Influences of Diet on the Life Histories of Aquatic Insects[1,2]

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Benthic species are partitioned into functional feeding groups based on food-acquiring mechanisms. Effects of food quality on voltinism, growth rate, and size at maturity are demonstrated for representatives of gougers and shredders, collectors, and scrapers. Food quality for predators is uniformly high, but food quantity (prey density) obviously influences their life histories. A food switch from herbivory to predation, or some ingestion of animal tissues, in the later stages is a feature of the life cycle of many aquatic insects. Temperature interacts with both food quality and quantity in effects on growth as well as having a direct effect on control of metabolism. Thus further elaboration of the role of food in life history phenomena will require controlled field or laboratory studies to partition the effects of temperature and food.

Key words: aquatic insects, feeding strategies, functional groups, life histories

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Nous avons séparé les espèces benthiques en groupes, selon le type d'alimentation fonctionnelle fondé sur les mécanismes d'acquisition de la nourriture. Chez des représentants de creuseurs et de déchireurs, de collecteurs et de racleurs, nous démontrons les effets de la qualité de la nourriture sur le voltinisme, le rythme de croissance et la taille à la maturité. Pour les prédateurs, la qualité de la nourriture est uniformément haute, mais la quantité de nourriture (densité des proies) influe évidemment sur leurs cycles biologiques. Un changement de régime, d'herbivore à prédateur, ou une certaine absorption de tissus animaux aux stades ultérieurs est une caractéristique du cycle biologique de plusieurs insectes aquatiques. Il y a interaction de la température avec la qualité aussi bien que la quantité de nourriture dans ses effets sur la croissance, de même qu'un effet direct sur le contrôle du métabolisme. Des études plus poussées sur le rôle de la nourriture dans les phénomènes du cycle biologique nécessiteront des expériences de laboratoire ou des études contrôlées sur le terrain afin de séparer les effets de la température et de la nourriture.

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THE study of trophic relations in freshwater communities reveals a bewildering array of foods available and methods of resource utilization. As Hynes (1970, p. 192) suggested "It may seem inappropriate to consider the food of invertebrates in any biotope, as it is obviously as varied as the invertebrates themselves." Because of such complexity, it seems necessary to attempt some simplification in evaluating the general role of nutrition in controlling aquatic insect life histories — primarily growth (i.e. rate and maximum size attained). The stereotyping of food habits, based on what is eaten, at the generic or family level for aquatic insects has been criticized (e.g. Resh 1976; Fuller and Stewart 1977). However, the partitioning of taxa on the basis of food-acquiring mechanisms, that is, community functional role, rather than what is eaten, has proven useful in approaching certain ecological questions (Cummins 1973, 1974; Merritt and Cummins 1978; Wiggins and Mackay 1978). This approach, which stresses partitioning of food resources on a community basis, reveals that detrital utilization by shredders (coarse particle feeders) and collectors (fine particle feeders) dominates most forested headwater streams. This is in contrast to many terrestrial systems in which the insects feed primarily on living plant tissue.

Various aspects of food (diet) as a factor influencing life histories, or life history strategies, are examined. Since field data implicating food as a causal factor usually have other possible explanations, our task is akin to completing a jigsaw puzzle with most of the pieces missing. Furthermore, the interaction of abiotic factors, especially temperature, with food quality and quantity (food per unit of environment) confounds the

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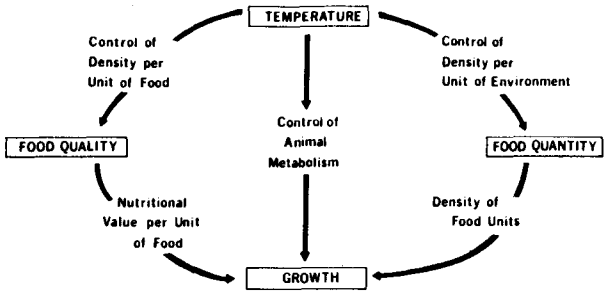


FIG. 1. Relationship between temperature and food in the control of macroinvertebrate growth.

problem (Fig. 1). A bias to lotic examples is evident both in the experimental data presented and literature cited because our research programs are directed to stream studies.

