

# BIOLOGY OF FRESHWATER CHIRONOMIDAE

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The family Chironomidae is the most widely distributed and frequently the most abundant group of insects in freshwater environments. An enormous amount has been written about their biology (51, 69), and yet the detailed ecology and life cycles of the great majority of species are unknown and most general faunistic works either ignore the Chironomidae or deal with them superficially (146). The primary reason for such deficiencies is the lack of readily available "keys" for their identification, coupled with the large number of species frequently encountered within even a small water body. The recent generic diagnoses and keys to larvae and pupae of the Holarctic region (214, 215), which will shortly be followed by a similar treatment of adult males, should do much to remedy this situation.

The first attempt to summarize the ecology of the Chironomidae was by Thienemann (189), and there have been two, more recent, reviews that provide useful summaries of the natural history of the group (136, 149).

## LIFE CYCLES

In temperate regions many species of Chironomidae are uni- or bivoltine, but the occurrence of three or four annual generations is not uncommon (25, 54, 73, 145, 147, 151, 161, 173, 174, 227, 228). A substantial number of species, especially among the subfamily Orthocladiinae, are multivoltine with continuous recruitment for much of the year (41, 143, 151, 220). Species inhabiting the profundal of deep lakes may require more than a year to complete their development (2, 76), whereas in the far north all species require at least two (123) and up to seven (24) years.

For most species the overwintering capability is not restricted to any particular instar, and in temperate regions development of some species may continue throughout the winter (127). *Paratendipes albimanus* larvae are known to remain as first or second instar larvae throughout the winter (202), and *Rheotanytarsus curtistylus* larvae pass most of the winter in the third instar (147). Under favorable conditions, many species are capable of very rapid development (89, 145), but larvae derived from the same batch of eggs may not necessarily all develop at similar rates (196). The subject of dispersal of chironomid larvae from the egg mass was reviewed by Davies (38).

The pupal stage is short lived and has been little studied in an ecological context (136). When development is complete, the pupa swims to the surface where the adult usually emerges within a few seconds (129). Oliver (136) states that adult midges live for a few weeks at the most, but for many species the length of adult life is no more than a few days (93, 196). In general, chironomids produce only a single egg batch, although, on the basis of ovarian structure, *Chironomus plumosus* females appear to be capable of producing up to three batches of eggs (209).

## INFLUENCE OF ENVIRONMENTAL CONDITIONS

### *Nature of Substratum*

Although chironomid species may exhibit a distinct preference for a certain type of substratum (95, 118), many are capable of using a variety of substrata (144). Several studies have identified the nature of the substratum as an important factor limiting the distribution of chironomid larvae (95, 101–103, 109).

The types of substratum available for colonization in aquatic habitats may broadly be classified as hard rock, soft sediment, submerged wood, and aquatic plants. A few species of chironomid live epizoically on other invertebrates. This aspect was reviewed by Steffan (176), who has also discussed the evolution of such associations (177).

Although well known in qualitative terms, the quantitative ecology of the chironomid fauna of hard rock surfaces, predominantly Diamesinae and Orthoclaadiinae (189), has been little studied. None of the species listed in *Limnofauna Europaea* (50) as characteristic of hygropetric situations (i.e. thin films of water on rock surfaces) is restricted to such places. They all occur also in springs or small streams. The Chironomidae inhabiting hard rock surfaces in glacier brooks have been particularly well described (44, 86, 163, 178, 179).

The fauna of soft sediments, including gravel as well as various grades of sand and silt, has been much more intensively studied than that of hard rock surfaces (95, 106, 144), primarily because of the relative ease with which quantitative samples can be obtained.

In a detailed study of the benthos of Loch Leven (106), no species of chironomid was found to be closely associated with sediments that consisted principally of pebbles. Chironomid larvae were also scarce in the "flint zone" of the River Thames (102). In marked contrast, chironomids were more abundant in gravel, in the organically polluted River Suprasl, than in nearby sediments that were rich in organic matter (133). Similarly, in a highly productive chalk stream, chironomids were more abundant in samples taken from gravel than in adjacent deposits consisting of sand and organic silt (144).

Whereas rock and gravel substrata are dominated by species of Orthocla-diinae and Diamesinae, the subfamilies Chironominae and Tanypodinae pre-dominate in finer sediments of sand and silt (106, 144). In general, a strong correlation has been found between the organic content of sediments and the density of most Chironominae and Tanypodinae (125); however, interactions between environmental factors may serve to obscure the relationship (199).

