if A_1, S_1, and C_1 are, respectively, the mean number of Ankistrodesmus, Scenedesmus and Chlamydomonas colonies on the stock-mix plate, then the numbers of viable cells per Nitzchia frustule in the stock mix are A_1/40Ds, S_1/40Ds and C_1/40Ds, respectively.

If the concentration of frustules in a given sample of suspended hind-gut contents is Dg frustules/μl, then in the 40 μl of suspension used per test plate, the number of frustules in the hind-gut sample is 40xDg. The number of potentially viable (i.e., if no loss of viability has occurred in the gut) Nitzchia cells is:

$$\% \text{ viability (in stock) x number of frustules}$$

$$= (D_1/40Ds) \times (40Dg)$$

$$= D_1 \times Dg/Ds.$$

The numbers of potentially viable cells per inoculation for the other three species are given simply by replacing D_1 with A_1, S_1 or C_1, which are the mean numbers of Ankistrodesmus, Scenedesmus or Chlamydomonas on the stock plate, respectively.

Now, if the mean number of Nitzchia colonies on the test plates is D_2, then the actual retained viability ("survival") rate for Nitzchia is:

$$D_2/\text{potential viability}$$

$$= (D_2/(D_1 \times Dg/Ds))$$

The "survival" rates for the other taxa are given by substituting for D_1 and D_2; thus for Ankistrodesmus:

$$(A_2/(A_1 \times Dg/Ds)) \times 100\%.$$

5.3 RESULTS

Specimens of all four algal species passed through the larval guts and still retained viability, under all three sets of environmental conditions, indicating incomplete digestion of such foods (Table 23). The proportion of Ankistrodesmus cells surviving passage was significantly greater (overall mean = 54.1%; $P < 0.001$) than those for Scenedesmus and Nitzchia, while the overall 'survival' rate for Chlamydomonas (0.46%) was significantly lower than all others ($P < 0.001$; 2-factor ANOVA on arcsine-square root transformed data, all treatments combined).

Contamination of tests, either during the larval dissection process or during the inoculation, was insubstantial: the mean number of colonies per control plate was <0.05% of the mean number of colonies per test plate. The data was re-worked using factors that allowed for selectivity of ingestion for each of the four food types. Because selectivity was low, the computed 'survival' rates, when adjusted for selectivity, were little different from the data of Table 23, and the general trends were unchanged.

5.4 DISCUSSION

The results are consistent with visual observations on apparent degree of digestion reported in Chapter 4. Chlamydomonas flagellates, for example, appeared to be

Table 23 Percentage survival (mean ± s.d.) of algal cells of 4 genera after passage through guts of *S. vittatum*

Treatment:	Nitzchia	Ankistrodesmus	Scenedesmus	Chlamydomonas
1. 19°, 5 mg/l	27.7 ± 10.4	62.4 ± 27.7	17.4 ± 4.3	0.08 ± 0.13
2. 10°, 5 mg/l	37.7 ± 15.3	60.3 ± 19.6	32.4 ± 5.7	1.04 ± 1.32
3. 10°, 1 mg/l	17.7 ± 8.1	37.8 ± 8.7	12.3 ± 4.4	0.08 ± 0.14
overall mean	28.7 ± 13.9	54.2 ± 21.1	21.9 ± 10.3	0.46 ± 0.91

Results of 2-way ANOVA:

Concentration effect: treatment 2 > treatment 3 ($P < 0.001$);
Alga effect: *Ankistrodesmus* > *Nitzchia*, *Scenedesmus* ($P < 0.001$);
Chlamydomonas < *Nitzchia*, *Scenedesmus* ($P < 0.001$); data transformed to arcsine- square-root before statistical treatment; above means are de-transformed (%).

easily broken down on ingestion: cells of this taxon also showed exceptionally high loss of viability in the present trial.

There is some suggestion of a link between retention of viability on passage through larval guts, and the nature of the wall of given types of algal cells. Of the four taxa used, Ankistrodesmus and Scenedesmus have a rigid cell wall, while that of Chlamydomonas is more delicate. Although Nitzchia has a rigid frustule, there is no continuous, thick envelope surrounding the cytoplasm, and therefore digestion proceeds without the need for the breakdown of a resistant outer wall.

For three of the four taxa (excepting the most resistant entity Ankistrodesmus), mean viability rates were lower at 19° C than at 10° C, probably reflecting the enhanced degree of digestion at higher temperatures observed earlier. For all four algae, mean viability rates (at 10° C) were lower for those at suspended solids concentration of 1 mg/l than for those at 5 mg/l ($P < 0.001$; 2-way ANOVA). This may have resulted from increased gut residence time at the lower concentration.

The findings are analogous to those made by Brown (1961) on digestion of algae in the mayfly Chloeon dipterum. In that study, some algae (diatoms, blue-green algae) were found to be viable when removed from the hind-gut, and viability was reduced as a function of gut residence time.

It is to be noted, however, that the retention of viability of algae after gut passage does not necessarily imply that the material made no nutrient contribution. A gut residence time of several hours could still allow for a significant input of nutritive substances through cellular leakage or excretion (Cummins 1973).

In summary, the present results indicate that algal food ingested by simuliid larvae retained viability on passage through the entire gut, giving clear evidence of incomplete digestion. Different types of algae had substantially different degrees of susceptibility to digestion.

CHAPTER 6 GENERAL DISCUSSION

6.1. Ecological Relevance of the Results:

The change in character of seston as it moves downstream is a dynamic and complex process. High densities of filter-feeding invertebrates at lake outlets have been linked to high densities of lacustrine algae, which generally have less refractory material content than other seston components such as particles of wood, leaves and needles. As the seston moves downstream, however, it is quickly modified by biological and physical processes, and augmented by new sources. Naiman (1983) has observed that seston in Quebec streams increased in food quality up to the sixth stream order, before declining slightly. This was thought to be due to partial breakdown of refractory material, rendering it more digestible to downstream organisms. Filter-feeding populations may influence their own densities and life histories, as well as those of other populations, by affecting downstream seston quality.

Since larval simuliids have been shown to have measurable impact on seston processing (Maciolek and Tunzi 1968, Morin et al. 1988), a knowledge of their selectivity toward the various classes of particulate matter, and their rates of feeding and digestion is important to an understanding of the functioning of stream ecosystems.

In another sense, the above type of information is important in providing insight into nutritional factors that may be significant to simuliid population dynamics and distribution. The notion that quality as well as quantity of food is important to secondary productivity has been demonstrated in certain other types of stream invertebrate (e.g., Fuller and McKay 1981, Lawson et al. 1984, Richardson 1984), and to some degree this has been shown in larval simuliids (Schroeder 1979, Ladle and Hansford 1981). Hart (1986) and Morin et al. (1988) have suggested that field populations of simuliids may be food-limited, and that their numbers and distribution may depend on food availability and food-related competition from congeners. A knowledge of the nutritional importance of the various food types, therefore, may contribute to the construction of predictive models for simuliid larval productivity and distribution among stream sites.

In Chapter 1, it was hypothesized that the feeding of simuliids in the study area incorporates two dimensions of selectivity (i.e., ingestive and digestive), and that the superimposition of these constitutes the effective feeding niche. The remainder of this Chapter discusses the present results in terms of selectivity of ingestion and selectivity of digestion under various conditions. The implications of the results are then discussed with respect to the actual nutritional importance of various potential foods in the habitat. This is followed by a discussion of the relevance

of the findings for simuliid control strategies.

6.2. Selectivity of Ingestion:

The findings of chapter 2 demonstrate that larval simuliids of the study area ingested a qualitatively wide range of algal and other available particulate matter in the seston. The size of particulate matter ingested was also distributed over a very wide range, and observed selectivity was related mainly to differences among physiological age groups in the ability to trap and ingest particles of certain size ranges. Apart from size, there was no evidence of selectivity based on the nature of the algal particle. Apparent food partitioning linked to larval habitat selection was shown to have resulted, in fact, from differing relative availabilities of the various algae in different riverine stretches. The overall lack of strong selectivity for the various types of algae is suggestive of a generalist strategy, thus allowing members of the simuliid community to colonize a wide range of stream habitats yielding different spectra of available foods.

6.2.1. Mechanisms of Selectivity:

The simuliid labral fan complex consists of three interacting fans: the large primary fan, and the smaller secondary and medial fans (Chance 1970). The primary fan is the major filtering organ (Craig and Chance 1982), consisting of 30-60 sickle-shaped rays. Ross and Craig

(1980) have provided some evidence that certain non-sieving filtration mechanisms, in which particles smaller than the spacings between adjacent filter fibers are trapped by means of contact/adhesion, operate to some degree in the feeding of larval simuliids. Braimah (1987a, 1987b) has identified the specific mechanisms that may operate in certain insect filter feeders under certain conditions of current velocity. The operation of a set of different mechanisms helps to show how particles of a considerable size range are captured and ingested by simuliid larvae. At the small end of the scale, reports of bacteria ingested by larval simuliids are well established (inter alia Fredeen 1964, Burton et al. 1973, Baker and Bradnam 1976, Wotton 1980). Wotton (1976) has shown that Metacnephia tredecimatum Edwards ingests particles of colloidal size (0.09 μm diameter). Merritt et al. (1978) reported particles ranging from < 2 μm to larger particles in a range 50-105 μm; and Merritt et al. (1982) observed particles ranging from 0.45 μm to more than 50 μm in P. mixtum/fuscum and St. mutata. The largest particle recorded from field material in the present work was a planar fragment of vascular plant tissue, measuring approximately 300 μm X 300 μm, recovered from a late-instar larva of C. ornithophilia. The largest ingested particle reported by Chance (1970) measured 345 μm diameter. In the present laboratory experiments (Chapter 2), bacterial-sized (0.2-0.5 μm) particles were captured, by three species, with efficiency comparable to that at which much larger (30 μm)

diatoms were taken. As a whole, the spectrum thus defined represents a range, in terms of particle volume, of more than 30 billion (3 X 10^{10}) times. The capability of capturing and ingesting particles of such a wide size range -- further evidence of a generalist strategy -- leads to maximum exploitation of the seston food resource by larvae of all species. Estimates of the impact of simuliid populations on seston loads in river systems have yielded variable results. Morin et al. (1988) for example, estimated that 32 - 55% of available seston was removed by (mainly) S. venustum/ verecundum with 0.8 - 1.4% being removed per linear meter. McCullough et al. (1979) calculated that filter feeders in a 1-m^2 area removed approximately 1% of the seston flowing over them each day. Maciolek and Tunzi (1968) estimated that simuliid larvae contributed significantly to the 60% of seston removed by filter feeders within a 0.4-km stream section below a lake.

C. ornithophilia was an exceptional case, in that selectivity towards particles 5-15 μm, and away from bacterial-sized particles relative to diatoms of about 30 μm dimension, was demonstrated. It is tempting to speculate that such differences may be related to its distinctive labral fan morphology. Craig and Chance (1982) observed that the microtrichia of S. vittatum are aligned parallel to the current, so that the only 'mesh' capable of sieving is formed by the primary fan rays, rather than the microtrichia. The microtrichia of C. ornithophilia, however,

are exceptionally long and fine, and appear to align normal to the current flow. If it were supposed that the microtrichia of C. ornithophilia represent an adaptation toward a sieving mechanism, in which the microtrichia themselves form a mesh of about 5-μm pore size, it follows that particles 5-15 μm diameter would more readily become lodged in the mesh of C. ornithophilia than in the 30-50 μm mesh formed by the primary rays in the other species. Alternatively, the long microtrichia of C. ornithophilia may act to retard or otherwise alter the flow of water between adjacent rays, leading to some degree of segregation of seston by size or shape. It is noteworthy that Kurtak (1978) observed higher capture efficiency for particles of 5-10 μm diameter relative to particles of other sizes, by C. dacotensis Dyar and Shannon, a species having microtrichial arrangement similar to that of C. ornithophilia.

Preferences for specific current velocities are shown by larvae of various species, and several authors have suggested that such preferences may be related to species-specific differences in labral fan structure (Kurtak 1978; Craig and Chance 1982). In the course of the present collections, it was noted that C. ornithophilia larvae frequently were found in microhabitats of relatively slow current velocity (e.g., under stones) as compared to other species. It is also plausible, therefore, that the distinct fan structure of this species is an adaptation to hydrodynamic requirements of a specific microhabitat.

The investment of long microtrichia, as in C. ornithophilia, would result in a reduction of fluid flow through the labral fan (Cheer and Koehl 1987a, 1987b). Because sieving is inherently more efficient than non-sieving mechanisms, however, and because the mesh of C. ornithophilia is apparently finer than that of the other species, the C. ornithophilia model would likely filter with maximal efficiency over a greater size range (i.e., 5 μm and greater, as opposed to 30-50 μm and greater). The C. ornithophilia microtrichial arrangement may thus represent a shift toward reduced flow volume per unit time, compensated by enhanced capture efficiency over a greater range of particle sizes. This would be ideally suited to the lake outlet habitat preferred by this species, where low current velocities are accompanied by a relatively rich food supply. More laboratory studies, examining capture efficiencies for particles of various sizes by C. ornithophilia and other species, at various current velocities, should prove useful to our understanding of simuliid feeding, by determining whether microtrichial arrangement and form is related to feeding selectivity.

6.2.2. Selectivity and Resource Partitioning:

Observations made during the study and information on simuliid bionomics gathered by others working in the study area (Lewis and Bennett 1974, 1975, Colbo 1979) suggest temporal and spatial distributions as niche segregation

mechanisms within the simuliid community. The present findings gauge the importance of selectivity toward various types of available food as a third segregation factor.

The present data provide evidence for intra-specific food resource partitioning, based on particle size and larval size/age. This type of niche segregation may be important in reducing competition among individuals where high densities of larvae of a range of instars co-exist in spatially restricted habitats. This situation occurs in most streams of the study area in the spring, where high densities of late-instar S. vittatum, C. ornithophilia, and occasionally P. mixtum and St. mutata co-habit lake outlets with early instars of spring-hatching generations of S. vittatum and S. venustum. It also occurs from mid- to late summer, when overlapping generations of S. venustum/ verecundum larvae exist in large numbers.

The present data indicate that inter-specific partitioning was less pronounced than intra-specific, in simuliid communities of the study area, and that it centred around one species, viz. C. ornithophilia. Here, too, selectivity was based on particle size, relating to a certain relatively narrow size range of small algae. It is possible that such partitioning serves to reduce competition between late instars of this species and those of S. vittatum, which often co-habit lake outlets in large densities.

Inter-specific competition in the study area may be reduced through a combination of feeding selectivity, (as between C. ornithophilia and others), differences in habitat preference and temporal distribution. Thus, C. ornithophilia and S. vittatum are generally more restricted to the immediate lake outlet area than are P. mixtum and St. mutata, which normally inhabit downstream stretches. Whilst direct competition between C. ornithophilia and S. vittatum may be relieved to some extent by inter-specific food partitioning, there are microhabitat differences between these two species (C. ornithophilia has a marked tendency to aggregate in large mono-specific clumps or to adhere to the bottom surfaces of stones). Likewise, P. mixtum and St. mutata have somewhat different habitat preferences (St. mutata tending to inhabit small tributaries and slower currents within larger streams (Colbo 1979)). At certain sites and times, however, all four 'winter' species were observed to occur together immediately below lake outlets in the study area. Under such conditions, inter-specific competition may be severe, and it seems unlikely that the degree of food-resource partitioning observed in the present data is sufficient in itself to explain co-existence. In such cases, food may not in fact be a limiting resource, and this may obviate the need for vigorous competition. Although S. venustum/verecundum inhabits both the immediate outlet area and downstream stretches, being a 'summer species' it is to a large degree separated from the other species

through temporal distribution. The diets of late-instar S. venustum/ verecundum and the bivoltine S. vittatum overlapped broadly, and little evidence was given of any partitioning mechanism between these two species. Distribution of S. venustum/ verecundum among streams in the area, however, appeared to be different from that of S. vittatum (i.e., there are 'S. vittatum streams'). Whether this is due to competitive exclusion or whether habitat choice plays a significant role in reducing competition between the two species is speculative at this point. The above niche partitioning mechanisms are summarized in Table 24.

