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Histology

CHANGES IN MICROSTRUCTURE OF GILLS IN RAINBOW TROUT, *SALMO GAIRDNERI* RICHARDSON, ADAPTED TO SEA WATER CONDITIONS

ZMIANY W MIKROSTRUKTURZE SKRZEL PSTRĄGA TĘCZOWEGO *SALMO GAIRDNERI* RICHARDSON INTRODUKOWANEGO DO MORZA

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Histological examination of gills of rainbow trout, *Salmo gairdneri* Rich. reared in freshwater ponds, introduced into the Baltic Sea, and kept in flow-through fresh water tanks and in tanks with the Baltic water showed marked changes to take place in the gill microstructure of those fishes kept in sea water. Increased numbers of chloride cells, decreased size of mucous cells as well as a reduction in laminated branchial epithelium adjacent to gill filament blood vessels have been observed.

INTRODUCTION

Stocking of aquatic habitats other than natural for the species with salmonid fishes has been described for many years (Kulmatycki, 1940). Those attempts gained a particular momentum in the 'sixties (Chrzan, 1963; Bartel, 1969; Trzebiatowski, 1973). Webb (1975) found that sea-dwelling rainbow trout, as opposed to those inhabiting fresh waters, utilised their food resources more efficiently, avoided energy losses for maintaining ionic equilibrium, and were less vulnerable to diseases. Similar were the conclusions drawn

from an experimental rearing of trout in a pond artificially enriched with NaCl (Epler and Cedrowski, 1971). In recent years good results have been also obtained when keeping salmonids, rainbow trout included, in cages placed in the Baltic inshore waters (Wiktor, 1976: pers.comm.). However, experiments of this kind produce numerous questions the elucidation of which is called for. For instance, it is interesting to know whether, and to what extent, an increase in ambient salinity produces morphological changes in rainbow trout osmoregulatory organs, possible changes in the gill microstructure presenting a particular interest.

Smith (1929) showed fresh water fishes to excrete most nitrogen compounds (ammonia, urea, amine compounds) by their gills. When studying eel, this author (1930) found that strongly hypertonic solutions of potassium, natrium and chlorine were also removed from a fish organism via gills too.

Gill microstructure in fish has been studied for many years (Plehn, 1901; Faussek, 1902; Krauss, 1936). A paper by Keys and Willmer (1932) proved most revealing in this respect; the authors described specific mucins negative cells found in eel's branchial epithelium, the so-called chloride cells containing granulated and strongly acidophilic cytoplasm. In the authors' opinion, those cells are responsible for the excretion of excessive ions. Bevelander (1935), on the other hand, maintained that the chloride-excreting cells were actually mucous cells and occurred not only in gills but also in mouth epithelium in *Fundulus*.

Liu (1942) observed a faster increase in number and size of chloride cells of *Macropodus opercularis* L., kept in water with a salinity gradient.

Burns and Copeland (1950) and Getman (1950) find the chloride cells in sea water-dwelling *Fundulus* and eel, respectively, to have a higher number of mitochondria than in the representatives of the species living in freshwater habitats.

Vickers (1961) suggested the chloride cells to be metamorphosed mucous cells, their development being stimulated by a gradual hyperosmotic adaptation of fishes. However, they are not confined to gills, being found in the epithelium of almost the entire internal part of fish head.

Changes in chloride cells morphology associated with fish adaptation to hyper-osmotic aquaceous habitat are reported by Robertson and Wexler (1960), Virabhandrachari (1961), Zaks and Sokolova (1961), Čusovitina (1963), Oliverau (1970), Shirai and Utida (1970), and Krajuškina (1972).

Scanning electron microscope (SEM) proved a valuable tool in obtaining detailed data on the chloride cell structure. Petrik and Bucher (1969) found, using SEM, that the free surface of a chloride cell usually showed an apical cavity filled with finely granulated substance of a glycoproteid nature. Hughes and Wright (1970) and Abel (1973) observed microvilli on the protruding surface of a chloride cell; most probably those microvilli are an attachment area for mucus covering the surface of branchial epithelium.

Recently, cytochemical methods have been more and more widely applied, which enables to locate individual ions in the chloride cells (Philpott, 1965; Petrik, 1968; Maetz and Bornacin, 1975).

As seen from above, many workers have studied the gill microstructure; each of those papers, however, deals with only one aspect of the problem, with a single element of cells forming the organ. There is a paucity of data on changes in the gill microstructure induced by a higher ambient salinity; when such data are reported, they are as a rule derived from observations on aquarium-kept fishes, the question being never treated in a holistic manner. The present paper is an attempt to fill the existing gap.

MATERIAL AND METHODS

The studies were carried out in the years 1971–1974 in the Department of Fish Anatomy and Embryology, Institute of Ichthyology, Academy of Agriculture, Szczecin.

The experimental material embodied 13 individuals of rainbow trout caught in the sea (originating from a stock previously introduced there, 9 individuals pond-reared, and 4 individuals each from seawater and running freshwater tanks).

Juveniles of both the fishes introduced to the sea and pond-reared were obtained in the Field Laboratory of the Institute of Inland Fisheries, Gdańsk-Oliwa, while the tank-reared fishes were raised in the PZW Trout Centre, Rumia.

To keep the fishes in tanks was aimed at obtaining uniform thermal and gaseous regime since the living conditions in natural environments (sea and ponds), due to obvious reasons, differed markedly and one might suppose that some changes in morphological and cytologica parameters could have been brought about by those differences.

One-year-old fishes were kept in 4 m^3 concrete tanks over the period of 16 weeks. The water was aerated; its temperature ranged within 11–13°, the temperature in the seawater tank being on the average higher by 1°C.

