Otoliths in Archaeology: Methods, Applications and Future Prospects

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Abstract

Otoliths are small structures found in the inner ear of teleost fish that act as organs of equilibrium and as direction and sound detectors. They possess unique characteristics that set them apart from other skeletal structures, notably a continuous growth structure deposited on a daily basis. While otolith analyses are widely employed in modern fisheries studies, they have slowly been increasing within archaeological and palaeoenvironmental research. This paper overviews the development and future prospects of otolith studies in archaeology. The main methods of analysis are outlined and major advances and research in each area detailed. In spite of some limitations, the benefits and unique information that otolith analyses can provide ensure that otoliths should be an important part of archaeological research. Continuing development of methods and technologies within this area will serve to further increase the importance and use of otoliths, while raising the profile of this unique resource.

Keywords

otolith; chemistry; morphology; palaeoenvironment; fisheries science; archaeozoology; isotopes

1. Introduction

Otoliths are small structures found in the inner ear of teleost fish that act as organs of equilibrium and as direction and sound detectors (Popper and Fay 2011). The three pairs of otoliths are termed the 'sagittae', 'lapilli' and 'asterisci', and are each contained within individual vestibules (Fig. 1) (Campana 2004). They form in the embryonic stages of the fish, grow continuously throughout its life, and are composed of alternating layers of calcium carbonate (usually in the mineral form aragonite) and protein, which are deposited on a daily basis (Campana and Neilson 1985; Pannella 1971; Payan et al. 2004).

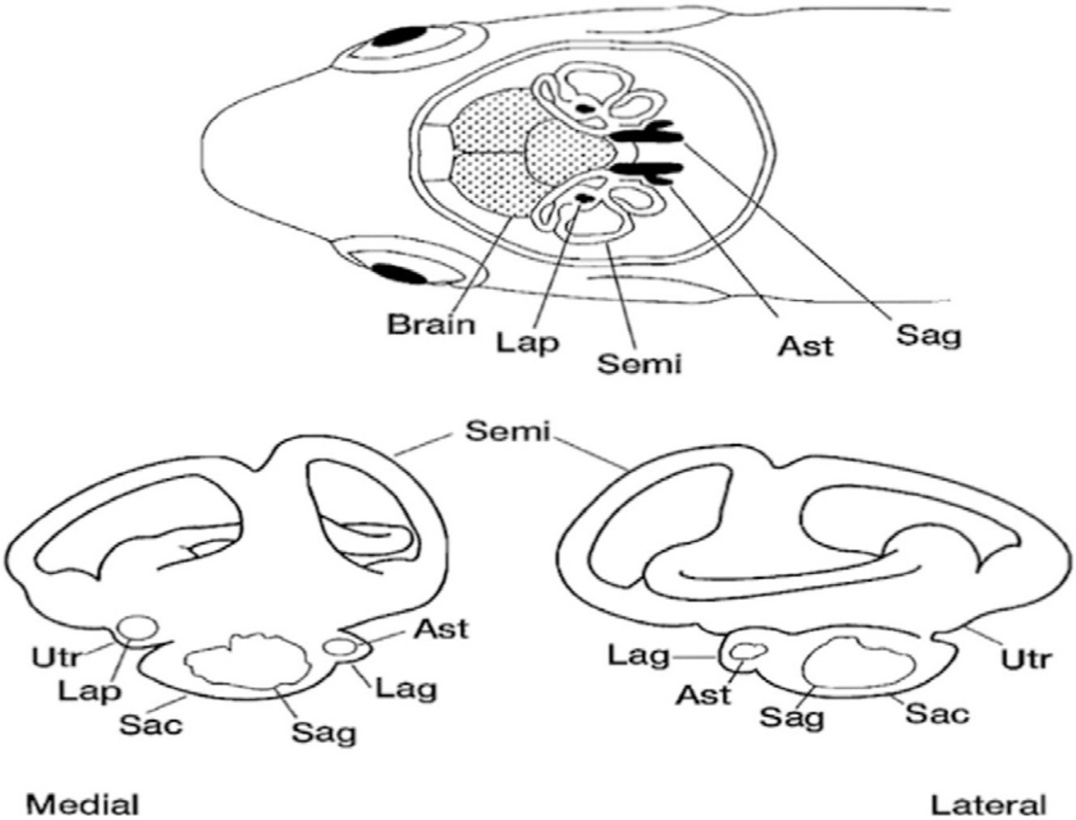

Fig. 1. Schematic of the location of the inner ear and three pairs of otoliths in the skull of a generalized teleost. *Top,* Dorsal view of the inner ear and otoliths in relation to the brain in a cutaway of a fish skull (modified from Secor et al. 1992). *Bottom,* Position of otoliths and otolith chambers in the inner ear of the teleost *Trichogaster (modified from Popper and Hoxter 1981)*. Ast, asteriscus; Lag, lagena; Lap, lapillus; Sac, sacculus; Sag, sagitta; Semi, semi-circular canal of labyrinth; Utr, utriculus (used with permission from Campana 2004:2).

Otoliths possess unique characteristics that set them apart from all other skeletal structures. Otolith growth is continuous and is maintained even through periods when somatic growth is virtually nonexistent (Campana 1990; Secor and Dean 1989). As they form, otoliths absorb elements from the ambient water, which vary in relation to environmental conditions, such as salinity and temperature. They are acellular, meaning that once the material in otoliths is deposited, it is generally not reworked or resorbed (Campana and Neilson 1985); otolith chemistry is thus a function of the environmental conditions experienced by the fish. This is a very important property of the otolith for palaeoenvironmental and archaeological applications. Their chemical composition affords the possibility of environmental reconstruction that, when matched with otolith biochronologies, can allow the lifetime of an individual fish to be placed retrospectively within time and space (Campana and Thorrold 2001:37).