In studies of field populations of European simuliids, Schroeder (1983a, 1986a, 1986b) found both inter-specific and intra-specific differences in diet between species co-habiting stream sites, on the basis of size distributions of certain diatoms or of the relative abundances of diatoms, other algae or detritus. Inter-specific differences in the ingested food particle spectrum were observed between larvae of Prosimulium rufipes Meigen and Eusimulium cryophilum Rubtsov, and between Simulium ornatum Meigen and S. reptans. However, not all of the studied assemblages of larval simuliids exhibited inter-specific differences, and intra-specific differences were generally considerably greater than inter-specific.

Table 24 Possible niche segregation mechanisms reducing competition and favouring co-existence among simuliid populations of the study area.

	St. mutata (late-instar)	P. mixtum (late-instar)	C. ornithophilia (late-instar)	S. vittatum (late-instar)
S. vittatum (late-instar)	habitat[1]	habitat[1]	food partitioning, microhabitat[2]	-
C. ornithophilia (late-instar)	habitat[1]	habitat[1]	-	-
P. mixtum (late-instar)	microhabitat[3]	-	-	-
S. verecundum (late-instar)	temporal	temporal	temporal	habitat[4]
all winter species (early-instar)	food partition, temporal	food partition, temporal	food partition, temporal	food partition, temporal
all summer species (early-instar)	food partition, temporal	food partition, temporal	food partition, temporal	food partition, temporal

[1] relative positions upstream/downstream
[2] C. ornithophilia has a tendency to "clump" and to adhere to undersides of stones
[3] St. mutata has a preference for slower current velocities, as compared to P. mixtum
[4] among streams

In summary, the presently observed differences in food utilization among simuliid populations may play a role -- but not an exclusive role -- in reducing competition among larvae of different age classes and, in the case of C. ornithophilia, between species. Selection of different feeding niches by different age-groups/species would favour co-existence of a range of developmental forms/species, and would tend to maximize the efficiency with which the overall seston resource is utilized at any given site.

6.3. Selectivity of Digestion:

The apparent adaptation of optimal digestive rates to warm or cool temperatures is consistent with the different temporal distributions of simuliid species of the study area. In S. verecundum, for example, degree of digestion was shown to be greater at higher temperatures, while the reverse relationship was observed for P. mixtum. These two species occur as larvae during the summer and winter months, respectively.

Larval populations of the bivoltine S. vittatum occur year-round, and this species must be able to digest food effectively over a temperature range of near 0° to the mid-20°s. Feeding efficiency responded significantly to changes in temperature, and this effect tended to increase gut residence time at lower temperatures. Enzymatic digestive activity likely responds to changes in temperature in the opposite way, and hence the temperature-efficiency

linkage may serve to maintain the degree of digestion above certain thresholds under conditions that would otherwise lead to very little utilization of ingested food. At warmer temperatures, however, the effect of decreased residence time was apparently overcome by the increases in digestive activity, and the final degree of digestion of food rose with temperature.

An additional compensatory mechanism may be the inverse correlation of feeding efficiency with PM concentration, ensuring that movement of food along the alimentary tract does not proceed at such a rapid rate at high PM concentrations (e.g., during spates) that the animal literally starves because of the very abundance of food. The findings suggest that the linkage of feeding efficiency (and hence ingestion rate) with ambient temperature, PM concentration and current velocity assisted larvae of the studied species to consume and digest food under the range of physical conditions encountered in their respective temporal niches. The mechanisms involved in effecting these linkages may include: (i) varying rapidity of movement of feeding organs, which may be controlled by temperature or by concentration (Hart and Latta 1986); (ii) intermittent feeding, which appears to be reactive to temperature and to PM concentration; and (iii) hydrodynamic factors, which may be influenced by larval behaviour, by fan morphology or by water temperature.

The above relationships are reflected in the proportionate utilization of the available food supply (U), which incorporates both ingestive and digestive processes. U shifted in the eurythermal S. vittatum, with both PM concentration and temperature. As the supply became sparser (i.e., lower concentration or lower current velocity) or as temperature increased, the proportionate utilization of food (diatoms) rose. There was no evidence that this species, C. ornithophilia or P. mixtum differed substantially in the relative utilization of available food.

Although environmental conditions play a role in determining the degree of digestion, they account for only part of the variation in digestion of algal cells. Great differences exist among algal types regarding susceptibility to digestion. In many cases, the cell wall may protect the cell membrane from mechanical damage of the ingestion/digestion process. Once the cell membrane is ruptured, the contents (e.g., food storage products) are free to disperse from the cell. Some algae are sufficiently resistant to digestion that they remain apparently intact regardless of environmental conditions (e.g., Chlamydomonas palmellae, various desmids). Other taxa are nearly always digested beyond visual recognition (e.g., Chlamydomonas flagellates). Still others are apparently intermediate in susceptibility to digestion (e.g., Nitzchia, Navicula, Scenedesmus, Ankistrodesmus). It is in the latter types that variability in degree of digestion and its correlation with

environmental conditions most often becomes evident in field collections taken from various sites and times of year. These findings help to explain the widely divergent reports of the apparent utilization of algae, based on visual observations of ingested material in field-collected larvae.

In summary, the larval feeding niche can be viewed as a construct of two dimensions: the breadth of the range of materials ingested, and the degree to which ingested foods are actually digested. Larvae proved invariably to be "generalists" in respect to the range of algae ingested. However, the degree of digestion of any alga, and (because algae differ in susceptibility to digestion) the range of algal types digested to a given degree, was shown to adapt to conditions of food availability and temperature. The survival value may lie in a certain plasticity, by which larvae adapt to low food delivery rates by extracting proportionately more from the available supply, this being effected through adjustments to feeding efficiency and degree of digestion. Similarly, in S. vittatum and S. verecundum at least, the proportion of food digested rose with increasing temperature. Colbo and Porter (1981) observed that the amount of food required to produce maximum growth in larval S. vittatum increased with increasing temperature over the range 15° to 25°C. The present findings suggest a mechanism by which this need is accommodated.

Although not studied specifically in the present work, re-ingestion of faecal material by downstream larvae may be important in nutrition at low temperatures or when seston is sparse. This would be particularly so in relation to algal material that is refractory to digestion, and which requires a certain amount of exposure to digestive influences before protective walls are broken down and cell contents are released. Wotton (1980) estimated the nutritional content of one faecal pellet as equivalent to bacteria filtered from as much as 100 ml of water. Faecal pellets are generally high in content of lipids, nitrogen and calories (Shepard and Minshall 1981). Given the low ingestion rates associated with such environmental conditions, the capture and ingestion of a single faecal pellet may represent a considerable nutritional advantage, even if the material is partially digested. The significance of ingested faecal pellets to the nutrition of simuliid larvae is a subject deserving further study.

6.4. Ecological Nutritional Role of Algal and Other Foods:

The relative value of the various algal types as food by larval black flies can be linked generally to susceptibility to digestion and thus, presumably, to the structure and composition of the cell. The flagellate form of Chlamydomonas, for example, has a relatively fragile cell wall that is susceptible to crushing. These cells, which appeared to be effectively digested under nearly all

conditions, and which lost nearly all viability on passage through larval guts, promoted high growth rates in larvae. The diatoms, which have only a thin membrane protecting the cytoplasm, and which were digested to at least some degree under all sets of environmental conditions, led to very high growth rates in all four larval species. Scenedesmus, Ankistrodesmus, Chlorella and Chlamydomonas palmellae all have a thick or rigid cell wall, and as food, led to generally lower growth rates among larvae.

The availabilities of different types of food, however, vary considerably among sites and seasons. The realized nutritional value of different foods in the field, hereafter referred to as "nutritional importance", must take into account the following factors: (i) seasonal abundance in the seston; (ii) susceptibility to capture; (iii) susceptibility to digestion; and (iv) inherent nutrient content. The present findings allow certain predictions of the relative nutritional importance, to larval simuliids, of classes of particulate matter constituting seston of the study area.

Diatoms must be of relatively great nutritional importance in the study area, as they were shown to be abundant in guts of field-collected larvae from streams representing a variety of ecological conditions; and because they are ingestible, digestible and highly nutritious, as shown in laboratory rearing trials. The nutritional importance of diatoms would be especially high for species

such as P. mixtum, St. mutata and S. verecundum, which usually occupy downstream habitats. Diatoms are one of the major components of the autochthonous periphytic stream flora and, as they are continuously washed from the substrate by flowing water, they typically become more abundant downstream.

For populations (chiefly C. ornithophilia, S. vittatum, S. venustum) which inhabit lake outlets, the relative nutritional importance of small (4-12μ) flagellate chrysophytes, chlamydomonads and other such forms of lacustrine planktonic algae, must be high, since these organisms appeared, in general, to be easily digested and furthermore, appeared to be abundant in local habitats. Especially high densities of these algae were observed in late-winter/early-spring collections at lake-outlet habitats in the present study; such numbers were not seen in habitats much further downstream (likely due to attrition). "Blooms" of small chlorophytes/chrysophytes may be of great importance to lake-outlet populations during periods of maximum increase in larval biomass. It is perhaps noteworthy that the microtrichial arrangement of the lake-outlet species C. ornithophilia seems ideally suited to apprehending particles of this size range. Hansford (1978) related high growth and abundance of S. austeni to seasonal blooms of phytoplankton in the River Stour (England). Carlsson et al. (1977) attributed huge larval simuliid populations below lake outlets to the abundance of fine

particulate food of lake origin; and Brown and Brown (1984) postulated that filter-feeding riffle insects compete for high-quality food items produced in upstream pools. Richardson (1984) observed both higher growth rates of the caddis larva Neureclipsis bimaculata L. and greater seston nutritional quality at a lake outlet habitat relative to downstream stretches, and took this to explain the accelerated voltinism and higher population densities of filter-feeding invertebrates below lake outlets. In productive lakes where high densities of such organisms exist, it would be expected that upstream individuals would exhibit greater rates of growth than downstream conspecifics. In such cases, productivity of the autochthonous periphytic flora cannot keep pace with nutrient input of lacustrine origin. Such situations are likely to be fairly common in the study area, where human populations have in places led to some degree of enrichment.

Neither leaf litter nor bacteria provided very high growth rates among the four species of larvae tested, and leaf litter produced particularly low rates of growth. However, high densities of leaf litter and associated bacteria may abound in stream seston, especially at times of the year (fall, spring) when decomposition of vascular plant material is rapid. Originating from terrestrial runoff, this allochthonous input is not limited by any factor of stream chemistry; it is limited chiefly by the abundance of deciduous woody plants near the stream banks. Most streams

in the study vicinity had a dense border, primarily of speckled alder. These materials may represent a major share of the nutritional input to simuliid populations in downstream habitats in situations of inherently low aquatic productivity, particularly at times of year when litter decomposition is rapid. Larval growth rates in such situations, however, would likely be relatively low. The extent to which the shed leaf material is "natured" (i.e., colonized by saprophytic bacterial and fungal flora) might influence its nutritional value (Ward and Cummins 1979) in a given stretch of stream at a given time of year. However, Cummins and Klug (1979) point out that while the nutritive value of micro-organisms may be higher than that of other detritus, the proportionate microbial biomass of ingested detritus is very low (0.03-10%). In fact, they attributed only 8% of the observed growth of the shredder Tipula abdominalis (Diptera: Tipulidae) to microbial biomass associated with a diet of natured leaves.

The present findings enable one to formulate certain hypotheses on simuliid larval distribution, abundance and productivity, based on quality, as well as quantity, of potential particulate foods. Working in the study area, Colbo (1982) observed certain patterns in mean wing-length and numbers of eggs among P. mixtum, St. mutata and C. ornithophilia adults, according to stream of larval origin, and to site within any given stream. Growth and fecundity were generally greater at upstream sites (near lentic

outlets) than at more downstream sites on the same stream. Outlets of lakes that were considered to be relatively high in primary productivity supported more productive larval populations.

Colbo's interpretations correspond with some of the findings of the present work. Although not included in the data of Chapter 2, subjective estimates were made, in the present study, of the relative abundances of algal and other materials in simuliid guts taken from a number of sites, including some of those in Colbo's study (details given in Appendix III). The summary observations are shown in Table 25. Mean wing-lengths and fecundities among the sites for all three species correspond in rank to the approximate proportion of gut contents composed of algal material. This pattern is consistent with the present findings, where algae were generally more valuable as food than were bacterial or detrital matter.

Given the abundance of planktonic algae at lake outlets and the relatively high degree of digestibility and nutritive value among various types of algae shown in the present work, and allowing for progressive downstream attritional loss of these, high productivities of larval populations might be expected in lake-outlet habitats relative to downstream stretches. This finding, too, was made in Colbo's study. Relatively enriched lentic bodies are also capable of conferring elevated downstream levels of

Table 25 Composition of seston observed at five sites, showing wing-length and fecundity data of P. mixtum females collected at same sites by Colbo (1982)

Site	Percent Algae[1]	Wing Length (mm) (mean, s.d.)	Eggs per female (mean, s.d.)
Beachy Cove Br.	> 90	2.33 ± 0.05	281.7 ± 16.9
Healey's Pond outlet	> 90	2.34 ± 0.05	278.6 ± 36.5
Little Power Pond outlet	> 80	2.13 ± 0.06	223.2 ± 14.1
Barking Kettle Pond outlet	< 10	2.04 ± 0.04	191.3 ± 17.3
Mt. Scio Farm Bog outlet	< 5	1.92 ± 0.06	145.8 ± 28.1

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1. remainder was detrital, fungal matter.

autochthonous primary productivity (chiefly diatoms and filamentous algae) if they provide an abundance of dissolved nutrients. Hence, it is hypothesized that even downstream sites on streams draining relatively enriched lentic bodies would themselves be relatively productive in terms of simuliid growth -- although not as much so as the headwaters of the same stream. This, too, is generally borne out in Colbo's data.

6.5. Relevance of Findings to Simuliid Control Strategies:

Initially, it was conjectured as to whether the degree of feeding specialization among species might be sufficient that the incorporation of a potent control agent into a given food organism would allow selective control of a target simuliid population. However, the data did not support this, at least for the study community.

Manipulation of the natural food supply was another of the possible control strategies considered. Because of the low dependence of simuliid larvae in the study area on periphytic material, there would be little point in attempting to alter the composition or productivity of the autochthonous riparian flora with a view to suppressing the numbers of certain species. Similarly, it does not seem likely that the relative abundances of algae in the seston could be altered in such a way as to manipulate the relative abundances of species in the larval simuliid community.

The absence of substantive differences among simuliid species of the study community regarding the size spectrum of particles ingested argues against the feasibility of using formulations of specific particle size to control a single target species. As for an ideal particle to maximize ingestion by larvae of the target population, several attributes are noted. First, the diameter of the particle should be in the approximate range 1-20 μm, to promote ingestion by all instars. Particles at the smaller end of this range, if denser than water, would tend to remain suspended in the water column longer than larger particles, thus increasing the downstream effect of the treatment. Finally, the size and composition of the optimal particle would be such as to allow digestion under the alkaline conditions of the gut lumen, over a suitable range of ambient temperatures and PM concentrations, in less than the expected gut residence time.

