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Title: Population and Production Ecology of Lipsothrix spp. (Diptera: Tipulidae)

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Craneflies of the genus Lipsothrix inhabit decomposing wood in streams. The life cycles and ecological relationships of L. nigrilinea (Doane) and L. fenderi Alexander were investigated to determine how they exploit and respond to the wood habitat and their role in degradation of woody debris in western Oregon. Surveys of the western states and provinces provided data on geographical distribution of the four western species, and a key is given to the five species known from America north of Mexico.

The non-adult stages are spent within single logs, primarily red alder (Alnus rubra), in headwater streams where disturbance by abrasion is minimized. The two species are sympatric in soft logs in constant contact with water. L. fenderi larvae are found in a wider variety of wood types, including harder wood, other species of wood, and in marginal habitats in which they are more susceptible to desiccation and interactions with the semi-terrestrial community. Habitat selection may relate to the specificity of ovipositing females.

Biological and behavioral characteristics of the life stages are described. Both species have a basic biennial life cycle with an ephemeral (1-8 days) adult stage. This long cycle may be possible because because the habitat is relatively predictable and constant. L. fenderi is smaller than L. nigrilinea, and some individuals emerge as annuals, probably in response to an indirect thermal cue in the fall. L. nigrilinea uses combined cues of temperature and descending water level, which more directly predict suitable conditions for emergence in

spring and summer. Some L. nigrilinea take three years or longer if they do not receive the water level cue in a portion of the log. A large degree of variability exists in size of both species, and especially L. nigrilinea, within a single log. Though growth rate differences are correlated with temperature and food quality, variability in timing of oviposition probably accounts for the majority of the difference. The life history traits of L. fenderi are more conducive to increasing reproductive quantity when compared to L. nigrilinea, which may be related to the association of L. fenderi with relatively less predictable habitats.

The mean biomass of L. nigrilinea was near 12.0 mg/100 cm^2, with low variation, while L. fenderi had low biomass in the fall (1.40 mg/100 cm^2) and peaked prior to emergence (12.65 mg/100 cm^2). Wood hardness was the major determinant of larval densities and feeding rates of both species. Egestion rates were estimated at 88% of dry weight per day in firm wood and 223% per day in highly decayed material. Egestion is increased by a factor of two between low (3°C) and high (15°C) temperatures encountered in the field. The total ecological impact will be the greatest where the highest abundance of the most suitable habitat is found, as in small streams during the middle stages of forest succession.

Population and Production Ecology of *Lipsothrix* spp. (Diptera:Tipulidae)

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POPULATION AND PRODUCTION ECOLOGY OF *LIPSOTHRIX* SPP. (DIPTERA:TIPULIDAE)

INTRODUCTION

Small streams are characterized as open systems controlled by the terrestrial community (Hynes 1970). Nutrient cycling and trophic processes within the stream are directly related to the forest canopy which reduces light and thus autotrophic production, and by the consequent introduction of vegetative material into the system. This input drives a heterotrophic community which utilizes and processes the material (Egglishaw 1964, Minshall 1967, Cummins 1973).

In low-order streams of the Pacific Northwest, woody debris is an important component of the allochthonous input. There may be 25-40 kg of wood (>10 cm dia) per m^2 compared with 4 in New Hampshire, 4-8 in Michigan, and 7 in central Idaho (Triska and Cromack 1980). This wood is highly refractory, and small streams lack the power to remove such large-sized material, so it is available to function as habitat and as a nutrient source for a relatively long period.

While woody debris remains in the stream, it is subjected to microbial decomposition, macro-invertebrate utilization and physical reduction. The patterns and mechanisms of these processes have been studied by an interdisciplinary group at Oregon State University and cooperating institutions. Investigations of the macro-organismal component have focused on taxa with potential impact on the mineralization of wood (Anderson et al. 1978, Anderson and Sedell 1979, Dudley and Anderson 1982). Most of the invertebrates are associated with the wood surface, but a group was also characterized that gouged into the wood. The gougers included the caddisfly *Heteroplectron californicum*, the elmid beetle *Lara avara*, and the snail *Juga plicifera* (= *Oxytrema silicula*). Cranefly (Tipulidae) larvae of the genus *Lipsothrix* were collected from tunnels in decayed alder.

Several characteristics of wood in streams appear to make this a unique spatial and nutritional resource. Attendant with its long

residency, wood is a relatively constant and predictable habitat when compared with other benthic substrates. Its toughness may exclude many predators and competitors from the internal portion, as well as reducing abiotic mortality. This toughness makes acquisition and ingestion of food difficult. Wood is also a poor source of nutrients, such that nearly all xylophagous organisms require at least an opportunistic association with cellulytic microbes in order to acquire sufficient energy, nitrogen, and other factors (Ausmus 1977).

The craneflies reported by Anderson et al. (1978) were subsequently identified as Lipsothrix nigrilinea (Doane) and L. fenderi Alexander . They were potentially important in the particle-size reduction of wood due to their habit of burrowing through the wood matrix. The unique qualities of the habitat and its low nutritional value were hypothesized to have resulted in the evolution of specialized life histories. In 1978, I initiated an ecological study of Lipsothrix spp., the objectives of which were:

1. to delimit the distribution of L. fenderi and L. nigrilinea with respect to habitat preferences and restrictions;

2. to describe their life cycles and how population dynamics are affected by environmental variables (e.g., temperature, food quality, water level, resource availability);

3. to study the impact of Lipsothrix spp. in the degradation and material recycling of woody debris, especially alder, in streams of the Pacific Northwest; and

4. to analyze the possible evolutionary consequences of association with the wood habitat, and to compare the life history traits exhibited by these two species in relation to their patterns of habitat utilization.

BACKGROUND

Wood in Streams: Role and Utilization

Wood in streams forms barriers which entrain mineral and organic material beneath or behind barriers (Anderson and Sedell 1979, Bilby and Likens 1980). These barriers also dissipate the energy of the water flow, thereby decreasing its potential to erode and remove material (Heede 1972, Fisher and Likens 1973). Consequently, a greater proportion of the available organic matter may be processed within the immediate stream section (Anderson et. al. 1978, Bilby 1981). Woody debris adds structural complexity to the stream habitat regulating and diversifying channel morphology (Hall and Baker 1975, Swanson and Lienkaemper 1978, Keller and Swanson 1979). In addition, the wood itself provides substrate and a long-term storage source of nutrients. Through all of these mechanisms, nutrient retention is enhanced within the watershed, supporting a larger and richer community of organisms at all trophic levels.

The mineralization of wood results from the action of microbial decomposition, invertebrate utilization and physical degradation (Ausmus 1977, Swift 1977, Triska and Cromack 1980). The magnitude of each component is largely dependent upon the physical character of the watershed. In larger streams, moving water and suspended material abrade surfaces and displace wood to the channel margins (Swanson and Lienkaemper 1978), altering the micro-environment and thus the suitability of the resource to organisms. Conversely, in small streams the lower frequency and intensity of disturbance allows biological processing to continue with less impact from hydraulic action. These first and second order streams contain an order of magnitude more wood as well (Anderson et al. 1978), so it is here that microbial and animal utilization would be expected to be most important.

Microbial processing of wood debris has been more extensively studied for terrestrial than aquatic systems. On land, a rather elaborate successional sequence of xylophilous decomposers has been

described (Shigo 1967). Bacteria are early opportunists and are associated with the wood surface, while a complex of fungi later penetrate into the cortical material. The species and patterns of decay are related to factors such as micro-climate (temperature and moisture) and location (Gilbertson 1980). This sequence is important to the processing which occurs in the aquatic environment because conditioning prior to entry into the stream will determine in part the rate and mechanisms of decomposition within the stream (Triska and Cromack 1980). Of particular significance in this context is attack by polypore dry-rot fungi, which softens the wood (Moore-Landecker 1972) and thus accelerates its degradation in water.

Upon entry into the stream, woody debris is subject to a different array of microbial decomposers. In general, aquatic wood decay occurs at the surface due to the inhibition of oxygen diffusion into the inner tissue. Bacteria, including filamentous actinomycetes, are common on the surface and may play some role (Buckley and Triska 1978, Aumen, pers. comm.). Only in the advanced stages of decomposition will fungal hyphae penetrate deeper than a few millimeters. Common terrestrial forms, such as basidiomycetes are rare (Cromack, pers. comm.), while soft-rot fungi (Savory 1954) and aquatic hyphomycetes may play a dominant role (Jones and Oliver 1964, Willoughby and Archer 1973, Sanders and Anderson 1979).

Microbial conditioning of wood is necessary prior to its utilization by invertebrates for two reasons. First, the refractory lignified tissue is mechanically impenetrable for most organisms. As wood decays, the structural integrity is broken down, making it easier to handle. Secondly, dead wood is a low quality food source, with nitrogen concentrations <0.2% as compared to 2.03% for alder leaves or 6-10% for algae (Anderson et al. 1978). As is the case with leaf inputs (Kaushik and Hynes 1968, Barlöcher and Kendrick 1973, Petersen and Cummins 1979), wood serves as a colonization site and nutrient source for microbes (Ausmus 1977, Swift 1977), which in turn provide nutrition for xylophagous invertebrates (Anderson and Sedell 1979, Martin 1979).

Feeding activity then increases the surface area available to the microbes and inoculates newly-opened habitats.

Anderson et al. (1978) identified 40+ invertebrate taxa which potentially had a role in the processing of stream wood. Dudley and Anderson (1982) extended this list to 185+ taxa. They discuss several modes of association with wood, ranging from casual use as substrate to obligate use of a single log, at least through a large part of the life cycle. It may provide a substrate for filter-feeding (Wallace and Sherberger 1974), pupation, emergence, for refuge from predators or physical disturbance, and for resting. In many streams with unstable substrata, firmly anchored logs and branches may provide a solid habitat for many organisms. While some scraper-grazer and collector-gatherer taxa utilize the wood surface for its periphyton and accumulated detritus (Pereira 1980), others ingest a portion of the wood tissue along with the aufwuchs material. Pereira et al. (1982) analyzed the gut contents of a wide range of aquatic insects collected from wood and indicated that their role in this habitat could be determined by the proportions of wood, diatoms and other forms of organic material in the guts. The guts of those considered to be obligate xylophages were consistently packed with wood fragments. These species are likely to play a significant, and possibly the dominant, role in the wood processing attributed to invertebrates. However, it is in the final stages of wood decomposition that one finds a large component of the wood community made up of relatively restricted organisms, especially tunneling forms. These belong primarily to the order Diptera (Teskey 1976, Dudley and Anderson 1982). In certain settings, Lipsothrix spp. may be dominant tunnelers (Rogers and Byers 1956, Anderson et al. 1978).

In headwater streams microbial and invertebrate succession are allowed to proceed without attenuation by disturbance. In such situations, there is no longer a clear distinction between aquatic and terrestrial processes, and much of the wood remains exposed yet moist for most of the year. The residency of this wood is related to its size, chemical composition, prior conditioning, as well as to the environmental parameters to which it is exposed. Some material is small

enough to be readily removed, while other pieces may remain in the channel for long periods, certainly more than 100 years in some cases (Triska and Cromack 1979). Thus, one would expect to find that the xylophilous communities predominate in these small streams.

It is expected that organisms adapted to life within well-decomposed wood will have evolved life history adjustments in relation to the unique characteristics of their habitat (Anderson et al. 1978). Those ecological determinants include tissue toughness, low food quality (relative to other resources available in the stream), long-term availability and habitat stability. Logs will undergo less thermal fluctuation throughout the year than the surrounding environment. (Savely 1939), and moisture level remains near saturation. A log occurs as a discrete unit and for organisms which cannot tolerate conditions outside for the majority of their life cycle, their habits must be oriented towards survival within this strictly delimited patch (Hamilton 1978).

Biology of Tipulidae

The family Tipulidae is the largest dipteran family (Byers 1978) with 1458 species recorded from the U.S. and Canada (Stone et al. 1956). Most craneflies are closely associated with water or moist terrestrial situations (Alexander 1920). Though Byers (1978) lists 34 genera in his key to aquatic tipulids, only a few of these are truly aquatic, and those that live in water typically move to shore for pupation (Rogers 1933, White 1951).

The biology of the Tipulidae has been reviewed by Pritchard (in press). There is little quantitative life history information on tipulids because most species, except for some grassland dwelling species of *Tipula* (Milne et al. 1965, Meats 1974, Myers and Iyer 1981), are not of economic importance. *Tipula abdominalis*, is a dominant leaf shredder in Michigan streams, and has been used in studies of growth and feeding in relation to food quality (Cummins et al. 1973, Petersen and Cummins 1974, Cummins and Klug 1979).

The tipulid life cycle begins with a short egg stage, the egg generally hatching within two to four weeks of oviposition (Rogers 1933). Egg diapauses are known, but are rare (Butterfield 1976b, Hartman and Hynes 1980, J. Gelhaus, pers. comm.). Egg morphology is reviewed by Hinton (1981). There are four instars (Hadley 1969), the first three quite rapid while growth slows in the fourth (Laughlin 1960, den Hollander 1975, Pritchard 1976). Synchrony of emergence is achieved in response to temperature (Meats 1975) or photoperiod (Butterfield 1976a). There are frequently more male adults collected than females (Barnes 1937, Freeman 1964, Hemmingsen 1965), possibly related to greater female mortality (Hadley 1971, Pritchard 1976).

Craneflies typically have a one-year life cycle, but timing may be constant in some species, while others show considerable variability. Differences in temperature can result in a species which is bivoltine in one region being capable of only one generation per year at a higher altitude or latitude (Brown and Duncan 1949, Nielsen et al. 1954, Coulson 1959, Freeman 1964, 1968). Two year life cycles may also result in this way (Hofsvang 1972, Brindle 1960), and extreme cases in the arctic of three years for two species (MacLean and Pitelka 1971) and four to five years for Pedicia hannai (MacLean 1973). An interesting case is the situation in which larvae of T. sacra from the same cohort emerge in different years, due to differences in growth rates (Pritchard 1976, 1978, Pritchard and Hall 1971).

The genus Lipsothrix is included in the subfamily Limoniinae. The five species known from America north of Mexico are all xylophages. Hynes (1965) described the larvae and pupae of the four western species, L. fenderi, L. hynesiana Alexander, L. nigrilinea and L. shasta Alexander. The biology of L. sylvia Alexander, a species found in headwater streams of the Appalachian region, was studied by Rogers and Byers (1956). The only other literature on the American species of Lipsothrix is of collection records (Alexander 1949, 1954, 1964).

Other craneflies have been found in wood (Alexander 1931, Rogers 1933, Savely 1938, Snow 1953, Wood 1952, Rogers and Byers 1956, Larking and Elbourne 1964, Teskey 1965, Hinton 1981). Although a few of these

occur in stream wood, there is little information on their habits or life cycles. Hinton (1955, 1957, 1967) studied the spiracular gills of pupae in two European species of Lipsothrix. The pore-bearing surface acts as a plastron for diffusion of dissolved oxygen into the trachea. Winterbourn (1980) and Anderson (in press) describe the habitat of Limonia nigrescens, a xylophagous species in New Zealand with many traits that are very similar to Lipsothrix.

MATERIALS AND METHODS

Field Analysis of Habitats, Habits and Life Cycles

The life histories of both L. fenderi and L. nigrilinea were largely unknown prior to this study so it was necessary to spend considerable effort on observations and descriptive ecology. Field surveys were conducted at two levels, with extensive collecting in several geographic regions and a more intensive analysis in areas of western Oregon. Field work was performed in conjunction with an on-going study of the invertebrate fauna associated with wood in streams. Regional sampling was conducted in streams and other aquatic habitats associated with many forested regions of the western states and British Columbia. Included were the Olympic Mountains of Washington; the Coast Range 60 miles north of Vancouver, British Columbia; the Willamette Valley, and the Coast, Cascade, Blue, Ochoco, Strawberry and Siskiyou Mountains of Oregon; the Coast Range, Sierra Nevada, and southern Cascades of California; and the northern Rockies of central Idaho and Wyoming (see Dudley and Anderson 1982). L. sylvia were obtained in Pennsylvania by the author and in North Carolina (Coweeta Experimental Forest) by N.H. Anderson.

At a given site, pieces of wood were removed from the water and probed with forceps and a pocket knife. Any Tipulidae larvae found were placed in alcohol, along with a bit of the wood and any associated organisms. Macro- or micro-habitat characteristics which might relate to the presence or absence of Lipsothrix spp. were measured or observed at each site.

Macrohabitat characteristics included the dominant overstory vegetation, the percent canopy cover was visually estimated, and the amount of wood debris (as surface area available/100 m section) in the stream. Other physical factors noted were directional orientation of the watershed, elevation, water temperature, average channel width and estimated stream order. A subjective evaluation of habitat stability was made based on substrate type, erosion and water level fluctuation.

Finer resolution habitat parameters were species of wood, its state of decomposition or decay class (see Table 2), and the toughness or hardness of the material. The orientation of the log was noted as was its extent of submergence and associated benthic substrates. Biological microhabitat characteristics included the portion of the log inhabited by larvae, the depth of penetration by each larval size class, and the density of larvae per unit of wood surface area.

Identification of wood species was often difficult due to decay-related alterations, but a separation was made at least to coniferous or broad-leafed wood. The decay class scheme is a means of estimating or averaging a general condition of the substrate by comparing several characteristics of decay. Hardness is important because it influences oviposition, feeding rate, and abrasion. A penetrometer was fashioned from a spring and hypodermic needle to quantify hardness, but due to local heterogeneity in a log, decay class gave an adequate and simplier index of hardness.

The intensive field sampling was necessary to determine the life cycle patterns of the two species. A series of streams was sampled approximately monthly in the Coast and western Cascade Ranges of Oregon from fall 1977 to spring 1979. Streams were chosen at 10-15 mile intervals to represent a range of elevations and habitat types (Fig. 1, Table 1).

Sampling consisted of removing with a pocket knife a piece of wood about 10 x 10 x 2 cm. The size varied somewhat, but an attempt was made to collect about 100 cm^2, based on surface area. One to three logs were sampled at each site, and, if possible, the same log or logs were used on each occasion. The material was placed in plastic bags and frozen in the lab for later analysis. The frozen samples were thawed, broken or cut, and picked through under a dissecting microscope to isolate organisms. Fragmented material was placed in a pan of water in which remaining larvae could be more easily seen. It is likely that despite thorough searching there was some bias favoring larger animals. Lipsothrix larvae and pupae were removed to a separate container for weighing, and other taxa were enumerated unless they were abundant

enough to consider for life cycle analysis (e.g. Austrolimnophila badia, Xylophagus sp. - see Appendix 5). Larval densities were estimates as the number per surface area of inhabited wood.

Instars could not be distinguished because tipulid head capsules enlarge during each stadium (Freeman 1964, Hemmingsen 1965, Pritchard 1976) and are withdrawn into the thoracic region. Dry weights of individuals were thus used to interpret population growth dynamics at each field site. Larvae were oven-dried at 60°C for at least 48 hours, and weighed on a Cahn electrobalance (Model 4100).

For some experiments requiring live weights, excess water was removed by placing larvae on a paper towel for 30 seconds prior to weighing.

The monthly field samples were also analyzed to estimate sex ratios. During the emergence period, sex could be determined from pupae, and from pupal exuviae which remain with the log after adults emerge. The sex of larvae could not be determined as in Pritchard (1976). Instead, logs were brought in from the field and the proportion of males and females determined from reared pupae or adults.

Experimental Procedures for Laboratory Rearing

To substantiate growth and development trends and phenomena observed in the field, larvae were reared in the laboratory. Examination of feeding rates, larval and adult behaviors, and biotic interactions also required lab conditions. The basic methodolcgies are described here and more detail is given in the Results section for various experiments.

Natural Substrates. The most direct method for rearing was to bring logs or pieces of wood into the laboratory. The wood was kept saturated but largely exposed to air because larvae are sensitive to low oxygen tensions and will leave the wood if kept in standing water which is too deep. Larvae could be maintained either within their habitat or free from wood by aerating the water. Most rearing was done in a controlled-environment room at 15°C with a 16-hour light cycle.

Despite the ease of handling, the use of natural substrates poses several technical difficulties. Larvae cannot be observed due to their sub-surface habits, and the habitat must be destroyed in order to sample them. In the process of removing larvae from a log, many are injured so that the sample size is further reduced by the sampling procedure.

Artificial Media. An artificial medium was prepared in order to maintain more controllable experimental conditions. Soft wood that had been inhabitated by Lipsothrix larvae, but was not overly decayed, was processed for approximately five seconds in a Waring blender. This reduced the material to a fairly homogeneous texture, while maintaining some structural integrity so that mastication was still necessary. Water was added or filtered off to obtain a medium that was fully wetted but without excess water. The resulting cake was lightly patted into a petri dish to provide a layer 4-5 mm deep. Placing the medium into capillary tubes (2 mm dia.) or between glass plates was unsuitable because introduced larvae escaped or died from oxygen deficiency.

The qualities of this medium could be manipulated by using different wood types, culturing at different temperatures, or by the addition of nutrients, antibiotics, or excess water. For some experiments greater cohesion was obtained by the addition of agar. A solution of 2 agar:100 water (by weight) was mixed into warm wood medium. Just enough solution was used to congeal the mixture. Larval densities and species composition were also manipulated in the wood medium.

Obtaining and Handling Experimental Animals. Larvae were obtained by bringing in logs from the field and cutting the logs open. Much time and care were expended in exposure and removal, yet I rarely achieved 50% survival due to wounding or other stress. Larvae were first placed in a pan with shallow water for 1-2 days before introduction into experimental dishes so that dead or stressed individuals could be removed. During this period larvae cleared their hindguts, which was important for growth and feeding experiments.

The test animals were placed into the dishes and covered. They generally bored into the medium immediately. The preparation was not disturbed through the course of an experiment. When an experiment was terminated, larvae were removed by dispersing the media in water. Handling is thus easier, and more controlled, than it was with natural substrates.

Rearing from the egg stage was attempted. Adults which emerged in the laboratory could be induced to oviposit into wood, the rearing medium, or on a wet paper towel. Lab oviposition was only moderately successful due to the small numbers of eggs oviposited and high egg mortality. Artificial insemination was also attempted by macerating the terminal abdominal segments of the male and mixing this with unfertilized eggs (after Fremling 1967), but no development was observed in the eggs.

Laboratory Studies of Growth and Feeding

Growth Rates and Developmental Patterns. The effect of temperature was studied by cutting each of six Lipsothrix-infected logs into four pieces, and placing these in pans with water in controlled-temperature chambers at 3°, 8°, and 15°C. One series was frozen as a control for initial conditions. After the desired period, the wood was cut open, and the animals removed, dried and weighed.

Food quality may be altered by thermal enhancement of microbial production, so two replicate experiments were conducted, using the prepared medium, to separate temperature and food quality effects on growth. A block design was used in which larvae were reared at different temperatures and concurrently, the standard media were manipulated at a constant temperature by addition of a nutrient solution. In some cases, antibiotics were added to retard microbial growth, and also blended wood of different types and qualities were used.

The effect of temperature on induction of pupation was tested using the standard medium, but in 100 ml jars rather than petri dishes. Large

larvae were placed 1°, 3°, 8°, and 15°C and examined daily to determine the date of pupation. The possible interactive effect of moisture was studied by adding excess water to one of the pair of treatments at each temperature.

To test the hypothesis that water level might play a role in the induction of pupation, standard samples were collected from above and below low water level at two of the field sites and analyzed separately to compare development of pupae. The effect of submergence was also tested in artificial streams at the Oak Creek Aquatic Entomology Laboratory during the typical emergence period of each species. Two logs containing L. fenderi were cut into halves and one of each pair set 70% submerged and the other 10% submerged. A cage was placed over the set-up so that adults could be collected. The same was done for L. nigrilinea, except with one log cut into three sections and held 20%, 50%, and 80% submerged.

Feeding and Processing Rates. Experiments were designed to examine the role of Lipsothrix spp. in the degradation of wood of different qualities. Ingestion rate per se could not be determined accurately, but was not critical to the degradation studies. The important effect was the combined impact of disruption of wood by passage through the gut and the sloughing of wood particles due to larval activity. Temperature, food quality and toughness were factors which were considered.

Frass is often eliminated to the log exterior. By collecting the frass, or by spraying the log with a wash bottle at regular intervals, one could estimate larval impact. Frass collecting was done in one experiment with logs held at 2°, 9° and 15°C and outdoors (February through April). Another experiment involved spraying logs held at 3°, 8° and 15°C. These were the same logs used to study larval growth rates. Using larval biomass values from that study, processing could be expressed per gram of animal tissue. A third experiment designed to study larval impact involved the use of the agar/wood medium. Larvae were introduced into a series of treatments manipulating wood type,

nutrients, temperatures, and after a set period of time the petri dishes were sprayed with the wash bottle. Loosened material was filtered and dry-weighed to indicate processing or larval activity.

Field Studies

Colonization and Growth in Non-Colonized Wood. Uninfested wood was distributed to 35 small streams to assess the colonizing abilities of L. fenderi and L. nigrilinea. Decayed alder logs were obtained from a moist terrestrial site, where fungal conditioning was appropriate and neither larvae nor eggs of Lipsothrix would occur. The logs were cut into pieces approximately 15 x 15 x 40 cm. Each was positioned in a stream so that a portion was above water to allow oviposition, while remaining partially submerged during low water.

The streams selected for the colonization study were in the Coast and Cascade Mountains from 10 to 1800 m elevation. Vegetation types included old-growth and second-growth Douglas fir stands, young and mature alder groves, and clearcuts. Logs were distributed in April 1977 and removed in October 1977, when density and biomass of larvae were determined.

Processing Rates. To corroborate the lab studies of processing rates, I attempted to determine field processing rates in logs of various qualities in the presence and absence of Lipsothrix. The non-infested logs were cut in half, air-dried and weighed. Photographs were taken for before and after treatment comparisons. The logs were set into slow riffle sections of Berry Creek, approximately halfway submerged to allow oviposition. Berry Creek is a controlled-flow stream (Warren et al. 1964), so it was expected that current would play a relatively small but seasonally constant role in wood degradation.

The experimental half log was exposed to oviposition while the control portion was covered with screen to inhibit oviposition. The screen was stapled to a wood frame and propped so that it touched neither the log nor the substrate allowing normal current flow around

the log. The cages were removed from November to April when Lipsothrix adults were absent, so that all logs would be similarly affected by extrinsic factors such as rain splash and the presence of other detritivorous organisms.

The experiments included three pairs of freshly cut alder, three pairs of solid but seasoned alder with bark intact, four pairs of highly decayed alder, and one pair from a dry-rotted branch. All logs remained in the creek from August 1977 to November 1979. Logs were dry-weighed before and after treatment, to give an index of degradation due to Lipsothrix. In addition, portions of the outer surface of the logs were removed and wood densities compared by dry-weighing and estimating volume by water displacement. This technique was employed to indicate some impact differences which were not apparent from whole log weights.

The above experiment served to roughly estimate degradation rates of woods of different qualities in the field. This may relate to the time required for wood to decompose to the next decay class. Such processes are complex, involving microbial activity, invertebrate processing, and erosive factors. To examine the role of erosion, alder wood of three decay classes was maintained in artificial streams at Oak Creek. They were placed at three levels of submergence, fully and half submerged, with the third just at water level. No animals were allowed to colonize, though microbial differences potentially existed, and dry weights were compared before and after.

Studies of Adults

The behavior of several adults was observed in cages in the lab. Cages were 20 x 20 x 60 cm wood frames covered with Nytex® mesh and with a sliding glass front. These were used for studies of emergence, orientation, courtship and mating, oviposition, feeding and other activities.

Adults that emerged in the lab were released in the field for observation of flight behaviors. Additionally, 60 sticky traps, constructed of plastic-coated (20 x 30 cm) cardboard covered with

Tanglefoot®, were hung at different heights above, and distances from, Berry Creek. By capturing adults I hoped to examine some aspects of dispersal behavior, especially whether there was any orientation with respect to the stream the juvenile habitat.

The reproductive efforts (sensu Price 1974) of L. fenderi and L. nigrilinea were compared as a measure of the importance of direct reproductive allocation. Size and numbers of eggs per female were found by dissecting the ovarioles from post-teneral adults that emerged in the laboratory. The egg mass, ovipositor and other reproductive tissues were dried and weighed separately of the rest of the other organs. Male allocation was estimated by removing the final two abdominal segments which bore the genitalia and other reproductive organs. A comparative assessment of female reproductive behavior was made based on observations of the two species and on oviposition habits and site preferences of adults provided with various materials in cages or under screens in the artificial streams.

RESULTS AND INTERPRETATION

CHARACTERIZATION OF ORGANISMS AND HABITATS

Keys to the Immature Stages of the North American Species of the Genus Lipsothrix

The keys to the larvae and pupae are modified from Hynes (1965). General distributions of the four western species are shown in Fig. 2, and county distributions of L. fenderi and L. nigrilinea from Oregon in Fig. 3. All five species are found tunneling in sodden, partially- or well-decayed wood associated with forested headwater streams.

Larvae:

1. Spiracular disk with lobes expanded; creeping welts clearly evident and bearing gold or dark pile (Fig. 4).....2
   Spiracular disk with lobes forming a terminal cone; creeping welts not obviously expanded and pile not apparent (Fig. 6).....4
2. Anal lobes with elliptical, bulbous expansions (Figs. 4, 8b).....3
   Anal lobes with no bulbous expansions (Fig. 8a); Coast R., N. California..... hynesiana
3. Spiracle with a darkened central area; pile on creeping welts brown, thoracic integument darkened (Fig. 4); Coast and Cascade Mts., C. Washington to S. Oregon, Wallowa Mts. .....nigrilinea
   Spiracle without a darkened central area; integument and pile light or golden; N. California and S.W. Oregon.....shasta
4. Anal lobes subequal in size; eastern United States.....sylvia
   Anal lobes with anterior pair 5 or 6 times longer than posterior set (Fig. 6); Coast Range - S.W. British Columbia to C. Oregon, W. Cascades - Washington and Oregon.....fenderi

Pupae:

1. Breathing horns cuplike, with dorsocephalic edge of each horn extending forward (Figs. 6, 8i-k).....3
   Breathing horns without such extension (Fig. 8g,h).....2
2. Anterior edge of horns crenulate; apices of the leg sheaths extend to middle of abdominal segment IV (Fig. 5, 8h).....nigrilinea
   Anterior edge of horns not crenulate (Fig. 8g); apices of leg sheaths to posterior margin of abdominal segment IV..... shasta
3. Dark seam extending from dorsal base to forward extension of breathing horn (Fig. 7)..... fenderi
   Dark seam extending from dorsal base past forward extension to the ventrocephalic margin of the breathing horn.....4
4. Dorsocephalic extension pointed or acute (Fig. 8k).....sylvia
   Dorsocephalic extension rounded (Fig. 8j).....hynesiana

No further reference will be made to L. sylvia, L. shasta nor L. hynesiana. The macrohabitat characteristics of L. fenderi and L. nigrilinea will first be covered, followed by discussion of the finer scale aspects of their ecological relations.

Habitat Characteristics of Lipsothrix nigrilinea

Geographic Distribution. In western Oregon this species occurs generally throughout the Tsuga heterophylla region as defined by Franklin and Dyrness (1973). Larvae were collected from near sea level to 1100 meters in the Cascade Mountains. Only two collections have been made east of the Cascade crest (Fig. 3), even though >50 streams were sampled. Both of these were from streams in relatively mesic mixed-conifer forests with a well-developed hardwood riparian zone.

Larvae are found in headwater streams, as in Figure 9. Only four third-order (Leopold et al. 1964) streams studied were inhabited from ten times that many examined, and only in places where wood debris had washed down and accumulated out of the main current. In the smaller

streams, suitable wood is scattered more randomly along the watercourse. Typical L. nigrilinea streams are low gradient (<4%), but larvae are also found in wood in steep hillside seeps. Larvae were never found in wood covered with silt, so logs in the water must be subject to significant flow. This may account for their absence from floodplain streams in the Willamette Valley.

A factor which appeared to be an important distributional determinant was constancy of streamflow. The wood must remain saturated all year yet be protected from severe and frequent disturbance. This factor is a probable reason for the general absence of L. nigrilinea in the rain-shadow region east of the Cascades and in other drier regions. In these areas there is often a large seasonal fluctuation in water level (USGS, 1978). Both high and low flows will leave wood uninhabitable, by abrasion or by desiccation. The anomalous central and eastern Oregon collections were from streams where flow level remained nearly constant year-round, as was evident from the relatively undisturbed vegetation along the stream banks. The stream near the Metolius River (Jefferson Co.) illustrates this because there is extensive spring activity in this area which maintains consistent flows.

Local Distribution. Although Douglas fir (Pseudotsuga menziesii) and other common conifers (western hemlock - Tsuga heterophylla, western red cedar - Thuja plicata) are the predominant types of wood debris in western Oregon streams, no larvae were found in them. Red alder (Alnus rubra) was the most common host material, but big leaf maple (Acer macrophyllum) was occasionally inhabited. White alder (Alnus rhombifolia) is probably utilized where it occurs, but because of identification problems it is lumped with red alder in this study. Identification of decayed wood is extremely difficult, but identity can often be inferred from the riparian vegetation or from portions of the log which extend into the terrestrial environment. I estimate that 95% of the L. nigrilinea collected were from alder. L. nigrilinea was only collected from one coniferous wood; several very large larvae were found

at low densities (<1/200 cm^2) in decayed western red cedar from an old-growth stream where no hardwood material was available.

The altitudinal limit appears to be related to suitable habitat, as alder is rare and/or scrubby at 1100 m, and big leaf maple is absent. Shrub-like trees such as vine maple (Acer circinatum), Sitka alder (Alnus sinuata), and willow (Salix spp.) were not colonized. This unsuitability may be due in part to the small size of the stems, although larvae have been taken from alder pieces <2 cm dia. at lower elevations.

Wood must become appropriately conditioned before it is suitable for Lipsothrix colonization (Table 2, Fig. 10). The conditioning period necessary upon entry into the stream depends on the previous history of the log. Fresh wood remained submerged with minimal erosion for at least two years before becoming habitable (this study, and Anderson, unpublished data). From personal observations, wood which initially decayed terrestrially was suitable after one year in the stream. This wood appeared uniformly dark while water-decayed wood was only stained near the surface. Wood which initially underwent decay in a moist terrestrial site was dark, or grey-colored, often had a fibrous texture and felt somewhat slimy. This type of wood also required about one year of conditioning, though it was frequently not utilized by L. nigrilinea. Wood that undergoes dry rot while still standing is very soft and is suitable for oviposition and larval colonization upon saturation.

Relationship with Forest Successional Stages. As part of the general field survey, 'suitable' wood was sampled from streams in vegetation types representing the seral stages of forest succession. L. nigrilinea larvae were found in recent clearcuts (with young alder present), older clearcuts (>15 years following cutting, alder mature), second-growth Douglas fir forests (alder dying out), and old-growth conifer forests. Larvae were rare if the second growth forest was a nearly pure stand of Douglas fir with very little hardwood present. Six recent clear cuts which had been burned yielded no larvae. In natural

open areas, such as meadow streams, they are present but not common, being found in only one of eight sites sampled.

Figure 11 presents the data from the colonization experiment in which preconditioned alder logs were transported to a variety of habitat types. Ten logs, including most at higher elevations, were lost or unavailable to animals. High colonization rates occurred in all treatments but densities of larvae differed between treatments. The densities in old-growth and recent clearcut sites are not significantly different, while densities increase significantly during forest maturation. With advancing maturity, and loss of alder, the densities then decrease. The number of colonists would appear to be related to the amount of suitable habitat in the channel, and thus to the number of adults in each vegetation type.

Habitat Characteristics of Lipsothrix fenderi

Geographic Distribution. This species is also associated with small streams of the Tsuga heterophylla region of western Oregon. While its range does not extend to the more xeric forests of southern Oregon and east of the Cascades, L. fenderi apparently occurs further north than does L. nigrilinea. It extends into the cooler coastal streams of southern British Columbia (Figs 2, 3). This species is common near sea level and the highest collection was from 900 m in the Cascades.

Within its range, L. fenderi inhabits nearly all of the streams where L. nigrilinea occurs as well as habitats unsuitable for its congener. These include non-flowing seeps and intermittent, but moist, first-order streams. L. fenderi were collected from silt-laden emergent logs in slow-moving or isolated backwaters of the South Fork of the Hoh River, a sixth-order stream with a wide flood plain in Olympic National Park, Washington. This species was therefore expected, but not found, in the floodplain streams of the Willamette Valley. The transect stream with a morphology most similar to valley streams, Watkins Creek, was inhabited almost solely by L. fenderi. Disturbance from high waterflows has a limiting influence which is probably similar for both species.

Local Distribution. In streams where both Lipsothrix species occur, there is considerable spatial overlap within a log. However, L. fenderi has often been found in logs or portions of logs further above low water level. For instance, an 8-cm dia. branch which extended from the stream showed a clear pattern in which L. nigrilinea had emerged from the lower portion, L. fenderi was emerging primarily from a section extending 15 cm above this, and a third cranefly, the semi-terrestrial Austrolimnophila badia, was above the others (Fig. 12). All zones intergraded. Questions of resource overlap are considered in a later section.

Saturated alder is the predominant wood type inhabited (about 90% of collections) but there appears to be considerable opportunism in habitat utilization. L. fenderi larvae were collected at least five times from decayed Douglas fir and as many times from identifiable big leaf maple. When individuals were found in coniferous wood, alder wood was also available and inhabited by high densities of the craneflies.

The size of logs utilized and the time required before they are suitable for colonization appeared to be the same as for L. nigrilinea. However, each log exhibits considerable patchiness as a result of orientation to the water, contact with other substrates, microbial decay, and other factors. Because of the relatively catholic habits of L. fenderi, a greater proportion of a given log may be utilized than is the case for L. nigrilinea.

Relationship with Forest Successional Stages. General sampling showed that L. fenderi occurs in the four major successional stages. However, it was uncommon in old-growth situations, having been present in only four out of $\geq$15 sites sampled. Though alder is uncommon in old-growth, wood that appeared suitable in some of these streams yielded no larvae. Thus, it seems that L. fenderi is less capable of maintaining populations during periods of lowered resource abundance than is L. nigrilinea.

The preconditioned colonization logs were retrieved before the winter floods and maintained in artificial stream channels to allow L. fenderi eggs to hatch and larvae to grow until they were large enough for identification. A severe freeze disrupted this experiment, but remaining material indicated that colonization patterns were similar to those of L. nigrilinea (Fig. 11). Probably the only difference is that the old-growth treatments had the lowest colonization, as expected from the general surveys.

Biology and Behavior of Lipsothrix spp.

Many aspects of the biology of Lipsothrix nigrilinea and L. fenderi are similar, so this section is presented for Lipsothrix spp. Specific differences will be compared and discussed where appropriate.

Eggs. No Lipsothrix eggs were recovered from the field, so observations were based on eggs dissected from females or deposited in the laboratory. The eggs are cream-colored, oval-oblong but flatter on one side, and lack the stalk which is found on many cranefly eggs. There seems to be an adhesive substance associated with the surface which causes them to adhere to wood, although they are generally deposited under the wood surface. At 15°C eggs hatched in 18-28 days.

L. nigrilinea eggs are deposited from April through August. The dimensions are 0.050 mm by 0.025 mm, with an average weight of .012 mg (averaged from clutch weight divided by no. of eggs for 8 clutches, C.V. = 12.5%). L. fenderi eggs are deposited from September through November. There may be a facultative winter egg diapause since very few small larvae were found in the winter. The eggs of this species are slightly smaller, 0.045 mm by 0.025 mm at an average weight of .009 mg (7 clutches, C.V. = 5.5%).

Larval Morphology. Lipsothrix larvae are wormlike, being more slender and formless than typical tipulid larvae (Figs. 4, 6). Larvae are nearly terete with ventral creeping welts bearing numerous minute

spines (Byers 1978). Like many Diptera associated with wood, the body is largely without rigid features other than the heavily sclerotized head capsule (Teskey 1976). The mandibles are developed into strong gouging organs with three teeth (see Fig. 39).

Maximum body length of L. nigrilinea is near 30 mm with a head capsule approximately 2 mm wide. The compact thoracic segments are slightly expanded. L. fenderi is more slender at 1 mm wide while the length may be over 35 mm when relaxed. The cuticle is callow-colored and more easily torn in L. fenderi.

There are two spiracles on the posterior spiracular disc as in most tipulids. These may function as secondary gills by a plastron mechanism as in aquatic species like Tipula sacra (Pritchard and Stewart 1982). Two pair of finger-like papillae are located just antero-ventral to the disc, which, along with the anal lobes, may facilitate respiration (Pritchard in press). L. nigrilinea has compact structures, while the upper pair in L. fenderi is much elongated and trails behind the body. The anal papillae and thin cuticle may allow L. fenderi to live in more poorly oxygenated habitats than L. nigrilinea.

Little work was done with the very early stages. However, observations of eggs deposited on wet paper towels indicated that upon hatching, larvae swell to about four times their size by absorbing water. They then begin to feed and bore into the wood or under the paper towels. The mandibular teeth are not well-differentiated at this stage.

Location Within the Wood Habitat. The depth at which larvae occur is dependent on the size of the individual and the decay state of the wood. Small and medium larvae are found in the outer 5 mm of wood which is typically in decay class 5. Larger larvae are generally 5-15 mm below the surface. They are deepest in class-5 and class-4-m wood. L. fenderi has not been found deeper than 15 mm, while large L. nigrilinea may be up to 30 mm deep. At this depth, the wood is often more firm and not discolored. The larvae may inoculate this wood with fungi and

bacteria because there is generally some fungal stain radiating from the larval gallery.

The majority of collections and the highest densities of L. nigrilinea were from class-4 and 5 wood, which had typically experienced dry-rot before entry into the stream. Alder that has either fallen in fresh or has rotted in a moist terrestrial site is more fibrous in texture, highly discolored, and is much harder below the easily removed surface material. Such wood will be in decay classes 3 and 4-f. L. nigrilinea larvae from this material did not tunnel as deep, nor attain the size of those in the softer types. They comprised less than one quarter of all collections. L. fenderi are found in the same types of wood as L. nigrilinea but, in contrast, over 50% of the total collections were from wood in decay classes 3 and 4-f.

Larvae are often in the spring wood, or next to a layer which is formed by a wall-like front associated with the advancing zone of fungal colonization. This orientation might be due to the relative softness and ease of mastication of this wood. The fungal front and the winter wood are harder and could serve as a protective shield against erosion. L. fenderi is especially common up against harder surfaces, and 35-40% of the collections were from soft wood immediately under the hard outer surface layer. In petri dishes they would bore to the bottom and remain against the glass, while L. nigrilinea would be located throughout the medium.