A large array of data are able to be recovered from otoliths, including species identification, age and growth studies, seasonality, radiocarbon dating and trace element and isotope analysis, which are discussed in this paper. Information gained from such analyses can address broad and often key archaeological issues. Otolith studies frequently contribute to answering questions focusing on changes in fish population structures, including examining impacts of intense human predation, environmental change and habitat destruction. The determination of ecological baselines is an essential step toward restoring native fish populations to pre-industrialised fishing levels, and as fisheries catch records generally only provide information from the last hundred years or so, otoliths, along with other fish remains, hold vital information frequently used for establishing knowledge of ancient fish stocks. There are some issues intrinsic to using anthropogenically compiled assemblages (Reitz 2004), and Indigenous populations often had notable impacts on faunal populations (Holdaway and Jacomb 2000; Mannino and Thomas 2002; Wragg 1995); however, it is undeniable that impacts experienced after the industrialization of fishing have been unparalleled in human history. Otoliths also provide a wide range of information regarding the past occupants of a site; human subsistence strategies, fishing methods and technologies, trade routes, seasonality of site usage, and past human responses to environmental changes can all be examined through the analysis of these small carbonate structures.

Otolith analyses are widely employed in modern fisheries studies (for recent overviews, see Begg et al. 2005; Campana 2005; Elsdon et al. 2008; Sturrock et al. 2012), and have been slowly increasing in archaeological applications. In 1891, otoliths were excavated from an archaeological site in Rio Grande do Sul, Brazil, and identified to species through comparisons with modern samples collected from fish in nearby streams (Ihering 1891 in Fitch 1972). Despite these promising beginnings, otolith analysis seems to be absent from archaeological literature until the mid-20th century, when discussions of otoliths from archaeological sites start to re-appear (e.g., Niehoff 1952; Priegel 1963; Shumway et al. 1961; Witt 1960). Initially, these studies focused on species identification based on otolith shape, and size and age of the fish based on otolith size. The development of advanced analytical techniques over the recent past, including trace element and isotope analyses, as well as radiocarbon dating, has encouraged an expansion of these techniques, including archaeological and palaeoenvironmental applications.

A decade ago, Campana (2005) found that papers involving otoliths across all disciplines were being published at five times the rate they were in the 1970s; however, the areas of both environmental reconstruction (modern and ancient) and 'fossil' otoliths each made up <1% of the 862 papers published between 1999 and early 2004. A basic search of online databases, such as Web of Science, shows that while publications focusing on fish otoliths have increased over the past two decades, and archaeological papers within these have also steadily increased, they are still a relatively small area of research.

Despite some earlier reviews of otoliths in archaeology (Campana 1999; Campana 2005; Casteel 1976b; Van Neer 2000; Weisler 1993) and coverage of otoliths in general icthyoarchaeology texts, no specialist overview on the state of the art of otolith analysis applications in archaeology has appeared for more than a decade. As such, this paper overviews the development of otolith studies in archaeology, building on past reviews and discussing recent technological developments. The main methods of analysis are outlined and major advances and significant studies in each area discussed. There are some limitations to the review; the publications included in this paper are all written in English, therefore, a significant amount of research and developments that have been published in non-English languages have been excluded. In addition, there has been an attempt to avoid "grey literature" (unpublished reports) and focus on peer-reviewed publications, which may have excluded some important research, but such literature is not always widely available. We do not hope to include every publication, but rather provide examples of the type of research that can be undertaken on otoliths. Despite these limitations, this paper provides a broad review of the current state of archaeological analyses of fish otoliths.

2. Sample Collection and Preservation

While the numbers of otoliths recovered during archaeological excavations can be low, or even non-existent at some sites, others contain significant assemblages from numerous or single fish species (Gabriel et al. 2012; Scartascini and Volpedo 2013). Otoliths do require certain site conditions to survive in the archaeological record; their aragonite structure makes them more susceptible to deterioration than bone in some situations. The alkaline matrix of shell middens provide some of the best conditions for preservation (Andrus 2011) and waterlogged sites such as cesspits or large deep refuse pits limit the impact of acid rain percolation, allowing for preservation of the otoliths of some taxa (Van Neer et al. 2002). Well preserved assemblages of otoliths have also been collected from other sites, such as earth mounds (Disspain et al. 2012a), lunettes and hearths (Long et al. 2014).

In order to enhance collecting otoliths from sites, wet sieving methods are advocated (Casteel 1976a; Ross and Duffy 2000). The sieve size used during collection will impact the size and number of fish remains collected from a site, and potentially taxa or species identification (James 1997; Nagaoka 2005; Ross and Duffy 2000; Ulm 2002; Weisler 1993). Zohar and Belmaker (2005) demonstrated that taxonomic diversity within a fishbone assemblage from Arrawarra-I, a coastal midden site in Australia, was higher when sieved through a 1 mm mesh, as opposed to a 6 mm or 3 mm mesh. As otoliths can vary greatly in size dependent on the species and size of the fish (see Furlani et al. 2007 for examples), Casteel (1976a) advocated wet-sieving samples and sorting with low-power magnification to ensure a comprehensive collection of fish remains.

Sites with large quantities of fish bone can sometimes be devoid of otoliths (e.g., Butler and Chatters 1994). This can be attributed to a number of factors including discard methods; fish heads may be removed at the time of catch, and returned to the water, or may be removed at the time of cooking and thrown into a fire where burning makes them fragile and more likely to deteriorate completely (Lubinski 1996). The Indigenous people of the Murray River and Lakes, South Australia, removed the head of the Murray cod and baked it on hot coals, while that of the catfish was cut off and thrown to the dogs (Berndt et al. 1993:105-106). In Kenya (Lake Turkana), fish smaller than 250 mm in length are processed whole while larger specimens (>250 mm) are decapitated (Stewart and Gifford-Gonzalez 1994). It is also possible for fish heads to be eaten whole, with digestion eroding otoliths sometimes completely, or beyond recognition (Jones 1986; Nicholson 1993). Taphonomic processes can contribute to a loss of samples; as they are composed of calcium carbonate in the form of aragonite, which is chemically less stable than the hydroxy-apatite of bones, otoliths can dissolve in acidic conditions (Nicholson 1996). As well as being eaten, smaller and more fragile otoliths are less likely to survive in archaeological sites than those that are more robust. This can lead to an over-representation of taxa that have more durable otoliths and/or an under-representation of those with small, fragile otoliths of more robust species. Misidentification may also impact the frequency with which otoliths are recovered from sites; otolith shapes are species specific, and unless researchers are aware of this, some samples may be easily overlooked and misidentified as shell or other material.