The phenomenon of intermittent feeding should be studied further, examining various simuliid species under various physical conditions of the environment. The implications for field or laboratory dosing programs involving particulate formulations are important. Under conditions where intermittent feeding occurs, short dosing regimes would tend to produce relatively poor results since only a certain proportion of larvae would be feeding during the dosing interval. In such cases it might be more effective to apply an equal amount of formulation over a

longer dosing period. Any laboratory or field dosing trial run at relatively low temperatures or high levels of suspended material should therefore include an assessment of the proportion of the target population that was actively feeding during the dosing period. This requirement applies to particulate formulations but it also applies to dissolved or emulsified insecticides because of the tendency of many such chemicals to quickly become adsorbed to particulate matter already present in the riverine water and thus become in effect particulate agents.

Using diatoms as indicators, it was shown that the degree of digestion occurring in the larval gut in S. verecundum and S. vittatum is lower at lower temperatures; in P. mixtum the reverse was found. There may therefore be an optimum temperature, specific to each species, for the efficacy of any particulate formulation (such as a micro-capsule or bio-control agent) that depends upon digestion of an outer coat before release of the agent or active ingredient into the larval gut. Screening and evaluation of such control agents should therefore be carried out over a range of water temperatures corresponding to that experienced by the species under field conditions. Dosage rate or other factors might then be adjusted, in practice, to water temperature occurring at the time of dosing.

For agents that are somewhat resistant to digestion, or for any agent in use under environmental conditions that are unfavourable for digestion, release of the 'active ingredient' may occur only after a considerable period in the gut and may thus take place only when the particle has been ingested by a second, or subsequent, larva. The general effect would be increasing mortality rates with distance downstream from the dosage point. Superimposing the effect of attrition, the resulting pattern would be one of increasing mortality rate with progression downstream until a peak is reached, and then subsequent decline. The spatial position of the peak could be expected to vary according to such factors as larval age (and thus gut residence time), total PM concentration, water temperature, and the rate at which the formulation sediments or is otherwise lost. All of these factors can be expected to vary considerably, both temporally and among different sites.

As more knowledge is gained of ingestive efficiencies for various types of particle, and of relationships between environmental conditions and feeding/digestion rates, much of the unpredictability that is frequently experienced in field dosing programs may be removed.

6.6. Achievement of Thesis Objectives:

All four objectives set out in Chapter 1 were achieved, as outlined below.

Larvae of simuliid species in the study area did not ingest certain types (i.e., genera) of algae selectively, but populations were shown to prefer certain fractions of the available spectrum based on algal particle size (1). Different algae and other materials representative of the seston differed substantially in nutritional value, but no substantial differences among simuliid species were observed as to which foods were most nutritious (2). Extrinsic factors had significant effects on both ingestion rates and the degree to which ingested materials were digested (3). Different forms of algae displayed greatly different degrees of resistance to digestion in larval guts (4).

SUMMARY OF CONCLUSIONS

1. With some exceptions, feeding selectivity by larvae on algae of the seston was relatively low for six Newfoundland simuliid species.
2. Smaller particles of the seston were relatively more abundant in the mid-guts of smaller larvae of all species than of larger larvae, while larger algae were more heavily represented in guts of late instars. This was probably related to the differences in dimensions of the filtering and ingestive apparatus.
3. Among the age-species populations examined, first-instar P. mixtum was unique in that it heavily utilized the periphyton, by grazing or possibly deposit feeding, for acquisition of food material. Other populations utilized the seston. There was no evidence of predation.
4. Consistent with the lack of selectivity of feeding, larval diets were strongly correlated with the selection of algae available in the seston. The algal food of headwater populations in lake-fed streams included a preponderance of lacustrine flora, whereas for downstream populations, the autochthonous algal flora was more heavily represented in larval diets.
5. Whilst larvae situated in different stretches of stream exhibited different spectra of ingested food, choice of substrate had no influence on larval diet.
6. Bacteria (represented by Micrococcus and Pseudomonas)

were ingested by larvae of all 4 species tested (P. mixtum, St. mutata, S. vittatum, C. ornithophilia) in laboratory trials. Whereas the first 3 species ingested bacteria and the much larger diatoms (about 30 μm) with roughly equal efficiency, C. ornithophilia was less efficient in capturing bacteria than it was in capturing the larger particles.

7. Late-instar C. ornithophilia collected from the field contained an especially high relative abundance of particles of the 5-15 μm size range and was notably different from other species in this regard.
8. Although no strong evidence was given for selectivity or partitioning on the basis of particle quality or phylogeny, the data provide evidence for some degree of resource partitioning based on particle size. Evidence for intra-specific partitioning in this form was considerably stronger than for inter-specific. The various species had widely overlapping diets. The feeding niche of late-instar C. ornithophilia, however, was different from those of three other species with which its larvae co-exist in winter habitats, possibly due to preference towards small particles of a certain size range (5-15 μm). Food niche breadths of early-instar larvae in all species were narrower than for late-instar conspecifics, probably due to selectivity by smaller larvae toward smaller algae.
9. The presently observed differences in food utilization by

simuliid populations may serve to reduce competition among larvae of different age classes and, in the case of C. ornithophilia, between species, thus allowing co-existence in the same or closely associated habitats. A combination of niche separation mechanisms may be involved, including food resource partitioning based on particle size, and other factors such as micro-habitat differences or temporal distribution.

10. The unique morphology of the C. ornithophilia labral fan as compared to those of other species examined may have some relationship with the different selectivity characteristics in this species.
11. Ingestion rates, as measured by the passage of marker among algal foods in laboratory trials, varied with water temperature, in larvae of all three species tested. In S. vittatum, a eurythermal species, ingestion rates rose with increased temperature. P. mixtum and C. ornithophilia failed to feed substantially at the warmer temperatures, a finding consistent with the stenothermal biology of these species and temporal restriction to the colder months of the year. Ingestion rates were not significantly different under different conditions of water current velocity. Larvae of different physiological age showed no significant differences in ingestion rates. Residence times of ingested material in the mid-gut were generally reduced at higher temperatures.

12. Feeding **efficiency** (i.e., amount of food ingested per amount presented to the labral fans by the current per unit time) for all three of the above species increased with increasing temperature, with decreasing PM concentration and with decreasing water current velocity.
13. The proportion of time larvae of S. verecundum spent actively filter feeding increased with increased temperature and with decreased PM concentration.
14. The 'completeness' of digestion, using diatoms as digestible indicators, was measured under various environmental conditions in laboratory trials, with S. verecundum, S. vittatum and P. mixtum. In the 'summer species' S. verecundum, the degree of digestion increased with increasing temperature and decreasing PM concentration but in the 'winter species' P. mixtum, the reverse temperature relationship was shown. In the eurythermal S. vittatum, the degree of digestion did not vary markedly with PM concentration, and increased with temperature over only part of the range examined (1-20°). Neither physiological age nor current velocity appeared to be strong determinative factors with regard to degree of digestion. In no situation did ingestion occur without a substantial degree of digestion.
15. It is hypothesized that a form of compensatory system, perhaps based on intermittent feeding or varying rapidity of movement of the mouthparts, exists in S.

vittatum, such that a certain degree of digestion is maintained under conditions (i.e., low temperature, high PM concentrations) that would otherwise lead to very little utilization of ingested food. The system seemed to be 'offset' toward a greater degree of digestion at warmer temperatures. Thus, the degree of food utilization (a function of feeding efficiency and degree of digestion) relative to the rate at which food was delivered by the current, rose as the PM concentration declined, and as temperature increased.

16. Although environmental conditions were important in determining the degree of digestion, some types of algae were inherently more readily digestible than others. Those with a thin, fragile cell wall appeared to be relatively easily digested, while those with a thick, rigid wall were not prone to rapid digestion. Diatoms, which have a siliceous frustule but no firm outer cell wall, were rather easily digested.
17. Algal cells of the taxa Ankistrodesmus, Chlamydomonas, Nitzchia and Scenedesmus all passed through the guts of S. vittatum larvae in laboratory trials, and retained viability to some degree, giving evidence of incomplete digestion. Less than one percent of cells of Chlamydomonas, a thin-walled alga, retained viability, while the corresonding proportions for the other green algae and the diatom were far higher (21.9 - 54.2%).
18. Larvae of S. verecundum, S. vittatum, C. ornithophilia

and *P. mixtum* were laboratory reared on standardized suspensions of different algal, bacterial and detrital foods. All diets produced some increase in mean larval size, but some foods yielded greater increases than others. Diatom ration generally produced greater increases than did all other foods. A thin-walled green alga (*Chlamydomonas*) produced generally greater increases in size than did thick-walled green algae (*Ankistrodesmus*, *Chlorella*, *Scenedesmus*), suggesting a relationship between digestibility and nutritional value. Bacterial diets produced lower larval growth than did algal diets, overall. Leaf litter yielded the least larval growth. Little difference was observed among the four simuliid species regarding the relative values of the different foods, giving little evidence of specialization by any species for any class of food.

19. The overall value, as larval food, of any suspended particulate material in streams was considered to be a function of its availability in the seston, its ingestibility, its digestibility and its nutrient content.

20. The quality, as well as the quantity, of seston must be considered in any investigation of simuliid nutrition as it relates to distribution and productivity. By considering the amount and types of available algal and other material in the seston, predictions can be made concerning the likely productivity of larval populations

at sites representing different ecological conditions at different times.

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APPENDIX I

Life Cycles and Ecology of Simuliid Species Studied:

Field and laboratory studies were carried out using the six most common simuliid taxa indigenous to insular Newfoundland.

The following synopsis uses the information of Lewis and Bennett (1973, 1974) and Colbo (1979).

Prosimulium mixtum Syme and Davies is a widespread univoltine species which overwinters in the larval stages. Larval growth progresses slowly throughout the winter and then increases in rate as stream temperatures rise in the spring. Adults emerge in late April or May, depending on seasonal temperatures. Females are autogenous on the first gonotrophic cycle and eggs are laid in June. Hatching of eggs occurs in early autumn and the cycle is repeated. P. mixtum is a serious man-biting pest in Newfoundland; it probably attacks a range of mammalian hosts.

The yearly life cycle of univoltine Stegopterna mutata Malloch is approximately similar to that of P. mixtum. Like P. mixtum it is autogenous. It differs in that it is allotriploid and parthenogenic. Although closely associated with P. mixtum in habitat, St. mutata appears to prefer micro-habitats of somewhat slower current velocity. Both species are normally found in downstream sections (i.e.,

other than at outlets) of streams of small or medium size such as are abundant on the Avalon Peninsula. Occasionally, however, St. mutata is found co-habiting lake outlets with C. ornithophilia. St. mutata is very common in smaller streams.

The anautogenous Cnephia ornithophilia Davies et al. is unique from other local simuliids in that larval populations occur almost exclusively at lake outlets, where larvae aggregate, often in very dense clusters, in slowly-flowing water. It is not clear whether the tendency to aggregate is related to shortage of available substrates in a rather spatially "condensed" habitat or is a more strictly behavioural phenomenon. Like the above species, it overwinters as a larva, emerging in the spring. It is believed to attack avian hosts.

Simulium vittatum Zetterstedt is multivoltine in the study area, having one generation overwintering in the larval stages (emerging in the spring and ovipositing shortly thereafter) and overlapping generations completing larval development throughout the summer, with oviposition and egg-hatch into late summer (Colbo, pers. comm.). Females are primarily autogenous on the first gonotrophic cycle. S. vittatum larvae are often found in large numbers near lake outlets during the winter (frequently co-existing with C. ornithophilia), but they are by no means restricted to these upstream habitats. Females of this species will attack man

but it is not as serious a pest in this regard as are P. mixtum and S. venustum/verecundum.

Local members of the S. venustum/verecundum species complex are anautogenous and mammalophilic. The overwintering stage is the egg. S. venustum Say complex hatches early in the spring and is found in late April, May and June covering all available substrates, often in vast numbers, near lake outlets. The multivoltine S. verecundum Stone & Jamnback hatches later -- around mid-June -- and is normally found on trailing vegetation in more downstream situations. Subsequent generations (2-3) develop in streams of a wide size range throughout the summer.

Simulium tuberosum Lundstrom is either univoltine or bivoltine but apart from this it is similar in most ecological respects to S. venustum/verecundum.

During winter months, larvae of the 'winter species' P. mixtum, St. mutata, C. ornithophilia and S. vittatum, develop slowly until spring, when growth proceeds more rapidly until pupation and emergence of adults in April/May. At this time, eggs of the 'summer species', S. venustum, S. verecundum, S. tuberosum and S. vittatum hatch, leading to high larval densities on all available substrates showing increasing asynchrony of development as the summer progresses. Shortly following the emergence of the last members of the summer populations, the eggs of the 'winter species' begin to hatch. Of these taxa, only S. vittatum is

year-round in its temporal distribution.

In the present study, the taxonomic nomenclature for the Simuliidae developed by Crosskey (1987) was used.

APPENDIX II

Collection Schedule and Details:

All collections in the field study are shown in Table 2, together with the number of larvae dissected in each sample. Further details follow.

B1. Beachy Cove Bk., 77-10-27

Water sample was taken several metres downstream from Hughes Pd. i.e., at the outlet, in slowly flowing water. Cnephia ornithophilia were collected from trailing grass. Water temperature was 7.5°C.

B2. Beachy Cove Bk., 77-10-28

Water sample from rapidly flowing section about 50 m downstream from Hughes Pd. outlet. Prosimulium mixtum collected from trailing grass. Water temperature 7°C.

H1. Healey's Pond outlet, 78-02-13

Water sample taken ca. 15 m downstream from Healey's Pond (10 m below bridge) in moderately rapid water at 1130 h. Fourth-instar (approximately) C. ornithophilia, P. mixtum, Stegopterna mutata and 4th, 6th instar S. vittatum were taken on trailing vegetation (chiefly mint stems). Weather: strong winds, cloudy; water temperature 0.5°C.

B3,4. Beachy Cove Bk., 78-03-14

Water samples taken from 2 sites: "UP" (at Hughes pd. outlet, in slow water -- B3), and "DN" (ca. 150 m downstream from UP site in rapid water -- B4), 1100-1200 h. Late-instar C. ornithophilia, which normally inhabits lake outlets and is rarely encountered in the downstream stretches of streams, were collected from UP site and late-instar P. mixtum, which is normally found in stretches other than the headwaters, from DN site, all on trailing vegetation. Weather: clear, cold; water temperature 0.5°C.

H2,3. Healey's Pond outlet, 80-03-17

Water sample from ca. 5 m downstream from Healey's Pond. Late-instar larvae of all 4 major "winter species" (ie. P. mixtum, C. ornithophilia, St. mutata and S. vittatum) collected from (H2) trailing stem of aquatic macrophyte (Mentha) and (H3) bottom surfaces of 3 rocks, at 1100-1200 h. Water temperature 1°C. This collection occurred during a peak period of snow melt.

H5. Healey's Pond outlet, 81-02-11

From 5 m downstream from Healey's Pd. in water of moderate flow velocity. Larvae (S. vittatum, P. mixtum, C. ornithophilia) taken from stem of aquatic macrophyte (Mentha) at 1300-1400 h. Water temperature 10°C.

B5. Beachy Cove Bk., 78-07-03

Water sample and larval collection taken ca. 20 m downstream from Hughes Pond outlet at 1500 h. Late-instar S. vittatum and S. venustum of all instars were taken from trailing grass. Water temperature 20°C. Flow volume relatively low at 5-10 l/sec.

G1. Goat Cove Bk., 79-06-16

This brook is fed by a bog and maintains low temperatures year-round relative to other brooks in the area. Water sample and larvae collected ca. 10 m upstream from the culvert for the Tucker's Hill Road, at 1615 h. Late-instar S. venustum were collected from a trailing aquatic macrophyte and late-instar larvae of this species and of Simulium tuberosum were taken from the surface of submerged rock in rapid water. Water temperature 14°C.

B6. Beachy Cove Bk. (site 1), 79-06-16

Water sample and larval collection from same point as for collection B2, at 1700 h. S. venustum/verecundum of all instars were taken from aquatic macrophyte (Carex) and from rock surface. Water temperature 19°C.