Most studies indicate that, within certain limits, larvae are unselective in terms of the sizes of particles used for construction of their cases or tube retreats (18). Nevertheless, particle sizes in sediments may play an important role in determining the distribution of larvae of some species (109, 117, 219).

A conflict may sometimes occur between the nutritional value of sediment and its suitability for the construction of tubes. The distribution of *Chironomus lugubris* in a bog lake was shown to be related to the age of particles and their consequent microbial loading (116). In contrast, larvae of *Glyptotendipes paripes* were associated with large particles, suitable for case building, but of low nutritional value (112).

Chironomid larvae in general are confined to the surface layers of soft sediments (53, 153), but some species penetrate more deeply (14) and depth of sediment may be limiting to population density in some instances (68, 115). In stony streams the hyporheos may be an important component of the biota (27, 56, 175), but the significance of this habitat in relation to populations of Chironomidae is unknown.

Chironomid larvae commonly colonize the surface of submerged logs (110, 134). The majority of larvae associated with wood probably feed on the associated "aufwuchs." There are, however, several species of Orthocla-diinae (29) and Chironominae (148) that are genuine, and perhaps obligate, miners in wood. Larvae of *Symposiocladius lignicola* are found only in the outer layers of firm, not waterlogged, wood and they ingest wood fibers (28). It is not known whether such larvae derive their nutrition from microorganisms associated with the decomposition of timber or, less likely, whether they carry a symbiotic gut fauna that is capable of digesting cellulose.

The presence of macrophytes in aquatic ecosystems may result in a very substantial increase in the surface area available for colonization by in-vertebrates. Boerger and colleagues (16) showed that aquatic plants increased

the available surface area by between 5 and 10 times in an Alberta stream, but they harbored only 30 to 40% of the total chironomids. Work carried out on another North American stream (121) showed that, when expressed in terms of number of animals per unit of surface area, significantly fewer invertebrates were found on macrophytes than on bare substrates. Most studies have, however, demonstrated a positive relationship between the distribution of macrophyte beds and the abundance and/or diversity of Chironomidae (8, 42, 120, 125, 144, 168, 192).

Various patterns of microdistribution have been demonstrated for Chironomidae and other invertebrates on submerged macrophytes (41, 193), and such patterns may be closely related to features of plant morphology (193). Plants may also affect chironomid distribution by influencing the nature of the bottom deposits (125).

Representatives of a number of genera of Orthoclaadiinae (29) and Chironominae (148) have been recorded mining in the soft tissues of plants, but in many instances such behavior does not appear to be obligatory.

### *Water Quality*

At pH values of less than 5.5, many aquatic animals experience difficulties with calcium regulation, whereas below pH 5.0 problems also arise in relation to sodium regulation (64). Many species of chironomid are tolerant of a wide range of pH, from 6.0 to 9.0 (156), but outside of this range decreasing pH results in the occurrence of fewer species (42, 152, 171).

The relative sensitivity of aquatic invertebrates, including chironomids, to low pH was studied in a series of ponds, ranging from pH 8.2 to 2.8 (65). Sensitive species were unable to maintain high levels of sodium at low environmental pH. Tolerance of acidic conditions appears to be partially related to body size (216), and the ability to tolerate a wide range of pH seems to occur most frequently within the Chironominae and especially in the tribe Chironomini. Of 71 species listed by Roback (156) only seven occurred at pH < 5.5 and, of these, five belonged to the Chironomini. *Chironomus plumosus* was usually the only species found in a series of lakes affected by acid mine-drainage when the pH was < 6.0, and there was also measurable free acidity (63). The ability to withstand highly acid conditions may be enhanced by the buffering capacity of hemoglobin, which is present in the hemolymph of all Chironomini (74).

Despite the fact that larvae of *C. attenuatus* have been recorded living under a wide range of pH (156), they were found, under laboratory conditions, to have a relatively narrow range of favorable pH, which varied somewhat according to developmental stage (190). *Sergentia albescens* is most susceptible to acidification at the time of adult emergence (10).

In addition to creating difficulties in relation to ion balance, reduced pH may also result in an increase in the length of time spent by larvae in creating a

current of water through their tubes (200), and may thereby reduce the time available for feeding.