Food Resources of Aquatic Insects

The range of organic materials potentially available as foods for aquatic insects extends from the highly refractory to the readily assimilable. The relative nutritional gradient is perhaps: (1) wood; (2) terrestrial leaf litter; (3) fine particulate organic matter (FPOM); (4) decomposing vascular hydrophytes and filamentous algae; (5) living algae, especially diatoms; and (6) animal tissues. Considerable evidence has accumulated (e.g. Bärlocher and Kendrick 1973a, b) that the microbial flora associated with categories 1–4 is the primary source of nutrition for aquatic insects. Monk (1976) demonstrated a weak cellulase activity in gut extracts of several aquatic insects but found no correlation between the occurrence of cellulase and the abundance of cellulose in the diet. However, *Tipula* and other shredders have been shown to have hind gut symbionts that may be instrumental in the assimilation of products of cellulose degradation (Meitz 1975).

Gougers and Shredders

These functional groups encompass those species that feed on coarse particulate organic matter (CPOM) (food categories 1 and 2) and reduce the particle size by chewing-gouging and mining wood, and skeletonizing leaf litter. Woody detritus, the most refractory material in aquatic habitats, has a processing time of at least decades. In water, microbial degradation of wood occurs largely on exposed surfaces (Anderson and Sedell 1979). Initially food is available to invertebrates only through gouging at the surface, but when tissue softens, the inner tissues are mined. Although wood debris offers an extremely nitrogen-poor diet (C to N ratio 300–500:1), in western coniferous forests it supports a considerable fauna (Anderson et al. 1978). Life-history strategies suggested for species that exploit wood as a food source were (1) long life cycles with low metabolic activity; (2) high ingestion

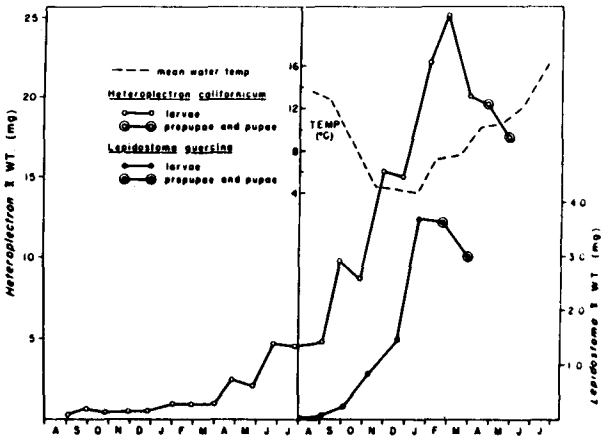


FIG. 2. Life cycles of the wood gouger *Heteroplectron californicum* and the leaf shredder *Lepidostoma quercina*, expressed as mean individual weight at each sample interval at Berry Creek, Benton Co., Oreg. Water temperature is given as mean monthly temperature.

rates to provide sufficient assimilative gut contact with the microbial flora to meet the animal's nutrient requirements; (3) supplemental feeding on higher quality food (especially the periphyton film); or (4) some combination of the above.

Examples of xylophages include the elmid beetle, *Lara avara*, the calamoceratid caddisfly, *Heteroplectron californicum*, the craneflies, *Lipsothrix nigrilinea* and *L. fenderi*, and midges of the genus *Brillia*. Life cycle studies of the dipterans are incomplete. *Lara avara* and *H. californicum* both grow slowly; the former probably requires 3 yr or more to complete development and the latter has a 2-yr life cycle. Microbial symbionts capable of digesting cellulose have not been demonstrated in the hind guts of either species.

The growth pattern of *H. californicum* is compared with that of a typical leaf shredder, *Lepidostoma quercina*, in the same stream (Fig. 2). The major growth period for both species is from September to February when water temperature ranges from about 12 to 4°C. *Lepidostoma quercina* is univoltine, with an instantaneous growth rate (IGR) of 2.7% $\cdot d^{-1}$, whereas *H. californicum* has a 2-yr cycle with an IGR of 0.9% $\cdot d^{-1}$.

