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Otoliths as a proxy for seasonality: The case of *Micropogonias furnieri* from the northern coast of San Matías Gulf, Río Negro, Patagonia, Argentina

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ABSTRACT

This article presents the preliminary results of a seasonality study on *Micropogonias furnieri* otoliths from the northern coast of the San Matías Gulf, Río Negro, Argentina. First, we analyze modern *M. furnieri* otoliths from a reference collection, which provides a necessary framework for assessing the viability of the method. Data from the modern reference collection comprise more than 360 otolith section cuts from fish with known capture dates that span a whole year. Second, we analyze otolith section cuts from zooarchaeological fish remains, a total of 61 samples, collected from different archaeological sites along the northern coast of the San Matías Gulf, Patagonia, Argentina. Using data from the two analyses, we generate a strong macro-regional model of seasonality. A comparison between the modern and ancient otoliths also provides insights into the seasonality of human occupation and *M. furnieri* exploitation along the Northern Río Negro coastline from the mid-to late Holocene. Our data show that *M. furnieri* fishing activities in the area primarily took place between November and January. Application of our method demonstrates its advantages and limitations for more general application in a wider range of archaeological studies.

1. Introduction

A crucial aspect in understanding ancient human adaptive strategies is addressing occupation seasonality in a given region or in the exploitation of a particular resource (Bettinger, 2001). A variety of archaeofaunal methods allow estimation of seasonality from different archaeological contexts (Casteel, 1976; Monks, 1981; Wheeler and Jones, 1989; among others). Examples include, the study of mollusk growth patterns (Andrus, 2011; Colonese et al., 2011, 2012; Lobbia, 2012); assessment of fusion sequences of bone elements (Kaufmann, 2009); the eruption, substitution, growth, and wear sequences of teeth in animal jawbones (Kaufmann, 2009; Borella et al., 2014); high resolution isotopic relation (O^{18}) analysis of otoliths growth rings (Patterson, 1998; Hufthammer et al., 2010; Celis Hernández, 2011); and quantification of growth rings in hard elements such as otoliths, vertebrae, pectoral spines, teeth (Casteel, 1976; Campan, 1992; Schiavini et al., 1992; Van Neer, 1993; Van Neer et al., 1993, 1999, 2004; Higham and Horn, 2000; Bolle et al., 2004), among many others.

Here, we develop a growth ring model for whitemouth croaker (*Micropogonias furnieri*) otoliths using modern reference specimens, which we apply to otoliths collected from different archaeological sites along the coast of the San Matías Gulf (SMG), Río Negro Province, Argentina (Fig. 1). Whitemouth croaker otoliths are commonly recovered together with other archaeological remains – bone, shell, lithic weights, and lithic debris – in surface assemblages in the area (Favier Dubois et al., 2008, 2009). The specimens studied here are from sites dating between *c.* 6000 BP through *c.* 400 BP (Scartascini et al., 2009). *M. furnieri* otoliths were recovered in large quantities, which permits analysis of different lines of evidence relating to chronology (Favier Dubois, 2013), allometry (Scartascini et al., 2009), geoarchaeology (Favier Dubois and Scartascini, 2012), and paleoecology (Scartascini and Volpedo, 2013). In this paper, the otolith seasonality model we develop is applied to 61 zooarchaeological otolith specimens recovered from two sites along the northern coast of the San Matías Gulf.