By living within the wood, Lipsothrix is also buffered against other environmental parameters. Savely (1939) showed that the internal terrestrial wood environment remains cooler than air or the log surface during high temperature periods and warmer when the air is cold. Wood which is emergent from the water often freezes superficially. Residual heat or heat of microbial respiration keeps the internal portions unfrozen. Frozen larvae of both species have been found in the winter in logs where larvae survived in deeper tunnels. All dead individuals were within 0.5 cm of the wood surface. On the other hand, when the summer air temperature was 33°C and the stream water 16°C, the inhabited portion of a log (at 1.0 cm) was 13°C. No larvae were observed to die

due to high temperatures, but respiratory costs may potentially be increased.

Larval Gallery - Locomotion and Orientation. A tube-like, non-branching gallery oriented approximately in a plane with the log surface is formed by larval feeding (Fig. 13). It is no wider than the larva within. Galleries longer than 15 cm were uncommon, but it was difficult to accurately follow a galley because it tends to wind extensively. Several galleries may be in close proximity, but they do not appear to merge. Only one individual is found per gallery, although some L. fenderi have been found which could potentially contact each other. The gallery opens to the surface, but in the field this opening is difficult to observe.

A slight taper may be apparent towards one end of the gallery, possibly because it was bored when the larva was younger. There is an abruptly wider, apical section of the gallery of large L. fenderi. The larva will often be found doubled over within. L. nigrilinea do not turn around but remain with the head directed forward.

Larval locomotion involves slow peristaltic contractions which force the setae-covered creeping welts against the walls of the gallery. Larvae removed from the gallery are clumsy and their movement is ineffective.

Feeding. Larvae feed by extending the head out of the thorax, cutting a piece of wood while the body is braced against the gallery walls, and then retracting the head to pull in the fragment. There is some mastication before the particle moves into the digestive tract. However, wood fragments in the frass are often similar in size to that of the bite taken, about 0.5 x 0.5 mm. This may indicate that nutritive quality of the particle is changed by digestive processes during gut passage without further maceration of the food. When removed to water or to an undesirable substrate, the animal will readily void the hind gut but will hold the material in the foregut and midgut for over

10 days. Gut contents accounted for 20% of the larval dry weight, ranging from 0 to 50% (n = 20).

There is a pouch off the hindgut of Lipsothrix which is packed with filamentous bacteria (M. Klug, pers. comm.). It is unclear what the role of these associates is, but they may be cellulase-producing. They could be important especially during times of stress, by providing nutrients not available in the food or by inoculating the food held in the gut (Wigglesworth 1965). Attempts to sterilize larvae by rearing in media laced with Tetracycline were inconclusive.

Frass is eliminated as a loosely aggregated pellet. Some of this may be extruded to the log surface, although both species pack some material in the gallery and in spaces in the wood where it is likely to be re-ingested. The frass is rarely observed in the field, because it is either washed off underwater, or falls off due to wind, rain, or its own weight. In a few cases, a log surface may be covered with a mat of what appears to be Lipsothrix feces.

L. nigrilinea larvae actively feed in the winter. At 1°C in the lab there is observable activity. L. fenderi, on the other hand, seems to be less active during cold periods. The doubled-over posture is particularly common in the winter, and is associated with quiescent behavior.

Larval Defensive or Escape Behavior. Observations throughout this study indicate that L. nigrilinea are much more active than L. fenderi. They responded when disturbed by bracing themselves in the gallery. Larvae bit at a probe, posturing in a defensive manner with the head slightly upraised. Upon encountering another individual, a retreating or diverging motion is exercised. Smaller larvae appear subordinate, migrating from experimental dishes when larval densities are high (pers. observ.).

L. fenderi shows little response to disturbance, though they will bite at a probe. They may be pulled more easily from the gallery.

There is no significant response to encountering another individual and larvae in a dish of water will often become entangled with each other.

Larval populations may experience two types of mortality which could potentially be avoided by immigration from a log: desiccation when a log is stranded out of water, or suffocation when the wood is resting in non-aerated standing water. It was initially assumed that Lipsothrix larvae would not leave the larval habitat because (1) they did not survive placed in an artificial stream with alternate foods, (2) suitable wood is very patchily distributed and unlikely to be encountered by migrants, and (3) they do not occur in benthic collections. However, L. nigrilinea exits from logs brought into the lab and allowed to dry in the air or placed in standing water. L. fenderi never exited from a log so manipulated.

To ascertain whether emigration has any role in the field, uninhabited logs were placed next to colonized logs in five creeks. One L. nigrilinea larva was collected which could not have been oviposited into an experimental log, suggesting that this species may successfully migrate. No L. fenderi larvae were found.

Pupal Preparation. Prior to pupation, the larvae modify the gallery to facilitate pupal development and emergence. The pupal chamber of L. nigrilinea is prepared by widening the terminal section of the larval gallery about 20 mm below, and parallel to, the wood surface. This chamber then curves upward to terminate in a turret-like structure (Fig. 14). The top of the turret is flush with the surface and a canal resembling a moat is formed around it, 2-5 mm deep. It is presumed that the purpose of forming the structure is to clear loose material away to provide firm support for emergence of the imago. A similar turret structure is produced by Limonia nigrescens in New Zealand (Anderson, in press), and Tricyphma inconstans builds a mud turret (Rogers 1933), but this is otherwise a very elaborate procedure for the Tipulidae. L. fenderi exhibits a simpler procedure. The distal end of the larval gallery is already expanded. This becomes the pupation chamber and the gallery is only widened to the exterior. A disc of wood at the surface

is partially cut out but left undisturbed. This cap-piece resembles a manhole cover and is pushed out at emergence. The log surface is usually firm, so there is sufficient support for exit by the teneral adult.

Both species have an active non-feeding prepupal stage in which the final instar larva voids all gut contents. Developing organs (respiratory fans, genitalia) are visible through the cuticle. Prepupae comprised <5% of the 4th instar larvae collected during the emergence period, indicating that this stage is rapid, probably lasting less than one week.

Pupae. The pupa (or pharate adult) lies ventral-surface down in the pupal chamber until ready to emerge. The external genitalia are well-developed within their sheath so sexes are identifiable. The dorsal-cephalic respiratory organs are elaborated into two large forward-directed fan-like spiracular gills (Fig. 8). Hinton (1955, 1967) has studied the fine structure of the fans of the European L. remota and L. nervosa. They are unusual in bearing a cuticular network of canals which retain air. These plastrons facilitate the inward diffusion of oxygen from air or water.

The pupal stage lasted a minimum of 11 days for males and 16 days for females at 15°C (pers. observ., $n \geq 10$, 18 respectively). Pupae are mobile, though only when disturbed. They are more tolerant of dry conditions than are the larvae, surviving out of water at room temperature for several hours whereas larvae shrivelled and died within one hour.

Adult Emergence. At emergence the pharate adult proceeds up the chamber by peristaltic contractions until the head and thorax extend beyond the exit. The pupal exuviae splits dorsally, and the imago begins to emerge by repeated sinusoidal movements. When the head and thorax are free, the legs are drawn up and then extended to be used for support to pull the abdomen out. Emergence took less than 10 minutes for eight individuals observed. Pupae reared outside of their chamber

were frequently unsuccessful in emerging. In about one half of the observations, they lost legs or did not fully eclose from the pupal exuviae.

Emergence usually occurs early in the morning, but is not highly synchronized. Individuals were observed to emerge during the day in the field. Under a 16-hour light cycle in the laboratory, emergence occurred throughout the day and in the dark.

The teneral adult rests after walking a few centimeters from the emergence site and eliminates the fluid used in swelling the body to split the pupal exuviae. The body is hardened enough for flight within 10 minutes. There is no external change in L. fenderi after this, while the black dorsal line and the cuticle of L. nigrilinea are fully pigmented after about six hours.

Adult Biology. The adult morphology of Lipsothrix is typical of most craneflies. Legs are long but account for only 6-8% of body dry weight. The wings are held over the abdomen in a plane parallel to the substrate, or may be held straight out from the body (Fig. 15).

Adults were maintained in the lab in cages provisioned with water and a honey-water solution, as Rogers (1933) suggests that tipulids may feed on floral nectar. Craneflies, however, are typically non-feeding as adults. Unmated L. nigrilinea females lived approximately 5 days (1-6 days, n=12) and unmated males 8 days (1-12 days, n=14). Mated males and females lived only 3 to 4 days.

Adult behavior of L. nigrilinea in the field was examined by releasing 10 males and 5 females individually. They flew to the stream vegetation, or if landing on the ground, hesitated and then either flew or climbed into the brush. Those released in the sun all immediately flew back to the riparian zone. The flies perched upside down on branches and either remained still or would exhibit a bobbing behavior described later. Desiccation is a major mortality source for tipulid adults (Freeman 1968), and some of these responses result in decreased moisture loss.

Three L. nigrilinea were captured on the Berry Creek sticky traps. All were on the downstream side as if they had been moving upstream, but the sample size was too small for significance. They were within 2 m vertical and horizontal to the stream.

L. fenderi adults appeared to be more susceptible than L. nigrilinea to sticky trap capture. Five males, 7 females and 5 of unknown sex were collected within 2.2 m of the stream on 14 of 55 traps. Of these, 10 individuals were on the downstream side, one was upstream, and for 6 the position could not be established. The number from the downstream side and the proximity to the natural habitat suggest that there is local movement in an upstream direction. It was not possible to examine the role of long-range dispersal for either species, but considerable numbers of larvae colonized the experimental logs previously uninhabited in streams indicating that this dispersal is significant.

Mating Behavior. Males and females of both species exhibit bobbing behavior similar to that noted by Hemmingsen (1952). The body is raised to full leg extension, and lowered to almost touching the substrate, at a rate of 1.5 times per second. This is done for 5 to 10 seconds, they then rest and repeat the behavior. Upon contact with a female, the male does pushups at nearly twice the rate. The role of this behavior may relate to mate attraction, but this is unclear because females continue to do pushups even during copulation.

Unmated males actively clamber along the cage walls until they chance to touch the leg of the female, who is more quiescent. Rogers (1933) felt that tipulid mate finding was primarily by contact. The male becomes agitated and attempts to climb onto the dorsum of the female, at the same time groping with his claspers for her abdomen and genitalia. A non-receptive female holds her abdomen to the substrate and will struggle until she escapes. A receptive female allows the male to extend his claspers under her abdomen from above. On establishing a firm grasp on the genitalia just above the valves of the ovipositor, he then twists fully around so that copulation takes place with the male

above and parallel the female (Fig.15b). They may remain in copulation for several hours, even overnight.

Other males will disturb a copulating pair, and in 14 out of 38 observations broke the coupling. Otherwise, the female walks or flies away with the male still attached. Only once was an intruding L. nigrilinea male successful in copulating with the abandoned female before she escaped. Nonetheless, such "spite behavior" (Hamilton 1970) can decrease the fitness of other competing males. Previously mated males commonly attempted to copulate again, and females also did so on occasion. However, it was not known when and if sperm was passed.

An early emerging L. fenderi male could not be induced to copulate with an abnormally late female L. nigrilinea, which is not surprising because the two species are evolutionarily distant (Hynes 1965).

Oviposition Behavior and Habitat Suitability. Female Lipsothrix deposit eggs individually into sodden wood. They repeatedly probe the substrate with their ovipositor, searching for a suitable soft spot or crevice. The ovipositor valves are then forced 1-3 mm deep, the final abdominal segment folding upward to allow penetration. There is a side to side jerking motion as the egg is deposited. In the laboratory both species required a substrate that extended from the water, as was noted by Rogers and Byers (1956) for L. sylvia. L. nigrilinea was able to oviposit into a portion of the wood which was 2 mm submerged but L. fenderi never used submerged portions.

Oviposition site preferences of both species was examined by providing five females in lab cages with several choices of material. Wood pieces approximately 15 x 10 cm were set slanting into a dish of water. After one week, when nearly all craneflies had died, the wood was removed and about one half of each piece examined closely for eggs. The other halves were then set into aerated water in order to determine whether the eggs would hatch. Wet paper towels were also provided in each experiment, since L. nigrilinea was known to deposit eggs, which subsequently hatched, on this substrate. A few of the eggs recovered from the wood were placed on the paper towels to hatch.

Table 3 presents the results of this experiment. There was no clear preference for wood species by L. fenderi. Texture seemed to be a more appropriate determinant of choice, since many eggs were deposited on soft Douglas fir. These treatments were terminated too early to determine whether hatching occurred in the atypical woods. L. nigrilinea, however, exhibits a very clear preference for the substrate which is also the one most commonly utilized in nature. It does make some 'wrong' choices, as is evidenced by oviposition into Douglas fir. Therefore, L. nigrilinea probably uses texture as an oviposition cue as well, but is more discriminating than its congener in determining suitability. It should be noted that both species deposited a small number of eggs in each substrate when only a single type of material was presented.

An experiment was set up under somewhat more natural conditions to test the long-term suitabilities of some different wood types. Class 4-m alder (exposed and submerged), class 4 Douglas fir (previously inhabited by L. fenderi), hemlock and cedar were provided in a laboratory stream. These were caged, and adults of both species were introduced. Larvae of both species were found the following summer in only the emergent alder. There was apparently no oviposition into the wholly submerged material. The previous experiments indicated that oviposition occurs in coniferous woods, especially by L. fenderi. If that was true in this experiment, then there may be some inhibitory or toxic effect of such wood on the development of the craneflies. This would account for the lack of hatching of the few L. nigrilinea eggs deposited in Douglas fir from Table 3.

Reproductive Allocation and Parental Care. Determination of the relative allocation of biomass to reproduction versus other functions is a useful means of comparing strategies used to increase fitness (Cody 1966, Price 1974). This assessment was made using percent of dry weight of reproductive tissues, by comparing egg numbers and sizes, and by comparing behavior related to reproduction.

L. nigrilinea females produce an average of 185 eggs (n = 22, range = 106-380). The eggs are initially soft and cannot be dissected intact from the ovarioles for 8 to 10 hours after emergence. Eggs are presumably hardened enough for oviposition after the same period. There are usually about 10 soft, spherical ova which have not completed oogenesis. These bodies are also found in females a few days old, which may mean that oogenesis continues throughout the adult life span or that these ova never fully develop. L. fenderi produces an average of 138 eggs (n = 16, range = 60-198). They are all fully developed at emergence, and an equivalent period is required for hardening.

L. fenderi apportions a larger part of its biomass to immediate reproductive apparatus than does L. nigrilinea (Table 4). This holds true for the relative weight of eggs and oviposition equipment, egg number per unit body weight, and total allocation as measured by female abdominal weights and by weights of genital segments. On the other hand, allocation to individual progeny, or reproductive quality, is greater for L. nigrilinea as suggested by its larger eggs in absolute terms or fewer eggs per unit body weight. The allocation to reproduction actually increases with adult size of females, while no such correlation exists for L. fenderi. This will be discussed in a later section.

There were some behavioral traits displayed by the two species which suggest that L. nigrilinea invests greater effort into progeny success. As stated previously, both species oviposit eggs singly, however L. fenderi frequently 'dumped' eggs in the laboratory by leaving many unprotected on a substrate or the cage bottom (including 2 out of 5 in the oviposition experiment). This may also occur in nature because on four occasions females which appeared healthy were encountered (approximately 40 females were collected in the field) whose abdomens were devoid of eggs. On the other hand, of $\geq$ female L. nigrilinea in the laboratory, none dumped eggs until they were near death. None of the $\geq$ 22 females collected from the field had oviposited all or even most of their eggs. Saving of eggs and the possible continued oogenesis may represent a type of bet-hedging (Schaffer 1974) should dispersers

find additional available habitats. Clumping of eggs is likely detrimental because larvae of tipulids are known to be cannibalistic (Barnes 1937), so there is an additional parental advantage to distributing eggs individually and widely in order to avoid sibling interactions. The tighter oviposition site discrimination by L. nigrilinea is further indication that it puts relatively more effort into reproductive quality.

ENVIRONMENTAL MODIFICATION OF GROWTH RATES

Differences in growth rates between individuals and populations may be the major determinants of size variability and voltinism (annual, biennial, or triennial) for both species. Factors which can influence growth rates include temperature, food quality, density-dependent competition, and genetic variability. Temperature and food quality are especially important parameters for detritivorous organisms (Iversen 1974, Sweeney 1978). They play a role at all times, especially since the low mobility of Lipsothrix keeps animals exposed to the same microhabitat. Populations are assumed to be genetically homogeneous because of the difficulty in testing this factor. This is probably valid when compared with the other mechanisms. Competitively-attenuated growth is also assumed to be a relatively insignificant factor, at least when comparing population differences between field sites. L. nigrilinea is more fully treated in this section than L. fenderi, but results should apply to both due to physiological similarities.

Thermal Effects on Growth

Field Evidence. The following analysis is based on the hypothesis, covered in the Life Cycles section, that Lipsothrix spp. have at least a two-year life cycle. The growth of both species was estimated from the transect data for larvae in their first year (Table 5, Appendices 2,3). The estimates were for samples combined on a regional and elevational basis in which temperature was assumed to be the primary

determinant variable. The four regions compared were represented by high and low elevation Coast Range sites, and high and low Cascade Range sites. Both coastal groups were combined for L. nigrilinea because of their lower abundance in that region. Only the first year of the life cycle is considered in this analysis because any quantitative trends were obscured by the variability in later sizes. Temperature comparisons between sites are not available due to the lack of site-specific temperature data. All sites had a similar, dense canopy.

The data show some trend of slower growth occurring at the cooler temperatures at higher elevations. The low Coast Range samples produced the most rapid growth rates as well as the largest larvae at the end of the season. There is a complicating factor, in that the warmer sites also have the longest growing season. Emergence, oviposition, and egg hatching may occur earlier in these sites, and the warm season also lasts later into the fall. The net accumulation of thermal units is thus considerably greater at warm sites. Growth rates are much reduced at all sites from about November to March on account of the low winter temperatures.

The logs distributed for colonization studies provided clearer evidence of temperature control of growth. Food quality differences are minimized because all of the logs were initially similar in conditioning. The mean dry weights of L. nigrilinea larvae from individual logs was determined after approximately six months of growth. L. fenderi could not be analyzed because logs were removed before larvae could experience significant growth under field conditions. The weights from each site were compared with three potential indices of temperature: elevation, directional orientation of the watershed, and canopy cover. The last was necessarily subjective because seasonal and microhabitat differences could not be measured. It was based on visual estimations of percent open sky at several points on the stream and on at least two dates.

While elevation appeared to be an important determinant of growth rates in the transect data analysis, a significant relationship for the colonization log data was found only with relative cover (Fig. 16).

Hence, solar radiation is suggested to override elevation in streams subject to different degrees of canopy development. Within- and between-sample variability could be partly due to differences in time of hatching. However, it was previously shown that time of emergence showed minimal relationship to altitude and temperature, so oviposition dates should be similar between sites.

The weights analyzed above (Fig. 16) give justification to the curves fit to the transect data. Their range (0.14-0.83 mg) overlaps with the range of mean weights of first year L. nigrilinea larvae from the three transect regions in October (0.07-0.44 mg, see Appendix 2). The growth rates in the latter streams may be lower because they did not include open canopy streams.

Temperature Studies in the Laboratory. Figure 17 gives the results of an experiment in which six inhabited logs were cut into sections and maintained for 58 days at 3°, 8°, 15°C. L. nigrilinea larvae were then removed and weighed. Assuming initial size distribution was random with respect to treatments, there appears to be a clear difference between treatments both in average weight gain and in proportions of the population which have grown to larger size classes. Data were not analyzed statistically because differential mortality due to size confounds results. The similarity between 8° and 15° suggests that the advantage of higher temperature is greatest in the lower range of temperatures this species may encounter in the field.

To provide better control for temperature studies, three L. nigrilinea larvae per petri dish were kept at 3°, 8° and 15°C for 30 days, and live weights were compared before and after treatment (Fig. 18). Mortality was moderately high, and variability in wetness and gut contents probably introduced considerable error, but some trends are apparent. All larvae lost weight in the cold treatment, and of those that actually gained weight in the 8° and 15° treatments, the amount increased was higher at 15° for both species. A net gain was only recorded in the 15° group. None of these gains is as great as occurred in the field at similar temperatures.

Food Quality and Growth

The Role of Food Quality. The use of wood as a food source is impeded by the very low nutritional quality of wood (Anderson et al. 1978). Several strategies exist for wood feeders: (1) They may produce cellulase to break down cellulose into suitable components (Lasker and Giese 1956); (2) symbionts may be harbored in the digestive tract to break down wood material or to provide nutrients directly (Wigglesworth 1965); and (3) external conditioning by fungi and bacteria may render the material more usable (Ausmus 1977). Some of these microbes may continue activity within the gut, acting as opportunistic symbionts (Graham 1967). No cellulase activity was reported from the guts of Lipsothrix, despite the presence of symbiotic bacteria (M. Klug, pers. comm.). Nutritional enrichment by environmental microbes is likely to be essential for Lipsothrix. Conditioning by fungi should be especially important due to their ability to penetrate the wood matrix.

An increase in the nutritional quality of the food resource can increase the growth rate of insects (Anderson and Cummins 1979). Food quality may interact with and override temperature in determining growth rates (Cummins and Klug 1979). This is because an increase in temperature results in a thermal enhancement of microbial production more directly than it affects the insect itself.

The actual determinants of food quality to Lipsothrix are difficult to define because the nutritional requirements are unknown. Two general indices which are commonly associated with microbial activity are the lignin:cellulose ratio and the percent nitrogen. Table 6 gives values of these two factors from various types of wood.

Despite the expected importance of nitrogen content, it appeared to be poorly correlated with the presence of larvae. Nitrogen does increase with decay class, but even non-decayed wood had values within the range utilized. The light-colored class 3 and 4-m wood is the most favorable habitat, especially of L. nigrilinea, yet the darker, sub-optimal material inhabited by L. fenderi contained higher nitrogen

levels. Decayed coniferous wood also had sufficient nitrogen but was seldom used by the craneflies.

An increase in lignin:cellulose ratio seemed to be a better indicator of suitability than nitrogen, at least for different wood species. Lignin is a structural hardener in trees and higher contents may render material unsuitable to detritivores. However, the L:C ratios increase with decay class when considering alder alone. This is because lignin is less easily degraded by decomposers than is cellulose, so the absolute amount remains more constant. The slight increase in lignin:cellulose did not correlate with larval presence so this index also does not provide adequate predictive potential, at least within the primary wood species of interest. In addition, it may be that some constituent of coniferous wood reduces or deters feeding (or oviposition).

Laboratory Studies of Food Quality. In conjunction with the laboratory experiments testing thermal effects on growth rate, several treatments were included in an attempt to separate the effects of food quality from temperature. The 8°C incubator was employed because this temperature most nearly approximated stream temperatures, and because excessive mortality occurred with enriched media at 15°C.

Some limitations of the laboratory experiments must first be discussed. In order to control for food texture, only blended media were used. The manipulation of the media may result in changing other characteristics as well. The increased surface area allows exaggerated growth of microbes, especially bacteria, with attendant changes in food quality and oxygen availability. Antibiotics that were included in some treatments (Tetracycline, sodium benzoate, or potassium sorbate) neither eliminated microbes nor could they be used without a potentially confounding impact on the gut microbes of the insects. Autoclaving the media apparently altered it so that larvae refused to feed. Many of these factors may, in fact, remove or mask cues which are necessary to stimulate feeding or growth.

A series of treatments was set up with pre-weighed larvae of both species. Control media was blended from typical class 4-m Lipsothrix wood while 'new' was wood which had held Lipsothrix but was light-colored and less decayed (class 3). 'Cedar' was from the one coniferous log containing L. nigrilinea, which had a high nitrogen content, but may have been of low quality because lignin values were also high. The nutrient-enrichment treatments entailed stirring into the media a nutrient mixture suggested by V. Brookes to simulate fungal enrichment (brewer's yeast + casein powder + vitamin complex + wheat germ). Results are given in Figure 19.

The L. fenderi data were ambiguous, so are not presented. In no L. nigrilinea treatment was positive mean growth observed after 30 days. However, larvae in the two 'low quality' treatments (new, cedar) lost significantly more weight than in 'better quality' treatments. The nutrient-enriched 'new' was superior to all others in three respects. Survival was greater, more animals gained weight, and those that gained grew more. It was the only treatment comparable with the increased temperature treatment described earlier. The 'control + nutrient' may have suffered from microbial depletion of oxygen since bacterial infection was evident. No feeding by larvae in the 'cedar' treatment was observed. The other materials appeared to be suitable, since feeding occurred, but the relative lack of growth in the 'new' treatment compared with the same material with nutrients added suggests that food quality may have some impact on larval growth in the field.

Food Choice by Larvae. Growth is obviously dependent on acceptance and utilization of food. In the temperature section, it was suggested that some manipulations of the food source may remove larval feeding cues. To test whether they can indeed sense quality and make choices, L. nigrilinea larvae were placed into arenas in which they were free to migrate between food patches. In two-way experiments with 'new' and conditioned alder media placed next to each other, no migration was observed with five larvae in each side, while feeding commenced in both sides. Four types of media were then placed into a square dish such that a different medium was in each corner. New alder, conditioned

alder, nutritionally enhanced alder, and cedar were used. Four larvae were introduced into each corner and none dispersed. Only in cedar were the hind guts evacuated and no feeding observed.

Lipsothrix apparently do not search for the better quality resources which could increase their growth. This makes ecological sense because the benefit of finding a better quality log or patch is probably outweighed by the risk entailed by leaving a log. Migrating individuals would be exposed to greater predation pressure, and must utilize a different food source. To establish whether growth is possible on other materials, alder leaves which had been leached and microbially colonized in the laboratory for over one month and then blended were tested as a food. Larvae placed in this medium would not feed even after three weeks. This suggests that Lipsothrix cannot survive on other materials found in the stream, but only in wood.

One is left to conclude that while food quality is certainly important for larval metabolism, the determinant of "quality" in the field may be more complex than a single chemical component. Furthermore, the nutritional quality of individual habitats may not alone control the growth rate (nor the habitat selection) of the associated organisms. The important factor may involve the rate of nutrient acquisition rather than the absolute nutrient concentration. Some other quality, such as hardness, could overwhelm the chemical factors. This element will be examined in a later section.

LIFE CYCLE ANALYSIS

The life cycles of the two Lipsothrix species were examined by analyzing the size composition of larvae and pupae collected from the transect stations. Each log delimits a discrete habitat, and the individuals within were treated as a population. Sequential sub-samples from the log were assumed to be representative of that population. The sampling intensity was restricted because destructive. Only a few larvae (generally <10) could be taken in a fairly small piece of wood on each sampling date. Even with these precautions, it was often difficult

to accurately monitor single populations, so the data were also analyzed by grouping stations together.

L. nigrilinea

Variability - A Statement of the Problem. The initial analysis of the size distribution of larvae over time suggested a complex life cycle. There is a large degree of variability in the system, as indicated by the presence of co-occurring individuals of all size classes at nearly all times of the year (Fig. 20).

The variability of size-class distribution is further complicated by a large range of pupal sizes, and a very long emergence period (Fig. 21). Individual pupae may differ by almost an order of magnitude in weight, and this cannot be attributed to sexual size dimorphism. These data are based on field-collected samples, so no lab artifacts have been introduced.

A model is first proposed to explain the patterns, or lack of pattern, observed in analysis of field data. Supporting data are then presented to justify this model.

Model for the Life Cycle of L. nigrilinea. The life cycle hypothesized is that L. nigrilinea is predominantly a biennial species, but exhibits developmental plasticity which allows a non-deterministic life span. Some portion of the population is extended to a 3-year life cycle. Given certain circumstances, even a 4-year cycle is possible.

The diversity in size classes which results from this life cycle is compounded because the population does not respond synchronously to a single pupation cue. The predominant cue is a drop in water level, which stimulates individuals on a very local basis. In this manner, emergence occurs at one site for several months as the water recedes. Some larvae will continue growing without emerging in a given year if they are not exposed to the cue or are not ready to respond. Additional variability in size class distribution is the result of disparate timing of hatching because of the extended oviposition period for the

population. Environmentally-induced differences in growth rate yield additional variability.

Evidence for a Biennial Life Cycle. Biennial life cycles are relatively uncommon among tipulids (Pritchard, in press), as well as aquatic insects (Hynes 1970, p. 276), in relatively mild temperate regions such as western Oregon. As stated previously, there is a large spread of larval weights at a given site and time without clear separation of cohorts. However, by plotting the weights of all individuals obtained from the Green Creek site against the date collected, there is some indication of multiple cohorts occurring within a single log (Fig. 22). An envelope encircles larvae that may belong to a single cohort or year class. Pupae were collected from April through August, so larvae of the following generation probably hatched from May to September. Horizontal lines indicate size classes, and it appears that most larvae reach the third size class (early 4th instar) during their first year of growth. Relatively little growth would occur during the winter due to cooler temperatures.

The suggested biennial life cycle becomes more apparent if the assigned cohorts are visualized as extensions of each other. The smallest cohort fits an exponential growth model for the warm months (r^2 = .76), while the larger individuals are too widely spread to fit closely to a curve. Pupae weigh less (approximately two-thirds) than the corresponding larvae due to loss of gut contents and energy loss during development, so that the pupae shown came from much larger larvae. Cohort separation was not readily apparent for most of the other sites sampled.

Some corroborating evidence supports the proposed biennial life cycle. First, in several experiments, non-infested logs were placed into streams in early spring and left for more than a year. In none of these situations were any craneflies observed to emerge the following spring. Emergence would have been obvious because the pupal exuviae remain with the log. Larvae were present, and in the following year adults emerged from most of these logs. Second, the logs which were

distributed in early spring to 35 streams to monitor colonization capabilities were retrieved in the late fall after larvae had experienced one growth season. The maximum weight of any larva removed was 1.56 mg and the average was 0.38 mg. These logs were similar in quality to the transect logs so that growth rates were expected to be near field rates. The average size of male adults was 2.05 mg, and females 4.31 mg, and adults weigh approximately one half of their final larval weight. Thus,at least two years are required to accumulate sufficient biomass for production of adults.

Emergence Pattern and Pupation Cues. Among most insect populations, including aquatic insects, emergence occurs during a relatively discrete period. The pattern is generally a result of synchronous pupal development in response to photoperiod or thermal accumulation (Hynes 1970, p. 285). The emergence period is typically related to the season. If a population uses a thermal cue, emergence is delayed if temperature change is late. Accordingly, emergence occurs later among populations at higher altitudes, latitudes, or in other cooler habitats. Nonetheless, there is considerable synchrony on a local scale. Population synchrony also insures that males and females are concurrently present, which is important for short-lived adults.

In contrast, L. nigrilinea exhibits little synchrony, emerging from April through August with no definite peak (Fig. 23). These data are the sum of monthly collections of pupae and pupal exuviae from the transect logs. Pupae collected would have emerged during the month, while exuviae were assumed to represent emergence during the previous month. The large number in the July sample was primarily due to 19 exuviae from a single log. There is also no apparent local synchronization of development. The mean length of emergence period at individual sites was 2.8 months in the Cascades and 3.8 months in the Coast Range streams (excluding three sites where only one pupa was collected). One Cascade stream and three Coastal streams produced adults over the full 5-month period, and in two of these streams individuals were from a single log.

The above results argue against a discrete thermal accumulation mechanism as the primary pupation cue. Temperatures do not vary enough within a water-saturated log (Savely 1939) to cause a large difference, especially under the temperature-moderating canopy. The induction of pupation by water level decline was hypothesized to account for this variability. Stream levels recede slowly as dry seasons approach (Appendix 1), such that different logs, and different portions of a single log, become exposed over a long period of time. Larvae within these microhabitats may respond to exposure, resulting in minimal population synchrony.

Rogers and Byers (1956) noted that emergence of L. sylvia could be forced early by removing a log containing the larvae from the stream to the lab. I have observed the same phenomenon, but, in both of these cases temperature cues may have been involved because lab temperatures were higher than those in the field. To test the water level mechanism, a prime alder log containing many large individuals was cut into three equal sections and these placed horizontally into an artificial stream with one 80% submerged, one 50% and the third only 20% submerged. Temperatures approximated normal temperatures in Oak Creek, and were nearly uniform in each piece. Logs remained in place from May 12 through the entire emergence period, and emerging adults were enumerated (Fig. 24). The absence of emergence from the 80% submerged log indicates that water level is a primary pupation cue. This log contained large larvae which did not pupate during the experiment. The 50% log yield the most adults because more larvae were initially present.

Another experiment showed that pupation period itself may be regulated by water level. When evidence of pupation was observed in a small log, it was submerged for 32 days. A single pupa could be seen at the mouth of the gallery, and it emerged when the wood was removed from the water. Isolated pupae placed underwater survived for about seven weeks before dying, more than four weeks beyond the normal duration. Hinton (1967) noted that a submerged larva of a European species

(L. remota) entered pupation, while a submerged pupa remained in that stage (pharate adult) without emerging.

The timing of emergence does not rely solely upon water level. There appears to be some interaction with temperature, or some individuals would be emerging in all seasons, especially from the logs in seeps or very small streams which would always have a large portion of wood out of water. I tested the interaction of temperature and moisture by placing 'very large' larvae in jars of wood media at four temperatures and two moisture levels. One had water added so there was a slight excess, while the other was held upside down until no water dripped out. Both pupation and emergence were observed through the summer (Table 7). Sample sizes were too small for statistical significance, but the trend was for lower moisture levels to enhance emergence. Secondly, warmer temperatures increased the likelihood of emergence, even in the wet treatment.

The interpretations of emergence pattern based on water level in concert with a thermal response are corroborated by field observations. Emergence only occurs in spring and summer even though some wood is out of water in fall and winter, which supports the idea of a temperature cue. Even though there are regional growth rate differences based primarily on temperatures, no emergence pattern exists in relation to temperature indices such as region, altitude, or date. Instead, early maturation was seen in some logs in the smallest streams such as Lone Cedar, Lewis, Darkey, Baker, and L. Alder. Water levels recede sooner in small streams resulting in earlier onset of the pupation cue.

The life cycle of L. nigrilinea may be examined with respect to appropriate cues which may predict suitable conditions for emergence. The larval habitat is rarely disrupted and is available at nearly all times such that the biennial life cycle is possible. Emergence is impossible under water. Being restricted to a log, Lipsothrix must wait until the log is out of water before it can leave, and furthermore, oviposition must occur near the air-water interface. The inverse

constraint is that if a log extends too far out of water, desiccation of larvae may result and oviposition is unlikely.

A thermal threshhold response coupled with a water level cue seems an ecologically appropriate mechanism cuing metamorphosis. A thermal cue could bring reproductives out in late spring and early summer, when adult mortality from storms or low humidity would be low. The preponderance of tipulid species emerge at this time (Rogers 1933). In turn, the suitability of a log for emergence cannot be predicted by a thermal mechanism, as each log will be on a different time schedule. Water level itself would be the better predictor of the local environmental conditions necessary for emergence.

The greatest rainfall in western Oregon is in the winter and tapers off through the spring and summer (Appendix 1). The emergence period of L. nigrilinea coincides with this decline. If sufficient biomass is accrued for adulthood, the thermal cue signals that the climate is suitable for adult survival, and water level insures directly that emergence is possible and indirectly that other wood is available for oviposition. Should stream levels rise during this period, the developmental flexibility of the pupa allows emergence to be arrested until levels again recede as the weather becomes favorable.

Environmentally Induced Extension of Life Cycles. It is apparent that a large portion of the variability in life cycle timing of L. nigrilinea is due to variation in water levels. This phenomenon also accounts in two ways for much of the variability in individual weights that was described earlier in this section. First, spreading of emergence over a long period obviously spreads oviposition and hatching time. Individuals of one year class within the same log may differ in age by five months. Secondly, some larvae which are large enough to emerge as typical biennials may not do so in the absence of their developmental cue. This occurs when a log is largely submerged all year. Developmental flexibility allows larvae to continue to grow the following year so that four cohorts may ultimately co-occur. A more

deterministic life cycle would be unsuitable in response to the biologically important, and stochastic, variable of water level.

I have no direct evidence that any animals collected were in their third year, however, several indirect observations and results suggest that triennials commonly occur. Though it was impossible to differentiate cohorts or growth rates of larvae beyond their first year from the transect data, there are occasional very large individuals which are hard to explain based on a strict biennial life cycle.

When the triennial option and the role of water level were hypothesized, I started taking samples of wood below and just above the water lines from a large log at two sampling sites. Table 8 indicates that greater numbers of 'very large' larvae remain below the waterline than above after emergence. Therefore, virtually no pupation occurred in the underwater portions, and larvae in these portions remain in place rather than migrating upward. The heaviest L. nigrilinea larvae collected during my study came from the submerged portion of the Thistle Creek log and the sole submerged pupa weighed 12.5 mg, which was one of the largest pupae collected in the study.

If adults are comprised of both 2- and 3-year individuals, then there may be some bimodality in size class frequencies. Variability in larval size and timing of pupation mask any clear differences, but Figure 21 suggests some pattern. The data seem to cluster into groups which have been subjectively divided by lines. Note that the very large individuals are clearly removed from the main group of the populations.

The final evidence of trienniality is from the submergence experiment at Oak Creek Laboratory. Many mature biennial larvae remained in the 80% submerged log into the winter, but died when the artificial streams froze. The average size for female adults which emerged from the 50% and 20% submerged treatments (Fig. 24) was significantly less ($p < .05$, Mann-Whitney Test for unequal samples, Zar 1974) than the field population. The smaller size may indicate that a larger proportion of the population within a log was induced to pupate by water level than would normally occur in the field. It follows that

in a wet year, more larvae will remain for the third year because less wood will be exposed. The submergence mechanism could even result in larvae being four or more years old.

Regional and Sex-Related Variability in Growth and Emergence. Considerable variation exists in life cycle patterns of L. nigrilinea between regions and habitats that is independent of water level. Differences in timing of development, whether in months or years, may result from differences in growth rates and developmental thresholds. Temperature and food quality will in part determine these processes, as was examined in the Growth Rates section. For the transect streams, mean temperatures decrease up an altitudinal gradient and with distance inland, and warmer temperatures yield greater growth. Additional variability may result from sex-related differences in growth and size.

Males emerge slightly earlier than do females (see Figs. 21 and 23). Their shorter pupation period accounts for most of this difference. The two-fold difference in size, however, must mean that as larvae, females either grow faster or for a longer time than males. Pritchard (1976) and Meats (1975) indicate that female growth is more rapid in the final instar for two species of Tipula, while male growth in T. oleracea may be arrested once sufficient size is reached (den Hollander 1975). Any sex-related differences in growth rates for Lipsothrix, which would have been indicated by two size class frequency peaks which become separated with time, were obscured by other variability. Growth is not arrested at a size threshold because this would argue against the wide weight range of pupae observed. There also seemed to be an increase in pupal size with later emergence which is expected if larvae continue to grow when not cued to emerge.

There is some size threshold of response to moisture by both sexes since small larvae will not pupate in a log taken from the water. Females benefit more from an increase in size than males due to their greater expense of reproduction, so it is likely that this threshold would be higher for females than males. If growth rates are similar, then it could be expected that females must wait until they become triennials more often than males, and males are more likely to be large

enough to emerge as annuals, as suggested by the cohort separation lines in Fig. 21. Longer life means more exposure to mortality, which may explain part of the male-biased sex ratio ($p < .05$, Wilcoxon signed rank test) in the Coast Range transect samples. In the cooler Cascades, males may not get large enough to emerge a year before females, resulting in the even sex ratio. Both male and female pupae appeared larger there (not significant due to variance from combining both year classes), which could result from a predominance of triennials.

Although the actual mechanisms remain unclear, some portion of the variability in life cycles observed is due to differences between individuals on the basis of sex. Additional differences in typical patterns are related to region, and more directly, to temperature differences resulting in modified growth rates of larvae. The emergence pattern itself was not affected due to the role of water level. The drawn-out oviposition period may be the most significant factor determining size variation within the population.

L. fenderi

This species presented the same difficulties as L. nigrilinea for interpreting the life cycle. There is again a wide range in the sizes of co-occurring larvae, and all size classes are present in nearly all months (Fig. 25). Coincident with the size variability observed for larvae, the range of pupal sizes is also wide (Fig. 26). However, L. fenderi differs from L. nigrilinea in that emergence is more synchronous over fewer months.

Model for the Life Cycle of L. fenderi. L. fenderi is also proposed to follow a biennial life cycle, but largely lacks the flexibility to extend growth for a third year. The emergence pattern is fairly synchronized because a general environmental cue, probably related to temperature, is more important than water level in the induction of pupation. This life cycle should result in relatively discrete cohorts. However, other factors account for the observed variability. Temperatures are decreasing during the fall emergence period. Eggs

deposited early hatch and the larvae grow during the fall, while later eggs may be dormant during the winter and then hatch as spring approaches. At least some individuals complete development in the year following oviposition while other, younger or smaller larvae remain until the following year. Additional variability results from growth rate differences, these being accentuated because of the wide range (relative to L. nigrilinea) of habitats utilized.

Length of Life Cycle. L. fenderi appears to follow a biennial life cycle. The data from the Dinner Creek samples indicate that larvae may be subjectively separated into two fairly distinct, co-occurring cohorts (Fig. 27). Growth starts from late fall to mid-winter, and by the following winter the average larva reaches the 'large' size class, or early 4th instar, with a weight somewhat under 1.0 mg. During the second year, growth is not as rapid, but continues until emergence in the fall. The biennial pattern is supported by the growth curves for combined data from the four transect regions (Appendix 3), and by analysis of expanded size-frequency histograms for all collections (Fig. 26).

Despite the similarity of this life cycle to that of L. nigrilinea, there is an important difference. At the end of the emergence period, very few larvae remain from the second-year cohort. It seems, therefore, that triennialism is rare for this species. Only two larvae, collected in the spring, were too large to be explained by the biennial cycle. On the other hand, the broad variability which exists in the first-year cohort in the fall suggests that larvae can complete development in one year as some fall-collected larvae are nearly twice the size of small pupae.

Emergence Pattern. Emergence of L. fenderi occurs from August through November with a clear peak in September (Fig. 28). Pupation is more synchronized at each site and also between sites than with L. nigrilinea. The data on pupae from the transect collections suggest that males emerge before females, at least in the Coast Range. In a log

in the laboratory, males first emerged four days earlier, peaked after three days, and rapidly tapered off while female emergence remained nearly constant for three weeks.

The importance of water level to emergence was tested by cutting two logs and placing half of each log 80% out of water in a caged pan. The other two pieces were placed in another pan with about 75% of the log under water. Temperature in the building was similar to outside temperature. Submergence of the log appeared to have little effect on pupation and emergence. From the exposed logs 31 males and 14 females emerged, while in the partially submerged log it was 21 males and 13 females (no difference at $p < .20$, chi-squared). A few larvae in the field were disproportionately large, and may have been inhibited from emerging by submergence. However, two observations were made of a pupa attempting to emerge underwater, without success, indicating that L. fenderi cannot arrest development if water levels rise. Water level would not be an ecologically appropriate cue because in the fall the level is just starting to rise (Appendix 1), so could not be an adequate predictor of suitability for emergence.

