Dietary Change during Development in the Freshwater Calanoid Copepod *Epischura lacustris* Forbes

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The diet of the freshwater calanoid copepod *Epischura lacustris* from C2 to adult stage was examined with predation experiments, grazing experiments, and stomach content analyses. There was a transition from an exclusively herbivorous diet in early copepodid stages to an omnivorous diet in adults. Laboratory predation experiments revealed that C2 and C3 were incapable of ingesting *Bosmina* (0.25–0.35 mm), but from C4 to C6, ingestion rate of *Bosmina* increased with developmental stage. The order or prey selection for adult *Epischura* was *Bosmina* over *Diaptomus* and *Cyclops*. Grazing rate on small algae (<10 μm) increased with developmental stage. Zooplankton remains were only found in the guts of stages older than C2; cladocerans and crustacean eggs were the most common zooplankton food. Algae with longest linear dimensions greater than 10 μm (e.g. *Sphaerocystis, Dinobryon,* and diatoms) were common in the guts of all developmental stages of *Epischura*. The occurrence of small unicells (<10 μm) in the guts decreased with developmental stage.

On a étudié le régime alimentaire du copépode d'eau douce *Epischura lacustris* du groupe des calanoïdes du stade C2 au stade adulte en faisant des expériences sur la prédation et sur le broutage et en faisant l'analyse des contenus stomacaux. On a noté le passage d'un régime exclusivement herbivore dans les premiers stades de copépodides à un régime omnivore chez les adultes. Des expériences sur la prédation en laboratoire ont révélé que les individus des stades C2 et C3 étaient incapables d'ingérer *Bosmina* (0,25 à 0,35 mm), mais que, en passant du stade de développement C4 à C6, le taux d'ingestion de *Bosmina* augmentait. Chez les adultes, les proies étaient par ordre d'importance *Bosmina*, puis *Diaptomus* et *Cyclops*. Le taux de broutage sur les petites algues (<10 μm) augmentait en passant d'un stade de développement à un autre. On n'a trouvé des restes de zooplancton que dans le tube digestif d'individus appartenant à des stades plus avancés que C2; les oeufs de cladocères et de crustacés constituaient les éléments du zooplancton le plus souvent ingérés. On retrouvait couramment dans le tube digestif des *Epischura* à tous les stades de développement des algues qui, dans leur plus grande longueur, mesuraient plus de 10 μm (p. ex. *Sphaerocystis, Dinobryon* et diatomées). Il y avait diminution du nombre de petits organismes unicellulaires (<10 μm) présents dans le tube digestif en passant d'un stade de développement à un autre.

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Epischura lacustris is one of the most common zooplankters in lakes of glaciated North America (Carter et al. 1980). The adult predatory feeding behavior of this calanoid copepod has been studied by many authors (Main 1961; Confer and Blades 1975; Strickler and Twombly 1975; Kerfoot 1977, 1978; Wong 1981a), especially with reference to its impact on the life history and morphology of the small cladoceran, *Bosmina* (Kerfoot 1975; Black 1980; Wong 1981b; Byron et al. 1984; Wong and Sprules 1985). Because of the emphasis on its predaceous feeding in these studies, investigators have tended to consider it only a carnivore in aquatic food webs (Sprules 1980; Sprules and Knoechel 1984), despite there being strong evidence that *Epischura* adults feed omnivorously on both algae and zooplankton prey (Main 1961; Chow-Fraser and Wong 1985; Wong and Chow-Fraser 1985). This biased view of its functional role is even more objectionable when we consider that the biomass of immature stages often surpasses that of adults throughout the year (Main 1961), and as yet, the predaceous feeding habit of immature instars has not been clearly demonstrated.

This tendency to consider only a portion of an animal's feeding habit is also evidenced in studies on other omnivorous calanoid copepods. For example, Folt and Goldman (1981) studied only the herbivorous feeding of *E. nevadensis* while Kerfoot (1978) concentrated only on its predaceous feeding. Kibby and Rigler (1973) reported only the grazing rates of *Limnocalanus macrurus* even though this calanoid copepod is an omnivore (Wong and Chow-Fraser 1985; Chow-Fraser and Wong 1985).

