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A Comparison of Whole and Thin-Sectioned Otolith Aging Techniques and Validation of Annuli for Arctic Grayling

Abstract

Information on age and growth is essential for the conservation and management of fish species. Age is often estimated using the banding structure in otoliths, but the technique used can influence the estimate, especially in slow-growing, long-lived species. Counts of translucent bands from both whole and thin-sectioned Arctic grayling (*Thymallus arcticus*) otoliths from the Kuparuk River, Alaska, gave similar age estimates. Age estimates from whole otoliths were less variable, particularly for older age groups, and were much easier to prepare and read than thin-sections. Comparison of growth of individual tagged fish to a von Bertalanffy growth model revealed that the translucent rings are true annuli. This approach to validation may be most useful in northern latitudes where other techniques are impractical. Our study shows that whole otoliths provide a fast, reliable, cost-effective technique for age estimation of this long-lived, slow-growing fish species common to the North American Arctic.

Introduction

Arctic grayling, *Thymallus arcticus* (Pallus), are widely distributed in the Arctic, often dominating fish communities in streams and lakes (Tack 1971, Carl et al. 1992). They are slow-growing, long-lived, and late-maturing, especially in the northernmost populations (Reed 1964, Beauchamp 1982, Northcote 1995). Information about age at maturity, longevity, and length-at-age is essential for the management and conservation of the species.

Age of fishes is typically estimated by counting bands in such hard parts as scales, fin rays, and sagittal otoliths, but both the hard part examined and the aging method used can yield different age estimates. Otoliths are considered the most accurate bony structures for estimating ages of slow-growing, long-lived species because they are less susceptible to resorbtion compared to more metabolically active parts (Beamish and McFarlane 1983). Lateral views of whole Arctic grayling otoliths yielded band counts which were more closely correlated with fish size than were band counts from scales, fin rays, whole and sectioned vertebrae, and whole and sectioned opercula (Yole 1975, Sikstrom 1983, Merritt and Fleming 1991). Cross-sections of otoliths have been advocated for long-lived, slow-growing species because differentiating closely spaced bands near the outside edge of an otolith can be difficult using whole otoliths. This occurs most often when the annual growth increment is small and fish have large otoliths (as is typical of older fish) and leads to an underestimate of the true age of the fish. For example, Power (1978) found that lateral views of whole otoliths yielded underestimates of age of Arctic whitefish (*Coregonus clupeaformis*) by up to 20 years when compared to otoliths cross-sectioned using the 'broken and burned' method. Barber and McFarlane (1987) and Kristoffersen and Klemetsen (1991) found that broken and burned otolith sections gave higher ages than surface-examined whole otoliths for some stocks of Arctic char (*Salvelinus alpinus*). Thin sections, in which a cross-section is sliced from the otolith and examined microscopically, have given higher estimates of ages than have whole otoliths or broken and burned sections for some species (Casselman 1983). Merritt and Fleming (1991) found that whole otoliths of Arctic grayling produced higher estimates of age than did broken and burned otoliths, but they did not examine thin-sectioned otoliths.

An additional problem in estimating the age of fish using hard parts is knowing the frequency of formation of the bands. Translucent bands on otoliths of Arctic grayling are assumed to represent annuli (Sikstrom 1983), but this assumption has not been tested because many of the validation methods are impractical at extreme northern

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latitudes. One approach that has been used in some species where other approaches cannot be used is to develop a von Bertalanffy growth model assuming the translucent bands are annuli and to determine if the model produces growth parameters (e. g., mean asymptotic length, L_∞) that are realistic (Casselman 1987, DeVries and Fric 1996, Burnham-Curtis and Bronte 1996). This method can indicate the reasonableness of the annuli assumption, although it is not definitive. The best technique for estimating the age of a fish is one in which the frequency of formation of the banding structure in the hard part has been validated.

Our objectives in this study were to: 1) compare age estimates for Arctic grayling using polished whole otoliths and otolith thin-sections, and 2) validate formation of otolith annuli by coupling the von Bertalanffy growth model with growth of individual tagged fish. We provide an alternate approach to validating annuli formation which may be useful in high latitudes where other techniques are impractical.

