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R. P. Rodríguez Mendoza: Otoliths and their applications in fishery science

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Review article

OTOLITHS AND THEIR APPLICATIONS IN FISHERY SCIENCE

R. P. Rodríguez Mendoza

Summary

Otoliths are structures located in the inner ear cavity of all teleost fish and serve as a balance organ and also aid in hearing. They have been used traditionally to obtain information about the taxon, age and size of fishes. This is very important because age, growth rate, and mortality rate are three of the most influential life history characteristics controlling the productivity of fish populations. Besides age and growth determination, otoliths have been the object of study in many different fields, such as fish biology (hearing and balance in fishes), larval fish ecology, species identification, fish stock identification and environmental reconstruction of the fish habitat. Thus, the purpose of this paper is to provide an overview of the traditional and current applications of the otoliths. Also, a short description of the traditional methods for age determination is included.

Keywords: otolith, fish, age determination, growth, developments, composition, identification

INTRODUCTION

Otoliths are structures located in the inner ear cavity of all teleost fish. They are isolated within a semi permeable membrane and bathed in an endolymphatic fluid. These structures serve as a balance organ and also aid in hearing (Campana, 1999; Campana and Thorrold, 2001). The structure of the otoliths is three dimensional but they do not necessarily grow at the same rate equally in all dimensions. Also, the size and shape vary considerably among species (Campana and Thorrold, 2001).

Otoliths are composed mainly of calcium carbonate ($CaCO_3$) mostly in the form of aragonite. Aragonite is also found in coral and sclerosponge skeletons,

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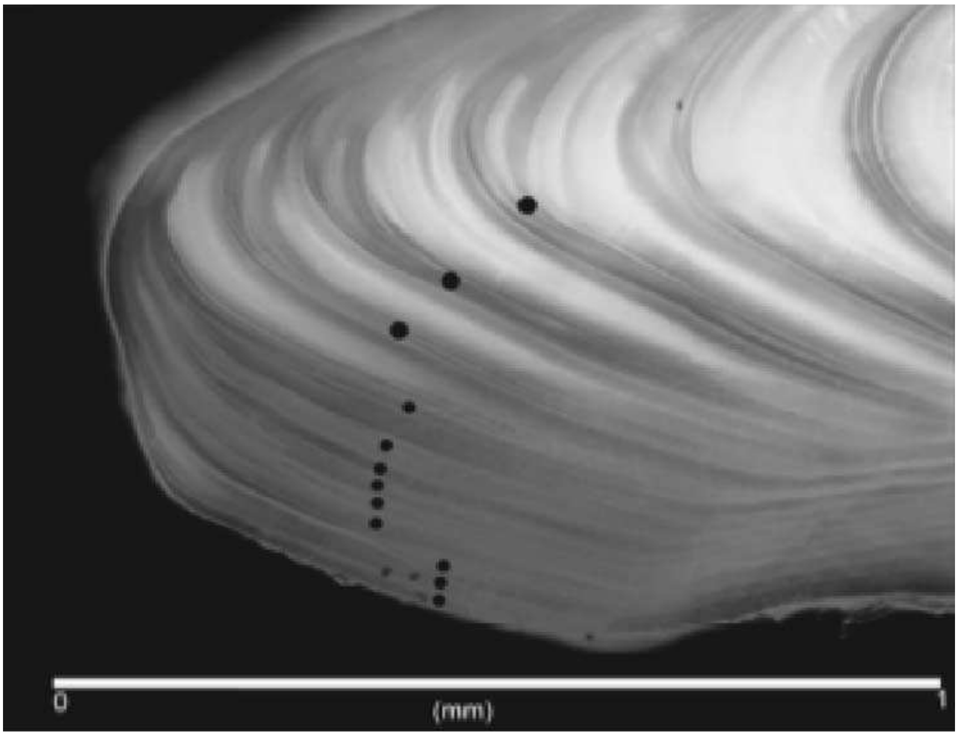

*Fig. 1. Transverse section of a yellowtail flounder (*Limanda ferruginea*) otolith (46 cm female), revealing the annuli (black dots). From: Campana and Thorrold (2001).*
*Slika 1. Poprečni presjek otolita žutorepe plosnatice (*Limanda ferruginea*) u 46 cm dugačke ženke s vidljivim anulima (crne točke). Izvor: Campana i Thorrold (2001).*

bivalve shells, and squid statoliths. The other 10 % of the otolith is minor and trace elements within the aragonite matrix that are derived from the water surrounding the fish. These impurities reflect the water chemistry, as well as the fish's metabolism (Telmer, 2004; Campana and Thorrold, 2001).

