ULTRASTRUCTURE OF MITOCHONDRIA-RICH CELLS IN THE GILL EPITHELIUM OF OREOCHROMIS NILOTICUS

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ABSTRACT

The mitochondria-rich (MR) cells (also called chloride cells) in the gill epithelium of adult tilapia Oreochromis niloticus were investigated at the light and electron microscopic levels. Three types of MR cells, the α, β, and accessory cells are observed. In addition to numerous mitochondria, a characteristic feature for the cytoplasm of the identified three types was the presence of a network of membranous tubules, the tubular system, connected to the basolateral plasma membrane. The β cells were found exclusively in the interlamellar regions of the filaments. In addition to their well-developed tubular system, they contained numerous deeply stained elongated mitochondria displayed closely packed cristae within a dense matrix. The cells were devoid of the apical structures that were previously described in other fish species. Small elongated cells were seen to be closely opposed to the lateral side of the β cells; they had a less-developed tubular system and were considered to be accessory cells. The α cells were present along the lamellae. In contrast to the β cells, they exhibited a well-developed granular endoplasmic reticulum and the tubular system was lesser developed than in β cells. The possible role of these three types of MR cells in osmoregulation during adult life is discussed.

Key words: mitochondria-rich cells; chloride cells; gill epithelium; Oreochromis niloticus; teleostei.

INTRODUCTION

The mitochondria-rich (MR) cells (also called chloride cells) of the gill epithelium plays a crucial role in the ionic regulation of fish **(Maetz, 1971; Pisam et al., 1995; Pisam et al., 2000)**. Whereas the ion-extruding activity of the gills of seawater fish has been demonstrated to be located in the chloride cells **(Foskett and Scheffey, 1982)**, and the importance of these cells is well known, the ion-absorptive function ascribed to these cells in freshwater fish has been

shown only indirectly. These cells have been described as rudimentary in freshwater fish **(Foskett et al., 1981)**. However, other physiological, biochemical and ultrastructural studies have established a close relationship between freshwater chloride cells and the uptake of monovalent and divalent ions **(Payan et al., 1981; Flik et al., 1985; Mayer-Gostan et al., 1987)** Furthermore, these cells show adaptive changes such as cell proliferation when the ion balance is disturbed by reduced water ion levels or by various types of water pollution **(McDonald 1983; Leino and McCormick 1984; Laurent et al., 1985; Avella et al., 1987).**

Teleost chloride cells are structurally characterized by many small mitochondria and an extensive system of small branching and anastomosing tubules, where ion-transporting enzymes such as Na^+/K^+-ATPase, Na^+/H^+ ATPase and transport Ca^{2+}-ATPase are located **(Hootman and Philpott 1979; Flik et al., 1985; Balm et al., 1988; Pisam et al., 1997; Pisam et al., 2000)**. The tubules have a lumen that is continuous with the extracellular space via orifices in the basolateral cell membrane **(Sardet et al., 1979; Laurent and Dunel 1980)**. Vesicles are present between the apical membrane and the tubular system in the apical cytoplasm **(Pisam 1981; Laurent 1984)**. This structure is typical of chloride cells of fish from freshwater and seawater.

Based on ultrastructural characteristics, two types of chloride cells were distinguished in different species of teleosts **(Doyle and Gorecki, 1961; Straus, 1963; Shirai and Utida, 1970; Pisam et al., 1987; Pisam et al., 1993)**: they were referred to as α and β chloride cells. The presence of accessory (A cell) cells is considered typical of seawater fish **(Dunel-Erb and Laurent 1980; Chretien and Pisam 1986; Pisam et al., 1988)**. These cells have been interpreted as immature *differentiating* chloride cells **(Sardet et al 1979; Hootman and Philpott 1980)**. In tilapia **(Wendellar Bonga and Van der Meij 1989)** accessory cells in freshwater fish, albeit in very low numbers are found. In 1995, Pisam et al. examined the apical structures of the two MR cell types in salmon and tilapia *maintained in freshwater*. In α cells, they consisted of isolated vesicles located close to the apical membrane, whereas they occupied the whole supranuclear region of β cells and originating from the juxtanuclear Golgi apparatus.