3. Species Identification

The sagittal otoliths are the largest of the three pairs of otoliths in most fish (in cyprinids, the asterisci are the largest (Macdonald et al. 2012)). Sagittal otolith shape varies widely and is recognised as being species- or genera-specific (see Fig. 2) (Furlani et al. 2007; Maisey 1987; Weisler 1993). This is one of the great advantages of otoliths, as shape allows identifications at species level, which is not always possible for the bones of closely related species. Additionally, when species identification is not easily determined using basic observations of otoliths, otolith shape analysis can be employed. This has been used in numerous modern studies (Jolivet et al. 2013; Paul et al. 2013; Vergara-Solana et al. 2013), as well as in conjunction with elemental analyses (Avigliano et al. 2014; Ferguson et al. 2011). It was recently applied to archaeological otoliths as a way to determine species (Chen et al. 2011), and has the potential to be more frequently incorporated into archaeological analyses.

When present at a site, otoliths play an important role in the identification of species within archaeological assemblages, and comprehensive otolith reference collections have been compiled and published (e.g., Campana 2004; Furlani et al. 2007; Nolf 2013; Smale et al. 1995; Stinton 1985; Tuset et al. 2008), or are available online (e.g., http://fishbone.nottingham.ac.uk/, http://hbs.bishopmuseum.org/frc/index.html,

http://www.shd-archzoo.co.uk/fishresources.html) in order to assist with these identifications. Species identification is useful because many fish species show marked seasonality of movement, which means that they may only be available for predation by human populations at certain times of the year. Consequently, the presence or absence of seasonal species in the archaeological record may convey information about the way people moved around the landscape throughout the year (Colley 1990; O'Connor 2000:141), although it may also indicate cultural choices. Changes over time in the species that are present in, or absent from, archaeological assemblages reflects these changing patterns and allows inferences to be made about the palaeoenvironmental conditions of the region, resource use, cultural preferences and foraging choices of the occupants of the area.

Once a species has been identified at a site, biological information about that species can provide further knowledge about the use of the site. For example, whether a fish is a schooling or solitary species, or their known environmental conditions such as food sources, water temperature, depth and salinity, can inform us about gross changes in environmental conditions surrounding the site, or appropriate technologies for capture e.g., pelagic fish are unlikely to be captured in near-shore stone-walled fish traps.

Examples of these sorts of studies abound in the literature (Disspain et al. 2012b; Fitch 1969; Rose 1996; Scartascini and Volpedo 2013). Fish remains, including otoliths, from hearths dated to between 25,000 and 32,000 years ago at Lake Mungo, were identified as golden perch, *Macquaria ambigua* (Bowler et al. 1970). This species has a high salinity tolerance, but breeding is induced by freshwater flows, which takes place in the spring when floodwaters flow down the Murray-Darling Rivers. At the time the hearths were formed, similar spring floods could have been expected with the annual melt of the periglacial snows in the catchment highlands. It was suggested the presence of immature fish at Mungo might have meant that the site was occupied soon after this spring period (Bowler et al. 1970).

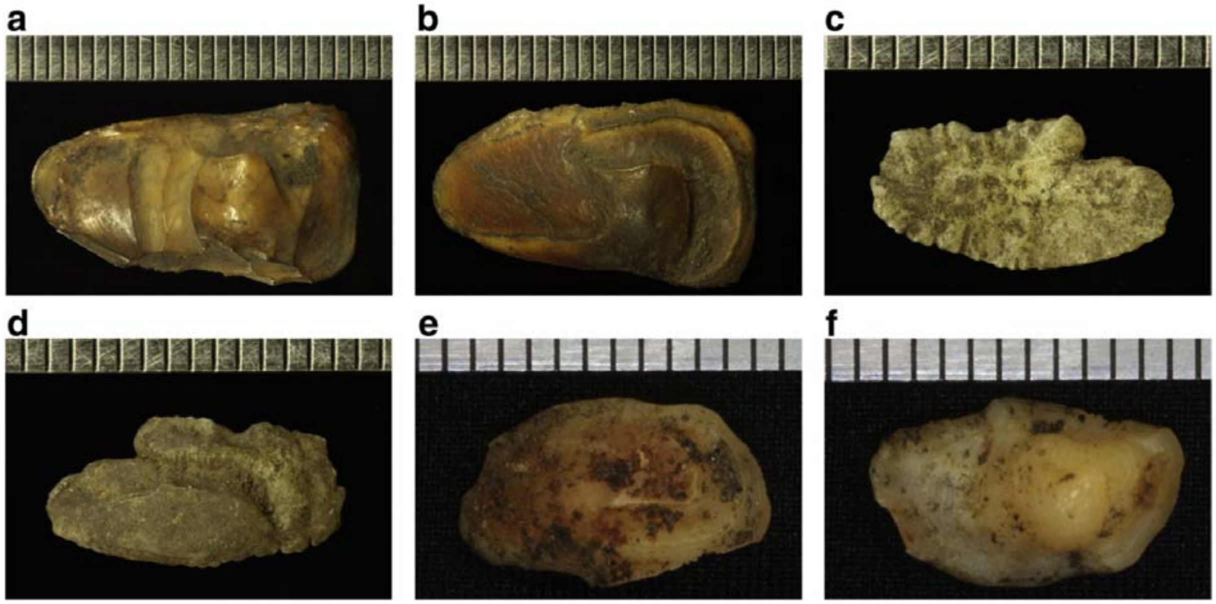

Fig. 2. Archaeological *Argyrosomus japonicus* (mulloway) otolith a, distal and b, proximal surface; archaeological *Macquaria ambigua* (golden perch) otolith c, distal and d, proximal surface; archaeological *Sciaena deliciosa* (lorna drum) otolith e, distal and f, proximal surface. Ruler along top indicate scale with gradations equal to 1 mm.

