Fourier Analysis of Otolith Banding Patterns to Discriminate among Hatchery, Tributary, and Lake Shore Incubated Sockeye Salmon (*Oncorhynchus nerka*) Juveniles in Tustemena Lake, Alaska

A Thesis
for the Degree of
Master of Science

by

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University of Alaska Fairbanks
Fairbanks, Alaska

May 1995

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Abstract

Otolith banding patterns formed during incubation were used to discriminate among hatchery and wild sockeye salmon (*Oncorhynchus nerka*) fry from Tustumena Lake, Alaska. Banding patterns were described by Fourier analysis of otolith luminance profiles. Amplitudes of individual Fourier harmonics were used as discriminant variables. Estimates of total correct classification of otoliths to hatchery or wild origin were as high as 83.1% using quadratic discriminant function analysis on 10 Fourier amplitudes. The maximum total classification rate estimate among hatchery and five wild groups was 45.7% using linear discriminant function analysis on 14 Fourier amplitudes. Although classification rates for any individual group of wild incubated fry never exceeded 64%, site specific information was evident for all groups because the probability of classifying an individual to its true incubation location was significantly greater than chance. Results indicate phenotypic differences in otolith microstructure amongst incubation sites separated by < 10 km.

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Acknowledgments

This project was initially funded by the U.S. Fish and Wildlife Service (USFWS). This support continued under the newly formed National Biological Survey (NBS). I would like to thank my supervisors for allowing me this opportunity and providing their support. In particular I would like to thank Carl V. Burger (NBS) and Dick Wilmot (National Marine Fisheries Service) who provided direction, support, and friendship. I would like to thank my committee members. My major advisor, Dr. James Reynolds, provided guidance and support throughout both my undergraduate and graduate careers. Dr. Leslie Holland-Bartels acted as both a committee member and supervisor, and she was the person who asked the important question of "so what ?" Dr. Ron Barry provided statistical support and review. Dr. Lew Haldorson provided a fresh prospective and helped me see past the numbers and statistics to the biology. I would like to thank Dr. Jeremy Collie who gave me encouragement as my initial advisor. Gary Sonnevil (USFWS) and staff helped in the field and with logistical support. Pat Shields , Alaska Department of Fish and Game (ADFG), helped with discussions on sample preparation and interpretation. Bob Oches (ADFG) and the staff at the Crooked Creek Hatchery provided hatchery fry and assistance during field sampling. My many friends and colleagues provided discussions, review, and made this endeavor an adventure in life. In particular I thank Nicola T. Hillgruber (meine Freundin aus Deutschland), Mary Whalen, Ruth Dodte, Deb Burwen, Steve Fleischman, Tom Taube, Greg Horton, Dan Nelson, Kurt Hensel, Dave Dawely, and Ken Cash. As always my Mother supported me through her love, even though she thought it a little odd for a grown person to study fish ears.

Introduction

The question of stock origin is a central issue in much of fisheries research and management. The term stock may be used to define a single species group that is reproductively and to some degree genetically discrete. On the other hand, a stock can be some subunit of fish that is convenient for management purposes (Larkin 1972; Ricker 1972; Ihssen et al. 1981). In Pacific salmon (*Oncorhynchus* sp.) biology the question of stock identification connotes mixed stock and wild/hatchery stock management. However, our quest for new and more accurate techniques is actually grounded on the dependence between stock (population) assessment and stock identification (Brown et al. 1985; Prager 1988).

An issue fundamental to fisheries science is that population parameters (e.g., growth, mortality, and reproductive rates) remain unknown and are estimated based on samples drawn from the population. These estimates are used to model dynamics, assess the condition of the population at future dates, and predict the potential effects of present and future management strategies . Stock assessment is predicated on the requirement that the parameter estimates are based on and applied to a stock for which they are meaningful (Brown et al. 1985; Prager 1988). This brings us to a very basic concept in

statistical estimation, perhaps the first question we hear when a statistician is consulted, "what is the population of interest"? Here "population" is used in the statistical sense, and perhaps the answer is straightforward, e.g., all the largemouth bass (*Micropterus salmoides*) in a landlocked farm pond or the 1989 cohort of Lake Washington sockeye salmon (*O. nerka*). However, as in the case of the Lake Washington sockeye salmon, even though the population of interest is easily defined in concept, often it will be mixed with other populations during periods when estimates of population parameters must be made. Hence a means of identifying or discriminating among individuals of several mixed populations or stocks is essential for assessment, management, and ecological research.

The stock concept in Pacific salmon management has been in use since the latter part of the 19th century (Ricker 1972). The life history of Pacific salmon includes a high degree of fidelity (homing) to discrete spawning areas (Ricker 1972; Blair and Quinn 1991). Evidence of a genetic component in homing has been presented for chinook salmon (*O. tshawytscha*) and pink salmon (*O. gorbuscha*) (McIsaac and Quinn 1988; Smoker et al. in press). This propensity for some degree of reproductive isolation can result in stocks

that are locally adapted to spawning, incubation, and rearing environments (Taylor 1991).

Evidence for genetically discrete stocks of Pacific salmon spawning within the same drainage have been demonstrated for pink salmon (Smoker et al. in press), sockeye salmon (Wilmot and Burger 1985), chinook salmon (Adams et al. in press), and chum salmon (*O. keta*) (Wilmot et al. in press). Holland-Bartels et al. (1994) argued that in cases where genetic evidence is not available, ecological and behavioral evidence often suggests that locally adapted stocks may co-exist within relatively small (<10 km) ranges. Individuals from several potentially discrete spawning stocks often rear in a common environment throughout much of their life. Early and late components of a sockeye salmon run may spawn in different environments (tributary versus lake shorelines), however, their young rear in a common lake environment (Burgner 1991). Therefore, attempts to investigate stock dynamics during the freshwater phase require some means of separating individuals. This involves either applying an artificial mark or measuring a natural mark.

Artificial marks have been used for many years and can be external or internal. Some of the first work which documented migrations and homing was done using Peterson disk tags. Other forms of external marking include fin removal or mutilation, branding and tattooing, and dyes (Nielsen 1992). Internal artificial marks are based on the introduction of some material or genetic code that is later recognizable. Coded wire tags have been used extensively in Pacific salmon (Jewell and Hager 1972; Nielsen 1992). More recently chemical marking of calcified structures (e.g., vertebrae, scales, and otoliths) has been used (Mulligan et al. 1987; Yamada and Mulligan 1990; Hendricks et al. 1991). Temperature changes during incubation have also been shown to induce distinct banding patterns in salmon otoliths (Volk et al. 1990). Genetic markers are multi-generational (Ihssen et al. 1981) and have been used with pink salmon (Lane et al. 1990; Gharrett et al. in press) and chum salmon (Seeb et al. 1990). The application and use of artificial marks requires the assumption that the marked individuals behave in the same manner as unmarked individuals. Naturally occurring marks circumvent this assumption, and may provide a method of stock discrimination where sample size and handling problems make the application of artificial marks impractical.

Naturally occurring marks are genotypic or phenotypic characteristics of individuals that are to some degree stock- or population-specific, at least within the admixtures of stocks under consideration. These marks can include: growth parameters (Ihssen et al. 1981); chemical composition (both somatic and skeletal) (Mulligan et al. 1987; Yamada et al. 1987; Edmonds et al. 1989; Rieman et al 1994); meristic and morphological (Fournier et al. 1986; Meng and Stoker 1984; Taylor 1986); genetic (protein enzymes and DNA) (Wilmot and Burger 1985; Adams et al. in press; Wilmot et al. in press); and the pattern and shape of calcified structures such as scales and otoliths (Ihssen et al. 1981). Calcified structures which form by accretion can develop different patterns as the result of environmental changes (e.g., temperature changes, food availability, habitat changes). When stocks experience consistent and different conditions, a record may be left in structures such as scale and otoliths (Brothers et al. 1976; Neilson and Geen 1984; Neilson et al. 1985a).

The spacing of scale circulii is a function of metabolism, and stocks may be separated based on circulii patterns where regular differences exist. Scale pattern analysis has been used to separate Pacific salmon to continent , region, (Cook and Lord 1977; Cook 1978), and drainage (Rowland 1969;

Cross et al. 1987) of origin. Scale shape has been used for discrimination among stocks of walleye (*Stizostedion vitreum*) (Jarvis et al. 1978; Riley and Carline 1982) and striped bass (*Morone saxatilus*) (Ross and Pickard 1990). As sockeye salmon spend 1-2 yr in freshwater, the characteristics of the scales formed during this phase can reflect differences among rearing environments. However, scales are of no use for separating individuals if the environmental differences occur prior to scale formation (e.g., during incubation or during the first few months after hatching).

Otoliths, on the other hand, are formed by the time salmonid embryos reach the eyed egg stage and are a potential repository for a record of differences among incubation environments (Neilson et al. 1985b; Brothers 1990; Volk et al. 1990). The examination of otolith elemental composition and microstructure has received much attention since Pannella (1971) reported on the occurrence of daily and even subdaily banding patterns.

Observed differences in the elemental composition of otoliths has been tied to the contrasting environments that parental females inhabit during egg development. The progeny of anadromous and resident brown trout (*Salmo trutta*), rainbow trout (*O. mykiss*), and sockeye salmon may be distinguished

by differences in their Sr/Ca (strontium/calcium) ratios (Kalish 1990; Reiman et al. 1994). These differences have been attributed to the higher ambient Sr/Ca ratio in saltwater. However, Reiman et al. (1994) cautioned that within-group variability requires further investigation. Differential incorporation of organics into the otolith crystalline matrix results in variation in optical densities seen as light and dark bands (Pannella 1971).

Increments (composed of alternating light and dark bands) are deposited on the otoliths of a wide range of fish species (Campana and Neilson 1985). Many fish species deposit increments at a rate of approximately one per day (Pannella 1971; Brothers et. al. 1976; Taubert and Coble 1977; Wilson and Larkin 1980; Marshall and Parker 1982; Campana 1983; Geen et al. 1985; Volk et al. 1984; Rice et al. 1985; Secor and Dean 1989). There is evidence that increment deposition is tied to an endocrine-driven, endogenous circadian rhythm (Campana and Neilson 1985). However, other factors such as water temperature, photoperiod, feeding frequency, food ration, and fish activity can modify or mask diurnal rhythms (Neilson and Geen 1982; Marshall and Parker 1982; Campana and Neilson 1985).

Life history events such as hatching, first feeding, and migration from fresh to salt water can be recorded on otoliths and used as reference points (Neilson and Geen 1985a; Marshall and Parker 1982; Volk et al. 1984; Brothers 1990). Rapid changes in water temperature of less than 2 °C can be used to induce banding in otoliths of embryos and fry (Volk et al. 1990). Stress induced by starvation, handling and transport may also cause distinct marks (Neilson and Geen 1984; Paragamian 1992; Hendricks et al. 1994).

Otolith shape and diameter were used to separate spring and fall stocks of herring (Messieh 1972). McKern et al. (1974) were able to separate winter and summer stocks of steelhead trout (*O. mykiss*) based on otolith nucleus size. Nucleus size was also used to separate steelhead and resident rainbow trout (Rybock et al. 1975). Currens et al. (1988) examined otoliths of juvenile steelhead and resident rainbow trout from the same locations sampled by Rybock et al. (1975) and found no significant difference in nucleus size. This discrepancy may be due to differences in the definitions used to delineate the nucleus area (Currens et al. 1988). Neilson et al. (1985b) demonstrated that nucleus size was influenced by temperature, but were unable to separate steelhead and resident rainbow trout (incubated under controlled conditions) based on nucleus size due to within-group variability. Therefore, the differences seen in nucleus size for wild

populations may have been due to differing life histories which expose developing fish to different thermal regimes (Messieh 1972; Rybock et al. 1975). Otolith shape was used to separate juvenile Atlantic salmon (*Salmon salar*) and brown trout (*S. trutta*) (L'Abe'e-Lund 1988). Hendricks et al. (1994) found a significant difference between the mean increment widths (first 15 increments) of hatchery and wild American shad (*Alosa sapidissima*) and were able to estimate hatchery contribution. Ambiguity in defining the border of the nucleus, check marks (e.g., hatching and first feeding), and establishing reference points and transects, may introduce error into increment counts, dimension measures, and increment width measurements (Wilson and Larkin 1982, Currens et al. 1988). Although validation (e.g., through chemical marking) should be used when defining increments and check marks (Neilson 1992; Hendricks et al. 1994), it is often difficult or impossible when examining otolith patterns developed under natural conditions. A method which allows for the examination of the variation or components of the overall banding pattern may provide a means to illuminate differences among groups of fish, while reducing the subjectivity introduced by artificial definitions of reference points, transects, and increment boundaries.

Fourier analysis allows for the decomposition of complex periodic functions into discrete subcomponents. Fourier analysis has been used to: assess population

structure of sea scallops (*Placopecten magellanicus*) by describing shell shape (Kenchington and Full 1994); quantify scale shape for discrimination of fish stocks (Jarvis et al. 1978; Riley and Carline 1982); and for otolith shape analysis (Bird et al. 1986; Castonguay et al. 1991; Campana and Casselman 1993; Friedland and Reddin 1994). Shape analysis, however, is dependent on the condition of the otolith at the time of collection and has little potential for illuminating differences that occurred in the past (e.g., during incubation). However, the banding pattern laid down during incubation should remain unchanged by subsequent life history events (Campana and Neilson 1985). The dark and light intensities (luminance values) across an otolith transect (luminance profile) can be represented by a complex periodic function and hence lend themselves to Fourier analysis.

To my knowledge, Fourier analysis has not been used to describe otolith banding patterns. Whereas others (Bird et al. 1986; Castonguay et al. 1991; Campana and Casselman 1993; Friedland and Reddin 1994) have used Fourier analysis for discrimination based on otolith shape, Fourier analysis has the potential for providing a means to analyze otolith banding patterns by decomposing the shapes of luminance profiles. Therefore, Fourier analysis of luminance profiles may allow for discrimination among fish which experience different incubation

environments, as may be the case for sockeye salmon rearing in Tustumena Lake, Alaska (Figure 1).

Based on a perception that Tustumena Lake sockeye salmon production was limited by spawning area rather than lake rearing capacity, the Alaska Department of Fish and Game (ADFG) began an enhancement program in 1976. Brood stock are taken from Bear and Glacier Flats creeks, eggs are incubated at the Crooked Creek hatchery, and emergent fry are fed for several weeks before being released into Tustumena Lake (Kyle 1992). Recent research demonstrated that a substantial amount of shoreline spawning by sockeye salmon occurs in Tustumena Lake (Burger et al. 1995). Furthermore, subtle differences in the timing of migrations and spawning between fish choosing tributary and shoreline areas suggest the existence of subpopulations (Burger et al. 1995). Further work to determine whether competitive interactions occur between hatchery and wild incubated fry, and whether differences exist in the life history of wild fry originating from the various spawning areas requires a method to discriminate among them.

Data indicate that sockeye salmon fry incubated at the ADFG hatchery and within the Tustumena Lake drainage experience different thermal regimes (Figure 2).

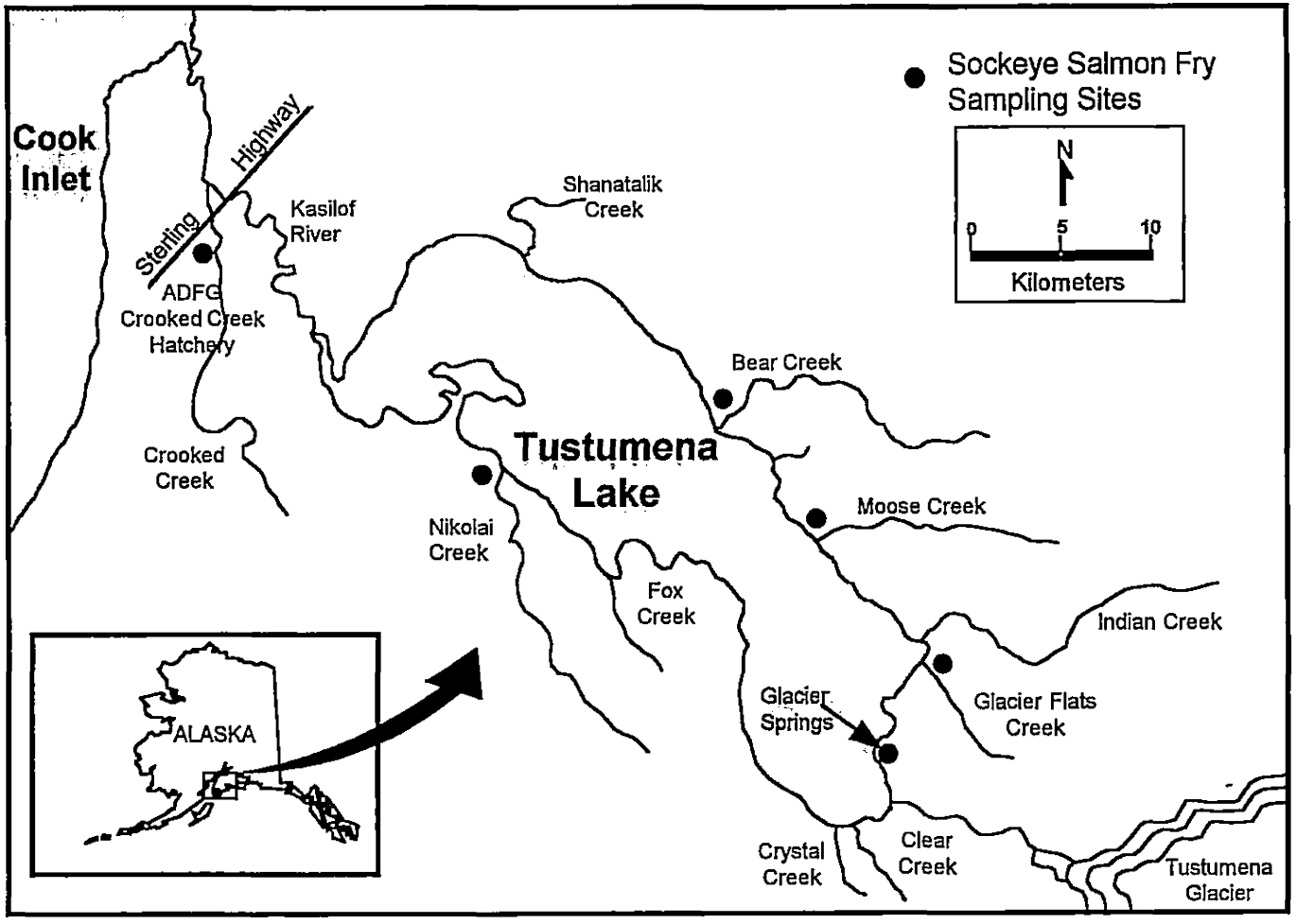

Figure 1. Sampling sites for sockeye salmon used in otolith pattern analysis, Tustumena Lake, Alaska, 1992.

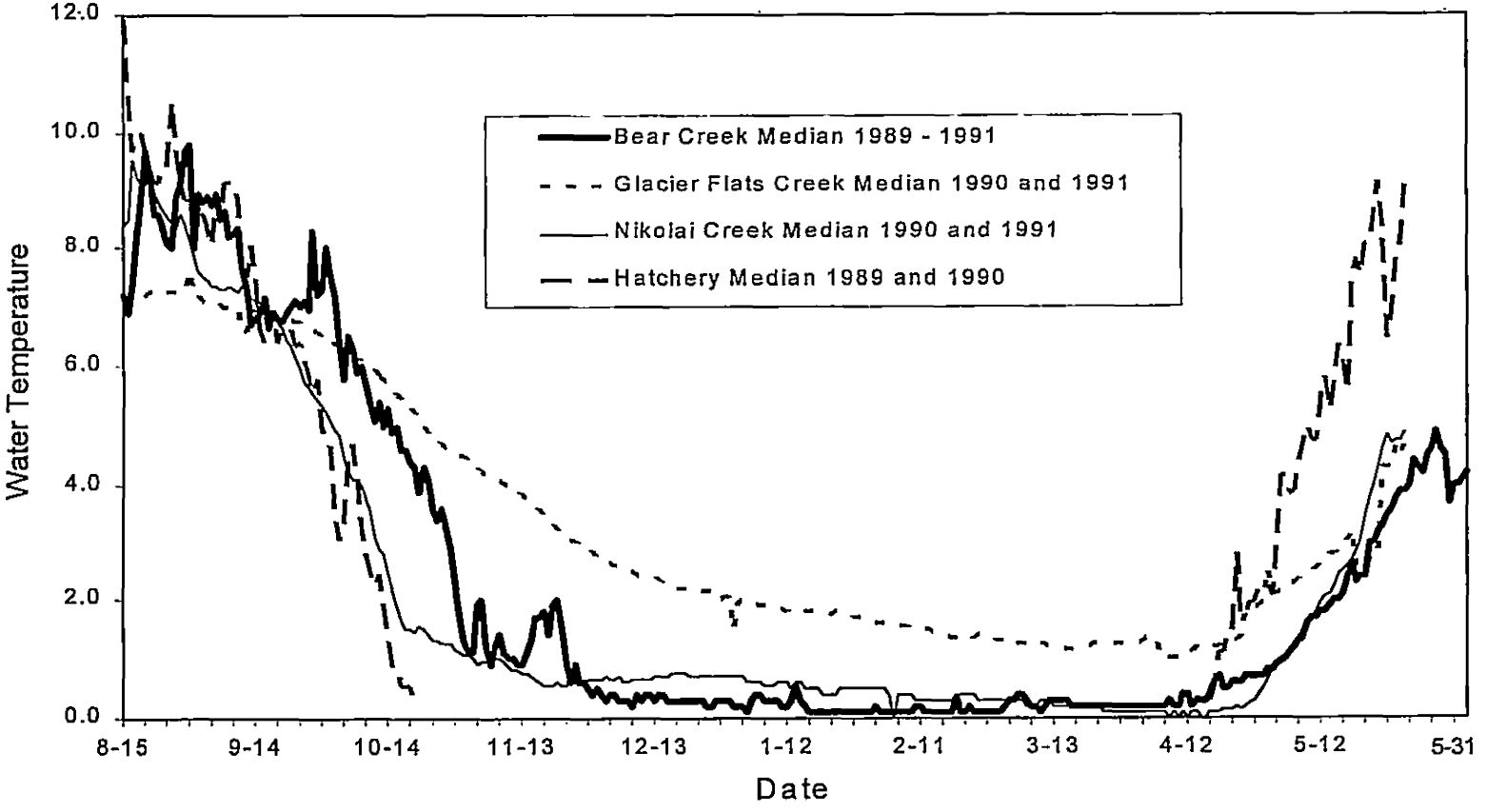

Figure 2. Daily median incubation water temperatures (°C) for the Alaska Department of Fish and Game Crooked Creek Hatchery, Bear, Glacier Flats, Nikolai, and Moose creeks. Years refer to brood year, i.e., 1989 brood year is for those fry spawned during the summer of 1989, emerging and migrating into Tustumena Lake during the spring of 1990. Hatchery temperatures were not monitored from mid-October through early April.

There are no data on lake intergravel water temperatures, but it is very likely that they differ from both hatchery and tributary temperatures due to the influence of glacial melt-water (Burger et al. 1995). Also, hatchery practices (e.g., prophylactic treatments, shocking, sorting, and artificial light/dark cycles) during incubation may induce a discernible pattern. Therefore, it is possible that the existing differences in the incubating environments of the juvenile sockeye salmon rearing in Tustumena Lake result in distinctive banding patterns in their otoliths.

The purpose of this study was to determine the feasibility of using otolith microstructure, as described by Fourier analysis, to discriminate among the various groups of sockeye salmon fry rearing within Tustumena Lake. To this end, samples of known-origin fry were collected and otolith banding patterns were quantified. My specific objectives were: 1) to develop standardized techniques for the measurement of otolith microstructure characteristics; 2) to test for differences in the characteristics among and between the major groups of sockeye fry (hatchery, Bear Creek, Glacier Flats Creek, Moose Creek, Nikolai Creek, and lake-shore incubated fry) in Tustumena Lake; 3) to determine the appropriate statistical classification method(s); 4) to make recommendations for the use of these methods to address management and ecological questions.

Study Area

Tustumena Lake is within the Kasilof River watershed on the Kenai Peninsula in south-central Alaska and is entirely within the bounds of the Kenai National Wildlife Refuge (Figure 1). Tustumena Lake is the largest lake (about 295 km^2) on the Kenai Peninsula, approximately 40 km long, 8 km wide, mean depth 124 m, and maximum depth 320 m. The lake is turbid ($\approx$ 50 NTU) and oligitrophic (light penetration only to about 2m, and total phosphorus averaging 3.7 µg/L during May-October); the result of melt water from the Tustumena Glacier (Kyle 1992).

Five species of Pacific salmon occur in the Tustumena Lake system. The most important to commercial and recreational fisheries are sockeye and chinook salmon. This system has supplied up to 20% (2 million fish) of Cook Inlet's total annual sockeye salmon harvest. Annual escapements average 241,100 fish (1981-1990) with a peak of 503,000 in 1985 (Reusch 1991). Estimated exploitation rates of Tustumena Lake sockeye salmon in the commercial fishery range from 50-85% (Kyle 1992). According to Kyle (1992) Bear, Glacier Flats, Moose, and Nikolai creeks, account for an average (1975-1990) of 96.2% of the sockeye salmon spawning in Tustumena Lake tributaries. Tustumena Lake sockeye salmon also use lake shoreline areas

for spawning. Burger et al. (1995) used radio telemetry to investigate the distribution of sockeye spawning and found that 31 to 46% (1989 -1991) of the radio-tagged fish presumably spawned along the lake shore. Natural production has been supplemented by ADFG since 1976. Brood stock has been taken from Bear and Glacier Flats creeks, and the eggs are incubated at the ADFG Crooked Creek Hatchery. Fry are fed for 1-2 wk and released back into Tustumena Lake. Fry plants have ranged from 400,000 (1978) to 17,050,000 (1984). Since 1988 the annual stocking level has been set at 6,000,000 fry. Hatchery-incubated fish have averaged 25.7% (1981-1990) of the estimated smolt outmigration (Kyle 1992).

Methods And Materials

Sample Collection and Selection

Wild incubated sockeye salmon fry were collected as they migrated from five incubation areas into Tustumena Lake (Figure 1). During 1992, funnel traps were used to monitor the timing of fry migrations from Bear, Glacier Flats, and Nikolai creeks. The funnel traps (1.2 X 1.2 m openings, 5 mm tapering to 3 mm square mesh netting, connected to a holding box) were operated 6 d per week from 22 April to 2 June (Figure 3). Traps were fished for 5-15 min per hour from 2200 hr to 0500 hr each night. A sample ($n \geq 100$) of fry were preserved in >80% ethyl alcohol (Butler 1992) every 7 d with an additional sample collected during peak migration. Fry in the holding box were stirred with a dip net and a blind dip was made. To reduce the possibility of biasing the sample with a single cohort, the entire sample was spread over several hours. Other wild stocks (Moose Creek and Glacier Springs) were sampled opportunistically 1 to 3 times during the same time period. In 1991 all hatchery brood stock were taken from Bear Creek. Eggs were incubated at the hatchery over the winter and after emergence (May 1992) the fry were held in raceways prior to release into the Tustumena Lake on 15 June 1992. Several hundred hatchery incubated fry were collected and preserved prior to their release into the lake. Hatchery fry were dip netted from hatchery

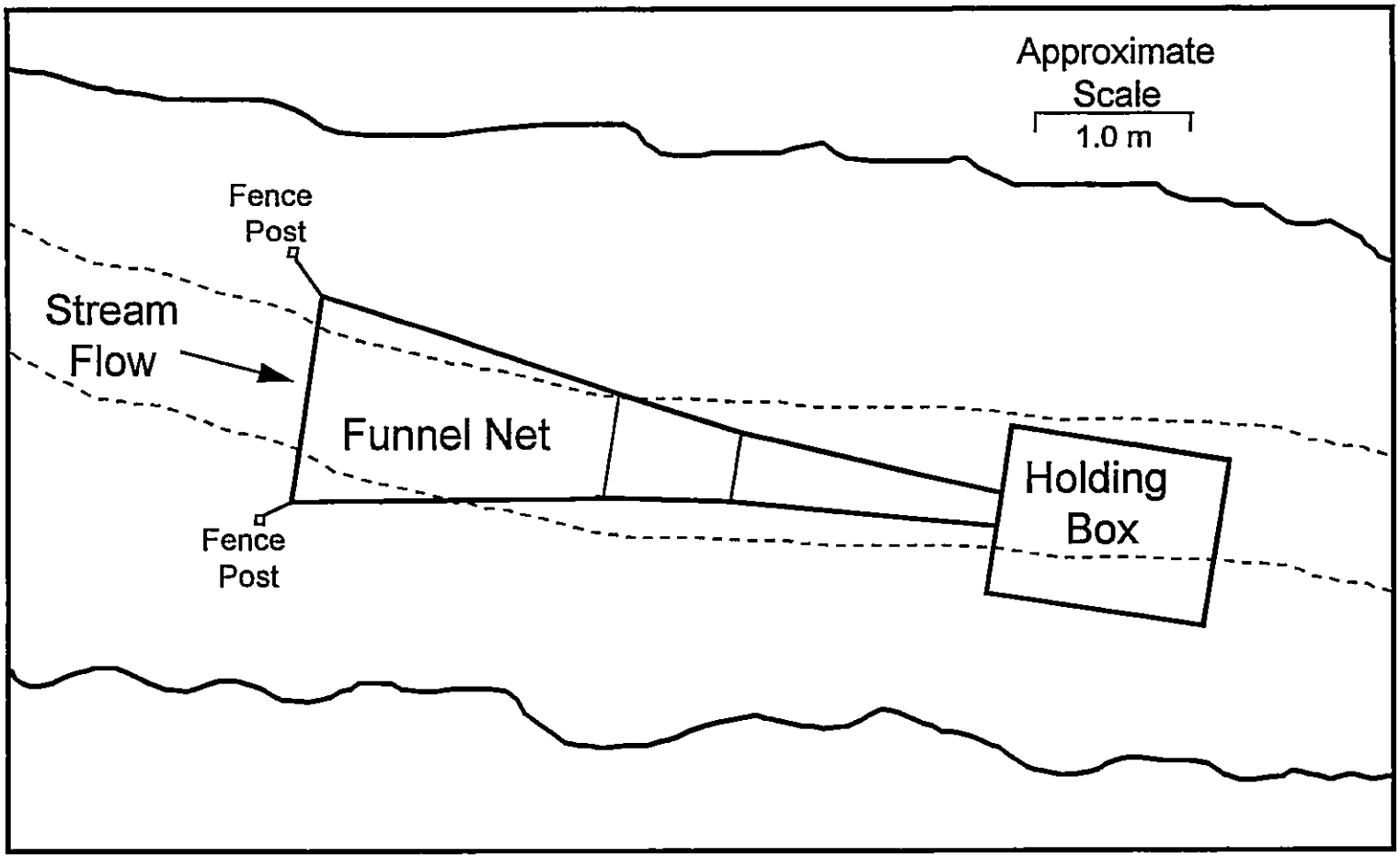

Figure 3. Funnel trap used to collected sockeye salmon fry migrating from incubation sites into Tustumena Lake, Alaska. Dashed lines indicate the location of stream thalweg.

raceways on 03, 14, and 15 June. Each hatchery sample consisted of ≥100 fry from 3-5 blind grabs taken in different areas of the raceways.

