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The Feeding Strategies of the Leech *Erpobdella octoculata* (L.): A Laboratory Study

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Abstract

The feeding behaviour of the freshwater leech *Erpobdella octoculata* was analysed by exposing potential invertebrate and vertebrate prey organisms (alive, wounded or dead) to leech attack in dishes, in the laboratory. The fact that *E. octoculata* is a macrophagous feeder that swallows living prey organisms whole (preferentially *Chironomus* larvae) is documented. However, it was repeatedly observed that adult leeches sucked the body fluids from wounded larvae. Likewise, cut pieces of earthworms, dead crustaceans and crushed water snails were attacked and the soft parts sucked in with the aid of the unarmed pharynx. Adult leeches sucked the body fluids from dead, decaying bodies of vertebrates (fish, newt larvae). Newly hatched young are blood suckers that rapidly attacked the wounded regions of *Chironomus* larvae and other invertebrates such as crushed water snails. It is concluded that the common leech *E. octoculata* is not only a predator, but also a fluid sucker and a scavenger. The ecological implications of this finding are discussed.

1. Introduction

In running waters throughout Europe, *Erpobdella octoculata* is one of the most common freshwater leeches (ELLIOTT and MANN, 1979; NEUBERT and NESEMANN, 1999). In streams that are polluted to some extent by organic substances, this species may occur in very high population densities (up to 900 individuals/m^2; SCHÖNBORN, 1985). This is largely due to the fact that the leeches feed extensively on oligochaetes such as *Tubifex* and on *Chironomus* larvae (ELLIOTT, 1973; TOMAN and DALL, 1997). In general, *E. octoculata* has been classified as a macrophagous, carnivorous predator that swallows its invertebrate prey organisms whole with the aid of an unarmed, musculous pharynx (HERTER, 1968; SAWYER, 1986; KUTSCHERA and WIRTZ, 2001).

Several quantitative analyses of the gut contents in natural *E. octoculata*-populations have been published (e.g., ELLIOTT, 1973; DALL, 1983; SCHÖNBORN, 1985; TOMAN and DALL, 1997). These studies led to the conclusion that, in its corresponding habitat, *E. octoculata* feeds predominantly on chironomid larvae (up to 80% of diet), followed by oligochaeta and other small invertebrates. Laboratory experiments on the food consumed by individual adult leeches that were kept in dishes corroborated and extended these results (YOUNG and IRONMONGER, 1979; 1980). However, corresponding studies with juvenile leeches (1–3 days after hatching) were not carried out. In spite of the importance of *E. octoculata* in aquatic ecosystems only one detailed study on the feeding behaviour of this species has been published (GREENE, 1974). This investigator used mature individuals of *E. octoculata*; he observed (and counted) the kinds and numbers of prey consumed, the influence of substrate on feeding efficiency and the effects of temperature on these processes. Only two kinds of prey

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organisms, *Chironomus* larvae and *Gammarus pulex,* were offered. In spite of the fact that GREENE (1974) pointed out that young leeches are hardly capable of feeding on chironomid larvae, the behaviour of juvenile *E. octoculata* was not studied.

The observations and experiments reported here were designed to answer the following questions: Does *E. octoculata* suck body fluids and soft parts of living and dead invertebrate and vertebrate prey organisms? How do newly hatched leeches obtain their food?

2. Material and Methods

Observations and experiments were carried out from February 1999 through September 2001. Adult individuals of the leech *E. octoculata* L. 1758 (dark pigmented variety, 30–35 mm body length at rest) were collected from the underside of stones at two sites: a slow running creek (Park Schönfeld, Kassel-Wehlheiden) and a rapidly running stream (Bergpark Kassel-Wilhelmshöhe). The leeches were cultured in the laboratory at room temperature (17–22 °C), using sand, stones and water from their habitat (KUTSCHERA, 1983). Under a natural photoperiod (ca. 12 h light/darkness) the animals produced cocoons between March and September. Juvenile unpigmented leeches (length at rest: 1.5–2.0 mm) were used for feeding experiments (1–3 days after hatching from cocoons) as illustrated for the related species *Trocheta bykowskii* (KUTSCHERA, 1986).