In comparison with studies on marine species (Allan et al. 1977; Fernandez 1979; Marshall and Orr 1956; Mullin and Brooks 1967; Paffenhöfer 1971, 1984), relatively little is known about diet changes that accompany the development of *E. lacustris*, or any other freshwater calanoid copepod. In this paper, we examine the dietary changes of *E. lacustris* from early copepodid to adult stages. We concentrate on both the

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TABLE 1. Description of study lakes. pH values are volume-weighted measurements from 1979 samples, except for Gull L. Data for Gull L. are taken from Ontario Ministry of Natural Resources, Minden, Ont. (unpubl. data).

Lake	Maximum depth (m)	Mean depth (m)	Volume (Mm^3)	pH
Gull	49.10	16.50	164.34	7.5
Mountain	31.39	13.43	44.12	6.5
Blue Chalk	21.95	9.37	4.70	6.0

predatory and herbivorous components of their feeding habit throughout their development from C2 to adult. We hope that such information will enable more accurate representation of all developmental stages of this calanoid copepod in future food web studies, so that studies of the energy budgets of plankton in lakes can be more realistic.

Methods and Materials

Three lakes were included in this study, Mountain, Blue Chalk, and Gull lakes, located in south-central Ontario. These lakes vary with respect to their basin morphology and water chemistry (Table 1) and were sampled at various times during 1981–84.

Predation Experiments

Epischura for predation experiments were collected from the epilimnion of Blue Chalk L. (May and June 1984) and Gull L. (August 1983). These samples included all developmental stages from C2 to adults. Prey for these experiments included *Bosmina longirostris* (0.25–0.35 mm, from the rostrum to base of the mucro) from laboratory cultures and adult stages of *Cyclops* spp. (0.8 mm, body length) and *Diaptomus minutus* (0.7 to 1.0 mm, body length) collected from Gull L.

For experiments with *Bosmina*, one predator was introduced into 200 mL of 64-μm-filtered lake water containing five prey individuals. We conducted 2, 4, 20, 12, and 12 experiments for each of the instars of *Epischura* ranging from C2 to C6, respectively. We also conducted 4, 3, and 2 experiments with adult *Epischura* using *Cyclops* as prey, at densities of 5, 10, and 15 prey$\cdot L^{-1}$, respectively; we similarly conducted 5, 3, and 4 experiments using adult *Diaptomus* as prey at densities of 5, 10, and 15 prey $\cdot L^{-1}$, respectively. In these predation experiments, one to three predators were added to beakers containing 1 L of 64-μm-filtered lake water.

Predation durations, ranging from 6 h (for *Bosmina*) to 12 h (for *Cyclops* and *Diaptomus*), were chosen so that some prey were still alive at the end of the experiments. All experiments were carried out at 10–15°C in total darkness. At the end of the experiments, all remaining animals were retained on a small 64-μm Nitex screen and examined with a stereomicroscope. Since no prey mortality was found in control containers (beakers with identical contents except predators), predation rates were determined from the difference between the initial number of prey and the number of prey found alive at the end of the experiments.

Grazing Experiments

In situ grazing experiments were conducted in Mountain L. in July 1981, Blue Chalk L. in June 1982, and Gull L. in June and August 1982. All experiments were conducted in the epilimnion; 5 experiments were conducted in Blue Chalk L., 11 in Gull L., and 2 in Mountain L.

We used the procedure of (Haney 1971) for in situ experiments. Animals were collected within the water column with a 2-L Haney grazing chamber. They were fed ^{14}C-labelled *Chlorella vulgaris* (in 1981), *Scenedesmus ovalis* (in 1982), and *Pediastrum* spp. (in 1982). The longest linear dimensions of these algal particles were 6–8 μm for *Chlorella*, 4–5 μm for *Scenedesmus*, and 30–40 μm for *Pediastrum* (coenobium). Algae were prepared for radioactive labelling according to Holtby and Knoechel's (1981) purge–uptake method. The specific activity of water in the grazing chamber generally ranged from 1000 to 5000 cpm$\cdot mL^{-1}$. Animals grazed in situ for 15 min. They were then filtered onto modified petri plates equipped with 64-μm Nitex screens and killed by immersion into hot water (at least 80°C). They were rinsed with filtered (64 μm) surface lake water and then stored on dry ice for no longer than 7 d. To determine the amount of radioactivity in the grazing chamber, 5-mL aliquots of the grazing chamber water were collected.