The available dates and samples of wild incubated fry were subsampled (Table A-1). When samples for multiple dates were available, subsamples were taken by selecting the peak migration date and then randomly selecting one to two dates prior to and after the peak date. In some cases (e.g., Glacier Springs) there was only one sampling date. Fry were selected from all three of the hatchery samples. From each selected date sample, 50 fry were randomly chosen by spreading the entire sample onto a dissection pan and selecting 50 random numbers to select individuals for otolith extraction.

Otolith Preparation

Teleost fishes have three otolith pairs (asterisci, lapilli, and sagittae) located in the vistibular apparatus within the cranium (Figure 4). Morphological terminology follows Pannella (1980). I chose the largest of the otoliths, the sagittae, as they were easily and consistently found; their morphology allows for identification of left and right otoliths after extraction; and their use is most prevalent in the literature (Secor et al. 1992). Also, my initial attempts at polishing lapilli failed to produce consistent results, and the smallest of the

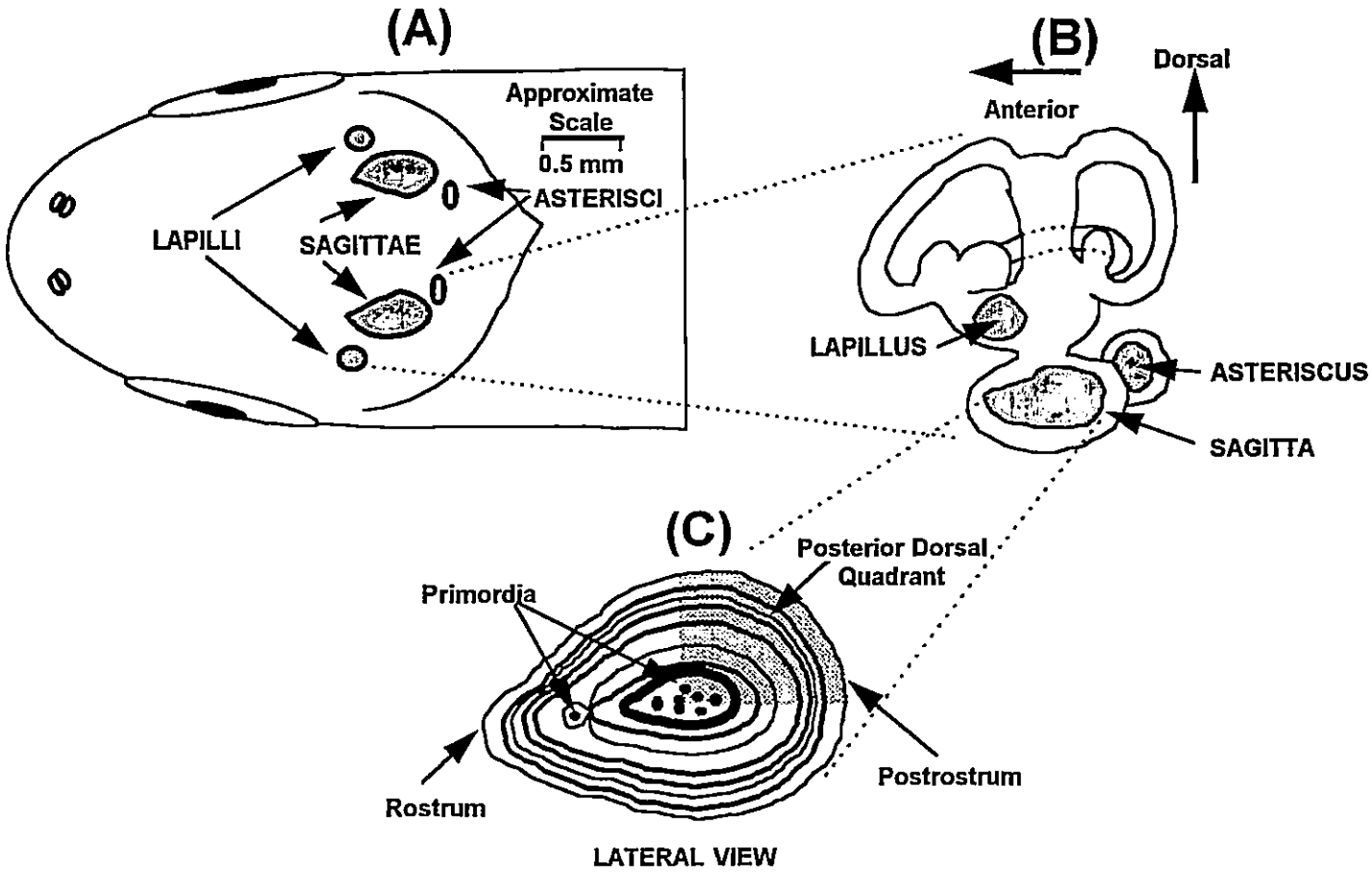

Figure 4. (A) Location of otolith pairs in sockeye salmon fry; (B) anatomy of vestibular apparatus (adapted from Secor et al. 1992); and (C) medial view of saggita with posterior dorsal quadrant delineated by stippled area.

otoliths (the asterisci) were rarely seen during extraction and appeared to be devoid of banding. Further use of the word otolith will refer to the sagittae.

Fry selected for otolith extraction were measured (fork length to nearest 0.1 mm) and both left and right otoliths were removed, cleaned and mounted sulcus side down on glass microscope slides using Crystal Bond thermal plastic resin. Otoliths were polished on the sagittal plane to the primordial zone using a lapidary wheel with 1.0 µm alumina paste. A 0.05 µm paste was used for a final polish. The slides were reheated and the otolith flipped so that the sulcus side was exposed, and the above polishing procedure was repeated. A metal probe was used to tap each otolith to position the polished surface parallel with the slide surface in an attempt to minimize the amount of resin between the otolith and the slide.

A random subsample of 25 otoliths was used to estimate the thickness of the polished sections. This was done by first calibrating the graduated fine focus adjustment knob of the microscope in µm as follows: 1) metal blades of known thickness (76 µm and 102 µm) were taped to a slide; 2) the microscope was focused on the surface of the blade and the position of the graduated knob recorded (R1); 3) the microscope was than focused on the

surface of the glass slide (R2); 4) the absolute difference between R1 and R2 was converted to μm/gradation = |R1-R2|/blade thickness in μm. This was repeated five times at each blade thickness and an average μm/gradation calculated. The otoliths were then placed on the microscope and R1 (in this case the surface of the otolith at the primordial region) and R2 were recorded three times. These readings were used to calculate a mean thickness for each otolith. As there was no way to verify the thickness of the resin between the otolith and the slide, these measurements represented a maximum thickness.

Feature Extraction

Otolith banding features were examined and extracted to databases using a microcomputer-based digital image analysis system. The system consisted of the following components: compound light microscope; video camera; image monitor; 640x480 frame grabber board (interfaces video camera to the computer and converts analog video images to digital images); and microcomputer (Figure 5). Optimas (Bioscan, Inc. Seattle WA) software was used for image enhancement and data extraction. The digitized image was composed of pixels with associated two dimensional location values (x, y) and a luminance intensity value (measured on a 256 value gray scale with 0 = black and 255 = white).

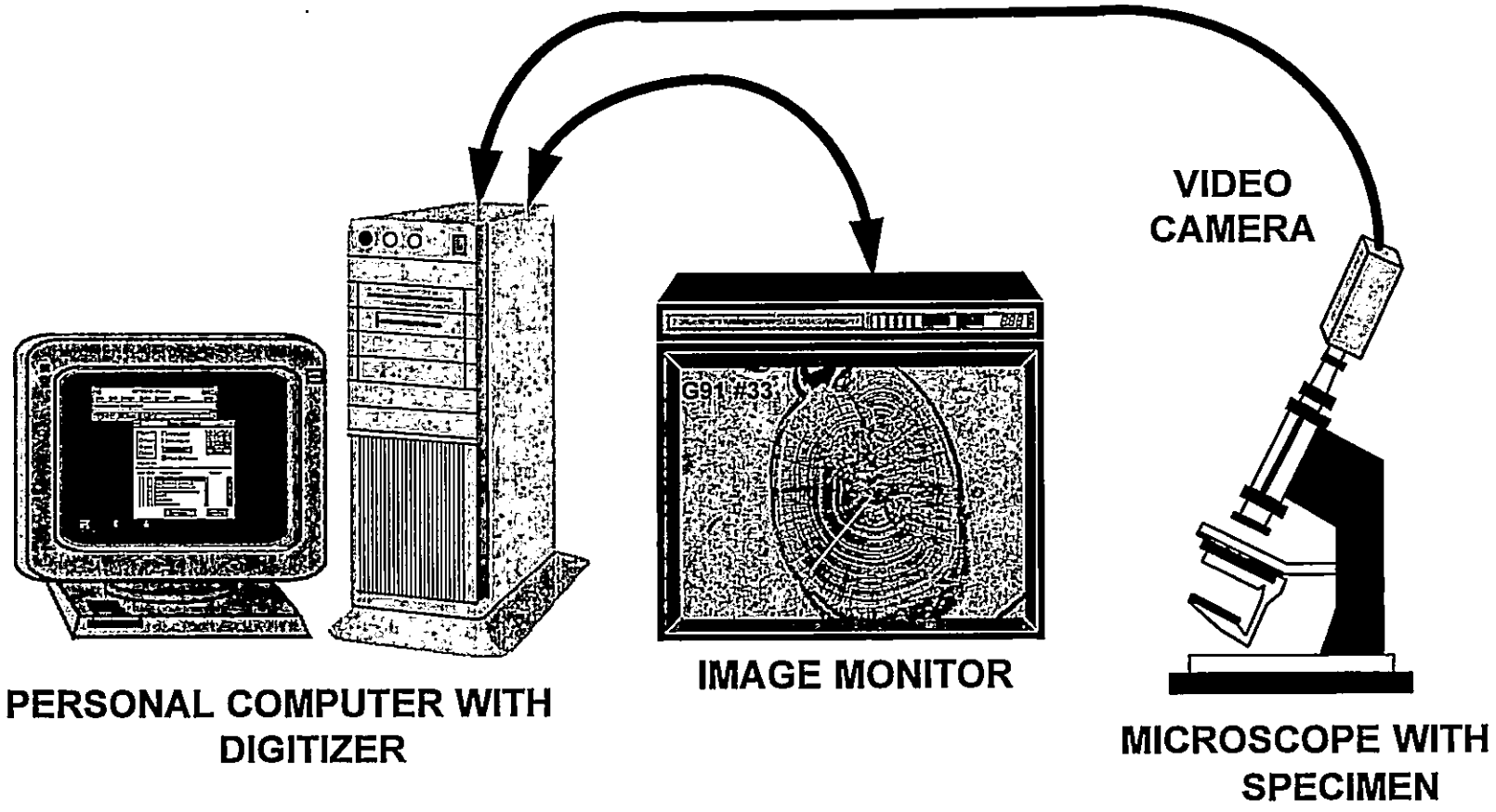

Figure 5. Computer based image analysis system used for the measurement of otolith banding patterns.

A planachromatic 40X, 0.65 NA (numerical aperture) objective and a green filter were used which resulted in a maximum resolution of about 0.42µm (Delly 1988). This closely matched the 0.58µm resolution of the digitized image (calibrated width of individual pixels). When projected on the monitor, the image was at 750X magnification. The software measurements were calibrated using a stage micrometer with 100µm graduations.

All measurements were taken in the posterior dorsal quadrant of each sagitta (Figure 4). This is the zone of the greatest growth and best increment definition (Pannella 1980; Marshall and Parker 1982; Wilson and Larkin 1982; Campana and Neilson 1985). Past studies have used standard reference lines with transects placed at consistent angles off the reference line (Wilson and Larkin 1982; West and Larkin 1987). To be applicable to future measurements on otoliths collected from older fish (e.g., age 1+ fish), the protocol I developed for the placement and length of measurement transects was not based on reference points that would change with fish or otolith growth.

The first consideration was to place a transect such that it would include the majority of the otolith formed during incubation, but not extend into the area formed after fry had moved into the common rearing environment of the lake. A

random sample of sixty-seven wild incubated fry otoliths: Bear Creek n=18; Glacier Flats Creek n=7; Moose Creek n=14; and Nikolai Creek n=28 were measured from the most posterior primordia to the otolith edge along three transects at 40°, 60°, and 80° angles off a reference line running from the rostrum through the most posterior primordia. This resulted in a total of 201 measurements. These measurements had a mean of 230.0 µm (range = 169.5 - 309.0 µm; standard deviation = 32.6 µm). Based on these data, a 95% prediction interval around the individual observations (i.e., using the sample standard deviation as opposed to the mean standard error to be conservative) was 165.8 - 294.2 µm. Therefore, I selected a distance of 160 µm for the end point of transects starting at central primordia. This would include approximately 55% to 96% of the zone formed during incubation with a 95% probability.

The posterior dorsal quadrant of each otolith image was focused on the monitor. The quadrant was examined and a portion was selected which included both a distinct primordium and clear banding (I subjectively eliminated areas with cracks, scratches, and where excessive polishing had obliterated bands). The image was rotated by turning the video camera until the majority of the banding was horizontally oriented. This was done to insure that the transects placed on the image would be perpendicular to the otolith bands. Prior to establishing the

transects, the contrast between light and dark bands was enhanced by applying a 3X3 edge detection convolution mask (Gonzalez and Wintz 1987).

The mask I used evaluated the image over a 3X3 pixel matrix and transformed the gray scale value of the central pixel as a function of the mask (a matrix) and the gray scale values of the pixel matrix. This is most easily illustrated with an example. Consider the following where the gray scale values in matrix g are going from lighter to darker values:

g Matrix

200	210	190
180	170	155
140	150	140

a Matrix

-1	-1	-1
1	1	1
1	1	1

Convolution Function:

$$g_{22} = \frac{\sum_{i=1}^{3}\left(\sum_{j=1}^{3} a_{ij} \cdot g_{ij}\right)}{3} = 111.6$$

200	210	190
180	111.6	155
140	150	140

The image is filtered pixel by pixel with the results stored in a memory buffer. In that way the transformed values are not used in subsequent calculations. Once the entire image has been filtered, the original image is replaced with the filtered

pixel values. The filter has little effect on the value of pixel g_{22} when the gray scale values of matrix g are nearly equal. However, gradient changes (edges between light and dark borders) are enhanced (Figure 6). The divisor (3) was subjectively chosen by observing the effects of values ranging from 1 - 12. Note that when the divisor is set to 9, pixel g_{22} is a weighted average. By replacing all the values in the a matrix with 1 with a divisor of 9, the convolution acts as an averaging filter.

A primordium was selected as a reference for transect positions, and a software macro established three transect lines. To avoid including the primordium, the center transect began 10 mm above the start point. The other two transects were positioned 5 mm to the left and right of the center transect (Figure 6).

Along each transect, 256 luminance values were measured at an interval of about 0.586 mm. Each luminance value was averaged over a width of 5.81 mm (five pixels). Thus each otolith had three 150-mm 256 value luminance transects extracted to spreadsheet data files. The luminance values (L) were averaged over the three transects (i = 1-3) at each of the j = 1-256 intervals:

$$\overline{L}_j = \sum_{i=1}^{3} L_{ij} / 3$$

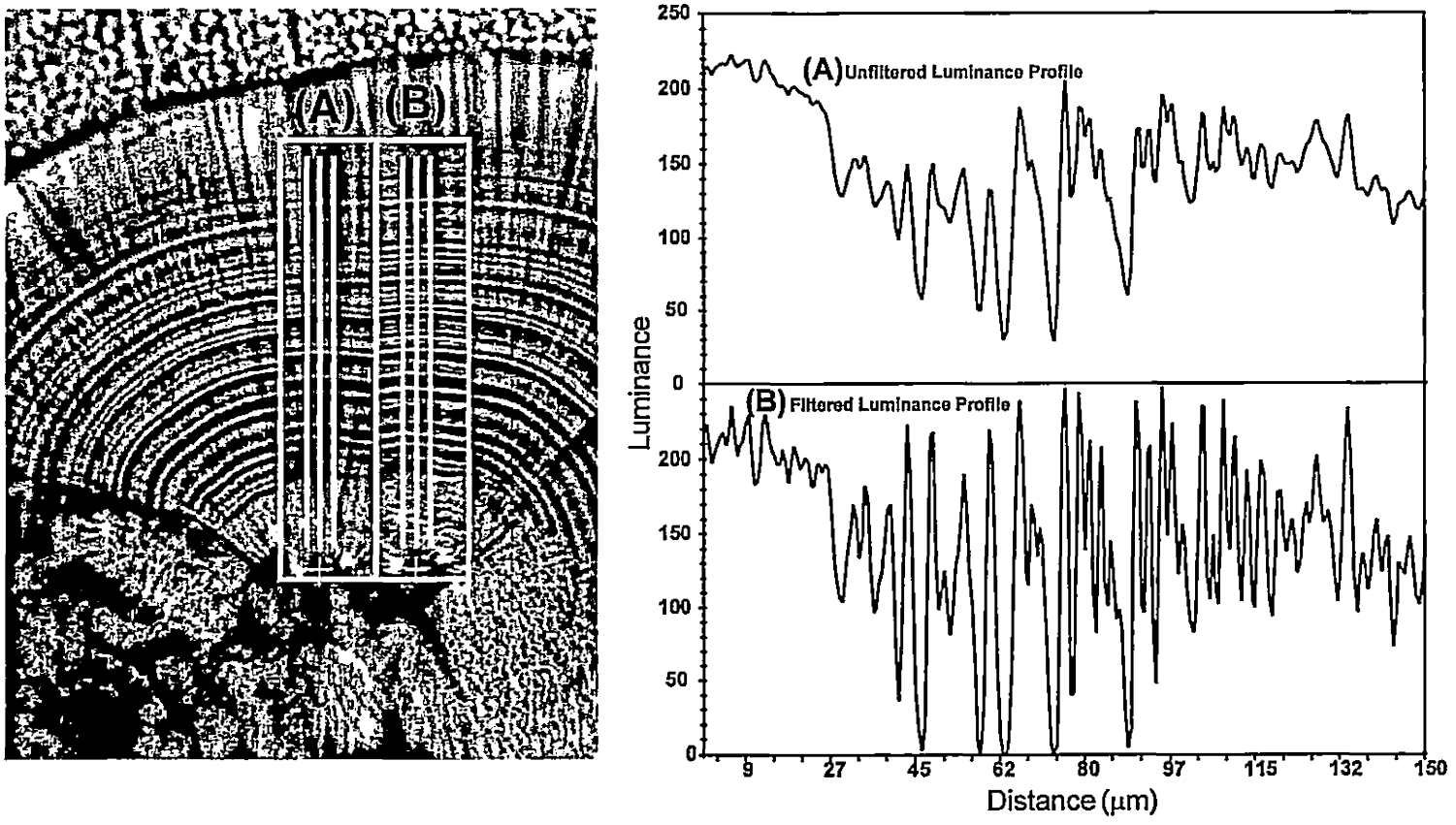

Figure 6. Digital otolith image with 150-μm transect lines showing the banding pattern before (A) and after (B) application of convolution edge detection filter. Section (A) is an offset of section (B). The luminance profile plots are for the unfiltered (A) and filtered (B) images.

This resulted in one average luminance profile per otolith. Each luminance profile consisted of a series of n = 256 luminance values along a 150 mm transect. Average luminance values were then standardized to have a mean = 0 and standard deviation = 1 by subtracting the profile mean and dividing by the profile standard deviation.

Fourier Transformation

The average luminance profiles were transformed into a Fourier series using a Fast Fourier Transformation (FFT) algorithm (Gonzalez and Wintz 1987). FFT decomposed the series into component cosine functions. Cosines are additive such that the luminance value at any given point can be described as:

$$L_i = A_o + A_i \bullet \cos(i\theta - \phi_i)$$

where:

L_i = luminance value at point i along the transect;

A_o = the amplitude of the 0th harmonic (mean luminance);

A_i = the amplitude of the ith harmonic;

$i\theta$ = the polar angle of the ith harmonic; and

ϕ_i = the phase angle of the ith harmonic;

The above form is adapted from Fourier description of shapes where the shape is defined by radii from a centroid using polar angle coordinates. This can easily applied to describing the shape of a luminance profile if we consider the profile to be an unrolled shape perimeter and the coordinates along the x axis as distances along a transect rather than degrees around a polar plot (Jarvis et al. 1978). The luminance profile will be exactly described by a summation of n = 256 harmonics at each point of the transect. However there are only n/2 = 256/2 =128 unique harmonics (Jarvis et al. 1978). Individual harmonics represent a cosine with i cycles, and an amplitude of A_i, offset by A_0. The portion of the pattern accounted for by individual or subsets of harmonics can be seen by setting all other harmonics to zero and performing an inverse FFT (Figure 7).

In practice, software algorithms produced a complex number for each point along the luminance profile. This complex number was of the form:

$$z = x + yi$$

where: x = a real number; and

yi = an imaginary number.

Then the amplitude for a given harmonic was defined as:

$$A_i = |z| = \sqrt{x^2 + y^2}$$

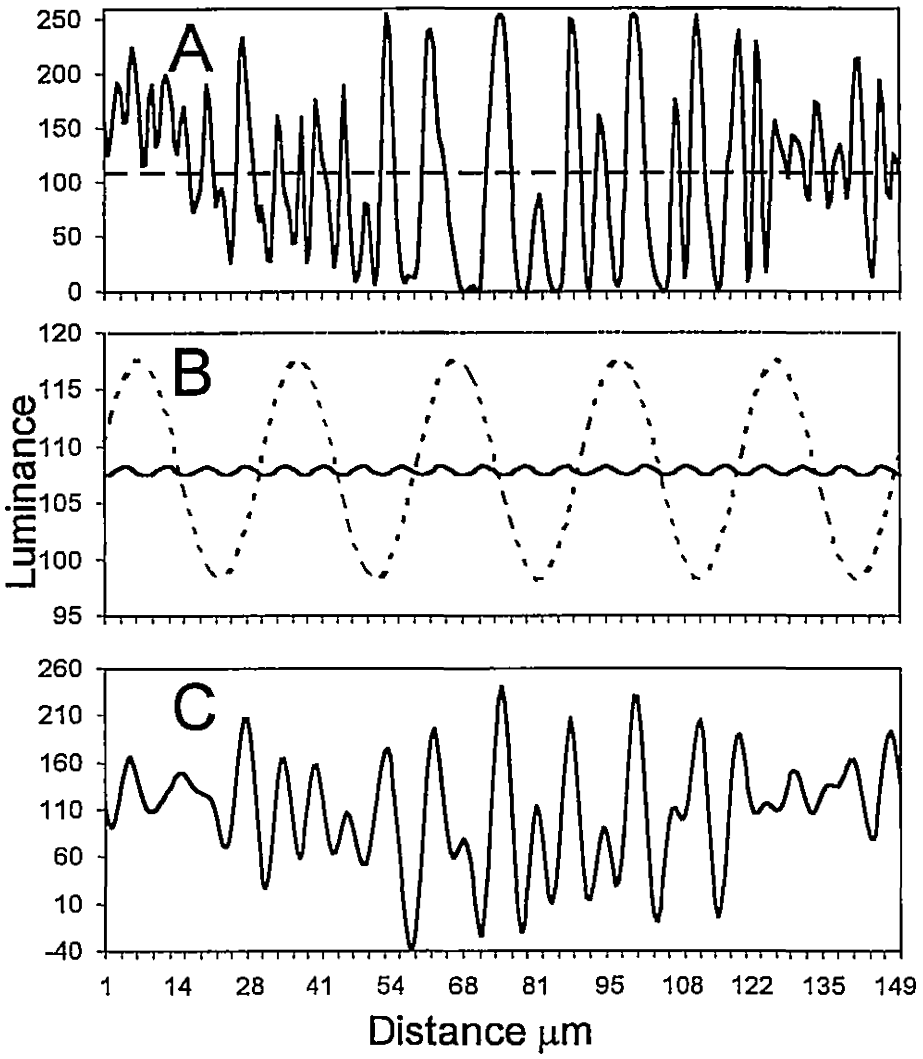

Figure 7. Fourier analysis of randomly selected otolith luminance profile. **A)** luminance profile (solid line) and series described by the 0th Fourier harmonic (dashed line); **B)** series described by the 5th harmonic (dashed line) and the 20th harmonic (solid line); **C)** series described by a subset of 11 harmonics composed of the 0th harmonic and 10 harmonics associated with the 10 largest amplitudes (harmonics: 1, 12, 13, 14, 16, 21, 22, 23, 24, 25).

Fourier analysis and calculations of amplitudes were done using Microsoft Excel version 4.0 functions (Microsoft Corp., Redmond, WA).

The variance of each harmonic was given by:

$$V_k = A_k^2 / 2$$

These variances are additive (Jarvis et al. 1978) making it possible to determine the proportion of the total variation accounted for by individual and subsets of harmonics as :

$$C_k = A_k^2 / \sum_{k=0}^{n/2} A_k^2$$

The individual amplitudes were used as variables in statistical analyses. Others have focused on Fourier amplitudes for shape analysis (Bird et al. 1986; Castonquay et al. 1991; Campana and Casselman 1993; Kenchington and Full 1994). Although the phase angle (ϕ) contains shape information, ϕ is distributed in a circular manner and is often bimodal (Campana and Casselman 1993). Therefore, there are no means to transform ϕ to approximate normality.

Data Sets

Data sets were developed to: 1) test for differences between left and right otoliths; 2) test for differences between readers; 3) estimate discriminant functions; and 4) test discriminant functions.

Luminance profiles were recorded on 1203 otoliths. Of these there were 427 pairs (left and right from the same fish) available for testing differences between left and right otolith luminance profiles. To test for consistency between observers, a random sample of 50 otoliths were remeasured independently by a second observer. The second observer was first instructed in transect placement, image enhancement, and data acquisition on five otoliths not used in the test. The second observer then extracted the luminance profiles from the 50 otoliths without further instruction.

The general procedure for developing and testing discriminant models requires that a set of characteristics of known origin individuals are used to estimate discriminant functions; this is commonly known as the learning data set (McLachin 1992). The learning data are used to estimate the group distribution functions which are used to develop classification rules. The test data set is also composed of observations from known origin individuals, however they are held

back from the model building process. The test data are used in the evaluation of the discrimination rules developed with the learning data.

First a data set with only one otolith per fish was made. When paired otoliths were present, left or right otolith values were randomly deleted. This resulted in a data set of 776 luminance profiles. This data set was subdivided into learning and test data sets. For the test data set, a random sample of 25 luminance profiles was taken from each of the six groups (total = 150). The remaining 626 observations made up the learning data set.