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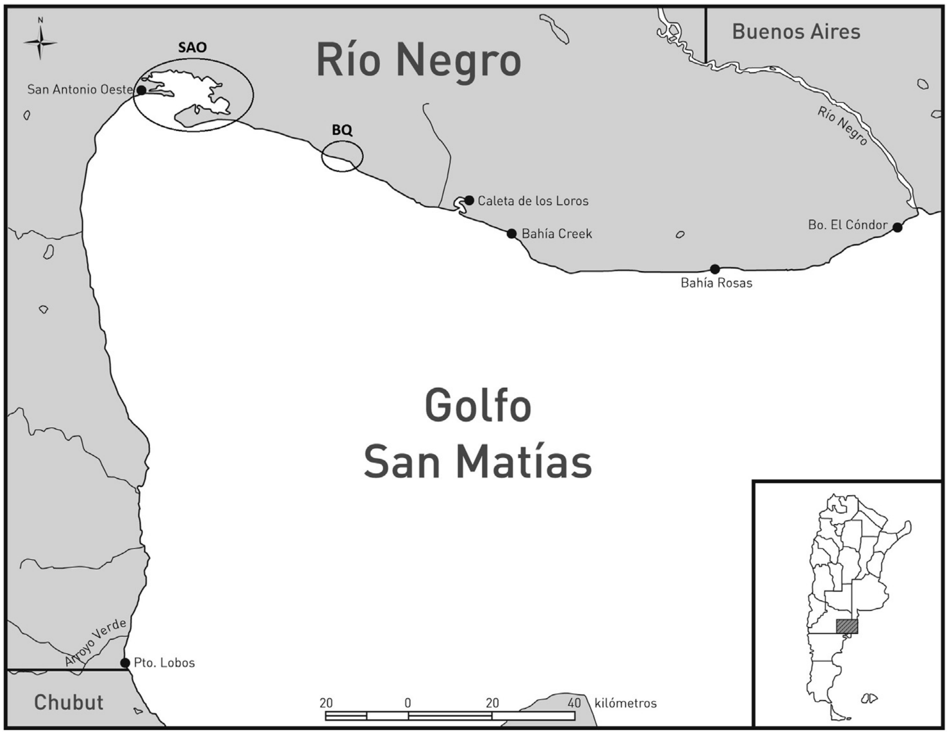

Fig. 1. Map of the study area and the sites addressed in this article.

2. Background

In temperate and sub-polar waters the growth cycle of fish is directly related to photoperiod, water temperature, food availability, and marine bio-productivity (Loeng, 1988; Cardinale et al., 2002). On the basis of these parameters, we know that during the summer months productivity is higher and fish growth rate increases; the reverse occurs during winter months. This differential growth rate (seasonality) can be observed across various hard structures of the fish, such as their vertebra, opercular bones, spine, scales, and otoliths (Wheeler and Jones, 1989).

Otolith development, the main focus of this article, is the result of the interaction between fish ecology – growth rate, physiology, condition – and environmental conditions (Campana and Neilson, 1985; Gutierrez and Morales-Nin, 1986; Radtke and Shafer, 1992; among others). The otoliths of teleost fishes are complex polycrystaline bodies composed mainly of calcium carbonate forming as aragonite and small quantities of other minerals buried within an organic matrix in the vestibular apparatus (Campana, 1999; Volpedo and Echeverría, 2000). The aggregation of calcium is an extracellular process that is regulated by hormones and influenced by variation in environmental temperature and by the chemical composition of the water (Morales-Nin, 1991; Avigliano and Volpedo, 2013; Avigliano et al., 2014).

In general, during periods of rapid growth the otolith forms an opaque ring, and during periods of slow growth it forms a translucent or hyaline ring (Casselman, 1987). Thus, the structure of the otolith growth rings corresponds to specific periods of the year, both in the Northern and Southern Hemisphere, although these can vary depending on the latitude that fish inhabit (Beckman and Wilson, 1995 in Van Neer et al., 2004: 458).

This method has been applied successfully in different parts of the world, including the North Sea, Australia, and Patagonia (Van Neer et al., 1993, 2004; Higham and Horn, 2000; Cahiza, 2003; Svoboda, 2013; among others). Nevertheless, the use of otoliths for seasonality analysis is not without its problems and certain aspects have to be carefully considered before proceeding with analysis.

One challenge is that it is not possible to gauge seasonality from the study of a single otolith. The reason for this is that both types of rings – opaque and hyaline – can be observed at different times of the year, and therefore this type of analysis requires multiple otoliths. With multiple otolith samples the proportional variation in ring frequency for different seasons can be observed. A second challenge is the collection and recording of samples; otoliths from unknown or insecure origin and chronology should be avoided, as this minimizes the possibility of mixing elements from different seasons.