Methods

Fish Collection

Arctic grayling were collected from a reach of the upper Kuparuk River near where it crosses the Dalton Highway on the North Slope of Alaska (68°N, 149°W; Figure 1). As part of a long-term study of the population dynamics of Arctic grayling begun in 1985, fish have been collected, anesthetized (MS-222), weighed (±1 g), measured (±0.1 cm total length (TL)), tagged (Floy FD-68B T-bar anchor tags), and released into the Kuparuk River (Figure 1). During July-August 1986-1992 we seined, measured and froze 531 fish. Later, sex of each specimen was determined, and both sagittal otoliths were removed and stored dry in envelopes.

Aging Technique Comparison

Age estimates from whole and thin-sections should differ most in larger, older fish (Casselman 1987); therefore, sub-adult and adult fish 21.5 to 43.6 cm TL (26 males, 20 females) were used to compare techniques. One otolith from each fish was read whole and the other was thin-sectioned. The distal surface of each whole otolith was polished for 3 to 5 sec using 400-grade wet-dry sandpaper and a drop of clove oil which made the translucent bands more distinct (DeVries and Frie 1996). Thin-sections (about 0.18 mm thick) were made by embedding unpolished, whole otoliths in black wax on a cardboard backing and cutting them transversely through the sulcus acusticus on the dorsal-ventral axis with a diamond saw (Secor et al. 1992, Almeida and Sheehan 1997). Exploratory work revealed that this section (Figure 2a) had the most distinct translucent bands.

Opaque and translucent band pairs in each of two preparations were counted twice on separate occasions by two readers. Readers had no knowledge of their previous readings, the other reader's results, or the total length of the fish. Polished whole and thin-sectioned otoliths were placed on a black background (proximal-side down for whole otoliths) and wetted with liquid dish soap or a 50/50 glycerin/water solution to enhance the translucent bands. The otoliths were then observed through a microscope at magnifications of 10X to 50X with reflected light. Neither reader had previous experience reading otoliths, so they were trained at the National Marine Fisheries Service Age and Growth Lab (Woods Hole, MA) at the start of this project.

Age was estimated by assuming that each opaque and translucent band pair represented one year; the opaque bands result from fast, summer growth and translucent bands from slow, winter growth (Sikstrom 1983, Jearld 1983, Secor et al. 1992). A translucent band that generally followed the overall shape of the otolith was considered to be an annulus. If a translucent band appeared faint, very narrow, ephemeral and discontinuous, it was considered a "check," meaning a false annulus that was not counted (Figure 2b). An incomplete opaque band at the edge of an otolith was assigned a "+," which represented incomplete summer growth. Readings of polished whole otoliths were generally done on the dorsal and ventral lobes (Figure 2b), where translucent bands were usually easiest to identify. For the thin-sections, counts were done along the sulcus, where the translucent bands were best-defined (Figure 2b). Thin-sections were often turned over and counted on the other side, particularly when the thin-sections had relatively large numbers of annuli.

Repeated measures ANOVA was used to determine if there was any significant difference in age between readers or techniques. The age esti-

