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Age determination of a long-lived coregonid from the Canadian North: comparison of otoliths, fin rays and scales in inconnu (*Stenodus leucichthys*)

Kimberly L. Howland[1,2], Michel Gendron[3], William M. Tonn[1] & Ross F. Tallman[2]

[1)] *Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, T6E 2G9 (e-mail: HowlandK@dfo-mpo.gc.ca)*
[2)] *Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6*
[3)] *Ducks Unlimited Canada, Unit 1–614 Norris Court, Kingston, Ontario, Canada, K7P 2R9*

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We examined otoliths, pelvic fin rays and scales of inconnu to determine precision of age estimates within and between readers, and to compare relative accuracy of estimates from different structures. Our main objective was to determine if readability and estimates from fin rays and scales, which can be non-lethally removed, were similar to those of otoliths, which are generally considered the most reliable ageing structure. Among- and within-reader variation was low for both fin rays and otoliths, but higher for scales. Variation tended to increase with fish length for all structures. Scales were most difficult to read and had age estimates that were significantly lower than the other structures at ages of ten years and greater. Age estimates and readability of fin rays and otoliths were similar.

Introduction

Proper age determination is critical for assessments of fish stocks. Estimates of demographic characteristics such as age structure, age at maturity, reproductive life span and age-specific schedules of fecundity, mortality and growth using inaccurate ages can lead to substantial errors in management, especially for long-lived species (Mills & Beamish 1980, Chilton & Beamish 1982, Beamish & McFarlane 1983). Thus, the evaluation of accuracy and precision of different ageing methods is a crucial component of age and growth studies (Chilton & Beamish 1982, Beamish & McFarlane 1983). Readability may vary among ageing structures with some providing more reliable age estimates than others. Therefore, fish from a new species, stock or population should be treated as if being aged for first time (Beamish & McFarlane 1983). Ideally, several different structures should be compared, and if similar ages are obtained using each, then the most accessible or easily aged one should be used (Chilton & Beamish 1982).

The inconnu, *Stenodus leucichthys*, is a highly migratory coregonid found in large rivers and lakes of northwestern North America and northern Eurasia (McPhail & Lindsey 1970). The inconnu, like many other northern fish, is long-lived, and exhibits relatively slow rates of growth, particularly at older ages and in parts of its range where it experiences lower levels of exploitation (Stein *et al*. 1973, Brown 2000, K. L. Howland unpubl. data). The species forms an important resource for subsistence, recreation and commercial use. Given that inconnu are particularly vulnerable to exploitation and environmental disturbance (Howland *et al*. 2000), it is essential that proper ageing methods are used in managing this resource.

The majority of published ages for inconnu have been obtained using scales only, as these were the traditional structure of choice for age determination in the past (Fuller 1955, Alt 1973, Yole 1975). However, decreased somatic growth in later years, as seen in this species, can present difficulties in estimating ages from scales where annuli can become crowded and sometimes indistinguishable (Chilton & Beamish 1982). Problems with resorption, lack of annulus formation, and difficulties with interpretation of scales are also frequently reported (Chilton & Beamish 1982). A number of studies on other coregonid species have demonstrated that scales often under age fish where ages are known (e.g., Sych 1971, Mills & Beamish 1980) and typically give lower age estimates than either fin rays or otoliths, particularly in populations containing long-lived, slow-growing individuals (Aass 1972, Power 1978, Barnes & Power 1984, Mills & Beamish 1980).