Living prey organisms (*Asellus aquaticus*, *Gammarus pulex*, *Lymnaea peregra*) were collected from the natural habitat of the leeches. Earthworms (*Lumbricus terrestris*) of medium size (length: ca. 3–5 cm) were obtained from the underside of large stones at the shore of the corresponding creeks and streams. Other water snails (*Physa fontinalis*, *Bithynia tentaculata*) were collected from ponds and rivers in the vicinity of Kassel. *Chironomus* larvae and *Tubifex* worms were purchased from a local Aquarium-shop. Dead bodies of vertebrates (juvenile *Gasterosteus aculeatus*, *Triturus vulgaris* larvae) were found at regular intervals at the shore of lakes close to the running waters where *E. octoculata* is abundant. The dead juvenile fish and newt larvae were used 1–3 days after collection; they were kept in pond water in open petri dishes.

For the experiments depicted in Figs. 1–4, adult healthy specimens were starved for 4–5 days prior to their use. Petri dishes of 10 cm diameter and 100 ml capacity were filled with 75 ml water from the corresponding habitat. Usually, a single predator was placed into each dish and allowed to acclimatize for 1 h (low light conditions, room temperature). The leech came to rest at the edge of the dish. A living, crushed (wounded), or dead prey organism was introduced to the centre of the dish. The following chain of events was either observed and recorded or photographed (KUTSCHERA, 1983; 1986).

The investigations depicted in Figs. 5 and 6 were carried out as described above; newly hatched leeches were used instead of adult individuals. The sequence of events shown in Fig. 6 was obtained as follows. One newly hatched *E. octoculata* was placed into a drop of pond water on a glass plate and a small, crushed *Chironomus* larvae was added. A rubber ring (diameter: 1 cm; high: 1,5 mm) was added and the sample covered with a glass slide. The behaviour of the juvenile leech was examined under a fluorescence microscope (Zeiss, Oberkochen, Germany) during the subsequent hour. Images were taken with a digital camera (Olympus DP 10, Olympus, Hannover, Germany).

All observations (duration: 5 min to 1 h) were repeated at least 10 times with different individuals. Representative pictures are presented for illustration of the results.

3. Results

3.1. Adult Leeches and Invertebrate Prey

All members of the Erpobdellidae are equipped with a sucking pharynx provided with muscular folds. Usually, *Erpobdella* is a macrophagous feeder and prey organisms (for instance, *Chironomus* larvae) are consumed whole. This behaviour is illustrated in Figure 1. Prey-captures are induced when random probing brings the mouth area of an adult *Erpobdella* into chance contact with the insect larvae: the leech grasps the prey with its mouth and swallows it. The chain of events shown in Figure 1 A, B takes 1–2 min, depend-

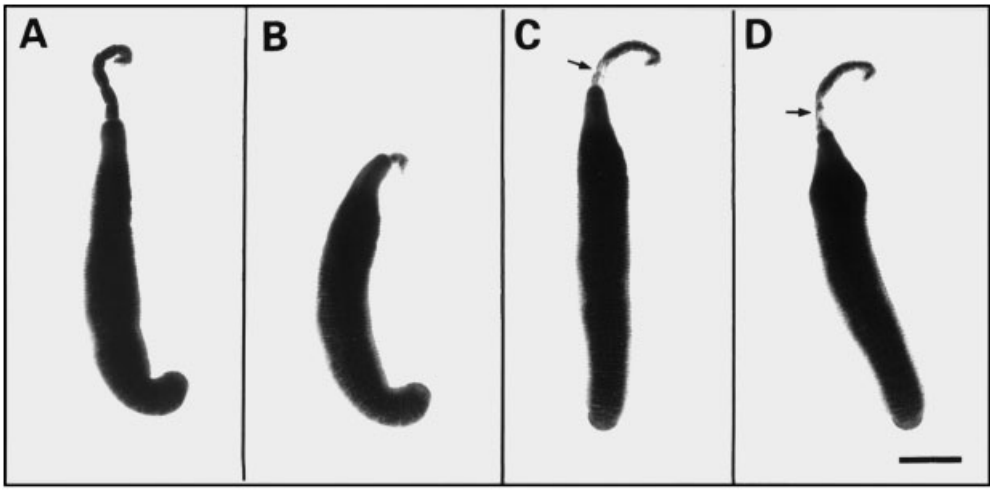

Figure 1. Capture and feeding behaviour of an adult *E. octoculata*. The leech grasps the prey (a large *Chironomus* larvae) and swallows it (A, B). When a wounded larvae is presented, the leech sucks off the body fluids from those parts of the prey where the exoskeleton is damaged (D, C). Arrow: region of the *Chironomus* larvae where the red-coloured content has been extracted by the leech. Scale bar = 1 cm.

ing on the size of the chironomid larvae. One day after the leech has swallowed the larvae the complete transparent exoskeleton can be found in the water. The internal (soft) parts of the prey have been digested out, notably the red haemoglobin. Occasionally I have observed that an adult leech partially swallowed a wounded chironomid larvae. Thereafter, the fluids of the prey were sucked off and the pale exoskeleton regurgitated from the pharynx of the leech. A representative sequence is depicted in Figure 1C, D. These observations indicate that *E. octoculata* is capable of sucking the body fluids of insect larvae.

