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LIFE CYCLES REPRODUCTION AND DIETS OF *DINA DUBIA* AND *ERPOBDELLA PUNCTATA* (HIRUDINEA: ERPOBDELLIDAE) IN CANAGAGIGUE CREEK, ONTARIO

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EXECUTIVE SUMMARY

Life cycles, reproduction and diets of *Dina dubia* and *Erpobdella punctata* (Hirudinea: Erpobdellidae) in Canagagigue Creek, Ontario

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The life histories and food habits of two species of leeches, *Dina dubia* and *Erpobdella punctata*, in an industrially polluted creek are described. Most individuals of both species completed their life cycles in about one year, but many required nearly two years to reach sexual maturity and a portion of each year class appeared to survive to breed two or more times. The number of viable young produced was 3.5X greater for E. *punctata* than for D. *dubia*. The former also grew more rapidly and attained a greater maximum size (1946 vs. 725 mg live weight). Both species fed most frequently on Chironomidae and Oligochaeta. However, D. *dubia* consumed more prey characteristic of riffle areas (Simuliidae, Tanytarsini, Orthocladinae), while E. *punctata* ate more prey commonly associated with lentic conditions (Tubificidae, Chironomini, Crustacea).

Despite the greater reproductive success of E. *punctata*, D. *dubia* were more abundant in the creek. We attribute this to differences in microhabitat preference and oxygen requirements (or thermal tolerances) which result in spatial separation of the two species and favour the survival of D. *dubia*.

MANAGEMENT PERSPECTIVE

In recent work on Canagagigue Creek, we found that leeches contained residues of chlorophenols from 10 to 100X higher than other benthic invertebrates and fish. There is evidence from the literature that leeches have a considerable bioaccumulation capacity for other synthetic organic compounds such as DDT and mirex, and even metals. We have therefore suggested that leeches may serve as excellent "early warning" indicators of contamination, and have recommended their use in biomonitoring.

In order to determine pathways for the bioaccumulation of contaminants by these organisms, details of their life histories (e.g. trophic status, longevity) must be known. Unfortunately, the biology of Canadian leech species is poorly known. The present study, believed to be the first of its kind in eastern Canada, provides background information on the reproduction, growth, life cycles and food habits of two species of leeches in an Ontario stream. The work was conducted under contract to the senior author from A-Base funds

SOMMAIRE ADMINISTRATIF

Cycle vital, reproduction et régime alimentaire de Dina dubia et Erpobdella punctata (Hirudinée : Erpobdellidé) dans le ruisseau Canagagigue, Ontario

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On décrit le cycle vital et les habitudes alimentaires de deux espèces de sangues, Dina dubia et Erpobdella punctata, dans un ruisseau subissant la pollution industrielle. La plupart des individus des deux espèces ont terminé leur cycle vital en l'espace d'environ 1 an, mais nombre d'entre eux ont nécessité près de deux ans pour atteindre la maturité sexuelle et une partie de chaque classe annuelle a semblé survivre pour se reproduire deux fois ou plus. La progéniture viable était 3,5 fois plus nombreuse dans le cas d' E. punctata que dans celui de D. dubia. La première espèce présentait également une croissance plus rapide et atteignait une taille maximale plus grande (1946 mg comparativement à 725, en poids vif). Les deux espèces se nourrissaient le plus souvent de Chironomidés èt d'Oligochètes. Toutefois, D. dubia consommait plus de proies caractéristiques des zones de rides (Simuliidae, Tanytarsini, Orthocladinae), tandis qu'E. punctata consommait plus de proies couramment liées à des conditions d'eau calme (Tubificidae, Chironomini, Crustacea).

Malgré le succès d'E. punctata du point de vue de la reproduction, D. dubia était plus abondant dans le ruisseau. Nous attribuons ce phénomène à des différences dans les préférences à l'égard des micro-habitats et dans les besoins en oxygène (ou tolérances thermiques) qui entraînent une séparation spatiale des deux espèces et favorisent la survie de D. dubia.

PERSPECTIVES DE GESTION

Dans des travaux récents réalisés dans le ruisseau Canagagigue, nous avons constaté que les sangsues contenaient 10 à 100 fois plus de résidus de chlorophénols que d'autres invertébrés benthiques et le poisson. La documentation scientifique nous indique que les sangsues sont douées d'une forte capacité de bioaccumulation d'autres composés organiques synthétiques tels le DDT et le mirex, et même des métaux. Par conséquent, nous estimons que les sangsues pourraient être d'excellents organismes indicateurs de la contamination capables de donner une "alerte précoce" et nous recommandons leur utilisation dans le système de surveillance biologique.

Pour pouvoir déterminer les voies de bioaccumulation des contaminants par ces organismes, nous devons connaître les détails relatifs à leur cycle vital (par exemple, état trophique, longévité). Malheureusement, on connaît mal la biologie des espèces de sangsues vivant au Canada. La présente étude, que l'on croit être la première du genre dans l'Est du Canada, fournit des renseignements de base sur la reproduction, la croissance, le cycle vital et les habitudes alimentaires de deux espèces de sangsues dans un ruisseau de l'Ontario. Le travail a été réalisé en vertu d'un contrat accordé à l'auteur principal à partir de fonds de base A.

Abstract

The life cycles of *Dina dubia* and *Erpobdella punctata* were described from semimonthly (monthly in winter) collections made at 2 sites on Canagagigue Creek between May 1982 and July 1983. Observations on reproduction were made in the creek and in a flow-through stream tank. Most individuals of both species completed their life cycles in about 1 yr, but some required 2 or more yr to reach sexual maturity. The estimated average fecundity (138-173 young adult^{-1}), growth rate and maximum size (1946 mg live weight) of *E. punctata* were all greater than for *D. dubia* (47-50 young adult^{-1}; maximum size 725 mg), but *D. dubia* was much more abundant in Canagagigue Creek. Both species fed most frequently on Chironomidae and Oligochaeta with the total variety of prey consumed reflecting the diversity of prey available at the site. The habitat preferences of the leeches were apparent from their diets: *D. dubia* ate relatively more animals associated with riffle habitats, *E. punctata* ate relatively more pool-dwelling organisms. The greater abundance of *D. dubia* at our study sites is attributed to this difference in habitat preference.