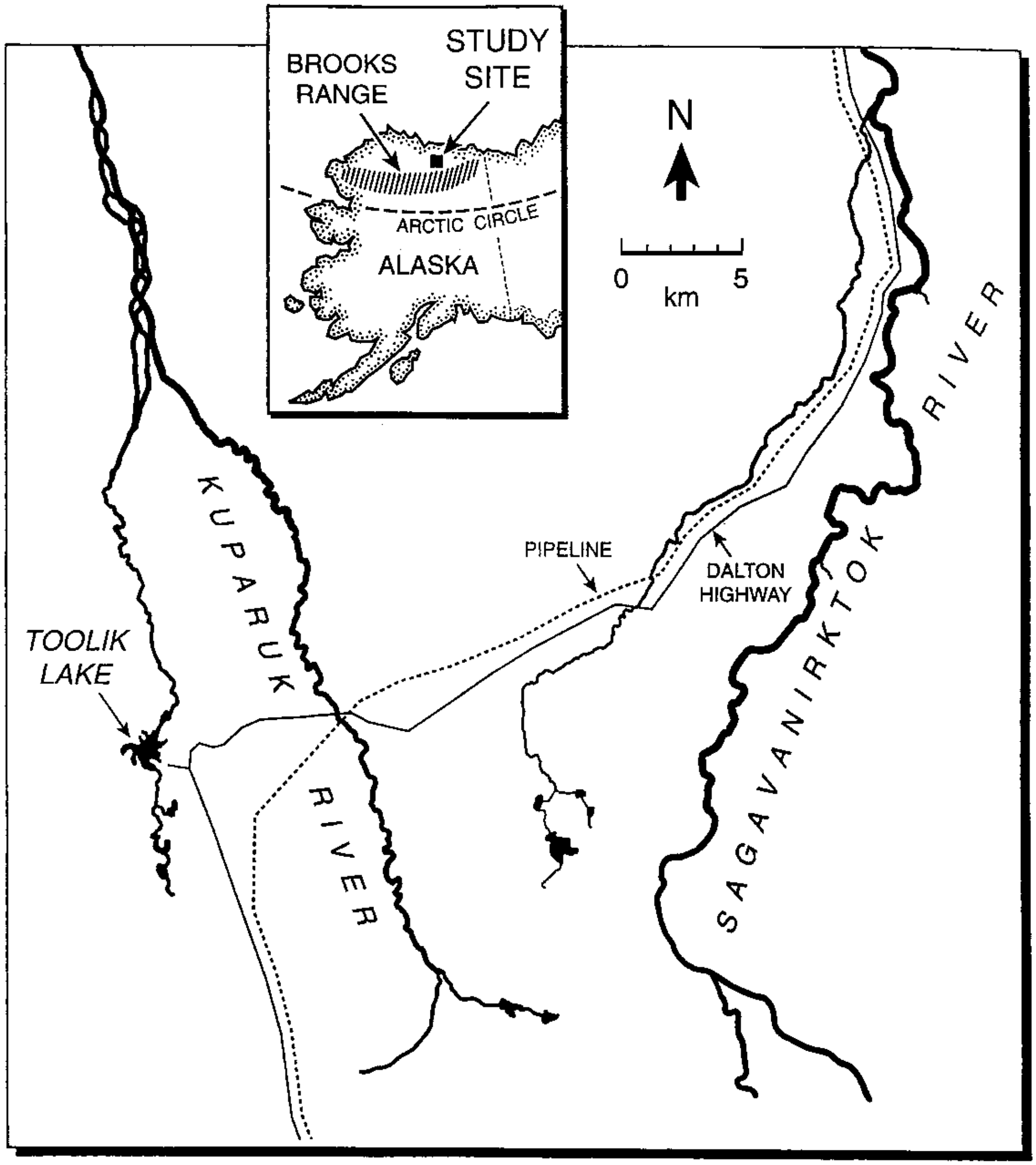

Figure 1. Map of the study area in the upper Kuparuk River watershed. Fish were captured near where the haul road crosses the Kuparuk River.

mate (by method) was the repeated measure and reader the main effect (Statview 4.5, Abacus Concepts 1992). To examine the variability in age estimate by method, we plotted standard deviation against age and used a t-test to determine if standard deviations differed between methods. The mean and standard deviation from four readings (two readers, two reads per method) were computed for each otolith for each method.