The individuals caught were killed and sections of gills from the central part of the first gill arch taken for analyses. The tissue sections were fixed in 10% buffered formalin and paraffin blocks were made. 5–7 mm thick serial sections were obtained using a rotating microtome. The tissue mount were stained using PAS and Mallory techniques as well as with hemalaun and eosin.

Chloride and mucous cells visible on cross-sections of gill filaments were counted and measured; additionally, laminated epithelium height was measured on the side of filament blood vessels.

The numerical data obtained were analysed statistically in order to detect any changes in the morphology of the studied organ that could be related to the hyper-osmotic conditions of living.

RESULTS

Although the increased salinity-induced changes in morphology of the fishes examined were not the main object of the present study, it seemed purposeful to include this

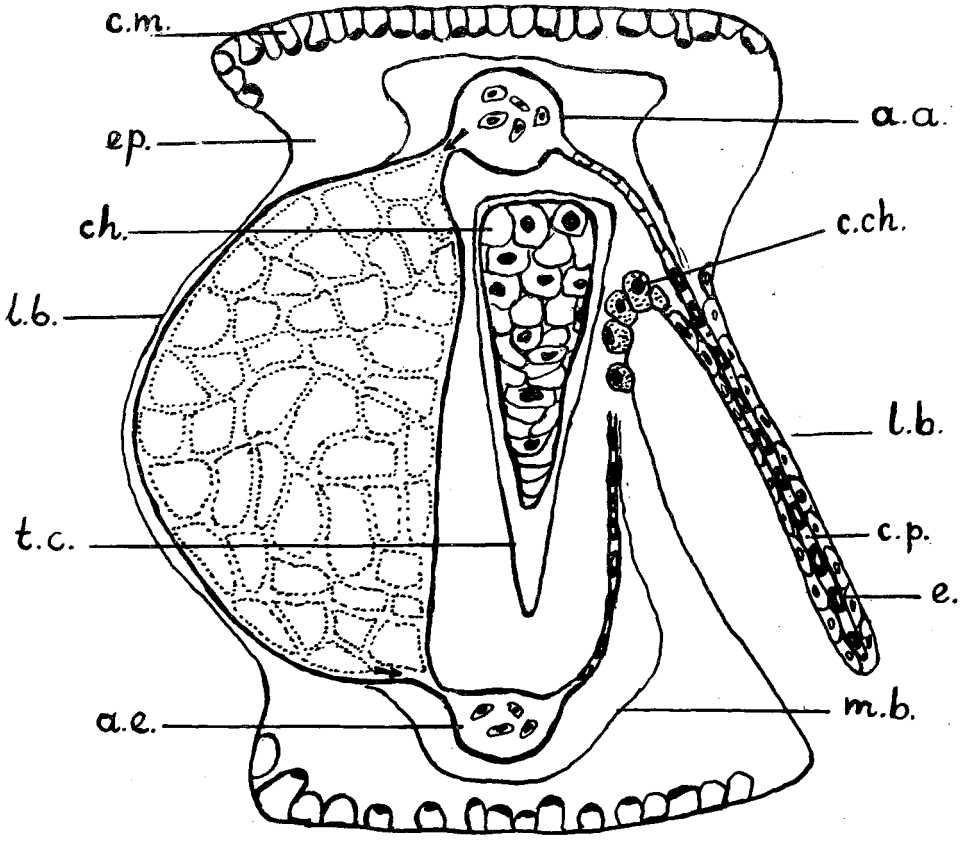

Fig. 1. Sagittal section of rainbow trout gill filament (a diagram)
Left: Branchial lamella in a section parallel to its surface.
Right: Sagittal section. For explanations see text.

question in the preliminary stage of the project, additional information and a more general beckground for histological analyses being thus gained.

The fishes kept in tanks showed a uniform size and weight (a mean difference of 10 g can be regarded as insignificant here). On the other hand, the fishes obtained from the sea were, on the average, heavier and longer by 44.6% and 9.4%. respectively than those reared in ponds.

Microstructure of a rainbow trout gill filament is pictured in Fig. 1. A cartilaginous selvage (ch.) is visible in the central part of the filament and blood vessels, afferent (a.a.) and efferent arteries (a.e.) on its ends. The selvage, surrounded by a connective tissue capsule (t.c.) is separated from branchial epithelium (ep.) by means of a basal membrane (m.b.) to which lumpish cells of branchial epithelium adjoin. The epithelium adhering to blood vessels is arranged in several layers, the topmost one being composed of mucous cells (c.m.) showing a strongly positive PAS reaction. These cells can also be found on

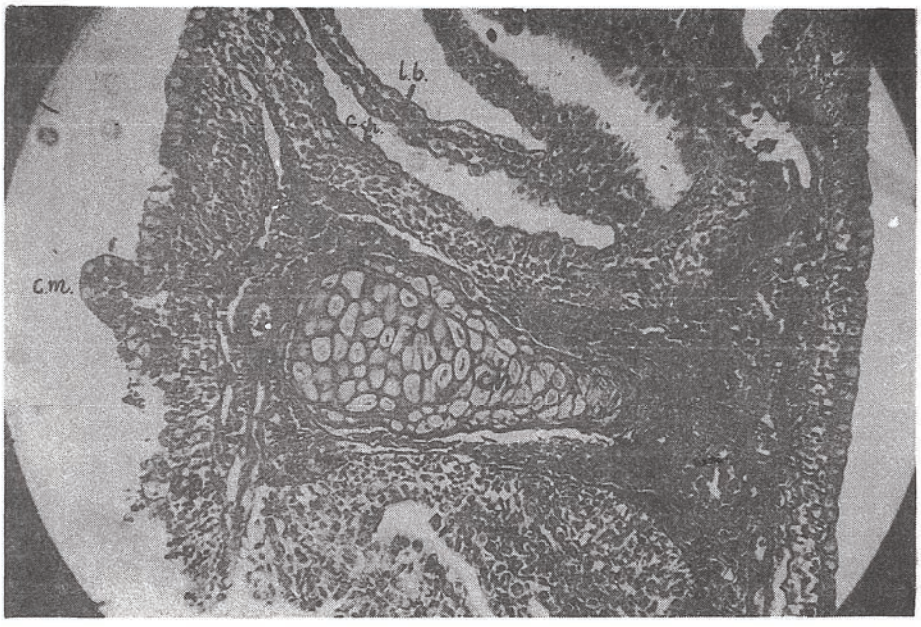

Fig. 2. Sagittal section through rainbow trout gill filament. For explanations see text. Mallory, 240x.