Photoperiod is unlikely to cue emergence due to darkness within a log. Thermal accumulation could be involved, but the synchrony between sites, despite differences in temperature indices such as altitude, region and to a lesser extent canopy cover, may suggest otherwise. A direct response to change in temperature may be possible. There is a cooling of stream temperatures around early September (Appendix 1), which would signal the approach of the winter season.

Factors Resulting in Variability. A large portion of the size variability of L. nigrilinea, especially of pupae, was related to the indeterminate timing of the life cycle. At first, one would expect low variability for L. fenderi due to its shorter emergence period. This may be partly true for larvae of one cohort within a single log, as evidenced by the greater ease of cohort separation in field data analysis. Adult weight is also more consistent, as indicated by a

smaller coefficient of variation for this species (see Table 4), though the absence of triennials reduces variability.

Considerable variability still exists in these populations, part of which is due to growth rate differences. As with L. nigrilinea, growth was less in higher and inland sites (Table 5). Also, L. fenderi utilizes a wider range of wood types and decay classes, even within one log, than does L. nigrilinea. These microhabitats vary in nutritional quality so growth rates of the larvae within may differ as well.

Differences in the timing of growth may result in additional variability. Figure 26 illustrates the sizes of pupae collected on various sampling dates. The overlay indicates what I believe to represent pupae of different year classes. Most are considered biennials, while several may be annuals since they are much smaller than some larvae which are one year old. All eggs are oviposited in the fall, but disproportionately few early instar larvae were found in the late fall and winter months (see Fig. 25), despite careful picking under a dissecting microscope. In early spring, there was a sudden jump in numbers. These data suggest that while some eggs hatch in the fall, hatching is retarded until the late winter or spring for most. The fall-hatching individuals grow during the remaining season, and may attain sufficient size for pupation the following fall as relatively small adults. Two sub-cohorts may be apparent in the transect data (Appendix 3b).

The adult data showed that females are larger than males. It was not determined whether females grew at a faster rate or if males slowed biomass accumulation beyond some threshold. Such sex-related variability may still add another source of variability to account for the range of larval sizes observed.

Size and Reproduction

There is a certain advantage to Lipsothrix, particularly L. nigrilinea, remaining within a log until the following year. By growing to a larger size, the individual reproductive potential may be

increased. However, the intrinsic rate of increase may be lowered due to the greater age at reproduction. Large individuals may be stronger fliers, less prone to predation, and more resistant to other mortality factors (Calow 1977). Consequently, the decreased intrinsic rate may be balanced by the higher reproductive quality profferred by older and larger reproductives.

In an earlier section (Table 4), it was shown that L. fenderi allocates a larger portion of its mass to reproductive tissue than does L. nigrilinea, as would be expected for smaller, fugitive-type species (Hutchinson 1951). However, a paradoxical relationship with size exists for L. nigrilinea. There is a significant positive correlation between female size and reproductive allocation (Fig. 29; r^2 = .61 without the three points with asterisks, r^2 = .45 with all points). The asterisks represent large (probably triennial) individuals which emerged early in the season, and thus may not have replenished reserves which were necessary for winter maintenance. Egg weight appeared to be nearly fixed, so this increase is associated with greater numbers of eggs produced than would have been predicted by a geometric biomass increase with size, with the proportionate reproductive allocation held constant.

The benefit from larger size is likely to be less than from a gain in fecundity beyond certain sufficient adult dimensions. As biomass accumulation increases, a greater proportion of biomass may be channeled into reproduction at the expense of size. Thus, increasing larval size in L. nigrilinea may provide both an advantage against mortality, as well as an increase in fecundity which could further offset the reduction of 'r' resulting from the longer life cycle. Its life-cycle flexibility allows this advantage, and may lead to a trade-off between the 'security' of an early response to a weak environmental cue and the 'risk' and potential benefit of delaying the response. It was not within the scope of this study to substantiate that increased reproductive allocation and attendant life history traits actually result in increased fitness.

A poor relationship between size and reproductive allocation was found for L. fenderi (linear correlation provided best fit; $y = 1.82x + 60.7$, $r^2 = .14$), which may reflect a lesser ability to balance outputs within the limits of its life cycle. The range of allocation values was between 59 and 70%. A strategy of early reproduction may consequently be favored if there is less benefit to increasing size for another year, especially if larval mortality is fairly high.

POPULATION SIZE AND DYNAMICS

Larval Density

This section deals with the numerical density of larvae found within a log, and the factors related to the typical numbers attained in a variety of wood types and situations. This information can then be combined with estimates of wood availability in the section on processing to estimate the ecological role of Lipsothrix spp. in different habitats on a per-area basis.

Larval densities may be related in part to the availability of suitable wood. It was shown in the Habitat section (Fig. 11) that the highest densities of L. nigrilinea, and probably of L. fenderi, were found in streams associated with the mid-stages of forest succession, where there is the greatest abundance of suitable habitat due to the influx of dying wood, especially alder. The endemic populations are able to increase rapidly through the localized dispersal of adults.

Wood type is likely to be an important determinant of larval density. The transect data were analyzed with respect to densities by comparing the total numbers of each species, adjusted by the number of samples, taken from single logs through the study. Values presented in Figure 30 are minimum estimates because in summing all dates together, some samples are included which contained few larvae due to microhabitat quality or temporary reduction following emergence.

Class-3 wood was utilized by both species, although logs have a mosaic of qualities, and the inhabited portions may have been slightly

more decayed. General field surveys suggest that actual densities in class-3 material are somewhat lower. L. fenderi reached high densities in class-4f material, while it was not favored by L. nigrilinea. Class-4m wood is the prime habitat of L. nigrilinea, and several of these logs in the field had few or no L. fenderi. However, there was no statistical difference in densities of the two species in the transect logs (t-test, $p < .10$), indicating that this is a high quality habitat for both. The very soft class-5 wood is also heavily colonized where abrasion is low enough for such wood to occur. As with other wood favorable to both species, utilization is based primarily on the degree of association with water. The log with both species was fully saturated in a small permanent creek, while the log in which only L. fenderi were found was in a very small seep above the stream (Durkey Creek).

There is a trend for larval densities to increase with decay class, and the highest densities of both species, and especially L. fenderi occur in class 5 alder. This suggests that decayed material may be able to support more animal biomass, possibly due to the enhanced nutritional quality provided by decomposer organisms. The role of stream erosive power is important, in that it may remove soft material and not allow development of these high densities. This is indicated by the experiment in the Oak Creek artificial streams, in which L. nigrilinea adults were allowed to oviposit into soft logs where there was low stream velocity. When these pieces were removed the following year all structural integrity was lost from the wood, largely due to larval feeding, yet larvae were at a higher density ($1.4/cm^2$) than was found in nature. Although conditions were somewhat artificial, it appears that ultimate density may be controlled more by wood condition than by the length of time it remains available.

Mortality

The changes in animal density with time are useful for quantifying material processing and assessing the evolutionary importance of various

mortality factors to the population. However, attempts to generate mortality curves were unsuccessful for several reasons: 1) early stages were not adequately sampled so the initial population sizes were unknown; 2) variability in larval sizes made it difficult to determine which cohort they were from; 3) growth is not constant through the life cycle so weight is a poor index of larval age; 4) co-occuring cohorts were sampled rather than subsequent years of the same cohort; and 5) the choice of logs to sample was biased towards larger, more stable ones, while other unsampled log types may have different mortalities associated with them. Consequently, the density changes for single cohorts (Fig. 31) give a rough estimation of mortality, suggesting that it is low (2- to 4-fold reduction from peak density to the following year) and is similar for both species within the substrates sampled.

Mortality to Lipsothrix populations may result from abiotic factors (erosion and displacement, temperature extremes, desiccation) and biotic sources (competitive exclusion and predation, including cannibalism). In the absence of quantitative data, observations and habitat characteristics are given which are related to mortality. I hypothesize that L. fenderi experiences greater mortality than does L. nigrilinea in all stages, and that such mortality is in part due to its association with less hospitable habitats. Table 9 indicates that although there is considerable overlap between the two species, L. fenderi was more frequently alone. No sample with L. nigrilinea exclusively was wood which L. fenderi avoids, while the latter was found alone primarily in wood avoided by L. nigrilinea (see Fig. 30).

Abiotic mortality. Catastrophic or chronic disturbance associated with waterflow has considerable impact on these populations. At least five sticks or small logs, including three being monitored, were lost during storms. Also, 10 of the 35 logs distributed to assess colonization were lost during the experiment. L. fenderi is more commonly associated with semi-aquatic logs, and these are often more susceptible to disturbance since they may be less imbedded in the substrate. Though survival in the displaced logs was unlikely, some

L. fenderi survived in a log that was moved 2 meters, because the wood was firm. Other wood is subject to surface erosion, and at two sites known populations of L. fenderi were eliminated by scouring of part of the monitored logs. L. nigrilinea larvae survived because they were deeper in the wood. The eggs and early instars of L. fenderi are especially prone to disturbance, as high water comes in fall and winter before enough growth can occur to enable deeper boring by newly hatched larvae. Most L. nigrilinea are in the third or fourth instar by this time.

Death due to desiccation of larvae may occur in the summer and fall if wood is isolated too far out of water. L. nigrilinea has an advantage because it is found in wood which is in close contact with water. Since L. fenderi are commonly associated with semi-aquatic habitats, they are more frequently subject to desiccation. In a wet year, survival is high in the marginal habitats, but in a drier year, or if water courses change slightly, some wood will become drier than larvae can tolerate. During 1978 rainfall was normal, yet at four sites drying logs were found which contained dead larvae. Only once were L. nigrilinea larvae found which were killed by desiccation, in a log which had been moved out of water. L. nigrilinea has a physiological and a behavioral advantage as well. In the rare event that a log dries, larvae may respond by emerging or by migrating. When a log was placed out of water in the lab, only 2 of 48 larvae remained within. L. fenderi larvae do not emerge in direct response to water level, and all larvae died in place when a log was allowed to slowly dry.

Extreme temperature is the third form of abiotic mortality. A log is generally buffered from high temperatures by the water, and riparian vegetation, while low temperatures may be important. Both species are active at near freezing temperatures, but wood which is emergent from the water is subject to superficial freezing in winter. Freeze-killed L. nigrilinea were found once, at Berry Creek, while other larvae 1.0 cm deep in the wood survived. Logs containing this species, however, are rarely subject to freezing since water levels are up in winter. On ten occasions L. fenderi logs have been found frozen. It

seems that this species is more tolerant of freezing, as larvae were taken alive from the frozen material, but at four of these sites dead larvae were collected as well.

Biological Mortality. In laboratory media Lipsothrix spp. larvae were preyed upon by several burrowing forms, including Dicranota, Pedicia, Xylophagus, tabanids, Rhyacophila and hydrophilids. Small stages were also ingested by detritivores such as Austrolimnophila and oligochaetes (pers. observ.). In addition, L. nigrilinea was observed to prey upon L. fenderi and Barnes (1937) indicated that cannibalism occurs among early instars of tipulids. The potential exists for competition between all of these taxa.

The marginal zone between aquatic and terrestrial systems shares components of both communities (Dudley and Anderson 1982). L. fenderi, whose range includes these semi-aquatic habitats, is associated more frequently, and at higher densities, with more taxa of potential competitors (Table 10) and predators (Table 11) than is L. nigrilinea. Those competitors more commonly found with L. nigrilinea are fully aquatic and gouge the wood surface, or are found in sub-optimal habitats as suggested by lower cranefly densities (Appendix 4). Xylophagus is the most likely unrelated predator within wood, while the others occasionally bore into very soft wood. Disease and parasitism were not documented in this study, but are felt to be relatively unimportant for tipulids in water (Hadley 1969, but see Carter 1976).

The larval galleries of both Lipsothrix species do not typically join, but at high densities in soft wood the walls may break down, allowing the potential for interactions within and between the two species. Experiments in escape-proof petri dish arenas (Table 12) suggested that (1) L. nigrilinea may reduce the density of smaller individuals, probably by cannibalism, (2) L. nigrilinea may reduce L. fenderi as larval densities increase, and (3) L. fenderi has little impact on L. nigrilinea larvae. When escape was allowed, an increase in larval densities to approximately maximum field densities resulted in an increase in migration of smaller individuals of L. nigrilinea (large larvae remained unchanged) but no migration with similar densities of

L. fenderi (pers. observ). Field densities of L. fenderi were higher than those of L. nigrilinea (see Fig. 30), which may in part be explained by its lack of migration in response to density or other factors. I suggest that when high densities of L. nigrilinea occur, larger individuals may exclude both smaller larvae and L. fenderi larvae. Two 4-m logs were examined which held only very large L. nigrilinea larvae ($\bar{x}$ = 3.30 mg). The logs were submerged such that pupation was inhibited, yet oviposition was possible by both species, and I believe that the lack of small L. nigrilinea and any L. fenderi was due to predation by the high density of probably triennial larvae.

Adult Mortality. Adult mortality is virtually undocumented. L. nigrilinea are tougher and larger, so are presumably less susceptible to physical damage. Desiccation is a primary mortality factor for other tipulid populations, as is bird predation (Butterfield and Coulson 1975). Both are minimized as adults released in the field were observed to remain near water and protective vegetation. The black dorsal line may give L. nigrilinea a camouflage advantage over the very callow and easily visible L. fenderi. Both species have been observed landing on spider webs (esp. Tetragnatha spp) without difficulty, but the only indication of differential mortality is that six dead L. fenderi were collected from spider webs while no L. nigrilinea were seen in webs.

In summary, the probability of survival at all stages seems to be lower for L. fenderi than L. nigrilinea . There may be a greater loss of eggs and larvae to abiotic factors and environmental extremes due to life cycle timing and habitat association. The same is true of most biotic factors. These disadvantages to L. fenderi may be in part balanced by utilization of a wider variety of habitats. Their relatively shorter life cycle may be a response to some of these habitats being less predictable, while the relatively benign typical habitat of L. nigrilinea allows the life cycle extension discussed earlier.

Biomass and Production

The data in Figure 31, while not amenable to the direct calculation of secondary production using the average cohort method (Hynes and Coleman 1968), are used to estimate the biomass of Lipsothrix present (Fig 32). For the transect logs the biomass of L. nigrilinea is greater than that of L. fenderi. Early instars of each species contribute relatively insignificantly to the totals. Biomass of L. nigrilinea is nearly constant through the year while L. fenderi peaks just prior to emergence. This is consistent with the hypothesis that L. nigrilinea populations may be regulated, and that the longer life cycle tends to ameliorate biomass peaks, while there is more fluctuation in L. fenderi biomass as a result of less consistency in numbers and a greater proportion of annuals. The July-August L. nigrilinea value is an underestimate because it excludes the questionable value for triennials shown with dashed lines. The September-October value is an overestimate because the second year larvae just entered the very large size class, so are actually smaller than the factor used to generate biomass figures.

To estimate adult production, the emergence data from the transect samples (Figs. 20, 25) were adjusted for the number of logs sampled (n=23). This yielded estimates of 0.0443 L. nigrilinea adults per cm^2 of log surface area and 0.0436 for L. fenderi. Considering sex ratios, and multiplying by average adult dry weights, this works out to L. nigrilinea adult production of 0.124 mg/cm^2 or 1.24 g/m^2 of available log surface area. L. fenderi adult production was calculated to be 0.071 mg/cm^2 or 0.71 g/m^2. These values may then by multiplied by two (because pre-pupal larvae are approximately twice the weight of the resulting adults) to estimate the final production value for populations in the habitat sampled.

Adult production values of2.48 $g/m^2/yr$ for L. nigrilinea and L. fenderi are only slightly larger than the estimated standing crop averages for larvae (by a factor of approximately 2, Figure 32). These values were derived from independent data, which lends credence to the

validity of the estimates. The larval biomass values were actually underestimates of the true standing crops, as they did not include most triennial larvae since these were too scarce to provide accurate density estimates, while triennials were included in the adult production figures. Although secondary production could not be estimated because of inadequate mortality information, the actual cohort production of each species is not considerably greater than the adult production estimates given, probably by less than a factor of two. This is because most production occurs during the final instar, when mortality is probably low. Despite the 2+ year life cycles, the annual production estimates should be similar, because two or three cohorts will be growing simultaneously, though an abundance of triennials will boost this considerably.

IMPACT OF LIPSOTHRIX ON WOOD DEGRADATION

The role of Lipsothrix spp. in the reduction of large organic debris in streams requires the estimation of feeding rates and wood processing rates under various conditions encountered in the field. Dependent factors include resource quality and quantity, tissue toughness, temperature, and population density. Quantity, or resource availability, was discounted as a factor regulating feeding rates because, once successful oviposition has occurred, there is apparently an abundant supply of wood available per individual. Density-related competitive interactions might potentially affect rates as well as feeding site selection. However, the effort expended on interference competition was assumed to be insignificant in relation to other environmental factors related to feeding effort, while competitively-induced habitat displacement and population changes could not be adequately estimated in terms of their quantitative effect on processing. Therefore, the primary variables which I will consider are wood quality, toughness, and the effect of temperature on processing rates.

Laboratory Studies

Feeding Rates in Artificial Media. Laboratory experiments were initially undertaken to indicate approximate feeding rate, and how it is affected by temperature and food quality. By presenting 12 larvae with charcoal or fluorescein dye incorporated into blended wood between microscope slides, a gut passage time of approximately six to eight hours was estimated.

Petri dishes with wood and agar media were used for further experiments. Three larvae were introduced into each dish, and after 10 days, larvae were removed and the media was cut and rinsed. Feeding activity and egestion resulted in production of fine particles that could be washed off and collected. Processing of control alder, non-conditioned and nutrient-enriched alder, and cedar is compared in Fig. 33.

There is a trend for processing rate to increase in response to increased temperatures, and to decrease as food quality is enhanced. The results are confounded by the fact that in the 'cedar' and the 'control + nutrients' treatments, larvae remained active on the surface without extensive feeding. This may have been related to the modification of feeding cues discussed in the Growth Rate section. The food quality relationship was best illustrated by comparing the high values for the non-conditioned treatment and the low values for this type of wood with nutrients added. The high values with non-conditioned wood fits the interpretation of increased consumption of low quality foods in order to acquire sufficient nutrients (Hargrave 1972, Iversen 1974, Slansky and Feeny 1977, Grafius and Anderson 1980).

Processing Rates from Natural Substrates in the Laboratory. Laboratory studies using whole logs rather than blended wood media indicated that hardness is a primary factor determining natural feeding rates. Larvae commonly shunt feces to the log exterior where the pellets can be collected. Assimilation efficiency is low (Anderson et al. 1978), so egestion is a good index of processing. This technique

was used with a set of logs which contained L. nigrilinea larvae, maintained at 14°C. The class-3 logs were solid alder, and the two class-4 alder logs probably underwent some dry-rot prior to entry into the stream. Class 5 was represented by a single soft and discolored log. Fecal collections were made at 10, 21, and 24 days, and the class-5 log was sampled 7 times in 77 days. At least 20 fecal collections were taken each time from each log. Larvae were removed from the logs and weighed at the end of the experiment. Processing rates (Fig. 34) are expressed as percent of dry body weight per day, using mean larval weights (which were extrapolated over the experimental period to be 0.90 to 1.20 mg).

It is quite clear that highly decomposed wood is processed more rapidly by Lipsothrix than wood in an earlier decay class (223% vs 88% of the body weight per day). At rates > 1-2 x body weight per day, Lipsothrix activity will have a major effect on the mineralization of this recalcitrant material in streams. These rates are realistic, as is evidenced by a 53.2 g piece of class 5 alder in a lab stream which, after 12 months exposure to Lipsothrix, was reduced to the point where only 5 g or so retained any structural integrity.

Hardness appeared to be the major determinant of processing in this experiment, overwhelming food quality effects, especially considering that the two class 3 logs differed greatly in the extent of fungal colonization while the rates of utilization were similar. Therefore, it was hypothesized that if temperature affected natural rates, it would be as a result of influencing larval activity rather than microbial production. Fig. 34b suggests a trend for more material to be processed with an increase in temperature. Table 13 gives the values, with wood losses (1.5 - 3.5 x body weight daily) similar to estimates in Fig. 34. The logs were sprayed at the end of the experiment in order to mimic particle reduction in the field since erosion will also remove wood disturbed by larval activity. The wide variance is due to texture differences between logs in each treatment, further suggesting that wood hardness plays an overriding role in wood degradation due to Lipsothrix.

Field Studies of Processing

The impact of Lipsothrix spp. in the field was estimated by comparing caged and exposed logs maintained in the controlled section of Berry Creek from August 1977 to July 1979. Percent loss of dry weight for five types of wood is given in Table 14.

There was no impact on wood which was in decay class 1, as it was not colonized by Lipsothrix in two years. A few individuals had colonized the outer portions of the class-2 branches and logs. This wood was extensively colonized by Chironomidae (primarily Brillia and Symposiocladius) in both treatments, and had decayed to class-3 at the termination of the experiment. The small (6.6%) difference for the 'damp' class 4-5 logs is misleading because there was a large change in volume which was not reflected by weight change (Fig. 35b). The 'dry-rotted' 4-5 logs showed a very clear difference, almost 20% of the weight loss being due to Lipsothrix feeding.

The weight differences of the class-2-3 treatments do not reflect the changes in surface quality and texture due to feeding since the main mass of the logs is unaffected. Figure 35a illustrates the surface utilization by Lipsothrix. The wood density difference of the portions of wood affected by larval boring is a better indicator of impact. To estimate volume reduction, the infested outer portion wood was cut away and oven dried. After weighing, the wood was dipped into waterproof latex paint to fill up boring holes and to inhibit water absorption by wood tissue. Specific gravity of infested wood and control wood was measured by water volume displacement. Table 15 presents the density values obtained by this method. Class-3 material showed a significantly lower density as a result of larval feeding while there was no difference between the softer wood. Erosion would have had much less effect on the harder logs, and I believe that softer logs have similar densities due to abrasion of material weakened by Lipsothrix activity. Note that the class 5 wood has the same density as it had at the initiation of this experiment. This may imply that a minimum density is reached, at which point any further processing causes loss of the

tissue. It appears that density may be the most suitable measure of impact on firm wood, while weight loss provides a better index for soft wood.

Material excavated to the surface by larvae was sloughed off by rain, wind, or other forces. Erosion by the stream, however, was minimized for most treatments in this controlled stream (though it had considerable effects on the softer wood), so microbial decay probably accounted for the rest of the weight reduction of sound wood. Some error was introduced because the drying methods were different before and after treatment.

The percent weight loss of logs due to larval activity is related to the surface:mass ratio. A large log in suitable condition would be less impacted by Lipsothrix than several with equivalent total volume and weight but smaller diameters. After adjusting the previous data for surface area, the amount of weight loss during the study due to Lipsothrix spp. was 412 mg/cm^2 for the class 4-5 logs, and only 13 mg/cm^2 for a class-2-3 branch. A value of 27 mg/cm^2 was estimated from the density figures for the class 2-3 seasoned logs. During much of the experiment larvae were small, so on a per day basis, these estimates will be low.

Ecosystem Role in Relation to Physical Processing

The preceding experiments illustrate the importance of history in determining degradation rates for alder wood. Dry-rotted logs can be colonized through much of the matrix quite rapidly, whereas those which enter the stream in decay classes 1 or 2, or even 3 will only be affected at the surface layer. The course of degradation once a log becomes available to Lipsothrix is determined to a large degree by the amount of abrasion due to waterflow. Erosion of wood will vary with stream size and run-off dynamics, local physical structure, and extent of submergence of the log. The following experiment points out how local positioning can affect wood reduction by physical processing and microbial decay in the absence of Lipsothrix.

Three pieces of alder without larvae (live wood, class 2 seasoned wood, and class 4-m dry-rotted material) were each cut into three equal sections. They were placed into an artificial stream trough so that one of each type was (a) fully submerged, (b) 50% submerged, and (c) above but just touching the water. Current velocity was approximately 30 cm/sec. The trough was screened to prevent oviposition. After 22 months, the wood was dried and weighed, and density was determined by volume displacement with two replicates from each piece (Table 16). No pre-experiment weights were taken so that only obvious patterns were observed.

Two observations can be made from the submergence experiment. First, the erosive force of the water flow had a significant impact only upon the soft material. The non-submerged soft piece was nearly identical with its initial condition; the fully submerged was extensively reduced but still relatively entire. However, the constant disturbance at the water surface reduced the half-submerged piece to an eroded fragment (Fig. 36c). The second observation was that there was no density difference for the soft (Class 5), nor for the new (Class 1) treatments, while the out-of-water seasoned wood (Class 2-3) was less dense than the two in-water treatments. The emergent wood had large growths of dry-rot fungi (Polyporaceae) (Fig 36b), suggesting that its lower density was the result of greater microbial decay. The live wood out of water was 50% covered with white fungal mycelia while no other treatment had external evidence of fungi (Fig. 36a). One might conclude that sound alder will degrade more rapidly in the semi-terrestrial habitats, but once it is softened, microbial decay is less important because most of the usable constituents have been removed. Erosion will then increase wood loss in streams faster than occurs out of water.

Table 17 provides estimates of the impact of both Lipsothrix species in various habitats. These data take into account the size of the stream, the availability of alder wood from riparian vegetation, prior conditioning or decay class of the wood, temperature, and larval

population sizes in the different streams. The total processing may be expressed as an equation:

$$\text{Proc.} = \sum_{c=3}^{5} (N \cdot F \cdot T \cdot S)_c \text{ where } N = \text{mg of larvae/cm}^2,$$

F = feeding rate/mg of larvae/unit time, T = thermal index, S = surface area of available wood, and C = decay class of the wood. Most elements are approximated since the supporting data lacked statistical significance.

Erosional disturbance is a dominant factor regulating the impact by Lipsothrix spp. in stream systems. Class 5 wood will only be found in seeps and first-order streams because in larger streams water flow abrades the soft material. This abrasion removes suitable cranefly habitat, thus reducing or retarding population densities and impact. The remaining log would be more solid, such that associated larvae would feed relatively slowly. There is also a greater chance of larger streams removing wood to the banks or downstream where other processes are responsible for degradation.

DISCUSSION

This study was initially oriented, in part, towards clarification of the role of Lipsothrix spp. in ecosystem processes. Most aquatic studies of this type treat the populations of the subject organisms as discrete entities within generalized environments. This is a realistic simplification when dealing with some systems in which resources are evenly distributed, of similar qualities and predictability, and the organisms are capable of movement between foraging microhabitats or materials. This approach is unrealistic when dealing with a system possessing a large degree of heterogeneity in both the resource patterns and the life cycles of the organisms. This problem was confounded because it centered on two species about which very little was known, living in a unique and poorly known habitat. Consequently, much of the effort involved the observation and characterization of Lipsothrix biologies and life histories.

Overview of Life Cycles: Cohort Asynchrony Within and Between Years

A general model of the life cycles of both species of Lipsothrix is presented in Figure 37. This incorporates the time of oviposition and emergence, proportions emerging in a given year, and the general growth patterns of a cohort. The two forms of variability encompassed, size of individuals of a cohort and variable timing of emergence (within and between years), are large for the family Tipulidae. Most studies indicate a much narrower local period of emergence and tighter cohort size ranges (Freeman and Adams 1972, Mendl 1973, Pritchard, in press), though different levels of voltinism are not uncommon on a regional basis (Coulson 1959, Hofsvang 1972). The latter studies include species that are typically bivoltine or univoltine, but due to the colder temperatures and attenuated growth periods associated with higher altitudes or latitudes, the local populations will instead follow a longer annual or biennial life cycle. Such life cycle extension may also be the case for Lipsothrix spp. along an altitudinal gradient.

Emergence of individuals from a single cohort in different years is largely undocumented. Pritchard (1976) cites several examples in which such "cohort-splitting" occurs. Most involve situations in which splitting results from some individuals growing more slowly due to different conditions experienced during their lifetime. Conditions can include resource quality (Pritchard 1976), temperature (Mutch 1981), and resource availability (Jonassen 1971, Benech 1972) .

There are several factors which may result in local variability in Lipsothrix growth. While most animals sample various foraging patches and thus average the conditions in all, Lipsothrix larvae are restricted to one portion of a single log. Individuals in close proximity may have very different growth patterns as a result of heterogeneity in microhabitat quality. Endogeneous variability in growth rate due to sex could not be established, but it is likely that female larvae grow more rapidly during part of their cycle, as indicated by Pritchard (1976) and Meats (1974) for two species of Tipula, to assimilate energy for egg production. Laughlin (1960) suggested a genetic component to growth rate differences in T. oleracea, but it is doubtful that physiology would account for more growth rate difference than feeding behavior and other environmentally produced variability.

Factors resulting in growth rate differences explain only part of the variability seen in Lipsothrix. The phenomenon of water level-induced pupal development is a largely undocumented but key element. White (1978) found that the elmid beetle Stenelmis sexlineata required a lowering in water level to induce pupation and adult development. Larvae of several dryopoid species would remain in the larval stage indefinitely if kept in water (Brown 1973). Even ducks may enter reproductive condition using water level as a cue (Braithwaite and Frith 1969), so this seems to be a suitable phenomenon indicating a change in environmental conditions. The relative lack of mobility of Lipsothrix is significant because other species are able to 'choose' habitats in which they may then 'wait' for the developmental cue. Lipsothrix, especially L. nigrilinea may exhibit the very large range in emergence

dates, as well as cohort splitting as a result of its inability to choose the height of its habitat in relation to water level.

The Ecosystem Role of Lipsothrix spp.

Particle Reduction of Woody Debris. The amount of wood reduction which can be attributed to Lipsothrix spp. in a variety of habitat types was estimated in the Results section. Processing increases threefold within the range of wood hardness encountered, while nutritive quality and temperature are of secondary importance. Tissue toughness has been shown in other studies to override quality as a determinant of consumption rate (Soohoo and Fraenkel 1966), and this effect may be magnified because Lipsothrix larvae cannot select foraging habitats. Temperature plays an interactive role in degradation rates by enhancing microbial activity and hence food quality (Ward and Cummins 1978), and in turn will allow slower ingestion rates by larvae to gain the same nutritional equivalent (Cummins and Klug 1979, Cammen 1980). But, because wood hardness overrides quality, the only significant temperature effect will be to increase feeding activity as a direct thermodynamic response. Besides regional differences, there will also be significant temperature differences depending on vegetation type, as Ringler and Hall (1975) showed with clearcut, partially cut and old-growth watersheds. One would expect greater processing per individual per unit time with the decreased canopy and greater thermal input of more open habitats.

The size of the larva obviously determines how much it may ingest. Population heterogeneity may in this context play an important role in processing. Extension of the life cycle beyond two years overwhelms other differences for both species in terms of lifetime processing (Table 18). Most consumption is by the fourth instar, and I would estimate this to range from 90 to 99% of the L. nigrilinea individual total and 80 to 95% of the L. fenderi total. Scriber and Slansky (1981) state that based on 10 feeding studies, an average of 58% of consumption of plant material by insect larvae took place in the final instar, which

emphasizes that in general, the early stages are relatively insignificant in terms of impact. A log containing L. nigrilinea, which remains mostly submerged, may undergo more degradation than an exposed log because larvae are forced to remain within. Likewise, L. fenderi in a warmer stream may emerge as annuals, while in a higher or covered site, growth may be slower but more wood is consumed by the larvae which remain as biennials. Lipsothrix individuals which emerge early, however, also distribute progeny early into other habitats. In a fully colonized log, density-dependent mortality reduces the impact of the next generation, while newly available or undercolonized logs may decompose faster due to early dispersal of progeny.

Several other environmental factors influence the role of Lipsothrix in particle size reduction. As noted, population density and impact increase as wood decays and softens. However, in streams larger than about second-order and in clearcut streams, erosion becomes more important, and will inhibit this decay sequence (Dudley and Anderson 1982). Densities within a stream section also change with vegetation type during forest succession, as illustrated by the idealized scheme in Figure 38. L. nigrilinea maintains itself at low densities and growth rates in mature forests until some disturbance agent opens the canopy and soil for early seral species, including alder. Populations will increase as alder wood begins to enter the stream. Local recolonization is important and the enhanced thermal regime may increase both growth of the population and its impact on processing. L. fenderi experiences even more dramatic fluctuation. Being less numerous in old growth situations (see Fig. 11), it is more dependent on immigration from other habitats to newly available materials. Due to its greater capacity for increase, wider habitat utilization, and tolerance of higher densities, L. fenderi will soon reach higher population levels. As the forest matures, this species loses ecosystem dominance but has played a large role during the period of high resource abundance.

The result is that alder, which itself decays more rapidly than other woods (Baker et al., in press), is processed most rapidly when it is most abundant. This is in essence an ecosystem process which

enhances nutrient cycling at a stage when nutrient dynamics are undergoing their greatest fluxes (Fisher and Likens 1973).

Secondary Production. Secondary production of L. nigrilinea was estimated to be on the order of 5.0 $g/m^2/yr$ for the transect logs. These values are based on quadrupling the adult production (final larval biomass approximately = 2X adult production) which was roughly equivalent to doubling the maximum larval biomass. Waters (1969) uses a turnover ratio (production: mean biomass) of 5 for benthic insect production. My conservative value of two is due to the longer life cycles and lower mortality experienced by Lipsothrix. Nevertheless, production is greater than that of Simuliidae (2.2 $g/m^2/yr$), which are dominant species in similar streams (Speir 1976), or Lepidostoma quercina, an abundant leaf detritivore (0.19 $g/m^2/yr$, Grafius and Anderson 1979). The higher value is because the habitat of Lipsothrix spp., although nutritionally poor on a weight basis, is abundant where it occurs. Production values for a stream reach would be much lower because the suitable habitat patches are sparsely distributed within the stream. Mean larval biomass may range from 34.7 mg/m^2 in first- and second-order mid-forest succession streams to near zero in third-order old-growth or early succession streams, so fine particle production by Lipsothrix larvae may range from 0 to 30.3 $g/m^2/yr$. If there is significant re-ingestion of fecal material, as is likely, these figures are an overestimate.

Evolutionary Consequences of Xylophagy

Woody Debris as a Habitat. There are relatively few wood-associated species and the standing crop of aquatic invertebrates on wood may be two orders of magnitude less than the standing crop on leaf packs. What are the evolutionary barriers to the colonization of woody debris in streams, how have they been overcome by Lipsothrix spp., and what are the advantages and consequences of this particular choice of habitat?

Wood is highly refractory, and requires development of mouth parts and musculature capable of handling tough tissue. In fact, there is a high degree of analogous adaptation of mouth parts of several aquatic xylophages, including Lipsothrix (Fig. 39). Wood is nutritionally very poor, with C/N ratios >300 (Anderson et al. 1978). Alder wood, however, may range from 30 to 300, depending on the extent of conditioning by aquatic or terrestrial micro-organisms, which provide the bulk of nutrition to xylophages. The nitrogen content is still several times lower than in other foods in streams, such as leaves and diatoms (Anderson et al. 1978).

There are four general classes of mortality which impact all organisms. These include resource availability, predation and disease, inter- and intra-specific competition, and abiotic mortality. All have been discussed in the Results section, and Table 19 summarizes how Lipsothrix copes with each. In fact, once the hurdle of xylophagy is cleared, there appear to be definite advantages to internal habitation of stream wood. The physiological aspects of xylophagy are relatively unexplored, and may hold the most important keys to understanding the utilization of, and restriction to, wood as a resource (Cummins and Klug 1979).

Evolutionary Advantage of Life Cycle Extension. One of the life history consequences of detrital wood utilization appears to be the extension of the life cycle. This is indicated for both terrestrial (Hamilton 1978) and aquatic (Anderson et al. 1978) environments. Because of the low nutritional quality of wood, a long life cycle may be necessary to acquire sufficient nutrients for adequate size and reproduction. However, there may also be some advantage to extending generation time.

Although low food quality will depress growth rates, the question remains as to why the organisms do not sacrifice size to keep age at reproduction constant. Another aquatic xylophage, Lara avara (Elmidae), may live for 3 or more years, but is about an order of magnitude heavier than other detritus and algae feeding elmids. Other insects in dead wood are also larger than related taxa in different

habitats (Cerambycidae - Monsour and Monsour - Bek 1934, Camponotus ants - Borror and DeLong 1976, Siricidae-Furniss and Carolin 1977). Lipsothrix are not notably large for the family Tipulidae, however the scant literature on the Limoniinae may suggest that they, and especially L. nigrilinea, are relatively large for their subfamily (Hadley 1969).

The increased size of wood-feeding invertebrates implies that nutritional deficiency may not be the sole reason for extended life cycles. Calow (1977) details three advantages of increased size to the individual. First, larger females produce more offspring. Second and third, larger size and the attendant greater strength confer both a competitive advantage and greater predator immunity to the individual. If juvenile mortality is high, then very few individuals are able to even reach a size that will make these advantages available. However, mortality within these logs is relatively low, such that a relatively large proportion of a single clutch reaches maturity. When juvenile mortality is low in relation to adult mortality, Schaffer (1974) suggests that increases in the age at reproduction will be selectively advantageous. This may be especially true since greater age and larger size produce an adult cranefly better able to resist both predators and abiotic mortality.

Comparative Life History Adaptations in Relation to Habitats. Despite the general similarities, there are differences between the two Lipsothrix species which may be related to their habitats. A dead log offers a habitat that, when compared with the benthic substrate or to other typical larval tipulid habitats, is both constant and predictable with respect to environmental perturbation. Different logs, however, may vary in their suitability and in the risk of mortality to animals within. If durational stability (habitat favorability in relation to generation time) is high, then selection should favor traits characteristic of so-called 'K-selected' populations, such as decreased fecundity and dispersal with increases in age at reproduction, competitive and defensive ability, and parental care (MacArthur and Wilson 1967, Southwood and Comins 1976). Despite the conceptual

limitations of the 'r-K continuum' when it is applied to natural systems (Grime 1979), it is a useful framework for comparing some traits in this system.

L. fenderi is sympatric with L. nigrilinea yet extends into some habitats considered more marginal. Several lines of evidence indicate that its populations experience greater mortality. Comparing the two species, L. nigrilinea has characteristics of 'K-selected' populations, while L. fenderi exhibits traits of a fugitive or 'r-type' species, as indicated in Table 20. Selection for reproductive traits of L. fenderi seens to have favored quantitative ones over those increasing reproductive quality, as suggested by 'sloppy' traits such as poor distinction of oviposition site quality, tolerating high densities, dumping eggs, or even emerging out of season without eggs.

The dichotomous grouping of life history traits results in some oversimplification. One exception in the comparison of these traits above relates to the overriding necessity for dispersal, which is typically thought to be more important for fugitive species. Suitable logs are patchily distributed within the watershed. Adults disperse to find suitable oviposition sites because larvae are incapable of significant dispersal. L. nigrilinea adults are also potentially better dispersers than L. fenderi due to their greater strength for flying, though approximately equal colonization occurred in the experimental logs placed in many watershed types. It is apparent that dispersal is of equal if not greater import in the life cycle of the so-called 'K' species, contrary to the typical pattern. This is important because if L. nigrilinea is to maintain its competitive superiority over L. fenderi, it must disperse nearly as well, due to L. fenderi's more rapid rate of increase in new habitats. Otherwise, the habitat will deteriorate before L. nigrilinea becomes fully established. At the same time, L. nigrilinea has the advantage that it is able to maintain populations in old-growth situations within atypical wood, so is already present if suitable wood enters the stream.

The large degree of variability in life cycles probably results from two seemingly opposing environmental characteristics. First, the

predictable constancy of a log allows greater developmental flexibility just as it allows, rather than causes, increased size and age. Secondly, stochastic variability (water level changes, temperature differentials, etc.) between logs and portions of logs results in population variability in size and in timing of developmental stages. While this at times entails some reduction of parental fitness, den Boer (1968) points out that variability within the cohort may ultimately confer an advantage if part of the cohort survives or does better as a result of 'spreading the risk' of mortality. A monotypic phenotype or population would be more susceptible to extinction in an environment where some mortality sources are highly stochastic.

L. nigrilinea possesses considerable phenotypic plasticity, especially in timing, because it must respond to a habitat which is suitable for emergence for only a short period when water level is low. On the other hand, it suffers relatively little mortality from biotic or abiotic factors due to its habitat preference. A change in emergence suitability, such as if water level rises abruptly, is tolerated because there is a high certainty that the habitat will be suitable when levels descend after a few days or the following year. The flexible developmental response to water level in an otherwise nearly constant habitat makes possible the advantage of accruing greater size without serious risk of desiccation and other mortality. The primary cost of this strategy is lack of population synchrony, and whatever deficit in rate of increase may be imposed by a greater age at reproduction. In the absence of the ultimate emergence cue of water level, a proximate cue such as thermal accumulation or an endogenous cue may induce metamorphosis. An interesting extension to these studies would be to rear larvae under constant conditions which are suitable for emergence to discern whether these cues will result in emergence at an 'optimal' size, which would maximize the rate of increase.

Because L. fenderi is more catholic in its habitat utilization, it cannot be assured the same predictability of future habitat suitability. In 'good' habitats, it may survive if competitor and predator densities (including L. nigrilinea) are sufficiently low, while

in marginal or more temporary habitats, good survival may occur in a wetter or more benign year. Consequently, this species pupates in response to indirect cues which carry some predictive capacity, such as temperature. The population may benefit from more synchronous emergence, and it has largely foregone the risks (and advantages) of remaining within the log. This strategy is more deterministic than the dual cue of L. nigrilinea, and occasionally leads to individual errors, such as emerging underwater or dying from desiccation in the marginal logs.

The likelihood of mortality is a factor which tends to balance the advantage of increasing life cycle duration. The longer an individual remains within a log, the more likely it is to experience stochastic abiotic mortality, density-caused competition, and other negative impacts. It seems reasonable to assume that while both sexes gain by the size advantage the males may do better to emerge at a smaller size and younger age. Reproductive material is metabolically expensive to produce, so the cost of sperm to the males is energetically much less than the cost of the reproductive apparatus of females. Also, mating can occur soon after emergence, so the mission may be completed much earlier for males, with less risk of death while the reproductive value is still high (Stearns 1976). Migration is probably the role of females since mate-finding would be more successful near the larval habitat before dispersal (Dingle 1972).

Flexibility in development can allow male Lipsothrix, especially L. nigrilinea, to follow a strategy different than that of females. Early reproduction (males appeared to less commonly become triennials) is selectively advantageous because if there is no mate selection for large males, the male 'r' would be greater. This is possibly one reason why, with some insects in which the sex is not fixed, the smaller individuals generally become males (Charnov et al. 1981). By remaining longer within a log, female larvae may experience additional mortality, resulting in the male-biased sex ratio of L. nigrilinea.

