Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations?[1]

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Abstract: The chronological properties of otoliths are unparalleled in the animal world, allowing accurate estimates of age and growth at both the daily and the yearly scale. Based on the successes of calcified structures as environmental proxies in other taxa, it was logical that researchers should attempt to link otolith biochronologies with otolith chemistry. With the benefit of hindsight, this anticipation may have been naive. For instance, the concentrations of many elements are lower in the otolith than in corals, bivalves, seal teeth, or the other bony structures of fish, making them less than ideal for elemental analyses. Nevertheless, there is growing interest in the use of otolith chemistry as a natural tag of fish stocks. Such applications are directed at questions concerning fish populations rather than using the fish as a passive recorder of the ambient environment and do not rely upon any explicit relationship between environmental variables and otolith chemistry. The questions that can be addressed with otolith chemistry are not necessarily answerable with genetic studies, suggesting that genetic and otolith studies complement rather than compete with each other. Thus, we believe that otolith applications have the potential to revolutionize our understanding of the integrity of fish populations and the management of fish stocks.

Résumé : Les propriétés des otolithes sur le plan de la chronologie sont sans équivalent dans le monde animal, car elles permettent d'estimer avec précision l'âge et la croissance à une échelle tant quotidienne qu'annuelle. Étant donné les succès obtenus par l'emploi des structures calcifiées comme substituts des conditions environnementales chez d'autres taxons, il était logique pour les chercheurs de tenter de faire le lien entre la biochronologie et la chimie des otolithes. Rétrospectivement, cette approche peut sembler naïve. Par exemple, les concentrations de nombreux éléments sont plus faibles dans les otolithes que dans les coraux, les bivalves, les dents de phoques ou les autres structures osseuses des poissons, ce qui en fait de bien mauvais candidats à l'analyse élémentaire. Toutefois, on note un intérêt croissant pour l'emploi de la chimie des otolithes comme marque naturelle des stocks de poissons. De telles applications visent à répondre à des questions sur les populations de poissons plutôt qu'à utiliser les poissons comme enregistreurs passifs du milieu ambiant, et ne se fondent pas sur une relation explicite entre les variables environnementales et la chimie des otolithes. Les questions auxquelles peut répondre la chimie des otolithes ne sont pas nécessairement abordables par l'étude génétique, de sorte que les travaux sur les otolithes et les études génétiques vont se compléter plutôt que se concurrencer. Nous pensons ainsi que les applications de l'étude des otolithes peuvent révolutionner aussi bien notre compréhension de l'intégrité des populations de poissons que la gestion des stocks halieutiques.

[Traduit par la Rédaction]

Introduction

The collection of age-structured information has always been a major preoccupation of fisheries science. Perhaps as a result, studies of fish have dominated progress in the field of age determination for several decades. To give some idea of the magnitude of the resources allocated to this activity, it is interesting to speculate on the global extent of age determinations based on otoliths. After an informal survey of 30 fisheries laboratories around the world, we have determined that a minimum of 800 000 otoliths were aged worldwide in 1999, at an approximate cost of $8 million CAN. An unknown but much larger number of scales and vertebrae were also aged, albeit at a considerably lower unit cost. On the basis of known numbers, well over 1 million fish were aged last year, and the actual number is probably closer to 2 million. In contrast, the number of individuals of other taxonomic groups that are aged on a routine basis, either as part of harvest calculations or otherwise, appears to be at least one to two orders of magnitude smaller. For example, only a few tens of thousands of nonfish aquatic animals (primarily bivalves) are aged annually in support of research or resource management. Age determinations of terrestrial animals are much lower in number again.

There are several reasons for the apparent emphasis on age determinations in the study of fishes compared with other animals. (*i*) Most fishes have life spans that exceed 1 year, and many have life spans of more than 20 years. As such, age and age composition are important characteristics of individuals and populations, respectively. The impact of the "baby boom" on human populations provides a useful analogy. (*ii*) Fish are much easier to age than most other organisms. For example, some animals such as the lobster lack