Data Transformation

Parametric methods require assumptions which include normality. Although discriminant analysis is a multivariate technique, tests for multivariate normality are limited (Johnson and Wichern 1988). Lilliefor's Test (a modification of the Kolomogorov-Smirnov Test) was used to assess univariate normality for individual amplitudes (Daniel; 1990, Systat 1992). Tests of normality to determine the necessity of transformation were only done on learning data sets. In that way the test data did not influence the resulting models. Normal probability plots were used to visually assess normality. Transformations were selected from the family

of power transforms known as Box-Cox Power Transformations (Sokal and Rohlf 1981; Johnson and Wichern 1988) The general form of the transformation is:

$$X' = (X^{\lambda} - 1) / \lambda \quad \text{where } \lambda \neq 0; \text{ and}$$
$$X' = ln(X) \qquad \text{where } \lambda = 0.$$

The lambda (λ) value for each variable was found by finding λ which maximized the log-likelihood function:

$$L = \frac{v}{n} \bullet \ln(S^{2}_{x'}) + (l - 1)\frac{\upsilon}{n}\sum \ln(X)$$

where: $\upsilon = df = (n-1)$; and

S^{2}_{x} = variance of the Box - Cox transformed X

The "best" value of λ is that value which maximizes L (Sokal and Rohlf 1988). Lambda was evaluated over a range of 0.10 - 1.00 in increments of 0.05.

Classification

Classification is the formulation of a rule which assigns (predicts) the group membership of a individual based on some set of measurements/characteristics. A variety of statistical techniques are available with recent reviews found in McLachlin (1992) and Huberty (1994). Although the form of the data at hand provides guidance for selection of statistical techniques; on a pragmatic level the success (classification rate) of the rule in assigning individuals to the correct group is the most important

criteria under a stock separation program. Data sets were examined for violations of model assumptions (e.g., multivariate normality) during initial variable selection and rule formulation. Classification rate estimates were then used for model refinement and comparisons among models. I confined my analyses to the use of linear discriminant analysis (LDF), quadratic discriminant analysis (QDF), and logistic regression.

Discriminant Analysis:

Parametric discriminant analysis uses the learning data set to estimate the multivariate density function of each of the m groups to be separated. Estimates of group membership probabilities are often incorporated into discriminant models (SAS a 1990, Huberty 1994). Using sample sizes as estimates of group proportions is not warranted unless sampling has been strictly group proportional (Huberty 1994). As I had no prior knowledge of "at large" group proportions, equal proportions for all groups was assumed. Therefore, group weighting factors which are often seen in discriminant distance and probability calculations were dropped from the following formulas.

One of the problems presented by Fourier analysis of luminance values is the large number of variables available for the discriminant model. In my case the Fourier analysis of 256 luminance values generated up to 128 amplitude variables. Variable selection in this case is not straightforward and efforts to find the most parsimonious model are recommended (Williams 1983; McLachlan 1992). A general rule is to restrict the number of discriminant variables to $p \leq n_i/3$ (Williams and Titus 1988). As a starting point, I used two methods to select initial subsets of variables, stepwise LDF and ANOVA. The first method (stepwise LDF) assumes multivariate normality and equal covariance matrices and is therefore most appropriate for developing linear discriminant classification rules (SAS 1989 b). The second method (ANOVA) provided initial data sets for the development of quadratic discriminant rules.

A forward/backward stepwise LDF was done using SAS PROC STEPDISC (SAS 1989 b). A forward/backward stepwise discriminant selection process proceeds much the same as in multiple regression analysis. Of the p variables, one is selected for inclusion based on Wilk's lambda (Λ, a multivariate equivalent to the F ratio) which is a measure of how much the inclusion of the variable contributes to separation of the group centriods (means in the univariate case). The remaining p-1 variables are then

reevaluated for their effect on Λ given the variable(s) already included in the model. An additional variable enters the model if the Λ-to-enter criteria is met. Before proceeding forward a backward selection is done. Variables in the model are reevaluated and any that do not meet a Λ-to-remain criteria are dropped. The SAS default significance level ($P = 0.15$) for variable entry and removal was used for all stepwise procedures. This sequence is repeated until none of the remaining variables meet the Λ-to-enter criteria (McLachlan 1992). However, blind acceptance of stepwise methods may not result in the best possible discrimination or may cause extraneous variables to be included in the model (SAS 1989 b; McLachlan 1992). The reason for this is that the measure of variable importance (Λ) is based on separation among group centriods and not on classification results (Huberty 1994). The SAS STEPDISC procedure assumes multivariate normality and equality of within group covariance matrices and hence selects the "best" subset of variables for a linear discriminant model.

The second method of variable selection employed SAS ANOVA (PROC GLM). Univariate ANOVA was done on individual amplitudes to test for significant differences among groups. Amplitudes that were significantly ($P \leq 0.01$) different were included in the initial model. These two methods

were used to develop models for discriminating among both m = 2 groups (hatchery versus wild) and m = 6 groups (hatchery, Bear Creek, Glacier Flats Creek, Glacier Springs, Moose Creek, and Nikolai Creek).

Starting with these reduced sets of p amplitudes, refinement was done by running PROC DISCRIM (SAS 1989 a) on all combinations of p -1 amplitude sets and examining the estimated misclassification rates (Figure 8). For example, if initially 31 amplitudes were selected by stepwise discrimination, first the error rate for the full 31 variable model was estimated. Then all possible 30-amplitude model error rates were estimated. The model with the lowest error rate was selected and then all possible 29-amplitude model error rates were calculated and compared to select a 29-amplitude model. This process was continued until the k=1 amplitude model was reached. Classification rates were estimated using crossvalidation (also known as the leave-one-out technique) (McLachlan 1992). Crossvalidation involves holding out one observation from the learning data, developing a discriminant rule based on the N-1 data set, and using the rule to classify the observation that was held out. The process is repeated N times. The three models that resulted in the lowest error rates were used for classification of the test data set.

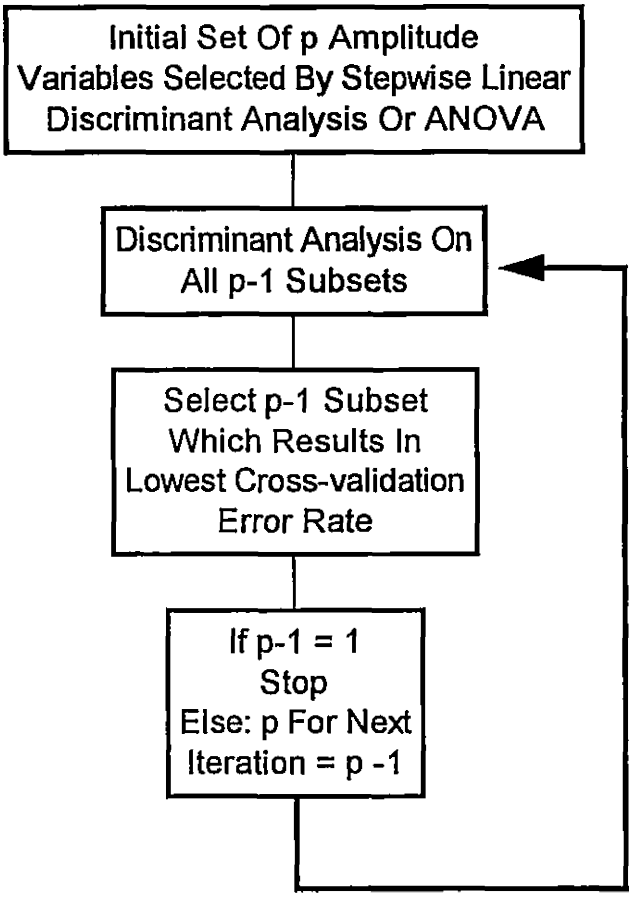

Figure 8. Procedure used to test all possible subsets of p-1 amplitude variables. The value of p was reduced by 1 after each iteration by selecting the set of p-1 variables which resulted in the lowest cross-validation error rate.

Linear Discriminant Analysis:

Linear Discriminant Analysis (LDF) assumes multivariate normality and homoscedasticity (common covariance structure among groups). The Mahalanobis distance of an individual observation vector from a given group i mean vector is:

$$D_i^2 = (x - \bar{x}_i)' C^{-1} (x - \bar{x}_i)$$

where:

x = the vector of measurements from an individual;
$\bar{x}_i$ = the mean vector for the ith group; and
C^{-1} = the inverse of the pooled covariance matrix

The posterior probability of group membership is estimated as:

$$p(i|x) = \frac{\exp(-0.5 \cdot D_i^2 \cdot (x))}{\sum_{i=1}^{m} \exp(-0.5 \cdot D_i^2 \cdot (x))}$$

where: p(i|x) = the probability of membership to group i given the observed vector x. An observation is assigned to the group where D^2 is minimized or conversely where p(i|x) is maximized.

The distance between the mulitvariate mean vectors of any two groups i and j can be generalized as:

$$D_{(i|j)}^2 = (\bar{x}_i - \bar{x}_j)' \cdot C^{-1} \cdot (\bar{x}_i - \bar{x}_j)$$

Quadratic Discriminant Analysis:

Quadratic Discriminant Analysis (QDF) assumes multivariate normality. However, the assumption of equal covariance is relaxed. D^2 is calculated using the within group covariance matrices:

$$D_i^2 = (x - \bar{x}_i)' \cdot C_i^{-1} \cdot (x - \bar{x}_i)$$

where: C_i^{-1} = the inverse of the covariance matrix for the ith group.

The probability of group membership in QDF is the same as was calculated above for LDF.

Tests for departures from normality were done as previously mentioned. The assumption of homoscedasticity was tested using Bartlet's log-likelihood ratio (SAS 1989 a, McLachlan 1992). The test statistic is:

$$Q = \sum_{i=1}^{m} n_i \cdot \log(|C|/|C_i|)$$

where:

$|C|$ = the determinant of the covariance matrix for group i;

$|C_i|$ = the determinant of the pooled covariance matrix.

Under H_o: $C_1 = C_2 = \ldots = C_m$, Q will be distributed as chi-square with 1/2(m-1)p(p+1) df. The significance level for Q was set at $P \leq 0.1$ (SAS 1989 a).

Logistic Regression:

When the assumptions required by LDF and QDF are not met, discrimination based on logistic regression may be more optimal (Prager and Fabrizio 1990). Logistic regression models the probability of observing a categorical membership or response variable using explanatory variables (Agresti 1990). The general relationship takes the form:

$$\pi_i = \frac{\exp(\beta_o + \beta_i x)}{(1 + \exp(\beta_o + \beta_i x))}$$

where:

p_i = the probability of observing response i given the observed vector x;

b_o = an intercept; and

b_0 = a vector of regression coefficients.

To put the model in a linear form, the log of the odds ratio is estimated as:

$$ln(\pi_i / 1 - \pi_i) = \beta_0 + \beta_i x$$

The value of p_i is then calculated using the equation above.

In instances where the distances among groups are small, logistic regression may out perform LDF, particularly if the LDF assumption of normality is not met (McLachlan 1992). Logistic regression is also particularly suited for models where explanatory variables are a mixture of continuous and binary observations.

Variable selection was done in the same manner as LDF and QDF models. SAS PROC LOGISTIC using a forward/backward selection provided one initial set of variables (SAS 1990 b). The same ANOVA results as described under discriminant analysis provided a second set of variables. Error rates were calculated using a leave-one-out approximation (SAS 1990 a; Huberty 1994). The same looping procedure used for discriminant analysis was used to look at all combinations of k-1 variables. As stepwise selection and error rate estimates were only available for binary classifications, logistic regression was only done under the m = 2 (Hatchery versus Wild) scenario.

Model Comparisons:

Pairwise comparisons of discriminant rules were done using McNemar's test for related samples (Daniel 1990; Huberty 1994). The classification results of two discriminant rules were arranged in a table:

		Rule 2	
		Correct	Incorrect
Rule 1	Correct	n_{11}	n_{12}
	Incorrect	n_{21}	n_{22}

where: n_{11} = number classified correctly by both rules;

n_{12} = number classified correctly by Rule 1 but incorrectly by Rule 2;

n_{21} = number classified incorrectly by Rule 1 but correctly by Rule 2; and

n_{22} = number classified incorrectly by both rules.

The test statistic was: $z = (n_{12} - n_{21})^2/(n_{12}+n_{21})$ Which was compared to the standard normal distribution. The overall experimentwise error rate was set at 0.1 for pairwise comparisons (Daniel 1990). Then the individual comparison significance level was a = 0.1/(k(k-1), where k is the total number of pariwise comparisons. For example, to make three pairwise comparisons, a was set to 0.1/(3(3-1) = 0.017.

To determine if the classification rates were greater than expected by chance, the observed number (o_g) classified to the correct origin was compared to the expected number (e_g). The expected number was calculated under an assumption of equal probabilities of classification into each of the possible origins. If observations were assigned by chance to an origin an if classifications were independent, the probability would be 1/m, where m = the number of possible origins. Then the expected number classified to origin g

would become $e_g = 1/m \bullet n_g$, where n_g = the number of individuals whose true origin was location g. The test statistic was:

$$z = \frac{(o_g - e_g)}{\sqrt{e_g(n_g - e_g)/n_g}}$$

Under the null hypothesis: $o_g - e_g = 0$, z follows the standard normal distribution (Huberty 1994).

Results

Otolith Samples

Otoliths were extracted and polished from a total of 775 sockeye salmon fry (Table 1; Table A-1). The difference between the actual sample size and the target sample size (50) reflects the loss of otoliths during extraction, breakage, and excessive polishing. Glacier Springs is an exception, as there was only one date the target sample was 100. The loss of otoliths ranged from 4 to 32%. The mean thickness of the polished otoliths was 69.4 μm (range 33.7 - 112.3 μm; SD 17.8 μm; N = 25).

Variation in the preserved lengths of fry probably reflects incubation environment or temporal differences. Hatchery fry (mean = 29.3 mm) were significantly larger (t = 10.78, $P \leq 0.001$) than wild fry (mean = 27.6 mm). Mean lengths were significantly different among the six locations (ANOVA, F = 48.12, df = 5, 769, $P < 0.001$). Pairwise comparisons (Tukey) indicated that the hatchery and Glacier Springs fry were similar and larger than fry from other locations (Figure 9). This is to be expected as hatchery fry were all sampled in June and most had been fed for several weeks. The Glacier Springs fry were also sampled later than most other wild fry.

Table 1. Sample location, date (day-of-year), mean, range, and standard error (SE) of preserved fork length (mm) for Tustumena Lake, Alaska, sockeye salmon fry used in otolith pattern analysis.

Location	Day Of Year	Date	Fork Length Mean	Range	SE	N
Hatchery	155	03-Jun	28.3	26.1 - 31.7	1.13	40
	166	14-Jun	30.1	27.4 - 34.5	1.60	47
	167	15-Jun	29.3	25.7 - 33.8	1.73	48
Bear Creek	111	20-Apr	27.8	24.8 - 29.3	0.93	47
	139	18-May	27.4	25.2 - 29.2	0.89	48
	142	21-May	27.3	25.0 - 29.8	0.98	38
	154	02-Jun	27.3	24.5 - 28.9	1.01	49
Glacier Flats Creek	113	22-Apr	26.9	24.7 - 31.6	1.48	34
	118	27-Apr	27.1	25.8 - 29.1	0.82	34
	125	04-May	27.3	25.4 - 32.9	1.55	49
	150	29-May	28.9	24.7 - 33.7	2.47	46
Glacier Springs	154	02-Jun	28.8	25.3 - 31.4	1.27	85
Moose Creek	120	29-Apr	26.5	22.1 - 29.7	1.87	37
	143	22-May	26.9	23.5 - 28.9	1.12	40
Nikolai Creek	118	27-Apr	27.4	24.4 - 29.1	0.97	44
	125	04-May	28.1	26.4 - 29.7	0.76	49
	146	25-May	27.3	25.0 - 29.4	1.05	40

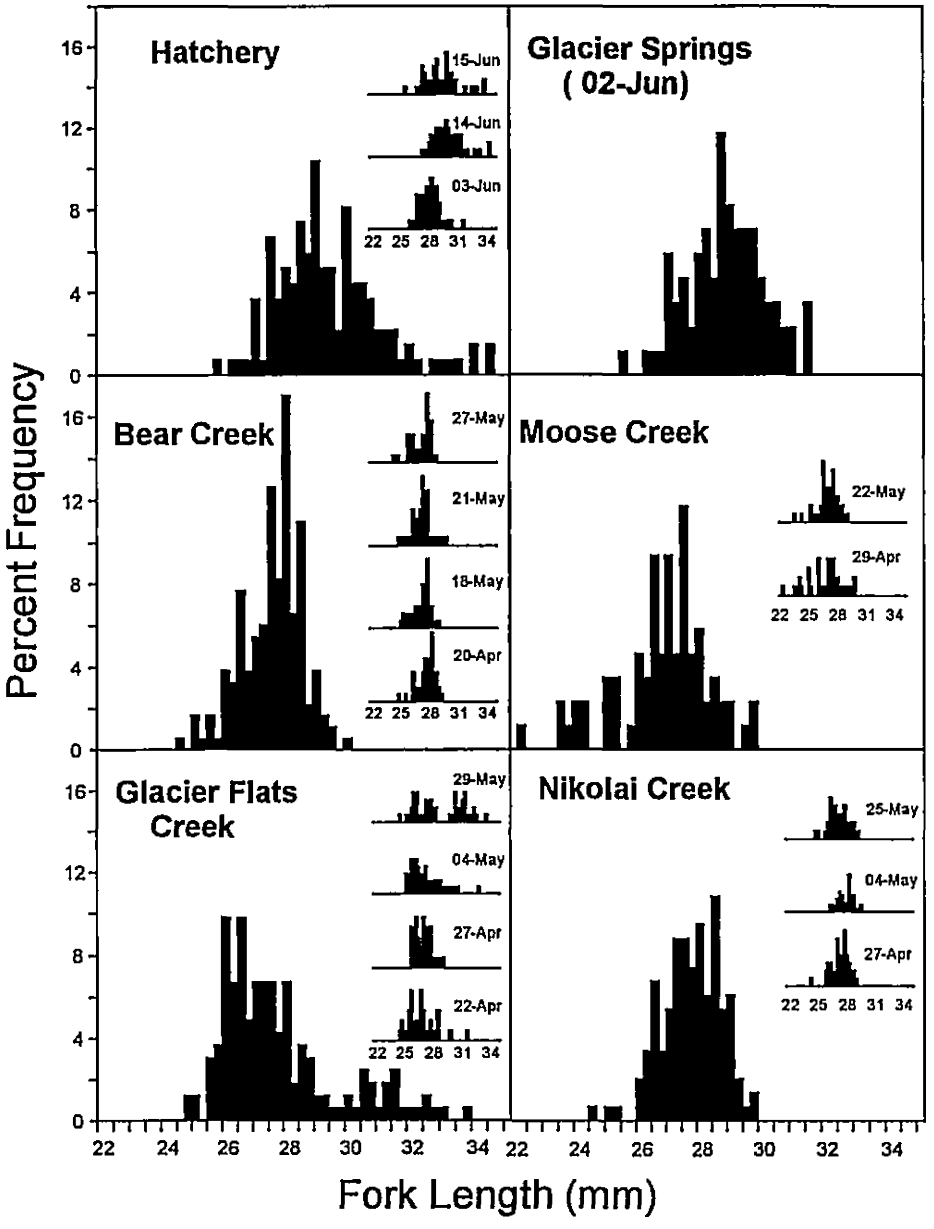

Figure 9. Percent frequency preserved length distributions of sockeye salmon fry used in otolith pattern analysis, Tustumena Lake, Alaska, 1992. Insert histograms are distributions by sample date for each location.

Pairwise comparisons (Tukey) among the other wild fry groups indicated that Moose Creek fry were smaller ($P < 0.001$; Figure 9) than other wild groups. Although thermographs were not run on Moose Creek, available data suggest that fry incubating in Moose Creek experienced lower water temperatures in the spring than did fry in the other tributaries. On 22 May, Moose Creek water temperatures were recorded as 3°C (2200 hr) and 1°C (0500 hr), as compared to Nikolai Creek (7°C -2200 hr; 3°C -0500 hr); 21 May Bear Creek (7°C -2200 hr; 2°C -0500 hr), and Glacier Flats Creek (5°C -2300 hr; 2.5°C -0500 hr). Observations indicated that ice and snow along Moose Creek's drainage persisted longer than on other creeks. This may have been due to shading from the more developed riparian vegetation in the form of large trees (*Populus* sp. and *Picea* sp.) on the Moose Creek drainage as compared to Bear, Glacier Flats, and Nikolai creeks. Data are not available to determine if the apparent thermal differences observed between Moose Creek and other drainages are consistent from year to year.

Variation among the tributary environments and fry behavior is also seen in the occurrence of feeding (J. Finn unpublished data). Little feeding, as indexed by the percentage of stomachs containing food items, was observed in Bear (0.2%), Moose (0.0 %), and Nikolai (0.7 %) creeks. On the other

hand 33.4 % of the Glacier Flats Creek and 86.0 % of the Glacier Springs fry stomachs contained food (predominantly chironomid larvae, pupae, and adults). It appeared that some proportion of the Glacier Flats Creek fry remain in the creek to feed prior to migrating to the lake. This may have resulted in the bimodal length distribution seen in the 29 May Glacier Flats sample (Figure 9). The Glacier Spring fry were similar to the late (29 May) Glacier Flats Creek fry in terms of percent feeding and yolk sac. As Glacier Springs fry were only sampled on a single date (02 June), it was not possible to determine if fry emerging earlier in the spring area had a lower incidence of feeding and higher proportions of yolk sacs. Moose Creek fry had a higher percentage of yolk sac than the other tributaries (Figure 10).

Assessment Of Normality

The distributions of the untransformed amplitude variables were all significantly non-normal (Lilleifor's Test; $D_{max} > 0.059$; $P < 0.001$; Table A-2). Square-root transformation normalized 73 of the 128 amplitudes, but 43% were still significantly non-normal (Table A-2). The Box-Cox power transformations normalized 122 of the amplitudes, leaving only 4.7% significantly non-normal (Table A-2; Figure 11). It appeared that the

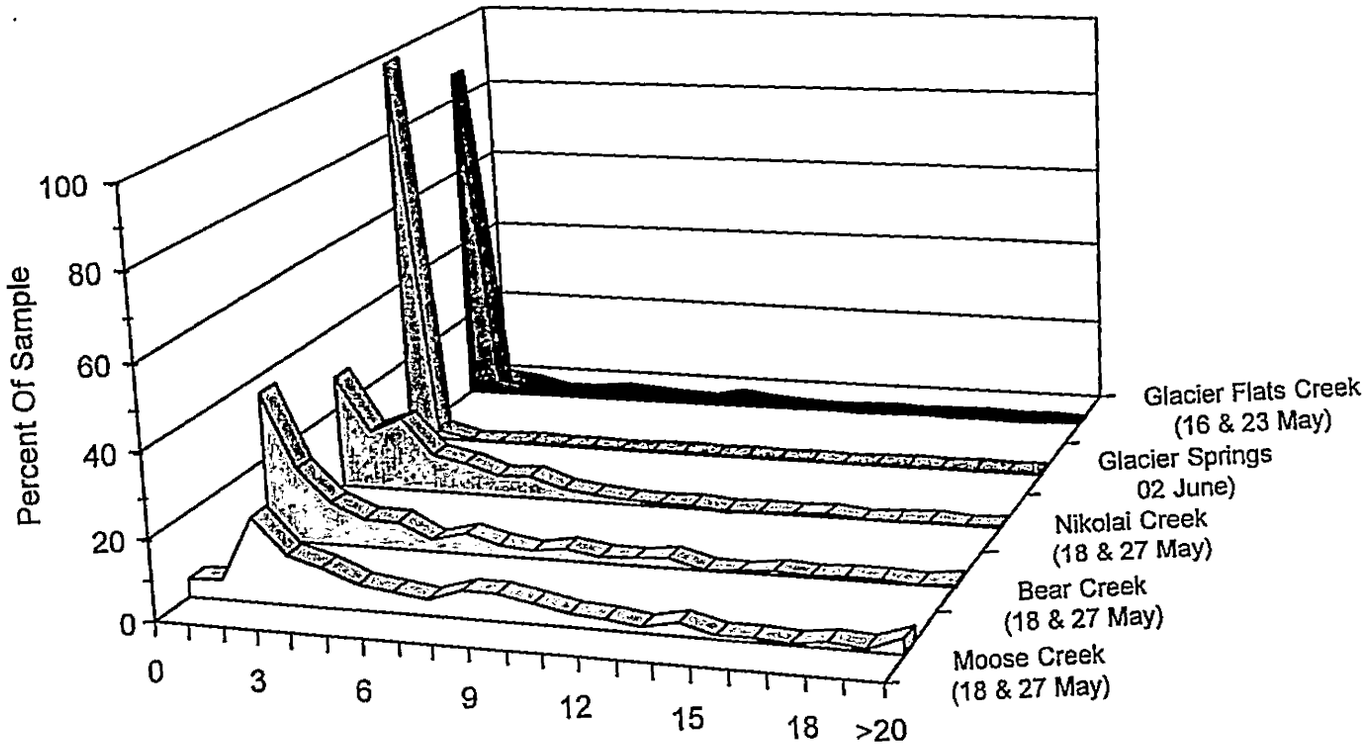

Figure 10. Yolk-sac weight as percent of total preserved (fromalin) weight for sockeye salmon fry, Tustumena Lake, Alaska, 1992. Sample dates in parentheses.

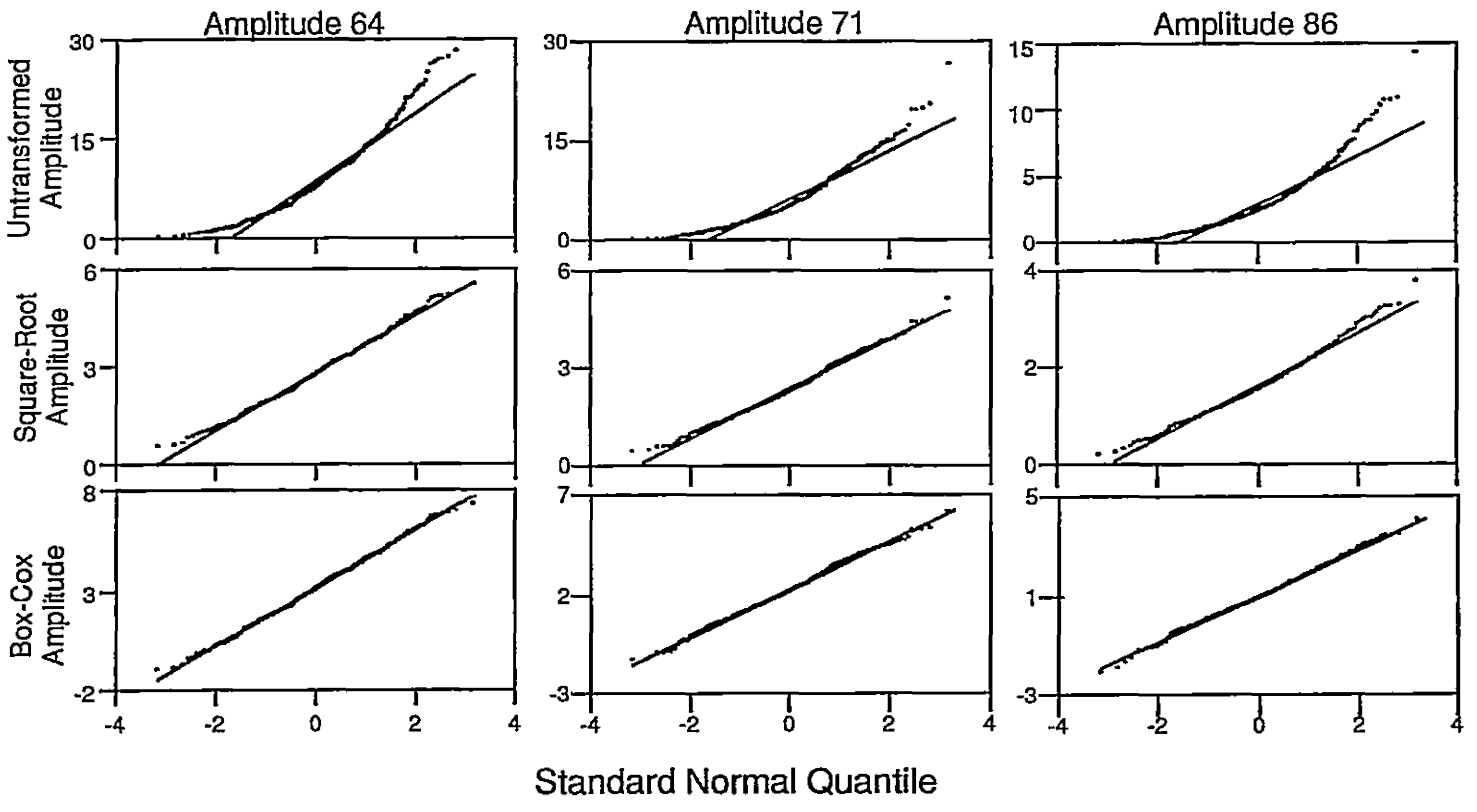

Figure 11. Normal probability plots for untransformed, square-root, and Box-Cox power transformed Fourier amplitude variables. Straight line represent the linear relationship between the amplitude variable and the standard normal quantile that is expected if the variable is normally distributed. Amplitudes 64, 71, and 81 are from a randomly selected otolith.

distributions of the amplitudes varied to such a degree that the individual assessment for transformation was necessary. Box-Cox transformed amplitudes were used in subsequent analyses, and further use of the word amplitude will refer to transformed values unless specifically stated.