B7. Beachy Cove Bk. (site 2), 79-06-16

This collection was made several kilometres downstream from collection B6, at a point several metres upstream from where the brook passes under Tucker's Hill Road, at 1630 h. The two collections were made within 0.5 h of each other, the purpose being to compare the available food spectrum near the headwater of a lake-fed stream with that in the lower reaches of the same stream. Here, S. venustum/ verecundum (final-instar) were taken from trailing vegetation and from a rock surface: S. vittatum (final-instar) were collected from the same rock surface. Water temperature 17°C.

M1. Mt. Scio Bk., 79-05-12

This small brook drains a boggy area atop Mt. Scio. The collection was made in moderately rapid water just downstream from a small pool which was in turn only a few metres below a large boggy area of negligible flow rate. P. mixtum and St. mutata were taken, at 1500-1600 h, from the surfaces of two submerged rocks. The larval collection from the top of the rocks was preserved separate from the collection taken from the bottom surfaces. One of the objects was to compare food spectra available to larvae inhabiting the respective surfaces. Water temperature 7°C.

H4. Healey's Pond outlet, 80-04-30

Water samples and larval collections taken from ca. 4 m downstream from Healey's Pd. in slowly moving water from stems of Mentha or from rock surfaces. There was a very great density of 2nd-instar S. venustum, with some late-instar S. vittatum on the rocks. P. mixtum and St. mutata were collected from the mint stems at the same site. Water temperature 6°C. (1300-1400h).

F1. Flat Rock Bk., 80-05-09

Water samples and larval collections were taken (a) in slow water near the outlet of a small pond which feeds this brook (C. ornithophilia) and (b) ca. 75 m downstream from the headwater, in rapid water just below the culvert for the road to Flat Rock (P. mixtum, St. mutata), at 1330-1400 h. Water temperature 10°C. This is a small brook of flow volume ca. 5 l/sec.

APPENDIX III

Supplementary Observations of Larval Gut Contents (Ch. 2):

To obtain a broader view of the general spectrum of available and ingested simuliid larval food, collections and general observations were made at sites over a wider area than represented in the 14 collections listed in Appendix II.

Late-instar P. mixtum larvae collected 80-04-23 from Island Pond Bk., north of Gander, Newfoundland had very little algal material in the guts, with an estimated 95% of the volume of matter apparently fungal or decomposed vascular plant fragments. Late-instar St. mutata collected 80-04-23 from a small unnamed brook near the Main Point turnoff on the Gander Bay Road consisted of about 80% vascular plant detritus. At Flat Rock (collection F1) the gut contents of late-instar P. mixtum, St. mutata, and C. ornithophilia was estimated to comprise less than 1% algal matter, the remainder being chiefly fungal material (as was the case for the seston).

By contrast, larvae from all collections at Beachy Cove Bk. and Healey's Pd. Bk. contained a very high (more than 90%) relative volume of algae, chiefly small chrysophytes, chlamydomonads and cryptophytes, plus Dinobryon and in one case (#B1,2) Chroococcus. P. mixtum collected 81-05-07 from an unnamed stream draining a bog approximately 100 km west

of St. John's along the Trans Canada Highway contained a very great proportion of diverse diatoms and chlorophyte filaments. And 4th-instar larvae of S. venustum collected 81-05-07 from a pond outlet in the same general vicinity showed gut contents consisting mainly of diatoms (chiefly Tabellaria), small crysophytes etc., Dinobryon and filaments.

At Little Power Pond outlet, more than 80% of both the seston and larval gut contents were composed of algal material, as observed on several dates. At Barking Kettle Pond outlet by contrast, very little algal material was observed in either seston or larval guts (less than 10%), and samples (winter and spring) taken from a point several hundred metres downstream were similar to the outlet sample. The non-algal material appeared to be composed mainly of unidentifiable detritus. At Mt. Scio Farm Bog outlet, proportionately even less algal material (less than 5%) was encountered, in spring and autumn samples.

In each case, the composition of the gut contents, in terms of proportion of algae, detritus, etc., was reflective of that of the associated seston.

APPENDIX IV

Tables A1-A11:

Sample means for gut-content and seston analyses of field-collected larvae, for each collection (Chapter 2): r_i and p_i values for all larval populations and seston'.

'In Tables A1 to A11, values shown are for mean r_i (x100%) or in the case of seston, p_i (x100%). Values corresponding to each enumerated algal taxon are given for each larval population. F probability (%) is given, for each algal type, for 1-way ANOVA comparing population means. Standard errors are not included due to lack of space in tables. However, an asterisk is used to indicate that the seston value (p_i) lies outside the 95% C.L. of estimated mean r_i. Lower-case letters indicate inclusion in Student-Newman-Keuls ranges. Means followed by different letters differ significantly ($P < 0.05$). Numbers of larvae in each collection are given in Table 2. For seston, n=1 for each collection.

Table A1 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collections B1,B2.

	BEACHY CV. UP, 77-10-27		BEACHY CV. DN, 77-10-28					
Algal type	Seston	C. ornith. mid-instar	Seston	P. mixtum 1st-instar	P. mixtum 2nd-instar	P. mixtum mid-instar	St. mutata mid-instar	F prob.(%)
Chroococcus	43.97	20.27* b	29.89	1.56* a	20.13* b	30.98 b	37.22 b	0
Microcystis	0.24	0.05*	0.09	0.00*	0.37	0.25	0.07	43.6
Bluegreen filaments	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
All bluegreen algae	44.21	20.32* b	29.98	1.56* a	20.50* b	31.23 b	37.29 b	0
Ankistrodesmus	4.75	7.57 b	1.19	0.69 a	2.41 a,b	1.60 a,b	1.67 a,b	0
Scenedesmus	0.00	0.23* b	0.00	0.00 a	0.00 a	0.02 a	0.00 a	0
Elakatothrix	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Chlorella	-	-	-	-	-	-	-	-
Cosmarium	0.06	1.10* b	0.00	0.00 a	0.00 a	0.00 a	0.00 a	0
Closterium	0.00	0.00	0.00	0.00	0.00	0.01	0.00	80.9
Staurastrum	0.00	0.06	0.00	0.00	0.00	0.00	0.05	9.7
Arthrodesmus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Euastrum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Tetraedron	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
All desmids	0.06	1.15* b	0.00	0.00 a	0.00 a	0.01 a	0.05 a	0
Chlorophyte filaments	-	-	-	-	-	-	-	-
All green algae	4.81	8.96* b	1.19	0.69* a	2.41 a,b	1.64 a,b	1.72 a,b	0

Table A1 (cont'd)

	BEACHY CV. UP, 77-10-27		BEACHY CV. DN, 77-10-28					
Algal type	Seston	C. ornith. mid-instar	Seston	P. mixtum 1st-instar	P. mixtum 2nd-instar	P. mixtum mid-instar	St. mutata mid-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Dinobryon	42.02	54.63* b	63.45 b	1.00* a	63.15 b	55.79* b	49.21*b	0.0
Chrysosomatidae	0.06	1.07	0.09	8.64	1.06	0.00*	0.23	35.3
Chrysophyte A	-	-	-	-	-	-	-	-
Chrysophyte B	-	-	-	-	-	-	-	-
Chrysophyte C	-	-	-	-	-	-	-	-
Dictyosphaeria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Meridion	0.00	0.00	1.02	0.00*	0.00*	0.15	0.11	
Asterionella	3.65	4.14 c	2.22	0.00* a	0.82* a,b	5.16* b	2.41 abc	0.0
Diatoma	0.00	0.26	0.00	2.08	0.34	0.02	0.28	65.4
Rhizoselenia	2.07	3.27 a,b	0.51	1.56 a	6.47* b	1.36* a,b	4.28* a,b	0.4
Achnanthes	0.30	0.93* a,b	0.34	15.98* b	0.94 a,b	0.27 a	0.51 a	0.1
Tabellaria flocculosa	0.00	0.53	0.43	18.74*	0.89	1.27	0.51	0.3
Tabellaria fenestrata	0.24	0.07*	0.00	1.25	0.00	0.09	0.16	88.9
All Tabellaria	0.24	0.60	0.43	19.99*	0.89	1.36	0.67	0.1
Synedra (<20um)	0.91	0.61 a,b	0.51	18.11* b,	0.36 a	1.00 a	1.50 a,b	0.04
Synedra (>20um)	0.92	2.40* c	0.17	0.00* a	0.43 a,b	1.52* c	1.11* b,c	0
All Synedra	1.83	3.01 a,b	0.68	18.11* b	0.79 a	2.52 a,b	2.61* a,b	0.5

Table A1 (cont'd)

Algal type	BEACHY CV. UP, 77-10-27 Seston	C. ornith. mid-instar	BEACHY CV. DN, 77-10-28 Seston	P. mixtum 1st-instar	P. mixtum 2nd-instar	P. mixtum mid-instar	St. mutata mid-instar	F prob.(%)
Cymbella	0.00	0.03	0.00	0.58	0.00	0.05	0.11	62.3
Gomphonema	0.06	0.23	0.00	19.82	0.09	0.23*	0.51	11.3
Eunotia (<30um)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Eunotia (>30um)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Fragilaria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Navicula (~8um)	-	-	-	-	-	-	-	-
Nitzschia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Centric diatoms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	-	-	-	-	-	-	-	-
Misc. pennate diatoms (>35um)	0.42	0.64	0	0	0.02	0	0.01	0
All diatoms[m]	6.94	10.60 a,b	4.70 a,b	76.56* b	4.95 a	9.76* a,b	7.27 a,b	6.3
Gleno-/Peridinium	0.00	0.07	0.09	0.00*	0.14	0.00*	0.00*	66.9
Gymnodinium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
All filaments	-	-	-	-	-	-	-	-
Total	100.11	99.42	100.91	99.91	97.78	99.79	100.00	

[m] except Rhizoselenia

Table A: Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collections B3,B4.

Algal types	BEACHY CV. UP, 78-03-14 Seston	C. ornith. late-instar	BEACHY CV. DN, 78-03-14 Seston	P. mixtum late-instar	F prob.(%)
Chroococcus	0.00	0.00	0.00	0.00	-
Microcystis	0.56	0.09*	0.00	0.17	29.3
Bluegreen filaments	0.00	0.13	0.12	0.05	57.0
All bluegreen algae	0.56	0.21*	0.12	0.22	71.3
Ankistrodesmus	16.25	14.15	8.12	6.28	7.4
Scenedesmus	0.00	0.00	0.00	0.00	-
Elakatothrix	0.00	0.00	0.00	0.00	-
Chlorella	0.42	1.18	0.71	0.27	40.2
Cosmarium	0.00	0.00	0.00	0.00	-
Closterium	0.00	0.00	0.00	0.00	-
Staurastrum	0.00	0.03	0.00	0.00	76.4
Arthrodesmus	0.00	0.05	0.00	0.00	76.4
Euastrum	0.00	0.00	0.00	0.00	-
Tetraedron	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	-
All desmids	0.00	0.08	0.00	0.00	44.1
Chlorophyte filaments	0.00	0.03	0.12	0.14	82.0
All green algae	16.67	15.52	8.95	6.69	4.4

Table A2 (cont'd)

Algal types	BEACHY CV. UP, 78-03-14 Seston	BEACHY CV. UP, 78-03-14 C. ornith. late-instar	BEACHY CV. DN, 78-03-14 Seston	BEACHY CV. DN, 78-03-14 P. mixtum late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	-
Keratella	0.28	0.00*	0.00	0.08	11.8
Dinobryon	1.81	3.16	0.71	0.78	1.9
Chrysosomatidae	0.56	0.56	0.24	0.04*	1.9
Chrysophyte A	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.69	2.02	0.71	0.62	6.1
Chrysophyte C	0.00	0.00	0.00	0.00	-
Dictyosphaeria	0.00	0.00	0.00	0.00	-
Meridion	3.75	5.29	4.24	10.75*	1.9
Asterionella	2.50	2.33	0.47	0.81	16.9
Diatoma	63.61	63.89	74.47	72.83	12.0
Rhizoselenia	0.00	0.00	0.00	0.00	-
Achnanthes	0.69	0.54	2.00	0.21*	
Tabellaria flocculosa	1.67	1.93	0.59	1.11*	40.9
Tabellaria fenestrata	1.81	0.66	0.71	0.28	45.3
All Tabellaria	3.48	2.59	1.30	1.38	25.8
Synedra (<20um)	0.83	0.36*	1.18	1.13	2.8
Synedra (>20um)	3.33	2.71	3.41	3.57	84.9
All Synedra	4.17	3.07	4.59	4.70	53.3

Table A2 (cont'd)

Algal types	BEACHY CV. UP, 78-03-14 Seston	BEACHY CV. UP, 78-03-14 C. ornith. late-instar	BEACHY CV. DN, 78-03-14 Seston	BEACHY CV. DN, 78-03-14 P. mixtum late-instar	F prob.(%)
Cymbella	0.00	0.00	0.00	0.00	-
Gomphonema	0.14	0.25	1.29	0.46*	40.9
Eunotia (<20um)	0.00	0.00	0.24	0.08*	12.0
Eunotia (>20um)	0.00	0.08	0.00	0.00	76.4
Fragilaria	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.00	-
Navicula (~8um)	-	-	-	-	-
Nitzchia	0.00	0.00	0.00	0.00	-
Centric diatoms	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	0.00	0.04	0.00	0.03	95.0
Misc. pennate diatoms (>35um)	0.14	0.00*	0.00	0.10	10.3
All diatoms	78.47	78.08 a	88.59	91.36 b	1.1
Gleno-/Peridinium	0.83	0.32*	0.59	0.06*	10.2
Cymnodinium	0.14	0.23	0.12	0.15	99.0
All filaments	0.00	0.16	0.24	0.19	79.9
Total	100.01	100.01	100.03	100.00	

Table A3 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collection B5.