Some species of chironomid are tolerant of a wide range of salinity (154). *Chironomus salinarius* has been recorded from freshwater (198) as well as in chloride concentrations of up to 41% (155, 181). This species is also tolerant of extreme changes in salinity in pools subject to evaporation (132).

Lake Lenore, in central Washington, has been studied over a 24-year period during which its salinity has steadily declined (213). Most previously unreported species colonized this lake when the salinity range was 2–3 ppt. Several taxa that did not appear in the “sodium bicarbonate type” Lake Lenore until the salinity level had fallen to less than 3 ppt occurred at much higher levels of salinity in “sodium magnesium sulphate type” lakes in Saskatchewan (154). This suggests that ion composition, as well as salinity, is an important factor influencing chironomid distribution (61).

Many species of chironomid larvae are tolerant of poorly oxygenated conditions. In the Chironominae such tolerance is related to the possession of hemoglobin, and larvae of *Chironomus dorsalis* have been reported to extend their tubes as much as 20 mm above the sediment surface in order to maintain an oxygen concentration of more than  $7 \text{ mg l}^{-1}$  at the tube entrance (85). As oxygen levels decline, various species have been shown to increase the length of time spent pumping water through their tubes (78, 85). Growth of *Chironomus anthracinus* in Lake Esrom is known to be inhibited when oxygen levels fall to less than 4% saturation in summer (78). Chironomid densities in part of the Great Slave Lake were found to be negatively correlated with oxygen concentration (123), but this was probably indicative of a positive correlation with the organic content of sediments.

Nearly all species of chironomid exhibit preferences for certain water depths (138), even in shallow water bodies (34). Some species show changes in depth preference that are associated with age (123); distribution in relation to depth may also be modified in response to changes in temperature (196) or pollution (123). Such interactions probably explain observed differences in the distribution of certain species between water bodies. For example, depth was found to have little influence on the distribution of *Heterotrissocladius changi* in one lake (123), but elsewhere this species was confined to a narrow littoral/upper profundal zone (164).

Chironomid larvae apparently do not migrate in response to falling water level, and many species can survive a degree of drying. In contrast, many species rapidly exploit a rise in water level (111).

Temperature is one of the major factors controlling rates of growth and development in aquatic insects (4), and the adult body size of a number of insects depends largely on temperatures experienced during larval development (185). In addition to a direct effect on metabolism, temperature is also likely to have an indirect effect through its influence on food quality and quantity (185).

There are few published data on the influence of environmental temperature on egg development in the Chironomidae (184). Eggs of *Chironomus plumosus* hatched in 1.5 to 2 days at temperatures between 22° and 25°C (196); in another study they were found to take 3, 6.5, and 14 days to hatch at temperatures of 24°, 16°, and 9°C respectively (67). At temperatures below 8°C, eggs of this species failed to hatch (67).

Considerably more information is available on the temperature relations of larval chironomids (35, 104, 183, 184). Under favorable conditions, larval development of many species may be extremely rapid (89, 104). Rate of development is largely temperature dependent, but there is evidence that food quality may also have a significant effect (203).

Mackey (104) studied growth and development of a range of species at different temperatures. At 15°C larval development required between 5 and 48 days for completion. In these experiments larvae were collected from the field so that their initial ages were not accurately known. Some of the stated times for development may thus be substantial underestimates. Support for this view is found in work done elsewhere (220) in which larvae of *Thienemanniella vittata* that were derived from eggs, and therefore of known age, took about 20 days to complete development at 15°C, whereas Mackey's (104) estimate for the same species was only 5.2 days at this temperature.

Larvae reared at lower temperatures are usually longer than those reared at higher temperatures (104). In most species, rates of growth and development increase with a rise in temperature, but in *Cricotopus bicinctus* an increase in temperature from 15° to 20°C produced an increased rate of development, but not of growth (104). It may be assumed that larger larvae give rise to correspondingly larger adults, and this has been demonstrated for at least one species of chironomid (228). In many insect species the number of eggs laid is positively correlated with female body size and hence negatively correlated with temperature experienced during larval development (185), but there appears to be no direct evidence for this within the Chironomidae.

