many social species [9]. Oophagy, as outlined above, may also be a plausible first step in the evolution of trophic egg production by worker bees as found in eusocial species such as in the Meliponini [10].

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**Umbra pygmaea, an Acid-tolerant Fish**

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*Umbra pygmaea* (De Kay) (Fig. 1) is a small fish species that was introduced into the Netherlands in the 1920s. Its original area of distribution is in the eastern USA. Today it is widespread in the south-eastern part of the Netherlands and in the province of Limburg in Belgium, where it is particularly abundant in acidified soft-water ecosystems with a low pH, such as moorland pools ("vennen"), and usually the only fish species [1, 2]. It can be found as well in circumneutral waters but there, probably due to predation by large fish, quantities are low.

This fish is very well adapted to survive adverse circumstances, such as poor oxygen conditions, extreme temperatures, high acidity and also temporary desiccation of its environment. The swim bladder plays an essential role as an additional respiratory organ [3, 4]. As the ventral and pectoral fins can be moved independently, it can not only swim in the water, but can move equally well in the mud at the bottom. The fish is, however, quite sluggish, making it an easy prey for larger fish and fish-eating birds.

In the moorland pools *U. pygmaea* is particularly abundant (up to 20 kg ha⁻¹) in waters with an alkalinity less than 0.1 meq l⁻¹, a pH range between 3.5–4.0, and a Ca²⁺ concentration of less than 100 μmol l⁻¹. The species has even been found at a Ca²⁺ concentration as low as 15 μmol l⁻¹ [2]. The lowest pH level at which the fish has been observed under natural conditions is 3.2. In the laboratory the fish could be kept at a pH of 2.8 (i.e., the lowest pH value ever measured in a Dutch aquatic environment), although with considerable mortality [3].

In general, fish exposed to acid water at pH 5 or lower show considerable loss of ions, mainly via the gills. This leads to a drop in plasma electrolytes, which is considered the major cause of death in acid water and which usually occurs below pH 4–4.5. *U. pygmaea* maintains normal blood plasma osmolarity and ion levels at low pH, even in very soft freshwater [2]. One of the morphological factors that contributes to this tolerance is the gill structure. The gill epithelium is the most vulnerable site of a fish and decreased branchial ion uptake and increased branchial permeability account for most of the net...
The maturation of the gonads takes place from October to April. The female deposits 100–1200 eggs (size 1.8–1.9 mm) in April and May. At a temperature of 10°C hatching takes place after 14 days. The larvae are then 5 mm and still have a yolk sac. When they have grown to 7 mm the yolk has been used up completely. Possibly the parent fish takes care of the fry, since during the whole reproduction season the fish live in pairs. Also eggs and fry seem extremely tolerant to acid water; these were observed in pools with a water pH ≥ 3.5 [2]. In other species of fish, eggs and fry are usually very sensitive to low pH [6]. No temperate fish species other than *U. pygmaea* is known to us that reproduces successfully below pH 4.5. The food consists mainly of benthic invertebrates, and a small zooplankton component. Nematocera form 84% of the food [2]; consequently the fish may be applied as a control agent for mosquitoes in acidified water systems. In the last few decades at least 60% of the Dutch moorland pools have been acidified [7]. This resulted in fundamental changes in the aquatic vegetation and a strong reduction in the microbiological activity in decomposition processes [8]. The changed conditions have also had profound consequences for the fauna. At present the fauna of the acidified moorland pools is mainly composed of insect larvae, water beetles and water bugs. In these systems *Umbra pygmaea* and the larvae of *Odonata* function as top predators. In some pools these are perhaps kept in check by grebes. Further research is needed to confirm the latter aspect.

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