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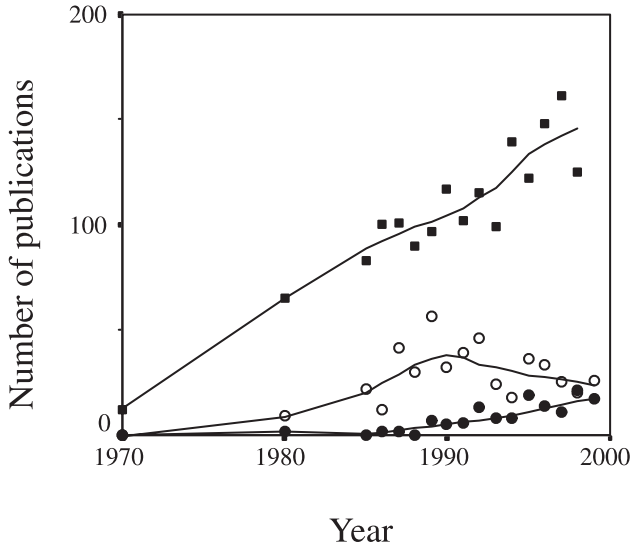
Fig. 1. Trends in annual numbers of primary publications describing otolith annuli (■), otolith microstructure (○), and otolith chemistry (●). On a percentage basis, otolith microstructure papers reached a peak in the late 1980s, while papers on otolith chemistry have been increasing steadily over the past decade. LOWESS curves have been fitted to each time series.



permanent or bony structures upon which age determinations can be based. (*iii*) 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. Unlike birds and mammals, fish have indeterminate growth patterns that are heavily influenced by the environment. As a result, fish growth and production are less predictable than those of homeotherms and require frequent measurement if productivity calculations or population characteristics are to be adjusted for environmental change. For example, the impact of global warming on a hypothetical fish population might be to increase growth rate, reduce longevity, reduce the age of sexual maturity, and increase the rate of natural mortality. Without accurate age data, the net effect on the abundance and productivity of the population would be difficult to predict.

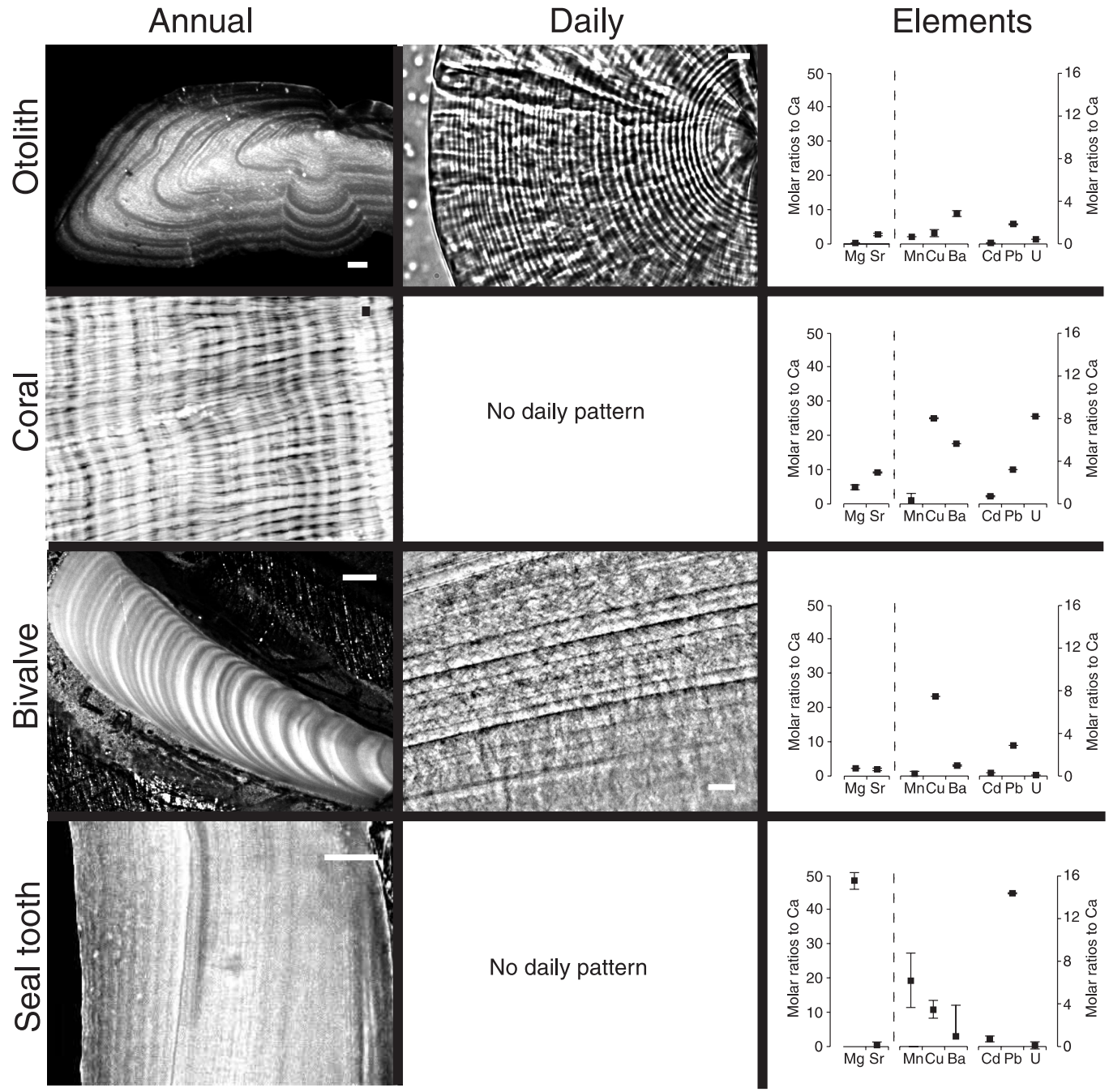
One might normally expect the progression of otolith research in the primary literature to be associated with the development and refinement of techniques for determining annual age, since otoliths provide the most accurate age determinations over the broadest age range (Secor et al. 1995). In fact, three separate otolith disciplines appear to have evolved over the past 100 years (Fig. 1). Beginning with Reibisch's observations of otolith annuli in 1899, there has been continued and growing interest in the use of the otolith as an indicator of annual age. Many applications in age estimation are now considered routine, even if accuracy continues to be an issue (Secor et al. 1995). With the development of otolith microstructure examination in the early 1970s, the otolith literature became preoccupied with this new approach and its capabilities for determining the daily age of a fish with unprecedented precision (Pannella 1971; Campana and Neilson 1985). In light of the similar focus on age-structured information in both of these disciplines, the evolution of microstructural work from macrostructural examinations appears logical. However, the relatively sudden development of otolith elemental analyses in the 1980s appeared not to follow such a logical progression. Relatively few of the elemental analyses to date have taken advantage of the otolith growth pattern, and at first glance, there is no obvious transition between the earlier otolith work and the elemental papers, which have increased exponentially in number during the past decade. How, then, to interpret this sequence of events?

