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Effects of the 2022 Oder River environmental disaster on fish gill structure

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ABSTRACT: The 2022 Oder River disaster was one of the most significant harmful events in recent European river history, with an estimated 60% reduction in fish biomass in the lower section of the river. While the prevailing hypothesis attributes associated fish kills to toxins from golden algae *Prymnesium parvum*, our histopathological study on the gills of 2 common cyprinid fish species, namely vimba bream *Vimba vimba* (L.) and roach *Rutilus rutilus* (L.), collected from the lower Oder River at 3, 4, and 6 mo after the disaster, suggests another mechanism. Vimba bream showed damage to the epithelial layer of lamellae and increased mucus production. Roach exhibited interlamellar cell mass (ILCM), lamellar damage, including hypertrophy of epithelial cells, lamellar fusion, as well as significant thickening of the water—blood barrier compared to controls. These findings suggest that adverse factors, most likely the increase in toxin concentrations resulting from reduced water levels together with elevated temperatures and low precipitation, triggered the formation of ILCM, increasing the susceptibility of fish to hypoxia. Fish species with a capacity for adaptive interlamellar hyperplasia, such as common bream *Abramis brama*, roach, and common perch *Perca fluviatilis*, accounted for the largest number of deaths during the disaster. Vimba bream, which showed no ILCM, were observed only sporadically, with mortality confined to a single area of the Oder. In conclusion, fish capable of adaptive hyperplasia, whereby the gills attempt to protect themselves by developing ILCM, appear to be particularly vulnerable in conditions of aquatic hypoxia.

KEY WORDS: Oder River disaster · Hypoxia · Adaptive hyperplasia · Gill lesions · Vimba bream · *Vimba vimba* · Roach · *Rutilus rutilus*

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1. INTRODUCTION

The 2022 Oder River catastrophe stands out as one of the most devastating ecological disasters in recent European river history. From the end of July to the beginning of September 2022, in 5 Polish provinces (Silesia, Opolskie, Lower Silesia, Lubuskie, and West Pomerania), a high level of incidental disease and mortality was observed in various fish species in the Oder River. The disaster affected mainly fish species that prefer cold water habitats (IOŚ-PIB 2023). The observed fish deaths were not a continuous phenomenon; they occurred with varying intensity in different sections of the Oder River and its associated reservoirs over different time intervals. Interestingly, during this sensitive period, some river sections showed no dead fish (IOŚ-PIB 2023).

The percentages of dead fish observed in individual provinces were as follows (downstream): Silesia and Opolskie (Gliwicki Canal), 3%; Lower Silesia, 10.5%; Lubuskie, 18.6%; and West Pomerania, 67.9% (IOŚ-PIB 2023). In the lower section of the river, fish biomass decreased by an estimated 60% (Szlauer-Łukaszewska et al. 2024). The highest quantity of

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dead fish in the West Pomeranian province was observed during the periods of 13–17 and 19–25 August 2022. At the same time, the concentration of pollutants measured in fish samples examined did not deviate from the levels characteristic of environmental pollution in rivers in Poland (IOŚ-PIB 2023). However, in the year 2022, high water temperature (>24°C), high ammonium concentration (>4 mg l^{-1}), and relatively low nitrate concentration (<6.5 mg l^{-1}) were observed in the middle Oder (Sługocki & Czerniawski 2023). In addition, the salinity of the river was very high (maximum 1.4 g l^{-1}) and oxygen concentration was exceptionally low, with a minimum of 0.26 mg l^{-1} dissolved oxygen in surface waters in the lower Oder on 22 August 2022 (Sługocki & Czerniawski 2023).

The official reports emphasize that the disaster was associated with significantly increased conductivity, increased water temperature, and elevated chloride and sulfate content, but also high solar radiation (EPA 2023, IOŚ-PIB 2023). A role was also attributed to major variations in water parameters in the Oder River (Kucharski et al. 2022, Absalon et al. 2023, Sobieraj & Metelski 2023). According to the official report, at the time of low oxygen concentration, fish died suddenly without showing any signs of being affected. It has been suggested that this may have been influenced by changes in the gills that caused a disruption in gas exchange with subsequent hypoxia. Fish deaths occurred abruptly during periods of aquatic hypoxia (IOŚ-PIB 2023).

The prevailing hypothesis suggested that the catastrophic event may have been directly triggered by harmful toxins, namely prymnesins, emitted by golden algae *Prymnesium parvum* (Schulte et al. 2022, Absalon et al. 2023, EPA 2023, Free et al. 2023, IOŚ-PIB 2023, MacErlean 2023, Sobieraj & Metelski 2023, Szlauer-Łukaszewska et al. 2024).

The main organs of fish used in histopathological examinations are the gills, liver, and kidneys, depending on the goal of analyses. Fish gills are multifunctional organs that constitute the primary site for respiratory gas exchange, ion regulation, acid–base balance, and nitrogenous waste excretion in most fishes and are in constant contact with the environment (De Jager & Dekkers 1975, De Jager et al. 1977, Hughes 1984a,b, 1990, Wolf et al. 2015, Gilmour & Perry 2018, Fernandes 2019, Wegner & Farrell 2024). The gills are comprised of lamellae, thin plate-like structures containing blood capillaries covered with a delicate water–blood barrier (epithelial layer). As such, gills are often the first organs to exhibit adverse effects from environmental stressors. At the same time, recent research has demonstrated the adaptability of gills and their capacity to adjust to changing environmental conditions (Nilsson 2007, Wolf et al. 2015, Gilmour & Perry 2018, Fernandes 2019, Wegner & Farrell 2024). However, histopathological studies on gills are relatively rare, as they demand extensive expertise, both in specimen preparation (Hughes 1984a,b, 1990) and in the accurate interpretation of findings (De Jager & Dekkers 1975, De Jager et al. 1977, Jakubowski 1992, Satora & Jakubowski 1995, Satora & Romek 2010, Satora & Wegner 2012).