4. Fish Size

Fish grow larger the longer they live, though growth capacity is dependent on both internal (nervous, endocrinological and neuroendocrinological) and external ecological factors (salinity, temperature, food) (Boeuf et al. 1999; Boeuf and Payan 2001; Neuheimer et al. 2011). While somatic growth can be slowed or interrupted, otolith growth is continuous (Campana and Neilson 1985). Growth is a three-dimensional process, with the length, width and depth of an individual organism all changing over time. This relationship enables the size of a fish at the time of its death to be determined by analysing the weight(s) of its otolith(s) (Quinn and Deriso 1999:180). Similarly, otolith length can also be used (Casteel 1974). We acknowledge that numerous other skeletal elements can be used to reconstruct fish size, and may be better suited to the task in some cases; however, as this is a review of otoliths, we will focus solely on research relating to their use in fish size determination. Numerous archaeological studies utilising otolith weight (or length):fish length relations, validated by modern-day samples, have been conducted (e.g., Balme 1983; 1995; Gabriel et al. 2012; Moss 2011; Shumway et al. 1961; Witt 1960). It is important to note that that while there is a strong correlation between otolith size and fish size within species, specific relationships do not correspond between species. Small fish species do not necessarily have small otoliths, and large fish do not always have large otoliths (see Weisler 1993:Figure 2 for an example of otolith length:fish length within and across different species). There are some issues with this method, as otolith growth and somatic growth can sometimes become uncoupled (Wilson et al. 2009) because, as mentioned earlier, some constant amount of calcification occurs onto the otolith despite fluctuations in somatic growth rate (Secor and Dean 1992). In addition, ancient otoliths can experience breakage and deterioration, meaning that calculations based on their size need to be taken as minimum length values only. Despite these complications, otolith size can give good indications of fish size, and is an extremely valuable attribute of the otolith for use within archaeology and marine science applications.

The size of fish present in the archaeological record may be indicative of the fishing techniques that were employed by local Indigenous populations: spearing in shallow water usually results in the capture of larger specimens, as they are easier to hit; gill nets have a high degree of size selectivity, capturing a narrow size range of fish dependent on the net's mesh size (Balme 2013); fish traps of stone, netting or wicker-work will catch all fish over a certain size; and hook and line fishing tends to catch predatory fish whose size can be dependent on the size of the hook (O'Connor 2000:141-3). Past fishing methods can inform about the technological skills and knowledge of a society, and may indicate the relative importance of fish in the diet and community, based on the time and energy involved in fishing (Colley 1987).

An example of this, comes from sites in the lower Darling River region of western New South Wales, Australia, where the spatial distribution and uniform size of >500 otoliths implied that nets were the most likely fishing technique used at the site (Balme 1995). From this observation, it was concluded that people must have been able to make string from vegetable fibre, have had a social organisation that allowed them considerable time to make and maintain the nets, and that they were aware of the water conditions under which netting was effective (Balme 1995). Thus, information about otolith size allows inferences beyond merely fish size, enabling researchers to deduce information concerning Indigenous technologies, subsistence strategies and social structures.

Changes in fish size over time, through comparisons with modern size data, enable investigations into the effects that human predation, habitat alteration and environmental degradation have had on individual species. An early study indicated the mean lengths of present day *Aplodinotus grunnien,* freshwater drum, in the vicinity of a number of archaeological sites along the Mississippi River, Missouri, were generally smaller than those from 3600 to 7000 years ago (Witt 1960). Estimates of *Maccullochella peeli,* Murray cod, (4250 - 6410 years BP) size based on otolith weight (Disspain et al. 2012b) were used to suggest that the general size of *M. peeli* has declined over time since very large (>2200 mm TL) fish were found in the archaeological record. Both of these studies suggested habitat alteration and intensive human predation as likely causes for the decreases in fish size and demonstrate that even basic analyses of fish otoliths can result in significant findings concerning past fish population structures.

5. Age Structure

Since the late nineteenth century, otoliths have been recognised as accurate indicators of the age of individual fish. The appearance of the aragonite on the organic matrix within the otoliths changes depending on physiological and environmental factors. These variations result in the formation of bands, or annuli, within the otolith's structure. They are defined by two zones; a slow growth zone, that, when viewed under a transmitted light source, appears as thin bands, darker in colour, and a fast-growth zone that appears as thick, lighter-coloured, or hyaline, bands (see Fig. 3) (Casteel 1972; Pannella 1971). Aragonite and organic compounds are found in both zones, with greater concentrations of organic compounds in the fast growth zones, and greater concentrations of aragonite in the tight carbonate bandings of the slow growth zones (Jolivet et al. 2008; Schöne and Gillikin 2013). It is known that development and growth are influenced by both internal and external factors (Boeuf and Payan 2001), but it is widely accepted that these growth bands in the otoliths of temperate fish coincide with seasonal variations in environmental conditions. Therefore, an examination of a cross-section of an otolith, and counting the annuli, can estimate the age of the fish at the time of its death.