Lipsothrix Biology and the Implications for Community Ecology

Streams are characteristically perturbed by seasonal high water flows. Although these events are predictable on a seasonal basis, there are few non-predatory aquatic insects which have life cycles greater than the annual periodicity of this disturbance. Either enough stochasticity exists such that these events cannot be 'predicted' accurately, or they are intense enough that avoidance is necessary either by eggs or with the cushion of large numbers of offspring. Detritivores are especially likely to be annuals because their food resources are generally available on a seasonal basis (Ross 1963).

In only a few aquatic microhabitats are conditions temporally stable enough to allow associated species to evolve multi-annual life cycles. Woody debris is apparently one such resource, so the associated community, while possessing less taxonomic diversity, seems to exhibit a greater latitude of potential and realized life histories. The system is still representative of a non-equilibrium community (Connell 1978), in which disturbance usually prevents a self-replacing climax to persist. Log disturbance, or maturational deterioration, may preclude the development of fauna living much more than two years. Biennialism, as found in the genus Lipsothrix, may thus be common among xylophagous insects in the same manner that biennialism was the reproductive strategy most suited to plants occupying the moderately disturbed intermediate stages of vegetative succession (Hart 1977).

The wood habitat may be suitable for examining processes, such as biotic interactions or successional development, which are more ephemeral or non-existent in the rest of the stream. The two species of Lipsothrix, for instance, do exhibit both morphological and behavioral traits which are assumed to confer different ecological advantages within a competitive framework as discussed previously. With regard to successional patterns, the stream log system is interesting because in addition to being one of the only stream components which clearly exhibits successional sequences, the process seems to be more additive than one involving species replacement. In other words,

species richness of associated organisms increases with log degradation (Dudley and Anderson 1982) as early taxa cause alterations which facilitate colonization by later ones. Pioneers are themselves still present throughout the cycle because they are more opportunistic in their use of wood, and habitat complexity increases as decay becomes internalized, allowing greater diversity of utilization.

Some recent interest in evolutionary processes within stream communities has focused primarily on vagile benthic insects (Hildrew and Townsend 1976, Peckarsky 1979, Wiley 1981). These organisms may be as difficult to use for illustrating theoretical evolutionary processes as are bird communities, because of the problems of monitoring specific groups or individuals, and identifying interacting factors in temporally and spatially heterogeneous patches. Semi-sessile grazers (Hart and Resh 1980) and filter-feeders (McAuliffe 1982) offer the advantage of reduced mobility but may still suffer from the problem that their life cycles are geared towards surviving abiotic disturbance more so than competition, and probably represent one end of the competitive spectrum. Rather than suggesting that future work on biotic interactions in streams take place in logs, it is reasonable to suggest that such work take place within the context of the disturbance cycles encountered by organisms, as Sousa (1979) has done in marine intertidal communities. In this manner, stream ecology can then be incorporated into a larger body of knowledge concerning the maintenance of structure in natural communities.

LITERATURE CITED

Alexander, C.P. 1920. The crane-flies of New York. Part II. Biology and phylogeny. Cornell Univ. Agr. Exp. Stn. Mem. 38: 691-1133.

Alexander, C.P. 1931. Deutsche limnologische Sunda Expedition. The craneflies (Tipulidae, Diptera). Arch. Hydrobiol. Suppl. 9, Tropische Binnengewasser 2:135-191.

Alexander, C.P. 1949. Records and descriptions of North American crane-flies (Diptera), Part VIII. The Tipuloidea of Washington. Am. Midl. Nat. 423: 257-333.

Alexander, C.P. 1954. Records and descriptions of North American crane-flies (Diptera) Part IX. The Tipuloidea of Oregon, I. Am. Midl. Nat. 51: 1-86.

Alexander, C.P. 1964. Undescribed species of Nearctic Tipulidae (Diptera). IV. Great Basin Nat. 24: 19-25.

Anon. 1978. Water resource data for Oregon. USGS Water Data Rept. OR-78-1.

Anderson, N.H. and K.W. Cummins. 1979. The influences of diet on the life histories of aquatic insects. J. Fish. Res. Bd. Canada 36: 335-342.

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Ent. 24: 351-77.

Anderson, N.H., J.R. Sedell, L.M. Roberts, and F.J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. Am. Midl. Nat. 100 (1): 64-82.

Ausmus, B. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. In: Lohm, U. and T. Persson (eds.) Soil organisms as components of ecosystems, Proc. 6th Int. Coll. Soil Zool., Ecol. Bull. (Stockholm) 25: 180-192.

Baker, J.H., R.Y. Morita and N.H. Anderson. 1983. Bacterial activity associated with decomposition of woody substrates in a stream sediment. Appl. Envir. Microbiol. (in press).

Barlöcher, F. and B. Kendrick. 1973. Fungi in the diet of Gammarus pseudolimnaeus (Amphipoda). Oikos 24: 295-300.

Barnes, H.F. 1937. Methods of investigating the bionomics of the common cranefly, Tipula paludosa Meigen, together with some results. Ann. Appl. Biol. 24: 256-268.

Benech, V. 1972. Le polyvoltinisme chez Baetis rhodani Pictet (Insecta, Ephemeroptera) dans un ruisseau a truites de Pyenees-Atlantiques, le Lissuraga. Ann. Hydrobiol. 3: 141-171.

Bilby, R.E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62: 1234-1243.

Borror, D.J., D.M. DeLong and C.A. Triplehorn. 1976. An introduction to the study of insects, 3rd ed. Holt, Rinehart and Winston, New York.

Braithwaite, L.W. and H.J. Frith. 1969. Waterfowl in an inland swamp in New South Wales. III. Breeding. CSIRO Wildlife Res. 14: 65-109.

Brindle, A. 1960. The larvae and pupae of the British Tipulinae (Dipt, Tipulidae). Trans. Soc. Brit. Entom. 14: 63-114.

Brown, H.P. 1973. Survival records for elmid beetles, with notes on laboratory rearing of various dryopoids. Entomol. News 84: 278-284.

Brown, E.S. and A.B. Duncan. 1949. A list of Tipulinae (Diptera, Nematocera) of the Solway area, with some notes on the habitats of the adults. Scott. Nat. 61: 156-168.

Buckley, B.M. and F.J. Triska. 1978. Presence and ecological role of nitrogen-fixing bacteria associated with wood decay in streams. Verh. Int. Verein. Limnol. 20: 1333-1339.

Butterfield, J.E.L. 1976a. The response of development rate to temperature in the univoltine cranefly Tipula subnodicornis Zetterstadt. Oecologia (Berl.) 25: 89-100.

Butterfield, J. 1976b. Effect of photoperiod on a winter and on a summer diapause in two species of cranefly (Tipulidae). J. Ins. Physiol. 22: 1443-46.

Butterfield, J. and J.C. Coulson. 1975. Insect food of adult red grouse Lagopus lagopus scotius (Lath). J. Anim. Ecol. 44: 601-608.

Byers, G.W. 1978. Tipulidae. Ch. 19 In: R.W. Merritt and K.W. Cummins (eds). An introduction to the aquatic insects of North America. Kendall-Hunt, Dubuque, Iowa.

Calow, P. 1977. Ecology, evolution and energetics: A study in metabolic adaptation. Adv. Ecol. Res. 10: 1-62.

Cammen, L.M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores Oecologia (Berl.). 44: 303-310.

Carter, J.B. 1976. A survey of microbial, insect and nematode parasites of Tipulidae (Diptera) larvae in northeast England. J. Appl. Ecol. 13: 103-122.

Charnov, E.L. 1981. Sex ratio evolution in a variable environment. Nature 289: 27-33.

Cody, M.L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199: 1302-1310.

Coulson, J.C. 1959. Observations on the Tipulidae (Diptera) of the Moor House Nature Reserve, Westmorland. Trans. R. Entom. Soc. Lond. 111: 157-174.

Cummins, K.W. 1973. Trophic relations of aquatic insects. Ann. Rev. Ent. 18: 183-206.

Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147-172.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck and V.I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54: 336-345.

den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. Acta. Biotheor. 18: 165-194.

den Hollander, J. 1975. The growth of larvae of Tipula oleracea L., 1758 (Diptera, Tipulidae). Tijdschr. Entomol. 118: 67-82.

Dingle, H. 1972. Migration strategies of insects. Science 175: 1327-35.

Dudley, T. and N.H. Anderson. 1982. A survey of the invertebrates associated with wood debris in aquatic habitats. Melanderia 39: 1-21.

Egglishaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463-476.

Fisher, S.G. and G.E. Likens. 1973. Energy flow in Bear Brook, New Hampshire. An integrative approach to stream metabolism. Ecol. Monogr. 43: 421-491.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Pac. Northwest For. and Range Exp. Stn. Gen. Techn. Rep. PNW-8.

Freeman, B.E. 1964. A population study of Tipula species (Diptera, Tipulidae). J. Anim. Ecol. 33: 129-40.

Freeman, B.E. 1968. Studies on the ecology of adult Tipulidae (Diptera) in southern England. J. Anim. Ecol. 37: 339-62.

Freeman, B.E. and C.A. Adams. 1972. The spatial and temporal distribution of adult Tipulidae (Diptera) in southern England. J. Anim. Ecol. 37: 339-362.

Fremling, C.R. 1967. Methods for mass-rearing Nexagenia mayflies (Ephemeroptera: Ephemeridae). Tr. Am. Fish. Soc. 96: 407-410.

Furniss, R.L. and V.M. Carolin. 1977. Western forest insects. USDA-F.S. Misc. Publ. #1339.

Gilbertson, R.L. 1980. Wood-rotting fungi of North America. Mycologia 72: 1-49.

Grafius, E. and N.H. Anderson. 1979. Population dynamics, bioenergetics, and role of Lepidostoma quercina Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. Ecology 60: 433-441.

Grafius, E. and N.H. Anderson. 1980. Population dynamics and role of two species of Lepidostoma (Trichoptera: Lepidostomatidae) in an Oregon coniferous forest stream. Ecology 61: 808-816.

Graham, K. 1967. Fungal-insect mutualism in trees and timber. Ann. Rev. Ent. 12: 105-126.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester.

Hadley, M. 1969. The adult biology of the crane-fly Molophilus ater Meigen. J. Anim. Ecol. 38: 765-90.

Hadley, M. 1971. Aspects of the larval ecology and population dynamics of Molophilus ater Meigen. (Diptera: Tipulidae) on a Pennine moorland, J. Anim. Ecol. 40: 445-66.

Hall, J.D. and C.O. Baker. 1975. Biological impacts of organic debris in Pacific Northwest streams. p. 1-13. In: Logging debris in streams; a workshop. Oregon St. Univ., Corvallis.

Hamilton, W.D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature, Lond. 228: 1218-1220.

Hamilton, W.D. 1978. Evolution and diversity under bark. p. 154-175. In: Mound, L.A. and N. Waloff (eds.). Diversity of insect faunas. Symp. R. Ent. Soc. Lond. #9.

Hargrave, B.T. 1972. Prediction of egestion by the deposit-feeding amphipod Hyalella azteca. Oikos 23: 116-124.

Hart, D.D. and V.H. Resh. 1980. Movement patterns and foraging ecology of a stream caddisfly larva. Can. J. Zool. 38: 1174-1185.

Hart, R. 1977. Why are biennials so few? Am. Nat. 111: 792-794.

Hartman, M.J. and C.D. Hynes. 1980. Environmental factors influencing hatching of Tipula simplex eggs (Diptera: Tipulidae). Pan-Pac. Entom. 56: 268-272.

Hemmingsen, A.M. 1952. Oviposition of craneflies from different localities. Vidensk. Medd. Dan. Naturlist, Foren. Kjobenhaven 123: 81-110.

Hemmingsen, A.M. 1965. The lotic cranefly, Tipula saginata Bergroth, and the adaptive radiation of the Tipulinae, with a test of Dyar's law. Vidensk. Medd. Naturalist. Foren. Kjobenhavn 128: 93-150.

Hildrew, A.G. and C.R. Townsend. 1976. The distribution of two predators and their prey in an iron rich stream. J. Anim. Ecol. 45: 41-57.

Hinton, H.E. 1955. The structure of the spiracular gill of Lipsothrix (Tipulidae), with some observations on the living epithelium isolated in the gill at the pupa-adult moult. Proc. R. Ent. Soc. Lond (A) 30: 1-14.

Hinton, H.E. 1957. The structure and function of the spiracular gill of the fly Taphrophila vitripennis. Proc. R. Soc. (B) 147: 90-120.

Hinton, H.E. 1967. Structure of the plastron in Lipsothrix, and the polyphyletic origin of plastron respiration in Tipulidae. Proc. R. Ent. Soc. Lond (A) 42: 35-38.

Hinton, H.E. 1981. Biology of insect eggs. Pergamon Press, Oxford.

Hofsvang, T. 1972. Tipula excisa Schum. (Diptera, Tipulidae), life cycle and population dynamics. Norw. J. Entom. 19: 43-48.

Hutchinson, G.E. 1951. Copepodology for the ornithologist. Ecology 32: 571-577.

Hynes, C.D. 1965. The immature stages of the genus Lipsothrix in the western United States (Tipulidae: Diptera). Pan-Pac. Entom. 41: 165-172.

Hynes, H.B.N. 1970. The ecology of running waters. Univ. Toronto Press. 555 pp.

Hynes, H.B.N. and M.J. Coleman. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13: 569-573.

Iversen, T.M. 1974. Ingestion and growth in Sericostoma personatum in relation to the nitrogen content of ingested leaves. Oikos 25: 278-282.

Jonasson, P.M. 1971. Population studies of Chironomus anthracinus. p. 220-231. In: P.J. den Boer and G.R. Gradwell (eds.). Dynamics of Populations. Centre for Agric. Publ. and Documentation, Wageningen.

Jones, E.B.G. and A.C. Oliver. 1964. Occurrence of aquatic hyphomycetes on wood submerged in fresh and brackish water. Trans. Brit. Mycol. Soc. 47: 45-48.

Kaushik, N.K. and H.B.N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. J. Ecol. 56: 229-243.

Keller, E.A. and F.J. Swanson. 1979. Effects of large organic material on channel form and fluvial processes. Earth. Surf. Proc. 4: 361-380.

Larkin, P.A. and C.A. Elbourne. 1968. Some observations on the fauna of dead wood in live oak trees. Oikos 15: 79-92.

Laughlin, R. 1960. Biology of Tipula oleracea L.: Growth of the larvae. Ent. Exp. Appl. 3: 185-97.

Leopold, L.B., M.G. Wolman and J.P. Miller. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.

McAuliffe, J.R. 1982. Colonization patterns, competition and disturbance in stream benthic communities. In: J.R. Barnes and G.W. Minshall (eds.). The testing of general ecological theory in lotic ecosystems. Sympos. N. Am. Benthol. Soc. 1981. Plenum Press, New York. (in press).

MacLean, S.F. 1973. Life cycle and growth energetics of the arctic cranefly Pedicia hannai antenatta. Oikos 24: 436-43.

Maclean, S.F. and F.A. Pitelka. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24: 19-40.

Martin, M.M. 1979. Biochemical implications of insect mycophagy. Biol. Rev. 54: 1-21.

Meats, A. 1970. Susceptibility of the leatherjackets Tipula oleracea and T. paludosa to soil flooding. Ann. Appl. Biol. 65: 25-30.

Meats, A. 1974. A population model for two species of Tipula (Diptera, Nematocera) derived from data on their physiological relations with their environment. Oecologia (Berl.) 16: 119-138.

Meats, A. 1975. The developmental dynamics of Tipula paludosa and the relation of climate to it growth pattern, flight season and geographical distribution. Oecol. 19: 117-28.

Mendl, H. 1973. Limoniinen aus dem Breitenbach (Diptera: Tipulidae). Arch. Hydrobiol. 71: 255-270.

Merritt, R.W. and D.L. Lawson. 1979. Leaf litter processing in floodplain and stream communities. In: R.R. Johnson and J.F. McCormick (eds.). Strategies for protection and management of floodplain wetland and other riparian ecosystems. USDA Forest Service Gen. Tech. Rep. WO-12, Washington, DC.

Milne, A., R. Laughlin and R.E. Coggins. 1965. The 1955 and 1959 population crashes of the leatherjacket, Tipula paludosa Meigen in Northumberland. J. Anim. Ecol. 34: 529-544.

Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland spring brook community. Ecology 48:139-149.

Monsour, K. and J.J. Monsour-Bek. 1934. On the digestion of wood by insects. J. Exp. Biol. 11: 243-256.

Moore-Landecker, R. 1972. Fundamentals of the fungi. Prentice-Hall, Englewood Cliffs, N.J.

Mutch, R.A. 1981. Life histories of two insect shredders and their role in detritus degradation in Rocky Mountsin streams. Ph.D. Diss., Univ. of Calgary.

Myers, J.H. and R. Iyer,. 1981. Phenotypic and genetic characteristics of the European cranefly (Tipula paludosa) following its introduction and spread in western North America. J. Anim. Ecol. 50: 519-532.

Nielsen, P., O. Ringdahl and S.L. Tuxen. 1954. In: The zoology of Iceland. Diptera 1, 3, Pt. 48. Copenhagen and Reykjavik.

Peckarsky, B.L. 1979. Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams. Limnol. Oceanogr. 24: 59-68.

Pereira, C.R.D. 1980. Life history studies of Cinygma integrum Eaton (Ephemeroptera: Heptageniidae) and other mayflies associated with wood substrates in Oregon streams. M.S. thesis, Oregon St. Univ., Corvallis.

Pereira, C.R.D., N.H. Anderson and T. Dudley. 1982. Gut content analysis of aquatic insects from wood substrates. Melanderia 39: 23-33.

Petersen, R.C. and K.W. Cummins. 1974. Leaf processing in a woodland stream. Freshwat. Biol. 4: 343-368.

Price, P.W. 1974. Energy allocation in ephemeral adult insects. Ohio J. Sci. 74: 380-87.

Pritchard, G. 1976. Growth and development of larvae and adults of Tipula sacra Alex. (Insecta: Diptera) in a series of abandoned beaver ponds. Can. J. Zool. 54: 206-84.

Pritchard, G. 1978. Study of dynamics of populations of aquatic insects: the problem of variability in life history exemplified by Tipula sacra Alex. (Diptera; Tipulidae). Verh. Int. Ver. Theor. Angew. Limnol. 20: 2634-40.

Pritchard, G. 1980. Life budgets for a population of Tipula sacra (Diptera; Tipulidae). Ecol. Entom. 5: 165-173.

Pritchard, G. 1983. Biology of Tipulidae. Ann. Rev. Ent. (in press).

Pritchard, G. and H.A. Hall. 1971. An introduction to the biology of craneflies in a series of abandoned beaver ponds, with an account of the life cycle of Tipula sacra Alex. (Diptera; Tipulidae) Can. J. Zool. 49: 467-482.

Pritchard, G. and M. Stewart. 1982. How cranefly larvae breathe. Can. J. Zool. 60: 310-317.

Ringler, N.H. and J.D. Hall. 1975. Effects of logging on water temperature and dissolved oxygen in spawning beds. Trans. Am. Fish. Soc. 104: 111-121.

Rogers, J.S. 1933. The ecological distribution of the crane-flies of northern Florida. Ecol. Monogr. 3: 1-74.

Rogers, J.S. and G.W. Byers. 1956. The ecological distribution, life history, and immature stages of Lipsothrix sylvia (Diptera: Tipulidae). Occas. Pap. Mus. Zool. Univ. Michigan No. 572:

Ross, H.H. 1963. Stream communities and terrestrial biomes. Arch. Hydrobiol. 59: 235-242.

Sanders, P.F. and J.M. Anderson. 1979. Colonization of wood blocks by aquatic hyphomycetes. Trans. Brit. Mycol. Soc. 73: 103-197.

Savely, H.E. 1939. Ecological relationships of certain animals in dead pine and oak logs. Ecol. Monogr. 9: 321-385.

Savory, J.G. 1954. Damage to wood caused by micro-organisms. J. Appl. Bacteriol. 17: 213-218.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108: 783-790.

Scriber, J.M. and F. Slansky. 1981. The nutritional ecology of immature insects. Ann. Rev. Entom. 26: 183-211.

Shigo, A.L. 1967. Successions of organisms in discoloration and decay of wood. p. 237-239. In: J.A. Romberger and P. Mikola. International Review of Forestry Research II. Academic Press, New York.

Slansky, F. and P. Fenny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. Ecol. Monogr. 47: 209-228.

Snow, W.E. 1953. Stratification of arthropods in wet stump cavities. Ecology 39: 83-88.

Soohoo, C.F. and G. Fraenkel. 1966. The selection of food plants by ruminants. In: J. Harborne (ed.) Phytochemical Ecology. Proc. Phytochem. Soc., Symp. 1971.

Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227-254.

Southwood, T.R.E. and H.N. Comins. 1976. A synoptic population model. J. Anim. Ecol. 405: 949-965.

Speir, J.A. 1976. The ecology and production dynamics of four species of blackflies in western Oregon streams. Ph.D. Diss. Oregon St. Univ., Corvallis. 297 p.

Stearns, S.C. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47.

Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote, and J.R. Coulson. 1965. A catalogue of the Diptera of America. U.S.D.A. Handbook 276.

Swanson, F.J. and G.W. Lienkaemper. 1978. Physical consequences of large organic debris in Pacific Northwest streams. USDA For. Serv. PNW For. and Range Exp. Stn. Gen. Tech. Rept. #69.

Sweeney, B.W. 1978. Bioenergetics and developmental response of a mayfly to thermal variation. Limnol. Oceanogr. 23: 461-477.

Swift, M.J. 1977. The roles of fungi and animals in the immobilization and release of nutrient elements from decomposing branch-wood. In: Lohm, U. and T. Persson (eds.) Soil Organisms as Components of Ecosystems. Proc. 6th Int. Coll. Soil Zool., Ecol. Bull. (Stockholm) 25: 193-202.

Taylor, L.R. 1974. Insect migration, flight periodicity and the boundary layer. J. Anim. Ecol. 43: 225-238.

Teskey, H.J. 1976. Diptera larvae associated with trees in North America. Mem. Ent. Soc. Canada no. 100.

Triska, F.J. and K. Cromack. 1980. The role of wood debris in forests and streams. In: Waring, R.H. (ed.) Forests: Fresh Perspectives from Ecosystem Analysis, Proc. 40th Ann. Biol. Coll., Oregon St. Univ. Press, Corvallis.

Wallace, J.B. and F.F. Sherberger. 1974. The larval retreat and feeding net of Macronemum carolina Banks (Trichoptera: Hydropsychidae). Hydrobiol. 45: 177-184.

Ward, G.M. and K.W. Cummins. 1978. Effects of food quality on growth of a stream detritivore, Paratendipes albimanus (Meigen) (Diptera: Chironomidae). Ecology 60: 57-64.

Warren, C.K., J.H. Wales, G.E. Davis and P. Doudoroff. 1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manag. 28: 617-660.

Waters, T.F. 1969. The turnover ratio in production ecology of freshwater invertebrates. Am. Nat. 103: 173-185.

White, D.S. 1978. Life cycle of the riffle beetle, Stenelmis sexlineata (Elmidae). Ann. Ent. Soc. Am. 71: 121-125.

White, J.H. 1951. Observations of the life history and biology of Tipula lateralis Meig. Ann. Appl. Biol. 38: 748-58.

Wigglesworth, V.B. 1965. The Principles of Insect Physiology. Methuen, London.

Wiley, M.J. 1981. Interacting influences of density and preference on the emigration rates of some lotic chironomid larvae (Diptera: Chironomidae). Ecology 62: 426-438.

Willoughby, L.G.G. and J.F. Archer. 1973. The fungal spora of a freshwater stream and its colonization pattern on wood. Freshwat. Biol. 3: 219-239.

Winterbourn, M.J. 1980. Benthic communities of South Island beech forest streams. Beech Res. News 7: 5-10.

Wood, H.G. 1952. The crane-flies of the Southwest Cape (Diptera; Tipuloidea). Ann. So. Afr. Mus. 39: 1-327.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.

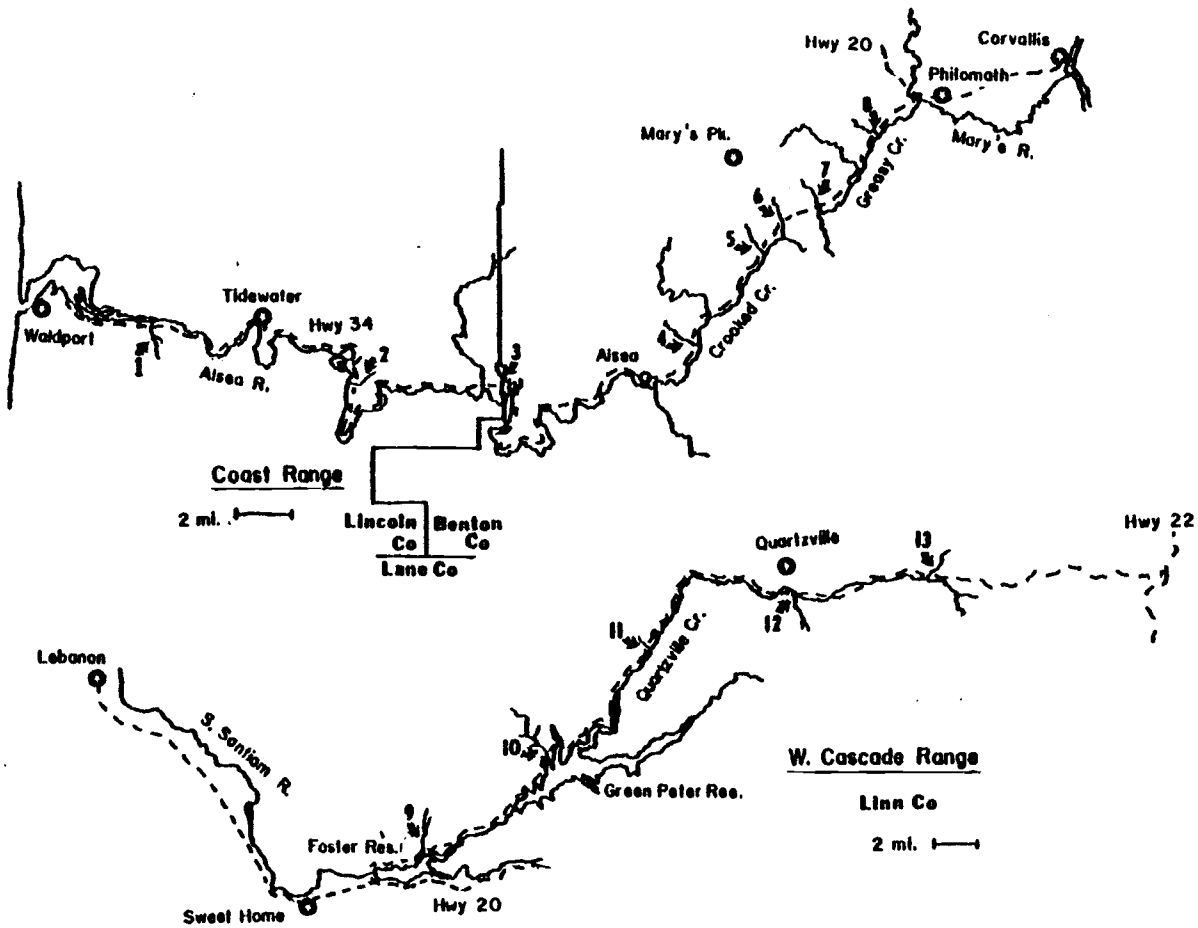


Fig. 1. Sampling sites for monthly transect collections, descriptions in Table 1. Numbered arrows denote the streams sampled, dashed lines indicate roads.

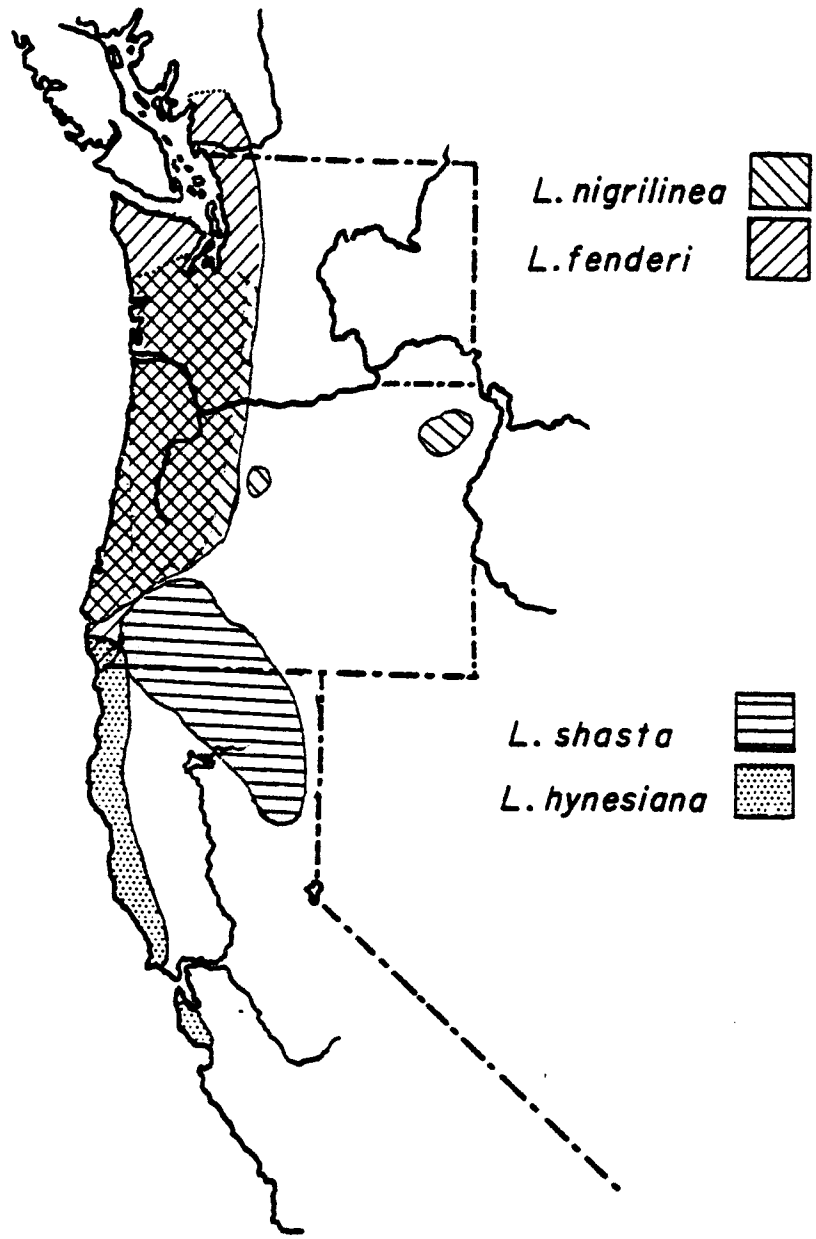


Fig. 2. Distributions of western species of Lipsothrix.

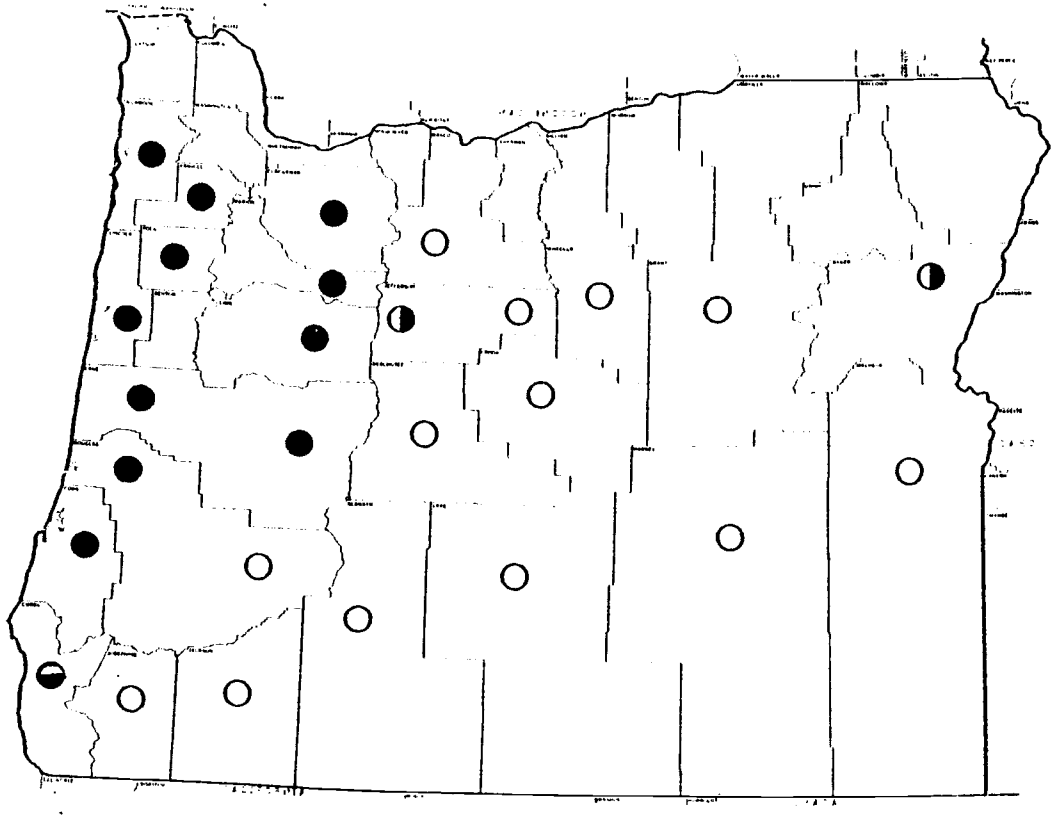
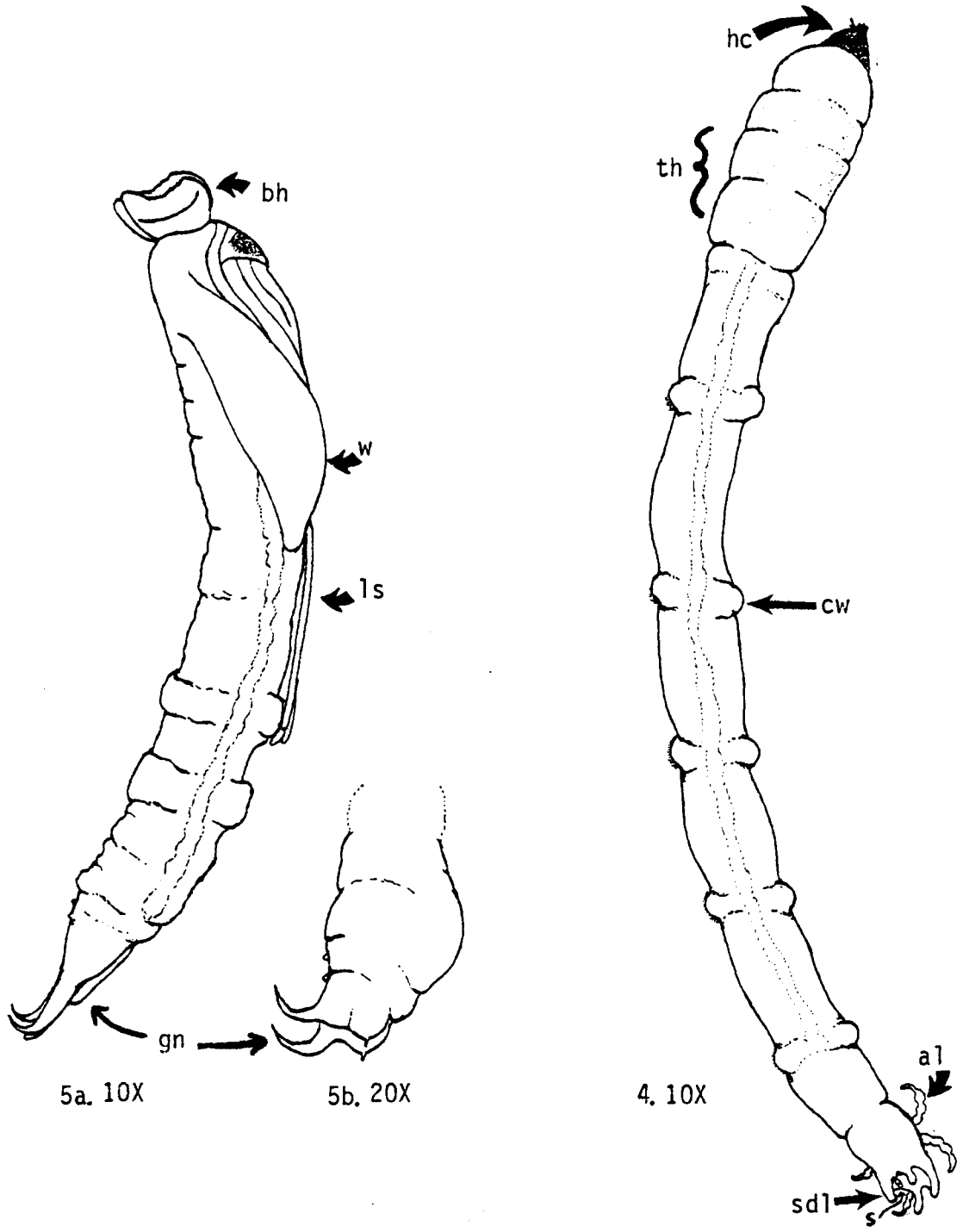
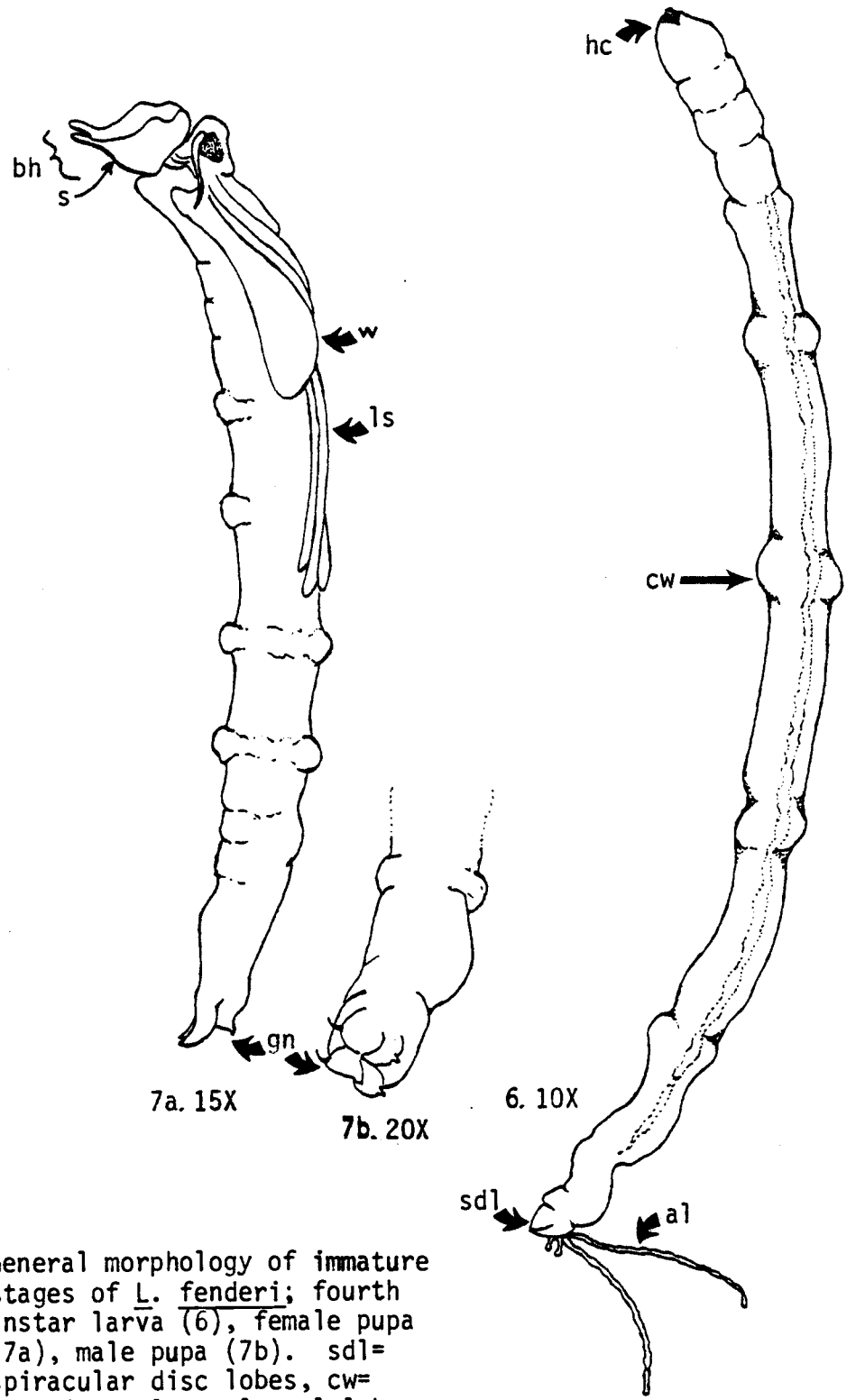


Fig. 3. Distributions of L. nigrilinea and L. fenderi in Oregon. Closed circles indicate both species collected, vertical half-closed= L. nigrilinea only, horizontal half-closed =L. fenderi only, open means sampled but no larvae found. Larvae were in Coast Range only in Douglas Co., Cascades only in Jefferson Co., as represented by two symbols in each of these counties.



Figs. 4-5. General morphology of immature stages of L. nigrilinea; fourth instar larva (4), female pupa (5a), male pupa (5b). sdl=spiracular disc lobes, cw=creeping welts, al=anal lobes, s=spiracle, hc=head capsule, th=thorax, gn=developing genitalia, bh=breathing horns, ls=leg sheaths, w=wing buds. illus. Wendy Madar.



Figs. 6-7. General morphology of immature stages of L. fenderi; fourth instar larva (6), female pupa (7a), male pupa (7b). sdl= spiracular disc lobes, cw= creeping welts, al=anal lobes, hc=head capsule, gn =developing genitalia, bh=breathing horns, s=darkened seam, w=wing buds, ls=leg sheaths. illus. Wendy Madar.