The pattern in the otolith is composed of a number of concentric shells with different radii. Depending on the amount of organic material in each shell or zone, its appearance will vary from extremely opaque to complete hyaline (transparent). The first zone is the nucleus of the otolith. The opaque zones in the otoliths are formed during the period of greatest growth and the hyaline zone is laid down usually during the period of slowest growth. These zones are also called rings (Fig. 1).

Any major change in the environment in which a fish lives is likely to produce a ring. In the earth's temperate zones differences between summer

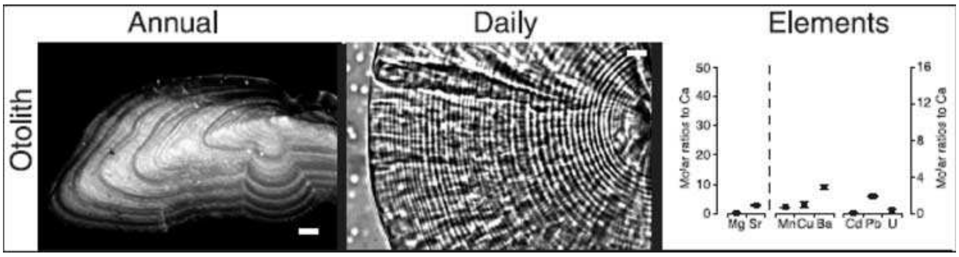

*Fig. 2. Representative growth patterns and elemental composition of fish otoliths. The images of annual patterns are from Atlantic cod (*Gadus morhua*). The daily increment images are from Atlantic herring (*Clupea harengus*) Scale bar = 1 mm for annual patterns and 10 mm for daily patterns. From: Campana and Thorrold (2001).*
*Slika 2. Reprezentativni uzorci rasta i elementalnog sastava ribljih otolita. Slike godišnjih uzoraka potječu od atlantskog bakalara (*Gadus morhua*). Slike dnevnih inkrementacija potječu od atlantske haringe (*Clupea harengus*). Mjerilo iznosi 1 mm za godišnje uzorke i 10 mm za dnevne uzorke. Izvor: Campana i Thorrold (2001).*

and winter are marked by both changes in water temperatures and amounts of food available. Equally marked changes occur also in the tropics, for example, many rivers are subject to seasonal floods. During the floods, food is abundant and the fish grow rapidly. In the dry season the food becomes scarce and the fish very often starve. Still, some fish live in uniform environments, notably in the polar and tropical regions and consequently no rings whatsoever are laid down in their skeletal structures (Holden and Raitt, 1974).

Daily increments of growth have been detected on fish otoliths (Fig. 2). The width of these increments averages 1 to 2 µm in larval anchovies (*Engraulis mordax*) and 3 to 4 µm in the larger hake (*Merluccius* spp.), (Moyle and Cech, 2004). In a recent study, daily increments were also found in juvenile skipjack tuna (*Katsuwonus pelamis*) otoliths, measuring 15–40 µm (Tanabe et al., 2003).

One of the most appreciated characteristics of the otoliths is the lack of resorption. This means that once the material has been deposited, the organism will not use again these minerals even in periods of starvation. Lack of resorption is not shared with any other calcified structure (like scales and bones) in fish or other vertebrates (Bilton, 1974 cited by Campana and Thorrold, 2001). Another special characteristic of otoliths is that they form the only calcified structures known to grow throughout the lifetime of the fish in a continual way.

All the facts mentioned before provide the basis on which otoliths can be used as powerful tools for age determination. This is very important because age, growth rate, and mortality rate (growth and mortality are both based on age information) are three of the most influential life history characteristics controlling the productivity of fish populations.

Besides age and growth determination, otoliths have been the object of study in many in different fields, such as, fish biology (hearing and balance in fishes), larval fish ecology, species identification, fish stock identification, environmental reconstruction of the fish habitat (Campana, 1999; Brazner et al., 2004; Campana, 2005; Humphreys et al., 2005; Popper et al., 2005).

Thus, the purpose of this paper is to provide an overview of the traditional and current applications of the otoliths in Fishery Science.

