Notes on the feeding biology of *Ecnomus tenellus* (Rambur, 1842)

(Trichoptera, Ecnomidae)

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Based on container experiments and field observations the net-spinning behaviour of larvae of *Ecnomus tenellus* is reported for the first time. Thus, at least 3rd to 5th instar larvae construct funnel-shaped capture nets, loosely woven of fine silky threads and associated with silky tunnel-shaped retreats. In the littoral zone of Danish lakes, the capture nets and retreats are normally placed in crevices underneath or between stones. Once in contact with the fine threads of the capture net, a prey is rapidly attacked by the *Ecnomus* larva, seized by its mandibles, and quickly redrawn to the retreat for consumption. Feeding experiments have shown that partial prey consumption of soft, fleshy prey parts often occurs, at least when relatively large invertebrate prey are captured. Accordingly, detritus-like material of apparently animal origin dominated the foregut content of 3rd to 5th instar *Ecnomus* larvae sampled in 9 Danish lakes. However, a wide spectrum of invertebrate prey could actually be identified, including Nematoda, Oligochaeta, Tardigrada, small crustaceans (Copepoda, Cladocera and Ostracoda), insect larvae (Ephemeroptera and Chironomidae) and Hydrachnellae. Whereas large prey are normally fragmented, relatively smaller prey is often eaten in whole. With its predacious net-spinning behaviour *E. tenellus* may compete with co-existing polycentropodid species. There is evidence that *E. tenellus* is favoured by eutrophication in Danish lakes at the expence of polycentropodids.

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Introduction

The distribution of *Ecnomus tenellus* (Rambur, 1842) covers an extremely large geographical area, including Europe, the former USSR and to the east China, Taiwan and Japan (Lepneva, 1964; Botosaneanu & Malicky, 1978). Moreover, this species occurs in North Africa, Asia Minor, Iran, India, Sri Lanka and Tibet (Lepneva, 1964; Malicky, 1983).

The habitats of *E. tenellus* include a large variety of freshwaters, such as lakes, ponds, channels and large slow-flowing rivers.

It is therefore quite surprising that so relatively little is actually known about the biology of the species, including life history and feeding biology of the larva (i.e. Edington & Hildrew, 1981). This could be due to the fact that the Ecnomidae is only a small family in the otherwise well-studied European area, including only one species in addition to *E. tenellus*. By comparison, the Ecnomidae is a large family in the Afrotropical region with more than 50 species of the genus *Ecnomus* (Barnard & Clark, 1986). About a hundred species are known on a worldwide basis (Malicky, 1973).

Summarising the available information on feeding biology, larvae of *E. tenellus* seem to be predacious (Higler, 1977; Stroot et al., 1988). However, it is not known how the larvae actually catch their prey, although Wesenberg-Lund (1911), Edington & Hildrew (1981) and Stroot et al. (1988) suggest a net-spinning behaviour. The main purpose of the present study was therefore to verify this suggestion and to examine the diet of *E. tenellus*.

Methods

Larvae of *E. tenellus* were sampled from April to November in 12 Danish lakes of different eutrophy: Arreskov Sø, Dallund Sø, Langesø, Nørresø, Sarup Sø, Søbo Sø, Sønderby Sø (in Funen), Furesø, Store Hulsø (in northern Zealand), Store Økssø (in northern Jutland), Jels Midtsø and Vedsted Sø (in southern Jutland). The larvae were mostly handpicked from stones or occasionally wooden sticks in the littoral zone of the lakes and immediately placed in either 80% ethanol or Kahle's fluid. In Arreskov Sø, Langesø, Sønderby Sø and Store Økssø, however, stones of the littoral zone were brushed clean, the detached material including invertebrates being sieved (mesh size 200 or 500 μm) and preserved in 80% ethanol, and finally the larvae sorted by hand.

Instar analysis was performed on a total of 423 larvae, the head capsule width being measured using a micrometer at 50 times magnification. Second to 5th instar larvae were easily recognized according to Table 1.

Gut analysis was made on 30 larvae (3rd to 5th instar) sampled in 9 of the lakes mentioned above (Table 2). The foregut of each larva was dissected and transferred to 99.9% ethanol, then mounted in euparal on a glass slide, and finally the foregut content carefully released. Slides were examined at 150-600 times magnification.