Comparison Of Left and Right Otoliths and Observers

Amplitudes were not significantly affected by otolith position (left versus right) or observer. The difference between the two otoliths (left and right) was only significant (Randomized Block ANOVA; $P \leq 0.05$) for 13 (10.2%) out of the 128 amplitudes (Table A-3). Significant differences between observer measurements were found for only 3 (2.4%) out of 128 (Randomized Block ANOVA; $P \leq 0.05$) comparisons between the two observers (Table A-4). These results justified randomly using either left or right otoliths for discriminant analysis. Although not a rigorous test, it appears that the method used for feature extraction is repeatable and can be performed with limited instruction.

Hatchery versus Wild

Comparisons (ANOVA) of hatchery and wild amplitudes resulted in significant differences for 54 (42.2%) at the $P < 0.05$ level and 30 (23.4%) at the $P <$

0.01 level (Table A-5). Although hatchery amplitudes were neither consistently higher nor lower than wild amplitudes, the largest differences were seen in amplitudes 20 - 28 (Figure 12). Stepwise discriminant analysis initially selected 29 amplitudes. Of the 29 amplitudes selected by stepwise discriminant analysis, 18 (62.1%) were significantly different in the previous ANOVA. These subsets of amplitudes (30 from ANOVA and 29 from stepwise discrimination) formed the starting points for looping procedures to select more parsimonious subsets of amplitudes.

Linear Discriminant Analysis:

During the looping process on the 29 amplitudes selected by STEP DISCRIM, the total crossvalidation classification rates ranged from 0.646 to 0.861 for models with p = 29 through 1 (Table A-6; Figure 13). The models which resulted in the three highest total LDF classification rates (0.861, 0.860, and 0.859) included 24, 26, and 20 amplitudes. The LDF classification rates based on crossvalidation were > 84% for both hatchery and wild otoliths (Figure 13). However, when LDF was used to classify the test data the classification rates dropped (Table 2). The best classification of test data was 60.0% (hatchery) and 77.6% (wild) using the twenty amplitude model. As the assumption of equality of covariance's was rejected (Bartlet's log-likelihood

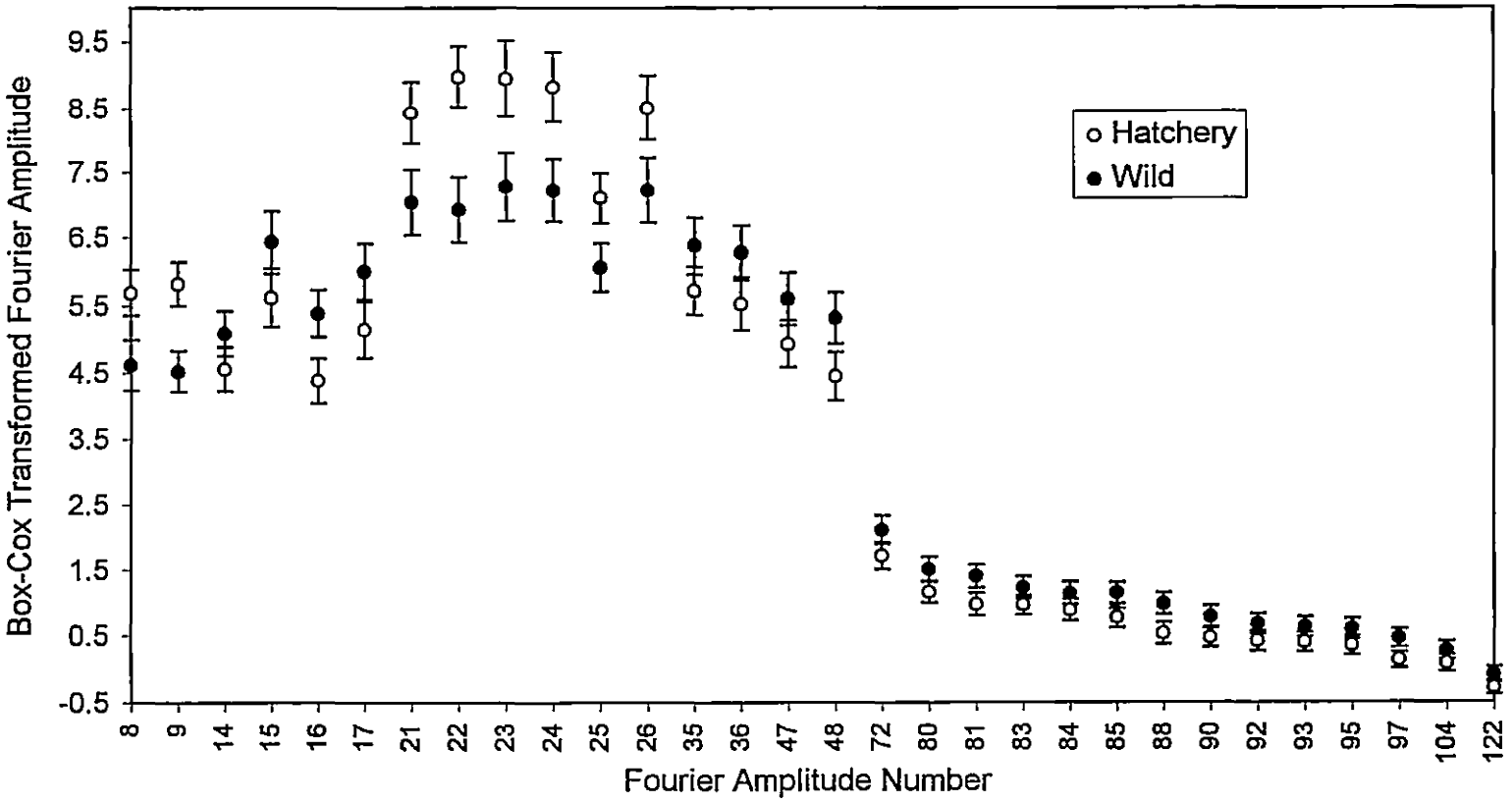

Figure 12. Mean and 95% confidence intervals for 30 highly significant (ANOVA, $P < 0.01$) Box-Cox transformed Fourier amplitudes from hatchery (solid circles) and wild (open circles) sockeye salmon fry otoliths, Tustumena Lake, Alaska.

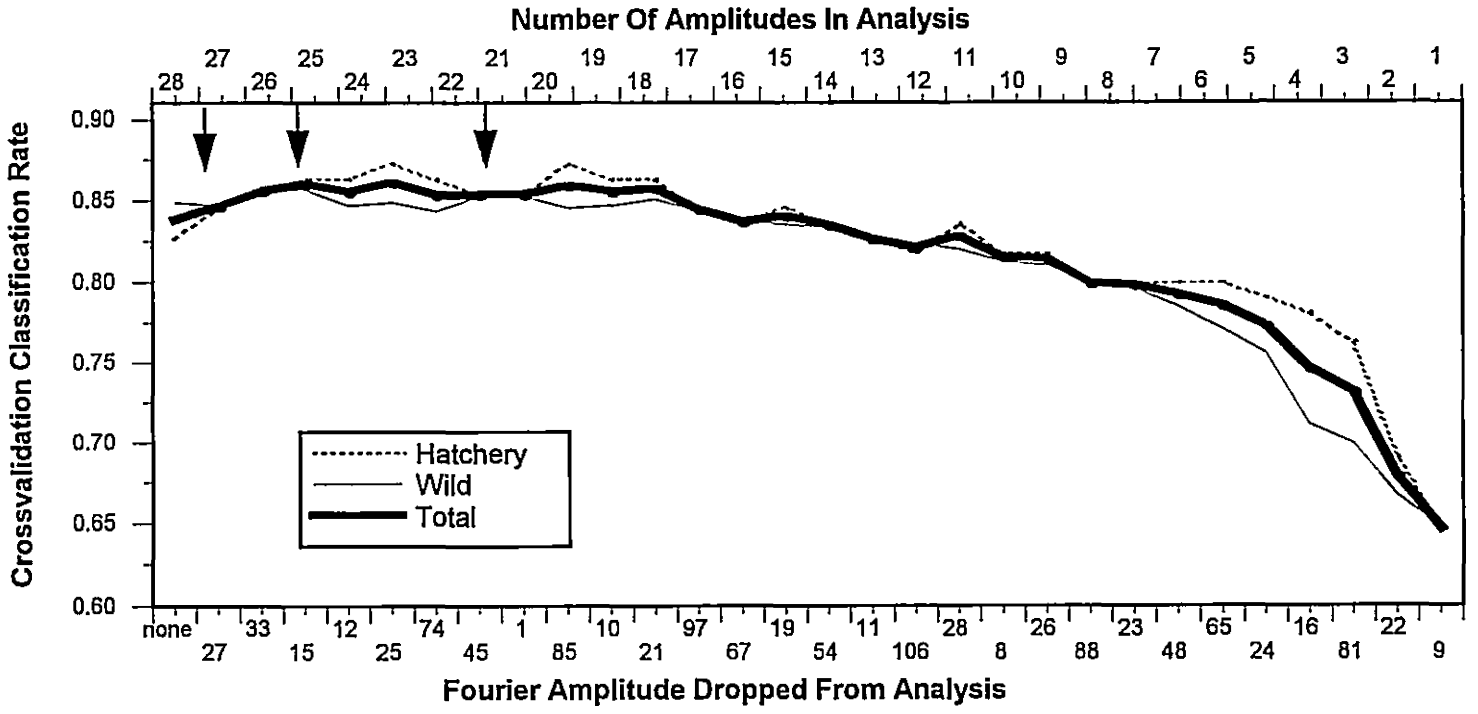

Figure 13. Crossvalidation classification rates (proportion correctly classified) for linear discriminant function analysis on Box-Cox transformed amplitudes from hatchery and wild sockeye salmon fry otoliths, Tustumena Lake, Alaska, 1992. The initial model included 29 amplitudes selected by stepwise discriminant analysis. At each analysis an additional amplitude was dropped (lower X axis), the upper X axis indicates the number of amplitudes used for each analysis. The arrows (upper X axis) indicate the models selected for comparison.

Table 2. Classification success, number and percent (in parentheses) correctly classified, using linear (LDF) and quadratic (QDF) discriminant analysis for hatchery and wild sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. Amplitude selection based on subsets from 29 amplitudes from stepwise LDF. Actual numbers of hatchery and wild otoliths were 110 and 516 (crossvalidation) and 25 and 125 (test data)

	Classification Success											
	Crossvalidation Estimate						Test Data					
	Hatchery		Wild		Total		Hatchery		Wild		Total	
Twenty Amplitude Models[1]	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent	Number	Percent
LDF	96	(87.3)	436	(84.5)	532	(85.0)	14	(56.0)	96	(76.8)	110	(73.3)
QDF	71	(64.5)	461	(89.3)	532	(85.0)	12	(48.0)	107	(85.6)	119	(79.3)
Twenty four Amplitude Models[2]												
LDF	96	(87.3)	438	(84.9)	534	(85.3)	15	(60.0)	97	(77.6)	112	(74.7)
QDF	66	(60.0)	476	(92.2)	542	(86.6)	9	(36.0)	110	(88.0)	119	(79.3)
Twenty six Amplitude Models[3]												
LDF	95	(86.4)	442	(85.7)	537	(85.8)	15	(60.0)	95	(76.0)	110	(73.3)
QDF	65	(59.1)	479	(92.8)	544	(86.9)	10	(40.0)	109	(87.2)	119	(79.3)

[1] Model included amplitudes: 8, 9, 10, 11, 16, 19, 21, 22, 23, 24, 26, 28, 48, 54, 65, 67, 81, 88, 97, and 106.

[2] Model included amplitudes: 1, 8, 9, 10, 11, 16, 19, 21, 22, 23, 24, 26, 28, 45, 48, 54, 65, 67, 74, 81, 85, 88, 97, and 106.

[3] Model included amplitudes: 1, 8, 9, 10, 11, 12, 16, 19, 21, 22, 23, 24, 25, 26, 28, 45, 48, 54, 65, 67, 74, 81, 85, 88, 97, and 106.

ratio, $P < 0.001$) a QDF discriminant rule appeared to be appropriate. However, QDF did not perform as well as LDF (Table 2). QDF resulted in higher correct classification of wild otoliths for both crossvalidation estimates and test data results. However, QDF did poorly in classification of hatchery otoliths, where test data classifications ranged from 36 - 48%. Therefore, use of the models selected from the stepwise variables would require that one ignore the apparent violation of the equality of covariance assumption and use LDF, or use QDF and accept hatchery classifications of < 65% (crossvalidation estimate) and < 50% (test data estimate).

Quadratic Discriminant Analysis:

Starting with the 30 highly significantly different (ANOVA, $P \leq 0.01$) amplitudes (Table 3), the models which resulted in the three highest QDF total crossvalidation classification rates included 11 (83.0%), 13 (82,7%), and 10 (82.6%) amplitudes (Table A-7). The QDF classification rates for the hatchery and wild otoliths did not converge until the total number of amplitudes in the model was reduced to 12 (Figure 14). In comparison to the previous models based on initial stepwise selection, the classifications were

Table 3. Mean and standard deviation (SD) for 30 highly significant (ANOVA, $P < 0.01$) Box-Cox transformed Fourier amplitudes of hatchery and wild sockeye salmon fry otoliths, Tustumena Lake, Alaska, 1992.

wild sockeye salmon otoliths, Tustumena Lake, Alaska, 1992.

	Hatchery		Wild	
Amplitude	Mean	SD	Mean	SD
8	5.69	1.79	4.62	2.01
9	5.82	1.72	4.53	1.64
14	4.56	1.77	5.09	1.76
15	5.62	2.25	6.43	2.50
16	4.39	1.77	5.39	1.86
17	5.15	2.20	6.00	2.17
21	8.43	2.53	7.04	2.67
22	8.98	2.41	6.92	2.67
23	8.95	3.00	7.28	2.78
24	8.82	2.76	7.22	2.56
25	7.10	2.04	6.05	1.87
26	8.50	2.60	7.22	2.64
35	5.71	1.87	6.38	2.27
36	5.53	2.05	6.28	2.15
47	4.93	1.83	5.60	2.05
48	4.45	1.95	5.32	2.02
72	1.71	1.07	2.11	1.20
80	1.15	0.87	1.51	0.99
81	0.97	0.91	1.40	0.94
83	0.95	0.78	1.23	0.91
84	0.88	0.88	1.14	0.94
85	0.76	0.78	1.14	0.88
88	0.53	0.87	0.98	0.88
90	0.46	0.75	0.78	0.89
92	0.42	0.77	0.67	0.80
93	0.40	0.74	0.63	0.79
95	0.35	0.75	0.60	0.81
97	0.13	0.63	0.45	0.72
104	0.08	0.64	0.27	0.70
122	-0.28	0.54	-0.08	0.61

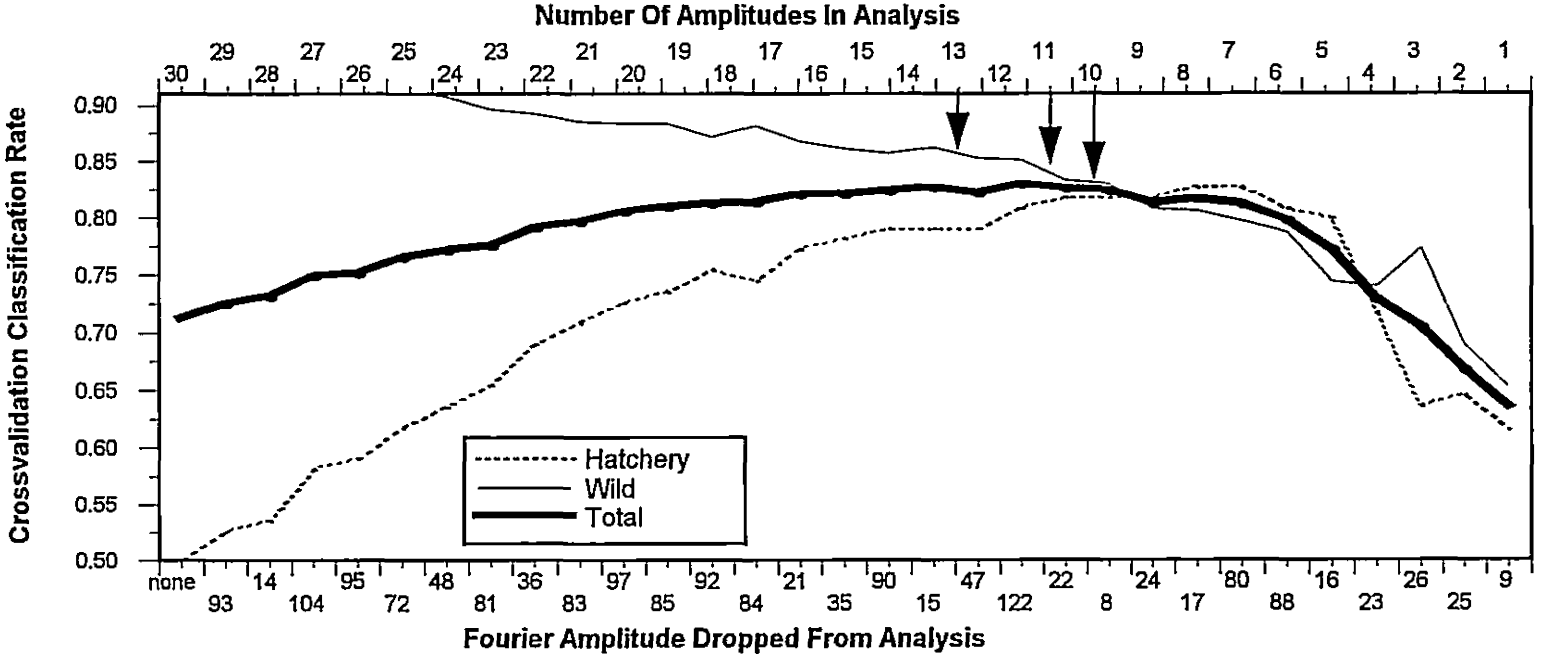

Figure 14. Crossvalidation classification rates (proportion correctly classified) for quadratic discriminant function analysis on Box-Cox transformed Fourier amplitudes from hatchery and wild sockeye salmon fry, Tustumena Lake, Alaska, 1992. The initial model include 30 amplitudes found to be significantly different (ANOVA, $P < 0.01$) between hatchery and wild fry otoliths. At each step an additional amplitude was dropped (lower X axis), the upper X axis indicates the number of amplitudes used at each step. The arrows (upper X axis) indicated models selected for comparison.

more consistent between hatchery and wild otoliths (Table 4). Use of QDF discrimination was supported by the rejection of the equality of covariance matrices assumption for three models (Bartlet's log-likelihood ratio, $P \leq 0.001$). It appeared that using separate group covariance matrices had little effect on the classification rates of hatchery and wild otoliths (Table 4). The exception was the 13 amplitude model where QDF resulted in 52% hatchery and 76.8% wild otolith test data classification.

The QDF 10 amplitude model was selected for further comparisons. Although the 13 and 11 amplitude models had higher total crossvalidation rates than the 10 amplitude model, none of the pairwise comparisons indicated a significant difference among the models (McNemar's test, $|z| \leq 1.567$, $P \geq 0.058$). The QDF 10 amplitude model resulted in nearly equal hatchery versus wild rates and allows for unequal covariance matrices.

Logistic Regression:

Logistic regression did not classify hatchery and wild otoliths as well as discriminant function analysis. Stepwise logistic regression selected 20 amplitudes. Although total crossvalidation classification rates ranged from 81.9 to 91.1%, there was a wide discrepancy between hatchery and wild

Table 4. Classification success, number and percent (in parentheses) correctly classified, using quadratic (QDF) discriminant classification for hatchery and wild sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. Amplitude selection based on subsets from the 30 most significantly different (ANOVA, $P < 0.01$) amplitudes. Actual numbers of hatchery and wild otoliths were 110 and 516 (crossvalidation) and 25 and 125 (test data).

	Classification Success								
	Crossvalidation Estimate			Test Data		
	Hatchery	Wild	Total	Hatchery	Wild	Total
Ten Amplitude Model[1]	90 (81.8)	430 (83.3)	520 (83.1)	19 (76.0)	90 (72.0)	109 (72.7)
Eleven Amplitude Models[2]	89 (80.9)	439 (85.1)	528 (84.3)	16 (64.0)	99 (79.2)	115 (76.7)
Thirteen Amplitude Models[3]	87 (79.1)	445 (86.2)	532 (85.0)	13 (52.0)	96 (76.8)	109 (72.7)

[1] Model included amplitudes: 8, 9, 16, 17, 23, 24, 25, 26, 80, and 88.

[2] Model included amplitudes: 8, 9, 16, 17, 22, 23, 24, 25, 26, 80, and 88.

[3] Model included amplitudes: 8, 9, 16, 17, 22, 23, 24, 25, 26, 47, 80, 88, and 122.

otolith classifications (Table A-8; Figure 15). Wild otoliths were classified correctly > 95% even when only one amplitude was used. However, the best hatchery classification was 64.5% using both 19 and 18 amplitudes (Table A-8). Logistic regression does not predict group membership per se, rather it models the probability of an event (in this case hatchery origin). Therefore, the apparently high wild classification rates are actually the models inability of predicting a hatchery event so that most observations were classified as non-events (i.e., wild origin).

Model Comparisons:

The previous analyses resulted in one model that warranted further comparison. The models produced from stepwise LDF were not considered as the assumption of homogeneity was not met. Although the stepwise QDF total classifications ranged from 85.0 - 86.9%, the difference between hatchery and wild classifications was > 24.8% (Table 2). Logistic regression models were not considered due to the disparity between the hatchery and wild otolith classification rates (Table A-8, Figure 15). On the other hand the 10 amplitude QDF model from the looping process (10-QDF) using the 30 most significant (ANOVA) amplitudes met model selection criteria (Table 4).

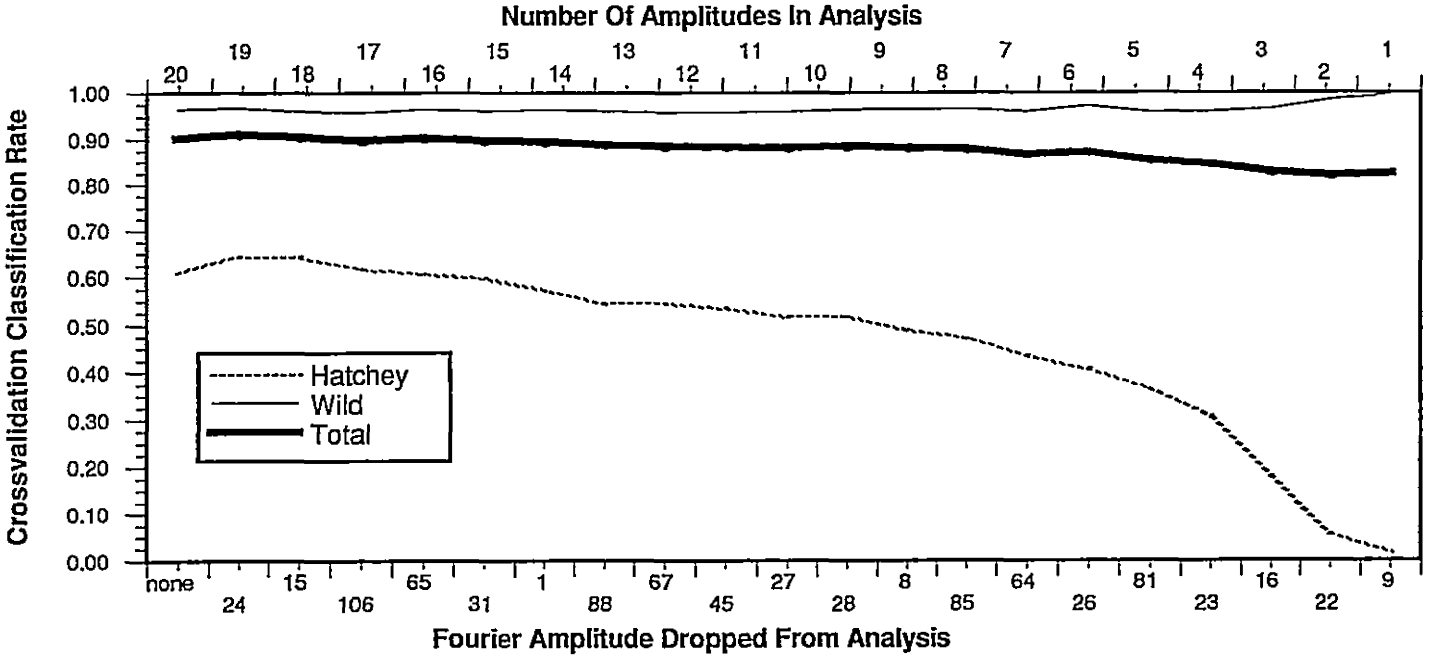

Figure 15. Logistic regression crossvalidation classification rates (proportion correctly classified) of hatchery and wild sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. At each step an additional amplitude was dropped (lower X axis), the upper X axis indicates the number of amplitudes used at each step.

Using the group mean amplitudes, the proportions of the total hatchery and wild luminance profiles explained by the Fourier harmonics associated with the 10 amplitudes in model 10-QDF were 0.152 and 0.120 (Table A-9). Therefore, the classifications rates that were realized with model 10-QDF were based on approximately 12.0-15.2% of the total variation of the luminance profiles. The proportions of otoliths from individual wild locations that were classified to hatchery origin ranged from 0.127 to 0.201 (Figure 16, Table 5). These proportions were not significantly different ($\chi^2 = 3.39$, df = 4, $P > 0.495$). Therefore, it appeared that none of the wild groups were disproportionately misclassified to hatchery origin.

It did not appear that the 10-QDF model classification of wild otoliths was affected by sample date. To determine if sample date affected classification, I examined the proportions of wild otoliths classified to hatchery and wild origin for individual locations by sample date (Table 6). There was no indication that date affected the classification of Bear Creek otoliths ($\chi^2 = 4.44$, df = 3, $P = 0.217$). Although Glacier Flats otoliths showed more variation over the sample dates, the differences were not significant ($\chi^2 = 6.45$, df = 3, $P = 0.092$). The Moose and Nikolai creeks classifications also were not

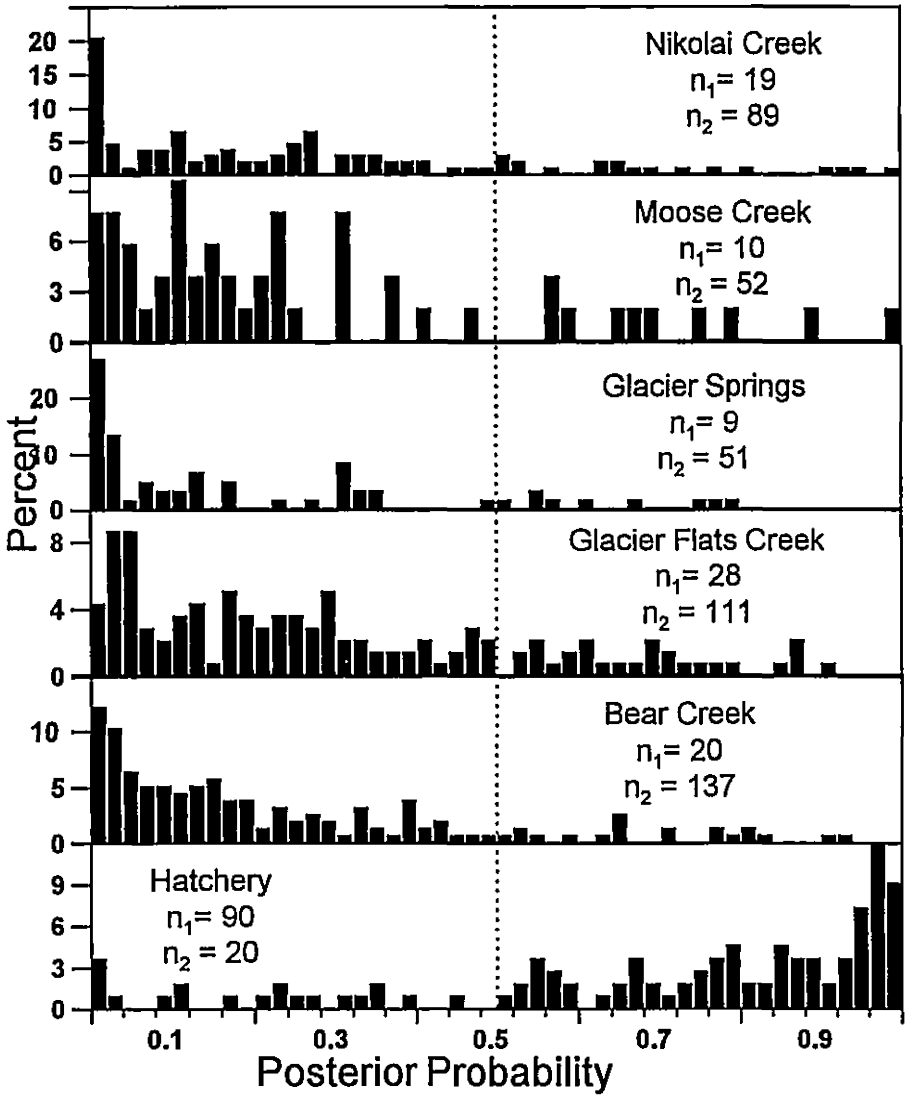

Figure 16. Distributions of crossvalidation posterior probabilities of otoliths being classified to hatchery origin for six groups of sockeye salmon fry from Tustumena Lake, Alaska. Probabilities based on quadratic discriminant analysis using Box-Cox transformed Fourier amplitudes: 8, 9, 16, 17, 22, 23, 24, 25, 26, 80, and 88. Labels indicate true origin, n_1 = number classified as hatchery, n_2 = number classified as wild. Observations falling to the right of the vertical dashed line (0.5 probability level) were classified as hatchery.