In the laboratory, animals were sorted and identified with the aid of a dissecting microscope. We measured the prosome length for each animal and then placed each into individual scintillation vials. Animals were digested overnite in 0.25 mL of NCS (Amersham) tissue solubilizer at 50°C. We then followed Chow-Fraser and Knoechel's (1985) method for scintillation counting. Radioactivity in the animals ranged from 3 to 100 counts above background, but were usually between 30 and 60 cpm$\cdot$animal^{-1}.

The prosome length of 20 individuals of each developmental stage was measured from preserved zooplankton samples (70% alcohol) from Blue Chalk L. The range of these measurements were used as an index for estimating the developmental stage of *Epischura* in the in situ grazing experiments, since only prosome lengths were recorded.

Laboratory grazing experiments were conducted with animals from Gull L. (August 1982). Five adults were placed in 1 L of 64-μm-filtered lake water and were acclimatized in beakers at 10°C for 2 h prior to experimentation. One millilitre of labelled *Scenedesmus* or *Pediastrum* was then introduced into the beaker and gently mixed with a glass rod. Animals were allowed to graze for 30 min and were then killed with hot water, rinsed, sized, and placed individually into scintillation vials. Other details of the procedure were essentially as already described. In these experiments, radioactivity in each animal ranged from 5 to 150 counts above background.

Stomach Content Analysis

Animals for stomach content analyses were collected from Blue Chalk L. during June 1984 by vertical tows of the epilimnion. They were stored in Lugol's iodine solution to preserve the algal and zooplankton material in the guts.

The prosome length and developmental stage were recorded for each animal. Stomachs were dissected out with fine pins with the aid of a dissecting microscope. They were then transferred onto a slide and gently squashed under a glass coverslip, with addition of a dilute glycerin–water solution. Contents were examined at 200× and 400× magnification using a phase-contrast light microscope.

The results of stomach content analyses are dependent on the availability of food items in the water column, the different digestibility of the various food types, the condition of the stomach dissected out for examination, and the correctness of the stomach content identification. Since we anticipated that experience would enable a more thorough identification of later relative to early specimens, we examined developmental stages in random order.

Statistical Analyses

Grazing rates of *Epischura* (all developmental stages) were regressed against prosome length, regardless of lake origin, with a least-squares regression analysis (Sokal and Rohlf 1981). Lake-by-lake regression equations were also generated and analysis of covariance (Sokal and Rohlf 1981) was used to determine differences among slopes and intercepts of these lakes. Nonparametric analyses included the Kruskal–Wallis test and the Mann–Whitney *U*-test (Zar 1984).

Results and Discussion

Predation Experiments

Generally, adult *Epischura* had very low predation rates on adult *Cyclops* and *Diaptomus*, the maximum mean ingestion rate being only 0.5 prey·predator^{-1}·d^{-1}. They did not have measurable ingestion rates when presented with adult *Cyclops* at prey densities of 5 or 15 prey·L^{-1}; at a prey density of 10·L^{-1}, there was a mean predation rate of 0.4 prey·predator^{-1}·d^{-1}. *Epischura* adults appeared to have higher ingestion rates when presented with adult *Diaptomus;* at prey densities of 5 and 15 prey·L^{-1}, they had a mean ingestion rate of 0.2 and 0.5 prey·predator^{-1}·d^{-1}, respectively, although no measurable ingestion rate was recorded at a prey density of 10·L^{-1}. We did not attempt to conduct predation experiments with immature stages of *Epischura* using these two prey species, since predation rates would likely be too low to measure.