Some chironomids are known to be able to complete their development at very low temperatures (135). Under arctic conditions, development may be protracted (24). A species of *Procladius* from Lake Hazen, where temperatures never exceed 4°C, requires 3–4 years to develop fully (135), and a 7-year life cycle has been noted for *Chironomus* spp. inhabiting tundra ponds (24).

It has been suggested that the Chironomidae as a whole are preadapted to cold (23) or even freezing (34) conditions by virtue of having initially evolved in areas subject to such conditions. Certainly, tolerance of freezing is widespread among members of the Chironomidae and has been demonstrated in all sub-families and in temperate as well as arctic species (34, 137). Preparation for overwintering may be accompanied by a reduction in water content. This has been observed in larvae in temperate zones, but in the arctic the tendency is

much more marked and may result in larvae becoming noticeably shrivelled (34). Chironomid larvae have no apparent ability to resist freezing when in contact with ice crystals (34).

When larvae overwinter in areas where freezing is likely, they frequently, though by no means invariably, construct cocoons and empty their guts (34, 36, 137). Although cocoons confer no advantage in terms of ability to withstand freezing of body fluids, larvae in cocoons overwinter markedly better than those without (34). The benefit may be in conferring increased resistance to mechanical damage, and it is significant that similar cocoons may be constructed by larvae forced to withstand other types of stress such as desiccation (59) or oxygen depletion (162).

Pupation appears to be primarily under the control of light, although temperature may have a modifying influence (135). Some individuals may pupate and emerge in small numbers under conditions that are generally unfavorable; others fail to emerge when conditions appear to be ideal for the majority of the population (35, 47). According to Danks (35), such individuals may buffer the population in years of unusually harsh environmental conditions when the main population is destroyed or severely depleted.

The emergence behavior of adult midges is influenced by a variety of environmental factors, including temperature (204), and has often been the subject of study (26, 87, 130, 204). In the arctic, emergence is timed to coincide with rising or peak water temperature (37). In temperate regions, emergence is more variable and may be primarily under the control of temperature, light, or a combination of the two (48, 88, 93, 139, 204).

### Food

Oliver (136) briefly reviewed the feeding strategies of chironomid larvae, and Monakov (122) divided them into four types on the basis of feeding behavior: filter-feeders, scrapers, predators, and mixed feeders.

Few chironomids appear to be restricted rigidly to a single mode of feeding. The filter-feeding methods of *Chironomus plumosus* and *Rheotanytarsus* were described by Walshe (201), but *C. plumosus* may also scrape material from around its tube (68), and at least one *Rheotanytarsus* species may behave similarly (personal observation). One exceptional species, which may be confined to a specific feeding method because of the unusual morphology of its mouthparts (166), is *Odontomesa fulva*. The larva of this species apparently feeds by alternately swallowing and expelling water, thereby filtering suspended particles by means of the numerous setae associated with its mouthparts (122).

Food quality and quantity have been identified as the principal environmental factors influencing rates of growth in aquatic animals (4), with consequent effects on duration of life cycle, size at maturity, fecundity, and survivorship.

Food quality is extremely difficult to define, especially for a group of insects like the Chironomidae, which have varied natural diets. The development of artificial diets in relation to the nutritional requirements of insects was reviewed by Vanderzant (197), but little quantitative work has been done on the nutrition of aquatic insects.

Larval Tanypodinae are generally stated to be carnivorous, but few are obligate carnivores (136). Detritus and diatoms also figure prominently in the diet of many Tanypodinae (105, 187). The gut contents of three species of this subfamily from a variety of habitats in northern England and Scotland were invariably dominated by finely particulate detritus, with diatoms and larger particles of detritus also represented (7).

Normally detritivorous species have sometimes been found to be facultative predators. *Chironomus attenuatus*, for example, has been found to consume oligochaetes (96), and this may explain the negative correlation sometimes observed between numbers of *Chironomus* larvae and the number of oligochaetes in samples of sediment (20, 96). Predation is relatively uncommon in the Orthocladiinae, but larvae of *Cardiocladius* are reported to feed on larval Simuliidae (29).

The most frequently recorded material in chironomid guts is detritus (7, 75, 113, 122, 125, 187). Some authors have suggested that detritus is not readily digested (123, 157), but not all have agreed with this view (107). A study of carbohydrases present in a variety of invertebrates, including *Chironomus*, led to the conclusion that the bulk of the material ingested by deposit and filter-feeding animals is indigestible (15). Furthermore, the rapid rate of passage through the gut (75, 220) allows little time for extensive digestion to occur.

