# MAYFLIES AS FOOD

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**ABSTRACT**

Mayflies are ubiquitous in freshwater environments. As a result, they are a common and important component in the flow of energy through ecosystems, both aquatic and terrestrial. Many predators include mayflies on their menu of organisms consumed including invertebrates, vertebrates and at least one plant. This paper examines the diversity of organisms that consume mayflies. Some of the more interesting aspects of this predation are discussed. A list of 224 predators is included as a table.

## INTRODUCTION

Each year I spend some time perusing the Ephemeroptera portion of the North American Benthological Society's (NABS) *Annual Bibliography on Benthic Biology*. Invariably, papers are encountered that discuss predators of mayflies. Some of these predators have rather intriguing names such as dipper, wagtail, bluegilled bully, shortjawed kokopu, gulf coast waterdog, edible nest swiftlet, or Pyrenean desman.

I have often wondered about how many different kinds of animals eat mayflies. Well, I have finally gotten around to compiling such a list. This is the first time that such a compilation has been made for mayflies.

The purposes of this paper are (1) to compile a list of the predators of mayflies and (2) to discuss some of the more interesting aspects of this predation. This is a rather unusual approach because, rather than studying the prey of a predator, I will be examining the predators of a prey.

## METHODS AND MATERIALS

Initially, my goal was to compile an exhaustive list of all the predators of mayflies. It was soon apparent to me that this goal was not practical. Many of the papers I examined contained only small bits of information about mayflies as prey and thus could not be located using a keyword search of a database (e.g., BIOSIS). An exhaustive list could only be compiled by paging through all volumes of all appropriate journals.

A more efficient strategy that I adopted for this paper was to compile as many predators as I could in the time available. During this compilation, I tried to place more emphasis on the diversity of predators rather than the total number of predators.

I used the following sources to initially search for papers on predators: *NABS Annual Bibliography on Benthic Biology*, 1965-present (which, in later years, has been compiled by searching BIOSIS); *Eatonia*, 1954-1980; *The Mayfly Newsletter*, 1990-present; proceedings of previous mayfly conferences; books on mayflies, such Leonard and Leonard (1962); various books on aquatic entomology and ecology; and my reprint collection. The references cited at the end of papers examined were particularly valuable. These references led to many additional sources that could not have been located by keyword searches or would have been overlooked based on their title alone.

Predators, involved in manipulative studies of feeding behavior, are not included.

## RESULTS AND DISCUSSION

I have compiled a total of 224 predators of mayflies. These predators, along with a published reference, are listed in Table 5 at the end of this paper. The scientific name of the predator is written exactly as it appeared in the reference. No attempt was made to update the taxonomy of these 224 species.

Unfortunately, space prohibits me from discussing all of these predators in this paper, so my emphasis will be on some of the more interesting aspects of predation on mayflies.

### Were Mayflies Eaten?

The predators listed in Table 5 were identified as feeding on mayflies by gut or fecal analysis or by direct observation of feeding. The direct analysis of feces, though, may be misleading. Rabinowitz and Tuttle (1982) observed gray bats, *Myotis grisecens*, feeding on mayflies, but few of the bats' fecal pellets contained mayfly parts. They hand fed one bat a mixture of insects which included 60% mayflies. None of the fecal pellets from this animal collected after feeding contained any mayfly parts. Another bat was fed only mayflies (n = 274). Only 60% of this bat's fecal pellets contained parts of mayflies (wings). This species tends to remove the wings from mayflies before feeding, thereby eliminating the only body part that can pass through its digestive system. Thus, use of fecal pellets to analyze the importance of mayflies in the diet of the gray bat underestimates the actual amount consumed.

Turner (1983) encountered the same problem with the blue and white swallow, *Notiochelidon cyanoleuca*, in Venezuela. Mayflies were present in 53.7% of the food boluses of nestlings but only 0.6% of the feces.

Another difficulty with interpreting gut analyses is that the results can be reported three different ways: (1) percent occurrence - if half of the individuals consumed mayflies, the frequency of occurrence is 50%; (2) percent relative abundance – if 50 of the 100 food particles in the gut of a predator are mayflies, the percent relative abundance is 50%; and (3) percent volume – if mayflies make up half the volume of the gut, they contribute 50% of the volume. Knowing what the author means by "50% mayflies in the gut" is critical to a proper interpretation.