Table 5. Numbers and proportions (in parentheses) of wild sockeye salmon fry otoliths classified into hatchery and wild origin (Classification Location) based on quadratic discriminant analysis using 10 Box-Cox transformed Fourier amplitudes. The number classified to hatchery represents misclassified individuals. Proportions are within each wild group.

Classification Location	Location Of True Origin					Total
	Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek	
Hatchery	20 (0.127)	28 (0.201)	9 (0.150)	10 (0.192)	19 (0.176)	86
Wild	137 (0.873)	111 (0.799)	51 (0.850)	42 (0.808)	89 (0.824)	430
Total	157	139	60	52	108	516

Table 6. Numbers and proportions (in parentheses) of wild sockeye salmon fry otoliths by sampling date classified into hatchery and wild origin (classification location) based on quadratic discriminant analysis using 10 Box-Cox transformed Fourier amplitudes. Number classified as hatchery represents misclassified individuals. Proportions are with each wild group and date.

Location Of True Origin	Classification Location	Date			
		20-Apr	18-May	21-May	02-Jun
Bear Creek	Hatchery	5 (0.13)	2 (0.05)	7 (0.21)	6 (0.14)
	Wild	34 (0.87)	39 (0.95)	26 (0.79)	38 (0.86)
		22-Apr	27-Apr	04-May	29-May
Glacier Flats Creek	Hatchery	2 (0.05)	6 (0.15)	7 (0.21)	13 (0.30)
	Wild	25 (0.64)	23 (0.56)	42 (1.27)	41 (0.93)
		29-Apr	22-May		
Moose Creek	Hatchery	4 (0.10)	6 (0.15)		
	Wild	19 (0.49)	23 (0.56)		
		27-Apr	04-May	25-May	
Nikolai Creek	Hatchery	5 (0.13)	8 (0.20)	6 (0.18)	
	Wild	29 (0.74)	32 (0.78)	28 (0.85)	

significantly different among the sample dates ($\chi^2 = 0.716$, df = 1, $P = 0.398$; and $\chi^2 = 0.355$, df = 2, $P = 0.837$).

In six out of the 10 amplitudes used in the 10-QDF model, hatchery means were greater than wild means (Figure 17). The average profile of the hatchery standardized luminance values appeared to have more pronounced banding than the wild profile, particularly in the first 60 - 70 µm of the transect (Figure 18a). When luminance profiles were reconstructed using only the Fourier harmonics associated with the 10 amplitudes in the 10-QDF model, this trend is accentuated (Figure 18b). It is possible that regular hatchery practices, such as: cleaning, application of fungicides, and artificial light cycles, resulted in a more distinct banding pattern. As the hatchery water supply is directly from Crooked Creek's water column, water temperature may have fluctuated more widely than in the more buffered intergravel environment (Figure 2).

Six Group Classification

When the amplitudes were tested for differences among the six groups (i.e., Hatchery, Bear Creek, Glacier Flats Creek, Glacier Springs, Moose Creek, and Nikolai Creek), 105 (80.0%) were significantly different (ANOVA, $P \leq$

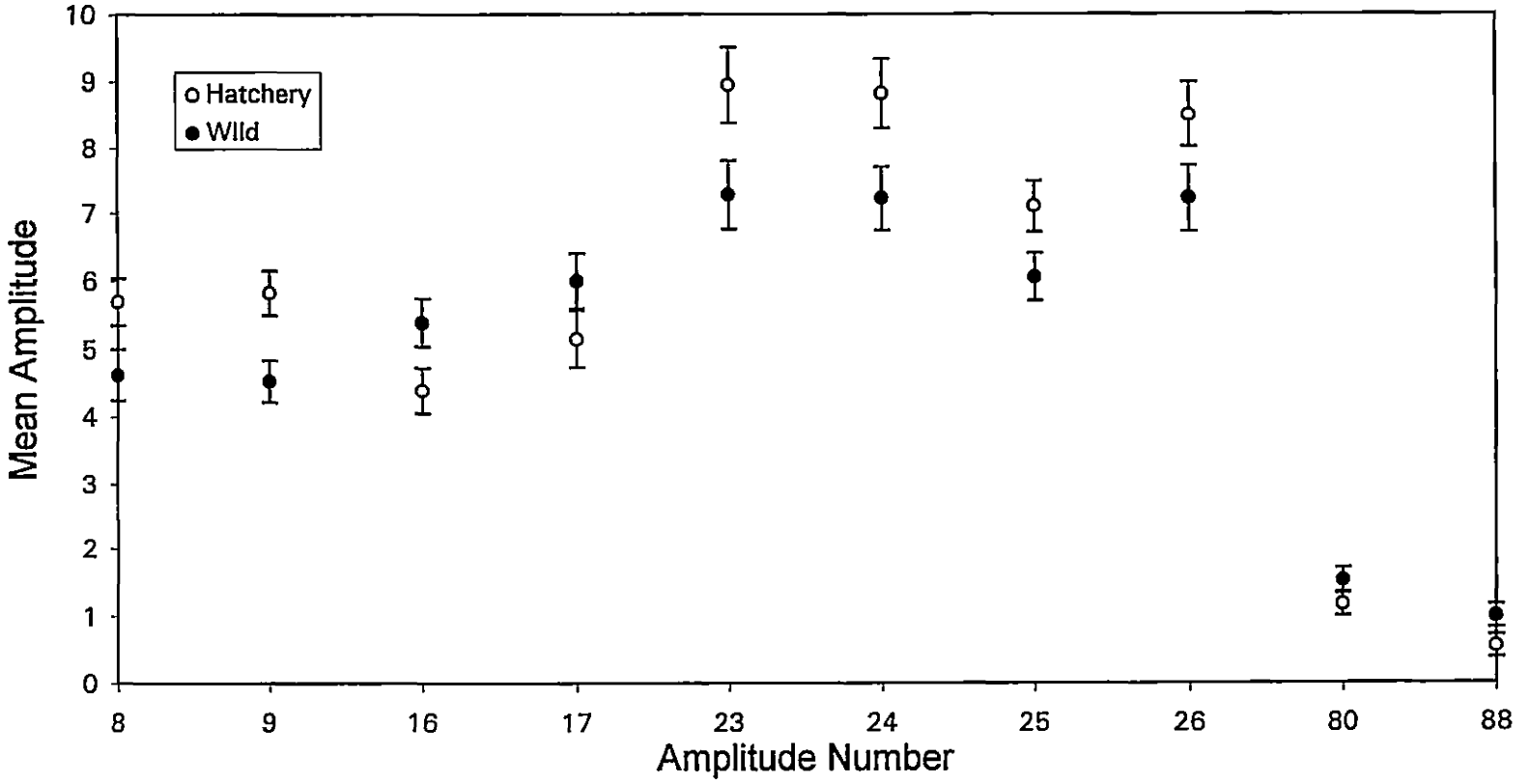

Figure 17. Means and 95% confidence intervals (vertical bars) of Box-Cox transformed Fourier amplitudes hatchery and wild origin sockeye salmon fry otoliths used in quadratic discriminant analysis.

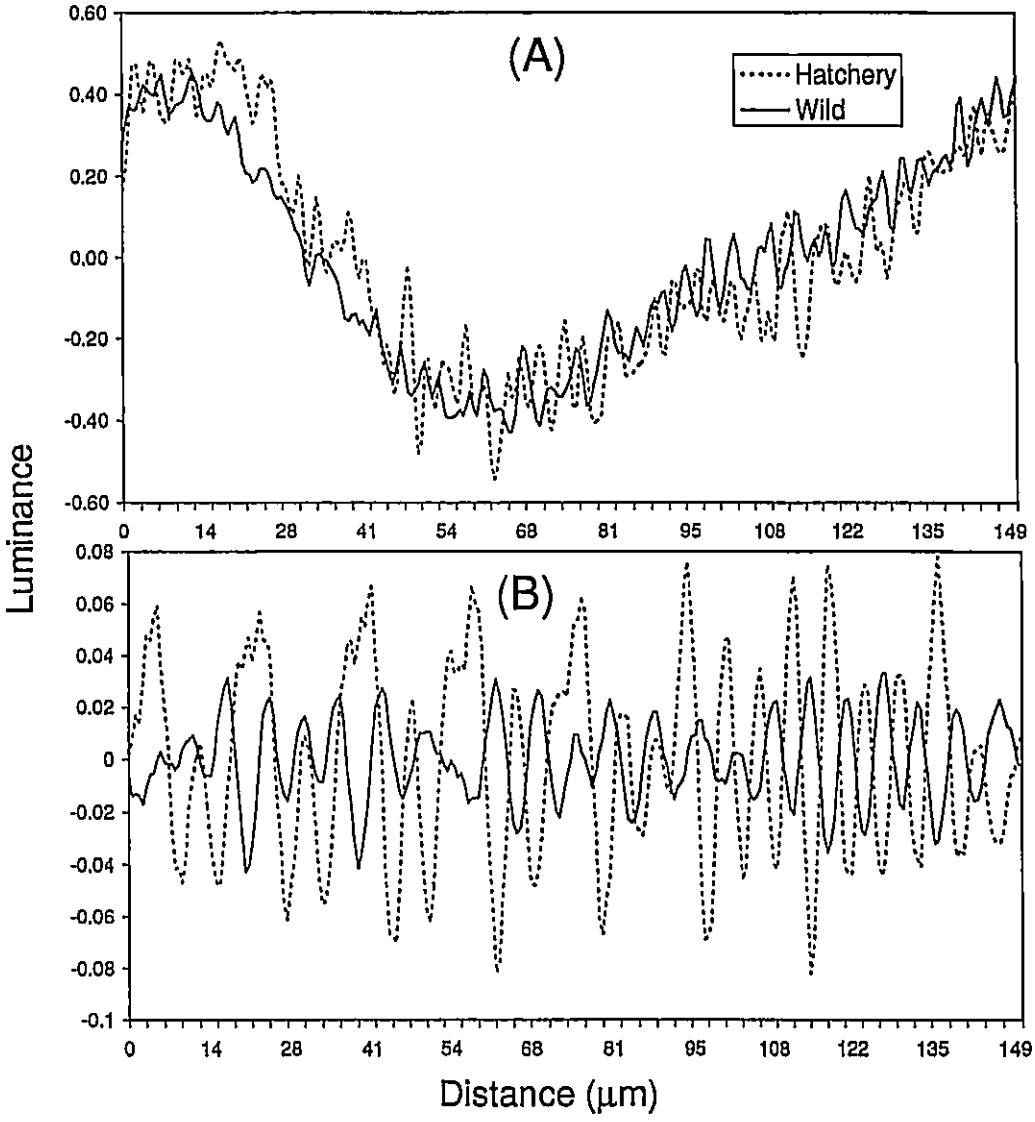

Figure 18. (A) mean standardized hatchery and wild sockeye salmon fry otolith luminance profiles; and (B) reconstruction of mean standardized hatchery and wild sockeye salmon fry otolith luminance profiles based on the Fourier harmonics associated with amplitudes 8, 9, 16, 17, 23, 24, 25, 26, 80, and 88.

0.05), and 90 (70.3%) were highly (ANOVA, $P \leq 0.01$) significant (Table A-10). Stepwise discriminant analysis initially selected 43 amplitudes. The starting points for the looping procedures were the 43 amplitudes selected by stepwise discrimination and the 40 most significantly different (ANOVA) amplitudes. The choice of 40 amplitudes from the ANOVA results was essentially to provide approximately the same number of amplitudes as were selected by stepwise discrimination (43). As the minimum group size was 52 (Moose Creek), my goal was to determine if models using $p \leq 3/52 = 17$ amplitudes had potential for discriminating among all six groups.

Linear Discriminant Analysis:

Starting with the 43 amplitudes selected by stepwise discrimination, 44 LDF model were evaluated during the looping procedure. Total crossvalidation classification rates ranged from 0.247 to 0.550 (Table A-11). No distinct peak was evident and the general trend was a decline from a total rate of 0.533 to 0.443 from the 43 through the 7 amplitude model (Figure 19). The total classification rate declined rapidly with fewer than 7 amplitudes. Hatchery, Glacier Springs, and Nikolai Creek otoliths were correctly classified at rates > 0.50 for all but the $p < 5$ models (Figure 19). Bear, Glacier Flats, and Moose

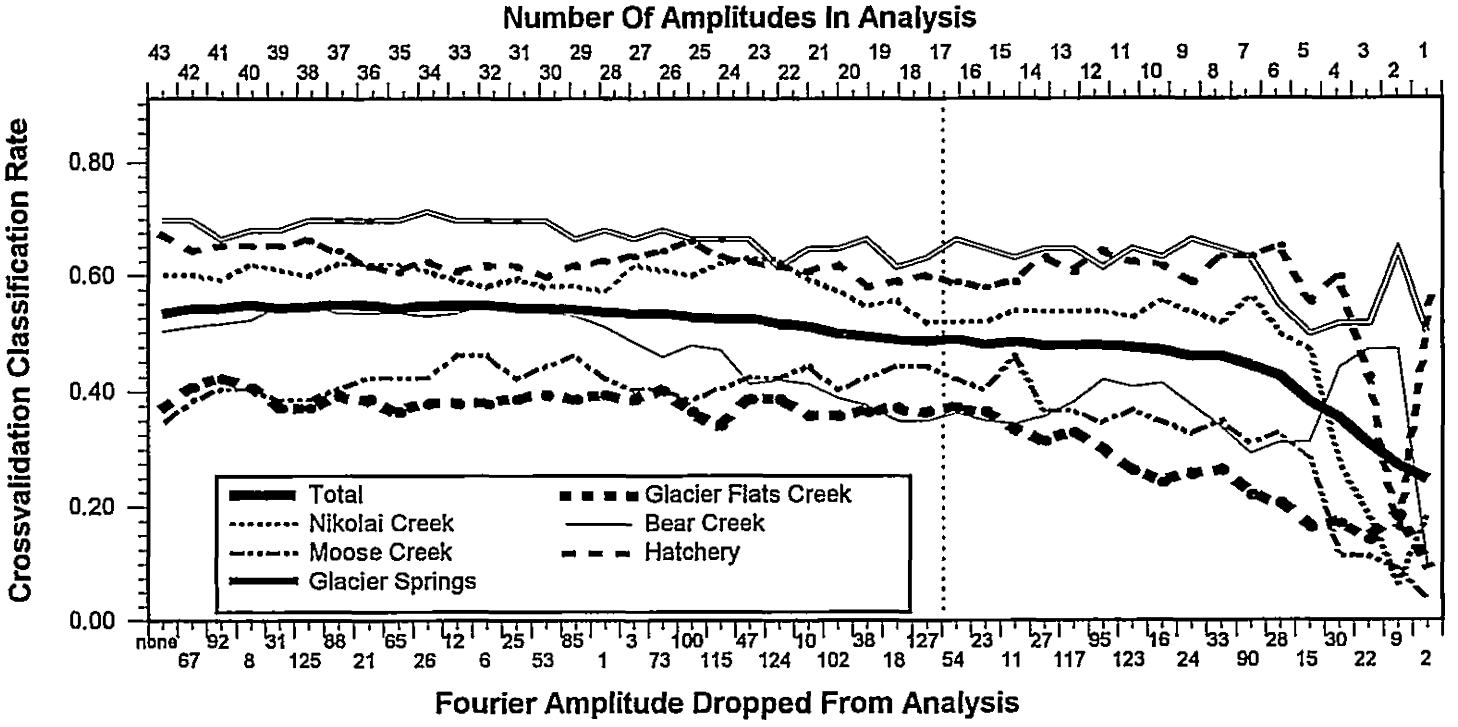

Figure 19. Crossvalidation classification rates (proportion correctly classified) for linear discriminant function analysis on Box-Cox transformed amplitudes from six groups of sockeye salmon fry otoliths, Tustumena Lake, Alaska, 1992. The initial model included 43 amplitudes selected by stepwise discriminant analysis. At each analysis an additional amplitude was dropped (lower X axis), the upper X axis indicates the number of amplitudes used for each analysis. The vertical dashed line indicates the $n_i/3 = 17$ variable model.

creeks otoliths classified at lower than the total rate for all but the $p < 5$ amplitude models.

When the restriction of $p \leq 17$ amplitudes was considered, the three highest total LDF crossvalidation rates occurred with the 16 (48.9%), 17 (48.5%), and 14 (48.4%) amplitude models (Table A-11). Covariance matrices were significantly different (Bartlet's log-likelihood ratio, $P \leq 0.017$) for the 16 and 17 amplitude models, but were not significantly different ($P = 0.102$) for the 14 amplitude model. Therefore, the 14 amplitude LDF, 16 and 17 amplitude QDF models were compared. Crossvalidation classification rates ranged from: 52.7 - 59.1% (Hatchery); 34.4 - 40.8 (Bear Creek); 33.8% (Glacier Flats Creek); 40.0 - 63.3% (Glacier Springs); 13.46 - 46.2% (Moose Creek); and 21.15 - 53.7% (Nikolai Creek; Tables 7 - 9). Comparisons of the three models indicated that the total crossvalidation rate of the 14 amplitude LDF model total was significantly higher than the 16 (McNemar's test, $z = 3.482$, $P < 0.001$) and 17 (McNemar's test, $z = 3.064$, $P < 0.001$) amplitude QDF models (Table 10). There was no significant difference between the crossvalidation rates of the 16 and 17 QDF models (McNemar's test, $z = -0.762$, $P = 0.223$). The test data total classification rates were similar for all three models

Table 7. Linear discriminant function crossvalidation and test data classification success, number and percent (in parentheses) for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox Fourier amplitudes. Number of amplitudes in model[1] = 14; selected from 43 amplitudes from stepwise discrimination. Actual totals are the true number of otoliths from each location, estimated totals are the number classified into each location.

Crossvalidation Results

	Classification Success												Actual
Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Total
Hatchery	65	(59.09)	10	(9.09)	15	(13.64)	4	(3.64)	10	(9.09)	6	(5.45)	110
Bear Creek	12	(7.64)	54	(34.39)	16	(10.19)	17	(10.83)	26	(16.56)	32	(20.38)	157
Glacier Flats Creek	18	(12.95)	17	(12.23)	47	(33.81)	27	(19.42)	17	(12.23)	13	(9.35)	139
Glacier Springs	5	(8.33)	3	(5.00)	8	(13.33)	38	(63.33)	5	(8.33)	1	(1.67)	60
Moose Creek	7	(13.46)	5	(9.62)	3	(5.77)	5	(9.62)	24	(46.15)	8	(15.38)	52
Nikolai Creek	9	(8.33)	17	(15.74)	5	(4.63)	6	(5.56)	13	(12.04)	58	(53.70)	108
Estimated Total	116		106		94		97		95		118		

Test Data Results

	Classification Success												Actual
Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Total
Hatchery	13	(52.00)	2	(8.00)	4	(16.00)	1	(4.00)	3	(12.00)	2	(8.00)	25
Bear Creek	1	(4.00)	5	(20.00)	4	(16.00)	6	(24.00)	4	(16.00)	5	(20.00)	25
Glacier Flats Creek	3	(12.00)	5	(20.00)	3	(12.00)	7	(28.00)	5	(20.00)	2	(8.00)	25
Glacier Springs	4	(16.00)	0	(0.00)	7	(28.00)	14	(56.00)	0	(0.00)	0	(0.00)	25
Moose Creek	3	(12.00)	8	(32.00)	3	(12.00)	1	(4.00)	5	(20.00)	5	(20.00)	25
Nikolai Creek	4	(16.00)	3	(12.00)	3	(12.00)	1	(4.00)	0	(0.00)	14	(56.00)	25
Estimated Total	28		23		24		30		17		28		

[1] Amplitudes in model: AMP2, AMP9, AMP15, AMP16, AMP22, AMP24, AMP27, AMP28, AMP30, AMP33, AMP90, AMP95, AMP117, and AMP123.

Table 8. Quadratic discriminant function crossvalidation and test data classification success, number and percent (in parentheses) for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox Fourier amplitudes. Number of amplitudes in model1 = 16; selected from 43 amplitudes from stepwise discrimination. Actual totals are the true number of otoliths from each location, estimated totals are the number classified into each location.

Crossvalidation Results

Classification Success

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	58	(52.73)	16	(14.55)	16	(14.55)	4	(3.64)	5	(4.55)	11	(10.00)	110
Bear Creek	14	(8.92)	60	(38.22)	19	(12.10)	11	(7.01)	24	(15.29)	29	(18.47)	157
Glacier Flats Creek	15	(10.79)	27	(19.42)	47	(33.81)	23	(16.55)	14	(10.07)	13	(9.35)	139
Glacier Springs	3	(5.00)	9	(15.00)	15	(25.00)	25	(41.67)	3	(5.00)	5	(8.33)	60
Moose Creek	11	(21.15)	13	(25.00)	6	(11.54)	3	(5.77)	7	(13.46)	12	(23.08)	52
Nikolai Creek	7	(6.48)	31	(28.70)	13	(12.04)	6	(5.56)	10	(9.26)	41	(37.96)	108
Estimated Total	108		156		116		72		63		111		

Test Data Results

Classification Success

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	14	(56.00)	1	(4.00)	2	(8.00)	3	(12.00)	3	(12.00)	2	(8.00)	25
Bear Creek	5	(20.00)	5	(20.00)	5	(20.00)	0	(0.00)	3	(12.00)	7	(28.00)	25
Glacier Flats Creek	4	(16.00)	3	(12.00)	6	(24.00)	3	(12.00)	5	(20.00)	4	(16.00)	25
Glacier Springs	4	(16.00)	2	(8.00)	5	(20.00)	12	(48.00)	2	(8.00)	0	(0.00)	25
Moose Creek	2	(8.00)	8	(32.00)	3	(12.00)	3	(12.00)	3	(12.00)	6	(24.00)	25
Nikolai Creek	4	(16.00)	5	(20.00)	1	(4.00)	1	(4.00)	1	(4.00)	13	(52.00)	25
Estimated Total	33		24		22		22		17		32		

[1] Ampiltudes in model: AMP2, AMP9, AMP11, AMP15, AMP16, AMP22, AMP23, AMP24, AMP27, AMP28, AMP30, AMP33, AMP90, AMP95, AMP117, and AMP123.

Table 9. Quadratic discriminant function crossvalidation and test data classification success, number and percent (in parentheses) for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox Fourier amplitudes. Number of amplitudes in model1 = 17; selected from 43 amplitudes from stepwise discrimination. Actual totals are the true number of otoliths from each location, estimated totals are the number classified into each location.

Crossvalidation Results Classification Success													
Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	59	(53.64)	18	(16.36)	15	(13.64)	7	(6.36)	4	(3.64)	7	(6.36)	110
Bear Creek	14	(8.92)	64	(40.76)	20	(12.74)	14	(8.92)	17	(10.83)	28	(17.83)	157
Glacier Flats Creek	14	(10.07)	26	(18.71)	47	(33.81)	24	(17.27)	13	(9.35)	15	(10.79)	139
Glacier Springs	4	(6.67)	9	(15.00)	14	(23.33)	24	(40.00)	5	(8.33)	4	(6.67)	60
Moose Creek	11	(21.15)	9	(17.31)	8	(15.38)	4	(7.69)	9	(17.31)	11	(21.15)	52
Nikolai Creek	6	(5.56)	32	(29.63)	13	(12.04)	5	(4.63)	12	(11.11)	40	(37.04)	108
Estimated Total	108		158		117		78		60		105		

Test Data Results Classification													
Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	12	(48.00)	1	(4.00)	3	(12.00)	4	(16.00)	2	(8.00)	3	(12.00)	25
Bear Creek	4	(16.00)	6	(24.00)	6	(24.00)	0	(0.00)	3	(12.00)	6	(24.00)	25
Glacier Flats Creek	4	(16.00)	2	(8.00)	7	(28.00)	2	(8.00)	5	(20.00)	5	(20.00)	25
Glacier Springs	3	(12.00)	2	(8.00)	2	(8.00)	16	(64.00)	2	(8.00)	0	(0.00)	25
Moose Creek	2	(8.00)	10	(40.00)	3	(12.00)	1	(4.00)	2	(8.00)	7	(28.00)	25
Nikolai Creek	3	(12.00)	4	(16.00)	1	(4.00)	2	(8.00)	2	(8.00)	13	(52.00)	25
Estimated Total	28		25		22		25		16		34		

[1] Amplitudes in model: AMP2, AMP9, AMP11, AMP15, AMP16, AMP22, AMP23, AMP24, AMP27, AMP28, AMP30, AMP33, AMP54, AMP90, AMP95, AMP117, and AMP123.

Table 10. Total crossvalidation and test data classification rates (proportion correctly classified) using linear (LDF) and quadratic (QDF) discriminant analysis on Box-Cox transformed Fourier amplitudes from sockeye salmon fry otoliths, Tustumena Lake, Alaska.

Model[1]	Crossvaldation	Test Data
17 Amplitudes		
QDF	0.388	0.373
16 Amplitudes		
QDF	0.380	0.353
14 Amplitudes		
LDF	0.457	0.360

[1]Models selected by looping procedure starting with 43 amplitudes selected by stepwise LDF.

(McNemar's test, $|z| \leq 0.832$, $P \geq 0.203$). Based on these results, the 14 amplitude LDF (14-LDF) model was selected.

Quadratic Discriminant Analysis:

Using the 40 most significant (Table 11, Table A-10) amplitudes, a total of 41 QDF models were evaluated during the looping procedure. The total crossvalidation classification rates appeared to be relatively stable through the 40 - 10 amplitude models (Figure 20), ranging from 0.294 to 0.417 (Table A-12). Increases in the classification rate were primarily due to improvement in the rates for Glacier Springs and Moose Creek.

The three highest classifications occurred with the 17 (42.2%), 15 (43.0%), and 14 (42.4%) amplitudes models (Table A-12, Figure 20). The use of QDF was justified as, the covariance matrices were significantly different for all three models (Bartlet's log-likelihood ratio, $P < 0.001$). QDF crossvalidation rates ranged from: 47.3 - 49.1% (Hatchery); 42.7 - 48.4% (Bear Creek); 34.5 - 41.0% (Glacier Flats Creek); 43.3 - 51.7% (Glacier Springs); 21.2 - 28.8% (Moose Creek); and 47.2 - 50.0% (Nikolai Creek; Tables 12 - 14). Test data classification resulted in a maximum total classification of 33.3% (Table 13) and an individual location maximum classification of 48.0% (Nikolai Creek;

Table 11. Mean and standard deviation (SD) for the 40 most significant (ANOVA, $P < 0.01$) Box-Cox transformed Fourier amplitudes for six groups of sockeye salmon fry otoliths, Tustumena Lake, Alaska. Number in parentheses next to location names indicate sample size.