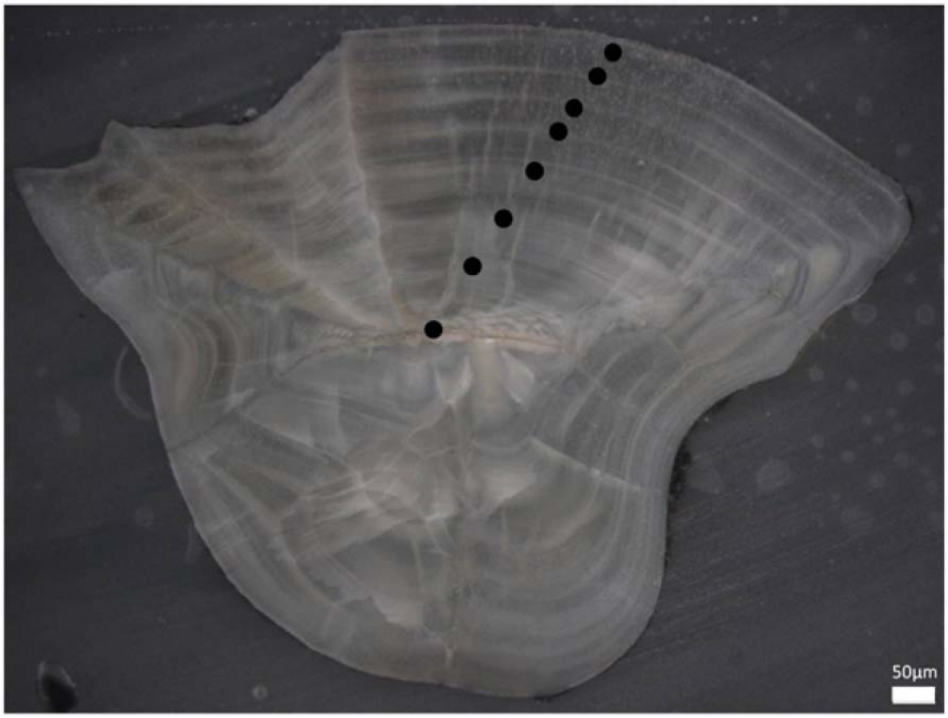

Fig. 3. Transverse section of an archaeological *Argyrosomus japonicus* (mulloway) otolith, with black spots indicating increments. Otolith is aged to 7 years; the edge increment is hyaline, indicating the fish died in the warm season.

It is important to determine for individual species that the bands are indicative of an annual cycle; this can be done by using modern reference material (Ferguson et al. 2014; Higham and Horn 2000). It is particularly difficult to age fish from tropical environments using otoliths increments, as there is less seasonal fluctuation in tropical waters compared with temperate, meaning that growth cycles are not as strongly related to environmental conditions (Giardina et al. 2014; Green et al. 2009). Validation that one increment equals one year is also required, as not all axes within an otolith show a complete growth record (Campana 2001). Measures must also be taken to avoid distorted results caused by reader bias (Campana 2001); multiple readers can be used, or one reader can count the annuli more than once with no recollection of previous results. Discrepancies in counts should be reported (for examples, see Disspain et al. 2011; Ferguson et al. 2014). In order to avoid reader discrepancies, another method for determining the age of a fish that has begun to be explored involves using the weight of an otolith to calculate the fish's age; this method also requires validation with modern samples and may result in an underestimate because to taphonomic processes that have caused the otolith to weigh less (Matić-Skoko et al. 2011).

As heavy fishing pressure often reduces the size and/or age structure of local or regional populations, temporal changes in the size or age of individuals from a particular species are one of the most common means of assessing changes in human predation pressure and the impacts on aquatic ecosystems (Erlandson and Rick 2008; Erlandson and Rick 2010; Mannino and Thomas 2002). One of the great advantages of average size or age studies for zooarchaeological assemblages is that they can be readily compared to palaeontological, historical, and recent ecological data sets to construct relatively long and continuous records of change in marine ecosystems (Erlandson and Rick 2008:10).

An example of changes in age structure of a population comes from a study on Atlantic croaker, *Micropogonias undulatus.* In this study, otoliths that were recovered from archaeological sites in Florida, USA showed that Atlantic croaker grew more slowly and lived much longer than those in modern times (15 years versus 7 years) (Hales and Reitz 1992). Through comparisons of the age and growth of the fish with modern studies, it was determined that the population had changed dramatically over time, perhaps in response to exploitation or habitat alteration. Another study, investigating baselines for the recovery of the Baltic Sea cod fishery, reconstructed demographics from a Neolithic population (4500 BP) to show that cod were on average larger, older, and had lower total mortality than the heavily exploited modern stocks (Limburg et al. 2008).

6. Edge Increment Analysis

In addition to providing an estimate of age of death of the fish, the annuli can also provide information about the season of death. By recording the nature of the edge increment, whether it was laid down in a warm (fast growth) or cool (slow growth) season, the season of fish capture can be determined. This in turn, can provide information relating to site occupation and movement of people within the landscape. Analysis of edge increments has, however, been criticized since the outside surface of the otolith may deteriorate through time in archaeological deposits, and a range of factors (e.g. temperature, salinity, geographical location, diet and age of the fish) may influence when increments are formed as well as the clarity of the edge increment (Carlson 1988; Plug et al. 2012; Van Neer et al. 2004). The methods can also be problematic, with different results obtained by different readers, but good seasonality estimations can be obtained when a large sample size can be analysed, and when studies of modern samples of the same species have been conducted to demonstrate when edge increments are laid down (Higham and Horn 2000; Scartascini et al. 2015; Van Neer et al. 1993; Van Neer et al. 1999). The age and season of death were determined for an assemblage of black drum *(Pogonias cromis)* from a late Prehistoric site on the lower Texas coast (Smith 1983). The seasonality study was enhanced by a comparative study of modern otoliths from the immediate region, and revealed occupation of the site from late fall to early spring. Daily increments can also be used to indicate when fish were targeted; a study analysing daily growth increments from archaeological fish otoliths was conducted on an assemblage from a late Palaeolithic site in Egypt (Van Neer et al. 1993). The well-preserved otoliths at the site had widely-spaced outer growth lines, indicative of fast growth. This fast growth was thought to coincide with the flood season of the Nile. The daily increments showed that the fish were captured after the maximum of the flood.

7. Trace Element Analysis

Elements are incorporated into the calcium carbonate matrix of otoliths as they grow and can provide us with information about the environment the fish lived in. This knowledge can in turn be used in palaeoenvironmental reconstructions and examining changes in local conditions. This is possible because concentrations of elements vary, and are influenced by salinity, temperature, ambient water chemistry (Elsdon and Gillanders 2004; Elsdon et al. 2008; Sturrock et al. 2012), the bedrock type the water is exposed to, and the physiology of the fish (Campana 1999; Kalish 1989). Precise relationships are not always clear and species-specific responses to experiments have been found (e.g., Hamer et al. 2006; Morales-Nin et al. 2012; Wells et al. 2003), meaning that caution is required if extrapolating among species. Generally, trace elements incorporated into the surface of the otolith reflect the physical and chemical characteristics of the ambient water. In some systems, such as lakes, open oceans and bays, elemental concentrations can be relatively stable over time (Jarvie et al. 2000). Reconstructing the movements of fish based on otolith elemental concentrations in such stable environments relies on predictable relationships being established between ambient conditions and internal otolith structures. In contrast, in estuaries and coastal regions, elemental concentrations can vary greatly with time, with differences varying over the scales of days to seasons and even over tidal cycles on individual days (Elsdon and Gillanders 2006; Elsdon et al. 2008). In such regions, information on temporal changes in water chemistry through time can aid interpretation of otolith chemistry patterns.