For example, the relative abundance of mayflies in the gut of the Pacific giant salamander, *Dicamptodon tenebrosus*, varies between 30 and 69%, yet mayflies occupy only 1-26% of the volume of the gut (Parker, 1994). Just the opposite occurs in the Oklahoma salamander, *Eurycea tynerensis* (Tumlison *et al.*, 1990): the relative abundance of mayflies in the gut is 19% but they occupy 46% of the volume. This is explained by examining the food items other than mayflies. The Pacific giant salamander eats a lot of mayflies (high relative frequency) but also consumes much larger prey items (such as megalopterans, fish and small salamanders) which greatly affect volume. The Oklahoma salamander consumes many more chironomids than mayflies, which results in a low relative frequency for mayflies. However, the mayflies consumed are much larger than the chironomids and thus occupy a larger volume of the gut.

The gut analyses of some predators require special techniques. For example, Reynoldson and Bellamy (1975) analyzed the guts of small turbellarians for the presence of mayfly proteins using serological techniques. Reilly and McCarthy (1990) used a similar immunological technique for corixids, while Giller (1986) used electrophoresis to determine the presence of mayfly proteins in the gut of notonectids.

## Mayflies as Predators of Mayflies

Some mayflies are predators of other mayflies. *Siphlonisca aerodromia* nymphs begin their lives as detritivores but these agile, rapid swimmers become more carnivorous as they age, feeding on the likes of *Siphlonurus*, *Leptophlebia* and *Ephemerella* (Gibbs and Mingo, 1986). The sand-dwelling heptageniid, *Pseudiron centralis*, prefers chironomids as food, but 5% of its foregut contents were composed of early instars of *Baetis*, *Centroptilum* and *Ephoron* (Soluk and Clifford, 1984). Agnew (1962), in his study of *Centroptiloides bifasciata*, found remains of baetid nymphs in two of seven guts analyzed. Finally, Muttkowski and Smith (1929), while conducting a feeding analysis of *Ephemerella* sp., examined one nymph with 50% of its gut filled with *Heptagenia* nymphs.

## Some Predators Prefer Mayflies

Fishes that feed predominantly on mayflies (based on percent relative abundance in the gut) are listed in Table 1. Young freshwater stingrays, *Potamotrygon magdalenae*, feed exclusively on mayflies (Caira and Orringer, 1995). These authors noted that 2 of the 15 juvenile stingrays examined were also parasitized by a cestode, which implicated its mayfly prey as being the intermediate host.

While the relative frequency of mayflies in the gut of the fish in Table 1 can be very high, some species exhibit quite a range of preference such as young smallmouth bass, *Micropterus dolomieu* (Easton *et al.*, 1996), bluegilled bully, *Gobiomorphus hubbsi*, and torrentfish, *Cheimarrichthys fosteri* (Scrimgeour and Winterbourn, 1987).

Downes (1978) has observed six species of ceratopogonids (Diptera) feeding on mayflies. Typically the female ceratopogonid enters the mayfly swarm, lands on the thorax

**Table 1.** Percent relative abundance of mayflies in the gut of eight species of fishes. Ranges are provided for some species. Number in parentheses indicates the mean value. Superscript after the name of the organisms identifies reference: [a]Caira and Orringer, 1995; [b]Easton *et al.*, 1996; [c]Scrimgeour and Winterbourn, 1987; [d]Glova *et al.*, 1992; [e]Vives, 1987; [f]Denoncourt and Stauffer, 1993.

| Species | % Relative Abundance in Gut |
|---|---|
| Freshwater stingray (young)[a] | 100 |
| Smallmouth bass (young)[b] | 19-99 (61) |
| Bluegilled bully[c] | 13-91 (71) |
| Torrentfish[c] | 1-82 (51) |
| Brown trout[d] | 41-73 |
| Slender madtom[e] | 52-60 (58) |
| Common river galaxias[d] | 27-60 |
| American eel[f] | 58 |

of a male, pierces his head with her mouthparts, and begins feeding. Quite often the mayfly prey are larger that the fly. Feeding may continue for up to 30 minutes in some species. The three genera listed in Table 5, *Bezzia, Probezzia* and *Palpomyia*, commonly feed on mayflies. In fact, the four *Palpomyia* species observed by Downes (1978) in Scotland fed only on mayflies during his observation period.