Some larval chironomids are capable of completing their development on a diet of bacteria alone (157, 225). On the other hand, larvae of *Chironomus riparius* that live in an environment where bacteria are sufficiently abundant to fulfill their theoretical dietary needs apparently feed selectively on some other component of the detritus and digest only about half of the bacteria that are consumed (6). Even if larvae do not derive their full carbon and nitrogen requirements from microorganisms, microbial biomass may still be of critical importance in chemically modifying detritus so as to render it usable by insects (31) or in supplying particular substances that are essential for growth (6). Conditioning by microorganisms may also be necessary to render organic matter palatable to invertebrates (83, 116, 118, 141, 195). Even sand grains may act as surfaces for microbial attachment and thus have a high nutritional value (119).

The growth of *Paratendipes albimanus* has been related to seasonal changes in microbial biomass (202). In rivers at least, the life cycle of this species seems to be remarkably constant over a wide geographical area (145, 202), with a single annual generation emerging in June. When experimentally fed on de-

tritus that was derived from hickory leaves and had a high microbial biomass, larvae grew faster than on "natural" stream detritus and were able to complete a second annual generation (203).

The primitive habitat in which the chironomids began their evolution is considered by some (23) to have been rich in diatoms. Algae, and diatoms in particular, are frequently a conspicuous component of the diet of chironomid larvae (79, 80, 123, 124, 127, 173). Brook (21) noted the periodic disappearance of algae from filter beds and concluded that this was attributable to the feeding of insects, and especially Chironomidae. Similarly, grazing by chironomids was reported to reduce substantially the amount of periphyton on reedstems (108).

In contrast, the impact of grazing by midge larvae in a small woodland stream was felt to be insignificant (30) and Williams (220) concluded that chironomid grazing was insufficient to account for the decline in numbers of epiphytic diatoms in a small river. Nevertheless, the peak in numbers of chironomid larvae, mostly Orthocladiinae, in the chalk streams of southern England is closely synchronized with the spring diatom bloom (143, 220), and variations in the quality and quantity of planktonic algae have been correlated with a sevenfold increase in chironomid biomass (79). Seasonal cycles in the growth of *Chironomus anthracinus* were also shown to be controlled by fluctuations in the density of phytoplankton (78).

In spite of such observations, the relevance of algae in chironomid nutrition has sometimes been questioned. Rodina (157) suggested that bacteria associated with algae were the main source of energy. However, diatoms have been found to be well assimilated (158), and periods of high assimilation rate in *Chironomus plumosus* corresponded with blooms of *Melosira* and *Stephanodiscus* (75).

Relatively few aquatic insects are known to ingest fresh macrophyte tissue. A number of chironomid species mine in leaves of aquatic plants and ingest some plant tissue in the process (136). Berg (13) records some *Cricotopus* larvae as feeding exclusively on leaves of *Potamogeton*, and it has been suggested that *Cricotopus* larvae have potential as biological control agents of *Myriophyllum spicatum* (82), since they feed extensively on its submerged apical buds (81).

A few chironomid larvae are parasitic such as those of *Baeoctenus*, which eat the gills of the swan mussel, *Anodonta* (29), and *Symbiocladius*, which parasitizes mayfly nymphs (217).

There have been few studies concerning changes in the diet of chironomid larvae in the course of their development. In lakes, planktonic first instar larvae feed on suspended algae and detritus but may also derive some nutriment from remains of the yolk sac (38, 136). First instar larvae of several epiphytic Orthocladiinae living in a chalk stream were found to feed selectively on diatoms, whereas later instars fed, more or less indiscriminately, on diatoms

and detritus (220). First instar larvae of *Chironomus plumosus* were also found to feed selectively on diatoms (80), although this was not true in the River Thames where fine detritus (tripton) was their sole food (105).

McLachlan and colleagues (114) found that all larval instars living on stony surfaces in fast flowing streams were selective only in terms of particle size. *Chironomus anthracinus* larvae in Lake Esrom also selected diatoms in relation to their size (78).

The first recorded instance of feeding by adult chironomids was by Oliver (135), who noted feeding on nectar from arctic flowers by two species of *Smittia*. Since then, feeding on honeydew and nectar has been found to be widespread (40, 169).

