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Biology of the acid-tolerant fish species *Umbra pygmaea* (De Kay, 1842)

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In The Netherlands, the mudminnow *Umbra pygmaea* mainly occurs in water bodies with a pH ranging from 3.5 to 4.0, an alkalinity less than 0.1 meq l⁻¹ and a calcium content below 100 µmol l⁻¹. The abundance of mudminnows is inversely related to the pH and the presence of predatory fish species. Experimental studies show that *U. pygmaea* is extremely acid-tolerant. Exposure to media with pH values ranging from 4.0 to 7.0 did not cause mortality or significant changes in blood plasma osmolarity and haematocrit. At pH 3.0 no mortality was recorded although a strong decrease in the plasma osmolarity was observed. Exposure to pH 2.8 and calcium concentrations of 100 or 500 µmol l⁻¹ for 10 days caused 70% and 40% mortality respectively. The growth, reproduction and feeding of mudminnows are described. Age-growth and length-age relationships were calculated. Gonadal development started between September and January. The highest Gonado Somatic Index was recorded in spring. Spawning occurred from April to May. Fecundity of a sample of females was assessed. Nematocera provided the main item of diet of *U. pygmaea*; the microfauna ingested was dominated by Cladocera. The adaptations of mudminnows to acid environments are discussed.

I. INTRODUCTION

The East American mudminnow, *Umbra pygmaea* (De Kay, 1842), is one of the five now living representatives of the Umbridae (Wilson & Veillieux, 1982). The world distribution of the umbrids is shown in Fig. 1. *Umbra pygmaea* is native in inland waters in the eastern part of the U.S.A. (Schrenkeisen, 1938; Wheeler, 1969). About 70 years ago this species was introduced into Western Europe. Subsequently, *U. pygmaea* has been recorded from France, (Spillmann, 1959), The Federal German Republic (Ladiges & Voigt, 1965; Muus & Dahlstrøm, 1968), The Netherlands (Kleijn, 1968; Vooren, 1972; Leuven *et al.*, 1984a, b) and Belgium (Poll, 1949; Burney, 1984).

In North America, *U. pygmaea* has been found in quiet, mud-bottomed, often heavily vegetated streams, sloughs and ponds, particularly along the margins (Lee, 1980). However, little is known about the ecology and life history of this fish species.

In Europe, *U. pygmaea* has been observed in small rivers, lakes, pools, ditches and sluggish or stagnant waters in peat bog areas (Vooren, 1972). Recently it has been reported that the East American mudminnow is extremely acid-tolerant and survives in waters where no native fish can live (Leuven *et al.*, 1984a, b). The distribution of *U. pygmaea* in The Netherlands has been extended during recent decades. Many acid and acidifying soft-water systems have been invaded by this species.

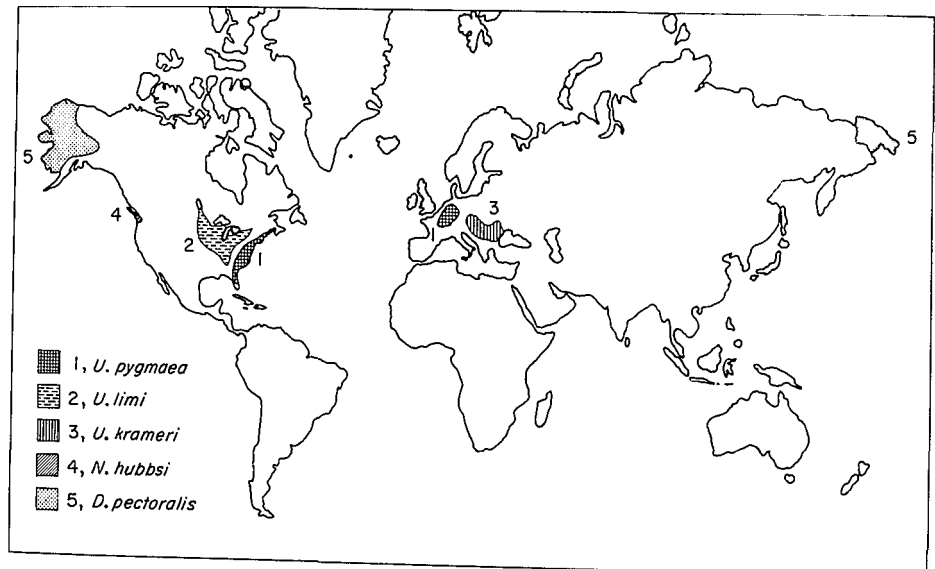


FIG. 1. The world distribution of the Umbridae (after Spillman, 1959; Ladiges & Voigt, 1965; Vooren, 1972; Scott & Crossman, 1973; Wilson & Veillieux, 1982, Leuven *et al.*, 1984b).

In acid ecosystems, *U. pygmaea* may play a significant role as a top predator. In America the same phenomenon has been described for the related species *U. limi* (Kirtland) (Rahel & Magnuson, 1983). Thus the biology of mudminnows is of special interest because they seem to be well adapted to acid water. So far, little is known about the physiological and ecological mechanisms which enable these umbrids to live under acid conditions.

In the present paper the occurrences of *U. pygmaea* in relation to water quality (particularly pH) and presence of predatory fish species are described. Moreover, data are presented on growth, feeding and reproduction of mudminnows. The acid-tolerance was studied in a laboratory experiment.

II. METHODS

FIELD STUDIES

In 1983 the fish assemblages were investigated in 96 isolated soft-water systems (alkalinity ≤ 2 meq l^{-1}). Most waters (moorland pools and small lakes) are situated in the southern and eastern parts of The Netherlands. In order to get a reasonably complete list of fish species, 54 waters were sampled at least three times with different types of fishing gear, i.e., V-shaped dipnets, fykes, gill-nets and seine-nets. A survey of the entire water body was made and the presence and relative abundance of *U. pygmaea* determined. The remaining 42 waters were sampled only once. If *U. pygmaea* was present in a catch, 5–40 individuals were collected at random and preserved in 70% ethanol. At the laboratory the sex, length and total weight were recorded. The opercular bone was removed and used for age determination.

The relationship between length and weight was described by the power function:

$$W = \alpha L^{\beta} \quad (1)$$

where W is body weight, L body length, and the constants α and β were estimated by curve fitting.

The age-length data for fish older than 50 days were fitted to the model (Brody, 1945):

$$L = L_x (1 - e^{-K(t-t_0)}) \quad (2)$$

where L is body length, t age, L_x the arithmetically determined ultimate length, and K and t_0 are species specific constants. The parameters in equation (2) were estimated according to Von Bertalanffy (1934, 1938). In addition, the equation

$$L = Pe^{kt} \quad (3)$$

where L is body length, t age, and k a species specific constant, was applied in order to describe the length-age relationship in younger fish (Brody, 1945). The time-derivative of equation (2)

$$G_1 = KL_x e^{-K(t-t_0)} \quad (4)$$

Where L is body length, t age, L_x the arithmetically determined ultimate length, and K and t_0 are species specific constants, gives a description of the growth-rate of the fishes.