There have been few studies on the ultrastructure of mitochondria-rich cells in the gills of freshwater fish. Moreover, the nature and possible origin of the structural diversity characteristic to gill MR cells is still a matter of debate. Therefore, the primary objective of the present study was to describe the ultrastructure of mitochondria-rich cells in the gills of the Oreochromis niloticus during adult life. Such study is crucial in order to find out whether the different types can be distinguished and to determine whether these types are considered either as different developmental stages of chloride cells or as specific cell-types.

MATERIALS AND METHODS

Ten sexually mature male and female tilapia (Oreochromis niloticus), formerly tilapia nilotica were obtained from laboratory stock in Department of Fish Health, Central Lab of Aquaculture, Abbasa, Egypt. They were kept in 200-liter aquaria containing non-chlorinated tap water, at 25°C with a daily 12-h photoperiod. For light microscopy, gill samples were fixed in 10% neutral buffered formalin, dehydrated in ascending ethanolic series, cleared in xylene and embedded in paraplast. Four to five micron sections were cut and stained with H and E, PAS and Masson's trichrome. For transmission electron microscopy, gill arches were dissected out and fixed for 24 hr at room temperature in 2.5 % glutaraldehyde in 0.07 sodium cacodylate buffer (pH 7.6). They were postfixed for 1 hr at room temperature in 1% osmium tetroxide using the same buffer, dehydrated in ethanol and embedded in Epon 812. Semithin sections were stained with an aquous solution of 1% toluidine blue. Ultrathin sections were obtained using diamond knife, mounted on 200-mesh copper grids. They were double stained with uranyle acetate and lead citrate and examined at 80 kV with JEOL 100 c electron microscope.

RESULTS

Light Microscopy :

The gill of Oreochromis niloticus consisted of four branchial arches (Fig. 1), each of which bears filaments from which lamellae radiate. The gill arches consisted of loose connective tissue containing a cartilagenous rod, some skeletal muscle fibers and large venous sinuses in their apical regions (Fig. 2). Each filament was supplied by afferent arteriole and is drained by efferent arteriole. The region of the filaments located between two adjacent lamellae is referred to as the interlamellar region (Fig. 3). The core of each filaments contained a longitudinally arranged capillaries enclosed in a very thin connective tissue layer (Fig. 3). The gill filaments and lamellae were covered by a simple epithelium consisting of three main cell types: the flattened epithelial cells (pavement cells), mucous cells and the mitochondria-rich (chloride) cells. The cytoplasm of the mucous cells was PAS positive (Fig. 4), in contrast to the PAS negative pavement and chloride cells (Fig. 5).

Electron Microscopy :

Many mitochondria-rich (chloride) cells were recognized among the epithelial cells of both gill filaments and lamellae. The mitochondria-rich cells were ovoid or elongated in shape with elongated euchromatic nuclei (Fig.6). The apical cell membrane was covered by a thin cytoplasmic layer of the neighboring pavement cells (Fig. 6). The cell displayed a well-developed tubular sys-

tem made up of long anastomosing tubules, which formed a loose network (Fig. 7). The elongated mitochondria were deeply stained and displayed numerous closely packed cristae within a dense matrix (Fig. 8). The endoplasmic reticulum appeared as interconnected cisternae located preferentially in the perinuclear region (Fig. 8). Numerous small electron-lucent or dense small vesicles and multivesicular bodies were also observed within the apical cytoplasm (Fig. 7, 9). These cells were exclusively encountered in the interlamellar regions of the filaments. The distribution and structural peculiarities of these mitochondria-rich cells suggest that the latter were β cells.

Some of the β chloride cells were associated with smaller cells with variable shape that were closely opposed to their lateral sides (Fig. 10). These cells were attached to the β chloride cells by shallow apical junctions. They were always linked to adjacent pavement cells by tight junctions (Fig. 11). The cells exhibited a well-developed tubular system with no or just a few small electron-lucent vesicles in their apices (Fig. 12), and were considered to be accessory (A) cells.

A few mitochondria-rich cells were structurally intermediate between accessory cells and β chloride cells. They were exclusively found in the epithelium of the lamellae. They were elongated with much lighter cytoplasm and their apical surface was separated from the external medium by a layer of pavement cell cytoplasm (Fig. 13). Their granular endoplasmic reticulum was more extensive and the tubular system was less developed than in β cells. In some areas the rER cisternae were seen to be continuous with the adjacent membranous tubules (Fig. 13, 14). Golgi areas, which were scarce in β and accessory cells, were common; the nuclei were euchromatic. Their apical cytoplasm contained fewer elongated mitochondria and sparse tubules (Fig. 13, 14).

