

B. Historical

F.J. Meunier, J. Panfili

Estimates of the age of individual living organisms are needed in many types of studies. The methods developed to collect age information may be very old, as in the case of dendrochronology, i.e. estimating the age of trees from their annual growth rings. In fact, knowledge in this field has existed for many centuries, as was noted by Leonard de Vinci and by Montaigne (1580-1581) in accounts of his travels in Italy: "... the Artist... told me that all the trees show as many rings as they have years... The part of the trunk oriented towards the north is narrower, shows the tighter rings...; so whatever the wood that we show him, he prides oneself on being able to age the tree...". Meanwhile, the Swedish monk Hederström (1759) was the first to propose in an 18th century treatise that vertebral rings in fish could be counted to estimate their age. However, the first serious attempts for estimating the age of Vertebrates were not made until the end of the 19th century. Normally, the ages of animals were estimated on the basis of repeated features in a calcified organ or a hard tissue, for which reason the various methods were summarized by the term "sclerochronology". Within this field, more precise words were developed to characterize specialized approaches (scalimetry, otolithometry, skeletochronology).

Studies of cyclic patterns recorded in the CS of fishes are very numerous, and they cannot all be included here. However, a certain number of references concerning the theoretical aspects of this field of research are useful, as they highlight advances in our understanding of the growth of hard parts and their ability to record time (Bagenal, 1974; Bagenal & Tesch, 1978; Summerfelt & Hall, 1987; Baglinière *et al.*, 1992). These studies can be traced back to the beginning of the 20th century but the ideas and underlying background for this science were laid down even earlier.

We thus initially deal with works which gradually developed into the methodologies usually used today for bony fishes (Osteichthyans). We then consider the history of more recent work which has permitted the development of similar approaches in cartilaginous fishes (Chondrichthyans).

1. Osteichthyans

1.1. Scalimetry

Leeuwenhoek (1696), and then Réaumur (1716), suggested that concentric peaks (i.e. *circuli*) on the surface of a fish scale corresponded to

the various stages of growth. Kuntzman (1824), later challenged the validity of using the *circuli* as indicators of annual growth. Several authors concentrated on the relationship between adjacent *circuli* and plates (Agassiz, 1833-1844; Peters, 1841). Steenstrup (1861), followed by Baudelot (1873), showed that new *circuli* were added to the periphery of the scale throughout growth. Hoffbauer (1898, 1900) observed in carp that the growth of the scale was more significant in periods of food abundance and that, when food was scarce, the scale *circuli* were narrower. He then proposed the use of these structures as a means of obtaining the average age of fish and suggested practical applications based on carp.

In spite of some reservations (Brown, 1903; Tims, 1906), ichthyologists at the turn of the 20th century developed a method of individual age estimation in fishes starting from the variations in the arrangements of the circular peaks and other ornamentations on the surface of elasmoid scales (Walter, 1901; Thomson, 1904; Hoffbauer, 1905; Dahl, 1907; Esdaile, 1912, *inter alia*).

Johnston (1905, 1907, 1908, 1910) discovered and described the marks of reproduction ("spawning marks") on the scales of salmon and provided the foundations of the technique of back-calculation to follow the annual growth of fish. Dahl (1911) analysed the causes of the false marks and with Lea (1911), he gave the first practical applications of scale measurement (calculation of successive sizes in individual fish).

Conscious that the use of the scale in the age estimation rested on assumptions rather than on well established facts, Masterman (1913) published a critical study on salmon in which he demonstrated the necessity of proving the cogency of his method, by combining morphological, experimental and statistical observations. In fact, what he raised was the significant question of the validation of interpretative assumptions. In the experimental domain it was Winge (1915), on Gadidae, who developed the use of marked and recaptured animals, although Johnston (1907) had already practised this technique on salmon. Following these pioneer works, many practical studies based on scales were published in specialized reviews of ichthyology and fisheries.