Numerous researchers have examined how environmental variables influence otolith chemistry and then used such relations to interpret environmental histories of modern fish. The most widely investigated trace elements have been Sr:Ca and Ba:Ca; they appear to reflect environmental parameters either linearly or non-linearly, and as such they are ideal for determining fish movement (Bath et al. 2000; Elsdon and Gillanders 2005; Gillanders and Munro 2012; Hamer et al. 2006). Alternate elements, including Mn (Elsdon and Gillanders 2003; Elsdon and Gillanders 2006) and Mg (Arkhipkin et al. 2009; Wells et al. 2003), among others (e.g., Campana et al. 2000; Morales-Nin et al. 2012; Tanner et al. 2013) have also been studied for their suitability as environmental indicators, with varying results. Changes in the elemental concentrations within otoliths can only be used to reconstruct past environmental conditions and fish life history patterns, if concentrations of elements within otoliths change in a predictable manner with environmental variables. Although trace element analysis across an otolith can demonstrate potential variation in habitats utilized by a fish throughout its life, it may also demonstrate movement of water masses around a stationary fish. Thus, some information on the life history of the fish and how environmental conditions change is useful to properly interpret such data.

As discussed above, definitive reconstructions often require prior knowledge of the differences in water chemistry within environments (Elsdon and Gillanders 2004; Elsdon et al. 2008). This is not possible for archaeological studies, and caution is required in identifying fine scale spatial differences in movement of prehistoric fish based on trace elemental analyses. As a result, few studies have analysed trace elements in archaeological otoliths to determine past environmental habitats. One study used modern relationships between ambient water concentrations, salinity and otolith elemental concentrations (sourced from Elsdon and Gillanders 2004) to analyse data from archaeological *Argyrosomus japonicus* and *Acanthopagrus butcheri* otoliths (Disspain et al. 2011). The assemblage was recovered from mid-to-late Holocene shell middens along the Coorong, an estuary at the mouth of the Murray River, South Australia. The elemental analysis revealed fluctuating levels of salinity in the river and the estuary that were significantly lower than the hypersaline conditions experienced in some areas today (Disspain et al. 2011). This information suggests significant change in environmental conditions associated with river regulation. Additionally, trace element data from otoliths of two freshwater species (*Maccullochella peelii* and *Macquaria ambigua*) from mid-to-late Holocene sites further upstream reinforced that, prior to human interference, water of the Murray River experienced fluctuating salinity levels; however, as a result of historical barrage construction and water management strategies, the river is now predominantly fresh (see Fig. 4) (Disspain et al. 2012b). These studies successfully expanded the examination of archaeological otoliths to include this analysis, although interpretations are generalized and further research is needed into the viability of archaeological otoliths for reliable trace elemental analyses.

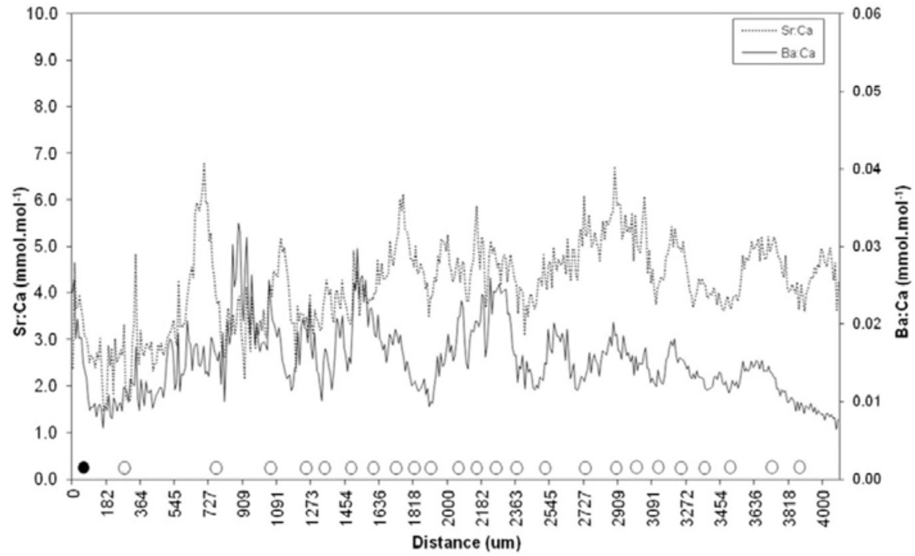

Fig. 4. Trace element data from an archaeological *Maccullochella peelii* (Murray cod) otolith showing fluctuations in salinity levels based on Ba:Ca levels. The spots on the chart indicate the location of the annuli along the profile (modified from Disspain et al. 2012b).

8. Isotope Analysis

A range of stable isotopes have been analysed in modern fish otoliths, while the most widely used elements in isotopic studies of archaeological otoliths are oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$), with fewer studies focusing on nitrogen ($\delta^{15}N$) (Rowell et al. 2010). Isotopic analyses of ancient fish remains can provide information on seasonality of site usage (Hufthammer et al. 2010), trade and provenance of fish (for bone and teeth applications, which could be applied to otoliths, see Barrett et al. 2008; Dufour et al. 2007; Lubinski and Partlow 2012) palaeoenvironmental conditions (Surge and Walker 2005; Walker and Surge 2006; Wang et al. 2013), fish migrations, and the effects of human predation and habitat alteration on fish populations (Rowell et al. 2010; Rowell et al. 2008).