This preliminary study aimed to investigate the histomorphology of gills of 2 common cyprinid fish species, vimba bream *Vimba vimba* (L.) and roach *Rutilus rutilus* (L.), that survived the 2022 Oder disaster. In this way, we compared a species (roach) that saw higher mortality rates and has the ability for gill remodeling (interlamellar hyperplasia) to protect the gill (Kiejkowski 2016) with a species (vimba bream) that experienced lower mortality rates and is not known to use interlamellar hyperplasia. The fish were obtained within a period of 3 to 6 mo after the catastrophe from a lower section of the Oder River in West Pomerania, from 3 closely located sites near the city of Szczecin. Several dead individuals were still observed floating on the water at the 3 sampling time points (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/d161p029_supp.pdf).

2. MATERIALS AND METHODS

The research material was collected within a period of 3 to 6 mo after the catastrophe (the highest fish mortality in West Pomerania was observed on 13–17 and 19–25 August 2022). Live fish were collected at 3 time points (16 November 2022, 12 December 2022, and 25 February 2023), at 3 sites, respectively: Stepnica, Regalica, and Dąbie (Fig. S1) in West Pomerania (lower Oder River) by the Regalica Fishermen's Cooperative (contract of 2019-04-10 with the Director of the Regional Water Management Board in Szczecin of the State Water Holding Company) as part of the standard monitoring of the Oder River. Water parameters were measured during fish harvesting as part of standard river monitoring (Table 1). Electrolytic conductivity and pH were measured with a CPC-461 multi-parameter meter, and oxygen and temperature were measured with a Hach HQ 1130 series meter equipped with a probe for measuring dissolved oxygen in water.

A total of 42 fish were used in the study (21 roach and 21 vimba bream), with 7 individuals of each species sampled at each time point. Immediately after collec-

Table 1. Values of the water parameters during fish sampling

Site	Date	Oxygen (mg l^{-1})	Temperature (°C)	pH	Conductivity (µS cm^{-1})
Stepnica	16 Nov 2022	11.6	6.1	7.99	1492.3
Regalica	12 Dec 2022	10.6	5.8	7.96	1392.3
Dąbie	25 Feb 2023	13.6	4.8	7.67	963.0

tion, the fish were euthanized with an overdose of buffered MS 222 (pH 8.0, ethyl 3-aminobenzoate methanesulfonic acid, 1 g l^{-1}; Acros Organics) (Sinha et al. 2014). All gill arches were removed from each fish under a stereomicroscope (Carl Zeiss Discovery V12) in phosphate-buffered saline; the second gill arch from the right side was taken and placed in 4% formaldehyde in phosphate buffer (pH 7.4) for 12 h. For further research, 3 individuals from each species at each of the 3 time points (roach, n = 9, total length = 32–35 cm, 508–636 g; vimba bream, n = 9, 26–37 cm, 314–898 g) were used for histological examination of the gill. The tissues were then dehydrated in ethanol, treated with xylene, embedded in paraplast wax, and serially cross-sectioned using a rotary microtome (HM 310). Dewaxed sections (2–5 µm) were processed with Mayer's H&E Y (Diapath), Alcian blue, and periodic acid-Schiff (PAS). Sections were then dehydrated through a graded ethanol series and mounted in distyrene plasticizer and xylene (DPX) medium under coverslips. Photographs were taken using a Nikon 2000 SE light microscope with a Zeiss camera and NIS-Elements Br software.

Measurements of the water–blood barrier were conducted using the same microscope–computer setup. Morphometric analysis was performed on selected slides cut at the appropriate angle to eliminate errors associated with improper sectioning. Measurements were taken on specimens where all elements forming the barrier were visible. The results of water–blood barrier measurements in roach gills were compared with the results of Kiejkowski (2016) (control). Gill preparations of roach selected for comparison of the water–blood barrier (control) originated from individuals obtained from fish ponds in Podkarpacie during the spring season (water oxygen saturation 90%). Gills of the control specimens were approximately 50% covered by interlamellar cell mass (ILCM) (see Fig. 2f) (Kiejkowski 2016). A total of 63 measurements of the water–blood barrier were conducted on 7 roach individuals (present study), and 63 measurements were performed on preparations from 7 control individuals (Kiejkowski 2016). The results of the water–blood barrier measurements were compared using a 2-sample *t*-test with unequal variance. In the case of vimba bream, 57 measurements of the water–blood barrier were conducted on 6 individuals.

For scanning electron microscopy (SEM), gill filaments from the second gill arches of 4 specimens (2 roach and 2 vimba bream) were dehydrated in ascending concentrations of ethanol from 30 to 100%. Samples used for SEM studies were critical-point dried, mounted on stubs, sputter-coated with gold, and examined with a Quanta-200 MK2 scanning electron microscope at an accelerating voltage of 15 kV.