The appearance of otolith chemistry as a significant theme in recent otolith research is probably not a simple consequence of the overall increase in number of age or otolith studies. Instead, we suggest that it has developed in anticipation of the otolith's properties as an environmental recorder, based almost exclusively on the successes of calcified structures as environmental proxies in other aquatic organisms (Chivas et al. 1985; Holmden et al. 1997; Dettman et al. 1999). We now know that there are few parallels between otolith chemistry and that of calcified material in aquatic invertebrates, at least beyond the superficial observation that both are composed primarily of calcium carbonate (Campana 1999). Nevertheless, elemental and isotopic assays of otoliths continue to increase in popularity, despite analytical requirements and a range of applications that appear considerably more restrictive than are present in similar studies of other organisms. So why is the pace of research in this discipline proceeding so quickly? As we will argue below, accelerated research into otolith chemistry applications is proceeding because of the unique chemical and chronological properties of the otolith. These properties, in turn, allow applications and questions to be answered that are simply not possible in other organisms or calcified structures. In the following pages, we offer an interdisciplinary overview of otoliths and otolith applications, which frequently strays across taxonomic and methodological boundaries. The intention is to provide a broad, and occasionally philosophical, perspective on the direction that the field has taken, as well as some thoughts on its future direction. A comprehensive review of the field is not the subject of this paper; that has been addressed elsewhere (Campana 1999). Rather, the goal is to contrast progress in the otolith field with that on other structures and other organisms and thus attempt to fathom why we have moved in the direction that we have.

General properties of calcified structures in aquatic organisms

Growth bands in calcified structures corresponding to daily, seasonal, or annual patterns are common in a number of aquatic phyla. Annual density or optical bands are found in coral skeletons, bivalve shells, and mammal teeth, as well as fish otoliths (Fig. 2). 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. Age estimates of 100 years or more have been recorded from several deepwater fishes based on otolith

Fig. 2. Representative growth patterns and elemental composition of fish otoliths, corals, bivalves, and seal teeth at various scales. The images of annual patterns are from Atlantic cod (*Gadus morhua*), coral (*Siderastrea* sp.), Arctic surfclam (*Mactromeris polynyma*), and grey seal (*Halichoerus grypus*). The daily increment images are from Atlantic herring (*Clupea harengus*) and Arctic surfclam. Annuli are visible in all of the taxa, but consistent daily growth patterns were evident only in otoliths and bivalves. Scale bar = 1 mm for annual patterns and 10 μm for daily patterns. All elemental data are means of three replicate analyses of the same specimen (±SE), expressed as molar ratios to Ca (Mg:Ca, Sr:Ca ($\times 10^{-3}$); Mn:Ca, Cu:Ca, Ba:Ca ($\times 10^{-6}$); Cd:Ca, Pb:Ca, U:Ca ($\times 10^{-8}$)). Broken lines separate data referenced to left- and right-side *y*-axes.



