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Cellular contributions to the otolith formation in teleosts: A review

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The teleost otolith is the most reliable age determinant and has been commonly applied for fisheries research such as population studies etc. However, the mechanism of otolith formation has been only insufficiently studied. In order to clarify the present status and future directions of such basic research, I briefly review here the recent cytological studies on the structure and functions of the teleost inner ear epithelium. Ultrastructural studies suggest that the mitochondria-rich cells and the squamous epithelial cells are involved in ion transport. However, the ion species transported by these cells are yet unknown. Especially, precise understanding of the transport mechanisms of calcium and bicarbonate, and of the distribution of such transport systems in the saccular epithelium is essential to elucidate the mechanisms of calcium carbonate crystallization onto the otolith. On the other hand, the transitional epithelium and the squamous epithelium are responsible for the production of otolith matrix. The sensory epithelium also has some secretory functions; however, controversial results have been reported on the nature of the secretory products. The detailed nature of secretory products of each cell type remains to be investigated in future.

Key words: otolith formation, sacculus, endolymph, teleost fish

INTRODUCTION

The teleost otolith is the most reliable age determinant and has been commonly used for fisheries research such as population studies etc. (Secor et al. 1995a). Since Pannella (1971) found the presence of daily growth increments in the microstructure of teleost otoliths, the otolith has also been used to determine the daily age of larvae and juveniles. Moreover, recent technical developments in microanalysis of otolith trace elements enable us to read environmental events which an individual fish has experienced. For example, strontium/calcium ratio in the otolith was indicated to reflect environmental salinity in laboratory-reared fish (Secor et al. 1995b, Tzeng 1996, Kawakami et al. 1998) and the ratio has been applied to document the history of environmental salinity in wild fish (Secor and Piccoli 1996, Tzeng et al. 1997, Otake and Uchida 1998, Radtke et al. 1998). While there have been many extensive studies on the application of fish otoliths to fisheries research, the mechanism of otolith formation has been insufficiently studied. In order to clarify the present status and future directions of such basic research, I briefly review here the recent cytological studies on the structure and functions of the teleost inner ear epithelium. The mechanism of otolith formation must be studied from the two points of views; that is, ion transport and matrix synthesis, since the otolith is composed of calcium carbonate crystals (Carlström 1963) and organic matrix (Mugiya 1968). In the present review, the structure and distribution of ion-transporting cells and otolith-matrix-producing cells in the saccular epithelium will be described with special emphasis.

GROSS STRUCTURE OF THE TELEOST OTOLITH ORGANS

Gross structure of the teleost otolith organs was well documented in Lowenstein (1971) and a good example of tilapia (*Oreochromis niloticus*) otolith organs was described in detail by Saitoh and Yamada (1989). In brief, teleost otolith organs consist of three membranous sacs called the utriculus, sacculus, and lagena, each containing a single dense calcareous otolith called the lapillus, sagitta, and asteriscus, respectively. In most of species, the sagitta is the largest among the three otoliths and most frequently used for the fisheries research. Histological characteristics of the otolith organs are thus best documented in the sacculus. The present review will also deal with the sacculus unless otherwise noticed.

HISTOLOGICAL CHARACTERISTICS OF THE SACCULUS

Histological characteristics of the sacculus were documented in tilapia (Saitoh and Yamada 1989), rainbow trout (*Oncorhynchus mykiss*; Mayer-Gostan et al. 1997, Takagi and Takahashi 1999), and turbot (*Scopthalumus maximus*; Mayer-Gostan et al. 1997). A schematic representation of the transverse section of the teleost fish sacculus is shown in Figure 1. The saccular wall is a single-layer epithelium surrounded by a thin connective tissue layer. Three types of epithelia, i.e., the sensory epithelium, transitional epithelium and squamous epithelium, are distinguished. The thickest part of the epithelium is the sensory epithelium which is composed of sensory hair cells and supporting cells. Nuclei of these cells are stratified in two layers; hair cell nuclei are lined in the apical zone and supporting cell nuclei in the basal. Another type of cells, the columnar cells which are laying the most peripheral region of the sensory epithelium, is distinguished in the rainbow trout and the turbot. Eighth nerve fibers are innervated into the sensory hair cells. Next to the sensory epithelium, the transitional epithelium is extended, which gradually becomes thinner to form the squamous epithelium. Mitochondria-rich cells (MRCs) are dispersed in the epithelium, but their distribution is species