Over 50 species of *Podagritis* wasps (Hymenoptera: Sphecidae) are distributed throughout South America, Australia and New Zealand and they feed exclusively on Diptera (Harris, 1990). However, Harris (1990) discovered two species in New Zealand, *P. albipes* and *P. cora*, that are rather unusual – they provision their nests almost exclusively with *Deleatidium* mayflies. Female wasps wait on rocks in the stream until they encounter a *Deleatidium* nymph in the process of molting to the subimago. The wasps have been observed to actually pull the subimago from the nymphal exuviae. Females also collect subimagos as they float on the water surface. The mayflies are stung and are used to provision nests which the wasps make along the shores of the stream.

Two species of flies are also involved in this food web (Harris, 1990). A muscid fly, *Spilogona* sp., competes with the wasps for subimagos emerging on the rocks in the stream. Also, the larvae of *Anabarynchus* sp., a therevid fly, burrows through the soil along the edge of the stream. When this larva encounters a provisioned nest of *Podagritis*, it consumes the *Deleatidium*.

## Variations in Feeding

Dudgeon (1989) has shown that not only does the preference for mayflies by the nymphs of the damselfly, *Euphaea decorata*, increases as they age, but also the number of genera consumed (Table 2). Twelve percent of the prey consumed by small nymphs was composed of two genera of mayflies, while large nymphs fed on five genera which represented 36% of the prey consumed.

Mayflies make up a larger portion of the food of young smallmouth bass, *Micropterus dolomieu*, and rock bass, *Ambloplites rupestris* (Rabeni, 1992), but make up a larger portion of the food of older white suckers, *Catostomus commersoni* (Chen and Harvey, 1995), and common river galaxias, *Galaxias vulgaris* (Cadwallader, 1975a). The change in the food preference of galaxias occurs when it moves from quiet water to riffles once it has attained a length of 40 mm (Cadwallader, 1975a). Riffles have a greater diversity of food items.

The diet of the Gulf coast waterdog, *Necturus beyeri*, changes with age also (Bart and Holzenthal, 1985). Table 3 shows how this salamander prefers *Leptophlebia* mayflies when younger and *Stenonema* mayflies when older.

The Eurasian dipper, *Cinclus cinclus*, consumes more mayflies during the breeding season (Ormerod and Tyler, 1991) as does the black duck, *Anas rubripes* (Reinecke and Owen, 1980).

**Table 2.** Relative abundance of mayflies in the gut of *Euphaea decorata* nymphs. Values for three age groups of *E. decorata* are shown along with the genera of mayflies consumed (Dudgeon, 1989).

| Size of Nymphs | | |
|---|---|---|
| Small<br>12% | Medium<br>26% | Large<br>36% |
| *Choroterpes*<br>*Baetis* | *Baetis*<br>*Choroterpes*<br>*Isca*<br>*Compsoneuriella* | *Baetis*<br>*Compsoneuriella*<br>*Ephemerellina*<br>*Choroterpes*<br>*Isca* |

Ormerod and Tyler (1991) also showed how the frequency of mayflies in the diet of dippers is affected by the type of stream in which it forages. For example, the frequency of mayflies in the diet is between 1% and 3% for adults and nestlings, respectively, when foraging in an acidic stream. The frequency greatly increases to 67% for adults and 38% for nestlings when foraging in a circumneutral stream. Mayflies were simply more abundant in the circumneutral stream.

### Variety

The salamander, *Leurognathus marmorata* feeds on 10 species of mayflies (Martof and Scott, 1957). In addition to the genera listed in Table 2, *Euphaea decorata* also consumed six genera of mayflies (*Baetiella, Pseudocloeon, Epeorus, Habrophlebiodes, Serratella* and *Teloganodes*) in much smaller quantities for a total of 11 genera (Dudgeon, 1989). Teslenko (1997), however, may have discovered the premier mayfly predators – two species of stoneflies, *Skwala pusilla* and *Kamimuria exilis*, each of which consumes 18 species of mayflies.

### Energetics

The production of a mayfly has been shown to directly influence the production of walleye, *Stizostedion vitreum*, in Ontario, Canada (Ritchie and Colby, 1988). During even years, when the production of *Hexagenia limbata* was high (7660 mg/m$^2$), the abundance of walleye was approximately three to five times higher than during odd years when *H. limbata* production was lower (1930 mg/m$^2$). Ritchie and Colby (1988) concluded that higher numbers of *Hexagenia* probably reduce carnivory and predation on young walleyes and increase fecundity of females.