TRADITIONAL USES OF OTOLITHS

Age determination of fishes

Otoliths are a focus of attention by fisheries scientists because of the precision of age estimates based on annuli and the relative ease of otolith preparation and annuli enumeration. Indeed, the clarity of annual increments in the otoliths of fish species from both marine (e. g., *Pogonias cromis*; Campana and Jones, 1998) and freshwater habitats (*Aplodinotus grunniens*; Pereira et al., 1995) can be quite remarkable (Campana and Thorrold, 2001).

The exact age determination of fish is one of the most important elements in the study of their population dynamics. It forms the basis for calculations leading to knowledge of the growth, mortality, recruitment and other fundamental parameters of their populations (Holden and Raitt, 1974).

Thus, otoliths provide some of the best examples of biochronologies in the animal kingdom, combining annual sequences of up to 110 years in adult fishes with daily chronologies of up to a year during the larval and juvenile stages (Campana and Thorrold, 2001).

Age estimation of most larval and juvenile fishes is possible thanks to the presence of easily discernable daily increments in otoliths, making a remarkably accurate and precise method (Campana and Neilson, 1985; Tanabe et al., 2003).

These data have been used to determine growth rates during early life history, estimate pelagic larval durations of reef–associated species, and examine the effects of physical processes on larval survival through back–calculation of hatch date distributions. It is also possible to reconstruct instantaneous daily growth rates of larval fish from increment width trajectories, based on an empirical relationship between otolith size and fish size (Campana and Jones, 1992).

Direct reading of the otoliths

There are several methods to prepare the otoliths that will be observed. The variety of methods used is explained in more detail in Holden and Raitt (1974). However, the simplest method is to immerse the whole otolith in a clear liquid such as water or a solution of alcohol, illuminate it from above, and view it against a dark background. This method is suitable only if the otoliths are relatively thin and translucent and all the rings can be seen.

In many species the outer rings become very narrow once the growth rate of the fish slows down. These narrow rings sometimes grow only on the underside of the otolith, and can only be seen when a cross section of the otolith is prepared. When investigating any species of fish it is always necessary to check, by examining cross section, whether these narrow rings are present before accepting an age based on viewing the whole otolith from above. Failure to understand this type of growth patterns in otoliths can result in gross underestimates of age.

In other cases, such as otoliths in the sole (*Solea solea*) and the plaice (*Pleuronectes platessa*) a different technique is used. It is called the 'burning technique'. A prepared cross section is gently burned over a very low flame until it is slightly charred. The appearance of the rings is changed and a narrow black ring is produced at each change from hyaline to opaque material reading outwards from the nucleus of the otolith (Holden and Raitt, 1974).

Then, to determine the age, opaque rings are counted from the nucleus to margin along the longest axis of the otolith. The periodicity in the formation of the rings must also be established.

Another important step when determining age of fish is age validation. Age validation studies are required for accurate age determination and are essential for fisheries catch–at–age models, to assess the health of a fishery resource or to correctly interpret the dynamics of a fish population.

Validation methods include chemical marking, using oxytetracycline, length–frequency, and identification of the first annulus, marginal increment analysis, tag–recapture analysis and bomb radiocarbon assays to assess the accuracy of these age determination methods and examine growth (Dwyer et al., 2003).

One of the most used methods (because of its relative simplicity), is the marginal increment method (MI). It is based on estimating the marginal increment of the otolith of each fish for age class and estimates the profile of the mean monthly marginal increment. The marginal increment is measured as the distance from the inner margin of the outermost translucent ring to the periphery of the otolith. Measurements are always made along the longest axis.

The marginal otolith increment increases when an opaque band forms and drops to zero when a new translucent band begins to form. If increments are formed yearly, the mean marginal increment over time should show one mode and the peak should correspond to the time the yearly opaque ring formed; in this case the age corresponds to the increment. The size of the growth zone varies with time of sampling during the year and the age of the fish. Because younger fish grow faster than older individuals, a larger marginal increment is expected. For this reason, quantitative marginal increment analyses should be standardized for age (Pajuelo and Lorenzo, 2003).

When it has been possible to view the zones or rings, count them satisfactorily and establish their formation conforms to a definite time–pattern, there is possible to age the fish.

The terms age, age group and year–class are frequently used. The age of a fish a certain period of time refers to the period of time from birth to a given point of time. When the age of the fish has been established it can be assigned to the appropriate age group which is an integral number of years according to a convention based on an arbitrarily–adopted birthday.