Otoliths, fin rays, spines and various other hard parts can potentially be used as an alternative to scale ages. Otoliths are generally considered to contain the best permanent record of fish growth and have been shown to be more accurate than scales in most cases (e.g., Beamish & McFarlane 1987, Barbieri *et al*. 1994). A disadvantage of otoliths is that their removal is lethal to the fish which can be a problem when dealing with small populations, trophy fisheries, endangered species or when tagging and releasing individuals (Jearld 1983). The removal of otoliths also causes visible damage to the head which is often undesirable when sampled fish are to be used for commercial sale (K. L. Howland pers. obs.). Fin rays and spines appear to vary substantially among species with respect to their readability. Some studies have found these structures to have relatively high accuracy and precision (e.g., Beamish & Harvey 1969, Mills & Beamish 1980), however in other cases authors have reported difficulties in interpretation or ages that are significantly lower than otoliths (e.g., Erickson 1983, Barber & McFarlane 1987, Welch *et al*. 1993). Where fin rays are shown to be as accurate as otoliths, there is a major advantage in that they can be used when live sampling protocols are desired. Although ageing of inconnu with otoliths has been used in more recent studies (e.g., Brown 2000) there has never been a comparison of the effectiveness of these alternative ageing structures for this species.

In this study we examined otoliths, pectoral fin rays and scales of inconnu from a lightly-exploited (relatively slow-growing) population in the Canadian Arctic to: (1) determine precision and bias of age estimates within and between readers for each of the three ageing structures, and (2) to determine if readability and age estimates from fin rays and scales, which can be non-lethally removed, are similar to those of otoliths, which are generally considered the most reliable ageing structure.

Materials and methods

All inconnu included in this study were collected by gillnet from the Arctic Red River, Northwest Territories, Canada in 1992 and 1993. Scales, pectoral fin rays and otoliths were collected from individual fish along with other biological data (fork length, weight, sex and maturity) as part of a larger study on the life histories of coregonids in this river system. A total of 80 (1992: $N = 42$; 1993: $N = 38$) samples were selected to provide an approximately equal representation across eight 100 mm length intervals ranging from 200 mm to 1000+ mm. With the exception of the 200–299 mm and the 1000+ intervals where there were insufficient samples available, a total of 12 individuals were included in each length category.

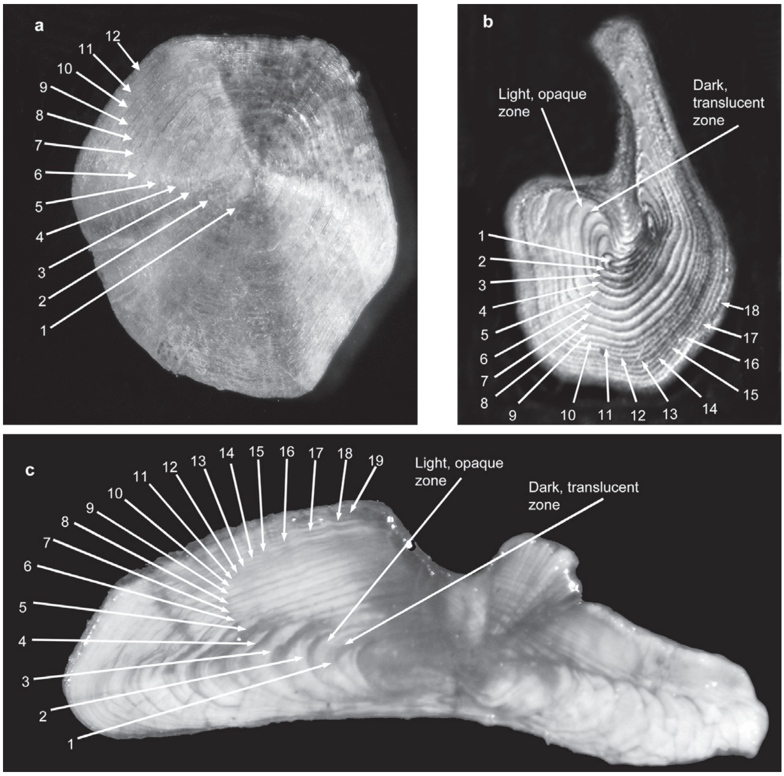

Fig. 1. Examples of different ageing structures from the same fish: (**a**) scale, (**b**) fin ray section showing alternating opaque and translucent growth zones, (**c**) surface of broken and burned otolith showing alternating opaque and translucent zones.