To fit the data to the models, the GLM and NLIN regression procedures of SAS (1982) were applied. For statistical comparison of the length-weight and length-age relationships for males and females the best fitting equations (1, 2) were transformed to linear models using logs. Statistical differences between the equations calculated were tested using F tests (Fisher, 1924).

Prior to spawning, the ovaries of some specimens were preserved for counting the total number of eggs per fish. The length-fecundity and weight-fecundity relationships were described by the model

$$Y = aX^b \quad (5)$$

(Babiker & Ibrahim, 1979).

The oesophagus and stomach of the preserved mudminnows were dissected and the contents identified.

From January until May 1984 approximately 20 individuals of *U. pygmaea* were sampled fortnightly in the Groot Huisven. This moorland pool is situated East of Oisterwijk (51°35'N 5°16'E) and has a surface area of 5 ha and a maximum depth of 1.5 m. The physico-chemical properties of the Groot Huisven are given in Table I. All fishes captured were preserved in 70% ethanol. The Gonado Somatic Index (GSI) of a fish was calculated as:

$$\text{GSI} = (\text{gonad weight}) / (\text{body weight} - \text{gonad weight})^{-1} \times 100\%.$$

At all locations, pH measurements were carried out with a Metrohm E488 pH-meter and a model EA152 combined electrode. Alkalinity was measured by titration of 100 ml of water with 0.01 M HCl down to pH 4.2 and the acidity by titration with 0.01 M NaOH up to pH 8.2. Electrical conductivity (EC) and temperature were measured with a model 33 YSI-SCI portable conductivity meter. The measured conductivity was corrected for temperature and pH according to Vangenechten *et al.* (1981). A Dentan model FN5 meter was used for the measurement of the turbidity.

Water samples were passed through a Whatman GF/C filter, collected into two 100-ml iodinated polyethylene bottles and preserved by adding 0.5 ml of a 200 mg l⁻¹ HgCl₂ solution. In one of the two samples some grains of citric acid were added in order to prevent precipitation of metals. All samples were transported to the laboratory in a refrigerated container and stored at -20° C until analysis.

LABORATORY STUDIES

Fully controlled laboratory experiments were performed in order to study the acid-tolerance of *U. pygmaea*. The experimental set-up has been described by Roelofs *et al.* (1984). All experiments were conducted in glass containers (25 × 25 × 30 cm) which were placed in a water bath. The temperature of the water bath was maintained at 20° C by means of a Neslab type Coolflow 75 cooling aggregate. The medium in each aquarium was continuously refreshed (1 litre h⁻¹) from black polyethylene stock containers by means of a Multifix Constant pump unit. To avoid oxygen deficiency or high carbon dioxide pressures, an inundated air-tube was placed in each container. All experiments

TABLE I. The ranges of some physico-chemical parameters of 21 Dutch waters harbouring *Umbra pygmaea* and the average values of these parameters for the Groot Huisven

Parameter	Range*	Groot Huisven†
pH	3.5–8.1	4.9
Alkalinity (meq l ⁻¹)	0–1.930	0.040
Acidity (meq l ⁻¹)	0.042–0.305	0.150
EC _{18°C} ^{##} (μS cm ⁻¹)	0–383	59
Cl ⁻ (μmol l ⁻¹)	140–1320	319
NO ₂ ⁻ (μmol l ⁻¹)	0.5–1.75	0.5
NO ₃ ⁻ (μmol l ⁻¹)	0.5–13.5	6.0
NH ₄ ⁺ (μmol l ⁻¹)	140–1320	61
PO ₄ ⁻⁻⁻ (μmol l ⁻¹)	0.0–8.73	0.14
SO ₄ ⁻ (μmol l ⁻¹)	80–515	147
Na ⁺ (μmol l ⁻¹)	98–1120	289
K ⁺ (μmol l ⁻¹)	25–175	37
Ca ⁺⁺ (μmol l ⁻¹)	15–870	84
Mg ⁺⁺ (μmol l ⁻¹)	10.6–282	99
Si (μmol l ⁻¹)	0.78–108	1.3
Fe (μmol l ⁻¹)	3.9–45.2	18.3
Mn (μmol l ⁻¹)	0.8–233	1.3
Al (μmol l ⁻¹)	2.3–53.9	11.2
Cd (nmol l ⁻¹)	0.0–23.0	0.9
Turbidity (ppm)	1.8–10.4	6.6

*Range in average for 21 sites (1983).

†Average values 1984 (*n* = 19).

TABLE II. The chemical composition of the water used in the experiments in μmol l⁻¹

Ca ⁺⁺	100 or 500	SO ₄ ⁻	32.0
K ⁺	11.4	Cl ⁻	800 or 1600
Na ⁺	532	F ⁻	0.08
Mg ⁺⁺	60.1	Br ⁻	0.94
Si ⁺⁺	0.17	I ⁻	0.003
H ₃ BO ₂	0.49	HCO ₃ ⁻	2.7
P	0.007	+ trace elements	

were conducted in synthetic culture media (Table II), prepared by the addition of sea salt and CaCl₂ to twice demineralized water.

After acclimatization to the basic medium (pH = 5.7), replicates of 10 individuals were exposed to water of different pH and calcium content. In order to prevent shock effects the pH in the aquaria was changed gradually. All fish were incubated at the ultimate pH for a period of 10 days. During the experiments the animals were fed *Tubifex*. The pH of the media was adjusted daily by adding H₂SO₄ or KOH. The mortality rate of the fishes was recorded and probability of survival predicted using PROBIT analysis (SAS, 1982).

After cutting off the tails of anaesthetized fish, blood was collected from the caudal blood vessels in heparinized haematocrit capillaries. After centrifugation of the blood in a

TABLE III. The presence and relative abundance of *Umbra pygmaea* (%) in poorly buffered waters in The Netherlands with different pH (*n*, number of waters sampled; N.D., not determined)

	pH < 5 (<i>n</i> = 28)	pH ≥ 5 (<i>n</i> = 26)	3.5 < pH < 8.1 (<i>n</i> = 96)
Presence	21	25	22
Relative abundance*	100	1.6	N.D.

*Percentage *U. pygmaea* of the total number of fish caught.

Heraeus-Christ haematocrit centrifuge (3 min) the haematocrit percentage was measured and the osmolarity of the plasma estimated with a Vogel osmometer. The blood parameters ($P < 0.05$) were tested for statistical significance with the Kruskal & Wallis one-way analysis by ranks.