With these data, an age–length key is made (Table 1). Only now it is possible to fit the von Bertalanffy curve and compute the growth parameters.

Back–calculation analysis

Back–calculation analysis is often used to estimate fish length at a previous age or date. Growth back–calculations can be derived from a series of growth increments (either daily or yearly) and represent one of the most powerful applications of the otolith. Since the fish length: otolith length relationship can be determined, the widths of the daily (or yearly) growth increments in an otolith reflect the daily (or yearly) growth rates of the fish at that age and on those dates (Campana, 2004a).

For example, one of the most used methods for doing this is based on a body proportional hypothesis applied to a power relationship between the fish length and the otolith radius (Francis, 1990 cited by Pajuelo and Lorenzo, 2003) (Fig. 3). Other methods use regression and the Fraser–Lee equation.

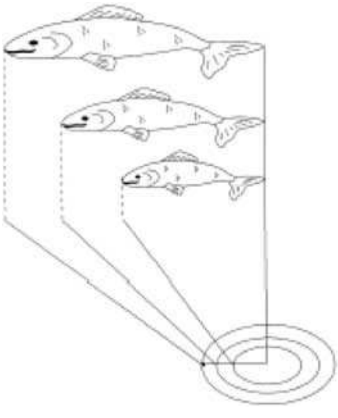

Fig. 3. A simple example using otolith back–calculations to estimate retrospective growth histories of fish. From: Jones (1992).
Slika 3. Jednostavan primjer uporabe otolita za procjenu retrospektivnog rasta ribe s pomoću povratnog izračuna. Izvor: Jones (1992).

In the method used by Francis (1990), the radius of the *i*th band (Ri) and the radius of the otolith at capture (Rc) are measured for the analysis. The first one (Ri) is the distance from the center of the otolith to the outer margin of the translucent ring. The second is the distance from the center of the otolith to the periphery.

The data can be fitted by regression of the log T L and log of the otolith radius (R). The length of an individual when the *i*th band was laid down (Li, mm) is calculated using $Li=(Ri/Rc)^{v}$ Lc, where Lc is the length at capture and v is a constant derived from the power function which describes the relationship of between the fish length and the otolith radius.

Then again, the data can be fitted to the von Bertalanffy curve and compute the growth parameters.

In a study of the growth of the common two banded seabream (*Diplodus vulgaris*), Pajuelo and Lorenzo (2003) estimated the growth parameters by the two methods described above (direct otolith reading and back–calculation methods) which gave similar results in this species.

Still, some constraints appear to most procedures in back–calculations. One of the most important is the assumption that the fish–otolith relationship is not only linear, but does not vary systematically with the growth rate of the fish. Many studies have demonstrated that otoliths of slow–growing fish tend to be larger and heavier than those of fast–growing fish of the same size, whether at the daily or yearly scale. Such a systematic variation implies that growth back–calculations made with any of the traditional equations will tend to underestimate previous lengths at age, with the degree of error varying with the range of growth rates that are present in the population (Campana, 2004a).

OTHER USES OF OTOLITHS AND RECENT DEVELOPMENTS

Otoliths have a distinct shape which is often characteristic of the species of fish (Fig. 4). Thus fish, seal and seabird biologists, as well as taxonomists and archaeologists, often rely on the shape and size of preserved or undigested otoliths to reconstruct the species and size composition of the diet of fish predators. (Campana and Casselman, 1993; Campana, 2004a). The basis for these types of studies is either a reference collection of otoliths from the local fish species or published atlases (Campana, 2005). For example, Harvey et al. (2000) presented a compilation of images of otoliths of 63 fish species of the North Pacific Ocean, including the relationship between the otolith length and fish length, Assis (2003) published a comprehensive examination of asteriscal otoliths in teleosts and Campana (2004b) published a photographic atlas of otoliths from fishes of the northwest Atlantic.