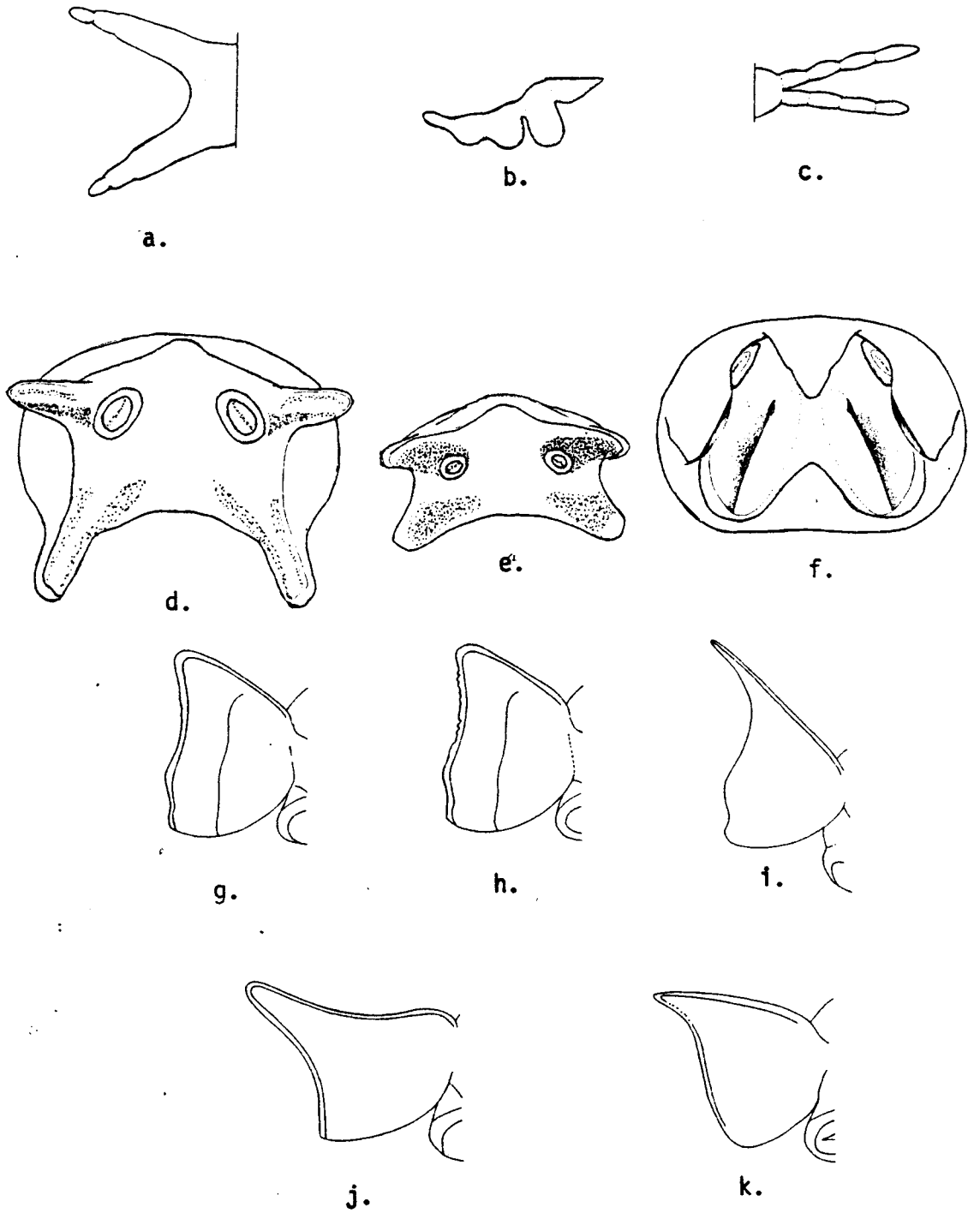


Fig. 8. Lipsothrix spp. key characters; a.-c. anal lobes of L. hynesiana, L. shasta, L. sylvia, respectively; d.-f. spiracular discs of L. hynesiana, L. nigrilinea, L. fenderi, respectively; g.-k. pupal breathing horns of L. shasta, L. nigrilinea, L. fenderi, L. hynesiana, L. sylvia, respectively. Illustrations from Hynes (1965).

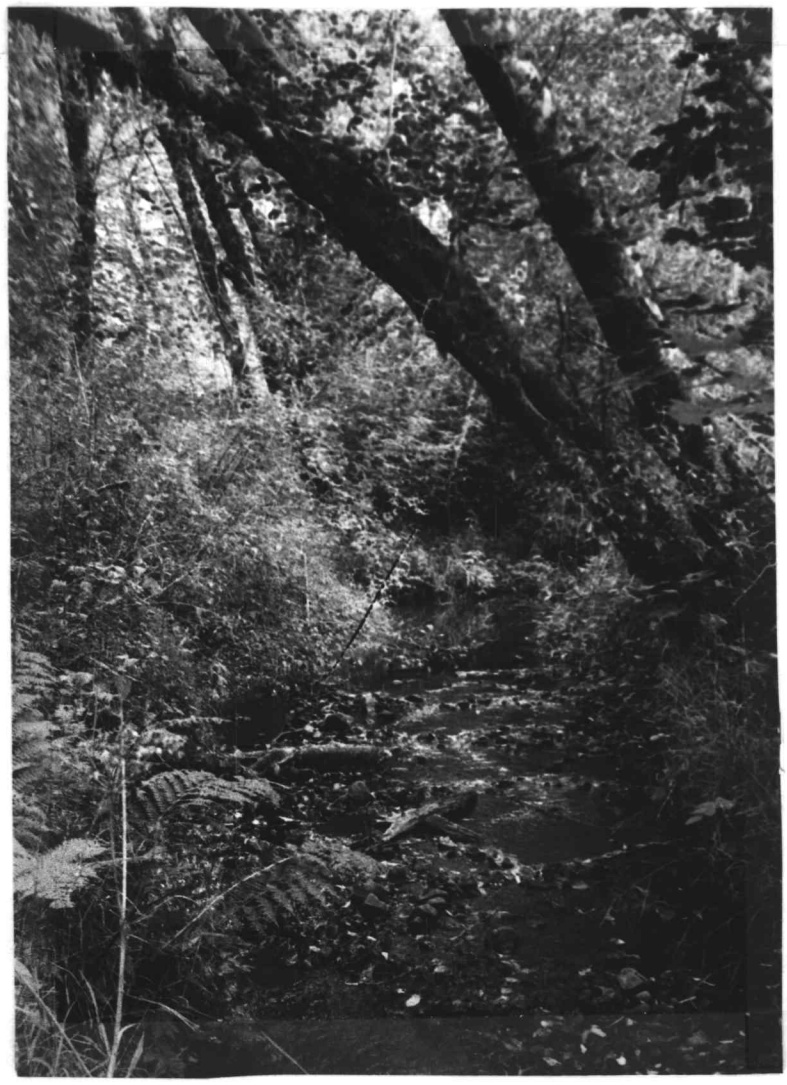


Fig. 9. Typical second order Lipsothrix stream, with alder and maple overstory.

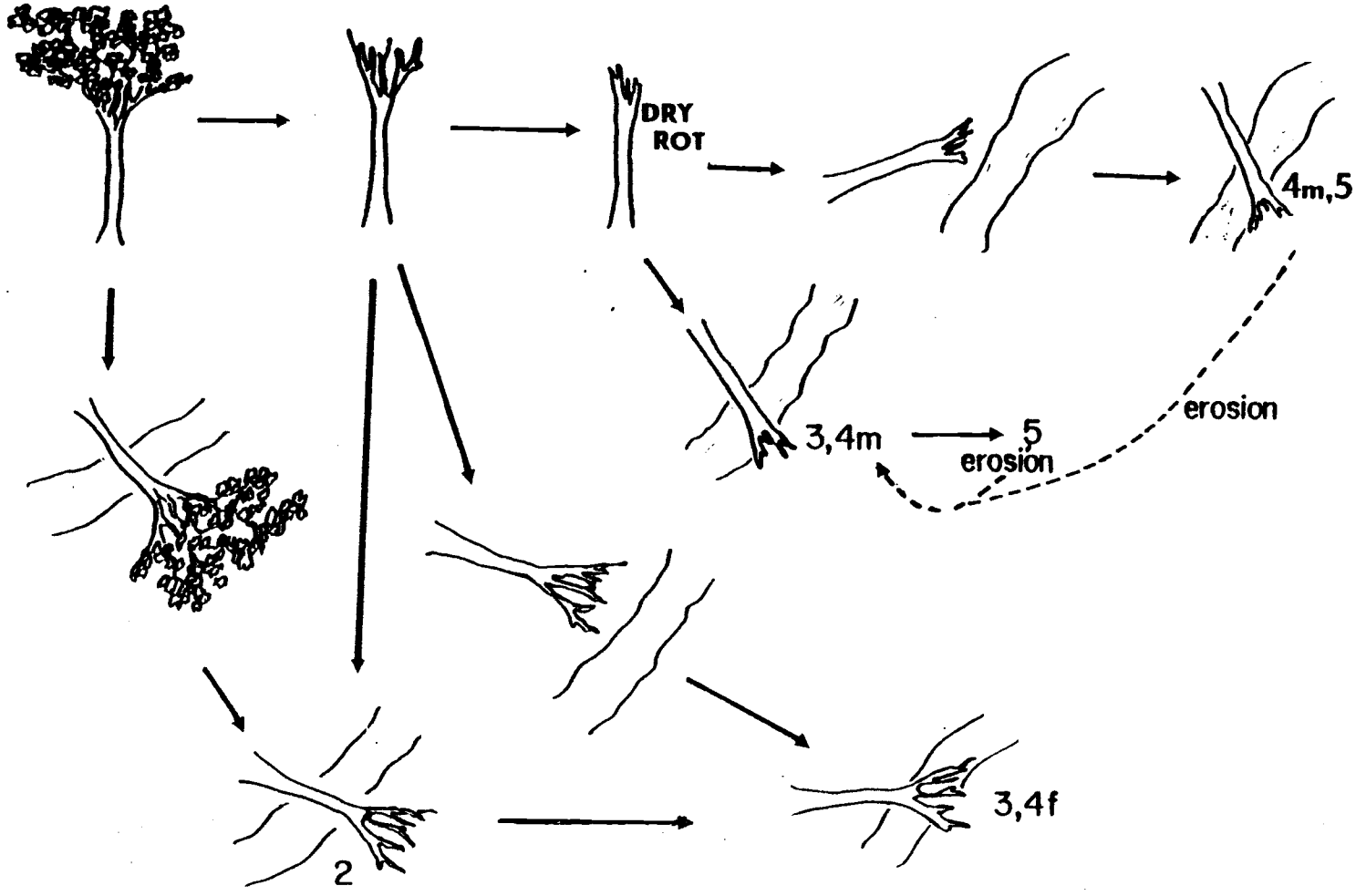


Fig. 10. Schematic illustration of the pathways of alder decomposition. Wood which remains standing may undergo dry-rot, and follow a sequence of decay classes terminating in the class-5 stage either in or out of water; Wood which does not dry-rot instead decays to the class-4f stage. Class-5 wood may be returned to class-4m by erosion.

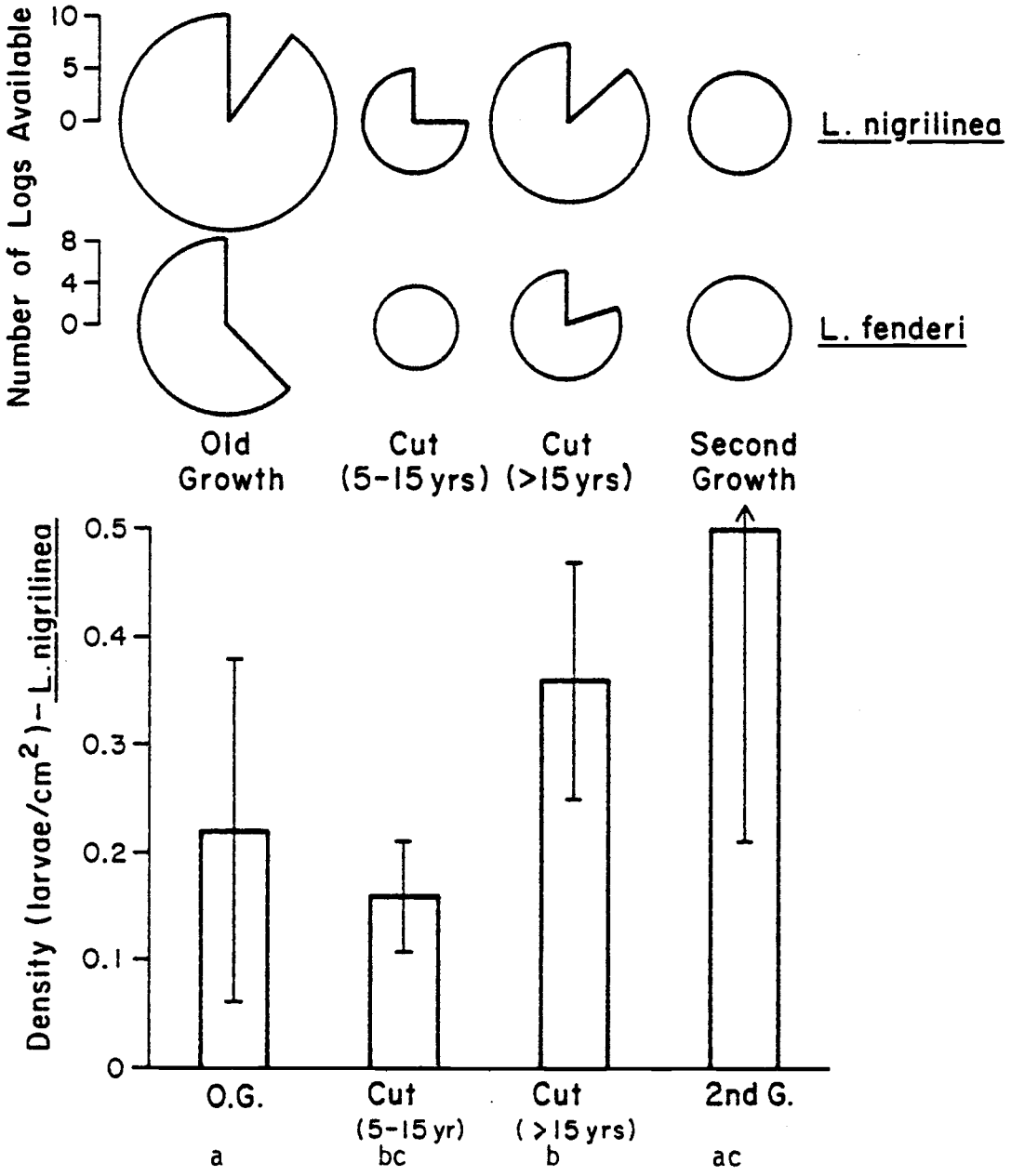


Fig. 11. Colonization of uninfested experimental logs by Lipsothrix in four forest stages. Diameters of circles signify number of logs available, the closed portion represents proportion colonized. Bars below indicate density of L. nigrilinea in colonized logs with standard deviation; significant differences between pairs indicated by matched letters (Newman-Keuls multiple range comparison for unequal sample sizes, $p<.05$).

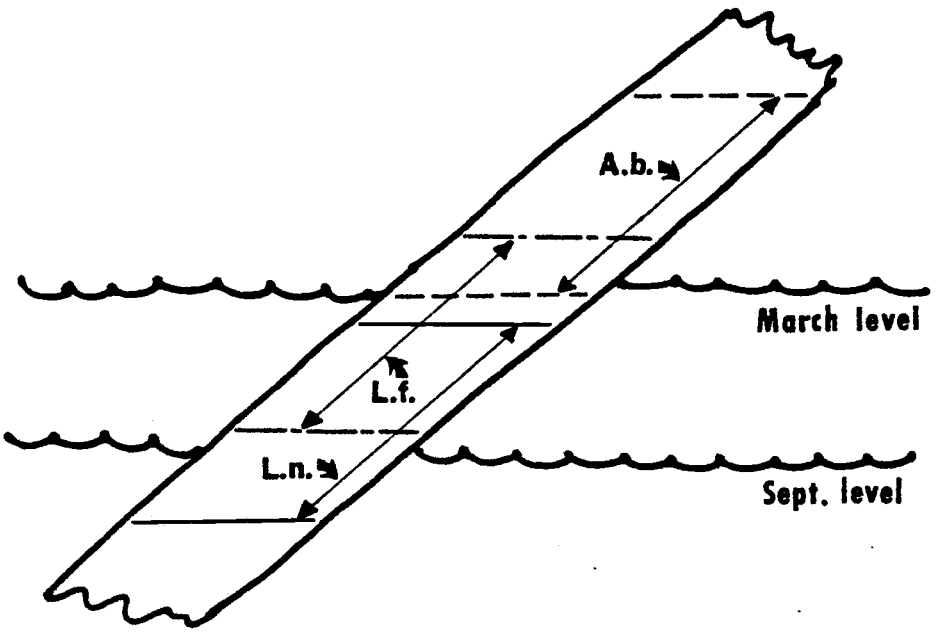
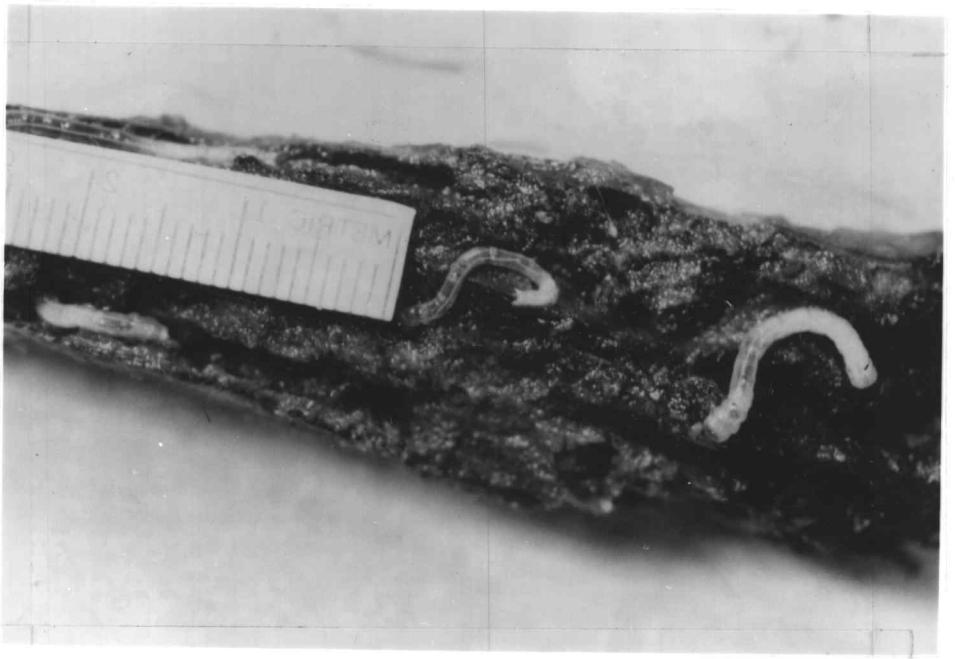
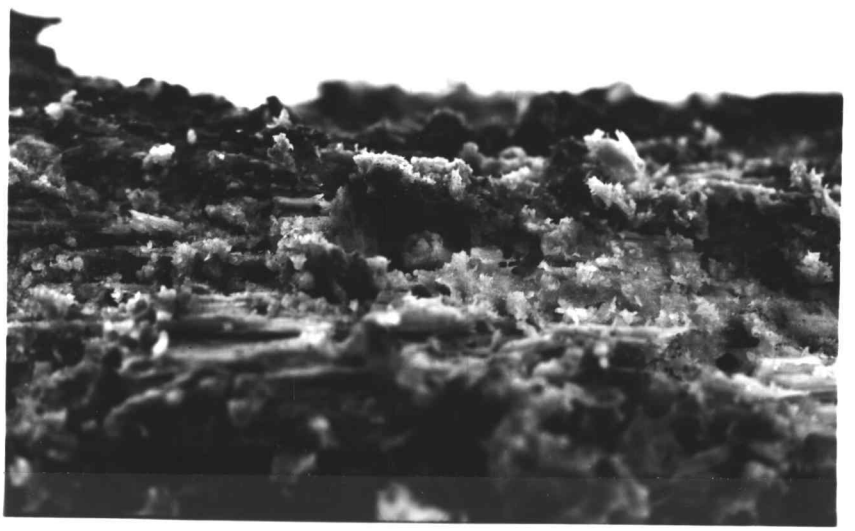


Fig. 12. Idealized representation of zones of overlap and non-overlap of the three primary tipulids in stream wood, L. fenderi, L. nigrilinea and Austrolimnophila badia, in relation to water levels.



13.

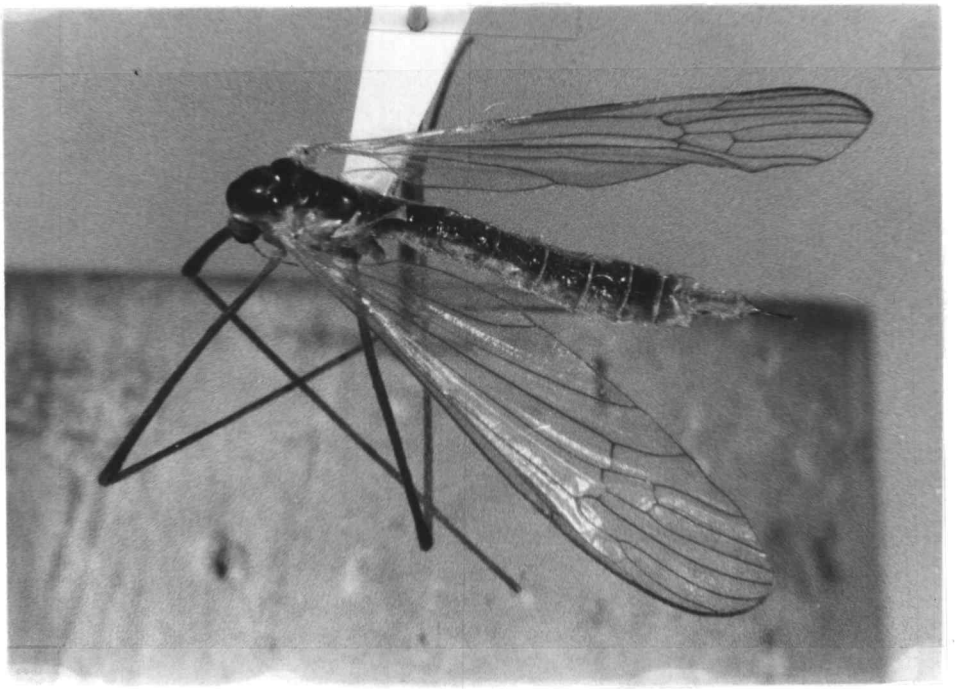


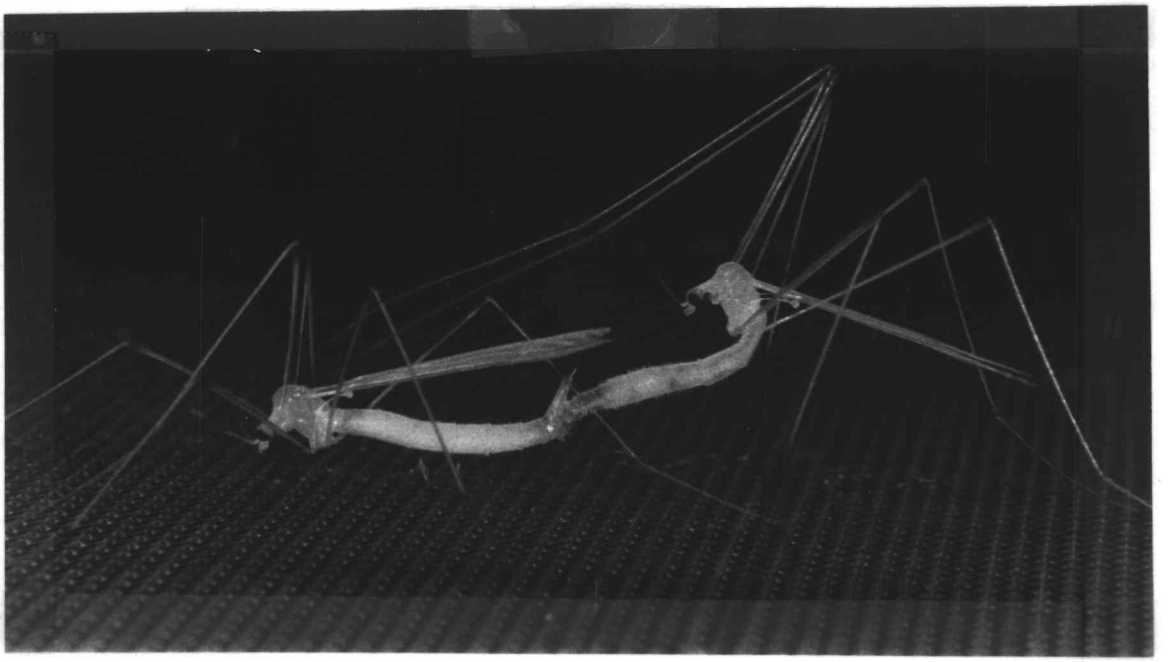
14.

2X

Figs. 13-14. Natural habitats of L. nigrilinea; larvae on alder and in galleries (13); pupation turret (14).

a.
5X





b. 3X

Fig. 15. Adults of Lipsothrix spp.; a. L. nigrilinea female showing median black line; b. L. fenderi mating, with female in fore position and male behind.

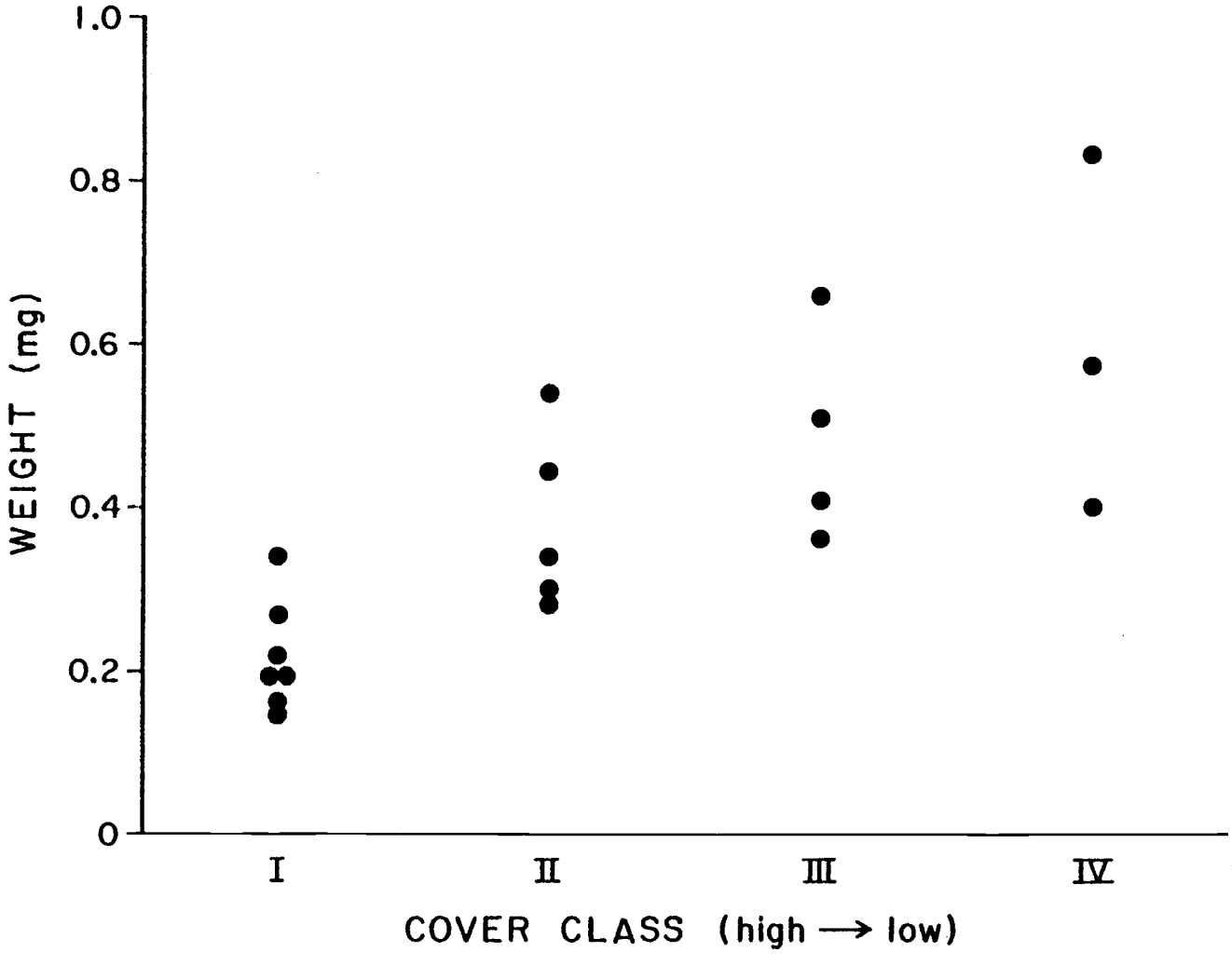


Fig. 16. Growth of L. nigrilinea in relation to canopy cover. Each point refers to mean weight for larvae in an experimental log at one creek; cover and growth are significantly correlated (Spearman rank r_s = .84, $p<.01$).

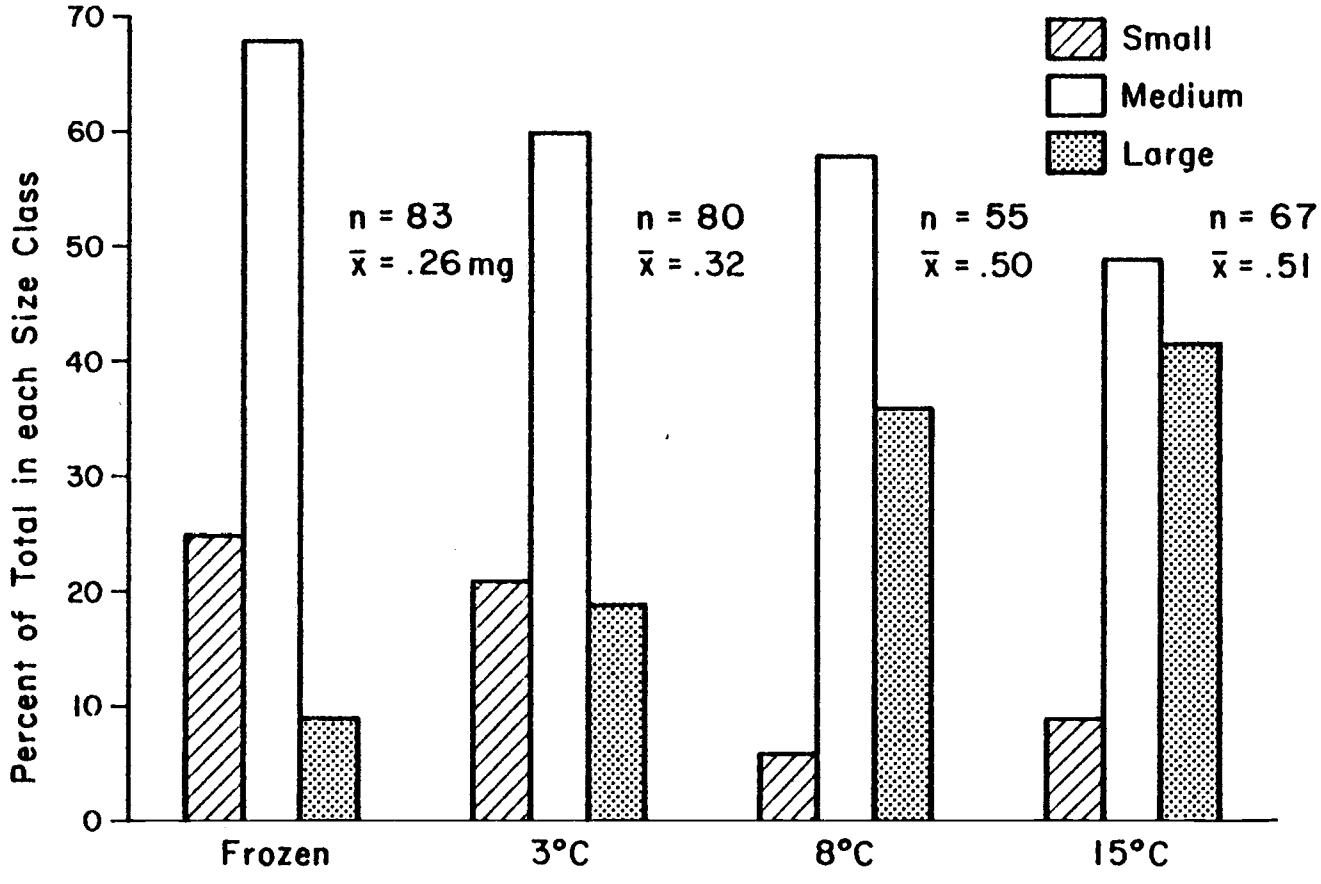


Fig. 17. Size class distribution and weights of L. nigrilinea in logs at three temperatures for 60 days, with an initial frozen control for comparison.

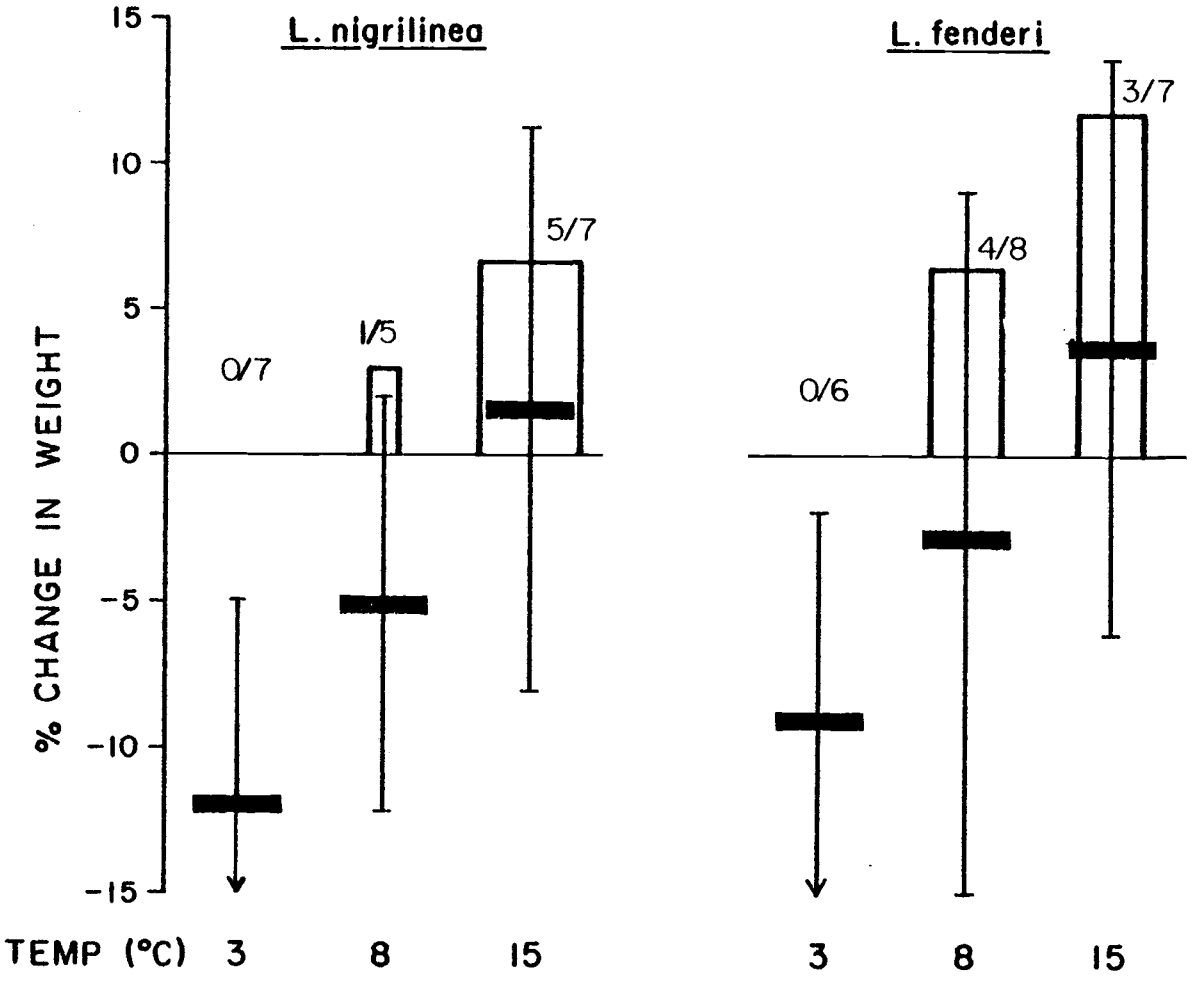


Fig. 18. Weight change of Lipsothrix vs. temperature after 50 days in petri dishes with blended wood media. Horizontal bar=mean % change with S.D. as vertical line, histogram height= mean change of larvae which gained and width suggests proportion of experimental animals which gained; linear correlation for L. nigrilinea $y=2.3x-31.6$, $r^2=.46$, for L. fenderi, $y=2.9x-42.4$, $r^2=.22$.

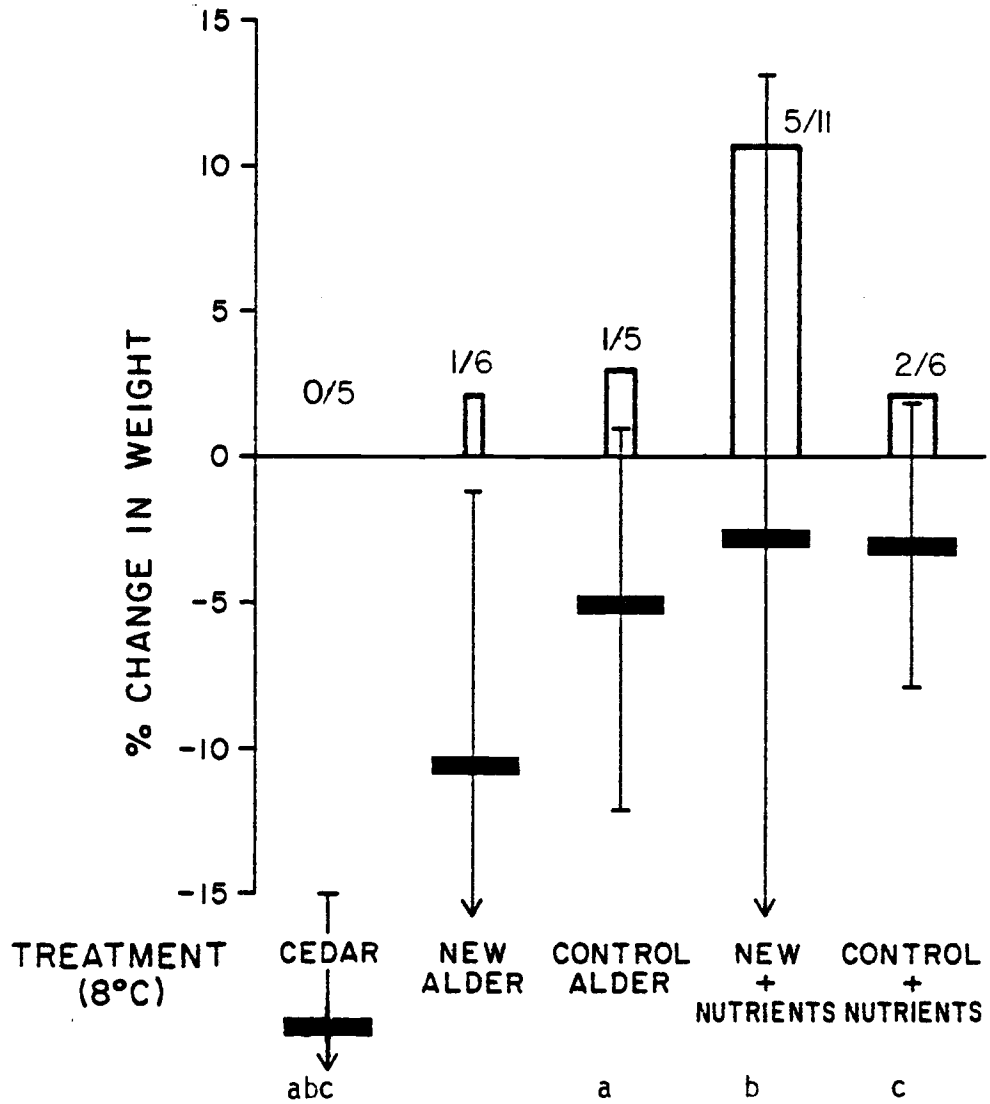


Fig. 19. Weight change of L. nigrilinea vs. analogues of food quality after 50 days in petri dishes with experimental media. Horizontal bar=mean % change with S.D. as vertical line, histogram height=mean change of larvae which gained weight and width suggests proportion of experimental animals which gained; letters indicate pairs which were significantly different (Newman-Keuls multiple range comparison, $p<.05$).