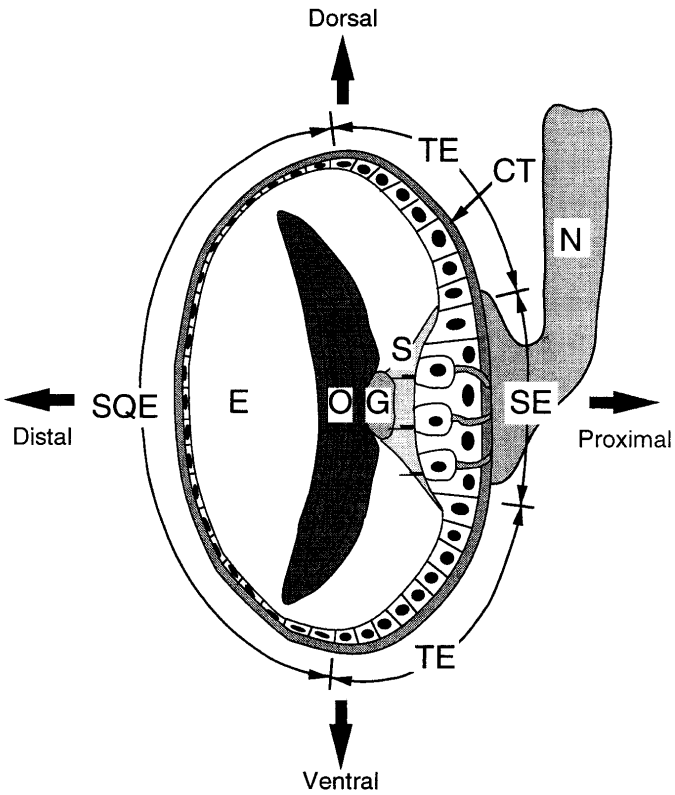

Fig. 1. Schematic representation of the transverse section of a teleost left sacculus. The saccular wall is a single-layer epithelium surrounded by a thin connective tissue layer (CT). The saccular epithelium is divided into sensory epithelium (SE), transitional epithelium (TE) and squamous epithelium (SQE). The eighth nerve fibers (N) are innervated into the SE. The otolith membrane, which is composed of a subcupular meshwork (S) and a gelatinous layer (G), fixes the otolith (O) over the SE. The sacculus is filled with endolymph (E). Mitochondria-rich cells are dispersed in the epithelium, but they are not drawn in the figure because their distribution varies depending on the species.

specific. The otolith membrane, which is composed of a subcupular meshwork and a gelatinous layer, fixes the sagitta over the sensory epithelium. The sacculus is filled with endolymph.

ION-TRANSPORTING CELLS IN THE SACCULAR EPITHELIUM

Electrolyte composition of the saccular endolymph was studied in several teleost species (Enger 1964, Fänge et al. 1972, Kalish 1991, Payan et al. 1997, 1999) and was best documented in the rainbow trout (Mugiya and Takahashi 1985, Takagi 1997, Payan et al. 1997, 1998, 1999). The most characteristic feature of the saccular endolymph is a high potassium concentration compared with plasma. In the rainbow trout, the endolymph potassium levels were reported to be 34–124 mM. Bicarbonate concentrations are much higher in the endolymph than in the plasma, whereas calcium concentrations are lower in the endolymph (Mugiya and Takahashi 1985, Takagi 1997, Payan et al. 1997, 1998, 1999).

Since the sagitta grows in the endolymph without touching the saccular epithelium, the electrolyte composition and concentrations of the endolymph, including calcium and bicarbonate, must be finely regulated in order to lead stable

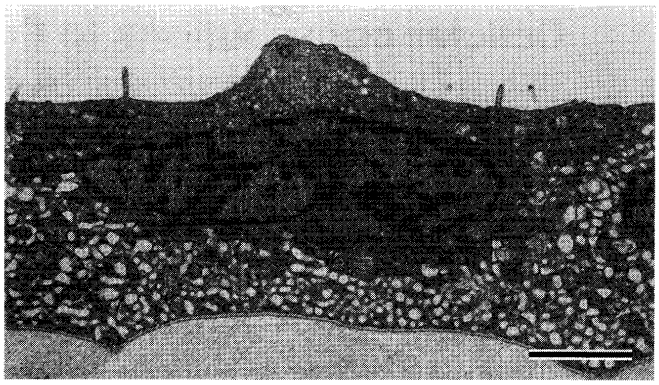

Fig. 2. A small flat mitochondria-rich cell in the squamous epithelium of the rainbow trout sacculus. Bar=2 μm.

crystallization of calcium carbonate onto the sagitta. Ultrastructural studies suggest that the MRCs and the squamous epithelial cells in the saccular epithelium are responsible for the regulation of the endolymph electrolyte composition.