A third concern is that raised by Van Neer et al. (2004) when they registered differences in growth rate of the marginal ring of two species – *Pleuronectes platessa* and *Melanogrammus aeglefinus* – depending on geographic location, the year under study, and ontogenetic age (Bolle et al., 2004). As a result of these considerations, counting of marginal opaque and hyaline ring frequencies can be imprecise for certain species. In this sense, it is important to take into consideration that the physiology of the fish (e.g., reproduction, physical condition, and other life history variables) as well as the different ecological strategies employed by fish in different habitats (e.g., estuary habitation fomenting growth and maturity, migratory displacements, population interconnectivity) may also influence marginal ring growth rates.

A final potential limitation that has to be accounted for is the degree to which otolith preservation is impacted by taphonomic processes. Although there is little concrete information on this, Van Neer et al. (1993) observed that diagenesis can lead to the recrystalization of *Oreochromis niloticus* otoliths, making it in turn difficult to study their edges. Svoboda and Moreno (2013), in their analysis of modern-day creole perch (*Percichthys trucha*) otoliths exposed to the open air for 46 months and then buried for a further 26 months, concluded that there were no fundamental changes in the physical structure of otoliths affecting the collection of growth-ring data. Evidence for changes in the physical structure of the otoliths by taphonomic effects requires further study, and there may be significant variability between species. Present day experiments with negative results such as those presented by Svoboda and Moreno (2013) are valuable, but a limitation is that they do not assess long-term variability in growth rates, such as those often observed in paleozoological samples (Borrero, 1991).

An alternative that complements and increases reliability of ring-frequency analysis is analysis of terminal-ring width. Various scholars (Higham and Horn, 2000; Van Neer et al., 2004) have observed that the width of the terminal ring correlates to different periods in the year and allows for greater precision in the quantification method. For example, a narrow as opposed to a wide opaque ring could suggest different moments during the same season, such that the narrow opaque ring corresponds to the state of the productive season – end of winter – while a wider opaque ring would mean the middle of summer.

In Argentina, there are only two previous examples of the use of otolith rings as a proxy to determine seasonality, though neither of these were from marine contexts. Pioneering work in this respect is that of Cahiza (2003) at Guanacache Lake, in northeast Mendoza Province. On the basis of a study into *P. trucha* otoliths recovered from archaeological sites in the area, the author proposes the seasonal consumption of this resource during the period between September and April, thus coinciding with the hottest months of the year. The other case study is recent work by Svoboda (2013) on creole perch (*P. trucha*) from the lower Río Chubut valley. Although very few otoliths were sampled ($n = 4$), the author observes differences between the two studied assemblages, one of creole perch fished during autumn–winter and another group fished during summer.

This type of work is lacking along a large sector of the Argentine coastal environment. The only similar studies are those by Campan (1992) on fish vertebrates in Tierra del Fuego coast, and those by Lobbia (2012) and Steffan and Morsan (2013) on *Mytilus* valves.

3. Methodology

We collected 1500 otoliths of *M. furnieri* from the surface of archaeological sites at different points along the San Matías gulf coast in the Rio Negro Province. A complete description of the assemblages, as well as their main taphonomic and contextual characteristics have been presented in previous articles (Scartascini et al., 2009; Favier Dubois and Scartascini, 2012; Scartascini, 2012).

As a reference baseline for this article, we used 360 otoliths *sagittae* from adult *M. furnieri* specimens collected from fishing catches in Mar del Plata harbor. *M. furnieri* presently has a southern distribution limit north of the study area (Scartascini and Volpedo, 2013). Each otolith was sectioned and measured. We selected 30 otoliths for each month of the year, thereby collecting a representative sample across the annual cycle of the species, which in turn allowed us to further adjust the precision of the method.

The sectioning of the otoliths from the external edge to the core was undertaken using a handheld edge cutter machine (optic type), with a diamond wheel (two wheels were used, a coarse one to file down quickly and a fine one to achieve a precise finish). In some cases, otoliths were baked over an aluminum flat grill, so as to produce a greater contrast between the rings (Christensen, 1964). The ring reading was done on the filed face of the otoliths. To this end, a drop of immersion oil was used to obtain a higher resolution. The otoliths were examined with transmitted light using a stereomicroscope (Nikon SMZ 10A). Age was determined by counting opaque rings, which are visible as clear and fine lines next to the hyaline rings, which are dark and wide (due to roasting), each pair together represent a year (Cotrina, 1991). With this data, we generated an annual curve of ring counts that allowed us to establish the number of opaque/hyaline rings and to observe relative variability in frequency by month of capture.