Résumé

Les cycles vitaux de Dina dubia et Erpobdella punctata ont été décrits à partir de collections semi-mensuelles (mensuelles en hiver) réalisées à 2 endroits dans le ruisseau Canagagigue entre mai 1982 et juillet 1983. Les observations sur la reproduction ont été réalisées dans le ruisseau et dans un réservoir à circulation continue. La plupart des individus des deux espèces ont terminé leur cycle vital en l'espace d'environ 1 an, mais nombre d'entre eux ont nécessité près de deux ans pour atteindre la maturité sexuelle et une partie de chaque classe annuelle a semblé survivre pour se reproduire 2 fois ou plus. La fécondité moyenne estimée (progéniture de 138-173 par adulte), le taux de croissance et la taille maximale (1946 mg en poids vif) étaient tous plus grands dans le cas d'E. punctata que dans celui de D. dubia (progéniture de 47-50 par adulte; taille maximale de 725 mg), mais D. dubia était néanmoins beaucoup plus abondant dans le ruisseau Canagagigue. Les deux espèces se nourrissaient le plus souvent de Chironomidés et d'Oligochètes; la variété totale des proides consommées reflétait la diversité des proies présentes dans le site. Les préférences des sangsues en ce qui a trait à l'habitat étaient apparentes à partir de leur régime alimentaire : D. dubia consommait relativement plus d'animaux liés à des habitats caractérisés par des rides, tandis qu'E. punctata consommait relativement plus d'organismes caractéristiques des eaux calmes. La plus grande abondance de D. dubia dans nos sites d'études est attribuable à cette différence dans la préférence à l'égard de l'habitat.

Introduction

Many species of non-parasitic Hirudinea have very broad geographical distributions and live in a wide variety of freshwater habitats (Mann 1961, Sawyer 1972). This ecological success is at least partially due to their flexible life histories and feeding habits (e.g. Aston and Brown 1975, Young and Ironmonger 1982a, Dall 1983). Erpobdella punctata (Leidy 1870) is found throughout North America and has been shown to vary life history strategies in response to temporal stability of the habitat (Sawyer 1970) or the presence of a competitor (Davies et al. 1977). Dina dubia Moore and Meyer 1951, is also widely distributed, occurring from the Great Lakes region to Alaska, but little is known of its biology (Herrmann 1970, Sawyer 1972).

Both E. punctata and D. dubia are common in the lower reaches of Canagagigue Creek in hern Ontario. This study was undertaken to determine the basic life histories and feeding habits of these co-occurring species in an enriched, perennial stream. Such information is essential to understanding the role of these predators in streams, and the ways in which leeches accumulate organic contaminants (Metcalfe et al. 1984).

Canagagigue Creek is a tributary of the Grand River, which in turn empties into eastern Lake Erie. It receives domestic and industrial effluents from the town of Elmira, Ontario, as well as leachates from a disused chemical waste dump. Carey et al. (1983) have described physical and biological aspects of the creek with respect to the origin and fate of contaminants. We used two of their study sites for collections and observations on leeches: site CN3 was 1.7 km downstream of the Elmira Water Pollution Control Plant (WPCP) and had a benthic community dominated by Tubificidae (Oligochaeta) and Chironomidae (Diptera); site CN5 was 7.4 km downstream from WPCP and supported a diverse assemblage of meroptera, Trichoptera, Plecoptera and other invertebrates. Depth and current velocity were more uniform at CN3 than at CN5 which had alternating riffles and pools.

Methods

Each collection of leeches for life cycle and dietary analysis included specimens picked by hand from stones lifted gently from the streambed, and those caught in a dip net (300 um) after disturbing the substratum to dislodge the animals. Hand-picking was most effective for stones in shallow riffles and near the margins of the stream. The dip net was used in deeper water (> 40cm), along undercut banks and in vegetated backwaters. The collecting effort on each date involved a search of all available habitats for a period of 3 h or until at least 50 animals of each species were found. Since E. punctata was much less abundant than D. Dubia, each collection was composed of individual E. punctata from a variety of habitats (riffles, pools, undercut banks, etc.) in numbers approximately proportional to their relative abundance in each habitat, while samples of D. dubia were of[illegible] dominated by individuals from a smaller variety of habitats.

Leeches were placed individually in vials to retain gut contents regurgitated or defecated during handling (Bennike 1943). When air temperatures exceeded 10^{0}C, the vials were kept on ice until the animals were weighed. Each leech was weighed within 24 hours (usually within 6 hours) of collection, returned to its vial and preserved in 70% ethanol. Weights were measured to the nearest milligram on a Sartorius balance (model 2400) after blotting to remove excess water and mucus.

Gut contents were determined by exposing the entire length of the digestive tract through a middorsal incision and dissecting out the contents. Fecal material, enclosed in mucus strands adhering to the posterior end of the animal, and regurgitated items inside the vial were also examined. Intact food items were sorted from the gut contents, identified and counted under a dissecting microscope. More homogenous material was di[illegible]ed in a drop of glycerine and examined under a compound microscope. Numbers of oligochaetes were determined from counts of whole worms and intact cuticles, or estimated from the abundance of cuticular fragments and setae in the gut contents. Analysis of gut contents by direct examination has been used by numerous investigators to describe the diets of erpobdellids (e.g. Dall 1983, Davies and Everett 1975, Elliott 1973). Davies et al. (1978, 1981) cited Davies and Everett (1975) in asserting that erpobdellids occasionally ingest whole prey, but that they more commonly suck out body fluids. Davies and Everett (1975) presented no direct evidence of extensive feeding on soft tissues or fluids but did find that direct examination of gut contents underestimated the consumption of oligochaetes by *Nephelopsis obscura* when compared with assessment by serological techniques. Since our specimens were preserved prior to dissection, we expected that ingested body fluids would be evident as amorphous, coagulated material, either in the midgut or in the storage vial. Such material was seen in less than 1% of our specimens.

All *D. dubia* collected between 27 May and 24 August 1982, were dissected and food items identified and counted. Up to 20 randomly selected individuals from each collection during September 1982 through April 1983, were examined and the proportion containing prey was noted. The gut contents of all *E. punctata* collected from 12 May 1982 through 15 February 1983, were identified and counted. The typical diet of each species during the study period was considered to be the mean number of each prey taxon found in all the leeches dissected.