Otolith appearance and shape often vary geographically within a species, although there are mixed reports concerning the potential for stock discrimi-

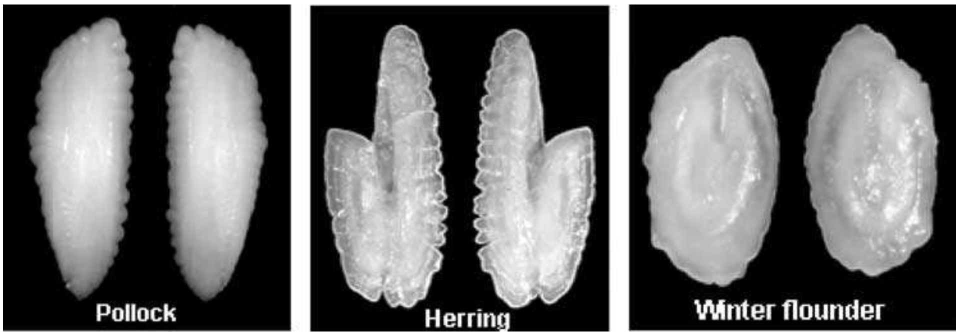

Fig. 4. Otoliths of different fish species. From: Campana (2004).
Slika 4. Otoliti različitih ribljih vrsta. Izvor: Campana (2004).

nation. In a comprehensive examination of the shape of all 3 otolith pairs, Campana and Casselman (1993) concluded that otolith shape did indeed vary among some stocks, although the stock variation appeared to be environmentally induced rather than genetically induced.

Another example using otolith morphometry was presented by Begg et al. (2001). In this case, the internal structures of the otolith where used for stock differentiation in the Georges Bank haddock (*Melanogrammus aeglefinus*). They found out differences in growth rates (and hence, otolith structure) of eastern and western Georges Bank haddock which appeared to derive mainly from differences in the stock's environmental conditions (water temperature and diet), showing the usefulness of otoliths in stock studies. Cardinale et al. (2004) used hatchery releases of cod into the wild, recaptured after several years, to demonstrate that both genetic and environmental influences control otolith shape. Several laboratory experiments confirmed that the relationship between otolith and somatic growth is mediated by temperature and/or other modifiers of growth rate, such that slow–growing fish produce relatively large otoliths (Oozeki and Watanabe, 2000; Strelcheck et al., 2003 cited by Campana, 2005).

Recent studies have used the elemental composition of the otoliths to infer the timing of day–to–day environmental changes and changes in the physical habitat For example; the change in the calcium/strontium ratio can be used in combination with increment number to estimate the dates of migration of anadromous and catadromous species (Kennedy et al., 2002). Other trace elements, such as K, Mn, Li, Mg and Ba have also proved their utility as natural tags of the nursery ground origins of juvenile fish and spacio–temporal distribution of stocks, as for the American shad (*Alosa sapidissima*) inhabiting the Connecticut, Hudson and Delaware rivers in North America (Thorrold et al., 1998), the Pacific swordfish (*Xiphias gladius*) (Humphreys et al., 2005) and the Atlantic cod stocks (*Gadus morhua*) along the north shore of Quebec in Canada (Methot et al., 2005).

The major developments using otolith microstructure (daily growth increments) for purposes other than just early life history descriptions or routine age validation, are presented in studies which used larval age composition for and/or daily increment width series to infer population exposure to regional or size–selective mortality events (Searcy and Sponaugle 2001; Pepin et al., 2002; Wilson and Meekan, 2002 cited by Campana, 2005). Otolith microstructure has also been used to determine the duration of residence as pelagic larva (Pasten et al., 2003).

The applicability of the bomb–radiocarbon (produced by the atmospheric testing of thermonuclear devices in the 1950's and 1960's) for validating the ages of long–lived species around the world was broadened when the radiocarbon histories for the northwest Pacific (Kerr et al., 2004; Kerr et al., 2005) and northeast Atlantic (Kalish et al., 2001 cited by Campana, 2005) demonstrated that the years during which the bomb signal increased were similar in other areas of the world, even if the radiocarbon levels themselves were not. A remarkable methodological advance has been the development of an improved radiochemical assay for ^{226}Ra, which improved the precision of radiometric age estimates by a factor of 2 to 10 (Andrews et al., 1999). Also, Clear et al. (2000) demonstrated the successful use of a novel otolith marker (strontium chloride) for age validation in a larger scale tag–recapture study of southern bluefin tuna, *Thunnus maccoyii*.

The most significant developments in population dynamics revolved around the use of growth–back calculations to assess the influence of size–selective mortality on previous life history stages (Campana, 2005). For example, Gronkjaer and Schytte (1999) used the radius of the otolith hatch check as an unambiguous marker to demonstrate that larvae that we smaller at hatch were less likely to survive to the first weeks of life.