Stable isotope analyses of fossilized fish otoliths to examine palaeoenvironmental conditions were investigated in the mid-20th century (e.g., Devereux 1967); however, archaeologists did not embrace the method until approximately 30 years later (e.g., Andrus et al. 2002; Patterson 1998). These analyses are becoming increasingly popular and important for understanding past environmental and cultural changes, encouraging the development of new methods, such as the use of a Sensitive High Resolution Ion MicroProbe (SHRIMP II) for detailed fine scale in situ micro-analyses of oxygen isotopes (Aubert et al. 2012). The accretionary nature of otoliths, combined with advances in mass spectrometry and micro-sampling techniques enable the recovery of high-resolution isotope profiles, representing time-specific indices of environmental conditions experienced by individual fish throughout life.

Oxygen isotope ($\delta^{18}O$) ratios in otoliths are determined primarily by water temperature (Rowell et al. 2008; Surge and Walker 2005), and can consequently provide information on environmental change (Wang et al. 2011; West et al. 2011; West et al. 2012; Wurster and Patterson 2001), seasonality of site usage (Hufthammer et al. 2010), fish location and migration. As water temperatures increase, the uptake of $\delta^{18}O$ in otoliths decreases (Rowell et al. 2008). Oxygen isotopes are robust tracers of the marine stage of life history because large and systematic differences exist between marine and inland water isotope values, and the oxygen isotopic composition of fish otoliths depends upon the temperature, salinity and isotopic composition of the ambient water, not food (Elsdon and Gillanders 2002; Thorrold et al. 1997). Despite the well defined relationship between temperature and $\delta^{18}O$ ratios, water salinity can also have an effect (Gillanders and Munro 2012), while temperature and salinity can interact to influence ratios (Elsdon and Gillanders 2002). Additionally, evaporation increases ocean surface $\delta^{18}O$, whereas precipitation reduces it (Ashford and Jones 2007). The $\delta^{18}O$ composition of lake waters depends primarily on the $\delta^{18}O$ composition of the precipitation falling on the lake surface and catchment, and on the evaporation/precipitation balance of the water body. A progressive depletion of $\delta^{18}O$ in rain and surface water occurs with increasing latitude, increasing elevation, and increasing distance inland from the ocean (Dansgaard 1964; Nelson et al. 1989; Stewart and Taylor 1981).

In contrast with oxygen, carbon isotopes in otolith aragonite are deposited in disequilibrium with the ambient water (Iacumin et al. 1992). The carbon in otolith aragonite is a mixture of carbon derived from ambient dissolved inorganic carbon (DIC) and that derived from diet (metabolic carbon). DIC has a distinct isotopic composition compared to metabolic carbon, and the proportions of each incorporated into otolith aragonite are controlled by the metabolism of the fish (Kalish 1991; Shephard et al. 2007). Therefore, $\delta^{13}C$ values within otoliths, which reflect levels of metabolically derived carbon, are sensitive to changes in metabolic activity levels, which can allow insights into ontogenic changes in fish metabolism (Ashford and Jones 2007; Jamieson et al. 2004; Shephard et al. 2007). Carbon isotopes in fish otoliths from the late Holocene have been analysed to examine metabolic rates (Wurster and Patterson 2003), while comparisons of $\delta^{13}C$ values within and among modern and archaeological otoliths have provided informative trends related to ontogenetic change (Wang et al. 2011).

$\delta^{15}N$ in tissue is commonly used in ecological studies to determine trophic level, trophic structure and food chain length (Post 2002; Vander Zanden et al. 1997). This is possible, because the ratio of ^{15}N to ^{14}N ($\delta^{15}N$) increases as one moves from lower to higher levels of the food chain (Rowell et al. 2010). Nitrogen isotopes are influenced by species, tissue, type of consumer (e.g., carnivore, herbivore) and habitat type (marine, freshwater or terrestrial) (Vander Zanden et al. 1997). Studies of $\delta^{15}N$ in archaeological otoliths can assist in establishing pre-disturbance ecological benchmarks, or baselines, an essential first step for documenting ecosystem change in response to anthropogenic alterations (Rowell et al. 2010).

The "carbonate clumped isotope thermometer'" approach is another method used to investigate past changes in climate, and it can potentially be applied to parts of the geological record where the isotopic composition of water is unknown, eliminating the need to make assumptions regarding these values (Ghosh et al. 2006; Schauble et al. 2006). This can specifically be applied to otoliths from the archaeological record, but to date only modern otoliths have been analysed.

The expanding array of stable isotopic analyses is of great value to icthyoarchaeology, and is more frequently being adopted as a method of choice for researchers examining a wide variety of questions. As with other assays, frequent collaboration with fisheries scientists and geochemists will only serve to increase its applicability to the analysis of ancient samples.

9. Radiocarbon Dating

Radiocarbon dating is widely used within archaeology, and, being organic, otoliths lend themselves successfully to this method. As marine organisms exhibit older apparent radiocarbon ages caused by the uptake of carbon that has already undergone radioactive decay through long residence in the ocean (Ulm 2006), it is important to know the marine carbon reservoir correction, or δR value, for the geographic origin of the samples (for an example, see Higham and Hogg 1995). Numerous studies have incorporated radiocarbon dating of otoliths (e.g., Favier Dubois and Scartascini 2012; Hufthammer et al. 2010; Scartascini and Volpedo 2013). One example is the information obtained from the dating of otoliths collected at sites on the northern coast of the San Matías Gulf, Argentina (Favier Dubois and Scartascini 2012). Radiocarbon dating places fishing activities between ca. 6000 and ca. 5000 ^{14}C BP at two sites, Bajo de la Quinta, and Bahia Creek, while another site, Bahia de la San Antonio showed greater continuity between ca. 5300 and ca. 890 ^{14}C BP. Calibration of the radiocarbon ages and δR correction of the otoliths pushed the older ages further back and brought forward the more recent. Based on these radiocarbon dates, the past coastal conditions of the area were reconstructed (as demonstrated in simulated digital elevation models (Favier Dubois and Scartascini 2012)); the sea level was higher, creating small inlets and canals, while today, the coastline has been filled in and straightened as a result of geomorphic evolution. Favier Dubois and Scartascini (2012) propose that these small inlets would have been highly favourable for the use of nets and other mass capture techniques, such as traps.