The feeding behavior of newly hatched leeches was observed in the laboratory using animals which emerged from cocoons collected in the field and held at room temperature in petri plates of stream water. Potential prey items were taken alive from dip net collections made at CN5 and offered individually to the leeches. The leeches' responses were observed under a dissecting microscope. Prey which were not consumed immediately were observed periodically for up to 2 weeks. The organisms offered were: Oligochaeta (Tubificidae and Naididae), Gastropoda (*Physa* and Lymnaeidae), Ostracoda, Copepoda, Amphipoda, Insecta (Ephemeroptera, Trichoptera, Coleoptera: Dytiscidae, Diptera: Chironomidae) and Pisces (larval *Notropis* sp.). The prey offered to the leeches spanned the entire range of individual size for each group present in the stream.

In 1982, cocoons were hand-picked (using forceps) from stones lifted from the streambed.. All cocoons were taken from each randomly selected stone until a total of at least 50 were obtained. Cocoons were examined under a dissecting microscope and classified as: hatched - empty, with an end plug missing; damaged - empty, with end plugs intact and an irregular hole in the wall; developing - with visible embryos; or dead - albumen opaque. Embryos were counted. Damaged cocoons were considered to have been eaten by invertebrate predators (Bennike 1943) since no empty cocoons were found with ruptures or tears consistent with damage from shifting of the substratum.

In 1983, observations on the reproduction of both species were made in a flow-through stream tank located in a laboratory trailer at CN3. Stream water was pumped into a 215 x 4[illegible] 17cm fish hatching trough at a rate of ca. 5 L min^{-1} through a filter system with Grade No. 2 silica sand as the filtering medium. This reduced, but did not eliminate, suspended solids and had no effect on dissolved oxygen. Water temperature was monitored continuously and was always within 0.5^{0}C of the stream itself. Aluminum trays (20 x 40 cm), perforated by 1.5 mm holes about 1 cm apart on the bottom and downstream ends, were suspended in the tanks to a depth of about 15 cm. Shelter and an initial supply of food were provided by the epilithic community (minus leeches) of 3 stones (ca. 10 cm in greatest diameter) taken from the streambed and placed in each tray. Dense populations of chironomid larvae (mainly Tanytarsini) appeared in the trays within a few days.

Leeches were collected at CN3 and CN5 on 28 April 1983, at which time no fresh cocoons of any species were present in the stream. Leeches expected to be sexually mature (i.e. >300 mg live weight, see below) were confined in groups of 5 in 3 trays each. As animals died the survivors were shifted among tanks to maintain 5 animals in at least one tank for as long as possible. Numbers of cocoons and surviving adults were recorded at intervals of 1-3 days throughout the breeding season, i.e. until the last animal died.

Daily rates of cocoon production were estimated by dividing the number of new cocoons by the product of the number of surviving animals and the number of days since the last count. Cocoons were harvested and the numbers of embryos were recorded on 12 May, 15 June and 29 June.

Results

Dina Dubia

Reproduction

Deposition of cocoons had begun before the first collecting trip on 12 May 1982, and cocoons with embryos in the early stages of cleavage were found as late as the first week of September. The greatest concentrations of cocoons were found on cobbles near the water's edge or in riffles. Hatching (emergence of the young from the cocoon) began in the first week of June. Newly hatched Dina (2-5mg live weight) were collected through mid-October (fig. 1). Of 726 cocoons examined, 81 (11.2%) were dead or appeared to have been damaged by predators. The mean number of embryos cocoon^{-1} was 7.1 (range 2-14).

The 15 D. dubia (300-400 mg) confined in the stream tanks in 1983, deposited a total of 119 cocoons ($\bar{x}$ = 7.9 cocoons leech^{-1}) from 2 May until the last animal died on 21 June. Adults survived an average of 24.8 d (range 4-54 d). The daily rate of cocoon production tended to increase over time as stream temperature increased (fig. 2). Cocoons produced in captivity contained slightly fewer embryos ($\bar{x}$ = 6.7, n=93, range 2-12) than did those in field collections the previous year. Assuming 11.2% mortality during development (from field observations in 1982) and 6.7 to 7.1 young cocoon^{-1}, average total fecundity of D. dubia was 46.9 - 49.7 young adult^{-1}.

Microdistribution and life cycle

D. dubia were not randomly distributed among the available microhabitats at either site. In early May of both years, most Dina were found under stones embedded in fine aerobic mud and gravel near the banks of the stream. From early June through August 1982, most animals were found on cobbles in riffles, among strands of Cladophora when algal growth was luxuriant, otherwise under the stones. Most smaller Dina (<100 mg) remained in the riffles until the following spring, but larger individuals were commonly found under boulders and cobbles in deeper runs and pools in late autumn and winter. In mid-July 1983, water temperature was high (22^0-30^0C, fig. 2) and no _Dina_ were found in riffles. All specimens were found buried in aerobic, muddy gravel near the margins of the creek.

This non-random distribution within the stream contributed to the absence or underrepresentation of certain size classes in various collections (e.g. animals weighing < 100 mg in December, or <150 mg in late summer and March, fig. 1.). Examination of the size-frequency distributon over the entire study period (fig. 1) suggests that individual _D. dubia_ weighing from 5 to > 300 mg were present in Canagagigue Creek throughout the year. From April through June of both years, average individual size appeared to be greater at CN3 than at CN5. No such difference was seen when both sites were sampled in J[illegible] August and November.

No _Dina_ with distinct clitella were seen in 1982. Clitellate animals were found from late April through May 1983, the smallest of which weighed 70 mg, and the first cocoons were seen in the stream in the first week of May.

Recruitment was continuous from June through October. Growth appeared to be most rapid from September through mid-November, then stopped until April or early May. The average size of potentially mature _D. dubia_ (i.e. those >70 mg live wieght) decreased with the onset of the breeding season as most of the larger animals died by the end of June; moribund leeches were frequently observed in the stream at this time. Leeches which were not sexually mature (< 70 mg) at the beginning of May grew rapidly through June and were probably responsible for cocoons deposited from July onwards. Some of these survived the summer, grew rapidly in autumn and developed clitella the following spring. A small fraction of these animals evidently survived until at least September of their second year as shown by the presence of few individuals weighing > 300 mg during August. The largest _D. dubia_ collected, which weighed 725 mg in late May 1982, may have been nearly 3-yr old.