BEACHY CV., 78-07-03

Algal types	Seston	S. vittatum	S. venustum/verecundum			F prob.(%)
		late-instar	2nd-instar	4th-instar	6th-instar	
Chroococcus	3.03	0.83*	1.89*	0.79*	0.86*	65.0
Microcystis	1.93	1.73	0.64*	0.38*	0.93*	3.5
Bluegreen filaments	1.93	3.57 b	0.21* a	3.16 b	3.34* b	0.01
All bluegreen algae	6.89	6.13	2.74*	4.33*	5.13*	13.6
Ankistrodesmus	11.84	6.13* a	56.15* c	17.34* b	6.56* a	0.01
Scenedesmus	0.28	0.10*	0.00*	0.06*	0.16*	1.2
Elakatothrix	0.00	0.00	0.00	0.00	0.00	-
Chlorella	4.41	3.43 a	18.70* b	4.15 a	2.05* a	0.0
Cosmarium	0.00	0.27*	0.00	0.21*	0.05	5.8
Closterium	0.00	0.00	0.00	0.09	0.01	56.0
Staurastrum	0.09	0.04*	0.00*	0.00*	0.09	2.3
Arthrodesmus	0.00	0.02	0.00	0.04	0.00	71.2
Euastrum	0.18	0.07*	0.00*	0.07*	0.04*	17.6
Tetraedron	0.00	0.03	0.00	0.05	0.00	36.9
Netrium	0.00	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	0.00	-
All desmids	0.27	0.43 b	0.00*a	0.37 a,b	0.19 a,b	0.4
Chlorophyte filaments	0.55	2.02*	2.56	2.77*	1.86*	70.3
All green algae	17.35	12.11*a	77.41*c	24.69*b	10.82*a	0.0

Table A3 (cont'd)

BEACHY CV., 78-07-03

Algal types	Seston	S. vittatum	S. venustum/verecundum			F prob.(%)
		1 te-instar	2nd-instar	4th-instar	6th-instar	
Zooplankton	0.00	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	0.00	0.02	56.1
Dinobryon	59.50	69.27* b	10.62* a	57.90 b	79.50* b	0.0
Chrysosomatidae	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte A	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte C	0.00	0.00	0.00	0.00	0.00	-
Dictyosphaeria	0.00	0.07	0.00	0.24	0.05	29.6
Meridion	0.28	0.27	0.00*	0.13	0.13	0.9
Asterionella	2.57	2.29 a,b	1.38* a	2.33 a,b	3.41 b	0.6
Diatoma	3.21	1.58*	1.32*	1.91*	2.25	15.8
Rhizoselenia	0.00	0.00	0.00	0.00	0.00	-
Achnanthes	0.73	0.36*	1.87	1.35	0.55	72.6
Tabellaria flocculosa	1.01	0.92	1.06	0.42*	0.53*	84.2
Tabellaria fenestrata	0.00	0.92*	0.00	0.10	0.39*	0.02
All Tabellaria	1.01	1.84	1.06	0.52*	0.92	18.1
Synedra (<20um)	-	-	-	-	-	-
Synedra (>20um)	-	-	-	-	-	-
All Synedra	2.94	2.54 a,b	0.99* a	3.18 b	2.22 a,b	0.3

Table A3 (cont'd)

BEACHY CV., 78-07-03

Algal types	Seston	S. vittatum late-instar	S. venustum/verecundum 2nd-instar	4th-instar	6th-instar	F prob.(%)
Cymbella	0.00	0.06*	0.15*	0.05*	0.14*	72.4
Gomphonema	0.09	0.30	0.72	0.21	0.44	98.5
Eunotia (<20um)	0.00	0.00	0.00	0.19*	0.03	0.7
Eunotia (>20um)	0.09	0.06*	0.00*	0.00*	0.13	3.7
Fragilaria	0.00	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.09*	0.00	0.13*	0.13*	5.6
Diatom B1	0.00	0.00	0.00	0.00	0.00	-
Navicula (~8um)	0.00	0.23*	0.00	0.52*	0.13	5.6
Nitzchia	0.00	0.00	0.00	0.00	0.00	-
Centric diatoms	0.00	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	0.28	0.29	0.15*	0.22	0.23	24.5
Misc. pennate diatoms (>35um)	0.00	0.20*	0.34	0.39*	0.31	83.9
All diatoms	11.20	9.87	7.99	10.50	10.82	59.4
Gleno-/Peridinium	5.05	2.28*	1.23*	1.78*	2.39*	1.9
Gymnodinium	0.00	0.00	0.00	0.00	0.00	-
All filaments	2.48	5.59*	2.77	5.94	5.20*	5.8
Total	99.99	99.73	99.99	99.44	99.73	

Table A4 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collections Bo,B7.

	BEACHY CV. SITE I, 79-06-16					BEACHY CV. SITE II, 79-06-16				
		S. venustum/verecundum					S. vittat.	S.venust./verec.		
Algal taxa	Seston	2nd-inst. veg'n	4th-inst. veg'n	6th-inst. veg'n	6th-inst. rock	Seston	late-inst rock	6th-inst. veg'n	6th-inst. rock	F prob.
Carococcus	0.41 [m.]	5.01*a	11.96*b	29.55*c	13.96*b	0.00	0.00 a	0.00 a	0.04 a	0.0
Microcystis	0.20	0.07*	0.14	0.15	0.00*	0.00	0.00	0.00	0.00	3.7
Bluegreen filaments	0.20	0.80	1.22	1.17	0.52	0.70	1.87	1.36	1.11	88.0
All bluegreen algae	0.82	5.88* b	13.32* b	30.87* a	14.48* b	0.70	1.87 b	1.36 b	1.16 b	0.0
Ankistrodesmus	5.12	6.18 b	4.95 ab	4.36 ab	5.35 ab	1.58	1.66 a	1.32 a	0.51*a	0.02
Scenedesmus	0.92	0.00*	0.44	0.51	0.09*	0.00	0.24*	0.11	0.35	39.8
Elakatothrix	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Chlorella	6.76	8.65	3.81	2.34*	4.20	0.00	0.00	0.07	0.04	0.0
Cosmarium	0.61	0.49	0.89	0.26	0.17*	0.00	0.04	0.00	0.07	1.0
Closterium	0.31	0.27 ab	0.00*a	0.05*a	0.18 ab	1.23	2.17 c	0.93 abc	1.27 bc	0.04
Staurastrum	0.21	0.07	0.05*	0.05*	0.00*	0.00	0.00	0.00	0.00	23.0
Arthrodesmus	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	59.3
Euastrum	0.00	0.00	0.22	0.17	0.00	0.13	0.04*	0.00*	0.00*	0.9
Tetraedron	0.31	0.07*	0.05*	0.05*	0.13	0.00	0.07	0.08	0.00	63.0
Netrium	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	59.3
Micrasterias	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00	5.9
All desmids	1.43	0.91	1.28	0.59	0.60*	1.41	2.31	1.01	1.34	42.1
Chlorophyte filaments	15.66	10.36 ab	11.83 ab	13.97 ab	16.82 b	1.94	6.60 ab	2.61 a	2.29 ab	0.01
All green algae	29.89	26.06	22.41*	21.85*	27.05	4.93	10.84	4.57	4.55	0.01

[m.] These were difficult to see in seston sample -- very likely an under-estimate

Table A4 (cont'd)

Algal taxa	BEACHY CV. SITE I, 79-06-16 S. venustum/verecundum Seston	2nd-inst. veg'n	4th-inst. veg'n	6th-inst. veg'n	6th-inst. rock	BEACHY CV. SITE II, 79-06-16 S. vittat. S.venust./verec. Seston	late-inst rock	6th-inst. veg'n	6th-inst. rock	F prob.
Zooplankton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	59.3
Keratella	0.41	0.00*a	0.00*a	0.60 c	0.38 b	0.00 a	0.00 a	0.00 a	0.00 a	0.0
Dinobryon	21.49	24.59 b	32.40*a	21.62 b	19.41 b	0.00 c	0.00 c	0.09 c	0.00 c	0.0
Chrysosomatidae	4.81	0.15*	0.15*	0.05*	0.34*	0.35	0.22	0.08*	0.00*	
Chrysophyte A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Dictyosphaeria	0.00	1.61*	0.54	0.31	0.34*	0.00	0.00	0.00	0.00	1.9
Meridion	0.00	0.00	0.00	0.00	0.00	0.00	0.32*	0.39	0.11	1.7
Asterionella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Diatoma	4.81	8.49 ab	2.90 a	2.55*a	6.75 ab	38.38	45.61 c	59.17 c	63.24*c	0.0
Rhizosolenia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Achnanthes	2.86	1.72	0.81*	0.89*	0.51*	7.39	5.08	2.67*	2.29*	0.1
Tabellaria flocculosa	2.15	1.38	2.98	1.57	1.73	1.76	0.88*	1.99	0.98	27.2
Tabellaria fenestrata	0.00	0.07	0.11	0.10	0.18	0.00	0.35	0.12	0.24	90.1
All Tabellaria	2.15	1.45	3.09	1.67	1.90	1.76	1.23	2.11	1.22	46.6
Synedra (<20um)	2.70	1.04	1.14	0.97	1.11	3.34	0.90	1.62	1.33	-
Synedra (>20um)	13.00	25.73*a	19.54 a	15.38 a	24.04*a	1.06	0.52 b	1.15 b	0.35*b	0.0
All Synedra	15.70	26.77 a	20.68 a	16.35 a	25.15*a	4.40	1.42*b	2.77 b	1.68*b	0.0

Table A4 (cont'd)

Algal taxa	BEACHY CV. SITE I, 79-06-16 S. venustum/verecundum Seston	2nd-inst. veg'n	4th-inst. veg'n	6th-inst. veg'n	6th-inst. rock	BEACHY CV. SITE II, 79-06-16 S. vittat. S.venust./verec. Sesto	late-inst rock	6th-inst. veg'n	6th-inst. rock	F prob.
Cymbella	0.10	0.12 ab	.07 ab	0.19 ab	0.13 a	0.18	0.05*b	0.30 ab	0.55 ab	6.4
Gomphonema	0.41	1.18 b	1.01 b	0.84*b	1.05 b	13.03	18.10 a	9.92*b	9.80 b	0.0
Eunotia (<20um)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Eunotia (>20um)	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.39	0.20	29.2
Fragilaria	0.82	0.00*b	0.00*b	0.00*b	0.29 b	8.27	6.12 a	6.19 a	6.81 a	0.0
Pinnularia	0.00	0.00	0.00	0.09	0.08	0.00	0.00	0.00	0.04	50.4
Diatom B1	0.00	0.00	0.00	0.00	0.05	0.35	0.14*	0.16	0.07*	7.6
Navicula (~8um)	0.00	0.00 b	0.10 b	0.24 b	0.04 b	0.00	1.50*a	1.00*ab	0.80*ab	0.0
Nitzchia	2.25	0.87*c	1.14*c	0.56*c	1.09*c	19.01*	4.90*b	7.24*b	5.94*b	0.0
Centric diatoms	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.19	0.08	57.9
Misc. pennate diatoms (<35um)	7.16	0.19*	0.41*	0.21*	0.09*	0.18	0.07	0.52	0.23	-
Misc. pennate diatoms (>35um)	0.20	0.00*	0.00*	0.04*	0.00*	0.70	1.78	1.06	1.23	-
All diatoms	36.64	41.27 b	30.21 bc	23.68*c	37.23 bc	93.84	87.04 a	93.90 a	94.29 a	0.0
Gleno-/Peridinium	3.38	0.34*b	0.85*b	0.65*b	0.12*b	0.00	0.00 b	0.00 b	0.00	0.0
Gymnodinium	0.51	0.19	0.05*	0.19	0.00*	0.00	0.00	0.00	0.00	4.0
All filaments	15.86	11.16	13.05	15.14	17.34	2.64	8.47	3.37	3.40	0.03
Total	97.95	100.00	99.93	99.82	99.44	99.82	99.97	100.00	100.00	

Table A5 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collection HI.

HEALEY'S PD., 78-02-13

Algal taxa	Seston	P. mixtum mid-instar	C. ornith. mid-instar	St.mutata mid-instar	S. vittat. mid-instar	S. vittat. late-instar	F prob.(%)
Chroococcus	0.00	0.02	0.00	0.00	0.00	0.12	16.4
Microcystis	0.00	0.00	0.00	0.00	0.00	0.00	-
Bluegreen filaments	0.47	0.72 a	0.56 a	4.48*b	1.49 a,b	0.66 a,b	2.4
All bluegreen algae	0.47	0.74 a	0.56 a	4.48*b	1.49 a,b	0.78 a,b	2.8
Ankistrodesmus	0.00	0.77*	0.27*	0.88	0.09	0.04	17.2
Scenedesmus	0.00	0.00	0.00	0.00	0.00	0.00	-
Elakatothrix	0.16	1.04*	1.09*	2.88	0.71	1.58*	4.0
Chlorella	-	-	-	-	-	-	-
Cosmarium	0.16	0.00*	0.04*	0.00*	0.00*	0.00*	
Closterium	0.00	0.00	0.02	0.00	0.00	0.03	65.8
Staurastrum	0.00	0.00	0.02	0.29	0.00	0.01	4.0
Arthrodesmus	0.31	0.00*	0.15*	0.00*	0.00*	0.08*	0.8
Euastrum	0.00	0.00	0.04	0.00	0.00	0.00	34.5
Tetraedron	0.00	0.00	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	0.00	0.00	-
All desmids	0.47	0.00*	0.27*	0.29	0.00*	0.12*	0.06
Chlorophyte filaments	0.47	1.34*	0.99*	2.05	1.74	1.68*	68.7
All green algae	1.10	3.65*	2.62*	6.10	2.54	3.42*	5.2

Table A5 (cont'd)

HEALEY'S PD., 78-02-13

Algal taxa	Seston	P. mixtum mid-instar	C. ornith. mid-instar	St.mutata mid-instar	S. vittat. mid-instar	S. vittat. late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.05	0.00	0.00	0.04	72.0
Keratella	0.00	0.08	0.00	0.00	0.00	0.10	28.2
Dinobryon	34.22	17.16*	24.03*	4.45	17.42*	27.48*	1.1
Chrysosomatidae	0.00	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte A	0.00	0.00	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.47	0.22*	0.04*	0.43	0.15	0.00*	5.1
Chrysophyte C	0.00	0.00	0.00	0.00	0.00	0.00	-
Dictyosphaeria	0.00	0.00	0.00	0.00	0.00	0.00	-
Meridion	0.63	0.52 a	1.06 a,b	4.21 b	1.24 a,b	0.65 a	0.2
Asterionella	0.16	0.00	0.00	0.00	0.00	0.00	-
Diatoma	0.00	0.03 a	0.57*a	1.73*b	0.15 a	0.27*a	0.0
Rhizoselenia	0.00	0.00	0.00	0.00	0.00	0.00	-
Achnanthes	0.47	3.11*	5.03*	3.06	2.97	1.77	42.3
Tabellaria flocculosa	38.28	49.73*	37.74	32.88	46.17	46.59*	22.6
Tabellaria fenestrata	3.28	2.87	6.37*	2.32	4.01	4.84*	4.4
All Tabellaria	41.56	52.60*	44.11	35.20	50.18	51.43*	37.9
Synedra (<20um)	2.34	3.76 b	1.27*a	2.74 a,b	0.48*a	0.50*a	0.01
Synedra (>20um)	12.34	7.79*	9.84*	11.99	13.75	7.46*	38.6
All Synedra	14.69	11.55	11.11*	14.73	14.23	7.95*	40.2

Table A5 (cont'd)

HEALEY'S PD., 78-02-13

Algal taxa	Seston	P. mixtum mid-instar	C. ornith. mid-instar	St.mutata mid-instar	S. vittat. mid-instar	S. vittat. late-instar	F prob.(%)
Cymbella	0.00	0.00	0.07	0.00	0.00	0.04	28.6
Gomphonema	1.25	7.25*a	5.27*a	20.29 b	6.00*a	3.84 a	0.7
Eunotia (< 20um)	0.00	0.00	0.00	0.00	0.00	0.00	-
Eunotia (> 20um)	0.63	0.12*a	0.21*b	0.88*b	0.00 a,b	0.12*a	0.0
Fragilaria	0.16	0.00*a	0.02*a,b	0.00*a,b	0.00*a,b	0.03*a,b	6.2
Pinnularia	0.00	0.00	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.00	0.00	0.00	-
Navicula (~8um)	-	-	-	-	-	-	-
Nitzchia	0.00	0.00	0.00	0.00	0.00	0.00	-
Centric diatoms	0.00	0.00	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	1.25	1.13	1.73*	0.43	0.30*	0.16*	1.8
Misc. pennate diatoms (>35um)	0.15	0.10	0.28	0.72	0.36	0.06*	16.9
All diatoms	61.09	76.80*	70.90*	84.12*	76.57*	66.61	7.6
Gleno-/Peridinium	0.16	0.00*	0.09*	0.00*	0.00*	0.02*	2.0
Gymnodinium	2.50	1.17*	1.72*	0.43	1.84	1.56*	48.2
All filaments	0.94	2.56*	1.54*	6.52	3.23	2.34*	2.3
Total	100.01	99.80	100.01	100.01	100.01	99.62	

Table 6. Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collections H?,H3.