3. RESULTS

The results of measurements of oxygen, temperature, pH, and electrolytic conductivity taken during the harvesting of the fish are shown in Table 1.

3.1. Histomorphology

3.1.1. Vimba bream

The essential internal structure of the lamellae was preserved (Fig. 1b–e), with only a few pillar cell bodies observed to be displaced in relation to the lamellar blood sinus (Fig. 1a). Clavate lamellae (lamellar aneurism) (Fig. 1d), vascular congestion (Fig. 1c), exfoliation of epithelial cells, and conglomerates of dead epithelial cells (Fig. 1d) were observed. Epithelial lifting, involving the detachment of the single layer of epithelium from the supporting cells, was observed within the lamellae (Fig. 1e). Characteristic damage of the surface of the epithelial cells, resembling epithelial cell rupture, was visible (Fig. 1a,e). Occasionally, there was a small amount of ILCM at the base of the lamellae (Fig. 1e). Mucous cells were located at the base and on the distal parts of the lamellae (Fig. 1b,c), and some small patches of mucus were visible on the gills (Fig. 1b,c). The mean (±SD) thickness of the water–blood barrier measured in the lamellae of vimba bream (n lamellae = 58) was 3.71 ± 1.20 µm.

3.1.2. Roach

There were no differences in the gill structure of fish from different sampling timepoints and between fish from the same sampling timepoint. In all roach specimens, the spaces between lamellae were filled