By comparison, adult *Epischura* from Blue Chalk L. had high predation rates on *Bosmina*. We found that predation rate on *Bosmina* increased with developmental stage (Kruskal–Wallis test, $P < 0.05$), from a mean rate of 3 prey·predator^{-1}·d^{-1} at C4 to 6 prey·predator^{-1}·d^{-1} at C6 (Fig. 1). Predation rates of C5 and C6 were statistically similar (Mann–Whitney *U*-test, $P > 0.05$), but those of C4 were statistically lower than C5 and C6 combined (Mann–Whitney *U*-test, $P < 0.01$), suggesting that predation rate is proportional to predator size. There was, however, no measurable ingestion rate on *Bosmina* for C2 and C3 stages.

Individual variation in daily predation rate of *Bosmina* was high. Such high variability in predation rate may be the result of intermittent feeding behavior of *Epischura*, and also reflects the difficulty associated with successful capture and ingestion of *Bosmina* by this predator (Kerfoot 1978; Wong 1981b).

Main (1961) conducted predation experiments with *E. lacustris* using *Bosmina coregoni* as prey but concluded that *Bosmina* was not a suitable prey for *Epischura*, since he obtained extremely low predation rates. The reason for his low rates relative to ours is probably because he used prey >0.5 mm, which were likely too big to be ingested by *E. lacustris* (Wong 1981a; Wong and Sprules 1985). Main also obtained results different from ours in that he measured high predation rates for *Epischura* feeding on *Diaptomus*. We believe that the probable reason for this discrepancy is that Main conducted predation experiments in 2-mL depression chamber slides. Since *Diaptomus* defends itself by outswimming the predator, experiments conducted in such unrealistically small volumes would artificially inflate predation rates for *Diaptomus*. In another study, Folt and Goldman (1981) observed that *E. nevadensis* adults ingested adult *Diaptomus* at high rates in the laboratory, but did not have high predation rates in the field. Thus, *Epischura* probably do not prey on adult *Diaptomus* at high rates in nature, and this is supported by our data.

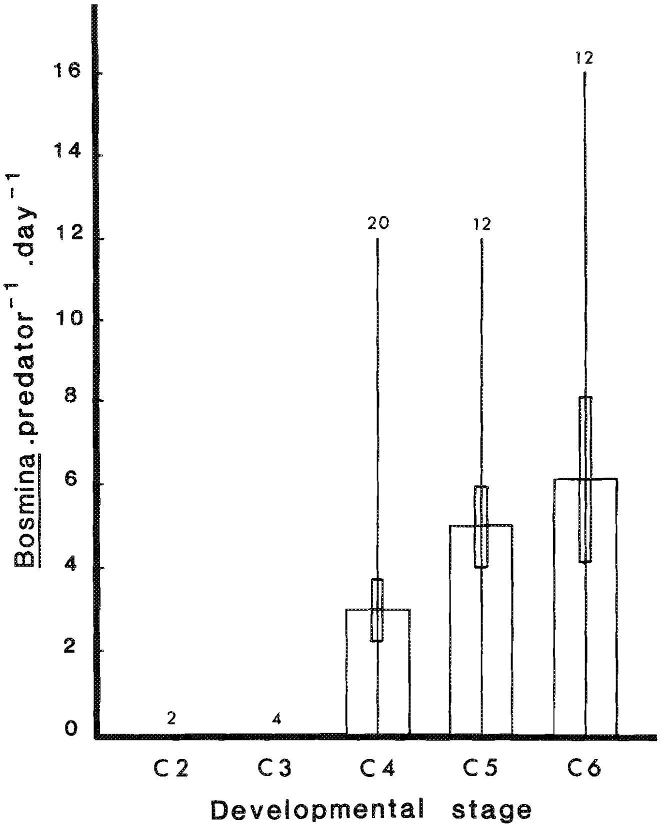

FIG. 1. Predation rate (mean ± 1 SE) by *Epischura lacustris* of various developmental stages on *Bosmina longirostris*. Numbers on top of bars indicate sample size.

Grazing Experiments

In total, 61 in situ individual grazing rates were measured in the three lakes; 21 were from Blue Chalk, 27 from Gull, and 13 from Mountain L. The grazing rate when *Chlorella* was used as tracer declined logarithmically with body size (Fig. 2). Since we were unable to identify the developmental stage of the animals, we present the size range for each of the copepodid stage (Blue Chalk L.) below the *x*-coordinate in Fig. 2. As in the predation experiments, no C1 and relatively few C2 were present in samples because grazing data were collected in all three lakes between June and August when C1 and C2 were scarce relative to other stages.