The MRCs. The MRCs are characterized by abundant mitochondria in the cytoplasm. Size, shape and distribution of the MRCs in the sacculus varied greatly depending on the species. For example, in the tilapia, MRCs are squamous or cuboidal in shape and are distributed in the lateral wall of the sacculus forming an oval patch (Saitoh and Yamada 1989, Saitoh 1990). In the rainbow trout, on the other hand, they are located in the transitional epithelium around the sensory epithelium and form dense meshwork, spreading cellular processes and connecting each other (Mayer-Gostan et al. 1997, Takagi 1997). In the rainbow trout, flattened small MRCs are also localized in patches in the squamous epithelium opposite to the sensory epithelium (Mayer-Gostan et al. 1997, Pisam et al. 1998, Takagi unpublished observations, Fig. 2). In brown trout (*Salmo trutta fario*), the MRCs are distributed in the utriculus but not in the sacculus (Becerra and Anadón 1993).

Ultrastructure of the MRCs is described in blue gourami (*Trichogaster trichopterus*; Popper and Hoxter 1981), tilapia (Saitoh and Yamada 1989, Saitoh 1990), goldfish (*Carassius auratus*; Saitoh 1990), brown trout (Becerra and Anadón 1993), rainbow trout (Takagi 1997, Pisam et al. 1998), and turbot (*Psetta maxima*; Pisam et al. 1998). The most distinct cytological features of the MRCs are the presence of abundant mitochondria and highly developed system of anastomosing membranous tubules. The tubules open to the basolateral membrane of the cell. All these characteristic features are common to the cells involved in active ion transport. Moreover, the MRCs are rich in Na^+, K^+-ATPase (Mayer-Gostan et al. 1997, Takagi 1997), which is an enzyme directly or indirectly associated with the transepithelial transport of various ions in the ion-transporting cells (cf. De Renzis and Bornancin 1984, McCormick 1995). However, actual ion species which are transported by the MRCs are unknown at present.

The squamous epithelial cells. In tilapia (Saitoh and Yamada 1989), the lateral membranes of the squamous epithelial cells show complex infoldings forming the intercellular canalicular system. I found similar lateral-membrane infoldings in the rainbow trout squamous epithelial cells

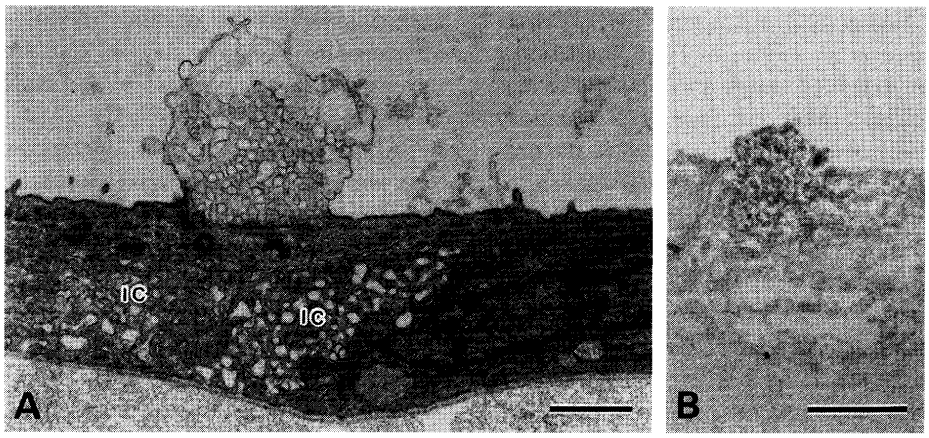

Fig. 3. Squamous epithelial cells of the rainbow trout sacculus. A. The lateral membrane of the squamous epithelial cells have complex infoldings forming the intercellular canalicular system (IC). A vesicle is arising from the apical surface of the cell. Bar=1 μm. B. The vesicle arising from the squamous epithelial cell shows the positive reaction (black precipitates) toward the antiserum against the EDTA-soluble otolith matrix. Bar=1 μm.