Removal, preparation and reading of ageing structures

Scales

Several scales were taken from each fish from above the lateral line and just posterior to the dorsal fin and stored dry in a coin envelope. If necessary, scales were cleaned prior to reading. They were then placed between glass plates, magnified on a microfiche reader (20×) and the number of annuli was estimated. Annuli were defined as the regions where there was crowding of circuli and/or "cutting over" or breaks in circuli (Alt 1969, Bagenal & Tesch 1978, Jearld 1983; Fig. 1a).

Pectoral fins

Pectoral fin rays were chosen over pelvic fin rays for this comparison since they are slightly smaller and thus easier to remove and store. The two structures have not been found to differ significantly when examined in other coregonids (e.g., Mills & Beamish 1980). The pectoral rays were removed from each fish by cutting with bone cutters at the base of the fin from as close to the body as possible and pulling the first three rays away from the remainder of the fin. For larger fish, excess material at the tip of the first three rays was removed from approximately three centimeters from the base. The clipped fin rays were placed in coin envelopes where they were stored dry. They were later dipped in epoxy resin, dried and serially sectioned using a low-speed saw. An initial cut was made to remove the rough edge at the base of the fin. Three 0.5 mm cross-sections of the first three rays were then cut, mounted on a microscope slide and read at 64× magnification using a compound microscope. We considered each annual increment (annulus) to consist of a wide, light, opaque (summer growth) zone and an adjacent narrow, translucent, hyaline (winter growth) zone, that together formed a continuous ring around the center of the ray when viewed under transmitted light (Chilton & Beamish 1982, Jearld 1983; Fig. 1b).

Otoliths

Otoliths were removed, cleaned and stored dry in coin envelopes. Otoliths were prepared for reading using a modified version of the "break and burn" technique (Chilton & Beamish 1982). They were allowed to soak in glycerin for at least three weeks prior to preparation to improve clarity of the rings and to prevent shattering during cross-sectioning. One otolith from each pair was broken in transverse cross-section through the nucleus by repeatedly scoring the surface with a scalpel blade. The broken surface on both halves of the otolith was then polished smooth using fine grit sandpaper mounted on a grinding wheel. The polished surfaces were carefully burned in an alcohol flame to produce a distinct banding pattern. Otoliths were mounted in plasticine and a drop of mineral oil was placed on the burnt surface to improve the contrast between growth zones. Ages were read using a dissecting microscope at 20–40× magnification. An annulus was considered to consist of a wide, light, opaque zone and an adjacent narrow, dark, translucent, hyaline zone, as seen when the burned otolith was viewed under reflected light (Jearld 1983; Secor *et al*. 1992; Fig. 1c).

Each ageing structure was read twice by two different readers (first and second authors). Reader A had no previous age reading experience and reader B had previous experience with reading otoliths only. Thus, prior to conducting the study, practice materials were examined, and the above-described criteria for identifying annuli were followed to help standardize techniques. Ageing structures were each assigned a random five digit number and reads were done in random order. Readers were not provided with information on fish size, and were unable to compare estimates among different readings of the same structure or between different structures from the same fish. The capture date was provided to ensure that fish were assigned to the proper year-class using January first as a common birth date.

When estimating ages, readers also recorded a readability factor on a scale of one to four: 1 = very good readability, total confidence in age estimate; 2 = good readability, high confidence in age estimate; 3 = poor readability, age estimate may be off by one to two years; 4 = unreadable, no age estimate can be made. This allowed us to quantitatively compare perceived readability between different structures.

Analyses

Precision and bias

Age bias plots (Campana *et al*. 1995) were used to look for systematic differences and evaluate consistency of age estimates within and between readers for each ageing structure.

Precision of age estimates within and between readers was compared using the coefficient of variation (CV) expressed as a ratio of the standard deviation to the mean of age estimates for a given fish (Chang 1982) and written as:

$$\mathrm{CV}_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R-1}}}{X_j} \qquad (1)$$

where X_{ij} was the *i*th age determination of the *j*th fish, and R was the number of times each fish was aged. The CV was averaged across all samples to determine average precision within and between readers for each structure.