HEALEY'S PD., 80-03-17:

Algal taxa	Seston	MACROPHYTE SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	ROCK SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	F prob.
Chroococcus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Microcystis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Bluegreen filaments	0.00	0.74*ab	2.21*b	0.79*ab	1.04*ab	7.19 b	0.76*ab	0.63*a	1.90*b	0.98*ab	0.00 c	0.0
All bluegreen algae	0.00	0.74*ab	2.21 b	0.79*ab	1.04*ab	7.19 b	0.76*ab	0.63*a	1.90*b	0.98*ab	0.00 c	0.0
Ankistrodesmus	0.60	4.76	8.12	1.97*	5.18	1.56	4.45*	6.61	2.91*	4.48*	0.00	13.1
Scenedesmus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.03	0.02	0.00	90.3
Elakatothrix	0.00	0.02	0.00	0.20*	0.04	0.00	0.09	0.21	0.00	0.01	0.00	4.2
Chlorella	6.40	0.49*a	2.45*a	1.45*a	0.79*a	0.94 a	0.75*a	15.76*b	2.45*a	1.91*a	0.00 a	0.0
Cosmarium	0.00	0.00	0.08	0.00	0.13	0.00	0.00	0.15	0.00	0.00	0.00	52.3
Closterium	0.00	0.00 a	0.00 a	0.00 a	0.00 a	0.00 a	0.00 a	0.00 a	0.00 a	0.03 a	0.39 b	0.0
Staurastrum	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Arthrodesmus	0.00	0.10	0.38	0.13	0.20	0.00	0.04	0.17	0.10	0.18*	0.00	90.8
Euastrum	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	85.5
Tetraedron	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.92	-
Micrasterias	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
All desmids	0.40	0.09*a	0.46 a	0.13*a	0.33 a	0.00 a	0.04*a	0.32 a	0.10*a	0.24 a	4.31 b	0.5
Chlorophyte filaments	0.40	0.52 a	0.00*a	0.33 a	0.20 a	3.75 b	0.33 a	0.40 a	0.16*a	0.20*a	0.00 a	0.3
All green algae	16.80	5.88 *a	11.03 a	4.08*a	6.54*a	6.25 a	5.66*a	23.34 b	5.65*a	6.86*a	4.31 a	

Table A6 (cont'd)

HEALEY'S PD., 80-03-17:

Algal taxa	Seston	MACROPHYTE SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	ROCK SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	F prob.
Zooplankton	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.02	0.00	0.00	0.00	0.00	0.06	0.13	0.00	0.06	0.00	86.5
Dinobryon	44.40	85.47*b	69.37 b	88.32*b	87.35*b	5.00 a	72.23 b	58.97*b	73.35*b	81.05*b	5.10a	0.0
Chrysosomatidae	0.40	0.00*	0.35	0.00*	0.03*	0.00	0.06*	0.53	0.03*	0.14*	0.00	9.2
Chrysophyte A	0.80	0.10*a	11.89*c	0.00*a	0.08*a	0.63 a	0.07*a	5.30*b	0.21*a	0.14*a	0.00a	0.0
Chrysophyte B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.09	0.00	87.9
Chrysophyte C	0.40	0.10*	0.12	0.10*	0.25	0.31	0.07*	0.21	0.07*	0.29	0.00	69.3
Dictyosphaeria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Meridion	1.60	0.17*	0.00*	0.08*	0.10*	0.00	0.10*	0.39*	0.05*	0.09*	0.00	
Asterionella	0.00	0.13	0.00	0.40	0.32*	0.00	0.38	0.58*	0.26	0.36	0.00	63.2
Diatoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Rhizoselenia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Achnanthes	1.20	0.99*a	0.00*a	0.30*a	0.04*a	5.00 b	0.21*a	0.71*ab	0.28*a	1.63ab	1.19ab	6.8
Tabellaria flocculosa	9.60	5.68ab	3.28 a	3.40*a	2.50*a	48.75 b	13.91ab	3.63*a	13.75ab	3.48*a	4.31ab	1.8
Tabellaria fenestrata	0.00	0.13 a	0.00 a	0.13 a	0.30*a	3.75 b	0.06 a	0.65 a	0.25 a	0.26*a	0.00a	1.1
All Tabellaria	9.60	5.81 a	3.28 a	3.40*a	2.81*a	52.50 b	13.97ab	4.28*a	13.00ab	3.74*a	4.31a	1.2
Synedra (<20um)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Synedra (>20um)	8.00	0.99*	1.40*	1.57*	0.59*	14.38	5.49	2.52*	3.64	2.37*	1.18	4.7
All Synedra	8.00	0.99*	1.40*	1.57*	0.59*	14.38	5.49	2.52*	3.64	2.37*	1.18	4.7

Table A6 (cont'd)

HEALEY'S PD., 90-03-17:

Algal taxa	Seston	MACROPHYTE SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	ROCK SUBSTRATE: P. mixtum late-instar	C. ornith late-instar	St. mutata late-instar	S. vittat late-instar	Peri-phyton	F prob.
Cymbella	0.40	0.00*a	0.00*a	0.00*a	0.00*a	0.00 a	0.00*a	0.08*a	0.00*a	0.04*a	0.00 a	0.6
Gomphonema	1.20	0.13*a	0.27 a	0.05*a	0.12*a	6.56 b	0.03*a	0.37*a	0.68 a	1.25 a	1.57ab	0.2
Eunotia (<20um)	10.00	0.05*a	0.12*a	0.05*a	0.08*a	2.19 c	0.23*a	0.68*bc	0.29*ab	0.35*ab	1.57bc	0.0
Eunotia (>20um)	0.00	0.05	0.00	0.00	0.03	0.00	0.32	0.05	0.08	0.01	1.18	4.7
Fragilaria	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	79.60	-
Navicula (~8um)	0.40	0.00	0.00	0.03	0.00	0.00	0.00	0.19	0.09	0.03	0.00	73.2
Nitzchia	0.40	0.00*	0.00*	0.05*	0.02*	0.00	0.06*	0.12*	0.00*	0.06*	0.00	25.8
Centric diatoms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	-	-	-	-	-	-	-	-	-	-	-	-
Misc. pennate diatoms (>35um)	0.40	0.07*	0.00*	0.05*	0.00*	0.00	0.00*	0.35	0.09*	0.04*	0.00	-
All diatoms	37.20	7.39*a	5.06*a	5.97*a	4.10*a	80.63cb	20.80 a	10.30*a	18.47 a	9.97*a	90.59 c	0.0
Gleno-/Peridinium	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.05	0.00	0.00	0.00	80.4
Gymnodinium	0.00	0.29	0.00*	0.70	0.63*	0.00	0.29	0.46*	0.34	0.42*	0.00	8.5
All filaments	0.40	1.26 b	2.21 b	1.12*b	1.24*b	10.94 c	1.10*b	1.03*b	2.06*b	1.18*b	0.00 a	0.0
Total	100.00	99.99	100.03	99.99	100.02	100.01	100.00	100.00	100.02	100.00	100.00	

Table A7 Relative proportionate abundances of algal taxa in simuliid gut-c[illegible]tent samples and in seston: collection H4.

HEALEY'S PD., 80-04-30

Algal taxa	Seston	S. vittatum late-instar	S.venust./ver. 2nd-instar	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Chroococcus	0.00	0.00	0.00	0.00	0.00	-
Microcystis	0.00	0.00	0.00	0.00	0.00	-
Bluegreen filaments	0.00	0.71*	0.48	0.35*	0.59*	37.5
All bluegreen algae	0.00	0.71	0.48	0.35	0.59*	37.5
Ankistrodesmus	14.71	2.48*a	12.86 b	0.60*a	3.11*a	0.01
Scenedesmus	0.00	0.00	0.17	0.00	0.00	56.5
Elakatothrix	0.00	0.00	0.00	0.00	0.00	-
Chlorella	0.00	0.00	0.00	0.00	0.00	-
Cosmarium	0.00	0.00	0.00	0.00	0.03	56.5
Closterium	0.00	0.00	0.00	0.00	0.00	-
Staurastrum	0.00	0.00	0.00	0.00	0.00	-
Arthrodesmus	0.00	0.08	0.16	0.05	0.05	96.2
Euastrum	0.00	0.00	0.00	0.00	0.00	-
Tetraedron	0.00	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	0.00	-
All desmids	0.00	0.08	0.16	0.05	0.08	92.5
Chlorophyte filaments	0.00	0.47	0.37	0.36*	0.19	70.9
All green algae	14.71	3.03*ab	13.57 b	1.00*a	3.39*ab	0.02

Table A7 (cont'd)

HEALEY'S PD., 80-04-30

Algal taxa	Seston	S. vittatum late-instar	S.venust./ver. 2nd-instar	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	0.00	0.00	-
Dinobryon	61.76	89.19* b	74.42* a	95.10* c	87.60* b	0.01
Chrysosomatidae	0.98	0.00* a	0.86 b	0.00* a	0.07* a	0.0
Chrysophyte A	0.49	0.68 ab	1.23* b	0.10* a	0.82 ab	2.6
Chrysophyte B	0.00	0.09	0.00	0.00	0.16	11.7
Chrysophyte C	0.00	0.77*	0.98	0.42*	0.85*	53.3
Dictyosphaerla	0.00	0.00	0.00	0.00	0.00	-
Meridion	0.00	0.04	0.38	0.09	0.09	71.8
Asterionella	0.00	0.21*	0.00	0.02	0.13	7.6
Diatoma	0.00	0.00	0.00	0.00	0.00	-
Rhizoselenia	0.00	0.00	0.00	0.00	0.00	-
Achnanthes	0.00	0.34	0.34	0.00	0.06	64.6
Tabellaria flocculosa	15.69	1.68*	1.82*	1.60*	2.93*	
Tabellaria fenestrata	0.49	0.03*	0.00*	0.02*	0.00*	
All Tabellaria	16.18	1.71*	1.82*	1.62*	2.93*	
Synedra (<20um)	-	-	-	-	-	-
Synedra (>20um)	0.98	2.41	3.68*	0.92	2.97*	4.2
All Synedra	0.93	2.41 ab	3.68* b	0.92 a	2.97* ab	4.2

j. A single chain biased this count upward.

Table V (cont'd)

HEALEY'S PD., 30-04-30

Algal taxa	Seston	S. vittatum late-instar	S.venust./ver. 2nd-instar	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Cymbella	0.00	0.00	0.00	0.05	0.00	56.5
Gomphonema	0.49	0.15*	0.37	0.00*	0.08*	28.7
Eunotia (<20um)	1.47	0.15*	0.85	0.00*	0.00*	6.3
Eunotia (>20um)	0.00	0.03	0.00	0.00	0.00	56.5
Fragilaria	0.00	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.00	0.00	-
Navicula (~8um)	0.00	0.02	0.17	0.02	0.03	66.7
Nitzchia	0.00	0.14	0.54	0.00	0.03	6.8
Centric diatoms	0.00	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	-	-	-	-	-	-
Misc. pennate diatoms (>35um)	0.49	0.08*	0.00*	0.04*	0.10*	-
All diatoms	19.61	5.28* a,b	8.30* b	2.75* a	6.32* a,b	0.2
Gleno-/Peridinium	0.98	0.17*	0.16*	0.00*	0.03*	
Gymnodinium	1.47	0.09* b	0.00* a	0.27* b	0.17* a,b	0.01
All filaments	0.00	1.18*	0.85	0.71*	0.79*	47.8
Total	100.00	100.01	100.00	99.99	100.00	

j. A single very long chain of T. flocculosa biased this count upward.

Table A6 Relative proportionate abundances of algal taxa in simulild gut-content samples and in seston: collection B5.

HEALEY'S PD., 81-02-11

Algal taxa	Seston	C. ornith. late-instar c.	S. vittatum late-instar c.	Periphyton	F prob.(%)
Chroococcus	0.00	0.00	0.00	0.00	-
Microcystis	0.00	0.00	0.02	0.00	76.4
Bluegreen filaments	0.11	0.05 a	0.08 a	0.77 b	5.0
All bluegreen algae	0.11	0.05 a	0.10 a,b	0.77 b	6.5
Ankistrodesmus	1.82	1.45	0.58*	0.38	36.2
Scenedesmus	0.00	0.00	0.00	0.00	-
Elakatothrix	0.11	0.47	0.83*	0.00	20.1
Chlorella	0.34	0.13*	0.21	0.00	35.9
Cosmarium	0.00	0.02	0.00	0.00	76.4
Closterium	0.00	0.00	0.00	0.00	-
Staurastrum	0.00	0.02	0.02	0.00	94.5
Arthrodesmus	0.00	0.00	0.13	0.00	19.3
Euastrum	0.00	0.00	0.00	0.00	-
Tetraedron	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	-
All desmids	0.00	0.05	0.15	0.00	50.8
Chlorophyte filaments	0.00	0.43*	0.46*	1.15	
All green algae	2.28	2.53	2.24	1.53	95.8

c. from macrophyte stem.

Table A8 (cont'd)

HEALEY'S PD., 81-02-11

Algal taxa	Seston	C. ornith. late-instar c.	S. vittatum late-instar c.	Periphyton	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.02	0.00	76.4
Dinobryon	91.91	91.15 b	91.14 b	2.30 a	0.0
Chrysosomatidae	0.57	0.88	0.04*	0.00	29.3
Chrysophyte A	0.00	0.05	0.00	0.00	76.4
Chrysophyte B	8.83	19.84 b	0.52*a	0.76 a	0.1
Chrysophyte C	0.80	0.06*	0.27*	0.00	7.7
Dictyosphaeria	0.00	0.00	0.00	0.00	-
Meridion	0.00	0.00	0.00	0.00	-
Asterionella	0.00	0.84*	0.77*	0.00	32.2
Diatoma	0.00	0.00	0.00	0.00	-
Rhizoselenia	0.00	0.00	0.00	0.00	-
Achnanthes	0.00	0.30*a	0.02 a	8.81 b	0.0
Tabellaria flocculose	2.73	1.82*a	3.95 b	69.73 c	0.0
Tabellaria fenestrata	0.00	0.35 a	0.31*a	4.98 b	0.6
All Tabellaria	2.73	2.16*a	4.25 b	74.71 c	0.0
Synedra (<20um)	0.11	0.13 a	0.06 a	1.15 b	3.7
Synedra (>20um)	0.23	0.69*a	0.40*a	7.66 b	0.0
All Synedra	0.34	0.82*a	0.46 a	8.81 b	0.0

c. from macrophyte stem.

Table A8 (cont'd)

HEALEY'S PD., 81-07-11

Algal taxa	Seston	C. ornith. late-instar c.	S. vittatum late-instar c.	Periphyton	F prob.(%)
Cymbella	0.00	0.00	0.00	0.00	-
Gomphonema	0.11	0.13 a	0.05 a	1.15 b	4.1
Eunotia (<20um)	0.46	0.13* a	0.03* a	1.15 b	2.0
Eunotia (>20um)	0.00	0.00	0.00	0.00	-
Fragilaria	0.00	0.00	0.00	0.00	-
Pinnularia	0.00	0.00	0.00	0.00	-
Diatom B1	0.00	0.00	0.00	0.38	-
Navicula (~8um)	0.23	0.21	0.00*	0.00	43.6
Nitzchia	0.00	0.13	0.11	0.38	47.6
Centric diatoms	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	0.00	0.03	0.07	0.00	76.8
Misc. pennate diatoms (>35um)	0.00	0.00	0.00	0.00	-
All diatoms	3.87	4.85 a	5.91* a	95.40 b	0.0
Gleno-/Peridinium	0.46	0.22	0.04*	0.00	23.7
Gymnodinium	0.00	0.21	0.14	0.00	69.2
All filaments	0.11	0.53* a	0.66* a	1.92 b	1.6

c. from macrophyte stem.

Table A9 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collection G1.