The growth of the scale surface layer is indefinite and is closely linked, in certain areas and during clearly-defined seasons, with variations in the external medium. It is known that, during poor seasons, the interval separating the *circuli* is narrower and/or that new *circuli* are formed that do not match the first (Ombredane & Baglinière, 1992); this narrowing or discordance is very clear under transmitted light and was first named *annuli*. From the discovery of these *annuli* was born the measurement of scales: the age estimation of fish and estimates of individual growth (Dahl, 1907, 1911; Graham, 1929; Vibert & Lagler, 1961; Daget & Le Guen, 1975, *inter alia*).

Although empirical in its early stages at the beginning of the 20th century, scalimetry was capable of offering very satisfactory results on many occasions, in particular for the species of interest for fisheries. However, Walter (1901), Brown (1903), Dahl (1911) and others, showed that serious causes of error could appear with the occurrence of false marks or false *annuli*, because scales may also record various significant biological events and stresses (physiological wounds, shocks, poor summer conditions), whether periodical or not. Moreover, in certain species, the *annuli* are difficult to observe, making age estimation very delicate or impossible. Other species lack scales. Ichthyologists then turned to other CS, otoliths and/or bones, which also record the events that affect growth.

1.2. Otolithometry

Otolithometry is another method of age estimation that is very widely used in Teleost species (Stevenson & Campana, 1992). This branch of science was also developed at the end of the 19th century, starting with the work of Reibisch (1899). The otolith, a calcium carbonate concretion of the inner ear, with theoretically indefinite growth, is not strictly an element of the skeleton, but its mineral-bearing nature gives it similar properties as far as sclerochronology is concerned. Originally, as with scales, otoliths have been used to study seasonal and annual growth cycles, and there is now an abundant literature on the subject. Their observation as whole parts or after preparation is capable of providing accurate age estimations (Vibert & Lagler, 1961, *inter alia*). However, the discovery by Pannella (1971) of daily increments inside the otolith structure has opened up new fields of investigation. Specialists were enabled to reconstruct the specific stages in the life history of individuals, most of the time for larvae and juveniles. Otolith microstructure is thus a very sensitive recorder that covers a wide time scale. Nevertheless, the techniques used to reach the finest scale can be expensive and time-consuming. More recently, at the beginning of the 1980s, it was discovered that otoliths also incorporated chemical elements from their environment (biotic and abiotic) via complex physiological processes. Chemical analysis of otolith contents offered new methods of research and areas of interest, particularly in ecology and the reconstruction of life history traits. Here also the techniques are expensive and still under development. The number of studies of otolith works is already large, and symposia devoted solely to otolith research and its applications have already occurred during the past ten years (Secor *et al.*, 1995a; Fossum *et al.*, 2000). Recently, otoliths have been increasingly used for age estimation of fish and they are also valuable in other fields than the study of age and growth (Fossum *et al.*, 2000).

1.3. Skeletochronology

If the development of fish skeletochronology began a few years after the first steps in scale measurement, the first applications appeared, in fact, in the middle of the 18th century, with the work of Hederström (1759). This author, generally ignored, was shocked by the fabulous longevities usually ascribed at that time to common fish like pike (more than 200 years, see also Casselman, 1974). Having observed that the vertebrae of several species showed rings, he suggested that they could offer an index of age. The enumeration of these rings on the vertebrae of several species (pike, cod, perch, eel, bream) gave him, for the age of these animals, values close to those accepted today. On the basis of his results, Hederström created the foundations of stock management techniques, certainly awkward, but probably the first in the field of aquaculture. Published in Swedish this work remained unknown for many years and it was necessary to wait until 1904 to find studies based on bones, in connection with scales and otoliths (Heincke, 1904, 1908; Cunningham, 1905). An endorsement must be made on the work of Clerk (1927), the first modern author to develop skeletochronology. He made a comparative study of the "growth periodicity of bones" in Osteichthyans, Amphibians and Mammals. He insisted much on the fact that growth is a complex phenomenon under the control of external factors (such as the influence of the environment and the climate) as well as internal factors. He recognized that cyclic structures appear in the periostic bone and showed that certain bones, through the abundance of their periostic formations, are more suitable than others for the analysis of the cyclic growth on the one hand, and that the processes of rebuilding involves the destruction of these structures on the other.