annuli, while even tropical species routinely attain ages of 30 years or more. Although the accuracy of extremely old age estimates has been questioned, sensitive assays of bomb radiocarbon and ^{210}Pb:^{226}Ra ratios have generally confirmed longevity estimates where validation has been attempted (Campana 1999). Otolith annuli are narrow compared with annual bands in calcified structures of other organisms, often on the order of 20–50 μm in width (Fig. 2). This is indicative of a low rate of calcification, while the failure of otolith growth models based only on inorganic molecules and pH (Romanek and Gauldie 1996) suggests that otolith crystallization is under the control of soluble organic molecules within the endolymphatic fluid (Belcher et al. 1996; Falini et al. 1996).

Daily growth increments in calcified structures are not as common as annual patterns and are restricted to species in which the depositional environment of the structure can be controlled by the organism without subsequent resorption (Fig. 2). Examples of such structures include fish otoliths (Campana and Neilson 1985), bivalve shells (Richardson 1988), and squid statoliths (Jackson 1990). Under normal circumstances, higher vertebrates do not produce daily growth patterns (Neville 1967). The presence of easily discernable daily increments in otoliths provides a remarkably accurate and precise method for age estimation of most larval and juvenile fishes (Campana and Neilson 1985). 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). Such information remains the envy of ecologists working on marine invertebrates where, for instance, information on larval durations is based on the time for pelagic larvae to reach competency when reared in the laboratory.

The chronological properties of otoliths are, then, unparalleled in the animal world. Therefore, it was perhaps only natural that researchers attempted to link this information with data on the environment inferred from chemical analyses of otolith growth increments. However, it is not immediately obvious that otolith geochemistry is influenced by processes similar to those affecting other calcified structures in either aquatic vertebrates or invertebrate phyla. We conducted a comparative, but cursory, analysis of the minor and trace element chemistry of a typical otolith, coral skeleton, bivalve shell, and seal tooth using laser ablation inductively coupled plasma mass spectrometry (ICP-MS). There were significant differences in the concentrations of divalent metal ions capable of substituting for Ca among each of the structures that we examined (Fig. 2). The scale of these differences was not sensitive to the particular species selected for analysis. The coral skeleton contained high levels of Sr and U, while Mg and Pb values were elevated in the seal tooth. Otoliths, however, were characterized by consistently low levels of all these ions, confirming Campana et al.'s (1997) observation that otolith aragonite is relatively free of trace metal contaminants. This observation does not imply that otolith chemistry fails to record temperature or water composition, since correlations between otolith and water chemistry may still exist even if absolute levels of elements are different. Nonetheless, the data highlight the fact that otolith elemental analyses remain challenging compared with assays of other calcified structures. Many of the elements of interest, including those likely to be indicative of pollution exposure such as Ni, Cu, and Pb, are present in concentrations at or below the detection limits of even the most sensitive mass spectrometers (e.g., Sie and Thresher 1992; Thorrold and Shuttleworth 2000).

Given the analytical constraints associated with otolith chemistry, might other calcified structures provide more information on environmental conditions experienced by individual fish? Preliminary studies on the chemistry of vertebrae (Mulligan et al. 1983) and scales (Wells et al. 2000) suggest that both structures have promise. To provide a baseline comparison of the chemical composition of each of these structures, we analyzed scales, vertebrae, and otoliths from juvenile spot (*Leiostomus xanthurus*) reared under controlled laboratory conditions using solution-based ICP-MS (Fig. 3). Here, as would be expected of any fish species, otoliths were characterized by lower levels of Mg:Ca, Mn:Ca, and Ba:Ca than either scales or bones. Again, however, it was also clear that otoliths provided superior chronological records, either at the daily or at the annual level (or both) (Fig. 3).

Unique properties of the otolith

There is little doubt that current interest in otolith chemistry is driven by the chronological capabilities of these structures rather than any unique chemical properties. Nonetheless, otoliths do have several properties that set them apart from all other skeletal structures and without which many of the current applications would be impossible.