Validation

A von Bertalanffy growth model was fitted to length-at-age data with the equation: $L_t = L_\infty (1-e^{-k(t-t_0)})$ where L_t is the total length (cm) at age

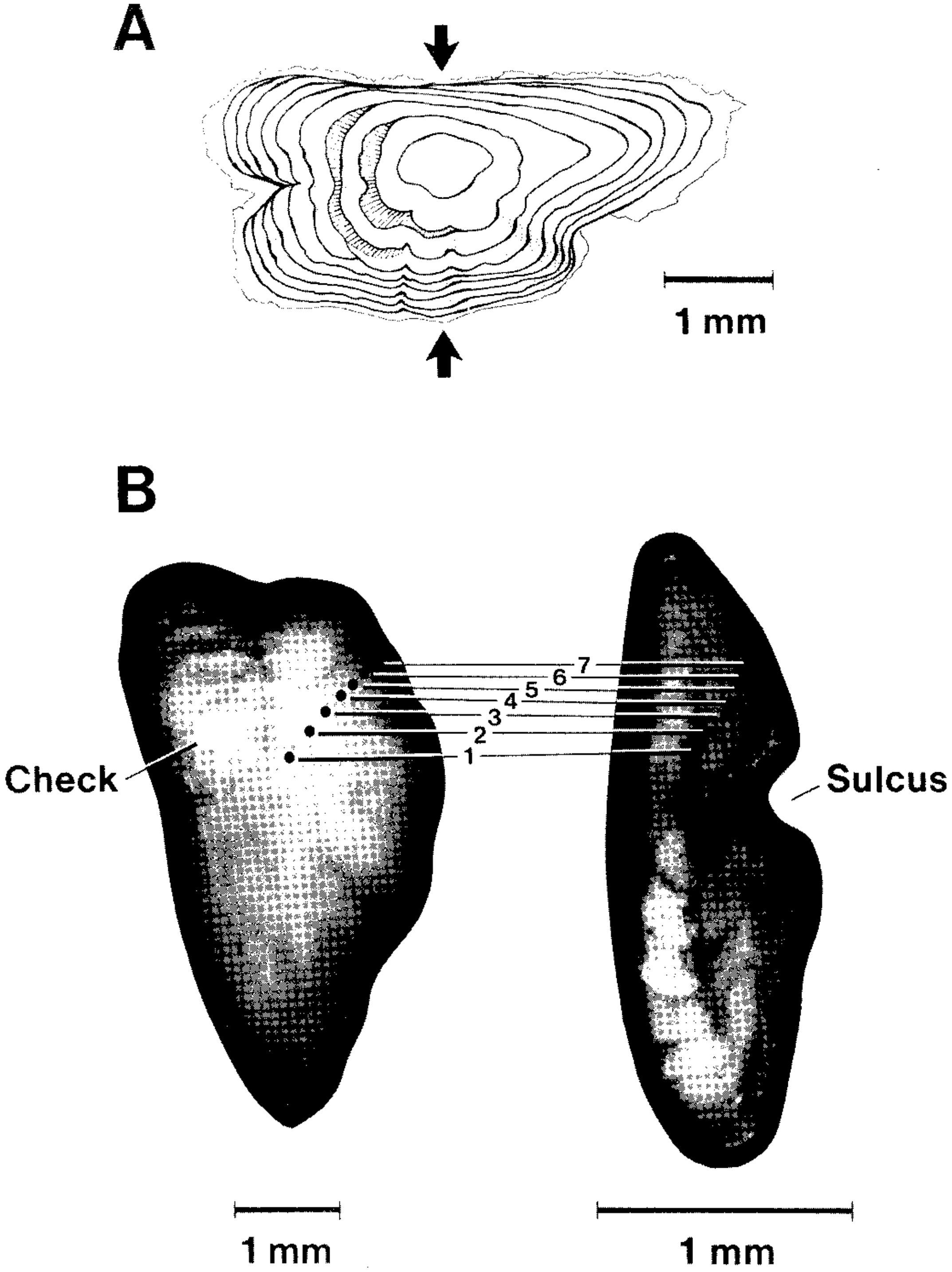

Figure 2. a) Diagram of an Arctic grayling otolith. The arrows indicate the cross section used for thin-sectioning otoliths in this study. b) Photographs of the lateral surface of a polished whole otolith (left) and corresponding thin-section (right) taken from an age-7 Arctic grayling, with dots indicating annuli. Size scales are different in the two photographs.

t (years), L∞ is the asymptotic total length, k is the growth coefficient, and t_0 is the hypothetical age of otolith formation using a nonlinear curve fitting package (SAS 1985). In developing this model, we assumed that translucent bands were formed annually. Polished whole otoliths were used to estimate the age of 193 males, 166 females and 76 immature fish (≤ 25 cm TL). Immature fish were used in both male (n = 269) and female (n = 242) growth curves.