The degradation of deciduous leaves by shredders has received considerable attention in the last decade and was recently reviewed by Anderson and Sedell (1979). From the viewpoint of dietary effects on life histories, some salient features of the shredder function are

1. Life cycles of many shredders (e.g. *Tipula* and many caddisflies) are keyed to the autumnal pulse of leaf fall, with the major growth period occuring in the late autumn and winter.

2. Shredders selectively feed on the leaves maximally colonized (conditioned) by microorganisms, especially aquatic hyphomycete fungi. This is shown by the posi-

tive correlation between selective feeding and density of microbial flora (Bärlocher and Kendrick 1973a, b), nitrogen content (Iversen 1974), and respiration rate and ATP content per unit weight of leaf (M. Ward, R. Speaker, and K. Cummins unpublished data). Thus, the rate of leaf degradation (e.g. *Alnus, Tilia, Fraxinus,* fast; *Carya,* intermediate; *Quercus, Fagus* and conifers, slow) is a good predictor of shredder feeding preference.

3. Although shredders selectively feed on the best conditioned substrate, they can make an adjustment in feeding rate to maintain their growth rate.

Food Quality of *Alnus* Leaves for *Clistoronia magnifica*

Compared with many common riparian species, *Alnus* leaves are high in nitrogen, rapidly conditioned, and one of the most palatable species for benthic invertebrates (Iversen 1974; Otto 1974; Petersen and Cummins 1974; Anderson and Grafius 1975). Therefore, alder leaves have been used as a standard for comparison in short-term growth studies of various Trichoptera at Oregon State University. However, when the limnephilid *C. magnifica* was reared through the entire larval stage and compared with field collected specimens, it became apparent that laboratory-conditioned alder leaves were inadequate to produce normal growth. A diet including a supplement of wheat grains or enchytraeid worms in addition to alder leaves has enabled continuous rearing of *C. magnifica* (Anderson 1976, 1978). Feeding experiments with individuals from the laboratory culture indicate that development time was at least 10 wk longer and mortality more than twice as high on alder leaves compared with a supplemented diet (Fig. 3). Mean pupal weight was only 22.65 (±1.04) mg on the nonsupplemented diet as compared with 37.90 (±2.32) mg on the leaves plus supplement.

Laboratory-conditioned leaves were compared as food with leaves incubated in a stream to test the possibility that an inferior microbial flora developed on laboratory-conditioned leaves. Conditioning time was 2–3 wk at 12–15°C in the field and at 15°C in the laboratory. Fecal production was greater with the stream-conditioned leaves than for the laboratory-conditioned leaves (Table 1), which suggests that the former were more palatable. On the evidence of their development to fifth instar and on final weights, larvae fed on field-conditioned leaves were judged to be marginally more advanced than those fed on laboratory-conditioned leaves. However, the differences in weights are not significant ($P > .05$), and both are markedly below the weights of larvae receiving a wheat supplement. Low fecal production by control larvae is attributed to higher assimilation of the wheat diet. Thus, laboratory conditioning is apparently not a major factor in reduced growth rates on the nonsupplemented detritus diet.

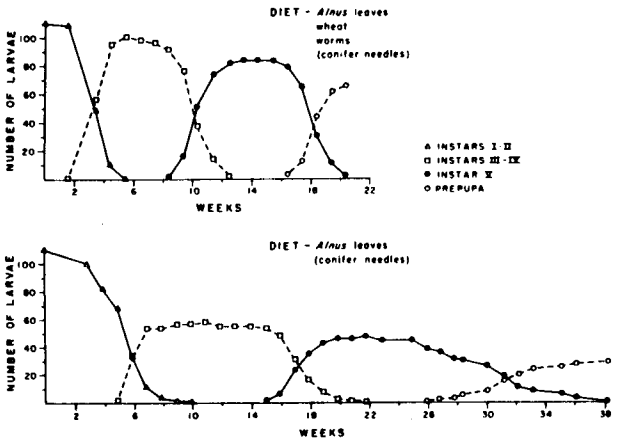


FIG. 3. Rate of development and survival of *Clistoronia magnifica* larvae reared on *Alnus* leaves compared with a control of *Alnus* plus a supplement of wheat grains and enchytraeid worms. Both series reared at 15°C, with conifer needles and sand for case material.