The data suggested that D. dubia which hatch early in the summer (June-July) can complete their life cycle in one year. Animals which hatch later in the season (August-October) first reach sexual maturity in July of the following year, and a larger fraction of this group survives to breed in May of the next year.

Food habits.

The average numbers of prey found in 328 D. dubia collected in Canagagigue Creek between 27 May and 24 August 1982, is shown in Table 1. A greater variety of prey was eaten at CN5 (31 taxa) than at CN3 (19 taxa), but oligochaetes and chironomid larvae comprised over 80% of the diet at both sites. The major differences in diet between leeches at the two sites were in the relative importances of Naididae, Tubificidae and Orthocladiinae (Table 2).

While the most frequently eaten prey (Oligochaeta and Chironomidae) predominated in the guts of leeches of all sizes, both the variety and numbers of individual prey eaten increased with size of D. dubia at CN5, but not at CN3 (Table 3). This did not reflect smaller gut volumes at CN3, but rather the larger average size of prey items. Over 90% of the specimens examined from CN3 during the summer (May-August) contained recognizeable prey items except on 6 August when 22% was empty. Feeding rates declined more in August at CN5, the proportion of empty leeches rose from 12% overall during May-July to 62% in August. None of 15 animals inspected in each of September and October was empty. Four of 10 were empty in November, as were all of those examined in December (n=15) and March (n=20). Feeding resumed in April.

Erpodbella punctata

Reproduction

Cocoons of E. punctata were most commonly found on the undersides of boulders and cobbles where the depth of water was at least 30cm and current speed was less than about 20 cm s[illegible]. Young were first seen hatching from cocoons on 2 June 1982, and no cocoons with viable eggs or embryos were found after August. Of 245 cocoons examined, 36 (14.7%) were dead or had been attacked by predators. The mean number of embryos cocoon^{-1} was 8.5 (range 2-15).

The 12 clitellate E. punctata ($\bar{x}$ = 968 mg, range = 438-1623 mg) confined in 1983, produced a total of 286 cocoons, an average of 23.8 cocoons leech^{-1}. The adults lived an average of 52.7 d (range 14-76 d). Daily cocoon production was high in the first week, then tended to parallel water temperature, reaching a peak when mean daily stream temperature first remained above 20^{0}C (fig. 2). Cocoons produced in the stream tanks contained an average of 6.8 embryos cocoon^{-1} (n = 208, range = 1-14). On the basis of these field and laboratory observations, total fecundity of E. punctata was 138.0-172.6 y[illegible] adult^{-1}, assuming 14.7% mortality prior to hatching.

Microdistribution and life cycle

This species was more abundant at CN5 than at CN3, but, as with D. dubia, larger individuals made up relatively more of the catch at CN3 (fig. 3). Seasonal and size-specific changes in the microdistribution of E. punctata were very pronounced. Recently hatched individuals were found in stony riffles in June and early July. In late July, nearly all specimens weighing <350 mg were found in backwaters, especially in association with aquatic or submerged terrestrial vegetation. Large E. punctata (>500 mg) were found most frequently among trailing vegetation along undercut banks, or under boulders in deep (> 50 cm) pools in all seasons. During the period from July through November, large individuals were often seen swimming away or burrowing into the gravel after being disturbed when stones in deep water were turned over. These animals were very difficult t[illegible]ch, and this is reflected in Figure 3. Kick sampling was much more effective in winter when the animals were less active.

The weights of all E. punctata collected from both CN3 and CN5 are shown in Figure 3. These data suggest that animals weighing up to about 300 mg in May are one year old, those 300-700 mg are two years old, and a few individuals may live four years (up to 1900 mg). Clitellate specimens were found from late April through May, the smallest weighing 119 mg. Thus, most E. punctata appear to attain sexual maturity in their first year of life. Moribund adults were seen on most collecting trips in June and early July, suggesting that adult mortality is heavy just after the breeding season. This was also noted among captive animals.

Food habits

The diet of E. punctata was similar to that of D. dubia in general composition and variety of prey eaten (Table 1), although it ate more oligochaetes, larval Chironomini and Ephemeroptera, and fewer Tanytarsini and Orthocladiinae. All E. punctata examined from CN3 had eaten Tubificidae, but too few leeches were collected there to allow meaningful comparisons of diet between sites.

The most frequently eaten prey at CN5 was Naididae, followed by Tanytansini, Tubificidae, Chironomini and Orthocladiinae (Table 2). Other prey were consumed by 38% of E. punctata but these accounted for < 15% of the total diet. Larger E. punctata ingested prey of a wider range of sizes than did smaller ones, so that the variety of prey ingested increased with size of leech (Table 4), but only very large individuals (> 400 mg) ate significantly more prey items.

Nearly 75% (80 of 107) of E. punctata dissected between May and November 1982, contained prey. Feeding appeared to continue at a low rate throughout the winter, with 9 of 14 animals collected in December and February each having 1 or 2 prey items in their guts. One specimen (1945 mg) collected on 25 June 1982, produced a cocoon during the 4 h interval between capture and weighing. Since it contained 2 Chironomus, 3 Tubificidae and

2 Ostracoda, reproduction did not appear to interrupt feeding.

Feeding Behavior in the Laboratory

Newly hatched D. dubia and E. punctata were behaviorally indistinguishable in the laboratory. Both were slightly negatively phototropic and continuously searched the culture dishes in an apparently random manner. Searching did not appear to be affected by the presence of either whole or damaged prey (Oligochaeta and Chironomidae) when introduced either separately or simultaneously. Detection of prey seemed to depend entirely upon direct contact with the prey's integument by the oral region of the leech, and such contact resulted in immediate application of suction. Prey which escaped an attack were not effectively pursued but were often contacted again as the leech resumed its searching. The maximum diameter of prey which could be ingested appeared to be about the same as the relaxed diameter of the leech's head. Live Copepoda, Caenis, Dytiscidae and Hyalella azteca (Amphipoda) of apparently appropriate size did not elicit attacks, nor did Physa of any size. Dead individuals of all of these, as well as Notropis cornutus (Pisces), were eaten immediately on contact. Active searching and feeding continued until the midgut was completely full. Satiated animals became quiescent but were active again within 24 hr. No cannabalism (except on experimentally exposed embryos) was observed, although larger individuals frequently attacked and swallowed prey which had already been partially ingested by smaller leeches.