Readability and relative accuracy

Readability was compared between structures by computing a mean readability from four readings (two readers, two reads per structure) for each sample for each ageing structure. Pairwise comparisons between the readability of different structures were then made using the two-tailed *t*-test with Bonferroni adjustment.

Although annulus formation has not been formally validated for inconnu, we have observed seasonal patterns in the marginal increment deposition on the otoliths that suggest a single translucent band (winter growth) is laid down sometime between February and May, and that growth of the lighter opaque zone occurs mainly between early June and late September (Howland *et al.* 2001). Given our previous observations

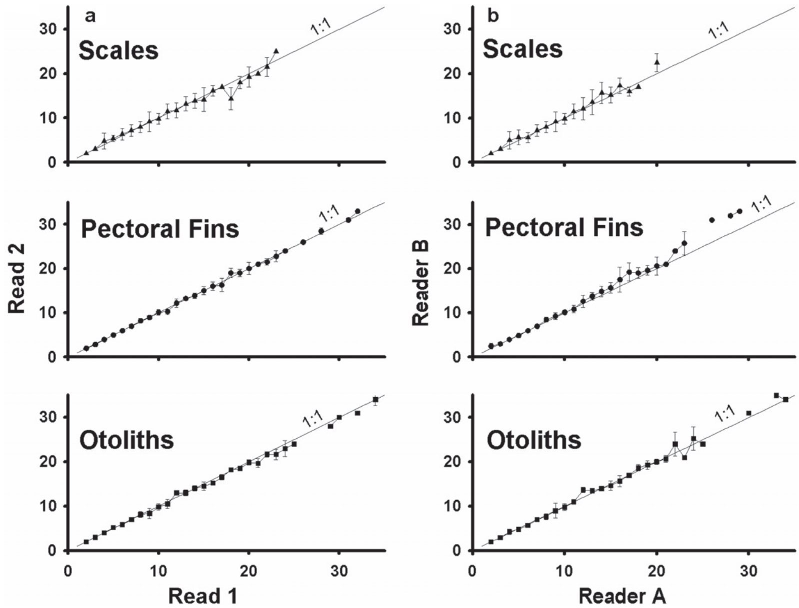

Fig. 2. Age bias plots for pairwise age comparisons (**a**) between reads within readers and (**b**) between readers. Each data point represents the mean age assigned (**a**) during read 2 for all fish assigned a given age during read 1, and (**b**) by reader B for all fish assigned a given age by reader A. Each error bar represents 1 standard deviation from the mean. The solid black line indicates the 1:1 equivalence.

and the fact that otoliths have been validated in a number of other species (*see* Beamish & McFarlane 1987), we chose to compare age estimates from scales and pectoral fin rays with those from otoliths, under the assumption that otoliths are a valid method for ageing inconnu. The relative accuracy of hard structures was assessed by computing a mean age per sample for each structure from four readings (two readers, two reads per hard structure). Mean ages from pectoral fin rays and scales were then regressed on mean otolith ages and plots were examined for deviations from the 1:1 line. The average CV between estimates from corresponding pairs of structures was calculated using the above described formula by Chang (1982) and comparisons among the mean age estimates from different ageing structures were made using the two-tailed *t*-test with Bonferroni adjustment.

Results

Precision and bias

Scales had the lowest precision as indicated by the high CV and standard deviation of age estimates both within and between readers; pectoral fin rays and otoliths had higher precision as indicated by the lower levels of within- and between-reader variation (Table 1 and Fig. 2). Within- and between-reader variation tended to increase with fish age for all three ageing structures, suggesting that level of precision can be expected to be lower when ageing older individuals (Fig. 2).

There did not appear to be any within-reader bias, however there was some evidence of between-reader bias in reading pectoral fin rays, with reader B tending towards higher age estimates than reader A at ages > 20 years (Fig. 2).

Table 1. CV of age estimates for individual fish averaged across samples for each age structure

	Between readers			Within readers		
Ageing structure	Read 1	Read 2	Read 1 + 2 combined	Reader A	Reader B	Reader A + B combined
Scales	0.115	0.091	0.104	0.050	0.094	0.072
Pectoral Fins	0.031	0.038	0.034	0.015	0.017	0.016
Otoliths	0.030	0.035	0.032	0.028	0.017	0.022

Readability and relative accuracy

Scales had significantly lower readability than either otoliths or pectoral fin rays; otoliths and fins did not differ significantly in terms of their readability (Table 2).