The feeding behaviour of 3rd (4 specimens) and 4th (4 specimens) instar larvae collected alive at Dallund Sø in September 1992 and 5th (5 specimens) instar larvae collected at Søbo Sø in June 1985 was studied. Each larva was transferred to and kept in a small glass container with a bottom substrate of stones, sand particles and coarse detritus. The behaviour of the larvae was studied in detail using a stereolupe at 6-50 times magnification. After 2 days of acclimatization live potentiel macroinvertebrate prey (chironomid larvae and *Asellus aquaticus* L.) was introduced.

Table 1. Head capsule widths (mm) of 2nd to 5th instar larvae of *Ecnomus tenellus*.

Instar	Range	Mean	S.D.	n
2	0.26-0.29	0.28	0.02	2
3	0.36-0.46	0.41	0.02	132
4	0.57-0.73	0.63	0.03	94
5	0.80-1.02	0.92	0.05	49

In order to examine the possible importance of eutrophication on the competition between larvae of *E. tenellus* and Polycentropodidae, an *Ecnomus*-index defined as *Ecnomus* (larvae m^{-2} stone-area)/(*Ecnomus* + Polycentropodidae) (larvae m^{-2} stone-area) was calculated for standardized samples of littoral stones (see Dall et al., 1983) from 30 Danish lakes of differing eutrophy (expressed as secchi depth and lakewater summermean concentration of total-phosphorus). Data from the following lakes were used: Store Økssø in northern Jutland (present study; County of North Jutland, unpublished), Hald Sø, Tjele Langsø, Viborg Nørresø, Viborg Søndersø in Viborg County (Bio/consult, 1984, 1986, 1987b; Viborg Amtskommune (Viborg County Council), 1983; Viborg County Council, unpublished), Borre Sø, Bryrup Langsø, Jul Sø, Mossø, Ravn Sø, Stilling-Solbjerg Sø, Ørn Sø in Århus County (Bio/consult, 1987a, 1988, 1990a, 1990b, 1990c, 1990d; Andersen, 1982, 1986; Windolf, 1988, 1990a, 1990b, 1990c), Rørbæk Sø in Vejle County (Dall, 1978; Vejle Amt (Vejle County Council), 1991), Sunds Sø in Ringkjøbing County (Bio/consult, 1990e, 1990f), Kvie Sø in Ribe County (Bio/consult and Ribe County Council, unpublished), Arreskov Sø, Dallund Sø, Langesø, Nordby Sø, Nørresø, Sarup Sø, Søbo Sø,

Table 2. Physical and chemical characteristics of nine Danish lakes, where the diet of *Ecnomus tenellus* was investigated. The data presented are summer means (1 May-1 October). All lakes are alkalic, except Store Økssø which is acid and humic (mean pH 4.2, mean acidity 0.14 $mmoll^{-1}$).

Lake locality	Year	Secchi depth (m)	Chlorophyll-a ($\mu g\ l^{-1}$)	Total nitrogen ($\mu g\ l^{-1}$)	Total phosphorous ($\mu g\ l^{-1}$)
Arreskov Sø	1990	0.25	150	3200	280
Langesø	1990	0.78	130	2800	420
Sønderby Sø	1991	0.78	130	1900	1600
Nørresø	1989	0.58	49	1700	110
Søbo Sø	1983-88	0.75-0.99	50-66	2200-3200	90-120
Furesø	1975-76	1.61-2.20	34	840-890	540-570
Vedsted Sø	1980	2.02	14	830	37
Jels Midtsø	1977-89	1.92-2.27	9.4-32	6200	44
Store Økssø	1980	1.86	32	480	50

Søholm Sø and Sønderby Sø in Funen County (Fyns Amt (Funen County Council), 1992a, 1992b, 1992c; Funen County Council, unpublished), Arresø, Bastrup Sø, Esrum Sø, Fugle Sø, Gurre Sø and Sjælsø in Frederiksborg County (Dall et al., 1984; Olesen et al., 1991; Vandkvalitetsinstituttet, 1991; Water Consult & Frederiksborg Amt (Frederiksborg County Council), 1992a, 1992b; Frederiksborg County Council, unpublished; Bioconsult & Frederiksborg County Council, unpublished; Database of The Danish Environmental Research Institute).