	Hatchery (110)		Bear Creek (157)		Glacier Flats Creek (139)		Glacier Springs (60)		Moose Creek (52)		Nikolai Creek (108)	
Amplitude	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	19.02	4.03	17.31	4.78	19.94	5.83	19.67	6.32	19.79	5.21	21.42	5.81
2	4.46	1.27	3.71	1.09	5.16	1.43	5.68	1.28	3.97	1.06	3.94	1.08
3	4.10	1.69	3.55	1.49	4.52	1.64	5.36	1.61	4.36	1.59	4.09	1.54
5	5.20	1.84	4.06	1.76	5.24	2.13	4.90	2.29	4.27	2.10	4.84	2.01
6	3.98	1.52	3.54	1.37	3.98	1.68	4.11	1.27	3.91	1.27	4.62	1.76
8	5.69	1.79	4.31	1.85	4.42	1.94	4.44	1.93	4.45	1.96	5.50	2.17
9	5.82	1.72	4.22	1.50	4.56	1.64	3.96	1.58	4.50	1.54	5.26	1.69
10	4.90	1.49	4.34	1.35	4.24	1.61	4.04	1.31	4.49	1.45	5.33	1.68
11	5.05	1.71	5.38	1.87	5.07	1.76	4.62	1.60	4.95	1.87	6.01	1.96
12	5.18	1.94	5.80	2.13	5.22	2.16	5.02	2.04	5.09	2.07	6.56	2.02
16	4.39	1.77	5.27	1.77	5.58	1.83	5.17	1.85	5.48	1.92	5.39	1.98
21	6.43	2.53	6.80	2.55	7.11	2.80	6.75	2.62	7.06	2.67	7.45	2.70
22	6.98	2.41	6.70	2.54	7.43	2.67	6.70	2.64	6.81	2.74	6.77	2.79
23	8.95	3.00	7.14	2.89	7.69	2.93	6.87	2.71	6.93	2.60	7.35	2.49
24	6.82	2.76	7.24	2.58	7.26	2.54	7.11	2.40	7.95	3.01	6.86	2.36
25	7.10	2.04	6.17	1.80	6.18	2.08	5.87	1.94	6.07	1.82	5.83	1.66
26	8.50	2.60	7.11	2.63	7.84	2.57	6.47	2.42	7.49	2.94	6.88	2.60
27	8.21	2.44	7.44	2.97	8.28	2.52	7.84	2.66	7.56	2.50	6.38	2.28
28	10.13	3.32	9.48	3.48	9.79	3.92	10.70	3.44	9.89	3.83	8.04	2.99
30	7.77	2.42	7.64	2.73	7.76	2.47	7.94	2.72	8.57	2.54	6.40	2.78
31	6.95	1.97	6.69	2.49	6.73	2.10	7.25	2.16	6.82	2.20	5.66	2.03
33	7.47	2.48	8.00	2.75	7.13	2.58	7.16	2.64	6.73	2.84	6.21	2.68
47	4.93	1.83	5.21	2.02	5.14	2.05	5.39	1.86	5.87	2.02	5.26	2.00
48	4.45	1.95	5.80	2.10	5.00	1.99	5.06	1.97	5.41	1.59	5.11	2.02
60	3.06	1.45	3.71	1.41	2.95	1.42	3.31	1.50	3.29	1.46	3.63	1.50
63	2.71	1.23	3.27	1.24	2.48	1.25	2.95	1.05	2.81	1.40	3.06	1.13
66	2.55	1.32	2.98	1.35	2.20	1.24	2.69	1.21	2.70	1.48	2.80	1.17
73	1.76	1.05	2.11	1.16	1.60	1.16	2.30	1.34	1.92	1.12	2.23	1.17
79	1.40	0.90	1.49	1.18	1.25	0.97	2.10	1.05	1.55	1.10	1.64	1.01
80	1.15	0.87	1.58	0.98	1.19	0.91	1.81	1.09	1.37	0.96	1.71	0.95
81	0.97	0.91	1.45	0.94	1.13	0.84	1.73	1.01	1.33	0.79	1.53	0.99
83	0.95	0.78	1.39	0.89	0.95	0.95	1.53	0.95	1.11	0.73	1.23	0.86
85	0.76	0.78	1.18	0.74	0.88	0.98	1.55	0.90	1.08	0.84	1.22	0.85
86	0.83	0.89	1.18	0.91	0.82	0.85	1.46	0.96	0.82	0.97	1.04	0.96
88	0.53	0.87	1.11	0.83	0.78	0.80	1.36	0.97	0.77	0.87	0.93	0.92
90	0.46	0.75	0.93	0.89	0.56	0.84	1.20	0.96	0.55	0.88	0.72	0.82
92	0.42	0.77	0.70	0.75	0.40	0.84	0.97	0.80	0.68	0.66	0.81	0.80
95	0.35	0.75	0.59	0.81	0.29	0.75	0.93	0.79	0.54	0.79	0.85	0.75
97	0.13	0.63	0.56	0.68	0.27	0.71	0.58	0.79	0.44	0.73	0.45	0.73
102	0.18	0.60	0.56	0.70	0.16	0.62	0.36	0.52	0.34	0.67	0.27	0.70

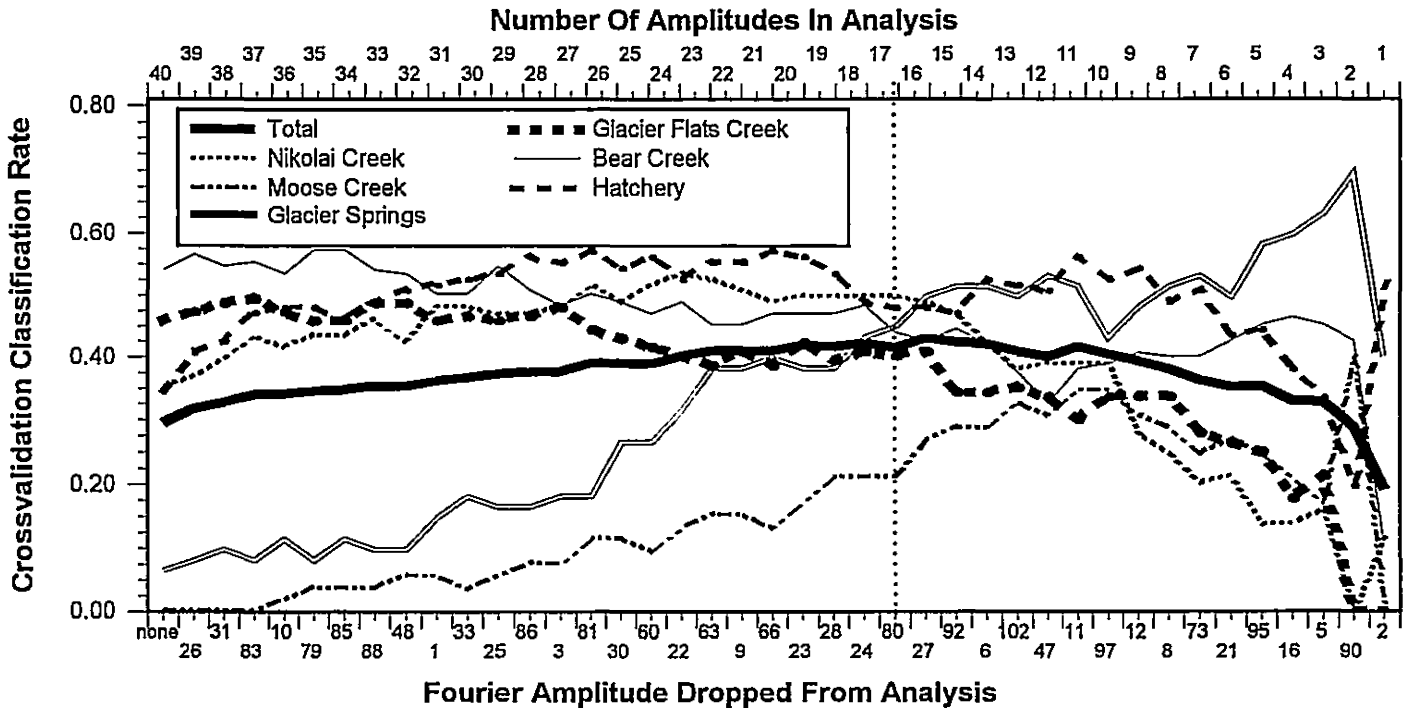

Figure 20. Crossvalidation classification rates (proportion correctly classified) for quadratic discriminant function analysis on Box-Cox transformed amplitudes from six groups of sockeye salmon fry otoliths, Tustumena Lake, Alaska, 1992. The initial model included 40 most significantly different amplitudes based on ANOVA. At each analysis an additional amplitude was dropped (lower X axis), the upper X axis indicates the number of amplitudes used for each analysis. The vertical dashed line indicates the $n_i/3 = 17$ variable model.

Table 12. Quadratic discriminant function crossvalidation and test data classification success, number and percent (in parentheses), for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. Number of amplitudes in model1 = 14; selected from the 40 most significantly different among groups based on ANOVA. Actual totals are the number of otoliths from each location and the estimated totals are the number classified to each location.

Crossvalidation Results

Classification Success

Origin	Hatchery	Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek	Actual Total
Hatchery	52 (47.27)	7 (6.36)	21 (19.09)	10 (9.09)	8 (7.27)	12 (10.91)	110
Bear Creek	13 (8.28)	70 (44.59)	22 (14.01)	8 (5.10)	26 (16.56)	18 (11.46)	157
Glacier Flats Creek	22 (15.83)	21 (15.11)	48 (34.53)	21 (15.11)	11 (7.91)	16 (11.51)	139
Glacier Springs	5 (8.33)	4 (6.67)	8 (13.33)	31 (51.67)	5 (8.33)	7 (11.67)	60
Moose Creek	3 (5.77)	17 (32.69)	9 (17.31)	2 (3.85)	15 (28.85)	6 (11.54)	52
Nikolai Creek	14 (12.96)	18 (16.67)	9 (8.33)	6 (5.56)	10 (9.26)	51 (47.22)	108
Estimated Total	109	137	117	78	75	110	

Test Data Results

Origin	Hatchery	Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek	Actual Total
Hatchery	8 (32.00)	1 (4.00)	8 (32.00)	2 (8.00)	2 (8.00)	4 (16.00)	25
Bear Creek	3 (12.00)	6 (24.00)	8 (32.00)	2 (8.00)	1 (4.00)	5 (20.00)	25
Glacier Flats Creek	7 (28.00)	3 (12.00)	9 (36.00)	2 (8.00)	2 (8.00)	2 (8.00)	25
Glacier Springs	2 (8.00)	2 (8.00)	10 (40.00)	10 (40.00)	0 (0.00)	1 (4.00)	25
Moose Creek	3 (12.00)	9 (36.00)	5 (20.00)	2 (8.00)	4 (16.00)	2 (8.00)	25
Nikolai Creek	2 (8.00)	4 (16.00)	6 (24.00)	1 (4.00)	2 (8.00)	10 (40.00)	25
Estimated Total	25	25	46	19	11.001	24	

1 Amplitudes in model: AMP2 AMP5 AMP6 AMP8 AMP11 AMP12 AMP16 AMP21 AMP47 AMP73 AMP90 AMP95 AMP97 AMP102.

Table 13. Quadratic discriminant function crossvalidation and test data classification success, number and percent (in parentheses), for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. Number of amplitudes in model1 = 15; selected from the 40 most significantly different among groups based on ANOVA. Actual totals are the number of otoliths from each location and the estimated totals are the number classified to each location.

Crossvalidation Results

Classification Success

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	53	(48.18)	6	(5.45)	22	(20.00)	9	(8.18)	8	(7.27)	12	(10.91)	110
Bear Creek	13	(8.28)	67	(42.68)	22	(14.01)	6	(3.82)	29	(18.47)	20	(12.74)	157
Glacier Flats Creek	21	(15.11)	20	(14.39)	57	(41.01)	20	(14.39)	8	(5.76)	13	(9.35)	139
Glacier Springs	5	(8.33)	4	(6.67)	8	(13.33)	30	(50.00)	6	(10.00)	7	(11.67)	60
Moose Creek	4	(7.69)	17	(32.69)	7	(13.46)	2	(3.85)	14	(26.92)	8	(15.38)	52
Nikolai Creek	15	(13.89)	15	(13.89)	10	(9.26)	7	(6.48)	8	(7.41)	53	(49.07)	108
Estimated Total	111		129		126		74		73		113		

Test Data Results

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	8	(32.00)	2	(8.00)	9	(36.00)	1	(4.00)	2	(8.00)	3	(12.00)	25
Bear Creek	3	(12.00)	6	(24.00)	9	(36.00)	1	(4.00)	1	(4.00)	5	(20.00)	25
Glacier Flats Creek	6	(24.00)	2	(8.00)	9	(36.00)	2	(8.00)	4	(16.00)	2	(8.00)	25
Glacier Springs	2	(8.00)	2	(8.00)	8	(32.00)	11	(44.00)	1	(4.00)	1	(4.00)	25
Moose Creek	3	(12.00)	10	(40.00)	4	(16.00)	2	(8.00)	3	(12.00)	3	(12.00)	25
Nikolai Creek	1	(4.00)	4	(16.00)	6	(24.00)	1	(4.00)	2	(8.00)	11	(44.00)	25
Estimated Total	23		26		45		18		13		25		

1 Amplitudes in model: AMP2 AMP5 AMP6 AMP8 AMP11 AMP12 AMP16 AMP21 AMP47 AMP73 AMP90 AMP92 AMP95 AMP97 AMP102.

Table 14. Quadratic discriminant function crossvalidation and test data classification success, number and percent (in parentheses), for hatchery and five wild groups of sockeye salmon fry otoliths based on Box-Cox transformed Fourier amplitudes. Number of amplitudes in model1 = 17; selected from the 40 most significantly different among groups based on ANOVA. Actual totals are the number of otoliths from each location and the estimated totals are the number classified to each location.

Crossvalidation Results

Classification Success

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	54	(49.09)	6	(5.45)	22	(20.00)	10	(9.09)	6	(5.45)	12	(10.91)	110
Bear Creek	9	(5.73)	76	(48.41)	22	(14.01)	9	(5.73)	22	(14.01)	19	(12.10)	157
Glacier Flats Creek	21	(15.11)	20	(14.39)	57	(41.01)	17	(12.23)	8	(5.76)	16	(11.51)	139
Glacier Springs	4	(6.67)	4	(6.67)	11	(18.33)	26	(43.33)	7	(11.67)	8	(13.33)	60
Moose Creek	5	(9.62)	18	(34.62)	8	(15.38)	4	(7.69)	11	(21.15)	6	(11.54)	52
Nikolai Creek	16	(14.81)	15	(13.89)	9	(8.33)	5	(4.63)	9	(8.33)	54	(50.00)	108
Estimated Total	109		139		129		71		63		115		

Test Data Results

Origin	Hatchery		Bear Creek		Glacier Flats Creek		Glacier Springs		Moose Creek		Nikolai Creek		Actual Total
Hatchery	11	(44.00)	0	(0.00)	7	(28.00)	1	(4.00)	1	(4.00)	5	(20.00)	25.0001
Bear Creek	3	(12.00)	6	(24.00)	7	(28.00)	2	(8.00)	2	(8.00)	5	(20.00)	25
Glacier Flats Creek	6	(24.00)	4	(16.00)	8	(32.00)	2	(8.00)	3	(12.00)	2	(8.00)	25
Glacier Springs	1	(4.00)	2	(8.00)	8	(32.00)	11	(44.00)	1	(4.00)	2	(8.00)	25
Moose Creek	3	(12.00)	9	(36.00)	7	(28.00)	2	(8.00)	2	(8.00)	2	(8.00)	25
Nikolai Creek	2	(8.00)	3	(12.00)	6	(24.00)	0	(0.00)	2	(8.00)	12	(48.00)	25.0001
Estimated Total	26		24		43		18		11		28		

1 Amplitudes in model: AMP2 AMP5 AMP6 AMP8 AMP11 AMP12 AMP16 AMP21 AMP27 AMP47 AMP73 AMP80 AMP90 AMP92 AMP95 AMP97 AMP102.

Table 14). Comparisons among the three models did not result in an obvious "best" model. Both total crossvalidation (McNemar's test, $|z| \leq 1.153$, $P \geq 0.124$) and test data ($|z| \leq 0.655$, $P \geq 0.256$) were not significantly different (Table 15). For the sake of parsimony, the 14 amplitude quadratic model (14-QDF) was chosen fro comparison with the 14-LDF model from the stepwise discriminant procedure.

Model Comparisons:

The total crossvalidation and test data classification of the 14-LDF and 14-QDF models were not significantly different ($z = 1.19$, $P > 0.11$; and $z = 0.94$, $P > 0.17$). When crossvalidation and tests data classification rates for individual locations were compared the 14-LDF model values were higher for four out of the six locations (Tables 16 and 17). Huberty (1994) suggested that a linear classification may provide greater across sample stability when the sample to discriminant variable ratio (n_l / p) is small or moderate, although no guidance was given on for the definition of small. Huberty (1994) cautioned that such generalizations were based on the $m = 2$ group case. Given the apparent equality of the classification success of the 14-LDF and 14-QDF rules and the potential for higher stability of the linear rule, I chose the 14-LDF model for further examination.

Table 15. Total crossvalidation and test data classification rates (proportion correctly classified) using quadratic (QDF) discriminant analysis based on Box-Cox transformed Fourier amplitudes from sockeye salmon fry otoliths, Tustumena Lake, Alaska.

Model[1]	Crossvaldation	Test Data
14 Amplitudes		
QDF	0.427	0.313
15 Amplitudes		
QDF	0.438	0.320
17 Amplitudes		
QDF	0.444	0.333

[1]Models selected by looping procedure starting with the 40 most significant amplitudes based on ANOVA.

Table 16. Crossvalidation classification success comparisons, number and percent (in parentheses) correctly classified, for sockeye salmon fry otoliths using linear (14-LDF) and quadratic (14-QDF) discriminant analysis based on Box-Cox transformed Fourier amplitudes. The actual number refers to the true number of otoliths from each location.

Cox transformed Fourier amplitudes.

Location	14-LDF[1]	14-QDF[2]	Actual Number
Hatchery	65 (59.09)	52 (47.27)	110
Bear Creek	54 (34.39)	70 (44.59)	157
Glacier Flats Creek	47 (33.81)	48 (34.53)	139
Glacier Springs	38 (63.33)	31 (51.67)	60
Moose Creek	24 (46.15)	15 (28.85)	52
Nikolai Creek	58 (53.70)	51 (47.22)	108

[1] Amplitudes in model: 2, 9, 15, 16, 22, 24, 27, 28, 30, 33, 90, 95, 117, and 123.

[2] Amplitudes in model: 2, 5, 6, 8, 11, 12, 16, 21, 47, 73, 90, 95, 97, and 102.

Table 17. Test data classification success comparisons, number and percent (in parentheses) correctly classified, for sockeye salmon fry otoliths using linear (14-LDF) and quadratic (14-QDF) discriminant analysis based on Box-Cox transformed Fourier amplitudes. The actual number refers to the true number of otoliths from each location

Cox transformed Fourier amplitudes.

Location	14-LDF[1]	14-QDF[2]	Actual Number
Hatchery	13 (52.00)	8 (32.00)	25
Bear Creek	5 (20.00)	6 (24.00)	25
Glacier Flats Creek	3 (12.00)	9 (36.00)	25
Glacier Springs	14 (56.00)	10 (40.00)	25
Moose Creek	5 (20.00)	4 (16.00)	25
Nikolai Creek	14 (56.00)	10 (40.00)	25

[1] Amplitudes in model: 2, 9, 15, 16, 22, 24, 27, 28, 30, 33, 90, 95, 117, and 123.
[2] Amplitudes in model: 2, 5, 6, 8, 11, 12, 16, 21, 47, 73, 90, 95, 97, and 102.

To determine if the numbers of otoliths classified to their true location were greater than chance, I compared observed values to expected values based on equal probabilities. Given that there were six groups and under the assumption of equal probability of classification, the probability of an individual being assigned to any one location was 1/6. Although the classification rates for the m = 6 groups case were considerably lower than for the m = 2 case, individuals were assigned to their true location at a higher probability than would be expected by chance ($z > 4.82$, $P \leq 0.001$; Figure 21). Therefore, the otolith banding patterns as measured by the selected Fourier amplitudes all contained some degree of location specific information.

The standardized luminance profiles indicated among group variation (Figure 22). The Bear, Moose, and Nikolai creek profiles appeared to be the most similar. When the profiles were reconstructed using the Fourier harmonics associated with the 14-LDF model amplitudes, the hatchery, Glacier Flats Creek, and Glacier Springs profiles appear to be dominated by a cycle with a period of two (Figure 23). The higher period cycle are more dominant in the Bear, Moose, and Nikolai creek profiles (Figure 23). This may be due to a larger degree of noise or variation in the otolith from those tributaries.

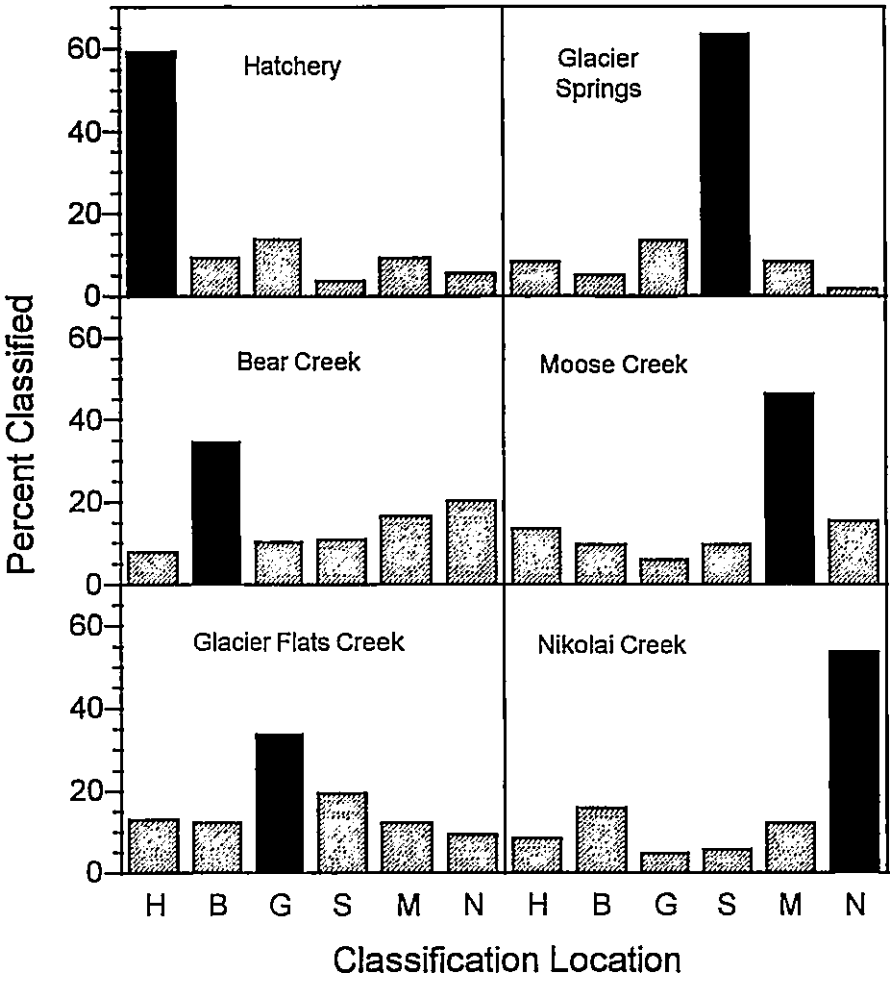

Figure 21. Linear discriminant crossvalidation classifications (percent) using Box-Cox transformed Fourier amplitudes from sockeye salmon fry otoliths, Tustumena Lake, Alaska. Insert labels are location of origin; classification locations are H = hatchery, B = Bear Creek, G = Glacier Flats Creek, S = Glacier Springs, M = Moose Creek, and N = Nikolai Creek. The percentages of individuals correctly classified are shown by solid bars. The amplitude numbers used in the discriminant model were: 2, 9, 15, 16, 22, 24, 27, 28, 30, 33, 90, 95, 117, and 123.

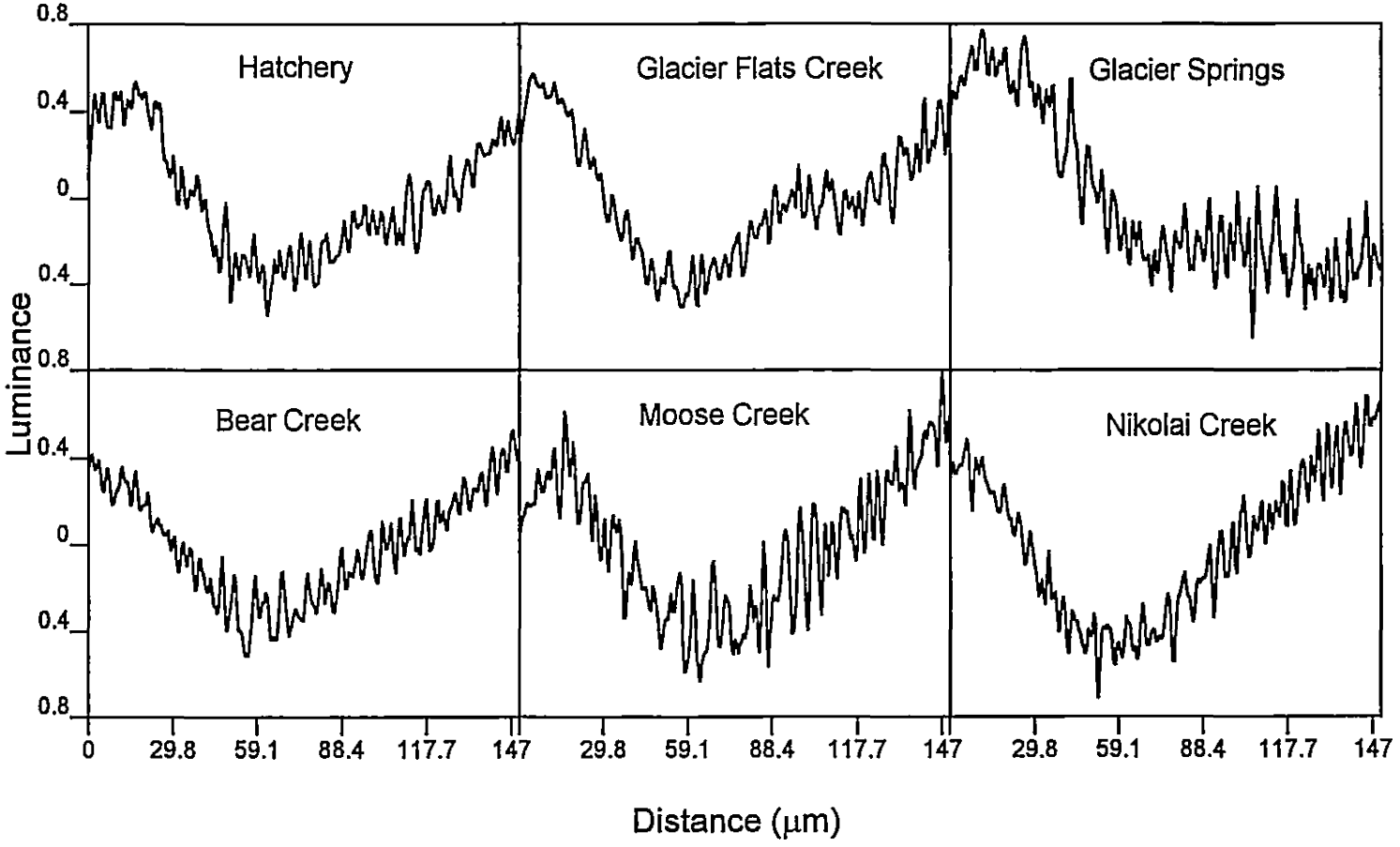

Figure 22. Mean standardized luminance profiles by location for sockeye salmon fry otoliths, Tustumena Lake, Alaska.