The negative slope of the regression (Fig. 2) indicates that *Epischura* decreases its grazing on small algae such as *Chlorella* as it grows from C2 to adult. Consequently, the feeding of adult animals on such small cells is almost negligible. These low grazing rates on small algae were also reported in other omnivorous calanoid copepods (Kibby and Rigler 1973; Chow-Fraser and Wong 1985).

There is considerable individual variation associated with grazing rates of a single body size. Such high variability is not uncommon for field animals, and is not associated with differences in tracer cells used, since there was very high variability

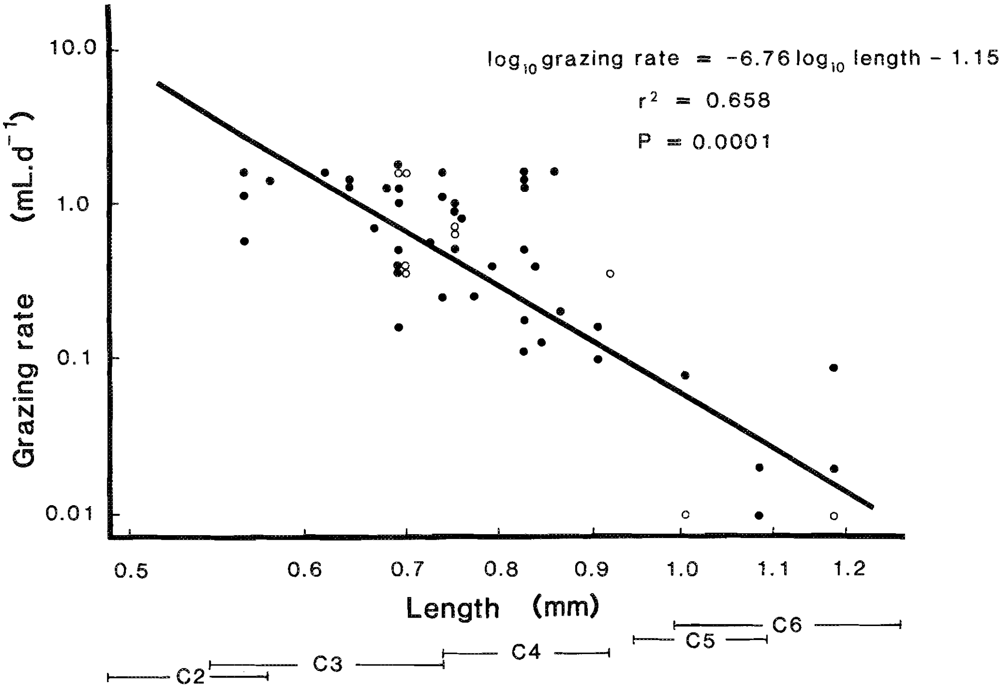

FIG. 2. Grazing rate versus prosome length for *Epischura lacustris*. Tracer cells used were *Chlorella*. Solid line represents least-squares regression through data. Two overlapping data points are represented by open circles.

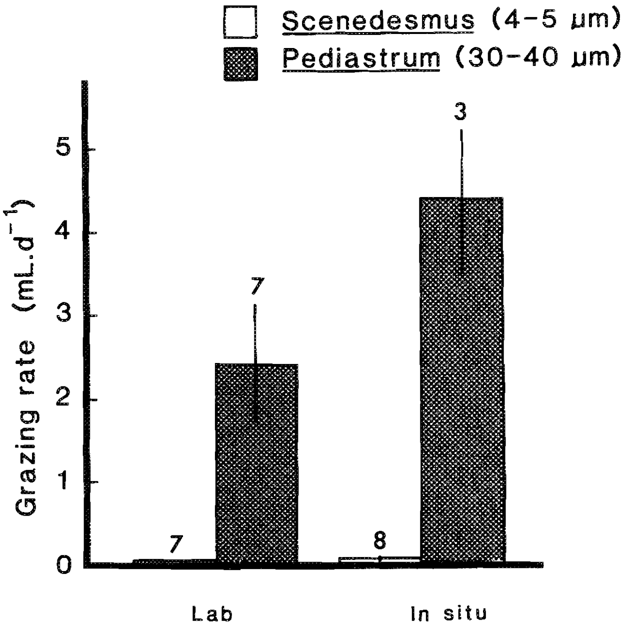

FIG. 3. In situ and laboratory grazing rate (mean ± 1 SE) of adult *Epischura lacustris*. Tracer cells used were *Scenedesmus* and *Pediastrum*. Numbers on top of bars indicate sample size.