CHEMICAL ANALYSIS

Magnesium, manganese and iron were estimated with a Beckman model 1272 Atomic Absorption Spectrophotometer, and aluminium and cadmium with an IL Video AA/AE Spectrophotometer. Sodium and potassium were determined flame-photometrically and sulphate gravimetrically using a Technicon I Autoanalyser. Orthophosphate (Henriksen, 1965), nitrate and nitrite (Kamphake *et al.*, 1967), chloride (O'Brien, 1962), ammonia (Grasshoff & Johannsen, 1977) and silicon (Campbell & Thomas, 1970) were analyzed colorimetrically with a Technicon II Autoanalyser.

III. RESULTS

CHARACTERIZATION OF THE HABITATS

In 1983 *U. pygmaea* was observed in 21 (22%) of 96 soft waters investigated (Table III). The ranges of the physico-chemical properties of these habitats are shown in Table I. *U. pygmaea* has a rather wide range of occurrence with respect to the pH of the water. The habitats are characterized by low alkalinity and ionic content. In some systems the acidity and (heavy) metal concentrations are rather high. Figure 2 illustrates that *U. pygmaea* mainly occurs in waters with a pH between 3.5 and 4.0, an alkalinity below 0.1 meq l^{-1} and a calcium concentration below $100 \mu\text{mol l}^{-1}$. These waters are relatively small (< 10 ha) and shallow (average depth 1.5 m). The vegetation is mainly dominated by *Juncus bulbosus* L., *Molinea caerulea* (L.) Moench and *Sphagnum* spp.

The presence and the average relative abundance of *U. pygmaea* in comparison with other fish species are given in Table III. The presence of *U. pygmaea* in soft waters seems to be independent of the pH. The percentage of water bodies which harbour mudminnow populations is more or less the same for systems of different pH-classes. The average relative abundance of *U. pygmaea*, however, is strongly related to the pH. In circumneutral and alkaline waters (pH ≥ 5) the mudminnows only account for 1.6% of the total number of fish in the catches. In these systems *U. pygmaea* can be accompanied by *Abramis brama* (L.), *Blicca bjoerkna* (L.), *Cyprinus carpio* L., *Esox lucius* L., *Lepomis gibbosus* L., *Perca fluviatilis* L., *Rutilus rutilus* (L.), *Scardinius erythrophthalmus* (L.) and *Tinca tinca*

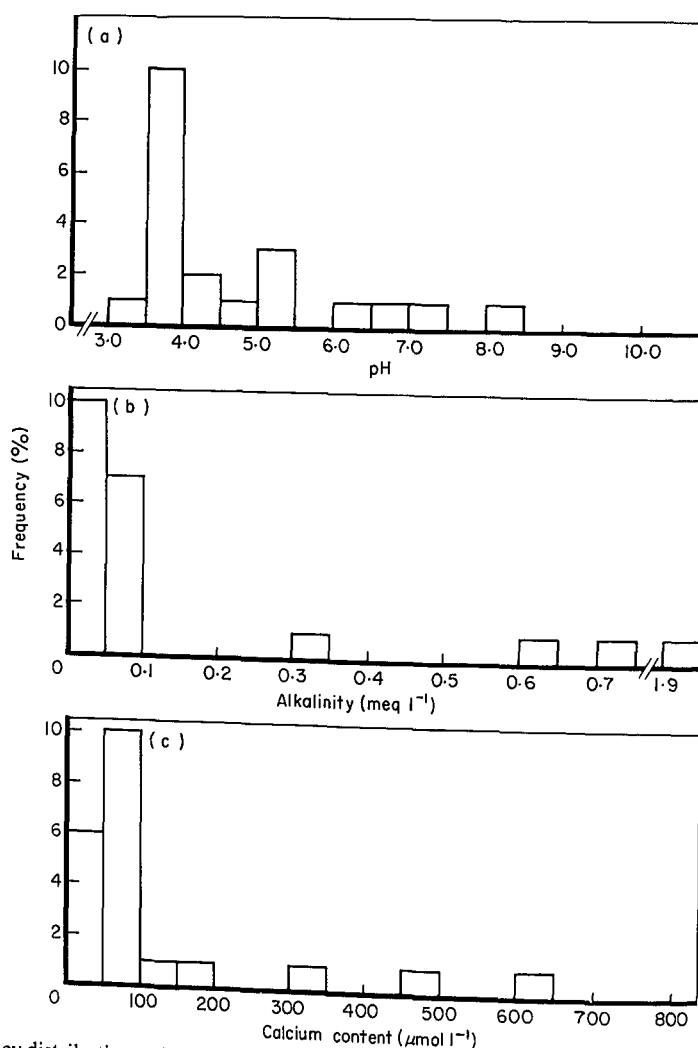


FIG. 2. Frequency distributions of the (a) pH, (b) alkalinity and (c) calcium content of 21 waters harbouring *Umbra pygmaea*.

(L.). The average relative abundance of *U. pygmaea* in extremely acid waters is 100%; in these systems all native fish species are absent.

For 12 waters the relative numbers of mudminnows per system were calculated (Fig. 3). The sampling in each water investigated was more or less similar. More than 90% of the fishes were captured in the extremely acid waters in which the predatory species *Esox lucius* and *Perca fluviatilis* were absent. In waters harbouring these species the relative number of mudminnows was always low. For five waters the minimum standing stock of mudminnows was estimated (Table IV). The total biomass per unit of surface area varied between 0.8 and 21.3 kg ha⁻¹.

FOOD

The composition of the stomach contents of 152 mudminnows is shown in Fig. 4. More than 80% of the ingested macro-invertebrates were Nematocera;

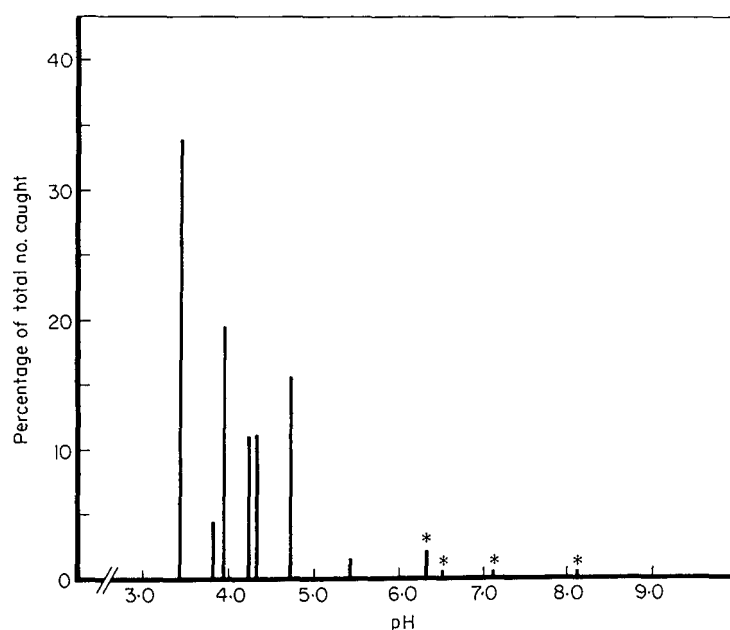


FIG. 3. The relationship between the number of mudminnows as a percentage of the total number ($n = 1019$) caught and the pH of the waters sampled. (* *Perca fluviatilis* and/or *Esox lucius* present.)