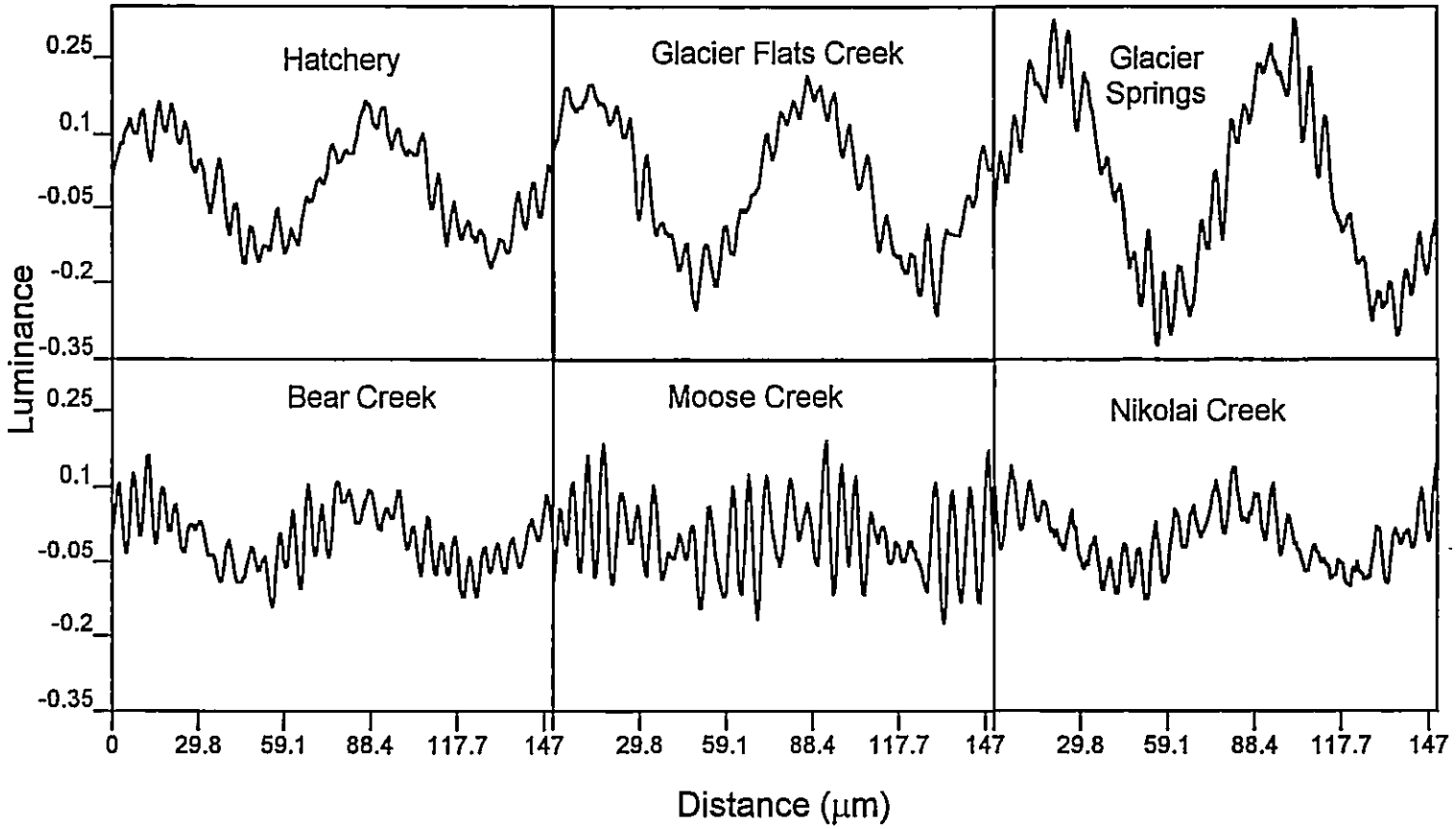

Figure 23. Reconstruction of mean standardized luminance profiles by location for sockeye salmon fry otoliths, Tustumena Lake, Alaska. Profiles were reconstructed using the Fourier harmonics associated with amplitudes: 2, 9, 15, 16, 22, 24, 27, 28, 30, 33, 90, 95, 117, and 123.

Discussion

These analyses of otolith banding patterns represent a first attempt at using Fourier analysis to provide discriminant variables based on luminance profiles. The Fourier amplitudes provide continuous variables which lend themselves to statistical discriminant analysis. The comparison between two observers, although not rigorous, indicated that the method of feature extraction I used was repeatable and potentially robust. Total classification, hatchery versus wild, rates of 83.1% (crossvalidation) and 72.7% (test data) were achieved with quadratic discriminant analysis using 10 Box-Cox transformed Fourier amplitudes (Table 4). While attempts to discriminate among of otoliths from wild fry did not result in total classification rates greater than 45.7% for crossvalidation or 37.3% for test data (Table 15), the evidence suggests that site specific information was contained within the banding patterns.

The use of otolith banding patterns formed during incubation has several desirable qualities. In the case of sockeye salmon it is relatively easy to collect the progeny of known origin spawning groups as the basis of discriminant models upon while they migrate from incubation sites into rearing

environments. Also subsequent growth and environmental conditions should not affect the banding laid down during incubation (Campana and Neilson 1985). Although attempts to discriminate among wild stocks of other fish species using otolith and scale shape analysis have had some success, the evidence indicates that the degree of success is most probably a function of the difference in growth rates amongst the stocks (Campana and Casselman 1993).

Tagging data on lake whitefish (*Coregonus clupeaformis*) indicated the existence of 5 to 11 temporally and spatially discrete groups in Lake Huron (Casselman et al. 1981). Using scale and otolith shape analysis, Casselman et al. (1981) were able to achieve classification rates of 80-85%. However, they concluded that classification success was a function of temporal and spatial separation as well as growth rate differences. Classification of adult mackerel (*Scomber scombus*) from the Gulf of Saint Lawrence, Northwest Atlantic continental shelf, and North Sea regions ranged from 36 to 90% (Catonguay et al. 1991). The classification rates between the Northwest Atlantic groups were lowest (36 to 68%). While separation between Northwest Atlantic and North Sea groups were 60 to 90%. Friedlend and Reddin (1994) found similar results using otolith shape analysis on Atlantic

salmon stocks from the United States, Canada, Ireland and United Kingdom. Classification rates were 84 to 91% between the eastern and western Atlantic salmon stocks. Correct classification between US and Canadian stocks was 62 to 69%. Correct classification between Irish and United Kingdom stocks was similar (64 to 73%). Riley and Carline (1982) used scale shape analysis on walleye stocks within Lake Erie and concluded that separation was poor due to within group variability. Campana and Casselman (1993) used otolith shape analysis on Atlantic cod (*Gadus morhua*) stocks and found that reasonable classification was possible among stocks with different growth rates. However, cod stocks with similar growth rates classified poorly. Campana and Casselman (1993) stated that the utility of otolith shape as a means to discriminate among Atlantic cod stocks depended on differential growth rates and the consistency of the environment that a given stock experiences over the lifetime of the fish. Therefore, if the purpose of research is to determine if growth or survival differs amongst co-mingled stocks, the use of characteristics formed during incubation have a higher potential for utility than characteristics such as adult otolith shape.

Separation of hatchery otoliths from wild otoliths has been previously done using thermally induced banding (Brothers 1990; Volk et al. 1990),

identification of stocking check marks, increment counts, and increment widths (Paragamian et al. 1992; Hendricks et al. 1994). These methods rely on observers consistently identifying a hatchery mark. Investigators who have attempted to delineate among hatchery and wild groups of fish using existing otoliths characteristics have met with mixed results. Rybock (1975) found differences in the nucleus diameters of hatchery steelhead trout versus wild rainbow trout. Both Neilson et al. (1985b) and Currens (1988) were unable to find similar differences; this disparity may have been due to differences in the definitions used to delineate the otolith nucleus (Currens 1988). Rybock (1975) relied on acid etching (HCl) to define a hatching check and was unable to find such a check in 29% of the otoliths examined. During initial examination of otoliths I identified a possible hatching check on hatchery origin otoliths. This check was similar to that which was described by Marshall and Parker (1982). However, I felt that objective identification was not tenable, and I was unable to find such a check on 58% of a sample of 113 wild origin otoliths examined. Although verification of hatching checks would have been possible with hatchery fish, validation of wild fry would not have been logistically possible.

There are few studies available for comparison with the hatchery versus wild otolith classifications rates achieved in my study. Although induced thermal banding results in 100% marking (Volk et al. 1990), I am unaware of published findings which demonstrate the rate at which induced marks are recognized from admixtures of hatchery and wild otoliths. Using oxytetracycline (OTC) validation, Paragamian et al. (1992) determined that the presence of hatch and check marks and increment counts allowed researchers to distinguish between hatchery and wild kokanee salmon (a nonanadromous form of sockeye salmon). However, these authors did not report a classification rate for hatchery otoliths which were not marked with OTC. Hendricks et al. (1994) used hatch and stocking checks as well as increment counts to achieve a total classification rate of 89% for hatchery and wild American shad (*Alosa sapidissima*). These classifications were based on the ability of trained observers to recognize hatchery versus wild patterns and not on statistical classification.

The low classification rates observed for discriminant analysis on $m = 6$ groups certainly do not suggest that the present method is directly useable for the separation of the various wild subcomponents of sockeye fry in Tustumena Lake. What is intriguing is that site specific information is

apparently available within the otolith microstructure formed during incubation. For all wild groups the probability of an individual being classified to it's true incubation location was significantly greater than chance (Figure 21). It should be noted that these are differences among incubation sites that were < 10 km apart. And it also indicates that differences exist that may lend themselves to the separation of groups of fish when they are rearing in a common freshwater environment. The separation of Pacific salmonid stocks based on scale pattern analysis has been restricted to discriminating among freshwater origins (Cook and Lord 1977; Cook 1978; Rowland 1969; Cross et al. 1987). This is because the scale characteristics do not occur prior to emergence from incubation environments. However, emerging genetic and behavioral data are demonstrating the existence or potential for within-drainage diversity (Burger et al. 1995; Holland-Bartels et al. 1994).

Temporal and spatial differences in the distributions of sockeye salmon spawning within Tustumena Lake has been documented. Spawning occurs over a period >30 d (Burger et al. 1995). Within Nikolai Creek sockeye salmon spawn over a distance of >20 km (Kyle 1992). Spawning in Bear and Moose creeks occurs over >10 km of their drainages. While spawning is restricted to about 4 km of Glacier Flats Creek. Further work to quantify

within and among tributary variation in spawning habitat is ongoing (C. Woody, National Biological Survey, pers. comm.). I would propose that further sampling be done to illuminate potential differences in otolith banding patterns within tributaries. For example, collection of outmigrating fry should be stratified along a drainage. Further, other measures of separation (e.g., otolith elemental composition and DNA analysis) should be made simultaneously. In combination the various methods may provide more refined discrimination (Wood et al. 1989).

One area for improvement is variable selection. The looping procedure I used (Figure 8) did not include all possible subsets of amplitudes. Once an amplitude was removed (e.g., deleted at the p = 15 amplitudes step) it was not evaluated at smaller p subsets. The plots of classification rates that were generated during the looping procedures (Figures 13, 14, 19, and 20) did not result in clearly defined maximums. Indeed, discrimination among six groups resulted in four equivocal models. Further work is necessary to develop and apply algorithms that will evaluate all possible subsets of p amplitudes to refine the discriminant capabilities of the present method (Huberty 1994). Not only would this potentially improve discrimination, it would allow researchers

to concentrate on amplitude subsets that meet variable-to-sample ratio criteria (Williams and Titus 1988).

Behavioral and genetic evidence for the existence of subpopulations of sockeye salmon within Tustumena Lake has been presented (Burger et al. 1995). The present study indicated that phenotypic differences in sockeye fry otoliths which develop during incubation have a potential for discrimination. With refinement, such discrimination would allow for estimation of population parameters (e.g., mortality and growth functions) for the various groups of sockeye salmon fry during their freshwater residence. This method also has the potential for research to assess potential hatchery and wild stock interactions.

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Appendices

Table A-1. Summary of dates from which wild outmigrant sockeye salmon fry were preserved (ethanol), Tustumena Lake, Alaska, 1992. Dates from which samples were used in Fourier analysis of otolith banding patterns are indicated by *.

Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek
20 April *	22 April *			20 April
27 April	27 April *		29 April *	27 April *
04 May	04 May *			04 May *
11 May	16 May			11 May
18 May *			17 May	18 May
21 May *	23 May		22 May *	20 May
28 May	29 May *			25 May *
02 June *		02 June *		01 June

Table A-2. Lilleifor's test of normality for untransformed, square-root transformed, and Box-Cox power transformed Fourier amplitudes from sockeye salmon fry otoliths. D_{max} = maximum distance between observed and hypothesized distributions; P = the significance of D_{max}; * $P \leq 0.05$; ** $P \leq 0.01$; lambda = the Box-Cox coefficient.

	Untransformed		Square-Root Transformed		Box-Cox Power Transformed		
Amplitude	D_{max}	P	D_{max}	P	D_{max}	P	Lambda (λ)
1	0.062	0.000 **	0.024	0.461	0.034	0.083	0.65
2	0.113	0.000 **	0.053	0.000 **	0.033	0.093	0.25
3	0.082	0.000 **	0.023	0.550	0.022	0.623	0.40
4	0.069	0.000 **	0.017	0.967	0.018	0.917	0.45
5	0.077	0.000 **	0.025	0.446	0.025	0.446	0.50
6	0.095	0.000 **	0.037	0.043 *	0.019	0.830	0.35
7	0.094	0.000 **	0.032	0.117	0.03	0.185	0.40
8	0.08	0.000 **	0.027	0.290	0.033	0.101	0.45
9	0.084	0.000 **	0.029	0.209	0.024	0.475	0.40
10	0.082	0.000 **	0.027	0.331	0.017	0.991	0.35
11	0.066	0.000 **	0.031	0.147	0.024	0.461	0.40
12	0.089	0.000 **	0.031	0.157	0.025	0.442	0.45
13	0.083	0.000 **	0.029	0.220	0.029	0.220	0.50
14	0.076	0.000 **	0.03	0.187	0.02	0.757	0.40
15	0.064	0.000 **	0.023	0.534	0.023	0.534	0.50
16	0.086	0.000 **	0.028	0.264	0.023	0.519	0.40
17	0.083	0.000 **	0.025	0.414	0.02	0.808	0.45
18	0.065	0.000 **	0.019	0.890	0.019	0.890	0.50
19	0.069	0.000 **	0.019	0.882	0.02	0.752	0.45
20	0.073	0.000 **	0.025	0.422	0.023	0.553	0.55
21	0.065	0.000 **	0.026	0.392	0.026	0.392	0.50
22	0.073	0.000 **	0.039	0.024 *	0.039	0.024 *	0.50
23	0.07	0.000 **	0.032	0.134	0.032	0.134	0.50
24	0.063	0.000 **	0.024	0.456	0.024	0.456	0.50
25	0.064	0.000 **	0.023	0.571	0.029	0.230	0.40
26	0.061	0.000 **	0.026	0.339	0.026	0.339	0.50
27	0.064	0.000 **	0.029	0.213	0.029	0.213	0.50
28	0.045	0.004 **	0.042	0.009 **	0.033	0.107	0.60
29	0.065	0.000 **	0.032	0.132	0.032	0.132	0.50
30	0.064	0.000 **	0.024	0.472	0.024	0.472	0.50

continued

(Table A-2 continued)

	Untransformed		Square-Root Transformed		Box-Cox Power Transformed		
Amplitude	D_{max}	P	D_{max}	P	D_{max}	P	Lambda (λ)
31	0.079	0.000 **	0.026	0.375	0.021	0.724	0.45
32	0.065	0.000 **	0.017	1.000	0.017	1.000	0.50
33	0.075	0.000 **	0.025	0.398	0.025	0.398	0.50
34	0.084	0.000 **	0.033	0.096	0.033	0.096	0.50
35	0.066	0.000 **	0.024	0.502	0.021	0.692	0.45
36	0.062	0.000 **	0.021	0.694	0.026	0.363	0.45
37	0.069	0.000 **	0.021	0.735	0.021	0.735	0.50
38	0.056	0.000 **	0.019	0.869	0.019	0.869	0.50
39	0.061	0.000 **	0.018	0.920	0.02	0.755	0.55
40	0.064	0.000 **	0.022	0.638	0.022	0.638	0.50
41	0.072	0.000 **	0.026	0.388	0.028	0.286	0.45
42	0.077	0.000 **	0.032	0.128	0.032	0.135	0.40
43	0.071	0.000 **	0.022	0.633	0.022	0.633	0.50
44	0.075	0.000 **	0.024	0.499	0.024	0.478	0.45
45	0.077	0.000 **	0.021	0.696	0.02	0.760	0.45
46	0.071	0.000 **	0.023	0.587	0.025	0.411	0.45
47	0.069	0.000 **	0.02	0.752	0.017	0.974	0.45
48	0.08	0.000 **	0.022	0.628	0.024	0.499	0.45
49	0.074	0.000 **	0.017	1.000	0.017	1.000	0.45
50	0.09	0.000 **	0.029	0.210	0.023	0.537	0.40
51	0.074	0.000 **	0.023	0.520	0.023	0.582	0.45
52	0.079	0.000 **	0.03	0.193	0.018	0.942	0.40
53	0.062	0.000 **	0.032	0.138	0.029	0.205	0.45
54	0.073	0.000 **	0.015	1.000	0.018	0.939	0.40
55	0.078	0.000 **	0.019	0.856	0.019	0.862	0.40
56	0.077	0.000 **	0.026	0.358	0.026	0.348	0.40
57	0.081	0.000 **	0.022	0.602	0.019	0.874	0.35
58	0.078	0.000 **	0.025	0.407	0.021	0.684	0.40
59	0.072	0.000 **	0.027	0.323	0.025	0.442	0.40
60	0.094	0.000 **	0.037	0.045 *	0.026	0.369	0.35
61	0.094	0.000 **	0.037	0.044 *	0.027	0.295	0.30
62	0.116	0.000 **	0.056	0.000 **	0.022	0.606	0.25
63	0.086	0.000 **	0.044	0.007 **	0.036	0.054	0.30
64	0.077	0.000 **	0.044	0.005 **	0.036	0.049 *	0.40
65	0.091	0.000 **	0.042	0.011 *	0.022	0.612	0.30
66	0.097	0.000 **	0.035	0.066	0.019	0.836	0.30
67	0.109	0.000 **	0.049	0.001 **	0.022	0.607	0.30
68	0.093	0.000 **	0.033	0.093	0.02	0.757	0.30
69	0.094	0.000 **	0.038	0.029 *	0.018	0.914	0.35
70	0.106	0.000 **	0.048	0.002 **	0.022	0.646	0.30
71	0.103	0.000 **	0.047	0.003 **	0.035	0.061	0.35
72	0.12	0.000 **	0.06	0.000 **	0.032	0.137	0.30
73	0.107	0.000 **	0.055	0.000 **	0.028	0.250	0.30
74	0.119	0.000 **	0.054	0.000 **	0.034	0.079	0.30
75	0.113	0.000 **	0.05	0.001 **	0.023	0.548	0.30
76	0.108	0.000 **	0.046	0.003 **	0.015	1.000	0.25
77	0.107	0.000 **	0.045	0.005 **	0.03	0.202	0.35
78	0.099	0.000 **	0.052	0.000 **	0.034	0.076	0.35
79	0.1	0.000 **	0.04	0.020 *	0.015	1.000	0.30

(continued)

(Table A-2 continued)

	Untransformed		Square-Root Transformed		Box-Cox Power Transformed		
Amplitude	D_{max}	P	D_{max}	P	D_{max}	P	Lambda (λ)
80	0.11	0.000 **	0.046	0.003 **	0.02	0.781	0.30
81	0.116	0.000 **	0.062	0.000 **	0.029	0.211	0.25
82	0.1	0.000 **	0.037	0.042 *	0.034	0.089	0.25
83	0.108	0.000 **	0.043	0.009 **	0.019	0.838	0.25
84	0.122	0.000 **	0.059	0.000 **	0.023	0.553	0.25
85	0.111	0.000 **	0.048	0.001 **	0.027	0.334	0.25
86	0.113	0.000 **	0.046	0.003 **	0.021	0.699	0.30
87	0.101	0.000 **	0.062	0.000 **	0.031	0.168	0.25
88	0.105	0.000 **	0.042	0.010 **	0.018	0.905	0.30
89	0.097	0.000 **	0.037	0.037 *	0.026	0.389	0.30
90	0.111	0.000 **	0.047	0.003 **	0.027	0.325	0.30
91	0.091	0.000 **	0.035	0.071	0.02	0.768	0.30
92	0.076	0.000 **	0.025	0.423	0.024	0.458	0.35
93	0.083	0.000 **	0.031	0.141	0.018	0.903	0.35
94	0.105	0.000 **	0.043	0.008 **	0.03	0.176	0.40
95	0.106	0.000 **	0.044	0.006 **	0.032	0.123	0.40
96	0.1	0.000 **	0.037	0.039 *	0.02	0.790	0.25
97	0.113	0.000 **	0.051	0.000 **	0.021	0.720	0.25
98	0.097	0.000 **	0.047	0.003 **	0.016	1.000	0.25
99	0.09	0.000 **	0.034	0.085	0.029	0.237	0.35
100	0.096	0.000 **	0.033	0.093	0.024	0.516	0.35
101	0.075	0.000 **	0.023	0.530	0.02	0.747	0.40
102	0.077	0.000 **	0.035	0.069	0.03	0.171	0.45
103	0.087	0.000 **	0.032	0.116	0.03	0.190	0.35
104	0.085	0.000 **	0.025	0.452	0.024	0.514	0.40
105	0.074	0.000 **	0.023	0.552	0.019	0.877	0.35
106	0.063	0.000 **	0.031	0.158	0.03	0.202	0.45
107	0.083	0.000 **	0.035	0.063	0.026	0.372	0.40
108	0.07	0.000 **	0.025	0.443	0.019	0.869	0.40
109	0.08	0.000 **	0.025	0.422	0.019	0.868	0.40
110	0.059	0.000 **	0.029	0.220	0.029	0.220	0.50
111	0.067	0.000 **	0.024	0.477	0.022	0.648	0.55
112	0.062	0.000 **	0.034	0.074	0.031	0.149	0.45
113	0.079	0.000 **	0.027	0.313	0.024	0.456	0.45
114	0.079	0.000 **	0.039	0.022 *	0.042	0.010 **	0.40
115	0.085	0.000 **	0.027	0.318	0.026	0.381	0.40
116	0.08	0.000 **	0.025	0.429	0.019	0.816	0.45
117	0.073	0.000 **	0.048	0.001 **	0.038	0.030 *	0.35
118	0.083	0.000 **	0.023	0.541	0.017	0.996	0.45
119	0.084	0.000 **	0.032	0.135	0.032	0.122	0.40
120	0.075	0.000 **	0.029	0.231	0.026	0.361	0.45
121	0.078	0.000 **	0.022	0.596	0.018	0.940	0.40
122	0.069	0.000 **	0.04	0.017 *	0.037	0.038 *	0.40
123	0.074	0.000 **	0.023	0.588	0.028	0.261	0.45
124	0.086	0.000 **	0.028	0.277	0.019	0.821	0.40
125	0.073	0.000 **	0.025	0.415	0.021	0.677	0.40
126	0.082	0.000 **	0.032	0.132	0.038	0.033 *	0.30
127	0.072	0.000 **	0.027	0.300	0.025	0.395	0.45
128	0.104	0.000 **	0.045	0.004 **	0.035	0.068	0.35

Table A-3. Test of differences between left and right sockeye salmon fry otolith Box-Cox transformed Fourier amplitudes using randomized block ANOVA. Significance levels are $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$.

Amplitude	F	P > F	Amplitude	F	P > F	Amplitude	F	P > F
1	0.54	0.463	44	2.90	0.089	87	1.99	0.159
2	7.90	0.005 **	45	0.12	0.729	88	4.34	0.038 *
3	3.69	0.055	46	0.87	0.351	89	3.05	0.081
4	1.70	0.193	47	1.75	0.187	90	0.06	0.807
5	1.59	0.208	48	0.25	0.617	91	0.32	0.572
6	6.33	0.012 *	49	0.03	0.863	92	2.69	0.102
7	0.25	0.617	50	0.00	0.956	93	0.97	0.325
8	2.81	0.094	51	1.86	0.173	94	6.38	0.012 *
9	0.52	0.471	52	0.68	0.410	95	0.73	0.393
10	0.14	0.708	53	0.01	0.920	96	0.03	0.863
11	0.06	0.807	54	4.27	0.039 *	97	0.57	0.451
12	0.64	0.424	55	2.69	0.102	98	0.58	0.447
13	0.04	0.842	56	1.11	0.293	99	2.22	0.137
14	3.19	0.075	57	3.11	0.079	100	2.15	0.143
15	2.61	0.107	58	1.10	0.295	101	3.52	0.061
16	1.44	0.231	59	1.28	0.259	102	1.18	0.278
17	0.37	0.543	60	1.21	0.272	103	0.05	0.823
18	0.48	0.489	61	0.06	0.807	104	0.09	0.764
19	0.03	0.863	62	1.50	0.221	105	2.77	0.097
20	0.07	0.791	63	0.61	0.435	106	2.69	0.102
21	0.25	0.617	64	3.88	0.050 *	107	0.03	0.863
22	3.14	0.077	65	2.67	0.103	108	0.28	0.597
23	2.73	0.099	66	0.62	0.431	109	0.69	0.407
24	0.80	0.372	67	0.17	0.680	110	3.74	0.054
25	3.94	0.048 *	68	0.03	0.863	111	1.41	0.236
26	0.92	0.338	69	0.41	0.522	112	1.53	0.217
27	0.22	0.639	70	1.06	0.304	113	0.41	0.522
28	0.04	0.842	71	6.33	0.012 *	114	1.25	0.264
29	0.05	0.823	72	0.91	0.341	115	1.20	0.274
30	0.18	0.672	73	2.50	0.115	116	2.01	0.157
31	0.10	0.752	74	0.04	0.842	117	0.00	0.975
32	2.75	0.098	75	0.04	0.842	118	0.01	0.920
33	0.19	0.663	76	0.46	0.498	119	0.34	0.560
34	4.00	0.046 *	77	4.73	0.030 *	120	0.87	0.351
35	0.02	0.888	78	0.09	0.764	121	0.22	0.639
36	0.59	0.443	79	0.02	0.888	122	0.28	0.597
37	4.33	0.038 *	80	0.99	0.320	123	0.81	0.369
38	3.39	0.066	81	0.57	0.451	124	0.26	0.610
39	0.15	0.699	82	0.78	0.378	125	0.05	0.823
40	0.18	0.672	83	17.64	0.000 **	126	0.24	0.624
41	0.38	0.538	84	1.24	0.266	127	0.05	0.823
42	0.71	0.400	85	4.49	0.035 *	128	0.62	0.431
43	1.54	0.215	86	0.32	0.572			

Table A-4. Test of differences between two observer's measurements on sockeye salmon fry otolith Box-Cox transformed Fourier amplitudes using randomized block ANOVA. Significance levels are *$P \leq 0.05$ and **$P \leq 0.01$.

Amplitude	F	P > F	Amplitude	F	P > F	Amplitude	F	P > F
1	0.80	0.375	44	3.07	0.086	87	6.17	0.016 *
2	0.08	0.778	45	0.24	0.626	88	0.88	0.353
3	0.60	0.442	46	0.19	0.665	89	0.33	0.568
4	1.35	0.251	47	0.07	0.792	90	0.23	0.634
5	1.52	0.223	48	0.15	0.700	91	0.10	0.753
6	0.92	0.342	49	0.57	0.454	92	0.61	0.438
7	2.06	0.157	50	0.02	0.888	93	0.56	0.458
8	0.32	0.574	51	1.14	0.291	94	1.72	0.196
9	0.88	0.353	52	2.93	0.093	95	0.48	0.492
10	0.49	0.487	53	0.11	0.742	96	0.00	0.950
11	0.00	0.947	54	0.01	0.921	97	0.22	0.641
12	1.03	0.315	55	2.20	0.144	98	1.32	0.256
13	0.12	0.730	56	0.01	0.921	99	0.96	0.332
14	0.08	0.778	57	0.21	0.649	100	0.38	0.540
15	0.03	0.863	58	0.13	0.720	101	1.14	0.291
16	0.09	0.765	59	0.33	0.568	102	0.53	0.470
17	0.15	0.700	60	0.66	0.420	103	0.05	0.824
18	0.25	0.619	61	0.05	0.824	104	2.09	0.154
19	0.27	0.606	62	1.43	0.237	105	0.02	0.888
20	2.50	0.120	63	0.34	0.562	106	1.94	0.170
21	0.40	0.530	64	0.02	0.888	107	1.32	0.256
22	0.03	0.863	65	0.94	0.337	108	0.07	0.792
23	0.08	0.778	66	0.05	0.824	109	0.49	0.487
24	3.18	0.080	67	0.82	0.369	110	0.35	0.557
25	0.62	0.435	68	0.15	0.700	111	0.01	0.921
26	1.85	0.180	69	1.24	0.271	112	3.43	0.070
27	3.12	0.083	70	1.13	0.293	113	0.85	0.361
28	2.74	0.104	71	0.54	0.466	114	1.51	0.225
29	1.22	0.275	72	0.03	0.863	115	3.37	0.072
30	0.57	0.454	73	0.14	0.710	116	0.90	0.347
31	0.34	0.562	74	0.10	0.753	117	0.04	0.842
32	0.04	0.842	75	0.20	0.657	118	1.23	0.273
33	0.00	0.947	76	0.92	0.342	119	0.11	0.742
34	3.54	0.066	77	0.03	0.863	120	0.17	0.682
35	4.82	0.033 *	78	0.01	0.921	121	8.81	0.005 **
36	0.15	0.700	79	0.07	0.792	122	1.35	0.251
37	0.26	0.612	80	3.85	0.055	123	0.22	0.641
38	0.07	0.792	81	0.11	0.742	124	2.22	0.142
39	2.09	0.154	82	0.85	0.361	125	0.12	0.730
40	0.47	0.496	83	0.01	0.921	126	0.77	0.384
41	3.26	0.077	84	0.07	0.792	127	1.75	0.192
42	0.62	0.435	85	0.27	0.606	128	1.29	0.261
43	0.23	0.634	86	0.15	0.700			

Table A-5. Tests for differences between hatchery and wild sockeye salmon fry otoliths Box-Cox transformed Fourier amplitudes using ANOVA. Significance levels are * $P \leq 0.05$ and ** $P \leq 0.01$.