### *Other Animals*

Although chironomids are a frequently recorded component of the diet of fish, there are few statements as to the likely impact of fish on chironomid populations. Macan's (98) review of the influence of predation on freshwater animal communities contains only one reference to the Chironomidae. Several authors have suggested that although fish may feed heavily on stream invertebrates, such predation has relatively little effect on either abundance or diversity (3, 52, 191, 229). Other studies, mostly on lakes or other still waters, that have dealt specifically with Chironomidae suggest that fish predation may have an important influence on population size (71, 72, 150, 183). Bream were estimated to consume about 30–35% of the standing crop of Chironomidae in Lake Balaton between May and November (150). Even greater levels of predation probably occurred in localities where bream were aggregated (188).

Fish that feed on Chironomidae may show a high degree of selectivity. Coho salmon fry did not coincide with the peak drift of larvae but they preyed heavily on pupae and adults at the time of emergence (131). Similarly, heavy predation by fish and a freshwater prawn together accounted for the loss of 50% of the midges emerging from Lake Kasumigaura in Japan (72). By contrast, bream in the River Thames fed selectively on larvae and, in June especially, on *Parachironomus biannualatus* even though other species were up to 15 times more abundant (105). Such selectivity is likely to be caused, at least in part, by differences in behavior that make certain species or life stages more, or less, available. Sometimes, however, it also appears to be related to size of larvae. Thames bream mostly took larvae that were shorter than 3 mm (105). Brook sticklebacks also selected for small larvae even though they were physically capable of taking all sizes of prey (194).

The impact of predatory birds on populations of Chironomidae is probably very small, but the availability of chironomids as food at certain times of year may have a considerable influence on the distribution and population size of some bird species. The preference of spring-migrating hirundines and swifts for

a particular lake was explained in terms of the emergence of large species of midge (186), which are preferred to smaller insects (207). Chironomids are an important component of the diet of some diving ducks (11) and may also be important for dabbling ducks (32, 33). Emerging chironomids are especially important for some species of ducklings in their first few days of life (32, 180).

Many species of invertebrates are known to consume chironomid larvae (12, 46, 183, 196), but few authors have suggested that invertebrate predators have a significant impact on chironomid numbers. The leech *Erpobdella octoculata* feeds largely on chironomid larvae (46, 58). In certain circumstances it has been suggested that availability of chironomid larvae may limit the population size of this leech (46).

Midge larvae and *Caenis* (Ephemeroptera) nymphs were the most common elements in the diet of Odonata nymphs in a South Carolina pond (12). Several studies indicate that Odonata may have a significant effect on the density of chironomid populations (12, 120, 183).

Records of invertebrates feeding on other life stages of Chironomidae are scarce. Schlee (170) reviews the literature pertaining to feeding by representatives of several families of adult Diptera on chironomid adults and larvae, and Wiles (218) reported aquatic mites consuming chironomid eggs. The freshwater prawn, *Macrobrachium nipponense*, consumes large numbers of pupae and adults at emergence. (72).

With the exceptions of larval water-mites and mermithid nematodes, the literature contains few references to parasites of Chironomidae. Parasitization of adult midges by water mites has been extensively studied (17, 93), and a useful review of this topic was provided by Smith & Oliver (172).

There is little information relating the effect of parasitization by mites to the population dynamics of the host midges, but heavy infestations have been found to cause sexual anomalies (167). References to sexual abnormalities caused by mermithid infections are frequent (1, 93, 167, 226). Heavy infestations were found to diminish the populations of several species of *Cricotopus* (93).

Larval *Chironomus plumosus* are frequently infested by the ciliate *Tetrahymena chironomi* (45). Up to a quarter of a million may be present in the haemocoel, with fatal consequences.

References to fungal parasites of Chironomidae are surprisingly scarce in view of the frequency of their occurrence in other Nematocera such as mosquitoes (208). *Entomophthora conica* has been recorded from an aerial adult *Chironomus*, which died within 12 hours, presumably as a result of the infection (39). This fungal species was also recorded on the corpses of three other chironomid genera but was much more commonly associated with Simuliidae (39). Fungi of the family Coelomycetaceae are well-known pathogens of mosquito larvae, and two species were found parasitizing chironomid larvae in a Canadian lake (208).