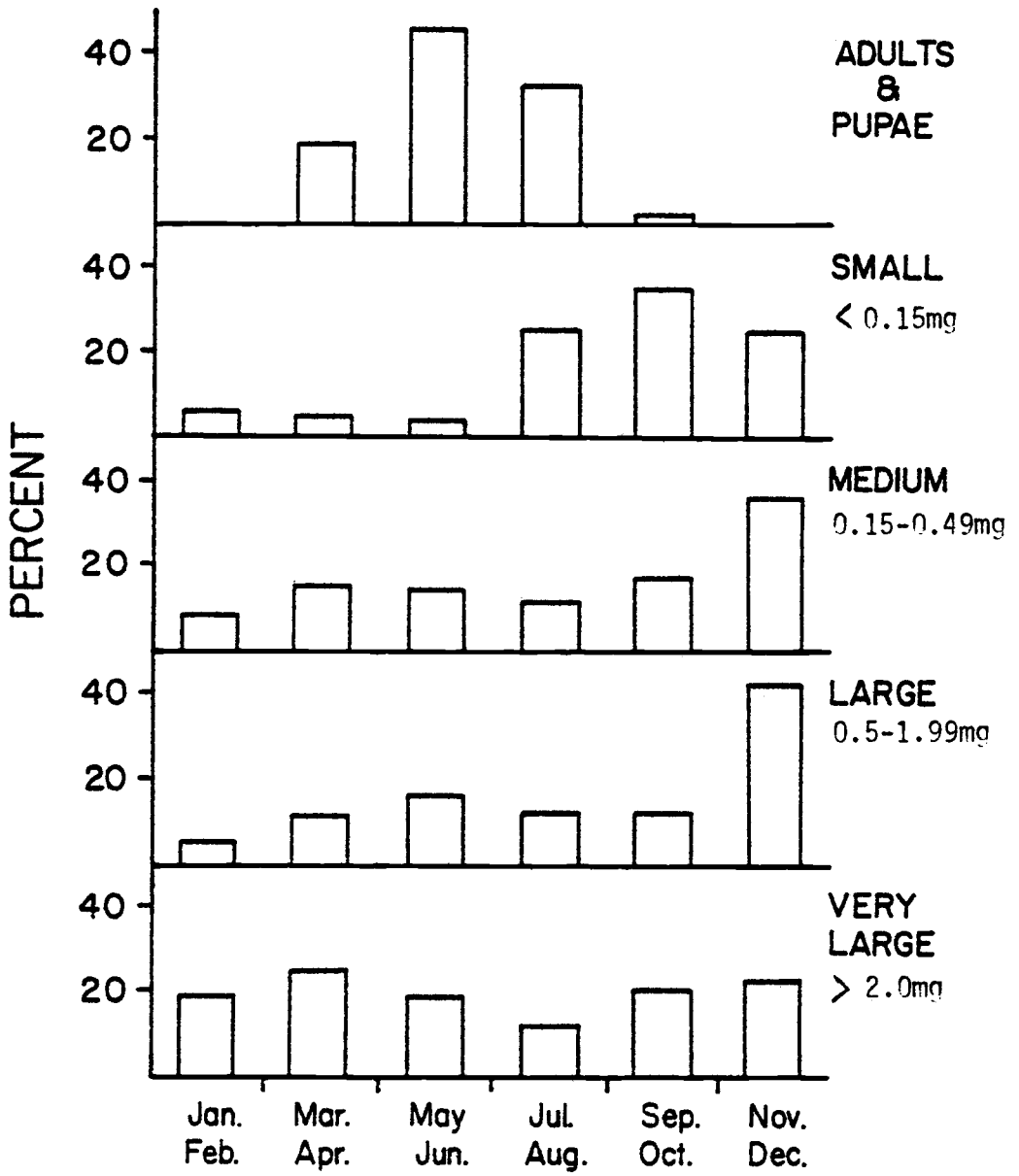


Fig. 20. Seasonal distribution of size classes of L. nigrilinea in the Coast Range. Histograms add horizontally to 100%.

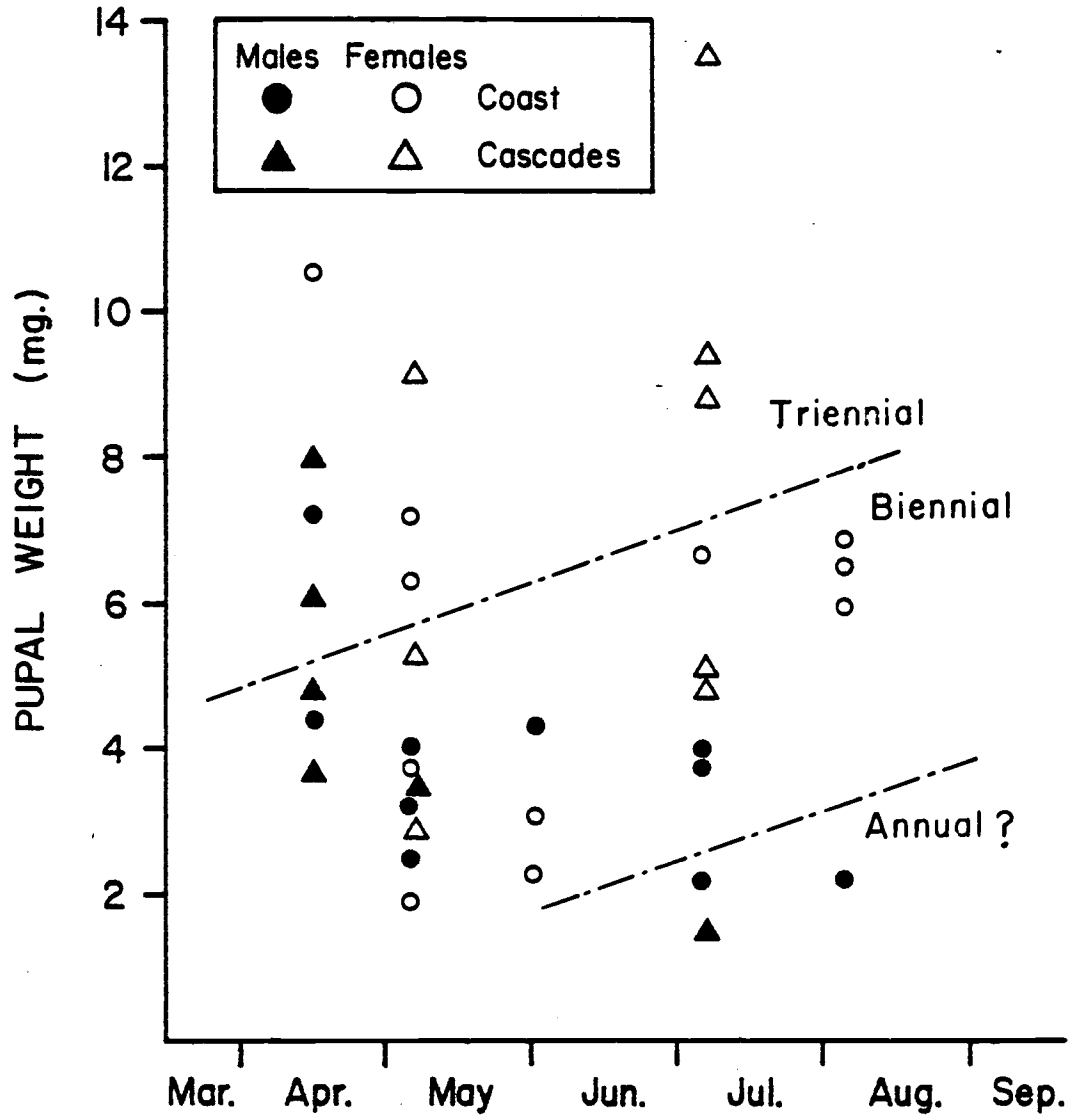


Fig. 21. Weight and collection date of L. nigrilinea pupae. Mean weight and standard error of: ♂♂-Coast 3.8(1.4)mg, Cascades 4.7(2.1); ♀♀-Coast 5.6(2.6), Cascades 7.5(3.4); neither pair significantly different (t-test, p .1).
Overlay indicates cut-off lines between individuals suggested to be from different year classes.

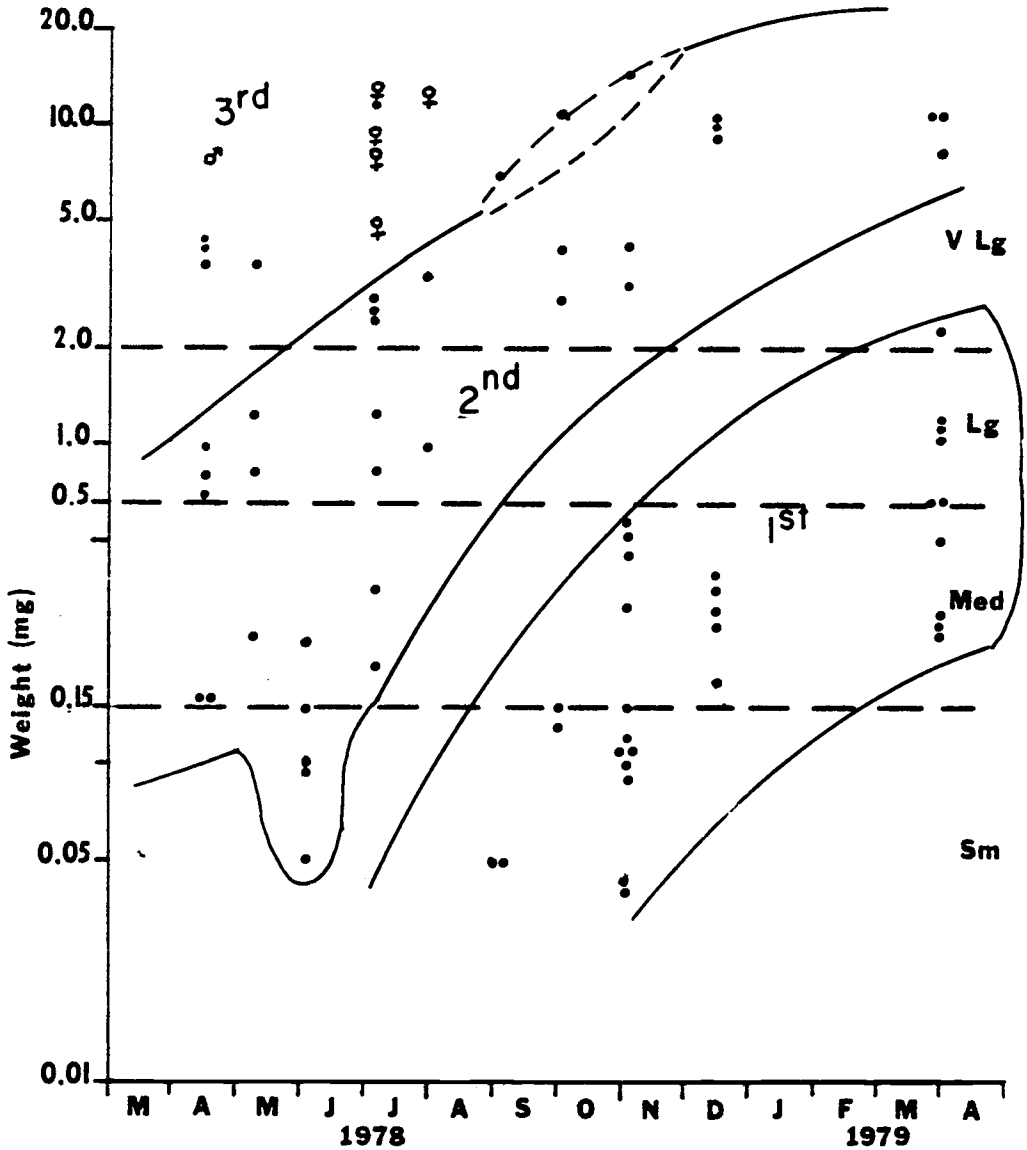


Fig. 22. L. nigrilinea larval and pupal weights vs. collection date from a single log at Green Cr. (Linn Co.). Horizontal lines indicate size classes. Gender symbols=pupae. Overlay indicates approximate year classes, with dashed lines where cut-off is unclear. First year cohort fits exponential equation, $y=.015e^{.01x}$, $r^2=.55$.

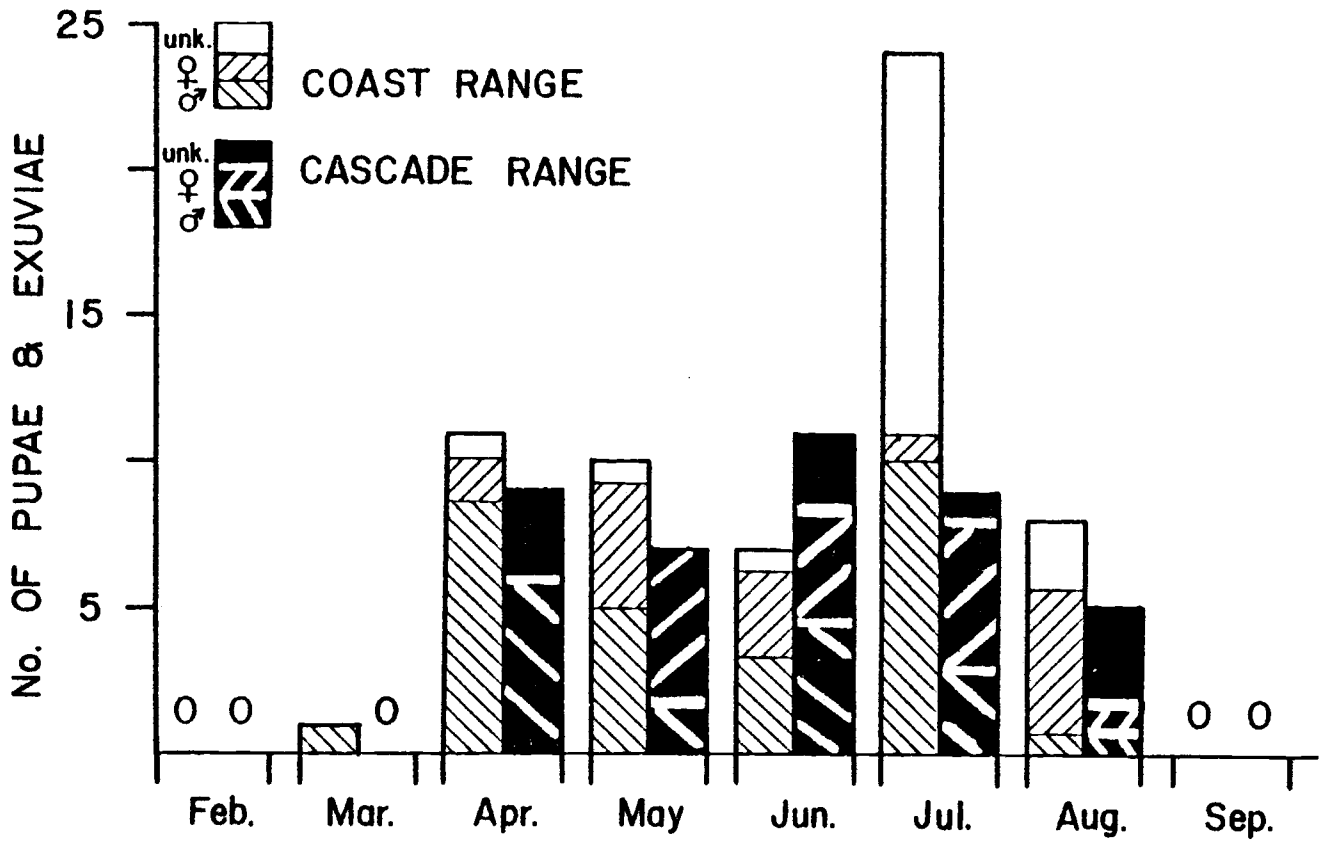


Fig. 23. Emergence pattern of L. nigrilinea from transect collections of pupae and pupal exuviae. Sex ratio in Cascade samples does not vary significantly from 1:1, Coast sex ratio is significantly unequal--29♂:14♀ (Wilcoxon signed rank, $p<.05$).

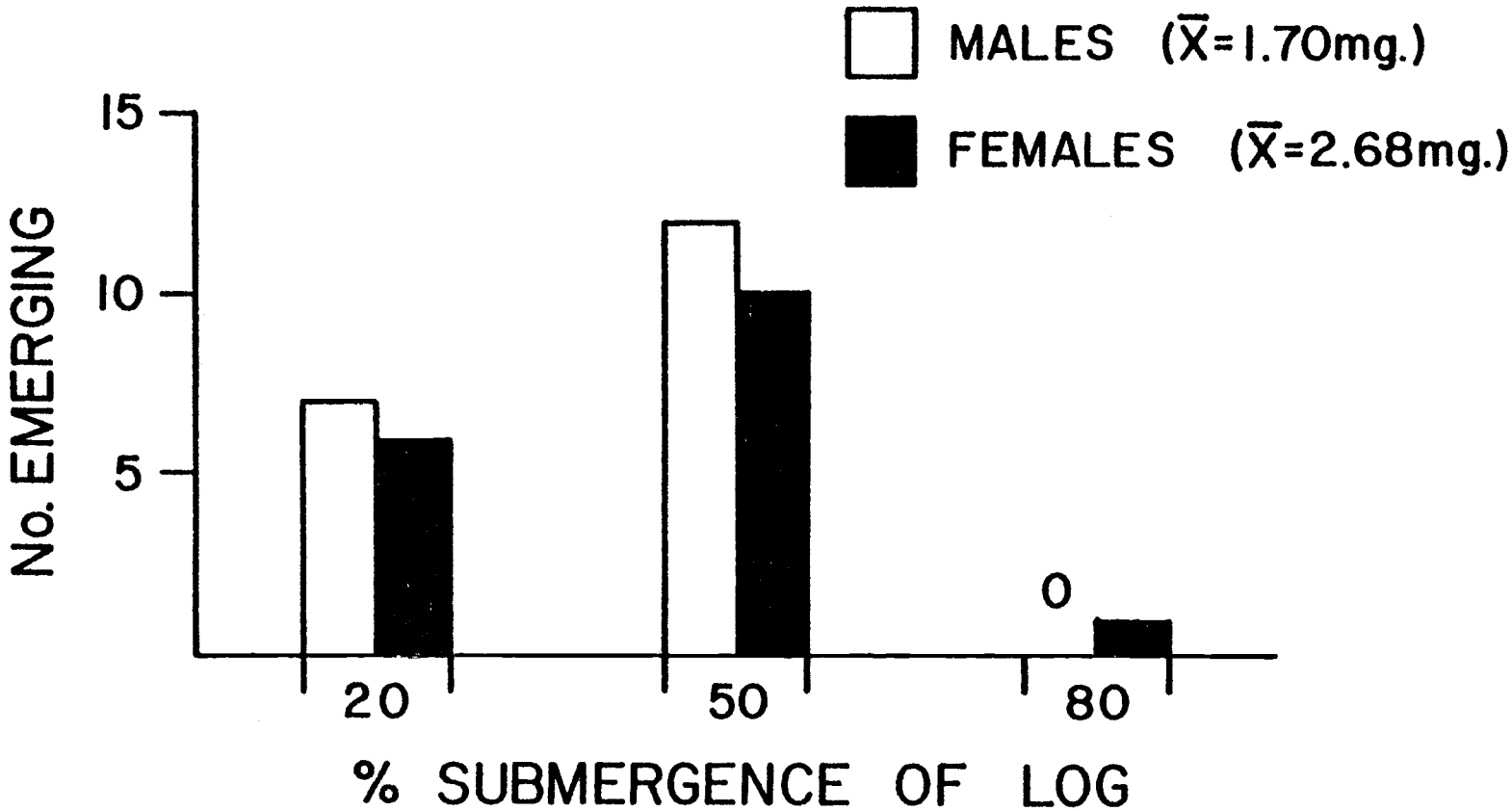


Fig. 24. Induction of emergence of L. nigrilinea in response to water level. One log was cut into equal portions; total population size was unknown.

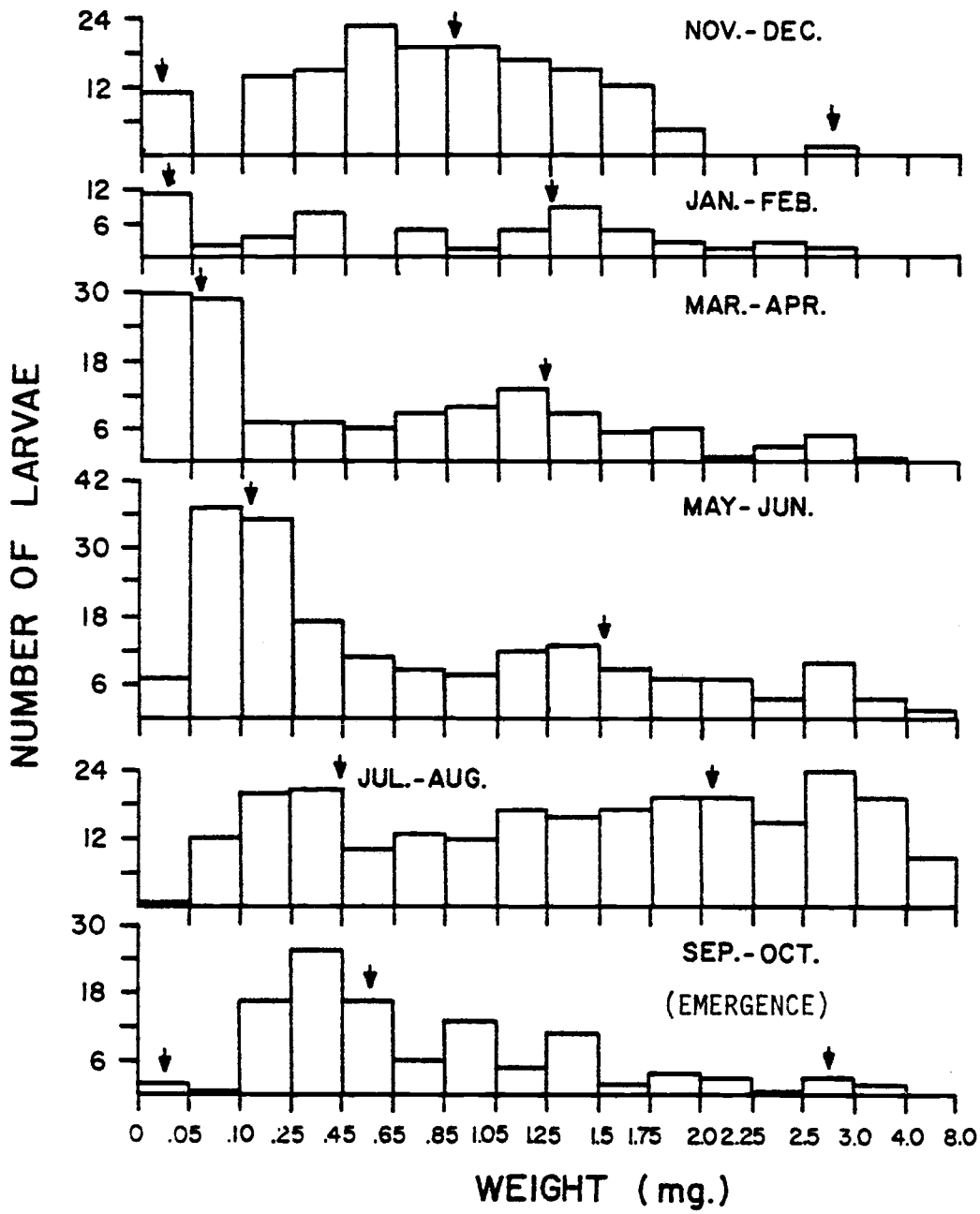


Fig. 25. Size class distributions of L. fenderi larvae at different times of the year (1978) from Coast and Cascade collections. Abscissa is an arbitrary scale, not logarithmic; arrows indicate approximate cohort means.

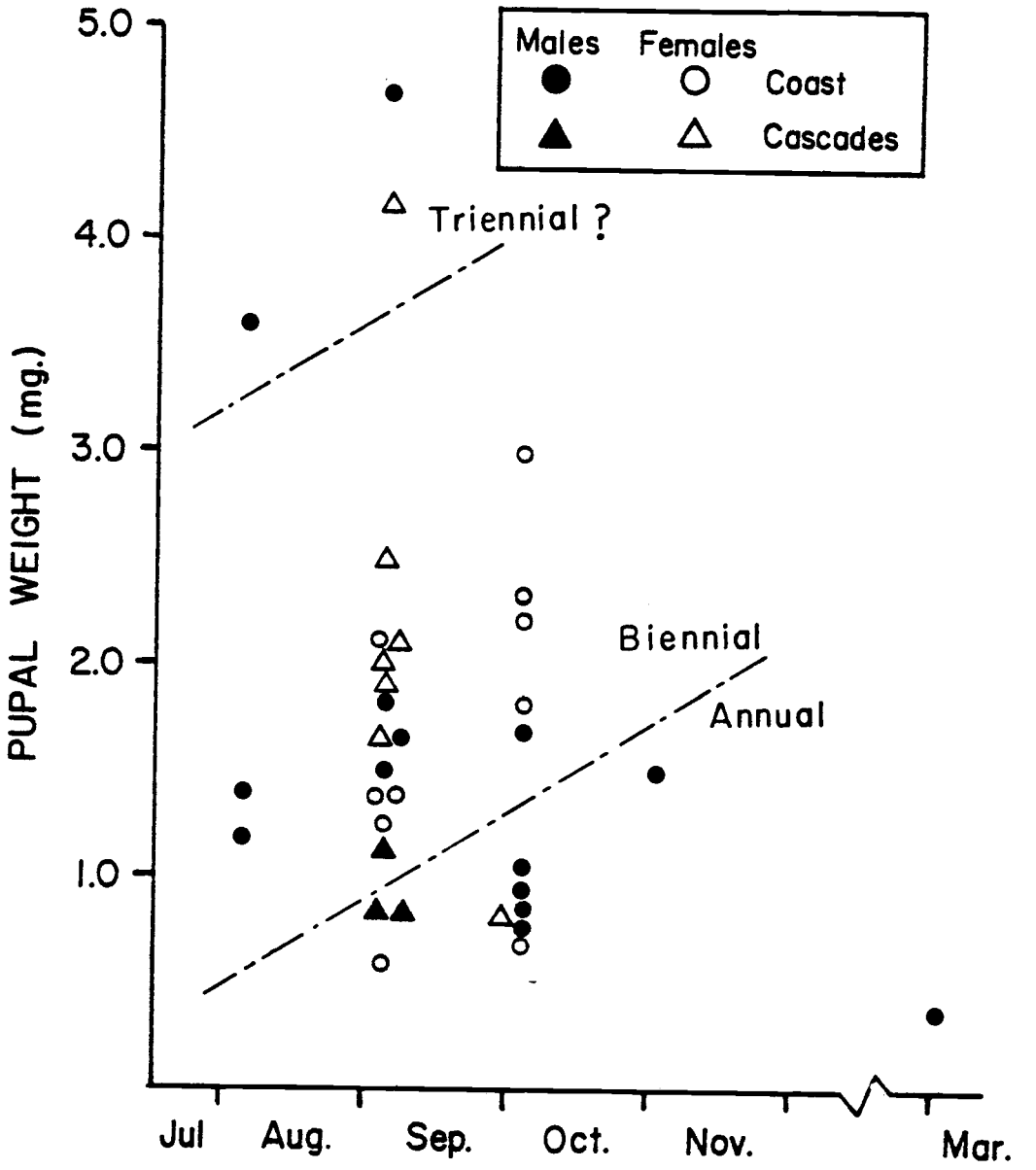


Fig. 26. Distribution of weight and collection date of L. fenderi pupae.
Overlay indicates cut-off lines between individuals suggested to be from different year classes.

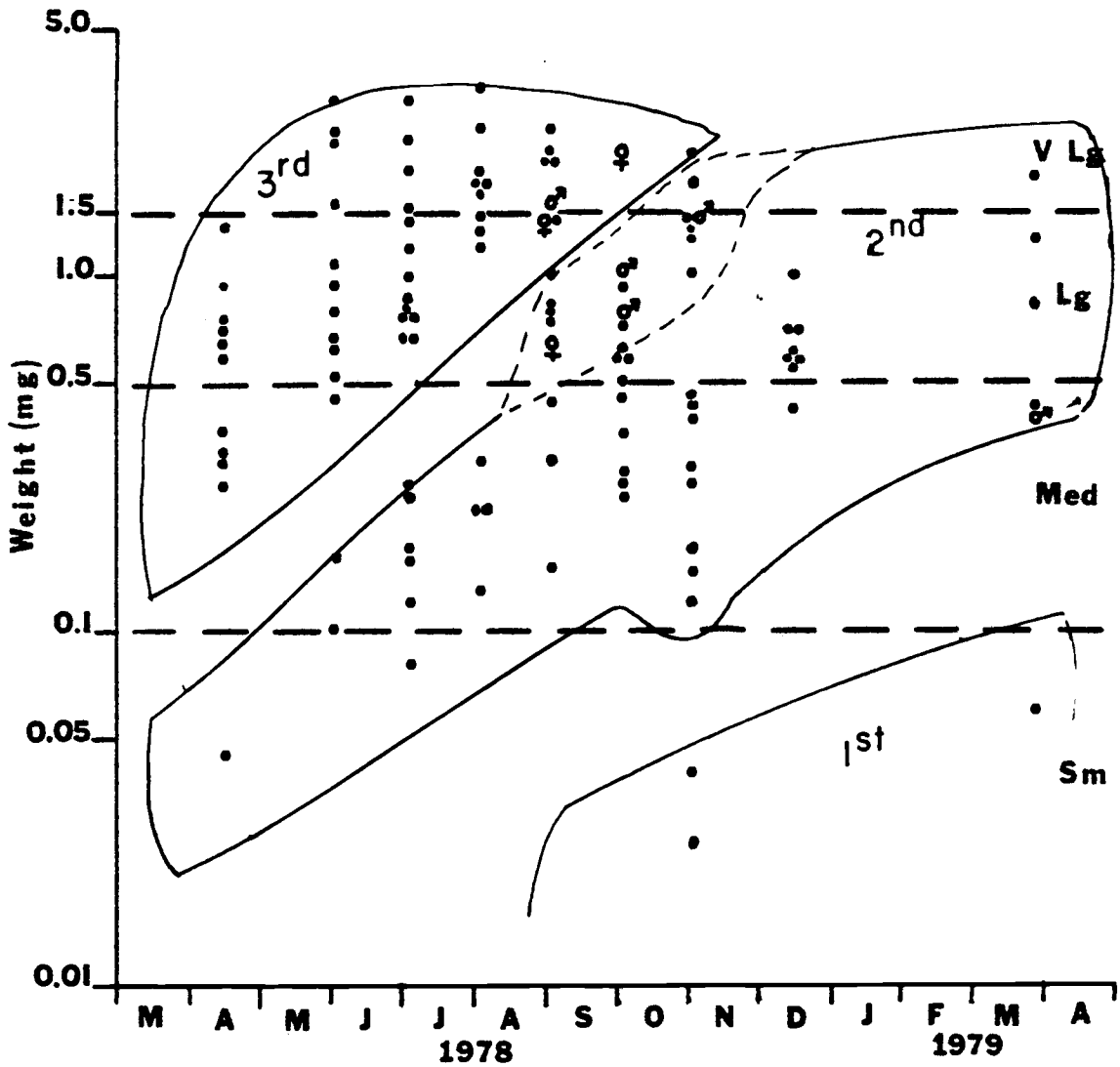


Fig. 27. L. fenderi larval and pupal weights vs. collection date from a single log at Dinner Cr. (Benton Co.). Horizontal lines indicate size classes. Gender symbols=pupae. Overlay indicates approximate year classes, with dashed lines where cut-off is unclear. First year cohort (March to December) fits exponential equation, $y=.068e^{.008x}$, $r^2=.59$.

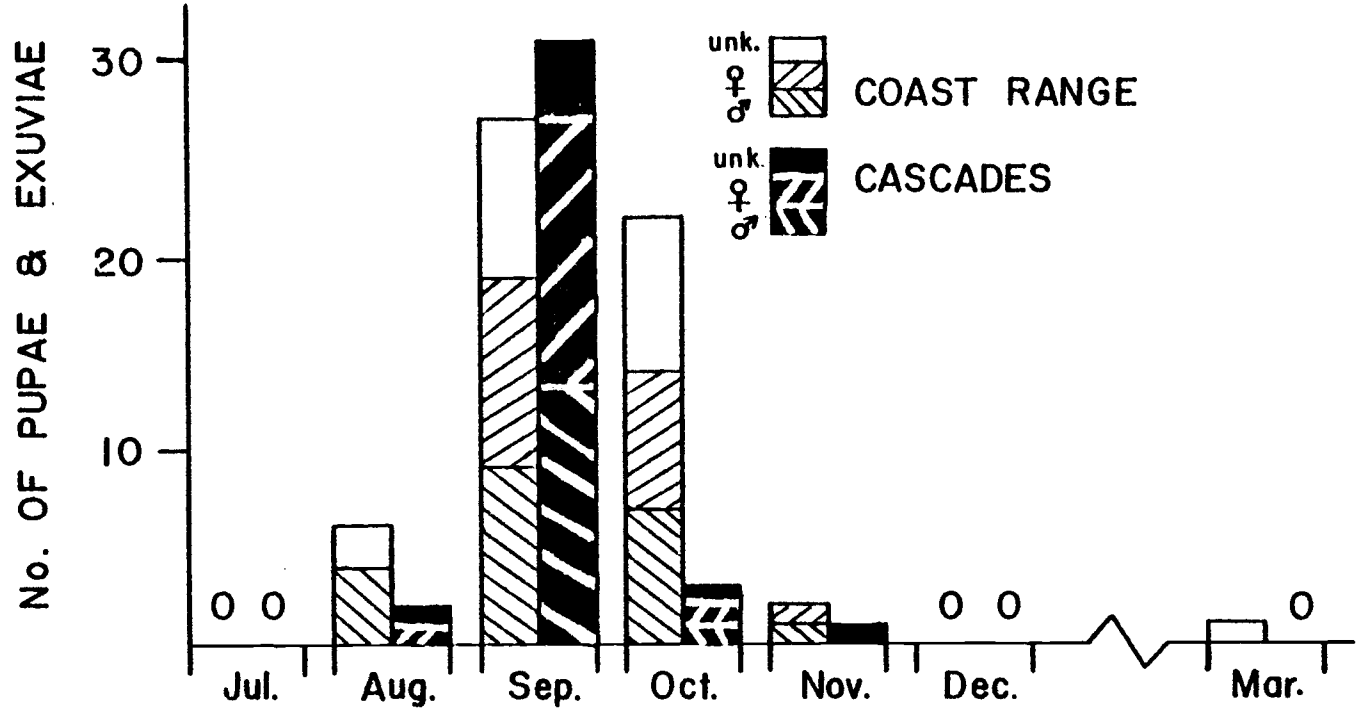


Fig. 28. Emergence pattern of L. fenderi from transect pupae and pupal exuviae collections. Sex ratios do not vary significantly from 1:1. (Wilcoxon signed rank, $p<.05$).

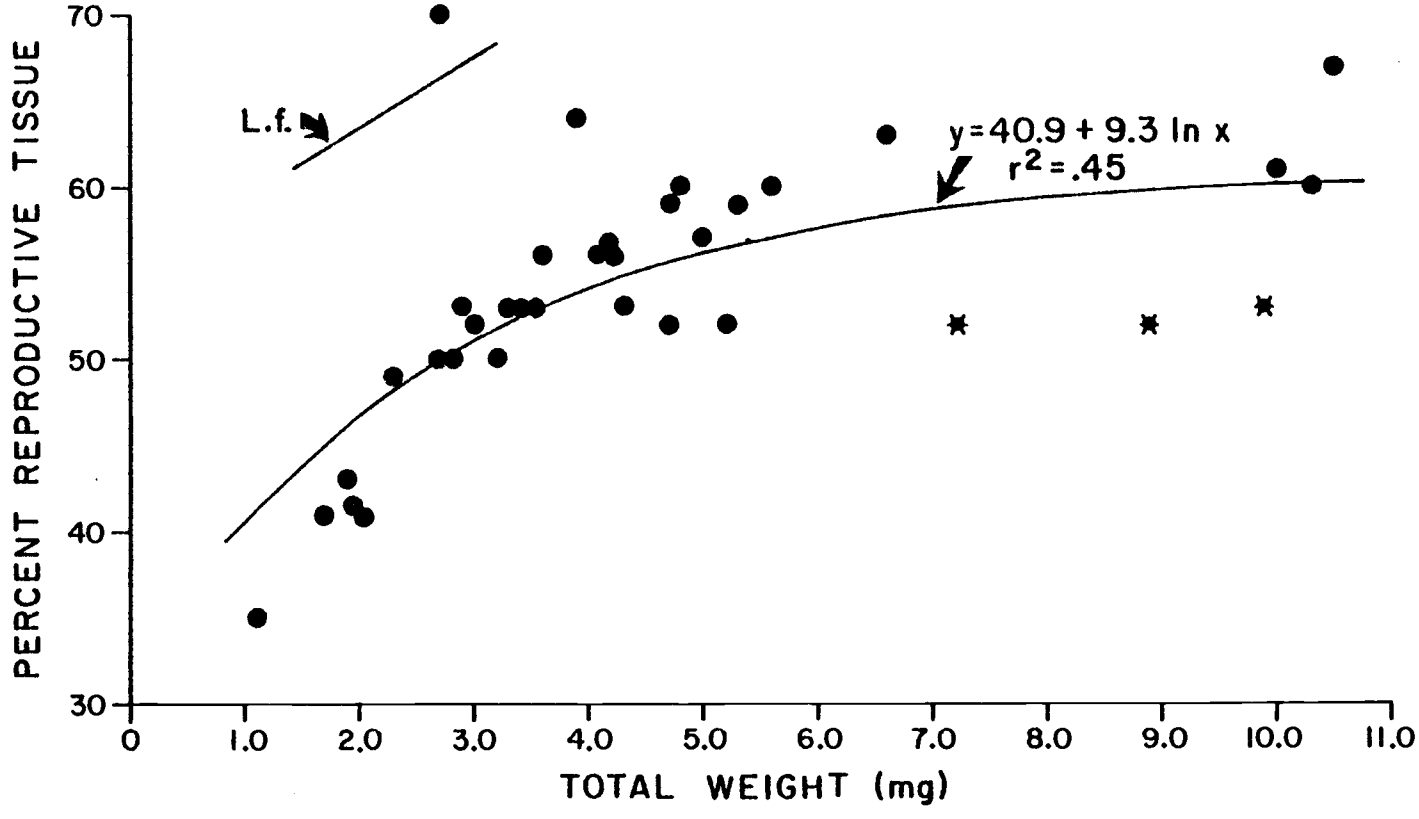


Fig. 29 . Relationship between L. nigrilinea adult female dry weight and the percentage allocation to reproductive tissue. L.f.=the same relationship for L. fenderi, indicating the range of values for females between 1.2 and 4.2 mg. Asterisks explained in text.

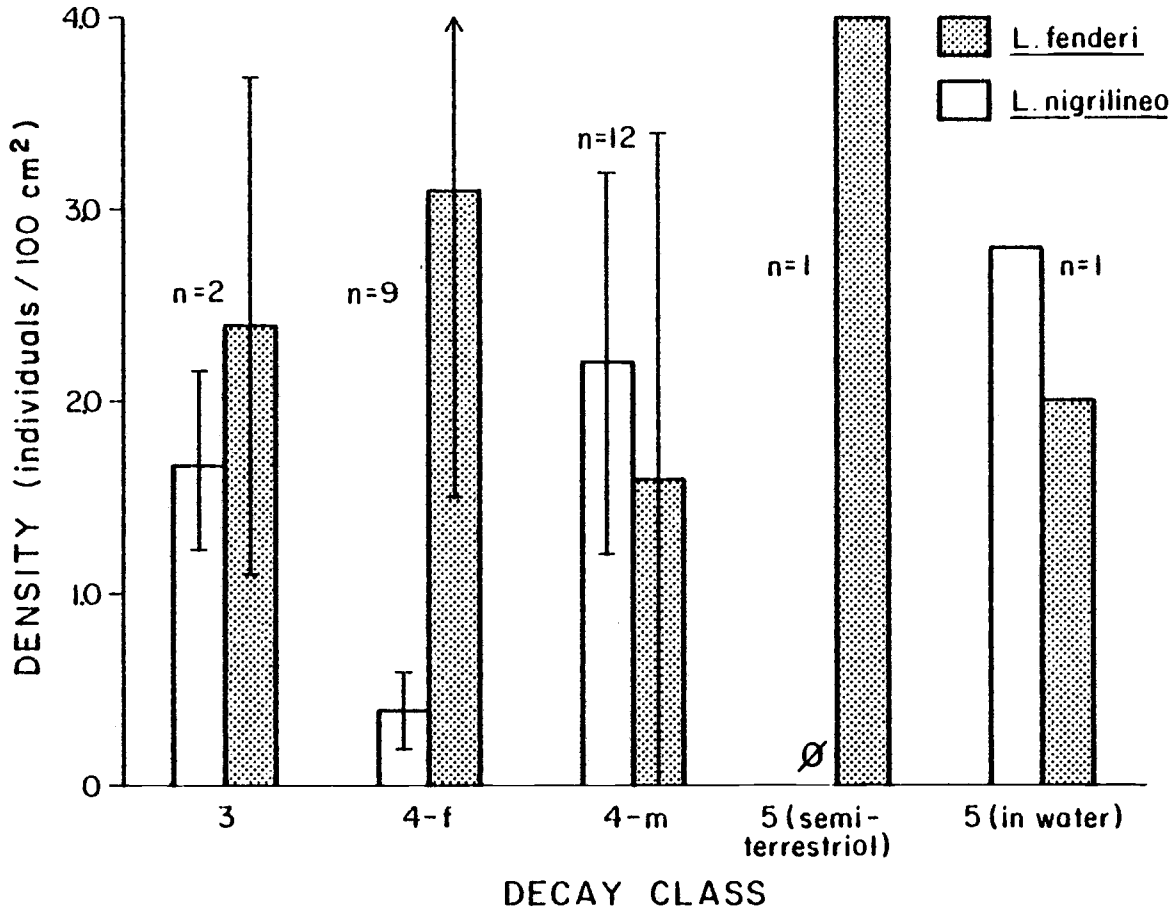


Fig. 30. Mean larval densities of L. fenderi and L. nigrilinea over all sampling dates in transect logs of each decay class. Standard error given if more than one log was sampled. Densities did not differ between species for classes 3 and 4-m; L. nigrilinea < L. fenderi in class 4-f (t-test, $p<.001$), N.S. for classes 3, 4m (t-test, $p<.20$).