TABLE IV. The estimated minimum standing stock of some mudminnow populations

Sites	Coordinates	pH*	Alkalinity* (meq l^{-1})	Minimum standing stock (kg ha^{-1})
Klein Aderven	51°34' 5°13'	4.7	0.065	8.7
Groot Huisven	51°35' 5°16'	4.3	0.018	0.8
Peetersven	51°22' 5°28'	3.9	0	18.2
Kiezelven	51°24' 5°36'	3.8	0	1.4
Gat van Klercks	51°23' 5°55'	3.6	0	21.3

*Average values 1983.

Ephemeroptera and Acarina each represented 5%. Only a small number of Gastropoda, Corixidae and Odonata were recorded (total < 5%). The importance of the Oligochaeta could not be estimated because only remnants of chaetae were found. Figure 5 shows that most of the Nematocera ingested were Chironomidae (49.7%) and Orthoclaadiinae (36.7%), while only low percentages of Tanypodinae (8.6%), Ceratopogonidae (6.0%) and Chaoboridae (1%) were recorded. The zooplankton ingested consisted of about 90% Cladocera, 10% Copepoda and few Ostracoda and Rhizopoda [Fig. 4(b)]. The composition of the diet and the relative importance of several food items varied with age and habitat.

AGE AND GROWTH

The weight-length relationship of the mudminnows in the Groot Huisven is

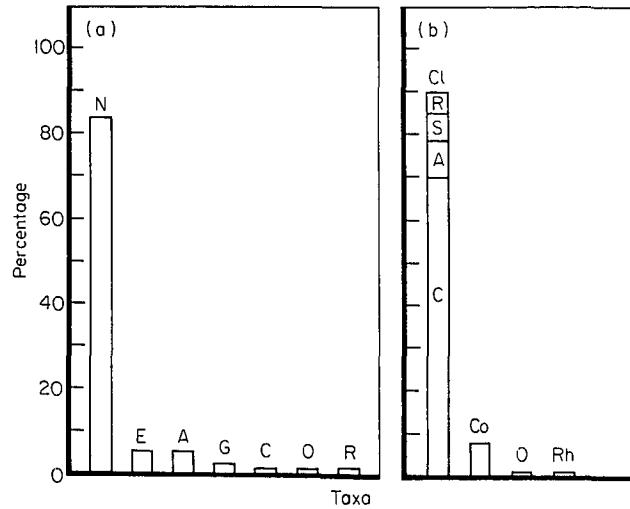


FIG. 4. The relative number of several food items of *Umbra pygmaea*. (a) Macrofauna: Nematocera (N), Ephemeroptera (E), Acarina (A), Gastropoda (G), Corixidae (C), Odonata (O) and Remainder (R). (b) Microfauna: Cladocera (Cl), Copepoda (Co), Ostracoda (O) and Rhizopoda (Rh); the Cladocera are subdivided into *Chydorus sphaericus* (C), *Acantholeberis curvirostris* (A), *Simocephalus vetulus* (S) and the remainder species (R).

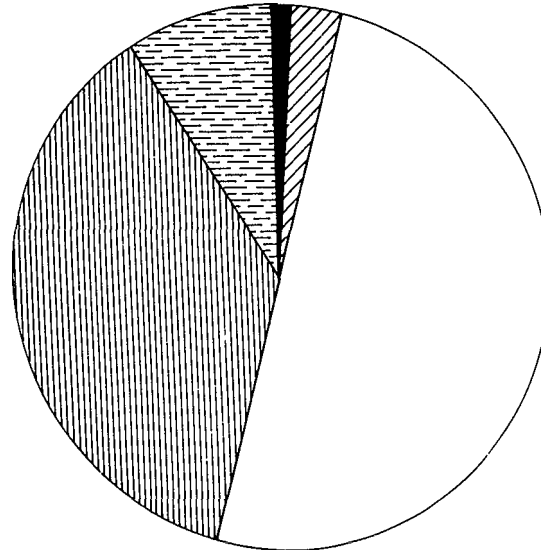


FIG. 5. The relative abundance of Nematocera taxa in the stomachs of *Umbra pygmaea*. ■, *Chaoborus*; ▨, Ceratopogonidae; ▩, Orthocladiinae; □, Chironominae; ▩, Tanypodinae.

given in Fig. 6. Fitting of 547 data pairs to a power function (equation 1) resulted in

$$W = 0.0034 L^{3.55}$$

where W is in g; L in cm, and $r = 0.97$. Because the weight-length relationship for males and females did not differ statistically ($P > 0.51$), no sex discrimination was made in the data presented (Fig. 6).

Figure 7 shows the age-length relationship for *U. pygmaea*. This relationship was significantly different for the two sexes ($P < 0.0001$). For males, females and the total population of fish older than 50 days the parameter estimates of

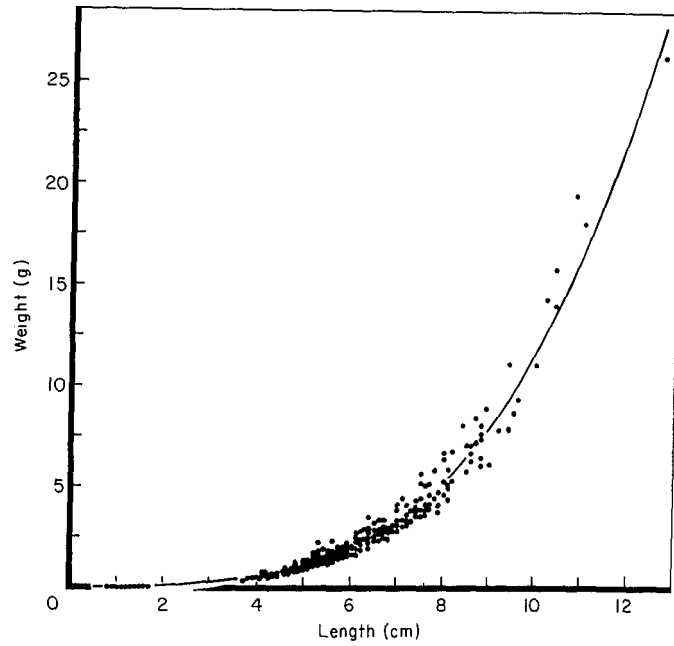


FIG. 6. The length-weight relationship of *Umbra pygmaea* ($n = 547$).