(Fig. 3A). The small flattened MRCs located in the squamous epithelial cells in the rainbow trout and the turbot also have similar structures (Pisam et al. 1998). Pisam et al. (1998) suggested that the small flattened MRCs are responsible for the secretion of potassium, which is highly concentrated in the endolymph, since similar lateral-membrane infoldings are observed in potassium-secreting epithelia in other animals (Berridge 1970, Ellis and Goertemillar 1974). Saitoh and Yamada (1989) suggested that the tilapia squamous epithelium was involved in the humoral control of the endolymph. Therefore, it is highly likely that the squamous epithelial cells other than MRCs are also involved in the ion transport.

OTOLITH-MATRIX-PRODUCING CELLS IN THE SACCULAR EPITHELIUM

The otolith organic matrix includes proteins, carbohydrates and lipids (Mugiya 1968), and generally divided into two fractions, water-soluble and -insoluble fractions. Both fractions are mainly composed of proteins and rich in acidic amino acids (Degens et al. 1969, Baba et al. 1991, Asano and Mugiya 1993, Sasagawa and Mugiya 1996). Some components of the water-soluble fractions have calcium-binding capacity and have been suggested to have important roles in mineralization of the otolith (Baba et al. 1991, Asano and Mugiya 1993, Sasagawa and Mugiya 1996). Several glycoproteins have also been biochemically demonstrated in the otolith matrix (Baba et al. 1991, Asano and Mugiya 1993, Sasagawa and Mugiya 1996).

Baba et al. (1991) reported that almost all the cells in the saccular epithelium of walleye pollock (*Theragra chalcogramma*) were positive to the antiserum against the whole otolith matrix and suggested these cells as otolith-matrix-producing cells. However, they did not distinguish MRCs in their study. Takagi and Takahashi (1999) showed that trout MRCs were immunonegative toward the antibody raised against the EDTA-soluble proteins of the otolith. Thus, the results of Baba et al. (1991) may indicate that all the saccular epithelial cells, except for the MRCs, are otolith-matrix-producing cells. In the present review, functions of each epithelium in the sacculus on the otolith-matrix production are discussed independently.

The sensory epithelium. In tilapia (Saitoh and Yamada 1989) and rainbow trout (Takagi unpublished observations), both the sensory hair cells and supporting cells are equipped with apocrine-like extrusions of cytoplasm and dilations of vesicles. These cells are also reported to contain rough endoplasmic reticulum and Golgi apparatus in the rainbow trout and the turbot (Pisam et al. 1998). In the rainbow trout and turbot, the columnar cells laying the most peripheral region of the sensory epithelium have highly extended and dilated endoplasmic reticulum and contain electron-dense spherical granules (Pisam et al. 1998, Takagi and Takahashi 1999). Apical membrane of these cells are frequently equipped with the dilations of vesicles (Takagi and Takahashi 1999). These data strongly suggest that all the cells in the sensory epithelium have secretory function. Although the data available at present suggest that the sensory epithelial cells produce the component(s) of otolith matrix or otolith membrane, there is still controversy on the nature of the secretory products. Baba et al. (1991) reported that the antibody against the calcium-binding protein, which was contained in the walleye pollock otolith, reacted with the sensory hair cells. Because the calcium-binding protein was extracted from the otolith with 10% EDTA solution, their result indicates that the hair cells produce one of the EDTA-soluble proteins of the otolith matrix. In the rainbow trout, on the other hand, the columnar cells laying the most peripheral region of the sensory epithelium are involved in the production of otolith matrix, since the antibody against the EDTA-soluble otolith matrix strongly bound with the columnar cells but showed no specific reaction with the sensory hair cells and the supporting cells (Takagi and Takahashi 1999). In contrast, Davis et al. (1997) reported that the cells at the edge of the sunfish saccular sensory epithelium produce the 95 kDa glycoprotein which was specifically contained in the otolith membrane. They considered these cells as supporting cells. From the morphological characteristics and their localization, however, these cells may be equivalent to the columnar cells in the rainbow trout.