GOAT CV., 79-06-16

Algal taxa	Seston	S.venustum/verecundum,6th-instar from leaf	S.venustum/verecundum,6th-instar from rock	S.tuberosum late-instar	F prob.(%)
Chroococcus	0.00	0.53	0.22	0.39	67.4
Microcystis	0.00	0.00	0.00	0.00	-
Bluegreen filaments	0.23	0.13	0.39	0.43	60.1
All bluegreen algae	0.23	0.66	0.51*	0.82	94.6
Ankistrodesmus	0.11	0.05	0.06	0.17	88.0
Scenedesmus	0.00	0.00	0.00	0.00	-
Elakatothrix	0.00	0.00	0.00	0.00	-
Chlorella	-	-	-	-	-
Cosmarium	1.12	1.30	1.85	1.48	78.7
Closterium	0.45	0.40	0.56	0.70	63.4
Staurastrum	0.11	0.31	0.40	0.15	72.8
Arthrodesmus	0.00	0.00	0.00	0.00	-
Euastrum	0.00	0.00	0.00	0.00	-
Tetraedron	0.00	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	-
All desmids	1.69	2.01	2.80	2.32	70.0
Chlorophyte filaments	0.00	0.37*	0.23	0.99*	3.5
All green algae	1.80	2.43	3.09	3.48	57.3

Table A9 (cont'd)

GOAT CV., 79-06-16

Algal taxa	Seston	S.venustum/verecundum,6th-instar from leaf	S.venustum/verecundum,6th-instar from rock	S.tuberosum late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	0.00	-
Dinobryon	0.00	0.00	0.00	0.00	-
Chrysosomatidae	0.00	0.00	0.00	0.00	-
Chrysophyte A	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.00	0.00	0.00	0.00	-
Chrysophyte C	0.00	0.00	0.00	0.00	-
Dictyosphaeria	0.00	0.00	0.00	0.00	-
Meridion	1.69	1.73	1.59	1.28	61.9
Asterionella	0.00	0.00	0.00	0.00	-
Diatoma	0.00	0.00	0.06	0.04	76.7
Rhizoselenia	0.00	0.00	0.00	0.00	-
Achnanthes	0.00	0.43*	1.05*	0.40	17.5
Tabellaria flocculosa	1.80	2.06	4.01*	2.85	11.7
Tabellaria fenestrata	0.00	0.00	0.00	0.00	-
All Tabellaria	1.80	2.06	4.01*	2.85	11.7
Synedra (<20um)	-	-	-	-	-
Synedra (>20um)	0.45	0.04*	0.16	0.00*	8.6
All Synedra	0.45	0.04*	0.16	0.00*	8.6

Table A9 (cont'd)

GOAT CV., 79-06-16

Algal taxa	Seston	S.venustum/verecundum,6th-instar from leaf	S.venustum/verecundum,6th-instar from rock	S.tuberosum late-instar	F prob.(%)
Cymbella	0.23	0.05*	0.00*	0.05*	17.6
Gomphonema	3.37	3.08	3.44	3.18	87.1
Eunotia (<20um)	0.90	0.28*	0.27*	0.60	38.0
Eunotia (>20um)	0.00	2.32*	1.69*	1.30	44.7
Fragilaria	12.26	23.49*	19.58	20.58	49.1
Pinnularia	0.00	0.00	0.00	0.00	-
Diatom Bl	56.69	49.39	43.49*	39.49	51.7
Navicula (~8um)	14.06	8.33*	13.09	16.65	22.9
Nitzchia	3.71	4.33	4.94	6.24	51.9
Centric diatoms	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	2.23	0.92*	1.72	2.41	8.0
Misc. pennate diatoms (>35um)	0.45	0.40 a	1.00 b	0.53 a,b	5.7
All diatoms	95.39	95.08	95.60	92.61	21.9
Gleno-/Peridinium	0.00	0.00	0.00	0.00	-
Gymnodinium	0.00	0.00	0.00	0.00	-
All filaments	0.23	0.50	0.62	1.43*	9.7
Total	97.42	98.17	99.20	96.91	

Table A10 Relative proportionate abundances of algal taxa in simulid gut-content samples and in seston: collection MI.

MT. SCIO, 79-05-12

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Chroococcus	0.00	0.00	0.00	-
Microcystis	0.00	0.21	0.00	60.0
Bluegreen filaments	2.05	0.36* a	0.95* b	2.3
All bluegreen algae	2.05	0.57*	0.95*	13.2
Ankistrodesmus	0.00	0.00	0.06	60.0
Scenedesmus	0.00	0.07	0.00	60.0
Elakatothrix	0.00	0.00	0.00	-
Chlorella	1.02	1.65	0.97	63.3
Cosmarium	2.81	1.29*	2.07	3.9
Closterium	1.02	0.29*	0.76	41.2
Staurastrum	0.51	0.08*	0.13*	24.6
Arthrodesmus	0.00	0.00	0.00	-
Euastrum	0.26	0.14	0.07*	48.6
Tetraedron	0.00	0.00	0.00	-
Netrium	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	-
All desmids	4.60	1.80* a	3.02* b	2.7
Chlorophyte filaments	19.18	21.22	16.38	41.9
All green algae	24.81	24.74	20.43	50.9

Table A10 (cont'd)

MT. SCIO, 79-05-12

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	-
Dinobryon	2.81	1.28*	3.94	7.2
Chrysosomatidae	0.00	0.00	0.00	-
Chrysophyte A	0.00	0.00	0.00	-
Chrysophyte B	0.00	0.00	0.00	-
Chrysophyte C	0.00	0.00	0.00	-
Dictyosphaeria	0.00	0.00	0.00	-
Meridion	0.00	0.00	0.00	-
Asterionella	0.00	0.07	0.06	91.2
Diatoma	0.00	0.00	0.00	-
Rhizoselenia	0.00	0.00	0.00	-
Achnanthes	0.00	0.14	0.00	29.0
Tabellaria flocculosa	26.09	34.07*	32.04*	37.7
Tabellaria fenestrata	3.32	5.97*	4.75	25.4
All Tabellaria	29.41	39.94*	36.79*	18.3
Synedra (<20um)	-	-	-	-
Synedra (>20um)	0.51	0.00* a	0.69 b	0.0
All Synedra	0.51	0.00* a	0.69 b	0.0

Table A10 (cont'd)

MT. SCIO, 79-05-12

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	F prob.(%)
Cymbella	0.09	0.00	0.00	-
Gomphonema	0.00	0.08	0.06	90.1
Eunotia (<20um)	30.69	22.93	24.11	50.0
Eunotia (>20um)	2.82	5.49	5.80*	68.9
Fragilaria	0.00	0.00	0.00	-
Pinnularia	0.51	0.00*	0.26	13.9
Diatom B1	0.09	0.00	0.00	-
Navicula (~8um)	0.51	0.00*	0.20	9.1
Nitzchia	0.26	0.14	0.33	69.0
Centric diatoms	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	-	-	-	-
Misc. pennate diatoms (>35um)	1.53	1.22	1.61	61.5
All diatoms	66.50	70.14	69.91	79.5
Gleno-/Peridinium	0.00	0.00	0.00	-
Gymnodinium	0.00	0.00	0.00	-
All filaments	21.23	21.59	17.33	43.6
Total	96.17 (100.01)[m]	96.73 (98.93)[m]	95.23 (99.40)[m]	

[m]Counts of certain fungal filaments, significant interms of volume, were taken but it was decided in retrospect that the counts were not really representative of abundance. The total therefore is exclusive of the representation of these counts. Total in parentheses includes fungal counts.

Table A11 Relative proportionate abundances of algal taxa in simuliid gut-content samples and in seston: collection F1.

FLAT ROCK, 80-05-09

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	C. ornith. late-instar	F prob.(%)
Chroococcus	0.00	0.00	0.00	0.00	-
Microcystis	0.54	4.39	0.76	0.13*	5.7
Bluegreen filaments	0.54	4.42*	2.92*	0.86	2.4
All bluegreen algae	1.08	8.72* b	3.68 a	0.99 a	0.1
Ankistrodesmus	0.54	4.45	1.80	1.12*	29.2
Scenedesmus	0.00	0.00	0.00	0.00	-
Elakatothrix	0.00	0.00	0.00	0.00	-
Chlorella	0.00	0.00	0.00	0.00	-
Cosmarium	2.17	1.17	1.18	1.92	54.6
Closterium	1.09	2.38 b	0.54 a	0.42 a	3.4
Staurastrum	0.54	1.88	3.00*	0.64	18.2
Arthrodesmus	0.00	0.71	1.13	1.83	50.2
Euastrum	0.54	1.33	1.66	1.05*	71.3
Tetraedron	0.00	0.53	0.48	0.09	67.4
Netrium	0.00	0.00	0.00	0.00	-
Micrasterias	0.00	0.00	0.00	0.00	-
All desmids	4.35	8.00*	8.23*	6.06	41.3
Chlorophyte filaments	3.80	10.49* b	4.05 a	0.55* a	0.01
All green algae	8.70	22.95* c	14.13* b	7.74 a	0.01

Table A11 (cont'd)

FLAT ROCK, 80-05-09

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	C. ornith. late-instar	F prob.(%)
Zooplankton	0.00	0.00	0.00	0.00	-
Keratella	0.00	0.00	0.00	0.00	-
Dinobryon	55.43	32.88* a	44.06* b	62.17 c	0.07
Chrysosomatidae	0.54	0.00* a	3.94 b	13.32* c	0.0
Chrysophyte A	0.00	0.00	0.00	0.00	-
Chrysophyte B	0.00	0.00	0.00	0.89	6.6
Chrysophyte C	0.00	0.63	1.39	0.79*	69.0
Dictyosphaeria	0.00	0.00	0.00	0.00	-
Meridion	0.00	0.00	0.00	0.00	-
Asterionella	0.00	0.00	0.00	0.00	-
Diatoma	0.00	0.00	0.00	0.00	-
Rhizoselenia	0.00	0.00	0.00	0.00	-
Achnanthes	0.54	0.00*	0.19*	0.00*	7.7
Tabellaria flocculosa	10.87	15.40 b	9.30 a,b	3.32* a	2.2
Tabellaria fenestrata	0.54	3.36	2.28	0.25	4.6
All Tabellaria	11.41	18.76 b	11.58 a,b	3.57* a	1.3
Synedra (<20um)	-	-	-	-	-
Synedra (>20um)	1.09	1.39	1.03	0.91	80.6
All Synedra	1.09	1.39	1.03	0.91	80.6

Table A11 (cont'd)

FLAT ROCK, 80-05-09

Algal taxa	Seston	P. mixtum late-instar	St. mutata late-instar	C. ornith. late-instar	F prob.(%)
Cymbella	1.63	0.24*	0.76	0.44*	49.1
Gomphonema	0.54	0.00*	0.14*	0.52	12.2
Eunotia (<20um)	6.52	9.75	10.44	3.83*	3.0
Eunotia (>20um)	2.17	0.44*	0.58*	0.09*	6.1
Fragilaria	0.00	0.00	0.00	0.00	-
Pinnularia	1.63	0.00* a	0.76 b	0.31* a,b	4.6
Diatom B1	0.00	0.00	0.00	0.00	-
Navicula (~8um)	0.00	0.00	0.29	0.00	57.7
Nitzchia	1.09	0.49	0.57	0.44	80.8
Centric diatoms	0.00	0.00	0.00	0.00	-
Misc. pennate diatoms (<35um)	1.09	1.12	1.44	0.51	55.3
Misc. pennate diatoms (>35um)	1.63	1.31	3.71	1.15	16.3
All diatoms	32.07	33.49 b	31.86 b	11.96* a	0.3
Gleno-/Peridinium	2.17	0.19*	0.66*	1.83	2.7
Gymnodinium	0.00	0.00	0.00	0.00	-
All filaments	4.35	14.91* c	6.98* b	1.42* a	0.01
Total	99.99	98.86	99.72	99.69	

APPENDIX V

Tables B1-B9:

Larval Growth Data (Chapter 3)

Table 61 Growth parameters of larvae of S. verecundum reared simultaneously on various diets, Trial 1 .

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Pre-treatment	(29)	480.14 ± 112.19	-
Chlamydomonas	23	1306.13 ± 344.73	1
Navicula	20	1212.30 ± 248.13	2
Bacillus subtilis	19	806.58 ± 263.18	3
Chlorella	11	689.82 ± 157.96	4
Leaves	7	611.76 ± 151.18	5
Escherischia coli	1	570.64 ± 0	6
Scenedesmus	1	490.80 ± 0	7
No food	3	195.91 ± 1.64	8

a of [illegible]
b in arbitrary areal size units (see text for explanation)
c based on size data

Table 62 Growth parameters of larvae of S. verecundum reared simultaneously on various diets, Trial 2.

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Pre-treatment	(33)	364.67 ± 94.62	-
Navicula	13	1982.69 ± 906.72	1
Chlamydomonas	9	1660.67 ± 722.21	2
Tetra	8	1261.88 ± 656.25	3
Scenedesmus	15	1194.60 ± 461.00	4
Chlorella	13	1189.15 ± 618.13	5
B. subtilis	14	1087.43 ± 516.71	6
E. coli	9	852.77 ± 346.06	7
Leaves	11	501.25 ± 101.58	8
no food	9	425.93 ± 149.38	9

a of 25
b in arbitrary areal size units (see text for explanation)
c based on Size data

Table B3 Growth parameters of larvae of S. verecundum reared simultaneously on various diets, Trial 3 .

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Pre-treatment	(22)	105.84 ± 31.84	-
Navicula	24	1959.13 ± 279.85	1
Chlorella	31	1400.00 ± 412.32	2
B. subtilis	17	1371.59 ± 450.58	3
Pseudomonas aeruginosa	25	1045.64 ± 247.15	4
Scenedesmus	25	910.44 ± 262.53	5
Leaves	22	610.99 ± 233.41	6
No food	25	534.88 ± 152.68	7
Chlamydomonas	0	- ± -	8

a of 30-35
b in arbitrary areal size units (see text for explanation)
c based on Size data

Table 8. Growth parameters of larvae of *C. ornithopaillia* reared simultaneously on various diets, Trial 4.

Food	Number of Survivors[a]	Size ($\bar{X}$ ± s.d.)[b]	Rank[c]
Pre-treatment	(13)	239.58 ± 90.74	-
Saviculia	12	3419.67 ± 919.48	1
B. subtilis	12	2513.08 ± 794.12	2
P. aeruginosa	14	2480.21 ± 790.24	3
Chlorella	10	2163.10 ± 647.44	4
Leaves	12	1832.08 ± 736.36	5
Scenedesmus	12	1113.58 ± 323.52	6
no food	12	1020.75 ± 529.49	7
Chlamydomonas	0	- ± -	8

a of 20
b in arbitrary areal size units (see text for explanation)
c based on Size data

Table B5 Growth parameters of larvae of P. mixtum reared simultaneously on various diets, Trial 5 .

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Pre-treatment	20	489.25 ± 102.28	-
Navicula	15	1203.27 ± 262.71	1
Chlorella	9	850.56 ± 186.65	2
P. aeruginosa	11	725.64 ± 196.96	3
Leaves	14	664.79 ± 104.42	4
Scenedesmus	15	647.85 ± 236.86	5
B. subtilis	6	632.67 ± 103.43 [d.]	6
No food	7	553.14 ± 123.92	7
Chlamydomonas	0	- ± -	8

a of 20
b in arbitrary areal size units (see text for explanation)
c Based on Size data

Table 6. Growth parameters of larvae of S. vittatum reared simultaneously on various diets, Trial 6.

Food	Number of Survivors[a]	Size ($\bar{X}$ ± s.d.)[b]	Rank[c]
Pre-treatment	(27)	521.30 ± 149.45	-
Nitzschia	20	1242.60 ± 423.36	1
Chlamydomonas palmella	14	1180.57 ± 279.22	2
Tetra	21	952.29 ± 330.79	3
Ankistrodesmus	14	775.93 ± 223.40	4
Chlamydomonas	17	699.47 ± 166.23	5
B. subtilis	13	604.31 ± 194.29	6
P. aeruginosa	18	602.78 ± 192.72	7
Scenedesmus	4	446.50 ± 188.24	8
Chlorella	0	- ± -	9
Leaves	0	- ± -	9

a of 25
b in arbitrary areal size units (see text for explanation)
c based on Size data

Table 67 Growth parameters of larvae of S. verecundum reared simultaneously on various diets, Trial 7 .