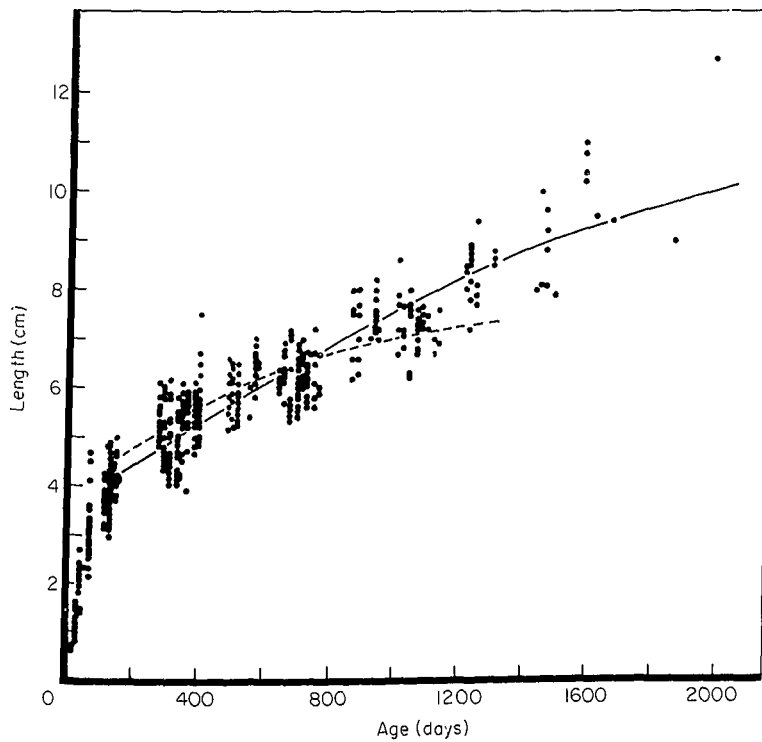
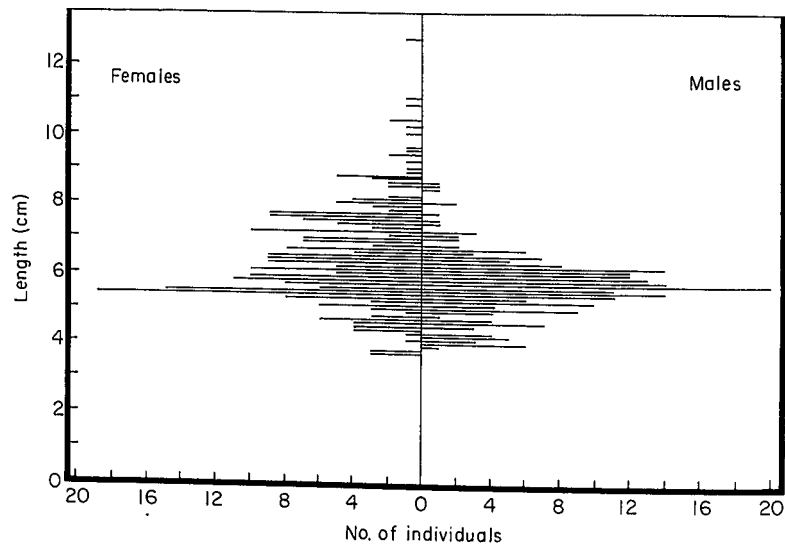


FIG. 7. The age-length relationship of *Umbra pygmaea* ($n = 547$). The curves drawn are calculated according to Von Bertalanffy (1934, 1938) and Brody (1945). — — —, ♂; — — — ♀.

TABLE V. Parameter estimates for the age-length model $L = L_{\infty}(1 - e^{-K(t-t_0)})$ [equation 2] for *Umbra pygmaea*

	n	L_{∞} (cm)	t_0 (year)	K (year ⁻¹)	r
♀	264	15.9 ± 2.3	-1.52 ± 0.23	0.152 ± 0.005	0.88
♂	234	8.2 ± 1.4	-1.12 ± 0.21	0.52 ± 0.04	0.69
Population	498	16.0 ± 2.3	-1.02 ± 0.15	0.178 ± 0.004	0.79

FIG. 8. The length-frequency distribution of male and female *Umbra pygmaea* ($n = 451$).

equation 2 are given in Table V. The predicted ultimate length of females is approximately twice that of males. Also, t_0 and K are different for males and females.

In determining the length-age relationship of fish younger than 50 days, the sexes were not separated because sex determination of young fish is difficult. Putting the 105 age-length data pairs into equation 3 resulted in:

$$L = 0.4089 e^{11.83t}$$

where L is in cm, t in years, and $r = 0.86$.

The growth of *U. pygmaea* is also sex-dependent. Using equation 4, it was calculated that the growth rate of both sexes decreases with age. Initially males grow faster than females; the growth rate for both sexes is similar when they are about 150 days old, after which females grow faster than males of the same age. These differences result in a similar length for males and females at an age of approximately 660 days (Fig. 7). Females older than 660 days are usually longer than males. The predicted ultimate lengths are 15.9 ± 2.3 and 8.2 ± 1.4 cm for females and males respectively (Table V).

The length-frequency distribution of the mudminnows sampled is presented in Fig. 8. The longest female and male were 12.7 and 8.6 cm respectively. The predicted ultimate lengths given in Table V agree with these values. The lengths most frequently measured were 5.7 and 5.4 cm for males and females respectively.

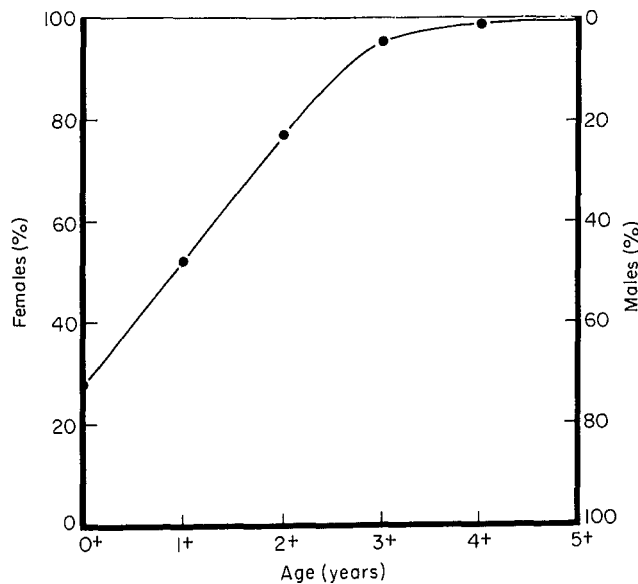


FIG. 9. The sex ratio of *Umbra pygmaea* in relation to age.