Similarly we processed, section-cut, and examined 61 otoliths from two archaeological sites (described above) from the northern coast of the San Matías Gulf (San Antonio Oeste and Bajo de la Quinta). Even though these 61 otoliths were from surface collections, they had a clear temporal and spatial origin. Otoliths form discrete concentrations in this coastal landscape. There is also a clear relationship between the chronology of the sites and the geographic location and landforms where they occur (Favier Dubois and Scartascini, 2012). We used assemblages in which *M. furnieri* otoliths had been directly dated (Table 1), and from which basic geoarchaeological and assemblage formation studies were carried out (Favier Dubois and Kokot, 2011; Favier Dubois and Scartascini, 2012; Favier Dubois, 2013; among other authors.). Finally to reduce the ontogenetic age variation, we used samples of adult fish (estimated size greater than 360 mm).

Table 1
Location and chronology of otoliths used in seasonality analysis. All dates correspond to *M. furnieri* otoliths. Site codes: SAO: San Antonio Oeste, BQ: Bajo de la Quinta.

Site	*Locus*	Chronology	Frequency	Reference
SAO	Playón Cem.	*c.* 4500 BP	20	Scartascini et al. (2009)
	No K	*c.* 3600 BP	8	Scartascini et al. (2009)
	Saco Viejo	*c.* 1600 BP	10	Favier Dubois (2013)
BQ	Sec. Otolitos	*c.* 6000 BP	18	Scartascini et al. (2009)
	LNO	*c.* 1300 BP	5	Favier Dubois and Scartascini (2012)
Total			61	

4. Results

4.1. Modern-day reference collection

The first general tendency that could be observed from examining the modern samples was that the hyaline edge was present during the whole year, although in varying proportions. Within this sample, the otoliths collected between the months March and August, Autumn–Winter, did not have any observable variation and had 100% hyaline edges.

Conversely, the opaque edges were only visible during the warmer months, between September and February. The model showed a gradually rising number of opaque edges from the beginning of Spring going into Summer. The peak frequency in opaque edges was between December and January with an abrupt fall in their frequency after January (Fig. 2). The resulting model suggests two points during the year that are clearly differentiated and thus easy to separate: the otoliths recovered in Autumn–-Winter that had 100% hyaline edges and the otoliths recovered in Spring–Summer exhibited opaque edges, although the frequency of this edges varied proportionally during this period (from 3.3% to 86.7%).

Poisson regression analysis was applied to achieve a higher precision of model examining the frequency of opaque edges across the warmer months. We calculated the median and the confidence levels (95%) of each month (Fig. 3).

A general linear model using the Poisson distribution on count data was used to test the null hypothesis of homogeneous distribution in opaque bands throughout the various months, with the

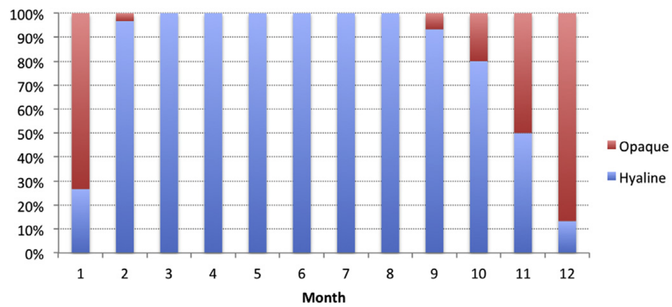

Fig. 2. Seasonal percentage (%) changes in edge type (hyaline/opaque) for modern *M. furnieri* samples.

months used as factors. The results suggested differences in the occurrence of opaque bands ($p < 0.001$). Group A, covering the months of February, September and October, in which the average percentage of opaque edged otoliths was 10% with a confidence level of between 0.1% and 16.7%, and a high degree of dispersal. Group B, covering the months of November, December, and January, in which the percentage of opaque edged otoliths was 70%, with a confidence interval of between 53.3% and 90%, and a low level of dispersal (Fig. 4).