The maximum estimated age of inconnu using scales was 11–13 years lower than that obtained using either pectoral fin rays or otoliths (Table 3). Likewise, the overall mean age based on scale estimates was significantly lower than mean ages based on either fins or otoliths; mean ages of fin rays and otoliths did not differ from each other (Table 3).

Direct comparisons of age estimates for the same fish from different hard structures revealed that there was poor agreement between scale and otolith ages as indicated by the high average CV and the large deviation from the 1:1 line for the scale–otolith regression (Fig. 3a). Estimates of scale age tended to be slightly higher than those of otolith age at ages of less than ten years (although this difference was not significant), but at ages of ten and greater, scale ages were significantly lower than otolith ages (Table 4 and Fig. 3a). Fish of age ten and up, as estimated from otoliths, ranged in fork length from 540–1180 mm. In contrast to scales, pectoral fin ray ages, showed very good agreement with otoliths, as indicated by a low average CV and only a slight deviation from the 1:1 line on the fin-otolith regression (Fig. 3b). Estimates of fin ray age were not found to differ significantly from those of otolith age at ages above or below ten years (Table 4).

The tendency for scales to underage otoliths and fins at older ages resulted in overestimates of growth rate and underestimates of longevity (Fig. 4).

Discussion

Age estimates from pectoral fin rays were similar to those from otoliths, while estimates from scales were substantially lower at ages greater than nine years, suggesting that this was the least accurate ageing method, particularly for older fish. The common problem of poor accuracy when using scales to age older fish (Beamish & McFarlane 1987) is related to the fact that scale growth is directly linked to somatic growth rate and therefore may slow dramatically or even

Table 2. Mean readability of each ageing structure and pairwise comparisons of readabilities among ageing structures using the two-tailed *t*-test with Bonferonni adjustment. *P* values and $t_{\alpha = 0.017, \text{df} = 154}$ for each set of comparisons are indicated above and below the diagonal, respectively.

Ageing structure	Mean ± SD readability	Pair-wise comparisons		
		Scale	Pectoral fin	Otolith
Scales	2.05 ± 0.432	–	$P < 0.0001$	$P < 0.0001$
Pectoral fins	1.62 ± 0.551	$t = 5.32$	–	$P = 0.708$
Otoliths	1.58 ± 0.439	$t = 6.47$	$t = –0.375$	–

Table 3. Range and mean of age estimates for each ageing structure along with results of pair-wise comparisons of the age estimates among ageing structures using two-tailed *t*-test with Bonferonni adjustment. *P* values and $t_{\alpha = 0.017, \text{df} = 154}$ for each set of comparisons are indicated above and below the diagonal, respectively.

Ageing structure	Age range	Mean ± SD age	Pair-wise comparisons		
			Scale	Pectoral fin	Otolith
Scales	2–22	10.6 ± 4.44	–	$P < 0.018$	$P < 0.013$
Pectoral fins	2–33	12.8 ± 6.55	$t = –2.40$	–	$P = 0.851$
Otoliths	2–35	13.0 ± 6.97	$t = –2.52$	$t = 0.188$	–

cease with age (Beamish & McFarlane 1993). Otolith growth in contrast, is thought to be temporally driven, thus annuli continue to be laid down even when somatic growth ceases (Beamish & McFarlane 1993).