branchial lamellae. The lamellaer (l.b.) are equipped with a fine network of capillary blood vessels. The lamella epithelium is formed by one layer of flat cells, supporting cells (c.p.) providing for the internal space between both epithelium walls. Among the rainbow trout branchial epithelium cells mentioned there are some cells differing in their size, shape and stronger reaction to acidic stains. These cells, have been found to be identical with those described by Keys and Willmer (1932) from eel, therefore the name "chloride cells" (c.ch.) suggested by the two authors is adopted here. Chloride cells are mostly seen in groups of 5 to 10, more seldom single, within the intralamellar part of the epithelium at bases of the lamellae (Fig. 3). They are rounded, oval or irregular in shape, with large nuclei situated in the basal or central part of cells; cytoplasm strongly eosinophilic, characteristically granulated. Chloride cells in rainbow trout gills do not rest on basal membrane; they are usually seen in the surface layer of epithelium, their apical part protruding above the other cells. This arrangement seems to provide a better contact with water flushing the gills.

The mounts show the general plan of the microscopic structure of various filaments to be similar regardless of the actual habitat of a fish individual examined. With respect to some elements, however, considerable differences, both quantitative, can be observed; those differences are found primarily in chloride and mucous cells as well as in the laminated epithelium (Table 1, Fig. 4–15).

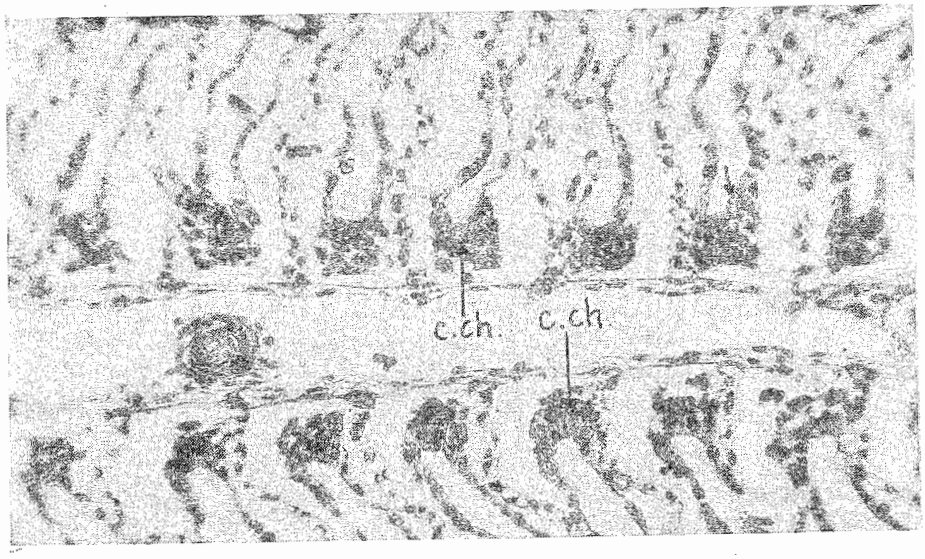

Fig. 3. Longitudinal section through gill filament. Groups of chloride cells at the base of branchial lamellae. Hemalaun and eosin. 330x.

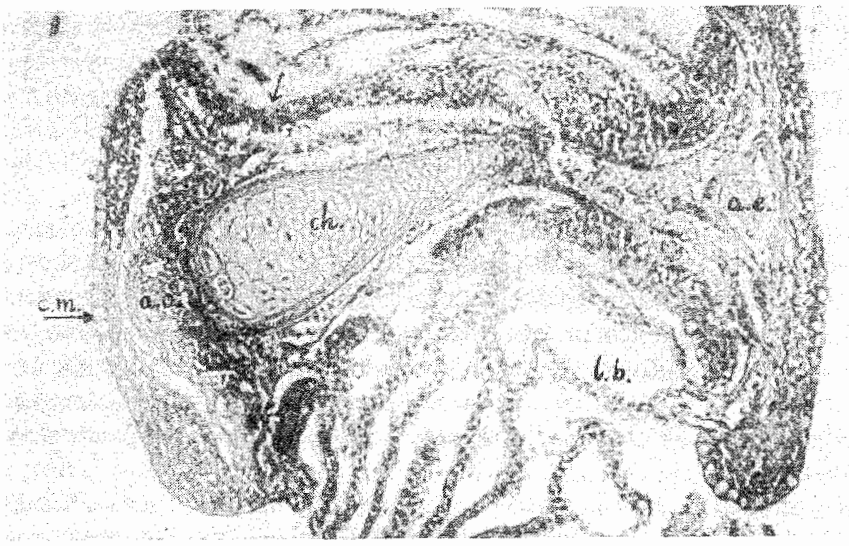

Fig. 4. Sagittal section through gill filament of rainbow trout reared in sea. For explanations see text. Hemalaun and eosin. 150x.