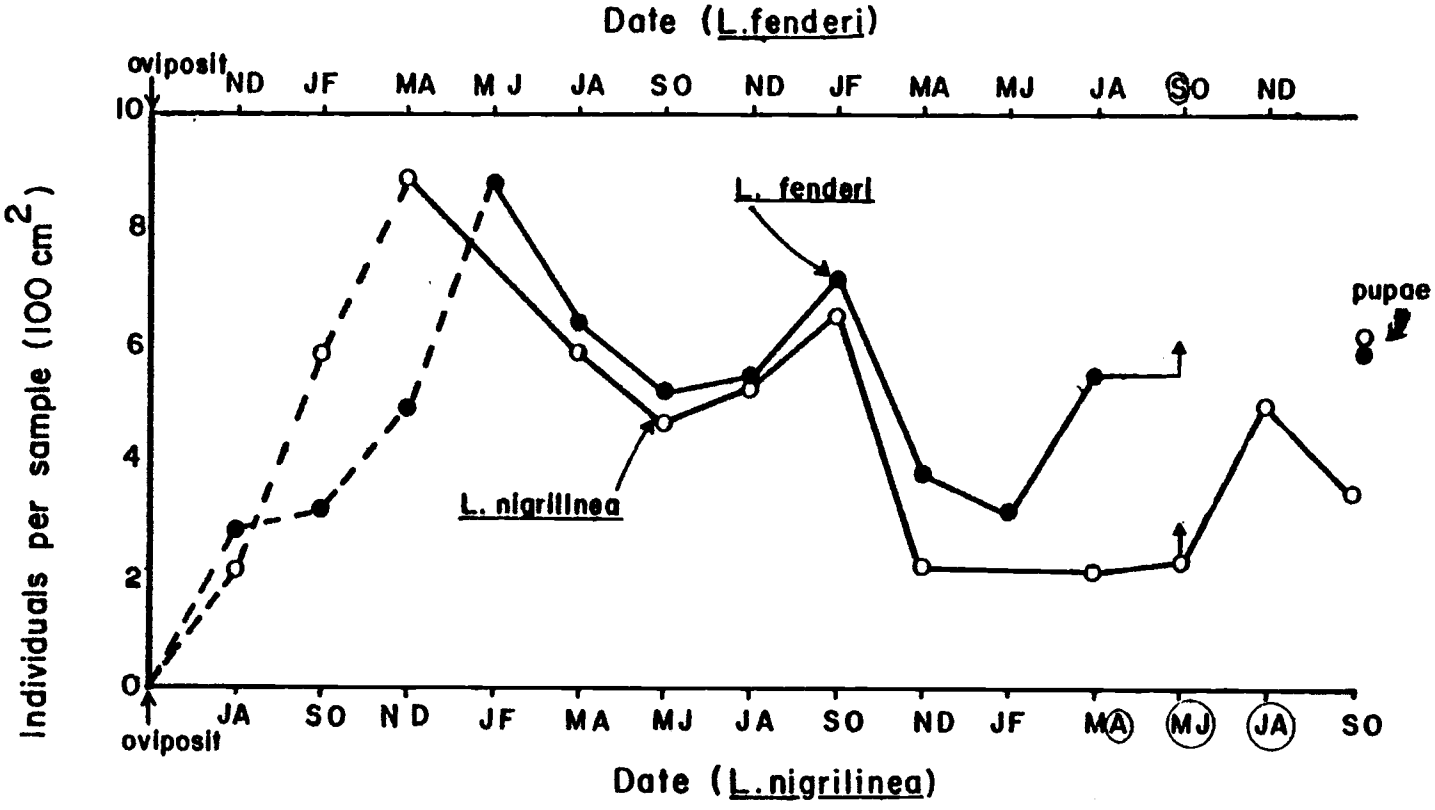


Fig. 31. Density of a single cohort of L. nigrilinea and L. fenderi over life cycle, based on transect logs which contained larvae throughout the sampling period. Pupal densities at far right are mean totals per log over whole emergence period for each species; dashed lines represent period when many larvae were too small for recovery; months of emergence are circled. The anomalous increases are due to small sample sizes for some months and size classes.

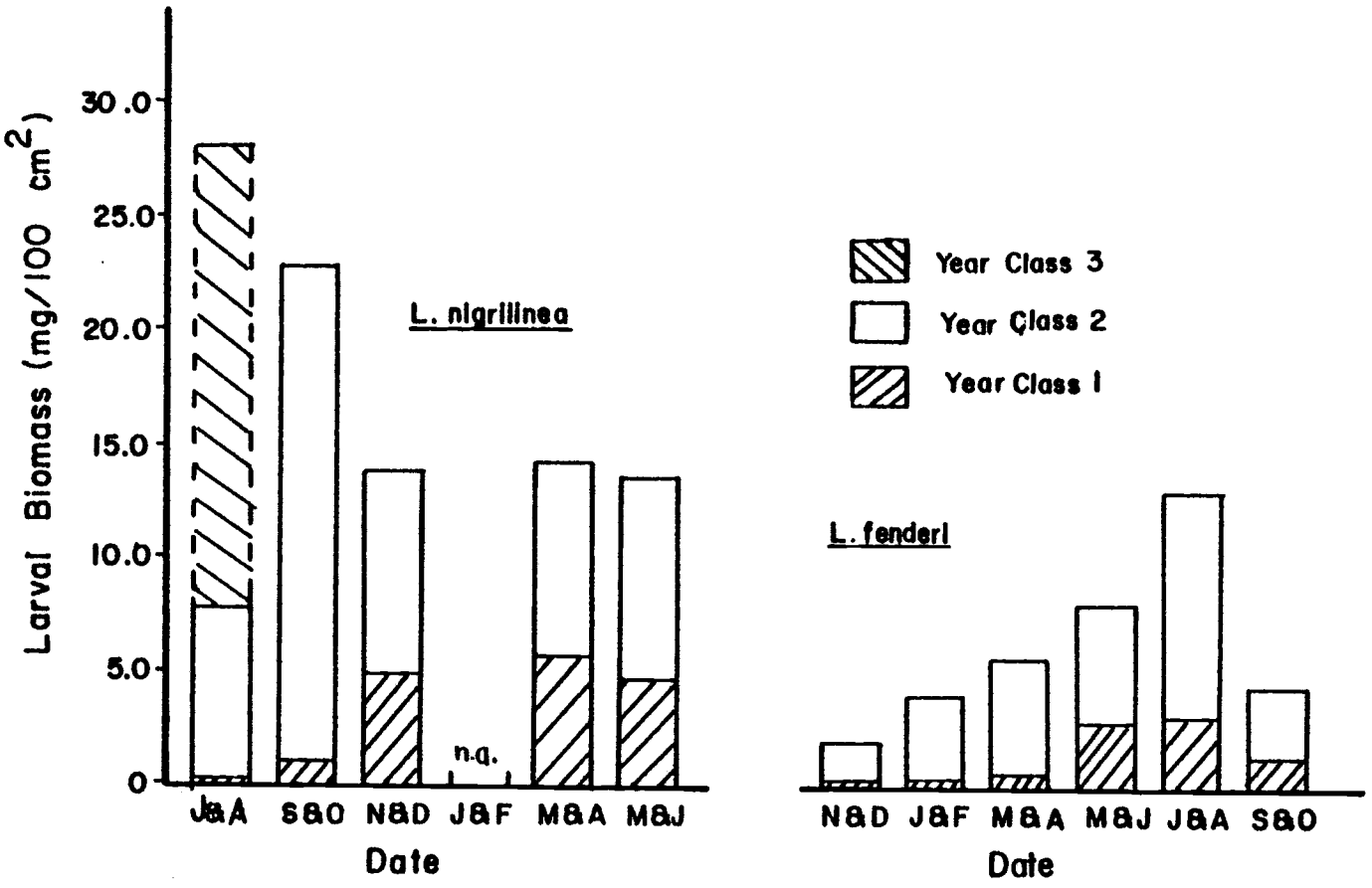


Fig. 32. Mean biomass of L. nigrilinea and L. fenderi over bimonthly intervals from transect collections. Year three larvae were underrepresented, and inflate the estimate, so this group is indicated by the dashed histogram.

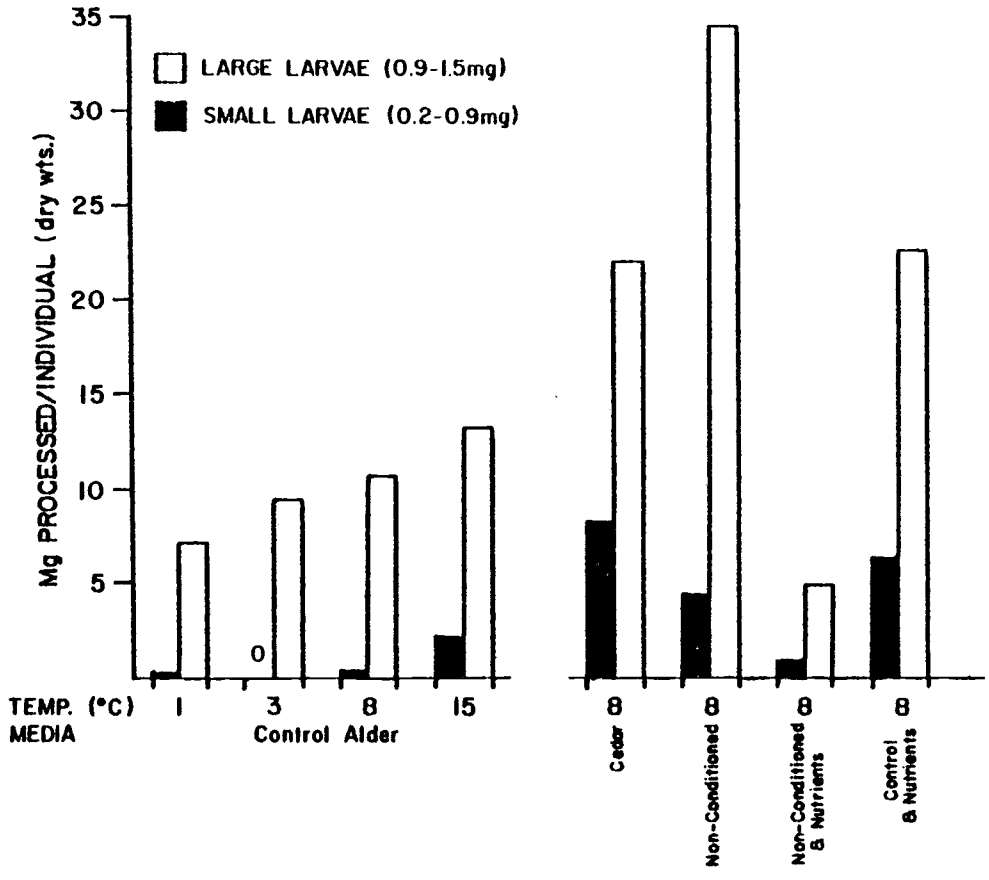


Fig. 33. Processing rates in vitro of L. nigrilinea and L. fenderi in response to temperature and food quality. Control media was macerated class 4-m alder; Non-conditioned was non-discolored class 3 alder; cedar was similar in texture to class 4-m. Only trends are shown because feces from individual larvae were not separated.

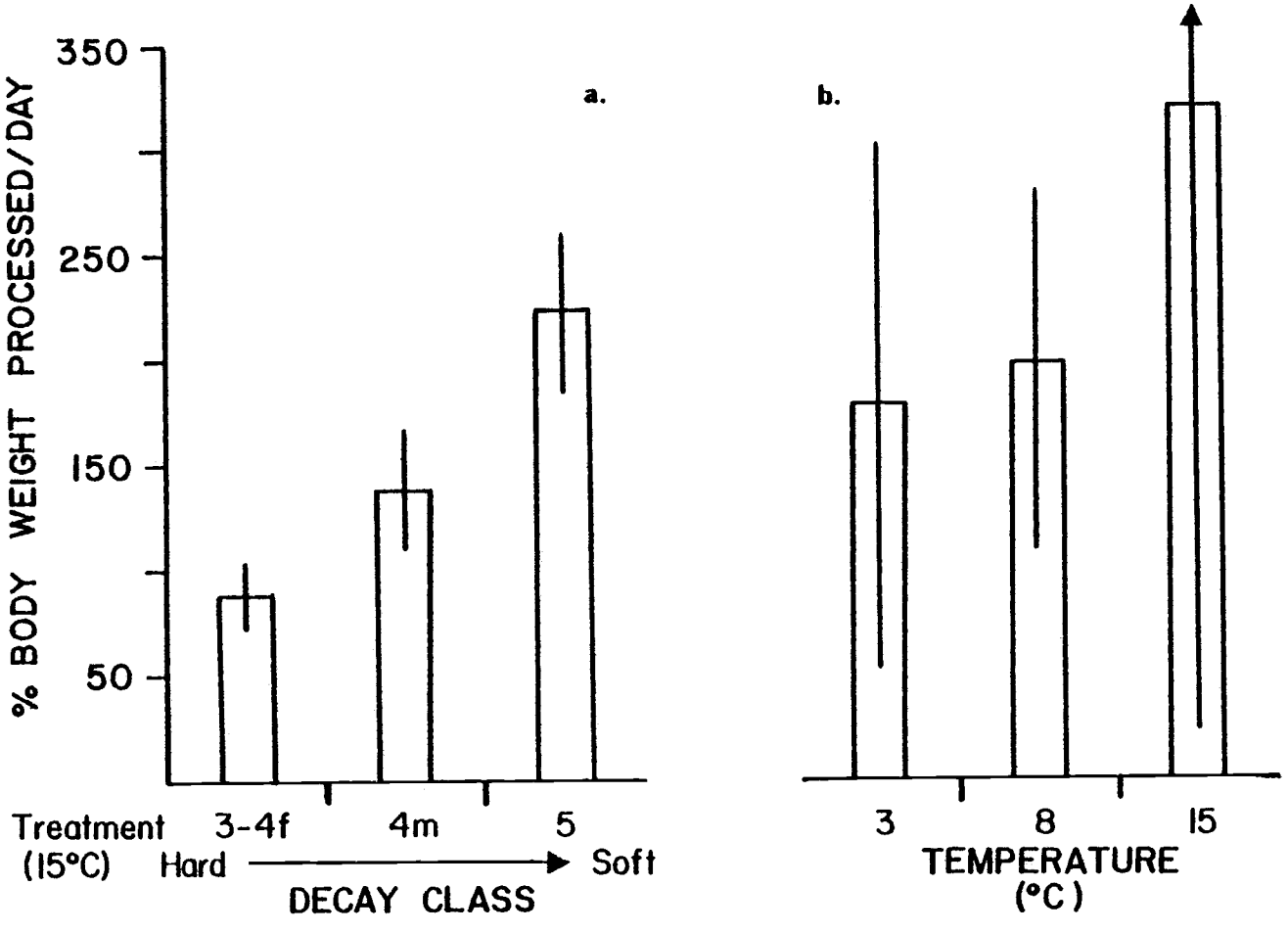


Fig. 34. Processing rates in vivo of L. nigrilinea in response to: a. decay class (hardness); and b. temperature. Expressed as mean % of body weight processed/day , standard deviation among logs of each treatment. Processing is significantly related to decay class (ANOVA, F=14.24, $p<.05$), though only a trend occurs with temperature (F=1.77).

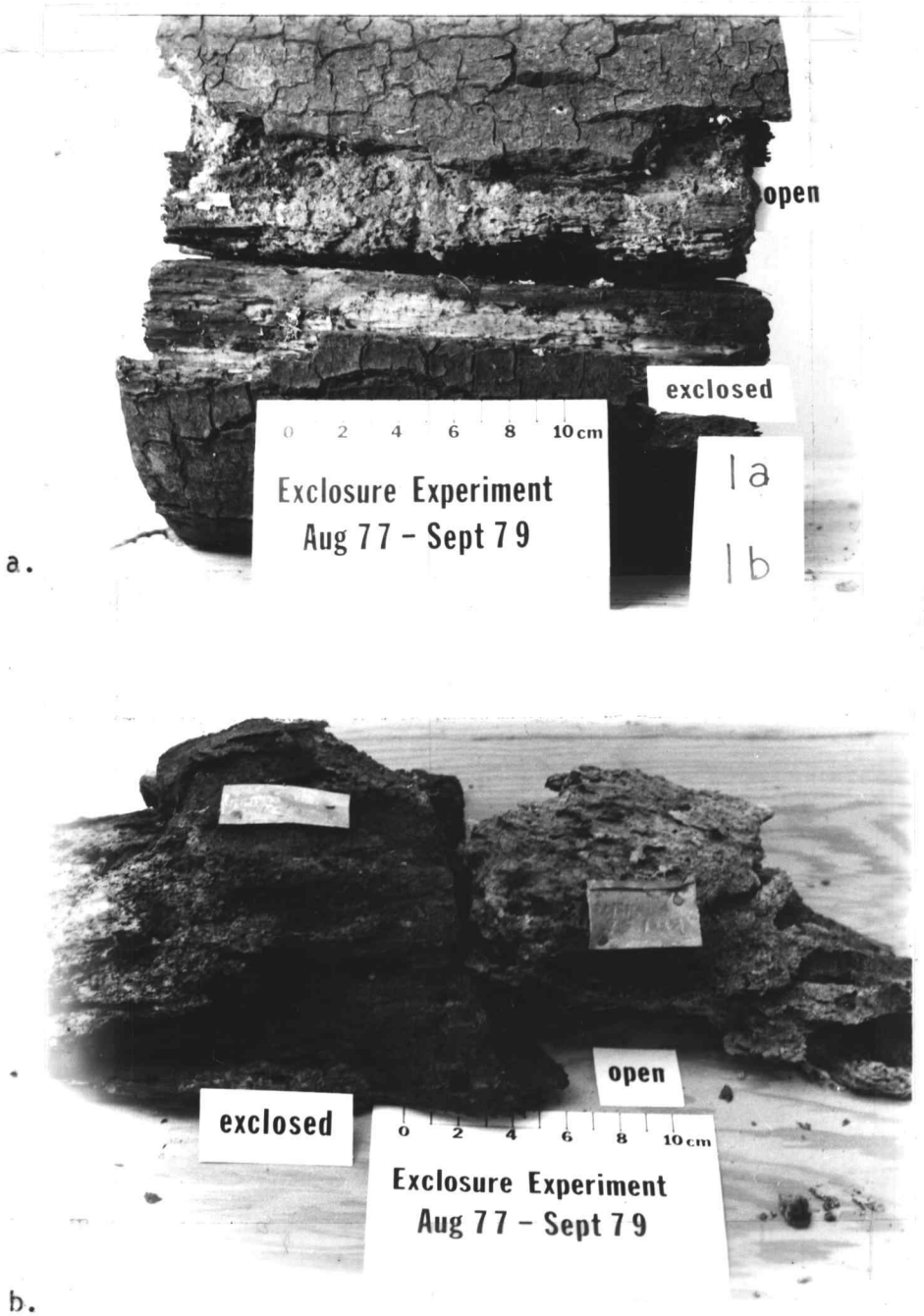


Fig. 35. Comparison of experimental logs in presence (open) and absence (exclosed) of Lipsothrix spp. for 2 years in the field. a. Class 3 log; b. Class 5 log.

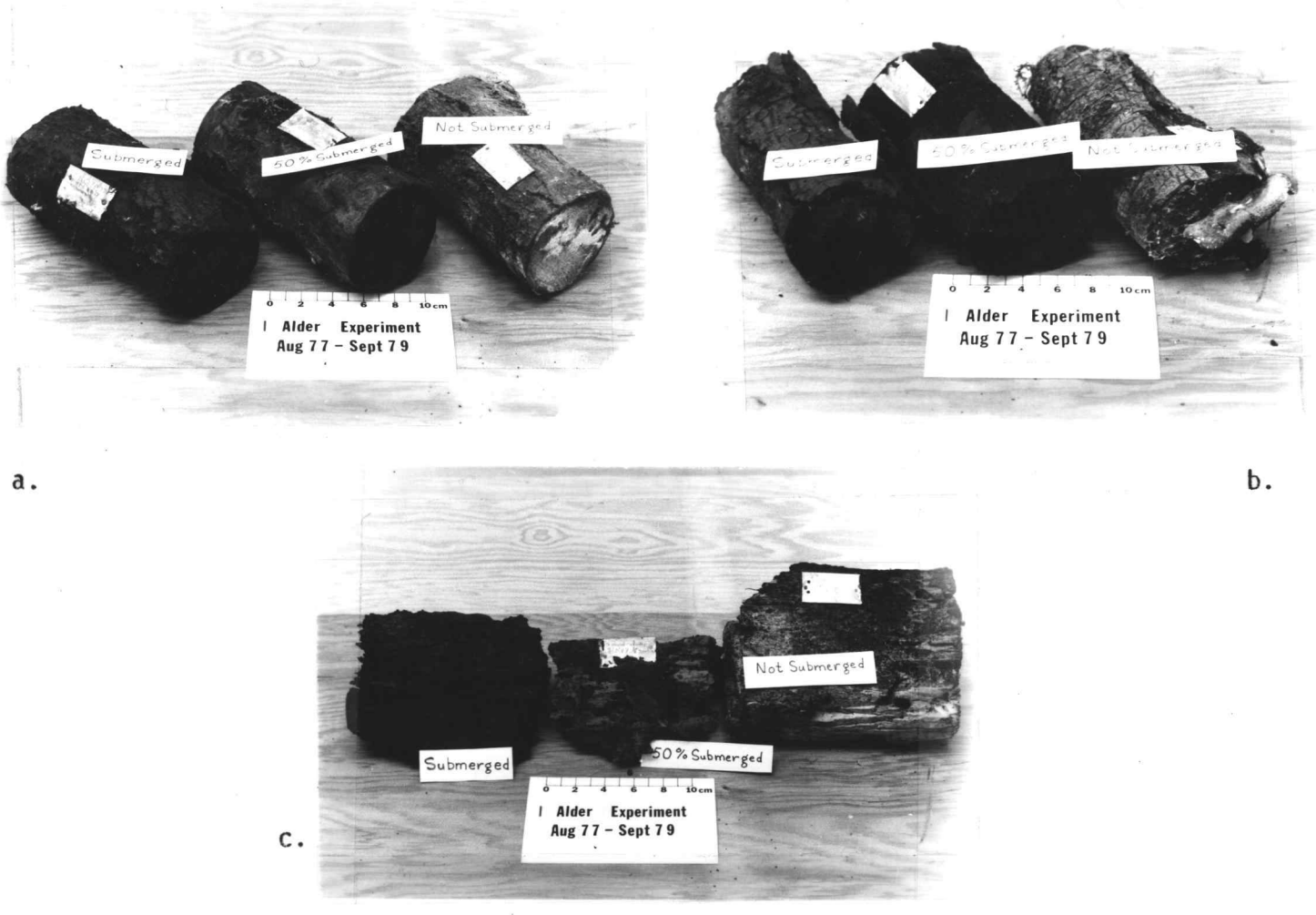


Fig. 36. Physical processing of 3 classes of alder wood maintained at 3 levels of submergence in an artificial stream: a. Class 1; b. Class 3; c. Class 5.

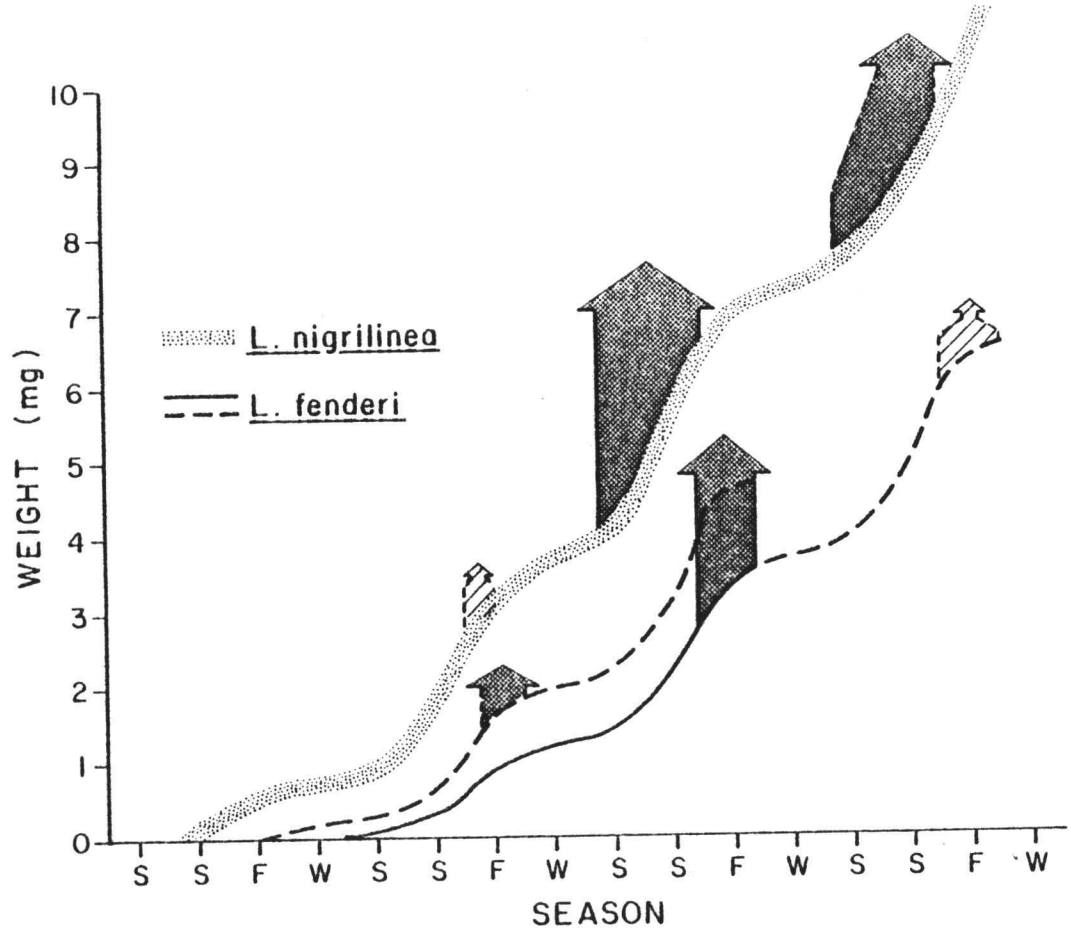


Fig. 37. Synoptic growth patterns of L. nigrilinea and L. fenderi. Solid line shows general L. fenderi pattern, dashed lines show hypothetical early sub-cohort and third year individuals, stipled L. nigrilinea line suggests wider variance in individual sizes; stipled arrows indicate major emergence periods, slashed arrows are hypothetical, width of arrowhead suggests relative importance of each emerging group.

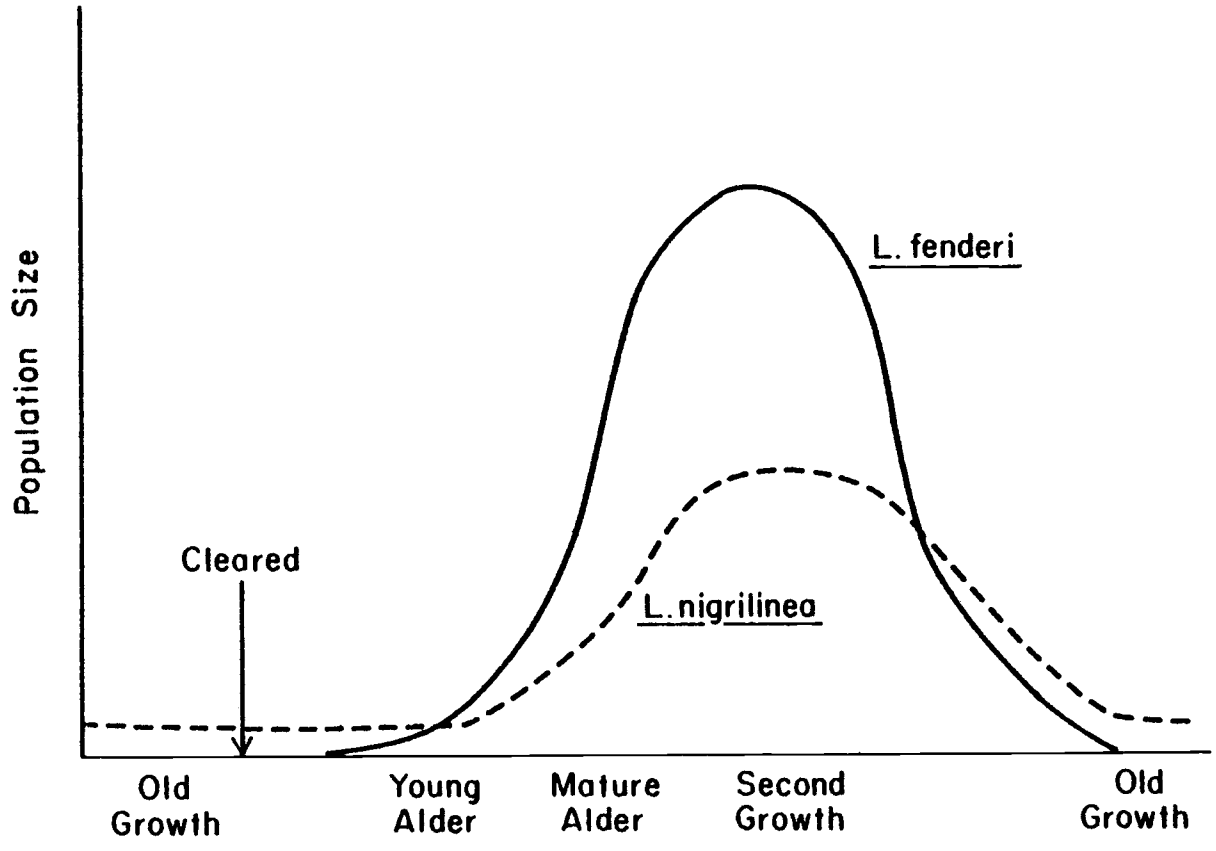


Fig. 38. Population size of L. nigrilinea and L. fenderi in streams with respect to successional stage of the riparian vegetation.

a.
100X

b. 305X

c. 135X

Fig. 39. Mandibles of three xylophagous aquatic insects showing analogous morphology of feeding structures. a. Lipsothrix nigrilinea; b. Lara avara (Elmidae:Coleoptera); c. Heteroplectron californicum (Calomoceratidae:Trichoptera). SEM courtesy of K. Luchessa and C. Hawkins.

Site	# logs sampled	Elev.(m)	Stream order	Riparian vegetation	Species
Coast Range					
1 L. Darkey Cr.	2	15	2	mat.AlRu-AcMa	B
"	2	"	seep	"	L.f.
2 Smallwood Cr.	3	30	2	AlRu-PsMe-AcMa	B
3 "County Line"	6*	90	1	mat. AlRu	B
4 Baker Cr.	1	110	1-2	mat. AlRu	B
5 L. Alder Cr.	1	300	1-2	PsMe-young AlRu	B
6 "Chintimini"	3	410	1	PsMe-ThPl-AlRu	B
7 Dinner Cr.	3	275	2	mat. AlRu-PsMe	B
8 Watkins Cr.	1	105	1-2	AlRu-AcMa	L.f.
Cascade Range					
9 Lewis Cr.	3	300	1-2	AlRu-AcMa-PsMe	B
10 Thistle Cr.	4	290	3	AlRu-young & mat-open	B
11 "Lone Cedar"	2	325	1	AcMa-AlRu-PsMe-open	B
12 Green Cr.	2	580	2	AcMa-PsMe-TsHe-ThPl	B
13 Bruler Cr.	1	860	2	TsHe-ThPl-AcMa-AlRu	L.n.

Table 1. Transect collection sites and site descriptions. AlRu=Alnus rubra, AcMa=Acer macrophyllum, PsMe=Pseudotsuga menziesii, ThPl=Thuja plicata, TsHe=Tsuga heterophylla. L.n.=L.nigrilinea, L.f.=L.fenderi, B=both species present. mat=mature stand, *=sticks (≤ 4 cm dia) were sampled.

	Decay Class					
	1	2	3	4f	4m	5
Bark	intact	intact	detached, but firm	absent or detached	absent or detached	absent
Structural integrity	sound, hard	sound, hard	sound interior, outer portion softer but firm	firm throughout but fibrous	outer portion easily removed, mealy, interior firm	inner and outer tissue easily sloughed
Microbial evidence	none	surface bacteria and fungi	some internal mycelia, not deep unless previously dry-rotted	extensive internal mycelia, non-dry-rotted	extensive mycelia	same
Color	original	surface darkening	outer stained inner original	dark stained throughout, grey	same as 3	dark throughout
Lignin (%)	-	17.5 - 18.5	-	21.5 - 52.0	17.0 - 23.0	>23
Cellulose (%)	-	47.0 - 50.0	-	24.0 - 39.0	44.5 - 51.0	44.5
Nitrogen (total)	-	0.15 - 0.32	-	0.32 - 0.33	0.39 - 0.50	0.45
Density, (mg/cm^3)	50	30	-	20	10-15	5-12
Associated organisms	grazers and collectors; surface associated	same as 1, some surface gougers (*Lara*, *Cinygma*, *Brillia*)	same as 2, surface gougers few *L. fenderi*, orthoclads	surface and shallow internal gougers, *L. fenderi*, orthoclads	surface and internal gougers, *L. nigrilinea*, *L. fenderi*, orthoclads	same as 4m, more diverse and deeper internal fauna, (*Xylophagus*, *Limonia*, Mycetophilids, other Diptera, Oligochaetes

Table 2. Alder wood decay classes (modified from Triska and Cromack 1980, Dudley and Anderson 1982, K. Cromack, unpublished data).

Material (Decay Class)	L. fenderi		L. nigrilinea	
	No. of eggs	Hatching success	No. of eggs	Hatching success
Alder (4-m)	30	unk.	20	high***
Alder (4-f)	not tested	-	0	-
Alder (5)	12	unk.	3	high
Douglas fir (4)	14	unk.	3	0*
Douglas fir (4-terrestrial)	not tested	-	0	-
Hemlock (4)	4	unk.	not tested	-
Paper towels	6	unk.	0	0**

Table 3. Number of eggs deposited and surviving on various oviposition materials presented to 5 females of L. fenderi and L. nigrilinea. *=no hatching upon transferral to paper towels, **=high based on other experiments, ***=hatched when transferred to paper towels; numbers represent minimum numbers of eggs deposited.

Animal tissue	♀ L. nigrilinea n	$\bar{x}$	Diff.	♀ L. fenderi n	$\bar{x}$	♂ L. nigrilinea n	$\bar{x}$	Diff.	♂ L. fenderi n	$\bar{x}$
Adult weight (mg)	50	4.31(2.06)	**	32	2.37(0.64)	74	2.05(0.87)	**	43	0.97(0.27)
C.V. (%)		48			27		42			28
Abdomen (%)	34	53.6(7.4)	**	28	65.0(3.2)	43	5.3(1.1)	**	29	8.7(2.4)
Egg #	26	187(67)	**	16	138(42)					
Egg weight	6	40.6(8.5)	**	11	55.3(3.9)					
		0.012			0.009					
Egg #/mg		43.4			60.1					
Ovipositor (%)	9	3.4(1.3)	*	13	5.2(1.7)					
Head and thorax (%)[1]	34	30.9(5.2)	**	26	22.0(2.3)	43	64.7(4.5)	*	29	59.1(2.7)
Wings (%)	18	3.4(0.7)	n.s.	10	3.1(0.4)	29	5.2(1.1)	*	22	6.2(1.4)
Legs (%)	28	16.5(2.6)	*	21	13.2(1.3)	34	29.9(5.0)	n.s.	16	32.3(3.3)
Pupal weight (mg)[2]	40	6.29(2.46)	**	17	2.72(0.88)	48	4.06(1.76)	**	17	1.58(1.07)

Table 4. Allocation of dry weight biomass to various adult tissues. [1]-'abdomen'=whole for ♀♀, final 2 segments for ♂♂, rest of ♂ abdomen included in 'head and thorax', [2]-pupal biomass included for comparison with adults. Standard errors in parentheses, *=$p<.05$, **=$p<.01$ by Mann-Whitney U, with Z approximation for $n_1+n_2>30$. Percentages do not add to 100 due to unequal sample sizes.

Species	Region	Weight
L. nigrilinea (July 1)	Coast Range-low, -high	1.30
	Cascades-low < 400 m	1.00
	-high > 500 m	1.10
L. fenderi	Coast Range-low < 110 m	0.80
(Oct. 1)	-high > 110 m	0.70
	Cascades-low < 300 m	0.70
	-high > 325 m	0.52

Table 5. Estimated average weight of larvae from 4 regions of transect collections at the end of one year, the terminal date given in parentheses (see Appendices 2,3).

Substrate	Decay Class	n	N	L	C	L:C
Decayed alder	5	3	0.45(0.11)	22.8(3.5)	44.5	0.51
Non-decayed alder	2	4	0.31(0.06)	17.5(0.7)	50.0	0.35
Light alder with Lipsothrix*	4-m	2	0.33(0.04)	17.2(0.6)	51.4	0.33
Dark alder with Lipsothrix**	4-f	3	0.55(0.04)	21.5(1.1)	38.8	0.55
Douglas fir with L. fenderi	4-f	1	0.32	37.3	31.5	1.18
Decayed stream wood (no Lipsothrix)[1]	3-5	8	0.32(0.10)	52.4(20.9)	23.6(15.0)	2.22
Decayed stream wood (Lipsothrix)[2]	4-5	9	0.39(0.11)	23.4(6.2)	44.5(7.4)	0.53
Frass (Cerambycidae in Cl. 3 alder)	'5'	1	0.49			
Alder sticks[3], surface	4	2	0.71,1.03	19.5		
internal	2	2	0.15,0.18	20.5		
Hemlock sticks[3], surface	3-4	2	0.60,0.44	30-36		
internal	2	2	0.05			
Douglas fir sticks[3], surface	3-4	2	0.42,0.69	36		
internal	2	2	0.05			

Table 6. Percent chemical composition of certain woods. L=lignin, C=cellulose, N=total nitrogen, *=preferred L. nigrilinea habitat, **=preferred L.fenderi habitat, [1]=alder, douglas fir and cedar, [2]=alder, single douglas fir, [3]=N.H. Anderson, unpublished data. Standard errors in parentheses. Analysis by O.S.U. Agricultural Chemistry Laboratory.

Treatment	Emergence (♂:♀) at: 1°C	3°C	8°C	15°C
Saturated media	0	0	0	0:1
Days to emergence	-	-	-	33
Moist media	0	1:0*	3:0	2:2
Days to emergence $\bar{x}$	-	50*	40.5	28.0

Table 7. Effects of temperature and water saturation on induction of pupation and emergence of L. nigrilinea in laboratory media. Four larvae initially in each treatment, with 75 or 100% survival in all except 15°C-Saturated (25%). *=one individual pupated after 50 days but spent 2 months as a pupa until it died.

	Above Waterline		Below Waterline	
	Green Cr.	Thistle Cr.	Green Cr.	Thistle Cr.
Number of Pupae	16	8	1	0
Number of 'very large' larvae (post emergence)	1	0	9	4
Recruitment (young of year)	18	17	12	5

Table 8. Pupation of L. nigrilinea with respect to water level. Collections were taken from a log, above and below the waterline, at two sites; pupation was significantly related to water level (Fisher exact, $p < .001$). Recruitment may also be inhibited by water level, but there was no statistical difference (t-test, $p < .20$).

Density no./100 cm^2	n	Percent of samples containing:				
		L.n. only	L.n.>L.f.*	L.n.≈L.f.	L.f.>L.n.*	L.f. only
High (≥20)	29	10	14	17	3	55
Medium(≥10)	68	22	7	19	19	32
Low (<10)	168	32	5	13	6	44

Table 9. Relative percent of L. fenderi and L. nigrilinea occurring in individual transect samples. L.n.=L. nigrilinea, L.f.=L.fenderi ; *dominance means samples contained ≥70% of a single species.

Competitor Taxa	Frequency of Association with: *L. nigrilinea*	*L. fenderi*
Austrolimnophila badia	11%	37% +
Lumbricidae	7	29 +
Orthocladiinae (≥3spp)*	34 +	18
Symmerus sp.	2	4 +
Tipula sp.	2	5 +
*Lara avara**	6 +	2
Diplopoda	0	7 +
Syrphidae	1 +	0
Asellus sp.	1	2 +
Psychodidae	2 +	0
Ptilodactylidae	0	1 +
Pyrochroidae	0	1 +
Oligochaeta	0	2 +
Isoptera	0	1 +
Unknown	2 +	1
Total groups	10	13
Mean # Individuals/sample	.53	2.04

Table 10. Percent of transect samples which contain potential competitors within the wood, with mean density of all competitors per 100 cm^2 at bottom. '+' indicates the *Lipsothrix* species most frequently associated with each competitor; *=aquatic species.

Predator Taxa	Frequency of Association with: *L. nigrilinea*	*L. fenderi*
Xylophagus sp.	2%	13% +
Dicranota sp.*	7	10
Hydrophilidae	1	5 +
Chilopoda	0	2 +
Rhyacophila spp.*	6 +	0
Ceratopogonidae	2 +	0
Tanypodinae	0	1 +
Carabidae	0	1 +
Empididae	0	1 +
Tabanidae	0	1 +
Staphylinidae	1 +	0
Total groups	6	8
Mean Density/sample	.21	.39

Table 11. Percent of transect samples which contain potential predators within the wood, with mean density of all predators per 100 cm^2 at bottom. '+' indicates the *Lipsothrix* species most frequently associated with each predator; *=aquatic species.

n	Duration (days)	Number of larvae		Mean % survival (S.D.)	
		Species 1	Species 2	Species 1	Species 2
2	50	3-4 L.n. (L)	5-6 L.n. (M)	83.4(23.5)	10.0(14.1)*
2	30	3 L.f. (L)	4 L.n. (M)	66.7(0)	87.5(17.7)
2	50	none	4-5 L.n. (M)	--	90.0(14.1)*
1	61	15 L.n.(L&M)	15 L.f.(L&M)	53.3	13.3
1	61	6 L.n.(L&M)	5 L.f.(L&M)	83.3	80.0

Table 12. The effect of interactions on larval survival among and between Lipsothrix spp. of different sizes at various densities and species compositions in artificial arenas. L.n.=L. nigrilinea, L.f.=L. fenderi; (L)=large and (M)=medium size class individuals; 30,50 day trials were in 10 cm dia petri dishes, 61 day trials in larger glass bowls; different larval densities were due to mortality independent of the experiments; *=significant difference between treatment and control (t-test, $p<.05$), suggesting predation by larger individuals; in the final two treatments, 50% reduction of L.n. and 85% reduction of L.f. suggests predation by L.n. on both L.f. and small L.n.

T(°C)	# logs	mg Processed per cm^2 d^{-1}	mg Animals cm^{-1}	*Lipsothrix* x Density ($\#/cm^2$)	mg Processed per mg Animal d^{-1}
15	6	.072	.040	.053	3.19(3.02)
8	5	.065	.033	.045	1.96(0.82)
3	5	.035	.020	.050	1.78(1.22)

Table 13. Processing of logs by *Lipsothrix* spp. in laboratory at different temperatures. Processing is measured by rinsing egested material from the log surface, along with material softened by feeding activity after 55 days. (Biomass and density of larvae in 6 frozen control logs were .034 mg/cm^2 and .111 larvae/cm^2)

Treatment	n pairs	Decay class	Exclosure - Control (g)	Available Surface area(cm^2)	% Loss by *Lipsothrix*	Impact (mg/cm^2)
Live wood	3	1→2	none*	--	0	--
Branch, seasoned	1	2→3	15.7	120	<1	13
log, seasoned	3	2→3	-228.0	1600	ambiguous	27**
moist, dry-rotted	2	4m→5	152	390	6.6	389
dry, dry-rotted	2	4m→5	113	260	19.8	435

Table 14. Tissue loss of logs of different decay classes, manipulated to include or exclude oviposition. Differences between pairs represent processing attributed to *Lipsothrix* spp. over the two year experimental period. *=not colonized, **=estimated from other data due to ambiguous results in this treatment

Type	Initial density* (g/cm^3)	n	Open Wood Density	Open Animals	Control Wood Density	Control Animals	Difference (t-test)
Live wood	.560	2	.554	Ø	—	Ø	
Branch, seasoned	—	1	.226	L. n.?	.302	Ø	N.S.
log, seasoned	.275	4	.165 (.017)	L. n., L. f.!, Ch.	.192 (.024)	Ch, L.f.(-)	p<.05
moist, class 5	.117	3	.112 (.004)	L. n.!, L. f.!, Ch.	.118 (.031)	Ch., L.f.(-)	N.S.
dry, class 5	.116,.10	2	.116 (.008)	L.n.!	.112	Ø	N.S.