The transitional epithelium. No species difference is evident in the ultrastructure of the transitional epithelium among tilapia (Saitoh and Yamada 1989), rainbow trout

(Pisam et al. 1998, Takagi and Takahashi 1999, Takagi 2000) and turbot (Pisam et al. 1998). In brief, transitional epithelial cells contain extended rough endoplasmic reticulum, prominent Golgi apparatus and numerous secretory granules, indicating that these cells are involved in the production of proteinaceous materials. The apical surface of these cells are frequently associated with cytoplasmic extrusions and vesicles, which confirms the secretory activity of these cells. The transitional epithelial cells of the rainbow trout contain two types of secretory granules which are immunoreactive to the antibody against the EDTA-soluble otolith matrix (Takagi 2000). Therefore, the transitional epithelium in the rainbow trout certainly produces the otolith matrix. Considering the close similarities in their ultrastructures among several teleost species, it is most probable that the transitional epithelium is generally involved in the production of the otolith matrix.

The squamous epithelium. The squamous epithelial cells also have secretory functions, and nature of the secretory products of these cells has been best documented in the rainbow trout. Like the squamous epithelial cells of the walleye pollock, those of the rainbow trout are also immunopositive toward the antibody against the EDTA-soluble otolith matrix (Takagi and Takahashi 1999). The ultrastructural features of the immunoreactive cells indicate that these cells produce and secrete proteinaceous material(s) (Takagi and Takahashi 1999). It is also reported that the secretory granules contained in the apical part of the trout squamous epithelial cells react with the antibody against the EDTA-soluble otolith matrix (Takagi 2000). Moreover, the vesicles arising from the apical surface of the trout squamous epithelial cells are also immunoreactive to the antibody (Fig. 3B). All these data indicate that the squamous epithelial cells are involved in the production of the otolith matrix. As described above, the squamous epithelial cells have intercellular canalicular system, and thus are suggested to have ion-transporting activity. I found that the squamous epithelial cells with the intercellular canalicular system have secretory activity in the rainbow trout (Fig. 3A). Therefore, the squamous epithelial cells in the rainbow trout may have multiple functions, ion transport and otolith-matrix production. Saitoh and Yamada (1989) reported that the squamous epithelial cells of tilapia also have the intercellular canalicular system and secretory blebs. They suggested, however, that the squamous epithelium is involved in the humoral control of the endolymph. Further comparative studies on the nature of secretory products of the squamous epithelial cells in fishes other than the rainbow trout are required.

SUMMARY AND FUTURE DIRECTIONS

In the present review, the structure and distribution of ion-transporting cells and otolith-matrix-producing cells in the saccular epithelium are described. In the teleost sacculus, the MRCs and the squamous epithelial cells are suggested to have ion-transporting activity. However, the ion species transported by these cells are yet unknown. Especially, precise understanding of the transport mechanisms of calcium and bicarbonate, and of the distribution of such transport systems in the saccular epithelium is essential to elucidate the mechanism of calcium carbonate crystallization onto the otolith. Identification of various ion-transporting proteins, such as Ca^{2+}-ATPase and Na^{+}/Ca^{2+} exchanger, is prerequisite to the clarification of their ion-transporting mechanisms.

Although the number of species examined so far is not yet enough, the transitional epithelium and the squamous epithelium are responsible for the production of otolith matrix. The sensory epithelium also have some secretory functions; however, controversial results have been reported on the nature of the secretory product(s). The detailed nature of secretory products of each cell type remains to be investigated in future. In order to determine the secretory product(s) of each cell, immunohistochemistry with the specific antibody for each component of the otolith matrix and the otolith membrane is inevitable. Only the producing cells of the 42 kDa calcium-binding protein of the walleye pollack otolith and those of the 95 kDa glycoprotein of the sunfish otolith membrane have been identified. Further characterization of each component of the otolith matrix is essential to understand the cellular mechanism of the otolith matrix production.

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LITERATURE CITED

Asano, M. and Mugiya, Y. 1993. Biochemical and calcium-binding properties of water-soluble proteins isolated from otoliths of the tilapia, *Oreochromis niloticus*. Comp. Biochem. Physiol. 104B: 201–205.

Baba, K., Shimizu, M., Mugiya, Y. and Yamada, J. 1991. Otolith matrix proteins of walleye pollock; biochemical properties and immunohistochemical localization in the saccular tissue. *In* Mechanisms and phylogeny of mineralization in biological systems. Suga, S. and Nakahara, H. (eds.), pp. 57–61, Springer-Verlag, Tokyo.