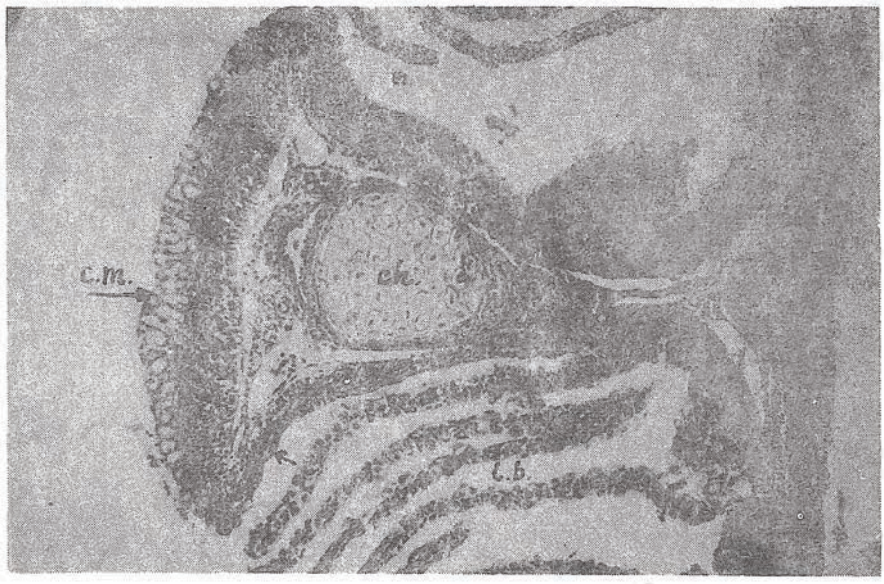

Fig. 5. Sagittal section through gill filament of rainbow trout reared in pond. For explanations see text. Hemalaun and eosin. 150x.

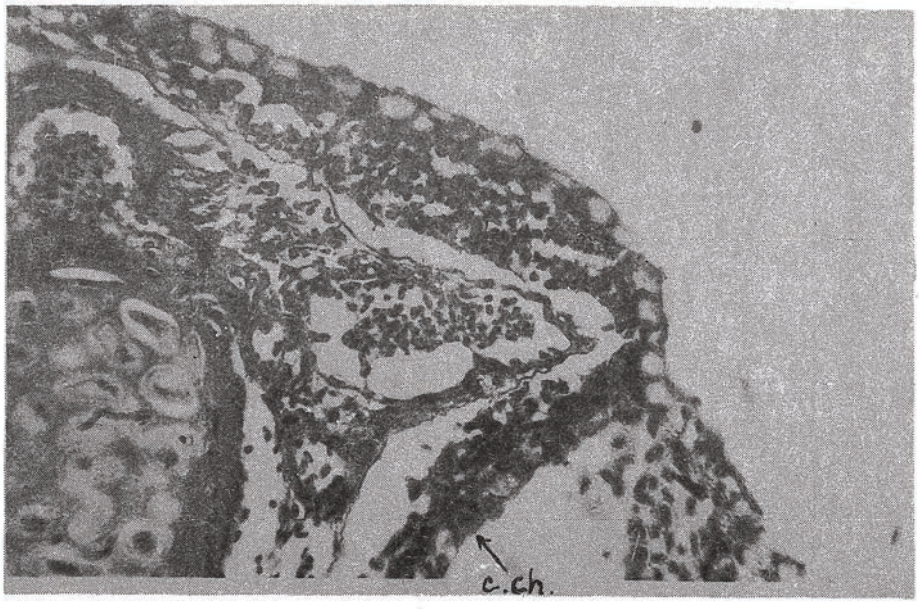

Fig. 6. Chloride cells in gill filament of rainbow trout reared in sea. Hemalaun and eosin. 330x.

Table 1

Changes in laminated epithelium height, number and size of chloride and mucous cells in rainbow trout gills

Object of study	Laminated epithelium height (μm)		Chloride cells				Mucous cells			
			No.		Diameter (μm)		No.		Diameter (μm)	
	$\bar{x}$	±	$\bar{x}$	±	$\bar{x}$	±	$\bar{x}$	±	$\bar{x}$	±
Large fish from sea	76.6	18.2	33.3	4.3	15.1	1.7	75.0	8	18.5	1.5
Large fish from pond	119.3	21,3	23.4	3.6	12.8	1.3	64.6	5	21.4	1.4
Small fish from seawater	64.3	12.9	31.6	4.7	12.24	2.2	29.1	2.7	12.8	1.3
Small fish from fresh water	85.0	19.3	16.0	2.0	11.6	1.2	31.9	3.7	18.7	1.5

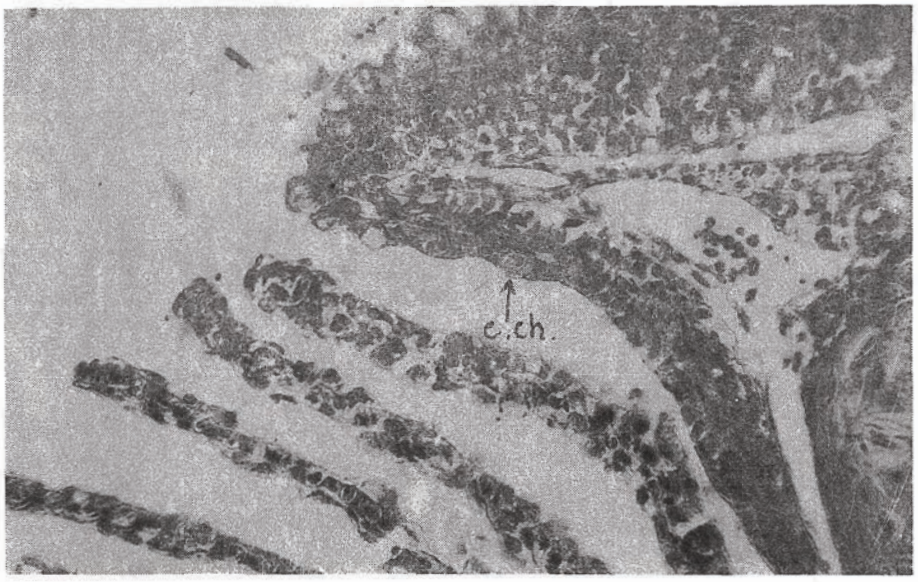

Fig. 7. Chloride cells in gill filament of rainbow trout reared in pond. Hemalaun and eosin. 330x.