Results

Gut analysis (Table 3) revealed that 3rd to 5th instar larvae of *E. tenellus* digest a large variety of aquatic invertebrates, e.g. Nematoda, Oligochaeta, Tardigrada, small crustaceans like Copepoda, Cladocera and Ostracoda, insect larvae like Ephemeroptera and Chironomidae, and Hydrachnellae. The different kinds of animal material were mostly heavily disintegrated, although some smaller prey was ingested in whole. Also fragments (e.g. legs) of larger invertebrate prey occurred. However in several larvae, only a minor part of the gut content could actually be identified as invertebrate items. Thus, most of the foregut content appeared as amorphous material, which might be termed "detritus". This "detritus" was probably animal tissue. There was no traces of plant material including algae, except in one case where small diatoms were found attached to fine sand grains.

In the container experiments each 3rd to 5th instar larva immediately constructed a tunnel-shaped retreat of silk (Fig. 1). Retreats were in most cases placed in crevices, e.g. under a stone or between two stones. Sand grains and coarse detritus particles were incorporated in the retreats. From either both or occasionally only one of the tunnel openings a funnel-shaped net was spun. However, retreats and funnels were sometimes more irregularly constructed. The nets were all loosely woven of very fine silky threads. The length of the retreats was approx. 20-25 mm, whereas funnels were up to 60 mm in diameter and could be more than 50 mm in length.

Both larval retreats and nets were found in the natural habitats of *E. tenellus*. They normally occurred underneath stones and in crevices between stones, but were occasionally found on top of the stones. However, as nets were loosely woven and streched between solid objects, they collapsed when sampled. Also retreats collapsed during sampling, but they were nevertheless more easily recognized be-

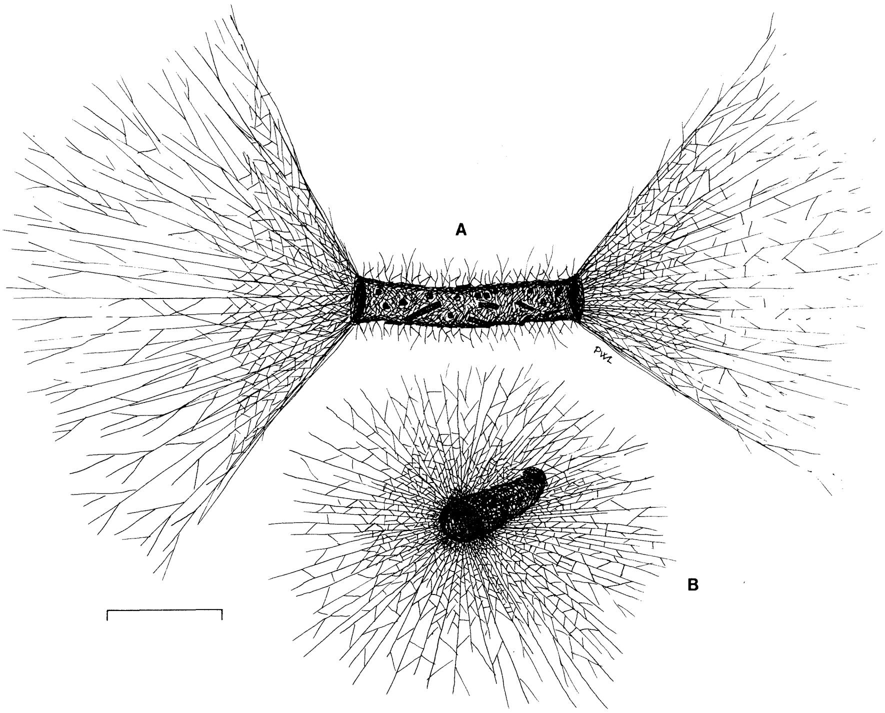

Fig. 1. Typical capture net and retreat of *Ecnomus tenellus*.
A, lateral view; B, apical view. Scale: 10 mm.

cause of the incorporated building material like sand grains and/or detritus.