The Pyrenean desman, *Galemys pryenaicus*, commonly feeds on mayflies, which occur in 96% of all the guts examined (Castién and Gosálbez, 1995). However, these mayflies only represent 16% of the food ingested by volume. While mayflies don't account for a large volume of the food consumed, Castién and Gosálbez (1995) believe the amount is critical to allow this homeotherm to thermoregulate. Mayflies are small but abundant in the stream and are easily captured and consumed.

Overall, mayflies represent 29% of the gross energy ingested for black ducks (Reinecke and Owen, 1980).

To show what some animals go through to acquire enough food, Ormerod and Tyler (1988) calculated that green sandpipers, *Tringa ochropus*, consume 9,500 to 11,000 *Baetis* nymphs per day!

### Humans

Not to be outdone by other carnivores, some *Homo sapiens* have also acquired a taste for mayflies. Bodenheimer (1951) described how mayflies are prepared in North Vietnam (con-vo or phu-du), China and Japan for consumption. The people of Malawi make a paste out of mayflies (*Caenis kungu*) and mosquitoes called kungu (Fladung,

**Table 3.** Percent occurrence of two genera of mayflies in the gut of the Gulf Coast waterdog (*Necturus beyeri* ) in different age classes (Bart and Holzenthal, 1985).

| | % Occurrence in Gut | | | | | |
|---|---|---|---|---|---|---|
| Age Class (Years) | 0-1 | 1-2 | 2-3 | 3-5 | 5-6 | 6-7 |
| *Leptophlebia* | 48 | 44 | 30 | 40 | 25 | 25 |
| *Stenonema* | - | 12 | 10 | 80 | 75 | 100 |

1924). The inhabitants near the shores of Lake Victoria collect emergent insects ("lakeflies"), which includes *Povilla* mayflies (Bergeron *et al.*, 1988). These insects are dried, ground into a flour, and formed into a dried cake for consumption. Swarms of mayflies (perhaps *Plethogenesia*) are collected in New Guinea, cooked and then eaten (Szent-Ivany and Ujházy, 1973). Even 17th century Incas ate raw nymphs (*Euthyplocia* or *Campylocia*?) or made them into a spicy sauce (Gillies, 1996).

## Plants

I have not been able to locate any printed reference to carnivorous plants consuming mayflies. I do have, however, a photograph that I removed from an advertisement several years ago. It shows a small mayfly that has been captured by what appears to be a thread-leaf sundew, *Drosera filiformis*. I believe this photograph was part of an advertisement for a book on carnivorous plants, but, to date, I have not been able to locate this book or the source of this photograph.

## Nutritional Analysis

Since a number of economically important animals, such as fish and ducks, consume mayflies, several individuals have analyzed their nutritional value. Table 4 represents a summary of the information found in these papers.

**Table 4.** List of papers that include nutritional analysis of mayflies. Abbreviations: [A]amino acids, [C]calories, [F]fiber, [H]carbohydrates, [L]lipids, [M]minerals, [P]proteins, [S]ash, [V]vitamins, [W]water. Analysis by Bergeron *et al.* (1988) is of an insect flour composed of *Povilla*, chaoborids and chironomids.

| Source | A | L | V | M | C | H | P | S | W | F |
|---|---|---|---|---|---|---|---|---|---|---|
| Albrecht and Breitsprecher (1969) | | • | | | | • | • | • | • | |
| Albrecht and Wünsche (1972) | • | | | | | | | | | |
| Bell *et al.* (1994) | | • | | | | | | | | |
| Bergeron *et al.* (1988) | • | • | • | • | • | | • | • | • | • |
| Block (1959) | • | | | | | | | | | |
| Cummins and Wuycheck (1971) | | | | | • | | | | | |
| Driver *et al.* (1974) | • | | | | • | | • | • | • | |
| Ghioni *et al.* (1996) | | • | | | | | | | | |
| Hanson *et al.* (1985) | | • | | | | | | | | |
| Okedi (1992) | | • | • | • | | | • | • | • | • |
| Reinecke and Owen (1980) | | • | | | • | • | • | • | | • |

Okedi (1992) observed that the traditional protein sources for some Africans (domestic animals, fish and wildlife) have declined over the years. He considered using the lakeflies mentioned previously as a source of protein. His analysis along with that of Bergeron *et al.* (1988) show that these insects are high in protein, minerals, B vitamins, and essential amino acids. They are also low in fat and moisture thus contributing to a long shelf life. The insect cakes have a high digestibility and the fact that *Povilla* occurs in huge swarms makes them relatively easy to capture. Suitable commercial harvesting techniques need to be designed before this potential source of food can be utilized.