Otolith growth is continual

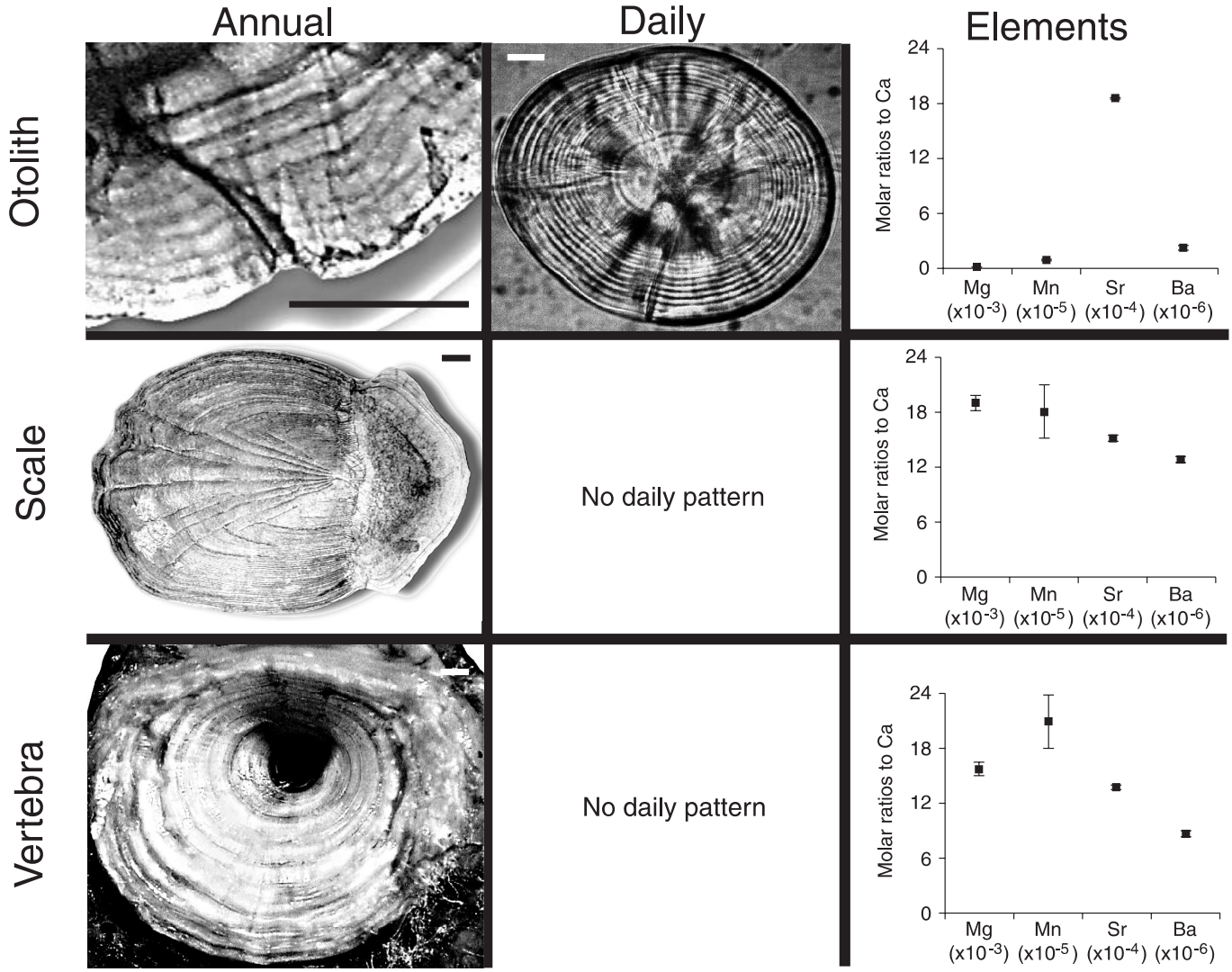
In part, this is because the otolith is one of the few calcified structures that is nonskeletal. The shells of bivalves, the tests of coral, and the bones of fish and mammals all serve key support or protection functions for their host. Since the growth of skeletal elements necessarily conforms to that of the organism, there is no requirement for continued growth during periods of nonfeeding or poor growth. The same principle applies to scales and teeth. In contrast, it appears that otolith growth is maintained even through periods when somatic growth is nonexistent (Maillet and Checkley 1990), and if not daily in old fishes, then at least seasonally. The advantage of a continuous growth pattern is most evident in studies of old fish in which annulus counts from scales and bones grossly underestimate those visible in the otolith (Beamish and McFarlane 1995). Clearly, a complete chronology is required if the environment corresponding to a previously deposited growth increment is to be accurately dated.

Could the unique and continued growth of the otolith be due to its nature as an organ of balance? Perhaps. For reasons that are still unclear, the vestibular organs of the fish (three otolith pairs) and squid (statolith pair) are the only calcified structures known to grow throughout the lifetime of the animal. Presumably, this is a reflection of their unique mode of calcification — a form of biomineralization with no epithelial contact, which is rarely encountered in other taxa or structures (Payan et al. 1997; Campana 1999). The fact that otolith growth is tightly linked to the natural endocrine rhythm of the fish (Campana and Neilson 1985) is probably also relevant, although the cause–effect relationship is unclear.