Ecnomus larvae normally resided in their retreats, regularly making respiratory undulations. Then, when introduced prey came in contact with the fine threads of their nets at distances of 25-30 mm from the retreat openings, the movements of the prey provoked the *Ecnomus* larvae to attack. These attacks were extremely rapid, the prey being seized by means of the mandibles and finally quickly redrawn to the retreat. Here the prey was consumed. The abdominal integument of larger chironomid larvae was either penetrated or the larvae were simply cut into two pieces, whereupon the soft body tissue was eaten up bit by bit. Smaller chironomids, however, were swallowed in whole anterior end first. Preyed *Asellus aquaticus* were attacked ventrally, their soft tissue being eaten bit by bit, leaving the heavily sclerotized parts unharmed.

Calculated *Ecnomus*-index values of 0.80-1.00 and densities of maximally 478 larvae m^{-2} stone-area were obtained in highly eutrophic and alkalic lakes with low secchi depths, 0.25-0.78 m (Fig. 2) and high concentrations of total-phosphorus, 115-1600 μg l^{-1} (Fig. 3), whereas index values of 0-0.50 were primarily found in less eutrophic lakes. Thus, dominance of Polycentropodidae actually occurred in two of the highly eutrophic lakes studied. High densities of Polycentropodidae (maximally 565 larvae m^{-2} stone-area) were found in several lakes.

A high *Ecnomus*-index was found in the acid (pH 4.2), oligotrophic Store Økssø. Moreover, *E. tenellus* was the most abundant macroinvertebrate (432 larvae m^{-2} stone-area) inhabiting the littoral stones of this lake.

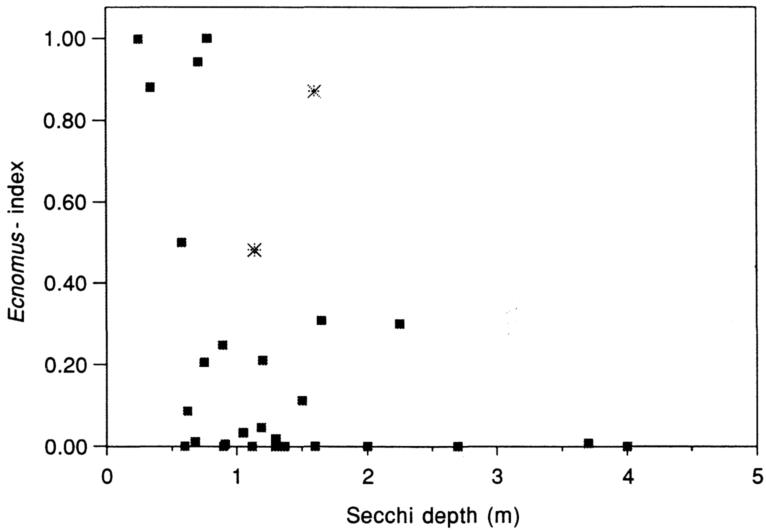

Fig. 2. Relationship between *Ecnomus*-index and secchi depth in 30 Danish lakes. The secchi depth is expressed as mean for the period 1 May-30 September. Asterisks: acid lakes (pH 4.2-5.4); squares: alkalic lakes. See text for further explanation.

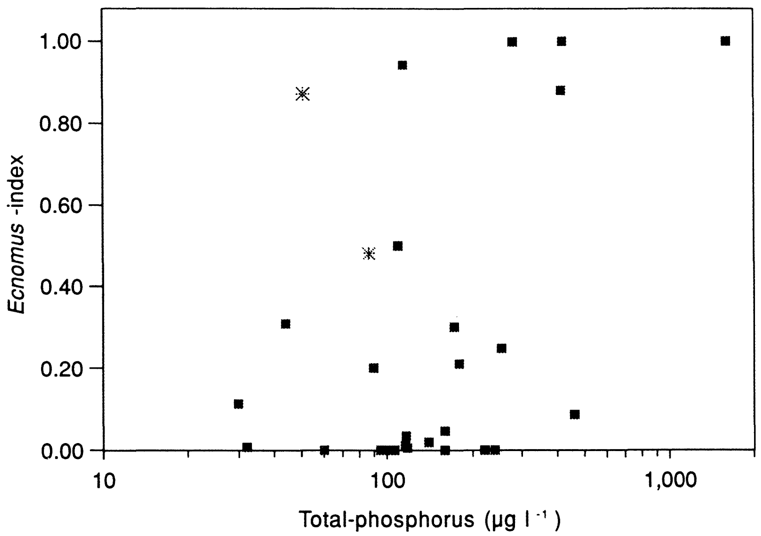

Fig. 3. Relationship between *Ecnomus*-index and lakewater concentration of total-phosphorus in 30 Danish lakes. The concentration of total-phosphorus is expressed as mean for the period 1 May-30 September. Asterisks: acid lakes (pH 4.2-5.4); squares: alkalic lakes. See text for further explanation.