Amplitude	F	P > F	Amplitude	F	P > F	Amplitude	F	P > F
1	0.44	0.507	44	0.59	0.443	87	4.17	0.042 *
2	0.13	0.719	45	0.00	0.950	88	23.35	0.000 **
3	0.46	0.498	46	0.53	0.467	89	3.390	0.066
4	0.36	0.549	47	9.85	0.002 **	90	12.120	0.001 **
5	6.31	0.012 *	48	16.83	0.000 **	91	1.550	0.214
6	0.00	0.947	49	4.51	0.034 *	92	9.350	0.002 **
7	0.11	0.740	50	0.01	0.920	93	7.620	0.006 **
8	26.79	0.000 **	51	1.25	0.264	94	4.550	0.033 *
9	55.45	0.000 **	52	0.02	0.888	95	8.530	0.004 **
10	5.94	0.015 *	53	0.16	0.689	96	4.970	0.026 *
11	1.63	0.202	54	2.79	0.095	97	18.470	0.000 **
12	4.27	0.039 *	55	6.40	0.012 *	98	5.780	0.017 *
13	3.44	0.064	56	0.81	0.368	99	4.460	0.035 *
14	8.12	0.005 **	57	1.59	0.208	100	1.330	0.249
15	9.85	0.002 **	58	2.06	0.152	101	2.590	0.108
16	26.66	0.000 **	59	5.63	0.018 *	102	5.590	0.018 *
17	13.78	0.000 **	60	4.73	0.030 *	103	4.810	0.029 *
18	0.10	0.752	61	4.91	0.027 *	104	6.880	0.009 **
19	2.88	0.090	62	2.09	0.149	105	0.280	0.597
20	1.25	0.264	63	2.74	0.098	106	0.004	0.950
21	25.01	0.000 **	64	0.09	0.764	107	0.000	1.000
22	55.50	0.000 **	65	1.13	0.288	108	1.20	0.274
23	31.94	0.000 **	66	0.75	0.387	109	0.04	0.842
24	34.58	0.000 **	67	0.05	0.823	110	1.40	0.237
25	27.55	0.000 **	68	1.12	0.290	111	0.36	0.549
26	21.43	0.000 **	69	0.94	0.333	112	1.38	0.241
27	6.35	0.012 *	70	1.68	0.195	113	3.58	0.059
28	3.34	0.068	71	2.48	0.116	114	2.35	0.126
29	1.24	0.266	72	10.70	0.001 **	115	4.83	0.028 *
30	0.64	0.424	73	3.96	0.047 *	116	3.90	0.049 *
31	2.72	0.100	74	0.68	0.410	117	0.72	0.396
32	0.07	0.791	75	5.15	0.024 *	118	1.84	0.175
33	1.19	0.276	76	0.41	0.522	119	0.93	0.335
34	1.65	0.199	77	3.35	0.068	120	0.03	0.863
35	8.25	0.004 **	78	2.67	0.103	121	2.19	0.139
36	11.15	0.001 **	79	1.54	0.215	122	10.09	0.002 **
37	5.41	0.020 *	80	12.14	0.001 **	123	5.20	0.023 *
38	2.07	0.151	81	19.42	0.000 **	124	2.39	0.123
39	0.48	0.489	82	4.37	0.037 *	125	0.10	0.752
40	0.31	0.578	83	8.51	0.004 **	126	1.38	0.241
41	0.46	0.498	84	6.84	0.009 **	127	0.14	0.708
42	0.13	0.719	85	17.40	0.000 **	128	0.65	0.420
43	0.00	0.950	86	4.92	0.027 *			

Table A-6. Linear discriminant function crossvalidation classification rates (proportion correctly classified) for hatchery and wild sockeye salmon fry otoliths based on Box-Cox transformed amplitudes, Tustumena Lake, Alaska. The initial amplitudes selection was based on stepwise linear discriminant analysis.

Number Of Amplitudes In The Model	Amplitude Removed	Classifcation		
		Hatchery	Wild	Total
29	none	0.827	0.849	0.838
28	27	0.846	0.847	0.846
27	33	0.855	0.857	0.856
26	15	0.864	0.857	0.860
25	12	0.864	0.847	0.855
24	25	0.873	0.849	0.861
23	74	0.864	0.843	0.853
22	45	0.855	0.853	0.854
21	1	0.855	0.853	0.854
20	85	0.873	0.845	0.859
19	10	0.864	0.847	0.855
18	21	0.864	0.851	0.857
17	97	0.846	0.843	0.844
16	67	0.836	0.837	0.837
15	19	0.846	0.835	0.840
14	54	0.836	0.833	0.835
13	11	0.827	0.826	0.826
12	106	0.818	0.824	0.821
11	28	0.836	0.820	0.828
10	8	0.818	0.812	0.815
9	26	0.818	0.810	0.814
8	88	0.800	0.798	0.799
7	23	0.800	0.797	0.798
6	48	0.800	0.785	0.792
5	65	0.800	0.771	0.786
4	24	0.791	0.756	0.773
3	16	0.782	0.711	0.747
2	81	0.764	0.700	0.732
1	22	0.691	0.667	0.679
1	9	0.646	0.647	0.646

Table A-7. Summary of quadratic discriminant crossvalidation classification rates (proportion correctly classified) based on Box-Cox transformed amplitudes for hatchery and wild sockeye salmon fry otoliths, Tustumena Lake, Alaska. The initial amplitudes were the 30 highly significant (ANOVA, $P < 0.01$) amplitudes.

Number Of Amplitudes In The Model	Amplitude Removed	Classification		
		Hatchery	Wild	Total
30	none	0.500	0.926	0.713
29	93	0.527	0.924	0.726
28	14	0.536	0.928	0.732
27	104	0.582	0.919	0.750
26	95	0.591	0.913	0.752
25	72	0.618	0.913	0.766
24	48	0.636	0.907	0.772
23	81	0.655	0.897	0.776
22	36	0.691	0.893	0.792
21	83	0.709	0.886	0.797
20	97	0.727	0.884	0.806
19	85	0.736	0.884	0.810
18	92	0.755	0.872	0.813
17	84	0.746	0.882	0.814
16	21	0.773	0.868	0.821
15	35	0.782	0.861	0.821
14	90	0.791	0.857	0.824
13	15	0.791	0.862	0.827
12	47	0.791	0.853	0.822
11	122	0.809	0.851	0.830
10	22	0.818	0.833	0.826
9	8	0.818	0.830	0.824
8	24	0.818	0.808	0.813
7	17	0.827	0.806	0.817
6	80	0.827	0.797	0.812
5	88	0.809	0.787	0.798
4	16	0.800	0.744	0.772
3	23	0.718	0.740	0.729
2	26	0.636	0.773	0.705
1	25	0.646	0.690	0.668
1	9	0.618	0.653	0.636

Table A-8. Summary of logistic regression crossvalidation classification (proportion correctly classified) for hatchery and wild sockeye salmon fry otoliths using Box-Cox transformed Fourier amplitudes. The initial 20 amplitudes were selected by stepwise logistic discrimination.

Number In Model	Amplitude Removed	Classification		
		Hatchery	Wild	Total
20	none	0.609	0.965	0.903
19	24	0.645	0.967	0.911
18	15	0.645	0.961	0.906
17	106	0.618	0.957	0.898
16	65	0.609	0.965	0.903
15	31	0.600	0.961	0.898
14	1	0.573	0.963	0.895
13	88	0.545	0.961	0.888
12	67	0.545	0.957	0.885
11	45	0.536	0.957	0.883
10	27	0.518	0.959	0.882
9	28	0.518	0.963	0.885
8	8	0.491	0.965	0.882
7	85	0.473	0.965	0.879
6	64	0.436	0.959	0.867
5	26	0.409	0.971	0.872
4	81	0.364	0.957	0.853
3	23	0.309	0.959	0.845
2	16	0.182	0.965	0.827
1	22	0.055	0.983	0.819
1	9	0.018	0.994	0.823

Table A-9. Hatchery and wild sockeye salmon fry otolith luminance profile Fourier harmonic mean amplitudes, variances, and proportion of total variance explained by individual harmonics.

	Hatchery			Wild		
Harmonic Number	Mean Amplitude	Variance Of Harmonic	Proportion Of Total Variance	Mean Amplitude	Variance Of Harmonic	Proportion Of Total Variance
1	19.02	180.98	0.1398	19.40	188.25	0.1489
2	4.46	9.94	0.0077	4.41	9.70	0.0077
3	4.10	8.40	0.0065	4.22	8.89	0.0070
4	4.57	10.45	0.0081	4.45	9.92	0.0078
5	5.20	13.51	0.0104	4.66	10.87	0.0086
6	3.98	7.92	0.0061	3.99	7.95	0.0063
7	4.33	9.39	0.0073	4.27	9.12	0.0072
8	5.69	16.19	0.0125	4.62	10.67	0.0084
9	5.82	16.93	0.0131	4.53	10.24	0.0081
10	4.90	11.98	0.0093	4.50	10.12	0.0080
11	5.05	12.75	0.0099	5.30	14.04	0.0111
12	5.18	13.40	0.0104	5.64	15.90	0.0126
13	5.83	17.00	0.0131	6.28	19.70	0.0156
14	4.56	10.40	0.0080	5.09	12.94	0.0102
15	5.62	15.81	0.0122	6.43	20.70	0.0164
16	4.39	9.63	0.0074	5.39	14.51	0.0115
17	5.15	13.26	0.0102	6.00	17.99	0.0142
18	6.54	21.38	0.0165	6.62	21.93	0.0173
19	5.88	17.29	0.0134	6.26	19.62	0.0155
20	8.01	32.10	0.0248	7.66	29.35	0.0232
21	8.43	35.52	0.0274	7.04	24.77	0.0196
22	8.98	40.30	0.0311	6.92	23.96	0.0189
23	8.95	40.08	0.0310	7.28	26.50	0.0210
24	8.82	38.93	0.0301	7.22	26.07	0.0206
25	7.10	25.21	0.0195	6.05	18.33	0.0145
26	8.50	36.17	0.0279	7.22	26.09	0.0206
27	8.21	33.69	0.0260	7.50	28.15	0.0223
28	10.13	51.29	0.0396	9.44	44.59	0.0353
29	7.68	29.49	0.0228	7.35	27.00	0.0213
30	7.77	30.15	0.0233	7.54	28.43	0.0225
31	6.95	24.15	0.0187	6.56	21.55	0.0170
32	7.20	25.94	0.0200	7.13	25.40	0.0201
33	7.47	27.93	0.0216	7.16	25.66	0.0203
34	6.60	21.80	0.0168	6.94	24.07	0.0190
35	5.71	16.33	0.0126	6.38	20.35	0.0161
36	5.53	15.29	0.0118	6.28	19.70	0.0156
37	6.15	18.89	0.0146	6.75	22.78	0.0180
38	6.50	21.09	0.0163	6.85	23.45	0.0185

(continued)

(Table A-9 continued)

Harmonic Number	Hatchery Mean Amplitude	Hatchery Variance Of Harmonic	Hatchery Proportion Of Total Variance	Wild Mean Amplitude	Wild Variance Of Harmonic	Wild Proportion Of Total Variance
39	7.12	25.35	0.0196	7.32	26.81	0.0212
40	6.40	20.46	0.0158	6.54	21.38	0.0169
41	5.97	17.85	0.0138	5.83	16.97	0.0134
42	5.29	13.97	0.0108	5.21	13.59	0.0107
43	6.26	19.59	0.0151	6.27	19.65	0.0155
44	5.43	14.73	0.0114	5.58	15.60	0.0123
45	5.46	14.90	0.0115	5.45	14.83	0.0117
46	5.18	13.43	0.0104	5.34	14.27	0.0113
47	4.93	12.17	0.0094	5.60	15.66	0.0124
48	4.45	9.91	0.0077	5.32	14.13	0.0112
49	4.69	10.99	0.0085	5.12	13.11	0.0104
50	4.46	9.96	0.0077	4.48	10.02	0.0079
51	4.69	11.00	0.0085	4.93	12.13	0.0096
52	4.43	9.82	0.0076	4.41	9.71	0.0077
53	4.71	11.08	0.0086	4.78	11.45	0.0091
54	4.01	8.03	0.0062	4.30	9.25	0.0073
55	3.80	7.21	0.0056	4.24	8.97	0.0071
56	3.87	7.48	0.0058	4.03	8.12	0.0064
57	3.59	6.44	0.0050	3.78	7.14	0.0056
58	3.62	6.56	0.0051	3.87	7.51	0.0059
59	3.44	5.91	0.0046	3.85	7.40	0.0059
60	3.06	4.69	0.0036	3.40	5.77	0.0046
61	2.77	3.85	0.0030	3.07	4.72	0.0037
62	2.62	3.44	0.0027	2.80	3.91	0.0031
63	2.71	3.68	0.0028	2.93	4.29	0.0034
64	3.17	5.03	0.0039	3.13	4.89	0.0039
65	2.86	4.10	0.0032	2.72	3.70	0.0029
66	2.55	3.25	0.0025	2.67	3.56	0.0028
67	2.56	3.29	0.0025	2.54	3.22	0.0025
68	2.33	2.71	0.0021	2.46	3.04	0.0024
69	2.40	2.87	0.0022	2.53	3.20	0.0025
70	2.10	2.21	0.0017	2.26	2.56	0.0020
71	2.09	2.19	0.0017	2.29	2.62	0.0021
72	1.71	1.46	0.0011	2.11	2.23	0.0018
73	1.76	1.54	0.0012	2.00	2.00	0.0016
74	1.80	1.61	0.0012	1.89	1.79	0.0014
75	1.58	1.25	0.0010	1.84	1.69	0.0013
76	1.57	1.23	0.0010	1.64	1.34	0.0011
77	1.57	1.23	0.0010	1.79	1.60	0.0013
78	1.48	1.10	0.0008	1.67	1.39	0.0011
79	1.40	0.98	0.0008	1.54	1.18	0.0009
80	1.15	0.67	0.0005	1.51	1.14	0.0009
81	0.97	0.47	0.0004	1.40	0.98	0.0008
82	1.10	0.61	0.0005	1.31	0.85	0.0007
83	0.95	0.45	0.0004	1.23	0.75	0.0006

(continued)

(Table A-9 continued)

Harmonic Number	Hatchery			Wild		
	Mean Amplitude	Variance Of Harmonic	Proportion Of Total Variance	Mean Amplitude	Variance Of Harmonic	Proportion Of Total Variance
84	0.88	0.39	0.0003	1.14	0.65	0.0005
85	0.76	0.29	0.0002	1.14	0.65	0.0005
86	0.83	0.35	0.0003	1.05	0.55	0.0004
87	0.70	0.24	0.0002	0.88	0.39	0.0003
88	0.53	0.14	0.0001	0.98	0.48	0.0004
89	0.70	0.25	0.0002	0.87	0.38	0.0003
90	0.46	0.11	0.0001	0.78	0.30	0.0002
91	0.59	0.17	0.0001	0.69	0.24	0.0002
92	0.42	0.09	0.0001	0.67	0.23	0.0002
93	0.40	0.08	0.0001	0.63	0.20	0.0002
94	0.43	0.09	0.0001	0.61	0.19	0.0001
95	0.35	0.06	0.0000	0.60	0.18	0.0001
96	0.30	0.05	0.0000	0.48	0.11	0.0001
97	0.13	0.01	0.0000	0.45	0.10	0.0001
98	0.19	0.02	0.0000	0.37	0.07	0.0001
99	0.22	0.02	0.0000	0.38	0.07	0.0001
100	0.22	0.02	0.0000	0.30	0.05	0.0000
101	0.18	0.02	0.0000	0.30	0.04	0.0000
102	0.18	0.02	0.0000	0.35	0.06	0.0000
103	0.10	0.00	0.0000	0.25	0.03	0.0000
104	0.08	0.00	0.0000	0.27	0.04	0.0000
105	0.14	0.01	0.0000	0.18	0.02	0.0000
106	0.15	0.01	0.0000	0.15	0.01	0.0000
107	0.12	0.01	0.0000	0.12	0.01	0.0000
108	0.04	0.00	0.0000	0.12	0.01	0.0000
109	0.10	0.01	0.0000	0.09	0.00	0.0000
110	-0.01	0.00	0.0000	0.07	0.00	0.0000
111	0.04	0.00	0.0000	0.08	0.00	0.0000
112	-0.02	0.00	0.0000	0.06	0.00	0.0000
113	-0.07	0.00	0.0000	0.04	0.00	0.0000
114	-0.12	0.01	0.0000	-0.01	0.00	0.0000
115	-0.16	0.01	0.0000	-0.01	0.00	0.0000
116	-0.15	0.01	0.0000	-0.02	0.00	0.0000
117	-0.12	0.01	0.0000	-0.07	0.00	0.0000
118	-0.15	0.01	0.0000	-0.06	0.00	0.0000
119	-0.11	0.01	0.0000	-0.05	0.00	0.0000
120	-0.08	0.00	0.0000	-0.07	0.00	0.0000
121	-0.14	0.01	0.0000	-0.05	0.00	0.0000
122	-0.28	0.04	0.0000	-0.08	0.00	0.0000
123	-0.24	0.03	0.0000	-0.09	0.00	0.0000
124	-0.15	0.01	0.0000	-0.06	0.00	0.0000
125	-0.13	0.01	0.0000	-0.11	0.01	0.0000
126	-0.17	0.01	0.0000	-0.09	0.00	0.0000
127	-0.08	0.00	0.0000	-0.06	0.00	0.0000
128	-0.36	0.06	0.0000	-0.29	0.04	0.0000

Table A-10. ANOVA tests for differences among Box-Cox transformed Fourier amplitudes of sockeye salmon fry otoliths from six locations (hatchery, Bear Creek, Glacier Flats Creek, Glacier Springs, Moose Creek, and Nikolai Creek), Tustumena Lake, Alaska. Significance levels are * $P < 0.05$ and ** $P < 0.01$.

Amplitude	F	P > F	Amplitude	F	P > F	Amplitude	F	P > F
1	8.50	0.000 **	44	1.11	0.354	87	3.59	0.003 **
2	38.34	0.000 **	45	0.89	0.487	88	10.07	0.000 **
3	13.04	0.000 **	46	2.38	0.037 *	89	4.55	0.000 **
4	2.14	0.059	47	7.51	0.000 **	90	9.25	0.000 **
5	7.31	0.000 **	48	6.47	0.000 **	91	3.49	0.004 **
6	6.45	0.000 **	49	2.45	0.033 *	92	7.83	0.000 **
7	4.81	0.000 **	50	3.41	0.005 **	93	3.82	0.002 **
8	11.32	0.000 **	51	3.72	0.003 **	94	5.01	0.000 **
9	18.79	0.000 **	52	2.77	0.017 *	95	10.76	0.000 **
10	10.17	0.000 **	53	4.23	0.001 **	96	2.51	0.029 *
11	6.28	0.000 **	54	2.74	0.018 *	97	6.89	0.000 **
12	8.27	0.000 **	55	4.78	0.000 **	98	4.50	0.000 **
13	4.03	0.001 **	56	3.41	0.005 **	99	2.44	0.033 *
14	3.55	0.004 **	57	3.63	0.003 **	100	4.81	0.000 **
15	5.19	0.000 **	58	2.31	0.043 *	101	4.38	0.001 **
16	5.94	0.000 **	59	3.56	0.004 **	102	7.30	0.000 **
17	3.74	0.002 **	60	5.78	0.000 **	103	5.54	0.000 **
18	1.85	0.101	61	3.87	0.002 **	104	5.59	0.000 **
19	2.09	0.065	62	2.59	0.025 *	105	2.10	0.064
20	2.35	0.040 *	63	7.10	0.000 **	106	3.57	0.003 **
21	5.94	0.000 **	64	4.68	0.000 **	107	2.98	0.011 *
22	12.63	0.000 **	65	4.24	0.001 **	108	1.96	0.083
23	7.50	0.000 **	66	5.87	0.000 **	109	1.57	0.166
24	8.22	0.000 **	67	3.76	0.002 **	110	2.75	0.018 *
25	6.15	0.000 **	68	4.09	0.001 **	111	1.90	0.092
26	7.41	0.000 **	69	2.69	0.020 *	112	3.97	0.001 **
27	8.07	0.000 **	70	5.12	0.000 **	113	1.34	0.246
28	6.16	0.000 **	71	3.67	0.003 **	114	2.09	0.065
29	4.40	0.001 **	72	4.13	0.001 **	115	5.37	0.000 **
30	6.36	0.000 **	73	6.17	0.000 **	116	4.23	0.001 **
31	5.86	0.000 **	74	4.92	0.000 **	117	3.23	0.007 **
32	2.01	0.075	75	3.77	0 002 **	118	1 67	0.140
33	6.40	0.000 **	76	3.39	0.005 **	119	1.81	0.109
34	0.91	0.474	77	2.71	0.020 *	120	1.75	0.121
35	4.46	0.001 **	78	3.38	0.005 **	121	2.73	0.019 *
36	5.01	0.000 **	79	6.18	0.000 **	122	3.41	0.005 **
37	2.77	0.017 *	80	8.21	0.000 **	123	3.47	0.004 **
38	5.33	0.000 **	81	8.53	0.000 **	124	2.05	0.070
39	1.82	0.107	82	5.62	0.000 **	125	5.02	0.000 **
40	2.04	0.071	83	7.19	0.000 **	126	3.66	0.003 **
41	1.78	0.115	84	5.73	0.000 **	127	3.91	0.002 **
42	1.62	0.153	85	9.26	0.000 **	128	0.66	0.654
43	0.91	0.474	86	6.59	0.000 **			

Table A-11. Summary of linear discriminant function crossvalidation classifications (proportion correctly classified) for six groups of Tustumena Lake, Alaska, sockeye salmon fry otoliths using Box-Cox transformed Fourier amplitudes. The initial 43 amplitudes were selected by stepwise linear discriminant analysis.

Number in Model	Amplitude Removed	Classification						
		Hatchery	Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek	Total
43	none	0.673	0.503	0.374	0.700	0.346	0.602	0.533
42	67	0.646	0.510	0.410	0.700	0.385	0.602	0.542
41	92	0.655	0.516	0.425	0.667	0.404	0.593	0.543
40	8	0.655	0.522	0.410	0.683	0.404	0.620	0.549
39	31	0.655	0.548	0.374	0.683	0.385	0.611	0.543
38	125	0.664	0.548	0.374	0.700	0.385	0.602	0.545
37	88	0.646	0.535	0.396	0.700	0.404	0.620	0.550
36	21	0.618	0.535	0.389	0.700	0.423	0.620	0.548
35	65	0.609	0.535	0.367	0.700	0.423	0.620	0.542
34	26	0.627	0.529	0.381	0.717	0.423	0.611	0.548
33	12	0.609	0.535	0.381	0.700	0.462	0.593	0.547
32	6	0.618	0.548	0.381	0.700	0.462	0.583	0.549
31	25	0.618	0.541	0.389	0.700	0.423	0.593	0.544
30	53	0.600	0.535	0.396	0.700	0.442	0.583	0.543
29	85	0.618	0.529	0.389	0.667	0.462	0.583	0.541
28	1	0.627	0.510	0.396	0.683	0.423	0.574	0.536
27	3	0.636	0.484	0.389	0.667	0.404	0.620	0.533
26	73	0.646	0.459	0.403	0.683	0.404	0.611	0.534
25	100	0.664	0.478	0.367	0.667	0.385	0.602	0.527
24	115	0.636	0.471	0.345	0.667	0.404	0.620	0.524
23	47	0.627	0.414	0.389	0.667	0.423	0.630	0.525
22	124	0.618	0.420	0.389	0.617	0.423	0.630	0.516
21	10	0.609	0.414	0.360	0.650	0.442	0.593	0.511
20	102	0.618	0.389	0.360	0.650	0.404	0.574	0.499
19	38	0.582	0.376	0.367	0.667	0.423	0.546	0.493
18	18	0.591	0.350	0.374	0.617	0.442	0.556	0.488
17	127	0.600	0.350	0.367	0.633	0.442	0.519	0.485
16	54	0.591	0.363	0.374	0.667	0.423	0.519	0.489
15	23	0.582	0.350	0.367	0.650	0.404	0.519	0.479
14	11	0.591	0.344	0.338	0.633	0.462	0.537	0.484
13	27	0.636	0.357	0.317	0.650	0.365	0.537	0.477
12	117	0.609	0.382	0.331	0.650	0.365	0.537	0.479
11	95	0.646	0.420	0.302	0.617	0.346	0.537	0.478
10	123	0.627	0.408	0.266	0.650	0.365	0.528	0.474
9	16	0.618	0.414	0.245	0.633	0.346	0.556	0.469
8	24	0.591	0.376	0.259	0.667	0.327	0.537	0.459
7	33	0.636	0.338	0.266	0.650	0.346	0.519	0.459
6	90	0.636	0.293	0.223	0.633	0.308	0.565	0.443
5	28	0.655	0.312	0.209	0.550	0.327	0.500	0.425
4	15	0.555	0.312	0.166	0.500	0.289	0.472	0.382
3	30	0.600	0.440	0.173	0.517	0.115	0.278	0.354
2	22	0.427	0.471	0.144	0.517	0.115	0.185	0.310
1	9	0.164	0.471	0.187	0.650	0.096	0.065	0.272
1	2	0.564	0.096	0.101	0.500	0.039	0.185	0.247

Table A-12. Summary of quadratic discriminant function crossvalidation classification (proportion correctly classified) for six groups of sockeye salmon fry otoliths, Tustumena Lake, Alaska. The initial amplitudes were the 40 most significantly different among the groups based on ANOVA.

Number In Model	Amplitude Removed	Classification						
		Hatchery	Bear Creek	Glacier Flats Creek	Glacier Springs	Moose Creek	Nikolai Creek	Total
40	none	0.346	0.541	0.460	0.067	0.000	0.352	0.294
39	26	0.409	0.567	0.476	0.083	0.000	0.370	0.317
38	31	0.427	0.548	0.489	0.100	0.000	0.398	0.327
37	83	0.473	0.554	0.496	0.083	0.000	0.435	0.340
36	10	0.482	0.535	0.475	0.117	0.019	0.417	0.341
35	79	0.482	0.573	0.460	0.083	0.039	0.435	0.345
34	85	0.464	0.573	0.460	0.117	0.039	0.435	0.348
33	88	0.491	0.541	0.489	0.100	0.039	0.463	0.354
32	48	0.509	0.535	0.489	0.100	0.058	0.426	0.353
31	1	0.518	0.503	0.460	0.150	0.058	0.482	0.362
30	33	0.527	0.503	0.468	0.183	0.039	0.482	0.367
29	25	0.536	0.548	0.460	0.167	0.058	0.472	0.374
28	86	0.564	0.510	0.468	0.167	0.077	0.472	0.376
27	3	0.555	0.484	0.482	0.183	0.077	0.482	0.377
26	81	0.573	0.503	0.446	0.183	0.115	0.519	0.390
25	30	0.546	0.490	0.432	0.267	0.115	0.491	0.390
24	60	0.564	0.471	0.417	0.267	0.096	0.519	0.389
23	22	0.527	0.490	0.403	0.317	0.135	0.537	0.402
22	63	0.555	0.452	0.389	0.383	0.154	0.528	0.410
21	9	0.555	0.452	0.410	0.383	0.154	0.509	0.411
20	66	0.573	0.471	0.389	0.400	0.135	0.491	0.410
19	23	0.564	0.471	0.425	0.383	0.173	0.500	0.419
18	28	0.536	0.471	0.396	0.383	0.212	0.500	0.416
17	24	0.491	0.484	0.410	0.433	0.212	0.500	0.422
16	80	0.482	0.440	0.403	0.450	0.212	0.500	0.414
15	27	0.482	0.427	0.410	0.500	0.269	0.491	0.430
14	92	0.473	0.446	0.345	0.517	0.289	0.472	0.424
13	6	0.527	0.420	0.345	0.517	0.289	0.426	0.421
12	102	0.518	0.376	0.353	0.500	0.327	0.380	0.409
11	47	0.509	0.325	0.338	0.533	0.308	0.389	0.400
10	11	0.564	0.382	0.302	0.517	0.346	0.389	0.417
9	97	0.527	0.389	0.338	0.433	0.346	0.389	0.404
8	12	0.546	0.408	0.338	0.483	0.308	0.278	0.393
7	8	0.491	0.401	0.338	0.517	0.289	0.250	0.381
6	73	0.509	0.401	0.281	0.533	0.250	0.204	0.363
5	21	0.436	0.427	0.266	0.500	0.269	0.213	0.352
4	95	0.446	0.452	0.252	0.583	0.250	0.139	0.354
3	16	0.382	0.465	0.180	0.600	0.212	0.139	0.330
2	5	0.336	0.452	0.216	0.633	0.173	0.157	0.328
1	90	0.200	0.427	0.000	0.700	0.404	0.000	0.288
1	2	0.527	0.102	0.000	0.400	0.000	0.120	0.192