Otolith growth occurs in isolation from the environment

This property of the otolith is clearly not shared by calcified exoskeletons, scales, or teeth, but perhaps surprisingly, nor is it shared by bones. While the bones of a fish or mammal are not in direct contact with the external environment, they are exposed to the physiological environment of the organism much more than in the case of the otolith. Only the

Fig. 3. Representative annular growth patterns of otoliths, scales, and vertebrae from a tautog (*Tautoga onitis*). The otolith daily growth pattern is from a larval haddock (*Melanogrammus aeglefinus)*, while the elemental assays (mean ± SE) are based on otoliths, scales, and vertebrae from each of three young spot (*Leiostomus xanthurus*) reared in the laboratory. Scale bar = 0.5 mm for annual patterns and 10 μm for daily patterns.



otolith is isolated within a semipermeable inner ear membrane and bathed in an endolymphatic fluid that is considerably more regulated than is the composition of blood plasma (Payan et al. 1997; Campana 1999). Presumably, the physical and chemical isolation of the inner ear is a prerequisite of its unique mode of calcification. However, it seems likely that such a level of isolation from the environment is not ideally suited for tracking environmental conditions.

The otolith is not subject to resorption

Lack of resorption is a prerequisite for the preservation of a complete growth and environmental record. This is probably the most important property of the otolith and is one that is not shared with any other calcified structure in fish or other vertebrates. Even periods of starvation, which can result in resorption of scales and bones (Bilton 1974), do not resorb previously deposited otolith material (Campana and Neilson 1985). Of course, the acellular nature of the otolith sets it apart from bone and teeth, which are always susceptible to metabolic reworking. Biomineralization in most invertebrates is also acellular, thus ensuring that resorption due to metabolic causes does not occur.

The crystalline structure of the otolith is aragonite

Of the three crystalline forms of calcium carbonate found in otoliths and other calcified structures, it is the metastable aragonite form that makes up all of the otoliths used in age and environmental studies (Carlström 1963). Aragonite is also found in coral and sclerosponge skeletons, bivalve shells, and squid statoliths. However, among the vertebrates, only the aragonitic otoliths of teleosts are useful age indicators; fish more primitive than teleosts have calcitic otoconia, while more advanced vertebrates have otoconia composed of hydroxyapatite. This apparent quirk of evolution is not necessarily an advantage, although the slightly higher specific gravity of aragonite (2.93) over that of calcite (2.71) and

vaterite (2.65) may be related to the otolith's role as a gravity receptor. There is no obvious reason why aragonitic otoliths would serve as superior recorders of age or environmental conditions compared with any other polymorph of calcium carbonate. Yet there is no question that the mode of calcification in aragonitic otoliths is unique compared with other biomineralized structures (Suga and Nakahara 1991). Similarly, the intricate and highly species-specific shape of aragonitic otoliths is both striking and puzzling (Harkonen 1986). While the diverse shapes are obvious indicators of a carefully controlled biomineralization process, there is no known function for the diversity in size and shape across species. Nevertheless, it is tempting to speculate that the combination of species-specific shapes, aragonitic composition, and unique method of calcification is indirectly responsible for the time-keeping and environmental recording properties of otoliths.

Otolith chronologies and environmental reconstruction

Otoliths provide some of the best examples of biochronologies in the animal kingdom, combining annual sequences of up to 110 years in adult fishes (Boehlert et al. 1989; Pereira et al. 1995) with daily chronologies of up to a year during the larval and juvenile stages (Campana and Neilson 1985). It was perhaps only natural that researchers should attempt to link this information with data on the temperature or water composition inferred from chemical analysis of otoliths sectioned to reveal the growth increments. These endeavors were initially predicated, often explicitly, on correlations between temperature or water chemistry and the elemental composition of biogenic aragonite found in the skeletal material of marine invertebrates such as corals (Radtke 1989). However, as we have demonstrated, the chemistry of otolith aragonite is quite different from the aragonite found in the skeletal material of marine invertebrates. Are there reasons, then, to believe that otolith chemistry is a function of the environmental conditions experienced by individual fish? The answer would appear to be a strongly qualified "yes."

Despite statements to the contrary (Thresher 1999), it is indeed possible to reconstruct environmental histories from otolith chronologies. For instance, stable isotopes of oxygen in otoliths are deposited close to isotopic equilibrium and with a well-defined fractionation effect due to ambient temperature (Patterson et al. 1993; Thorrold et al. 1997*a*). Several studies have used stable isotope analyses of oxygen isotopes to reconstruct temperature histories in both ancient and modern water masses (Patterson 1998; Weidman and Millner 2000). Experimental evidence indicates that otolith chemistry is also an accurate proxy for concentrations of at least some trace elements (e.g., Sr, Ba) in the ambient environment (Farrell and Campana 1996; Bath et al. 2000). Otolith Sr, for example, serves as an excellent proxy for ambient salinity and has often been used to reconstruct a history of anadromous migrations (Secor 1992).