even for data corresponding to one tracer species. Some of the variation may be attributed to the overlapping size of developmental stages; however, the highest individual variation was associated with C4 where there was no overlap in size with other stages. Comparison of regression equations for each lake (analysis of covariance) indicated that sopes and intercepts were statistically homogeneous ($P > 0.05$). Therefore, differences in lakes did not have any significant effect on the grazing rates of animals in the overall regression analysis.

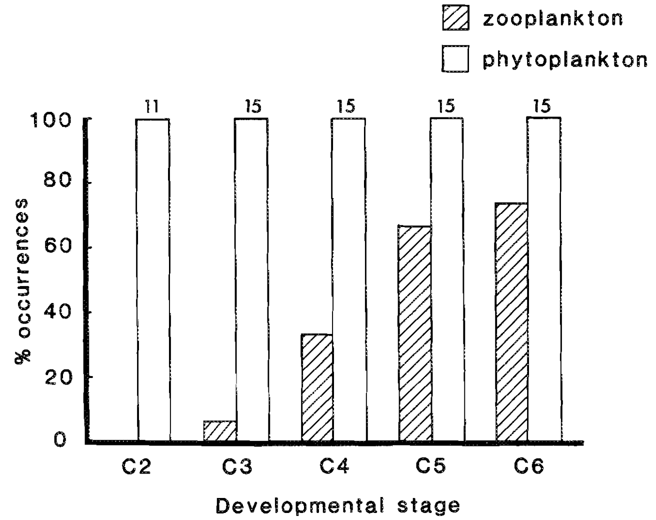

FIG. 4. Percent occurrence of zooplankton and phytoplankton in the guts of *Epischura lacustris* of various developmental stages.

Epischura adults grazed at higher rates on *Pediastrum* than on *Scenedesmus* in the laboratory and field studies (Mann–Whitney, $P < 0.025$ for both; Fig. 3). Grazing rates were generally less than 0.05 $\mathrm{mL \cdot d^{-1}}$ when *Scenedesmus* was used, compared with mean rates of 2.43 and 4.36 $\mathrm{mL \cdot d^{-1}}$ in laboratory and field experiments, respectively, when *Pediastrum* was used.

Stomach Content Analysis

Results of stomach content analyses (Fig. 4) substantiated all findings of the predation and grazing experiments (Fig. 1 and 2, respectively). We found algal remains in all of the animals regardless of developmental stage; however, the percent occur-