The range of the tools for skeletochronological studies grew rapidly, from hard spines to soft fin rays, endoskeletal parts of pectoral fins, *cleithra*, supra-occipital, opercular, vertebrae. Menon (1950) drew up an exhaustive list species by species. Authors usually employ either whole parts or slices, exploiting the differences in transparency of the osseous layers deposited during the seasons: opaque zones during the growing season, translucent *annuli* during slow growth. When the *annulus* is reduced to a narrow line of annual growth cessation, a simple histological method earlier developed for Tetrapods (Klevezal & Kleinenberg, 1967; Smirina, 1974; Pascal & Castanet, 1978, *inter alia*), based on staining with haematoxyline, facilitates the observation of these chromophilic rings (Meunier *et al.*, 1979; Boët, 1981; Meunier & Pascal, 1981). The use of bones for age estimation is nevertheless limited to Osteichthyans species, in which scalimetry and otolithometry give doubtful results. Access to the skeleton is often more difficult than the simple removal of scales, or even of otoliths.

2. Chondrichthyans

The first works on sclerochronology for Chondrichthyans are much more recent (by at least a half century) than those relating to Osteichthyans. Sharks and skates lacking both an osseous skeleton and otoliths (reduced only to fine calcium carbonate granules), it was necessary to use other tissues to record skeletal growth marks. Generally speaking, specialists use the vertebral bodies, of which the cartilaginous structure is fairly well known (Ridewood, 1921; Moss, 1977; Hoening & Walsh, 1982) or spines of the dorsal fins, when these exist (Squaliformes and Heterodontiformes), and whose morphogenesis has also been studied on several occasions (Markert, 1896; Goodrich, 1907; Peyer, 1957; Holden & Meadows, 1962; Maisey, 1979). Growth marks were also described on the teeth (Tanaka, 1990) but these did not give rise to skeletochronological applications.

Since the work of Ridewood (1921), it has been known that in many Chondrichthyans, the vertebral bodies present concentric rings of calcareous cartilage separated by rings from slightly or uncalcified cartilage, giving the vertebrae different properties of transparency to light. These rings are more or less visible at the surface of the vertebral cones. This regular alternation of calcified and less calcified sectors probably corresponds to more or less regular cyclic phenomena. Haskell (1949) was the first to clearly formulate the assumption of a close connection between these vertebral rings and the growth of the animals, and who proposed to use vertebral sections to estimate age. The first effective practical use for the age estimation for a skate was published by Ishiyama (1951) and for sharks by Parker & Stott (1965). These first studies were followed by new applications, particularly in the past two decades.

A second approach to age estimation in Chondrichthyans is based on the study of the spines of the dorsal fins. However, this concerns only taxa which possess these spines (i.e. Heterodontiformes and certain Squaliformes). The spines of the dorsal fins have a structure similar to that of the teeth and cutaneous denticles. They consist of dentine organised around a long cavity and covered with enamel or emailoid (Markert, 1896; Maisey, 1979). Unlike teeth and the cutaneous denticles, which are subject to replacement, these spines are capable of growing indefinitely, with rhythmic discontinuities. If those are synchronized with a seasonal rate/rhythm they can be used for age estimation (Kaganovskaia, 1933; Bonham *et al.*, 1949; Holden & Meadows, 1962).

With the development of skeletochronological studies for Chondrichthyans, the same difficulty in automating reading techniques as for Osteichthyans arises. Some studies on vertebral bodies have been

performed. Densitometric analyses of quantitative variations in minerals, either direct by X-ray spectrometry, or indirect, on the basis of radiographs, are the most promising methods. However, this implies that the growth target criteria of the skeletal structures are sufficiently well established to be used as a support for automation (Cailliet & Tanaka, 1990).

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