There is also good reason to believe that interpreting geochemical records from otoliths will be more difficult than from other environmental proxies such as invertebrate skeletons. Indeed, given the number of opportunities for significant decoupling, it is perhaps surprising that any detectable relationship exists between water and otolith chemistry. For instance, otolith aragonite precipitates from the endolymphatic fluid, the composition of which is regulated by membranes that separate the blood plasma from the ambient environment and the endolymphatic fluid from the blood plasma. It is possible, however, that Ca analogs such as Sr and Ba are moving across these membranes via para- or trans-cellular Ca channels (Kalish 1991; Mugiya and Yoshida 1995), in which case the environment may be able to exert a strong influence on subsequent element:Ca ratios in the otolith. There is also the likelihood of physiological processes altering levels of organic ligands, and hence free ion concentrations, within the blood plasma (Kalish 1991). In a serendipitous finding, at least for otolith researchers, it appears that the endolymphatic fluid is buffered from at least some of the temporal variability that characterizes the chemistry of the blood plasma (Payan et al. 1997). Aquatic environments are, in turn, less subject to high-frequency ("white noise") environmental variations than are the norm in terrestrial habitats, which may also increase the signal-to-noise ratio of chemical proxies in otoliths compared with the skeletal structures of terrestrial organisms.

Taken together, there appears to be hyperbole on both sides of the debate concerning the environmental effect on otolith chemistry. We believe that a consensus is emerging that while some elements in otoliths are useful as proxies of ambient environmental conditions, many, and perhaps most, elements are linked to the environment either indirectly or not at all (Campana 1999). So why are so many people carrying out elemental and isotopic analyses of the otolith? For at least two reasons: the excellent chronological properties of otoliths and the observation that otoliths appear to be immune to resorption. These two properties are unparalleled by any other skeletal structure in fishes and have provided fisheries ecologists the opportunity to address questions that were simply not possible with either scales or vertebrae. As such, the fact that otolith research evolved from studies of annuli to daily growth increments to elemental analyses was not a coincidence. Rather, it was a reflection of the importance of age-structured spatial information to studies of fish. Yet as we discuss below, there is a third reason for the growing interest in otolith composition, and it has to do more with the question being asked rather than the means for answering it.

What's the question: the fish or the environment?

Given that only a handful of elements are likely to be useful in reconstructing environmental history, is it possible that data on otolith chemistry could be useful even if it were not possible to make detailed inferences about the physicochemical environment? The recent explosion of papers using otolith chemistry suggests that this is the case. Certainly the questions being tackled with otolith geochemistry are very different from those being addressed with other environmental proxies. Chemical assays of invertebrate and mammal skeletons tend to be used to infer some feature of the environment, whereas chemical assays of otolith are directed at questions concerning the fish itself. For example, oxygen

isotope assays of coral annuli are generally used to reconstruct the temperature regime of the local ocean (Leder et al. 1996), trace metal assays of bivalves serve as pollution sentinels (Brown and Luoma 1995), and radioisotope assays of mammalian antlers indicate the extent of nuclear fallout (Tiller and Poston 2000). In each case, the interest is in the location or environment, not the organism being assayed. In contrast, otolith assays have been directed at questions concerning fish migration patterns (Thorrold et al. 1997*b*) or the extent of mixing between populations (Edmonds et al. 1991), where the focus is squarely on the fish. Indeed, the potential for significant migration, in both vertical and horizontal directions, has meant that the few attempts to reconstruct the environmental conditions of a given location from otolith chronologies have been from freshwater environments, where fish movements are constrained (Patterson et al. 1993; Patterson 1998).

By now, it should be clear that assays of otolith geochemistry are being used to address questions about fish that are simply not suited to assays of other organisms. Nevertheless, it has also become clear that these applications are driving otolith research well beyond what one would normally expect based on the chemical properties of otoliths. Is this an example of expectations not matching reality, or of inappropriate methods being used to address difficult issues? Not at all. Instead, we argue that the questions being addressed would be difficult or impossible to answer through other means. To support this statement, we offer three examples.

Atlantic cod (*Gadus morhua*) stock mixing

In a recent study, the trace element composition of the otolith (the elemental fingerprint) was used to track and identify members of four adjacent Atlantic cod stocks during a winter mixing period, using the fingerprints of the spawning aggregations as a reference (Campana et al. 1999). In this study, the elemental fingerprint was used as a natural tag, with many of the same strengths and limitations of conventional tagging, but with the advantage of a very large sample size of recaptures ($n \approx 2700$). Concurrent microsatellite DNA studies of the same fish were less able to distinguish among the various populations (Ruzzante et al. 1999), presumably because of periodic mixing among the spawning aggregations.