The response of adult *Erpobdella* to dead or wounded invertebrates was analysed in detail. Earthworms (*Lumbricus terrestris*), placed into the water, were not attacked by the predator. However, when a hungry *E. octoculata* encountered the cut surface of a wounded earthworm a rapid response was observed: the leech sucked the blood (and other fluids) from the wounded region of the prey (Fig. 2A). The dead body of a *Gammarus pulex* was also attacked (Fig. 2B), provided that the carrion had not decayed for longer than 2 days. The response to other decaying dead invertebrates (*Asellus aquaticus*) was similar to that shown in Figure 2. Adult *E. octoculata* also sucked the body fluids from the soft parts of crushed water snails (*Lamnaea peregra, Physa acuta*, *Bithynia tentaculata*). The reaction times of individual *Erpobdella* to crushed snails were determined (duration: 3–6 min); it was similar to that reported by SEABY *et al*. (1995).

3.2. Adult Leeches and Vertebrate Prey

The leech *Erpobdella octoculata*, which inhabits the underside of stones, may hardly be capable of capturing living aquatic vertebrates such as fishes or newt larvae. To my knowledge, such a behaviour has not yet been reported in the literature (HERTER, 1968; SAWYER, 1986; KUTSCHRA and WIRTZ, 2001) and was not observed during the course of this study.

However, dead bodies of fish and larvae of amphibians were readily attacked. It was found that *E. octoculata* is also a scavenger, feeding on decaying bodies of three spine

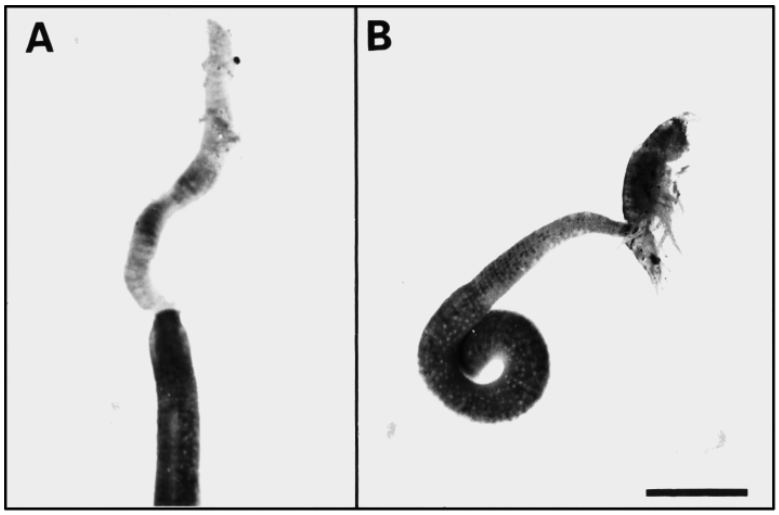

Figure 2. Adult *E. octoculata* that sucks off the body fluids from the wounded (cut) surface of a living earthworm (*Lumbricus terrestris*) (A) and the dead (decaying) body of a *Gammarus pulex* (B), respectively. Scale bar = 1 cm.

sticklebacks (*Gasterosteus aculeatus*), which were abundant in the habitat of the leeches (Fig. 3 A, B) and on corpses of newt larvae (*Triturus vulgaris*) (Fig. 4). It should be noted that these tetrapod larvae were not found in the running waters in which the leeches were collected. Nevertheless, Figure 4 clearly demonstrates that *E. octocualta* is attracted by this dead vertebrate prey organism and a strong sucking (i.e., feeding) response is apparent.