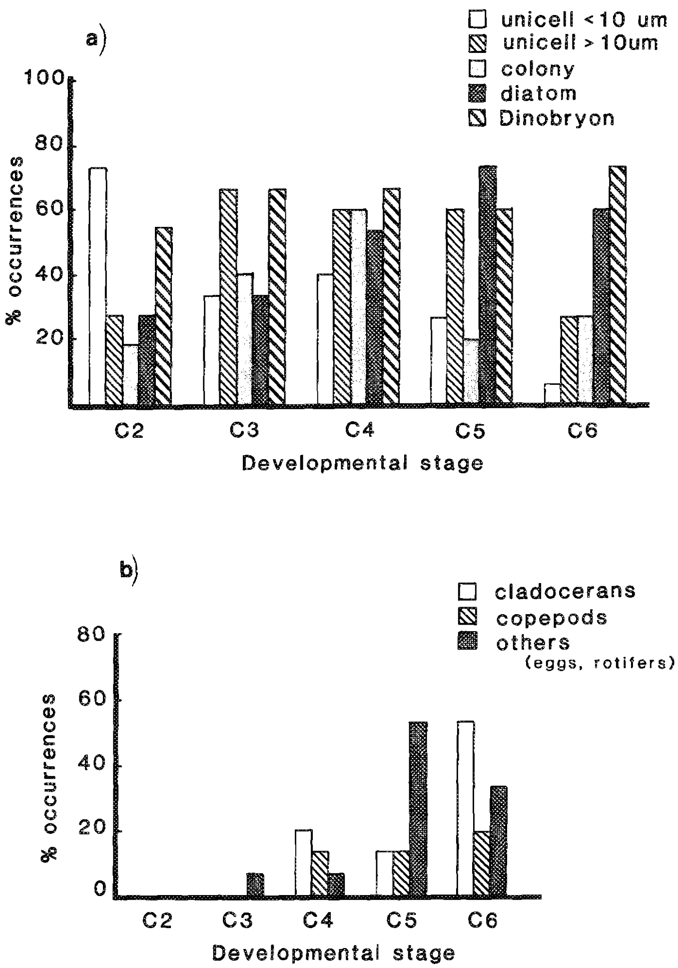

FIG. 5. Percent occurrence of (a) zooplankton and (b) phytoplankton in guts of *Epischura lacustris* of various developmental stages.

rence of animal remains increased with developmental stage, from 0% occurrence in C2 guts to 70% in adults.

Animal remains chiefly included cladocerans and copepods, although a large number of crustacean eggs were also present in the later instars (Fig. 5a). Adults were most predaceous on cladocerans, presumably *Bosmina*, but instars younger than C4 did not ingest any cladocerans. Since *Epischura* does not ingest the carapace of *Bosmina*, our estimate of the percent occurrence of cladocerans in these guts is probably conservative because we were not always able to distinguish the soft tissues of *Bosmina* from the mush present in the stomachs. The relative occurrence of copepod parts did not exceed 25% in any developmental stage, and substantiates the low predation rate of *Epischura* on *Diaptomus* and cyclopoids.

We categorized the algal remains into five groups: unicells <10 μm, unicells >10 μm, colonial forms, diatoms, and *Dinobryon* cells or colonies (Fig. 5b). By far, the most common food item in all developmental stages was *Dinobryon*. It occurred in at least 55% of guts of all stages. Small unicells were most common in C2, and became progressively rarer in the older stages; large cells, by contrast, were most common in the intermediate stages (C3 to C5), and relatively unimportant in C2 and C6. The dominant diatom was *Cyclotella*, and this was present in a large percentage of guts in the older instars. Colonial forms, especially *Sphaerocystis* and *Coelosphaerium*, were commin in C3 and C4, but were relatively uncommon in the stomachs of older or younger stages.

TABLE 2. Relative abundance of zooplankton in Blue Chalk L. (data from M. Arts, Department of Zoology, University of Toronto.) Samples were collected with a vertical townet from sediment to lake surface (mesh size 130 μm; mouth area 1590 cm^2; 70% efficiency)

Sampling date	Zooplankton taxa	Density (no.$\cdot$L^{-1})	Size range (mm)	Mean size (mm)
3 June 1982	Nauplii	16.69	0.12–0.39	0.23
	Daphnia	3.29	0.62–1.88	1.17
	Holopedium	0.65	0.62–2.00	1.31
	Bosmina	2.49	0.21–0.74	0.42
	Diaptomus	29.07	0.23–1.00	0.62
	Cyclopoids	28.84	0.32–1.47	0.69
17 June 1982	Nauplii	16.05	0.11–0.53	0.22
	Daphnia	6.96	0.42–2.49	1.47
	Holopedium	0.22	1.22–2.53	1.80
	Bosmina	9.69	0.27–0.73	0.47
	Diaptomus	44.81	0.32–1.22	0.65
	Cyclopoids	65.10	0.35–1.48	0.63

The low percent occurrence of small cells in C6 is consistent with the observation that adult *E. lacustris* grazed on *Scenedesmus* and *Chlorella* at low rates. The relatively large contribution of colonial forms, diatoms, and *Dinobryon* in the gut contents of C2 and C3 precludes the notion that early instars are incapable of ingestion large phytoplankton. Immature *E. lacustris* ingests a large variety and size of algae; adults, on the other hand, mostly ingest large cells.