Discussion

This study clearly demonstrates that at least 3rd to 5th instar larvae of *E. tenellus* are net-spinners, constructing tubular retreats with attached funnel-shaped capture nets. The nets have the same purpose as those of many spiders, although the threads of *Ecnomus* nets are apparently not sticky. The *Ecnomus* nets and retreats, thus, bear close resemblance to those of polycentropodids such as *Cyrnus* and *Holocentropus* (e.g. Wesenberg-Lund, 1911). Moreover, the prey capturing behaviour of *Ecnomus* is similar to that of these two genera, as described by Wesenberg-Lund (1911).

The net-spinning behaviour of *Ecnomus* species is previously reported only once. Thus, Gasith and Kugler (1973) found irregular hunting nets in *E. galilaeus* Tjeder and *E. gedrosicus* Schmid from Lake Tiberias, their nets usually being attached to the underside of stones or other suitable supports.

However, Barnard & Clark (1986) report that larvae of the African *E. menelli* Barnard & Clark and *E. thomasseti* Mosely both live in silk tubes, that sometimes meanders over surfaces of various substrates, or often shelter in crevices covered in silk. In my opinion, Barnard and Clarks description of silky structures could very well refer to capture nets associated with tubular retreats. I therefore suggest, that construction of capture nets is common or may even be the rule among *Ecnomus* species.

Construction of a tubular silken retreat is probably the rule among *Ecnomus* and other Ecnomidae, e.g. reported for Australian *Ecnomus* and *Ecnomina,* the latter constructing galleries within thin layers of silt that accumulate on stone surfaces (Dean & Bunn, 1989).

With their net-spinning and retreat building behaviour Danish *E. tenellus* are typically associated with solid objects like stones and sometimes wooden sticks. Further, they seem to prefer placing their retreats and nets in crevices, e.g. underneath or between stones. Consequently, they are typically inhabitants of the littoral zone of Danish lakes at water depths of 0-1 metre. A few other authors have found *E. tenellus* on a stony bottom (Jenkins, 1977; Schleuter & Tittizer, 1988), although most records in fact are from submersed vegetation, e.g. *Chara* beds (Jenkins, 1977), *Stratiotes* plants (Higler, 1977, 1978) and submersed parts of other emergent and floating-leaved macrophytes (Dvorak & Best, 1982). Also artificial *Stratiotes* plants provide a suitable substrate for *E. tenellus* larvae, often occurring in surprisingly high numbers (Higler, 1978). Therefore, any solid substrate including macrophytes seem to be suitable for *E. tenellus.*

The observed preference for a stony habitat in Danish lakes may, however, only be apparent as the submersed vegetation of the lakes has declined dramatically during the last century.

The results of this study indicate that partial prey consumption is common among larvae of *E. tenellus,* at least when relatively large invertebrate prey are captured: The fleshy tissue of the prey is excavated, leaving heavily sclerotized parts like legs and head capsules. Thus, without knowing the actual feeding behaviour of *E. tenellus,* a normal gut analysis would reveal that "detritus" is an important food source for the species.

Partial prey consumption has received only little attention in food studies. However, its importance has been clearly demonstrated in two *Rhyacophila* species (Trichoptera) by Martin & Mackay (1982). Further, it has been noted in Plecoptera by Winterbourn (1974) and Malmquist & Sjöström (1980).

Although "detritus"-like material dominated the foregut content of *E. tenellus* larvae in the present study, a large selection of invertebrates could be identified, mostly being relatively small prey. Other studies of the foregut content of *E. tenellus* have demonstrated a predaceous diet. Thus, Higler (1977) recorded a diet of *Stylaria lacustris* (L.) (Oligochaeta), Cladocera, Ostracoda and

Table 3. Gut content of 30 larvae of *Ecnomus tenellus*. Sampling sites: Arreskov Sø (Arr), Furesø (Fur), Jels Midtsø (Jel), Langesø (Lan), Nørresø (Nør), Store Økssø (StØ), Søbo Sø (Søb), Sønderby Sø (Søn) and Vedsted Sø (Ved).