In this manner, it was possible to discriminate two separate opaque edged otoliths groups, thereby refining the model. In summary, the model was able to define three 'seasons' or moments during the year: a) Autumn/Winter months (100% hyaline edges), b) Spring months (10% opaque edges) and, c) Summer months (70% opaque edges).

4.2. Results from the archaeological sample

All the archaeological otolith samples were from adult specimens, given that their maximum estimated length was above 360 mm (Table 2). Age was also calculated through the counting of rings on the otoliths (Fig. 5), estimated as being at least 11 years, supporting estimation based on maximum length. No changes were recorded in the external morphology (shape) of current and archaeological otoliths (Scartascini et al., 2009), or in the internal structure (distribution and resolution of the rings) (Fig. 5).

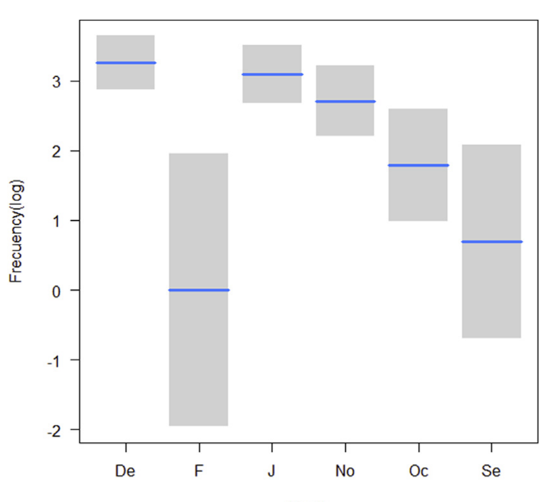

Fig. 3. Poisson regression graph, with median and confidence level (95%) for opaque edges during the warmer months.

Table 2
Archaeological otolith samples showing provenience; age, estimated size (mm), and edge type (hyaline or opaque).

Otolith No.	Provenance	Age	Estimated size (mm)	Edge
1	SAO SV	19	499.4	Hyaline
2	SAO SV	19	585.6	Hyaline
3	SAO SV	18	552.2	Hyaline
4	SAO SV	23	451.8	Opaque
5	SAO SV	12	443.2	Opaque
6	SAO SV	12	531.6	Hyaline
7	SAO SV	22	491.6	Opaque
8	SAO SV	24	448.4	Opaque
9	SAO SV	25	405.2	Hyaline
10	SAO SV	17	515.2	Hyaline
11	SAO PC	17	413.4	Opaque
12	SAO PC	11	438	Hyaline
13	SAO PC	18	439.2	Hyaline
14	SAO PC	33	460.2	Opaque
15	SAO PC	18	462	Hyaline
16	SAO PC	21	479.4	Opaque
17	SAO PC	20	480.2	Opaque
18	SAO PC	14	481.4	Opaque
19	SAO PC	18	486	Hyaline
20	SAO PC	15	486.8	Opaque
21	SAO PC	25	487	Hyaline
22	SAO PC	22	490.2	Opaque
23	SAO PC	20	490.8	Opaque
24	SAO PC	18	493	Opaque
25	SAO PC	11	499.4	Opaque
26	SAO PC	22	501.6	Opaque
27	SAO PC	24	505.8	Opaque
28	SAO PC	28	510.4	Opaque
29	SAO PC	13	520.6	Opaque
30	SAO PC	20	528	Opaque
31	SAO No K	20	385.2	Opaque
32	SAO No K	21	405.4	Opaque
33	SAO No K	20	462.6	Opaque
34	SAO No K	22	465.4	Opaque
35	SAO No K	19	466.8	Opaque
36	SAO No K	19	477.4	Opaque
37	SAO No K	18	480.2	Opaque
38	SAO No K	13	493	Opaque
39	BQ Sec OTO	25	384.4	Opaque
40	BQ Sec OTO	20	388.6	Opaque
41	BQ Sec OTO	31	389.2	Opaque
42	BQ Sec OTO	20	390.6	Opaque
43	BQ Sec OTO	36	391.2	Hyaline?
44	BQ Sec OTO	16	392.4	Opaque
45	BQ Sec OTO	38	392.6	Opaque
46	BQ Sec OTO	23	394.2	Opaque
47	BQ Sec OTO	20	397.2	Hyaline
48	BQ Sec OTO	18	403.6	Opaque
49	BQ Sec OTO	25	405.8	Opaque
50	BQ Sec OTO	22	406.6	Opaque
51	BQ Sec OTO	20	407.4	Hyaline
52	BQ Sec OTO	16	408.6	Opaque
53	BQ Sec OTO	14	409.8	Opaque
54	BQ Sec OTO	20	411.2	Opaque
55	BQ Sec OTO	23	426.2	Opaque
56	BQ Sec OTO	28	429.6	Opaque
57	BQ LNO	22	567.2	Opaque
58	BQ LNO	20	571.8	Opaque
59	BQ LNO	29	584.6	Opaque
60	BQ LNO	19	586.2	Opaque
61	BQ LNO	26	586.8	Opaque