Higher quality food is required during the final instar when growth is rapid and fat reserves are being laid down prior to pupation. A series of 26 *C. magnifica* larvae that had been reared from week 12 to 17 on alder leaves were split into two groups after 50% of the individuals had molted to the final instar. One group was continued on alder leaves while the other received leaves and a supplement of wheat plus worms. Mean time to pupation was a further 17 wk for the alder group as opposed to only 7 wk for those that received the supplement. Even more striking were the differences in survival and pupal weight: alder, ($n = 4$), $\bar{x} = 15.0$ mg; supplement ($n = 11$), $\bar{x} = 39.8$ mg. Pupae from the stock culture (fed a supplement diet) averaged 40.1 mg. Thus, the addition of the supplement for the final 5–7 wk of the larval stage provided sufficient nutriment to allow normal weight to be regained.

Food Quality of Basswood (*Tilia*) and Hickory (*Carya*) Leaves for *Tipula abdominalis*

Recent work at the Kellogg Biological Station (M. Ward, R. Speaker, and K. Cummins unpublished data) has shown that the shredder, *T. abdominalis*, can increase its feeding rate to compensate for poor food quality and thus maintain a typical growth rate. Two levels of food quality were obtained by using hickory and basswood leaves. These were incubated with natural stream microorganisms for 9 wk at 10°C. Respiration rates were 30% higher for the basswood leaves, indicating greater microbial conditioning than for hickory and, consequently, a higher food quality. *Tipula abdominalis* larvae grew at the same rate in a 1-wk experiment when fed either type of leaf separately. The weight loss of the hickory leaves was about 30% greater than the basswood, but the efficiency of food

TABLE 1. Growth, development, and fecal production of *Clistoronia magnifica* larvae reared on laboratory-conditioned *Alnus* leaves (n = 40), field-conditioned *Alnus* leaves (n = 40), and a control of leaves plus wheat grains (n = 20). Larvae reared for 18 d at 15°C.

	Lab leaves	Field leaves	Control
$\bar{x}$ Initial wt (mg)	10.56±1.11[a]	10.56±1.11	10.56±1.11
$\bar{x}$ Final wt (mg)	11.40±0.77	12.24±0.63	19.75±3.67
% molted	68	82	95
Feces (mg/mg·d)	0.31	0.46	0.27

[a]95% confidence interval.

conversion to growth (relative growth rate/consumption) (Waldbauer 1968) for *T. abdominalis* larvae on basswood was twice that on hickory. That is, the larvae ingested hickory leaves more rapidly, compensating for the lower food quality.

Feeding by *T. abdominalis* larvae was minimal on both basswood and hickory leaves when the conditioning time was reduced to 2 or 3 wk. With only this type of food available many of the larvae attempted to crawl out of the experimental chambers and those that remained did not grow.

The compensatory effect of food quality in overriding direct temperature effects on shredder growth is shown in Table 2. Basswood leaves conditioned at 5°C were of higher quality than hickory leaves at 10°C. When expressed per unit of temperature time (degree days), the growth rates of *T. abdominalis* and the caddisfly *Pycnopsyche guttifer* were higher on basswood than on hickory leaves.

The above experiments suggest that the overall shredder feeding strategy is selection of the highest quality (greatest microbial biomass) food available in a given leaf accumulation, increased feeding rate if the best available is not of sufficient quality to maintain growth in the normal range, and emigration if quality or quantity is below some minimal level. Temperature control of the general metabolic rate of shredders is compensated to some extent by the temperature-mediated effects on food quality. In addition, as demonstrated for *C. magnifica* (Anderson 1976), some intake of high protein (animal) food may be required for individuals to achieve an appropriate mature weight.