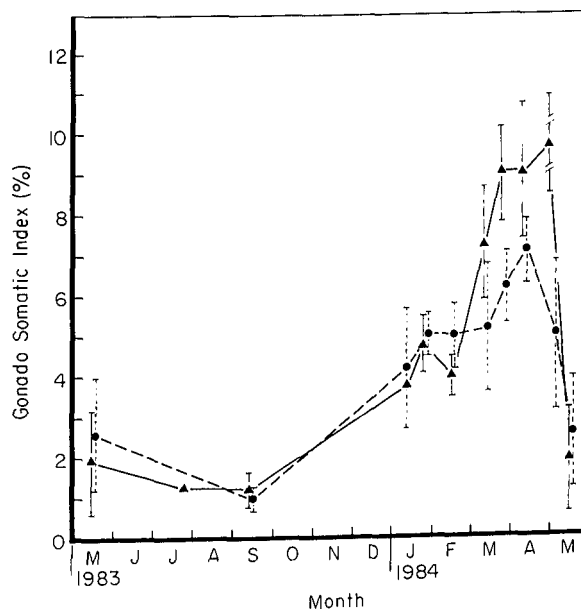


FIG. 10. The average Gonado Somatic Index (GSI), with standard deviations, of *Umbra pygmaea* in the Groot Huisven during 1983 and 1984. The highest GSI for females has a s.d. of 10.5%. \blacktriangle — \blacktriangle , ♀; \bullet — \bullet , ♂.

REPRODUCTION

Of the *U. pygmaea* caught 53% were females. However, the sex ratio depends on the age of the fishes (Fig. 9): within the group of 0+ fish 72% were males, but at age 6 years the percentage of males had decreased to 0%.

Figure 10 shows that gonadal development started between September and January, the highest average GSI was reached in spring, the maximum GSI was 10.5% and 25.4% for males and females respectively, and that spawning occurred

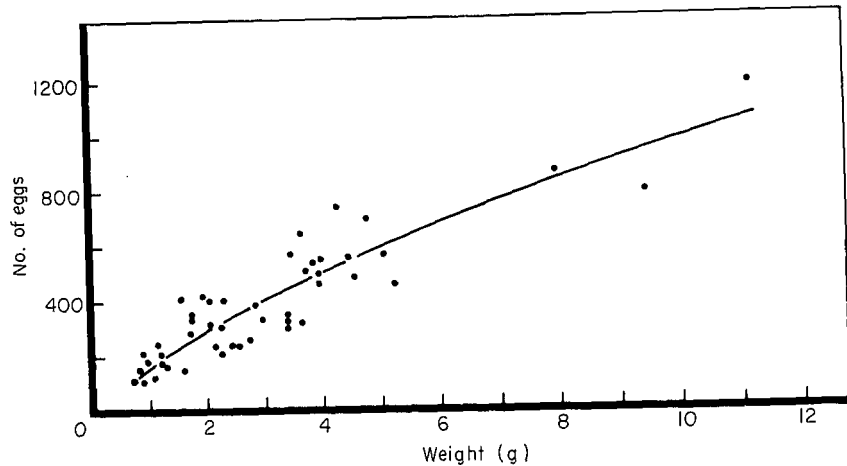


FIG. 11. The fecundity of *Umbra pygmaea* in relation to the body weight ($n=50$).

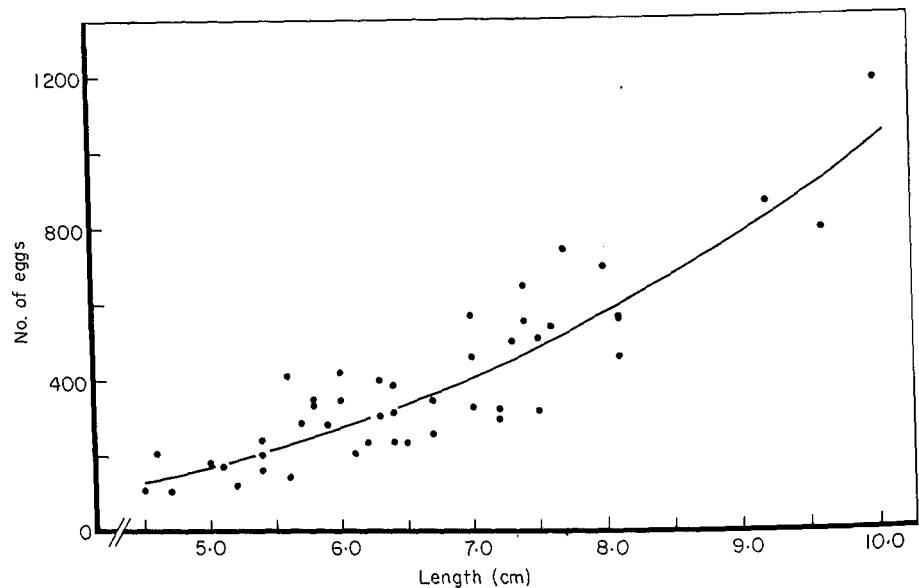


FIG. 12. The fecundity of *Umbra pygmaea* in relation to the length ($n=50$).

from April to May. Gonadal maturation was observed in all fishes older than 1 year, and in 0+ fishes with a length exceeding 4.7 cm. The reproduction of mudminnows seems not to be affected by low pH. The eggs and fry of *U. pygmaea* were observed in waters with a $\text{pH} \geq 3.5$.

The fecundity-weight and fecundity-length relationships are illustrated in Figs 11 & 12 respectively. The fecundity rises with increasing weight and length. The estimates of the fecundity are given by the equations:

$$F = 2.15 W^{5.11} \quad (n=49; r=0.88)$$

$$F = 2.67 L^{2.58} \quad (n=49; r=0.88)$$

where F is fecundity (i.e., number of eggs just before spawning), W weight in g, and L length in cm.

TABLE VI. LC(E) values expressed in pH with 95% confidential limits C.L., for *Umbra pygmaea* incubated in culture media with different calcium contents (*E*, percentage expected mortality)

	$(Ca^{2+}) = 100 \mu mol l^{-1}$		$(Ca^{2+}) = 500 \mu mol l^{-1}$			
	pH	95% C.L.	pH	95% C.L.		
LC01	2.60	1.82	2.73	2.63	2.14	2.70
LC50	2.86	2.73	2.95	2.79	2.75	2.87
LC99	3.12	3.00	3.81	2.95	2.87	3.51

ACID-TOLERANCE AND WATER CALCIUM LEVELS

Compared with the survival after 10 days in media with a calcium content of $100 \mu mol l^{-1}$, the probability of *U. pygmaea* survival was higher in media with a calcium content of $500 \mu mol l^{-1}$ (Fig. 13). Some lethal concentrations (LC) and their 95% confidence limits are presented in Table VI. The average osmolarity of the blood plasma of fish incubated in media with different pH and calcium content varied between 182 and $322 mOsmol l^{-1}$ ($n = 110$) (Fig. 14a) and it is evident that the osmolarity of the blood is approximately $300 mOsmol l^{-1}$ under normal conditions, i.e., $pH > 3$. After exposure of mudminnows to media with a pH of 2.8 or 3, significantly lower osmolarity levels were recorded than in fish exposed to water at $pH > 4$ ($P \leq 0.008$). The plasma osmolarities of fish exposed to media with different calcium contents and a $pH \geq 4$ were of the same magnitude and varied between 261 and $322 mOsmol l^{-1}$. Although in media at pH 3 the osmolarity was reduced by about 15% at both calcium concentrations used, no mortality was observed during the experimental period. However, a decrease of the osmolarities by approximately 25% resulted in a probability of death of < 0.40 and 0.70 in water at pH 2.8 and a calcium content of $500 \mu mol l^{-1}$ and $100 \mu mol l^{-1}$ respectively (Fig. 13).