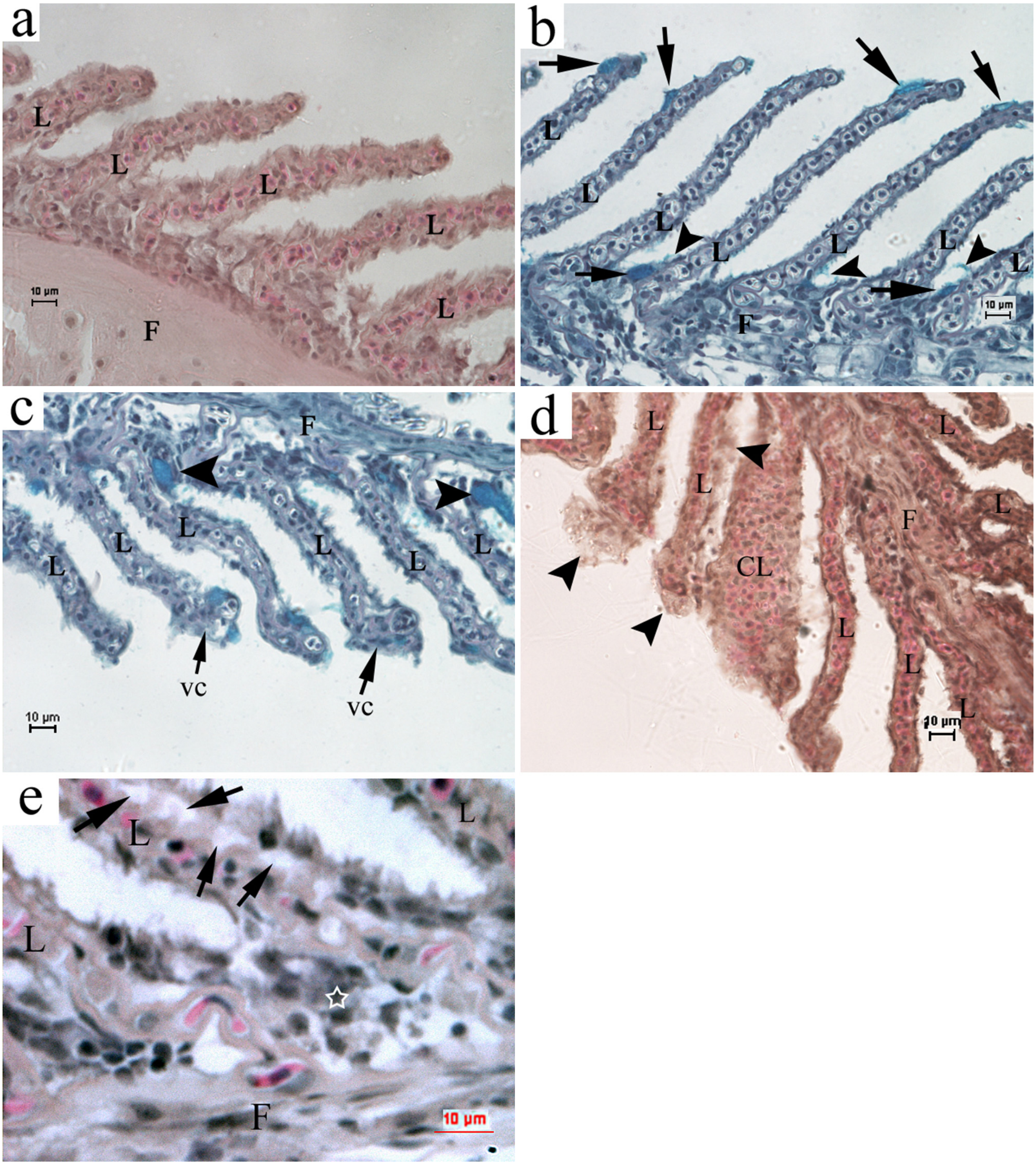

Fig. 1. Light microscopy of vimba bream *Vimba vimba* samples. (a,b) Sagittal section of the gill filament (F) and lamellae (L) of a bream from the field site Stepnica (lower Oder) 3 mo after the Oder River disaster. (a) Disrupted internal structure of lamellae is visible: pillar cell bodies are displaced in relation to the lamellar blood sinus with erythrocytes, and damage to pavement cells is visible. H&E staining. (b) Mucous cells (arrows) are visible at the base and on the distal parts of the lamellae, and patches of mucus (arrowheads) flow over the lamellae. The typical structure of pillar cell bodies and lamellar blood sinus is visible. Alcian blue staining. (c,d) Sagittal section of the gill filament (F) and lamellae (L) of a bream from Regalica (lower Oder) 4 mo after the disaster. (c) Vascular congestion (VC) in peripheral blood vessels and mucous cells (arrowheads), as well as changes to pavement cells resulting in epithelial lifting. Alcian blue staining. (d) A single clavate lamella (CL). Conglomerates of dead epithelial cells in the process of exfoliation (arrowheads) are visible. H&E staining. (e) High magnification of sagittal section of the gill filament (F) and lamellae (L) of a bream from Dąbie (lower Oder) 6 mo after the disaster. Visible epithelial lifting (arrows) and damage to the epithelium. A small number of interlamellar cells between adjacent lamellae is visible (white star). H&E staining

with ILCM, reaching a maximum of half the height of the lamellae (Fig. 2a–e). Mucous cells were present in large numbers at the end of the ILCM in the interlamellar spaces (Fig. 2a–e). There were numerous lamellar fusions within the protruding lamellae (Fig. 2a). Ionocytes were located on lamellae (Fig. 2c). The epithelial cells remained attached to the basal lamina (Fig. 2b,e). There was severe hypertrophy of epithelial cells and epithelial thickening/hypertrophy in the protruding parts of lamellae (Fig. 2b,e).

A comparison of the gills from control fish (Kiejkowski 2016) and fish from the present study revealed some differences. These pertained to the structure of epithelial cells, the thickness of the water–blood barrier, and the amount of ILCM. In control fish, the protruding parts of lamellae were covered by a single layer of flat pavement cells (Fig. 2f); in the present study, hypertrophy of epithelial cells was observed (Fig. 2b,e).

Thickness of the water–blood barrier in lamellae (control vs. present data) showed statistically significant differences between the averages, which was 1.052 µm for fish obtained during the spring (March) from fish ponds in Podkarpacie (Kiejkowski 2016) and 2.095 µm for fish from the Oder (present data), (Student's t-test: 2-sample assuming unequal variances, df = 86, $t = 9.239$, $p < 0.0001$). Simultaneously, the gills and the amount of ILCM covering the gills in fish obtained from ponds differed from those observed in the present study. In roach from Podkarpacie, single mucous cells were observed, whereas ILCM extended to about 1/3 of the length of the lamellae (Fig. 2f). In our study, an increase in mucous cells was observed, and the ILCM extension reached approximately half the length of the lamellae (Fig. 2a,d).

3.3. SEM

3.3.1. Vimba bream

Observations of the surface of the lamellae of vimba bream conducted using SEM revealed numerous strong distortions of the epithelium covering the lamellae (Fig. 3). It was not possible to distinguish boundaries between individual pavement cells (Fig. 3). Additionally, the pavement cells exhibited uneven surfaces (Fig. 3).

3.3.2. Roach

On the surface of the protruding portions of roach lamellae, pavement cells with clearly defined boundaries between them were visible (Fig. 4a,b). The layered arrangement of pavement cells was observed in some preparations (Fig. 4a). Furthermore, the surface of the epithelial cells covering the protruding lamellae was undulated (Fig. 4a,b), and pavement cells formed numerous protrusions (Fig. 4a,b). In 2 individuals sampled 4 mo after the disaster at the Regalica field site, individual *Trichodinella* sp. parasites were observed on the free ends of the gill lamellae (Fig. 4c).

4. DISCUSSION

Observations in this study revealed different pathological lesions in the gills of vimba bream and roach. Despite the differences in the type of damage, the lesions in both species would likely limit the normal function of the gill. In vimba bream specimens, mucus hypersecretion and changes in the lamellae due to disruption of internal blood flow and deformation of the epithelium (Figs. 1 & 3) may reduce the efficiency of the countercurrent exchange system. The observed pathologies were present in all individuals of vimba bream collected from 3 time points.

Vimba bream sampled at the same time and the same site show individual variation in the degree of pathological lesions. Fish exhibiting both severe (Fig. 1a,d,e) and mild gill lesions (Fig. 1b) were observed, suggesting inter-individual variation in pathological responses. Reports indicate that during the Oder disaster, there were areas where fish mortality was not observed, and the fish showed no signs of deteriorated health or condition (IOŚ-PIB 2023).

Some fish during the disaster were found to host gill parasites, including *Capriniana pixium*, *Trichodinella* sp., and monogeneans of the genus *Diplozoon*; however, parasites were not present in invasive quantities (IOŚ-PIB 2023). A few dead individuals observed during material collection for this study were not examined, but their mortality may have been caused by parasites. Weakened fish, whose gill regeneration processes were disrupted by pollutants (Table 1), may have been more susceptible to parasite infestations, potentially resulting in mortality.