**Table 5.** List of predators of mayflies. A reference that identifies each species as a predator is provided. Scientific names are exactly as they appear in the reference.

| Predator | Reference |
|---|---|
| Platyhelminthes – Turbellaria | |
| *Dugesia tigrina* | Gee and Young (1993) |
| *Polycelis nigra* | Reynoldson and Bellamy (1975) |
| *P. tenuis* | " |
| Arthropoda – Crustacea | |
| *Gammarus fossarum* | Dumont and Verneaux (1976) |
| *Orconectes propinquus* | Capelli (1980) |
| Arthropoda – Chelicerata | |
| *Tetragnatha elongata* | Williams *et al.* (1995) |
| *T. versicolor* | " |
| Arthropoda – Uniramia | |
| Ephemeroptera | |
| Baetidae | |
| *Centroptiloides bifasciata* | Agnew (1962) |
| Ephemerellidae | |
| *Ephemerella* sp. | Muttkowski and Smith (1929) |
| Heptageniidae | |
| *Pseudiron centralis* | Soluk and Clifford (1984) |
| Siphlonuridae | |
| *Siphlonisca aerodromia* | Gibbs and Mingo (1986) |
| Odonata - Anisoptera | |
| Aeshnidae | |
| *Anax imperator* | Blois (1985) |
| *A. junius* | Folsom and Collins (1984) |
| *Aeshna canadensis* | Pritchard (1964) |
| *A. eremita* | " |
| *A. interrupta lineata* | " |
| *A. cyanea* | Blois (1985) |
| Corduliidae | |
| *Cordulia shurtleffi* | Pritchard (1964) |
| Gomphidae | |
| *Lanthus vernalis* | Wallace *et al.* (1987) |
| *Ophiogomphus severus* | Koslucher and Minshall (1973) |
| Libellulidae | |
| *Leucorrhinia hudsonica* | Pritchard (1964) |
| *L. proxima* | " |
| *Libellula depressa* | Blois (1985) |
| Odonata - Zygoptera | |
| Calopterygidae | |
| *Hetaerina americana* | McCafferty (1979) |
| Euphaeidae | |
| *Euphaea decorata* | Dudgeon (1989) |
| Coenagrionidae | |
| *Enallagma anna* | Koslucher and Minshall (1973) |
| *Ischnura elegans* | Thompson (1978) |
| *Pyrrhosoma nymphula* | Lawton (1970) |
| Plecoptera | |
| Perlidae | |
| *Acroneuria abnormis* | Johnson (1981b) |