Weakfish (*Cynoscion regalis*) natal homing

Isotopic and elemental fingerprints of juvenile weakfish otoliths collected in their natal estuary were used to characterize and differentiate among adjacent estuarine habitats along the east coast of the United States (Thorrold et al. 1998). Several years later, adult weakfish from the same year-classes were collected when they returned to spawn in the estuaries. Otolith cores corresponding to the juvenile phase of the adults were assayed and the resulting fingerprints compared with reference fingerprints from the year in which the adult fish were spawned. A high degree of homing to natal estuaries (>85%) was demonstrated in some, but not all, of the subpopulations. Concurrent analyses of hypervariable markers, including microsatellite DNA and introns, were unable to detect significant genetic heterogeneity among juveniles from the various estuaries. These results were entirely consistent with a metapopulation model of weakfish population structure in which genetic exchange was accomplished through less than perfect natal homing.

Recruitment of coral reef fish

To determine the extent of local recruitment by a damselfish (*Pomacentrus moluccensis*) with a pelagic larval phase, Jones et al. (1999) chemically marked the otoliths of millions of developing embryos spawned around Lizard Island on the Great Barrier Reef. The ratio of marked to unmarked otoliths in fish collected immediately before settlement on the same reef tract was then used to estimate the relative contribution of recruits from the local area. This study was not only the first to demonstrate that larvae do actually return to their natal reef, but also suggested that the rate of self-recruitment of *P. moluccensis* to Lizard Island may be as high as 60%. No other study to date has been able to properly address this issue.

In these three examples, the successful results of each study took advantage of the chemical and (or) time-keeping characteristics of the otolith. In both the Atlantic cod and weakfish examples, otoliths were used as natural tags. These studies required only that the elemental and isotopic fingerprints from the reference samples were sufficiently different to allow unknown fish to be accurately classified to either a stock or a natal estuary. Although variations in the physicochemical environment probably generated the distinctive fingerprints, it was not necessary to reconstruct any aspect of the environment based on the otolith chemistry assays. It is conceivable that conventional tagging could have been carried out to produce similar results, but at a prohibitive cost. Why were the genetic approaches unsuccessful? Genetic markers are, of course, the archetypal natural tags and have been used to remarkable advantage in many population-level studies. Yet the failure of the genetic approach in each of the above studies was not at all surprising. As noted in the review by Ferguson and Danzmann (1998), genetic markers are ideally suited for many questions, particularly those focused on parental or evolutionary linkages, but are not necessarily well suited to localized stock identification or mixing issues. In particular, genetic markers would not be expected to perform well in instances where there is significant mixing among the groups of interest (e.g., among stocks). That was certainly the case in the above examples, where mixing rates were shown to exceed 1%. So for these types of studies, genetic markers were neither capable of nor appropriate for the question being asked. Are we suggesting that otolith elemental fingerprints are somehow superior to genetic assays? Not at all. In the absence of differences among groups, neither genetic nor otolith assays can be interpreted in terms of the similarity/dissimilarity of the groups. However, if differences exist, genetic analyses can be used to infer population structure, whereas elemental differences cannot. By corollary, the genetic structure of a population would be expected to remain relatively stable from year to year, whereas the corresponding elemental fingerprint might change. Therefore, genetic differences can be used to characterize populations, while differences in the elemental fingerprint merely reflect a different environmental history, which may or may not apply to the entire population. On the other hand, otolith elemental fingerprints formed under environmental influence are well suited for tracking those same populations, or subsets thereof,

whether or not genetic differences are evident. So for tracking and mixing applications, the unusual properties of the otolith must be viewed as an advantage.

In conclusion, otoliths have become an indispensable tool to fisheries scientists. Otolith biochronologies provide information on age and growth with unparalleled precision and accuracy. Although the analysis of age composition data based on otolith growth increments is routine in many laboratories around the world, it is easy to forget that the number and complexity of age-structured analyses of fish are matched only by age-structured studies on human demographics. The chemical composition of otoliths also affords the possibility of environmental reconstructions that, when matched with otolith biochronologies, may allow an individual fish to be retrospectively positioned in space and time throughout its life. We are clearly some way from realizing this goal. Nonetheless, the application of otolith chemistry as a natural tag is already providing unique information on spatial distributions at the population level. We believe that this information will not only increase our understanding of the integrity of fish stocks, but may also fundamentally alter the way that we view the assessment and management of exploited fish populations.

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