The studied otoliths exhibited very clear banded structures, which greatly facilitated the reading of their rings. The results showed that 79% of the otoliths from the archaeological assemblage had opaque edges, as opposed to 21% with hyaline edges.

Both sites tended towards opaque edged otoliths, which in turn strongly suggests that exploitation of the whitemouth croaker (*M. furnieri*) was undertaken during the warmer months. Table 3 indicates that all the samples had percentages above 50% for opaque edges, meaning that they belonged to Group B, specimens captured during the months of November, December, and January.

Table 3
Number of otoliths analyzed and percentage of opaque edges by *locus*.

Site	Sector	Opaque	Hyaline	% Opaque	Total
SAO	Playón Cem.	15	5	75%	20
	No K	8	0	100%	8
	Saco Viejo	5	5	50%	10
BQ	Sec. Otolitos	15	3	83.30%	18
	LNO	5	0	100%	5
Total					61

5. Discussion and final considerations

The results of this study of modern and archaeological white croaker otoliths demonstrated that on the basis of counting and classifying otolith edges (opaque/hyaline) it is possible to reliably identify the season of exploitation of *M. furnieri* in San Matías Gulf during Middle and Late Holocene.

The otolith ring model provides an interpretative framework for splitting the year into two blocks of six months each. One block corresponds to the colder months, in which only hyaline edges were observed, and another block is associated with warmer months, where there were also opaque edges in varying proportions. Hyaline edges were found in all studied otoliths, meaning that they had no value in determining the seasonality for individual cases. The model did suggest that the presence of opaque edged otoliths provided sufficient evidence to indicate exploitation during warm months.

The degree of resolution available for the warmer months was refined on the basis of statistical analysis. Consequently, the median proportion of opaque edges and their confidence levels make it possible to divide this period into two trimesters - Groups A and B in the analysis. Thus, the study of the modern sample allowed clear differentiation of three 'seasons' of capture of *M. furnieri*: one season corresponding to the cold months, and two to the warmer months (Group A and B). The implications of this study are macro-regional, given that modern specimens were considered from Buenos Aires province to Norpatagonia, the southern limit of this species distribution.

In other parts of the world, variations in the rhythm of the marginal ring growth has been attributed to geographical differences in the fishes' distribution areas (Van Neer et al., 2004). For this reason, validation of this method in other littoral sectors within the distribution area of *M. furnieri* (for instance along coastal Uruguay and Southern Brazil) will allow us to define the broader applicability of the model.

Application to the ichthyo-archaeological sample from the coast of San Matías Gulf indicates that *M. furnieri* was predominantly fished during the warmer months of the year, especially between November and January. This three-month period correlates well with the modern ecology of the species in the southern fishing bank (Volpedo and Fernández Cirelli, 2006). For example, today this species arrives at the coast of Buenos Aires province during the warmer months, the contemporary southern limit of the species, to spawn. This produces an annual growth ring that is physically registered on otoliths in the form of an opaque ring (Volpedo, 2001). Thus, the results of this preliminary study suggest that prehistoric fishers were taking advantage of the species arrival during the spawning season.