10. Current Issues, Challenges and a Way Forward

Otoliths offer unique and significant information to archaeological research, but they also present some challenges, as detailed throughout this paper. Therefore, there are a number of key methodological issues that require further investigation and refinement. First, such issues are related to factors influencing the presence of otoliths at archaeological sites and also what their elemental/isotopic data actually mean. Discard patterns affect the numbers of otoliths that are initially deposited in archaeological sites; heads (including the otoliths) may be removed from the fish at capture and thrown back into the water, or they may be burnt in campfires to dispose of the sharp bones. In addition, as with any organic remains, specific conditions are required to ensure survival within a site. Otoliths survive best in alkaline sediments, such as those provided by shell middens, and may deteriorate within other more acidic sediments. Numerous studies have examined the effects that taphonomic and diagenetic processes – physical (e.g., trampling, scavenging, temperature, drainage and wave activity etc.), chemical (e.g., sediment pH levels and chemical structure) and biological (e.g., microbial action in sediments) (e.g., Nicholson 1992; Zohar et al. 2008) have on fish bone preservation in general, but studies focused on otoliths are lacking.

In addition to influencing preservation, taphonomic and diagenetic processes can also alter the morphological and chemical properties of otoliths (Andrus and Crowe 2002). A number of studies have examined the effects that processing methods (cooking and burning) have on fish bone and flesh (Fernandes et al. 2014; Lubinski 1996; Nicholson 1995; Richter 1986; Willis et al. 2008; Zohar and Cooke 1997); however, very little has been done to determine the effects that these processes have on the trace element and isotopic information stored within fish otoliths (for an exception, see Andrus and Crowe 2002). In addition, elements within a site matrix may be post-depositionally absorbed into an otolith's structure, influencing any chemical data that is collected for palaeoenvironmental research from the otolith's edge. In spite of the fact that otoliths are considered chemically inert, handling, preservation and processing methods have been found to impact the integrity of some elements for modern day samples (Milton and Chenery 1998; Proctor and Thresher 1998). This impact can be lessened by employing consistent methods of preparation and storage for all samples, but it is difficult to determine processes that otoliths underwent prior to deposition, and what impacts these may have had on their integrity. If relatively minor factors such as how long an otolith remains in a fish's head after death (Proctor and Thresher 1998) affect its chemical composition, thousands of years of burial and post-depositional modification are likely to have even greater effects. This is significant because assumptions regarding changes in environmental conditions and associated human responses are frequently made based on the isotopic or trace elemental data from archaeological otoliths. Therefore, it is imperative to ascertain whether these data are altered by factors after the death of the fish. This is one area of otolith research that requires further investigation.

As is often the case in archaeological research in general, a key issue is misidentification. As the shapes of otoliths are species-specific, some samples may be incorrectly identified as broken shell, stone or seeds during the sorting process. Even if otoliths are identified, the species they came from may be incorrectly determined. This is where access to large modern-day otolith reference collections and published atlases for individual study regions would be highly beneficial; however, if species distributions have changed, or local extinctions have occurred, this may remain an issue. Hopefully, with the increase of otolith analyses within archaeology, researchers will be more aware of the presence of otoliths within their collection and identification will improve.

Small assemblage size is often problematic; it is much more common to recover a few otolith samples from an archaeological site, than the large assemblages ideally required to conduct environmental reconstructions. When only small sample sizes of otoliths are available, it can be difficult to make substantial claims based on the resulting data set. While small numbers of otoliths can be used to test methodological approaches and make some inferences about site use and fish populations (e.g., Disspain et al. 2011), large assemblages of hundreds of samples can be used to investigate changes over time and to make more significant claims. Compounding this issue is the fact that some analyses are destructive, and as ancient otoliths are fragile, rare and usually subjected to a wide range of morphological and chemical analyses, it is important to examine how multiple applications can be combined on assemblages without too much damage to the collection (Schaerlaekens et al. 2011; Therkildsen et al. 2010), and to carefully plan the sequence of analyses to enable as much data as possible to be collected.

Some of these issues may be circumvented by incorporating developments from within modern fisheries, or other sciences, into archaeological analyses. The ongoing research into how different environmental and physiological factors influence otolith chemistry, or how different fish species are affected by these variables, is highly beneficial in that findings can be incorporated into trace elemental and isotopic analyses of archaeological samples, allowing fewer assumptions to be made regarding fish life history. New techniques for sample acquisition and analyses requiring smaller sample sizes encourage the application of techniques previously deemed too destructive for archaeological specimens (e.g., Shiao et al. 2014).

Ongoing development of comprehensive and readily available reference collections of modern data for comparative analysis regarding all aspects of otolith analysis, and including a wide range of species, would also be advantageous. Some physical collections, online databases and published atlases are available for use by researchers, and continuous additions and updates to these collections only increase their value. In short, open communication and cooperation between the fields of archaeology and modern fisheries science, with the integration of archaeological, historical and modern data sets, and the standardisation of common methods, is highly beneficial to both research areas, with many objectives and outcomes of research overlapping.

11. Conclusion

In spite of the limitations and issues that analysing archaeological otoliths presents, the benefits and unique information that analyses provide suggest that otoliths should be an important part of archaeological research. Otoliths provide information regarding past fish population structures, including changes resulting from human predation, habitat destruction and environmental change, as well as assisting with the establishment of baselines for rehabilitating native species to pre-impact levels. They also provide information on human subsistence strategies, fishing methods and technologies, trade routes, seasonality of site usage, and past human responses to environmental changes. Otoliths from archaeological sites contribute information to palaeoenvironmental studies, with chemical analyses providing significant data about past climates and water conditions. This paper has detailed many of the applications of archaeological otoliths; however, continuing development of methods and technologies within this area will only serve to further increase the importance and use of otoliths, while raising the profile of this unique resource.

Acknowledgements

We thank Gretchen Grammer (University of Adelaide) for advice of age determination of otoliths, Gregory Maes (James Cook University) for advice on DNA applications, and Fiona Petchey (University of Waikato) for advice on radiocarbon dating studies. SU is the recipient of an Australian Research Council Future Fellowship (FT120100656). BMG acknowledges funding via an ARC Discovery grant (DP110100716) and Future Fellowship (FT100100767).

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