Gut content	No. of larvae	No. of prey per larva	Larval instars	Sampling sites
Nematoda (d)	1	1	5	Søb
Stylaria lacustris (d)	1	1-?	4	Arr
Naididae (d)	2	1-?	4	Arr, Ved
Tardigrada	1	1	3	Arr
Copepoda (d)	4	1-3	5	Jel, Søb
Cladocera (d)	6	1-5	4, 5	Arr, StØ, Søb, Ved
Ostracoda (d)	3	1	5	Jel, Søn
Ephemeroptera, nymphs (f)	2	1	5	Jel, Søb
Chironomidae, larvae (d)	2	1	4, 5	Arr, Jel
Chironomidae, larvae (w)	1	1	4	Arr
Hydrachnellae (d)	2	1-2	5	Jel, StØ
"Detritus" (probably animal tissue)	13	-	4, 5	Fur, Jel, Lan, Nør, Søb, Søn
Humic detritus	2	-	5	StØ
Gut empty	2	-	4, 5	Jel, Søn

(d) Disintegrated prey, (w) whole prey, (f) only fragments of prey.

chironomids in some Dutch broads, whereas Stroot et al. (1988) only found heavily fragmented Cladocera (1-2 specimens per larva) in larvae from a French locality. However, Stroot et al. (1988) also reported an uropod fragment of a juvenile *Gammarus* in one full-grown *Ecnomus* larva collected in a Belgian pond.

In conclusion larvae of *E. tenellus* seem to exploit a wide spectrum of invertebrate prey. As suggested by Stroot et al. (1988) it is likely that the composition of ingested prey reflects the supply of available prey items, rather than a selection among different prey.

Other species of the genus *Ecnomus* are probably predators like *E. tenellus*. Thus, studies of the European *E. deceptor* McL. (Stroot et al., 1988) and the African *E. menelli, E. thomasseti* (Barnard & Clark, 1986) and *E. relictus* Vaillant (Vaillant, 1953) revealed remains of oligochaetes, copepods and chironomid larvae in the foregut. In addition, Gasith & Kugler (1973) report that Israeli *E. galilaeus* and *E. gedrosicus* prey on small invertebrates. However, the diet of the Australian *E. pansus* Neboiss seems to be particularly diverse, including blue-green algae, filamentous and unicellular green algae and diatoms in addition to invertebrate prey such as Cladocera, Copepoda, Rotifera, Trichoptera, Chironomidae and terrestrial insect fragments (Chessman, 1986).

Predatory habits are also found among Australian *Ecnomina,* although algae may form an appreciable proportion of the gut content in at least one species (Chessman, 1986).

With their predacious net-spinning behaviour Danish *E. tenellus* may compete with co-existing polycentropodid species like e.g. *Polycentropus flavomaculatus* (Pictet), *Cyrnus flavidus* McL., *C. crenaticornis* (Kolenati), *C. trimaculatus* (Curtis), *Holocentropus dubius* (Rambur) and *H. picicornis* (Stephens), probably showing the same feeding habit with comparable food demands (e.g. Higler, 1977). However, as demonstrated by Higler (1977, 1978), different polycentropodid species are either separated spatially or temporally. Thus, temporal separation may reduce competition among species, assuming that larvae of different size have different food demands.

The data presented in this paper do not permit conclusions to be drawn concerning temporal separation between *E. tenellus* and different species of Polycentropodidae.

On the other hand, the data indicate that polycentropodid species are far more abundant than co-existing *E. tenellus* on stony bottom in the littoral zone of oligotrophic and moderately eutrophic Danish lakes. In contrast, *E. tenellus* seems to replace the polycentropodids in highly eutrophic Danish lakes, at the same time occurring in high densities, comparable to the densities obtained by Polycentropodidae in less eutrophic lakes. Thus, eutrophication apparently favours *E. tenellus* at the expence of polycentropodids.