DISCUSSION

The heterogencity of the mitochondria rich (chloride) cells has been noted by several investigators **(Shirai and Utida, 1970; Richman et al., 1987; Pisam et al., 1987; Pisam, 2000)**. In the present study, three types of mitochondria rich cells have been identified: β, α and accessory cells. Ultrastructurally, the characteristic features of the β cells in the gill of Oreochromis niloticus include:1) mitochondrial profiles that are abundant and large with dense matrices and densely paeked cristae; 2) a well developed cytoplasmic tubular system; 3) a lack of a vesiculotubular system in the apical cytoplasm. They were exclusively found in the interlamellar region of the filaments. With the exception of the lack of vesiculotubular system, the β cells described in the present study had ultrastructure and distributional pattern features reminiscent of those β cells described in other fishes **(Pisam and Caroff, 1985; Karnaky, 1986; Chretien and Pisam, 1986; Pisam et al., 1987, 1993; Pisam et al., 1995; Rojio et al., 1997)**. The exact functional roles of the apical structures have not been determined yet. In this respect it has been reported

that the apical structures do not correspond to lysosomes; they are strictly located in the apical region of the cell, have homogenous contents, and are relatively similar in size. Moreover in contrast to lysosomes, they are not endowed with cytidine monophosphate activity **(Pisam et al, 2000)**. They may correspond to carbohydrate-containing secretory granules originating from the trans-Golgi network **(Pisam et al., 1995)**. The numerous mitochondria and an extensive tubular system together with the absence of apical structures that have been revealed in the present study suggest that the Oreochromis niloticus β cells are active and likely to be mainly involved in ionic transfers rather than secretory functions. A similar conclusion regarding homologous cells was reached by several investigators **(Wendellar-Bonga et al, 1990; Pisam et al., 1993; Shikano and Fujio, 1998 a, b)**. Our interpretation may also concur with those of **Hwang et al. (1994)** who suggested that the β mitochondria-rich cells of the gills might be involved in the active uptake of Ca^{++}. They proposed that, in tilapia, the increase in the body Ca^{++} content observed after hatching may be due to the differentiation of chloride cells.

The accessory cells, revealed in the present study, have the ultrastructure characteristics of the accessory cells found in freshwater fish **(Laey, 1983, Leino and McCormick, 1984, Chretien and Pisam, 1986 and Pisam et al., 1989; Wendellar Bonga and Van der Meij, 1989)**. They are closely apposed to the lateral side of the β cells in the interlamellar region of the filaments. In comparison to the β cells, the accessory cells observed in the present study show a less developed tubular system. Their apex is devoid of apical structures. Based on the presence of less developed tubular system, **Wendellar-Bonga and van der Meij (1989), Hootman and Philpot (1980) and Pisam (1981)** proposed that the accessory cells may correspond to young β cells with which they are associated. In tilapia, the percentage of accessory cells is correlated with the rate of increase of the total number of chloride cells **(Leino and McCormik, 1984; Wendellar Bonga et al., 1990)**. This relationship supports the interpretation of these cells as young stages rather than as a specific type of chloride cell. In contrast to the aforementioned proposal, the present study clarified that the accessory cells are always found to be adjacent to the lateral side of the β cells and not at their base as would be the case for young cells involved in epithelial renewal. Thus, they should be considered as a cellular type with an origin and a mode of differentiation different from those of the mitochondria rich cells to which they are adjacent, as was demonstrated in the guppy after ^{3}H thymidine radioautography **(Chr tien and Pisam, 1986)**.

It is possible that there are different types of accessory cells, since several authors have reported that, in seawater fish or euryhaline seawater adapted fish, apical cytoplasmic processes of accessory cells interdigitate with the apical cytoplasm of neighboring mature chloride cells **(Sardet et al. 1979; Dunel and Laurent 1980; Hwang and Hirano 1985; Chretien and Pisam 1986; Pisam et al. 1988)**. Neither **Leino and McCormick (1984)**, nor our group have observed

this type of interdigitation in fathead minnors or Oreochromis niloticus, respectively.