The haematocrit values of the blood are presented in [Fig. 14(b)]. The haematocrit ranged from 42 to 72% ($n = 110$). The lowest values were recorded in fish exposed to water at pH 5. The levels measured after exposure to pH 3 were significantly higher than those at higher pH levels ($P \leq 0.045$).

IV. DISCUSSION

In The Netherlands, *U. pygmaea* has been observed in waters with low alkalinity, pH and ionic content and relatively high (heavy) metal concentrations and carbon dioxide pressure. In our experimental media with calcium contents of 100 and $500 \mu mol l^{-1}$, after 10 days 50% mortality occurred at pH (pH LC50) 2.86 and 2.79, respectively. Under laboratory conditions the pH LC50 ($[Ca^{2+}] = 140 \mu mol l^{-1}$) for *U. limi* was 3.05 (Rahel & Magnuson, 1983). Thus, *U. pygmaea* seems to be more acid-tolerant than *U. limi*. In naturally acid waters the abundance of most fish species is low (EIFAC, 1969; Tonn & Magnuson, 1982; Rahel & Magnuson, 1983). Recently many authors have described the deleterious impacts of acidifying precipitation on fish populations in poorly buffered waters. Also cultural acidification results in the loss of fish species or even entire fish

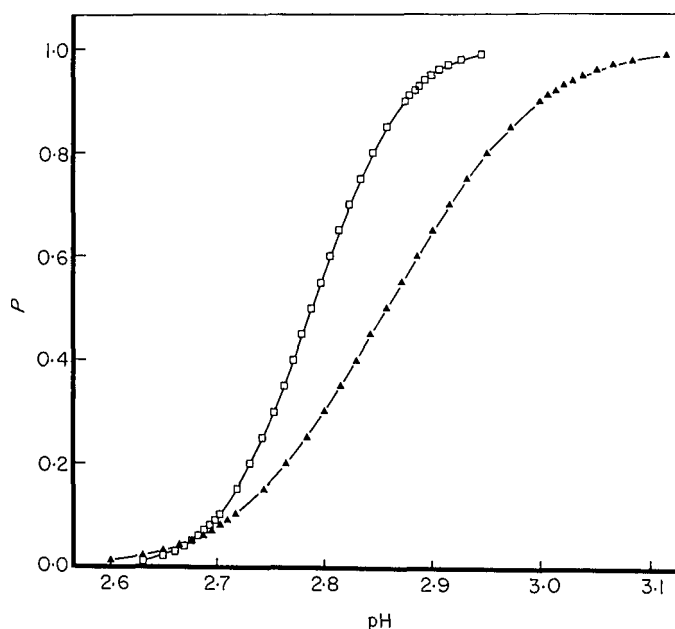


FIG. 13. The probability of survival for 10 days of *Umbra pygmaea* in relation to the pH and calcium concentration of the experimental media. □—□, $Ca^{2+} = 500 \mu\text{mol l}^{-1}$; ▲—▲, $Ca^{2+} = 100 \mu\text{mol l}^{-1}$.

assemblages (Schofield, 1976; Wright & Snekvik, 1978; Drabløs & Tollan, 1980; Harvey *et al.*, 1981; Overrein *et al.*, 1981; Johnson, 1982). Acute exposure to water with a pH between 3.5 and 5.0 is lethal for most fish species. The European Inland Fisheries Advisory Commission (1969) has concluded that it is unlikely for any fish species to survive for more than a few hours in waters with a pH ranging from 3.0 to 3.5. In the present paper, however, it has been pointed out that *U. pygmaea* tolerates this pH range. Rahel & Magnuson (1983) also found the closely related central mudminnow (*U. limi*) to be extremely acid-tolerant. The mechanisms enabling these fish species to live in acid water are not well known. Undoubtedly both umbrid species have evolved special physiological and structural adaptations to acid water. Therefore, a comparison of the biology of acid-sensitive species with that of mudminnows may elucidate some of these mechanisms.

Osmoregulatory stress, impaired gas exchange, reproductive failure, and changes in the predator-prey systems are considered as the main reasons for the decline or disappearance of fish populations in acidifying systems (Fromm, 1980; Overrein *et al.*, 1981; Wood & McDonald, 1982; McDonald, 1983a; Howells *et al.*, 1983). Furthermore, it is evident that not only the pH but also the changes in other environmental factors (alkalinity and ion content, heavy metal concentrations and carbon dioxide pressure) may be involved in the mortality of fish in acid waters (EIFAC, 1969; Fromm, 1980; McDonald, 1983a; Howells *et al.*, 1983).

OSMOREGULATION

Stress under acid circumstances normally results in deterioration of the ionic and acid-base regulation, increased mucus secretion, changes in gill structure and

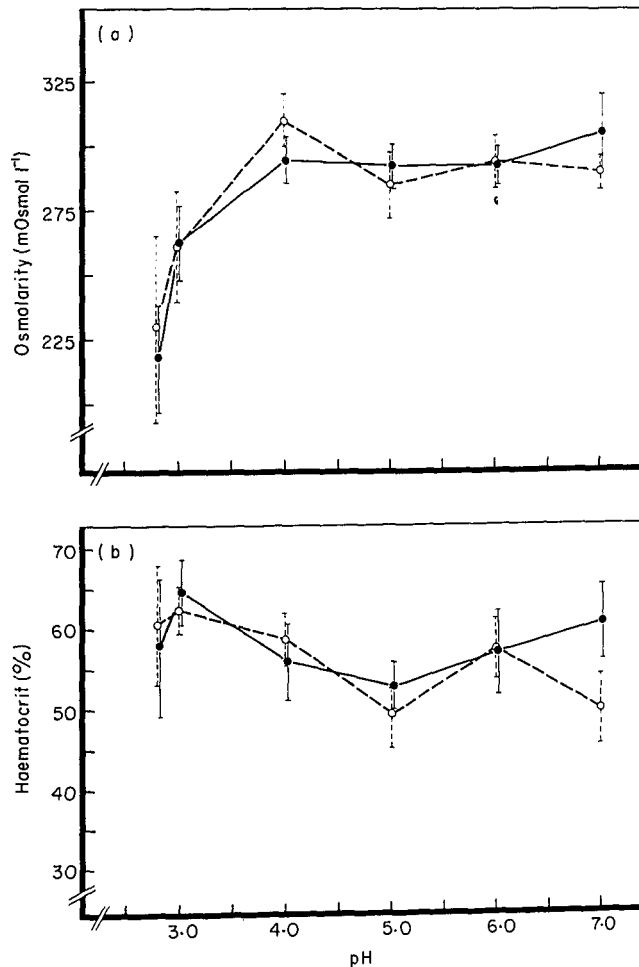


FIG. 14. The osmolarity of the plasma (a) and the haematocrit of the blood (b) of *Umbra pygmaea* after a 10-day incubation in water of various pHs at two calcium concentrations (Mean \pm S.D.; $n=10$).
 ●—●, $\text{Ca}^{2+} = 500 \mu\text{mol l}^{-1}$; ○—○, $\text{Ca}^{2+} = 100 \mu\text{mol l}^{-1}$.