We assessed the validity of assuming that translucent bands are annuli by comparing length data from tagged and recaptured fish to the predictions of the von Bertalanffy growth model. Data from tagged fish were of two types: 1) adult fish that had been caught at least twice and were killed to determine their age-at-final-capture and backcalculated age-at-previous-capture, and 2) juvenile fish that had been tagged at a small size where initial age could be well-estimated and were later recaptured several times. Fish used for the validation were not used to develop the von Bertalanffy growth model. A total of 50 adult fish (22 females and 28 males) were used to determine the age-at-final-capture (based on whole otoliths). Age-at-previous-capture was backcalculated by subtracting the number of years between previous capture and final capture from the age-at-final-capture. A total of 11 females and 24 males were tagged as juveniles and recaptured over a period of 7 years. Initial age was estimated using whole otoliths from fish of the same size from the same year-class and subsequent ages estimated by adding years-at-large since initial capture. The length data for both age-at-final-capture and the age-at-previous-capture were then compared to the length-at-age predictions of the von Bertalanffy growth model using the 95% confidence limits of predicted lengths (Draper and Smith 1981). If the translucent bands are annuli, we expect less than 5% of the length-at-age data from the tagged fish to lie outside the 95% confidence limits.

Results

Technique Comparison

Whole and thin-sectioned otoliths gave the same age estimates, but age estimates from thin-sections were more variable than those from whole otoliths. We found no difference in the estimated age of a fish by method or by reader, indicating that both methods gave similar age estimates (Table 1). We also found no difference in age estimates by technique between males and females (F= 0.52, p=0.66). Age estimates from thin-sections were more variable at every age, and variation increased more rapidly with age for thin-sections than for whole otoliths (Figure 3). The mean standard

TABLE 1. Results of a repeated measures ANOVA relating estimated age to reader (first or second) and technique (thin-sectioned or whole) otoliths factors.

Source	df	Mean Square	F-value	p-value
Reader	1	38.5	0.722	0.39
Subject (Group)	92	53.39		
Measurement Technique	3	0.037	0.031	0.99
Technique Reader	3	1.48	1.25	0.28
Technique Subject (Group)	276	0.99		

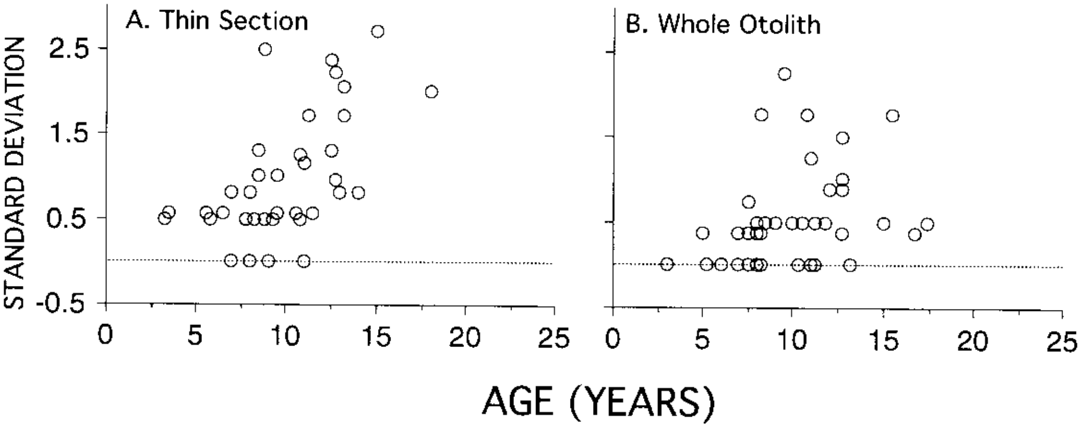

Figure 3. Relationship between standard deviation and age for thin-section (n = 46) and whole otolith (n = 46) techniques.

deviation for thin-sectioned otoliths age estimates (0.92) was significantly higher (n=46, t=3.11, p<0.001) than the mean standard deviation for whole otolith age estimates (0.51). The higher variation in thin-section age estimates resulted from difficulty interpreting the banding structure, not from differences between readers. Thin-sections had faint rings, especially near the outer edges, confusing discontinuities, and the first annulus was often difficult to discern. Readers felt interpreting rings on the thin-sections required more judgment decisions than did interpreting rings on whole otoliths.