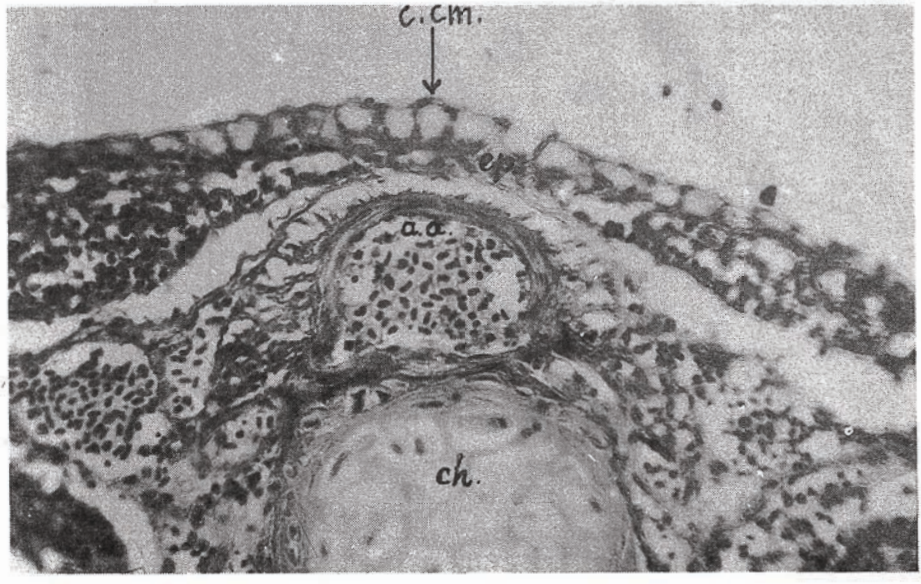

Fig. 8. Laminated epithelium from gill afferent artery in filament of rainbow trout reared in sea. Hemalaun and eosin. 330x.

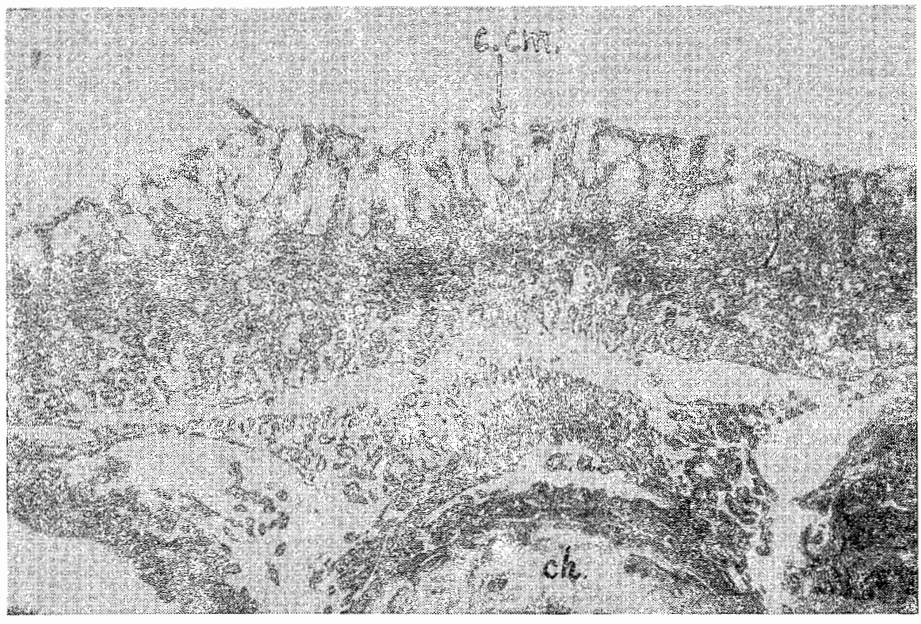

Fig. 9. Laminated epithelium from gill afferent artery in filament of rainbow trout reared in pond. H emalaun and eosin. 330x.

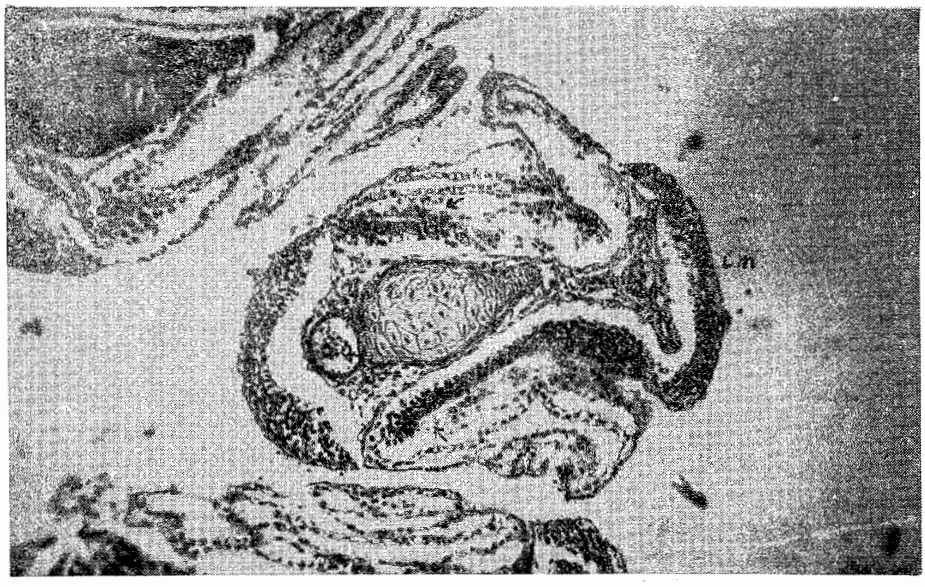

Fig. 10. Sagittal section through filament of rainbow trout kept in seawater tank. Hemalaun and eosin. 150x.