Becerra, M. and Anadón, R. 1993. Fine structure and development of ionocyte areas in the labyrinth of the trout (*Salmo trutta fario*). J. Anat. 183: 463–474.

Berridge, M. J. 1970. A structural analysis of intestinal absorption. Symp. R. Ent. Soc. Lond. 5: 135–151.

Carlström, D. 1963. A crystallographic study of vertebrate otoliths. Biol. Bull. 125: 441–463.

Davis, J. G., Burns, F. R., Navaratnam, D., Lee, A. M., Ichimiya, S., Oberholtzer, J. C. and Greene, M. I. 1997. Identification of a structural constituent and one possible site of postembryonic formation of a teleost otolithic membrane. Proc. Natl. Acad. Sci. USA 94: 707–712.

Degens, E. T., Deuser, W. G. and Haedrich, R. L. 1969. Molecular structure and composition of fish otoliths. Mar. Biol. 2: 105–113.

De Renzis, G. and Bornancin, M. 1984. Ion transport and gill ATPases. *In* Fish physiology, Vol. XB Gills. Hoar, W.S. and Randall, D. J. (eds.), pp. 65–104, Academic Press, New York.

Ellis, R. A. and Goertemillar, C. C. 1974. Cytological effects of salt-stress and localization of transport adenosine triphosphatase in the lateral nasal glands of the desert iguana, *Dipsosaurus dorsalis*. Anat. Rec. 180: 285–298.

Enger, P. S. 1964. Ionic composition of the cranial and labyrinthine fluids and saccular D.C. potentials in fish. Comp. Biochem. Physiol. 11: 131–137.

Fänge, R., Larsson, Å. and Lidman, U. 1972. Fluids and jellies of

the acousticolateralis system in relation to body fluids in *Coryphaenoides rupestris* and other fishes. Mar. Biol. 17: 180–185.

Kalish, J. M. 1991. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74: 137–159.

Kawakami, Y., Mochioka, N., Morishita, K., Tajima, T., Nakagawa, H., Toh, H. and Nakazono, A. 1998. Factors influencing otolith strontium/calcium ratios in *Anguilla japonica* elvers. Environ. Biol. Fishes 52: 299–303.

Lowenstein, O. 1971. The labyrinth. *In* Fish physiology, Vol. V Sensory systems and electric organs. Hoar, W.S. and Randall, D. J. (eds.), pp. 207–240, Academic Press, New York.

Mayer-Gostan, N., Kossmann, H., Watrin, A., Payan, P. and Boeuf G. 1997. Distribution of ionocytes in the saccular epithelium of the inner ear of two teleosts (*Oncorhynchus mykiss* and *Scophthalmus maximus*). Cell Tissue Res. 289: 53–61.

McCormick, S. D. 1995. Hormonal control of gill Na^+,K^+-ATPase and chloride cell function. *In* Cellular and molecular approaches to fish ionic regulation. Wood, C. M. and Shuttleworth, T. J. (eds.), pp. 285–315, Academic Press, New York.

Mugiya, Y. 1968. Calcification in fish and shell-fish—VII. Histochemical similarities between the otolith and the macula region of sacculus in juvenile rainbow trout, with special reference to the otolith formation. Bull. Japan. Soc. Sci. Fish. 34: 1096–1106.

Mugiya, Y. and Takahashi, K. 1985. Chemical properties of the saccular endolymph in rainbow trout, *Salmo gairdneri*. Bull. Fac. Fish. Hokkaido Univ. 36: 57–63.

Otake, T. and Uchida, K. 1998. Application of otolith microchemistry for distinguishing between amphidromous and non-amphidromous stocked Ayu, *Plecoglossus altivelis*. Fisheries Sci. 64: 517–521.

Pannella, G. 1971. Fish otoliths: Daily growth layers and periodical patterns. Science 173: 1124–1127.

Payan, P., Kossmann, H., Watrin, A., Mayer-Gostan, N. and Boeuf, G. 1997. Ionic composition of endolymph in teleosts: Origin and importance of endolymph alkalinity. J. Exp. Biol. 200: 1905–1912.

Payan, P., Borelli, G., Boeuf, G. and Mayer-Gostan, N. 1998. Relationship between otolith and somatic growth: consequence of starvation on acid-base balance in plasma and endolymph in the rainbow trout *Oncorhynchus mykiss*. Fish Physiol. Biochem. 19: 35–41.