Moreover, the regenerative potential of fish gills could have been impaired by pollution, as electrolytic conductivity levels (Table 1) consistently exceeded the permissible threshold (850 $\mu S\ cm^{-1}$) (IOŚ-PIB 2023). At 3 and 4 mo after the disaster, the electrolytic conductivity values (Table 1) remained comparable to those recorded during the disaster (IOŚ-PIB 2023).

Planned comparative studies on *Vimba vimba* from individuals in non-stressful conditions are expected

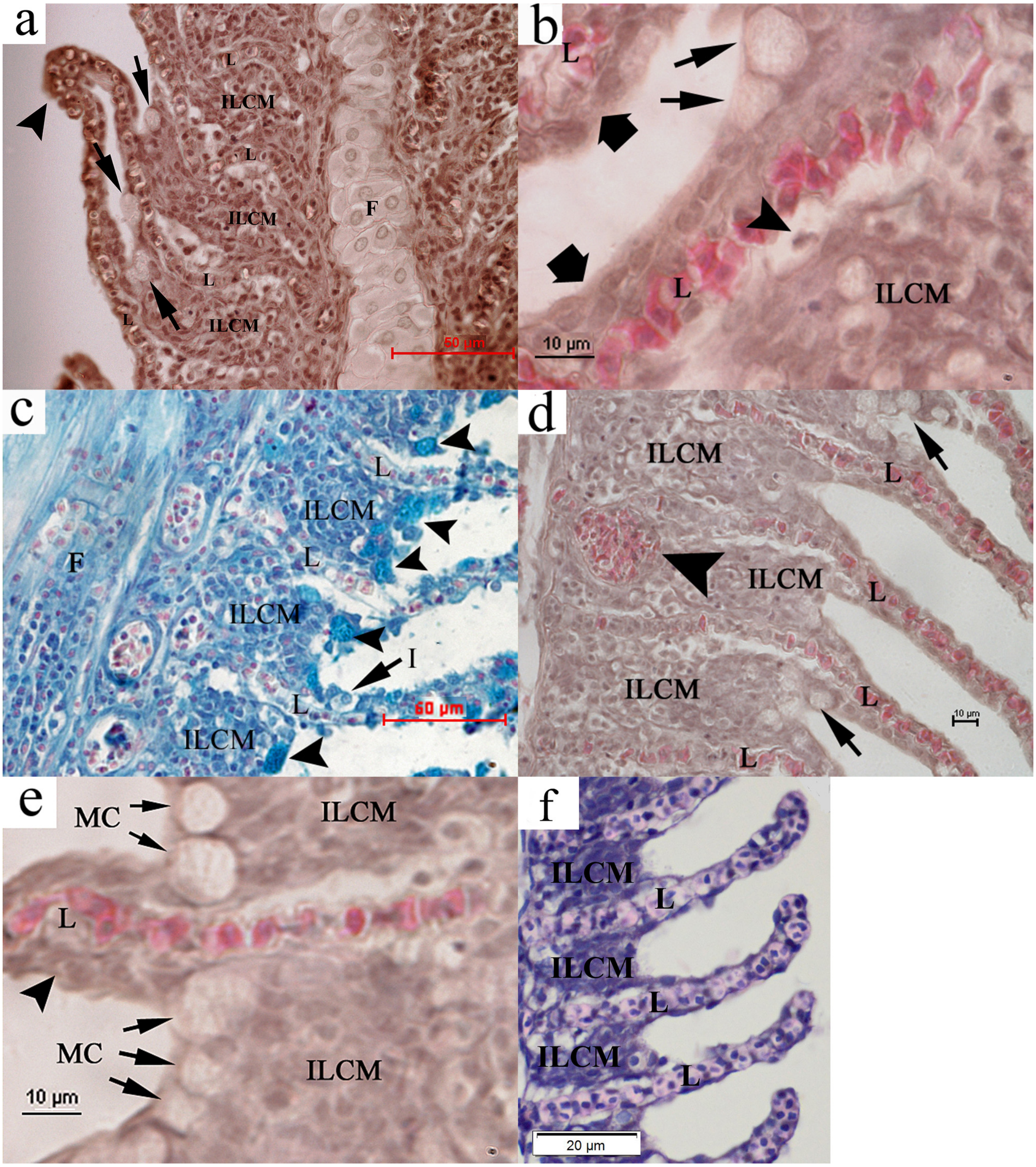

Fig. 2. Light microscopy of roach *Rutilus rutilus* samples. (a,b) Sagittal section of the gill filament (F) and lamellae (L) of a roach from Stepnica (lower Oder) 3 mo after the disaster. (a) Interlamellar cell mass (ILCM) filling the interlamellar spaces, reaching halfway up the lamellae. Fusion of protruding lamellae, and mucous cells (arrows) are visible. H&E staining. (b) High magnification of lamellae (L). Mucous cells (arrows), with visible necrotic nucleus (arrowhead) in the ILCM, and epithelial thickening (fat arrows). H&E staining. (c,d) Sagittal section of the gill filament (F) and lamellae (L) of a roach from Regalica (lower Oder) 4 mo after the disaster. (c) ILCM filling the spaces between adjacent lamellae (L). Numerous mucous cells (arrowheads) and a single ionocyte (I) are visible. PAS staining. (d) ILCM filling the interlamellar spaces, reaching halfway up the lamellae. Numerous mucous cells are visible (arrows), along with a single lamellar telangiectasis (arrowhead). Pavement cells appear hypertrophic. H&E staining. (e) Sagittal section of a gill lamella (L) of a roach from Dąbie (lower Oder) 6 mo after the disaster. High magnification of the lamella, showing epithelial thickening (arrowheads), ILCM, and numerous mucous cells (MC). H&E staining. (f) Sagittal section of lamellae of *R. rutilus* from fish ponds in Podkarpacie during the springtime (March). ILCM extends to about 1/3 of the length of the lamella. Note that the protruding parts of lamellae are covered with a single layer of flat pavement cells. H&E staining (from Kiejkowski 2016)