Of the three structures we compared, scales had the lowest levels of precision suggesting they are the most difficult to read for inconnu. This was also supported by the assigned scores for readability which were significantly worse for scales than for fins or otoliths. Both readers felt scale ages were generally more difficult to interpret and had lower confidence in estimates they made from scales. Some of this difficulty was related to the presence of what appeared to be incomplete annuli in all ages of fish, and problems with crowding of growth zones near the outer edge of the scales on older fish. Crowding near the scale edge made it difficult to distinguish zones of well spaced, complete circuli and zones of "crossed over", closely spaced circuli (annuli). We felt this ageing structure was the most difficult for inexperienced readers to age since the annuli are less distinct and the criteria for their determination more subjective than that of fin rays and otoliths. Despite the relative differences between scales and the other structures examined in this study, the levels of precision we had in ageing scales from inconnu (Table 1) were low when compared with other studies with scales (e.g., white crappie, *Pomoxis annularis,* $CV_{between\text{-}reader}$ = 0.586 (Boxrucker 1986); striped bass, *Morone saxatilus,* $CV_{between\text{-}reader}$ = 0.189 (Welch *et al.* 1993)). Thus, scales are likely to be sufficient for ageing fish in situations where a quick non-lethal ageing method is required given that the population of interest does not contain any individuals aged ten or greater.

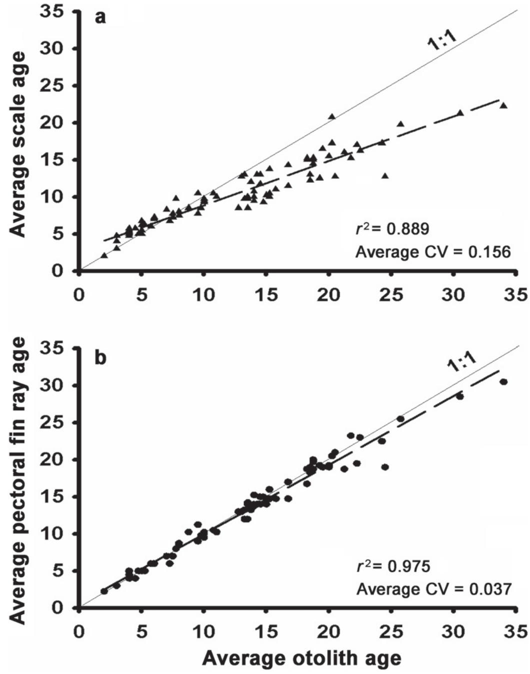

Fig. 3. Comparison of average scale and pectoral fin ray ages with otolith age estimates. Each data point represents the mean age estimate for each fish based on two reads by each of two readers. Regressions for each of the above plots are represented by the dotted lines.

Table 4. Mean estimated age for each ageing structure along with pair-wise comparisons of the estimated ages among structures for samples where estimated otolith ages were < 10 years of age and where otolith ages were ≥ 10 years. Pair-wise comparisons were made using the two-tailed *t*-test with Bonferonni adjustment. *P* values and $t_{\alpha = 0.017}$ for each set of comparisons are indicated above and below the diagonal, respectively.

Ageing structure	Mean ± SD age	Pair-wise comparisons		
		Scale	Pectoral fin	Otolith
Samples where otolith ages < 10 y				
Scales	6.09 ± 1.71	–	*P* = 0.252	*P* = 0.140
Pectoral fins	5.51 ± 1.95	*t* = –0.269	–	*P* = 0.789
Otoliths	5.37 ± 1.82	*t* = 1.501	*t* = 1.158	–
Samples where otolith ages ≥ 10 y				
Scales	13.0 ± 3.49	–	*P* < 0.0001	*P* < 0.0001
Pectoral fins	16.4 ± 4.75	*t* = –4.24	–	*P* = 0.648
Otoliths	16.9 ± 5.18	*t* = –4.53	*t* = 0.458	–

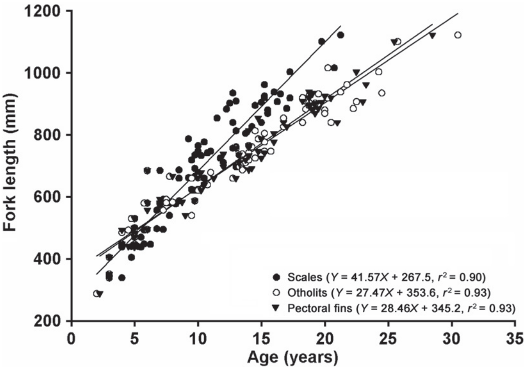

Fig. 4. Growth rates based on scale, pectoral fin ray and otolith age estimates. Each data point represents the mean age estimate for a given structure based on four reads (two reads by each of two readers). Linear regressions for each of the above plots are represented by the solid lines.