There is little evidence that intraspecific competition for food ever occurs in natural populations of Chironomidae, although the community inhabiting stone surfaces in a swiftly flowing river was thought to be limited by the availability of suitable food particles (114). Competition for space has been shown to occur in populations of *Chironomus anthracinus* in parts of Lake Esrom (77). Competition for space has also been demonstrated in laboratory populations (219), but the significance of such studies to natural situations where larval drift probably plays an important part in adjusting population density and minimizing intraspecific competition requires further investigation.

Evidence for interspecific competition involving Chironomidae is also sparse. Competitive interactions between populations of *Chironomus hyperboreus* and *Tanytarsus gracilentus* was proposed as a partial explanation for the population dynamics of the latter species (94). Wiley (219) provided laboratory and field data suggesting that competitive interactions play an important part in determining the spatial distribution of chironomid larvae in a Michigan stream.

Associations of chironomid larvae with other animals, usually regarded as commensal or phoretic, were reviewed by Steffan (176). The association of larvae of the genus *Ichthyocladius* with catfish in South America is the only known instance of chironomids using a vertebrate host (49).

## CHIRONOMIDAE AS INDICATORS OF WATER QUALITY

Species of Chironomidae are to be found in almost every imaginable freshwater habitat (136, 143). Consequently, they may be expected to be potentially useful as indicators of water quality (9, 143, 221). This potential usefulness has long been recognized in relation to the classification of lakes (19, 165). Historically, lake classification theory has been based on the response of the chironomid community to the availability of dissolved oxygen (206), but the availability of food is said to be the primary mechanism governing chironomid succession (205). According to Sæther (165), it is only in lakes of advanced eutrophy, or where oxygen levels are particularly low for other reasons, that oxygen concentration comes into effect. Brundin (22) showed that lake typology based on chironomid communities probably has worldwide validity, and a scale of grading with 15 categories ranging from extreme oligotrophy to extreme eutrophy has been proposed (165). The relative numbers of chironomid larvae and oligochaetes together with the distributional patterns of individual species may also be helpful in pinpointing localized areas of pollution (165).

Several authors have successfully used subfossil chironomid head capsules retrieved from lake sediments to trace the trophic history of lakes (70, 205, 216).

It is suspected that deformities, especially of larval mouthparts, are the result of pollution (60, 62, 206). Such deformities are thought to be caused by

industrial or agricultural pollution rather than by domestic wastes (60, 62, 84). Characteristic deformities of this kind may offer a useful extension of the more traditional methods for biological assessment of water quality (60).

Only relatively recently have attempts been made to classify rivers using chironomid associations in a similar way to the lake typology concept. In general, rivers support a much more diverse community than the profundal zone of lakes, and they present a wider range of environmental conditions so that taxonomic and sampling difficulties are much more severe. Furthermore, qualitative and quantitative changes in fauna may be both rapid and substantial, leading to difficulties in the interpretation of data (126).

Biological surveillance data is frequently summarized, either in the form of diversity indices or pollution indices (66). Chironomid diversity alone may not be a good indicator of total invertebrate diversity (159), and interpretation of the spatial distribution of invertebrate communities is not substantially affected by failure to identify Chironomidae below family level (126). Pollution indices that are designed for use in rivers either include Chironomidae as a single taxon or use only selected "indicator" species (66). Specific identification may not, therefore, be justified for routine monitoring purposes (126), at least within the limitations imposed by the present state of knowledge regarding the ecological preferences and tolerances of most species.

Some workers, however, have suggested that chironomids may ultimately provide a sensitive means of classifying running waters, and the available ecological data for many Nearctic species was summarized by Beck (9). Collection of pupal exuviae, by means of drift or by skim nets, avoids the difficulties associated with sampling of benthos and is being investigated as a practical means of river classification (222, 223). However, this type of sampling may not be capable of pinpointing sources of pollution in the same way as sampling of benthos (5); considerably more research on the ecology of individual species is required for the full and proper interpretation of such data.

### *Responses to Pollution*

Although the responses of the chironomid fauna of lakes to eutrophication are well known and form the basis of lake classification systems (165), the effects of organic pollution on the chironomid fauna of rivers have been less well investigated. Chironomid species richness in rivers is not necessarily well correlated with water quality (92). The influence of pollution on the density and production of Chironomidae in running waters was discussed in some detail by Losos (97).