Annuli Validation

The von Bertalanffy growth model exhibited the classic asymptote at older ages, and estimates of L_∞ were similar to the largest fish measured for both sexes. Fish were 5 to 43.6 cm TL and from 0 to 22 years old. The largest female was 40.7 cm TL and 11 years of age, while the oldest female (22 years) was only 36 cm TL. The largest male was 43.6 cm TL and 11 years old, while the oldest male (22 years) was 42.6 cm TL. The parameters (± 95 % confidence limits) of the von Bertalanffy growth model equations were: female - $L\infty = 37.9$ (37.2 - 38.4), $k = 0.27$ (0.26 - 0.28), $t_0 = -0.4$ (-0.5 - -0.2), $r^2 = 0.96$; male - $L\infty = 41.6$ (40.9 - 42.4), $k = 0.22$ (0.21 - 0.23), $t_0 = -0.5$ (-0.7 - -0.3), $r^2 = 0.98$. The growth equations indicate that males ($L\infty = 41.6$ cm) reach a larger maximum size than do females ($L\infty = 37.9$) but grow more slowly (Figure 4a & b).

Only 2.6% of the 187 observations of length-at-age from tagged fish were outside the 95% confidence interval for the predicted length-at-age (Figure 4). Adult fish used for otolith age estimates were typical of fish from the Kuparuk River (females: ave. 34.7 cm TL, range 27.5 to 37.1 cm TL; males: ave. 36.6 cm TL, range 27.5 to 39.8 cm TL). These fish were approximately 8 - 9 years old; the oldest fish was 13 years old and the youngest backcalculated age was 6 years. Time between previous capture and final capture of tagged fish ranged from 1 to 5 years; 24 fish were recaptured after 1 year, 16 after 2 years, 8 after 3 years, 1 after 4 years and 1 after 5 years. For females, no length-at-final-capture and only 1 length-at-previous-capture fell outside the 95% confidence interval (Figure 4a). One observation is less than the 2.2 observations (5% of 44 observations) expected to lie outside the 95% confidence limit. For males, no length-at-final-capture and 2 length-at-previous-captures fell outside the 95% confidence interval (Figure 4b). Approximately 3 observations are expected to lie outside the 95% confidence limits (2.8; 5% of 56). In all cases, the length-at-age estimates for both final-capture and previous-capture were well within the range of the data used to construct the von Bertalanffy growth model.

The length-at-age and the growth pattern of fish tagged as juveniles also closely followed the von Bertalanffy growth model (Figure 4e & f). For both males and females, the average initial size at tagging was 24 cm TL with an estimated age of 4 years. Fish were at large for between 3 and 7 years between initial and final capture and were recaptured 3 to 6 times. Final size ranged from 33 to 40 cm TL and final age ranged from 6 - 12 years. Of the 38 estimates of length-at-age for females and 49 estimates for males, only two length-at-age observations (one male, one female) lie outside the 95% confidence interval. Overall, growth curves for individual fish lie within the 95% confidence interval, although one or two individuals apparently grew much faster at younger ages than expected based on the von Bertalanffy growth model.