Fins and otoliths were both perceived to have good readability as indicated by the scores given by readers. Likewise, precision within and between readers was high for both structures. The high readability and precision of fins was likely due to the fact that they had clearer annuli than scales, and fewer checks or "false" annuli. Both readers, did, however, note that the centers of the fin ray sections were often difficult to interpret. This problem has also been noted by others (e.g., Barber & McFarlane 1987). We found the pattern within the center area was inconsistent among samples making it hard to distinguish the first year of growth. We suspect that the appearance of the center may depend on the manner in which the fin is removed from the fish during sampling. If the fin is cut too far from the body the core may not be seen and in some cases the first annulus may be missing. Thus, if fins are to be used, it is important to educate field workers in proper techniques of removal. Fins were found to be the most time consuming and labor intensive structure to prepare. However, they have better archival properties than broken and burned otoliths. The rings on fins maintain their clarity and the mounted thin sections are durable. We conclude that pectoral fin rays offer a suitable non-lethal alternative to otoliths for ageing of inconnu, given their similarity to otoliths with respect to age estimates, precision and readability.

The annuli on otoliths were generally found to be clear even towards the outer edge for the older fish included in the study. Although there can be problems with identifying the center and first annulus in otoliths if they have not been sectioned through the nucleus (e.g., Barber & McFarlane 1987), the otoliths of inconnu are relatively large (KLH pers. obs.) and therefore forgiving in this respect. The most common problem in interpretation noted by both readers was the presence of checks and what appeared to be shadow bands or double rings toward the outer edge of the otoliths on some older fish. These usually occurred along the faster growing longitudinal axis. This problem could usually be solved by reading on a part of the otolith where the bands were more closely spaced (e.g., along the axis parallel to the sulcus; Fig. 1c) since checks were not usually present there. We found otoliths to be relatively fast and easy to prepare, although care must be taken to prevent over-burning. Broken and burned otoliths are not as well suited to archiving as scales and fin ray sections. They appear to lose clarity as the contrast between growth zones created by burning fades over time. We have also found that otoliths become quite brittle and are easily damaged following burning. This can be a problem if the structure is to be read on multiple occasions or by multiple readers as noted by Baker and Timmons (1991).

Given that the majority of past studies of inconnu used scales, it is quite likely that rates of growth for inconnu were overestimated, and longevity severely underestimated. For example, prior to studies in our lab and those of Brown (2000), the maximum recorded age for inconnu was only 20 years (Alt 1973). Brown (2000) obtained a maximum age of 28 years and in this study the maximum estimated age using otoliths was 35 years. Thus, caution should be exercised in relying on scale-based data for management decisions and in some cases re-examination of populations may be necessary.

We suggest that scales should only be used in heavily exploited inconnu populations where the majority of individuals are under the age of ten. For example, in the Buffalo River, NWT (a tributary of Great Slave Lake), the majority of fish are in the six- to eight-year-old range and have relatively fast rates of growth due to previously high rates of exploitation (Day & Low 1993), thus scales are relatively easy to read and likely provide accurate ages (C. Read pers. comm.). It should be noted, however, that inconnu in the Great Slave Lake area, NWT are the only commercially fished inconnu population in North America. In most other areas of North America, inconnu populations are only lightly exploited by subsistence and recreational fisheries and should therefore be expected to contain older fish. Thus, scales are not recommended as they are likely to provide inaccurate ages. For most North American populations, ageing with pectoral fins or otoliths should be considered as a more reliable alternative to ageing with scales. If scales are to be used in populations with older fish, we suggest that they be combined with otoliths or fins which can be used to age larger and presumably older individuals. For example in the population we examined during this study otoliths or fins would be recommended for ageing fish over the length of 540 mm.

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