Table 15. Density of outer 2.5 cm of logs after two years in the field, that were manipulated to allow or exclude oviposition. L. n.=L. nigrilinea; L.f.=L. fenderi; Ch=Chironomidae; *=measurement done separately on wood of same origin; ?=presence of larvae questionable, i.e. no larvae seen but gouging evident; !=high density of larvae; (-)=low densities of larvae.

Type	0% Submergence		50% Submergence		100% Submergence	
	Final Wt. (g)	Density (mg/cm^3)	Final Wt.	Density	Final Wt.	Density
Live wood	381.5	507 (11)	345.0	523 (10)	356.0	497 (6)
bark only		783 (91)		561 (25)		545 (69)
general appearance	50% mycelial cover, bark tight		wood solid, darker, bark loose		solid, darker, only part of bark loose	
Seasoned, Class 2	160.0	165 (15)	188.0	231 (12)	144.0	254 (4)
bark only		569 (96)		848 (296)		417 -
appearance	more than 4 g fungal sporocarp (Polyporaceae)		clean		clean	
Dry-rooted wood, 4m	69.0	78	10.5	80	33.0	88
appearance	same as start		darkened, fully eroded		similar to start, partially eroded	

Table 16. Final weights and densities (specific gravity) of three rot classes of alder at three levels of submergence, in an artificial stream without Lipsothrix spp. S.D. in parentheses, n=2 for density values in first two treatments; differences for live wood are significant (one-way ANOVA, $F=4.00$, $p<.05$) and for class 2 wood are not ($F=33.92$, $p<.05$).

	Coniferous forest or Old-growth	Clearcut or young alder	Second-growth mature alder
Seep or first order (<2m)	(3) 0.15	(3) 0.9	(6) 8.2
Second order (2-4m)	(2) 0.17	(2) 1.0	(4) 22.1
Third order (>4m)	(2) 0	(2) 0	(5) 0.03

Table 17. Estimated annual impact of Lipsothrix spp. in various stream types, expressed as grams of wood processed per meter of stream length. Estimates are based on quantification of all wood types from 50 or 100 m sections of 2-7 streams of each type (n in parentheses).

Species	Oviposition date	Voltinism	Maximum weight (mg)	Estimated consumption (g)
L. nigrilinea	Aug 1	Biennial	4.5	3.1
"	May 1	Biennial	6.0	5.2
"	May 1	Triennial	12.0	12.9
L. fenderi	Sept 1	Annual	1.75	0.6
"	Oct 1	Biennial	4.0	2.4

Table 18. Lifetime consumption of class 4-m wood during the life cycle by L. nigrilinea and L. fenderi of different ages and starting times. Estimated by assuming 150% of body weight/day consumption in winter, 200% in spring and fall, and 300% in summer. A curve was fit to values obtained, and the area under the curve approximated total consumption.

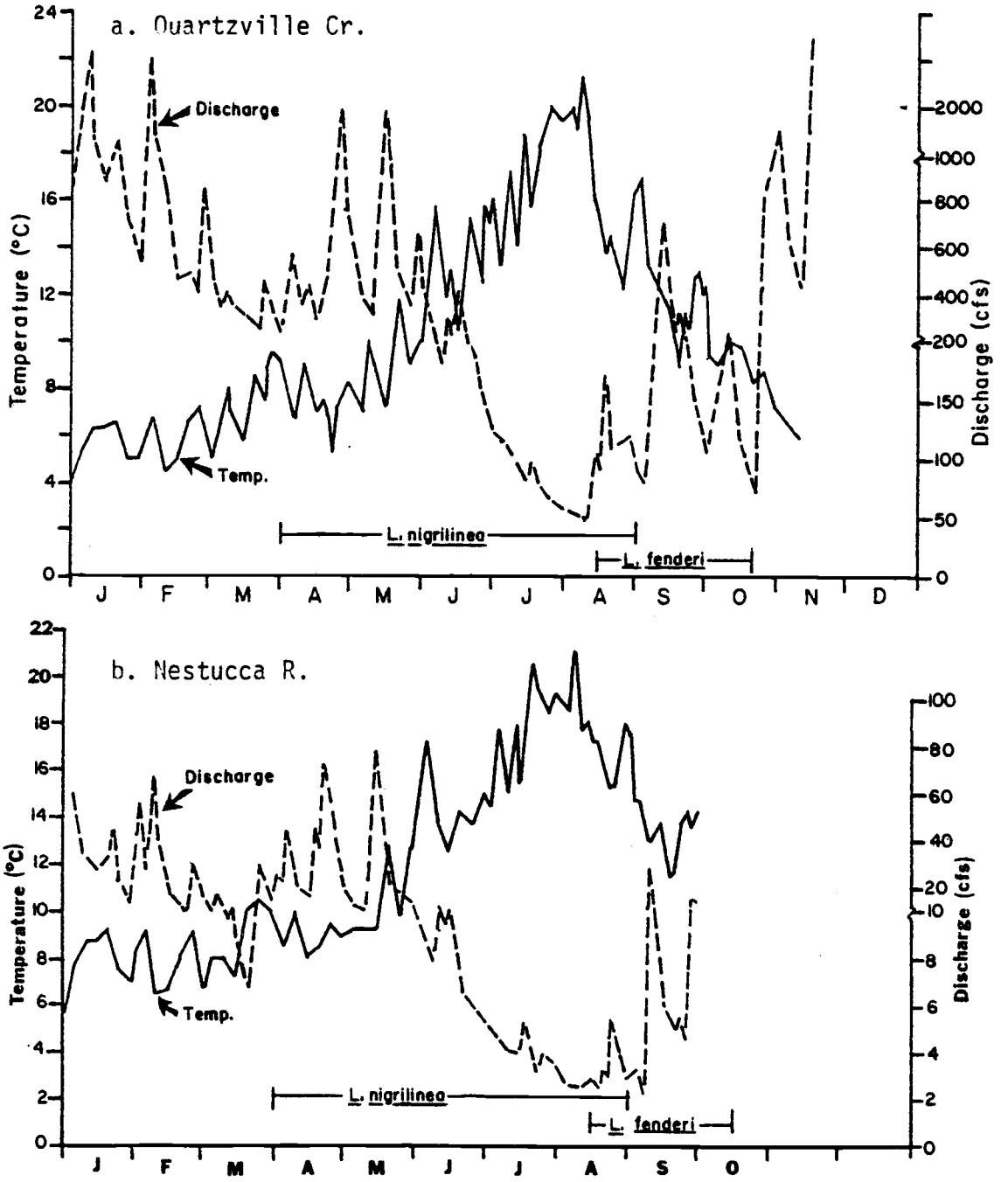
Population Problem	Characteristics of Xylophily by *Lipsothrix* spp.
Resource Acquisition	Eat saturated wood with associated microbes--once encountered, wood is in high short-term (all seasons) and long-term (many years) abundance; Microbes further vectored by larval boring; Gut symbionts may provide additional nutrients.
Predation	Low predator abundance and richness internally; Intrageneric & intraspecific predation may be important, especially at high densities; Single egg oviposition decreases risk of cannibalism Disease and parasitism low for isolated larvae within; Imago stage is short--avoids high risk external environment.
Competition	Interspecific: low abundance and richness; Intraspecific and intrageneric may be important but little opportunity for interaction--generally galleries do not connect; Emergence periods and time of maximal size non-overlapping; Some habitat differences (depth in wood, wood quality) may separate species.
Physical Mortality	High habitat stability: Wood and water buffer temperature and moisture extremes; Logs are relatively resistant to abrasion and habitat displacement.

Table 19. *Lipsothrix* and the Environment: some consequences and advantages of association with woody debris in streams.

	L. nigrilinea	L. fenderi
Host	Alder, other species at low density	Alder, other species at high density
Habitat preference	Narrow, more predictable substrates	Broad, often marginal & poor quality substrates
Life cycle	Biennial-triennial	Annual-biennial
Emergence cue	Water level&temperature flexible response	Temperature? less flexible
Adult size $\bar{x}$(S.D.),C.V.	4.31(2.06),0.48 2.05(0.87),0.42	2.37(0.64),0.27 0.97(0.27),0.28
Egg number	185 (42.5/mg)	138 (60.1/mg)
Egg size	0.012 mg	0.009 mg
Oviposition	Single eggs,high substrate specificity	Single eggs,may dump, less specific
Reproductive allocation	53.6%, increase with female size	65.0%, less increase
Population density	Lower, may regulate	Higher, no regulation
Larval migration	Yes	No
Competitive ability	Potentially displaces L. fenderi	Potentially excluded
Predator avoidance	Larva-active, tough aggressive Adult-cryptic, not in webs	Larva-passive, fragile Adult-yellow(visible), in webs, fragile
Colonizing ability	Good,maintain population until habitat is available,strong fliers	Good,more dispersive to new habitats, greater numbers

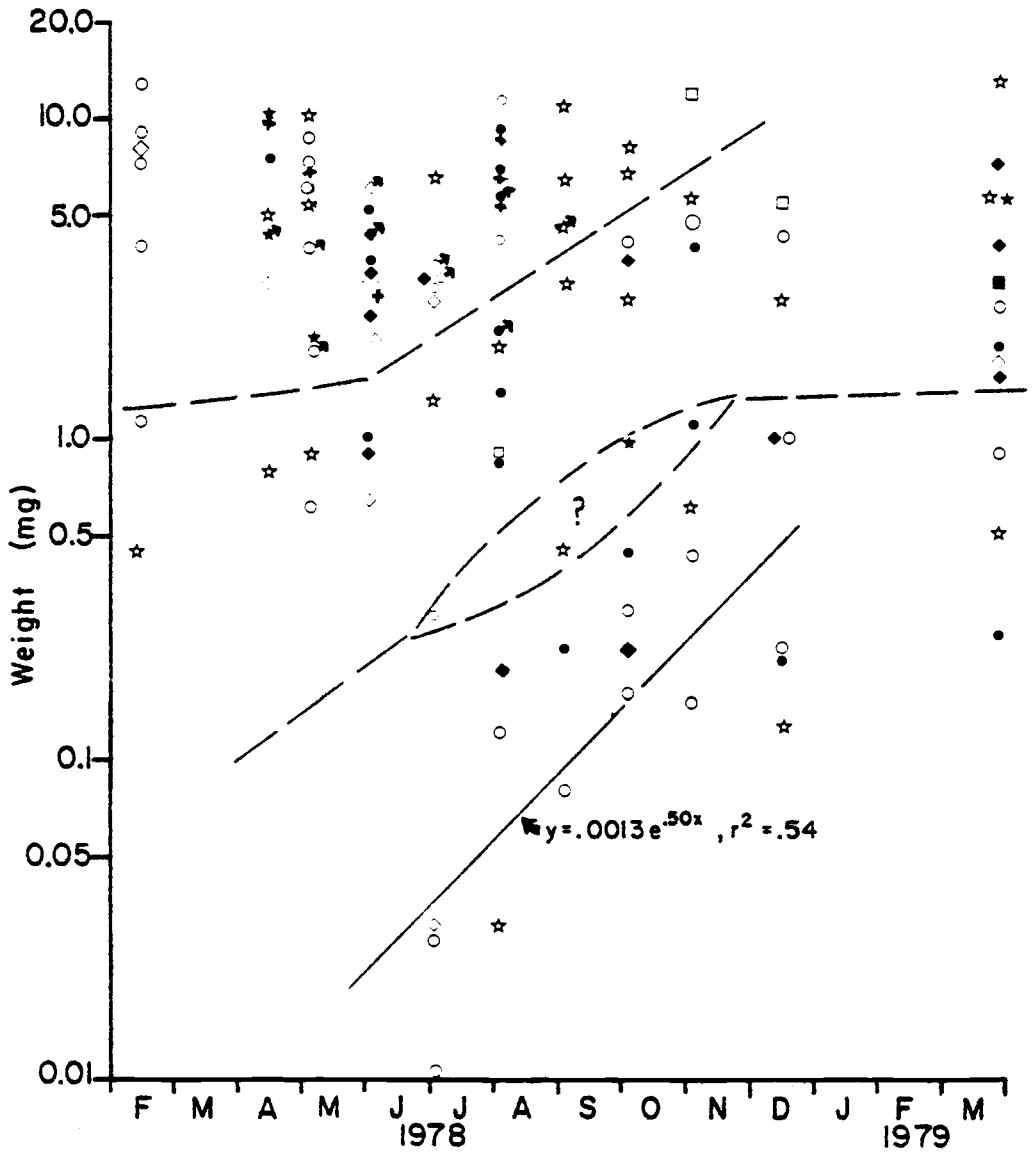
Table 20. Life history traits of Lipsothrix spp., to compare overall strategies.

APPENDICES

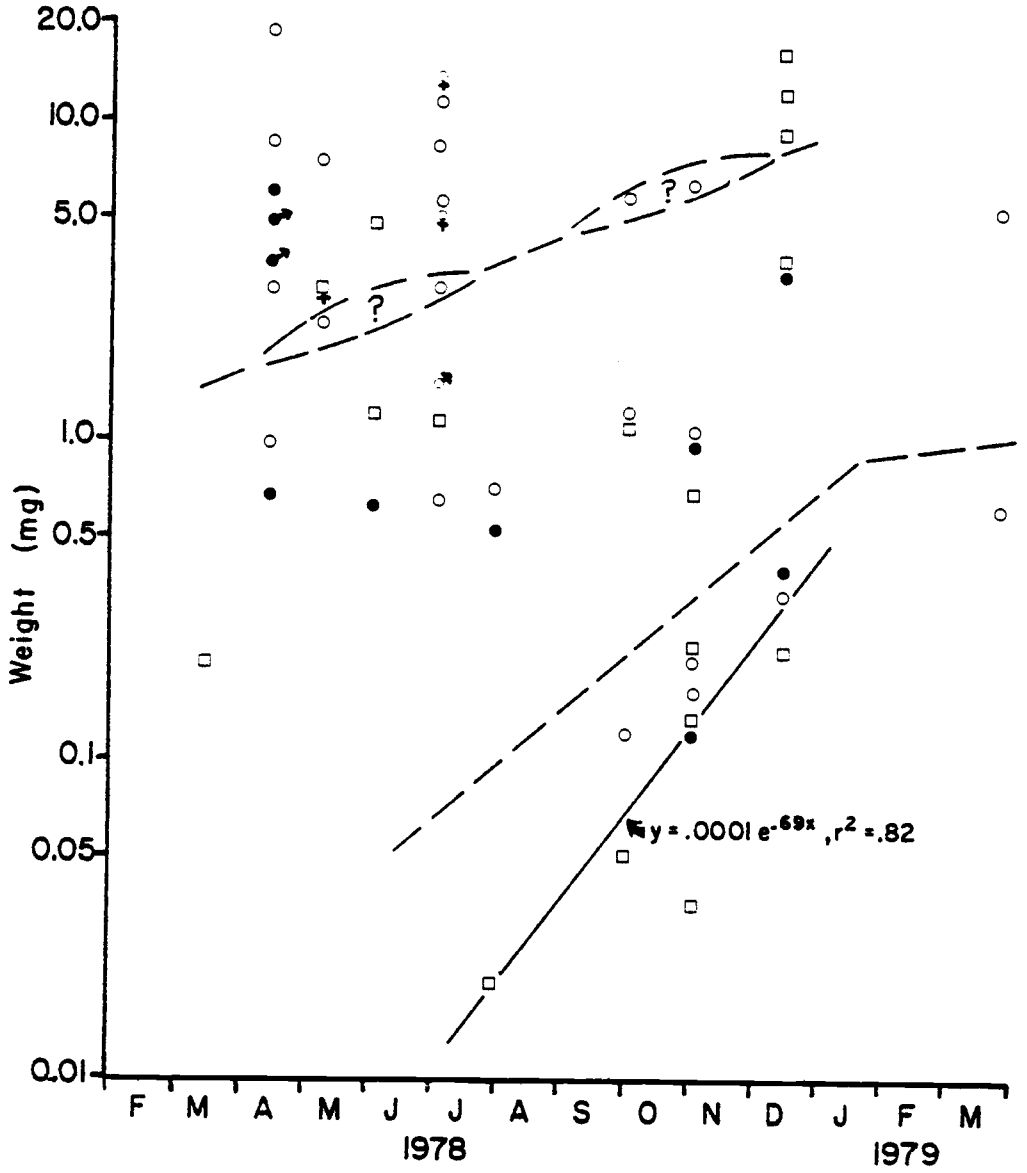


Appendix 1. USGS 1978 discharge and temperature records for a coastal and a Cascade river, compared with emergence periods of L. nigrilinea and L. fenderi over all sites.
a. Quartzville Cr., Linn Co., OR--elev. 320 m.
b. Nestucca R., Yamhill Co., OR--elev. 542 m.

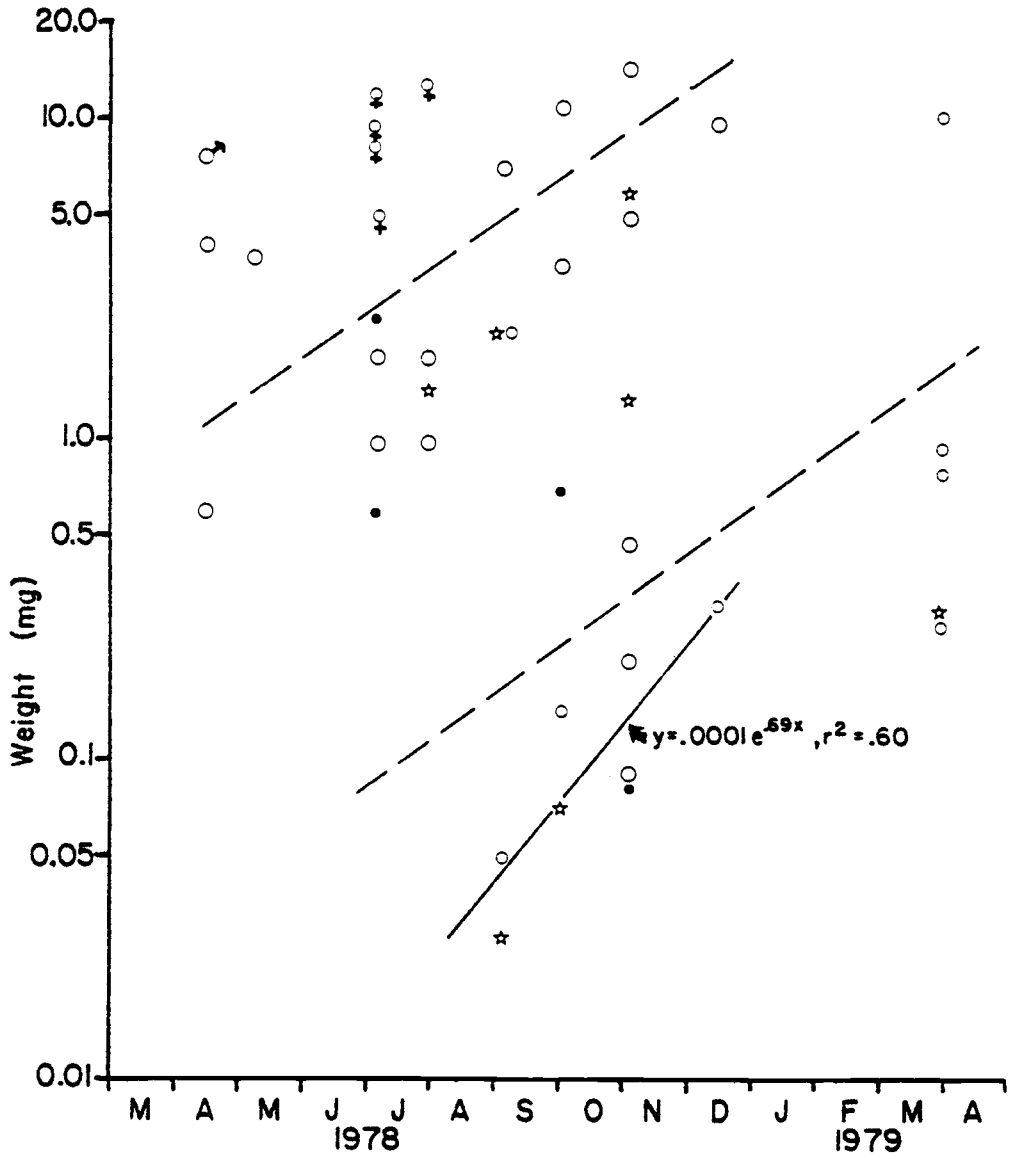
Appendix 2. Mean weights of L. nigrilinea cohorts from transect collections. Symbols represent means of animals from single samples which appeared to be of a single year class; dashed lines separate those estimated to be first, second or third year larvae; multiple entries in a year class represent different logs sampled; pupae indicated by gender symbols. Solid lines represent exponential regressions of first year larvae from summer of oviposition to late fall or December; for regression equation, ordinate is arranged numerically (e.g.-Jan.=1, June=6).



2a. Coast Range L. nigrilinea collections. ●=L. Darkey, ○=Smallwood, ◆=County Line, ★=Baker, □=L. Alder, ☆=Chintimini, ◇=Dinner, ■=Watkins.

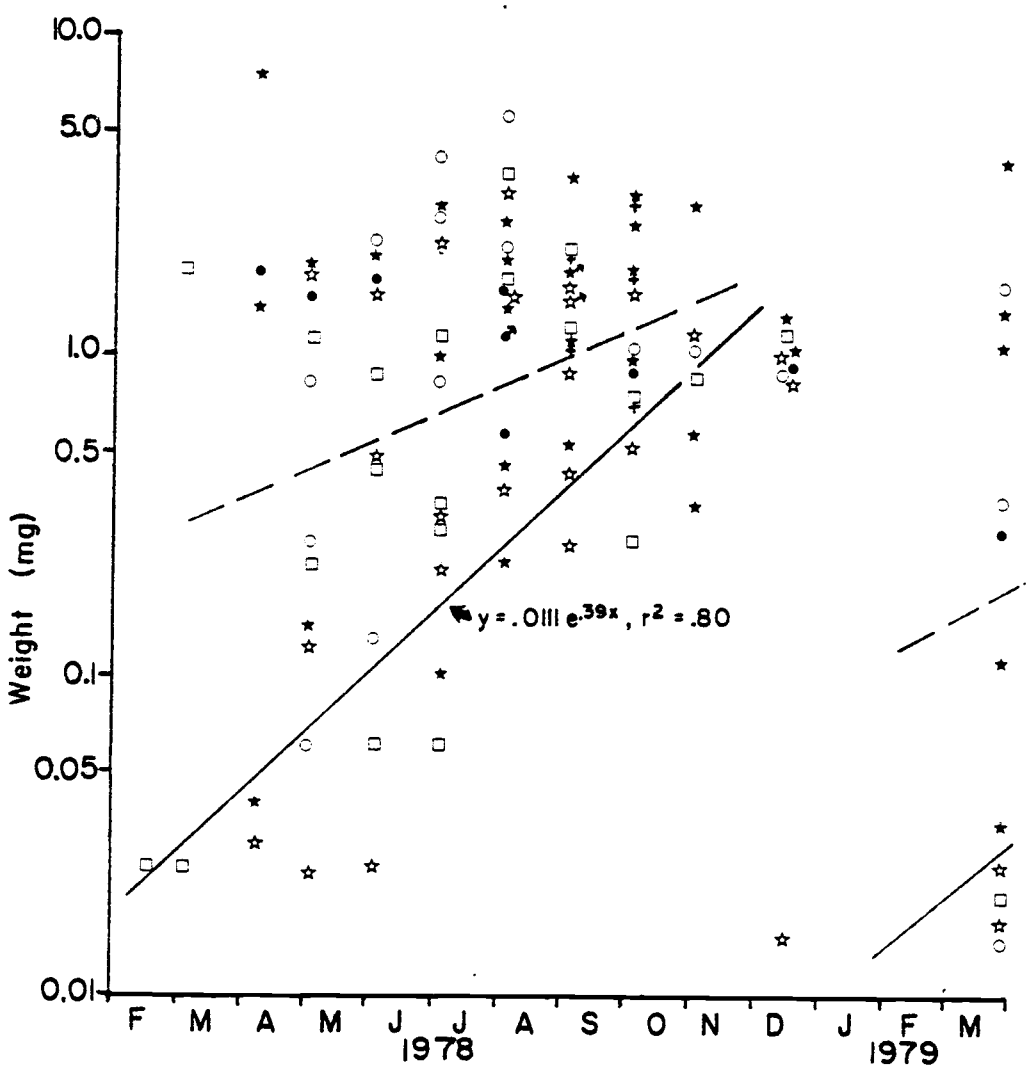


2b. Low Cascades L. nigrilinea collections. ●=Lew-is, ○=Thistle, □=Lone Cedar.

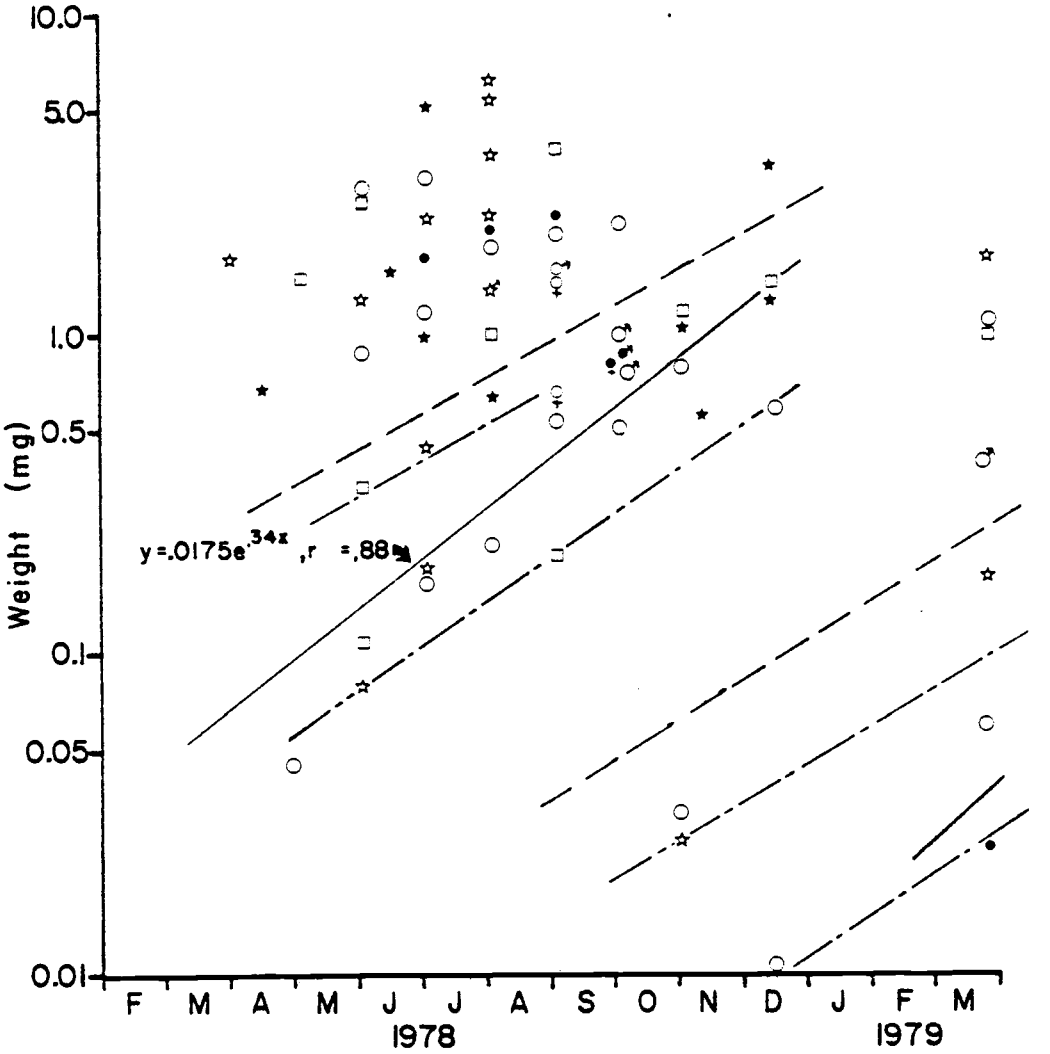


2c. High Cascades L. nigrilinea collections. ○=Green (falls log), ●=Green (side channel), ☆=Bruler.

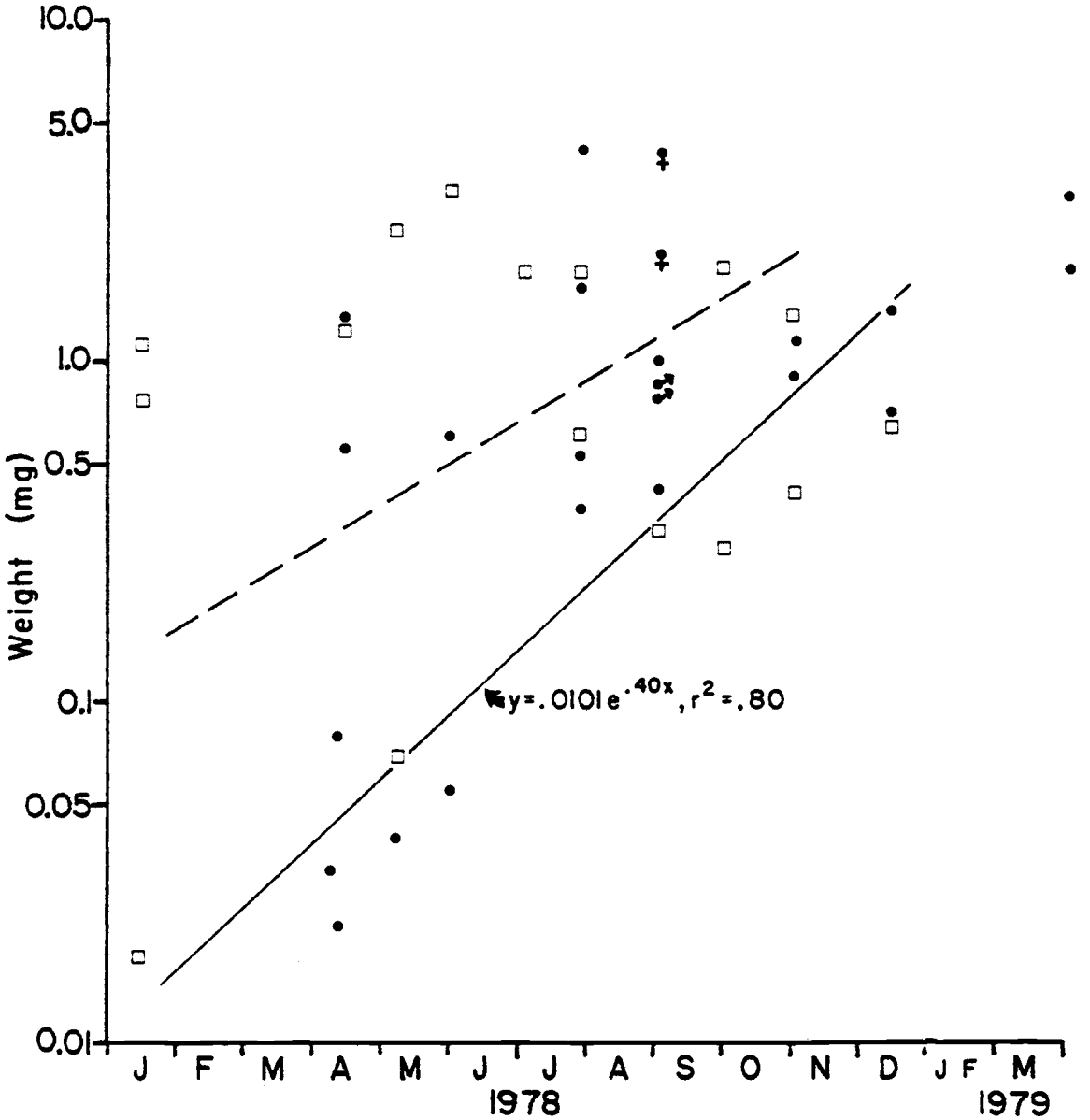
Appendix 3. Mean weights of L. fenderi cohorts from transect collections. Symbols represent means of animals from single samples which appeared to be of a single year class; dashed lines separate those estimated to be first or second year larvae; multiple entries in a year class represent different logs sampled; pupae indicated by gender symbols. Solid lines represent exponential regressions of first year larvae from early spring following oviposition to late fall or December, including 1979 cohort; for regression equation, ordinate is arranged numerically (e.g.- Jan.=1, June=6).



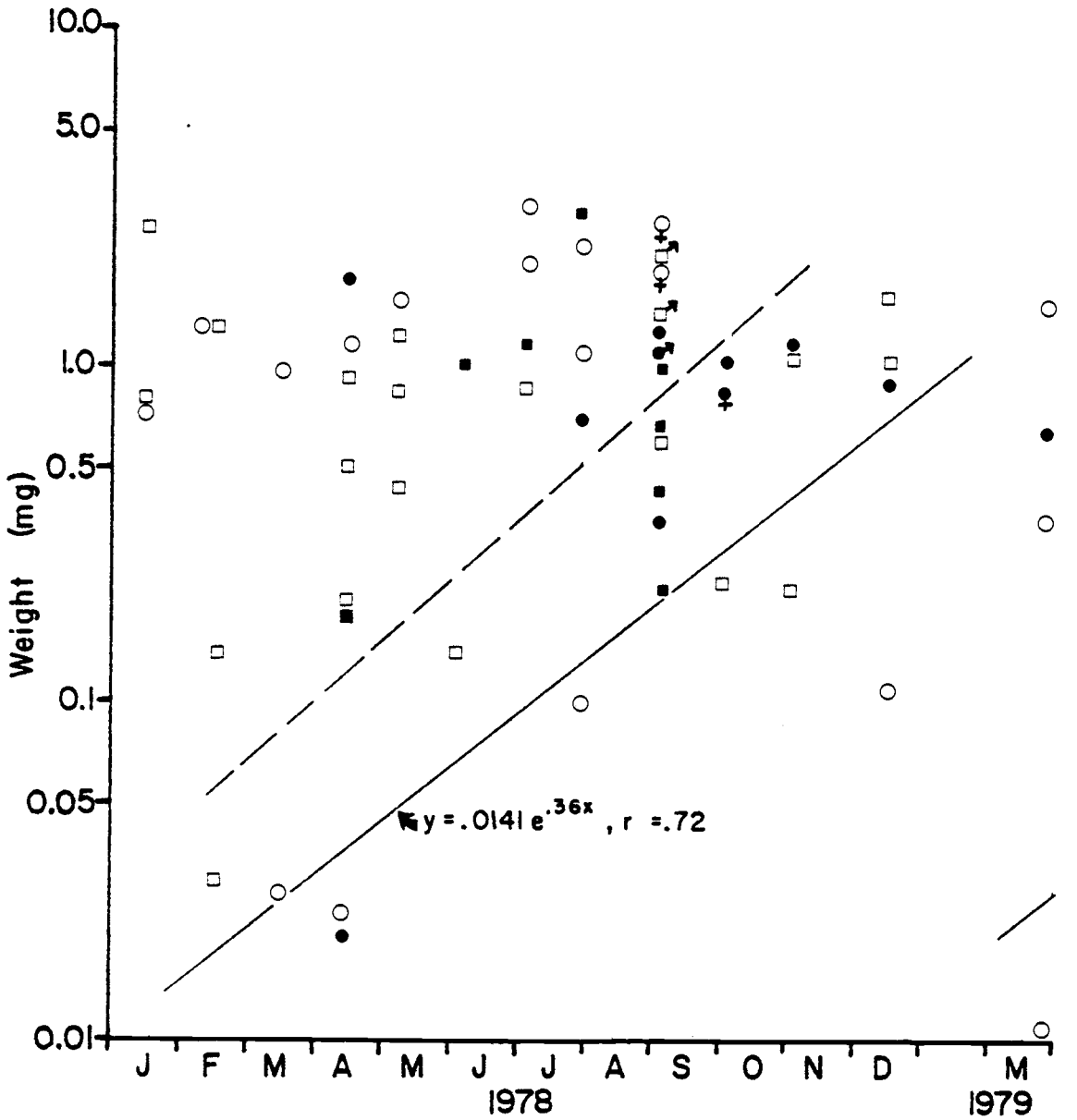
3a. Low Coast Range L. fenderi collections. ★=L. Darkey (stream), ☆=L. Darkey (seep), □=Smallwood, ○=County Line, ●=Baker.



3b. High or inland Coast Range L. fenderi collections. □=L. Alder, ☆=Chintimini, ○=Dinner (gate), ★=Dinner (gangplank), ●=Watkins. Uneven-dashed lines indicate sub-cohorts (see text).



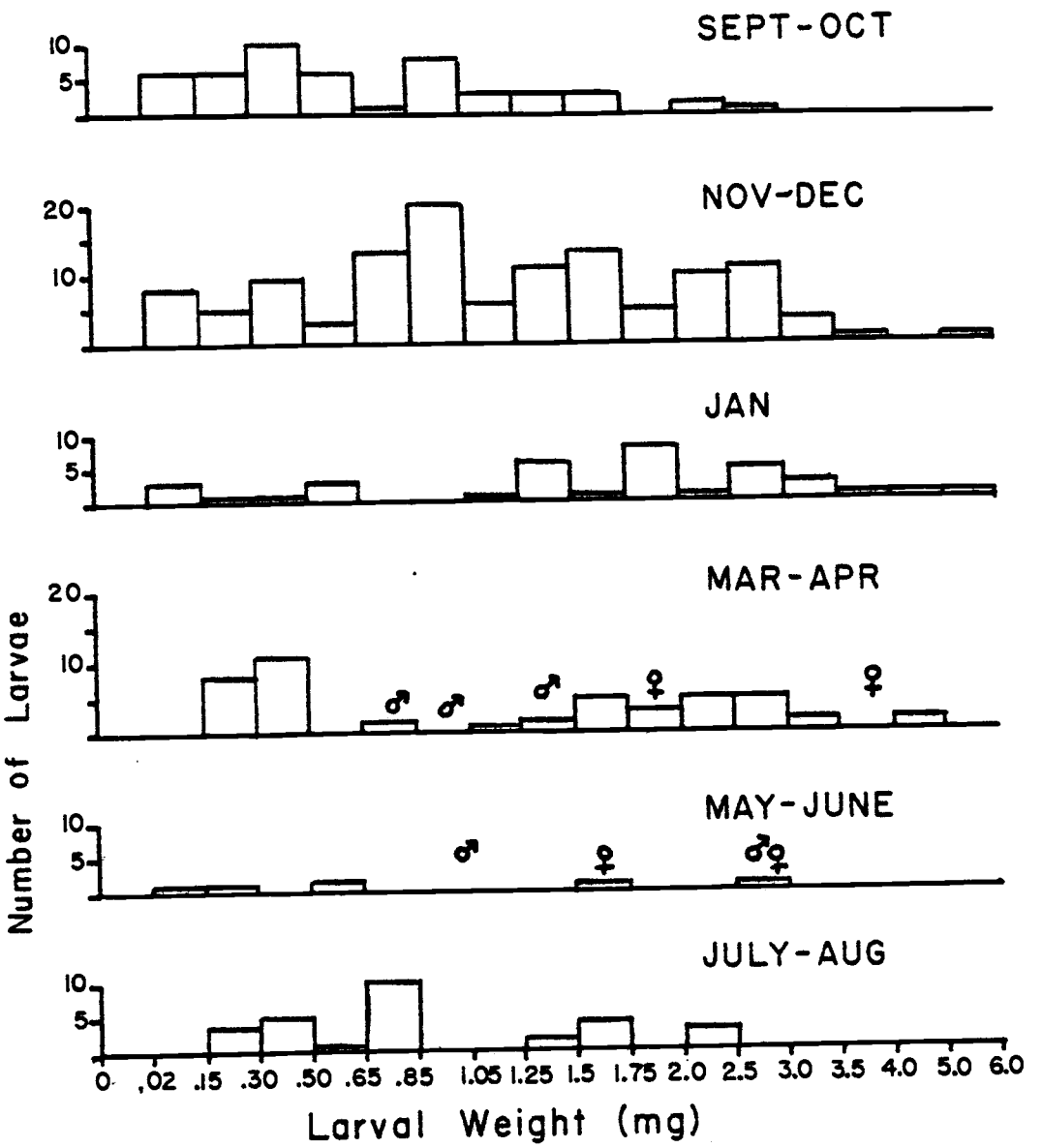
3c. Low Cascades L. fenderi collections. ●=Lewis, □=Thistle.



3d. High Cascades L. fenderi collections. ○=Lone Cedar (lower), ●=Lone Cedar (upper), □=Green (side channel), ■=Green (falls log).

Taxon	*Lipsothrix* absent n=11		*L.n.* only n=72		*L.n.*>*L.f.*[1] n=17		*L.n.* *L.f.* n=40		*L.n.*<*L.f.*[1] n=24		*L.f.* only n=112	
	F	D	F	D	F	D	F	D	F	D	F	D
Austrolimnophila badia (Tipulidae)	36.4	4.8	11.1	1.9	11.8	1.0	20.0	1.4	66.7	1.9	30.4	2.9
*Dicranota sp. (Tipulidae)	9.0	1.0	6.9	1.2	5.9	1.0	12.5	1.4	25.0	1.5	6.2	1.5
Symmerus sp. (Mycetophilidae)	18.2	2.0	1.4	2.0	5.9	1.0	0	-	0	-	5.4	3.0
**Orthocladiinae (Chironomidae)	54.6	4.2	27.8	5.9	58.8	7.9	42.5	6.0	33.3	4.2	5.4	4.2
Xylophagus sp. (Xylophagidae)	18.2	1.5	2.7	1.0	0	-	7.5	1.0	12.5	1.0	12.5	1.5
Oligochaeta-most *Dendrodrilus rubidus*	27.3	2.3	8.3	1.3	0	-	7.5	1.7	25.0	2.8	29.5	2.2
Other boring predators	>9.1	1.0	6.9	1.0	0	-	10.0	1.0	16.7	1.2	18.8	1.1

Appendix 4. Frequencies and densities of common associated species with different densities of *L. nigrilinea* and *L. fenderi*. F=frequency of occurrence of taxon (% of all samples), D=density of taxon when it occurs (#/100 cm^2), *=predator, **=truly aquatic. Other species are given in text (Tables and). [1]-dominance means ≥70% in a sample.



Appendix 5. Larval size distribution of Austrolimnophila badia during one year from transect collection data. It probably has a one year life cycle, though a few individuals may remain until the second year. Gender symbols indicate individual weights of pupae, which emerged during April-June in 1979.