Discussion

Cross-sections (broken and burned or thin-sections) of otoliths, rather than whole otoliths, have been advocated for aging long-lived, slow-growing fishes (Power 1978; Beamish 1979a, 1979b; Barber and McFarlane 1987; Kristoffersen and Klemetsen 1991). Worthington et al. (1995), however, suggested using aging methods that are uncomplicated and cost-effective, so long as the methods provide reliable data. Our study, like those of Baker and Timmons (1991) and Burnham-Curtis and Bronte (1996), demonstrates that for some species whole otoliths need only be polished to produce age estimates similar to and more precise than estimates derived from cross-sections even in a long-lived, slow growing species. Thin-sectioning did not yield different ages nor did it improve the precision of age estimates compared to those from whole otoliths. Thin-sections had very faint rings, especially near the outer edges, a sometimes indistinguishable first annulus, and confusing discontinuities. In addition, they were time-consuming to prepare, fragile and difficult to store. Similar difficulties were reported for

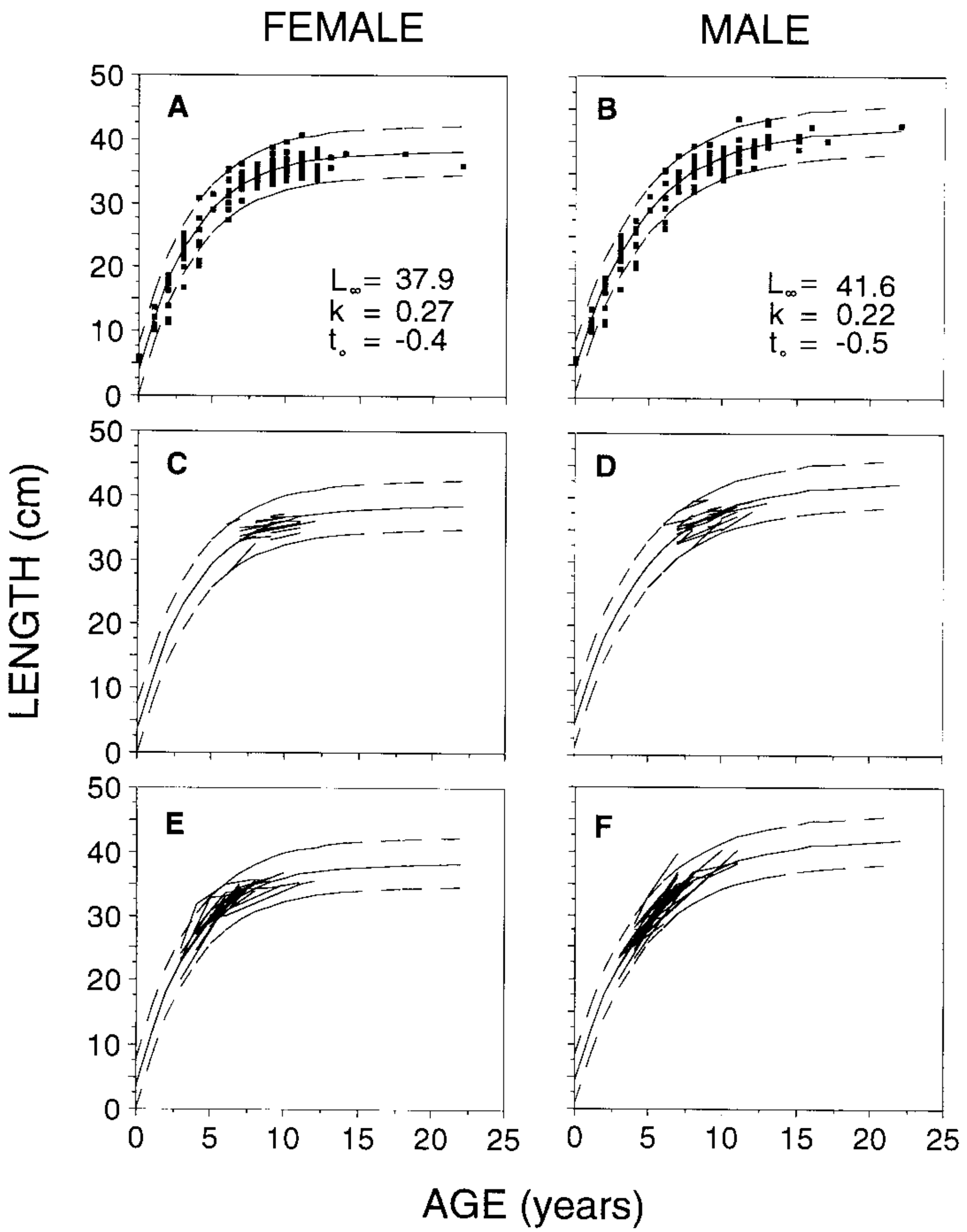

Figure 4. von Bertalanffy growth model compared to length-at-age data. A and B) Length-at-age data for Kuparuk River Arctic grayling used to parameterize the von Bertalanffy growth model (A: female, n = 242; B: male, n = 269). C and D) Age-at-length-at-final recapture and length-at-age-at-previous capture of tagged adult fish (C: female, n = 22; D: male, n = 28). E and F) Length-at-age-at-recapture for fish tagged as juveniles. (E: female, n = 11; F: male, n = 24). The curved solid line in each panel is the mean prediction of the von Bertalanffy growth model; curved dotted lines are the upper and lower bounds of the 95% confidence interval for a predicted length. Symbols in panels A and B indicate individual fish length and age estimates. Short straight solid lines in panels C, D, E and F connect the lengths-at-age for individual fish measured several times to indicate growth.

broken and burned Arctic grayling otoliths (Merritt and Fleming 1991). We recommend the use of whole otoliths for estimating age of Arctic grayling as they were much easier to prepare and read than thin-sections and provided the same age estimates.

The comparison between tagged fish growth and the von Bertalanffy growth model predictions indicate that the translucent bands represent annuli. The length-at-age data for virtually all (97.3%) adult and juvenile fish lie within the 95% confidence interval, and the pattern of individual fish growth over time is consistent with the von Bertalanffy growth model. The strongest evidence is the conformation of size-at-age of the juvenile fishes to the model because these fish are rapidly growing and the confidence limits are