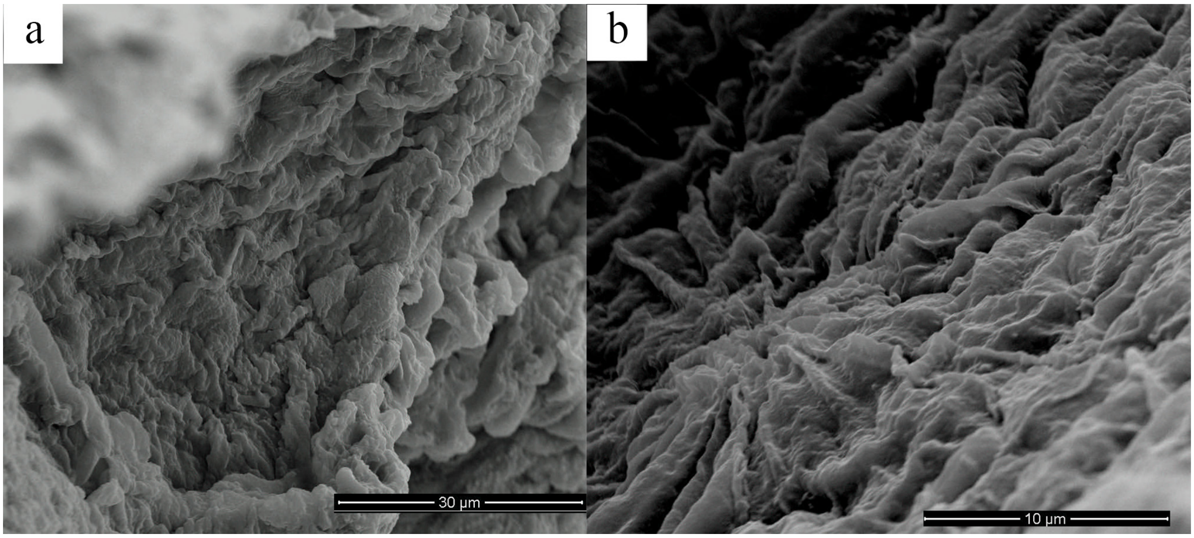

Fig. 3. Scanning electron micrographs of the gill lamellae epithelium of a vimba bream *Vimba vimba* sampled at Stepnica 3 mo after the disaster. (a) Strongly distorted surface of the lamella. The typical arrangement of pavement cells cannot be distinguished. (b) Blurred boundaries between individual epithelial cells and their distortions, elevations, and folding. Note: regardless of the location and date of sampling, all vimba bream individuals exhibited a similar spectrum of gill damage, ranging from mild to severe, which may indicate inter-individual variability