The α MR cells have the same ultrastructural characteristics as the α cells found in freshwater juvenile salmon and tilapia **(Pisam et al., 1995)**. In comparison to β cells, their granular endoplasmic reticulum is more extensive, the tubular system less developed, their apical cytoplasm contained fewer elongated mitochondria and they are exclusively found in the epithelium of the lamellae. The distinctive ultrastructure and distribution pattern of the α cells might led us to propose that they represent a distinctive mitochondria-rich cell types rather than they are developmental stage of β cells. This conclusion concur with that of **Pisam et al. (2000)** demonstrating that in brown trout, the α cells appear at a later developmental stage than the b cells because they are only seen after yolk sac resorption. β and α cells are thus different mitochondria-rich cell types and not developmental stages of the same cell type as postulated by **Wendelaar-Bonga and van der Meij (1989)** in tilapia. The α cells have a well-developed tubular system, in keeping with the findings of **Shikano and Fujio** in the guppy **(1998a)** and in chum salmon fry **(1998b)**, which showed that Na^+ K^+ ATPase activity was higher in α than in β MR cells. The α cells might thus be particularly involved in Na^+ and K^+ transfers.

Figure 1 : Photomicrograph of a light microscopic section of Oreochromis niloticus gill showing the four branchial arches from which filaments and lamellae radiate. H & E X 40.

Figure 2 : Photomicrograph of a light microscopic section of Oreochromis niloticus gill showing the structure of the gill arches. Note cartilagenous rod, skeletal muscle fibers and large venous sinuses in their apical regions. H & E X 100.

Figure 3 : Photomicrograph of a light microscopic section of Oreochromis niloticus gill showing the structure of the gill lamellae. Note central capillaries and delicate connective tissue layer around them. Masson's Trichrome. X 400.

Figure 5 : Photomicrograph of a section of Oreochromis niloticus gill showing the gill filaments and lamellae were covered by a simple epithelium covering the gill lamellae. Note the PAS-positive mucous cells in contrast to PAS-negative pavement and chloride cells. PAS X 1000 .