Food	Number of Survivors[a]	Size ($\bar{X}$ ± s.d.)[b]	Rank[c]
Pre-treatment	(21)	64.80 ± 9.32	-
Sitrachia	11	441.91 ± 237.44	1
Tetra	3	290.48 ± 74.03	2
Ankistrodesmus	12	212.08 ± 57.24	3
P. acetabulosa	2	97.07 ± 30.62	4
Chlamydomonas	0	- ± -	5
Chlamydomonas (palmella)	0	- ± -	5
Scenedesmus	0	- ± -	5
Chlorella	0	- ± -	5
S. subtilis	0	- ± -	5
Leaves	0	- ± -	5

a of 28
b in arbitrary areal size units (see text for explanation)
c based on Size data

Table 55 Growth parameters of larvae of S. vittatum reared simultaneously on various diets, Trial 8 .

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Pre-treatment	(30)	107.75 ± 25.20	-
Nitzschia	20	1190.40 ± 486.70	1
Chlamydomonas	18	813.22 ± 212.29	2
Oscillatoria	15	749.93 ± 341.96	3
Ankistrodesmus	9	386.44 ± 144.91	4
Tetra	11	363.18 ± 133.26	5
B. subtilis	10	296.10 ± 121.86	6
Chlorella	4	292.50 ± 69.84	7
Scenedesmus	3	233.67 ± 76.74	8
P. aeruginosa	3	231.33 ± 41.77	9
no food	8	173.50 ± 44.24	10
Leaves	0	- ± -	11
Chlamydo. palmella	0	- ± -	11

a of 30 b in arbitrary areal size units (see text for explanation)
c based on Size data

Table 19 Growth parameters of larvae of C. ornithophilia reared simultaneously on various diets, Trial 9 .

Food	Number of Survivors[a]	Size ($\bar{X} \pm$ s.d.)[b]	Rank[c]
Tetra	14	1476.00 ± 394.50	1
Chlamydomonas flagellates	11	1374.82 ± 363.09	2
B. subtilis	17	1258.71 ± 360.01	3
Chlorella	13	1217.69 ± 356.27	4
Oscillatoria	14	1109.07 ± 432.02	5
Nitzchia	15	1079.80 ± 221.46	6
Ankistrodesmus	9	945.78 ± 287.37	7
no food	13	872.69 ± 267.65	8
Leaves	19	831.95 ± 192.07	9
P. aeruginosa	5	736.00 ± 184.20	10
Scenedesmus	14	722.07 ± 231.15	11
Chlamydomonas palmellae	13	666.62 ± 279.59	12

a of 20

b in arbitrary areal size units (see text for explanation)

c Based on Size data

APPENDIX VI

Tables C1 - C7:

Supplementary tables on Larval Feeding Rates, Efficiency and Digestion Rates (Chapter 4)

Table C1 Percentage of time (mean ± s.d.) larvae of S. verecundum spent in filter-feeding mode during laboratory observations under different conditions of temperature and PM concentration.

Concentration: (cells/ul)	Temperature 17.5°C	19.0°C	21.0-23.5°C
3.0 - 5.1	99.74 ± 0.78 n=19	95.68 ± 5.08 n=8	98.60 ± 4.43 n=10
22 - 25	77.15 ± 25.20 n=12	94.34 ± 4.80 n=5	-
100 - 113	24.76 ± 27.24 n=8	56.30 ± 24.57 n=5	86.02 ± 30.97 n=16
189 - 201	12.18 ± 13.98 n=3	19.82 ± 15.75 n=6	78.58 ± 24.81 n=12

Table C2 Percentage of time (mean ± s.d.) larvae of S. verecundum spent in filter-feeding mode during laboratory observations under different conditions of water current velocity and PM concentration at 21-23.5°

	Stirring speed			
	7 cm/s	9 cm/s	15 cm/s	28.5 cm/s
Concentration: (cells/ul)				
3.0 - 5.1	99.15 ± 1.92 n=9	97.00 ± 8.61 n=11	98.60 ± 4.43 n=10	99.78 ± 0.31 n=10
100 - 113	96.76 ± 10.37 n=14	99.90 ± 0.35 n=15	86.02 ± 30.97 n=16	98.53 ± 5.68 n=15

Table C3 Degrees of digestion (D)[1] of Navicula diatoms in guts of late-instar S. verecundum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature	
	19.5° C	11.5° C
50 mg/l	0.343 (35.9 ± 11.0)	0.199 (26.5 ± 3.2)
10 mg/l	0.944 (76.3 ± 3.8)	0.237 (29.1 ± 20.0)
2 mg/l	0.980 (81.9 ± 0.9)	0.520 (46.1 ± 17.1)
0.4 mg/l	0.999 (88.7 ± 2.5)	0.894 (71.0 ± 9.4)

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	11564	4	26.86	0.000
Temperature	5672	1	52.70	0.000
Conc. x Temp.	.2301	4	5.34	0.002
Explained	19538	9	20.17	0.000
Residual	3229	30		
Total	22767	39		

[1]D = proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

Table C4 Degrees of digestion D[1] of Navicula diatoms in guts of early-instar S. verecundum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature	
	19.5° C	11.5° C
50 mg/l	0.317 (34.2 ± 13.4)	0.191 (25.9 ± 8.2)
10 mg/l	0.739 (59.3 ± 6.9)	0.294 (32.8 ± 10.3)
2 mg/l	0.963 (78.9 ± 2.8)	0.532 (46.9 ± 8.9)
0.4 mg/l	0.976 (81.0 ± 2.7)	-

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	5960	3	28.04	0.000
Temperature	2982	1	42.09	0.000
Conc. x Temp.	618	2	4.36	0.026
Explained	12018	6	28.28	0.000
Residual	1488	21		
Total	13506	27		

[1]D - proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

Table C5 Relative feeding efficiencies[1] (mean ± s.d.) for larvae of 3 species in laboratory trials at different temperatures and concentrations, at 9 cm/s current velocity.

Concentration	Temperature 22°C	11-12°C	0.5-1°C	P (Temp Effect)[2]
A. S. vittatum				
50 mg/l	0.37 ± 0.14	0.14 ± 0.05	0.06 ± 0.03	< 0.01
10 mg/l	1.26 ± 0.65	0.86 ± 0.18	0.27 ± 0.06	< 0.05
2 mg/l	7.12 ± 3.48	3.94 ± 2.87	1.17 ± 0.28	< 0.05
0.4 mg/l	11.67 ± 4.19	5.35 ± 2.13	-	< 0.05
P (Conc. Effect)[2]	< 0.005	< 0.005	< 0.01	
B. C. ornithophilia				
50 mg/l	didn't feed	0.13 ± 0.08	0.09 ± 0.04	N.S.
10 mg/l	didn't feed	0.83 ± 0.56	0.60 ± 0.32	N.S.
2 mg/l	didn't feed	3.00 ± 1.35	0.81 ± 0.20	N.S.
0.4 mg/l	didn't feed	7.40 ± 2.16	-	
P (Conc. Effect)		P < 0.05	P < 0.05	
C. P. mixtum				
10 mg/l	no test	0.83 ± 0.48	0.62 ± 0.13	N.S.
2 mg/l	no test	3.61 ± 1.41	2.19 ± 0.96	N.S.
P (Conc. Effect)		P < 0.05	P < 0.05	

[1]Efficiency is equal to passage rate/(concentration x velocity); figures represent relative values only, since units have no absolute significance.

[2]Kruskal-Wallis one-way ANOVA

Table C6 Degrees of digestion (D)[1] of Nitzchia diatoms in guts of late instar S. vittatum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature[2] 22° C	11-12° C	0.5-1° C	P (Temp Effect)
10 mg/l	0.764 b (60.9 ± 15.3)	0.306 a (33.6 ± 9.1)	0.263 a (30.8 ± 1.5)	< 0.001
2 mg/l	0.969 b (79.8 ± 8.2)	0.354 a (36.5 ± 6.2)	0.484 a (44.1 ± 10.3	< 0.001
0.4 mg/l	0.923 b (73.9 ± 13.1)	0.380 a (38.0 ± 6.8)	0.381 a (38.1 ± 5.8)	< 0.001
P (Conc. Effect)	N.S.	N.S.	N.S.	

Ranges: 22° treatments > 11-12° treatments (P < 0.01)
0.5-1° treatments not significantly different from 11-12°

[1] D = proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).
Supplementary data from a separate run using 50 mg/l PM concentration was also used to develop the variable U (means were 0.720, 0.630 and 0.757).

Table C7 Degrees of digestion (D)[1] of Nitzchia diatoms in guts of late-instar P. mixtum under different conditions of temperature and PM concentration, at 9 cm/s current velocity.

Concentration	Temperature[2] 11° C	1° C
10 mg/l	0.431 (41.0 ± 8.6)	0.985 (83.0 ± 9.4)
2 mg/l	0.741 (59.4 ± 21.2)	0.991 (84.5 ± 4.5)

Results of two-way ANOVA testing concentration and temperature effects:

Source of variance	Sum of squares	df	F	F prob.
Concentration	396	1	2.50	0.140
Temperature	4501	1	28.46	0.000
Conc. x Temp.	284	1	1.80	0.205
Explained	5182	3	10.92	0.001
Residual	1898	12		
Total	7080	15		

[1]D - proportion of diatom frustules with < 40% of contents remaining. Raw data was transformed to its arcsine-square-root. In each cell above, the detransformed mean of D is followed by transformed mean (± s.d.) (in degrees).

[2]Means for the two temperature treatments at 10 mg/l PM concentration were significantly different from each other ($P < 0.001$; 1-way ANOVA).

APPENDIX VII

Definition of Electivity and Related Indices (Chapter 2):

Selectivity:

$$E_i = (r_i - p_i)/(r_i + p_i)$$

Ivlev 1961

$$D_i = (r_i - p_i)/(r_i + p_i - 2r_ip_i)$$

Jacobs 1974

$$W_i = (r_i/p_i)/\Sigma_i^j(r/p)$$

for 'j' food items

Vanderploeg and Scavia 1979a

$$E^*_i = (W_i + 1/j)/(W_i - 1/j)$$

Vanderploeg and Scavia 1979b

Dietary overlap:

$$C = \frac{2\sum_i^j (r_{ia} \times r_{ib})}{\sum_i^j (r_{ia})^2 + \sum_i^j (r_{ib})^2}$$

Horn 1967

for 'j' algal taxa; a and b are the species being compared.

$$B_f = 1 - 0.5 \sum_i^j |r_{ia} - r_{ib}|$$

Feinsinger et al. 1981

Schroeder 1987a (after Schoener 1968).

Niche breadth:

$$B_h = 1/\sum_i^j (r_i^2/p_i)$$

Hurlbert 1978

$$B_s = 1/\sum_i^j (r_i/p_i)^2$$

Schoener 1974

$$R = B_r / B_p$$

where $$B_p = 1 / \sum_i^j p_i^2$$

and $$B_r = 1 / \sum_i^j r_i^2$$

Schroeder (1987a) after Levitten (1978)

Table D1 Comparative analysis, using three niche-breadth indices, of simulated data for environment and diet samples for two foraging species (A and B).

Counts for 11 "food" classes:

Environment	Species "A"	Species "B"
32	36	36
21	23	23
18	15	15
15	16	16
11	13	13
10	8	8
8	10	10
4	4	4
2	2	10
2	2	12
1	1	5
B_h (Hurlbert 1978)	0.9837	0.6641
B_s (Schoener 1974)[1]	1.016	0.174
R (Schroeder 1987a)	0.958	1.193

[1]multiplied by n for comparative purposes

Table D2 Mean values of D_i (Jacobs 1974) for six algal taxa or groups, all collections (compare values with E_i values of Table 9).

	Dinobryon	Asterionella	Achnanthes	Gomphonema	all small algae	all large algae
P. mixtum						
1st-instar	-.99	-1.00	+.98	0.99	+.99	-.99
2nd-instar	+.08	-.70	+.65	-	+.46	-.04
mid-instar	-.09	+.25	+.71	+.64	+.01	-.03
late-instar	+.12	+.74	-.88	-.89	-.19	+.18
	**	**	**	**	**	**
St. mutata						
mid-instar	-.44	-.01	+.62	+.96	+.48	-.53
late-instar	+.30	1.00	-.60	-.73	-.27	+.34
	**		**	**	**	**
C. ornithophilia						
mid-instar	0.00	+.01	+.68	+.48	+.08	-.23
late-instar	+.06	+.10	-.40	-.39	-.21	+.02
			**	**	**	**
S. vittatum						
mid-instar	-.04	-	+.74	+.79	-.27	-.04
late-instar	+.30	+.05	-.10	-.01	-.18	+.12
	**		**	**		
S. verecundum						
2nd-instar	-.22	-.57	0.00	+.61	+.12	-.18
mid-instar	+.01	-.04	-.04	+.36	0.00	0.00
late-instar	+.02	+.03	-.18	+.03	-.11	+.02
		*		**	**	*
Mean, all groups[1]					-0.044	0.011
X^2 prob. among age groups[2]					<0.0001	<0.0001
X^2 prob. among species[3]					0.2972	0.0064

[1] 1st-instar P. mixtum omitted
[2] comparing 2nd/mid/late-instar groups (all species combined); Kruskal-Wallis 1-way ANOVA.
[3] comparing late-instar samples among the different species (Kruskal-Wallis 1-way ANOVA).
* above (i.e., within cell) means differ significantly (* $P < 0.05$; ** $P < 0.01$).

GLOSSARY OF TERMS

A. Variables and Indices:

r_i: the relative abundance of individuals of any algal taxon ("i") in larval gut contents. Equal to the ratio of the number of cells of taxon "i" to the total number of algal cells in the sample.

p_i: relative abundance of taxon "i" in seston.

E_i: Ivlev's (1961) index of selectivity.

D_i: Jacobs' (1974) index of selectivity.

V: an index expressing the relative abundance of certain large particles (30-μm diatoms) versus that of very small (less than 1 μm) particles (bacteria). Equal to the number of diatom frustules per unit volume of gut contents (which contained only diatoms and bacteria).

V_e: the value of V that would be expected if larvae showed no selectivity based on particle size.

V_o: the observed value of V.

Passage rate: the rate of passage of gut-contents, expressed relative to the total mid-gut length, per hour.

D: an index of degree of digestion. Equal to the proportion of ingested diatoms retaining less than 40% of the cytoplasm, and corrected for the proportion of such in the stock sample.

U: index of relative utilization of food, taking into account both ingestion and digestion. U = Feeding efficiency x Degree of digestion.

B. Physical terms:

PM: suspended particulate matter.

PM Concentration: concentration of suspended particulate matter, expressed in mg/l dry weight.

FPOM: Fine particulate organic matter (< 1 mm).

UTOM: ultra-fine particulate organic matter (0.5 - 50 μm).

C. Ecological Terms:

Allochthonous: originating from source other than the compartment under consideration.

Autochthonous: originating from the compartment under consideration.

lentic: pertaining to still waters.

lotic: pertaining to running water.

periphyton: algal (or other) material attached to surface of a submerged object (rock, plant, etc.).

seston: algal (or other) matter existing as suspended particulate matter in lake or stream water.

tychoplanktonic: planktonic organisms occurring largely near the shores of the lakes.

D. Methodological terms:

Vortexed: A laboratory procedure, using a machine designed specifically for the purpose, to suspend particulate matter in a fluid, by means of rapidly revolving the vessel containing the fluid.

Sonication: Exposure of a fluid to ultra-sonic sound in

order to disperse clumped particulate matter.