*Chironomus riparius* is frequently exceedingly abundant under organically polluted conditions (57, 84) and has often been regarded as an indicator of organic pollution (43, 57). *C. riparius* is by no means restricted to polluted waters and may also be dominant in temporary or newly created water bodies, or in water subject to other forms of pollution where few other species are

present. It should perhaps be more properly regarded as an opportunistic species with a remarkably wide range of ecological tolerance that, combined with a potentially rapid rate of development (91), enables it to exploit situations where there is little competition from other insects.

Stress, attributable to pollution by heavy metals, eliminated virtually all invertebrates, except for chironomids and oligochaetes in two North American streams (224). In addition to directly toxic effects, heavy metals may also influence invertebrates by depressing primary production and consequently producing an increase in oxygen concentration at the sediment/water interface (90).

In general, it is members of the subfamily Chironominae that are tolerant of heavy metal contamination, but there are notable exceptions. *Cricotopus* larvae were found to be particularly resistant to electroplating waste containing chromium and copper, as well as to cyanides (182). Another orthoclaadiine was one of the few invertebrates found in an upland stream contaminated by zinc (5).

Most studies of heavy metal pollution have related the distribution of invertebrates to contamination of the water column rather than of the sediment. This may be justified on the grounds that the environment of tubicolous larvae corresponds closely to conditions in the water column (140), but a few studies have considered the role of heavy metals in sediments (210–212).

The relative susceptibility of different life stages to pollutants has rarely been studied. Eggs of *Chironomus tentans* are much less susceptible to copper toxicity than larvae, and fourth instar larvae were 12 to 27 times more resistant to copper stress than first instars (55). Thus, toxicity testing on older larvae may considerably underestimate the sensitivity of this species.

Oil pollution may result from drilling operations, refining processes, transportation of oil, or disposal of waste oil and may also result in the introduction of materials such as salts, heavy metals, acids, and caustic substances (190). Oil refinery effluents have a high organic content which may be exploited by aquatic organisms, notably Chironomidae, during effluent retention in holding ponds (196). The response of chironomid communities to oiled substrata was investigated in a Canadian river (160). Orthoclaadiinae were more abundant on oiled than on unoiled substrata, whereas the opposite was true of Chironominae and Tanypodinae. Colonization of oiled substrata was related to the development of algae, which were absent from unoiled substrata (160).

Phillips (142) reviewed the use of biological indicator organisms to quantify organochlorine pollution in aquatic environments. He concluded that the use of any organism to elucidate the comparative pollution of different locations or even to monitor changes at any one location is open to criticism because of interference by other parameters. His work contains no specific reference to Chironomidae, and it appears that the responses of chironomids to organochlorines and pesticides, in general, have not been widely investigated.

*Chironomus tentans* larvae were found to take up and excrete the herbicides terbutryn and fluoridone much more rapidly than rainbow trout (128); development of this species beyond the second instar is prevented by the herbicide atrazine at a concentration of 1.33 ppm (100). Lindane, at a concentration of 7.3 ppb, also prevents development of this species beyond the second instar (99).

## CONCLUDING REMARKS

The family Chironomidae is remarkable, not only for its diversity but also because of the wide range of tolerance of many species to environmental conditions. Environmental factors often interact in a manner which is poorly understood, so that ecological data derived from separate studies often appears to be contradictory. In the profundal of deep lakes, where conditions are relatively stable and predictable (19), the population dynamics of chironomid species and the structure of the community may be explained relatively easily. In rivers, and indeed in the littoral zone of lakes, conditions are considerably more variable and the chironomid community correspondingly more complex.

In contrast to most groups of aquatic insects, most studies of the Chironomidae have been synecological in character, with consequent constraints on the amount of detail that could be obtained regarding individual species. There is a striking lack of detailed, autecological studies, which, ideally, should consider the influence of environment on all stages in the life cycle and combine both field and laboratory investigations.

The way forward is perhaps shown by the work of Ward & Cummins (202, 203) on *Paratendipes albimanus*. It must also be considered, however, that in temperate stream ecosystems, multivoltine species, principally Orthoclaadiinae, that have overlapping generations and continuous recruitment are of greater significance to the ecosystem as a whole than those, like *P. albimanus*, that have only one or two discrete generations. Such populations also deserve detailed study.

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