Collectors

In contrast to shredders that feed on CPOM that is colonized by microbes both on the surface and throughout the matrix, collectors utilize fine particulate organic matter (FPOM) that is primarily surface-colonized by bacteria. The sources of FPOM food and its nutritional quality varies considerably. Much of it is fecal material produced by shredders and other functional groups that is recycled or "spiralled" (Wallace et al. 1977) by the stream biota. Other sources are wood and leaf fragments produced by physical abrasion and microbial maceration, senescent periphytic algae, planktonic algae, aquatic macrophyte fragments, small animals, and particles formed by the flocculation of dissolved organic matter. The organic layer on stones, described by Madsen (1972) as a matrix of bacteria, extracellular material, fungi, and organic and inorganic particles, may be used by collectors or by scrapers (see below).

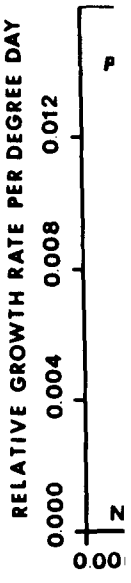
Black fly larvae typify collectors that filter FPOM from the water column. Gut filling times are about 20–30 min (Ladle et al. 1972). Since the food is passed so rapidly, the nutritional value is probably derived by stripping bacteria from the refractory detritus particles. Carlsson et al. (1977) have documented a relationship between the type of food available and the life cycle of some Lapland black flies. The larvae at lake outfalls occur in denser aggregations and have faster growth than the same or other species occurring further downstream. Phytoplankton and coarse detritus (> 2 μm) occurred in similar amounts in all reaches, so they concluded that small particles, from 2 μm down to colloidal size, were the resource that maintained the huge larval aggregations at the lake outlet. This material is produced by decomposition on the lake bottom in winter and is washed into the river during ice melt.

The influence of food quality, as indicated by particle-associated respiration rate or ATP content, on the growth of the collector-gatherer midge, *Paratendipes albimanus*, is shown in Fig. 4 and 5. All food materials were wet sieved to the same particle size range before use. The oak and hickory leaves had been conditioned

TABLE 2. Comparison of growth rates of two shredder species on high (basswood, *Tilia americana*) and medium (hickory, *Carya glabra*) quality leaf litter at different temperatures. Experiments conducted for 28 d in experimental stream channels under controlled flow and normal photoperiod conditions.

Leaf type	Mean temp (°C)	Degree days	% Loss/ deg day	Respiration of leaves ppm O_2/g DW·h^{-1}	Relative growth rate (% body wt) *Tipula abdominalis* per day	*Tipula abdominalis* per deg day[a]	*Pycnopsyche guttifer* per day	*Pycnopsyche guttifer* per deg day[a]
Basswood	5	147	0.38	0.022	2.22	0.424	4.70	0.895
Hickory	10	282	0.27	0.013	3.51	0.348	5.19	0.515

[a]The factoring out of temperature in these calculations assumes that growth is very low at 0°C.



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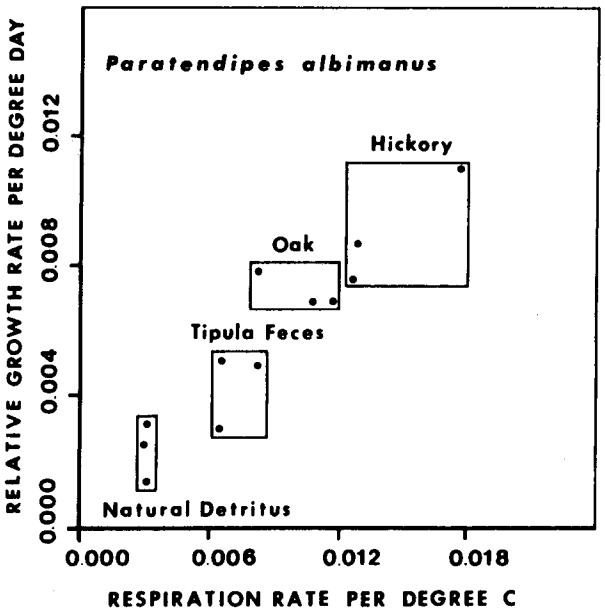