impeded oxygen uptake and transport (Fromm, 1980; Wood & McDonald, 1982; McDonald, 1983a). Our experimental data show that when the pH of the media varies between 7 and 4, plasma osmolarity of *U. pygmaea* is maintained at a relatively constant level. Exposure to pH 3 results in a marked decrease of the osmolarity but not in mortality. Water at pH 2.8 causes severe haemodilution and mortality.

McDonald (1983a) surmised that not only the pH but also the calcium content of the water is of considerable importance. It is well known that calcium in the water improves the survival of freshwater fish in acidified water (Wright & Snekvik, 1978; Leivestad *et al.*, 1980; McDonald *et al.*, 1980; Brown, 1981; McDonald, 1983b). The results of our experiments support these findings also.

Since water and ion balance is under endocrine control, hormones are undoubtedly closely implicated in the process of adaptation to acid water (Wendelaar Bonga *et al.*, 1984a, b). Studies on the role of the endocrine system in the adaptation mechanism of *U. pygmaea* to acid environments are in progress.

GAS EXCHANGE

Acid-intolerant fish often respond to acid exposure by an increased release of mucus from mucous cells in the gill area. A number of authors have suggested that a thick mucous layer upon the gills would impede oxygen transfer and contribute to tissue hypoxia (McDonald, 1983a). Further, an acid discharge in aquatic systems may liberate sufficient carbon dioxide from (bi)carbonate in the water and in the sediment to be either directly toxic or, in the pH-range 5–6, even lethal for fish (EIFAC, 1969).

Acid stress leads to blood acidosis, and thus will interfere with haemoglobin-O₂ transport via the well-known Bohr & Root effect (cf. Packer, 1979). However, mucus accumulation, and increased CO₂ pressures and blood acidosis, do not necessarily impair gas exchange in mudminnows. Investigations by Geyer & Mann (1939) and Safford Black (1945) have shown that the swimbladder of mudminnows acts as a supplementary organ for respiration, enabling air-breathing. Safford Black (1945) pointed out that under respiratory stress *U. limi* draws extensively on the oxygen in its swimbladder. Carbonnier (1874) (cf. Poll, 1949) had already noticed that air-breathing of *U. pygmaea* resulted in a decrease of opercular movement. It still remains to be established whether a decrease in opercular movement reduces the effects of acid media on other gill functions, e.g., ion regulation. Furthermore, mudminnows are sluggish fish, and their low activity will result in a low respiration rate. The haematocrit of the blood of *U. pygmaea* ranged from 42% to 72%. In comparison with other fish species, the upper limit is relatively high. For other air-breathing fishes Johansen (1970) described a maximum haematocrit of 47%. The haematocrit of the blood of *U. pygmaea* tended to increase with decreasing pH. The same phenomenon has been observed for *Salmo gairdneri* Richardson (Wood & McDonald, 1982). Whether the increased haematocrit results in a higher gas exchange capacity is unknown.

REPRODUCTIVE FAILURE

Many fish species show reproductive failure in acid environments. The reproduction process may be negatively affected by reduced spawning (Beamish & Harvey, 1972), decreased functioning of the gametes (EIFAC, 1969), failure of fertilized eggs to develop or hatch (Peterson *et al.*, 1980), and hatching of deformed fry (Runn *et al.*, 1977). In an acid moorland pool (average pH: 4.9) we observed normal development of gonads and the presence of fertilized eggs and fry of *U. pygmaea*; even at pH 3.5 successful reproduction was observed.

PREDATOR-PREY RELATIONS

Acidification of fresh water affects aquatic biota at all trophic levels (Drabløs & Tollan, 1980; Overrein *et al.*, 1981; Johnson, 1982). Key organisms for transferring energy from lower to higher trophic levels may be wiped out by acidification. In acid waters this will negatively affect the population density and growth of fish. According to Paszkowski (1984), *U. limi* is a generalist feeder, capable of using a variety of foraging sites and food items. We have established that Nematocera are the most important food items in the diet of *U. pygmaea*. The same has been described for *U. limi* (Maw, 1968). Many Nematocera species are acid-tolerant and there is no evidence that the biomass of Nematocera is reduced in acidified

waters (Leuven *et al.*, 1986). Therefore, it is unlikely that in acid waters the abundance and productivity of mudminnows is limited by their food supply.

Rahel (1984) reported that *U. limi* coexists with centrarchids, cyprinids and fish predatory species like *Perca flavescens* Mitchell: it appeared to coexist by selecting a different microhabitat from that of its potential predators. Clady (1974) found only one *U. limi* in the stomachs of 400 smallmouth bass, *Micropterus dolomieu* Lacépède, in a Michigan bog lake, although the mudminnows were abundant in the shallow parts of the lake. Contrastingly, our data indicate that the abundance of *U. pygmaea* may be influenced by the presence of the fish predatory species *Perca fluviatilis* and *Esox lucius* (Fig. 3). However, in some low alkalinity waters that did not harbour fish predators the abundance of mudminnows was also low. In addition to predation, other factors, e.g. complete freezing or dessication of the pool, may be important for the abundance of *U. pygmaea*.

Arnholz & Ahl (1936) (cf. Geyer, 1940) noticed that for a population of *U. krameri* Walbaum the ratio between females and males was 1.5. For *U. pygmaea* the sex ratio was also in favour of the females (1.1) and highly dependent on the age of the fish. Vitali & Braghieri (1984) described the same phenomenon for *Barbus barbus plebejus* (Valenciennes) and *Leuciscus cephalus cabeda* (Risso). The populations of these fishes also showed a preponderance of females, especially at old age.

Mudminnows have so far been economically unimportant. Maw (1968) and Slavin *et al.* (1977) noted that mudminnows may be possible agents for mosquito control in semi-permanent pools. Much attention has been given to the osteology and the phylogenetical relationships of Umbridae (Cavender, 1969; Sytcevskaia, 1976; Obrhelova, 1978; Wilson & Veillieux, 1982). Kligerman *et al.* (1975, 1984) used *U. pygmaea* for mutagens tests. In the present study it has been shown that mudminnows are extraordinarily acid-tolerant, so they may be useful as an experimental model for the study of the physiological adaptation of fish to acid water.

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