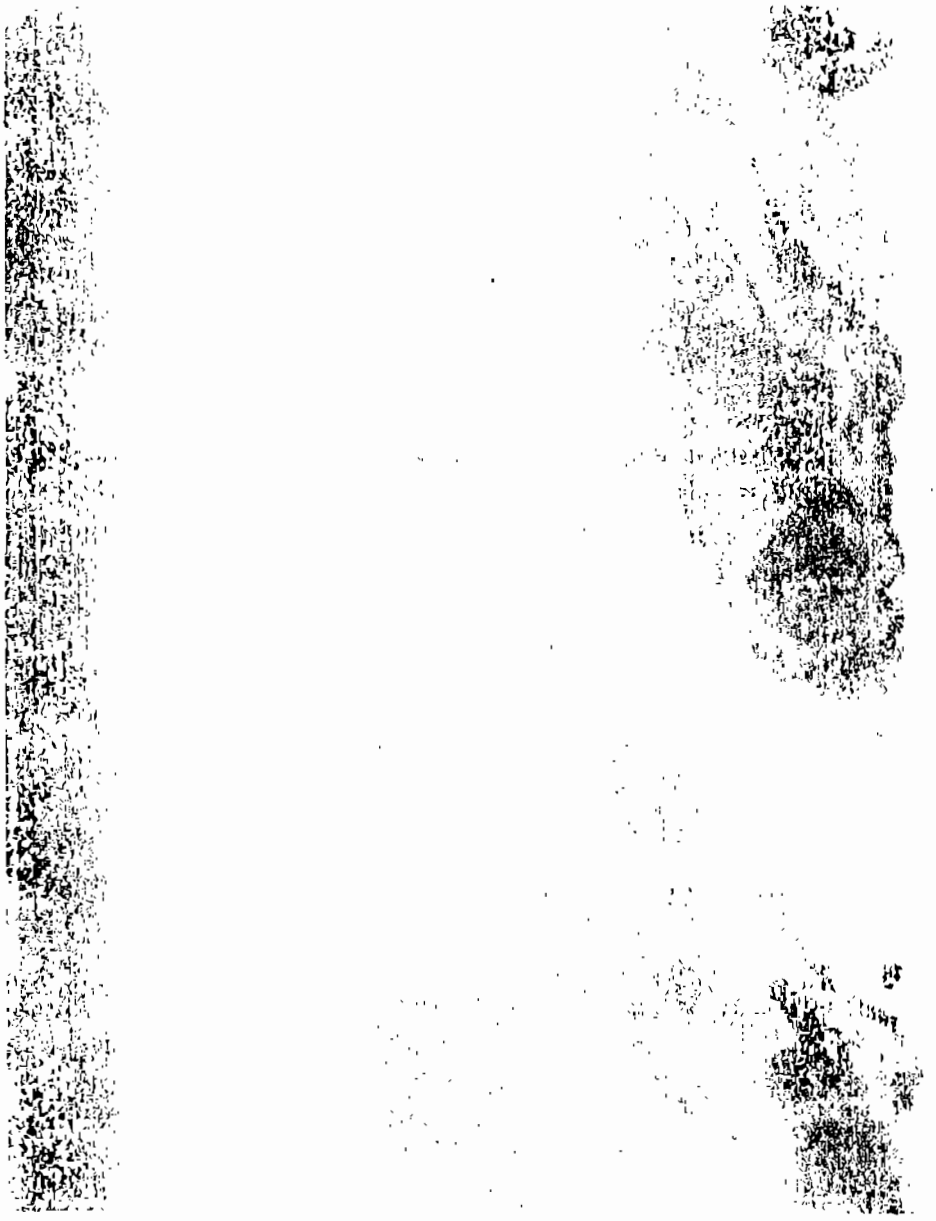

Figure 5 : Photomicr[illegible] Oreochromis niloticus gill showing the central capill[illegible] [illegible] toluidine blue X 250

Figure 6 : Transmission electron micrograph of Oreochromis niloticus gill. General view for β cell (B) and its relation to accessory cells (AC). (X 9000)

Figure 7 : TEM of β cell showing numerous elongated dark mitochondria (U), well-developed tubular system (T), multivesicular bodies (V), few rER tubules (r), few small vesicular system (double arrowheads), and adjacent accessory (A) cell. X10000.

Figure 8 : Higher magnification of the β cell cytoplasm showing numerous elongated dense mitochondria with closely packed cristae (U), few rER tubules (r) and well developed tubular system (T). X 22000.

Figure 9 : β cell at higher magnification showing a well developed tubular system (T) and numerous dense mitochondria (U). X22000.

Figure 10 : TEM of β (P) and accessory (A) cells. Note elongated heterochromatic nucleus (n) of A cell and few mitochondria (U). X10000.

Figure 11 : A well-developed junction complex (J) between the accessory (A) and pavement (V) cells. X 17000.