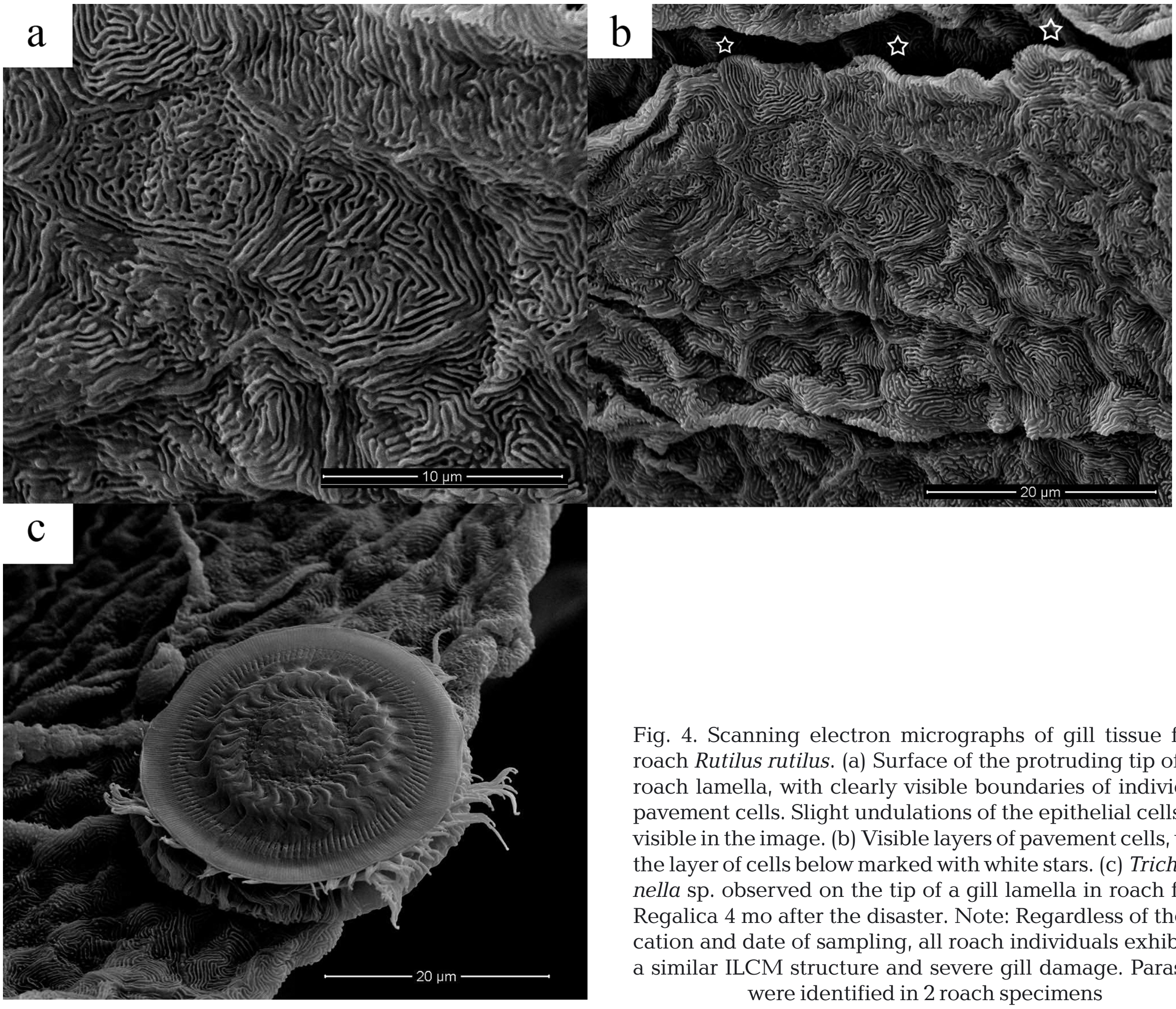

Fig. 4. Scanning electron micrographs of gill tissue from roach *Rutilus rutilus*. (a) Surface of the protruding tip of the roach lamella, with clearly visible boundaries of individual pavement cells. Slight undulations of the epithelial cells are visible in the image. (b) Visible layers of pavement cells, with the layer of cells below marked with white stars. (c) *Trichodinella* sp. observed on the tip of a gill lamella in roach from Regalica 4 mo after the disaster. Note: Regardless of the location and date of sampling, all roach individuals exhibited a similar ILCM structure and severe gill damage. Parasites were identified in 2 roach specimens

to provide crucial insights into the 2022 Oder disaster, particularly regarding the mechanisms of gill protection in fish lacking the capacity for adaptive interlamellar hyperplasia.

In roach, a mass of interlamellar cells, covering about half of the lamellar length, along with an abundance of mucous cells involved in mucus production, significantly reduced the surface area of the gills (Fig. 2a–e). Gas exchange would also potentially be impeded by numerous lamellar fusions and epithelial thickening/hypertrophy (Fig. 2a,b,d,e) by increasing the thickness of the water–blood barrier.

When compared to roach from fish ponds in Podkarpacie (southeastern Poland) (Kiejkowski 2016), the water–blood barrier in roach from the Oder was statistically significantly thicker. While in roach from control sites, the gill lamellae were covered by a single layer of flat pavement cells on the protruding part of the lamellae (Fig. 2f), we observed differences in the structure of epithelial cells expressed by hypertrophy in the gills of the Oder fish (Fig. 2b,d). Additionally, numerous mucous cells and a substantial amount of mucus were identified in the present study (Fig. 2b,c,e).

Furthermore, the ILCM in roach from the Oder extended to approximately half the height of the lamellae, with single necrotic nuclei visible in the interlamellar cells (Fig. 2b). In contrast, in roach from Podkarpacie, the ILCM extended to about one-third of the height of the lamellae, and no necrotic nuclei were observed within its structure (Fig. 2f).

Unlike the roach from the Oder, the roach from Podkarpacie exhibited a typical gill lamella structure, with pillar cell bodies and lamellar blood sinuses without any pathologies, ensuring efficient gas exchange in the protruding part of the lamellae (Fig. 2f) (Kiejkowski 2016).

In our study, similar to vimba bream, the roach displayed no signs of healing at any of the 3 time points studied (which is uncharacteristic in cases of contamination by gold algae toxins) (IOŚ-PIB 2023). The gill lesions in roach significantly reduced the surface area available for gas exchange. Fish rely on maintaining an optimal gill surface area and diffusion distance for oxygen uptake, along with efficient water flow through the interlamellar channels and proper blood flow within the lamellae to sustain a sufficient diffusion gradient (Ojha & Hughes 2001, Gilmour & Perry 2018, Wegner & Farrell 2024). The observed alterations in roach gills significantly impair these basic functions, posing a heightened risk in sudden hypoxic conditions.

The thickening of the water–blood barrier in the lamellae reduces the efficiency of oxygen extraction from the ventilatory stream (Wegner & Farrell 2024), while lamellar fusion also significantly reduces oxygen extraction. The mucus covering the gas exchange surface further exacerbates this issue by creating an additional water–blood barrier (Mallatt 1985). Moreover, separation of the epithelial layer from supporting cells, through the distortion of the lamellar epithelium, disrupts water flow across the gills (Ojha & Hughes 2001), and vascular congestion, along with clavate lamellae, disturbs proper blood flow within the lamellae and thus oxygen uptake.

