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].

This research was partly financed by grants from the Deutscher Akademischer Austauschdienst and from the Graduiertenförderung des Landes Baden-Württemberg given to R. E. Stark.

Received February 24 and October 3, 1989


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 Fig. 1. Umbra pygmaea (De Kay, 1842)
The epithelium covering the gills increases in thickness in water of pH 3.5 when compared to pH 4 or 4.5 [5]. This structure undoubtedly limits the oxygen uptake capacity of the gills. This low capacity is probably compensated for by the swim bladder, which functions as an accessory respiratory organ, and has a respiratory surface twice that of the gills [3].

Under acid circumstances in the pH range of 3.5–4.0 the fish seems to function optimally. The males reach a length of 8.4 cm, while the females may reach a size of 13.4 cm. The maximum age that could be established is 8 years. The fish becomes mature within a year.

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 mosquitos in acidified water systems. In the last four 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.

Table 1. Surface area of gill lamellae (mm² per g body weight) of *U. pygmaea* (pers. observations) and other teleost species (data from [9]).

<table>
<thead>
<tr>
<th>Species</th>
<th>Surface Area (mm² per g body weight)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Umbra pygmaea (De Kay)</td>
<td>136</td>
</tr>
<tr>
<td>Callionymus lyra L.</td>
<td>168</td>
</tr>
<tr>
<td>Cottus bubalis Euphrasen</td>
<td>453</td>
</tr>
<tr>
<td>Tinea tinca (L.)</td>
<td>383</td>
</tr>
<tr>
<td>Salmo trutta L.</td>
<td>339</td>
</tr>
<tr>
<td>Trachurus trachurus (L.)</td>
<td>745</td>
</tr>
</tbody>
</table>

Received April 27 and September 18, 1989


**Dominance Behavior Among Ant Females**

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Antagonistic behavior, leading to the formation of reproductive rank orders, is known to play an important role in the control of reproduction in colonies of social insects. Hierarchies have been reported from bumblebees as early as 1802 [1], and they have been studied in detail in several species of wasps (e.g., [2]). In ants, dominance interactions are known to occur among cofoundresses in young colonies [3, 4], among workers [5–7], and among virgin females [8], but little attention has been paid to the behavior of inseminated females in established colonies. I here report the first case of linear dominance hierarchies among inseminated females in mature colonies of ants. (Additional data will be presented in more detail by J. Heinze and T. A. Smith.) In incipient colonies of the Australian meat ant, *Iridomyrmex purpureus*, the cofoundresses engage in ritualized antennation bouts, which result in a lower frequency of egg-laying by the subordinate female. Once the colony grows larger, the queens escape dominance conflicts by permanently separating within the nest (oligogyny) [4]. In established colonies with several fertile females (polygyny), however, the queens are often found clustered together or seem to ignore each other’s presence. Individual females in polygynous nests of the fire ant, *Solenopsis invicta* [9], or the Argentine ant, *Iridomyrmex humilis* [10], may differ substantially in their reproductive success. It has been suggested that differences in fecundity result from intrinsic physiological factors [10]. In *Leptothorax (Myrafant) curvispinosus*, differential reproduction is caused by the way individual queens handle the