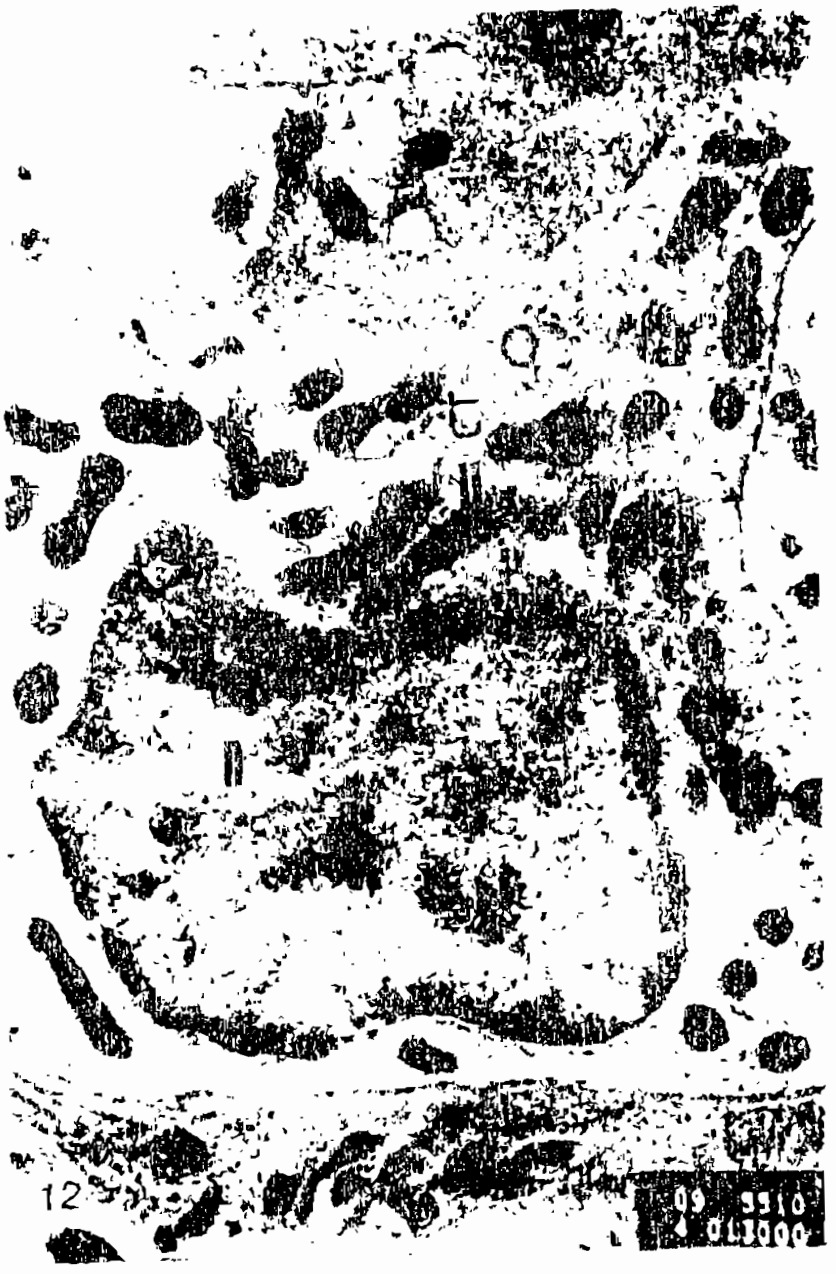

Figure 12 : Accessory cell at a higher magnification. Note nucleus (n), mitochondria (L), tubular system (T). X 13000

Figure 13 : A general view of a (A) cell. Note the nucleus (n), mitochondria (U), rER (r) and ill developed tubular system (T). X 8000.

Figure 14 : Higher magnification of a (A) cell showing large number of rER tubules (r), mitochondria (M) ill-developed tubular system (T). X 13000.

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الملخص العربى

دراسة التركيب الدقيق للخلايا الغنية بالميتوكوندريا فى النسيج الطلائى المبطن لخباشيم أسماك البلطى النيلى

المشتركون فى البحث

هـانى السـيد مرعـى

قسم الخلية والأنسجة - كلية الطب البيطرى - جامعة المنصورة

أجريت هذه الدراسة على خياشيم أسماك البلطى النيلى حيث تم أخذ العينات من الأجزاء المختلفة للخياشيم وتم تجهيزها للفحص بكل من الميكروسكوب الضوئى والإلكترونى، تم تمييز ثلاثة أنواع من الخلايا الغنية بالميتوكندريا وهى خلايا آلفا وبيتا والخلايا المساعدة. تميزت خلايا بيتا بموقع متميز حيث تركز وجودها فى المناطق الواقعة بى صفائح الخيوط الخيشومية كما تميز سيتوبلازم تلك الخلايا بوجود جهاز أنبوبى متطور والعديد من الميتوكندريا بالإضافة إلى عدم وجود التركيبات القمية والتى تم تميزها فى أنواع الأسماك الأخرى، بالنسبة للخلايا المساعدة فلقد تميز سيتوبلازم تلك الخلايا بوجود جهاز أنبوبى غير متطور وظهرت كخلايا طويلة تقع بجانب السطح الوحشى لخلايا بيتا. أما خلايا آلفا فلقد تم التعرف عليها فى جميع مناطق الصفائح الخيشومية ومقارنة بخلايا بيتا تميزت تلك الخلايا بوجود شبكة إندوبلازمية محببة وجهاز أنبوبى غير متطور أو مضمحل. كما تم فى هذه الدراسة مناقشة الدور الوظيفى المحتمل ومنشأ تلك الأنواع المختلفة من الخلايا الخيشومية الغنية بالميتوكندريا ودورها المتوقع فى تنظيم الضغط الإسموزى داخل جسم الأسماك.