Discussion

Interpretation of the life cycles of *D. dubia* and *E. punctata* was complicated by the wide range of size classes represented in most collections, and the absence of certain size clases from some collections. The first was due in part to the prolonged recruitment periods of both species, but could also be predicted on the basis of their foraging and feeding behavior. Greene (1974) described *Erpobdella octoculata* as 'not a deadly stalker and capturer of prey but rather a slow, clumsy, opportunistic wanderer dependent upon food happening to come into contact with its mouth'. Davies et al. (1982) found that *Nephelopsis obscura* detects and reacts to prey only on direct contact rather than by distant chemosensory detection. These reports are in perfect accord with our observations on young *D. dubia* and *E. punctata*. The large chance component of encountering and successfully ingesting prey should lead to great variation in size among leeches of the same age since feeding allows growth which, in turn, increases the range of size of prey which can subsequently be ingested and increases the probability of encountering suitable prey.

The basic life cycles of the two species were generally the same, although *E. punctata* had a shorter reproductive period and appeared to grow faster, attaining a much larger size than did *D. dubia*. Most individuals of both species completed their life cycles in about 1 yr, but some required 2 or more years to reach sexual maturity. It is unclear if these longer living individuals breed more than once. Davies and Everett (1977) reported complete postreproductive mortality in *N. obscura*, and all of our confined animals died so iteroparity seems unlikely. Growth slowed or stopped in winter. Similar life histories have been reported for *E. punctata* from an intermittent stream in Michigan (Sawyer 1970) and for both *E. punctata* and *N. obscura* from permanent ponds in Alberta (Davies and Everett 1977, Davies et al. 1977). Prolonged periods of recruitment are common among other aquatic invertebrates which feed as adults, e.g. many Hemiptera, Coleoptera and Odonata, most of which are also predaceous. While this could have adaptive value in minimizing intraspecific competition for prey (Harper and Magnin 1969), Butler (1984) has cautioned that life history parameters may not be the direct result of natural selection. For leeches, prolonged reproduction and recruitment may simply be a consequence of variable growth rates due to the large chance component of encounters with suitable prey. The resulting long breeding season, with individuals maturing at different ages, offers the additional benefit of ensuring genetic mixing within the population as has been noted for the common Nearctic mayfly Stenacron interpunctatum by McCafferty and Huff (1978).

Examination of gut contents indicated that the diets of D. dubia and E. punctata in Canagagigue Creek were also similar to those of erpobdellids elsewhere, consisting mainly of oligochaetes and chironomid larvae but including most other invertebrates of appropriate size found in the stream (Cross 1976, Davies et al. 1981, Young and Ironmonger 1979, Dall 1983). The predominance of Naididae, Simuliidae and Tanytarsini in the diet of D. dubia suggests that this species forages mainly on the upper surfaces of stones in fast water. The greater proportions of Tubificidae, Chironomini and small Crustacea eaten by E. punctata seems most consistant with foraging more in softer sediments in pools. Our laboratory observations on feeding behavior indicate that selective feeding on oligochaetes and chironomid larvae reflects the ease with which these organisms are detected by foraging leeches. Potential prey with projecting setae or cerci usually fled without provoking an attack when contacted by a foraging leech. These observations support the hypothesis that cuticular projections confer protection against some (Otto and Sjostrom 1983) but not all (Corkum and Clifford 1981) kinds of predators. Both the examination of gut contents and observations in the laboratory suggest that D. dubia and E. punctata feed primarily on whole prey organisms. We expected that leeches which fed only on the body fluids of prey would contain amorphous, coagulated material, at least in the fore- and midguts, but we found no such specimens.

The most striking differences between our observations and previously published results were in the fecundity of the species studied. Sawyer (1972) reported that isolated *D. dubia* from southern Michigan produced an average of 7.9 cocoons leech^{-1}, each containing an average of 4.15 eggs. Specimens from Canagagigue Creek produced the same number of cocoons, but each contained more embryos (6.7-7.1), so total fecundity was about 1.4x greater. Isolated individual *E. punctata* from Michigan (Sawyer 1970) and Alberta (Davies et al. 1977) produced an average of about 10 cocoons leech^{-1}, containing 5.0-5.6 eggs cocoon^{-1}. The fecundity of animals of similar size in the present study was at least 3x greater (23.8 cocoons leech^{-1} with 6.8-9.1 embryos cocoon^{-1}). Young and Ironmonger (1982b) found that fecundity of leeches was greater in more eutrophic British lakes, so our larger estimates of the reproductive capacities of *D. dubia* and *E. punctata* may reflect the enriched trophic conditions in Canagagigue Creek. Since our stream tanks duplicated the thermal and chemical regimes of the creek and provided access to food, shelter and potential mates throughout the breeding season, our higher estimates of fecundity are probably also due to these more natural conditions of confinement than in the studies by Davies et al. (1977) and Sawyer (1970, 1972).

Since it has been found that erpobdellid leeches can vary their life histories in response to local conditions (e.g. Aston and Brown 1975, Murphy and Learner 1982), we expected that *D. dubia* and *E. punctata* might grow faster at the more enriched site CN3 than at CN5. Practical problems prevented detailed intersite comparisons: too few animals were found at CN3 in summer, and ice cover prevented collecting at CN5 in winter. If collections taken at both sites within a few days of each other are compared in isolation, the average sizes of both species were larger at CN3 than CN5. This suggests faster growth at the more enriched site. However, inspection of the total collections s[illegible] that the catches at each site complement one another, certain samples from CN5 often containing size classes obviously missed at CN3, and vice versa. This suggests that growth rates were similar at both sites, but that certain size classes were more accessible at certain times at each site. These temporal differences in catchability are most clearly related to the age-specific microhabitat preferences observed for both species, and the physical differences between the sites. The shallow riffle habitat where most smaller leeches were found at CN5 was much less extensive at CN3. The deeper water at CN3 necessitated more extensive use of the dip net for catching specimens, thus biasing the collections toward larger individual size.