**Table 5** (continued)

| Predator | Reference |
|---|---|
| *A. californica* | Sheldon (1969) |
| *A. carolinensis* | Schmidt and Tarter (1985) |
| *Agnetina capitata* | Fuller and Hynes (1987) |
| *Claassenia sabulosa* | Allan (1982) |
| *Dinocras cephalotes* | Berthélemy and Lahoud (1981) |
| *Hesperoperla pacifica* | Fuller and Stewart (1977) |
| *Kamimuria exilis* | Teslenko (1997) |
| *Neoperla clymene* | Vaught and Stewart (1974) |
| *Paragnetina mediá* | Fuller and Hynes (1987) |
| *P. immarginata* | Johnson (1981b) |
| *Perla bipunctata* | Lucy *et al.* (1990) |
| *P. marginata* | Berthélemy and Lahoud (1981) |
| *Perlesta placida* | Snellen and Stewart (1979) |
| *Phasganophora capitata* | Johnson (1981b) |
| Perlodidae | |
| *Arcynopteryx compacta* | Berthélemy and Lahoud (1981) |
| *Clioperla clio* | Feminella and Stewart (1986) |
| *Cultus aestivalis* | Fuller and Stewart (1979) |
| *Frisonia picticeps* | Sheldon (1972) |
| *Hydroperla crosbyi* | Oberndorfer and Stewart (1977) |
| *Isogenoides zionensis* | Fuller and Stewart (1977) |
| *Isoperla acicularis* | Berthélemy and Lahoud (1981) |
| *I. moselyi* | " |
| *I. difformis* | Malmqvist *et al.* (1991) |
| *I. grammatica* | " |
| *I. namata* | Feminella and Stewart (1986) |
| *I. fulva* | Fuller and Stewart (1977) |
| *I. viridinervis* | Lavandier (1982) |
| *Kogotus modestus* | Allan (1982) |
| *K. nonus* | Walde and Davies (1987) |
| *Megarcys ochracea* | Teslenko (1997) |
| *M. signata* | Allan (1982) |
| *Oroperla barbara* | Sheldon (1972) |
| *Perlinodes aurea* | " |
| *Perlodes microcephalus* | Berthélemy and Lahoud (1981) |
| *Skwala curvata* | Sheldon (1972) |
| *S. parallela* | Fuller and Stewart (1977) |
| *S. pucilla* | Teslenko (1997) |
| *Stavsolus* sp. | Teslenko (1997) |
| Hemiptera | |
| Corixidae | |
| *Cymatia bonsdorfi* | Reilly and McCarthy (1990) |
| *Cenocorixa bifida hungerfordi* | Reynolds and Scudder (1987) |
| *C. expleta* | " |
| Notonectidae | |
| *Notonecta hoffmanni* | Fox (1975) |
| *N. glauca* | Giller (1986) |
| *N. viridis* | " |
| Megaloptera | |
| Sialidae | |
| *Sialis fuliginosa* | Dumont and Verneaux (1976) |
| Corydalidae | |
| *Corydalus cornutus* | Stewart *et al.* (1973) |
| *Nigronia serricornis* | Fuller and Hynes (1987) |

**Table 5** (continued)

| Predator | Reference |
|---|---|
| *Protohermes grandis* | Yoshida *et al.* (1985) |
| Trichoptera | |
| Polycentropodidae | |
| *Polycentropus variegatus* | Dudgeon and Richardson (1988) |
| Hydropsychidae | |
| *Arctopsyche irrorata* | Wallace (1975) |
| *Hydropsyche simulans* | Rhame and Stewart (1976) |
| *Parapsyche almota* | Dudgeon and Richardson (1988) |
| *P. elsis* | " |
| Rhyacophilidae | |
| *Rhyacophila acutiloba* | Manuel and Folsom (1982) |
| *R. carolina* | " |
| *R. minor* | " |
| *R. septentrionis* | Dumont and Verneaux (1976) |
| *R. vaccua* | Thut (1969) |
| *R. vaefes* | " |
| *R. vepulsa* | " |
| Limnephilidae | |
| *Drusus discolor* | Bohle (1983) |
| Odontoceridae | |
| *Odontocerum albicorne* | Dumont and Verneaux (1976) |
| Hymenoptera | |
| Sphecidae | |
| *Podagritus albipes* | Harris (1990) |
| *P. cora* | " |
| Diptera | |
| Tipulidae | |
| *Dicranota bimaculata* | Dumont and Verneaux (1976) |
| Muscidae | |
| *Spilogona* sp. | Harris (1990) |
| Therevidae | |
| *Anabarynchus* sp. | " |
| Ceratopogonidae | |
| *Bezzia varicolor* | Downes (1978) |
| *Palpomyia flavipes* | " |
| *P. nemorivaga* | " |
| *P. quadrispinosa* | " |
| *P. semifumosa* | " |
| *Probezzia venusta* | " |
| Phylum Chordata | |
| Chondrichthyes | |
| *Potamotrygon magdalenae* | Caira and Orringer (1995) |
| Osteichthyes | |
| Anguillidae | |
| *Anguilla anguilla* | Sinha and Jones (1967) |
| *A. australis schmidtii* | Cadwallader (1975b) |
| *A. dieffenbachii* | " |
| *A. japonica* | Tzeng *et al.* (1995) |
| *A. rostrata* | Denoncourt and Stauffer (1993) |
| Balitoridae | |
| *Noemacheilus barbatulus* | Maitland (1965) |