In a comprehensive analysis and classification of damage to the gills of fish caused by various factors, epithelial necrosis, rupture, and mucus secretion are considered the greatest threat to fish life — these changes are believed to reflect the 'direct deleterious effect' of irritants (Mallatt 1985). Heavy metals, organic toxicants, and other irritants induce similar overall frequencies of lesions, although gill epithelial necrosis is more commonly associated with heavy metals than with organic toxicants or other irritants (Mallatt 1985). On the other hand, hypersecretion of mucus by branchial mucous cells and hypertrophy of branchial epithelial cells are also most frequently associated with heavy metals. Heavy metals are least frequently associated with clavate lamellae (Morgan & Tovell 1973, Mallatt 1985).

According to the official report on the 2022 Oder disaster, the fish in the river died suddenly. It has been suggested that this may have been influenced by changes in the gills resulting in disrupted gas exchange with subsequent hypoxia (IOŚ-PIB 2023). It has also been suggested that pathomorphological changes in the gills may have been a consequence of toxins produced by golden algae (Schulte et al. 2022, Absalon et al. 2023, EPA 2023, Free et al. 2023, IOŚ-PIB 2023, MacErlean 2023, Sobieraj & Metelski 2023, Szlauer-Łukaszewska et al. 2024).

However, the report stressed that the concentration of pollutants measured in the examined fish samples did not deviate from the levels characteristic of environmental pollution in rivers in Poland (IOŚ-PIB 2023). This may be explained by the fact that, as water temperature increases, waterborne toxicants become lethal to fish at lower concentrations (Mallatt 1985). At the same time, another important factor, namely oxygen levels, were dramatically low at the time of the disaster (IOŚ-PIB 2023). In the second half of August 2022, the oxygen concentration in the Oder River in the West Pomeranian province fell below 1 mg l^{-1} (IOŚ-PIB 2023), compared to 10.6–13.6 mg l^{-1} during the collection of roach and vimba bream specimens in the present study (Table 1).

Analyses of the species composition of the dead fish along the lower Oder showed that the greatest losses occurred in the populations of common bream *Abramis brama* (L.), roach, and common perch *Perca fluviatilis* (L.) (IOŚ-PIB 2023, Tański & Pender 2023, Szlauer-Łukaszewska et al. 2024). The gill of common bream and perch (Fig. S2) defends itself against parasites by ILCM (Molnár & Székely 1999, Dezfuli et al. 2003, Robaczyński 2016), and a similar defense response can be induced by toxins (Nilsson 2007, Nilsson et al. 2012, Gilmour & Perry 2018). In contrast, vimba bream, which displayed minimal ILCM growth, were observed only sporadically, with mortality confined to only one area of the Oder River (IOŚ-PIB 2023, Tański & Pender 2023). This indicates that states of aquatic hypoxia combined with severe water pollution and resulting damage to the gill pose a serious threat to species with the ability to defend themselves against toxins with adaptive hyperplasia (reversible remodeling). Species with low gill respiratory surface area values per 1 g of body mass, such as the pikeperch *Stizostedion lucioperca* (L.) (Satora & Wegner 2012), also appear particularly vulnerable (IOŚ-PIB 2023, Tański & Pender 2023, Szlauer-Łukaszewska et al. 2024).

Many fish species use ILCM to protect the gill from parasites and toxins (Dezfuli et al. 2003, Nilsson et al. 2012, Gilmour & Perry 2018, Satora et al. 2022). In 'classical' reversible gill remodeling, cell masses that limit functional surface area are lost when oxygen availability is reduced by hypoxia or when oxygen demand is increased by exercise or high temperature (Nilsson 2007, Gilmour & Perry 2018). However, in the presence of persistent irritants like gill parasites or toxins, ILCM remains even under hypoxic conditions, posing a serious threat to fish survival (Nilsson et al. 2012, Satora et al. 2022).

This preliminary study aims to contribute to the understanding of one of the largest ecological disasters in recent European river history. However, to fully explain the causes and course of the catastrophe, it is necessary to conduct research under conditions similar to those that prevailed on the Oder in July and August 2022. Fish gills have the ability not only to remodel themselves but also to completely regenerate gill filaments and lamellae, although to date, this capacity has only been documented in a limited number of fish species (Jonz 2024). Comparative studies with unaffected individuals of the same species such as vimba bream are essential to evaluate the significance of the gill alterations described in this study. Finally, given the enormous regeneration potential of fish gills, it is not entirely certain whether the described findings still reflect the situation present during the events.

5. CONCLUSIONS

The adaptability of gill structure and function, closely linked to the metabolic demands and physiological requirements of a fish, is crucial for maintaining homeostasis and ensuring survival in diverse environmental conditions (Wolf et al. 2015, Gilmour & Perry 2018). However, the primary limiting factor for gill function remains the oxygen content of the water (Wegner & Farrell 2024).

Fish capable of adaptive interlamellar hyperplasia (reversible remodeling), whereby the gill attempts to protect itself by developing an ILCM and thickening the gill epithelium, appear to be particularly vulnerable in conditions of aquatic hypoxia.

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