narrow. Adult grayling growth is asymptotic as predicted, but confidence limits in this region of the growth curve are large. This analysis allowed us to follow the growth of individual fish from 4 years old until they were 12 years old. We followed them through the rapid growth phase and into the asymptotic growth phase where detection of annuli becomes problematic. By coupling juvenile growth with an analysis of adult growth we were able to validate formation of annuli over the age range of 3 to 13 years. Determining the timing and frequency of otolith increment formation using known age fish and marking otoliths is the most definitive method of validation (Geffen 1992, DeVries and Frie 1996), but the application of chemicals to mark otoliths in wild fish populations is currently restricted by the United States Food and Drug Administration. Until this kind of information is available for Arctic grayling, our analysis indicates that the assumption of annular formation of translucent bands in Arctic grayling otoliths is reasonable.

Testing the von Bertalanffy growth model based on the assumption of annual ring formation and using tagged fish provides an alternative method for validating otoliths in fish populations at high latitudes and remote areas where other methods are not feasible. Incremental edge analysis, in which fish are captured year-round to analyze the development of translucent and opaque bands on otoliths (Beamish and McFarlane 1983), is not possible because Arctic waters are often inaccessible from November to May. Analysis of the changes in length-frequency distributions over time (McNew and Summerfelt 1978, Weatherley and Gill 1987) does not work well because as the year-classes age, the length distribution of individual cohorts overlap and become indistinct. Identifying individual age cohorts becomes impossible for older fish. Gauldie (1990) suggested that in some temperate and tropical fish species, weight varies widely within a year and the banding structure of otoliths may be linked to gains in weight rather than length. This might limit the usefulness of the von Bertalanffy growth model based on length as a validation method in some fish populations. In Arctic grayling, as in many northern latitude species (e.g., Fechhelm et al. 1995), growth in length and weight show a strong positive correlation ($r^2 = 0.96$), and their rapid growth in the summer (up to 80 g and 1.5 cm TL) followed by no growth over winter is ideal for the production of distinct annual bands on otoliths (Jearld 1983, Secor et al. 1992, Deegan and Peterson 1992). Thus, northern fish have ideal growth characteristics for using the von Bertalanffy growth model linked to tagged fish growth to validate the banding structure of otoliths.

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