FIG. 4. Relative growth rate (Waldbauer 1968) of *Paratendipes albimanus* fed four diets (all sieved to the same particle size) compared at three temperatures (10, 15, 20°C) on the basis of substrate respiration rate ($\mu LO_2 \cdot mg\ AFDW^{-1} \cdot h^{-1} \cdot °C^{-1}$). Modified from Ward and Cummins (1978).

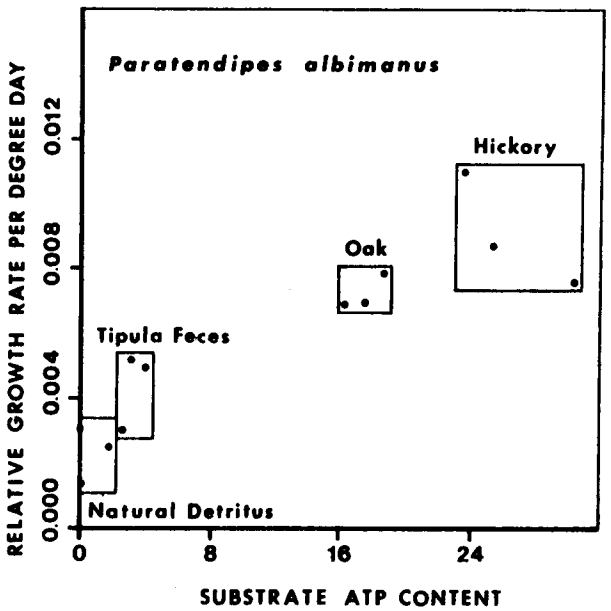

FIG. 5. Relative growth rate of *Paratendipes albimanus* fed four diets compared with substrate ATP content as an index of microbial biomass (μM ATP/mg AFDW). See Fig. 4 caption for additional details.

in aerated batch cultures with aquatic hyphomycete fungi inocula for 2 wk. The leaves were dried, ground, and wet sieved to the appropriate size range. The experiments were conducted at three temperatures (10, 15, and 20°C). Each of the three points for each food type represents a temperature in Fig. 4 and 5. Although in all cases the higher temperature produced the highest growth rate on a given food, it is clear that food quality outweighed the direct effect of temperature on larval growth.

Scrapers

This functional group is typified by glossosomatid caddisflies, representatives of the baetid, heptageneid, and ephemerellid mayflies, and psephenid beetle larvae (Merritt and Cummins 1978). Scrapers are dependent primarily on autochthonous production as a food resource but their mode of feeding also results in ingestion of detritus, as well as the organic layer on stones (Madsen 1972). The nutritional content of live algal cells is high; Cummins and Wuycheck (1971) report differences of several hundred calories per gram between diatoms and detritus.

Previous studies indicated that *Glossosoma nigrior* from first-order streams were much smaller than those in a third-order stream (Cummins 1973, 1975). Gut content analysis revealed that larvae in the small stream consumed more detritus whereas those in the third-order stream fed predominantly on diatoms. The interaction of temperature and food on growth of *G. nigrior* is shown in Table 3. The ratio of gross primary production to community respiration (P/R) is a reflection of the available algal food, and the data indicate a strong relationship between P/R and the final larval (prepupal) weights.

As shown by Gose (1970), the amount of accumulated temperature can influence the number of generations of a scraper species, and it probably affects the maximum size attained by individuals in a given cohort. There was a 20% greater accumulation of day degrees in the third-order stream, which is undoubtedly a con-

TABLE 3. Dry weights of *Glossosoma nigrior* prepupae from six sites in the Augusta Creek watershed, Kalamazoo and Barry Co., Mich. (collected Nov. 11–12, 1977).