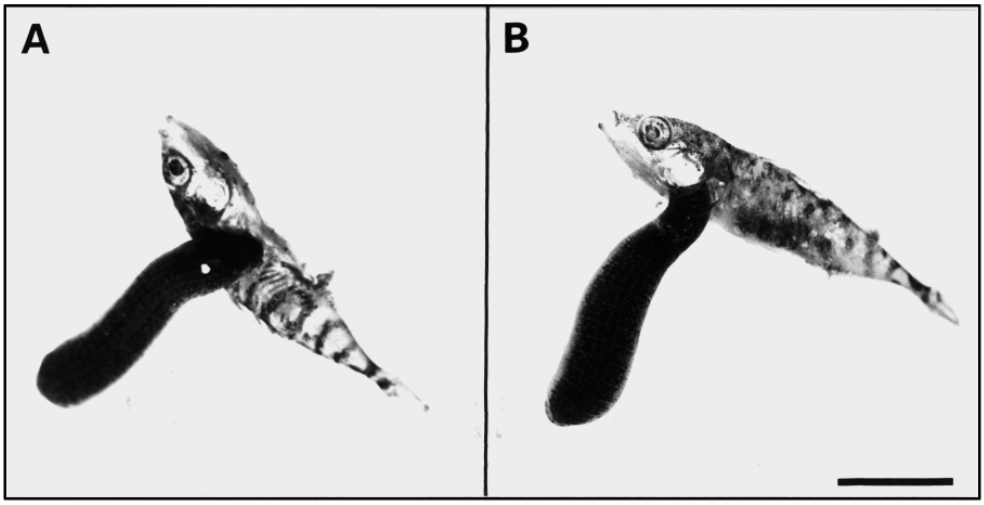

Figure 3. Adult *E. octoculata* that feeds on the dead body of a young fish (*Gasterosteus aculeatus*). The leech comes into chance contact with the prey, instantly grasps the fish and attempts to swallow parts of the dead body (A). After random probing the leech creeps into the body of the fish and feeds on the soft parts of the carrion (B). Scale bar = 1 cm.

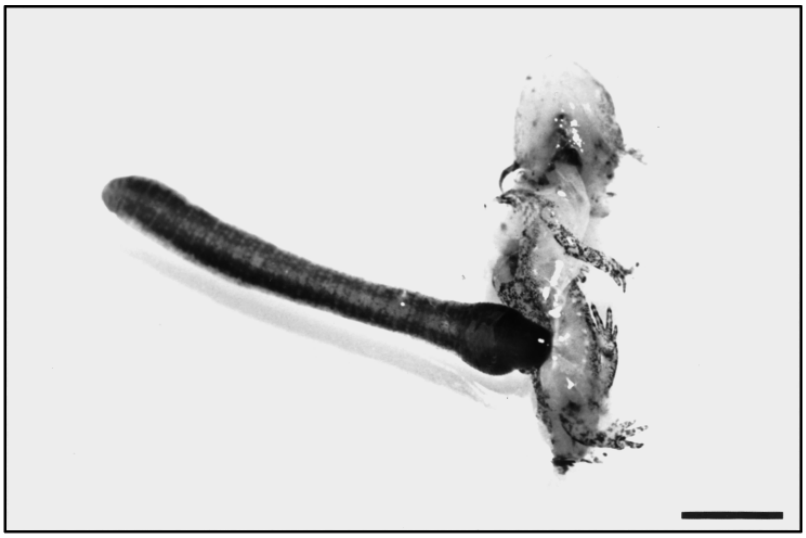

Figure 4. Adult *E. octoculata* that feeds on the dead (decaying) body of a newt larvae (*Triturus vulgaris*). Note the contracted pharynx of the scavenger. Scale bar = 1 cm.

3.3. Feeding Behaviour of Juvenile Leeches

About 3 weeks after cocoon deposition the young leeches hatch via two holes that are formed after the terminal 'plugs' have disappeared (KUTSCHERA, 1983; 1986). The juvenile *E. octoculata* (length about 1,5 mm at rest) are unpigmented and sometimes remain within the translucent egg capsule for another 1–2 weeks (Fig. 5 A). Juvenile leeches are not capable of feeding on the comparatively large, sturdy *Chironomus* larvae, which are the food of choice of the adults (Fig. 1). In *Chironomus* populations one can occasionally observe rather small individuals (length: 1–2 mm). I have never observed newly hatched *E. octoculata* feeding on these insect larvae. However, wounded or dead chironomid larvae are readily attacked by these potential predators. This behaviour is shown in Figure 5. A living insect larvae was wounded with a forceps so that a small amount of red haemoglobin leaked into the water. Five juvenile leeches were rapidly attracted and sucked the red-coloured body fluid from the wounds of the prey (Fig. 5 A, B).