Microhabitat preferences also explain why D. dubia was much more abundant than E. punctata even though the individual fecundity of the latter was over 3.5 x greater. Most D. dubia were found in areas with strong to rapid currents; most E. punctata occurred in pools or sheltered areas. While these distributions could not be quantified by our collecting methods, this difference was clearly reflected in the diets of the two species. D. dubia ate more prey characteristic of riffles such as Simuliidae, Tanytarsini and Orthocladiinae, while E. punctata consumed relatively more Tubificidae, Chironomini and Crustacea, prey more commonly associated with pools. This spatial separation appears to benefit D. dubia in two ways: the epilithic fauna in riffles offers greater densities of easily accessible prey than are found in pools (especially insects (Sprules 1940)) and susceptibility to fish predation is much greater in deeper, slower water. Leeches comprised 10-48% by weight of the stomach contents of 4 common fish species at CN3 in May (unpublished data), so predation may be the more important factor in Canagagigue Creek.

While interspecific interactions cannot be ruled out on the basis of our observations, we do not suggest that D. dubia competively excludes E. punctata from the more favourable riffle habitats. Herrmann (1970) concluded that D. dubia is more of a cold stenotherm than is E. punctata. Since tolerance to high temperatures is often greater when dissolved oxygen concentrations are high, thermal stress on Dina may be minimal in areas of rapid current in an enriched, warm-water stream such as Canagagigue Creek. E. punctata is more tolerant of low oxygen concentrations (Sawyer 1974) and is a more active species, often swimming freely in the water column. We feel that these differences in oxygen requirements (or thermal tolerance) and behaviour, rather than competitive interactions, result in spatial seperation of the two species, to the numerical advantage of D. dubia.

Acknowledgements

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Table 1. The average numbers of various prey items eaten by *Dina dubia* (n=328) and *Erpobdella punctata* (n=107) from Canagagigue Creek. + = <0.01.

Taxon	D. dubia	E. punctata
Oligochaeta		
Naididae	1.36	1.63
Tubificidae	0.58	1.08
Bivalvia		
Sphaeriidae	0.01	0.01
Gastropoda		
Physa	+	0.02
Arachnida		
Hydracarina	+	
Crustacea		
Cladocera	0.02	0.01
Dytiscidae	0.01	0.03
Diptera		
Tipulidae	0.01	
Simuliidae	0.42	0.09
Chironomidae		
Tanypodinae	0.15	0.09
Diamesinae	0.02	0.01
Chironomini		
Chironomus	0.12	0.29
Cryptochironomus	+	0.03
Microtendipes	0.02	0.05
Phaenopsectra		0.04
Polypedilum	0.12	0.07
Stictochironomus	0.01	
Tanytarsini	0.91	0.36
Orthocladiinae		

Table cont..

Taxon	*D. dubia*	*E. punctata*
Copepoda	0.03	0.11
Ostracoda	0.07	0.22
Insecta		
Ephemeroptera		
Baetidae	0.10	0.09
Ephemerellidae		0.03
Heptageniidae		0.01
Caenidae		0.01
Ephemeridae		0.02
Trichoptera		
Hydroptilidae	0.03	0.01
Hydropsychidae	0.01	0.04
Coleoptera		
Elmidae	0.01	
Brillia		0.01
Corynoneura	0.02	
Cricotopus	0.93	0.61
Eukiefferiella	0.04	0.04
Nanocladius	0.10	0.03
Rheocricotopus	0.01	
Smittia - group	+	
Thienemanniella	0.15	0.18
Empididae	0.03	0.01
Tabanidae	+	0.01
Pisces	0.01	

Table 2. Percentage composition of the diets of <u>Dina dubia</u> and <u>Erpobdella punctata</u> at stations CN3 and CN5, May-August 1982.

	<u>D. dubia</u>		<u>E. punctata</u>
	CN3	CN5	
Naididae	14.7	30.9	25.8
Tubificidae	26.7	2.3	12.5
Simuliidae	8.6	7.4	1.6
[illegible]ypodinae	2.1	2.2	1.8
Chironomini	5.6	4.6	10.4
Tanytarsini	20.3	15.2	7.9
Orthocladiinae	17.5	32.6	23.1
Other Insecta	1.8	4.8	5.9
Other	1.0	0.2	0.6

Table 3. Mean (± 95% c.l.) numbers of taxa and individual prey eaten by *Dina dubia* of various sizes at stations CN-3 and CN-5, May to August 1982.

	CN-3			CN-5		
Size class (mg)	n	Taxa	individuals	n	Taxa	individuals
1-15	31	2.10 ± 0.48	2.87 ± 0.84	30	1.73 ± 0.40	3.17 ± 1.50
16-30	24	3.00 ± 0.57	5.38 ± 1.58	20	2.80 ± 1.07	5.85 ± 4.19
31-50	11	3.00 ± 1.16	4.91 ± 2.56	12	3.08 ± 1.32	5.00 ± 3.51
51-100	14	3.43 ± 1.25	9.57 ± 7.33	12	3.42 ± 1.34	9.83 ± 7.06
101-150	10	1.90 ± 0.79	2.80 ± 1.54	21	4.24 ± 0.59	9.43 ± 5.06
151-250	19	2.00 ± 0.51	3.73 ± 1.40	27	5.03 ± 0.80	15.37 ± 3.81
251-350	10	2.40 ± 0.84	5.40 ± 2.87	8	5.50 ± 1.48	24.25 ± 3.23
>350	11	2.55 ± 1.01	5.91 ± 3.28	0	-	-

Table 4. Mean (± 95% c.l.) numbers of taxa and individual prey eaten by Erpobdella punctata of various sizes from Canagagigue Creek stations CN-3 (n=15) and CN-5 (n=91).