Stream site	Stream order	Degree days[a]	P/R[b]	*N*	Mean dry wt (mg)	C.V. (%)
Smith Cr.	1	2398	0.39	28	1.512	13.1
B. Ave.	1	2443	0.73	32	1.666	12.3
Upper 43rd	2	2863	1.76	34	4.018	17.7
Lower 43rd	3	3006	—	27	4.638	21.6
C Ave.	3	—[c]	—	40	3.749	17.3
Nagel's	3	2811	1.70	26	4.507	11.5

[a]Based on mean weekly temperatures.
[b]Gross primary production community respiration measured over 24-h period in circulating chambers (D. L. King and K. W. Cummins unpublished data).
[c]Temperature regime approximately the same as Nagel's.

tributing factor to the larger size of the *G. nigrior* larvae, but the data also implicate food quality (e.g. ratio of algal cells to detritus) and quantity (e.g. density of algae per unit of rock surface).

Predators

Predators, that is, species that feed on live prey by active capture, have high assimilation efficiencies (75–85%, Heiman and Knight 1975). Although food quality is uniformly high, the quantity (prey density) can vary significantly. Thus, effects of food on the life cycles of predators occur as density effects, both in numbers or biomass of predators, or differences in generation time.

Azam and Anderson (1969) compared populations of *Sialis californica* in a stream section where chironomid populations were high due to enrichment with sucrose and urea, with an upstream nonenriched section. *Sialis californica* was univoltime in the enriched area whereas a portion of the population required 2 yr in the control section. Azam (1969) was able to simulate the growth patterns that resulted in 1- and 2-yr life cycles by using different levels of rations in feeding experiments.

Johnson (1973) demonstrated with damselfly larvae that searching movement increases as prey density falls from high to low, but at very low prey densities the larvae remain stationary and again wait for prey, presumably because of the high metabolic cost of increased searching.

Inter- and intraspecific competition and territoriality were important factors affecting the life cycle of the damselfly, *Pyrrhosoma nymphula*, in Macan's (1977) 20-yr study of trophic relations in Hodson's Tarn, England. Larvae of *P. nymphula* feed primarily on planktonic Crustacea as a "sit and wait" type of predator. When prey are scarce, *P. nymphula* can fast for long periods. They may take two full summers to complete development if they do not obtain enough food to complete it in one. When predator density was high, there were two size-groups at the end of the summer. Macan suggests that the large larvae had obtained vantage points where food was frequently within reach, while the small larvae were relegated to inferior feeding sites. He proposed that the starvelings would eventually die unless good feeding sites became vacant. When fish were in the pond, their predation on large larvae would lead to vacancies in optimal feeding sites which would then be filled by small larvae. Macan postulates a self-regulating population mechanism whereby a substantial consumption of large larvae by fish does not greatly reduce the numbers of damselflies reaching maturity because the loss of large larvae allows the small larvae to exploit the copepod population.

Resh (1976) demonstrated that food quality affected the life cycle of the sponge-feeding leptocerid caddisfly, *Ceraclea transversa*. Larvae that occur during the summer feed on the sponge, *Spongilla lacustris*, and reach the nonfeeding prepupal stage is early autumn at the time the colonial sponge declines and produces gemmules. Larvae that emerge later in the summer also feed on sponge but only reach the third or fourth instar before the sponges become inedible due to gemmulation. Thus, they are forced to shift to a detritus diet and growth is suspended until spring when there is a return to sponge feeding. Larvae of this cohort are significantly smaller than those that complete growth before overwintering. Resh indicates that the two cohorts operate as independent functional units in the larval stages, but presumably there is some gene flow between the two populations. Both cohorts have a univoltine life cycle so the differences in food quality do not greatly affect the duration. However, larvae of the second cohort are actively feeding for longer, which exposes them to more environmental hazards, and the smaller size of adults indicates a lower fecundity.