In an earlier article, we observed that the *M. furnieri* sizes registered for the sites in the area strongly suggested a mass fishing strategy of adult specimens (Scartascini et al., 2009). Stone weights were recovered in association with fish remains in these assemblages. These artifacts have been interpreted as belonging to nets, thereby reinforcing the hypothesis that a mass fishing strategy was employed (Scartascini and Cardillo, 2009). Taking into account that these archaeological sites are located in protected littoral environments such as bays and sheltered coastal areas with soft seabeds, they would have been camps for prehistoric mass fishing. This

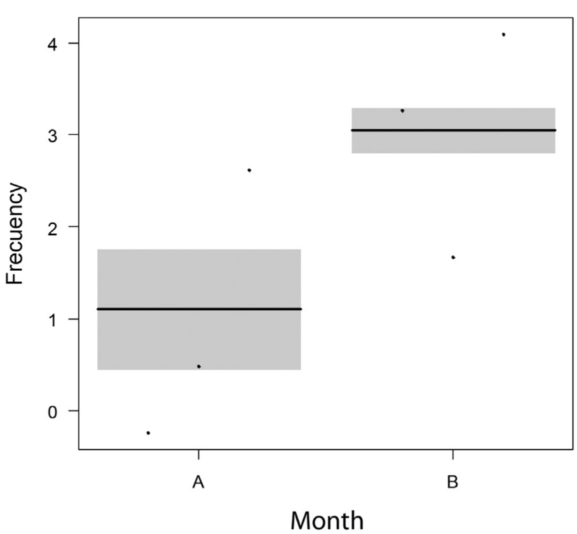

Fig. 4. Poisson regression graph, with median and confidence level (95%) for Group A and B. Note that there is no overlap between the groups, and that Group A had higher variance than Group B.

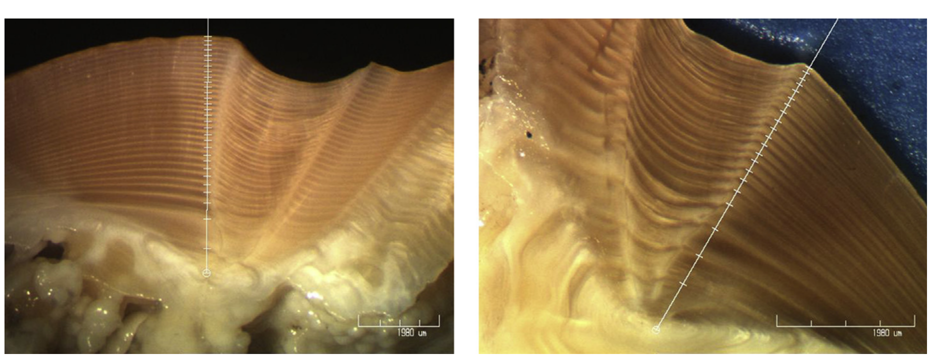

Fig. 5. Current (left) and archaeological (right) *M. furnieri* otolith section cuts. Observe the opaque (fine and clear lines) and hyaline (dark and wide) rings, clearly visible in both specimens. In the archaeological specimen, 22 rings were counted and the edge corresponded to an opaque ring.

study shows that the intense fishing of *M. furnieri* in the area followed a seasonal pattern, a pattern that appears to have been upheld for at least six millennia. This in turn implies marked knowledge of local coastal environments by hunter–gatherer groups who took advantage of the predictability of these coastal resources, in this case *M. furnieri*. In order to confirm the pattern observed here, it is necessary to undertake new studies into *M. furnieri* as well as other fish species found in the archaeological assemblages of the area (Scartascini, 2012). Other taxa that can supply data on resource seasonality and seascape exploitation in San Matías Gulf should be included in future studies, for instance mollusks and sea lions (Borella et al., 2011; Steffan and Morsan, 2013). This in turn will help to produce a more holistic narrative of human exploitation of San Matías Gulf area during the Middle and Late Holocene.

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