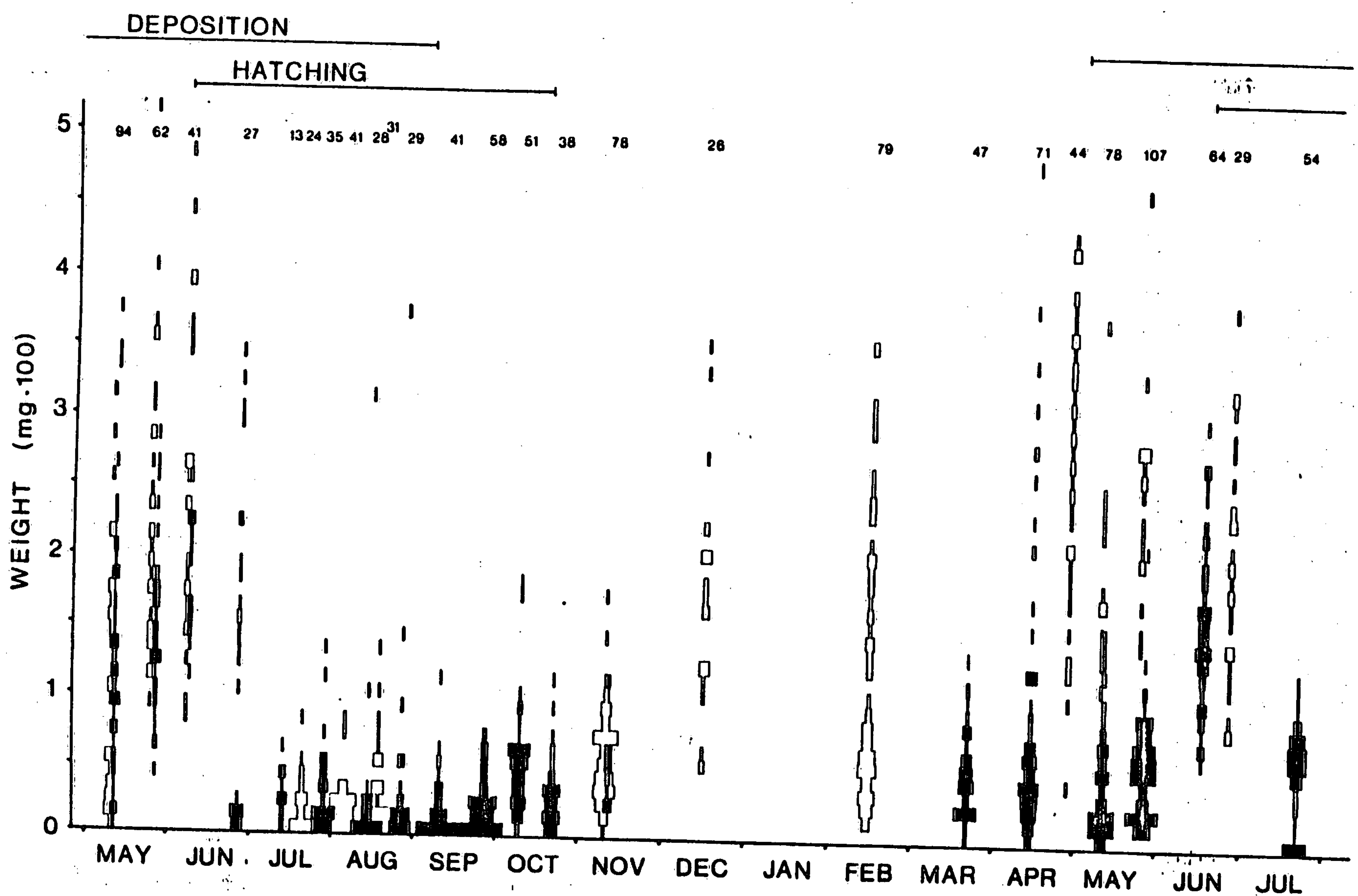
Size class (mg)	n	Taxa	Individuals
1-15	13	0.77 ± 0.33	3.46 ± 1.64
16-30	12	1.66 ± 0.55	4.58 ± 2.30
31-50	11	1.27 ± 0.60	1.82 ± 0.90
51-100	29	1.96 ± 0.48	4.17 ± 1.50
101-200	21	2.28 ± 0.46	3.66 ± 0.84
201-400	10	2.50 ± 0.86	7.80 ± 4.09
>400	10	3.79 ± 0.72	14.30 ± 4.84

Captions for Figures

Figure 1. Numbers and weights of _Dina dubia_ collected from sites CN3 (open symbols) and CN5 (solid) between May 1982 and July 1983. The smallest symbols indicate one animal. Approximate times of cocoon deposition and hatching are also indicated.

Figure 2. Rates of cocoon production by captive _Dina dubia_ (■) and _Erpobdella punctata_ (▲) and daily maximum and minimum water temperatures (•).

Figure 3. Numbers and weights of _Erpobdella punctata_ collected from sites CN3 (open symbol) and CN5 (solid) between May 1982 and July 1983. The smallest symbols indicate one animal. Approximate times of cocoon deposition and hatching are also indicated.