The number of chloride cells in the two experimental variants was found to be higher in the seawater-dwelling individuals. Large rainbow trout past their 18th month in the sea showed the number of those cells to be higher by 42.3%. Still greater differences were revealed in the tank-reared trout: after 16 weeks of rearing, the Baltic individuals showed, their number of chloride cells to be higher by 97.5% on the average compared to the fishes kept in fresh water.

As seen from Table 1, the quantitative differences are accompanied by the qualitative ones. Chloride cells diameters in the seawater fishes; are 20% larger than those measured in the freshwater fishes.

Somewhat different were the proportions among mucous cells. The sections of gill filaments of rainbow trout introduced to the sea showed higher numbers of those cells. The pond individuals contained lower numbers of them (by 16% on the average), but the cells diameters here were on the average larger by 15.6%. No significant differences in the amounts of mucous cells were recorded between younger individuals; the size of those cells, however, was 46% larger in the freshwater tank fishes compared to the rainbow trout kept in tanks filled with sea water.

The two experimental groups of fishes revealed also some differences between their laminated epithelium heights. As seen from Table 1, the freshwater rainbow trout – both those kept in tanks and in the pond – have their laminated epithelium much higher than the seawater individuals, the differences averaging to 55.7% and 32.2% in older and younger fishes, respectively. This finding is illustrated by Figs. 8, 9, 14 and 15.

DISCUSSION AND CONCLUSIONS

The results obtained in the course of the present project confirm the well-known opinion of other workers (Parry, 1958; Morgan and Tovell, 1973; Olson and Fromm, 1973; Morgan, 1974) on considerable hyperosmotic adaptation power in freshwater salmonid, rainbow trout *Salmo gairdneri* Rich. It is evidenced by higher increments observed in the individuals from the same culture living in the sea, in a pond, and under experimental conditions.

With regard to the gill histology studied here, significant qualitative and quantitative differences were found. The gills are known to be the weakest barriers for the ionic penetration owing to their structure (large area, delicate epithelium) and a permanent contact with water.

In relation to chloride cells, the differences are found in the amount of them, their numbers being higher in fishes living in sea water, as well as in their size. Particularly in this latter case, the differences seem to point out to the increase in the importance (cf. numbers) and activity (cf. size) of those cells in the process of maintaining the equilibrium between the organism's internal environment and the external milieu.

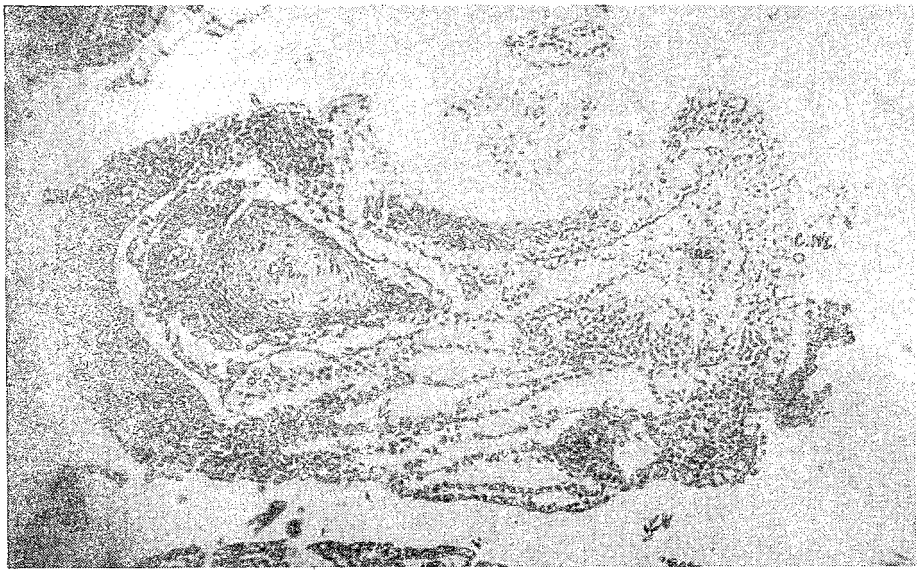

Fig. 11. Sagittal section through filament of rainbow trout kept in freshwater tank. Hemalaun and eosin. 150x.

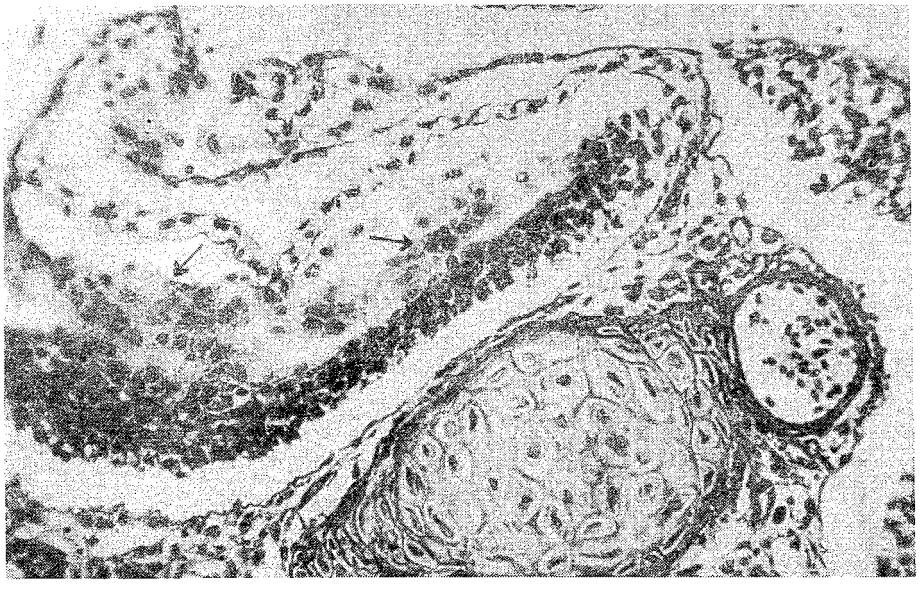

Fig. 12. Chloride cells in gills of rainbow trout kept in seawater tank. Hemalaun and eosin. 330 x.