**Table 5** (continued)

| Predator | Reference |
|---|---|
| *N. fasciolatus* | Dudgeon (1987) |
| Catostomidae | |
| *Catostomus commersoni* | Chen and Harvey (1995) |
| Centrarchidae | |
| *Ambloplites rupestris* | Johnson and Dropkin (1993) |
| *Lepomis auritus* | " |
| *L. gibbosus* | " |
| *L. megalotis peltastes* | Laughlin and Werner (1980) |
| *Micropterus dolomieu* | Easton *et al.* (1996) |
| *M. salmoides* | Godinho and Ferreira (1994) |
| Cichlidae | |
| *Crenicichla lipidota* | Lobón-Cerviá *et al.* (1993) |
| Clariidae | |
| *Clarias gariepinus* | Adámek and Sukop (1995) |
| Cottidae | |
| *Cottus cognatus* | Petrosky and Waters (1975) |
| *C. gobio* | Dumont and Verneaux (1976) |
| Cyprinidae | |
| *Barbus callensis* | Kraiem (1996) |
| *Gobio gobio* | Przybylski and Banbura (1989) |
| *Notropis atherinoides* | Mendelson (1975) |
| *N. dorsalis* | " |
| *N. hudsonius* | Johnson and Dropkin (1993) |
| *N. spilopterus* | " |
| *N. volucellus* | " |
| *Phoximus phoxinus* | Maitland (1965) |
| *Rhinichthys atratulus* | Fuller and Hynes (1987) |
| Cyprinodontidae | |
| *Fundulus catenatus* | Fisher (1981) |
| *F. diaphanus* | Johnson and Dropkin (1993) |
| Eleotridae | |
| *Gobiomorphus breviceps* | Cadwallader (1975b) |
| *G. hubbsi* | Scrimgeour and Winterbourn (1987) |
| Esocidae | |
| *Esox lucius* | Ritchie and Colby (1988) |
| Galaxiidae | |
| *Galaxias postvectis* | McDowall *et al.* (1996) |
| *G. vulgaris* | Cadwallader (1975b) |
| Gasterosteidae | |
| *Gasterosteus aculeatus* | Maitland (1965) |
| Gobiidae | |
| *Tukugobius wui* | Dudgeon (1987) |
| Ictaluridae | |
| *Noturus exilis* | Vives (1987) |
| *N. miurus* | Burr and Mayden (1982) |
| Mormyridae | |
| *Gnathonemus tamandua* | Petr (1968) |
| *G. cyprinoides* | " |
| *Hippopotamyrus pictus* | Olatunde and Moneke (1985) |
| *Hyperopisus bebe* | Petr (1968) |
| *Marcusenius senegalensis* | Olatunde and Moneke (1985) |
| *Momyrus rume* | Petr (1968) |
| *M. hasselquisti* | " |
| *M. macrophthalmus* | " |
| *M. deliciosus* | " |
| *Petrocephalus bane* | " |

**Table 5** (continued)

| Predator | Reference |
|---|---|
| *P. bovei* | Olatunde and Moneke (1985) |
| Percidae | |
| *Etheostoma blennioides* | Hlohowskyj and White (1983) |
| *E. caeruleum* | " |
| *E. flabellare* | Fuller and Hynes (1987) |
| *E. lepidum* | McClure and Stewart (1976) |
| *E. rubrum* | Knight and Ross (1994) |
| *Gymnocephalus cernuus* | Ogle *et al.* (1995) |
| *Perca flavescens* | Hayes *et al.* (1992) |
| *Percina sçiera* | McClure and Stewart (1976) |
| *Stizostedion vitreum* | Ritchie and Colby (1988) |
| Pinguipedidae | |
| *Cheimarrichthys fosteri* | Scrimgeour and Winterbourn (1987) |
| Poeciliidae | |
| *Gambusia affinis* | Miura *et al.* (1979) |
| Salmonidae | |
| *Oncorhynchus kisutch* | Johnson (1981a) |
| *O. tshawytscha* | " |
| *O. mykiss* | Dedual and Collier (1995) |
| *Salmo salar* | Levings *et al.* (1994) |
| *S. trutta* | Cadwallader (1975b) |
| *Salvelinus fontinalis* | Forrester *et al.* (1994) |
| *Thymallus thymallus* | Sempeski and Gaudin (1996) |
| | |
| Amphibia – Urodela | |
| Plethodontidae | |
| *Desmognathus quadramaculaus* | Martof and Scott (1957) |
| *Eurycea tynerensis* | Tumlison *et al.* (1990) |
| *Leurognathus marmorata* | Martof and Scott (1957) |
| Salamandridae | |
| *Euproctus asper* | Montori (1992) |
| *Notophthalmus v. viridescens* | Burton (1977) |
| *Salamandra salamandra* | Kuz'min (1992) |
| *Triturus cristatus* | Avery (1968) |
| *T. helveticus* | " |
| *T. vulgaris* | " |
| Dicamptodontidae | |
| *Dicamptodon tenebrosus* | Parker (1994) |
| Ambystomatidae | |
| *Ambystoma texanum* | Whitaker *et al.* (1980) |
| *A. tigrinum nebulosum* | Collins and Holomuzki (1984) |
| Proteidae | |
| *Necturus beyeri* | Bart and Holzenthal (1985) |
| *N. punctatus* | Meffe and Sheldon (1987) |
| Hynobiidae | |
| *Onychodactylus fischeri* | Kuz'min (1990) |
| | |
| Reptilia – Testudines | |
| Trionychidae | |
| *Trionyx muticus* | Williams and Christiansen (1981) |
| *T. spiniferus* | Cochran and McConville (1983) |
| Chelydridae | |
| *Chelydra serpentina* | Lagler (1943) |
| Kinosterniidae | |
| *Sternotherus odoratus* | " |