DEPOSITION
HATCHING
WEIGHT (mg·100)
0
1
2
3
4
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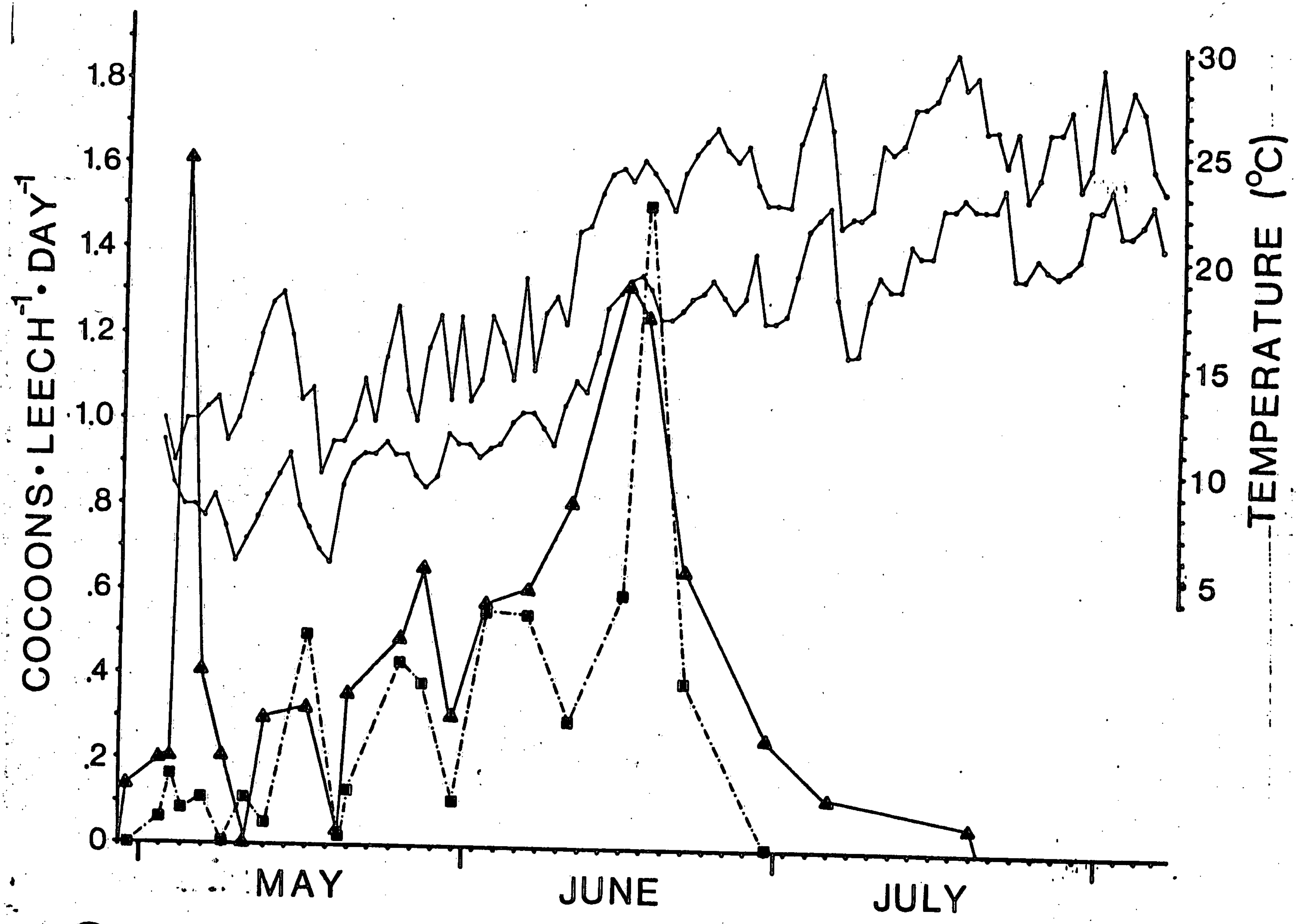
94 62 41 27 13 24 35 41 28 31 29 41 58 51 38 78 26 79 47 71 44 78 107 64 29 54
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL

Fig. 1



COCOONS • LEECH⁻¹ • DAY⁻¹
0
.2
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.6
.8
1.0
1.2
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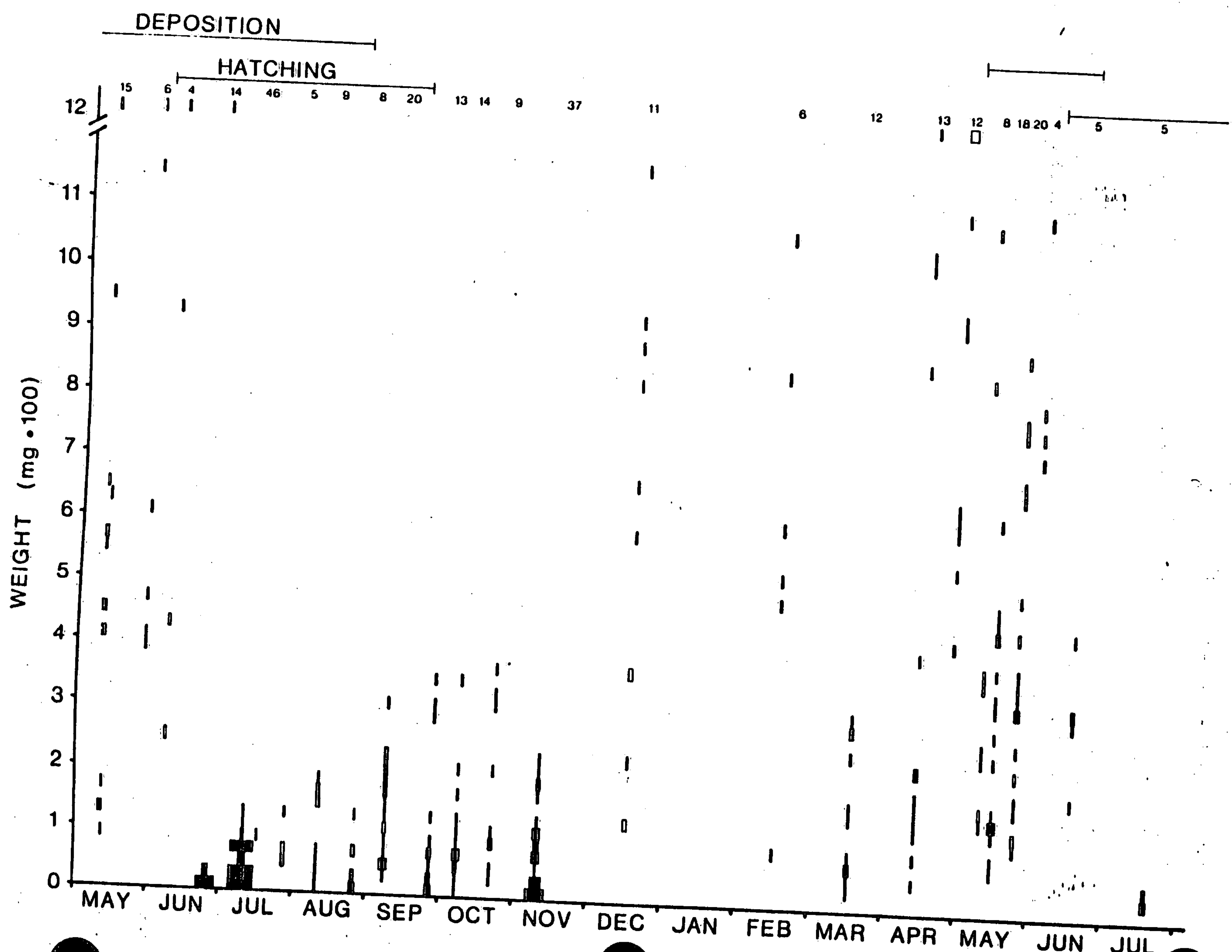
MAY
JUNE
JULY
TEMPERATURE (°C)
5
10
15
20
25
30


DEPOSITION
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