Main (1961) likewise observed greater than 30% occurrence of colonial algae in the stomachs of C5 and C6 animals. Diatoms such as *Synedra* and *Navicula* were commonly ingested (15–20%); however, *Dinobryon* were absent, even though they were present in the water column. The difference between his results and ours is perplexing, since *Dinobryon* were commonly found in the guts of other calanoid omnivores, *E. lacustris*, and *Senecella calanoides* in Gull L. (Chow-Fraser and Wong 1985). We speculate that its absence in the stomachs of Main's animals probably reflects the relative scarcity of *Dinobryon* in his lake at the time of sampling.

We can give a qualitative evaluation of *Epischura*'s food preference, since we noted the relative abundance of zooplankton and phytoplankton in Blue Chalk L. at roughly the same time of the season when samples were collected for the stomach content analysis. The most common prey items in the lake on both June sampling dates were diaptomids and cyclopoids (Table 2). Because cladocerans were less abundant than copepods in the water column, but were found in disproportionately high numbers in guts, we suggest that *Epischura* selectively feeds on cladocerans, presumably *Bosmina*. This trend of selective feeding is probably stronger if we consider that assessment of cladocerans in our analyses is conservative.

The dominant algae in Blue Chalk L. were forms larger than 30 μm. *Dinobryon* colonies, as well as diatoms such as *Tabellaria*, *Cyclotella*, and *Asterionella*, were prevalent (Table 3). Thus, it is not surprising that these algae were found in abundance in the stomachs of *Epischura*. *Cryptomonas* was also relatively abundant, but these were seldom in guts. Since these algae are naked, even if they had been ingested, they may have been macerated beyond recognition. It is surprising, though, that colonial forms such as *Sphaerocystis* and *Aphanocapsa* were present in guts, since these were relatively scarce in the water column. Thus, *E. lacustris* appears to select for these

TABLE 3. Biomass concentration of phytoplankton in Blue Chalk L. Sample was collected on 10 June 1982 from the epilimnion of the lake.

Phytoplankton taxa	Biomass ($mg \cdot m^{-3}$)
Colonial	
Sphaerocystis	25.67
Aphanocapsa	8.65
Chroococcus	12.48
Oocystis	9.01
Unicells	
Cryptomonas	48.54
Chlorella	32.13
Mallomonas	36.56
Diatoms	
Asterionella	54.84
Tabellaria	63.31
Cyclotella	170.36
Others	
Dinobryon	395.57

colonial forms in Blue Chalk L. This is also consistent with the observation that *Epischura* appeared to select for *Sphaerocystis* in Gull L. (Chow-Fraser and Wong 1985).

General Discussion

This study represents one of the few studies on the diet changes that accompany development of an omnivorous freshwater calanoid copepod. The results of two other studies (Elster 1936; Maly and Maly 1974) are consistent with the present findings. Elster (1936) studied the diet of *Heterocope borealis*, noting that the intensity of carnivorous feeding increased during copeodid development, and that all stages included a large quantity of *Cyclotella, Asterionella*, and *Synedra* in their guts. Maly and Maly (1974) noted a shift to larger algal particles with development of *Diaptomus shoshone* from C2 to adult; at C4, they became predatory, and thereafter maintained an omnivorous diet. It appears that the diet of freshwater omnivorous calanoids develops from soley herbivorous to completely omnivorous, with the transition to predaceous feeding at C4. Further investigation should be conducted to determine if the change to omnivory in C4 is accompanied by the development of sharp mandibular teeth in *Epischura*, similar to that noted by Maly and Maly (1974) for *D. shoshone*.

Proper evaluation of an animal's status in the food web requires detailed information on its feeding ecology. In this study, we have examined changes in ingestion rates of *E. lacustris* on various prey items during development. By examining rate changes, we have presented a more complete picture of the feeding of *Epischura* and have shown that C2 to C6 instars exert a differential impact on the phytoplankton and zooplankton prey in the water column. Future dietary studies of omnivorous copepods should include both the predatory and herbivorous components of their feeding habit so that the relative proportion of time spent on each feeding mode and the energetic consequences of switching food habit can be investigated.

Acknowledgments

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