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Outil, méthodes et connaissances
dans le but d’une exploitation durable
Understanding otolith biomineralization: from physico-chemical signatures to numerical modelling

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Condensé

Introduction
Fish otoliths, calcified structures located in the inner ear, are actual biological and environmental archives. Their accretionary growth results from a strict physiological control of the organism, but is influenced by the environmental conditions in which the fish lives. For instance, environmental variables such as temperature and salinity, as well as season-based or age-based metabolic variations are known to influence the deposit rate and the incorporation of chemical elements. This accretionary process often leads to the formation of a sequence of structures (rings), whose periodicity goes from the day to the season. Otolith analysis then offers a unique potential to reconstruct, at a daily and/or yearly scale, environmental parameters as well as individual life traits (age, growth patterns, migration patterns,...), and provides the mean to acquire information at different biological level: the individual level, in terms of individual life traits, the population level regarding age-based population statistics or spatio-temporal population structures, the environmental level in terms of reconstruction of temporal series of environmental parameters. Over than a million of otoliths are thus analyzed yearly worldwide for fish stock assessment as well as ecological studies.

Although otolith analysis is now recognized as an invaluable source of information, the decoding of the metabolic and environmental information archived by the otolith remains critical and new tools are needed to achieve a robust calibration of the archive. The last decade has mainly focused on the detection of significant statistical links between environmental and/or metabolic conditions and otolith signatures. Such an empirical framework actually led to significant scientific advances (eg., the calibration of $\delta^{18}O$ signal as a proxy of the temperature). However, in many situations, the otolith signal remained non-interpreted. These difficulties stress the needs for characterizing and understanding the biological basis of the biomineralization processes.
Within the framework of the project ANR JC OTOCAL, these issues have been addressed from a multidisciplinary point of view in order to characterize and to model the processes involved in the otolith formation, and their modulation by environmental factors and the physiology of the organism. Two major topics have been jointly investigated: enriching the multivariate structural and chemical characterization of fish otoliths, modelling otolith formation.

Enriching otolith characterization
To better understand otolith biomineralization processes and to bring new insight on local physico-chemical features and on global characteristics (shape, spatial distribution, etc.), news tools are required. A set of image processing tools have been developed to automate the extraction of geometric information from otolith images (otolith shape history, growth axis, growth rings etc.). It relies on a level-set representation of the 2D otolith growth and on an efficient variational setting to fit this model to a given image. Besides, regarding the physico-chemical characterization of otolith structures is concerned, previous work has mainly focused on elemental or isotopic analyses either using global (e.g., dissolved otoliths) or local (eg transects on thin slides) analytical methodologies. In contrast, in our project, a specific emphasis has been given to the characterization of the organic and mineral components of micro- and macro-scale otolith structures. Among different analytical techniques, we have demonstrated the great potential of Raman microspectrometry for jointly and quantitatively characterizing these organic and mineral fractions up to a one-micron spatial sampling resolution. Such a spatial resolution is typically in the range of a tenth to half of a daily growth increment for the considered otoliths. To be able to link observed variations with environmental parameters (eg temperature, food), most samples (juvenile and adult hakes) were obtained from fish reared in controlled conditions.

With a view to understanding and exhibiting the relationships between these various 1D and 2D signatures of the otolith sampled at different resolutions, an appropriate framework has been proposed to perform a multivariate statistical analysis adapted to otolith growth and shape.

Modelling otolith formation
Within the framework of the DEB (Dynamic Energy Budget) theory, a 2D numerical model of the accretionary growth of fish otoliths has been developed. The DEB theory provides a generic, parsimonious and biologically- and mathematically-sound formulation of the transfer of energy fluxes at the individual level. Stating otolith formation as a DEB product, otolith growth and opacity result of elementary metabolic fluxes (i.e., somatic growth and maintenance growth fluxes). In addition to this direct metabolic modulation, a biomineralization-specific temperature effect is considered as calcium carbonate precipitation is known to be temperature-dependent. From these two elementary components, this model conforms to the relationships observed empirically in different experiments regarding the effects of metabolism and environmental conditions (i.e., food availability and temperature) on global otolith characteristics (growth and opacity) and provide a clear interpretation of the interactions between these two (opposite in some cases) effects. By combining this DEB-based otolith model from otolith shape model issued from level-set representations of the 2D otolith growth estimated from images, a 2D otolith model is derived to simulate opacity otolith images accounting for opacity anisotropy. Numerical experiments for otolith data issued from controlled experiments (e.g., fish reared at constant feeding and varied temperature or conversely) provide a validation of the proposed model.
Prospect
Reported results provide new insights on the effects of fish metabolism and environmental conditions on the formation of the otolith. On one hand, the analytical characterization of the organic and mineral fractions of the otolith challenges the current view of micro- and macrostructure composition. On the other hand, model simulations validate basic concepts on otolith formation, i.e. the physiological control of the otolith formation through fish maintenance and growth energy fluxes and a temperature-dependent modulation of the precipitation of calcium carbonate.
From these novel advances, three research directions seem particularly promising: the analysis of the relationship between RAMAN otolith characterization and otolith macroscopic features (opacity, growth, etc.) as well as endolymph features (e.g., concentration in calcification precursors) under different metabolic and environmental conditions, the integration in the DEB-based model of the dynamics of chemical otolith signatures (e.g., stable isotopes, chemical elements), the exploitation of the DEB-based otolith model both for assisting in the interpretation of otolith patterns for given environmental and metabolic conditions and for reconstructing individual life traits (e.g., growth, food availability, etc.) from given otolith signatures. Regarding the latter issue, the DEB-based model is particularly appealing as it provides a mechanistic formulation to investigate the combination of otolith markers to other biochemical or electronic markers (e.g., markers of soft tissues, records of electronic tags, etc.).