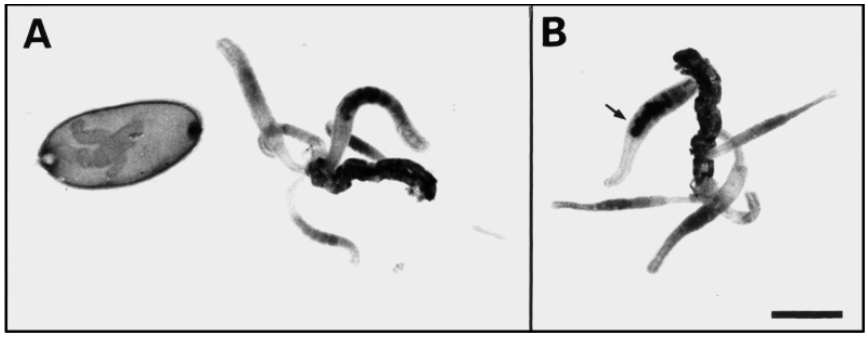

Figure 5. Feeding behaviour of five newly hatched (juvenile) *E. octoculata*. One cocoon with two young leeches is shown on the left side of the picture (A). Ten minutes later one satiated leech leaves the prey organism. Note the dark-coloured gut of the juvenile leech (arrow). (B) Scale bar = 0,25 mm.

The blood sucking behaviour of juvenile *E. octoculata* was analysed in more detail with the aid of a fluorescence microscope. For technical reasons, a small, wounded insect larvae, about half the size of that shown in Figure 5, was used. The time sequence displayed in Figure 6A–D demonstrates that a juvenile leech rapidly attacks the prey organism and sucks body fluids until its gut is filled with red-coloured material. After feeding, the young *E. octoculata* rested for about 6–8 h. During this time period, the gut contents were digested by the blood sucker. Thereafter, the juvenile leeches were hungry again and the sequence of events described in this section could be repeated after the addition of another (wounded or dead) *Chironomus* larvae.

Neither adult nor juvenile *E. octoculata* attacked wounded or decaying bodies of conspecifics, i.e., no cannibalism was observed during the course of this study. This observation is in accordance with that of other investigators (SAWYER, 1986). However, it should be pointed out that DAVIES and EVERETT (1975) noted cannibalism in monocultures of the erpobdellid leech *Nephelopsis obscura*.