Payan, P., Edeyer, A., De Pontual, H., Borelli, G., Boeuf, G. and Mayer-Gostan, N. 1999. Chemical composition of saccular endolymph and otolith in fish inner ear: lack of spatial uniformity. Am. J. Physiol. 277: R123–R131.

Pisam, M., Payan, P., LeMoal, C., Edeyer, A., Boeuf, G. and Mayer-Gostan, N. 1998. Ultrastructural study of the saccular epithelium of the inner ear of two teleosts, *Oncorhynchus mykiss* and *Psetta maxima*. Cell Tissue Res. 294: 261–270.

Popper, A. N. and Hoxter, B. 1981. The fine structure of the sacculus and lagena of a teleost fish. Hear. Res. 5: 245–263.

Radtke, R. L., Dempson, J. B. and Ruzicka, J. 1998. Microprobe analyses of anadromous arctic charr, *Salvelinus alpinus*, otoliths to infer life history migration events. Polar Biol. 19: 1–8.

Saitoh, S. 1990. Localization and ultrastructure of mitochondria-rich cells in the inner ears of goldfish and tilapia. Jpn. J. Ichthyol. 37: 49–55.

Saitoh, S. and Yamada, J. 1989. Ultrastructure of the saccular epithelium and the otolithic membrane in relation to the otolith growth in tilapia, *Oreochromis niloticus* (Teleostei: Cichlidae). Trans. Amer. Micr. Soc. 108: 223–238.

Sasagawa, T. and Mugiya, Y. 1996. Biochemical properties of water-soluble otolith proteins and the immunobiochemical detection of the proteins in serum and various tissues in the tilapia *Oreochromis niloticus*. Fisheries Sci. 62: 970–976.

Secor, D. H. and Piccoli, P. M. 1996. Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19: 778–793.

Secor, D. H., Dean, J. M. and Campana, S. E. 1995a. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Secor, D. H., Henderson-Arzapalo, A. and Piccoli, P. M. 1995b. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? J. Exp. Mar. Biol. Ecol. 192: 15–33.

Takagi, Y. 1997. Meshwork arrangement of mitochondria-rich, Na^+,K^+-ATPase-rich cells in the saccular epithelium of rainbow trout (*Oncorhynchus mykiss*) inner ear. Anat. Rec. 248: 483–489.

Takagi, Y. 2000. Ultrastructural immunolocalization of the otolith water-soluble matrix in the inner ear of rainbow trout just-hatched fry. Fisheries Sci. 66: 71–77.

Takagi, Y. and Takahashi, A. 1999. Characterization of otolith soluble-matrix producing cells in the saccular epithelium of rainbow trout (*Oncorhynchus mykiss*) inner ear. Anat. Rec. 254: 322–329.

Tzeng, W. N. 1996. Effects of salinity and ontogenic movements on strontium : calcium ratios in the otoliths of the Japanese eel, *Anguilla japonica* Temminck and Schlegel. J. Exp. Mar. Biol. Ecol. 199: 111–122.

Tzeng, W. N., Severin, K. P. and Wickstrom, H. 1997. Use of otolith microchemistry to investigate the environmental history of European eel *Anguilla anguilla*. Mar. Ecol. Prog. Ser. 149: 73–81.

魚類耳石形成における細胞の役割（総説）

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耳石は硬骨魚類の最も信頼性の高い齢査定形質として水産学上用いられているが，その形成機構には不明な点が多い．本総説では耳石形成に関与する内耳上皮細胞の形態と機能に関する研究をレビューし，今後の研究の方向性を探る．内耳小嚢上皮におけるイオン輸送はmitochondria-rich cellsと扁平上皮細胞において行われている．今後これらの細胞で実際に輸送されているイオンの種類やそのメカニズムに関する研究が必要である．特に耳石の構成成分であるカルシウムイオンと重炭酸イオンの輸送機構や，それがどの細胞で行われているかを知ることが，耳石形成機構を解明する上で必要不可欠である．一方，耳石有機基質は移行上皮細胞と扁平上皮細胞において産生されている．感覚上皮細胞も分泌活性を有するが，その産生物に関してはいまだに一定の見解が得られていない．今後，各細胞の分泌物の性状に関する詳細な研究が必要である．

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