Assuming an almost spherical shape of chloride cells, one can prove using the numerical data that mean volume of a chloride cell in a fish adapted to saline waters (rainbow trout from the sea) is more than 60% larger. Furthermore, considering the fact that their mean numbers are 43% larger than the respective numbers in fishes inhabiting fresh waters, appropriate calculations will show the gills of fishes living in the sea over the equal area to contain chloride cells of the total volume nearly 130% larger. Therefore the chloride cells' efficiency in those fishes should exceed the efficiency of chloride cells in the pond fish gills by the same factor, assuming Krogh's (1937) suggestion on the two-way chloride excretion performed by the cells discussed. Similar differences in the total volume of those cells are seen in juvenile forms living for 16 weeks in saline water, although the phenomenon is expressed morphologically in a different way. It is worth noticing that the volume percentage ratio (132%) is almost the same here as in mature individuals. The results, presented in Table 1, showing a considerable increase in the juveniles' chloride cells number following a relatively short period of life in sea water, are consistent with the results obtained for acipenserids (Krajuškina and Vasileva, 1975) or rainbow trout (Morgan, 1974). The latter author additionally informs that chloride cells appear in rainbow trout on the 28th day of life and are morphologically identical with those cells in adults.

The fact that the qualitative changes have taken place after a short period of time tends to confirm the opinion expressed by Shirai and Utida (1970) on the existence of two types (A and B) of chloride cells, type B (poorly acidophilic) becoming type A (functioning chloride cells), given a change in an actual habitat. Type B would correspond to the so-called "substitute cells" reported earlier by Conte and Liu (1967). However, the cells discussed by the authors mentioned can be regarded as an inactive form of chloride cells activated by an increased salinity whereby the number of chloride cells increases.

The differences in mucous cells, although existing, are not as big as in the previously discussed cells and there are no grounds for supposing, as did Bevelander (1935, 1946), Munshi (1964), and Vickers (1961), that they can be transformed into chloride cells, their spatial arrangement tending to preclude such possibility, too. The excreted mucus protects the organism against direct receiving of, for instance, changes in pH, changes in contents of some chemical compounds, pollutants, etc.

Finally, the third index of changes in the gill microstructure, i.e., the branchial laminated epithelium height, has not been basically considered by other workers. However, the gill filaments of rainbow trout reared in the sea showed a lower number of cell layers, particularly so nearby the filament blood vessels. It can be supposed then, that the multiplication of branchal epithelium layers in fishes kept in fresh water presents an additional protective barrier against a loss of ions from the fish body.

The following conclusions can be drawn as a summary of the abovediscussed findings:

1. After 18 months of life in the Baltic waters, rainbow trout significantly increased (by 42.3%) their number of chloride cells in branchial epithelium compared to the individuals kept in fresh water; the increase in number is accompanied by an increase

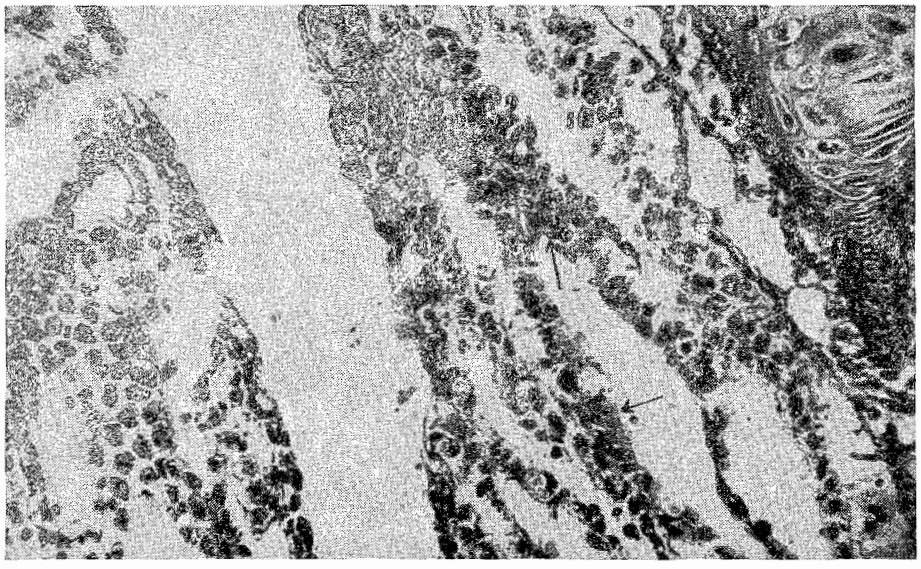

Fig. 13. Chloride cells in gill of rainbow trout kept in freshwater tank.
Hemalaun and eosin. 330x.