**Table 5** (continued)

| Predator | Reference |
| --- | --- |
| Emydidae | |
| *Chrysemys picta marginata* | Lagler (1943) |
| *Emys blandingii* | " |
| *Graptemys geographica* | " |
| Aves | |
| Apodiformes | |
| *Aerodramus fuciphagus* | Langham (1980) |
| *Chaetura pelagica* | Leonard and Leonard (1962) |
| *C. vauxi* | Bull and Beckwith (1993) |
| Anseriformes | |
| *Anas rubripes* | Reinecke and Owen (1980) |
| *Aythya valisineria* | Bartonek and Hickey (1969) |
| *Bucephala clangula* | Eadie and Keast (1982) |
| *Hymenolaimus malacorhynchos* | Collier and Lyon (1991) |
| Charadriiformes | |
| *Himantopus h. leucocephalus* | Pierce (1986b) |
| *H. novaezealandiae* | " |
| *Ibidorhyncha struthersii* | Pierce (1986a) |
| *Larus delawarensis* | Welham (1987) |
| *Tringa ochropus* | Ormerod and Tyler (1988) |
| *Sterna sandvicencis* | Greenwood (1986) |
| Passeriformes | |
| *Acrocephalus arundinaceus* | Bibby and Green (1983) |
| *A. schoenobaenus* | " |
| *A. scirpaceus* | " |
| *Bombycilla cedrorum* | Leonard and Leonard (1962) |
| *Cinclus cinclus* | Ormerod and Tyler (1991) |
| *Hirundo rustica* | Loske (1992) |
| *Locustella luscinioides* | Bibby and Green (1983) |
| *Motacilla cinerea* | Bures and Král (1987) |
| *Notiochelidon cyanoleuca* | Turner (1983) |
| *Tachycineta bicolor* | Blancher and McNicol (1991) |
| Mammalia | |
| Rodentia | |
| *Glaucomys* sp. | Leonard and Leonard (1962) |
| *Zapus princeps* | Vaughan and Weil (1980) |
| Insectivora | |
| *Galemys pyrenaicus* | Castién and Gosálbez (1995) |
| *Sorex palustris navigator* | Conaway (1952) |
| Chiroptera | |
| *Lasiurus borealis* | Whitaker (1972) |
| *Myotis grisescens* | Rabinowitz and Tuttle (1982) |
| *M. lucifugus* | Anthony and Kunz (1977) |
| *Pipistrellus pipistrellus* | Swift *et al.* (1985) |
| Primates | |
| *Homo sapiens* | Fladung (1924) |
| Plantae – Tracheophyta | |
| Angiospermae | |
| Nepenthales | |
| *Drosera filiformis*? | See text for explanation |

## Behavior

Being so nutritionally rich, and being preyed upon by well over 200 species (see Table 5), mayflies have evolved defense mechanisms to reduce the chance of predation. Peckarsky (1996) has shown that behaviors such as drifting, swimming, scorpion posturing and timing of activity are all influenced by the presence of predators and are used to avoid predation. Edmunds and Edmunds (1980) have hypothesized that life history attributes of mayflies, such as short adult life, mass emergence, mating swarms, timing of emergence and remote nuptial flights all reduce the chance of predation.

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