A shift from algal or detrital feeding to predation has been demonstrated in later larval stages for several stoneflies and caddisflies (Siegfried and Knight 1976; Fuller and Stewart 1977; Winterbourn 1971; Wiggins 1977). The more unusual switch from predation to heavy algal feeding was reported for the stonefly, *Stenoperla prasina* (Winterbourn 1974) and *Acroneuria californica* (Siegfried and Knight 1976); in both instances this was apparently a response to an alternative food that was available for a limited period. As pointed out previously, the ingestion of animal tissue in the later stages of the growth cycle may be an important feature of the life cycle of many species of aquatic insects.

Discussion

Differences in growth rate directly affect duration of life cyles (i.e. voltinism), size attained at maturity (and therefore fecundity, which is positively correlated with female size), and survivorship. Temperature and food quality and quantity are control parameters with significant interactions on rate of growth. Thus isolation of the role of food in life histories is difficult to achieve without controlled laboratory or field experiments. As pointed out by Pritchard (1979), the duration and timing of aquatic insects life cycles are more indeterminate than is usually suggested. He cites examples of cohort splitting, where individuals of the same cohort may have 1, 2-, or even 3-yr life cycles. Detrimental effects of a poor diet will be most apparent with multivoltine species because those that have a univoltine (or longer) cycle usually have a period of arrested development of variable length that can be shortened to increase the feeding interval (Pritchard 1976).

The recent work of Sweeney and Vannote (1978) has convincingly shown that adult body size and fecundity of a number of aquatic insects depend largely on thermal conditions during the larval period. Changes of 2 or 3 deg Celsius either warmer or cooler than the optimum temperature regime can affect both the rate

and duration of larval growth to the extent that adult size is significantly reduced. Thus, in any study of growth, it is important to separate as far as possible the direct (animal metabolism) and indirect (food quality and quantity) effects of temperature.

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Benthic Life Histories: Summary and Future Needs[1,2]

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WATERS, T. F. 1979. Benthic life histories: summary and future needs. J. Fish. Res. Board Can. 36: 342–345.

The symposium indicated many ways in which greater knowledge of benthic life histories can be used to develop and improve techniques such as sampling, taxonomic methods, and bioassays. Benthic organisms' diet and physical environment, factors variable in nature, were shown to be capable of modifying certain life history features such as growth rate and voltinism. The lack of accumulated life history data and the need to tailor sampling schedules to life history events were commonly identified elements in the symposium. Future research needs included (1) basic data on benthic life history, (2) improved taxonomy of immature benthic invertebrates, and (3) understanding the entire life history of an organism in relation to the seasonal progression of its environment. Management implications of benthic life history information included more applicable data from long-term bioassays on all life history stages, and improved management of stream fisheries through habitat alteration to manipulate benthic production.

Key words: life history, benthos, symposium

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Au cours du colloque, on a indiqué plusieurs façons d'utiliser de meilleures informations sur le cycle biologique d'organismes benthiques afin de mettre au point et améliorer les techniques telles que l'échantillonnage, les méthodes taxonomiques et les analyses biologiques. On a démontré que le régime alimentaire et le milieu physique des organismes benthiques, facteurs variables dans la nature, peuvent modifier certaines caractéristiques du cycle biologique, telles que le rythme de croissance et le voltinisme. Parmi les points communément identifiés au cours du colloque, on note le manque de données accumulées sur les cycles biologiques et le besoin d'échelonner l'échantillonnage selon les événements de ces cycles. Parmi les besoins futurs en recherche, on compte: (1) les données de base sur le cycle biologique benthique, (2) une taxonomie améliorée des invertébrés benthiques immatures et (3) la compréhension du cycle biologique complet d'un organisme en relation avec l'évolution saisonnière de son milieu. Pour ce qui est de la manière dont les gestionnaires peuvent utiliser les connaissances sur les cycles biologiques benthiques, on note des résultats plus facilement applicables d'analyses biologiques à long terme sur tous les stades du cycle biologique. On note aussi une meilleure gestion des pêches fluviales par altération de l'habitat et manipulation de la production de benthos.

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