Campana (2005) criticizes the fact that very few papers have been published concerning their role in fish balance and hearing, which are two of the main functions of otoliths. However, some studies have made important contribution in these areas, such as the one from Riley and Moorman (2000), who demonstrated that the lapilli, but not the sagittae, are required by the fish for balance and survival. Popper (2003) provided an important review on the effects of anthropogenic sounds on fishes. Also, Popper et al. (2005) raised several questions that still need to be answered to improve the understanding and significance of the structure and function of the ear in fishes.

Mass marking techniques of juvenile fish have also taken advantage of the recording properties of the otoliths. The sensitivity of the otolith increment characteristics to temperature changes have been used during the past two decades to induce specific patterns functioning as a permanent identifier for that fish (Volk et al., 2005). For example, continued use of this technique to manage the Prince William Sound pink salmon fishery has demonstrated greater precision of hatchery contribution estimates with far smaller sample

Table 1. Age–length key for all fish of Diplodus vulgaris *of the Canarian Archipielago (April 2000–March 2001). From: Pajuelo and Lorenzo (2003).*
Tablica 1. Ključ odnosa dob–dužina za sve Diplodus vulgaris *iz Kanarskog otočja (travanj 2000. — ožujak 2001.). Izvor: Pajuelo i Lorenzo (2003).*

Size — Veličina (mm)	Age groups (years) — Dobna skupina (godine)								
	I	II	III	IV	V	VI	VII	VIII	IX
130	7								
140	20								
150	43	3							
160	75	7							
170	59	21							
180	27	38	1						
190	9	44	3						
200	3	26	2						
210	1	12	8						
220		3	11						
230			14						
240		1	12	1					
250			11	6					
260			2	9					
270			1	6	2				
280				3	3				
290				2	4				
300					3	2			
310					1	2			
320						1	2		
330							1	1	
340								1	1
350									1
360									1
370									

sizes and much faster results than the traditional coded–wired tagging program could provide (Joyce and Evans, 2001). Otolith thermal marking is also providing unprecedent data on high seas distribution and migratory characteristics of Pacific salmon that may have important implications for predicting specific run sizes (Kawana, 2001).

Moreover, a new technique for transgenerational marking of embryonic otoliths has been recently described by Thorrold et al. (2006), promising significant advancements in the study of larval dispersal and population connectivity in marine fishes. The technique provides a new means of mass–marking larvae of benthic– and pelagic–spawning fishes from multiple populations over extended spawning periods and is based on maternal transmission of ^{137}Ba from spawning females to egg material that is ultimately incorporated into the otoliths of embryos produced.

Concluding remarks

Otoliths are one of the most reliable tools for determining the age of a fish. Since age is used to establish growth rates of a fish species and age compositions of a certain population, otoliths are a powerful tool in fisheries management. Otolith chemistry and microstructure analysis have developed greatly in the recent years and have showed a wide range of applications for stock identification and other environmental studies concerning fish habitats. However, there are still several areas of otolith research that need further development. For example, to avoid overfishing, the management of deepsea fishes requires the development of new methods to validate the age determined from the otoliths, because many species appear to have long life spans and grow slowly. Also, the development of otolith growth models, apart from improving the accuracy of back–growth calculations, would simplify the methods for reconstructing life histories and environmental exposures.

Sažetak

OTOLITI I NJIHOVA PRIMJENA U RIBARSTVU

R. P. Rodríguez Mendoza

Otoliti su strukture locirane u šupljini unutarnjeg uha svih riba iz nadreda *Teleostei* i služe kao organ za ravnotežu te također pomažu osjetilu sluha. Tradicionalno se rabe da bi se dobile informacije o klasifikaciji, dobi i veličini riba. To je izuzetno važno jer su dob, stopa rasta i stopa mortaliteta tri najbitnija životna obilježja koja kontroliraju produktivnost ribljih populacija. Osim u određivanju dobi i rasta, otoliti su bili predmet istraživanja u raznim područjima, kao što su biologija riba (sluh i ravnoteža kod riba), ekologija ribljih ličinki, određivanje vrsta, određivanje ribljega stoka i rekonstrukcije ribljega staništa. Cilj je ovog rada da pruži pregled tradicionalnih i recentnih načina primjena otolita. Osim toga, uključen je i kratak opis tradicionalnih metoda određivanja dobi.

Ključne riječi: otolit, riba, određivanje dobi, rast, razvoj, sastav, određivanje

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