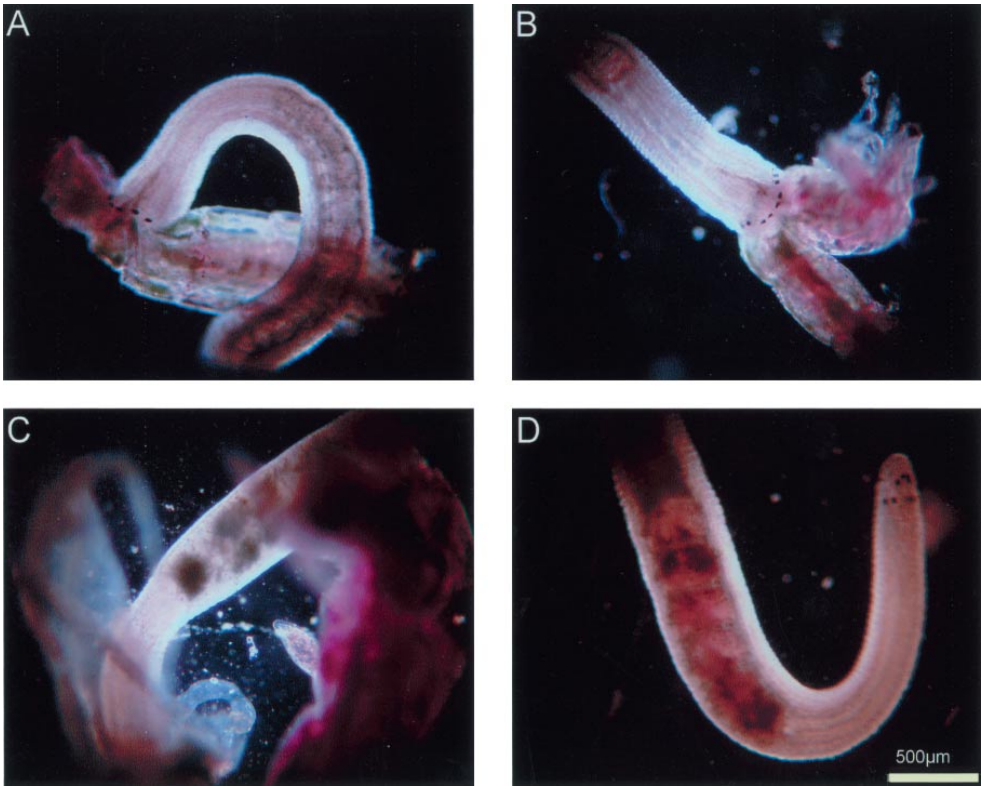

Figure 6. Juvenile *E. octoculata* that sucks the body fluids of a small *Chironomus* larvae, as revealed by fluorescence microscopy. The prey organism has been wounded with a forceps. The leech sucks the body fluids from the insect larvae (A, B). Ten minutes later, the gut of the blood feeder was filled in part (C) and after 1 h entirely with soft material extracted from the body of the prey organism (D). Scale bar = 0,5 mm.

4. Discussion

Numerous studies have shown that *E. octoculata* and other erpobdellids are macrophagous feeders that forage primarily at night (SAWYER, 1986). Since *Erpobdella* has neither jaws nor a proboscis, it usually swallows its invertebrate prey organisms whole. If the active 'circumnavigating' hungry *Erpobdella* happens to contact a potential prey organism, the leech attempts to seize and swallow it. This behaviour, described by ELLIOTT (1973), GREENE (1974), YOUNG and IRONMONGER (1980) and SAWYER (1986), is depicted in Fig. 1A, B and can be regarded as the 'standard-feeding' of *Erpobdella*. The chain of events shown in Fig. 1 C, D, i.e., the capture, sucking behaviour and release of the empty exoskeleton of a *Chironomus* larvae, has not yet been recorded in detail. It is likely that the erpobdellid leech displays the behaviour of a fluid feeder, i.e., the prey organism is sucked off until part of or all body fluids are removed. Since other dead invertebrates (crustaceans, water snails) and wounded earthworms are also attacked, hungry *E. octoculata* can be classified as predators and opportunistic feeders of body fluids. This conclusion is in accordance with laboratory experiments on comparative speeds at which *E. octoculata* responded to crushed (dead) invertebrate prey (SEABY *et al*., 1995). It should be noted that the rapid response of the leech to wounded earthworms shown in this study was not reported by the authors cited above.

An unexpected result of this investigation was the finding that *E. octoculata* rapidly attacked dead bodies of vertebrates (fish, amphibians). It is likely that this leech is attracted to any carrion it may encounter. Hence, the 'worm leech' *E. octoculata* is not only a predator and fluid sucker, but also a scavenger like the common species *Haemopis sanguisuga* (HERTER, 1968; SIDDALL and BURRESON, 1996; KUTSCHERA and WIRTZ, 2001). It should be noted that DAVIES and EVERETT (1975) mentioned that some species of the genus *Erpobdella* may be scavengers. However, direct experimental proof in support of this hypothesis, notably with respect to vertebrates as sources of food, has not yet been provided for the species investigated here. In fact, SAWYER (1986) classified *E. octoculata* as a macrophagous feeder that predates preferentially on aquatic invertebrates and swallows prey organisms whole.

BLINN and DAVIES (1989) have shown that close predator-prey relationships can evolve in isolated freshwater ecosystems. In the Montezuma Well (Arizona, USA) the endemic species *Erpobdella montezuma* and two amphipod prey organisms (*Hyalella montezuma* and *H. azteca*) occupy the same habitat. Through the use of mechanoperception, this leech species feeds preferentially on one of these amphipods. In contrast, neither *E. punctata* nor *Nephelopsis obscura*, which were not found in the Montezuma Well, displayed highly developed capabilities to detect this specific prey organism by mechanoreception. These leech species are common in many aquatic ecosystems of North America and feed on a variety of prey organisms such as Oligochaeta, Chironomidae, Mollusca and Cladocera (DAVIES *et al*., 1988; BLINN and DAVIES, 1989).

According to Sawyer (1986) the most important factor that determines the relative abundance and distribution of *E. octoculata* is the availability of food. The fact that this common Palaearctic leech species is so widely distributed throughout different freshwater habitats in Europe may in part be due to the fact that it is not only a macrophagous predator. In the absence of the preferred food (living *Chironomus* larvae) this opportunistic freshwater leech will switch to other modes of feeding: the sucking of liquid contents from wounded or dead invertebrate and vertebrate prey organisms.

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