E. tenellus also dominates over polycentropodids in the highly acid, oligotrophic and humic Danish lake, Store Økssø, at the same time being surprisingly abundant. Accordingly, acidification is reported to favour *E. tenellus* in Dutch lakes, reducing species richness in Polycentropodidae as well as in Trichoptera in general (Leuven et al., 1987).

Also organic or toxic pollution seems to reduce the competition from polycentropodids (Urk & Vaate, 1990).

Therefore in conclusion, different types of increased environmental stress seem to favour *E. tenellus* at the expense of polycentropodids. However, the basis for this competitive avantage in *E. tenellus* is not known.

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Dansk sammendrag

Det er ved laboratorie- og feltundersøgelser for første gang påvist, at i det mindste 3.-5. stadie larver af vårfluen *Ecnomus tenellus* spinder net, hvori de fanger forskellige byttedyr. *Ecnomus*-larverne bygger endvidere faste boliger (»retræter«) i form af op til 20-25 mm lange, ret løst vævede rør, til hvilke der i hver ende er knyttet et nærmest tragtformet, løst spundet fangnet (Fig. 1). Fangnettene kan være op til 60 mm brede og 50 mm lange. I retræterne er ofte indbygget forskelligt materiale, så som sandskorn, små bladstykker o. lign. Retræterne og fangnettene er fæstnet til faste genstande, i en række undersøgte danske søer normalt til sten på lavt vand. Her anbringes retræter og net normalt i hulrum mellem stenene, ofte på undersiden af løstliggende sten, idet dog stenenes overside undertiden også anvendes. Retræter og fangnet kan også findes fæstnet til rankegrøde (undervandsvegetation), hvor en sådan findes.

Ecnomus-larverne er meget hurtige rovdyr. Berører eller indvikles et muligt byttedyr i fangnettets meget fine, ikke-klæbende tråde, udløser dette straks et lynhurtigt angreb fra *Ecnomus*-larvens side. Herunder gribes byttet med mandiblerne og trækkes lynhurtigt ned i retræten, hvor det fortæres.

Laboratorieundersøgelser har vist, at små byttedyr normalt fortæres hele, mens større bytte bides itu og de bløde dele spises, således at de hårde, sklerotiserede dele efterlades. Den sidstnævnte måde at fortære et fanget bytte på viser sig ved, at fortarmindholdet hos 30 undersøgte *Ecnomus*-larver fra 9 danske søer med forskelligt indhold af plantenæringsstoffer (Tabel 2) hovedsagelig består af »detritus«, tilsyneladende af dyrisk oprindelse (Tabel 3). En del forskellige byttedyr kunne dog samtidig identificeres, idet disse dog typisk var meget findelte: Rundorme (Nematoda), børsteorme (Oligochaeta), bjørnedyr (Tardigrada), små krebsdyr som

vandlopper (Copepoda), daphnier (Cladocera) og muslingekrebs (Ostracoda), nymfer/larver af døgnfluer (Ephemeroptera) og dansemyg (Chironomidae), samt vandmider (Hydrachnellae).

Larven af *E. tenellus* har samme levevis som larver, der tilhører den nærtstående vårfluefamilie, Polycentropodidae. Alle konstruerer de således net til fangst af byttedyr og lever tilsyneladende også af de samme byttedyr. *Ecnomus* og de forskellige arter af Polycentropodidae konkurrerer derfor som udgangspunkt om både plads og føde.

Data fra undersøgelser af smådyrfaunaen på stenbund i 30 danske søer tyder på, at *Ecnomus* begunstiges på bekostning af Polycentropodidae i stærkt næringsstofberigede søer (dvs. søer med højt fosforindhold i vandfasen og ringe gennemsigtighed om sommeren på grund af stor planktonalgevækst). Sådanne søer har således typisk et *Ecnomus*-indeks på 0,80-1,00 (*Ecnomus*-indeks = *Ecnomus* (antal m^{-2}) / (*Ecnomus* + Polycentropodidae) (antal m^{-2}), mens *Ecnomus*-indekset er lavt (0-0,50) i mindre næringsrige søer, hvor polycentropodider således dominerer (Fig. 2 og 3).

Dominans af *Ecnomus* er også fundet i den sure (pH 4,2), brunvandede, men rene Store Økssø, hvilket er i overensstemmelse med hollandske søundersøgelser.

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