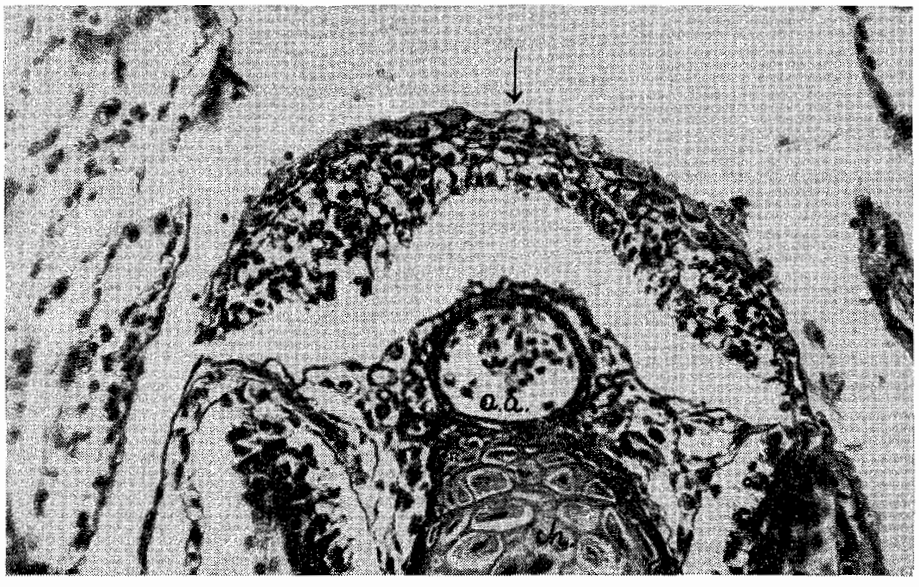

Fig. 14. Laminated epithelium from gill afferent artery in rainbow trout kept in seawater tank.
Hemalaun and eosin. 330 x.

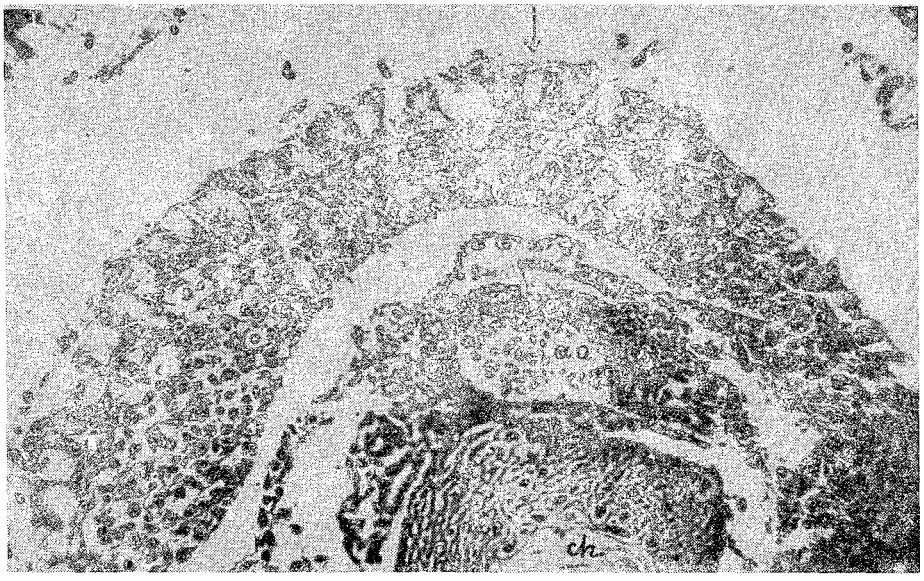

Fig. 15. Laminated epithelium from gill afferent artery in rainbow trout kept in freshwater tank. Hemalaun and eosin. 330x.

in cell size, which results in an almost two-fold rise of total volume of those cells in rainbow trout in the sea.

2. A considerable increase in chloride cells total volume is also observed in juvenile trout subject to a short-duration influence of a higher salinity; in this case, however, the observed increase results from the direct quantitative increment of those cells rather than from a size increment.
3. Rainbow trout subject to a high-salinity medium decrease the height of laminated epithelium surrounding the gill filament blood vessels.
4. Changes in the gill microstructure evidence the high plasticity of rainbow trout and the species' adaptive ability to withstand hyper-osmotic habitats, which to a certain extent explains successful attempts of rearing this species in the sea.

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ZMIANY W MIKROSTRUKTURZE SKRZELI PSTRĄGA TĘCZOWEGO *SALMO GAIRDNERI* RICHARDSON INTRODUKOWANEGO DO MORZA

Streszczenie

Przeprowadzono badania histologiczne skrzeli pstrągów tęczowych ***Salmo gairdneri*** Rich. hodowanych w stawie z wodą słodką i introdukowanych do Bałtyku oraz pstrągów przetrzymywanych przez 16 dni w basenach z wodą słodką i wodą bałtycką.

Stwierdzono, że niezależnie od środowiska z jakiego pochodziły osobniki ogólny plan budowy mikroskopowej jest jednakowy, jednakże w odniesieniu do niektórvch elementów strukturalnych wystąpiły znaczne różnice. U pstrągów bytujących w wodzie morskiej zaobserwowano zwiększenie ilości komórek chlorkowych, zmniejszenie rozmiarów komórek śluzowych oraz redukcję nabłonka wielowarstwowego po stronie naczyń krwionośnych.

Ц. Цыковска

ИЗМЕНЕНИЯ В МИКРОСТРУКТУРЕ ЖАБР РАДУЖНОЙ ФОРЕЛИ (SALMO GAIRDNERI RICH.), ИНТРОДУЦИРОВАННОЙ В МОРЕ

Р е з ю м е

Проведены гистологические исследования жабр радужнои форели (Salmo gairdneri Rich.), выращиваемой в пресноводном пруду и интродуцированной в

Балтийское море, а также форели, выдерживаемой в течение 16 недель в бассейнах с пресной водой.

Установлено, что независимо от среды, из которой происходили исследуемые особи, общий план микроскопического строения является одинаковым, однако в отношении некоторых структурных элементов наблюдались значительные расхождения. У форели, обитающей в морской воде, наблюдалось увеличение количества хлоридных клеток, а также редукция многослойного эпителия со стороны кровеносных сосудов.

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